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**ARBUSCULAR MYCORRHIZA: A LINKAGE OF PLANT, SOIL AND SURFACE
HYDROLOGIC PROCESSES IN A SOUTHWEST GRASSLAND**

by

Mary Elizabeth O'Dea

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A Dissertation Submitted to the Faculty of the
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For the Degree of

**DOCTOR OF PHILOSOPHY
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THE UNIVERSITY OF ARIZONA

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Mary Elizabeth O'Dea entitled Arbuscular Mycorrhiza: A Linkage of Plant, Soil and Surface Hydrologic Processes in a Southwest Savanna

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ABSTRACT

A three-year randomized field study was undertaken to evaluate the effects of prescribed burning and the intense rainfall events associated with the summer monsoon of southern Arizona, specifically examining the interchange between the plant, soil and surface hydrologic processes within a savanna. The effects of fire and rainfall treatments were evaluated by examining their specific effects on vegetation, arbuscular mycorrhizal fungi (AMF), soil structure, soil nutrient capital, surface runoff and sediment. In addition to the field study, two factorial greenhouse studies were completed in conjunction with the field study. The objectives of the greenhouse studies were: 1) to test the effects of prescribed fire and high intensity rainfall on AMF infectivity potential, and 2) to examine the effect of mycotrophy on the biomass production of native and introduced grasses grown in pasteurized and native soils. A third study examined the development of an empirical model to estimate sediment production from the field study's plots. The objectives of this third study were: 1) to develop the empirical model using two years of collected sediment, and 2) to compare model estimates with the commonly used Revised Universal Soil Loss Equation (RUSLE) model. The results of these studies indicate that an integrated mechanism exists between the plant community and biotic and physical soil processes, which when disturbed affect the hydrology of the watershed.

INTRODUCTION

Within an ecosystem, plant and soil processes interact to affect surface hydrology through their influence on surface roughness, soil structure, evaporation, transpiration and through their relationship with soil biota. We know that by both explicit research and intuition that the processes that characterize the watershed, such as the geomorphology, hydrology, soil and vegetation are linked together. But what is not well understood are the linkages and drivers that can advance or disrupt this integrated system.

In the perennial grasslands and savannas of southern Arizona, arbuscular mycorrhizae (AM) are unique and measurable linkages between soil, plant and surface hydrologic processes. AM fungi (AMF) are obligate biotrophs, dependent upon the formation of a symbiotic relationship with a host plant for its carbon source. Depending upon its response to colonization, the host plant may receive benefits from the relationship, such as improved nutritional benefits or protection from pathogens (Miller 1987, Wilson and Hartnett 1998). Additionally, current agronomic literature has described the role of AM in maintaining soil structure, aggregate stability (Schreiner et al. 1997) and the role of AM in the binding of micro-aggregates (Tisdall and Oades, 1982, Wright and Upadhyaya 1998). Yet, little is understood as to how this biotic relationship functions in the wildland ecosystem, particularly in terms of its role in watershed erosion and recovery from fire.

Fire within the grasslands of Arizona is a normal disturbance, generally starting as the result of human-caused ignitions or the dry lightning strikes, which precede the summer monsoon rains (Wright and Bailey 1982). Within a watershed, fire and rainfall events act as disturbances upon the soil surface, affecting the plant and soil communities, and the surface hydrology. Removal of above ground vegetation not only removes soil surface cover, it also affects the flow of carbon between plant leaf area, roots and the mycorrhizal fungi. The disruption of the AM linkage between plant and soil processes affects plant community recovery from the disturbance (Rashid et al. 1997, Smith et al. 1999), as well as the role of the AMF in soil aggregation and structural stability.

The surface 10cm of soil appears to be highly influential to many plant, soil and surface hydrologic processes in the semi-arid grassland (Dunne et al. 1991), as it is the interface between the atmosphere and the soil system. The soil structure at this interface influences the initial movement of gas and water from the atmosphere into the soil matrix, influenced by structural characteristics such as aggregate stability, pore sizes and their distribution. Through mediation of soil water and gas movement, soil structure affects plant and soil microbial activity, water infiltration and storage. In turn, the stability of the structure is dependent upon the presence and function of soil biotic processes to maintain itself, as through the mechanical binding of aggregates by roots, hyphae or mucilage (Tisdall and Oades 1982). Given the common dependence of soil and plant processes to one another, a change within one would generate a change in the other. As a common linkage, the AMF couples soil and plant processes through its affect on both plant community dynamics and soil structural stability. It could then be argued that a

disruption in the functioning of the AM would disrupt plant and soil processes, which would in turn affect the surface hydrology (Figure. 1).

The multi-functional nature of AM in watershed processes lends itself to examination as a quantifiable linkage between certain plant, soil, and hydrologic processes under disturbed and stable conditions. The purpose of this study is to quantify the effects of prescribed fire and the intense rainfall events associated with the summer monsoon on plant and soil processes, and how changes in these processes may affect the surface hydrology of southern Arizona grasslands and savannas.

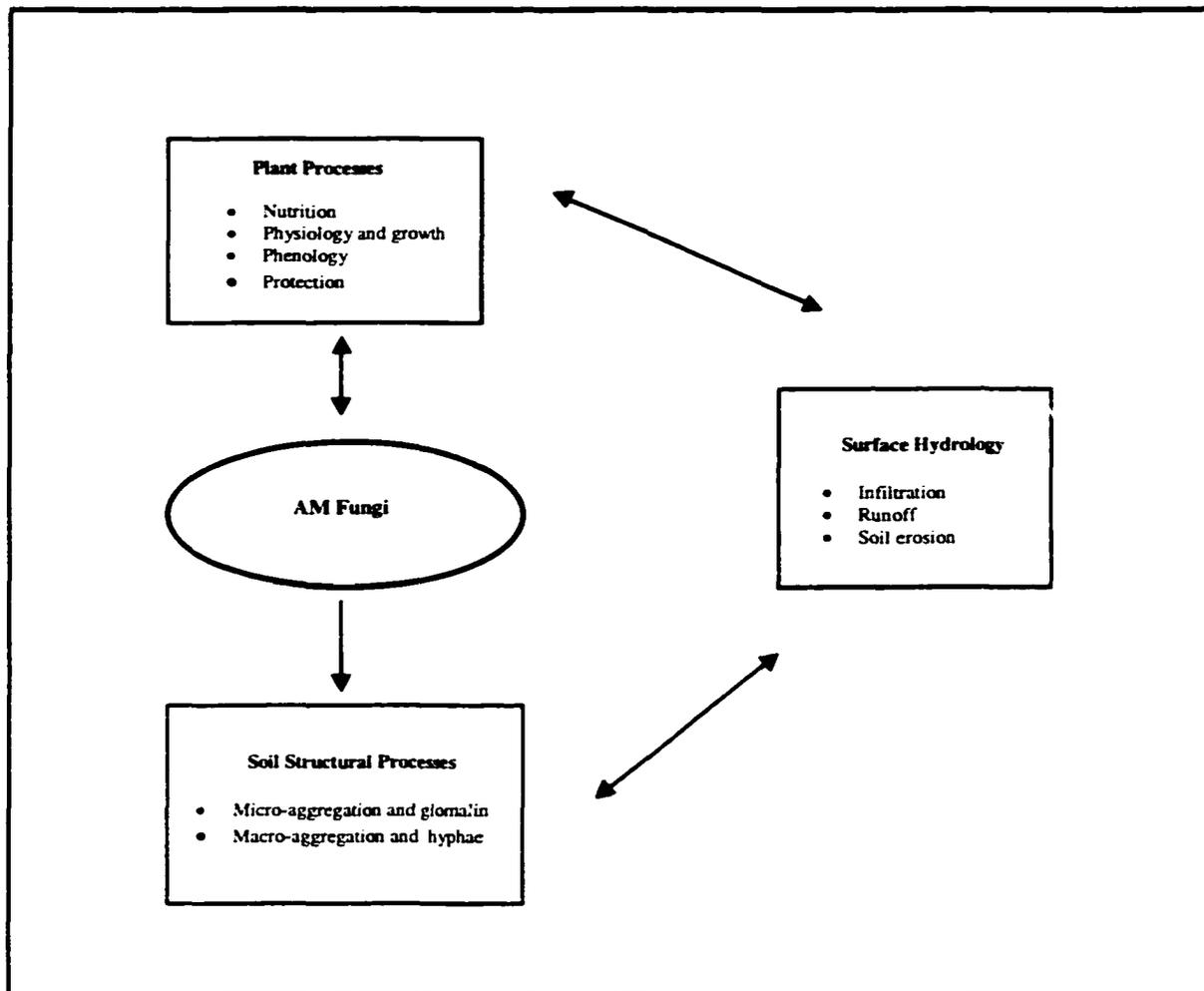


Figure 1. The coupled effect of AM on of plant and soil processes, and its affect on the surface hydrology of the watershed.

OBJECTIVES OF THIS RESEARCH

Objectives

This study was established to evaluate the effects of prescribed burning and the intense rainfall events associated with the summer monsoon of southern Arizona on the functioning and interchange between plant, soil and surface hydrologic processes within a savanna. The role of AMF was also to be evaluated as a common and functional linkage between plant and soil processes, and as an indirect mediator of surface hydrology. The effects of fire and rainfall treatments were evaluated by examining their specific effects on vegetation, AMF, soil structure, soil nutrient capital, surface runoff and sediment yield.

H₀: Prescribed fire and rainfall treatments will diminish plant cover in the short-term (i.e. first two post-treatment summer growing seasons), but will not have any detrimental effects on community structure (i.e. species richness and abundance).

The nature of fire within the perennial grasslands is one of relatively quick consumption of fuels with little heat flux to the soil, therefore permanent damage to the bud bank of the perennial grasses was not expected. Rapid re-sprouting of aboveground leaf area was expected before the end of the first summer growing season. Although the amount of the leaf area would likely be diminished in the short-term, it was expected that pre-burn levels of leaf area would be reached within 2 years of burn.

Since minimal damage to existing plants was expected, there was no expected

shift in community composition. Changes within the grassland community were quantified in terms of species regeneration, abundance, and aerial cover in response to treatment application.

H₁: Prescribed fire and rainfall treatment effects on AM fungi will parallel changes in plant cover. Soil fungal biomass and activity (i.e. plant colonization and protein production) will be diminished in the short-term, but will recover by the second post-treatment growing season.

The activity of the AMF is closely tied to that of the plant community. As the plant community recovers from the disturbance, it is expected that recovery of the fungal community will be coupled to it. Treatment effect on the AMF was quantified through examination of live fungal biomass, spore number, fungal species abundance and richness, and soil protein levels following treatment application.

Many of the perennial grasslands of the southwest are populated by native species, which evolved upon the site and by non-native species that were introduced to supplement range forage. From earlier surveys many of the introduced species appear to be either facultatively or non-mycorrhizal in nature. In comparison, many of the native species appear to be either mycorrhizal or facultatively mycorrhizal as determined by high rates of fungal colonization (Trappe 1981). Therefore, the effect of mycorrhizal fungal colonization on the growth and phenology of introduced and native perennial grasses was also tested.

H₂: Prescribed fire and rainfall treatment effects on soil structural parameters will be 1) an increase in bulk density, 2) a decrease in silt and clay portions with the sampled bulk soil, and 3) decreases in surface infiltration rates and wet aggregate stability during the first post-treatment growing season.

Comparisons among treatments may provide observable changes in soil parameters, which in turn may lead to quantifiable changes in surface water runoff and soil erosion.

H₃: Surface runoff volumes and sediment yield will be significantly different from the control during the first post-treatment summer growing season.

H₄: Sediment yield from hillslope erosion will be correlated to changes in AM activity, decreases in plant cover and a decrease in aggregate stability following treatment application.

Explanation of Dissertation Format

The format of this dissertation includes an overall introduction of this study's objectives, a review of current literature on the topics associated with this study, and experimental methodology. The results and discussions of the study are presented as papers, with figures and table numbers contiguous starting with the first paper (Appendix 1). All three papers are written around the theme of treatment effects upon the linkage between plant, soil and hydrologic processes within a southeastern Arizona savanna .

REVIEW OF CURRENT KNOWLEDGE

Grassland Communities and Arbuscular Mycorrhizal Fungi

The ecology of the Southern Arizona grasslands has been reviewed by McClaran (1995). The perennial grass communities are found on a variety of soil types and conditions limited primarily by available soil moisture and nitrogen (Whitford 1986, Wright 1980). The plant communities are represented by a diverse representation of at least 89 genera and more than 363 species of the grass family alone, with both introduced and native C₃ and C₄ grasses present (Gould 1993), and many of the grasses are mycorrhizal (Trappe 1981).

Mycorrhizae are common symbiotic relationships between plants and certain genera of soil fungi. In grasslands, the ubiquitous arbuscular mycorrhizal fungi (AMF) are obligate biotrophs, unable to photosynthesize or decompose organic substrates. This heterotrophic inability to produce their own energy makes them dependent upon a host plant for their carbon source. In turn, depending on its mycorrhizal response the plant can receive benefits from the symbiotic relationship, such as improved nutritional status or protection from pathogens. The ecology of arbuscular mycorrhizae (AM) in grass- and shrublands has been thoroughly reviewed by Miller (1987).

The functioning of the plant community appears to be inextricably linked to that of the soil's biotic community. Changes in the plant community structure, even its

composition can trigger changes within the soil ecosystem. The inherent linkage of the two systems demonstrates a positive-feedback mechanism, which when disturbed can lead to total system degradation and the decreased ability of either community to deal with the stress (Nelson and Allen 1993). A disruption of this soil-plant linkage has been associated with the Schlesinger et al. (1990) desertification scenario. In this scenario there is a heterogeneous allocation of resources (e.g. soil moisture, plant available nutrients, shifts in plant community dominance, and declines in mycorrhizal regeneration) over the landscape (Doerr et al.1984, Hunt et al. 1988, Perry et al. 1990, Reeves et al. 1979, Schlesinger et al. 1990). Within the desertification scenario, as vegetative cover becomes distributed in a heterogeneous pattern, so do the other site resources required for a healthy biotic soil community. Furthermore, the grassland community would shift from one with dispersed woody vegetation to one dominated by the woody vegetation and non- or facultatively mycorrhizal plants. In severely disturbed Colorado rangelands, Reeves et al. (1979) found that the early seral establishment of primarily non-mycorrhizal annuals could be explained in large part to their lack of dependence on the integrity of surface soils, which are contrary to the needs of the perennial mycorrhizal grasses.

The stability of AMF populations is dependent upon the nature of the physical environment and the mycorrhizal plant community. Disturbances that remove or suppress populations of obligate and facultative mycotrophs appears to lead to a decline or removal of AM inoculum, an obligate biotroph (Harris and Paul 1987). As the number of fungal propagules are reduced to a critical level or eliminated, so to are the chances for successful introduction of plants dependent upon the mycorrhizal colonization (Allen 1988, Miller

1987, Trappe 1981). Following severe disturbance, soil foodwebs favoring bacteria over fungi may develop, leading to increased decomposition rates and nutrient mineralization. Under this new environment of increased available N the establishment of non-mycorrhizal or facultative annuals, such as cheat grass (*Bromus tectorum*) may be favored over a mycorrhizal perennial (Trent et al. 1994).

The response of plants to mycorrhizal infection shapes plant community structure and influences competition dynamics. Within the tallgrass prairie, the suppression of the mycorrhizal fungi resulted in both structural and compositional changes within the plant community, including an increase in species richness and diversity (Smith et al. 1999). Two possible mechanisms have been put forth to explain mycorrhizal mediation of community dynamics. One is that there is a selective allocation of site resources through hyphal connections. Or, it is proposed that there is a relative response of a plant to colonization that in comparison with its neighbors, affects its ability to dominate within a community (Hartnett and Wilson 1999). Additionally, mycorrhizae appear to mediate the regeneration, as well as the competition dynamics of some native grasses and introduced forbs. Although the mechanisms are not completely understood, the lack of competitiveness of many native species may be due to a net positive response of the introduced species to native AMF. And it is this net positive (or super response) which give the introduced species an advantage over the native plant. In the northern United States, *Centaurea maculosa* is an invasive forb in native fescue grasslands. When the forb is grown with a native bunch grass, *Festuca idahoensis* in the presence of AMF, the forb is able to grow more than two-thirds the size of the native grass. However, without the presence of the AMF the native grass has the marked

advantage (Marler et al. 1999).

Fire Within the Grassland Watershed

Plant Processes

Fire, and its associated erosion events are normal disturbances in Arizona grasslands. Fires start as the result of human-caused ignition or dry lightening strikes, which precede the summer monsoon rainstorms. Historically, large prairie fires usually occurred during the drought years that had followed years of above-average rainfall (i.e. ENSO) and fuel production (Wright and Bailey 1982). The role of fire in maintaining the grass community structure through the suppression of woody vegetation has been well documented (Martin 1983, McPherson 1995, Wright and Bailey 1982). However, lacking in current literature is a quantification of wildland system productivity losses due to soil erosion, and the effects of soil losses on community dynamics. Moreover, unlike most agricultural crops, perennial grasslands may be impacted by multiple disturbance regimes throughout their life. In Southwest grasslands, little is known about the linkages between soil erosion and grassland community dynamics with various disturbance histories.

Fire effects on the semidesert grasslands are reviewed by Wright and Bailey (1982). Plant response appears to be a function of the season of burning, as well as the general climatic conditions before and after the fire (Ford 1999). Following spring fires, which occurred under dry soil conditions (i.e. following winter drought), notable community recovery has taken up to three years (Wright 1979). Within southeastern

Arizona grasslands, blue grama (*Bouteloua gracilis*), side-oats grama (*B. curtipendula*), Rothrock grama (*B. rothrockii*) and wolftail (*Lycurus pheloides*) have been harmed by spring fires which followed winters of below-average rainfall. However, with favorable soil moisture conditions many species do not show as significant of losses. Black grama (*B. eropida*) has also been shown to be harmed by drought conditions, as well as severely damaged by fire even during wetter years (Wright and Bailey 1982). Lehmann lovegrass (*Eragrostis lehmanniana*.) appears to be susceptible to early summer fire (Cable 1965), however it is highly successful in re-establishing itself by seed in post-fire sites. Successful seedling establishment is dependent upon adequate soil moisture and the pattern of summer rainfall for genera, including *Eragrostis*, *Muhlenbergia* or *Bouteloua* (Biedenbender and Roundy 1996, Bock et al. 1995, Wilson and Briske 1979).

Bunchgrass communities, such as those of the desert grasslands are characterized by fine fuel accumulations around the bud bank of perennial grass species. Long fire-free periods allow for the accumulation of fuels, and a higher incidence of mortality following fire. The larger the grass clump, the greater the accumulation of fuels, and a higher probability of fatality. Since seedbanks are generally unharmed during grassland fires, plants which are readily established from seed are important contributors to the post-fire community (Steuter and McPherson 1995, Wright 1979). In turn, it is these characteristics of the grass community which appear to increase their susceptibility to exotic plant invasions (Mack 1981), such as the cheat grass (*Bromus tectorum*) of the Great Basin or Lehmann lovegrass (*E. lehmanniana*) of the Southwest.

Mycorrhizae

Given that the magnitude and duration of heating are the drivers of plant damage following a fire, it is not unreasonable that they are also important to AMF propagules and their infectivity. Within the sand prairie of Illinois, a 3-year depression in spore abundance for a variety of AMF was attributed to a heat effect, as well as to changes in the host plant community (Dhillion and Anderson 1993). Klopatek et al. (1988) also reported a significant and highly positive correlation between soil temperature and AMF infection of plant roots. Additionally, it has been put forth that low levels of post-fire mycotrophy may be due to a plant's requirement for limiting nutrients (i.e. total N, Ca, Mg and K) whose uptake is not enhanced by a mycorrhizal association (Anderson and Menges 1997). The physical reduction of propagule number through the loss of surface soil layers also affects AMF infectivity. Habte (1989) reported that the number of active AM propagules significantly declined with soil depth with significant decreases reported for soil losses greater than 7.5 cm. Additionally, he proposed that the lack of infectiveness may be the result of either physical or chemical changes within the soil that is induced by the erosion, but provided no data to support this hypothesis (Habte 1989).

Surface Hydrology

The effect of fire on infiltration, overland flow and erosion in Southwestern wildlands has been reviewed by Baker (1988). He reported that many of the factors that affect infiltration (amount of water that can move through the soil surface in a given amount of time) can be detrimentally affected by fire, including the amount and type of

vegetation, soil texture and porosity, and level of soil organic matter. The primary hydrologic effect of prescribed burning is its impact on infiltration, and consequentially on overland flow. Given the heterogeneous distribution of soil moisture over the landscape, there is a variable fire effect on the soil and vegetation parameters that affect infiltration rates and water storage capacities, such as evapotranspiration and soil organic matter. In the Southwest, soil erosion is an episodic or discontinuous process, dependent on the large convective summer storms. Under the intense rainfall of summer storms, soil loss after a burn is driven primarily by the frequency and size of exposed areas, and slope. Additionally, overland flow (runoff) succeeding prescribed burning is directly related to slope steepness, and indirectly related to re-vegetation rates (Baker 1988). In turn, vegetative cover can account for a large amount of the variance in the amount of eroded soil (Meeuwig 1970).

Prescribed burning appears to decrease infiltration rates in many plant types, including oak and juniper, perennial bunchgrasses and short grass. Hester et al. (1997) reported that although there were significant decreases in infiltration rates on burned sites, there were no corresponding changes in the soil structure (i.e. bulk density or aggregate stability). Changes in infiltration rates were attributed to loss of soil cover to protect against raindrop energy and to slow overland flow, as well to the seasonal timing of the burning. However, there appears to be a disparity in results within the same region of southeastern Arizona. While Simanton and Renard (1981) found that there was more runoff and erosion from spring fires, Emmerich and Cox (1992) did not. It appears that in both situations, when vegetation is senescent, as in the fall or winter there is a decrease in

the disturbance of fire on plant and soil properties. These studies, like Hester et al. (1997) concluded that soil erosion was caused by the lack of organic matter protecting the exposed soil surface and slowing the overland flow. Yet, none of these studies examined the integrated role of vegetation and below ground processes in mitigating erosion and runoff responses in semi-arid systems.

Studies evaluating the functioning of the semi-arid systems have recognized the important interactions of vegetation, overland flow and erosion in the dynamic re-distribution of resources over the landscape (Ludwig et al. 1997, Tongway and Ludwig 1994, Schlesinger et al. 1990). There is a natural feedback mechanism, which affects both the plant and hydrologic processes within the semi-arid system. Semiarid plant community establishment and productivity are primarily limited by available soil moisture, nutrients, and their spatial distribution over the landscape (Belsky 1994, Breshears and Barnes 1999, Whitford 1986). In turn, the spatial distribution of the water is a function of differences between functional plant types (e.g. bare patches, grassland or woodland) in terms of interception, overland flow, evaporation, plant water use, and climate (Breshears and Barnes 1999). Therefore, vegetation type has a prominent role in runoff and erosion processes because: 1) each type has a consistent hydrologic behavior, and 2) there is a dynamic relationship between types in terms of water and sediment exchange (Reid et al. 1999). By examining the exchange as a source to a sink (Ludwig et al. 1997), areas of significant runoff and sediment contributions (i.e. bare patches) act as sources, and can contribute on average 3 times more sediment than a grass patch, and 24 times more than a woodland patch (Reid et al. 1999).

Many studies (Bennett 1974, Hester et al. 1997, Smith et al. 1990, Thurow et al. 1986) have operated upon the accepted premise that the primary drivers of surface runoff and erosion are the lack of soil surface protection, as well as the force of raindrop impact to dislodge soil material and disperse soil particles. As expected, vegetation characteristics, such as cover and type, moderated the primary impact of fire on soil erosion. However, this premise does not account for the dynamic interaction of plant and soil biotic processes which are important to soil aggregation and the maintenance of the soil structure. It does not account for the response of these processes to disturbance, and how this response may demonstrate itself in terms of the soil's susceptibility to erosion. Moreover, changes in plant community dynamics and surface hydrologic processes are tied to surface soil characteristics, yet this commonality has not often been addressed.

Soil Processes

Soil structure plays an intricate role in the assemblage of biotic processes present in semi-arid grasslands, through its influence on bulk density, water movement, aeration, heat transfer and porosity. In addition, soil structure characteristics influence water infiltration and overland flow, as well as soil erosion through aggregate size distribution and stability (Armstrong and Stein 1996, Blackburn et al. 1992, Granger 1992). A number of physical, chemical and biological factors contribute to its development, including the physical activity of plant and soil fauna, freezing and thawing, soil microbial activity, colloidal particle and sorbed cation interactions, and the decay of organic matter (Pritchett 1979, Ritter et al. 1995, Tate 1987). Organic matter, which is usually sparse in more arid ecosystems (Whitford 1986), appears to play a critical role in the stability of water stable

aggregates (Tate 1987). The largest quantities of organic carbon appear to be associated with larger soil aggregates (> 0.5 mm diam.) suggesting the importance of organic matter in the stabilization of macro-aggregates (Lu et al.1998).

Tisdall and Oades (1982) reported the significant contributions of soil biotic activities to soil aggregation in grassland soils. Plant roots and fungal hyphae are active in the initiation and maintenance of soil macro-aggregates through the mechanical binding of smaller aggregates and particles together. Mucilage and soil humic substances are primarily responsible for the micro-aggregation of soil particles. Current agronomic literature has described the role of AM in maintaining soil structure, aggregate stability (Schreiner et al.1997), and the binding of micro-aggregates (Tisdall and Oades, 1982, Wright and Upadhyaya 1998). A glycoprotein , glomalin has recently been discovered and is unique to the AMF within the taxonomic order Glomales (Wright and Upadhyaya 1996). These findings report that glomalin acts in a manner similar to known proteins secreted by soil bacteria, and are important to micro-aggregation within soils. Through the maintenance of aggregation and aggregate stability, the integrity of the soil structure can be influenced. Yet, little is understood as to how this biotic relationship functions in the wildland ecosystem, particularly in terms of its role in the erosion process. Therefore a number of common land use practices, such as livestock grazing or the use of prescribed fire can have significant impacts on the soil matrix through their influence on the biotic and physical processes affecting aggregate formation and structure stability (Armstrong and Stein 1996, Gang et al. 1998, Warren 1987).

PRESENT STUDY

Research Methods

Experimental Design

Field Study

The study area was located in southern Arizona (Appendix 4), characterized by oak woodlands in the drainages, and perennial grass species occupying the uplands (Figure 2). The site was located within the Appleton-Whittel Research Ranch, where livestock grazing has been excluded from the landscape for more than 30 years. Within the study site the dominant grass species included the genera *Eragrostis intermedia*, *Bouteloua spp.* and *Muhlenbergia spp.*. Mimosa (*Mimosa aculeaticarpa* Ortega var. *biuncifera* (Benth.) Barneby), velvet mesquite (*Prosopis velutina*), rabbit brush (*Chrysothamnus nauseosus*) and various cacti were also present. The soil is a White House (Fine, mixed, superactive, thermic Ustic Haplargids) fairly deep, well-drained gravelly loam that formed in fan alluvium from mixed sources, with 1 to 3 % slope.

The study design was a randomized complete block (block = replication) with a split-strip plot design and four applied treatments. The four treatments were a control, a prescribed burn, a rainfall simulation, and a rainfall simulation and prescribed burn interaction, with 6 replicates for each treatment (Appendix 5). Six blocks were established on a hillslope (1-3 % slope) in a systematic manner from a random start. Within each block 4 walled runoff subplots with catchments were established, for a total



Figure 2. Overview of research site



(a)



(b)

Figure 3. View of plot during (a) the winter season and (b) the summer season

of 24 subplots for the study and 6 subplots for each treatment (Figure 3). Catchments placed at the base of each subplot were fabricated from sheet metal, and consisted of a collection basin with a removal lid. Two sizes of catchments were used, one size for the plots receiving the rainfall treatments (capacity of 480 liters) and one for the others that did not (capacity of 120 liters). Logistical constraints on the application of the rainfall simulation required that all the plot runoff was to be captured, therefore larger catchments were installed. Given the results of another study (Emmerich and Cox 1992) on a similar local rangeland site, large volumes of runoff were not expected and smaller catchments were used on the remaining subplots. Depth of runoff was routinely measured, and the catchments pumped out following the settling out of the sediment. Losses from evaporation or potential leakage were not accounted for in this study. Additionally, a delay in the installation of the smaller catchments may have resulted in the loss of both sediment and runoff from at least two storm events in the first year. Moreover, it had been the original intention of this study to measure runoff volume and sediment yield through out the year, examining both annual and seasonal variations. Yet, due to the lack of sufficient winter precipitation, there were no measurable amounts of sediment or runoff during the winter seasons of 1999 and 2000, leaving only the monsoon rainfall events to be observed.

Plots measured 9 m by 10 m, and each subplot was 3m wide by 10m long with a 3m buffer between subplots. Permanent points for soil, vegetation and mycorrhizal fungal parameters were randomly and systematically established to allow multiple sampling within each plot. Within each subplot, 3 sampling points were established for the

measurement of vegetation and fungal parameters, and 6 sampling points for soil parameters. A total of 288 sampling points were established, with 72 sampling points within each treatment. A raingage was stationed at the site for the duration of each monsoon season (1998 and 1999). In addition, a complete meteorological station was present at the Appleton-Whittel Research Ranch office, approximately 1.5 miles (2.4 kilometers) from the research site. A 30-yr. rainfall record for the meteorological station is available in Appendix 6.

Two treatments were applied: a late spring prescribed burn and a simulated monsoon rainfall-erosion event. The low-intensity prescribed burn was applied the last week of May 1998 using a drip torch. Greater than 90 % of the vegetation was removed. A water drop test showed post-fire hydrophobicity to not be present. The second treatment, a simulated monsoon rainfall-erosion event, was applied with a rotating boom rainfall simulator (Swanson 1965) during the last week of June 1998. Given the unpredictable nature of the monsoon season, the simulated rainfall event was applied to ensure a heavy rainfall event that generated sediment production. The simulator rained for 40 minutes at 63.5 mmhr^{-1} for an average rainfall depth of 43.2 mm. Runoff was noted to begin 4 minutes after the start of the simulation, with observable soil erosion beginning at 8.5 minutes from the start. The simulation was stopped when substantial sediment production was observed and catchment capacity was nearly surpassed. Marked pins had been placed within the plots to view changes in the soil surface profile. The rainfall simulation accounted for approximately 45% of the total rainfall for the 1998 monsoon season (95.6 mm), a season which lasts from approximately July 1 to October 1.

The simulated event was within the 30-year documented range of rainfall events for the area, comparable to a natural event with an annual return period of 3.3 years. A natural rain event of 34.6 mm occurred in August of 1997 and accounted for approximately 46% of the total monsoon rainfall for 1997 (76.0 mm). The volume of runoff generated by the simulation was measured. However, experimental design and weather limitations did not allow for the collection of sediment produced during the application of the simulated rainfall treatment. The monsoon rain season began the day after the simulation, not allowing the draining of the catchments and collection of the sediment.

Measured vegetation variables were perennial grass cover (%), herbaceous annual cover (%), shrub cover (%), grass bunch and shrub basal areas (cm^2), number of seedlings and ramets, and plant species presence and frequencies. Variables were measured within quadrat plots (0.5m by 0.5m) centered on the point marker for an approximate 2.5% area sample. Within a subset quadrat (0.25 m by 0.25 m), total percent rock and cryptogam cover were also noted. A total of 72 vegetation points were sampled, with a total of 18 sampling points per treatment. Vegetation variables were sampled before treatment application (1997) and biannually following the end of the post-treatment growing seasons (1998 and 1999), April and October respectively. However, with winter rainfall substantially decreased in 1998 and 1999 winter germinates were too few to sample.

Sampled soil variables included: gravimetric soil moisture at 0-5 cm and 6-10 cm depths, bulk density at 0-5 cm and 6-10 cm (kgm^{-3}) depths (Blake and Hartge 1986), soil particle distribution (%)(Gee and Bauder 1986), wet-sieved stable aggregates

(%)(Kemper and Rosenau 1986), surface infiltration rates (mmhr^{-1}), total organic soil carbon and nitrogen ($\mu\text{g/g}$)(Matejovic1997)), and total Kjeldahl orthophosphate ($\mu\text{g/g}$) (Bowman and Delfino1982). Surface infiltration rates were measured using a disc permeameter under unsaturated field conditions (Perroux and White 1988, White and Sully 1987, Sullivan et al. 1996). Soil samples were taken in the top 10 cm of soil since this depth appears to be highly influential on the biological and physical processes of semi-arid soils (Dunne et al. 1991). Soil cores (2cm by 15 cm) were removed at sampling points in early October following the end of the monsoon season, composited or separated according to experimental design. Samples for bulk density were taken in the winter when the soil had a higher moisture content, and allowed for recovery of complete cores.

Mycorrhizal fungal variables were measured from composite soil samples taken from each subplot. Three samples were collected from each subplot. Each sample was separated into two subsamples, with one representing a depth from 0-5 cm and one from 6-10 cm. Each composite sample represented one treatment replicate, for a total of 6 samples representing a treatment. Samples were examined for spore count (Silva 1994, Stutz and Morton 1996), total live hyphal biomass ($\mu\text{g/g}$) (Ames et al. 1984, Silva 1994), total soil protein ($\mu\text{g/g}$) and glomalin ($\mu\text{g/g}$)(Wright and Upadhyaya 1996). Additionally, AMF spore counts were done on 100 g sediment samples collected from each subplot at the end of the monsoon season (Silva 1994, Stutz and Morton 1996). Soil samples were collected prior to treatment application (1997) and again following the summer growing seasons (1998 and 1999). In addition, soil samples were taken from the study site for use

in two greenhouse studies.

Greenhouse Study

Two factorial experiments examined the effect of fungal infection on the growth of dominant perennial grasses, and the effect of treatment on mycorrhizal fungal inoculum and infectivity.

One study examined the effect of mycorrhizal fungal infection on the growth and phenology of 5 grasses that dominate the research site: blue grama (*Bouteloua gracilis*), sideoats grama (*B. curtipendula*), wolftail (*Lycurus phleoides*), Plains lovegrass (*Eragrostis intermedia*), and Lehmann lovegrass (*E. lehmanniana*). Approximately 1 kg of native soil was collected from the surface soil layer (0 to 15 cm) around the field research site, outside of the experimental plots and heavily trafficked pathways. The soil was then mixed 1:1 (v/v) with silica sand (no. 60), and half of the mixture was pasteurized. All seeds were surface sterilized with 1 % sodium hypochlorite for 5 min. Each grass species was planted into 12 Ray Leach Cone-tainers™ (164 ml) filled with native (non-pasteurized) soil mixture and 12 containers filled with the pasteurized soil for a total of 24 containers per grass species. Following germination, seedlings were culled to one plant per container. Plants were grown at temperatures between 22 and 32°C, and watered as needed. No fertilizer was applied. Plants were monitored for phenological changes and were harvested at 120 days. Three plants from each treatment were checked

for mycorrhizal fungal infection through the examination of 50 pooled root segments (Silva 1994). The remaining 9 plants were individually separated in to root and foliar material, dried for 3 days at 70°C, and weighed.

Ten plants from each of the species represented in the greenhouse study were randomly selected from the research site, harvested and examined for fungal colonization in the same manner as their greenhouse counterparts. The sampled plants were taken outside of the subplots and high traffic pathways. Plants were not taken from inside the subplots so as not to disturb other experiments, particularly the hydrology results. The examination of the field specimens was done to compare the potential effect of the greenhouse environment on the infection results.

The second factorial study examined the effect of treatment on the infectivity of the mycorrhizal fungi. For each field treatment (i.e. control, prescribed burn, rainfall simulation, simulation and burn), approximately 100 g of soil was taken from a depth up to 15 cm from each subplot, and then composited. The soil for each treatment was mixed 1:1 (v/v) with silica sand (no. 60), placed in tube containers, and planted with 3 surface sterilized seeds of Sudan grass (*Sorghum sudanese* (Piper) Staph). The Sudan grass was chosen because of its consistent fast germination and growth, and high capacity for mycorrhizal fungal colonization. Following germination, seedlings were culled to one plant per container. Plants were grown in a greenhouse at temperatures between 22 and 32°C, and watered as needed. No fertilizer was applied. Plants were harvested at 90 days following seed set. For each treatment, 100 randomly selected root sections were

evaluated for mycorrhizal fungal infection using a grid-line intersection (Silva 1994) . In addition, these pots were also used as pot cultures to examine mycorrhizal fungal diversity through spore taxonomic identification and count (Stutz and Morton 1996).

Data Analysis

Field study

Hydrologic, soil, fungal and plant variables were evaluated by analysis of variance and covariance following the experimental design, a complete randomized split-strip plot design. Additionally, Pearson's test of correlation and regression analysis of variables related to sediment yields, runoff volumes and glomalin levels were evaluated. Stepwise regression and response surface analysis were used to the model upland sediment yield. Principal components analysis (PCA) was used to examine the linear relationship and relative contributions of the quantitative variables to the model. All statistical tests were performed using SAS statistical software (SAS Institute, Inc. 1990).

Greenhouse Study

The bioassays were analyzed as factorial experimental designs. Comparisons of soil treatment (i.e. pasteurized versus native) were made using analysis of variance to quantify treatment effects within grass species on mean colonization rates, as well as mean shoot and root growth. The second comparison of field treatment effects (i.e.

control, prescribed burn, simulated rainfall, and simulation and burn) on the mean infection potential of mycorrhizal inoculum was also made with analysis of variance.

Summary of Results

Ecosystems are assemblages of interacting biotic and abiotic, or environmental components. More often viewed as concepts rather than as tangible entities, ecosystems do have specific attributes, including: structure, function, complexity, interaction or interdependency, no inherently defined spatial dimension, and they possess a temporal component (Kimmons 1987). The structure of the ecosystem results from the linking of its biotic and physical components with their function expressed through the flow of energy and matter. The organization of the system (i.e. organism, forest stand or watershed), both in time and space determines the level of interaction or interdependency of the components on one another. Disturbances within the system, whether environmental or anthropogenic in nature affect the function of the system by impacting system components and linkages, affecting inherent feed-back mechanisms and energy flows within the system. Linkages between components are critical to the functioning of the ecosystem. Defining the critical linkages and how disturbance affects their functioning are important tasks within ecosystem science. To manage or conserve an ecosystem is to understand not only the immediate impact of a cultural practice, but also the cumulative impacts of repeated disturbance on the structure, function and linkages of the ecosystem. This dissertation was undertaken to examine the role of arbuscular mycorrhizal fungi (AMF) as a biotic linkage between surface hydrologic and plant processes in a semi-arid grassland ecosystem (Figure 1).

AMF are ubiquitous in the grasslands and savannas of southern Arizona, affecting both soil and plant processes. Southern Arizona grasslands are inhabited by many genera of perennial bunch grasses, some of which have been documented to be mycorrhizal, or allow the fungal colonization of their root system. However, in the studies represented here, the representatives of each genera tested responded to fungal colonization in its own fashion. Under greenhouse conditions, non-colonized lovegrass (*Eragrostis spp.*) appeared to produce greater biomass, higher shoot to root ratios and earlier seed set compared to colonized lovegrass. Yet, the grama (*Bouteloua spp.*) and wolftail (*Lycurus phleoides*) appear to react in opposite fashion. Both genera were considerably less productive when not colonized by AMF, and neither produced an inflorescence during the tenure of the study (120 days). Differences in plant response to colonization by the AMF provide insight into plant community competitive dynamics following site disturbance.

Within the perennial grassland, prescribed burning in the spring and associated monsoon rainfall events did affect the infectivity of the AM fungal inoculum in the tested sorghum grass. Prescribed fire and severe rainfall events significantly diminished the amount of fungal inoculum in the soil, both AM spores and live hyphal biomass. The decline in the inoculum is considered in large part a result of high amounts of surface erosion in plots treated with prescribed burns. When compared with the control, the highly eroded treatments had significantly higher spore numbers within the collected sediment and lower numbers within the bulk soil samples collected from treatment plots. However, high soil losses did not completely explain the decline in root infectivity, specifically within the prescribed burn treatment. Examination of runoff volume and sediment spore counts within

the prescribed burn only treatment were not significantly different from the control following the first post-treatment season, even though the sediment yield was. Additionally, bulk soil spore counts within the prescribed burn only treatment did not significantly differ from the counts within the rainfall simulation treatment, yet soil from the burn treatment had significantly lower infection rates compared to the simulation treatment. These results indicate that the prescribed burn, whether through soil heat flux or changes within the host plant, may have also been detrimental to the fungal community. Due to the limitations of the greenhouse study's experimental design and the current inability to examine AMF in axenic culture, the fire damage hypothesis was not testable. It was clear though that the undisturbed site or control had the greatest quantity of AM inoculum following the first post-treatment growing season, and was reflected in the highest infection rate (number of fungal infection per unit length of root) compared with all of the other treatments.

Within the study site, native perennial grass cover and abundance were significantly lower in the burned plots compared with the unburned, even after two growing seasons. The comparatively severe decline in residual grasses within the simulation and burn treatment suggests that erosion itself also inhibits community recovery. Soil loss may cause injury to the root system or damaged growing points below the surface, beyond that damage usually associated with fire. In addition, the herbaceous annual cover continued to have a strong presence within the most disturbed plots. Seedling and ramet production was most evident within the first growing season for all treatments following application. Significantly greater regeneration of new individuals was also evident following the first post-treatment season, with the majority of seedlings being plains lovegrass (*Eragrostis*

intermedia). As with the herbaceous cover trends, the greatest number of seedlings and ramets were also present in the most disturbed plots, specifically those plots treated with the rainfall simulation and burning. With the decrease in the recovery of residual grasses, and the treatment's negative impact on AMF infection potential, both the native plains (*E. intermedia*) and introduced Lehmann (*E. lehmanniana*) lovegrasses appear to have distinct competitive advantages over other site grasses in re-establishing the burned site.

The fungal community, most particularly the AMF have an important role in the sustainability of the desert grassland watershed. However, the fungal community as a whole is likely to be important to maintaining soil structure. The hyphae mechanically bind microaggregates and particles together, much in the same fashion as plant roots (Tisdall and Oades 1982). Following the first post-treatment season, live fungal biomass levels showed no significant response to treatments. However, by the second year, levels for the biomass were significantly higher within the rainfall simulation treatment compared with the burned treatments. The higher fungal biomass production was not unexpected given the concurrently higher plant productivity within the same treatment comparisons. Both the plant and fungal communities responded positively to the higher rainfall treatment levels in 1998, as well as the increased natural rainfall totals of the 1999 growing season. These increases in fungal biomass production may explain the diminished erosion rate within disturbed plots despite the lack of vegetative cover.

Unlike the general fungal community, the AMF secrete the unique glycoprotein glomalin, which has been demonstrated to play a role in soil micro-aggregation (Wright and Upadhyaya 1996). Levels of total extractable glomalin (TG) were highest within the control

following the first post-treatment year, with the lowest levels within the burned treatments. These results were not surprising given that the AMF are obligate biotrophs, as well as given the previously discussed possible reasons for decreased AMF infectivity. The difference between burned and unburned treatments was more evident for TG levels after the second year. The prescribed burn reduced the total glomalin capital within the soil matrix, with aggregate stability significantly correlated to soil glomalin levels. The reduction in glomalin levels reflected the general response of the AMF to the fire disturbance, which included observable reductions in propagules and levels of infectivity that are comparable to those reported by Gibson and Hetrick (1988) and Habte (1989).

As the structural stability of the soil profile declines there are potential changes in soil porosity and particle size distribution, which are measurable in soil bulk density and surface water infiltration rates. A regression on experimental soil and biotic parameters revealed a significant relationship between infiltration rates (mmhr^{-1}) and plant cover, fungal biomass levels, TG and % sand particle ($R^2 = 0.45$) (O'Dea 2000, unpublished data). All of these measured changes are indirect measures of changes in structural changes in the surface soil profile. It should be noted that given the design of the experiment, the partitioning of biotic and abiotic contributions (e.g. raindrop impact) to structural changes cannot be assessed. However, as the organization of the soil profile changes, one should expect direct and measurable changes in the permeability of surface water through the soil profile. Results from this study demonstrated that as soil aggregates weaken (i.e. decreased number of water-stable aggregates) and increases in bulk density become evident, water infiltration declines and there is a measurable increase in surface runoff and soil erosion on

the hillslope.

Erosion within the watershed is an important concern to watershed management, and to ecosystems in general. Upland erosion is a mode of site resource allocation, including the redistribution of soil particle size classes, nutrients and propagules. With increased erosional disturbance there is a heterogeneous allocation of these site resources over the landscape, affecting channel processes, nutrient cycling and general ecosystem productivity. Within the desert grassland of this site, erosion was found to be a continual process, with substantial sediment yields measured within the control plots both field seasons. Captured sediment revealed a 100- fold increase in total organic C, N and spore number compared to bulk soil surveys within the treated and control plots. These results have lead to the insight that these grassland sites are not inherently unproductive, but are systems with resources continually on the move. It is as if the site resources (e.g. C, N) are moving targets, dependent upon the presence of adequate dams (i.e. vegetative cover) or brakes to allow their deposition and availability to the system.

Understanding the cumulative effects of all disturbances within the watershed, including rainfall events on the plant, fungal and soil parameters are important to understanding hillslope runoff and erosion events. The glue that keeps the soil together is both figuratively and literally meshed within the feedback mechanism between the fungal and plant communities, affecting both plant community dynamics and the structural stability of the soil. The multi-functional nature of AM in watershed processes has shown itself to be a quantifiable linkage between certain plant, soil, and hydrologic processes under disturbed and stable condition.

**APPENDIX A. A PRESCRIBED FIRE AND MONSOON RAINFALL IN A
SOUTHERN ARIZONA SAVANNA: THE INTEGRATED ROLE OF PLANT AND
SOIL PROCESSES IN SURFACE HYDROLOGY**

Abstract:

A 3-yr random design field study was undertaken to quantify the integrated effects of prescribed fire and the summer monsoon on the plant and fungal communities, soil structure and surface hydrology of a southeastern Arizona savanna. Six blocks with walled subplots ($n = 24$) were installed on a hillslope to measure changes to plant, fungal, soil and hydrologic variables in response to prescribed burning and simulated high intensity rainfall. The most significant changes following the first season were within the soil structure and surface hydrology of the burned treatments. Significant ($p \leq 0.05$) declines in perennial grass cover and infiltration rates, as well as large increases in runoff volume and sediment production were observed in response to the prescribed burning. In the second year, significant changes in the fungal community, and not the soil organic carbon levels were correlated to changes in the soil structure and sediment yield. The effect of the prescribed fire continued to be evident in both plant and soil variables, particularly within the simulation and burned treatment. The results of this study indicate that a feedback mechanism exists between the plant community and biotic and physical soil processes, which when disturbed affect the hydrology of the hillslope.

INTRODUCTION

The interactions of vegetation, runoff and erosion are important drivers in the dynamic distribution of resources over the semi-arid landscape (Ludwig et al. 1997, Tongway and Ludwig 1994, Schlesinger et al. 1990). There is a natural feedback mechanism between the plant community and hydrologic processes, where perturbation of one affects the functioning of the other. Plant community characteristics, such as composition, range and productivity are dependent upon the availability of soil water and limiting nutrients (Belsky 1994, Breshears and Barnes 1999, Whitford 1986). In turn, water distribution is dependent upon the hydrologic differences between functional plant types (i.e. woodland canopy, vegetated areas, and bare patches) with respect to interception, runoff, evaporation, plant water use, and climate (Breshears and Barnes 1999, Reid et al. 1999). Therefore, a continuum of resources (i.e. soil water, nutrients) is established over the landscape by the vegetation pattern, changing only in response to disturbance.

Disturbances, such as fire and drought, within the semi-arid environment are important influences on vegetation. Within the savannas of Arizona, fire is an historic disturbance resulting from both human-caused and dry lightning strikes which precede the summer monsoon rainstorms (Wright and Bailey 1982). Fire in these systems generally result in the reduction of woody plants, and an increase in herbaceous plant diversity and abundance (Martin 1983, McPherson 1995, Wright and Bailey 1982). Many perennial grasses are harmed by fire, with plant response appearing to be sensitive to the

season of burning and the general climatic conditions before and after the fire (Ford 1999). Spring fires under dry soil conditions appear to be most detrimental to plant communities, with notable recovery sometimes taking up to three growing seasons (Wright 1980). Long fire return intervals allow fuels to accumulate, increasing the incidence of mortality of perennial plants following burning (Steuter and McPherson 1995). However, seed banks are generally unharmed during grassland fires and favor the establishment of forbs and some grasses, such as *Eragrostis spp.* in the post-fire community (Biedenbender and Roundy 1996, Bock et al. 1995, Wright and Bailey 1982). With the reduction or elimination of certain functional plant types (i.e. woody canopies) from the landscape, surface runoff and erosion responses are affected by increases in exposed soil surface. Timing and extent of recovery for the savanna is in large part a function of plant and soil response to characteristics of the disturbance.

Prescribed burning strongly influences infiltration rates and consequentially runoff (Baker 1988). Following fire, changes in the hydrologic response have been attributed to the lack of plant cover, particularly in terms of the protection of exposed soil surface from raindrop impact and the impedance of overland flow. But no changes in the soil structure in response to prescribed fire were reported (Hester et al. 1997). In contrast, the lack of plant cover has also been reported as not being a dominant factor controlling the runoff response immediately following a prescribed burn (Emmerich and Cox 1992), alluding to the influence of changes within the soil structure. Additionally, prescribed burning in the spring has been reported to produce greater runoff and sediment yield than fall burns (Simanton and Renard 1981).

Soil structure influences water infiltration, runoff, and erosion through aggregate size distribution and stability (Armstrong and Stein 1996, Blackburn et al. 1992, Granger 1992). Prescribed fire can have significant impacts on the soil matrix through its influence on the biotic and physical processes affecting aggregate formation and structural stability (Armstrong and Stein 1996, Warren 1987). As soil organic matter is generally limited in the more arid ecosystems (Whitford 1986), its removal can result in the immediate loss of water stable aggregates (Tate 1987). Moreover, focusing only on plant contributions to aggregate stability and soil organic matter overlooks the significant contributions of the soil microflora and fauna, particularly those of the fungi within grassland soils (Tisdall and Oades 1982). Arbuscular mycorrhizae (AM) are common symbiotic relationships between a majority of grass genera and arbuscular mycorrhizal fungi (AMF) (Trappe 1981). The fungi are obligate biotrophs in this relationship, meaning that they are dependent upon the host plant to act as an energy source. AMF are ubiquitous in grassland soils affecting both plant community dynamics (e.g. growth, phenology), as well as having a prominent role in soil aggregation and stability through the mechanical binding of hyphae and the secretion of glycoproteins (i.e. glomalin) (Schreiner et al. 1997, Tisdall and Oades, 1982, Wright and Upadhyaya 1998).

Glomalin is a unique protein secreted by the AMF and it has an important role in soil aggregation and stability. Its relationship to aggregation is similar to characteristics attributed to rhizosphere mucilage and other soil proteins secreted by bacteria (Wright and Upadhyaya 1996). Fire and erosion often have a two-fold impact on these obligate biotrophs. Disturbance reduces the abundance of plant hosts, as well as significantly

reducing the ability of the fungi to establish a symbiotic relationship with the remaining plants (Dhillon and Anderson, 1993, Habte 1989). Without this symbiotic relationship with host plants, the function of the fungi within the soil structure is reduced. Moreover, without the symbiotic relationship with the fungi, many grasses are at a competitive disadvantage for re-establishment following site perturbation (Hartnett and Wilson 1999, Marler et al. 1999, Moora and Zobel 1996). While significant research on the contributions of the soil biota to soil structure has been investigated in agricultural systems, little is understood as to how this biotic relationship functions in the wildland ecosystem, particularly in terms of its role in the erosion process.

A three year random design study was undertaken to quantify the integrated effects of prescribed fire and the summer monsoon on the plant community, soil structure and surface hydrology of a southeastern Arizona savanna. This study should provide insights into how disturbance characteristics, such as timing or magnitude influence plant and soil interactions, and consequentially influence runoff and sediment production over the landscape.

METHODS AND MATERIALS

The Elgin, Arizona study area was located in a savanna, characterized by oak woodlands in the drainages, and perennial grass species occupying the uplands. The site was located within the Appleton-Whittel Research Ranch, where livestock grazing has been excluded from the landscape for more than 30 years. Within the study site the

dominant grass species included the genera *Eragrostis intermedia*, *Bouteloua spp.*, *Lycurus* and *Muhlenbergia spp.*. Mimosa (*Mimosa biuncifera*), rabbit brush (*Chrysothamnus nauseosus*) and various cacti were also present. The soil is a White House (Fine, mixed, superactive, thermic Ustic Haplargids) fairly deep well-drained gravelly loam that formed in fan alluvium from mixed sources, with 1 to 3 % slope.

The study was a randomized complete block (block = replication) with a split-strip plot design and four applied treatments. The four treatments were a control, a prescribed burn, a rainfall simulation, and a rainfall simulation and prescribed burn interaction, with 6 replicates for each treatment. A prescribed fire treatment was randomly applied to half of the plots ($n = 6$) in late May 1998. The plots were then split equally into strips for the application of a simulated monsoon rainfall event (63.5 mmhr^{-1} for 40 min.) using a rotating-boom rainfall simulator (Swanson 1965) at the end of June 1998, approximately one month after the prescribed burn. The depth of rainfall used in the simulation was determined on site during the event. Given the unpredictable nature of the monsoon season, the simulated rainfall treatment was applied to ensure a heavy rainfall event that generated sediment production. Therefore, the simulation was run until substantial sediment production was observed and catchment capacity was nearly surpassed. The volume of runoff generated by the simulation was measured. However, experimental design and weather limitations did not allow for the collection of sediment produced during the application of the simulated rainfall treatment. The monsoon rain season unexpectedly began the day after the simulation, not allowing the draining of the catchments and collection of the sediment.

Six blocks were established on a hillslope, each containing 4 walled runoff subplots (3m by 10m) with a sediment catchment. Twelve permanent sampling points were established within each subplot to measure plant (n=3), fungal (n=3) and soil parameters (n=6). All sampling occurred following the summer growing season, ending with the culmination of the summer monsoon season. Samples were taken both prior to treatment application (1997) and following treatment application (1998 and 1999). Vegetation variables were measured within quadrat plots (0.5m by 0.5m) centered upon the point marker for a 2.5% area sample. The variables measured included percent aerial cover, grass bunch basal area (clump circumference at soil surface), and number of grass seedlings and ramets. Within a quadrat subset (0.25 m by 0.25 m), percent total rock cover and cryptogam presence were also noted. Soil and fungal samples were collected from soil cores (2cm by 10cm) and composited according to the experimental design. Soil samples for bulk density and fungal variables were composited by subplot (subplot = treatment) and depth (0-5 cm, 6-10 cm), while the remaining soil samples were composited by subplot. Measured variables were bulk density (Blake and Hartge 1986), soil particle-size distribution (Gee and Bauder 1986), aggregate stability (Kemper and Rosenau 1986), infiltration rate (Perroux and White 1988, White and Sully 1987, Sullivan et. al. 1996), live fungal biomass (Ames et. al. 1984) and total extractable glomalin (TG) (Wright and Upadhyaya. 1998). Aggregate stability was measured using a wet sieving technique, and infiltration rates were measured using a disc permeameter under unsaturated soil conditions.

Runoff volumes and dried sediment weights were measured for each subplot during the monsoon season, approximately July 1 through to October 1. Runoff volumes were calculated from the runoff depth captured in the catchments after storms. There was no adjustment for potential evaporation or pan leakage. Monsoon rainfall data were collected for 2 years following treatment application. Local meteorological data was available from the Audubon Research Ranch, Elgin, Arizona located approximately 2.4 kilometers miles from research site (Table 1). In relation to the last 10 years, the

Table 1. Rainfall totals by season for years 1990 to 1999.

	Rainfall (mm)				
	Winter (Jan to Mar)	Spring (Apr to Jun)	Monsoon (Jul to Sep)	Fall (Oct to Dec)	Total
1989	21.8	5.9	68.5	42.1	138.3
1990	14.4	11.8	146.7	33.5	206.4
1991	65.7	3.3	72.8	48.8	190.6
1992	62.6	27.8	81.4	69.9	208.7
1993	91.6	6.8	82.1	8.3	188.8
1994	31.2	13.0	88.9	73.0	206.1
1995	20.0	2.1	63.0	22.0	107.1
1996	12.0	6.0	71.8	13.5	103.3
1997	36.5	9.9	76.0	24.0	146.4
1998	52.8	22.0	95.6	11.8	182.2
1999	2.0	22.3	108.1	6.0	138.4

monsoon rainfall season of 1998 (95.6 mm) was above average, with the 1999 (108.1 mm) well above average. Rainfall records show that site annual totals (1989 to 1999) were above average in 1998, with below-average totals in 1999 attributed to a dry winter and fall. Except for a below-average fall, average rainfall totals for all seasons were well above normal in 1998.

Effects of prescribed fire and simulated rainfall on plant (cover, basal area, seedling number), soil microflora (live fungal biomass, total soil protein), and soil (bulk density, percent stable aggregates, infiltration rates, particle size distribution) variable responses were analyzed using analysis of variance (SAS Institute, Inc. 1990). There were no significant block by treatment interactions and plots were used as replicates. Mean comparisons of treatment within each year were made using least-squares means.

RESULTS

Vegetation

Prior to treatment application there were no significant differences among plots for perennial grass aerial cover or grass bunch basal area. There was a significant ($p = 0.0026$) block effect for annual herbaceous cover in 1997 that appeared to be due to the lower slope placement of two blocks, but no significant block by treatment interaction was present. In 1998 the significance of the block effect had decreased ($p = 0.0579$).

Following the 1998 and 1999 summer growing seasons there were significant treatments effects on perennial and annual plant cover, as well as perennial grass basal area. For perennial grass cover, a significant treatment effect was observed in 1998 ($F = 4.92$, $df = 3$, $p = 0.0001$) and 1999 ($F = 4.96$, $df = 3$, $p = 0.0001$). For both years following treatment, perennial grass cover was significantly diminished on the burned plots (Table 2). The recovery of the perennial vegetation following the prescribed burn was slow, with little difference between 1998 and 1999. There were also significant treatment effects for perennial grass basal area in 1998 ($F = 4.17$, $df = 3$, $p = 0.008$) and 1999 ($F = 5.04$, $df = 3$, $p = 0.013$). The mean basal area of grass clumps within the simulation and burn treatment were approximately 7.5 times lower than values for the prescribed burn only treatment, and at least 10 times lower than the remaining unburned treatments (Table 2).

While perennial grass coverage of the soil surface decreases, annual forb coverage was greatest within the simulation and burn treatment. As with perennial grass cover and basal area, a significant treatment effect on annual forb cover was also observed in 1998 ($F = 2.02$, $df = 3$, $p = 0.02$) and 1999 ($F = 3.80$, $df = 3$, $p = 0.0001$). In 1998, all treatments had significantly ($p \leq 0.05$) greater annual cover compared with the control, only the burned treatments continue to have greater annual cover and less perennial cover in 1999 (Table 2). By the end of the second summer growing season the recovery

Table 2. Comparison among treatments of mean seasonal plant variables¹.

Treatments		Cover (%)		Basal Area (cm ²)	
		1998	1999	1998	1999
Perennial	Control	20.4 ^b	31.9 ^a	254.8 ^a	285.5 ^{ab}
	Prescribed burn	9.0 ^c	19.0 ^b	185.3 ^{ab}	158.2 ^{ab}
	Simulated rainfall	29.8 ^a	30.8 ^a	319.8 ^a	332.6 ^a
	Simulation and burn	11.2 ^c	15.0 ^b	45.7 ^b	80.3 ^b
Annual	Control	0.9 ^c	5.3 ^b		
	Prescribed burn	1.9 ^b	10.1 ^a		
	Simulated rainfall	1.9 ^b	3.8 ^b		
	Simulation and burn	3.2 ^a	9.5 ^a		

¹Significant ($p \leq 0.05$) differences among treatment means for each plant variable are denoted with different letters.

of the perennial grass cover and basal area was beginning, yet coverage values were still lower than those within the unburned plots.

Regeneration of the perennial grass community was primarily through vegetative means, specifically with the re-sprouting of residual grass clumps and few new individuals being established. Seedlings were found within all treatments both years, yet none were found to survive the proceeding winter due to the lack of precipitation. In 1998 a significant ($F = 3.55$, $df = 4$, $p = 0.040$) treatment effect was observed, as well as a significant ($p = 0.0009$) treatment by block interaction. The significant block by treatment interaction was attributed to the lack of seedling production in 2 of the 6 blocks, as well the high variability in seedling number in the simulation and burn treatment compared with the other treatments. The greatest number of seedlings was found within the plots treated with the rainfall simulation, with the simulation and burn treatment (3.4

seedlings/m²) having a significantly ($p \leq 0.05$) greater number compared with other treatments (< 1 seedling/m²). There was no significant treatment effect on seedling counts in 1999, with seedling counts less than 1 seedling/m². There was also no significant treatment effect on ramet formation in either 1998 or 1999. Ramet formation (0.4 ramets/m²) was highest in the simulation and burn treatment compared to the other treatments (0.0 ramets/m²) in 1998, yet no new and few residual ramets were observed within the treatment in 1999.

The above-average seasonal rainfall of 1999 was reflected in productivity increases within the plant community, as well as in increased live fungal biomass levels (Table 3). While there was no significant treatment response in 1998, there was a significant ($F = 2.09$, $df = 3$, $p = 0.103$) effect on biomass levels in 1999. Levels were highest within the simulated rainfall treatment, significantly ($p \leq 0.05$) higher than levels within the burned treatments. Unlike fungal biomass levels, there was a significant treatment effect on total glomalin (TG) levels in both 1998 ($F = 2.69$, $df = 3$, $p = 0.079$) and 1999 ($F = 6.77$, $df = 3$, $p = 0.003$). For both years, protein levels were higher within the control, significantly ($p \leq 0.05$) higher than protein levels within the burned treatments (Table 3).

Table 3. Comparison among treatments of mean seasonal live fungal biomass and glomalin protein levels¹.

Treatments	Live fungal biomass ($\mu\text{g/g}$ soil)		Total glomalin ($\mu\text{g/g}$ soil)	
	1998	1999	1998	1999
Control	17.1 ^a	58.0 ^{ab}	2.080 ^a	2.130 ^a
Prescribed burn	19.9 ^a	48.7 ^b	1.334 ^b	1.214 ^b
Simulated rainfall	17.4 ^a	72.3 ^a	1.498 ^{ab}	2.392 ^a
Simulation and burn	16.8 ^a	46.5 ^b	1.408 ^b	1.426 ^b

¹Significant ($p \leq 0.05$) differences among treatment means for each fungal variables are denoted with different letters.

Changes within the soil matrix

Differences among treatments were observed for the soil variables evaluated after the two post-treatment monsoon seasons (Table 4). A significant treatment effect was observed for bulk density in both 1998 ($F = 3.63$, $df = 3$, $p = 0.0141$) and 1999 ($F = 2.99$, $df = 3$, $p = 0.311$), including a significant depth by treatment interaction in 1998 ($F = 2.21$, $df = 3$, $p = 0.0991$). Bulk density measurements for all treatments were significantly ($p \leq 0.05$) higher than the control following the first post-treatment season, yet only the simulation and burn treatment was significantly ($p \leq 0.05$) higher than the control in 1999. In 1998, samples taken within the plots treated with the rainfall simulation had significant ($p \leq 0.05$) increases in bulk density with depth (i.e. 0-5 cm and 6-10 cm), but these changes were not evident in 1999.

Table 4. Comparison of among treatments surface soil variables (10 cm depth)¹.

Treatments	Bulk density (kgm ⁻³)		Aggregate stability (PSA)		Infiltration rate (mmhr ⁻¹)	
	1998	1999	1998	1999	1998	1999
Control	1.53 ^b	1.50 ^b	0.74 ^a	0.64 ^{ab}	14.4 ^a	12.8 ^a
Prescribed burn	1.65 ^a	1.59 ^{ab}	0.75 ^a	0.59 ^b	9.7 ^b	8.0 ^b
Simulated rainfall	1.70 ^a	1.54 ^b	0.82 ^a	0.73 ^a	15.3 ^a	13.8 ^a
Simulation and burn	1.64 ^a	1.62 ^a	0.83 ^a	0.58 ^b	10.0 ^b	8.9 ^b

¹Significant ($p \leq 0.05$) differences among treatment means for each soil variable are denoted with different letters.

Aggregate stability, measured by percent water-stable aggregates (PSA) sized 150 to 300 μm , was not affected by treatment the first season. However, there was a significant ($F = 2.14$, $df = 3$, $p = 0.009$) treatment effect on aggregate stability in 1999, with a significantly lower percent of stable aggregates within the burned treatments compared to the rainfall simulation treatment (Table 4). Significant treatment effects on infiltration rates (mmhr^{-1}) were also recorded in 1998 ($F = 9.11$, $df = 3$, $p = 0.0001$) and 1999 ($F = 8.58$, $df = 3$, $p = 0.0001$), with significantly lower rates within the burned treatments compared with the unburned (Table 4).

Correlative relationships between soil and plant variables illustrated the integrated relationship of the soil structure to the biotic components of the watershed (Table 5). Perennial plant cover was moderately correlated to TG levels, which in turn was correlated to aggregate stability and sediment yield. Levels of fungal biomass within the soil were moderately correlated to soil texture, bulk density and aggregate stability, sediment sand and silt content, as well sediment yield ($p = 0.105$). Additionally, soil organic C levels were also correlated to bulk density, as well as to the silt content of the

soil. Moreover, soil texture size classes were correlated to bulk density and aggregate stability, particularly percent sand size class.

Surface Runoff and Sediment Yield

Measured runoff volumes in 1999 were higher than volumes measured in 1998, due in large part to the above average depth of monsoon rainfall. There was a significant treatment effect for both 1998 ($F = 14.01$, $df = 3$, $p = 0.0001$) and 1999 ($F = 7.78$, $df = 3$, $p = 0.0001$). For both years, runoff volume derived from storm events was significantly ($p \leq 0.05$) greater within the simulation and burn treatment (Table 6).

The simulated rainfall treatments contributed approximately 40% of the total seasonal rainfall and approximately 53% of the runoff for the 1998 monsoon season. Excluding the contributions of the simulation, the runoff volume in 1998 from the simulated rainfall only treatment was significantly higher than volumes recorded for the remaining treatments. The lack of a significant response in the prescribed burn treatment is due in part to experimental error. Logistical delays in the installation of catchment pans for these treatments may have caused the loss of both sediment and runoff from at least two storm events in the first year. It is reasonable to expect that the sediment yield and runoff depth would have been significantly higher than the control.

Table 5. Significant correlation coefficients (r) to show relationships between soil and plant variables (n=48).

	Bulk Soil									Sediment		
	Plant Cover	Fungal biomass	TG	C _{organic}	Sand	Silt	Clay	Bulk density	Agg. stability	Sand	Silt	Yield
Plant cover	1.000		0.481***									
Fungal biomass		1.000	0.291*		-0.584***		-0.446***	0.453***	0.420**	0.672***	-0.389**	-0.242
TG	0.481**	0.406*	1.000						0.279*			-0.461**
C _{organic}				1.000		-0.421**		0.346**				
Sand		-0.584***			1.000	-0.423**		0.324*	0.275*	0.302*	-0.315*	-0.286*
Silt		0.660***		-0.421**	-0.423**	1.000	0.441**	-0.289*		-0.356*		
Clay		-0.446**				0.441**	1.000	-0.324*		-0.419**		
Bulk density		0.453***		0.346**	0.324*	-0.289*	-0.324*	1.000	0.390**	0.517***	-0.404**	
Agg. stability		0.420**	0.279*		0.275*			0.390**	1.000			

*, **, *** Denote significance at 5 %, 1%, and 0.1% levels, respectively.

Table 6. Comparisons among treatments and years of mean monsoon season runoff volumes and sediment yield¹.

Treatments	Runoff volume (liters)			Sediment yield (kgm ⁻²).	
	Simulation	Total seasonal mean		Total seasonal mean	
	1998	1998	1999	1998	1999
Control	0 ^c	175.3 ^c	443.2 ^b	1.7 ^c	1.8 ^a
Prescribed burn	0 ^c	182.0 ^c	451.9 ^b	2.8 ^b	2.2 ^a
Simulated rainfall	279.0 ^b	544.0 ^b	592.3 ^b	2.9 ^b	1.9 ^a
Simulation and burn	415.0 ^a	890.3 ^a	828.5 ^a	4.1 ^a	2.3 ^a

¹Significant ($p \leq 0.05$) differences among treatment means for each hydrologic variable are denoted with different letters.

Mean sediment production showed a significant ($F= 5.34$, $df = 3$, $p = 0.011$) treatment effect the first post-treatment season, with little difference among treatments at the end of the second season (Table 6). In 1998, sediment yield from the simulation and burn treatment was greater than the other treatments. The control produced the least amount of sediment, while there was no significant difference between the prescribed burn and simulated rainfall treatments. Following the 1999 season, the sediment yield from the simulation and burn treatment was the greater than the remaining treatments.

DISCUSSION

Prescribed fire and the high intensity rainfall events associated with the summer monsoon were effective disturbances in the Arizona savanna. The integrated effects of the disturbance produced structural changes in the plant community and surface soil depths, consequentially contributing to hillslope runoff and erosion responses.

Vegetation

The length of the recovery period for the burned perennial grass community was longer than expected. The above-average summer rainfall in 1998 and 1999, as well as moist soil conditions preceding the burn were expected to mitigate plant damage and support a greater growth response following the fire. Aerial cover from remnant perennial individuals within the burned treatments was approximately 50 – 75 % the cover of the unburned treatments, with the lowest abundance of re-sprouting observed within the simulation and burn treatment. On the other side of the spectrum, the continued higher productivity of the grass community within the rainfall simulation treatment is likely the result of the one-time simulated rainfall event, illustrating the important effect of climatic controls on the plant community.

Aside from the regeneration of the residual perennials, regeneration of new individuals within the grass community appeared to be predominately influenced by environmental factors rather than treatment characteristics. The largest seedlings counts

were recorded in 1998 within the subplots treated with the rainfall simulation, although seedlings were found in all treatments both years. Even though seedlings were found in all treatments at the end of the summer season none were able to survive the winter droughts, suggesting strong environmental influences on long-term survival. Ramets were also observed in 1998 within the simulation and burn and control treatments, but few survived to the 1999 survey. Additionally, no new ramets were observed in 1999. Environmental or climatic factors appeared to mitigate ramet survival while prescribed fire appeared to have no influence on either seedling or ramet number. Recovery of the remnant the perennial grass community, as well as the successful establishment of new recruits appeared to be primarily dependent on winter and summer rainfall totals rather than on the characteristics of the spring prescribed burn.

Within this plant community, prescribed fire or large rainfall events alone do not seem to pose a long-term threat to the stability of the system. It is their interaction that appears to damage the perennial grass community and inhibit its ability to recover. While burning alone may damage above ground growing points (Steuter and McPherson 1995), erosion of soil around the plant exposes previously protected plant parts. Desiccation of exposed roots, as well as damage to below-ground growing points may explain the disproportionate decline of the perennial plants within the simulation and burn treatment compared to the prescribed burn treatment.

At the end of the second growing season in 1999 annual forb cover within the burned treatments ($\geq 9.5\%$) continued to be a significant contributor to the structure of

the residual plant community. With the slow recovery of the remnant perennial community and lack of new grass recruits, the increased forb presence may point to the beginning of a modified structure the savanna community. While the changes to the community may not be long-term there are ramifications to the hydrologic dynamics of the system. Evapotranspiration (ET) rates and overland flow processes are strongly affected by vegetative cover density and leaf area, influencing soil moisture levels, erosion dynamics and the routing of water over the hillslope.

Changes within the soil matrix

Decreases in measures of bulk density and infiltration rates within the burned treatments suggest that prescribed burning affects the structural integrity of surface soil layers. However, common measures of structural integrity, such as measurements of percent water-stable aggregates may not be appropriate or sensitive enough to detect changes in the organic carbon (C) limited soils of the desert grassland. Typically, water-stable aggregates are reported within much larger size classes (e.g. > 1 mm). Levels of soil organic C appear to play a critical role in the stability of water stable aggregates (Tate 1987), especially in association with larger soil aggregates (> 0.5 mm diam.)(Lu et. al.1998). Within this study, there were no stable aggregates larger than 0.3 mm. As positive correlation appears to exist between soil organic C levels and aggregate stability (Wright and Upadhyaya 1998), the lack of larger aggregates was expected given the organic C levels within the study's soils were on average 1.1 % (O'Dea, unpublished data).

The lack of larger stable aggregates does not preclude the structure of the desert grassland or savanna from being considered stable. Tisdall and Oades (1982) reported the significant contributions of soil biotic activities to soil aggregation in grassland soils. Both plant roots and fungal hyphae have been found to actively initiate and maintain of soil aggregates through the mechanical binding together of particles and smaller aggregates. Additionally, mucilage and other glycoproteins secreted by the soil biota, such as fungi are important drivers in micro-aggregation processes. Wright and Upadhyaya (1998) reported a highly significant correlation ($r^2 \geq 0.84$) between aggregate stability and glomalin, a glycoprotein produced by the ubiquitous AMF within grassland systems.

Within this study, there were no significant differences in percent water-stable aggregates among treatments following the first post-treatment season. However, the greater number of stable aggregates within the unburned treatments mirrored the results of both live fungal biomass and glomalin measures at the end of the second season. The percent of water-stable aggregate, fungal biomass and glomalin levels were highest in the simulated rainfall and control treatments, all significantly correlated to one another (Table 5). The presence of significant correlative relationships between the biotic and physical characteristics of the desert grassland's soil may lead to important clues regarding its structural characteristics and stability. For unlike other soils where organic C is not a limiting factor, organic C levels were not correlated to the aggregate stability, fungal or perennial plant parameters of soils within this study. Within this study

aggregate stability of the soil appears to be strongly influenced by the fungal community, as well as soil texture.

Sediment Yield and Runoff

First year runoff volumes were greatest within the simulation treatments, with the largest runoff volumes within the simulation and burn treatment for both 1998 and 1999. All of the treatments, including the control produced sediment both sampling years. Erosion losses within the simulation and burn subplots were the highest of all the treatments both in 1998 and 1999. Of particular interest was the unexpectedly high sediment production in 1998, approximating a soil loss from the subplots of 5 tons/acre/year (1cm depth) in 4 of the 6 blocks. Sediment production among the remaining treatments was as expected, as the burned plots produced a greater erosion response than the unburned ones. Due to experimental methodology we were not able to separate out the actual sediment contributions of the rainfall simulation treatment. However, in practical terms, it has been suggested that the first year response within the rainfall simulation only treatment would not have been different from the control had it also received 40% more rainfall in 1998. Additionally, a conclusive statement regarding the contribution of the rainfall simulation treatment on sediment production within the burned plots was not possible. The simulation event may have produced a quantity of sediment equivalent to the difference between the burned treatments, or it could have primed the system to be more susceptible to proceeding storms events.

Desert grassland soils appear to have inherently low levels of organic carbon, on average 1.1 % in this study, but this limitation does not exclude the existence of relative stability for the soil structure. The lower levels of soil organic matter within these systems appears to require a shift in perspective towards what may be the primary contributor to aggregate stability, the fungal community. This study found no correlation between organic C levels and aggregate stability. Yet, the fungal variables were found to correlate well with soil variables representative of the soil structure. Live fungal biomass levels had moderate to moderately high significant correlation to not only aggregate stability, but also bulk density, soil texture and sediment yield (Table 5). Additionally, biomass and glomalin levels were substantially reduced within the burned treatments, as were surface infiltration rates. The relationship of fungi to aggregate stability is not new to the literature (Schreiner et. al. 1997, Tisdall and Oades 1982), however the relationship had not been examined outside an agricultural context.

As the soil structural characteristics appear to be dependent upon the presence of an active fungal community, the fungal community is dependent upon an active plant community. Without plant hosts the activity of the obligate biotroph AMF diminishes, and apparently so does the production of the glomalin protein and a portion of the fungal biomass. Prescribed fire disrupts the linkage between the plant and fungal communities, with recovery of the fungal community dependent in many ways on the recovery of the vegetation. As the vegetation and fungal community recovers, aggregate stability begins to increase and sediment production appears to decline. Until the vegetation begins to

recover, soil erosion continues as the surface remains exposed and less vegetation is present to mitigate overland flow, increasing the susceptibility of the fungal community to decline.

SUMMARY

Prescribed fires are set in the spring to precede the summer monsoon in an attempt to mimic the natural fire regime of the desert grassland and savanna. It is often put forth that this is the opportune time to set the fires since native vegetation evolved under these fire regimes. For most, the desired outcome of these prescribed fires is to reduce woody vegetation, and produce a more diverse and native grassland community. However, fire also affects the soil and hydrologic processes within the grassland or savanna. Therefore, prescribed fire is a disturbance to the watershed or landscape, not just the plant community.

A feedback mechanism exists between plant and soil processes, which when disturbed affects the hydrology of the watershed. The prescribed fire's perturbation of the plant community disrupts below ground processes linked to the activity of the plants, including those important to the maintenance of the soil's structural stability. In this study, reductions in fungal biomass and glomalin production appeared to be linked to decreases in aggregate stability, increases in bulk density, and subsequently decreasing infiltration rates and greater erosion in the C-limited grassland. As soil was eroded away so were the fungi, leaving progressively less fungi in the surface soil layers. The slow

post- prescribed fire recovery of the plant community also appeared to affect the recovery of the fungal community, especially the biotrophic AMF. Historically, the importance of vegetative cover to overland flow processes and ET have been well accepted, yet its role in soil aggregation is often simplified to only examining the contributions of roots without examining its linkage to the soil biota. The results of this study call to attention the importance of examining the cumulative effects of site disturbances, whether fire or raindrop impact on the processes which mitigate the structural stability of the soil matrix.

The occurrence of prescribed fires preceding large, erosive rainfall events is not improbable. Within the 30-year rainfall record of the study site large events had been recorded, with the most recent occurring the year before the experimental treatments were applied. Prescribed fire is a useful tool in the maintenance of the desert grasslands. However, it needs to be recognized that the fire affects the functioning of the entire watershed, not just the plant community.

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APPENDIX 2. FIRE AND ARBUSCULAR MYCORRHIZAE IN THE DESERT GRASS COMMUNITIES OF SOUTHEASTERN

Abstract:

Two factorial greenhouse studies were completed in conjunction with a field study to examine the effects of prescribed fire and the summer monsoon on the AM fungal (AMF) community, and the role of AMF in the regeneration of the post-fire grass community. The objectives of the greenhouse studies were: 1) to test the effects of prescribed fire and high intensity rainfall on AMF infectivity potential, and 2) to examine the effect of mycotrophy on the biomass production of native and introduced grasses grown in pasteurized and native soils. Results indicate that prescribed fire has a significant ($p \leq 0.05$) and negative impact on AMF infection potential. Grass root colonization was significantly ($p \leq 0.05$) lower in plants grown in soil exposed to the prescribed burn. Grass response to mycorrhizal colonization varied within and among the species examined. Within this study the lovegrasses (*Eragrostis spp.*) appeared to be facultatively mycorrhizal, producing greater shoot biomass and earlier inflorescences without colonization. The opposite results were observed for the grama (*Bouteloua spp.*) and wolftail (*Lycurus phleoides*) grasses. For these grasses, larger shoot:root ratios and inflorescences were present when they were colonized. Clear differences among the grasses demonstrated that their responses to colonization, as well as the effect of burning on AMF infection potential provides important insights in to the development of the post-fire desert grassland community.

INTRODUCTION

Southwest grasslands evolved with fire as an important shaper of the grass community (McPherson 1995, Wright and Bailey 1982). Prescribed fire is a land management tool utilized to create desired grassland communities through the removal of unwanted vegetation, usually targeting the plant's lifestage that is most susceptible to lethal damage from the fire. However, its use in the restoration of native grasslands in southern Arizona has not been successful in the removal of some introduced species, such as Lehmann lovegrass (*Eragrostis lehmanniana*). In the Southwest, Lehmann lovegrass was introduced along with other South African grasses in the early part of the 20th century to enhance domestic livestock forage in the grasslands. Following prescribed fires, lovegrass seed germination has been found to be higher on burned sites compared with unburned sites, with the greatest numbers of seedlings occurring following prescribed fires timed with seasonal plant senescence (Biedenbender and Roundy 1996, Ruyle and Cox 1988). Greater numbers of individuals, from both ramet formation and seedling establishment following fire have also been noted for other lovegrass, including the Arizona native *E. intermedia* and the Africa native *E. pallens* (Bock et al. 1995, Yeaton et al. 1988) compared with other grass species common to their respective sites. Successful seedling establishment of semi-arid grassland species, such as *Eragrostis*, *Muhlenbergia* or *Bouteloua spp.* (Biedenbender and Roundy 1996, Wilson and Briske 1979) is dependent upon adequate soil moisture and the pattern of summer rainfall. Ford (1999) suggests that the response of *Bouteloua gracilis* to fire is

predominately neutral or positive. Plant response appears to be a function of the season of burning and general climatic conditions before and after the fire. Yet a clear mechanism for these fire-induced differences in plant responses has not been determined.

Mycorrhizae, specifically the arbuscular mycorrhizae (AM) have well documented roles in plant nutrition, growth and phenology (Miller 1987, Trappe 1981). However, there has been little focus on these symbiotic relationships in terms of grass species occupying the desert grasslands of Arizona with the exception of blue grama (*B. gracilis*) (Hays et al. 1982). But what has not been examined is the role this relationship would play in the recovery of a grassland community following fire. Additionally, little is known about the effects of fire on the AM fungal (AMF) in the semi-arid grasslands. The magnitude and duration of soil temperature fluctuations appear to influence the extent of mycotrophy. For example, decreases in AMF propagules (Dhillion and Anderson 1993, Habte 1989), AM infection of plant roots (Klopatek et al 1988), and AMF species composition (Gibson and Hetrick 1988) have been attributed to the temperature effects of burning. Additionally, the number of active AM propagules and infectivity significantly decline with soil depth (Habte 1989). Therefore, as soil erodes away the numbers of propagules proportionally drop with depth.

The objective of this study was to evaluate potential impacts of AM on the competition dynamics of 5 dominant grass species following prescribed fire and rainfall erosion disturbances in a southeastern Arizona grassland. Treatment effect on the infectivity of the fungal inoculum, levels of live fungal biomass and AMF spore number

were evaluated, as well as the impact of mycorrhizal relationship on the grass species' growth and seed production.

METHODS

Study Site

The study area was a small-watershed in a southern Arizona savanna. The grass community dominated by perennial grasses, including *Lycurus phleoides*, *Bouteloua spp.*, *Muhlenbergia spp.*, and *Eragrostis spp.*. The soil is an alluvium derived from andesite, rhyolite, limestone and quartzite (pH = 5.9, ave. extractable P = 18.6 ppm (17.5 ppm – 20.2ppm). The study design was a randomized complete block (block = replication) with a split-strip plot design. Six blocks were established along a hillslope, with each block split into two plots. A late-spring prescribed burn was randomly applied to half of the plots. The plots were then split again into strips and the rainfall simulation treatment applied with a rotating-boom rainfall simulator (Swanson 1965) to simulate an erosional rainfall event. This treatment was not randomly applied because of the logistical and physical constraints of moving the simulator across the study site. The four treatments that resulted were a control, a prescribed burn, a simulated rainfall event, and a simulation and burn, with each treatment replicated in each block (n= 6). Each treatment was represented by walled subplots with sediment catchments at their base. Soil and sediment samples were collected from all of the subplots at the end of the first post-treatment growing season, which coincided with the end of the summer monsoon (approximately July 1 to October 1). At this time, AMF spores were counted within the

bulk soil and sediment samples, bulk soil fungal biomass levels were measured, and the greenhouse studies were initiated.

Greenhouse

Two factorial greenhouse studies were established to 1) examine the effects of treatment on the infectivity potential of the mycorrhizal fungal inoculum, and 2) the effect of mycorrhizal infection on the growth and timing of seed production of the 5 predominant perennial grasses within the research site.

Study 1 – Infectivity potential of soil inoculum following treatment

Soil samples of approximately 100 g were collected to a depth of 15 cm from each of the subplots at the field site, with all soil samples being composited by treatment (i.e. control, prescribed burn, simulated rainfall event, simulation and burn). The soil samples were mixed 1:1 (v/v) with silica sand (no. 60) the day of collection. For each treatment, 10 Ray Leach Cone-tainers™ (164 ml) were filled with the soil mixture and planted with 3 sudan (*Sorghum sudanese* (Piper) Staph.) grass seeds that had been surface sterilized with 1 % sodium hypochlorite for 5 min. Sudan grass was chosen because of its consistent growth under greenhouse conditions and its high capacity for mycorrhizal fungal colonization. Following germination, seedlings were culled to one plant per container. Plants were grown in a greenhouse at temperatures between 22 and 32°C, and watered as needed. No fertilizer was applied. Plants were harvested at 90 days following seed set. For each treatment, 100 randomly selected root sections from the 10 plants were evaluated for AMF infection using a grid-line intersection method (Silva

1994). Soil cores (2 cm x 10 cm) were also taken from the field study site, and levels of live fungal biomass (Ames 1982, Silva 1994) and numbers of AMF spores (Silva 1994, Stutz and Morton 1996) were measured. Comparison of colonization means among treatments was made using one-way analysis of variance computations on the mean. Significant differences among treatment means were isolated using least significant difference measures with SAS statistical software (SAS Institute, Inc., 1990).

Study 2 – Effect of mycorrhizal infection on the growth and timing of seed production

Seeds from the five most dominant grasses were collected from the research site in late summer of 1998. The grass species examined were wolftail (*Lycurus phleoides*), blue grama (*Bouteloua gracillis*), side-oats grama (*B. curtipendula*), plains lovegrass (*Eragrostis intermedia*), and Lehmann lovegrass (*E. lehmanniana*). Approximately 1 kg of soil was taken from undisturbed portions of the research site, outside of high traffic pathways and experimental plots, and mixed 1:1 (v/v) with silica sand (no. 60). Half of the soil mixture was pasteurized. All seeds were surface sterilized with 1 % sodium hypochlorite for 5 min. Each grass species was planted in to 12 Ray Leach Cone-tainers™ (164 ml) filled with either native (non-pasteurized) soil mixture, pasteurized soil mixture or a control (a 1:1 (v/v) mix of pasteurized and native soil mixtures) for a total of 36 containers per species. Following germination, seedlings were culled to one plant per container. Plants were grown at temperatures between 22 and 32°C, and watered as needed. No fertilizer was applied. Plants were monitored for phenological changes

and were harvested at 120 days. Three plants from each treatment were checked for AMF infection through the examination of 50 root segments (Silva 1994). The remaining 9 plants were separated in to root and foliar material, dried for 3 days at 70°C, and weighed.

Ten plants from each of the species represented in the greenhouse study were randomly selected from the research site, harvested and examined for fungal colonization in the same manner as their greenhouse counterparts. The sampled plants were taken outside of the subplots and high traffic pathways. Plants were not taken from inside the subplots so as not to disturb other experiments, particularly the hydrology results. The examination of the field specimens was done to compare the potential effect of the greenhouse environment on the infection results. Additionally, mean AMF spore counts (Silva 1994, Stutz and Morton 1996) and levels of live fungal biomass (Ames et al. 1984) were measured for both bulk soil and sediment samples collected from each subplot at the end of the monsoon season

Comparisons of shoot and root dry weight means among soil treatments were made using analysis of variance computations for each grass species. Comparison of colonization means among grass species was made using analysis of variance computations on the mean. Significant differences among treatment means were isolated using least significant difference measures with SAS statistical software (SAS Institute, Inc., 1990).

RESULTS

Study 1

Mycorrhizal infection potential, as measured by fungal infections per unit length of root was significantly ($F = 201.10$, $df = 3$, $p = 0.0001$) different among treatments, with levels of infection substantially diminished in soil samples from the prescribed burn treatments (Table 7). Plants grown in soil taken from the control and the simulated rainfall treatments had the highest mean colonization rates, significantly ($F = 169.28$, $df = 3$, $p = 0.0001$) higher than plants grown in soil from burned treatments.

Changes in fungal inoculum were observed for bulk soil and sediment pan AMF spore counts, but not for live hyphal biomass levels. There were no significant differences among the treatments for total live soil fungal biomass, which represents all fungi present at the site, not just the AMF. Within the bulk soil, significant ($F = 7.60$, $df = 3$, $p = 0.0026$) treatment effects on AMF spore counts were observed. AMF spore numbers were highest within the control, significantly greater than other treatments. The spore count was the lowest in the simulation and prescribed burn treatment (Table 7). Within the sediment samples a significant treatment effects ($F = 2.96$, $df = 3$, $p = 0.0054$) on sediment spore counts were observed. The number of AMF spores significantly ($p > 0.002$) lower in the control compared to the subplots treated with the rainfall simulator.

Table 7. Mean infection points per unit root length of sudan grass (*Sorghum sudanese* (Piper) Staph), live fungal biomass levels and spore numbers as measures of AMF inoculum potential and viability following site disturbance¹. Mean standard errors are in parentheses.

Treatment	Root Infection (per unit root length)	Live fungal biomass (mg per g soil)	Number of AMF spores (per g soil)	
			Bulk soil	Sediment Pan
Control	0.91 ^a (0.03)	19.92 (2.017)	18.3 ^a (1.04)	7.8 ^c (1.43)
Prescribed burn	0.13 ^c (0.04)	17.12 (8.290)	14.2 ^b (2.20)	12.6 ^b (2.23)
Simulated rainfall	0.71 ^b (0.04)	17.39 (1.682)	15.0 ^b (1.91)	19.5 ^a (1.73)
Simulation and burn	0.06 ^c (0.07)	16.80 (4.482)	12.5 ^b (2.5)	19.2 ^a (3.07)

¹Significant ($p \leq 0.05$) differences among treatment means within each fungal variable is denoted by different letters.

Study 2

All species germinated and became mycorrhizal. Using mean number of infections per unit root length as a measure of the mycorrhizal colonization, there were significant ($F = 2.35$, $df = 4$, $p = 0.0735$) differences in among grass species grown in native soil. The wolftail grass (*Lycurus phleoides*) had significantly ($p > 0.05$) greater colonization (0.093 ± 0.016 S.E. infections per unit root length) than the other species examined (infections per unit root length ≤ 0.064). There were no significant differences in colonization rates among the grama grasses (*Bouteloua spp.*) and the lovegrasses (*Eragrostis spp.*), with colonization means of $0.057 (\pm 0.009$ S.E.) and $0.064 (\pm 0.004$ S.E.) infections per unit root length, respectively. However, there were important differences among the species in response to mycorrhizal colonization.

Colonization status (i.e. colonized or not colonized) appeared to be an important factor in comparing differences among species in shoot and root dry weights (g).

Inoculated wolftail and grama grasses had higher shoot and lower root biomass, resulting in significantly ($p = 0.001$) higher shoot:root ratios than their non-infected counterparts (Table 8). In addition, within the time frame of this study, inflorescences were only observed in the colonized grama and wolftail grasses. In contrast, the uncolonized lovegrass had significantly ($p > 0.001$) higher shoot biomass and shoot:root ratios than their infected lovegrass counterparts (Table 8). Unlike the Lehmann lovegrass, the native plains lovegrass had significantly ($p = 0.001$) higher root biomass when grown in the pasteurized soil compared to the native soil. In addition, inflorescence within the uninfected lovegrass group appeared on average approximately 2 weeks before the colonized plants (Table 8).

Table 8. Mean dry weight comparisons of the shoots and roots of grass species (n=10) grown in pasteurized and native (non-pasteurized) soils. Mean standard errors are in parentheses.

Grass Species	Soil Treatment	Mean dry weight per plant (g)		
		Shoot	Root	Shoot:Root
<i>Lycurus phleoides</i>	Native	0.490 (0.018)	0.674 (0.326)	0.727 (0.050)
	Pasteurized	0.455 (0.025)	2.449 (1.278)	0.186 (0.137)
<i>Bouteloua gracillis</i>	Native	0.362 (0.021)	0.586 (0.109)	0.618 (0.065)
	Pasteurized	0.275 (0.059)	1.100 (0.214)	0.248 (0.259)
<i>B. curtipendula</i>	Native	0.350 (0.027)	0.365 (0.086)	0.959 (0.062)
	Pasteurized	0.259 (0.061)	0.556 (0.099)	0.466 (0.264)
<i>Eragrostis intermedia</i>	Native	0.445 (0.052)	0.994 (0.115)	0.447 (0.018)
	Pasteurized	0.702 (0.124)	1.269 (0.137)	0.553 (0.071)
<i>E. lehmanniana</i>	Native	0.427 (0.049)	1.234 (.228)	0.346 (0.049)
	Pasteurized	0.646 (0.131)	0.777 (0.148)	0.831 (0.137)

DISCUSSION

Late-spring prescribed fires appeared to disrupt the mycorrhizal communities within the studied southern Arizona grassland, as evidenced by decreases in propagule number and mycorrhizal formation in test plants. The infection potential of the AMF was severely diminished in the first post-treatment season following the prescribed fire, with the decline appearing to be related to erosion losses of inoculum and fire damage. The smallest number of AMF spores was found within the bulk soil samples of the simulated and burned treatment, yet the numbers for all of the treatments were lower than the control. Within the sediment samples, the control treatment had the least amount of AMF spores, with the highest losses associated with the rainfall simulation treatments. The sediment spore counts related well to the soil losses from each treatment, in which all treatments had sediment yields significantly higher than the control. Following the first post-treatment season, soil loss from the simulation and burn treatment (4.1 kgm^{-2}) was nearly 2.5 times greater than the soil loss from the control (1.7 kgm^{-2}) (O'Dea 2000, unpublished data). The results from this study are also similar to those reported by Habte (1989) and Amaranthus and Trappe (1993), who found that as soil surface layers are eroded away the numbers of AM propagules and fungal infectivity proportionally decreased. However, it is not clear from the methodology of this study that the decline in infectivity is only due to the erosional loss of propagules.

Although the greatest number of AMF spores was found within the sediment pans of the simulated rainfall treatments, the spore count for the prescribed burn treatment was significantly different from both the control and the simulation treatments. Moreover, all

treatments had fewer spores in the bulk soil when compared to the control. Results from the greenhouse studies show the colonization rates of grasses grown in soil taken from the burned treatments were much lower than the rates reported for either of the unburned treatments. These results suggest that a portion of the decline in infectivity may not be explained only by the erosional loss of propagules from the plot, but suggest that the prescribed burning may have damaged the AMF community. The fungi may have been physically damaged by the heat flux through the soil, or the declines in infectivity may be attributed to nutritional changes associated with plant host damage. In either case, the methodology of this study did not examine either explanation.

While all of the grasses in this study were mycorrhizal, the growth response to colonization was distinctly different among the species. The lovegrass appeared to be facultatively mycorrhizal, thriving without mycorrhizal colonization. Without colonization, substantially higher shoot to root ratios were measured for the lovegrass when compared to the blue grama and the wolftail grasses. Above ground biomass production was greatest for the introduced African Lehmann lovegrass compared to all of the other non-colonized grasses. Additionally, both of the non-colonized lovegrasses formed inflorescences weeks before their infected counterparts. Similar findings were reported by Yeaton et al. (1988) for *E. pallens*, a native lovegrass of South African savannas, but without the examination of the role of mycotrophy. In the African study, greater production of above ground biomass was reported for the grass following annual burning, with a greater number of tillers and earlier seed production also observed. The reported annual burning may have led to a decline in mycorrhizal infection potential or to a similar disruption of the soil biota (van Reenen et al.

1992), which may have then led to the creation of an environment for the African lovegrass similar to that of the Arizonan lovegrasses discussed in this study.

In comparing the two lovegrasses, both species had significantly higher shoot production and shoot: root ratios when they were not colonized. In response to colonization, root production was significantly lower in the plains lovegrass than it was when it was not colonized. The opposite relationship was observed in the Lehmann lovegrass, where the lowest root production was recorded when the grass was not colonized. Overall comparison of root production among the grasses showed that the lovegrasses had considerably higher root production when colonized than did the other grasses. Without colonization it appears that the Lehmann lovegrass may not require as large of a root system as the plains lovegrass to maintain the shoot biomass in the absence of the mycorrhizal association. These results lead to further questions to be addressed in the future. Specifically, to questions regarding the effect of mycotrophy on plant resource allocations between the shoot and root systems.

In contrast to the lovegrass, production of above ground biomass significantly declined in the grama and wolftail grasses without mycorrhizal colonization, a reduction in shoot to root ratios of between 50 to 70 %. Without mycorrhizal colonization, the grasses appear to allocate more energy to root system production at the expense of above ground biomass. As with the below ground comparison of the lovegrasses, the differences in the grama grass responses are also worth noting. The shoot:root ratio of the side-oats grama was 50 to 60% greater than the ratio for the blue grama, under colonized and non-infected conditions. Although both grammas have less above ground biomass without colonization, the

side-oats grama did not produce the greater root biomass evident for both the blue grama and the wolftail grasses. The result of this phenomenon appears to be that the shoot: root ratios for the side-oats grama were not as reduced without colonization as they were for the other grasses. It is clear that responses to colonization occur within genera, as well as between them. Differences in growth strategies in response to mycotrophy may give one species a competitive advantage over another, even those within the same genus. However, this discussion is outside the scope of the current study.

No inflorescences were observed for the non-colonized grama and wolftail grasses during the study, but they were observed in colonized plants. It is not known if the non-colonized grasses would have flowered had the study continued. However, the early production of inflorescences on the non-colonized lovegrasses, compared with both the colonized lovegrasses and the other grasses, appears to give it a competitive advantage in regeneration. Clear differences among the grasses demonstrated that their responses to colonization may provide important insights in to the development of the post-fire desert grassland community.

With a decrease in AMF presence, the competitive advantage for re-establishment on the burned site appears to favor the lovegrass, particularly the Lehmann lovegrass over the other grasses from the study site. Under general conditions, the seed banks of the grass community are not expected to be significantly damaged during grassland fires (Biedenbender and Roundy 1996, Bock et al. 1995, Wright 1979), allowing for a viable seed source to be present for the regeneration of the disturbed community. The

mycorrhizal responses of individual grass species, along with the fire damage to antecedent plants and the AMF appear to have the potential to influence the competitive interactions and structure of the community, not unlike those observed within the tallgrass prairie (Smith et al. 1999). Additionally, the severity of the AMF response to fire may also explain delays in the recovery of disturbed communities. The recovery time of mycorrhizal dependent species, such as the grama and wolftail grasses may be a function of AMF recovery and not necessarily just seedling recruitment. Given the relatively short fire frequencies associated with the desert grasslands, it appears that the interaction of fire and the AMF have meaningful roles in shaping the grassland communities.

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APPENDIX 3. BELOW-GROUND MITIGATION OF UPLAND EROSION PROCESSES IN A DESERT GRASSLAND

Abstract:

Within a desert grassland in southeastern Arizona, the interaction of prescribed fire and the summer monsoon significantly ($p \leq 0.05$) affected the plant, fungal, and soil properties important to upland erosion processes. The fungal properties of the soil, and not levels of soil organic matter, appeared to strongly influence the characteristics of the soil structure. These structural changes in turn created measurable changes in both runoff and upland erosion processes. The integrated nature of the soil fungal and physical properties allowed for the development of a new perspective on measuring soil erodibility and the modeling of upland erosion in desert grasslands and savannas.

INTRODUCTION

Within an ecosystem, plant and soil processes interact to affect surface hydrology through their influence on surface roughness, soil structure, evaporation, and through their relationship with soil biota. In the Southwest, decreases in perennial grass cover and the erosion of uplands can initiate a decline in watershed condition. Both explicit research and intuition indicate that the processes that characterize the watershed, such as the geomorphology, hydrology, soil and vegetation, are linked together. But what is not well known are the process linkages or the drivers that create the dynamic and integrated ecosystem.

Mycorrhizae provide unique and measurable linkages between soil and plant processes. Mycorrhizae are symbiotic associations between host plants and certain fungi. In the case of arbuscule mycorrhizae (AM), the host plant acts as a source of carbon for the fungi. The plant in turn can receive nutritional benefits and protection from pathogens. Recent agronomic literature has described the role of AM in maintaining soil structure, aggregate stability (Schreiner et al.1997), as well as the contributions of the soil fungal community and the AMF to micro-aggregation (Tisdall and Oades 1982, Wright and Upadhyaya 1998). Yet, little is understood as to how this biotic relationship functions in the wildland ecosystem, particularly in terms of its role in the erosion process.

The impact of fire on plant and hydrologic processes in Southwestern grasslands has been well examined (Baker 1988, McPherson 1995, Hester et al. 1997). As expected, vegetative cover mitigates the impact of fire on erosion by protecting the soil surface.

Moreover, the disturbance appears to strongly influence the biotic soil community through its linkage to the vegetation (Nelson and Allen 1993). Reeves et al. (1979) and Doerr et al. (1984) reported significant declines in mycorrhizal regeneration and growth within highly disturbed systems, similar to those described for the desertification scenario suggested by Sclesinger et al. (1990). Instability within the ecosystem leads to a breakdown in the feedback mechanism between the plant and soil communities, decreasing the ability of either community to deal with the stress of a disturbance. It has been suggested that the lack of regeneration of many native mycorrhizal plant species may be linked to this breakdown (Allen 1988, Miller 1987, Reeves et al. 1979).

Soil erosion is an important consideration in the management of wildlands. Hillslope erosion can contribute to channel sediment load, yet the sediment may not be deposited in the channel. In semi-arid grasslands there may be a limited number of permanent channels. Therefore, erosion may be more relevantly thought of as a means by which soil resources are redistributed over the landscape. In addition, traditional erosion prediction models, such as the Revised Universal Soil Loss Equation (RUSLE) may not perform as well as they do on the agricultural lands for which they were developed. Semi-arid grassland soils, unlike most agricultural soils have on average less than 5 % organic carbon and a heterogeneous distribution of soil organic matter over the landscape. Given the nature of these systems erosion models, such as the RUSLE may not be effective given their assumptions for determining soil erodibility (Renard et. al. 1997).

The objectives of this study were: 1) to examine the effects of prescribed burning and the high intensity rainfall events of the summer monsoon on the plant and soil fungal communities and soil structure in relation to experimental plot sediment production, 2) to develop and evaluate an experimental erosion estimation model incorporating physical and biotic soil components, and 3) to compare the experimental model to the commonly used RUSLE.

METHODS AND MATERIALS

The Elgin, Arizona study area was located in a savanna, characterized by oak woodlands in the drainages, and perennial grass species occupying the uplands. The site was located within the Appleton-Whittel Research Ranch, where livestock grazing has been excluded from the landscape for more than 30 years. Within the study site the dominant grass species included the genera *Eragrostis intermedia*, *Bouteloua spp.*, *Lycurus* and *Muhlenbergia spp.*. Mimosa (*Mimosa biuncifera*), rabbit brush (*Chrysothamnus nauseosus*) and various cacti were also present. The soil is a White House (Fine, mixed, superactive, thermic Ustic Haplargids) fairly deep well-drained gravelly loam that formed in fan alluvium from mixed sources, with 1 to 3 % slope.

The study was a randomized complete block (block = replication) with a split-strip plot design and four applied treatments. The four treatments were a control, a prescribed burn, a rainfall simulation, and a rainfall simulation and prescribed burn

interaction, with 6 replicates for each treatment. The blocks were split into plots and the prescribed fire treatment was randomly applied to half of the plots ($n = 6$) in late May 1998. The plots were then split equally into strips for the application of a simulated monsoon rainfall event (63.5 mmhr^{-1} for 40 min.) using a rotating-boom rainfall simulator (Swanson 1965) at the end of June 1998, approximately one month after the prescribed burn. Given the unpredictable nature of the monsoon season, the simulated rainfall treatment was applied to ensure a heavy rainfall event that generated sediment production. Therefore, the simulation was run until substantial sediment production was observed and catchment capacity was nearly surpassed.

Six blocks were established on a hillslope, each containing 4 walled runoff subplots (3m by 10m) with a sediment catchment. Twelve permanent sampling points were established within each subplot to measure plant ($n=3$), fungal ($n=3$) and soil variables ($n=6$). All sampling occurred following the summer growing season, ending with the culmination of the summer monsoon season. Percent aerial cover and genera abundance measurements for the perennial grasses were made within quadrat plots (0.5m by 0.5m) centered upon the point marker. Soil samples (2cm by 10cm) were collected at their respective sampling points, and tested for total organic carbon ($\mu\text{g/g}$) (Matejovic 1997), live fungal biomass ($\mu\text{g/g}$ of soil) (Ames et. al. 1984), easily (EEG) and total extracted glomalin (TG) ($\mu\text{g/g}$ of soil) (Wright and Upadhyaya 1998), particle size distribution (%) (Gee and Bauder 1986), and percent water-stable aggregates (PSA) (Kemper and Rosenau 1986). Aggregate stability was measured using a wet sieving technique. Only two water-stable aggregates sizes reported here, PSA100 (150 – 300 μm)

and PSA200 (74 – 149 μm). There were no water-stable aggregates larger than 300 μm recorded for soil samples taken from the field study site.

Monsoon rainfall data were collected for 2 years following treatment application. Local meteorological data were available from the Audubon Research Ranch, Elgin, Arizona, located approximately 2.4 kilometers miles from the research site. In relation to the last 10 years, the monsoon rainfall season of 1998 (95.6 mm) was above average, with the 1999 season (108.1 mm) well above average. Rainfall records show that the annual totals for the site were above average in 1998 compared to the period average from 1989 to 1999. The below-average totals in 1999 were attributed to a dry winter and fall. Except for a below-average fall, average rainfall totals for all seasons were well above normal in 1998.

A comparison of upland sediment was made between the experimental model developed in this study and the Revised Universal Soil Loss Equation (RUSLE). RUSLE model software is freely provided to the public by the United States Department of Agriculture, with complete documentation also available (Renard et al. 1997). The RUSLE model is described as follows:

$$A = R * K * L * S * C * P$$

Where A is the estimated average soil loss per unit of area based upon a user selected K and R. R is the rainfall-runoff erosivity factor, K is the soil erodibility factor, L is the slope length factor, S is the slope steepness factor, and C is the cover-management factor.

P is the support practice factor, which is generally only applicable to agronomic practices.

RUSLE erosion estimates were calculated for each subplot based upon input variables measured for each subplot, with all estimates converted to units of kgm^{-2} .

For this study, an R factor of 78 was calculated with rainfall data collected at the research site in 1998. L and S factors were based upon subplot dimensions (3 m by 10 m) and an average slope of 2 %. All of the remaining factors were calculated using the RUSLE software, with data input generated from subplot measurements of plant and soil variables taken in 1998 and 1999.

Examinations of treatment effects and time on the plant, fungal and soil means were made using analysis of variance. Significant differences among treatment means were isolated using least significant difference measures with SAS statistical software (SAS Institute, Inc., 1990). Correlation tests were evaluated on annual means for perennial grass (cover, genera), soil microflora (live fungal biomass, easily extractable and total glomalin), and soil (percent water-stable aggregates, total organic carbon, texture classes) variables using the Pearson correlation test. Stepwise regression and response surface analysis were used to model upland sediment yield. Principal components analysis (PCA) was used to examine the linear relationship and relative contributions of the quantitative variables to the model. All statistical tests were performed using SAS statistical software (SAS Institute, Inc. 1990).

RESULTS

Response to field treatments

In 1998, the first post-treatment season, there were measurable treatment effects observed in the plant and soil variables (Table 9). For the plant variables, the most significant treatment effect ($F = 4.92$, $df = 3$, $p = 0.0001$) was on percent aerial cover of the perennial grasses, with significant ($p \leq 0.05$) decreases in the burned treatments as compared to the unburned. There were no significant differences among years or treatments for the grass genera present, and only slight differences in ratios of grama to lovegrass were observed. For the fungal variables, there was no significant treatments effect on live fungal biomass levels, but there was for total glomalin (TG) ($F = 2.69$, $df = 3$, $p = 0.079$) and easily extractable glomalin (EEG) ($F = 3.43$, $df = 3$, $p = 0.041$) levels. For both specimens of glomalin, levels within the burned plots were significantly ($p \leq 0.05$) lower than levels in the control. In the soil variables, there was a greater percent of PSA200 within the simulated and burn treatment compared to the other treatments (Table 10). But aside from this difference there were no significant differences in percent stable aggregates, nor was there a significant treatment effect on soil particle size distribution in either year. There was a significant ($F = 5.34$, $df = 3$, $p = 0.011$) treatment effect on sediment production, with production significantly ($p \leq 0.05$) lower within the control.

In 1999, there continued to be a significant ($F = 4.96$, $df = 3$, $p = 0.0001$) treatment effect on perennial grass cover, with lower cover in the burned plots compared

with the unburned. There was a significant treatment effect on live fungal biomass levels and on TG glomalin levels ($F = 6.77$, $df = 3$, $p = 0.003$), which were both substantially higher in the unburned treatments compared with the burned (Table 9). A significant treatment effect ($F = 2.14$, $df = 3$, $p = 0.009$) was observed in the second year for PSA100, with the percent in the simulated treatment significantly ($p \leq 0.05$) higher than percents observed in the burned treatments (Table 10). Sediment production remained the highest within the simulation and burn treatment.

Table 9. Comparison of EEG and TG levels among treatments¹.

Year	Treatment	Grass Cover (%)	Live fungal biomass ($\mu\text{g/g}$ of soil)	EEG ($\mu\text{g/g}$ of soil)	TG ($\mu\text{g/g}$ of soil)
1998	Control	20.4 ^b	17.1 ^a	1.74 ^a	2.08 ^a
	Prescribed burn	9.0 ^c	19.9 ^a	0.98 ^b	1.33 ^b
	Simulated rainfall	29.8 ^a	17.4 ^a	1.25 ^{ab}	1.50 ^{ab}
	Simulation and burn	11.2 ^c	16.8 ^a	0.86 ^b	1.41 ^b
1999	Control	31.9 ^a	58.0 ^{ab}	1.72 ^a	2.13 ^a
	Prescribed burn	19.0 ^b	48.7 ^b	1.29 ^a	1.21 ^b
	Simulated rainfall	30.8 ^a	72.3 ^a	1.48 ^a	2.39 ^a
	Simulation and burn	15.0 ^b	46.5 ^b	1.07 ^a	1.43 ^b

¹Significant differences ($p \leq 0.05$) among treatment means for each variable are denoted by different letters.

Table 10. Comparison of aggregate stability and sediment yield among treatments¹.

Year	Treatment	Aggregate stability (PSA)		Sediment yield (kgm ⁻²).
		100 (150 – 300 µm)	200 (74 - 149µm)	
1998	Control	0.74 ^a	0.73 ^b	1.7 ^c
	Prescribed burn	0.75 ^a	0.78 ^b	2.8 ^b
	Simulated rainfall	0.82 ^a	0.75 ^b	2.9 ^b
	Simulation and burn	0.83 ^a	0.86 ^a	4.1 ^a
1999	Control	0.64 ^{ab}	0.66 ^a	1.8 ^a
	Prescribed burn	0.59 ^b	0.82 ^a	2.2 ^a
	Simulated rainfall	0.73 ^a	0.75 ^a	1.9 ^a
	Simulation and burn	0.58 ^b	0.86 ^a	2.3 ^a

¹Significant differences among treatment means within soil variables and years are denoted with different letters ($p \leq 0.05$) using least-square means.

Correlation among plant, fungal and soil variables

Data taken from 1998 and 1999 were composited, and correlations among the variables were examined (Table 11). Glomalin levels were correlated to plant cover levels, and TG was correlated to fungal biomass levels, PSA 100 and sediment yield. The levels of EEG were positively correlated with the grass genera, but negatively correlated to sediment yield. Fungal biomass was significantly correlated to both soil texture and aggregate stability (PSA 100 and PSA 200). Within the soil texture, the percentage of sand was significantly correlated to fungal biomass, percentage of silt, and aggregate stability and sediment yield.

Utilizing step-wise regression methods on the correlated variables, a significant linear relationship was observed between live fungal biomass and PSA100 in the prediction of sediment production off of experimental subplots (Figure 4). A significant

treatment effect ($F = 20.54$, $df = 3$, $p = 0.0002$) was observed for sediment production (Table 10), and treatment was therefore added to the regression model as an indicator variable (i.e. control = 1, prescribed burn = 2, simulated rainfall = 3, simulation and burn = 4). Regressed sediment estimates were moderately successful in their comparisons with actual sediment yields ($r^2 = 0.579$). In examining variable contributions to the model, first-year contributions of fungal biomass levels and PSA100 were highly significant, $p = 0.0194$ and $p = 0.0084$, respectively. However, in examining the added contributions of 1999 data the significance of the fungal biomass ($p = 0.157$) and PSA100 ($p = 0.042$) variables declined in the model, with fungal biomass contributions to error much lower compared to the other two variables. Significant autocorrelation between variables (Table 11) created a confused picture of the significant contributors within the sediment model. Principal component analysis (PCA) results (Table 12 and 13) showed that the significant correlation of fungal biomass to both glomalin and plant cover confused the regression results. Fungal biomass was the dominant contributor to the first eigenvector, and PSA100 the primary contributor to the third and sixth eigenvectors. Further examination of the response surface was done using the RSREG procedure (SAS Institute, Inc. 1990), which: a) tests model fit (i.e. linear, quadratic cross product, total regression), b) does canonical analysis on the predicted response surface, and c) does ridge analysis to search for the region of optimum response. Results of the examination of the response surface showed that the linear model ($p = 0.0028$) fit the data better than

Table 11. Significant correlation coefficients (r) to show relationships between soil and plant variables (n=48).

	Grass Cover	Grass genera	Fungal biomass	EEG	TG	C _{organic}	Sand	Silt	Clay	PSA100	PSA200
Grass cover	1.000	0.092	0.193	0.475**	0.481***	-0.158	-0.110	-0.086	0.259	-0.144	-0.086
Grass genera	0.092	1.000	0.046	0.236	-0.197	0.236	-0.143	0.147	0.1181	0.104	-0.032
Fungal biomass	0.193	0.046	1.000	0.037	0.291*	0.219	-0.584***	0.660***	-0.446***	0.420**	-0.389**
EEG	0.475**	0.236	0.037	1.000	0.590***	-0.118	0.056	0.117	-0.103	-0.088	-0.006
TG	0.481***	-0.197	0.406*	0.590***	1.000	-0.089	-0.036	-0.080	0.148	0.279*	0.008
C _{organic}	-0.158	0.236	0.219	-0.118	-0.089	1.000	0.234	-0.421**	-0.082	0.002	-0.023
Sand	-0.110	-0.143	-0.584***	0.056	-0.036	0.234	1.000	-0.423**	-0.085	0.275*	-0.319*
Silt	-0.086	0.147	0.660***	0.117	-0.080	-0.421**	-0.423**	1.000	0.441**	-0.261	-0.251
Clay	0.259	0.118	-0.446**	-0.103	0.148	-0.082	-0.085	0.441**	1.000	-0.137	-0.168
PSA 100	-0.144	0.104	0.420**	-0.088	0.279*	0.002	0.275*	-0.261	-0.137	1.000	-0.067
PSA 200	0.019	-0.032	-0.389**	-0.006	-0.043	0.240	0.319*	-0.251	-0.168	0.082	1.000
Sediment	-0.125	-0.252	-0.254	-0.458**	-0.286*	-0.032	-0.289*	0.174	0.201	-0.014	-0.107

*, **, *** Denote significance at 5 %, 1%, and 0.1% levels, respectively.

the other models examined ($p > 0.02$), and that there were no significant regions of optimum response (i.e. no minima or maxima).

Comparison of experimental and RUSLE model estimates for subplot sediment production

Estimates of sediment production from the subplots within the field study were compared using the experimental model and the RUSLE model. For this study, the experimental model developed in this study better estimated sediment production than RUSLE for the upland site described for this study (Figure 5).

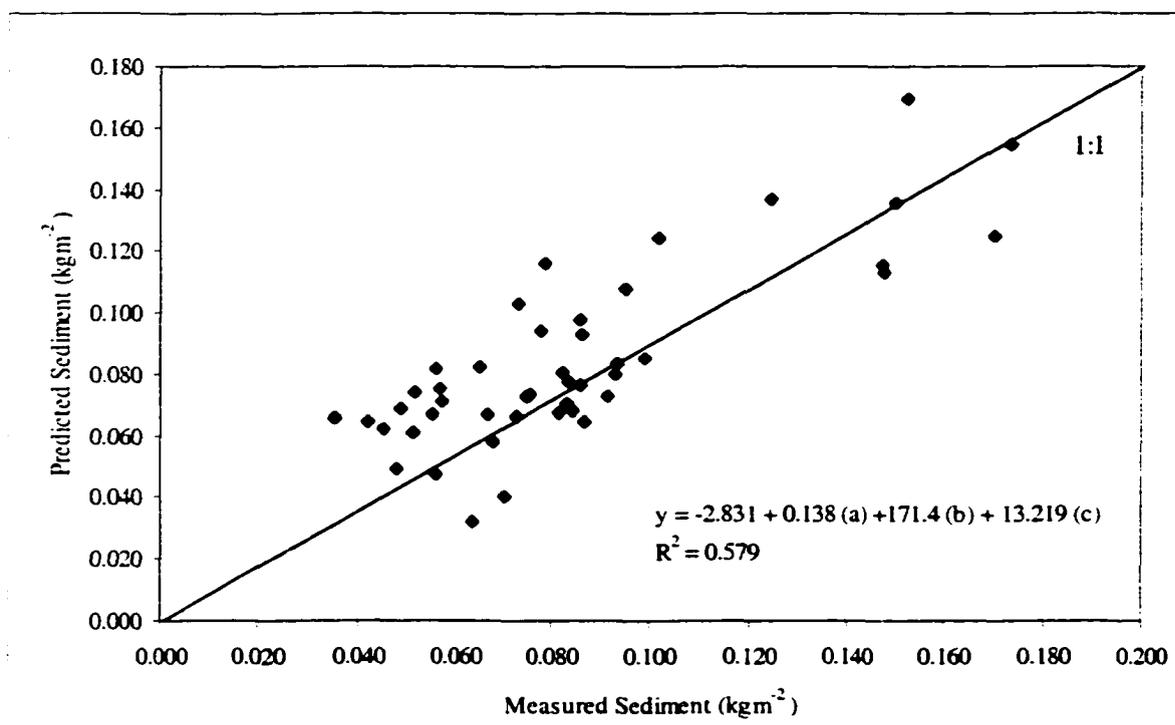


Figure 4. Prediction of average hillslope erosion (kgm⁻²) for all treatments as a function of live fungal biomass levels ($\mu\text{g/g}$ soil) and aggregate stability (%). Where a = treatment (indicator variable), b = amount of live fungal biomass, and c = percent stable aggregate.

Table 12. Eigenvalues of the correlation matrix.

Eigenvectors	Eigenvalue	Difference	Proportion	Cumulative
PC 1	2.921	0.508	0.243	0.243
PC 2	2.413	1.131	0.201	0.445
PC 3	1.283	0.158	0.107	0.551
PC 4	1.125	0.220	0.094	0.645
PC 5	0.905	0.166	0.75	0.721
PC 6	0.739	0.045	0.062	0.782
PC 7	0.694	0.165	0.58	0.840
PC 8	0.528	0.024	0.44	0.884

Table 13. Contributions of plant, fungal and soil parameters to eigenvectors.

	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8
Clay	-0.373	-0.110	-0.250	0.418	0.106	0.107	0.179	0.511
Sand	0.414	-0.036	0.148	0.088	-0.002	0.374	-0.463	0.569
Silt	0.462	0.111	0.163	0.090	0.236	0.251	-0.241	-0.207
Sediment yield	-0.233	-0.351	0.111	-0.384	0.276	-0.063	0.357	0.365
Fungal biomass	0.466	0.066	0.231	-0.079	0.021	-0.242	0.278	0.140
PSA 100	0.263	-0.096	0.579	0.108	0.123	0.532	0.232	-0.052
PSA 200	0.0286	-0.041	-0.187	0.169	0.748	-0.345	-0.203	-0.134
C _{organic}	0.201	-0.265	-0.474	0.314	0.003	0.245	0.512	-0.302
EEG	0.037	0.543	-0.160	0.105	0.007	0.271	0.081	-0.120
TG	0.0597	0.478	-0.240	-0.237	-0.169	-0.113	0.252	0.225
Perennial cover	-0.073	0.429	0.012	-0.202	0.500	0.204	0.209	0.099
Plant species	-0.056	0.300	0.381	0.640	-0.060	-0.365	0.138	0.180

Estimated values of sediment means from the experimental model were not significantly different from measured sediment (Table 14). The largest estimate errors of the experimental model are believed to be due in large part to experimental from subplot sediment catchments overflowing during large rainfall events. RUSLE sediment estimates of subplot sediment production were not as accurate as the experimental model, especially with first-year estimates. First year averages over estimated sediment production in the control, and under estimated production in the rainfall simulation plots. Yet, for both years it was a reasonable produced reasonable estimates for the prescribed burn only plots.

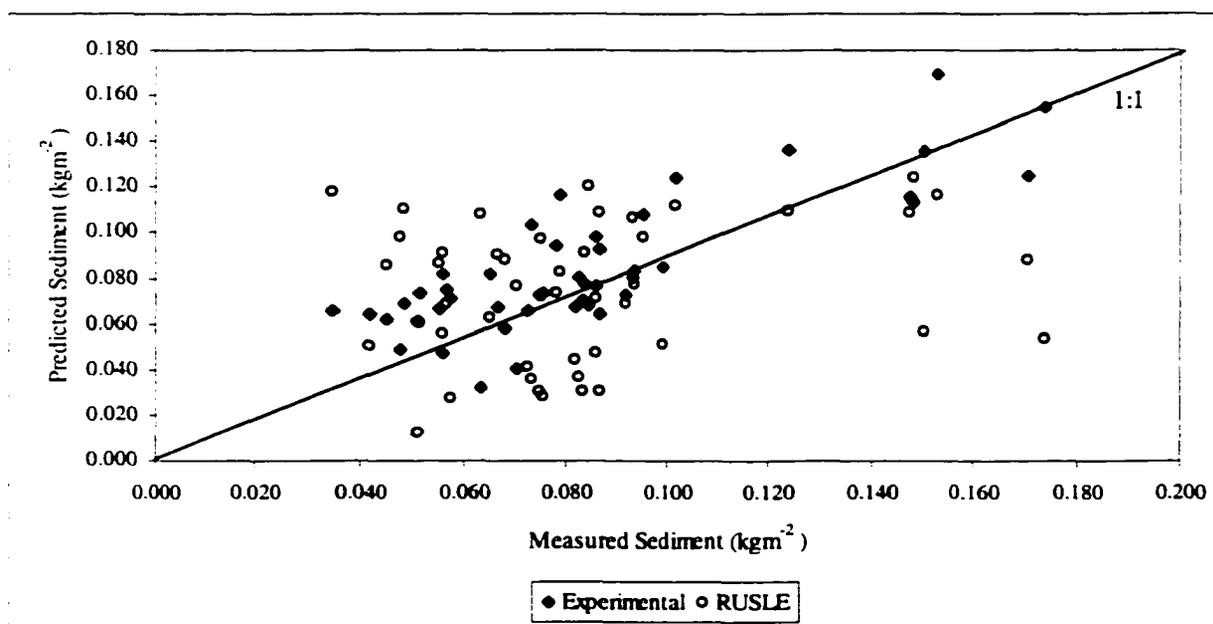


Figure 5. Comparison of experimental and RUSLE model estimations of average monsoon sediment yield from study subplots.

Table 14. Comparison among treatments of experimental model and RUSLE estimated sediment yield means. Standard errors are in the parentheses.

Year	Treatment	Actual Sediment Yield (kgm ⁻²)	Estimated Sediment Yields	
			RUSLE (kgm ⁻²)	Experimental (kgm ⁻²)
1998	Control	0.064 (0.008)	0.091 (0.008)	0.060 (0.010)
	Prescribed burn	0.080 (0.015)	0.077 (0.012)	0.089 (0.011)
	Simulated rainfall	0.098 (0.021)	0.076 (0.013)	0.097 (0.009)
	Simulation and burn	0.133 (0.013)	0.091 (0.012)	0.138 (0.009)
1999	Control	0.063 (0.007)	0.072 (0.014)	0.066 (0.002)
	Prescribed burn	0.075 (0.005)	0.059 (0.017)	0.069 (0.003)
	Simulated rainfall	0.073 (0.007)	0.045 (0.015)	0.071 (0.002)
	Simulation and burn	0.085 (0.006)	0.072 (0.011)	0.078 (0.002)

DISCUSSION

Response to field treatments

Following the first post-treatment season, results from the field study suggested that the prescribed fire and its interaction with the monsoon had a strong influence primarily on plant and fungal protein variables. Few observable changes were evident for live fungal biomass, aggregate stability or soil particle size distributions. Yet, there was a significant erosion and runoff response. At the end of the second season, while there

continued to be significant responses of the plant and fungal communities to treatment, there were also significant treatment responses in aggregate stability. Within the burned plots, plant, fungal and aggregate stability variables were significantly lower than comparable variables not exposed to the prescribed burning. While there appeared to be no significant difference in sediment production among treatments, runoff volumes were still highest within the burned plots.

Continued overland flow was expected given the continued lack of plant cover within the burned plots, as well as decreases in surface infiltration rates (Chapter 1). The decline in sediment production and lack of treatment effect was not expected the second year given the continued increases in overland flow observed within the burned plots. The decline in sediment production with the continued high volumes of runoff may be due in part to the formation of erosion pavement (Kinnell et al. 1993). Erosion pavements and surface seals are able to reduce soil infiltration rate, and may increase erosion by increasing runoff without increasing erosion. Factors important to determining levels of erosion appear to be the soil chemical and physical properties that determine soil sealing and erodibility (Baumhardt et al. 1990, Le Bissonnais and Singer 1993), as well as the biotic components influential on the soil structure (Tisdall and Oades 1983).

Significant correlations between plant, fungal, soil and sediment variables illustrate the important role of the soil fungal properties. In carbon limiting systems, such as the desert grassland or savanna, it appears that levels of live fungal biomass are more strongly related to the structural components of the soil than levels of organic carbon.

In light of the apparent increased importance of fungal properties over soil organic matter, the development of the experimental model was intriguing.

The significant correlation of fungal properties, specifically between the levels of live fungal biomass and fungal protein levels were of initial interest. In comparing the fungal variables, the examination of the eigenvectors from the PCA analysis clearly demonstrated the importance of fungal biomass levels and aggregate size to the model's development. The majority of the estimation error for the experimental model was not attributed to variability in model parameters, but to the loss of sediment and runoff during large storm events when the capacity of the sediment catchment was exceeded and overflowed.

Experimental Model Comparison with RUSLE

Traditional erosion prediction models, such as the RUSLE may not perform as well as they do on the agricultural lands for which they were developed. Semi-arid grassland soils, unlike most agricultural soils have on average less than 5 % organic carbon and a heterogeneous distribution of soil organic matter over the landscape (Chadwick et al. 1994, Tate 1987). Given the nature of these systems, erosion models such as the RUSLE may not be effective in estimating erosion losses given their assumptions for determining soil erodibility (Renard et. al. 1997).

In comparing the experimental model and RUSLE, the erosion estimates were not significantly different from the actual sediment amounts collected from each subplot. The high correlation ($r^2 = 0.82$) of estimated erosion losses to actual losses demonstrate the significant correlations between the plant, fungal and soil properties reported in the field study. However, the successful sediment production modeling with fungal and soil variables within this study may be attributable to the small sampling size and empirical nature of the model. Testing the model over larger landscapes with a greater diversity in plant, fungal and soil properties will assist in examining the application of this model outside of the grassland for which it was developed for. However, the higher level of accuracy of this experimental model compared with the RUSLE on the tested grasslands does raise questions about the RUSLE assumptions used in the determination of soil erodibility, particularly on soils with low organic carbon levels.

SUMMARY

Within the desert grasslands and savannas of southeast Arizona, the interaction of prescribed burning and the summer monsoon strongly influences erosion losses from these wildlands. Through their impact on the plant and fungal communities, as well as the soil structure these disturbances influence both upland runoff and erosion dynamics. Modeling erosion losses within these systems with traditional models developed in agricultural systems may not prove to be effective, especially in wildland systems with inherently low levels of organic carbon. Utilizing the integrated nature of the soil fungal properties and the structural characteristics of the soil, rather than organic matter,

provides a new perspective in the examination soil erodibility and upland erosion modeling.

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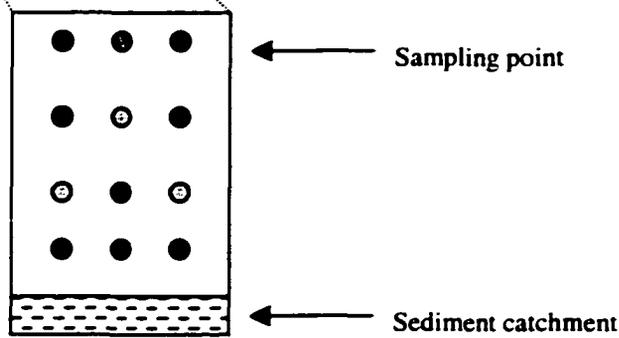
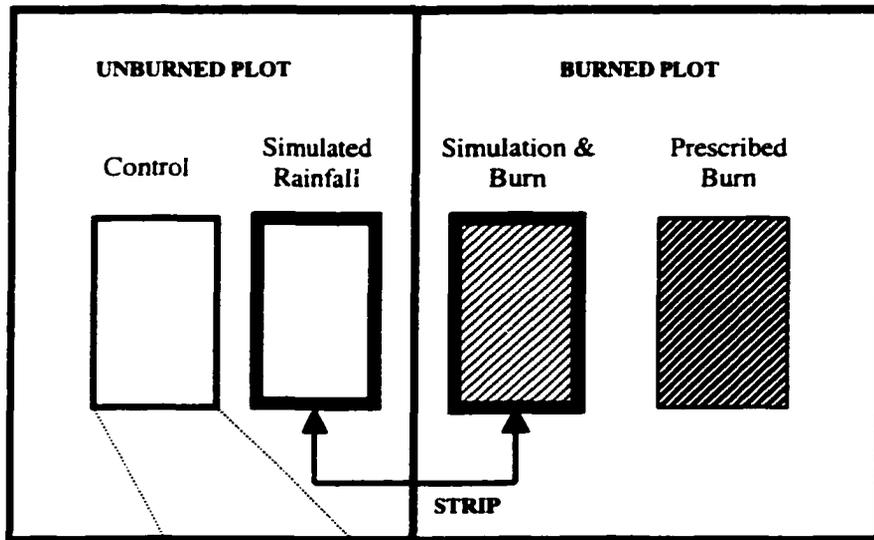
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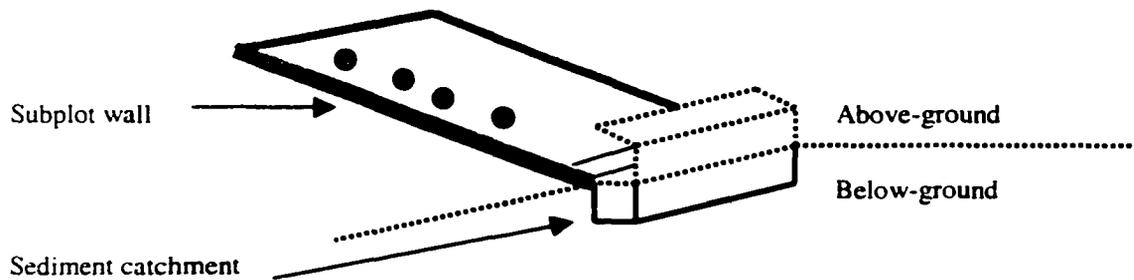
Appendix 4. Map of research site location.



Appendix 5. Block schematic with subplot (= treatment) layout. Treatments are control, prescribed burn, simulated rainfall, and simulation and burn.



Over-view of plots



Side-view of subplot

Appendix 6. A 30-year rainfall record from the meteorological station at the Audubon Research Ranch, Elgin, Arizona. Rainfall depths are reported in millimeters.

Year	Designated Monsoon Season												Total
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
1968	6.6	12.8	16.5	4.3	0.0	0.0	42.3	40.0	2.1	2.3	5.9	10.6	143.4
1969	4.6	10.0	6.5	2.4	4.9	0.0	59.0	40.4	14.3	0.8	9.3	4.1	156.3
1970	0.0	7.7	15.3	2.9	0.0	0.9	46.1	53.2	19.8	1.0	0.0	7.3	154.2
1971	--	--	--	--	--	--	--	--	--	--	--	--	--
1972	--	--	--	--	--	--	--	--	--	--	--	--	--
1973	--	--	--	--	--	--	--	--	--	--	--	--	--
1974	16.2	0.0	2.7	0.2	1.0	1.2	55.8	14.1	33.7	21.6	2.9	1.1	150.5
1975	9.4	0.0	8.5	7.7	0.0	0.0	65.8	13.3	35.3	0.0	10.5	5.9	156.4
1976	3.7	14.4	3.1	8.2	1.5	3.2	73.2	22.7	22.3	6.8	8.0	5.5	172.6
1977	--	--	--	--	--	--	--	--	--	--	--	--	--
1978	35.6	34.0	13.1	0.9	4.5	5.3	22.1	19.4	3.8	25.7	36.8	0.2	201.4
1979	40.8	7.2	11.3	0.0	3.1	4.6	8.2	24.0	5.7	0.2	2.8	1.3	109.2
1980	10.6	21.8	7.8	0.9	0.0	7.1	10.1	37.7	24.4	0.5	0.0	6.6	127.5
1981	10.9	10.6	28.7	10.5	2.1	3.6	52.2	17.5	6.0	10.7	0.0	0.0	152.8
1982	12.9	5.1	6.8	1.3	3.2	0.1	22.6	32.4	28.1	0.0	9.9	35.2	157.6
1983	20.0	19.4	33.8	3.4	3.0	1.5	45.0	36.4	74.0	26.0	18.6	5.9	287.0
1984	23.7	0.0	0.0	5.9	2.3	7.2	49.6	63.5	11.9	13.0	9.6	51.9	238.6
1985	22.6	9.1	2.3	10.6	0.0	5.8	44.9	23.9	27.5	23.8	16.1	2.6	189.2
1986	4.6	14.7	13.3	5.2	5.5	9.5	26.0	69.6	9.0	5.2	4.3	19.6	186.5
1987	3.4	14.7	5.0	24.8	4.3	5.9	9.1	61.4	20.9	4.3	4.1	19.9	177.8
1988	12.0	3.2	4.2	8.1	0.0	7.5	47.1	44.9	14.1	30.8	7.3	1.7	180.9
1989	11.2	4.9	5.7	0.0	4.9	1.0	37.1	20.7	10.7	40.6	0.0	1.5	138.3
1990	7.0	3.3	4.1	3.0	1.8	7.0	62.6	64.3	19.8	9.0	5.5	19.0	206.4
1991	22.1	24.8	18.8	0.0	0.0	3.3	18.6	26.2	28.0	5.8	7.8	35.2	190.6
1992	16.1	13.6	32.9	5.5	22.3	0.0	34.8	35.1	11.5	2.7	0.0	34.2	208.7
1993	68.0	18.9	4.7	0.0	6.8	0.0	18.8	56.3	7.0	5.3	0.0	3.0	188.8
1994	3.0	9.9	18.3	0.0	0.9	12.1	31.5	41.4	16.0	0.0	31.0	42.0	206.1
1995	7.5	12.5	0.0	2.0	0.0	0.1	12.5	40.5	10.0	0.0	17.0	5.0	107.1
1996	1.5	9.0	1.5	1.5	1.0	3.5	52.7	13.3	5.8	0.0	9.0	4.5	103.3
1997	16.5	12.5	7.5	9.4	0.5	0.0	6.0	67.5	2.5	4.5	4.5	15.0	146.4
1998	1.2	36.2	15.4	22.0	0.0	0.0	51.2	30.4	14.0	0.2	7.2	4.4	182.2
1999	0.0	1.0	1.0	17.5	0.0	4.8	36.9	38.2	33.0	0.0	0.0	6.0	138.4
MEAN 1968-1999	14.0	11.8	10.3	5.7	2.6	3.4	37.2	37.4	18.3	8.6	8.1	12.5	169.9

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