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UNDERSTORY PLANT COMMUNITY DYNAMICS IN SOUTHWESTERN PONDEROSA PINE FOREST RESTORATION

by Julie E. Korb

A Dissertation
Submitted in Partial Fulfillment
of the Requirements for the degree of
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Approved:

W Wallace Covington
W. Wallace Covington, Ph.D., Chair

Peter Z. Fulé, Ph.D.

Nancy C. Johnson, Ph.D.

Margaret M. Moore
Margaret M. Moore, Ph.D.

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ABSTRACT

UNDERSTORY PLANT COMMUNITY DYNAMICS IN SOUTHWESTERN PONDEROSA PINE FOREST RESTORATION

JULIE E. KORB

The research in this dissertation focused on three major components related to understory plant community dynamics in southwestern ponderosa pine forest restoration in northern Arizona. Our first goal was to compare different understory plant monitoring sampling techniques and sampling sizes. Our results illustrated that the sampling technique chosen for monitoring herbaceous and shrub species richness and foliar cover in restoration studies can greatly influence the ability to detect change. We found that large area sampling techniques were the most effective at capturing species richness and rare and exotic species.

Our second goal was to quantify the effect of restoration tree thinning versus thinning and prescribed burning on propagule densities of arbuscular mycorrhizal (AM) fungi and ectomycorrhizal (EM) fungi and their relationships to plant community properties. Our results indicated that population densities of AM fungi increased rapidly following restoration thinning as well as thinning and prescribed burning treatments in northern Arizona ponderosa pine forests. The relative amount of infective propagules of AM fungi was significantly negatively correlated with overstory tree canopy cover and litter cover and positively correlated with herbaceous understory species richness and graminoid cover. In addition, our results indicated that restoration thinning alone and thinning and prescribed burning had no significant effect on EM fungal propagule densities even though their host plant was significantly reduced in thinning treatments.

Our third goal was to quantify the effect of slash pile burning on AM fungal propagule densities, the soil seed bank, soil physical and chemical properties and extant vegetation. In addition, we tested seed and soil amendments for native plant establishment on severely burned slash piles. Our results indicated that severe slash pile burning had a negative effect on AM fungal propagule densities, the soil seed bank and extant vegetation and changes soil physical and chemical properties. In addition, our results indicated that a seed and soil amendment is necessary to facilitate the establishment of native plants on severely burned slash piles in southwest ponderosa pine forests.

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This dissertation is dedicated to Mother Earth
and all the people who strive to restore and protect
the land for future generations

PREFACE

I wrote this dissertation in manuscript format. This dissertation contains an introduction, literature review, three journal manuscript chapters, and a conclusion with management recommendations. Methods for each study are provided in each of the manuscript chapters. Scientific names were taken from *Colorado Flora-western slope* (Weber and Wittmann 1996). Species that were not found in the *Colorado Flora* were taken from *Intermountain Flora* (Cronquist et al. 1972, 1977, 1984, 1989, 1994, 1997) and *Arizona Flora* (Kearney and Peebles 1960). Species were identified as native or non-native from these floras.

CHAPTER 1

INTRODUCTION

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests prior to Euro-American settlement (1870-1890) were dominated by large, old trees intermixed with grassy meadows. Early accounts by explorers qualitatively described pre-Euro-American ponderosa pine forests as being much more open and park-like. Cooper (1960) quotes Lt. Edward Beale's impression of northern Arizona, "It is the most beautiful region I ever remember to have seen in any part of the world. A vast forest of gigantic pines, intersected frequently with open glades, sprinkled all over with mountains, meadows, and wide savannas, and covered with the richest grasses, was traversed by our party for many days."

Quantitative reconstruction of presettlement southwestern ponderosa pine forests also indicates open, park-like stands. Covington and others (1997) determined that presettlement ponderosa pine stands consisted of approximately 60 stems/ha at the Gus Pearson Natural Area, Arizona. Fulé and others (1997) also found on average 65.3 ponderosa pine trees/ha at Camp Navajo, Arizona Similarly, several early National Forest inventories showed a range of 7 to 116 stems/ha in presettlement southwestern ponderosa pine forests (Covington and Moore 1994a).

Presettlement southwestern ponderosa pine forests were regulated by a vital ecological attribute--fire. Low intensity fires carried by grassy understories recurred every 2-20 years in southwestern ponderosa pine ecosystems prior to Euro-American settlement and played a major role in regulating the structure, composition, and stability of these ecosystems (Baison and Swetnam 1997, Fulé et al. 1997). These frequent, low-intensity fires, along with grass competition, prevented dense ponderosa pine regeneration and maintained the open, park-like structure of presettlement ponderosa pine stands (Harrington and Sackett 1990). Ponderosa pine seedlings were able to establish themselves in small, exposed areas such as where trees had died and produced enough fuel to allow high-intensity fires to occur and eliminate grass competition (White 1985).

The frequent fires in ponderosa pine forests were the combination of both natural lightning and human-caused ignitions. Native Americans purposely set fires for a variety of reasons including driving game, increasing spring harvests, and clearing land for farming. As a result, Native Americans may have had a major impact on the development of these forests in the southwest at lower elevations where they inhabited (Veblen and Lorenz 1991, Covington et al. 1994). In contrast, in southwest ponderosa pine systems at higher elevation, Native Americans did not have a major impact on fire behavior (Baison and Swetnam 1997). Evidence of ponderosa pine evolution with fire is seen in selected survival adaptations such as bark thickness and high crown levels (Mutch 1970, Moore et al. 1999).

Three main anthropogenic influences are responsible for the dramatic alterations in the structure and function of ponderosa pine forest ecosystems: grazing, logging, and fire exclusion (Cooper 1960, Covington and Moore 1994a, Covington et al. 1994, Covington et al. 1997). In addition, climatic oscillations may have also altered ponderosa pine forest ecosystems (Covington and Moore 1994a, Savage and Swetnam 1990). Global warming projections indicate that increased drought in the Southwest may result in forests becoming more susceptible to high intensity fires in the future (Swetnam 1990).

Grazing

Prior to European settlement, ponderosa pine ecosystems in the Southwest evolved mainly without large hoofed herbivores (Covington et al. 1994). However, in the mid- to late-1800's, grazing by domestic livestock began in southwestern ponderosa pine forests. Intense grazing by sheep resulted in reduced grass fuel loads, which reduced the competition of grasses with pine seedlings for soil moisture, reduced low-intensity grass fires, and increased the exposure of mineral seedbeds due to excessive livestock trampling (Cooper 1960). The combination of intense grazing, good ponderosa pine seed years, and favorable climatic conditions permitted the germination and successful establishment of large numbers of ponderosa pine trees in the Southwest during the early 1900's (Arnold 1950, Savage et al. 1996, Schubert 1974).

Logging

Heavy logging of old-growth trees began simultaneously with sheep overgrazing the ponderosa pine understory. Increased resource demands from an increasing human population led to over-harvesting of old-growth ponderosa pine forests. Specifically, the demand for railroad bridges and ties from railroad development in the late 1800's along with a demand for building materials and mining timbers resulted in extensive tree harvesting. Over-harvesting of old trees coupled with irruptions of young trees changed the ponderosa pine forest structure from old-growth stands to younger stands and created unusually high fuel loads (Covington et al. 1994).

Fire Exclusion

Changes in the structure and function of ponderosa pine forests occurred prior to organized fire suppression efforts by almost one to two decades (Savage and Swetnam 1990). However, Euro-American fire exclusion efforts have resulted in an increased severity for large crown fires, previously rare or nonexistent, and longer mean fire intervals. Large crown fires have a high rate of spread (6035-12070 m/hour) and taller flame heights (24-46 m) than the low intensity fires that were common in presettlement ponderosa pine forests (Covington and Moore 1994b). Evidence of increasing fire size and intensity in ponderosa pine forests has been documented. Swetnam (1990) indicated a trend of increasing fire loads and higher numbers of larger areas burned from lightning-caused fire in the Southwest. Specifically, Swetnam (1990) cited postsettlement fires in ponderosa pine forests in New Mexico that ranged between 4,047-8094 hectares, which are large in comparison to his inferred average fire size of 1,214 hectares in presettlement southwestern ponderosa pine forests. Mean fire intervals have also increased substantially since Euro-American settlement. For example, the mean presettlement fire interval between 1637 and 1883 was 3.7 years for all fires and 6.5 years for widespread fires at Camp Navajo, Arizona (Fulé et al. 1997). Since 1883, fires have been completely excluded from this area.

Anthropogenic effects associated with Euro-American settlement have resulted in numerous young, small trees; fewer old, large trees; increased forest fuel loads; lower herbaceous production and diversity; altered fire regimes; and changed wildlife habitats in southwestern ponderosa pine forests (Cooper 1960, Vose and White 1991, Covington and Moore 1994a, Covington et al. 1997, Fulé et al. 1997). As a consequence there has been an overall change in forest structure and function altering soil moisture availability, decomposition rates, tree health (e.g., carbon, water, nutrient, growth, and insect resistance), nutrient cycling, microbial populations, net primary production and susceptibility to invasive exotics (Covington and Sackett 1984, Swezy and Agee 1991, Sutherland et al. 1991, Covington and Sackett 1992, Wright 1996, Covington et al. 1997, Feeney et al. 1998).

One of the primary goals of ecological restoration is to reverse the degradation of ecosystems by restoring system structure, function and natural disturbance regimes to emulate conditions prior to degradation (Sauer 1998). In order to accomplish this goal, reference conditions (the range of historical or natural variability in ecological structures and processes that reflect evolutionary history, disturbance regimes, and abiotic and biotic conditions) must be determined prior to restoration (Moore et al. 1999). In identifying reference conditions, it is also important to identify a spatial and temporal context. Disturbances may create different successional stages of ecosystems at different spatial scales within the area to be restored and therefore produce a shifting mosaic of patches (White and Walker 1997). Reference conditions are useful for identifying the restoration potential of a site, evaluating the success of restoration, and creating a benchmark against which to evaluate current conditions (Fulé et al. 1997, White and Walker 1997). Reference conditions can be determined from historical data from the site (e.g., historic field notes, photographs, etc.); contemporary data from sites that have not been degraded; on-site information (e.g., seed banks, fire scars, dead and down woody material, soil characteristics, species composition); and traditional indigenous knowledge (e.g., understanding indigenous peoples' burning, foraging, planting methods, and medicinal uses of species in the area) (Fulé et al.1997, White and Walker 1997, Naveh 1998, Sauer 1998).

The herbaceous understory is an important component of ponderosa pine forest ecosystems, comprising 95-99 % of plant species diversity and providing fuel continuity that allowed surface fires to sweep across the landscape before settlement. The current reduction in understory plant production and diversity of ponderosa pine forests has contributed to the alteration of the natural fire regime and the loss of habitat for numerous wildlife, bird, and insect species. Thus, a major objective of restoring southwestern ponderosa pine forests is to increase herbaceous and shrub understory production and diversity to reference conditions. We had three major objectives for our research related to understory plant community dynamics in southwestern ponderosa pine forest restoration in northern Arizona. 1) Our first objective was to compare different understory plant monitoring sampling techniques and sampling sizes and determine if different sampling techniques would influence the ability to detect change in restoration treatments. 2) Our second objective was to quantify the effect of restoration tree thinning versus thinning and prescribed burning on propagule densities of arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi and their relationships to plant community properties. 3) Our third objective was to quantify the effect of slash pile burning on AM propagule densities, the soil seed bank, physical and chemical soil properties and the extant vegetation. In addition, we tested seed and soil amendment for native plant establishment on severely burned slash piles. The results from these data provide us with a better understanding of understory plant community dynamics in southwestern ponderosa pine forest restoration in northern Arizona and provide information that can be integrated into ponderosa pine forest adaptive ecosystem management.

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CHAPTER 2

LITERATURE REVIEW

Introduction

Plant ecologists have been trying to describe and model the underlying mechanisms behind plant succession since the inception of the field. Still today, there is little consensus regarding the underlying mechanisms that direct successional change and it is unlikely that one model will ever fit all the diverse situations encountered in the field. Cowles (1899), just over a hundred years ago, summarized succession best as a "variable approaching a variable, not a constant." In light of this, successional theories developed over the years have been useful in understanding some of the mechanisms that are responsible for driving successional changes in plant communities. Ecologists have also been intrigued with the dynamics of community structure in ecosystems for years. Community structure is the result of multiple interactions among species, environmental variability, perturbations and chance events (Samuels and Drake 1997). Spatial and temporal scales are crucial to understanding the dynamic nature of communities and whether communities converge towards a single or multiple states. In this literature review I will address two main topics regarding plant community dynamics: 1) I will describe the major plant successional models and 2) I will address the concept of alternative community states and its relevance to ecological restoration.

Successional Models

Succession is defined as a process where one plant community changes into another usually following some type of disturbance (Crawley 1997). While this definition is simple, the mechanisms underlying the process are more complex and less understood. The debate regarding what mechanisms drive succession began in the early 1900's between Cowles and Clements. At the heart of the debate was how nature was viewed and whether abiotic or biotic factors were driving succession. Cowles (1899) and others after him, notably Gleason, looked at a community as individual species interacting with each other driven primarily by local abiotic factors (soil, light, temperature, wind, etc.). Cowles believed that a community was composed of species with similar abiotic ecological requirements, which allowed species to coexist (Barbour et al. 1997). In contrast, Clements (1916) viewed the community as being much like a single, integrated organism and that changes in the community were driven primarily by biotic factors. Gleason (1917) and Egler (1954) challenged Clements' organismic view even though it dominated successional theory for the majority of the mid 1900's.

Connell and Slayter's Successional Models

Connell and Slayter (1977) presented three different models for describing successional change following some type of disturbance. These three models were: facilitation, tolerance, and inhibition. The primary difference between these three models is the mechanism that determines how species are able to establish during succession. The facilitation model was based on the relay floristics concept developed by Clements (1916) where species that establish early in the community allowed for the establishment of later successional species by modifying their environment. This model states that only early successional species can colonize a recently disturbed site (Connell and Slayter 1977). The second model, tolerance, is based more on the initial floristics concept developed by Egler (1954) where all species are present at the beginning of succession but some are better competitors, live longer, and are bigger than seral species. In this model, early successional species do not increase or reduce the rates of later successional species (Connell and Slayter 1977). In addition, the sequence of species during succession is driven primarily by their life history traits and their ability to tolerate stress. The third model, inhibition, emphasizes that once species are established they prevent the invasion of other species by occupying space or by suppressing their growth through nutrient acquisition (Barbour et al. 1997). Other species are only allowed to colonize a site when the initially established colonists either are damaged or killed, which results in opening up space and releasing nutrients and therefore results in succession that leads from short-lived to long-lived species (Connell and Slayter 1977).

Connell and Slayter's three models of succession provide a simplistic cartoon of a rather complex ecological process. The three different models represent three different pathways of succession that all have been documented in field studies and can be tested through experiments (Barbour et al. 1997). These models can also be used in the context of ecological restoration in whether to encourage or discourage early colonizing species based upon the successional model that represents the plant community. At the same time however, Connell and Slayter's different successional models are too simplified and do not represent the true complexity of succession. In addition, some authors feel that the three models are not mutually exclusive and have too much overlap among them to be truly useful in plant successional theory (Walker and Chapin 1987). For example, in primary succession facilitation may be one of many mechanisms driving succession, not the only mechanism. Huston and Smith (1987) noted that these three models of succession are relative and that all three can occur simultaneously with different degrees of importance.

Grime's Successional Model

Grime (1979) applied life history trait theories to succession in an attempt to explain the mechanisms behind succession. Grime's model predicts a general relationship between habitat, species life form, longevity, and life history traits (Barbour et al. 1997). Grime distinguished three primary strategies of plants during succession based on their life history traits and their habitats. These strategies include: 1) ruderals that favor temporary habitats with abundant resources; 2) competitors that favor predictable habitats with abundant resources; and 3) stress tolerators that favor habitats with low resources (Grime 1977). While these three strategies are distinct, Grime (1977) recognized that most plants use some combination of these strategies due to their adaptation to disturbance, competition, and stress. At the center of Grime's (1977) successional theory is that the amount of change in species turnover through succession is positively related to the amount of productivity. Grime's model predicts lower species change on infertile, less productive soil and higher species change on fertile, productive soil (Barbour et al. 1997).

Similar to Connell and Slayter's model, Grime's successional model provides a simplified view of succession so that we can gain a better understanding of community organization and how species interact for limited resources. In addition, Grime's model is a useful tool for understanding the range of variability in plants due to life history traits (Barbour et al. 1997). Although, Grime's model does not permit quantitative predictions because the model is too simplistic, his general theories regarding evolutionary tradeoffs and competition can be experimentally tested. A disadvantage of Grime's model is that most species do not fall neatly into one of the three strategies of plants and represent some mixture of the three along a continuum of plant strategies, which Grime recognized. In addition, an individual species may change its strategy based upon its life stage or habitat. For example, a species may be considered a ruderal as a seedling but as a tolerator as an adult. Finally, Grime's model is based on a set of assumptions regarding the mechanisms of plant interactions and evolutionary tradeoffs among plant life traits. Specifically, Grime views the ability to compete as being able to exploit resources rapidly rather than being able to tolerate resource depletion (Grace 1990).

Tilman's Successional Model

In contrast to Grime's successional theory that predicts species change with a competitive environment Tilman's (1985) resource-ratio hypothesis predicts the opposite scenario. Tilman's hypothesis has two key elements: 1) interspecific competition for resources, and 2) long-term patterns of supply for limiting resources (Barbour et al. 1997). This hypothesis assumes that succession will be directional and predictable only when limiting resources are directional and predictable. If resources loop back during succession then plant communities will also loop back and be retrogressive rather than directional (Tilman 1988). At the center of the resource-ratio hypothesis is the notion that each species is a superior competitor at a given ratio of resources. Species are able to coexist because each species is relatively more limited by another resource than the other species and because the superior competitor is often unable to occupy all the space (Tilman 1988). As a result, if several species compete for the same single limited resource, the species with the smallest need for this resource will be able to displace the other species by increasing its abundance and depleting the limited resource (Tilman 1997a).

Tilman's resource-ratio hypothesis is more complex and dynamic than the previous successional models offered by Connell and Slayter (1977) and Grime (1977, 1979). Tilman's model is useful because it can be tested directly through experimental studies by manipulating limiting resources, including light. In addition, field observational studies can be conducted to see if a resource gradient exists in nature and to see how plant communities respond along the gradient. Studies such as these have been conducted in different environments and have shown that plant communities correspond to nutrient and light gradients (Pastor et al. 1984, Tilman and Wedin 1991). Models based on resource competition can be applied on both temporal and spatial gradients (Huston and Smith 1989). Some shortcomings of Tilman's model, which he himself recognized, include the failure to incorporate the existing or potential species pool into his model and the role of herbivory in succession (Tilman 1988). However, a benefit of Tilman's model is that it can be modified to incorporate more specific plant traits and non-resource variables and environmental variables. Tilman's model is based upon particular assumptions about the mechanisms of plant resource use. Tilman defines competition in terms of being able to tolerate low resource levels (Grace 1990). Tilman's model as well as Grime's model fails to distinguish between species adaptation to resource levels and non-resource conditions (Grace 1990). Another disadvantage of both Tilman and Grime's model is that they are based upon populations rather than individual organisms, which therefore makes it more difficult to interpret the true complexity of succession (Huston 1994). Huston and Smith (1987) pointed out that the resource-ratio hypothesis groups numerous components that give a population a competitive ability into a single parameter—resources—that does not allow the population to respond to environmental conditions with the same amount of flexibility if individual components were investigated. For example, if a researcher is only investigating the effects of a limiting resource (nitrogen) on a population then other factors such as precipitation, which may have a larger influence on the population than nitrogen, may be overlooked due to the simplicity of the model.

Huston's Successional Model

Huston's successional model is based upon the interactions of individual organisms rather than populations. Huston and Smith (1987) believe that an individual-based model using life history and physiological traits offers the most comprehensive model to understand the complexity of successional dynamics at different scales, which is known as the dynamic equilibrium model. The dynamic equilibrium model is based upon opposing forces of two factors: 1) competitive interactions that lead to competitive exclusion, and 2) mortality-causing disturbances that do not lead to competitive exclusion (Huston 1994). Specifically, there are three main premises for this model: 1) competition for resources occurs in all plant communities and varies both spatially and temporally; 2) plants can change the availability of resources and therefore alter the criteria for being competitively successful; and 3) physiological constraints prevent one species from dominating all environmental conditions (Huston and Smith 1987). In this model, species diversity is reduced by either competition or the inability of organisms to recovery following disturbance. However, a major contribution of this model for understanding species diversity is that similar disturbance frequency and intensity are recognized to have dramatically different effects on species diversity depending on the rate of competitive displacement (Huston 1994).

Huston's model provides a useful tool to explore the causes of variation in successional patterns based upon the interactions of individual species that can also be interpreted at the population level in the context of plant functional groups. Because this model is based upon individual organisms rather than populations, patterns of species diversity under different environmental conditions can be explored. Huston's model allows the competitive ability of an individual organism to be based on its life history traits and its interactions within explicit environmental conditions rather than averages of life history traits for populations and averages of environmental conditions as in Tilman's model (Huston and

Smith 1987). The dynamic equilibrium model allows the interpretation of succession beyond the successional replacement of species to understanding the complex variety of successional mechanisms (Huston and Smith 1987). A disadvantage of the dynamic equilibrium model is that it is more difficult to experimentally test because more than one factor is affecting plant succession. As a result, factorial studies with at least three levels of each factor are needed in order to test this model. These tests are more logistically difficult to manipulate and as a result fewer experiments have been conducted to test this theory (Huston 1994). In addition, successional species interactions are more difficult to predict because this model is inherently more complex than previous models and has no mathematical basis.

Alternative Community States

The concept of alternative community states originated from the work of Lewontin (1969) who was investigating the concept of stability. Lewontin (1969) explained community structure through two opposing ways. His first explanation focused on the importance of history in explaining patterns of species, populations and communities, which is associated with multiple stable points. His second explanation emphasized the importance of fixed forces without any reference to historical events in explaining patterns of species, populations and communities (single stable point) (Lewontin 1969). In the early 1970's, ecologists recognized the occurrence of different communities in similar environments and developed mathematical models of species interaction with several interaction points (Noy-Meir 1975, May 1977), which supported the concept of multiple stable points (Petraitis and Dudgeon 1999). A community is considered to have one unique stable point if it returns to its original state following any disturbances and all initial conditions "like a marble seeking the bottom of a cup" (May 1977). In contrast, a community is considered to have alternative community states if a system's trajectory is influenced by the initial conditions. In this scenario, a system may return to its original state following a small perturbation or it may change to a new state following a large perturbation "like the ball in a pin-ball machine" (e.g., the community may bounce around to numerous new states) (May 1977).

A system's history matters under the concept of alternative community states and is unimportant under the concept of a single community state. History is important because it is needed to interpret observed differences in the structure of communities in the same locality. The disturbance history of an area will often interact with competitive interactions among species and the intensity and timing of the disturbance will often affect community dynamics (Hughes 1989, Berlow 1997). For example, a study by Harper (1969 in Sutherland 1974) showed that grazing by rabbits promoted high herbaceous diversity in many parts of Britain during the end of the 19th century and that the removal of rabbits from disease and exclosures decreased herbaceous diversity and promoted the establishment and persistence of woody vegetation. Herbaceous vegetation in these systems was maintained by rabbits for 60-75 years despite the potential to be dominated by woody vegetation. The removal of rabbits from this system allowed the system to cross a critical threshold to change to another stable point, woody vegetation. The fact that simply returning the rabbits back to the system would not revert the system to its original state because the rabbits would be unable to remove trees suggests alternative communities states for this system. As a result, understanding the history or initial conditions of the system is crucial to the identification of alternative community states. Without the knowledge that rabbits existed in this community prior to their removal, the system would most likely be defined as a separate stable system instead of a system with multiple stable points. In addition to the knowledge of historical perturbations, knowledge of a system's historical and current species pool (the number of species potentially able to exist in a particular community) is also important in explaining variation in communities (Partel and Zobel 1998). Law and Morton (1993) suggested that the ability for a system to have alternative states was more likely with a large species pool and therefore suggested that species-rich systems with strong interactions were more likely to have alternative states than species poor systems. In addition, the order of species arrival plays an important role in the community structure of alternative states (Drake 1991). As stated by Dudgeon and Petraitis (2001), "in many ecosystems, the distributions and abundances of organisms carry the signatures of historical events" and the history of species relationships that no longer exist may be the invisible keys to understanding extant community structure (Samuel and Drake 1997).

The debate surrounding the existence of multiple stable points in communities persists despite the large amount of empirical evidence illustrating their existence. Connell and Sousa (1983) pointed out three reasons for the lack of evidence of multiple stable points in communities: 1) the physical environment is different in the different states; 2) external controls are necessary to maintain one of the alternative states; and 3) inappropriate time and spatial scales are used in studies to test multiple stable points. Peterson (1984) refuted Connell and Sousa's reasons for the lack of evidence of multiple stable points through empirical studies conducted in various environments. Temporal and spatial scales play a critical role in determining whether or not alternative community states exist or whether the patterns observed are successional changes that will ultimately result in community convergence to a single stable state. For example, Dudgeon and Petraitis (2001) noted that most studies that suggest convergence in late succession for marine systems are conducted in experimental clearings of less than 3 m^2. The small size of the clearings leads to a large edge effect from the surrounding community and the ability of the surrounding community to aid in the reestablishment of the original assemblage (Dudgeon and Petraitis 2001). In contrast, large clearings greater than 30 m^2 in marine systems have shown variable results from community convergence to divergence (Connell et al. 1997, Knowlton 1992). These results suggest that large experimental clearings allow much of the area to extend beyond the edge effect and therefore species recruitment has sufficient time and space to establish and develop into divergent species assemblages (Dudgeon and Petraitis 2001). As a result, providing sufficient time and space in experiments testing the existence of alternative community states is crucial because an area has to be large enough to extend beyond the edge effect from the surrounding community. In addition, studies that suggest alternative community states need to be of long enough to rule out the argument that the multiple stable points are an artifact of the length of the study and that an adequate amount of time was not provided to allow equilibrium to be reached (Samuels and Drake 1997).

Alternative Community States and Ecological Restoration

Understanding if a system has alternative community states is important for ecological restorationists trying to reverse degradation because of the potential implications this knowledge can have on how and if systems can be restored. If all communities converged to a single stable point, ecological restoration would be much easier because all degradation in systems would be along a linear gradient with time being the only factor preventing a system being restored following a disturbance (Samuels and Drake 1997). In contrast, if all systems were represented by divergence, the communities would be idiosyncratic and structured by chance making restoration of a system impossible and entirely due to chance (Samuels and Drake 1997). A crucial component to understanding the ability for multiple stable points in a community is the critical threshold at which change occurs in a system. Wissel (1984) warns that dramatic changes at thresholds in systems with alternative states may be irreversible if caused by humans. He cites examples of increased eutrophication in lakes and introduction of pests as changes that may be irreversible (Wissel 1984). As a result, being able to predict critical thresholds for irreversible events is crucial to preventing permanent changes (Knowlton 1992). A critical threshold has two characteristics: 1) it is a boundary in space and time between two or more states; and 2) the shift across the boundary is not reversible within a reasonable timeframe without intervention by humans (Friedel 1991).

The concept of alternative community states is relevant to southwestern ponderosa pine systems. Similar to the example presented earlier regarding the removal of rabbits leading to alternative community states of herbaceous and woody dominated communities, the removal of fire in ponderosa pine systems may have led to alternative herbaceous and woody community. The reintegration of fire into ponderosa pine ecosystems has not been able to return the system to a community that consists of few trees intermixed with grassy meadows (Covington and Sackett 1984). Instead, other mechanisms such as tree removal through thinning have been necessary, which suggests an alternative community state (Covington et al. 1997). The concept of multiple community states has relevance to understory plant community dynamics in southwestern ponderosa pine forests in the context of ecological restoration because a major goal of ponderosa pine restoration is to increase native plant diversity and productivity. As a result, an important question regarding the existence of multiple states in ponderosa pine systems is whether the herbaceous understory will have similar composition and structure to pre-disturbance states or whether the history of the site will matter and the existing species pool and order of species recruitment will allow other species assemblages to maintain their own alternative state.

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CHAPTER 3

CHOOSING THE APPROPRIATE SAMPLING TECHNIQUE TO DETECT CHANGE—AN EXAMPLE FROM PONDEROSA PINE RESTORATION

ABSTRACT

While there is no one correct method for sampling vegetation, the sampling design chosen may greatly influence the conclusions researchers can draw from restoration treatments. Considerations when designing vegetation sampling protocol include the size and shape of the sampling plot, the number of replicates and their location within the study area, and the frequency of sampling. We installed 20 point-intercept transects (50-m long), 8 belt transects (10 x 50-m), 10 adapted Daubenmire transects (four 0.5 x 2-m plots) and 4 Modified-Whittaker plots (20 x 50 m with smaller nested plots) in treatment and control units to measure understory herbaceous and shrub response in a forest restoration experiment that tested thinning and prescribed burning methods. Point-intercept transects on average recorded at least twice as much plant cover as did adapted Daubenmire transects and Modified-Whittaker plots taken at the same location for all control and treatment units. Point-intercept transects and adapted Daubenmire plots on average captured fewer rare and exotic species in the control and treatment units in comparison to the belt transects and Modified-Whittaker plots. Modified-Whittaker plots captured the highest species richness in all units. Early successional understory response to restoration treatments was likely masked by the response of the herbaceous community to yearly climatic variation (dry vs. wet years). Species richness and abundance were higher in wet years than dry years for all control and treatment units. Our results illustrate that sampling design can greatly influence the ability to measure species richness and abundance. In addition, our results suggest that restoration studies should be conducted for a sufficient length of time so that restoration treatment responses can be detected.

INTRODUCTION

Ecological monitoring is a major component of numerous ecological restoration projects. Monitoring is the repetition of measurements over time for the purpose of quantifying change (MacDonald 1991), providing information about plant populations, community processes, and management techniques (Sutter 1996). Monitoring is often the tool used to define "success" in restoration projects and provides the justification for restoration treatments by being able to quantify restoration treatment effects (Sauer 1998). As a result, choosing an appropriate monitoring design that is compatible with the restoration project goals is crucial to the evaluation of any ecological restoration treatment.

Currently, extensive efforts are underway to restore ponderosa pine forests across the western United States. Ponderosa pine restoration aims to reverse the degradation caused by historical land management practices of heavy grazing, intensive logging of old-growth trees, and fire suppression. A major goal of ponderosa pine restoration is restoring ecosystem structure and function within a range of natural variability. Specifically, increasing native diversity, abundance and productivity of the herbaceous understory is a major component to restoring ecosystem structure (Covington et al. 1997). It is therefore important to have a monitoring sampling technique that will reliably and precisely detect change in the herbaceous understory of ponderosa pine forests that have undergone restoration. In particular, early detection of exotic and rare species in areas that have undergone restoration treatments is fundamental to assessing the "success" of restoration projects because exotics can be problematic and because rare natives are often given special management attention.

Numerous vegetation sampling techniques are outlined in sampling textbooks (Mueller-Dombois and Ellenberg 1974; Krebs 1989; Kent and Coker 1994; and Barbour et al.1999) and in the scientific literature (Etchberger and Krausman 1997; Stohlgren et al. 1995a; Stohlgren et al. 1998). However, determining the sampling technique that is most appropriate for restoration monitoring objectives can be difficult since there is no one "correct" sampling technique applicable to all study designs. Sutter (1996) outlined four criteria of monitoring techniques that must be met in order to reliably and precisely detect change. These included: (1) data need to have a known and acceptable level of precision; (2) data sampling techniques need to be repeatable across time and personnel; (3) data need to be collected for a long enough time to capture responses to treatments; and (4) techniques need to be feasible, realistic, and inexpensive enough to be maintained long-term. In addition, monitoring techniques need to be adaptable so that new variables that were not anticipated at the beginning of the study can be incorporated into the existing monitoring protocol.

We were concerned that different monitoring sampling techniques and sampling sizes would result in inconsistent data and that these results would affect our ability to detect change in the herbaceous and shrub understory response to restoration treatments. The specific objectives of this study were to: 1) compare four sampling techniques with equal sample sizes to quantify changes in herbaceous species richness and abundance in control and restoration treatment units; 2) compare four sampling techniques with unequal sample sizes in the same experimental setting; and 3) determine the effect of yearly climatic variation on the ability of different sampling techniques to detect change in response to restoration treatments.

METHODS

Experimental Design

We established three blocks of four different treatments during the summer of 1998 within an approximate 688 hectare area of the Fort Valley Experimental Forest and adjacent Coconino National Forest. Each treatment unit is approximately 16 hectares. Treatment units within each block were randomly assigned one of two treatments: (1) no thinning nor burning (control); and (2) thinning to a low level of trees more similar to the forest density prior to settlement, and prescribed burning.

The vegetation at the study site consists of pure ponderosa pine stands, which contain a few large, yellow-barked trees intermixed with numerous small black-barked postsettlement trees. Perennial grasses such as squirreltail (*Elymus* *elymoides*), mountain muhly (*Muhlenbergia montana*), Arizona fescue (*Festuca arizonica*), sedges (e.g., *Carex geophila)* and numerous forbs (*Antennaria* sp., *Cirsium* sp., *Lupinus argenteus, Solidago* sp.) dominate the understory. Soils are moderately well-drained clay and clay loams that are of volcanic origin (Covington et al. 1997). Annual precipitation ranges from 43 to 64 cm with an average of 50 cm in the Flagstaff area (Shubert 1974). Precipitation patterns follow scattered snowfall and rain during the winter months and a pronounced drought in May and June, followed by frequent monsoon rains in July and August (Vose and White 1991). Daily mean temperatures range from –5° C to 17° C (Sackett 1980).

Field Sampling

Four different vegetation monitoring techniques were established in the three control units and the three replicate treatment units. The original monitoring sampling design consisted of 20 systematically located permanent plots on a grid system within each unit. All vegetation sampling techniques were overlaid on this grid system. The four sampling techniques consisted of (1) the line-intercept method, (2) an adapted Daubenmire transect, (3) a belt transect, and (4) a Modified-Whittaker plot. We chose the first three sampling techniques because they are traditional sampling techniques that are well established and commonly used in monitoring vegetation. We chose the Modified-Whittaker plot design because recent studies have illustrated that it is more robust at capturing species diversity than traditional sampling techniques (Stohlgren et al. 1998). Four randomly located plots on the 20-plot grid system were chosen in each unit for a direct, paired comparison of the four techniques, hereafter referred to as the paired sampling technique comparisons. Figure 1 illustrates the layout of the sampling techniques at each plot. In addition, we compared the four techniques based on the total area sampled for each method; hereafter referred to as the unpaired sampling technique comparisons. For this comparison, the number of sampling plots in each unit was: 20 point-intercept transects, 10 Daubenmire transects, 8 belt transects, and 4 Modified-Whittaker plots. We used twenty point-intercept transects for each unit because this was the original sampling protocol for the study. We used 10 Daubenmire transects so that the average area recorded for plant foliar cover (40 m^2) was the same between this technique and the 4 Modified-Whittaker plots within each unit. Finally, we used eight belt transects so that the average area recorded for species composition (4000 m^2) was the same between this technique and the 4 Modified-Whittaker plots within each unit. For both the paired and unpaired sampling techniques we recorded the amount of time it took to survey the vegetation, which did not include the time to set up the plots. We collected this information so that we could determine the cost of the different sampling techniques in comparison to the amount of data we collected (e.g., species richness).

Point-intercept Transect

The point-intercept method uses a 50-m transect laid parallel to the environmental gradient (Figure 1). The primary objective of the point-intercept transect is to quantify plant foliar frequency, as a surrogate for plant cover/abundance (Buckner 1985). Every 30 cm along the transect, for a total of 166 point measurements, plant and substrate (litter, rock, wood, or bare mineral soil) was recorded. For all plant hits, the species was identified and its height was recorded. Plant abundance was determined by dividing the number of first plant hits by 166 points. Individual species abundance was determined by dividing the number of individual species' hits by the total number of plant hits.

Daubenmire Transect

One adapted Daubenmire transect, consisting of four 0.5 x 2 m plots, was overlaid on each line-intercept transect. Plots were located at 10, 20, 30, and 40 m alternating to the left and right of the transect (Figure 1). The main objective of the Daubenmire transect is to quantify plant foliar cover of most species in an area (Stohlgren et al. 1998). Daubenmire plant cover classes (e.g., 0-5, 5-25, 25-50%, etc.) were not used because they tend to overestimate species cover because the smallest size class averages cover to be 2.5 %/species. Instead, for each plot we estimated the percent cover of each species to the nearest quarter percent using cardboard cutouts of known sizes as visual guides. Ocular estimation of plant cover is a commonly used method for determining plant dominance, succession, and treatment response in vegetation analysis (Hatton et al. 1986). The estimates can total > 100% because percent cover was estimated independently for each species and independent of canopy position. Individual species abundance was determined by averaging the species' abundance in the four plots/transect. The percent cover of litter, rock, wood, and bare mineral soil was also determined for each plot.

Belt Transect

A 10 x 50 meter belt transect was centered over each 50-m line intercept transect (Figure 1). The primary objective of the belt transect is to obtain a species list of the area (Kent and Coker 1994). All herbaceous and shrub species within the belt were recorded. We did not record any plant cover or substrate data.

Modified-Whittaker Plot

We placed the Modified-Whittaker plot (Stohlgren et al. 1995b) to the left of the line-intercept transect at 0 meters (Figure 3.1). The Modified-Whittaker plot is a 20 x 50-m nested plot design consisting of 10 1-m^2 plots with detailed plant and substrate information (six systematically arranged around the inside of the 1000-m^2 plot perimeter and four systematically arranged around the outside of the 100-m^2 perimeter), two 10-m^2 plots (in diagonally opposite corners of the plot), one 100-m^2 plot (in plot center), and one 1000-m^2 plot that documents species composition. The main objectives of the Modified-Whittaker plot are to quantify plant foliar cover and height for most species at an area, provide cover and frequency data that has low spatial autocorrelation, and to develop species-area curves based on the nested design to predict the number of species in a larger area (Stohlgren et al. 1995). Within each 0.5 x 2 m plot (1 m^2), species cover was estimated using the ocular estimate method to the nearest quarter percent similar to the methodology described for the adapted Daubenmire transects. Individual species abundance was determined by averaging the species' abundance of the ten 1-m^2 plots per a Modified-Whittaker plot. In addition, mean plant height and different substrate covers were also documented for each 1 m^2 plot.

Statistical Analyses

Multivariate analysis of variance (MANOVA) repeated measures was used to determine the effects of different sampling techniques and time on herbaceous species richness and abundance in control and treatment units for data collected in 1999 and 2000. We used the Shapiro Wilks test to determine if data met the normality assumption and Leven's test if data met the homogeneity of variance assumption (Milliken and Johnson 1984). Tukey's Honestly Significant Difference (HSD) test was used to make post-hoc multiple comparisons of means between sampling techniques. Significant differences were accepted at alpha ≤ 0.05.

RESULTS

Paired Sampling Technique Comparisons

The four different sampling techniques that were paired for a direct comparison within the control and treated units had greater variation in species richness than plant foliar cover. The point-intercept transects recorded a significantly lower number of species for both years in the control and treatment units in comparison to the other three techniques (Figures 3.2a and 3.2b). The Modified-Whittaker plots recorded the highest number of species out of the four sampling techniques (Figures 3.2a and 3.2b). In addition, the Modified-Whittaker plots recorded a significantly higher number of exotic and annual species for both years than any of the other sampling techniques (Table 3.1). The point-intercept transects captured the fewest exotic and annual species, followed by the Daubenmire transects and belt transects; however, these differences were not significant. There was no significant difference between the number of species recorded in the treatment units between 1999 and 2000. Similarly, there was no significant difference between the number of species recorded in the control units between 1999 and 2000. However, species richness was lower in 2000 for all the control and treatment units than in 1999 (Figures 3.2a and 3.2b). Plant foliar cover was not significantly different in the control units between the three sampling techniques (Figure 3.3a). In contrast, in the treatment units, average foliar cover values were significantly higher in 1999 and 2000 using point-intercept transects than Daubenmire plots and Modified-Whittaker plots (Figure 3.3b).

Modified-Whittaker plots took significantly longer (p=.001) on average than the other sampling techniques to survey four replicates. Modified-Whittaker plots took an average of 341 minutes for one person to survey four plots in comparison to 55 minutes for four point-intercept transects, 43 minutes for four Daubenmire transects, and 46 minutes for four belt transects.

Unpaired Sampling Technique Comparisons

The four different sampling techniques had significant variation for species richness and plant foliar cover within control and treated units for both years with uneven replicates of sampling techniques in each unit: 20 point-intercept transects, 10 Daubenmire transects, 8 belt transects, and 4 Modified-Whittaker plots. Similar to the paired sampling technique comparisons, the point-intercept transects recorded the lowest number of species for both 1999 and 2000 in comparison to the other three techniques even with an additional 16 transects within each unit (Figures 3.4a and 3.4b). The belt transects recorded a significantly higher number of species than the previous two sampling techniques although it was not significantly different from the Modified-Whittaker plots (Figures 3.4a and 3.4b). Similar to the paired sampling technique comparisons, the line-intercept transects captured the fewest exotic and annual species, followed by the Daubenmire transects; however, these differences were not significant (Table 3.2). The belt transects and Modified-Whittaker plots recorded significantly more exotic and annual species than the other two sampling techniques (Table 3.2). For example, Dalmatian toadflax (*Linaria dalmatica* (L.) P. Mill.) was recorded in all three treatment units and one control using the belt transects and the Modified-Whittaker plots but was only recorded in one treatment unit using the line-intercept transects and Daubenmire transects. Similarly, Rusby's Milkvetch (*Astragulus rusbyi* Greene) was recorded in only one treatment or control unit using the line intercept transects and Daubenmire transects. In contrast, it was found in two controls and two treatment units using the Modified-Whittaker plot and in two control and one treatment unit using the belt transect. This species is listed as a threatened species by the state of Arizona. The Modified-Whittaker plots offer good detection of exotic and rare species and the ability to quantify change in abundance where the belt transects only offer good detection because no cover values are recorded with belt transects. There was no significant difference between the average number of species recorded in the control between 1999 and 2000 and treatment units between 1999 and 2000. However, there was lower species richness in 2000 than 1999 for all of the control and treatment units (Figures 3.4a and 3.4b). The point-intercept transects recorded significantly higher plant foliar cover than Daubenmire transects and Modified-Whittaker plots in both the control and treatment units in 1999 and 2000 (Figures 3.5a and 3.5b). Specifically, foliar cover from the point-intercept transects was more than double the average foliar cover from the Daubenmire transects and Modified-Whittaker plots.

There was no significant difference between the average time it took for one person to survey four Modified-Whittaker plots (341 minutes) in comparison to 20 point-intercept transects (321 minutes). Daubenmire transects and belt transects took significantly less (p=.001) time with an average of 128 minutes to survey 10 Daubenmire transects and an average of 133 minutes to survey 8 belt transects for one individual.

DISCUSSION

Species Richness

Species diversity is one of the most frequently sampled attributes in vegetation studies (Ricklefs and Schluter 1993) and increasing native plant diversity is one of the most cited goals of ecological restoration (e.g., Bugg et al. 1997, Johnson 1996, Kindscher and Tieszen 1998). Species diversity is often used interchangeably with species richness. Species richness however is one of two components that define species diversity, the other being species evenness (Kent and Coker 1994). Having a sampling technique that is robust in capturing species richness should be desirable in restoration monitoring protocol. Choosing a sampling technique that maximizes the detection of species richness while not compromising financial and time restraints is imperative in ecological restoration studies. In addition, determining the appropriate scale for capturing species diversity is important because relationships between species richness and other community attributes such as productivity can be dependent upon the scale of study (Grytnes 2000). For example, a recent study by Stohlgren and others (1999) found that at the 1-m^2 plot scale areas rich in species were less invaded by exotic species; however, at the 1000-m^2 plot scale areas rich in species were the most heavily invaded by exotic species.

In our study the Modified-Whittaker plot served as the baseline for species richness comparisons because it captured the most species. Assuming there is some true but number of species, the method that captures the highest species richness must be closest to the "truth." The direct comparison of sampling techniques at one location supported the well-known concept that an increase in sampling area will increase species richness detection (Rapson et al. 1997). The grain (the minimal scale sampled), the extent (the farthest distance between samples), and the number of samples influence the positive relationship between species richness and area (Palmer and White 1994). In our study, the point-intercept transect sampled the smallest total area (< 0.1-m^2) and found the fewest species, followed by the Daubenmire transect (4-m^2), the belt transect (500-m^2) and the Modified-Whittaker plot (1000-m^2), which captured the most species. When more belt transects were added so that the sampling area was equal to the area surveyed in Modified-Whittaker plots there was no significant difference in species richness, although Modified-Whittaker plots returned slightly higher numbers.

Other methodology comparison studies in various ecosystems have documented low species detection using point-intercept transects in comparison to other sampling techniques (Kinsinger et al. 1960, Etchberger and Kraussman 1997, Stohlgren et al. 1998). A high degree of spatial autocorrelation is another possible reason, in addition to their small sampling area, why transect methods failed to capture higher levels of species richness (Stohlgren et al. 1998). Due to the spatial arrangement of the sampling technique, point-intercept transects and

Daubenmire transects tend to record redundant information on species richness while at the same time missing many species (Stohlgren et al. 1998). However, in our study Daubenmire transects captured significantly more species than the point-intercept transects, which is probably the result of the larger sampling area surveyed.

Modified-Whittaker plots on average took five times longer for one individual to survey four plots in comparison to sampling four replicates of the other sampling techniques. Modified-Whittaker plots also captured five times as many species as the point-intercept technique for the paired sampling technique comparisons. There was no significant difference between the time it took one individual to survey four point-intercept transects, four Daubenmire transects and four belt transects. However, Daubenmire transects captured twice as many species, and belt transects captured three times as many species, as the point-intercept transects. For the unpaired sampling technique comparisons there was no significant difference between the time it took one individual to survey four Modified-Whittaker plots in comparison to 20 point-intercept transects, although on average the four Modified-Whittaker plots captured over twice as many species as the 20 point-intercept transects. In addition, there was no significant difference between the amount of time it took to survey ten Daubenmire transects and eight belt transects but belt transects captured twice as many species. Finally, there was no difference between the average number of species captured using eight belt transects in comparison to four Modified-Whittaker plots even though the eight belt transects took less than half the time to survey. These data illustrate how the amount of data collected is related to the time it takes to collect the data. The type of sampling technique chosen to measure herbaceous and shrub species richness needs to incorporate the amount of time available for sampling, the detail of information required and the focus of the understory in a multi-objective sampling design that incorporates other landscape parameters such as fuels, trees, etc. For example, if only a species list is needed, the belt transect provides the most information for the cost. Alternatively, if a species list, species abundance data, and capturing rare and exotic species is important then the Modified-Whittaker provides the most information for the cost.

Species Abundance

Increasing native herbaceous and shrub foliar cover is an important goal in many ecological restoration treatments (Covington et al. 1997, Lovich and Bainbridge 1999) and therefore it is important to have a robust sampling technique to accurately measure foliar cover included in restoration monitoring. Species abundance is some measure of the amount of a species in a sample (Chiarucci et al. 1999). Plant foliar cover is one of the most widely used abundance measurements because it is not biased by the size or distribution of individual species (Floyd and Anderson 1987). Numerous sampling techniques have been designed by ecologists to quantify plant foliar cover. The three most commonly used techniques include the point-intercept, the line-intercept, and ocular estimation (Buckner 1985). These three methods all have strengths and weaknesses, but when used appropriately their weaknesses can be minimized.

Point-Intercept

It is difficult to determine a baseline for foliar cover as was done with species richness because the sampling techniques in our study produced varied results and the actual cover of individual species in the treatment units is unknown. Because one technique provides more species cover than another technique does not necessarily mean that the technique providing the higher cover is more accurate. Regardless, we can draw some general conclusions about the two sampling techniques used in this study from other published data that have compared these sampling techniques and their precision. The point-intercept transect is a very robust technique for measuring foliar cover when it is used appropriately (Brady et al. 1995). This sampling technique was designed to be limited to a "dimensionless" point where the probability of a particular species being contacted by a point is a strict function of its abundance (Buckner 1985). This requirement is often violated because of the extra time needed to sample small points with a vertical projection, thereby compromising the accuracy and objectivity of the method. Researchers have shown, however, that the violation of point size and point projection can be minimized when an optical device with fine cross hairs is attached to a sturdy tripod.

In our study, the point-intercept method recorded twice as much foliar cover as the Daubenmire transects and Modified-Whittaker plots in the paired sampling technique comparisons. Point-intercept plant foliar cover values were almost three times higher than Daubenmire transect and Modified-Whittaker plot values in the unpaired sampling technique comparisons. These results are consistent with other studies that have documented an overestimation of foliar cover when point-line intercept transects were not used appropriately (Sharp 1954, Buckner 1985, Frank and McNaughton 1990, Stohlgren et al. 1998). As early as 1952, Goodall illustrated the large effect that point size has on cover values. For example, when measuring cover of a grass species he found that a pin diameter of 4.75 mm recorded a cover of 71 percent, a pin diameter of 1.84 mm recorded 66.5 percent cover and pin diameter reduced to a point with almost no diameter resulted in 39 percent cover. Similarly, Wilson (1963) found that the error in cover estimates doubled with a doubling of the pin diameter or halving of the leaf breadth. In addition, he found that there was an interaction between pin diameter and leaf size, preventing the use of an error correction value because leaf size will vary with age and environment (Wilson 1963).

Our original sampling technique was designed to be consistent with the prescribed fire monitoring protocol. In our study, we used a point that varied between 5-10 mm and a point that was not controlled for vertical projection. These two violations of the point-intercept sampling technique, along with the comparison of our data with other studies that used a similar point size, suggests that our point-intercept foliar cover values overestimated the actual foliar cover. Other evidence that suggests our sampling technique overestimated cover includes a study that found systematically located points overestimated foliar cover in comparison to randomly located points along a transect (Whysong and Miller 1987) and a study that found species with small, outstretched leaves such as grasses and legumes increased pin contact and therefore overestimated their cover (Glatzle et al. 1993). In our study we used systematically located points along a transect to measure cover and our vegetation was dominated by grasses and sedges.

Ocular Estimation

Visual estimation of plant cover is one of the most common measurements in plant ecology (Kennedy and Addison 1987). Ocular estimates are normally taken within a 1 m^{-2} area because one of the requirements for accuracy is that observations must be made from a vertical perspective within a bounded plot (Buckner 1985). Ocular estimates can either be estimated to the nearest predetermined percent (e.g., closest 1 percent) or they can be categorized into published cover classes (e.g., Daubenmire or Braun-Blanquet, Mueller-Dombois and Ellenberg 1974). In this study we did not categorize ocular estimates into published cover classes because of the inherent problems with overestimating cover values when ocular estimates are categorized, which has been documented in numerous studies in many ecosystems (Floyd and Anderson 1987, Hatton et al. 1986, Stohlgren et al. 1998). Instead, we estimated cover values to the nearest quarter percent within 1-m^2 plots and used cutout visual aids of different percents as suggested by Tilman (1997) to reduce inconsistencies between observers. Even taking these measures to reduce bias in cover estimates, the mental integrations involved in ocular estimation make cover estimates inherently variable between observers, though observers experienced with the technique can be consistent within their own observations (Buckner 1985). A study by Sykes and other (1983) showed that there was reasonable agreement among observers using ocular estimation for 4-m^2 quadrats but that larger 50-m^2 and 200-m^2 quadrats had large inconsistencies between observer estimates with clear tendencies of some observers to consistently over- or underestimate cover. To increase consistency in ocular estimates it has been recommended that observers practice reading cover for species before sampling begins and to periodically compare values among observers throughout the field season (Anderson and Kothmann 1982). In our study, both the Daubenmire transects and the Modified-Whittaker plots used ocular estimates for species cover values. In the direct comparison plots (sixteen 1-m^2 plots for the Daubenmire transects and forty 1-m^2

plots in the Modified-Whittaker plots per a unit) there was no significant difference between foliar cover values using these two techniques in comparison with the point-intercept technique. In addition, there was no significant difference in foliar cover values between the two sampling techniques when both the Daubenmire transects and Modified-Whittaker plots had forty 1-m^2 plots within each sampling unit. This consistency between the two sampling techniques, along with the known violations made using the point-intercept technique, suggest that foliar cover values using ocular estimation were more accurate than foliar cover values using the point-intercept method.

CONCLUSION AND RECOMMENDATIONS

The sampling technique chosen for monitoring herbaceous and shrub species richness and foliar cover in restoration studies can greatly influence the ability to detect change. When choosing a sampling technique, decisions must be made about plot size and shape, the parameters to be measured, and the frequency, precision and location of measurements (Stohlgren 1994). Reference conditions are often cited as the goal for restoration treatments. This study illustrates that the type of sampling technique used to determine reference conditions should be similar to the sampling technique used to monitor change or the data may lead to inaccuracy, confusion, or apparent over- or under-achievement of goals. Large area sampling techniques were the most effective at capturing species richness and rare and exotic species. Modified-Whittaker plots returned on average the highest species richness in all sampling technique comparisons and captured the most rare and exotic species. In comparison, point-intercept transects captured the fewest species. Our study with two years post treatment data was not conducted over a long enough timeframe to detect foliar cover change in response to restoration treatments. Change in foliar cover was likely masked by the herbaceous community response to yearly climatic variation (dry vs. wet years). The year of 1999 was a wet summer (May-September) with 27.51 cm of rain in comparison to the summer of 2000, which received 11.26 cm of rain (NOAA). The average summer precipitation is 20.83 cm (NOAA). These changes in precipitation were evident in the herbaceous community with lower species richness and foliar cover in 2000 for the control and treatment units than recorded in 1999 for all units.

Point-intercept transects using an optical device to eliminate error are recommended in revegetation studies where objectivity and repeatability are of primary importance and capturing species diversity is of secondary importance (Buckner 1985). In studies where capturing species diversity and cover values of rare and exotic species are of primary importance we recommend Modified-Whittaker plots. Determining the sampling technique that should be used for a particular study needs to take into consideration numerous factors such as the level of sampling precision, project goals, and financial and personnel constraints. Finally, when choosing a sampling technique for long-term monitoring of restoration treatments, it is important to test sampling techniques to make sure they will meet the objectives of the particular study rather than simply using a particular sampling technique because it is well established and recommended.

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Table 3.1 Total number of exotic and annual species captured in 1999 and 2000 for paired plots using different sampling techniques in the control and treatment units with similar sampling sizes. Data are expressed as means (N=3) ± SE.

	Line-Intercept Transect	Daubenmire Transect	Belt Transect	Modified Whittaker Plot
Control Plots				
Exotic 1999	0 ± 0 a	0.33 ± .33 a	1.33 ± .33 b	2.33 ± .68 b
Exotic 2000	0 ± 0 a	0.33 ± .33 a	0.33 ± .33 a	2.00 ± .57 b
Annual 1999	0.66 ± .33 a	1.67 ± .33 a	2.33 ± .33 a	6.00 ± 1.52 b
Annual 2000	0 ± 0 a	1.00 ± .58 a	1.00 ± 0 a	3.33 ± .33 b
Treatment Plots				
Exotic 1999	0.33 ± .33 a	2.33 ± 1.33 b	3.00 ± 1.52 b	4.00 ± .64 b
Exotic 2000	0.67 ± .33 a	1.33 ± .88 a	3.00 ± 1.1 a	4.00 ± .57 b
Annual 1999	0.67 ± .33 a	3.67 ± 1.67 a	6.00 ± 1.5 a	10.00 ± 2.1 b
Annual 2000	0.67 ± .33 a	2.33 ± .88 a	5.67 ± 1.4 a	8.00 ± .58 b

Number of samples within a plot: line-intercept transect N=4, Daubenmire transect N=4, belt transect N=4, modified Whittaker plot N=4. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques.

Table 3.2 Total number of exotic and annual species captured in 1999 and 2000 in the control and treatment units using different sampling techniques with different sampling sizes. Data are expressed as means (N=3) ± SE.

	Line-Intercept Transect	**Daubenmire Transect**	**Belt Transect**	**Modified Whittaker Plot**
Control Plots				
Exotic 1999	0 ± 0 a	0.33 ± .33 a	2.67 ± .33 b	2.33 ± .88 b
Exotic 2000	0.33 ± .33 a	0.33 ± .33 a	1.27 ± .33 b	2.00 ± .57 b
Annual 1999	2.67 ± .88 a	1.67 ± .33 a	5.33 ± .88 b	6.00 ± 1.52 b
Annual 2000	1.00 ± .58 a	1.00 ± .58 a	3.00 ± 1.33 b	3.33 ± .33 b
Treatment Plots				
Exotic 1999	0.67 ± .33 a	1.33 ± .88 a	3.67 ± .76 b	4.00 ± .64 b
Exotic 2000	1.00 ± .58 a	0.67 ± .67 a	3.67 ± .67 b	4.00 ± .57 b
Annual 1999	2.33 ± .67 a	3.67 ± .33 a	8.00 ± 3.0 b	10.00 ± 2.0 b
Annual 2000	2.67 ± .88 a	3.33 ± .33 a	7.00 ± 1.1 b	8.00 ± .58 b

Number of samples within a plot: line-intercept transect N=20, Daubenmire transect N=10, belt transect N=8, modified Whittaker plot N=4. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques.

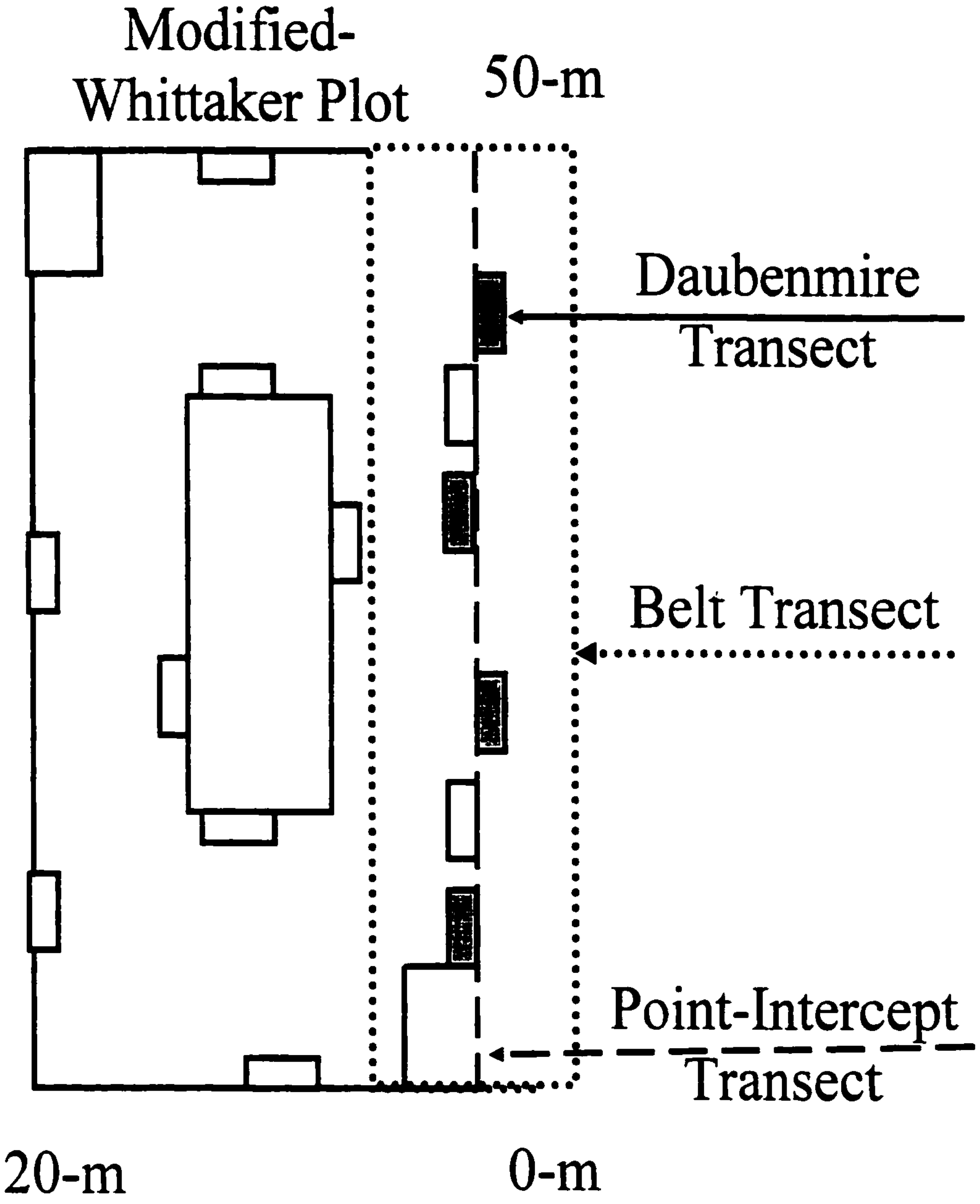

Figure 3.1 Layout of the four sampling techniques for direct paired comparisons. The point-intercept transect is shown in hatch marks (50-m), the belt transect is outlined in dots (10 x 50-m), the adapted Daubenmire transect has four shaded plots (0.5 x 2-m) and the Modified Whittaker plot is shown in solid lines (20 x 50-m) with smaller nested plots of various sizes (ten 0.5 x 2-m plots, two 2 x 5-m plots and one 5 x 20-m plot).

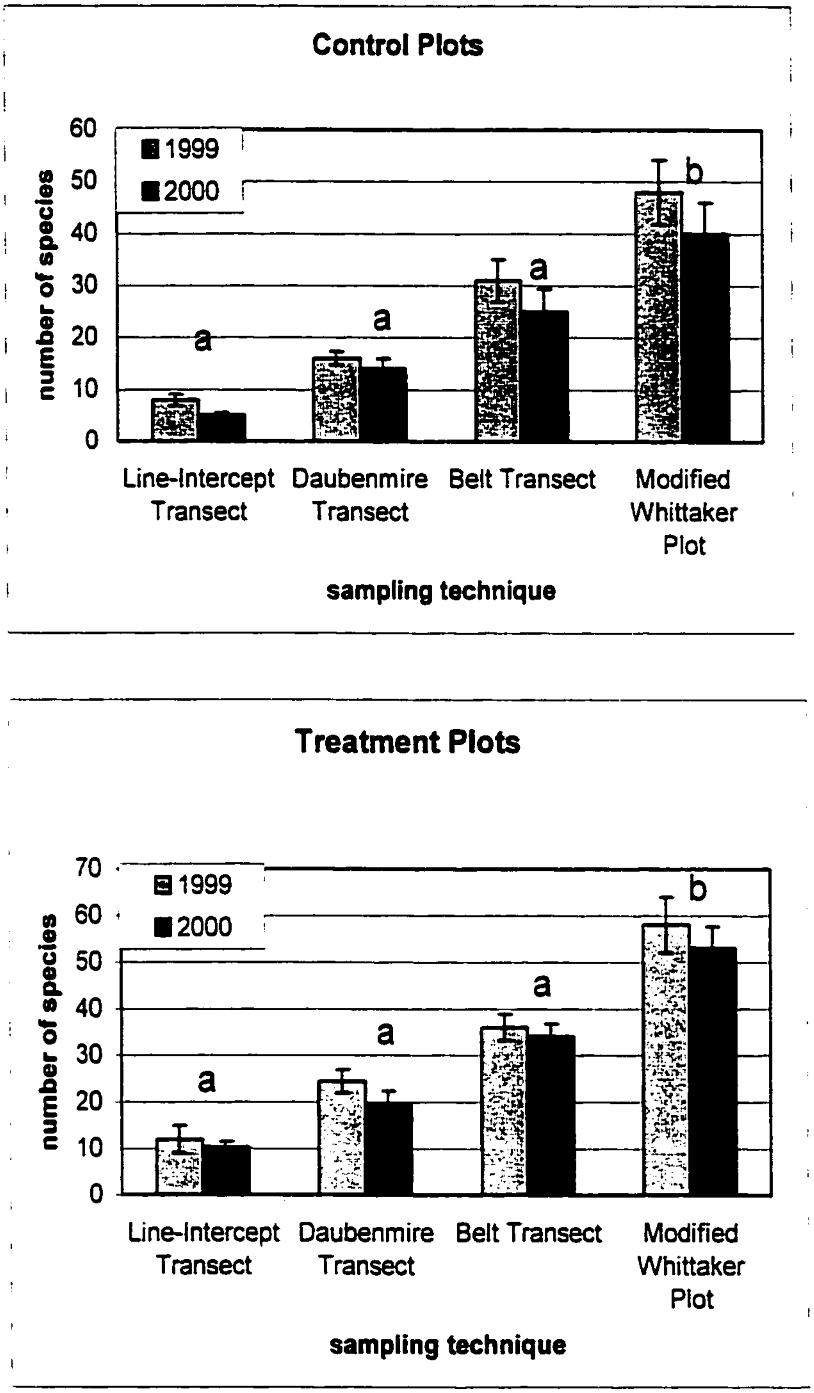

Figure 3.2a-b Total species richness for paired control (a) and treatment (b) plots in 1999 and 2000 using four different sampling techniques. Data are expressed as means (N=4) ± SE. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques. There was no significant difference between the number of species recorded between 1999 and 2000 for individual sampling techniques.

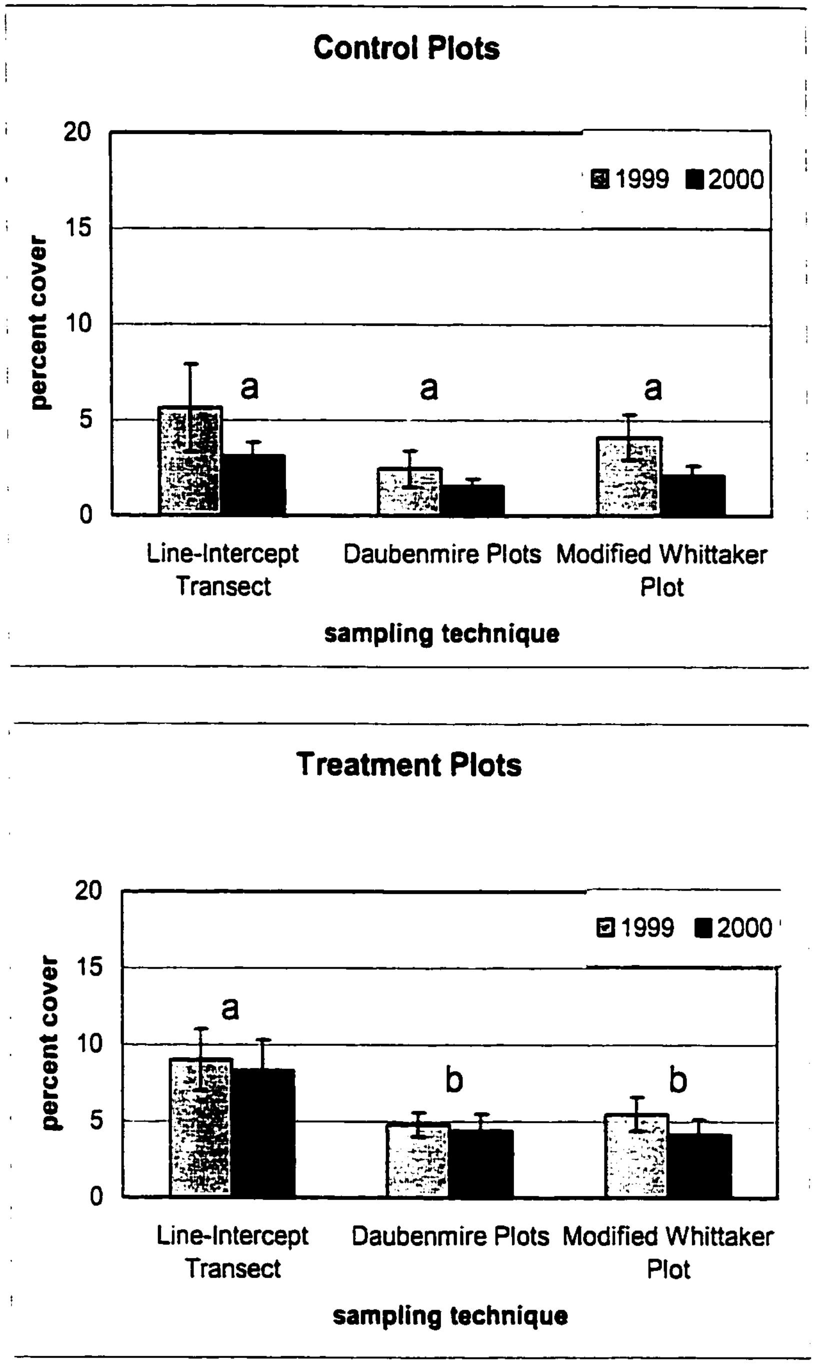

Figure 3.3a-b Total plant foliar cover for paired control (a) and treatment (b) plots in 1999 and 2000 using four different sampling techniques. Data are expressed as means (N=4) ± SE. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques. There was no significant difference between total plant foliar cover between 1999 and 2000 for individual sampling techniques.

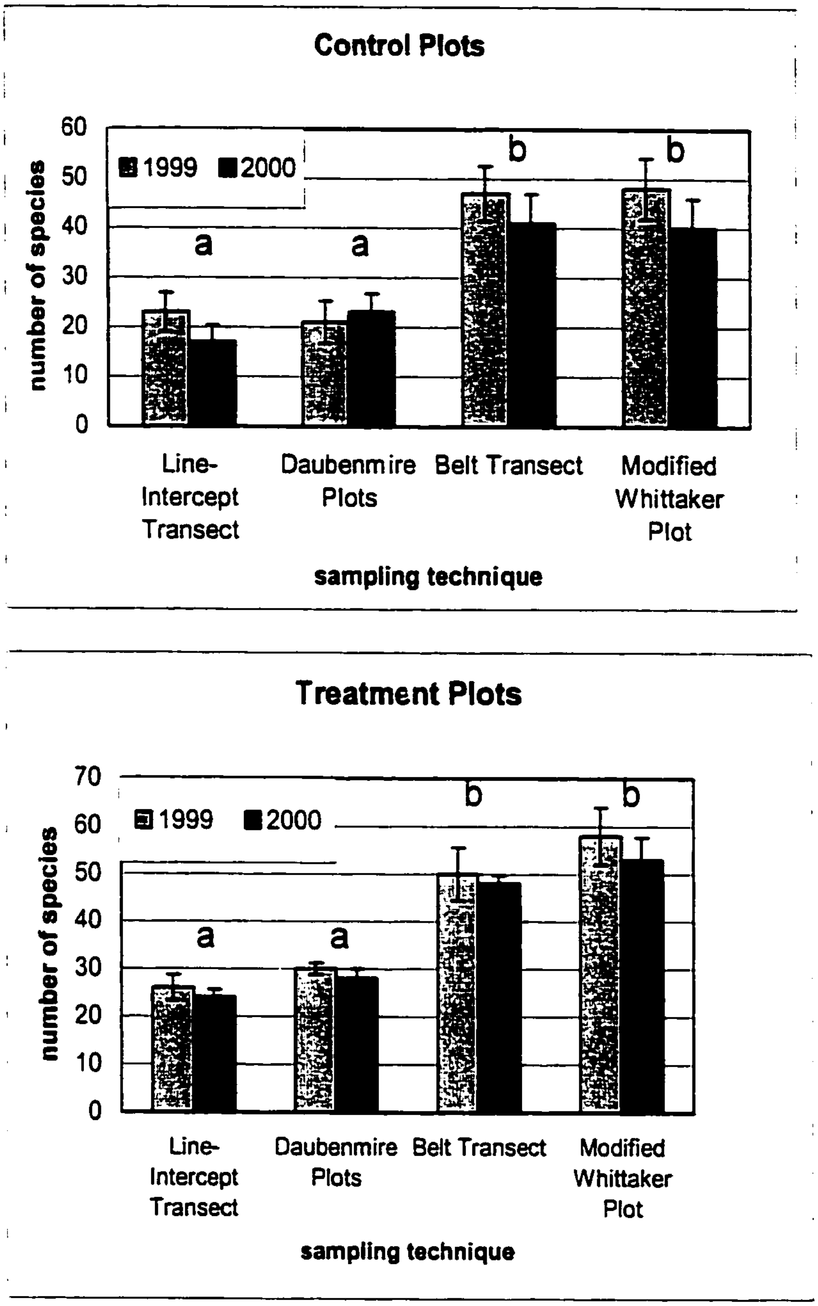

Figure 3.4a-b Total species richness for all control (a) and treatment (b) plots in 1999 and 2000 using four different sampling techniques. Data are expressed as means (N=20 point-intercept transect; N=4 adapted Daubenmire transects; N=8 belt transects; N=4 Modified-Whittaker plots) ± SE. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques. There was no significant difference between the number of species recorded between 1999 and 2000 for individual sampling techniques.

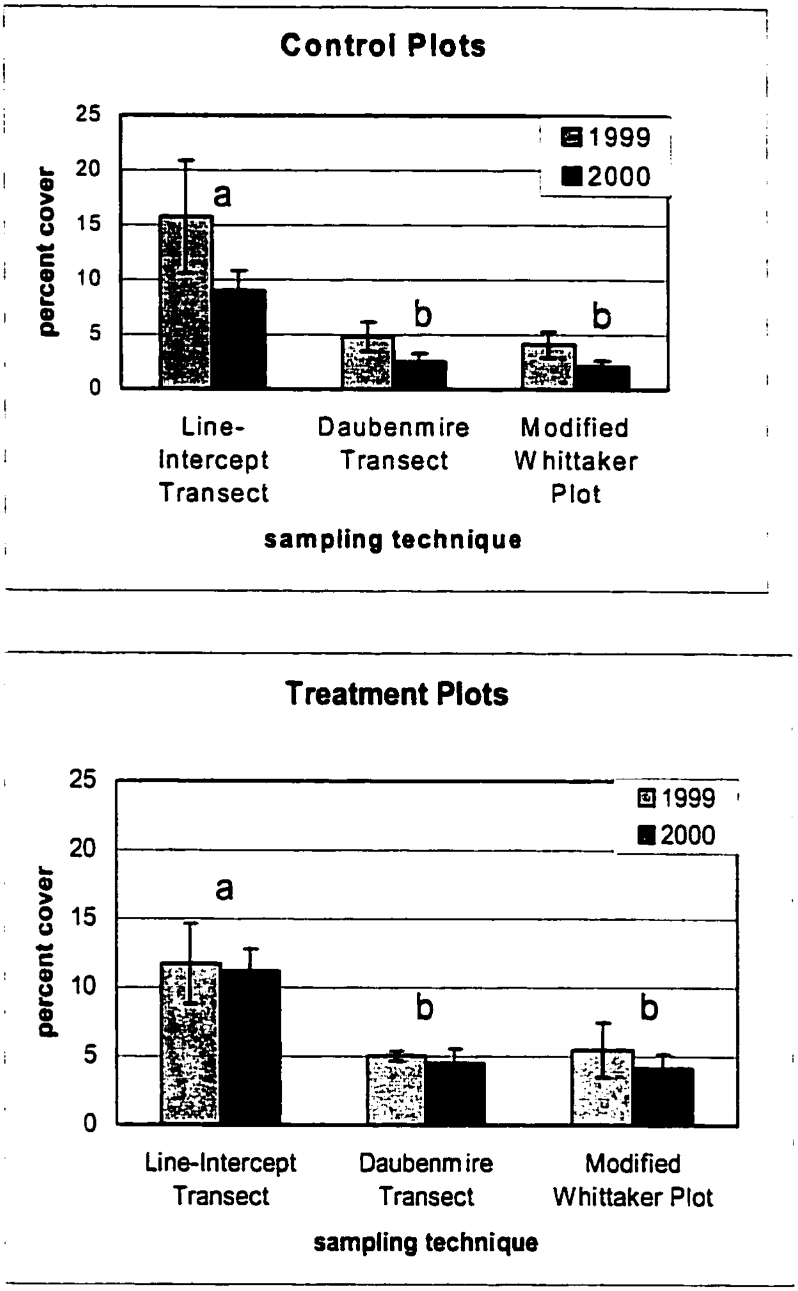

Figure 3.5a-b Total plant foliar cover for all control (a) and treatment (b) plots in 1999 and 2000 using four different sampling techniques. Data are expressed as means (N=20 point-intercept transect; N=4 adapted Daubenmire transects; N=8 belt transects; N=4 Modified-Whittaker plots) ± SE. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques. There was no significant difference between total plant foliar cover between 1999 and 2000 for individual sampling techniques.

CHAPTER 4

ARBUSCULAR MYCORRHIZAL PROPAGULE DENSITIES RESPOND RAPIDLY TO THINNING AND PRESCRIBED BURNING IN TWO SOUTHWESTERN PONDEROSA PINE RESTORATION TREATMENTS

ABSTRACT

The inoculum potential for arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi was investigated in thinned only, thinned and prescribed burned, and unthinned and unburned control stands in northern Arizona ponderosa pine forests. A corn (*Zea mays*) bioassay was used to determine the relative amount of infective propagules of AM fungi and a ponderosa pine (*Pinus ponderosa*) bioassay was used to determine the relative amount of infective propagules of EM fungi. Two blocks of thinned only and unthinned and unburned control stands ~ 16 hectares in size were sampled at the Fort Valley Experimental Forest, near Flagstaff, Arizona. Four blocks of thinned and prescribed burned and unthinned and unburned control stands each ~ 16 hectares in size were sampled at the Mount Trumbull Resource Conservation Area, near Fredonia, Arizona. Soil cores for the bioassays were collected along 10 transects within each stand. The relative amount of infective propagules of AM fungi was significantly higher in samples collected from the thinned only and thinned and prescribed burned stands than their paired controls. In contrast, restoration treatments had no significant effect on the relative amount of infective propagules of EM fungi. The relative amount of infective propagules of AM fungi was significantly positively correlated with graminoid cover and herbaceous understory species richness and negatively correlated with overstory tree canopy cover and litter cover. These results indicate that population densities of AM fungi rapidly increase following restoration thinning and thinning and prescribed burning treatments in northern Arizona ponderosa pine forests. This has important implications for restoring the herbaceous understory of these forests because most understory plants depend upon AM associations for normal growth.

INTRODUCTION

Prior to Euro-American settlement in the1880's, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests in the American Southwest were characterized by herbaceous understories dominated by grasses intermixed with large trees (Cooper 1960). Low intensity grass-fueled fires every 2-20 years played a major role in determining the structure, composition, and stability of these ecosystems (Fulé et al. 1997). Euro-American settlers drastically changed these forest ecosystems through heavy livestock grazing, intensive logging of old-growth trees, and fire suppression. Today these forests are often characterized by a large number of small trees with closed canopies, deep deposits of dead organic material on soil surfaces, and little herbaceous understory. This forest structure has greatly reduced species diversity and has created a high risk for catastrophic fires. Efforts are currently underway to reverse structural and functional ecosystem changes caused by historical land management practices by returning ponderosa pine forests to a more open savannah-like structure and reintegrating the natural disturbance regime of fire in aims to restore ecosystem diversity (Covington and Moore 1994). Tree thinning and prescribed burning are two major components of this restoration effort.

A major objective for ponderosa pine forest restoration is to increase herbaceous understory diversity and production to levels that emulate reference conditions (Covington et al. 1997). Mycorrhizae are a critical link between aboveground plants and the soil system, playing an important role in plant nutrition, nutrient cycling, and the development of soil structure (Allen 1991, Smith and Read 1997). Many tree species are highly dependent on ectomycorrhizal (EM) fungi (Mikola 1970) and most herbaceous plants are associated with arbuscular mycorrhizal (AM) fungi (Smith et al. 1998). Consequently, numerous researchers have suggested a relationship between the recovery time of disturbed ecosystems and the abundance of infective propagules of mycorrhizal fungi (Reeves et al. 1979, Allen and Allen 1980, Bentivenga and Hetrick 1991, Noyd et al. 1995). In addition, Perry and others (1989) refer to the strong link between plants and the soil biota as the "bootstrapping hypothesis" that suggests that through close mutual interactions that some ecosystems are able to literally pull themselves up by their own "bootstraps", thus creating conditions to allow the system to persist over time (Perry et al. 1989). These authors showed that mycorrhizae helped facilitate succession following natural wildfires where different species of plants formed mutualistic relationships with the same fungi throughout succession in forests in the northwestern United States. Other studies suggest that the role of mycorrhizae in facilitating succession may be dependent on the nutrient status of soil (Allen and Allen 1990). Because ponderosa pines are strongly EM and many of the native understory grasses and forbs are strongly AM, we predicted that densities of AM fungal propagules should increase and EM fungal propagules should decrease in response to restoration thinning and prescribed burning in ponderosa pine forests, with the changes correlated to host plant abundance. The specific objectives of this study were to: 1) quantify the effect of restoration thinning and thinning and prescribed burning on AM and EM fungal propagule densities; and 2) assess the relationships between mycorrhizal fungal propagule densities and plant community and soil properties.

METHODS

Experimental Design

This research was conducted at two sites: the Fort Valley Experimental Forest and adjacent areas near Flagstaff, Arizona (hereafter referred to as Fort Valley) and the Mt. Trumbull Resource Conservation Area northwest of Grand Canyon National Park, Arizona (hereafter referred to as Mt. Trumbull). Two experimental blocks were established during the summer of 1998 at Fort Valley and four experimental blocks were established during the summer of 1999 at Mt. Trumbull. Treatment stands within each block were ~ 16 hectares. Treatments at Fort Valley were randomly assigned one of two treatments: (1) no thinning or burning (control); or (2) thinning to a low level of replacement trees based upon presettlement tree densities. Thinning treatments at Fort Valley received prescribed burning treatments following the sampling for this study during the summer of 2001. Treatments at Mt. Trumbull were randomly assigned the same two treatments with the addition of prescribed burning to thinning. Specific details of the thinning treatments at Fort Valley are outlined in Fulé and others (2001a) and specific details of the thinning treatments at Mt. Trumbull are outlined in Fulé and others (2001b). Twenty systematically located permanent plot centers were located in each stand at Fort Valley and Mt. Trumbull. At each of these permanent plots we sampled herbaceous understory and overstory tree composition and abundance, fuel loads, and tree canopy cover.

Soil Field Sampling

At Fort Valley, soil samples were randomly taken from 10 of the 20 systematically placed plots centers along a 50-m transect within each of the 4 stands (2 blocks x 2 treatments) in late May 1999, six months after thinning, and again in May 2000, eighteen months after thinning. At Mt. Trumbull soil samples were randomly taken from 10 of the 20 systematically placed plot centers along a 50-m transect within each of the 8 stands (4 blocks x 2 treatments) in late June 2000, five months after thinning and three months after burning. Two samples at 20 meters along each transect (one for the AM bioassay and one for the EM bioassay) were taken and immediately placed into 4 cm diameter x 20 cm diameter deep Conetainers (Stuewe and Sons, Inc., Corvallis, Oregon USA) for "bait-plant bioassays" (Brundrett and Abbott 1994). Soils were collected to a depth of 15 cm using a hand trowel. We took samples to this depth because AM fungal propagule densities are generally highest in the surface 15 cm (Smith and Walker 1981). A third sample was taken at the same location for soil chemical analyses. This sample was frozen until it was analyzed.

Vegetation Field Sampling

At Fort Valley, we recorded pretreatment data for the herbaceous understory and overstory tree composition and abundance, fuel loads, and tree canopy cover in 1998. Post thinning treatment data were collected in 1999 and 2000. These data were not significantly different between the two years, therefore only post treatment data from 2000 is presented because it is further along the trajectory of restoration. At Mt. Trumbull, we recorded pretreatment data for the herbaceous understory and overstory tree composition and abundance, fuel loads, and tree canopy cover in 1999. Post treatment data was collected in 2000.

We surveyed the herbaceous and shrub understory community along the same 50-m transects where soil samples were collected for AM and EM bioassays and soil chemical analyses. Every 30 cm along the 50-m transect, for a total of 166 points, substrate (plant, litter, soil, wood, rock) was recorded. If the substrate was a plant, the species was identified and its height was recorded. We determined plant cover by dividing the number of first plant hits by 166 points for each transect. Overstory tree data was collected in 400 m^2 circular plots centered on each plot center. Tree species and diameter at breast height (dbh, 1.37 m) were recorded for all live and dead trees greater than 1.37 m in height.

In addition, at the same 30 cm intervals along the 50-m transect, tree canopy cover and fire severity in areas treated with prescribed burning were recorded. We determined tree canopy cover by recording the presence or absence of tree canopy from a vertical projection. Fire severity was determined based upon descriptions in the Western Regional Fire Monitoring Handbook (NPS, 1992). Areas with charred litter, upper duff and wood were recorded as lightly burned areas, areas with litter mostly consumed, duff deeply burned and wood recognizable were recorded as moderately burned areas, and areas with litter and duff consumed leaving white ash and soil often reddish were recorded as severely burned. We used a 15-m planar transect located in a random direction from the plot center to measure forest floor litter and duff depths. Every 1.5 m, litter and duff were recorded following guidelines outlined in Brown (1974).

Lab Analysis

Bait-plant bioassays are designed to detect all types of viable mycorrhizal fungal propagules including spores, fragments of mycorrhizal roots and extraradical hyphae and, therefore, may more accurately quantify total mycorrhizal fungi than direct counts of sporocarps, spores, or colonized root lengths (Brundrett et al 1994, Johnson et al. 1999). We used a corn (*Zea mays*) bioassay to determine the relative amount of infective propagules of AM fungi and a ponderosa pine bioassay to determine the relative amount of infective propagules of EM fungi. Corn is mycotrophic with many species of AM fungi and grows rapidly and uniformly; these advantages outweigh the disadvantage of not using a native host plant (Johnson et al 1999). Plants were placed in a greenhouse and watered every 3 days until they were harvested at 6 weeks. Because pine seedlings grow more slowly than corn seedlings, pine seedlings were harvested at 12 weeks. Roots were carefully washed free from the soil and weighed. Following mycorrhizal analysis, we dried the roots in an oven at 70° C for 24 hours and then reweighed them. Shoot lengths and dry root and shoot weights were also measured. Corn roots were prepared for AM analysis by cutting roots into 2.5 cm segments, taking a random subsample of the cut roots of a known mass, clearing roots in 5 percent KOH, and then staining roots with trypan blue in lactoglycerin (Koske and Gemma 1990). The gridline intersect method using a dissecting microscope was used to measure the proportion of root length containing AM fungal structures: arbuscules, vesicles, coils, internal mycorrhizal hyphae and external mycorrhizal hyphae (Giovannetti and Mosse 1980). We measured pine roots for fungal propagule density through direct examination using a dissecting microscope to quantify the proportion of root tips colonized with EM fungi (Gehring and Whitham 1991). Root tips were classified either as a living or dead EM tip or a living or dead non-mycorrhizal tip. Different morphological types and colors were also recorded.

Soil Analysis

Soil samples from each transect were analyzed for pH, total N, total P and organic C at the Bilby Research Soil Analysis Laboratory, Flagstaff, Arizona. Soil pH was determined in a 1:1 slurry by pH meter. Total N and P was measured using a Kjeldahl digestion of the soil material followed with the analysis of N and P by automated colorimetry using a Technicon auto-analyzer (Parkinson et al 1975). Organic C was determined by loss on ignition. Samples were heated in crucibles for 24 hours in a muffle furnace at 425° C and organic matter was estimated from net weight loss.

Statistical Analysis

We used analysis of variance (ANOVA) for a randomized block design in SPSS version 8 (SAS Institute 1997) to determine the effect of thinning and prescribed burning on mycorrhizal propagule densities and vegetation and soil properties and on the proportion of AM fungal structures for the 2000 data. Significance for analysis of variance tests was accepted at alpha [0.05. Multivariate analysis of variance (MANOVA) repeated measures was used to determine the effects of thinning on mycorrhizal propagule densities and vegetation and soil properties for data collected in 1999 and 2000. Comparisons for thinned only treatments were accepted at alpha [0.10 because there were only two replicate blocks. The Shapiro Wilks test was used to test data for normality and Leven's test was used to test for homogeneity of the variance (Milliken and Johnson 1984). Root infection data were arcsin square root transformed prior to analysis and bait plant length and weight, herbaceous plant abundance, graminoid cover and soil properties were square root transformed to improve normality and homoscedasticity assumptions (Zar 1984). Multiple regression was used to determine the relationship between infectivity and plant and community properties. Simple correlation analysis was used to determine the relationship between root infectivity and bait plant characteristics (length and weight).

RESULTS

Stand Characteristics

Pretreatment, there were no significant differences between control and treatment stand data for vegetation and site characteristics at the Fort Valley study site (1998) or at the Mt. Trumbull study site (1999) (Tables 4.1 and 4.2). Following thinning treatments, there were significantly less trees/hectare and tree canopy cover in the thinned only and thinned and prescribed burned units than their respective controls (Tables 4.1 and 4.2). At the Fort Valley study site, there were approximately 182 trees/hectare in the thinned only units and 1426 trees/hectare in the paired controls. At the Mt. Trumbull study site, there were approximately 336 trees/hectare in thinned and prescribed burn units compared to 1298 trees/hectare in the paired controls. Although the average herbaceous cover tended to be higher in treated units than in control units, the differences were not significant (Table 4.1). The herbaceous plant communities in the experimental units at Fort Valley were dominated by graminoids followed by non-legume forbs, legumes, and woody shrubs. Similar abundance patterns were present at

Mt. Trumbull except there were more legumes than non-legume forbs. Sedges, *Carex* sp., dominated the herbaceous cover for both study sites along with C_3 grasses including *Elymus elymoides* (Rafinesque) Swezey (squirreltail) and *Poa fendleriana* (Steudel) Vasey (muttongrass). Mountain Muhley (*Muhlenbergia montana* (Nuttall) Hitchcock) was the only abundant C_4 grass in the experimental units at Fort Valley and it was consistently less common than the abundant C_3 grasses. There were no abundant C_4 grasses in the experimental units at Mt. Trumbull.

Approximately 21 percent of the area treated with prescribed fire remained unburned following prescribed burning at Mt. Trumbull (Table 4.3). Of the area that burned, approximately 20 percent was lightly burned, 38 percent was moderately burned, and 21 percent was severely burned. There were no significant differences between soil properties in the treated and control units (Table 4.4). However, at both sites, organic C and total N levels appeared to be higher in both treated units in comparison to their paired controls and total P was slightly higher in the thinned and prescribed burned units at Mt. Trumbull than their controls, although none of these differences were statistical significant.

Mycorrhizal Infectivity

Mycorrhizal fungi colonized all bait-plants and colonization levels were influenced by restoration treatments at both sites. At Fort Valley infective propagule densities of AM fungi were significantly higher in the thinned units than their paired controls for both study years (MANOVA: 1999 F= 12.1407, p=0.0734; 2000 F=20.3451, p=0.0458; Figure 4.1a). Infective propagule densities of AM fungi at Mt. Trumbull were significantly higher in soils from the thinned and prescribed burned units in comparison to their paired controls (F=20.129, p=0.008; Figure 4.2a). Corn bioassay plants grown in the Fort Valley thinned only soils had significantly more vesicles and less hyphae than corn grown in their paired control soils (F=2.1601, p=0.05; F=5.4437, p=0.001; Figure 4.3a.) whereas there was no difference between the relative proportion of AM fungal structures in the Mt. Trumbull thinned and prescribed burned soils and their controls (Figure 4.3b). Unlike the AM fungi, there was no significant difference in the relative amount of infective propagules of EM fungi in samples collected from treated units in comparison to their controls for 1999 or 2000 at Fort Valley (MANOVA 1999 F=0.0846, p=0.7985; 2000 F=4.6877 p=0.1628; Figure 4.1b) or at Mt. Trumbull in 2000 (F= 0.4689 p=0.6754; Figure 4.2b). Sparsely branched bifurcated tips were the dominant EM morphotype for all stands.

AM colonization of the corn bait plants was not correlated with corn shoot weight or corn root weight (r^2= -0.037 and r= 0.031, pµ0.05). EM colonization of the pine bait plants was not correlated with pine shoot weight (r^2= 0.11, p=0.74) but was positively correlated with pine root weight (r^2= 0.28, p=0.04). For all 14 study units combined, about 85% of the variance of AM infectivity was explained by graminoid cover (square root cover), species richness, tree canopy cover and litter cover (F= 13.12 p=0.0009; Table 4.5). In contrast, for all study units combined trees/hectare, tree canopy cover, or litter cover did not explain the variance of EM infectivity (F=0.101, p=0.9573; Table 4.5)

DISCUSSION

During the first two years, restoration treatments had no significant effect on the overall cover of herbaceous AM plants even though plant cover did increase in the restoration treatments. AM abundance was highly correlated to grass cover and therefore areas with higher grass cover (restoration treatments) also had higher propagule densities of AM fungi. Contrary to our expectations, restoration treatments did not change EM propagule densities illustrating that even though their host plant density was significantly reduced, EM fungi are able to maintain viable propagules for at least two years following thinning and one year following thinning and prescribed burning. Other studies have shown variable affects of tree thinning on EM fungal densities depending on the disturbance intensity. For example, clearcutting a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest in western Montana significantly reduced the number of EM roots and affected adjacent uncut stands for at least 7.6 m into the stand (Harvey et al 1980). In contrast, predisturbance population densities of EM fungi were maintained for 2 years after clearcutting an aspen (*Populus tremuloides* Michaux) stand (Visser et al. 1998). Prescribed fire also has varied effects on EM fungi ranging from dramatic reductions in propagule densities and diversity after intense wildfires (Visser 1995) to no significant changes (Baar et al. 1999). A study of a low intensity wildfire showed little change in EM fungal composition or densities (Jonsson et al. 1999). This study suggested that if the organic layer where EM mycelia are concentrated remains largely undamaged then fire would have little or no impact on EM fungi. This explanation may account for the lack of changes in EM fungal propagule densities to restoration thinning and thinning and prescribed burning in this study.

In contrast to EM fungi, AM fungi responded rapidly to restoration treatments in northern Arizona pine forests. Propagule densities of AM fungi increased by an average of 20 percent in thinned and thinned and burned units compared to control units. Two main processes control population densities of mycorrhizal fungi following disturbance: immigration of new propagules from nearby areas and survival and spread of residual propagules (Warner et al. 1987). Rapid colonization of AM fungi has been illustrated in other studies. Gould and others (1996) found that AM propagule densities increased significantly within 9 months of mining reclamation and increased 10-fold the following spring after seeding. Similarly, Johnson and McGraw (1988) found that taconite tailings that were initially devoid of AM fungi were colonized within weeks of reclamation seeding. It was hypothesized that spores were transferred to the reclaimed tailings by both biotic (animals) and abiotic (wind and water) vectors (Johnson and McGraw 1988).

In the present study, it is likely that AM fungi spread from preexisting mycorrhizal hyphae in living and dead plant roots. These live and dead roots systems and their mutualistic mycorrhizal associations represent the mechanism for the "bootstrapping hypothesis" (Perry et al. 1989). The persistence of these associations under unrestored conditions (dense, closed forest canopies and high fuel loads) and their ability to respond rapidly to tree removal and prescribed fire suggests that AM associations may facilitate succession of this community to its previous dominance of herbaceous AM hosts. A study by Kovacic and others (1984) found that AM hosts and AM fungal abundance were significantly higher under beetle-killed ponderosa pine stands than under live ponderosa pine stands in northern Colorado. While the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) outbreak was of epidemic proportions, its function in reducing live tree stand densities promoted changes in belowground AM fungal densities and aboveground herbaceous production. Other studies in different ecosystems have also shown changes in AM propagule densities with changes in tree densities. A successional study of AM propagule densities across a grassland to forest chronosequence showed AM inoculum potential increased with increasing grass cover and decreased in later successional sites with EM trees (Johnson et al. 1991). Similarly, a study by Benjamin and others (1989) illustrated that herbaceous plants had lower AM colonization as tree density and shading increased, possibly because these plants had insufficient photosynthetic capability to support AM infection.

Soil disturbance has been reported to generally reduce AM propagule densities due to the destruction of the hyphal network during the break-up of the soil macrostructure (Reeves et al. 1979, Fairchild and Miller 1988). Consequently, one might predict that propagule densities should decrease following tree thinning due to soil disturbance from mechanized logging equipment. This effect was not observed in our study, which indicates that either soil disturbance was not severe enough to have destroyed AM fungal propagules or that the sites were rapidly colonized by AM fungal spores and residual hyphae. In addition, because sunlight and photosynthetic capacity is greater in thinned stands, herbaceous host root densities probably increased with tree removal that would allow the herbaceous plant community could support more hyphae. Rives and others (1980) also found no reduction in population densities of AM fungi following soil disturbance. It has been suggested that AM propagule densities in seasonal grasslands may be relatively tolerant of disturbance because their AM fungal communities produce high densities of perennating spores (Jasper et al. 1991).

Prescribed fire has variable affects on AM propagule densities ranging from decreased AM propagule densities (Klopatek et al. 1988, Dhillion and

Anderson 1993), to no change (Anderson and Menges 1997, Rashid et al. 1997), to increases in AM propagule densities (Bentivenga and Hetrick 1991). Similar to soil disturbance, the effect of prescribed fire on AM propagules is highly dependent on the disturbance intensity. Because fire intensity can span three orders of magnitude (Pyne et al. 1996), soil is not heated uniformly during prescribed burns and therefore soil samples from burned areas are likely to contain highly variable levels of AM fungi making the assessment of fire on AM fungi difficult. In our study, similar variance in the inoculum potential of soils from thinned-only and thinned-burned units suggest that these forests were not significantly affected by prescribed fire, which were mostly low intensity burns of short duration. Approximately 40 % of the study area was lightly burned or remained unburned following the prescribed fire and approximately 38 % was only moderately burned. In contrast, high intensity burns of long duration in slash pile burning at the Fort Valley study site significantly reduced AM propagule densities by 98 percent (Chapter 5). Simulated laboratory fires have shown that heating field soil above 80° C almost completely eliminates AM fungi (Pattinson et al. 1999). Understanding the maximum soil temperature and duration that AM fungi can withstand at different soil depths will be crucial to understanding the effects of prescribed fire on AM fungi propagule densities in southwestern ponderosa pine forest restoration.

IMPLICATIONS FOR RESTORATION

Some evidence suggests that ponderosa pine understory communities prior to the mid 1880's were dominated by warm-season (C_4) grasses, which are often strongly mycotrophic (Cooper 1960, Pearson et al. 1971, Wilson and Hartnett 1998). However, current ponderosa pine forests are dominated by species that often form no mycorrhizal associations (e.g., *Carex geophila*) or C_3 grasses that are often weakly mycotrophic (Wilson and Hartnett 1998). This community possibly became established because of suppression of natural fires that historically would minimize competition between ponderosa pine and herbaceous plants and shade-tolerant C_3 grasses are better adapted to these environments. Without the reduction of EM tree competition and reintroduction of fire, the understory of southwestern ponderosa pine forests will likely continue to be dominated by nonmycotrophic *Carex* and weakly mycotrophic C_3 grasses. Noyd and others (1995) demonstrated that strongly mycotrophic C_4 grasses, *Andropogon gerardii* (big bluestem) and *Schizachyrium scoparium* (little bluestem), were unable to grow or survive as seedlings in soil where AM fungi were eliminated, but establishment of the C_3 grass *Elymus canadensis* (Canada wild rye) was unaffected by AM fungi availability. Similarly, Hetrick and others (1994) found that C_4 grasses were competitively superior to C_3 grasses when grown in the presence of AM fungi, but C_3 grasses were competitively superior in soils without AM fungi. As a result, one can predict that increased populations of AM fungi in the thinned only and thinned and prescribed burned restoration stands may assist in the replacement of weakly mycotrophic species by strongly mycotrophic species, thereby increasing C_4 grass cover and leading to the maintenance of a stable sward of mycorrhizal compatible species (Francis and Read 1994, Johnson 1998).

Enhancing AM propagules does not always result in a favorable community as shown in a study by Marler and others (1999) where AM fungi enhanced the competitive superiority of spotted knapweed (*Centaurea maculosa* Lam.) over a native bunchgrass. In addition, our results suggest that restoration thinning may have caused a shift in the species composition of the AM fungal community at the Fort Valley study site where taxa that form abundant vesicles increased in the thinned treatments. These changes in AM species may directly influence aboveground plant community composition and structure because taxa of AM fungi differ greatly in their effects on plant fitness. Specifically, species of the Gigasporaceae family do not form vesicles and therefore an increase in vesicles could suggest a reduction in AM species of this taxon or an increase in other species that do readily form vesicles. Future studies of AM in ponderosa pine restoration areas will require analysis of the species composition of the fungal communities to determine if a shift in the fungal community is occurring in response to restoration treatments and whether these shifts impact the plant community composition.

Recent research in a variety of environments has shown that mycorrhizal interactions may be important determinants of plant diversity, ecosystem variability, and productivity (Hartnett and Wilson 1999, van der Heijden et al. 1998a, van der Heijden et al. 1998b, and Klironomos et al. 2000). Host plant species composition influences AM fungal species composition (Johnson et al. 1992, Bever et al. 1996, Eom et al 2000), which provides evidence for current feedback models between soil communities and plant community structure (Bever et al. 1997). Future studies of ponderosa pine restoration treatment areas are needed to more fully understand responses of AM fungal communities and assess feedbacks between AM fungal and plant communities. Our results indicate that AM propagule densities respond rapidly to thinning and prescribed burning in southwestern ponderosa pine restoration treatments. This has important implications for land managers trying to restore the herbaceous understory of these forests because most understory plants depend upon AM associations for normal growth.

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Table 4.1 Vegetation and site characteristics for the Ft. Valley control and thinned units for pretreatment 1998 data and post treatment 2000 data. Data are expressed as means (N=2) ± SE.

	Pretreatment 1998		Post treatment 2000	
Variable	Control Stand	Treatment Stand	Control Stand	Treatment Stand
trees/hectare	1415.1 ± 392	1162 ± 141.4	1426.2 ± 330 a	182.3 ± 34 b
tree canopy cover (%)	62.37 ± 5.5	57.61 ± 3.8	61.03 ± 4.41 a	34 ± 2.95 b
herbaceous cover (%)	9.67 ± 1.92	9.23 ± 1.2	9.06 ± 1.76	11.22 ± 1.4
Simpson's diversity index	2.92 ± .44	2.89 ± .38	2.88 ± .62	3.61 ± .46
litter load (kg/ha)	14211.5 ± 1508.04	14133.76 ± 1980.12	14363.7 ± 1508.04	15625.13 ± 2598.97
duff load (kg/ha)	25127.12 ± 2006.04	25338.22 ± 3266.01	25836.25 ± 3103.27	26379.49 ± 3266.01

Values indexed by a different letter are significantly different at the $p \leq 0.05$ level between paired control and treatment units for the same sampling year.

Table 4.2 Vegetation and site characteristics for the Mt. Trumbull control and thinned/prescribed burned units for pretreatment 1999 data and post treatment 2000 data. Data are expressed as means (N=4) ± SE.

	Pretreatment 1998		Post treatment 2000	
Variable	Control Stand	Treatment Stand	Control Stand	Treatment Stand
trees/hectare	2128.47 ± 700.9	1866.67 ± 786.1	2193.1 ± 355 a	336.3 ± 119 b
tree canopy cover (%)	58.96 ± 5.8	53.15 ± 6.98	61.51 ± 5.73 a	33.49 ± 7.1 b
herbaceous cover (%)	6.54 ± 1.32	6.21 ± 1.52	6.13 ± 1.94	10.61 ± 5.26
Simpson's diversity index	2.26 ± .32	2.31 ± .26	2.43 ± .24	2.33 ± .43
litter load (kg/ha)	13873.7 ± 1204.34	13655.83 ± 1866.04	13500.23 ± 1991.9 a	6169.03 ± 2393.47 b
duff load (kg/ha)	229855.6 ± 2877.57	23034.1 ± 3146.52	23239.7 ± 218.77 a	10100.63 ± 1760.77 b

Values indexed by a different letter are significantly different at the $p \leq 0.05$ level between paired control and treatment units for the same sampling year.

Table 4.3 Mean substrate burn severity for Mt. Trumbull thinned/prescribed burned units. Lightly burned areas had charred litter and duff, moderately burned areas had litter and duff mostly consumed, and severely burned areas have litter and duff consumed leaving white ash. N=4 ± SE, 10 replicates in each block.

Severity Level	Mean (in percent)
Not Applicable (Rock)	4.6 ± 3.18
Not Burned	16.4 ± 7.77
Lightly Burned	19.4 ± 7.66
Moderately Burned	37.8 ± 11.15
Severely Burned	21.0 ± 5.35

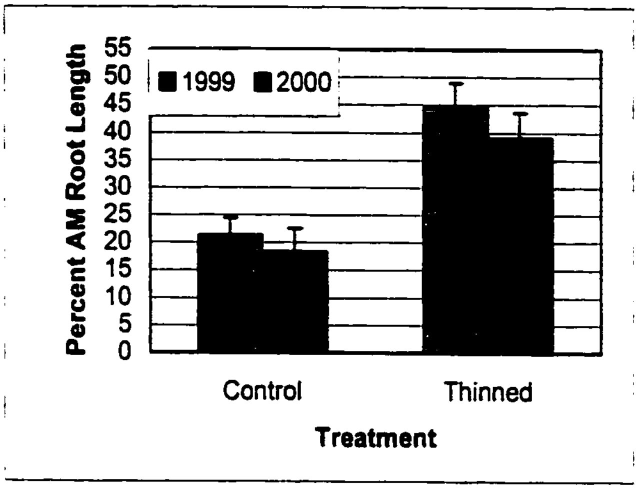
Table 4.4 Post treatment soil characteristics (pH, Organic C, Total N, Total P) for the Ft. Valley control and thinned units and the Mt. Trumbull control and thinned/prescribed burned units in 2000. Data are expressed as means (N=2) ± SE at Ft. Valley, (N=4) ± SE at Mt. Trumbull, 10 replicates in each block.

	Fort Valley		Mt. Trumbull	
Variable	CT	T	CTB	TB
pH	5.74 ± .11	5.7 ± .11	6.4 ± .02	6.40±.07
C (% loss on ignition)	8.81 ± .63	10.75 ± 1.19	0.97 ± 1.05	12.03 ± 1.43
Total N (mg/Ng)	1.38 ± .1	1.61 ± .16	2.04 ± .17	2.27 ± .31
Total P (mg/Pg)	0.93 ± .05	0.91 ± .03	1.20 ± .14	1.47 ± .20

Treatments were: control for Ft. Valley thinned units (CT), Ft. Valley thinned units (T), Mt. Trumbull control for thinned/prescribed burned units (CTB), and Mt. Trumbull thinned/prescribed burned units (TB).

Table 4.5 Multiple regression analysis results for AM and EM infectivity and plant community characteristics for the six Ft. Valley study units and eight Mt. Trumbull study units combined.

Dependent variable and predictors	Coefficient	t	P	R^2	df	F	P
Multiple regressions							
AM infectivity				0.853	4,13	13.12	.0009
Constant	7.17	0.38	0.715				
Sqrt graminoid cover	15.53	3.05	0.014				
Species richness	-3.81	-1.28	0.231				
Tree canopy cover	-0.34	-2.5	0.034				
Litter cover	0.30	1.12	0.291				
EM infectivity				0.029	3,10	0.101	0.9573
Constant	30.89	3.26	0.008				
Trees/hectare	.0004	0.18	0.861				
Tree canopy cover	-0.054	-0.46	0.655				
Litter cover	0.0804	0.52	0.617				



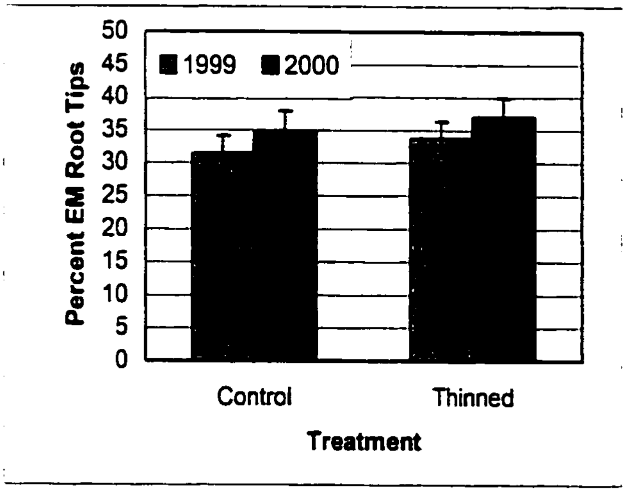
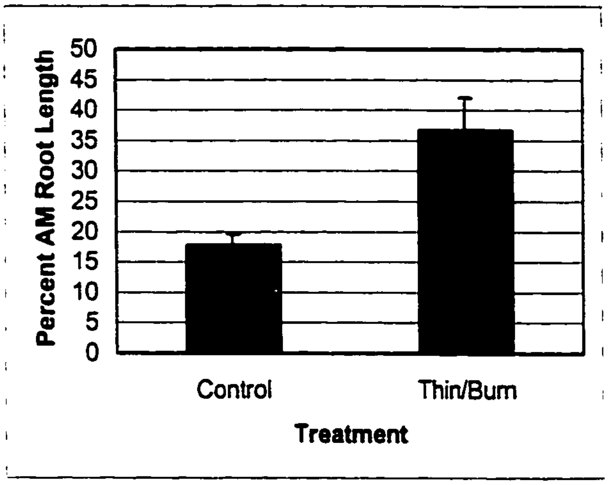


Figure 4.1a-b. The relative amount of mycorrhizal propagules indicated by (**a**) percent AM colonized root length in corn and (**b**) EM root tips in ponderosa pine from bait-plant bioassays from the Ft. Valley thinned only and paired control units in 1999, six months after thinning and 2000, eighteen months after thinning. Differences between the units were determined by MANOVA repeated measures on arcsin square root transformed data.



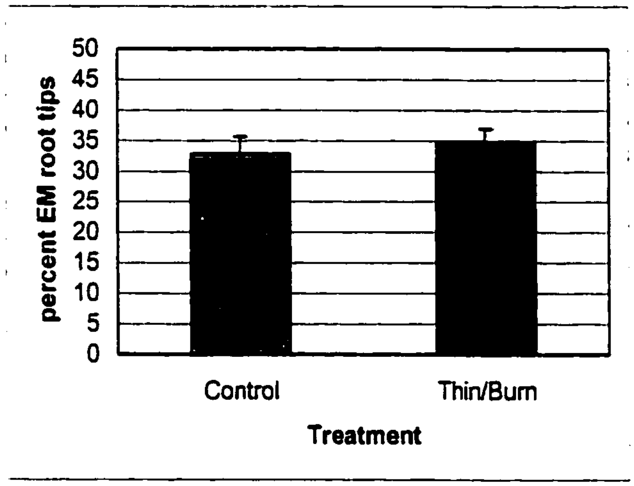


Figure 4.2a-b. The relative amount of mycorrhizal propagules indicated by (**a**) percent AM colonized root length in corn and (**b**) EM root tips in ponderosa pine from bait-plant bioassays from the Mt. Trumbull thinned and prescribed burned and paired control units for 2000, five months after thinning and three months after burning. Differences between the units were determined by ANOVA on arcsin square root transformed data.

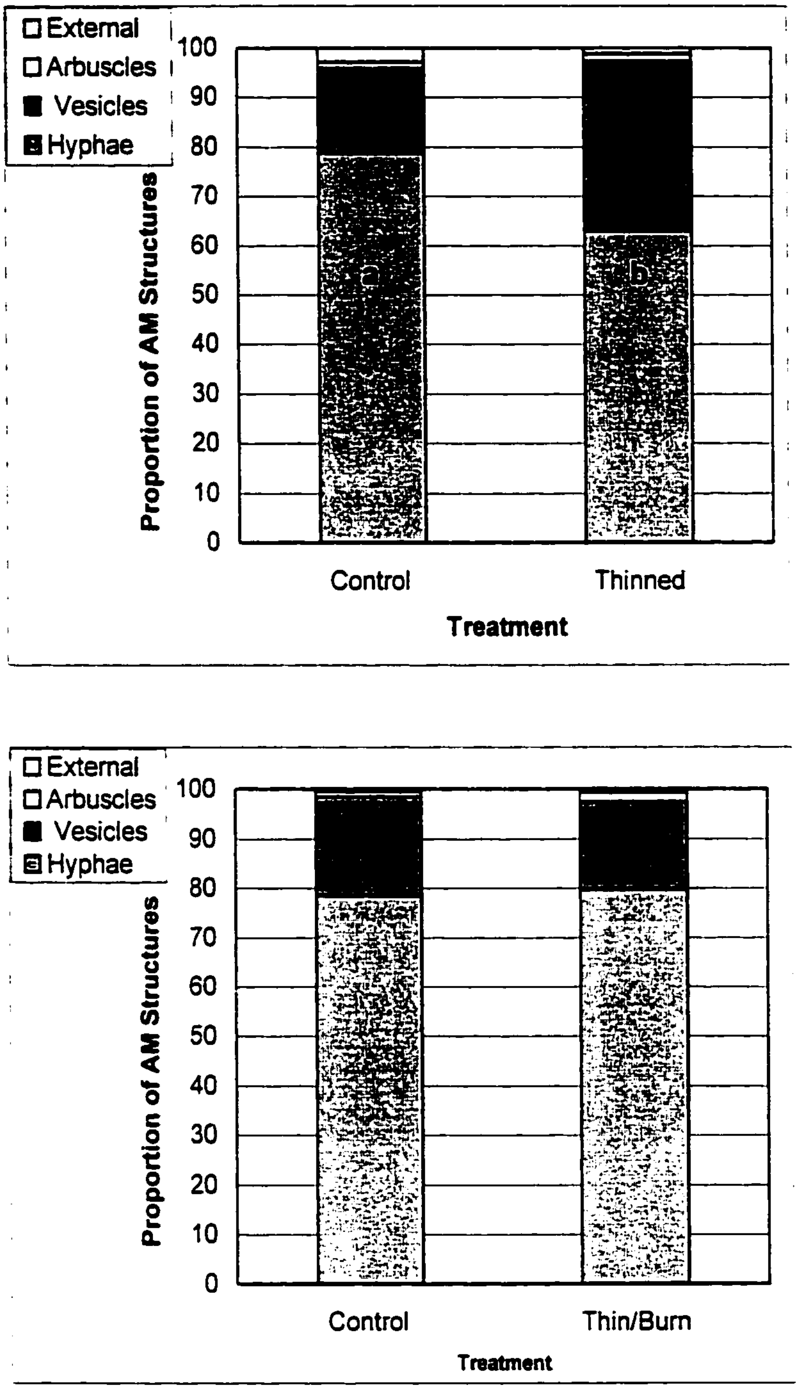


Figure 4.3a-b. The proportion of different AM fungal structures within colonized corn roots grown in soils collected from (**a**) the Ft. Valley thinned only and paired control units and (**b**) the Mt. Trumbull thinned and prescribed burned and pair control units. Values indexed by different letters are significantly different at the p[0.05 between treatments.

CHAPTER 5

THE EFFECTS OF SLASH PILE BURNING ON SOIL ABIOTIC AND BIOTIC PROPERTIES AND NATIVE PLANT ESTABLISHMENT

ABSTRACT

Thinning dense forest stands creates tremendous quantities of slash. Burning slash piles is a preferred method of slash removal because it allows land managers to burn large quantities of slash under more controlled conditions than broadcast burning. However, burning slash piles can have adverse effects such as soil sterilization and enhanced establishment of exotic plants. This study investigated the effects of slash pile burning on soil abiotic and biotic variables and plant establishment on burned slash pile scars. Slash piles were created following tree thinning in two adjacent ~16-ha ponderosa pine (*Pinus ponderosa*) restoration treatments in the Coconino National Forest near Flagstaff, Arizona. Ponderosa pine forest restoration consists of thinning trees and prescribed fire to reduce unnaturally high tree densities and fuel loads in order to restore ecosystem structure and function. We selected thirty slash pile scars and measured arbuscular mycorrhizal (AM) propagule densities, the soil seed bank, and soil physical and chemical properties along a fire intensity gradient across each burned slash pile scar. In addition, we established five 1-m^2 plots in each slash pile scar to quantify the effect of soil and seeding amendments on herbaceous plant growth and AM propagule densities. The five treatments consisted of a control (no treatment), soil amendment (AM propagules), sterilized soil amendment (no AM propagules), seed amendment, and a seed/soil amendment (both plant and AM propagules). Without amendments, the relative amount of AM fungal propagule densities, number of viable seeds in the soil seed bank, and extant vegetation was significantly lower and soil properties were significantly different outside than inside slash pile scars. Seed/soil amendments had significantly higher cover of native forb and graminoid species in comparison to the other treatments. In addition, the seed/soil treatments had higher plant density, cover, and height than the seed only treatments. These results illustrate that adding both seed and living soil to slash pile scars can increase cover of desirable native forbs and grass.

INTRODUCTION

Southwestern ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests prior to Euro-American settlement were dominated by open stands of large old-growth trees intermixed with grassy meadows. Low intensity fires carried by grassy understories recurred every 2-20 years in southwestern ponderosa pine ecosystems and played a major role in determining the structure, composition, and stability of these ecosystems (Cooper 1960). These frequent, low-intensity fires, along with grass competition, controlled ponderosa pine regeneration and maintained the open, park-like structure of presettlement ponderosa pine stands (Harrington and Sackett 1990). Heavy livestock grazing, intensive logging of old-growth trees, and fire suppression following Euro-American settlement resulted in dense forests consisting of numerous small trees, along with other structural and functional changes to the ecosystem (Covington et al. 1997). Ponderosa pine restoration aims to restore ecosystem structure and function primarily through tree thinning and prescribed fire.

A major dilemma in ponderosa pine restoration is the disposal of the slash (tree crowns, bole tips, small boles) created during tree thinning (Brown et al. 1977). Currently, three different slash removal methods are used in restoration of forests near Flagstaff, Arizona. The first method is associated with whole-tree harvesting. Large piles of unmarketable small diameter trees and slash are concentrated in piles along roads and burned under appropriate weather conditions. Land managers currently prefer this method because it reduces harvest-created fire hazards, burns more efficiently with less smoke, and allows burning under broader weather conditions (Hardy 1996). The second and third slash removal methods are associated with harvesting using a feller-buncher. The second method disperses small diameter trees and slash across the thinned area and burns the entire area under appropriate weather conditions in spring or fall. The third method is a combination of the first two methods and consists of dispersing the small slash and piling the large slash.

The importance of arbuscular mycorrhizae (AM) fungi in plant community composition and structure has received increasing recognition over the past few years (Gange et al. 1993, Hartnett and Wilson 1999, Jordan et al 2000). Studies show AM propagule densities are significantly reduced in severely disturbed soil (Reeves et al. 1979, Jasper et al.1989). Similarly, AM fungi colonization (Schenck et al. 1975, Pattinson et al. 1999), spore densities, and species richness are reduced (Dhillon et al. 1988, Gibson and Hetrick 1988) in severely burned areas. These mutualistic fungi can improve plant establishment, nutrient uptake, drought tolerance, and protection from plant pathogens, and they may be necessary for reestablishing vegetation in severely disturbed soil environments (Gould et al. 1996). Consequently, to increase the establishment of native grasses and forbs in slash pile scars where AM fungi have been significantly reduced or eliminated it may be necessary to reinoculate AM fungi with unburned soil that contains viable AM propagules. In addition, a seed amendment may be necessary to increase the availability of viable native seeds due to seed destruction by fire.

We hypothesized that severely burned slash pile scars would have significantly reduced propagule densities of plants and AM fungi as well as altered soil physical and chemical properties. In addition, we hypothesized that soil amendments containing viable AM propagules and seed amendments would increase the establishment of native plants in severely burned slash pile scars in southwestern ponderosa pine forests. The specific objectives of this study were to: 1) determine the effect of slash pile burning on densities of plant and AM fungal propagules and soil physical and chemical properties; and 2) determine the effect of soil and seed amendments on the rate of native herbaceous plant establishment within burned slash pile scars.

METHODS

Experimental Design

This research was conducted on the Coconino National Forest near Flagstaff, Arizona, at 2250 m elevation in two adjacent ~16 hectare units that were treated in the winter of 1999 with tree thinning and broadcast prescribed fire in the spring of 2000. Piles of slash were created during tree thinning treatments and were burned in February 2000. Over 50 slash piles (averaging 9 m in diameter and 3-4 m tall) were created from the thinning treatments. Estimated total fuel mass consumed for each slash pile averaged between 1.5 and 3.5 tons (Hardy 1996). We randomly chose 30 slash piles of similar size to minimize variation in fire severity among piles.

The vegetation at the study site consisted of pure ponderosa pine stands, with few large trees intermixed with numerous small trees. Perennial grasses such as squirreltail (*Elymus elymoides* (Rafinesque) Swezey), mountain muhly (*Muhlenbergia montana* Nuttall), and numerous forbs dominated the understory. Soils are moderately well-drained clays and clay loams of volcanic origin (Covington et al. 1997). Annual precipitation ranges from 43 to 64 cm with an average of 50 cm in the Flagstaff area (Shubert 1974). Precipitation patterns include scattered snowfall and rain during the winter months, a pronounced drought in May and June, followed by frequent monsoon rains in July and August (Vose and White 1991). Daily mean temperatures range from -5° C to 17° C (Sackett 1980).

Field Sampling

Fire Intensity Gradient

We established a 6 m transect across each of the 30 slash pile scars. We assumed that these transects represent fire intensity gradients with gradient sampling points 3 m inside the pile (hottest), 1.5 m inside the pile, the pile edge, and 3 m outside the pile (coolest), running due north from a random starting location along the scar edge (Figure 1a). We collected soil samples along each transect in May 2000 (three months after burning) and May 2001 (fifteen months after burning). Soils were collected to a depth of 15 cm using a hand trowel. We took samples to this depth because AM fungal propagule densities are generally highest in the surface 15 cm (Smith and Walker 1981). Soil samples were immediately placed into 4 cm diameter x 20 cm deep Conetainers (Stuewe and Sons, Inc., Corvallis, Oregon USA) for bait-plant bioassays (Brundrett and Abbott 1994).

In addition, in May 2000, soil samples were taken along the transect using a 5 cm diameter metal core to a depth of 5 cm. Soil seed bank cores were placed on top of 2 cm of sterilized soil in 11 x 11 cm plastic containers in an un-heated greenhouse and watered daily by an automatic mist system for 4 months. Species that emerged were identified, counted, and removed. In addition, sterilized soil was placed in plastic containers without seed bank cores to determine if there was any greenhouse contamination. Soil samples for physical and chemical soil analyses were taken to a depth of 10 cm using a hand trowel, and frozen until analysis.

Seed/Soil Amendments

Five 1-m^2 (.05 m x 2 m) plots were randomly located within each slash pile scar at least 1 meter from the scar edge and at least one meter from each other and were randomly assigned one of five treatments: no treatment (a control), a soil amendment (AM propagules), a sterilized soil amendment (no AM propagules), a seed amendment, or a seed/soil (plant and AM propagules) amendment (Figure 1b). Soil for the soil amendment and sterilized soil amendment was collected from topsoil that was stockpiled from road construction in a nearby restoration thinning treatment unit. In a previous study, we determined that AM propagule densities at this site were relatively high using a corn bait plant bioassay. Approximately 40 percent of the root length of assayed corn was colonized with AM fungi (Chapter 4). This soil was used as our soil AM inoculum. Soil taken from the same location was steam sterilized for 48 hours to create a soil amendment without AM fungi but with the same physical properties as the AM inoculum soil amendment. Twenty thousand cm^3 of soil was added to each 1-m^2 plot soil treatment, resulting in an average soil depth of 2 cm across the plot. During the collection of the soil for the soil amendment treatments in June 2000 we took twenty soil cores to quantify the soil the seed bank using the same procedures described earlier in the text.

In May 2001, soil samples were taken from the experimental plots in each slash pile scar to quantify AM propagule densities using bait plant bioassays, fifteen months following burning and eleven months after soil amendments were added to the slash pile scars. Soil samples were taken to a depth of 15 cm using a hand trowel.

Seeding amendments consisted of native grass and forb species that were abundant in the extant vegetation surrounding the slash pile scars (Table 1). Seeds were purchased from the nearest regional source that had available seed: Colorado Native Seed in Salida, Colorado. To ensure the purity of the seed, we grew seed out in a greenhouse and in the field and found no seed impurity. We sowed 8.4 grams of grass seed and 2.8 grams of forb seed to each 1-m^2 seeding treatment, representing equal proportions of grasses and forbs by weight. Seeds were added in early July 2000, five months after burning, to coincide with the monsoon rains in late summer and mimic treatments that would be implemented by land managers (e.g., no supplemental water was added). In September 2000, seven months after the piles were burned and in September 2001, nineteen months after the piles were burned, all seedlings and mature plants in each of the five 1-m^2 plots were identified and counted for all thirty slash pile scars. In addition, the cover of each individual species was determined using the ocular estimate method to the nearest 10th of a percent, individual plants were noted for their phenological stage (e.g., rosette, flower, or seed) and the average height for each individual plant was recorded.

Lab Analysis

We used a corn (*Zea mays*) bioassay to determine the relative amount of infective propagules of AM fungi. Corn is mycotrophic with many species of AM fungi and grows rapidly and uniformly; these advantages outweigh the disadvantage of not using native host plants (Johnson et al. 1999). Bait-plant bioassays are designed to detect all types of viable mycorrhizal fungal propagules including spores, fragments of mycorrhizal roots and extraradical hyphae, and therefore may more accurately quantify total mycorrhizal fungi than direct counts of sporocarps, spores, or colonized root lengths (Brundrett et al. 1994, Johnson et al. 1999). Corn plants were placed in a greenhouse and watered every 3 days until they were harvested at 6 weeks. Corn roots were prepared for AM analysis by cutting roots into 2.5 cm segments, taking a random subsample of the cut roots of a known mass, clearing roots in 5 percent KOH, and then staining roots with trypan blue in lactoglycerin (Koske and Gemma 1990). The gridline intersect method using a dissecting microscope was used to measure the proportion of root length containing AM fungal structures: arbuscules, vesicles, coils, internal mycorrhizal hyphae and external mycorrhizal hyphae (Giovannetti and Mosse 1980).

Soil Analysis

Soil samples from each slash pile gradient transect were analyzed for pH, total N, total P and organic C at the Bilby Research Soil Analysis Laboratory, Flagstaff, Arizona. Soil pH was determined in a 1:1 slurry by pH meter. Total N and P were measured using a Kjeldahl digestion of the soil material followed with the analysis of N and P by automated colorimetry using a Technicon auto-analyzer (Parkinson et al 1975). Organic C was determined by loss on ignition. Samples were heated in crucibles for 24 hours in a muffle furnace at 425° C and organic matter was estimated from net weight loss.

Statistical Analysis

We used multivariate analysis of variance (MANOVA) repeated measures in SPSS version 8 (SAS Institute 1997) to determine the effect of slash pile burning on AM propagule densities and seed/soil amendment plant community variables for data collected in 2000 and 2001. We used analysis of variance (ANOVA) to determine the effect of slash pile burning on the soil seed bank and soil chemical properties for data collected in 2000. The ShapiroWilk test was used to test data for normality, and Leven's test was used to test for homogeneity of the variance (Milliken and Johnson 1984). Prior to analysis, root infection data were arcsin square root transformed, soil seed bank densities and some individual seeded species variables were log (x+1) transformed, and soil properties were square root transformed to improve normality and homoscedasticity assumptions (Zar 1984). Tukey's Honestly Significant Difference (HSD) test was used to make multiple comparisons of means following a significant ANOVA result.

RESULTS

Fire Intensity Gradient

Mycorrhizal fungi did not colonize all bait-plants. Bait-plants grown in soils collected from 3 m and 1.5 m inside the slash pile scar had significantly lower densities of AM propagules than samples from the scar edge and 3 m outside the scar three and fifteen months following burning (Figure 5.1). Infective propagule densities of AM fungi were also significantly lowered at the scar edge in comparison to 3 m outside the slash pile scar for this same time period. There was a significant increase in infective propagule densities of AM fungi between three and fifteen months after burning at the scar edge and 3 m outside the scar with no significant change between the two sampling periods at 1.5 m and 3 m inside the slash pile scar (Figure 5.2).

There were significantly more exotic and ruderal (native species that prefer disturbed habitats) seeds/m^2 at 3 m outside the pile than 3 m inside the scar or at the scar edge three months after burning (Figure 5.3). Sixty-eight percent of the seeds/m^2 at 3 m outside the scar were exotic, 26 percent were ruderal and only 6 percent were non-ruderal natives. Mullein (*Verbascum thapsus* L.), an early successional species of disturbed habitats, dominated the exotic seed bank 3 m outside the pile with 368 seeds/m^2. Dalmation toadflax (*Linaria dalmatica* (L.) P. Mill.) made up the remaining exotic seed bank with 45 seeds/m^2. The most dominant ruderals included pineland marshtail (*Laennecia schiedeana* (Less.) Nesom) and spreading fleabane (*Erigeron divergens* Torrey & Gray). The most common natives were *Carex* spp. and *Muhlenbergia montana*.

Changes in physical and chemical soil properties were evident three months following burning along the fire intensity gradient. Soil pH was significantly lower 3 m outside the scar in comparison to the scar edge and 3 m inside the scar (Figure 5.4a). In contrast, total N and organic C were significantly higher 3 m outside the scar in comparison to the scar edge and 3 m inside the scar (Figures 5.4b-c). There was no significant difference in total P between any of the locations along the fire intensity gradient (Figure 5.4d).

Seed/Soil Amendments

Soil samples from the control plots and those treated with sterilized soil amendment had significantly lower infective propagule densities of AM fungi than samples from the seed/soil amendments fifteen months following burning and eleven months after soil amendments were added to the slash pile scars

(Figure 5.5). AM hyphal colonization in the seed/soil amendments was more abundant than AM colonization by vesicles or arbuscules (Figure 5.4). The soil seed bank of the soil amendments had on average 256 seeds/m^2. The most abundant species in the seed bank was *Carex* spp. Other abundant species included: *Muhlenbergia montana, Verbascum thapsus* and *Laennecia schiedeana.*

Seedlings established only in the seed amendment and seed/soil amendments during the first growing season seven months after burning and two months after seeding. Only native forb and graminoid seeded species established with no natural regeneration of ruderals or exotics. There was significantly higher plant cover of forbs and graminoids in the seed/soil amendments than the seed amendments two months after seeding (Figure 5.5a and 5.5b).

During the second growing season in 2001 there was no significant difference in exotic plant cover between any of the amendment treatments, but the seed/soil amendments had the lowest exotic cover (Figure 5.6a). The most abundant exotic species was *Verbascum thapsus*. Other exotic species included bull thistle (*Cirsium vulgare* (Savi) Tenore), amaranth (*Amaranthus albus* L.), and *Linaria dalmatica.* During the 2001 growing season, ruderal species had significantly higher plant cover in the control, soil amendment, and sterile soil amendment treatments than the seed or the seed/soil amendment treatments (Figure 5.6b). The most abundant ruderal species was *Laennecia schiedeana,* an early colonizing biennial cudweed. There was no significant difference in native forb or graminoid plant cover in 2001 for the control, sterilized soil amendment or soil amendment treatments (Figures 5.6c-d). The seed amendments had significantly higher native forb and graminoid cover than the control, sterilized soil amendment, and soil amendment treatments but had significantly less native forb and graminoid cover in comparison to the seed/soil amendments (Figures 5.6c-d).

Seventeen species flowered the second growing season, in 2001. *Elymus elymoides* was the most abundant flowering species followed by showy goldeneye (*Heliomeris multiflora* Nuttall), spike muhly (*Muhlenbergia wrightii* Vasey), and blue grama (*Bouteloua gracilis* Humboldt). The seed/soil amendments had the highest total number of flowering individuals (41) followed by the seed amendments (27), soil amendments (17), sterile soil amendments (8), and the controls (6). Three non-native species flowered in the control, sterilized soil, or soil amendments: *Verbascum thapsus*, *Linaria dalmatica*, and *Amaranthus albus*.

Individual Seeded Species

Three seeded graminoid species, junegrass (*Koeleria macrantha* (Ledebour) Schultes), muttongrass (*Poa fendleriana* (Stuedel) Vasey), and little bluestem (*Schizachyrium scoparium* (Michaux) Nash) did not germinate in any of the seeded amendments during the 2000 or 2001 growing seasons (Table 5.1). In addition, two seeded forb species, narrow leaf paintbrush (*Castilleja linariifolia* Benthem) and prairie smoke (*Geum trifolium* Pursh) did not germinate in any of the seeded amendments for either growing season (Table 5.1). Nine species in 2000 and 13 species in 2001 established as seedlings or mature plants in the seed amendments. In the seed/soil amendments, 10 species in 2000 and 14 species in 2001 established as seedlings or mature plants. Species that did not germinate in the first growing season but did germinate during the second growing season included: scarlet bugler (*Penstemon barbatus* (Cavanilles) Roth), wand penstemon (*Penstemon virgatus*), foothills golden banner (*Thermopsis divaricarpa* Nelson), and Rocky Mountain iris (*Iris missouriensis* Nuttall). Eight of the nine seeded species that were established in 2000 in the seed amendments increased their average cover and height. Three of these species significantly increased their average cover and four species significantly increased their average height by 2001 (Table 5.2). Nine of the ten seeded species that were established in 2000 in the seed/soil amendments increased their average cover and average height. Five of these species significantly increased their cover and their average height (Table 5.3). In contrast, five seeded species significantly decreased in density in the seed/soil amendments and only one species increased in density (Table 5.3). *Lupinus argenteus* showed almost no change in plant cover and only a small height increase between the two growing seasons in both the seed and seed/soil amendments (Tables 5.2 and 5.3). *Elymus elymoides* and scarlet gilia (*Ipomopsis aggregata* Pursh) had the highest average density, cover and height in both the seed and seed/soil amendments, but these values were significantly higher in the seed/soil amendments (Tables 5.2 and 5.3).

DISCUSSION

Fire Intensity Gradient

Biotic and abiotic changes that occurred in the slash pile scars are consistent with numerous other studies that have measured changes in severely burned areas (DeBano et al. 1979, Dickinson and Kirkpatrick 1987, Moreno and Oechel 1991). Fire severity depends on burning intensity, burning duration, fuel loading, vegetation type, fire climate, soil texture and moisture, and organic matter (Neary et al. 1999) and can be qualitatively assessed following a burn based upon litter, duff, and wood consumption (NPS 1992). All of the slash pile scars in this study had litter and duff consumed, leaving white ash with often reddish soil that is characteristic of severely burned areas (NPS 1992). When duff layers ignite, large amounts of heat can be transferred to the soil with temperatures above 350° C for several hours (DeBano et al. 1998). In addition, ash created from glowing combustion retards heat dissipation upwards, causing more heat to penetrate the soil (Sackett and Haase 1994). Soil surface maximum temperatures in heavy slash burns are usually around 500-700° C (Rundel 1983). Temperatures at 10 cm in mineral soil can reach over 250° C and temperatures at 22 cm in mineral soil can reach over 100° C during heavy slash burns (Roberts 1965).

Arbuscular Mycorrhizae

Slash pile burning significantly reduced AM fungal propagule densities for the fifteen months monitored in this study. This result is consistent with other studies that have shown large declines in AM propagule densities following severe burning (Berch et al. 1993). A study by Klopatek and others (1988) found that soil temperatures of 80-90° C reduced AM fungal propagule densities between 30-40 percent in wet soils and between 50-85 percent in dry soils. Temperatures over 94° C resulted in a near total loss of AM propagules (Klopakek et al. 1988). AM hyphae are abundant in the litter and duff horizon and the complete consumption of this horizon during severe burning may directly result in the large decline of ting (St. John et al. 1983). In addition, AM hyphae in the soil may be more susceptible to high temperatures than AM hyphae protected in roots (Pattinson et al. 1999). In our study the litter and duff horizon was completely consumed, which may explain the low presence of AM fungi in the burned slash pile scars.

A rapid recolonization of AM fungi was evident fifteen months following the burn at the scar edge and 3-m outside the scar where physical soil disturbance most likely initially resulted in low AM fungal propagule densities. Other studies have shown increased AM mycorrhizal activity following low intensity burning where AM hyphae most likely survived in the roots of nearby plants (Rashid et al. 1997) or as propagules deeper in the soil profile where soil heating was not severe (Pattinson et al.1999). In addition, AM propagule densities at the same study site showed rapid increases within months of the initial tree thinning treatment, which is consistent with these results of rapid recolonization following low severity disturbance (Korb et al. in press).

Soil Seed Bank

Viable seeds in the soil seed bank were almost completely consumed in the slash pile scar and at the scar edge during burning. The majority of the viable seeds at this study site are located in the top 5 cm of mineral soil and in the litter/duff horizon (Korb et al. 2000). The complete consumption of the litter and duff horizon along with soil heating due to the severity of the burn are most likely responsible for the low number of viable seeds in the soil (Moore and Wein 1977). Studies in other ecosystems with severe burning have also shown low numbers of viable seeds following burning (Hassan and West 1986, Zammit and Zedler 1988, Schimmel and Granström 1996). Odion and Davis (2000) showed that excessive heat killed viable seeds and that there was a significant positive relationship between increasing maximum surface temperature during burning and seed mortality. Other explanations for the low number of viable seeds in the soil could be due to spatial distribution of seeds both horizontally (seeds are normally clustered) and vertically (seeds could be too deep to germinate or too deep to emerge if they do germinate) (Odion and Davis 2000).

Soil Properties

Soil physical and chemical properties exhibited changes in the slash pile scars. Soil pH values were significantly higher 3 m in the slash pile scar and at the scar edge than 3 m outside scar, a result that is consistent with other studies of slash pile burning (Fuller et al. 1955, Ballard 2000). Soil pH generally increases following burning due to hydrolysis of base cation oxides that are abundant in ash following severe burns (Ballard 2000). In contrast, total nitrogen was significantly lower 3 m in the slash pile scar and at the scar edge than 3 m outside of the scar, which is consistent with results from a slash pile burn study that occurred near our study area (Klemmedson 1976). Total nitrogen has been shown to either decrease (Baird et al. 1999, Ellingson et al. 2000) or increase (Covington et al. 1991) following burning. A decrease in total nitrogen following burning indicates that soil temperatures during burning volatilized nitrogen at the soil surface (Ellingson et al. 2000). Nitrogen begins to volatize at temperatures of 200° C and over half of the nitrogen present in the organic matter can be lost at temperatures over 500° C (Weast 1988). Numerous studies have shown that while total nitrogen may decrease with burning, ammonium-nitrogen (NH_4-N) immediately increases due to pyrolysis of forest floor material and nitrate-nitrogen (NO_3-N) increases usually a year following burning due to nitrification of the high NH_4-N produced after burning (Covington et al. 1991, Covington and Sackett 1992, Ellingson et al. 2000). Organic C was also significantly lower 3 m in the slash pile scar and at the scar edge than 3 m outside the scar, which is congruent with another slash pile burn study where soil organic matter decreased with severe burning (Roberts 1965). In severely burned areas aboveground organic matter is completely ashed or significantly reduced. The location of the majority of organic matter pools in the ecosystem (either above- or belowground) will influence how susceptible the system is to organic matter and nutrient losses in response to fire (Neary et al. 1999). Total phosphorus showed no significant difference in response to burning. Ninety-four to ninety-eight percent of the main phosphorus source is located in the soil and not in the litter layer and therefore phosphorus does not respond to severe burning in the same way that nitrogen does (Neary et al. 1999).

Seed/Soil Amendments

The size and severity of a disturbance influences the character of the seedling environment and the type of species that are able to establish in the disturbed environment (Pickett et al. 1987, Chambers et al. 1990). Severe disturbance is often cited as an important precursor to exotic species invasions (Symstad 2000). Severely burned slash piles either remain unvegetated (Covington et al. 1991) or are invaded by exotic aggressive species with little presence of native species for numerous years following burning (Dickinson and Kirkpatrick 1987). Some studies have shown that native plant recolonization following fire is greatly influenced by AM fungi and seed availability (Martin et al. 1975, Klopatek et al. 1988). In our study, AM fungal propagule densities and the soil seed bank were severely reduced or eliminated following slash pile burning. As a result, we were interested in identifying restoration treatments that would encourage native plant establishment and discourage exotic plant establishment. Seed/soil amendments promoted the highest species richness and abundance of native plant establishment on severely burned slash pile scars and the lowest species richness and abundance of exotic and ruderal plant establishment. Direct seeding amendments on ash were also successful at native plant establishment but had lower native species richness and less than half the native plant cover of the seed/soil amendments. The control, sterilized soil amendment, and soil amendment treatments had very low native species richness and plant cover and higher exotic plant cover than the other amendment treatments.

Arbuscular Mycorrhizae

AM fungal propagule densities were significantly higher in the seed/soil amendments than the sterilized soil amendment or control treatments fifteen months following burning and eleven months following soil amendment treatments. Congruent with our results, numerous studies have shown that AM fungi propagule densities will remain low in severely disturbed soil environments unless efforts are made to restore topsoil to the surface (Reeves et al. 1979, Rives et al. 1980, Gould et al. 1996). The increased availability of AM fungi from the soil (AM propagule) amendments along with native seed amendments may be responsible for the higher native plant abundance found in the seed/soil amendments than that found in the other amendment treatments. Other studies have found that AM fungi can promote the establishment of native plant cover in disturbed habitats (Grime et al. 1987, Gange et al. 1990, Smith et al.1998). Investigating the effect of seeding and AM inoculum on plant establishment in tallgrass prairies, Smith and others (1998) found that placing AM inoculum directly under native plant seeds significantly increased AM fungal colonization and plant cover of native seeded prairie species. Hartnett and others (1994) found that AM fungi had varying results on seedling germination and establishment depending on the individual species. For example, AM fungi increased C_3 seedling emergence but had no effect on C_4 seedling emergence (Hartnett et al. 1994). In addition, AM fungi increased flowering of C_4 grasses in burned prairies but had no effect in unburned prairies, suggesting that soil warming and increased nutrient release from burning may be more beneficial to plants grown in soil with AM fungi than without (Hartnett et al. 1994). In our study we had higher seedling emergence of both C_3 and C_4 grasses in the seed/soil (AM propagules) amendment treatments than seeding on the ash (no AM propagules) or the sterilized soil amendment treatments.

Soil Seed Bank

The soil used in our soil amendment treatments had relatively low numbers of viable seeds/m^2 in comparison to other seed bank studies (Pratt et al. 1984, Baskin and Baskin 1998). The soil amendment treatments did not have any seedlings three months after they were established and had low exotic and ruderal cover and even less native grass and forb cover fifteen months after they were established, indicating that adding soil alone without a seed amendment does not increase the rate of native plant establishment in severely burned areas through viable seeds in the soil seed bank. *Verbascum thapsus* and *Laennecia schiedeana* both were found in the soil seed bank and as established plants in the soil amendment treatments. These plants may have established from viable seed in the soil seed bank or the seeds of these two species could have blown in from nearby seeding plants during the first growing season that surrounded the burned slash pile areas (Korb, personal observation).

Seeding/Individual Species

More seeds germinated, established as mature plants, grew taller, had more cover, and were more likely to reproduce in the treatments that included living soil than those without soil. This difference may be the result of the large amount of ash that is commonly found in severely burned areas that may cause salinity and high osmotic values that can prevent seed imbibition and germination (Kutiel and Naveh 1987). Some seeded species failed to germinate. Germination requirements are usually only met for a short time frame in the field, especially in semi-arid environments where water availability is restricted to certain months of the year. In our study, the combined soil water and temperature requirements for germination were probably not met for all of the seeded species since five seeded species never established as seedlings. Seedling death after germination also probably contributed to the lower number of seedlings than the number of seeds seeded (Chambers 2000).

In our study, *Elymus elymoides* had the highest plant cover of any seeded species and was the most abundant species reaching the reproductive stage. *Elymus elymoides* has been recommended as a native restoration grass because of its ability to establish and grow rapidly (Jones 1998). Concurrent with our results, Chambers (2000) found that *Elymus canadensis* had the highest seed entrapment and retention and highest survival after emergence in a variety of soil surface environments. In addition, a study by Noyd and others (1995) illustrated that *Elymus canadensis* can support a large AM hyphal network both internally and externally that can help spread AM infectivity and the establishment of other species. *Verbascum thapsus* was the most abundant exotic species establishing in all the treatments. *Verbascum thapsus* is a biennial species that produces over 100,000 seeds per plant, with 95 percent of the seeds falling within 5 meters of the parent plant, and has seeds that can remain viable in the soil seed bank for over 100 years (Gross and Werner 1978). A study by Gross (1980) showed that *V. thapsus* seedlings grew 4-7 times faster and produced 2000 percent more biomass when growing in bare sites in comparison to vegetated sites. These results are congruent with our findings where *V. thapsus* was most abundant in our bare control, sterilized soil and soil amendments and less abundant in our seed and seed/soil amendments where there was competition from other vegetation. In our study there was evidence that slash pile burning promoted the establishment of a fire-adapted species, tobacco (*Nicotiana attenuata* Torrey), which was present in the soil seed bank. *Nicotiana attenuata* is a post fire annual that cues its germination with cellulose combustion products found in wood smoke and takes advantage of the high nitrogen environments commonly found after burning (Lynds and Baldwin 1998). Even though our slash piles were severely burned, species adapted to fire are able to survive higher fire severities than non-adapted fire species (Keeley 1987).

Other Abiotic/Biotic Variables

Numerous other variables could also be playing a critical role in the successful establishment of native plants in severely burned areas treated with seed/soil amendments. Specifically, soil physical properties, soil surface characteristics (e.g., microtopography, temperature), soil nutrient levels, and water availability are all important in seedling establishment (Chambers 2000). In addition, individual species' life history and physiological traits are important determinants of whether or not species can establish in different environments (Grime 1979). In our study, the seed/soil amendments may have provided a soil environment that was less prone to surface wind erosion than the ash that seeds were directly seeded onto in the seed amendment treatments and also may have provided a better environment to trap wind-blown seeds (Chambers et al. 1990).

Another important variable that may have played a role in the rapid increase in plant cover between seven and nineteen months following burning was the pulse of inorganic nutrients that is often associated with increased plant productivity following burning (Anderson and Menges 1997). Studies that were conducted near our study site in ponderosa pine forests showed an increase in seedling establishment of herbaceous species (Vose and White 1987), an increase in herbaceous production (Harris and Covington 1983) and an increase in ponderosa pine seedling growth (Sackett 1984) following prescribed fire, attributed to the nutrient pulse of inorganic nitrogen into the system from burning. In addition, there also could be interactions between a pulse of available ammonium and AM fungi because AM fungi are able to increase the uptake of ammonium (Johansen et al. 1992). In our study, there were larger plants (aerial cover and height) and a higher number of plants reaching their reproductive stage than another nearby study that was conducted during the same time frame and seeded with similar species to look at different seed/soil/mulch amendments on abandoned roads (Elseroad 2001). One major difference between these studies was the absence of fire in the abandoned road study, which suggests that a nutrient pulse following burning may be partially responsible for the larger plants we found in severely burned slash scars. Other explanations such as soil compaction on roads may also explain the larger plants we found in the slash pile scars in comparison to the abandoned road study.

MANAGEMENT IMPLICATIONS

The severity of a burn is a critical factor that controls the post-fire herbaceous community structure (Moreno and Oechel 1991). Revegetation of a disturbed system is a substrate/soil driven process and is governed by the availability of seeds (Wali 1999). Our results illustrate that severely burned slash pile scars have significantly reduced AM fungal propagule densities, viable seeds in the soil seed bank and extant vegetation, altered soil physical and chemical properties and are susceptible to exotic species invasion. From these results we recommend land managers minimize burning large piles of slash that will result in severe soil heating, vegetation changes, and biotic and abiotic soil changes. Management decisions about slash removal need to take into consideration numerous factors such as the feasibility of other slash removal techniques including chipping and broadcast burning slash, the effects of these alternative techniques on ecosystem structure and function, and financial and personal constraints. Under scenarios where slash pile burning is the only realistic management option for reducing large amounts of fuel safely, we recommend that slash should be piled and burned on roads that are to be obliterated to minimize additional soil disturbance within the restoration treatment areas. We also recommend that severely burned slash pile scars should be treated with seed and soil amendments within the first growing season following burning to increase the rate of native plant establishment and discourage the invasion of exotic species. Native seeds of species common in the area should be used from a local source to minimize genetic contamination for seeding amendments and soil for the soil amendment treatments should be taken from stockpiled soil created during road building for the restoration treatments.

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Table 5.1 Species list for slash pile seed amendments and seed/soil amendments.

Grasses	
Bouteloua gracilis	Blue Grama
Elymus elymoides	Bottlebrush Squirreltail
Festuca arizonica	Arizona Fescue
Koeleria macrantha	Junegrass *
Muhlenbergia wrightii	Spike Muhly
Poa fendleriana	Mutton Grass *
Schizachyrium scoparium	Little Bluestem *
Forbs	
Artemisia ludoviciana	Prairie Sage
Castilleja linariifolia	Narrow leaf Paintbrush *
Geum triflorum	Prairie Smoke *
Heliomeris multiflora	Showy Goldeneye
Ipomopsis aggregata	Scarlet Gilia
Iris missouriensis	Rocky Mountain Iris
Linum lewisii	Blue Flax
Lupinus argenteus	Lupine
Oxytropis lambertii	Showy Locoweed
Penstemon barbatus	Scarlet Bugler
Penstemon virgatus	Wand Penstemon
Thermopsis divaricarpa	Foothills Golden Banner

* Species that did not germinate or did not establish as seedlings during the 2000 or 2001 growing season.

Table 5.2 Seeded species' average density, cover and height for the seed amendment plots in 2000 and 2001. Data are expressed as means (N=30) ± SE.

Species	Average Density		Average Cover (%)		Average Height (cm)	
	2000	2001	2000	2001	2000	2001
Bouteloua gracilis	1.10 ±.63 a	0.38 ±.25 a	0.03 ±.01 a	0.07 ±.03 a	0.51 ±.22 a	0.90 ±.43 a
Elymus elymoides	4.06 ±1.4 a	2.07 ±.47 a	0.10 ±.03 **a**	2.02 ±.96 **b**	1.72 ±.38 **a**	15.1 ±2.4 **b**
Festuca arizonica	0.07 ±.03 a	0.07 ±.02 a	0.01 ±.01 a	0.07 ±.03 a	0.20 ±.21 a	1.93 ±1.4 a
Muhlenbergia wrightii	0.65 ±.62 a	0.24 ±.09 a	0.02 ±.02 a	0.17 ±.09 a	0.17 ±.12 **a**	1.86 ±.74 **b**
Artemisia ludoviciana	0 ± 0 a	0.03 ±.02 a	0 ± 0 a	0.02 ±.01 a	0 ± 0 a	0.27 ±.06 a
Heliomeris multiflora	0.37 ±.08 a	0.40 ±.10 a	0.01 ±.01 **a**	0.48 ±.21 **b**	0.23 ±.13 **a**	4.67 ±1.5 **b**
Ipomopsis aggregata	0.24 ±.15 a	0.69 ±.18 a	0.02 ±.01 **a**	1.07 ±.45 **b**	0.24 ±.22 **a**	7.55 ±3.4 **b**
Linum lewisii	0.17 ±.09 a	0 ± 0 a	0.01 ±.01 a	0 ± 0 a	0.31 ±.21 a	0 ± 0 a
Lupinus argenteus	0.07 ±.03 a	0.07 ±.03 a	0.02 ±.01 a	0.02 ±.01 a	0.28 ±.14 a	0.24 ±.21 a
Oxytropis lambertii	0.21 ±.10 a	0.10 ±.08 a	0.03 ±.01 a	0.22 ±.21 a	0.34 ±.17 a	1.28 ±1.2 a
Penstemon barbatus	0 ± 0 **a**	0.72 ±.31 **b**	0 ± 0 **a**	0.51 ±.21 **b**	0 ± 0 **a**	1.10 ±.43 **b**
Penstemon virgatus	0 ± 0 a	0.03 ±.02 a	0 ± 0 a	0.02 ±.01 a	0 ± 0 a	0.10 ±.03 a
Thermopsis divaricarpa	0 ± 0 a	0.03 ±.02 a	0 ± 0 a	0.01 ±.01 a	0 ± 0 a	0.24 ±.05 a

*Only seeded species that germinated and established as seedlings in either 2000 or 2001 are presented. Values indexed by different bold letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between years for different sampling attributes.

Table 5.3 Seeded species' average density, cover and height for the seed/soil amendment plots in 2000 and 2001. Data are expressed as means (N=30) ± SE.

Species	Average Density		Average Cover (%)		Average Height (cm)	
	2000	2001	2000	2001	2000	2001
Bouteloua gracilis	17.5 ±4.7 **a**	0.44±.22 **b**	0.35 ±.06 a	0.26 ±.10 a	2.31 ± .19 a	3.03 ± 1.1 a
Elymus elymoides	17.3 ±2.8 **a**	3.86 ±.69 **b**	0.41 ±.07 **a**	6.12 ±1.3 **b**	3.55 ± .24 **a**	19.1 ± 2.1 **b**
Festuca arizonica	0.55 ±.35 a	0.13 ±.07 a	0.02 ±.01 a	0.14 ±.07 a	0.41 ± .18 a	3.55 ± 1.9 a
Muhlenbergia wrightii	3.55 ±1.3 **a**	0.69 ±.19 **b**	0.13 ±.04 **a**	0.82 ±.30 **b**	1.10 ± .24 **a**	9.38 ± 2.7 **b**
Artemisia ludoviciana	0.79 ±.54 a	0.45 ±.24 a	0.06 ±.04 a	0.14 ±.07 a	0.41 ± .16 a	1.10 ± .36 a
Heliomeris multiflora	0.23 ±.13 a	0.38 ±.12 a	0.04 ±.02 **a**	0.36 ±.13 **b**	0.34 ± .21 **a**	4.93 ± 1.7 **b**
Ipomopsis aggregata	1.79 ±.51 a	1.10 ±.19 a	0.12 ±.02 **a**	2.16 ±.49 **b**	1.34 ± .22 **a**	15.3 ± 3.6 **b**
Iris missouriensis	0 ±0 a	0.03 ±.01 a	0 ±0 a	0.01 ±.01 a	0 ± 0 a	0.41 ± .16 a
Linum lewisii	2.17 ±.57 **a**	0.66 ±.28 **b**	0.11 ±.04 a	0.13 ±.07 a	1.13 ± .24 a	3.55 ± 1.4 a
Lupinus argenteus	0.03 ±.01 a	0.03 ±.01 a	0.01 ±.01 a	0.01 ±.01 a	0.07 ± .05 a	0.30 ± .06 a
Oxytropis lambertii	0.96 ±.30 **a**	0.17 ±.11 **b**	0.06 ±.02 a	0.28 ±.22 a	1.34 ± .32 a	1.34 ± .36 a
Penstemon barbatus	0 ±0 **a**	0.97 ±.29 **b**	0 ±0 **a**	0.59 ±.13 **b**	0 ± 0 **a**	2.65 ± .52 **b**
Penstemon virgatus	0 ±0 a	0.31 ±.12 a	0 ±0 a	0.18 ±.18 a	0 ± 0 **a**	1.01 ± .31 **b**
Thermopsis divaricarpa	0 ±0 a	0.38 ±.06 a	0 ±0 a	0.12 ±.07 a	0 ± 0 a	2.27 ± 1.4 a

*Only seeded species that germinated and established as seedlings in either 2000 or 2001 are presented. Values indexed by different bold letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between years for different sampling attributes.

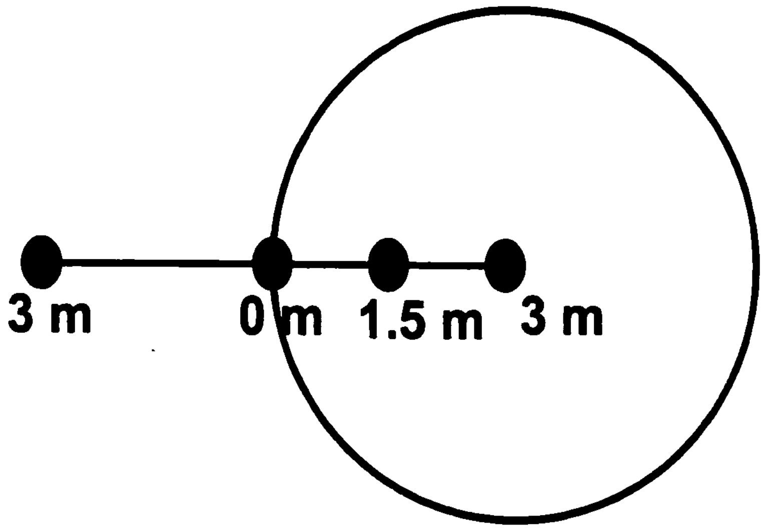

Figure 5.1a

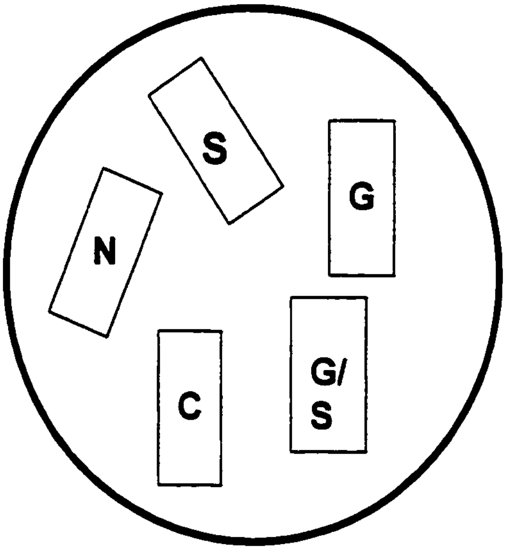

Figure 5.1b

Figure 5.1a-b a). Fire intensity gradient across each of the slash pile scars, b). amendment treatments for slash pile scars: no treatment (a control) (C), a soil amendment treatment (AM propagules) (S), a sterilized soil amendment (no AM propagules) (N), a seed amendment (G), and a seed/soil amendment (plant and AM propagules) (G/S).

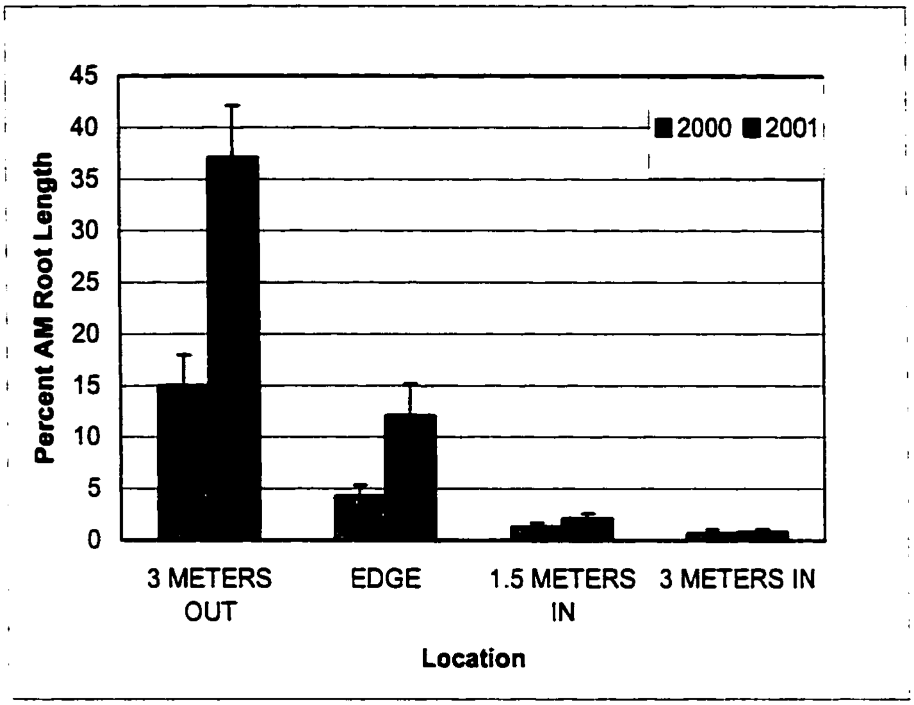

Figure 5.2 The relative amount of mycorrhizal propagules indicated by percent AM colonized root length in corn from bait-plant bioassays along the fire intensity gradient in 2000 and 2001, seven months and nineteen months following burning. Differences between the locations along the fire intensity gradient were determined by MANOVA repeated measures on arcsin square root transformed data.

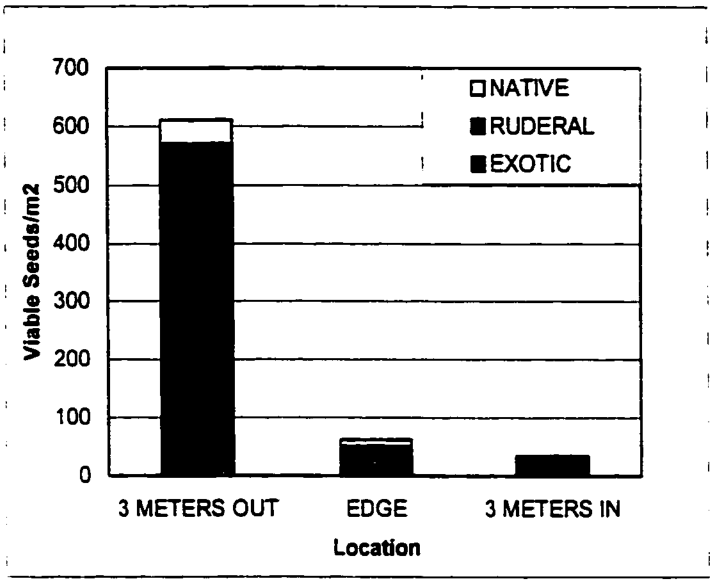

Figure 5.3 The number of native, ruderal, and exotic seeds per m^2 along the slash pile gradient in 2000, seven months after burning. Differences between the locations along the gradient were determined by ANOVA on log(x+1) transformed data.

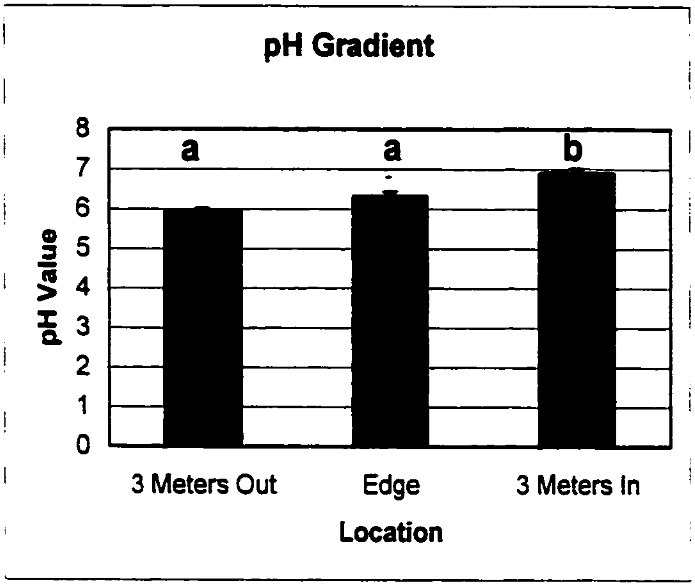

Figure 5.4a

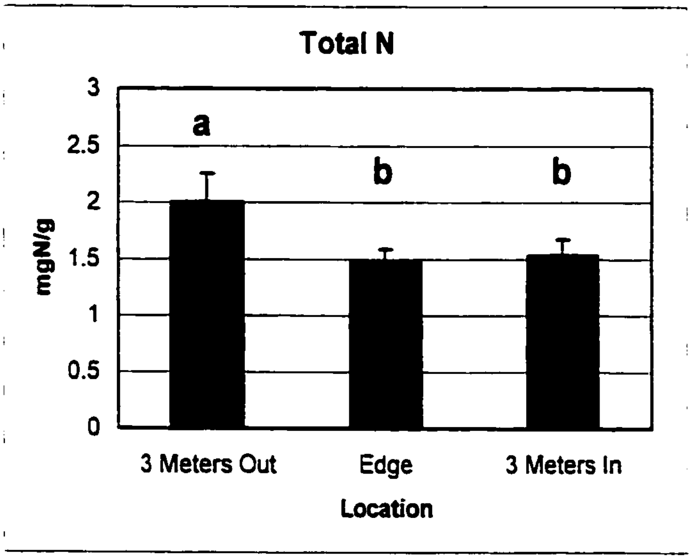

Figure 5.4b

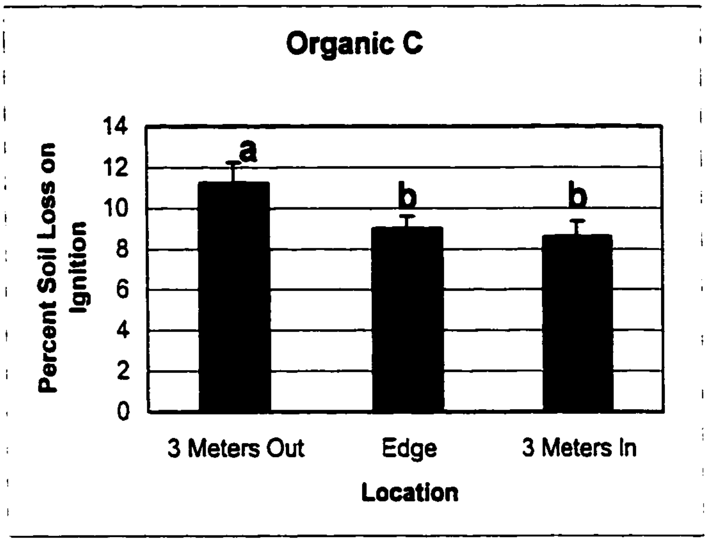

Figure 5.4c

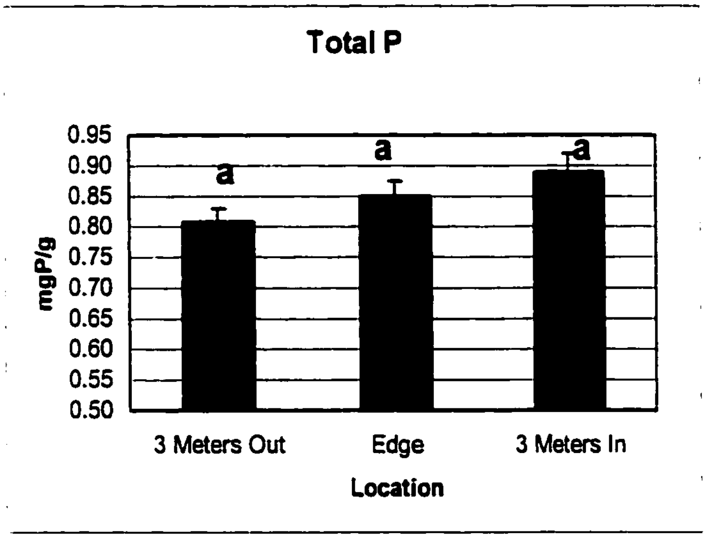

Figure 5.4d

Figure 5.4a-d Soil chemical properties a). soil pH, b). total N, c). organic C, d). total P along the fire intensity gradient for 2000. Differences between the locations along the fire intensity gradient were determined by ANOVA on square root transformed data. Values indexed by different letters are significantly different at the $p \leq 0.05$ level.

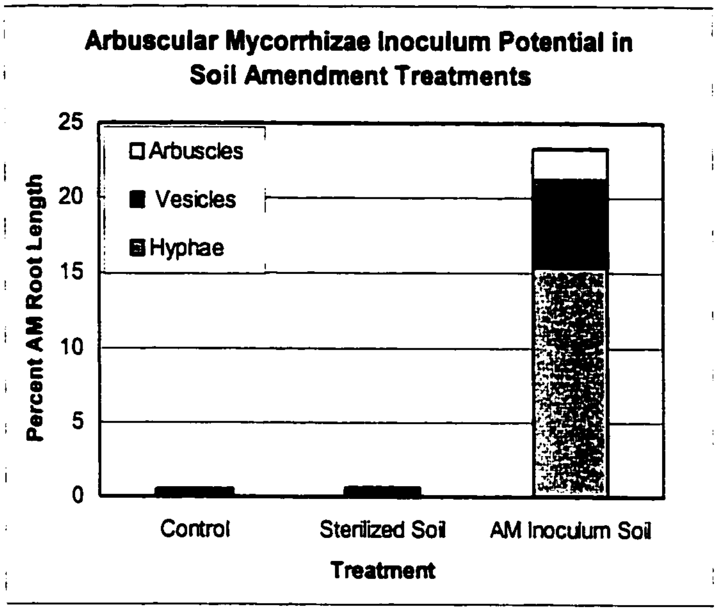

Figure 5.5 The relative amount of different AM fungal structures within colonized corn roots grown in soils collected from the control, sterilized soil (no AM inoculum), and seed/soil (AM inoculum) amendment plots. Differences between the AM fungal structures were determined by ANOVA on arcsin square root transformed data.

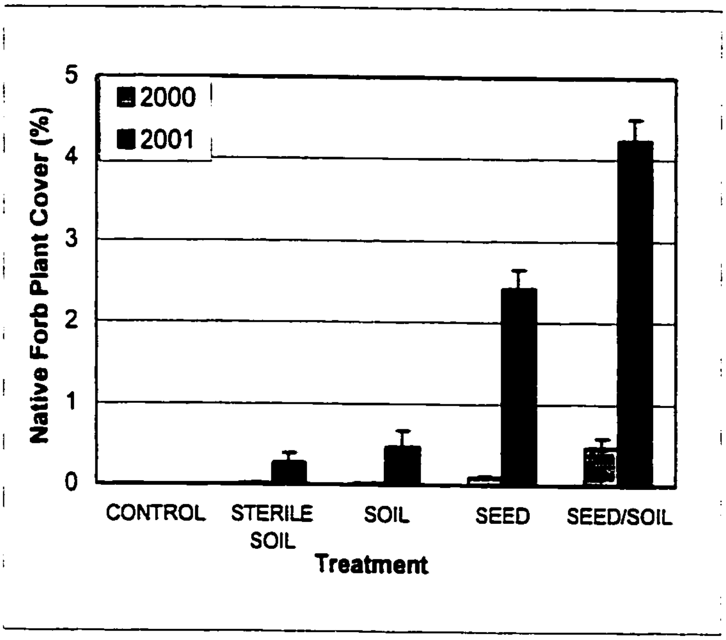

Figure 5.6a

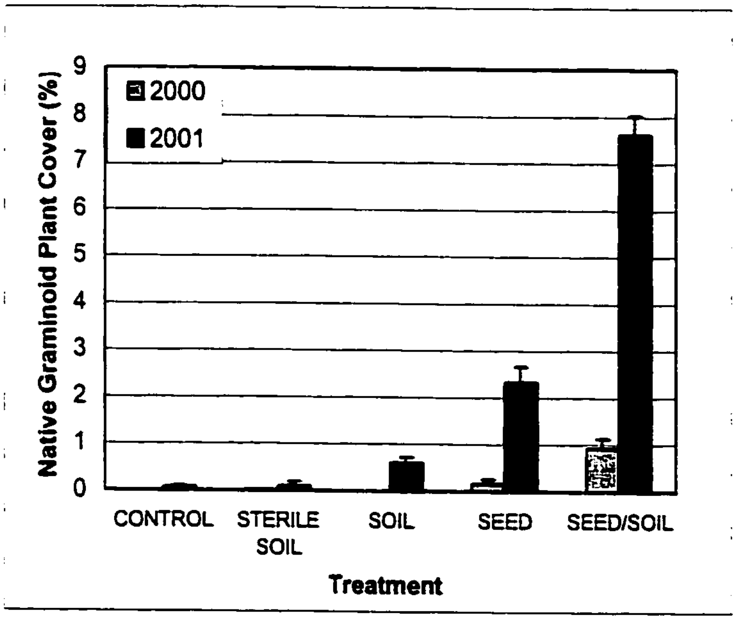

Figure 5.6b

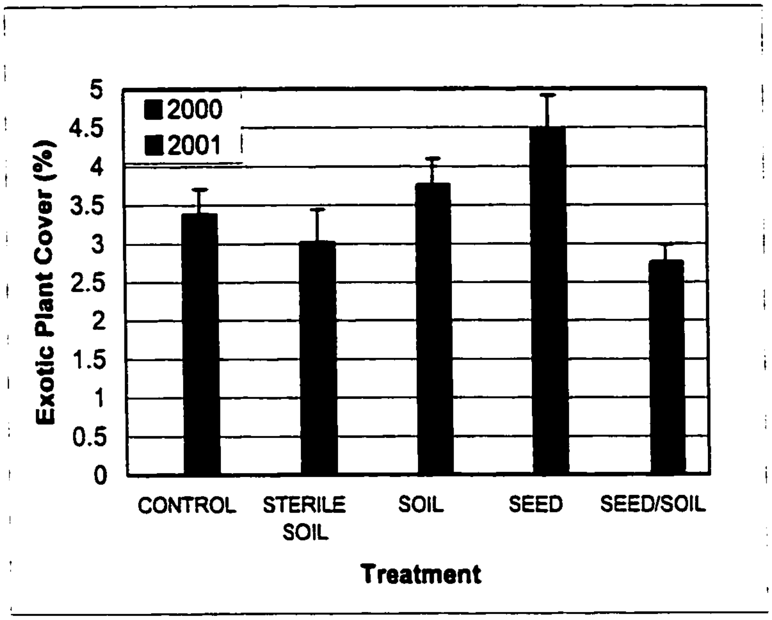

Figure 5.6c

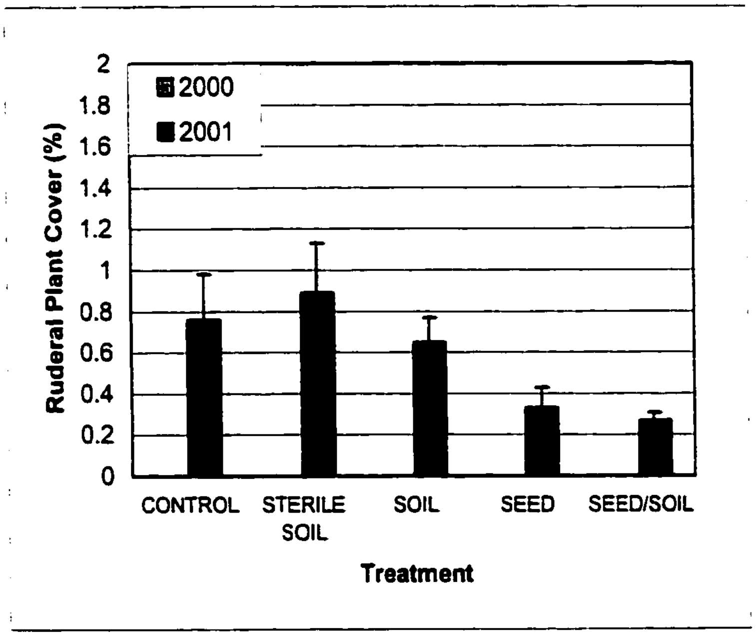

Figure 5.6d

Figure 5.6a-d Average number of a). forb, b). graminoid, c). exotic, d). ruderal seedlings established under different seed/soil amendment treatments: a control, no treatment, a soil amendment, a sterilized soil amendment, a seed amendment, and a seed/soil amendment. Differences between treatments were determined by MANOVA repeated measures.

CHAPTER 6

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The results of the studies in this dissertation have direct implications for lay people, scientists, and land managers who are involved in ponderosa pine restoration projects in the southwest and can be integrated into ponderosa pine forest adaptive ecosystem management. These studies investigated three different aspects of understory plant community dynamics in southwestern ponderosa pine forests. The herbaceous understory is an important component of ponderosa pine forest ecosystems. The postsettlement reduction in understory plant production and diversity of ponderosa pine forests has contributed to the alteration of the natural fire regime and the loss of habitat for numerous wildlife, bird, and insect species.

Any of the land management recommendations from these studies should be placed in the context of the particular restoration treatment in which it is being applied. Ponderosa pine restoration is an evolving field that incorporates a diversity of individual interests from people who are trying to put theory and knowledge into practice. The results from these studies need to be balanced with the practicality of their applicability in different management situations (e.g., availability of funding, personnel, project goals, etc.). Therefore, these results do not represent a final answer to the questions proposed but rather a base of knowledge in which discussions can begin.

The first objective of this dissertation was to determine whether different understory plant monitoring sampling techniques and sampling sizes would result in inconsistent data and if this would influence the ability to detect change in ponderosa pine restoration treatments. The results illustrated that the sampling technique chosen for monitoring herbaceous and shrub species richness and foliar cover in restoration studies can greatly influence the ability to detect change. Specifically, the results from this study showed that large area sampling techniques were the most effective at capturing species richness and rare and exotic species. Modified-Whittaker plots returned on average the highest species richness in all sampling technique comparisons and captured the most rare and exotic species. In comparison, point-intercept transects captured the fewest species. When choosing a sampling technique, decisions must be made about plot size and shape, the parameters to be measured, and the frequency, precision and location of measurements (Stohlgren 1994). Reference conditions are often cited as the goal for restoration treatments. This study illustrates that the type of sampling technique used to determine reference conditions should be similar to the sampling technique used to monitor change or the data may lead to inaccuracy, confusion, or apparent over-achievement of goals.

There is no one correct method for monitoring the herbaceous understory and therefore decisions about the type of monitoring technique to be used to detect change needs to be based upon the study's research goals, the study site and vegetation, and the availability of funding and personnel. Sutter (1996) outlined four criteria of monitoring techniques that must be met in order to reliably and precisely detect change. These included: (1) data need to have a known and acceptable level of precision; (2) data sampling techniques need to be repeatable across time and personnel; (3) data need to be collected for a long enough time to capture responses to treatments; and (4) techniques need to be feasible, realistic, and inexpensive enough to be maintained long-term.

Point-intercept transects using an optical device to eliminate error are recommended in revegetation studies where objectivity and repeatability are of primary importance and capturing species diversity is of secondary importance (Buckner 1985). In monitoring the effects of restoration treatments, we recommend a combination of sampling techniques to overcome the disadvantages of individual sampling techniques. For example, in ponderosa pine restoration studies the combined use of Modified Whittaker plots to capture species diversity and cover values of rare and exotic species along with point-intercept transects to accurately measure total species cover would minimize the disadvantages of both techniques. To ensure accuracy, point-intercept transects would need to be carefully located and done with an optical device with fine cross hairs attached to a sturdy tripod. Otherwise, ocular estimates are likely to be more accurate.

The second objective of this dissertation was to quantify the effect of restoration thinning alone and thinning and prescribed burning on arbuscular mycorrhizae (AM) and ectomycorrhizae (EM) fungal propagule densities and assess the relationships between mycorrhizal fungal propagule densities and plant community properties in southwestern ponderosa pine forests. The results indicated that population densities of AM fungi can rapidly increase following restoration thinning alone and thinning and prescribed burning. The relative amount of infective propagules of AM fungi was significantly negatively correlated with overstory tree canopy cover and litter cover and positively correlated with herbaceous understory species richness and graminoid cover.

These results have application to land managers who are trying to increase herbaceous understory richness and abundance. Some evidence suggests that prior to the mid 1880's, ponderosa pine understory communities were dominated by warm-season (C_4) grasses, which are often strongly mycotrophic (Cooper 1960, Pearson et al. 1971,Wilson and Hartnett 1998). For example, data from plots measured in 1912 showed that C_4 grasses predominated over C_3 grasses (Arnold 1955). In addition, Pearson and others (1970) stated that the timing of grazing by cattle can influence C_3/C_4 grass ratios. They stated that grazing of cattle between June and October favored C_3 grass establishment because cattle would only lightly graze Arizona fescue, the predominant C_3 grass, because it was approaching maturity (e.g. forming seeds). Instead cattle grazed heavily on immature Mountain muhly, the dominant C_4 grass, which lowered its abundance and therefore favored the establishment of Arizona fescue (Arnold 1955). However, current ponderosa pine forests are dominated by species that often form no mycorrhizal associations (e.g., *Carex* spp.), or C_3 grasses that are often weakly mycotrophic (Wilson and Hartnett 1998). This community has been established because the natural fires that historically would minimize competition between ponderosa pine and herbaceous plants have been suppressed and shade-tolerant C_3 grasses are better adapted to these environments. Without the reduction of EM tree competition and reintroduction of fire, the understory of southwestern ponderosa pine forests will likely continue to be dominated by weakly nonmycotrophic *Carex* and weakly mycotrophic C_3 grasses. One can predict that increased populations of AM fungi in the thinned only and thinned and prescribed burned restoration stands may assist in the replacement of weakly mycotrophic species by strongly mycotrophic species, thereby increasing C_4 grass cover and leading to the maintenance of a stable sward of mycorrhizal compatible species (Francis and Read 1994, Johnson 1998). This has important implications for land managers trying to restore the herbaceous understory of these forests because most understory plants depend upon AM associations for normal growth.

Future studies of AM in ponderosa pine restoration areas will require analysis of the species composition of the fungal communities to determine if a shift in the fungal community is occurring in response to restoration treatments and whether these shifts impact the plant community composition. Recent research in a variety of environments has shown that mycorrhizal interactions may be important determinants of plant diversity, ecosystem variability, and productivity (Hartnett and Wilson 1999, van der Heijden et al. 1998a, van der Heijden et al. 1998b, and Klironomos et al. 2000). Therefore, future studies in ponderosa pine restoration treatment areas are needed to more fully understand responses of AM fungal communities and assess feedbacks between AM fungal and plant communities.

The third objective of this dissertation was to determine the effect slash pile burning on densities of plant and AM fungal propagules and soil physical and chemical properties and determine the effect of soil and seed amendments on the rate of native herbaceous plant establishment within burned slash pile scars. The results indicated that without amendments, the relative amount of AM fungal propagule densities, number of viable seeds in the soil seed bank, and extant vegetation were significantly lower and soil properties were significantly different outside than inside slash pile scars. Seed/soil amendments had significantly higher cover of native forb and graminoid species in comparison to the other treatments. In addition, the seed/soil amendments had higher plant density, cover, and height than the seed only amendments. These results illustrate that adding both seed and living soil to slash pile scars can increase plant cover of desirable native forbs and grasses.

From these results we recommend land managers minimize burning large piles of slash that will result in severe soil heating, vegetation changes, and biotic and abiotic soil changes. Management decisions about slash removal need to take into consideration numerous factors such as the feasibility of other slash removal techniques including chipping and broadcast burning slash, the effects of these alternative techniques on ecosystem structure and function, and financial and personal constraints. Under scenarios where slash pile burning is the only realistic management option for reducing large amounts of fuel safely, we recommend that slash should be piled and burned on roads that are to be obliterated to minimize additional soil disturbance within the restoration treatment areas. We also recommend that severely burned slash pile scars should be treated with seed and soil amendments within the first growing season following burning to increase the rate of native plant establishment and discourage the invasion of exotic species. Native seeds of species common in the area should be used from a local source to minimize genetic contamination for seeding amendments and soil for the soil amendment treatments should be taken from stockpiled soil created during road building for the restoration treatments.

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