ENVIRONMENTAL CONTROLS OVER FOREST SUCCESSION OF A FORMER OAK SAVANNA, JIM'S CREEK, WILLAMETTE NATIONAL FOREST, OREGON

by

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A THESIS

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Oregon white oak (*Quercus garryana*) savanna is an imperiled ecosystem in Oregon's Willamette Valley. Over the past 150 years, changes to fire regimes have resulted in the succession of oak savanna to woodland and forest. Analysis of a former oak savanna at Jim's Creek, Willamette National Forest, revealed that Douglas-fir (*Pseudotsuga menziesii*) now dominates much of the historic savanna with oaks restricted to remnant meadows and meadow edges. Canonical correspondence analysis (CCA) identified slope, pH, soil nitrogen, and silt and clay content as important factors associated with current distribution of Oregon white oak, Douglas fir, Ponderosa pine (*Pinus ponderosa*) and incense cedar (*Calocedrus decurrens*). Mature living oaks were found in areas with high pH, soil nitrogen, clay content and water-retaining microtopography. Meadows have been

retained in areas with shallow soil, high clay and low silt content. Thus, this study identified environmental variables that characterize current oak refuges within former savanna.

This thesis includes my co-authored materials.

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CHAPTER I

INTRODUCTION

Historic and Current Oak Savanna

Oak savanna is believed to have existed in North America for 20-25 million years (Barry and Spicer 1987). When Euro-Americans began settling the Midwestern United States, oak savanna was found from Minnesota to Texas and had been relatively stable there for thousands of years (Nuzzo 1986). Approximately 12,000,000 ha of oak savanna were found in the upper Midwestern United States when settlement of the region began in the early nineteenth century (Nuzzo 1986). In the Pacific Northwest, oak savanna is estimated to have covered 500,000 ha prior to Euro-American settlement around 1850 (Vesely and Tucker 2004). Today, oak savanna is considered critically endangered in both the Midwestern United States and Oregon's Willamette Valley (Noss et al. 1995).

In the Pacific Northwest, Oregon white oak (*Quercus garryana*) was the dominant tree of historic oak savanna. It is the principal native oak in Oregon and the only native oak in British Columbia and Washington (Stein 1990). Oregon white oak has the widest range of any oak species in the Pacific Northwest (Vesely and Tucker 2004), occurring from Vancouver Island, British Columbia to southern California.

Prior to the settlement of the Pacific Northwest by Euro-American settlers, Oregon white oak savanna was a major ecosystem in Oregon's Willamette Valley (Thilenius 1968, Hulse et al. 2002) and covered approximately 213,580 ha (Hulse et al. 2002). Today, more than 99% of the oak savanna historically present in the Willamette Valley has been destroyed or severely degraded (Noss et al. 1995). Approximately 40% was lost to agriculture, and roughly 10% was lost to urbanization and development of rural areas, while nearly 32% has succeeded to forest as a consequence of reductions in fire frequencies (Hulse et al. 2002).

Historically, the savanna was maintained by frequent, low-intensity fires ignited by Native Americans and occasional lightning strikes (Boyd 1986, Agee 1993, Whitlock and Knox 2002). Recurring fires in the savanna maintained fire-tolerant species such as Oregon white oak (Stein 1990) and ponderosa pine (*Pinus ponderosa,* Oliver and Ryker 1990). Oaks have thick bark (Stein 1990) and the ability to re-sprout following fires that make mature oaks fire resistant (Stein 1990, Howard 1991). Because young Douglas-fir (*Pseudotsuga menziesii*), the primary species that has successfully invaded oak savanna (Stein 1990), is fire-intolerant (Hermann and Lavender 1990, Uchytil 1991), it was historically prevented from establishing in high densities in the savanna. However, in the absence of fire, it is often able to populate savanna in high densities.

Whereas Douglas-fir is shade-tolerant and can be found in stands with greater than 2,500 tree/ha, Oregon white oak is shade-intolerant (Stein 1990). Oregon white oak is generally slow growing and reaches a height of 15 to 27 m under favorable conditions (Stein 1990). In contrast, Douglas-fir grows more rapidly and experiences its fastest growth between the first 20 and 30 years of age, and trees 76-m tall are common in low elevation old-growth forests (Hermann and Lavender 1990). Thus, in the absence of fire, Oregon white oak is often overtopped and shaded out by faster growing, taller, shade-tolerant trees such as Douglas-fir (Stein 1990).

Invasion of Oregon white oak savanna has resulted in different plant community types across the landscape. While many areas of former oak savanna have become densely forested, some are filling in only slowly or appear to be relatively stable. Furthermore, most living oaks appear to be restricted to certain environmental conditions despite Oregon white oak being tolerant of a wide range of growing conditions (Stein 1990). It is likely that environmental variables, such as soil and site physiographic factors, may influence the successional dynamics of oak savanna, allowing some areas to be easily invaded, while succession is restricted in other areas.

Life History Characteristics, Site Factors and Succession

Because of the reduction of fire frequency, historic savanna in the Willamette Valley has succeeded to conifer forest mostly dominated by Douglas-fir (Stein 1990, Franklin and Dyrness 1998). In the southeastern part of the Willamette Valley, Douglas-fir, ponderosa pine and incense cedar (*Calocedrus decurrens*) occur as components of Oregon white oak communities (Thilenius 1968). Douglas-fir and incense cedar now occupy large areas of the landscape, including former oak savanna, in high densities, while remnant prairie and savanna appear to be confined to small areas of refugia. It is likely that these refugia have not been invaded because different abiotic tolerances of tree species influence successional dynamics. Consequently, living Oregon white oak may be confined to certain soil and site physiographic conditions that have allowed remnant savanna to persist because Douglas-fir and incense cedar are unable to establish or mature there.

Soil moisture has been shown to be important in savanna community structure, as savanna and grassland composition often vary across soil moisture gradients (Kirkman et al. 2001; Ringrose et al. 1998; Skarpe 1996; Benshahar 1991; Belsky 1990; Walker 1987; Johnson and Tothill 1985). Most of these studies have been large-scale regional analyses, and the effect of rainfall on community composition often depends on soil texture and type and vegetative physiology. It is possible, however, that heterogeneous microtopography influencing soil moisture at the site level may influence conifer invasion of oak savanna in the Willamette Valley.

Soil texture also has been important in describing plant community structure in other savanna ecosystems. Williams et al. (1996) examined savannas in northern Australia and found decreasing canopy cover correlated with increasing clay content. Johnson and Tothill (1985) found decreasing woodland cover associated with high clay content in savannas worldwide. Soil texture may be an important variable in maintaining current oak savanna through its effect on soil moisture availability. In the Willamette Valley, oak is often found in soils with a subsurface clay layer that limits water infiltration (Stein 1990). Clay has high water tension and can have limited moisture availability in comparison to coarser soil textures (Chapin et al. 2002). During dry Pacific Northwest summers, these soils likely become droughty. Oregon white oak and ponderosa pine are both highly drought tolerant (Stein 1990, Oliver and Ryker 1990, Wilken and Burgher 2000), at least in part due to their quick establishment of a deep taproot when they are young (Stein 1990, Oliver and Ryker 1990). In contrast, Douglas-fir and incense cedar are not tolerant of droughty conditions as seedlings (Hermann and Lavender 1990, Powers and Oliver 1990). Douglas-fir tolerates a wide range of conditions but grows best on soil that is deep with good aeration (Hermann and Lavendar 1990). Incense cedar can also grow in various soil conditions but thrives in deep clay loams and deep sandy loam or coarse-textured pumice soils that are well-drained (Powers and Oliver 1990).

Soil depth may be an important factor influencing successional dynamics by limiting species' abilities to successfully establish or mature. Oregon white oak communities in British Columbia are often found on shallow soil and rock outcrops (Klinka et al. 1996). Heikens and Robertson (1995) found that remnant oak savanna barrens occur on shallower soils than neighboring xeric forest in southern Illinois. Arabas (2000) looked at serpentine barrens in Pennsylvania and Maryland and found that pine (*Pinus rigida*) savanna was associated with shallow soils, oak (*Q. stellata* and *marilandica*) woodlands were found on intermediate-depth soils and hardwood forests (excluding oaks) were associated with well-developed soils. Douglas-fir and incense cedar both require deep soils for optimal growing conditions (Hermann and Lavender 1990, Powers and Oliver 1990), and may be restricted to areas of adequate soil depth.

The amount of heat that areas experience because of aspect or as a function of slope and aspect (heat load) might protect certain savanna areas from invasion. Douglas-fir seedlings do best in partial shade, especially on south-facing exposures (Hermann and Lavender 1990). Oregon white oak and ponderosa pine, however, are both tolerant of exposure (Stein 1990, Gray et al. 2005). Oregon white oak communities in British Columbia are often found on south-facing slopes, but Douglas-fir and evergreen Pacific madrone (*Arbutus menziesii*) communities predominate on north and protected south-facing slopes (Klinka et al. 1996). Mast et al. (1997) found that Douglas-fir forest invasion of a ponderosa pine grassland was greatest on north facing slopes in the Rocky Mountains. They attributed differential invasion of north and south facing slopes to cooler temperatures and higher moisture in the north slopes.

At a former oak savanna in the Willamette Valley foothills, Day (2005) found the highest densities of young trees (< 25 years) on south edges of prairie and savanna, and the age and species' distributions of trees in these areas were indicative of ongoing invasion. Day proposed that older trees found along the south edges were likely "nursing" saplings by providing sufficient shade. Day also found that north edges had the lowest tree densities and attributed this to an inability of most trees to establish in the harsh conditions and low shading that likely characterize them.

Soil nutrient content may also play a fundamental role in tree community structure and forest successional dynamics of former savannas. In British Columbia, Oregon white oak is associated with soils with moderate to high nitrogen content (Klinka et al. 1996). It is uncertain whether this correlation results from the growth requirements of the oak or as a feedback mechanism from oaks' presence. Gambel oak (*Q. gambelii Nutt.*) has been shown to increase nitrogen availability in ponderosa pine forest in

Arizona (Klemmedson 1991). Douglas-fir growth, on the other hand, can be nitrogen limited (Steinbrener 1981; Shaw et al. 1998; Piatek et al. 2003). If Oregon white oaks are creating nitrogen-rich micro-sites in addition to providing shade for saplings, it is likely that they are creating suitable conditions for Douglas-fir to establish in the absence of fire.

Generalizing environmental controls on tree community structure in savannas is difficult because mechanisms of control may vary among different regions or topographic areas. For example, in wet climates or depressional areas high clay content can limit plant growth because soils become waterlogged and do not drain well. In drier climates or topographic areas, clay might prevent vegetation from accessing water during droughts because of its high water tension properties. However, based on studies of savanna worldwide and the current conditions that Oregon white oak is generally associated with, one would suspect that the remnant oak savanna in the Pacific Northwest may be edaphically controlled by factors such as soil depth, aspect, heat load, slope and/or soil texture.

Successional Dynamics and Current Tree Community Composition of a Former Oak Savanna in the Willamette Valley

There is currently great impetus to restore oak savanna throughout the Pacific Northwest because of its imperiled status. The decline of oak habitats has resulted in large losses in local and regional biodiversity (Gumtow-Farrier and Gumtow-Farrier 1994). Increased tree density and fuels accumulation are an additional consequence of this succession, both of which foster the conditions for catastrophic wildfires. However, little is known about how environmental characteristics have influenced succession of oak savanna, or how environmental factors define current oak refugia. Although the vegetative structure of Oregon white oak communities around the Pacific Northwest has been examined (Thilenius 1968, Klinka et al. 2002), there are no studies describing current tree community structure of former oak savanna as a function of environmental variables. Erickson (2002) differentiated Oregon white oak communities in British Columbia based on environmental variables using indirect gradient analysis. However, no studies have been done using direct gradient analysis. Consequently, studies are lacking that identify how environmental variables influence current savanna refugia or the current distributions of trees in a former oak savanna.

I examined the current tree community structure and oak savanna refugia of a former oak savanna at Jim's Creek in the foothills of Oregon's Willamette Valley as a function of environmental variables. This site was historically predominantly savanna with open-grown Oregon white oak, Douglas-fir, ponderosa pine and incense cedar (Day 2005). The site is now dominated by Douglas-fir and incense-cedar. Patches of savanna and prairie remain scattered within the forest matrix and oak appears to be confined within close proximity of these areas.

Dendrochronological data indicate that 75% of the trees currently found at Jim's Creek are less than 125 years of age (Day 2005). Euro-American settlement began at approximately 1850, which was associated both with declines in anthropogenic ignitions and later with active fire suppression. The rapid influx of trees proceeding Euro-

American settlement and the presence of formerly open-grown trees scattered beneath Douglas-fir, provide evidence that Jim's Creek was predominantly savanna prior to the reduction in fire frequencies.

Jim's Creek has experienced the effects of post-settlement fire suppression but has remained free of other anthropogenic disturbances such as grazing, logging or agriculture, with the exception of a 25-ha ponderosa pine plantation (Day 2005). For these reasons, it is an ideal site to study successional trajectories of a former oak savanna in terms of the relationships between environmental variables and current community structure. In addition, snags and logs have been left undisturbed across the site and offer insight into the historical tree community structure. The site ranges in elevation from 600 m to 1000 m above sea level and represents both the high-elevation limit of Oregon white oak's former range, and an important part of Oregon white oak's former range.

I addressed three main questions in this study: 1) Is the extent of Douglas-fir invasion of a former oak savanna influenced by environmental variables? 2) In areas that have resisted invasion, is succession influenced by environmental variables? 3) Where and under what conditions are oak refugia found?

Canonical Correspondence Analysis (CCA) was used to investigate how slope, heat load, soil depth and texture, microtopography, pH and organic matter and soil nitrogen are related to the current distribution of Oregon white oak, Douglas-fir, ponderosa pine and incense cedar in a former oak savanna. Direct gradient analysis was chosen to describe species and size class distributions because the main objective was to describe tree community structure as a function of environmental variables.

Non-metric multidimensional scaling (NMS) was selected to supplement the CCA because plots without trees were unable to undergo ordination. Plots were ordinated solely on environmental variables without using tree densities. Plots were then labeled by community type to determine if environmental variables were predictive of community type. NMS is an indirect gradient analysis that works well with data that is nonnormally distributed and does not make linear assumptions among variables (Bruce and McCune 2002).

I used t-tests to examine whether remnant savanna and prairie were environmentally different from areas that have undergone succession. They were also applied to determine whether the distribution of large (DBH>25 cm) oaks at Jim's Creek is related to environmental variables. The distributions of living and dead oaks within community types were analyzed using Kruskal-Wallis tests to determine if oak densities differed among community types.

This study is part of a larger collaborative project between the University of Oregon and the U.S.D.A. Forest Service funded by the Joint Fire Science Program. Dr. Bart Johnson, from the University of Oregon Department of Landscape Architecture, Dr. Scott Bridgham, from the University of Oregon Center for Ecology and Evolutionary Biology, and Jane Kertis and Jennifer Lippert from the U.S.D.A. Forest Service are the principal investigators. The overlying goal of the project is to investigate the potential to integrate oak savanna restoration with fuels management. If successful, this strategy has the potential to combine the conservation objective of protecting an imperiled ecosystem with the social objective of reducing the risk of catastrophic wildfire. To do so, the project is investigating the historic and current distributions of oak savanna in the Willamette Valley and relating them to environmental variables. The information gathered from this project will be applied to a stakeholder-informed evaluation of alternative approaches to restoration at both site and landscape scales.

Ecological information is greatly needed to guide oak savanna restoration efforts in the Willamette Valley. It is important to understand which microclimatic and edaphic conditions have allowed some areas of oak savanna to successfully resist invasion while other areas are now densely forested. This information can inform management strategies for restoring and maintaining oak savanna across the full range of environmental conditions of its historic distribution.

CHAPTER II

ENVIRONMENTAL CONTROLS OVER FOREST SUCCESSION OF A FORMER OAK SAVANNA, JIM'S CREEK, WILLAMETTE NATIONAL FOREST, OREGON

Introduction

Oregon white oak (*Quercus garryana*) savanna was once a major ecosystem in Oregon's Willamette Valley (Thilenius 1968; Hulse et al. 2002). Historically, oak savanna persisted because of frequent, low-intensity fires ignited by Native Americans and occasional lightning strikes (Boyd 1986; Agee 1993, Whitlock and Knox 2002). However, since the time of Euro-American settlement of the western United States, anthropogenic ignitions appear to have been declining over time, and active fire suppression became a prominent land management strategy (Agee 1993). Conifer invasion of Oregon white oak savanna due to reduced fire frequency, along with urbanization and intensive agricultural practices, has contributed to the decline of oak savanna throughout western Oregon (Erickson 1993, Noss et al. 1995, Barnhart 1996).

The decline of oak habitats has resulted in large losses in local and regional biodiversity (Gumtow-Farrier and Gumtow-Farrier 1994), and Oregon white oak savanna is now considered an endangered ecosystem (Noss et al. 1995). Furthermore, changes to fire dependent systems have resulted in higher tree density and fuels accumulation, which have also created conditions that increase the risk of catastrophic wildfires (Arno and Allison-Bunnell 2002). Thus, restoration of oak savanna can serve both biodiversity and fuels management objectives.

However, the causes and consequences of fire frequency changes in former oak savanna are complex. Mature oaks are fire-tolerant, and frequent, low-intensity burns historically prevented most other trees species from invading oak savannas. Although many areas of former oak savanna have become densely forested as a consequence of reduced fire frequency and extent, some are filling in only slowly or appear to be relatively stable. It is likely that environmental factors influence the succession of oak savanna and the stability of the remaining refuges. Other studies have revealed the importance of soil and site characteristics in the community structure of savannas, but most of these have focused on tropical or mid-western U.S. savannas (Benshahar 1991, Bowman 1991, Heikens and Robertson 1995, Williams 1996, Arabas 2000, Ruggiero et al. 2002). Oregon white oak communities in the Willamette Valley have been described based on plant community structure and environmental characteristics (Thilenius 1968), and Erickson (2002) related environmental variables to Oregon white oak community structure at the northern extent of its range in British Columbia. No studies have examined how environmental variables such as soil and site physiographic characteristics might influence successional dynamics of former Oregon white oak savanna in the Willamette Valley. Furthermore, no studies have used environmental characteristics to define current tree community structure of former Oregon white oak savanna.

I sought to answer three primary questions in this study. First, is the extent of Douglas-fir invasion of a former oak savanna dependent on environmental variables? Second, in areas that have resisted invasion, to what extent is succession restricted by environmental variables? Third, where and under what conditions are oak refugia found? Ordination and other analyses were used to investigate how nine environmental variables are related to the current distribution of the four dominant tree species.

Methods

Study Area

Jim's Creek (122°25'W, 43°30'N) is a 276-ha site in Oregon's Willamette National Forest. It lies on a mostly south-southwest facing slope between a ridgetop and the Middle Fork Willamette River in the lower elevations of the Cascade Mountains. It ranges in elevation from 600 m to 1000 m above sea level. Jim's Creek lies approximately 25 km south of the city of Oakridge, where average annual precipitation is 116 cm. The climate is Mediterranean with summer drought and most of the precipitation between November and April.

There is substantial evidence that historically Jim's Creek was a savanna with open-grown Oregon white oak, Douglas-fir (*Pseudotsuga menzeisii*), ponderosa pine (*Pinus ponderosa)* and incense cedar (*Calocedrus decurrens*) (Bailey and Winkler 2002, Day 2005). Today, Jim's Creek is mostly woodland and forest dominated by Doulgas-fir between 75 and 125 years old (Day 2005). Many of the formerly open-grown oak and Ponderosa pine now persist only as snags and logs within the forest matrix. Living oaks, many in declining health, are mostly confined to remaining savanna pockets and unforested prairie edges.

Sampling Methods

Five stratified random belt transects were established across the site (Figure 1). Transects were oriented north-south to run mostly up and down the slope from the river to the ridge. To determine transect locations, the site was divided into five equal-width segments running from east to west. Within each segment, a single transect location was randomly selected. An east-west unpaved road that bisects the site served as a dividing point for identifying north and south segments of the transects. Two of the five transects were terminated at the north edge of the road because of a pine plantation on the south side. Otherwise, transects ran from the top of the ridge on the northern boundary of the site to the paved highway along the Middle Fork Willamette River that sets the site's southern boundary. Transects were 30-m wide and between 240 and 660-m long, totaling 3420 m in length. Transects were initiated a minimum of 20 m from the road to avoid areas where vegetation had been affected by the road.

Vegetative Data

Every 60 m along each transect a 200-m^2 circular plot was established. The species, size-class and number of all live trees and snags with a diameter at breast height (DBH=137-cm height) were recorded within the plot. Oak logs and conifer logs > 75-cm DBH were also recorded. DBH was recorded to the nearest cm for all oaks and any tree

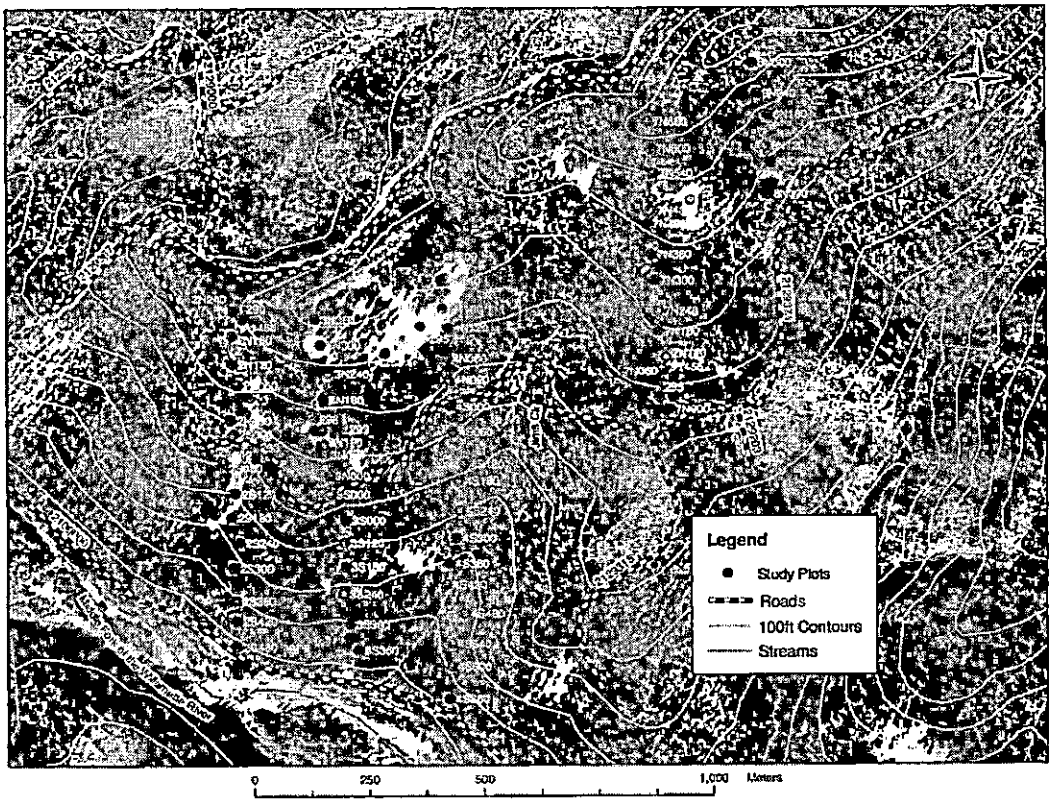


Figure 1. Location of study plots at Jim's Creek. Plots were located along transects that ran from the top of the ridge on the northern boundary of the site to the paved highway along the Middle Fork Willamette River that sets the site's southern boundary.

larger than 50 cm. Trees were tallied into the following DBH size classes: >0 to 12 cm, >12 to 25 cm and >25 to 50 cm. Oaks were assigned one additional size class, >50 cm, whereas conifers were assigned size classes for >50 to 75 cm, >75 to 100 cm, and >100 cm.

Because large conifers and oaks of any size are relatively uncommon on the site, the 200-m^2 plots were too small for accurate estimates of their densities. To improve accuracy, data was recorded for all oaks and conifers $\geq$ 75cm DBH within a larger 900-

m^2 plot centered on the 200-m^2 plot and bounded by the belt transect. The DBH of all oak logs and snags were also recorded within the 900-m^2 plot.

Canopy cover was recorded between July and September at the center of every plot using a spherical densiometer (Lemmon 1956). Plots were classified based on percent canopy cover into one of the following community types (adapted from Packard 1993): prairie (0-5% canopy cover), savanna (6-25% canopy cover), woodland (26-60%) and forest (>60%). Two additional community types, edge and transition, were defined spatially (regardless of canopy cover) because observations suggested that they were important for analyzing successional dynamics. Edges were defined as the tree-line boundary separating forest or woodland from savanna or prairie. At Jim's Creek this boundary is typically quite distinct. Transitions are areas adjacent to a current or historic savanna or prairie that are densely treed but appear to have different community structure than surrounding woodland or forest. Live and dead oaks are often found in this zone and it appeared to represent a unique community type. However, no transition plots were sampled within the stratified random belt transects. This was not surprising since this zone encircles prairie or savanna, and the proportional area of prairie or savanna is very low. To incorporate this community type in analyses, additional plots were established outside the transects. Transition plots were located within a broad zone characterized by scattered concentrations of dead and/or live oaks along the prairie or savanna boundary with woodland or forest. The plot center was randomly located within the zone of oaks (if any) but did not necessarily include any oaks. This was typically 15 to 30 m from the edge and was never less than 8 m so as to avoid including part of the savanna or prairie.

Because prairie and savanna plots were poorly represented by the random transects, seven additional plots were selected to represent these community types as well.

The actual proportions of the site occupied by different community types were analyzed using air photos in conjunction with transect data information. The percentage of prairie, edge and transition were defined as follows: the savanna and prairie included areas with no or low tree densities. Because edges were defined as including both part of the prairie and savanna and part of the more densely treed areas surrounding them, the outer 8-m wide perimeter of the area with few or no trees was excluded from prairie and savanna so as not to overlap with the edge and not to include the rooting zone of adjacent areas that were densely treed. The edge included the outer 8-m perimeter of the areas with few or no trees in addition to the 8-m ring of more densely treed areas that encircled it, forming a 16-m wide envelope around the prairie and savanna. The transition zone formed another 16-m wide ring around the edge. Of the remaining area, which was either forest or woodland, the proportions of sampled plots that were forest and woodland were used to estimate the actual proportions of these community types across Jim's Creek.

Environmental Variables

At every 200-m^2 plot, environmental variables were recorded. Percent slope was recorded as the average of one up-slope and one down-slope measurement taken with a clinometer. Aspect was recorded using a compass and was later transformed to an index of solar aspect (Parker 1982). Horizontal and vertical microtopographies were visually assigned a quantitative value ranking from most water shedding to most water collecting:

(1) convex, (2) flat, (3) undulating, and (4) concave. Horizontal and vertical microtopographies were summed to an overall microtopography value for the plot as a surrogate for water shedding and collecting capability (two represents maximum water shedding and eight represents maximum water collecting). Percent cover of surface rock and exposed rock were recorded in cover classes based on ocular estimates using the Braun-Blanquet method (Braun-Blanquet 1932) with a Daubenmire modification (Daubenmire 1959). Soil depth was measured using a .635-cm steel bit attached to a battery-operated drill to a maximum depth of 1.5 m. A preliminary analysis of power indicated that eight replicates of soil depth were necessary because measurements were often obstructed by soil rocks. The maximum depth was used for statistical analyses. Heat load was calculated using slope in radians and folded aspect (McCune and Keon 2002).

Mineral soil samples were randomly extracted using an Eigelkamp soil auger. Three replicates to 20-cm depth were collected from each plot and composited. Ten samples of the organic layer were randomly extracted from each plot using a tulip planter and were composited. Samples were transported immediately to the lab for analysis. Soil pH was determined using a pH meter in a 1:1 soil-water slurry. Soil bulk density was calculated based upon oven-dry mass (at 60 °C) and the volume of the cores. Soil texture was assessed using the hydrometer method (adapted from Gee and Bauder 1986) and sand was later isolated with a 53-μm mesh sieve, which was then oven-dried and weighed. Total carbon and nitrogen levels were measured using a Costech Analytical CHN analyzer.

Statistical Analyses

Community stand structure was defined by the densities of trees in different size classes. Because Oregon white oak, Douglas-fir, ponderosa pine and incense cedar comprised 98% of all trees sampled, my analysis was confined to these four dominant species.

Heat load and slope were log transformed, and soil nitrogen, organic layer nitrogen, soil depth and aspect were square-root transformed to normalize their distributions. Solar aspect index was found to be highly correlated with heat load (r = -0.87) and was removed from subsequent analyses. Soil and organic layer carbon were highly correlated with soil (r = 0.76) and organic layer (r = 0.94) nitrogen, respectively and were removed from the analyses because previous studies have shown that Douglas-fir are limited by nitrogen and respond to nitrogen fertilization (Steinbrener 1981; Shaw et al. 1998; Piatek et al. 2003).

The influence of environmental factors on stand structure was analyzed using Canonical Correspondence Analysis (CCA). CCA is a direct gradient analysis technique that ordinates community structure based on environmental variables (McCune and Grace 2002). Samples are weighted on total abundance, amplifying distributions of rare species-size class distributions. CCA ordinations were run using PC-ORD (Version 4, McCune and Mefford, 1999).

The main matrix was composed of tree densities for twenty-two species by size class variables. Six plots with no trees were excluded from the CCA because PC-ORD cannot perform ordination on empty rows. Nine environmental variables were used in the analysis: pH, percent clay, percent silt, soil nitrogen, organic layer nitrogen, heat load, slope, soil depth and microtopography. Percent surface rock and percent exposed rock were excluded from analyses because outliers in both categories resulted in distributions that were strongly skewed with a few plots with high values, creating ordinations that were unstable. Graphical examination of the data suggested that these variables were not important in explaining stand structure.

The environmental variables in each plot were ordinated with Non-metric Multidimensional Scaling (NMS). Community types (i.e., prairie, savanna, woodland, forest, transition, edge) were overlain on the resulting graph to qualitatively evaluate whether environmental variables were predictive of community type. This analysis was necessary to see if plots with no trees, which could not be included in the CCA, were environmentally distinct. NMS is an indirect gradient method that uses rank distances without assumptions of normality to ordinate sample units along axes with minimal stress and acceptable stability (McCune and Grace 2002). NMS was run using Sorenson (Bray-Curtis) distance in PC-ORD (Version 4, McCune and Mefford, 1999). Random starting configuration was used with 40 real data runs. The nine environmental variables previously mentioned were modified using general relativization so that all variables were given equal weight in the analysis (McCune and Grace 2002).

To test for environmental constraints on succession of the historic vegetation to forest or woodland, environmental variables in savanna and prairie were compared against transition, woodland and forest with t-tests using JMP IN ver. 5.1 (SAS Institute Inc., Cary, NC). Edge plots were not included in this analysis because, by definition, they contain both prairie or savanna and a more densely-treed community type, and environmental measurements were recorded on the plot as a whole. To test whether oak distribution was characterized by environmental variables, plots with surviving large (DBH > 25 cm) oaks were compared to plots without large oaks using t-tests. Oaks > 25 cm DBH were classified as large trees because they represented the largest 24% of the oaks found at Jim's Creek.

Kruskal-Wallis tests were used to investigate whether living and dead oak densities differed among community types. Densities were log transformed to normalize their distributions.

Results

Tree Community Structure

A total of 970 live trees of the four dominant species and 60 oak snags and logs were sampled from 2003 to 2005. Of the 79 plots sampled, there were 5 prairie, 7 savanna, 10 edge, 7 transition, 17 woodland and 33 forest plots. Because transects were located randomly, the center of edge plots included variable proportions of prairie and other more densely-treed community types, so edge plots were excluded from the comparison of average tree density among community types. Prairie and savanna plots were combined because they were representing similar community types and were uncommon across the site.

Distinct species and size class distributions are evident among community types (Table 1 and Figure 2). Douglas-fir was the dominant species across the site and Oregon

Table 1. Tree densities by community type. Mean densities (trees/ha) ± one standard error are given for each of the four dominant tree species within each community type. The Jim's Creek total density is derived from weighted averaging of community types based on the proportional area of each community type across the site from air photo analysis.

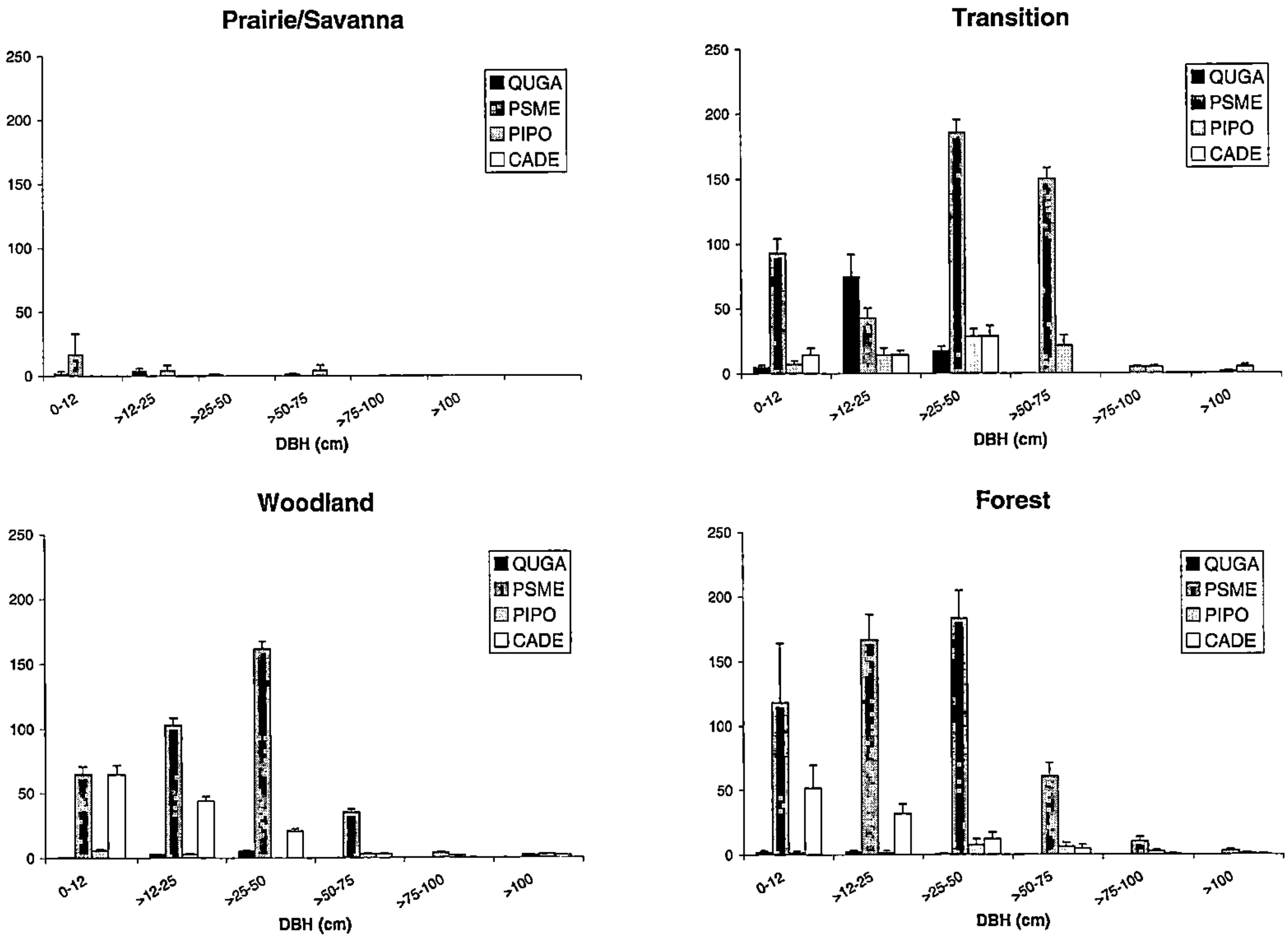
Community Type	Oregon white oak	Douglas-fir	Ponderosa pine	Incense cedar	Total
Prairie/savanna (n=12)	7 ± 4	17 ± 17	8 ± 6	0	32
Transition (n=7)	97 ± 52	478 ± 65	81 ± 41	57 ± 41	712
Woodland (n=17)	8 ± 5	371 ± 43	16 ± 6	134 ± 45	526
Forest (n=33)	5 ± 3	542 ± 48	21 ± 6	101 ± 23	669
Jim's Creek	**10**	**438**	**21**	**98**	**567**

white oak was least common. The highest mean tree density was found in the transition zone followed by the forest and woodland, with the prairie and savanna having the lowest density. Douglas-fir dominated the transition, woodland and forest. Douglas-fir was the dominant small tree (DBH > 0-12 cm) in the prairie and savanna, even though oak and ponderosa pine were the only larger trees established there.

Environmental Variables and Tree Community Structure

Canonical correspondence analysis revealed species-specific patterns of size-structured tree distribution in environmental space (Figure 3). The first axis (eigenvalue = 0.233) was most strongly correlated with percent clay, followed by soil nitrogen, pH and percent silt (Table 2) and was significant when Monte Carlo permutations were performed ($p = 0.01$). This axis represents a gradient from acidic soil high in silt to more

Figure 2. Mean densities of size-classes by community type: Oregon white oak (QUGA), Douglas-fir (PSME), ponderosa pine (PIPO) and incense cedar (CADE) in different community types.


Prairie/Savanna
Transition
Woodland
Forest
QUGA
PSME
PIPO
CADE
0
50
100
150
200
250
0-12
>12-25
>25-50
>50-75
>75-100
>100
DBH (cm)

basic soil high in clay and nitrogen. Of the tree community structure variance explained by the environmental variables, 73.3% was represented in the first axis (p = 0.01). The second axis (eignenvalue = 0.129) primarily represents a gradient in slope; soil nitrogen and heat load were also moderately correlated with this axis.

Although a large portion of the tree community composition was explained as a function of environmental variables, stand structure was not well defined in the CCA as a function of species-size class densities. The first and second axes only represented 7.7% and 4.3% of the variance in the species data, respectively. However, non-metric multidimensional scaling of the plot tree densities produced a very similar grouping of species by size-class and explained 84.6% of the community variance (data not shown). The primary focus of this research, however, was to understand how environmental variables relate to current tree community structure of a former oak savanna, rather than to define current stand structure based on vegetative patterns, and environmental variables were much more strongly correlated with tree community composition in the CCA.

Oaks of every size class scored negatively on the first axis, with larger oaks tending to have smaller axis one scores, indicating they were found in more basic soils with high clay and soil nitrogen. All of the ponderosa pine size classes scored negatively on the first axis, and five of six size classes were found in the lower left quadrant, indicating they were also associated with more basic soils high in clay and soil nitrogen. Four of six Douglas-fir size classes scored positively on the first axis, suggesting they were found in more acidic soils with lower clay content and soil nitrogen. The

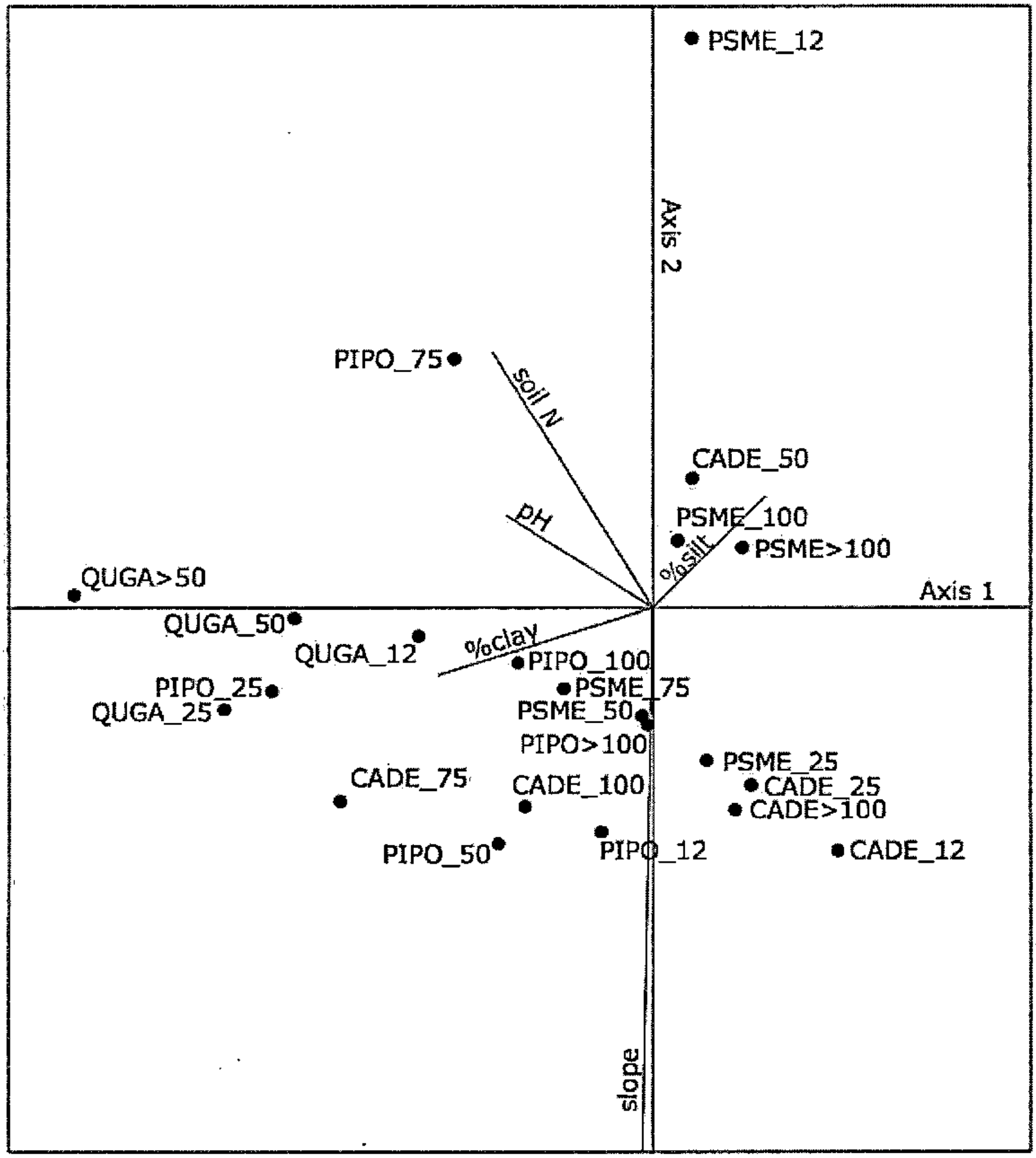


Figure 3. Biplot of the CCA ordination. Twenty-two size class-species tree densities were ordinated using nine environmental variables (pH, soil depth, soil and organic layer nitrogen, percent silt and clay, microtopography, heat load and slope): QUGA = *Quercus garryana* (Oregon white oak), PSME = *Pseudotsuga menziesii* (Douglas-fir), PIPO = *Pinus ponderosa* (ponderosa pine), CADE = *Calocedrus decurrens* (incense cedar). Numbers following the four-digit species code represent the maximum DBH for that size class. For example, PSME_12 represents Douglas-fir > 0-12 cm and PSME_25 represents Douglas-fir > 12-25 cm. A > sign preceeding a number indicates a size class in which all trees had a DBH larger than that number.

smallest Douglas-fir trees were positively correlated with Axis 2, indicating an association with areas with low slope. One plot located on a bench with a large number of small Douglas-fir trees (1250 trees/ha) was responsible for this size class appearing as an outlier in the ordination. When the CCA was run without this plot, slope was no longer an important variable in explaining the distribution of trees, but soil nitrogen, percent silt and clay and pH still remained important (data not shown). Because this plot represented the site of greatest small-sized Douglas-fir invasion at Jim's Creek, it was not removed from the analyses.

Table 2. CCA results. Eigenvalues, correlations of environmental variables, and species-environment correlations for the two axes in the CCA. Correlations of environmental variables are intraset correlations (ter Braak 1986). Species-environment correlations are Pearson correlations between sample scores based on the species data and sample scores that are linear combinations of the environmental variables.

	Axis 1	Axis 2
Eigenvalue	0.233	0.129
pH	-0.586	0.129
Percent clay	-0.859	-0.083
Percent silt	0.445	0.156
Soil nitrogen	-0.654	0.356
Organic layer nitrogen	0.106	0.087
Heat load	0.044	-0.338
Slope	-0.030	-0.871
Soil Depth	-0.177	0.272
Microtopography	-0.336	-0.212
Pearson Spp-Env Correlation	0.773	0.557

Five of six incense cedar size classes scored negatively on the second axis, suggesting increasing occurrence with increasing slope. The one incense cedar size class that scored positively on the first axis was clustered with large Douglas-fir (DBH > 75 cm) and was associated with high silt.

Environmental Variables and Community Types

Non-metric multidimensional scaling of the environmental variables showed distinct patterns of community types in relation to environmental variables. A three-dimensional solution represented 85.2% of the variation between the distances in the ordination and the original data space (stress = 14.6). Axes 1, 2 and 3 represented 35.4%, 30.5% and 19.3% of this variation, respectively (only Axes 1 and 2 are shown in Figure 4). Acceptable stability was attained (instability = 0.0001) with 86 iterations for the final solution. Fifty randomized runs were completed. Monte Carlo test results were significant for all three axes ($p < 0.05$), indicating that similar final stress could not have been reached by chance alone. The first axis was negatively correlated with microtopography ($r = -0.73$), percent clay ($r = -0.52$), soil nitrogen ($r = -0.48$) and soil depth ($r = -0.48$). The second axis was negatively correlated with organic layer nitrogen ($r = -0.61$) and percent silt ($r = -0.51$) and positively correlated with percent clay ($r = 0.61$), and soil nitrogen ($r = 0.49$). The third axis was correlated with soil depth ($r = 0.67$) and microtopography ($r = -0.69$).

The positioning of community types in ordination space to a great extent reflected the relative spatial distribution of the community types across the landscape (Figure 4).

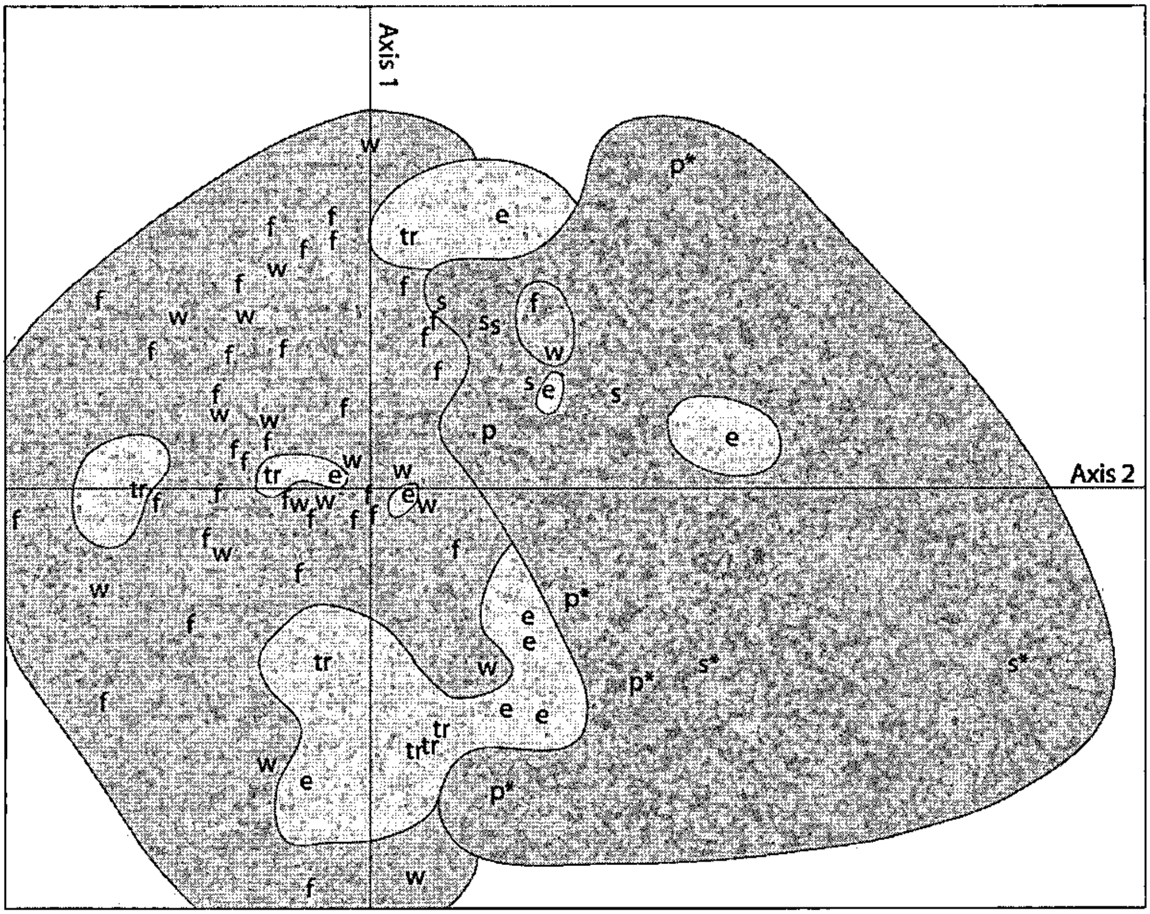


Figure 4. NMS of plots labeled by community type. Non-metric multidimensional scaling ordination of the all the plots (n= 79) identified by community type at Jim's Creek (p= prairie, s= savanna, e= edge, tr= transition, w= woodland, f= forest) based on nine environmental variables (pH, soil depth, soil and organic layer nitrogen, percent silt and clay, microtopography, heat load and slope). Lines enclosing plots were drawn by the author for ease of visual interpretation and have no statistical basis. Community types occupy the ordination space similar to actual physical space. Savanna and prairie plots score positively on the second axis and woodland and forest plots score negatively, with edge and transition plots typically displaying intermediate values.

Forest and woodland plots were distributed along all of axis 1 but scored mostly negatively on axis 2, indicating an association with higher percent silt and organic layer nitrogen, and lower percent clay and soil nitrogen. Savanna and prairie plots were also distributed along the length of axis 1 but corresponded positively to axis 2, indicating the opposite situation, occupying areas with higher clay and soil nitrogen, and lower silt and organic layer nitrogen. The edge and transition plots were centrally located on the second axis and span the entire first axis, occupying the zone of the ordination space intermediate between the woodland and forest on the one hand, and the prairie and savanna on the other, just as they do in physical space.

Oak Distributions

The densities of living oaks differed significantly among community types ($p < 0.001$, Table 3). The edge had a significantly higher density of living oaks than the prairie and savanna ($p = 0.003$), the woodland ($p < 0.001$) and the forest ($p < 0.001$). The transition zone had the highest mean density of living oaks, but was only significantly higher than the forest ($p = 0.007$).

Table 3. Oak densities by community type. Mean density (trees/ha) ± one standard error of living and dead oaks found in each community type. To examine whether oak distributions differed among community types, Kruskal-Wallis tests were performed. The densities of living oaks were significantly different among community types ($p < 0.001$), but densities of dead oaks were not ($p = 0.18$).

	Prairie and Savanna	Edge	Transition	Woodland	Forest
Living oaks	7 ± 4	52 ± 14	97 ± 52	8 ± 5	5 ± 3
Dead oaks	4 ± 2	13 ± 5	11 ± 6	3 ± 2	11 ± 4

The mean densities of dead oaks were not significantly different among community types ($p = 0.18$). However, the density of dead oaks in the edge was significantly higher than in the woodland ($p = 0.05$).

Prairies, Savannas and Areas with Large Oaks

Prairie and savanna had significantly shallower soil, less organic layer nitrogen and silt and more clay and soil nitrogen than transition zone, woodland and forest combined (Table 4). These results were also consistent with the patterns evident in the NMS analysis of community types (Figure 4). After making a sequential Bonferroni correction, soil depth, organic layer nitrogen and percent silt and clay remained significant (Rice 1989).

Table 4. Comparison of environmental variables for community types. Mean ± standard error of prairie and savanna ($n = 12$) versus transition, woodland and forest ($n = 57$). Means were compared using t-tests.

	Transition, Woodland and Forest	Prairie and Savanna	p-value
Soil depth (cm)	82 ± 5	34 ± 6	<0.001
Organic layer nitrogen (g/cm^2)	0.163 ± 0.011	0.082 ± 0.013	<0.001
Percent silt	40.2 ± 0.7	35.1 ± 1.2	0.001
Percent clay	20.9 ± 0.7	24.9 ± 0.9	0.002
Soil nitrogen (g/cm^2)	0.173 ± 0.007	0.284 ± 0.050	0.04
pH	6.06 ± 0.04	6.23 ± 0.13	0.23
Microtopography	4.85 ± 0.22	5.25 ± 0.53	0.38
Slope	33 ± 2	31 ± 4	0.49
Heat load	0.950 ± 0.007	0.950 ± 0.013	1.00

Large (DBH > 25 cm) living oaks constituted 24% of the total living oaks sampled. Areas with large oaks had significantly higher clay content, soil nitrogen, microtopography values (indicating a tendency to live in areas with a larger water collecting capacity) and pH than areas without large oaks (Table 5). Clay content was only significantly higher in areas with large oaks when applying a sequential Bonferroni correction (Rice 1989).

Table 5. Environmental characteristics of areas with large living oaks. Comparison of environmental variables (mean ± standard error) of plots with large living oaks (DBH > 25 cm, n = 14) and plots without large living oaks (n = 65). Means were compared using t-tests.

	Areas with large oaks	Areas without large oaks	p-value
Percent clay	27.8 ± 1.2	21.2 ± 0.6	<0.001
Soil nitrogen (g/cm^2)	0.250 ± 0.024	0.189 ± 0.012	0.016
Microtopography	6 ± 0.5	4.7 ± 0.2	0.021
pH	6.30 ± 0.10	6.05 ± 0.04	0.036
Percent silt	37.8 ± 1.8	39.5 ± 0.6	0.37
Heat load	0.9591 ± 0.0110	0.9483 ± 0.0059	0.39
Slope	31 ± 2	33 ± 2	0.69
Organic layer nitrogen (g/cm^2)	0.154 ± 0.025	0.146 ± 0.010	0.808
Soil depth (cm)	73 ± 13	71 ± 5	0.98

Proportional Area of Community Types

Forest was the most widespread community type across Jim's Creek, constituting 57% of the site. Woodland was also relatively abundant and covered 28% of the site.

Prairie and savanna, edge and transition zone were uncommon and constituted 5%, 4% and 5%, respectively.

Discussion

Succession of a Former Oak Savanna

Tree ages and growth forms indicate that Jim's Creek was historically a savanna with lower densities of trees than are present there today. When growing in open conditions, Oregon white oak has low, laterally spreading branches and a round crown (Stein 1990), as a result of maturing with little or no competition for light. Most large oaks at Jim's Creek show signs of substantial canopy loss. However, analysis of original canopy architecture based on branches and branch stubs suggests that most of the large (DBH > 25 cm) oaks at Jim's Creek had open-grown structure as they were maturing. Fifty-three percent showed branching patterns that indicate they were fully open grown and 23% were partially open grown. Thus, it appears that three-quarters of these large oaks matured in an environment with access to full or partial sunlight without being overtopped by other trees.

Today, however, transition, woodland and forest constitute 91% of the site. Dendrochronological data from the site indicate that 75% of all living trees are 125 years old or less (Day 2005). Furthermore, 67% of all living trees established at Jim's Creek within the last 75-125 years (Day 2005) following fire suppression and an apparent reduction in fire ignitions by non-native American settlers. These findings suggest that although Jim's Creek is currently primarily woodland and forest composed mainly of

Douglas-fir, a large portion of these trees were not a component of the site until a reduction in fire frequencies occurred across the Willamette Valley. This large influx of trees within the past 125 years (Day 2005), along with the high proportion of open-growth form large oaks, indicates that Jim's Creek has undergone succession from a predominantly open savanna to more densely-treed community types.

This evidence of change in tree community structure within the past 125 years suggests that the different community types currently at Jim's Creek represent different successional trajectories from a historic oak savanna. Succession appears to have proceeded non-uniformly across the site in large extent due to environmental factors (Figure 3, Table 4); the community types classified in this study (prairie/savanna, edge, transition, woodland and forest) and environmental differences among them reveal that certain site physiographic and soil conditions allow areas to resist or succumb to succession.

Environmental Controls Over Tree Community Structure and Community Type

Oregon white oak can grow in a wide range of environmental conditions but is often outcompeted by taller, rapidly growing species (Stein 1990). In general, Douglas-fir grows twice as quickly as oak at Jim's Creek (Day 2005), and light shade can maximize survival and growth of first-year Douglas-fir trees on south facing exposures (Hermann and Lavender 1990), such as those that characterize Jim's Creek. It is likely that the historic oaks and large trees at Jim's Creek provided enough shading and moisture for Douglas-fir saplings to establish by creating a "nursing" effect. Once established, Douglas-fir would be able to overtop the oaks and shade them out, as oaks are shade intolerant (Stein 1990).

While succession appears to be ongoing in certain areas across the site, it appears to be restricted in others by edaphic factors. Day (2005) provides evidence that invasion of prairie and savanna at Jim's Creek is continuing on south edges where young Douglas-fir is being shaded. Invasion of north edges, however, appears to be arrested, and harsh conditions, such as insufficient shade in droughty areas, appear to be important in maintaining prairie and savanna at Jim's Creek. Remnant prairie and savanna are characterized by relatively shallow soil and high clay while transition, woodland and forest have deeper soil and higher silt content (Table 4). Although Douglas-fir grows on a wide range of soil types, it thrives on soils that are deep and well-aerated (Hermann and Lavender 1990). The most successful area of small-sized (> 0-12 cm) Douglas-fir establishment was on a bench with deep soil (> 1.5 m) and a large (DBH = 181 cm) ponderosa pine in the plot contributing to 73% canopy cover. It also appears to be a site of moisture accumulation, further favoring Douglas-fir establishment. Incense cedar also tolerates a variety of soil types but generally grows best on deep, sandy loam with good drainage (Powers and Oliver 1990). The high densities of Douglas-fir and incense cedar in the woodland and forest, which were associated with high silt and low clay content (Figure 4), suggest that these areas may have provided more suitable conditions for successful invasion early on.

Many of the living oaks at Jim's Creek are found growing on clayey soils (Figure 3, Table 5) that may be difficult for Douglas-fir and incense cedar to colonize. Oaks are often found on heavy clay soils that are droughty during the dry summer months (Stein 1990), but such sites may be too harsh for establishment of Douglas-fir seedlings (Youngberg 1955). Overall, Douglas-fir appear much less able to occupy droughty sites than do Oregon white oak, ponderosa pine and incense cedar (Hermann and Lavender 1990). Incense cedar is more tolerant than ponderosa pine once it is established, but incense cedar seedlings are drought intolerant (Powers and Oliver 1990).

Soil texture has been shown to be important in distinguishing community types in other savanna ecosystems, with savanna woodlands occurring mostly on coarse-textured soils and savannas occurring on fine-textured soils (Johnson and Tothill 1985). Williams et al. (1996) examined large-scale tropical savanna structure in Australia and found decreasing tree cover and basal area with increasing soil clay content. Clay has high water tension properties, which can often limit water availability to species as soils dry (Chapin et al. 2002). In the Midwestern U.S., remnant savanna is associated with dry sites high in sand rather than clay (Nuzzo 1986, Apfelbaum and Haney 1990), as much of the original mesic savanna in the region has been converted to agriculture or succeeded to dense forests in the absence of fire (Curtis 1959, McCune and Cottam 1985, Nuzzo 1986).

Shallow soil has also been linked to the persistence of other savannas across the landscape. Heikens and Robertson (1995) found that remnant oak savanna barrens were found on shallower soils than neighboring xeric forest in southern Illinois. Arabas (2000) looked at serpentine barrens in Pennsylvania and Maryland and found that pine (*Pinus rigida*) savanna was associated with shallow soils, oak (*Q. stellata* and *marilandica*) woodlands were found on intermediate-depth soils and hardwood forests (excluding oaks) were associated with well-developed soils.

At Jim's Creek, areas that have already undergone succession appear to have different nutrient characteristics than remnant prairie and savanna. The transition, woodland and forest had significantly more nitrogen in the organic horizon than prairie and savanna (Table 4). However, litter of the prairie and savanna had a similar percent nitrogen concentration as litter in the transition, woodland and forest ($p = 0.46$). The higher nitrogen in the organic horizon of the transition, woodland and forest appears to be a direct consequence of a significantly higher litter mass in the organic layer compared to that in the prairie and savanna (59.36 ± 3.40 g/m^2 for transition, woodland and forest; 30.94 ± 6.55 g/m^2 for prairie and savanna; $p = 0.002$). On the other hand, savanna and prairie had higher soil nitrogen than the transition, woodland and forest. The presence of nitrogen-fixing forbs such as lupines and clovers (Fabaceae, personal observation) in the savanna may contribute to higher soil nitrogen found in these community types, and like the nitrogen in the organic layer, seems most likely to represent a feedback mechanism of succession rather than a factor influencing it. While savanna and prairie represent one end of the nitrogen gradient and woodland and forest represent the other end, the nitrogen content of transition and edge areas are intermediate between the prairie and savanna and the woodland and forest (Figure 4). Previous research in central Oregon found that soil properties (pH, extractable ammonium, potential mineralizable nitrogen, soil organic matter) of transition zones are intermediate between conifer forest and prairie currently being invaded, but more closely resembled those of forests (Griffiths et al. 2005).

Griffiths et al. defined a transition zone as encompassing the forest-prairie edge to the area where grass is no longer found on the forest floor, which would include the edge and the part of the transition zone nearest the savanna in this study. The intermediate characteristics of transition and edge in this study suggest that characteristics such as nitrogen content or pH of savannas may be rapidly influenced by bio-feedback mechanisms of invading Douglas-fir due to processes such as changes in litterfall.

Environmental Conditions Characterizing Oak Refugia

The different densities of living oaks among community types suggests that living oaks are concentrated within certain areas across the site. The edge appears to be an important refugia for living oaks as it had higher mean densities than all other community types except the transition zone. The edge seems to be especially important for the largest (DBH > 50 cm) living oaks, as six of seven of the largest oaks were found there, despite the fact that the edge represented only 13% of sampled plots. In addition, nine of twenty-one small (DBH < 12 cm) living oaks were also found there. The edge likely has higher living densities because oaks may still obtain sufficient sunlight there.

The transition zone also appears to be an important habitat for living oaks, but it appears suitable for high densities of Douglas-fir and incense cedar as well (Table 1). More than half (47 of 89) of mid-sized (DBH > 12-25 cm) living oaks were found in the transition, and 11 of 27 of large (DBH > 25-50 cm) living oaks were also found there, despite the fact transition only represented 9% of sampled plots. The highest mean density of living oaks occurred in the transition zone, but was only significantly higher than the oak density in the forest. While, two of seven transition plots had exceptionally high living oak densities (nearly 300 trees/ha), three plots had no living oaks, so the oak densities found within the transition zone were quite variable. Furthermore, only the presence of living and dead oaks were examined in this study, and many of the living trees found in the transition appear to have compromised health. Additionally, the mean canopy cover of the transition plots would categorize them as woodland, and the woodland had relatively low oak densities. Thus, it seems likely that the close proximity of the transition zone to the prairie and savanna may allow for substantial diffuse light in plots with high densities of living oaks, but the seemingly declining health of many of the oaks suggests that the transition zone may not remain as longstanding oak refugia.

The environmental conditions of prairie and savanna appear to be difficult places for trees to establish. The prairie and savanna had relatively low densities of living oaks, but half of the savanna and prairie plots had no trees at all. However, enough oaks and pines establish there with Douglas-fir being able to establish there only infrequently, indicating these areas are more long-term oak refugia.

Current oak refugia appears to be confined to small areas across the site. The prairie, savanna, edge and transition seem to be the most important community types for oaks today, but they only constitute a small proportion of the site. Conversely, oaks were found in the lowest density in the forest, the most widespread community type at Jim's Creek, indicating that living oaks are relatively rare across the majority of the site.

However, the densities of dead oaks among community types suggest that the current distribution of oaks across the site does not reflect their historic distribution.

Dead oak densities were not significantly different among community types, except between the woodland and edge, suggesting that a large portion of Jim's Creek was viable oak habitat prior to a reduction in fire frequencies. Whereas the forest does not appear important for living oaks today, nearly half of all dead oaks >12 cm were found in the forest; half of the largest dead oaks were also found there despite none of the largest living oaks being found there. These findings indicate that historically oaks were able to thrive in the area that is currently forest despite the high densities of Douglas-fir found there today.

Oak distribution was also associated with relatively high pH values. Oregon white oak is often associated with pH values ranging from 4.8 to 5.9 (Stein 1990), but the pH values measured in this study were higher (Table 5). The association of oaks with higher pH may be partially explained by differences in litter quality of oaks and Douglas-fir. Previous research has shown that litter of an eastern U.S. species, penduculate oak (*Quercus robur),* can have an acidifying effect on soil, but high soil clay content can offset this acidification (Beniamino et al. 1991). Coniferous species are known to acidify the surrounding soil (Jonsson et al. 2003), although they are subject to the same offset of effect by high clay content. However, Douglas-fir have been shown to have a greater acidifying effect on soil than oak species in as little as three years (Augusto et al. 2001).

Large (DBH > 25 cm) oaks occurred with high soil nitrogen (Table 5). My results are similar to those of Klinka et al. (1996) who classified forest communities in British Columbia. Klinka et al. found Oregon white oak occurring on nitrogen-medium to nitrogen-rich soil and Douglas-fir-Oregon grape communities on sites that were nitrogen-poor to -medium within the same biogeographic region. Douglas-fir densities are highest in the transition, woodland and forest at Jim's Creek and these areas had significantly less soil nitrogen.

Large oaks were also found on water collecting microtopography (Table 5). These areas in which water collects may offer microsite refuge for oaks that are often associated with high clay content. To my knowledge, no other studies have related the distribution of large Oregon white oak to a microtopographic gradient.

Conclusion

The tradeoffs for different tree species in terms of their tolerances for fire, shade and drought appear to be important in the successional dynamics of a former oak savanna at Jim's Creek, Willamette National Forest. Oregon white oak and ponderosa pine were historically maintained in the savanna because of their fire tolerance (Agee 1993, Stein 1990); Douglas-fir and incense cedar were unable to establish in high densities because they are intolerant of fire until they attain maturity (Hermann and Lavender 1990, Powers and Oliver 1990). In the absence of fire, shade-tolerant Douglas-fir and incense cedar were able to establish and the mean density of the site is currently 567 trees/ha. Because Douglas-fir grows twice as quickly (Day 2005) and much taller (Hermann and Lavender 1990, Stein 1990) than Oregon white oak, current oak refugia are confined within close proximity of remnant prairie and savanna where there is sufficient sunlight for a shade-intolerant (Stein 1990) species. Remnant prairie and savanna appear to have resisted invasion because shallow soil and high clay content have prevented young, drought-intolerant Douglas-fir (Hermann and Lavender 1990) and incense cedar (Powers and Oliver) from establishing.

Current tree distribution across the site is associated with soil clay and silt content, slope, pH and soil and organic layer nitrogen. Soil pH and nitrogen may reflect biotic feedback mechanisms resulting from changes in vegetation, rather than causing the changes in the vegetation per se. The persistence of remnant savanna, however, does appear to be edaphically controlled, probably most importantly by shallow soil depth and high clay content. The effects of clay content may be primarily expressed through low moisture availability during the summer drought, but this study could not confirm this hypothesis.

Although current oak refugia at Jim's Creek was characterized in this study, it is important to note that oaks once inhabited more variable conditions. Areas that are currently occupied by forest and woodland were a primary component of historic oak savanna structure, although differences in soil texture and depth may have resulted in successful invasion of these areas by Douglas-fir earlier on.

The understanding that edaphic features have led to differential rates of succession at Jim's Creek has important implications for savanna restoration and long-term management at the site. Oaks have been excluded from a large part of their historic habitat because of reductions in fire frequencies. They now mostly exist in the most extreme edaphic conditions. Consequently, restoration that is only focused on their current distribution will not reintroduce them to their full range of habitats. Reintroduction of fire or other disturbance regimes will be necessary in the more mesic sites to inhibit succession into Douglas-fir forests.

CHAPTER III

CONCLUSION

Environmental variables appear to have influenced the succession of a former Oregon white oak (*Quercus garryana*) savanna and the stability of remaining oak refugia at Jim's Creek, Willamette National Forest, Oregon. By associating environmental characteristics with conifer invasion and areas that have remained prairie and savanna, abiotic characteristics have been linked to the successional dynamics of oak savanna in Oregon's Willamette Valley. This study is part of a larger collaborative project between the University of Oregon and the U.S.D.A. Forest Service funded by the Joint Fire Science Program. The overlying goal of the project is to investigate the potential to integrate oak savanna restoration with fuels management. By providing an understanding of how environmental variables influence the successional dynamics of oak savanna, this study will help guide restoration and fuels management efforts of Oregon white oak savanna throughout the Willamette Valley.

Historically, Jim's Creek was predominantly a savanna with scattered open-grown trees (Day 2005). Mature oaks are fire-tolerant and frequent, low-intensity fires maintained the savanna by preventing invasion from less fire-tolerant species, such as Douglas-fir (*Pseudotsuga menziesii*) and incense cedar (*Calocedrus decurrens*). With the reduction of fire frequencies, fire-intolerant species have invaded the site and the current mean density is 567 trees/hectare. Douglas-fir is the dominant species within all community types, and living oaks are currently concentrated in the prairie, savanna, edge and transition zone. Because Douglas-fir grows twice as quickly and much taller than Oregon white oak, current oak refugia are restricted to areas where there is sufficient sunlight for oak, which is shade-intolerant.

The current distribution of oak savanna at Jim's Creek, however, does not reflect its historical range. The large numbers of dead oaks found in the forest indicate that this community type was once viable habitat for oak even though it is characterized by high densities of Douglas-fir and incense cedar today.

Soil depth and texture appear to be important in explaining why some areas (the forest, woodland and transition zone) underwent succession early on, while other areas have resisted invasion. Douglas-fir and incense cedar are tolerant of a wide range of growing conditions but thrive in deep soil. Douglas-fir grows best on well-aerated soil while incense cedar thrives on soil with good drainage. Because the transition, woodland and forest had higher soil silt content and deeper soil, it is likely that these areas were more suitable for Douglas-fir and incense cedar establishment.

Thus, remnant prairie and savanna appear to be edaphically controlled, primarily by high soil clay content and shallow soil. Young Douglas-fir and incense cedar are drought-intolerant and are likely unable to establish under the harsh conditions characterizing remnant prairie and savanna. Oak, however, is drought-tolerant and is often associated with soils high in clay. At Jim's Creek, oaks of all sizes were associated with relatively high clay content, suggesting that they have been confined to areas that are too droughty for Douglas-fir and incense cedar to invade. Furthermore, large oak (DBH > 25 cm) was found in water collecting microtopography, which may offer some relief in the harsh conditions in which oak is often found.

To evaluate the relationship of environmental variables to current tree community structure of a former oak savanna, several statistical methods were applied to the data. First, the distribution of species-size classes were described as a function of environmental variables using Canonical Correspondence Analysis (CCA). CCA is a direct gradient analysis (McCune and Grace 2002) that was used to examine how the densities of different species-size classes were related to environmental conditions. One advantage of using CCA was that a high percentage of the variance between species-size classes and environmental variables was explained. Additionally, samples are weighted based on total abundance, amplifying distributions of rare species-size class distributions, which were all oak and pine size classes in this study.

One shortfall of CCA is that categorical variables were unable to ordinated. Variables such as slope position and the presence of earthflows and swales were therefore not considered. Preliminary analyses with indirect gradient analyses using only plots with trees showed these variables to be unimportant indicators of tree densities, but the outcome cannot be predicted had they been included in a direct gradient ordination involving all of the plots. One disadvantage in using direct rather than indirect gradient analysis was that a smaller percentage of the overall tree community structure was explained, but a much larger portion of the community structure based on environmental variables was explained.

One major statistical issue faced was the integration of six plots with no trees. Several methods were attempted to include them in the CCA, but all produced skewed results. Consequently, CCA was run without these plots and revealed that current tree community structure of a former oak savanna was related to soil silt, clay and nitrogen content, pH and slope.

To include plots with no trees in analyses, an additional ordination technique was applied. Plots were labeled by community type and ordinated solely on environmental variables using Non-metric Multidimensional Scaling (NMS). NMS is an indirect gradient analysis that works well with data that are non-normally distributed and does not make linear assumptions among variables (Bruce and McCune 2002).

Similar variables were important in ordinating plots in both the CCA and NMS. Both analyses revealed that clay and silt content and soil nitrogen were important in ordinating plots based on tree densities as well as by community type. Thus, similar environmental variables appeared to be predictive of species-size class distributions and community type.

Differences in soil and site physiographic characteristics among community types were further analyzed using t-tests. Remnant prairie and savanna were found to have shallower soil and higher clay content than areas that had already undergone succession, which were characterized by deeper soil and higher silt content. To analyze the consequences of succession for the distribution of oaks at Jim's Creek, Kruskal-Wallis tests were used to examine live and dead oak densities within each community type. Living oak densities were different among communities, but dead oak densities were not.

Water availability was not directly investigated in this study and may be a key control of successional trajectories and current tree community structure. Several variables found to be important in this study, including microtopography, clay content and soil depth are likely to influence water availability but may not accurately reflect water stress. It would be useful to examine water stress of oak versus Douglas-fir along a soil texture and microtopographic gradient to determine if these variables were maintaining oak refugia because of their influence on soil moisture.

Different nitrogen requirements of species may also influence successional dynamics of a former oak savanna. Oak at Jim's Creek was associated with high soil nitrogen. It seems likely that this correlation reflects a feedback mechanism from the switch from oak litter, as well as the dense herbaceous layer of the prairie and savanna, to conifer litter through succession. However, Douglas-fir have been shown to be nitrogen limited; if oak is creating a nitrogen-rich micro-environment, it is may also be aiding Douglas-fir establishment. As succession progresses, changes to immobilization and mineralization rates may occur that affect nitrogen availability. For example, decomposition of grass and oak litter versus conifer litter probably differs. Consequently, further research examining net nitrogen mineralization-immobilization dynamics could supplement this study. Only total soil nitrogen was examined, which may differ significantly from plant available nitrogen. Other nutrients that have been shown to be limiting to plant growth, such as phosphorus, could also be analyzed.

There is currently great impetus to restore oak savanna because of its imperiled status. Oak savanna is a critically endangered ecosystem in the Pacific Northwest and Midwestern United States, with more than 99% of its original habitat destroyed or severely degraded by agriculture, grazing or fire suppression (Nuzzo 1986; Noss et al. 1995). Information about how environmental conditions influence successional dynamics is greatly needed for successful restoration of these ecosystems. Other studies throughout the Pacific Northwest have worked to characterize current community structure of Oregon white oak and relate environmental variables to community structure (Thilenius 1968, Klinka et al. 1996, Erickson 2002), but none have revealed how soil and site physiographic factors describe tree community structure or influence successional dynamics. Furthermore, these studies have only focused on macro-scale distribution of Oregon white oak communities across the landscape. By identifying environmental variables associated with invasion of a former Oregon white oak savanna and characterizing current oak refugia in the Willamette Valley, this research has described the importance of abiotic factors in the succession of former Oregon white oak savanna.

APPENDIX A

PLOT OVERLAYS FROM CCA

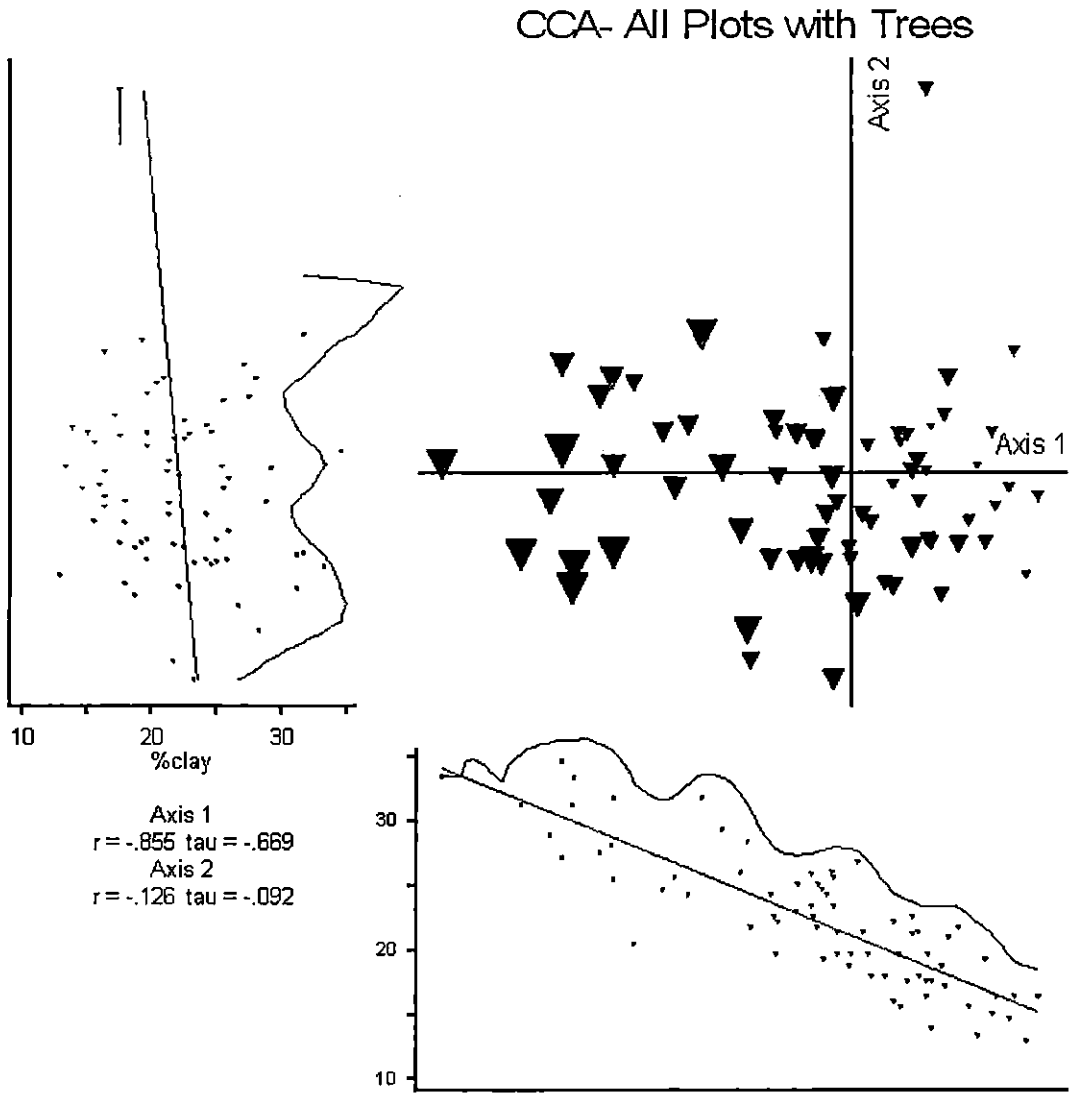


Figure 5. Percent clay overlay.

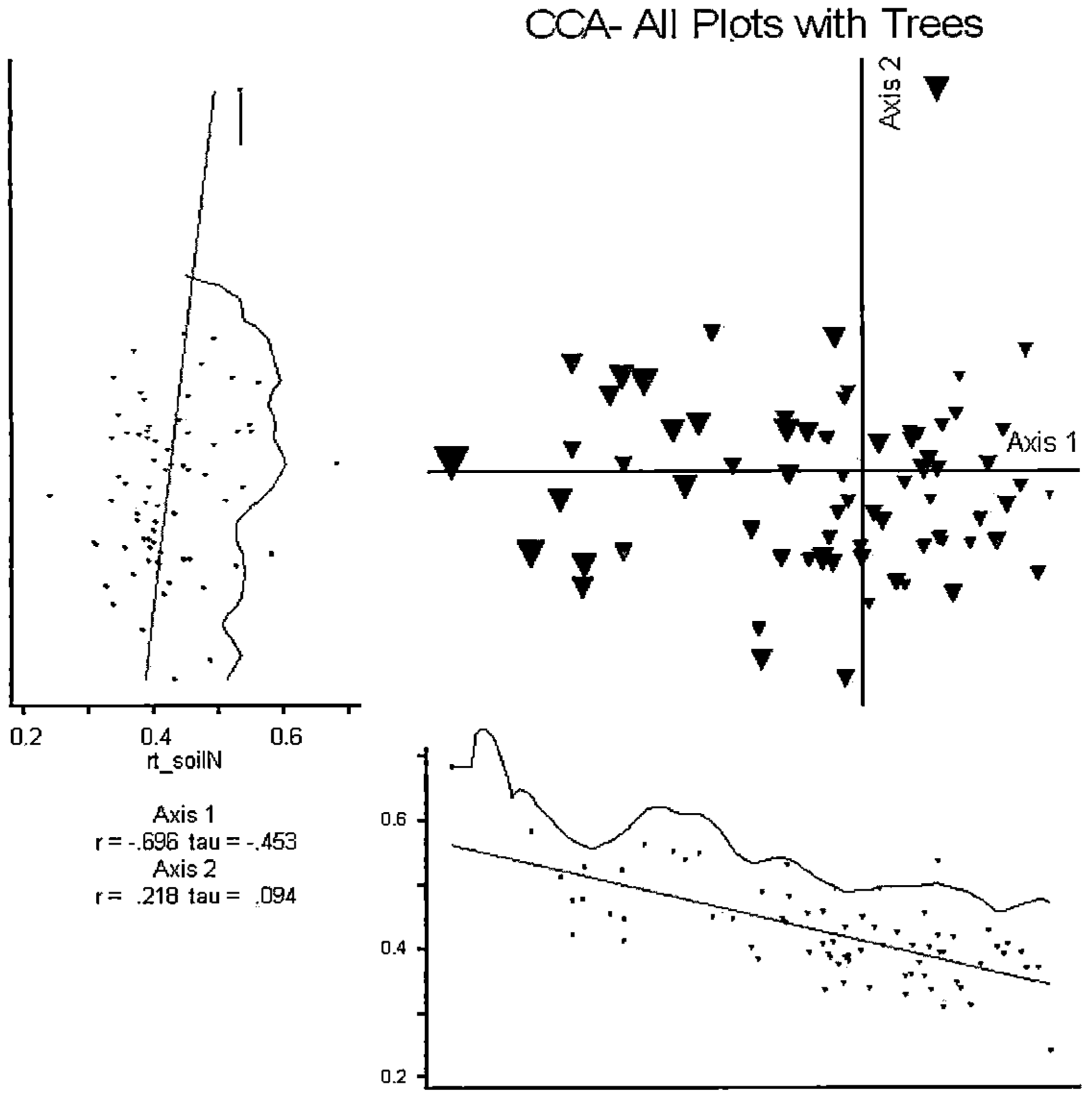


Figure 6. Percent silt overlay.

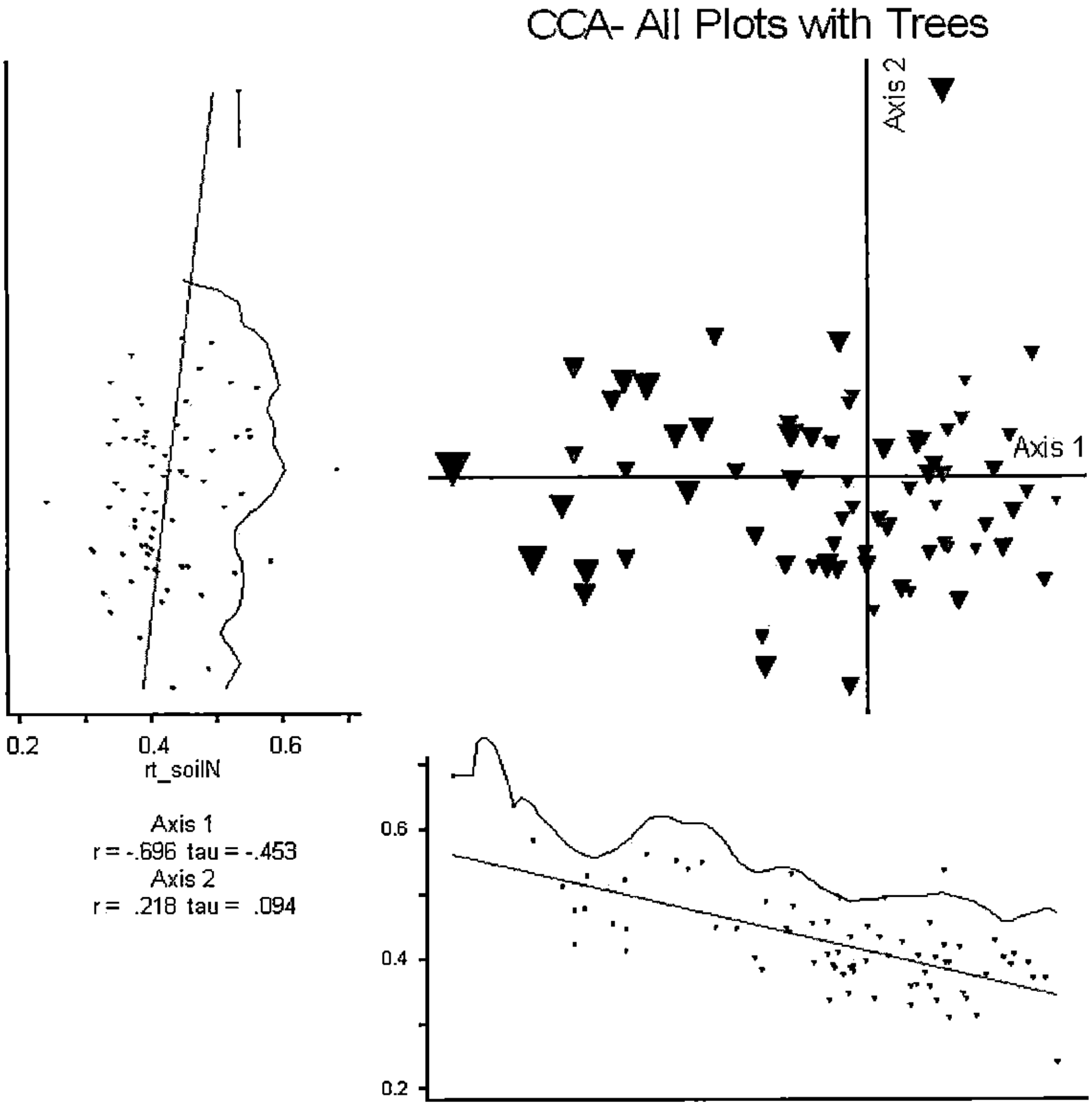


Figure 7. Soil nitrogen overlay.

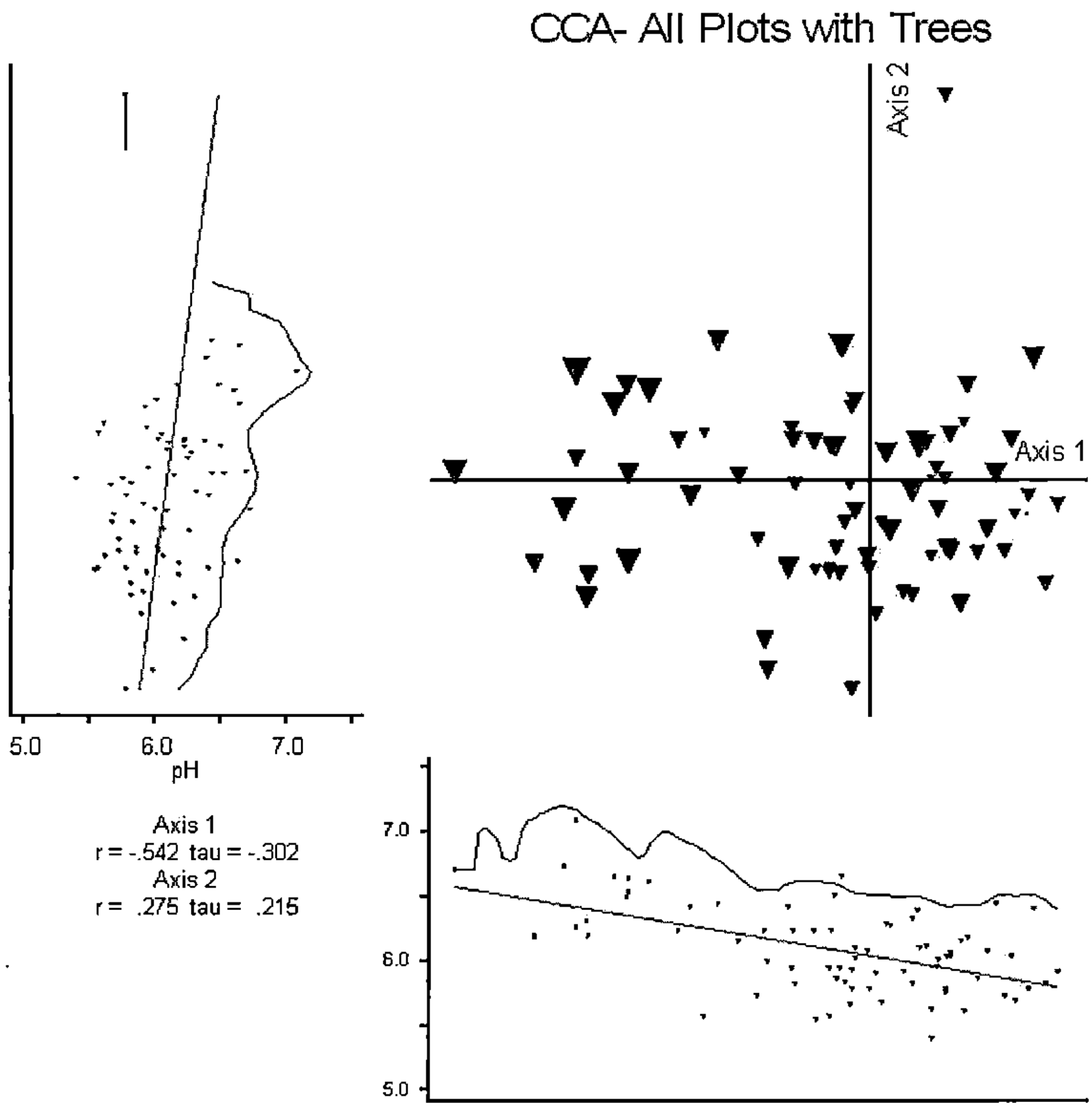


Figure 8. pH overlay.

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