ENVIRONMENTAL AND VEGETATIONAL GRADIENTS ON AN ARIZONA

PONDEROSA PINE LANDSCAPE: IMPLICATIONS FOR

ECOLOGICAL RESTORATION

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ABSTRACT

ENVIRONMENTAL AND VEGETATIONAL GRADIENTS ON AN ARIZONA PONDEROSA PINE LANDSCAPE: IMPLICATIONS FOR ECOLOGICAL RESTORATION

SCOTT R. ABELLA

This research was performed in northern Arizona ponderosa pine (*Pinus ponderosa*) forests to enhance the ecological basis for restoration projects currently ongoing in these forests. My objectives were to: (i) develop a forest ecosystem classification on a 110,000-ha ponderosa pine landscape, (ii) determine geomorphic and soil gradients associated with the distribution of plant communities on this landscape, (iii) assess potential contributions of the soil seed bank for reestablishing understory communities, and (iv) determine understory responses to forest-floor manipulations in an existing ecological restoration experiment. I identified 10 landscape ecosystem types on this landscape, ranging from black cinders/*Phacelia* ecosystems low in available moisture and total N, to mesic basalt/*Festuca* and aspen/*Lathyrus* ecosystems. Distribution of plant communities was chiefly correlated with soil texture and resource levels reflecting influences of parent materials. Soil seed bank composition was partly ecosystem-specific, and was dominated by graminoids and short-lived forbs such as aspen fleabane (*Erigeron divergens*). I did not detect any short-term (2 year) treatment effects on understory vegetation in the forest-floor manipulation experiment.

ACKNOWLEDGEMENTS

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PREFACE

This dissertation is written in journal format and contains an introduction, literature review, four manuscript chapters, and a concluding chapter. The manuscript chapters are meant as stand-alone documents to be submitted to peer-reviewed journals. Methods are contained within each of the manuscript chapters, but redundancy is minimal among chapters because of the different focuses of the studies of each chapter. Differences in style among the manuscript chapters may be evident and reflect the style of the target journals, which are *Journal of Biogeophy* (Chapter 3), *Plant Ecology* (Chapter 4), *Canadian Journal of Botany* (Chapter 5), and *Western North American Naturalist* (Chapter 6).

CHAPTER 1

INTRODUCTION

This research was undertaken to provide ecological information in support of efforts aimed at restoring northern Arizona ponderosa pine (*Pinus ponderosa*) forests. Since European settlement of northern Arizona beginning ca. 1875, most of these forests have been subjected to heavy livestock grazing and to exclusion of historically frequent (< 10 yr on average) surface fires (Covington et al. 1994, Fulé et al. 1997, Allen et al. 2002). As a result, contemporary forests are dominated by dense small-diameter trees, sharply contrasting with the open stand structures and productive understories of presettlement forests (Cooper 1960, Moore et al. 1999). These dense contemporary forests are considered to be outside a range of natural variability thought to characterize presettlement forests (Moore et al. 1999, Allen et al. 2002). Ecological restoration in these forests seeks to approximately return fire regimes, tree structure, understory vegetation, and ecosystem functions to within a range of variability consistent with these forests' evolutionary environment (Covington et al. 1997, Moore et al. 1999). Restoration treatments in ponderosa pine forests chiefly include mechanical thinning of small-diameter trees and reintroducing surface fire through prescribed burning (e.g., Lynch et al. 2000, Fulé et al. 2001). Particularly for understory vegetation, supplemental treatments such as exotic species removal or seeding of native species may be needed on some sites to meet ecological restoration objectives (Covington et al. 1997, Abella 2004).

All research in this dissertation was performed in ponderosa pine forests surrounding the city of Flagstaff in northern Arizona, which has been a center of

ecological restoration efforts in southwestern ponderosa pine forests (e.g., Moore et al. 1999, Fulé et al. 2001). The general objectives of my research on this landscape were to: (i) develop a forest ecosystem classification, (ii) identify environmental gradients associated with plant community distribution, (iii) determine soil seed bank composition and its response to fire-related cues, and (iv) measure understory responses to forest-floor treatments in an existing ecological restoration experiment. Studies pertaining to each of these objectives are presented in four independent manuscript chapters following a literature review chapter. The literature review summarizes applications of ecosystem classification and forest site classification in southwestern United States forests. The dissertation concludes with a chapter synthesizing major conclusions of this research and identifies topics for future research. My emphasis in all chapters is on increasing our understanding of the ecology of the ponderosa pine landscapes we are trying to restore, and suggesting how results relate to applied ecological restoration.

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CHAPTER 2

LITERATURE REVIEW

Introduction

A major challenge confronting restorationists in southwestern United States

ponderosa pine (*Pinus ponderosa*) forests is developing strategies for restoring large

landscapes. In Arizona and New Mexico alone, ponderosa pine-dominated landscapes

occupy more than 3.4 million hectares (Brown 1994). These landscapes also are

heterogeneous, containing arrays of soil orders, topography, and plant communities

(Schubert 1974, Brown 1994). Sites within landscapes exhibit different levels of

ecological properties, suggesting that ecological restoration is most accurate if treatments

are based on site-specific knowledge of ecological properties (Covington et al. 1997).

Treating each site as if it were entirely unique, however, would present a daunting

challenge for estimating levels of many past and present ecological properties,

developing treatments, and monitoring treatment outcomes on large landscapes.

Furthermore, a tenet of ecosystem management is that we need to manage landscapes as

wholes, not as collections of independent points (Franklin 1993, Covington et al. 1999).

Partitioning landscapes into classification units comprised of collections of

similar sites has a long history in ecological research and management, including plant

community classification (Whittaker 1962), site index grouping (Carmean 1975), soil

surveys (Jones 1969), and ecosystem classification (Cajander 1926). If mapped, these

classifications allow their variable(s) of interest to be extrapolated from specific points to

other mapping units within classification strata. A certain degree of error is inherent in

this extrapolation for several reasons, because (i) ecological systems often occur on continuums, meaning any classification will not be perfect, (ii) accuracy depends on how well a given variable of interest is correlated with the classification, (iii) levels of variables and correlations with the classification system may change through time, and (iv) other reasons such as compounding of measurement errors during extrapolation. Despite these limitations, classification is a practical tool for communicating information about numerous sites in landscapes to facilitate their management (Whittaker 1962).

Ecosystem classification, also called ecological land classification, ecological site typing, and other terms, is becoming increasingly popular in the scientific literature as a means to partition landscapes into relatively homogenous ecosystem units (e.g., Barnes et al. 1982, Hix and Pearcy 1997, Goebel et al. 2001). Inherently multivariate and interdisciplinary, ecosystem classification identifies sites exhibiting similar abiotic (geomorphology and soils) and vegetational characteristics (Pregitzer and Barnes 1984, Archambault et al. 1990, Meilleur et al. 1994). The main difference between ecosystem classification and traditional plant community classification is that ecosystem classification emphasizes persistent abiotic ecosystem components, with vegetation of secondary importance (Spies and Barnes 1985, McNab et al. 1999, Palik et al. 2000). Like any classification system (Pregitzer et al. 2001), ecosystem classification is not designed to simultaneously meet all the estimation objectives for a landscape (Nolet et al. 1995). However, the intuitive appeal of studying landscapes as reoccurring ecosystem mosaics comprised of interrelated environmental complexes and plant communities, has gained ecosystem classification's general acceptance in the scientific literature (e.g., Barnes et al. 1982, Host et al. 1988, Palik et al. 2003).

In this chapter, I summarize (i) examples where ecosystem classification has been used to estimate ecological properties across landscapes, and (ii) site classifications in southwestern United States forests. Ecosystem classification has been little developed to date in southwestern forests. Given the large landscapes needing restoration in southwestern forests and the range of ecological properties useful to estimate to enhance the knowledge base for restoration (Covington et al. 1997), ecosystem classification may be particularly useful in the future in the southwestern United States.

Ecosystem Classification Applications

Ecosystem classification automatically provides baseline soils, geomorphic, and vegetation data through its development, and the classification subsequently provides a useful ecosystem framework for studying a variety of ecological properties among ecosystems. Diverse studies, ranging from predicting distributions of archaeological sites (Ferone et al. 1997), estimating ecosystem-specific nutrient cycling (Zak and Pregitzer 1990), reconstructing presettlement forest composition through General Land Survey records (Fralish et al.1991), and prioritizing ecological restoration (Palik et al. 2000), have been undertaken within and made more accurate by an ecosystem classification framework (Table 2.1). In the following sections, I present examples where ecosystem classification has been applied to estimate ecological properties relevant to ecosystem management.

Table 2.1. Examples of ecological properties studied and estimated in an ecosystem classification framework. Literature citations are not intended to be exhaustive, but to provide examples of representative studies. Not all properties will be relevant to all landscapes, and some properties may correspond with classified ecosystems more closely on some landscapes than on others.

Ecological Property	References
Nitrogen cycling	Zak et al. 1989, Wilson et al. 1999
Understory productivity	Mitchell et al. 1999
Tree growth	Host et al. 1988, Jose and Gillespie 1997
Tree mortality	Hix et al. 1987, Palik and Pederson 1996
Community composition	Meilleur et al. 1994, Abella and Shelburne 2004
Seed bank composition	Abella 2005
Bird habitat	Kashian et al. 2003
Species diversity	Lapin and Barnes 1995, Kirkman et al. 2004
Rare plant species	Abella et al. 2003
Succession	Host et al. 1987, Host and Pastor 1998
Presettlement forests	Fralish et al. 1991
Prioritizing restoration	Palik et al. 2000
Range degradation	Weixelman et al. 1997
Fire behavior	Sims and Uhlig 1992
Archaeological sites	Ferone et al. 1997

Nitrogen Cycling

In a series of studies, Zak et al. (1986, 1989) and Zak and Pregitzer (1990) compared N cycling among nine ecosystem types occurring along soil texture and drainage gradients on glacial landforms of a forested northern Michigan landscape. Potential net N mineralization averaged about 50 µg N g^{-1} in dry oak (*Quercus*) ecosystems on outwash plains or on moraines without fine-textured soil banding (Zak et al. 1989). Mineralization was sharply higher in two sugar maple (*Acer saccharum*) ecosystems on moraine landforms with fine-textured bands, averaging 93-128 µg N g^{-1}. Potential net nitrification averaged < 5 µg N g^{-1} in 8/9 ecosystems, but averaged 45 µg N g^{-1} in a moist *Acer saccharum–Osmorhiza* ecosystem. Litterfall N concentrations of trees that grew in multiple ecosystems also differed among ecosystems for several species. Northern red oak (*Quercus rubra*) litterfall, for example, averaged 0.8% N in outwash plain ecosystems compared to 1.1% N in moist morainal ecosystems (Zak et al. 1986). Net N mineralization was strongly correlated with overstory biomass ($r^2 = 0.82$) and annual biomass increment ($r^2 = 0.85$), both of which displayed predictable patterns among ecosystem types (Host et al. 1988).

These studies illustrated that ecosystem properties such as nutrient cycling, species composition, and productivity were interrelated with each other, and with the glacial landforms and soil textural properties forming the foundation of the ecosystem classification. The authors also emphasized that variability in N cycling can be as high among ecosystems within a region as between regions (Zak et al. 1989). They hypothesized that some of the nine ecosystem types within their study landscape were N-limited, whereas others were not.

Tree Mortality

On a Georgia Coastal Plain landscape, Palik and Pederson (1996) found that causes of longleaf pine (*Pinus palustris*) mortality were partly correlated with site factors associated with different ecosystem types (Goebel et al. 2001). Lightning mortality was most frequent on coarse-textured, excessively drained xeric sites. The authors hypothesized that pines on these xeric sites were more likely to die after being struck by lightning because they were already stressed by low moisture levels. Windthrow mortality, in contrast, was most frequent on sites in low topographic positions with high water tables. Rooting depth was restricted on these sites, increasing longleaf pine's susceptibility to windthrow.

Tree Growth

Differences in tree growth have routinely been found among classified ecosystems. For example, pignut hickory (*Carya glabra*) site index$_{50}$ ranged from 14-23 meters across six ecosystem types in Indiana's Hoosier National Forest (Jose and Gillespie 1997). Annual woody biomass production was lowest in a dry-slope ecosystem (2127 kg ha^{-1} yr^{-1}) and highest in a bottomland ecosystem (3353 kg ha^{-1} yr^{-1}). Differences in tree growth among classified ecosystems also have been reported in Wisconsin hardwood forests (Hix 1988), Michigan jack pine (*Pinus banksiana*; Kashian et al. 2003) and hardwood forests (Host et al. 1988), Georgia longleaf pine savannas (Mitchell et al. 1999), Arizona ponderosa pine forests (Abella 2005), and in other areas. Because ecosystem classification is based on environmental variables associated with soil moisture and nutrient levels affecting tree growth, it is not surprising that ecosystem classification has strongly predicted forest productivity on a range of landscapes.

Plant Species Diversity

On a 4000-ha northern Michigan forested landscape, Lapin and Barnes (1995) found that Shannon's diversity index ranged from 0.61 in excessively drained, nutrient-poor glacial outwash ecosystems, to 2.21 in loamy, nutrient-rich moist ecosystems. Plant diversity thus appeared positively correlated with soil-resource levels, well captured by the ecosystem framework. Kirkman et al. (2004) compared Shannon's diversity among ecosystem types on a 13,000-ha longleaf pine landscape previously classified by Goebel et al. (2001). These authors concluded that species diversity was affected both by environmental factors and prescribed burning frequency. Interestingly, the authors noted that ecosystem types were correlated with both these factors. Unproductive ecosystems were not burned frequently because of slow fuel accumulation, and seasonally flooded ecosystems also were not burned frequently because of limited periods of dry fuels.

Presettlement Forest Composition

Fralish et al. (1991) reconstructed 1806-1807 (presettlement) forest composition in the Illinois Shawnee Hills from General Land Office records and related these witness tree data to an ecosystem classification. Presettlement composition closely corresponded with the present-day ecosystem classification. Post oak (*Quercus stellata*), for example, was abundant in dry ecosystems on rocky, south-facing slopes. Drainages cut in sandstone bedrock consisted of mesic hardwoods such as tulip-poplar (*Liriodendron tulipifera*). Reconstructed presettlement basal area ranged from 9 m^2 ha^{-1} on rocky south slopes to 22 m^2 ha^{-1} in drainages. Fralish et al. (1991) also sampled contemporary old-growth forests on these ecosystem types, and noted that contemporary composition differed to a certain extent from presettlement composition likely because of fire

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suppression or other factors. Similar to presettlement forest composition, however, contemporary composition was strongly ecosystem specific. This illustrates an important principle that a given ecosystem type can support different plant communities at different times. These data also illustrate that the ecosystem classification viably predicted forest composition for a 200-year period, owing to the persistence of the topographic and soil factors on which the ecosystem framework was based.

Forest Site Classification in the Southwest

Early site classification efforts in the Southwest focused on grouping sites according to soil surveys, site index, or generalized topographic features or vegetation types (Jones 1969, Leven et al. 1972). Clary et al. (1966), for example, suggested stratifying sites by soil series and topographic position for estimating forage production in ponderosa pine forests of northern Arizona's Beaver Creek watershed. Radloff and Betters (1978) and Omi et al. (1979) later suggested using multivariate statistics for grouping sites on Colorado and California landscapes.

Habitat typing (Daubenmire 1952) likely has been the most extensively developed site classification method in southwestern forests (Muldavin et al. 1990). Habitat typing is basically plant community classification chiefly of late-successional vegetation, and soil properties typically are not measured or only qualitatively assessed (e.g., Pfister and Arno 1980, Hanks et al. 1983). Barnes et al. (1998) concisely summarized the history and nature of habitat typing, and noted that habitat typing has made major contributions to our understanding of vegetation ecology. Cook (1996) discussed some assumptions and problems with traditional habitat typing, particularly about climax vegetation concepts on which habitat typing rests. Habitat types are not necessarily synonymous

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with ecosystem types because multiple climax vegetation types may occur on similar environmental complexes, and some environmental complexes may not support climax vegetation due to recurrent disturbances (Cook 1996, Barnes et al. 1998). It is not necessarily appropriate to say that one classification is better than another, because ecosystem classification and habitat typing classify different things (Barnes et al. 1998).

Two qualities that I believe make ecosystem classification particularly useful in the context of southwestern forest restoration are: (i) Ecosystem classification is based on semi-permanent abiotic landscape features, thought to change relatively little during vegetation transitions or forest succession. (ii) By incorporating quantitative soil and environmental variables, ecosystem classification better explains vegetation-environment ecological relationships and mechanisms than classification based strictly on plant community characteristics. Ecosystem classification's utility also can be enhanced if successional trajectories in the presence or absence of disturbance can be developed for individual ecosystem types (Kirkman et al. 2000). Land managers then have ecosystem and current vegetation maps available for management planning (Palik et al. 2000).

Terrestrial ecosystem surveys (TES), developed for several southwestern national forests since the late 1980s (Ganey and Benoit 2002), also deserve mention for site classification. These surveys provide map unit descriptions similar to traditional USDA soil surveys, with the exceptions that TES classifies soils only to the family level and provides minimal soil profile descriptions, but lists expected understory species (e.g., U.S. Forest Service 1995). It is unclear, however, how the species lists were obtained (U.S. Forest Service 1995). To a user, TES may seem akin to traditional soil surveys, just termed differently. It is well-established that ecosystem types typically do not equate

with soil taxonomic units (e.g., Host et al. 1988, Abella et al. 2003), although soil survey data can greatly assist development of ecosystem classifications. There are no known published TES and ecosystem classification comparisons, which are needed to assess the role of TES in southwestern forest site classification.

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CHAPTER 3

FOREST ECOSYSTEMS OF AN ARIZONA PINUS PONDEROSA LANDSCAPE: MULTIFACTOR CLASSIFICATION AND IMPLICATIONS FOR ECOLOGICAL RESTORATION

ABSTRACT

Aim I developed an ecosystem classification on a 110,000-ha Arizona *Pinus ponderosa* P. & C. Lawson (ponderosa pine) landscape to support ecological restoration of these forests. Specific objectives included identifying key environmental variables constraining ecosystem distribution, and comparing plant species composition, richness, and tree growth among ecosystems.

Location The Coconino National Forest and the Northern Arizona University Centennial Forest, near the city of Flagstaff in northern Arizona, USA.

Methods I sampled geomorphology, soils, and vegetation on 66, 0.05-ha plots in open stands containing trees of pre-European settlement (ca. 1875) origin, and on 26 plots in dense postsettlement stands. Using cluster analysis and ordination of vegetation and environment matrices, I classified plots into ecosystem types internally similar in environmental and vegetational characteristics.

Results I identified 10 ecosystem types, ranging from dry, black cinders/*Phacelia* ecosystems to moist aspen/*Lathyrus* ecosystems. Texture, organic C, and other soil properties reflecting effects of parent materials structured ecosystem distribution across the landscape, with geomorphology locally important. Species composition also was ecosystem-specific, with C_3 *Festuca arizonica* Vasey (Arizona fescue), for instance,

abundant in mesic basalt/*Festuca* ecosystems. Mean *P. ponderosa* diameter increments ranged from 2.3-4.3 mm yr^{-1} across ecosystems in old-growth stands, and the ecosystem classification was robust in dense postsettlement stands.

Main conclusions Several lines of evidence suggest that although species composition may have been altered since settlement, the same basic ecosystems occurred on this landscape in presettlement forests, providing reference information for ecological restoration. Red cinders/*Bahia* ecosystems historically were rare and > 30% of their area has burned by crown fires since 1950, indicating priority could be given to restoring this ecosystem's remaining mapping units. Ecosystem turnover occurs at broad extents on this landscape, and restoration must accordingly operate across large areas to encompass ecosystem diversity. By incorporating factors driving ecosystem composition, this ecosystem classification represents a framework for estimating spatial variation in ecological properties relevant to ecological restoration.

Keywords

Ecosystem classification, geomorphology, soil, terrestrial ecosystem survey, vegetation-environment relationships, reference conditions, species richness.

INTRODUCTION

Geomorphology and soils vary across forest landscapes, forming mosaics of environmental complexes differing in productivities and capabilities for supporting plant communities (Hix, 1988; Archambault et al., 1990; Host & Pregitzer, 1992). Ecosystem classification is a tool for identifying interrelationships among environmental variables forming environmental complexes, discerning gradients constraining vegetation

distribution and productivity, and classifying volumetric environment-vegetation units into landscape ecosystems to facilitate ecosystem-specific management (Barnes et al., 1982; McNab et al., 1999). Goebel et al. (2001), for example, distinguished 21 ecosystem types along soil texture, drainage, and topographic gradients on an 11,000-ha southeastern USA *Pinus palustris* P. Mill. (longleaf pine) landscape. Palik et al. (2000) then used the ecosystem classification to develop models for prioritizing ecosystem-specific restoration based on the historical and current rarity of different ecosystems.

While ecosystem classification is increasingly being developed and utilized in eastern USA forests (e.g., Lapin & Barnes, 1995; McNab et al., 1999; Abella et al., 2003), little ecosystem classification or soil-site research has been published for vast southwestern USA *Pinus ponderosa* P. & C. Lawson (ponderosa pine) forests. Vegetation-based habitat classifications (Hanks et al., 1983; Muldavin et al., 1990) or soil or landform type classifications (Leven et al., 1972) have been more common in these forests, although recently the US Forest Service has published Terrestrial Ecosystem Surveys (TES) for several southwestern national forests (see Ganey & Benoit, 2002). These TES land classifications provide georeferenced maps and soil classification data similar to eastern US soil surveys (US Forest Service, 1995). Although TES has been extensively developed for southwestern *P. ponderosa* forests, there are no published TES and ecosystem classification comparisons. Ecosystem integrity in these forests has declined since settlement (ca. 1875), largely because of fire exclusion, increases in tree density, widespread crown fires, and other factors. Scientific consensus has emerged that these forests urgently need extensive ecological restoration, primarily including tree thinning and reintroduction of frequent surface fire (Covington et al., 1994; Moore et al.,

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1999; Allen et al., 2002). Developing ecosystem classification in southwestern *P. ponderosa* forests and comparisons with TES may be timely for assisting ecosystem-specific ecological restoration.

I undertook this study to develop a multifactor ecosystem classification on a 110,000-ha northern Arizona USA *Pinus ponderosa* landscape. Specific objectives included identifying primary environmental and vegetational gradients and their interrelationships associated with ecosystem distribution, comparing variables such as tree growth among classified ecosystems, and providing examples of applications for ecological restoration and hypothesis generation for future research.

METHODS

Study area

This study was performed between 1920-2660 m elevations in the Northern Arizona University Centennial Forest and the north half of the Coconino National Forest near the city of Flagstaff, AZ (Fig. 3.1). *Pinus ponderosa* is the dominant tree species and forms extensive pure stands, but sometimes occurs with *Quercus gambelii* Nutt. (Gambel oak) or *Populus tremuloides* Michx. (trembling aspen). Precipitation increases and temperatures decrease from east to west across the study area, with precipitation ranging from 42-56 cm yr^{-1}, snowfall from 152-233 cm yr^{-1}, and maximum mean daily temperatures from 15.7-17.5^{o}C (Western Regional Climate Center, Reno, NV, USA). Topography is primarily flat or undulating (slope gradients < 10%), occasionally punctuated by cinder cones, ravines, and low hills. Volcanic activity has been widespread, with the most recent eruptions occurring ca. 900 years ago in the Sunset Crater Volcanic Field in the northeastern part of the study area (Moore et al., 1976). Soil

parent materials include basalt, volcanic cinders, benmoreite, mixed igneous rocks, and limestone (Welch & Klemmedson, 1975). Major soil subgroups are Typic and Udic Argiborolls, Typic and Mollic Eutroboralfs, Typic Ustorthents, and Vitrandic Ustochrepts (US Forest Service, 1995). Lightning-ignited surface fires in presettlement forests on average occurred at least once every 10 years, maintaining open stand structures (Fulé et al., 1997). Most of the study area, however, has sustained fire exclusion, timber harvest, and heavy livestock grazing since settlement, which may have influenced contemporary ground-flora composition in some areas (Abella, 2004).

Site selection

I used a digital TES map (US Forest Service, 1995) in a geographic information system to randomly select six mapping units for sampling in each of 11 TES types (55, 500, 513, 523, 536, 551, 558, 570, 582, 585, and 611) encompassing a range of soils. I sampled a 0.05-ha (20 m × 25 m) plot in each mapping unit in areas exhibiting open canopies, relatively intact understories, and no apparent major recent disturbance. Areas dominated by presettlement-origin trees most frequently met these criteria. These 66 open-canopy plots were used to develop the ecosystem classification, and I sampled an additional 26 plots in dense postsettlement-origin stands in 536, 570, and 585 TES mapping units to ascertain classification viability in dense stands. These stands typically exceeded 1000 trees ha^{-1}, in contrast to typical densities of < 150 trees ha^{-1} in presettlement-origin stands.

Environmental measurements

I sampled plots from May-August 2003. On each plot, I recorded elevation, transformed aspect (Beers et al., 1966), slope gradient, and terrain shape index (McNab, 1989). Terrain shape index measures local topographic geometry, and I based measurements on

eight clinometer sightings every 45° to a change in topographic shape (Abella, 2003). I

measured surface rock cover by recording substrate every 0.3 m along a 25-m transect,

and obtained rock samples later identified by a geologist (Sam Bourque, Ecological

Restoration Institute, Flagstaff, AZ, USA). I collected composite soil samples of 0-15

and 15-50 cm depths from two pits per plot, and examined deeper layers to 150 cm or to

an impervious layer using a bucket auger. Soil samples were air dried, sieved through a

2-mm sieve, and analyzed for $CaCO_3$ equivalent (Goh et al.'s [1993] approximate

gravimetric method), texture (hydrometer method), pH (1:2 soil:0.01 M $CaCl_2$), and

organic C and total N (C/N analyzer after HCl removal of inorganic C) following Bartels

& Bigham (1996) and Dane & Topp (2002). I also estimated soil available water

capacity using Saxton et al.'s (1986) equations incorporating texture, gravel content, and

organic matter (organic C × 1.724). On three plots each of six ecosystem types, I

measured gravimetric 0-15 cm soil moisture (24 hr 105°C oven drying) averaged from

two soil cores each of 208-cm^3 per plot. I made measurements during the driest period of

the year, when moisture differences may be most critical, on 19 June 2004 after no

measurable precipitation had fallen since April (Western Regional Climate Center, Reno,

NV, USA). Measurement errors averaged < 5% based on a repeated measure every 10

samples for soil analyses and every six samples for moisture.

Vegetation measurements

In 15, 1-m^2 subplots per plot centered at 0.5, 5, 12.5, 20, and 24.5 m along plot axes, I

visually categorized areal percent cover of ground-flora species rooted in subplots as 0.1,

0.25, 0.5, and 1% up to 1% cover, at 1% intervals to 10% cover, and at 5% intervals

above 10% cover. Measurement error, based on remeasuring two randomly selected

subplots every six plots, averaged < 0.25% for total cover and < 0.25 species m^{-2}. I

inventoried species in whole plots on a presence/absence basis, and assigned these

species a frequency of 1 and the lowest cover for computing importance values (average

of relative frequency and relative cover summing to 100% on a plot basis).

Nomenclature follows USDA-NRCS (2004).

To measure tree growth, at 0.4 m above ground level I cored two dominant, open-

grown *Pinus ponderosa* of pre-settlement origin on each open-canopy plot. Cores were

sanded, mounted, and cross-dated using local tree-ring chronologies. I measured

diameter increment between ages of 50-150 yr at 0.4 m height to avoid potential

measurement inaccuracies due to missed piths, while providing a growth measure in the

early-middle life stage of *P. ponderosa* (Schubert, 1974). I used diameter increment as a

growth measure rather than site index because site index equations have not been

developed for old-growth, uneven-aged southwestern *P. ponderosa* stands sampled for

this study.

Statistical analysis

I developed the ecosystem classification by classifying and ordinating the environmental

matrix using cluster analysis (variables relativized by maximums, Euclidean distance,

Ward's linkage method) and principal components analysis (correlation matrix) in PC-

ORD (McCune & Mefford, 1999). I classified and ordinated the importance value

vegetation matrix using cluster analysis (Sørensen distance, -0.25 flexible beta linkage)

and non-metric multidimensional scaling (autopilot, thorough mode). After identifying

seven plot groupings in these analyses with 24 remaining plots chiefly of basalt parent

materials not clearly distinguished, I performed a second iteration of ordination and

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classification separately on these 24 plots. This analysis identified three plot groupings

distinguished by soil properties and plant composition. The final ecosystem classification

was based on plot groups internally similar in environmental properties and species

composition, and similarity of classification and ordination results increased the

classification's robustness. I compared means of environmental variables, species

richness, and *Pinus ponderosa* diameter increment among classified ecosystems using

one-way analysis of variance and Fisher's least significant difference in SAS JMP (SAS

Institute, 2002). Raw data approximated assumptions of equal variance (Levene test) and

normality (Shapiro-Wilk W test).

RESULTS AND DISCUSSION

Classification

I classified and named 10 landscape ecosystem types on the basis of diagnostic

environmental features and characteristic species along a continuum ranging from black

cinders/*Phacelia* ecosystems with the driest surface soils and lowest plant cover, to moist

aspen/*Lathyrus* and treeless park/*Symphyotrichum* ecosystems (Table 3.1, Fig. 3.2).

Other ecosystems differed more subtly, such as xeric basalt/*Muhlenbergia* ecosystems

differentiating from mesic basalt/*Festuca* ecosystems by exhibiting sandier soils, less

organic C, and more *Muhlenbergia montana* (Nutt.) A.S. Hitchc. (mountain muhly) than

Festuca arizonica Vasey (Arizona fescue). Seven ecosystems corresponded with a

respective TES type, whereas three ecosystems each occurred on combinations of the

551, 570, 582, and 585 TES types mostly containing basalt parent material (US Forest

Service, 1995). Of six plots sampled in the 582 TES type, for example, I classified four

into the mesic basalt/*Festuca* and two into the rocky basalt/*Sporobolus* ecosystems. This

increased internal mean Sørensen similarities of understory vegetation from 44% within

the 582 TES type to 55% within this study's mesic basalt/*Festuca* ecosystem. Results

suggest that TES broadly differentiated distinctively different ecosystems, but did not

detect multivariate interactions among environmental variables distinguishing closely

related ecosystems (Fig. 3.3). Similar to eastern US soil surveys, however, TES is a

starting point for understanding ecosystem distribution on this landscape (Pregitzer et al.,

2001). By identifying interrelationships, ecosystem classification is useful to refine or

complement TES in southwestern USA national forests.

Environmental complexes

Ecosystems primarily differentiated along soil gradients (Fig. 3.3), reflecting differences

among soil parent materials from the presence or absence of volcanic activity (Welch &

Klemmedson, 1975). Contrasting with ecosystem classification in the eastern USA

where geomorphology often forms an initial layer distinguishing ecosystems (Hix, 1988;

Host & Pregitzer, 1992; Abella et al., 2003), ecosystem distribution was not closely

associated with the geomorphic variables of aspect, slope gradient, or terrain shape index.

Slope gradients averaged < 8% in all ecosystems except for red cinders/*Bahia*

ecosystems, so most plots did not exhibit strong aspects. Terrain shape indices were near

zero reflecting fairly linear topography (McNab, 1989), averaging only slightly convex (-

2.1) in red cinders/*Bahia* ecosystems because of the convex cinder cones this ecosystem

often occupied. Park/*Symphyotrichum* ecosystems had weakly concave (1.9) terrain

shapes, consistent with this ecosystem's occurrence in depressions a few meters lower

than surrounding forested topography. While geomorphology may influence ecosystem

composition in rare, localized areas such as particularly deep ravines I did not sample

(Crawford Zimmerman et al., 1999), the flat to undulating topography on most of the landscape minimally affects ecosystem distribution.

Soil properties such as texture and organic C, in contrast to geomorphic variables, sharply differed among ecosystems (Table 3.2). Sand concentration from 0-15 cm in black cinders/*Phacelia* ecosystems exceeded 90% and averaged between 53-63% in red cinders/*Bahia* and limestone ecosystems. Clay basalt/*Gutierrezia*, rocky basalt/*Sporobolus*, and park/*Symphyotrichum* ecosystems exhibited the most 0-50 cm clay. High clay concentrations in park/*Symphyotrichum* ecosystems combined with the flat depressions parks occupy may explain early accounts that some parks seasonally were shallow lakes (Kircher, 1910), possibly much moister than they currently are after hydrological alterations from livestock tanks (Rusby, 1889). Siltier textures and higher organic C resulting in 0.03-0.05 m^3 m^{-3} greater water-holding capacities (Saxton et al., 1986) partly distinguished mesic basalt/*Festuca* ecosystems from other basalt ecosystems. Organic C and total N concentrations also were high in aspen/*Lathyrus* ecosystems, probably reflecting this ecosystem's high productivity where mean ground-flora cover was highest (35%). By occupying large volumes at a given weight, the low-density cinders in black and red cinder ecosystems (Moore et al., 1976) result in higher gravel and lower N and organic C contents volumetrically than on a weight basis (Welch & Klemmedson, 1975), decreasing soil fertility in these ecosystems.

Mean pH ranged from 5.9-7.0 across ecosystems, exceeding 6.5 in xeric limestone/*Bouteloua*, clay basalt/*Gutierrezia*, and cinder ecosystems (Table 3.2). The mesic limestone/mixed flora ecosystem had among the lowest 0-15 cm pH, and I also did not detect appreciable $CaCO_3$ equivalents in this ecosystem. $CaCO_3$ equivalent was the

only soil property not significantly different among ecosystems, with the highest but variable amount in the xeric limestone/*Bouteloua* ecosystem. While pH does not seem to be driven by carbonate equilibria on this landscape, high pH ecosystems apparently are associated with parent materials rich in exchangeable bases that also occupy dry sites where leaching rates may be slower.

Principal components analysis portrayed correlations among environmental variables and their relative importance in structuring the environmental matrix (Fig. 3.3a), with 40% of variance explained by principal component 1, 20% by component 2, and 10% by component 3. Component loadings were well balanced among 17 important environmental variables included in the analysis, consistent with ecosystem classification theory that multivariate combinations of environmental variables structure ecosystem distribution rather than single-factor gradients (Barnes et al., 1982; Host & Pregitzer, 1992; Goebel et al., 2001). Variables exhibiting the highest loadings on component 1 included 0-15 cm silt (loading = 0.35) and sand (-0.34), UTM easting (-0.29), 0-50 cm available water (0.29), 15-50 cm C and N (both 0.27), and 15-50 cm pH (-0.26). Based on three weather stations (Fig. 3.1) and a regional climate study (Jameson, 1969), UTM easting probably is partly correlated with a precipitation gradient increasing by ca. 14 cm yr^{-1} from east to west across the study area. Ecosystems containing soils with low water-holding capacities also tended to occur in eastern parts of the study area where low precipitation may amplify these dry-soil properties (Fig. 3.1). Dry-season gravimetric soil moisture differed by more than a factor of 20 across ecosystems, expressing these contrasting environmental complexes (Table 3.2). Parent material and its influence on soil properties, modified regionally by precipitation gradients and locally by rockiness or

geomorphic gradients, constrained the distribution, productivity, and composition of ecosystems on this landscape.

Species composition and richness

A total of 271 plant species occurred on the 66 open-canopy plots, with some species like *Phacelia sericea* (Graham) Gray (purplefringe) of black cinders/*Phacelia* ecosystems and *Symphyotrichum ascendens* (Lindl.) Nesom (western aster) of park/*Symphyotrichum* ecosystems, restricted to one ecosystem type (Table 3.3). *Muhlenbergia minutissima* (Steud.) Swallen (annual muhly), *Nama dichotomum* (Ruiz & Pavón) Choisy (wishbone fiddleleaf), and other annuals dominated black cinders/*Phacelia* ecosystems. These data concur with theories that annuals are successful in ecosystems of unpredictable moisture (Philippi, 1993), but may also be related to continuous disturbances caused by movements of the loose cinders (Fig. 3.2a). Grazing-resistant *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (broom snakeweed) or *Erigeron divergens* Torr. & Gray (spreading fleabane) dominated clay basalt/*Gutierrezia* or park/*Symphyotrichum* ecosystems, likely the most heavily grazed ecosystems (Clary, 1975). Mesic limestone/mixed flora ecosystems exhibiting intermediate soil resources (Table 3.2) shared species of many ecosystems and had no clear dominant species, seemingly consistent with hypotheses that intermediate resource levels promote species coexistence (Tilman & Pacala, 1993).

Grass distribution differentiated closely related basalt ecosystems, with C_4 *Muhlenbergia montana* important in xeric basalt/*Muhlenbergia* ecosystems and C_3 *Festuca arizonica* prominent in mesic basalt/*Festuca* ecosystems (Table 3.3). These distributions, combined with high importance of C_4 *Bouteloua gracilis* (Willd. ex Kunth)

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Lag. ex Griffiths (blue grama) in climatically dry ecosystems, support predictions that C_4 species have greater water-use efficiencies and competitive abilities in dry habitats than C_3 species (Wentworth 1983). Rocky basalt/*Sporobolus* ecosystems were distinguished by high importance of *Sporobolus interruptus* Vasey (black dropseed), *Lathyrus laetivirens* Greene ex Rydb. (aspen peavine), and *Pedicularis centranthera* Gray (dwarf lousewort). Legumes including *Lupinus argenteus* Pursh (silver lupine), *Vicia americana* Muhl. Ex Willd. (American purple vetch), and *Lathyrus lanszwertii* var. *leucanthus* (Rydb.) Dorn (Nevada vetchling) predominated in aspen/*Lathyrus* ecosystems. It is possible these legumes contributed to high soil N levels in this ecosystem (Crews, 1999). Park/*Symphyotrichum* ecosystems also contained several moist-affinity species including *Iris missouriensis* Nutt. (Rocky Mountain iris) and *Allium geyeri* S. Wats. (Geyer's onion) uncommon elsewhere.

Limestone ecosystems contained the most species per 500-m^2 plot, and richness per plot also averaged > 38 species in rocky basalt/*Sporobolus*, clay basalt/*Gutierrezia*, and red cinders/*Bahia* ecosystems (Fig. 3.4a). Black cinders/*Phacelia* and aspen/*Lathyrus* ecosystems, occupying extremes of productivity and soil-resource gradients, had the fewest species per plot. Aspen/*Lathyrus* ecosystems, however, exhibited high richness per 1-m^2 subplot, reflecting high species densities at fine grains in this ecosystem but rapid leveling off of species richness with increasing grain (Fig. 3.4b). Ecosystem distribution predicted spatial variation in species composition and richness on this landscape reasonably well, presumably because the ecosystem framework integrated factors constraining composition and richness (Lapin & Barnes, 1995).

***Pinus ponderosa* growth**

The oldest tree was dated to 1646 and all trees in the data set were of presettlement origin, recording growth rates in presttlement forests. Mean *Pinus ponderosa* diameter growth differed by nearly a factor of two across ecosystems (Fig. 3.5). The slowest growth occurred in red cinders/*Bahia* ecosystems, whereas the fastest growth occurred in aspen/*Lathyrus* ecosystems containing mixed *P. ponderosa-Populus tremuloides* forests. Growth rates also tended to be 0.7-0.8 mm yr^{-1} higher in mesic basalt than in rocky or xeric basalt ecosystems, probably reflecting the mesic basalt's greater rooting volume because of fewer rocks and more available water. While black cinders/*Phacelia* ecosystems contained inhospitable surface soils, variable but on average rapid diameter growth occurred once a tree established. This paradox may result because of minimal ground-flora competition, deep subsoils (> 1.5 m) consisting of alternating cinder-soil layers retaining subsoil moisture, or loose soils facilitating development of extensive, branched root systems (Haasis, 1921). Colton (1932) also noted rapid diameter growth near Sunset Crater in the study area, and Lindsey (1951) found that the greatest mean increment of 3.4 mm yr^{-1} among central New Mexico soils he studied occurred on volcanic cinder soils.

Previous research in southwestern *Pinus ponderosa* forests has been conflicting on whether *P. ponderosa* growth differs among land classification units (Meurisse et al., 1975; Stansfield et al., 1991). Mathiasen et al. (1987), for example, found that site index did not differ among seven vegetation-based habitat types in Colorado, New Mexico, and northern Arizona. Verbyla and Fisher (1989) also concluded that habitat types did not reliably predict *P. ponderosa* site index in southern Utah because of wide environmental variation within habitat types. Meurisse et al. (1975), however, reported site indices

ranging from 17-26 m (base age 100 yr) that differed significantly among 12 northern

Arizona soil series. My findings combined with those of Lindsey (1951) and Meurisse et

al. (1975) suggest that land classifications such as ecosystem classification are useful for

predicting *P. ponderosa* growth since these classifications incorporate environmental

variables affecting growth (Cox et al., 1960).

Classification in dense stands

A possible criticism of this ecosystem classification is that it was developed in open

presettlement-origin stands, whereas most of the landscape contains dense postsettlement

stands typically exceeding 1000 trees ha^{-1}, exhibiting low ground-flora cover, and often

requiring the most intensive restoration (Abella & Covington, 2004). Species

composition differentiated by ecosystem type even more strongly in dense than in open

stands, and ecosystems in dense stands also differentiated along rock cover, texture, and

other gradients like in open stands (Fig. 3.6). Mesic limestone/mixed flora ecosystems in

dense stands had sandy soil textures and no clear dominant species similar to their open

counterparts, while grass distribution and environmental gradients distinguished basalt

ecosystems. Ecosystem specificity of plant composition may have intensified in dense

stands because only high-fidelity species persisted below dense canopies, precluding

more widespread and opportunistic species able to occupy open stands.

Implications for ecological restoration

Reference conditions

Determining reference conditions is a major goal in restoration ecology, with reference

conditions for Arizona *Pinus ponderosa* forests usually considered to be ca. 1875

(European settlement) since this is the most recent time these forests are thought to have

been free of degrading factors such as fire exclusion (Moore et al., 1999). Three lines of

evidence suggest that ecosystems similar to those classified in this study occurred on this

landscape at the time of settlement: (1) abiotic variables such as soil texture forming

backbones of ecosystems are considered relatively stable landscape features (Palik et al.,

2000), (2) major differences in tree growth occurred among sites in prestttlement forests

(Fig. 1.5), and (3) historical reports and photos provide geographic-specific accounts of

occurrences of ecosystems like parks and sites exhibiting different soil texture and rock

cover (Rusby, 1889; Leiberg et al., 1904; Kircher, 1910). An important point is that

while grazing and other factors may have altered species composition of some

ecosystems since settlement (Hanson, 1924), these are similar ecosystem types but with

different species composition. A given ecosystem type may contain multiple species

compositions during different time periods (e.g., Archambault et al., 1989; Goebel et al.,

2001; Abella et al., 2003). This is consistent with a guiding premise of ecosystem

classification that vegetation comprises only one, and usually the least stable, of three

basic landscape ecosystem components of geomorphology, soils, and vegetation (Barnes

et al., 1982).

Reference conditions for herbaceous vegetation are not well known in *Pinus

ponderosa* forests similar to many ecosystems (Moore et al., 1999), hampering efforts to

define and restore target communities (Bakker et al., 2000). Although historical accounts

suggest that most native species presently on this landscape occurred in presettlement

forests, these accounts provide little information about species distributions and also

unfortunately occurred after initiation of heavy livestock grazing (Vasey, 1888; Britton,

1889). While herbarium records and other reconstructive methods (e.g., Kerns et al.,

2003) may provide additional clues to past composition, this study's information on contemporary ecosystems is one of the few currently available references on species-soil relationships. Although imperfect like other reference information and best used in combination with other data sources, contemporary ecosystems are an important source of reference information (White & Walker, 1997; Palik et al., 2000).

Current distributions among ecosystems for some species, for example, probably places approximate bounds on where these species occurred in presettlement forests (Table 3.3). In contrast to *Muhlenbergia montana*, for instance, *Festuca arizonica* is absent from dry ecosystems such as red cinders/*Bahia* ecosystems and likely did not occur in those ecosystems in presettlement forests because *F. arizonica* has a C_3 pathway poorly adapted to xeric sites (Sage & Monson, 1999). If a land manager has limited funds to purchase seeds for revegetating a rocky, loamy basalt site burned by wildfire, for example, revegetating the site with native species of the rocky basalt/*Sporobolus* ecosystem seems more accurate than using general species mixes that may or may not have grown on rocky basalt sites. Furthermore, experiments with current ecosystems such as reintroducing fire and comparing responses of different ecosystems may enhance our understanding of past composition of the diverse ecosystems on this landscape.

Prioritization and scale

Ecological restoration in the study area has largely been prioritized near the city of Flagstaff in the wildland-urban interface, which is prudent since recent wildfires in *Pinus ponderosa* forests have threatened settlements (Allen et al., 2002). This approach may not well prioritize other ecosystems farther from settlements, however, that also require restoration (Palik et al., 2000). Red cinders/*Bahia* ecosystems, for example, historically

were rare based on their soils distribution, occupying < 1840 ha or < 1.7% of the study area (US Forest Service, 1995). About 9/32 (28%) of this ecosystem's mapping units (> 30% of its area) also have been burned by crown fires since 1950, suggesting that red cinders/*Bahia* ecosystems are the most endangered landscape ecosystems in the study area. Priority could be given to restoring this ecosystem's remaining mapping units to forestall further losses by crown fires.

Ecosystem turnover occurs over broad extents on this landscape, with mapping units sometimes exceeding 1000 ha (US Forest Service, 1995), differing from ecosystem classifications in many eastern US forests where ecosystem turnover is spatially rapid (Lapin & Barnes, 1995; Goebel et al., 1999; McNab et al., 1999). Broad-extent turnover indicates that restoring dispersed mapping units of different ecosystems or large areas will be required to encompass ecosystem diversity in restoration on this landscape. Sizes of restoration units needed to encompass multiple ecosystem types, for instance, could be conceptualized as an ecosystem-area curve. Since financial and other resources often are limited for conducting restoration, estimating optimal sizes and distributions of restoration units for maximizing cumulative ecosystem diversity included in restoration is an important topic for future research.

CONCLUSION

Ecosystem distribution on this landscape followed the distribution of soil properties and parent materials, modified by regional precipitation gradients and locally by variables such as rock cover and geomorphology. An important area of future research is examining rare ecosystems such as springs or deep ravines (Crawford Zimmerman et al., 1999) I did not sample, which may be keystone ecosystems requiring special restoration

(Stohlgren et al., 1997). It is important to recognize that vegetation is one of the more transient and easily changed ecosystem components, whereas properties such as soil parent material are fixed for long time periods. This persistence suggests that the same basic ecosystems presently on this landscape occurred at the time of settlement. Multiple classifications, such as vegetation or stand condition classes, in combination with ecosystem classification likely will provide the most comprehensive site information database to guide restoration. A given ecosystem type may contain constituent sites widely differing in current conditions, with mesic basalt/*Festuca* ecosystems, for example, currently containing sites burned by crown fire or showing indications of overgrazing. Relatively intact sites within ecosystems, however, exhibited high degrees of similarity, suggesting that reference conditions within ecosystem types may be similar. This study provides an initial ecosystem framework for ecological restoration on this landscape that can be improved by future research measuring past species composition, fire regime, and stand structure reference conditions among ecosystems, estimating ecosystem-specific differences between reference and current conditions, identifying target communities for restoration, and replicating restoration experiments across ecosystem types to measure ecosystem-specific responses.

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Table 3.1 Summary of diagnostic environmental properties and examples of characteristic plant species of *Pinus ponderosa* landscape ecosystems, northern Arizona

_____

Black cinders/*Phacelia* (558)*

    Gravelly, surficial volcanic cinders 10-15 cm thick; low ground-flora cover; *Phacelia sericea, Nama dichotomum*

Red cinders/*Bahia* (513)

    Xeric, sandy loam soils; slow tree growth, moderate ground-flora cover; *Bahia dissecta, Muhlenbergia montana*

Clay basalt/*Gutierrezia* (523)

    Rocky, clay loam soils of climatically dry sites; slow tree growth; heavily grazed; *Gutierrezia sarothrae, Bouteloua gracilis*

Xeric limestone/*Bouteloua* (500)

    Sandy loam soils of neutral pH low in total N and organic C; climatically dry sites; *Bouteloua gracilis, Hymenopappus filifolius*

Mesic limestone/mixed flora (536)

    Climatically moist sandy loam soils; variable geomorphology; high plant diversity; *Festuca arizonica, Muhlenbergia montana*

Xeric basalt/*Muhlenbergia* (551, 570)†

    Lowest N and organic C of basalt ecosystems; *Muhlenbergia montana*

Rocky basalt/*Sporobolus* (570, 582, 585)

    High surface rock cover; slowest tree growth of basalt ecosystems; *Sporobolus interruptus, Pedicularis centranthera*

Mesic basalt/*Festuca* (551, 570, 582, 585)

    Silt loam soils high in N and organic C; rapid tree growth and productive understories; *Festuca arizonica, Carex geophila*

Aspen/*Lathyrus* (611)

    Mixed *Populus tremuloides-Pinus ponderosa*; deep sola > 1 m thick; high N and organic C; *Lathyrus lanszwertii, Lupinus argenteus*

Park/*Symphyotrichum* (55)

    Treeless basins 1 ha to > 1000 ha in size; clay loam soils with deep sola; heavily grazed; *Symphyotrichum ascendens, Allium geyeri*

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*Terrestrial ecosystem survey (US Forest Service, 1995) types on which ecosystems occurred are given in parenthesis.

†Basalt ecosystems also contained plots with benmoreite and mixed igneous parent materials.

Table 3.2 Soil properties of forest ecosystems of a northern Arizona *Pinus ponderosa* landscape. All variables are % by weight

except for pH

Variable	Depth (cm)	Black cinders	Red cinders	Clay basalt	Xeric limestone	Mesic limestone	Xeric basalt	Rocky basalt	Mesic basalt	Aspen	Park
Gravel	0-15	48a (17)*	39abc (23)	45ab (24)	11e (18)	22d (40)	36bc (19)	35bc (31)	31cd (24)	41abc (32)	37bc (23)
	15-50	38bc (25)	39abc (27)	54a (13)	26c (60)	49ab (33)	53a (30)	48ab (31)	36bc (39)	31c (48)	49ab (9)
Sand	0-15	93a (5)	63b (6)	30ef (17)	63b (19)	53bc (26)	45cd (44)	35def (14)	35def (23)	39de (15)	27f (22)
	15-50	87a (20)	57b (8)	24e (6)	51bc (20)	40cd (37)	35de (51)	31de (22)	35de (28)	37de (23)	31de (32)
Silt	0-15	6f (62)	28e (12)	38cd (20)	24e (15)	32de (31)	41bc (32)	44bc (9)	53a (15)	49ab (12)	42bc (21)
	15-50	10d (120)	32bc (14)	31bc (24)	25c (11)	31bc (58)	36b (14)	35b (20)	48a (18)	49a (10)	36b (31)
Clay	0-15	1d (123)	8c (15)	31a (35)	13c (69)	14c (36)	14c (55)	21b (18)	12c (17)	12c (27)	31a (25)
	15-50	4f (154)	10ef (42)	44a (17)	24cd (44)	29bc (45)	28bc (53)	34b (29)	17de (29)	14e (33)	34bc (20)
pH	0-15	6.5bcd (3)	6.6b (1)	6.6bc (4)	6.9a (3)	6.1ef (5)	6.3de (5)	6.0fg (2)	6.1fg (4)	6.4cde (3)	5.9g (3)
	15-50	6.7b (2)	6.8ab (1)	6.8b (4)	7.0a (2)	6.4c (8)	6.3cd (5)	6.0e (4)	6.2cde (3)	6.2cde (3)	6.1de (1)
$CaCO_3$†	0-15	0.8 (23)	0.0 (0)	0.0 (0)	3.3 (191)	0.1 (108)	0.7 (172)	0.4 (156)	0.3 (117)	0.3 (100)	0.3 (158)
	15-50	0.8 (138)	0.7 (244)	0.0 (0)	28.0 (195)	1.7 (132)	0.1 (214)	0.6 (218)	0.4 (70)	1.8 (217)	0.6 (220)

Organic C	0-15	1.5cde (63)	2.1bc (24)	1.3e (17)	1.1e (24)	1.3de (35)	1.3de (23)	1.9bcd (28)	2.2b (31)	3.1a (28)	1.6bcde (16)
	15-50	0.3d (51)	0.9bc (31)	1.0bc (37)	0.9bc (31)	0.8c (28)	1.0bc (24)	1.1bc (34)	1.2b (42)	1.7a (23)	1.0bc (16)
Total N	0-15	0.07f (36)	0.12bcd (23)	0.13bcd (17)	0.07f (39)	0.08ef (27)	0.09def (33)	0.11cde (18)	0.14bc (33)	0.26a (30)	0.15b (12)
	15-50	0.02e (111)	0.07d (20)	0.11b (13)	0.08cd (43)	0.07d (24)	0.08cd (35)	0.08cd (29)	0.10bc (34)	0.15a (18)	0.13ab (16)
Moisture‡	0-15	0.5d (60)	1.7cd (59)	___	4.1bc	___	___	___	5.6b (27)	10.7a (17)	8.4a (32)

*Values are mean (coefficient of variation). Means without shared letters within rows differ at $P < 0.05$.

†CaCO$_3$ equivalent.

‡Gravimetric soil moisture (% oven dry weight) measured 19 June 2004 during the driest period of the year in the study area; — not measured.

Table 3.3 Importance values and 0.05-ha plot frequencies for 24 common species in forest ecosystems of a northern Arizona *Pinus ponderosa* landscape. Species are arranged from dry to moist affinities, and values in bold represent ecosystems in which a species was most important

Species	Black cinders	Red cinders	Clay basalt	Xeric limestone	Mesic limestone	Xeric basalt	Rocky basalt	Mesic basalt	Aspen	Park
Phacelia sericea	**5 (50)***	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Nama dichotomum	**5 (33)**	0 (0)	<1 (33)	0 (0)	<1 (17)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Chenopodium graveolens	**22 (83)**	2 (100)	0 (0)	0 (0)	<1 (17)	<1 (20)	<1 (38)	0 (0)	0 (0)	<1 (17)
Muhlenbergia minutissima	**8 (33)**	0 (0)	0 (0)	0 (0)	<1 (17)	<1 (20)	<1 (38)	<1 (9)	0 (0)	<1 (17)
Bahia dissecta	**5 (100)**	**9 (100)**	0 (0)	<1 (67)	0 (0)	<1 (20)	0 (0)	<1 (27)	0 (0)	0 (0)
Bouteloua gracilis	**18 (83)**	**14 (100)**	**26 (100)**	**24 (100)**	2 (33)	<1 (20)	<1 (25)	0 (0)	0 (0)	1 (17)
Gutierrezia sarothrae	0 (0)	**1 (67)**	**6 (100)**	**2 (83)**	0 (0)	0 (0)	0 (0)	<1 (9)	0 (0)	0 (0)
Heliomeris longifolia	0 (0)	0 (0)	**6 (83)**	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Hymenoxys richardsonii	0 (0)	<1 (17)	**2 (100)**	**3 (100)**	<1 (33)	1 (80)	<1 (13)	<1 (18)	0 (0)	<1 (33)
Muhlenbergia montana	7 (17)	19 (83)	<1 (17)	10 (50)	11 (83)	**29 (100)**	7 (75)	13 (100)	5 (83)	0 (0)

Species										
Cirsium wheeleri	0 (0)	<1 (50)	<1 (100)	<1 (83)	**3 (83)**	**5 (100)**	**3 (100)**	**2 (91)**	<1 (50)	0 (0)
Elymus elymoides	**9 (83)**	**8 (100)**	**4 (100)**	**6 (83)**	**11 (100)**	**8 (100)**	**11 (100)**	**9 (100)**	**10 (100)**	2 (83)
Poa fendleriana	0 (0)	4 (67)	1 (67)	2 (100)	**4 (83)**	**5 (100)**	**10 (100)**	**4 (100)**	**4 (100)**	<1 (17)
Blepharoneuron tricholepis	0 (0)	0 (0)	<1 (17)	0 (0)	2 (67)	2 (80)	**5 (75)**	<1 (18)	0 (0)	<1 (17)
Sporobolus interruptus	0 (0)	0 (0)	0 (0)	0 (0)	<1 (33)	0 (0)	**6 (63)**	0 (0)	0 (0)	0 (0)
Carex geophila	0 (0)	<1 (17)	<1 (17)	<1 (17)	2 (83)	3 (100)	**9 (100)**	**11 (100)**	**6 (100)**	1 (50)
Festuca arizonica	0 (0)	0 (0)	0 (0)	3 (67)	9 (67)	9 (80)	1 (50)	**18 (100)**	**17 (100)**	0 (0)
Lupinus argenteus	0 (0)	0 (0)	0 (0)	<1 (17)	2 (50)	2 (60)	<1 (25)	**9 (100)**	**13 (100)**	<1 (33)
Vicia americana	0 (0)	0 (0)	0 (0)	<1 (17)	2 (100)	<1 (40)	1 (50)	2 (82)	**6 (100)**	0 (0)
Lathyrus lanszwertii	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	<1 (36)	**6 (67)**	0 (0)
Erigeron divergens	0 (0)	0 (0)	**11 (100)**	2 (100)	2 (83)	2 (80)	3 (75)	1 (73)	0 (0)	**19 (100)**
Muhlenbergia wrightii	0 (0)	0 (0)	3 (83)	0 (0)	0 (0)	0 (0)	<1 (13)	<1 (9)	0 (0)	**13 (100)**
Coreopsis tinctoria	0 (0)	0 (0)	<1 (17)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	**6 (83)**
Symphyotrichum ascendens	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	**6 (100)**

*Values are mean importance value (% frequency). Importance values are in % and are the average of relative cover and relative frequency.

Figure 3.1 Distribution of 66 sample plots and their classification into ecosystem types for a northern Arizona *Pinus ponderosa* landscape, USA (UTM zone 12). Geographic features are abbreviated as GF and weather stations as WS. Although at similar elevations (2128-2244 m), precipitation based on > 35 years of records averages 42 cm yr^{-1} at the eastern weather station 3 (Sunset Crater), 54 cm yr^{-1} at central station 2 (Flagstaff Airport), and 56 cm yr^{-1} at station 3 (Fort Valley). Ecosystem type abbreviations are as follows: AN = aspen/*Lathyrus*, BC = black cinders/*Phacelia*, CB = clay basalt/*Gutierrezia*, MB = mesic basalt/*Festuca*, ML = mesic limestone/mixed flora, PK = park/*Symphyotrichum*, RB = rocky basalt/*Sporobolus*, RC = red cinders/*Bahia*, XB = xeric basalt/*Muhlenbergia*, and XL = xeric limestone/*Bouteloua*.

Figure 3.2 Examples of ecosystems of a northern Arizona *Pinus ponderosa* landscape, USA. Black cinders/*Phacelia* ecosystems (a) contain dry surface soils of loose volcanic cinders, low ground-flora cover, and high importance of *Phacelia sericea* and other annuals (452800 mE, 3905545 mN, zone 12). Mesic basalt/*Festuca* ecosystems (b) have silt loam soils, high understory cover of *Festuca arizonica* and *Lupinus argenteus*, and rapid *P. ponderosa* diameter growth (438407 mE, 3916244 mN). Treeless park/*Symphyotrichum* ecosystems (c) occupy depressions, are heavily grazed, and have high abundance of *Symphyotrichum ascendens* and *Erigeron divergens* (425369 mE, 3887662 mN). Photos by S.R. Abella, summer 2003.

Figure 3.3 Principal components analysis ordination of environmental variables (a) and non-metric multidimensional scaling ordination of vegetation (b) of a northern Arizona

Pinus ponderosa landscape, USA. For soil variables, A = 0-15 cm and B = 15-50 cm.

UTM(x) partly portrays a geographic gradient of increasing precipitation from east to

west across the study area. Vector abbreviations for species in (b) are as follows:

BAHDIS = *Bahia dissecta*, BOUGRA = *Bouteloua gracilis*, CARGEO = *Carex geophila*,

ERIDIV = *Erigeron divergens*, FESARI = *Festuca arizonica*, GUTSAR = *Gutierrezia*

sarothrae, HYMRIC = *Hymenoxys richardsonii*, LUPARG = *Lupinus argenteus*,

MUHMON = *Muhlenbergia montana*, and SYMASC = *Symphyotrichum ascendens*.

Figure 3.4 Mean species richness per (a) 500-m^2 plot and (b) 1-m^2 subplot for forest

ecosystems of a northern Arizona *Pinus ponderosa* landscape, USA. Means without

shared letters differ at $P < 0.05$. Error bars are 1 SD.

Figure 3.5 Mean *Pinus ponderosa* diameter increment among forest ecosystems of a

northern Arizona *Pinus ponderosa* landscape, USA. Means without shared letters differ

at $P < 0.05$. Error bars are 1 SD.

Figure 3.6 Non-metric multidimensional scaling ordination of ground-flora vegetation

and ecosystem type classifications for 26 plots in dense *Pinus ponderosa* postsettlement

stands (> 1000 trees ha^{-1}), northern Arizona, USA. For soil variables, A = 0-15 cm and B

= 15-50 cm depth. Vector abbreviations for species in are as follows: ASTTRO =

Astragalus troglodytus, CARGEO = *Carex geophila*, MUHMON = *Muhlenbergia*

montana, PEDCEN = *Pedicularis centranthera*, and SPOINT = *Sporobolus interruptus*.
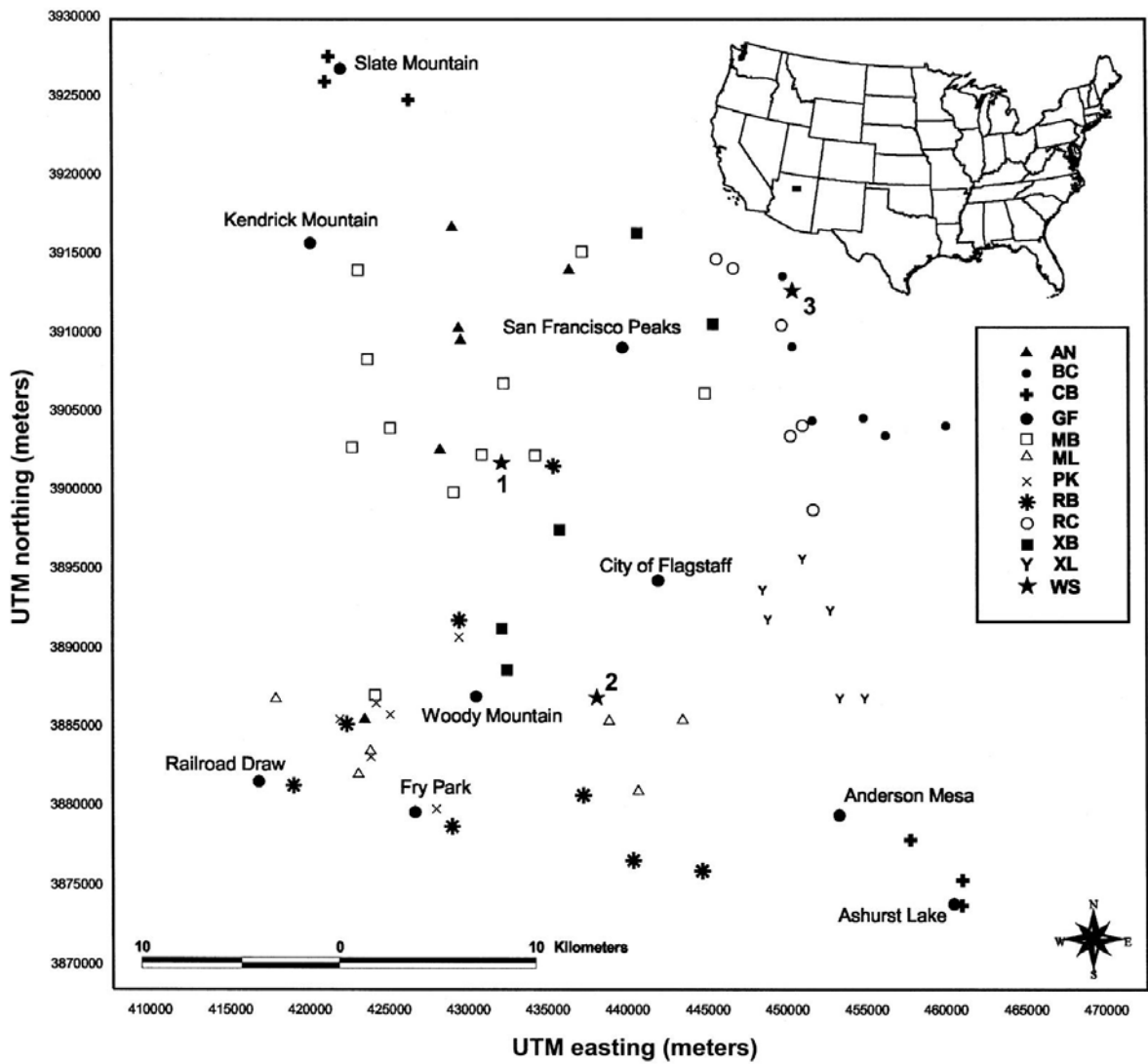
Figure 3.1

Figure 3.2 (a)

Figure 3.2 (b)

Figure 3.2 (c)
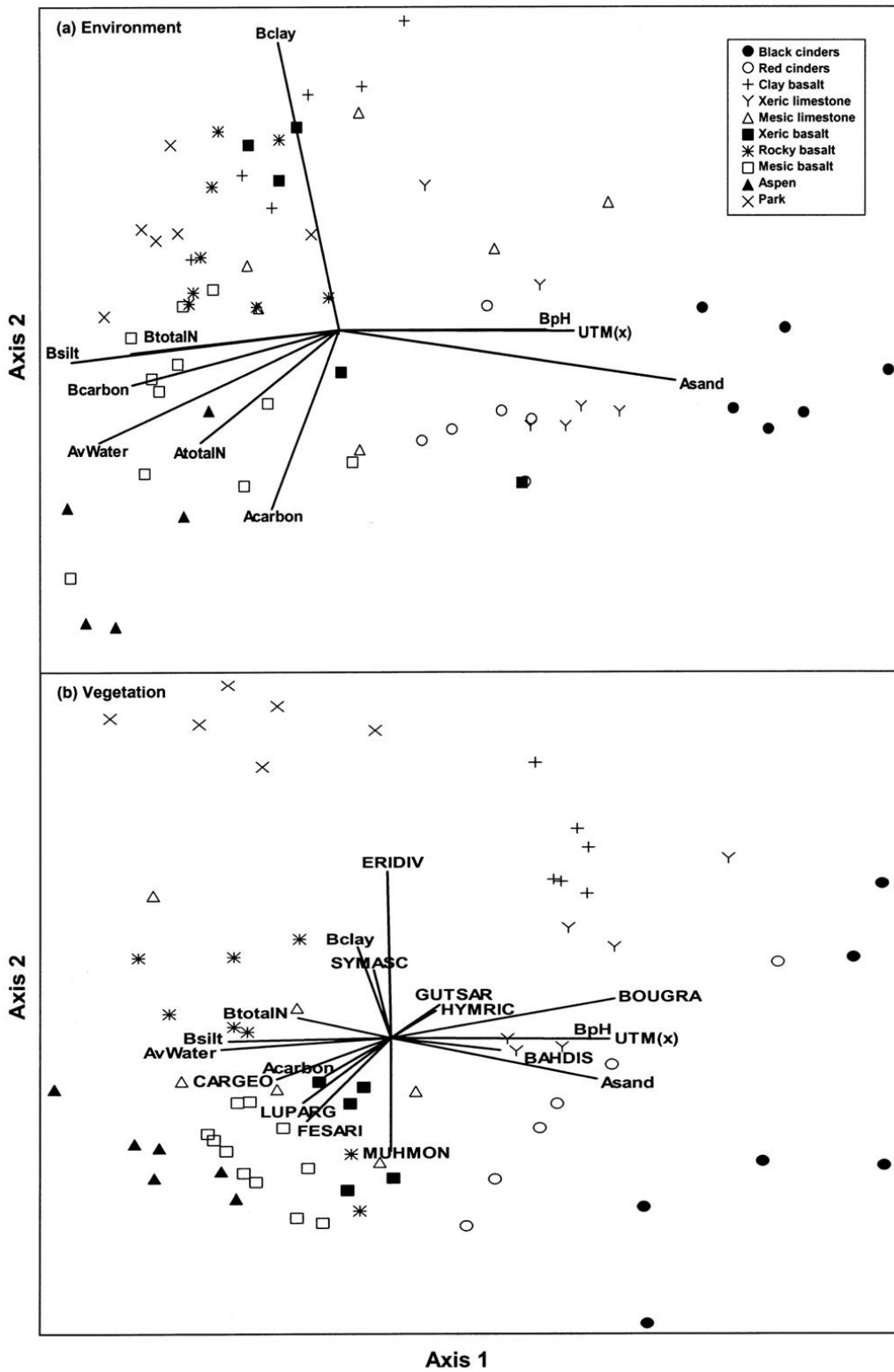
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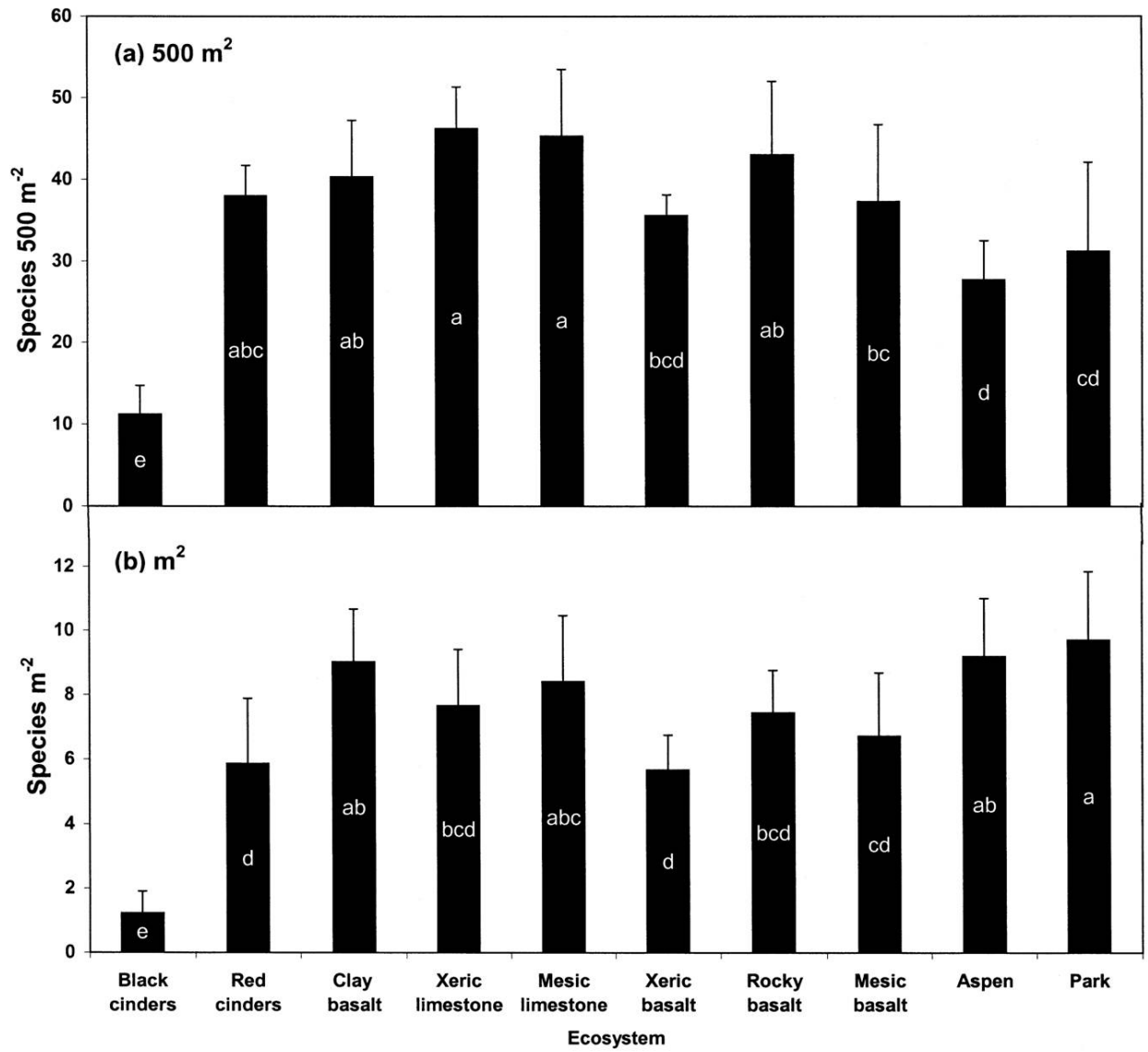
Figure 3.4
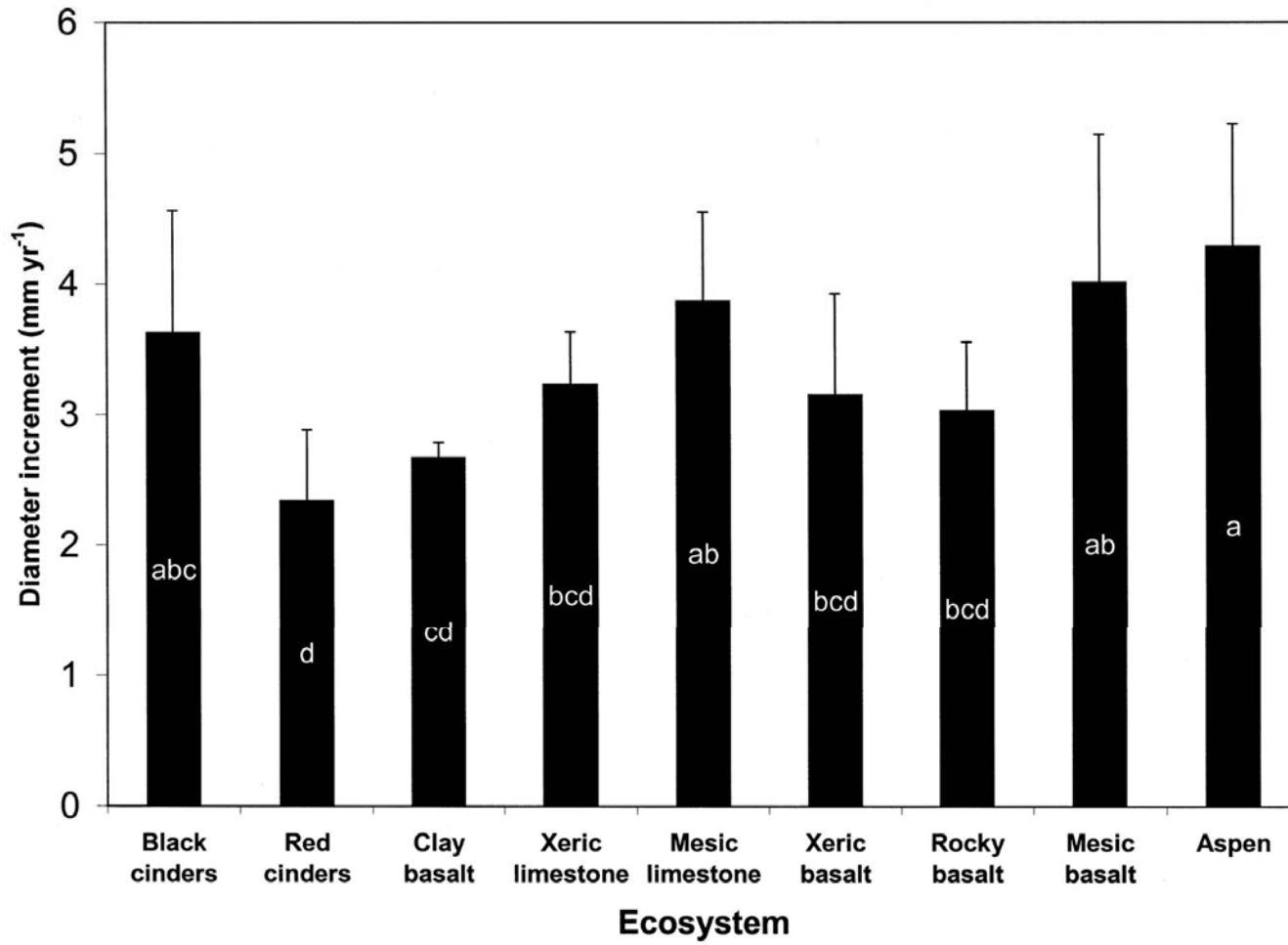
Figure 3.5
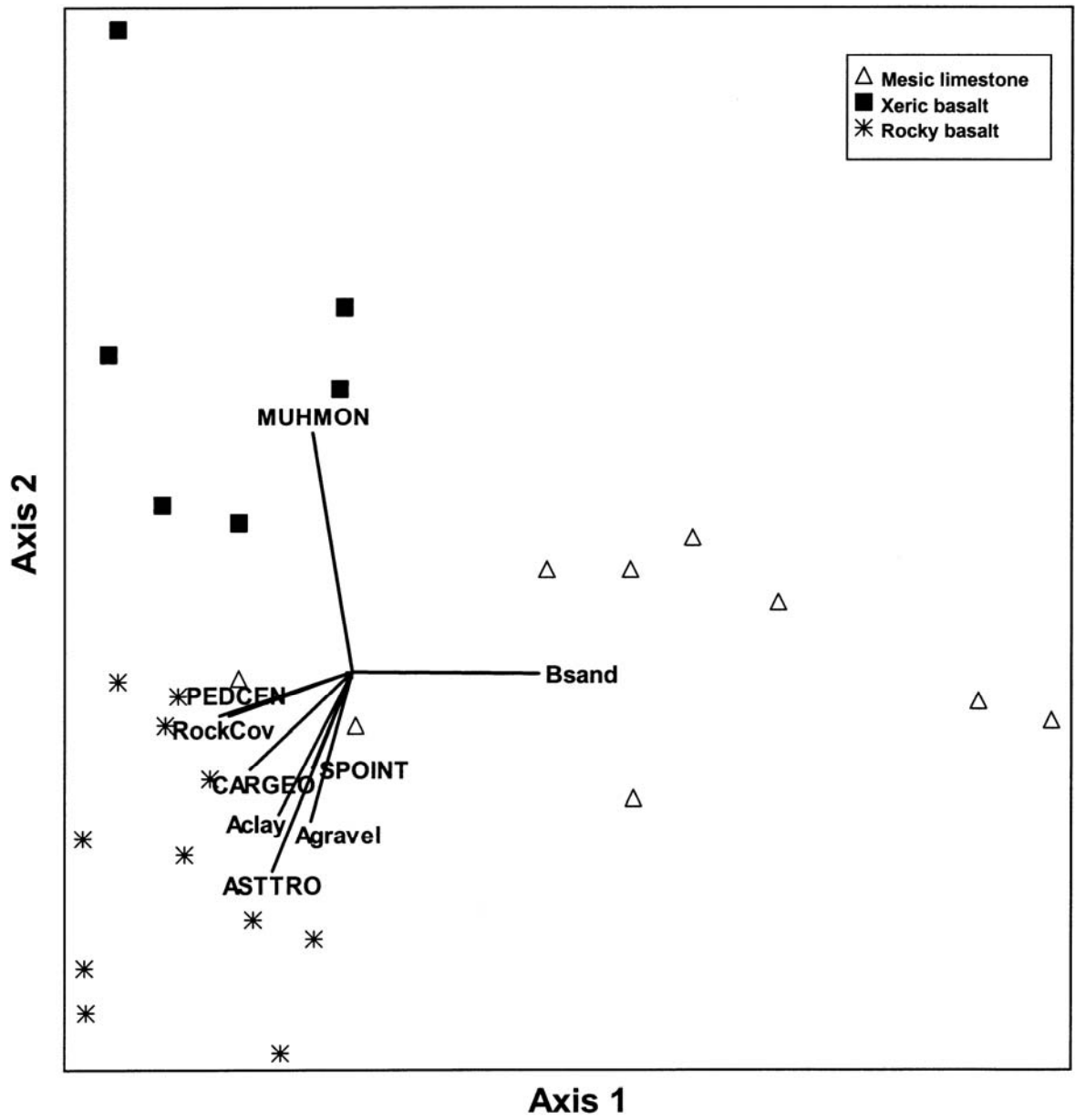
Figure 3.6

CHAPTER 4

VEGETATION-ENVIRONMENT RELATIONSHIPS AND ECOLOGICAL SPECIES GROUPS OF AN ARIZONA *PINUS PONDEROSA* LANDSCAPE, USA

Key words: Ecosystem classification, Forest, Geomorphology, Ground flora, Understory, Soil

Abstract

I developed ecological species groups, consisting of co-occurring plant species exhibiting similar environmental affinities, on a 110,000-ha *Pinus ponderosa* landscape in northern Arizona, USA to provide data on vegetation-environment relationships and species distributions. I measured geomorphology, soils, and vegetation on 66, 0.05-ha plots, and classified 52 of the 271 detected plant species into 18 ecological species groups. Species groups ranged from *Phacelia* and *Bahia* groups occupying xeric, volcanic cinder soils low in organic C and total N, to *Festuca* and *Lathyrus* groups characterizing moist, loam-silt loam soils. Upper 0-15 cm soil total N, for example, averaged only 0.09% on 12 plots where a *Bahia* group exhibited its highest importance, compared to 0.19% on 12 plots where a *Festuca* group was most important. Using discriminant analysis, I also built a model that correctly classified the most important of four grasses (*Bouteloua gracilis*, *Muhlenbergia montana*, *Sporobolus interruptus*, or *Festuca arizonica*) on 70-80% of plots based on five environmental variables related to soil moisture and resource levels. I applied this study's data in a regression tree model using abundances of key plant species to estimate diameter increment of old-growth *P. ponderosa*. The most rapid

P. ponderosa diameter growth averaging 4.9 mm/yr occurred on plots with high importance of *Lupinus argenteus* and *F. arizonica*. Soil parent material, affected by the presence or absence of volcanic activity, seems a primary factor constraining vegetation patterns on this landscape. My results on this semi-arid landscape support several general ecological species group principles chiefly developed in temperate regions, and suggest that vegetation-environment research has great potential for enhancing our understanding of *P. ponderosa* forests occupying vast areas of the southwestern United States.

Introduction

Ecological species groups consist of co-occurring plant species sharing similar environmental affinities (Spies and Barnes 1985; Godart et al. 1989; Grabherr et al. 2003). Species groups are based on the theory that evolutionary and community processes such as competition confine species to environmental complexes where they are best adapted (Host and Pregitzer 1992; Kashian et al. 2003). Species group research identifies environmental gradients correlated with species distributions, classifies species assemblages occupying similar environmental complexes, and relates species distributions to management-oriented variables such as tree growth (Bergeron and Bouchard 1984; Hix 1988; Host and Pregitzer 1991). Based on the principle that vegetation expresses environmental site conditions, once species groups are developed for an area their distribution can be used to rapidly estimate soil properties and other variables relatively difficult to measure (Pregitzer and Barnes 1982; Meilleur et al. 1992).

In North America, species groups have been most frequently developed for temperate ecosystems, including Michigan hardwood forests (Archambault et al. 1989; Simpson et al. 1990; Host and Pregitzer 1991) and Georgia Coastal Plain *Pinus palustris*

(longleaf pine) savannas (Goebel et al. 2001). Kashian et al. (2003), for example, classified eight species groups comprised of 31 species occurring along soil texture and drainage gradients on a Michigan *Pinus banksiana* (jack pine) landscape. Presence of a *Fragaria* group indicated soils containing fine-textured bands where *P. banksiana* height growth was rapid, whereas a *Rubus* group indicated sandy sites with slow *P. banksiana* growth. On a southern Appalachian landscape, soil solums averaged 120 cm thick when a *Sanguinaria* group typified by *Sanguinaria canadensis* (bloodroot) was abundant, compared to only 61 cm thick when this group was sparse (Abella and Shelburne 2004). Species-rich, productive sites were associated with thick soil solums, which could be readily identified without making soil measurements by observing the distribution of the *Sanguinaria* group. These studies illustrate that species groups have been useful on contrasting landscapes, and among-landscape differences can be expected in environmental variables affecting moisture, nutrients, and other factors constraining species distributions.

Occupying more than 3.4 million hectares in Arizona and New Mexico alone, southwestern United States *Pinus ponderosa* (ponderosa pine) forests inhabit a diversity of landscapes differing in topography and soil parent material (Brown 1994). This large environmental variation and few published soil-plant community data suggest that species group research may be useful in *P. ponderosa* forests. Ecosystem integrity has declined in these forests since European settlement (ca. 1875) from several factors, including exclusion of historically frequent surface fires, increasing density of small-diameter trees, and heavy livestock grazing (Covington et al. 1994; Allen et al. 2002). Ecological restoration, chiefly tree thinning and prescribed burning, is ongoing in *P.*

ponderosa forests to return ecosystem structure and function to within a range of variability thought to characterize presettlement forests (Fulé et al. 1997). I undertook this study to determine environmental gradients most strongly correlated with plant distributions by developing ecological species groups on a 110,000-ha Arizona *P. ponderosa* landscape to improve our understanding of the *P. ponderosa* landscapes we are trying to restore. I illustrate an application of these data by predicting diameter increments of old-growth *P. ponderosa* based on relative abundances of key plant species.

Methods

Study area

This study was performed at elevations between 1920-2660 m in northern Arizona, USA on the north half of the Coconino National Forest and on the Northern Arizona University Centennial Forest (Fig. 4.1). Based on Jameson's (1969) regional climate study and three weather stations each with > 35 years of records, precipitation increases and temperatures decrease from east to west across the study area. Mean total precipitation ranges from 42-56 cm/yr, snowfall from 152-233 cm/yr, and maximum mean daily temperatures from 15.7-17.5 ^{o}C (Western Regional Climate Center, Reno, NV). Slope gradients are less than 10% on most of the landscape, occasionally greater in deep ravines and on cinder cones. Volcanic activity has affected soil properties in many parts of the study area, with the most recent volcanic eruptions occurring ca. 900 years ago near Sunset Crater in the northeastern part of the study area (Moore et al. 1976). Major soil subgroups include Typic and Udic Argiborolls, Typic and Mollic Eutroboralfs, Typic Ustorthents, and Vitrandic Ustochrepts (U.S. Forest Service 1995). Forests are primarily pure *Pinus*

ponderosa, but *P. ponderosa* occurs with *Populus tremuloides* (trembling aspen) or

Quercus gambelii (Gambel oak) in some stands.

Site selection and ecosystem classification

I used a terrestrial ecosystem survey (TES) soil map (U.S. Forest Service 1995) of the

study area to randomly select six mapping units for sampling in each of 11 TES types

(55, 500, 513, 523, 536, 551, 558, 570, 582, 585, and 611) covering a range of soil types.

TES classifies soils to families and provides information similar to county soil surveys

common in the eastern United States (U.S. Forest Service 1995). I sampled one 20 x 25

m (0.05 ha) plot in each mapping unit (n = 66 plots) in areas exhibiting open canopies,

relatively intact understories, and no visual indications of major recent disturbance.

Areas dominated by old-growth trees most frequently met these criteria (Kerns et al.

2003). I did not sample springs, deep ravines, or other rare ecosystems (Crawford

Zimmerman et al. 1999), as my focus was on widespread landscape ecosystems

occupying > 95% of the study area.

Ecological species groups often are developed in conjunction with ecosystem

classification because species distributions can then be interpreted among environmental

gradients treated as continuums or compared among ecosystem types (e.g., Goebel et al.

2001). I classified the 66 plots into 10 ecosystem types (Fig. 4.1) internally similar in

environmental and vegetational characteristics described in detail in Abella (2005) using

methods similar to Abella et al. (2003). I named ecosystems based on diagnostic plant

species and environmental features such as soil parent material. Ecosystems ranged from

sandy-textured black cinders/*Phacelia* ecosystems containing dry volcanic cinder soils

and low plant cover, to silt loam mesic basalt/*Festuca* ecosystems with high cover of

Festuca arizonica (Arizona fescue), *Carex geophila* (White Mountain sedge), and

Lupinus argenteus (silvery lupine). Other ecosystems included treeless

park/*Symphyotrichum* ecosystems occupying depressions often with clay loam soils, and

aspen/*Lathyrus* ecosystems containing mixed *Pinus ponderosa-Populus tremuloides*

(trembling aspen) forests with loamy soils high in total N and plant cover.

Field and laboratory procedures

I sampled ground flora in 15, 1-m^2 subplots centered at 0.5, 5, 12.5, 20, and 24.5 m along

the bottom, middle, and top axes of each of the 66 plots. I visually categorized percent

cover of each species rooted in each subplot as 0.1, 0.25, 0.5, and 1% up to 1% cover, at

1% intervals to 10% cover, and at 5% intervals above 10% cover. Measurement error

averaged < 2% for total cover and < 0.5 species/m^2 based on remeasuring two randomly

selected subplots every six plots. I recorded species in whole plots on a presence/absence

basis, and assigned these species a frequency of 1 and the lowest cover value for

computing importance values. I calculated importance values on a plot basis for each

species as the average of relative frequency and relative cover (summing to 100% for

each plot). Sampling occurred from May-August 2003. Nomenclature follows USDA-

NRCS (2004).

Geomorphic variables I collected on each plot included slope gradient,

transformed aspect (Beers et al. 1966), and terrain shape index that measures local

topographic shape (McNab 1989). I measured rock cover every 0.3 m on a 25-m transect

by recording the percentage of rock intercepts out of 83 points. I collected composite soil

samples from 0-15 and 15-50 cm layers by digging a 50-cm deep pit at the northwest and

southeast corners of each plot.

Soil samples were air dried, sieved through a 2-mm sieve, and analyzed for $CaCO_3$ equivalent (Goh et al.'s [1993] approximate gravimetric method), texture (hydrometer method), pH (1:2 soil:0.01 M $CaCl_2$), and organic C and total N (C/N analyzer after HCl removal of inorganic C) following Bartels and Bigham (1996) and Dane and Topp (2002). Analysis of duplicate samples every 10 samples indicated that analytical error averaged < 5%. I estimated soil available water capacity for each plot from texture, gravel, and organic matter (organic C × 1.724) using Saxton et al.'s (1986) equations available online (http://hydrolab.arsusda.gov/soilwater/Index.htm).

I measured *Pinus ponderosa* diameter growth on all plots except for six treeless plots in park/*Symphyotrichum* ecosystems by coring two trees per plot at 40 cm above ground level. I selected trees for coring that were open-grown dominants of presettlement origin. Old-growth *P. ponderosa* can be readily identified by their bark color that turns from black to yellow-orange after ca. age 100 yr (Schubert 1974). Cores were mounted, sanded, and cross-dated using local tree-ring chronologies (Fulé et al. 1997). I used age 50-150 yr increment averaged on a plot basis as a growth measure for the early-middle life stage of *P. ponderosa* (Schubert 1974).

Statistical analyses

To identify environmental variables most strongly correlated with plant community composition, I ordinated the vegetation importance value matrix with environmental vectors using non-metric multidimensional scaling (autopilot, thorough mode) in PC-ORD (McCune and Mefford 1999). I used discriminant analysis (SAS Institute 1999) to model distributions of four major grasses based on environmental variables. I employed stepwise selection to identify variables for inclusion in the model, and I also manually

entered combinations of variables (Tabachnick and Fidell 1996). Five of the six variables identified in stepwise selection provided high discriminatory power for as few variables as possible. I used equal prior probabilities, and employed cross-validation (jackknifing) for examining model robustness (SAS Institute 1999).

I developed ecological species groups in an R-mode analysis (McCune and Grace 2002) including hierarchical cluster analysis (Sørensen distance and -0.25 Flexible Beta group linkage method) and non-metric multidimensional scaling in PC-ORD (McCune and Mefford 1999). I relativized importance values for these analyses by species sums of squares to emphasize habitat preferences, avoiding groupings based on the commonness or rarity of species (McCune et al. 2000). Species groups identified in non-metric multidimensional scaling were similar to those identified in cluster analysis, and I also examined raw data to refine groupings portrayed by these multivariate analyses (Kashian et al. 2003). I included 52 species in species groups, representing common species whose distributions could be assessed based on available data. While species groups identified in these analyses are a logical classification of species displaying similar environmental affinities, this classification is one of a few reasonable groupings (Kashian et al. 2003; Abella and Shelburne 2004). I used a regression tree model (Breiman et al. 1984) in S-PLUS software (Insightful Corporation 2001) to estimate *Pinus ponderosa* diameter increment based on importance values of plant species. Regression trees partition independent variables similar to a dichotomous botanical key, and provide point estimates for dependent variables corresponding to different levels of independent variables (McCune and Grace 2002). I input 15 major species to the regression algorithm, which retained four species in the final model.

Results and discussion

Community-environment gradients

Plant community composition was correlated with moisture-affecting soil physical properties such as texture, Universal Transverse Mercator (UTM) easting probably partly reflecting a precipitation gradient (Jameson 1969; Fig. 4.1), and soil-resource gradients such as total N (Fig. 4.2). Variables most strongly correlated (Pearson $r^2 > 0.2$) with axis 1 or 2 of the community ordination included 0-15 cm sand, 0-50 cm available water capacity, 15-50 cm silt, 0-15 cm organic C, 15-50 cm total N, UTM easting, and 15-50 cm pH. *Festuca arizonica* and *Lupinus argenteus* increased in community importance with increasing soil available-water capacity, and silt, organic C, and total N concentrations. *Bahia dissecta* (ragleaf bahia), in contrast, increased with increasing sand and decreasing available water, organic C, and total N.

Species composition was not strongly correlated ($r^2 < 0.08$) with the geomorphic variables of slope gradient, aspect, and terrain shape index. Gently sloping ravines and drainages on this landscape are common, but these topographic features apparently need to be especially large or steep before they appreciably affect vegetation patterns (Crawford Zimmerman et al. 1999). Soil parent material rather than geomorphology primarily structures vegetation patterns at broad extents on this landscape (Fig. 4.2). Parent material on this landscape largely depends on the presence or absence of volcanic activity and the age and type of volcanic material (Welch and Klemmedson 1975; Moore et al. 1976).

Modeling species distributions

Grasses had the highest average importance among plant lifeform functional groups in all 10 classified ecosystem types, and I modeled which one of four dominant grasses would have the highest importance value at different levels of five environmental variables using discriminant analysis (Table 4.1). The model correctly classified the most important grass on 80% of plots in resubstitution and 70% in cross-validation. Consistent with ordination results (Fig. 4.2), *Festuca arizonica* was most important on plots with high soil available-water capacity. *Bouteloua gracilis* (blue grama), however, dominated plots with lower water-holding capacities, higher pH (> 6.5), and also tended to occur in clay basalt/*Gutierrezia*, xeric limestone/*Bouteloua*, and cinder ecosystems where precipitation is sparse (Fig. 4.1). *Sporobolus interruptus* (black dropseed) occupied clayey sites and was largely restricted to plots of the rocky basalt/*Sporobolus* ecosystem exhibiting high surface rock cover (> 10%) usually occurring in the study area's south half. *Muhlenbergia montana* was important on a range of plots, but importance of this species declined while importance of *F. arizonica* increased in loam-silt loam mesic basalt/*Festuca* and aspen/*Lathyrus* ecosystems. These distributional differences could be related to photosynthetic pathways, with the C_4 *M. montana* more competitive on drier sites than the C_3 *F. arizonica* (Sage and Monson 1999).

Plots misclassified by the model mostly occurred where two species had nearly equal importance values. Misclassifications occurred for dry plots where *Bouteloua gracilis* and *Muhlenbergia montana* were co-dominant, and on plots of the mesic limestone/mixed flora ecosystem where *Festuca arizonica* and *M. montana* were co-dominant (Table 4.1). Nevertheless, this model's reasonably good accuracy suggests that development of quantitative species-environment models has potential for increasing our

understanding and predictive ability of plant distributions at plot scales on southwestern *Pinus ponderosa* landscapes.

Similar to grasses, many forbs occupied characteristic environmental complexes, illustrated for six species along soil texture and fertility gradients (Fig. 4.3). *Bahia dissecta*, for example, dominated plots sandier and lower in total N than *Lupinus argenteus*. Occupying a fairly narrow range of site conditions, *Pedicularis centranthera* (dwarf lousewort) occurred on plots containing 0.05-0.1% total N and 20-40% 15-50 cm sand. *Penstemon linarioides* (toadflax penstemon) occurrences were not soil-texture specific, but 0-15 cm pH exceeded 6.5 on 89% (8/9) of this species' occurrences. *Antennaria parvifolia* (small-leaf pussytoes) and *Vicia americana* (American vetch) exhibited similar distributions, occupying loam and silt loam sites of lower pH than *P. linarioides*. These data suggest that observing abundances of groups of species can facilitate rapid field assessments of environmental site conditions such as texture and soil N on this landscape.

Ecological species groups

I classified 18 ecological species groups comprised of 52 plant species, with groups differentiating along soil texture and other gradients (Fig. 4.4, Table 4.2). The *Phacelia* group, for example, consisting of *Phacelia serrata* (saw phacelia), *Penstemon clutei* (Sunset Crater beardtongue)*,* and *Physaria newberryi* (Newberry's twinpod), was restricted to plots in black cinders/*Phacelia* ecosystems containing the driest surface soils in the study area. Upper 0-15 cm sand concentration averaged 92%, 15-50 cm organic C only 0.2%, and 15-50 cm total N only 0.02% in the three plots where the *Phacelia* group occurred. Similarly, *Erysimum capitatum* (sanddune wallflower) and *Hymenoxys*

subintegra (Arizona rubberweed) comprising the *Erysimum* group were restricted to red cinders/*Bahia* ecosystems, and also indicated sandy sites low in organic C and total N. In contrast, the *Festuca* group, composed of *Festuca arizonica, Lupinus argenteus,* and *Carex geophila*, indicated moist, loam-silt loam productive soils rich in C and N. On 13 plots where total importance of the *Festuca* group exceeded 30% (range = 30-51%), 0-15 cm silt averaged 52%, 15-50 cm organic C 1.5%, and 15-50 cm total N 0.13%. Although overlapping in distribution, the *Muhlenbergia* group typified by *Muhlenbergia montana* indicated sandier textures and lower soil-resource levels than the *Festuca* group. Upper 0-15 cm silt concentration averaged 19% lower, and 15-50 cm organic C and total N were half as concentrated on the 13 plots where the *Muhlenbergia* group was most important (importance values = 26-43%) compared to the 13 plots where the *Festuca* group was most important.

In a vegetation classification of central and northern Arizona, Hanks et al. (1983) also noted that *Festuca arizonica* occupied moister sites than *Muhlenbergia montana* which occurred over a broader range of dry-moist sites. Korstian (1917) similarly reported that *F. arizonica* was most abundant on moist sites in west central New Mexico *Pinus ponderosa* forests. My results also agree with Hanson's (1924) finding in the study area that *Bouteloua gracilis* and *Bahia dissecta* were dominants on dry cinder soils. Lindsey (1951), however, reported that *B. dissecta* and *F. arizonica* both occupied cinder benches consisting of volcanic ash on a New Mexico *P. ponderosa* landscape, whereas these species exhibited little distributional overlap in my study (Table 2). Merkle (1962) found that *Arenaria fendleri* (sandwort) was among the most important forbs in two park grasslands near the Grand Canyon north of my study area, consistent with my finding that

this species in the *Symphyotrichum* group characterized park/*Symphyotrichum* ecosystems. Species group research in other regions has noted the importance of among-landscape differences in species distributions (Pregitzer and Barnes 1982; Host and Pregitzer 1991), important to clarify for *P. ponderosa* regions in future research.

My results on this semi-arid landscape support several general species group principles chiefly developed on temperate landscapes (e.g., Spies and Barnes 1985; Grabherr et al. 2003; Kashian et al. 2003). For example, authors in eastern USA forests have concluded that while some species groups are restricted to only one ecosystem type, most groups occur in several ecosystems but are quantitatively most important in only a few (Archambault et al. 1989; Abella and Shelburne 2004). My results concur with this principle because only a few groups such as the *Phacelia* and *Erysimum* groups were restricted to one ecosystem type, and quantitative distributional differences were important for distinguishing closely related groups like the *Festuca* and *Muhlenbergia* groups (Table 4.2). Species groups also typically are reported to more strongly indicate environmental complexes rather than single-factor gradients (Spies and Barnes 1985; Archambault et al. 1989; Meilleur et al. 1992), which also concurs with my results. While a soil texture gradient corresponded with the *Bahia* group's distribution, for example, many groups could not be differentiated along individual gradients. The *Hymenopappus* group, for instance, occurred on a range of soil textures illustrated by *Penstemon linarioides*'s distribution (Fig. 4.3). High importance of this group, however, was indicative of dry soils, often of the xeric limestone/*Bouteloua* or clay basalt/*Gutierrezia* ecosystems resulting from combinations of clayey or sandy textures, low precipitation, and low-moderate organic C concentrations.

Scale and factors resulting in different environmental complexes are key

differences between my study and previous species group research in temperate eastern

USA forests. Spatially rapid turnover in species composition has been reported for some

eastern forests, with dominance of species groups shifting at extents < 100 m for instance

in southern Appalachian forests (Abella and Shelburne 2004). Plant community and

species group turnover occurs at broader extents on this landscape, where soil mapping

units containing similar plant communities exceeding 1000 ha are not uncommon (U.S.

Forest Service 1995). These scale differences likely occur because environmental factors

constraining species distributions change at broader scales on this landscape. For

example, soil drainage and depth to water table changed over short distances and directed

species distributions on several eastern USA landscapes (Archambault et al. 1989;

Goebel et al. 2001). These variables were not closely associated with species

distributions in my study (Welch and Klemmedson 1975). These comparisons illustrate

that past events, such as glaciation in Michigan (Host and Pregitzer 1992) or volcanic

activity on this landscape (Moore et al. 1976), differ among landscapes yet similarly

create environmental complexes affecting species distributions.

Estimating tree growth

I applied this study's data by predicting diameter growth of open-grown, old-growth

Pinus ponderosa based on importance values of four plant species in a regression tree

model (Fig. 4.5). The model's terminal nodes represent predicted *P. ponderosa* annual

diameter increments (Insightful Corporation 2001). For example, the most rapid

diameter growth of 4.9 mm/yr is predicted if importance of *Lupinus argenteus* exceeds

8% and importance of *Festuca arizonica* exceeds 17%. Low importance of these species

and greater importance of *Sporobolus interruptus* indicates slower diameter growth, probably because *S. interruptus* indicates rocky sites where tree rooting may be restricted (Table 2). Plots where none of these species were important exhibited the slowest diameter growth of 2.6 mm/yr, with these plots often dominated by *Bouteloua gracilis* in climatically dry areas where sparse precipitation combined with soils holding little available water may limit *P. ponderosa* growth. Daubenmire (1961) and Stansfield et al. (1991) also found that plant species predicted tree growth fairly reliably in *P. ponderosa* forests. Vegetation-environment research has potential for increasing our understanding of *P. ponderosa* forest ecology, providing a foundation for ecological restoration and management in these forests.

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Table 4.1. Discriminant functions classifying which one of four dominant grasses is predicted to have the highest importance value at difference levels of five environmental variables for an Arizona *Pinus ponderosa* landscape.

	Bouteloua gracilis n=19[a]	*Festuca arizonica* n=17	*Muhlenbergia montana* n=18	*Sporobolus interruptus* n=5
Variable	——————— discriminant functions ———————			
Constant	-1403	-1362	-1368	-1386
15-50 cm pH	17.61649	15.91682	15.787	8.74846
0-50 cm AWC[b]	1406	1575	1465	1478
0-15 cm clay (%)	0.83406	0.48799	0.66308	0.74321
15-50 cm gravel (%)	1.7305	1.94237	1.83275	1.85903
UTM (easting)[c]	0.0055	0.00538	0.00543	0.00556
Resubstitution accuracy[d]	——————— % classified into groups ———————			
Bouteloua gracilis	**74**	0	16	11

Festuca arizonica	0	**88**	12	0
Muhlenbergia montana	17	6	**56**	22
Sporobolus interruptus	0	0	0	**100**
Cross-validation accuracy	**63**	**88**	**50**	**80**

[a] Number of plots where a species exhibited the highest importance value among the four modeled species out of 59 plots where at least one of these species occurred.

[b] AWC = available water capacity (Saxton et al. 1986).

[c] UTM = Universal Transverse Mercator coordinates in meters, partly correlated with a gradient of increasing precipitation from east to west across the study area (Jameson 1969).

[d] Classification accuracy by resubstitution into the discriminant function. Values in bold are % correctly classified into a group. Overall classification accuracy using equal priors was 80% for resubstitution and 70% for cross-validation. Tabachnick and Fidell (1996) provide methodological details for discriminant analysis.

Table 4.2. Summary of ecological species groups and their environmental affinities for an Arizona *Pinus ponderosa* landscape between 1920-2660 m elevations.

Dry-site groups

Phacelia group: Restricted to dry, gravelly, black cinder soils of the Sunset Crater volcanic field low in organic C and total N (BC)[a]

    Phacelia serrata, Penstemon clutei, Physaria newberryi

Aristida group: Characteristic of dry, gravelly, sandy or sandy loam black or red cinder soils on or near cinder cones (BC, RC)

    Aristida arizonica, Brickellia eupatorioides, Penstemon ophianthus

Erysimum group: Characteristic of dry, sandy loam red cinder soils on or near cinder cones (RC)

    Erysimum capitatum, Hymenoxys subintegra

Hymenopappus group: Most abundant on climatically dry limestone or basalt soils (XL, CB)

    Hymenopappus filifolius, Plantago argyraea, Penstemon linarioides

Bouteloua group: Climatically dry sites on soils with various parent materials (BC, RC, XL, CB)

    Bouteloua gracilis

Bahia group: Most abundant on red and black cinder soils and less abundant on basalt or limestone soils (BC, RC)

    Bahia dissecta, Nama dichotomum, Chenopodium graveolens, Muhlenbergia minutissima

Gutierrezia group: Frequent on climatically dry limestone or basalt soils (XL, CB)

   Gutierrezia sarothrae, Hymenoxys richardsonii, Eriogonum racemosum

Dry-moist groups

Muhlenbergia group: Dry-moist soils including black and red cinders, limestone, and basalt (most dominant in XB)

   Muhlenbergia montana, Geranium caespitosum, Pseudocymopterus montanus, Lotus wrightii

Oxytropis group: Diverse group of dry-moist soils of a variety of parent materials (several ecosystems)

   Oxytropis lambertii, Artemisia carruthii, Penstemon virgatus, Packera multilobata, Thalictrum fendleri, Poa fendleriana

Elymus group: Widespread species occurring on 97% of plots and consistently of medium-high abundance (all ecosystems)

   Elymus elymoides

Intermediate and moist-site groups

Sporobolus group: Characteristic of loamy or clay loam basalt soils with high (> 10%) surface rock cover (RB)

   Sporobolus interruptus, Lathyrus laetivirens, Pedicularis centranthera

Blepharoneuron group: Provisional group with both species most abundant on moist basalt and limestone soils (RB, MB, ML)

   Blepharoneuron tricholepis, Ceanothus fendleri

Solidago group: Common on limestone and moist basalt soil (ML, MB)

   Solidago velutina, Potentilla subviscosa, Antennaria parvifolia, Vicia americana

Festuca group: Dominant on moist, loam-silt loam basalt soils with high organic C and total N (MB, AN)

    Festuca arizonica, Lupinus argenteus, Carex geophila

Lathyrus group: Restricted to aspen ecosystems containing moist, loamy soils with high organic C and total N (AN)

    Lathyrus lanszwertii, Populus tremuloides

Erigeron group: Occupied all soils except cinder soils but most abundant in two ecosystem types (CB, PK)

    Erigeron divergens, Antennaria rosulata

Muhlenbergia wrightii group: Abundant in treeless parks but also occurred on limestone and basalt forested soils (PK, ML, MB)

    Muhlenbergia wrightii

Symphyotrichum group: Dominant in parks containing deep, primarily clay loam soils (PK)

    Symphyotrichum ascendens, Allium geyeri, Arenaria fendleri, Coreopsis tinctoria, Iris missouriensis

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[a] Ecosystem types where species groups were most characteristic are given in parenthesis: AN = aspen/*Lathyrus*, BC = black cinders/*Phacelia*, CB = clay basalt/*Gutierrezia*, MB = mesic basalt/*Festuca*, ML = mesic limestone/mixed flora, PK = park/*Symphyotrichum*, RB = rocky basalt/*Sporobolus*, RC = red cinders/*Bahia*, XB = xeric basalt/*Muhlenbergia*, and XL = xeric limestone/*Bouteloua*.

Figure 4.1. Location of 66 sample plots and their ecosystem type classifications on a 110,000-ha Arizona *Pinus ponderosa* landscape, USA (UTM zone 12). Geographic features are abbreviated as GF and weather stations as WS. Although at similar elevations (2128-2244 m), precipitation averages 56 cm yr^{-1} at Fort Valley (station 1), 54 cm yr^{-1} at the Flagstaff Airport (station 2), and 42 cm yr^{-1} at Sunset Crater (station 3). Ecosystem type abbreviations are as follows: AN = aspen/*Lathyrus*, BC = black cinders/*Phacelia*, CB = clay basalt/*Gutierrezia*, MB = mesic basalt/*Festuca*, ML = mesic limestone/mixed flora, PK = park/*Symphyotrichum*, RB = rocky basalt/*Sporobolus*, RC = red cinders/*Bahia*, XB = xeric basalt/*Muhlenbergia*, and XL = xeric limestone/*Bouteloua*.

Figure 4.2. Non-metric multidimensional scaling ordination of a 66 plot × 271 plant species importance value matrix for 10 ecosystem types of an Arizona *Pinus ponderosa* landscape. Vector lengths are proportional to the strengths of relationships between community composition and variables associated with vectors. Community composition was more closely related to soil properties reflecting parent materials than to geomorphic variables. For soil variables, A = 0-15 cm and B = 15-50 cm. UTM(x) = Universal Transverse Mercator easting and is partly correlated with a precipitation gradient. Vector abbreviations for species are as follows: BAHDIS = *Bahia dissecta*, BOUGRA = *Bouteloua gracilis*, CARGEO = *Carex geophila*, ERIDIV = *Erigeron divergens*, FESARI = *Festuca arizonica*, GUTSAR = *Gutierrezia sarothrae*, HYMRIC = *Hymenoxys richardsonii*, LUPARG = *Lupinus argenteus*, MUHMON = *Muhlenbergia montana*, and SYMASC = *Symphyotrichum ascendens*.

Figure 4.3. Distribution of six forbs along soil texture and fertility gradients on an Arizona *Pinus ponderosa* landscape. Distributions represent the 12 plots where a species was most important or all occurrences if a species occurred on fewer than 12 plots.

Figure 4.4. R-mode non-metric multidimensional scaling ordination of 49 species constituting 15 ecological species groups of an Arizona *Pinus ponderosa* landscape. Three species (*Bouteloua gracilis*, *Elymus elymoides*, and *Muhlenbergia wrightii*) forming single-species groups are not shown. Species are abbreviated by the first three letters of each of the genus and species names, and their full names and group identities are given in Table 4.2.

Figure 4.5. Regression tree model estimating diameter growth of open-grown, old-growth *Pinus ponderosa* based on importance values of plant species. Terminal nodes represent predicted *P. ponderosa* diameter increment in mm/yr, with standard deviations given as a measure of variability of predicted estimates (predicted value ± standard deviation). This model did not include plots in black cinders/*Phacelia* ecosystems because of unusually high tree growth variability or plots in treeless park/*Symphyotrichum* ecosystems. Abbreviations for plant species are as follows: LUPARG = *Lupinus argenteus,* FESARI = *Festuca arizonica,* CARGEO = *Carex geophila*, and SPOINT = *Sporobolus interruptus*.
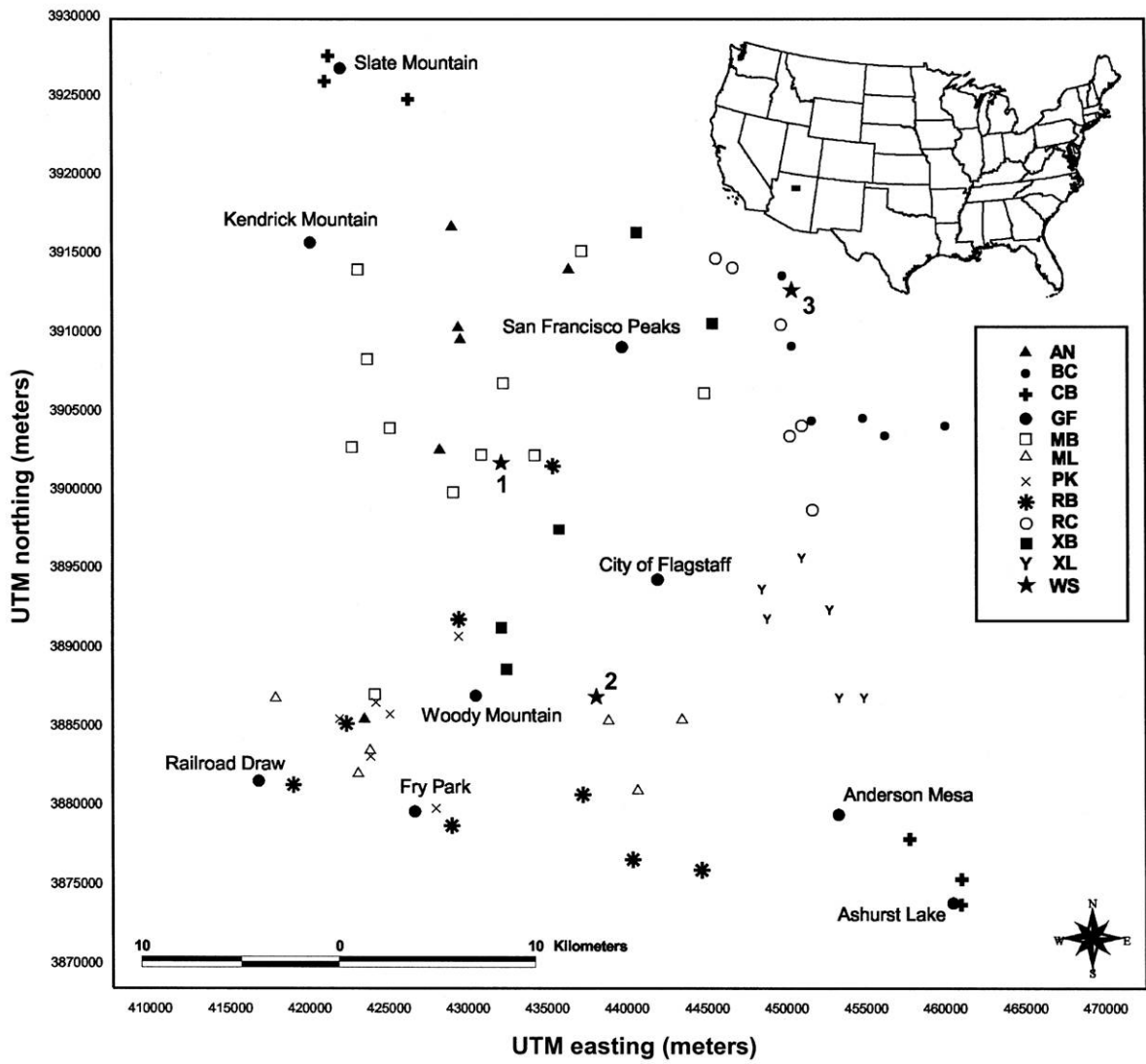
Fig. 4.1
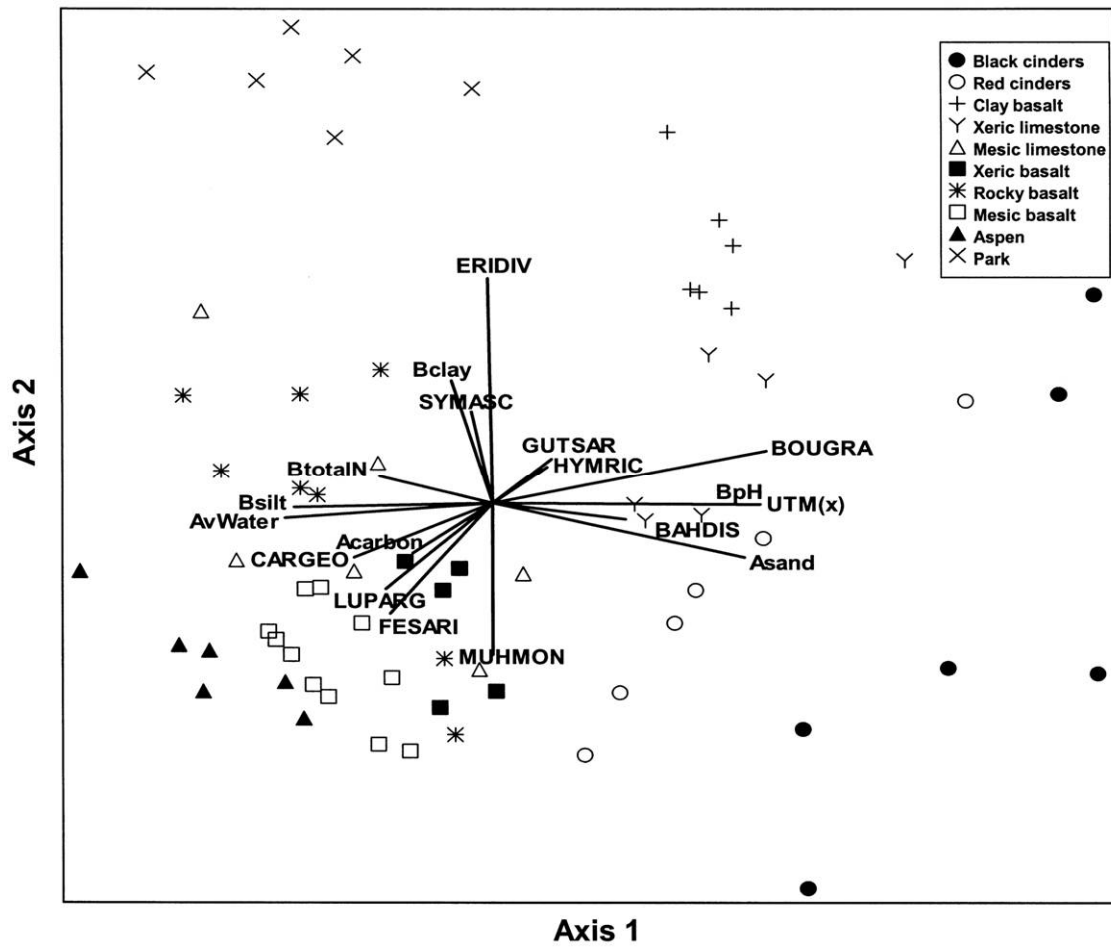
Fig. 4.2
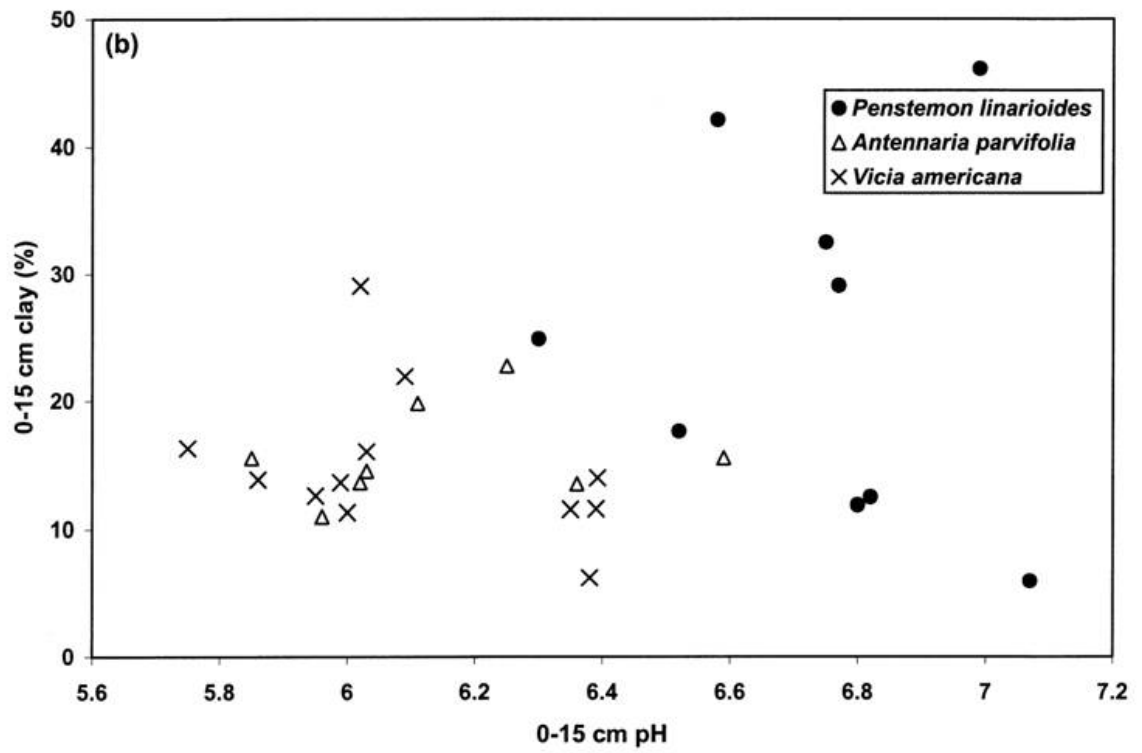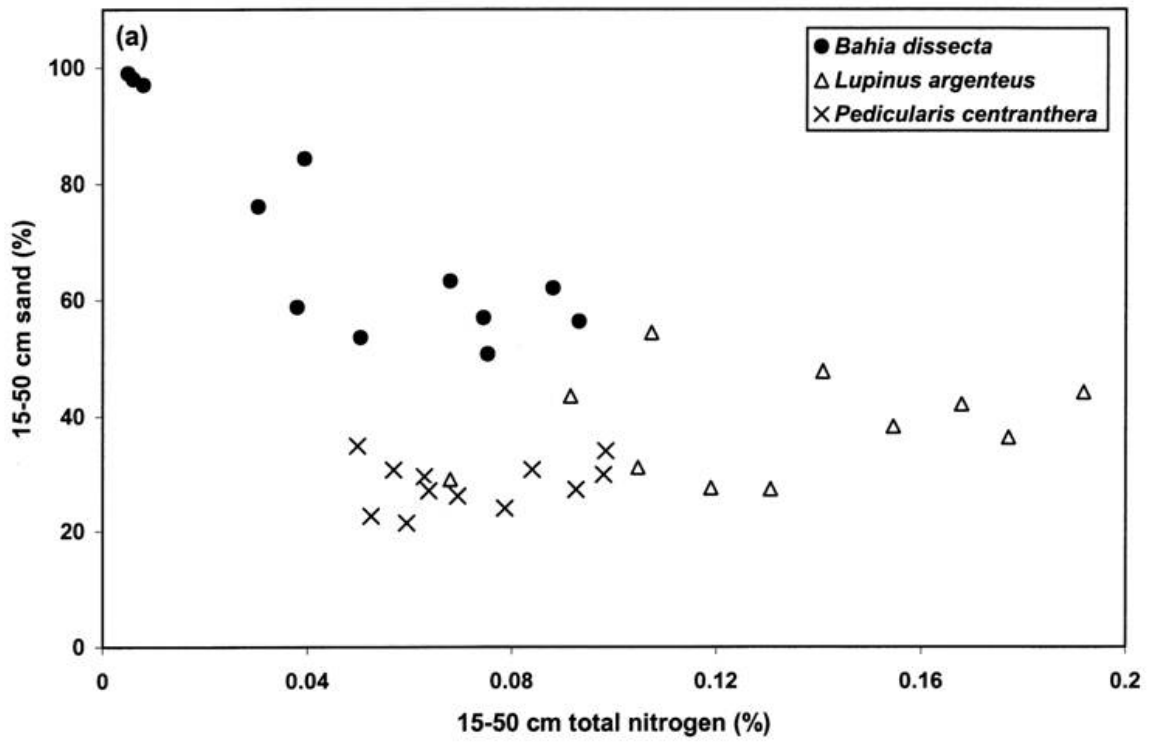
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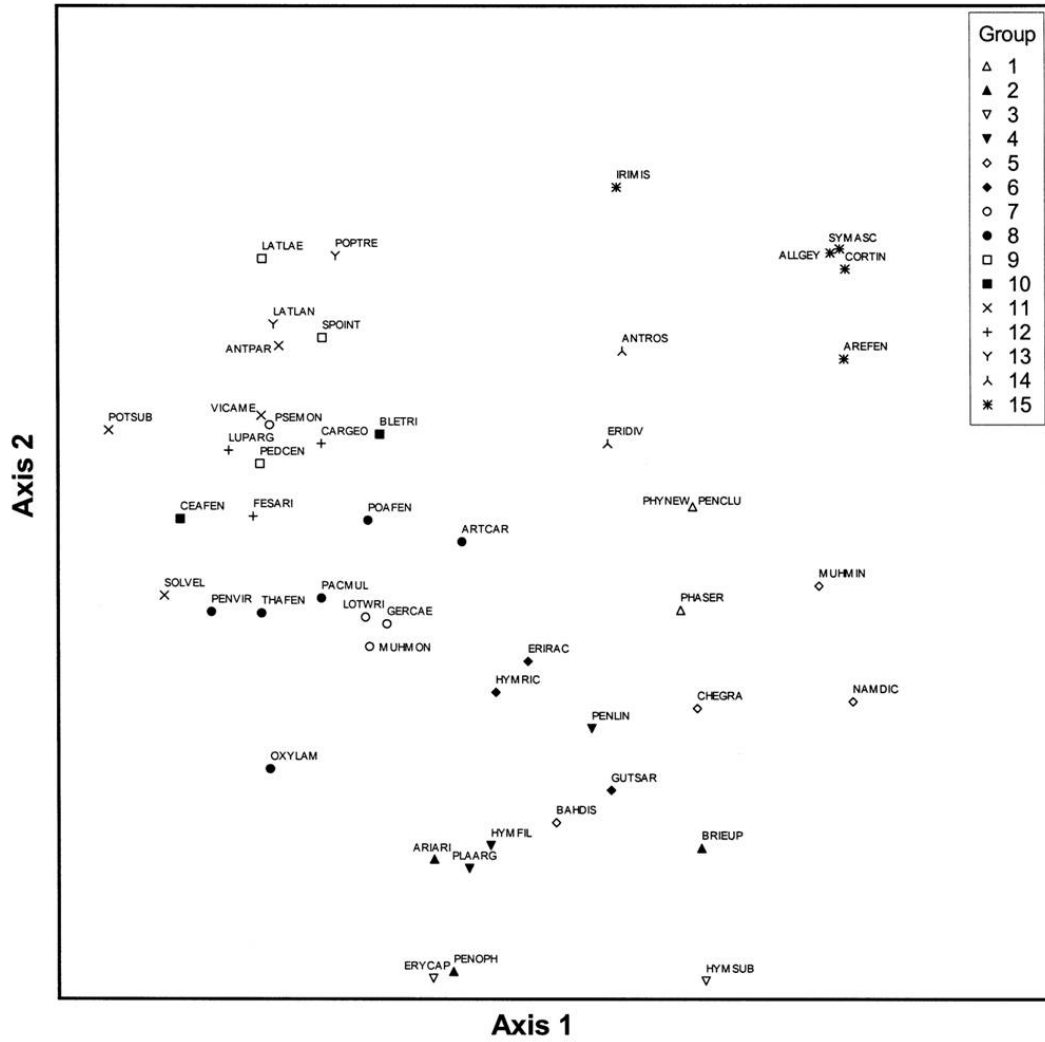
Fig. 4.4
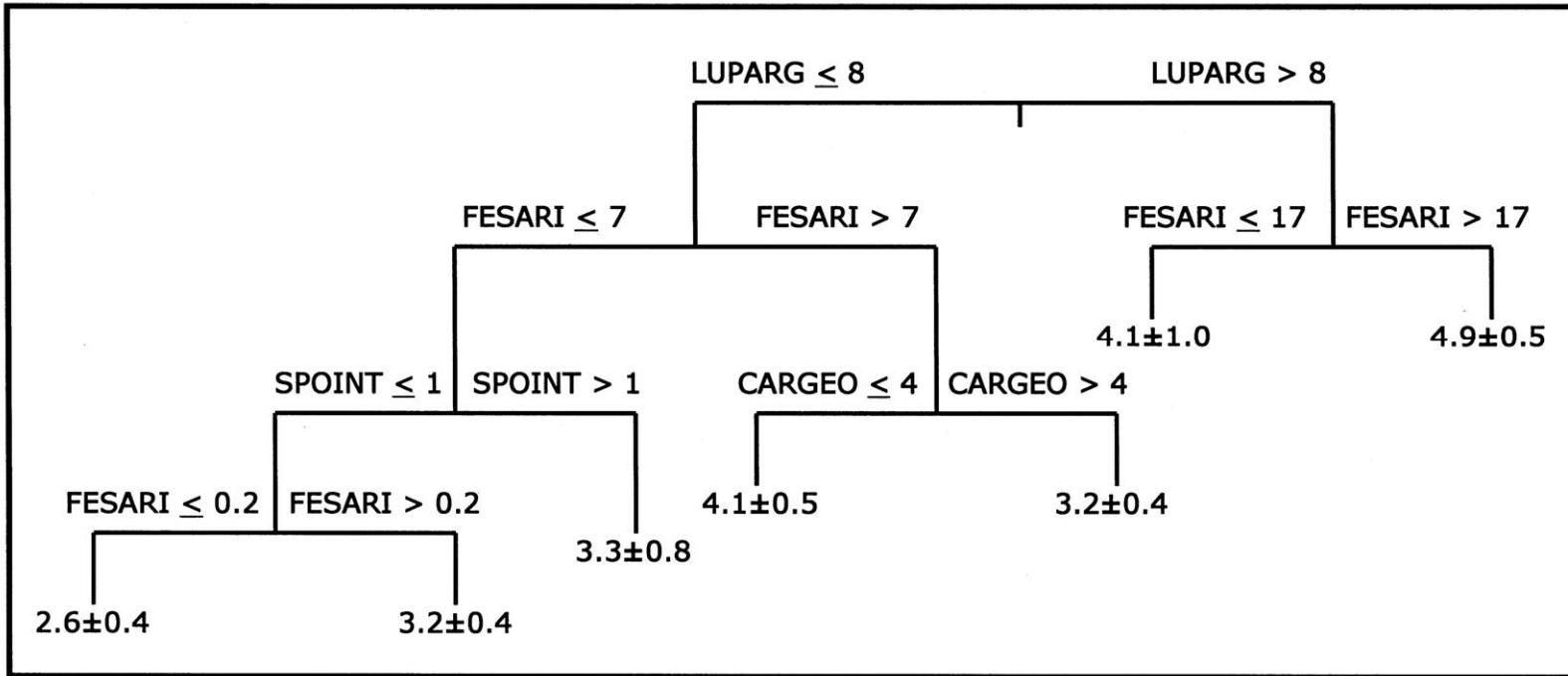
Fig. 4.5

CHAPTER 5

SEED BANKS OF AN ARIZONA *PINUS PONDEROSA* LANDSCAPE: RESPONSES TO ENVIRONMENTAL GRADIENTS AND FIRE CUES

Abstract: We measured soil seed banks of 102 plots on a 110 000-ha Arizona *Pinus ponderosa* landscape, and determined seed bank responses to fire cues and tree density, compared seed bank composition among ecosystem types, and assessed the utility of seed banks for ecological restoration. Liquid smoke increased community-level seed bank emergence in greenhouse experiments, whereas 100°C heating had minimal effect and *P. ponderosa* charred wood decreased emergence. We detected 103 total species in seed bank samples, and 280 species in aboveground vegetation. *Erigeron divergens* was the most frequent seed bank species, and with the exception of *Gnaphalium exilifolium*, species detected in seed banks also occurred aboveground. Although a dry, sandy-textured black cinders ecosystem exhibited the greatest seed density, seed bank composition was more ecosystem-specific than was seed density. Major graminoids including *Carex geophila* and *Muhlenbergia montana* were common in seed banks, whereas perennial forbs were sparse particularly in areas of high tree density. Our results suggest that smoke may increase emergence from seed banks in these forests, seed banks can assist establishment of major graminoids but not forbs during ecological restoration, and ecosystem-specific seed bank composition occurs to a certain extent across the landscape.

Introduction

Soil seed banks consist of stored, viable seeds that can emerge when germination requirements are met, which for some species occurs after canopy-reducing disturbance or after fire (Thompson 1987; Halpern et al. 1999; Odion and Davis 2000). In frequent-fire ecosystems, fire-related cues such as smoke, heat, ash, or charred wood may stimulate germination of some species that otherwise exhibit low germination (Baldwin et al. 1994; Dixon et al. 1995; Blank and Young 1998). Burne et al. (2003), for example, found that two *Grevillea* shrub species in Australian heath ecosystems germinated only on plots sprayed with liquid smoke, while Roche et al. (1997) reported that aerosol smoke sharply increased germination from 5 to 246 seeds/m^2 in seed banks of Australian *Eucalyptus* forests. In California chaparral, Keeley et al. (1985) found that germination of about half of 30 tested species responded positively to heating or to additions of *Adenostoma fasciculatum* (chamise) charred wood, with responses to these cues consistent with the post-fire distribution of these species. These studies suggest that seed bank exposure to fire cues can affect post-fire community succession in frequent-fire ecosystems, and may influence our impression of seed bank composition in greenhouse emergence studies.

Surface fire historically was prevalent in western United States *Pinus ponderosa* (ponderosa pine) ecosystems, and reintroducing fire along with tree thinning is increasingly proposed for ecological restoration of these forests (Fulé et al. 1997; Allen et

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al. 2002). Tree density has increased and understory vegetation has declined in these forests during a post-settlement period of fire exclusion beginning in the late 1800s (Covington et al. 1994). Previous seed bank research in *P. ponderosa* forests has been limited and conflicting, ranging from estimates of 8 seeds/m^2 on a northern Arizona site (Vose and White 1987) to more than 13 000 seeds/m^2 on an Oregon site (Pratt et al. 1984). Predicting seed bank characteristics of *P. ponderosa* forests is further complicated since these forests share attributes of many ecosystems, by being coniferous forests that usually have small seed banks (Roberts 1981), often shrub- or grass-dominated ecosystems that may have large or small seed banks (Warr et al. 1993), and in dry regions frequently surrounded by deserts that have large seed banks (Guo et al. 1998). Fire-seed bank relationships also have been little studied in these forests, despite fire's historical prevalence and potentially extensive reintroduction during restoration, making it difficult to foretell potential seed bank contributions to community dynamics during ecological restoration.

We examined composition and responses to fire cues of soil seed banks of a northern Arizona *Pinus ponderosa* landscape proposed to receive extensive restoration treatments. Since this landscape contains a range of soil and ecosystem types that may undergo restoration, we also focused on landscape-scale variation in seed bank characteristics across environmental gradients. Our specific objectives were to: (1) determine seed bank responses to the fire cues of heat, charred wood, and smoke using greenhouse experiments, (2) compare seed bank characteristics among environmental gradients and regional landscape ecosystems, and (3) assess the potential role of seed banks for the restoration of forest understories.

Methods

Study area

We collected seed bank samples between 1920-2660 m elevations on a 110 000-ha landscape surrounding the city of Flagstaff, Arizona in the Northern Arizona University Centennial Forest and the north half of the Coconino National Forest (study area SE corner 35°01'N, 111°23'W; SW corner 35°04'N, 111°53'W; NW corner 35°29'N, 111°51'W; NE corner 35°23'N, 111°31'W). Based on three weather stations, total precipitation across the study area ranges from 42-56 cm/yr, snowfall from 152-233 cm/yr, and maximum mean daily temperatures from 15.7-17.5°C (Western Regional Climate Center, Reno, NV). Soil parent materials include volcanic cinders, basalt, benmoreite, and limestone, with major soil subgroups including Typic and Udic Argiborolls, Typic and Mollic Eutroboralfs, Typic Ustorthents, and Vitrandic Ustochrepts (U.S. Forest Service 1995). Slope gradients are <10% over most of the study area, and cinder cones, ravines, and low hills punctuate this undulating topography. Before fire exclusion beginning in the late 1800s, return intervals for primarily lightning ignited surface fires averaged <10 yr (Fulé et al. 1997). Livestock grazing has been widespread since the late 1800s, and grazing by *Cervus elaphus* (Rocky Mountain elk) and other ungulates also occurs (Clary 1975). Tree species include *Pinus ponderosa* which forms extensive pure stands, *Quercus gambelii* (Gambel oak), and less commonly *Populus tremuloides* (trembling aspen), *Pinus edulis* (two-needle pinyon), and *Juniperus* spp. Understories are dominated by graminoids including *Festuca arizonica* (Arizona fescue), *Muhlenbergia montana* (mountain muhly), *Carex geophila* (White Mountain sedge), *Bouteloua gracilis* (blue grama), and *Elymus elymoides* (squirreltail).

Field procedures and ecosystem classification

We sampled 66, 0.05-ha (20 × 25 m) plots by sampling one plot in each of six randomly selected mapping units of 11 soil types (numbered 55, 500, 513, 523, 536, 551, 558, 570, 582, 585, and 611) mapped in a Terrestrial Ecosystem Survey (TES) of the study area (U.S. Forest Service 1995). These 66 plots are termed ecosystem plots in this paper and were classified into ecosystem types based on multivariate analyses of environment and vegetation characteristics using methods described in Abella (2005) similar to Abella et al. (2003). We identified 10 ecosystem types, ranging from a dry, coarse-textured black cinders ecosystem, to moist, nitrogen-rich aspen and treeless park ecosystems (Table 5.1). Four primarily basalt ecosystems differentiated from each other along soil texture and rockiness gradients, and xeric and mesic limestone ecosystems of similar texture differentiated along a regional precipitation gradient (Western Regional Climate Center, Reno, NV). Park ecosystems occupied depressions ranging in size from 2 to >1000 ha, receive exceptionally heavy grazing (Clary 1975), and were dominated by *Erigeron divergens* (spreading fleabane), *Muhlenbergia wrightii* (spike muhly), and *Symphyotrichum ascendens* (western aster). Ecosystem plots were located below open canopies, which usually occurred around old-growth trees (White et al. 1991). An additional 36 plots, 18 in open areas and 18 under dense canopies (*Pinus ponderosa* density >1000 trees/ha), were sampled in the 536, 570, and 585 TES types.

We measured seed banks, soils, geomorphology, and aboveground vegetation on all 102 plots. Using a 4.2-cm diameter cylinder, we collected seed bank samples of 70 cm^3 from 0-5 and 5-10 mineral soil depths in each of 15, 1-m^2 subplots per plot, resulting in a composite plot sample of 1050 cm^3 for each depth. Subplots were located at 0.5, 5,

12.5, 20, and 24.5 m along the south, center, and north plot axes. Although litter can trap seeds (e.g., Halpern et al. 1999), we focused on mineral soil seed banks because our open-canopy plots contained patchy, sparse litter layers. Sampling occurred from mid-May to August 2003, and seed bank collections likely primarily represent the persistent seed bank (Baskin and Baskin 2001) since sampling occurred before most species had dispersed seeds. We also categorized areal cover of each plant species rooted in subplots, inventoried all species in whole plots on a presence/absence basis, and recorded Oi-horizon thickness, slope gradient, aspect, and elevation of each plot. Composite soil samples of 0-15 and 15-50 cm depths were collected from two pits per plot, air dried and sieved through a 2-mm sieve, and analyzed for $CaCO_3$ equivalent (Goh et al.'s [1993] approximate gravimetric method), texture (hydrometer method), pH (1:2 soil:0.01 M $CaCl_2$), and organic C and total N (C/N analyzer after HCl removal of inorganic C) following Bartels and Bigham (1996) and Dane and Topp (2002). We also estimated soil available water capacity from texture, gravel content, and organic matter (organic C $\times$ 1.724) using Saxton et al.'s (1986) equations available online (http://hydrolab.arsusda.gov/soilwater/Index.htm).

General seed bank procedures

Using the emergence method (Warr et al. 1993), we performed an initial summer seed bank compositional study on untreated 0-5 and 5-10 cm samples started in the greenhouse the same day each sample was collected and provided a mid-May 2003 to January 2004 germination period, and five subsequent experiments on 0-5 cm samples stored at $-5^{o}C$ for 4-6 months after collection. We performed experimental treatments in January 2004, and gave experimental samples a January-October 2004 germination

period. Square plastic pots of 700 cm^3 served as experimental units. We filled these pots

with 120 cm^3 of seed bank soil 1 cm thick overlaying 300 cm^3 of sterile potting soil

(United Industries Co., St. Louis, MO). Pots were randomly arranged on benches in a

Northern Arizona University greenhouse maintained at 24°C, given four hours (6:00-8:00

am and pm) of daily artificial lighting except for May-August, watered daily, and

monitored for emergence every two weeks. We randomly interspersed 24 pots

containing only potting soil to check for seed contamination. *Conyza canadensis*

(Canadian horseweed) was a contaminant in the summer study, so we deleted this species

from the summer data. Nomenclature and native/exotic species classifications followed

USDA-NRCS (2004).

Known-seed and seed bank experiments

Concurrently with seed bank experiments, we performed a known-seed

experiment testing heat and smoke effects on emergence of locally collected seeds stored

at -5°C for four months of six species common in northern Arizona *Pinus ponderosa*

forests. Our purpose was to determine if emergence requirements were met for these

species, addressing a criticism of the seed bank emergence method (Warr et al. 1993).

This experiment was a three-factor, split-plot factorial design consisting of two levels of

the whole plot factor heat (none, exposure to 100°C for 30 minutes), two levels of the

subplot factor liquid smoke (none, 60 ml of 10% smoke), and six levels of species

(*Elymus elymoides*, *Festuca arizonica*, *Geranium caespitosum* [pineywoods geranium],

Lupinus argenteus [silvery lupine], *Penstemon barbatus* [beardlip penstemon], or

Thalictrum fendleri [Fendler's meadow-rue]). Three replicate pots were used for each of

the 24 treatment combinations, and seeds were lightly pressed in four rows of four seeds

in each pot (16 seeds/pot) on 120 cm^3 of locally collected basalt soil overlaying 300 cm^3 of potting soil.

Experiment 1 of the seed bank experiments tested heat, liquid smoke, and ecosystem type effects on emergence density and species richness in a factorial, three-factor experiment using samples from 33 randomly selected ecosystem plots. Each of four samples per plot received either no treatment, a 100°C 30 minute heat exposure, 60 ml of 10% liquid smoke by volume, or heat + smoke (33 plots × 4 pots each = 132 total pots). We heated pots containing potting and seed bank soil in an electric oven, and prepared liquid smoke solutions by diluting commercially available liquid smoke (Wright's Brand, Roseland, NJ) with deionized water. Previous research has found that air smoke and different kinds of liquid smoke exhibit similar effects on germination (van Staden et al. 2000). Experiment 2 was a two-factor experiment using the remaining 33 ecosystem plots testing ecosystem types and treatments, which included a 50°C 30 minute heat exposure, addition of 30 ml of *Pinus ponderosa* charred wood intermixed with the seed bank soil, 100°C 30 minute heating + charred wood, and 100°C 30 minute heating + charred wood + 10% liquid smoke (33 plots × 4 pots each = 132 total pots). We prepared charred wood (blackened with no visible bark remaining) by burning *P. ponderosa* logs and grinding burned pieces to pass a 4-mm sieve.

Experiment 3 was a two-factor experiment testing canopy types (open or dense) and treatments, consisting of a single or double (30 days after initial application) 100°C 30 minute heat exposure, or a single or double addition of 60 ml of 10% liquid smoke. We used nine plots for each canopy type in this experiment (18 plots × 4 pots each = 72 total pots). Experiments 4 and 5 each included nine dense-canopy plots, with Experiment

4 including the same treatments as Experiment 1 and Experiment 5 including the same

treatments as Experiment 2 (9 plots × 4 pots each = 36 total pots for each experiment).

Statistical analyses

We analyzed the known-seed experiment using analysis of variance (ANOVA)

with 60-day percent emergence as the response variable. Raw data approximated equal

variance (Levene test) and normality (Shapiro-Wilk W test) assumptions. After square

root transforming emergence density and species richness to meet assumptions, we also

used ANOVA to analyze experimental seed bank data. In all seed bank experiments, we

defined plots as a random blocking variable because four seed bank samples per plot

were extracted for treatment from composite plot samples. We compared mean square-

root transformed emergence density among ecosystem types using one-way ANOVA.

We performed analyses with SAS JMP (SAS Institute 2002) and used Tukey's test for

multiple comparisons. Seed bank data are known for their variability (Baskin and Baskin

2001), so we also highlight trends not statistically significant at $P < 0.05$ but potentially

ecologically insightful. We also ordinated summer study seed bank composition

(emergent seeds/m^2 relativized by plot totals) and aboveground vegetation importance

values (average of relative frequency and relative cover summing to 100% on a plot

basis) using non-metric multidimensional scaling (autopilot, thorough mode) in PC-ORD

(McCune and Mefford 1999).

Results and Discussion

Summer compositional study

We identified 53 species in 0-5 cm, 44 species in 5-10 cm, and 66 species overall

in 0-10 cm untreated samples from the 102 plots. *Erigeron divergens* was the most

frequent species with a 35% 0-10 cm frequency, followed by *Verbascum thapsus* (common mullein) with a 25% frequency (Table 5.2). Seven other species exhibited 0-10 cm frequencies ≥ 10%, including *Gnaphalium exilifolium* (slender cudweed), *Carex geophila*, *Chamaesyce serpyllifolia* (thymeleaf sandmat), *Muhlenbergia minutissima* (annual muhly), *Erigeron flagellaris* (trailing fleabane), *Poa pratensis* (Kentucky bluegrass), and an unidentified forb. Of the 29 most common species, 14% were exotics, 27% were grasses, none were shrubs or trees, 34% were perennials, 10% were biennials, 41% were annuals, and 14% were short-lived annuals-perennials. Although 87% of species were more frequent in 0-5 cm than in 5-10 cm samples, most species occurred at both depths.

Four dominant aboveground graminoids, including *Carex geophila*, *Festuca arizonica*, *Muhlenbergia montana*, and *Poa fendleriana* (muttongrass), exhibited seed bank frequencies ≥ 2%, while fewer dominant aboveground forbs were frequent seed bank species. While little correspondence between seed bank and aboveground composition has been widely reported for forests (Roberts 1981), our findings indicate that if a species was detected in the seed bank it almost always also occurred aboveground. For example, *E. divergens* occurred aboveground on 34/36 (94%) plots in which it was detected in the seed bank, greater than the 67% expected by chance from its aboveground frequency. *Poa pratensis* occurred aboveground on all 10 plots in which it was detected in the seed bank, *M. montana* on all nine plots, and *Coreopsis tinctoria* (golden tickseed) on all three plots. *Gnaphalium exilifolium* was an exception, detected in 13% of seed bank samples but absent aboveground. *Elymus elymoides* was the most prevalent aboveground species that was sparse in seed banks, occurring aboveground in

97% of plots but in only 1% of seed bank samples. The exceptionally high seed viability of this species with no special germination requirements apparently renders a seed bank unnecessary for its success (Young and Evans 1977). Furthermore, *E. elymoides* would not be predicted to form a persistent mineral soil seed bank (Thompson et al. 1993) because the species has heavy, awned seeds, that are 2-3 mg heavier than the smooth seeds of other grasses such as *P. fendleriana* and *M. montana* common in seed banks.

Known-seed experiment

In the known-seed experiment testing heat and liquid smoke effects for assessing emergence requirements, *Elymus elymoides* exhibited 88-90% emergence across treatments (Table 5.3), consistent with McDonough (1970) who reported high germination of *E. elymoides* seeds collected in Utah. *Festuca arizonica* emergence also was high across treatments, ranging from 67-79%. The forbs *Geranium caespitosum*, *Lupinus argenteus*, and *Thalictrum fendleri* had lower emergence than the grasses, and did not significantly respond to smoke or to 100°C heating. Emergence of *L. argenteus* was 37-56% lower than the 79% emergence of Wyoming seeds under alternating 15-25°C temperatures reported by Romme et al. (1995). *Thalictrum fendleri*'s low emergence of 13-29%, however, is consistent with Hoffman's (1985) results for Colorado seeds. *Penstemon barbatus* did respond strongly to smoke, with smoke increasing emergence by 44% over the 19% control emergence. This may represent an evolutionary response (Baskin and Baskin 2001) to frequent fires long characteristic of *Pinus ponderosa* forests in which *P. barbatus* is common. Keeley and Fotheringham (1998) found that air smoke increased germination of *Penstemon centranthifolius* (scarlet bugler) by 30% in California chaparral, suggesting that responses to smoke in southwestern United States

Penstemon may not be uncommon. Results of this experiment suggest that greenhouse emergence requirements at least of these tested species would likely be met if their seeds occurred in seed bank samples.

Seed bank experiments

Treatment means in Experiment 1 ranged from 1237-1591 seeds/m^2 and 1.6-2.1 spp/120 cm^3. While not statistically significant at $P < 0.05$, greater emergence and species richness occurred after liquid smoke additions (Fig. 5.1, Table 5.4). Ecosystem type was not significant and did not interact with heat or liquid smoke. Treatment was significant in Experiment 2, with emergence after *Pinus ponderosa* charred wood additions averaging 391 seeds/m^2 less than the 1200 seeds/m^2 emerging when charred wood was applied with 100°C heating + liquid smoke (Fig. 5.1). Reduced emergence after charred wood addition contrasts with the California chaparral results of Keeley et al. (1985), who found that *Adenostoma fasciculatum* charred wood significantly increased germination of six of 12 annuals tested while reducing only one species, increased two of six *Phacelia* species, and did not affect four herbaceous perennials. Our findings agree with those of Lodhi and Killingbeck (1982), however, who found that *P. ponderosa* needles and materials were allelopathic and reduced germination of *Andropogon gerardii* (big bluestem) and *Schizachyrium scoparium* (little bluestem) in North Dakota *P. ponderosa* forests. While charred wood of species other than *P. ponderosa* may have enhanced emergence in our experiment, *P. ponderosa* is a major or sole source of woody material across most of the study area.

Treatment and canopy type both were significant at $P < 0.10$ in Experiment 3 (Table 5.4), with multiple heat or smoke applications increasing emergence only for

open-canopy plots (Fig. 5.2). Similar to Experiment 1 (Fig. 5.1), smoke caused greater

emergence than heat for both canopy types, with overall means of 1308 seeds/m^2 and 2.3

spp/120 cm^3 for smoked samples compared to 775 seeds/m^2 and 1.3 spp/120 cm^3 for

heated samples. While heat-stimulated species such as *Ceanothus fendleri* (Fendler's

ceanothus) occur in *Pinus ponderosa* forests (Huffman 2003), our results suggest that

smoke promotes community-level seed bank emergence more strongly than heat, at least

at the levels of smoke and heat tested in this study. Smoke also induced greater

emergence than heat in seed banks of an Australian *Eucalyptus* forest (Read et al. 2000).

Canopy type also was a fairly strong main effect in Experiment 3, with overall

means of 625 seeds/m^2 and 1.2 spp/120 cm^3 for dense-canopy plots, and 1458 seeds/m^2

and 2.4 spp/120 cm^3 for open-canopy plots (Fig. 5.2). Sparse mineral soil seed banks

below dense canopies could result from minimal seed inputs because of depauperate

aboveground vegetation (Harper 1977), reduced seed viability by burial below possibly

allelopathic *Pinus ponderosa* litter (Lodhi and Killingbeck 1982), or appreciable numbers

of seeds not detected in the mineral soil samples could have been trapped in Oi horizons

(Strickler and Edgerton 1976), which averaged 3.5 cm thick in dense-canopy plots

compared to only 2.0 cm in open-canopy plots. Consistent with our results, Springer

(1999) detected 16 species in 0-5 cm seed banks of open plots in *P. ponderosa* forests

near the Grand Canyon, compared to only seven species in dense-canopy plots.

Smoke more than doubled emergence and species richness of seed banks from

dense-canopy plots in Experiment 4, but differences were not significant because of high

within-treatment variability (Fig. 5.3). Similar to Experiment 2 with open-canopy plots

(Fig. 5.1), charred wood decreased emergence in dense-canopy samples of Experiment 5

(Fig. 5.4). Emergence after exposure to charred wood averaged only 278 seeds/m^2, 787 seeds fewer than a 50°C heat treatment and at least 324 seeds fewer than any other treatment. Heat and smoke apparently partially counteracted charred wood's negative effects, because greater emergence occurred when heat or smoke was applied with charred wood than when charred wood was applied alone.

We detected 78 total species in the experimental samples, including 37 species not detected in the summer study. Most of these new species occurred in fewer than three samples each, making it difficult to ascertain if these species occurred simply because of the additional samples, the cold storage period, or the treatments. For example, the only occurrences of *Ceanothus fendleri*, previously identified as a heat-stimulated species (Huffman 2003), were in two samples receiving 100°C heat in Experiment 2. *Nicotiana attenuata* (coyote tobacco), previously shown to germinate most strongly after smoke exposure (Baldwin et al. 1994), emerged from only one sample which received liquid smoke in Experiment 1. Other new species detected during the experiments included *Pinus ponderosa*, the exotic *Linaria dalmatica* (Dalmatian toadflax), and the perennial forbs *Heliomeris multiflora* (showy goldeneye), *Hymenoxys bigelovii* (Bigelow's rubberweed), *Lotus wrightii* (Wright's deervetch), *Oenothera flava* ssp. *taraxacoides* (yellow evening-primrose), *Oxytropis lambertii* (purple locoweed), *Potentilla plattensis* (Platte River cinquefoil), and *Thlaspi montanum* (alpine pennycress). Common species in the summer study, such as *Erigeron divergens*, *Verbascum thapsus*, *Nama dichotomum* (wishbone fiddleleaf), and *Poa fendleriana*, also were the most common overall in the experiments.

In summarizing these experiments, (a) liquid smoke increased community-level emergence and species richness, (b) heat had minimal effects and did not interact with smoke, (c) *Pinus ponderosa* charred wood when added alone reduced emergence, (d) ecosystem type did not interact with treatments, (e) open-canopy plots had much greater seed density and species richness than closed-canopy plots, and (f) pinpointing individual species that increased or decreased emergence as a result of these factors is difficult because many species were sparse. Studying seeds of known species or seed banks expected to contain certain species could help identify species-specific responses (e.g., Ralphs and Cronin 1987; Clark and Wilson 1994).

Comparisons among ecosystems and environmental gradients

Mean 0-5 cm seed density in the summer study ranged from 417 seeds/m^2 in the xeric limestone ecosystem to 3333 seeds/m^2 in the park ecosystem, whereas for unclear reasons, the park ecosystem exhibited the lowest seed density after cold storage averaged across the experiments (Fig. 5.5). The xeric, gravelly black cinders ecosystem exhibited the third highest seed density in the summer study and the highest overall density by more than 600 seeds/m^2 in the experiments, driven by high abundance of the annuals *Nama dichotomum*, *Chenopodium graveolens* (fetid goosefoot), and *Muhlenbergia minutissima*. High variability within ecosystems, however, precluded the statistical significance of any seed-density differences among ecosystems. Measured soil and topographic variables also were not strongly correlated with seed density, with Pearson correlations (*r*), for example, of -0.23 with pH, 0.15 with % gravel, 0.10 with total N, 0.28 with % clay, and -0.10 with available soil water.

Seed bank composition more strongly differentiated along ecosystem and environmental gradients than did seed density, but less strongly than aboveground vegetation (Fig. 5.6). Seed bank compositional patterns are more pronounced if similar ecosystems are grouped, by combining, for example, the black and red cinder ecosystems. While not restricted to the cinder ecosystems, *Nama dichotomum* and *Muhlenbergia minutissima*, for instance, attained their highest abundance in these sandy ecosystems. Sand content of the upper 15 cm averaged 70% in the 21 plots in which *N. dichotomum* was detected in seed bank samples, but only 37% in the 45 plots in which this species was not detected. Park and clay basalt ecosystems, both exhibiting the most 0-15 cm clay (Table 5.1) and receiving heavy grazing (Clary 1975), contained the only seed bank occurrences of *Coreopsis tinctoria*, *Gutierrezia sarothrae* (broom snakeweed), and *Oenothera flava* ssp. *taraxacoides*, and the highest abundance of *Erigeron divergens*. *Poa pratensis* was most prominent in the mesic, N-rich aspen ecosystem, while seven of the 11 (64%) plots in which *Carex geophila* was detected in the seed bank were from the aspen or mesic basalt ecosystems. Seed bank distribution of these species followed environmental gradients affecting the distribution of their aboveground vegetation. Other species, such as *Verbascum thapsus* and *Gnaphalium exilifolium*, exhibited little apparent association with specific ecosystems or environmental gradients, with their seed deposition likely more closely associated with past disturbances than with environmental gradients.

Regional comparisons

Our overall summer study average of 1600 seeds/m^2 (0-5 cm) is sharply greater than previous findings of 186 seeds/m^2 (litter + 0-3 cm soil) in a South Dakota *Pinus*

ponderosa stand (Wienk et al. 2004), and 8-22 seeds/m^2 (Vose and White 1987) and 25-600 seeds/m^2 (Korb et al. 2004) for the 0-5 cm depth at sites near Flagstaff encompassed by our investigation's study area. Our overall 0-10 cm average of 2500 seeds/m^2, however, is much lower than estimates of 13 000-14 000 seeds/m^2 (litter + 0-10 cm depth) by Pratt et al. (1984) in a Washington *P. ponderosa* stand, which these authors explained may not be typical of area forests because of exceptional numbers of exotic species and proximity to other community types. Springer's (1999) results of 1200 seeds/m^2 (0-5 cm) for *P. ponderosa-Quercus gambelii* forests near the Grand Canyon at Mt. Trumbull 190 km north of our study area most closely correspond to our results. Our detection of 103 total species in seed bank samples is much greater than detection in previous studies in *P. ponderosa* forests, which ranged from three (Vose and White 1987) to 57 species (Pratt et al. 1984). Elevated species detection in our study could result from our large number of sample sites and ecosystem types, the experimental treatments, or other factors.

Eighteen of 38 (47%) species detected by Springer (1999) in seed banks at Mt. Trumbull also were detected in our study, including the major species *Erigeron divergens*, *Chamaesyce serpyllifolia*, *Poa pratensis*, *Verbascum thapsus*, *Nama dichotomum*, *Muhlenbergia minutissima*, and *Verbena bracteata* (bigbract verbena). Probably reflecting differences in regional species pools, *Artemisia tridentata* (big sagebrush), *Collinsia parviflora* (maiden blue-eyed Mary), *Leonurus cardiaca* (common motherwort), *Viola canadensis* (Canadian white violet), and *Chenopodium berlandieri* (pitseed goosefoot) were abundant at Mt. Trumbull but were not detected in our study. We detected <10% of the species Pratt et al. (1984) detected, with congruent species

mainly including exotics such as *Verbascum thapsus*, *Bromus tectorum*, and *P. pratensis* that Springer (1999) also detected. These observations suggest that some species may be fairly widespread in seed banks throughout *P. ponderosa* forests, but substantial regional differences in seed bank composition can be expected in this widespread forest type.

Implications for ecological restoration

Seed banks are useful in ecological restoration if desired species occur in the seed bank and conditions promoting their germination can be created (van der Valk and Pederson 1989). Since we identified 280 aboveground species on plots and 103 species in seed bank samples, many species of the study area do not form persistent seed banks, were too infrequent in seed bank samples to be detected, or have germination requirements we did not meet (Warr et al. 1993). Species notably common aboveground with >40% plot frequencies but absent from seed bank samples included *Astragalus humistratus* (groundcover milkvetch), *Cirsium wheeleri* (Wheeler's thistle), *Polygonum douglasii* (Douglas' knotweed), *Pseudocymopterus montanus* (alpine false springparsley), and *Vicia americana* (American vetch). The four perennial forbs in our known-seed experiment (Table 5.3) also were absent from seed bank samples. With some exceptions such as Cohen et al.'s (2004) study in a North Carolina *Pinus palustris* (longleaf pine) forest, our study concurs with previous studies reporting few perennial forbs in forest seed banks (Warr et al. 1993). Because many perennial forbs also disperse seeds only short distances (Ehrlén and van Groenendael 1998), our study supports observations that colonization by perennial forbs can be expected to be slow after thinning and burning during *Pinus ponderosa* forest restoration, particularly in dense stands containing few aboveground seed sources (Vose and White 1987; Abella 2004).

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In contrast to the paucity of perennial forbs, many dominant, native graminoids such as *Muhlenbergia montana* and *Carex geophila* were detected in seed banks of both open- and dense-canopy plots. This may explain why these graminoids often initially increase fairly rapidly after thinning and burning (Abella and Covington 2004). Short-lived, native forbs also were fairly common in our seed bank samples, suggesting that perennial forbs are likely the most seed-limited functional group in these forests (Turnbull et al. 2000). Given increasing concern about exotic species invasions in *Pinus ponderosa* forests, attention could be given to establishing desirable, perennial forbs more rapidly than may occur from natural colonization during restoration (Bakker et al. 1996). Seeding and outplanting have shown some success in *P. ponderosa* forests (Steed and DeWald 2003; Springer and Laughlin 2004), but have not been extensively tested to date. Enhancing on-site seed production and germination possibly through timely burning or grazing reductions (White et al. 1991; Kinucan and Smeins 1992) also may assist recovery of perennial forbs during restoration. Our study suggests that during restoration in northern Arizona *P. ponderosa* forests, seed banks can facilitate establishment of major native graminoids, supply seeds of short-lived native forbs but also of some exotic species, and may exhibit enhanced emergence after prescribed fire although timing of fires may be important.

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Table 5.1. Summary of soil properties and aboveground vegetation based on 0.05-ha plots for forest ecosystems of a *Pinus ponderosa* landscape, northern Arizona.

Ecosystem	Texture [a]	Total N (%) [b]	pH	Cover (%) [c]	Spp/500 m^2	Dominants [d]
Black cinders	Sand	0.04-0.10	6.28-6.69	1-10	7-17	PS, BG, BD
Red cinders	Sandy loam	0.10-0.18	6.51-6.68	12-31	32-42	BD, MM, BG
Clay basalt	Clay loam	0.10-0.16	6.30-6.99	16-28	33-52	BG, ED, GS
Xeric limestone	Sandy loam	0.02-0.09	6.66-7.14	16-30	39-54	BG, HF, HR
Mesic limestone	Sandy loam	0.05-0.10	5.75-6.60	7-26	31-55	FA, MM, EE
Xeric basalt	Loam	0.07-0.13	6.01-6.68	8-21	34-40	MM, EE, PF
Rocky basalt	Loam	0.08-0.14	5.85-6.25	6-15	33-55	SI, CG, PF
Mesic basalt	Silt loam	0.09-0.24	5.61-6.36	7-48	22-54	FA, CG, LA
Aspen	Loam	0.15-0.34	6.03-6.59	13-57	20-32	FA, LA, LL
Park	Clay loam	0.13-0.18	5.65-6.07	24-34	19-45	ED, MW, SA

[a] Soil properties represent a 0-15 cm depth.

[b] Values are minimum-maximum based on plot means.

[c] Areal ground-flora cover.

[d] BD = *Bahia dissecta*, BG = *Bouteloua gracilis*, CG = *Carex geophila*, ED = *Erigeron divergens*, EE = *Elymus elymoides*, FA = *Festuca arizonica*, GS = *Gutierrezia sarothrae*, HF = *Hymenopappus filifolius*, HR = *Hymenoxys richardsonii*, LA = *Lupinus argenteus*, LL = *Lathyrus lanszwertii* var. *leucanthus*, MM = *Muhlenbergia montana*, MW = *Muhlenbergia wrightii*, PF = *Poa fendleriana*, PS = *Phacelia serrata*, SA = *Symphyotrichum ascendens*, and SI = *Sporobolus interruptus*.

Table 5.2. Seed bank characteristics and correspondence to aboveground vegetation for the 30 most frequent species detected in summer seed bank samples of 102, 0.05-ha plots on a *Pinus ponderosa* landscape, northern Arizona.

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Species[a]	0-5 cm depth[b]		5-10 cm depth		0-10 cm overall		Aboveground	
	Fr (%)	Seeds/m^2	Fr (%)	Seeds/m^2	Fr (%)	Seeds/m^2	Fr (%)	AG:SB[c]
Agrostis scabra (P)	4	2500	3	417	6	2500	2	17
Androsace septentrionalis (A-P)	2	1667	2	833	3	2500	3	33
Arenaria lanuginosa (P)	3	417	0	0	3	417	25	33
Artemisia dracunculus (P)	1	417	2	417	2	833	6	100
Bromus tectorum (A)*	1	417	1	417	1	833	39	100
Carex geophila (P)	8	417	4	833	12	833	75	92
Chamaesyce revoluta (A)	1	417	1	417	2	417	0	0
Chamaesyce serpyllifolia (A)	10	1250	5	833	12	2083	14	8
Chenopodium graveolens (A)	4	2500	6	833	8	2917	26	63
Coreopsis tinctoria (A-P)	3	833	1	833	3	1250	7	100

Drymaria molluginea (A)	1	417	2	833	2	833	0	0
Erigeron divergens (B)	26	2500	17	833	35	2500	67	94
Erigeron flagellaris (B)	6	833	5	417	10	833	32	70
Erigeron formosissimus (P)	1	417	1	417	2	417	31	100
Festuca arizonica (P)	2	417	1	417	2	833	56	100
Gnaphalium exilifolium (A)	9	833	6	1250	13	2083	0	0
Laennecia schiedeana (A)	5	2500	5	1250	7	3750	9	29
Linum aristatum (A)	0	0	2	417	2	417	9	50
Linum australe (A)	1	417	1	417	2	417	23	100
Muhlenbergia minutissima (A)	9	833	6	2500	12	2500	9	25
Muhlenbergia montana (P)	7	417	3	417	9	833	67	100
Nama dichotomum (A)	5	1667	4	2083	7	2500	7	29
Poa compressa (P)*	2	1250	0	0	2	1250	14	100
Poa fendleriana (P)	4	1250	4	417	7	1250	83	100
Poa pratensis (P)*	6	2500	7	3333	10	5834	38	100
Portulaca oleracea (A)	4	2083	2	417	4	2500	4	25

Pseudognaphalium macounii (A-B)	5	833	2	417	6	833	7	33
Verbascum thapsus (B)*	20	4583	14	2083	25	5834	35	64
Verbena bracteata (A-P)	1	417	1	417	2	417	1	0
Unidentifed forb[d]	10	2083	12	1667	17	2917	—	—

[a] A = annual, B = biennial, P = perennial, and * = exotic species following USDA-NRCS (2004).

[b] Fr = frequency (% of 102 plots in which a species occurred); seeds/m^2 is the maximum seed density recorded for a species.

[c] Concordance between aboveground vegetation (0.05-ha plots) and seed bank occurrences, indicating the percent of plots in which a species occurred in the 0-10 cm seed bank and also occurred in the aboveground vegetation. For example, *Erigeron divergens* occurred in the aboveground vegetation in 34/36 (94%) plots in which it was detected in the 0-10 cm seed bank.

[d] Specimens had glabrous, slightly lobed, numerous basal leaves and were possibly a *Veronica* sp.

Table 5.3. Mean % emergence after heat and liquid smoke treatments for six species common in northern Arizona *Pinus ponderosa* forests.

Species	Control	Heat	Smoke	Heat + Smoke
Elymus elymoides	88 a (12)	88 a (14)	90 a (8)	88 a (14)
Festuca arizonica	79 ab (18)	77 ab (17)	67 a-d (11)	71 abc (5)
Geranium caespitosum	31 d-g (40)	35 c-g (27)	31 d-g (35)	27 efg (58)
Lupinus argenteus	23 fg (31)	42 b-g (43)	35 c-g (27)	29 d-g (33)
Penstemon barbatus	19 fg (33)	13 g (87)	63 a-e (35)	56 a-f (19)
Thalictrum fendleri	21 fg (69)	13 g (100)	15 g (65)	29 d-g (54)

Note: Values are mean (coefficient of variation [%]). Means without shared letters differ at *P*< 0.05 (Tukey's test).

Table 5.4. Summary of analysis of variance for five experiments testing fire-related cues, ecosystem type, and canopy effects on 0-5 cm soil seed banks of a *Pinus ponderosa* landscape, northern Arizona.

Effect		Seeds/m^2		Species richness	
Experiment 1	*DF*	*F*	*P*	*F*	*P*
Heat	1	0.45	0.51	0.32	0.57
Smoke	1	1.11	0.30	0.67	0.42
Heat × smoke	1	0.08	0.78	0.11	0.74
Ecosystem	9	1.66	0.16	1.59	0.18
Heat × ecosystem	9	0.88	0.54	0.44	0.91
Smoke × ecosystem	9	0.52	0.85	0.94	0.49
Heat × smoke × ecosystem	9	0.34	0.96	1.03	0.43
Block	23	7.77	<0.01	6.64	<0.01
Experiment 2					
Treatment	3	4.27	0.01	3.66	0.02

Ecosystem	9	1.25	0.31	1.16	0.36
Treatment × ecosystem	27	1.31	0.18	1.11	0.36
Block	23	7.87	<0.01	6.89	<0.01
Experiment 3					
Treatment	3	3.00	0.04	3.02	0.04
Canopy	1	3.34	0.09	2.33	0.15
Treatment × canopy	3	0.27	0.85	0.02	1.00
Block	16	5.30	<0.01	6.43	<0.01
Experiment 4					
Heat	1	0.53	0.47	0.49	0.49
Smoke	1	1.55	0.22	0.83	0.37
Heat × smoke	1	2.15	0.16	2.20	0.15
Block	8	3.30	0.01	2.85	0.02
Experiment 5					
Treatment	3	3.36	0.04	1.98	0.14
Block	8	7.34	<0.01	6.53	<0.01

Note: *DF* = degrees of freedom, *F* = *F*-statistic, and *P* = probability of a greater *F*-statistic.

Fig. 5.1. Soil seed bank 0-5 cm (a) seed density and (b) species richness among fire-related treatments of Experiments 1 and 2 for a *Pinus ponderosa* landscape, northern Arizona. Means without shared letters within an experiment differ at $P < 0.05$ (Tukey's test). Error bars are standard errors of the mean.

Fig. 5.2. Soil seed bank 0-5 cm (a) seed density and (b) species richness among canopy types and single or double treatment applications in Experiment 3 for a *Pinus ponderosa* landscape, northern Arizona. Open canopies and multiple heating or smoke applications induced the most emergence and greatest species richness. Means without shared letters differ at $P < 0.05$ (Tukey's test). Error bars are standard errors of the mean.

Fig. 5.3. Soil seed bank 0-5 cm (a) seed density and (b) species richness for fire-related treatments in Experiment 4 on samples collected from dense *Pinus ponderosa* forests, northern Arizona. Although there was a trend for greater emergence and species richness from smoke applications, treatment means did not differ significantly ($P > 0.05$). Error bars are standard errors of the mean.

Fig. 5.4. Soil seed bank 0-5 cm (a) seed density and (b) species richness for fire-related treatments in Experiment 5 on samples collected from dense *Pinus ponderosa* forests, northern Arizona. Means without shared letters differ at $P < 0.05$ (Tukey's test). Error bars are standard errors of the mean.

Fig. 5.5. Mean seed densities for (a) the summer study and (b) experiments averaged across treatments among forest ecosystems of a *Pinus ponderosa* landscape, northern

Arizona. Seed density was variable within ecosystems and did not differ significantly (P > 0.05) among ecosystems. Error bars are standard errors of the mean for total seed density in (a) and for 0-5 cm seed density in (b).

Fig. 5.6. Non-metric multidimensional scaling ordination of (a) aboveground vegetation and (b) summer study seed bank composition of a northern Arizona *Pinus ponderosa* landscape. Letters indicate ecosystem types: BC = black cinders, RC = red cinders, CB = clay basalt, XL = xeric limestone, ML = mesic limestone, XB = xeric basalt, RB = rocky basalt, MB = mesic basalt, AN = aspen, and PK = park. Vector abbreviations for species are as follows: BAHDIS = *Bahia dissecta*, BOUGRA = *Bouteloua gracilis*, ERIDIV = *Erigeron divergens*, FESARI = *Festuca arizonica*, LUPARG = *Lupinus argenteus*, MUHMON = *Muhlenbergia montana*, NAMDIC = *Nama dichotomum*, and SYMASC = *Symphyotrichum ascendens*.
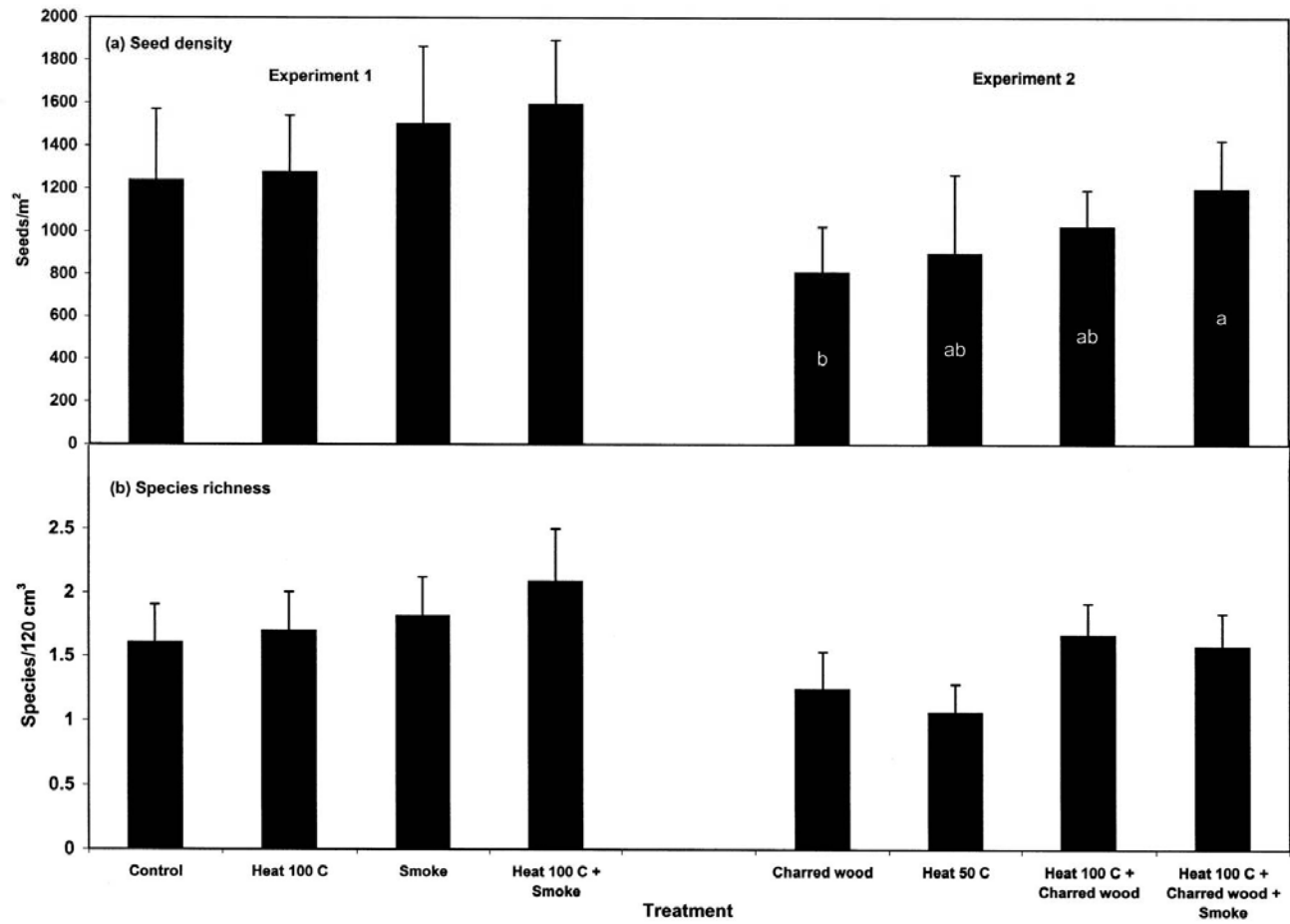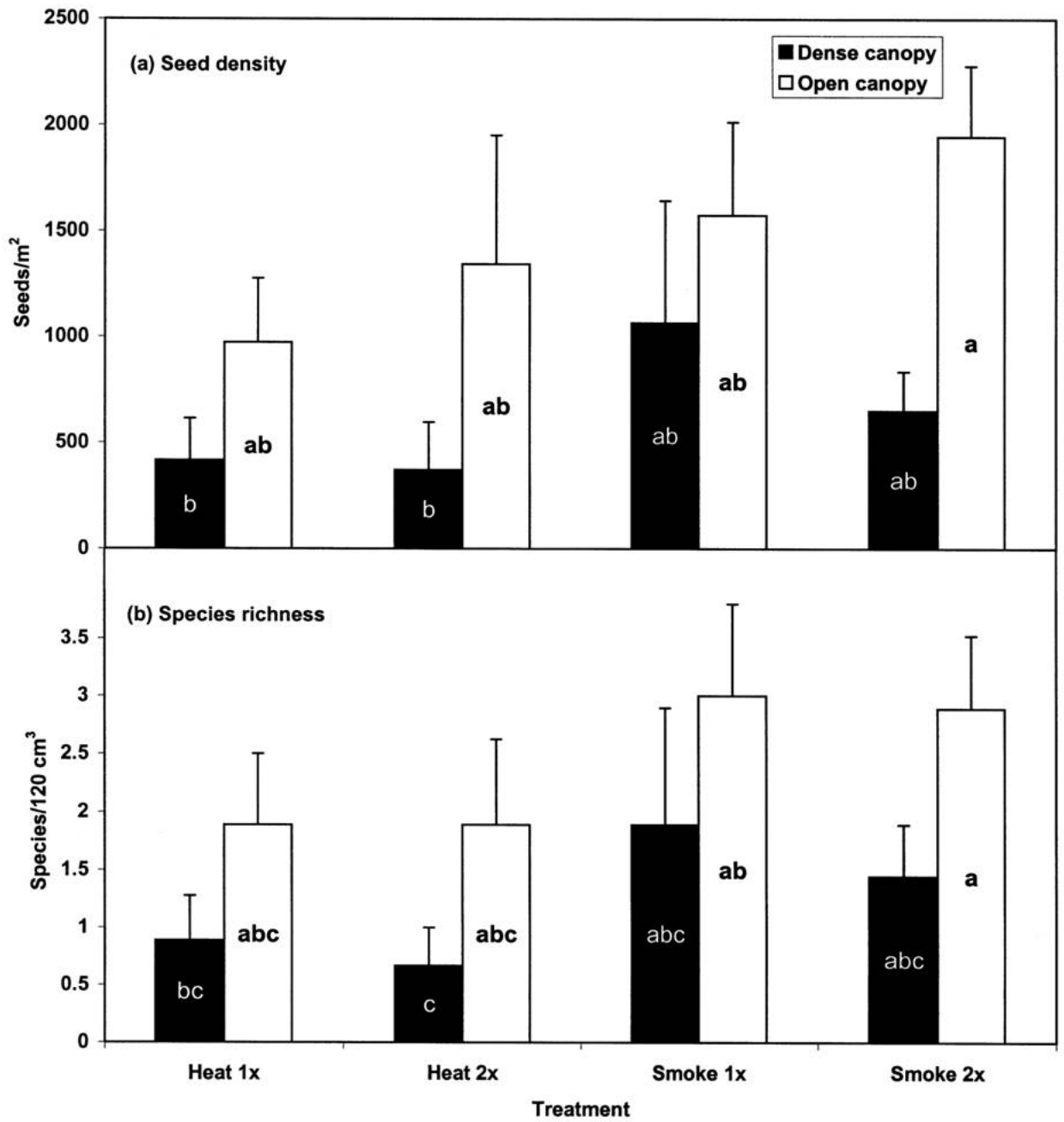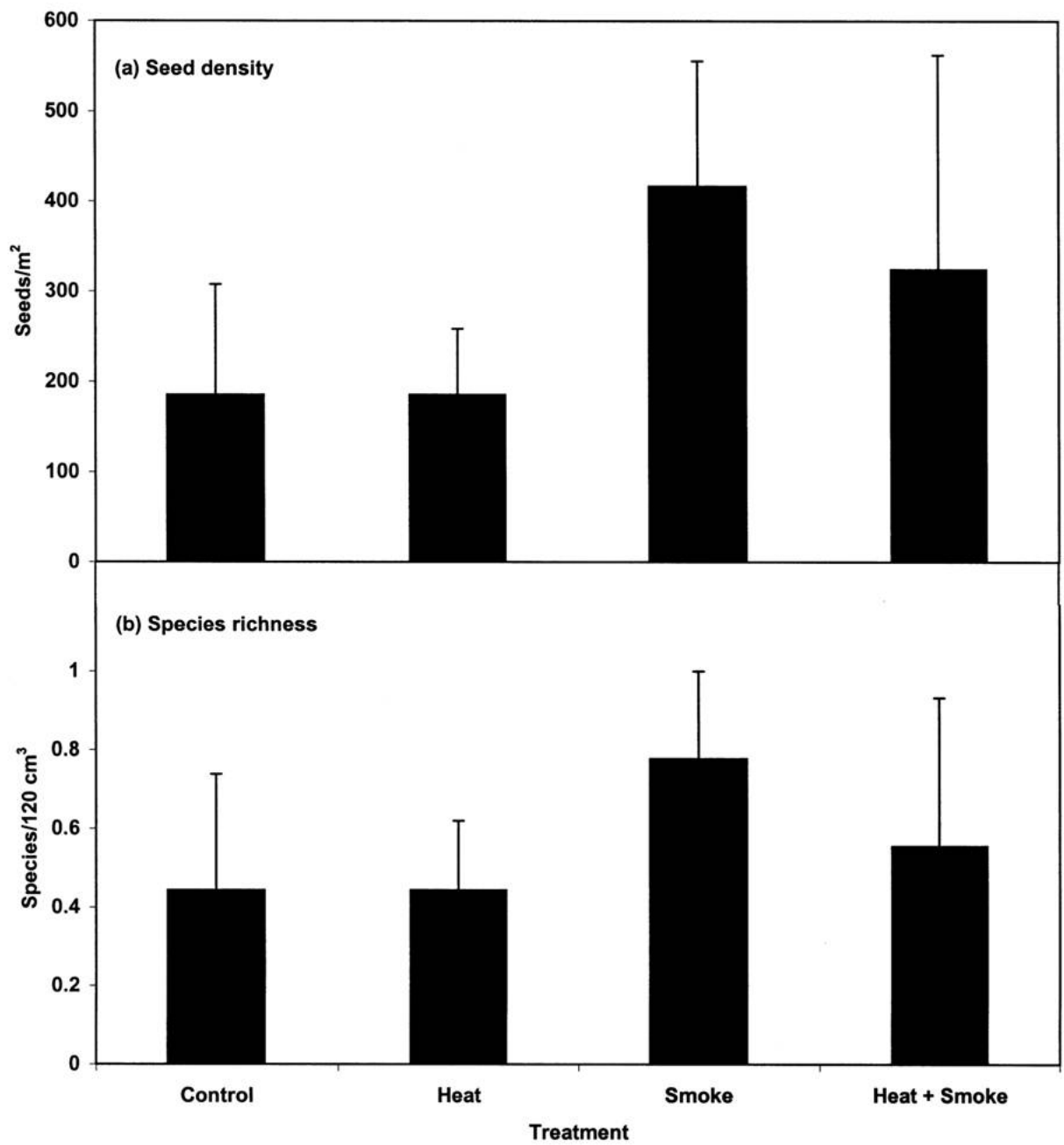
Fig. 5.1

Fig. 5.2

Fig. 5.3

Fig. 5.4

Fig. 5.5

(a) Aboveground vegetation

(b) Seed bank

Axis 2

Axis 1
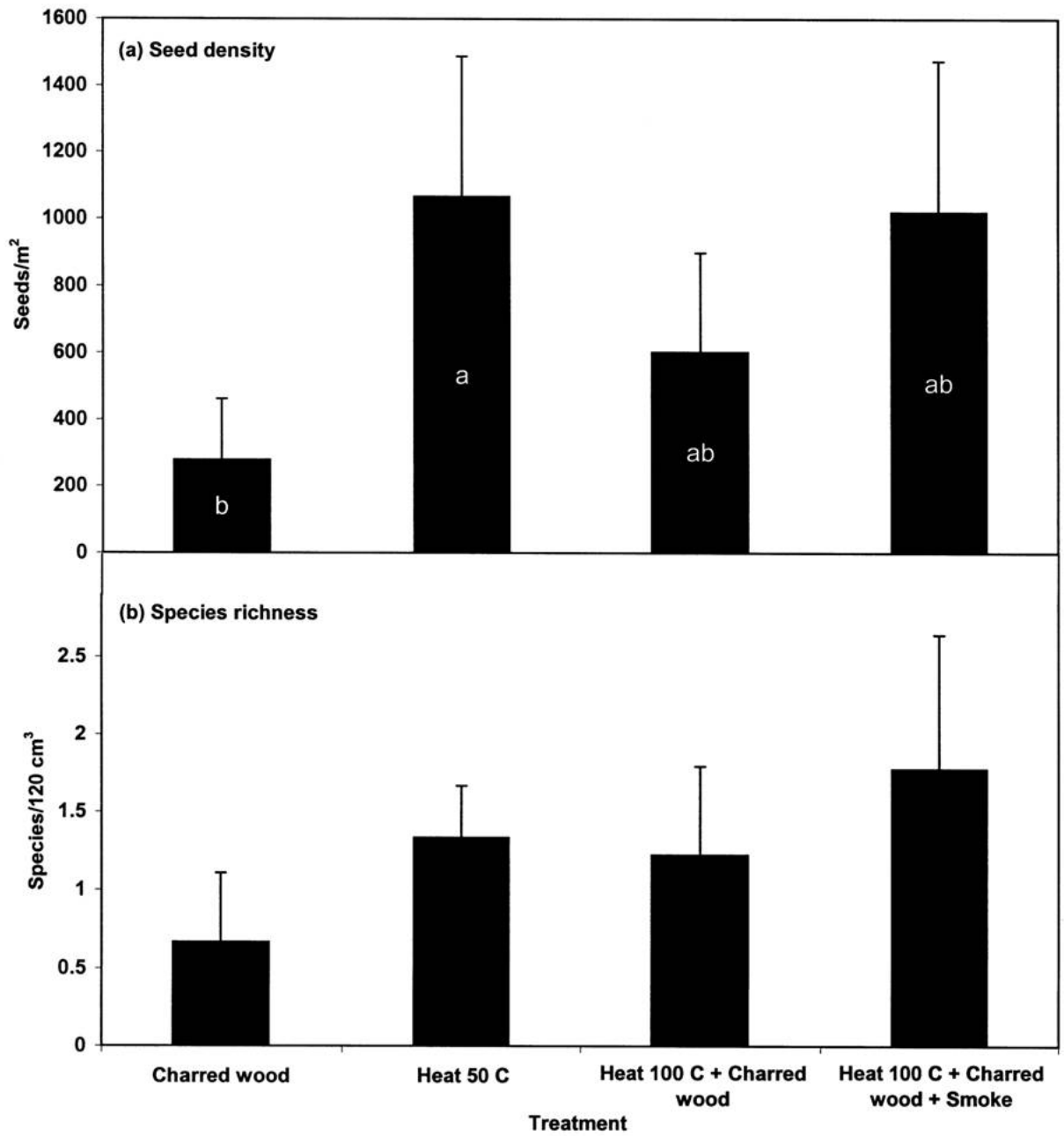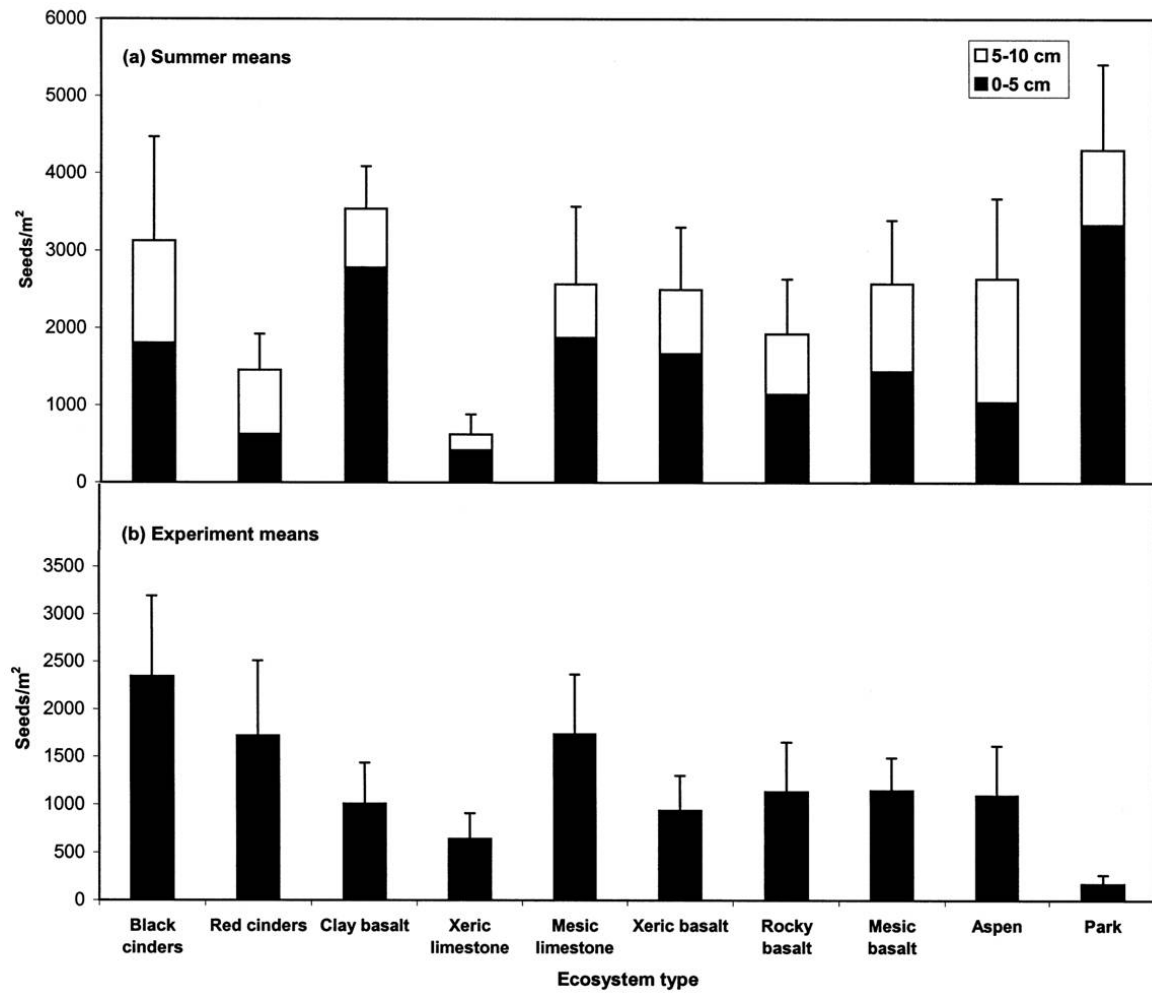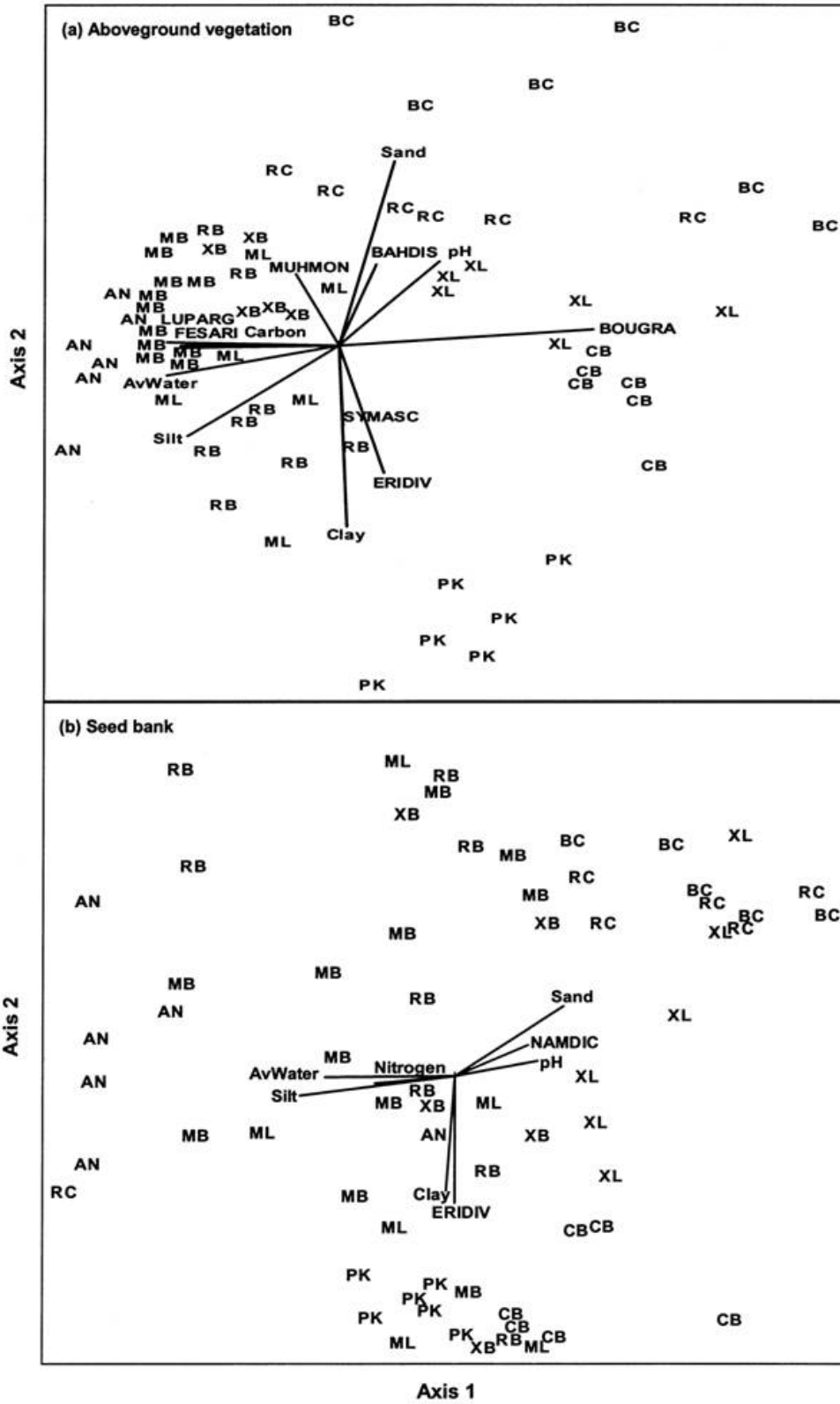
Fig. 5.6

CHAPTER 6

FOREST-FLOOR TREATMENTS IN ARIZONA PONDEROSA PINE RESTORATION ECOSYSTEMS: NO SHORT-TERM EFFECTS ON PLANT COMMUNITIES

ABSTRACT.—Leaf litter has accumulated during fire exclusion and tree density increases in post-settlement southwestern *Pinus ponderosa* forests, and may limit the establishment and emergence of understory vegetation that has recovered slowly during forest restoration. I performed an experiment in northern Arizona *P. ponderosa* forests to ascertain community responses to forest-floor scarification and Oi removal on 36, 100-m^2 plots overlaid on an existing thinning and burning restoration experiment. Contrasting with findings from many other forest types, forest-floor treatments had no effect on community diversity or composition during the 2-yr experiment, with post-treatment Sørensen similarities as high as 97% within treatments and no indication from successional vectors of possible longer term effects. An absence of response to these fairly drastic treatments is surprising given these forests' exceptionally heavy Oi horizons and large proportions of conifer litter. Based on sparse A-horizon seed banks averaging < 300 seeds/m^2 and paltry aboveground vegetation, I hypothesize that seed shortages particularly for native perennials partly precluded a treatment response. Since extensive unvegetated areas at these restoration sites could be colonized by exotics, a conservative management strategy is to test seeding or outplanting of desirable native species to fill unoccupied sites. It is important to report "no treatment effect" experiments such as this

one to avoid biasing meta-analyses, and for future research to clarify combinations of factors limiting understory communities to identify treatments that may more rapidly promote recovery of native species during ecosystem restoration in this region.

Key words: leaf litter, O horizon, soil, ground flora, seed bank, seed limitation, species diversity.

INTRODUCTION

Leaf litter directly and indirectly influences understory vegetation in plant communities. Decomposition of litter can immobilize some nutrients while releasing others, and produce allelopathic chemicals (Klemmedson et al. 1985). Accumulated litter intercepts light, affects soil microclimates, and can trap seeds or form physical barriers to plant emergence (Facelli and Pickett 1991). Litter also can be a filter in some plant communities regulating fine-grain species richness and species distributions by affecting plant germination and establishment (Sydes and Grime 1981). In a New York deciduous forest, for example, Beatty and Sholes (1988) found that removal of thick litter layers from treefall pits caused pit species composition to converge with that of treefall mounds, and all forbs colonizing litter-removed pits had previously been restricted to mounds.

In experiments in a variety of ecosystems, litter addition has often decreased germination, establishment, and species richness (Monk and Grabrielson 1985, Horman and Anderson 2003), whereas litter removal has resulted in increases at least in the short term for some species (Goldberg and Werner 1983, Vellend et al. 2000). Carson and Peterson (1990), for example, found that litter removal from 1-m^2 plots in New Jersey old fields increased plant density within 45 days, with *Oxalis stricta* (common yellow oxalis)

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increasing by 530 plants/m^2. Plant community responses to litter manipulations may vary with community type, the composition and quantity of litter, species pools and propagule availability, resource levels, and other factors (Xiong and Nilsson 1999).

After fire exclusion and increases in tree density since the late 1800s, many contemporary southwestern United States *Pinus ponderosa* (ponderosa pine) forests contain large amounts of litter from *P. ponderosa* needles, cones, bark, and wood (Covington and Sackett 1984). O horizons comprising forest floors, which include recognizable litter (Oi horizon) and decomposed duff (Oe+a horizon), were > 5 cm thick and weighed > 3000 g/m^2 in dense northern Arizona *P. ponderosa* stands surpassing 1500 trees/ha (Wollum and Schubert 1975, Klemmedson 1976, Fulé and Covington 1994). These depths and weights equal or exceed those of many world forests (Bray and Gorham 1964, Vogt et al. 1986), suggesting that litter may particularly affect or limit plant communities in contemporary *P. ponderosa* forests.

I performed an experiment in northern Arizona *Pinus ponderosa* forests to test the hypotheses that removing litter and scarifying the forest-floor increases plant species richness and diversity, changes community composition, and differentially affects individual species. By overlaying this experiment on an existing ecological restoration experiment that included tree thinning and prescribed burning, I sought to measure whether forest-floor manipulations could promote native plant establishment which has often been slow in this region after thinning and burning (Abella 2004).

METHODS

Study Area

I performed this experiment in the 1200-ha Fort Valley Experimental Forest (35°16'N, 111°43'W) in the Coconino National Forest, 15 km northwest of the city of Flagstaff in northern Arizona. Elevation is ca. 2300 m, and soils are primarily basalt-derived and classified as Mollic Eutroboralfs and Typic Argiborolls (USDA Forest Service 1995). Annual precipitation averages about 55 cm and half falls as snow (Western Regional Climate Center, Reno, NV). Forests are pure *Pinus ponderosa*, with graminoids dominating understory communities including *Carex geophila* (White Mountain sedge), *Elymus elymoides* (squirreltail), *Festuca arizonica* (Arizona fescue), *Muhlenbergia montana* (mountain muhly), and *Poa fendleriana* (muttongrass). Presettlement (pre 1875) tree densities averaged about 60 trees/ha, and fires primarily from lightning ignitions occurred on average at least once every 10 years (Covington et al. 1997). Likely from a combination of livestock grazing, fire exclusion, and increased tree density, ground flora declined after settlement, persisting only below canopy gaps or as isolated occurrences on litter-choked forest floors below dense canopies (Vose and White 1991).

This experiment was overlaid on 9 sites of an existing ecological restoration experiment initiated in 1998-1999 with goals of approximately reestablishing presettlement stand structure, reducing fuels, and increasing understory vegetation (Fulé et al. 2001a). These 9 sites in the restoration experiment included three 14-ha sites for each of 3 restoration prescriptions: control (no thinning, no burning), medium restoration (3-6 thin prescription + prescribed burning), and intensive restoration (2-4 thin prescription + prescribed burning). Thinning prescriptions represent ratios at which evidence (stumps, snags, and fallen logs) of presettlement tree locations were replaced by

postsettlement trees retained during thinning. The 2-4 prescription most sharply reduced

tree densities, and Fulé et al. (2001a) describe prescriptions in more detail. Restoration

prescriptions served as blocks in the current experiment to more accurately compare

responses to forest-floor treatments, because forest-floor and vegetation characteristics

differed among prescriptions prior to this experiment (Table 6.1).

<center>Experimental Design and Treatments</center>

I randomly located four 10 m × 10 m (0.01 ha) plots at each site for a total of 36

plots ($n = 9$ for each treatment), with plots at a site separated by 3 m and arranged in a 2

× 2 square. One of 4 forest-floor treatments was randomly assigned to each plot at each

site in a factorial design consisting of 2 levels of scarification (none, O horizon scarified)

and 2 levels of Oi horizon removal (none, Oi removed). Scarification was performed to

possibly bring seeds to the soil surface while creating a variegated establishment surface

for dispersed seeds (Chambers 2000). Oi horizons were removed to expose mineral soil

for a seed bed, while eliminating thick litter layers that possibly form a barrier to

emergence from soil seed banks (Horman and Anderson 2003). I performed scarification

treatments by hand by dragging a 45-cm wide metal rake across plots to break up O

horizons and the upper few cm of mineral soil. I removed Oi horizons by raking litter off

plots using a 75-cm wide plastic rake, with removals per plot ranging from 290-2200 kg

oven-dry weight. Oe+a horizons were thin or absent except in control restoration

prescriptions that had not been thinned or burned, and I retained these horizons on plots

during Oi removal. Observations during treatment application indicated that no apparent

damage occurred to existing vegetation during treatments since treatments were applied

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by hand and rakes moved over existing vegetation. I performed treatments in April 2003, and I raked Oi removal plots again in April 2004 to remove litterfall.

Vegetation and Environmental Sampling

I sampled ground flora on plots in April 2003 before treatment and in August-October after treatment in 2003 and 2004. I collected pre-treatment data as a covariate for repeated measures analysis of variance (ANOVA). Each plot contained six 1 m × 1 m subplots that were located at the plot corners and at the midpoints of the south and north plot edges. Areal percent cover of plant species rooted in each subplot was categorized as 0.1, 0.25, 0.5, or 0.75% cover below 1% cover, at 1% intervals to 10% cover, and at 5% intervals above 10% cover. I also recorded species on a presence/absence basis on whole plots. I calculated importance values (average of relative frequency and relative cover) for each species on each plot, and I assigned a frequency of 1 to species occurring only on whole plots for calculating importance values. Nomenclature and native or exotic classifications follow USDA-NRCS (2004).

I assessed sampling reproducibility by remeasuring a subplot every 3 plots, and by checking for consistency of species identification and detection on 2 plots inventoried twice by 2 different observers. Repeated measurements for subplots on average differed from original measurements by 0.17 species/m^2, and exhibited Sørensen similarities (based on percent cover) of 98%. Repeated and original measurements for plots differed by 1 species/100 m^2, and also varied by 1 species on average among observers who sampled plots during the experiment. I was present during all sampling periods, and low measurement error suggests that results from this experiment represent actual occurrences and not sampling artifacts.

I measured litterfall by installing 2 litter traps randomly located around the edge of each plot. Traps consisted of a 0.15-m^2 plastic bucket 30 cm tall. I collected an Oi horizon sample of 1 m^2 on each plot before treatment in April 2003, and I oven dried Oi and litterfall samples at 70°C. I gravimetrically measured moisture of the 0-10 cm mineral soil on Oi removal and control plots by oven drying a 415-cm^3 sample per plot at 105°C for 24 hr. Soil moisture was measured 9 June 2004 during the driest period of the year in this region when no measurable precipitation had fallen since April (Western Regional Climate Center, Reno, NV).

Seed Bank Procedures

I collected fifteen 208-cm^3 seed bank samples per plot of the 0-5 cm A horizon from control and Oi removal plots, and combined these samples on a plot basis (18 composite samples). I also collected Oe+a samples from control plots in control restoration prescriptions (3 composite samples) and Oi samples from all control plots (9 composite samples). Oi and Oe+a samples were collected as grab samples each of ca. 15 g (field moist), and I sieved Oi samples through a 4-mm sieve. Samples were collected and started in a greenhouse on 25 June 2004. I selected this collection and germination period to estimate which species may emerge in the field during monsoon rains typically beginning in July in this region. I placed 120 cm^3 of each horizon of each plot in separate 700-cm^3 plastic pots filled with 300 cm^3 of sterile soil (United Industries Co., St Louis, MO), randomly arranged pots in a greenhouse maintained at 24°C without artificial lighting, watered samples daily, and monitored emergence for 6 months.

Statistical Analysis

I analyzed the response variables of species/m^2, species/100 m^2, and Shannon's diversity index as a repeated measures ANOVA with pretreatment data as a covariate and restoration prescriptions as blocks using the following model: 2003 and 2004 y = covariate + blocks + scarification + Oi removal + scarification × Oi removal. To track community compositional changes of individual plots across sampling periods, I computed Sørensen similarities for importance value and presence/absence data. I compared Sørensen similarities among treatments using a 2-factor ANOVA model consisting of scarification and Oi removal with restoration prescriptions as blocks. Raw data approximated equal variance and normality assumptions, and I performed analyses in SAS JMP (SAS Institute 2002). I also ordinated community data (importance values) with successional vectors using non-metric multidimensional scaling (autopilot, thorough mode) in PC-ORD (McCune and Mefford 1999).

<center>RESULTS</center>

Forest-floor treatments did not significantly affect species richness or diversity during the 2-year experiment based on repeated measures ANOVA (Table 6.2). The covariate (pre-treatment data) and blocks (restoration prescription) were significant in all ANOVA models, indicating only that the covariate was correlated with post-treatment data and that the restoration prescriptions differed before and after treatment reducing variance in treatment means. Time was significant only for species/m^2, with slight increases occurring on average across all treatments from 2003 to 2004 (Fig. 6.1).

High Sørensen similarities averaging > 75% indicated that little compositional change occurred between post-treatment 2003 and 2004 measurements for individual plots in any treatment (Fig. 6.2). Lower similarities between pre- and post-treatment

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2003 measurements simply reflect season-of-sampling effects (spring versus fall) since similarities did not differ significantly among treatments. Successional trajectories from repeated-measures community ordination provided no evidence that plots of like forest-floor treatments converged in species composition, indicating only loose groupings of plots within restoration prescriptions (Fig. 6.3).

Forest-floor treatments had no clear effect on frequencies of individual species, with only restoration prescription and time effects apparent for some species (Table 6.3). Exotic species *Linaria dalmatica* (Dalmatian toadflax) and *Verbascum thapsus* (common mullein) were more frequent in restoration than in control prescriptions, with seedlings of *V. thapsus* increasing in frequency from 2003 to 2004. Short-lived but primarily native species including the annuals *Chenopodium graveolens* (fetid goosefoot), *Muhlenbergia minutissima* (annual muhly), and *Nama dichotomum* (wishbone fiddleleaf) also were more frequent in restoration prescriptions and exhibited overall increases through time. The annual *Laennecia schiedeana* (pineland marshtail) and *Pinus ponderosa* seedlings, however, sharply decreased from 2003 to 2004, but these decreases appeared largely independent of forest-floor treatments. In contrast, frequencies of the perennials *Carex geophila*, *Festuca arizonica*, *Geranium caespitosum* (pineywoods geranium), *Muhlenbergia montana*, *Poa fendleriana*, and *Solidago velutina* (three-nerve goldenrod) changed little or not at all during the experiment.

Nine species emerged from seed bank samples collected in 2004, with *Elymus elymoides* the most frequent (Fig. 6.4). *Gnaphalium exilifolium* (slender cudweed), an annual, was the only species detected in seed bank samples that did not occur in the aboveground vegetation of at least one plot. Seed density averaged less than 300

seeds/m^2 except for a higher density in Oi horizons of control forest-floor treatments in intensive restoration prescriptions. This high average density of 1250 seeds/m^2 occurred because of one plot containing an unusually high seed density. Approximately equal seed densities were detected in A-horizon samples from control and Oi removal forest-floor treatments, and A-horizon seed densities in the control forest-floor treatment were identical among restoration prescriptions

Discussion

Absence of Treatment Effects

Scarification and Oi removal forest-floor treatments had no measurable effect on plant community composition or species richness during the 2-year experiment, and successional trajectories provided little evidence for potential long-term effects (Fig. 6.3). Sampling included complete species inventories of well-replicated plots and was reproducible across years, ruling out inadequate sampling as a reason for the observed absence of treatment effects. Results contrast with many other published studies in a variety of forest types where some type of community response to litter manipulations has occurred in less than 3 years (Beatty and Sholes 1988, Carson and Peterson 1990, Vellend et al. 2000). Furthermore, Xiong and Nilsson's (1999) meta-analysis found that effects of litter manipulations on plant establishment were greater in field than in greenhouse experiments, in 2-year versus 1-year experiments, in communities with large amounts of litter, and in coniferous compared to deciduous forests, all of which characterized my experiment. Treatments also were fairly drastic removing up to 2200 kg of litter on a plot, and my plot sizes of 100 m^2 were much larger than the $\leq$ 1 m^2 in

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many litter experiments although treatment effects did not occur in my experiment at 1-m^2 grains either.

<div align="center">Limitations to Treatment Response</div>

A number of factors may have limited ground-flora responses to treatments in this experiment, including climate, *Pinus ponderosa*-associated variables other than litter, grazing, competition with existing vegetation, nutrients, and seed limitations (DiTommaso and Aarssen 1989). A period of below-average annual precipitation has occurred in the study area since 1999 after restoration treatments were implemented, and 2002 was a particularly dry year before my experiment was initiated (Fig. 6.4). However, growing-season and total precipitation were near or slightly above normal during both post-treatment years in 2003-2004.

High densities of *Pinus ponderosa* in post-settlement forests are well known to reduce understory vegetation, presumably from shading, allelopathic litter production, and competition for water (Moir 1966, Lodhi and Killingbeck 1982, Naumburg and DeWald 1999). For example, plant cover and diversity increased during trenching experiments severing *P. ponderosa* roots in Oregon (Riegel et al. 1992) and in Northern Arizona (Fulé et al. 2001b). Although tree densities were sharply reduced in restoration prescriptions in my experiment (Table 6.1), there was no trend for effects of forest-floor treatments to be greater on lower tree density plots. Tree densities in restoration prescriptions still exceeded presettlement densities by ca. 100-300 trees/ha, however, and may still have been too high for forest-floor treatments to elicit a response (McLaughlin 1978, Moore and Deiter 1992, Abella and Covington 2004).

Grazing by livestock and other ungulates affects community composition in northern Arizona *Pinus ponderosa* forests (Clary 1975). Although livestock grazing has been excluded from the study area since at least 1998, Huffman and Moore (2003) found that heavy *Cervus elaphus* (Rocky Mountain elk) grazing reduced *Ceanothus fendleri* (buckbrush) in the study area. Grazing thus may have affected composition during my experiment. Since plant cover averaged < 10% on plots in this experiment, it does not seem plausible that all niches and microsites were filled and that competition from existing vegetation precluded a treatment response. Nutrient availability could have been limiting, but prescribed burning before this experiment may have released nutrients at least in the short term (Covington and Sackett 1986, Kaye and Hart 1998).

Seed bank data indicated that A-horizon seed banks were sparse or essentially absent, and aside from one plot, few seeds were trapped in O horizons so few seeds were likely removed by forest-floor treatments (Fig. 6.3). Sparse seed banks particularly of perennial forbs also were previously reported in the study area (Vose and White 1987, Korb et al. 2004) and typify many northern Arizona *Pinus ponderosa* forests (Abella 2005). In their seed budget study, Vose and White (1987) also found that seed rain was fairly impoverished, ranging from 14-547 seeds/m^2/yr and concentrated around existing plants. Propagule limitations have been reported in about 50% of seed-augmentation experiments, and have been particularly severe in communities such as in my experiment that exhibit sparse seed banks, paltry aboveground vegetation producing few seeds, and much bare ground (Turnbull et al. 2000). Seeding and outplanting have shown success in the limited areas in which they have been studied in Arizona *P. ponderosa* forests (Steed

and DeWald 2003, Springer and Laughlin 2004), and testing for propagule limitation in these forests is an important research need.

<center>Potential Long-Term Species Composition</center>

Species composition and diversity at the onset of this experiment did differ between controls and restoration prescriptions that included thinning and burning, consistent with previous research at these sites completed in 2002 (Abella and Covington 2004). Aside from transitions in *Pinus ponderosa* seedlings and short-lived species like *Laennecia schiedeana*, *Chenopodium graveolens* and *Verbascum thapsus*, community composition as a whole was fairly stagnant in restoration prescriptions in 2003-2004 during the present experiment (Table 6.3). Apparently there was an initial increase in plant cover after the 1998-1999 restoration treatments, driven primarily by species such as *Carex geophila* that do form fairly large persistent seed banks, but little change since. Bartha et al. (2003) reported a similar pattern in a 40-yr study of a New Jersey old-field succession, where the number of colonizing species rapidly declined after the first few years of succession. However, increases in colonization rates then occurred after dry years during "colonization windows" in their study, which has not occurred to date in the present experiment except possibly for undesirable species like *V. thapsus*. The biennial *V. thapsus*, usually thought to rapidly decline following initial post-disturbance increases (Gross and Werner 1978), remained frequent in restoration areas, even sharply increasing on control forest-floor plots in the intensive restoration prescription 6 years after restoration treatments (Table 6.3). Although this species was not detected in my seed bank samples, possibly because its germination requirements were not met at the time of

sample collection (Baskin and Baskin 1981), this species is known to form large and persistent seed banks (Gross and Werner 1978).

Extensive bare ground providing colonization sites for exotic species such as *Verbascum thapsus* is a concern given increasing unease about exotic species invasions in northern Arizona forests (Sieg et al. 2003). Since these unoccupied microsites could continue to fill with exotics like *V. thapsus*, *Linaria dalmatica*, or additional undesirable species that are not presently found in current species pools, a conservative management strategy is to test seeding or outplanting of native perennials for vegetating unoccupied ground.

Non-Significant Results

This paper reports a main finding of "no treatment effect" on plant communities from fairly drastic forest-floor manipulations in a well-sampled experiment that likely would have detected trends had they existed. Under-reporting of non-statistically significant but properly collected and analyzed data, a form of publication bias, has long been suspected in ecology and increasingly is being quantitatively assessed (Møller and Jennions 2001, Murtaugh 2002). Reporting of non-significant results is particularly important to avoid biasing meta-analyses, which are increasingly used to synthesize research findings in ecology (Osenberg et al. 1999, Gurevitch and Hedges 1999). Results of my experiment contrast sharply with results of most published papers in a recent meta-analysis of leaf-litter manipulation experiments, which found strong treatment effects in many other ecosystems (Xiong and Nilsson 1999). This does not mean that leaf litter has no influence on plant communities in *Pinus ponderosa* forests, but rather that treatment responses were precluded by other factors important to identify in future research to find

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ways to increase native plant cover. If seed shortages prevented responses, for example, it is unclear whether seeding would be more successful with or without litter. This experiment portrays that economically and ecologically effective treatments supplementary to thinning and burning still need to be identified and tested for promoting native vegetation more rapidly in restoration *P. ponderosa* ecosystems.

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Table 6.1. Plot characteristics of a forest-floor manipulation experiment in *Pinus ponderosa* ecological restoration blocks, northern Arizona.

Treatment[a]	Stand density[b]	Oi horizon	Litterfall	Soil moisture[c]
Control ER	—Trees/ha—	—g/m^2—	—$g/m^2/yr$—	—%—
C	1333 (95)[d]	1302 (63)	129 (20)	6.8 (25)
S	1300 (66)	1349 (55)	118 (50)	—
R	700 (52)	1117 (39)	153 (25)	6.3 (13)
S+R	1233 (68)	1318 (33)	164 (54)	—
Medium ER				
C	333 (96)	893 (41)	95 (7)	7.4 (30)
S	333 (35)	643 (17)	109 (30)	—
R	133 (86)	573 (38)	128 (72)	5.2 (6)
S+R	267 (43)	723 (48)	127 (74)	—
Intensive ER				
C	300 (67)	821 (24)	75 (55)	8.3 (28)
S	400 (25)	687 (79)	74 (41)	—
R	167 (92)	702 (20)	105 (47)	5.3 (36)
S+R	267 (115)	778 (28)	92 (8)	—

^a ER = ecological restoration prescription. Abbreviations for forest-floor treatments are as follows: C = control, S = scarification, R = Oi removal, and S + R = scarification + Oi removal.

^b Densities represent all stems > 1 cm diameter at 1.4 m. Trees and Oi weight were measured after ecological restoration but before forest-floor treatments.

^c Percent of oven dry weight measured in June 2004 for a 0-10 cm depth; — not measured.

^d Values are mean (coefficient of variation).

Table 6.2. Summary of repeated-measures analysis of variance for forest-floor treatments in northern Arizona *Pinus ponderosa* ecosystems.

Effect	Species/m^2		Species/100 m^2		Diversity[a]	
	F[b]	P[b]	F	P	F	P
Between subjects						
Blocks	14.78	<0.01	18.84	<0.01	16.70	<0.01
Covariate	29.15	<0.01	19.84	<0.01	26.53	<0.01
S[c]	0.32	0.58	0.10	0.76	0.90	0.35
R	0.03	0.87	0.02	0.89	0.28	0.60
S × R	0.62	0.44	0.06	0.81	1.02	0.32
Within subjects						
Time	5.11	0.03	0.00	1.00	1.29	0.27
Time × block	0.65	0.53	0.51	0.60	1.57	0.23
Time × S	0.01	0.92	0.22	0.65	0.02	0.90
Time × R	1.10	0.30	0.26	0.61	0.77	0.39
Time × S × R	0.54	0.47	0.00	0.98	0.00	0.96

[a] Shannon's diversity index.

[b] *F*-statistic and probability of a greater *F*.

[c] Abbreviations for forest-floor treatments: S = scarification, R = Oi removal.

Table 6.3. Mean 2004 1-m^2 percent frequency and change from 2003 to 2004 for the 25 most frequent species among ecological restoration prescriptions and forest-floor treatments in northern Arizona *Pinus ponderosa* forests ($n = 3$ for each category).

Species	CC[a]	CS	CR	CSR	MC	MS	MR	MSR	IC	IS	IR	ISR
Carex geophila	44 (0)[b]	33 (0)	39 (0)	44 (0)	72 (+16)	44 (0)	39 (-11)	56 (0)	56 (0)	50 (0)	50 (+6)	44 (-12)
Ceanothus fendleri	0 (0)	0 (0)	0 (-6)	11 (0)	6 (0)	0 (0)	0 (0)	0 (0)	6 (-5)	17 (0)	0 (0)	0 (-6)
Chenopodium graveolens	0 (0)	6 (0)	0 (0)	0 (0)	33 (+22)	39 (+17)	33 (+16)	33 (+16)	11 (+11)	17 (+11)	22 (+22)	17 (+11)
Cirsium wheeleri	0 (0)	0 (0)	11 (+5)	6 (0)	22 (+5)	17 (+6)	11 (+5)	0 (0)	28 (+17)	28 (+6)	33 (+5)	22 (-6)
Elymus elymoides	61 (0)	61 (0)	56 (-5)	67 (0)	72 (+16)	66 (+16)	78 (0)	56 (0)	89 (+11)	94 (+22)	78 (+11)	72 (0)
Erigeron divergens	0 (0)	0 (0)	11 (+11)	11 (+11)	6 (+6)	0 (0)	0 (0)	6 (+6)	0 (-6)	6 (0)	11 (+5)	6 (+6)
Festuca arizonica	0 (0)	6 (0)	6 (0)	17 (0)	0 (0)	11 (0)	11 (0)	6 (+6)	17 (0)	17 (0)	11 (0)	11 (0)
Geranium caespitosum	0 (0)	0 (0)	6 (0)	17 (0)	0 (0)	6 (0)	6 (-5)	0 (0)	17 (0)	0 (0)	17 (0)	0 (0)
Hieracium fendleri	6 (0)	0 (0)	0 (-6)	0 (-6)	6 (+6)	0 (0)	6 (+6)	0 (0)	11 (0)	17 (+6)	6 (-5)	11 (0)
Laennecia schiedeana	0 (0)	0 (0)	6 (-5)	6 (-11)	17 (-22)	0 (-11)	22 (-17)	28 (-5)	6 (-33)	17 (-33)	17 (-16)	17 (-5)
Linaria dalmatica	0 (0)	0 (0)	0 (0)	0 (0)	6 (+6)	11 (0)	0 (-6)	11 (0)	0 (0)	0 (0)	11 (+5)	0 (0)
Lotus wrightii	0 (-6)	0 (0)	6 (+6)	6 (0)	17 (0)	0 (-6)	0 (0)	11 (0)	11 (+5)	11 (+5)	28 (0)	11 (0)
Muhlenbergia montana	22 (0)	33 (0)	11 (0)	17 (0)	17 (0)	22 (0)	6 (0)	0 (0)	28 (0)	6 (0)	17 (0)	0 (0)
Muhlenbergia ramulosa	6 (+6)	11 (0)	0 (0)	11 (+11)	11 (0)	17 (+17)	0 (0)	11 (+11)	28 (+11)	17 (0)	22 (+11)	22 (+5)

Nama dichotomum	0 (0)	0 (0)	0 (0)	0 (0)	6 (+6)	0 (0)	6 (-5)	0 (0)	17 (+17)	0 (0)	11 (+11)	22 (+11)
Packera multilobata	0 (0)	0 (0)	6 (+6)	0 (0)	11 (0)	11 (+5)	17 (0)	17 (+6)	22 (0)	17 (0)	22 (+11)	0 (0)
Pinus ponderosa	6 (0)	6 (0)	0 (0)	0 (0)	11 (-28)	11 (-33)	6 (-33)	22 (+5)	6 (-11)	11 (-17)	0 (-28)	6 (-5)
Poa fendleriana	11 (0)	11 (0)	33 (0)	17 (0)	0 (0)	11 (0)	17 (0)	6 (0)	17 (-5)	6 (0)	0 (0)	11 (+5)
Potentilla crinita	6 (0)	0 (0)	17 (0)	22 (-6)	0 (0)	0 (0)	6 (0)	0 (0)	0 (0)	0 (0)	6 (0)	0 (0)
Potentilla subviscosa	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	6 (0)	11 (-6)	0 (-6)	0 (0)	0 (0)	0 (-6)
Pseudocymopterus montanus	6 (0)	0 (0)	6 (-5)	0 (0)	6 (0)	6 (0)	6 (0)	0 (0)	22 (+5)	0 (-6)	11 (0)	6 (0)
Pseudognaphalium macounii	0 (0)	11 (+5)	0 (0)	0 (0)	0 (-6)	0 (0)	0 (0)	0 (-6)	6 (0)	6 (-5)	0 (0)	11 (0)
Solidago velutina	22 (0)	6 (0)	39 (0)	17 (0)	17 (0)	6 (0)	17 (0)	0 (0)	6 (0)	0 (0)	22 (0)	11 (0)
Verbascum thapsus	0 (0)	0 (0)	0 (-6)	6 (0)	11 (0)	17 (+6)	22 (+11)	28 (+28)	56 (+17)	56 (+28)	39 (+17)	33 (0)
Vicia americana	6 (+6)	11 (0)	6 (0)	22 (-6)	6 (0)	6 (0)	17 (+6)	11 (0)	6 (0)	17 (0)	33 (0)	6 (0)

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[a] The first letter identifies the ecological restoration prescription (C = control, M = medium, and I = intensive), and the following

letter(s) identifies the forest-floor treatment (C = control, S = scarification, R = Oi removal, and SR = scarification + Oi removal).

[b] Values are mean 2004 frequency (% change from 2003 to 2004).

Fig. 6.1. Mean plant species richness and diversity among ecological restoration prescriptions and forest-floor treatments in northern Arizona *Pinus ponderosa* forests. Error bars are 1 standard deviation.

Fig. 6.2. Mean multivariate similarities through time based on species importance values (IV) and presence/absence (P/A) among ecological restoration prescriptions and forest-floor treatments in northern Arizona *Pinus ponderosa* forests. Error bars are 1 standard deviation.

Fig. 6.3. Non-metric multidimensional scaling successional vectors of understory composition among ecological restoration prescriptions and forest-floor treatments in northern Arizona *Pinus ponderosa* forests.

Fig. 6.4. Seed bank composition by species and soil horizon among control and Oi removal forest-floor treatments and ecological restoration prescriptions in northern Arizona *Pinus ponderosa* forests. Seeds/m^2 are standardized to represent a 0-5 cm depth (0.05 m^3), with the Oi horizon representing material passing a 4-mm sieve. ARELAN = *Arenaria lanuginosa*, ELYELY = *Elymus elymoides*, ERIDIV = *Erigeron divergens*, GNAEXI = *Gnaphalium exilifolium*, LAESCH = *Laennecia schiedeana*, MUHMON = *Muhlenbergia montana*, MUHRAM = *Muhlenbergia ramulosa*, POAFEN = *Poa fendleriana*, and PSEMAC = *Pseudognaphalium macounii*.

Fig. 6.5. Recent and long-term precipitation records measured at the Flagstaff Airport, northern Arizona, obtained from the Western Regional Climate Center (Reno, NV).
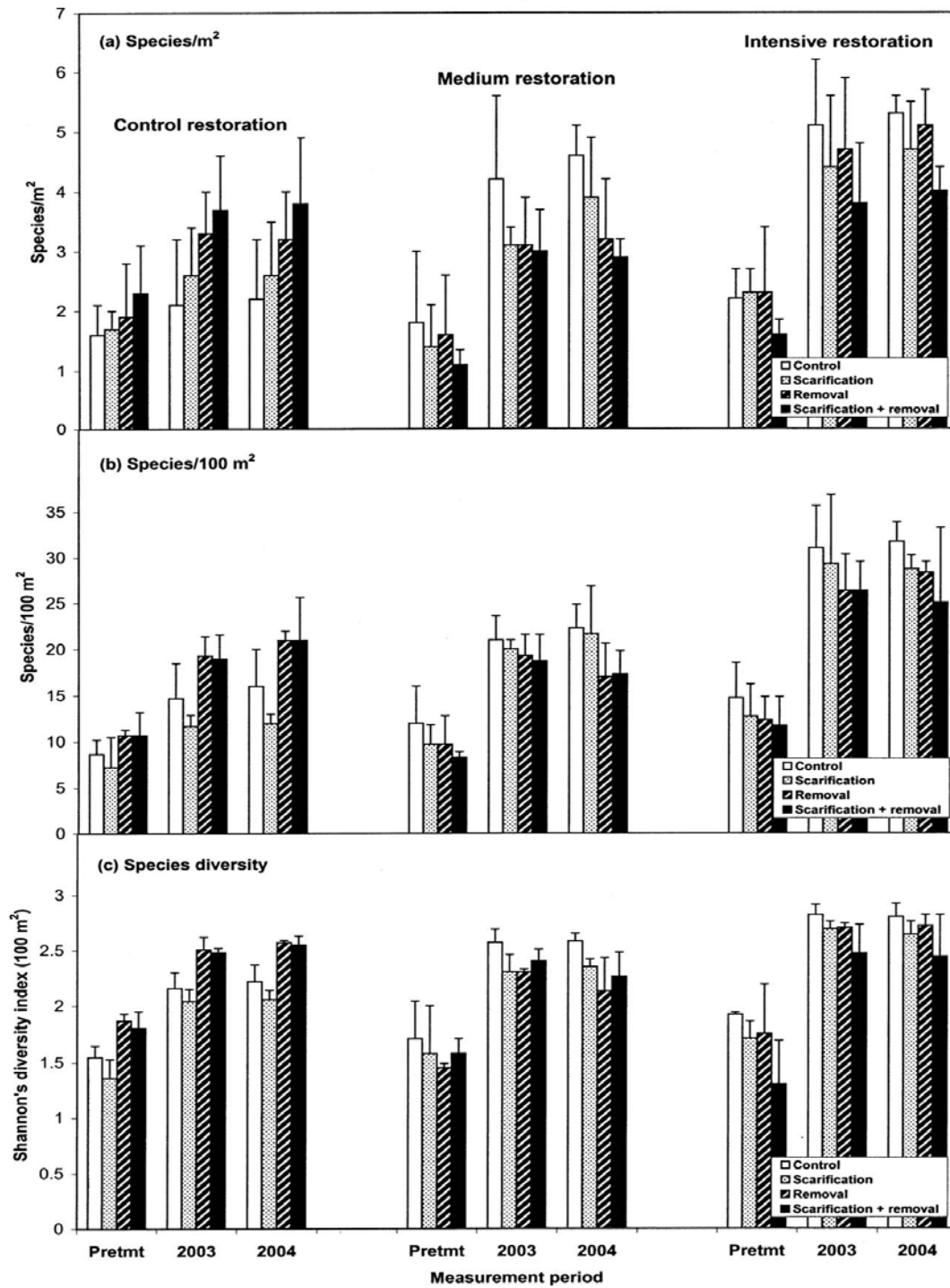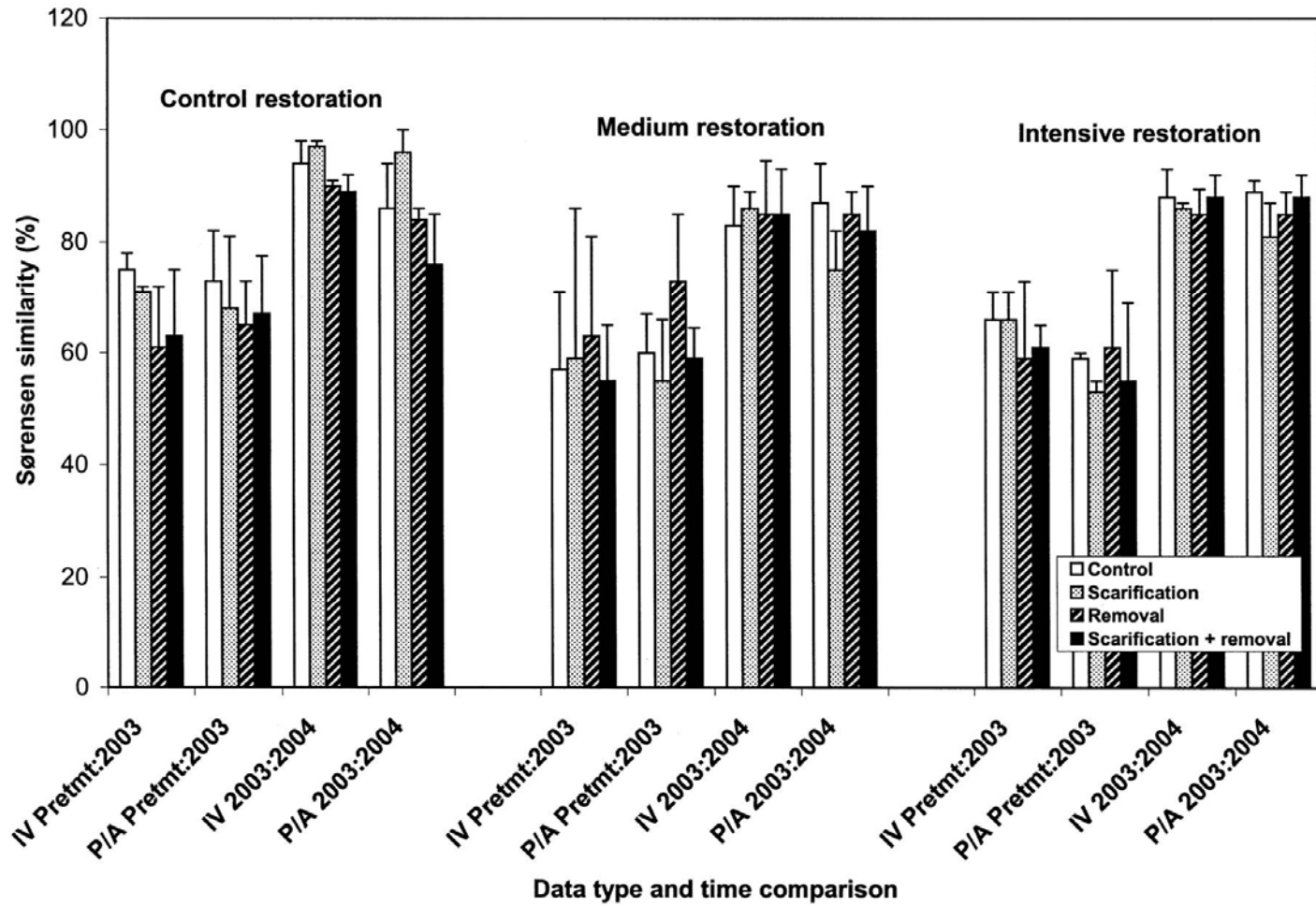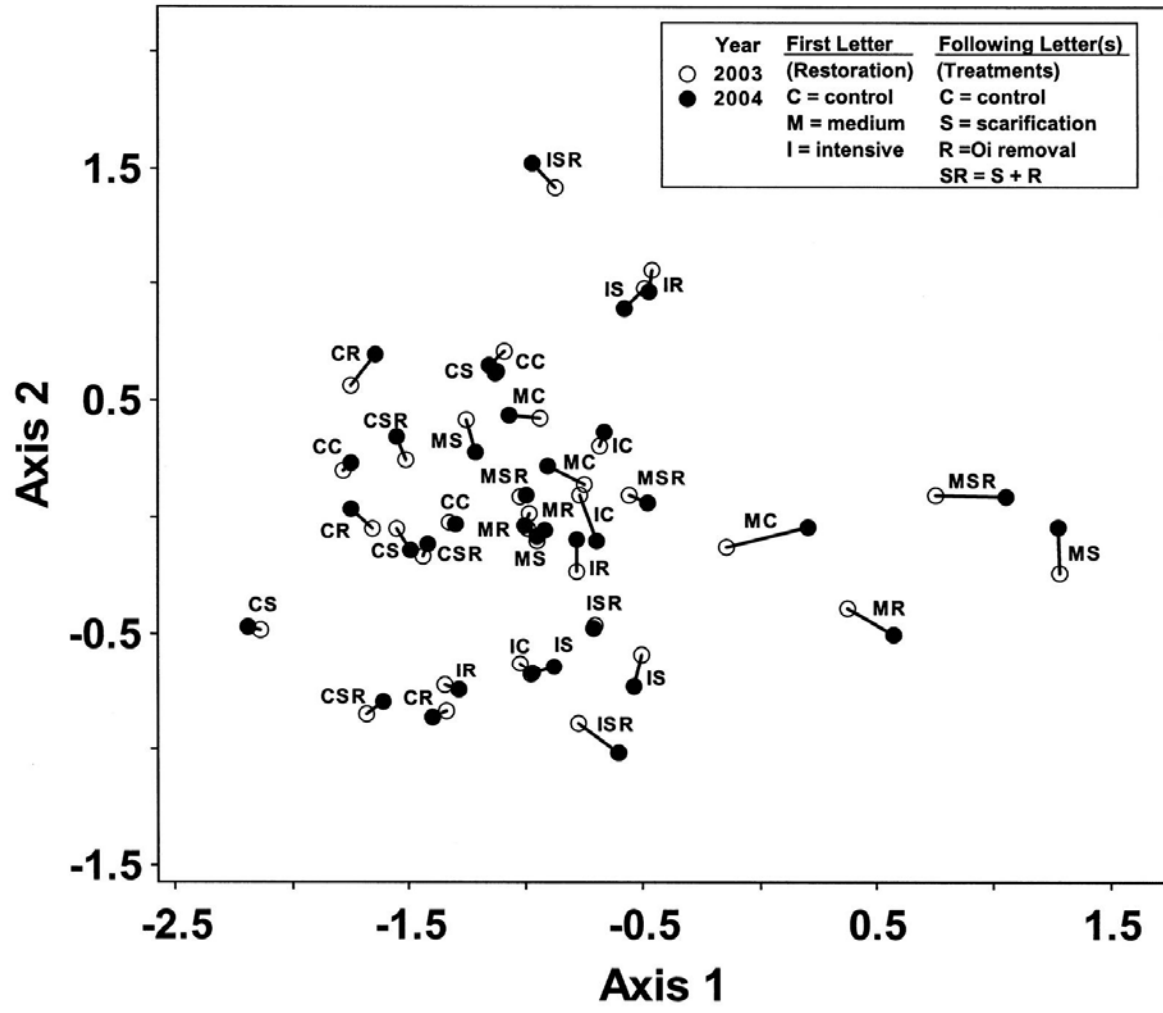
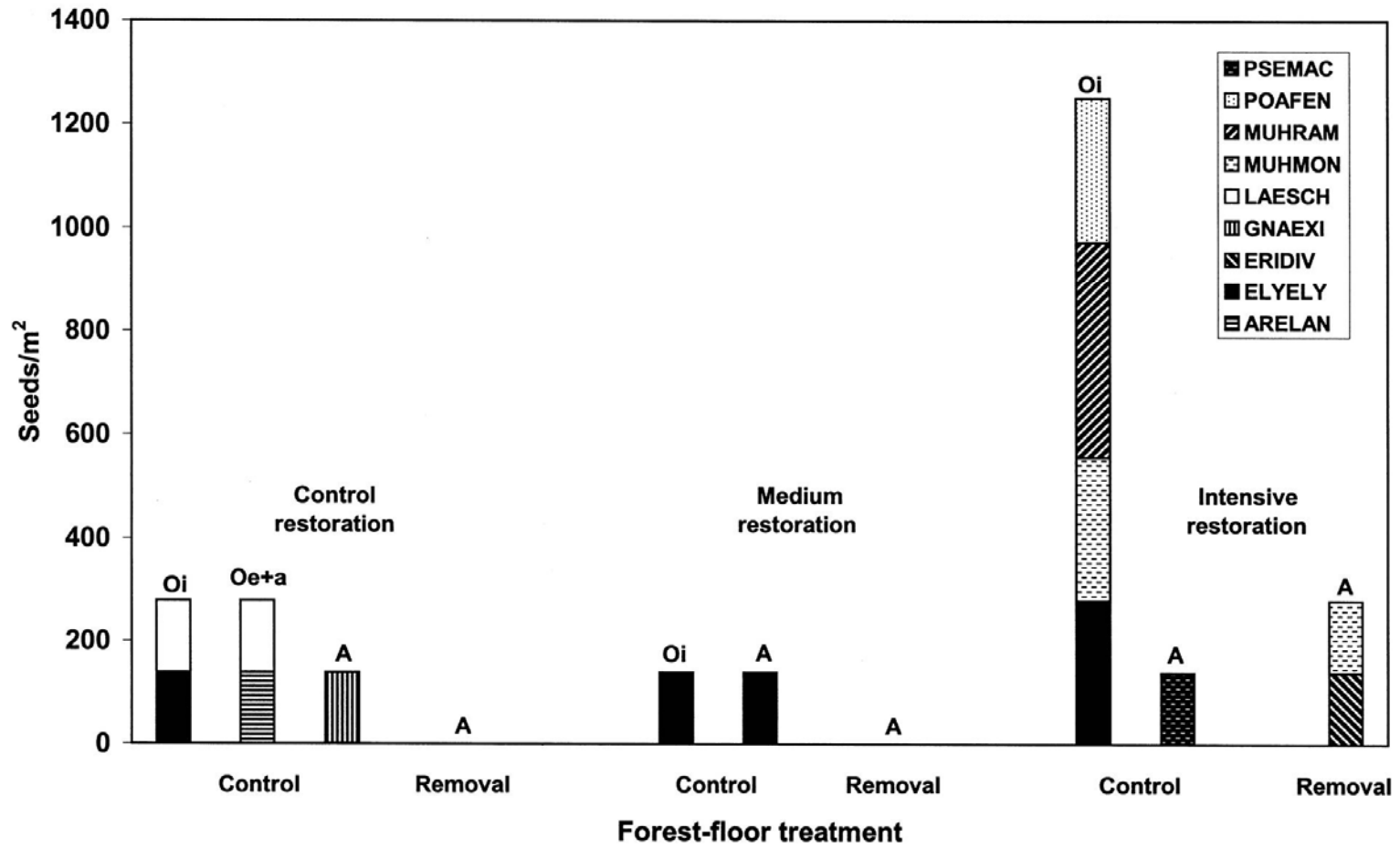**Fig. 6.1**

Fig. 6.2

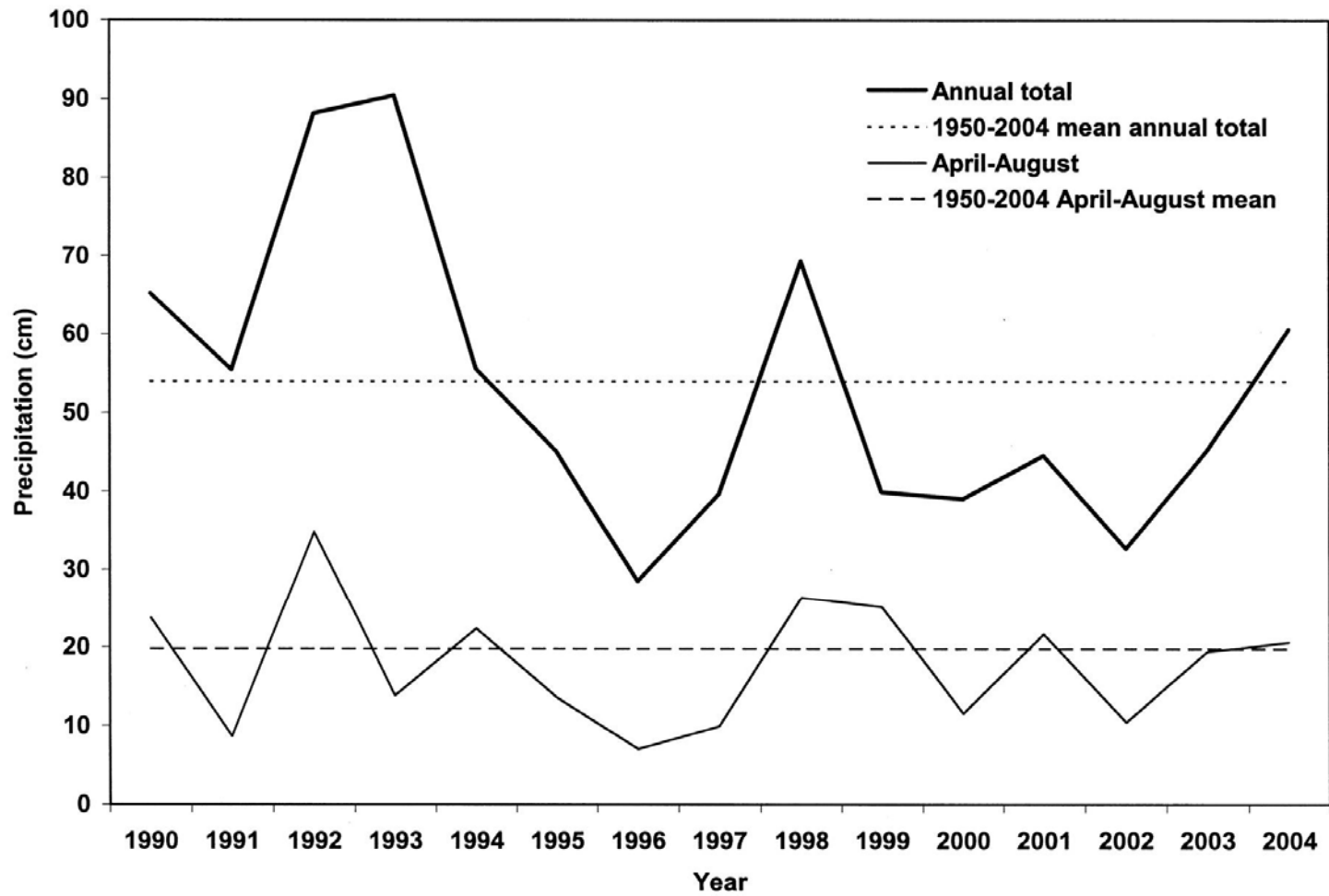**Fig. 6.3**

Fig. 6.4

Fig. 6.5

CHAPTER 7

CONCLUSION

This research developed a forest ecosystem classification on a 110,000-ha northern Arizona ponderosa pine (*Pinus ponderosa*) landscape (Chapter 3), determined environmental gradients associated with plant community distribution and classified ecological species groups (Chapter 4), measured soil seed bank composition and responses to fire-related cues (Chapter 5), and assessed plant community dynamics after forest-floor manipulations in an existing ponderosa pine restoration experiment (Chapter 6). Major conclusions I have drawn from these studies include the following:

1. Forest sites on this landscape could be readily classified into ecosystem types internally similar in environmental and vegetational characteristics. Such an ecosystem framework improves our understanding and aptitude for estimating variability in ecological properties such as soil moisture and resource levels across forest landscapes.

2. Soil properties such as texture reflecting parent materials were closely associated with ecosystem distribution. In contrast to many landscapes, geomorphic variables were not closely associated with the distribution of most ecosystems.

3. Diameter increment of old-growth ponderosa pine could be estimated fairly accurately based on ecosystem distribution.

4. Ecosystem turnover occurs at broad extents on this landscape, and restoration must accordingly operate across large areas to encompass ecosystem diversity.

5. Owing to the persistence of environmental features on which the ecosystem classification was based, the ecosystem framework provides a reference for the nature and distribution of ecosystem types in both presettlement and contemporary forests.

6. Plant species composition differed markedly among ecosystems in contemporary forests. Groups of species occupied characteristic environmental complexes, and species distributions closely corresponded with spatial variation in ponderosa pine growth.

7. A few key environmental variables readily predicted distributions of major graminoids and forbs across the landscape. These variables include soil texture, total N, rock cover, and geographic precipitation patterns.

8. Soil seed bank composition was partly ecosystem specific. Several native graminoids were detected in seed bank samples, whereas perennial forbs were sparse. Seed banks can supply propagules of desirable natives such as mountain muhly (*Muhlenbergia montana*) and muttongrass (*Poa fendleriana*) in several ecosystems on this landscape.

9. Liquid smoke increased emergence from seed bank samples in greenhouse experiments, suggesting that fire-related cues may be important in regulating post-burning responses in ponderosa pine communities.

10. In the forest-floor experiment, Oi removal and scarification had no detectable influence on understory composition or diversity in two post-treatment years. Several factors could have precluded a response, including climate. Seed availability may have been particularly limiting for native perennial forbs.

Based on this research, I identify the following topics in need of additional study:

1. Rare ecosystems such as springs or deep ravines I did not study could be included in a future ecosystem classification. These may be keystone ecosystems that if restored could provide large gains in biodiversity and ecosystem function.

2. Ecosystem classification could be applied to other southwestern ponderosa pine landscapes to examine within and among landscape patterns in ecosystem composition and reference conditions.

3. Assessing whether presettlement tree densities, patterns, or fire regimes show any consistent trends among ecosystems or can be predicted from abiotic variables may assist reference condition estimation. These variables may be partly ecosystem specific or specific to groups of ecosystems if they were affected by site environments in presettlement forests. On the other hand, variables such as tree spatial patterns could be more closely related to microsite ecology or other factors largely independent of landscape ecosystems.

4. Studying whether different ecosystem types respond differently to restoration or require different levels of treatments could assist restoration planning. For example, does understory vegetation in productive ecosystems respond more

rapidly to thinning and burning than understory vegetation in unproductive ecosystems?

5. Determining reference conditions for herbaceous vegetation is challenging. Can herbarium records or other methods be used to provide clues to past ecosystem-specific species composition on this landscape?

6. Fire cues affected emergence from seed bank samples in a greenhouse experiment. These findings need to be tested in the field where factors such as timing of burns may be important.

7. The forest-floor experiment could be expanded to include trenching, seed addition, or other treatments to ascertain understory responses to these manipulations.