Long-Term Vegetation Dynamics of Ponderosa Pine Forests

by Jonathan David Bakker

A Dissertation

Submitted in Partial Fulfillment

of the Requirements for the degree of

Doctor of Philosophy

in Forest Science

Northern Arizona University

August 2005

Approved:

Margaret M. Moore

Margaret M. Moore, Ph.D., Chair

W. Wallace Covington, Ph.D.

Laura E. DeWald

Laura E. DeWald, Ph.D.

Catherine Gehring, Ph.D.

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

Abstract

Long-Term Vegetation Dynamics of Ponderosa Pine Forests

Jonathan David Bakker

I examined the vegetation dynamics of ponderosa pine (*Pinus ponderosa*) forests in northern Arizona. Most field work was conducted on the Hill plots, five grazing exclosures established in 1912 and sampled in 1941 and 2004. Meta-analytic techniques were used to combine the results from individual sites. Overstory vegetation increased in dominance since 1941, but less where subject to continued livestock grazing than where protected from livestock grazing since 1912. A state-and-transition model for overstory vegetation dynamics is proposed, suggesting that historical development of the overstory is the result of interactions between livestock grazing, fire history, climate, and seed production.

Between 1941 and 2004, understory species density and herbaceous plant density both declined by 37%, shrub cover by 69%, herbaceous cover by 59%, graminoid cover by 45%, and forb cover by 82%. Declines were due to the increased overstory rather than grazing effects, as were apparent differences between grazing treatments in 2004. Community-level variables masked interspecific differences in temporal dynamics and in response to grazing treatment and overstory condition. Using Indicator Species Analysis, three times more species were identified as indicators of 1941 as of 2004; few species increased in cover during this interval. More species were indicators of grazing treatments in 1941 and of overstory condition in 2004, suggesting that the dominant structuring force in this ecosystem has changed over time. Some species responded to grazing, some to overstory condition, and some to both forces. Most species were consistent indicators across sites.

I developed a new, proportional method of reconstructing historical tree diameters. This method can be used to model overstory growth and estimate historical tree sizes; such information is essential when accounting for overstory-understory relations in these forests.

This study demonstrated that livestock grazing can have complex long-term effects on overstory vegetation, and provided a quantitative analysis of long-term changes in the understory vegetation of southwestern ponderosa pine forests. Since understory community-level variables are affected primarily by the overstory, the observed declines might be reversed if the overstory is thinned as part of ecological restoration activities, though responses of individual species may vary.

Acknowledgements

Margaret Moore was an ideal major professor, encouraging me to pursue my interests and providing the resources necessary to do so. Thank you, Margaret. Wally Covington, Laura DeWald, and Kitty Gehring reviewed earlier versions of this research, and 'made things work' in spite of their own busy schedules.

Mike Hannemann and Katherine Sánchez Meador (Coconino National Forest) and Rick Miller (Arizona Game and Fish) helped locate sites and maintain fences. Sites are located on the Coconino National Forest and NAU Centennial Forest, and I thank both forests for permission to conduct this research. Ralph Baierlein helped preserve the integrity of the Big Fill site by educating fellow horse riders about it. Susan Olberding provided access to historical data, which were collected by George Glendening and are housed in the Fort Valley Experimental Station Archives (Flagstaff, AZ). Robert Hill established the Hill plots, on which Chapters 2 through 4 are based, and Gus Pearson and Theodore Woolsey Jr. established the Woolsey plots, on which Chapter 5 is based.

The Ecological Restoration Institute (ERI) continues to be an exceptional place to work, involving wonderful people doing important and timely tasks. I thank Wally Covington, Pete Fulé, Diane Vosick, and Doc Smith for their support of the many activities conducted by ERI. I also thank the Woolsey team (Andy Sánchez Meador, Dave Huffman, Dave Bell) for discussions, ERI botanists (Daniel Laughlin, Mark Daniels, Steve Buckley, Rob Hastings, Judy Springer, and others) for assistance with fieldwork, and ERI undergraduates (Jake Dyer, Ben deBlois, Danielle Gift, Bob Ivens,

and many others, all capably supervised by Don Normandin) for assistance with field and lab work.

Finally, I thank my wife Erika for her continued love and support, and my children, Aidan, Linnea, and Marijka, for putting up with a small apartment and a busy father. This work is dedicated to them.

This research was supported by the ERI, the School of Forestry, McIntire-Stennis appropriations (project 0194878), and the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service, grant number 2003-35101-12919.

Table of Contents

Page

List of Tables

List of Figures

Page

Preface

This dissertation has been prepared in journal format, resulting in some redundancy among chapters. Chapter 2, "Long-term effects of livestock grazing on overstory vegetation in southwestern ponderosa pine forests", will be submitted to *Forest Ecology and Management*. Chapter 3, "Dynamics of herbaceous vegetation in a southwestern ponderosa pine forest, 1941-2004", will be submitted to *Rangeland Ecology and Management*. Chapter 4, "Indicator species of temporal dynamics, livestock grazing effects, and overstory vegetation in southwestern ponderosa pine forests", will be submitted to *Ecological Applications*. Chapter 5, "A new, proportional method for reconstructing historical tree diameters" has been accepted for publication in the *Canadian Journal of Forest Research.*

For ease of presentation, scientific names of species are presented without authorities. All nomenclature follows the USDA NRCS Plants Database (http://plants.usda.gov/).

Chapter 1

Introduction

Long-term studies can broaden our understanding of concepts such as reference conditions, invasion of exotic species, vegetation dynamics, and successional theory (Pickett et al. 2001; Bakker et al. 2002). Remeasurements of plots established in long-term studies have demonstrated large changes in species composition (Tilman et al. 1994; Crawley et al. 2005) and forest structure (Moore et al. 2004).

Remeasurements of historical studies are also important because long-term effects may be contingent upon site differences, interannual variability, or other factors (Bakker et al. 2003; Yeo 2005; Young et al. 2005). For example, perennial grasses in a desert grassland exhibited little response to two decades of protection from livestock grazing (Chew 1982) but increased significantly after four decades of protection (Valone et al. 2002; Valone & Sauter 2005), likely due to the episodic occurrence of conditions suitable for seedling establishment. Contingent effects may be particularly important when they involve changes in life form dominance (House et al. 2003).

An historical perspective is necessary to ensure that appropriate reference conditions are used when evaluating ecological data (Egan & Howell 2001). The use of recent conditions as baselines without recognition of changes that occurred prior to that point has been termed the shifting baseline syndrome (Pauly 1995), and can result in inappropriate expectations of potential ecological development (Rosenberg et al. 2005).

Southwestern ponderosa pine (*Pinus ponderosa*) forests are much denser at present than they were prior to Euro-American settlement (Cooper 1960; Fulé et al. 1997; Moore et al. 2004). Grazing by livestock has been suggested as one of the main causal factors of this change (Belsky & Blumenthal 1997), though few tests of this relationship have been published.

Based on known overstory-understory relationships (Arnold 1950; Jameson 1967; Moore & Deiter 1992; Naumburg & DeWald 1999), the increased dominance of the overstory should have large effects on the herbaceous and shrub understory vegetation in these forests. Similarly, herbivory can have significant effects on understory vegetation (Arnold 1950; Johnson 1956; Smith 1967; Rambo & Faeth 1999). Recent models suggest that livestock grazing should negatively affect plant diversity in semiarid environments such as the Southwest (Olff & Ritchie 1998; Cingolani et al. 2005).

Qualitative assessments from historical photographs and early written accounts suggest that the understory was abundant (Leopold 1951; Cooper 1960), a conclusion that is consistent with historical reconstruction models (Covington & Moore 1994) and observed vegetation responses following contemporary thinning experiments (Casey 2004; Wienk et al. 2004; Moore et al. *in review*). However, quantitative data about long-term changes in understory vegetation in this region are rare, and can only be obtained from historical studies. Such data are required at the community level (e.g., plant density, total cover) and for individual species.

Dissertation Structure

The objective of this research is to examine the vegetation dynamics of ponderosa pine forests in northern Arizona, including temporal dynamics, overstory-understory relationships, and grazing effects. I focus on changes between 1941 and 2004. While conditions in 1941 are obviously not 'reference' or 'presettlement' (Moore et al. 1999), the changes that have occurred since then provide insight into the overall trajectory of change that has occurred in these forests in recent decades.

Much of the dissertation is based on data obtained from five grazing exclosures established in 1912. These exclosures were established after several decades of intense livestock grazing, but before the pulse of ponderosa pine regeneration that occurred throughout many southwestern forests (Pearson 1950; Savage et al. 1996). Other publications based on these sites include Talbot & Hill (1923), Merrick (1939), and Arnold (1950).

While examining the ecological questions that frame each chapter, I also demonstrate a variety of methods that can be used in such studies. In Chapters 2 through 4, I use meta-analytic techniques to combine results from multiple sites. These techniques are often used to analyze the results of published studies, but the issues they address are very similar to those in multi-site studies (Gurevitch & Hedges 1999).

In Chapter 4, I apply Indicator Species Analysis (Dufrêne & Legendre 1997) to multiple sites, assessing the consistency of indicators spatially and temporally. These analyses require careful consideration of the logic of permutation tests, but can be effectively applied to binary (presence/absence) data, thereby permitting meta-analytical comparisons with published studies.

In Chapter 5, I describe a proportional method of reconstructing historical tree diameters. Accurate diameter reconstructions are important because diameter is required in studies of stand structural dynamics (Foster et al. 1996) and is used in allometric equations to estimate many variables, including understory production (Bojorquez Tapia et al. 1990).

References

Arnold, J.F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. Journal of Forestry **48**:118-126.

Bakker, J.P., R.H. Marrs, and R.J. Pakeman. 2002. Long-term vegetation dynamics: successional patterns and processes. Introduction. Applied Vegetation Science **5**:2-6.

Bakker, J.D., S.D. Wilson, J.M. Christian, X. Li, L.G. Ambrose, and J. Waddington. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications **13**:137-153.

Belsky, A.J., and D.M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. Conservation Biology **11**:315-327.

Bojorquez Tapia, L.A., P.F. Ffolliott, and D.P. Guertin. 1990. Herbage production-forest overstory relationships in two Arizona ponderosa pine forests. Journal of Range Management **43**:25-28.

Casey, C.A. 2004. Herbaceous biomass and species composition responses to ponderosa pine restoration treatments. M.Sc. thesis. Northern Arizona University, Flagstaff, AZ.

Chew, R.M. 1982. Changes in herbaceous and suffrutescent perennials in grazed and ungrazed desertified grassland in southeastern Arizona, 1958-1978. American Midland Naturalist **108**:159-169.

Cingolani, A.M., I. Noy-Meir, and S. Diaz. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecological Applications **15**:757-773.

Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Monographs **30**:129-164.

Covington, W.W., and M.M. Moore. 1994. Southwestern ponderosa forest structure: Changes since Euro-American settlement. Journal of Forestry **92**:39-47.

Crawley, M.J., A.E. Johnston, J. Silvertown, M. Dodd, C. de Mazancourt, M.S. Heard, D.F. Henman, and G.R. Edwards. 2005. Determinants of species richness in the Park Grass Experiment. The American Naturalist **165**:179-192.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Egan, D., and E.A. Howell. 2001. The historical ecology handbook: A restorationist's guide to reference ecosystems. Island Press, Washington, DC.

Foster, D.R., D.A. Orwig, and J.S. McLachlan. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. Trends in Ecology and Evolution **11**:419-424.

Fulé, P.Z., W.W. Covington, and M.M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications **7**:895-908.

Gurevitch, J., and L.V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology **80**:1142-1149.

House, J.I., S. Archer, D.D. Breshears, R.J. Scholes, and NCEAS Tree-Grass Interactions Participants. 2003. Conundrums in mixed woody-herbaceous plant systems. Journal of Biogeography **30**:1763-1777.

Jameson, D.A. 1967. The relationship of tree overstory and herbaceous understory vegetation. Journal of Range Management **20**:247-249.

Johnson, W.M. 1956. The effect of grazing intensity on plant composition, vigor, and growth of pine-bunchgrass ranges in central Colorado. Ecology **37**:790-798.

Leopold, L.B. 1951. Vegetation of southwestern watersheds in the nineteenth century. The Geographical Review **41**:295-316.

Merrick, G.D. 1939. Revegetation of deteriorated range land in northern Arizona. M.A. Thesis. Duke University, Durham, NC.

Moore, M.M., and D.A. Deiter. 1992. Stand density index as a predictor of forage production in northern Arizona pine forests. Journal of Range Management **45**:267-271.

Moore, M.M., W.W. Covington, and P.Z. Fulé. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. Ecological Applications **94**:1266-1277.

Moore, M.M., D.W. Huffman, P.Z. Fulé, W.W. Covington, and J.E. Crouse. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Science **50**:162-176.

Moore, M.M., C.A. Casey, J.D. Bakker, J.D. Springer, P.Z. Fulé, W.W. Covington, and D.C. Laughlin. *In review*. Herbaceous response to restoration treatments in a ponderosa pine forest, 1992-2004. Rangeland Ecology and Management

Naumburg, E., and L.E. DeWald. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. Forest Ecology and Management **124**:205-215.

Olff, H., and M.E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution **13**:261-265.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution **10**:430.

Pearson, G. A. 1950. Management of ponderosa pine in the southwest as developed by research and experimental practice. USDA Forest Service, Washington, DC.

Agriculture Monograph No. 6.

Pickett, S.T.A., M.L. Cadenasso, and S. Bartha. 2001. Implications from the Buell-Small succession study for vegetation restoration. Applied Vegetation Science **4**:41-52.

Rambo, J.L., and S.H. Faeth. 1999. Effect of vertebrate grazing on plant and insect community structure. Conservation Biology **13**:1047-1054.

Rosenberg, A.A., W.J. Bolster, K.E. Alexander, W.B. Leavenworth, A.B. Cooper, and M.G. McKenzie. 2005. The history of ocean resources: modeling cod biomass using historical records. Frontiers in Ecology and the Environment **3**:78-84.

Savage, M., P.M. Brown, and J. Feddema. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ecoscience **3**:310-318.

Smith, D.R. 1967. Effects of cattle grazing on a ponderosa pine-bunchgrass range in Colorado. US Department of Agriculture, Washington, DC. Technical Bulletin 1371.

Talbot, M.W., and R.R. Hill. 1923. Progress report on the range study plots on the Coconino National Forest comprising a description of project and digest of data. Unpublished report, Coconino National Forest, Flagstaff, AZ. 32 p.

Tilman, D., M.E. Dodd, J. Silvertown, P.R. Poulton, A.E. Johnston, and M.J. Crawley. 1994. The Park Grass Experiment: insights from the most long-term ecological study. Pages 287-303 *in* R.A. Leigh and A.E. Johnston (editors). Long-term experiments in agricultural and ecological sciences. CAB International, Wallingford, UK.

Valone, T.J., and P. Sauter. 2005. Effects of long-term cattle exclosure on vegetation and rodents at a desertified arid grassland site. Journal of Arid Environments **61**:161-170.

Valone, T.J., M. Meyer, J.H. Brown, and R.M. Chew. 2002. Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. Conservation Biology **16**:995-1002.

Wienk, C.L., C.H. Sieg, and G.R. McPherson. 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. Forest Ecology and Management **192**:375-393.

Yeo, J.J. 2005. Effects of grazing exclusion on rangeland vegetation and soils, east central Idaho. Western North American Naturalist **65**:91-102.

Young, T.P., D.A. Petersen, and J.J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters **8**:662-673.

Chapter 2

Long-Term Effects of Livestock Grazing on Overstory Vegetation in Southwestern Ponderosa Pine Forests

Preface

In this chapter, I examine the long-term effects of livestock grazing on overstory vegetation in southwestern ponderosa pine forests and propose a state-and-transition model of overstory dynamics in these forests.

Abstract

Livestock grazing has been suggested as a causal factor contributing to high tree densities in southwestern ponderosa pine forests, though few experimental tests of the effects of continued grazing or the cessation of grazing have been conducted in these forests. Grazing exclosures were established in 1912 at five sites in a southwestern ponderosa pine forest, and the overstory vegetation inside and outside of these exclosures was measured in 1941 and 2004. Canopy cover of regeneration was significantly higher inside exclosures in 1941, and both canopy cover and tree density were higher inside exclosures in 2004. Tree basal area was higher, and trees were smaller, inside exclosures. In addition, trees were younger inside exclosures at sites that had not received interim silvicultural treatments. These results indicate that grazing has complex and long-term effects on the overstory vegetation. A state-and-transition model of overstory dynamics

in southwestern ponderosa pine forests is presented which suggests that the contemporary overstory structure is the result of interactions between livestock grazing, fire history, climate, and seed production. Livestock grazing contributed to the pulse of ponderosa pine regeneration in the early 1900s, but contemporary forests would be even denser than they are at present if grazing had not continued to occur in these forests.

Introduction

Beginning with Aldo Leopold's 1924 article and Charles Cooper's 1960 monograph, a large body of evidence has documented significant changes in the overstory of ponderosa pine (*Pinus ponderosa*) forests in the southwestern United States since Euro-American settlement of the region in the late 1800s. Lines of evidence pointing to increased tree densities include repeat photography (Gordon et al. 1992; Hart & Laycock 1996; Mast et al. 1997; Fig. 2.1), written accounts of early explorers (Leopold 1951), stand reconstruction modeling (Covington & Moore 1994; Fulé et al. 1997), and remeasurements of historical permanent plots (Moore et al. 2004).

Grazing by livestock has been proposed as one of the major mechanisms causing increased tree densities (Belsky & Blumenthal 1997). The conventional understanding is that livestock grazing reduces the competitive dominance of the herbaceous layer (Larson & Schubert 1969; Elliott & White 1987), permitting large numbers of ponderosa pine seedlings to establish (Pearson 1923; Madany & West 1983; Belsky & Blumenthal 1997). Intense grazing has coincided with invasion by woody plants in other ecosystems (Archer 1994), though pine establishment in northern California was greatest when meadows were moderately grazed (Norman & Taylor 2005).

Many studies of livestock grazing have been observational studies of relict areas, where topographic features prevent access by livestock. Relict areas are either sampled alone (Jameson et al. 1962; Mason et al. 1967; Mason & West 1970; Thatcher & Hart 1974; Madany & West 1984; Rowlands & Brian 2001) or are compared to nearby grazed areas (Rummell 1951; Schmutz et al. 1967; Madany & West 1983; Guenther et al. 2004). Differences between relict and grazed areas are attributed to grazing, often with little consideration of grazing intensity or duration.

Relict areas can provide valuable insights into reference conditions (Moore et al. 1999), including criteria about ecosystem structure and function with which to evaluate the success of active management actions such as thinning small trees and reintroducing low-intensity fires (Covington et al. 1994; Moore et al. 1999; Allen et al. 2002). However, they may not be appropriate for describing anticipated vegetation dynamics, particularly if historical events have constrained potential vegetation development. For example, large areas of the southwestern United States were grazed very intensely in the late 1800s, and in manners that are recognized to have been unsustainable (Haskett 1936; Abruzzi 1995; Fredrickson et al. 1998). This grazing history may have had long-term effects on the vegetation, suggesting that experimental studies of areas that are now protected from grazing with areas that continue to be grazed might be more appropriate for describing anticipated vegetation dynamics. Comparisons would have to be made over long time scales to account for temporal heterogeneity (Valone & Sauter 2005) and the long life span of woody plants. Few such studies have been conducted in ponderosa pine forests (e.g., Arnold 1950). Vegetation dynamics are likely to be non-linear in environmentally heterogeneous semiarid communities (Rietkerk & van de Koppel 1997;

Briske et al. 2005), suggesting that state-and-transition models (Westoby et al. 1989) may be useful for describing the dynamics of southwestern ponderosa pine ecosystems.

In this study, I examine the overstory vegetation inside and outside five grazing exclosures in northern Arizona. Exclosures were established in 1912 and measured in 1941 and 2004. My objectives were to examine the relationship between long-term grazing and overstory structure and age distributions, and to describe a state-and-transition model for overstory dynamics in southwestern ponderosa pine forests.

Methods

Study Sites

R.R. Hill established five grazing exclosures, called the Hill plots, in 1912. Sites are located within 25 km of Flagstaff, AZ, vary in soil type, and span the elevational range of the ponderosa pine forest type (Table 2.1). Exclosures were designed to exclude livestock but not wild ungulates (Fig. 2.1).

Early researchers felt these sites were ‘overgrazed’ in 1912 (Talbot & Hill 1923). Though subjective, this term suggests that an intensity and severity of grazing that are not sustainable. Hill (1918) related overgrazing to the number of livestock an area could support. In a later publication based on these sites, Merrick defined overgrazing as “any degree of use which removed such a large portion of the principal forage plants that they would be reduced in vigor or killed out” (1939:10). Grazing histories are summarized in Tables 2.1 and 3.1. Grazing intensities were much lower in 2004 (Tables 2.1, 3.1).

Field Methods

The overstory vegetation inside and outside exclosures was sampled in 1941 and 2004 using the line transect method (Canfield 1941). Areas were divided into 10-20 contiguous strata, and each stratum was sampled with 2-4 lines (Table 2.1; Fig. 3.1). Lines were 15.24 m (50 ft) lengths of wire rope stretched taut along the ground. The 1941 data were collected by G. Glendening and published in summary form by Arnold (1950), who focused on overstory-understory relationships.

Four sites were selectively harvested before the exclosures were built, and several sites received subsequent silvicultural treatments, including two in recent decades (Table 2.1). These activities were implemented across both grazing treatments (i.e., inside and outside of exclosures), and are considered part of the inter-site variability. Five strata outside the exclosure at Black Springs were destroyed by an interstate highway in the 1950s, so I established replacement strata on the other side of the exclosure. Analyses were restricted to lines that were not within localized disturbances (powerline right-of-ways, etc.) or prescribed burns (Table 2.1). In total, 520 lines from 1941 and 480 lines from 2004 were analyzed.

Canopy cover was measured as the percentage of the line directly beneath tree crowns, and tree density as the number of trees within a 1.22 m (4 ft) wide belt centered on the line. In 1941, canopy cover and tree density were measured separately for mature trees and regeneration of each species, and regeneration was further divided into 1919, 1929, and >1929 age classes (Glendening 1941). In 2004, there was minimal regeneration so canopy cover and tree density were measured in total for each species.

In 2003-2004, the overstory vegetation was also measured within four to seven 400 m^2 (20 x 20 m) plots within each grazing treatment at each site. These plots were measured to obtain contemporary overstory information relevant to chart quadrats on which the understory vegetation has been mapped periodically between 1912 and 2004 (J.D. Bakker, *unpub. data*). Plots were centered on the chart quadrats and therefore overlapped somewhat; analyses were based on the total area sampled (Table 2.4). Species identity and diameter at breast height (DBH) were recorded for all live trees taller than breast height (1.37 m above ground level); trees were also cored at stump height (40 cm above ground level) and aged using standard dendrochronological methods (Stokes & Smiley 1968).

Analysis

Variables analyzed were: canopy cover and density of regeneration, mature trees, and total (regeneration + mature) in 1941, density within each regeneration age class in 1941, and total canopy cover and total tree density in 2004. Canopy cover data were arcsin (square root x) transformed and tree density data log (x + 1) transformed for analysis, but back-transformed data are presented for clarity. I used Wilcoxon tests to test whether variables differed between grazing treatments at each site.

I used meta-analytic techniques (Hedges & Olkin 1985; Gurevitch & Hedges 2001; Lipsey & Wilson 2001) to assess the significance of grazing effects across all sites. These techniques were developed to combine the results of multiple studies, which is conceptually and analytically similar to combining results from multiple sites (Gurevitch & Hedges 1999; a similar application of these techniques is found in Yeo [2005]). In the following presentation, I use the notation of Gurevitch & Hedges (2001). Formulae not provided here are reported in Hedges & Olkin (1985), Gurevitch & Hedges (2001), and Lipsey & Wilson (2001).

For each variable, the grazing effect size (d_{ij}) of the j^{th} site in the i^{th} class (i.e., year; 1941 or 2004) was calculated as:

[2.1] $$d_{ij} = \frac{\overline{X}_{ij}^{In} - \overline{X}_{ij}^{Out}}{s_{ij}} J$$

where $\overline{X}_{ij}^{In}$ and $\overline{X}_{ij}^{Out}$ are the mean values inside and outside the exclosure, s_{ij} is the pooled standard deviation of the two groups, and J is a correction factor for small sample sizes. Positive and negative grazing effect sizes indicate larger responses inside and outside of exclosures, respectively. Effect sizes are in standard deviation units and are commonly interpreted as follows: 0.2 is small, 0.5 is medium, 0.8 is large, and >1 is very large (Gurevitch & Hedges 2001).

Effect sizes from the five sites were combined using a mixed effects model, which assumes random variation in effect size among sites in addition to variation within sites (Becker 1988; Gurevitch & Hedges 2001). Grazing effect sizes were weighted by the inverse of their variance (w_{ij}^{*}; combination of sampling and effect size variances), thus weighting intensely sampled sites more heavily than less intensely sampled sites. The formulae for the cumulated grazing effect size (d_{i+}^{*}) and its standard deviation (s_{i+}^{*}) are:

[2.2] $$d_{i+}^{*} = \frac{\sum_{j=1}^{k_i} w_{ij}^{*} d_{ij}^{*}}{\sum_{j=1}^{k_i} w_{ij}^{*}}$$

$$[2.3] \qquad s_{i+}^{*} = \sqrt{\frac{1}{\sum_{j=1}^{k_i} w_{ij}^{*}}}$$

where *k* is the number of sites in class *i* (Gurevitch & Hedges 2001). The cumulated grazing effect size was assessed for significance by dividing it by its standard deviation to form a *z*-statistic, which was then compared to a *Z*-distribution using $\alpha = 0.05$ (Lipsey & Wilson 2001).

G^2 likelihood-ratio chi-square tests were used to determine whether the proportion of trees in each regeneration age class (1919, 1929, > 1929) differed between grazing treatments at each site in 1941. The Cochran-Mantel-Haenszel (CMH) test was then used to test whether the proportion of trees in each age class differed between grazing treatments after blocking across sites.

Kolmogorov-Smirnov tests examined whether diameter and age distributions differed between grazing treatments at each site in 2004, and across the three sites that did not receive recent silvicultural treatments (Table 2.1).

The quadratic mean diameter (QMD) and basal area (m^2/ha; measured at breast height) were calculated for each grazing treatment and site. Statistical tests were not used because these variables were calculated in the aggregate for each grazing treatment and site (i.e., calculations were based on the total area sampled) so there were no measures of intra-site variability.

Statistical analyses were conducted using JMP (v. 5.1.2) and SPSS (v. 12.0) software. Meta-analyses were conducted in Microsoft Excel 2002.

Results

Ponderosa pine comprised > 99% of the overstory in both years. Other species encountered included pinyon pine (*Pinus edulis*) and junipers (*Juniperus deppeana* and *J. monosperma*) at Big Fill, limber pine (*Pinus flexilis*) at Reese Tank, and Gambel oak (*Quercus gambelii*) at Rogers Lake. Since ponderosa pine comprised most of the overstory, comparisons were made for all trees rather than for individual species.

Overstory Structure

In 1941, the cumulated grazing effect size for canopy cover of mature trees was not significant (Table 2.2) because mature tree canopy cover was higher inside the exclosure at Big Fill but outside the exclosure at Black Springs (Fig. 2.2a). Canopy cover of regeneration was significantly higher inside than outside exclosures, while total canopy cover was marginally significantly ($0.1 < p < 0.05$) higher inside exclosures (Table 2.2; Fig. 2.2a). Canopy cover was about twice as high at Reese Tank as at other sites. In 2004, total canopy cover was significantly greater inside exclosures (Table 2.2), though it did not differ between grazing treatments at Black Springs or Reese Tank (Fig. 2.2b).

The density of mature trees did not differ between grazing treatments (Table 2.2; Fig. 2.2c). Regeneration and total tree densities were significantly higher inside exclosures at three sites and outside the exclosure at Reese Tank (Fig. 2.2c); these responses counteracted each other so that neither cumulated grazing effect size was significant (Table 2.2). In 2004, total tree density was significantly greater inside exclosures (Table 2.2), though it did not differ between grazing treatments at Black Springs or Reese Tank (Fig. 2.2d).

Densities of individual age classes were much higher at Reese Tank than at any other site, particularly for the 1919 and 1929 age classes, and were significantly higher outside the exclosure at this site (Table 2.3). At most other sites, densities of individual age classes were higher inside exclosures. As a result of these counteracting responses, cumulated grazing effect sizes for densities of individual age classes did not differ between grazing treatments, though the 1919 age class was marginally significantly more abundant inside exclosures (Table 2.2).

Diameter distributions in 2004 differed significantly between grazing treatments at Reese Tank and Rogers Lake and marginally significantly at Big Fill and Black Springs (Fig. 2.3: left column). Diameter distributions did not differ between grazing treatments at Fry Park, where only 18 trees were sampled outside the exclosure. Maximum diameters ranged from 51 cm at Reese Tank to 96 cm at Fry Park. Overall, trees were smaller at sites that did not receive recent silvicultural treatments. QMD was higher outside the exclosures at all sites except Reese Tank (Table 2.4). On average, total basal area was 30% higher inside than outside exclosures.

Age Distributions

In 1941, the distribution of regeneration age classes differed significantly between grazing treatments (Fig. 2.4). Overall, the 1919 age class accounted for a higher proportion of the trees outside exclosures and the > 1929 age class for more of the trees inside exclosures. However, no age class dominated the regeneration at all sites; most regeneration was from the 1919 age class at Fry Park and Reese Tank, the 1929 age class at Big Fill and Rogers Lake, and the >1929 age class at Black Springs.

In 2004, age distributions differed significantly between grazing treatments at Black Springs, Reese Tank, and Rogers Lake, and marginally significantly at Big Fill (Fig. 2.3: right column). Trees were older inside exclosures at Black Springs and Reese Tank but outside exclosures at Big Fill and Rogers Lake. Overall, trees were marginally significantly younger inside exclosures at sites that have not received recent silvicultural treatments.

Discussion

Long-Term Effects of Grazing

This study demonstrates that overstory dynamics in the Southwest are complex. In contrast to earlier suggestions that livestock grazing causes increased tree densities (Belsky & Blumenthal 1997), I found fewer trees and less canopy cover in areas where livestock grazing continued than where it ceased in 1912 (Fig. 2.2; Table 2.4). These effects were already evident in 1941 and are still present today. Our understanding of the interaction between livestock grazing and ponderosa pine regeneration may have been hindered because the regional increases in tree density were so dramatic (Moore et al. 2004) that the factors affecting these increases were assumed to have been relatively uniform across the landscape.

Our understanding has also been hindered because few studies have compared overstory structure in grazed and previously grazed areas in this ecosystem. Exclosure studies are more common in lower elevation non-forested ecosystems (e.g., Valone et al. 2002; Courtois et al. 2004; Yeo 2005). In addition, overstory species may differ in response: in an Idaho forest, ponderosa pine seedlings were ten times as abundant inside the exclosure whereas Douglas-fir (*Pseudotsuga menziesii*) seedlings did not differ in density between grazing treatments (Zimmerman & Neuenschwander 1984).

Parks and natural areas were often grazed by livestock before their establishment as protected areas, and thus can be viewed as large-scale grazing exclosures. For example, Grand Canyon National Park (GCNP) was heavily grazed by sheep and cattle from the late 1800s until it was fenced to exclude livestock grazing in the late 1930s (Fulé et al. 2002). Contemporary tree densities are higher in GCNP (Grandview site; 955 t/ha ≥ 2.5 cm DBH) than at an adjacent site in Kaibab National Forest, which continued to be grazed (830 t/ha ≥ 2.5 cm DBH, comprising 689 live t/ha and 141 cut t/ha) (Fulé et al. 2002). Similarly, contemporary tree densities are higher within Walnut Canyon National Monument (WCNM; 883 t/ha ≥ 10 cm DBH) than in adjacent areas managed by the USDA Forest Service (311 t/ha ≥ 10 cm DBH) or the Arizona State Land Department (161 t/ha ≥ 10 cm DBH) (Menzel 1996). While these differences are partly due to selective overstory harvests outside WCNM, they also reflect the restrictions on grazing that occurred after it was established in 1917 (Cheney 1982). Reconstructed forest structures at the time of Euro-American settlement did not differ between sites in either study (Menzel 1996; Fulé et al. 2002), indicating that these differences are a response to subsequent land management practices.

In other ecosystems, higher woody plant densities are often found in ungrazed than grazed areas (Glendening 1952; Bock et al. 1984; Chesterfield & Parsons 1985; Kenney et al. 1986; Cheal 1993; Spooner et al. 2002; Mengistu et al. 2005). Similar effects have been reported with respect to ponderosa pine regeneration, though this research has received little attention. Ponderosa pine regeneration was noted to be more abundant within other fenced exclosures in northern Arizona than in adjacent areas that continued to be overgrazed by livestock (Pearson 1923, 1933). Heidmann et al. (1982) indicated that ponderosa pine regeneration could be maximized by grazing prior to but not for several years after seedling germination.

Mechanisms for Higher Density Inside Exclosures

Current tree densities may be higher inside exclosures for several reasons, including release of older seedlings from grazing pressure, increased seedling establishment inside exclosures, and increased seedling mortality outside exclosures. The relative importances of these mechanisms are unclear, and may vary among sites.

When the exclosures were built in 1912, regeneration was present but had been damaged by repeated browsing (Hill 1917; Talbot & Hill 1923). Protection by exclosures would have increased the survival of these trees and permitted rapid height growth, since ponderosa pine seedlings can recover from browsing (Hill 1917; Pearson 1931; Gardner & Hubbell 1943; Schubert 1974; Karl & Doescher 1998). For example, 57 regeneration (~ 90 t/ha) were present inside the Big Fill site in 1912; of these, five had died by 1914 (Hill 1917) and 'practically all' survived to 1921 (Hill 1921). In contrast, most of the 45 regeneration (~ 70 t/ha) outside the exclosure were dead by 1914 (Hill 1917) and only two remained alive in 1921 (Hill 1921). Similarly, Pearson (1923, 1933) noted that regeneration in 1918 was 'noticeably better' inside than outside other exclosures in northern Arizona, "due more to the growth of old seedlings than appearance of new ones" (Southwestern Forest and Range Experiment Station 1937:11).

Regeneration densities were much higher in 1941 (Table 2.3) than can be accounted for by the regeneration already present in 1912 (Hill 1917), indicating that many trees germinated after the exclosures were built. Herbaceous vegetation increased greatly after the exclosures were built (Arnold 1950), and herbaceous vegetation and tree recruitment density are positively correlated in other ecosystems (Spooner et al. 2002). In southwestern ponderosa pine forests, herbaceous vegetation can prevent frost-heaving, which is a significant mortality agent for pine seedlings (Haasis 1923). However, survival and growth of ponderosa pine seedlings are poor under tall grass cover in southwestern ponderosa pine forests (Pearson 1942), likely due to competition with herbaceous vegetation for water and nitrogen (Pearson 1942; Larson & Schubert 1969; Elliott & White 1987). Pine seedlings that germinated within the exclosures likely experienced intense competition with herbaceous vegetation, though many were still able to establish (Table 2.3).

Soils outside exclosures would have been very different from those inside (Krzic et al. 1999; Frank et al. 2003). By exposing the mineral soil and reducing the prevalence of the herbaceous layer, grazing would have promoted germination relative to conditions within the exclosures. However, trampling and/or browsing by livestock can kill seedlings, particularly in the first few years after germination (Pearson 1950; Eissenstat et al. 1982; Jiménez et al. 2005). Early scientists in the region clearly felt this was an important mechanism. Both Hill (1917) and Pearson (1923, 1933) attributed lower regeneration densities outside exclosures to damage by livestock, primarily sheep. Established seedlings would have been more likely to survive grazing damage, which may explain why more of the regeneration recorded outside exclosures in 1941 was from the oldest (1919) age class (Fig. 2.4) and why trees were older outside exclosures in 2004 at sites that had not received recent silvicultural treatments (Fig. 2.3: right column).

Several other studies have shown that heavy grazing may reduce seedling densities, though light to moderate grazing does not (Hill 1917; Young et al. 1942; Pearson et al. 1971; Currie et al. 1978; Allen & Bartolome 1989; cf. Skovlin et al. 1976). In northern California, the highest rates of establishment by seedlings of ponderosa pine and other tree species were during periods of moderate livestock grazing (Norman & Taylor 2005).

Regeneration Ages

Cores were taken at a 40 cm height, so knowledge of when trees germinated requires an understanding of how long it takes them to reach that height. Dendrochronological analyses at the root-shoot boundary provide accurate germination data (Savage et al. 1996) but were well beyond the scope of this study. Instead, I used published data to estimate seedling height growth. Cormier (1990) found that seedling height growth in northern Arizona is negatively related to elevation and slope, and that damaged seedlings take a year longer to reach a given height. Applying his equation for uninjured seedlings yields estimates of 12 years at Reese Tank (due to the higher elevation) and 8-9 years at all other sites. Hill (1917) estimated that seedlings will reach breast height in 15 years if uninjured but may require 35 years if browsed repeatedly. Assuming exponential growth (Cormier 1990), trees would therefore require 12 years to reach 40 cm if uninjured and 26 years if browsed. Ponderosa pine seedlings take 8-13 years to reach 35 cm in central Colorado (Kaufmann et al. 2000), averaged 40 cm tall after five years in eastern Arizona (Jones 1971), and averaged < 15 cm tall after five years in burned areas of north-central Arizona (Sackett 1984). Therefore, I assume that trees germinated 8-12 years before they reached 40 cm if they were uninjured. Trees that were injured by livestock grazing (potentially any trees except those that established inside exclosures after 1912) would have germinated even earlier.

Seedlings that were damaged by repeated browsing before the exclosures were built may be evident as peaks in the contemporary age distributions within the first 10-15 years after the exclosures were established. These peaks are evident inside the exclosures at Reese Tank and Rogers Lake and outside the exclosures at four sites (Fig. 2.3: 1915, 1920, and 1925 age classes).

In some locations in northern Arizona, much of the regeneration germinated in 1919 (Pearson 1950; Savage et al. 1996). Pronounced peaks inside the exclosures at four sites and outside the exclosures at Big Fill and Rogers Lake (Fig. 2.3: 1930 age class) might correspond with this age class. The 1929 and >1929 age classes accounted for a sizable proportion of the regeneration in 1941 (Fig. 2.4), but are much more poorly represented within the contemporary stand (Fig. 2.3: 1940 and later age classes), possibly due to higher mortality rates because of competition with established regeneration.

Site History

Several aspects of site history are directly relevant to this study, including fire history, abiotic factors, silviculture, and grazing history. Surface fires have been identified as important for ponderosa pine regeneration (Bailey & Covington 2002), but these sites have not burned since they began to be studied in 1912 and likely had not burned since the 1870s or 1880s (Fulé et al. 1997). Given the low densities of mature trees in these forests a century ago (Moore et al. 2004), relatively little fine fuel had likely accumulated by the time seedlings germinated and established on these sites. Therefore, fire may have been less important for creating safe sites for seedling germination and establishment than it is under contemporary conditions, when pine litter is much more prevalent (Sackett 1984).

Reese Tank is located at a north-facing aspect at a higher elevation than the other sites (Table 2.1), suggesting that the cooler, wetter climate might have contributed to higher levels of regeneration at this site (Fig. 2.2c). However, data from the Gus Pearson Natural Area (GPNA), an unlogged site at about the same elevation as the other sites, indicate that elevation was not a major factor. In 1992, GPNA had 3097 t/ha, > 99% of which were < 70 years old (Mast et al. 1999), indicating that ample regeneration can establish at lower elevations comparable to that of the other Hill plots.

Silvicultural practices remove mature trees that are seed sources while creating openings and scarified sites in which seedlings can establish (Schubert 1974). Mean regeneration and mature tree densities were positively correlated in 1941 ($r^2 = 0.483$; $p = 0.0258$; $n = 10$ site x grazing treatment combinations), suggesting that regeneration density was limited in part by seed production (Fig. 2.2c). However, regeneration densities were much higher at Reese Tank, which did not received its first overstory harvest until 1940, than at the other sites, which were selectively harvested before the exclosures were built (Table 2.1). Therefore, it is apparent that logging is not required for large numbers of seedlings to establish. Similarly, Meagher (1950) considers site disturbance from logging of secondary importance with respect to pine regeneration compared to factors such as climate and seed production.

Recent silvicultural treatments at the Black Springs and Reese Tank sites (Table 2.1) explain some of the observed differences in overstory vegetation in 2004. For example, total canopy cover and tree density in 2004 did not differ between grazing treatments at these sites but did at all other sites (Fig. 2.2b,d). The thinnings at these sites removed most of the small diameter (< 15 cm DBH) trees (Fig. 2.3), reducing the difference in QMD between grazing treatments (Table 2.4). These silvicultural treatments likely also altered tree age distributions: trees were older inside exclosures at these sites but younger inside exclosures at other sites (Fig. 2.3).

Early range scientists considered all five sites to be overgrazed when the exclosures were built (Talbot & Hill 1923). The first large herds of livestock arrived in northern Arizona in the 1870s (Schlegel 1992), suggesting that overgrazing occurred for up to 35-40 years. Several decades after the exclosures were built, livestock densities had been reduced (Pearson 1933; Merrick 1939) but the Fry Park and Rogers Lake sites were still considered overgrazed (Table 2.1) and had the lowest regeneration densities outside exclosures (Table 2.3). Woody plants are most affected by livestock grazing when they are young (Archer 1994), and these effects remain evident for long periods due to their long life spans. Therefore, the grazing effects that are evident in 2004 (Fig. 2.2, 2.3) are the long-term consequences of grazing in the early 1900s rather than the effects of recent grazing.

A State-and-Transition Model for Southwestern Ponderosa Pine Overstory Vegetation

Clementsian models of vegetation succession (Clements 1916; Sampson 1919) suggest that the removal of a disturbance will permit the vegetation to gradually resemble its pre-disturbance conditions. However, protection from grazing in 1912 was insufficient and even deleterious with respect to overstory structure (Fig. 2.2); densities were even higher than they were in areas that continued to be grazed. Therefore, a Clementsian model is inadequate for explaining overstory dynamics in these forests.

Such a model does not account for multiple successional pathways (Cattelino et al. 1979), thresholds between alternate stable states (Westoby et al. 1989; Briske et al. 2005), or the unexpected effects of multiple disturbances (Paine et al. 1998).

I suggest that vegetation dynamics in these forests are more accurately explained by a state-and-transition model (Fig. 2.5). The pulses of ponderosa pine regeneration that occurred in the Southwest in the early 1900s were the result of interactions between several factors, including grazing regime, fire history, climatic conditions, and seed production (Meagher 1950). If these factors had not coincided, the results may have been very different (Paine et al. 1998).

Prior to Euro-American settlement, these forests are generally considered to have been maintained by surface fires in an open and park-like state (Cooper 1960), with abundant herbaceous vegetation in the understory. Grazing intensity was low, increasing greatly around 1870 with the arrival of Euro-American settlers and their large herds of domestic livestock (Haskett 1936; Schlegel 1992; Abruzzi 1995). While grazing greatly reduced the understory vegetation, particularly near water sources and along livestock driveways (Clary 1975), it had minimal effects on overstory dynamics for several decades: relatively little overstory regeneration had occurred by the time the grazing exclosures were built in 1912 (Fig. 2.3). However, grazing reduced the herbaceous biomass that carried surface fires, and was accompanied in the early 1900s by forest management decisions to actively suppress fires (Pearson 1933; Cooper 1960).

Dendroclimatological analyses in northern Arizona indicate that the period from 1905 to 1922 was the longest wet interval in more than 1400 years (Salzer 2000). Several years with good seed production also occurred during this period (Pearson 1950).

The coincidence of these factors permitted the germination and establishment of large numbers of pine seedlings, particularly in areas where grazing continued to occur. If the climate had been drier, or if years with good seed production had not occurred, the effects might have been very different. Pearson summarized the factors that led to the germination of many pine seedlings in northern Arizona in 1919 as "an excellent seed crop falling on a heavily grazed soil [coinciding] with the wettest summer on record" (1950:120). He noted that seedlings did not establish on heavily grazed areas, though he also noted that they did not establish on areas where complete exclusion of livestock favored luxurious grass and weed, which appears to contradict the results of this study (Fig. 2.2). Perhaps the understory was not as abundant at the sites reported here as in the areas he was referring to, or perhaps some seedlings established although most did not.

As the ponderosa pine regeneration grew, a transition between states was crossed. The nature of this threshold is unclear, but may relate to the development of a closed forest canopy, together with corresponding declines in understory production and increases in litter and woody fuel accumulation. This new state represents a significant departure from the historical norm: ecological processes such as surface fire could no longer eliminate the established regeneration and recreate presettlement conditions (Archer 1994; House et al. 2003). Once this had occurred, the only way to restore presettlement conditions was - and remains - through intentional management activities such as overstory thinning and the introduction of prescribed fires (Covington et al. 1994). If livestock grazing had been excluded from large areas, this threshold would have been crossed more rapidly (as indicated by the higher densities inside exclosures), and these ecosystems would have been at risk from stand-replacing disturbances earlier.

Presently, forests are at increased risk of stand-replacing disturbances such as crown fires. These disturbances function very different ecologically than those noted in these forests historically, and therefore represent another threshold. In addition, these post-disturbance communities contain few trees and may be dominated by introduced herbaceous species (Griffis et al. 2001; Crawford et al. 2001). Restoring post-disturbance communities to presettlement conditions is essentially impossible, at least within several decades or centuries.

Management Implications

Contemporary conditions in southwestern ponderosa pine forests are widely acknowledged to be unprecedented: tree densities are much greater than they were historically, and the risk of crown fire is also greatly increased (Covington et al. 1994; Allen et al. 2002). However, this study suggests that contemporary forests would contain even more, smaller trees if grazing by livestock had not continued to occur since the early 1900s. One implication is that livestock grazing might serve as a potential tool to control ponderosa pine densities. While clearly beyond the scope of this study, an assessment of such activities would have to identify the minimum grazing intensity to achieve these results; it may be that grazing at low intensities, as practiced currently in Coconino National Forest (Table 3.1), would have minimal effects on the overstory vegetation (Hill 1917; Schubert 1974). In addition, the potential benefits would have to be weighed against economic and ecological costs.

The grazing that occurred in the late 1800s and early 1900s is quantitatively and qualitatively different from that occurring afterwards. The number of cattle in Arizona is estimated to have quintupled between 1866 and 1900 (Schlegel 1992) while the number of sheep increased from less than a thousand in 1870 to more than 860,000 in 1900 (Haskett 1936). Abruzzi (1995) estimated that the Aztec Land and Cattle Company stocked the Little Colorado River basin with 2-3 times more livestock than the land could support in the 1890s. The intensity and duration of grazing were not regulated before the Forest Service was established (Breen 1907; Hill 1917; Dutton 1953), whereas current grazing intensities are greatly reduced (Table 3.1) because livestock grazing is ecologically informed and managed, and because of declining forage production due to overstory growth (Moore & Deiter 1992).

These results illustrate that livestock grazing, and protection from livestock grazing, can have significant long-term effects on overstory vegetation and that grazing history therefore must be considered when extrapolating results from one site to another. For example, permanent plots that have been fenced against livestock grazing for long periods (e.g. Moore et al. 2004) may differ in overstory structure from areas that experienced continued grazing. Conversely, areas that have never been grazed by livestock may also be atypical: relict areas usually exhibit lower tree densities than nearby grazed areas (Rummell 1951; Madany & West 1983; Schmutz et al. 1967; cf. Harris et al. 2003; Guenther et al. 2004).

Conclusions

This study has provided a quantitative analysis of the relationship between long-term grazing and overstory vegetation in southwestern ponderosa pine forests. Tree canopy cover and density were higher inside than outside grazing exclosures, indicating that the relationship between grazing and overstory regeneration is more complex than previously thought. Tree diameter and age distributions also varied between grazing treatments; trees were larger outside exclosures and older outside exclosures at sites that had not received recent silvicultural treatments. A state-and-transition model is presented that explains overstory dynamics in these forests as the result of interactions between livestock grazing, fire history, climate, and seed production.

In the last known publication related to these study sites, Arnold (1950) noted that understory plant cover was declining in 1941, and attributed this decline to the increasing prevalence of overstory regeneration. In other research (Chapters 3 and 4), I re-examine the dynamics of the herbaceous vegetation with respect to grazing treatment and overstory vegetation, and extend these analyses to the present.

References

Abruzzi, W.S. 1995. The social and ecological consequences of early cattle ranching in the Little Colorado River Basin. Human Ecology **23**:75-98.

Allen, B.H., and J.W. Bartolome. 1989. Cattle grazing effects on understory cover and tree growth in mixed conifer clearcuts. Northwest Science **63**:214-220.

Allen, C.D., M. Savage, D.A. Falk, K.F. Suckling, T.W. Swetnam, T. Schulke, P.B. Stacey, P. Morgan, M.Hoffman, and J.T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications **12**:1418-1433.

Archer, S. 1994. Woody plant encroachment into southwestern grassland and savannas: rates, patterns and proximate causes. Pages 13-68 *in* M. Vavra, W.A. Laycock, and R.D. Pieper (editors). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

Arnold, J.F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. Journal of Forestry **48**:118-126.

Bailey, J.D., and W.W. Covington. 2002. Evaluating ponderosa pine regeneration rates following ecological restoration treatments in northern Arizona, USA. Forest Ecology and Management **155**:271-278.

Becker, B.J. 1988. Synthesizing standardized mean-change measures. British Journal of Mathematical and Statistical Psychology **41**:257-278.

Belsky, A.J., and D.M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. Conservation Biology **11**:315-327.

Bock, C.E., J.H. Bock, W.R. Kenney, and V.M. Hawthorne. 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. Journal of Range Management **37**:239-242.

Breen, F.S. 1907. Forest reserves as seen at close range. Forestry and Irrigation **13**:180-183.

Briske, D.D., S.D. Fuhlendorf, and F.E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. Rangeland Ecology and Management **58**:1-10.

Canfield, R.H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry **39**:388-394.

Cattelino, P.J., I.R. Noble, R.O. Slatyer, and S.R. Kessell. 1979. Predicting the multiple pathways of plant succession. Environmental Management **3**:41-50.

Cheal, D.C. 1993. Effects of stock grazing on the plants of semi-arid woodlands and grasslands. Proceedings of the Royal Society of Victoria **105**:57-65.

Cheney, B. 1982. Effects of grazing at Walnut Canyon National Monument. Appendix A in K. Davis. Fire history of Walnut Canyon National Monument. 1987. Unpublished report. USDI National Park Service, Flagstaff Area National Monuments, Flagstaff, AZ.

Chesterfield, C.J., and R.F. Parsons. 1985. Regeneration of three tree species in arid south-eastern Australia. Australian Journal of Botany **33**:715-732.

Clary, W.P. 1975. Range management and its ecological basis in the ponderosa pine type of Arizona: the status of our knowledge. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. Research Paper RM - 158. 35 p.

Clements, F.E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institute, Washington, DC. Publication 242. 512 p.

Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Monographs **30**:129-164.

Cormier, K.L. 1990. Modeling natural regeneration of even-aged ponderosa pine following shelterwood cutting in northern Arizona. M.Sc. thesis. Northern Arizona University, Flagstaff, AZ. 69 p.

Courtois, D.R., B.L. Perryman, and H.S. Hussein. 2004. Vegetation change after 65 years of grazing and grazing exclusion. Journal of Range Management **57**:574-582.

Covington, W.W., and M.M. Moore. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. Journal of Forestry **92**:39-47.

Covington, W.W., R.L. Everett, R.W. Steele, L.I. Irwin, T.A. Daer, and A.N.D. Auclair. 1994. Historical and anticipated changes in forest ecosystems of the Inland West of the United States. Journal of Sustainable Forestry **2**:13-63.

Crawford, J.A., C.-H.A. Wahren, S. Kyle, and W.H. Moir. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. Journal of

Vegetation Science **12**:261-268.

Currie, P.O., C.B. Edminster, and F.W. Knott. 1978. Effects of cattle grazing on ponderosa pine regeneration in central Colorado. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. Research Paper RM-201. 7 p.

Dutton, W.L. 1953. Forest grazing in the United States. Journal of Forestry **51**:248-251.

Eissenstat, D.M., J.E. Mitchell, and W.W. Pope. 1982. Trampling damage by cattle on northern Idaho forest plantations. Journal of Range Management **35**:715-716.

Elliott, K.J., and A.S. White. 1987. Competitive effects of various grasses and forbs on ponderosa pine seedlings. Forest Science **33**:356-366.

Frank, D.A., C.A. Gehring, L. Machut, and M. Phillips. 2003. Soil community composition and the regulation of grazed temperate grassland. Oecologia **137**:603-609.

Fredrickson, E., K.M. Havstad, R. Estell, and P. Hyder. 1998. Perspectives on desertification: south-western United States. Journal of Arid Environments **39**:191-207.

Fulé, P.Z., W.W. Covington, and M.M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications **7**:895-908.

Fulé, P.Z., W.W. Covington, M.M. Moore, T.A. Heinlein, and A.E.M. Waltz. 2002. Natural variability in forests of the Grand Canyon, USA. Journal of Biogeography **29**:31-47.

Gardner, J.L., and D.S. Hubbell. 1943. Some vegetational responses after eight years of protection from grazing. Ecology **24**:409-410.

Glendening, G.E. 1941. Work plan - summer 1941; Hill study plots - Coconino. Unpublished document. Fort Valley Archives, Flagstaff, AZ. 3 p.

Glendening, G.E. 1952. Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. Ecology **33**:319-328.

Gordon, B.R., G.P. Parrott, and J.B. Smith. 1992. Vegetation changes in northern Arizona: the Alexander Gardner photos. Rangelands **14**:308-320.

Griffis, K.L., J.A. Crawford, M.R. Wagner, and W.H. Moir. 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. Forest Ecology and Management **146**:239-245.

Guenther, D., T.J. Stohlgren, and P. Evangelista. 2004. A comparison of a near-relict site and a grazed site in a pinyon-juniper community in the Grand Staircase-Escalante National Monument, Utah. Pages 153-162 *in* C. van Riper III and K.L. Cole (editors). The Colorado Plateau: cultural, biological, and physical research. University of Arizona, Tucson, AZ.

Gurevitch, J., and L.V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology **80**:1142-1149.

Gurevitch, J., and L.V. Hedges. 2001. Meta-analysis: combining the results of independent experiments. Pages 347-369 *in* S. M. Scheiner and J. Gurevitch (editors). Design and analysis of ecological experiments. Oxford University Press, New York, NY.

Haasis, F.W. 1923. Frost heaving of western yellow pine seedlings. Ecology **4**:378-390.

Harris, A.T., G.P. Asner, and M.E. Miller. 2003. Changes in vegetation structure after long-term grazing in pinyon-juniper ecosystems: integrating imaging spectroscopy and field studies. Ecosystems **6**:368-383.

Hart, R.H., and W.A. Laycock. 1996. Repeat photography on range and forest lands in the western United States. Journal of Range Management **49**:60-67.

Haskett, B. 1936. History of the sheep industry in Arizona. Arizona Historical Review **7**:3-49.

Hedges, L.V., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, Orlando, FL.

Heidmann, L.J., T.N. Johnson Jr., Q.W. Cole, and G. Cullum. 1982. Establishing natural regeneration of ponderosa pine in central Arizona. Journal of Forestry **80**:77-79.

Hill, R.R. 1917. Effects of grazing upon western yellow-pine reproduction in the national forests of Arizona and New Mexico. USDA, Washington, DC. Bulletin 580. 27 p.

Hill, R.R. 1918. Can an over-grazed range come back? Unpublished progress report. Fort Valley Archives, Flagstaff, AZ. 8 p.

Hill, R.R. 1921. Notes taken on Coconino trip with Grazing Examiner M. W. Talbot, Fall of 1921. Unpublished report. Fort Valley Archives, Flagstaff, AZ. 20 p.

House, J.I., S. Archer, D.D. Breshears, R.J. Scholes, and NCEAS Tree-Grass Interactions Participants. 2003. Conundrums in mixed woody-herbaceous plant systems. Journal of Biogeography **30**:1763-1777.

Jameson, D.A., J.A. Williams, and E.W. Wilton. 1962. Vegetation and soils of Fishtail Mesa, Arizona. Ecology **43**:403-410.

Jiménez, J., E. Jurado, O. Aguirre, and E. Estrada. 2005. Effect of grazing on restoration of endemic dwarf pine (*Pinus culminicola* Andresen et Beaman) populations in northeastern Mexico. Restoration Ecology **13**:103-107.

Jones, J.R. 1971. Mixed conifer seedling growth in eastern Arizona. USDA Forest Service, Fort Collins, CO. Research Paper RM-77. 19 p.

Karl, M.G.S., and P.S. Doescher. 1998. Ponderosa pine aboveground growth after cattle removal of terminal tissue. Journal of Range Management **51**:147-151.

Kaufmann, M.R., C.M. Regan, and P.M. Brown. 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. Canadian Journal of Forest Research **30**:698-711.

Kenney, W.R., J.H. Bock, and C.E. Bock. 1986. Responses of the shrub, Baccharis pteronioides, to livestock exclosure in southeastern Arizona. American Midland Naturalist **116**:429-431.

Krzic, M., R.F. Newman, K. Broersma, and A.A. Bomke. 1999. Soil compaction of forest plantations in interior British Columbia. Journal of Range Management **52**:671-677.

Larson, M.M. and G.H. Schubert. 1969. Root competition between ponderosa pine seedlings and grass. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. Research Paper RM-54. 12 p.

Leopold, A. 1924. Grass, brush, timber, and fire in southern Arizona. Journal of Forestry **22**:1-10.

Leopold, L.B. 1951. Vegetation of southwestern watersheds in the nineteenth century. The Geographical Review **41**:295-316.

Lipsey, M.W., and D.B. Wilson. 2001. Practical meta-analysis. SAGE Publications, Thousand Oaks, CA.

Madany, M.H., and N.E. West. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology **64**:661-667.

Madany, M.H., and N.E. West. 1984. Vegetation of two relict mesas in Zion National Park. Journal of Range Management **37**:456-461.

Mason, L., and N.E. West. 1970. Timber Top Mesa: a relict area in Zion National Park. Proceedings of the Utah Academy of Sciences, Arts and Letters **47**:284-285.

Mason, L.R., H.M. Andrews, J.A. Carley, and E.D. Haacke. 1967. Vegetation and soils of No Man's Land Mesa Relict Area, Utah. Journal of Range Management **20**:45-49.

Mast, J.N., P.Z. Fulé, M.M. Moore, W.W. Covington, and A.E.M. Waltz. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. Ecological Applications **9**:228-239.

Mast, J.N., T.T. Veblen, and M.E. Hodgson. 1997. Tree invasion within a pine / grassland ecotone: an approach with historic aerial photography and GIS modeling. Forest Ecology and Management **93**:181-194.

Meagher, G. 1950. Reproduction of ponderosa pine. Journal of Forestry **48**:188-191.

Mengistu, T., D. Teketay, H. Hulten, and Y. Yemshaw. 2005. The role of enclosures in the recovery of woody vegetation in degraded dryland hillsides of central and northern Ethiopia. Journal of Arid Environments **60**:259-281.

Menzel, J.P. 1996. Historical changes in forest structure in the ponderosa pine type, Walnut Canyon area, northern Arizona. M.Sc. thesis. Northern Arizona University, Flagstaff, AZ.

Merrick, G.D. 1939. Revegetation of deteriorated range land in northern Arizona. M.A. thesis. Duke University, Durham, NC. 37 p.

Moore, M.M., and D.A. Deiter. 1992. Stand density index as a predictor of forage production in northern Arizona pine forests. Journal of Range Management **45**:267-271.

Moore, M.M., W.W. Covington, and P.Z. Fulé. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecological Applications **94**:1266-1277.

Moore, M.M., D.W. Huffman, P.Z. Fulé, W.W. Covington, and J.E. Crouse. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Science **50**:162-176.

Norman, S.P., and A.H. Taylor. 2005. Pine forest expansion along a forest-meadow ecotone in northeastern California, USA. Forest Ecology and Management *In press*.

Paine, R.T., M.J. Tegner, and E.A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1**:535-545.

Pearson, G.A. 1923. Natural reproduction of western yellow pine in the southwest. USDA Forest Service, Washington, DC. Bulletin 1105. 143 p.

Pearson, G.A. 1931. Recovery of western yellow pine seedlings from injury by grazing animals. Journal of Forestry **29**:876-894.

Pearson, G.A. 1933. A twenty year record of changes in an Arizona pine forest. Ecology **14**:272-285.

Pearson, G.A. 1942. Herbaceous vegetation a factor in natural regeneration of ponderosa pine in the southwest. Ecological Monographs **12**:315-338.

Pearson, G.A. 1950. Management of ponderosa pine in the Southwest as developed by research and experimental practice. USDA Forest Service, Washington, DC. Agriculture Monograph 6. 218 p.

Pearson, H.A., L.B. Whitaker, and V.L. Duvall. 1971. Slash pine regeneration under regulated grazing. Journal of Forestry **69**:744-746.

Rietkerk, M., and J. van de Koppel. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. Oikos **79**:69-76.

Rowlands, P.G., and N.J. Brian. 2001. Fishtail Mesa: a vegetation resurvey of a relict area in Grand Canyon National Park, Arizona. Western North American Naturalist **61**:159-181.

Rummell, R.S. 1951. Some effects of livestock grazing on ponderosa pine forest and range in central Washington. Ecology **32**:594-607.

Sackett, S.S. 1984. Observations on natural regeneration in ponderosa pine following a prescribed burn in Arizona. USDA Forest Service, Fort Collins, CO. Research Note RM-435. 8 p.

Salzer, M.W. 2000. Dendroclimatology in the San Francisco Peaks region of northern Arizona, USA. Ph.D. Dissertation. University of Arizona, Tucson, AZ. 211 p.

Sampson, A.W. 1919. Plant succession in relation to range management. US Department of Agriculture, Washington, DC. Bulletin No. 791. 76 p.

Savage, M., Brown, P.M., and Feddema, J. 1996. The role of climate in a pine forest regeneration pulse in the southwestern United States. Ecoscience **3**:310-318.

Schlegel, P.A. 1992. A history of the cattle industry in northern Arizona, 1863-1912. M.A. thesis. Northern Arizona University, Flagstaff, AZ. 113 p.

Schmutz, E.M., C.C. Michaels, and B.I. Judd. 1967. Boysag Point: a relict area on the North Rim of Grand Canyon in Arizona. Journal of Range Management **20**:363-368.

Schubert, G.H. 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. Research Paper RM-123. 71 p.

Skovlin, J.M., R.W. Harris, G.S. Strickler, and G.A. Garrison. 1976. Effects of cattle grazing methods on ponderosa pine-bunchgrass range in Pacific Northwest. USDA Forest Service, Pacific Northwest Research Station, Portland, OR. Technical Bulletin 1531. 40 p.

Southwestern Forest and Range Experiment Station. 1937. Annual report and program. USDA Forest Service, Southwestern Forest and Range Experiment Station, Tucson, AZ.

Spooner, P., I. Lunt, and W. Robinson. 2002. Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. Ecological Management and Restoration **3**:117-126.

Stokes, M.A., and T.L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago, Chicago, IL.

Talbot, M.W. and R.R. Hill. 1923. Progress report on the range study plots on the Coconino National Forest comprising a description of project and digest of data. Unpublished report. Fort Valley Archives, Flagstaff, AZ. 32 p.

Thatcher, A.P., and V.L. Hart. 1974. Spy Mesa yields better understanding of pinyon-juniper in range ecosystem. Journal of Range Management **27**:354-357.

Valone, T.J., and P. Sauter. 2005. Effects of long-term cattle exclosure on vegetation and rodents at a desertified arid grassland site. Journal of Arid Environments **61**:161-170.

Valone, T.J., M. Meyer, J.H. Brown, and R.M. Chew. 2002. Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. Conservation Biology **16**:995-1002.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management **42**:266-274.

Yeo, J.J. 2005. Effects of grazing exclusion on rangeland vegetation and soils, east central Idaho. Western North American Naturalist **65**:91-102.

Young, V.A., G.B. Doll, G.A. Harris, and J.P. Blaisdell. 1942. The influence of sheep grazing on coniferous reproduction and forage on cut-over western white pine areas in northern Idaho. The University of Idaho Bulletin **37**:1-46.

Zimmerman, G.T., and L.F. Neuenschwander. 1984. Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas-fir/ninebark habitat type. Journal of Range Management **37**:104-110.

Table 2.1. Summary statistics for the Hill plots in northern Arizona. Additional details are in Table 3.1.

	Big Fill	Black Springs	Fry Park[1]	Reese Tank[2]	Rogers Lake
Abbreviation	BF	BS	FP	RT	RL
Location	SW¼ Sec 21, T21N, R8E,	SW¼ Sec 8, T20N, R7E	NE¼ Sec 31, T20N, R6E	NE¼ Sec 8, T23N, R7E	NW¼ Sec 8, T20N, R6E
Current jurisdiction	Coconino National Forest	Coconino National Forest	Coconino National Forest	Coconino National Forest	Centennial Forest[3]
Exclosure area (ha)	0.618	0.786	0.840	0.669	0.574
Mean elevation (m)	2070	2100	2170	2490	2220
Disturbance history[4]					
Localized	PL 1946	PL ca. 1954	None	RD ca. 1978	None
Generalized	SH 1896, 1919, 1947	SH 1902; PCT 1976, 1997	SH 1910	SH 1940,1978,1989; PCT 1964; PB 1999 (west half)	SH 1905
Grazing intensity[5]					
Before 1912	Overgrazed	Overgrazed	Overgrazed	Overgrazed	Overgrazed
1912-1924	Overgrazed	Heavy	Overgrazed	Moderate	Overgrazed
1924-1938	Heavy	Heavy	Overgrazed	Moderate	Overgrazed
Contemporary	None since 2000	None since ca. 1960	Light	None since ca. 1992	Light
Number of undisturbed lines sampled, inside and outside exclosures					
1941	In-80; Out-80	In-40; Out-40	In-80; Out-80	In-20; Out-20	In-40; Out-40
2004	In-71; Out-80	In-37; Out-36	In-80; Out-78	In-12; Out-6	In-40; Out-40

[1] also known as Frye Park

[2] also known as Rees Tank

[3] Some of the chart quadrats at this site are located on land within Coconino National Forest

[4] Data obtained from unpublished documents in Fort Valley Archives and from Coconino National Forest (J. Rolf, *pers. comm.*). Codes: PB = prescribed burn; PCT = pre-commercial thinning; PL = power/phone line built through site; RD = road built through site; SH = selective overstory harvest.

[5] Historical data from Merrick 1939; contemporary data from unpublished data on file at Coconino National Forest.

Table 2.2. Cumulated grazing effect size ($d^*_{i+} \pm s^*_{i+}$) in 1941 and 2004 for canopy cover and tree density variables. Effect sizes are combined across the five Hill plots. Positive and negative effect sizes indicate larger responses inside and outside of exclosures, respectively. Mature trees and regeneration were measured separately in 1941 but not in 2004; regeneration was further classified by age class in 1941. *P*-values indicate whether effect sizes are significantly different from zero, which indicates no difference between grazing treatments; values ≤ 0.05 are in bold. Data are presented in Fig. 2.2, Table 2.3, and Appendix 2.1.

Variable	Effect size	*p*
Canopy Cover		
1941 Mature Trees	0.01 ± 0.19	0.481
1941 Regeneration	0.60 ± 0.18	**<0.001**
1941 Total	0.22 ± 0.17	0.095
2004 Total	0.65 ± 0.22	**0.002**
Tree Density		
1941 Mature Trees	0.17 ± 0.13	0.089
1941 Regeneration	0.47 ± 0.39	0.118
1919 Age Class	0.26 ± 0.19	0.084
1929 Age Class	0.42 ± 0.37	0.126
>1929 Age Class	0.26 ± 0.36	0.238
1941 Total	0.41 ± 0.40	0.153
2004 Total	0.85 ± 0.27	**<0.001**

Table 2.3. Mean density (t/ha) of regeneration by age class (1919, 1929, and >1929), inside and outside grazing exclosures at five sites in northern Arizona in 1941. Data are back-transformed to original units; standard deviations are not shown as they are asymmetric (see Fig. 2.2). Values in the 'Overall' category are weighted by the degrees of freedom at each site. Within each site and age class, different letters indicate statistically significant differences between grazing treatments, as determined by Wilcoxon tests. Site abbreviations are in Table 2.1, cumulated grazing effect sizes in Table 2.2, and a summary of untransformed data in Appendix 2.1.

Age Class	Grazing Treatment	BF	BS	FP	RT	RL	Overall
1919	In	326 a	167 a	340 a	2119 a	71 a	330
	Out	58 b	55 b	116 b	5702 b	71 a	194
1929	In	816 a	260 a	91 a	1681 a	1621 a	559
	Out	235 b	144 a	63 a	5365 b	76 b	250
>1929	In	543 a	559 a	37 a	311 a	1291 a	410
	Out	94 b	825 a	63 a	798 b	69 b	197
Total	In	1685	986	468	4111	2983	1299
	Out	387	1024	242	11,865	216	641

Table 2.4. Sampling intensity and structural characteristics (quadratic mean diameter [QMD] and basal area [BA]) inside and outside grazing exclosures at five sites in northern Arizona in 2004.

	Trees Sampled		Area Sampled (ha)		QMD (cm)		BA (m^2/ha)	
Site	In	Out	In	Out	In	Out	In	Out
Big Fill	320	250	0.136	0.248	13.1	15.9	31.6	20.2
Black Springs[1]	112	83	0.216	0.251	29.0	34.4	34.3	30.7
Fry Park	64	18	0.163	0.223	30.3	41.8	28.3	11.1
Reese Tank[1]	71	120	0.121	0.167	31.6	27.6	46.0	42.5
Rogers Lake	461	127	0.235	0.305	16.6	28.0	42.5	25.7
Mean					24.1	29.5	36.6	26.0
SD					8.6	9.6	7.5	11.7

[1] Received silvicultural treatments in last 20 years (Table 2.1)

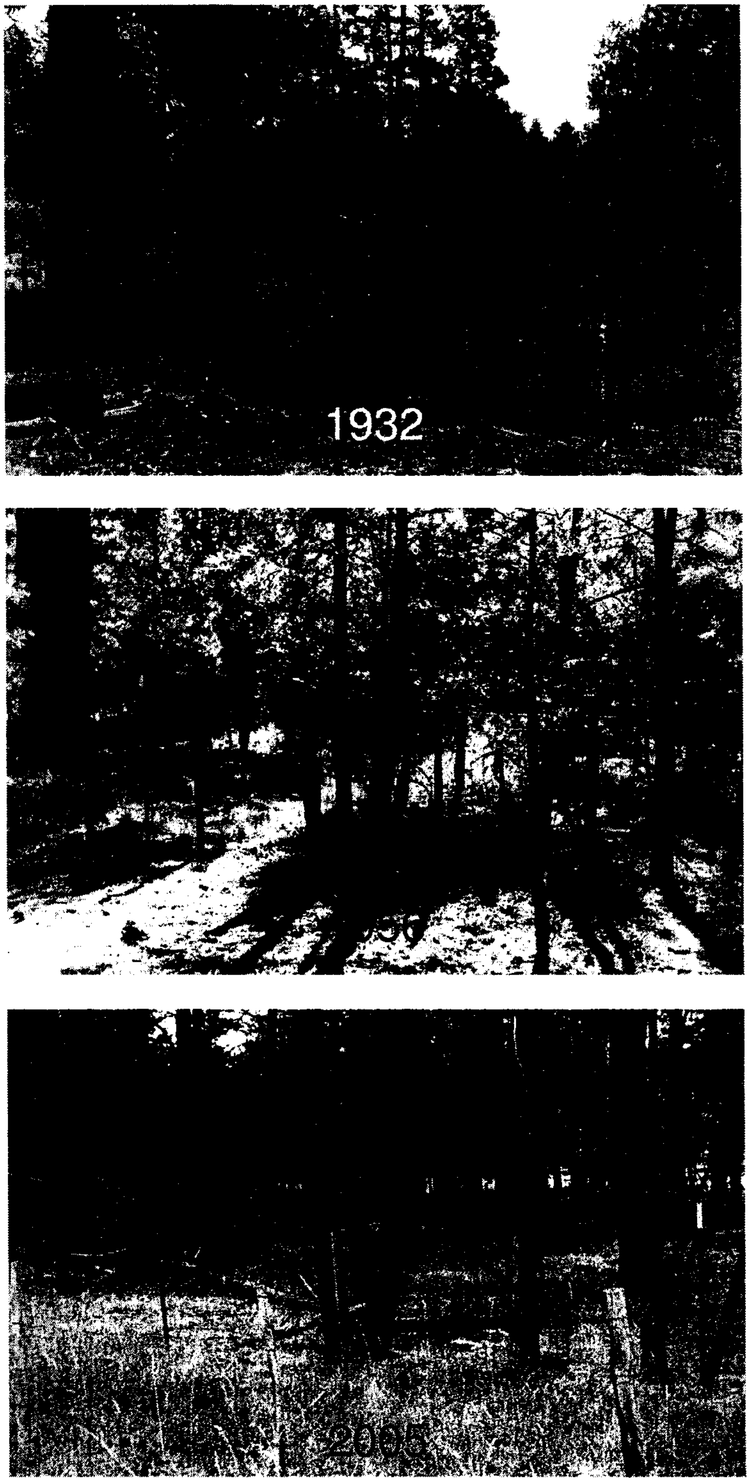


Figure 2.1. 1932 (top), 1956 (middle), and 2005 (bottom) photographs of the livestock exclosure at Rogers Lake. The 1932 photo was taken by J.D. Jones (US Forest Service photo 269997), the 1956 photo by T.M. Smith (US Forest Service photo 485803), and the 2005 photo by J.D. Bakker.

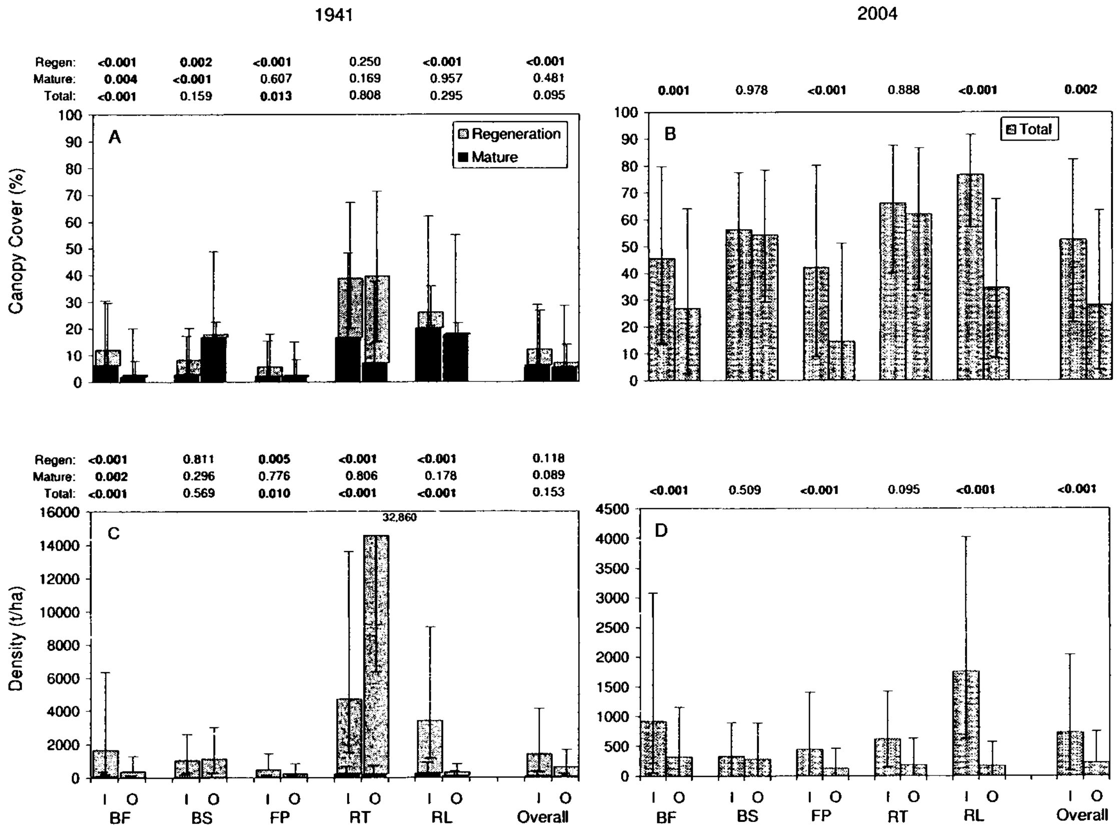


Figure 2.2. Mean (± SD) canopy cover (top) and tree density (bottom) inside (I) and outside (O) grazing exclosures at five sites in northern Arizona in 1941 (left) and 2004 (right). Mature trees and regeneration were measured separately in 1941 but not in 2004. Data are back-transformed to original units. *P*-values above sites are from Wilcoxon tests for differences between grazing treatments, and those above the 'Overall' category are from a meta-analysis of grazing effect sizes (Table 2.2). *P*-values ≤ 0.05 are in bold. To avoid overlapping error bars, the bars representing mature trees and regeneration are slightly offset. Site abbreviations are in Table 2.1. Note difference in scale of y-axis for tree density in 1941 and 2004.

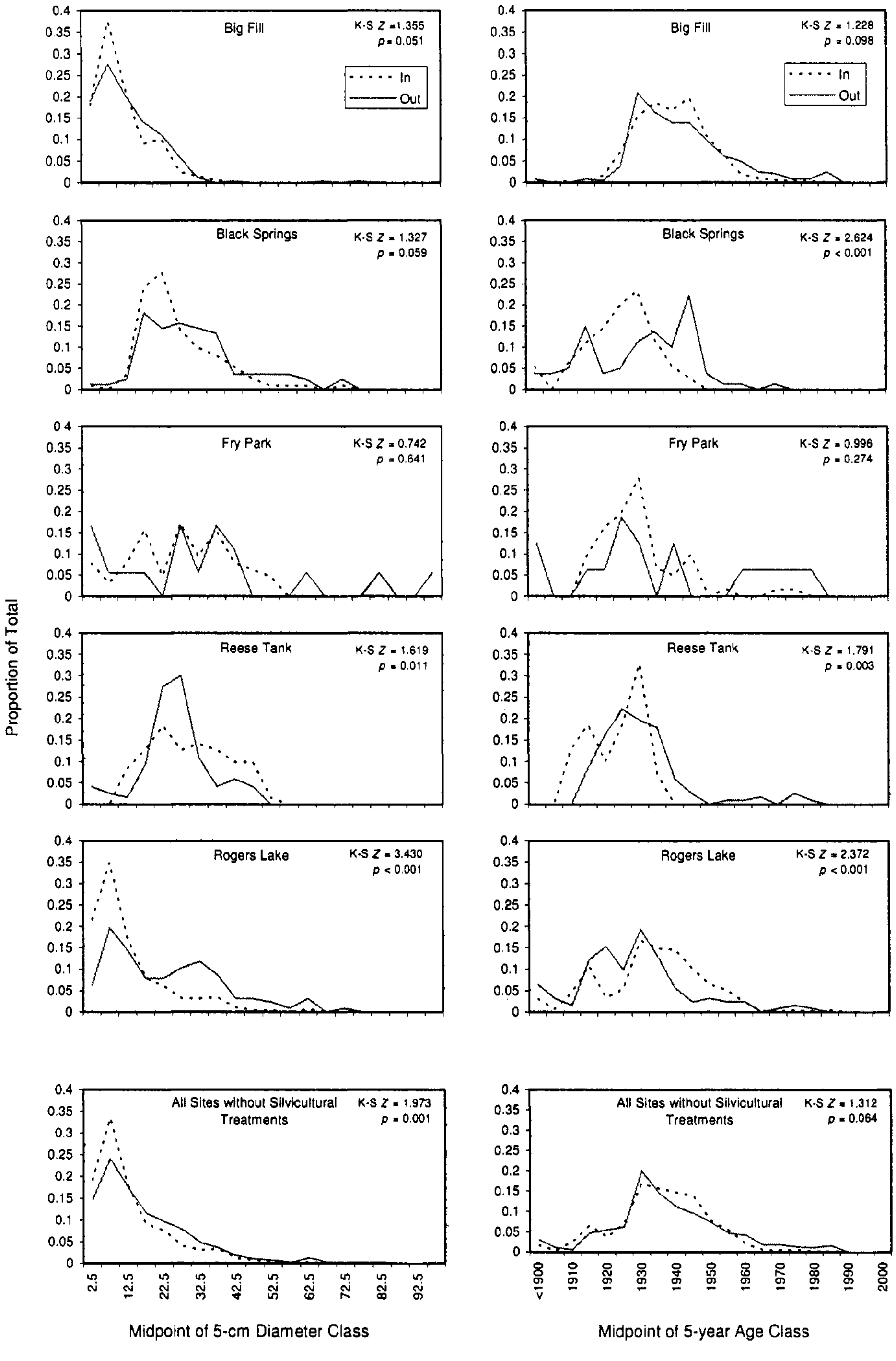


Figure 2.3. Diameter (left) and age (right) distributions inside and outside grazing exclosures at five sites in northern Arizona in 2004. Since the number of trees and area sampled varied between grazing treatments (Table 2.4), distributions are presented as proportions. Data are grouped for presentation but were ungrouped for analysis with Kolmogorov-Smirnov (K-S) tests. Note that the Black Springs and Reese Tank sites received silvicultural treatments within the last 20 years (Table 2.1).

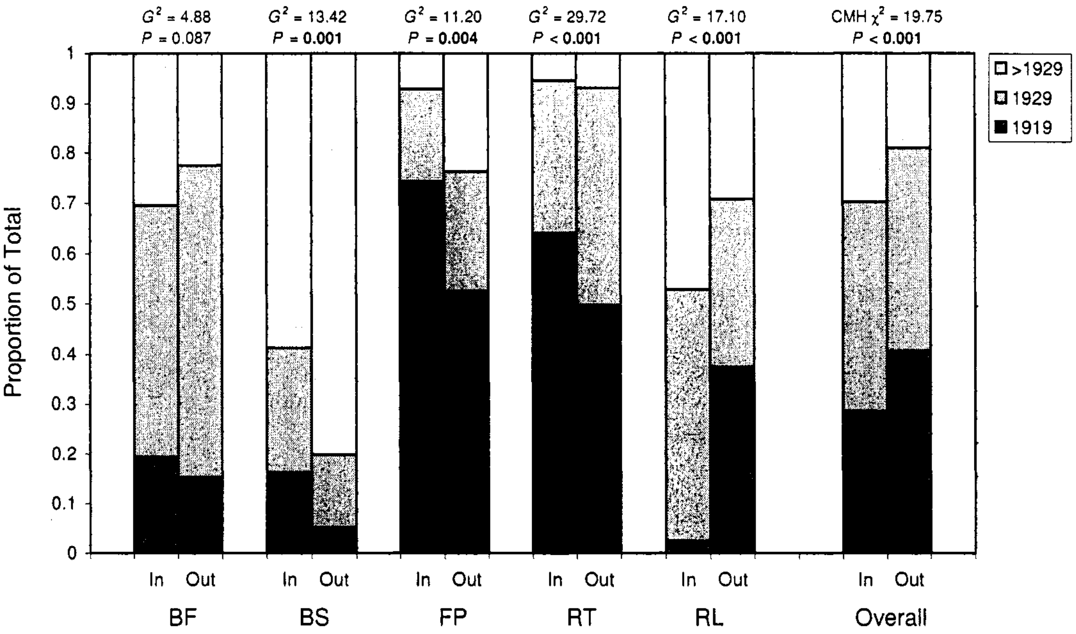


Figure 2.4. Proportion of overstory regeneration classified in 1941 as belonging to the 1919, 1929, or >1929 age class inside and outside grazing exclosures at five sites in northern Arizona. Results of G^2 likelihood-ratio chi-square tests for differences between grazing treatments are presented above sites, and those from a Cochran-Mantel-Haenszel test for overall differences between grazing treatments are above the 'Overall' category. P-values $\leq$ 0.05 are in bold. Site abbreviations are in Table 2.1, and regeneration densities are in Table 2.3.

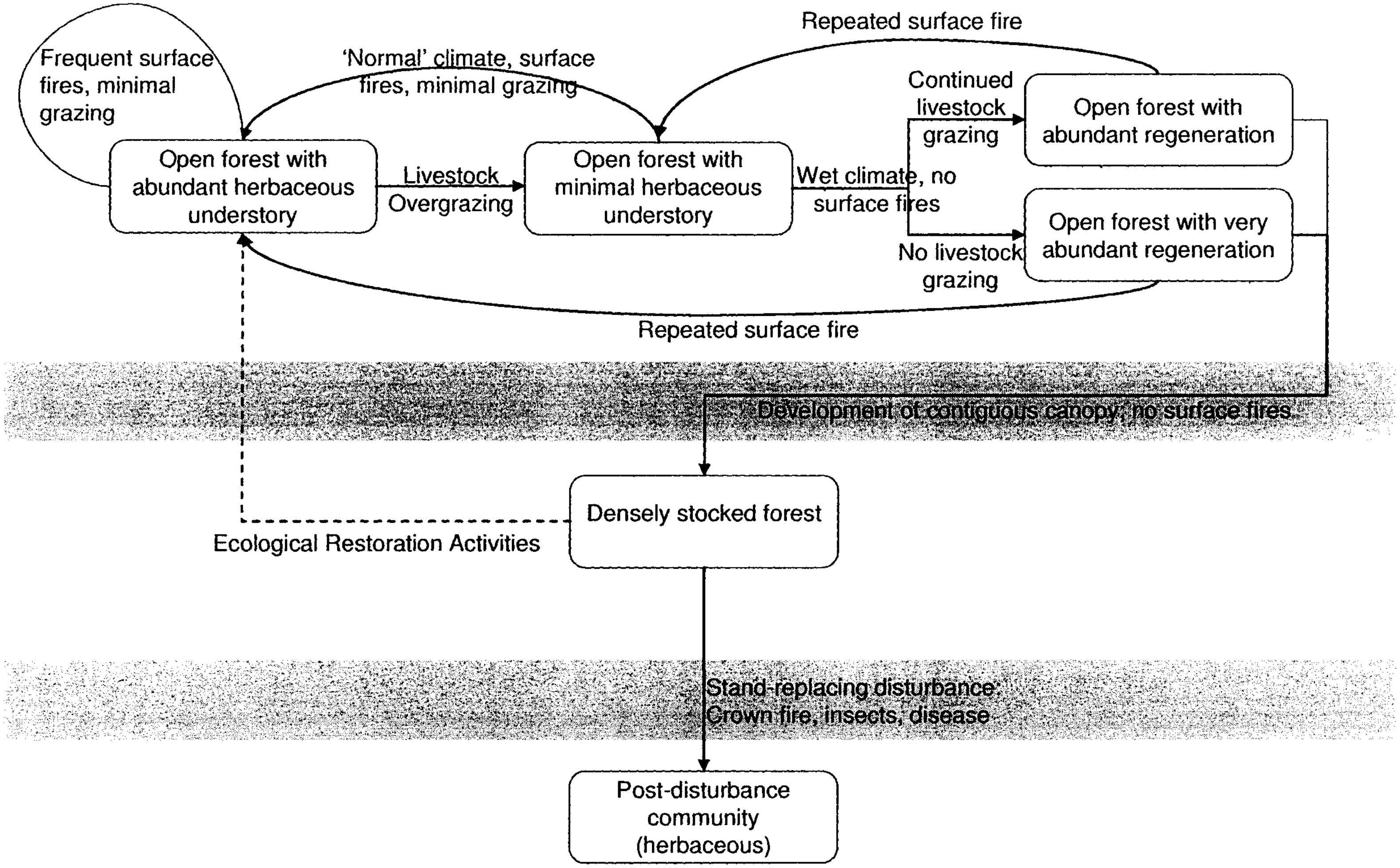


Figure 2.5. A state-and-transition model of overstory dynamics in southwestern ponderosa pine forests. Grey bars indicate thresholds between alternate states, and dashed lines represent management activities.

Chapter 3

Dynamics of Herbaceous Vegetation in a Southwestern Ponderosa Pine Forest, 1941-2004

Preface

In this chapter, I examine the effects of increasing overstory vegetation and long-term livestock grazing on community-level characteristics (species density, plant density, plant cover) of the understory vegetation in southwestern ponderosa pine forests.

Abstract

The long-term dynamics of understory (herbaceous and shrub) vegetation are much more poorly understood than the dynamics of overstory (tree) vegetation. I examined the effects of overstory vegetation and long-term livestock grazing on the understory vegetation at five sites in a southwestern ponderosa pine forest in 1941 and 2004. Response variables were negatively correlated with overstory vegetation in both years. Most variables did not differ between grazing treatments in 1941 but were greater outside exclosures in 2004. However, many of the apparent differences between grazing treatments were due to differences in overstory vegetation between grazing treatments rather than to grazing effects. After controlling for overstory effects, graminoid cover was higher inside exclosures in 1941 but did not differ between grazing treatments for other variables. Between 1941 and 2004, species density and herbaceous plant density

each declined by 37%, shrub cover by 69%, herbaceous cover by 59%, graminoid cover by 45%, and forb cover by 82%. These declines were primarily attributable to the increasing dominance of the overstory. Since overstory effects are the dominant force affecting the understory in this ecosystem, the herbaceous and shrub understory should respond positively to ecological restoration activities that reduce the dominance of the overstory.

Introduction

Long-term studies can broaden our understanding of concepts such as reference conditions, invasion of exotic species, vegetation dynamics, and successional theory (Pickett et al. 2001; Bakker et al. 2002; Rango et al. 2005). Remeasurements of long-term studies have demonstrated large changes in species composition (Tilman et al. 1994; Crawley et al. 2005) and forest structure (Moore et al. 2004; Chapter 2). Long-term studies are also important to detect responses that are contingent upon site differences, interannual variability, or other factors (Bakker et al. 2003; Yeo 2005; Young et al. 2005). For example, perennial grasses in a desert grassland exhibited little response to two decades of protection from livestock grazing (Chew 1982) but increased significantly after four decades of protection (Valone et al. 2002; Valone & Sauter 2005); the lag in response was attributed to the episodic nature of suitable conditions for seedling establishment.

Contingent effects may be particularly important when they involve changes in life form dominance (House et al. 2003). In northern Arizona, the establishment of large numbers of ponderosa pine (*Pinus ponderosa*) seedlings in the early 1900s is thought to have resulted from the interaction of several factors, including intense livestock grazing, fire suppression, favorable climatic conditions, and the production of large seed crops (Pearson 1950), although responses to these factors are more complex than originally envisioned (Chapter 2).

This pulse of pine regeneration has affected ecosystem structure and function and produced an alternate stable state that is irreversible at decadal time-scales without anthropogenic intervention (House et al. 2003). Based on known overstory-understory relationships (Arnold 1950; Jameson 1967; Dodd et al. 1972; McLaughlin 1978; Bojorquez Tapia et al. 1990; Moore & Deiter 1992; Naumburg & DeWald 1999), the growth of the overstory should have large effects on the herbaceous and shrub understory vegetation in these forests. Herbivory can also have significant effects on understory vegetation (Arnold 1950; Johnson 1956; Smith 1967; Krueger & Winward 1974; Olff & Ritchie 1998; Rambo & Faeth 1999). Recent models suggest that livestock grazing should negatively affect plant diversity in semiarid environments such as the Southwest (Olff & Ritchie 1998; Cingolani et al. 2005).

In a 1936 report to the United States Senate, it was estimated that the grazing capacity of southwestern ponderosa pine forests and other open forests had declined by one-third since Euro-American settlement (Clapp 1936). This decline was attributed to the loss of valuable forage plants, their replacement with unpalatable, annual, and/or exotic species, a reduction in density of palatable forage plants, and the growth of the overstory. However, the relative importance of these factors is unclear. Qualitative assessments from historical photographs and early written accounts suggest an abundant understory (Leopold 1951; Cooper 1960), a conclusion that is consistent with historical reconstruction models (Covington & Moore 1994) and observed vegetation responses following contemporary thinning experiments (Casey 2004; Wienk et al. 2004; Moore et al. *in review*). However, quantitative data about long-term changes in understory vegetation in this region are rare, and can only be obtained from historical studies.

My first objective in this study was to assess the relative importance of overstory and grazing effects on the understory vegetation of southwestern ponderosa pine forests. To do so, I analyzed vegetation data obtained in 1941 and 2004 from inside and outside of five long-term experimental grazing exclosures. My second objective was to quantify the magnitude of change and to assess the relative importance of overstory and grazing effects in these changes.

Methods

Field Sampling

This study was conducted on the Hill plots, a series of five grazing exclosures established on the Coconino National Forest (Arizona) in 1912. Sites vary in soil type (Table 3.1) and span the elevational range of the ponderosa pine forest type (Table 2.1). Livestock grazing intensities at the time of each measurement are shown in Table 3.1, and grazing histories are summarized in Table 2.1.

At the Fort Valley Experiment Station, precipitation from Sept 1940 to Aug 1941 totaled 83.4 cm, or 148% of the long-term mean (1909-2004; USDA FS 2004). Precipitation from Sept 2003 to Aug 2004 totaled 35.6 cm, or 63% of the long-term mean.

The vegetation inside and outside of each exclosure was sampled in 1941 and 2004 using the line transect method (Canfield 1941). Each area was divided into 10-20 contiguous strata, and each stratum was sampled with 2-4 lines (Fig. 3.1). In 1941, lines were located by randomly selecting X,Y starting coordinates relative to the origin of each stratum. 1941 data were collected by G.E. Glendening and published in summary form by Arnold (1950), who focused on overstory-understory relationships. In 2004, the same starting coordinates were used where possible (79% of lines), otherwise new random coordinates were generated. Lines were 15.24 m (50 ft) long and oriented parallel to the long axis of the stratum. Overstory canopy cover was measured as the proportion of the line directly beneath a tree crown, and tree density as the number of trees within a 1.22 m (4 ft) wide belt centered on the line (see Chapter 2 for details).

Five strata outside the exclosure at Black Springs were destroyed by an interstate highway built in the 1950s, so replacement strata were established on the other side of the exclosure. Several sites received silvicultural treatments between 1941 and 2004 (Table 2.1), but these generalized disturbances were applied inside and outside the exclosures and are considered part of the intersite variability. Other areas were subject to localized disturbances (powerline right-of-ways, etc; Table 2.1); lines in these areas were omitted from analyses. In total, 520 undisturbed lines were measured in 1941 and 480 undisturbed lines in 2004. The Black Springs and Reese Tank sites were omitted from analyses of grazing effects in 2004 (see below) because they had not been grazed by livestock for a number of years (Table 3.1) and grazing impacts were therefore expected to be minimal.

For herbaceous plants (graminoids and forbs), the rooted portions of live plants directly underneath the line were measured. For shrubs, the plant canopy was projected down onto the line and this distance was measured. Distances were recorded to the nearest ~0.3 cm (0.01 ft) in 1941 and to the nearest 0.25 cm in 2004. Total species density (*sensu* Gotelli & Colwell 2001) was calculated as the number of species (both herbaceous and shrub) recorded on a line. The density of individual herbaceous plants (hereafter, herbaceous plant density) was calculated as the sum of the number of recorded distances for all herbaceous species on a line. The density of individual shrubs could not be calculated since it is unknown how many times the canopy of each plant overlapped the line. The percent cover of each species on each line was calculated as the sum of the recorded distances divided by the line length. Covers of herbaceous and shrub species were analyzed separately since they were measured using different methods. Herbaceous cover data were analyzed in total and separately by life form (graminoid, forb). All nomenclature is based on the USDA NRCS plants database (2004).

Overstory and Grazing Effects

Variables analyzed were total species density (number of species per line, including both herbaceous plants and shrubs), herbaceous plant density (number of herbaceous plants per line), shrub cover, and herbaceous plant cover (total, graminoid, forb). Densities were log $(x + 1)$ transformed and cover data were arc-sin (square root x) transformed for analysis, but back-transformed data are presented for clarity.

Overstory effects were assessed using multiple regression with tree canopy cover and tree density as dependent variables. All lines from all sites were included in these analyses, which were conducted separately for each year.

Meta-analytic techniques (Chapter 2; Lipsey & Wilson 2001; Gurevitch & Hedges 2001) were used to assess the significance of grazing effects across sites. These techniques were developed to combine the results of multiple studies, which is conceptually and analytically similar to combining results from multiple sites (Gurevitch & Hedges 1999; Yeo [2005] provides a comparable application of these techniques). In the following presentation, I use the notation of Gurevitch & Hedges (2001). Formulae not provided here are reported in Hedges & Olkin (1985), Gurevitch & Hedges (2001), and Lipsey & Wilson (2001).

I performed two analyses, one using the transformed data and one using the residuals after adjusting for overstory effects. I compared the effect sizes from the two analyses to assess how important grazing effects were once overstory effects were taken into account. I also converted the effect sizes into correlation coefficients so that I could compare overstory and grazing effects using the same metric.

The grazing effect size (d_{ij}) of the j^{th} site in the i^{th} class (i.e., year; 1941 or 2004) was calculated as:

$$[3.1] \qquad d_{ij} = \frac{\overline{X}_{ij}^{In} - \overline{X}_{ij}^{Out}}{s_{ij}} J$$

where $\overline{X}_{ij}^{In}$ and $\overline{X}_{ij}^{Out}$ are the mean values inside and outside the exclosure, s_{ij} is the pooled standard deviation of the two groups, and J is a correction factor for small sample sizes. Positive and negative grazing effect sizes indicated larger responses inside and outside of exclosures, respectively. Effect sizes are in standard deviation units and are commonly interpreted as follows: 0.2 is small, 0.5 is medium, 0.8 is large, and >1 is very large (Gurevitch & Hedges 2001). Effect sizes were converted into correlation coefficients (r_{ij}) using the formula:

$$r_{ij} = \frac{d_{ij}}{\sqrt{d_{ij}^2 + \frac{N(N-2)}{n_{ij}^{In} n_{ij}^{Out}}}} \quad [3.2]$$

where N is the total sample size, and n_{ij}^{In} and n_{ij}^{Out} are the sample sizes of each grazing treatment.

Effect sizes from the five sites were combined using a mixed effects model, which assumes random variation in effect size among sites in addition to variation within sites (Becker 1988; Gurevitch & Hedges 2001). The grazing effect size from site j was weighted by the inverse of its variance (w_{ij}^* ; combination of sampling and effect size variances), thus weighting intensely sampled sites more heavily than less intensely sampled sites. The formulae for the cumulated grazing effect size (d_{i+}^*) and its standard deviation (s_{i+}^*) are:

$$d_{i+}^* = \frac{\sum_{j=1}^{k_i} w_{ij}^* d_{ij}^*}{\sum_{j=1}^{k_i} w_{ij}^*} \quad [3.3]$$

$$s_{i+}^* = \sqrt{\frac{1}{\sum_{j=1}^{k_i} w_{ij}^*}} \quad [3.4]$$

where k is the number of sites in class i (Gurevitch & Hedges 2001). For each class, the cumulated grazing effect size was assessed for significance by dividing it by its standard deviation to form a z-statistic, which was then compared to a Z-distribution using $\alpha = 0.05$ (Lipsey & Wilson 2001).

The correlation coefficient for the grazing effect size at each site was converted to a z-score (z_{ij}), and the weighted average z-score (z_{i+}) was calculated as the sum of the product of each z_{ij} and its weight (w_{ij}^{z}):

$$z_{ij} = \frac{1}{2}\ln\left(\frac{1+r_{ij}}{1-r_{ij}}\right) \tag{3.5}$$

$$w_{ij}^{z} = \frac{n_{ij}-3}{\sum_{j=1}^{k_i}\left(n_{ij}-3\right)} \tag{3.6}$$

$$z_{i+} = \sum_{j=1}^{k_i} z_{ij} w_{ij}^{z} \tag{3.7}$$

The common correlation coefficient across sites was estimated by converting z_{i+} back to a correlation coefficient (r_{i+}):

$$r_{i+} = \frac{e^{2z_{i+}}-1}{e^{2z_{i+}}+1} \tag{3.8}$$

Temporal Dynamics

Since the starting coordinates used in 1941 were not available for all lines and the precision with which lines were relocated is unknown, I did not use lines as experimental units to examine the magnitude of change between 1941 and 2004. Instead, I averaged across all undisturbed lines (those not subject to localized disturbances) within each stratum and use these strata means in analyses of temporal dynamics. Strata that were not measured in both years were omitted from analyses of temporal dynamics.

I performed two analyses as described above for grazing effects, one using the transformed data and one using the residuals after adjusting for overstory effects in each year. Similar meta-analytic techniques were also used, except that: i) temporal effect sizes were calculated using the mean values in 1941 and 2004 rather than inside and outside exclosures, and ii) sampling variances were calculated using a formula that accounted for the correlation between 1941 and 2004 data (Becker 1988; Lipsey & Wilson 2001). All else being equal, a site with larger correlation between data, either positively or negatively, will have a smaller variance and therefore a larger weight. Negative temporal effect sizes indicate a decline in the response variable between 1941 and 2004 and positive values indicate an increase between 1941 and 2004. Cumulated temporal effect sizes and standard deviations were calculated for each grazing treatment using formulae [3.3] and [3.4].

Cumulated temporal effect sizes from the two grazing treatments were tested for equality using the homogeneity statistic Q (Gurevitch & Hedges 2001). Between-class homogeneity (Q_B) is calculated as:

$$[3.9] \qquad Q_B = \sum_{i=1}^{2} \sum_{j=1}^{k_i} w_{ij}^* \left(d_{i+}^* - d_{++}^* \right)^2$$

where w_{ij}^* is the weight of the jth site in the ith class (grazing treatment), d_{i+}^* is defined in formula [3.3], and d_{++}^* is the grand cumulated temporal effect size across both grazing treatments. Q_B is distributed as a χ^2-statistic with one degree of freedom, since there are two classes being compared. If Q_B was statistically significant, indicating that the temporal dynamics of a response variable differed between grazing treatments, the cumulated temporal effect size of each grazing treatment was reported. If Q_B was not significant, the grand cumulated temporal effect size was reported.

Results

Overstory Effects

Total species density, herbaceous plant density, and herbaceous cover variables were negatively correlated with overstory vegetation in 1941 and 2004 (Table 3.2; Fig. 3.2). Shrub cover was not correlated with overstory vegetation in 1941 but slightly positively correlated with it in 2004. Correlations with overstory vegetation were stronger in 2004 than 1941 (Table 3.2: r-values; Fig. 3.2: F-values), but predicted values of response variables were smaller (Fig. 3.2: fit lines).

Grazing Effects

Total species density (number of species per line) and herbaceous plant density (number of individual herbaceous plants per line) responded in the same fashion to grazing treatment. Neither variable differed between grazing treatments in 1941, but both were significantly lower inside exclosures in 2004 (Fig. 3.3a,b, 3.4a,b: open symbols; Appendix 3.1). After accounting for overstory effects, neither density differed between grazing treatments in either year (Fig. 3.4a,b: filled symbols).

Shrub cover was low and did not differ between grazing treatments in either year (Fig. 3.3c, 3.4c). Herbaceous cover and forb cover responded in the same fashion to grazing. Neither variable differed between grazing treatments in 1941, but both were significantly lower inside exclosures in 2004, though not after accounting for overstory effects (Fig. 3.3d,f, 3.4d,f; Appendix 3.2). Graminoid cover was significantly higher inside exclosures in 1941 but outside exclosures in 2004 (Fig. 3.3e, 3.4e: open symbols). After accounting for overstory effects, graminoid cover remained higher inside exclosures in 1941 but did not differ between grazing treatments in 2004 (Fig. 3.4e: filled symbols).

Temporal Dynamics

The temporal dynamics of herbaceous plant density differed between grazing treatments ($Q_B = 5.19$, $p = 0.023$): density declined in both grazing treatments, but declined more inside than outside exclosures (Fig. 3.3b, 3.5b: open symbols). After accounting for overstory effects, however, the temporal dynamics of plant density did not differ between grazing treatments ($Q_B = 2.77$, $p = 0.096$) or years (Fig. 3.5b: filled symbol).

The temporal dynamics of graminoid cover also differed between grazing treatments ($Q_B = 4.3$, $p = 0.038$); graminoid cover declined inside exclosures but did not change outside exclosures (Fig. 3.3e, 3.5e: open symbols). After accounting for overstory effects, however, the temporal dynamics of graminoid cover did not differ between grazing treatments ($Q_B = 2.27$, $p = 0.132$) or years (Fig. 3.5e: filled symbol).

For all other response variables, temporal dynamics did not differ between grazing treatments ($p > 0.05$). Species density, herbaceous cover, and forb cover all declined between 1941 and 2004 (Fig. 3.3, 3.5: open symbols), though not after accounting for overstory effects (Fig. 3.5: filled symbols). Shrub cover declined between 1941 and 2004 (Fig. 3.3c, 3.5c: open symbol), but increased after overstory effects were accounted for (Fig. 3.5c: filled symbol).

Discussion

Overstory Effects

This study illustrates that the overstory vegetation is the dominant force affecting understory dynamics in these forests, and that failure to account for its effects can alter the conclusions of a study. Although several variables differed between grazing treatments (Fig. 3.3), many of these differences were no longer significant after accounting for overstory effects (Fig. 3.4, 3.5), indicating that they were due to differences in overstory vegetation between grazing treatments (Chapter 2). Overstory-understory relationships are widely recognized (e.g., Arnold 1950, 1953; Glendening 1952; Smith 1967; McConnell & Smith 1970; Thompson & Gartner 1971; Ffolliott 1983; Mitchell & Bartling 1991; Moore & Deiter 1992), but should be explicitly accounted for when studying factors controlling the understory vegetation in forested ecosystems. Most studies of grazing effects in forest ecosystems have either considered overstory effects to be part of the variability between grazing treatments (e.g., Potter & Krenetsky 1967; Tiedemann & Berndt 1972) or have intentionally sampled non-treed openings (e.g., Schwan et al. 1949; Rambo & Faeth 1999).

A few studies have assessed the importance of overstory effects relative to other factors. Livestock grazing patterns differ between vegetation types, and vegetation responses to grazing therefore also differ between vegetation types (Smith 1967). Logging reduces the tree canopy and therefore has beneficial effects on the understory, though these positive effects may be offset by the accumulation of logging slash (Arnold 1953). In 1975, Clary et al. concluded that intermediate stand densities provide an economically optimal balance between timber and grazing practices. Some studies have suggested that cover of grazing sensitive grasses was positively correlated with overstory vegetation in grazed areas because livestock were less likely to graze beneath the overstory (Arnold 1950; McPherson & Wright 1990), though there was no indication of a positive correlation between overstory vegetation and graminoid cover in my study (Fig. 3.2e).

Correlations between overstory and understory variables were not as strong in my study (Fig. 3.2) as in other studies (Clary 1969; Ffolliott 1983; Mitchell & Bartling 1991; Moore & Deiter 1992). Many of these studies used understory biomass as the response variable (Ffolliott 1983), but the relationship between the overstory and understory biomass may differ in magnitude and sign from the relationship between it and understory cover (McPherson & Wright 1990). In addition, basal area is commonly used as the independent variable (Ffolliott 1983), although some studies have used canopy cover and/or tree density (McPherson & Wright 1990; Mitchell & Bartling 1991; Nemati & Goetz 1995) as in this study.

Overstory effects were stronger than grazing effects: for all variables, the correlation coefficient for overstory effect was larger in absolute value than that for grazing effects using the residuals after accounting for overstory effects (Table 3.2). Also, most variables did not change significantly between 1941 and 2004 (i.e., effect sizes not significantly different than zero; Fig. 3.5) after overstory effects were taken into account. Since overstory-understory relations are so important in these forests, an accurate knowledge of the historical overstory, either via permanent plots (Moore et al. 2004) or via reconstruction techniques (Chapter 5) is essential when seeking to understand historical understory vegetation dynamics in these forests.

Overstory effects were more pronounced in 2004 than 1941, likely due to the growth and increasing canopy of trees (Chapter 2). Overstory-understory relationships were consistently stronger in 2004 (Table 3.2; Fig. 3.2: *F*-values), and the difference between effect sizes calculated using data and those calculated using residuals after accounting for overstory effects were more pronounced in 2004 than 1941 (Fig. 3.4). Southwestern ponderosa pine forests are widely recognized to be at high risk of crown fire, insect attack, and other disturbances because of the increased overstory (Fulé et al. 1997; Moore et al. 2004). This change in life form dominance is irreversible at decadal time-scales without anthropogenic intervention (House et al. 2003). Since the declines in understory vegetation between 1941 and 2004 are largely attributable to overstory effects (Fig. 3.5), they might be reversed by ecological restoration activities which reduce the dominance of overstory vegetation (e.g., Casey 2004; Wienk et al 2004; Moore et al. *in review*).

While the herbaceous plant basal cover measurements in this study are low compared to measurements of foliar cover, they are within the range of values reported from other studies using the line intercept method. Total herbaceous plant cover was < 1% in another northern Arizona ponderosa pine forest (Arnold 1953) and 5-8% in New Mexico ponderosa pine forests (Potter & Krenetsky 1967). A similar range of values has also been recorded in other ecosystems: 0.25% herbaceous cover in a pinyon-juniper woodland (Jameson et al. 1962), 3% perennial grass cover in a desert grassland protected from grazing for 28 years (Schmutz & Smith 1976), and 0.5 to 6.2% perennial grass cover during 45 years of sampling a sagebrush steppe (Anderson & Inouye 2001).

Grazing Effects

Historical factors can have long-term legacy effects (e.g., Abruzzi 1995; Floyd et al. 2003) and alter the successional trajectory of ecosystems. This is particularly true when the legacy effects involve a change to dominance by long-lived woody plants (House et al. 2003), as has been documented in desert grasslands (Glendening 1952; Bock et al. 1984; Roundy & Jordan 1988; Archer 1994) and on these sites, where long-term protection from grazing increased the dominance of the overstory (Chapter 2). Grazing exclosure studies (e.g. Potter & Krenetsky 1967; Smith 1967; Zimmerman & Neuenschwander 1984; Rambo & Faeth 1999) can provide insight into how plant communities are expected to change if grazing ceases.

Although grazing effects were smaller than overstory effects (Table 3.2), some differences were detected between grazing treatments after accounting for overstory effects (Fig. 3.4: filled symbols). Total species density and herbaceous plant density both tended to be higher inside exclosures in 1941 but did not differ between grazing treatments in 2004 (Fig. 3.4: filled symbols). Guenther et al. (2004) found no difference in number of species per square meter between a pinyon-juniper relict area and a nearby area grazed at an unspecified intensity, whereas Stohlgren et al. (1999) found fewer species per square meter in ungrazed than 'moderately grazed' grasslands. In an Arizona ponderosa pine forest, Rambo & Faeth (1999) found lower species richness in meadows ungrazed for 8-9 years than in meadows grazed to > 70% utilization. The effects of grazing on diversity can vary with environmental conditions (Harrison et al. 2003; Pykälä 2004) and among years (Loeser et al. 2005).

The effects of grazing on herbaceous cover also varied between years. In 1941, no effect on total herbaceous cover was found due to counteracting responses of graminoids and forbs (Fig. 3.3), as has also been noted elsewhere (McPherson & Wright 1990; Harris et al. 2003). In 2004, total herbaceous cover was higher in grazed areas, particularly after accounting for overstory effects (Fig. 3.4d), though others have reported no difference between grazing treatments (Zimmerman & Neuenschwander 1984; Stohlgren et al. 1999; Guenther et al. 2004) or, more commonly, higher herbaceous cover in ungrazed areas (Rummell 1951; Schmutz et al. 1967; Smith 1967; Tiedemann & Berndt 1972; Peek et al. 1978; Allen & Bartolome 1989). Costello & Turner (1941) reported that 68% of the 22 sites they measured in ponderosa pine forests had higher plant cover in ungrazed areas.

Temporal Dynamics

Between-class homogeneity (Q_B) did not differ between grazing treatments for most variables, indicating that variables changed in similar fashions in both treatments. On average, species density and herbaceous plant density each declined by 37% between 1941 and 2004, shrub cover by 69%, herbaceous cover by 59%, graminoid cover by 45%, and forb cover by 82%. These declines were attributable to the increasing overstory (Fig. 3.5): most variables did not differ between years after accounting for overstory effects. Shrub cover was higher in 2004 than 1941, but this might be an artifact of the extremely high variability among lines (Fig. 3.3c).

1941 was much wetter than 2004, suggesting that climatic differences could confound the interpretation of temporal changes on these sites. However, plant cover and precipitation may not be directly correlated due to interspecific differences in response to precipitation and to stochastic variation in precipitation patterns (Anderson & Inouye 2001). In addition, the trends exhibited in these data are broadly similar to those recorded on permanent chart quadrats measured a few years earlier (1938, 2002-2003; J.D. Bakker & M.M. Moore, *unpub. data*). Also, overstory-understory relationships explain most of the temporal dynamics on these sites. Climatic differences would most likely be reflected in the residuals, but analyses of temporal effect sizes indicate that most residuals do not differ between years (Fig. 3.5).

Conclusions

This study has provided the first quantitative analyses of how the understory vegetation in southwestern ponderosa pine forests has changed between 1941 and 2004. Most community-level variables were negatively correlated with overstory vegetation in both years. Also, most variables did not differ between grazing treatments in 1941 but were greater outside exclosures in 2004. These differences were primarily due to overstory effects rather than to grazing effects. Graminoid cover was higher inside exclosures in 1941 after controlling for overstory effects, but no other variable differed significantly between grazing treatments. Variables declined significantly between 1941 and 2004, but these declines were due primarily to the increasing dominance of the overstory.

Conditions in 1941 are obviously not 'reference conditions' or 'presettlement' (Moore et al. 1999); between 1912 and 1941, grass cover declined by 25% beneath pine canopies, but almost doubled in open areas (Arnold 1950). Nonetheless, changes between 1941 and 2004 provide insight into the overall trajectory of change that has occurred on these sites in recent decades. In other research (Chapter 4), I examine interspecific differences in temporal dynamics and response to overstory and grazing effects. Future research will examine changes over longer timeframes (e.g., since 1912), including modeling the establishment and growth of the overstory and accounting for overstory-understory relationships (J.D. Bakker and M.M. Moore, *unpub. data*).

References

Abruzzi, W.S. 1995. The social and ecological consequences of early cattle ranching in the Little Colorado River Basin. Human Ecology **23**:75-98.

Allen, B.H., and J.W. Bartolome. 1989. Cattle grazing effects on understory cover and tree growth in mixed conifer clearcuts. Northwest Science **63**:214-220.

Anderson, J.E., and R.S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecological Monographs **71**:531-556.

Archer, S. 1994. Woody plant encroachment into southwestern grassland and savannas: rates, patterns and proximate causes. Pages 13-68 *in* M. Vavra, W.A. Laycock, and R.D. Pieper (editors). Ecological implications of livestock herbivory in the west. Society for Range Management, Denver, CO.

Arnold, J.F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. Journal of Forestry **48**:118-126.

Arnold, J.F. 1953. Effect of heavy selection logging on the herbaceous vegetation in a ponderosa pine forest in northern Arizona. Journal of Forestry **51**:101-105.

Bakker, J.P., R.H. Marrs, and R.J. Pakeman. 2002. Long-term vegetation dynamics: successional patterns and processes. Introduction. Applied Vegetation Science **5**:2-6.

Bakker, J.D., S.D. Wilson, J.M. Christian, X. Li, L.G. Ambrose, and J. Waddington. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications **13**:137-153.

Becker, B.J. 1988. Synthesizing standardized mean-change measures. British Journal of Mathematical and Statistical Psychology **41**:257-278.

Bock, C.E., J.H. Bock, W.R. Kenney, and V.M. Hawthorne. 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. Journal of Range Management **37**:239-242.

Bojorquez Tapia, L.A., P.F. Ffolliott, and D.P. Guertin. 1990. Herbage production-forest overstory relationships in two Arizona ponderosa pine forests. Journal of Range Management **43**:25-28.

Canfield, R.H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry **39**:388-394.

Casey, C.A. 2004. Herbaceous biomass and species composition responses to ponderosa pine restoration treatments. M.Sc. thesis. Northern Arizona University, Flagstaff, AZ.

Chew, R.M. 1982. Changes in herbaceous and suffrutescent perennials in grazed and ungrazed desertified grassland in southeastern Arizona, 1958-1978. American Midland Naturalist **108**:159-169.

Cingolani, A.M., I. Noy-Meir, and S. Diaz. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecological Applications **15**:757-773.

Clapp, E.H. 1936. The major range problems and their solution: a résumé. Pages 1-70 *in* The western range. US Government Printing Office, Washington, DC. Senate Document 199.

Clary, W.P. 1969. Increasing sampling precision for some herbage variables through knowledge of the timber overstory. Journal of Range Management **22**:200-201.

Clary, W.P., W.H. Kruse, and F.R. Larson. 1975. Cattle grazing and wood production with different basal areas of ponderosa pine. Journal of Range Management **28**:434-437.

Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Monographs **30**:129-164.

Costello, D.F., and G.T. Turner. 1941. Vegetation changes following exclusion of livestock from grazed ranges. Journal of Forestry **39**:310-315.

Covington, W.W., and M.M. Moore. 1994. Southwestern ponderosa forest structure: Changes since Euro-American settlement. Journal of Forestry **92**:39-47.

Crawley, M.J., A.E. Johnston, J. Silvertown, M. Dodd, C. de Mazancourt, M.S. Heard, D.F. Henman, and G.R. Edwards. 2005. Determinants of species richness in the Park Grass Experiment. The American Naturalist **165**:179-192.

Dodd, C.J.H., A. McLean, and V.C. Brink. 1972. Grazing values as related to tree-crown covers. Canadian Journal of Forest Research **2**:185-189.

Ffolliott, P.F. 1983. Overstory-understory relationships: southwestern ponderosa pine forests. Pages 13-18 *in* E.T. Bartlett and D.R. Betters (editors). Overstory-understory relationships in western forests. Colorado State University Experiment Station, Fort Collins, CO.

Floyd, M.L., T.L. Fleischner, D. Hanna, and P. Whitefield. 2003. Effects of historic livestock grazing on vegetation at Chaco Culture National Historic Park, New Mexico. Conservation Biology **17**:1703-1711.

Fulé, P.Z., W.W. Covington, and M.M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications **7**:895-908.

Glendening, G.E. 1952. Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. Ecology **33**:319-328.

Gotelli, N.J., and R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters **4**:379-391.

Guenther, D., Stohlgren, T.J., and Evangelista, P. 2004. A comparison of a near-relict site and a grazed site in a pinyon-juniper community in the Grand Staircase-Escalante National Monument, Utah. Pages 153-162 *in* C. van Riper III and K.L. Cole (editors). The Colorado Plateau: cultural, biological, and physical research. University of Arizona, Tucson, AZ.

Gurevitch, J., and L.V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology **80**:1142-1149.

Gurevitch, J., and L.V. Hedges. 2001. Meta-analysis: combining the results of independent experiments. Pages 347-369 *in* S. M. Scheiner and J. Gurevitch (editors). Design and analysis of ecological experiments. Oxford University Press, New York, NY.

Harris, A.T., G.P. Asner, and M.E. Miller. 2003. Changes in vegetation structure after long-term grazing in pinyon-juniper ecosystems: integrating imaging spectroscopy and field studies. Ecosystems **6**:368-383.

Harrison, S., B.D. Inouye, and H.D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. Conservation Biology **17**:837-845.

Hedges, L.V., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, Orlando, FL.

House, J.I., S. Archer, D.D. Breshears, R.J. Scholes, and NCEAS Tree-Grass Interactions Participants. 2003. Conundrums in mixed woody-herbaceous plant systems. Journal of Biogeography **30**:1763-1777.

Jameson, D.A., J.A. Williams, and E.W. Wilton. 1962. Vegetation and soils of Fishtail Mesa, Arizona. Ecology **43**:403-410.

Jameson, D.A. 1967. The relationship of tree overstory and herbaceous understory vegetation. Journal of Range Management **20**:247-249.

Johnson, W.M. 1956. The effect of grazing intensity on plant composition, vigor, and growth of pine-bunchgrass ranges in central Colorado. Ecology **37**:790-798.

Krueger, W.C., and A.H. Winward. 1974. Influence of cattle and big game grazing on understory structure of a Douglasfir-ponderosa pine-Kentucky bluegrass community. Journal of Range Management **27**:450-453.

Leopold, L.B. 1951. Vegetation of southwestern watersheds in the nineteenth century. The Geographical Review **41**:295-316.

Lipsey, M.W., and D.B. Wilson. 2001. Practical meta-analysis. SAGE Publications, Thousand Oaks, CA.

Loeser, M.R., S.D. Mezulis, T.D. Sisk, and T.C. Theimer. 2005. Vegetation cover and forb responses to cattle exclusion: implications for pronghorn. Rangeland Ecology and Management **58**:234-238.

McConnell, B.R., and J.G. Smith. 1970. Response of understory vegetation to ponderosa pine thinning in eastern Washington. Journal of Range Management **23**:208-212.

McLaughlin, S.P. 1978. Overstory attributes, light, throughfall, and the interpretation of overstory-understory relationships. Forest Science **24**:550-553.

McPherson, G.R., and H.A. Wright. 1990. Effects of cattle grazing and *Juniperus pinchotti* canopy cover on herb cover and production in western Texas. American Midland Naturalist **123**:144-151.

Merrick, G.D. 1939. Revegetation of deteriorated range land in northern Arizona. M.A. Thesis. Duke University, Durham, NC.

Miller, G., N. Ambos, P. Boness, D. Reyher, G. Robertson, K. Scalzone, R. Steinke, and T. Subirge. 1995. Terrestrial ecosystem survey of the Coconino National Forest. USDA Forest Service, Southwestern Region, Albuquerque, NM.

Mitchell, J.E., and P.N.S. Bartling. 1991. Comparison of linear and nonlinear overstory-understory models for ponderosa pine. Forest Ecology and Management **42**:195-204.

Moore, M.M., and D.A. Deiter. 1992. Stand density index as a predictor of forage production in northern Arizona pine forests. Journal of Range Management **45**:267-271.

Moore, M.M., W.W. Covington, and P.Z. Fulé. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. Ecological Applications **94**:1266-1277.

Moore, M.M., D.W. Huffman, P.Z. Fulé, W.W. Covington, and J.E. Crouse. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Science **50**:162-176.

Moore, M.M., C.A. Casey, J.D. Bakker, J.D. Springer, P.Z. Fulé, W.W. Covington, and D.C. Laughlin. *In review*. Herbaceous response to restoration treatments in a ponderosa pine forest, 1992-2004. Rangeland Ecology and Management

Naumburg, E., and L.E. DeWald. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. Forest Ecology and Management **124**:205-215.

Nemati, N., and H. Goetz. 1995. Relationships of overstory to understory cover variables in a ponderosa pine/gambel oak ecosystem. Vegetatio **119**:15-21.

Olff, H., and M.E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution **13**:261-265.

Pearson, G.A. 1950. Management of ponderosa pine in the southwest as developed by research and experimental practice. USDA Forest Service, Washington, DC. Agriculture Monograph No. 6.

Peek, J.M., F.D. Johnson, and N.N. Pence. 1978. Successional trends in a ponderosa pine/bitterbrush community related to grazing by livestock, wildlife, and to fire. Journal of Range Management **31**:49-53.

Pickett, S.T.A., M.L. Cadenasso, and S. Bartha. 2001. Implications from the Buell-Small succession study for vegetation restoration. Applied Vegetation Science **4**:41-52.

Potter, L.D., and J.C. Krenetsky. 1967. Plant succession with released grazing on New Mexico range lands. Journal of Range Management **20**:145-151.

Pykälä, J. 2004. Cattle grazing increases plant species richness of most species trait groups in mesic semi-natural grasslands. Plant Ecology **175**:217-226.

Rambo, J.L., and S.H. Faeth. 1999. Effect of vertebrate grazing on plant and insect community structure. Conservation Biology **13**:1047-1054.

Rango, A., L. Huenneke, M. Buonopane, J.E. Herrick, and K.M. Havstad. 2005. Using historic data to assess effectiveness of shrub removal in southern New Mexico. Journal of Arid Environments **62**:75-91.

Roundy, B.A., and G.L. Jordan. 1988. Vegetation changes in relation to livestock exclusion and rootplowing in southeastern Arizona. The Southwestern Naturalist **33**:425-436.

Rummell, R.S. 1951. Some effects of livestock grazing on ponderosa pine forest and range in central Washington. Ecology **32**:594-607.

Schmutz, E.M., C.C. Michaels, and B.I. Judd. 1967. Boysag Point: a relict area on the North Rim of Grand Canyon in Arizona. Journal of Range Management **20**:363-368.

Schmutz, E.M., and D.A. Smith. 1976. Successional classification of plants on a desert grassland site in Arizona. Journal of Range Management **29**:476-479.

Schwan, H.E., D.J. Hodges, and C.N. Weaver. 1949. Influence of grazing and mulch on forage growth. Journal of Range Management **2**:142-148.

Smith, D.R. 1967. Effects of cattle grazing on a ponderosa pine-bunchgrass range in Colorado. US Department of Agriculture, Washington, DC. Technical Bulletin 1371.

Stohlgren, T.J., L.D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications **9**:45-64.

Thompson, W.W., and F.R. Gartner. 1971. Native forage response to clearing low quality ponderosa pine. Journal of Range Management **24**:272-277.

Tiedemann, A.R., and H.W. Berndt. 1972. Vegetation and soils of a 30-year deer and elk exclosure in central Washington. Northwest Science **46**:59-66.

Tilman, D., M.E. Dodd, J. Silvertown, P.R. Poulton, A.E. Johnston, and M.J. Crawley. 1994. The Park Grass Experiment: insights from the most long-term ecological study. Pages 287-303 *in* R.A. Leigh and A.E. Johnston (editors). Long-term experiments in agricultural and ecological sciences. CAB International, Wallingford, UK.

USDA, FS. 2004. Fort Valley Coop Station. http://www.rmrs.nau.edu/weather/stations/ftv_coop/. Accessed November 15, 2004.

USDA, NRCS. 2004. The PLANTS Database, Version 3.5. http://plants.usda.gov. Accessed February 15, 2005.

Valone, T.J., and P. Sauter. 2005. Effects of long-term cattle exclosure on vegetation and rodents at a desertified arid grassland site. Journal of Arid Environments **61**:161-170.

Valone, T.J., M. Meyer, J.H. Brown, and R.M. Chew. 2002. Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. Conservation Biology **16**:995-1002.

Wienk, C.L., C.H. Sieg, and G.R. McPherson. 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. Forest Ecology and Management **192**:375-393.

Yeo, J.J. 2005. Effects of grazing exclusion on rangeland vegetation and soils, east central Idaho. Western North American Naturalist **65**:91-102.

Young, T.P., D.A. Petersen, and J.J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters **8**:662-673.

Zimmerman, G.T., and L.F. Neuenschwander. 1984. Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas-fir/ninebark habitat type. Journal of Range Management **37**:104-110.

Table 3.1. Summary statistics for the Hill plots in northern Arizona. Additional details are in Table 2.1.

	Big Fill	Black Springs	Fry Park	Reese Tank	Rogers Lake
Substrate[1]					
Parent material	Limestone	Limestone / Sandstone	Basalt / Cinders	Mixed Igneous	Basalt / Cinders
Soil	Typic Haploboroll	Mollic Eutroboralf	Typic Argiboroll	Mollic Eutroboralf	Typic Argiboroll
Soil texture	Fine sandy loam	Fine sandy loam	Loam	Sandy loam	Loam
Livestock type					
1939-41	Cattle[2]	Cattle[2]	Cattle	Sheep	Sheep
2002-04	None since 2000	None since ca. 1960	Cattle	None since ca. 1992	Sheep
Average Grazing intensity (AUM/ha)[3]					
1939-41	0.58	1.01	1.35	0.17	-[4]
2002-04	0	0	0.03	0	0.18
Dates sampled					
1941	8/26-9/3	8/5-8/6	8/13-8/22	9/4-9/8	8/7-8/11
2004	9/20-9/27	9/1-9/17	9/8-10/1	9/16-9/17	9/2-9/8
Number of undisturbed lines sampled					
1941	In-80; Out-80	In-40; Out-40	In-80; Out-80	In-20; Out-20	In-40; Out-40
2004	In-71; Out-80	In-37; Out-36	In-80; Out-78	In-12; Out-6	In-40; Out-40

[1] From Miller et al. (1995)

[2] Near sheep driveway

[3] animal unit months per ha; larger values indicate higher grazing intensity. 1939-41 data are from the Fort Valley Archives (US Forest Service, Rocky Mountain Research Station, Flagstaff, AZ) and 2002-04 data are from annual range inspections on file at the Coconino National Forest.

[4] Data not available; classified as 'overgrazed' by Merrick (1939)

Table 3.2. Correlation coefficients (*r*) for overstory effects and grazing effects (both overall effect and using residuals after accounting for overstory effects) on the Hill plots in northern Arizona. Note that negative correlations with overstory indicate a decline in the response variable as the importance of the overstory increases, whereas negative correlations with grazing indicate a response that was larger outside than inside exclosures. Statistically significant ($p \leq 0.05$) correlation coefficients are shown in bold.

Response Variable	Overstory	Grazing	
		Overall	Residuals
Species Density			
1941	**-0.22**	0.10	0.13
2004	**-0.38**	**-0.27**	-0.09
Herbaceous plant density			
1941	**-0.46**	0.04	0.07
2004	**-0.61**	**-0.43**	-0.21
Shrub Cover			
1941	0.05	-0.00	-0.00
2004	**0.19**	0.15	-0.01
Herbaceous Cover			
1941	**-0.48**	-0.01	0.03
2004	**-0.64**	**-0.44**	-0.22
Graminoid Cover			
1941	**-0.34**	**0.31**	**0.29**
2004	**-0.61**	**-0.41**	-0.18
Forb Cover			
1941	**-0.34**	-0.27	-0.14
2004	**-0.40**	**-0.29**	-0.11

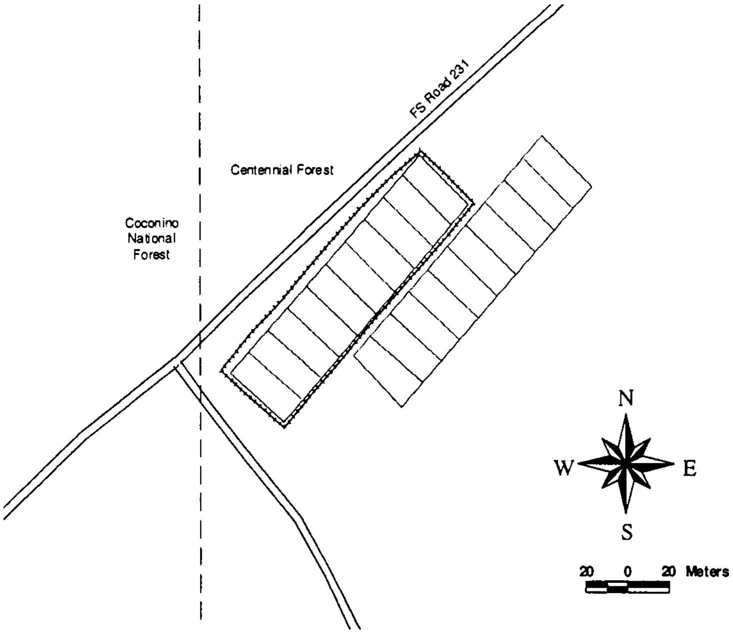


Figure 3.1. Layout of Rogers Lake site, showing the grazing exclosure (hatched lines) and strata boundaries (single lines) inside and outside each grazing treatment. Each stratum was sampled with four 15.24 m (50 ft) lines running parallel to the long axis of the stratum. The X,Y coordinates of the start of each line are relative to the western corner of the stratum. All five sites have a similar layout, differing in number and size of strata.

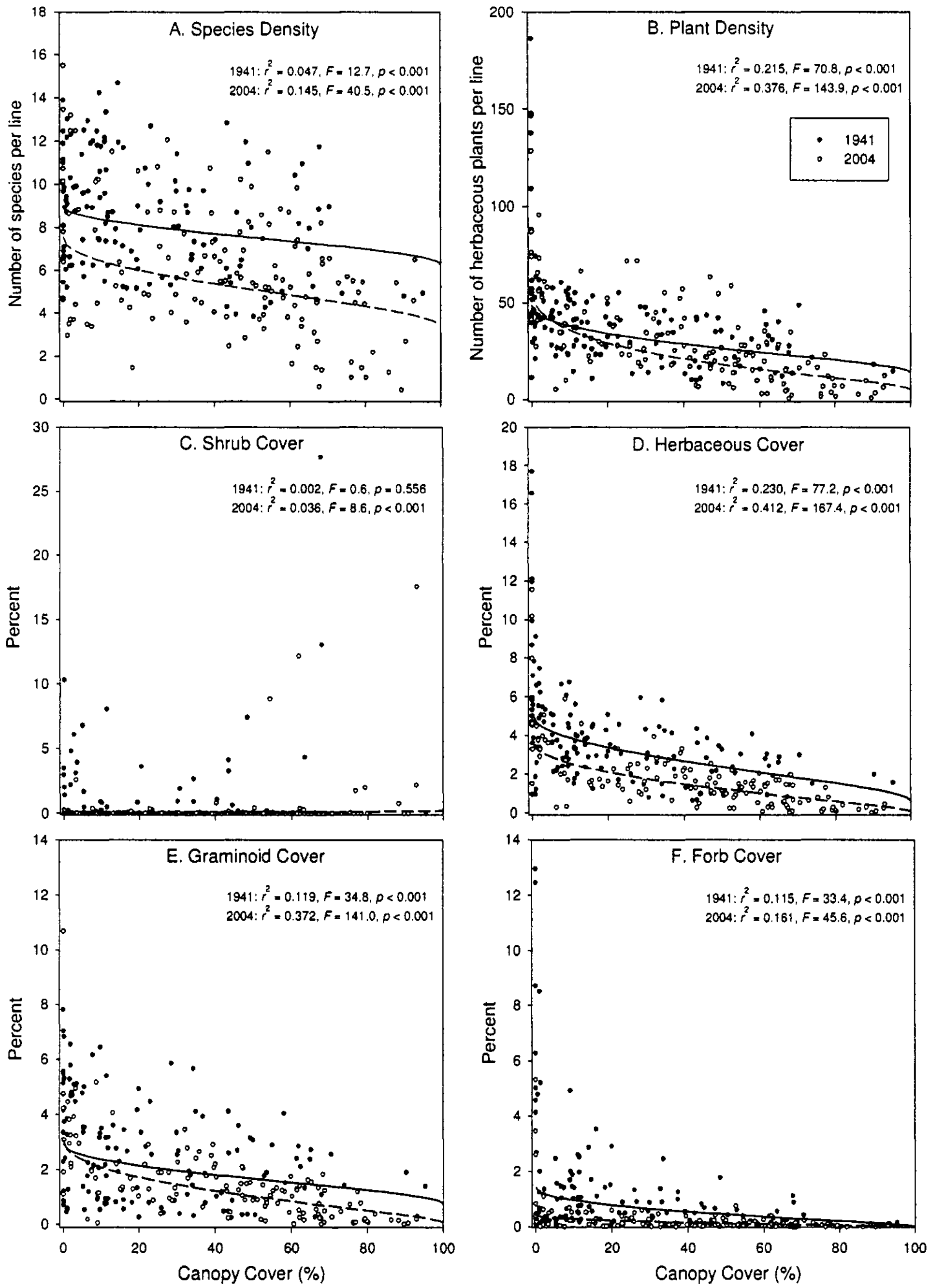


Figure 3.2. Relationships between tree canopy cover and understory variables (species density, herbaceous plant density, and covers of shrubs, all herbaceous plants, graminoids, and forbs) in 1941 (solid lines, filled symbols) and 2004 (dashed lines, open symbols) across five sites in northern Arizona. Data are back-transformed to original units. For clarity, strata means are shown rather than all lines. The reported statistics refer to the multiple regression using tree canopy cover and density as dependent variables, but response variables are plotted against canopy cover since it explained most of the variation in response variables.

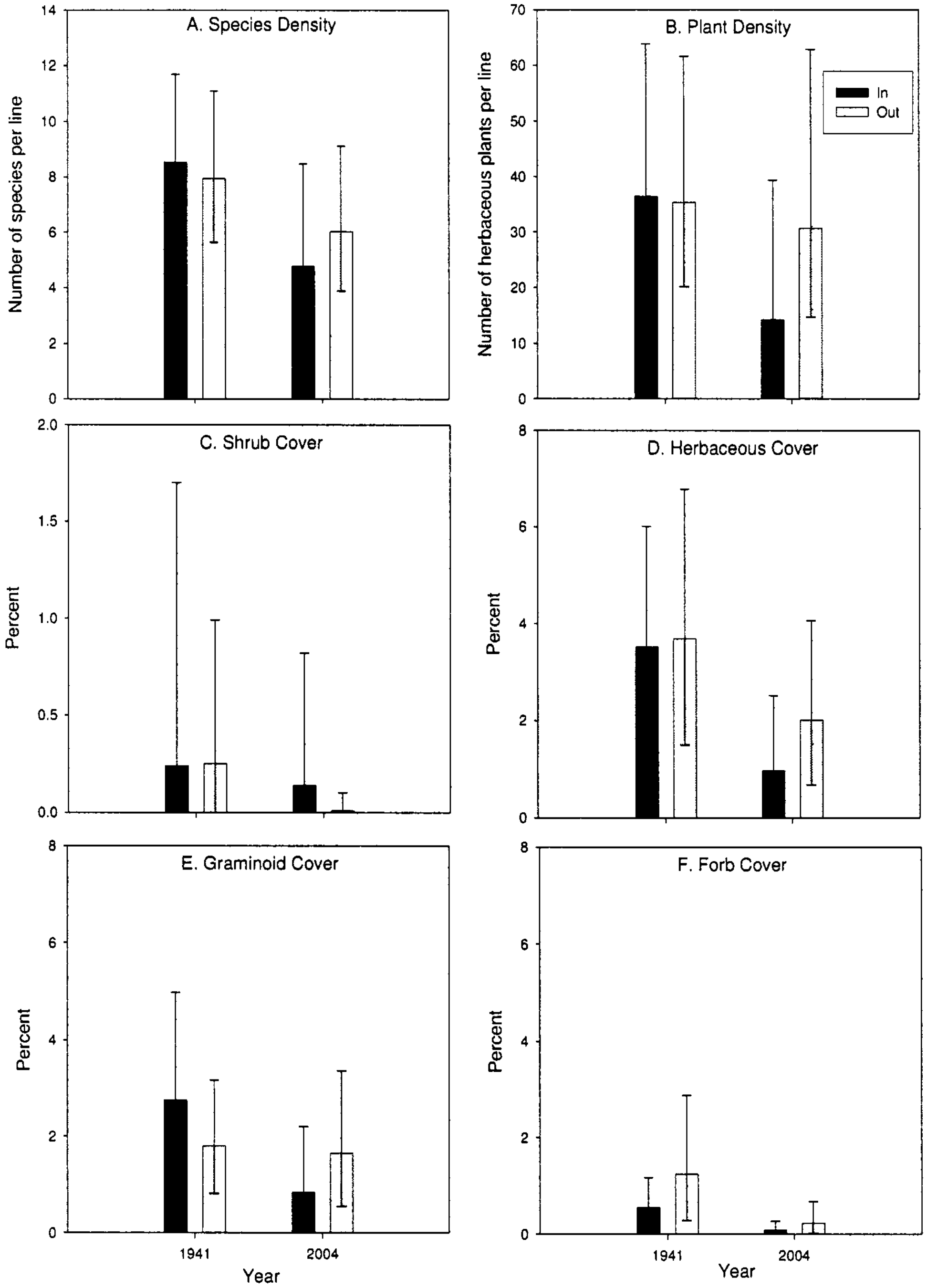


Figure 3.3. Mean (± SD) species density, herbaceous plant density, and covers of shrubs, all herbaceous plants, graminoids, and forbs inside and outside exclosures in 1941 and 2004 across five sites in northern Arizona. These data are not adjusted for overstory effects (Fig. 3.2) but are weighted by the degrees of freedom at each site and back-transformed to original units. Significant differences are shown in Fig. 3.4 (grazing effect sizes) and 3.5 (temporal effect sizes). Untransformed data are summarized in Appendices 3.1 and 3.2.

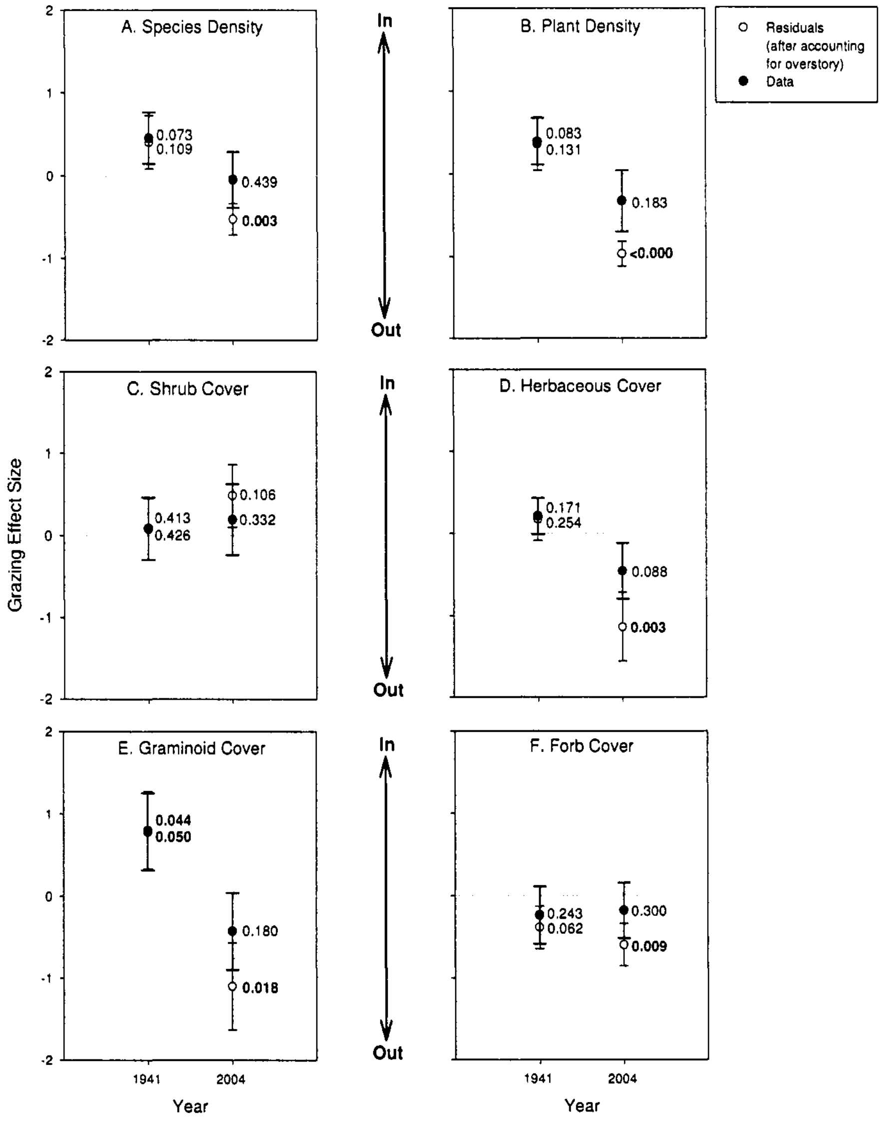


Figure 3.4. Cumulated grazing effect size (mean $d^*_{i+} \pm s^*_{i+}$) for species density (number of species per line), herbaceous plant density (number of herbaceous plants per line), and percent covers of shrubs, all herbaceous plants, graminoids, and forbs in 1941 and 2004 across fives sites in northern Arizona. Positive and negative effect sizes indicate larger responses inside and outside exclosures, respectively, and the horizontal line at zero indicates no difference between grazing treatments. Open symbols indicate effect sizes using transformed data, and filled circles indicate effect sizes calculated from residuals after accounting for overstory effects (Fig. 3.2). The *p*-value reported beside each data point indicates whether that effect size is significantly different from zero; *p*-values ≤ 0.05 are in bold. Effect sizes can be interpreted as follows: 0.2 is small, 0.5 is medium, 0.8 is large, and >1 is very large (Gurevitch & Hedges 2001).

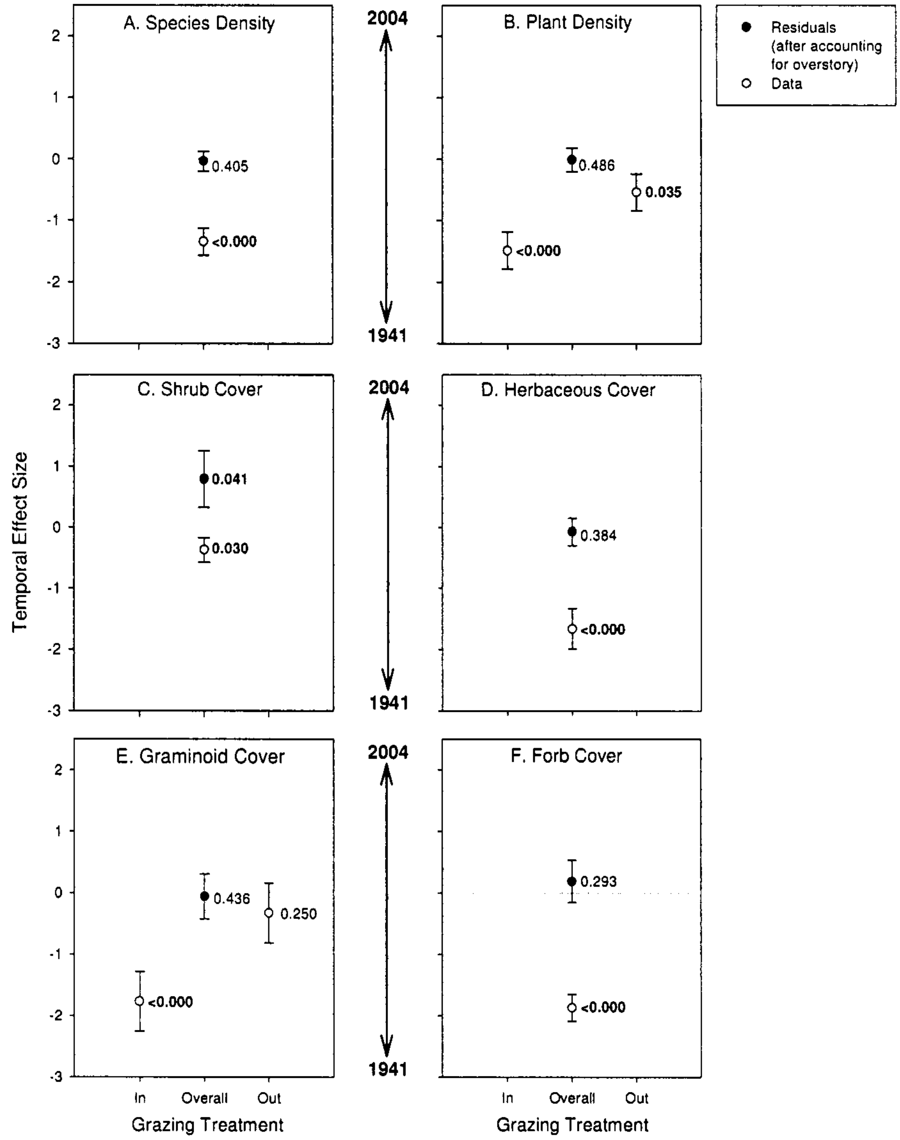


Figure 3.5. Cumulated temporal effect size (mean ± SD) for species density (number of species per line), herbaceous plant density (number of herbaceous plants per line), and percent covers of shrubs, all herbaceous plants, graminoids, and forbs at five sites in northern Arizona. Effect sizes are reported across both grazing treatments ($d^*_{++} \pm s^*_{++}$) unless they differed between grazing treatments, in which case the effect size for each treatment ($d^*_{i+} \pm s^*_{i+}$) is reported. Negative and positive effect sizes indicate larger responses in 1941 and 2004, respectively, and the horizontal line at zero indicates no difference between years. Open symbols indicate effect sizes using transformed data, and filled circles indicate effect sizes calculated from residuals after accounting for overstory effects (Fig. 3.2). The p-value reported beside each data point indicates whether that effect size is significantly different from zero; p-values $\leq$ 0.05 are in bold. Effect size interpretation is as reported in Fig. 3.4.

Chapter 4

Indicator Species of Temporal Dynamics, Livestock Grazing Effects, and Overstory Vegetation in Southwestern Ponderosa Pine Forests

Preface

Understory community-level variables (species density, total herbaceous plant cover, etc.) are much more strongly affected by the overstory than by grazing treatments (Chapter 3), but individual species may not respond identically to these forces. In this chapter, I identify understory species that are indicators of grazing treatments, overstory condition, and long-term temporal dynamics in southwestern ponderosa pine forests.

Abstract

Community-level variables may mask interspecific differences in response to disturbance. I used Indicator Species Analysis (ISA) to identify indicators of grazing treatments, overstory conditions, and temporal dynamics in southwestern ponderosa pine (*Pinus ponderosa*) forests. In doing so, I describe how to correctly permute data for ISA, use meta-analytic techniques to assess the consistency of indicators by combining results from multiple sites, and evaluate a simplified ISA based on binary (presence/absence) data. Combining data from five sites reduced the number of significant indicators by 20-25%. Species that occurred at multiple sites were more likely to be indicators than those present at a single site. The simplified ISA yields very similar results as those from the

classical ISA, but requires much less data and could easily be applied in meta-analyses of published literature. Three times more species were indicators of 1941 than 2004, indicating that the abundance and frequency of many species declined during this interval. More species were indicators of grazing treatments in 1941 and of overstory effects in 2004, suggesting that the dominant structuring force affecting understory species in this ecosystem has changed over time. Some species responded mostly to grazing (e.g., *Elymus elymoides*, *Muhlenbergia montana*), some to overstory effects (e.g., *Bromus tectorum*, *Carex* spp., *Sporobolus interruptus*), and some to both forces (e.g., *Erigeron divergens*, *Bouteloua gracilis*, *Trifolium longipes*, *Hesperostipa comata*, *Festuca arizonica*).

Introduction

Community-level variables are commonly used (e.g., Chapter 3) and indicate broad ecological patterns (Magurran 2004), but often mask interspecific differences (Weiss & Reice 2005). Similarly, multivariate methods permit analyses of the response of the entire community (e.g., Laughlin et al. 2004) but, by themselves, do not clarify whether these responses are being driven by a subset of species in the community. In-depth analyses are often required to identify differences in response between groups of species (functional groups) or individual species.

Plants have been classified into functional groups for decades (e.g., Arnold 1955; Dansereau & Lems 1957; Knight & Loucks 1969). Basic distinctions among graminoid, forb, shrub, and tree life forms permit comparisons among widely disparate ecosystems (Lavorel et al. 1997, 1999; Diaz et al. 1999; Pillar 1999). Species can also be classified on the basis of their expected responses to the dominant structuring processes of an ecosystem (Landsberg et al. 1999; Lavorel et al. 1997, 1999; McIntyre et al. 1999; Kahmen & Poschlod 2004), such as by classifying plants as grazing tolerant or grazing resistant (e.g., Arnold 1950; Adler et al. 2005). However, the importance of structuring processes can vary with the extent, frequency, and selectivity of disturbances (Hadar et al. 1999; McIntyre et al. 1999). If the structuring disturbance varies spatially or temporally, or if multiple disturbances structure the community, a single classification scheme with broad applicability may not exist. For example, frequent surface fires were a dominant structuring process historically in southwestern ponderosa pine (*Pinus ponderosa*) forests, but have been excluded from the ecosystem for more than a century (Pyne 2001). At present, plants in these forests are growing in a very different environment containing thick litter layers and heavy shade (Naumburg & DeWald 1999), suggesting that the dominant structuring process at present might be more accurately described by the different environmental conditions and the *absence* of fire (Moir 1966).

The identification of species that indicate or are associated with particular habitats or ecological conditions also has a long ecological history (e.g., Korstian 1917). An indicator species is defined as "an organism whose characteristics (e.g., presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest" (Landres et al. 1988:317). Zacharias & Roff (2001) make a helpful distinction between indicators of composition and of condition. Composition indicators are used to characterize habitats or communities and, therefore, are most useful in landscape-scale assessments (e.g., Salovaara et al. 2004). Condition indicators are used to monitor environmental change within specific habitats or communities and are the focus of this paper (though for simplicity I simply refer to indicators throughout the paper).

By definition, the identification of indicator species requires comparisons between two or more groups. These groups might consist of experimental treatments within a site (e.g., inside and outside a grazing exclosure), different sites, or measurements of the same site at different times. When more than two groups are sampled, the identification of significant indicators will depend on the scale at which comparisons are conducted (Dufrêne & Legendre 1997). For example, consider a study of three groups (*a*, *b*, *c*). Species may occur in one group, two groups (*a* and *b*, or *a* and *c*, or *b* and *c*), or all three groups. A species that occurs in *a* and *b* may not be an indicator of either but may distinguish *a* and *b* from *c*.

To have broad relevance, indicators should be associated with the same group at multiple sites. However, surprisingly few studies have investigated the consistency of indicator species. Studies of benthic communities and lepidopterans have concluded that actual indicator taxa are of limited applicability due to strong spatiotemporal heterogeneity (Zacharias & Roff 2001; Bustos-Baez & Frid 2003; Frid 2003; Poyry et al. 2005; Weiss & Reice 2005). I am unaware of any assessments of the consistency of terrestrial vascular plant indicator species, but suspect that consistent indicators may be more common due to their sessile growth habit. Also, terrestrial plant communities are generally less diverse than the macrobenthos, so species are more likely to occur at multiple sites (cf. Saetersdal et al. 2005).

The methods used to sample communities can also affect which, if any, species are identified as indicators. In benthic studies, logistic constraints prevent the collection of more than a few samples per site (e.g., Weiss & Rice 2005), so efforts to identify indicators have low power. In terrestrial plant communities or other environments where multiple samples per site can be easily obtained, indicators can be identified and assessed using statistically rigorous procedures such as Indicator Species Analysis (ISA; Dufrêne & Legendre 1997).

The focus of this chapter is the identification of indicator species of overstory conditions, grazing treatments, and temporal dynamics in southwestern ponderosa pine forests. In identifying these indicators, I describe how to correctly permute data for ISA, use meta-analytic techniques to assess the consistency of indicators by combining results from multiple sites, and evaluate a simplified ISA based on binary (presence/absence) data.

Indicator Species Analysis

While several methods of identifying indicator species have been described in the literature (Hill 1979; Dufrêne & Legendre 1997), one of the most appealing methods is Indicator Species Analysis (ISA). Advantages of ISA are that it accounts for both the abundance and frequency of species and is calculated independently for each species in the assemblage (Dufrêne & Legendre 1997; McGeoch & Chown 1998). In addition, ISA can be applied to any typology (classification of experimental units into groups), including *a priori* classifications such as the levels of an experimental factor. ISA involves the calculation of an Indicator Value (*IV*) for each species in each group, and the use of Monte Carlo randomizations to assess the significance of each *IV*.

Indicator Values

The classical Indicator Value (*IV*) of species *i* in group *j* is the product of its abundance (specificity; A_{ij}) and frequency (fidelity; B_{ij}):

[4.1] $$A_{ij} = \frac{\bar{x}_{ij}}{\sum_j \bar{x}_{i\cdot}}$$

[4.2] $$B_{ij} = \frac{n_{ij}}{n_{\cdot j}}$$

[4.3] $$IV_{ij} = A_{ij} \times B_{ij} \times 100$$

where $\bar{x}_{ij}$ is the mean cover of species *i* within group *j*, $\sum_j \bar{x}_{i\cdot}$ is the sum of the mean cover of species *i* in all groups, n_{ij} is the number of plots in group *j* occupied by species *i*, and $n_{\cdot j}$ is the total number of plots in group *j*. Formulae are described in more detail in Dufrêne & Legendre (1997) and McCune & Grace (2002).

IV_{ij} ranges between 0 (species *i* is absent from group *j*) and 100 (species *i* occurs on all plots within group *j* and does not occur in other groups). Uncommon species will have low B_{ij} values and therefore low IV_{ij} values that are unlikely to be statistically significant. Ubiquitous species (i.e., species present in all groups at a given level of the typology) have high B_{ij} values and therefore higher IV_{ij} values, but are unlikely to be statistically significant as permutations of the data (see below) will also yield high B_{ij} values. The highest IV_{ij} values will occur for species that are much more common in one group within the typology. Dufrêne & Legendre (1997) suggest that species *i* be considered a 'strong' indicator of group j if $IV_{ij} > 25$. This occurs, for example, when it occurs on at least 50% of the plots in group j and also has at least 50% of its total abundance in group j.

Dufrêne & Legendre (1997) suggest identifying the group j in which $IV_{i.}$ is at its maximum and assessing the significance of this maximum $IV_{i.}$ via a permutation test. However, it frequently happens that the maximum $IV_{i.}$ does not occur in the same group j at all sites; if species i is not a significant indicator of group j, the maximum $IV_{i.}$ may be equally likely to occur in another group. Therefore, I propose a modification to these steps: i) assess the statistical significance of IV_{ij} for all groups at all sites, ii) combine the IV_{ij} from all sites where species i occurred, and iii) identify the maximum $IV_{i.}$ based on the combined data. The second step can, of course, be omitted if a single site is being studied.

The statistical significance of IV_{ij} is assessed via Monte Carlo randomizations. Computer intensive permutation tests are increasingly popular methods (Manly 1997) but, as with all statistical methods, can be used incorrectly. Anderson & ter Braak (2003) note that exact permutation tests for multi-factorial analysis of variance (ANOVA) require that: i) the correct exchangeable units be permuted, and ii) permutations be restricted to occur within levels of terms of smaller or equal order as the term being tested. These requirements also apply to permutation tests of IV_{ij}. The correct exchangeable units in a permutation test of a factor are identified by the term that would form the denominator mean-square of the F-ratio to test that factor in an ANOVA. For example, if a single data vector is obtained from each plot within each group (e.g., level of a factor), the plots form the error term for the analysis of the factor and therefore are the correct exchangeable units. However, if plots are subsampled, the subsamples must either be permuted together or pooled to yield a single data vector per plot (e.g., Peterson & McCune 2001). If the individual subsamples were permuted, the variability among subsamples would be erroneously combined with the variability among plots.

In this study, the overstory (tree) and understory (herbaceous and shrub) vegetation were sampled in two years on multiple lines inside and outside a grazing exclosure at each of five sites. As described below, different analyses were required to identify understory species that were indicators of overstory condition (in the open or under the canopy) and of grazing treatment (inside or outside exclosure) and year (1941 or 2004).

Analyses of overstory condition sought to relate the abundance and frequency of understory species to the overstory canopy above the lines on which they occurred, so lines were the correct exchangeable units for these analyses. Including lines from areas where species *i* did not occur would have deflated the calculated *IV*, and would have confounded overstory-related differences with differences in species occurrence among grazing treatments and/or sites. Therefore, I analyzed the data from all site x grazing combinations where species *i* occurred together.

Grazing treatments were nested within sites, so permutations to assess the significance of indicators of grazing treatments also had to be restricted to occur within sites. The same logic applied to analyses of temporal dynamics. These restrictions cannot currently be specified in programs that calculate *IV* (PC-ORD [v. 4.35; McCune & Mefford 1999], IndVal [v. 2.1; Dufrêne 2004], and Appendix 4.1), so I analyzed each site separately and combined the results across sites using meta-analytic techniques.

In conventional meta-analyses (e.g., Chapters 2 and 3), effect sizes calculated at k sites are combined to yield a cumulated effect size. Since effect sizes cannot be calculated for *IV*s, I combined the p-values using a weighted Z-transform (Whitlock 2005). This approach is particularly appropriate for combining multiple tests of the same hypothesis (Rice 1990). The p-value for species i in group j (a grazing treatment or year) at site k, as determined by Monte Carlo randomizations, was converted to a Z-score, and the Z-scores from all sites were combined using the formula:

$$Z_{ijk}^{w} = \frac{\sum_{k=1}^{s} w_{\cdot jk} Z_{ijk}}{\sqrt{\sum_{k=1}^{s} w_{\cdot jk}^{2}}} \tag{4.4}$$

where $w_{\cdot jk}$ is the weight (sample size) for group j at site k, and s is the total number of sites at which species i was present. Z_{ijk}^{w} was converted back to a p-value for the combined effect. The weighted mean IV ($\overline{IV}_{ij\cdot}$) was calculated by combining the *IV*s for species i from group j at all sites where it occurred. The group j in which the weighted mean $\overline{IV}_{ij\cdot}$ was at a maximum ($\overline{IV}_{i\cdot\cdot}$) was identified. Species i was considered to be an indicator of this group if the combined p-value for $\overline{IV}_{i\cdot\cdot}$ was statistically significant using $\alpha = 0.05$.

Analysis of Presence / Absence Data

The classical ISA described above has been used in numerous studies (e.g., Peterson & McCune 2001; Salovaara et al. 2004; Poyry et al. 2005; Rentch et al. 2005) and is the primary method used in this study, but the calculation of IV_{ij} requires the raw data (abundance of species i on every plot). Since raw data are generally unpublished, the classical ISA is therefore of limited utility for calculating IV_{ij} from published literature.

An alternate simplified ISA has been proposed which is calculated using presence/absence data (Dufrêne & Legendre 1997; Dufrêne 2004). These data are easily summarized in tables or appendices; all that needs to be reported is the total number of plots in group *j* and the number of plots within group *j* on which species *i* occurs. The simplified ISA could therefore be utilized in meta-analyses of published literature. However, I am unaware of any published comparisons of the results of classical and simplified ISAs.

For the simplified ISA, formula [4.1] for specificity (A_{ij}) is modified to:

$$[4.5] \qquad A_{ij} = \frac{n_{ij}}{n_{i.}}$$

where n_{ij} is the number of plots in group *j* occupied by species *i*, and $n_{i.}$ is the total number of plots occupied by species *i*. B_{ij} and IV_{ij} are calculated as above. In practice, this can be implemented by transforming the data to binary data (0 = absence, 1 = presence) and calculating the classical ISA on the transformed data. If a species is equally abundant on all plots where it occurs, the classical and simplified ISAs yield identical results. As variability in abundance among plots increases, the classical and simplified ISAs give differing weights to A_{ij}, and therefore yield different results.

Methods

Field Sampling

This study was conducted on the Hill plots, a series of five grazing exclosures established in northern Arizona in 1912. Exclosures were built to prevent grazing by livestock but not by wild ungulates (Fig. 2.1). Additional details about the sites, exclosures, and grazing histories are provided in Tables 2.1 and 3.1.

The vegetation inside and outside of each exclosure was sampled in 1941 and 2004 using the line transect method (Canfield 1941). Each area was divided into 10-20 contiguous strata, and each stratum was sampled with 2-4 lines (Fig. 3.1). Sampling intensity varied among sites and years (Table 3.1). In 1941, lines were located by randomly selecting X,Y starting coordinates relative to the origin of each stratum. In 2004, the same starting coordinates were used where possible (79% of lines), otherwise new random coordinates were generated. Lines were 15.24 m (50 ft) long and oriented parallel to the long axis of the stratum. Overstory canopy cover was measured as the proportion of the line directly beneath a tree crown (see Chapter 2 for details). 1941 data were collected by G. Glendening and published in summary form by Arnold (1950); to my knowledge, data about individual species have never been published.

Five strata outside the exclosure at Black Springs were destroyed by an interstate highway in the 1950s, so replacement strata were established on the other side of the exclosure. Several sites received silvicultural treatments between 1941 and 2004 (Table 2.1), but these generalized disturbances were applied inside and outside of the exclosures and are considered part of the intersite variability. Areas subject to localized disturbances (powerline right-of-ways, etc; Table 2.1) were omitted from analyses. In total, 520 undisturbed lines were measured in 1941 and 480 lines in 2004.

For herbaceous plants (graminoids and forbs), the rooted portions of live plants directly underneath the line were measured. For shrubs, the plant canopy was projected down onto the line and this distance was measured. Distances were recorded to the nearest ~ 0.3 cm (0.01 foot) in 1941 and to the nearest 0.25 cm in 2004. The recorded distances were summed and divided by the line length to yield the percent cover of each species on each line.

Taxonomy

All nomenclature is based on the USDA NRCS plants database (2004), and species nativity follows USDA NRCS (2004) and Kearney & Peebles (1942). Species lists from 1941 were available for all sites. Most species were identified to species or genus, though some were identified by common names (a few others were assigned unknown codes; these were omitted from further analyses). Historical nomenclature was rectified using several lines of evidence. First, herbarium specimens were consulted for synonymy and common names. At least 45 specimens collected by G. Glendening on these sites in 1941 are housed in the herbarium at Arizona State University (Tempe, AZ), and other specimens collected from the region in the early 1900s are housed in various southwestern herbaria. Second, synonymy was traced via early reports (Read 1915; Talbot & Hill 1923; Merrick 1939), floras (Hitchcock 1971; Kearney & Peebles 1942), and the USDA NRCS (2004) plants database. Third, species lists compiled for other studies on these sites (unpublished data in Fort Valley Archives, Rocky Mountain Research Station, USDA Forest Service) were consulted.

To be conservative in my analysis of changes between 1941 and 2004, I combined species that are difficult to distinguish. In 1941, for example, one researcher recorded *Erigeron formosissimus* but no *Erigeron speciosus* at a site while another researcher recorded *E. speciosus* but no *E. formosissimus* at the same site. Since these species have very similar morphologies, both researchers were likely referring to the same species. It is unclear which researcher was correct in their identification, however, so I combined these species and refer to them as *E. formosissimus*, which was more commonly recorded than *E. speciosus* (Table 4.1). Plants that were classified to the genus level in 1941 were also combined at the genus level in 2004 (Table 4.1). For simplicity, however, I refer to species throughout the paper.

Calculation of Indicator Values

I calculated indicator values (IV_{ij}) using an *IV* function (Appendix 4.1) written for R software (R Development Core Team 2005). Calculated *IV*s were assessed for statistical significance using Monte Carlo randomizations with 9999 permutations.

Comparisons of the results of this *IV* function with results from PC-ORD and IndVal indicated that all three programs yield identical *IV*s, but do not always yield similar *p*-values. For some species, *p*-values obtained via the *IV* function are lower than those obtained via PC-ORD and IndVal. This discrepancy appears to be due to the fact that the *IV* function compares the calculated IV_{ij} against the permutation-based IV_{ij}, whereas PC-ORD and IndVal compare the calculated maximum $IV_{i.}$ against the maximum $IV_{i.}$ from each permutation. As such, PC-ORD and IndVal are actually answering a different hypothesis (What is the probability of obtaining, in any group, an $IV_{i.}$ equal to or greater than the calculated value?) than the *IV* function (What is the probability of obtaining, in group *j*, an IV_{ij} equal to or greater than the calculated value?). The hypothesis addressed by the *IV* function is more directly relevant to this study.

The analyses of overstory effects identified indicator species of open areas (no tree canopy above line) and shaded areas (tree canopy > 0% above line). To minimize the effect of grazing treatments on overstory analyses, the analysis of each species was restricted to the site x grazing combinations on which it occurred. All lines from these combinations were analyzed together since lines were the exchangeable units.

Analyses of indicator species of grazing treatments and years were conducted separately for each site so that permutations were restricted to occur within sites. Comparisons of grazing treatments were not conducted for the Black Springs and Reese Tank sites in 2004. The Black Springs site was omitted because it had not been grazed for about four decades (Table 3.1) and differences in herbaceous vegetation due to grazing impacts were therefore expected to be minimal. The Reese Tank site was omitted because it had not been grazed in more than a decade and because it was sampled at a much lower intensity than the other sites due to a prescribed fire on about half of the site in 1999 (Table 2.1).

For analyses of temporal dynamics, I did not use lines as experimental units because the starting coordinates used in 1941 were not available for all lines and because the precision with which lines were relocated is unclear. Instead, I averaged across all undisturbed lines within each stratum and use these strata means to identify species as indicators of 1941 or 2004. Strata that were not sampled in both years were omitted from analyses of temporal dynamics.

For species *i*, the data for group *j* from all sites where that species occurred were combined by calculating the weighted mean *IV* ($\overline{IV}_{ij\cdot}$) and by using the weighted *Z*-transform (Whitlock 2005) to combine *p*-values. The group in which the weighted mean *IV* was maximized ($\overline{IV}_{i\cdot\cdot}$) was identified. The indicator status of species *i* with respect to this group was then assessed by examining the statistical significance of $\overline{IV}_{i\cdot\cdot}$, its magnitude, and the consistency with which it indicated that group across sites. Statistical significance was assessed using $\alpha = 0.05$. Species were considered to be 'strong' indicators if $\overline{IV}_{i..} > 25$ (Dufrêne & Legendre 1997). Consistency was determined by examining whether species that were significant indicators overall (combined p-value $\leq$ 0.05) were significant indicators of opposing groups at individual sites (p-value $\leq$ 0.05 for group j at one site and for the opposite group at another site).

To assess the effect of combining data from multiple sites on the number of indicators identified, I compared the number of species that were indicators of grazing treatments and years at individual sites with the number that were indicators once data from all sites were combined. I also used contingency analysis to assess the relationship between the number of sites a species occurred at and the likelihood it was a significant and consistent indicator overall.

The data used to identify indicators of grazing treatments in 1941 and 2004 were transformed into binary (presence/absence) data and simplified ISAs were conducted for each site. The simplified and classical ISAs were compared by i) noting whether they identified the same group as having the maximum IV and ii) tallying the number of species that were identified as statistically significant indicators by either or both methods. These comparisons were conducted using individual tests (each species in each site and year; 430 tests total) and combined tests (each species in each year, all sites combined; 197 tests total).

Results

Species Richness and Exotic Species

One hundred twenty-seven species were identified across all sites and years. In 1941, 88 species were identified, including a single individual of one exotic species

(*Verbascum thapsus*). Arnold (1950) noted that *Poa pratensis*, another exotic species, occurred at some sites, but since it was not distinguished from *Poa fendleriana* during the 1941 data collection, it is unclear what proportion it comprised of the *Poa* spp. recorded that year.

In 2004, 113 species were identified, including 12 exotics: *Agropyron cristatum*, *Atriplex rosea*, *Bromus tectorum*, *Convolvulus arvensis*, *Erodium cicutarium*, *Kochia scoparia*, *Lactuca serriola*, *Linaria dalmatica*, *Salsola tragus*, *Taraxacum officinale*, *Tragopogon dubius*, and *Verbascum thapsus*. Several other exotic species (*Poa compressa*, *Poa pratensis*, *Polygonum aviculare*) were also identified but were combined with congenerics to permit comparisons with 1941 data (Table 4.1).

Indicators of Overstory Condition

Fifty species were indicators of overstory condition in at least one year (Table 4.2). Although relatively few lines were in the open (29% in 1941, 17% in 2004), 30 species were significant indicators of these areas in one year and nine were significant indicators in both years (Table 4.2). Eighteen species were strong indicators in at least one year (Fig. 4.1). Notable indicators of areas in the open included *Antennaria* spp., *Bouteloua gracilis*, *Erigeron divergens*, and *Sporobolus interruptus*.

Most lines were under tree canopies. Nine species were indicators of these areas in one year, and two were significant indicators in both years (Table 4.2). *Festuca arizonica* was the only strong indicator of these areas (Fig. 4.1), though other indicators included *Bromus tectorum*, *Carex* spp., *Cirsium* spp., and several legumes.

No species were significant indicators of one overstory condition in 1941 and the opposite in 2004.

Indicators of Grazing Treatments

Seventy-two species were significant indicators of grazing treatments at one or more sites in at least one year. Combining the results from all sites reduced the number of significant indicators by 25%, to 54 (Table 4.3). Three dominant graminoids (*Bouteloua gracilis* and *Koeleria macrantha* in 1941, *Muhlenbergia montana* in 2004) were inconsistent indicators: the combined p-values were significant, but they were significant indicators of conditions inside exclosures at some sites and conditions outside exclosures at other sites. *Blepharoneuron tricholepis* and *Poa* spp. switched from being indicators of conditions inside exclosures in 1941 to indicators of conditions outside exclosures in 2004.

Eighteen species were consistent indicators of conditions inside exclosures in one year and four were consistent indicators in both years (Table 4.3). Notable indicators of conditions inside exclosures included *Rosa woodsii*, *Artemisia carruthii*, *Festuca arizonica*, and *Hesperostipa comata* (Table 4.3; Fig. 4.2). Twenty-one species were consistent indicators of conditions outside exclosures in one year, and six were consistent indicators in both years (Table 4.3). Notable indicators of conditions outside exclosures included *Elymus elymoides*, *Gutierrezia sarothrae*, *Antennaria* spp., and *Trifolium longipes* (Table 4.3; Fig. 4.2).

Species that occurred at a single site were less likely to be indicators of one grazing treatment over the other, whereas species that occurred at multiple sites were more likely to be significant and consistent indicators of grazing treatments (Fig. 4.4a).

In 95.3% (410 of 430) of individual tests (species in each site and year), the classical and simplified ISAs identified the same grazing treatment as having the maximum *IV*. *IV*s were lower for the simplified method than the classical method, but in no test did the two methods identify opposite grazing treatments as statistically significant indicators. In 135 tests, species were identified as statistically significant indicators by both methods. In 19 tests, species were identified as significant indicators by the classical ISA only, and in two tests, species were identified as significant indicators by the simplified ISA only.

When the results from all sites were combined, the two methods identified the same grazing treatment as having the maximum *IV* in 95.9% (189 of 197) of tests. Once again, in no test did the two methods identify opposite grazing treatments as statistically significant indicators. In 63 tests, species were identified as statistically significant indicators by both methods, compared to five by the classical ISA only, and one by the simplified ISA only.

Indicators of 1941 or 2004

Sixty-four species were significant indicators of one year over the other at one or more sites. Combining the results from all sites reduced the number of significant indicators by 20%, to 51 species (Table 4.4). Two species (*Elymus elymoides* and *Poa* spp.) were inconsistent indicators.

Thirty-six species were consistent indicators of 1941 (Table 4.4), including *Achillea millefolium*, *Muhlenbergia montana*, *Antennaria* spp., *Hymenopappus filifolius*, *Artemisia carruthii*, and 20 other strong indicators (Fig. 4.3). Thirteen species were indicators of 2004 (Table 4.4; Fig. 4.3). Only three species (*Carex* spp., *Muhlenbergia minutissima*, *Verbascum thapsus*) that were indicators of 2004 were recorded in both years; covers of these species increased between 1941 and 2004, while covers of most other species declined (Table 4.4). Several indicators of 2004 were exotic species (*Linaria dalmatica*, *Taraxacum officinale*, *Bromus tectorum*, and *Verbascum thapsus*).

Species that occurred at a single site were less likely to be significant indicators of one year over the other, whereas species that occurred at multiple sites were more likely to be significant and consistent indicators (Fig. 4.4b).

Discussion

Utility of Indicator Species Analysis

Combining the results from multiple sites reduced the number of significant indicators by 20-25%, suggesting that some identifications of indicators at individual sites were spurious. Consistency could obviously not be assessed for species that occurred at a single site; the indicator status of these species should be regarded as tentative unless supported by published data or until studies are conducted at additional sites. These species were less likely than expected to be indicators (Fig. 4.4), possibly because they were sampled at lower intensities than species that occurred at multiple sites.

Conversely, species that occurred at multiple sites were more likely than expected to be indicators (Fig. 4.4). This is partly because the outcome of individual tests may differ even if they are examining identical underlying effects. Gurevitch & Hedges (1999) note that there is only a 68% chance that two reasonably powerful tests (power = 0.80) will arrive at the same conclusion about whether an effect is significant. By combining tests, meta-analysis can detect situations where the overall effect is significant though individual tests are not. For example, *Orthocarpus* spp. was not a significant indicator of conditions inside exclosures in 1941 at any of the three sites where it occurred ($p = 0.121$, 0.502, and 0.055), yet was a significant indicator ($p = 0.043$) of this grazing treatment once data from the three sites were combined. The increased likelihood that widespread species are significant indicators is also beneficial as these species are more likely than species with narrow distributions to have broad relevance and be generalizable to other studies (Zacharias & Roff 2001).

The simplified and classical ISAs yielded very similar results on both individual and combined tests, suggesting that the simplified ISA could be used in meta-analyses of published studies. For example, the generality of indicator species identified in this study could be assessed by comparing these results with those from published studies. Since ISAs are conducted independently for each species, studies can be drawn from across the distributional range of each species. Indicator status can then be assessed across all ecosystems represented, or differences between ecosystems can be examined. To illustrate this, I surveyed the literature for studies that reported frequency data for species inside and outside of livestock grazing exclosures. Eight studies were identified that reported results for at least one species recorded in this study (Appendices 4.2 and 4.3). I used the *IV* function (Appendix 4.1) to calculate the simplified *IV* for each species in each grazing treatment (since species are analyzed independently, the order of data in the input file is inconsequential). For studies involving several exclosures, each exclosure was analyzed separately, *p*-values were combined using the weighted-*Z* transform, and the weighted mean *IV* was calculated. Summary data are presented in Table 4.5 and are discussed within the text below (see *Important and Consistent Indicators of Grazing Treatments and Overstory Conditions*).

Indicators of Temporal Dynamics

While some studies have demonstrated increased cover in response to protection from grazing (e.g. Robertson 1971; McLean & Tisdale 1972) and others have found little change (e.g., Turner 1971; Courtois et al. 2004), few have noted declines of the magnitude reported here: covers of individual species often declined by > 80% (Table 4.4), though species that were not indicators of conditions in 1941 would not have declined as greatly in cover. In terms of total herbaceous cover, graminoid cover, or forb cover, these declines are entirely attributable to the growth of the overstory (Chapter 3; House et al. 2003). However, this study demonstrates that community-level responses mask interspecific differences: species differ in indicator status among years, overstory conditions, and grazing treatments.

Three times more species were indicators of 1941 over 2004 (Table 4.4; Fig. 4.3). With the exception of a few species (*Comandra umbellata*, *Euphorbia* spp., *Gaillardia pinnata*, *Orthocarpus* spp.), most of these indicators were still present in 2004, though at much lower levels. For example, *Agoseris* spp. was present on five sites in 1941 but only one site in 2004, and *Muhlenbergia wrightii* on four sites in 1941 and one in 2004. Some species that were indicators of 1941 were also indicators of specific grazing and/or overstory conditions in 2004, suggesting that their declines in abundance were not equal among habitats. For example, *Achillea millefolium*, the strongest indicator of 1941 (Fig. 4.3), was not a significant indicator of overstory condition or grazing treatment that year (Tables 4.2, 4.3) but was a strong indicator of conditions outside exclosures and in the open in 2004 (Fig. 4.1, 4.2). It may have been eliminated from habitats where it was weaker competitor and persisted in habitats in which it was a strong competitor.

In contrast, most of the species that were indicators of 2004 were not recorded in 1941. Several exotic species (e.g., *Linaria dalmatica, Bromus tectorum, Taraxacum officinale*) likely invaded since 1941. Other species may have been present but either not recorded due to their short stature and insignificance as forage (e.g., *Drymaria molluginea*, *Chenopodium graveolens*), or recorded as unknowns, which were excluded from these analyses. For example, specimens of *Helianthella quinquenervis* and *Pyrrocoma crocea* were collected by G. Glendening in 1941, but these species were not recorded on data sheets. Unfortunately, the herbarium labels for these specimens do not contain unknown codes that could be matched with the unknown codes on data sheets (S. Doan, Arizona State University herbarium, *pers. comm.*).

Carex spp. was the only dominant species that was an indicator of conditions in 2004 (Table 4.4); *Muhlenbergia minutissima* and *Verbascum thapsus*, the other indicators of 2004 that were also recorded in 1941, accounted for small proportions of the herbaceous cover. The increased cover of *Carex* spp., coupled with the decline in overall herbaceous cover (Chapter 3), mean that it accounts for a larger proportion of the total cover in 2004 than it did in 1941. *Carex* spp. are non-mycorrhizal (van der Heijden et al. 1998) and grow well under low light conditions (Naumburg & DeWald 1999), and therefore may have a competitive advantage over other species under the current conditions.

Livestock grazing and shading by the tree overstory, the two structuring forces measured in this study, appear to have switched in importance between 1941 and 2004. In 1941, grazing intensity was high (Table 3.1), and tree canopy cover low (mean = 15%; Chapter 2), and more species were indicators of grazing treatments than overstory conditions (39 vs. 29). In 2004, grazing intensity was much lower but tree canopy cover had increased to 40%, and more species were indicators of overstory conditions than grazing treatments (31 vs. 26). Relatively few species responded in the same manner in both years (Tables 4.2, 4.3), possibly because of these differences in the nature of the structuring forces.

Important and Consistent Indicators of Grazing Treatments and Overstory Conditions

When applied to hierarchical typologies, ISA can be used to identify the level of the hierarchy where a species is the strongest indicator (Dufrêne & Legendre 1997). The maximum $\overline{IV}_{i..}$ calculated in this study cannot be used in this fashion, since comparisons did not involve hierarchical typologies; the exchangeable units varied among typologies and the number of sites across which data were combined varied among species and years. However, comparisons of $\overline{IV}_{i..}$ can identify species associated with particular treatments. For example, species can be grouped by the combination of grazing indicators (inside, outside, neither) and overstory indicators (open, under, neither) that they represent (Table 4.6). These patterns are not functional groups *per se*, as they identify responses to both forces rather than to a single structuring disturbance. It should be recognized that the classification of lines by overstory condition does not account for stand structure or light characteristics, which affect the presence and abundance of graminoids in ponderosa pine forests (Naumburg & DeWald 1999). Also, the cover of a species might or might not be correlated with tree canopy regardless of whether it is an indicator of an overstory condition.

Species such as *Elymus elymoides*, *Aristida arizonica*, and *Chenopodium graveolens* were indicators of conditions outside exclosures (Table 4.3) but not of overstory condition (Table 4.2), suggesting that they increased under grazing but were not significantly affected by the overstory (Table 4.6). *E. elymoides* is considered to be grazing resistant (Arnold 1950; Schmutz et al. 1967) primarily because its awns deter grazing on mature plants (Office of Grazing Studies 1914; Sampson 1924). It is a significant indicator of conditions outside exclosures in pine forests of New Mexico (Table 4.5) but was generally unresponsive to protection from grazing in northern Utah shrub communities (Rice & Westoby 1978). It was a significant indicator of conditions inside exclosures in salt-desert range (Table 4.5), possibly because the salt-desert range was grazed in the winter; *E. elymoides* is considered good forage when it has not yet flowered (Sampson 1924). Madany & West (1983) reported that it was more abundant on an ungrazed mesa than on a nearby plateau that was ungrazed for two decades. *E. elymoides* has a relatively high ability to grow under dense pine canopies, though it does grow better in the open (Naumburg & DeWald 1999; Naumburg et al. 2001).

Many species were indicators of conditions outside exclosures and in the open (Table 4.6). A number of these are annual forbs (e.g., *Erigeron divergens*, *Erigeron flagellaris*, *Polygonum* spp.), which is consistent with a life history strategy of capitalizing on disturbances and early seral habitats (Peek et al. 1978; Laughlin et al. 2004). *Polygonum* spp. was also a significant indicator of conditions outside exclosures in New Mexico pine forests, though *E. divergens* and *E. flagellaris* were not (Table 4.5). Other species indicative of conditions outside exclosures in the open included *Bouteloua gracilis*, *Antennaria* spp., *Achillea millefolium*, and *Hymenopappus filifolius*. Numerous studies have reported that *B. gracilis* and *Antennaria* spp. are more common in grazed than ungrazed areas (Costello & Turner 1941; Johnson 1956; Schmutz et al. 1967;

McLean & Tisdale 1972; Brand & Goetz 1986; Willms et al. 2002). Sampson (1924) stated that *A. millefolium* 'glories in full sunlight' and is often abundant in moderately overgrazed areas, which agrees with the ISA results reported here and with Tiedemann & Berndt (1972), though other studies have found it to be an indicator of conditions inside exclosures (Table 4.5; Costello & Turner 1941) and del-Val & Crawley (2005) consider it a species whose abundance decreases when herbivores are present. *Gutierrezia sarothrae* was also an indicator of these conditions in 1941 and is a recognized indicator of overgrazed areas (Costello & Schwan 1946), though other studies have found it to be more common inside exclosures (Table 4.5).

A few species (e.g., *Dalea* spp., *Oxytropis lambertii*, *Trifolium longipes*) were indicators of areas outside exclosures and under the canopy (Table 4.6) All of these species are legumes, though the ecological significance of this is unclear. Covers of these species spanned the range of tree canopies, but were not correlated with tree canopy cover (data not shown). *T. longipes* was not a significant indicator of conditions outside exclosures in an Idaho mixed conifer forest (Table 4.5).

Species such as *Artemisia campestris*, *Muhlenbergia montana*, *Helianthella quinquenervis*, *Pseudocymopterus montanus*, and *Rosa woodsii* were indicators of areas inside exclosures but not of overstory condition (Table 4.6), suggesting that they are more responsive to grazing than to shading from the overstory. *A. campestris* was more common on an ungrazed mesa than a nearby grazed area in southern Utah (Guenther et al. 2004). Some studies have reported that *M. montana* is more common in ungrazed than grazed areas (Madany & West 1983; Johnson 1956), but it was a significant indicator of conditions outside exclosures in New Mexico ponderosa pine forests (Table

4.5) and considered to be favored by light grazing in Colorado (Smith 1967). *M. montana* has a relatively low ability to grow under dense pine canopies (Naumburg et al. 2001). Although it was not an indicator of overstory condition, *M. montana* cover is negatively correlated with tree canopy, though this relation explains little of the variation in its cover (1941: $r^2_{adj} = 0.026, p = 0.003$, n = 300; 2004: $r^2_{adj} = 0.112, p < 0.001$ n = 173). *P. montanus* was a marginally significant ($p = 0.088$) indicator of conditions outside exclosures in New Mexico ponderosa pine forests (Table 4.5).

Hesperostipa comata, *Erigeron formosissimus*, and *Orthocarpus* spp. were indicators of areas inside exclosures and in the open (Table 4.6), suggesting that they occur in sunny, protected habitats. *H. comata* was more abundant in areas protected from cattle grazing (Costello & Turner 1941) and on an ungrazed mesa than a nearby grazed area (Guenther et al. 2004), though it was a significant indicator of conditions outside exclosures in the ponderosa pine forests of British Columbia (Table 4.5). A long-term demographic study in Idaho demonstrated that fall grazing increased the longevity of *H. comata* plants (West et al. 1979). *H. comata* cover declined greatly over time inside exclosures (McLean & Tisdale 1972), suggesting that it occupies relatively seral habitats.

In contrast, *Festuca arizonica*, *Cirsium* spp., *Ceanothus fendleri*, *Lotus wrightii*, and *Solidago* spp. were indicators of areas inside exclosures and under the canopy (Table 4.6), suggesting that they occur in shady habitats protected from livestock grazing. Early reports describe *F. arizonica* as being able to withstand grazing (Office of Grazing Studies 1914; Sampson 1924) and as favored by light grazing (Smith 1967; cf. Costello & Turner 1941), which appears to contradict the fact that it was an indicator of areas inside exclosures. However, *F. arizonica* has a limited ability to reseed (Sampson 1924;

Laughlin et al., *in review*) and continued clipping reduces its prevalence relative to other grasses (Pearson 1942), suggesting that continued grazing killed mature plants outside exclosures and that subsequent regeneration did not occur. Early reports also describe *F. arizonica* as 'somewhat tolerant of shade' (Sampson 1924), and Naumburg et al. (2001) rank it as intermediate in ability to grow under dense pine canopies. *F. arizonica* cover was not correlated with tree canopy in 1941 ($p = 0.419$) but negatively correlated with it in 2004 ($r^2_{adj} = 0.038$, $p = 0.009$, n = 153).

Arenaria spp. and *Sporobolus interruptus* were not indicators of grazing treatments but were indicators of areas in the open (Table 4.6). In contrast, Smith (1967) reported that *Arenaria fendleri* was more abundant on grazed than protected areas. *S. interruptus*, an endemic species, has been the subject of little research to date. It has been characterized as tolerant of grazing (Arnold 1950) and as a favored forage of livestock (Office of Grazing Studies 1914; Sampson 1924; Clary & Pearson 1969), but my results suggest that it is more strongly affected by shade than by grazing. The overstory increased most inside exclosures (Chapter 2), and *S. interruptus* cover declined by 31% inside compared to 4% outside exclosures.

Bromus tectorum, *Carex* spp., and *Eriogonum racemosum* were not indicators of grazing treatment but were indicators of areas under the canopy (Table 4.6). Other studies have found that *B. tectorum* is a significant indicator of conditions outside exclosures (Table 4.5) or have reported inconsistent responses to protection (Rice & Westoby 1978). *Carex* spp. accounted for most of the herbaceous biomass under ponderosa pine forests in the Black Hills of South Dakota (Thompson & Gartner 1971), though its cover was negatively correlated with ponderosa pine canopy cover in Colorado (Nemati & Goetz 1995).

Inconsistent Indicators of Grazing Treatments

In 1941, *Koeleria macrantha* was an indicator of conditions inside exclosures at three sites but of conditions outside the exclosure at a fourth site. Published data are also inconsistent with respect to the grazing indicator status of *K. macrantha*: its longevity is not affected by fall grazing (West et al. 1979) but it was a significant indicator of conditions outside exclosures in some studies and inside exclosures in others (Evanko & Peterson 1955; Table 4.5). Its response may be affected by other variables such as the type of grazing animal or the intensity and duration of grazing.

Blepharoneuron tricholepis and *Poa* spp. were indicators of conditions inside exclosures in 1941 but of conditions outside exclosures in 2004 (Table 4.3; Fig. 4.2). These reversals may be due to several factors, including species-specific responses to grazing and to overstory vegetation. The reduced grazing pressure at present may have permitted these species to reestablish outside exclosures, and the increased overstory (Chapter 2) may have reduced their abundance inside exclosures. Mean cover of *B. tricholepis* and *Poa* spp. increased by 939% and 273%, respectively, outside exclosures while declining inside exclosures by 86% and 53%, respectively. *B. tricholepis* has a low ability to grow under dense pine canopies (Naumburg et al. 2001).

In addition, the switch in indicator status by *Poa* spp. could reflect changing representation of species within this genus. *P. fendleriana* and *P. pratensis* occurred on the sites in 1941 (Arnold 1950) but were not distinguished during the 1941 measurements. *P. fendleriana* has been reported to be more abundant in ungrazed than grazed areas (Schmutz et al. 1967; Guenther et al. 2004), while *P. pratensis* is more abundant in grazed areas (Costello & Turner 1941; Schwan et al. 1949), though it is not a consistent indicator of this grazing treatment (Table 4.5; Brand & Goetz 1986). However, an ISA of individual *Poa* spp. in 2004 indicated that *P. fendleriana* and *P. compressa* were significant indicators of conditions outside exclosures while *P. pratensis* was not an indicator of grazing treatment. In addition, *P. compressa* and *P. pratensis* were indicators of conditions in the open while *P. fendleriana* was not an indicator of overstory condition. This highlights the importance of identifying plants to species rather than simply to genus, as has been discussed for benthic invertebrates by Weiss & Rice (2005). Other examples from this study of contrasting indicator status within the same genus include *Erigeron*, *Hymenopappus*, and *Muhlenbergia.*

No species were indicators of conditions outside exclosures in 1941 and inside exclosures in 2004, likely because of the dramatic differences in grazing history and environmental conditions between these areas and times (Chapters 2, 3).

Recommendations for Indicator Species Analyses

To close, I offer some recommendations for using Indicator Species Analysis (ISA) and combining the results of multiple sites or studies:

1. To the extent possible, identify all individuals to the species level, as congeneric species may differ in indicator status.

2. Consider the proper exchangeable units for the permutations tests (Anderson & ter Braak 2003). Where appropriate, such as when a factor is nested within sites, that factor could be analyzed separately at each site and the results combined using meta-analytic techniques.

3. The results of an ISA depend on the typology used (Dufrêne & Legendre 1997), so comparisons of ISAs from multiple studies require that the same typology be used in each study. Simple pairwise comparisons are more likely to be comparable between studies than comparisons among multiple levels. Groups included in the typology should be described in detail for the benefit of future researchers.

4. Ensure that the sample size within each group is sufficient to sample the vegetation. Doing so will also provide enough samples to permit an adequate number of permutations. If there are *m* samples per group and *n* samples in total, the number of possible permutations is:

$$[4.6] \qquad {}^{n}C_{m} = \frac{n!}{(n-m)!m!}$$

For example, $n = 20$ samples can be permuted into two groups of $m = 10$ 184,756 times.

5. At a minimum, report the sample size and frequency of all species in all groups, so that the simplified *IV* can be calculated. Digital appendices and other repositories permit the archiving of these data in an accessible manner (Parr & Cummings 2005).

6. If reporting the significance level of an *IV*, report the actual *p*-value rather than just noting if the value is $< \alpha$ (e.g., * < 0.05, ** < 0.001, etc.). Small differences in *p*-value make a large difference in the *Z*-scores inputted into the weighted *Z*-transform, particularly at the tails of the *Z*-distribution.

7. To prevent publication bias in future meta-analyses (Gurevitch & Hedges 2001), publish data for all species, regardless of whether or not they were significant indicators.

Conclusions

Indicator Species Analysis (ISA) was used to identify indicators of overstory conditions, grazing treatments, and temporal dynamics in a southwestern ponderosa pine forest. Meta-analytic techniques demonstrated that most species were consistent indicators of grazing treatments and/or years across sites. Species that occurred at multiple sites were more likely to be indicators than those present at a single site. The classical ISA and simplified ISA produced very similar results, indicating that the simplified ISA could be applied in meta-analyses of published literature. Three times more species were indicators of 1941 than 2004, indicating that many species declined in abundance and frequency during this interval. More species were indicators of grazing treatments in 1941 and of overstory effects in 2004, suggesting that the dominant structuring force in this ecosystem has changed over time. Some species responded mostly to grazing (e.g., *Elymus elymoides*, *Muhlenbergia montana*), some to overstory effects (e.g., *Bromus tectorum*, *Carex* spp., *Sporobolus interruptus*), and some to both forces (e.g., *Erigeron divergens*, *Bouteloua gracilis*, *Trifolium longipes*, *Hesperostipa comata*, *Festuca arizonica*).

References

Adler, P.B., D.G. Milchunas, O.E. Sala, I.C. Burke, and W.K. Lauenroth. 2005. Plant traits and ecosystem grazing effects: comparison of U.S. sagebrush steppe and Patagonian steppe. Ecological Applications **15**:774-792.

Anderson, M.J., and C.J.F. ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. Journal of Statistical Computation and Simulation **73**:85-113.

Arnold, J.F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. Journal of Forestry **48**:118-126.

Arnold, J.F. 1955. Plant life-form classification and its use in evaluating range conditions and trend. Journal of Range Management **8**:176-181.

Bock, C.E., J.H. Bock, W.R. Kenney, and V.M. Hawthorne. 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. Journal of Range Management **37**:239-242.

Brand, M.D., and H. Goetz. 1986. Vegetation of exclosures in southwestern North Dakota. Journal of Range Management **39**:434-437.

Bustos-Baez, S., and C. Frid. 2003. Using indicator species to assess the state of macrobenthic communities. Hydrobiologia **496**:299-309.

Canfield, R.H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry **39**:388-394.

Chew, R.M. 1982. Changes in herbaceous and suffrutescent perennials in grazed and ungrazed desertified grassland in southeastern Arizona, 1958-1978. American Midland Naturalist **108**:159-169.

Clary, W.P., and H.A. Pearson. 1969. Cattle preferences for forage species in northern Arizona. Journal of Range Management **22**:114-116.

Costello, D.F., and H.E. Schwan. 1946. Conditions and trends on ponderosa pine ranges in Colorado. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Costello, D.F. and G.T. Turner. 1941. Vegetation changes following exclusion of livestock from grazed ranges. Journal of Forestry **39**:310-315.

Courtois, D.R., B.L. Perryman, and H.S. Hussein. 2004. Vegetation change after 65 years of grazing and grazing exclusion. Journal of Range Management **57**:574-582.

Dansereau, P., and K. Lems. 1957. The grading of dispersal types in plant communities and their ecological significance. Contributions de l'Institut Botanique de l'Université de Montreal **71**: 5-52.

del-Val, E., and M.J. Crawley. 2005. Are grazing increaser species better tolerators than decreasers? An experimental assessment of defoliation tolerance in eight British grassland species. Journal of Ecology *In press*

Díaz, S., M. Cabido, M. Zak, E. Martínez Carretero, and J. Araníbar. 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. Journal of Vegetation Science **10**:651-660.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Dufrêne, M. 2004. IndVal webpage. http://mrw.wallonie.be/dgrne/sibw/outils/indval/home.html. Accessed June 20, 2005.

Evanko, A.B., and R.A. Peterson. 1955. Comparisons of protected and grazed mountain rangelands in southwestern Montana. Ecology **36**:71-82.

Frid, C.L.J. 2003. Managing the health of the seafloor. Frontiers in Ecology and the Environment **1**:429-436.

Gardner, J.L., and D.S. Hubbell. 1943. Some vegetational responses after eight years of protection from grazing. Ecology **24**:409-410.

Guenther, D., T.J. Stohlgren, and P. Evangelista. 2004. A comparison of a near-relict site and a grazed site in a pinyon-juniper community in the Grand Staircase-Escalante National Monument, Utah. Pages 153-162 *in* C. van Riper III and K.L. Cole,(editors). The Colorado Plateau: cultural, biological, and physical research. University of Arizona, Tucson, AZ.

Gurevitch, J., and L.V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology **80**:1142-1149.

Gurevitch, J., and L.V. Hedges. 2001. Meta-analysis: combining the results of independent experiments. Pages 347-369 *in* S.M. Scheiner and J. Gurevitch (editors). Design and analysis of ecological experiments. Oxford University Press, New York, NY.

Hadar, L., I. Noy-Meir, and A. Perevolotsky. 1999. The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. Journal of Vegetation Science **10**:673-682.

Hill, M.O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, NY.

Hitchcock, A.S. 1971. Manual of the grasses of the United States. 2nd edition. Dover, New York, NY.

House, J.I., S. Archer, D.D. Breshears, R.J. Scholes, and NCEAS Tree-Grass Interactions Participants. 2003. Conundrums in mixed woody-herbaceous plant systems. Journal of Biogeography **30**:1763-1777.

Johnson, W.M. 1956. The effect of grazing intensity on plant composition, vigor, and growth of pine-bunchgrass ranges in central Colorado. Ecology **37**:790-798.

Kahmen, S., and P. Poschlod. 2004. Plant functional trait responses to grassland succession over 25 years. Journal of Vegetation Science **15**:21-32.

Kearney, T.H., and R.H. Peebles. 1942. Flowering plants and ferns of Arizona. US Department of Agriculture, Washington, DC. Miscellaneous Publication 423.

Knight, D.H., and O.L. Loucks. 1969. A quantitative analysis of Wisconsin forest vegetation on the basis of plant function and gross morphology. Ecology **50**:219-234.

Korstian, C.F. 1917. The indicator significance of native vegetation in the determination of forest sites. The Plant World **20**:267-287.

Krueger, W.C., and A.H. Winward. 1974. Influence of cattle and big game grazing on understory structure of a Douglasfir-ponderosa pine-Kentucky bluegrass community. Journal of Range Management **27**:450-453.

Landres, P.B., J. Verner, and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology **2**:316-328.

Landsberg, J., S. Lavorel, and J. Stol. 1999. Grazing response groups among understorey plants in arid rangelands. Journal of Vegetation Science **10**:683-696.

Laughlin, D.C., J.D. Bakker, M.T. Stoddard, M.L. Daniels, J.D. Springer, C.N. Gildar, A.M. Green, and W.W. Covington. 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. Forest Ecology and Management **199**:137-152.

Laughlin, D.C., M.M. Moore, J.D. Bakker, C.A. Casey, J.D. Springer, P.Z. Fulé, and W.W. Covington. *In review.* Assessing targets for the restoration of herbaceous vegetation in ponderosa pine forests. Restoration Ecology

Lavorel, S., S. McIntyre, J. Landsberg, and T.D.A. Forbes. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends in Ecology and Evolution **12**:474-478.

Lavorel, S., S. McIntyre, and K. Grigulis. 1999. Plant response to disturbance in a Mediterranean grassland: how many functional groups? Journal of Vegetation Science **10**:661-672.

Madany, M.H. and N.E. West. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah . Ecology **64**:661-667.

Magurran, A.E. 2004. Measuring biological diversity. Blackwell, Oxford, UK.

Manly, B.F.J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall, Boca Raton, FL.

McCune, B. and M.J. Mefford. 1999. PC-ORD: Multivariate Analysis of Ecological Data. Version 4.35. MjM Software, Gleneden Beach, OR.

McCune, B. and J.B. Grace. 2002. Analysis of ecological communities. MJM Software Design, Gleneden Beach, OR.

McGeoch, M.A. and S.L. Chown. 1998. Scaling up the value of bioindicators. Trends in Ecology and Evolution **13**:46-47.

McIntyre, S., S. Lavorel, J. Landsberg, and T.D.A. Forbes. 1999. Disturbance response in vegetation - towards a global perspective on functional traits. Journal of Vegetation Science **10**:621-630.

McLean, A. and E.W. Tisdale. 1972. Recovery rate of depleted range sites under protection from grazing. Journal of Range Management **25**:178-184.

Merrick, G.D. 1939. Revegetation of deteriorated range land in northern Arizona. M.A. Thesis. Duke University. Durham, NC.

Moir, W.H. 1966. Influence of ponderosa pine on herbaceous vegetation. Ecology **47**:1045-1048.

Naumburg, E., and L.E. DeWald. 1999. Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance. Forest Ecology and Management **124**:205-215.

Naumburg, E., L.E. DeWald, and T.E. Kolb. 2001. Shade responses of five grasses native to southwestern U.S. *Pinus ponderosa* forests. Canadian Journal of Botany **79**:1001-1009.

Nemati, N. and H. Goetz. 1995. Relationships of overstory to understory cover variables in a Ponderosa pine/Gambel oak ecosystem. Vegetatio **119**:15-21.

Office of Grazing Studies. 1914. Notes on National Forest range plants: Part I: Grasses. Washington, D.C. 224 p.

Parr, C.S., and M.P. Cummings. 2005. Data sharing in ecology and evolution. Trends in Ecology and Evolution **20**:362-363.

Pearson, G.A. 1942. Herbaceous vegetation a factor in natural regeneration of ponderosa pine in the southwest. Ecological Monographs **12**:315-338.

Peek, J.M., F.D. Johnson, and N.N. Pence. 1978. Successional trends in a ponderosa pine/bitterbrush community related to grazing by livestock, wildlife, and to fire. Journal of Range Management **31**:49-53.

Peterson, E.B. and B. McCune. 2001. Diversity and succession of epiphytic macrolichen communities in low-elevation managed conifer forests in western Oregon. Journal of Vegetation Science **12**:511-524.

Pillar, V.D. 1999. On the identification of optimal plant functional types. Journal of Vegetation Science **10**:631-640.

Poyry, J., S. Lindgren, J. Salminen, and M. Kuussaari. 2005. Responses of butterfly and moth species to restored cattle grazing in semi-natural grasslands. Biological Conservation **122**:465-478.

Pyne, S.J. 2001. The fires this time, and next. Science **294**:1005-1006.

R Development Core Team. 2005. R: A Language and Environment for Statistical Computing. Vienna, Austria. http://www.R-project.org. Accessed June 1, 2005.

Read, A.D. 1915. The flora of the Williams division of the Tusayan National Forest, Arizona. Plant World **18**:112-123.

Rentch, J.S., R.H. Fortney, S.L. Stephenson, H.S. Adams, W.N. Grafton, and J.T. Anderson. 2005. Vegetation-site relationships of roadside plant communities in West Virginia, USA. Journal of Applied Ecology **42**:129-138.

Rice, W.R. 1990. A consensus combined *P*-value test and the family-wide significance of component tests. Biometrics **46**:303-308.

Rice, B., and M. Westoby. 1978. Vegetative responses of some Great Basin shrub communities protected against jackrabbits or domestic stock. Journal of Range Management **31**:28-34.

Robertson, J.H. 1971. Changes on a sagebrush-grass range in Nevada ungrazed for 30 years. Journal of Range Management **24**:397-400.

Saetersdal, M., I. Gjerde, and H.H. Blom. 2005. Indicator species and the problem of spatial inconsistency in nestedness patterns. Biological Conservation **122**:305-316.

Salovaara, K.J., G.G. Cardenas, and H. Tuomisto. 2004. Forest classification in an Amazonian rainforest landscape using pteridophytes as indicator species. Ecography **27**:689-700.

Sampson, A.W. 1924. Native American forage plants. John Wiley & Sons, New York, NY.

Schmutz, E.M., C.C. Michaels, and B.I. Judd. 1967. Boysag Point: a relict area on the North Rim of Grand Canyon in Arizona. Journal of Range Management **20**:363-368.

Schwan, H.E., D.J. Hodges, and C.N. Weaver. 1949. Influence of grazing and mulch on forage growth. Journal of Range Management **2**:142-148.

Smith, D.R. 1967. Effects of cattle grazing on a ponderosa pine-bunchgrass range in Colorado. USDA Forest Service, Washington, DC. Technical Bulletin 1371.

Talbot, M.W., and R.R. Hill. 1923. Progress report on the range study plots on the Coconino National Forest comprising a description of project and digest of data. Unpublished report. USDA Forest Service, Rocky Mountain Research Station, Fort Valley Archives, Flagstaff, AZ. 32 p.

Thompson, W.W., and F.R. Gartner. 1971. Native forage response to clearing low quality ponderosa pine. Journal of Range Management **24**:272-277.

Tiedemann, A.R., and H.W. Berndt. 1972. Vegetation and soils of a 30-year deer and elk exclosure in central Washington. Northwest Science **46**:59-66.

Turner, G.T. 1971. Soil and grazing influences on a salt-desert shrub range in western Colorado. Journal of Range Management **24**:31-37.

USDA, NRCS. 2004. The PLANTS Database, Version 3.5. http://plants.usda.gov. Accessed February 15, 2005.

van der Heijden, M.G.A., J.N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I.R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature **396**:69-72.

Weiss, J.M., and S.R. Reice. 2005. The aggregation of impacts: using species-specific effects to infer community-level disturbances. Ecological Applications **15**:599-617.

West, N.E., K.H. Rea, and R.O. Harniss. 1979. Plant demographic studies in sagebrush-grass communities of southeastern Idaho. Ecology **60**:376-388.

Whitlock, M.C. 2005. Combining probability from independent tests: the weighted Z-method is superior to Fisher's approach. Journal of Evolutionary Biology *In press.*

Willms, W.D., J.F. Dormaar, B.W. Adams, and H.E. Douwes. 2002. Response of the mixed prairie to protection from grazing. Journal of Range Management **55**:210-216.

Zacharias, M.A., and J.C. Roff. 2001. Use of focal species in marine conservation and management: a review and critique. Aquatic Conservation: Marine and Freshwater Ecosystems **11**:59-76.

Zimmerman, G.T., and L.F. Neuenschwander. 1984. Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas fir/ninebark habitat type. Journal of Range Management **37**:104-110.

Table 4.1. Taxa combined in 1941 and/or 2004 to permit comparisons between years. Taxa were combined either because they are difficult to distinguish or because the 1941 data were collected at the genus level. Percentages refer to the proportion of the cover attributable to each species. For example, *Antennaria* spp. were not distinguished in 1941, so *A. rosulata* and *A. parviflora* (which comprised 73.9 and 26.1% of the combined cover, respectively) were combined at the genus level in 2004.

Taxa	Dominant Species in Taxa	Additional Species in Taxa	Year
Antennaria spp.	*A. rosulata* (73.9%)	*A. parviflora* (26.1%)	2004
Arenaria spp.	*A. fendleri* (99.8%)	*A. lanuginosa* (0.2%)	2004
Artemisia carruthii	*A. carruthii* (69.0%)	*A. ludoviciana* (31.0%)	2004
Astragalus spp.	*A. humistratus* (70.6%)	*A. castaneiformis* (17.6%), *A. tephrodes* (11.8%)	2004
Brassicaceae spp.	Brassicaceae spp. (85.7%)	*Lesquerella* sp. (14.3%)	1941
Brassicaceae spp.	*Thlaspi montanum* (28.6%)	*Arabis* spp. (20.0%), *Despidium pinnatum* (20.0%), *Lepidium densiflorum* (20.0%), *Draba* spp. (11.4%)	2004
Chenopodium spp.	broad-leaved *Chenopodium* spp.[1]		1941
Erigeron formosissimus	*E. formosissimus* (81.9%)	*E. speciosus* (18.1%)	1941
Heliomeris multiflora	*Gymnolomia* spp. (69.1%)	*Viguiera* spp. (30.1%)	1941
Orthocarpus spp.	*Orthocarpus* spp. (50.0%)	*O. luteus* (43.8%), *O. purpureoalbus* (6.2%)	1941
Penstemon spp.	*P. virgatus* (57.4%)	*P. linarioides* (31.7%), *P. barbatus* (10.9%)	2004
Poa spp.	*P. fendleriana* (68.0%)	*P. pratensis*[2] (23.4%), *P. compressa*[2] (8.6%)	2004
Polygonum spp.	*P. douglasii* (56.0%)	*P. aviculare*[2] (44.0%)	2004
Potentilla spp.	*P. crinita* (73.0%)	*P. hippiana* (27.0%)	2004
Senecio spp.	*Packera multilobata*[3] (74.1%)	*S. actinella* (18.5%), *S. spartioides* (7.4%)	2004
Solidago spp.	*S. velutina* (53.3)	*S. nana* (46.7%)	2004
Symphyotrichum spp.[4]	*S. ascendens* (83.0%)	*S. falcatum* (17.0%)	2004

[1] It is nearly impossible to differentiate the broad-leaved *Chenopodium* spp. (*C. album*, *C. berlandieri*, *C. fremontii*, and *C. incanum*), although they are easily distinguished from *C. graveolens* and *C. leptophyllum*

[2] Exotic species

[3] Formerly *Senecio multilobata*

[4] *Aster* spp. in 1941

Table 4.2. Significant indicators of areas in the open (O; no canopy above line) or under (U) the tree canopy in 1941 and 2004 on the Hill plots in northern Arizona. Indicator Values (*IV*s) for each year were calculated using all site x grazing (SxG) combinations on which a species occurred (range = 0 to 10). *P*-values were calculated by permuting the data 9999 times. Data are not reported if the *p*-value was not statistically significant.

	1941				2004			
Species	SxG	Trt	*IV*	*P*	SxG	Trt	*IV*	*P*
Achillea millefolium	8				7	O	25.5	0.0072
Agoseris spp.	9	O	22.4	0.0002	1			
Antennaria spp.	8	O	52.0	0.0001	7	O	44.1	0.0001
Arenaria spp.	5	O	26.9	0.0001	3	O	43.8	0.0001
Aristida purpurea	4				4	O	7.2	0.0075
Artemisia carruthiii	10				8	O	26.7	0.0005
Astragalus spp.	9				3	O	13.1	0.0020
Blepharoneuron tricholepis	7				6	O	37.6	0.0001
Bouteloua gracilis	8	O	34.0	0.0030	6	O	28.5	0.0024
Bouteloua simplex	1	O	37.6	0.0024	1			
Bromus tectorum	0				4	U	10.2	0.0117
Carex spp.	10	U	18.7	0.0086	9			
Ceanothus fendleri	5	U	6.8	0.0081	4			
Chamaesyce serpyllifolia	0				4	O	15.3	0.0247
Cirsium spp.	8	U	12.4	0.0004	8	U	13.0	0.0034
Cyperus fendlerianus	0				2	O	7.7	0.0368
Dalea spp.	2				1	U	13.6	0.0294
Drymaria molluginea	0				2	O	9.0	0.0402
Elymus trachycaulus	1				1	O	11.8	0.0359
Erigeron divergens	10	O	30.8	0.0001	9	O	21.3	0.0001
Erigeron flagellaris	9	O	13.6	0.0003	6	O	32.4	0.0001
Erigeron formosissimus	8	O	16.6	0.0250	6	O	16.8	0.0116
Eriogonum racemosum	6	U	8.8	0.0429	5			
Festuca arizonica	9	U	30.1	0.0002	9	U	26.2	0.0024
Gailliardia pinnata	2	O	10.9	0.0016	0			
Gutierrezia sarothrae	3	O	44.2	0.0001	3			
Hesperostipa comata	2	O	8.8	0.0357	1	O	26.1	0.0284
Houstonia wrightii	6				3	O	14.5	0.0017
Hymenopappus filifolius	2	O	29.5	0.0021	2			
Hymenopappus mexicanus	3				2	O	6.2	0.0250
Hymenoxys richardsonii	3	O	29.0	0.0122	1			
Ipomopsis multiflora	2	O	20.5	0.0002	2			
Koeleria macrantha	8	O	16.6	0.0177	7			
Lotus wrightii	10	U	10.0	0.0137	5			
Machaeranthera gracilis	4	O	9.5	0.0253	1			
Muhlenbergia minutissima	1				5	O	34.6	0.0001
Muhlenbergia rigens	4				4			
Muhlenbergia wrightii	5				2	O	28.1	0.0001

	1941				2004			
Species	SxG	Trt	*IV*	*P*	SxG	Trt	*IV*	*P*
Orthocarpus spp.	4	O	14.1	0.0013	0			
Oxalis spp.	3	O	22.4	0.0361	3			
Oxytropis lambertii	3	U	16.9	0.0268	2			
Penstemon spp.	9				7	O	11.6	0.0097
Plantago spp.	3	O	16.7	0.0035	1			
Poa spp.	10				9	O	39.0	0.0117
Polygonum spp.	6	O	28.8	0.0001	6	O	23.0	0.0141
Portulaca oleracea	2				3	O	18.5	0.0010
Potentilla spp.	9				7	O	24.9	0.0001
Solidago spp.	7				6	U	14.7	0.0222
Sporobolus interruptus	4	O	28.0	0.0234	4	O	28.3	0.0083
Trifolium longipes	5	U	21.0	0.0484	4			

Table 4.3. Significant indicators of grazing treatments (inside or outside of exclosures) in 1941 and 2004 on the Hill plots in northern Arizona. Indicator Values (*IV*s) are the weighted mean of the *IV*s from all sites where a species occurred (range = 0 to 5). *P*-values were calculated for each site by permuting the data 9999 times, and combined across sites using a weighted *Z*-transform. Data are not reported if the combined *p*-value was not statistically significant. Note that all five sites were used for this comparison in 1941 but only three sites were used in 2004 due to differences in recent grazing history (see Methods for details).

	1941				2004			
Species	Sites	Trt	*IV*	*P*	Sites	Trt	*IV*	*P*
Achillea millefolium	4				2	Out	40.4	0.0000
Agoseris spp.	5	Out	31.9	0.0001	1			
Antennaria spp.	4	Out	35.4	0.0004	2	Out	41.2	0.0001
Aristida arizonica	2	Out	24.0	0.0001	0			
Aristida purpurea	2	Out	37.8	0.0000	2			
Artemisia campestris	2	In	22.5	0.0000	2			
Artemisia carruthii	5	In	43.3	0.0000	3	In	16.3	0.0001
Blepharoneuron tricholepis	4	In	36.9	0.0000	2	Out	27.4	0.0065
Bouteloua gracilis	5	Out*	28.6	0.0058	3	Out	33.9	0.0035
Bouteloua simplex	1	Out	33.8	0.0001	1	Out	12.8	0.0011
Ceanothus fendleri	4	In	5.8	0.0240	1			
Chamaesyce serpyllifolia	0				3	Out	17.0	0.0040
Chenopodium graveolens	0				2	Out	20.5	0.0002
Cirsium spp.	5	In	14.5	0.0001	3			
Comandra umbellata	1	In	20.0	0.0001	0			
Dalea spp.	2				1	Out	7.7	0.0147
Drymaria molluginea	0				1	Out	9.1	0.0152
Elymus elymoides	5	Out	45.1	0.0002	3	Out	52.9	0.0000
Ericameria nauseosus	2	Out	5.9	0.0356	1			
Erigeron divergens	5	Out	29.4	0.0001	3	Out	16.0	0.0388
Erigeron flagellaris	5	Out	16.0	0.0000	3			
Erigeron formosissimus	4	In	18.4	0.0003	2			
Euphorbia spp.	2	Out	7.3	0.0073	0			
Festuca arizonica	5	In	32.6	0.0030	3	In	27.9	0.0165
Gutierrezia sarothrae	2	Out	56.2	0.0002	2			
Heliomeris multiflora	5	In	20.2	0.0000	3			
Helianthella quinquenervis	0				1	In	27.5	0.0001
Hesperostipa comata	1	In	11.1	0.0025	1	In	9.9	0.0033
Heterotheca villosa	3	In	16.3	0.0002	0			
Hymenopappus filifolius	1	Out	29.7	0.0005	1			
Hymenopappus mexicanus	2	In	21.6	0.0004	1			
Hymenoxys richardsonii	3	Out	41.5	0.0002	1			
Koeleria macrantha	5	In*	19.9	0.0001	3			
Lappula occidentalis	0				1	Out	6.4	0.0293

	1941				2004			
Species	Sites	Trt	*IV*	*P*	Sites	Trt	*IV*	*P*
Lithospermum multiflorum	2				1	In	8.8	0.0062
Lotus wrightii	5	In	12.5	0.0291	2			
Muhlenbergia minutissima	1	Out	20.0	0.0001	3			
Muhlenbergia montana	5	In	59.2	0.0000	3	In*	41.2	0.0192
Muhlenbergia rigens	3	In	9.2	0.0049	3			
Muhlenbergia wrightii	4				1	Out	15.8	0.0012
Orthocarpus spp.	3	In	6.0	0.0428	0			
Oxalis spp.	2	Out	44.3	0.0004	2			
Oxytropis lambertii	2	Out	10.8	0.0080	1			
Plantago spp.	2	Out	18.2	0.0000	0			
Poa spp.	5	In	43.0	0.0000	3	Out	54.6	0.0000
Polygonum spp.	3	Out	28.8	0.0091	2	Out	27.3	0.0004
Portulaca oleracea	2				2	Out	12.1	0.0204
Potentilla spp.	5	In	19.4	0.0057	3			
Pseudocymopterus montanus	4				2	In	18.8	0.0000
Pyrrocoma crocea	0				1	In	12.5	0.0277
Rosa woodsii	2	In	40.1	0.0004	1	In	69.9	0.0001
Solidago spp.	5				3	In	14.8	0.0001
Tetradymia canescens	1	In	13.9	0.0014	1			
Trifolium longipes	3	Out	25.3	0.0082	2	Out	59.7	0.0000

* Although the combined indicator value for this species is statistically significant, it is an inconsistent indicator in this year because it is a significant indicator of conditions inside exclosures at one or more sites and of conditions outside exclosures at one or more sites

Table 4.4. Significant indicators of conditions in 1941 or 2004 on the Hill plots in northern Arizona. Indicator Values (*IV*s) are the weighted mean of the *IV*s from all sites where a species occurred (range = 1 to 5). *P*-values were calculated for each site by permuting the data 9999 times, and combined across sites using a weighted *Z*-transform. Data are not reported if the combined *p*-value was not statistically significant. Percent change in mean cover is also reported; 'n/a' indicates that a species was not present in 1941.

Species	Sites	Year	*IV*	*P*	% Change[1]
Achillea millefolium	4	1941	65.4	0.0000	-78
Agoseris spp.	5	1941	32.8	0.0000	-100
Antennaria spp.	4	1941	57.0	0.0000	-93
Aristida arizonica	2	1941	46.4	0.0000	-99
Artemisia campestris	2	1941	22.8	0.0002	-87
Artemisia carruthii	5	1941	51.9	0.0000	-80
Astragalus spp.	5	1941	21.0	0.0006	-94
Bahia dissecta	1	2004	30.8	0.0001	n/a
Blepharoneuron tricholepis	4	1941	22.7	0.0494	-36
Bouteloua gracilis	5	1941	34.6	0.0002	-40
Bromus tectorum	3	2004	11.1	0.0087	n/a
Carex spp.	5	2004	42.9	0.0036	+106
Chamaesyce serpyllifolia	3	2004	24.2	0.0000	n/a
Chenopodium graveolens	3	2004	30.9	0.0000	n/a
Comandra umbellata	1	1941	17.5	0.0065	-100
Drymaria molluginea	1	2004	17.5	0.0067	n/a
Elymus elymoides	5	1941*	54.6	0.0162	-28
Epilobium brachycarpum	3	1941	25.8	0.0003	-83
Erigeron divergens	5	1941	35.6	0.0000	-60
Erigeron formosissimus	4	1941	32.0	0.0096	-58
Eriogonum racemosum	4	1941	17.4	0.0154	-73
Euphorbia spp.	2	1941	16.3	0.0018	-100
Festuca arizonica	5	1941	37.2	0.0149	-41
Heliomeris multiflora	5	1941	28.4	0.0008	-72
Helianthella quinquenervis	1	2004	30.0	0.0092	n/a
Heterotheca villosa	3	1941	28.0	0.0001	-95
Hymenopappus filifolius	1	1941	56.7	0.0001	-94
Hymenopappus mexicanus	2	1941	23.8	0.0013	-88
Ipomopsis multiflora	1	1941	26.3	0.0011	-95
Koeleria macrantha	5	1941	22.8	0.0016	-61
Linaria dalmatica	2	2004	27.8	0.0000	n/a
Lotus wrightii	5	1941	25.9	0.0000	-90
Lupinus spp.	4	1941	28.6	0.0000	-88
Machaeranthera gracilis	2	1941	27.6	0.0000	-99
Muhlenbergia minutissima	4	2004	22.4	0.0023	+470
Muhlenbergia montana	5	1941	64.3	0.0000	-75
Muhlenbergia rigens	3	1941	11.1	0.0442	-92
Oxalis spp.	2	1941	35.1	0.0004	-98
Oxytropis lambertii	2	1941	25.5	0.0145	-85
Penstemon spp.	5	1941	29.8	0.0009	-83

Species	Sites	Year	*IV*	*P*	% Change[1]
Phlox speciosa	2	2004	45.0	0.0000	n/a
Plantago spp.	2	1941	18.4	0.0024	+3
Poa spp.	5	2004*	44.3	0.0205	+21
Potentilla spp.	5	1941	39.9	0.0002	-86
Pyrrocoma crocea	1	2004	20.0	0.0498	n/a
Schizachyrium scoparium	2	1941	43.7	0.0004	-97
Senecio spp.	4	1941	18.6	0.0130	-81
Symphyotrichum spp.	5	1941	28.9	0.0001	-95
Taraxacum officinale	2	2004	18.3	0.0006	n/a
Verbascum thapsus	2	2004	9.7	0.0188	+1351
Vicia spp.	4	1941	35.6	0.0000	-91

* Although the combined indicator value for this species is statistically significant, it is an inconsistent indicator because it is a significant indicator of conditions inside exclosures at one or more sites and of conditions outside exclosures at one or more sites

[1] Percent change is calculated as (2004-1941)/1941, using mean cover at all sites where each species occurred.

Table 4.5. Summary of published data regarding the grazing indicator status of species recorded on the Hill plots (Appendices 4.2 and 4.3). Data are from studies reporting frequency data for species inside and outside livestock grazing exclosures. The IV function (Appendix 4.1) was used to calculate the simplified Indicator Value (*IV*) for each species. The grazing treatment (Trt) with the maximum *IV* is noted, as well as additional information about the study. The reliability of the indicator status of a species can be assessed by comparing these results with those from the Hill plots (Table 4.3). Significant *p*-values are shown in bold. Note that some of the species reported in sources were combined with other species for analysis on the Hill plots (Table 4.1).

Species	Name in Source	State	Ecosystem^1	Elev. (m)	Sites	Trt	*IV*	*P*	Source^2
Achillea millefolium	*Achillea millefolium*	ID	MC forest	3000	1	In	8.2	0.4577	4
Achillea millefolium	*Achillea millefolium*	ID	MC forest	1400	1	Out	37.6	0.0883	6
Achillea millefolium	*Achillea millefolium*	BC	Fescue grassland	1110	2	In	48.1	**0.0004**	7
Achillea millefolium	*Achillea millefolium*	OR	Pine forest	1200	1	Out	49.4	**0.0298**	8
Aristida purpurea	*Aristida purpurea*	AZ	Desert grassland	1500	1	In	5.7	**0.0001**	3
Artemisia carruthii	*Artemisia wrightii*	NM	Pine forest	2530	2	In	5.7	0.0882	1
Astragalus spp.	*Astragalus humistratus*	NM	Pine forest	2530	2	In	6.8	**0.0213**	1
Bahia dissecta	*Bahia dissecta*	NM	Pine forest	2530	1	In	1.0	0.4949	1
Bouteloua gracilis	*Bouteloua gracilis*	NM	Pine forest	2530	2	Out	14.4	**0.0042**	1
Bouteloua gracilis	*Bouteloua gracilis*	AZ	Desert grassland	1500	1	In	11.5	0.1978	3
Brassicaceae spp.	*Thlaspi fendleri*	NM	Pine forest	2530	2	Out	10.1	**0.0001**	1
Brassicaceae spp.	*Descurainia pinnata*	CO	Salt-desert	1524	2	In	5.1	0.8291	2
Brassicaceae spp.	*Lepidium densiflorum*	CO	Salt-desert	1524	2	Out	22.0	**0.0000**	2
Bromus tectorum	*Bromus tectorum*	CO	Salt-desert	1524	3	Out	30.0	**0.0000**	2
Bromus tectorum	*Bromus tectorum*	BC	Fescue grassland	1070	1	Out	9.0	0.1375	7
Bromus tectorum	*Bromus tectorum*	OR	Pine forest	1200	1	In	2.5	0.4950	8
Elymus elymoides	*Sitanion hystrix*	NM	Pine forest	2530	2	Out	21.5	**0.0061**	1
Elymus elymoides	*Sitanion hystrix*	CO	Salt-desert	1524	3	In	13.3	**0.0047**	2
Erigeron divergens	*Erigeron divergens*	NM	Pine forest	2530	2	Out	1.6	0.5719	1
Erigeron flagellaris	*Erigeron flagellaris*	NM	Pine forest	2530	2	In	38.8	0.4467	1
Eriogonum alatum	*Eriogonum alatum*	NM	Pine forest	2530	2	In	6.9	**0.0123**	1
Festuca arizonica	*Festuca arizonica*	NM	Pine forest	2530	1	In	3.0	0.1240	1

Species	Name in Source	State	Ecosystem[1]	Elev. (m)	Sites	Trt	*IV*	*P*	Source[2]
Gutierrezia sarothrae	*Gutierrezia sarothrae*	CO	Salt-desert	1524	3	In	13.8	0.5396	2
Gutierrezia sarothrae	*Gutierrezia sarothrae*	AZ	Desert grassland	1370	2	In	43.8	**0.0128**	5
Hesperostipa comata	*Stipa comata*	BC	Pine forest	730	2	Out	77.3	**0.0000**	7
Heterotheca villosa	*Chrysopsis villosa*	NM	Pine forest	2530	2	In	39.3	**0.0013**	1
Hymenopappus filifolius	*Hymenopappus filifolius*	NM	Pine forest	2530	1	Out	2.7	0.3379	1
Hymenoxys richardsonii	*Actinea richardsoni*	NM	Pine forest	2530	2	Out	36.5	**0.0000**	1
Ipomopsis multiflora	*Gilia multiflora*	NM	Pine forest	2530	1	In	7.6	0.0947	1
Koeleria macrantha	*Koeleria cristata*	NM	Pine forest	2530	2	Out	2.6	0.2088	1
Koeleria macrantha	*Koeleria cristata*	ID	MC forest	1400	1	Out	16.9	0.0581	6
Koeleria macrantha	*Koeleria cristata*	BC	Fescue grassland and pine forest	910	5	Out	42.5	**0.0009**	7
Koeleria macrantha	*Koeleria cristata*	OR	Pine forest	1200	1	In	12.5	**0.0274**	8
Lappula spp.	*Lappula redowskii*	CO	Salt-desert	1524	3	Out	40.7	**0.0000**	2
Lappula spp.	*Lappula redowskii*	BC	Fescue grassland	850	1	Out	48.0	**0.0001**	7
Muhlenbergia montana	*Muhlenbergia montana*	NM	Pine forest	2530	1	Out	7.0	**0.0061**	1
Orthocarpus spp.	*Orthocarpus purpureo-albus*	NM	Pine forest	2530	2	In	2.6	0.1932	1
Phlox speciosus	*Phlox longifolia*	CO	Salt-desert	1524	3	In	17.8	**0.0004**	2
Plantago spp.	*Plantago purshii*	NM	Pine forest	2530	2	Out	15.8	0.1041	1
Plantago spp.	*Plantago purshii*	CO	Salt-desert	1524	2	Out	28.5	**0.0000**	2
Poa spp.	*Poa pratensis*	ID	MC forest	3000	1	Out	14.7	**0.0001**	4
Poa spp.	*Poa pratensis*	BC	Fescue grassland	1070	1	In	41.1	**0.0001**	7
Poa spp.	*Poa pratensis*	OR	Pine forest	1200	1	In	50.6	0.4987	8
Polygonum spp.	*Polygonum sawatchense*	NM	Pine forest	2530	2	Out	13.2	**0.0003**	1
Polygonum spp.	*Polygonum douglasii*	OR	Pine forest	1200	1	In	5.0	0.2480	8
Pseudocymopterus montanus	*Pseudocymopterus montanus*	NM	Pine forest	2530	2	Out	3.1	0.0877	1
Rosa woodsii	*Rosa woodsii*	ID	MC forest	1400	1	In	17.9	0.0691	6
Sporobolus cryptandrus	*Sporobolus cryptandrus*	NM	Pine forest	2530	2	Out	1.0	0.9944	1
Taraxacum officinale	*Taraxacum officinale*	ID	MC forest	3000	1	In	4.6	**0.0285**	4
Taraxacum officinale	*Taraxacum officinale*	BC	Fescue grassland	1010	2	Out	36.8	0.1432	7

Species	Name in Source	State	Ecosystem[1]	Elev. (m)	Sites	Trt	*IV*	*P*	Source[2]
Taraxacum officinale	*Taraxacum officinale*	OR	Pine forest	1200	1	Out	27.5	**0.0003**	8
Trifolium longipes	*Trifolium longipes*	ID	MC forest	1400	1	Out	1.3	0.7497	6
Vicia spp.	*Vicia americana*	ID	MC forest	3000	1	In	5.3	**0.0001**	4

[1] Ecosystem: MC Forest = Mixed-conifer forest; Pine forest = Ponderosa pine forest

[2] Sources:

1 = Gardner & Hubbell 1943 (100 0.1 m^2 quadrats per grazing treatment, measured in 1942)
2 = Turner 1971 (480 2 x 10 ft [0.6 x 3.0 m] subplots per grazing treatment, measured in 1963; data are summarized across four pairs of watersheds [one fenced and one unfenced in each pair] and three soil types)
3 = Bock et al. 1984 (800 points per grazing treatment, measured in 1981)
4 = Zimmerman & Neuenschwander 1984 (450 0.1 m^2 microplots per grazing treatment; measured in 1978)
5 = Chew 1982 (60 or 276 0.1 m^2 quadrats per grazing treatment in each of two vegetation types, measured in 1976 and 1977)
6 = Peek et al. 1978 (40 0.1 m^2 microplots per grazing treatments, measured in 1976)
7 = McLean & Tisdale 1972 (50 0.1 m^2 frames per grazing treatment at each of 7 sites; measured in 1968-1970)
8 = Krueger & Winward 1974 (40 1 x 2 ft [0.3 x 0.6 m] plots per grazing treatment, measured in 1972; data from area open to game only [ungrazed] and area open to cattle and game [grazed])

Table 4.6. Cross-classification of species based on indicator status with respect to overstory condition (columns; data in Table 4.2) and grazing treatment (rows; data in Table 4.3).

		Overstory Condition		
		In Open	Neither	Under Canopy
Grazing Treatment	Outside	*Achillea millefolium* *Antennaria* spp. *Bouteloua gracilis* *Erigeron divergens* *Erigeron flagellaris* *Gutierrezia sarothrae* *Hymenopappus filifolius* *Polygonum* spp.	*Aristida arizonica* *Chenopodium graveolens* *Elymus elymoides*	*Dalea* spp. *Oxytropis lambertii* *Trifolium longipes*
	Neither	*Arenaria* spp. *Sporobolus interruptus*		*Bromus tectorum* *Carex* spp. *Eriogonum racemosum*
	Inside	*Hesperostipa comata* *Erigeron formosissimus* *Orthocarpus* spp.	*Artemisia campestris* *Helianthella quinquenervis* *Muhlenbergia montana* *Pseudocymopterus montanus* *Rosa woodsii*	*Ceanothus fendleri* *Cirsium* spp. *Festuca arizonica* *Lotus wrightii* *Solidago* spp.

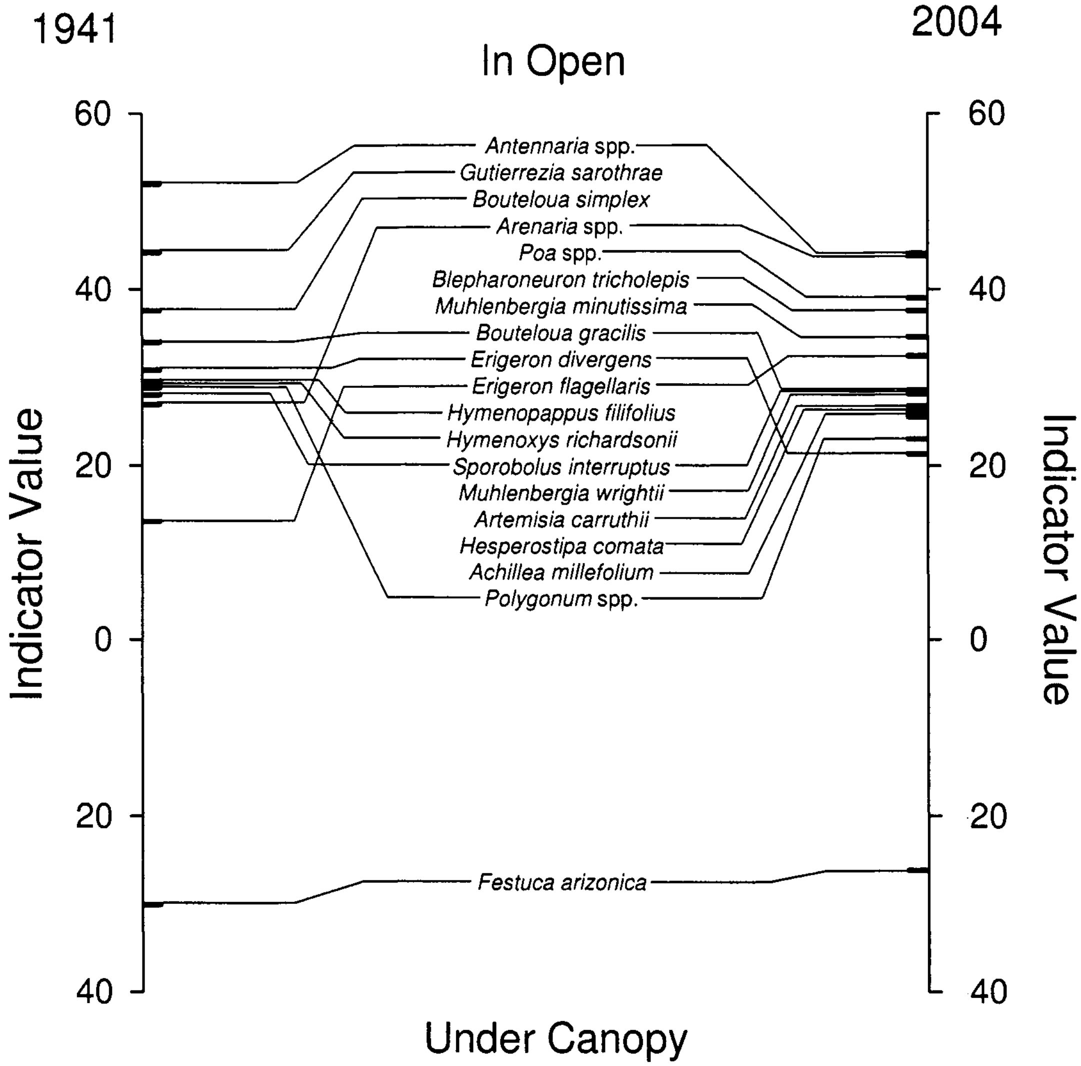


Figure 4.1. Strong indicator species (Indicator Value > 25 in at least one year) of conditions in the open (top) or under the tree canopy (bottom) in 1941 (left) and 2004 (right) on the Hill plots in northern Arizona. All statistically significant indicator species of overstory conditions are listed in Table 4.2. See Methods for details of how Indicator Values were calculated.

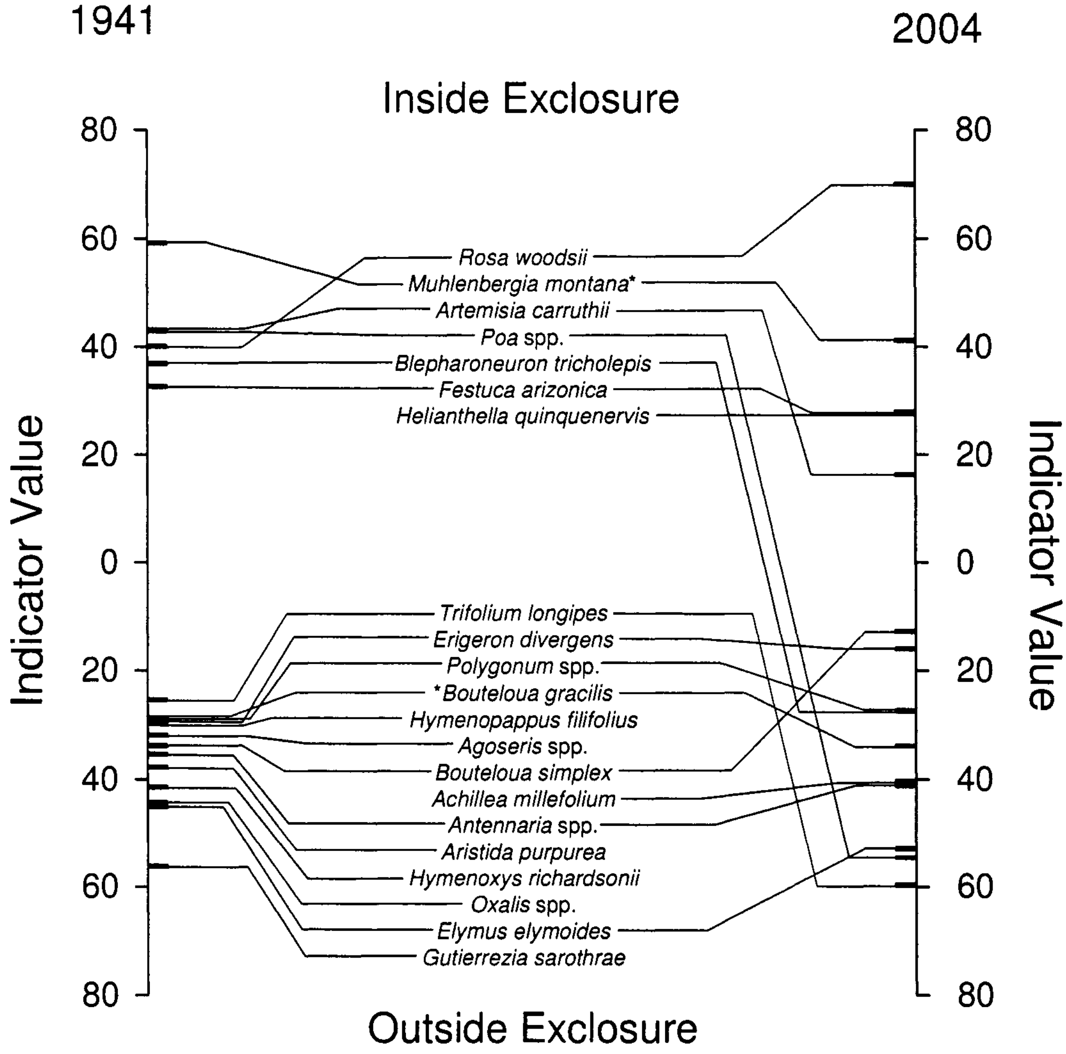


Figure 4.2. Strong indicator species (Indicator Value > 25 in at least one year) of conditions inside (top) and outside (bottom) grazing exclosures in 1941 (left) and 2004 (right) on the Hill plots in northern Arizona. All statistically significant indicator species of grazing treatments are listed in Table 4.3. See Methods for details of how Indicator Values were calculated. A '*' indicates that a species was an inconsistent indicator of one grazing treatment over the other in that year.

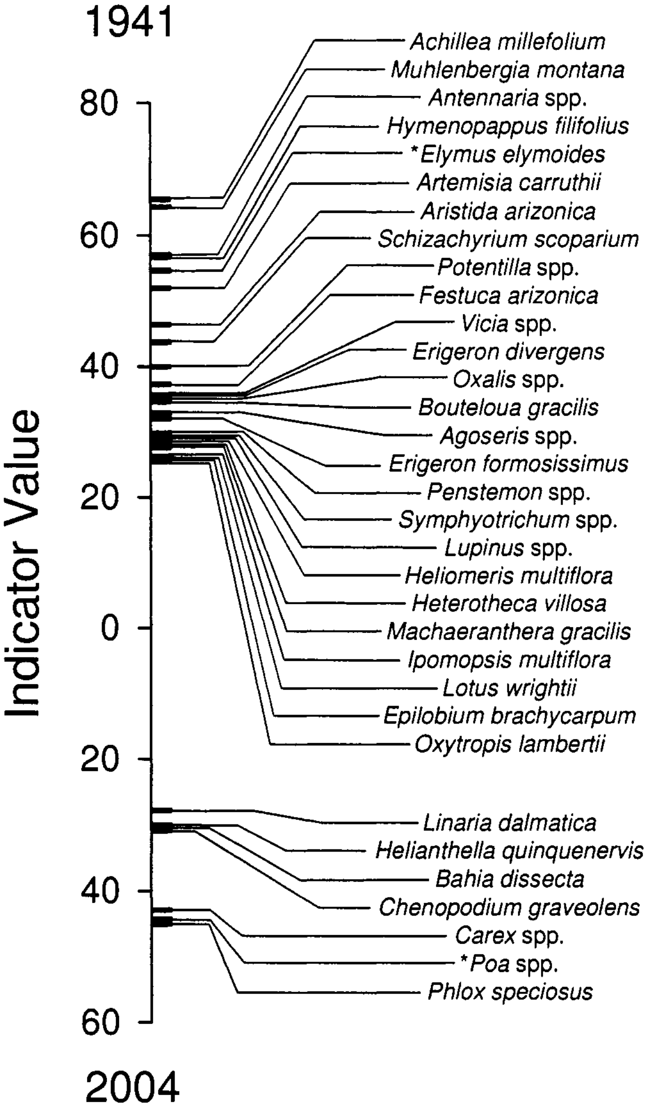


Figure 4.3. Strong indicator species (Indicator Value > 25) of conditions in 1941 (top) or 2004 (bottom) on the Hill plots in northern Arizona. All statistically significant indicator species of 1941 or 2004 are listed in Table 4.4. See Methods for details of how Indicator Values were calculated. A '*' indicates that a species was an inconsistent indicator of one year over the other.

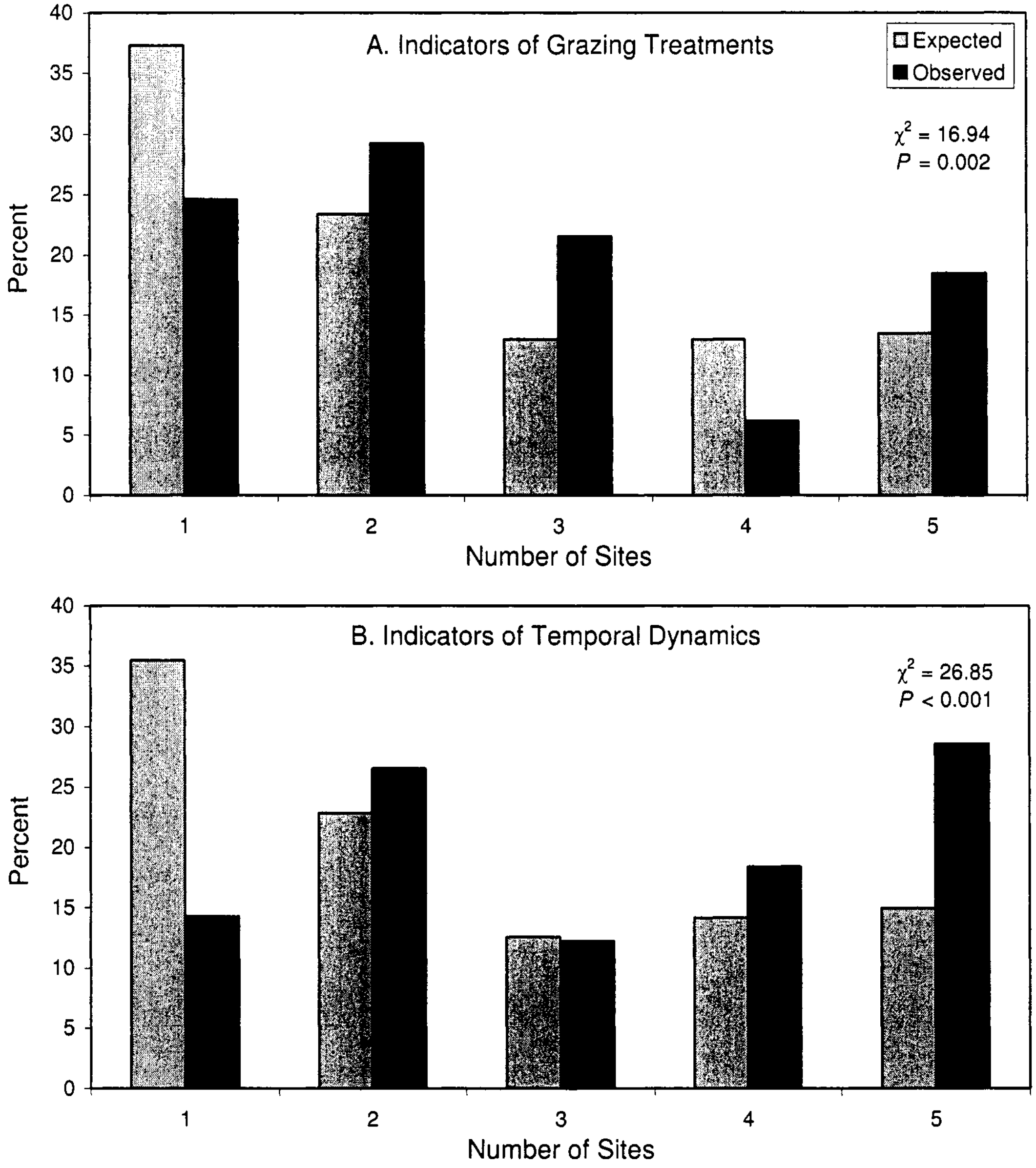


Figure 4.4. Percentage of species that were significant and consistent indicators of (a) grazing treatments and (b) years as a function of the number of sites at which they occurred in northern Arizona. 'Expected' is the percentage of all species that occurred on that number of sites, and 'Observed' is the percentage of all significant and consistent indicators that occurred on that number of sites.

Chapter 5

A New, Proportional Method for Reconstructing Historical Tree Diameters

Preface

Previous chapters have demonstrated important effects of the overstory on understory vegetation, which indicates that analyses of historical understory dynamics require accurate models of overstory growth and estimates of historical tree size. In this chapter, I present a new, proportional method for reconstructing historical tree diameters that helps address this need.

Abstract

Accurate methods of reconstructing historical tree diameters from increment cores are important because diameter is used in allometric equations to predict stand characteristics and to study stand dynamics. The conventional reconstruction method assumes that the pith is in the centre of the stem. This is often incorrect, as evidenced by an index (*PII*) quantifying the deviation between the geometric radius of the stem and the chronological radius of a core. I propose a new method which assumes that growth is proportional around the stem and, unlike the conventional method, cannot yield negative historical diameters. These methods were evaluated by calculating the deviations between reconstructed diameters and historical diameter measurements of 164 ponderosa pine (*Pinus ponderosa*) trees from permanent plots in Arizona and New Mexico.

Deviations varied with *PII* for the conventional method but not for the proportional method, and varied with tree age for both methods at one site. These methods could be used in tandem with the proportional method applied where the increment from outer ring to pith is measured, and the conventional method applied where this increment cannot be measured.

Introduction

Tree diameter is used in allometric equations to estimate many variables, including tree biomass (Gholz et al. 1979; Omdal et al. 2001), understory production (e.g., Bojorquez-Tapia et al. 1990) and forest carbon stocks and fluxes (Jenkins et al. 2003). Studies of stand structural dynamics (Foster et al. 1996) also often require the reconstruction of historical tree diameters. Accurate diameter reconstructions are therefore important for understanding and modeling forest dynamics and for making management decisions.

A stem cross-section provides the complete radial growth series of a tree but can only be obtained by killing it, which is unacceptable in most situations (Rozas 2003). In addition, results from studies of cross-sections may not be applicable in the field as they require information about stem geometry that cannot be obtained without sectioning the tree (e.g., Biging and Wensel 1988). Increment cores provide a non-destructive and operationally feasible method of obtaining growth data. Multiple cores per tree can increase the accuracy of diameter growth estimates (Matérn 1961; Iles 1974), but also greatly increase the amount of required processing time, effort, and core storage space. I sought a method of reconstructing historical diameters that could be applied to a single increment core per tree, regardless of where on the stem the core was obtained from.

Much attention has been devoted to methods for correctly identifying tree age (Duncan 1989; Villalba and Veblen 1997; Wong and Lertzman 2001; Rozas 2003; Clark and Hallgren 2004; Gutsell and Johnson 2004) but less attention has been given to methods for quantifying radial growth increment (e.g., Biging and Wensel 1988) or reconstructing historical tree diameter (Dolph 1981). In this paper, I describe a new method for reconstructing historical diameters and compare it with the conventional method by calculating the deviations between diameters reconstructed by each method and historical diameter measurements of trees on permanent plots.

Description of Reconstruction Methods

Stem Geometry

The pith, or chronological centre of a stem (*sensu* Norton et al. 1987), often does not correspond with the geometric centre (Williamson 1975; Biging and Wensel 1988; Singleton et al. 2003). Analysis of the deviation between these two points requires a stem cross-section (e.g., Singleton et al. 2003). However, an increment core can be used to describe the difference between the chronological and geometric radii using a pith increment index (*PII*):

$$[5.1] \qquad PII = \frac{2I_P - DIAM_{IB}}{DIAM_{IB}} \times 100$$

where I_P is the radial increment from outer ring to pith (chronological radius) as measured on an increment core, and $DIAM_{IB}$ is the inside bark diameter at coring height (twice the geometric radius). *PII* is positive when chronological > geometric radius, zero when chronological = geometric radius, and negative when chronological < geometric radius. If the pith is off-centre, the chronological radius varies around the stem, and *PII* differs between cores taken at different locations around the stem.

The Conventional and Proportional Methods

Conventional diameter reconstructions involve measuring the radial increment between the outer ring and the historical date of interest (I_H) and subtracting twice this measurement from inside bark diameter (e.g., Fulé et al. 1997). This method assumes that the chronological and geometric centres are equal, and that radial growth has been symmetric. When *PII* is positive, it can yield negative reconstructed diameters.

The proportional diameter reconstruction method involves multiplying the current diameter by the proportion of radial growth that occurred before the historical date of interest (G). G is calculated as:

$$G = \frac{I_P - I_H}{I_P} \qquad [5.2]$$

This method assumes that growth has been proportional around the stem, which is not always true (Norton et al. 1987) but is a less restrictive assumption than those of the conventional method. In particular, no assumption is made about the location of the pith relative to the geometric centre of the stem. Also, reconstructed diameters are always positive since $G \geq 0$.

An example (Fig. 5.1) illustrates these methods. An increment core that intersects the pith of a tree with a current inside bark diameter of 40 cm is used to reconstruct the tree's historical diameter (10 cm; in practice this is unknown) at the date of interest. The stem is assumed to be circular, and growth to have been proportional around the stem. If the chronological and geometric centres are identical, growth was radially symmetric and both methods yield the correct reconstructed diameter (Fig. 5.1a). Similarly, both methods yield the correct reconstructed diameter if the pith is off-centre but the core is taken where the chronological and geometric radii are equal (dashed lines in Fig. 5.1b,c). The points where these radii are equal cannot be identified in the field, however, so it is unlikely that cores will be taken at these points. For cores taken elsewhere around the stem, the proportional method yields the correct reconstructed diameter since *G* is unaffected by *PII* (Fig. 5.1b,c). In contrast, diameters reconstructed by the conventional method vary with core location, as illustrated by the extremes presented here. The conventional method underestimates the historical diameter if *PII* is positive (Fig. 5.1b) and overestimates it if *PII* is negative (Fig. 5.1c).

Case Studies

Data Collection

The conventional and proportional reconstruction methods were tested on 102 trees from a permanent plot in Arizona and validated on 62 trees from permanent plots in New Mexico. These plots were established in the early 1900s as part of a long-term study of growth and yield in ponderosa pine (*Pinus ponderosa* Laws.) (Pearson 1923). The Arizona plot (COC S1A; hereafter COC) is in the Fort Valley Experimental Forest, Coconino National Forest, 10 km northwest of Flagstaff, AZ. The New Mexico plots (CIB S1A and CIB S2A; hereafter jointly referred to as CIB) are in the Cibola National

Forest, 30 km south of Magdalena, NM. Historical data are stored in the Fort Valley Archives, US Forest Service Rocky Mountain Research Station, Flagstaff, AZ.

Contemporary measurements were gathered as part of a larger project (Moore et al. 2004). For this study, I used data from all live ponderosa pine trees that i) had been tagged and measured in 1914 or 1915 (COC and CIB, respectively), and ii) had cores on which I_P could be measured (i.e., no broken cores or heart rot). Sampled trees were $\geq$ 100 years old and spanned a 70 cm range of diameter at breast height (*DBH*; 137 cm) (Table 5.1). Small trees were not included because initial measurements were restricted to trees $\geq$ 9.14 cm *DBH*.

Cores were extracted at stump height (40 cm) because the larger project required a more accurate assessment of tree age than was possible with cores taken at breast height. Cores were mounted, sanded, and cross-dated using standard dendrochronological techniques (Stokes and Smiley 1968). For cores that missed the pith, the pith location and number of rings between the inner ring of the core and the pith (hereafter rings-to-pith) were estimated with a pith locator (Applequist 1958). Use of a pith locator is rapid and efficient but assumes that radial growth has been symmetric and constant near the centre of the tree (Rozas 2003). I_P and I_H were measured to the nearest mm. On cores that missed the pith, I_P was measured by positioning the pith locator on the core and measuring from the centre of the pith locator to the outer ring. *PII* and *G* were calculated for each increment core (Table 5.1).

Outside bark diameter at stump height (DSH_{OB}) was measured, and inside bark diameter (DSH_{IB}) was calculated using Myers' (1963) bark thickness equations for old-growth ponderosa pine. The DSH_{IB} of each tree at the historical measurement date (1914 for COC, 1915 for CIB) was reconstructed using the conventional and proportional method, and reconstructed diameters were then converted to DBH_{OB} for comparison with historical diameter measurements. Conversions were made using Myers' (1963) bark thickness equations and a *DSH-DBH* regression developed from other ponderosa pine trees on the Coconino and Cibola National Forests (J. Bakker et al., *unpub. data*):

[5.3] $DBH_{OB} = -0.5413 + 0.9313\ DSH_{OB}$ ($r^2 = 0.9928$; $P < 0.0001$; $n = 3387$)

I used this regression because published equations (e.g., Hann 1976) do not use the same stump height as this study.

Comparisons with Historical Diameters

Reconstructed diameters were compared with actual diameters measured in 1914-1915. The deviation (D_m) between the diameter reconstructed by each method (DBH_{Hm}) and the historical diameter (DBH_H) was calculated as:

[5.4] $D_m = DBH_{Hm} - DBH_H$

where $m = C$ for conventional method and $m = P$ for proportional method. Since D is expected to be correlated with historical diameter, I calculated the percent deviation ($\%D_m$) between reconstructed and historical *DBH* as:

[5.5] $$\%D_m = \frac{D_m}{DBH_H} \times 100 = \frac{DBH_{Hm} - DBH_H}{DBH_H} \times 100$$

Percent D_m is > 0 when the historical diameter is overestimated and < 0 when it is underestimated.

Wilcoxon signed rank tests were used to determine whether the mean $\%D_m$ was significantly different from 0 at each forest. Chi-squared goodness of fit tests determined whether the observed proportions of trees for which each method performed best (had smallest $|\%D|$) differed significantly from those expected by chance at each forest.

I postulated that $\%D_m$ might be related to *PII*, tree age, and rings-to-pith. Since *PII* is a proxy for the deviation between the chronological and geometric centres of a stem, $\%D_C$ should be related to it but $\%D_P$ should not (Fig. 5.1). While correlation with historical diameter was accounted for, age-diameter relationships are weak for ponderosa pine (Pearson 1950) and $\%D_m$ might be related with tree age (i.e., age at stump height when historical diameters were measured). The ability to identify the location of the pith decreases as the distance between the inner ring and pith increases (Rozas 2003), so $\%D_P$ might be related to rings-to-pith (since it requires the radial increment from outer ring to pith) while $\%D_C$ is not.

I used model selection to quantify the importance of explanatory variables (see Burnham and Anderson [2002; section 4.4] and Johnson and Omland [2004] for details). The three variables (*PII*, tree age, rings-to-pith) were combined in all seven possible combinations for each method at each forest. The model containing all variables was assessed for overall significance; if it was not significant, further testing was not warranted. If it was significant, the fit between model i and the data was examined by calculating an Akaike Information Criterion ($\mathrm{AIC_c}$) score normalized as an Akaike weight (w_i). The relative importance of a variable is Σw_i (maximum = 1) for all models containing that variable, and the model averaged coefficient for the variable is the sum of the products of the coefficient from model i and w_i (Burnham and Anderson 2002).

Results

At COC, the conventional method overestimated historical diameter (DBH_H) by 8.3% ($T^+ = -884.5$, $p = 0.003$; Table 5.2) while the proportional method overestimated DBH_H by only 0.1% ($T^+ = 198.5$, $p = 0.510$). The proportional method performed best for 64.7% of trees ($\chi^2 = 8.82$; $p = 0.003$). Percent D_C was negatively related to *PII* (Fig. 5.2a) and tree age (Fig. 5.2b), but there was little evidence of a relation with rings-to-pith (Table 5.3). Percent D_P was not related to *PII* (Fig. 5.2c) or rings-to-pith, but was negatively related to tree age (Table 5.3; Fig. 5.2d).

At CIB, the conventional method underestimated DBH_H by 1.3% ($T^+ = 207.5$, $p = 0.147$; Table 5.2) while the proportional method underestimated it by 8.6% ($T^+ = 678.5$, $p < 0.001$). The proportional method performed best for 53.2% of trees ($\chi^2 = 0.26$; $p = 0.612$). Percent D_C was negatively related to *PII* (Fig. 5.2a) but not to tree age (Fig. 5.2b) or rings-to-pith (Table 5.3). Percent D_P was not related to any of the explanatory variables (Table 5.3; Fig. 5.2c,d).

Discussion

The case studies provide support for using the proportional method rather than the conventional method to estimate historical tree diameter. Diameters reconstructed via the proportional method were unrelated to *PII* (Table 5.3; Fig. 5.2c), while those reconstructed via the conventional method (Fig. 5.2a) were overestimated when *PII* was negative (chronological < geometric radius) and underestimated when *PII* was positive (chronological > geometric radius).

The fact that the proportional method is not affected by core location (Fig. 5.1) has practical advantages during fieldwork. For example, a common practice is to measure stump height on the uphill side of the tree but to obtain increment cores from the side-slope to minimize reaction wood and get the most accurate assessment of growth possible from a single core (Stokes and Smiley 1968). If cores are going to be used to reconstruct historical diameters via the proportional method, they could be taken where stump height is measured, or elsewhere around the stem if necessary.

Deviations between historical and reconstructed diameters varied between forests (Table 5.2), indicating that variables other than core location were also important. While this difference may reflect variation in growth form between sites, it may also relate to tree age, which was an important explanatory variable at COC but not at CIB (Table 5.3). More young trees were sampled at COC (27 trees vs. 1 tree < 20 years old at CIB), and historical diameters of young trees were more likely to be overestimated, especially via the conventional method (Fig. 5.2b). The reason for this overestimation is unclear, but may relate to juvenile growth rates and patterns. The proportional method reduced the range of *%D* values for these young trees much more than it affected the range of *%D* values for older trees (Fig. 5.2d).

Historical diameter measurements were not made on small trees where the conventional method is most likely to yield negative diameters (Fig. 5.1b). An assessment of the implications of reconstruction method on stand characteristics would require a detailed study of all trees on a site, including these smaller trees, and would require multiple cores per tree to account for the effect of core location on diameters reconstructed by the conventional method.

Deviations between reconstructed and historical diameters were not related to rings-to-pith (Table 5.3), possibly because most cores missed the pith by only a few rings

(Table 5.1). For cores that miss the pith by a large amount or lack the arcs of inner rings (Rozas 2003), the proportional method cannot be used because I_P cannot be measured accurately. Although the conventional method is affected by core location, it remains useful for these cores and for others that do not reach the pith due to heart rot, exceptionally large stem diameter, or other factors.

I suggest that these methods be used in tandem, with the proportional method applied where the increment from outer ring to pith is measurable and the conventional method applied where this increment cannot be measured. Such an approach should be less biased than using the conventional method alone, although the implications of combining both methods in a study should be further studied.

References

Applequist, M.B. 1958. A simple pith locator for use with off-centre increment cores. Journal of Forestry **56**:141.

Biging, G.S., and L.C. Wensel. 1988. The effect of eccentricity on the estimation of basal area and basal area increment of coniferous trees. Forest Science **34**:621-633.

Bojorquez Tapia, L.A., P.F. Ffolliott, and D.P. Guertin. 1990. Herbage production-forest overstory relationships in two Arizona ponderosa pine forests. Journal of Range Management **43**:25-28.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York, NY.

Clark, S.L., and S.W. Hallgren. 2004. Age estimation of *Quercus marilandica* and *Quercus stellata*: applications for interpreting stand dynamics. Canadian Journal of Forest Research **34**:1353-1358.

Dolph, K.L. 1981. Estimating past diameters of mixed-conifer species in the central Sierra Nevada. USDA Forest Service. Research Note PSW-353.

Duncan, R.P. 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). New Zealand Natural Sciences **16**:31-37.

Foster, D.R., D.A. Orwig, and J.S. McLachlan. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. Trends in Ecology and Evolution **11**:419-424.

Fulé, P.Z., W.W. Covington,, and M.M. Moore. 1997. Determining reference conditions for ecosystem management in southwestern ponderosa pine forests. Ecological Applications **7**:895-908.

Gholz, H.G., C.C. Grier, A.G. Campbell, and A.T. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Forest Research Lab, Oregon State University, Corvallis, OR. Research Paper 41.

Gutsell, S.L., and E.A. Johnson. 2004. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. Journal of Ecology **90**:153-166.

Hann, D.W. 1976. Relationship of stump diameter to diameter at breast height for seven tree species in Arizona and New Mexico. USDA Forest Service. Research Note INT-212.

Iles, K. 1974. Geometrical considerations affecting the determination of basal area growth by increment boring methods. M.Sc. thesis. Oregon State University, Corvallis, OR.

Jenkins, J.C., D.C. Chojnacky, L.S. Heath, and R.A. Birdsey. 2003. National-scale biomass estimators for United States tree species. Forest Science **49**:12-35.

Johnson, J.B., and K.S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution **19**:101-108.

Matérn, B. 1961. On the precision of estimates of diameter growth from increment borings. *In* Proceedings of the 13th Congress, International Union of Forest Research Organizations, September 1961, Vienna. Pt. 2(2), Sect. 25/8.

Moore, M.M., D.W. Huffman, P.Z. Fulé, W.W. Covington, and J.E. Crouse. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Science **50**:162-176.

Myers, C.A. 1963. Estimating past diameters of ponderosa pines in Arizona and New Mexico. USDA Forest Service. Research Note RM-7.

Norton, D.A., J.G. Palmer, and J. Ogden. 1987. Dendroecological studies in New Zealand. 1. An evaluation of tree age estimates based on increment cores. New Zealand Journal of Botany **25**:373-383.

Omdal, D.W., W.R. Jacobi, and C.G. Shaw III. 2001. Estimating large-root biomass from breast-height diameters for ponderosa pine in northern New Mexico. Western Journal of Applied Forestry **16**:18-21.

Pearson, G.A. 1923. Natural reproduction of western yellow pine in the southwest. USDA Forest Service, Washington, DC. USDA Bulletin 1105.

Pearson, G.A. 1950. Management of ponderosa pine in the southwest as developed by research and experimental practice. USDA Forest Service, Washington, DC. Agriculture Monograph No. 6.

Rozas, V. 2003. Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. Plant Ecology **167**:193-212.

Singleton, R., D.S. DeBell, D.D. Marshall, and B.L. Gartner. 2003. Eccentricity and fluting in young-growth western hemlock in Oregon. Western Journal of Applied Forestry **18**:221-228.

Stokes, M.A. and T.L. Smiley. 1968. An introduction to tree-ring dating. Univ. Chicago, Chicago, IL.

Villalba, R., and T.T. Veblen. 1997. Improving estimates of total tree ages based on increment core samples. Écoscience **4**:534-542.

Williamson, R.L. 1975. Out-of-roundness in Douglas-fir stems. Forest Science **21**:365-370.

Wong, C.M., and K.P. Lertzman. 2001. Errors in estimating tree age: implications for studies of stand dynamics. Canadian Journal of Forest Research **31**:1262-1271.

Table 5.1. Summary statistics for trees from the Coconino (COC) and Cibola (CIB) National Forests used to reconstruct outside bark diameter at breast height (DBH_{OB}) in 1914-1915 from DBH_{OB} measurements and increment cores obtained in 1997-2001.

	COC (n = 102)		CIB (n = 62)	
	Mean ± SD	Range	Mean ± SD	Range
DBH_{OB} in 1997-2001 (cm)	52.5 ± 10.2	36.1 - 86.6	38.8 ± 9.4	14.7 - 64.5
DBH_{OB} in 1914-1915 (cm)	28.5 ± 12.8	10.2 - 63.5	24.6 ± 7.3	9.9 - 45.5
Stump height centre date	1844 ± 49	1702 - 1905	1824 ± 44	1606 - 1896
Rings-to-pith[a]	6 ± 4	0 - 20	5 ± 4	0 - 17
Pith Increment Index (*PII*; %)	-5.2 ± 9.8	-28.0 - 25.3	-9.5 ± 13.4	-40.0 - 30.5
Percentage of radial growth before 1914-1915 (*G*)	51 ± 17	21 - 82	57 ± 11	31 - 88

[a] Estimated number of rings between inner ring of core and pith

Table 5.2. Deviations (*D*) and percent deviations (*%D*) between historical diameters (Table 5.1) and reconstructed diameters using the conventional and proportional methods for trees from the Coconino (COC) and Cibola (CIB) National Forests.

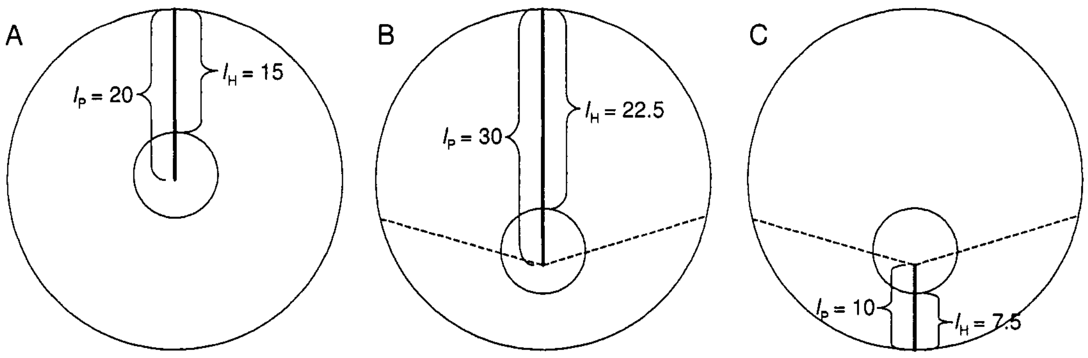
	COC (*n* = 102)		CIB (*n* = 62)	
	Mean ± SD	Range	Mean ± SD	Range
Conventional Method				
D (cm)	0.7 ± 4.0	-9.5 - 10.3	-0.7 ± 3.4	-8.6 - 6.7
%D	8.3 ± 22.5	-31.1 - 86.0	-1.3 ± 16.9	-27.2 - 56.0
Proportional Method				
D (cm)	-0.7 ± 2.8	-9.1 - 4.7	-2.3 ± 2.8	-10.1 - 3.8
%D	0.1 ± 11.9	-27.6 - 31.5	-8.6 ± 12.2	-40.7 - 25.2

Note: Positive and negative deviations indicate that the historical diameter was overestimated or underestimated, respectively.

Table 5.3. Results of model selection estimating the relative importance of three explanatory variables to the percent deviation (%*D*) between historical diameters (Table 5.1) and reconstructed diameters using the conventional and proportional methods for trees from the Coconino (COC) and Cibola (CIB) National Forests.

	COC (n = 102)		CIB (n = 62)	
	$\sum w_i$	Coefficient	$\sum w_i$	Coefficient
Conventional Method				
PII	1.0000	-1.34	1.0000	-0.66
Tree age	1.0000	-0.17	0.4059	-0.02
Rings-to-pith	0.2526	-0.02	0.2399	-0.01
Proportional Method				
PII	0.5188	-0.09	-	-
Tree age	0.9974	-0.09	-	-
Rings-to-pith	0.2516	0.00	-	-

Note: Larger summed Akaike weights ($\sum w_i$; maximum = 1) indicate increased evidence of the importance of a variable relative to the other variables in the model set (see Burnham and Anderson [2002] and Johnson and Omland [2004] for details). Summed Akaike weights and coefficients were not calculated for the proportional method at CIB as the model containing all variables was not significant ($P = 0.989$). The model containing all variables was significant for the proportional method at COC ($P = 0.0006$) and for the conventional method at COC ($P < 0.0001$) and CIB ($P = 0.0001$).



A:
$PII = 0\%$
$G = 0.25$

$DBH_{HC} = 10$ cm
$\%D_C = 0\%$

$DBH_{HP} = 10$ cm
$\%D_P = 0\%$

B:
$PII = +50\%$
$G = 0.25$

$DBH_{HC} = -5$ cm
$\%D_C = -150\%$

$DBH_{HP} = 10$ cm
$\%D_P = 0\%$

C:
$PII = -50\%$
$G = 0.25$

$DBH_{HC} = 25$ cm
$\%D_C = 150\%$

$DBH_{HP} = 10$ cm
$\%D_P = 0\%$

Figure 5.1. Idealized stem cross-sections illustrating the reconstruction of a historical diameter using the conventional method (DBH_{HC}) and proportional method (DBH_{HP}). Reconstructions are based on the current inside bark diameter (outer circle; 40 cm in these examples) and a single increment core (thick vertical line). Increments are measured on the core from the outer ring to the historical date of interest (I_H; required for both methods) and from the outer ring to the pith (chronological radius; I_P; required for the proportional method). The historical diameter (inner circle) is 10 cm in these examples but in practice is unknown. Pith increment index (*PII*) is a measure of the difference between the chronological radius of the core and the geometric radius of the stem, and *G* is the proportion of radial growth that occurred before the historical date of interest. In (A), the pith and geometric centre of the stem are equal and both methods correctly reconstruct the historical diameter. In (B) and (C), the pith is off-centre and the dashed lines indicate where the chronological and geometric radii are equal. The proportional method correctly reconstructs the historical diameter regardless of where the core is taken, while the conventional method can underestimate it (B) or overestimate it (C).

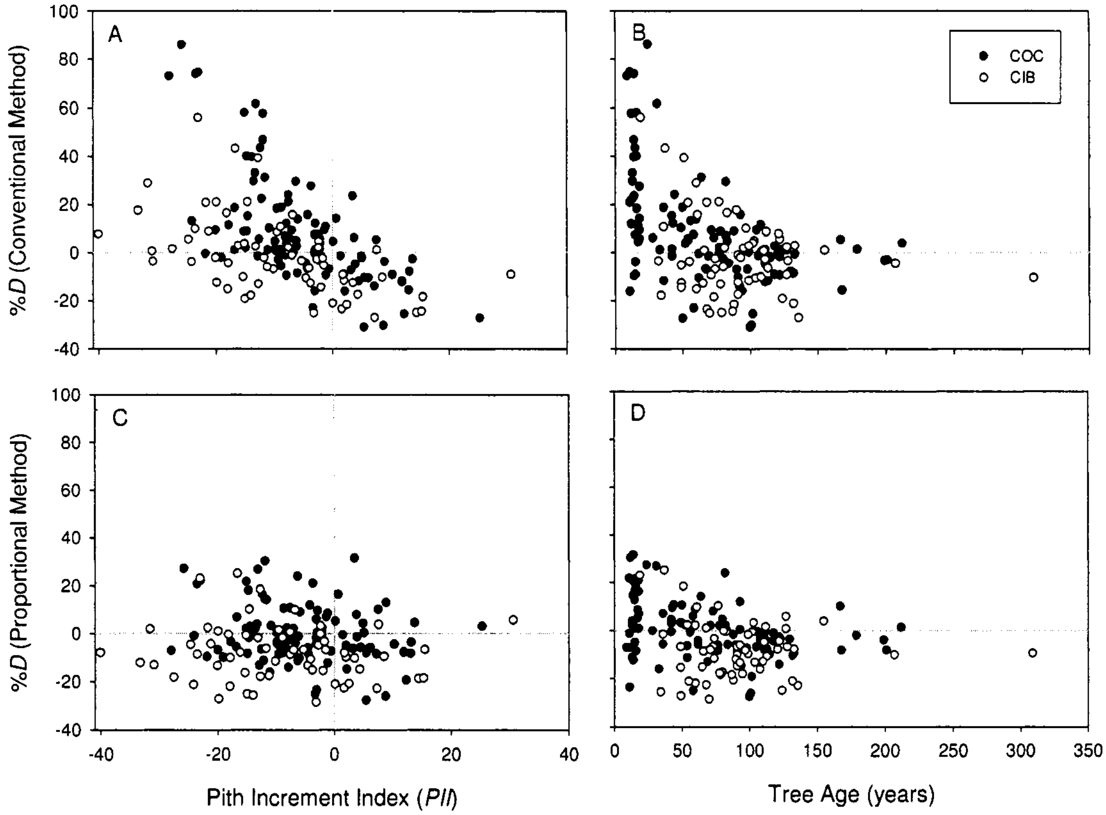


Figure 5.2. Scatterplots of percent deviation (*%D*; Table 5.2) between historical diameters (Table 5.1) and reconstructed diameters using the conventional method (top) and proportional method (bottom) for trees from the Coconino (COC) and Cibola (CIB) National Forests. For the conventional method, *%D* is negatively related to pith increment index (*PII*) at both sites (A) and to tree age at COC (B). For the proportional method, *%D* is not related to *PII* at either site (C) but is negatively related to tree age at COC (D). Horizontal and vertical zero lines are shown for reference. Model selection results are presented in Table 5.3.

Chapter 6

Conclusions and Implications

Vegetation Dynamics

The overall goal of this research was to examine vegetation dynamics within southwestern ponderosa pine forests. The observed increase in overstory vegetation has been noted in numerous other studies (e.g., Moore et al. 2004), but the complex and long-term effects of livestock grazing on the overstory have not been recognized. Overstory increases were smaller where livestock grazing continued than in areas protected from livestock grazing since 1912 (Chapter 2). One implication of these results is that livestock grazing might be used to control overstory regeneration, particularly in the first few years after germination. However, more research would be required to assess the feasibility of this as a management action; the required grazing intensities and ecological and economic costs may be prohibitive. A state-and-transition model for overstory vegetation dynamics is presented which suggests that the contemporary overstory structure is the result of interactions between livestock grazing, fire history, climate, and seed production.

This study provides one of the first quantitative analyses of long-term changes in the understory vegetation of southwestern ponderosa pine forests. Between 1941 and 2004, species density and herbaceous plant density both declined by 37%, shrub cover by 69%, herbaceous cover by 59%, graminoid cover by 45%, and forb cover by 82%

(Chapter 3). These declines are attributable to the increasing dominance of the overstory rather than to grazing effects. Experiments to identify the relative importance of mechanisms controlling overstory-understory relations in these forests would be valuable. Potential mechanisms include belowground competition for water and nutrients, reduced establishment of understory plants because of the accumulation of pine litter, and the interception of light and/or precipitation by the overstory.

Individual species differed in temporal dynamics and in response to grazing and overstory effects (Chapter 4). Three times more species were indicators of 1941 than 2004. Many species declined greatly in abundance and frequency during this interval; only a few (notably *Carex* spp. and introduced species) increased in cover. More species were indicators of grazing treatments in 1941 and of overstory effects in 2004, suggesting that the dominant structuring force in this ecosystem has changed over time. Some species responded mostly to grazing (e.g., *Elymus elymoides*, *Muhlenbergia montana*), some to overstory effects (e.g., *Bromus tectorum*, *Carex* spp., *Sporobolus interruptus*), and some to both forces (e.g., *Erigeron divergens*, *Bouteloua gracilis*, *Trifolium longipes*, *Hesperostipa comata*, *Festuca arizonica*). Species may respond in the same manner via different mechanisms. For example, *E. elymoides* is an indicator of areas outside exclosures because its awns deter grazing while *B. gracilis* is an indicator of the same condition because of its low stature (Arnold 1950). Analyses of individual species may identify other mechanisms explaining how and why species respond to grazing and/or overstory conditions.

Species that occurred at multiple sites were more likely to be significant indicators than those present at a single site. Most species were consistent indicators, though a few were inconsistent indicators of grazing treatment or years. The reasons for these inconsistencies among sites are unclear and deserve further study. In addition, a few species were indicators of ungrazed areas in 1941 but of grazed areas in 2004.

Given the dominant influence of overstory effects on the understory vegetation, analyses of historical understory dynamics require accurate models of overstory growth and estimates of historical tree size. The conventional method of reconstructing historical tree diameters assumes that the pith is in the centre of the stem, which is often incorrect. I developed a new, proportional method for reconstructing tree diameters (Chapter 5). The new method assumes that growth is proportional around the stem but makes no other assumptions about the location of the pith. By comparing diameters reconstructed by these two methods with historical diameter measurements on trees from permanent plots in Arizona and New Mexico, I demonstrated that the degree the pith was off-center affected the accuracy of diameters reconstructed with the conventional method but not those reconstructed with the proportional method.

Data from 1941 obviously do not represent presettlement reference conditions (Moore et al. 1999), though conditions in 1941 and changes since then provide insight into the overall trajectory of change that has occurred in these forests in recent decades. However, future research should address vegetation dynamics over longer time scales to assess the changes that occurred prior to 1941. For example, the vegetation on these sites was measured periodically between 1912 and 1941 on chart quadrats (J.D. Bakker and M.M. Moore, *unpub. data*). Many additional studies could be conducted on the Hill plots. For example, studies might examine the effects of long-term livestock grazing and growth of the overstory on plants (e.g., species-area curves), cryptogamic crusts, microbes (e.g., mycorrhizae [Frank et al. 2003]), and wildlife (e.g., small mammals, insects [Rambo & Faeth 1999]).

Efforts should be made to identify other extant data sets and to remeasure other long-term study areas. Future generations will thank us if we make a priority of preserving these data and sites. None of the work reported here would have been possible if the data collected in 1941 had not sat in a drawer for 60 years rather than being discarded.

Ecological Restoration

The results of this study highlight the importance of an adaptive management approach to the ecological restoration of southwestern ponderosa pine forests. Temporal dynamics and apparent differences between grazing treatments were attributable to the overstory, suggesting that the observed declines might be reversed by thinning the overstory (Casey 2004; Wienk et al. 2004; Moore et al. *in review*). Relevant areas of research include management of introduced species, the application of assembly rules to restoration, and spatial and temporal variation in restoration success.

Species-specific responses to restoration are more poorly understood than community-level responses. Species may be limited by a lack of seed, microsites, or other factors. Also, some species were present at many more sites in 1941 than 2004 (Table 4.3), suggesting that they have disappeared from the local species pool at individual sites. If these species are desired in the post-restoration treatment community, they may have to be seeded or transplanted into the local area.

Analytical Methods

A variety of methods were demonstrated that can be used in future studies. Meta-analytic techniques (Chapters 2 through 4; Gurevitch & Hedges 2001; Lipsey & Wilson 2001; Whitlock 2005) can be used to combine the results from multiple sites and to compare results with published data.

Indicator species analysis (ISA; Chapter 4; Dufrêne & Legendre 1997) permits the identification of species that are more abundant and/or frequent in one group than in another group(s). A number of recommendations regarding the use of ISA are presented, as well as the code to conduct these analyses in R (Appendix 4.1). A simplified ISA using presence/absence data yields results very similar to those from the classical ISA but can be easily calculated using summary data that can be reported in the literature. It is therefore recommended for use in future studies. Conducting ISAs at multiple sites permits an assessment of the consistency of indicators and reduces the likelihood of spurious results from individual sites. The correct exchangeable units must be identified for the permutation tests used to assess the significance of indicator values.

The proportional tree diameter reconstruction method (Chapter 5) can be used to reconstruct historical stem diameters more accurately than the conventional method. Accurate reconstructions are important when accounting for overstory effects in studies of historical understory vegetation dynamics. The proportional method requires knowledge about radial growth between the pith and outer ring which will not always be available, particularly for trees with heart rot or exceptionally large stem diameters. Therefore, the proportional and conventional reconstruction methods should be used in tandem, with the proportional method applied where the increment from outer ring to pith is measured, and the conventional method applied where this increment cannot be measured.

References

Arnold, J.F. 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. Journal of Forestry **48**:118-126.

Casey, C.A. 2004. Herbaceous biomass and species composition responses to ponderosa pine restoration treatments. M.Sc. thesis. Northern Arizona University, Flagstaff, AZ.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Frank, D.A., C.A. Gehring, L. Machut, and M. Phillips. 2003. Soil community composition and the regulation of grazed temperate grassland. Oecologia **137**:603-609.

Gurevitch, J., and L.V. Hedges. 2001. Meta-analysis: combining the results of independent experiments. Pages 347-369 *in* S.M. Scheiner and J. Gurevitch (editors). Design and analysis of ecological experiments. Oxford University Press, New York, NY.

Lipsey, M.W., and D.B. Wilson. 2001. Practical meta-analysis. SAGE Publications, Thousand Oaks, CA.

Moore, M.M., W.W. Covington, and P.Z. Fulé. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. Ecological Applications **94**:1266-1277.

Moore, M.M., D.W. Huffman, P.Z. Fulé, W.W. Covington, and J.E. Crouse. 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. Forest Science **50**:162-176.

Moore, M.M., C.A. Casey, J.D. Bakker, J.D. Springer, P.Z. Fulé, W.W. Covington, and D.C. Laughlin. *In review*. Herbaceous response to restoration treatments in a ponderosa pine forest, 1992-2004. Rangeland Ecology and Management

Rambo, J.L., and S.H. Faeth. 1999. Effect of vertebrate grazing on plant and insect community structure. Conservation Biology **13**:1047-1054.

Whitlock, M.C. 2005. Combining probability from independent tests: the weighted Z-method is superior to Fisher's approach. Journal of Evolutionary Biology *In press*.

Wienk, C.L., C.H. Sieg, and G.R. McPherson. 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. Forest Ecology and Management **192**:375-393.

Appendix 2.1. Density (t/ha) of regeneration age classes at five sites in northern Arizona in 1941. The mean ± SD and minimum-maximum values are presented for each site x grazing combination. These data are untransformed, whereas those in Table 2.3 are back-transformed to original units. Site abbreviations are in Table 2.1.

Age Class	Grazing Trt	BF	BS	FP	RT	RL
1919	In	679±1331 a	229±363 a	565±926 a	5086±8126 a	121±355 a
		0-7535	0-1615	0-4306	0-31,754	0-1615
	Out	101±333 b	81±230 b	209±517 b	8880±8020 b	121±355 a
		0-1615	0-1076	0-2691	0-31,754	0-1615
1929	In	1756±2567 a	350±449 a	141±350 a	2422±2702 a	2489±3075 a
		0-12,378	0-1615	0-2153	0-11,302	0-17,760
	Out	410±757 b	229±470 a	94±254 a	7723±6790 b	108±250 b
		0-3229	0-2153	0-1076	538-25,833	0-1076
>1929	In	1063±1899 a	821±1005 a	54±184 a	431±541 a	2328±2851 a
		0-10,764	0-4306	0-1076	0-1615	0-12,378
	Out	148±373 b	1251±1275 a	94±254 a	1238±1462 b	94±207 b
		0-2153	0-4306	0-1076	0-4844	0-538

Appendix 3.1. Species density, plant density, and shrub cover inside and outside of grazing exclosures at five sites in northern Arizona in 1941 and 2004. The mean ± SD and minimum-maximum values are presented for each site x grazing combination. These data are untransformed, whereas those in Fig 3.3 are back-transformed to original units. Site abbreviations are in Table 2.1.

	Species Density (species / line)		Plant Density (herbaceous plants / line)		Shrub Cover (%)	
Site	In	Out	In	Out	In	Out
1941						
BF	6.4±2.0 a	7.5±2.7 a	34.3±18.1	42.1±15.3	0.79 ± 1.94	3.39±3.80
	2-15	3-14	4-76	14-77	0-12.40	0-17.10
BS	10.4±2.4	7.4±2.6	42.7±14.6	28.7±17.5	0.07±0.42	0.00±0.01
	5-16	1-13	25-96	2-75	0-2.64	0-0.04
FP	10.0±3.1	10.4±2.5	53.5±37.0	62.5±45.2	0.55±1.98	0.01±0.11
	2-17	4-17	8-194	16-225	0-13.20	0-1.00
RT	7.8±2.5	7.0±2.8	41.4±10.9	27.4±12.2	0.00±0.01	0.06±0.23
	3-12	4-16	25-62	10-49	0-0.04	0-1.00
RL	12.1±3.0	8.3±2.5	39.0±17.0	28.4±14.4	6.68±9.69	0.28±0.69
	4-17	3-13	4-73	6-62	0-41.10	0-3.52
2004						
BF	4.0±2.7	4.2±1.6	17.1±18.5	34.9±18.1	0.18±0.42	0.25±0.76
	0-14	1-8	0-103	4-97	0-1.87	0-5.13
BS	6.9±2.0	6.3±2.2	22.4±13.3	29.4±20.5	0.17±1.02	0.02±0.05
	4-11	3-12	7-59	8-90	0-6.22	0-0.23
FP	6.3±3.3	9.8±3.7	33.0±33.3	58.9±50.7	0.05±0.25	0.01±0.06
	1-15	1-17	2-176	2-301	0-1.77	0-0.36
RT	3.5±2.5	2.7±2.3	14.6±16.5	7.8±7.6	-	-
	0-8	1-6	0-58	1-19		
RL	6.6±3.0	7.3±2.6	17.6±12.7	32.0±16.0	4.86±6.86	0.00±0.02
	2-13	3-13	2-52	8-71	0-24.64	0-0.13

Appendix 3.2. Herbaceous cover (total, graminoid, forb) inside and outside of grazing exclosures at five sites in northern Arizona in 1941 and 2004. The mean ± SD and minimum-maximum values are presented for each site x grazing combination. These data are untransformed, whereas those in Fig 3.3 are back-transformed to original units. Site abbreviations are in Table 2.1.

	Herbaceous Cover (%)		Graminoid Cover (%)		Forb Cover (%)	
Site	In	Out	In	Out	In	Out
1941						
BF	3.55±2.18	4.91±2.26	3.37 ±2.18	4.65±2.20	0.18±0.17	0.26±0.21
	0.24-8.10	1.14-11.74	0.08-7.78	1.12-11.72	0-0.70	0-1.14
BS	3.78±1.83	3.67±2.72	2.96±1.69	1.14±1.19	0.82±0.53	2.54±2.25
	1.06-9.58	0.08-9.78	0.64-8.92	0.04-5.14	0.14-2.72	0-7.80
FP	4.89±3.17	5.61±5.17	3.68±2.26	1.35±1.45	1.21±1.39	4.26±4.19
	0.68-13.66	0.58-24.04	0-11.20	0.18-8.44	0.06-6.92	0.08-15.90
RT	3.39±1.09	2.52±1.04	3.10±1.16	2.35±1.04	0.29±0.18	0.17±0.15
	2.04-6.08	0.82-4.38	1.70-5.88	0.48-4.36	0-0.70	0.02-0.58
RL	2.86±1.67	1.81±1.28	1.65±1.42	0.48±0.29	1.22±0.86	1.33±1.18
	0.10-8.32	0.16-4.88	0-6.66	0.10-1.20	0.08-3.92	0.06-4.52
2004						
BF	0.94±1.08	2.47±1.79	0.86±1.03	2.40±1.78	0.07±0.11	0.08±0.10
	0-4.45	0.08-7.68	0-4.38	0.05-7.51	0-0.57	0-0.52
BS	1.77±1.45	1.54±1.12	1.58±1.38	1.32±1.02	0.19±0.16	0.22±0.62
	0.21-5.45	0.20-4.71	0.10-5.36	0.11-4.68	0-0.87	0-3.76
FP	2.10±2.70	2.84±2.80	1.92±2.51	1.89±1.69	0.19±0.26	0.95±1.50
	0.03-14.44	0.05-12.14	0.02-13.50	0-8.35	0-1.23	0-7.41
RT	0.76±0.85	0.58±0.57	0.70±0.79	0.56±0.55	0.06±0.08	0.02±0.02
	0-2.82	0.02-1.33	0-2.58	0.02-1.31	0-0.25	0-0.05
RL	0.56±0.47	2.41±1.64	0.39±0.37	2.05±1.49	0.18±0.18	0.37±0.31
	0.03-1.80	0.49-7.73	0.02-1.69	0.49-6.92	0-0.69	0-1.05

Appendix 4.1. *IV* function to calculate Dufrêne & Legendre's (1997) Indicator Value for all species in all groups in R (R Development Core Team 2005). Text to the right of a '#' are comments describing the code.

```
# R Code to Calculate Dufrêne & Legendre's (1997) Indicator Value for all species in all groups
# JBakker, June 13 2005

# Required Format:
# Data in txt format, with treatment in first column (coded as 1 or 2)
# Must have only 2 groups, and must have >1 species (can use a dummy species)
# No spaces in column headings (use '.' instead)
# All data values >= 0 (no blank cells)
# Number of permutations controlled by 'numitr' variable below

# Obtain Data and Group files
sppmatrix <- read.table(file.choose(),header=TRUE)

# Set initial values for variables
grps <- sppmatrix[1]
data <- sppmatrix[,2:dim(sppmatrix)[2]]
numspp <- (ncol(sppmatrix)-1)
relabu <- c()
relfrq <- c()
indval <- c()
rand <- c()
pval <- c()
numitr = 9999

# Calculate mean and presence/absence in each group
grp.1 <- subset(data,grps==1)
count1 <- nrow(grp.1) # number of lines in group 1
count3=(grp.1>0) # TRUE if >0, else FALSE
x.1 <- as.vector(mean(grp.1)) # mean abundance of species in group 1
grp.2 <- subset(data,grps==2)
count2 <- nrow(grp.2) # number of lines in group 2
count4=(grp.2>0) # TRUE if >0, else FALSE
x.2 <- as.vector(mean(grp.2)) # mean abundance of species in group 2

# Calculate Actual Specificity
a.1 <- c()
a.2 <- c()
for(i in 1:numspp) {
        if((x.1[i]+x.2[i])==0) {
```

```
                a.1[i] <- 0
                a.2[i] = 0
        } else {
                a.1[i] <- x.1[i]/(x.1[i]+x.2[i])
                a.2[i] = x.2[i]/(x.1[i]+x.2[i])
        }
}
A <- c(a.1,a.2) # vector of relative abundances
relabu <- cbind(relabu,A)
relabu.actual <- relabu[,1]

# Calculate Actual Fidelity
b.1 <- matrix(ncol=numspp)
b.2 <- matrix(ncol=numspp)
for(i in 1:numspp) {
        b.1[1,i] = sum(count3[,i], na.rm=TRUE)
        b.2[1,i] = sum(count4[,i], na.rm=TRUE)
}
b1 <- b.1/count1
b2 <- b.2/count2
B <- c(t(b1),t(b2))
relfrq <- cbind(relfrq,B)
relfrq.actual <- relfrq[,1]

# Calculate Actual IV
IV<-A*B*100
indval <- cbind(indval,IV)
indval.actual <- indval[,1]

# Calculate Permutational IVs
# rand.grps<-c()
for(i in 1:numitr) {
cat("\n","Iteration ", i)

rand<-sample(t(grps))
rand.df<-data.frame(rand)
data.perm <- cbind(rand.df,data)
# rand.grps<-cbind(rand.grps,rand) # Matrix of permutations of group identities

# Calculate mean and presence/absence in each group
grp.1.perm <- subset(data.perm,rand.df==1,select=2:dim(data.perm)[2])
count1 <- nrow(grp.1.perm) # number of lines in group 1
count3=(grp.1.perm>0) # TRUE if >0, else FALSE
x.1.perm <- as.vector(mean(grp.1.perm)) # mean abundance of species in group 1
grp.2.perm <- subset(data.perm,rand.df==2,select=2:dim(data.perm)[2])
count2 <- nrow(grp.2.perm) # number of lines in group 2
```

```
count4=(grp.2.perm>0) # TRUE if >0, else FALSE
x.2.perm <- as.vector(mean(grp.2.perm)) # mean abundance of species in group 2

# Calculate Permutation Specificity
a.1.perm <- c()
a.2.perm <- c()
for(i in 1:numspp) {
        if((x.1.perm[i]+x.2.perm[i])==0) {
                a.1.perm[i] = 0
                a.2.perm[i] = 0
        } else {
                a.1.perm[i] = x.1.perm[i]/(x.1.perm[i]+x.2.perm[i])
                a.2.perm[i] = x.2.perm[i]/(x.1.perm[i]+x.2.perm[i])
        }
}
A.perm <- c(a.1.perm,a.2.perm) # vector of relative abundances
relabu <- cbind(relabu,A.perm)

# Calculate Permutation Fidelity
b.1.perm <- matrix(ncol=numspp)
b.2.perm <- matrix(ncol=numspp)
for(i in 1:numspp) {
        b.1.perm[1,i] = sum(count3[,i], na.rm=TRUE)
        b.2.perm[1,i] = sum(count4[,i], na.rm=TRUE)
}
b1.perm <- b.1.perm/count1
b2.perm <- b.2.perm/count2
B.perm <- c(t(b1.perm),t(b2.perm))
relfrq <- cbind(relfrq,B.perm)

# Calculate Permutation IV
IV.perm<-A.perm*B.perm*100
indval <- cbind(indval,IV.perm)
}

# Calculate p-value for each species in each group
indval.perm <- indval[,2:dim(indval)[2]]
numcls <- nrow(indval) # number of species x group combinations

gt.IV <- matrix(0,nrow=numcls)
count5 = (indval.perm >= indval.actual)
for(k in 1:numcls) {
        gt.IV[k,] = sum(count5[k,], na.rm=TRUE)
}
pval=(gt.IV+1)/(numitr+1)
```

```
# Output results
out <- cbind(rep(1:2,each=numspp), relabu.actual, relfrq.actual, indval.actual, pval)
colnames(out) <- c("Grp","A","B","IV","pval")
rownames(out) <- rep(colnames(data),2)
out

write.table(out, file="IV.results.txt", append=FALSE, sep=" ",
col.names=c("Grp","A","B","IV","pval"))
```

Appendix 4.2. Number of lines occupied by plant species inside and outside of grazing exclosures at fives sites in northern Arizona in 1941. The number of lines sampled is reported in Table 3.1, and details about species combined at the generic level are in Table 4.1.

Species[1]	Big Fill		Black Springs		Fry Park		Reese Tank		Rogers Lake	
	In	Out	In	Out	In	Out	In	Out	In	Out
Achillea millefolium	0	0	16	9	43	42	7	4	37	33
Agoseris spp.	1	10	3	1	7	65	2	0	2	12
Allium spp.	0	0	0	0	0	1	0	0	0	0
Antennaria spp.	0	0	2	5	35	58	2	1	19	16
Arenaria spp.	0	0	4	1	14	12	0	0	3	0
Aristida arizonica	6	22	6	15	0	0	0	0	0	0
Aristida purpurea	7	30	7	20	0	0	0	0	0	0
Artemisia campestris	16	0	0	0	20	0	0	0	0	0
Artemisia carruthii	27	8	28	6	55	20	5	1	25	14
Asclepias spp.	0	2	0	0	0	0	0	0	0	0
Astragalus spp.	3	15	7	0	2	1	1	3	4	3
Blepharoneuron tricholepis	3	0	19	2	47	2	0	0	23	5
Bouteloua gracilis	58	80	8	12	0	4	5	10	5	0
Bouteloua simplex	0	0	0	0	0	27	0	0	0	0
Brassicaceae spp.	0	1	1	0	3	4	0	0	0	1
Bromus spp.	0	0	0	1	3	0	6	2	1	0
Carex spp.	4	2	8	14	50	34	6	5	3	12
Castilleja spp.	0	0	0	0	1	0	1	1	0	0
Ceanothus fendleri	5	0	1	0	7	2	0	1	0	0
Chenopodium spp.	0	0	0	0	0	3	0	0	0	0
Cirsium spp.	5	1	10	0	11	7	7	0	12	4
Comandra umbellata	16	0	0	0	0	0	0	0	0	0
Dalea spp.	1	0	1	0	0	0	0	0	0	0
Elymus elymoides	40	46	20	15	38	62	18	18	34	40
Elymus trachycaulus	0	0	0	0	0	1	0	0	0	0
Epilobium brachycarpum	0	0	4	8	2	3	0	0	12	6
Ericameria nauseosus	1	7	1	1	0	0	0	0	0	0
Erigeron divergens	5	9	8	11	13	58	2	4	9	10
Erigeron flagellaris	1	6	0	4	1	25	1	4	2	5
Erigeron formosissimus	0	0	9	5	16	6	2	5	18	9
Eriogonum alatum	8	3	0	0	0	0	1	0	0	0
Eriogonum racemosum	3	2	12	6	0	0	0	1	6	0
Euphorbia spp.	3	10	0	0	0	3	0	0	0	0
Festuca arizonica	45	48	2	0	41	4	19	18	15	4
Fragaria spp.	0	0	0	1	0	0	0	0	0	0
Gaillardia pinnata	2	4	0	0	0	0	0	0	0	0
Gaura spp.	1	0	0	0	0	0	0	0	0	0
Geranium caespitosum	3	0	0	0	0	0	0	0	0	0
Gilia spp.	0	0	0	0	0	0	1	0	0	0
Gutierrezia sarothrae	5	56	0	0	0	0	0	1	0	0
Heliomeris longifolia	0	0	0	0	0	0	2	1	0	0
Heliomeris multiflora	7	0	10	0	19	2	3	3	27	20
Hesperostipa comata	9	1	0	0	0	0	0	0	0	0
Heterotheca villosa	0	0	14	5	15	2	0	0	1	0
Hieracium fendleri	2	0	1	0	1	0	0	0	2	0
Houstonia wrightii	0	0	1	2	8	3	0	0	5	1

Species[1]	Big Fill		Black Springs		Fry Park		Reese Tank		Rogers Lake	
	In	Out	In	Out	In	Out	In	Out	In	Out
Hymenopappus filifolius	15	29	0	0	0	0	0	0	0	0
Hymenopappus mexicanus	0	0	1	0	26	2	0	0	0	0
Hymenoxys richardsonii	0	0	1	30	0	0	1	0	1	12
Ipomopsis multiflora	7	8	0	0	0	0	0	0	0	0
Iris missouriensis	0	0	0	0	0	1	0	0	0	2
Koeleria macrantha	1	0	18	0	30	7	2	6	7	2
Lathyrus spp.	1	0	0	0	0	0	0	0	0	0
Linum lewisii	1	5	0	0	0	0	2	0	0	0
Lithospermum multiflorum	0	0	1	0	5	1	0	0	0	0
Lotus wrightii	9	11	12	3	8	4	1	1	14	2
Lupinus spp.	13	26	0	0	9	10	0	5	3	0
Machaeranthera gracilis	3	8	3	4	0	0	0	0	0	0
Muhlenbergia minutissima	0	0	0	0	0	16	0	0	0	0
Muhlenbergia montana	58	61	21	11	74	7	20	20	22	6
Muhlenbergia rigens	15	6	0	0	2	0	0	0	3	0
Muhlenbergia wrightii	1	0	2	0	3	5	0	0	2	0
Oenothera spp.	2	0	0	1	0	1	0	0	0	0
Orthocarpus spp.	0	0	0	0	3	0	1	0	5	1
Oxalis spp.	0	0	0	0	4	54	0	0	0	1
Oxytropis lambertii	0	7	0	0	0	0	7	7	0	0
Penstemon spp.	5	9	11	1	27	10	0	1	9	6
Plantago spp.	2	18	0	5	0	0	0	0	0	0
Poa spp.	19	3	36	8	60	31	13	10	23	22
Polygonum spp.	3	2	0	0	5	53	0	0	1	5
Portulaca oleracea	4	0	0	0	0	4	0	0	0	0
Potentilla spp.	3	0	20	24	23	27	5	1	17	9
Pseudocymopterus montanus	0	0	0	1	5	3	5	4	7	1
Rhus trilobata	4	0	0	0	0	0	0	0	0	0
Ribes spp.	0	0	0	0	1	0	0	0	0	0
Rosa woodsii	0	0	0	0	0	0	1	0	24	11
Saxifragaceae spp.	0	0	0	0	0	0	0	0	1	0
Schedonnardus paniculatus	0	0	0	1	0	0	0	0	0	0
Schizachyrium scoparium	38	18	0	1	0	0	0	0	0	0
Senecio spp.	1	0	3	2	7	21	0	0	0	1
Solidago spp.	1	0	25	25	7	11	3	0	1	0
Sporobolus interruptus	0	0	32	24	14	16	0	0	0	0
Symphyotrichum spp.	2	3	22	4	0	10	0	1	27	24
Tetradymia canescens	12	2	0	0	0	0	0	0	0	0
Thalictrum fendleri	2	0	2	0	5	0	0	0	1	3
Trifolium longipes	0	0	0	1	2	31	0	0	27	25
UNK CHA	0	0	1	0	0	0	0	0	0	0
UNK COMP1	0	0	0	0	0	2	0	0	0	0
UNK ERI	0	0	0	0	0	0	0	0	1	0
UNK W1	0	0	0	2	0	7	1	0	0	0
UNK W2	0	0	0	0	0	1	1	0	0	0
UNK W3	2	12	0	0	1	1	1	0	0	0
UNK W4	1	2	2	0	0	0	0	0	0	0
UNK W5	2	2	1	0	5	16	0	0	4	4
UNK W6	0	0	0	0	0	0	0	0	1	0
Verbascum thapsus	0	1	0	0	0	0	0	0	0	0
Vicia spp.	0	0	0	3	25	25	1	1	16	1

[1] Species with unknown codes ("UNK ...") were not analyzed.

Appendix 4.3. Number of lines occupied by plant species inside and outside of grazing exclosures at five sites in northern Arizona in 2004. The number of lines sampled is reported in Table 3.1, and details about species combined at the generic level are in Table 4.1.

Species[1]	Big Fill		Black Springs		Fry Park		Reese Tank		Rogers Lake	
	In	Out	In	Out	In	Out	In	Out	In	Out
Achillea millefolium	0	0	4	1	8	37	5	0	7	20
Agoseris spp.	0	0	0	0	0	1	0	0	0	0
Agropyron cristatum	0	0	0	0	0	2	0	0	0	0
Amaranthus powellii	1	0	0	0	0	0	0	0	0	0
Ambrosia psilostachya	0	0	0	2	0	1	0	0	0	0
Antennaria spp.	0	0	2	8	17	47	1	0	8	8
Arenaria spp.	0	0	1	0	16	13	0	0	0	0
Aristida arizonica	0	0	0	1	0	0	0	0	0	0
Aristida purpurea	0	3	1	1	0	1	0	0	0	0
Artemisia campestris	4	1	0	0	0	4	0	0	0	0
Artemisia carruthii	8	0	17	4	27	16	1	0	7	2
Astragalus spp.	1	0	1	0	0	6	0	0	0	0
Atriplex rosea	1	1	0	0	0	0	0	0	0	0
Bahia dissecta	8	11	0	0	0	0	0	0	0	0
Blepharoneuron tricholepis	0	0	1	5	18	19	0	0	1	20
Bouteloua gracilis	30	74	0	6	1	1	0	0	0	5
Bouteloua simplex	0	0	0	0	0	10	0	0	0	0
Brassicaceae spp.	2	4	0	2	0	4	0	0	0	0
Bromus tectorum	7	7	0	7	0	2	0	0	0	0
Calylophus hartwegii	0	0	0	0	0	1	0	0	0	0
Carex spp.	6	0	24	24	53	53	1	2	25	25
Castilleja spp.	0	0	0	0	2	0	0	0	0	0
Ceanothus fendleri	0	0	1	3	3	2	0	0	0	0
Chaetopappa ericoides	0	2	0	0	0	0	0	0	0	0
Chamaesyce fendleri	1	0	0	0	0	0	0	0	0	0
Chamaesyce serpyllifolia	4	5	0	0	0	28	0	0	0	4
Chenopodium graveolens	10	20	0	0	0	0	1	2	0	7
Chenopodium leptophyllum	0	0	0	0	0	0	0	0	0	1
Chenopodium spp.	0	0	0	0	0	1	0	0	0	0
Cirsium spp.	1	2	18	7	16	9	3	0	5	0
Convolvulus arvensis	0	0	0	0	0	1	0	0	0	0
Cyperus fendlerianus	0	0	0	0	0	2	0	0	0	1
Dalea spp.	0	0	0	0	0	6	0	0	0	0
Drymaria leptophylla	0	0	0	0	1	0	0	0	0	0
Drymaria molluginea	0	0	0	0	1	8	0	0	0	0
Echeandia flavescens	0	0	1	0	0	0	0	0	0	1
Elymus elymoides	34	36	34	27	33	58	5	3	35	39
Elymus trachycaulus	0	0	0	0	0	4	0	0	0	0
Epilobium brachycarpum	0	0	1	3	0	0	0	0	1	0
Ericameria nauseosus	0	2	0	0	0	0	0	0	0	0
Erigeron divergens	6	1	11	7	2	22	0	1	1	11
Erigeron flagellaris	8	2	0	1	0	31	0	0	1	3
Erigeron formosissimus	0	0	6	3	10	7	0	0	12	5
Eriogonum alatum	2	3	0	0	1	0	0	0	0	0
Eriogonum racemosum	1	0	9	3	0	0	0	0	2	1
Erodium cicutarium	1	0	0	0	0	0	0	0	0	0

Species[1]	Big Fill		Black Springs		Fry Park		Reese Tank		Rogers Lake	
	In	Out	In	Out	In	Out	In	Out	In	Out
Festuca arizonica	30	42	0	6	45	5	11	5	5	4
Gaura spp.	0	0	0	0	0	2	0	0	0	0
Geranium caespitosum	2	0	0	0	0	0	3	0	0	0
Gutierrezia sarothrae	8	14	0	0	0	2	0	0	0	0
Heliomeris multiflora	3	0	13	7	4	6	0	0	7	12
Helianthella quinquenervis	0	0	0	0	0	0	0	0	11	0
Hesperostipa comata	7	0	0	0	0	0	0	0	0	0
Heterosperma pinnatum	0	0	0	0	0	0	0	0	0	2
Heterotheca villosa	0	0	0	5	0	0	0	0	0	0
Hieracium fendleri	0	0	0	0	0	0	0	0	0	1
Houstonia wrightii	0	0	0	1	0	5	0	0	1	0
Hymenopappus filifolius	1	5	0	0	0	0	0	0	0	0
Hymenopappus mexicanus	0	0	0	0	3	1	0	0	0	0
Hymenoxys richardsonii	0	2	0	0	0	0	0	0	0	0
Ipomopsis multiflora	1	1	0	0	0	0	0	0	0	0
Iris missouriensis	0	0	0	0	0	2	0	0	1	0
Kochia scoparia	0	1	0	0	0	0	0	0	0	0
Koeleria macrantha	1	0	6	10	4	3	0	0	1	1
Lactuca serriola	1	0	0	0	0	0	0	0	0	0
Lappula occidentalis	0	0	0	0	0	5	0	0	0	0
Lathyrus spp.	0	0	0	0	5	7	0	0	1	0
Linaria dalmatica	15	14	0	0	0	12	0	0	0	0
Linum australe	1	0	0	0	0	1	0	0	0	0
Lithospermum multiflorum	0	0	0	0	7	0	0	0	0	0
Lomatium spp.	2	0	0	0	0	0	0	0	0	0
Lotus wrightii	0	1	3	2	5	2	0	0	0	0
Lupinus spp.	0	0	0	0	2	0	1	1	0	0
Machaeranthera canescens	2	0	0	0	0	4	0	0	0	0
Machaeranthera gracilis	0	1	0	0	0	0	0	0	0	0
Monroa squarrosa	0	0	0	0	1	1	0	0	0	0
Muhlenbergia minutissima	1	0	0	1	8	38	0	0	0	9
Muhlenbergia montana	27	27	11	15	67	8	6	2	3	7
Muhlenbergia rigens	0	5	0	0	2	1	0	0	5	0
Muhlenbergia wrightii	0	0	0	0	3	14	0	0	0	0
Nama dichotomum	1	0	0	0	0	0	0	0	0	0
Oxalis spp.	0	0	0	0	1	1	0	0	0	1
Oxytropis lambertii	0	4	0	0	0	0	1	0	0	0
Penstemon spp.	3	3	2	1	15	9	0	0	1	0
Phaseolus angustissimus	0	3	0	0	0	0	0	0	0	0
Phlox speciosa	0	0	0	0	8	10	0	0	13	4
Plantago spp.	0	0	0	3	0	0	0	0	0	0
Poa spp.	18	27	33	22	27	67	1	0	29	39
Polygonum spp.	0	0	8	6	5	11	0	0	3	23
Portulaca oleracea	1	1	0	0	0	19	0	0	0	0
Potentilla spp.	4	0	2	3	15	22	0	0	2	8
Pseudocymopterus montanus	0	0	0	0	16	1	1	0	7	0
Pyrrocoma crocea	0	0	0	0	0	0	0	0	5	0
Rhus trilobata	2	0	0	0	0	0	0	0	0	0
Ribes spp.	0	0	0	0	1	0	0	0	0	0
Rosa woodsii	0	0	0	0	0	0	0	0	28	2
Salsola tragus	1	0	0	0	0	0	0	0	0	0
Schizachyrium scoparium	1	1	0	0	0	0	0	0	0	0

Species[1]	Big Fill		Black Springs		Fry Park		Reese Tank		Rogers Lake	
	In	Out	In	Out	In	Out	In	Out	In	Out
Senecio spp.	1	2	3	0	2	3	0	0	1	0
Solidago spp.	2	0	15	7	22	4	0	0	7	0
Sporobolus cryptandrus	0	0	0	2	0	0	0	0	0	0
Sporobolus interruptus	0	0	25	20	10	10	0	0	0	0
Symphyotrichum spp.	0	0	1	1	1	5	0	0	7	0
Taraxacum officinale	0	0	0	0	0	16	0	0	2	0
Tetradymia canescens	7	6	0	0	0	0	0	0	0	0
Thalictrum fendleri	1	2	0	0	3	0	0	0	1	1
Townsendia exscapa	0	0	0	0	0	1	0	0	0	0
Tragopogon dubius	0	1	0	0	0	3	0	0	0	0
Tragia ramosa	1	0	0	0	0	0	0	0	0	0
Trifolium longipes	0	0	0	0	7	52	0	0	17	24
UNK-ONAGRACEAE	0	1	0	0	0	0	0	0	0	0
Verbascum thapsus	3	1	0	0	0	6	0	0	0	0
Vicia spp.	0	0	0	0	5	7	1	0	0	0
Wyethia arizonica	0	0	0	0	0	0	0	0	2	0

[1] Species with unknown codes ("UNK ...") were not analyzed.