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Environmental Gradients, Community Boundaries, and Disturbance the Darlingtonia Fens of Southwestern Oregon

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ENVIRONMENTAL GRADIENTS, COMMUNITY BOUNDARIES, AND DISTURBANCE: THE *DARLINGTONIA* FENS OF SOUTHWESTERN OREGON

by

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Portland State University

DISSERTATION APPROVAL

The abstract and dissertation of Deborah Ann Tolman for the Doctor of Philosophy in Environmental Sciences and Resources:Geography were presented May 9, 2003, and accepted by the dissertation committee and the doctoral program.

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ABSTRACT

An abstract of the dissertation of Deborah Ann Tolman for the Doctor of Philosophy in Environmental Sciences and Resources: Geography presented May 9, 2003.

Title: Environmental Gradients, Community Boundaries, and Disturbance: The
Darlingtonia Fens of Southwestern Oregon

The *Darlingtonia* fens, found on serpentine soils in southern Oregon, are distinct communities that frequently undergo dramatic changes in size and shape in response to a wide array of environmental factors. Since few systems demonstrate a balance among high water tables, shallow soils, the presence of heavy metals, and limited nutrients, conservative efforts have been made to preserve them. This dissertation investigates the role of fire on nutrient cycling and succession in three separate fens, each a different time since fire. I specifically analyze the spatial distributions of soil properties, the physical and ecological characteristics of ecotones between Jeffrey pine savanna and *Darlingtonia* fens, and the vegetation structure of fire-disturbed systems. Soil, water, and vegetation sampling were conducted along an array of transects, oriented perpendicular to community boundaries and main environmental gradients, at each of the three fens. Abrupt changes in vegetation, across communities, were consistently identified at each of the three sites, although statistical analysis did not always identify distinct mid-canopy communities. Below-ground variables were likewise distinguished at the fen and savanna boundary for two of the three sites. At the third site, discontinuities did not align with the fen boundaries, but followed fluctuations in soil NH_4. My results suggest that below-ground discontinuities may be more important than fire at preserving these uniquely-adapted systems, while vegetation undergoes postfire succession from fen to mid-canopy to savanna after approximately 100 years since fire. Although restoration of ecosystem structure and processes was not the primary focus of this study, my data suggest that time since fire may drive ecosystem processes in a trajectory away from the normal succession cycle. Moreover, time since fire may decrease overall vigor of *Darlingtonia* populations.

DEDICATION

For Craig Stephen Revels, who has provided me with support and guidance in my academic pursuits, and with love and understanding during my social life, without which I could not have produced this document.

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CHAPTER 1

INTRODUCTION

Despite recent efforts to protect the uniquely adapted *Darlingtonia* fens of southwestern Oregon and northern California, these communities have become smaller and less diverse (Borgias and Beigel 1996, Borgias and Beigel 1998). Few other systems demonstrate such a delicate balance among high water tables, shallow soils, the presence of heavy metals, and limited nutrients in the context of fire as a primary restraint on succession cycles. For nearly 50 years ecologists have recognized that the size and shape of these fens can change dramatically from one year to the next in response to an array of environmental factors, particularly fire and nutrient availability (Folkerts 1982, Mellichamp 1983, Becking 1997, Ulloa 1998, Gotelli 2002). That these communities have received limited attention among researchers is somewhat surprising. They have been addressed at varying levels of significance in previous research on the eastern seaboard where their most similar carnivorous plant neighbors reside, but in all instances studies have been exclusive of the Pacific Northwest serpentine soil systems.

Few studies have considered the combined role of disturbance and soil properties on vegetation patterns within serpentine soil systems (Arabas 1997). Even fewer have addressed the role of fire as a mechanism for maintaining diversity of serpentine soil communities, or have examined the long-term effects of changes in soil moisture and nutrient supply on community composition across boundaries, or framed system complexity within the context of nutrient availability and succession.

Whittaker's (1954) work was among the first to document climate and soil parent material as factors controlling the vegetation communities on serpentine bedrock (Kruckeberg 1954, Whittaker 1954, Waring 1969, White 1971, Kruckeberg 1984, Brooks 1987). Some authors consider *Darlingtonia* fens as a fire subclimax or a disclimax ecosystem, because they depend on fire to release many nutrients bound up in the organic matter from previous growth, and to eliminate mid-canopy competitors (Whittaker 1954, Folkerts 1982, Franklin and Dyrness 1988). Nevertheless, the underlying processes explaining the driving variables in these systems are poorly understood and have been left largely unaddressed.

In particular, there are several fundamental questions concerning the role of fire and water in serpentine ecosystems that merit consideration. First, what is the role of soils in defining the vegetation boundaries of these communities? Second, does fire influence boundary-defining processes? Third, and perhaps most importantly, is the structural and compositional diversity of these communities influenced by the combined effects of environmental gradients and fire? Fire-induced nutrient transformations and post-fire nutrient availability have attracted considerable attention from a wide range of researchers (Christensen 1977, 1985, Andreau, et al. 1996), yet generalizations to serpentine communities are difficult.

In this study I address these questions by examining the environmental gradients, community boundaries, and the role of disturbance (fire) in the *Darlingtonia* fens and pine savannas of serpentine soil ecosystems in southwestern Oregon. My guiding hypothesis is that, in the absence of fire, *Darlingtonia* fen communities become smaller because of increasing nutrient availability favoring a subsequent change in vegetation dominance. If a relative change in plant nutrients is contingent on the development of new communities, then a conceptual model of nutrient availability can be developed to show how these systems operate across a larger temporal context. Such a model necessitates an understanding of the spatial and temporal dynamics of subterranean processes across community boundaries.

History: Gradients, Ecotones, Vegetation Structure, and Succession

Gradients

The historical development of theories that link vegetation structure and spatial pattern follows several logical progressions. One approach is to address vegetation patterns as patches set in a background matrix. This avenue focuses on deviations from homogeneity, where the configuration and structure of pattern becomes important. While much of the work in patch theory addresses other approaches such as population genetics and population dynamics, heterogeneity is interpreted as an expression of the overall spatial complexity (Wiens 1995). In the past two decades, emphasis on the description of spatial patterns of plant communities has incorporated techniques for detecting and defining patch boundaries, or ecotones. For example, gradients are considered a form of spatial variation in which boundaries are indistinct (Gauch 1982, O'Neill et al. 1992, Wiens 1995, Gosz 1991). These ecotones can be interpreted as the next stage of understanding not only patches themselves but also the complex interfaces between distinct plant communities (Cadenasso et al. 1997).

Ecotones

The framework for researching ecotones in serpentine soil ecosystems is found in the study of plant community dynamics (Miles 1979). Ecotones are transition zones between two communities (Holland 1988), however, their relevance depends on which theoretical perspective - community (Clements 1936), individualistic (Gleason 1926) or continuum (Whittaker 1956) - is adopted to explain the structure of the plant community or vegetation. The community concept implies a group of co-adapted species with common limits along a gradient. By contrast, the individualistic concept sees the coexisting species as the results of similar requirements and tolerances, and of chance, while the continuum concept builds on this and continuity of vegetation changes where the optima and limits for each species are independently distributed along environmental gradients (Austin 1985). The concept of a continuum has been widely accepted since Whittaker's gradient analysis studies on vegetation in the Great Smoky Mountains (1956) and Curtis' indirect gradient analysis of a prairie in Wisconsin (1955, 1959). Since then variants of the continuum concept have been proposed, most notably the major species concept (Gauch and Whittaker 1972), which states that "major" species are regularly distributed along a gradient with optima evenly-spaced, while "minor" species are independently distributed. Additionally, the independent strata concept (Goodall 1963) proposes that each stratum (e.g., herbs, shrubs, and trees) partitions the gradient independently of the others. Given that the modern synthesis is closer to the views of Gleason and Whittaker, less attention has been focused on the community hypothesis and on the ecotone concept (Crawley 1986).

Closely associated with the concept of ecotone and an emergent perspective in biogeography, edge dynamics research analyzes the systematic energy that flows within linkages among soil moisture, disturbance history, plant response, and soil nutrients (Veblen 1989). One key aspect of edge dynamics is a strong inclination toward overcoming the traditional separation of study that is common with population, community, ecosystem, and landscape ecology. While methodology varies among researchers, emphasis on numbers of species at multiple temporal and spatial scales to explain long-term patterns of species and habitat diversity are key components in understanding modern directions of research (Veblen 1989). Other aspects include an emphasis on understanding patterns and agents of change at any hierarchical (population to the biosphere) or spatial (centimeters to thousands of kilometers) scale, depending on the characteristics of the disturbance itself. To this end, Delcourt and Delcourt's (1988, 1992) explicit use of variable temporal and spatial scaling show degrees of interconnecting ecosystem processes which may redefine attributes of a new system. Malanson's (1996, 1997) synthesis of changes in mass, matter, and energy fluxes across gradual abiotic gradients demonstrate typical ecotone methods and approaches. Cairns (1994, 1996) has focused on measuring net primary productivity with the use of physiologically mechanistic models in alpine ecotones. Both authors prescribe analysis of complex systems that are linked through the exchange of energy, matter, and information where feedback loops, significant space-time discontinuities, thresholds, and limits make it difficult to distinguish cause from effect. Similarly, Kellman's (1997) work on soils and nutrient limitations of tropical savannas and Meentemeyer's (1977, 1978, 1982, 1984, 1985) work on biogeochemical cycles are essential foundations for detailed boundary analysis such as that in the present study.

Vegetation Structure and Succession

Contrasting views on the spatial structure of vegetation communities have directly influenced the theory of succession (Austin 1985, 1990) (Table 1.1). Thus far, succession theory does not encompass all properties of vegetation dynamics, particularly those involved in the creation and maintenance of ecotones. Terrestrial ecologists have generally concentrated their studies on homogeneous areas between ecosystems (Bormann and Likens 1979, Keddy 1991, MacArthur 1972). As a result, properties of boundaries may be overlooked and their spatial representation is often reduced to a generalized line on a map.

Table 1.1 Some key studies in the development of succession theory.

Clements (1916, 1936)	community concept
Gleason (1917, 1926)	individualistic concept
Watt (1947), Zedler and Goff (1973)	spatio-temporal dynamics
Whittaker (1953, 1956)	continuum concept
Egler (1954)	inhibition mechanisms
Margalef (1968), Odum (1969)	ecosystem dynamics
Heinselman (1973), Levin and Paine (1974), Grubb (1977)	disturbance dynamics
Whitaker and Levin (1977), White (1979), Sousa (1979, 1984), Paine and Levin (1981), Connell and Keough (1985), Pickett and White (1985)	spatio-temporal dynamics and disturbance dynamics
Peet and Christensen (1980)	population dynamics
Runkle (1982, 1985), Hibbs (1982), Shugart (1984)	gap dynamics
Pickett et al. (1987a,b), Urban et al. (1987)	hierarchy perspective
Huston and Smith (1987), Smith and Huston (1989)	individual dynamics

Numerous ecological studies appearing in the 1920s, 1930s, and 1940s (Gleason 1926, Clements 1936, Watt 1947) pursued the interpretation of vegetation structure and composition through analysis of plant community associations in the context of succession. Whittaker (1953, 1965, 1970, 1972, 1973, 1977), however, was among the first to recognize differences in plant associations based on their functional roles in the landscape. Instrumental to the development of this approach was Whittaker's research on serpentine soils in southern Oregon of "mesic temperate savannas" (Whittaker 1954, 1960, 1970).

Since the 1950s, researchers have documented climate and soil parent material as factors controlling the vegetation communities on serpentine bedrock (Kruckeberg 1954, Whittaker 1954, Waring 1969, White 1971, Kruckeberg 1984, Brooks 1987). This literature indicates that soils high in metals toxic to plants, low in macronutrients, and high in Mg:Ca ratio explain the inability of most plant species to become established under serpentine conditions. While a more extensive array of studies from the 1970s and 1980s implicates various disturbances such as fire as important factors contributing to the structure and composition of vegetation in plant communities (Levin and Paine 1974, Grubb 1977, White 1979, Heinselman 1981, Sousa 1984, Pickett and White 1985), Huston's (1994) account of the aspects of fire-induced habitats identifies moisture as an index for change in diversity for grassland, savannah, temperate and tropical forest ecosystems. Few researchers have explored the specific processes influenced by fire on serpentine communities.

Most researchers claim an increased nutrient availability immediately following a fire (Wilbur 1985, Trabaud 1994, Wan et al. 2001). These results are consistent with Christensen's (1977) finding on pine savannas in the southeastern United States. Data collected from single heathland fires suggest that nutrient availability is generally low in undisturbed communities and is increased in the short term by mineralization of organically-bound nutrients during fire (Christensen 1977, Rundel 1981). Although usually not emphasized in papers dealing with fire-caused nutrient changes, soil nutrient concentrations tend to be highly variable after a fire (Wilbur and Christensen 1983, Adams et al. 1994, Trabaud 1994). This variation appears to be the result of local differences in fire intensity and the uneven distribution of ash. Plummer (1963) and Agee (1993) both document similar within-site condition variations in nutrient availability and fire intensity. A recent meta-analysis on the fire effects of nitrogen pools claimed variability was dependent on seven environmental factors, none of which had any single effect on total soil nitrogen amount (Wan et al. 2001). Thus, the post-fire environment may vary considerably with regard to the potential availability of limiting community resources.

Data from Wilbur and Christensen (1983), as well as Chandler and Anderson (1975), suggest that mesic savannas are limited by nitrogen and phosphorous availability. In this case, burning results in an enrichment of most available nutrients, including phosphorous (Wilbur and Christensen 1983). The increased soil fertility which follows fire is short-lived with most nutrients returning to pre-fire levels by the second growing season (Wilbur and Christensen 1983). Thus, there appears to be a range of post-fire nutrient availability. Both pre-burn and post-burn measures of nutrient availability may be necessary to adequately describe and better indicate the cycling process.

The most convincing evidence for an increase in nutrient availability following a fire in serpentine communities comes from a study of a pine-wiregrass savanna in North Carolina (Christensen and Muller 1975, Christensen 1977). This research shows increased nitrate and higher ammonium concentrations as the result of ash production and post-fire environmental changes that favor high mineralization rates. Christensen and Muller (1975) found that many nutrients in ash not immediately available following burning in a pine savanna are more amenable to microbial mineralization following the natural drying of the peat near the soil surface. Surface drying of peat has been shown to enhance nitrification in a variety of organic soils (Wilbur and Christensen 1983).

While most studies suggest that fire can increase the availability of soil ammonium and nitrate (Christensen and Muller 1975, Christensen 1977, Covington et al. 1991), Plummer (1963) and Folkerts (1982) reported that savanna soils of the southeast contained little to no ammonium. However, the results of Wilbur and Christensen (1983) showed significantly higher levels of soil ammonium in some burned areas during the first growing season. Some authors have reported that ash is rich in NH_4 content rather than NO_3 immediately following fire (Wells and Skunk 1931, Christensen and Muller 1975). Data on ammonium availability after fires have shown varied results depending on heat and duration of fire.

Similarly, Carriera et al. (1994) found no immediate changes in soil NO_3 after a fire. This finding is typical for Mediterranean-type shrublands and California chaparral having medium to low organic matter levels in the upper soil horizon (Carriera et al. 1994). However, soil nitrate increased a few weeks after a fire and is attributed to enhanced microbial mineralization and nitrification (Carriera et al. 1994). These findings are similar to Wilbur's (1985) results from the Coastal Plain of North Carolina, that showed soil pH and concentrations of extractable Ca, Mg, K, NH_4, and PO_4 increase after a fire. Wilbur (1985) concluded that changes in nutrient cycling were the result of ashfall rather than soil heating and sterilization and that after-burn microbial processes merit particularly close attention.

Riggan et al. (1994) demonstrated that concentrations of mineral nitrogen in soils vary in response to fire intensity, which may explain the presence of ammonium in savanna soils immediately following a fire. Results from the same study showed NH_4 in surface soils rises less than during more moderate heating by fires on test plots with standing vegetation. Soils experiencing intense fires are subject to the greater heating below the soil surface and demonstrate the highest volatilization rates, which implies vertical partitioning of some soil nutrients.

Conflicting evidence from Christensen's study (1977) in the pine-wiregrass savanna indicated that burning results in an initial enrichment of available soil nutrients while NO_3 and NH_4 concentrations remained unchanged. Because of the dependence of nitrifying bacteria on moisture, increases in nitrate concentration after a fire may be caused by increases in nitrifying bacteria stimulated by an increase in ammonium ions. However, a decline in ammonium levels, or a return to pre-fire levels, could occur at rates faster than sampling could capture.

The abundance of water in these types of systems should explain a prevalence of the more reduced form of nitrogen, NH_3. If true, ammonia should also be observed in similar soils that have not been burned recently. Roberts et al. (1958), for example, found low levels of ammonia in southeastern savanna soils but no increases in ammonium or nitrate following fire. In spite of these low levels, Christensen (1977) noted that plant growth in the season following fire was significantly better in burned than in unburned soil. This finding suggests either that some factor other than nutrients may be operating or that the nutrients are present but are not detectable.

Fire in serpentine ecosystems appears to reset ecosystem N cycling over time. Despite the general tenet of a temporary post-fire enhancement of mineral N availability (Pickett and White 1985), high fire frequency could lead to a substantial depletion of total N pools simply because the losses cannot be replaced fast enough by N_2 fixation in regenerating stands. Additionally, there is a risk of nutrient loss through volatilization or increased runoff. However, minimal relief in savannas reduces the potential for runoff, and savanna fires rarely exceed 180°C, an unlikely temperature for volatilizing nitrogen (Rundell 1981).

In areas of frequent fires (3 to 5 year return interval), high concentrations of nutrients previously held in the standing crop are found in the soil, emphasizing the beneficial aspects of ash (Wilbur 1985, Trabaud 1994). In many grassland soils, nitrate is often singled out because of its apparent deficiency and its comparatively high concentrations after burning. Although speculation is abundant, the questions of why savanna soils are generally low in nitrate and why nitrate concentrations increase after fire have largely been left unanswered.

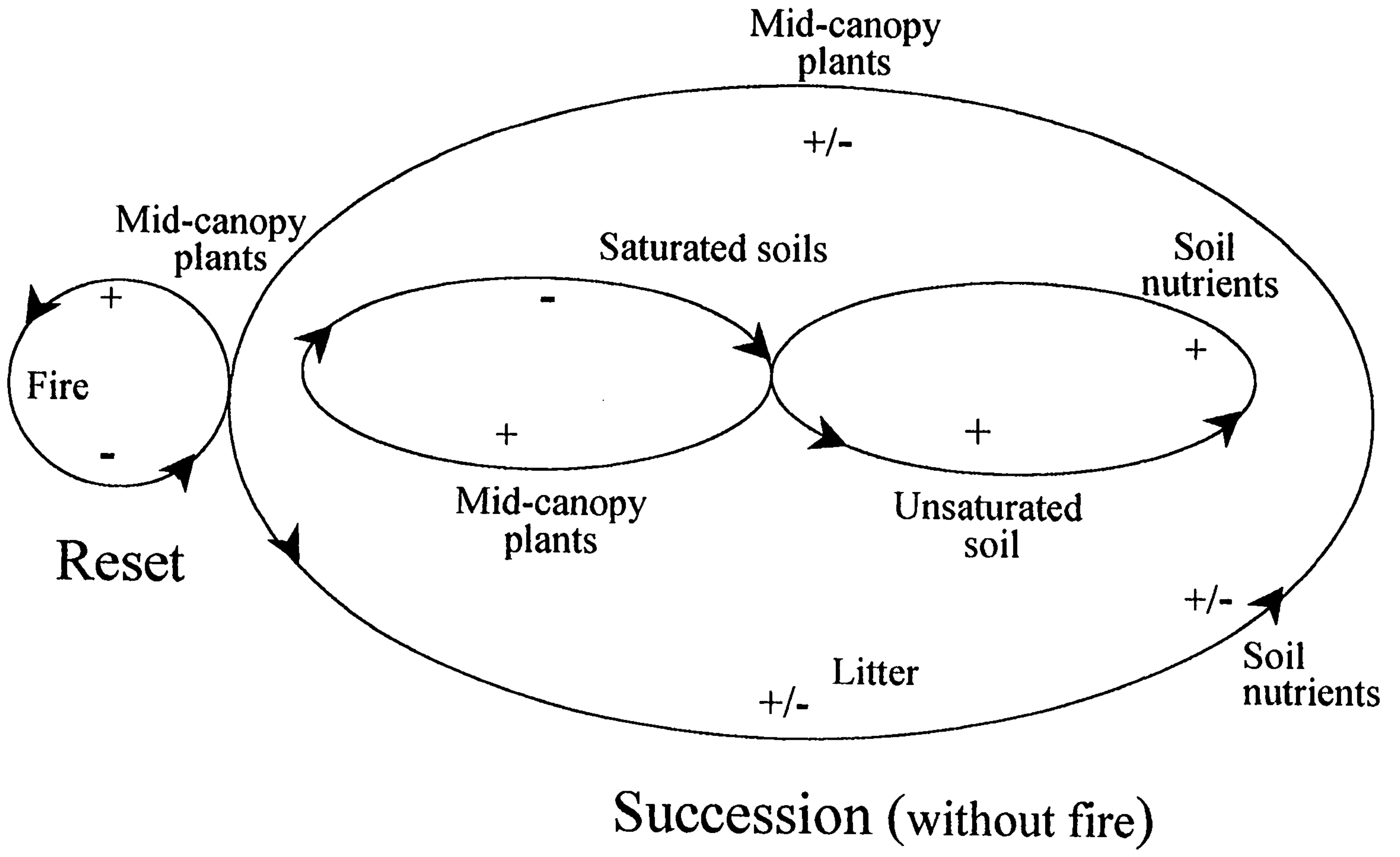
Taken together, these studies lead to several generalizations concerning the study of fire and nutrient extent in serpentine soil ecosystems. First, these studies relied on interpretations of vegetation structure and/or composition to characterize or explain the dynamic nature of these communities, but largely ignored the processes of boundary dynamics or edge discontinuities in the soil. Several above- and below-ground variables in these ecosystems are theoretically quantifiable, but little quantitative data has been compiled to evaluate their relative importance.

Second, relatively little research has examined the vegetation and floristics in transition areas. Although several recent studies describe and review the general concept of boundary dynamics/transition areas (Holland 1988, Naiman et al. 1989, Naiman and Decamps 1990, Hansen and di Castri 1992), detailed research is lacking. Few studies have attempted to explore simultaneous but differential impacts of ecological variables using correlations between species distribution and distributions of elements in the soils; studies by White (1971) and Arabas (1997) are notable exceptions. Third, the majority of studies regarding transition and boundary areas focus on techniques for examining the overall shape and form of landscape boundaries and plant community transition areas. The methods used in these studies describe the spatial pattern of the linear boundaries between adjacent plant community and vegetation types. Some elements of these types of analyses are commonly used for determining scale-dependent patterns over time in a spatial context. Far fewer studies address variation in serpentine soils using both spatial and temporal perspectives. In short, a good deal is inferred through mosaic and patch study in the landscape, but far less is known about the mechanisms underlying changes in vegetation composition and structure (Kent et al. 1997).

A few studies have addressed the roles of disturbance and soil in analyses of floristic and environmental data across vegetation boundaries using 'edge detection' methods such as a moving-window analysis and Mantel's test (Kent et al. 1997). Various analytical approaches to locate discontinuities have been devised but many of these are suited only to univariate data and are inappropriate to characterize transition areas (Kent et al. 1997). The present study adopts a multivariate approach, using a physical agent (fire), and examines its effects on the dynamics of nutrient flow across the ecotones and parallel to the environmental gradients of the plant community. To this end, this dissertation is an exploration of the role of fire as a mechanism for maintaining the serpentine soil communities. It examines the long-term effects of gradients in soil moisture and nutrient supply on community composition across boundaries, and frames the system within the complexity of nutrient availability and succession.

A 'nutrient availability' hypothesis portrays *Darlingtonia* fen communities as dynamic systems operating at a number of different spatial and temporal scales where fire, saturated soil, and low nutrient availability are linked in reciprocal processes (Figure 1.1). In this model, succession proceeds toward the development of a community that decreases soil moisture levels (left inner nested loop of Figure 1.1). At the point of decreasing saturated soils, two outcomes may result: additional growth in the mid-canopy plants or continued drying of the soil (right nested circle of Figure 1.1). Either way, removal of excess moisture may contribute to a higher availability of soil nutrients which then facilitates the establishment of mid-canopy shrub vegetation (top side of the outer loop). As a result of the increase of mid-canopy vegetation, litter

Figure 1.1 A conceptual model describing states and processes linking hypothetical elements of ***Darlingtonia*** fen ecosystems. Arrows indicate directional movement over time while +/-'s indicate increases and decreases in indicated states, respectively.



on the soil surface accumulates, leading to additional soil nutrients (outer loop of Figure 1.1). However, fire may intercede and reset the system by burning the mid-canopy and the litter (Clinton et al. 1993), eliminating the nitrogen and enabling the development of a survival mechanism such as carnivory. If fire plays a paramount role in maintaining the *Darlingtonia* fens of southwestern Oregon, as it does in the southeastern United States, then irrespective of the moisture regime and soil conditions, the absence of fire results in the elimination of *Darlingtonia* fens through the subsequent increase and encroachment of mid-canopy shrub seedlings.

Study Approach and Objectives

The key to long-term understanding and management of fire-dependent ecosystems lies in answering important ecological questions about these fens. Three *Darlingtonia* serpentine soil ecosystems were chosen for their burn histories, their distinct ecotones, and their unique times since the last fire. Specifically, my research objectives were:

- to determine the presence of biogeochemical gradients across the boundaries of the communities,
- to identify the effects of disturbance on boundary composition and structure, and
- to examine the historic effects of fire on western fen communities.

The methodology for this study includes an analysis of physical and chemical characteristics of the soil (e.g., pH, NH_4 and NO_3, and soil texture) as natural below-ground gradients, a characterization of the ecotones found at these sites, and an analysis of the community response of these serpentine soil ecosystems to fire and fire suppression within the larger context of succession.

The outcomes of this project have both management and theoretical implications. First, the role of the ecotones, their dynamics, and their impacts on diversity need to be identified to ensure effective present and future management. Second, this research provides an ecological basis for developing management strategies by the United States Forest Service and The Nature Conservancy by describing community structure and ecosystem dynamics as they relate to disturbance and succession. Finally, this project evaluates a successional model for western *Darlingtonia* fens, and provides a conceptual basis for future studies in these and other uniquely adapted ecosystems.

Dissertation Structure

This dissertation includes the introduction, three core chapters, and a brief summary and conclusion. Each of the three core chapters is presented in a self-contained or "stand alone" format, including a methods, results, and a discussion section, designed to answer specific questions related to the succession of *Darlingtonia* fens. Chapter 2 examines the environmental gradients that provide the details for underground biogeochemical processes - the below ground components of the system. This chapter also examines the spatial distributions of soil properties in *Darlingtonia* fens. In Chapter 3, I characterize the vegetation and the below-ground discontinuities of the ecotones between the communities at each of the three sites. Plant communities commonly display structural or functional discontinuities across landscapes. Thus, this chapter links the inherent abiotic characteristics of

Darlingtonia fen communities with distinct assemblages of plants. Chapter 4 explores the larger context of succession in these communities, by examining the role of ecotones and environmental gradients in shaping vegetative structure and community structure over time. In sum, this study attempts to predict the outcomes of uniquely adapted systems on serpentine soil ecosystems in the Pacific Northwest and link these in the larger context to identical systems on the east coast. Finally, in Chapter 5, I summarize the overall conclusions for the study, and consider their implications for conservation management in southwestern Oregon.

CHAPTER 2

SPATIAL PATTERNING OF SOIL NITROGEN GRADIENTS ACROSS COMMUNITY BOUNDARIES IN *DARLINGTONIA* FENS OF VARYING FIRE HISTORY

Soil nitrogen gradients in terrestrial ecosystems are often conceptualized as having explicit but mutually dependent above- and below-ground components (Smith et al. 1986, Hook et al. 1991, Jackson and Caldwell 1993). While there is a rich history of soil ecological research and a wide recognition of the importance of soil chemical and physical properties (Huston 1979, Tilman 1988, Robertson et al. 1988, Keddy 1989), the extent to which below-ground processes can affect above-ground community structure and pattern has been largely understated. This is especially true for serpentine soil ecosystems.

Darlingtonia fens are part of a complex mosaic of fen and pine savanna communities found on serpentine soils in southwestern Oregon and northern California. Plant carnivory is an important characteristic of these serpentine ecosystems and reflects the unique soil requirements of contrasting plant growth forms that also include a grass understory, and a pine overstory, but disfavors plants of an intermediate stature, such as mid-canopy shrubs (Figure 2.1) (Whittaker 1960). Few other ecosystems demonstrate a comparable balance among high water tables, shallow soils, the presence of heavy metals, and limited nutrients where fire is the primary factor restricting the formation of a closed canopy forest in the succession cycle. Although a number of species are common to these communities, the dominant understory species includes the carnivorous plants *Darlingtonia californica* and the

Figure 2.1 *Darlingtonia* fen at Eight Dollar Mountain in southwestern Oregon.

sedge *Carex mendocum* while scattered Jeffrey pine *(Pinus jeffreyi)* constitute the upper canopy (Whittaker 1954, Franklin and Dyrness 1988).

In the fen ecosystems of southwestern Oregon, two important gradients or factors are believed to influence the vegetative patterns and composition (Proctor and Woodell 1975, Mellichamp 1983). The most important is vegetative position relative to soil moisture. Fens reside in perennial streams and typically are characterized by a rich floral community dominated by *Darlingtonia californica* and *Carex mendosum.* The second factor is position relative to fire intensity which ultimately depends on hydrology. Unburned vegetation growing on saturated soils can create distinct patterns of vegetation growth between fen and savanna. If this is the case, then soil nutrients should reflect these discontinuities with corresponding transitions in vegetative patterns

Soil patterning is unclear on serpentine soils and specific processes that appear to underlie soil variability are poorly understood. Even less certain is the persistence of vegetative patterns: are vegetative patterns controlled by soil variability or gradients, and how and to what extent do these gradients change over a shorter period of time, particularly in response to fire. Several above- and below-ground variables in these ecosystems are theoretically quantifiable, yet few studies have attempted to evaluate their relative importance. Thus this chapter examines the subterranean gradients on serpentine soils at three sites having different fire histories to determine the composition of plant communities associated with *Darlingtonia* fens in southwestern Oregon. My objectives are to:

- determine the presence of biogeochemical gradients in these study sites, and

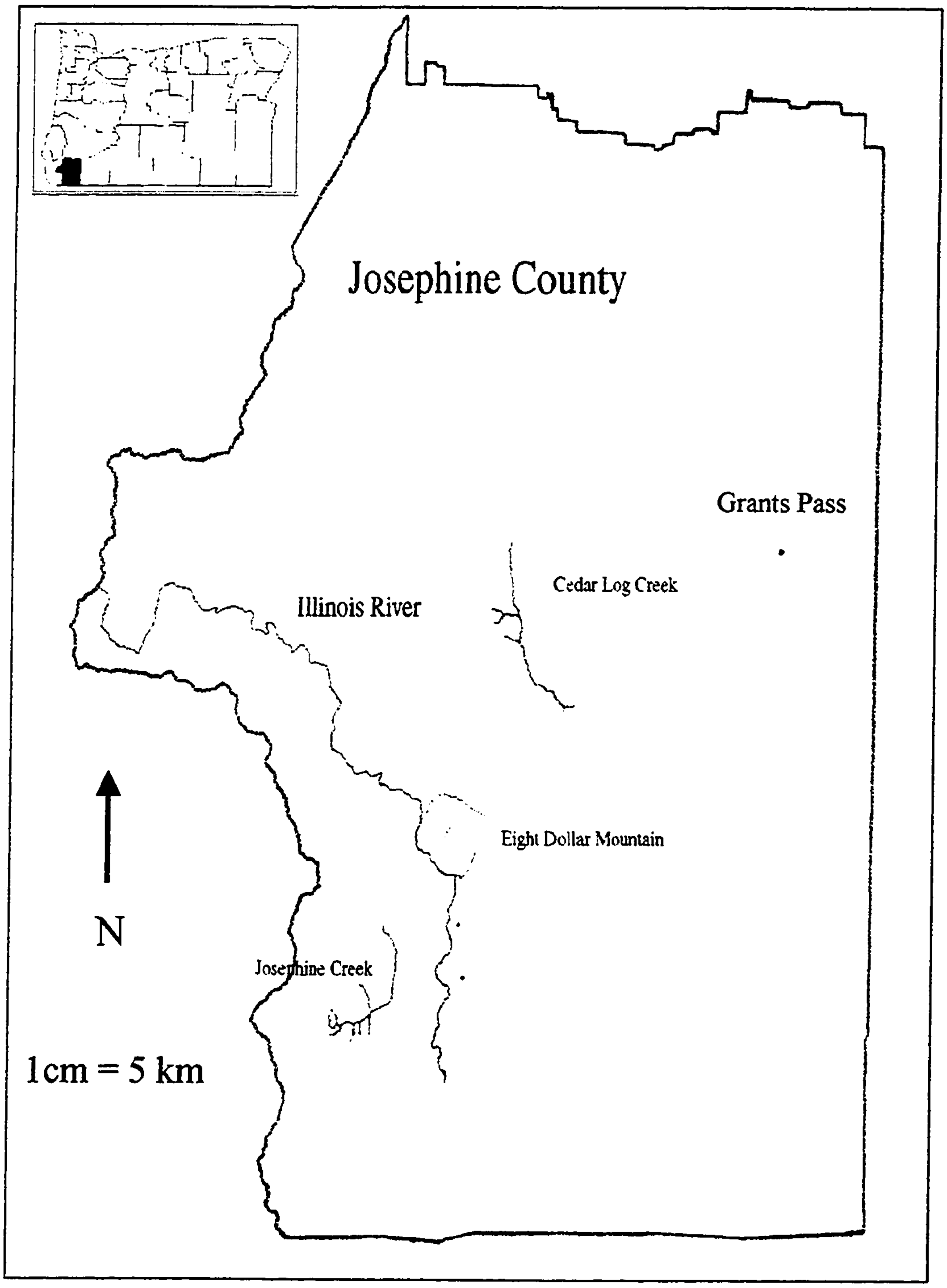
- determine if length of time since fire influences the biogeochemical gradients.

My hypothesis is that, over time and in the absence of fire, the soil nitrogen gradients in *Darlingtonia* fens become more pronounced in the absence of fire and increased community dominance by late successional species. Using a 'nutrient availability' model approach, longer fire return intervals should show lower soil moisture levels (left inner nested loop of Figure 1.1) while fire-determined biogeochemical gradients should be steeper at sites with the shortest time since fire. As time since fire increases, soil nutrient levels should be greatest in the study site with the longest time since fire following the establishment of a mid-canopy shrub community.

Study Site

This research was conducted in three *Darlingtonia* fens, each approximately .5-1 ha in extent and located within the Siskiyou National Forest in southwestern Oregon (42° 07' 30" N, 123° 37' 30" W, elevation 700 m) (Figure 2.2). Climatological data from Grants Pass, Oregon, ≈ 40 km from the study sites indicate that precipitation, almost entirely as rain, averages 140 cm annually with most occurring from November through May (Oregon Climate Service 2001). The climate is Mediterranean with cool, wet winters and distinctive warm and dry summers from June to September. Mean maximum temperatures at Grants Pass over the past 30 years for January and July were 9° and 31° C. Mean minimum temperatures for the same months were 5° and 11° C. It is during the comparatively dry months of August and September that maximal fuel loads and sources of ignition (primarily lightning) interact to result in fire events, the majority of which were, until the summer of 2002,

Figure 2.2. Study sites, Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain, located in Josephine County, Oregon.



small in spatial extent due to fuel breaks of bare serpentine rock and topographic discontinuities (Frost 2000).

The study area is located within the Josephine ultramafic sheet, a geologic region of southwestern Oregon characterized by unweathered rock fragments underlain by Jurassic-aged marine sediments (White 1971, Orr et al. 1992). Surface sediments consist of weathered ultramafic rock (serpentinite and partly serpentinized peridotite) which contributes to the serpentine soil chemistry: 1) high levels of exchangeable magnesium relative to other cations; 2) lower calcium levels than those found on nonserpentine soils; 3) lower levels of nitrogen, phosphorus, and potassium than are required for normal plant growth; and 4) high concentrations of heavy metals (chromium and nickel) with molybdenum levels insufficient for normal plant growth (Walker 1954, Kruckeberg 1984).

The fen soils belong to a laterite clay series rich in olivine and pyroxene minerals and serpentinized to various extents giving them a dark, blue-green color (Becking 1997). Immediately surrounding the fens are shallow red soils with stony profiles that vary in surface depth depending on age of the laterite, amount of erosion or surface movement to which it has been subjected, degree of fracturing and alteration of the parent rock, history of precipitation in the area, vegetative cover, and composition of the parent rock (Ramp and Peterson 1979). The upper surface (depth from 0-.3m) is typically dark, reddish-brown soil with minor organic residue and abundant to minor amounts of iron oxide pellets and chromite grains (variable amounts of relatively unweathered peridotitie boulders) (Ramp and Peterson 1979), slightly acidic in pH (6.6 to 6.8) and low in nutrients (Walker 1954, Kruckeberg

1984). Beneath this (.3-1m), a yellow-brown soil with variable amounts of partly weathered peridotite occurs. A mid-canopy shrub community soil, surrounding the fen at Eight Dollar Mountain, is intermediate in both hydroperiod and organic layer, slightly more than the savanna, and slightly less than the fen, but still saturated for most of the year.

The sites used in this study were selected for their distinct boundaries, unique vegetative requirements, and burn histories. Two of the study sites, Cedar Log Creek and Josephine Creek, include pine savanna and fen plant communities. The third site, Eight Dollar Mountain, is forested adjacent to a mesic shrub community and most closely resembles the southeastern United States' carnivorous plant communities. This shrub community (unique to the Eight Dollar Mountain site) is characterized by *Rhamnus californica* and *Rhododendron occidentalis* while scattered Jeffrey pine *(Pinus jeffreyi)* and incense-cedar *(Calocedrus decurrens)* constitute the upper canopy (Whittaker 1954, Franklin and Dyrness 1988). The three sites differ in time since last fire: five years (Cedar Log Creek), eight years (Josephine Creek), and approximately one hundred years (Eight Dollar Mountain) since fire. The Eight Dollar Mountain site combines the longest time period since fire, a closed canopy forest within 100 m of the fen center, and a major area of species endemism (Table 2.1). The boundaries common to these three communities represent discontinuities between different vegetation forms, with an emphasis on biological interaction between adjacent communities (Clements 1916).

Table 2.1. Summary of characteristic differences between the three study sites in southwestern Oregon.

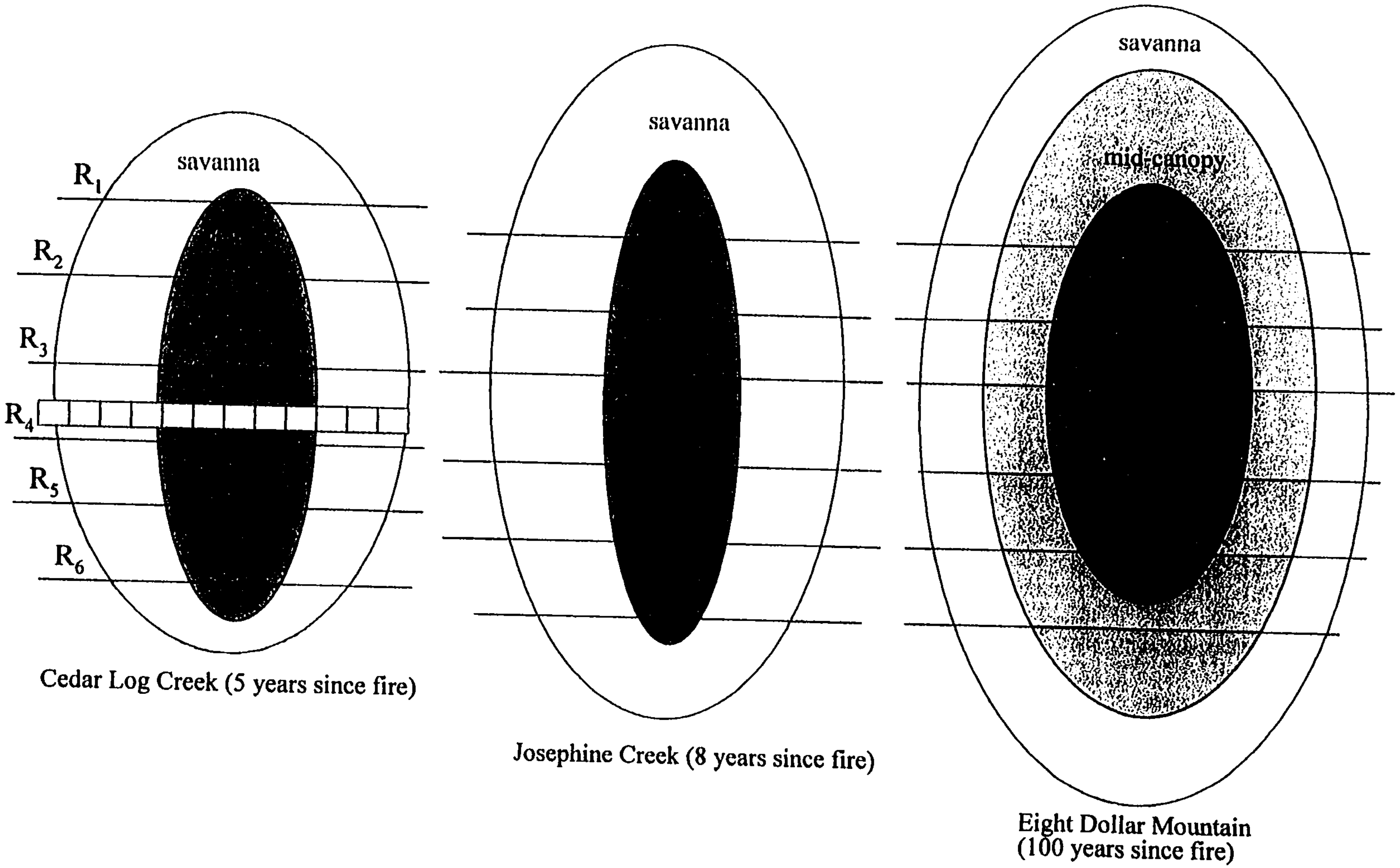
Study site	Length of time since last fire	Within-site communities	Size (ha)
Cedar Log Creek	5 yrs	Fen and savanna	.5
Josephine Creek	8 yrs	Fen and savanna	.5
Eight Dollar Mountain	100 yrs	Fen, savanna, and mid-canopy shrub	1.0

The 1986 burn in the Josephine Creek site was a ground fire, removing all flammable herbaceous biomass and most of the accumulated litter. Only the lower needles of pines were scorched by the fire. The 1996 burn in the Cedar Log Creek site was a prescribed fire that burned over both savanna and fen entirely. Both burns mimicked natural late summer fire regimes for the area (Borgias and Beigel 1998). The extensive Biscuit fire of 2002 did not reach any of the three sites.

Field Sampling

Six transects, oriented perpendicular to community boundaries and to the main environmental gradients (perennial stream and topography) (Knapp 1984, Palmer and Dixon 1990), were established at each of the three study sites (Figure 2.3). Each transect contained at least twelve soil and twelve vegetation sample plots, with six transects in each of the three separate sites. I sampled linearly along these 12 plots, contiguously and all 1m^2 apart. This sampling method allowed for six replications of twelve soil and twelve vegetation sample plots each 1 m^2. Because the Eight Dollar Mountain site contained an extra community, I used an additional 72 sample plots to include the sampling of mid-canopy shrubs. Transects of the Eight Dollar Mountain

Figure 2.3. Sampling design for Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain site. Numbered transects (R_c) run perpendicular to the community boundaries and adjacent squares illustrate the placement of contiguous 1m² quadrats from which soils were sampled. Eight Dollar Mountain contains the same transects but more quadrats (3 per community) due to the extra community. Not to scale.



Cedar Log Creek (5 years since fire)

Josephine Creek (8 years since fire)

Eight Dollar Mountain
(100 years since fire)

site extended across the mid-canopy boundary and into the savanna by an additional 15 meters to accommodate an increase in sample plot size (5x5 m) and to characterize structure across the entire site.

I recorded species presence and percent cover in each of the 230 quadrats (1 m^2) along the transects during the peak of the growing season (June, July, and August) and again in late summer (September and October). Percent cover for each species was estimated using one of six cover classes (<1%, 1-4%, 5-25%, 26-50%, 51-75%, and 76-100%). Plants were identified to species level where possible; nomenclature follows Jepson (1958). Because some plants remained in a vegetative state throughout the season, identification to this level was not always possible, resulting in several species being grouped at the genus level. Each species was noted for its presence and catalogued according to its: 1) life form, 2) life history (perennial versus annual), 3) phenological observations, and 4) native versus nonnative status.

For each quadrat in the three sites, I also recorded the following:

1. Soil surface characteristics such as bare ground, water, and exposed rock, measured as percent cover and
2. Air temperature, relative humidity, and slope angle, aspect, and elevation, at five separate locations using a laser rangefinder.

Soils Analyses

Soil variation across community boundaries was assessed using soil samples collected along transects at each site during June, July, August and September over four consecutive years (1999 - 2002). One core (12 cm deep and 3 cm in diameter; 340 cm^3) was taken from each 1m^2 plot for chemical and physical characteristics:

NO_3, NH_4, soil moisture, bulk density, pH, CEC, soil texture, and organic matter. In mid-canopy areas (Eight Dollar Mountain site) where soil variability was higher, 3 cores were taken randomly within a plot and composited. All soil cores were taken between shrub root zones. Soil pits were dug within each community at each site and described using SCS soil survey guidelines (Borine 1983).

Soil samples collected for nutrient analysis were air dried at 70° C for 48 hours and passed through a 2 mm sieve to remove stones and coarse roots. All subsequent analyses were performed on this sieved material. Soil pH was determined in a 1:1 soil-water paste (McLean 1982). Soil ammonium and nitrate were extracted in a 1:10 soil 2 N KCl solution using the Bremmer method (Bremmer et al. 1965). Extracts were analyzed colorimetrically on a Technicon II auto analyzer. Organic matter content was determined by loss on ignition (Shulte and Hopkins 1996) and cation exchange capacity (CEC) by extraction with 1 N ammonium acetate solution (Rhoades 1986). Physical soil characteristics (sand, silt and clay) were determined by pipette according to MacKeague (1978). Soils were also analyzed gravimetrically for soil moisture according to Western States Laboratory Proficiency Testing Standards.

Statistical analyses

In order to ordinate vegetation of the study sites, I used canonical correspondence analysis (CCA) (Ter Braak 1986) by means of the CANOCO program v.3.1 (Ter Braak 1987). Vegetation data for the analysis were based on percent cover estimates for each quadrat along the transects and were recorded during the peak of the growing season (June). The species matrix included percent cover of only the indicator variables of each community, since the objective was to gain information on community location relative to biogeochemical gradients. These species were: *Ceanothus pumila*, *Eriophorum crininger*, *Festuca idahoensis*, *Arctostaphylos viscida*, *Tofieldia glutinosa*, *Hastingsia bracteosa*, *Darlingtonia californica*, *Sanguisorba microcephala*, *Rudbeckia californica*, and *Carex mendocum* which characterized large communities of heliophytes (plants tolerating full sun). *Rhododendron* and *Rhamnus* characterized the mid-canopy plants while Jeffrey pine and incense-cedar constituted the upper canopy community. Site scores were screened for outliers (> 2 standard deviations from site score) prior to analysis; three samples were found outside of distinctive clusters of vegetation by running a principal components analysis (PCA) and removing them from the total (n=227 samples).

The environmental matrix of the CCA included nine soil variables: soil moisture (gravimetric water determination), bulk density, pH, NO_3, NH_4, organic matter, sand, silt, clay, and cation exchange capacity. Bulk density and pH are continuous variables while soil moisture is a proportionate variable (wet: dry wt./vol.) ranging from 22 to 573%. I transformed the variables cation exchange capacity, soil pH, NO_3, NH_4, and bulk density. Soil moisture, organic matter, sand, silt, and clay and variables of vegetation abundance required square root and arcsine transformations prior to analysis to more closely approximate the assumptions of normality (Jongman et al. 1995).

Since a primary goal of this analysis was to identify the relationship between community composition patterns in relation to soil variables, I removed rarer species that might obscure the analysis of the data (Gauch 1982). Species with mean cover values less than one percent or a frequency of less than 10% were also eliminated from the analysis. The final analysis incorporated both soil and species variables (Tables 2.2 and 2.3). Nineteen vegetation variables and 11 soils variables comprised the matrices for the analysis.

I performed multivariate analyses using the program CANOCO v. 3.1. Species variables were ordinated with respect to soil variables using CCA (Ter Braak 1986). Significance levels for the first and second axes were set at $p \leq 0.05$. A forward-selected CCA ordination was then used to determine which soil variables accounted for the greatest amount of variance in the distribution of the plants. This process chooses variables that explain significant ($p \leq 0.05$) and independent directions of total variation in the spatial distribution of plant vegetation. The significance of each variable added in this fashion was tested using a Monte Carlo permutation test with 999 unrestricted permutations. Following the CCA, I used a non-parametric median test between sites to confirm that the communities represented statistically different populations (Sokal and Rolf 1982).

Among multivariate methods, the eigenvector method (Canonical Correspondence Analysis) preserves the chi-square distance among points, and is appropriate when the responses of the dependent variables are expected to be unimodal along environmental gradients. Unimodality for this analysis was confirmed using an unconstrained analysis, detrended correspondence analysis (DCA), on the species data; all gradient lengths were greater than 3.5 and indicated high spatial variability among species.

Table 2.2. Species data for the three study sites. Variable codes presented in the results appear in parentheses. Numbers represent values recorded during the growing season. All variables listed were included in the CCA (n=227).

Species (Variable names)	**Eight Dollar Mountain**	**Josephine Creek**	**Cedar Log Creek**
	Range (%cover) (median)	Range (%cover) (median)	Range (%cover) (median)
Darlingtonia (lDca)	2-90 (25)	8-99 (60)	1-80 (30)
Tofieldia (Tofield)	0	1-10 (3)	1-40 (15)
Arctostaphylos (lManzan)	2-65 (15)	5-10 (7.5)	10-25 (15)
Agrostis (Agrostis)	1-55 (5)	5-15 (5)	3-35 (10)
Carex (Carex)	1-90 (35)	1-98 (20)	5-75 (10)
Rudbeckia (Rudbeck)	7-95 (30)	1-5 (3)	2-45 (17.5)
Rhododendron (Rhodo)	1-99 (50)	1 (0)	2-45 (12.5)
Ceanothus (Ceanoth)	1-5 (2)	5-40 (0)	1-30 (15)
Hastingsia (Hastings)	3-90 (20)	1-90 (15)	10-20 (15)
Sanguisorba (Sanguis)	1-45 (17.5)	1-20 (3)	2-55 (12.5)
Pinus jeffereyi (Pjeff)	5-100 (50)	2-50 (12.5)	2-100 (25)
Festuca (Festuca)	10-90 (75)	5-30 (20)	3-75 (17.5
Calocedrus (Libocedr)	1-60 (5)	0 (0)	5-25 (10)
Rhamnus (Chokeche)	1-100 (10)	0 (0)	10-65 (25)

Table 2.3. Summary of soil data for all three sites as used in the environmental matrix. Variable codes used in the results appear in parentheses. Numbers represent values recorded during the growing season. All variables listed were included in the CCA (n = 227).

Soil (Variables)	**Range (median)**
pH (pH)	5.1-7.7 (6.8)
Soil moisture (%) (smoist)	3-573 (65.0)
Cation exchange capacity meq (cec)	18.8-56.5 (36.1)
Bulk density (g/cm^3)(lgbdens)	.74 - 1.97 (1. 3)
Time since fire (tsfire)	5, 8 or 100 years
soil NO_3 (ppm) (sNO_3)	.1-5.7 (.8)
soil NH_4 (ppm) (sNH_4)	2 - 455.5 (24. 4)
Sand (%) (sand)	41- 89 (59.0)
Silt (%) (silt)	6-29 (16.0)
Clay (%) (clay)	4-38 (22.0)
Organic matter (%) (orgmat)	4.2-38. 3 (13.6)

Results

Vegetation

To determine plant community associations, two tree species, four shrub species, and ten herbaceous species were inventoried from all quadrats at the three sites. One tree species, Jeffrey pine, along with nine herbaceous genera, *Darlingtonia, Eriophorum, Hastingia, Festuca, Rudbeckia, Sanguisorba, Tofieldia, Agrostis*, *Arctostaphylos* and *Carex* (stellulatae group), were recorded at each of the three sites. Incense-cedar and two of the four shrub species, *Rhamnus* and *Rhododendron,* were present at the Eight Dollar Mountain site. These two shrub species dominated a mid-canopy community of the Eight Dollar Mountain site while the remaining two shrub species (*Ceanothus* and *Arctostaphylos*) were represented in the savanna communities at all three sites.

Soils

Several biogeochemical gradients were produced from the CCA analysis. Cedar Log Creek (5 years since fire) showed a slight soil NO_3 gradient across communities from the fen (lower values) to the savanna (higher values) (Table 2.4). Nitrate levels at this site were the lowest of the three sites (.6 ppm in the fen and .9 ppm in the savanna). Soil ammonium levels at this site were also lowest but were considerably higher than NO_3 levels (14 to 33 times higher) with decreasing values from center of fen to savanna, across all transects. A strong soil moisture gradient was present at Cedar Log Creek from the fen to the savanna with gravimetric moisture as low as 21% in the savanna community and supersaturated conditions in the fen community. There are no clear bulk density, soil texture, or cation exchange capacity

Table 2.4. Soil variables and median values for all communities, fen, mid-canopy (mc), and savanna (sav) at each site. Mid-canopy vegetation is restricted to the Eight Dollar Mountain site. Soil texture at all three sites is sandy clay loam.

Site	median soil NO_3 (ppm) fen mc sav	median soil NH_4 (ppm) fen mc sav	avg pH	bulk density (g/cc) fen mc sav	soil moisture (%) fen mc sav	CEC (meq/ 100g) fen mc sav	organic matter (%) fen mc sav	slope (%)
Eight Dollar Mountain (100 years since fire)	(.9)(1)(2.5)	(171)(65)(7)	6.6	(.9)(1)(1.4)	(328)(86)(11)	(31)(36)(31)	(20)(19)(7)	2-5
Josephine Creek (8 years since fire)	(.7) - (1. 4)	(40) - (29)	6.8	(1.5) - (1.6)	(110) - (69)	(26) - (31)	(11) - (9)	2-5
Cedar Log Creek (5 years since fire)	(.6) - (.9)	(20) - (13)	6.7	(1.3) - (1. 4)	(71) - (21)	(39) - (47)	(12) - (13)	10

gradients at Cedar Log Creek, however bulk density levels were similar to both the Josephine site (8 years since fire) and the savanna community at the Eight Dollar Mountain site. Organic matter levels were relatively consistent across communities with a median site pH of 6.7.

Josephine Creek (8 years since fire) showed a slight soil NO_3 gradient across communities from the fen to the savanna (Table 2.4). However, there was a stronger soil NH_4 gradient from the fen to the savanna with the levels of NH_4 dropping slightly from 40 ppm in the fen to 29 ppm in the savanna. As with the Cedar Log Creek site, levels of NH_4 were considerably higher than the NO_3 levels (30 to 40-fold greater). Organic matter levels decreased from fen to savanna but there were no apparent gradients for soil texture, bulk density or cation exchange capacity. The median pH was 6.8 at this site.

In general, two strong gradients occurred at the Eight Dollar Mountain site (100 years since fire); a soil NO_3 gradient that increased from fen to savanna and an NH_4 gradient that decreased from fen to savanna with NH_4 levels superseding NO_3 levels in some cases by a factor of 200 (Table 2.4). This range of values coincides with changes in organic matter that were highest in the fen, lowest in the savanna and intermediate in the mid canopy community. Additional gradients at this site were soil texture with a sand gradient decreasing from fen to savanna, a clay gradient that increased from fen to savanna, and a bulk density gradient that increased from fen to savanna and from source of fen to the outlet. The median pH of this site was 6.6.

Canonical Correspondence Analysis

The canonical coefficients represent the weight that each soil variable contributed to the ordination axes and the inter-set correlations reflect the correlation between the environmental variables and the ordination axes (Table 2.5). Both axes 1 and 2 of the CCA ordination were significant ($p \leq 0.05$) with high eigen values (λ_1=0.46, λ_2=0.29). Species-soil correlations (0.790 for axis 1, 0.795 for axis 2) accounted for 15% of the variance explained by the soil variables. Six out of ten soil variables (soil moisture, NO_3, NH_4, CEC, bulk density, and clay) were significant at $p \leq 0.001$. Results of the approximate t-tests and the inter-set correlations (Table 2.5) showed that soil chemical factors such as NH_4 make significant contributions to axis 1, whereas axis 2 likely represents a gradient that is related to the physical properties of the soil affected by either time since fire or soil moisture. All results indicated that plant species separate widely.

The first CCA axis ordered sites along an NH_4 gradient (-.66) and soil moisture (-.58) ranging from recently burned sites (5 and 8 years) to long-time since fire (100 years) (Figure 2.4a). Species occurred across a range of moisture conditions with *Darlingtonia*, *Sanguisorba*, and *Hastingsia* clumping tightly in a wetter habitat while *Ceanothus*, *Arctostaphylos* (lManzan) and *Festuca* clump more tightly in the drier habitats (Figure 2.4b). In these sites, the savanna separated from the fen and the mid-canopy communities of the Eight Dollar Mountain site. Along the second axis, bulk density occurred as a slight gradient from Jeffrey pine savanna to *Darlingtonia* fen community types, increasing from low to high, respectively. Separation within sites across communities and between all three sites (Figures 2.4a and 2.4b) was clear with

Table 2.5. Summary of canonical coefficients, approximate t-test scores, and inter-set correlations of environmental variables. Significance ($\alpha \leq 0.05$) is indicated by * (between sites) and ** (within sites).

	Canonical coefficients		**t-values of Canonical coefficients**		**Inter-set correlations**	
Environmental Variable (label)	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Soil moisture (smoist)**	-.24	.43	-2.51	4.51	-.58	-.14
pH (pH)*	-.06	.09	-1.01	1.61	.15	.21
Soil N0$_3$-N (sNO$_3$)**	44	-.05	7.71	-.92	.44	-.20
Soil NH$_4$-N (sNH$_4$)**	-.64	.08	-6.03	.81	-.66	-.27
Organic matter (orgmat)*	-.14	.01	-1.11	.11	-.35	-.53
Cation exchange capacity (cec)**	.05	-.40	.50	-4.23	.15	-.27
Soil bulk density (bdens)**	-.23	.60	-2.45	6.48	.26	.66
Soil texture (sand)*	.49	-.15	1.96	-.60	-.45	-.37
(silt)*	.30	-.19	2.79	-1.77	.45	.05
(clay)**	.35	.63	1.75	3.21	.39	.46

Figure 2.4a. CCA ordination sample scores by sites. Circles correspond to plant species for each site. Prefixes 1, 2, or 3 identify specific sites.

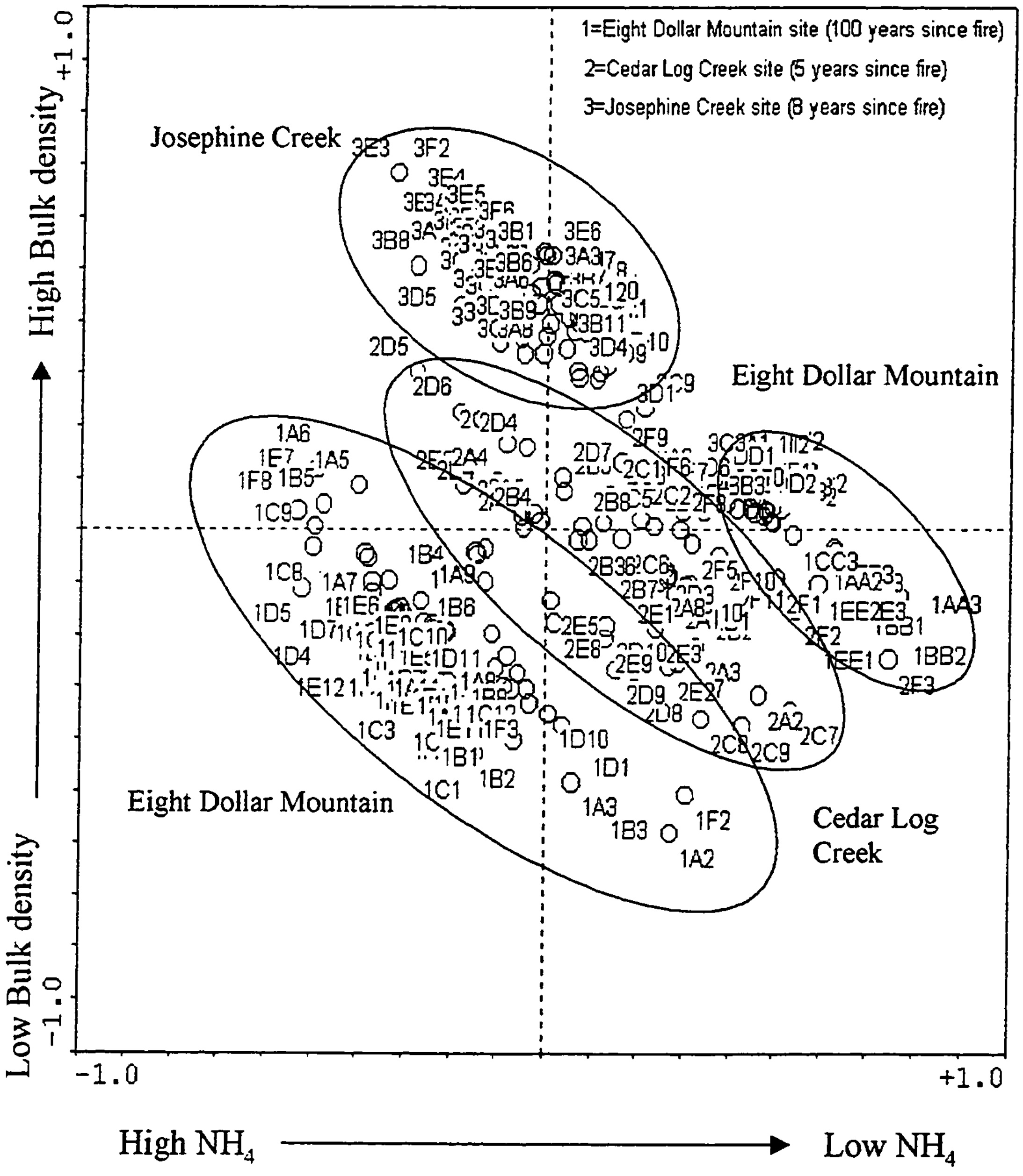


Figure 2.4b. CCA ordination of sample scores for environmental variables. Small circles correspond to plant species (Table 2.2); large circles indicate plant communities. Species identifiers and abbreviations for environmental variables follow Table 2.2.

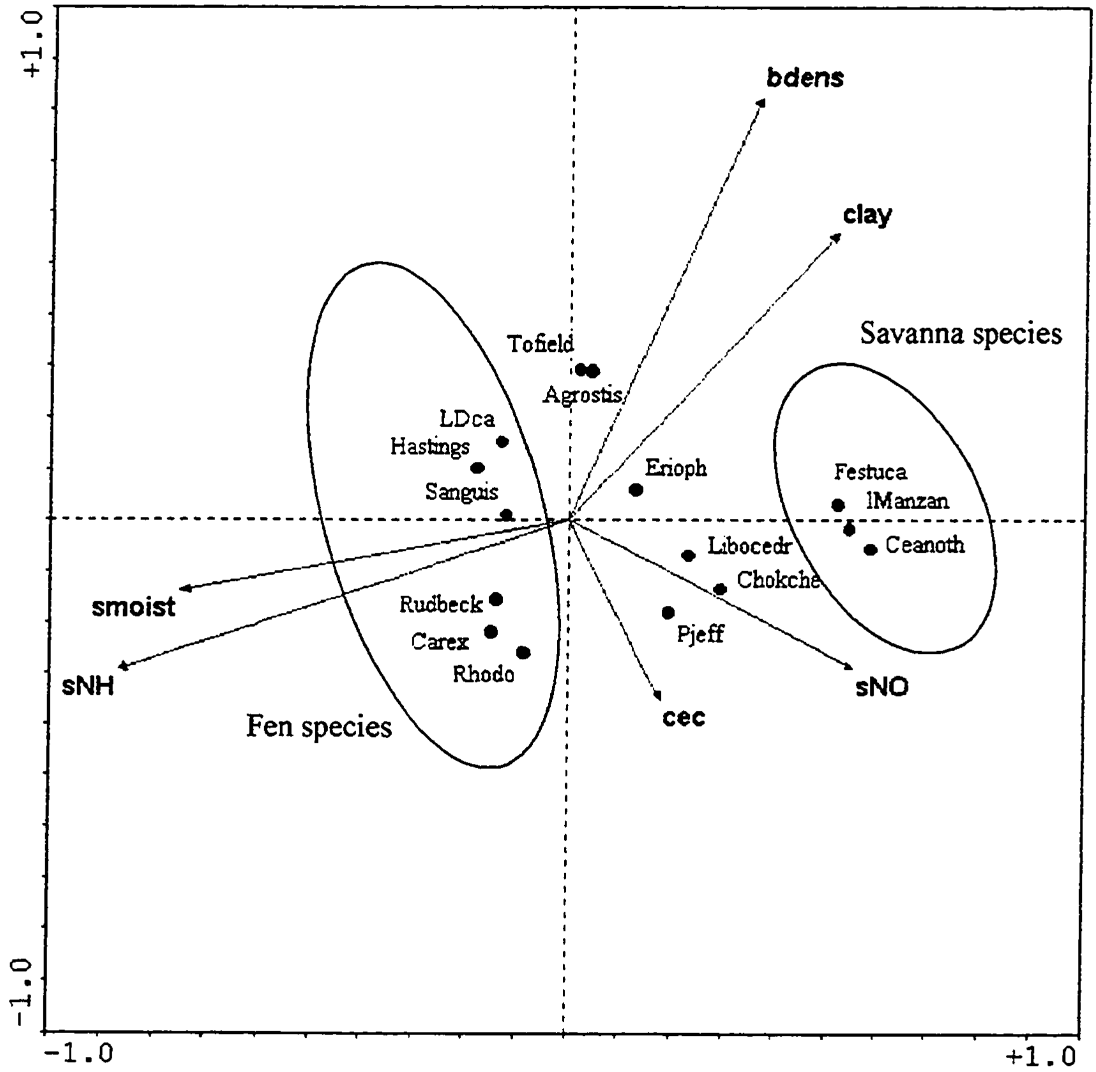
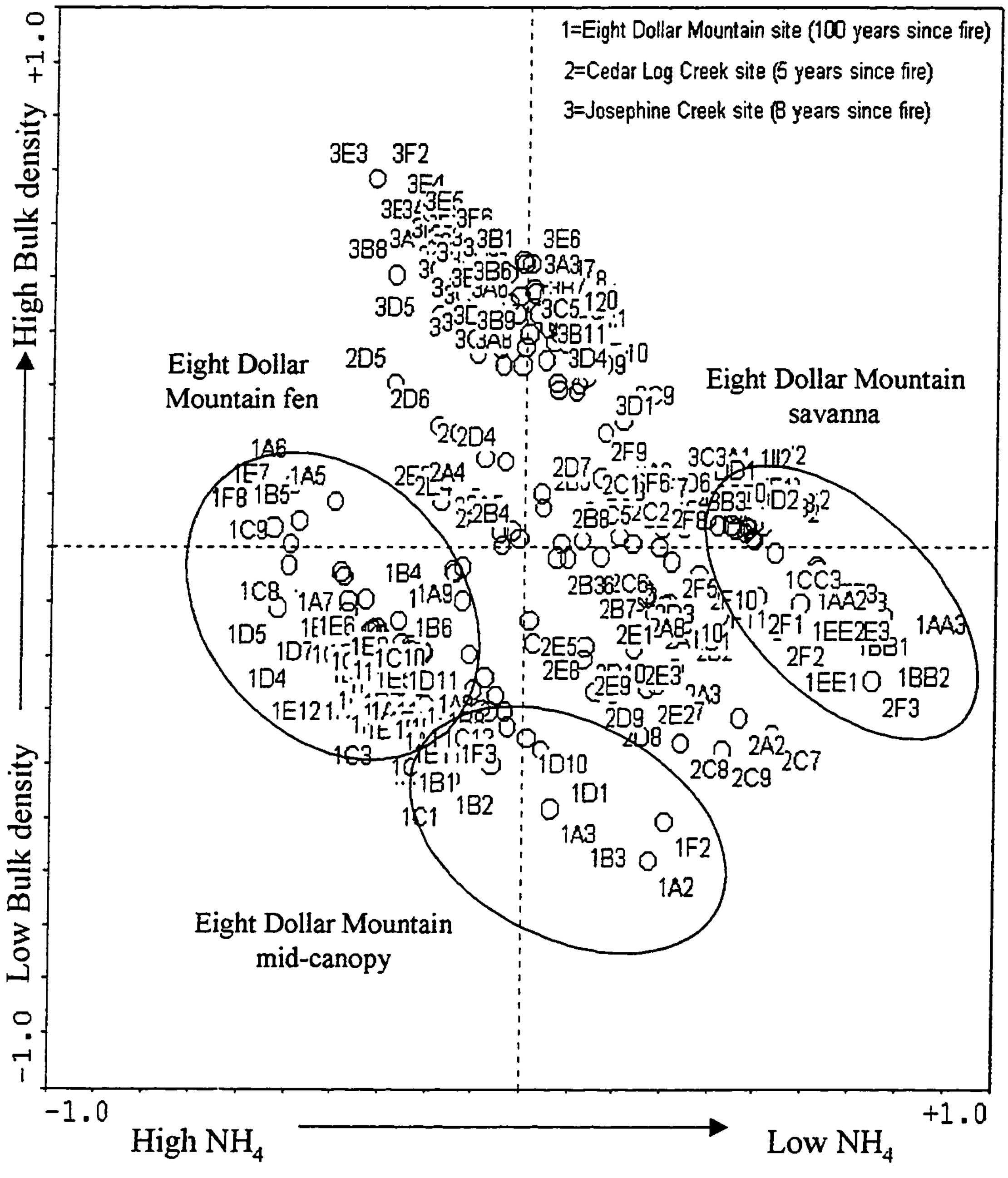


Figure 2.4c. CCA ordination of sample scores and sites showing intra-site distinction. Prefixes of either 1, 2, or 3 indicate groupings of inter-site quadrats at Eight Dollar Mountain.



the exception of the savanna community in the Eight Dollar Mountain site (Figure 2.4c). The non-parametric median comparison (Sokal and Rolf 1982) indicated significant differences in soil NH_4 ($p < 0.001$) and bulk density ($p < 0.001$) between sites.

Discussion

The results of this ordination analysis show clear differences can be observed in the types of plants grouped within sites and between communities in southern Oregon serpentine communities. Specifically, the analysis indicates that soil-related variables offer some explanation about patterns and distributions of plant species in combination with time since the last burn. These variables must be included when considering management options for this ecosystem, as should the ultimate value placed on effects of fire on those below-ground variables.

Use of Kruskal and Wallis (Sokal and Rolf 1982) median comparisons shows statistically significant differences in soil NH_4 and bulk density between sites. Soil ammonium accounts for a major portion of the variance in the gradient analysis; .79 of the species-soil correlation and 15% of the variation in spatial distribution of plants within each site. These results are consistent with Bedford's (1999) review of nutrient poor fens and bogs in temperate North America and with Andreu et al. (1996) in their study of soil ammonium changes following burning. *Rhododendron*, *Rudbeckia*, and *Carex* (Figure 2.4b) occupy sites having high NH_4 relative to *Ceanothus, Festuca,* and *Arctostaphylos* whereas shrub community plants (incense-cedar (Libocedr) and *Rhamnus* (Chokche)) occur somewhere between the wettest sites for *Darlingtonia* and the driest sites of *Ceanothus* and *Festuca*. Along with community separation by soil

NH_4, the ordination separates the three sites based on the length of time since the last burning (Figure 2.4a). These findings suggest age related soil characteristics at Eight Dollar Mountain where NH_4, NO_3, and organic matter levels are highest.

Examination of the sample numbers on these sites (Figure 2.4a) shows that sites 2 and 3 are juxtaposed. The Josephine Creek site (8 years since fire) values do not correspond with increasing time since fire where they would hypothetically exist; intermediate between the Eight Dollar Mountain site (100 years since fire) and the Cedar Log Creek site (5 years since fire). This suggests that either 8 years is insufficient time to build higher soil NH_4 levels than those found at Cedar Log Creek (5 years since fire) or that the slightly higher sand content at this site creates effectively drier (higher matric potential) soil conditions.

Both soil texture and bulk density are important in shaping post fire communities. The ordination values show that bulk density (strongly correlated with sand content) accounts for some spatial distribution of communities. Specifically, savanna plants increase in dominance with increasing bulk density. Fine-textured soils, on the other hand, with high total pore space such as silt loams, clays, and clay loams, generally have lower bulk densities than sandy soils, especially if organic matter is present (Brady and Weil 1996). This relationship is most evident at the Eight Dollar Mountain site (100 years since fire) where organic matter content is highest in the fen community, lowest in the savanna, and intermediate in the mid-canopy shrub community (Figure 2.4c). Plant species and thus communities separated widely, thereby demonstrating that soil variables such as soil moisture, pH, bulk density, CEC, and soil texture, may contribute to site differentiation as strongly as time since fire (Figure 2.4b).

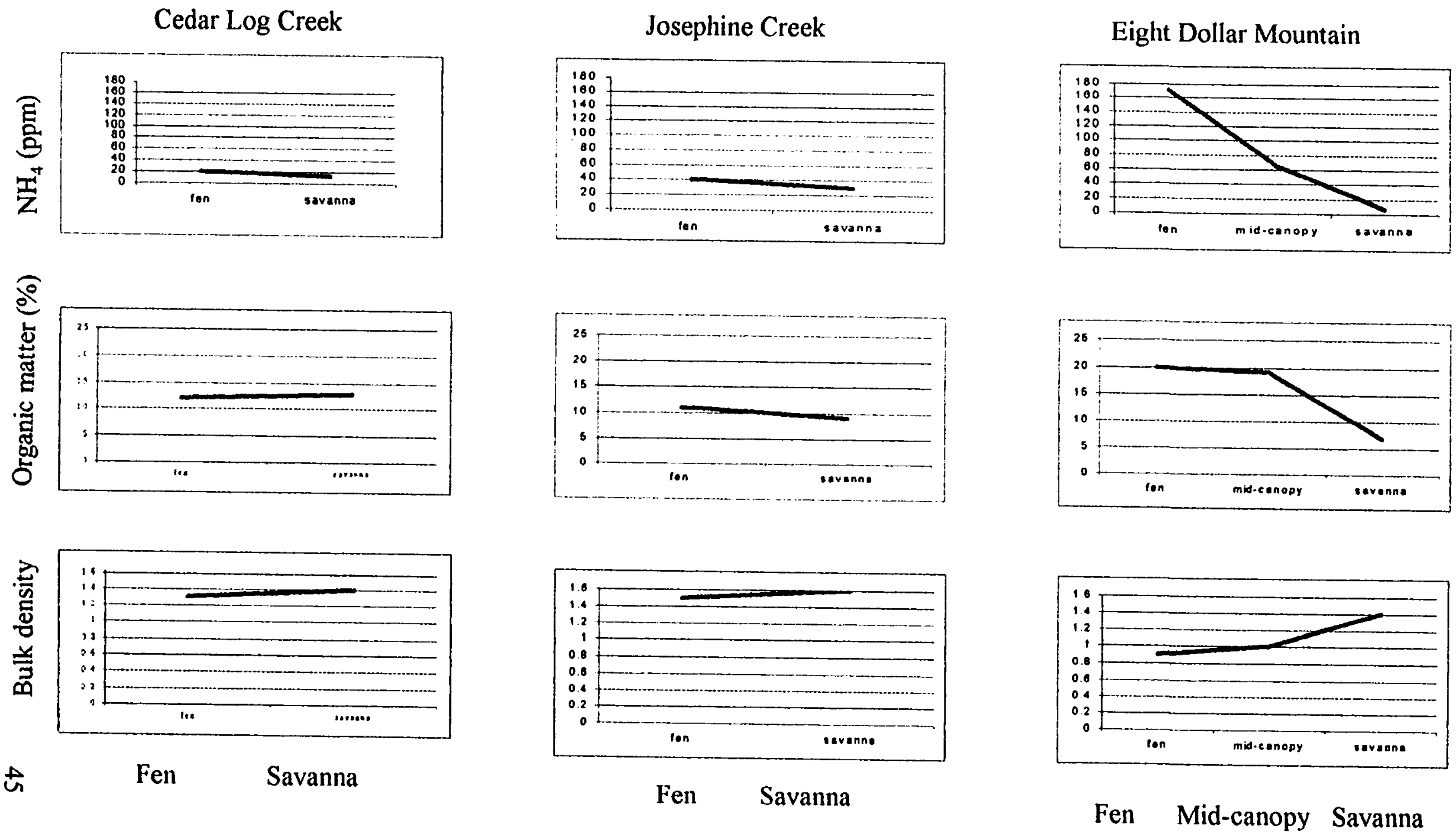
Flammable litter and branch dieback, both produced by savanna species, encourage frequent fire. In the event of a fire, litter is reduced and invading vegetation is eliminated, thus temporarily inhibiting soil development. By contrast, the absence of fire at the Eight Dollar Mountain site promotes the development of the current vegetation over successionally relevant time periods (i.e. approximately 100 years) causing litter decay and the development of a relatively nutrient-rich humus. This is commensurate with findings from studies on serpentine soils in the northeastern U.S. (Knox 1984, Latham 1993, Arabas 1997) where fire suppression and adequate moisture conditions promote litter accumulation and decomposition that raise soil organic matter and soil ammonium levels. At the Eight Dollar Mountain site, mid-canopy species may draw down moisture levels adjacent to the fen and facilitate faster decomposition contributing to higher soil ammonium levels. Earlier research has shown that surface plant distributions can influence below-ground variables and nitrogen cycling through differences in litter quality and quantity (Hobbie 1992), and in nitrogen poor systems small changes in the soil organic matter fraction can have large effects on ecosystem N dynamics (Wedin and Tilman 1990, Wedin and Pastor 1993).

In summary, the findings from the CCA on soil gradients yield information concerning the relative importance of spatial and environmental processes operating at stand and landscape scales in the *Darlingtonia* systems. Overall four main soil relationships exist with these serpentine sites (Figure 2.5): soil NH_4 increases, organic matter increases, and bulk density decreases with increasing time since fire which suggests that much of the pattern of plant distributions within a site can be attributed to soil ammonium and soil moisture while at a landscape scale, soil ammonium may be a larger factor determining the presence of communities within a site. In the 'nutrient availability' model (Figure 1.1), following hypothesis testing, succession without fire proceeds toward increasing soil ammonium levels. At a point of decreasing soil moisture levels presumably by mid-canopy plants, decomposition proceeds, the clay content of the soil gains a higher level of ammonium ions that are tightly held on the micelle and soil organic matter and soil ammonium levels in the soil increase.

Soil gradients likely play a role in maintaining the carnivorous fens of these sites. At the point of decreasing water-saturated soils, along the gradients between fen and savanna, soil nutrients increase, notably NH_4. This is particularly evident in these systems given increases in silicate clay content and subsequently higher levels of CEC. In a biogeochemical context, increases in clay contribute to the soil nutrient levels by subsequently elevating the NH_4 levels in the direction of the mid-canopy (Table 2.4).

Ultramafic rock contributes significantly to the CEC of serpentine soils through the decomposition of primary minerals to montmorillonite clays. Similarly, organic matter levels increase the number of micelles in the soil and reflect changes in bulk density from fen (low) to savanna (high) at the Eight Dollar Mountain site. In these serpentine soils, cation exchange sites are occupied primarily by Mg^{++} where the strength of cation adsorption (in decreasing order are: $Ca^{++} > Mg^{++} > K^+ = NH_4^+ > Na^+$

Figure 2.5. Summary of the four main soil relationships (NH_4, organic matter, bulk density and percent sand) for all plant communities at the Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain sites.



dictates that any open sites would accept Mg over NH_4^+. Consequently, soil moisture contributes to the nutrient status of saturated soils forcing the replacement of NH_4^+ with Mg^{++} and leaving the former in the soil solution and available for plant growth. Thus under particularly wet conditions, by nature of the strengths of adsorption sites, NH_4 would automatically be more available for plant growth.

These results support the hypothesis that, over time, accumulation of organic matter and clay content are essential to the development of a mid-canopy plant structure. While an increase in soil moisture across communities results in an increase in organic matter which slows decomposition and decreases bulk density, over time and in the larger context, a point of decreasing soil moisture levels by established mid-canopy plants facilitates decomposition. If succession proceeds with continued drying, then an increase in the decomposition process increases soil organic matter and leads to higher soil ammonium levels. As a result, the clay content of the soil gains a higher level of ammonium ions that are tightly held on the micelle. The role of the mid-canopy community appears to be mitigation of super-saturated conditions thus enabling the organic matter to decompose and contribute to soil ammonium levels. These soil-related variables and their subsequent levels are essential to the understanding of uniquely adapted systems and must be considered when determining the management of rare and endangered plant communities, as should the role of fire on the variables themselves. Knowledge of mid-canopy community age would likely support this hypothesis further. Incorporating post fire data from each site's plant community immediately after an experimental burn is needed to test the nutrient availability hypothesis further. Such research will make it easier to understand succession in these communities, predict how they vary over time, and foster enlightened management of uniquely adapted communities.

CHAPTER 3

ECOTONE CHARACTERIZATION OF JEFFREY PINE SAVANNA AND *DARLINGTONIA* FENS

Ecotones that separate savannas from wetland areas serve as important biogeochemical transition zones linking two distinctly different ecosystems (Johnston 1993) and promote structural and functional diversity across landscape gradients (O'Neill et al. 1986, Gosz 1993). These transition zones often reflect inherent abiotic distinctions (Johnston 1993) contributing to the development of unique plant and animal assemblages (Robertson et al. 1988, Petts 1990). Despite an increasing awareness of ecotones as functional components of landscapes (Naiman et al. 1989, Naiman and Decamps 1990, Holland et al. 1990, Gosz 1991, Hansen et al. 1992, Johnston 1993, Risser 1993), little is known about the mechanisms causing gradual changes in vegetation composition and structure (Kent et al. 1997) or the below-ground properties responsible for discontinuous vegetation patterns across these transitional areas.

Jeffrey pine (*Pinus jeffreyi*) savannas and *Darlingtonia* fens are part of a complex vegetation mosaic of serpentine soil-related plant communities in southwestern Oregon and northern California separated by distinct ecotones. Savanna vegetation gives way to fen vegetation which reflects unique soil requirements that favor contrasting plant growth forms such as carnivorous plants (*Darlingtonia californica),* grass understory, and a pine overstory, but disfavors plants of an intermediate stature, such as mid-canopy shrubs (Whittaker 1960). Few other ecosystems demonstrate such a comparable balanced diversity among permanent serpentine seeps, shallow xeric soils, the presence of heavy metals and limited nutrients, and where fire regime prohibits the formation of closed canopy forests (Whittaker 1960, 1961). Although a number of species are common to these communities, the majority of understory species includes large communities of *Darlingtonia* and sedges (*Carex mendocum)*, while scattered Jeffrey pine dominate the upper canopy (Whittaker 1954, Franklin and Dymess 1988).

The savanna-fen ecotones are unusually abrupt, both floristically and physiognomically, and can create high variability in the spatial characteristics of local plant communities. Perennial springs presumably maintain the savanna-fen ecotone in these southwestern Oregon ecosystems (Glasheen 1979, Stansell 1980), while the maintenance of similar boundaries for pine savannas in the southeastern United States is attributed to fire (Wells and Skunk 1931, Christensen 1977, Christensen 1985, Rome 1988). Although the size and shape of these communities can change dramatically in response to an array of environmental factors, the specific characteristics of these boundary ecotones are poorly understood.

This chapter characterizes and quantifies the physical aspects of the ecotones between Jeffrey pine savannas and *Darlingtonia* fens dominated by herbaceous species. I focus on the biological and physical characteristics of community boundaries rather than the more homogenous adjacent communities. Primarily, I test the hypothesis that discontinuities exist between these uniquely-adapted plant systems and that hydrophytic vegetation characterizes the boundaries. My main objectives are threefold:

- identify changes in community patterns from a *Darlingtonia californica/Pinus jeffreyi* association to a *Darlingtonia californica/Rhamnus californica/Pinus jeffreyi* association at the boundaries between these communities,
- determine if time since fire in part influences the distribution patterns of the individual plant species
- determine the role of perennial springs in shaping vegetation patterns across community boundaries.

Study Site Characteristics

I conducted my research in three savanna/fen ecosystems, each .5-1 ha, located within the Siskiyou National Forest in southwestern Oregon (42° 07' 30" N, 123° 37' 30" W; ≈ 700 m elevation) (Figure 2.2). All three sites are relatively undisturbed by human activity with the exception of fire which has been suppressed in one site for one hundred years.

The study area was located within the Josephine ultramafic sheet, a geologic region of southwestern Oregon (Figure 3.1). Both savanna and fen communities occupy soils characterized by unweathered rock fragments (lithosols) underlain by Jurassic-aged marine sediments (White 1971, Orr et al. 1992). Surface sediments consist of weathered serpentinite and partly serpentinized peridotite that results in a soil chemistry having: 1) high levels of exchangeable magnesium; 2) lower calcium levels; 3) low levels of nitrogen, phosphorus, and potassium; and 4) high concentrations of heavy metals (chromium and nickel) with molybdenum levels insufficient for normal plant growth (Walker 1954, Kruckeberg 1984).

Figure 3.1 Study sites Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain located on the ultramafic geology (purple shaded) in Josephine County, Oregon. Figure from Ramp and Peterson (1979).

I chose my study sites for their distinct ecotones, unique vegetative requirements, and burn histories. The ecotones common to these communities represented discontinuities between different vegetation forms with an emphasis on biological interaction (a tension zone) between adjacent communities (Clements 1916, van der Maarel 1976). In this sense, ecotones differ from simple edges or boundaries of plant communities. Two of the study sites, Cedar Log Creek and Josephine Creek, included pine savanna and fen plant communities while the third site, Eight Dollar Mountain, was forested adjacent to a mid-canopy shrub community. Time since last fire was: five (Cedar Log Flat), eight, (Josephine Creek), and approximately one hundred (Eight Dollar Mountain) years respectively (Ulloa 1998). The Eight Dollar Mountain fen site combined the longest time period since fire, an open canopy forest within 100 m of the center of the fen (the mid-canopy shrub community), and a major area of species endemism. All three fen ecosystems reside on serpentine soil and ranged from 4 - 12 m in width and 300 - 600 m in length while the savannas surrounding the fens are expansive (1-300 km^2). All three sites are located on moderate slopes (2-10 %).

Savanna vegetation is dominated by Jeffrey pine with a floristically-rich herbaceous ground cover dominated by *Festuca idahoensis* grasses (Borgias and Rudd 1999). This vegetation occurs on shallow red soils with rocky surface horizons and lower stony profiles that vary in surface depth depending on age of the laterite, amount of erosion or surface movement to which it has been subjected, degree of fracturing, history of precipitation in the area, vegetative cover, and composition and alteration of the parent rock (Ramp and Peterson 1979). The upper surface (depth from > .3 m to

30 m) is typically dark, reddish-brown soil with minor organic residue and abundant to minor amounts of iron oxide pellets and chromite grains (variable amounts of relatively unweathered peridotite boulders) (Ramp and Peterson 1979), slightly acidic in pH (6.6 to 6.8), and low in nutrients (Walker 1954, Kruckeberg 1984). Beneath this, a yellow-brown soil with variable amounts of partly weathered peridotite occurs. The subsequent soils from the weathering of this metamorphic rock give rise to mesic, mollic Haploxeralfs especially in the savanna communities. Generally these soils are shallow gravelly clay loams, high in bases. Bedrock is generally found within one meter of the surface.

The fens are dominated by *Darlingtonia* and *Carex* and lack tree canopy species. Similar to the savannas, the fens reside on serpentine soil and contain a floristically-rich subdominant herbaceous ground cover of local and regional endemics. Unlike the savanna soils, fen soils range from a sandy loam to a clay in the subsurface horizon with direct evidence of ground water input. Typically the fens are inundated in late fall and winter, and experience drying in summer with increased evapotranspiration rates. During drought years, savanna fires burn into the fens and thus are likely to have an important role in the development of vegetative structure and composition (Agee 1991, Frost 2000). Fire suppression and landscape fragmentation has eliminated most extensive lightning-ignited fires in the study area (Frost 2000). The 1986 burn in the Josephine Creek site was a prescribed ground fire that removed all flammable herbaceous biomass and most of the accumulated litter; the fire scorched only the lower needles of pines (Borgias and Beigel 1998). The 1996 burn in the Cedar Log Creek site was also a prescribed fire that burned over both communities

(Borgias and Beigel 1998). Both burns occurred during the late summer corresponding to the natural fire regime for the area (Borgias and Beigel 1998). The Biscuit fire of 2002 did not burn any of the three sites in the study area.

The shrub community present at Eight Dollar Mountain is characterized by *Rhamnus californica* and *Rhododendron occidentalis* while scattered Jeffrey pine and incense-cedar constitute the upper canopy (Whittaker 1954, Franklin and Dyrness 1988). This shrub community forms a narrow, 15 m band around the fen before it joins with the savanna. The area is intermediate in both hydroperiod and organic layer, slightly more than the savanna, and slightly less than the fen, but still saturated for most of the year.

Field Sampling

I used the same six transects as in Chapter 2, oriented perpendicular to community ecotones and presumed environmental gradients (Knapp 1984, Palmer and Dixon 1990) at each of the three study sites in order to locate vegetation discontinuities (Figure 2.3). Each transect contained at least twelve 1 m^2 vegetation quadrats, and was replicated six times at each site. Transects at the Eight Dollar Mountain site extended an additional 15 m to ensure sampling of the shrub to savanna ecotone. Sample plot size was increased to 5 x 5 m in both the shrub and savanna communities. Sampling was arranged as a randomized complete block design with six transects in each of three separate blocks (sites). Sampling at the Eight Dollar Mountain site included an additional 72 sample plots, to include the mid-canopy shrubs. Vegetation samples were collected from a total of 227 quadrats over 18 transects. Collectively, the transects contained 2,682 m^2 of sampling area. Each quadrat was sampled for: % cover of each species in the quadrat and the circumference of the largest stems found at 2 cm height, and any evidence of animal, insect, or human activity.

Vegetation data were recorded during the peak of the growing season (June, July, and August) and again in late summer (September and October). Plants were identified to species level, wherever possible followed Jepson (1968). Some plants remained in a vegetative state throughout the season and were identified at the genus level resulting in the grouping of several species. Percent cover for each species was visually estimated using one of six cover classes (<1%, 1-4%, 5-25%, 26-50%, 51-75%, and 76-100%). Each species was noted for its presence and catalogued according to its: 1) life form, 2) life history (perennial versus annual), 3) phenological observations, 4) native versus nonnative status, 5) vigor, and 6) distance to the ecotone. I also noted habitat preferences for each taxon, for example edge versus community interior and habitat characteristics (aspect, slope angle, orientation, elevation, air temperature, relative humidity, and soil surface characteristics). Along each transect I recorded: 1) cover of all plant species present within each $1m^2$ quadrat and an estimated overhead foliage in both mid to upper canopies, using an imaginary $1m^2$ vertical column and 2) vigor of all ground cover, shrub, and tree species, using a dichotomous system of 0=dead and 1=live. I did not distinguish among all grass species since individual plants were often dessicated and difficult to identify, however I distinguished between grass genera.

Soil variation across community boundaries was assessed by collecting soil samples along transects within each site during June, July, August and September.

One core (12 cm deep and 3 cm in diameter; 340 cm^3) was taken from each 1 m^2 plot for chemical and physical characteristics: NO_3, NH_4, soil moisture, bulk density, pH, CEC, soil texture, and organic matter. In shrub areas where soil variability was high, cores were taken randomly within a plot and composited. All soil cores were consistently taken between shrub root zones. Soil profiles were described in each community at each site and described following Soil Conservation Survey (SCS) soil survey guidelines (Borine 1983).

Soils collected for nutrient analysis were air dried at 70° C for 48 h and passed through a 2 mm sieve to remove stones and coarse roots. All subsequent analyses were performed on this sieved material. Soil pH was determined in a 1:1 soil-water paste (McLean 1982). Soil ammonium and nitrate were extracted in 1:10 soil 2 N KCl solution using the Bremmer method (Bremmer et al. 1965). Extracts were analyzed colorimetrically on a Technicon II auto analyzer using techniques described by Lachat (1989). Physical soil characteristics (sand, silt, clay) were determined by pipette according to MacKeague (1978). Organic matter content was determined by loss on ignition (Shulte and Hopkins 1996) and cation exchange capacity (CEC) by extraction with 1 N ammonium acetate solution (Rhoades 1986). Soils were also analyzed gravimetrically for soil moisture according to Western States Laboratory Proficiency Testing Standards.

Water samples, conducted on the same six soil transects, were collected in the fens only for NO_3 (nitrate) and NH_4 (ammonium) content, pH, DO (dissolved oxygen), temperature, conductivity, and redox potential to determine whether the fens acted as sinks for either nitrate or ammonium. Water chemistry analyses were performed at Portland State University.

Data Analyses

I used several methods to describe and compare patterns of change in vegetation and environmental factors across the ecotones in these communities. An initial stratification of vegetation into two or three classes (savanna, fen, or shrub community) was made on each transect using the two-way indicator species analysis (TWINSPAN) (Hill 1979) (Appendix A). This numerical classification technique groups vegetation samples based on floristic dissimilarity. An ordination of vegetation abundance data (all transects combined) was performed using detrended correspondence analysis (DCA) (Hill and Gauch 1980) to determine compositional similarity among plots and to detect discrete clusters of vegetation. This technique is comparatively free of distortion for samples with high beta diversity (high community differentiation) (Gauch 1982). Distributions of species abundance relative to soil properties (soil texture, soil moisture, CEC, bulk density, NO_3 and NH_4, and organic matter) were explored with canonical correspondence analysis (CCA) using CANOCO v.3.1 (ter Braak 1987) for all 227 plots plus the additional indices of water NO_3 and NH_4.

I used two methods to determine the presence of hydrophytic vegetation and the boundaries of communities, both of which relied on the hydrophyte list developed with the wetland indicator status of plant species (Reed 1988)(Tables 3.1 and 3.2). The first method was a measure of dominance using the "50% rule" (National Research Council 1995) as the dominance ratio (Wakely and Lichvar 1997). This method identifies hydrophytic vegetation if >50% of the 10 most dominant species (as determined by abundance) has a wetland indicator status of facultative (FAC), facultative wetland (FACW), or obligate (OBL). I used a weighted average index as a second method; a modification of the prevalence index used in the 1989 federal wetland delineation manual (USDA 2002) based on the indicator status (OBL=1, FACW+=2, FACW=3, FACW-=4, FAC+=5, FAC=6, FAC-=7, FACU+=8, FACU=9, FAC-=10, UP=11) of each species in the quadrat weighted by its abundance (Wentworth and Johnson 1986, Wentworth et al. 1988). The use of both methods, the 50% rule and the prevalence index, characterizes the plant community as a whole through its species composition (NRC 1995). *A priori* information regarding these communities indicated threshold values to be in the range of 3 - 5 (Wentworth and Johnson 1986).

Twelve environmental variables (soil moisture by volume, soil NO_3, soil NH_4, soil texture (sand, silt, and clay), bulk density, pH, organic matter, CEC, water NO_3 and water NH_4) were reduced to principal components using PCA (ter Braak 1986) for each quadrat of each transect. Both water chemistry variables (NO_3 and NH_4) were retained in the final analysis and were used to indicate ecotone locations at each of the sites. Median differences in vegetative and environmental variables within communities and across sites were compared non-parametrically using Kruskal-Wallis H-test (1968) to determine if they represented the same statistical populations.

I then used a moving split-window technique to identify vegetation discontinuities in the principal components analysis (PCA) axis scores (Webster and Wong 1969, Ludwig and Cornelius 1987, Johnston et al. 1992). Boundary definition involves

Table 3.1. Species data for study sites. Numbers represent values recorded during the growing season. All variables listed were included in the CCA (n=227).

Genus	**Eight Dollar Mountain**	**Josephine Creek**	**Cedar Log Creek**
	Range (% cover) (median)	Range (% cover) (median)	Range (% cover) (median)
Darlingtonia	2-90 (25)	8-99 (60)	1-80 (30)
Tofieldia	0	1-10 (3)	1-40 (15)
Arctostaphylos	2-65 (15)	5-10 (7.5)	10-25 (15)
Agrostis	1-55 (5)	5-15 (5)	3-35 (10)
Carex	1-90 (35)	1-98 (20)	5-75 (10)
Rudbeckia	7-95 (30)	1-5 (3)	2-45 (17.5)
Rhododendron	1-99 (50)	1 (0)	2-45 (12.5)
Ceanothus	1-5 (2)	5-40 (0)	1-30 (15)
Hastingsia	3-90 (20)	1-90 (15)	10-20 (15)
Sanguisorba	1-45 (17.5)	1-20 (3)	2-55 (12.5)
Pinus	5-199 (50)	2-50 (12.5)	2-100 (25)
Festuca	10-90 (75)	5-30 (20)	3-75 (17.5
Calocedrus	1-60 (5)	0 (0)	5-25 (10)
Rhamnus	1-100 (10)	0 (0)	10-65 (25)

Table 3.2. Hydrophytic indicator species for the Eight Dollar Mountain, Cedar Log Creek, and Josephine Creek study sites (USDA 2002).

Species (habitat type/location in site)	**Hydrophytic indicator**
Rhamnus californica (shrub/mid-canopy)	Facultative
Rhododendron occidentalis (shrub/mid-canopy)	Facultative
Pinus jeffreyi (tree/savanna)	Upland
Ceanothus pumilus (shrub/savanna)	Upland
Rudbeckia californica (perennial herb/fen)	Facultative U
Festuca idahoensis (graminoid/savanna)	Upland
Hastingsia bracteosa (perennial herb/fen)	Obligate
Sanguisorba macrophylla (perennial herb/fen)	Facultative W
Tofieldia glutinosa (perennial herb/fen)	Obligate
Arctostaphylos viscida (shrub/savanna)	Upland
Calocedrus decurrens (tree/mid-canopy and savanna)	Upland
Agrostis spp. (graminoid/fen)	Facultative
Eriophorum crininger (perennial herb/fen)	Obligate
Carex mendocum (graminoid/fen)	Facultative W
Darlingtonia californica (perennial herb/fen)	Obligate

locating a discontinuity within a theoretically continuous change of vegetation. The window (a four-quadrat window width) was placed over a data set of sequential quadrat values in a transect. Dissimilarity values between each window half (squared Euclidean distance [SED], Ludwig and Reynolds 1988) was calculated, and the window was then moved along the transect to produce a series of dissimilarity values between window halves along the transect to estimate autocorrelation (i.e., the greater the distance, the greater the dissimilarity). Distance plotted against transect position indicated abruptness in the rate of changes among species and environmental variables.

Results

Vegetation characteristics across ecotones

Vegetation patterns changed in all study sites (Figures 3.2, 3.3, 3.4). I recorded a total of 15 species in the 6 transects at each of the three sites. Five species (33%) were perennials, two were trees, four were shrubs and two were grasses. Ten of the 15 species (66%) occurred on over half of the transects in two sites, Cedar Log Creek and Josephine Creek, and contributed to > 30% of one or more community frequency values in all sites. All species were present at Eight Dollar Mountain where 27% of the species were obligate hydrophytes (OBL), 13% were facultative wetland (FACW), 20% were facultative (FAC), 7% were facultative upland (FACU), and 40% were upland (UP). Vegetation was significantly hydrophytic in all three fens (54% OBL) while the savannas were comprised of upland dominants (70% UP).

Figure 3.2. Species composition across the savanna and fen communities at Cedar Log Creek.

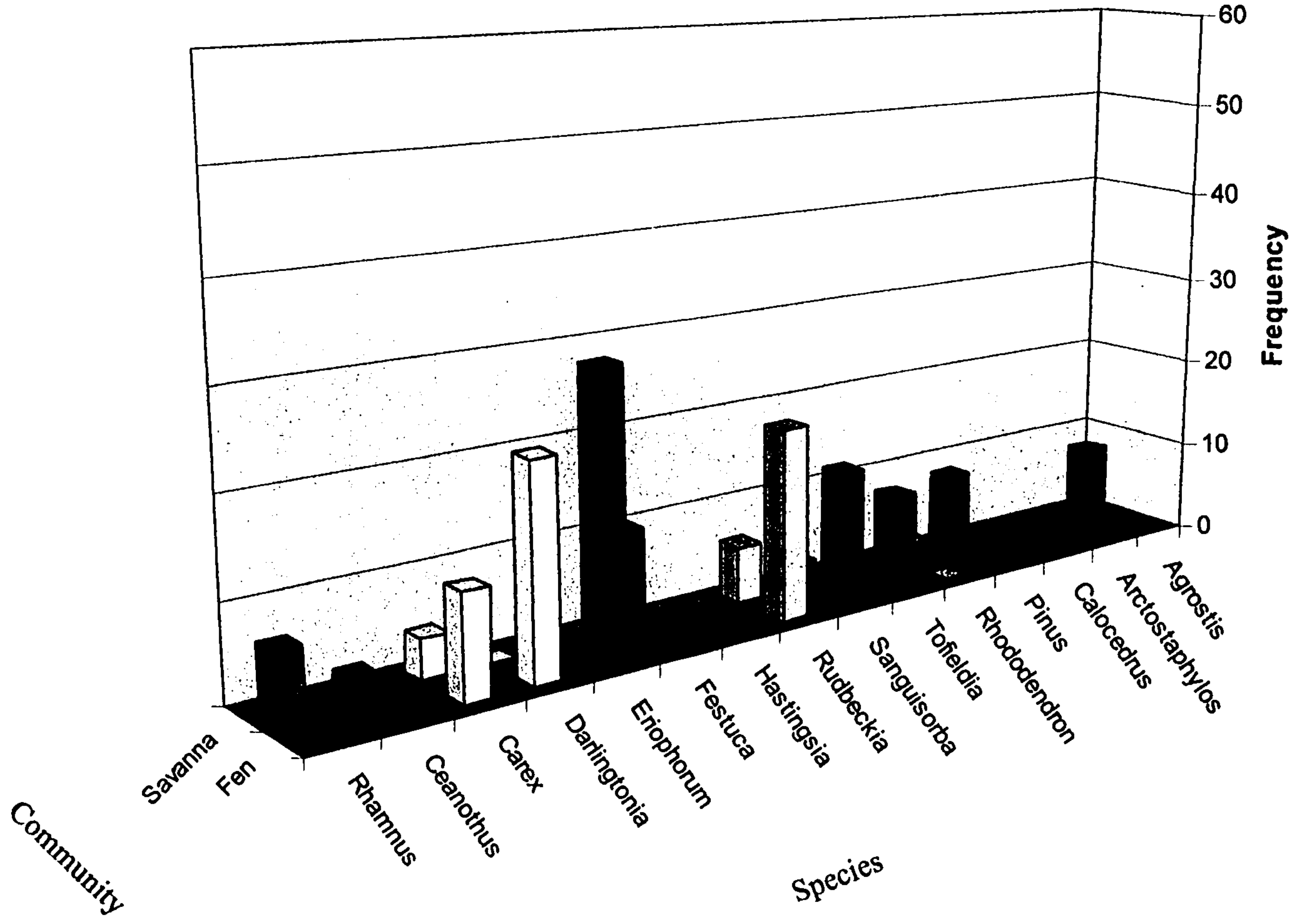


Figure 3.3. Species composition across the savanna and fen communities at Josephine Creek.

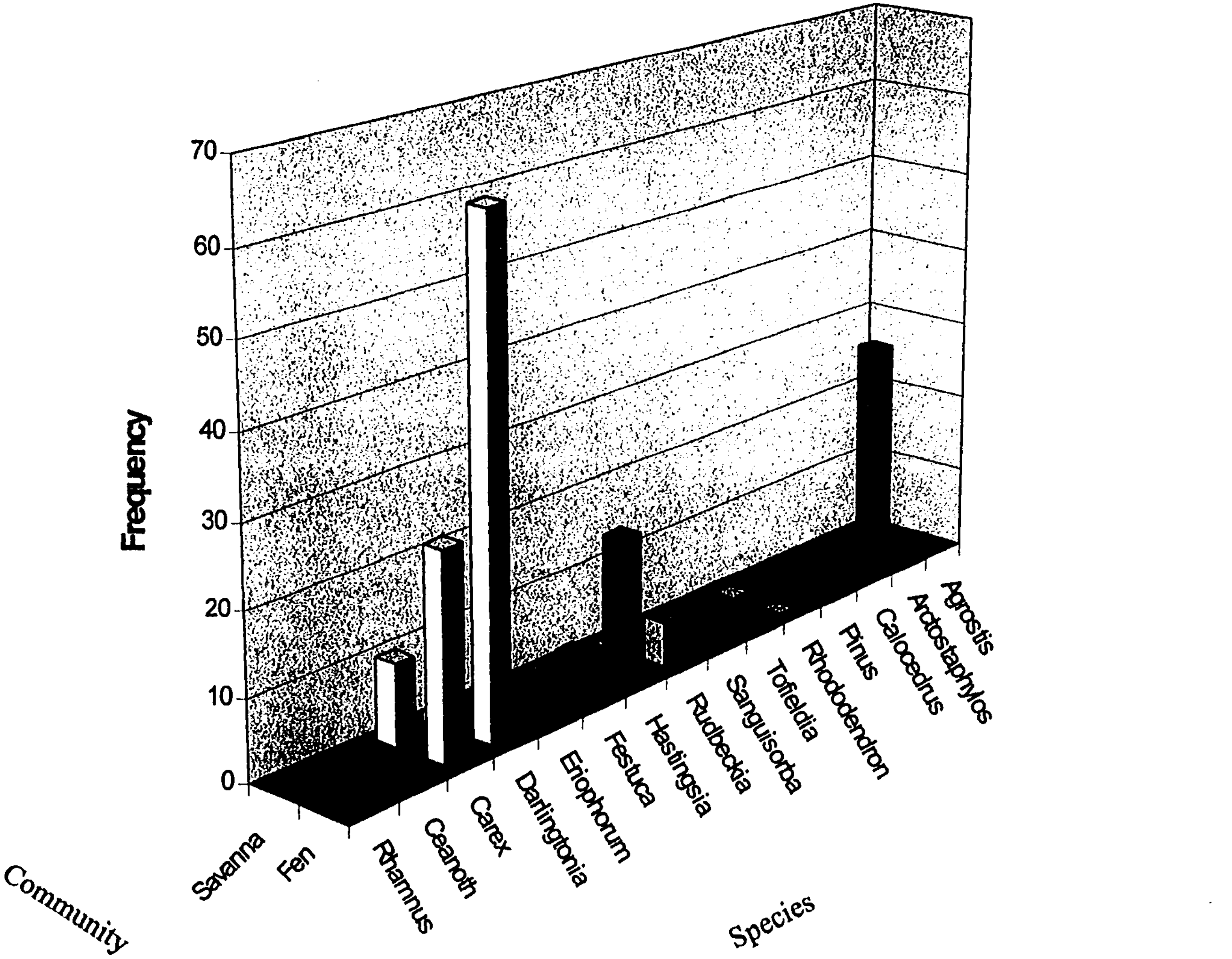
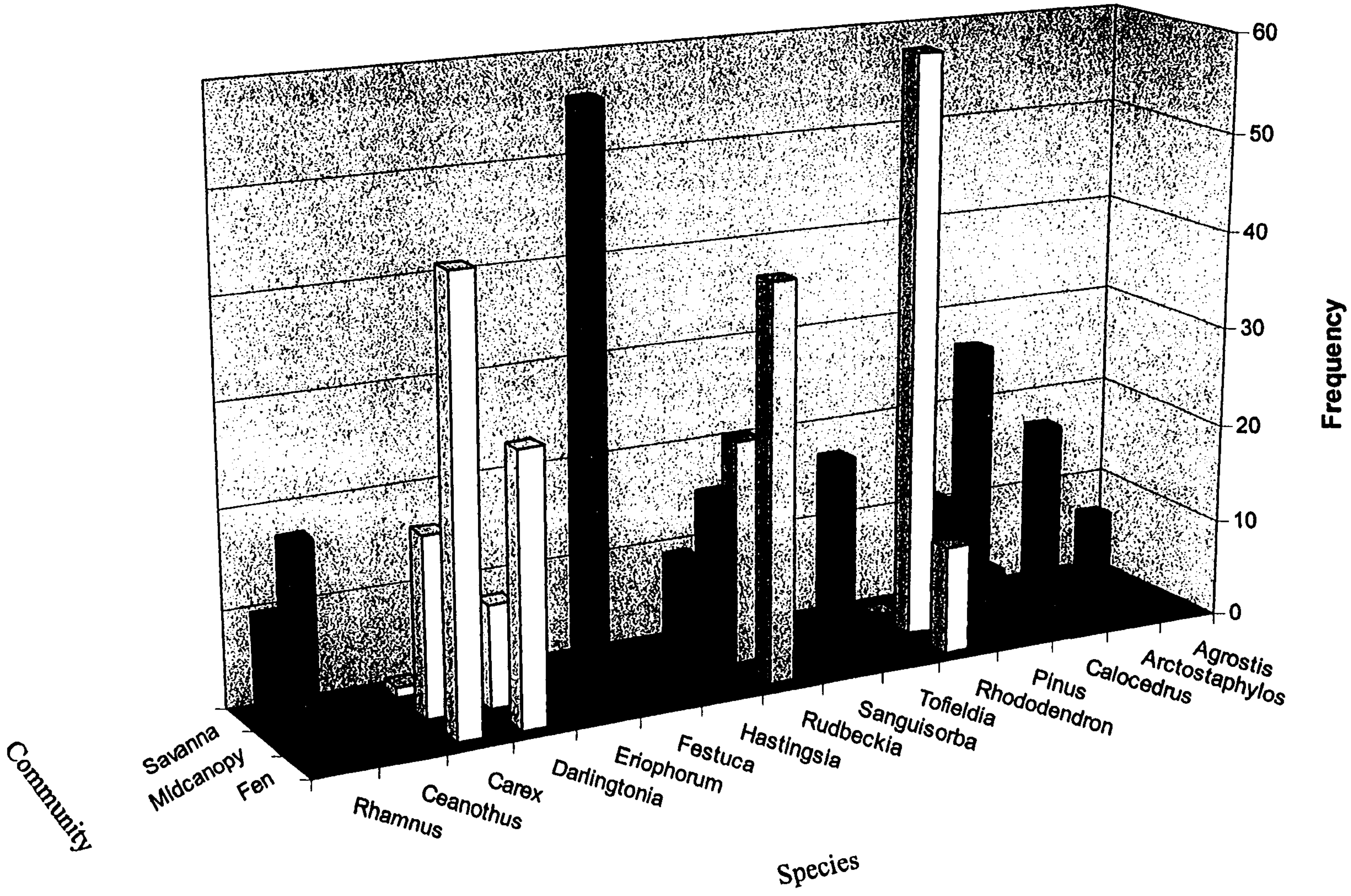


Figure 3.4. Species composition across savanna, mid-canopy (shrub), and fen communities at Eight Dollar Mountain.



Differences in median percent cover were greatest between communities at each site, with fens having a greater percent cover than the savannas. *Darlingtonia, Rudbeckia,* and *Sanguisorba* were the most common fen species. *Darlingtonia, Hastingsia, Rudbeckia*, and *Carex* represented one half of the total plant cover while *Festuca, Pinus jeffreyi*, and *Arctostaphylos* (LManzan) dominated the savanna at the Eight Dollar Mountain site. The dominant mid-canopy shrub species at the Eight Dollar Mountain site were *Rhamnus* (Chokche) and *Rhododendron. Sanguisorba, Rudbeckia*, and particularly *Carex* were common in the adjacent communities at all three sites.

Both the dominance ratio for hydrophytic vegetation and the species prevalence index values (based on weighted averages) were consistent for savanna and fen communities at all three sites. Non-parametric median comparisons (Kruskal-Wallis H-test) show fens differed significantly ($p \leq 0.001$) from savannas for all three sites (Chapter 2). Differences between the dominance ratio and the prevalence index identified the mid-canopy quadrats at Eight Dollar Mountain (National Research Council 1995, Wakely and Lichvar 1997) indicating that the indices reliably separated hydrophytic from nonhydrophytic plant communities. Floristic similarity in each community, based on 15 indicator species, changed significantly ($p \leq 0.001$) from fen to savanna communities in the Cedar Log Creek and Josephine Creek sites while at Eight Dollar Mountain the significant ($p \leq 0.001$) change was from savanna to mid canopy shrub community. Variations in slope had no impact along the transects at the sites.

Carex was an important and spatially variable component of ground cover species at the three sites. At Cedar Log Creek and Eight Dollar Mountain, *Carex* decreased toward the savanna end of the moisture gradient along the transects. However, in the Josephine Creek site, the persistence of *Carex* obscurred differences between savanna and fen communities in 30% of the quadrats (Figures 3.2, 3.3, 3.4).

Boundary Detection

The initial stratification of communities across the ecotones using TWINSPAN identified vegetation boundaries between the savanna and the fen in all 18 transects at the three sites and between the savanna and the mid-canopy shrub communities in the six transects at Eight Dollar Mountain (Appendix A). The moving window analysis of PCA scores showed sharp peaks of environmental discontinuity within the transects at Eight Dollar Mountain more closely associated with soil NH_4 than the hydrologic boundary (Figures 3.5 and 3.8). All of the transects at Josephine Creek and Cedar Log Creek, but only in 30% of the transects of Eight Dollar Mountain (Figures 3.6, 3.7, and 3.8), showed high contrast toward the center of the fen community. Broader contrast peaks along some transects (Figure 3.6, transects a, c, and f, and Figure 3.8, transects d and f) reflected a more gradual change and more overlap among adjacent communities.

In the second stratification, distinctly separated groups of vegetation (fen and savanna) were apparent in the DCA for Eight Dollar Mountain; a strong dissimilarity gradient among quadrats occurred between the wettest and the driest sites, indicating the presence of the mid-canopy shrub community. Savanna and fen quadrats were clustered with little separation by either axis (Figure 3.9). These plots were dominated

Figure 3.5. Generalized plan view of the Eight Dollar Mountain site with a cross section of the transect below. The moving window results illustrate the hypothesized location of high contrast values.

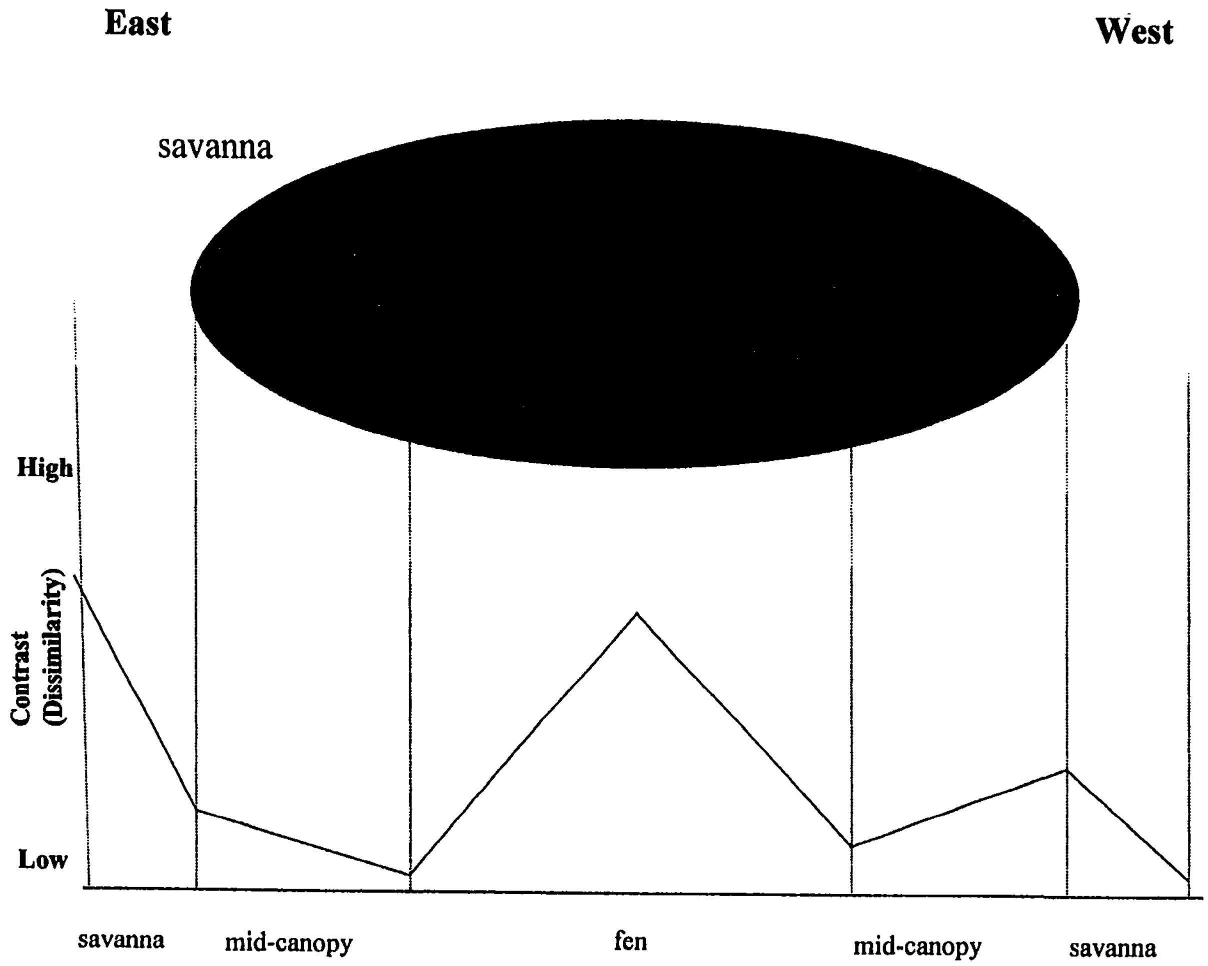
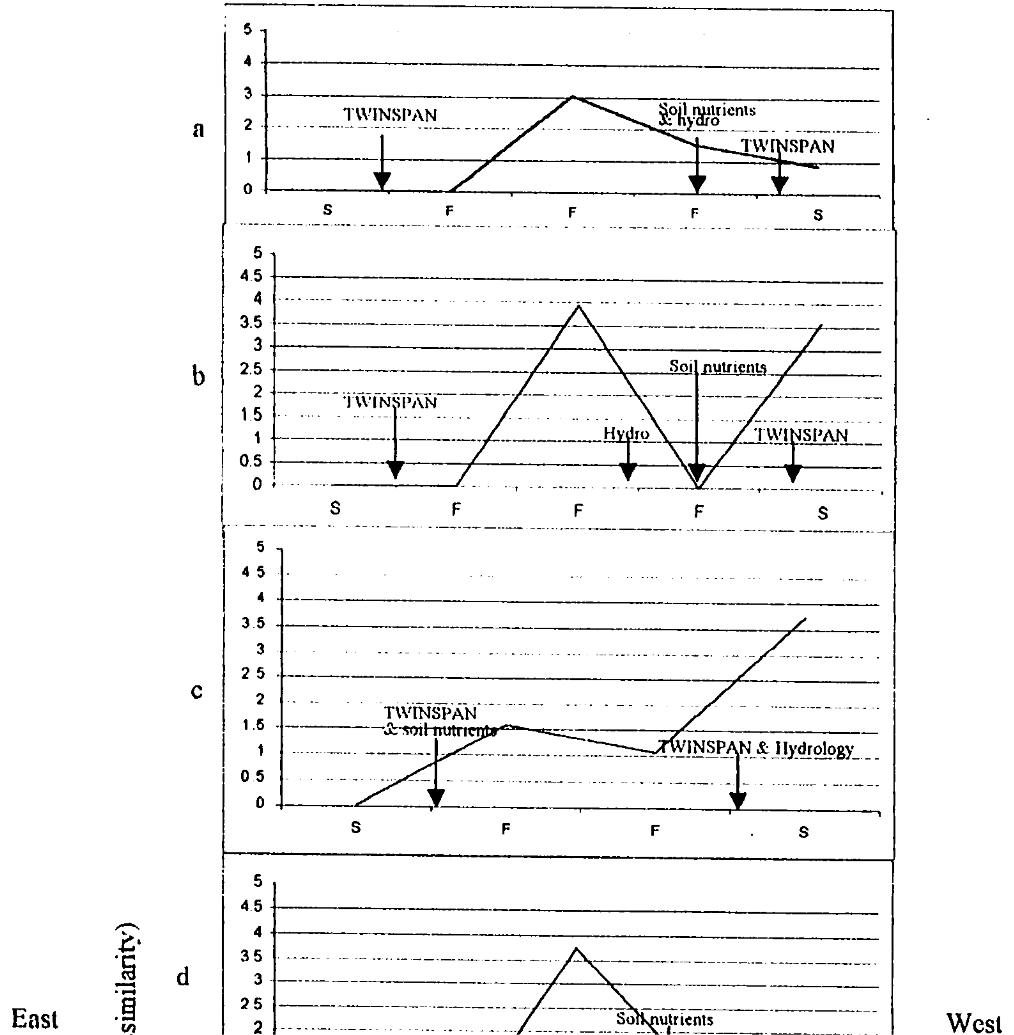
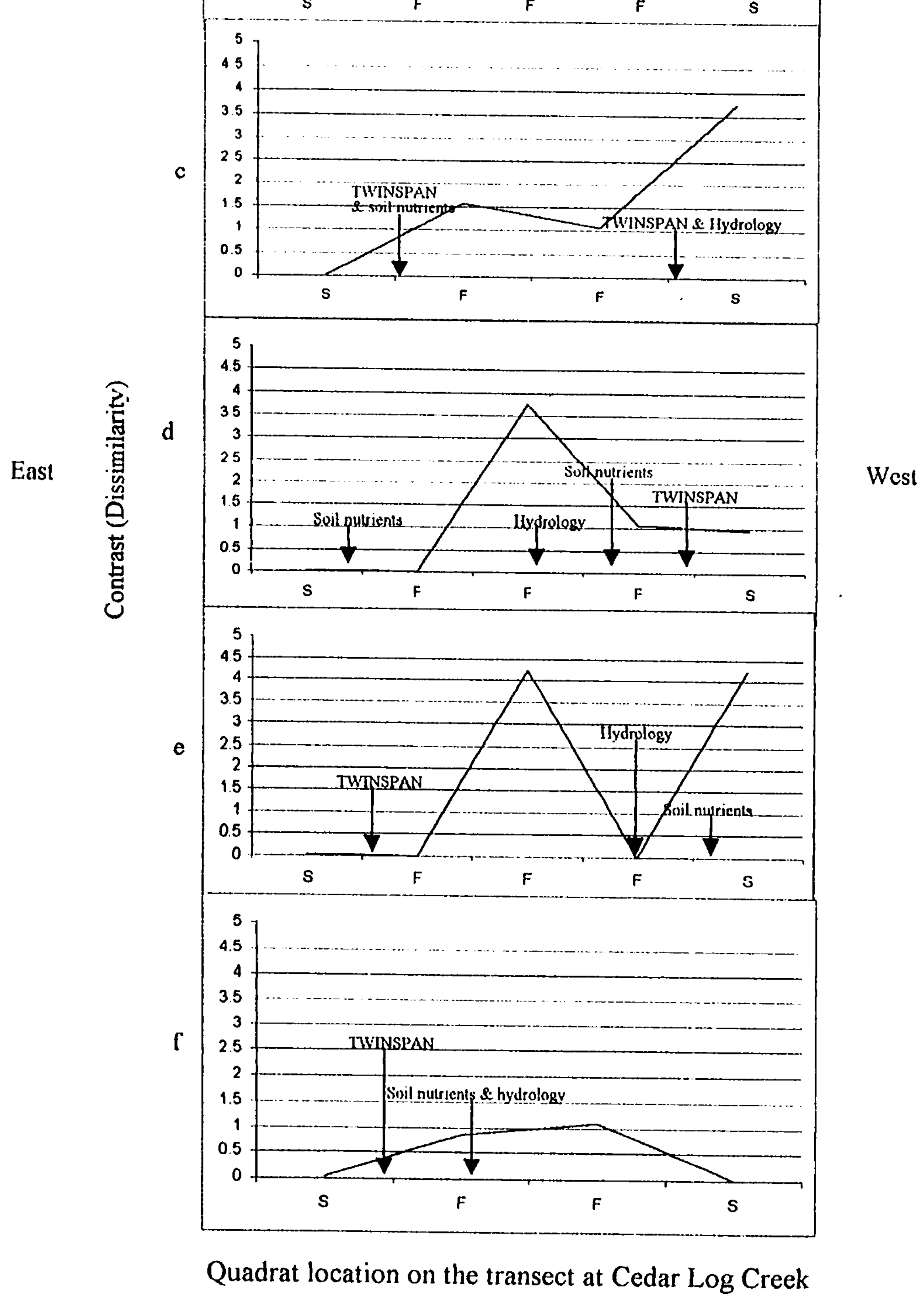


Figure 3.6. Environmental and vegetation discontinuities for each transect (a-f) of the Cedar Log Creek site. Arrows on the x-axis indicate hydrology (1st CCA axis) and soil moisture (2nd CCA axis), and vegetative boundary (TWINSPAN). Peaks in moving window analysis (squared Euclidean distance) indicate abrupt changes (high contrast values) in PCA scores. S=savanna, F=fen

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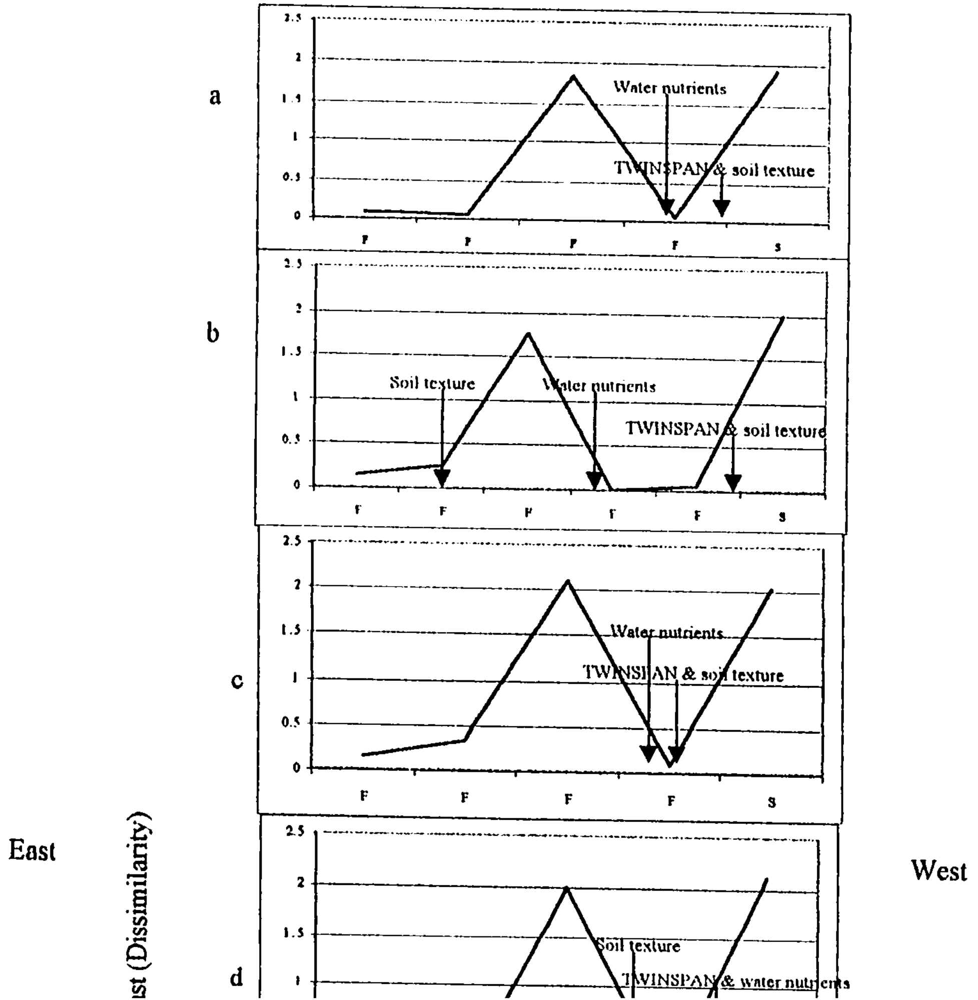
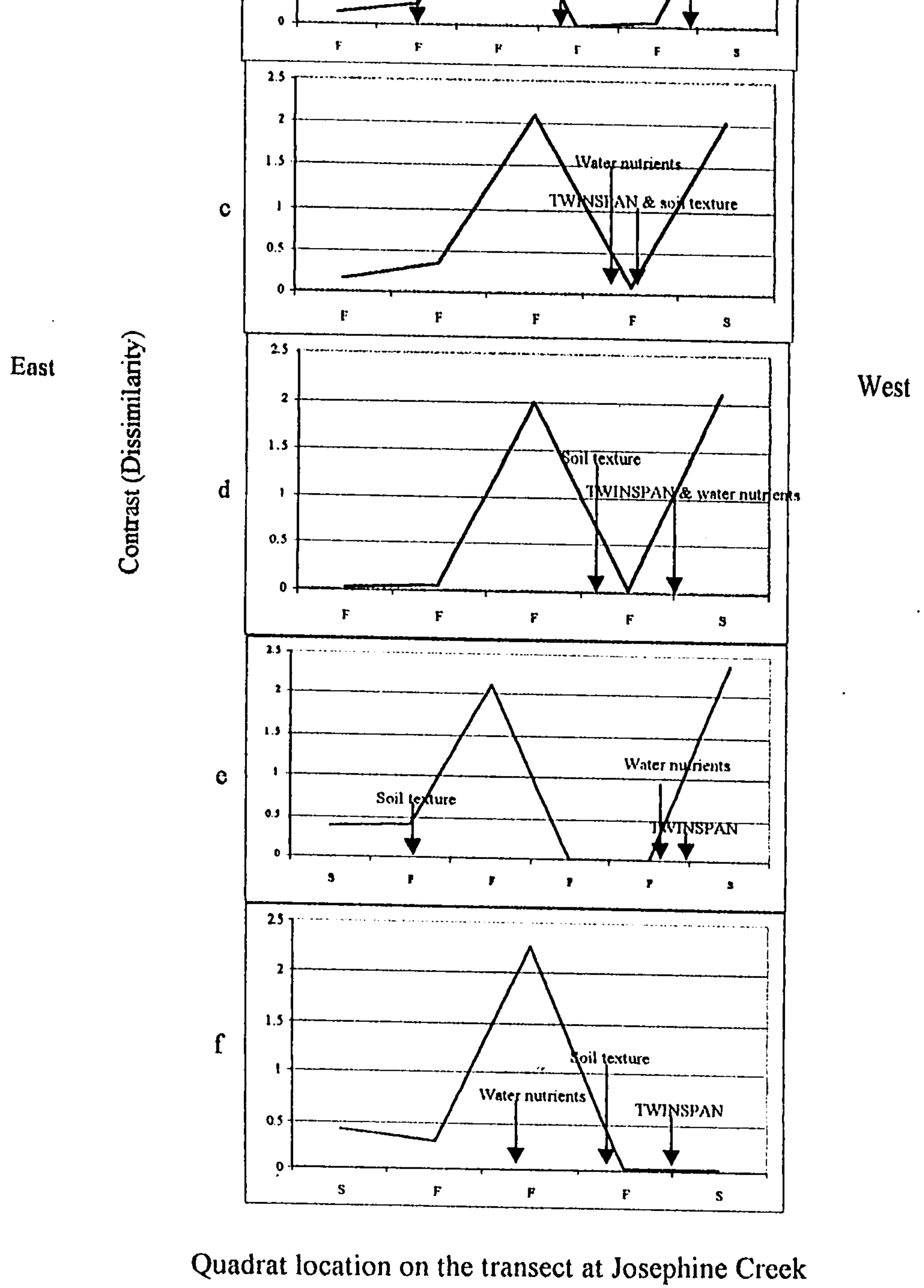
Quadrat location on the transect at Cedar Log Creek

Figure 3.7. Environmental and vegetation discontinuities for each transect (a-f) of the Josephine Creek site. Arrows on the x-axis indicate water NO_3 (1st CCA axis) and soil texture (2nd CCA axis) and vegetative boundary (TWINSPAN). Peaks in moving window analysis (squared Euclidean distance) indicate abrupt changes (high contrast values) in PCA scores. S=savanna, F=fen

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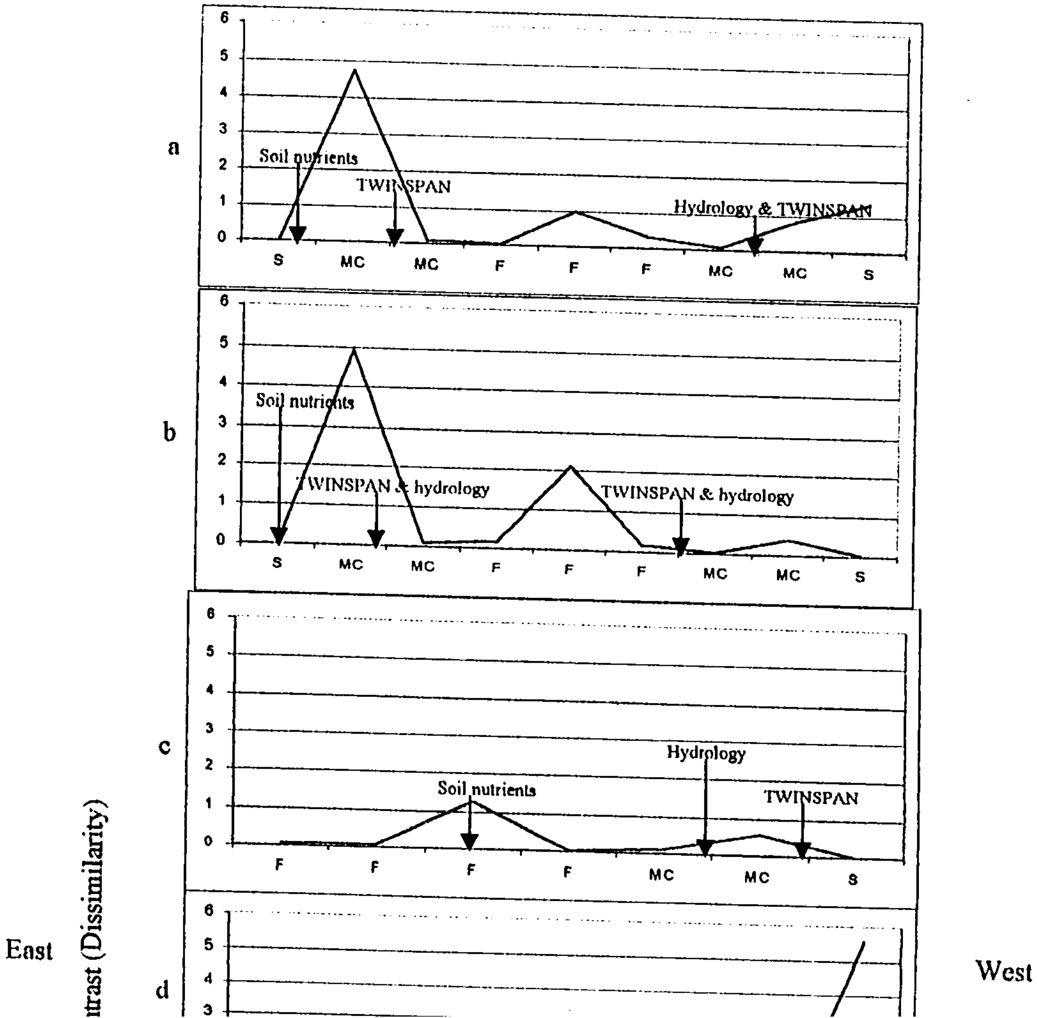
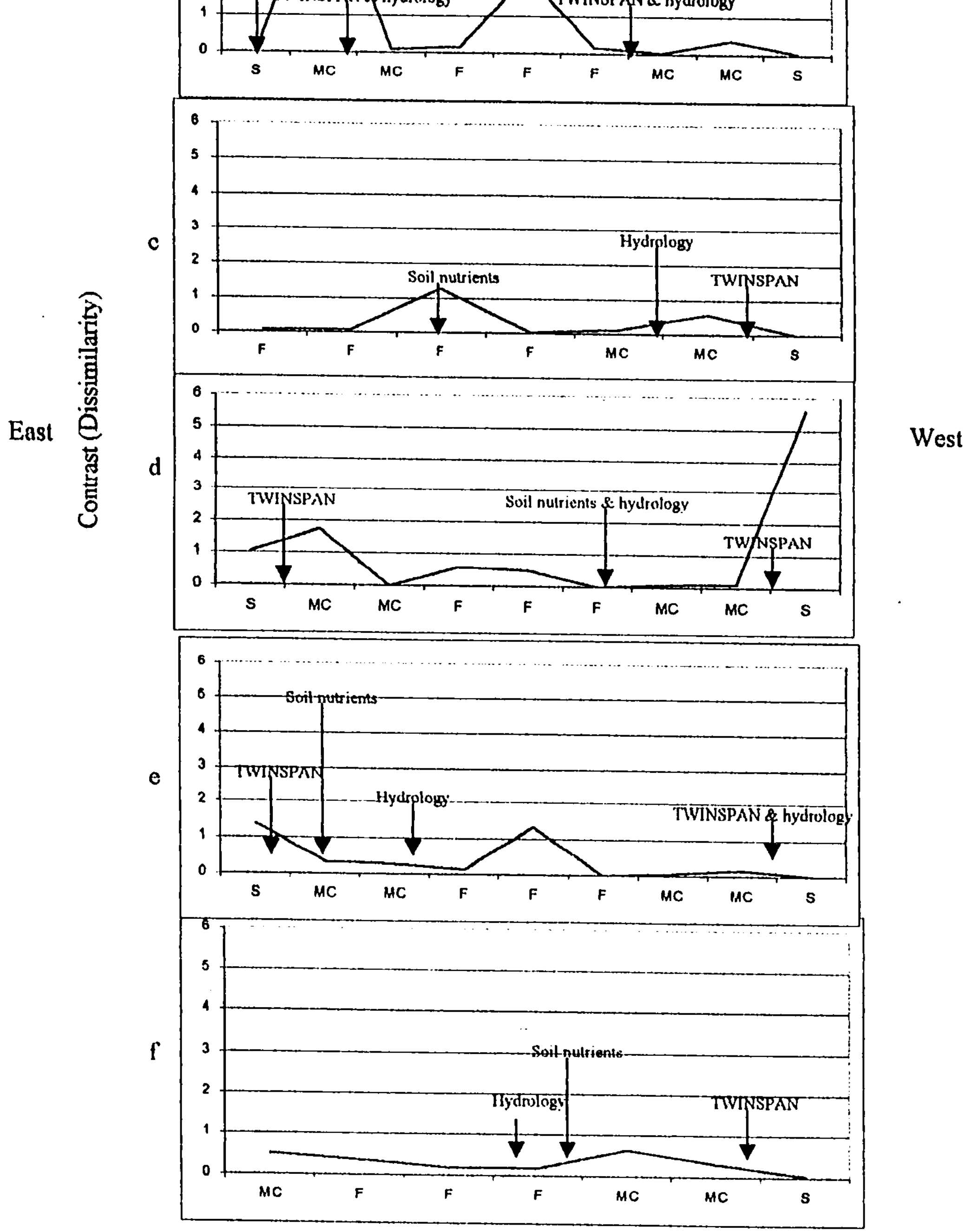
Quadrat location on the transect at Josephine Creek

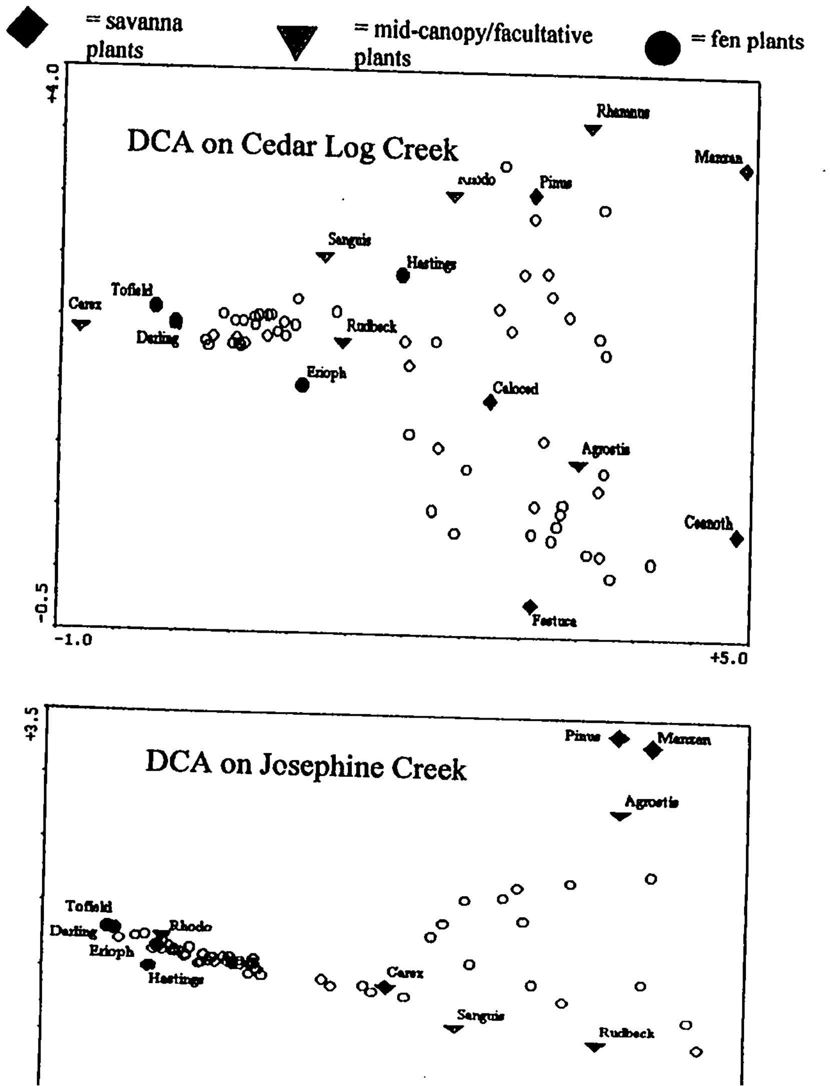
Figure 3.8. Environmental and vegetation discontinuities for each transect (a-f) of the Eight Dollar Mountain site. Arrows on the x-axis indicate soil nutrients (1st CCA axis) and hydrology (2nd CCA axis) and vegetative boundary (TWINSPAN). Peaks in moving window analysis (squared Euclidean distance) indicate abrupt changes (high contrast values) in PCA scores. S=savanna, F=fen, MC=mid-canopy

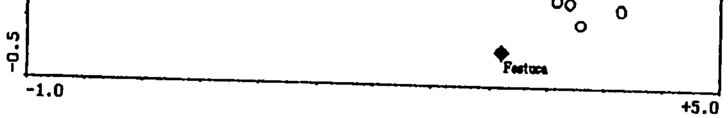


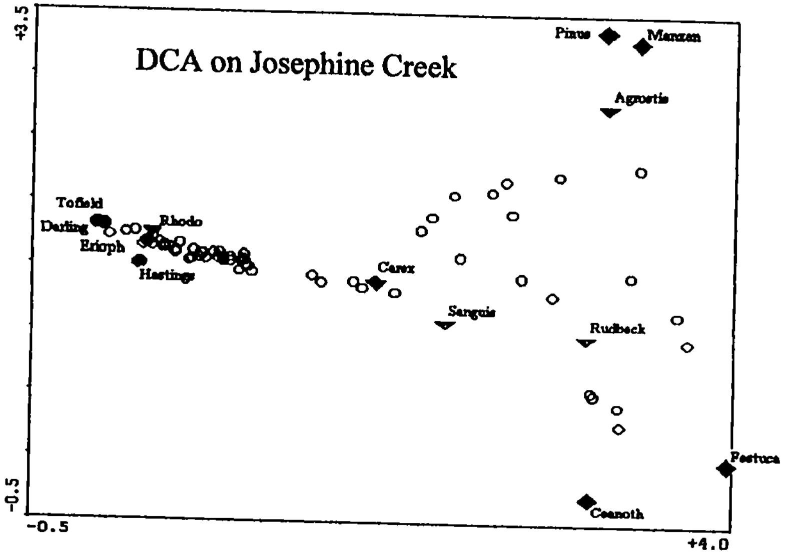


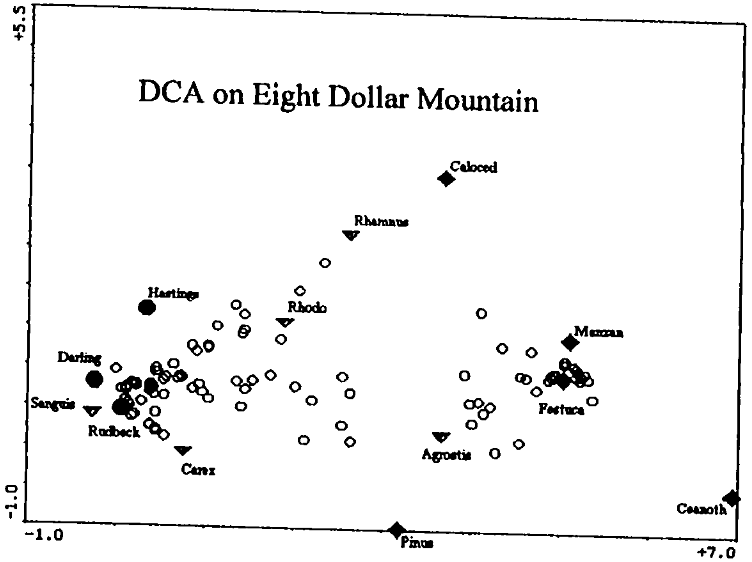
Quadrat location on the transects at Eight Dollar Mountain

Figure 3.9. Detrended correspondence of vegetation (DCA) at each site indicating community separation.




-0.5
-1.0
+5.0
Festuca


DCA on Josephine Creek
+3.5
-0.5
-0.5
+4.0
Pinus
Manzan
Agrostis
Tofield
Darling
Rhodo
Erioph
Hastings
Carex
Sanguis
Rudbeck
Festuca
Ceanoth


DCA on Eight Dollar Mountain
+5.5
-1.0
-1.0
+7.0
Caloced
Rhamnus
Hastings
Rhodo
Manzan
Darling
Sanguis
Rudbeck
Carex
Festuca
Agrostis
Ceanoth
Pinus

by upland species of either *Arctostaphylos, Ceanothus, Festuca* and *Agrostis* spp. for the driest sites, or by the obligate species, *Darlingtonia, Hastingsia, Rudbeckia*, and *Carex* for the wettest sites. The mid-canopy shrub community was characterized by large differences in DCA scores on both axes and was less tightly clustered than the other sites, indicating greater compositional variation among this communitys' quadrats. Mid-canopy quadrats were typically dominated by *Rhamnus* and *Rhododendron,* as woody species, and *Agrostis, Rudbeckia,* and *Sanguisorba* as herbaceous species.

Edaphic factors across ecotones

Savanna soils at Cedar Log Creek and Eight Dollar Mountain are characterized by rocky and gravelly A horizons that vary between 0 to 5 cm in thickness. A horizons at Josephine Creek extend down to 20 cm. Textures of AB and Bt horizons are sandy loam and clay, respectively, at all three sites. Also lower clay contents are present in Bw horizons at all three sites with few to no redoximorphic features (i.e., concentrations or depletions of Fe^{2+}).

Significant changes in physical and chemical soil properties occurred in the top 10 cm of soil along all transects. Soil moisture typically defines the fen and drops sharply at the ecotone preceding the savanna. In this manner soil moisture occured as a gradient across each study site (Table 3.3a) and differed significantly within sites (Table 3.3b). There was a notable decrease in soil moisture from fen to shrub to savanna community in the Eight Dollar Mountain site with similar and significant ($p \leq 0.05$) decreases from fen to savanna communities in the other two sites. There were no significant differences in soil moisture among the three sites.

Table 3.3a. Median ranks of abiotic characteristics for each site. Values with * and ** are significantly different at $p \leq 0.05$ and $p \leq 0.001$, respectively (Kruskal-Wallis H Test).

Variable	Median	**Eight Dollar Mountain**	**Cedar Log Creek**	**Josephine Creek**
Soil moisture (by volume)	.43%	75.5 *	50.1 *	130.0 *
Soil NO_3	.97ppm	100.1 ns	48.2 ns	93.2 ns
Soil NH_4	2.5ppm	68.5 *	55.2 *	139.8 *
Organic matter	.6%	61.2 *	113.5 *	143.3 *
CEC	2.5meq/100g	86.7 *	168.3 *	98.3 *
Bulk density	1.1g/cc	130.9 *	117.8 *	38.3 *
pH	1.8	109.6 *	102.3 *	72.2 *
Sand	1.1%	65.9 *	58.7 *	143.3 *
Silt	.8%	114.9 *	148.7 *	58.4 *
Clay	.8%	128.4 *	109.8 *	43.0 *

Table 3.3b. Median ranks of abiotic characteristics across communities (savanna, shrub, and fen) at each site. Values with asterisks (* and **) are significantly different at $p \leq 0.05$ and $p \leq 0.001$, respectively (Kruskal-Wallis H Test).

		Cedar Log Creek		Josephine Creek		Eight Dollar Mountain		
Variable	Median	Savanna	Fen	Savanna	Fen	Savanna	Mesic shrub	Fen
Soil moisture (by volume)	.485%	19.8 **	46.0**	23.5 **	42.5 **	16.5 **	49.5 **	78.4 * **
Soil NO_3	1.1ppm	32.3 ns	26.4 ns	37.1 ns	33.1 ns	38.9 **	37.4 **	77.1 **
Soil NH_4	2.6ppm	23.2 **	40.6 **	27.2 ns	37.8 ns	16.7 **	51.9 **	76.1 **
Organic matter	.7%	29.7 ns	30.5 ns	30.8 ns	38.7 ns	19.1 **	59.7 **	66.8 **
CEC	2.5meq/100g	40.0 **	14.4 **	39.5 ns	29.5 ns	41.5 ns	64.1 ns	44.2 ns
Bulk density	1.0g/cc	33.2 ns	25.0 ns	29.0 **	29.1 **	84.5 **	39.6 **	30.8 **
pH	1.8	31.0 ns	28.4 ns	34.9 ns	37.2 ns	68.7 **	36.4 **	78.4 **
Sand	1.2%	24.1 **	39.3 **	26.2 **	45.5 **	16.0 **	46.9 */**	81.2 **
Silt	.8%	34.8 ns	22.4 ns	41.5 ns	28.3 ns	82.3 **	53.8 **	22.8 **
Clay	.7%	32.8 ns	25.6 ns	32.5 ns	30.1 ns	83.6 **	53.8 **	18.5 **
Water NO_3	.08 ppm		46.5 *		67.5 *			49.5 *
Water NH_4	.8 ppm		65 *		28 *			70.5 *

Available soil nitrate and ammonium differed both within sites, across communities, and between sites ($p \leq 0.001$) with greater values of soil NH_4 occurring in the fens (Table 3.3b). Soil NO_3 values were higher in the savanna but were not significantly different from the fen levels. In contrast, at Josephine and Cedar Log Creek, soil NO_3 levels decreased from fen to savanna at Eight Dollar Mountain. Soil NH_4 values, on the other hand, were higher in the savanna at each site but were not significantly different from the fen values. In all cases, Cedar Log Creek had the lowest levels of soil NO_3 and NH_4 ($p \leq 0.05$) (Table 3.3a). Overall, the highest levels of soil NH_4 existed at Eight Dollar Mountain with NH_4 closely matched to the soil moisture gradient.

The highest organic matter values occurred in the fen and shrub communities at Eight Dollar Mountain (Table 3.3b). Organic matter levels were significantly different ($p \leq 0.05$) between communities at this site but did not differ significantly from either Josephine or Cedar Log Creek (Table 3.3a).

Bulk density varied spatially from fens (low) toward savannas (high) in each of the three sites. CEC differed significantly between fen and savanna only for the Cedar Log Creek site. Silt, pH, and clay values were similar across all communities for both Cedar Log Creek and Josephine Creek while significant differences occurred between communities ($p \leq 0.05$) for Eight Dollar Mountain. Percentages of sand varied within each site indicating significant differences ($p \leq 0.05$) between communities. Bulk density also varied significantly ($p \leq 0.05$) within each site except for Cedar Log Creek (Tables 3.3a and 3.3b).

Water NO_3 and NH_4 values (median = 0.08 and 0.8 ppm, respectively) were lower than the soil values at all three sites (Figure 3.10). Results of redox potential, dissolved oxygen, temperature, and conductivity at the sites were based on the average of five readings per site (Table 3.4).

The CCA of species distribution indicated that vegetation was constrained by: 1) soil moisture, soil NH_4 and NO_3 (sNH_4 and sNO_3) organic matter, silt and CEC at Cedar Log Creek, 2) soil NH_4 and NO_3, soil moisture, sand, silt, and water NO_3 (wNO_3) for Josephine Creek, and 3) soil moisture, sNH_4 organic matter, and soil texture at Eight Dollar Mountain (Figure 3.11). CCA axis 1 for Cedar Log Creek depicted a soil moisture gradient, representing 54% of the variation in species distribution whereas axis 1 for both Josephine Creek and Eight Dollar Mountain represented a nutrient gradient, explaining 46 and 73% of the variation in species distribution, respectively. Water nitrate was a more abundant nutrient than soil ammonium at the Josephine site. CCA axis 2 at Josephine Creek represented a soil textural gradient, explaining 24% of the residual variation while residual variation (19% and 23%) was explained by soil moisture and soil ammonium gradients for Eight Dollar Mountain and Cedar Log Creek, respectively.

I used a threshold value of 4 for the prevalence index to indicate the presence of hydrophytic vegetation; values above 4 were considered either mid-canopy shrub or savanna communities. This boundary criterion was consistent with contrast values of soil texture, nutrients and hydrologic conditions for hydrophytic vegetation in the Josephine and Cedar Log Creek sites. However, at the Eight Dollar Mountain site, this criterion was only consistent with hydrologic boundaries. I found the 50% rule

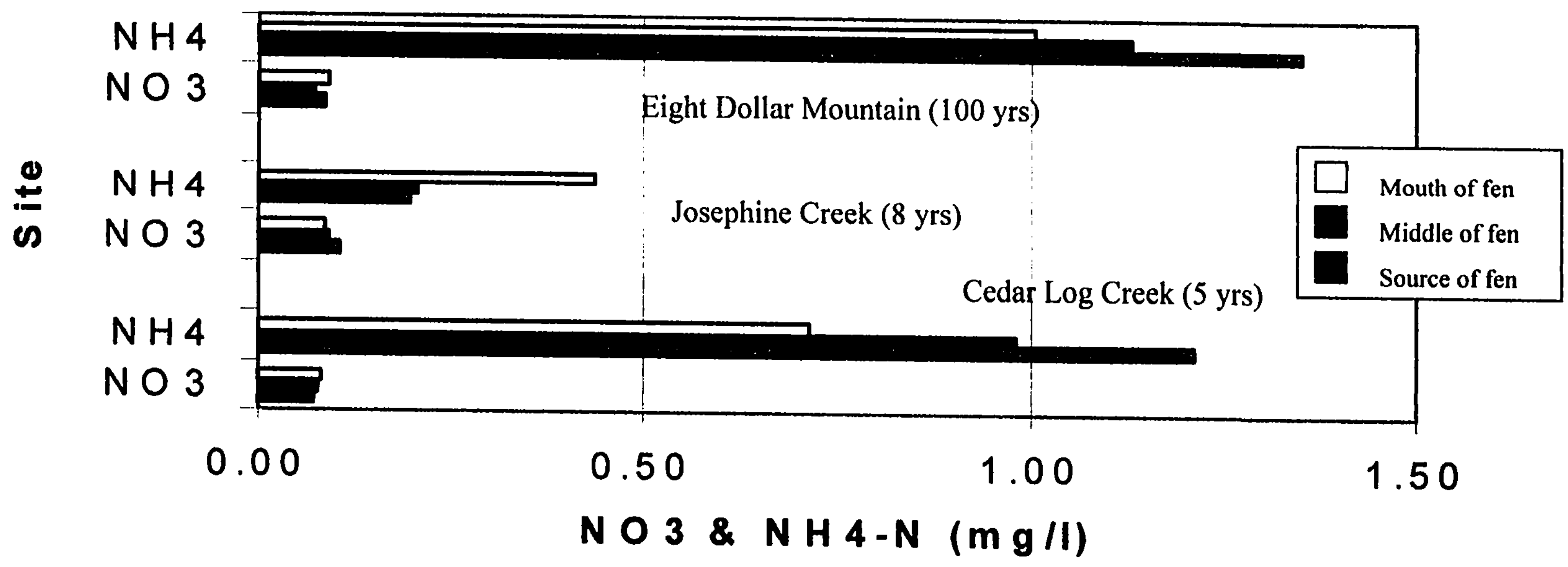
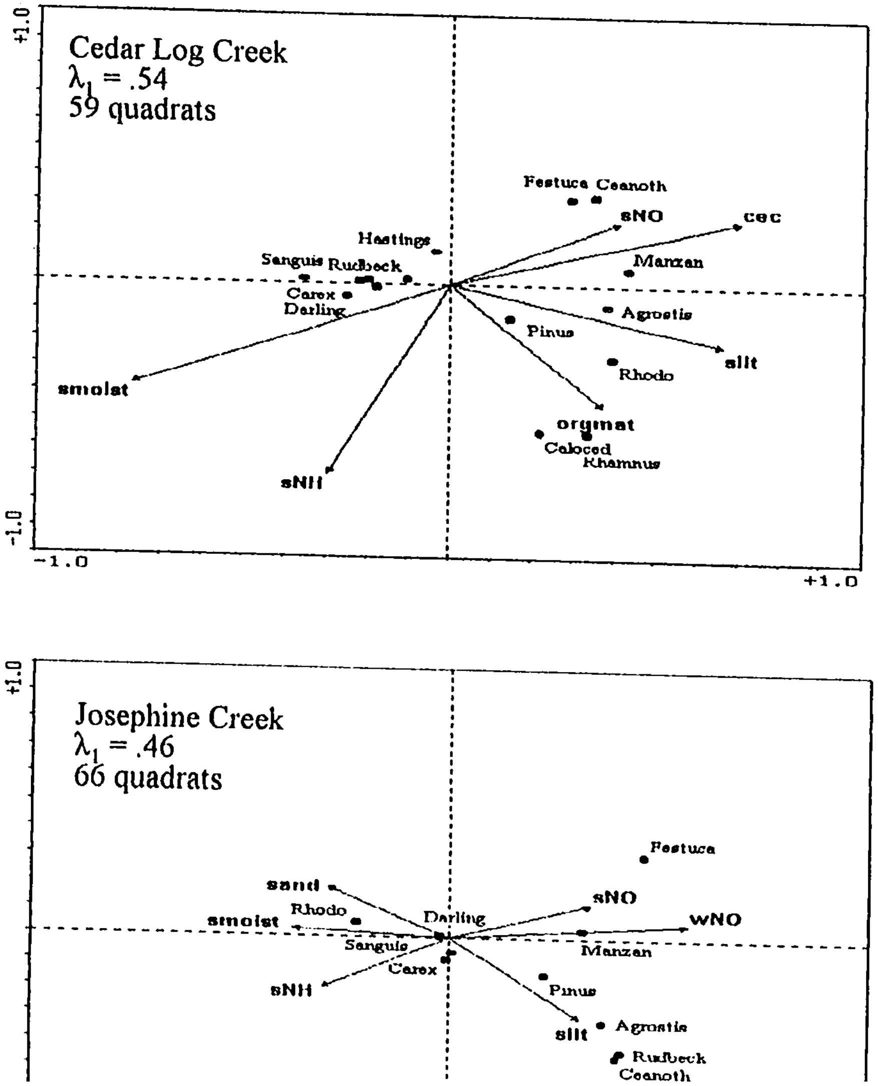


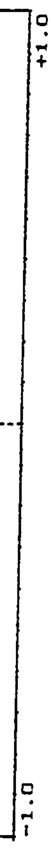
Figure 3.10. Water nitrogen at three *Darlingtonia* fens of varying time since last fire.

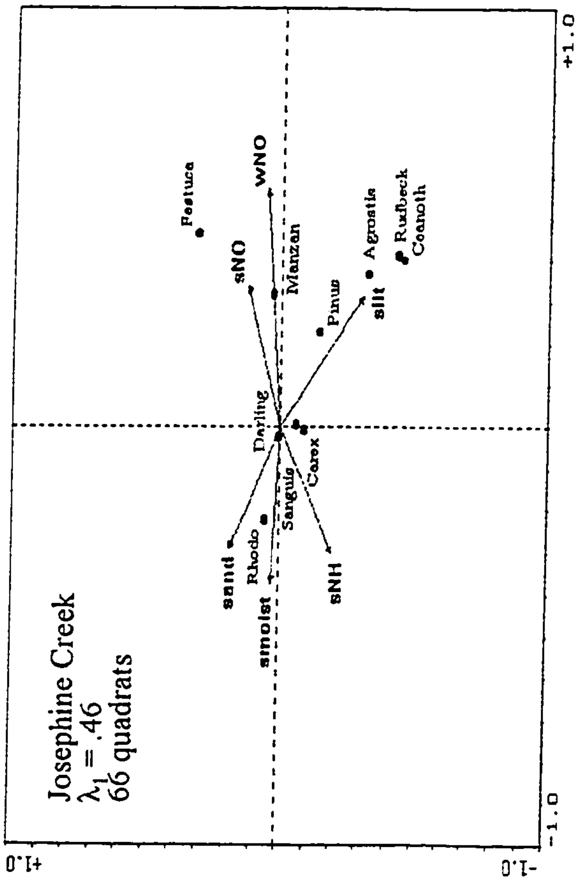
Table 3.4. Water temperature, pH, dissolved oxygen, conductivity, and redox potential at each site. Only redox readings were recorded at Josephine Creek.

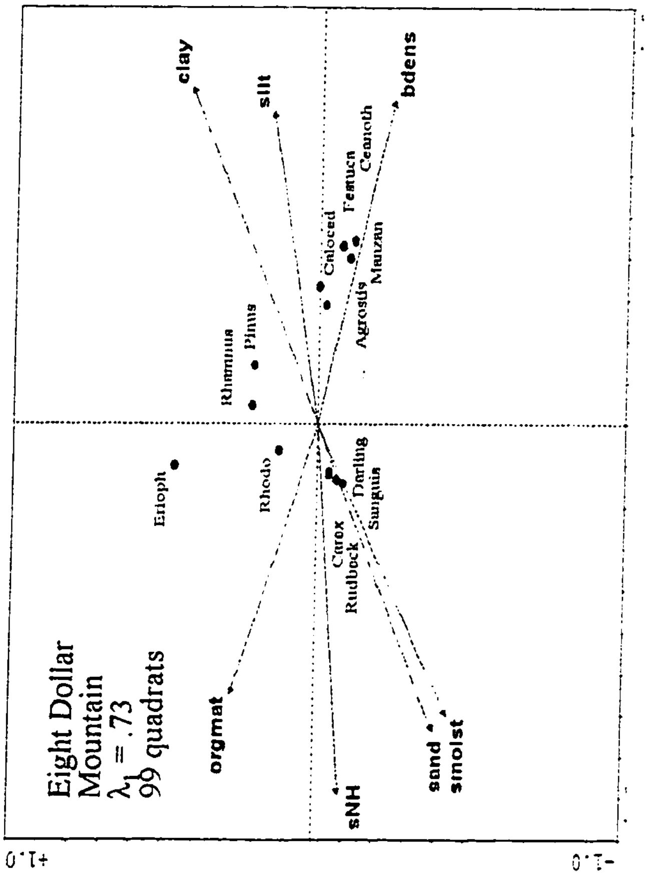
	Eight Dollar Mountain	**Cedar Log Creek**	**Josephine Creek**
Water temperature (° C)	13.8	10.7	-
pH	7.3	7.1	-
Dissolved oxygen (mg/L)	5	11.5	-
Conductivity (mmhos)	243	204	-
Redox potential (mV)	75-120	60-120	125-160

Figure 3.11. Canonical correspondence analysis results of transect quadrats by site. Smoist = gravimetric soil moisture, orgmat = organic matter, bdens = bulk density, sNH = soil NH_4, sNO = soil NO_3, and wNO = water NO_3.




+1.0
-1.0


Josephine Creek
λ_1 = .46
66 quadrats
Festuca
WNO
sNO
Manzan
Agrostis
Rudbeck
Ceanoth
Pinus
silt
Darling
Carex
Sanguis
Rhodo
sand
smoist
sNH
+1.0
-1.0
+1.0
-1.0


Eight Dollar
Mountain
λ_1 = .73
99 quadrats
clay
silt
bdens
Festuca
Ceanoth
Caloced
Manzan
Agrostis
Pinus
Rhamnus
Rhodo
Erioph
Darling
Sanguis
Carex
Rudbeck
orgmat
sNH
sand
smoist
+1.0
-1.0

method for determining the presence of hydrophytic vegetation inconsistent in determinations of sharp boundaries between the mid-canopy shrub community and the fen but consistent in determining the boundary between the mid-canopy shrub community and the savanna. Boundaries indicated by this method often matched the prevalence index boundaries, except where transects contained a mid-canopy shrub community. Hydrophytic vegetation boundaries determined by the prevalence index were not closely associated with vegetation compositional discontinuities identified with TWINSPAN (Figures 3.5-3.8).

In summary, the analyses TWINSPAN and moving windows, indicated that hydrophytic vegetation does not determe community boundaries with the exception of the fen community at the Eight Dollar Mountain site (100 years since the last burn). While the prevalence index and the DCA consistently separated all communities for each site, TWINSPAN and moving windows indicated that the fen and the mid-canopy communities could not be separated (Table 3.5). The 50% rule was the only analysis that consistently failed to separate communities within a site.

Discussion

To the casual observer, composition and structure of the ecotone boundaries at Cedar Log Creek and Josephine Creek appear sharp and abrupt between the fen and savanna communities. Eight Dollar Mountain contains equally abrupt ecotones with its inclusion of a third distinct shrub community. Statistical examination, however, reveals high species turnover rates (gradient lengths of 3.9 to 4.3) between communities but insufficiently different to be considered abrupt boundaries (van der Maarel 1976, Hobbs 1986). Recent interpretations of community dynamics suggest

Table 3.5. Results summary of ecotone analyses for all three sites.

		Discontinuities		
Site	Years since last fire	TWINSPAN	Moving windows	DCA and Prevalence index
Josephine Creek	5	Fen and savanna separation	Center stream peak	Fen and savanna separation
Cedar Log Creek	8	Fen and savanna separation	Center stream peak	Fen and savanna separation
Eight Dollar Mountain site	100	mid-canopy and savanna separation	Mid-canopy and savanna peaks	Fen, mid-canopy, and savanna separation

that the environmental discontinuities underlying these systems may characterize them as communities in transition (Hobbs 1986).

Traditionally, narrow ecotones have been identified by two key characteristics: 1) large differences in DCA scores between two communities (a separation of clusters) and 2) a high species turnover rate (between 10 and 25.5 Half Changes (HC)/100m) (Hobbs 1986) or change in species composition between communities within a short distance. Among my sites, the Eight Dollar Mountain site produces DCA scores that depict tightly clustered and separated fen and savanna communities while the 'mid-canopy' possesses plants common to both extremes. TWINSPAN also recognizes only two distinct classes, mid-canopy and savanna. Contrary to the DCA, the fen was not recognized as a separate and distinct community. Although gradient lengths are sufficiently high to be considered unimodal, HC values, used to calculate beta diversity (Whittaker et al. 1979), are less than the 10 and 25.0 HC/100 m needed to distinguish the mid-canopy as a separate community (Hobbs 1986). Species turnover rates are low, thus the shrub-dominated area at this site meets Hobbs' (1986) criterion for a *discontinuous transition* or van der Maarel's (1976, 1990) criterion for a " *limes divergens*"; a gradual change in environmental conditions and as a result, populations gradually merge into one another. In a "limes divergens" case, the boundaries are vague.

DCA scores for both Josephine and Cedar Log Creek sites depict only one vegetative group (the fen) that was tightly clustered and distinctly separated; the savanna community exhibited a strong gradient of increasing dissimilarity among its quadrats. These results contrast with those of the prevalence index and 50% dominance rule which, along with the TWINSPAN analysis, separated fens from the savanna communities. However, low species turnover rates, along environmental gradients at all three sites supports an ecotone interpretation similar to Hobbs' (1986) *discontinuous transition* or to van der Maarel's (1976) theoretical representation of a "*limes convergens*" where a coincidence of boundaries exists between two communities.

Most transects matching vegetation discontinuities at the Eight Dollar Mountain and the Cedar Log Creek sites are related to soil moisture and soil nutrients, with the exception of five transects (Figure 3.6, transects a, c, and f, and Figure 3.8, transects d and f). At the Josephine site, vegetation boundaries and water nutrients are more closely aligned. Together, these results are insufficient to fully interpret the processes responsible for changes that may be occurring at the boundary but support van der Maarel's (1976) theory that water, as a disturbance factor, creates a tension zone of uncertain, fluctuating environmental conditions. Water availability, within this context, could result in specific chemical and/or physical attributes that may influence interactions between adjacent ecological systems. Thus, the general distinction of these ecotones lies in their location relative to the reduced kinetic energy of the stream adjacent to the fen (Wiens et al. 1985, Forman and Godron 1986, Holland 1988, Naiman et al. 1989). Theoretically, water influences the boundary by deflecting sediment and organic matter to the edges, causing changes in the physical and edaphic gradients all along the fens (Forman and Godron 1981) or 'permeability' of the membrane as identified by Wiens et al. (1985).

Hypothetically, significant amounts of organic matter could accumulate at the boundaries between the fen and the savanna community in each site with water flow altering the soil characteristics at the fen boundary by slowing and dispersing any sediment to the community edge. Research with boundaries and beaver impoundments show this process facilitates the development of community structure at pond edges (Johnston and Naiman 1987). The work of Cadenasso et al. (1997) in upland forests with edges and gradients shows a similar effect related to sidewall vegetation that alters abiotic factors more dramatically than expected. Van der Maarel's (1976) ecotone research would suggest that Cedar Log Creek and Eight Dollar Mountain exemplify communities that may converge floristically, given enough time. My results appear to support van Leeuwen's (1966) prediction that species such as those found in the mid-canopy shrub community may reside in transitional zones associated with unstable environments. This may be especially true of Josephine Creek where sediment may not be sufficient enough to alter the soil characteristics at the edge.

Conclusion

Where many factors play a role in determining the composition and location of community boundaries, the role of water appears to be the most critical factor determining the fate of the fen and shrub communities in southwestern Oregon. Differences in soil structural and chemical properties from the fens to the savannas at all three sites may well be the result of processes that can influence decomposition and nutrient cycling characteristics at the ecotone level (Gosz 1981, Berg and McClaugherty 1987). As succession proceeds, fluctuating water tables lead to two possible outcomes: 1) either an increase in soil moisture levels, or 2) a decrease in soil moisture levels that enables adjacent species to occupy the boundary zone and alter the microhabitat. If sidewall vegetation should establish and further ameliorate the ecotone, this would explain the lack of differentiation between the fen and mid-canopy at Eight Dollar Mountain and the high contrast in the stream center at Josephine and Cedar Log Creek. These processes may well play a role in determining the rate of Carex invasion in these sites and the rate of community differentiation. Although studies at broader scales average the local (fine-scale) heterogeneity and are more predictable (ONeill et al. 1986) small-scale disturbance events such as sediment movement play key roles in releasing local nutrients, promoting patch scale recruitment of seedlings and ameliorating the soil at the ecotones. These small-scale processes have been known to turn subtle changes in the environment into measurable ecosystem responses (Gosz and Sharpe 1989).

CHAPTER 4

FIRE AND SUCCESSION IN SERPENTINE FENS OF SOUTHWESTERN OREGON

Fire in the Siskiyou Mountains of southwestern Oregon is an evolutionary force that influences soil properties, watershed hydrology, landscape patterns, wildlife habitat, fuel management, nutrient cycling, and forest structure and composition (Agee 1993, Chang 1996, Frost 2000). Vegetation structure and composition, particularly in the serpentine fens of southwestern Oregon, is adapted to and even dependent on fire's periodic occurrence (Atzet and Wheeler 1982, Agee 1991, Frost 2000). While the processes that link these systems to fire are still unclear, the ongoing attempts to manage them are even more puzzling.

The revegetation of many disturbed systems is primarily a substrate/soil driven process and governed by the presence or absence of soil organic matter (Wali and Freeman 1973, Tilman 1988, Gleeson and Tilman 1990). Fire potentially has a profound, long-term influence on nutrient cycles in ecosystem's by changing the form, distribution, and amount of soil nutrients as well as by changing species composition, plant growth, soil biota, leaching, and erosion (McNabb and Cromark 1990, Grogan et al. 2000). Most recent studies suggest that fire can increase the availability of soil ammonium (NH_4^+) and nitrate (NO_3^-) (Covington et al. 1991, Baldwin and Morse 1994, Kaye and Hart 1998) following the pyrolysis of organic material, an increase in N mineralization, and the leaching of total N from the forest floor into the soil immediately after fire (Wan et al. 2000).

Revegetation and succession following fire in these systems appears related to facilitation resulting from N fixation by pioneering plants or from plants that survive the disturbance. This chapter examines post-fire vegetation structure on serpentine fen substrates to assess the role of fire in shaping vegetation structure and succession on serpentine soils. I specifically examine: 1) the influence of species persistence and dispersal on the natural history of each site and to relate this to the fire history, and 2) the vegetation-induced environmental changes along with processes (below-ground) in order to predict the future of these plant systems.

Study Area

My study sites are located on the Josephine ultramafic sheet, a region of southwestern Oregon characterized by unweathered rock fragments (lithosols) and underlain by Jurassic-aged marine sediments (White 1971, Orr et al. 1992). Vegetation ranges from a floristically-rich herbaceous ground cover of endemics to low sclerophyllous shrubs to an open-canopy forest that excludes broad leaved trees and is dominated by a single, coniferous, tree species Jeffrey pine (*Pinus jeffreyi*) (Whittaker 1954, 1961). The associated vegetation grows on surface sediments consisting of weathered serpentinite and partly serpentinized peridotite.

Soils located where springs flow from the contact between the peridotite overburden and the metamorphosed serpentine below belong to a laterite clay series rich in olivine and pyroxene minerals. These soils are serpentinized to various extents giving them a dark, blue-green color (Coleman and Kruckeberg 1999). These fen soils range from a sandy loam to a clay in the subsurface horizon with direct evidence of ground water input. Most years the fens are inundated in late fall and winter and dry in summer with increased evapotranspiration rates. Immediately surrounding the fens, the soils are shallow and red with stony profiles that vary in surface depth, depending on age of the laterite. Factors influencing these much drier soils are erosion or surface movement, degree of bedrock fracturing, precipitation, vegetation cover, and composition and alteration of the parent rock (Ramp and Peterson 1979). In general, these soils are shallow gravelly-clay loams, high in bases and classified as mesic, mollic Haploxeralfs. The upper surface (.3 m to 1 m) is typically dark, reddish-brown with minor organic residue and varied amounts of iron oxide pellets, chromite grains and unweathered peridotitie boulders (Ramp and Peterson 1979). This portion of the soil profile is slightly acidic (pH 6.6 to 6.8). Bedrock occurs within 1 m of the surface in areas dominated by savanna vegetation.

Serpentine vegetation found on these soils is characteristically sparse and xerophytic. In the tree stratum, broad-leaved trees are absent and pines are numerous while sclerophyllous trees occur as shrubs on these sites. Savanna forests consist of an open-canopy dominated by Jeffrey pine (*Pinus jeffreyi*) and a floristically-rich herbaceous ground cover dominated by grasses, namely *Festuca idahoensis*. A rich herbaceous vegetation dominates the fens, primarily *Darlingtonia californica* and *Carex mendocum,* and lacks canopy species. Savanna vegetation differs drastically and physiognomically from the fens, but is no less floristically-rich in endemic ground cover.

Three low elevation (700 m), serpentine fen sites (Josephine Creek, Cedar Log Creek, and Eight Dollar Mountain) were located in 25,800 ha of the Josephine ultramafic sheet (42° 07' 30" N, 123° 37' 30" W) (Figures 2.2 and 3.1). Climatological data from Grants Pass, Oregon, approximately 40 km from the sites indicate that precipitation, almost entirely by rain, averages 140 cm annually with most occurring from November through May (Oregon Climate Service 2001). The climate is Mediterranean with cool, wet winters and distinctive warm and dry summers from June to September. Fire ignitions, primarily lightning, typically occur during the dry months of August and September under conditions of maximal fuel loads (Frost 2000). During drought years, fires in savanna forests burn into the fens and are thus likely to have an important role in the development of vegetative structure and composition (Agee 1991, Frost 2000). Pre-fire suppression era fires (1910 - 1930) were small because serpentine rock and other discontinuities in surface fuels acted as barriers to fire spread (Frost 2000). Since then, fire suppression and landscape fragmentation have limited the extent of lightning-ignited fires.

Similar to many other forests in the Klamath-Siskiyou region, little research has investigated fire history of the Jeffrey pine dominated communities. According to Atzet and Wheeler (1982), "fire infrequently occurs in this series" and no data are presented. Available reports on fire frequency are based on analyses of tree age classes and are considered only rough estimates (Frost 2000). According to Atzet and Martin (1992), frequency return intervals in the Jeffrey pine series average 50 years across southwest Oregon (Table 4.1). Similar forests of ponderosa pine in the Pacific Northwest typically have a fire frequency ranging from 5 - 25 years (Agee 1991).

The Josephine Creek site burned by a ground fire in 1986, removing all flammable herbaceous biomass and most of the accumulated litter; only the lower

Table 4.1. Summary of fire history in the Klamath Mountains (Atzet and Wheeler 1982, Lanner 1983, Frost 2000)

Area and vegetation	Location	Mean fire return interval	Fire severity	Period of record	Type of record	Size of sample area
Jeffrey pine/ ultramafic soils	National Forest lands across southwest OR	~ 50 years	Low severity	1540-1990	Composite of stand origin and disturbance data	31, 0.1 ha plots

needles of pines were scorched by the fire (Borgias and Beigel 1998). The Cedar Log Creek site was burned in 1996 by a prescribed fire that burned over the two communities entirely (Borgias and Beigel 1998). Both burns occurred in late summer typical of the natural fire regime for the area (Borgias and Beigel 1998). The extensive Biscuit fire of 2002 did not burn any of the sites in the study area.

A shrub community, present only at Eight Dollar Mountain, is characterized by *Rhamnus californica* and *Rhododendron occidentalis* while scattered Jeffrey pine and incense-cedar (*Calocedrus decurrens*) constitute the upper canopy (Whittaker 1954, Franklin and Dyrness 1988). This shrub community forms a narrow, 15 m band around the fen before it joins with the savanna. The area is intermediate in both hydroperiod and organic layer, slightly more than the savanna, and slightly less than the fen, but still saturated for most of the year. All three sites display distinct ecotones between the fen and savanna; the Eight Dollar Mountain site gains an extra ecotone formed by the shrub community (Figure 2.3).

Methods

I initially assessed the fire history of the sites from various sources, notably aerial photographs (1:15,840) taken between 1952 and 1996 and supplemented with historic records obtained from The Nature Conservancy, United States Forest Service, Bureau of Land Management, and Cornell University (R.H. Whittaker's special collections). Exact boundaries of past fires are rarely known but can be determined by sporadic fire histories available from air photographs.

I measured savanna composition and tree density using three circular-oblong plots. Two sites, Josephine and Cedar Log Creek (9.9 ha), included a fen and savanna. A third site, Eight Dollar Mountain (16.3 ha) encompassed fen, savanna, and mid-canopy shrubs. The sites were selected for their distinct community structure and composition, and burn histories: 3 years (Cedar Log Creek), 8 years (Josephine Creek) and 100 years (Eight Dollar Mountain) since fire. The tree stratum at each site is reduced to an open stand, dominated by Jeffrey pine, while the sclerophyllous 'tree' stratum at Eight Dollar Mountain consists of an understory shrub layer (< 5 m ht). All these sites were edaphically and topographically similar.

Tree species, age, and size data, were collected at each site, to identify changes in forest structure, composition, and the timing of stand replacing fire. Stand data, collected from trees located at each site, within the circular-oblong plots, included counts of live and dead seedlings (<1.4 m tall) and saplings (>1.4 m tall but <4 cm diameter at breast height (dbh)), dbh of all live and dead-standing trees (>4 cm dbh), and tree cores for live trees at each site. Tree rings were prepared following standard procedures (Stokes and Smiley 1968) and counted using a stereomicroscope. Since incense-cedar is generally killed by moderate and severe fires, I assumed that tree-ring counts for this species would indicate the minimum time since fire, excluding the time for establishment and early growth to reach coring height (30 cm). All tree ages were reported at coring height. I also examined soil profiles in each community to assess the relationship between soil type and tree/shrub regeneration success in saturated, mesic, and dry sites.

I measured a range of environmental variables at each site including elevation (m) and aspect and slope (degrees), using a laser rangefinder. I also recorded soil surface characteristics such as bare ground, water, and exposed rock measured as percent cover. I measured cover of duff and fine litter depth (mean of five observations per community), using four cover classes: class 0 = 0%, class 1 = 5 - 33%, class 2 = >33 - 66%, class 3 = >66% cover. Current and available historic vegetation data were used to establish snapshots of vegetation change, composition, and structure at the study sites, and I also noted the location and diameter of all fallen, intercepted boles.

Analysis

Because this study compared community types that may differ by above-ground biomass, litter alone was not necessarily a good surrogate of succession. Instead, I used an aggregate of four variables that are potentially related to succession in these sites: litter, Jeffrey pine canopy height, basal area, and tree density. I carried out a principal components analysis (PCA) to reduce the four highly correlated variables into a composite measure of succession (McCoy et al. 1999, Suding and Goldberg 1999) and created a succession index (SI) comprised of the site scores on the

1st axis. These scores minimize residual sums of squares after fitting straight lines to the data and reflect successional change. McCoy et al. (1999) found linear relationships to succession data with the variables litter, tree density, basal area, and canopy area. My PCA results yielded a first eigenvector accounting for 84% of the total variation and showed high correlation with the variables litter cover, tree density, basal area, and Jeffrey pine canopy height. PCA site scores on axis 1 were thus interpreted as a succession index (SI). I used this index in conjunction with estimated time since last stand-replacing fire based on maximum tree ages (Oliver and Larsen 1990) to compare sites. A constant of 2.29 was added to the succession index to eliminate negative values.

For comparison purposes, I ranked species in each community at all sites according to a species index (SPI), calculated as the mean of the product of their abundance and the SI at each site where they were present (McCoy et al. 1999). I standardized for sampling scale by calculating the species index for Jeffrey pine as the mean of the product of density (trees/ha) and the SI. A low species index value (1) indicates that species are most abundant early in a successional sequence while a high value indicates a late successional species.

Finally, I used a multinomial logistic regression procedure of combined and untransformed variables (SI and time since fire) (He et al. 2002) to analyze the survival versus disappearance of *Rhamnus* (mid-canopy indicator species) and *Darlingtonia* (fen indicator species) populations with respect to succession. Harrison et al. (2000) used logistic regression to analyze the survival versus disappearance of species with respect to population isolation, seep size, and distance from disturbance in turnover studies with serpentine populations. He et al. (2002) demonstrated a general positive interspecific relationship with occupancy and abundance models, i.e., locally abundant species tend to be widespread in space whereas rare species tend to be narrowly distributed and thus argue for using a logistic regression model in attempts to understand patterns of distribution that exist in communities with drastically different attributes (e.g., physiognomy and life history traits). Logistic regression calculates changes in the log odds of the dependent variable, not changes in the dependent variable itself, as in ordinary least squares regression. Thus, presence or absence of the dependent variable is treated as an event that either occurrs or does not occur.

Coefficients were estimated using a maximum likelihood estimation procedure. I converted the dependent variables, *Rhamnus* and *Darlingtonia* (% cover), to dummy variables ($0 \leq 33\%$, $1 = 34\text{-}66\%$, $2 = 67\text{-}100\%$) and used the succession index (SI) and litter as independent variables. Time since fire was a covariate. The model did not include canopy height, density, or basal area as independent variables because they are inherent measurements of the SI. Similar analyses by Suding and Goldberg (1999) were conducted on seedling establishment in productivity studies. Model goodness-of-fit was assessed by the likelihood ratio χ^2 statistic. Evaluation of the model is based on the "odds ratio" and its proximity to 1, thus, the later the stage of succession the closer the "odds ratio" is to 1.

Results

My floristic survey of serpentine *Darlingtonia* fen sites recorded 15 species, all of which occurred on at least two of the three sites (Chapter 3). Five species were perennials (33%), two were trees, four were shrubs and two were grasses. Ten species of the 15 (66%) occurred on over half of the transects in two sites, Cedar Log Creek and Josephine Creek. These species contributed to > 30% of one or more community frequency values within sites. All ten species were present at Eight Dollar Mountain.

Aerial photographs (1952-1996) of the Eight Dollar Mountain site revealed that the northwest and southeastern edges of the fen have experienced mid-canopy invasion for the past fifty years (Figures 4.1 and 4.2). In 1952, mid-canopy invasion was only slightly evident immediately northwest and southeast of the fen area (consistent green area) but largely absent below the tree canopy in the southeast and on the northeastern edge of the fen (Figure 4.1). The area at Eight Dollar Mountain had near-coverage (30 - 40%) of mid-canopy shrubs underneath the tree canopy by 1996 (Figure 4.2), most notably along its northwestern and southeastern edges. Successional rankings at Eight Dollar Mountain, Cedar Log Creek, and Josephine Creek (by SI) and species (by SPI) were distinctive with slight transitions in vegetative composition (Figure 4.3). Species presence data showed two main successional categories; an early to mid stage and a late seral stage. An early successional species (*Arctostaphylos*) (indicated by the low SPI value) was abundant at Eight Dollar Mountain, but rare at the other two sites. A group of mid-seral species, *Rhamnus* and *Rhododendron* (indicated by SPI values 0.24 and 0.39, respectively) was abundant at Eight Dollar Mountain while only rare to intermediate at Josephine and Cedar Log Creek. *Darlingtonia*, considered an early to mid-seral species, was more abundant on the earlier successional sites, Josephine and Cedar Log Creek. Later successional

Figure 4.1. Aerial photograph of Eight Dollar Mountain taken in 1952.
1 cm = .08 km.

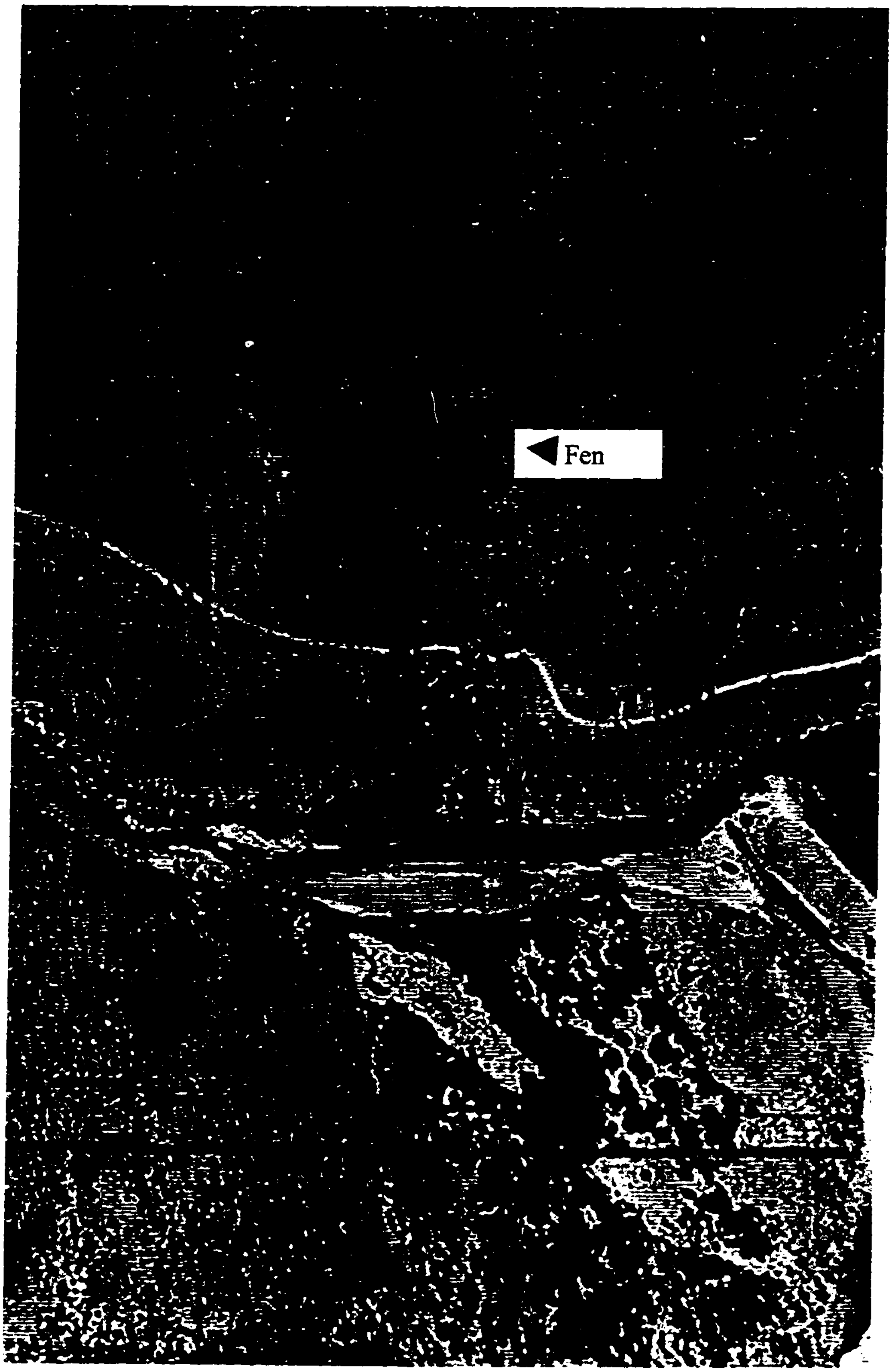


Figure 4.2. Aerial photograph of Eight Dollar Mountain taken in 1996.
1 cm = 1 km.

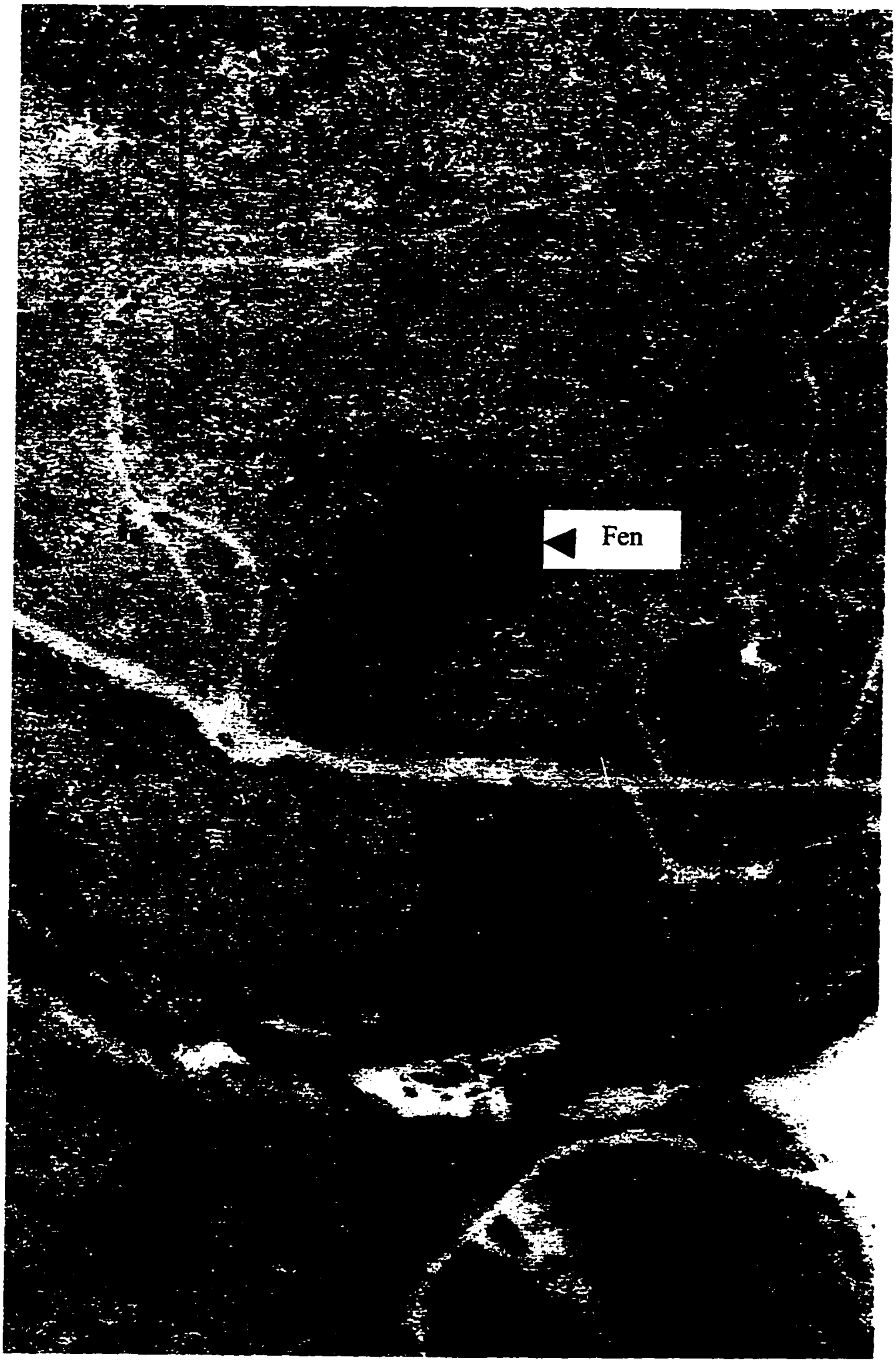
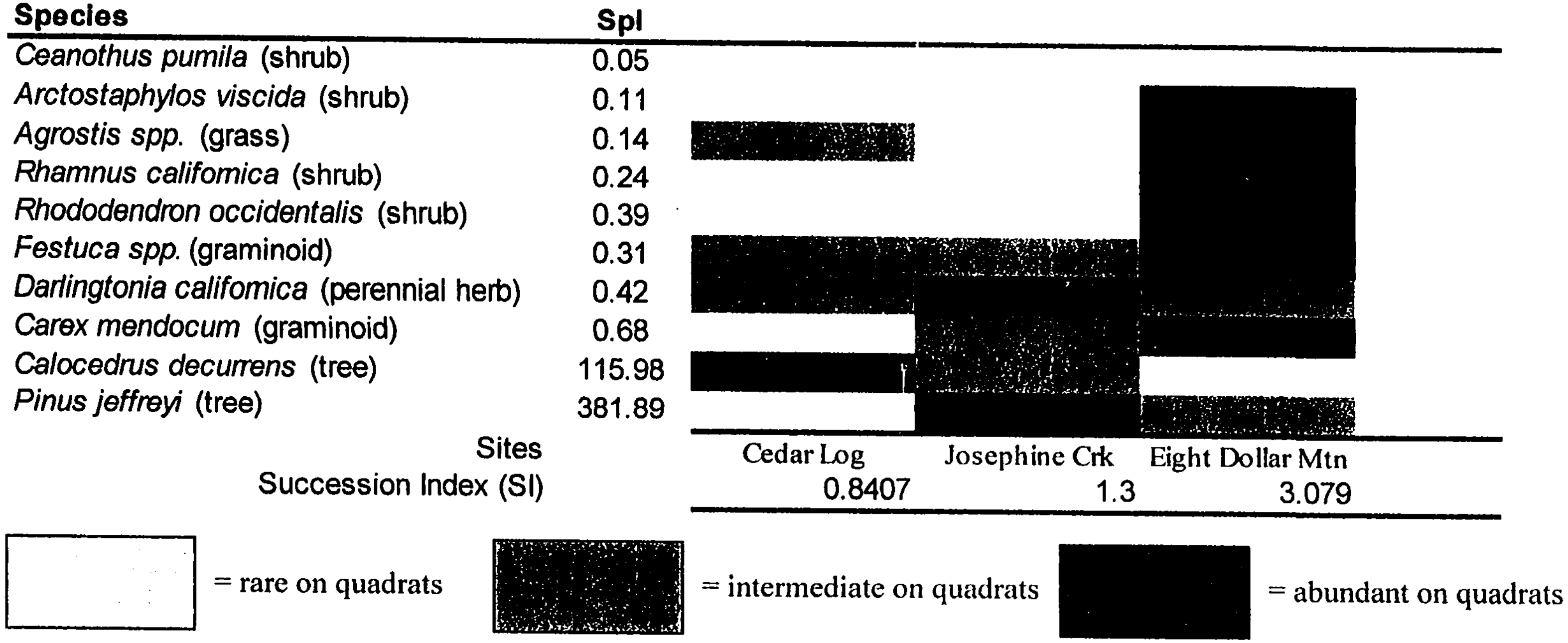


Figure 4.3. Presence of species (shaded) at Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain ranked by the succession index (SI) and the species index (SpI).



Species	**SpI**	Cedar Log	Josephine Crk	Eight Dollar Mtn
Ceanothus pumila (shrub)	0.05			
Arctostaphylos viscida (shrub)	0.11			■
Agrostis spp. (grass)	0.14	▨		■
Rhamnus califomica (shrub)	0.24			■
Rhododendron occidentalis (shrub)	0.39			■
Festuca spp. (graminoid)	0.31	■	▨	■
Darlingtonia califomica (perennial herb)	0.42	■	■	▨
Carex mendocum (graminoid)	0.68		▨	■
Calocedrus decurrens (tree)	115.98	■	▨	
Pinus jeffreyi (tree)	381.89		■	▨
Sites		Cedar Log	Josephine Crk	Eight Dollar Mtn
Succession Index (SI)		0.8407	1.3	3.079

☐ = rare on quadrats ▨ = intermediate on quadrats ■ = abundant on quadrats species (Jeffrey pine and incense-cedar) were also most abundant at the two younger sites.

Autecological traits (Table 4.2) for common species indicated that these sites experienced frequent low intensity burns, perhaps more frequent than the suggested fire return interval of ~50 years (Atzet and Wheeler 1982, Frost 2000). Both *Ceanothus* and *Arctostaphylos*, long-lived natives present at the sites, possess woody fruits which protect seed from fire or seed that require stratification, though the protection may not be sufficient for these to be classified as bradysporous. Other fire adaptations for both ponderosa and Jeffrey pine include thick bark and fire-activated seeds (Minore 1979, USDA 2003).

Age structures were determined from 129 - 187 trees sampled in each site (n=497) (Table 4.3). Tree rings were examined from 226 trees; 171 Jeffrey pine, 50 incense-cedar, three Douglas-fir *(Pseudotsuga menziesii)*, and two knobcone pine *(Pinus attenuata)*, none of which possessed fire scars. The Eight Dollar Mountain site consisted of a mixed Jeffrey pine and incense-cedar stand with tree age data ranging from 32 - 324 years. The Josephine and Cedar Log Creek sites had similar mixed stands of Jeffrey pine and incense-cedar (Table 4.3). The oldest live trees at these sites were 234 (Eight Dollar Mountain), 199 (Cedar Log Creek), and 334 years (Josephine Creek) old, respectively (Figure 4.4). Tree canopy height was greatest at Eight Dollar Mountain for both species (Table 4.4). In the most frequently burned areas (Josephine and Cedar Log Creek), fire scar dating was not instructive since the resulting low-intensity fires had not induced scarring.

Table 4.2. Autecology traits of indicator plants at Cedar Log Creek, Josephine Creek, and Eight Dollar

Species	Longevity	Shade tolerance	Resprouter	Seed	Relay	Initial
Ceanothus pumila (shrub)	early postfire	shade-intolerant	weak resprouter	postfire seedling estab.		on-site
Arctostaphylos viscida (shrub)	long-lived, native evergreen shrub	shade intolerant		hardcoated		early seral /fire
Agrostis spp. (grass)	perennial bunchgrass	shade-intolerant				
Rhamnus californica (shrub)	long-lived, native evergreen shrub	shade tolerant	obligate resprouter following fire		facultative seral	
Rhododendron occidentalis (shrub)	long-lived, native evergreen shrub	shade tolerant	resprouter following light fire		facultative seral	
Festuca spp. (graminoid)	perennial bunchgrass	shade intolerant	strong postfire regen following low severity fire		Secondary colonizer (on-site or off-site seed sources)	
Darlingtonia californica (perennial herb)	native perennial forb	unknown	vegetative reproduction by rhizomes		also seral species	Initial-offsite obligate colonizer
Carex mendocum (graminoid)						
Calocedrus decurrens (tree)	500+		no resprouting		facultative seral species	
Pinus jeffreyi (tree)	600+		no resprouting	off-site colonizer		early seral species on burned sites

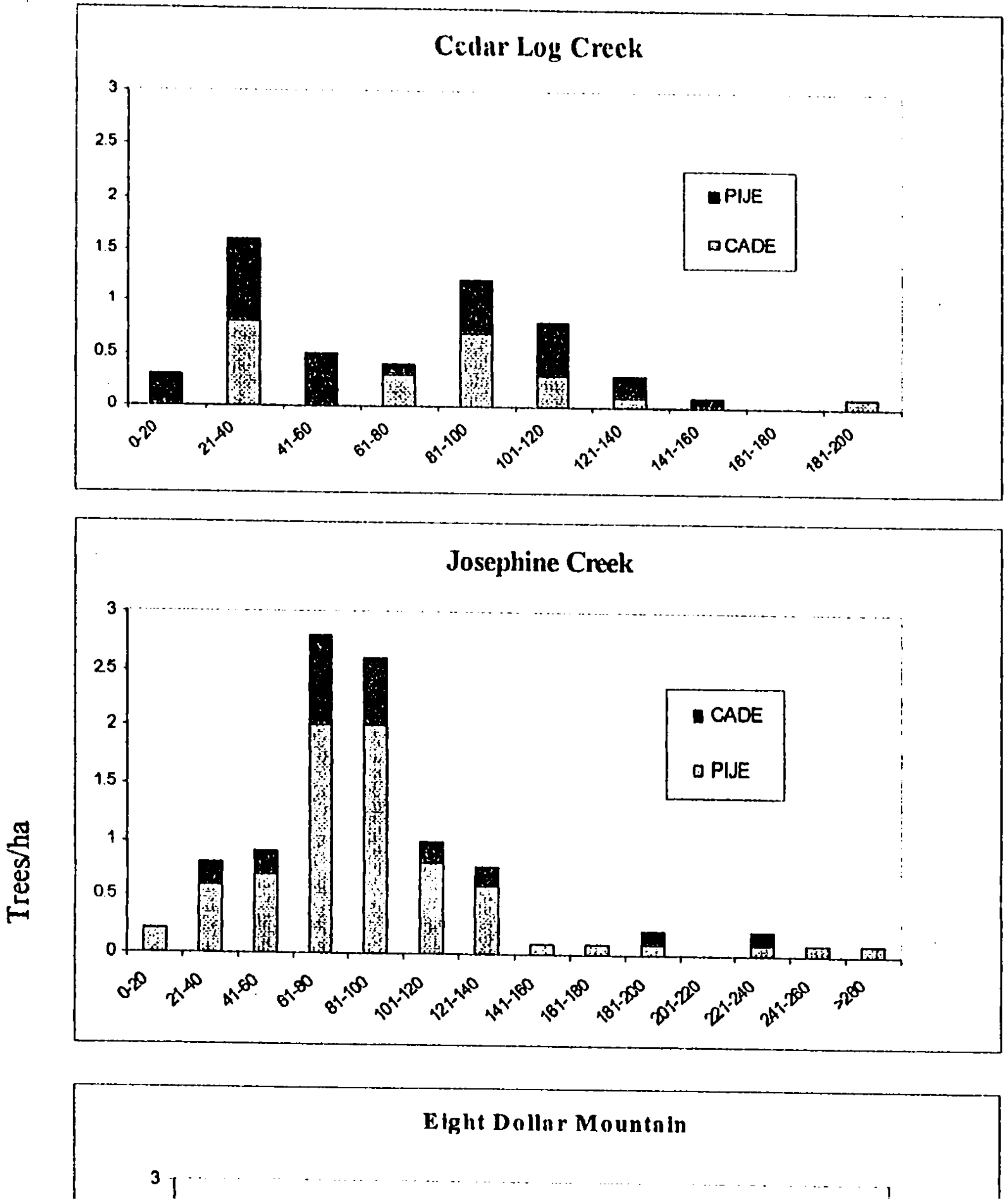
plants at Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain (Minore 1979, Lanner 1983).

	Resprouter	Seed	Relay	Initial	Notes
rant	weak resprouter	postfire seedling estab.		on-site	seed survive fire without litter; eliminated with high fire return interval (< 4 yrs)
rant		hardcoated		early seral /fire	hard-coated seed and capable of lying dormant for decades; fire stimulated germination of seeds
rant					seeds colonize recently disturbed sites having exposed mineral soil
nt	obligate resprouter following fire		facultative seral		short-lived seeds prone to rot:-- Seedling establishment is often episodic and coincides with periods of above normal rainfall . -- Although initial establishment may occur in burned or unburned stands during very wet years, continue
nt	resprouter following light fire		facultative seral		
rant	strong postfire regen following low severity fire		Secondary colonizer (on-site or off-site seed sources)		survives light fires; Plants may re-establish from seed after fire if temperatures are low enough to allow for survival of seed
	vegetative reproduction by rhizomes		also seral species	Initial-offsite obligate colonizer	
	no resprouting		facultative seral species		facultative seral species; highly susceptible to fire kill
	no resprouting	off-site colonizer		early seral species on burned sites	thick, corky bark that withstands high temperatures and a tall, erect bole free of lower limbs; buds develop thick scales able to withstand considerable amts of heat

Table 4.3. Tree age, diameter at breast height (dbh), density, and basal area at Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain. CADE = *Calocedrus decurrens*, PIJE = *Pinus jeffreyi*, PSME = *Pseudotsuga menziesii*.

		Age (years)		Density (trees/ha)		Basal area (m2/ha)		Diameter (dbh)			
Site	Species[a]	N	Range (yrs)	Live	Dead standing	Live	Dead standing	N	Median	Range (dbh)	% trees aged
Eight Dollar Mtn	CADE	3	(73-122)	8	0	1.38	0	8	23.5	(5-72)	38
	PIJE	66	(32-234)	120	0	655.10	0	120	38	(5-89)	55
	PSME	1	(117)	1	0	0.03	0	1	32.2	(32.2)	100
	Total			**129**	**0**	**656.51**	**0**				
Cedar Log Creek	CADE	23	(23-199)	65	40	164.76	14.52	65	28	(5-89)	35
	PIJE	30	(15-154)	108	49	222.60	28.9	108	17.5	(4-68)	28
	PSME	1	(34)	8	4	0.40	0.09	8	9	(9-25)	13
	Total			**181**	**93**	**387.76**	**43.51**				
Josephine Creek	CADE	24	(31-190)	40	15	44.78	4.57	40	23	(8-74)	60
	PIJE	75	(14-334)	144	23	324.43	8.34	144	15	(4.5-89)	51
	PSME	1	(0)	1	0	0.01	0	1	0	0	0
	PIAT	2	(36-68)	2	4	0.02	0.23	2	11.25	(11-11.5)	100
	Total			**187**	**42**	**369.24**	**13.14**				

Figure 4.4. Age structure comparison for Jeffrey pine (PIJE) and incense-cedar (CADE) at Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain.



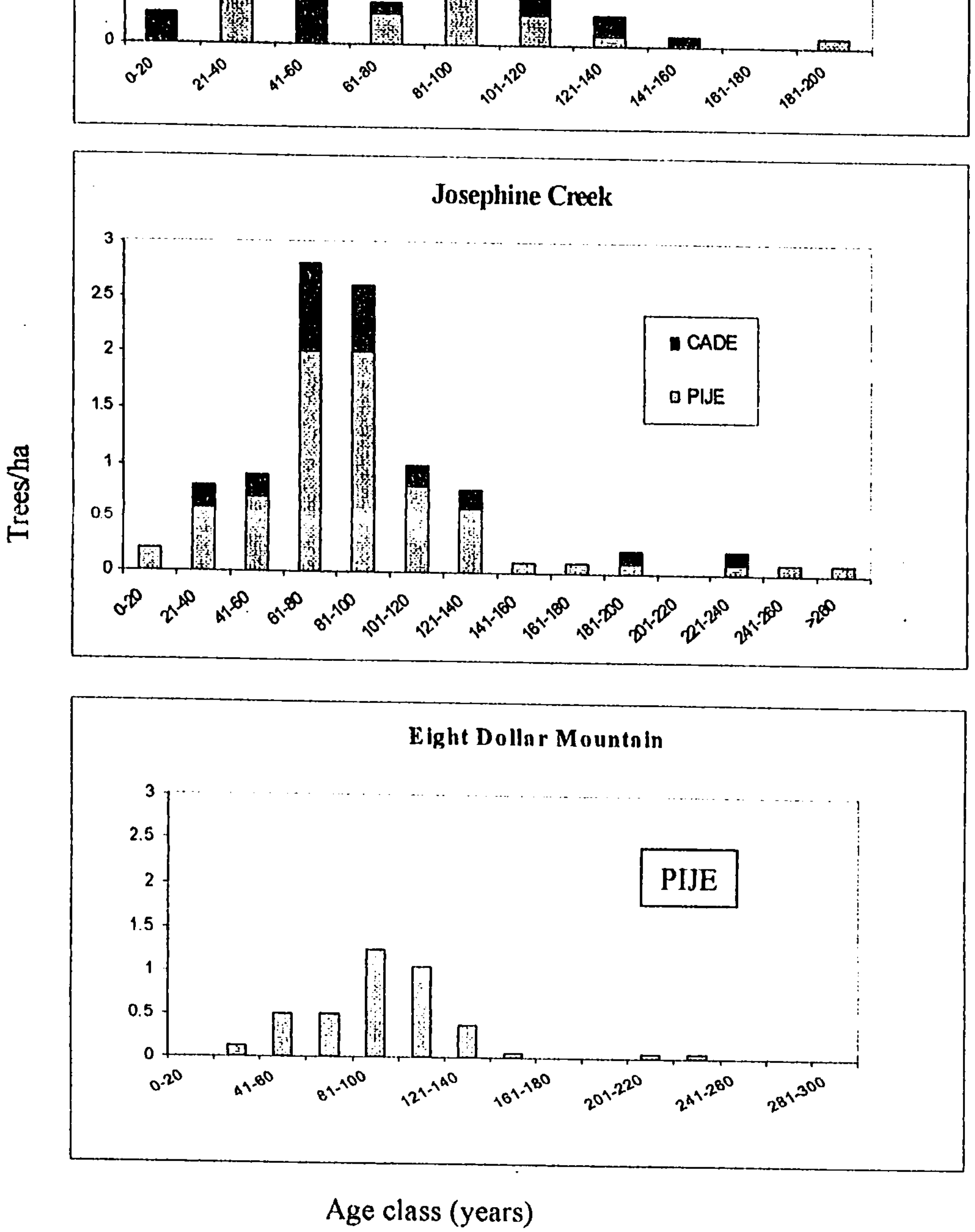

0
0-20
21-40
41-60
61-80
81-100
101-120
121-140
141-160
161-180
181-200
Josephine Creek
Trees/ha
3
2.5
2
1.5
1
0.5
0
CADE
PIJE
0-20
21-40
41-60
61-80
81-100
101-120
121-140
141-160
161-180
181-200
201-220
221-240
241-260
>280
Eight Dollar Mountain
3
2.5
2
1.5
1
0.5
0
PIJE
0-20
41-60
81-100
121-140
161-180
201-220
241-260
281-300
Age class (years)

Table 4.4. Tree canopy height (m) at Cedar Log Creek, Josephine Creek and Eight Dollar Mountain.

Site	Species[a]	N	Median	Range
Cedar Log Creek	CADE	61	9.5	4-24.4
	PIJE	79	9.1	4-25.9
	PSME	3	5	4-9.1
Josephine Creek	CADE	36	7.6	4.3-24.4
	PIJE	140	7.3	4-26.8
	PSME	1	6.1	0
	PIAT	2		4.6-6.1
Eight Dollar Mtn	CADE	7	11	5-27
	PIJE	120	21	4-56
	PSME	1	26	26

Tree and shrub structures

Seedlings, saplings, and understory trees of Jeffrey pine were common at the Eight Dollar Mountain site (longest time since fire) but rare at both younger sites (3 and 8 years since fire). Seedling recruitment of Jeffrey pine at the oldest site began within the last ten years (Table 4.5). Live pine saplings densities were low (8-10/ha) in all sites except Cedar Log Creek (32/ha) (Table 4.5). Jeffrey pine live tree ages ranged from 32 to 234 years (5-88 cm dbh) for the Eight Dollar Mountain site (median = 93). At Josephine and Cedar Log Creek sites, Jeffrey pine live trees ranged from 14 to 334 years (5 - 89 cm dbh) and 15 to 154 years (5 - 68 cm dbh) respectively. Rapid initial growth was rare among these trees indicating establishment under stressful conditions, a common characteristic of savanna communities. Live tree densities for Jeffrey pine and incense-cedar were fairly consistent across all sites (129-187 trees/ha). In general, tree mortality was highest among Jeffrey pine and incense-cedar at Cedar Log Creek (Table 4.3). Jeffrey pine had the highest live tree density and greatest basal area followed by incense-cedar at Josephine and Cedar Log Creek sites.

Incense-cedar seedlings and saplings were present at all three sites (Table 4.5) with 90% of these seedlings <50 cm tall. Live sapling densities of incense-cedar were low in all sites except at Cedar Log Creek (32/ha), which also had a comparatively high density of dead Jeffrey pine saplings (14/ha). At both of the younger sites, Josephine and Cedar Log Creek, incense-cedar seedlings have been present for 100-200 years (Table 4.3). Shrubs were present at the younger sites but were most prevalent at Eight Dollar Mountain where a thicket of *Rhamnus* and *Rhododendron*

Table 4.5. Live and dead standing seedling and sapling counts at Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain. CADE = *Calocedrus decurrens*, PIJE = *Pinus jeffreyi*, PSME = *Pseudotsuga menziesii*, PIAT = *Pinus attenuata*.

		Live (No./ha)		Dead standing (No./ha)	
Site	Species[a]	Seedling	Sapling	Seedling	Sapling
Eight Dollar Mtn	CADE	20	1	0	0
	PIJE	106	10	0	0
	PSME	0	0	0	0
	Total	**126**	**11**	**0**	**0**
Cedar Log Creek	CADE	1	1	0	10
	PIJE	2	32	5	14
	PSME	0	0	0	0
	Total	**3**	**33**	**5**	**24**
Josephine Creek	CADE	7	3	1	5
	PIJE	7	8	1	4
	PSME	0	0	0	0
	PIAT	0	0	0	1
	Total	**14**	**11**	**2**	**10**

stems (3-4 m ht), and a continuous canopy of foliage, dominated the understory community. Isolated shrubs at Josephine and Cedar Log Creek were short in stature (< 1.2 m) and contributed little to stand basal area. No seedlings of *Rhamnus* or *Rhododendron* were found at any of the sites.

Darlingtonia density

Darlingtonia was most abundant at the youngest site (3 years since fire) and outnumbered *Carex* on a median percent cover basis comparison ($p \leq 0.05$) (Table 2.2) (Kruskal-Wallis H test). While carnivorous plants densely covered the Josephine Creek fen, they declined considerably in percent cover (85% drop) at the Eight Dollar Mountain site (100 years since the last fire).

Soils and Surface Fuel Accumulation

Soil underneath the mid-canopy vegetation at the Eight Dollar Mountain site was distinguished from the Josephine and Cedar Log Creek sites by a thicker and darker A horizon and was typically a reddish-brown soil with greater amounts of organic residue. There were no significant differences among sites in soil texture (Table 2.4).

Pine needles, small twigs, and dead grass leaves comprised the litter component at each of the study sites. Litter depth was greatest at Eight Dollar Mountain, particularly in the mid-canopy shrub community (Table 4.6). Litter occurred at both Josephine and Cedar Log Creek but only as dead grass leaves; the needle component was virtually absent. Duff was not present at any site.

Table 4.6. Litter accumulation at all three sites.

Site	Median litter accumulation (cm)
Cedar Log Creek	.11
Josephine Creek	.15
Eight Dollar Mountain	.61

Logistic regression produced a significant litter cover term, particularly for the dependent variable *Rhamnus* (Table 4.7). The likelihood ratio χ^2 was highly significant ($P \leq 0.001$) and the percent correct predictions of indicator species *Darlingtonia* and *Rhamnus*, respectively, varied from 55% to 86% indicating good predictable performance. Used in a succession context, logistic regression analysis for succession indicated that for a one unit change in the density of *Rhamnus,* an "event" of succession was 7 times (88/12) more likely to occur with litter as a predicting variable.

Discussion

Based on natural histories and the vegetation-induced environmental changes in these sites *Darlingtonia* fens will show reduced percent cover in the absence of fire. Percent cover change of early seral species such as *Darlingtonia* and *Carex*, as well as tree age structure data, suggests that all three sites, Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain, would likely converge toward similar vegetative structure. Even though Cedar Log Creek has been more recently burned, there is an identical tree age structure and the site includes the oldest incense-cedar trees, considered a facultative seral species and eventually a codominant steady state species in the absence of fire (USDA 2002).

Table 4.7. Results of the multinomial logistic regression.

Variables in the Equation

Variable	B	S.E.	Wald	df	Sig
Litter	-0.022	0.38	0.003	1	0.955
TSF			4.006	2	0.135
TSF(1)	-0.297	0.383	0.602	1	0.438
TSF(2)	-0.736	0.368	4.004	1	0.045
Constant	0.274	0.257	1.139	1	0.286

Notes: (1) B is the estimated logit coefficient.

(2) S.E. is the standard error of the coefficient.

(3) Wald = [B/S.E.]2

(4) "Sig" is the significance level of the coefficient, for litter it is 95% confidence level

(5) A partial R = Wald statistic

Vegetation structure and floristic results indicate that the fen and surrounding vegetation are shaped by historic and current fire regimes. The transition from an open, two-phase vegetative community to a taller, nearly closed-savanna tree cover appears to be a function of time since fire, as noted by the current demographic structure of tree population, the changing composition at the three sites, and the current information regarding natural histories of key indicator species.

Floristic groups for Josephine Creek, Cedar Log Creek, and Eight Dollar Mountain include: (i) obligate colonizers that either persist or die out in later successional stages; (ii) shade-intolerant, hydro-successional species present only where soil water levels fluctuate; and (iii) resprouting species present only in areas lacking sufficient litter to maintain moisture long enough for them to perisist without fire. The time scale for vegetation changes appears to be at least 60 years to reach the mid-canopy shrub stage (assuming no fire) since a single stem age dated *Rhamnus* (2 cm dbh) at 60 years.

Germination requirements of both *Rhamnus* and *Rhododendron* seed are; temperatures less than about 23° C and low surface moisture to decrease rot sensitivity. The seeds from these species are also short-lived following animal dispersal, particularly by birds, (i.e., viable for 7-9 months) (Bullock 1978, Keeley 1987, Powers and Oliver 1990). *Rhododendron* and *Rhamnus* seeds do not appear to be dependent on fire-maintained systems (Keeley 1987). Long-term survival of *Rhamnus* beneath mature forests is rare (Zedler 1981, Keeley 1986, Keeley 1987), and seedlings are most common in old stands (60-100+ years) where long fire-free intervals allow for the build up of seedling production (Keeley 1986). Keeley (1987) and Zedler (1981) report that seedling establishment is often episodic and coincides with periods of above normal rainfall. Such events would most likely have occurred at Eight Dollar Mountain during a time when litter cover and moisture levels were high but water table was low. This combination of conditions corresponds to Graumlich's (1987) precipitation reconstruction of the Pacific Northwest when the area was uniformly wet, particularly from 1930 to 1950. To date, no research has indicated the presence of *Rhamnus* or *Rhododendron* seedlings beneath *Ceanothus* or *Arctostaphylos* shrubs and only limited seedling establishment beneath mixed hardwood forests. Similarly, seedlings are not evident at the Eight Dollar Mountain site possibly because of the current drought cycle.

Litter cover is strongly related to succession along with time since the last fire, and significantly predicts the probability of a succession event. This is especially true of *Rhamnus*-dominated communities. The logistic results indicate that with a one unit change in the litter component of a forest, the succession event is seven times more likely to occur (.875/.125). Odds ratios close to or equal to 1 indicate there is a greater chance the event will occur with a small change in the independent variable, as is the case with *Darlingtonia* or *Rhamnus* as the dependent variable.

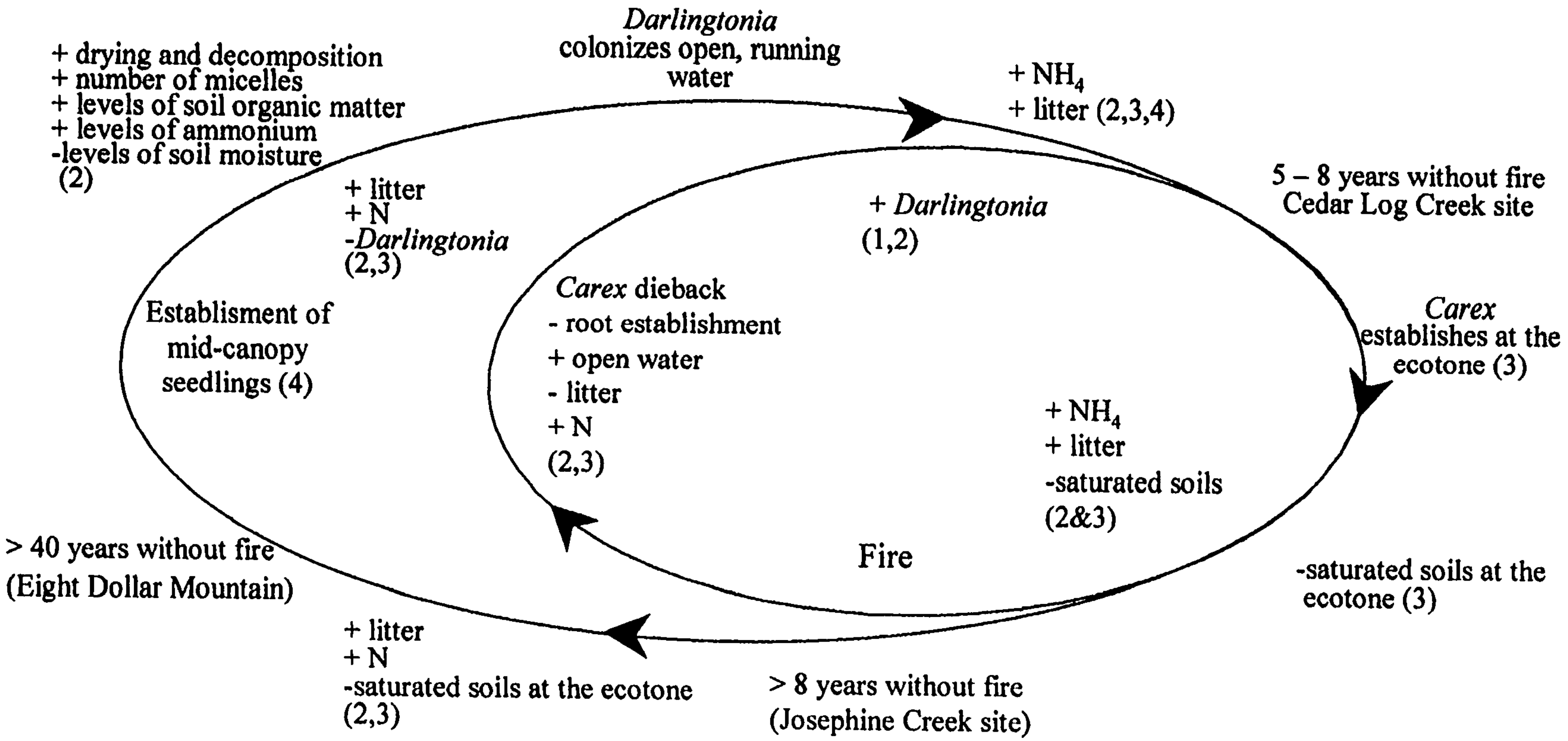
Succession in these serpentine fens appears to be facilitative (Connell and Slatyer 1977, Noble and Slatyer 1981). The primary colonization of the open serpentine fen is by a restricted suite of species dominated by *Darlingtonia*. *Darlingtonia* colonizes open water, promoting boggy conditions that can develop directly from wet sandy edges and thus accrete soil which can then be occupied by other perennials (Franklin and Dyreness 1988) (Figure 4.5 outer loop, upper right).

Carex, as a shade intolerant hydro-successional species capable of facilitating emergent marshes, is a likely second species to colonize saturated soils (Curtis 1959, Tiner 1991, Kudish 1992). A community of shrubby vegetation follows (approximately 40 years without fire) (Figure 4.5, outer loop, bottom left) and develops in the water-mediated soils (Curtis 1959, Tiner 1991, Kudish 1992). Harsh savanna communities on shallow and rocky, ferro-magnesium rich serpentine soils, possibly limit vegetation establishment except around rocks or existing vegetation. However, a change in climate and/or water table at Eight Dollar Mountain along with a litter base, provides enough foundation to support a shrub community (i.e., *Rhamnus*) at the fen to savanna ecotone.

Survival of any mid-canopy shrub seedlings is primarily underneath an already established canopy in the Eight Dollar Mountain site (100 years since the last fire). At Josephine and Cedar Log Creek sites, shrub seedlings have not established since recent burns. In fact, mid-canopy shrub seedlings were not observed at any of the three sites and only seedlings of trees were observed clumped around downed logs or at the base of existing *Arctostaphylos* and *Ceanothus* shrubs.

The fate of *Darlingtonia* in these systems is a concern and one that may be determined more by water than by fire (Figure 4.5). Juniper et al. (1989) suggest that *Darlingtonia californica*, unlike its southeastern relative, supports itself in an environment that may be more suited to the competitive invasion of other vigorous species. If so, then water plays an important role by removing the build up of nitrogen in the soil resulting from the sustained capture of insects. With chronic nitrogen deposition models, Ellison et al. (2002) found high levels of total nitrogen to severely

Figure 4.5. A hypothetical model of succession in the *Darlingtonia* fens showing the combined effects of environmental gradients, ecotones, and fire influencing structure and composition over time. Arrows denote direction over time and pluses/minuses indicate increases/decreases in the following stock. Numbers in parentheses refer to specific chapter results.



depress growth rates in a southeastern carnivorous plant, *Sarracenia purpurea*. This could explain the reduced *Darlingtonia* populations at Eight Dollar Mountain and suggest that fire may not be as important as running water to perpetuate carnivory.

Conversely, litter is most likely a driver in these systems and Jeffrey pine plays a major role in determining community flammability and ultimately facilitation in these sites at a landscape scale. Persistent litter forms a fuel bed which is deepest at Eight Dollar Mountain (Figure 4.5, outer loop, upper left). This fuel bed along with an open canopy from the Jeffrey pine allows rapid fuel drying during the summer months. Fuel connectivity between patches of litter around individual trees in these ecosystems is critical for fire spread during mid to late successional stages but also during mid-canopy seedling establishment. It may take several decades for some rocky sites to be colonized and support fires due to the patchiness of the fuel. A 40-year interval is likely to be sufficient to build up litter enough for these shrubs to establish. This time frame is consistent with estimated fire frequencies (Atzet and Wheeler 1982). Seedling establishment is often episodic and coincides with periods of above normal rainfall or during very wet years if the litter cover is sufficient (Keeley 1986). Fires are most likely to spread at the late-successional stage where *Rhamnus* and *Rhododendron* are already present and fuel is abundant, continuous, and relatively dry, at a time when these shrubs would resprout. Conversely, fire is unlikely beneath stands of broadleaved forest shrubs casting deep shade and maintaining higher fuel moisture. The regeneration strategies of many of the species at these study sites indicate that fire is an important historical factor continuing to shape these communities.

CHAPTER 5

SUMMARY AND CONCLUSIONS

R. H. Whittaker once noted of serpentine communities, "stand-to-stand regularity and predictability of patterning is an indication of stabilization" (1954: 281). At the same time, he claimed that empirical evidence supports the idea that Siskiyou serpentine vegetation was not a seral stage of the vegetation of neighboring soils, but was in fact its own distinctive climax with its own successional pathways. In this study, I explore several successon-related topics at three different *Darlingtonia* fens by examining the processes that explain why the fens exist where they do, how they differ from adjacent communities, and what environmental factors are responsible for their persistence.

The guiding hypothesis is that fire affects the spatial heterogeneity of the *Darlingtonia* fens, and that over time and in the absence of fire, these communities become smaller and less diverse in response to increasing nutrient availability. My results show that the processes maintaining these systems are complex and occur at two distinct spatial and temporal scales: within community processes on a seasonal time frame and, between communities at a landscape scale, over decades.

In Chapter 2, I demonstrated that soil ammonium and soil moisture are the most important variables explaining vegetation change across community boundaries. Ammonium levels generally decreased from the fen toward the savanna communities. While all three sites have this ammonium gradient, the greatest decline is at the Eight Dollar Mountain site. At two sites, recent prescribed burns may have been hot enough to liberate soil nitrogen while in the third case litter accumulation and subsequent decay (100 years without fire) may be contributing nitrogen to the system. In all cases, nitrogen levels are consistent with organic matter accumulations. Conversely, local soil moisture gradients increased in the direction of the fen for all sites with mesic levels detected at Eight Dollar Mountain in the mid-canopy shrub layer. Optimum locations of the dominant mid-canopy shrubs, *Rhododendron* and *Rhamnus,* were situated between the wettest sites for *Darlingtonia* and the driest sites for *Ceanothus* and *Festuca*. Along with community separation by soil NH_4 (slightly correlated with soil moisture), bulk density (strongly correlated with sand content) accounts for some spatial distribution of communities within a site, especially at the Eight Dollar Mountain site (100 years since fire).

The existence of these physical gradients, combined with the theoretical underpinnings to explain ecotones (Chapter 3), illustrates the importance of disturbance in these systems at both fine (community) and coarse (landscape) scales. Matching vegetation and soil nutrient discontinuities, or vegetation and water as in the case of Josephine Creek, implicate a physical factor, such as water, as the most important factor influencing vegetation structure and composition over time in these communities. Fluctuating environmental conditions at the boundary zone in the fen influences interactions with the adjacent vegetation, notably the facultative hydrophytic species found in all three sites, *Carex mendocum*. Moving water changes the physical and chemical characteristics of the boundary by deflecting sediment and debris to the edges where significant amounts of organic matter accumulate. This alters the physical structure of the boundary allowing *Darlingtonia* to act as sidewall vegetation for *Carex* and *Carex* to facilitate the entry of mid-canopy shrub seedlings by altering the structural makeup of the edges, and contributing to a less sandy, siltier soil structure. The TWINSPAN analysis did not distinguish the mid-canopy shrubs from the fen, possibly because of the interfusing nature of *Carex*. Though microhabitat events such as these occur on relatively small scales their importance in determining larger scale events should not be ignored.

At a landscape level, the presence of fire alters periodic small-scale disturbance events such as sediment movement in the fen by reducing live root masses at the ecotones and enables free-flowing water (Chapter 4) (Figure 4.5). Where local nutrients accumulate at any one of the ecotones, fire can either decrease the availability of ammonium in the short term by volatilization or increase ammonium by pyrolysis of organic material, by an increase in N mineralization, or by a leaching of N from the community floor into the soil. More importantly for *Darlingtonia*, fire can eliminate accumulated N levels, litter, and encroaching vegetation. Recent burns at Josephine Creek have eliminated litter cover and species composition suggests that a mid-canopy shrub layer is not likely to develop under a restored fire regime.

These findings illustrate the complex relationships among environmental gradients, community boundaries, and disturbance (water and fire) in maintaining the *Darlingtonia* fens of southwestern Oregon and northern California. Based on: 1) maximum savanna tree ages and the current demographic structure of tree populations, 2) the changing community composition since the last fire time, and 3) natural histories of key indicator species, litter, is the variable that best predicts the conditions leading to mid-canopy succession in these sites. These sites most likely require a litter accumulation greater than .2 cm in combination with 40 years without fire to develop a mid-canopy community. Together, litter, fire, and water play paramount roles in maintaining the *Darlingtonia* fens of southwestern Oregon. However, irrespective of the moisture regime and soil conditions, the absence of fire results in the decrease of *Darlingtonia* through the subsequent encroachment of either *Carex* or mid-canopy seedlings. Fire plays a critical role in these ecosystems as a driver of succession but appears less important than water as a disturbance factor, especially in light of removing the accumulation of soil nitrogen for *Darlingtonia californica*, specifically NH_4. Both environmental factors, fire and water, can influence many aspects of community ecology, structure and dynamics, and it is only through the inclusion of both these variables, along with soil properties, that complexity in the ecosystem and in uniquely adapted systems can be fully understood at two different temporal and spatial perspectives.

Implications

Fire and fire suppression play important roles in shaping the structure and composition of many plant communities in western North America (Agee 1993, Chang 1996). In the fen communities of southwestern Oregon, at least 8 years without fire are needed to develop a good seedbed before mid-canopy stage seedlings can emerge.

Management of the Siskiyou *Darlingtonia* fens has recently emerged as a conservation priority in the Pacific Northwest, due, in part, to their rich flora and fauna. From this study, conservation efforts aimed at preserving the biologically diverse flora and fauna of the *Darlingtonia* fen ecosystems must consider a more regional landscape perspective. Prescribed burns, in particular, need to include associated communities, particularly the mid-canopy shrub community, which is likely maintained by fire suppression. Based on the seedling requirement of the shrub species, prescribed burns in these systems should occur every 5 - 8 years. Furthermore, water management efforts, such as maintaining water levels, should not be understated as anthropomorphically lowering these levels may alter microhabitat processes and artificially hasten the demise of the *Darlingtonia* fens.

Further Research

Lacking appropriate definition of temporal scale or sufficient replication poses serious challenges for extrapolation and prediction of research results. Generalizations regarding ecosystem change require data collection over annual to decadal time scales. Thus, the greatest opportunities for further research in the *Darlingtonia* fens involve long-term monitoring or even short term controlled burns. Monitoring, should include continued seedling and sapling surveys to establish long term regeneration patterns following prescribed burning. Prescribed burns must include expanded research on fire behavior in these ecosystems (e.g., individual species' responses to burns, ecotone responses to burns, community responses to burns), as well as N tracer research in nutrient cycling, geomorphology and location of the fens relative to landslides, and genetic research regarding age of fens, is also crucial to predict potential fire effects on succession. More research on the litter component in these systems is required before its role in successional relationships can be fully understood, for example, does the mid-canopy litter have phytotoxic effects on either *Rhamnus* or *Rhododendron*. Secondly, are the competitive costs of germination in these systems outweighed by increased shading or increased water availability. Thirdly, information regarding post burn effects on gradients would be useful for a more comprehensive investigation.

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APPENDIX A

TWINSPAN Results

Cedar Log Creek transect A

```
                        1
                 5678943012

 3  LDca         -55--4----  000
 7  Sanguis      -443------  000
 8  Tofield      35---5----  000
 4  Erioph       54554522--  001
 6  Rudbeck      5555453---  001
 5  Festuca      ----2545--  01
 9  Pjeff        -------2--  01
 1  Ceanoth      --------5-  1
 2  Carex        -----55-55  1

                 0000000011
                 00000011
                 000001
```

Cedar Log Creek transect B

```
                 456781239

2  LDca          4554-----  00
6  Sanguis       4552-----  00
7  Tofield       455------  00
8  Pjeff         -5-------  00
5  Rudbeck       45554----  01
1  Ceanoth       -----5---  1
3  Erioph        55554-543  1
4  Festuca       -----5553  1
9  Agrostis      ----2---5  1

                 000001111
                 00001
```

Cedar Log Creek transect C

```
                 456731289

1  LDca          55513----   00
5  Sanguis       55543----   00
6  Tofield       -54-2----   00
7  Rhodo         5--3-----   00
2  Erioph        55552434-   01
4  Rudbeck       55533--42   01
3  Festuca       ----545--   1
8  Agrostis      --3545555   1

                 000011111
                     01111
```

Cedar Log Creek transect D

```
                         1
                  8456739012

 2  LDca          -555------  00
 7  Tofield       -4554-----  00
 3  Erioph        254554----  01
 5  Rudbeck       3433534---  01
 6  Sanguis       5555534---  01
 1  Chokeche      5-----55--  10
 8  Rhodo         -----545--  10
 9  Pjeff         -------3--  10
10  Libocedr      ------5---  10
 4  Festuca       -----4--44  11
11  Agrostis      ----2-5354  11

                  0000011111
                  0111100011
```

Cedar Log Creek transect E

```
                   456371289

 4   Rudbeck       5--55-44-   00
 5   Sanguis       ---3-----   00
 7   Pjeff         ---5-555-   00
 2   LDca          5551-----   01
 3   Erioph        45455555-   01
 8   Libocedr      3--4-----   01
 1   Chokeche      -------55   1
 6   Rhodo         -5---4-32   1
 9   1Manzan       --------5   1

                   000000001
                   00011111
                      00111
```

Cedar Log Creek transect F

```
                      11   1
                784569021231

  4  LDca       53--1-------  00
  5  Erioph     54-55-------  00
  3  Carex      345555------  01
  7  Rudbeck    455543------  01
  8  Tofield    1--2--------  01
  1  Chokeche   -----54-----  10
  9  Pjeff      -----554---3  10
  2  Ceanoth    --------2154  11
  6  Festuca    --------5555  11
 10  Agrostis   ------44---3  11

                000000111111
                000001001111
                00111
```

Josephine Creek transect A

```
                 1234567

1  LDca          55554--  0
2  Hastings      5555-13  0
4  Tofield       2--3--1  0
5  Rhodo         1------  0
3  Sanguis       2333543  1
6  Agrostis      553-555  1

                 0000111
```

Josephine Creek transect B

```
                312456789

1  LDca         5555555--  0
2  Hastings     54232----  0
4  Tofield      --121----  0
6  Agrostis     -55455554  0
3  Sanguis      212221343  1
5  Pjeff        --------2  1

                000000011
                0111111
                 0000
```

Josephine Creek transect C

```
                 1234567

1  LDca          55554--  0
2  Hastings      555----  0
6  Agrostis      322555-  0
3  Rudbeck       -----11  1
4  Sanguis       4314322  1
5  Pjeff         ------2  1

                 0000001
                 000111
```

Josephine Creek transect D

```
                    1234567

  1  LDca           55555--   0
  2  Hastings       451444-   0
  3  Rudbeck        ----223   1
  4  Sanguis        5--1222   1
  5  Agrostis       4423355   1

                    0000011
                    01111
```

Josephine Creek transect E

```
      451236789

1     LDca         55555544-   0
2     Hastings     -2443455-   0
3     Sanguis      ----1--13   1
4     Tofield      22--1---2   1
5     Agrostis     21545-2-5   1

                   000000001
                   00111111
```

Josephine Creek transect F

```
                 123945678

5  Agrostis     5555332-2  1
4  Tofield      -13222---  1
3  Sanguis      54---1---  1
2  Hastings     423-5545-  0
1  LDca         555455544  0

                000011111
                    00001
```

Eight Dollar Mountain transect A

```
                     1  11  11  1111
                     489016723455678123

  4  LDca            35555445522-------   00
  8  Sanguis         -54554554-2-------   02
  3  Carex           555555555444------   01
  6  Hastings        -55--553535-------   01
  7  Rudbeck         555554555-34------   01
  9  Rhodo           54---5555555------   01
 10  Pjeff           -----5----535-----   10
 13  Agrostis        -----3525-5-532---   10
  1  Chokeche        ---------45-11-545   110
  2  Ceanoth         -----------------1   110
  5  Festuca         ------------555555   111
 11  Libocedr        ------------1-----   111
 12  lManzan         ------------5-2455   111

                     000000000000111111
                     000000000111000111
                     000001111
                     01111
```

Eight Dollar Mountain transect B

```
                       11111   1  1 11
                    789120344565126378

 4  LDca            55543555--5-------   00
 7  Hastings        5553523-----------   00
 8  Rudbeck         55555555--4-------   00
 9  Sanguis         5455445---3-------   00
 3  Carex           5-555554525-4-----   01
 5  Erioph          ---------5--------   01
10  Rhodo           -----4555555------   01
11  Pjeff           ------5-5-55453---   10
 1  Chokeche        ------3--55-544544   110
12  Libocedr        ------------3-3---   1110
14  Agrostis        ------------4-4-1-   1110
 2  Ceanoth         -------------1-1-2   1111
 6  Festuca         ------------554555   1111
13  1Manzan         --------------3455   1111

                    000000000000111111
                    000000001111000111
                    00000011
                    000001
```

Eight Dollar Mountain transect C

```
                           111
                  123456789012

  2  Carex        555544241---   00
  7  Sanguis      445554143---   00
  3  LDca         555555555---   01
  5  Hastings     333555355---   01
  6  Rudbeck      555555555---   01
  8  Rhodo        ----31555---   01
  1  Chokeche     ------43344-   10
  4  Festuca      ---------555   11
  9  Pjeff        ---------5--   11
 10  Libocedr     ---------2--   11
 11  lManzan      ---------5-2   11
 12  Agrostis     ---------511   11

                  000000000111
                  000000111
                  000011
```

Eight Dollar Mountain transect D

```
   11   1  1 11 111
              802679145324516783

 4  LDca      3555455--4--------  00
 6  Hastings  5535543555--------  00
 7  Rudbeck   555555545---------  00
 8  Sanguis   555444524---------  00
 3  Carex     545515535---5-----  01
 9  Rhodo     ---5545555-5-1----  01
11  Libocedr  -------43-----1---  01
 1  Chokeche  -------555555344--  10
10  Pjeff     ----------555-5---  110
 2  Ceanoth   ----------2------3  111
 5  Festuca   ----------5--55555  111
12  1Manzan   --------------5-3-  111
13  Agrostis  -------------1532-  111

              000000000011111111
              000000011100011111
              0001111      00001
```

Eight Dollar Mountain transect E

```
                      111  111   111
                  478901256345123786

 8   Sanguis      -555555-----------   000
 3   Carex        5555555-55--------   001
 4   LDca         -555555-55--------   001
 6   Hastings     35555555-5--------   001
 7   Rudbeck      5555555554--------   001
 9   Rhodo        -55555555544------   01
 1   Chokeche     -------325-5555545   10
 2   Ceanoth      ------------231-2-   110
 5   Festuca      ------------555555   110
12   1Manzan      ------------555453   110
10   Pjeff        -----------------5   111
11   Libocedr     -----------------3   111
13   Agrostis     ---------------1-5   111

                  000000000001111111
                  000000011110111111
                  0111111     000001
```

Eight Dollar Mountain transect F

```
                         111111
                 647895123012345

  3  Carex       55553555-------  000
  4  LDca        3-----5--------  000
  6  Rudbeck     5545555555-----  000
  7  Sanguis     -----13--------  001
  8  Rhodo       ------555555---  001
  9  Pjeff       ------55-455---  001
  1  Chokeche    ------55355-444  01
  2  Ceanoth     --------------2  1
  5  Festuca     ------------455  1
 10  Libocedr    ------------5--  1
 11  lManzan     ------------334  1
 12  Agrostis    ------------41-  1

                 000000000000111
                 000000111111
                 011111001111
                  00001
```