LANDSCAPE DYNAMICS IN ASPEN AND WESTERN JUNIPER WOODLANDS ON THE OWYHEE PLATEAU, IDAHO

A Dissertation

Presented in Partial Fulfillment and Requirements for the

Degree of Doctor of Philosophy

in

Natural Resources

in the

College of Graduate Studies

University of Idaho

by
Eva K. Strand

May 2007

Major Professor: Dr. Lee A. Vierling, Ph.D.

AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Eva K. Strand, submitted for the degree of Doctor of Philosophy in Natural Resources and titled "Landscape dynamics in aspen and western juniper woodlands on the Owyhee Plateau, Idaho" has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate studies for approval.

Major Professor____________________________________Date__________
Lee A. Vierling

Committee
Members____Date__________
Stephen C. Bunting

____Date__________
Paul E. Gessler

____Date__________
Karen L. Launchbaugh

Department
Administrator_____________________________________Date__________
Karen L. Launchbaugh

Discipline's
College Dean______________________________________Date__________
Steven B. Daley Laursen

Final Approval and Acceptance by the College of Graduate Studies

____Date__________
Margrit von Braun

ABSTRACT

A century of altered fire regimes has affected the landscape vegetation dynamics in the Intermountain West. Suppression of wildfires has resulted in increases in woody plant cover in these semi-arid ecosystems, which has resulted in land cover changes affecting biogeochemical cycling, landscape composition, and habitat diversity. Recent developments in remote sensing technology, computational power, and a rapid development of analysis techniques have enabled us to quantify such changes at the landscape scale. Wavelet analysis is a powerful image analysis technique that is here applied in a novel fashion to fine scale remote sensing imagery to automatically detect the location and crown diameter of individual western juniper plants (*Juniperus occidentalis* ssp. *occidentalis*) expanding into sagebrush (*Artemisia* spp.) steppe at multiple scales. The produced marked point pattern of historical and current spatial juniper distribution was compared regionally and changes in foliar cover and above ground biomass were estimated across a 330,000 ha area on the Owyhee Plateau, Idaho. The above ground carbon accumulation rate from 1946 to 1998 was estimate to be 3.3 $gCm^{-2}yr^{-1}$ and 10.0 $gCm^{-2}yr^{-1}$ employing the wavelet and conventional texture analysis methods, respectively, with an additional 25% rise in belowground carbon accumulation in root stock. This research further demonstrates that estimates of carbon accumulation rates as a result of woody encroachment are highly dependent on the spatial and temporal scales of analysis. Conifer species, western juniper and Douglas-fir (*Pseudotsuga menziesii*) on the Owyhee Plateau, have further expanded into the biologically important quaking aspen (*Populus tremuloides*) habitats resulting in conifer dominance and occasional loss of aspen clones. Classification of remotely sensed imagery combined with spatially explicit modeling of aspen successional stages indicate that, in the absence of management activity, loss of seral aspen stands will continue to occur over the next centuries as a result of conifer expansion. Spatially explicit modeling results using the Tool for Exploratory Landscape Analyses (TELSA) show that a return to historic fire regimes that burn 12-14% of the modeled landscape per decade would minimize aspen loss by keeping the majority of aspen stands in early and mid seral woodland stages where conifers are subdominant. Furthermore, conifer dominance and aspen loss could be prevented by implementation of prescribed burning programs treating aspen and young conifer woodlands according to historic fire occurrence probabilities.

ACKNOWLEDGEMENTS

Without the support and encouragement from a number of individuals, completion of this work would not have been possible. First of all I would like to thank my major professor and graduate committee for invaluable guidance and support. Thank you Dr. Vierling for guiding me towards a broader and deeper understanding of remote sensing and the global carbon cycle and other research topics I have been pursuing and thank you for your insightful and constructive input and criticism of the manuscripts produced as part of this work. Thank you Dr. Bunting for somehow always making time to discuss complex ecological topics and modeling approaches in spite of your busy schedule. Thank you for introducing me to the beauty of western rangelands and sharing your skills in Dutch oven camp cooking. You are an exceptional mentor and friend. Thank you Dr. Gessler for encouraging me to begin this process and providing constructive criticism along the way. Thank you Dr. Launchbaugh for accepting me into your department, offering professional support and advice and, not to forget, times of laughter. Many thanks to the other co-authors Dr. Alistair Smith, Dr. David Hann, and Dr. Andrew Robinson and to my field assistants Ben Smith and Jacob Young. I could not have completed this work without your insight, encouragement, support and friendship. I sincerely acknowledge the Boise District of the BLM and the seed-grant from the University of Idaho for providing funding for this research. Many thanks also to the administration of the College of Natural Resources for enabling me to conduct this research while managing the Remote Sensing and GIS Teaching Laboratory, special thanks to Dr. Alton Campbell for encouragement and support. Many others have helped along the way and added fun memories to these years, graduate students, faculty, and staff at the CNR, there is not room to name you all. Special thanks go to Lee Anne Eareckson for encouragement and discussions during our many outdoor adventures. You are a good friend! Last but not least thank you Maja, Anna, and Katja for enduring the sometimes-difficult times while I was completing this work, I will make it worthwhile for all of us.

DEDICATION

I dedicate this dissertation to the aspen woodlands of the West and to all of those who appreciate their beauty and complexity
and to
my daughters
Maja, Anna, and Katja

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICIES

INTRODUCTION

Expansion of woody plants in arid and semi-arid ecosystems has been documented regionally and globally over the past 150 years (Scholes and Archer, 1997; Van Auken, 2000). Native and/or exotic woody plants are increasing in density in response to environmental changes, disturbance regimes and land use activities. Woody encroachment is a phenomenon of global concern with the potential to transform arid and semiarid lands covering approximately 45% of the Earth's land surface (Bailey, 1998). Human initiated fire suppression and excessive grazing are proposed causes of woody encroachment (Archer et al., 1995). However, climate change, CO_2 enrichment, nitrogen deposition and N_2-fixation by introduced species may further promote the shift from herbaceous vegetation to woody plants (Archer et al., 2001). Regardless of the cause, woody encroachment at the local to regional scale, often adversely affects herbaceous productivity, therefore also affecting the forage base for wildlife and commercial and subsistence grazing systems (Bovey, 2001; Miller et al., 2005). Furthermore, woody encroachment is often associated with decreased biodiversity, alterations in species composition, fire fuels, and in extreme instances, desertification (Bunting et al., 1999; Van Auken, 2000; Miller et al., 2005).

At the continental scale woody encroachment has been described as a land cover change affecting the global carbon budget by sequestering carbon from the atmosphere (Houghton and Goodale, 2004). Quantitative measures of this carbon sink have been estimated based on ecosystem process models and landscape inventories. However the uncertainty in these estimates is large (Houghton, 2003). This uncertainty has created a need for development of better remote sensing procedures and regional landscape scale analyses to further our understanding of the contribution of regional-scale woody encroachment on continental- to global scale biogeochemical budgets.

The expansion of conifer species into aspen (*Populus tremuloides*) habitats is of particular concern in the mountains of the western USA because this process is jeopardizing the long-term persistence of these keystone habitats (Kay, 1997; Bartos, 2001; Shepperd et al., 2001; Smith and Smith, 2005). Aspen in the western mountains is commonly seral to a number of conifer species and periodic fires are necessary to rejuvenate aspen stands and prevent dominance by the conifer species (Baker, 1925; Bartos and Mueggler, 1981; DeByle et al., 1987). Although the effects of fire have been documented at the stand scale, understanding of how the succession/disturbance dynamics in these aspen woodlands interact at the landscape scale is lacking.

The Owyhee Mountains in southwestern Idaho, located in the northern portion of the Great Basin, was selected for this research because the vegetative communities and ecological processes here are representative of those in many mountain ranges throughout the West. The overarching objective of this body of work is to gain a more holistic and broad scale understanding of the historic, current, and future succession/disturbance dynamics, within the study area.

Chapter 1, *Wavelet Estimation of Plant Spatial Patterns in Multi-temporal Aerial Photography*, describes the development and evaluation of a novel multi-scale remote sensing technique, 2-D wavelet analysis, and its application in extracting the location and crown diameters of individual western juniper (*Juniperus occidentalis* ssp. *occidentalis*) plants in black and white aerial photography. Chapter 1 was published in the peer-reviewed journal *International Journal of Remote Sensing* (Strand et al., 2006).

The expansion of western juniper into the shrub steppe on the Owyhee Plateau is further quantified in Chapter 2, *Net Changes in Above Ground Woody Carbon Stock in Western Juniper Woodlands, 1946-1998*. In this chapter the 2-D wavelet analysis technique and conventional remote sensing texture analysis are applied to historical (1939-1946) and current (1998-2004) aerial photography to quantify the regional changes in above ground woody carbon and woody plant cover. Effects of the spatial and temporal scale of analysis on the carbon accumulation estimates are quantified and discussed.

In Chapter 3, *Spatial Patterns on the Sagebrush Steppe/Western Juniper Ecotone*, the marked point pattern produced by the 2-D spatial wavelet analysis is the basis for analysis of the characteristics of the western juniper spatial patterns on the woodland/steppe ecotone. Through this analysis, significant spatial scales characterizing the spatial distribution of western juniper plants are identified. Via hypothesis testing, using two spatial statistical analysis techniques, Ripley's K (Ripley, 1981) and the pair-correlation function (Stoyan and Stoyan, 1994), we present statistical evidence that areas of fire refugia, seed dispersal processes, and competition for resources are tied to the observed spatial point pattern of western juniper and perpetuate the spread of the species into the shrub steppe at the ecotone. Chapter 3 has been accepted for publication in the scientific journal *Plant Ecology*.

The effect of conifer expansion on western aspen habitats is addressed in Chapter 4, *A quantitative approach for development of a state-and-transition model for aspen/conifer woodlands on the Owyhee Plateau, Idaho* and Chapter 5, *Landscape Composition in Aspen Woodlands under various Modeled Management Scenarios*. The overarching objective for these two chapters is to assess the effects of current and historic wildfire regimes and prescribed burning programs on landscape vegetation composition within two mountain ranges in the Owyhee Mountains in southwestern Idaho. A state-and-transition model (Westoby et al., 1989) for western aspen/conifer woodlands is developed in Chapter 4. This model is parameterized with data obtained via field surveys and interactions between aspen/conifer succession and fire disturbance are modeled in the computer simulation program Vegetation Dynamics Development Tool (VDDT). In Chapter 5, the non-spatial VDDT models are incorporated into the spatially explicit modeling framework, Tool for Exploratory Landscape Analyses (TELSA), and model scenarios for historical and current fire regimes as well as prescribed burning scenarios are developed and executed. The results from these simulations indicate that implementation of prescribed burning programs in aspen and young western juniper woodlands can mitigate for the lack of fire due to wildfire suppression, maintain aspen woodlands in early and mid seral stages and minimize the loss of aspen stands.

References

Archer S., Schimel D.S., and Holland E.A., 1995. Mechanisms of shrubland expansion: land use, climate, and CO_2?, Climatic Change, 29:91-99.

Archer, S., T.W. Boutton, and K.A. Hibbard 2001. Trees in grasslands: Biogeochemical consequences of woody plant expansion, in GlobalBiogeochemical Cycles in the Climate System, edited by E-D. Schulze, S.P. Harrison, M. Heimann, E.A. Holland, J. Lloyd, I.C. Prentice, D. Schimel, Academic Press, San Diego.

Bailey, R.G.,1998. Ecoregions: the ecosystem geography of the oceans and continents, Springer, New York.

Baker, F.S., 1925. Aspen in the central Rocky Mountain region. USDA Bull. 1291, p.47.

Bartos, D.L., 2001. Landscape Dynamics of Aspen and Conifer Forests. p. 5-14. Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Bovey, R.W., 2001. Woody plants and woody plant management, Marcel Dekker, New York.

Bunting, S.C., J.L. Kingery, and E.K. Strand, 1999. Effects of succession on species richness of the western juniper/sagebrush mosaic. Ecology and management of pinyon-juniper communities within the Interior West. USDA Forest Service GTR-RMRS-P-9. Pp. 76-81.

DeByle, N.V. C.D. Bevins, and W.C. Fischer, 1987. Wildfire occurrence in aspen in the interior western United States. Western Journal of Applied Forestry, 2:73-76.

Houghton, R.A., 2003. Why are estimates of the terrestrial carbon balance so different?, Global Change Biology, 9:500-509.

Houghton, R.A., and C.L. Goodale,2004. Effects of Land-Use Change on the Carbon Balance of Terrestrial Ecosystems, pp. 85 in Ecosystems and Landuse Change, edited by Defries, R.S., G.P. Asner, and R.A. Houghton, American Geophysical Union, Washington DC, USA.

Kay, C.E., 1997. Is aspen doomed? Journal of Forestry, 95: 4-11.

Miller, R.F., J.D. Bates, T.J. Svejcar, F.B. Pierson, and L.E. Eddleman, 2005. Biology, Ecology, and Management of Western Juniper, Technical Bulletin 152, Oregon State University, Agricultural Experiment Station.

Ripley, B.D., 1981. Spatial statistics. Wiley, New York, New York, USA.

Scholes, R.J., and S.R. Archer, 1997. Tree-grass interaction in savannas, Annual review Ecological Systems, 28:517-544.

Shepperd, W.D., D.L. Bartos, and S.A. Mata, 2001. Above-and below-ground effects of aspen clonal regeneration and succession to conifers, Canadian Journal of Forest Research, 31:739-745.

Smith, A.E. and F.W. Smith, 2005. Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA, Forest Ecology and Management, 213: 338-348.

Stoyan D., and H. Stoyan, 1994. Fractals, random shapes and point fields: methods of geometrical statistics. Wiley, Chichester, U.K.

Strand, E.K., A.M.S. Smith, S.C. Bunting, L.A. Vierling, B. Hann, and P.E. Gessler, 2006. Wavelet estimation of plant spatial patterns in multi-temporal aerial photography, International Journal of Remote Sensing*,* 27: 2049-2054.

Van Auken, O.W., 2000. Shrub invasions of North American semiarid grasslands, Annual Review Ecological Systems, 31:197-215.

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

CHAPTER 1: Wavelet Estimation of Plant Spatial Patterns in Multi-temporal Aerial Photography

Abstract

Wavelet analysis represents a powerful set of image processing techniques that have considerable potential to quantify ecologically relevant patterns at multiple scales. This letter provides a preliminary assessment of whether two-dimensional wavelets convolved with 1-m panchromatic aerial photography can be used to detect automatically the location and crown diameters of western juniper (*Juniperus occidentalis*) plants as they encroach upon a sagebrush (*Artemisia* spp.) steppe landscape. The juniper crown diameters derived from wavelet analysis produced a strong correlation with crown diameters measured via comparable hand-digitizing in a geographic information system (r=0.96, n=69) with a 5% commission and an 8% omission error. Through comparison with historical photography, we found that juniper plant cover increased 2.7 fold (from 2.7% to 7.3% total cover) during the period from 1939 to 1998 within the 15 ha study area. This approach has considerable potential for the long-term monitoring of vegetation change via aerial photograph and other remotely sensed imagery.

KEYWORDS: spatial pattern, encroachment, change detection, remote sensing, plant cover

1. Introduction

Woody plant encroachment upon lands formerly dominated by grasses and forbs is an ecological phenomenon of global concern (Archer *et al*. 1995, Asner *et al*. 2003). Woody species (e.g. *Quercus, Juniperus, Larrea, Prosopis*, and *Acacia*) are increasing in density in response to changes in environmental conditions such as fire suppression, excessive herbivory and climate change (Archer *et al*. 1995), resulting in forage reduction, decreased biodiversity, and at its extreme, desertification (Asner *et al*. 2003). This process is exemplified by western juniper, which over the past 100 years has been expanding into western U.S. sagebrush steppe (Miller and Rose 1995).

Previous methods for the remote identification of location and size of individual plants within imagery have applied hand-digitizing within geographic information systems (e.g. Ansley *et al*. 2001), user-defined gray-scale partitioning (e.g. Lahva-Giott *et al.* 2000), or textural analysis techniques (e.g. Asner *et al*. 2003). Although gray-scale partitioning and textural analysis can allow separate objects to be visually isolated within imagery they, in general, only provide information for an entire collection of objects (e.g. a cover map), rather than providing data on each object separately.

Up to March 2005, approximately one hundred peer-reviewed publications have incorporated wavelets in various aspects of remote sensing, with nearly three quarters of these publications focusing on image filtering, hyperspectral pixel analysis, image reconstruction, image registration, texture analysis, data fusion, and feature matching (e.g. Le Moigne *et al.* 2002, Ulfarsson *et al*. 2003). Although in the remote sensing community, wavelets have been used in the multi-scale assessment of urban areas (Myint *et a.* 2004), the full potential of these methods remains under-researched. In particular, 'ecological' feature recognition (i.e. plant location and sizes) at multiple scales is a promising application of wavelets to ecological problems, which have previously only used wavelet-based measures to identify potentially important analysis scales (Dale and Mah 1998).

In this preliminary study, we evaluate the potential of one form of wavelet analysis to identify and extract information on 'individual' juniper features from both historic and recently acquired high spatial resolution aerial photography.

2. Methods

2.1 Study Area and Aerial Photography

This study is centered on the Owyhee Plateau in southwestern Idaho (116° W Long, 43° N Lat), an area characterized by western juniper in a sagebrush steppe landscape. Western juniper (*Juniperus occidentalis*) occurs mainly as open savanna-like woodlands dissected by rocky canyons and riparian areas. Elevation ranges from 850 to 2560 m with an annual average precipitation ranging from 250 mm at lower elevations to 1000 mm at the crest of the mountain range. High spatial resolution (<1 m) panchromatic aerial photography was acquired for this area in 1939 (Figure 1a) and 1998 (Figure 1b), and serves as the basis for the wavelet analysis. These images are composed of dark juniper plants against a matrix of sagebrush steppe in multiple shades of gray for an area 15 ha in size. Prior to analysis in MatLab (2004) the sample image was converted to an ASCII matrix (390x390 pixels) with a 1 m pixel size.

2.2 Wavelet-based Image Feature Analysis

Following Ulfarsson *et al.* (2003), we employ the discrete wavelet transformation (DWT) to identify individual features within multi-temporal aerial photography. The DWT is performed by convolving ever-increasing sizes (i.e. dilation scales) of the wavelet shape, termed the basis function, with the imagery. The DWT differs from the continuous wavelet transformation (CWT) in that only discrete sets of dilation sizes are assessed, rather than a continuous distribution of possible sizes (Addison 2002). In wavelet analysis, the wavelet basis function, $\Psi(\mathbf{x})$, must meet certain mathematical criteria, including a finite energy (Equation 1) and a mean of zero (Equation 2):

$$Wavelet\ Energy\ Criterion: \int_{-\infty}^{\infty} |\Psi(x)|^2\, dx < \infty \tag{1}$$

$$Wavelet\ Mean\ Criterion: \int_{-\infty}^{\infty} \Psi(x)dx = 0 \tag{2}$$

Within this study, the Mexican hat wavelet (Equation 3) was selected due to its spherical shape and smooth edges approximating the appearance of a juniper plant in an aerial photograph.

$$\Psi(x, y) = (1-x^2 - y^2) * e^{-(x2+y2)/2} \qquad (3)$$

The 2-D Mexican Hat wavelet basis function was successively convolved, over a range of dilation scales, selected by the likely crown diameters of juniper trees (i.e. 1 to 10m in increments of 0.1m), with the aerial photograph to produce a wavelet intensity image corresponding to each dilation scale. This intensity image exhibited high values when features within the Image, I(**x,y**) were very similar to the size and shape of the wavelet function, Ψ(**x,y**), at that particular dilation scale. When the wavelets and the image features are similar a high intensity peak is created, while lower intensity, values are produced when the wavelet function is not similar to the image feature.

In this study, we were solely interested in identifying juniper plants, which appear as dark objects against a lighter sagebrush background (Figure 1). The wavelet analysis was coded in MatLab (2004) and the output of the analysis is a list of individual plant locations and estimated plant sizes (determined by the dilation with the highest value for the DWT). Although, this output contains data on individual trees, the results of the wavelet analysis were displayed in a GIS environment and overlaid onto the original aerial photographs, which allowed the direct assessment of plant cover and density.

2.3 Comparison to Alternative Measurement Techniques

We evaluate the wavelet analysis to be directly comparable to hand-digitizing in a GIS and to gray-scale partitioning. We used GIS software (http://www.esri.com) to measure 69 juniper crown diameters in the x and y directions directly from the orthorectified aerial photograph. When implementing the gray-scale binary partitioning we choose two thresholds such that at the lower threshold (90) all juniper trees in the image were recorded as woody plants, but also part of the darker background was included in the ‘woody plant’ category. At the higher threshold (140) no background was recorded as ‘woody plants’ however many juniper plants were recorded as background.

3. Results

Figure 1 demonstrates that the wavelet analysis identifies accurately the size and location of individual trees in both the 1939 and the 1998 imagery. The juniper crown diameters ranged from 2-9 m and were in good agreement with plant diameters directly measured in a GIS (Figure 2, $r = 0.96$). Figure 1e shows that a low gray-scale threshold (90) yields an under-prediction of juniper plants while Figure 1f illustrates that a high threshold (140) results in an over-prediction of juniper cover. These results demonstrate that in contrast to wavelet analysis, gray-scale partitioning is sensitive to the shade of the background.

Wavelet-derived juniper cover in the 1939 image was 2.7% compared to 1.0 % for the low gray-scale threshold (90) and 7.3 % for the high gray-scale threshold (140). The juniper cover in 1998 is estimated as 7.3% using the wavelet technique (Figure 1d). As such, it is apparent that gray-scale partitioning is sensitive to the selected threshold. Wavelet analysis of the 1998 photograph estimates 634 juniper plants within the 15 ha analysis area. The commission error is estimated to be less than 5%, representing features such as rock outcrops and small circular dense sagebrush patches that were misclassified as juniper plants. Occasional small juniper plants were not detected by the wavelet technique yielding an 8% omission error. The omission error might be reduced by the use of imagery with a finer pixel size.

4. Discussion

The wavelet analysis approach presented in this study has the potential of becoming an important tool for analysis of woody plant encroachment rates and may shed light on relationships between landscape patterns and ecological processes. Furthermore, the accurate identification of plant size and location will enhance our understanding of ecotone dynamics and plant responses to climate variability.

Quantifying objects within an image using wavelet analysis depends on the minimum object size, the spatial resolution of the image and the initial wavelet scale; as in general, the smallest applicable wavelet will be close to the cell size of the imagery. An advantage of the wavelet method is that it can be applied directly to images of any spatial resolution and thus could be an important tool to analyze vegetation features over multiple scales and over multiple image sources. In addition, the output of this technique is a point pattern of plant size, rather than a cover map, which can be broadly assessed with spatial analysis techniques.

Limitations of this technique can be expected in closed canopy environments such as forests, where clusters of objects may be incorrectly defined as larger individuals. However, such misclassifications can be limited through selecting a sensible maximum feature size. Wavelet analysis does not discriminate between vegetative species, rocks or other objects unless they are unique in shape or size, and as such this method does not directly provide a classified image. Furthermore, depending on the quality of the imagery, shadow effects may skew the size of objects as interpreted by the wavelet.

5. Conclusions

The wavelet analysis technique presented herein is a ‘rapid, objective, repeatable, and background invariant’ method for quantifying ecological patterns. Further research in plant ecology applications combining 2-dimensional multi-scale wavelet analysis of fine-scale landscape images (e.g. aerial photography, IKONOS or QuickBird) with spatial point pattern analysis techniques could yield important information about plant succession, biogeochemical properties, and landscape composition across large areas. This method is promising for the analysis of long-term ecological change because the earliest remotely sensed images of many areas are black & white aerial photography. Using such a technique to quantify vegetation change over decadal time periods stands to improve our understanding of how current environmental changes relating to climate, fire suppression, and invasive species are manifest at the landscape scale.

Acknowledgements

Pat Clark, USDA, Agricultural Research Service, Northwest Watershed Research Center, Boise, Idaho provided historic aerial photograph 1939.

References

Addison P.S., 2002, *The Illustrated Wavelet Transform Handbook* (Institute of Physics Publishing, The Institute of Physics, London, UK).

Ansley R.J., Wu X.B., and Kramp B.A., 2001, Observation: long-term increase in mesquite canopy cover in a north Texas savanna. *Journal of Range Management* **54**:171-176.

Asner G.P., Archer S., Hughes R.F., Ansley R.J., and Wessman C.A., 2003, Net change in regional woody vegetation cover and carbon storage in Texas Drylands, 1937-1999. *Global Change Biology* **9**:316-335.

Archer S., Schimel D.S., and Holland E.A., 1995, Mechanisms of shrubland expansion: land use, climate, and CO_2?. *Climatic Change* **29**:91-99.

Dale M.R.T., and Mah M., 1998, The use of wavelets for spatial pattern analysis in ecology. *Journal of Vegetation Science* **9**: 805-814.

Lahav-Ginott S., Kadmon R., and Gersani M., 2001, Evaluating the viability of *Acacia* populations in the Negev Desert: a remote sensing approach. *Biological Conservation* **98**: 127-137.

Le Moigne J., Campbell W.J., and Cromp R.F., 2002, An automated parallel image registration technique based on the correlation of wavelet features. *IEEE Transactions on Geoscience and Remote Sensing* **40** (8): 1849-1864.

MATLAB® 2004. Matlab and Simulink, Version 7.0.0.27 (R14). The MathWorks, Web site: http://www.mathworks.com/products/matlab/

Miller R.F., and Rose J.A., 1995, Historic expansion of *Juniperus occidentalis* (western juniper) in Southeastern Oregon. *Great Basin Naturalist* **55**:37-45.

Myint, S.W., Lam, N.S.N., and Tyler, J.M. 2004, Wavelets for urban spatial feature discrimination: Comparisons with fractal, spatial autocorrelation, and spatial co-occurrence approaches. *Photogrammetric Engineering & Remote Sensing*, **70**: 803-812.

Ulfarsson M.O., Benediktsson J.A., Sveinsson J.R., 2003, Data fusion and feature extraction in the wavelet domain. *International Journal of Remote Sensing* **24** (20): 3933-3945.

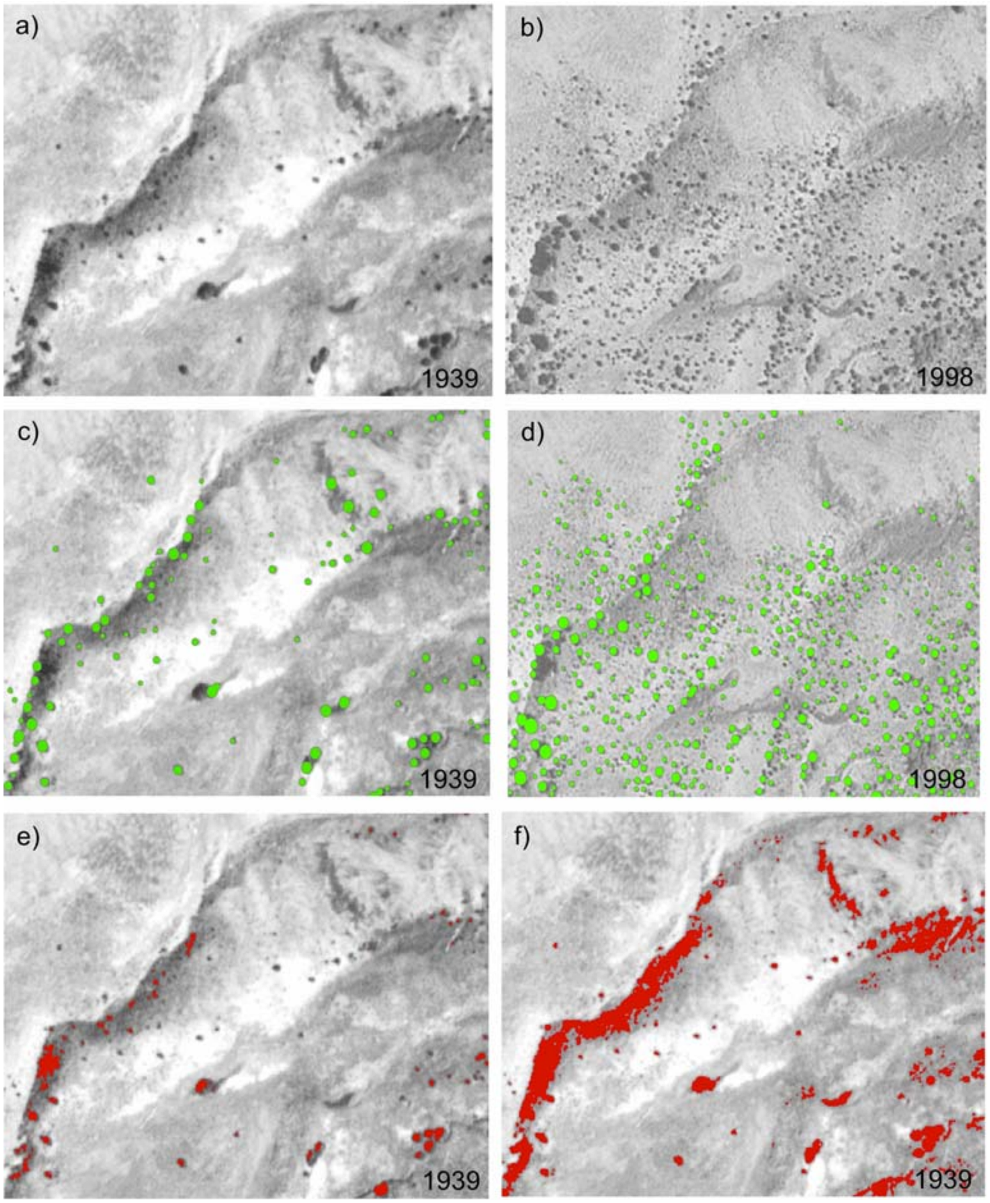


Figure 1. Aerial photograph of a western juniper / sagebrush steppe landscape (15 ha). a) Original aerial photograph 1939. b) Original aerial photograph 1998. c) and d) Projected juniper plant radii derived from wavelet analysis for the 1939 and 1998 photo. e) and f) Projected juniper cover year 1939 from gray-scale partitioning using thresholds of 90 and 140. The juniper cover estimated for the 1939 photo is 2.7% using wavelet analysis, 1.0% using the gray-scale threshold 90 and 7.3% using the gray-scale threshold 140. The juniper cover in 1998 is estimated to 7.3% using the wavelet technique. Source: The 1939 aerial photograph: USDA-SCS. The 1998 image: USGS (http://inside.uidaho.edu/geodata/USGS/DOQ.htm).

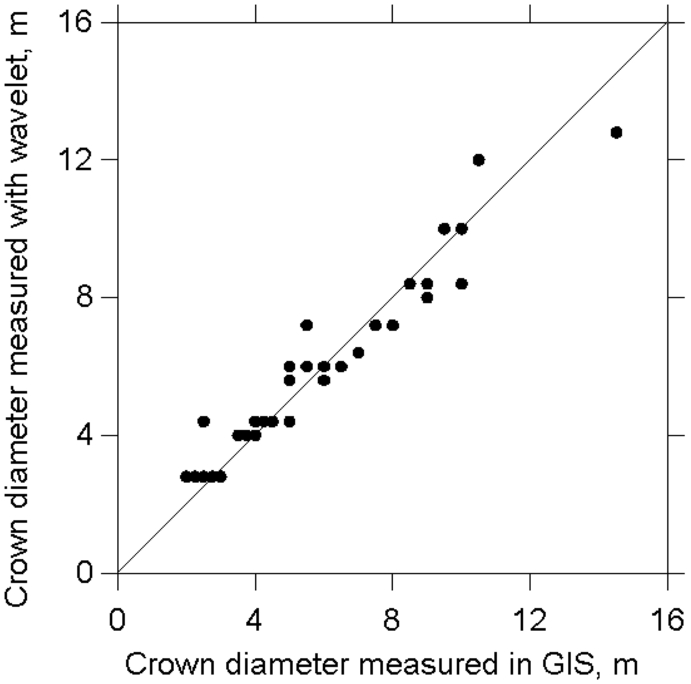


Figure 2. Plant size as determined by the wavelet analysis compared to measurements in a GIS environment.

CHAPTER 2: Net Changes in Above Ground Woody Carbon Stock in Western Juniper Woodlands, 1946-1998

Abstract

Although regional increases in woody plant cover in semi-arid ecosystems have been identified as a worldwide phenomenon affecting the global carbon budget, quantification of its impact on pools and fluxes via remote sensing has proven difficult. The challenge arises because although very large areas are affected, suggesting suitability of satellite remote sensing, the encroachment is governed by ecological processes that occur at a very fine spatial resolution (1-10 m) and, in many cases, at slow (decadal-scale) temporal rates; which are beyond the capabilities of most current satellite remote sensing systems. To overcome this, we present a quantitative analysis of historical and current aerial photography, which exhibits both the necessary spatial precision (1-m pixels) and time-series legacy (1930s to present), to imagery of western juniper (*Juniperus occidentalis* ssp. *occidentalis*) expanding into a sagebrush (*Artemisia* spp.) steppe landscape on the Owyhee Plateau, Idaho. Quantitative analysis is achieved through the implementation of both 2-D spatial wavelet analysis (SWA) and image texture analysis to time series aerial photography supported by field data, and allometric equations to quantify upper and lower bounds of the changes in above ground woody carbon. Analysis was applied over forty-eight 100-ha blocks across a 330,000-ha region. The 48 sampled areas were stratified by topography, soil characteristics, and land stewardship. Across the area we estimate a 3.3 $gCm^{-2}yr^{-1}$ and 10.0 $gCm^{-2}yr^{-1}$ above ground woody carbon accumulation rate for the wavelet and texture method, respectively, with an additional 25% rise in belowground carbon accumulation in root stock during the time period 1946 to 1998. Western juniper cover doubled from an average of 5.3 to 10.4 % over approximately 52 years. Woody biomass accumulation was significantly affected by soil properties with faster accumulations on deeper well-drained soils supporting the mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) plant associations. The estimates of carbon accumulation rates as a result of woody encroachment are highly dependent on the spatial and temporal scales of analysis. Specifically, at a 100-ha scale the above ground accumulation of woody carbon varied from -1.7 to 9.9 $gCm^{-2}yr^{-1}$, while at 1-ha scale the variability was –11 to 22 gCm^{-2}yr^{-1}. In terms of carbon accumulation rates due to woody encroachment these results are an order of magnitude less than previously suggested, which highlights the need for further assessments to wider environments.

KEYWORDS: carbon sequestration, woody encroachment, wavelet, texture analysis, Juniperus occidentalis, land cover change, remote sensing, aerial photography, Great Basin

1. Introduction

Current and the potential future changes in the Earth's climate system have stimulated great interest into further understanding the dynamics of the global carbon cycle such that options for management of carbon sources and sinks can be quantitatively evaluated (http://www.usgcrp.gov). Scientific information about carbon cycling and the interactions between the atmosphere, land surface and the oceans is essential for future strategic and successful carbon management. Although the majority of the increase in atmospheric CO_2 is considered due to fossil fuel combustion, a significant fraction of the increase arises from alterations in land cover and use (Houghton and Goodale 2004). These could include for example: agricultural management, wood harvest, plantations, fire management, woody encroachment, and natural disturbances. Houghton et al. (1983) clearly state that for improved understanding of the current warming climate we must focus research on recent changes in global carbon pools and fluxes, as although lag effects could exist, it is unlikely that pools and fluxes that have been relatively stable in recent history are the cause of changes in atmospheric CO_2 concentration (Houghton et al., 1983). However, detection of recent land cover and land use change over regional scales can be challenging because of lacking historical records and the large extent of affected land areas. Woody plant encroachment into lands previously covered by herbaceous or shrub-steppe vegetation has been documented world-wide over the past 150 years (Scholes and Archer, 1997; Van Auken, 2000). Native and/or exotic woody plant genera (e.g. *Quercus, Juniperus, Larrea, Prosopis, Acacia, Tamarisk* and *Yucca*) are apparently increasing in density in response to changes in environmental conditions, disturbance regimes and land use activities (Archer et al. 1995). Arid and semiarid lands cover approximately 45% of the Earth's land surface (Bailey, 1998) and the phenomenon of woody encroachment is not only widespread, but also has the potential to transform large areas of the Earth's terrestrial surface, and potentially affecting the global carbon budget.

At the continental scale, expansions of woody plants have been identified as contributing 0.06 $PgCyr^{-1}$ (Houghton, 2003, 1 Pg = 10^{15} g) to 0.12-0.13 $PgCyr^{-1}$ (Houghton et al., 1999; Pacala 2001) to the US carbon sink. These estimates are based on ecosystem process models and direct landscape inventories of on the ground carbon combined with reconstructions of land use change (Pacala, 2001). Such estimates of carbon sinks and sources emphasize large uncertainties (Pacala, 2001), creating a need for regional-scale analyses across various ecosystems. Stand to ecosystem scale carbon inventories characterizing woody plant expansions and thickening have recently been reported (Pare and Bergeron, 1995; Tilman et al., 2000; Archer et al., 2001; Norris et al., 2001; Asner et al., 2003; Law et al., 2003; Hicke et al., 2004; Hughes et al., 2006). Such studies typically quantify the above ground carbon accumulation over a certain time period, sometimes along a successional gradient or chronosequence, via stand scale measurements and allometric equations.

The study by Asner et al. (2003) additionally incorporated landscape scale topographic and edaphic variations and disturbance regimes and thereby allowed estimates to be extended from a local scale to a regional scale. Asner et al. (2003) estimated an average of 1.9 $gCm^{-2}yr^{-1}$ accumulation in above ground woody plants from 1937 to 1999 in Texas rangelands encroached by honey mesquite (*Prosopis glandulosa)*. Mesquite cover was quantified via textural analysis of aerial photography from 1937 and compared to 1999 estimates made via sub-pixel analyses of Landsat imagery. A local scale study at the site however, estimated the above ground carbon accumulation at a stand level to be approximately 35 $gCm^{-2}yr^{-1}$ over the 60-year time period (Hughes et al., 2006). Although Asner et al. (2003) emphasized that their regional scale estimate was likely to be low because riparian areas were excluded from the analysis, the difference between estimates made at the regional scale and the local scale is large, and underscores the need for regional scale analyses in order to discern area-wide trends. In order to facilitate such regional analyses, methodological developments are necessary, while to understand the contribution of regional-scale woody encroachment on continental- to global scale biogeochemical budgets, studies at additional sites are warranted.

In response to these needs we utilized a new methodological approach to quantify woody plant cover dynamics over a 60-year time period in the western juniper / sagebrush steppe ecosystem of southwestern Idaho. We applied an established image analysis method, namely 2-D spatial wavelet analysis (SWA) (Strand et al., 2005; Falkowski et al 2006; Strand et al., 2006a), to 1-m historic and current black and white aerial photography. In addition, to further evaluate the SWA methodology, we compared the results from the SWA to the texture analysis remote sensing technique used by Asner et al. (2003) and to stand-scale field data.

Our analyses were guided by a series of research questions relating to remote sensing methodology and biogeochemical cycling. The methodological objectives of this research are to estimate the minimum detectable juniper plant size in the application of SWA to 1-m panchromatic imagery and the level of canopy cover at which individual plants can no longer be detected due to tree clustering. We also compare the carbon accumulation rates estimated via SWA and texture analysis. Biogeochemical cycling questions that we intend to address are: 'What is the change in above ground woody carbon stock in the juniper zone of the Owyhee Plateau over a ~60-year time period?'; 'What are the effects of spatial scale on the estimate of changes in above ground woody carbon stock?' and finally, 'What broad scale environmental and land use variables have significantly affected the establishment of western juniper across the region'?

2. Methods

2.1. Study region

Our study is centered on a 400,000-ha area within the Owyhee Plateau of southwestern Idaho (116° W Long, 43° N Lat), an area characterized by western juniper woodlands (*Juniperus occidentalis* ssp. *occidentalis*) in a sagebrush (*Artemisia* spp.) steppe landscape. Western juniper encroachment into the sagebrush steppe is believed to have been occurring over the last 100-150 years (Miller et al., 2005; Bunting et al., 2005). This site is representative of a much larger region across the American West, where juniper species have in the last century greatly expanded to the current condition of juniper & pinyon woodlands occupying over 30 million hectares (West 1999). Of this area, 3.6 million hectares are dominated by western juniper (Miller et al., 2005), attesting to its significance as a species to observe. Although the total area affected by junipers have been estimated, actual encroachment rates are difficult to ascertain. Consequently, few studies exist that estimate the changes in the western juniper woodland carbon pools.

Western juniper in the study area occurs as open savanna-like woodlands at various stages of succession, dissected by rocky canyons and riparian areas. The two dominant sagebrush species are low sagebrush (*Artemisia arbuscula)* and mountain big sagebrush

(*Artemisia tridentata* ssp. *vaseyana)*. The area encompasses three mountain ranges: the Silver City Range in the north, South Mountain, and Juniper Mountain in the south. The elevation where juniper occurs ranges from approximately 1400 to 2560 m with an annual average precipitation ranging from 250 mm at lower elevations to 1000 mm at the crest of the mountain range. Juniper cover becomes sparse at elevations above 2000 to 2100 m due to cold winter temperatures and harsh conditions (Miller et al., 2005). Aspen (*Populus tremuloides*), Douglas-fir (*Pseudotsuga mensiezii*) and small patches of wet meadows and mountain shrub are infrequent components in the juniper-dominated landscape. Common mountain shrub species are shiny-leaf ceanotus (*Ceanothus veluntinus*), mountain snowberry (*Symphoricarpos oreophilus*), bittercherry (*Prunus emarginata*), and chokecherry (*Prunus virginiana*). Altogether approximately 70,000 ha of the study area comprises these various vegetation types leaving 330,000 ha in juniper woodland /sagebrush steppe cover.

Western juniper is a long-lived species with groups of individuals over 500 years old existing in areas of fire refugium (Miller et al., 2005). According to a landcover classification of juniper structural stages approximately 65% of the juniper cover on the Owyhee Plateau is composed of stand initiation and open young woodlands while another 16% is comprised of young multi-story woodlands leaving only 17% in the mature juniper class (Roth, 2004).

Soils that support sagebrush steppe and juniper woodlands on the Owyhee Plateau are dominated by xeric mollisols and alfisols (USDA-NRCS 1998) of igneous parent materials. Western juniper has encroached into many vegetation types; however, the encroachment rates can vary widely depending on several factors. Encroachment rates are relatively high on deeper soils supporting mountain big sagebrush, Idaho fescue (*Festuca idahoensis*) and aspen woodlands (Young and Evans, 1981; Eddleman, 1987; Bunting et al., 2005), while slower rates are observed on soils dominated by low sagebrush. Low sagebrush occurs on soils that are, in general shallow, stony loams or silt loams while mountain big sagebrush occurs on deeper well-drained loams or sandy loams with a higher content of organic material. The distribution of soils are partially a result of topographic position where the stony shallow loams are located on ridges and other wind exposed areas where over the centuries wind and water erosion works away the top soil layer. The deeper, richer soils are found on protected side slopes, in swales and valleys where top-soil has been allowed to build via pedogenesis and site productivity with contributions from sediment in water runoff. Therefore, juniper encroachment rates can be very heterogeneous even across short distances.

Euro-American settlement began when silver and other minerals were discovered in the Silver City Range in 1864. Before this era, the Piute, Shoshone and Bannock hunter and gatherer tribes inhabited the area (Owyhee Canyonlands History, 2003). Silver City quickly became a booming mining town and during this era the mountains around Silver City were cleared of wood for use in the mines and for fire-wood. Silver City quickly went from 'boom to bust' and by 1920 it was in reality a ghost town. All three mountain ranges have a history of sheep and cattle grazing beginning as early as the 1860's. The majority of the study region (71%) is comprised of public lands managed by the Bureau of Land Management. Remaining lands are managed by the State of Idaho (11%) or are in private ownership (18%). Today, the sparsely populated Owyhee Mountains are used primarily for summer range cattle grazing, hunting, camping, and outdoor recreation.

2.2. Disturbance and management practices

Since the end of the mining in the 1920's, most wood harvest in the juniper woodlands has been restricted to non-commercial wood-cutting with estimated minor impacts on the above ground woody carbon pool. Fire atlas data from the Bureau of Land Management 1957 – 2002 show that approximately 10% of the study region has burned in wildfires within this time period. Overlay analysis in a GIS (ESRI 1999-2005) with a recently developed land cover map reveal that the majority of the wildfires occurred at lower elevations in the sagebrush steppe where juniper plants, if present, are small (Roth, 2004). Only a few older juniper stands (1660 ha) have burned in wildfires, and thus the loss of woody carbon due to these fires can be considered negligible. Fire records were not available for the time period prior to 1957.

2.3. Analysis of aerial photography

Remote sensing data is today available from a multitude of sensors covering a variety of spatial, spectral and temporal resolutions. For long-term analyses (> 50 years) of landscape dynamics, current and historic aerial photography is available in many regions. Imagery with fine scale spatial resolution (~1 m) or sub-pixel analysis is required to accurately estimate levels of woody encroachment. For example, Asner et al. (2003) relied on sub-pixel analysis of Landsat 7 ETM+ imagery for estimates of current foliar cover of honey mesquite in Texas, while the only black and white aerial photography was available for the historic assessment of the same area.

We applied 2-D SWA to aerial photography (Strand et al., 2006a) to quantify the change in western juniper biomass from 1939-1946 to 1998-2004 on the Owyhee Plateau. Current aerial photography is available at 1-m pixel size (USDA 2004) and historical photography at a scale of 1:27000 is available for most of the study area from USGS (http://EarthExplorer.usgs.gov). For this detection of change we acquired ten black and white historical photos, each covering a 6x6 km area, from 1946 and three 6x5 km photos from 1939. The historical photos were georeferenced to the current imagery and resampled to 1-m pixel size, with an approximate RMSE of 10 m, in the ERDAS image processing software (Leica Geosystems, 1991-2003).

SWA stems from applications in medicine and astronomy and was recently adapted for landscape analysis within environmental remote sensing (Falkowski et al., 2006; Strand et al., 2006a,b). Within the field of medicine, wavelet analysis has been successful in object recognition in digital mammograms, magnetic-resonance and x-ray images (Unser et al., 2003) while at the macro-scale wavelet analysis is capable of detecting galaxies, clusters and voids within astronomic images (Slezak et al., 1992). Strand et al. (2006a) observed that a Mexican-hat 2-D wavelet can be convolved with remotely sensed imagery to quantify spatial patterns at multiple scales with the capability of automatically recording the diameter and location of individual objects, juniper plants in this specific application. The wavelet multi-scale convolution was coded in Matlab (Mathworks, 2004). In summary, the input to the wavelet code is a panchromatic aerial photograph in ASCII format and the output is a list of x-y coordinates and the diameter of individual trees detected within the image. For a detailed description of the 2-D SWA technique we refer to Strand et al. (2006a) and Falkowski et al. (2006).

In addition, we processed the black and white imagery according to the texture method used by Asner et al. (2003). Specifically, this texture analysis involved passing a 2x2 pixel filter across the image computing the mean, variance, and range within the kernel. Hudak and Wessman (1998) found that the ideal kernel size coincided with the size of the image objects to be detected (juniper plants in the present study). We repeated this moving window analysis with a kernel size of 5 m (the median crown diameter of the detectable trees based on the wavelet analysis was 4.75 m), for the historic and current aerial photography. Following the moving window analysis a supervised classification was performed on the three texture layers (mean, variance, and range) and the original image dividing the image into two classes; presence and absence of woody plants. Training data was derived from the aerial photographs.

Although current imagery from various sensors (e.g. Landsat, SPOT, ASTER) is available for the study region we chose to use black and white aerial photography resampled to 1-m spatial resolution for both current (1998-2004) and historic (1939-1946) cover and carbon estimates. Choosing consistent imagery allows us to 1) assess errors that may be present utilizing these techniques because current imagery can be calibrated to field conditions, 2) minimize errors associated with utilizing two different analysis techniques in historic and current analyses (i.e. Asner et al. 2003) and 3) improve spatial resolution over most freely available contemporary satellite sensors by using aerial photography.

2.4. Stand scale analysis - field verification

Although past studies observed that juniper crown diameters derived via SWA exhibited a strong correlation with crown diameters derived via hand digitizing in a GIS in open canopy juniper woodlands (Strand et al., 2006a), comparison of this method’s output to field measurements were clearly warranted. Furthermore, the collection of field-based data allows the evaluation of the methodological questions stated in the introduction.

In the summer of 2005 we established twenty 60x60-m plots with juniper foliar cover ranging from 1.2-61.8%. Within the established plots we recorded the spatial location of each individual juniper tree larger than 1 m tall with a Trimble GeoXT global positioning system (GPS) unit with a spatial accuracy of < 1 m. Plots were located such that trees were either in or out of the plot, i.e. no partial trees were present. Furthermore we recorded the maximum crown diameter, the crown diameter perpendicular to the maximum crown diameter, the height and the basal stem circumference of each juniper tree taller than 1 m within plots. Aerial photographs from 1998 and 2004 covering the field plots were then analyzed with 2-D wavelet analysis and crown diameters from the field and wavelet analysis were compared. We also compared the wavelet estimated juniper cover within the plots to field data and to cover estimated via a texture method.

2.5. Allometric estimate of biomass

Western juniper plant biomass was estimated from allometric equations developed by Gholz (1980) relating stem basal circumference to stem, branch, and foliar biomass:

$$\mathrm{B} = \exp(m + n \ln \mathrm{X})$$

where B is the above ground stem, branch or foliar biomass in kilograms, X is the stem basal circumference in centimeters and m and n are constants specific to western juniper stem, branch and foliar biomass in kilograms. Gholz's (1980) allometric equations did not incorporate biomass accumulation in root biomass. Following Law et al. (2001) we assumed the below ground carbon storage to be 25% of above ground woody carbon storage. We recognize that this estimate is associated with high uncertainty and therefore report above and below ground woody biomass separately. Biomass estimates were further converted to carbon by multiplication with 0.5 to account for the average carbon content of woody plant material (Schlesinger, 1997).

2.6. Landscape scale analysis

Landscape scale assessments of change in woody carbon over time can be complicated by the lack of information of historic and current woody plant cover, the topo-edaphic heterogeneity of the land, the effects of land use history and management practices (Asner et al., 2003), and variations in natural disturbance regimes. Other sources that contribute to the uncertainty are the large areal extent affected and the fine scale at which woody encroachment occurs (Houghton and Goodale, 2004). Image processing of high spatial resolution, limited extent, remotely sensed data such as aerial photography for areas the size of the Owyhee Plateau is time consuming. Therefore, to avoid unrealistic efforts in image processing while still obtaining statistically sound estimates of change in woody carbon stock for the region we stratified the landscape and analyzed samples of the aerial photographs within these strata.

Although attractive because of savings in effort and time, such stratification comes with its own challenges. Namely, it is important to select strata that are relevant to the ecological process observed (woody encroachment in this case), disturbance regimes, and management practices. With respect to expanding woodlands, studies have observed that structure and development are affected by landuse practices (Asner et al 2003) and topography, with specific onus on elevation and site exposure (Johnson and Miller 2006). Accelerated successional rates have also been reported on deeper and richer soils supporting mountain big sagebrush compared to shallow soils where low sagebrush represents the vegetation potential (Young and Evans, 1981; Eddleman, 1987; Bunting et al., 2005). Following these and other prior studies (e.g., Scott et al., 2002), we stratified the landscape based on elevation (USGS 1999), aspect, soil type (Owyhee County Soil Survey – USDA/NRCS 1998), and land stewardship. Another important ecological process in juniper woodlands affecting encroachment rates is the seed dispersal mechanisms, where seeds are adapted for spread by primarily berry eating birds and mammals (Maser and Gashwiler, 1977). Therefore, proximity analysis in GIS (NEAR function in ArcGIS) was used to evaluate how far current juniper plants had established from juniper plants present in historic photos to gain a better understanding of juniper encroachment rates across the landscape.

The 1:27000 scale 1946 photographs each covered a 6x6-km area. We randomly selected 8 photographs stratified by elevation and spatial location. Within these photos we randomly selected six 100 ha (1000 x 1000 m) areas stratified by sagebrush type (representative of the soil characteristics), aspect, and land stewardship. Altogether, net change in above ground carbon stock was estimated for 4800 ha representative of the 330,000-ha area over the selected time period. Beyond estimating the change in biomass and carbon stock for the entire sampled area we also evaluated the change at two different spatial scales, 1000 x 1000 m and 100 x 100 m (Figure 1) using both SWA and textural analysis. To further evaluate which environmental variables affect juniper encroachment at a landscape scale we statistically tested the effect of elevation, aspect, land stewardship, and sagebrush type (soil) with a single factor ANOVA with each of the 6x6 km photographs being the sampling unit (n=8).

3. Results

3.1. Stand scale analysis

Juniper crown diameters derived via the wavelet technique produced a strong unbiased correlation with crown diameters measured in the field (r=0.86, n=60), with a 19% omission error and 0% commission error (Figure 2). Plants with a crown diameter smaller than 2-3 m were not detected by the wavelet technique nor were they detectable in a GIS. However, even though these small plants comprised 55% of the number of juniper stems in the plots, they contain only 4% of the woody carbon across the sampled area (Figure 3).

We further compared the SWA estimated foliar plant cover to field data for 20 plots with juniper cover in the range 1.2 – 61.8 %. Cover estimates using SWA are accurate up to approximately 25% juniper cover, with increasing uncertainty in the range 25-55% due to crown clumping (r=0.81, Figure 4). In the canopy cover range of 25-55%, SWA is biased towards underestimating foliar cover and above 55% cover the method is unreliable for analysis of aerial photography. Considering all of the 20 plots, SWA estimated 10.7% total plant cover compared to the field estimate of 13.9%, yielding a relative underestimation of 23% over the study area. We attribute approximately 50% of the error in the cover estimate to the inability to detect plants < 2-3 m in size, and 50% of the error to misclassification due to clustering of trees in plots with > 25% plant cover. The texture method over-estimated woody plant cover 1.8 times on average for the 20 field plots (Figure 4).

3.2. Estimate of biomass and carbon from allometry

We found a strong correlation ($r^2 = 0.86$, n=454) linking crown diameter to stem diameter for western juniper plants within the field data, which enabled us to directly compute above ground biomass as a function of individual juniper plants identified using the SWA output of crown diameter (Figure 5).

3.3. Landscape scale analysis

Within the sampled forty-eight 100-ha blocks situated across the area, the western juniper plant cover increased one-fold, from 5.3 % to 10.4 % total cover, during the time period 1939-1946 to 1998-2004. Juniper plant density (plants > 3 m crown diameter) has increased by 128% with a higher proportion of the plant population in the smaller size classes compared to the size distribution 50-60 years ago. After image-based wavelet delineation of tree crown sizes, we computed the change in above ground woody plant biomass and carbon stock between the two time periods using the allometric equations by Gholz (1980). Overall 3.3 $gCm^{-2}yr^{-1}$ woody carbon accumulated over the sampled area above ground with an additional 0.8 $gCm^{-2}yr^{-1}$ estimated in root carbon stock. The variability in carbon accumulation rates increased with decreasing scale of analysis, as expected. At the 100-ha scale the above ground woody carbon stock accumulation varied from –1.7 $gCm^{-2}yr^{-1}$ to 9.9 $gCm^{-2}yr^{-1}$ while at the 1-ha scale the variation was –11.0 $gCm^{-2}yr^{-1}$ to 22.1 $gCm^{-2}yr^{-1}$.

Summarized over the entire sampled area the texture analysis yields an estimate of above ground carbon accumulation of 10.0 $gCm^{-2}yr^{-1}$ compared to 3.3 $gCm^{-2}yr^{-1}$ for SWA. Figure 6 shows an example of a historic and a current photo (1000 x 1000 m) superimposed with juniper cover areas estimated via the wavelet and texture method. For the area in Figure 6 SWA estimated juniper cover to be 2.5% in 1946 and 12.1% in 1998 while the texture method estimated 14.4% in 1946 and 61.1% in 1998. This figure illustrates how objects other than juniper plants and grayscale variations in the sagebrush steppe matrix can affect the texture based juniper cover estimate.

Among the topographic, soil, and stewardship variables statistically tested, only soil type had a significant effect on the above ground woody carbon accumulation ($p = 0.07$, $F = 3.81$, $n=8$, Table 1) within the 1400-2560 m elevation range.

The proximity analysis of current to historic juniper plants shows that western juniper plants in this area rarely establish farther away than ~50-100 m from an existing plant (Figure 7). When interpreting Figure 7 the reader should keep in mind that 44% of the plants in the current photo were present in the historic photo. The distance between a plant in the historic photo and the same plant in the current photo should be zero in the unachievable event of perfect georegistration, however georegistration errors of up to 10 m are not uncommon. The graph does not include1080 plants because they were located at distances 150-700 m from the closest 'historic' plant, representing approximately 1% of the recently established plants. These results are in agreement with previous spatial analyses of western juniper short- and long-distance spread mechanisms, estimating the short distance dispersal, aided by berry eating birds with small home ranges, to approximately 50-70 m (Strand et al., 2006b). The distance distribution in Figure 7 indeed represents the probability distribution of plant dispersal distance for western juniper.

4. Discussion

4.1. Comparison of 2-D wavelet and texture analysis

The 2-D wavelet analysis technique identifying plant size and spatial distribution has previously been identified as a remote sensing tool with the potential for analysis of current encroachment condition, rates of change, and ability to shed light on relationships between landscape patterns and ecological processes in arid and semi-arid landscapes (Strand et al., 2006a,b). Strand et al. (2006a) found a strong correlation between crown diameters estimated via SWA and those derived via hand-digitizing in a geographic information system. Through this research we provide further evidence that the crown diameters and positions of individual western juniper plants accurately portray the plant distribution on the ground in open canopy woodlands. SWA is limited in detecting plants that are smaller than 2-3 times the image pixel size and when the canopy closure within the stand approaches 50%. The omission in detecting plants with a crown diameter smaller than 2-3 m in crown diameter is of minor concern considering that the biomass contained in these small but numerous plants only contribute only approximately 4% to the over all above ground woody biomass across the landscape (Figure 3). In western juniper woodlands the commission errors of canopy cover were negligible while the omission errors amounted to 23% relative difference within the 20 field plots ranging from 1.2 – 61.8 % in canopy cover. It must also be recognized that SWA is sensitive to the shape of the objects of interest as the wavelet function is convolved with the image objects, represented by pixels, to produce high scores where the shape and size of the two coincide. Western juniper plants are commonly symmetrical and their image brightness is well represented by the Mexican hat wavelet function dilated at different scales to detect plants of varying size. This method may not be suitable for plants or image objects with more irregular shapes.

Texture analysis has previously been employed to estimate canopy cover (Asner et al., 2003) and shrub density (Hudak and Wessman, 1998, 2001). Hudak and Wessman (2001) found a weak ($r^2 = 0.2$) but significant relationship between image texture and woody plant canopy cover while the estimate by Asner et al. (2003) could not be validated because the analysis was performed only on historic (1937) data. Compared to field data the texture analysis technique in the case of western juniper overestimated canopy cover by a factor of 1.8 in the 20 field plots. This consistent overestimation of cover can be explained by the very nature of texture analysis in detecting edge. Both the variance and range component of the texture analysis are extremely sensitive to edge, such as the edge between a juniper plant and the surrounding sagebrush steppe matrix. Edges are emphasized and in the supervised classification of the texture images these edges are classified as juniper plants, hence overestimating the size of each plant. This phenomenon is apparent if the juniper cover map resulting from the texture analysis is laid over the aerial photograph in image processing software or GIS. Another shortcoming of the texture analysis is its sensitivity to image brightness and the contrast between juniper plants and surrounding sagebrush steppe. Juniper plants with a light background (high bare ground proportion for example) are easily identified using texture analysis, however if the background is darker (dense sagebrush or a dense herbaceous understory for example) the juniper plant may not be identified by texture analysis, while the shape sensitive wavelet accurately identifies these plants. Furthermore texture analysis does not discriminate between dark objects on a light background and light objects on a dark background. Hence such areas with fine-scale variability in brightness may mistakenly be classified as areas with high juniper cover. On the other hand, texture analysis is superior to SWA in identifying clusters of juniper trees, where the trees are too close together for adequate detection with the wavelet function.

We conclude that SWA and texture analysis are complementary and powerful remote sensing techniques with the ability to accurately estimate western juniper cover in panchromatic current and historical aerial photography. The strengths and limitations of the two methods result in an underestimate of juniper canopy cover for the wavelet method and an overestimate for the texture method providing a respective lower and upper bound for the change in woody carbon over time. In a detection of change between two time-periods we emphasize the advantage of using the same method for cover estimates for both time-periods. Each analysis technique has its own biases and when the same method is used in the temporal sequence, cancellation of errors is more likely than error propagation. However, temporal analysis of pools and fluxes with both an underestimating and overestimating method does improve the determination of the actual uncertainty within estimates and therefore we encourage the further application of such two-staged approaches to other aspects of biogeochemical cycling research.

4.2. Changes in woody plant cover and carbon accumulation

The research presented here confirms that western juniper over the past few decades has expanded into areas previously dominated by sagebrush steppe. The expansion occurs at significantly higher rates on deeper, well-drained soils capable of supporting mountain big sagebrush compared to shallow soils dominated by low sagebrush. Statistical analysis infers that within this study area there is no significant difference in management practices as they relate to juniper control between public, private and state land stewards nor does the topography represented by elevation and aspect significantly affect the juniper expansion at a 1000x1000-m scale. Although the effect of elevation is not statistically significant the highest rates of juniper expansion occurs at the 1800-2000 m elevation range compared to both lower and higher altitudes (Table 1). We can expected the encroachment rates to increase in areas of higher precipitation (i.e. higher elevation) while the drop in encroachment rates above 2000-2100 m can be explained by the cold winter temperatures and harsh conditions at these high altitudes (Miller et al., 2005).

Within the 4800-ha sampled area the wavelet and texture analyses estimate 3.3 $gCm^{-2}yr^{-1}$ and 10.0 $gCm^{-2}yr^{-1}$ accumulation rates of woody carbon over the ~60-year study period, respectively. Considering that field data shows that the wavelet method is underestimating cover and thereby biomass and carbon by ~23% and the texture method in average overestimates cover by 1.8 we can further constrain the estimate to the range 4.3 – 5.6 gCm^{-}

^{2}yr^{-1} where the lower bound is 23% higher than the wavelet estimate and the higher bound is 1.8 times lower than the texture estimate. Approximating the root biomass to be 25% of the above ground biomass increases this range to 5.4 – 7.0 gCm^{-2}yr^{-1} for above and below ground woody carbon.

Expansion of juniper woodlands eventually leads to a loss of the shade intolerant sagebrush plants (Bunting et al., 1999; Miller et al., 2005). The above ground carbon in sagebrush steppe of the Great Basin has been estimated to 440±180 gCm-2 (Bradley et al., 2006). Considering that the juniper cover averaged over the sampled 4800 ha area has increased from 5.3% to 10.4% replacing sagebrush steppe, we can calculate that over approximately 52 years (0.104-0.053)*440 = 22.4 gCm^{-2} sagebrush carbon has been lost averaging 0.43 gCm^{-2}yr^{-1} or less than 10% of the woody carbon accumulation caused by the juniper expansion.

The effect of woody plant encroachment on soil carbon pools and fluxes is uncertain. Honey mesquite (*Prosopis glandulosa*) encroachment in the semi-arid lands of Texas has been reported to both decrease (Jackson et al., 2002), increase (Geesing et al., 2000; Hibbard et al., 2001) and have no affect (Hughes et al., 2006) on the soil carbon in the upper soil layer. While estimating the affect of woody encroachment in western juniper woodlands on soil carbon is beyond the scope of this study, the wavelet method conveniently provides a spatial point pattern that may serve as a covariate for further studies of the redistribution or accumulation of soil carbon between areas below woody plant canopies and in sagebrush steppe interspaces. It is reasonable to hypothesize that the carbon accumulation (or loss) around previously or recently established juniper plants is related to the distance from the center of the plant. Geostatistical analysis techniques could here be employed to create a soil carbon estimate over the landscape utilizing soil properties available in the county soil survey and the juniper point pattern produced by the wavelet analysis. The point pattern produced by the wavelet analysis provides opportunities to tie secondary landscape properties such as soil properties, water usage, plant competition, fire fuel distribution, seed dispersal etc. to the juniper plant distribution (e.g. Strand et al., 2006b).

4.3. The need for landscape scale analyses

The spatial and temporal scale at which analyses are performed strongly influences estimates of woody carbon accumulation due to encroachment. We estimate the above ground woody carbon accumulation using SWA at three spatial scales. Over all, 3.3 $gCm^{-2}yr^{-1}$ above ground woody carbon accumulated within the 4800 ha sampled area. At the 1000 x 1000 m scale the above ground woody carbon stock accumulation varied from -1.7 to 9.9 $gCm^{-2}yr^{-1}$ while at the 100 x 100 m scale the variation was –11.0 to 22.1 $gCm^{-2}yr^{-1}$. Similar results have been found in Texas where honey mesquite is expanding into grasslands. In a regional assessment Asner et al. (2003) estimated a 1.9 $gCm^{-2}yr^{-1}$ above ground woody carbon accumulation over 62 years using remote sensing technology while at a plots scale Hughes et al. (2006) reported above ground woody carbon accumulations of 35-50 $gCm^{-2}yr^{-1}$ over ~60 years (Table 2) in the same general area. Similarly, Johnston et al. 1996 estimated a regional carbon accumulation rate of 16.9 $gCm^{-2}yr^{-1}$ in Minnesota oak savannas while Tilman et al. (2000) estimated the rate to be 180 $gCm^{-2}yr^{-1}$ in plots within the same ecosystem (Table 2). The reason for the much higher estimates at a plot scale can likely be traced back to selection of plot areas. In a study of carbon accumulation due to woody encroachment plots are selected in areas where encroachment has occurred, neglecting the fact that encroachment has not occurred uniformly across the landscape. In agreement with Asner et al. (2003) we found that soil properties significantly affect the biomass production and woody encroachment rates creating heterogeneity in the potential carbon storage and accumulation rates across regions.

Several researchers have explored temporal variations in biomass accumulation. Law et al. (2003) recorded remarkable differences in carbon accumulation rates along a chronosequence after a clearcut in ponderosa pine (*Pinus ponderosa*) where young regenerating stands were loosing carbon to the atmosphere, followed by an increase in carbon accumulation until the stands were 100-200 years of age when the carbon accumulation rates were reduced (Table 3). Similarly, Pare and Bergeron (1995) recorded higher carbon accumulation rates in Canadian boreal forest < 75 years of age while the rates were slower in the 75-200 year age stands. In Balsam fir (*Abies balsamea*) stands in New York, Sprugel (1984) observed carbon accumulation rates of 160 $gCm^{-2}yr^{-1}$ for stands younger than 55 years while the rates were reduced to 58 $gCm^{-2}yr^{-1}$ on average for older stands (Table 3). Assessments of carbon accumulation are commonly done at a stage in succession where the growth is likely to be the most rapid (20-100 year in age depending on the species). Law et al. (2003) show that both earlier and later in succession the carbon accumulation rates are lower in ponderosa pine systems and Miller et al. (2005) provide evidence that the most rapid biomass accumulation in western juniper stands occur between the onset of seed production (~30-50 years of age) and the time the trees reach maximum height (80-100 years depending on site conditions). The developing woodlands reach crown closure at 70-90 years on wet sites and 120-170 years on less productive sites (Miller et al., 2005) at which point one could expect a decrease in biomass accumulation rates. Canadell et al. (2007) present evidence indicating that most biological carbon sinks will over time level off and eventually reach zero, a process referred to as *sink saturation*. At this time no further carbon is removed from the atmosphere and there is no net carbon accumulation in the terrestrial ecosystem.

Landscapes are composed of a mosaic of vegetation types in patches of different age and structure classes, which are thought to be hierarchically nested (Allen and Starr, 1982; Urban et al., 1987; Turner et al., 1993). Within a life zone the potential natural plant community at a given location is dictated by topo-edaphic and climatic variables while plant succession combined with natural or human induced disturbances create patches of structural variability within the potential vegetation types (PVT). Two PVT's dominate the Owyhee Mountains; the western juniper woodland/mountain big sagebrush steppe and the western juniper woodland/low sagebrush steppe (Bunting et al., 2005). Within PVT's disturbance regimes (especially fire) influence the western juniper patchwork of different structural stages ranging from stand initiation to mature woodlands in areas where the soil and climatic conditions allow juniper establishment and a seed source is available (Bunting et al., 2005; Miller et al. 2005). The natural or historic range of variability is a useful concept, which describes the variability of ecosystem conditions and processes over time (Morgan et al., 1994; Swanson et al., 1994). The range of variability can, for example, describe the landscape composition of different age and structural classes where the patch mosaic at a given time period is affected by interactions with disturbance regimes. When comparing carbon pools and fluxes within ecosystems at a landscape scale between time periods it is important to understand not only the ability for the ecosystem to accumulate (or release) carbon along successional gradients but also to estimate the expected range of variability in landscape composition for the two time periods. Conceptually it is this change in range of variability that will explain the ecosystem carbon flux at the landscape scale. To better understand the change in carbon flux across regional extents samples must be collect randomly from a large enough area to adequately represent the structural variability within the landscape for the time periods of interest. Remote sensing technology provides avenues for mapping vegetative structure and disturbance events through time and is an invaluable asset in landscape scale assessments.

4.4. Carbon accounting

Woody encroachment has been identified as an ecological process that is contributing to the US carbon sink (Houghton and Goodale, 2004). Stand level analyses of carbon accumulation rates have been reported for many semi-arid ecosystems (San Jose et al., 1998; Tilman et al., 2000; Grünzweig et al., 2003; Hicke et al., 2004; Hughes et al., 2006, Table 3) however regional estimates are lacking (Asner et al., 2003). The results presented in this research and findings reported by Asner et al. (2003) show the importance of spatial scale, in estimates of changes in carbon pools and flux. At a landscape scale variability in soil productivity, topography, management objectives and natural disturbances creates a mosaic of vegetation structure with variable potential for carbon accumulation.

Considering this temporal and spatial variability at a landscape scale, the values previously used to estimate the contribution of woody encroachment to the US carbon sink may be too high. In a computation of the accumulation of woody carbon in juniper woodlands Houghton et al. (2000) used 65 $gCm^{-2}yr^{-1}$ for temperate pine and juniper woodlands compared to our estimate of 5.4 – 7.0 $gCm^{-2}yr^{-1}$ including above ground and root woody carbon. We are aware that we are not including possible changes in soil carbon in our estimate and it is not clear whether they were included in the estimate by Houghton et al. (2000). The seed dispersal mechanisms and distances are also clearly important, however not considered in previous estimates of the land area affected by woody encroachment. All non-forested non-cultivated areas cannot be assumed to be at immediate risk of woody encroachment for two reasons. 1) All such areas do not have the topo-edaphic and climatic characteristics necessary to support woody plants. 2) All areas where topo-edaphic and climatic variable allow for woody encroachment have not been exposed to seeds from these woody plants and may not be exposed for decades to come.

In a thought experiment we could assume that our average regional scale carbon flux estimate within the bounds of the wavelet and the texture analysis estimate (5.4 – 7.0 $gCm^{-2}yr^{-1}$) would apply to all pinyon-juniper woodlands in the Great Basin encompassing an area of 30 million ha (West, 1999) and calculate a 0.002 $PgCyr^{-1}$ contribution to the carbon sink proposed to be caused by woody encroachment (0.06-0.13 $PgCyr^{-1}$, Pacala, 2001; Houghton, 2003)

Another important consideration to make in the context of carbon accounting is the expected future of the recently created woodlands. Woody encroachment is in most areas undesirable from a management and conservation perspective and land stewards at all levels (private, state and federal) are likely to consider prescribed fire or other treatments to recover grassland or shrub steppe habitats by reducing the woody component. Certainly, before semi-arid lands are considered to be suitable for long-term carbon storage via woody plant encroachment or plantations the consequences for future land use and land cover changes must be seriously evaluated. Grassland or steppe habitats where woody encroachment has been allowed to proceed will be extremely difficult to restore to their original state. These lands will most likely eventually burn in natural wildfires under extreme conditions or persist for centennial time periods in a low productive state, none of which will result in removal of carbon from the atmosphere.

5. Conclusions

There is a need for landscape scale assessments to improve our understanding of the effect of ecological processes such as woody encroachment on the carbon fluxes between terrestrial ecosystems and the atmosphere. In such research it is important to capture the spatial and temporal variability over areas that are large enough to represent the ecosystem and its natural and managed disturbance regimes. Plot scale assessments cannot be directly extrapolated to large extents because of the natural variability in the topo-edaphic and climatic characteristics of the landscape, natural and human induced disturbance regimes, spread mechanisms of woody plant propagules, and temporal variability in carbon uptake along successional gradients. Remote sensing and geospatial analysis techniques are invaluable tools in such broad scale analyses. The 2-D wavelet analysis technique employed here provides a powerful remote sensing tool allowing for regional analyses of change in above ground woody carbon in open canopy savannas and woodlands at multiple spatial scales. Using this method in combination with conventional image texture analysis we estimate a 3.3 –10 $gCm^{-2}yr^{-1}$ woody carbon accumulated above ground in western juniper woodlands with an additional 25% estimated in root carbon stock from 1946 to 1998. This estimate is considerably lower than the 65-90 $gCm^{-2}yr^{-1}$ previously used to estimate the contribution of woody encroachment in western pine and juniper woodlands (Houthton et al., 2000) to the US carbon sink. Further research at regional to landscape scales across the West is warranted to further constrain the carbon cycle in western woodlands.

Acknowledgements

We would like to acknowledge the University of Idaho Research Office for providing funds via a seed grant for this research. We further thank the anonymous reviewers for their constructive criticism of this manuscript.

References

Allen, T.F.H., and T.B. Starr (1982), *Hierachy*, Chicago, Il, University of Chicago Press.

Archer, S., D.S. Schimel, and E.A. Holland (1995), Mechanisms of shrubland expansion: land use, climate, and CO_2?, *Climatic Change*, *29*, 91-99.

Archer, S., T.W. Boutton, and K.A. Hibbard (2001), Trees in grasslands: Biogeochemical consequences of woody plant expansion, in *GlobalBiogeochemical Cycles in the Climate System*, edited by E-D. Schulze, S.P. Harrison, M. Heimann, E.A. Holland, J. Lloyd, I.C. Prentice, D. Schimel, Academic Press, San Diego.

Asner, G.P., S. Archer, R.F. Hughes, R.J. Ansley, and C.A. Wessman (2003), Net change in regional woody vegetation cover and carbon storage in Texas Drylands, 1937-1999, *Global Change Biology, 9*, 316-335.

Bailey, R.G. (1998) *Ecoregions: the ecosystem geography of the oceans and continents*, Springer, New York.

Bradley, B.A., R.A. Houghton, J.F. Mustard, and S.P. Hamburg (2006), Invasive grass reduces above ground carbon stock in shrublands of the Western US, *Global Change Biology*, *12*, 1815-1822.

Bunting, S.C., J.L. Kingery and E.K. Strand (1999), Effects of succession on species richness of the western juniper woodland/sagebrush steppe mosaic, pp. 76-81 in *Proceedings: Ecology and management of pinyon-juniper communities within the Interior West. USDA For. Ser. Gen. Tech. Rep. RMRS-P-9*, compiled by Monsen, S.B. and R. Stevens.

Bunting, S.C., J.L. Kingery and M.A. Schroeder (2003), Assessing the restoration potential of altered rangeland ecosystems in the Interior Columbia Basin, *Restoration Ecology, 21*, 77-86.

Bunting, S.C., E.K. Strand, and J.L. Kingery (2005), Landscape characteristics of sagebrush-steppe/juniper woodland mosaics under varying modeled prescribed fire regimes, *Proceedings 23rd Tall Timbers Fire Ecology Conference*, Tallahassee, Florida. Tall Timbers Research, Inc., in press.

Canadell, J.G., D.E. Pataki, R. Gifford, R.A. Houghton, Y. Luo, M.R. Raupach, P. Smith, W. Steffen (2007), Chapter 6 Saturation of the Terrestrial Carbon Sink, in *Terrestrial*

Ecosystems in a Changing World, edited by Canadell, J.G., and D. E. Pataki, Springer-Verlag, Berlin, Heidelberg.

Conway-Welch, J. (1982), *The story of Silver City, Idaho – Gold town to Ghost town*, 115 pp., University of Idaho Press, Moscow, Idaho.

ESRI 1999-2005, ArcGIS software v. 9.1., Environmental Systems Research Institute Inc., Redlands, California, Web site: http://www.esri.com.

Eddleman, L.E. (1987), Establishment and stand development of western juniper in central Oregon, pp. 255-259 in *Proceedings- Pinyon-Juniper Conference General Technical Report INT-215*, edited by R.L. Everett,U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.

Falkowski, M.J., A.M.S. Smith, A.T. Hudak, P.E. Gessler, L.A. Vierling, and N.L.Crookston (2006), Automated estimation of individual conifer tree height and crown diameter via Two-dimensional spatial wavelet analysis of LIDAR data, *Canadian Journal of Remote Sensing*, *32*(1), 153-161.

Geesing, D, P. Felker, R.L. Bingham (2000), Influence of mesquite (*Prosopis glandulosa*) on soil nitrogen and carbon development implications for global carbon sequestration, *Journal of Arid Environments*, *46*, 157-180.

Gholz, H.L. (1980), Structure and productivity of *Juniperus occidentalis* in Central Oregon, *American Midland Naturalist, 103*, 251-261.

Grünzweig, J.M., T. Lin, E. Rotenberg, A. Schwartz, and D. Yakir (2003), Carbon sequestration in arid-land forest, *Global Change Biology,* 9, 791-799.

Hibbard, K.A., S. Archer, D.S. Schimel, D. Valentine (2001), Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna, *Ecology*, *82*, 1999-2001.

Hicke, J.A., R.L. Sherriff, T.T., Veblen, and G.P. Asner (2004), Carbon accumulation in Colorado ponderosa pine stands, *Canadian Journal of Forest Research, 34*, 1283-1295.

Houghton, R.A., J.E. Hobbie, J.M. Melillo, B. Moore, B.J. Peterson, G.R. Shaver, and G.M. Woodwell (1983), Changes in the carbon content of terrestrial biota and soil between 1866 and 1980: A net release of CO_2 to the atmosphere, *Ecological Monographs, 53*, 235-262.

Houghton, R.A., J.L. Hackler, and K.T. Lawrence (1999), The US carbon budget: contributions from land-use change, *Science, 285*, 574-578.

Houghton, R.A., J.L. Hackler, and K.T. Lawrence (2000), Changes in terrestrial carbon storage in the United States. 2: The role of fire and fire management, *Global Ecology and Biogeography*, *9*(2), 145-170.

Houghton, R.A. (2003), Why are estimates of the terrestrial carbon balance so different?, *Global Change Biology*, *9*, 500-509.

Houghton, R.A., and C.L. Goodale (2004), Effects of Land-Use Change on the Carbon Balance of Terrestrial Ecosystems, pp. 85 in *Ecosystems and Landuse Change*, edited by Defries, R.S., G.P. Asner, and R.A. Houghton, American Geophysical Union, Washington DC, USA.

Hudak A.T. and C.A. Wessman (1998), Textural analysis of historical aerial photography to characterize woody plant encroachment in South African savanna, *Remote Sensing of Environment, 66*(3), 317-330.

Hudak, A.T. and C.A. Wessman (2001), Textural analysis of high resolution imagery to quantify bush encroachment in Madikwe Game Reserve, South Africa, 1955-1996, *International Journal of Remote Sensing*, *22*(14), 2731-2740.

Hughes, R.F., S.R. Archer, G.P. Asner, C.A. Wessman, C. McMurtry, J. Nelson, and R.J. Ansley (2006), Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna, *Global Change Biology*, *12*, 1733-1747.

Jackson, R.B., J.L. Banner, E.G. Jobbagy, W.T. Pockman, and D.H. Wall (2002), Ecosystem carbon loss with woody plant invasion of grasslands, *Nature*, *418*, 623-626.

Johnson, D.D., and R.F.Miller (2006), Structure and development of expanding western juniper woodlands as influenced by two topographic variables. *Forest Ecology and Management,* in press.

Johnston, M.H., P.S. Homann, J.O. Engstrom, D.F. Grigal (1996), Changes in ecosystem carbon storage over 40 years on an old field/forest landscape in east-central Minnesota, *Forest Ecology and management*, *83*, 17-26.

Laclau, P. (2003), Root biomass and carbon storage of ponderosa pine in a northwest Patagonia plantation, *Forest Ecology and management, 173*, 353-360.

Law, B.E., P.E. Thornton, J. Irvine, P.M. Anthoni, and S. VanTuyl (2001), Carbon storage and fluxes in ponderosa pine forests at different developmental stages, *Global Change Biology, 7*, 755-777.

Law, B.E., O.J. Sun, J. Campbell, S. Van Tuyl, and P.E. Thornton (2003), Changes in carbon storage and fluxes in a chronosequence of ponderosa pine, *Global Change Biology, 9*, 510-524.

Leica Geosystems, ERDAS® Imagine, 1991-2003. Version 8.7, Leica Geosystems, GIS & Mapping, Atlanta Ga, USA, http://www.leica-geosystems.com/corporate/en/lgs_index.htm

Maser C. and Gashwiler J.S. 1977. Interrelationships of wildlife and western juniper. In: Proceedings of the western juniper ecology and management workshop in Bend Oregon p. 37-82, Editors: Martin R.E., Dealy J.E. and Caraher D.L. USDA Forest Service Portland Oregon GTR PNW-74.

MATLAB® 2004. Matlab and Simulink, Version 7.0.0.27 (R14). The MathWorks, http://www.mathworks.com/products/matlab/.

Miller, R.F., J.D. Bates, T.J. Svejcar, F.B. Pierson, and L.E. Eddleman (2005), Biology, Ecology, and Management of Western Juniper, *Technical Bulletin 152*, Oregon State University, Agricultural Experiment Station.

Morgan, P., G.H. Aplet, J.B. Haufler, H.C. Humphries, M.M. Moore, and W.D. Wilson. (1994), Historical range of variability: a useful tool for evaluating ecosystem change, *Journal of Sustainable Forestry, 2*(1/2), 87-111.

Norris, M.D, J.M Blair, L.C. Johnson, and R.B. McKane (2001), Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie, *Canadian journal of Forest Research, 31*, 1940-1946.

Owyhee Canyonlands History, 2003. Accessed November 13, 2006, http://www.endurance.net/oreana/owyheecanyonlands/owyheehistorygeology.htm

Pacala, S.W. (2001), Convergence of land-and atmosphere-based US carbon sink estimates. *Science, 292*, 2316-2320.

Pare, D., and Y. Bergeron (1995**)**, Above-Ground Biomass Accumulation along a 230-Year Chronosequence in the Southern Portion of the Canadian Boreal Forest **,** *Journal of Ecology*, *83*(6), 1001-1007

Roth, A. (2004), Fire patterns within a successional gradient of a sagebrush steppe/juniper woodland, M.S. Thesis, University of Idaho, Moscow, Idaho, USA.

SanJose, J.J., R.A. Montes, M.R. Farinas (1998), Carbon stock and fluxes in a temporal scaling from savanna to semi-deciduous forest, *Forest Ecology and Management*, *105*, 251-262.

Scholes, R.J., and S.R. Archer (1997), Tree-grass interaction in savannas, *Annual review Ecological Systems*, *28*, 517-544.

Schlesinger, W.H. (1997), *Biogeochemistry an Analysis of Global Change*, Academic Press, San Diego, California, USA.

Scott, J.M., C.R. Peterson, J.W. Karl, E.K. Strand, L.K. Svancara, and N.M. Wright (2002), *A Gap Analysis of Idaho: Final Report*, Idaho Cooperative Fish and Wildlife Research Unit, Moscow, ID.

Slezak, E., A. Bijaoui, and G. Mars (1992), Structures identification from galaxy counts – Use of wavelet transform, pp 175-180 in *Wavelets and applications* edited by Meyer, Y., Masson/Springer-Verlag, Paris/Berlin.

Sprugel, D.G. (1984), Density, biomass, productivity, and nutrient cycling changes during stand development in wave-regenerated balsam fir forest, *Ecological Monograph*, *54*, 165-186.

Strand, E K., L.A. Vierling, A.M.S. Smith, S.C. Bunting, D.B. Hann, and P.E. Gessler (2005), Wavelet Estimation of Plant Spatial Patterns in Multi-temporal Aerial Photography, Eos Trans. AGU, *86*(52)*,* Fall Meeting, San Francisco, Suppl., Abstract B43B-0278.

Strand, E.K., A.M.S. Smith, S.C. Bunting, L.A. Vierling, B. Hann, and P.E. Gessler (2006a), Wavelet estimation of plant spatial patterns in multi-temporal aerial photography, *International Journal of Remote Sensing*, *27*(9-10), 2049-2054.

Strand, E.K., A.P. Robinson, S.C. Bunting (2006b), Spatial Patterns on the Western Juniper/Sagebrush Steppe Ecotone, Plant Ecology in press.

Swanson, F.J., J.A. Jones, D.O. Wallin, and J.H. Cissel (1994), Natural variability – implications for ecosystem management, pp. 89-103 in. *Gen. Tech. Rep. PNW-GTR-318*, edited by Jensen, M.E., Bourgeron, and P.S. Portland, OR: U.S. Department of

Agriculture, Forest Service, Pacific Northwest Research Station. 376 p. (Everett, Richard L., assessment team leader; Eastside forest ecosystem health assessment).

Tilman, D., P. Reich, H. Phillips, M. Menton, A. Patel, E. Vos, D. Peterson, and J. Knops (2000), Fire suppression and ecosystem carbon storage, *Ecology*, *81*, 2680-2685.

Turner, M.G., R.V. O'Neill, R.H. Gardner, and S.M. Pearson (1993), Multiscale organization of landscape heterogeneity, pp. 81-87 in *Eastside Forest Ecosystem Health Report, Volume II. Ecosystem management: principles and applications,* edited by Jensen M.E. and P.S. Bourgeron, U. S. Department of Agriculture, National Forest System, Forest Service Research, Washington, DC.

Unser, M, A. Aldroubi, and A. Laine (2003), Guest Editorial: Wavelets in Medical Imaging, *IEEE Transactions on Medical Imaging, 22*, 285-287.

Urban, D.L., R.V. O'Neill, and H.H. Shugart (1987), Landscape Ecology, *Bioscience*, *37*, 119-127.

USDA – NRCS (1998), Owyhee County digital soil survey, SSURGO, Natural Resources Conservation Service, U.S. Department of Agriculture.

USGS (1999), National Elevation Data, U.S. Geological Survey (USGS), EROS Data Center, National Elevation Dataset , *Edition:* 1, Sioux Falls, SD, .Accessed May 2004 at http://seamless.usgs.gov

USDA (2004) United States Department of Agriculture Farm Service Agency Aerial Photography Field Office (USDA-FSA-APFO), 2004. Digital Ortho Image Western Owyhee County, Idaho. National Agriculture Imagery Program (NAIP), Salt Lake City, Utah.

Van Auken, O.W. (2000), Shrub invasions of North American semiarid grasslands, *Annual Review Ecological Systems*, *31*, 197-215.

West, N.E. (1999) Juniper-pinyon savannas and woodlands of western North America, pp 288-308 in *Savannas, Barrens, and Rock Outcrop Plant Communities of North America* edited by Anderson, R.C., J.S. Fralish, and J.M. Baskin, Cambridge University Press, London, England.

Young, J.A., and R.A. Evans (1981), Demography and fire history of a western juniper stand, *Journal of Range Management, 34*, 501-506.

Tables

Table 1. Effect of environmental variables on above ground woody carbon accumulation ($gCm^{-2}yr^{-1}$). Analysis of variance with 8 blocks (photographs)

Variable (n=8 blocks)	**Mean ± std**	**Min**	**Max**	**p**	**F**
Soil type				0.07	3.81
Supporting low sagebrush	2.0±1.8	0.12	4.54		
Supporting mountain big sagebrush	3.9±2.0	0.81	6.69		
Stewardship				0.29	1.33
BLM	3.3±2.2	0.07	5.95		
Private	3.8±2.0	1.36	6.31		
State	1.9±1.7	0.41	4.66		
Aspect (north and south)				0.88	0.022
North	3.3±1.9	0.76	6.00		
South	3.5±2.0	0.51	6.01		
Elevation				0.65	0.56
1400-1600 m	2.9±2.0	0.48	4.80		
1600-1800 m	3.1±2.0	0.48	6.19		
1800-2000 m	4.1±2.5	1.06	7.40		
> 2000 m	2.0±2.0	0.56	3.43		

Table 2. The effect of spatial scale on carbon accumulation estimates in three locations

Vegetation type	**Scale**	**Above ground carbon acc. (g C/m2/year)**	**Source**
Western juniper Idaho 1946-1998	Regional	3.3	This study
Western juniper Idaho 1946-1998	1 ha scale	-11-22	This study
Mesquite (*Prosopis glandulosa*) Texas 1937-1999	Regional	1.9	Asner et al. 2003
Mesquite (Prosopis glandulosa) Texas	Plot scale (age 20-60)	35-50	Hughes et al. 2006
Oak savanna Minnesota, includes soil & below ground C	Regional	16.9	Johnston et al. 1996
Oak savanna Minnesota, includes soil & below ground C	Plot scale (age0-59)	180	Tilman et al. 2000

Table 3. Carbon accumulation rates in various ecosystems, stand and regional estimates

Plant community	**Time since stand replacing distrbance (years)**	**Above ground carbon accumulation (g C/m2/year)**	**Source**
Western juniper / Low sagebrush, Idaho	Regional estimate	2.0	This study
Western juniper / Mountain big sagebrush, Idaho	Regional estimate	3.9	This study
Mesquite (*Prosopis glandulosa*) regional estimate, Texas 1937-1999	Regional estimate	1.9*	Asner et al. 2003
Mesquite (*Prosopis glandulosa*) individual plots	20-60	35-50	Hughes et al. 2006
Boreal forest, Canada	0-75	115	Pare and Bergeron 1995
Boreal forest, Canada	75-200	~50	Estimate from Pare and Bergeron 1995
Balsam fir (*Abies balsamea*) forest, New York	< 55	160	Sprugel 1984
Balsam fir (*Abies balsamea*) forest, New York	>55	58	Sprugel 1984
Ponderosa Pine (*Pinus ponderosa*), Colorado	Stand age ~100 years	9-70	Hicke et al. 2004
Ponderosa pine (*Pinus ponderosa*), central Oregon following clearcut	9-23 56-89 95-106 190-316	-124** 118** 170** 35**	Law et al. 2003
Ponderosa pine (*Pinus ponderosa*), central Oregon	Regional estimate	70**	Law et al. 2003
Ponderosa pine (*Pinus ponderosa*) plantation, Patagonia, Argentina	0-20	361 roots included	Laclau 2003
Aleppo pine (*Pinus halepensis*), Nevada	0-35	150 **	Grünzweig et al. 2003
Oak savanna, encroachment into old fields, Minnesota	Regional estimate	16.9**	Johnston et al. 1996
Oak savanna, Minnesota	0-59	180**	Tilman et al. 2000
Eastern red cedar (*Juniperus virginiana*), Kansas	35-70 years	130-230 ~400 inc. litter	Norris et al. 2001
Tropical grassland/savanna, Venezuela	0-51	392**	San Jose et al. 1998

***   shrub management was occurring within the study area**

**** includes below ground and soil carbon accumulation**

Figures

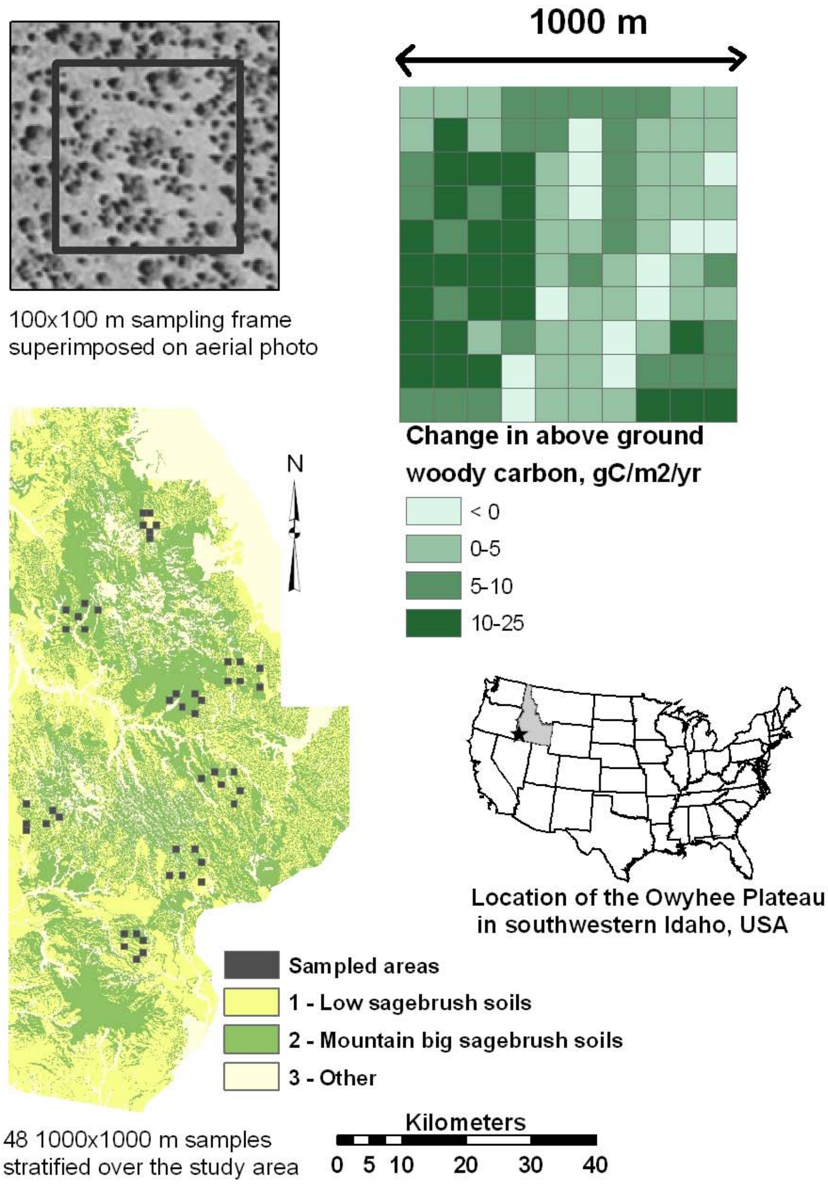


Figure 1. Sampling locations on the Owyhee Plateau. Estimates of carbon accumulation was performed at and three spatial scales: the total area of forty-eight 100 ha samples, by 100 ha and by 1-ha.

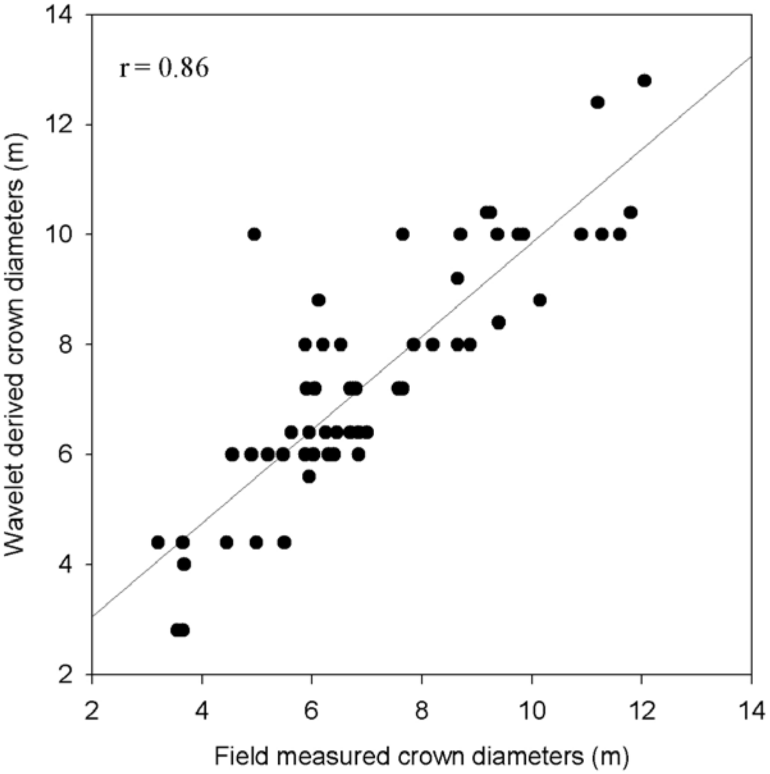


Figure 2. Comparison of wavelet derived and field measured crown diameters.

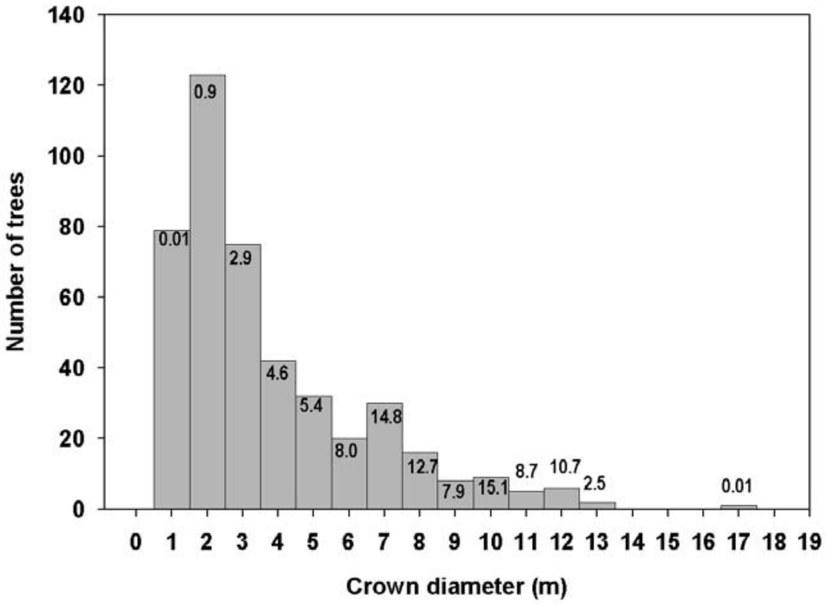


Figure 3. Size class histogram of juniper crown diameters and contribution to woody biomass. The numbers on the bars refer to the percent contribution of a size class to the total biomass in the 20 plots.

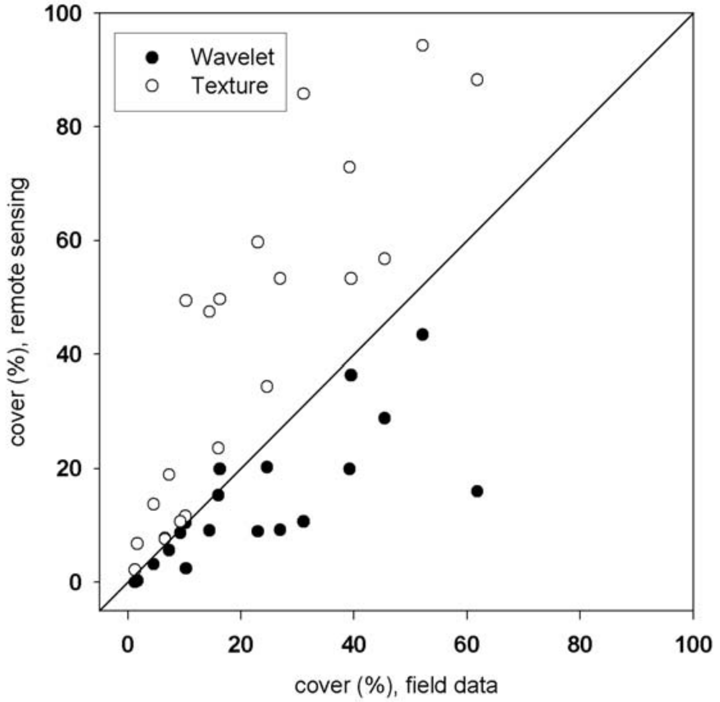


Figure 4. Juniper cover estimated via texture and 2-D wavelet remote sensing techniques compared to field estimates.

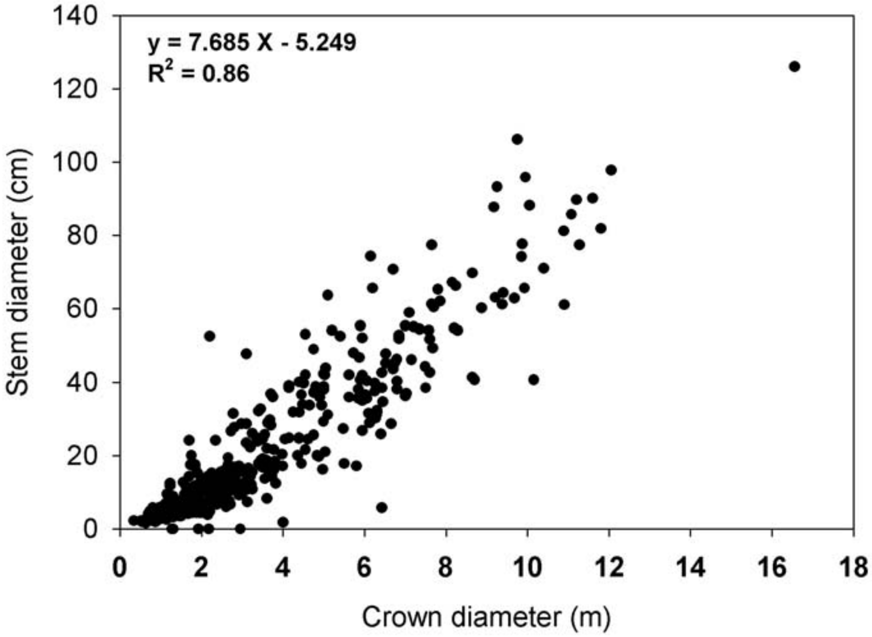


Figure 5. Stem diameter vs. crown diameter, field measurement**.**

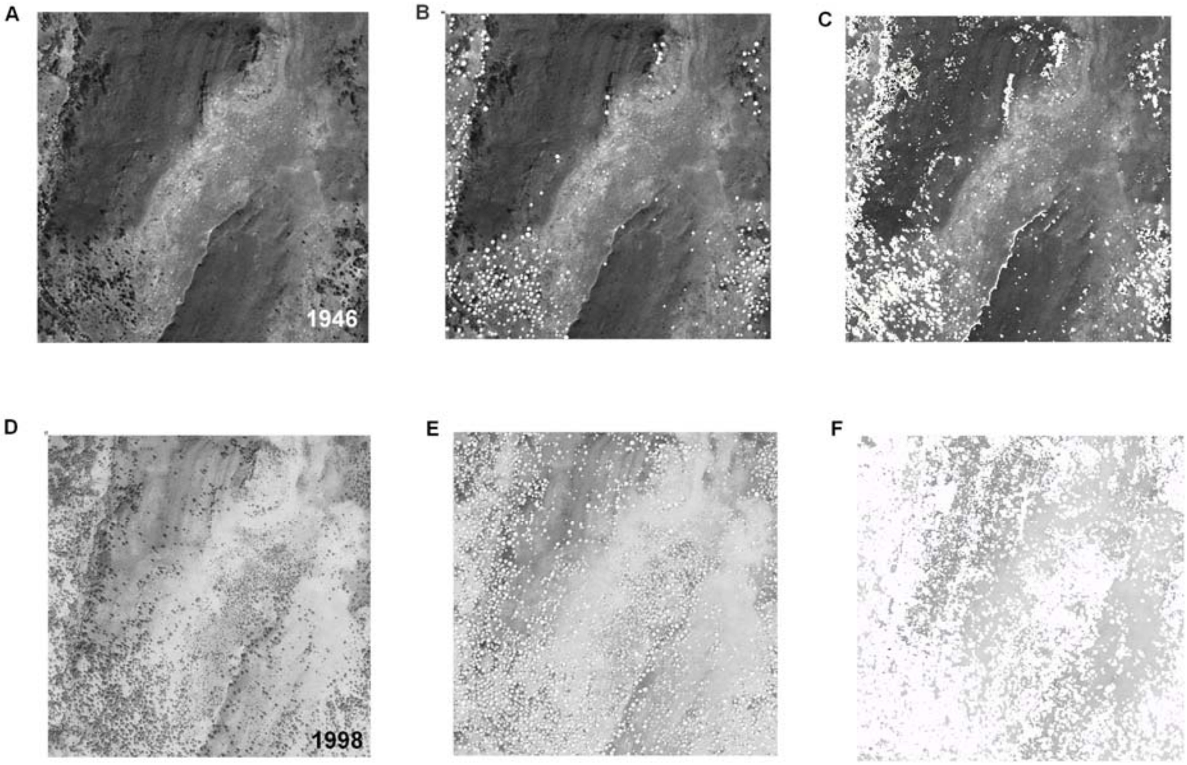


Figure 6. Above: Historic photo from 1946, ‘A’. In ‘B’ the crown diameters estimated via wavelet analysis are superimposed in white on the photo. In ‘C’ the areas of estimated juniper cover via texture analysis are colored white. Below: Photo from 1998, ‘D’. In ‘E’ the crown diameters estimated via wavelet analysis are superimposed in white on the 1998 photo. In ‘F’ the areas of estimated juniper cover via texture analysis are colored white.

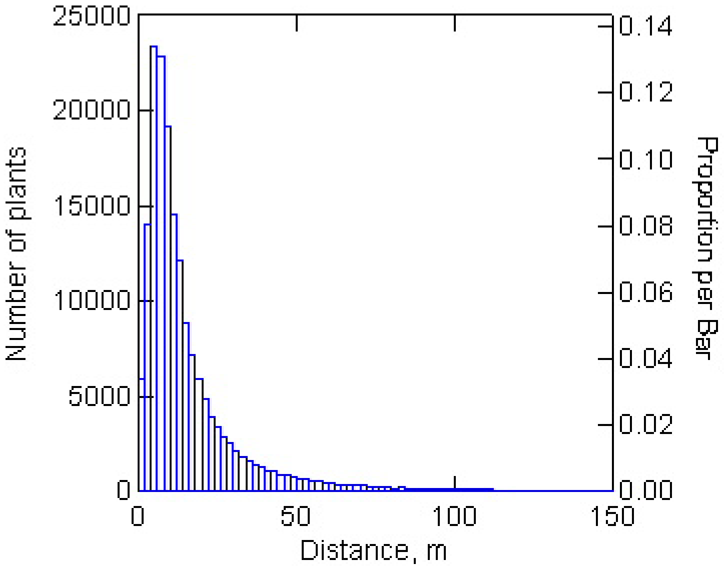


Figure 7. Histogram of the proximity of current (1998-2004) juniper plants to juniper plants present in the historic (1939-1946) photos. Plants that appear to be closer than ~10 m represents the same plant present in both photos (44% of the plants).

CHAPTER 3: Spatial Patterns on the Sagebrush Steppe /Western Juniper Ecotone

Abstract

Analysis of the spatial patterns of woody plants is important to better understand the ecological processes that govern the worldwide expansion of woody plants across semi-arid ecosystems. Second-order characteristics of a marked spatial point pattern of western juniper (*Juniperus occidentalis* subsp. *occidentalis*) were analyzed using Ripley's K-functions and the pair-correlation function *g*. The marked point process of crown diameters was produced via two-dimensional wavelet analysis of a fine scale aerial photograph at the woodland-steppe ecotone in the Reynolds Creek watershed in the Owyhee Mountains, southwestern Idaho.

Colonization of *J. occidentalis* stems from mature juniper trees growing in rocky, fire resistant areas. Although these areas introduce components of natural heterogeneity within the landscape, the selected study area is situated within a single soil type, and we modeled the expansion of juniper plants into previously juniper-free sagebrush steppe as a homogeneous point process with constant intensity.

Through this research we have identified two statistically significant spatial scales characteristic of *J. occidentalis* on the woodland/steppe ecotone: 1) We observed inhibition between *J. occidentalis* plants at distances <15 m, resulting in a regular pattern, rather than clumped or random. This short-distance inhibition can be attributed to competition for water and other resources. Recruitment of young *J. occidentalis* occurs significantly more often in a direction away from older plants, maximizing the utilization of water and light resources, and perpetuating the spread of the species into previously juniper-free shrub-steppe. 2) *J. occidentalis* on the ecotone exhibits significant clustering within a 30-60 m radius. Bivariate point pattern analyses provide evidence that, within a distance of 50-70 m, there is a spatial dependence in tree size such that medium trees are more likely than small trees to be close to large trees. We attribute these phenomena to the fact that juniper seeds are commonly dispersed by berry-eating birds with small territories (0.3-1 ha). Beyond a distance of 50-70 m, juniper plants are randomly distributed, suggesting that additional long-range seed dispersal processes are at work. We further acknowledge the importance of including a reference to spatial scale when formulating hypotheses in statistical analysis of spatio-temporal point patterns.

KEYWORDS: *marked point process; Ripley's K; pair-correlation function; spatial ecology; seed dispersal; wavelet*

1. Introduction

Woody plant encroachment into lands previously occupied by grasses, forbs and shrub-steppe is an ecological phenomenon of global concern. Over the past 150 years, most of the semi-arid grasslands and shrub-steppe in North America have experienced a change in composition and structure. Indigenous woody species are increasing in density in response to changes in landscape scale dynamics such as fire suppression, excessive herbivory, and climate change. Woody plants continue to expand, reducing forage for wildlife and domestic livestock, decreasing biodiversity, and contributing to desertification (Van Auken 2000). Woody plants of concern include for example various species of *Quercus, Juniperus, Larrea, Prosopis, Acacia, Yucca, Fluorensia* and *Haplopappus*. Woody plant encroachment is of concern worldwide, including the Mediterranean countries (Seligman and Henkin 2002), African savannas (Couteron and Kokou 1997; Hudak and Wessman 1998), Australian savannas (Walker and Gillison 1982) and South American grasslands (Schofield and Bucher 1986).

Expansion of juniper (*Juniperus* spp.) and singleleaf piňyon (*Pinus monophylla*) is of particular concern in many areas of the Great Basin in the western United States. Juniper has over the past 130 years been expanding into the sagebrush steppe, altering the species composition, fire fuels, and wildlife habitat of the region, with sometimes irreversible alterations of ecological processes such as fire regimes, hydrologic cycling and soil erosion rates (Burkhardt and Tisdale 1976; Tausch and West 1988; Miller et al. 2005). Currently, piňyon and juniper woodlands cover over 30 million hectares in the West of which 3.6 million hectares is western juniper (Miller et al. 2005).

The goal of this study is to characterize the spatial pattern of *J. occidentalis* size classes across the woodland/sagebrush steppe ecotone and to shed light on the ecological processes that have contributed to the expansion of juniper woodlands. *A priori*, we have formulated the following hypotheses:

H1. *Null*: Juniper plants are randomly distributed across the landscape.
Alternative: Across size classes, juniper plants are regularly placed over the area, rather than clustered or random, due to competition for water and other resources.

H2. *Null:* Mature juniper plants (size class large) are randomly placed across the landscape.

Alternative: Mature western juniper plants occur in clumped distributions. These large old trees grow in rocky areas where fire fuels are sparse, areas that for one reason or another have been acting as fire refugia for the juniper for centuries.

H3. *Null*: Juniper plants of all size classes (large, medium, small) are independently distributed across the landscape.

Alternative: There is a spatial dependence among juniper plants such that medium juniper plants are in general closer to the large plants then are the small plants within areas that are approximately 1 ha in size. This hypothesis is based on the seed dispersal process for juniper, aided by berry eating birds with relatively small home ranges (0.3-1 ha). Western juniper become prolific seed producers at an age of approximately 50 years (Miller and Rose 1995), creating a front of young juniper moving into the previously juniper-free sagebrush steppe.

Spatial statistical techniques have previously been applied to analyze patterns of plants within communities with the goal of understanding the connection between ecological patterns and processes. Schurr et al. (2004) characterized point patterns in semi-arid shrublands to determine whether seed dispersal or root competition is the shaping process of the Karoo shrub communities in South Africa. Succession and disturbance dynamics are other ecological processes that have been related to interspecific and intraspecific plant patterns (Fule' and Covington 1998; Park 2003). Here, we present statistical evidence that areas of fire refugia, seed dispersal processes, and competition for resources perpetuate the spread of *J. occidentalis* into previously juniper-free sagebrush steppe along the woodland/steppe ecotone.

2. Methods

2.2. Study area

The general research area, located on the Owyhee Plateau, covers about 550,000 ha of southwestern Idaho and southeastern Oregon. The area is dominated by western juniper woodlands (*Juniperus occidentalis* subsp. *occidentalis*) and sagebrush (*Artemisia tridentata* subsp. *vaseyana* and *Artemisia arbuscula*) steppe (116° W Long, 43° N Lat). Elevation ranges from 850 to 2560 m, and annual average precipitation varies from 250 mm at lower elevation to 1000 mm at the crest of the mountain range. *J. occidentalis* occurs mainly as open woodlands dissected by rocky river canyons and shrubby riparian areas. Aspen (*Populus tremuloides*), Douglas-fir (*Pseudotsuga menziesii*) and small patches of wet meadows and mountain shrub are infrequent components in the juniper-dominated landscape. Common mountain shrub species are shiny-leaf ceanotus (*Ceanothus veluntinus*), mountain snowberry (*Symphoricarpos oreophilus*), bittercherry (*Prunus emarginata*), and chokecherry (*Prunus virginiana*). The climate on the Owyhee Plateau is characterized by a warm dry summer and fall followed by moderate precipitation in winter (snow) and spring (rain+snow). The soils in the area are typically frigid, xeric loams and clay-loams of the soil orders mollisol, alfisol, and entisol.

Although pre-settlement woodlands of *J. occidentalis* were confined to rocky areas and ridges (Miller and Rose 1995), the current landscape composition comprises old multi-story juniper (18%), young-multi-story juniper (16%), and open young or stand initiation juniper (66%, Roth 2004). The expansion of *J. occidentalis* on the Owyhee Plateau has been explained by reduction in fine fuels due to late-19th century grazing, allowing juniper seedlings that would previously have been burned in wildfires to grow to mature trees. Miller and Rose (1995) further hypothesize that the mild wet winters and wet springs following the Little Ice Age in the mid 1800’s may have promoted a recruitment pulse of *J. occidentalis* in the area. The historic fire frequency of 30-40 years that would be adequate to keep *J. occidentalis* from expanding into the sagebrush steppe was interrupted in the early 1900’s (Burkhardt and Tisdale 1976). A century of fire suppression in the area therefore provides an opportunity to study the history of *J. occidentalis* recruitment using remotely sensed data combined with spatial analysis techniques.

2.2. Acquisition and field validation of point pattern

The point pattern of juniper plants was acquired via two dimensional wavelet analysis of fine scale aerial photography (Strand et al. 2006). 2-dimensional wavelet analysis is a rapid, objective, automatic, and repeatable method for determining size and location of individual objects from remotely sensed data over large areas. For this particular analysis we convolved a 2-dimensional Mexican hat (equation 1) wavelet (Addison 2002; Strand et al. 2006) with a USGS panchromatic orthophotograph with a 1-meter pixel resolution acquired in 1998. The analysis was performed in the Matlab (2004) software environment. The wavelet can be described mathematically:

$$\Psi(x, y) = (1 - x^2 - y^2) * e^{-(x2+y2)/2}$$

(1)

where $\Psi(x, y)$ represents the 2-dimensional Mexican hat wavelet function, in directions x and y. When the wavelet function and the image feature are nearly identical, a very high intensity peak is created. Lower intensity values are produced when the wavelet function is not similar to the image feature. The size of the wavelet can be altered to capture different features; thus, wavelets of consecutively larger sizes will highlight consecutively larger objects within an image. In this analysis we used wavelets to quantify the size of *J. occidentalis* crowns (dark gray) against a matrix of sagebrush steppe (shades of lighter gray) in the aerial photograph (Figure 1, *left*). The crown diameter and location of juniper plants were summarized as a marked point pattern and superimposed (white circles) on the photo in a geographic information system (Figure 1, *right*). We produced the marked point pattern for a 250 x 400 m area located within a single soil type. This particular soil is a shallow, well drained, loamy-skeletal, frigid argixeroll characterized by the *Artemisia arbuscula* vegetation association. Limiting the analysis to one soil type increases the likelihood that we are observing a homogeneous point process for which the sizes of the juniper plants would be indicative of their age.

A validation procedure suggested that 2-dimensional wavelet analysis of *J. occidentalis* plants depicts crown diameters accurately when compared with field measurements ($r=0.86$, $n=60$, $p<0.001$), however crowns smaller than 2-3 times the image pixel size have a high omission error (Strand et al. 2005). We compensated for this limitation of the wavelet analysis by adding missing 2-3 m plants via hand digitizing in a geographic information system. Juniper seedlings that are smaller than the 1-meter pixel size were not detected by the wavelet analysis and therefore not included the point pattern. We assume that this is of little consequence for our point pattern analysis, because our goal is to analyze the spatial patterns of plants recruited into the community, rather than seedlings, which have relatively uncertain survival.

2.3. Statistical analysis

The marked point pattern of juniper crown diameters was characterized using spatial analysis techniques. The simplest summary statistic for a homogeneous point pattern is the first-order intensity λ, defined as the number of points per unit area (Cressie 1991; Diggle 2003). The requirement of homogeneity and stationarity must be considered when analyzing a spatial point process. Natural landscapes are apparently rarely homogeneous but rather affected by topo-edaphic and hydrologic factors. We deliberately selected our study area within a single soil type to mitigate for natural heterogeneity in the landscape. Within the 250 x 400 m study area the old juniper plants grow on rocky outcrop and sparsely vegetated areas (fire refugia), features that apparently contribute to the heterogeneity of the landscape. Aside from these areas we however feel that the likelihood of juniper seed spread and establishment is mostly affected by the presence of previously established juniper plants and that homogeneity and stationarity with constant intensity are reasonable assumptions for the spatio-temporal process of juniper expansion into previously juniper-free areas. Spatial analysis of larger areas would likely require compensation for variations in first-order intensity caused by natural variations in soil characteristics and topography.

Point patterns are commonly characterized by the expected number of points that would fall within a circle of radius r around randomly chosen points. Under the condition of complete spatial randomness (CSR), the points are randomly distributed, and the number of points within a radius r is a random variable that is dictated by the intensity of the point pattern and the magnitude of r. Alternatively, for a clustered point pattern there are a higher number of points within radius r compared to CSR, and for a uniform point pattern there are fewer points within radius *r*. Ripley (1981) expressed this expected number of points as the K(r) function (equation 2):

$$\hat{K}(r) = \frac{A}{n^2} \sum_{i=1}^{n} \sum_{j=1}^{n} w_{ij}^{-1} I_r(|x_i - x_j|) \tag{2}$$

where A is the point pattern area, n is the number of points, $I_r = 1$ when $|x_i - x_j| < r$ and is otherwise 0. w_{ij} is a weighting function that accounts for edge effects. The expected value of K(r) for a random process is πr^2. Because the primary interest often is to determine if there is a significant deviation from CSR, K(r) is commonly expressed as:

$$\hat{L}(r) = \sqrt{\hat{K}(r)/\pi} \tag{3}$$

Note that L(r) – r = 0 when the point process is completely random (CSR), is larger than 0 for a clustered pattern and is less than 0 for a uniform point process.

Ripley's K-function is a cumulative function of the points within a distance *r*, i.e. each larger radius includes points of a smaller radius, and it is possible that information from two different scales may interfere with each other. The pair-correlation function g(r) (Stoyan and Stoyan 1994), also known as the O-ring statistic (Wiegand and Moloney 2004), is an alternative statistic that estimates the number of points within concentric rings rather than within a radius. The pair-correlation function is the first derivative of K with respect to *r* divided by $2\pi r$:

$$\hat{g}(r) = \frac{1}{2\pi r} \frac{d\hat{K}}{dr} \tag{4}$$

For a random point process $\hat{g}(r) = 1$. When g(r) takes on a value larger than 1 there are more points than expected at distances around radius *r,* indicating clustering at this distance. Values of g(r) smaller than 1 are indicative of inhibition in the point pattern at distance *r*, i.e. fewer points than expected for the given intensity.

Schurr et al. (2004) point out a number of differences in the interpretation of the cumulative function K(r) compared to the local function *g*(r). A maximum in K(r) indicates the typical clump size, although the typical plant distance cannot be directly inferred from this statistic. The cumulative function K(r) will commonly peak at larger distances compared to *g*(r). Furthermore, if *g*(r) shows only one peak, it can help to define the cluster size at the distance *r* at which the function approaches 1 (Stoyan and Stoyan 1994).

For a marked point pattern, the bivariate $K_{12}(r)$ can be computed to estimate the number of points of type (2) that are expected to occur within the radius *r* of points of type (1). $K_{12}(r)$ can be expressed:

$$\hat{K}_{12}(r) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_r(|x_i - y_j|) \tag{5}$$

where n_1 and n_2 are the number of points of type (1) and (2) respectively, and x_i are the locations of points of type (1) and y_j are the locations of points of type (2).

We computed the univariate K(r) and g(r) including all plants within the 250 x 400 m study area, and also for each size class of juniper plants (small, medium, large). Ripley's isotropic edge correction (Ripley 1988) was applied to account for edge effects in the analysis. The functions were computed for $r < 60$ meters, as it is prudent to restrict the estimation of K(r) to a maximum *r* of ¼ of the length of the smallest side of the analysis area (Baddeley and Turner 2005).

2.4. Null models for univariate and bivariate patterns

To test the significance of clustering or inhibition within a point process as expressed by the K(r) or g(r) function, it is necessary to compare the results to an appropriate null model (Wiegand and Moloney 2004). CSR normally serves as the null hypothesis for a univariate point process (Cressie 1991). Confidence envelopes can be computed using Monte Carlo simulation. We computed confidence envelopes by producing 1000 random plant patterns through Monte Carlo simulation for the univariate point pattern analyses of all trees and trees by size class. The random point patterns were conditioned upon the size of the study area and the number of points in the data set, to ensure consistency in first-order intensity.

Selection of an appropriate null model for significance testing of a bivariate point pattern requires insight in the biological processes that are being analyzed. Simple randomization of both point patterns may not answer the biological question asked and can lead to an inadequate statistical test (Wiegand and Moloney 2004). Wiegand and Moloney (2004) suggest that in studies of space-time point processes, such as relationships between seedlings and older trees, it is appropriate to randomize the seedlings while keeping the older trees fixed in space, because in this case randomization of the location for both the seedlings and the trees may obscure the attraction or repulsion between the two types. We adopted these suggestions in our choice of the bivariate null model and in all cases held the older cohort of trees fixed in space while randomizing the locations of the younger cohort. The spatial distribution of medium trees was tested against fixed large trees, and the small tree distribution was tested against fixed medium and large trees; see Table 1 for breakdown of the sizes. The distribution of small trees was also tested against large trees only, ignoring the presence of medium trees.

In the point pattern analysis the plant sizes were classified in three groups, large, medium and small. To rule out any influence of the size classification on the point pattern analysis we analyzed two sets of size classifications (Table 1). The large tree class was defined by a natural break in the data and was held constant in the two classifications. We hypothesize that these large trees are likely to be plants that survived the last wildfire in the area. The difference between the two classifications lies in the distribution of medium and small trees, where classification I contains 344 medium and 149 small trees while classification II contains 255 medium and 268 small trees.

2.5. Semi-variance

Spatial dependence for a stationary process can be evaluated by computing the mean difference between pairs of points at increasing lags (Cressie 1991). The computed pair-wise variances (equation 6) are commonly plotted against the lag distance in a semi-variogram. Spatial dependence in the data is observed if the variance takes on a lower value at shorter lags. The lag distance at which the variance becomes relatively constant is referred to as the range of influence for the spatial process. Locations that are farther apart than the range of influence are considered spatially independent.

$$\gamma(r) = \frac{1}{2n}\sum \left| x_i - x_{i+r} \right|^2 \tag{6}$$

where: $\gamma(r)$ is the semivariance for the interval distance class *r*, X_i is the measured crown diameter at location *i*, X_{i+r} is the measured crown diameter at location i+r and n is the number of pairs in lag interval *r*. We explored the fit of three different semi-variogram models, an exponential, a spherical, and a circular model. The best model was selected based on minimized sum of squares, and was compared to a null model where the point locations were held stationary while the point marks were randomized with 1000 replicates.

The statistical package 'R' (R Development Core Team 2004) was used for computations of the K(r) and *g*(r) functions, for the semi-variogram, and for Monte Carlo simulation of confidence envelopes. In particular, we used the R packages Spatstat (Baddeley and Turner 2005) and geoR (Ribeiro and Diggle 2001).

3. Results

The 2-D wavelet analysis within the 250 x 400 m study area resulted in 634 juniper trees recorded (Figure 1). The juniper crown diameters ranged from 1 to 12.8 m in a right-skewed distribution (Figure 2). Significant inhibition in the point pattern at short distances (<10-15 m) was observed for K(r) and 3-8 m for *g*(r) (Figure 3). The K-function expressed as 'L(r)-r' is 0 for CSR, values > 0 indicate clustering while values < 0 indicate inhibition. The *g*-function is 1 for CSR, *g*(r) > 1 indicates clustering and *g*(r) < 1 indicates inhibition. Dashed lines represent 95% confidence envelopes for CSR in all figures. We attribute the fine scale inhibition in Figure 3 to competition for water and other resources. The univariate K-function applied to all trees indicate significant clustering at distances of 30-50 m, while the *g*-function places this clustering at approximately 15 m.

Large trees show inhibition at close distances (<7-10 m) and clustering at intermediate distances (Figure 4a,d), supported by both K(r) and g(r). Again, K(r) depicts clustering at larger distances (>20 m) while for the *g*-function clustering is significant off and on at distances of 10-45 m. Medium trees also show inhibition at very close distances (<10 m) while clustering occurs at larger distances around 40 m according to the K-function and at 15 m according to the *g*-function (Figure 4b,e). Small trees do not show the short-distance inhibition observed for the larger tree classes (Figure 4c,f). On the contrary, the small trees are significantly clustered at short distances according to both K(r) and *g*(r). At longer distances the K-function for the small trees alternates between a significantly clustered (95% confidence envelope) and a random distribution.

Computation of the bivariate K(r) for medium trees in relation to large trees shows that medium trees do not tend to grow in the immediate proximity of large trees, however they tend to be clustered at distances 30-60 m away from larger trees (Figure 5a and 6a). Figure 5 here represents classification I, and Figure 6 represents results from classification II. Recruitment of small trees is significantly inhibited by large and medium trees at distances <15 m and small trees are thereafter randomly distributed within the 95% confidence interval (Figure 5b and 6b). Finally, we tested small trees versus large trees and found a significant inhibition at distances closer than 60 m (Figure 5c and 6c). The pair-correlation function was also computed for the bivariate analyses (Figure 5 d-f and 6 d-f), confirming the inhibition in all cases at short distances. At longer distances we find the oscillating *g*-function difficult to interpret for the bivariate analyses.

We computed the semi-variance for the crown diameters of *J. occidentalis* (Figure 7) and used ordinary least squares to fit an exponential model to the data (equation 7).

$$\gamma(r) = b_0 + c_0\,[1-\exp(-r/a_0)] \qquad (7)$$

where b_0 is the nugget, $3*a_0$ is the distance at which the semi-variance reaches 95% of the sill and c_0 is the partial sill (b_0+c_0 represents the sill). According to Isaaks and Srivastava (1989), data can be considered spatially correlated within a distance of $3*a_0$. The constants in this fitted exponential model are: $a_0 = 23.217$, $b_0 = 2.567$ and $c_0 = 0.805$. Comparing the three semi-variogram models (spherical, exponential and circular), the exponential model yields the lowest value for the minimized sum of squares (0.057). Based on this analysis we conclude that the range of influence is ~70 m ($3*a_0$) and that juniper trees that are located within this distance of one another are spatially dependent, i.e. trees that are closer together are more similar in crown diameter within this distance. Comparison of the exponential semi-variogram model to the null model reveals that the fitted semi-variogram model is statistically significant at a 95% confidence level within ~50 m. Beyond the range of influence, 50-70 m in this case, the crown diameters appear to be random.

4. Discussion

4.1. Comparing cumulative and local functions

Cumulative functions such as K(r) include the entire area of the circle when computing the expected number of points within radius r for a given point pattern intensity, while the local pair-correlation function $g(r)$ estimates the expected number of points within concentric rings around points. The two functions yield comparable results at short distances but the results and appropriate interpretation are quite different at longer distances. All analyses provided evidence of statistically significant inhibitions at short distances (<10-15 m) according to both the K- and the *g*-function, except for small trees. Small trees exhibit clustering at short distances according to both the K- and *g*-functions. In agreement with Stoyan and Stoyan (1994) we find that the K- and the *g*-functions indeed are different in appearance and it is reassuring that they are intended to represent different aspects of the point pattern. Stoyan and Stoyan (1994) suggest that a maximum in the univariate K-function indicate a typical cluster size in the point pattern while the first maximum in the *g*-function is indicative of the typical distance between plants. Furthermore, if the *g*-function has only one peak, the cluster size can be estimated at the distance where g falls to 1. In this analysis g tends to produce an oscillating function and consequently a typical clump size can not be inferred. It is also noticeable that the K-function produces results that are either significantly clustered or uniform, i.e. outside the confidence envelopes, more often than the *g*-function. The *g*-function rarely shows a significant deviation from CSR, except at short distances.

In analyses of plant encroachment, we argue that the cumulative K-function is more indicative of the ecological processes that affect the recruitment of woody plants into grass- and shrublands. The processes affecting the expansion of juniper into shrub-steppe are primarily competition for resources combined with the seed dispersal and recruitment mechanisms. *J. occidentalis* seed dispersal is primarily aided by birds foraging on juniper seeds (Lederer 1977; Salomonson and Balda 1977; Chambers et al. 1999). The territories of these birds vary in size, but are typically composed of relatively small (0.3-1 ha) areas (Lederer 1977; Salomonson and Balda 1977). Recruitment of new juniper plants will likely occur in areas that provide adequate safe sites for germination, emergence and establishment combined with sufficient resources for continued growth. It is sensible to assume that these favorable areas occur in homogeneous patches at various locations rather than being dictated by the pure distance from existing plants resulting in concentric circles of homogeneity.

From the univariate analysis of all trees (Figure 3), we can conclude that the typical interplant spacing is ~12-15 m based on the *g*-function and that the typical cluster size is 40-50 m based on the K-function. In summary, we agree with Schurr et al. (2004) that both cumulative and local point pattern analysis techniques are useful tools for ecologists. The selection of statistical analysis technique must depend on the ecological question asked and the patterns and processes at hand. Cumulative and local techniques yield answers to different questions and the two tools are complementary rather than competitive.

4.2. Seed dispersal

Juniper seeds are too large for wind dispersal and are adapted for seed spread primarily by berry-eating birds and mammals (Chambers et al. 1999). Female *J. occidentalis* plants produce large quantities of berries, a fleshy fruit about ¼ inch in diameter, beginning as early as 10-20 years of age and becoming significant at an age of 50-70 years (Miller and Rose 1995). Juniper berries are an important food source for many birds, particularly in the winter. The hard seeds within the berry commonly pass unharmed through the digestive tract of birds and are widely dispersed (Maser and Gashwiler 1977). Maser and Gashwiler (1977) observed 12 species of birds eating *J. occidentalis* berries on trees in eastern Oregon: Stellar's jay (*Cyanocitta stelleri*), pinyon jay (*Gymnorhinus cyanocephalus*), Clark's nutcracker (*Nucifraga columbiana*), American robin (*Turdus migratorius*), Townsend's solitaire (*Myadestes townsendi*), western bluebird (*Sialia Mexicana*), mountain bluebird (*Sialia currucoides*), Bohemian waxwing (*Bombycilla garrulous*), cedar waxwing (*Bombycilla *cedrorum*), European starling (*Sturnus vulgaris*), Brewer's blackbird (*Euphagus cyanocephalus*), and evening grosbeak (*Hesperiphona vespertina*). In addition Maser and Gashwiler (1977) observed four mammal species eating *J. occidentalis* berries directly from trees or that had fallen to the ground: yellow pine chipmunk (*Eutamias amoenus*), deer mouse (*Peromyscus maniculatus*), mantled ground squirrel (*Spermophilus lateralis*), and coyote (*Canis latrans*). Research by Schupp et al. (1997) show that *J. occidentalis* seeds are predominantly dispersed by birds on the Owyhee Plateau while the coyote is the only important seed dispersing mammal in the area. Although the coyote may locally be the only mammal important for dispersal of *J. occidentalis* it should be noted that the following mammals have been observed consuming berries from various juniper species: woodrats (*Neotama* spp.), Virginia opossum (*Didelphis virginiana*), Nuttal's cottontail (*Sylvilagus nuttallii*), desert cottontail (*Sylvilagus audubonii*), black-tailed jackrabbit (*Lepus californicus*), coyote (*Canis Latrens*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), black bear (*Ursus americanus*), ringtail (*Bassariscus astutus*), raccoon (*Procyon lotor*), mule deer (*Odocoileus hemionus*), white-tail deer (*Odocoileus virginianus*), and various types of livestock.

Based on plant migration theory, Clark et al. (1998) conclude that both short- and long-distance dispersal are important mechanisms to consider when assessing the migration rate of a plant species at the ecotone. Although rapid plant migration is primarily driven by long-distance dispersal events, such events are rare. The probability of occurrence for a long-distance dispersal event is greatly improved by a strong seed producing local population. A strong seed producing dense stand is created through short-distance dispersal of seeds filling in between the long-dispersed pioneers along the front of the ecotone.

Long-distance dispersal of *J. occidentalis* is likely affected by large frugivorous mammals such as coyote, fox and bears that have a long gut-retention time and travel long distances (Chambers et al. 1999). Migrating flocks of waxwings, robins and bluebirds may also contribute to long-distance dispersal of juniper seeds. At a finer scale, territorial, resident frugivorous birds with a short gut-retention time are largely responsible for the short distance dispersal of juniper seeds. Local dispersal leads to recruitment and increased density within existing stands. Examples of such local seed dispersers are the Townsend's soilitaire and the American robin (Lederer 1977; Salomonson and Balda 1977; Poddar and Lederer 1982).

Based on a study of 25 solitaire territories in *J. occidentalis* in the eastern Sierra Nevada Mountains in eastern California, Lederer (1977) determined that the size of the territories were on average 0.3 ha with a maximum size of 0.7 ha. Salomonson and Balda (1977) recorded territory sizes around 0.7 ha in northern Arizona in 1973-74. However, the following year the territory sizes averaged 5.5 times larger, possibly due to a season and area with lower juniper berry abundance. Territory sizes for the American robin has been reported to be 0.1 – 1 ha (Young 1956; Carothers et al. 1973). In the winter time the American robin migrates to below snowline and flocks of migratory robins may here contribute to long-distance seed dispersal.

We conclude that the observed spatial dependence of 50-70 m indicated by the range of influence in the semi-variogram (Figure 7) and the observed cluster size of 40-60 m estimated from the K-function (Figure 3 *top*) can possibly be attributed to the territory size of many of the short-distance seed dispersing birds in the area. Areas with a diameter of 40-60 m equals 0.2-0.4 ha and compares well to the average territory size of 0.3 ha recorded for solitaires and robins (Salomonson and Balda 1977). Beyond the range of influence the trees appear to be randomly distributed. We hypothesize that the oldest trees in each cluster are dispersed through the more random long-distance dispersal processes (Clark et al. 1998), likely to be carried out by coyotes and wider-ranging birds such as jays, blackbirds, nutcrackers or migratory flocks of waxwings. The observed pattern of juniper crown diameters can likely be explained by a combination of short- and long-dispersal mechanisms as described by Clark et al. (1998). This combination of long- and short-dispersal mechanisms contributes to the rapid migration of *J. occidentalis* into the shrub-steppe on the Owyhee Plateau.

4.3. Competition for resources

This analysis identifies a statistically significant fine scale inhibition (<15 m) for the large and medium size classes of *J. occidentalis* (Figure 4). Many scientists have observed low seedling establishment in the immediate area around older juniper plants (*e.g*. Burkhardt and Tisdale 1976; Tausch and West 1988). This phenomenon has been attributed to competition for water, light, and other resources. Another suggested reason for diminished plant recruitment and establishment near older plants is alterations to the nurse plant environment. Miller and Rose (1995) observed that most juvenile trees established beneath *Artemisia* species in the interspaces between mature *J. occidentalis*, using *Artemisia* as a nurse plant. Areas immediately under or close to mature juniper commonly show severely reduced plant cover, particularly of the shade intolerant shrub-steppe species such as *Artemisia*.

It has also been suggested that the reduction in understory species and lack of juniper establishment beneath or adjacent to mature juniper plants could be attributed to allelopathic compounds produced by the juniper itself (Jameson 1970). However, Josaitis (1991) shows through greenhouse studies that soils collected beneath older *J. occidentalis* plants contain significantly higher amounts of many nutrients, and produce significantly more biomass of shrub-steppe plants, such as Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Agropyron spicatum*), and bitterbrush (*Purshia tridentata*), compared to interspace soils. We conclude that although a majority of the seeds are dropped beneath mature trees, successful recruitment is uncommon there due to competition for resources and lack of appropriate nurse plants.

The small size class of juniper (Figure 4) shows clustering at short distances (< 6 m) and a random distribution thereafter. Van Auken et al. (2004) observed clustering of young juniper seedlings (*Juniperus ashei*), under and close to the canopy edge of mature trees in central Texas. Van Auken et al. (2004) further recorded the greatest survival of young *J. ashei* adjacent to mature trees but the greatest growth was observed in the open grassland habitat away from older trees. Note that the point pattern derived using wavelet analysis from 1-meter photography will not include the smallest juniper seedlings (<1 m in diameter). We see similar patterns in *J. occidentalis* woodlands as observed in *J. ashei* ecosystems where the greatest recruitment and growth occurs away from mature trees. We qualify this observation with the reservation that we do not observe clustering of seedlings adjacent to large trees, possibly due to the point pattern acquisition technique. At short distances we observe clustering of small *J. occidentalis* away from mature trees (Figure 4 and Figure 5c and 6c), however medium and large *J. occidentalis* display inhibition within 15 m. As the trees grow, the clusters of small trees most likely go through a process of self-thinning due to resource competition, commonly observed in forested systems (Stoyan and Penttinen 2000), resulting in the characteristic savanna-like western juniper woodlands.

4.4. Ecological applications of 2-D wavelet analysis

2-D wavelet analysis has recently been presented as a powerful image processing technique with promises in quantifying ecologically relevant patterns over extensive areas (Strand et al. 2006). Strand et al. (2006) demonstrates how 2-D wavelet analysis rapidly, objectively, and accurately produces a marked point pattern of plants from fine-scale current and historic remotely sensed imagery. The research presented here demonstrates for the first time the utility of this technique, combined with spatial statistics, in elucidating the underlying mechanisms of observed plant patterns, here exemplified by the tie between *J. occidentalis* plant patterns and the ecological processes affecting the juniper expansion along the woodland/steppe ecotone. 2-D wavelet analysis is an object oriented multi-scale remote sensing technique that differs from other techniques such as texture analysis (Hudak and Wessman 1998; Asner et al. 2003) and spectral classification of imagery (Whiteman and Brown 1998). Although these other methods have proven successful in estimating the cover and stem density within semi-arid woody plant communities, results are delivered in the form of thematic maps rather than marked point patterns. We suggest that 2-D wavelet analysis is particularly useful when the objective of the analysis is to study the placement and interactions between ecologically significant landscape features in relation to the ecological drivers within the system.

4.5. Hypothesis testing and point pattern statistics

The spatial arrangement of plants within a vegetative community is a result of complex ecological processes. Juniper woodlands are shaped through fire frequency, behavior, and effects, competition for water and other resources, and interactions with seed dispersing fauna and humans, among others. The observed point patterns of such woodlands can be an important source of information and aid in forwarding the understanding of the underlying ecological processes at work. In the light of the recent expansion of juniper woodlands in the West it is important to gather information that can add to the ecological understanding of the process-pattern relationships affecting this ecotone shift.

Point pattern statistics are particularly helpful in posing ecological and statistical hypotheses, and further, investigating how the hypotheses compare with empirical data (Stoyan and Penttinen 2000). Schurr et al. (2004) emphasize the importance of developing *a priori* hypotheses to restrict the number of analyses necessary and the number of relevant null models to those that are of interest for the ecological questions posed.

Our first null hypothesis (**H1**) states that *J. occidentalis* plants are randomly distributed in space with an alternative hypothesis stating that the plants are regularly placed due to competition for resources. Statistical analysis allows us to reject the null hypothesis and make the inference that *J. occidentalis* plants are indeed regularly spaced within a distance of 15 m. In the formulation of this hypothesis we omitted consideration of scale, *i.e*. we did not state the distance within which regularity could be expected or how the point pattern may unfold at longer distances. In addition to the hypothesized inhibition due to resource competition we observed a statistically significant clustering at distances of 30-60 m.

The second null hypothesis (**H2**) states that mature (large) *J. occidentalis* plants comply to CSR. Our alternative hypothesis was that the mature juniper plants occur in clumped distributions in areas where they have been able to escape fire for long periods of time. Again, in the hypothesis statement the scale at which clustering would be expected to occur was not clearly articulated. Statistical analysis however confirmed a strong significant clustering at distances >20 m, justifying rejection of **H2**, although inhibition was observed at shorter distances <10-15 m.

In the third hypothesis (**H3**) the null statement was that *J. occidentalis* plants of all size classes are independently distributed across the landscape, and the alternative hypothesis proposed spatial dependence with respect to plant size due to short-range seed dispersal by birds with relatively small home ranges (0.3-1 ha). We reject the null hypothesis and accept the alternative hypothesis based on the statistical analysis. The semi-variogram (Figure 7) fitted with an exponential model shows spatial dependence within a 50-70 m distance. The bivariate K-function shows that medium-sized trees are statistically more likely to be close to large trees than are small trees and that small trees are established away from large trees (Figure 5 and 6 a-c).

Through spatial analysis of *J. occidentalis* point patterns on the juniper woodland sagebrush steppe ecotone, we have identified two statistically significant spatial scales. The first is that inhibition between juniper plants occurs within distances of 10-15 m, resulting in a regular pattern at these distances. We attribute this short-distance inhibition to competition for water and other resources. The second spatial scale is that juniper plants show significant clustering at distances of 30-60 m, and show spatial dependence within 50-70 m. We attribute these phenomena to the short-distance seed dispersal by birds with small territories. We also acknowledge the importance of including reference to spatial scale when formulating hypotheses when characterizing spatial point patterns. The short-distance inhibition and the local seed dispersal process both contribute to the expansion of *J. occidentalis* into previously juniper-free sagebrush steppe.

The results presented here indicate that there is another seed dispersal process acting at longer distances that cannot be quantified by this analysis. If the short-distance (<100 m) seed dispersal process was the only mechanism for spread we would expect to see a more dense front of juniper plants of decreasing age at the ecotone, and expect a much longer distance of spatial dependence. A new hypothesis with regards to the long-distance dispersal process could be formulated such that long ranging mammals and birds distribute seeds randomly. The outlying juniper populations, initiated through long-distance dispersal, eventually coalesce through the short-distance dispersal process identified here into a scattered woodland savanna according to the migration process described by Clark et al. (1998). Point patterns for larger areas must be analyzed in order to make inferences about this long-distance seed dispersal process and its affect on the observed point pattern and the migration of juniper along the ecotone. In addition to spatial point pattern analysis, spatial simulation is another avenue for researching the migration of juniper along the ecotone. In such an experiment, artificial patterns created through hypothetical dispersal processes could be compared to the observed plant pattern.

Acknowledgements

We thank two anonymous reviewers for their insightful comments that have contributed to the contents and quality of this manuscript.

References

Addison PS (2002) The Illustrated Wavelet Transform Handbook, Institute of Physics Publishing. The Institute of Physics, London, UK.

Asner GP, Archer S, Hughes RF, Ansley RJ and Wessman CA (2003) Net change in regional woody vegetation cover and carbon storage in Texas Drylands, 1937-1999. Global Change Biology 9:316-335.

Baddeley A and Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. Journal of Statistical Software 12:1-42.

Burkhardt JW and Tisdale EW (1976) Cause of juniper invasion in Southeastern Idaho. Ecology 57:472-484.

Carothers SW, Balda RP and Haldeman JR (1973) Habitat selection and density of breeding birds of a coniferous forest in the White Mountains, Arizona. Pages 22-36 In: Carothers SW,

Haldeman JR and Balda RP (ed) Breeding birds of the San Francisco Mountain area and the White Mountains, Arizona. Mus. North. Ariz. Tech. Ser. 12. 54pp.

Chambers JC, Vander-Wall SB and Schupp EW (1999) Seed and seedling ecology of pinyon and juniper species in the pygmy woodlands of western North America. Botanical Review 65:1-38.

Clark JS, Fastie C, Hurtt G, Jackson ST, Johnson C, King G, Lewis M, Lynch J, Pacala S, Prentice C, Schupp EW, Webb III T and Wyckoff P (1998) Dispersal theory offers solutions to Reid’s paradox of rapid plant migration. BioScience 48:13-24.

Couteron P and Kokou K (1997) Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Aftica. Plant Ecology 132:211-227.

Cressie NAC (1991) Statistics for spatial data. John Wiley, Chichester, U.K.

Diggle PJ (2003) Statistical analysis of spatial point patterns. Second Edition. Oxford University Press, New York.

Fule’ PZ and Covington WW (1998) Spatial patterns of Mexican pine-oak forests under different recent fire regimes. Plant Ecology 134:197-209.

Hudak AT and Wessman CA (1998) Textural analysis of historical aerial photography to characterize woody plant encroachment in South African savanna. Remote Sensing of Environment 66: 317-330.

Isaaks EH and Srivastava RM (1989) An introduction to applied geostatistics. Oxford University Press Inc., New York, New York.

Jameson DA (1970) Degradation and accumulation of inhibitory substances from *Juniperus osteosperma* (Torr.) Little. Plant soil 33:213-224.

Josaitis RM (1991) The effects of western juniper occupancy on changes in soil characteristics in relation to shrub and grass establishment. Masters Thesis, University of Idaho, Moscow, Idaho, USA.

Lederer RJ (1977) Winter Territoriality and Foraging Behavior of the Townsend's Soiliataire. The American Midland Naturalist 97(1):101-109.

Maser C and Gashwiler JS (1977) Interrelationships of wildlife and western juniper. In: Proceedings of the western juniper ecology and management workshop in Bend Oregon p. 37-82, In: Martin RE, Dealy JE and Caraher DL (ed) USDA Forest Service Portland Oregon GTR PNW-74.

MATLAB® (2004) Matlab and Simulink, Version 7.0.0.27 (R14). The MathWorks, http://www.mathworks.com/products/matlab/.

Miller RF and JA Rose (1995) Historic expansion of *juniperus occidentalis* in southeastern Oregon. Great Basin Naturalist 55:37-45.

Miller RF, Bates JD, Svejcar TJ, Pierson FB, and Eddleman LE (2005) Biology, Ecology, and Management of Western Juniper. Technical Bulletin 152, June 2005, Oregon State University, Agricultural Experiment Station.

Park A (2003) Spatial segregation of pines and oaks under different fire regimes in the Sierra Madre Occidental. Plant Ecology 169:1-20.

Poddar S and Lederer RJ (1982) Juniper berries as and exclusive winter forage for Townsend's soilitaires. The American Midland Naturalist 108(1):34-40.

R Development Core Team (2004) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-00-3,http://www.R-project.org.

Ribeiro Jr. PJ and Diggle PJ (2001) geoR: A package for geostatistical analysis. R-NEWS Vol 1, No 2. ISSN 1609-3631. Available for download at: http://cran.r-project.org/doc/Rnews.

Ripley BD (1981) Spatial statistics. Wiley, New York, New York, USA.

Ripley BD (1988) Statistical inference for spatial processes. Cambridge University Press.

Roth A (2004) Fire patterns within a successional gradient of a sagebrush steppe/juniper woodland. Masters Thesis, University of Idaho, Moscow, Idaho, USA.

Salomonson MG and Balda RP (1977) Winter territoriality of Townsend's Solitaires (*Myadestes townsendi*) in a pinyon-juniper-ponderosa pine ecotone. The Condor 79:148-161.

Schofield CJ and Bucher EH 1986. Industrial contributions to desertification in South America. Trends in Ecology and Evolution 1:78-80.

Schupp EW, Gomez JM, Jimenez JE and Fuentes M (1997) Dispersal of *Juniperus occidentalis* (western juniper) seeds by frugivorous mammals on Juniper Mountain, southeastern Oregon. Great Basin Naturalist 57:74-78.

Schurr FM, Bossdorf O, Milton SJ and Schumacher J (2004) Spatial pattern formation in semi-arid shrublands: a priori predicted versus observed pattern characteristics. Plant Ecology 173:271-282.

Seligman N and Henkin Z (2002) Persistence in *Sarcopoterium spinosum* dwarf-shrub communities. Plant Ecology 164: 95-107.

Stoyan D and Penttinen A (2000) Recent applications of point process methods in forestry statistics. Statistical Science 15(1):61-78.

Stoyan D and Stoyan H (1994) Fractals, random shapes and point fields: methods of geometrical statistics. Wiley, Chichester, U.K.

Strand EK, Vierling LA, Smith AMS, Bunting SC, Hann DB and Gessler PE (2005). Wavelet estimation of plant spatial patterns in multi-temporal aerial photography, Eos transactions, American Geophysical Union, 86, 52, Fall Meeting, San Francisco, CA, December 5-9, 2005, Supplemental, B43B-0287.

Strand EK, Smith AMS, Bunting SC, Vierling LA, Hann DB and Gessler PE (2006). Wavelet Estimation of plant spatial patterns in multi-temporal aerial photography, International Journal of Remote Sensing, 27, 9-10, 2049-2054.

Tausch RJ and West NE (1988) Differential establishment of pinyon and juniper following fire. The American Midland Naturalist 119(1):174-184.

Van Auken OW (2000) Shrub invasions of North American semiarid grasslands. Annual Review Ecological Systems 31: 197-215.

Van Auken OW, Jackson JT and Jurena PN (2004) Survival and growth of *Juniperus* seedlings in *Juniperus* woodlands. Plant Ecology 175:245-257.

Walker J and Gillison AN (1982) Australian savannas. In: Ecology of Tropical Savannas Huntley BJ and Walker BH (ed), Springer Verlag, New York, pp. 5-24.

Whiteman G and Brown JR (1998) Assessment of a method for mapping woody plant density in a grassland matrix. Journal of Arid Environments 38: 269-282.

Wiegand T and Moloney KA (2004) Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104: 209-229.

Young H (1956) Territorial activities of the American Robin (*Turdus migratorius*). Ibis 98:448-452.

Tables

Table 1. Crown diameters of juniper by size class for classification I and II.

	Classification I		**Classification II**	
Size class	**Crown diameter (m)**	**Number of trees**	**Crown diameter (m)**	**Number of trees**
Large	> 6	77	> 6	77
Medium	4 - 6	344	4.4 - 6	225
Small	< 4	149	< 4.4	268

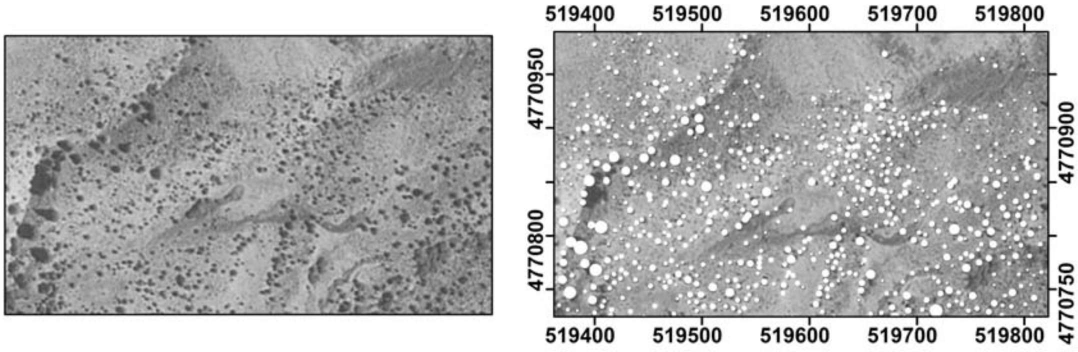


Figure 1. *Left:* Aerial photograph 1998 covering a 250 x 400 meter area. *Right:* Stem plot showing the relative diameters of juniper trees within the plot, derived from wavelet analysis of the 1998 photo.

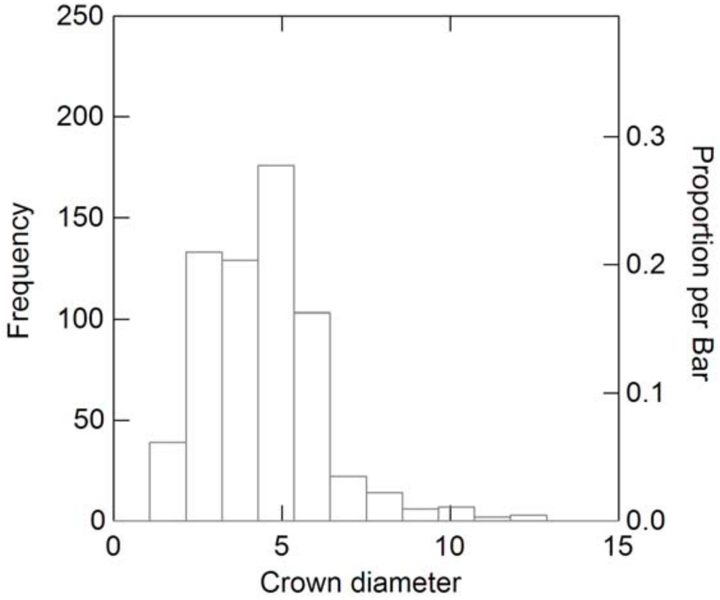


Figure 2. Histogram of juniper crown diameters as projected from the wavelet analysis.

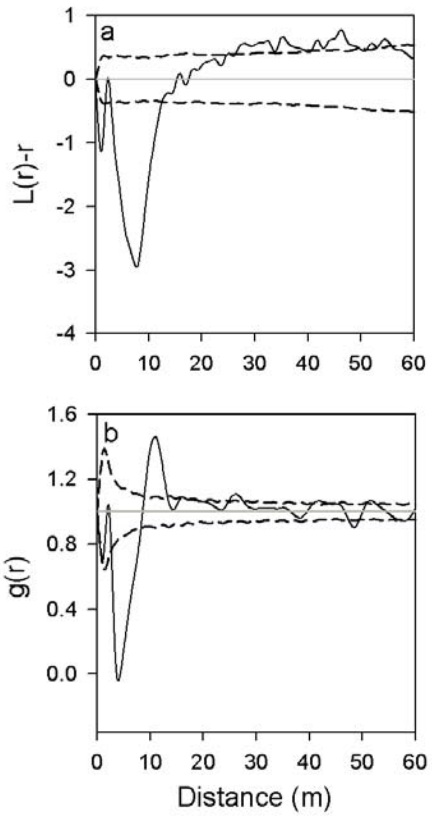


Figure 3. *Above*: Ripley's K expressed as L(r) –r for juniper trees of all size classes within the plot. *Below*: The pair-correlation function *g*(r) for all juniper trees. 95% confidence envelopes for the null hypothesis of no spatial patterns are displayed.

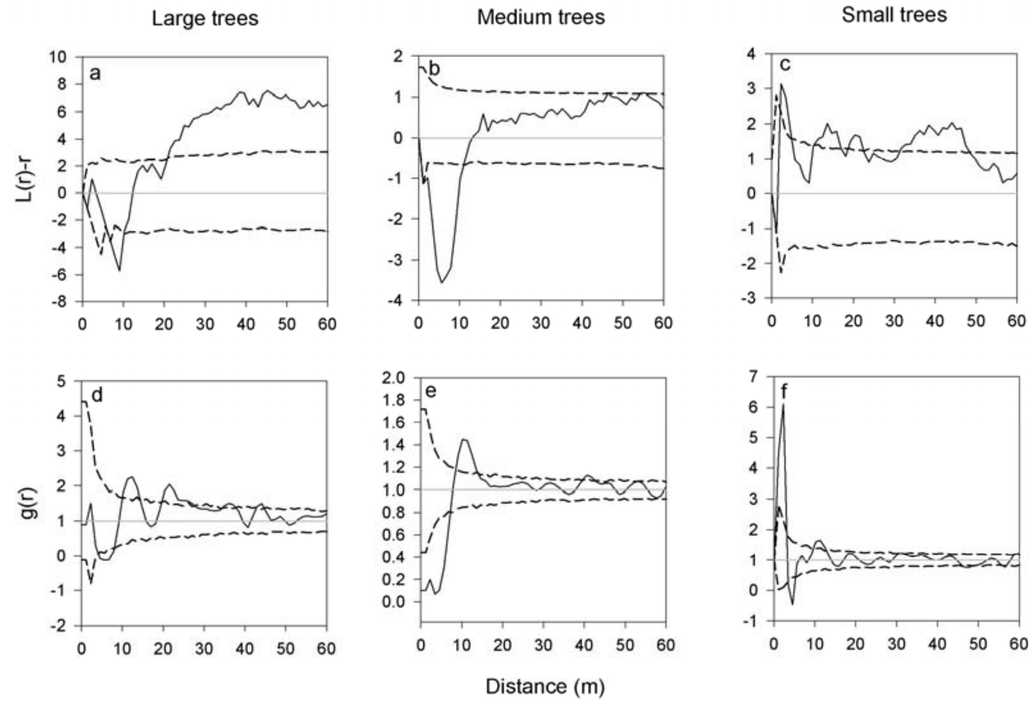


Figure 4. *Top row*: Ripley's K expressed as L(r) –r for large, medium, and small juniper trees within the plot. *Lower row*: The pair-correlation function *g*(r) for large, medium, and small juniper trees. 95% confidence envelopes for the null hypothesis of no spatial patterns are displayed.

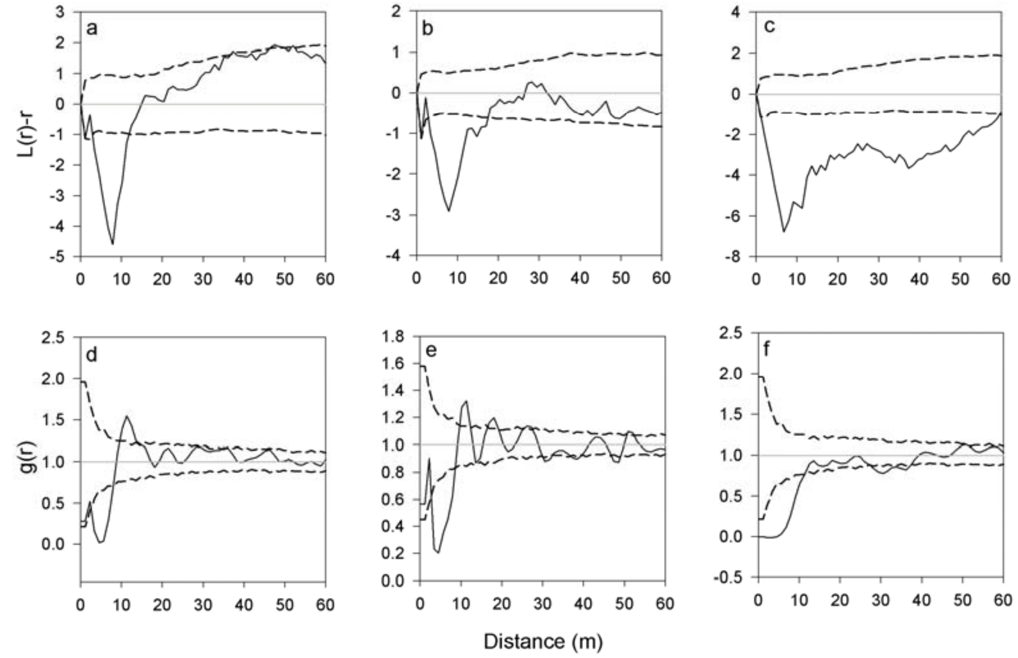


Figure 5. The K-function expressed as L(r) – r for a) medium to large trees, b) small trees in relation to large + medium trees and c) small trees in relation to large trees for ***Classification I***. The *g*-function for d) medium to large trees, e) small trees in relation to large + medium trees and f) small trees in relation to large trees for ***Classification I***. 95% confidence envelopes for the null hypothesis of no spatial patterns are displayed.

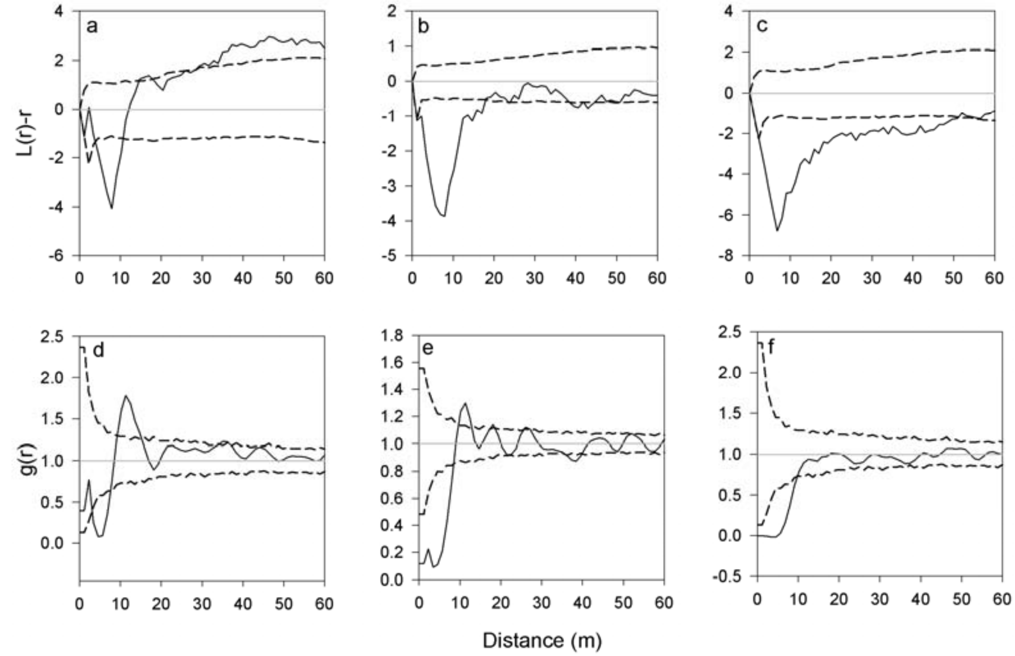


Figure 6. The K-function expressed as L(r) – r for a) medium to large trees, b) small trees in relation to large + medium trees and c) small trees in relation to large trees for ***Classification II.*** The *g*-function for d) medium to large trees, e) small trees in relation to large + medium trees and f) small trees in relation to large trees for ***Classification II***. 95% confidence envelopes for the null hypothesis of no spatial patterns are displayed.

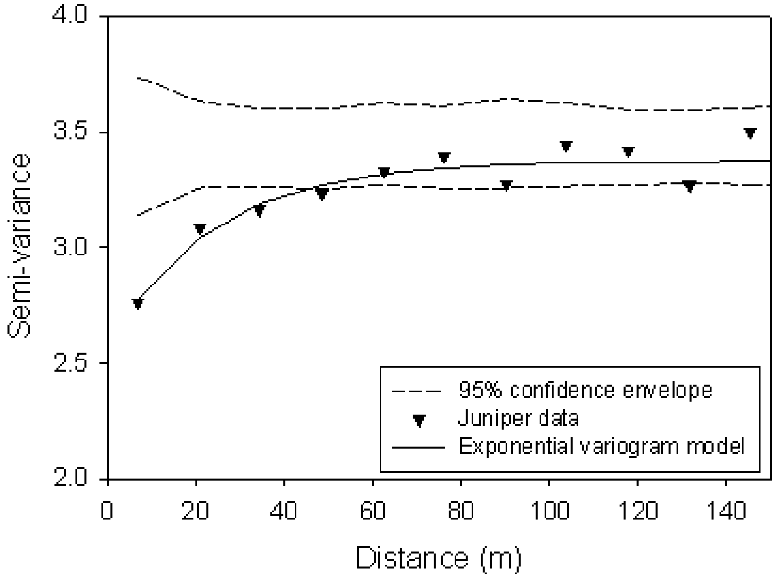


Figure 7. Semi-variogram of *J. occidentalis* crown diameters. Model fitting to an exponential model indicates a spatial dependence of approximately 70 m. The 95% confidence envelopes for the null hypothesis of no spatial patterns confirm that the spatial dependence is statistically significant within 50 m.

CHAPTER 4: A quantitative approach for development of a state-and-transition model for aspen/conifer woodlands on the Owyhee Plateau, Idaho

Abstract

Current decline of quaking aspen (*Populus tremuloides* Michx.) is of concern across the intermountain western United States. It has been postulated that current fire intervals, extents and intensities are not sufficient for the regeneration of aspen at historic rates, which has led to current aspen population declines. Although it is well known that the mixing of conifers into aspen stands and excessive browsing by herbivores negatively affect aspen establishment, it is poorly understood how these factors are manifested at a landscape scale through time.

Aspen in the Owyhee Mountains occur in three different biophysical settings, with each containing different successional trajectories. Pure aspen stands exist at high altitudes on south-facing slopes in an ecological niche where conifers are not likely to occur under current climate conditions. Aspen growing on wet microsites are experiencing slow rates of conifer establishment and will likely persist for many decades, although a high level of animal browsing is of concern for clone viability in many of these areas. Upland mixed aspen/conifer stands are experiencing rapid rates of conifer establishment. Increment cores from the oldest aspen and conifer stems here indicate that within the majority of the stands aspen and conifer species co-established on the site after the last disturbance, followed by a rapid transition to aspen/conifer woodlands when the conifer species begin to produce seed, leading to an exponential replacement of aspen within the stand.

We developed a conceptual state-and-transition model for upland aspen/conifer stands, that was parameterized based on field data in the vegetation dynamics computer simulation model Vegetation Dynamics Development Tool (VDDT). Modeling of varying fire regimes predict that a fire return interval of 30-60 years is desirable for maintenance of aspen in upland areas where conifers are present. Under the current fire regime the upland aspen/conifer stands will likely be lost within 80-200 years. Thresholds for the effect of conifer encroachment and browsing on aspen regeneration identified through this research are similar to those described by others across the West. We therefore suggest that the results presented for the Owyhee Plateau are likely applicable to broad areas of western aspen.

KEYWORDS: Aspen, succession, disturbance dynamics, encroachment, state-and-transition model, threshold, fire regimes, VDDT, vegetation dynamics simulation

1. Introduction

Quaking aspen (*Populus Tremuloides* Michx.) were among the pioneer species following the retreat of continental and alpine glaciers during the Pleistocene (Pielou, 1991). This glacial past helps explain the current spotty distribution of aspen in the high elevation mountainous areas of the semi-arid western states. Aspen is a clonal organism that reproduces primarily via vegetative root suckering in the western mountains, that requires some form of disturbance (Schier et al. 1985). When mature aspen trees are killed or stressed, the flow of the hormone auxin is suppressed and cytokinin can begin to stimulate root suckering (Schier et al., 1985). According to Barnes (1975), aspen clones can exist for centuries by self-regeneration after disturbance. Although aspen clones are long-lived, aspen trees are short-lived, normally living 100-150 years (Shepperd et al., 2001) with occasional stems over 200 years (Mueggler, 1989). Sexual aspen regeneration requires prolonged moist conditions and is extremely rare for Intermountain western aspen hence an aspen clone that is lost from the landscape will not likely be replaced through sexual reproduction (Mitton and Grant, 1996).

Aspen is an important community type in the western mountains. Second only to riparian ecosystems, aspen communities represent the most biologically diverse areas (Kay, 1997) and aspen decline cascades into losses of vertebrate species and vascular plants (Campbell and Bartos, 2001). As a result aspen has been described as an indicator of ecosystem integrity (Woodley, 1993), by some portrayed as a keystone community (Bartos, 2001) and valued by recreationists, artists and naturalists. Aspen communities produce high quality forage for wildlife and livestock (Mueggler, 1988) and reduced forage production in late seral conifer dominant aspen stands needs to be considered when determining carrying capacity for elk (*Cervus elaphus*), deer (*Odocoileus* spp.), and moose (*Alces alces*) as well as livestock stocking rates.

Aspen declines in the western United States (estimated on a per-state basis) range from 49% to 96% compared to historic distributions (Bartos, 2001). Aspen stands in the Intermountain West commonly occur in conjunction with conifer species such as Engelmann spruce (*Picea engelmannii;* Smith and Smith, 2005), Douglas-fir (*Pseudotsuga menziesii*; Heide, 2002; Roth, 2004), western juniper (*Juniperus occidentalis*; Wall et al., 2001; Roth, 2004), or subalpine fir (*Abies lasiocarpa*; Smith and Smith, 2005). Slow growing shade tolerant conifers begin to dominate over aspen late in succession, and will eventually out-compete and lead to the loss of aspen from the stand (Shepperd et al., 2001). Aspen growth rates are independent of the presence of conifers in early to mid-succession (Shepperd et al., 2001; Kaye et al., 2005), however Shepperd et al., (2001) estimate that conifers will begin to out-compete aspen at a stand age of 100-150 years.

It has long been accepted that fire stimulates aspen suckering (Bartos and Mueggler, 1981) and without stand-replacing fire conifer species will overtake many aspen sites (Baker, 1925). Aspen stands tend to grow on moist sites where fires are less intense and relatively easy to control (DeByle et al., 1987). Ironically, the presence of flammable conifers may be necessary to carry the stand-replacing fire that will revive the decadent aspen stand. Data presented by DeByle et al. (1987) imply that examples of fire induced aspen stand rejuvenation have been rare during the last century in the western states, and that fire suppression has been very effective in the last 50 years. Removal of competing vegetation and mechanical root stimulation are other agents that can promote aspen suckering and improve the survival likelihood of aspen clones (Prevost and Pothier, 2002; Shepperd, 2001). Bartos and Amacher (1998) warn that cutting alone in stands heavily dominated by conifers may not improve aspen suckering adequately due to a low soil pH caused by long term conifer dominance. In these areas fire may be necessary to increase pH and nutrients in the soil.

Browsing by wildlife and livestock has been shown to inhibit successful regeneration in aspen stands (Bartos and Campbell, 1998; Kay and Bartos, 2000, Kaye et al., 2005). Aspen regeneration is particularly affected within elk winter range in areas where elk are not hunted (Hart and Hart, 2001). Recent research (Kaye et al., 2005) confirms that high levels of elk browsing and conifer dominance negatively influence aspen establishment but do not affect the growth or mortality of individual mature aspen ramets.

Modeling of disturbance-succession dynamics is critical for predicting long-term trends at a landscape scale (Kaufmann et al., 1994). We suggest that a state-and-transition model (Westoby et al., 1989) can conceptually describe the succession/disturbance dynamics within the aspen ecosystem. Succession is a directional process in which one plant community sequentially replaces another through time. Successional theory originates in concepts developed by Clements (1916) where disturbed plant communities are predicted to return to a determined climax state, often the desired condition of the community. Clementsian succession theory has received much criticism in the recent decades (Briske et al., 2003) while hypothetical state-and-transition models (Westoby et al., 1989) have become widely accepted as a means of cataloging observations to better understand vegetation dynamics and interactions with management (Bestelmeyer et al., 2003). State-and-transition models portray multiple vegetative states along a single or multi-pathed succession gradient tied by transitional pathways. Agents such as fire, insect outbreaks, grazing or disease drive the transitions between the hypothetical vegetative states (Bestelmeyer et al., 2003). Land managers best utilize state-and-transition models not to establish a permanent ecosystem equilibrium, but rather to engage in opportunistic management that is flexible in nature, and guided by multiple described vegetative states, transitions, and defined measurable thresholds (Westoby et al., 1989). Friedel (1991) states that once a vegetative community has crossed a threshold into a more degraded state, significant management actions such as prescribed burning, mechanical or chemical treatments are necessary to return to the more desirable state, if reversal is possible at all. Recently, ecological thresholds have been interpreted as a switch from the dominance of negative feedbacks to positive feedbacks within the ecosystem (Briske et al. 2006). Dominance of negative feedbacks maintains resilience within the ecological system while a switch to positive feedbacks promotes development of the post-threshold (often non-desirable) vegetation state.

The state-and-transition model framework is particularly suitable for the disturbance-dependent aspen ecosystem, where the seral rather than the potential vegetation is the management objective, and where irreversible transitions into non-aspen communities can occur due to the reproductive strategy of western aspen. We establish the basis for our regional state-and-transition model by answering the following research questions:

Q I What are the characteristics of the biophysical settings within which aspen occurs on the Owyhee Plateau?

Q II Is the degree of conifer encroachment dependent on the time since conifer establishment in aspen stands? What environmental variables affect the rate of encroachment?

Q III What stand and environmental characteristics affect vegetative aspen establishment?

Q IV Is there evidence that aspen stands have recently, within the last 100 years, been converted to conifer stands in the Owyhee Mountains?

The overarching goal of this research is to enhance our understanding of the succession disturbance dynamics in aspen communities. We addressed this goal by developing and implementing a conceptual state-and-transition model in the computer software Vegetation Dynamics Development Tool (VDDT, 2003). The VDDT is a deterministic succession model with stochastic properties and the ability to output predictions of the future landscape compositions that would result from variety of management strategies (Kurz et al,. 2000; Merzenich and Frid, 2005). The VDDT model presented here focuses on fire dynamics, however the model is developed such that other disturbances including mechanical treatment, disease, and browsing could be incorporated in the future. The VDDT simulation was used to answer our fifth research question:

Q V How long will aspen persist on the landscape under different fire regimes?

2. Methods

2.1. Site Description

The Owyhee Plateau, covering about 440,000 ha of southwestern Idaho, is dominated by western juniper woodlands (*Juniperus occidentalis* subsp. *occidentalis*) and sagebrush (*Artemisia* spp.) steppe (116° W, 43° N). The Owyhee Mountains include three mountain ranges: Silver City Range in the north, and South Mountain and Juniper Mountain in the south. Elevation ranges from 1200 to 2560 m at the summit of the Silver City Range. Western juniper occurs mainly as open savanna-like woodlands dissected by rocky river canyons and shrubby riparian areas. Aspen, Douglas-fir and small patches of wet meadows and mountain shrub are infrequent components in the juniper-dominated landscape. Common mountain shrub species are shiny-leaf ceanothus (*Ceanothus veluntinus*), mountain snowberry (*Symphoricarpos oreophilus*), bittercherry (*Prunus emarginata*), and chokecherry

(*Prunus virginiana*). Commonly, aspen stands are located on cool northeast facing slopes, in concave snow and moisture accumulation areas on deep fine-loamy and loamy-skeletal mixed pachic or typic cryoborol soils with high water-holding capacity that are rich in organic material (USDA, 1998).

The climate on the Owyhee Plateau is characterized by a dry warm summer and fall, followed by moderate precipitation in winter (in the form of snow) and spring. Annual average precipitation varies with the elevation, from 250 mm at lower elevations, to 1000 mm at the crests of the mountain ranges. Annual precipitation in areas that support aspen is 400 mm or above (Oregon Climate Service, 1999). Elk and mule deer utilize the mountain woodlands for forage during the summer, however the winter range is located at a lower elevation where aspen is rare. Private, state, and federal lands are grazed by livestock during the summer months.

2.2. Field methods

Aspen clones were located on satellite and aerial imagery (USDA, 2004). Aspen clones larger than 0.4 ha in size and located at least 100 m apart were selected for sampling. We located plots along the elevation gradient (from 1700 m to the top of the mountain) and across the continuum of slope and aspect classes within the study area. Samples were collected from aspen along the entire successional gradient, from recently burned to completely dominated by conifers. A total of 82 aspen clones were sampled excluding stands that were restricted to the riparian zone or short-growing snow-bank aspen at the mountain crest.

Plots were located in the oldest part of the aspen clone and the following data were collected: UTM coordinates, elevation, slope, aspect, canopy cover of aspen and conifers in crown and below 2-m height, increment cores from the five oldest aspen and conifer trees (Wall et al., 2001), and a list of the six major vegetative species based on foliar coverage. Ocular estimates of foliar cover of perennial and annual grasses and forbs, as well as medium (0.5-2 m) and tall shrubs (> 2 m), were also recorded. To assess aspen clone regeneration and stem density we adopted the sampling method suggested by Kilpatrick et al. (2003) whereby circular plot size and number of subsamples are adjusted and collected to maintain 80% statistical confidence while minimizing the number of samples collected. Within the subplots we recorded three size classes of aspen and conifers (if present). Class 1 was composed of aspen suckers < 2 m tall, Class 2 represented aspen taller than 2 m but shorter than 75% of the height of mature aspen, and Class 3 represented the mature aspen trees. Class 1 aspen may or may not contribute to the aspen regeneration depending on the browsing pressure while Class 2 aspen is here considered to represent the recruitment to the aspen stand. If present, western juniper and Douglas-fir were sampled according to the same classification scheme. The outer boundary of the clone was recorded using ArcPad 6.0 (ESRI 2002) on a handheld pocket PC with a Teletype WAAS (Wide Area Augmented System) capable Global Positioning System unit with an estimated horizontal accuracy of 2-10 m. Signs of disturbance, i.e. fire scars, logging, and percent of the terminal leaders browsed were recorded.

Increment cores were extracted for age estimate using an increment borer at breast height for aspen and 30 cm above ground for the conifers. The increment cores were mounted and sanded with increasingly fine grit sand paper and the annual rings were counted using a stereo-microscope. Faint annual rings in aspen were stained with phloroglucinol solution before ring counting (Patterson, 1959). Through comparison of ring count at core height and at ground level we determined that the time to grow to core height was 4-6 years for aspen and 15-25 years for the conifers. Consequently we added 5 years to the age determined by the increment core for aspen, and 20 years for the conifers. Similarly, Smith and Smith (2005) recorded an average growth time to coring height of 5 years for aspen and 24 years for conifers on the Uncompahgre Plateau in Colorado. We here assume that the age of the oldest trees in the stand is indicative of the stand age and the time since the last major disturbance.

2.3. Community types

The aspen communities were in the field classified into three categories based on overstory composition: pure aspen, aspen/Douglas-fir, and aspen/western juniper. Pure aspen stands did not contain any conifer species. Stands were classified into the aspen/Douglas-fir association if the Douglas-fir was present and successfully reproducing; otherwise they were classified as aspen/western juniper stands. To better understand the biophysical distribution of aspen, Douglas-fir, and western juniper across the topography of the Owyhee Mountains (research question I, **Q I**), we performed an overlay analysis between a digital elevation model (USGS, 1999) and a recently developed cover type map (Roth, 2004) using a geographic information system (ESRI, 1999-2005).

2.4. Analysis of field data

The ages of the oldest aspen and the oldest conifer trees in encroached stands were compared to determine whether the aspen stand was experiencing conifer encroachment or had developed via co-establishment of aspen and conifers. To address research question II (**Q II**) we adapted the Chapman-Richards vegetation growth function to assess the successional rate of conifer establishment in aspen stands, following Yang et al. (2005). The Chapman-Richards function describes the closure of canopy as an exponential function of time since the last disturbance. We here adapted the exponential function to represent the proportion of conifers in the stand rather than the canopy closure of each species to characterize the seral development in upland aspen/conifer stands in the Owyhee Mountains.

$$f(t) = A\, e^{kt} \qquad (1)$$

where f(t) is the proportional cover of conifers in the aspen stand, which is close to 0 at $t = 0$ and approaches 1 at complete conifer dominance and the constant k represent the successional rate.

Besides time since the onset of conifer encroachment (t), environmental variables affect forest growth rates and successional development, for example terrain attributes, soil and climate data (Gustafson, 2003). Inspired by Gustafson (2003) we selected 10 landscape variables, which are likely to affect successional rates in our study area (Table 1). The successional rate (k) was modeled using a stepwise forward general linear modeling approach:

$$k = c + c1{*}X1 + c2{*}X2 + \ldots\ldots.. \qquad (2)$$

where c, c1, c2 etc. are constants and X1, X2 etc. are environmental variables (Table 1). We used the AIC information criterion (Akaike, 1973) modified for sample size, AICc (Hurvich and Tsai, 1989), for model selection.

Conifers and ungulate browsing affect aspen regeneration (e.g. Kaye et al., 2005). Other factors that potentially affect aspen regeneration are the stand age, disturbances such as logging and fire (represented by the presence of fire scars), and other site characteristics (Table 2). To address research question III (**Q III**), classification and regression tree analysis (CART, Breiman et al., 1984) was used to identify factors that affect aspen regeneration and determine threshold values for when aspen regeneration reaches a level near or below the desired 1200 stems/ha recommended by Bartos and Campbell (1998). CART is a non-parametric statistical method that can accommodate continuous as well as discrete variables without requirements of normality or linearity in the data. We employed a least squares binary partitioning algorithm in the CART analysis using the SYSTAT statistical software (SYSTAT, 2004).

2.5. Historical aspen stands

The persistence of aging aspen clones on the landscape is an important topic in aspen ecology and management. It has been suggested that aspen clones have persisted in the western mountains for centuries, possibly since the glacial retreats 10,000 years ago (Mitton and Grant, 1996). Considering such longevity aspen must previously have endured periods of infrequent fires, heavy ungulate browsing and climatic variations (Hessl, 2002) and the aspen decline today could be viewed as temporary. Despain (1990) suggested that aspen can maintain itself in a short shrub state under unfavorable conditions over time periods longer than 50 years.

With an estimated aspen decline of 61% in Idaho within the last 100 years (Bartos, 2001), evidence of historic dying or dead aspen stands in areas that are not currently covered by aspen would be expected. We hypothesize that remnants of decadent, conifer encroached aspen stands may exist in areas with environmental characteristics suitable for aspen vegetation such as cool slopes with high potential for snow accumulation.

To address research question IV (**Q IV** *Is there evidence of aspen stands that within the last 100 years have been converted to conifer stands?*), we compared the current aspen distribution to a spatial aspen habitat model. Many examples of strong correlations between terrain and soil attributes and vegetation types have been presented in the literature (e.g. Iverson et al. 1997, Gustafson et al., 2003, Falkowski et al., 2005). Potential vegetation type (PVT) is here defined as the environmental site potential affected by climatic, topographic, and edaphic factors. Following a Bayesian approach (Aspinall, 1992; Aspinall, 2000), the spatial aspen habitat model was created in a geographic information system (ESRI, 1999-2005), based on a 10-m digital elevation model (USGS, 1999) and the Owyhee county soil survey (USDA – NRCS, 1998). Model variables elevation, aspect, slope, solar insolation (Fu and Rich, 1999), and curvature were derived from the digital elevation model, the soil water-holding capacity was extracted from the soil survey, and all variables were tested for significance using the chi square statistic. Conditional probabilities for the presence of aspen were derived from 46 aspen/conifer training areas collected in 2002-2003 in the GIS, and then consequently incorporated in Bayes' theorem (following Aspinall, 2000) to compute aspen occurrence probability across the landscape.

The current land cover of aspen was mapped through image interpretation of a SPOT 5 satellite image from July 31, 2002 with a spatial resolution of 10 m in the green, red and near infrared bands and 20 m in the short wave infrared band. Pre-processing included conversion from digital numbers to at-sensor reflectance using the biases, gains, band pass values, and solar zenith angle specific to the SPOT 5 satellite instrument and the acquired image. Training areas for 46 aspen and aspen/conifer stands were delineated on the image and areas within 1.5 standard deviations from the reflectance means were mapped as stands containing aspen, encompassing an area of 14,200 ha. The map was validated with an independent dataset of 69 aspen locations collected in 2005 where 88% of the validation plots were within 30 m of areas mapped as aspen.

In the summers of 2004 and 2005 we visited 41 sites where aspen is likely to occur (>80% probability) according to the GIS aspen habitat model that did not show visible evidence of aspen according to the SPOT 5 image assessment. We expected to find remnant aspen stands, aspen in a shrub state or no evidence that aspen ever existed in the area.

2.6. Landscape dynamics modeling environment (Question V)

We constrained and parameterized the VDDT model based on successional rates and initial stand age distribution observed in the field data. The area in each successional stage along the aspen/conifer sere was calculated from an average of 10 Monte Carlo runs in VDDT 200 years into the future. Five fire regime scenarios were evaluated:

1. Current fire management (suppressed wildfire only). Fire atlas information for the area is available since 1957. Only one aspen stand within the study area above 1700 m has burned in wildfires during this time and two stands have been treated with prescribed fire. The current fire regime translates into a fire probability of 0.0002 (i.e. 1 in 5000 years) for the aspen woodlands, which is similar to the current fire return intervals computed by DeByle et al. (1987) for national forest lands in the interior West.
2. An average fire return interval of 25 years (probability 0.04).
3. An average fire return interval of 50 years (probability 0.02)
4. An average fire return interval of 75 years (probability 0.013)
5. An average fire return interval of 100 years (probability 0.01)

The persistence of aspen in stands severely affected by conifer encroachment with reduced aspen regeneration is poorly understood. Will these old stands return to a stand initiation phase of aspen after a disturbance or will the site come back as a conifer woodland with permanent loss of the aspen clone? We performed a sensitivity analysis to better understand how sensitive the model is to the persistence of aspen in old stands by modeling three scenarios under current wildfire conditions; aspen clones can persist in a poorly regenerating state for 25, 50 or 120 years and still come back as a stand initiation aspen stand after a disturbance.

3. Results

3.1. Biophysical preference of overstory species (Question I)

The preferred biophysical distribution for the three major overstory species, Douglas-fir, western juniper and aspen, in the Owyhee mountains was determined by overlay analysis in a GIS of a recently classified landcover map (Roth 2004) and a digital elevation model (USGS 1999). Douglas-fir occurs at 1800-2100 m elevation on all but the south-facing aspect (Figure 1), likely due to moisture limitations. Western juniper occurs in an elevation band at 1200-1900 m equally distributed among all aspects. Stands containing aspen occur at 1700-2100 m elevation on the cooler aspects and at 1900-2100 m on south-facing aspects (Figure 1). An ecological niche for aspen currently exists on south-facing aspects above 1900 m. Within this realized niche we observed 11 uneven-aged apparently self-regenerating aspen stands that were mostly free from conifers. Mueggler (1989) describes such areas of uneven-aged aspen stands where aspen appears to persist as a stable, self-regenerating ecosystem in the western mountains of the U.S. These stable aspen systems are, according to Mueggler (1989), unsuited for conifers or far away from conifer seed sources. Although the niche for pure aspen stands exists on south-facing aspects above 1900 m, the preferred biophysical setting, where the majority of the aspen is situated, occurs on northeast facing aspects around 1850-1950 m elevation.

3.2. Mixed and pure aspen stands

The majority of the 82 sampled stands were encroached to some degree by Douglas-fir (44% of the stands) or western juniper (41% of the stands) while the remaining 15% of the stands were pure aspen stands. Forty percent of the stands were encroached by both Douglas-fir and western juniper. The average age for the oldest Douglas-fir trees in the encroached stands was 101 years while the average age for the oldest western juniper trees was 68 years. The average age of the pure aspen stands was 77 years. Overall, the oldest trees cored, by species, were 143 years for aspen, 142 years for Douglas-fir and 124 years for western juniper. In pure aspen stands the age of the oldest aspen ramets may represent the time of the last stand–replacing disturbance, however the stand may also have been self-regenerating for a much longer period of time. Large aspen stems were present on the forest floor in many pure aspen stands indicating long-term occupancy of aspen in the area.

Analysis of the increment cores reveal that in 85% of the aspen stands containing conifers the oldest conifers were within 20 years in age of the oldest aspen ramets indicating co-establishment of the aspen and conifer species. In 15% of the stands the conifers were considerably younger than the oldest aspen indicating that conifers are here encroaching upon previously conifer free aspen stands. Ring counts of increment cores from the oldest trees in the aspen clones reveal that the majority of the aspen stands in the Owyhee Mountains were established in the early 1900's (Figure 2).

Based on the criteria specified by Bartos and Campbell (1998) listed in Table 3 we determine that 74% of the sampled aspen stands are at risk of loss. The most frequently occurring threat to the sampled aspen stands is poor regeneration in mixed aspen/conifer stands.

3.3. Disturbance and microsites

Signs of disturbance were observed in approximately half of the sampled aspen/conifer stands (Table 4). We recorded two forms of disturbance: logging and fire scars. The logged areas occurred only in the Douglas-fir zone on private and state managed lands. Typically the larger stems of Douglas-fir were removed, leaving stumps and gaps in the stand. No logging or cutting was recorded in the aspen/western juniper stands.

We recorded fire scars in 29% of the aspen/juniper stands (10 stands total) and in 19% of the aspen/Douglas-fir stands (7 stands total) even though the thin aspen bark is extremely sensitive to scorching by fire and aspen stands typically burn in a stand replacing fire regime (DeByle 1987). In aspen/Douglas-fir stands the fire scars were typically located on the uphill side of a few trees at the edge of stands while fire scars in aspen/western juniper stands sometimes occurred in patches throughout the stand, indicating movement of a patchy low severity fire through the stand. Evidence of fires in aspen stands, in the form of fire scars and charred snags, has previously been reported by Gruell (1978).

Thirteen of the sampled aspen/conifer stands occurred on wet microsites near springs or meadows with components of Kentucky bluegrass (*Poa pratensis*), California false hellebore (*Veratrum californicum*), and Sedge (*Carex* spp) in the understory.

3.4. Rates of succession (Question II)

Succession in aspen/conifer stands is largely driven by the conifer proportion within the stand. In estimating successional rates, we focused on the hill-side aspen/conifer stands and excluded stands on microsites and stands that had experienced logging or fire disturbance. Stepwise general linear model (GLM) analysis revealed that the most important variable in the stand development was time since conifers were introduced in the aspen stands. Among the environmental candidate variables (Table 1) only the climate variables and PVT (Table 5) were significant ($p<0.05$). Ratkowsky (1990) emphasizes the importance of parsimony and selection of boundary conditions and parameters that have physical meaning in development of nonlinear regression models. We used Akaike's information criterion for small sample sizes (Hurvich and Tsai 1989), which weighs parsimony and the maximum log-likelihood in model comparison, to select the best model for the rate of succession in upland aspen/conifer stands. Although all models were comparable (delta AICc < 2) we selected the model with the lowest AICc value ($R^2 = 0.63$, $F=114.4$, $p<0.001$) (Table 5).

$$f(t) = 0.0177\, e^{0.0315 * t} \qquad 0 < f(t) < 1 \qquad (3)$$

where f(t) is the cover proportion of conifers in the stand as a function of time (t) since the first conifers were established in the stand (Figure 3). At approximately 50-60 years after the establishment of conifers in the stand we see a rapid increase in conifer cover and after 100-140 years conifers dominate the stand. Although precipitation and PVT were not included in the selected model for reasons of parsimony, these variables were significant ($p<0.05$) indicating that successional rates increase with increased precipitation and are higher in aspen/western juniper stands than aspen/Douglas-fir stands.

Supported by a paired t-test ($\alpha = 0.05$) we conclude that stands growing on microsites show significantly slower successional rates of conifer establishment relative to upland aspen stands (Figure 3). Aspen/western juniper stands with fire scars also show significantly lower rates of conifer development ($\alpha = 0.1$) while successional rates in aspen/Douglas fir stands with fire scars were not significantly different from upland aspen stands.

3.5. Aspen regeneration (Question III)

Based on the CART analysis, the two variables with the most predictive power in estimating the level of regeneration in aspen stands are browsing and the level of conifer encroachment (Figure 4). The first split in the binary recursive partitioning occurs at a very low level of conifer encroachment. Stands with few or no conifers present regenerate adequately, with mean aspen regeneration of >1700 stems/ha. These stands are pure aspen stands growing in the niche habitat at elevation > 1900 m on south facing aspects or stands that have recently experienced a stand replacing fire or where large conifers have been mechanically removed. Stands with particularly low regeneration (< 500 stems/ha) occur in areas where the browsing is > 26% and where more than half the canopy cover consists of conifers (Figure 4). Aspen regeneration drops to levels below the recommended 1200 stems/ha when the browsing level reaches approximately 30% and the proportion of conifers in the stand reaches ~0.35-0.4 (Figure 5). To validate the results from the CART analysis we tested the predictability of aspen regeneration from browsing and conifer proportion using stepwise forward k-nearest neighbor non-parametric discriminant analysis (SAS 2005). Three classes of aspen regeneration, < 500 stems/ha, 500-1200 stems/ha and > 1200 stems/ha, could be predicted with a 70% accuracy from browsing and conifer proportion only.

3.6. Historical aspen stands (Question IV)

A map of aspen occurrence probability (Figure 6) was created via a Bayesian model with the following significant variables: elevation ($\chi^2 = 159.1$, df = 8, $p < 0.001$), slope ($\chi^2 = 15.1$, df = 5, $p < 0.01$), aspect ($\chi^2 = 46.6$, df = 7, $p < 0.001$), curvature ($\chi^2 = 9.3$, df = 4, $p < 0.05$), solar insolation ($\chi^2 = 27.0$, df = 6, $p < 0.001$), and water-holding capacity ($\chi^2 = 95.4$, df = 4, $p < 0.001$). Aspen and aspen/conifer areas mapped via remotely sensed data are overlayed on the aspen habitat map along with 41 points located in areas with high aspen probability but with no aspen cover for the South Mountain part of the study area (Figure 6). In 37% of the visited locations we found dead aspen stems (standing or on the ground) with no evidence of aspen regeneration while in 51% scattered aspen ramets were present and aspen was regenerating in forest gaps, along roads or trails, or at the edge of the conifer stand. In the remaining 12% of the visited sites there was no evidence that aspen had ever occurred on or near the site.

Comparing the spatial model of potential aspen habitat to the actual occurrence of aspen determined via remote sensing we estimate a region-wide conversion of 8000 ha of aspen woodlands to conifer woodlands, corresponding to a 69% loss of aspen woodlands. This estimate likely over predicted aspen loss since our field data show that in a portion (12%) of the areas mapped as aspen habitat there is no evidence that the area has ever supported aspen. Furthermore it is uncertain whether a large-scale disturbance will lead to aspen recruitment in these old stands or if the area will be converted to conifer woodlands. This estimate is however close to the estimate of 61% aspen loss in the state of Idaho in the last 100 years (Bartos 2001).

3.7. State-and-transition (ST) model

Successional rates and thresholds identified through statistical analysis of field data are here summarized in a conceptual state-and-transition model for upland aspen/conifer woodlands in the Owyhee Mountains. We suggest an ST-model with two states, where State I is composed of four phases and State II contains one phase (Figure 7). The transitions are described in Figure 7 and the five phases are defined as follows:

- Phase I (State I): Stand initiation, aspen < 2 m tall. This phase occurs after a disturbance such as fire, clear-cutting, or land slide and lasts for 5-10 years depending on the growth rate at the site. This phase is sensitive to excessive browsing. Young conifer seedlings may be present.

- Phase II (State I): Young and mature aspen woodland (> 2 m tall) with satisfactory regeneration (>1200 stems/ha as suggested by Bartos and Campbell, 1998). Conifer plants (if present) are not reaching into the crown of the stand and most are not yet seed-bearing. In the Owyhee woodlands this phase lasts until present conifers are ~50 years of age and prolific seed production has begun. The total canopy cover of conifers is less than 20%.

- Phase III (State I): Young or mature aspen woodland that is not reproducing satisfactorily (< 1200 stems/hectare). In this phase the lack of reproduction in aspen is due to factors other than conifer encroachment. The browsing pressure may be excessive. Disease such as leaf blight (*Venturia*) may continuously affect the young shoots and prohibit regeneration (Dance 1961). Aspen ramets may be aging and the production of the sucker inhibiting hormone auxin may be high. Conifer plants (if present) are not reaching into the crown of the stand and most are not yet reproducing. The total canopy cover of conifers is less than 25%.

- Phase IV (State I): Conifer/aspen woodlands where conifers are successfully reproducing but aspen is not. Conifers are dominating the stand. Mature aspen ramets may persist for several decades but due to ceasing aspen reproduction and prolific regeneration by conifers, conifers will eventually dominate the stand. The herbaceous biomass production in the understory is declining. In the Owyhee woodlands this phase begins ~50-60 years after conifers were introduced to the stand and lasts until aspen reproduction is severely affected or non-existent.

- Phase V (State II): Conifer woodland. Aspen regeneration ceased several decades ago and all mature aspen ramets are dead. A disturbance in this phase will not yield a return to the aspen cover type.

3.8. VDDT model results (Question V)

The conceptual ST-model (Figure 7) was parameterized using the field data and implemented in the landscape dynamics software VDDT and run under five different fire regimes 200 years into the future (Figure 8). The initial conditions reflected the age distribution found in the field data with 3% of the stands in the stand initiation phase (0-9 years), 1% of the stands in the age class 10-49 years, 72% of the stands in the age class 50-110 year and 24% of the stands older than 110 years. The bar chart (Figure 9) shows the percent area within each successional stage (Figure 8) for the five scenarios after the model has reached equilibrium in

200 years. Based on the assumptions described in the ST-model and the current fire probability calculated from recent fire perimeter data and land cover, we find that almost all upland aspen stands are expected to be permanently converted to conifer stands if current conditions persist for another 200 years (Figure 9). This model does not include stable aspen stands in areas free of conifers or aspen stands on microsites. Introduction of fire at an average return interval of 25 years will reduce the aspen loss to near zero and result in an aspen landscape composed of 35% stand initiation aspen, ~50% aspen woodlands and ~10% aspen/conifer woodlands. Fire regimes of 50-75-100 years average fire return interval results in an increasing loss of aspen and less aspen in early seral stages (Figure 9).

The persistence of aspen on the landscape was addressed with a sensitivity analysis evaluating three modeled scenarios under current wildfire conditions; aspen clones are capable of maintaining in a non-reproductive state for 25, 50, or 120 years and still return to stand initiation aspen after a disturbance. Non-reproducing stands older than 25, 50, or 120 years will in the model be permanently converted to a conifer stand and the aspen clone is lost. In the 'model world' this sensitivity analysis addresses the question of how long aspen will stay in the fourth box (conifer, non-reproducing aspen) and still return to box 1 (aspen young) after a disturbance (Figure 8). In the most pessimistic scenario, old aspen will return to young aspen only if disturbed within 25 years of conifer dominance (box 4 in Figure 8), almost all hillside aspen/conifer stands will disappear from the landscape within 80 years. If we believe that aspen will persist for 120 years in a non-reproductive state, only 20% of the upland aspen stands will be lost in 80 years, but most stands will be replaced by conifer woodlands in 180 years (Figure 9) in our study area.

4. Discussion

4.1. Successional rates and thresholds

In the quest to identify and quantify successional rates and ecological thresholds it is important to apply sampling strategies and analysis techniques that allow for detection of these phenomena. Statistical techniques with the underlying assumptions of linearity or normality are limited in detecting ecological thresholds as these assumptions rarely apply to ecological data (McCune et al. 2002). In this study we fitted a non-linear model grounded in the Chapman-Richards exponential canopy closure function and used non-parametric CART analysis to identify thresholds for detecting decreases in aspen regeneration along successional and browsing gradients.

This research is unique because aspen stands are sampled and analyzed along multiple gradients across the landscape: succession, elevation and browsing. Although our field surveys on the Owyhee Plateau were used to develop and parameterize the successional model, this model supports previous findings elsewhere that after a disturbance, aspen regenerates rapidly followed by a gradual increase in conifer cover through time in areas suitable for conifer growth (Wall et al.; 2001, Kaye et al., 2005; Smith and Smith, 2005). In agreement with Kaye et al. (2005) we found that conifers were in most of the sampled stands present early in succession, however they were subdominant due to slow initial growth rates.

An exponential increase in conifer cover relative to aspen cover beginning at 50-60 years after the first conifer trees established in the stand. We attribute this exponential increase in conifer cover to the onset of seed production at 20-30 years of age for Douglas-fir (Hermann and Lavender, 1990) and the start of prolific seed production in western juniper at 50-70 years of age (Miller and Rose, 1995). Although prolific seed production begins at 50-70 years of age on dry juniper woodland sites we have observed seed production as early as 25-35 years of age for western juniper growing on moist sites that support aspen. Douglas-fir seed generally fall within 100 m from cone-bearing trees (Hermann and Lavender, 1990), while western juniper seeds are dispersed by seed-eating birds in patches 0.3-1 ha in size (Lederer, 1977). After 50-60 years the conifer seedlings initially present in the stand can successfully produce and disperse seeds within the aspen stands, accelerating the conifer dominance exponentially. At the same time, aspen regeneration decreases as a result of the increasingly shady environment on the forest floor and a hormonal balance that is unfavorable for suckering and recruitment (Shepperd, 2001). The onset of seed production in conifers within the aspen stands well fit the description of an ecological *trigger* (Briske et al. 2006). A *trigger* represents a change in the biotic or abiotic environment that initiates threshold development (Briske et al. 2006). Lack of fire allows confers within aspen stands to become seed bearing, the *trigger*, attracting berry eating birds and mammals (in the case of juniper) leading to further spread of the conifer species. A positive feedback mechanism is initiated that will cause a shift in dominance from aspen to western juniper and eventually the system will cross a threshold where the diminishing aspen clone is no longer capable of vegetative reproduction eventually leading to the permanent aspen loss in the absence of a disturbance.

A second important step in aspen/conifer succession is the time when the conifer dominance has reached a level where it affects aspen regeneration. We conclude from our CART statistical analysis that when the proportion of conifers in the stand is above 0.35-0.5 (Figure 4, 5), 80-110 years after the first conifers were established in aspen upland stands, aspen regeneration drops below 1000 stems/ha. Similarly, when the browsing level exceeds 25-30% a decrease in aspen regeneration is observed (Figures 4, 5).

The thresholds for when conifer encroachment and browsing begin to affect aspen establishment identified through this research are similar to the guidelines for aspen stands at risk developed by Bartos and Campbell (1998) and through the Aspen Delineation Project (Burton 2004). Bartos and Campbell (1998) suggest that aspen stands with a conifer cover >25% are at risk of loss. We here show that aspen reproduction is negatively affected in aspen stands with a proportion of conifers > 0.35 (Figure 5). Burton (2004) suggest that browsing above 20% of the terminal leaders negatively affects aspen stands, while our CART anlysis identifies a drop in aspen regeneration at a threshold of 26% browsing. Although the onset of seed production and the cessation of aspen regeneration are important in aspen/conifer succession the crossing of the irreversible threshold from aspen woodlands to conifer woodlands does not occur until the clone will no longer respond to wild fire or other disturbance events.

4.2. Fire

Fire is an important ecological process in aspen that are seral to conifers. After a stand-replacing fire, quaking aspen regenerates quickly via root suckering. In the semi-arid western mountains aspen is commonly restricted to moist areas or areas where snow naturally accumulates. Due to moist conditions aspen stands burn only under very dry conditions and the fires are therefore generally stand replacing (DeByle et al., 1987; Romme et al., 2001). The thin bark of aspen is not resistant to fire, which contributes to this stand-replacing but relatively low severity fire regime. Although stand replacing fires are most common in aspen, fire scarred aspen trees were present in 17 of the 82 sampled stands. One could speculate that the small aspen patches (1-10 ha) in the Owyhee Mountains do not have a typical fire regime, rather fuel characteristics in the surrounding vegetation types control the frequency and intensity of the fires.

Fire scars in aspen/Douglas-fir stands were typically located at the edge of the stand, while fire scars in aspen/western juniper stands sometimes occurred in patches throughout the stand. Fires are more likely to start and sustain in the dryer aspen/western juniper stands and likely to burn more frequently and at a lower intensity, leaving patches of unburned junipers and scarred aspen trees. Successional rates in aspen/Douglas-fir stands with fire scars were not significantly different from undisturbed upland stands while aspen/western juniper stands with fire scars showed a significantly lower canopy cover of juniper compared to undisturbed stands of the same age. In these stands it is possible that mature trees in part of the stand survived a low severity fire that killed western juniper seedlings, some of the mature aspen and scarred others. In the aspen/Douglas-fir stands, on the other hand, the fire more likely burned the entire stand leaving a few fire scars at the ridge or edge of the stand. The oldest stands in these mountains, all free of fire scars, were found on wet microsites associated with springs or meadows.

Jones and DeByle (1985) suggested that the historical fire frequency in western aspen stands was 20-60 years with an average frequency of 50 years. Miller and Rose (1999) found fire return intervals ranging from 12 to 22 years in western juniper prior to 1987. Such frequent fires would not allow conifers to become dominant in the stand and the risk of having seed producing conifers present in or adjacent to the stand after a disturbance would be rather low. These previous findings are in agreement with our model results, suggesting fire return intervals of 30-60 years to avoid conversion of aspen stands to conifer woodlands.

As fires have become less frequent, succession is allowed to proceed to a later stage with higher conifer dominance before a fire occurs. Conifers present in the stand may now be large enough to withstand the flames of fire and become an instant seed source within the recovering aspen stand, accelerating succession in disturbed aspen/conifer stands. Manier and Laven (2001) recorded more abundant conifer regeneration compared to aspen regeneration in recently disturbed Colorado aspen stands and speculate that modern disturbances might have a different effect on aspen forest structure than did fires 100 years ago, suggesting that as conifers gradually replace aspen along the successional gradient fire regimes and effects are altered. DeByle et al. (1987) stated that the presence of flammable conifers might be necessary to carry the stand-replacing fire that will revive the decadent aspen stand, although severe fires may be harmful to aspen due to injury to near surface aspen roots (Schier et al. 1985). Consequently, as the landscape becomes dominated by conifers, increasing the availability of a conifer seed source and altering the fire regimes and effects in aspen/conifer stands, it will become increasingly difficult to restore aspen at a landscape scale.

4.3. Persistence of aspen on the landscape

Aspen in the Owyhee Mountains occur in three unique biophysical settings with entirely different stand development trajectories, not including aspen associated with riparian vegetation. The first biophysical setting includes aspen stands in areas where conifers are absent; in the Owyhee Mountains this occurs on southern aspects above 1900 m elevation. These aspen stands are multi-aged stands that appear to be self-regenerating through vegetative suckering. Aspen regeneration above the suggested threshold of 1200 stems/ha was occurring in 75% of these stands. Unless such stands are browsed heavily over long periods of time or are severely weakened by disease or climate change, they are likely to remain on the landscape for many decades. These aspen clones are not seral to conifers, rather aspen is here the potential natural community.

The second biophysical setting includes hillside upland aspen/conifer stands, here described in a succession model, conceptualized in a state-and-transition model and simulated into the future using the VDDT software. Data from the Owyhee Mountains is yet another example of the region-wide aspen decline observed in western aspen/conifer ecosystems (Bartos 2001; Kaye et al., 2005; Smith and Smith, 2005). Through our research we estimate that over 60% of aspen woodlands on the Owyhee Plateau have been or are in the process of rapidly being converted to conifer woodlands. The long-term persistence of upland aspen stands is highly dependent on the landscape scale dynamics between succession, fire, and herbivory. Results from the VDDT simulation indicate that under the current fire regime most of the hillside aspen will be permanently converted to conifer woodlands within 80-200 years. A fire return interval of 30-60 years is desirable in these areas if aspen woodland preservation is a management priority. Kaye et al. (2005), found that aspen growth and mortality was not affected by conifer encroachment and conclude, that '*long term preservation of aspen forests could be achieved by enhancing aspen recruitment*'. Succession can be described as a directional replacement of one plant community with another. According to successional theory, previously successional aspen models (Bartos et al., 1983) and the model developed here, the conifer dominance will continue to increase in the absence of a disturbance and a stand-replacing event or possibly selective removal of conifer trees is necessary to promote aspen regeneration for the long-term maintenance of upland aspen/conifer stands. Simply stimulating aspen recruitment without removal of conifers could at best yield a temporary advantage to aspen over conifers.

Our observational study of historical aspen stands in areas of expected aspen habitat but with no aspen present according to interpretation of satellite sensor imagery, reveal that many aspen clones (37% of our sampling locations) have indeed been permanently converted to conifers, while in other cases aspen only regenerates in forest gaps or along the forest edge, areas of adequate sun light. Not until these stands are exposed to a stand-replacing disturbance will we know for certain whether they will return to aspen or remain dominated by conifers.

Sensitivity analysis of the VDDT model reveal that the short-term persistence of the aspen/conifer system is highly dependent on the life expectancy of clones no longer reproducing adequately. However, even in the most optimistic case simulated, clone survival for 120 years after decline in aspen regeneration, nearly all upland aspen/conifer stands will convert to conifer woodlands within 200 years according to the succession-disturbance landscape model. This corresponds to 250-350 years after conifers were initially introduced to the stands, taking into account that the initial age of the stands in the simulation is 50-143 years.

The third biophysical setting includes aspen/conifer stands that grow on microsites in moist areas near springs, frequently flooding streams or wet meadows. Although these stands are being encroached by conifers, we found that the encroachment rates are significantly lower compared to those of upland aspen/conifer stands. The twelve microsite stands sampled are among the oldest aspen stands in the Owyhee Mountains and are typified by tall old aspen trees with a large stem diameter. The largest tree we cored was over 2 m in circumference, 23 m tall and 129 years old. The oldest tree cored was 143 years old. Apparently the moist conditions are not ideal for conifer growth and reproduction while aspen is thriving. The age and lack of fire scars in these stands suggest that fires are infrequent and stand replacing. One could speculate that aspen regeneration via seed is possible on these wet sites, although during the sampling we did not observe aspen ramets with different morphological characteristics within the same stand. Genetic analyses might reveal if sexual reproduction occurs in these stands. Aspen on wet microsites will likely persist for many decades. Even though conifer encroachment is a threat, the successional rate is slow. A more apparent threat to aspen degradation within these sites is high levels of animal use. Aspen regeneration was below 500 stems/ha in 7 of the 12 sampled microsite stands. The widespread presence of California false hellebore, a tall forb that is toxic to animals, is an indicator that these areas are or have been heavily used by herbivores (Cosgriff et al., 2004).

Aspen has likely existed in the Owyhee Mountains since the Pleistocene glacial retreats. According to our data, approximately one third of the stands grow on microsites or in conifer free niches where they can be expected to persist within a foreseeable future. The remaining two thirds of the aspen stands occur in conjunction with Douglas-fir or western juniper on dry upland sites. According to our succession-disturbance model, these stands are at risk of loss within 80-200 years under the current disturbance regime. If aspen stands have persisted for 10,000 years in these mountains and large areas now are at risk of loss within 80-200 years, we can conclude that either the region is currently experiencing conditions different than anything that has occurred since Pleistocene or aspen promoting ecological processes exist that have not been accounted for in this model.

4.4. Ecological and management implication

This research supports the observations widely reported in the literature that aspen in the west is declining and that conifer encroachment and excessive browsing are important considerations in aspen ecology and management. Not all aspen stands are at immediate risk of loss. For example, we have observed stable aspen stands growing in areas not suitable for conifers and aspen stands on microsites where conifer encroachment is slow. Two thirds of the aspen stands sampled in the Owyhee Mountains are, however, on a trajectory towards conversion to conifer woodlands in the absence of a large-scale disturbance or management activities.

Shepperd (2001) suggests a series of management techniques available for potential restoration of aspen stands, including commercial harvest, prescribed fire, mechanical root stimulation, removal of vegetative competition, protection of regeneration from herbivory and regeneration from seed. In selection of a management strategy it is important to consider the history and the trajectory of the aspen clone as well as the biophysical setting within the landscape (Shepperd, 2001). In guidelines for management of western juniper Miller et al. (2005) emphasize the importance of asking the right questions before selecting management action. What is the desired future condition? What factors are affecting proper ecological function? What is the current state of the site? What is the predicted outcome of a treatment?

An important question to consider is - *What are the consequences of no management activity*? The broad scale implications of altered fire regimes in the aspen ecosystem are currently manifesting itself as a region wide loss of aspen habitats. Because aspen is regarded one of the most species rich communities in the semi-arid mountains and by some considered a keystone species (as defined by Wilson, 1992) the loss of aspen will likely lead to an altered species composition and diversity at the landscape scale. Chong et al. (2001) for example sampled vascular plants and butterflies in Rocky Mountain National Park in Colorado. Although aspen only covered 1.2 % of the area, aspen stands contained 45% of the plant species sampled, of which 188 species were unique to aspen stands. Similarly, seven of the 33 butterfly species recorded in aspen stands were found only in aspen stands. Winternitz (1980) observed higher density and diversity of non-game birds in aspen stands compared to conifer stands and Jones (1993) reported an increase in bird species diversity with increasing size of aspen stands. Rumble et al. (2001) found that species diversity of birds was higher in pure aspen stands than in aspen/ponderosa pine (*Pinus ponderosa*) stands in the Black Hills of South Dakota. Based on such observations of diversity in aspen stands we can expect that a loss of aspen would cascade into loss or reduction of many plant, bird, and butterfly species. Aspen is furthermore well known for its high-quality and abundant forage (DeByle, 1985) for native ungulates and domestic livestock. For example, Beck et al. (2006) found that aspen is a preferred habitat for elk in the Jarbidge Mountains in Nevada and conclude that it is important to incorporate habitat selection when estimating an appropriate carrying capacity for maintenance of a healthy elk population. Estimates of carrying capacity without consideration of habitat selection may lead to overstocking that results in destructive alterations to the vegetation in the animal's preferred habitats. Ecologically, we are here faced with a positive feedback system where a decreasing aspen population becomes excessively utilized by herbivores, which further contributes to its decline. Other native ungulates that utilize aspen as a preferred habitat are deer *(Odocileus* spp.) and moose (*Alces alces*) (Barnett and Stohlgren, 2001; Shirley and Erickson, 2001).

Although alterations in fire regimes has been described as the major factor influencing the aspen woodlands and forest in the West it, may not be desirable or possible to return to historic fire regimes. Many western aspen stands may have passed a threshold of conifer encroachment where the expected fire effects are different than in the past and the large scale fires described historically may no longer return the system to aspen. Prescribed fire in combination with mechanical treatments is here an alternative to aspen restoration (Brown and DeByle, 1989; Bates and Miller, 2005). Further research is needed for better understanding of alterations of fire regimes and fire effects along the successional gradient in the aspen/conifer ecosystem.

The state-and-transition model developed here for quaking aspen in the Owyhee Mountains may act as a guideline for assessment of aspen stands and a decision support tool in management. The ST-model defines five phases of aspen including transitions between phases suggesting means of returning aspen stands to more desirable states. Identification of aspen stands at risk followed by proper management actions is a step forward in the maintenance of quaking aspen in the western mountains through time.

5. Acknowledgements

USDA Bureau of Land Management for partial funding of this project.
Field assistance by B. Smith and J. Young, College of Natural Resources, University of Idaho.

References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. p. 267-281 *in* B.N. Petrov, and F. Csaki, (eds.) Second International Symposium on Information Theory. Akademiai Kiado, Budapest.

Aspinall, R. 1992. An inductive modeling procedure based on Bayes theorem for analysis of pattern in spatial data. International Journal of Geographical Information Systems 6:105-121.

Aspinall, R., 2000. Bayesian Modeling with ArcView GIS, The GeoSpatial New West Intermountain GIS Conference, Kalispell, May 4, 2000.

Baker, F.S., 1925. Aspen in the central Rocky Mountain region. USDA Bull. 1291, p.47.

Barnes, B.V., 1975. Phenotypic variation of trembling aspen in Western North America. Forest Science 22:319-328.

Barnett D.T., and T.J. Stohlgren, 2001. Persistence of aspen regeneration near the national elk refuge and Gros Ventre Valley Elk Feedgrounds of Wyoming, p.27-37, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Bartos D.L., F.R. Ward and G.S. Innis, 1983. Aspen succession in the intermountain West: A deterministic model. USDA Forest Service GTR-INT-153, Ogden, Utah 60p.

Bartos, D.L., 2001. Landscape dynamics of aspen and conifer forests. p. 5-14. Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Bartos, D.L. and M.C. Amacher, 1998. Soil properties associated with aspen to conifer succession. Rangelands 20:25-28.

Bartos, D.L and W.F. Mueggler. 1981. Early succession in aspen communities following fire in western Wyoming. Journal of Range Management 34(4):315-318.

Bates J.D. and R.F. Miller 2005. Restoration of aspen woodland invaded by western juniper: Applications of partial cutting and prescribed fire, 16th International Conference for ecological restoration, August 24-26, Victoria, Canada.

Beck, J. L., J.M. Peek, and E.K. Strand, 2006. Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection, Journal of Wildlife Management 70:283-294.

Bestelmeyer, B.T., J.R. Brown, K.M. Havstad, R. Alexander, G. Chavez, and J.E. Herrick, 2003. Development and use of state-and-transition models for rangelands, Journal of Range Management, 56:114-126.

Breiman, L., J. J. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and Regression Trees. Wadsworth and Brooks Publishing, Monterey, California.

Briske, D.D., S.D. Fuhlendorf, and F.E. Smeins, 2003. Vegetation dynamics on rangelands; a critique of the current paradigms, Journal of Applied Ecology, 40:601-614.

Briske, D.D., S.D. Fuhlendorf, and F.E. Smeins, 2006. A unified framework for assessment and application of ecological thresholds, Rangeland Ecology and Management, 59:225-236.

Brown J.K. and N.V. DeByle 1989. Effects of prescribed fire on biomass and plant succession in western aspen, USDA Forest Service Research Paper INT-412.

Burton D. 2004. Aspen Delineation Project, BLM, U.S. Forest Service, and California Department of Fish. http://www.blm.gov/ca/pa/biology/aspen.html

Campbell, R.B., and D.L. Bartos, 2001. Aspen Ecosystems: Objectives for sustaining biodiversity. p. 299-307, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Chong, G.W., S.E. Simonson, T.J. Stohlgren, and M.A. Kalkhan, 2001. Biodiversity: Apen stands have the lead, but will nonnative species take over?, p. 261-271, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Cosgriff R., V.J. Anderson, and S. Monson, 2004. Restoration of communities dominated by false hellebore, Rangeland Ecology and Management 57:365-370.

Clements, F.E., 1916. Plant succession and the development of vegetation, Carnegie Inst. Washington Pub., 242:1-512.

Dance, B. W. 1961. Leaf and shoot blight of poplars (section *Tacamahaca*) caused by *Venturia populina* (Vuill.) Fabric. Can. J. Bot. 39:875-890.

DAYMET, 1980-1997. Daymet, University of Montana, Numerical Terradynamic Simulation Group, indexed by the Oak Ridge National Laboratory, Distributed Active Archive Center (ORNL DAAC), Accessed July 2004 http://www.daymet.org/

DeByle, N. V. 1985. Wildlife. Pages 135–152 in N. V. DeByle, and R. P. Winokur, editors. Aspen: ecology and management in the western United States. U.S. Forest Service General Technical Report RM-119**.**

DeByle, N.V., C.D. Bevins, and W.C. Fischer. 1987. Wildfire occurrence in aspen in the interior western United States. Western Journal of Applied Forestry 2:73-76.

Despain, D.G. 1990. Yellowstone vegetation: Consequences of environment and history in a natural setting. Roberts Rinehart Publishers, Inc.

ESRI 1999-2005. ArcGIS software v. 9.1. Environmental Systems Research Institute Inc., Redlands, California. Web site: http://www.esri.com.

ESRI 2002. ArcPad software v. 6.0. Environmental Systems Research Institute Inc., Redlands, California. Web site: http://www.esri.com.

Falkowski, M.J., P.E. Gessler, P. Morgan, A.T. Hudak and A.M.S. Smith, 2005. Mapping mixed-conifer forest fire fuels using ASTER imagery and gradient models. Forest Ecology and Management 217: 129-146.

Friedel, M.H., 1991. Range condition assessment and the concept of thresholds: A viewpoint., Journal of Range Management, 44:422-426.

Fu, P. and P.M. Rich, 1999. Design and implementation of the Solar Analyst: an ArcView extension for modeling solar radiation at landscape scales. Proceedings of the 19th Annual ESRI User Conference,San Diego, USA. Accessed May 2004 http://www.fs.fed.us/informs/download.php

Gruell G.E., 1978. Fire's influence on wildlife habitat on the Bridger-Teton National Forest, Wyoming, Volume II – Changes and causes, management implications. USDA Forest Service Research Paper INT-252 Intermountain Forest and Range Experiment Station and Intermountain Region.

Hart, J.H., and D.L. Hart, 2001. Interaction among cervids, fungi, and aspen in northwest Wyoming, p.197-205, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Hessl A. 2002. Aspen, elk, fire: The effects of human institutions on ecosystem processes, Bioscience, 52:1011-1022.

Heide, S.C., 2002. Comparison of methods to detect conifer encroachment into aspen stands using Landsat 7 ETM+ satellite imagery. Masters Thesis. University of Idaho. Moscow, Idaho.

Hermann, R.K. and D.P. Lavender, 1990. Pseudotsuga menziesii (Mirb.) Franco Douglas-fir. *in* Burns, Russell M.; Honkala, Barbara H., (technical coordinators). Silvics of North America. Volume 1. Conifers Agric. Handbook 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 527-540.

Hurvich, C.M, and C-L. Tsai 1989. Regression and time series model selection in small samples. Biometrica 76:297-307.

Iverson, L. R., M. E. Dale, C. T. Scott, A. Prasad. 1997. A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (U.S.A.), Landscape Ecology 12:331-348.

Jones B.W., 1993. The influence of grove size on bird species richness in aspen parklands. Wilson Bulletin 105:256-264.

Jones, R. and N.V. DeByle, 1985. Fire. p. 77-81, *in* DeByle and Winokur (editors) Aspen: Ecology and Management in the Western United States. USDA For. Serv. Gen. Tech. Rep. RM-119.

Kaufmann, M.R., R.T., Graham, D.A. Boyce, and others. 1994. An ecological basis for ecosystem management. General Technical Report RM-246, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft Collins, CO.

Kay, C.E. 1997. Is aspen doomed? Journal of Forestry 95:4-11.

Kay, C.E. and D.L. Bartos. 2000. Ungulate herbivory on Utah aspen: Assessment of long term exclosures. Journal of Range Management 53:145-153.

Kaye, M.W., D. Binkley, and T.J. Stohlgren, 2005. Effects of conifers and elk browsing on quaking aspen forests in the central Rocky Mountains, USA, Ecological Applications, 15:1284-1295.

Kilpatrick, S., D. Clause, and D. Scott, 2003. Aspen response to prescribed fire, mechanical treatments, and ungulate herbivory. USDA Forest Service Proceedings RMRS-P-29.

Kurz, W., S. Beukema, J. Merzenich, M. Arbaugh, S. Schilling, 2000. Long-range modeling of stochastic disturbances and management treatments using VDDT and TELSA. Pages 349-355 *in* Proceedings. Society of American Forests, Bethesda, MD.

Lederer, R.J., 1977. Winter territoriality and foraging behavior of the Townsend's soiliataire, American Midland Naturalist 97:101-109.

Manier, D.J. and R.L. Laven, 2001, Changes in landscape pattern and associated forest succession on the western slope of the Rocky Mountains, Colorado. p. 15-22. Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

McCune, B., J.B. Grace and D.L. Urban, 2002. Analysis of ecological communities. MjM Software Design, Gleneden, Oregon.

Merzenich, J. and L. Frid, 2005. Projecting Landscape Conditions in Southern Utah Using VDDT. *In:* M. Bevers and T.M. Barrett (comps.). 2005. Systems Analysis in Forest Resources: Proceedings of the 2003 Symposium; October 7-9, Stevenson, WA. General Technical Report PNW-GTR-656. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. pp. 157-163.

Miller, R.F. and J.A. Rose, 1995. Historic expansion of *Juniperus occidentalis* in southeastern Oregon. Great Basin Naturalist 55:37-45.

Miller, R.F. and J.R. Rose, 1999. Fire history and western juniper encroachment in sagebrush steppe, Journal of Range Management 62:550-559.

Mitton, B.J., and M.C. Grant, 1996. Genetic variation and the natural history of quaking aspen, Bioscience 46:25-31.

Mueggler, W.F., 1988. Aspen community types of the Intermountain Region. Gen. Tech. Rep. INT-250. Ogden, UT:US Department of Agriculture, Forest service, Intermountain Research Station.

Mueggler, W.F., 1989. Age distribution and reproduction of intermountain aspen stands, Western Journal of Applied Forestry 4:41-45.

Oregon Climate Service, 1999. Precipitation for Idaho: Average Monthly and Annual (1961-90), digital raster data, http://inside.uidaho.edu, University of Idaho Library, Moscow, Idaho

Patterson, A.E., 1959. Distinguishing annual rings of diffuse porous tree species, Journal of Forestry 57:126.

Pielou, E.C., 1991. After the ice age: The return of life to glaciated North America, p. 168, The University of Chicago Press, Chicago.

Prevost, M., and D. Pothier, 2002. Partial cuts in trembling aspen – conifer stand: effects on microenvironmental conditions and regeneration dynamics, Canadian Journal of Forest Research 33:1-15.

Ratkowsky, D.A.1990. Handbook of nonlinear regression models. Marcel Dekker, New York.

Romme, W.H., L. Floyd-Hanna, D.D. Hanna, and E. Bartlett, 2001. Aspen's ecological role in the West, p. 243-259, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Roth, A., 2004. Fire patterns within a successional gradient of a sagebrush steppe/juniper woodland, Dissertation, University of Idaho, Moscow, Idaho, USA.

Rumble, M.A., L.D. Flake, T.R. Mills, and B.L. Dykstra, 2001. Do pine trees in aspen stands increase bird diversity?, p. 185-191, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

SAS 2005. Version 9.1.3. SAS System for Windows. SAS Institute Inc. Cary, N.C.

Schier, G.A., W.D. Shepperd, J.R. Jones, 1985. Regeneration. *in* DeByle, Norbert V.; Winokur, Robert P., eds. Aspen: ecology and management in the western United States. Gen. Tech. Rep. RM-119. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 197-208.

Shepperd, W.D., 2001. Manipulations to regenerate aspen ecosystems. p. 355-365. Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Shepperd, W.D., D.L. Bartos, and S.A. Mata, 2001. Above-and below-ground effects of aspen clonal regeneration and succession to conifers, Canadian Journal of Forest Research, 31:739-745.

Shirley, D.M. and V. Erickson, 2001. Apen restoration in the Blue Mountains of northeast Oregon, p.101-115, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Smith, A.E. and F.W. Smith. 2005. Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA, Forest Ecology and Management, 213: 338-348.

SYSTAT 2004. SYSTAT Software Inc. version 11, Richmond, California, USA.

Tarboton, David G. 1997. A new method for the determination of flow directions and upslope areas in grid digital elevation models. Water Resources Research. 33:309-319.

United States Department of Agriculture Farm Service Agency Aerial Photography Field Office (USDA-FSA-APFO), 2004. Digital Ortho Image Western Owyhee County, Idaho. National Agriculture Imagery Program (NAIP), Salt Lake City, Utah. On line: http://insideidaho.org/data/USDA/archive/DOICCM2004_owyheewest_usda.tgz

USDA – NRCS, 1998. Owyhee County digital soil survey, SSURGO, Natural Resources Conservation Service, U.S. Department of Agriculture. On line: http://www.ncgc.nrcs.usda.gov/branch/ssb/products/ssurgo/

USGS, 1999. National Elevation Data, U.S. Geological Survey (USGS), EROS Data Center, National Elevation Dataset, *Edition:* 1, Sioux Falls, SD, Accessed May 2004 at http://seamless.usgs.gov.

VDDT, 2003. Vegetation Dynamics Development Tool, Version 4.4b, ESSA Technologies Ltd., Vancouver, B.C., Canada.

Wall, T.G., R.F. Miller, and T.J. Svejcar, 2001. Juniper encroachment into aspen in the Northwest Great Basin, Journal of Range Management, 54:691-698.

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

Wilson E.O. 1992. The diversity of life. New York: W.W. Norton and Company. 424 p.

Winternitz, B.L., 1980. Birds in aspen. Management of western forests and grasslands for nongame birds. USDA Forest Service General Technical Report INT-86. Intermountain Forest and Range Experiment Station, Ogden, UT.

Woodley, S.J., 1993. Kay, J. and G. Francis, editors. Ecological integrity and the management of ecosystems. St. Lucie Press, Del Ray Beach, FL.

Yang Z., W.B. Cohen, and M.E. Harmon, 2005. Modeling early forest succession following clear-cutting in western Oregon, Canadian Journal of Forest Research 35:1889-1900.

Tables

Table 1. Potential stand and landscape variables affecting successional rates in aspen stands.

Variable type	Variable (abbreviation in model)		Source
Stand	Age of oldest conifer in stand	(age)	Field data
	PVT (Douglas-fir or juniper)	(PVT)	Field variable
Climate	Average annual precipitation	(prec)	Daymet, 1980-1997
	Growing degree-days	(gdd)	Daymet, 1980-1997
	Average high July temp.	(tmax)	Daymet, 1980-1997
	Average low January temp.	(tmin)	Daymet, 1980-1997
	# of frost free days	(ffd)	Daymet, 1980-1997
Terrain	Elevation	(ele)	USGS 1999
	Solar insolation	(sol)	Fu and Rich 1999
	Landscape curvature	(curv)	DEM+Tarboton 1997
Soil	Water holding capacity	(whc)	USDA-NRCS 1998
	Organic matter	(om)	USDA-NRCS 1998

Table 2. Potential variables affecting aspen regeneration.

Variable	Variable type	Range
Conifer level	Continuous	0 to 1
Browsing	Continuous	0-100%
Stand age	Continuous	20-143 years
Elevation	Continuous	1721-2186 m
Logging	Discrete	yes or no
Fire scars	Discrete	yes or no
Wet microsite	Discrete	yes or no
PVT	Discrete	aspen, aspen/Douglas-fir or aspen/western juniper

Table 3. Characteristics of aspen stands at risk (following Bartos and Campbell 1998).

Risk factor	Pure aspen stands (12 stands)	Aspen/Douglas-fir (36 stands)	Aspen/juniper (32 stands)
Conifer > 25% cover	0	10	8
Aspen cover < 40%	0	13	11
Regeneration < 1200 stems/ha	4	26	25
Total at risk	4	28	27

Table 4. Distribution of sampled mixed aspen/conifer stands with different site characteristics.

Stand characteristic	Aspen/Douglas-fir (36 stands)	Aspen/western juniper (32 stands)
Logging	6	0
Fire scars	7	10
Microsites (springs, meadows)	7	6
Upland stands, no disturbance	17	16
Total	36	32

Table 5. Model selection for successional rates including the number of observations (n), number of model parameters (k), r-square, Akaike's information criterion for small sample sizes and delta AICc.

Model	n	k	R^2	AICc	Delta AICc
age	28	4	0.63	-18.1	0
age, ffd	28	5	0.65	-17.1	1.0
age, tmin	28	5	0.65	-16.9	1.2
age, prec, PVT	28	6	0.69	-16.7	1.4
age, prec	28	5	0.64	-16.3	1.8

Figures

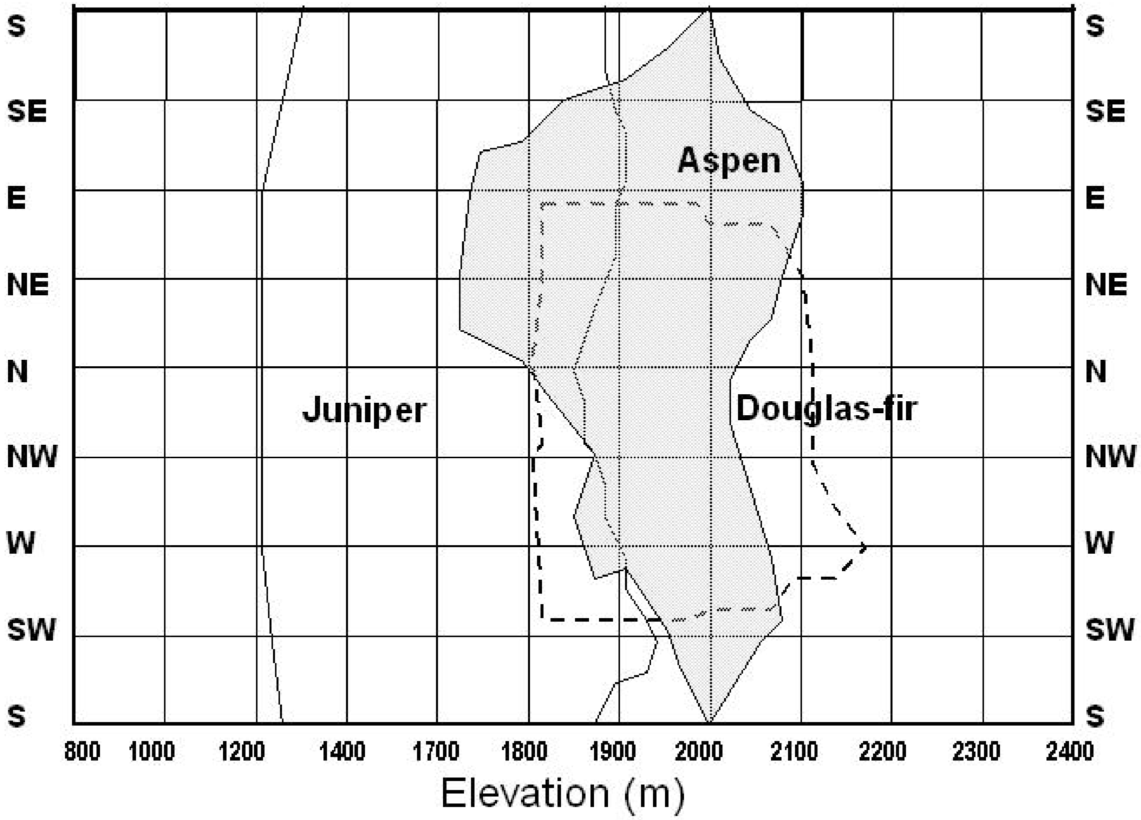


Figure 1. Distribution of aspen, Douglas-fir and western juniper with respect to elevation and aspect. Pure aspen stands exist in a niche at elevations above 1900 m on south-facing aspects.

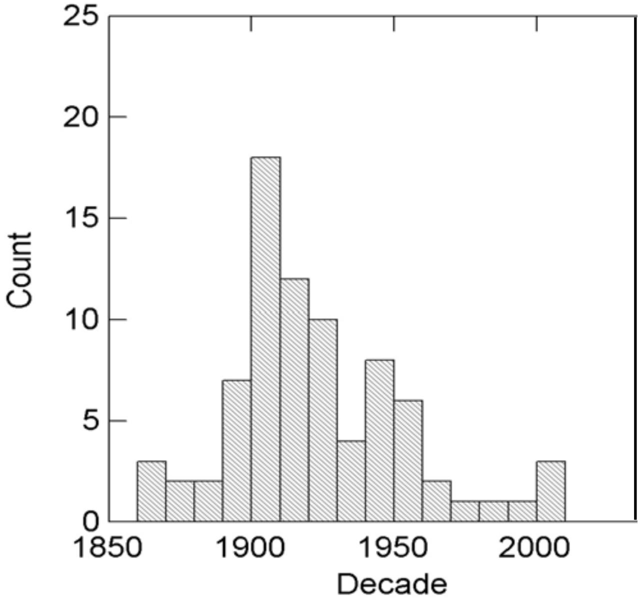


Figure 2. Decade of establishment for the oldest trees in the sampled aspen stands.

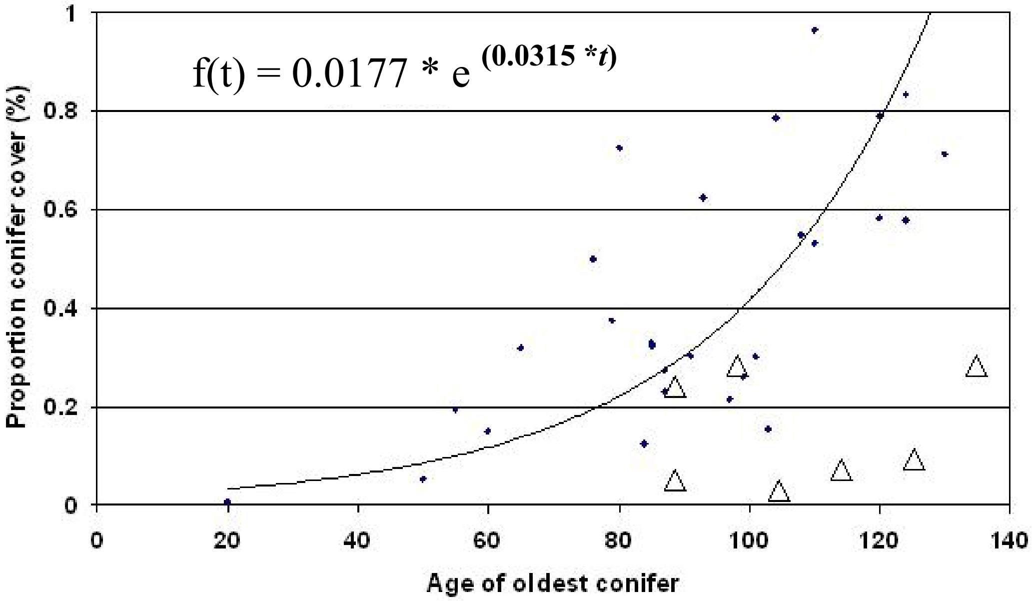


Figure 3. Successional rates in upland aspen/conifer stands. The conifer cover begins to increase exponentially after 50-60 years, at the onset of prolific seed production for both Douglas-fir and western juniper. The triangles represent stands on microsites experiencing significantly slower successional rates.

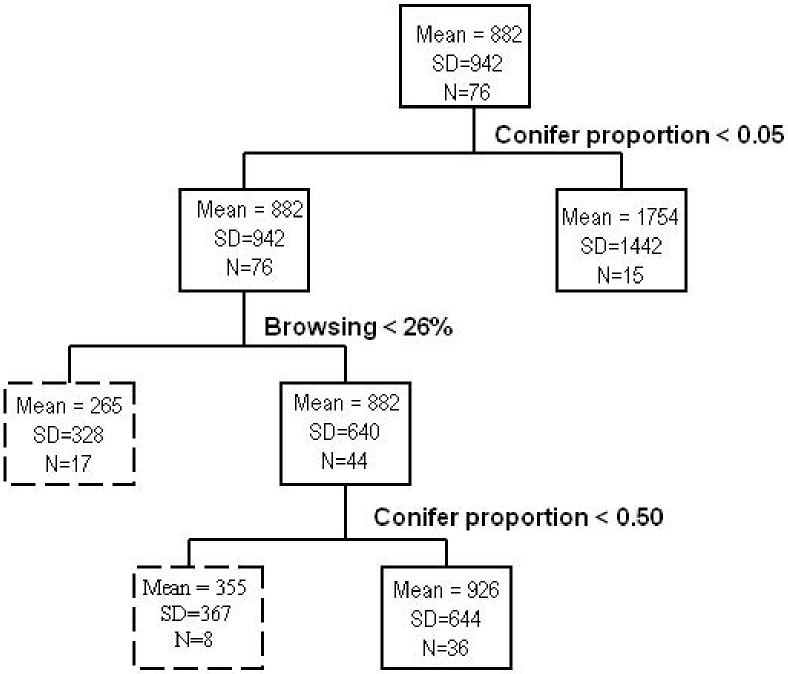


Figure 4. Classification and regression tree analysis show that the proportion conifer in the stand and the level of browsing are the most important variables affecting aspen regeneration. *Mean* here refer to aspen regeneration in stems per hectare.

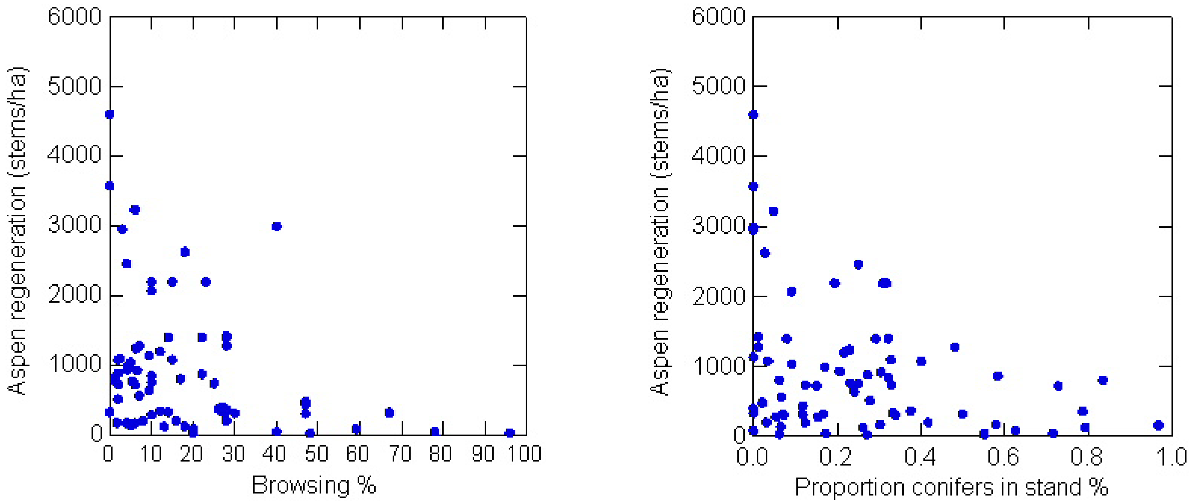


Figure 5. Aspen regeneration graphed against browsing and conifer encroachment levels.

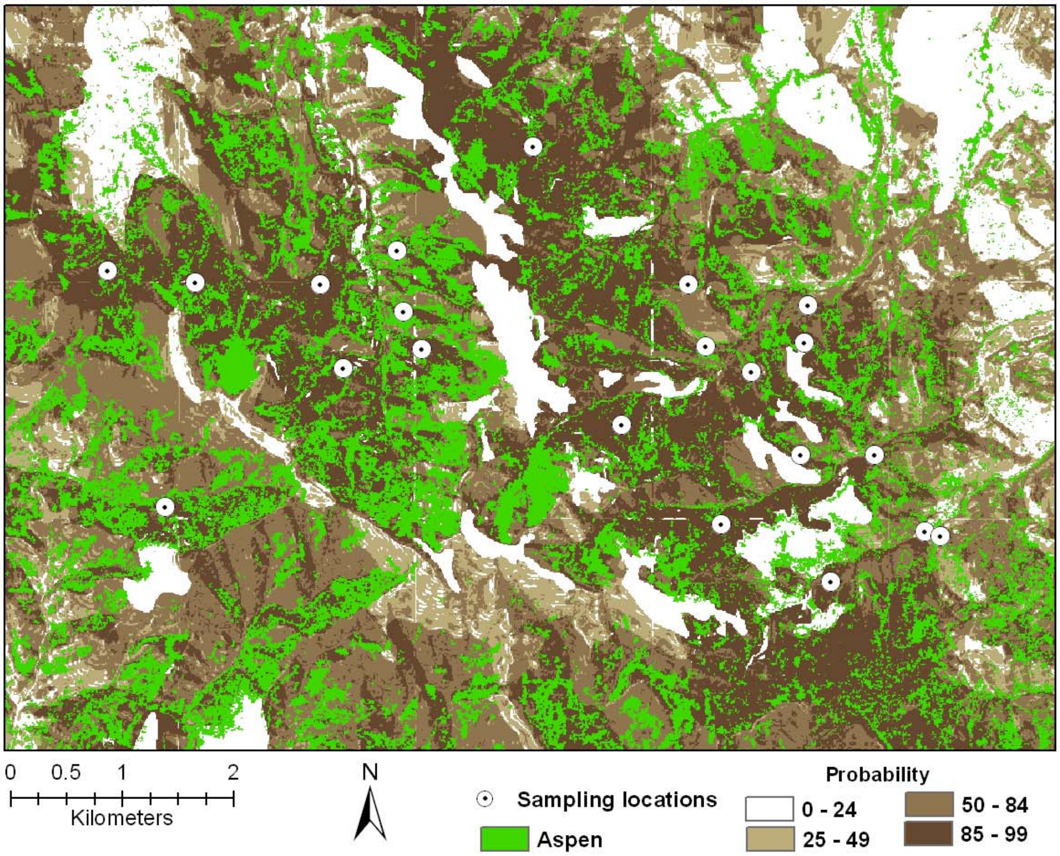
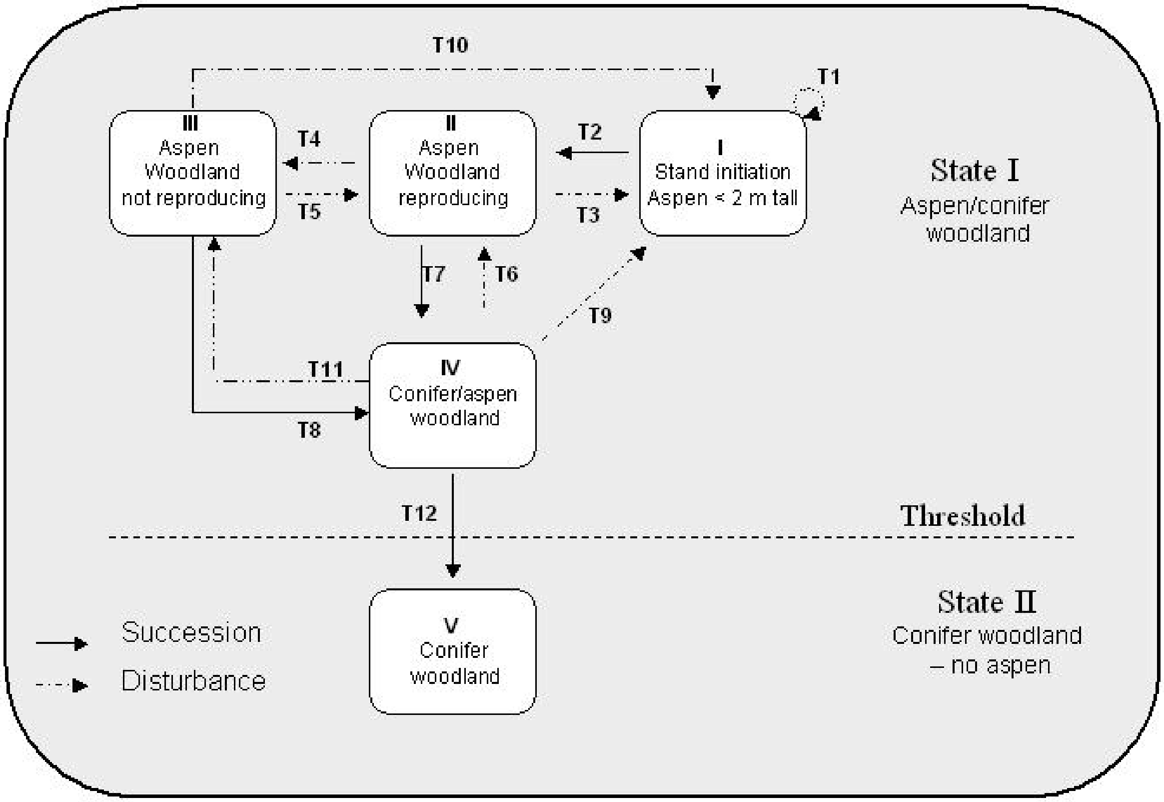


Figure 6. Predicted aspen occurrence probability overlayed with aspen stands mapped from remotely sensed imagery for the South Mountain area. Areas of high aspen probability yet lacking live aspen cover were field checked for remnant aspen stands.



Transition 1 (T1): *Stand initiation aspen to Stand initiation aspen*. Excessive browsing pressure, disease or frequent fires do not allow for aspen suckers to grow to mature trees, the stand is maintained in the stand initiation phase.

Transition 2 (T2): *Stand initiation aspen to Aspen woodland*. Lack of fire, disease, and/or excessive browsing allows succession to proceed and stand initiation aspen grows into an aspen woodland, often the desired phase.

Transition 3 (T3): *Aspen woodland to Stand initiation aspen*. Natural or prescribed fire will return young or mature aspen woodlands to stand initiation aspen. Clear-felling or disease can also return the stand to a stand initiation stage.

Transition 4 (T4): *Aspen woodland to non-regenerating aspen woodlands*. Aspen ramets may be very old and the production of the sucker inhibiting hormone auxin is high. The browsing pressure may be excessive with over 20-30% of the terminal leaders browsed. Disease such as leaf blight (*Venturia*) may continuously affect the young shoots and prohibit regeneration (Dance, 1961). Negative effects of climate-change could also cause this transition. This transition is not caused by conifer dominance (phase III does not have a dominant conifer component).

Transition 5 (T5): *Non-regenerating aspen woodland to-regenerating aspen woodland*. Reduced browsing pressure. Mechanical treatment that disturbs the auxin/cytokinine hormone balance to improve suckering and exposes the forest floor to more light (Shepperd, 2001). If climate change is the problem recovery is not likely.

Transition 6 (T6): *Conifer/aspen woodland to Aspen woodland*. Mechanical removal of conifers, particularly those producing seeds.

Transition 7 (T7): *Aspen woodland to Conifer/aspen woodland*. Conifers in the stand have reached a seed producing age and will rapidly begin to dominate the aspen stand.

Transition 8 (T8): *Aspen woodland (not reproducing) to Conifer/aspen woodland.* Conifers in the stand have reached a seed producing age and will rapidly begin to dominate the stand.

Transition 9 (T9): *Conifer/aspen woodland to Stand initiation aspen*. Natural or prescribed fire will return young or mature aspen woodlands to stand initiation aspen. Clear-felling or a land-slide will also return the stand to a stand initiation stage.

Transition 10 (T10): *Aspen/conifer woodland (not reproducing) to Stand initiation aspen*. Natural or prescribed fire will return aspen woodlands to stand initiation aspen unless the reason for the lack of aspen regeneration is climate change. Clear-felling may also return the stand to a stand initiation stage if the reason for the lack of aspen regeneration is excessive auxin production.

Transition 11 (T11): *Conifer/aspen woodland to Non-regenerating aspen woodland*. Mechanical removal of conifers in an attempt to increase aspen reproduction. Aspen reproduction may not increase due to other disturbances such as excessive browsing or high auxin levels in the live aspen ramets

Transition 12 (T12): *Confer/aspen woodland to Conifer woodland*. Continued conifer dominance and lack of aspen regeneration leads to an irreversible conversion of the aspen stand to a conifer stand.

Figure 7. Conceptual state-and-transition model for aspen/conifer woodlands, with narrative description of transitions present in model.

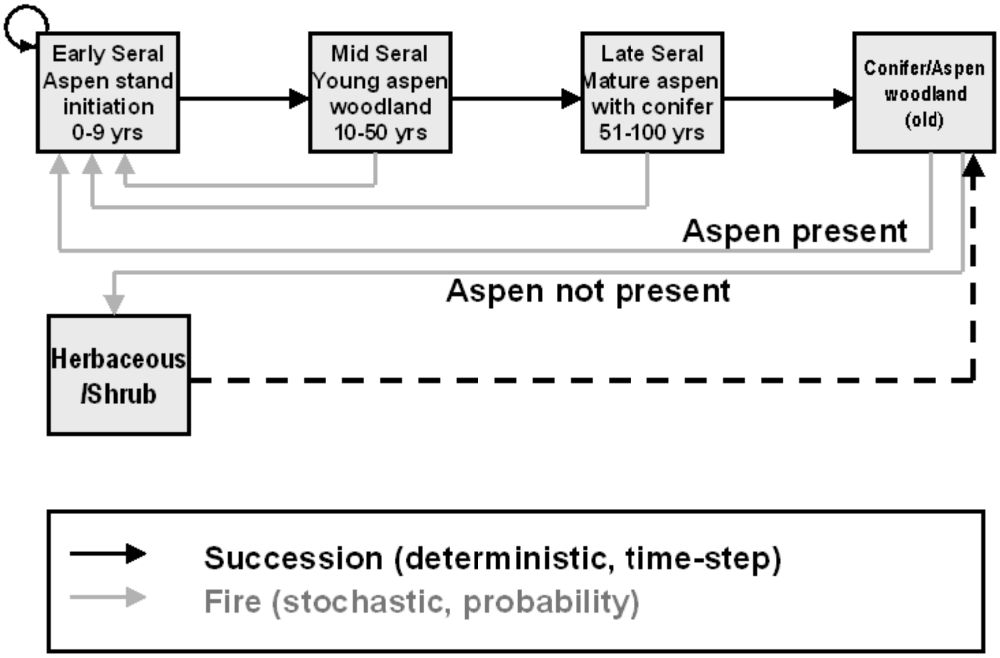


Figure 8. Simplified VDDT pathway diagram for the upland aspen/conifer communities in the Owyhee Mountains.

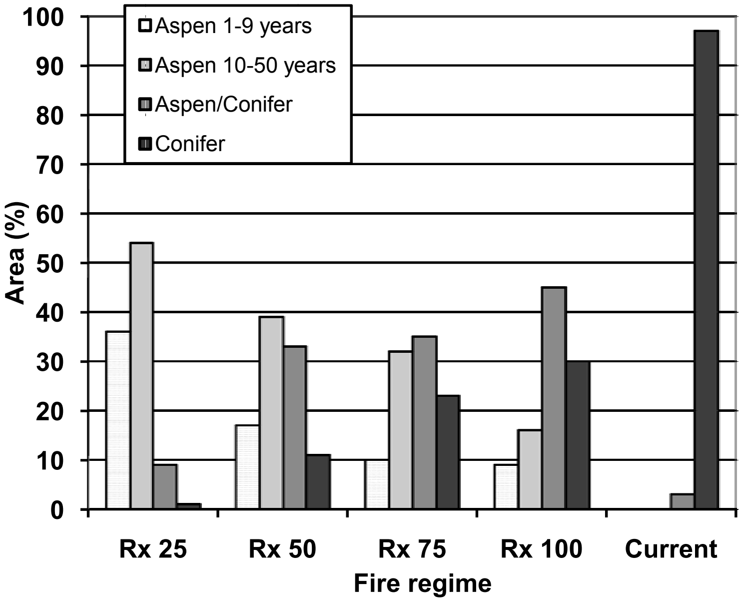


Figure 9. Age class distribution of upland aspen in different seral stages under a variety of modeled fire regimes.

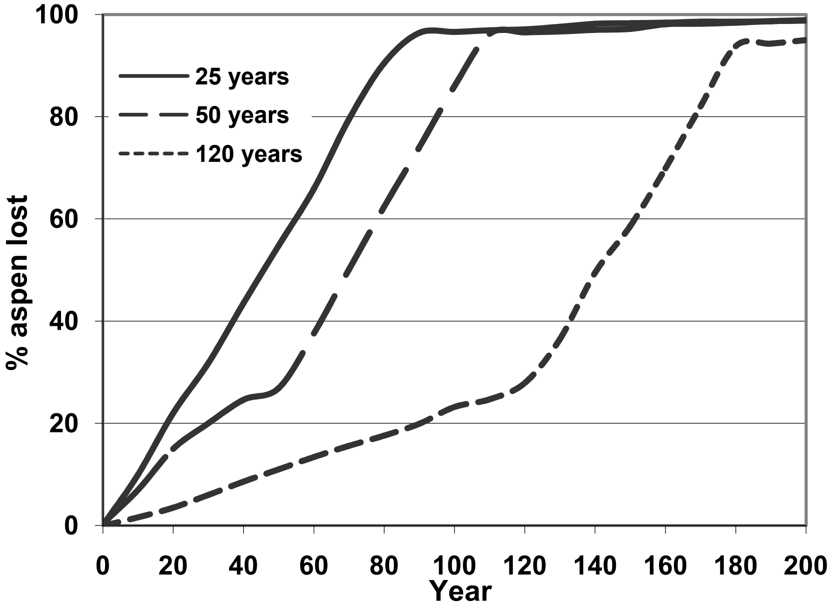


Figure 10. Upland aspen/conifer stands lost due to conifer encroachment over time under three different assumptions at the current fire regime: aspen can sustain in a non-regenerating state for 25, 50, or 120 years and still return to an aspen habitat type after a disturbance.

CHAPTER 5: Landscape Composition in Aspen Woodlands under various Modeled Management Scenarios

Abstract

Quaking aspen (*Populus tremuloides* Michx.) is declining across the intermountain western United States. Aspen habitats are among the most diverse plant communities in this region and loss of these habitats can result in landscape level ecosystem changes affecting watershed, biodiversity, and productivity. Western aspen is on the majority of sites seral to conifer species and long-term maintenance of these woodlands requires periodic fire. Over the past century fire intervals, extents, and intensities have been insufficient to regenerate aspen stands at historic rates, which has led to the aspen decline observed today. Although it is well known that fire rejuvenates aging aspen stands by promoting rapid regeneration, the effects of various fire regimes and management scenarios on aspen vegetation dynamics at broad spatial and temporal scales are unexplored. Here we assess the effects of current and historic wildfire regimes and prescribed burning programs on landscape vegetation composition within two mountain ranges in the Owyhee Mountains, Idaho, by using the Tool for Exploratory Landscape Analyses (TELSA), a spatially explicit landscape simulation framework. Model inputs are derived from a combination of field collected and remotely sensed data combined with local fire atlas information. Model outputs depict the structural landscape composition at selected time steps into the future under simulated management scenarios. Model results indicate that under current fire regimes and in the absence of management activities, loss of seral aspen stands will continue to occur over the next centuries. Historic fire regimes burning 12-14% of the modeled landscape per decade maintained, and would maintain into the future, the majority of aspen stands in early and mid seral woodland stages and minimize the loss of aspen. A fire rotation of 70-80 years was estimated for the historic fire regime while the current fire regime resulted in a fire rotation of 340-450 years, underscoring the current lack of fire in the system. Implementation of prescribed burning programs, treating aspen and young conifer woodlands according to historic fire occurrence probabilities, are predicted to prevent conifer dominance and loss of aspen stands.

KEYWORDS: Successional model, landscape dynamics, TELSA, VDDT, fire regimes, prescribed fire

1. Introduction

Population decline of quaking aspen (*Populus tremuloides*) across the intermountain western United States has caused concerns that the human alteration of succession and disturbance dynamics in this region are jeopardizing the long-term persistence of these woodlands (Kay 1997, Bartos 2001, Shepperd et al. 2001, Smith and Smith 2005). Aspen is a critical component of ecosystem diversity in the conifer dominated western mountains and provides a disproportionately diverse array of habitats for flora and fauna relative to its area proportion of the landscape cover (Winternitz 1980, Jones 1993, Kay 1997, Bartos 2001, Chong et al. 2001, Rumble et al. 2001). In the semi-arid West aspen commonly occurs as a disturbance dependent pioneer, seral to conifer species (Bartos 2001, Kaye et al. 2005, Smith and Smith 2005). It is well established that in mixed aspen/conifer stands periodic fires are necessary to prevent conifer dominance and possible loss of the aspen stand (Baker 1925, Bartos and Mueggler 1981, DeByle et al.1987). Aspen clones in the region reproduce primarily via vegetative suckering. Although quaking aspen is a prolific seed producer, the conditions required for successful germination and establishment are rare in the West (Mitton and Grant, 1996). An example of recent successful establishments of aspen seedlings followed the severe fires in Yellowstone in 1988 (Romme et al. 2005). All aspen stands are not seral to conifers. Aspen stands in certain biophysical settings and away from a conifer seed source have been observed to exist as self-regenerating uneven aged stands that do not appear to be at risk of rapid decline even in the absence of fire (Mueggler 1989, Romme et al. 2001, Strand 2007).

Although successional rates within pure and mixed aspen stands and interactions with fire and herbivory have been studied at the stand level there is a need for better understanding of these dynamics at the landscape scale over decadal time periods. Computer simulation models may be a means to better understanding of these dynamics in aspen landscapes. Early vegetation dynamics models were limited to applications at the stand level, for example the forest 'gap' models of the JABOWA family (Botkin et al. 1972), the individual tree model FOREST (Ek and Monserud 1974) and later spatially explicit stand level tree models such as SORTIE (Pacala et al. 1993). Due to the limited simulation extent (< 0.1-10 ha) these models focused on succession rather than disturbance. Models capable of simulating landscape change incorporating both succession and disturbance processes have evolved over the last 15 years (Mladenoff 2004), enabled by recent developments in landscape ecology, the availability of remotely sensed imagery, development of image processing techniques, and the improved computer power within geographic information systems (GIS).

Landscape scale succession-disturbance models are important tools in evaluation of habitat patterns in forests (Klenner et al. 2000) and assessment of fire regimes and management scenarios (Keane et al. 1997, Franklin et al. 2001, Bunting et al. 2005). The Tool for Exploratory Landscape Analyses, TELSA, (Essa Technology 2003) is a spatially explicit landscape dynamics model environment, allowing the user to explore the effect of natural and anthropogenic disturbances on landscape composition. Input data to this model are landscape units, potential natural plant communities, and initial vegetation types and structural stages, along with natural and management disturbance agents and pathways. Succession is treated as a deterministic variable with a constant pre-determined time period between successional states. Disturbance is a stochastic variable driven by user-defined probabilities. This stochastic component in landscape models results in many possible landscape configurations given the same input variables, allowing the range of variability in landscape composition to be explored and treated in statistically meaningful ways. TELSA interfaces with a GIS for input and output of data.

Modeling of structural landscape composition through time is challenging because of many interacting factors such as successional rates, disturbance regimes, disturbance agents and management activities. It can be helpful to begin the modeling effort by developing a conceptual model of the ecosystem. Strand (2007) developed such a conceptual state-and-transition model for upland western aspen in mixed aspen/conifer stands. The state-and-transition model describes vegetation states of aspen along the aspen-conifer successional gradient, e.g. stand initiation, young and mature woodlands and conifer dominated woodlands. These states are connected by transitional pathways, where natural disturbance or management action enables transitions among states. The conceptual model was implemented in the vegetation dynamics computer simulation model VDDT (Kurz et al. 2000, Essa Technology 2003b, Merzenich and Frid 2005) and parameterized with successional rates determined via field analysis of aspen stands along a successional gradient in the Owyhee Mountains, Idaho (Strand 2007). Although VDDT is a landscape scale computer simulation model with the capability of estimating landscape proportion within vegetation types and structural stages at user defined disturbance probabilities and pathways, the model is not spatially explicit and does not incorporate disturbance (fire) spread between landcover types adjacent to each other nor the effect of disturbance size on landscape composition. To compensate for these shortcomings the VDDT models can be transferred to the spatially explicit simulation tool TELSA, which is developed to directly interface with both GIS and VDDT.

In this paper we demonstrate the utility of spatially explicit modeling to enhance our understanding and estimate the effects of current and historic fire regimes on landscape vegetation composition and structure, with a particular emphasis on aspen woodland dynamics. In addition, although prescribed fire has been suggested and applied as a means of mitigating the frequent fire events common in the western mountains of the past with the goal of maintaining and restoring aspen woodlands (Brown and DeByle 1989, Shepperd 2001, Bates et al. 2004, Miller et al. 2005), little is known about how such management affect the vegetation composition and structure spatially at a landscape scale through time. We therefore also incorporated prescribed burning scenarios into our modeling runs. In particular, we intend to address the following research questions:

Q I. Can the historic fire regime required to maintain aspen stands prior to European settlement be simulated in the TELSA modeling environment?

Q II. What extent and frequency of fire (burned area per decade) is required to stabilize the current land cover composition within aspen woodlands?

Q III. What is the structural composition of aspen woodlands under historic and current fire occurrence probabilities? What is the structural composition under prescribed burning scenarios?

Q IV. What is the effect of fire size on the long-term maintenance of aspen woodlands?

This study is a part of a larger body of research working towards a more holistic understanding of the historic, current, and future vegetation dynamics in the semi-arid mountains of southwestern Idaho (Strand 2007).

2. Methods

2.1. Site Description

We selected the South Mountain and the Silver City mountain ranges because they contain vegetation communities representative of many mountain ranges of the Intermountain West for analysis. The South Mountain study area encompass 17,000 ha and the Silver City Range 20,000 ha and both occur on the Owyhee Plateau of southwestern Idaho (116° W, 43° N). Western juniper woodlands (*Juniperus occidentalis* ssp. *occidentalis*) and sagebrush (*Artemisia* spp.) steppe interspersed with pockets of aspen, mountain shrub species, and wet meadows comprise the landscape at altitudes above 1700 m. Common mountain shrub species are shiny-leaf ceanothus (*Ceanothus veluntinus*), mountain snowberry (*Symphoricarpos oreophilus*), bittercherry (*Prunus emarginata*), and chokecherry (*Prunus virginiana*). Western juniper is the dominant conifer species in the area but is gradually replaced by Douglas-fir (*Pseudotsuga menziesii* ssp. *glauca)* starting at 1850 m elevation in both mountain ranges. Douglas-fir is replaced by subalpine fir (*Abies lasiocarpa*) above 2400 m in the Silver City Range. Understory vegetation is composed of annual and perennial forbs and perennial grasses. Common grass species are mountain brome (*Bromus carinatus*), pinegrass (*Calamagrostis rubesence*), and bluegrass (*Poa* spp.) while common perennial forbs are sweet-cicely (*Osmoriza* spp.), Western meadow-rue (*Thalictrum occidentale*), nettleleaf horsemint (*Agastache urticifolia*), groundseal (*Senecio* spp.) and viola (*Viola* spp.). Annual forbs such as bedstraw (*Galium boreale*) and blue-eyed Mary (*Collinsia parvaflorum)* are common in many stands while annual grasses are rare. Aspen stands are commonly located on cool northeast facing hill slopes, in concave snow and moisture accumulation areas on deep fine-loamy and loamy-skeletal mixed pachic or typic cryoborol soils with high water-holding capacity that are rich in organic material (USDA 1998). Aspen occurs in three distinctly different biophysical settings with different successional trajectories and rates; pure aspen on south-facing aspects above 1900 m, aspen on wet micro sites and aspen/conifer stands on mountain hillsides (Strand 2007). The climates in areas that support aspen receive 400-1000 mm annual precipitation (Oregon Climate Service 1999) in the form of rain in the spring and fall, and snow during the winter months. The summer and early fall in the Owyhee Mountains are warm and dry.

European settlement in the area began in the 1860's when silver and other minerals were discovered in the Silver City range. Minerals were also mined around South Mountain in the late 1800's, however, never at the scale of Sliver City (Conway-Welch 1982). During the mining boom, the mountains around Silver City were cleared of wood for use in the mines and for fire wood. Silver City, like many towns in the West, quickly went from 'boom to bust' and by 1920 its population had dropped to levels such that many of the original woodlands could re-grow due to decreased wood demands. Both mountain ranges have a history of sheep and cattle grazing beginning as early as the 1860's.

Today the majority of this land is in public stewardship managed by the Bureau of Land Management, interspersed with a few private cattle ranches and state parcels. Summer recreation, camping, fishing and hunting attract a limited number of visitors each season. Aspen stands supply forage during the summer for the local native ungulates, elk (*Cervus elaphus*) and deer (*Odocileus spp.*), and for domestic livestock, however the winter range is located at a lower elevation where aspen is restricted to riparian areas.

2.2 Field data collection

A total of 82 aspen clones along elevational and succesional gradients were sampled across the study areas on South Mountain and in the Silver City Range. Within each clone we collected site characteristic information: slope, elevation, aspect, and UTM coordinates. We further collected stand characteristics: canopy cover of aspen and conifers in the crown and below 2-m height, increment cores from the five oldest aspen and conifer trees, stem counts of aspen and conifers in three height classes (< 2 m, 2 m up to 75% of the stand height, and trees taller than 75% of the stand height) and a list of the six major vegetative species based on foliar coverage. The increment cores were mounted and sanded and the annual growth rings were counted in a stereo-microscope for the age estimate. For a more detailed description of the field data collection refer to Strand (2007).

2.3. Model requirements and assumptions

Spatially explicit simulations in TELSA require spatially explicit information in the form of GIS data layers (digital maps) of the study area. Each landscape unit in the map must be classified hierarchically in a potential vegetation type (PVT), current cover type and current structural class. PVTs are groupings of habitat types or ecological sites with similar overstory composition in the absence of a disturbance and similar environmental requirements. For the sagebrush steppe/juniper woodlands we employed the PVT classification developed by Bunting et al. (2005) in the same general study area. Aspen woodlands were potentially present in three PVTs (Strand 2007): Pure aspen, aspen/western juniper, and aspen/Douglas-fir. In the simulation, aspen stands on pure aspen PVTs represent stands, which can be expected to self-regenerate and persist as uneven aged aspen stands for decades to come. Over time aspen on aspen/western juniper and aspen/Douglas-fir PVTs are assumed to become dominated by western juniper and Douglas-fir, respectively, and in the absence of a disturbance within a certain time period will be permanently converted to conifer stands. Aspen/conifer stands that burn before they are permanently converted to conifer stands are assumed to return to stand initiation aspen stands (Figure 1).

Each landscape unit is characterized by its PVT, but also by the current cover and structure. The current cover map represents the vegetation currently present on the ground and includes the climax vegetation classes represented by the PVTs with the addition of seral cover types such as grasslands, shrublands, and initiation woodlands. The structural classes within aspen succession include: stand initiation aspen, young aspen woodlands, mature aspen woodlands, aspen woodlands with conifers and conifer woodlands. Within the successional sequence (Figure 1), transition from one successional stage to the next occurs within a pre-determined time period. The length of time that aspen stays in each successional stage on this study site, was previously suggested by Strand (2007). Each PVT is composed of a similar sequence of cover and structural classes. For the sagebrush/juniper PVTs we used successional models developed by Bunting et al. (2005).

In general we make the assumption that PVTs are static, and consequently a landscape unit occupied by a PVT at the beginning of the simulation will stay within that PVT throughout the simulation. The land cover and structural vegetation stage within the landscape unit may change via the successional time step or revert to an earlier seral stage via a disturbance (i.e. fire). This static view of PVT works well in most ecosystems within reasonable time periods. In the aspen ecosystem, however, this static view is limited for two reasons. First**,** aspen has been observed to expand into adjacent areas with low canopy cover such as grasslands and sagebrush steppe. Such expansion of aspen clones was observed during field assessments and has also been reported by other researchers (Manier and Laven 2001). To accurately estimate the rate of aspen expansion into adjacent cover types, we recorded the decrease of aspen stem age along four transects perpendicular to the aspen/sagebrush steppe ecotone during the 2006 field season in the nearby Jarbidge Mountains. We here make the assumption that the aspen expansion rates are similar in the Jarbidge and Owyhee mountains as the two mountain ranges are located at similar latitudes and altitudes. Expansion of aspen could not be incorporated directly in the TELSA simulations but upper limits of aspen expansion were estimated based on expansion rates and the length of currently available aspen/sagebrush edge. Second, it is currently not known how long and under what conditions an aspen clone can persist after conifers dominate a site. It has been suggested that aspen clones can be sustained for decades in the absence of mature ramets nurtured only by transient suckers (Despain 1990). This hypothesis has not yet been tested (Hessl 2002); and we here assume that old mixed aspen/conifer stands permanently transition to conifer stands 120 years after aspen regeneration has diminished due to conifer dominance within a stand (Strand 2007). In such stands we do not expect a fire event to return the landscape unit to young aspen woodland but rather to young conifer woodlands, resulting in permanent loss of aspen within the landscape unit.

The current wildfire size distribution was calculated from a fire database provided by the Interior Columbia Basin Ecosystem Management Project (http://www.icbemp.gov/) for the interior Columbia River basin 1986-1992. The maximum allowable area burned in prescribed fires was set to 1000 ha per year in scenarios that included prescribed fire.

Current wildfire probability of occurrence in each PVT and structural stage was computed from an overlay analysis in a GIS (ESRI 1999-2005) of digital fire atlas data from 1957-2002 and a recently developed landcover map for the Owyhee Plateau (Roth 2004). Historic wildfire probabilities were estimated based on the 20-60 year fire interval suggested by Jones and DeByle (1985a) for aspen woodland with increasing fire probability later in succession where flammable confers are present. The fire occurrence probability for initiation juniper woodlands is estimated from the 40-50 year mean fire return interval suggested by Burkhardt and Tisdale (1976). As western juniper woodlands mature there is a decrease in understory productivity resulting in lower amounts of fine fuels and a reduced ability to carry fire in these older woodlands (Miller and Rose 1999, Bunting et al. 2005, Miller et al. 2005). For mid- and late seral juniper woodlands we used the same fire occurrence probabilities as those used by Bunting et al. (2005).

During the TELSA run, fires start in random locations according to the assigned probability. A fire that starts in a landscape unit may spread into an adjacent landscape unit if that unit is eligible for fire disturbance. The size of wildfires and prescribed fires were randomly assigned to each fire based on the pre-defined fire size probability distribution.

Six major assumptions and simplifications relating to aspen ecology and succession are important parts of this model. They are:

1) Aspen reproduction from seed is not included in this model.
2) Aspen is not allowed to spread laterally into other potential vegetation types in the absence of a disturbance.
3) Adjacency between vegetation types does not affect succession.
4) Fire will convert a conifer dominated aspen stand to an aspen dominated stand initiation structural stage regardless of the pre-disturbance conifer cover in the stand, i.e. no legacy effects are considered.
5) Aspen stands are permanently converted to conifer stands 120 years after aspen suckering has ceased due to conifer dominance (i.e. ~230 years after conifer initiation into the stand).
6) Insects, disease, and animal use affecting aspen and conifers are not included in this model.

These assumptions and simplifications and the effect they may have on the model outcome and interpretation are discussed in *section 4.2*.

2.4. Classification of potential vegetation types (PVT)

The digital Owyhee County soil survey (USDA 1998) provides a description of the potential vegetation for each mapped soil unit. In many instances several potential vegetation types occur within the same soil unit, for example aspen woodlands on north facing slopes and juniper woodlands or sagebrush steppe on south facing slopes. In such cases a digital elevation model (USGS 1999) and spatial overlay analysis in a GIS was used to separate the soil polygon into two PVTs. Decision rules developed by Strand (2007) were then applied as follows:

- Aspen occurring on south facing slopes at elevations > 1900 m were classified as aspen woodland PVT in which aspen will remain in self-regenerating uneven aged stands without encroachment from conifers.
- Aspen above 1850 m were classified into an aspen/Douglas-fir PVT where the potential vegetation is Douglas-fir in the absence of a disturbance.
- Aspen below 1850 m were classified into an aspen/western juniper PVT where the potential vegetation is western juniper in the absence of a disturbance.

2.5. Classification of current cover type

Broad land cover classes were classified via a maximum likelihood supervised classification procedure of a Landsat 7 Enhanced Thematic Mapper Plus (ETM+) image from August 2002, using the ERDAS Imagine image processing software (Leica Geosystems 1991-2003). Image preprocessing included conversion of the band digital numbers to spectral reflectance values using the biases, gains, and esun values specific to this image followed by an atmospheric correction according to the dark body subtraction method. Training data for the classification was obtained from previous studies in the Owyhee Mountains (Bunting et al. 1999, Yanish 2002, Roth et al. 2004, Strand 2007). Altogether over 1000 ground reference plots were included of which 120 were pure and mixed aspen stands. The ground reference locations were recorded using Garmin Map 76, Garmin Etrex and Trimble GeoXT GPS units. Polygons were drawn around these training areas and pixels within the polygons were randomly selected for the map validation process. Seventy-five percent of the ground reference plots were used for the classification and the remaining plots were used for an independent accuracy assessment. An error matrix, where mapped pixels are compared to ground verified areas for each mapped vegetation type, was created for both the PVT and the cover type classifications (Congalton 1991). Over-all accuracy, omission and commission errors and user's and producer's accuracy was computed according to methods outlined by Jensen (1996).

2.6. Classification of mixed aspen-conifer stands

We applied a linear spectral unmixing technique to map aspen along a seral gradient where the mid and late seral stages and old woodlands (Figure 1) are composed of a mixture of aspen and conifer trees along with understory grasses and forbs. The linear spectral unmixing was selectively applied within the aspen/conifer PVTs. Traditional image classification results in thematic maps where each image pixel is allocated to a single cover type. Linear mixture modeling (Settle and Drake, 1993) is a well established remote sensing technique designed to quantify the proportions of cover types occurring *within* a single pixel. This method has been successfully applied to create fraction and coverage maps from Landsat TM and other imagery in a variety of ecosystems (Adams et al. 1995, Drake et al. 1998, Roberts et al. 1998, Sabol et al. 2002, Chen et al. 2004).

Linear unmixing relies on the assumptions that there is no significant multiple scattering of radiation among the surface components and that each surface component has a reflectance that is significantly different from other components to allow for separation (Settle and Drake, 1993). We tested the separability of aspen, Douglas-fir, western juniper and mountain shrub species with the M-statistic (Pereira 1999) to confirm the applicability of spectral mixture analysis. Values of M larger than one indicates good separability between the two vegetation types, while smaller values indicate histogram overlap between the two classes.

Furthermore linear unmixing assumes that each surface component, commonly referred to as endmembers, is known and that the cover fractions within each pixel add to one. Linear spectral unmixing can be expressed as a series of linear equations:

$$f_1 y_{1,1} + f_2 y_{2,1} + f_3 y_{3,1} + \ldots\ldots + f_c y_{c,1} = x_1$$
$$f_1 y_{1,2} + f_2 y_{2,2} + f_3 y_{3,2} + \ldots\ldots + f_c y_{c,2} = x_2$$

.

$$f_1 y_{1,n} + f_2 y_{2,n} + f_3 y_{3,n} + \ldots\ldots + f_c y_{c,n} = x_n$$

$$f_1 + f_2 + f_3 + \ldots\ldots + f_c = 1$$

where *n* denotes the number of bands in the image, *c* is the number of endmembers, *f* is the proportion of each endmember, *x* is the pixel value and $y_{i,j}$ is the endmember spectrum for the *i*th ground cover type in the *j*th band (Settle and Drake, 1993). The first *n* equations are commonly referred to as the mixing equations while the last equation represents the sum-to-one constraint. Solutions to the system of equations can be found when $c < n$. In addition to the sum-to-one constraint it is also desirable to apply the positivity constraint, i.e. the fractions of endmembers must always be positive. Settle and Drake (1993) however demonstrated that an unbiased estimate of the fractions is lost when the positivity constraint is applied. We implemented the simplest solution to this problem, as described by Settle and Drake (1993), which involves solving the system of equations without applying the positivity constraint and then adjusting negative fractions to zero if they occur, followed by a renormalization of the fractions within each pixel. We implemented a principle component analysis (PCA) method to select endmembers along the aspen-conifer sere and confirmed the selection of spectrally pure endmember pixels using known locations of pure pixels from fine scale aerial photography and ground reference data (Smith et al. 1985, Theseira et al. 2002). We performed the image processing and linear mixture analysis in the ENVI image processing software (RSI 2005) with three endmembers: aspen, Douglas-fir and western juniper. The accuracy of the resulting fraction maps was assessed using field data collected in 82 aspen stands in the Owyhee Mountains (Strand 2007). Based on the sub-pixel proportion of aspen, each pixel within the aspen/conifer PVTs was classified into young aspen, aspen/conifer, conifer/aspen and conifer, the input classes for the TELSA model. The final raster map was smoothed using the *majorityfilter* function in ArcInfo Grid. We then converted the raster to a polygon coverage, the input format necessary for initializing TELSA. Polygons smaller than 0.2 ha were eliminated using the eliminate command in ArcInfo. Using pre-processing steps available in TELSA, we tessellated the landscape into landscape units approximately 1 ha in size. Tessellation allows disturbances to affect a portion of initial landscape units while the other portion is unaffected, allowing for a change in landscape structural composition within the original landscape units.

2.7. Model scenarios

To ensure that the assigned model parameters are realistic, we tested the model by subtracting 100 years from the age of each landscape unit followed by a simulation 100 years into the future using assigned successional rates, disturbance probabilities, and disturbance size distributions. The actual current landscape composition was then compared to the modeled composition. Future landscape compositions for the South Mountain and the Silver City areas were evaluated at 25, 50, 100 and 200 years from current time. Fire management regimes assessed for each mountain range included:

Scenario 1: Current fire management i.e. suppressed wildfire only.
Scenario 2: Historic wildfire probabilities.
Scenario 3: Historic wildfire probabilities with larger fires.
Scenario 4: Prescribed fire in aspen/conifer woodlands according to historic fire probabilities, no prescribed fire is applied in other cover types.
Scenario 5: Prescribed fire in aspen/conifer woodlands and young juniper woodlands according to historic fire probabilities.

Using a Monte Carlo approach, TELSA was run 10 times for each management regime in the South Mountain and Silver City study areas. Means and variances were then calculated from these results.

3. Results

3.1. Classification of PVT, cover, and structure

The area distribution of cover types and potential vegetation types within the two mountain ranges are listed in Tables 1 and 2 respectively. Independent validation data were used to assess the accuracy of the cover type and PVT maps. The overall accuracy for the five main PVTs was 80.2% (Table 3). The aspen PVTs (pure aspen, aspen/Douglas-fir, and aspen/western juniper) were here combined into one class. The majority of the error was caused by confusion between the two juniper woodland PVTs; western juniper/low sagebrush and western juniper/mountain big sagebrush. The producer's accuracy for the aspen PVTs was 98% and the user's accuracy was 86%. The overall accuracy for the cover type map was 72.3%, with most of the confusion occurring between the two juniper PVT types, the two sagebrush types and confusion of pure aspen with the mountain shrub class (Table 4).

The M-statistic calculations for the purpose of linear spectral unmixing were computed from the means and standard deviations of the reflectance values for the endmembers (data not shown). We also included a separability test between aspen and mountain shrub because these two cover types were commonly confused in the cover type classification. Satisfactory separability ($M > 1$) was found between aspen and Douglas-fir in all Landsat bands with the highest separability in the near infrared. Aspen and juniper were found separable in the near infrared reflectance band ($M = 1.95$) and juniper and Douglas-fir were separable in most reflectance bands. Poor separability ($M = 0.35$ at best in the near infrared) was computed between the aspen and mountain shrub classes, which may explain the confusion of these two types in the cover type classification.

Linear spectral unmixing was performed in areas classified as aspen or aspen/conifer mix to yield information about the proportions of aspen and conifers within pixels. A scatter plot of the principal component bands 1 and 2 resulted in a plot with three apices, where the pixels at each apex represent the three endmembers pure aspen, Douglas-fir and western juniper. The pixels at the apices were assigned endmember status and fraction maps of the three endmember components were derived. A statistically significant relationship ($p = 0.05$, $n = 83$, $r^2 = 0.52$) was found between the fraction map of aspen cover and ground reference data (Figure 2). The resultant landcover maps are shown in Figure 3.

3.2. Aspen expansion

The expansion of aspen into sagebrush steppe along the clone edge is graphed in Figure 4. The four transects show similar expansion rates of approximately 0.5 m per year (20 m expansion in 40 years). The length of the aspen/sagebrush steppe boundary within the South Mountain study area was computed as 68000 m. In the unlikely event that aspen expanded along all available edge the maximum area gained by aspen clones in 100 years would be 340 ha corresponding to 13% of the current aspen cover. These results are indicative of how assumption 2, aspen is not allowed to spread laterally in the model, affect the interpretation of the model results.

3.3. Fire occurrence, size and probabilities

Fire perimeter data from the Bureau of Land Management (BLM) 1957 – 2002 show that only 94 ha of the combined 37,000 ha study region has burned in wildfires within this time period. Overlay analysis in GIS reveal that none of these fires occurred on soils that support aspen woodlands. Fire records prior to 1957 are not available; however, Strand (2007) recorded fire scars in several aspen stands, particularly in aspen stands that are becoming dominated by western juniper at lower elevations. Prescribed fire in aspen stands has occurred in other areas on the Owyhee Plateau but up to this date not in areas that are included in this modeling effort.

The current wildfire size distribution calculated from the Interior Columbia Basin Ecosystem Management Project database resulted in the following size distribution: 90% of the wildfires were in the 0-1 ha size class, 5% in the 1-10 ha class, 3% in the 10-100 ha class and 2% in the 100-1000 ha class (Table 5). Information about the historical wildfire size distribution is not available for the study area and we therefore simulated two historical wildfire scenarios with two different fire size distributions (Scenarios 2 and 3, Table 5) to test the sensitivity of fire size within the model. Commonly, prescribed fires are in the size class 10-1000 ha (Scenarios 4 and 5, Table 5).

Current wildfire probabilities, estimated via overlay analysis between current cover types (Roth 2004) and a digital fire atlas in GIS, and historical wildfire probabilities based on literature references are listed in Table 6.

3.4. Management scenarios

To evaluate the input model parameters, we tested the model by subtracting 100 years from the age of each landscape unit followed by a simulation 100 years into the future using assigned successional rates, disturbance probabilities, and disturbance size distributions. The actual current landscape composition is compared to the modeled composition in Table 7. The model accurately simulated the current area of aspen using the inputs from 100 years back in time, which is important because this simulation focuses on dynamics in aspen woodlands. The simulated area of juniper woodlands is larger, and the area in sagebrush steppe and grasslands are smaller than the mapped current area for these cover types. This result suggests that the simulated successional rates within the juniper PVTs are slightly overestimated in the model. We attribute this to the fact that the juniper successional models were developed in a different study area on Juniper Mountain south of South Mountain. This deviation in juniper successional rates will have minor if any affects on this model focusing on aspen succession.

Future landscape composition of aspen seral stages was predicted under varying management scenarios for South Mountain and the Silver City Range (Figures 5 and 6). Under current wildfire regimes the early, mid, and late seral woodlands are predicted to decrease within the next 100 years while the old woodlands are predicted to increase. Continuation of current fire management is predicted to result in loss of aspen woodlands within the next 100 years with increasing losses in the following century.

Historical fire regimes predict an increase in early and mid seral woodlands while the area in late seral woodlands decreases and old woodlands maintain at current levels. Scenarios 2 and 3, historic fire probabilities with smaller and larger fire size distributions, yield similar results with an increase in the mean area of the early and mid seral aspen classes for the scenario with larger fire size compared to the smaller fire size. This difference is however within the variability of the 10 Monte Carlo runs.

Prescribed fire programs applied in aspen only (Scenario 4) and in aspen and young juniper (Scenario 5) results in a decrease in early and mid seral aspen woodlands. The area in late seral aspen woodlands initially decreases but reaches a stable level, similar to the current area, approximately 100 years into the future. The area in old aspen stands and the loss of aspen is similar for the prescribed fire and historical fire management scenarios. Under historical fire regimes a larger portion of the landscape is stable in mid seral woodlands while for the prescribed fire simulations a larger portion of the area stabilizes in late seral woodlands. According to these predictions, the aspen loss can largely be mitigated by implementation of prescribed fire programs.

Fire rotation is a measure of how many years it would take to burn an area equal to the study area under a given fire regime. Under historical fire probabilities our simulations indicate that the fire rotation for the two study areas was 70-80 years while at current fire management conditions the fire rotation is 340 years on South Mountain and 449 years in the Silver City area (Table 8). Fire rotations were also computed for the prescribed fire scenarios although these numbers may not be all that meaningful in the context of aspen management since the simulated prescribed fire programs here target aspen stands. According to this model the historical fire regimes, which are able to maintain the majority of aspen stands in early and mid seral woodlands, require that approximately 12-14% of the area burns per decade. Currently only 2-3% of the landscape burns per decade of which the majority of the area is sagebrush steppe rather than juniper or aspen woodlands.

4. Discussion

4.1. Remote sensing of aspen

Natural resource management has for the last 70-80 years relied on aerial photographs for remote sensing of rangeland and forest resources. As satellite imagery from a number of sensors (e.g. Landsat, SPOT, IKONOS) has become increasingly available researchers and scientists have begun to experiment with techniques for detecting aspen via automated and affordable image processing. Fine scale imagery (1-2 m pixel resolution) of forest canopies are difficult to classify using automated image classification methods because the picture elements are smaller than the objects to be classified, i.e. the aspen and conifer tree crowns. Within a crown the pixel values can vary from dark shadow to light sunlit leaves and the variance within a vegetation class is too large for successful classification using unsupervised or supervised classification techniques. This problem can to some extent be overcome by smoothing the image using a 3x3 or 5x5 neighborhood filters prior to classification (Heyman et al. 2003). Supervised classification of aspen and aspen/conifer stands into classes of pure aspen and three levels of aspen/conifer mixtures using Landsat 7 ETM+ data was explored with moderate success by Heide (2002). Pure aspen and Douglas-fir were here successfully classified while the classification accuracy of the three aspen/Douglas-fir mixtures was rather low. Many factors contribute to low accuracy in such a classification including georegistration errors, difficulties in assessing aspen and conifer proportions in the field and the fundamental fact that what contributes to producing a digital number of a single pixel in an image is obscure (Cracknell 1998).

Linear spectral unmixing constrained by the potential vegetation type, as presented here, offers several advantages. First of all, by only performing the linear spectral unmixing within aspen/conifer PVTs we minimize the possibility of including other vegetation types such as shrubs and meadows in the aspen/conifer classification. This is important because mesic broadleaf mountain shrub species cannot successfully be separated from aspen using multispectral data according to the M statistic. Secondly, the resulting aspen fraction map produced during the unmixing procedure provides aspen cover along a continuum rather than in discrete pre-defined classes. Following such a classification the user can bin the cover classes as desired or use the fraction cover map as is.

The spatial resolution of Landsat 7 ETM+ data (30 m pixels) is suitable for development of input maps to simulate landscape dynamics. Although these models are becoming increasingly powerful and can handle increasingly large landscapes and greater numbers of landscape units, maps at finer resolutions would result in software processing problems and unnecessarily long processing times. In applications where it is important to detect small aspen stands, finer resolution imagery than Landsat and different analysis techniques will yield higher accuracy maps (e.g. Heyman et al. 2003, Strand 2007).

A problem that remains unsolved in using remote methods for characterizing aspen succession is that the initial appearance of young conifer plants under the aspen canopy is difficult or impossible to detect during the growing season because of aspen leaves obscuring the understory, as well as during the winter due to snow and shadows in the understory. By the time the conifer crowns are visible within the aspen clone from an overhead perspective conifer dominance and reduced aspen regeneration is likely already occurring. Heide (2002) gained an improved classification accuracy in a supervised classification of aspen/conifer classes by stacking the bands from a summer and a fall Landsat scene. In the Owyhee study area this approach was investigated, however the mountainous terrain of the area results in phenological and snowcover variations along the elevational gradient, which unfortunately leads to multi-modal training spectra causing inaccuracies in the classification.

4.2. Model assumptions and their potential effects on model outcomes

The full complexity of interactions within ecosystems is neither feasible nor necessary to capture in a model to gain a better understanding for how the system functions. The model presented here is a form of deductive reasoning where the model results are a product of the input data and model assumptions. Here, we discuss the major assumptions and their potential effect on model outcomes.

1) *Aspen reproduction from seed is not included in this model.* It is well established that aspen in the semi-arid western mountains reproduces mainly via vegetative suckering and that aspen clones that exist today established hundreds or even thousands years ago (Baker 1925, Barnes 1966, Mitton and Grant 1996, Romme et al. 2005). Recruitment of new genetic individuals via sexual reproduction has however occurred periodically throughout the Holocene, for example aspen seedling establishment was widespread in Yellowstone National Park following the 1988 fires (Romme et al. 2005). Such aspen seedling establishment requires suitable substrate and climatic conditions, and specific requirements for germination and survival (Mitton and Grant 1996) occurring after severe burns in the West. We did not include the occurrence of such infrequent and severe fires because the occurrence probability and the probability of aspen establishment is not known and such a fire is unlikely to occur within the modeled time period due to the stochastic nature of these events combined with fire suppression. Indeed, such large infrequent fire events represent non-equilibrium conditions (Turner and Romme 1994) over the spatial and temporal extents addressed in this model. Including infrequent severe fires leading to aspen regeneration by seed would require modeling over a much longer time period and

extent and would show a much larger range of variability in stand structure in the aspen ecosystem. It is possible that aspen woodlands can be maintained by both frequent low severity fires promoting vegetative regeneration as suggested by Jones and DeByle (1985a), or infrequent severe fires promoting sexual regeneration (Romme et al. 2005, Kulakowski et al. 2006) or most likely a combination of the two processes. As stated by others (Turner and Romme 1994, Turner 1998, Kulakowski et al. 2006) it is difficult for humans to comprehend these rare disturbance events and the effect they have on the expected variability of a system.

2) *Aspen cannot spread into other potential vegetation types.* Expansion of aspen into adjacent shrub steppe or grasslands has been observed (Manier and Laven 2001). We calculated that aspen on South Mountain could expand as much as 340 ha in 100 years (13% of the current aspen cover) in the absence of fire if all aspen along aspen/sagebrush boundaries were expanding. This expansion would to some extent counteract the small aspen loss predicted under historical fire regime scenarios.

3) *Adjacency between vegetation types does not affect succession.* For example, in the current model the presence of a conifer seed source near an aspen stand does not affect the rate of succession. Incorporation of adjacency effects would result in variability in successional rates between stands far away and close to conifers. Adjacency effects would also increase successional rates in scenarios where only aspen stands are burned while conifer stands are left to mature and become a neighboring seed source to many aspen stands.

4) *Fire will convert a conifer dominated aspen stand to an aspen dominated stand initiation structural stage regardless of the pre-disturbance conifer cover in the stand, i.e. no legacy effects are considered.* It can be expected that an aspen stand with a high conifer cover, especially if the conifers are seed producing, is more likely to experience faster successional rates after a fire than a stand that housed only a few conifer seedlings prior to the fire. Western juniper seeds, for example, are persistent in the seed bank (Chambers et al. 1999) and may survive a low severity fire and

hence become an immediate source of juniper seedlings after a fire. Further research addressing the fire effects along the aspen/conifer successional gradient is required to better understand legacy effects and other consequences of this assumption.

5) *Aspen stands are permanently converted to conifer stands 120 years after aspen suckering has ceased due to conifer dominance, i.e. ~230 years after conifer initiation into the stand*. Reduced vegetative reproduction in aspen stands that are becoming dominated by conifers has been observed by several researchers in western mountains (Bartos and Campbell 1998, Kaye et al. 2005, Strand 2007). It is however not known how long an aspen clone can maintain in a non-reproductive state and still return to an aspen initiation woodland after a fire, hereafter referred to as the persistence time. The actual time an aspen clone can remain under conifer dominance could be significantly different from 120 years. The 120-year time period was selected because this can be considered the life expectancy of existing mature aspen ramets in the conifer-dominated stand. When all mature ramets are gone and the stand is no longer regenerating, permanent loss of the stand is assumed to have occurred resulting in a change from an aspen/conifer PVT to a conifer PVT. Strand (2007) showed that the length of the persistence time only affects the starting point of rapid aspen decline (see also Figures 5 and 6). The length of the persistence time is also extremely important when considering the possibility that one avenue for aspen rejuvenation is infrequent catastrophic wildfires creating a substrate suitable for aspen seedling establishment. In a scenario of effective fire suppression where large catastrophic fires (ones not possible to suppress) occur at an interval longer than the persistence time for all aspen clones in the area, local extinction of aspen will occur in aspen/conifer PVTs.

6) *Insects, disease, and animal use affecting aspen and conifers are not included in this model*. Fire is the only disturbance included in this model although we know that insects, disease, animal browsing, and wind felling, are examples of other disturbances affecting aspen and conifer succession (Hinds 1985, Jones and DeByle 1985b, Jones et al. 1985, Kay and Bartos 2000, Kaye et al. 2005). We deliberately did

not include any of these disturbance agents in the model to gain a clearer understanding of the effects of fire disturbance alone on the ecosystem. The Landfire rapid assessment program (http://www.Landfire.gov) has produced a series of reference condition (RC) models, which are intended to provide an estimate of the expected distribution of successional classes under pre-European settlement conditions. The Landfire RC model for aspen in the northern Great Basin incorporates an insect/disease disturbance in aging aspen/conifer stands every 200 years which reverts aspen to an earlier successional state and maintains aspen on the landscape. Regardless of whether the infrequent catastrophic event is a large severe fire promoting sexual reproduction in aspen, an infrequent disease outbreak, or a land slide it is questionable whether managers of aspen resources can rely on such infrequent stochastic events for ecosystem maintenance. Kulakowski et al. (2006, p. 1397) state that *human perceptions of ecosystems are often on time scales that are shorter than the cycles of natural variation within ecosystems*. With the help of field observations, mapping, and modeling we can begin to comprehend aspen ecosystem succession and disturbance dynamics at multiple spatial and temporal scales. The question is, can we *manage* aspen and other resources at such broad temporal scales?

4.3. Fire disturbance and landscape dynamics

Modeling results suggest that under a continuation of current fire regimes, aspen will continue to decline on both South Mountain and in the Silver City Range. Current mid and late seral aspen/conifer stands will continue to age over the next 50-100 years and eventually become permanently converted to conifer woodlands in the absence of a disturbance (Figures 5 and 6). Through simulations of succession-disturbance dynamics in TELSA under current and historic fire regimes and prescribed fire scenarios we are able to address the four questions posted in the introduction.

Q I. *Can we simulate the historical fire regime that maintained aspen stands prior to European settlement?*

Results produced under the historical fire regime conditions show a landscape where over half of the aspen area is in early or mid seral successional classes and the loss of aspen is low. In particular, predictions show 14% in the early seral stage, 45% in mid seral and 35% in late seral (late seral and old combined, see Figures 5 and 6). We predict a ~ 6% loss of aspen over the 200 year simulated time period even under historic fire regimes, which is likely due to caveats in the model assumptions. Within the model there is no avenue for aspen recruitment via seed or expansion of aspen into previously aspen free habitats such as sagebrush steppe or grasslands. Under stochastic and randomly distributed application of fire, by necessity, some aspen stands will by chance escape fire for a long enough time period to convert to conifer woodlands. Sexual reproduction of aspen is not likely to occur in the West, although such infrequent severe fire events enabling seedling establishment may be important for aspen regeneration long term. This model also did not include expansion of aspen into shrub and grasslands. We here estimate that the maximum estimated expansion rate for aspen on South Mountain (340 ha in 100 years or 13% of the current aspen area) would more than counteract the predicted loss of 6% in our model.

Obviously it is difficult to determine whether this is indeed a fair representation of fire regimes prior to European settlement, but comparisons can be made to the estimates of other researchers. The simulated historical fire regime results in a fire rotation of 70-80 years, which is somewhat longer than the mean fire frequency of 50 years suggested by Jones and DeByle (1985a). We also compared the area in successional classes to predictions presented as part of the Landfire rapid assessment RC models. For the aspen biophysical setting in mapping zone 18, which includes southern Idaho, the suggested distribution between successional stages is 14% in early seral, 40% in mid seral and 45% in the late seral class. This distribution between successional stages is very similar to our results. Loss of aspen woodlands is avoided in the Landfire RC models by including an insect/disease outbreak every 200 years, which reverts aging aspen stands to earlier successional stages.

Q II. *What extent and frequency of fire (burned area per decade) is required to stabilize the current land cover composition within aspen woodlands?*

Under historical conditions we predict that 12-14% of the landscape burned per decade and that this amount of fire largely maintained the aspen stands in early and mid seral stages. Current fire regimes, resulting in approximately 2% of the landscape burned per decade, is (according to model predictions) clearly not enough to avoid aspen loss or to maintain aspen in early and mid seral stages. Prescribed fire applied in aspen and young juniper woodland results in 5-6% of the landscape burned per decade while application of fire in aspen stands only results in 2% of the landscape burned per decade. By targeting only aspen/conifer stands, aspen could theoretically be kept on the landscape with minimal burning efforts. In reality this may not be a feasible management scenario considering that all surrounding conifer woodlands would be allowed to mature to late successional stages providing an increasing source of conifer seeds and probability for conifer establishment. Application of prescribed fire in both aspen and young juniper according to historic fire occurrence probabilities would both maintain aspen in a younger stage and eliminate the source of conifer seeds. Prescribed fire applied also in mature juniper woodlands was not considered due to the practical difficulty of burning such areas. In both prescribed fire scenarios, all conifer woodlands that currently exist in mature successional stages would therefore continue to mature and remain on the landscape.

Q III. *What is the structural composition within aspen woodlands under historical and current fire probabilities? What is the structural composition under prescribed burning scenarios?*

Landscape composition at user selected time intervals is reported by TELSA under defined disturbance regimes and initial landscape composition. The initial landscape composition is only important to gain understanding about a certain study area over a relatively short period. As the model is allowed to run for a sufficiently long time period the landscape composition at the equilibrium state is independent of the initial composition of the landscape. Under historic fire regimes approximately 60% of the aspen woodlands exist in an early or mid successional stage while this proportion is ~10% for current fire regimes and ~30% for the prescribed burning scenarios. Under the prescribed burning scenarios ~45% of the aspen end up in a late seral woodland, of which the majority are the self-regenerating pure aspen stands where prescribed fire was not applied. The amount of aspen in the old successional class and lost aspen woodlands is quite similar in the historic and the prescribed burning scenarios (Figures 5 and 6).

Q IV. *What is the effect of fire size on the long-term maintenance of aspen woodlands*

Historical fire regimes (Scenarios 2 and 3) were simulated with two fire size distributions (Table 5). Although the scenario with larger fires (Scenario 3) results in a larger area in early and mid seral woodlands, the difference is within the error bars generated via the Monte Carlo runs. Based on these results we conclude that there is no effect of fire size on the structural composition of aspen woodlands and the long-term maintenance of aspen woodlands. It is important to note that these results in the 'model world' do not necessarily apply to the 'real world'. A closer evaluation of the model assumptions leads us to believe that this model is not well suited to answer question Q IV. One could speculate that larger fires would benefit the fire dependent aspen woodlands in several ways. Larger fires would eliminate conifers over a larger area and thereby reduce the conifer seed source and probability of conifer establishment within newly established aspen stands. Modeling of this phenomenon would require the spatial model to account for seed dispersal to adjacent stands such that aspen stands that are closer to conifer woodlands would be more likely to experience conifer establishment and eventually dominance. Larger fires would also clear larger areas, which aspen could expand into as the clones grow. Aspen clones surrounded by closed conifer woodlands have no means of extending their area. The ability for aspen to expand into adjacent grass and shrub lands was not incorporated in this model. An improved model where the distance to seed source and expansion of existing aspen stands were included would likely show different results with regards to the importance of fire size.

4.4. Management implication

Over long term (i.e. centennial time periods) aspen will most likely remain a part of the western landscape unless the climate changes such that it is unfavorable for the species. Quaking aspen is apparently tolerant to a variety of fire frequencies and severities; vegetative reproduction occurs when fires are less severe and more frequent and reproduction via seed can occur after extensive severe fire events if the soil moisture and weather conditions are within the ‘window of opportunity’ for aspen regeneration (Romme et al. 2005). Even if aspen that is seral to conifers are eliminated from the landscape due to fire suppression, eventually a large-scale disturbance event will occur and pure aspen stands, riparian aspen, and aspen on microsites in the area may have the opportunity to initiate aspen establishment from seed. This optimistic outlook for aspen however does not offer a solution to the immediate concern over aspen declines in the West. Managers and scientists throughout the region are currently concerned about declining aspen populations and reproduction within aspen stands (Bartos 2001, Heide 2002, Kay 1997, Wall et al. 2001, Shepperd et al. 2001, Smith and Smith 2005). A century of fire suppression has been reported as one explanation for the current decline (Jones and DeByle 1985a, DeByle et al. 1987, Mueggler 1989, Shepperd 2001, Miller et al. 2005), particularly in areas where conifer species replace aspen as succession progresses in the absence of a disturbance. In other areas current aspen cover is higher than 100 years ago due to severe fires (Kulakowski et al. 2006) and vegetative expansion of aspen into other cover types (Manier and Laven 2001). Yet other aspen stands are not at risk of loss because they grow in areas that are not suitable for conifers (Mueggler 1989, Kulakowski et al. 2006, Strand 2007). Human activity and needs, and current fire policy makes it unlikely that aspen woodlands within the western mountains will return to historic fire regimes and active management has been proposed in locations where maintenance of aspen is a priority. Before engaging in management activities of any kind it is naturally important to make appropriate ecological assessments in the field to evaluate the current state of the aspen stands, their successional trajectories in a landscape context, and the presence of possible stressors. State-and-transition models such as that developed for aspen by Strand (2007) can assist in the understanding of the current state at the stand level.

Simulations of the historical fire frequency suggested by Jones and Debyle (1985a) maintain aspen on the landscape. In many areas it is not feasible or desirable to return to historic fire regimes and management activities such as prescribed burning is presented here as an alternative. The model predictions presented here suggest that in theory prescribed burning programs can mitigate aspen loss and maintain aspen woodlands in younger seral stages. Such restoration of aspen woodlands has been suggested (Brown and DeByle 1987, Bartos et al. 1991, Caprio and Graber 2000, Miller et al. 2005) and carried out in aspen restoration projects (e.g. Brown and DeByle 1989, Bates and Miller 2004, Bates et al. 2004). Prescribed fire has been described as the most economical restoration technique because it is a natural process where the vegetation will respond positively under the right burning conditions (Miller et al. 2005), furthermore, large areas can be treated. Disadvantages of fire treatments are the liabilities and risks, the possibility of weed establishment after the fire and smoke issues if the area is located near development (Miller et al. 2005). High intensity fires may also result in nutrient losses and a reduction in the recruitment of shrubs such as bitterbrush, sagebrush, and mountain-mahogany. Ecological factors that must be considered prior to burning are the fuels composition and structure, current understory composition, presence of weeds, and the successional stage of aspen woodland development (Miller et al. 2005). Other concerns are post-fire wildlife and animal use (Bartos and Campbell, 1998; Kay and Bartos, 2000, Hart and Hart, 2001, Kaye et al. 2005), which can jeopardize recently established aspen suckers and prevent the aspen clone recovery.

Where fire is undesirable for restoration, Shepperd (2001) has suggested a series of alternative management activities including commercial harvest, mechanical root stimulation, removal of competing vegetation, protection of regeneration from herbivory and regeneration from seed. Cutting of conifers followed by prescribed fire has also been applied (Bates and Miller 2004). The conifers on the ground here provide a fuel ladder that help carry the fire in aspen stands which are commonly difficult to burn.

Ecosystem management requires assessment of interactions between succession, natural disturbance regimes and management activities. Landscape dynamics models such as TELSA provide an avenue for managers, scientists and stakeholders to evaluate the long-term effect of changing natural disturbance regimes and management activities on landscape vegetation composition. All models have limitations. It is important to clearly understand the model assumptions during interpretation of model results and during the decision making process that follows a modeling exercise. The ultimate test of a model is not how accurate or truthful it is, but only whether one is likely to make a better decision with it than without it (Starfield 1997).

The modeling results presented here indicate that active management is necessary in areas where aspen is seral to conifers and aspen maintenance is a management goal unless we rely on infrequent catastrophic disturbance events to maintain these aspen resources.

5. Acknowledgements

USDA Bureau of Land Management for partial funding of this project
Field assistance by B. Smith and J. Young, College of Natural Resources, University of Idaho.

References

Adams, J.B., D.E. Sabol, V. Kapos, R.A. Filho, D.A. Roberts, M.O. Smith, and A.R. Gillespie, 1995. Classification of multispectral images based on fractions of endmembers: Application to land-cover change in the Brazilian Amazon. Remote Sensing of Environment 52:137-154.

Baker, F.S., 1925. Aspen in the central Rocky Mountain region. USDA Bull. 1291, p.47.

Barnes, B.V., 1975. Phenotypic variation of trembling aspen in Western North America. Forest Science 22:319-328.

Bartos, D.L., 2001. Landscape Dynamics of Aspen and Conifer Forests. p. 5-14. Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Bartos, D.L., and R.B. Campbell, 1998. Decline of Quaking Aspen in the Interior West – Examples from Utah. Rangelands 20:17-14.

Bartos, D.L, and W.F. Mueggler. 1981. Early succession in aspen communities following fire in western Wyoming. Journal of Range Management 34:315-318.

Bartos, D.L., W.F. Mueggler, and R.J. Campbell, 1991. Regeneration of aspen by suckering on burned sites in western Wyoming, Forest Research Paper INT-448, USDA Forest Service, Intermountain Reseach Station, Ogden, Utah, 10p.

Botkin D.B., J.F. Janak, and J.R. Wallis, 1972. Some ecological consequences of a computer model of forest growth, Journal of Ecology 60:849-873.

Bates J.D. and R.F. Miller, 2004. Restoration of aspen woodland invaded by western juniper: Applications of partial cutting and prescribed fire, 16th International Conference, Society for Ecological Restoration, August 24-26, Victoria, BC, Canada.

Bates, J.D., R.F. Miller, and K.W. Davies, 2004. Restoration of Quaking Aspen Woodlands Invaded by Western Juniper, Rangeland Ecology and Management 59: 88-97.

Brown J.K. and N.V. DeByle, 1989. Effects of prescribed fire on biomass and plant succession in Western aspen, United States Department of Agriculture, Firest Service, Intermountain Research Station, Research Paper INT-412, Ogden Utah.

Bunting, S.C., J.L. Kingery, and E.K. Strand, 1999. Effects of succession on species richness of the western juniper/sagebrush mosaic. Ecology and management of pinyon-juniper communities within the Interior West. USDA Forest Service GTR-

RMRS-P-9. Pp. 76-81.

Bunting, S.C., E.K. Strand, and J.L. Kingery, 2005. Landscape characteristics of sagebrush-steppe/juniper woodland mosaics under varying modeled prescribed fire regimes, Proceedings 23rd Tall Timbers Fire Ecology Conference, Tallahassee, Florida. Tall Timbers Research, Inc., in press.

Burkhardt, J.W., and E.W. Tisdale, 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57:472-484.

Caprio, A.C. and D.M. Graber, 2000. Returning fire to the mountains: Can we successfully restore the ecological role of pre-European fire regimes to the Sierra Nevada? P. 233-241. In D.N. Cole, S.F. McCool, W.T. Borrie and J. O'Loughlin (eds.). Wilderness Science in a Time of Change conreence. Volume 5: Wilderness Ecosystems, Threats, and Management. May 23-29, 1999, Missoula, Montana, RMRS-P-15-Vol5. USDA Forest Service, Intermountain Res. Sta., Ogden, Utah.

Chambers, J.C., S.B. Vander Wall, and E.W. Schupp, 1999. Seed and seedling ecology of pinyon and juniper species in the pygmy woodlands of western North America. Botanical Review 65:1-38.

Chen, X., L.A. Vierling, E. Rowell, and T. DeFelice, 2004. Using lidar and effective LAI data to evaluate IKONOS and Landsat 7 ETM+ vegetation cover estimates in a ponderosa pine forest. Remote Sensing of Environment 91:14-26.

Chong, G.W., S.E. Simonson, T.J. Stohlgren, and M.A. Kalkhan, 2001. Biodiversity: Apen stands have the lead, but will nonnative species take over?, p. 261-271, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Congalton, R.G. 1991. A review of assessing the accuracy of classifications of remotely sensed data, Remote Sensing of Environment 37:35-46.

Conway-Welch, J., 1982. The story of Silver City, Idaho – Gold town to Ghost town, University of Idaho Press, Moscow, Idaho, p. 115.

Cracknell, A.P. 1998. Synergy in remote sensing – what's in a pixel?, International Journal of Remote Sensing 19:2025-2047.

DeByle, N.V. C.D. Bevins, and W.C. Fischer. 1987. Wildfire occurrence in aspen in the interior western United States. Western Journal of Applied Forestry 2:73-76.

Despain, D.G., 1990. Yellowstone vegetation: Consequences of environment and history in a natural setting. Roberts Rinehart Publishers, Inc.

Drake, N.A., S. Mackin, and J.J. Settle, 1998. Mapping vegetation, soils, and geology in semiarid shrublands using spectral matching and mixture modeling of SWIR AVIRIS imagery. Remote Sensing of Environment 68:12-25.

Ek, A.R. and R.A. Monserud, 1974. FOREST: A computer model for the growth and reproduction of mixed species forest stands. Research Report A2635. College of Agricultural and Life Sciences, University of Wisconsin-Madison, Madison, WI, USA.

ESRI 1999-2005.ArcGIS version 9.1 Environmental Systems Research Institute Inc., Redlands, California. Web site: http://www.esri.com.

Essa Technology, 2003a. Tool for Exploratory Landscape Scenario Analyses (TELSA), version 3.1a, ESSA Technologies Ltd., Vancouver, B.C., Canada.

Essa Technology, 2003b. Vegetation Dynamics Development Tool (VDDT), Version 4.4b, ESSA Technologies Ltd., Vancouver, B.C., Canada.

Franklin J., A.D. Syphard, D.J. Mladenoff, H.S. He, D.K. Simons, R.P. Martin, D. Deutschman, and J.F. O'Leary, 2001. Simulating the effect of different fire regimes on plant functional groups in Southern California, Ecological Modelling, 142:261-283.

Hart, J.H., and D.L. Hart, 2001. Interaction among cervids, fungi, and aspen in northwest Wyoming, p.197-205, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Hessl, A., 2002. Aspen, elk, and fire: The effects of human institutions on ecosystem processes, Biocience 52:1011-1022.

Heide, S.C., 2002. Comparison of methods to detect conifer encroachment into aspen stands using Landsat 7 ETM+ satellite imagery, Masters Thesis, University of Idaho, Moscow, Idaho.

Heyman, O., G.G. Gaston, A.J. Kimberling, and J.T. Campbell, 2003. A per-segment approach to improving aspen mapping from high-resolution remote sensing imagery, Journal of Forestry 4:29-33.

Hinds, T.E., 1985. Diseases. p. 87-106, *in* DeByle and Winokur (Editors) Aspen: Ecology and Management in the Western United States. USDA For. Serv. Gen. Tech. Rep. RM-119.

Jensen, J.R. 1996. Introductory digital image processing. Prentice Hall.upper Saddle River, new Jersey, 318 p.

Jones B.W., 1993. The influence of grove size on bird species richness in aspen parklands. Wilson Bulletin 105:256-264.

Jones, J.R. and N.V. DeByle, 1985a. Fire. p. 77-81, *in* DeByle and Winokur (Editors) Aspen: Ecology and Management in the Western United States. USDA For. Serv. Gen. Tech. Rep. RM-119.

Jones, J.R. and N.V. DeByle, 1985b. Other physical factors. p. 83-86, *in* DeByle and Winokur (Editors) Aspen: Ecology and Management in the Western United States. USDA For. Serv. Gen. Tech. Rep. RM-119.

Jones, J.R. and N.V. DeByle, and D.M. Bowers, 1985. Insects and other invertebrates. p. 107-114, *in* DeByle and Winokur (Editors) Aspen: Ecology and Management in the Western United States. USDA For. Serv. Gen. Tech. Rep. RM-119.

Kay, C.E., 1997. Is aspen doomed? Journal of Forestry, 95: 4-11.

Kay, C.E. and D.L. Bartos. 2000. Ungulate herbivory on Utah aspen: Assessment of long term exclosures. Journal of Range Management 53:145-153.

Kaye, M.W., D. Binkley, and T.J. Stohlgren, 2005. Effects of conifers and elk browsing on quaking aspen forests in the central Rocky Mountains, USA, Ecological Applications, 15:1284-1295.

Keane, R.E., D.G. Long, D. Basford, B.A.. Levesque, 1997. Simulating vegetation dynamics accross multiple scales to assess alternative management strategies: Proceedings for GIS '97; 1997 February 17-20; Vancouver B.C. Fort Collins Co; GIS World Books. 640p.

Klenner, W., W. Kurz, and S. Beukema. 2000. Habitat patterns in forested landscapes: management practices and the uncertainty associated with natural disturbances. Computers and Electronics in Agriculture 27:243-262.

Kulakowski, D., T.T. Veblen, and B.P.Kurzel, 2006. Influences of infrequent fire, elevation and pre-fire vegetation on the persistence of quaking aspen (Populus tremuloides Michx.) in the Flat Tops area, Colorado, USA, Journal of Biogeography 33:1397-1413.

Kurz, W.A., S. Beukema, W. Klenner, J.A. Greenough, D.C.E. Robinson, A.D. Sharpe and T.M Webb, 2000. TELSA: the Tool for Exploratory Landscape Scenario Analyses. Computers and Electronics in Agriculture 27:227-242.

Leica Geosystems, ERDAS® Imagine, 1991-2003. Version 8.7, Leica Geosystems, GIS & Mapping, Atlanta Ga, USA, On line: http://www.leica-geosystems.com/corporate/en/lgs_index.htm

Manier, D.J. and R.L. Laven, 2001. Changes in landscape pattern and associated forest succession on the western slope of the Rocky Mountains, Colorado. p. 15-22. Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

McGarigal K. and W.H. Romme, 2003. Simulate landscape changes, GeoWorld July 2003. On line: http://www.umass.edu/landeco/research/rmlands/rmlands.html

Merzenich, J. and L. Frid, 2005. Projecting Landscape Conditions in Southern Utah Using VDDT. *In:* M. Bevers and T.M. Barrett (comps.). 2005. Systems Analysis in Forest Resources: Proceedings of the 2003 Symposium; October 7-9, Stevenson, WA. General Technical Report PNW-GTR-656. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. pp. 157-163.

Miller, R.F. and J.A. Rose, 1999. Fire history and western juniper encroachment in sagebrush steppe, Jouranl of Range Management 52:550-559.

Miller, R.F., J.D. Bates, T.J. Svejcar, F.B. Pierson, and L.E. Eddleman, 2005. Biology, ecology and management of western juniper. Technical Bulletin 152, Oregon State University Agricultural Experiment Station, Corvallis, OR.

Mitton, B.J., and M.C. Grant, 1996. Genetic variation and the natural history of quaking aspen, Bioscience 46:25-31.

Mueggler, W.F., 1989. Age distribution and reproduction of intermountain aspen stands. Western Journal of Applied Forestry 4:41-45.

Mladenoff D.J., 2004. LANDIS and forest landscape models, Ecological Modelling 180:7-19.

Oregon Climate Service, 1999. Precipitation for Idaho; Average Monthly and Annual (1961-90), digital raster data, http://inside.uidaho.edu, University of Idaho Library, Moscow, Idaho, USA.

Pacala, S.W., C.D. Canham, and J.A. Silander Jr., 1993. Forest models defined by field measurements. I. The design of a northeastern forest simulator, Canadian journal of Forest Research 23:1980-1988.

Pereira, J.M., 1999. A comparative evaluation of NOAA/AVHRR vegetation indexes for burned surface detection and mapping, IEEE Transactions on Geoscience and Remote Sensing, 37(1):217-226.

Research Systems Inc. 2005. ENVI software version 4.2, Boulder Colorado, USA.

Roberts, D.A., M. Gardner, R. Church, S. Ustin, G. Scheer, and R.O. Green, 1998. Mapping Chaparral in the Santa Monica Mountains Using Multiple Endmember Spectral Mixture Models. Remote Sensing of Environment 65:267-279.

Romme, W.H., L. Floyd-Hanna, D.D. Hanna, and E. Bartlett, 2001. Aspen's ecological role in the West, p. 243-259, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Romme, W.H., M.G. Turner, G.A. Tuskan, and R.A. Reed, 2005. Establishment, persistence, and growth of aspen (*Populus tremuloides*) seedlings in Yellowstone National Park, Ecology 86:404-418.

Rumble, M.A., L.D. Flake, T.R. Mills, and B.L. Dykstra, 2001. Do pine trees in aspen stands increase bird diversity?, p. 185-191, Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Roth, A., 2004. Fire patterns within a successional gradient of a sagebrush steppe/juniper woodland, Masters Thesis, University of Idaho, Moscow, Idaho, USA.

Sabol, D.E. Jr., A.R. Gillespie, J.B. Adams, M.O. Smith, and C.J. Tucker, 2002. Strucural stage in the Pacific Northwest forests estimated using simple mixing models of multispectral images. Remote Sensing of Environment 80:1-16.

Settle, J.J., and N.A. Drake, 1993. Linear mixing and the estimation of ground cover proportions. International Journal Remote Sensing 14:1159-1177.

Shepperd, W.D., 2001. Manipulations to regenerate aspen ecosystems. p. 355-365. Sustaining Aspen in Western Landscapes: Symposium Proceedings; 13-15 June 2000; Grand Junction, CO. USDA Forest Service Proceedings RMRS-P-18.

Shepperd, W.D., D.L. Bartos, and S.A. Mata, 2001. Above-and below-ground effects of aspen clonal regeneration and succession to conifers, Canadian Journal of Forest Research 31:739-745.

Smith, M.O., P.E. Johnson, and J.B. Adams, 1985. Quantitative determination of mineral types and abundances from reflectance spectra using principal component analysis. Journal of Geophysical Research 90:792-804.

Smith, A.E. and F.W. Smith, 2005. Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA, Forest Ecology and Management 213:338-348.

Starfield A.M. 1997. A pragmatic approach to modeling for wildlife management, Journal of Wildlife Management 61:261-270.

Strand, E.K. 2007. Chapter 4: Landscape dynamics in aspen and western juniper woodlands on the Owyhee Plateau, Idaho. Dissertation, University of Idaho, Moscow, Idaho, USA.

Theseira, M.A., G. Thomas, J.C. Taylor, F. Gemmell, and J. Varjo, 2002. Sensitivity of mixture modeling to end-member selection. International Journal of Remote Sensing 23:687-700.

Turner, M.G. 1998. Comparing large infrequent disturbances: What have we learned?, Ecosystems 1:493-496.

Turner, M.G. and W. H. Romme, 1994. Landscape dynamics in crown fire ecosystems, Landscape Ecology 9:59-77.

Wall, T.G., R.F. Miller, and T.J. Svejcar, 2001. Juniper encroachment into aspen in the Northwest Great Basin, Journal of Range Management, 54:691-698.

USDA – NRCS, 1998. Owyhee County digital soil survey, SSURGO, Natural Resources Conservation Service, U.S. Department of Agriculture. On line: http://www.ncgc.nrcs.usda.gov/branch/ssb/products/ssurgo/

USGS, 1999. National Elevation Data, U.S. Geological Survey (USGS), EROS Data Center, National Elevation Dataset, *Edition:* 1, Sioux Falls, SD. On line: http://seamless.usgs.gov

Winternitz, B.L., 1980. Birds in aspen. Management of western forests and grasslands for nongame birds. USDA Forest Service General Technical Report INT-86. Intermountain Forest and Range Experiment Station, Ogden, UT.

Yanish, C., 2002. Western juniper succession: Changing fuels and fire behavior. M.S. Thesis. University of Idaho, Moscow, Idaho.

Tables

Table 1. Areas of mapped cover types within the South Mountain and Silver City Range study sites.

Cover type	**South Mountain Area (ha)**	**Silver City Range Area (ha)**
Aspen woodland (pure aspen)	496	236
Aspen/Douglas-fir woodland	1371	2002
Aspen/Western juniper woodland	745	527
Bare/Rock	2	72
Ceanothus/Mesic shrub	299	365
Douglas-fir	298	923
Juniper woodland/Low sage open	1635	787
Juniper woodland/Low sage closed	1056	141
Juniper woodland/Mountain big sage open	4062	3321
Juniper woodland/Mountain big sage closed	3451	1259
Curlleaf mountain-mahogany	227	1983
Low sagebrush steppe	1335	2343
Mountain big sagebrush steppe	1729	5992
Wet meadow	42	189

Table 2. Areas of mapped potential vegetation types within the study area.

PVT	**South Mountain Area (ha)**	**Silver City Range Area (ha)**
Aspen woodland	496	236
Aspen/Douglas-fir woodland	1669	2925
Aspen/Western juniper woodland	745	527
Bare/Rock	2	72
Ceanothus/Mesic shrub	299	365
Juniper woodland/Low sage	4028	3272
Juniper woodland/Mountain big sage	9240	10571
Curlleaf mountain-mahogany	227	1983
Wet meadow	42	189

Table 3. Confusion matrix for PVT classification

	Ground reference PVT								
	Curlleaf mountain-mahogany	Juniper/low sagebrush	Juniper/ mtn big sagebrush	Meadow	Aspen	**Total**	error	Commission error %	User's accuracy (%)
Mapped PVT									
Curlleaf mountain-mahogany	9	0	4	0	1	**14**	5	35.7	64.3
Juniper / low sagebrush	0	19	4	0	0	**23**	4	17.4	82.6
Juniper / mountain big sagebrush	4	13	65	0	0	**82**	17	20.7	79.3
Meadow	0	0	2	2	0	**4**	2	50.0	50.0
Aspen	1	1	7	1	59	**69**	10	14.5	85.5
Total	**14**	**33**	**82**	**3**	**60**	**192**			
Omission error	5	14	17	1	1	**correct:**	**154**		
Omission error (%)	37.5	42.4	20.7	33.3	1.7	**total:**	**192**		
Producer's accuracy (%)	64.3	57.6	79.3	66.7	98.3	**total accuracy:**	**80.2**		

Table 4. Confusion matrix for cover type classification.

	Ground reference cover															
	Low Sage Brush	Mountain big sage	Bare/ Rock	Curlleaf mountain mahogany	Juniper/ low sage clsd	Juniper/ low sage open	Juniper/ mtn sage clsd	Juniper/ mtn sage open	Mtn shrub	Aspen	Aspen/ conifer	Douglas-fir	**Total**	Com-mission	Com-mission %	User's accuracy %
Mapped cover																
Low sagebrush	6	1	0	0	2	0	0	0	0	0	0	0	**9**	3	33.3	66.7
Mountain big sage	0	8	0	0	0	1	0	0	1	0	0	0	**10**	2	20.0	80.0
Bare/Rock	0	0	12	0	0	0	0	0	0	0	0	0	**12**	0	0.0	100.0
Curlleaf mtn-Mahogany	0	1	0	10	0	0	0	0	1	0	1	0	**13**	3	23.1	76.9
Juniper/Low sage open	1	1	0	0	10	1	1	0	0	0	0	0	**14**	4	28.6	71.4
Juniper/Low sage closed	0	0	0	0	1	7	0	0	0	0	0	0	**8**	1	12.5	87.5
Juniper/mtn sage open	1	0	0	0	0	0	16	0	1	0	1	0	**19**	3	15.8	84.2
Juniper/mtn sage closed	0	0	0	1	0	6	5	7	0	1	2	1	**23**	16	69.6	30.4
Mountain shrub	0	0	0	0	0	0	0	0	5	0	0	0	**5**	0	0.0	100.0
Aspen	0	0	0	0	0	0	0	0	4	7	1	0	**12**	5	41.7	58.3
Aspen/conifer	0	0	0	0	0	0	0	0	0	2	12	2	**16**	4	25.0	75.0
Douglas-fir	0	0	0	0	0	0	0	0	0	0	2	12	**14**	2	14.3	85.7
Total	**8**	**11**	**12**	**11**	**13**	**15**	**22**	**7**	**12**	**10**	**19**	**15**	**155**			
Omission	2	3	0	1	3	8	6	0	7	3	7	3		**correct:**		**112**
Omission error %	25.0	27.3	0.0	9.1	23.1	53.3	27.3	0.0	58.3	30.0	36.8	20.0		**total:**		**155**
Producer's accuracy %	75.5	72.7	100.0	90.9	76.9	46.7	72.7	100.0	41.7	70.0	63.2	80.0		**total accuracy:**		**72.3%**

Table 5. Distribution of the percent of fires in each size for the simulation scenarios.

Scenario	**Fire size 0-1** ha	**Fire size 1-10** ha	**Fire size 10-100 ha**	**Fire size 100-1000** ha
1	90	5	3	2
2	90	5	3	2
3	50	20	15	15
4	1	4	25	70
5	1	4	25	70

Table 6. Current and historic probability of wildfire occurrence in the major PVTs and structural stages on the Owyhee Plateau.

PVT	**Structural stage**	**Current wildfire probability**	**Historic wildfire probability**
Low sagebrush steppe	Grassland	0.00064	0.002
	Low sagebrush steppe	0.00064	0.005
Mountain big sagebrush steppe	Grassland	0.001	0.002
	Mountain big sagebrush steppe	0.001	0.02
Juniper woodlands/Low sagebrush steppe	Grasslands	0.00064	0.002
	Low sagebrush steppe	0.00064	0.02
	Stand initiation juniper	0.0008	0.01
	Open young woodland	0.0008	0.001
	Young multistory woodland	0.0005	0.002
	Old multistory woodland	0.0004	0.006
Juniper woodlands/Mtn big sagebrush steppe	Grasslands	0.001	0.005
	Low sagebrush steppe	0.001	0.02
	Stand initiation juniper	0.001	0.02
	Open young woodland	0.0007	0.01
	Young multistory woodland	0.0002	0.002
	Old multistory woodland	0.00009	0.001
Aspen woodlands with conifers	Young woodlands	0.005	0.0002
	Mature woodlands	0.0002	0.005
	Woodlands with conifer	0.0002	0.01
	Conifer / aspen woodlands	0.0002	0.02

Table 7. Comparison of the current cover type distribution and the 100-year simulated current cover type distribution for South Mountain.

Cover type	Current area ha	Simulated current ha
Aspen	2611	2610
Ceanothus / Mesic shrub	477	362
Curlleaf mountain-mahogany	223	117
Douglas-fir	298	284
Grasslands/Meadow	70	402
Juniper woodland	10193	11831
Sagebrush steppe	3053	1136

Table 8. Fire rotation and decadal proportion of the landscape burned under modeled fire regimes.

Study area	Scenario	Fire rotation (years)	Burned area per decade (%)
South Mountain	Current wildfire (1)	340	2.9
South Mountain	Historic fire probabilities (2)	82	12.2
South Mountain	Historic prob. large fires (3)	72	13.9
South Mountain	Prescribed fire in aspen (4)	466	2.1
South Mountain	Prescribed fire in aspen+young juniper (5)	192	5.2
Silver City	Current wildfire (1)	449	2.2
Silver City	Historic fire probabilities (2)	79	12.7
Silver City	Historic prob. large fires (3)	66	15.1
Silver City	Prescribed fire in aspen (4)	448	2.2
Silver City	Prescribed fire in aspen+young juniper (5)	178	5.6

Figures

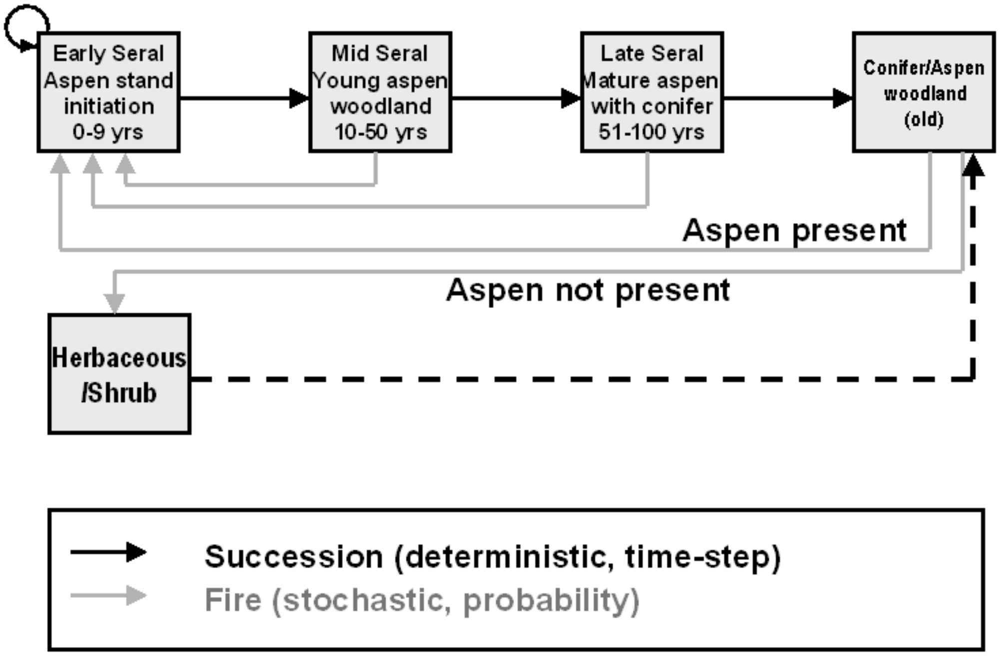


Figure 1. Simplified pathway diagram for upland aspen/conifer communities in the Owyhee Mountains.

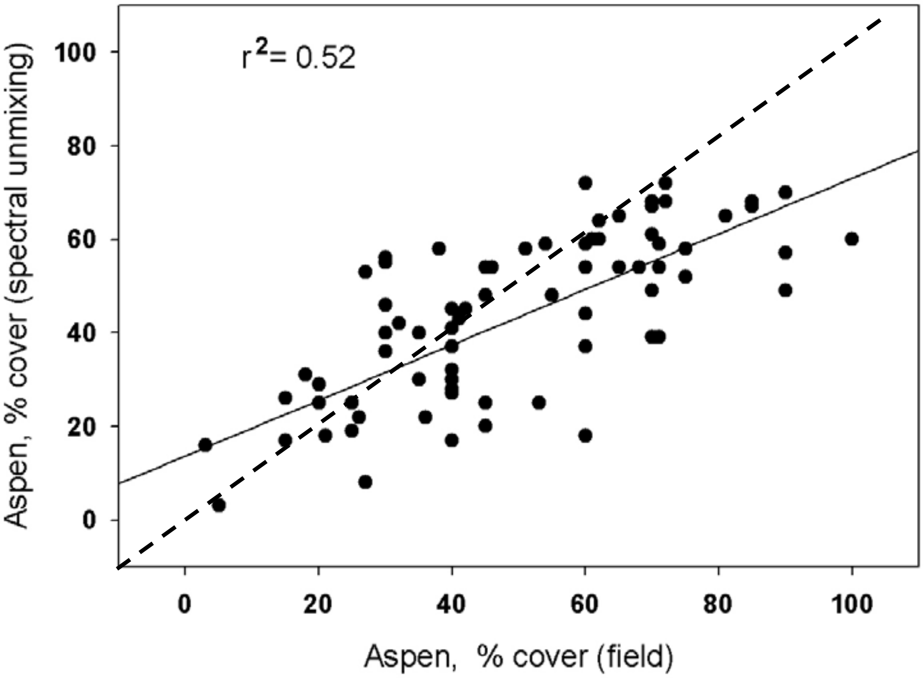


Figure 2. Aspen fraction predicted by linear spectral unmixing vs. field measurements. The dotted line represents the one-to-one line.

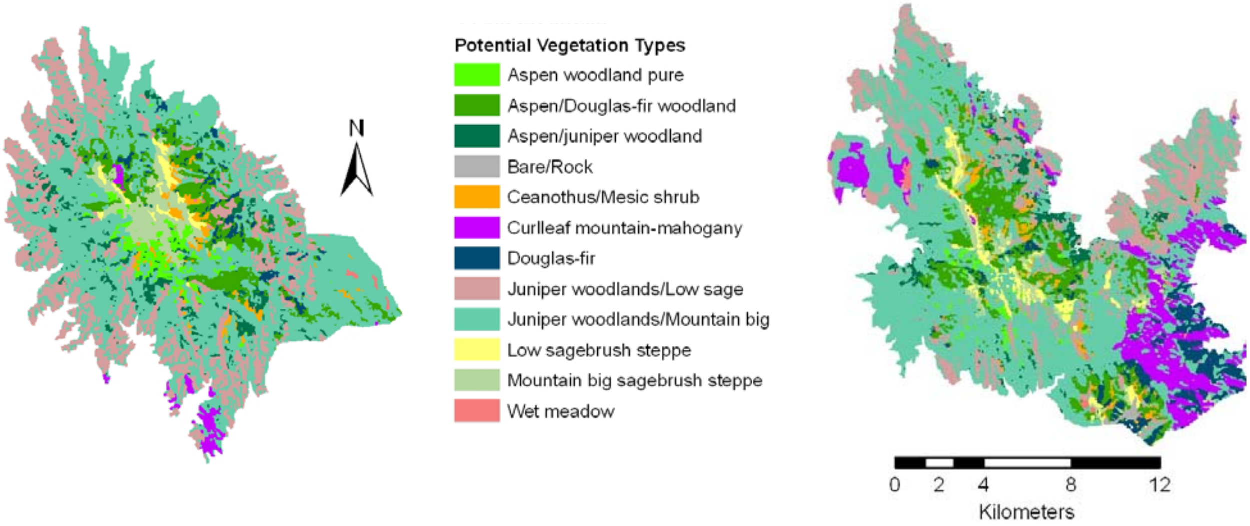


Figure 3. Potential vegetation maps of the South Mountain (left) and the Silver City (right) areas.

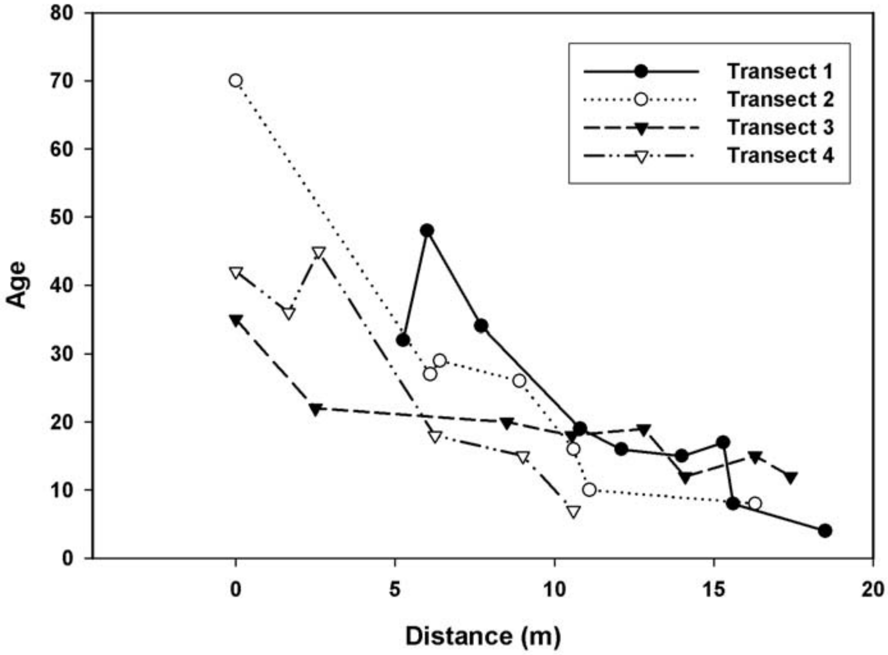


Figure 4. Gradient of aspen age at the aspen woodland / sagebrush steppe boundary. The x-axis represents the distance from the mature aspen stems along the stand edge.

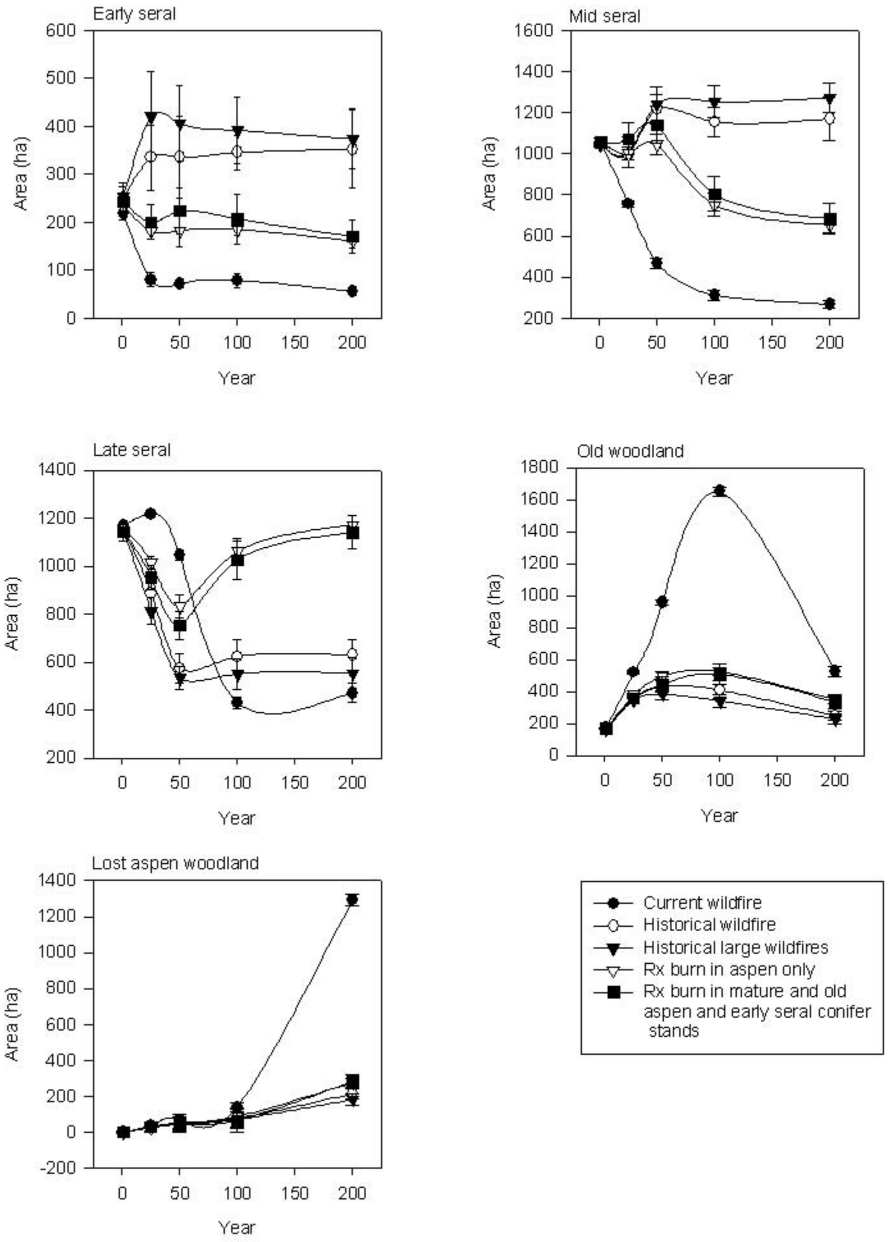


Figure 5. Area of aspen woodland in different seral stages under five simulated management scenarios on South Mountain. The total area in aspen vegetation is currently 2610 ha.

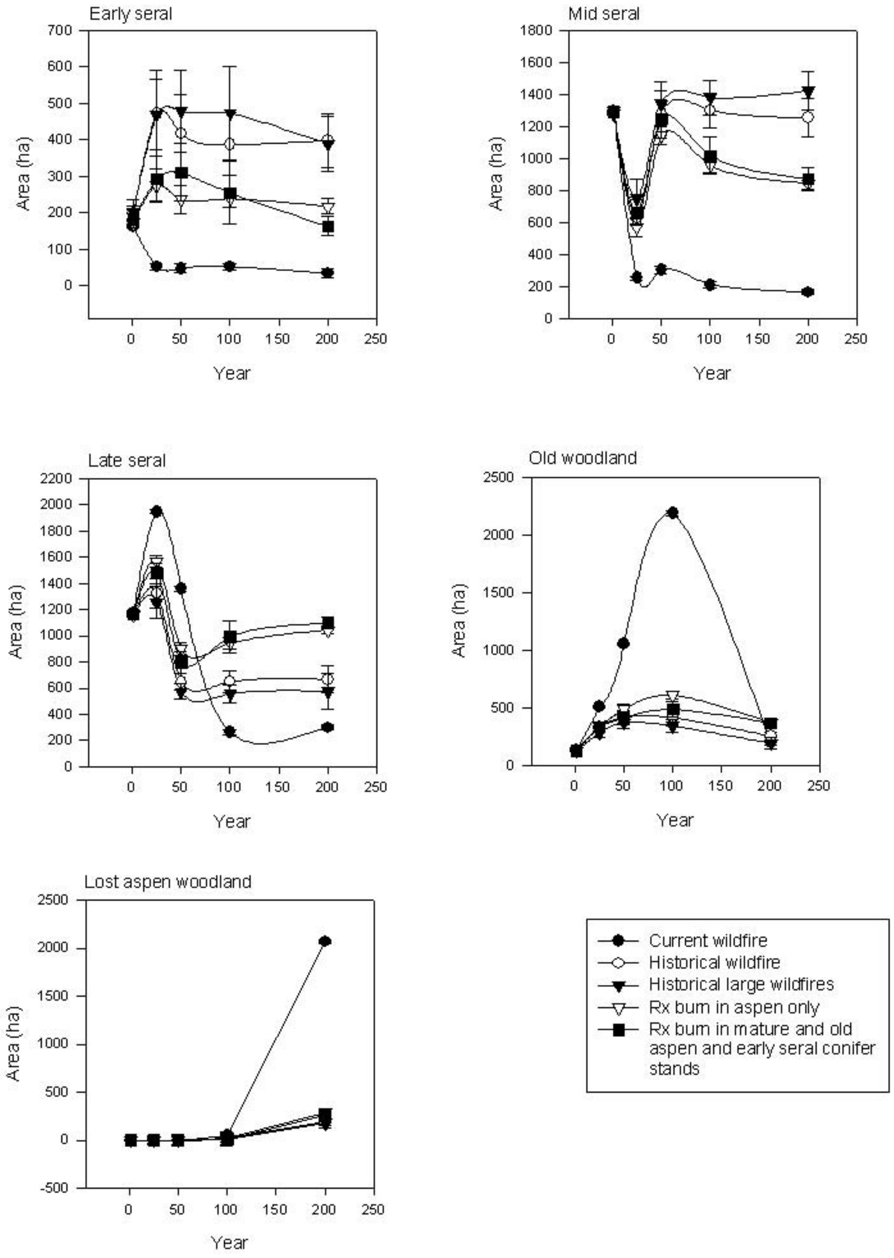


Figure 6. Area of aspen woodland in different seral stages under five simulated management scenarios in the Silver City Range. The total area in aspen vegetation is currently 2765 ha.

Appendix A. List of vascular plant species observed in the sampled aspen stands in the Owyhee Mountains (2004 - 2006)

Plant taxonomy follows that used by the United States Department of Agriculture Natural resources Conservation Service PLANTS Database (http://plants.usda.gov/) except for those marked with * which follows taxonomy according to:
Hitchcock C.L. and A. Cronquist, 1973, Flora of the Pacific Northwest, University of Washington Press, Seattle and London.

Scientific name	**Common name**	**Four-letter code**
<u>Trees</u>		
Abies lasiocarpa	Subalpine fir	ABLA
Acer glabrum	Rocky Mountain maple	ACGL
Juniperus occidentalis	Western juniper	JUOC
Populus tremuloides	Quaking aspen	POTR5
Pseudotsuga menziesii ssp. *Glauca*	Rocky Mountain Douglas-fir	PSMEG
<u>Mountain shrubs</u>		
Artemisia tridentata ssp. *vaseyena*	mountain big sagebrush	ARTRV
Ceanothus velutinus	snow brush	CEVE
Prunus emarginata	bitter cherry	PREM
Prunus virginiana	choke cherry	PRVI
Ribes cereum	wax current	RICE
Rosa woodsii	woods' rose	ROWO
Symphoricarpos oreophilus	mountain snowberry	SYOR2
Salix spp.	willow species	SALIX
<u>Perennial grasses</u>		
Agropyron trachycaulum	slender wheatgrass	AGTR
Bromus marginatus	mountain brome	BRMA4
Bromus inermis	smooth brome	BRIN2
Calamagrostis rubescens	pinegrass	CARU
Dactylis glomerata	orchard grass	DAGL
Festuca idahoensis	Idaho fescue	FEID
Melica bulbosa	oniongrass	MEBU
Phleum pretense	timothy	PHPR
Poa bulbosa	bulbous bluegrass	POBU
Poa pratensis	Kentucky bluegrass	POPR
Pseudoroegneria spicata	bluebunch wheatgrass	PSSP6

Annual grasses

None

Perennial forbs

Achillea millefolium	common yarrow	ACMI2
Agastache urticifolia	nettleleaf giant hyssop	AGUR
Agoseris spp.	agoseris	AGOSE
Anemone piperi	Piper's anemone	ANPI
Aquilegia Formosa	western columbine	AQFO
Arenaria congesta	ballhead sandwort	ARCO5
Arnica cordifolia	heartleaf arnica	ARCO9
Artemisia ludoviciana	white sagebrush	ARLU
Aster spp.	Aster	
Camassia quamash	camas	CAQU
Circaea alpina	small enchanter’s nightshade	CIAL
Claytonia lanceolata	lanceleaf springbeauty	CLLA
Collomia linearis	tiny trumpet	COLI2
Collomia graindiflora	grand collomia	COGR4
Corallorhiza maculata	summer coralroot	COMA25
Delphinium bicolor	little larkspur	DEBI
Delphinium occidentale	subalpine larkspur	DEOC
Descurainia pinnata	western tansymustard	DEPII
Fritillaria atropurpurea	spotted fritillary	FRAT
Geranium Richardsonii	Richardson’s geranium	GERI
Habenaria unalascensis	Alaskan rein orchid*	HAUN
Hieracium spp.	hawksweed	
Hydrophyllum capitatum	ballhead waterleaf	HYCA4
Lathyrus holochlorus	thinleaf pea	LAHO
Lithophragma bulbiferum	bulbous wood-star	LIBU2
Lithophragma parviflorum	smallflower woodstar	LIPA5
Lupinus sericeus	silky lupin	LUSE4
Lupinus spp.	lupin species	
Maianthemum racemosum	feathery false lily of the valley	MARAA
Maianthemum stellatum	starry false lily of the valley	MAST4
Mahonia repens	creeping barberry	MARE11
Mertensia	bluebell	
Myosotis	forget-me-not	MYOSO
Osmorhiza chilensis (also *berteroi*)	sweetcicely	OSCH
Osmorhiza occidentalis	western sweetroot	OSOC
Phacelia heterophylla	varileaf phacelia	PHHE2
Potentilla glandulosa	sticky cinquefoil	POGL9

Potentilla gracilis	sticky cinquefoil	POGR9
Pseudostellaria jamesiana	tuber starwort	PSJA2
Senecio hydrophiloides also *foetidus*	tall groundsel	SEHY
Senecio integerrimus	lambstongue ragwort	SEIN2
Senecio serra	tall ragwort	SESE2
Sidalcea oregana	Oregon checkerbloom	SIOR
Soilidago spp.	goldenrod	
Thalictrum occidentale	western meadow-rue	THOC
Veratrum californicum	California false hellebore	VECA2
Viola adunca	hookedspur violet	VIAD
Viola nuttallii	Nuttall's violet	VINU2
Viola purpurea	goosefoot violet	VIPU4
Wyethia amplexicaulis	mule-ears	WYAM
Wyethia helianthoides	sunflower mule-ears	WYHE2

Annual forbs

Castilleja applegatei	wavyleaf Indian paintbrush	CAAP4
Claytonia perfoliata	miner’s lettuce	CLPE
Collinsia parviflora	maiden blue eyed Mary	COPA
Galium boreale	northern bedstraw	GABO2
Nemophila breviflora	Great basin nemophila	NEBR
Polygonum douglasii	Douglas' knotweed	PODO4
Taraxacum officinale	common dandelion	TAOF

Appendix B. Location of sampled aspen stands in the Owyhee Mountains, Idaho

Owyhee Mountain Aspen Sites
Sampled in 2005
Map coordinates: UTM, zone 11, datum NAD27

Plot Number	Date	PVT	Elevation	Aspect	Slope	Easting	Northing
2005001	20050608	potr	1721	30	7	510385	4706610
2005002	20050608	potr	1728	25	3	509549	4707053
2005003	20050609	potr	1857	340	26	512354	4700037
2005004	20050609	potr/juoc	1960	10	12	511701	4699560
2005005	20050609	potr	1746	320	25	510510	4706101
2005006	20050610	potr/juoc	1586	40	25	523228	4712362
2005007	20050610	potr/juoc	1591	20	25	523035	4712402
2005008	20050610	potr/juoc	1617	330	50	520829	4712560
2005009	20050613	potr/psme	1857	330	45	519797	4764910
2005010	20050613	potr/psme	1882	70	15	521539	4763265
2005011	20050613	psme	1900	80	33	521534	4763169
2005012	20050613	potr	1948	100	35	521212	4762898
2005013	20050613	potr/psme	2003	60	35	521316	4763149
2005014	20050614	potr/abla	2062	70	15	523086	4762930
2005015	20050614	potr		210	15	518384	4767948
2005016	20050614	potr/psme	1851	20	12	513881	4773705
2005017	20050615	potr/psme	1911	60	25	513558	4773399
2005018	20050615	potr/psme	1991	50	10	513379	4772476
2005019	20050615	potr/psme	2027	40	10	513550	4771304
2005020	20050615	potr	2112	20	18	513702	4771172
2005021	20050615	potr	2084	165	10	516439	4767902
2005023	20050616	potr/juoc	1774	20	25	520805	4771688
2005024	20050616	potr/juoc	1810	320	15	520717	4771530
2005025	20050616	potr/juoc	1858	20	15	521023	4771162
2005026	20050616	potr/psme	1924	5	5	520608	4769393
2005027	20050616	potr	1987	300	10	520586	4768964
2005028	20050616	port/abla	2086	80	10	516626	4768205
2005029	20050620	potr/psme	1781	350	13	511792	4732062
2005030	20050620	potr/psme	1789	100	45	511381	4731829
2005031	20050620	potr/psme	1822	40	20	511275	4731886
2005032	20050620	potr/psme	1843	150	35	510856	4731644
2005033	20050621	potr	2186	180	25	506943	4730872
2005034	20050621	potr	2098	250	35	506664	4730235
2005035	20050621	potr	2068	100	15	506456	4729896
2005036	20050621	potr	2051	220	28	506570	4729860
2005037	20050621	potr	1996	250	25	507055	4729426
2005038	20050621	potr	2133	290	35	507132	4730316
2005039	20050621	potr	1845	60	25	509703	4733904
2005040	20050622	potr/psme	1909	20	30	509431	4734447
2005041	20050622	potr/psme	1931	70	20	509411	4734267

2005042	20050622	potr/psme	1991	100	35	508792	4733909
2005043	20050622	potr	1976	130	10	509018	4733814
2005044	20050622	potr/psme	1971	90	5	509209	4733210
2005045	20050622	potr-psme	1948	320	40	509687	4733179
2005046	20050622	potr/psme	1877	10	4	509910	4733458
2005047	20050623	potr/psme/juoc	1997	180	10	509668	4732255
2005048	20050623	potr/psme	2020	5	60	509802	4731883
2005049	20050623	potr/psme	1998	80	5	509660	4732160
2005050	20050623	potre/psme/juoc	1859	80	35	511651	4728550
2005051	20050624	potr/psme/juoc	1766	340	40	512528	4732375
2005052	20050624	potr/juoc	1819	30	40	508215	4736059
2005053	20050624	potr/juoc	1786	340	2	508884	4736270
2005054	20050624	potr/psme/juoc	1762	320	45	508454	4736651
2005055	20050624	potr/juoc	1834	260	5	503755	4730294
2005056	20050627	potr	2034	10	5	514090	4725850
2005057	20050627	potr/psme/juoc	1887	40	12	509713	4734644
2005058	20050627	potr/juoc	1896	80	30	510199	4734392
2005059	20050627	potr/juoc	1782	60	25	510752	4734382
2005060	20050628	potr/juoc	1915	20	8	517724	4726917
2005061	20050628	potr/juoc	1994	110	10	516725	4727772
2005062	20050628	potr/juoc	2049	50	15	516320	4727307
2005063	20050628	potr		290	13	517139	4727045
2005064	20050628	potr/juoc	2021	40	8	514638	4726291
2005065	20050628	potr/psme/juoc	2030	320	15	514581	4727396
2005066	20050628	potr/psme	2042	320	10	514505	4727018
2005067	20050628	potr/psme	1883	0	25	513169	4727873
2005068	20050629	potr/psme	1897	50	32	512797	4728182
2005069	20050629	potr/juoc	1903	340	25	512550	4727911
2005070	20050629	potr/psme	1791	60	25	512635	4729514
2005071	20050629	potr/psme	1953	20	3	511291	4730322
2005072	20050629	potr/psme	2003	20	12	511417	4730452
2005073	20050629	potr/psme	1978	90	10	511714	4730366
2005074	20050629	potr/psme/juoc	1854	60	10	512406	4730777
2005075	20050630	potr	1831	0	15	513200	4730020
2005076	20050630	potr	1641	20	3	507852	4737814
2005077	20050630	potr/juoc	1728	300	50	505828	4736979
2005078	20050714	potr	2080	34	47	520705	4768210
2005079	20050716	potr/juoc	1689	45	29	513733	4703455
2005080	20050718	potr/juoc	1682	350	7	514240	4702721
2005081	20050719	potr/juoc	1736	10	14	531389	4713774
2005082	20050719	potr/juoc	1650	10	25	527060	4713441
2005083	20050719	potr/juoc	1681	10	18	526820	4713339