EDAPHIC CONTROLS OVER SUCCESSION IN FORMER OAK SAVANNA, WILLAMETTE VALLEY, OREGON

by

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A THESIS

Presented to the Environmental Studies Program
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Master of Science

June 2008

"Edaphic Controls Over Succession In Former Oak Savanna, Willamette Valley, Oregon," a thesis prepared by Meghan Suzanne Murphy in partial fulfillment of the requirements for the Master of Science degree in the Environmental Studies Program. This thesis has been approved and accepted by:

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An Abstract of the Thesis of

Meghan Suzanne Murphy for the degree of Master of Science
in the Environmental Studies Program to be taken June 2008

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Oak savanna was a dominant ecosystem of Oregon's Willamette Valley prior to Euro-American settlement but has declined precipitously due to urbanization, agriculture, and reduced fire regimes. Some areas have retained their savanna structure while others have succeeded into woodland or forest. I investigated the relationships of current community type to edaphic (bulk density, texture, carbon, nitrogen, depth, and pH) and topographic (slope and heatload) factors at seven sites using analysis of variance and principal components analysis. Results indicate that edaphic and topographic conditions strongly influence successional pathways in former oak savanna, but the specific effects depend on site location. Soil moisture was also measured seasonally at three of the sites in community types representing the current successional stages. Results indicate that dry conditions restrict succession to dense forest, and that soil depth is an important control over soil moisture within the soil profile.

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ACKNOWLEDGMENTS

First I would like to thank my advisors, Dr. Scott Bridgham and Dr. Bart Johnson, for recruiting me to work on this project and for all of their help and advice. They dedicated an enormous amount of time and effort to helping me with field work, data analysis, and writing. From meetings to emails, they were always more than willing to make time for me and answer questions. They provided me with excellent guidance and advice. I am truly thankful for the opportunity to work with them.

I would like to acknowledge everyone who collected data for this project, including Karen Sonnenblick, Mark Gasser, Jonathan Day, Kate Skelton, Jenna Garmon, Adrienne Moll, and Gabe Yospin. I would especially like to thank Mark Gasser for his help installing the moisture wells; he was a great person to work with.

And finally, I would like to thank the members of the Bridgham lab group, Laurel Pfeifer, Lisa Turnbull, Kai Blaisdell, and Gabe Yospin, for their help and expertise with lab work, statistics, and giving presentations. I would also like to thank the Environmental Studies graduate students, staff, and faculty for supporting me throughout this process. I must also acknowledge the Joint Fire Science Program, which provided the funding for this project.

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CHAPTER I

INTRODUCTION

Oak savanna has been a major ecosystem in North America for many years, its existence dating back to 20-25 million years ago (Thomas and Spicer 1987). Twelve-hundred thousand hectares of oak savanna was present in the northern part of the Midwestern United States in the early1800s, which had been stable for thousands of years (Nuzzo 1986). Oak savanna is one of the most threatened ecosystems in the Midwestern United States and in the world (Henderson 2006). Oak savanna has declined in the United States for multiple reasons, and is currently considered critically endangered in the Midwestern United States and in the Willamette Valley, Oregon (Noss et al. 1995).

One of the primary reasons for the decline of savannas is tree invasion, resulting in large changes in community structure and composition. Some areas have succeeded to woodlands or forests, while others have maintained their savanna structure. In the Willamette Valley, about one-third of historic savanna has succeeded to conifer forest (Hulse et al. 2002).

An understanding of the edaphic and topographic factors underlying the ecological dynamics in former oak savanna in the Willamette Valley is imperative. To examine the relationships between environmental variables and succession, I did two separate studies. The first examines the relationships between edaphic and topographic factors and succession (Chapter 2). The second study looks at the effects of soil moisture on succession (Chapter 3).

Oregon White Oak Savanna

Oregon white oak (*Quercus garryana*) ranges from Vancouver Island, British Columbia to Southern California (Vesely and Tucker 2004), and was the dominant tree of historic savanna in the Willamette Valley. Approximately 500,000 ha of oak savanna were present in the Pacific Northwest prior to 1850 (Vesely and Tucker 2004). Typically, Oregon white oak is found below elevations of about 1150 m in Oregon (Vesely and Tucker 2004).

In the Willamette Valley, Oregon white oak savanna was a dominant ecosystem prior to Euro-American settlement, covering over 200,000 ha (Boyd 1999, Thilenius 1968, Hulse et al. 2002). The open, park like structure of the savanna was maintained by natural fires or fires set by the Native Americans. After Euro-American settlement in the Willamette Valley in the mid 1800s, the burning practices of the Native Americans were largely eliminated. In the early 1900s, fire suppression became a prominent land management strategy (Agee 1993). Conifer invasion of the savanna ecosystem due to reduced fire frequency, as well as urbanization and agriculture, have led to the decline of oak savanna in the Willamette Valley (Agee 1993, Vesely and Tucker 2004). Fire suppression has also resulted in higher tree densities and fuels accumulation, increasing the risk of catastrophic wildfire in the Willamette Valley (Arno and Allison-Bunnell 2002).

The decline of the oak savanna ecosystem has also resulted in a decrease of local and regional biodiversity (Gumtow-Farrier and Gumtow-Farrier 1994). Many species of birds and mammals depend on the oak savanna ecosystem, and some are becoming rarer. For example, the acorn woodpecker is currently listed as a Species of Concern and the western grey squirrel is listed as a Sensitive Species in Oregon (Oregon National Heritage Information Center 2007). Currently, less than 1% of the oak savanna ecosystem remains in Oregon (Noss et al. 1995, Hulse et al. 2002).

The loss of oak savanna has not been complete. Some areas in the Willamette Valley have maintained their savanna structure, while others have succeeded to woodlands or forests of various compositions. Environmental and soil conditions may be influencing the successional dynamics of oak savanna, allowing accelerated succession in some areas, while restricting tree invasion in others. The objective of my research is to understand how environmental factors have accelerated or restricted forest succession in former oak savanna, and, where succession has occurred, the factors that control its extent.

Vegetation and Soil Dynamics

Both above- and below- ground factors have affected successional trajectories in former oak savanna in the Willamette Valley. The life history strategies of different tree species influences how they respond to disturbances such as fire, as well as below-ground factors like moisture regime, soil texture and nutrients. In addition, these above- and below- ground factors influence tree species competition in former oak savanna.

Fire, Growth Rates, and Competition

The reduction of fire frequency has altered the vegetation dynamics in the Willamette Valley. The fires that once blazed through the valley kept tree density low, maintaining the scattered open-grown oak trees and a ground layer of grasses and forbs. The continuous ground layer of grasses and forbs created fine fuels, which burn easily and reinforced a regime of frequent, low intensity fires. Although Oregon oak seedlings are susceptible to fire, larger oaks are highly fire resistant (Stein 1990). Oregon white oaks also can re-sprout after fire (Stein 1990). The fire regime that kept the tree density low in the Willamette Valley also kept the competition experienced by the mature oaks for light, space, nutrients, and water to a minimum. Without fire as a disturbance, prairies and savannas in the Willamette Valley have experienced increased invasion by deciduous trees and conifers, mainly Douglas-fir, which are far less adapted to fire than the oaks (Stein 1990, Hermann and Lavender 1990, Day 2005).

The reduction in fire frequency in the Willamette Valley has resulted in dramatically higher tree densities in some areas. Recent studies of a mid-elevation site in the Willamette Valley show that this area was historically an Oregon white oak-ponderosa pine savanna that is now dominated by Douglas-fir forest (Winkler & Bailey 2002, Day 2005). Prior to Euro-American settlement, tree densities at Jim's Creek are estimated to be 17 trees/hectare, while post Euro-American settlement tree densities are around 582 trees/hectare (Day 2005).

In the absence of fire, several characteristics of Oregon white oak make it a poor competitor to Douglas-fir in all but the most stressful environmental conditions. Oregon white oak is a slow-growing tree, with growth rates of about 0.13 to 0.17 cm/year of bole wood production (Stein 1990). Higher growth rates are possible, and growth rates greater than 0.2cm/year have been documented (Stein 1990). Oregon white oak is also relatively short compared to coniferous trees, reaching a maximum height of around 27 m (Stein 1990), whereas old growth Douglas-fir can reach heights up to 76 m tall (Hermann and Lavender 1990). First-year Douglas-fir seedlings grow best under light shade (Hermann and Lavender 1990), thus finding an ideal environment at the base of an oak tree, where they are partially shaded. Older Douglas-fir seedlings prefer more sun than the first-years.

During the first five years of life the growth rate of Douglas-fir is relatively slow. Growth then accelerates and reaches a maximum growth rate at about 30 years of age (about 61 cm growth in height per year) (Hermann and Lavender 1990). Thus, young Douglas-firs growing under oaks soon grow tall and begin to shade the oaks. Oregon white oak is highly intolerant to shade (Stein 1990). It is only a matter of time until the oak will die due to lack of light, and it is common to find dead oaks under large Douglas-fir trees in the Willamette Valley (Stein 1990). The old oak trees essentially nurse their own death by providing an ideal habitat for Douglas-fir seedlings. This is the natural plant succession in most of the Willamette Valley in the absence of disturbances such as fire.

Rooting and Soil Dynamics

The rooting morphology of Oregon white oak is important for understanding why the species is able to survive under a broad range of environmental conditions. Oregon white oak can form a deep taproot and a well developed lateral root system (Stein 1990), which may lead to its ability to utilize both rare summer precipitation (with its lateral roots) and ground water (with its deep taproot). Seedlings develop a taproot quickly, which allows them to establish on dry or grassy sites (Vesely and Tucker 2004, Stein 1990). In Washington on coarse-textured glacial soil, Devine and Harrington (2005) found that the root morphology of Oregon white oak seedlings is dominated by a taproot, while small and large tree root morphologies tended to be dominated by large, shallow, first-order lateral root systems.

The taproots of Douglas-fir and Oregon white oak are similar in some ways but differ in important ways. Douglas fir is a potentially deep-rooting species, but grows a taproot only when there are no barriers in the soil (Hermann and Lavender 1990). When Douglas-fir roots hit obstructions in the soil such as bedrock, the taproot proliferates and grows laterally, instead of growing deeper (Hermann and Lavender 1990). Thus, Douglas-fir may not be able to exploit groundwater sources on shallow soils where bedrock would limit the growth of the taproot. On shallow soils, Oregon white oak may be able to tap groundwater sources that Douglas-fir cannot, since the roots of Douglas-fir tend to grow laterally when rooting depth is obstructed.

In addition, the shallow roots of Oregon white oak and Douglas-fir root morphologies differ. Oregon white oak tends to have denser surface roots than Douglas-fir (Krygier 1971). For example, in a root excavation of both species in the Willamette Valley, 11% of oak roots were found below 76 cm, whereas 28% of Douglas-fir roots were found below 76 cm in the same soil (Krygier 1971). Because a larger percentage of oak's roots remain in the shallower soil layers, this may enable oaks to take advantage of rare summer precipitation, which is important in the Willamette Valley where there is extreme summer drought. This may be part of the reason why Oregon white oak is able to establish and succeed in drier environments than Douglas-fir.

Overall, it appears that Oregon white oak has several main rooting advantages over Douglas-fir: 1) Douglas-fir will not form a taproot if there are obstructions in the soil profile, 2) Oregon white oak has more surface roots than Douglas-fir, and 3) Oregon white oak seedlings form a prominent taproot quickly.

Oregon white oaks are found on a wide variety of habitats and soils, from droughty exposed areas, to areas that are flooded for part of the year. Douglas-firs, however, prefer well-aerated deep soils and will not survive on soils with poor drainage or compaction. Oregon white oak can also occur in very wet areas, such as river terraces, flood plains, and heavy clay soils (Stein 1990). These habitats have a long wet season, but are droughty in the summer months. Douglas-fir roots are completely intolerant of soils with poor drainage, and tend to form lateral roots when they encounter a water table (Hermann and Lavender 1990). Douglas-fir prefers soils in a pH range of 5 to 6 (Hermann and Lavender 1990). Similarly, Oregon white oak is typically found in soils ranging from a pH of 4.8 to 5.9 (Stein 1990).

Soil texture has been linked to successional dynamics and could be influencing plant succession in the Willamette Valley. A study of savanna systems in Australia found that tree cover and basal area decreased with increasing clay content (Williams et al. 1996). A world-wide savanna study found that woodland cover decreased with increasing clay content (Johnson and Tothill 1985).

Soil texture can also have a profound effect on the level of soil moisture the plant experiences. Clay soils tend to hold onto water tightly (due to the increased surface area of the clay particles, leading to a greater surface tension between the clay particles and water), which limits the amount of moisture the roots experience (Chapin et al. 2002). In addition to holding water more tightly, clay soils also allow less infiltration, causing water to accumulate on the surface of clay soils. Clay soils are also droughty in summer.

The amount of nitrogen and organic matter in the soil also influence species distribution. Douglas-fir is typically found on acidic soils with high total nitrogen and low base saturation (Hermann and Lavender 1990). In the Pacific Northwest, Douglas-fir has been shown to be limited by nitrogen (Hermann and Lavender 1990). Similarly, a study in coastal British Columbia found Oregon white oak communities were associated with nitrogen-medium to nitrogen-rich soils (Klinka et al. 1996). Soil nutrient levels were found to be correlated with vegetation type in a study in a South African savanna system. Grass species were associated with lower nutrient (nitrogen, phosphorous, calcium, and magnesium) levels, while tree species were associated with medium to high levels of nutrients (Ben-Shahar 1991). The separation of grass and tree species could be due to differences in their nutritional requirements (Ben-Shahar 1991).

Soil depth has also been shown to be a determining factor in vegetation structure and composition (Bradfield and Scagel 1984, Heikens and Robertson 1995, Fulton and Prentice 1997, Arabas 2000). In particular, shallow soil appears to lead to areas with less or smaller trees. In a study of barrens and forest openings in Southern Illinois, soil depth was an important factor in discriminating among community types. Open-grown trees with prairie understory were associated with shallow and rocky soils (Heikens and Robertson 1995). Arabas (2000) found that in Pennsylvania and Maryland, pine savanna had the shallowest median soil depth, whereas hardwood forest and oak woodlands had the deepest soils, although these differences were not statistically significant. Pine woodland had intermediate soil depth in this study (Arabas 2000). On the British Columbia coast, Oregon white oak communities are found on shallow soils of rocky outcrops and on their adjacent steep and south-facing slopes (Klinka et al. 1996). Oregon white oak communities on the British Columbia coast were also found on deeper soils, but in areas with low rainfall (Klinka et al. 1996).

Soil moisture may be the environmental variable which has controlled the successional patterns in the Willamette Valley the most following the cessation of widespread fire. Oregon white oak has a unique ability to establish itself and persist in areas where precipitation is sparse and soils are shallow and/or droughty (Stein 1990). Douglas-fir will yield to Oregon white oak on droughty soils (Hermann and Lavender 1990). Since Oregon white oak is drought resistant, it may be able to establish seedlings in areas with low soil moisture. In contrast, Douglas-fir seedlings are limited by soil moisture in their first year (Hermann and Lavender 1990), restricting their establishment to areas with greater soil moisture. Oregon white oak communities were found on dry soils in British Columbia (Klinka et al. 1996).

Savanna structure in areas outside the Pacific Northwest has also been shown to be influenced by soil moisture, especially across precipitation and soil moisture gradients

(Prach and Rehounkova 2006, Ringrose et al. 1998, Skarpe 1996, Skarpe 1990, Johnson and Tothill 1985). A study in Australia showed that tree cover decreased with decreasing rainfall (Williams et al. 1996). In contrast, in a South African savanna system, soil moisture alone did not appear to be the determining factor affecting encroachment by woody plants (Ben-Shahar 1990). Rainfall in South Africa occurs in the summer, however, in the Willamette Valley, the summers (which are the growing seasons) are dry and the winters are wet. The climate of the Willamette Valley may make soil moisture a more important variable in the Oregon white oak savanna than found in the South African savanna system.

In addition to sub-surface soil factors, the organic layer may have an impact on successional trajectories in the Willamette Valley. Seedlings of Douglas-fir do not survive well in areas with a thick layer of duff (Hermann and Lavender 1990), but rather prefer a more mineral soil. Areas with a large amount of organic layer may inhibit the establishment of Douglas-fir. Douglas-fir may find it easy to establish in prairie/savannas since there is relatively little duff layer in these areas, provided other conditions are suitable for its establishment.

Hypotheses and Research Questions

The endangered status Oregon white oak savanna, as well as the resulting decrease in biodiversity and increased risk of catastrophic wildfire, has made oak savanna restoration imperative. A better understanding of the edaphic and topographic factors affecting succession in the Willamette Valley would strengthen the ability of land managers to assess successional trajectories. A description of the relationships between edaphic variables and succession in former oak savanna is needed to inform restoration strategies.

The relationships between community structure and environmental variables in former Oregon white oak savanna in the Willamette Valley have not been thoroughly examined at the landscape scale. However, one study at a mid-elevation site in the Willamette Valley (Jim's Creek) has suggested that remnant prairie and savanna have resisted invasion by Douglas-fir due to the high clay content and shallowness of the soil (Sonnenblick 2006).

Succession appears to be occurring at different rates under various edaphic and environmental conditions in the Willamette Valley. Some areas in the Willamette Valley have maintained their savanna structure while others have experienced succession.

I hypothesize that the distinct gradients in vegetation structures over short distances in the Willamette Valley are due to edaphic factors. My research focuses on the following questions: 1) How have edaphic and topographic conditions influenced succession in former oak savanna? 2) What are the characteristics of areas where succession has been restricted? 3) How has soil moisture influenced successional dynamics?

To answer these questions, I performed two separate studies. In the first study, I examined seven sites in the Willamette Valley that were chosen because they historically had a mosaic of oak savanna and prairie, and had undergone different successional trajectories. At each site, there were areas that had maintained remnant oak and prairie communities, as well as those that had succeeded to woodland or forest. I used Analyses Of Variance (ANOVAs) to investigate the relationships between community structure and edaphic variables, including bulk density, soil texture, carbon and nitrogen content, pH, and soil depth. Principal Components Analyses (PCAs) were used to supplement to the ANOVAs, describing the relationships between community type and edaphic and topographic variables in a multivariate context.

In the second study, I measured soil moisture seasonally throughout the soil profile at three of the seven sites to gain an understanding of the relationships between soil moisture and community type. The relationships between soil moisture and community type were evaluated using repeated measures ANOVAs.

This study is part of a larger project examining the potential for integrating fuels management with oak savanna restoration. This project is a collaboration between the University of Oregon and the USDA Forest Service, funded by the Joint Fire Science Program.

CHAPTER II

THE RELATIONSHIPS BETWEEN COMMUNITY TYPES AND EDAPHIC AND TOPOGRAPHIC FACTORS

Introduction

Oak savanna was a major ecosystem in the United States for millennia (Thomas and Spicer 1987), but has declined precipitously over the last few hundred years. The decline of oak savanna has lead to its current status as critically endangered in the Midwestern United States and in Oregon's Willamette Valley (Noss et al. 1995). In Oregon's Willamette Valley, Oregon white oak (*Quercus garryana*) savanna historically was a dominant ecosystem in the landscape (Hulse et al. 2002). Currently, less than one percent of the oak savanna ecosystem remains in the Willamette Valley (Noss et al. 1995, Hulse et al. 2002). Primary causes for decline of this ecosystem include agriculture, urbanization, and reduced fire frequency (Hulse et al. 2002). Reductions in fire frequency have allowed conifers and other tree species to invade the oak savanna, increasing tree densities. Coniferous trees such as Douglas-fir (*Psuedotsuga menziesii*) grow taller than the oaks and eventually overtop them, leading to higher mortality of the shade-intolerant oaks. Some areas in the Willamette Valley have maintained their savanna structure, while other areas have succeeded into woodlands and forests.

This study describes the edaphic and site physiographic conditions of historic oak savanna. Former oak savannas have undergone different successional trajectories, varying from areas that have maintained their savanna structure to areas that have succeeded into woodland or forest. In addition, the species composition in historic oak savanna has also changed. Some areas have infilled with oak or other deciduous trees, while others have infilled with conifers (primarily Douglas-fir), or some combination of the two (Stein 1990, personal observation). The differences in successional stages and species composition may be due to varying edaphic and site physiographic conditions.

This study investigates the relationships between edaphic and site physiographic factors and the current community types found in former oak savanna.

In particular, I focused on the following questions: How have soil variables (texture, nutrients, depth, pH, and bulk density) and topographic factors influenced succession in former oak savanna? How are these variables related to each other?

Methods

Study Areas

Seven sites were selected throughout the Willamette Valley to encompass a broad range of environmental conditions and the current successional stages found in former oak savanna. Sites are arranged from low to high average elevation in all figures and tables. Sites overlap in elevation and some have a substantial range in elevation (Table 2.1).

Table 2.1 Study sites in the Willamette Valley. Name, code, latitude/longitude, and elevation of seven sites in the Willamette Valley.

Site	Code	Latitude/Longitude	Elevation Range (m)	Mean Elevation (m)
Finley	FN	44°25′N, 123°19′W	85 – 165	125
Chip Ross	CR	44°34′N, 123°16′W	183 – 259	221
Mount Pisgah	MP	44° 0′N, 122° 58′W	171 – 347	259
South Eugene	SE	44°3′N, 123°6′37″W	201 – 347	274
Lowell	LW	43°55′N, 122°46′W	305 – 488	396
Brownsville	BR	44°23′N, 122°59′W	183 – 610	396
Jim's Creek	JC	122°25′W, 43°30′N	597 – 988	792

Soils series were determined from maps of each site, developed from the Pacific Northwest Ecological Research Consortium GIS data layers (http://www.fsl.orst.edu/pnwerc/wrb/access.html). Descriptions of each soil series are from the USDA Natural Resources Conservation Service (http://soils.usda.gov/technical/classification/osd/index.html).

Finley National Wildlife Refuge (FN) is located along the foothills of the Coast Range, about 15 km south of Corvallis, Oregon. FN has a rolling topography and ranges in elevation from 85 – 165 m above sea level. The lower elevations of FN contain mainly Jory and Bellpine series soils, which are deep well-drained silty clay loam Ultisols. Other soil series found in the lower elevations of Finley include Price, which are very deep, well drained clayey Inceptisols, and Hazelair, which are moderately deep silty clay loam Mollisols. The soils in the upper elevations of FN (Pigeon Butte) are Mollisols, including the Dixonville series, which are moderately deep, well-drained clayey soils on hills, and Woodburn, which are very deep, moderately well-drained silty soils (Table 2.2).

Chip Ross (CR) is a public park along the northern edge of the city of Corvallis, Oregon. CR is a small butte ranging in elevation from 183 – 259 m above sea level. Soils at CR include Dixonville, and a complex of Price-Ritner, which is a clayey moderately to very deep Inceptisol (Table 2.2).

Mount Pisgah (MP) is a public park located near the confluence of the Coast and Middle forks of the Willamette River, 7.5 km southeast of Eugene, Oregon and contains some of the highest quality oak savanna and prairie habitats left in the Willamette Valley. MP ranges in elevation from 171 – 347 m. MP soils are mainly Mollisols, including Witzel soils, which are shallow, well-drained, loamy soils, and Philomath, which are shallow, well-drained, clayey soils. Other soil series found at MP include Ritner, which are moderately deep, well-drained clayey-gravelly Inceptisols found on ridge tops and the sides of hills, Nekia, which are moderately deep, well-drained silty clay loam Ultisols found on foothills, and a complex of Dixonville-Philomath-Hazelair, which are moderately deep to shallow, clayey Mollisols found on hillsides (Table 2.2).

The South Eugene (SE) site is located on along the southern edge of the urban growth boundary of Eugene, Oregon and contains transects on both private and public land. SE ranges in elevation from 201 – 347 m. Soils at SE are primarily Mollisols, including Dixonville, a complex of Dixonville-Philomath-Hazelair, and Chehulpum, which are shallow, well-drained, loamy soils. Other soil series found at SE include

Witzel, Ritner, and Panther, which are deep to very deep clayey, poorly drained Inceptisols found in swales and concave slopes (Table 2.2).

The Lowell site (LW) is located along the eastern edge of Lowell, Oregon, just outside the urban growth boundary. This site is located on private land at the south end of the Willamette Valley and ranges in elevation from 305 – 488 m above sea level. LW is located in the foothills of the Cascades, and contains rolling to steeply sloped hillsides. Soils in LW are mainly Mollisols, including the Witzel series and a complex of Dixonville-Philomath-Hazelair. However, Inceptisols are also present at the site, including the Ritner series (Table 2.2).

The Brownsville site (BR) is located 6.5 km south of Brownsville on rolling to steep slopes at the eastern edge of the Willamette Valley. This site is located on private land and ranges in elevation from 183- 610 m above sea level. BR soils are mainly Mollisols, including the soil series Witzel and Philomath. Other soil series found at BR are Panther, Bellpine, and Ritner (Table 2.2).

Jim's Creek (JC) is in the Willamette National Forest in the lower elevations of the Cascade Mountains and ranges in elevation from 597 – 988 m above sea level. JC is near the upper elevation limit of Oregon white oak (1150 m) (Vesely and Tucker, 2004). JC is 25 km south of Oakridge, Oregon and contains mainly steeply sloped hillsides. JC soils are Inceptisols, and include several soil series: Klickitat, which are deep, well-drained, gravelly clay loam, Kinney, which are deep, well drained cobbly-loam soils, and McCully, which are deep, well-drained, fine-textured clay-loam soils (Table 2.2).

Plant Sampling Methods and Communities

We established transects using stratified random sampling to encompass the variety of environmental conditions and community types found at each site. Transects were oriented up and down slope to cover distinct changes in environmental gradients and community types, and were then randomly placed. Circular plots with an area of 200-m^2 were located every 60 meters along transects. Species and diameter at breast

Table 2.2 Soil series found at each site.

Site	Soil Series
FN	- **Jory:** fine, mixed, active, mesic Xeric Palehumults - **Bellpine:** fine, mixed, active, mesic Xeric Haplohumults - **Price:** fine, mixed, superactive, mesic Typic Haploxerepts - **Hazelair:** very-fine, smectitic, mesic Vertic Haploxerolls - **Dixonville:** fine, mixed, superactive mesic Pachic Ultic Argixerolls - **Woodburn:** fine-silty, mixed, superactive, mesic, Aquultic Argixerolls
CR	- **Dixonville:** fine, mixed, superactive, mesic Pachic Ultic Argixerolls - a complex of **Ritner** (clayey-skeletal, mixed superactive, mesic Typic Haploxerepts) and **Price** (fine, mixed, superactive, mesic Typic Haploxerepts)
MP	- **Witzel:** loamy-skeletal, mixed, superactive, mesic Lithic Ultic Haploxerolls - **Philomath:** clayey, smectitic, mesic, shallow Vertic Haploxerolls - **Ritner:** clayey-skeletal, mixed superactive, mesic Typic Haploxerepts - **Nekia:** fine, mixed, active, mesic Xeric Haplohumults - a complex of **Dixonville** (fine, mixed, superactive, mesic Pachic Ultic Argixerolls), **Philomath** (clayey, smectitic mesic, shallow Vertic Haploxerolls) and **Hazelair** (very-fine, smectitic, mesic Vertic Haploxerolls)
SE	- **Dixonville:** fine, mixed, superactive, mesic Pachic Ultic Argixerolls - a complex of **Dixonville** (fine, mixed, superactive, mesic Pachic Ultic Argixerolls), **Philomath** (clayey, smectitic mesic, shallow Vertic Haploxerolls) and **Hazelair** (very-fine, smectitic, mesic Vertic Haploxerolls) - **Witzel:** loamy-skeletal, mixed, superactive, mesic Lithic Ultic Haploxerolls - **Ritner:** clayey-skeletal, mixed superactive, mesic Typic Haploxerepts - **Panther:** very-fine, smectitic, mesic Vertic Epiaquolls - **Chehulpum:** loamy, mixed, superactive, mesic, shallow Ultic Haploxerolls
LW	- **Witzel:** loamy-skeletal, mixed, superactive, mesic Lithic Ultic Haploxerolls - **Ritner:** clayey-skeletal, mixed superactive, mesic Typic Haploxerepts - a complex of **Dixonville** (fine, mixed, superactive, mesic Pachic Ultic Argixerolls), **Philomath** (clayey, smectitic mesic, shallow Vertic Haploxerolls) and **Hazelair** (very-fine, smectitic, mesic Vertic Haploxerolls)
BR	- **Witzel:** loamy-skeletal, mixed, superactive, mesic Lithic Ultic Haploxerolls - **Philomath:** clayey, smectitic, mesic, shallow Vertic Haploxerolls - **Panther:** very-fine, smectitic mesic Vertic Epiaquolls - **Bellpine:** fine, mixed, active, mesic Xeric Haplohumults - **Ritner:** clayey-skeletal, mixed, superactive, mesic typic Haploxerepts
JC	- **Klickitat:** loamy-skeletal, isotic, mesic Humic Dystrudepts - **Kinney:** fine-loamy, isotic, mesic Andic Dystrudepts - **McCully:** fine, isotic, mesic Humic Dystrudepts

height (DBH) was recorded for every tree within a plot. Because large trees, including former savanna trees, are found in only low densities, oaks > 40 cm DBH and other species > 75 cm DBH were recorded in 30 m x 30 m square plots centered on the circular plot to more accurately assess their densities. Canopy cover was measured at each plot center using a spherical densitometer. Plots were classified as prairie/savanna, woodland, or forest based on canopy cover: prairie/savanna (0-25% canopy cover), woodland (26-60% canopy cover), and forest (> 60% canopy cover). Prairie and savanna were combined into one community type for this analysis because of the small number of prairie and/or savanna plots at any single site. We considered it appropriate to group savanna and prairie because savannas are essentially upland prairies with a small number of widely dispersed trees, and both have a continuous grassland ground layer. To incorporate an important ecotone, edge plots were also established on the tree line boundary separating a forest or woodland from a prairie/savanna.

The dominant tree species at all sites were Oregon white oak and Douglas-fir. The typical forest dominate was Douglas-fir at every site. Woodland was mixed deciduous- coniferous, typically dominated by oak and Douglas-fir. Oregon white oak was the dominant oak species at all sites. Ponderosa pine (*Pinus ponderosa)* was sampled at SE, LW, BR, and JC only. Incense cedar (*Calocedrus decurrens*) was sampled at FN, CR, LW, SE, MP, and JC, and big leaf maple (*Acer macrophyllum)* was sampled at FN, CR, SE, MP, and LW.

Environmental and Soil Sampling Methods

We measured environmental variables at each plot, with the exception that soil depth was measured in a subset of plots at all sites except JC, where soil depth was measured at every plot. Percent slope was measured with a clinometer as an average between one up-slope and one down-slope measurement. Aspect was recorded with a compass. Soil depth was measured with a 0.635-cm drill bit to a maximum depth of 1.22 m at eight (JC) or nine (all other sites) random locations throughout each plot. Soil depth, as it was measured in this study, is essentially the depth to obstruction.

We randomly sampled soils from 0-5 cm depth with a bulb planter and from 5-20 cm depth with an Eigelkamp soil auger. Each depth was sampled three times and composited. Soil bulk density was calculated based upon oven dry mass (at 60°C) and the volume of the auger (diameter = 5 cm) or bulb planter (diameter = 5.70 cm) cores. Soil pH was measured with a pH meter in a 1:1 soil-water slurry. Soil texture was determined using a modified hydrometer method (Gee and Bauder, 1986), and sand was isolated with a 53-µm sieve, which was then oven dried and weighed. Total carbon and nitrogen levels were measured with a Costech Analytical CN analyzer.

We randomly sampled the O-horizon layer 10 times throughout each plot using a bulb planter (diameter = 5.70 cm) and composited. Mineral matter was inadvertently included with the O-horizon in some sites, so the mineral component was separated from the organic matter with a 0.2-mm sieve for samples from FN, CR, MP, SE, LW, and BR. Organic layer samples with less than 30% carbon were assumed to have mineral matter contamination and were excluded from analysis. As this separation was only approximate, this process may have compromised our O-horizon data to an unknown extent.

Statistical Analyses

We used three-way analyses of variance (ANOVAs) to examine the effect of community type, site, and sample depth on percent carbon and nitrogen, texture, and bulk density (SPSS v. 16.0). Differences in percent nitrogen and carbon, texture, and bulk density at the two depths were analyzed by a paired t-test for each site. Percent carbon was natural log transformed to normalize its distribution. The number of 0-5 cm samples for the different variables ranged from 250 to 312 and the number of 5-20 cm samples ranged from 245 to 310. Bulk density was sampled at only 20 out of 81 plots at Jim's Creek. The number of plots in each community type at each site is listed in Table 2.3.

Plot data for each soil variable was calculated by taking the average weighted by depth across the soil profile. Carbon and nitrogen content (g/m^2) were calculated based on bulk density and their respective percents. Because of the large sample-to-sample variability in bulk density, we used the average bulk density for each distinct combination of site, community type, and depth, rather than the plot bulk densities. We also found that bulk density did not significantly vary among communities within a site.

Two-way ANOVAs were performed on the plot-level data to examine the effect of site and community type on bulk density, texture, percent carbon and nitrogen, carbon and nitrogen content (g/m^2), soil depth, and pH (SPSS v. 16.0). Carbon and nitrogen were analyzed as both percent and in g/m^2 because these measurements represent two ways that nitrogen could be varying in the environment, either as a percent of the total, or as a measure of the total amount over an area. Univariate ANOVAs were performed at each site individually for each soil variable and post-hoc multiple comparisons were used to determine differences among community types with Tukey's test of Honestly Significant Difference (HSD).

Table 2.3 Number of plots in each site by community type.

Site	**Prairie/ Savanna**	**Edge**	**Woodland**	**Forest**	**Total**
CR	11	7	11	8	**37**
FN	14	5	31	24	**74**
MP	8	8	8	4	**28**
SE	4	3	11	8	**26**
LW	8	6	9	12	**35**
BR	6	9	2	14	**31**
JC	12	11	24	34	**81**
Total	**63**	**49**	**96**	**104**	**312**

Two-way ANOVAs were used to analyze the organic layer. Jim's Creek was excluded from the analysis of the organic layer due to excessive mineral matter contamination. Table 2.4 lists the number of organic layer samples by community type in each site. Organic matter, carbon content, and nitrogen content (g/m^2) were natural log transformed to normalize their distributions.

Table 2.4 Number of organic layer samples in each site by community type.

Site	Prairie/ Savanna	Edge	Woodland	Forest	Total
CR	8	5	11	7	**31**
FN	12	5	31	24	**72**
MP	6	8	8	3	**25**
SE	3	1	11	8	**23**
LW	8	4	8	11	**31**
BR	4	10	2	14	**30**
Total	**41**	**33**	**71**	**67**	**212**

Soil depth was examined on a subset of plots at each site (Table 2.5). Soil depth was natural log transformed to normalize its distribution.

Table 2.5 Number of plots sampled for soil depth by site and community type.

Site	Prairie/ Savanna	Edge	Woodland	Forest	Total
FN	5	3	4	11	**23**
CR	7	7	10	8	**32**
MP	6	6	7	4	**23**
SE	3	1	11	9	**24**
LW	6	2	3	4	**15**
BR	4	10	2	13	**29**
JC	13	11	24	33	**81**
Total	**44**	**40**	**61**	**82**	**227**

The effects of topographic and soil variables were examined using principal components analysis (PCA) (Systat v. 12). Soil variables included soil depth, carbon (g/m^2), nitrogen (g/m^2), pH, percent clay and percent sand. These variables have been shown to be important in studies examining the effects of edaphic and environmental conditions on community structure and composition (Prach and Rhounkova 2006, Sonnenblick 2006, Williams et al. 1996, Johnson and Tothill 1985, Ben-Shahar 1990, Heikens and Robertson 1995). Slope and heatload are the topographic variables in the analysis. Heatload is a function of slope, aspect, and latitude and longitude.

Slope and soil depth were natural log transformed to normalize their distributions. Because soil depth was measured in a subset of plots, the PCAs were performed with and without soil depth. PCAs that included all sites were run. FN and JC were analyzed individually because they are the two primary sites in this study and contain the largest numbers of plots. FN and JC also represent the elevation extremes in this study; JC is highest elevation site, with steep, south-facing slopes, whereas FN is the lowest elevation site, with gentle slopes. All PCAs were rotated with the Varimax procedure.

Pearson correlations were performed in addition to the PCAs to examine the relationships among the soil and topographic variables, including elevation.

Results

Soils Analysis: Analyses of Variance

We observed strong interactions among the main effects of community type, site, and depth for all of our soil response variables (Table 2.6). The effect of community type depended upon site ($p < 0.05$) for all three-way ANOVAs. The effect of depth depended upon site for bulk density and soil texture ($p < 0.05$) and was marginally significant for percent nitrogen ($p = 0.067$). The effect of community type depended on depth for percent carbon ($p = 0.044$).

Table 2.6 Three-way ANOVA p-values for soil bulk density, texture, and percent carbon and nitrogen. Significant p-values are in bold ($\alpha = 0.05$), and marginally significant p-values are italicized ($\alpha = 0.10$).

Source	**Bulk Density**	**Clay (%)**	**Silt (%)**	**Sand (%)**	**Nitrogen (%)**	**Carbon (%)**
Community Type	*0.069*	0.573	0.556	0.683	0.131	**<0.001**
Depth	**0.048**	**0.026**	0.427	**0.011**	**<0.001**	**<0.001**
Site	0.425	**0.002**	**<0.001**	**<0.001**	**0.001**	**0.001**
Community Type x Depth	0.747	0.143	0.315	0.138	0.116	**0.044**
Community Type x Site	**0.012**	**<0.001**	**<0.001**	**<0.001**	**0.003**	**0.004**
Depth x Site	**<0.001**	**<0.001**	**0.010**	**0.012**	*0.067*	0.728
Community Type x Depth x Site	0.982	0.998	0.999	0.998	0.426	0.570

Similarly, the effect of community type depended upon site for all variables when they were integrated over the top 20-cm of the soil profile in the two-way ANOVAs ($p < 0.05$), except for bulk density and pH (Table 2.7). Community type had a marginal effect on bulk density ($p = 0.091$) and pH ($p = 0.084$).

Table 2.7 Two-way ANOVA p-values for variables integrated over the top 20-cm of the soil profile: bulk density, soil depth, texture, nitrogen, carbon, and pH. Significant p-values are in bold ($\alpha = 0.05$) and marginally significant values are italicized ($\alpha = 0.10$).

Source	**Bulk Density**	**Soil Depth**	**Clay (%)**	**Silt (%)**	**Sand (%)**	**Nitrogen (g/m^2)**	**Carbon (g/m^2)**	**Nitrogen (%)**	**Carbon (%)**	**pH**
Community Type	*0.091*	0.164	0.764	0.531	0.795	0.226	**0.002**	0.164	**<0.001**	*0.084*
Site	**<0.001**	**0.013**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.005**	**<0.001**	**<0.001**	**<0.001**
Community Type x Site	0.717	**<0.001**	**<0.001**	**0.002**	**<0.001**	**<0.001**	**0.012**	**0.006**	**0.026**	0.198

Bulk Density

The effect of community type on bulk density depended upon site ($p = 0.012$) ($n = 495$). Similarly, the effect of depth depended upon site ($p < 0.001$). Bulk densities varied among sites from 5-20 cm depth ($p < 0.001$), but not from 0-5 cm depth ($p = 0.16$) (Figure 2.1). Bulk density varied by depth within five of the seven sites (FN, CR, MP, LW, and JC) ($p < 0.05$). Bulk density was higher in the 5-20 cm increment at all sites except LW.

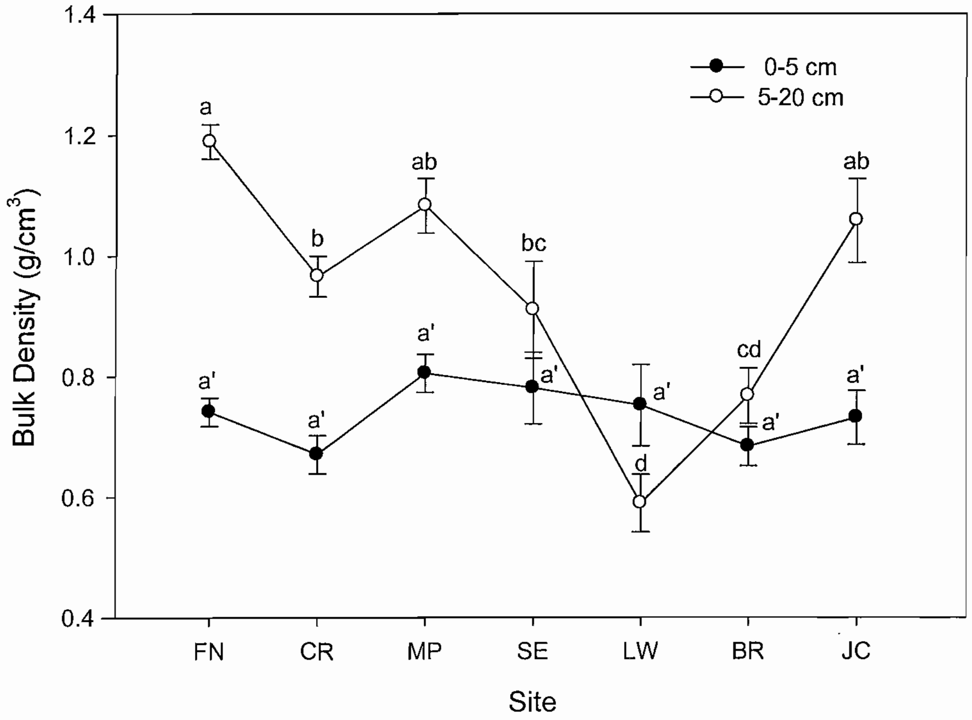

Figure 2.1 Bulk densities at two depths at seven sites. Mean bulk density (g/cm^3) ± one standard error at 0-5 cm and 5-20 cm depth within each site. Primes indicate the 0-5 cm depth. Unique letters represent significant differences among sites within the 0-5 cm and 5-20 cm depth at the $\alpha = 0.05$ level by Tukey's HSD.

Bulk density also varied among sites from 0-20 cm ($p < 0.001$) ($n = 254$). Community type had a marginally significant effect on bulk density ($p = 0.091$), but this effect did not depend on site ($p = 0.266$). Prairie/savannas and edges had higher bulk densities on average than woodlands and forests at three of the seven sites (CR, BR, and JC) (Figure 2.2).

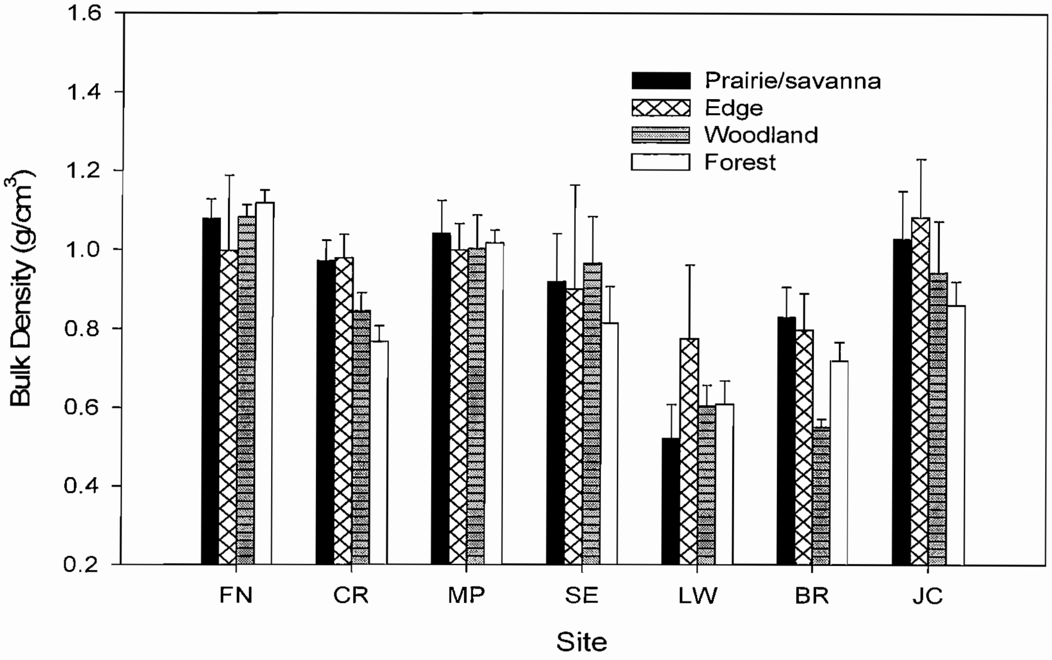

Figure 2.2 Bulk density in four community types at seven sites. Mean bulk density (g/cm^3) ± one standard error in each community type at each site.

Soil Texture

The effect of community type on percent clay, sand and silt depended upon site ($p < 0.001$) (Tables 2.6 and 2.7). Similarly, the effect of depth depended upon site for the three texture variables ($p < 0.05$).

Clay Content

The effect of community type on percent clay depended upon site ($p < 0.001$) (N = 622). Similarly, the effect of depth depended upon site ($p < 0.001$). Percent clay from 0-5 cm and 5-20 cm depth differed among sites ($p < 0.001$) (Figure 2.3). Percent clay was higher in the 5-20 cm depth at all sites except at JC, where it was higher in the 0-5 cm depth ($p < 0.001$). Overall, there is a decrease in clay content with increasing elevation (Figures 2.3 and 2.4).

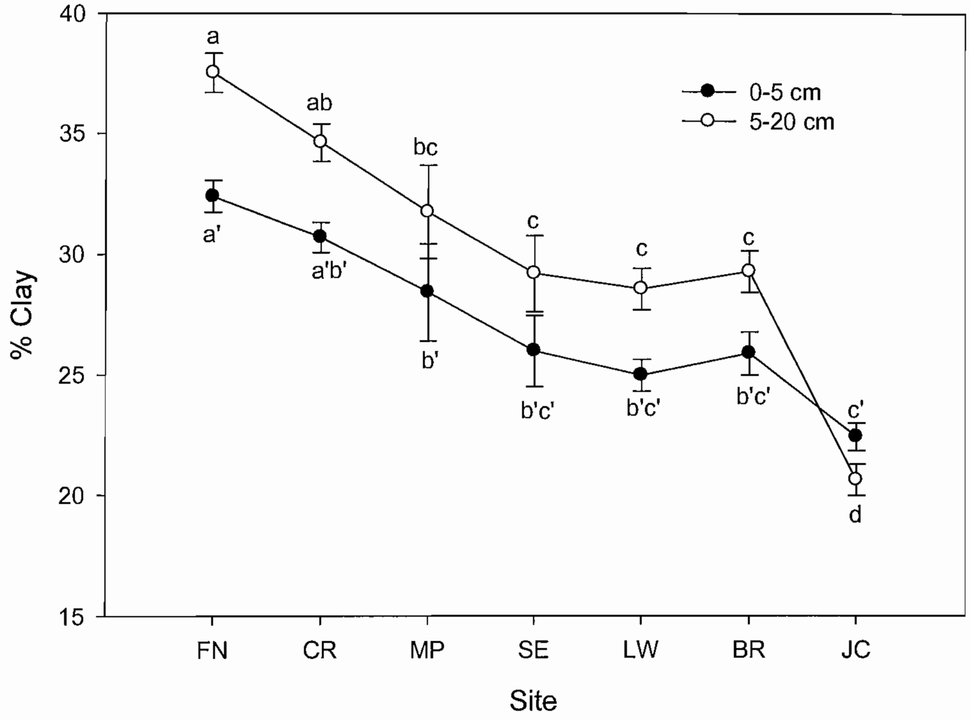

Figure 2.3 Percent clay at two depths at seven sites. Mean percent clay ± one standard error at 0-5 cm and 5-20 cm depth within each site. Primes indicate the 0-5 cm depth. Unique letters represent significant differences among sites within the 0-5 cm and 5-20 cm depth at the $\alpha = 0.05$ level by Tukey's HSD.

The effect of community type on percent clay from 0-20 cm depth depended upon site ($p < 0.001$) ($n = 309$). At the lowest elevation sites (FN and CR), percent clay was higher in forests than in prairie/savannas ($p < 0.05$). In contrast, percent clay was higher in prairie/savannas and edges than in forests at JC ($p < 0.01$) (Figure 2.4).

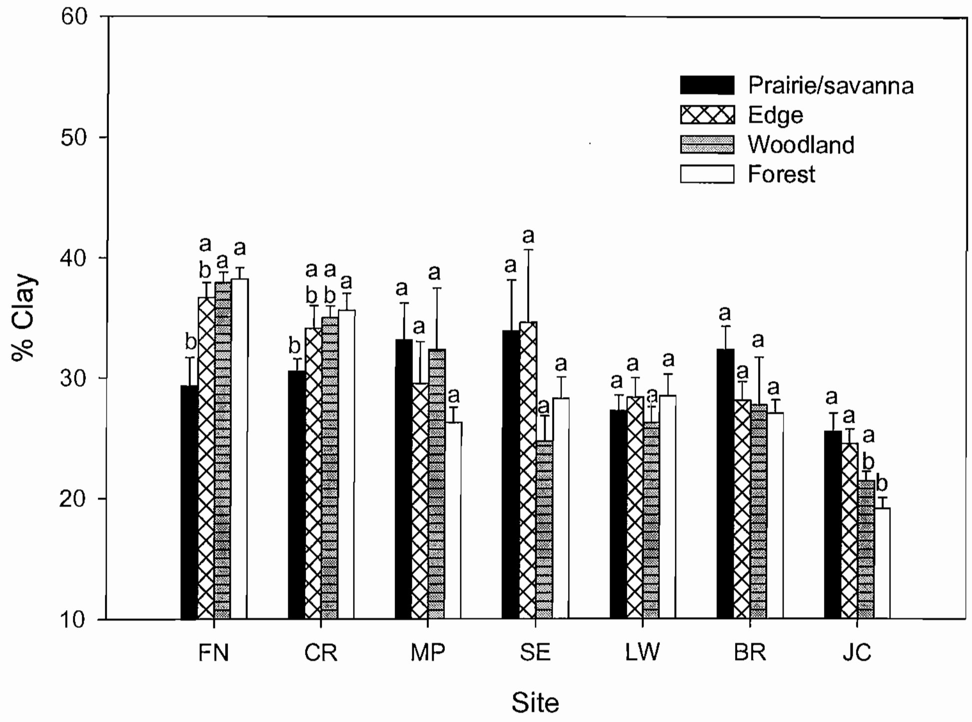

Figure 2.4 Percent clay in four community types at seven sites. Mean percent clay ± one standard error in each community type at each site. Unique letters represent significant differences among community types within a site at α = 0.05 by Tukey's HSD.

Silt Content

The effect of community type on percent silt depended upon site ($p < 0.001$) ($n = 622$). Similarly, the effect of depth depended upon site ($p = 0.01$). Percent silt at both the 0-5 cm and 5-20 cm depth differed among sites ($p < 0.001$). Percent silt was higher in the 0-5 cm depth than in the 5-20 cm at FN, MP, and LW ($p < 0.01$) (Figure 2.5).

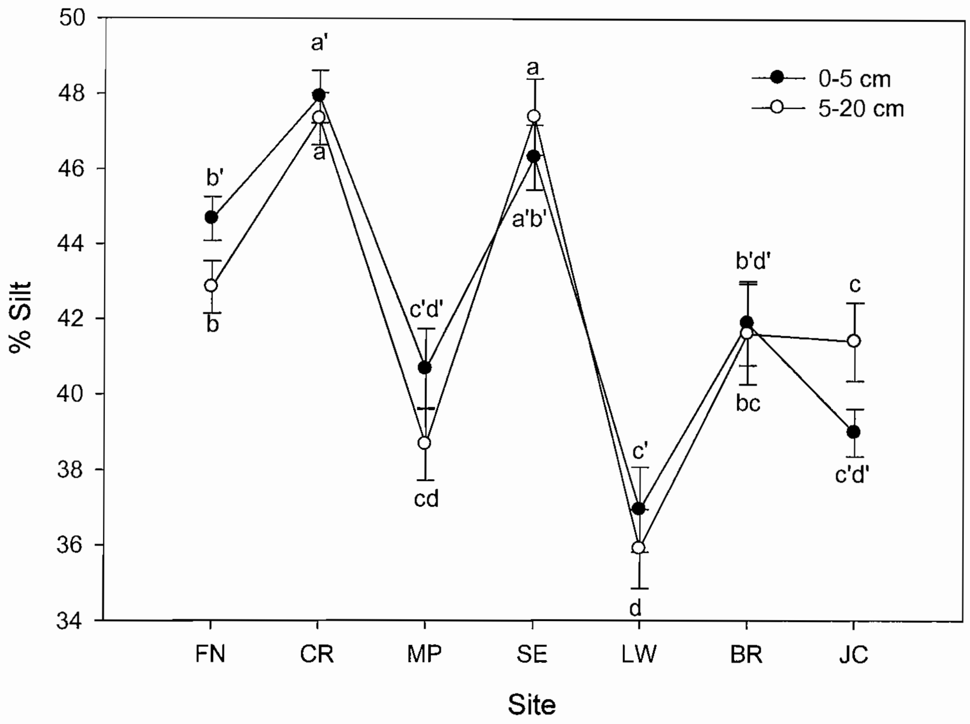

Figure 2.5 Percent silt at two depths at seven sites. Mean percent silt ± one standard error at 0-5 cm and 5-20 cm depth within each site. Primes indicate the 0-5 cm depth. Unique letters represent significant differences among sites within the 0-5 cm and 5-20 cm depth at the $\alpha = 0.05$ level by Tukey's HSD.

The effect of community type on percent silt from 0-20 cm depended upon site ($p = 0.002$) ($N = 309$). At BR, prairie/savannas had higher percent silt than edges and forests ($p < 0.02$). In contrast, at JC, woodlands had higher silt than prairie/savannas ($p = 0.037$) (Figure 2.6). Silt did not exhibit a clear pattern with elevation.

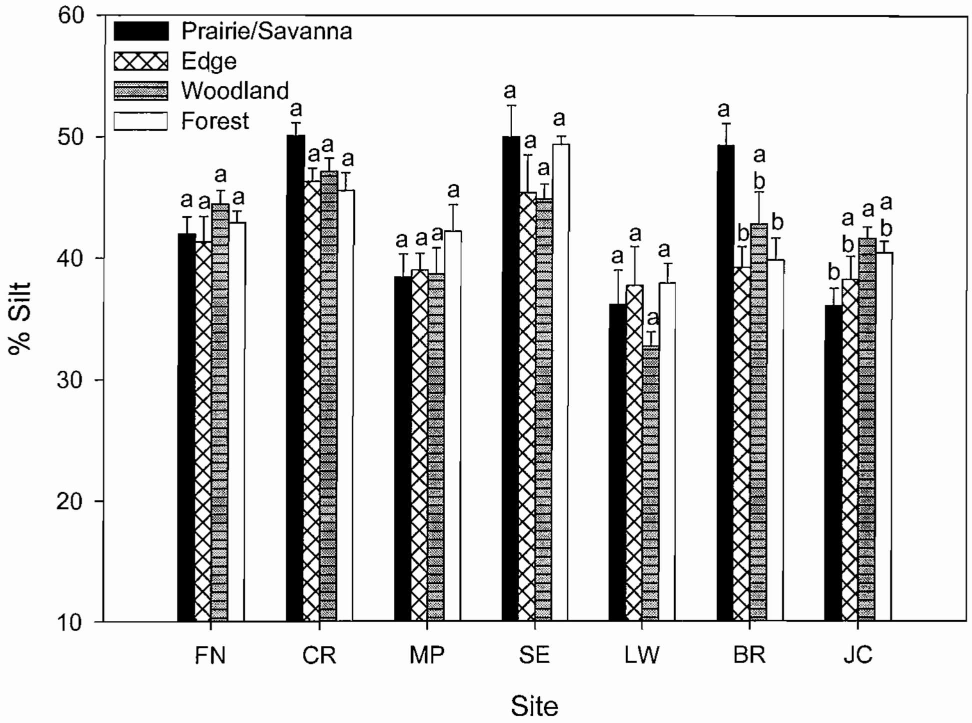

Figure 2.6 Percent silt in four community types at seven sites. Mean percent silt ± one standard error in each community type at each site. Unique letters represent significant differences among community types within a site at $\alpha = 0.05$ by Tukey's HSD.

Sand Content

The effect of community type on percent sand depended upon site ($p < 0.001$) ($n = 622$). Similarly, the effect of depth depended upon site ($p = 0.012$). Percent sand at both the 0-5 cm and 5-20 cm depths differed among sites ($p < 0.001$) (Figure 2.7). Percent sand was higher in the 0-5 cm depth than in the 5-20 cm depth at FN, CR, SE, LW, and BR ($p < 0.01$).

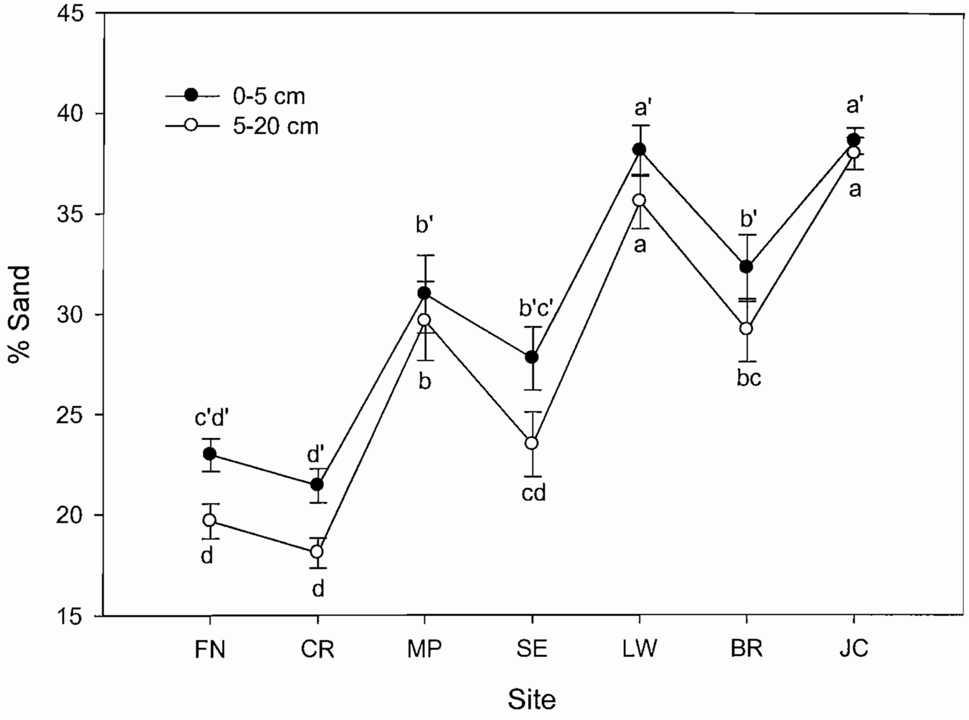

Figure 2.7 Percent sand at two depths at seven sites. Mean percent sand ± one standard error at 0-5 cm and 5-20 cm depth within each site. Primes indicate the 0-5 cm depth. Unique letters represent significant differences among sites within the 0-5 cm and 5-20 cm depth at the $\alpha = 0.05$ level by Tukey's HSD.

The effect of community type on percent sand from 0-20 cm depended upon site ($p < 0.001$) ($n = 309$). At FN, prairie/savannas had higher sand than woodlands and forests ($p < 0.001$) (Figure 2.8). Other sites showed variation in percent sand by community type, but not in a distinct pattern.

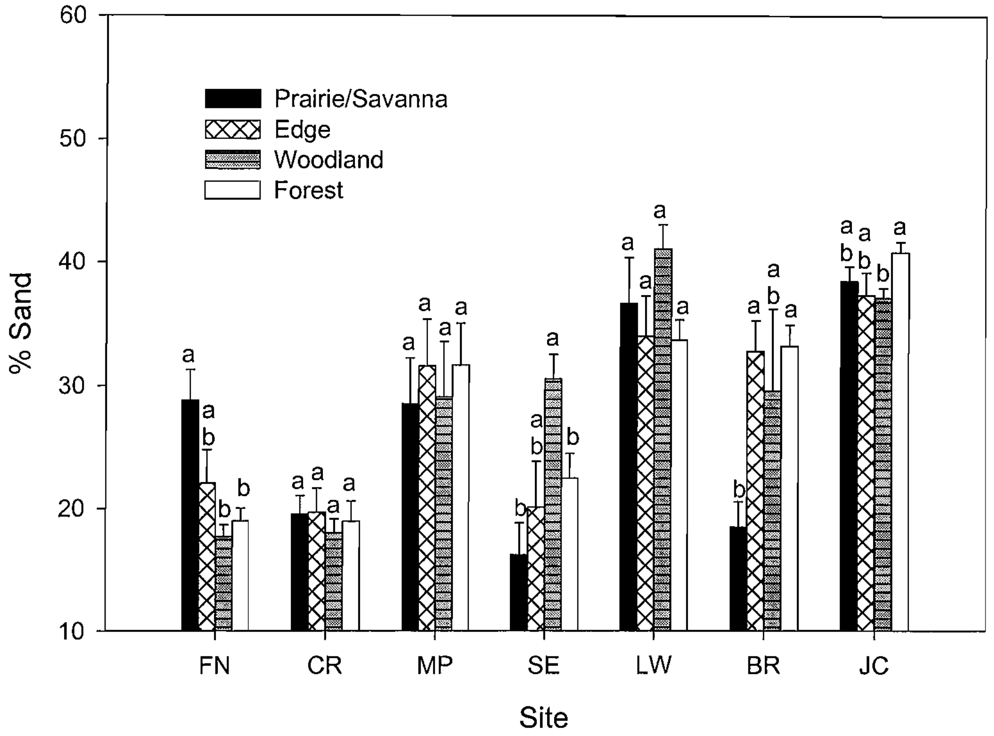

Figure 2.8 Percent sand in four community types at seven sites. Mean percent sand ± one standard error in each community type at each site. Unique letters represent significant differences among community types within a site at α = 0.05 by Tukey's HSD.

Carbon Content

The effect of community type on percent carbon depended upon site ($p = 0.004$) and depth ($p = 0.044$) ($n = 622$). Percent carbon at both the 0-5 cm and 5-20 cm depths differed among community types ($p < 0.001$) (Figure 2.9). Prairie/savannas had lower percent carbon than edges, forests, and woodlands within both the 0-5 cm and 5-20 cm depth ($p < 0.002$). Percent carbon was higher in the 0-5 cm depth than in the 5-20 cm depth in every community type ($p < 0.001$).

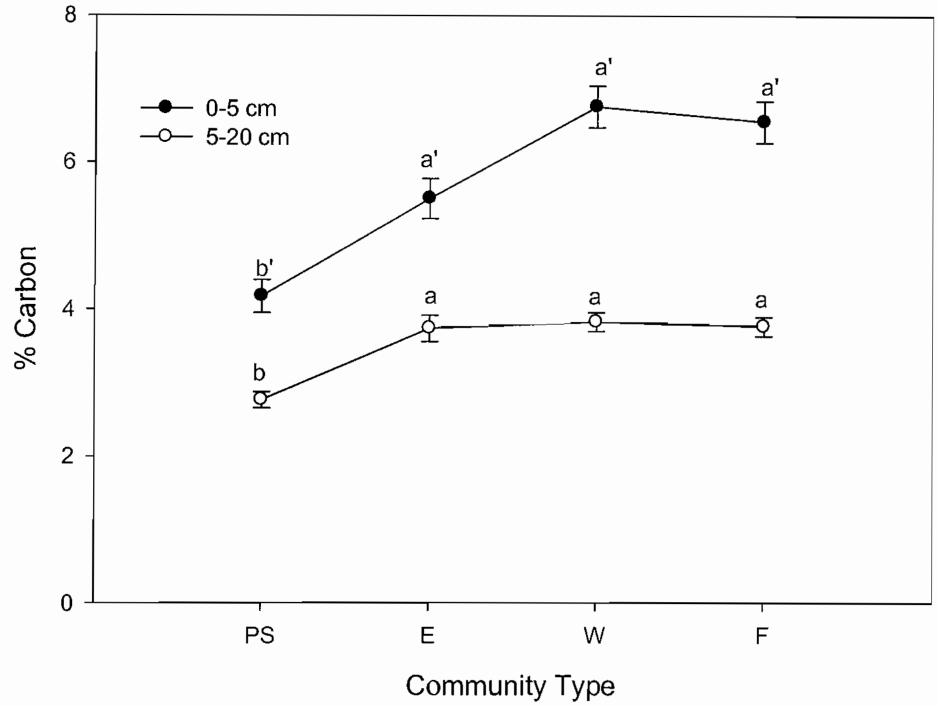

Figure 2.9 Percent carbon at two depths in four community types. Mean percent carbon ± one standard error at 0-5 cm and 5-20 cm depth within community type. PS is prairie/savanna, E is edge, W is woodland, and F is forest. Primes indicate the 0-5 cm depth. Unique letters represent significant differences among community types within the 0-5 cm and 5-20 cm depth at the $\alpha = 0.05$ level by Tukey's HSD.

The effect of community type on percent carbon from 0-20 cm depended upon site ($p = 0.026$) ($n = 308$). Similarly, the effect of community type on carbon (g/m^2) from 0-20 cm depended upon site ($p = 0.012$). Prairie/savannas had less percent carbon on average than edge, woodland, and forest at all sites (Figure 2.10A), and carbon in g/m^2 showed a similar result (Figure 2.10B), which illustrates the main effect of community type on carbon content ($p < 0.002$) (Table 2.7).

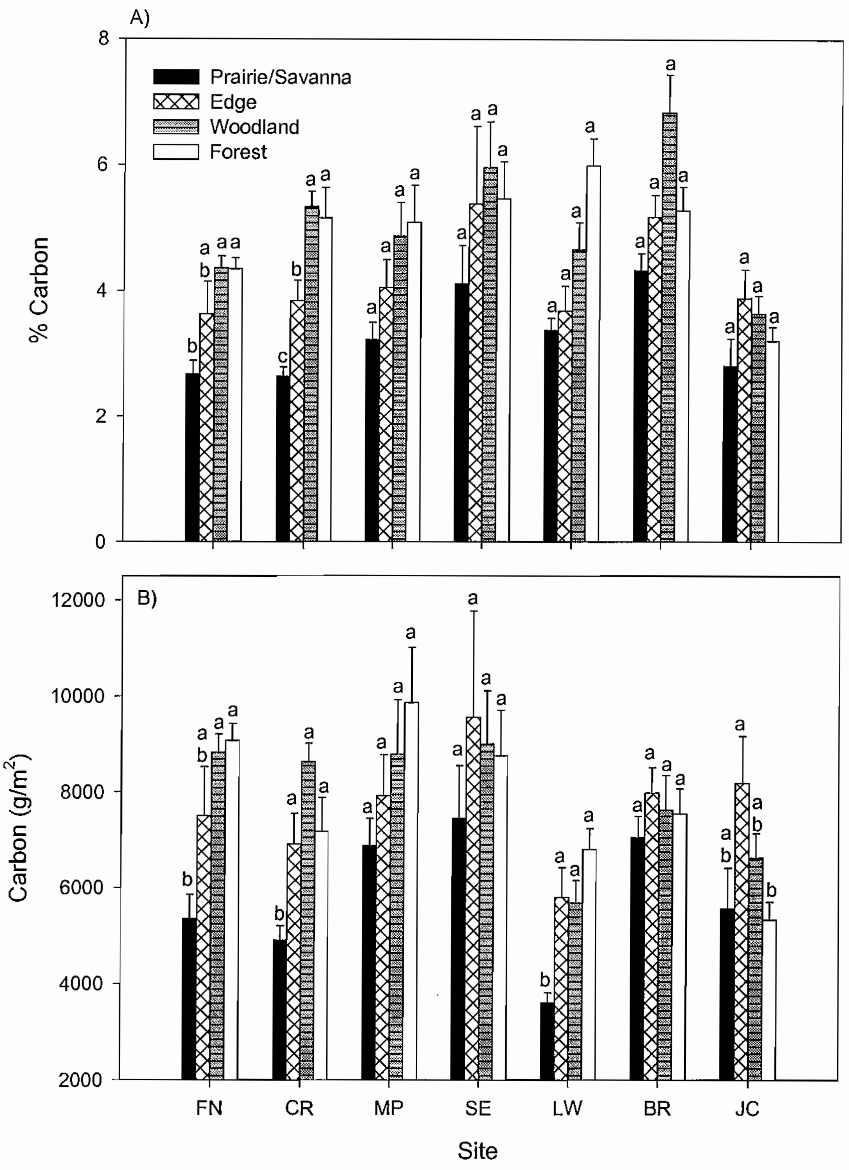

Figure 2.10 Soil carbon content. A) Percent carbon in four community types at seven sites. Mean percent carbon ± one standard error in four community types at seven sites. B) Carbon (g/m^2) in four community types at seven sites. Mean carbon (g/m^2) ± one standard error in four community types at seven sites. Unique letters represent significant differences among community types within a site at the $\alpha = 0.05$ level by Tukey's HSD

Nitrogen Content

The effect of community type on percent nitrogen depended upon site ($p = 0.003$) and marginally depended upon depth ($p = 0.067$) ($n = 622$). Percent nitrogen from 0-5 cm depth and from 5-20 cm depth differed among sites ($p < 0.001$). Percent nitrogen was higher in the 0-5 cm depth than in the 5-20 cm depth within every site ($p < 0.001$).

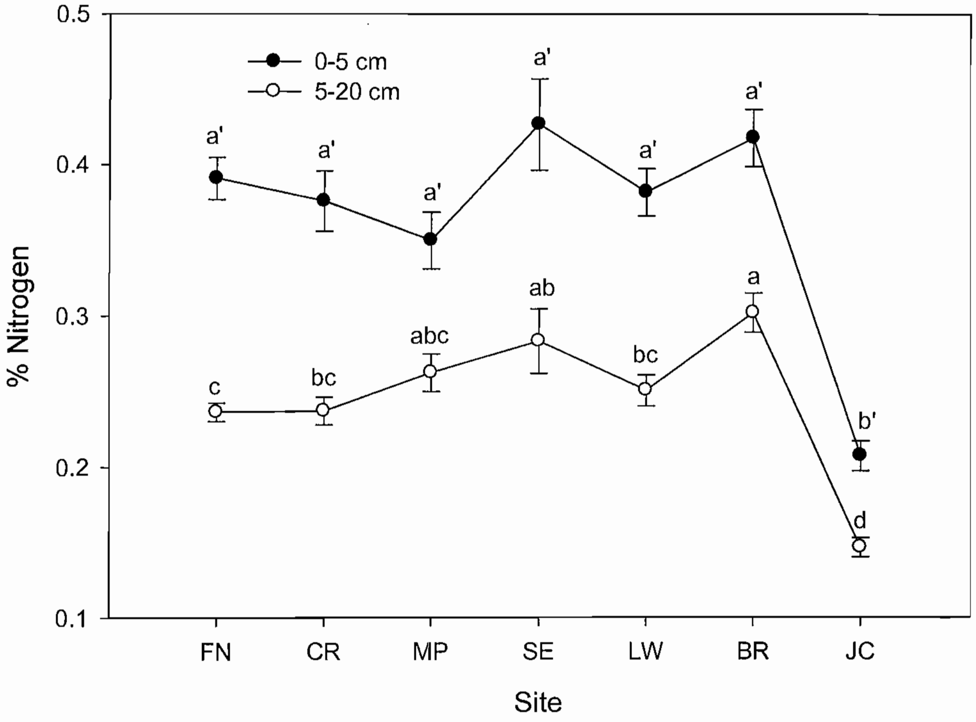

Figure 2.11 Percent nitrogen at two depths at seven sites. Mean percent nitrogen ± one standard error at 0-5 cm and 5-20 cm depth within each site. Primes indicate the 0-5 cm depth. Unique letters represent significant differences among sites within the 0-5 cm and 5-20 cm depth at the $\alpha = 0.05$ level by Tukey's HSD.

The effect of community type on nitrogen in both percent ($p = 0.006$) and g/m^2 ($p = 0.012$) from 0-20 cm depended upon site ($n = 307$). Woodlands and forests have significantly higher nitrogen content (g/m^2) than prairie/savannas at FN ($p < 0.02$) (Figure 2.12B). This trend is reversed at JC, where prairie/savannas and edges have significantly higher nitrogen content (g/m^2) than forests ($p < 0.02$). JC has lower nitrogen levels on average than the lower elevation sites (Figure 2.12).

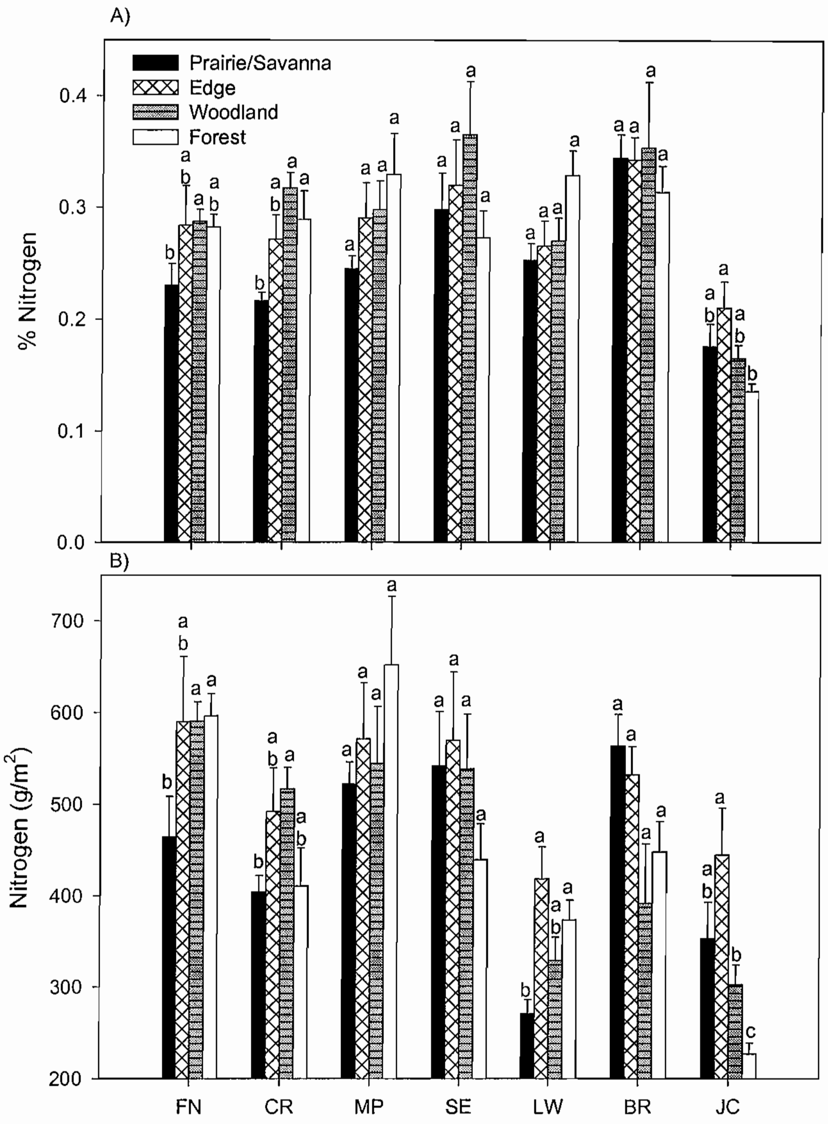

Figure 2.12 Soil nitrogen content. A) Percent nitrogen in four community types at seven sites. Mean percent nitrogen ± one standard error in four community types at seven sites. B) Nitrogen (g/m^2) in four community types at seven sites. Mean nitrogen (g/m^2) ± one standard error in four community types at seven sites. Unique letters represent significant differences among community types within a site at the $\alpha = 0.05$ level by Tukey's HSD

pH

Site significantly influenced soil pH ($p < 0.001$), however, this effect did not depend on community type ($p = 0.198$) ($n = 305$) (Table 2.7). Community type had a marginally significant effect on pH ($p = 0.084$). FN had a much lower pH than the other sites (Figure 2.13). In general, prairie/savannas had higher pH than edges, woodlands, and forests at CR, MP, SE, and JC, although these results were not statistically significant.

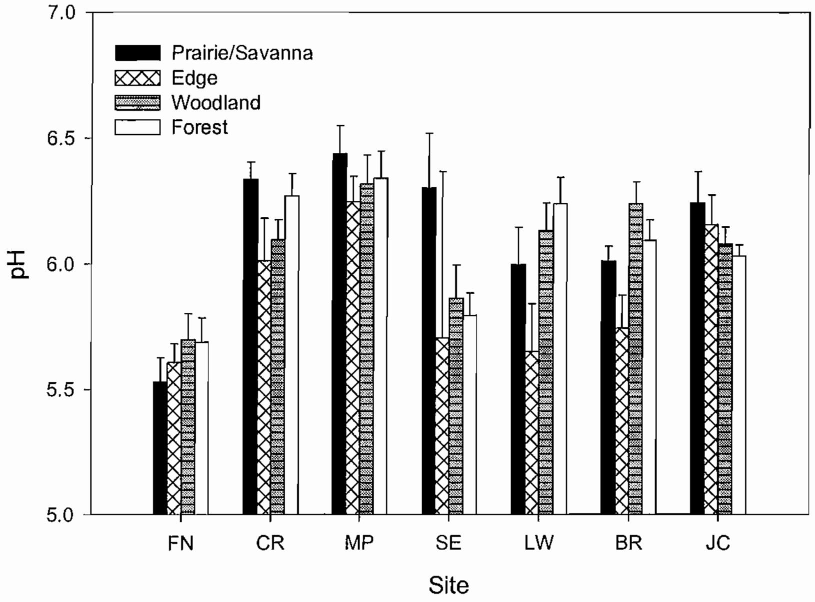

Figure 2.13 pH in four community types at seven sites. Mean pH ± one standard error in each community type at each site.

Soil Depth

The effect of community type on soil depth depended upon site ($p < 0.001$) ($n = 227$). Forests had deeper soils than prairie/savannas at FN ($p = 0.023$). Forests and woodlands had deeper soils than prairies and edges at JC ($p < 0.002$) (Figure 2.14). Other sites showed various patterns with community type.

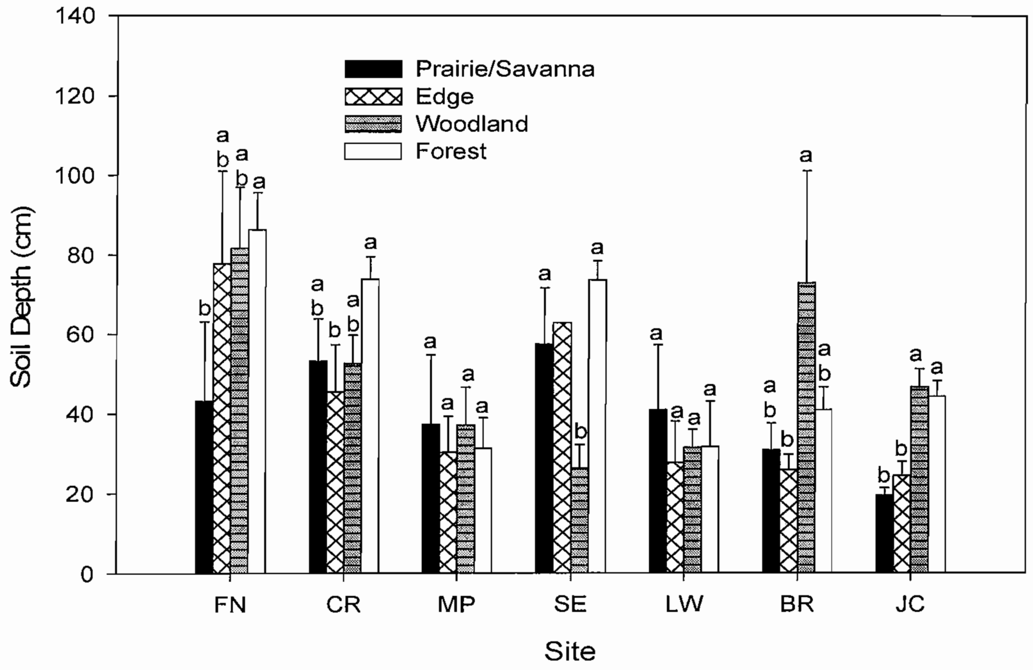

Figure 2.14 Soil depth in four community types at seven sites. Mean soil depth (cm) ± one standard error in each community type at each site. Unique letters represent significant differences among community types within a site at $\alpha = 0.05$ by Tukey's HSD.

Organic Layer Analysis: Analyses of Variance

The effect of community type on carbon content (% and g/m^2) depended upon site ($p < 0.05$) (Table 2.8). The effect of community type on the amount of bulk organic layer ($p = 0.056$) and nitrogen content (g/m^2) ($p = 0.074$) marginally depended upon site.

Table 2.8 Two-way ANOVA p-values for the organic layer.

Source	Bulk O-Layer (g/m^2)	Nitrogen (%)	Nitrogen (g/m^2)	Carbon (%)	Carbon (g/m^2)
Community Type	**0.003**	*0.062*	**0.003**	**<0.001**	**0.001**
Site	.404	**0.005**	0.405	0.224	0.480
Community Type x Site	*0.056*	0.445	*0.074*	**0.041**	**0.035**

Bulk Organic Layer

The amount of organic layer (g/m^2) was influenced by community type ($p = 0.003$), and marginally depended upon site ($p = 0.056$) ($n = 210$). Bulk organic layer was higher on average in forests and woodlands than in prairie/savannas at FN, CR, LW, and BR (Figure 2.15).

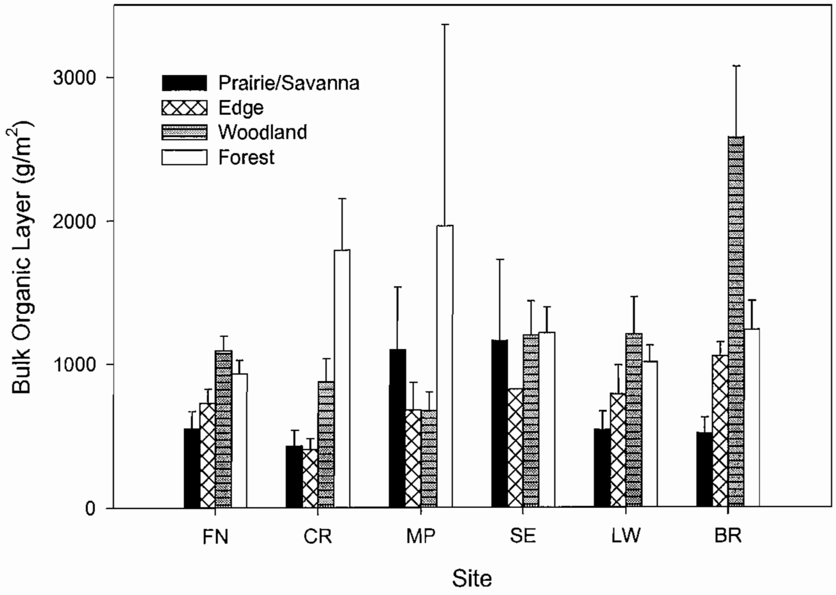

Figure 2.15 Bulk organic layer in four community types at six sites. Mean bulk organic layer (g/cm^3) ± one standard error in each community type at each site.

Carbon Content

Community type influenced percent carbon ($p < 0.001$) and grams of carbon per square meter ($p = 0.001$) in the organic layer, however, this effect also depended upon site ($p = 0.041$ and 0.035, respectively) ($n = 210$). In general, forests and woodlands had higher percent carbon than prairie/savannas at every site (Figure 2.16A), and carbon content in g/m^2 showed a similar result (Figure 2.16B).

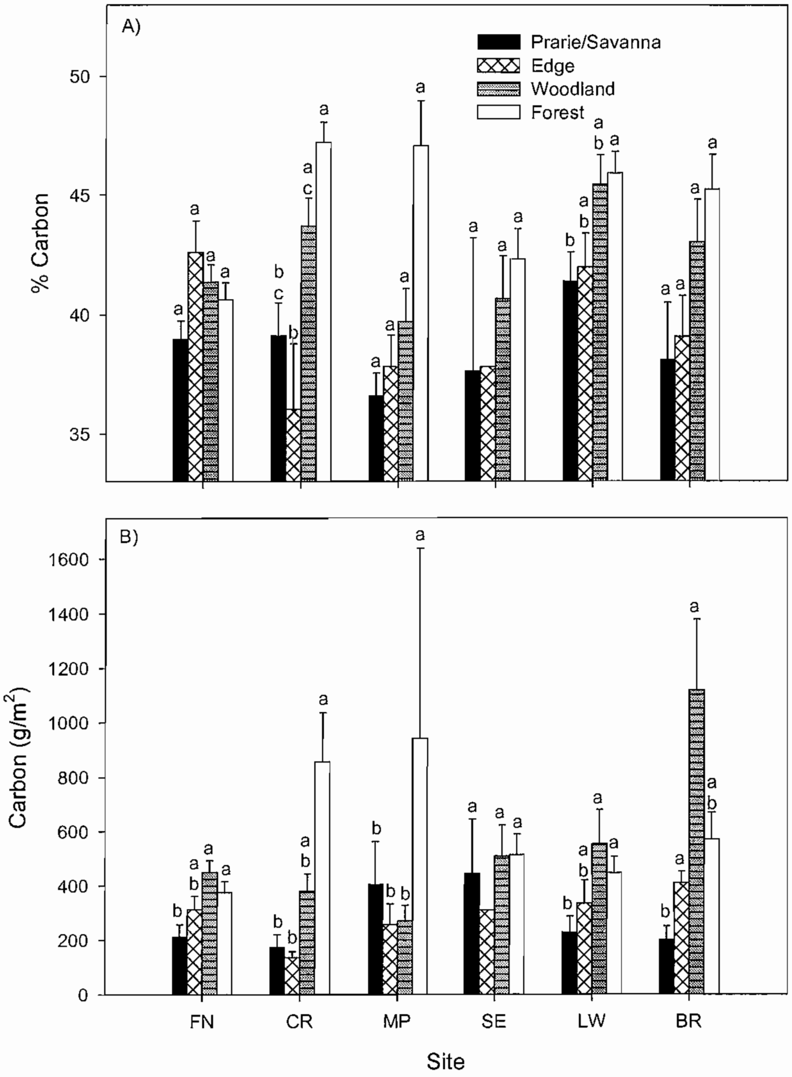

Figure 2.16 Organic layer carbon. A) Percent carbon in four community types at six sites. Mean percent carbon ± one standard error in four community types at six sites. B) Carbon (g/m^2) in four community types at six sites. Mean carbon (g/m^2) ± one standard error in four community types at six sites. Unique letters represent significant differences among community types within a site at the $\alpha = 0.05$ level by Tukey's HSD.

Nitrogen Content

Percent nitrogen varied by site ($p = 0.005$) and was marginally influenced by community type ($p = 0.062$) ($n = 210$). The effect of community type on percent nitrogen did not depend on site ($p = 0.445$) (Table 2.8). Grams of nitrogen per square meter varied by community type (p = 0.003), and the effect of community type marginally depended upon site (p = 0.074). In general, nitrogen (g/m^2) was lower in the prairie/savannas than in the forests (Figure 2.17B).

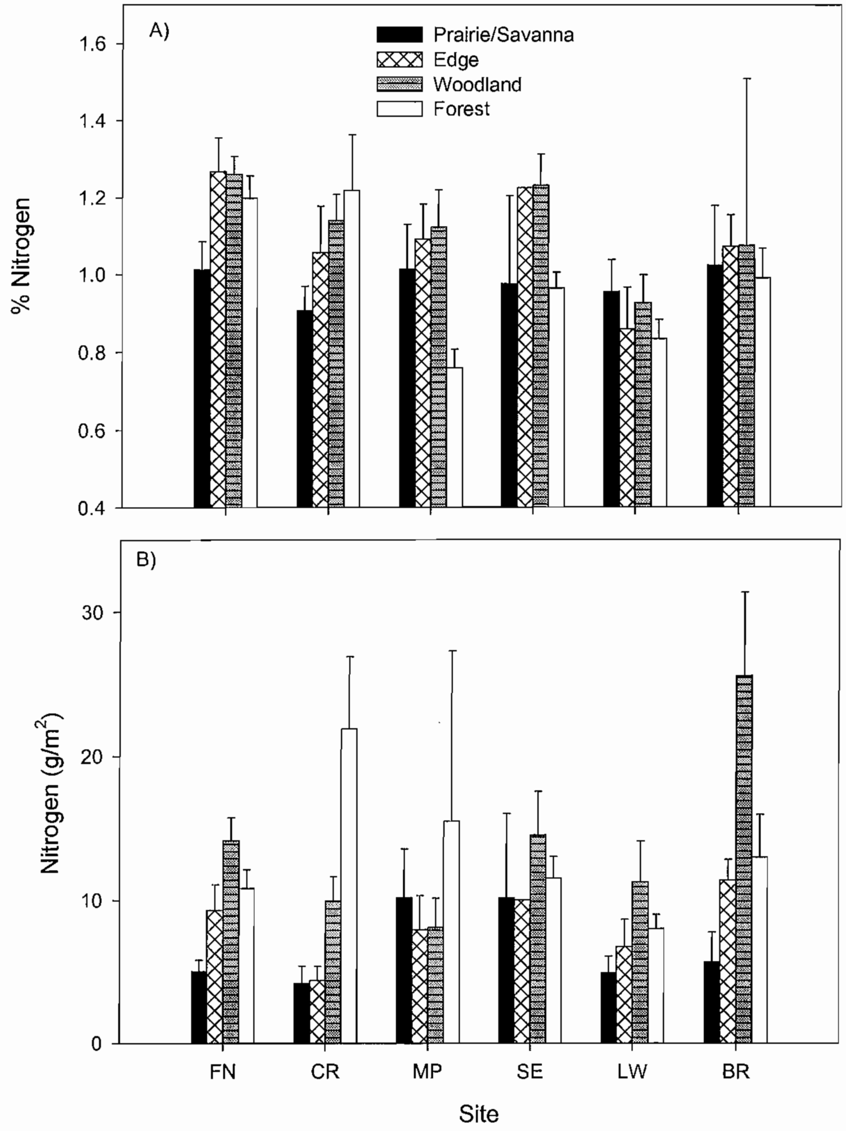

Figure 2.17 Organic layer nitrogen. A) Percent nitrogen in four community types at six sites. Mean percent nitrogen ± one standard error in four community types at six sites. B) Nitrogen (g/m^2) in four community types at six sites. Mean nitrogen (g/m^2) ± one standard error in four community types at six sites.

Relationships Among Soil Variables

Strong relationships existed between some of the soil variables (Table 2.10). Percent sand was negatively correlated with silt and clay. Nitrogen and carbon were strongly positively correlated. In addition, elevation was related to several soil variables. Elevation was negatively correlated with percent clay and nitrogen content (% and g/m^2), and was positively correlated with percent sand. Elevation was not included in the PCAs because elevation data was taken on a site level only.

PCAs were performed with and without soil depth because it was measured in only about two-thirds of the plots (see Methods). In a PCA that did not include soil depth, carbon, nitrogen, clay, sand, pH, heatload, and slope explained 61.0% of the variation in the data (n = 296). The first axis explained 35.5% of the variance and the second axis explained an additional 25.5% of the variance in the soil parameters across the seven sites. On the first axis, carbon, nitrogen, and clay loaded positively, while sand and heatload loaded negatively. On the second axis, clay loaded positively, while pH, sand, and slope loaded negatively (Table 2.9).

Table 2.9 Factor loadings for soil variables in the PCA including all seven sites. PCA does not include soil depth.

Variable	Factor 1	Factor 2
pH	0.148	-0.651
Percent Clay	0.545	0.572
Percent Sand	-0.539	-0.613
Nitrogen Content (g/m^2)	0.846	0.283
Carbon Content (g/m^2)	0.817	0.102
Heatload	-0.688	0.137
Slope	-0.143	-0.741

Figure 2.18 illustrates the relationships among the soil variables across the seven sites. Clay and sand are inversely related to each other. Carbon and nitrogen are closely related to each other. Areas that are high in clay are also high in nitrogen and carbon. In addition, steeply sloped areas tend to be high in sand and have high pHs.

Table 2.10 Correlation matrix for all soil variables measured. Correlations (R^2) greater than 0.5 are in bold.

	Bulk density	Clay (%)	Silt (%)	Sand (%)	C (%)	C (g/m^2)	N (%)	N (g/m^2)	pH	Soil depth	Heat-load	Slope	Ele-vation
Bulk density	1.000												
Clay (%)	0.192	1.000											
Silt (%)	0.288	0.020	1.000										
Sand (%)	-0.299	**-0.795**	**-0.623**	1.000									
C (%)	-0.426	0.123	0.040	-0.121	1.000								
C (g/m^2)	-0.095	0.312	0.091	-0.299	**0.814**	1.000							
N (%)	-0.309	0.317	0.096	-0.307	**0.816**	**0.694**	1.000						
N (g/m^2)	0.048	0.456	0.143	-0.445	**0.588**	**0.810**	**0.832**	1.000					
pH	-0.151	-0.073	-0.171	0.161	-0.061	-0.089	-0.076	-0.104	1.000				
Soil Depth	0.053	0.417	0.291	-0.499	0.129	0.188	0.083	0.093	-0.179	1.000			
Heat-load	-0.041	-0.251	-0.201	0.318	-0.129	-0.327	-0.303	-0.352	0.015	-0.241	1.000		
Slope	-0.399	-0.340	-0.201	0.388	-0.091	-0.265	-0.259	-0.412	0.266	-0.055	0.018	1.000	
Ele-vation	-0.230	**-0.635**	-0.220	**0.630**	-0.205	-0.285	**-0.512**	**-0.563**	0.213	-0.273	0.337	0.358	1.000

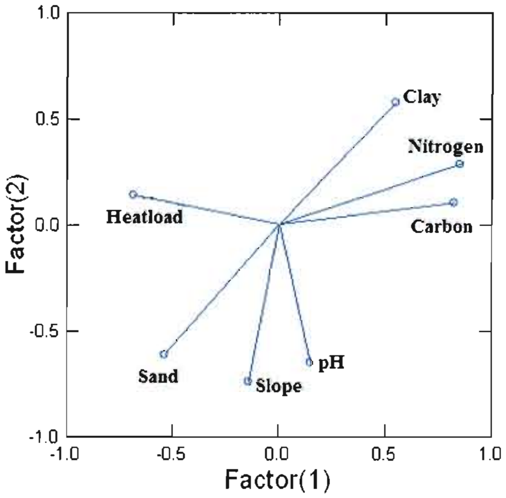

Figure 2.18 PCA vectors including seven sites, without soil depth.

I graphed each plot in the PCA by community type within each site (data not shown). Figure 2.19 shows the results of the same PCA, but plots the mean factor scores (± one standard error) for each community type within each site.

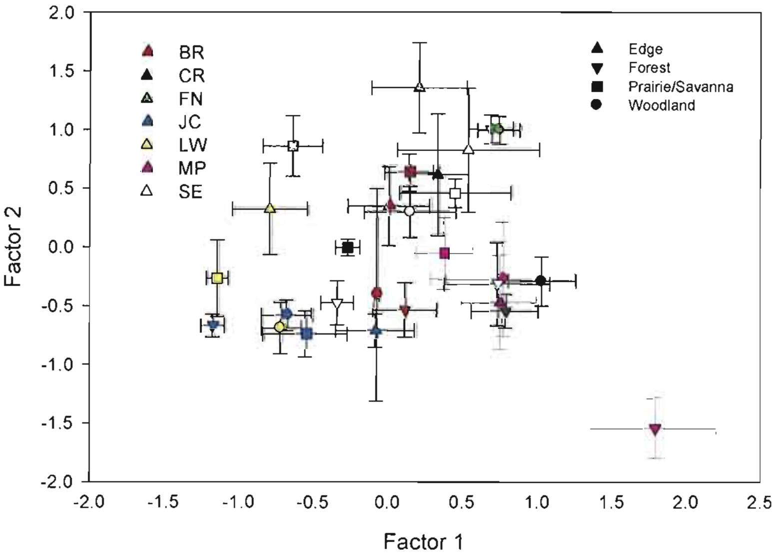

Figure 2.19 Factor loading scores in four community types at seven sites. Mean factor score ± one standard error for factors 1 and 2 in the PCA without soil depth.

Adding soil depth to the PCA slightly decreased the amount of variance explained to 54.5% (n = 207). The first axis explained 27.4% of the variation and the second axis explained an additional 27.1% of the variation in the soil parameters across seven sites. On the first axis, sand loaded positively while clay and soil depth loaded negatively. On the second axis, slope loaded positively, while carbon and nitrogen loaded negatively (Table 2.11). Adding soil depth to the PCA diminished the effect of slope dramatically and the effect of heatload somewhat (Tables 2.10 and 2.11).

Table 2.11 Factor loadings for soil variables in the PCA including all seven sites. PCA includes soil depth.

Variable	Factor 1	Factor 2
pH	0.035	0.099
Percent Clay	-0.801	-0.312
Percent Sand	0.870	0.249
Nitrogen Content (g/m^2)	-0.231	-0.911
Carbon Content (g/m^2)	-0.124	-0.872
Soil Depth	-0.750	0.085
Heatload	0.395	0.338
Slope	0.027	0.540

Similarly to the PCA without soil depth, clay and sand are negatively correlated with each other (Figure 2.20). Nitrogen and carbon levels also were highly correlated.

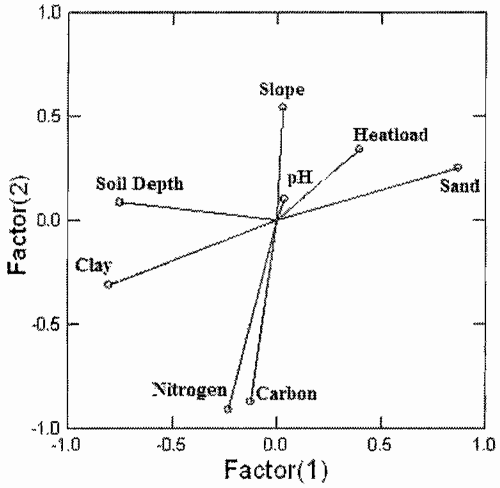

Figure 2.20 PCA vectors including seven sites, with soil depth.

I again graphed each plot in the PCA by community type and site (data not shown). Figure 2.21 shows these results, but plots the mean of each factor score by community type within each site.

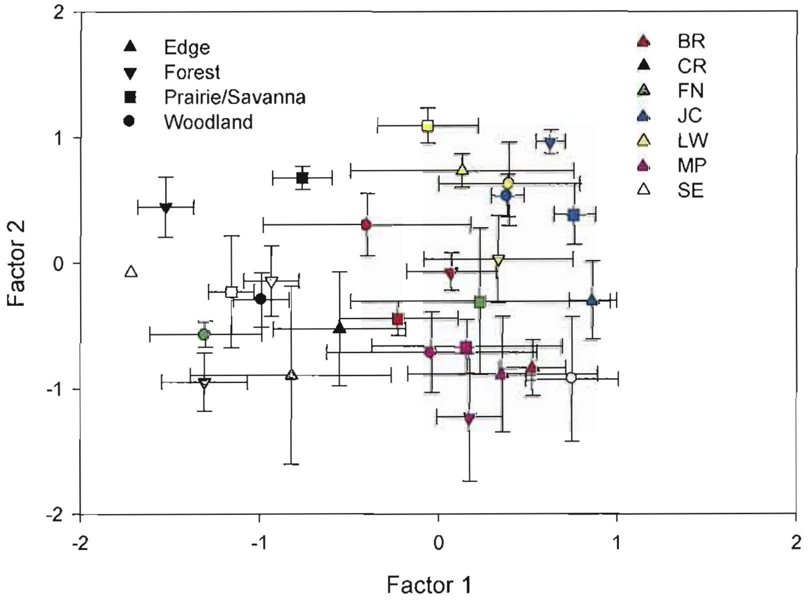

Figure 2.21 Factor loading scores in four community types at seven sites. Mean factor score ± one standard error for factors 1 and 2 in the PCA including soil depth.

Finley PCA

The PCAs at FN were performed with and without soil depth because soil depth was only measured at a subset of the plots. The inclusion of clay, sand, nitrogen, carbon, pH, heatload, and slope in the PCA together explained 58.4% of the variation in the data (n = 74). The first axis explained 30.8% of the variation and the second axis explained an additional 27.6% of the variation in the soil parameters at FN. On the first axis, nitrogen and carbon loaded positively, while heatload loaded negatively. On the second axis, percent sand loaded positively, while percent clay loaded negatively (Table 2.12). Slope and pH did not load onto either axis in a significant way.

Table 2.12 Factor loadings for soil variables in the PCA at FN. This PCA does not include soil depth.

Variable	Factor 1	Factor 2
pH	0.165	-0.248
Percent Clay	0.261	-0.814
Percent Sand	-0.008	0.945
Nitrogen Content (g/m^2)	0.959	0.008
Carbon Content (g/m^2)	0.915	-0.202
Heatload	-0.548	0.410
Slope	-0.039	0.327

Similarly to the other PCAs, clay and sand were negatively correlated to each other and carbon and nitrogen were closely related (Figure 2.22).

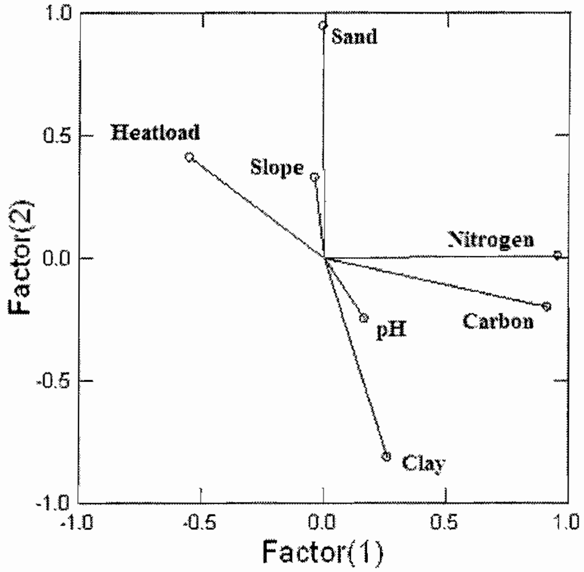

Figure 2.22 PCA vectors at FN only, without soil depth.

I graphed the factor scores of each plot by community type to see if community types would group together. Prairies tended to group together, and so did forests and woodlands (Figure 2.23).

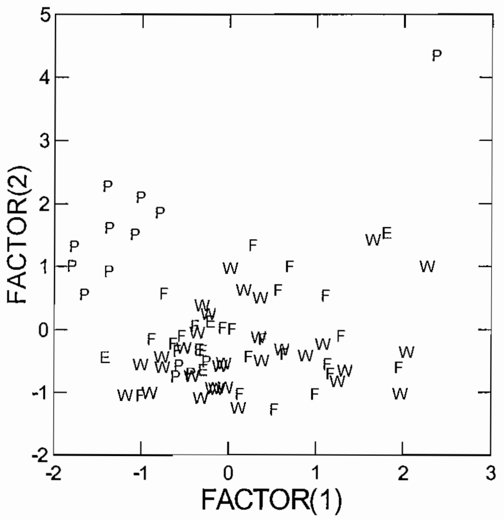

Figure 2.23 Plots by community type at FN (PCA without soil depth). F is forest, W is woodland, E is edge, and P is prairie/savanna.

To visualize the differences among community types at FN, I again graphed the mean factor scores for each community type (Figure 2.24). Prairie/savannas are distinct from forests, woodlands, and edges. The edge is between the prairie/savannas and the forests and woodlands. Prairie/savannas tended to load positively on factor 2 and negatively on factor 1, with a few exceptions.

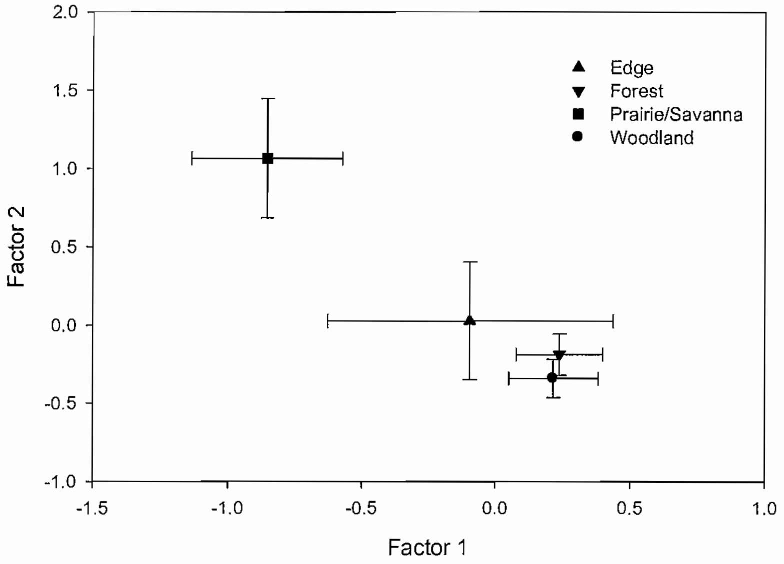

Figure 2.24 Factor loading scores in four community types at FN. Mean factor score ± one standard error for factors 1 and 2 in the PCA without soil depth.

Adding soil depth to the PCA of FN increased the amount of variance explained in the soil variables by over 10%. Clay, sand, nitrogen, carbon, pH, heatload, slope, and soil depth together explained 69.0% of the variation in the data at FN (n = 23). The first axis explained 42.0% of the variation and the second axis explained an additional 27.0% of the variation in the soil parameters at FN. On the first axis, sand and heatload loaded positively, while clay and soil depth loaded negatively. On the second axis, carbon and nitrogen loaded positively, while slope loaded negatively (Table 2.13). pH did not load onto either axis in a significant way.

Table 2.13 Factor loadings for the soil variables in the PCA of FN, including soil depth.

Variable	Factor 1	Factor 2
pH	0.081	0.420
Percent Clay	-0.930	-0.125
Percent Sand	0.927	0.011
Nitrogen Content (g/m^2)	0.113	0.895
Carbon Content (g/m^2)	-0.257	0.888
Soil depth	-0.948	0.031
Heatload	0.745	-0.223
Slope	0.154	-0.631

Areas that are high in clay also tend to have deeper soils (Figure 2.25). In addition, areas that have a high heatload also have high sand content.

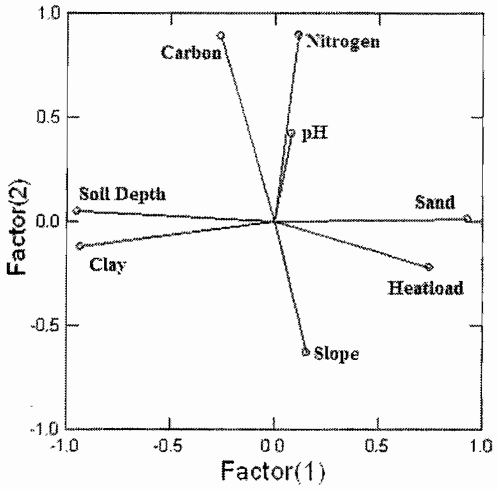

Figure 2.25 PCA vectors at FN, including soil depth.

I graphed the factors scores for each plot at FN by community type to see if there was any pattern with community type (Figure 2.26). Prairie/savannas tended to group together and so did forests and woodlands.

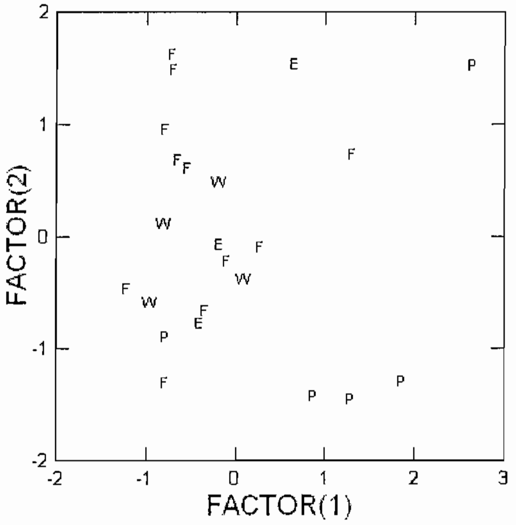

Figure 2.26 Plots by community type at FN (PCA including soil depth). F is forest, W is woodland, E is edge, and P is prairie/savanna.

In the PCA of FN including soil depth, I graphed the mean factor scores of each community type to better visualize the differences among them. Prairie/savannas are distinct from edges, woodlands, and forests at FN (Figure 2.27). The edges are between prairie/savannas and woodlands and forests. Prairie/savannas tended to load positively on axis one and negatively on axis two.

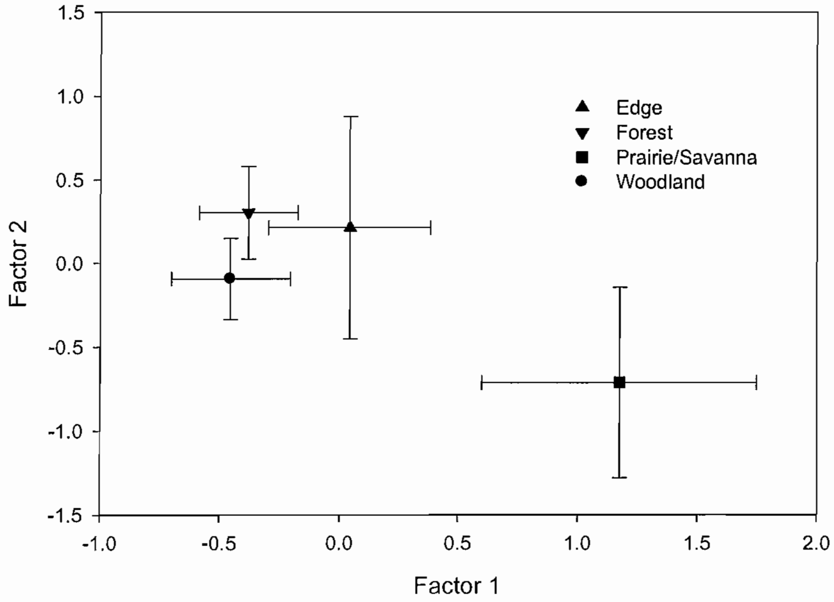

Figure 2.27 Factor loading scores in four community types at FN. Mean factor score ± one standard error for factors 1 and 2 in the PCA including soil depth.

Jim's Creek PCA

This PCA of JC was performed only once including soil depth because soil depth was measured at every plot at JC. Clay, sand, carbon, nitrogen, pH, slope, heat load, and soil depth together explained 50.7% of the variation in the data (n = 74). The first axis explained 31.9% of the variation and the second axis explained an additional 18.8% of the variation in the soil parameters. On the first axis, clay, nitrogen and carbon loaded postively, while sand loaded negatively. On the second axis, slope and pH loaded positively, while soil depth loaded negatively (Table 2.14). Heatload did not load onto either axis in a significant way.

Table 2.14 Factor loadings for soil variables in the PCA of JC, including soil depth.

Variable	Factor 1	Factor 2
pH	0.329	0.644
Percent Clay	0.743	0.229
Percent Sand	-0.499	0.245
Nitrogen (g/m^2)	0.914	0.134
Carbon (g/m^2)	0.803	-0.115
Soil depth	-0.017	-0.635
Heatload	-0.204	0.179
Slope	-0.351	0.714

Areas in JC that are high in clay are also high in nitrogen and carbon (Figure 2.28). Areas with steep slopes also tend to have high heatload and sand content.

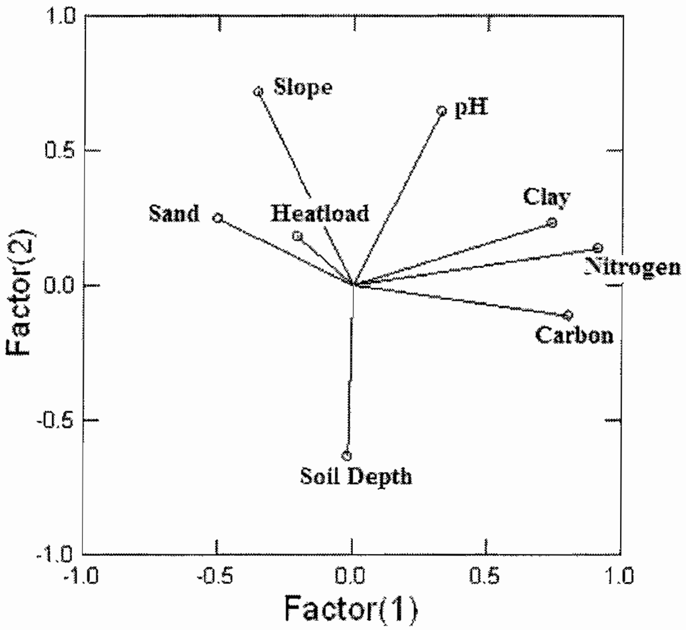

Figure 2.28 PCA vectors for JC, including soil depth.

I graphed the factor scores for each plot in the PCA of JC by community type (Figure 2.29). The grouping of community types was slightly less distinct than the PCAs at FN, although woodlands and forests tended to group separately from prairie/savannas and edges (Figure 2.29).

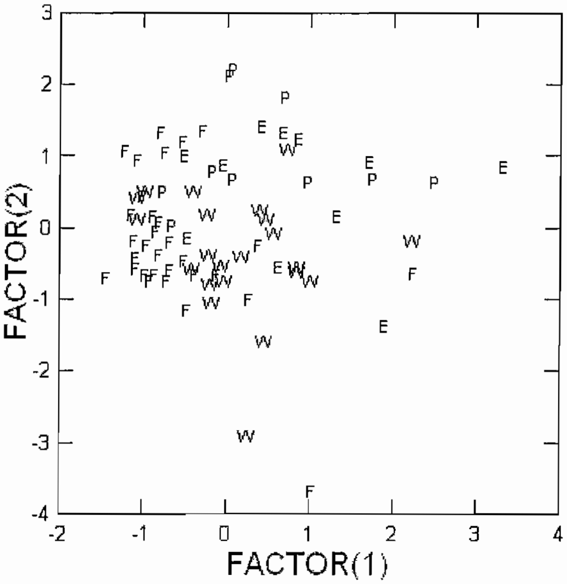

Figure 2.29 Plots by community type at JC (PCA includes soil depth). F is forest, W is woodland, E is edge, and P is prairie/savanna.

I graphed the mean factor scores by community type for the PCA of JC. Community types were somewhat more distinct at JC than at FN (Figure 2.30).

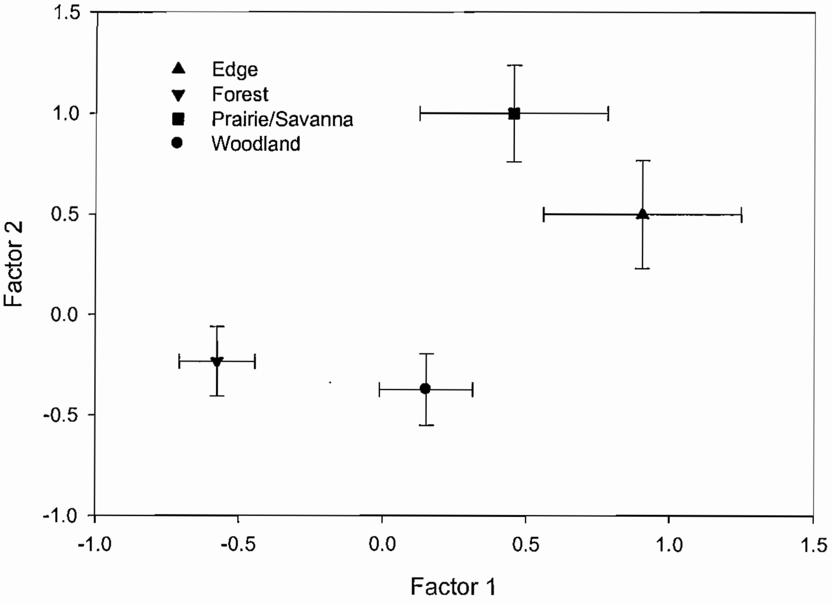

Figure 2.30 Factor loading scores in four community types at JC. Mean factor score ± one standard error for factors 1 and 2 in the PCA including soil depth.

Discussion

My results demonstrate that edaphic and topographic conditions have a strong influence on successional pathways in former oak savanna, but that the specific effects depend heavily on where the communities are located in the Willamette Valley. Although I had hypothesized that environmental factors would show consistent influences across the breadth of environmental conditions represented by the different sites, my results show a much more complex picture of environmental factors affecting succession and community structure in different ways depending on location. Overall, there was a stronger effect of site than of community type, which was illustrated in the ANOVA results by the consistent site by community type interaction (Table 2.7) and by similar results in the PCAs. In the PCA analysis, sites tended to group together consistently but community types did not group together independently of sites, though some community types showed similar patterns at more than one site (Figures 2.19 and 2.21). The average elevation of the seven sites ranged from 125 to 792 m and each contained unique topography, which may be part of the reason for the strong effect of site. Community types tended to be distinct within sites in the PCAs (Figures 2.27 and 2.30). In addition to the clustering of community types within sites, the sites are in general ordered from high elevation to low elevation as one follows from the lower left to upper right on the graph (Figure 2.19), suggesting that elevation plays a strong role in determining edaphic conditions.

Although a strong site effect was present in this study, edaphic conditions clearly have a strong influence on the successional pathways within sites. Low nitrogen content may be limiting succession in lower elevation sites, such as FN and CR (Figure 2.12B). In contrast, high nitrogen content may be inhibiting succession at higher elevation sites like JC (Figure 2.12B). Prairie/savannas tend to have a higher clay content than forests and woodlands at the higher elevation sites of JC, BR, MP, and SE (Figure 2.4). This trend is reversed at the lowever elevation sites of FN and CR (which are also close in proximity), where prairie/savanna areas tend to have a lower clay content than woodlands and forests (Figure 2.4).

Soil depth may be one of the more important variables in determining rates of succession. Prairie/savannas had significantly shallower soil depth than forests at both JC and FN in the ANOVA results (Figure 2.14). Prairie/savannas were strongly associated with shallow soils in the PCA results for both FN and JC (Table 2.13, Figure 2.27, and Table 2.14, Figure 2.30). FN and JC represent the elevation extremes in this study. Thus, if soil depth is restricting succession at these sites, it may be restricting succession at the more moderate elevation sites as well, although this was mot consistent at all of the other sites. This may be a result of historic grazing and land management at these sites.

JC has never had livestock grazing, agriculture, or logging, therefore, JC may represent the soil and topographic factors that are restricting succession with few confounding anthropogenic factors. Prairie/savannas tend to have shallow soils, high clay, high carbon and nitrogen, high pH, and steep slopes at JC (Figure 2.30). Further study is needed to determine the impacts of site history on successional trajectories at the other sites. Despite the potential influences of confounding factors such as grazing, I was still able to get strong statistical results.

In addition to the relationships between soil factors and community types, this study also illustrates the characteristics of soils in areas of former Willamette Valley oak savanna. As one would expect, soils that are high in carbon also tend to be high in nitrogen, and soils that have high clay content tend to be low in sand (Figure 2.18, Table 2.9). Areas that have steeper slopes tend to have higher sand content and higher pH (Figures 2.18 and 2.20). However, this last effect is most likely due to the presence of JC in the study, which is steeply sloped, has a high soil pH, and high sand content. JC is also the highest elevation site in this study, suggesting this may be characteristic of soils in higher elevations of the Willamette Valley.

Areas with high clay content tend to have deeper soils, however, this effect is most likely due to the presence of FN in the study (Figure 2.20). FN is in the lowlands of the Valley, with deep clay soils, which may also be characteristic of other low-elevation sites. In addition, there was an overall decrease in clay content as elevation increased (Figure 2.3).

Conclusions and Implications for Management

This study illustrates the importance of both site location and edaphic factors in determining successional trajectories in former oak savanna. Shallow soils appear to be one of the few characteristics that have restricted succession across a wide variety of sites in the Willamette Valley, while other factors appear to be having important but often site-specific influences. These results are important not only for understanding the complexities of how and why former oak savanna is changing, but for site managers who wish to redirect these trajectories. Restoration professionals in particular must take site factors such as elevation, topography, and soil characteristics into consideration when planning restoration and management of Oregon white oak savanna. Areas with soil and topographic characteristics more conducive to succession will require more management. It is important to restore these areas as well as those that may not be as prone to succession. If only areas that have resisted succession thus far are restored, the range of Oregon white oak savanna will be limited to the harshest environmental conditions, which are only a tiny fraction of its former range.

CHAPTER III

THE EFFECTS OF MOISTURE ON SUCCESSION

Introduction

Oak savanna was once a major ecosystem in the United States, but has declined over the last several hundred years (Thomas and Spicer 1987). In the early 1800s, approximately 12,000,000 ha of oak savanna were present in the northern part of the Midwestern United States (Nuzzo 1986). Multiple reasons underlie the decline of oak savanna, and it is currently considered critically endangered in the Midwestern United States and in Oregon's Willamette Valley (Noss et al. 1995).

One of the major reasons for the decline of oak savanna in the Willamette Valley, and also in the Midwestern United States, has been the reduction in fire regimes following Euro-American settlement (Henderson 2006, Hulse et al. 2002). In the Willamette Valley, the open, park-like structure of the savanna was maintained by natural fires or those set by the Native Americans (Boyd 1999, Agee 1993, Whitlock and Knox 2002). Oak savanna in the Willamette Valley is dominated by Oregon white oak (*Quercus garryana*), which is a highly fire tolerant species. Prior to the Euro-American settlement of the Willamette Valley, frequent low-intensity fires kept the tree density low, maintaining the open-grown oak trees and a ground layer of grasses and forbs. Without fire as a disturbance, Oregon white oak savannas are prone to tree invasion, especially by conifers (Stein 1990).

Remnant Willamette Valley oak savannas have experienced different levels of tree invasion; some areas have succeeded to woodland or forest, while other areas have maintained their open, park-like savanna structure. Succession in the Willamette Valley primarily has been driven by conifer invasion, principally Douglas-fir (Stein 1990), although infill in some areas has been dominated by Oregon white oak or big leaf maple (*Acer macrophyllum*). To date, however, there has been little investigation of the controls over forest succession in oak savanna following fire regime reduction, and in particular, on the mechanisms that explain the spatial variability in succession.

Soil nutrients, texture, depth, pH, and site physiographic factors appear to have affected the degree of succession in the Willamette Valley, both within and among sites (Chapter 2). In particular, soil and topography have a complex relationship with plant community type, and these relationships are highly dependent on site location (Chapter 2). Although these factors are strongly linked to successional trajectories, their primary effects may be through their control over other factors that plants experience.

Soil moisture, in particular, has been linked to successional dynamics in disturbed areas world-wide (Prach and Rehounkova 2006). Although climate and surrounding vegetation were found to be the most important factors influencing succession at the landscape scale in the review by Prach and Rehounkova (2006), soil moisture was the most important edaphic factor, followed by nitrogen, texture, and pH. Furthermore, because soils and soil moisture frequently show fine-scale spatial heterogeneity, differences in soil moisture may have important localized effects on succession within areas of former Willamette Valley savanna and prairie.

Oregon white oak has a unique ability to persist in areas with sparse precipitation and droughty soils (Stein 1990), which may give the species a competitive edge over Douglas fir in these areas. In the Pacific Northwest, Klinka et al. (1996) found Oregon white oak communities in British Columbia to be distinctive based on their association with the driest and shallowest environments. In the same study, Douglas-fir was found on moisture deficient sites, though these sites were not as dry as the sites where Oregon white oak was found.

As described in Chapter 1, limited soil moisture and shallow soils may favor Oregon white oak over Douglas-fir in some locations due to the differences in rooting dynamics, mainly by inhibiting Douglas-fir invasion. Oregon white oak has the ability to develop a deep taproot as well as an extensive lateral root system (Stein 1990, Devine and Harrington 2005). This gives Oregon white oak the ability to tap ground water resources with its deep taproot, and also to take advantage of rare summer precipitation with its shallow later roots, which may account for its ability to survive on droughty soils. The ability to take advantage of summer precipitation is especially important in the Willamette Valley, where there is summer drought. Douglas-fir will grow a taproot only when there are no barriers in the soil (Hermann and Lavender, 1990), which may limit its ability to obtain water in areas with shallow or rocky soils. In addition, Douglas-fir does not have as extensive a lateral root system as Oregon white oak, limiting its ability to utilize summer precipitation (Krygier 1971). Droughty soils thus may limit invasion by Douglas-fir, and allow these areas to maintain their savanna structure and/or dominance by oaks.

However, competitive interactions between Douglas-fir and Oregon white oak may be more complex than Douglas-fir being simply excluded from drier sites. Removal of Douglas fir in a former oak savanna increased soil moisture during the growing season (Devine and Harrington 2007), which may have been due in part to the increase in throughfall where Douglas fir were removed, and/or to the reduced water uptake by Douglas fir. Devine and Harrington (2007) conclude that competition for soil water may be an important reason for the Oregon white oak decline in areas invaded by Douglas fir, in addition to competition for light.

Soil depth can influence moisture availability by restricting the volume of soil available for water storage. The deeper the soil, the more water that can be stored in the soil profile. In a study of Willamette Valley oak savanna, soil depth affected community type, but the specific effects depended on site (Chapter 2). Soil depth was found to be significantly greater in forests than in prairies at two of the seven sites, and was greater in forest than in the forest-prairie edge at a third site. This suggests that soil depth maybe an important factor in determining community type, and because soil depth has a likely effect on soil moisture, it was important to incorporate in this study.

My research thus focused on the following questions: 1) How has soil moisture influenced succession in former oak savanna? 2) How is soil depth related to soil moisture? 3) Is soil depth or moisture driving the successional dynamics in former oak savanna?

Methods

Study Areas and Plant Communities

This study was conducted on a subset of the seven sites in the larger study described in Chapter 2. Jim's Creek (JC), Chip Ross (CR), and Finley (FN) were chosen for this study because they encompass a broad range of the environmental conditions and the current seral stages of succession found in former oak savanna. Twelve to fourteen soil moisture wells were installed at each site in key community types representing different successional stages and measured seasonally throughout one year. Basic vegetation data was taken previously (Chapter 2) and used to classify and select plots by community type for this study. At each site, moisture wells were installed in forest, edge, and prairie plots. Species and diameter at breast height were recorded for every tree within a plot. Canopy cover was measured at each plot center using a spherical densitometer. Forest was defined as having a canopy cover greater than 60% and prairie was defined as having few to no trees (< 5% canopy cover). The edge was defined as the tree-line boundary separating a forest or woodland from a savanna or prairie.

At FN, forest plots were categorized into two types, those dominated by oak with some fir and maple, and those dominated by fir with some oak (Table 3.1).

Table 3.1 Number of moisture well plots in each community type at FN.

Community type	Number of plots
Prairie	3
Edge	3
Forest, oak-fir-maple	3
Forest, fir-oak	3

At CR, moisture wells were installed in forest, edge, savanna and prairie plots (Table 3.2). Forest was broken down into two types, those dominated by fir with some oak and maple, and those dominated by oak with some fir. Because only two moisture wells were established in savanna plots at CR, savanna was not included as a community type in the statistical analysis.

Table 3.2 Number of moisture well plots in each community type at CR.

Community type	Number of plots
Prairie	3
Edge	3
Savanna	2
Forest, fir-oak-maple	3
Forest, oak-fir	3

At JC, moisture wells were installed in prairie, edge, meadow infill, and forest community types (Table 3.3). “Meadow infill” was defined as former meadow-savannas lightly infilled with trees, but not in a distinct pattern like in the edge. Infilled meadows are situated near a current meadow or savanna. This community type was unique to JC and displays a moderate rate of succession, faster than prairie but slower than forest. One of the forest plots at JC was a significant outlier for soil depth, not just for the 12 plots used in this study, but based on sampling of 81 plots at the site for the larger study (Chapter 2). This outlier was excluded from all analyses. In addition, a moisture well cap in an infilled meadow plot at JC was removed by an elk in March. Only three infilled meadow plots were included in the March sampling, rather than four.

Table 3.3 Number of moisture well plots in each community type at JC.

Community type	Number of plots
Prairie	3
Edge	4
Meadow infill	3
Forest	2

Moisture Well Installation, Monitoring, and Precipitation

PVC tubes (5-cm diameter) were installed with the slurry method (Sentek Sensor Technologies 2003) to the maximum depth possible within each plot, which ranged from 10 cm to a maximum tube depth of 130 cm. Soil moisture was measured with a soil moisture probe, the Diviner 2000 (Sentek Sensor Technologies, Stepney, Australia), starting at 10 cm depth and then at each successive 10 cm increment for the depth profile.

Moisture well readings were taken eight times from the spring of 2006 to the end of winter 2007 to encompass of the range of seasonal moisture levels. The climate of the Willamette Valley is Mediterranean, with summer drought and wet winters. CR and FN are near Corvallis, Oregon, where the long-term average annual precipitation is 104 cm. In 2006, the precipitation in Corvallis was 136 cm, which is slightly above average. In 2007, the precipitation was 97cm, which is slightly below average. JC is near Oakridge, Oregon, where the long-term average annual precipitation is 116 cm. In 2006, precipitation was 130 cm, slightly above average, whereas in 2007, precipitation was slightly below average (112cm) (Western Regional Climate Center 2007).

Soil Water Content Calibration

The Diviner 2000 contains a default calibration equation that is used to estimate soil water content, but this equation may not be accurate for a particular site due to differences in soil texture, depth, structure, vegetation, and other characteristics (Sentek Sensor Technologies 2001). To obtain absolute volumetric soil moisture readings, a laboratory calibration was performed with soil from the three sites (Sentek Sensor Technologies 2001, Platineanu and Starr 1997). Soils were sampled in forest and prairie vegetation types at JC, FN, and CR to a depth of 0-20 cm and 20-40 cm. Due to the high clay content of FN soils at depths greater than 40 cm, soils were sampled to a depth of 60 cm at this site.

Wells were installed in 18.9 L buckets to a depth of 20 cm with the slurry method (Sentek Sensor Technologies 2003) at three different moisture levels that spanned the range typically observed in the field. Soils were air dried to achieve low moisture levels. The maximum percent moisture in the field moisture wells was just under 52% moisture by volume, so this moisture content was used as the maximum moisture content for the calibration. Water was added to the medium and high moisture level soils until a volumetric water content of 26% and 52% was achieved, respectively. Soils were sealed in buckets and allowed to equilibrate until a constant soil moisture was read by the probe.

Then three soil cores were taken from each bucket and wet and dry oven weights were used to determine the gravimetric water content.

Bulk density was determined by the amount of dry soil added to the bucket divided by the total volume of soil. Volumetric water content (Θ) was calculated by multiplying the bulk density (p) by the gravimetric water content (W) (Sentek Environmental Technologies 1999).

$$\Theta = p*W$$

Volumetric water content (θ) is the percent moisture by volume. For example, if the volumetric water content is 1% (or 1 mm of volumetric water content per 10 cm of soil), that means it takes one liter of water to cover one square meter to a soil depth of 1 mm (Sentek Environmental Technologies 1999). Volumetric water content was plotted against the probe's reading (in scaled frequency, SF) to determine the calibration equation (Figure 3.1).

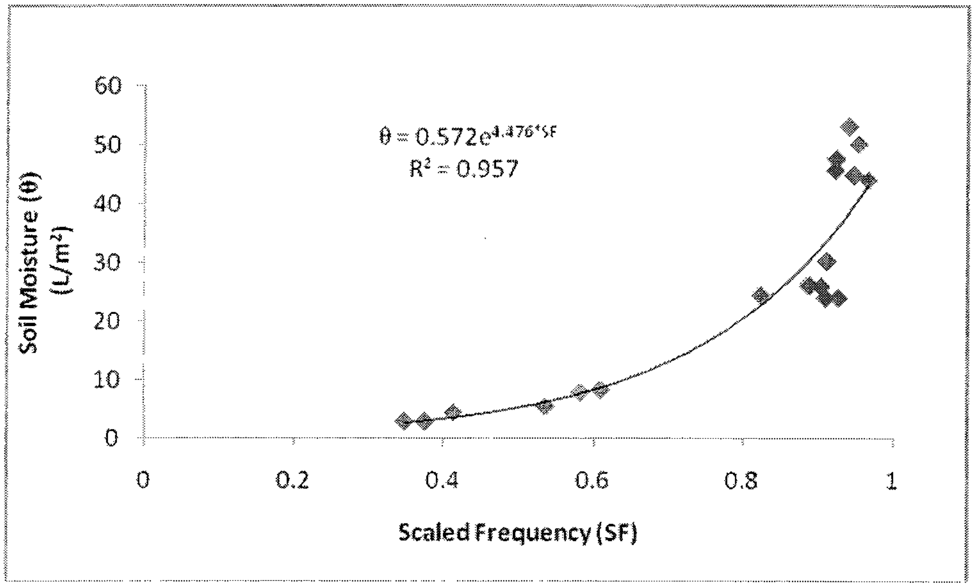

Figure 3.1 Calibration curve. The relationship between the probe reading in scaled frequency (SF) and soil moisture (θ) in L/m^2. Calibration equation: $\theta = 0.572*e^{4.476*SF}$

The potential effects of soil texture on the calibration were investigated by performing a multiple regression of the residuals from the calibration equation (Figure

3.1) against percent clay, silt and carbon, but none of these variables were significant (p = ns).

Data and Statistical Analyses

Repeated measures analyses of variance were used to analyze the relationship between community type and soil moisture over time at each site. Sites were analyzed individually for three reasons. First, although the community types that were the primary focus of this study (forest, prairie, and forest-prairie edge) were found at each site, the species composition of the forests differed, and at JC, infilled meadows were an important community type not present at the other sites. In addition, each site has a unique elevation range, topography, and climate. And finally, based on the results of Chapter 2, site plays an important role in determining how edaphic variables are related to community type.

Soil moisture was measured starting at 10 cm depth and at each successive 10 cm increment for the depth profile. The 10 cm depth reading, for example, represents the total soil moisture from 5 cm to 15 cm depth in L/m^2.

Soil moisture was summed from the surface to 15 cm depth (0-15 cm) using the reading at 10 cm and extrapolating to include the 0-5 cm depth increment. Soil moisture was summed from the surface to 25 cm depth (0-25 cm), to 35 cm depth (0-35 cm), to 45 cm depth (0-45 cm), and to the depth of the entire profile (profile) to a maximum depth of 1.22 m.

The depth of the soil profile varied by plot. Soil depth was measured with a 0.635-cm drill bit to a maximum depth of 1.22 m at eight (JC) or nine (FN and CR) random locations throughout each plot. Soil depth was averaged across all depth readings for use a covariate in analyses. The average soil depth for each plot was used as the cut-off for summing moisture across depth. For example, if the average soil depth was 32 cm, the soil moisture for the 0-35 cm, 0-45 cm, and the profile variables is: soil moisture from 0-15 cm + soil moisture from 15-25 cm + 0.7* soil moisture from 25-35 cm.

Soil moisture data were analyzed with repeated measures Analysis of Variance (ANOVA) (SPSS v. 16.0). The effect of community type on soil moisture was analyzed with and without soil depth as a covariate because the depth of the soil limits the amount of water in the soil profile. To examine the relationships between soil moisture and soil depth, each soil moisture variable at each time point within each site was regressed against the average depth of the profile. In addition, soil depth was also analyzed with a univariate ANOVA at each site to determine whether soil depth varied by community type.

Because there was often a significant interaction between time of sampling and community type, univariate ANOVAs were performed at each time point within each site. Post-hoc comparisons were made among community types at each time point for each moisture variable at each site with Tukey's test of Honestly Significant Difference (HSD). At JC, the soil moisture of the entire profile and from 0-45 cm were natural log transformed to normalize their distributions.

Results

Selected examples of moisture readings from a forest and a prairie plot at each site are shown in Figures 3.2, 3.3, and 3.4. Soil moisture was consistently lower in the shallower depths than in the deeper depths. The figures also show that surface soils dried out faster than deeper soils, and the shallower depths had greater variation in soil moisture than the deeper depths. Soils were driest in the late summer and early fall and wettest in late fall, winter, and spring. Note that prairies were generally shallower than forests and thus show moisture readings for fewer depth increments.

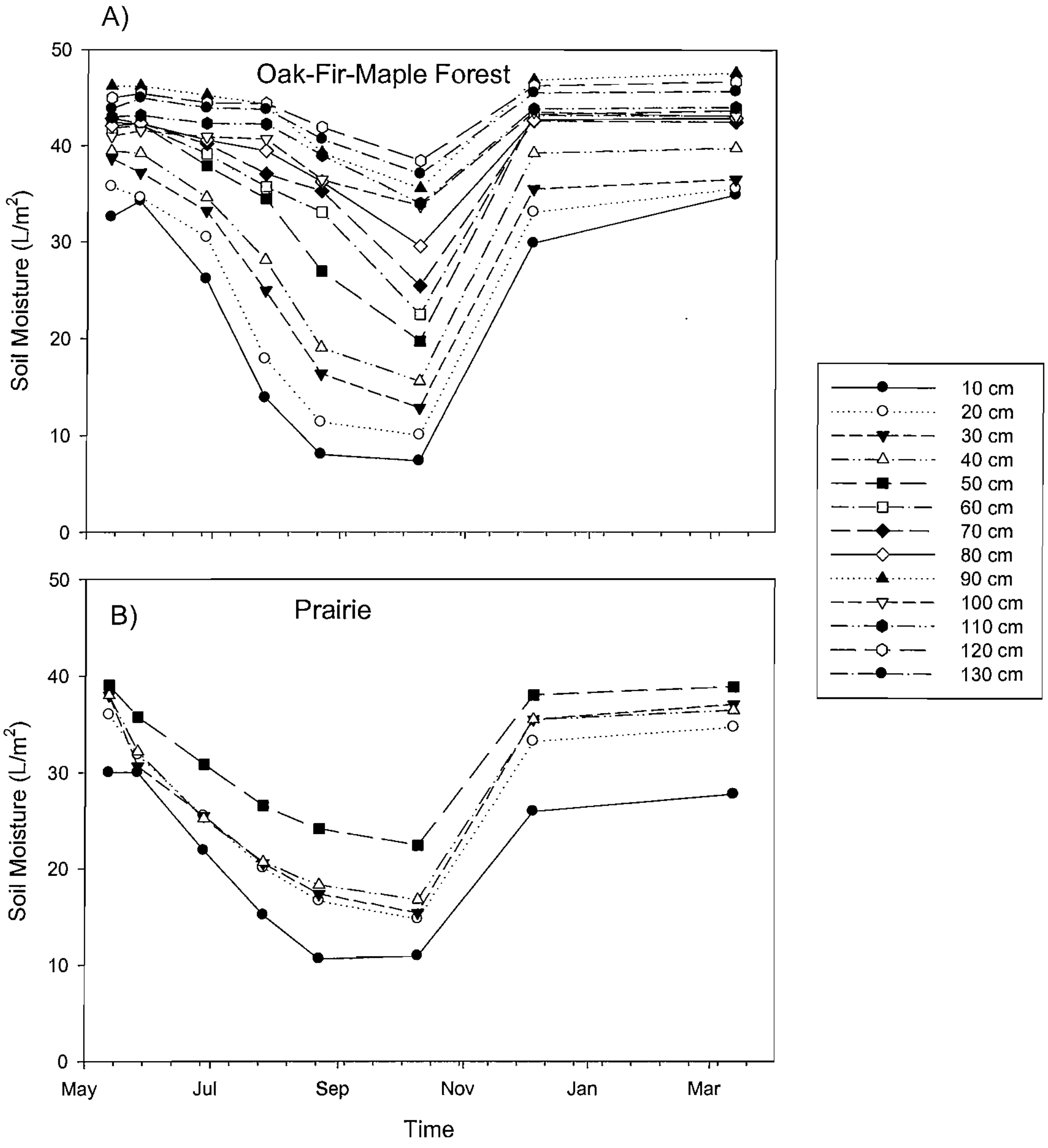

Figure 3.2 Soil moisture in 10 cm depth intervals at eight time points in A) an oak-fir-maple forest plot and B) a prairie plot at FN. Points represent the probe reading at each depth at each time point. The 10 cm reading is the total soil water content from 5-15 cm, the 20 cm reading is from 15-25 cm, and so on.

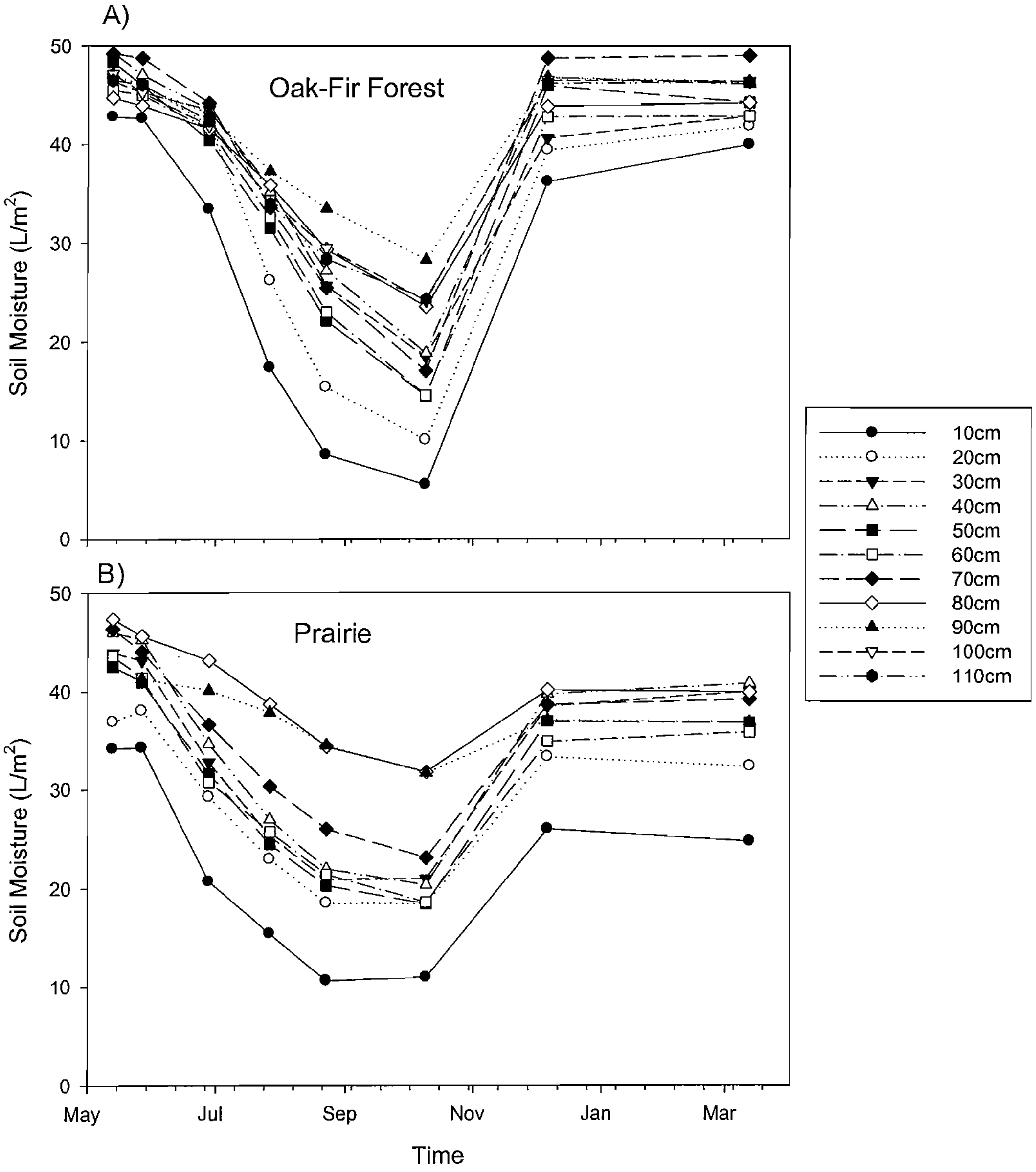

Figure 3.3 Soil moisture at eight time points in A) an oak-fir forest plot and B) a prairie plot at CR.

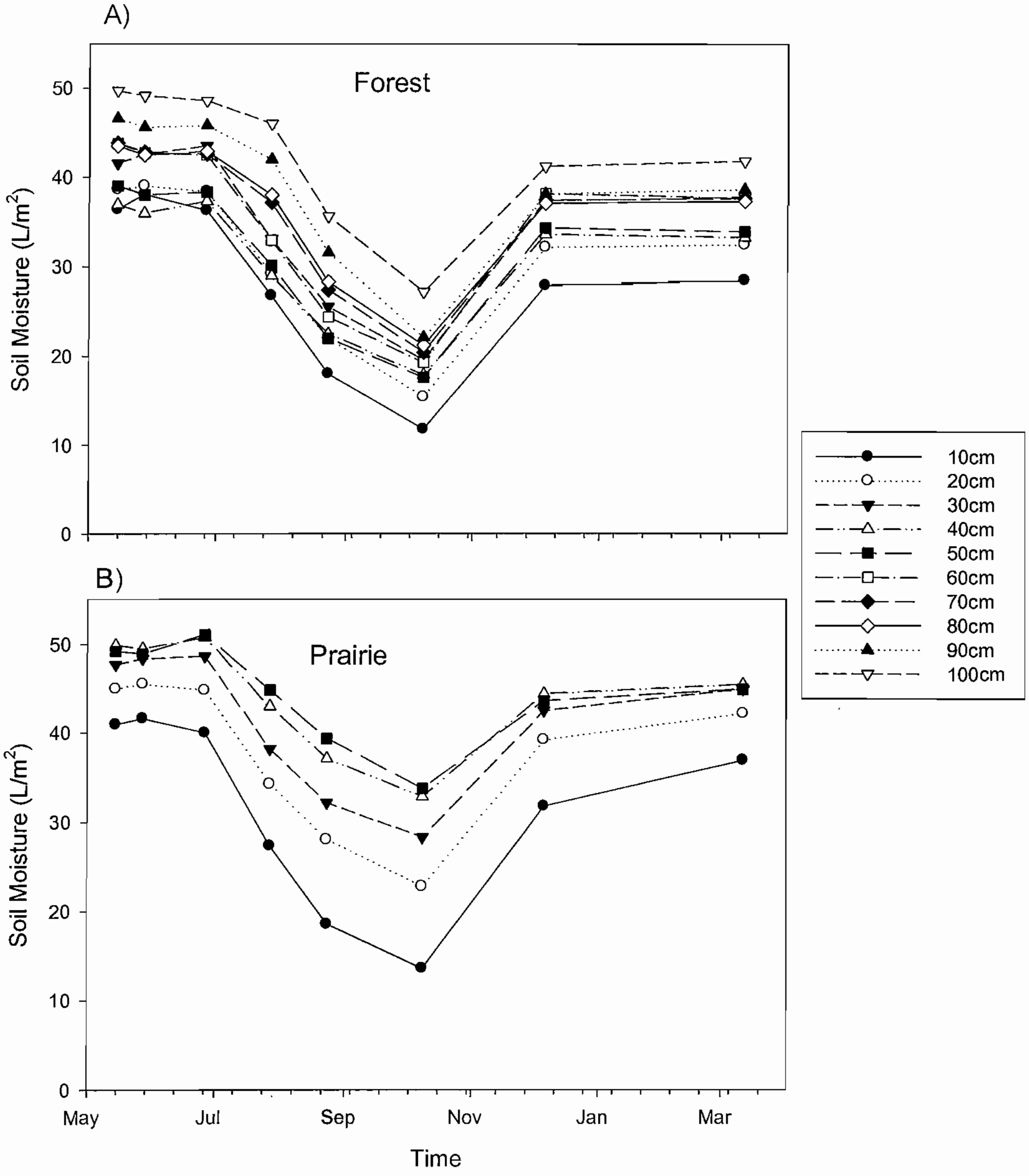

Figure 3.4 Soil moisture at eight time points in A) a forest plot and B) a prairie plot at JC.

Finley

Results from ANOVAs show that the effect of community type on soil water content from 0-15 cm, 0-25 cm, 0-35 cm, 0-45 cm, and for the entire profile depended upon time at FN both with and without the covariate of soil depth ($p < 0.05$) ($n = 12$) (Table 3.4). Time also had a strong direct effect on soil moisture in both analyses ($p < 0.001$).

Based on a univariate ANOVA, soil depth did not vary by community type at FN ($p = 0.41$). At FN, soil depth did not affect soil moisture from 0-15 cm or 0-25 cm ($p = 0.65$, $p = 0.17$, respectively), but did affect soil moisture from 0-35 cm, 0-45 cm and the entire profile ($p < 0.05$) (Table 3.4).

Table 3.4 FN repeated measures results for each soil moisture variable, including all eight time points, both without the covariate of soil depth and with the covariate. Significant p-values are in bold ($\alpha = 0.10$). For each variable, $n = 12$.

Source	0-15 cm	0-25 cm	0-35 cm	0-45 cm	profile
Without Covariate					
Community type	**0.017**	**0.051**	**0.043**	**0.037**	0.427
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Community type x Time	**0.004**	**0.005**	**0.003**	**0.002**	**0.049**
With Covariate					
Community type	**0.033**	**0.079**	**0.058**	**0.039**	0.140
Soil depth	0.653	0.173	**0.049**	**0.017**	**<0.001**
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Community type x Time	**0.005**	**0.005**	**0.003**	**0.002**	**0.017**

The correlation between soil depth and soil water content increased as the depth that soil moisture was summed over increased (Table 3.5). For soil moisture in the entire profile, the correlation with soil depth was always greater than 90% at all time points.

However, no significant correlation existed between soil depth and soil moisture from 0-15 cm at any time point.

Table 3.5 Correlations between soil moisture and soil depth at FN (R^2). Correlations significant at $\alpha = 0.10$ are indicated in bold. For each variable, n = 12.

Variable	**Mid - May**	**Late - May**	**June**	**July**	**August**	**Oct.**	**Dec.**	**March**
0-15 cm	0.030	0.050	0.010	0.025	0.030	0.022	0.142	0.156
0-25 cm	0.222	**0.281**	**0.251**	0.122	0.127	0.165	**0.338**	**0.350**
0-35 cm	**0.423**	**0.473**	**0.404**	**0.272**	**0.277**	**0.362**	**0.503**	**0.515**
0-45 cm	**0.540**	**0.525**	**0.506**	**0.390**	**0.398**	**0.442**	**0.598**	**0.563**
Profile	**0.936**	**0.942**	**0.935**	**0.931**	**0.943**	**0.926**	**0.969**	**0.968**

An example of the correlation between soil water content in the entire profile and soil depth is shown in Figure 3.5. Soil water content increased as soil depth increased.

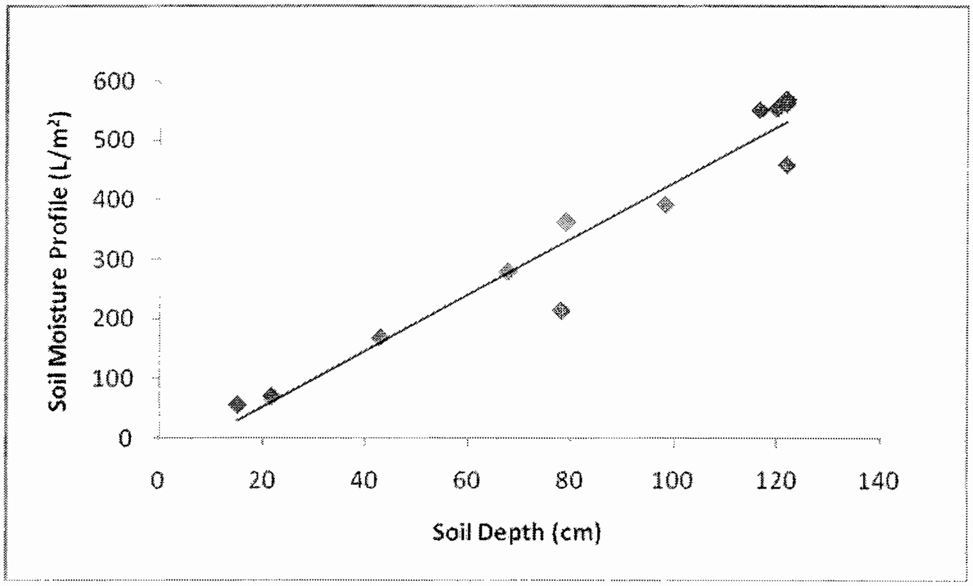

Figure 3.5 Soil moisture for the entire soil profile vs. soil depth at FN. Data is from mid-May ($R^2 = 0.936$).

At FN, differences among community types were present at different times of the year for the various moisture variables, with the soil moisture being most similar among communities in the driest months of late summer and autumn (Table 3.6). Soil moisture in the entire profile never varied by community type at any individual time point.

Table 3.6 Differences in soil moisture among community types at individual time points at FN. Significant p-values are in bold ($\alpha = 0.10$).

Variable	Mid - May	Late - May	June	July	August	Oct.	Dec.	March
0-15 cm	**0.021**	**0.036**	**0.011**	**0.039**	0.118	**0.099**	**0.036**	**0.022**
0-25 cm	**0.031**	**0.030**	**0.019**	**0.057**	0.151	0.216	**0.035**	**0.025**
0-35 cm	**0.046**	**0.030**	**0.017**	**0.041**	**0.099**	0.201	**0.027**	**0.019**
0-45 cm	**0.061**	**0.038**	**0.019**	**0.028**	**0.067**	0.158	**0.029**	**0.020**
Profile	0.489	0.441	0.385	0.393	0.527	0.641	0.354	0.306

Soils in the fir-oak forest contained more water in the 0-15 cm depth than soils in the oak-fir-maple forest in mid-May, late-May, June, July, August, October, and December ($p < 0.10$) (Figure 3.6). They also contained more water than the prairies in June, December, and March, and more water than edges in mid-May and March ($p < 0.10$). At this depth increment there was no significant differences in soil water content among the oak-fir-maple forests, prairies, or edges.

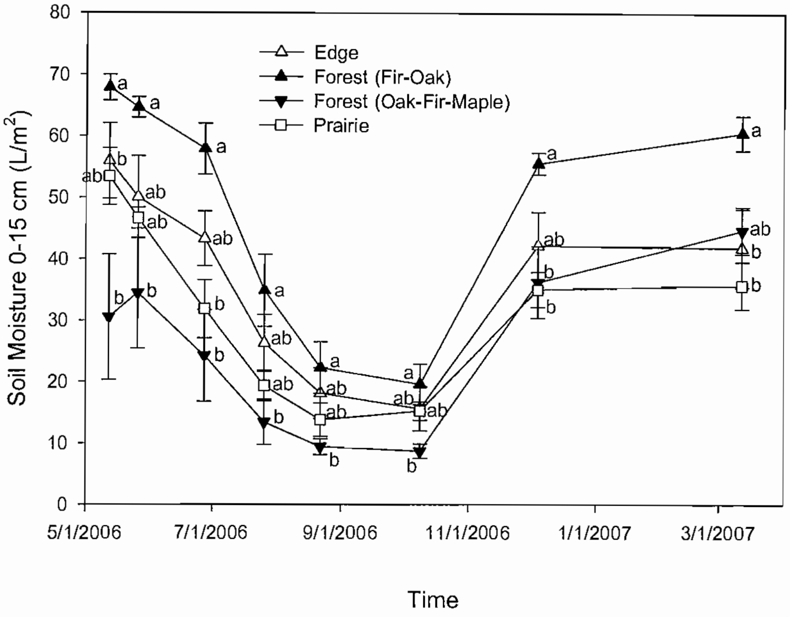

Figure 3.6 Soil moisture (L/m^2) from 0-15 cm ± one standard error at FN at eight time points in four community types. Unique letters represent significant differences among community types within a time point at the $\alpha = 0.10$ level by Tukey's HSD.

Soil water content in the entire profile did not differ significantly by community type at any time point due to high variance among plots (p = ns) (Table 3.6), but there was a trend for prairies and edges to be drier than both forest types on average (Figure 3.7).

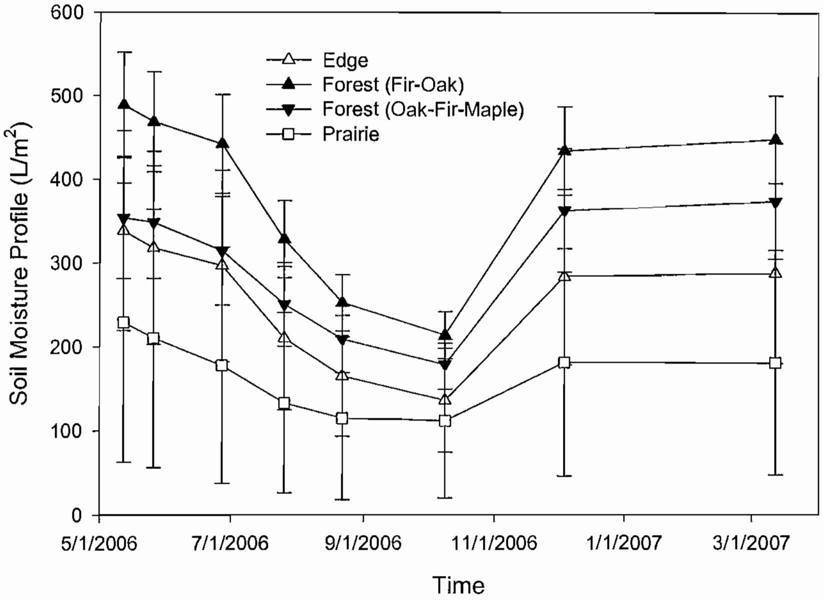

Figure 3.7 Soil moisture for the entire profile (L/m^2) ± one standard error at FN at eight time points in four community types.

Chip Ross

The effect of community type on soil water content from 0-15 cm, 0-25 cm, 0-35 cm, 0-45 cm, and for the entire profile depended upon time at CR, with and without the covariate of soil depth ($p < 0.05$) ($n = 12$) (Table 3.7). Time had a strong effect on all soil moisture variables in both analyses ($p < 0.001$).

Based on a univariate ANOVA, soil depth varied by community type ($p = 0.04$). Soil depth did not affect soil water content from 0-15 cm ($p = 0.291$), had a marginal effect on soil water content from 0-25 cm ($p = 0.096$), and affected soil water content from 0-35 cm, 0-45cm, and for the entire profile ($p < 0.05$) (Table 3.7).

The correlation between soil depth and soil water content increased as the depth that soil moisture was summed over increased (Table 3.8). The correlation between soil water content for the entire profile and soil depth was always greater than 89%. However, no correlation existed between soil depth and soil moisture from 0-15 cm at any time point (Table 3.8).

Table 3.7 CR repeated measures results including all eight time points without the soil depth covariate and with the covariate. Significant p-values are in bold ($\alpha = 0.10$). For each variable, n = 12.

Source	0-15 cm	0-25 cm	0-35 cm	0-45 cm	profile
Without Covariate					
Community type	**0.014**	0.275	0.299	0.231	**0.023**
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Community type x Time	**<0.001**	**0.001**	**0.002**	**0.019**	**<0.001**
With Covariate					
Community type	**0.014**	0.271	0.357	0.465	**0.047**
Soil depth	0.291	**0.096**	**0.020**	**0.007**	**<0.001**
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Community type x Time	**<0.001**	**<0.001**	**<0.001**	**0.010**	**0.002**

Table 3.8 Correlations between soil moisture and soil depth at CR (R^2). Correlations significant at $\alpha = 0.10$ are indicated in bold.

Variable	Mid - May	Late - May	June	July	August	Oct.	Dec.	March
0-15 cm	0.134	0.039	0.003	0.001	0.004	0.094	0.076	0.181
0-25 cm	**0.320**	0.219	0.088	**0.060**	0.026	0.008	**0.252**	**0.357**
0-35 cm	**0.506**	**0.447**	**0.303**	**0.319**	**0.304**	0.151	**0.492**	**0.560**
0-45 cm	**0.712**	**0.689**	**0.529**	**0.575**	**0.632**	**0.501**	**0.684**	**0.725**
Profile	**0.983**	**0.982**	**0.933**	**0.924**	**0.919**	**0.891**	**0.951**	**0.960**

An example of the correlation between soil water content in the entire profile and soil depth is shown in Figure 3.8. Soil water content increased as soil depth increased .

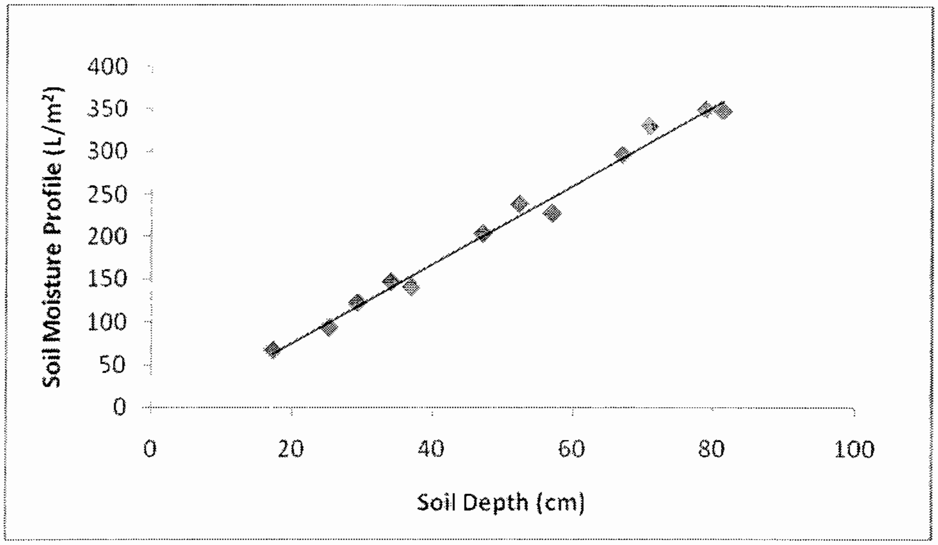

Figure 3.8 Soil moisture for the entire soil profile vs. soil depth at CR. Data is from mid-May ($R^2 = 0.983$).

At CR, differences among community types were present at different times of the year for the various moisture variables (Table 3.9). The soil water content of the entire profile varied by community type at every time point ($p < 0.10$).

Table 3.9 Differences among community types at individual time points at CR. Significant p-values are in bold ($\alpha = 0.10$).

Variable	Mid - May	Late - May	June	July	August	Oct.	Dec.	March
0-15 cm	**0.011**	**0.065**	**0.006**	**0.034**	**0.079**	0.121	0.329	0.115
0-25 cm	0.416	0.443	**0.080**	0.106	0.228	0.278	0.619	0.301
0-35 cm	0.297	0.272	0.143	0.209	0.433	0.668	0.445	0.252
0-45 cm	0.271	0.253	0.148	0.175	0.285	0.536	0.337	0.232
Profile	**0.023**	**0.023**	**0.013**	**0.021**	**0.041**	**0.092**	**0.030**	**0.024**

Prairies contained less water in the 0-15 cm interval than fir-oak-maple forests in mid-May, late-May, June and July ($p < 0.10$) (Figure 3.9). They also contained less water than oak-fir forests in mid-May and March, and less water than edges in mid-May and July ($p < 0.10$). There were no significant differences among community types in August, October, or December.

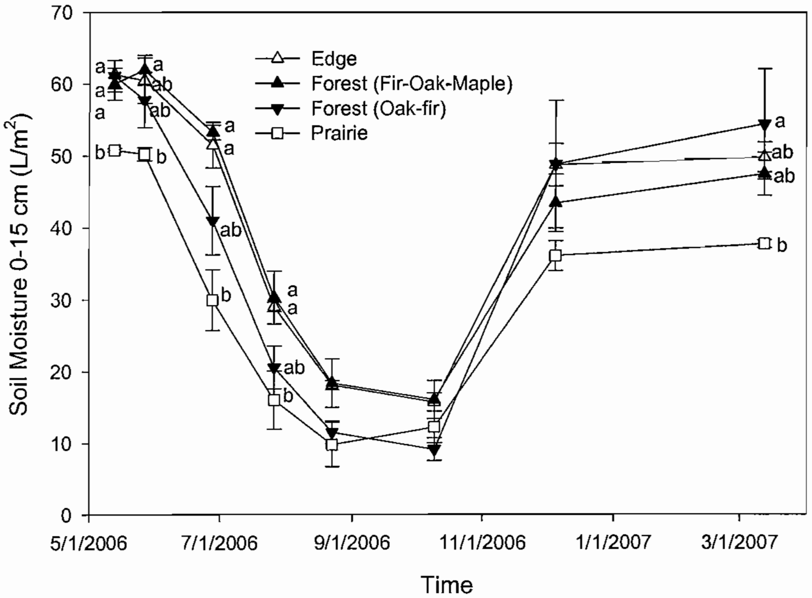

Figure 3.9 Soil moisture from 0-15 cm (L/m^2) ± one standard error at CR at eight time points in four community types. Unique letters represent significant differences among community types within a time point at the $\alpha = 0.10$ level by Tukey's HSD.

Prairies and edges contained less water in their entire profiles than oak-fir forests in mid-May, late-May, June, July, August, December, and March ($p < 0.10$) (Figure 3.10). At the driest reading in the beginning of October, edges contained less water in their entire profile than oak-fir forests ($p = 0.097$), but there was no difference between prairies and oak-fir forests at this time point ($p = 0.14$).

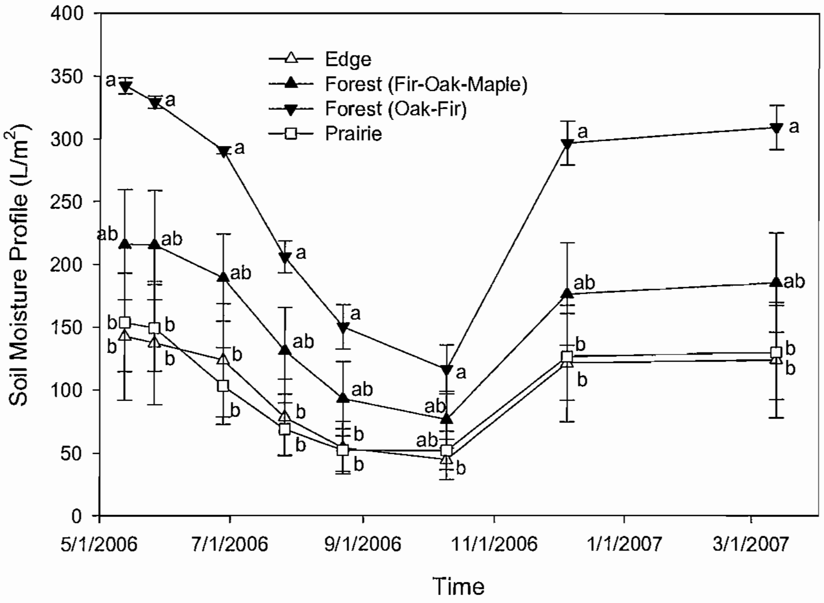

Figure 3.10 Soil moisture for the entire profile ± one standard error at CR at eight time points in four community types. Unique letters represent significant differences among community types within a time point at the $\alpha = 0.10$ level by Tukey's HSD.

Jim's Creek

The effect of community type on soil water content from 0-35 cm depended upon time, with and without the covariate of soil depth ($p = 0.036$) ($n = 12$ for all time points except March, where $n = 11$) (Table 3.10). There was no effect of community type on soil water content from 0-15 cm, 0-25 cm, 0-45 cm, or on the entire profile (p = ns) at JC, regardless of whether the covariate was included in the analysis. Time had a strong effect on water content for all depth intervals ($p < 0.001$).

Based on a univariate ANOVA, soil depth did not vary by community type at JC ($p = 0.34$). Soil depth did not affect soil water content from 0-15 cm ($p = 0.84$), but affected water content from 0-25 cm, 0-35 cm, 0-45 cm, and in the entire profile ($p < 0.10$) (Table 3.10).

Table 3.10 JC repeated measures results, including all eight time points without the soil depth covariate and with the covariate. Significant p-values are in bold (α =0.10). For each soil variable, n = 12 (except in March when n = 11).

Source	0-15 cm	0-25 cm	0-35 cm	0-45 cm	profile
Without Covariate					
Community type	0.755	0.452	0.256	0.284	0.290
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Community type x Time	0.416	0.442	**0.036**	0.740	0.746
With Covariate					
Community type	0.781	0.881	0.629	0.800	0.824
Soil depth	0.841	**0.092**	**0.009**	**0.003**	**0.003**
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Community type x Time	0.415	0.440	**0.036**	0.740	0.745

The correlation between soil depth and soil water content increased as the depth that soil water content was summed over increased (Table 3.11). The correlation between water content of the entire profile and soil depth was greater than 90% in mid-May, late May, June, December, and March, however, the correlation was not as strong in the driest months of July, August, and early October. No correlation existed between soil depth and soil water content from 0-15 cm (Table 3.11). An example of the correlation between water content in the entire profile and soil depth is shown in Figure 3.11. Water content increased as soil depth increased.

Table 3.11 Correlations between soil moisture and soil depth at JC (R^2). Correlations significant at $\alpha = 0.10$ are indicated in bold.

Variable	Mid - May	Late - May	June	July	August	Oct.	Dec.	March
0-15 cm	0.044	0.012	0.024	0.000	0.001	0.223	0.012	0.090
0-25 cm	**0.653**	**0.635**	**0.607**	0.208	0.193	0.103	**0.615**	**0.617**
0-35 cm	**0.878**	**0.874**	**0.863**	**0.432**	**0.399**	**0.346**	**0.817**	**0.806**
0-45 cm	**0.932**	**0.938**	**0.918**	**0.630**	**0.571**	**0.533**	**0.911**	**0.900**
Profile	**0.939**	**0.946**	**0.919**	**0.662**	**0.590**	**0.555**	**0.923**	**0.912**

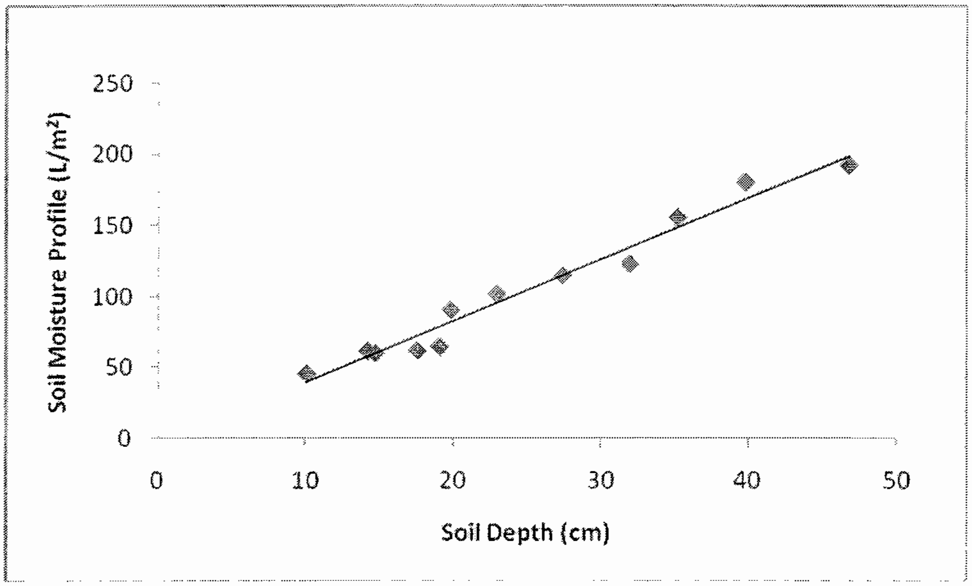

Figure 3.11 Soil moisture in the entire profile vs. soil depth at JC. Data is from mid-May ($R^2 = 0.939$).

No differences among community types were present at any individual time point at JC (Table 3.12), although there was a trend for prairies to contain less water than forests from 0-15 cm (Figure 3.12). There was also a trend for prairies, edges, and infilled meadows to be lower in soil moisture for the entire profile than forests (Figure 3.13).

Table 3.12 Differences in soil moisture among community types at individual time points at JC. No p-values were significant.

Variable	Mid - May	Late - May	June	July	August	Oct.	Dec.	March
0-15 cm	0.765	0.889	0.551	0.515	0.469	0.841	0.687	0.849
0-25 cm	0.612	0.592	0.600	0.297	0.229	0.437	0.615	0.675
0-35 cm	0.379	0.355	0.377	0.144	0.135	0.238	0.370	0.459
0-45 cm	0.389	0.377	0.401	0.204	0.163	0.203	0.411	0.361
Profile	0.394	0.384	0.406	0.208	0.165	0.205	0.419	0.356

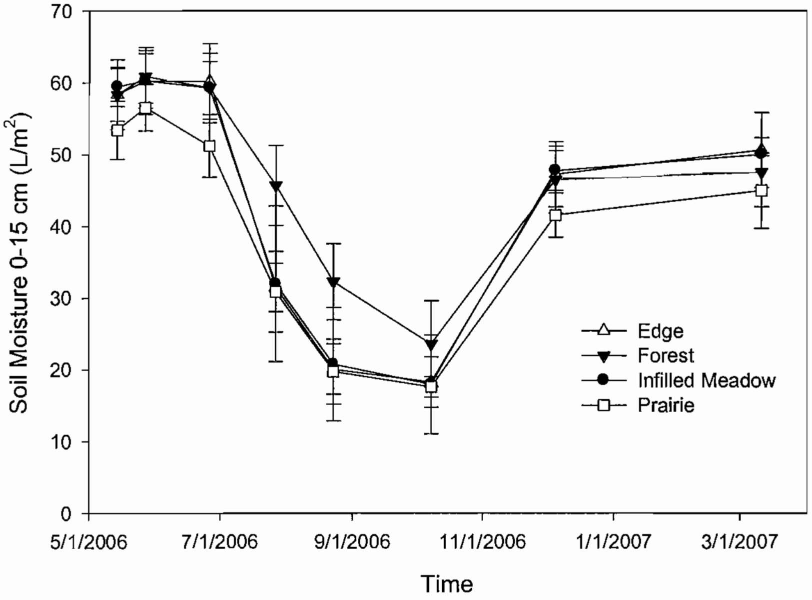

Figure 3.12 Soil moisture from 0-15 (L/m^2) ± one standard error at JC at eight time points in four community types.

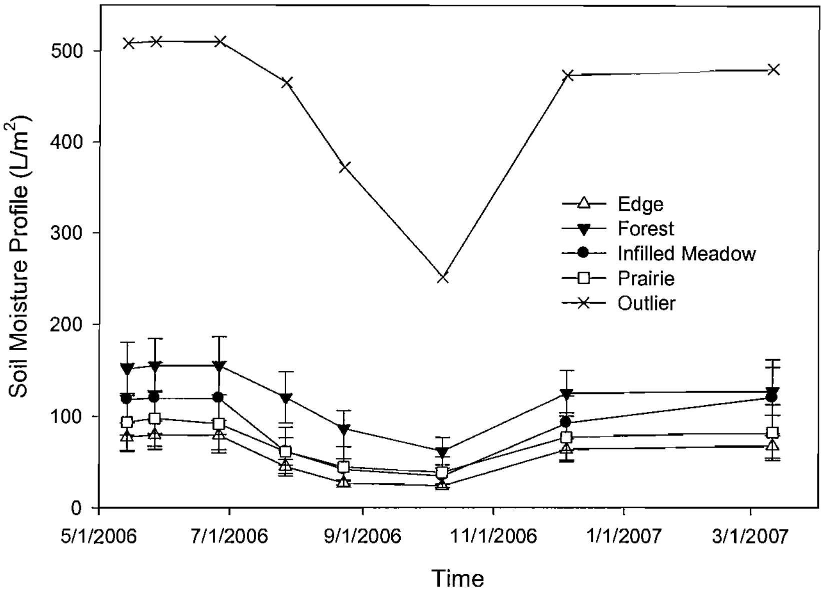

Figure 3.13 Soil moisture for the entire profile (L/m^2) ± one standard error at JC at eight time points in four community types. Note the magnitude of the outlier.

Comparison of Chip Ross, Finley, and Jim's Creek

The effect of soil moisture varied across the sites. FN and CR showed differences in soil moisture by community type (both as a main effect and as an interaction with time), but overall at JC there was no effect of community type on soil moisture (Tables 3.4, 3.7, and 3.10). Soil depth was never a significant covariate at the 0-15 cm moisture increment.

The correlation between soil moisture of the entire profile and soil depth was great than 89% at FN and CR and at most time points at JC (Tables 3.5, 3.8, and 3.11). However, the correlation between soil moisture and soil depth was weaker in the driest months at JC (Table 3.11). Soil moisture from 0-15 cm was never correlated with soil depth at any site.

Discussion

Prior to Euro-American settlement, frequent fires maintained prairie and oak savanna across large areas of the Willamette Valley. With the loss of historic fire regimes, succession has occurred rapidly in some areas and not at all in others. My results demonstrate that differences in soil moisture and soil depth play important roles underlying the spatial variability of forest succession following Euro-American settlement.

Successional pathways in former oak savanna appear to have been influenced by soil moisture. In general, areas that have experienced the least succession (prairies and edges) contain less water in the soil profile than areas that have experienced more succession (forests) (Figures 3.7, 3.10, and 3.13). This relationship between community type and soil moisture was consistent at each site, although it was not significant at JC (Figure 3.13). The lack of a significant community effect at JC could be due to the small number of replicates and the exclusion of the outlier, leaving only two forest plots in the analysis.

The amount of water present in the soil profile is highly dependent on soil depth. The strong correlation between soil depth and soil water is logical because the deeper the soil, the larger the volume of water the soil profile is able to hold. Since total soil moisture is so closely tied to soil depth, it is difficult to determine if one is a more important control over succession than the other. Based on this analysis, it appears that both are important controls over succession.

The shallower depths of the soil profiles tended to be drier and exhibited greater variation in moisture than the deeper depths (Figures 3.2, 3.3, and 3.4). This is most likely due to evaporation and to uptake by shallow plant roots. Soils in areas that have experienced less succession tend to be shallower (see Chapter 2), and these shallow soils are also dry. Trees trying to establish in these areas not only have less soil to exploit, but the soil they have access to is also drier than areas with deeper soils.

Soil moisture is highest in the late fall, winter, and early spring (Figures 3.2, 3.3, and 3.4). Soil moisture begins to decrease in the late spring/early summer, reaching a minimum in late summer/early fall. Oregon white oak begins to leaf out in the spring, when soil moisture is high, and continues to photosynthesize throughout the summer and into the fall, when it loses its leaves. The growing season of Oregon white oak is primarily during the driest time of the year, while Douglas-fir is able to photosynthesize year round in the lower elevations of the Willamette Valley. The ability of Douglas-fir to photosynthesize year round may give the species a competitive advantage over Oregon white oak in more mesic soils, but the extreme summer drought may prevent Douglas-fir from establishing or increase its mortality over time in harsher areas.

The rooting morphology of oaks is important to consider when thinking about the ability of Oregon white oak to survive in harsh areas. A study in glacial outwash soil found that Oregon white oaks developed a prominent taproot at a young age, which dominated the root morphology in seedlings and young trees (Devine and Harrington 2005). This may enable oaks to establish in dry areas as seedlings. As the trees age, however, the root systems of Oregon white oak became dominated by lateral roots (Devine and Harrington 2005). The shallow roots enable Oregon white oak to take advantage of rare summer precipitation, which is important in the Willamette Valley due to the extreme summer drought. Similar rooting morphologies of Oregon white oak were found in the Willamette Valley (Krygier 1971).

Several differences in rooting morphology may give Oregon white oak an advantage over Douglas fir in dry and/or shallow areas. The main rooting differences between Douglas-fir and Oregon white oak appears to be that Douglas-fir will grow a taproot only when there are no barriers in the soil (Hermann and Lavender 1990), which may limit its ability to obtain water in areas with shallow soils. On shallow soils, Douglas-fir may not be able to survive. In addition, Douglas fir has fewer shallow roots than Oregon white oak (Krygier 1971), thus, they may not be able to take advantage of summer precipitation. Physiological differences between the two species may also be determining the competitive advantages of one species over another under varying moisture conditions.

Oregon white oak may be able to survive in areas with shallower and drier soils for two main reasons: 1) Their ability to form a taproot when young allows them to obtain moisture from deeper soils that retain their moisture longer, allowing them to establish in dry/shallow soils, and 2) Their ability to form a prominent lateral root system as they age allows them to survive and mature on dry/shallow soils.

Conclusions and Implications for Management

My results suggest that drier and shallower soils are limiting the establishment of trees in former oak savanna in the Willamette Valley. Areas with high soil moisture and deep soils may be conducive to accelerated succession. In light of restoration efforts of Oregon white oak savanna in the Willamette Valley, areas with high moisture and deep soils may require more management than drier and shallower areas. However, areas with higher moisture and deeper soils also represent an important part of the historic range of variability of oak savanna, potentially with greater productivity and substantially different species composition and diversity. Although Oregon white oak has been excluded from much of this habitat type, not restoring areas that are conducive to succession will limit Oregon white oak to only the harshest sites, a small fraction of its former range.

This study focused on several key questions. First, I wanted to determine how soil moisture has influenced succession in former oak savanna. It appears that low soil moisture is associated with areas that have experienced less succession, suggesting that soil moisture may be restricting the establishment of trees. Secondly, I wanted to investigate the relationship between soil depth and soil moisture. Based on the results of this study, soil depth is an important control over soil moisture in the soil profile. And finally, I was interested in determining whether soil depth or moisture is the primary control over succession in Willamette Valley former oak savanna. Because both soil moisture and depth are related to successional dynamics in former oak savanna, and because soil moisture and soil depth are strongly correlated, it is difficult to determine which is a more important control over succession.

CHAPTER IV

CONCLUSION

Based on the combined results of the two studies, edaphic and topographic conditions appear to have influenced the successional dynamics in former Oregon white oak (*Quercus garryana*) savanna in the Willamette Valley. However, the specific effects of these conditions depends heavily on location. For example, soil texture appears to be strongly influencing succession within sites, but how texture is related to community type depends on site. Clay content was higher in the forests than in the prairie/savannas at Finley, whereas at Jim's Creek, clay content was higher in prairie/savannas than in forests. A similarly complex relationship between soil nitrogen content (g/m^2) and community type was also present in this study. At Finley, forests had higher nitrogen than prairie/savannas, whereas at Jim's Creek, prairie/savannas had higher nitrogen than forests. The complex relationships between soil characteristics, sites, and community types could be due in part to differences in elevation among the sites.

Soil depth appears to be restricting succession across most sites in this study, especially at Finley and Jim's Creek. Shallower soils were associated with areas that have experienced less succession (prairie/savannas and edges) at both of these sites. Although this relationship was less consistent at the other sites, site historical factors such as recent grazing may be influencing succession at these sites. Further investigation into the impacts of historical land use on succession is needed.

Soil moisture appears to have a dramatic influence on succession in former Oregon white oak savanna. Dry soil conditions are associated with areas that have experienced less succession, such as prairies and edges. Dry conditions may be restricting the establishment of trees in prairies and edges.

Soil depth is as an important control over soil moisture in the soil profile. Soil moisture and soil depth are related in that the deeper the soil, the higher the volume of moisture the soil can hold. Thus, as soil depth increases, so does the volume of soil water. Since soil moisture depends on soil depth, it is difficult to determine if one is a more important control over succession than the other. Based on this analysis, it appears that both are important controls over succession.

Final Thoughts and Implications for Management

Oregon white oak savanna existed under a broad range of environmental conditions in the Willamette Valley 150 years ago. Currently, it exits in a tiny fraction of its former range. Restoration of this endangered ecosystem is important not only culturally and ecologically, but also in terms of managing the risk of catastrophic wildfire.

Based on the results of this study, Oregon white oak savanna restoration efforts in the Willamette Valley must take edaphic and topographic factors into account as well as site location and history. The successional dynamics in former oak savanna in the Willamette Valley are complex, and vary highly by site factors. Some areas in the Willamette Valley will have edaphic and topographic conditions that are highly conducive to succession, and these areas will require more management. Restoration of a broad range of environmental conditions is important because currently, oak savanna is restricted to some of the harshest environments in the Willamette Valley. Although it will take more management to restore areas that are prone to succession, not doing so will restrict Oregon white oak savanna to a small portion of its former range, and the heterogeneity of its former range will be lost.

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