

AN ABSTRACT OF THE DISSERTATION OF

Craig A. Carr for the degree of Doctor of Philosophy in Rangeland Ecology and Management presented on October 16, 2007.

Title: An Evaluation of Understory Vegetation Dynamics, Ecosystem Resilience and State and Transition Ecological Theory in an Eastern Oregon Ponderosa Pine Forest

Abstract approved:

William C. Krueger

Relatively recent increases in ponderosa pine abundance have effected unprecedented changes to ecosystem structure and function. Efforts to restore ponderosa pine systems are often focused on the manipulation of tree structure and the re-introduction of a more natural fire regime. Successful restoration should also incorporate understory components but information addressing changes in understory species is minimal for Pacific Northwest ponderosa pine forests. Moreover, state and transition models (STM) derived from the concepts of non-equilibrium ecology may be appropriate for characterizing ecosystem dynamics in modern ponderosa pine forests, however this approach has not previously been used. The focus of this research was to evaluate ecosystem dynamics within a hypothesized STM framework and to experimentally assess the existence of model components with particular emphasis on understanding understory species dynamics.

The analyses of vegetation, soil, and environmental attributes measured in a eastern Oregon ponderosa pine forest indicated that increased ponderosa pine occupancy modified the under-canopy environment through alterations in light, nitrogen availability, and soil temperature and was related to reductions in understory species diversity caused by a major shift in understory character away from the dominance of perennial bunchgrasses. Light availability appeared to be the most influential driver in understory species distribution. Similar results were observed in a greenhouse experiment that identified high light intensity as significant in

generating increased *Festuca idahoensis* Elmer growth, biomass and vigor. A seed bank assessment to evaluate recovery potential from diminished understory conditions indicated that understory species dominant in open ponderosa pine forests do not form a persistent seed bank and can not be relied upon as a tool for their recovery.

These data described ecosystem dynamics in accordance with the hypothesized STM model. Loss of ecosystem resilience associated with a fire loss threshold can initiate additional degradation in the understory component, however, pine influenced alterations to the under-canopy environment did not appear irreparable and restoration practices that reduce pine occupancy should enhance the conditions for perennial bunchgrass growth. Successful restoration will require the re-introduction of desired understory species seeds or other viable plant material when considering stands that have lost the understory component.

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An Evaluation of Understory Vegetation Dynamics, Ecosystem Resilience and State
and Transition Ecological Theory in an Eastern Oregon Ponderosa Pine Forest

by
Craig A. Carr

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APPROVED:

Major Professor, representing Rangeland Ecology and Management

Head of the Department of Rangeland Ecology and Management

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Craig A. Carr, Author

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CONTRIBUTION OF AUTHORS

Dr. William Krueger assisted in the development and study design of each research component described in this thesis and was instrumental in editing the associated manuscripts. Dr. Duane Lammers assisted in the soil classification and was instrumental in writing and editing the soils descriptions.

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An Evaluation of Understory Vegetation Dynamics, Ecosystem Resilience and State and Transition Ecological Theory in an Eastern Oregon Ponderosa Pine Forest

CHAPTER 1: GENERAL INTRODUCTION

Introduction

Ponderosa pine (*Pinus ponderosa* Dougl.) forests are common throughout much of western North America. They occur from southern British Columbia through the Pacific Northwest and into California. Their distribution spans as far east as Nebraska and south into the American Southwest and northern Mexico (Figure 1).

Within the Pacific Northwest, ponderosa pine forests have a wide geographical range and can generally be found between 1200 and 1800 m elevation, separating higher elevation closed canopy forests dominated by Douglas fir (*Pseudotsuga mensizii* (Mirbel) Franco) from lower elevation grassland and shrubland vegetation types (Franklin and Dyrness 1973 and Agee 1993).

Ponderosa pine forests evolved under a regime of frequent, low-intensity surface fires. These fires limited understory pine regeneration and maintained an open park-like forest structure with a preponderance of large-diameter well spaced trees and a vigorous understory of herbaceous and/or shrubby species (Weaver 1943, Cooper 1960, Wright and Bailey 1982, and Agee 1993). In the time since European settlement, grazing, logging, and active fire suppression practices have combined to effect a substantial increase in the fire return interval and, along with favorable conditions for ponderosa pine seedling establishment, have generated substantial increases in pine density and canopy cover, reductions in understory growth and vigor, and have altered understory species composition. These alterations to ecosystem structure have lead to increased insect and disease outbreaks, limitations on available wildlife habitat, reduced forage production, and an increased risk and occurrence of severe stand-replacing wildfires (Weaver 1943, Dickman 1978,

Covington and Moore 1994, Covington et al. 1997, Tiedemann et al. 2000, and Allen et al. 2002).



Figure 1. North American distribution of ponderosa pine. Image edited from United States Geological Survey (1999).

Recognition of the unhealthy status of many arid forest systems and concern over the risk of stand-replacing wildfire has led to increased implementation of forest thinning and under-burning and has also generated significant interest in system restoration through the reintroduction of historic fire patterns. However, it is uncertain if the re-introduction of fire will stimulate the necessary processes for recovery of system structure and function. Several authors have discussed the permanence of the altered status, and the likelihood of multiple trajectories of ecosystem change (Arno et al., 1985, Johnson 1994, Johnson et al. 1994, Stephenson 1999, Tiedemann et al. 2000, and Griffis et al. 2001) implying that movement of contemporary stands in the direction of pre-European conditions may require efforts beyond simply re-introducing a more natural fire regime.

Many studies have investigated the impacts of fire on ecosystem components within contemporary forests (i.e. forests with altered structure and function) (eg. Covington and Sackett 1984, White 1985, White et al. 1991, Wright and Hart 1997, Busse et al. 2000, DeLuca and Zouhar 2000, and Robichaud 2000), tested the effectiveness of fire regime restoration, stand structure reconstruction, and their combination, (Arno et al. 1995, Youngblood and Riegel 1999, Fulé et al. 2001, Fulé et al. 2004 and Wallin et al. 2004), and debated the merits of structure based restoration (i.e. stand thinning) versus process based restoration (re-introduction of fire) (Stephenson 1999). Several publications identify fire as a keystone ecological process and that re-introduction of a more frequent fire regime combined with the reconstruction of stand structure will ensure the recovery of internal system feedbacks that provide for eventual stand restoration (e.g. Fulé et al. 1997 and Moore et al. 1999). However, changes in the hydrological, energy flow, or nutrient cycling processes may preclude the attainment and maintenance of more natural fire regimes, stand structures and feedback mechanisms suggesting non-equilibrium ecology-based models of ecosystem dynamics (i.e. State and Transition models) may be well suited for characterizing contemporary ponderosa pine ecosystem dynamics.

Historic Role of Fire in Ponderosa Pine Ecosystems

Although the specific fire history of a ponderosa pine ecosystem is dependent upon site characteristics, regional climatic conditions and land use history, these forests generally existed as a mélange of variable sized and aged ponderosa pine patches maintained spatially and temporally through periodic low-intensity surface fires (Cooper 1960, West 1969, Wright and Bailey 1982, White 1985, Morrow 1985, Savage and Swetnam 1990 and Agee 1993). Cooper (1960) described ponderosa pine stand evolution as a consequence of the shade intolerance of ponderosa pine, episodic seed production and seedling establishment, and frequent fire events. Savage and Swetnam (1990) also emphasized the importance of climatic variation to the pulse establishment of ponderosa pine seedlings.

Successful seedling establishment, generally associated with heavy seed crops and favorable growing season soil moisture, occurs preferentially in areas of exposed mineral soil and often in forest gaps created by individual tree or whole patch death (Cooper 1960, Wright and Bailey 1982, Habeck 1992 and Agee 1993). Tree mortality is associated with insect, disease, wind, lightning or other environmental stress events and frequently in some combination (Wright and Bailey 1982 and Pyne et al. 1996). New seedlings are either protected from immediate fire activity because of initial low fuel loads associated with intra-patch positions (Agee 1993) or inherently susceptible to fire because of their low stature, thin bark and placement within the fuel matrix of herbaceous vegetation and pine litter (Wright and Bailey 1982). Thus, seedlings within mature tree patches or open areas with adequate fuel loads will generally be removed by fire while those in gaps generated by tree loss may survive several years before a sufficient fuel load is present to carry a thinning fire. Future burns will thin pine saplings by killing the smaller, thin-barked trees while leaving the larger more vigorous trees (Biswell et al. 1973) to re-fill the gap initially created by the loss of the mature trees.

Thus fire promoted the maintenance of an open patchy ponderosa pine forest by killing saplings growing under mature trees or in open areas, exposing mineral soil to provide the seedbed required for recruitment to replace dead trees or patches, thinning regeneration patches once adequate fuels are present, and limiting the occurrence of stand-replacing events through reduced fuel accumulation. This pattern of death, recruitment and fire over time effectively maintained the spatial arrangement at the landscape scale.

Although fires in ponderosa pine forests typically had little direct impact on understory herbaceous and shrubby components, the maintenance of an open tree canopy, reduced pine sapling competition and limited litter accumulation generally enhanced the conditions for understory growth (Wright and Bailey 1982 and Agee 1993). Although there are exceptions, graminoid, forb and shrub species common in ponderosa pine understories recover quickly (1 – 3 years) after low-intensity surface fires (Wright and Bailey 1983 and Agee 1993).

Fire Frequency

The fire history literature presents a somewhat confusing picture with respect to the periodicity of fire (Romme 1980). Metrics including fire return interval (or fire free interval), mean fire return interval (or mean fire free interval), and fire frequency are area dependent and can vary significantly within the same study area (Romme 1980). Generally, as the area sampled increases the interval between fire occurrences in the sample area decreases (Arno 1983). Bork (1984) for example, described fire return intervals for ponderosa pine forests that varied by as much as 17 years where the smallest fire return intervals were calculated from the largest combined sample area.

Romme (1980) proposed the following definitions for terminology in connection with fire history:

“A fire return interval is the number of years between two successive fires documented in a designated area; the size of the area must be clearly specified.

Mean fire return interval is the arithmetic average of all fire intervals determined in a designated area during a designated time period; the size of the area and the time period must be specified.

Fire frequency is the number of fires per unit of time in some designated area; the size of the areas must be specified.

Fire rotation (or fire cycle) is the length of time necessary for an area equal to the entire area of interest to burn; the size of the area of interest must be clearly specified.”

The fire return interval and mean fire return interval are measures of fire periodicity commonly used in describing the fire regime of ponderosa pine forests (Baker and Ehle 2001). In contrast to southwestern ponderosa pine forests, relatively few fire history studies have been performed in ponderosa pine forests of the Pacific Northwest.

Weaver (1959) evaluated fire periodicity in ponderosa pine forests at the Warm Springs Indian Reservation on the east slope of the Cascade mountains in

Oregon by examining four individual ponderosa pine trees (or stumps) from four widely separated locations. Average fire return intervals for the four trees were 17, 11, 16, and 37 years. The 37 year fire return interval was for a ponderosa pine tree in higher elevation mesic conditions associated with mixed conifer forests where one would expect a longer fire free period.

Prior to active fire suppression (ca. 1914) the average fire return interval was 10 years in a seral ponderosa pine forest in the Blue Mountains of eastern Oregon (Hall 1973). Hall evaluated the fire scars on one ponderosa pine tree to acquire this fire return interval.

A more thorough investigation of the fire history on the Warm Springs Indian Reservation by Soeriaatmadja (1965) indicated average fire return intervals of 16.5 (75 fire scarred stumps sampled), 14.2 (123 fire scarred stumps sampled), 24.6 (64 fire scarred stumps sampled), and 30.2 years (43 fire scarred stumps) for 4 different locations within the reservation. Similar to Weaver (1959), the two largest fire return intervals were associated with more mesic conditions characteristic of climax mixed coniferous forests (Soeriaatmadja 1965).

Bork (1984) provided a complete cross dated set of mean fire return intervals for several locations throughout central Oregon ponderosa pine forests (Table 1). These data incorporated fire scars up to 1900 and indicated a regional mean fire return interval of 17 years. Although Bork provided site and regional fire return intervals based on individual tree fire scar history, she suggests that mean fire return intervals that incorporate plot means as the base data give a more accurate indication of mean fire return interval and is the most useful way of expressing the data.

Miller and Rose (1999) provided cross dated composite fire return intervals for ponderosa pine growing on the edge of the sagebrush steppe in southern Oregon. Mean fire return intervals within sample locations varied from 12 - 27 years while the range of fire return intervals was 3 – 54 years (Miller and Rose 1999). The composite mean fire return interval for the entire study area was 7.7 years (Miller and Rose 1999).

Table 1. Fire history data for three sites sampled by Bork (1984) in ponderosa pine forests of central Oregon.

	Cabin Lake	Pringle Butte	Lookout Mountain	Region
Trees Sampled	31	35	48	114
Range of # of fires per tree	1 – 8	4 – 30	2 – 10	1 – 30
Average plot MFRI	24 years	11 years	15 years	17 years
Average individual tree MFRI	7 years	4 years	8 years	6 years

Note: MFRI (mean fire return interval) calculated to 1900. Six 40 acre plots were sampled at each site, thus average plot MFRI was calculated as the sum of plot MFRI divided by 6.

Heyerdahl et al. (2001) evaluated fire frequencies of four watersheds in the Blue Mountains of eastern Oregon. The overstory vegetation of these sites was dominated primarily by ponderosa pine, however, Douglas fir and grand fir (*Abies grandis* (Dougl.) Forbes) were also present although in sub-dominant abundances. The southern more xeric watersheds exhibited mean fire return intervals of 14.2 and 16.4 years while the two northern watersheds, influenced climatically by moist maritime air traveling up the Columbia River gorge, had mean fire return intervals of around 35 years. Fire frequencies were evaluated for the period spanning 1687 – 1900.

Some research has recently challenged the view that frequent low-severity fire regimes were significant ecological forces in the evolution and maintenance of pre-settlement ponderosa pine forests (Baker and Ehle 2001 and Baker 2006). Shinneman and Baker (1997) suggested that dense thickets of pine regeneration and dense patches of older trees along with higher incidences of stand-replacing crown fires were common components of historic ponderosa pine forests. Baker and Ehle (2001) contended that fire return intervals used in developing ponderosa pine fire histories are uncertain because they do not adequately account for unburned areas or unrecorded fires, are based on biased sampling regimes, do not account for spatial

variability of the fire regime and do not consider the fire-free period between seedling germination and the first fire scar. Baker and Elhe (2001) suggested that reported mean fire return intervals for ponderosa pine forests may significantly underestimate the population mean fire return intervals and fire rotations. Although recognizing the limitations in applying fire return interval statistics (mean, median, composite, filtered) to the quantification of fire regimes, Fulé et al. (2006) suggested that these metrics are a repeatable indicator of fire frequency, and add to a greater body of converging evidence from which the character of historical fire regimes emerge. Moreover, a modern calibration of fire scar studies suggested that fire scar analyses accurately detected past fires, lending support to the currently accepted interpretation of ponderosa pine fire history as a regime of low-intensity surface fire (Fulé et al. 2006). Recent comprehensive fire scar studies have provided more evidence in support of frequent, low-severity surface fires as the dominant fire regime in pre-settlement ponderosa pine forests (Fulé et al. 2006, Van Horne and Fulé 2006 and C.E. Ferris, unpublished data as cited in Fule et al. 2006).

Contemporary Ponderosa Pine Forests

Post-settlement changes in ponderosa pine forest structure are often causally linked with fire exclusion and lengthened fire return intervals. Covington and Moore (1994) describe several factors related to European settlement that facilitated the reduction in fire frequency; roads and trails that reduced fuel continuity, intensive domestic livestock grazing in the late 1800s reduced herbaceous fuel abundance; and, active fire suppression limited the spread of fires once ignited. These factors combined with favorable conditions for ponderosa pine seed germination and seedling establishment effected unprecedented changes in the fire regime and forest structure in ponderosa pine ecosystems (Covington and Moore 1994 and Johnson 1994)

In ponderosa pine forests of the Pacific Northwest, Weaver (1943, 1959) suggested that the lack of fire had resulted in 1) the development of dense even-aged

stands of ponderosa pine reproduction; 2) large scale invasion of shade-tolerant, fire sensitive species (e.g. Douglas fir) into ponderosa pine forests; 3) wide spread epizootics of western pine beetle (*Dendroctonus brevicomis* LeConte), and; 4) a tremendous increase in fire hazard and occurrence of high severity stand replacement fires. Dickman (1978) reported a significant conversion from ponderosa pine to Douglas fir in ponderosa pine forests of the Umpqua National Forest, Oregon, and suggested that reduced fire frequency was the most likely cause of the invasion. Data from Heyerdahl et al. (2001, Figures 2 and 3) showed the substantial change in fire pattern occurring around 1900. A change in the relationship between cumulative area burned and date is evident ca. 1900 and indicated a decrease in the area burned and in the frequency of fire in the southern Blue Mountains of Oregon (Figure 2). A similar pattern is observed in the fire chart Figure 3 indicating relatively few post-1900 fire occurrences. Although the data presented in Figures 2 and 3 represent one southern Blue Mountains watershed (Dugout), the other three watersheds evaluated by Heyerdahl et al. (2001) showed similar trends.

Studies from ponderosa pine forests in the southwest (Cooper 1960), Idaho (Barrett 1988), and Montana (Gruell et al. 1982) suggested a common lengthening of the fire return interval, increase in tree densities and fuel loading, and escalation of occurrences of crown fires across the range of ponderosa pine forests (Covington and Moore 1994). These changes in fire regime and consequent alterations in forest structure have effected negative changes in other ecosystem attributes and processes including decomposition and nutrient cycling, hydrologic function, biological diversity, wildlife habitat, understory species abundance, and aesthetic value (Covington and Moore 1994, Johnson 1994, Tiedemann et al. 2000, Allen et al. 2002).

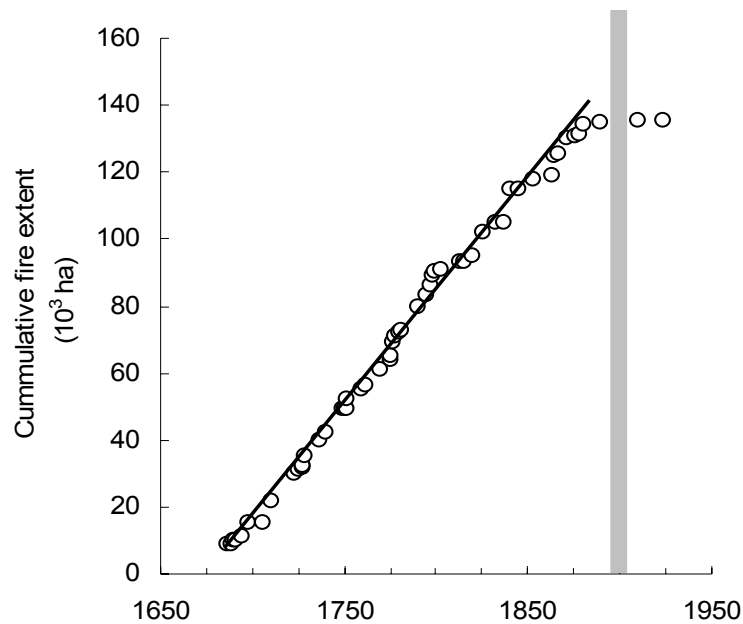


Figure 2. The cumulative fire extent of a southern Blue Mountains ponderosa pine forest. Trend line represents the best fit of the data for the period of 1687 to 1900. The shaded vertical bar identifies the year 1900. Adapted from Heyerdahl et al. 2001; data are approximate.

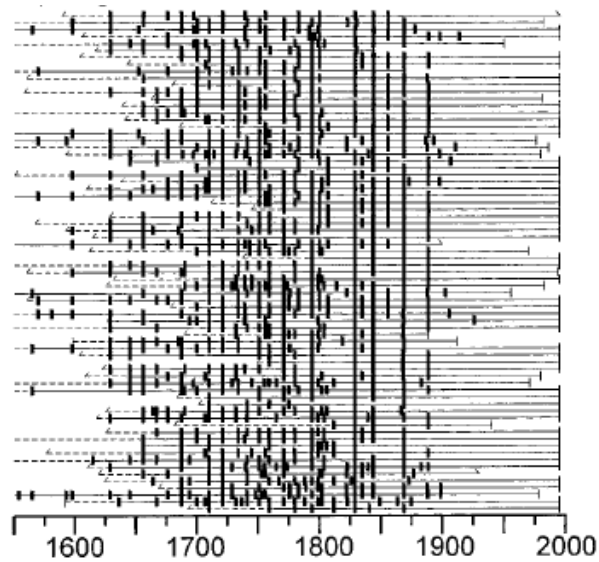


Figure 3. A fire history chart representing a southern Blue Mountains ponderosa pine forest, reproduced from Heyerdahl et al. (2001). Each horizontal line represents a sampling unit while the vertical lines indicate fire events.

Soils

The steady accumulation of relatively recalcitrant pine needle litter in contemporary ponderosa pine forests can disrupt decomposition and nutrient cycling thereby limiting availability of mineral sources of plant nutrients (Covington and Sackett 1984, Covington and Sackett 1990, Kaye and Hart 1998a and Selman et al. 2003). Moreover, lower under-canopy soil temperature and soil moisture associated with greater tree density may exacerbate the stagnation of nutrient cycling processes (Covington et al. 1997). Kaye and Hart (1998a) found almost double the rate of net nitrogen mineralization in pre-settlement openings when compared to post-settlement pole-sized ponderosa pine patches. They suggested that pre-settlement forests likely had higher ecosystem-level nitrogen cycling rates and that these rates likely declined with ponderosa pine ingress. Relict open patches also exhibited higher rates of microbial activity compared to dense post-settlement pine (Kaye and Hart 1998b).

An additional threat to ecosystem nutrient status in contemporary ponderosa pine forests is the increasing abundance of nutrients stored in standing live and dead trees, down trees, and litter. These nutrient reserves are unavailable for plant growth and are extremely vulnerable to loss through fire, particularly when considering contemporary high-severity and high-intensity fire regimes (Klemmedson 1975, Covington and Sackett 1984, Covington and Sackett 1990, and Tiedemann et al. 2000).

Hydrology

The hydrologic cycle can be generalized into four components: precipitation, runoff, evapotranspiration, and storage (Satterlund 1972). In arid and semi arid environments the effects of evapotranspiration dominate the water budget (Brandes and Wilcox 2000). Recent alterations in ponderosa pine forest structure have influenced the hydrologic cycle primarily through changes in the evapotranspirative demand and may be responsible for reduced water yields (Baker 1986 and Covington and Moore 1994). Moreover, increased competition for limited soil moisture has

negatively impacted tree growth, contributed to increased tree susceptibility to insect and disease attack, and reduced understory species vigor (Sartwell 1971, Riegel et al. 1992, Covington and Moore, 1994 and Tiedemann et al 2000).

In inland ponderosa pine forests of the Pacific Northwest, increased tree density is generally related to increased transpirational demands and thus higher growing season water use. Barrett and Youngberg (1965) and Barrett (1970) compared soil moisture use (the difference between spring and fall soil moisture) among central Oregon ponderosa pine stands of varying pine density and found that lower-density plots exhibited lower moisture use. The presence of a vigorous understory also increased water use relative to stands similar in tree density but without a significant understory component (Barrett and Youngberg 1965). Helvey (1975) found similar results in a ponderosa pine forest near Baker City, Oregon. In this study, heavily thinned plots expressed substantially lower moisture loss over the growing season. Baker (1986) identified an increase in watershed water yield associated with reducing ponderosa pine abundance in Arizona.

In both the Helvey (1975) and Baker (1986) studies, the reduction in water use associated with thinning treatments diminished over time. Both authors suggested that increasing vigor of understory and an expanding rooting profile of residual ponderosa pine trees eventually recapture soil moisture released through the thinning treatments. Moreover, Baker (1986) indicated that leaf area index of a thinned pine stand with a vigorous understory may exceed that of an untreated stand and will provide adequate transpirational surface area to equal that of the untreated stand. These results appear to correspond with Hibbert (1979) and Baker (2003) who indicated that reducing transpiration in arid ecosystems (<460mm annual precipitation) is difficult because all types of vegetation appear equally efficient at using the relatively small amount of available moisture.

The bulk of the precipitation that falls throughout ponderosa pine regions of the Pacific Northwest occurs as winter-time snow. Spring melt of the accumulated snow pack is the primary source of soil moisture, groundwater recharge, and stream flow in these ponderosa pine watersheds and as a consequence dominates the annual

hydrograph (Toews and Gluns 1986). Forest canopy structure influences snow accumulation and can subsequently moderate hydrological function. Numerous studies from a variety of forest types indicated that dense stand conditions that promote snow interception and subsequent ablation reduce the quantity of snow accumulated (e.g. Haupt 1951, Gary and Troendle 1982, Toews and Gluns 1986 and Moore and McCaughey 1997). Moreover, small openings, either patch clearcuts or natural clearings accumulated more snow than adjacent low-density forest sites (Haupt 1951; Gary and Troendle 1982 and Toews and Gluns 1986). These responses are mitigated by other factors that influence snow accumulation in forested watersheds including, climate, elevation, and topography (Moore and McCaughey 1997).

The increasing abundance of small-diameter trees associated with contemporary ponderosa pine forest structure may effect reductions in total snow accumulation and subsequently impede hydrological function. Haupt (1951) found that dense pole sized ponderosa pine stands exhibited low levels of snow accumulation when compared to more open or sapling structures. Baker (2003) suggested that creating forest openings in contemporary ponderosa pine stands may concentrate snow accumulation and increase soil moisture availability, however gains in soil moisture related to canopy structure influenced improvement in snow accumulation may be short-lived depending on the rate of root invasion and canopy re-establishment (Haupt 1979).

Understory Species Abundance

Numerous studies from a variety of ecosystems have been published that report on interactions between overstory and understory components. Ffolliot and Clary (1982) provided a relatively complete bibliography up to 1982 of publications describing these relationships. The general trend expressed throughout the literature is that increasing tree occupancy results in a decrease in understory abundance. Figure 4 displays this relationship for Arizona ponderosa pine forests (panel A) and Oregon mixed conifer forests (panel B). Krueger (1981) also described a non-linear

relationship between tree canopy cover and understory production and indicated that a sharp decline in understory abundance is initially observed at around 20 – 30% tree canopy cover.

The majority of the research pertaining to overstory-understory interactions has investigated the response in biomass of graminoid, forb, and shrubby species to differing levels of tree influence (measured by density, basal area, or canopy cover). For example, Rummell (1951), Moir (1966), McConnell and Smith (1970), Barrett (1982), Riegel et al. (1992), Uresk and Severson (1998), Wienk et al. (2004), and Moore et al. (2006) all indicated that understory production was lower under increasing levels of ponderosa pine abundance.

Krueger (1981) provided insight into the mechanisms associated with these relationships by suggesting that trees influence understory production by modifying the complex interaction of light, heat, litter accumulation and moisture and identified moisture as the dominant force governing understory herbaceous production in forested rangeland typical in eastern Oregon. Riegel et al. (1991, 1992, and 1995) used these hypotheses to direct their research of overstory – understory interaction in an eastern Oregon ponderosa pine forest and indicated that 1) below ground resources (nutrients and water) were the primary controlling factors in understory production (Riegel et al. 1992); 2) the combination of increased soil moisture and nitrogen provided the greatest response in understory production, although both moisture and nitrogen additions individually improved biomass response compared to the control (Riegel et al. 1991), and; 3) the composition of understory species was variously influenced by light availability, soil moisture and soil nutrients, the response determined by individual species physiological limitations or morphological adaptations (i.e. rhizomatous growth form) for resource capture (Riegel et al. 1995).

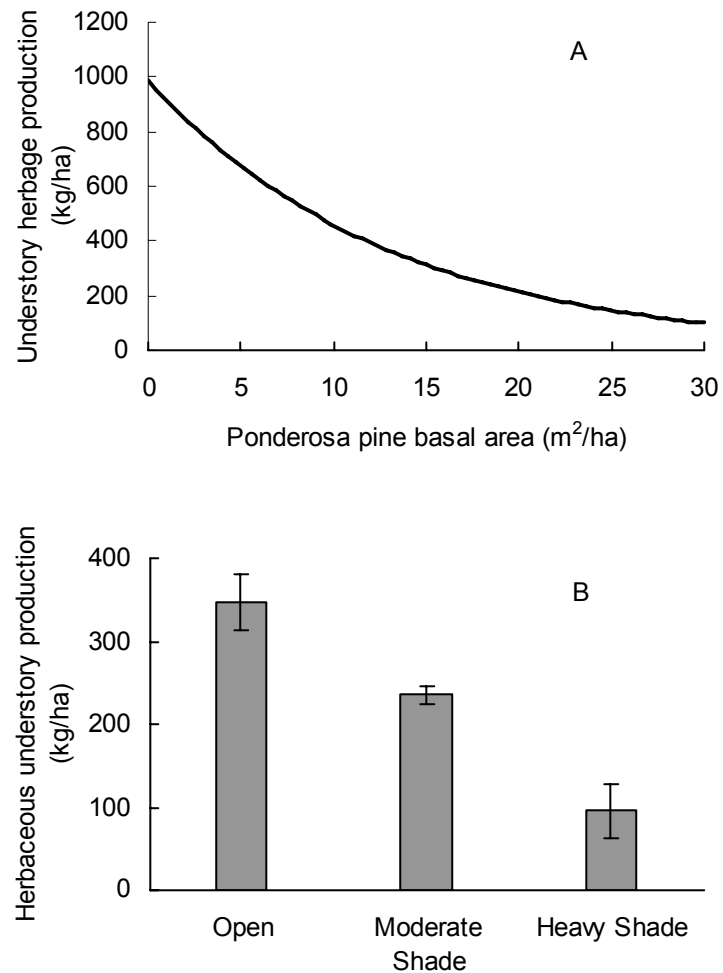


Figure 4. Relationship between understory herbaceous production and (A) basal area for a ponderosa pine forest in Arizona, and (B) overstory canopy cover for a mixed conifer forest in Oregon. Panel (A) adapted from Clary (1975) and panel (B) adapted from Hedrick et al. (1968). Error bars in B are \pm standard error.

Naumberg and DeWald (1999) also found that ponderosa pine stands with diminished overstories were associated with increased graminoid presence and abundance. Graminoid presence appeared related to tree diameter while light availability was the strongest predictor of understory graminoid species abundance (cover and density). However, the authors suggested that tree diameter may actually represent understory light conditions. Naumberg et al. (2001) expanded on their

discussion of the affects of light conditions on understory species and found that individual species responses to greenhouse shading treatments corresponded well with their field based observations.

Measures of understory species diversity have also been shown to be higher under reduced ponderosa pine overstory (Uresk and Severson 1998 and Korb and Springer 2003). Forest ingress has also been linked to a loss of dominant understory species (Greene and Evenden 1996)

A Contemporary View of Ponderosa Pine Ecology

The increased density, canopy cover, and basal area of pine trees common in contemporary ponderosa pine forests has impacted the growing conditions of understory species through alterations in above ground (light) and below ground (moisture and nutrient availability) resources. Although a common mechanism remains elusive, the general consequence of the transformation in forest structure has been reduced understory biomass, changes in understory species composition and a reduction in species diversity. As restoration of ponderosa pine forests involves re-establishing, to some degree, the natural ecosystem processes and structures (Friederici 2003), restoration activities in ponderosa pine forests need to include strategies that account for alterations in understory species. According to Moore et al. (2006), “the herbaceous understory should be a prime focus of land managers involved with forest restoration and conservation biology...”. However, the changes wrought by altered fire regimes in ponderosa pine forests may not simply be reversed through the re-introduction of fire. Rather, as alluded to by several authors (e.g. Arno et al. 1985, Johnson 1994, Johnson et al. 1994, Stephenson 1999, Tiedemann et al. 2000, Griffis et al. 2001, Allen et al. 2002 and Kaye et al. 2005), the potential exists for multiple trajectories of change and ecological thresholds in ponderosa pine ecosystem dynamics and non-equilibrium ecology concepts, including state and transition models, may be an appropriate theoretical framework from which to develop an improved understanding of the relationships among ponderosa pine

ecosystem structure, function, and process. Kaye et al. (2005) was the only publication found that specifically described the ecological changes in contemporary ponderosa pine forests in terms of ecosystem resilience and alternative stable states and suggest ponderosa pine forests have “shifted from a stable mixture of herbaceous plants and pines maintained by frequent surface fires to an alternative state with dense pine monocultures susceptible to large stand-replacing fires”.

Non-equilibrium Ecology

Non-equilibrium ecological theory emerged as a result of consistent observations, from a variety of ecosystems (i.e. aquatic, forest, grassland), of more than one stable community state. System dynamics did not follow the hypothesized concept of a single equilibrium state to which a system will tend, “from all initial conditions and following any disturbance” (May 1977, p. 471) rather, multiple stable states were possible indicating that many systems did not function in an equilibrium sense, thus, non-equilibrium ecology.

Although not yet a matter of convention, non-equilibrium approaches to describing ecosystem dynamics are established within the ecological literature and have been applied to a variety of ecosystems and ecosystem components (e.g. Holling 1973 and May 1977). Researchers have recognized that traditional linear succession approaches to ecosystem change inadequately characterize the observed vegetation dynamics in arid and semi-arid ecosystems (West et al. 1984, Westoby et al. 1989, Laycock 1991, Svejcar and Brown 1991). Emerging ecological concepts provide for multiple stable states, multiple successional pathways, and thresholds of ecosystem change (Westoby et al. 1989, Friedel 1991, George et al. 1992, West 1999, and Stringham et al. 2003), and investigate ecosystem dynamics in terms of natural variability (Fulé et al. 1997, Moore et al., 1999, Landres et al. 1999 and Fulé et al. 2002). A recent development in the theoretical approach to modeling non-equilibrium systems follows Stringham et al. (2001 and 2003). Their approach to understanding ecosystem dynamics builds upon initial state and transition concepts (eg. Westoby et

al. 1989, West 1999, and Friedel 1991) and is an attempt to organize complex ecological relationships into a model that will adequately predict ecosystem response to natural disturbances and / or management actions (Stringham et al. 2001 and 2003).

The state and transition model proposed by Stringham et al. (2003) (Figure 5) incorporates an ecological process approach whereby thresholds and transitions are defined by changes to one or more of the ecological processes of energy capture, hydrology and nutrient cycling. The following definitions and concepts explain the state and transition model as proposed by Stringham et al. (2003).

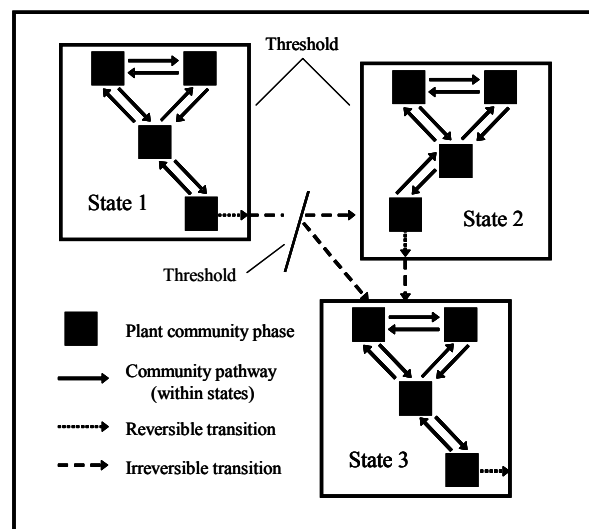


Figure 5. Conceptual state and transition model showing multiple stable state, transitions, and thresholds. Modified from Stringham et al. (2003).

A state is defined as a recognizable, resistant and resilient complex of soil and vegetation components and is bound by a threshold. Within a state, vegetation dynamics can be characterized by a linear succession-retrogression approach and ecosystem structure and function are thought to exist within the range of natural variability. Plant community phases can shift along bi-directional community pathways in response to natural and/or management pressures whose impacts on the

primary ecological processes are within the recovery capacity (resistance and resilience) of the state. Thresholds are defined as a boundary in space and time between any and all states, or along irreversible transitions, such that one or more of the primary ecological processes has been irreversibly changed and must be actively restored before return to a previous state is possible. Transitions are trajectories of change initiated by natural and/or management pressures which degrade one or more of the primary ecological processes. Reversible transitions exist within the confines of a state (i.e. system has not crossed a threshold) and are characterized by system recovery of degraded processes upon removal of the associated stress. Conversely, if a system is unable to recover damaged processes upon removal of the initiating stress then a threshold has been breached and the system is engaged in an irreversible transition toward a new state.

Considerable effort has been devoted to defining, describing, and cataloguing possible alternative stable states for numerous ecosystems (see Rodriguez Iglesias and Kothmann 1997), however less effort has been put toward developing a mechanistic understanding of thresholds. Thresholds exist primarily as an abstract concept and by virtue of the existence of more than one stable state. Ironically, however, multiple domains of stability exist only if thresholds are crossed, thus it is evident that thresholds are a fundamental component of state and transition modeling. An understanding of the mechanisms involved in threshold dynamics is crucial from a resource management perspective particularly with regard to the recognition of impending thresholds and development of ecosystem restoration strategies for sites where thresholds have been breached.

The Threshold Concept

The concept of an ecological threshold, although not always termed so, has been used variously to describe a boundary between one stable ecosystem and another. Holling (1973) considered ecological thresholds as a component of the dynamics of many ecosystems and described what is ostensibly a threshold, as the boundary around a domain of attraction within which exists a stable equilibrium.

Holling uses examples from various ecosystems to illustrate the concepts of multiple domains of attraction and suggests that populations forced, by some form of stress or perturbation, close to the boundary of the domain (threshold) can cross the boundary and enter into another domain of attraction. In describing threshold dynamics of tree encroachment into grass dominated rangelands Holling (1973) stated that returning to the original grass dominated domain from a tree-dominated domain can only occur with an explicit reduction of the trees and shrubs. Thus implying a level of extant irreversibility to thresholds.

May (1977) depicted thresholds as watershed boundaries between separate stable states. Thresholds are identified by a discontinuous relationship between a system control variable and system response variable. For example, a linear or gradual change in stocking rates may cause a non-linear (discontinuous) response in the forage community. (May 1977). Although May's depictions of multiple stable states are based on mathematical modeling, he does provide some indication of the potential mechanisms responsible for the thresholds indicated. For instance, he implicates plant competition for light and nutrients as a potential influence on the stability of a grazed grassland (May 1977).

Although Westoby et al. (1989) did not formally recognize thresholds in their seminal state and transition model, they do acknowledge the existence of transitions between alternative stable states that are not simply reversible within the linear succession framework. A series of 5 broad mechanisms were identified, 1) demographic inertia, 2) grazing catastrophe, 3) priority in competition, 4) fire positive feedback, and 5) a vegetation change that triggers a persisting change in soil conditions, as contributing to the existence of alternative stable states and could thus be considered mechanisms involved in threshold relationships (irreversible transitions).

Studying vegetation changes in Texas savannas, Archer (1989), described transitional thresholds that when crossed signal a change to an alternate stable system exposed to a new suite of successional mechanisms. Over time, alterations to various system components, like soil, seed bank, and vegetative regeneration, will prevent the

site from crossing back over the transitional threshold and into the original domain (Archer 1989). Thus, these transitional thresholds can be considered irreversible within the context of internal system dynamics. Alternatively, Archer (1989) stated that a system that retains control of these components remains within its stable confines and can return to equilibrium conditions upon removal of the stress.

Friedel (1991, p. 422) defined a threshold as “a boundary in space and time between 2 states” and addresses the issue of permanence by stating, “the shift across the boundary is not reversible on a practical time scale without substantial intervention by the manager”. Friedel indicates that thresholds offer a useful framework for identifying environmental change and her approach to detecting thresholds is based on the existence of multiple stable states and subsequent deduction of thresholds crossed.

Laycock (1991) used the same approach to defining thresholds as Friedel (1991) and indicated that recovery from a crossed threshold is difficult. Laycock (1991), however, acknowledged the abstract concept of thresholds and stated that in addition to identifying alternative stable states, efforts must be directed at identifying and understanding the mechanisms responsible for thresholds.

Tausch et al (1993) described vegetation-based thresholds and defined a threshold as a significant change in the species composition or functioning of a community in the response to some form of disturbance. These authors also addressed the irreversible nature of thresholds suggesting that returning the community back across a threshold is difficult or unattainable. In this paper, the authors expanded on the concept of a threshold and defined threshold mechanisms relative to biotic and abiotic component interactions leading to the classification of thresholds into 3 categories related to the conditions required for a threshold to be crossed and the trigger to initiate the breach. An important consideration of their definition of thresholds is that, regardless of a physical threshold breach, a threshold is considered crossed if all the conditions required for the threshold are present with the exception of the trigger but the trigger is a given future occurrence (i.e. fire) (Tausch et al. 1993).

Brown et al. (1999, p. 1113) defined thresholds as the “point of entry into a new domain or region of ecosystem function – the point in time when processes that result in a change in ecosystem function are entrained”. The authors make an important addition to the development of the threshold concept by suggesting that research and understanding be directed toward the destabilizing processes responsible for multiple stable states rather than focusing on the existence of stable states. This suggestion is made because system degradation (threshold breach) may occur prior to the expression of an alternative stable state (Brown et al. 1999). Thus, an understanding of the processes responsible for thresholds is more important than characterizing alternative states particularly in terms of recognizing the potential for system degradation prior to its occurrence. Several types of thresholds were proposed including, ecological threshold, damage threshold, and economic threshold, however it is the ecological threshold that appears to define the start of a conversion into a new domain of equilibrium (Brown et al. 1999).

Although Bestelmeyer et al. (2003) did not explicitly define thresholds in their adaptation of a state and transition model, their transitions represent typically irreversible changes and define the boundary between alternate stable states, thus fitting well with other definitions. Like Brown et al (1999), Bestelmeyer et al. (2003) also recognized the importance of understanding the mechanisms behind thresholds. The authors considered thresholds (irreversible transitions) a result of altered external or internal positive feed back mechanisms that influence one or more of the controls on the presence or abundance of particular plant species (Bestelmeyer et al. 2003). Three broad categories of control mechanisms were identified and include: 1) the dispersal of propagules to a site and subsequent reproduction, 2) ‘neighbor’ constraints, including the effects of competitors, predators, or parasites, as well as the tendency of certain life-forms to facilitate fire disturbance, and 3) ‘site’ constraints, including soil properties, hydrology, and climate (Bestelmeyer et al. 2003).

More recently Briske et al. (2005 and 2006) put forth a refined vision of the threshold concept. Although they stated that the Stringham et al. (2003) contribution to the threshold definition was a “valuable and necessary advance” because it

incorporated ecosystem resilience, Briske et al. (2005) felt that a functional interpretation of the ecological processes associated with thresholds was lacking. Briske et al. (2006) developed a framework for the evaluation and application of ecological thresholds within the arena of state and transition modeling. They proposed an ecosystem structure or function initiated feedback switch, from stabilizing negative feedback dominance to destabilizing positive feedback dominance, as the trigger that initiates threshold progression through 5 threshold categories, representing both structural and functional changes, each becoming increasingly difficult with respect to the likelihood of recovery.

Detecting Thresholds in the Field

There has been some discussion in the literature with respect to our ability to detect multiple stable states (see Connell and Sousa 1983, Peterson 1984, and Sousa and Connell 1985). Connell and Sousa (1983) expressed specific concerns with the lack of spatial and temporal constraints applied to tests of population or community stability and with the apparent lack of environmental consistency among supposed alternative stable states. Peterson (1984) however, indicated that environmental differences among stable states may in fact be the result of feedbacks between biotic and abiotic factors and that the feedback mechanism is likely involved in maintaining alternative states. Thus, it seems reasonable to evaluate stability (potential equilibrium) through the use of stabilizing feedback mechanisms that provide the conditions necessary for system self-replacement within recognized temporal and spatial extents that address the ecological scale of interest.

Attempts to identify thresholds and alternative stable states, often involve experimental design and analyses that model relationships exhibited among structural and functional attributes of a particular kind of ecosystem. Friedel (1991) employed multivariate analysis techniques of classification and ordination to compare sites with each other and provide some indication of a threshold breach by grouping similar sites. The author further suggested that non-linear relationships expressed between plant community composition and soil erosion status would indicate a possible

threshold. Similarly, Foran et al. (1986) utilized, in a combined fashion, cluster analysis and ordination along with correlations between ordination axes and environmental variables to elucidate potential thresholds (“condition states”) and the associated mechanisms.

Other researchers have identified stable equilibria through an understanding and quantification of system stability. Noy-Meir and Walker (1986) defined stability as the ability of a system to remain the same while external conditions change and quantified it by the variation in system attributes over time as indicated by the coefficient of variation. Resilience, defined by a system’s ability to recover after it has been altered, can be measured by assessing the correlation between system variables and the preceding value of the external factor (stress) (Noy-Meir and Walker 1986). The higher the resiliency the less correlation expected between the system variable and the stress. Seybold et al. (1999) also presented information specific to the quantification of resilience and resistance (stability) as applied to soil characteristics. Their approach involved measuring either the rate or amount of post-disturbance recovery in soil function (resilience) or the ratio of post-disturbance function to pre-disturbance function (resistance).

The testing of thresholds requires an understanding of or hypotheses regarding the mechanisms responsible for the threshold (mechanisms of recovery and change). Identification of the mechanisms allows the researcher to experimentally manipulate threshold components and test the responses in system structure and process against the expected results.

Petratis and Latham (1999) presented several approaches for testing the existence of multiple stable states. Focusing primarily on thresholds related to post-disturbance changes in vegetation species composition, they explained the use of analysis of variance, analysis of covariance, variance exploration, repeated measures analysis, and the partial Mantel test, to evaluate threshold potential relative to disturbance size and plant species recruitment.

Knoop and Walker (1985) investigated the existence of mechanisms responsible for two stable equilibria in South African savanna. Based on the

hypothesized function of the mechanisms involved in a state change (threshold), the researchers experimentally manipulated the threshold components and tested the results against the hypothesized relationship.

Research exploring thresholds of ecosystem change has also been performed in ponderosa pine forests. Covington et al. (1997) evaluated system response to several restoration treatments relative to an untreated control. Although not explicitly investigating the existence of thresholds, the authors were interested in system response to the re-introduction of the processes and structure thought to be responsible for maintaining feed back mechanisms required for system resistance and resilience. Griffis et al. (2001) analyzed understory species composition along a disturbance gradient of 4 disturbance levels and indicated the potential existence of thresholds with respect disturbance and exotic understory species establishment.

Project Rationale

Relatively recent increases in ponderosa pine abundance have affected ecosystem structure, function, and process (Covington and Moore 1994 and Allen et al. 2002). Fire regimes are trending toward longer fire return intervals and increasing preponderance of high severity crown fire. Alterations in soil processes have reduced soil moisture availability and water yields and promoted the stagnation of decomposition and nutrient cycling. Diminished understory plant vigor and biomass along with increasingly depauperate understories are evident across the range of ponderosa pine, the understory gradually replaced by thick mats of fallen pine needles.

The effects of ponderosa pine ingress on understory herbaceous components are not well understood. Only recently has an emphasis been placed on research that explores understory aspects other than production and within the context of an altered overstory status (e.g. Riegel et al. 1995, Naumburg and DeWald 1999, Moore et al. 2006 and Laughlin et al. 2006). A substantial effort has been directed at restoration programs for ponderosa pine ecosystems, many focused on manipulating tree

structure and re-introduction of fire at more frequent intervals. However, restoration objectives need to incorporate the understory component, as successful restoration projects will also enhance the recovery of native understory species (Moore et al. 2006). Thus, a more complete understanding of how alterations in pine abundance may influence understory species is required to assist in attaining restoration objectives in western ponderosa pine forests. An improved level of understanding should include understory responses to increasing pine abundance, mechanisms associated with these responses, and the potential for recovery from the altered conditions.

Several authors have asserted that ponderosa pine ecosystems exhibit non-equilibrium dynamics (e.g. Arno et al. 1985, Johnson 1994, Johnson et al. 1994, Stephenson 1999, Tiedemann et al. 2000, Griffis et al. 2001, Allen et al. 2002 and Kaye et al. 2005). Non-equilibrium dynamics can be characterized through state and transition models that identify and explain states, transitions, and ecological thresholds, however no research is available that has evaluated contemporary ponderosa pine forests within a state and transition framework. A state and transition model of contemporary ponderosa pine forests that links ecosystem structure and process will be useful in organizing the details of ecosystem dynamics and in predicting system response to management induced or naturally occurring events.

Research Objectives

Ponderosa pine trees modify the growing conditions for understory species. Increasing abundance of ponderosa pine trees in the time since European settlement has effected substantial changes to the understory in many ecosystems, however information specific to the magnitude, cause, and ease of system recovery from these changes is limited. The objectives of this research program were to:

1. Evaluate the effect of increasing ponderosa pine abundance on understory species composition.

2. Elucidate mechanisms associated with differences in understory species composition and linked to ponderosa pine site modifications.
3. Ascertain the degree to which changes in understory species composition have occurred and infer the level of ecosystem resilience remaining in ponderosa pine systems following a gradient of understory change.
4. Develop a state and transition model that describes the ecosystem dynamics of contemporary ponderosa pine forests.

Research Approach

Substituting space for time, the variability in understory species composition along a gradient of ponderosa pine abundance was evaluated. Understory and overstory species characteristics were sampled from 28 permanent plots established in ponderosa pine stands varying in stem density. Relationships among overstory and understory attributes were evaluated using cluster analyses, indicator species analyses, and ordination, to assess if levels of ponderosa pine abundance were associated with differing understory species composition.

The under-canopy growing environment, including light availability, soil moisture, nitrogen availability, and soil temperature, was described for each of the 28 plots. Relationships among under-canopy environment, ponderosa pine abundance, and understory species composition were evaluated using ordination analyses to elucidate potential mechanisms associated with understory species variability and ponderosa pine abundance. To corroborate the observational evidence indicating mechanisms of understory species variability, a green house experiment was also initiated to evaluate the effects of varying light and nutrient levels on the vigor of Idaho fescue. Idaho fescue was selected for this experiment because it is a common herbaceous understory species in these forests. A split plot factorial experimental testing 2 levels of each factor was performed.

A comparison of the germinable soil seedbank between ponderosa pine stands with and without an intact understory was completed using the seedling emergence

method to evaluate the potential for understory species recovery from depauperate conditions. MRPP was used to test for a difference in the seedbank composition between the two groups. Indicator species analysis was performed to evaluate species relationships with plot type (depauperate or intact).

A conceptual state and transition model characterizing ecosystem dynamics in contemporary ponderosa pine forests was developed using the data derived in the course of this research program and the currently accepted definitions of states, thresholds, transitions, and phase shifts.

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CHAPTER 2: SITE DESCRIPTION

Location

The study area was located in eastern Oregon approximately 8 km north of Seneca and 50 km south of John Day ($44^{\circ}12'52''$ N latitude, $118^{\circ}59'16''$ W; UTM zone 11 0341083, 4897978) (Figure 6). The elevation of the study area ranged from 1500 m to 1560 m and was situated in an area of gently sloping ($\sim 8\%$ slope gradient) north-facing hillsides. The area exists within a Ponderosa pine / Idaho fescue plant association (Johnson and Clausnitzer 1992) and is located in the John Day ecological province (Anderson et al. 1998) and the Continental Zone Highlands sub-region of the Blue Mountains Ecoregion (Bryce and Omernik 1997).

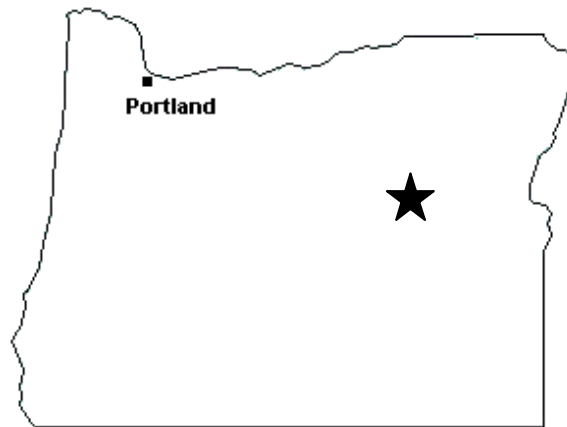


Figure 6. Location of study area within the state of Oregon.

Climate

The climate of the study area, and in general the eastern portion of Oregon, is significantly influenced by westerly mountain ranges. As warm and moist air masses from the Pacific Ocean move east, rising over the Coast Mountains and then again over the Cascade Mountains, much of the accumulated offshore moisture is released as a result of the cooling that occurs during uplift. As a consequence, areas east of the Cascade Mountains exist in a rain-shadow receiving very little precipitation. The coast range receives around 250 to 500 cm of precipitation per year, the west side of the Cascade Mountains averages approximately 200 – 300 cm per year, while the arid rain-shadow affected areas east of the Cascades range from 13 – 76 cm of precipitation annually (Taylor and Hannan 1999). The distance from the Pacific Ocean also influences the temperature patterns observed at our study location. In the absence of the temperature moderating influence of the Pacific Ocean, the diurnal and seasonal variability in temperatures in eastern Oregon can be quite extreme (Taylor and Hannan 1999). Seasonal variability in temperature in the vicinity of our study location can be evaluated in Figure 7. For example, in the month of August, the daily temperature flux averages almost 25°C, while seasonal variation in average maximum temperature almost reaches 26°C. Temperature variability is moderated in the winter months as the northern Rocky Mountains tend to block the full effect of southerly flowing Arctic air masses (Bryce and Omernik 1997).

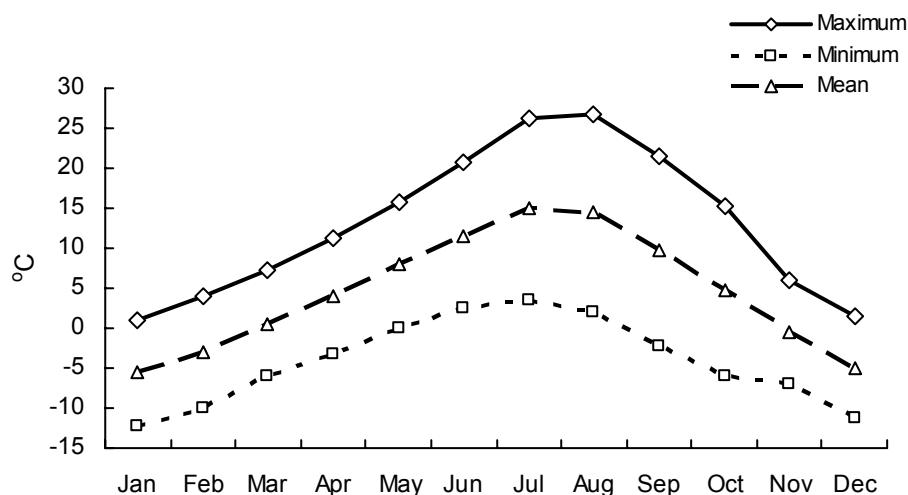


Figure 7. Average maximum, minimum, and monthly mean air temperatures recorded at Seneca, Oregon during the period of 1971-2000. Adapted from Oregon Climate Service (2007a).

The closest long-term weather station to the study area is located at Seneca (44°08'N latitude, 118°59' W longitude; 1420 m ASL). This weather station has been recording information since 1949 and these data, provided by Oregon Climate Service (2007a and b) were used to characterize the general climate of the study area. Seneca is approximately 100m lower in elevation than the sites used in this research project and exists in a relatively broad non-forested valley. Thus, it is expected that the study area received slightly more precipitation than that recorded at Seneca and that the temperature regimes differ slightly between the two areas. Cold air drainage funneling cool air into the valley at night likely decreases the frost free period in Seneca relative to the study sites on the hill sides above.

The area is characterized by warm summers and cold winters with average daily high and low temperatures of 24°C and 1.5°C and 4°C and -9°C for summer and winter respectively (Oregon Climate Service 2007a) (Figure 7). The area has a relatively short frost free period with the Oregon Climate Service (2007b) reporting, for the period of 1961 – 2002, that 50% of the last yearly 0°C temperature days

occurred by July 24 and 50% of the first yearly 0°C temperatures were experienced by August 6.

The area receives about 35 cm of precipitation annually. Approximately 50% of the annual precipitation accumulates in the winter months (November through March), much in the form of snow, however, a secondary peak, approximately 28% of the annual precipitation, occurs through the spring and early summer (April through June) (Oregon Climate Service 2007 a) (Figure 8). Localized convective thunderstorms are frequent throughout the summer months and can provide mid-summer moisture.

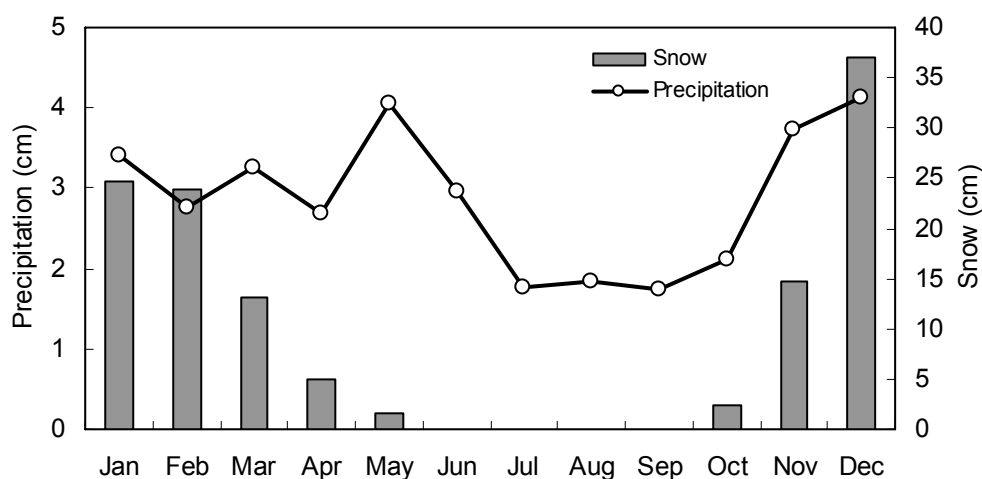


Figure 8. Average monthly precipitation (line) and snowfall (columns) recorded at Seneca, Oregon during the period of 1971-2000. Adapted from Oregon Climate Service (2007a).

Geology

The greater Blue Mountains area emerged through the Devonian and Jurassic periods (275 – 200 million years ago) as a series of off-shore islands and rock

formations that developed in association with subduction processes as the ocean floor collided with the North American craton (Orr et al. 1992 and Bryce and Omernik 1997). Five tectonostratigraphic terrains were accreted to the North American craton during this time and together form the geologic foundation of the Blue Mountains (Siberling and Jones 1984, Orr et al. 1992, and Leeman et al. 1995). Subsequent periods of intense volcanic activity, including the Clarno period (55 - 35 million years ago), John Day formation (35 million years ago), Strawberry Volanics (8 million years ago), and Columbia River Basalt flows (17.5 – 6 million years ago), Pleistocene glaciation (2 million – 11,000 years ago) and perpetual erosion and deposition all contributed to the development of the geologic landscape as it exists today (Orr et al. 1992 and Bryce and Omernik 1997).

The study area is located within the Izee terrain and is composed primarily of ultramafic serpentinite rock derived from peridotite. These serpentine formations are related to the Canyon Mountain Complex (Brown and Thayer 1977), a Permian ophiolitic rock formation located in the area immediately south of the city of John Day (Leeman et al. 1995). In addition to serpentine, the Canyon Mountain Complex contains argillites, cherts, gabbro, diorite, and volcanic tuffs (Orr et al. 1992). Keller creek shale (upper Jurassic and lower Triassic tuffaceous greywacke and black shale) of the Aldrich mountains group, more characteristic of the Izee terrain, is also found in adjacent areas. More recent volcanic events, particularly the eruption of Mt. Mazama approximately 6000 to 7000 years ago (Klimasauskas et al. 2002), have overlain much of the pre-Tertiary rock with an ash mantle of variable thickness.

Soils

The soils in our study area are influenced by a volcanic ash deposition associated with the eruption of Mt. Mazama approximately 6000 to 7000 years ago (Klimasauskas et al. 2002). These soils range in depth from about 25 to 100 cm and are developed in the air-fall volcanic ash over colluvium over residuum from serpentinite bedrock. Soil depth in this landscape is primarily in response to wind

driven erosion and deposition patterns where leeward landscape positions tend to exhibit thicker ashy materials. The ash-influenced mantle is composed of volcanic ash, local eolian material and colluvium, mixed by erosion and bioturbation. This mantle is ashy sandy loam or ashy loam and ranges in thickness from 8 cm in shallow soil to 37 cm in moderately deep soil. Based on laboratory data, determined in support of soil survey activities in the Blue Mountain region of eastern Oregon, the ashy mantle is expected to contain between 15 and 30 percent volcanic glass in the very fine sand fraction and have a sum of aluminum plus one-half iron (extracted by ammonium oxalate) of 0.3 to 0.8 percent. These properties are indicative of weathering of the young ash materials and meet criteria for vitrandic subgroups of Mollisols. Buried soil horizons, developed in residuum directly above bedrock contact, are very gravelly or very cobbly, sandy clay loam or sandy clay and may exhibit clay films as evidence of translocated clay. This clayey layer will restrict deep percolation of soil water during periods of saturation of soil material above, such as during Spring snowmelt.

Soils identified in the study area were classified in two families of Mollisols. Moderately deep soils on 25 of the plots classified in fine-loamy, mixed, superactive, frigid Vitrandic Haploxerolls and shallow soils on the other three plots classified in clayey-skeletal, smectitic, frigid Lithic Ultic Argixerolls (Soil Survey Staff 2006) (See Appendix A for complete soil descriptions). Base saturation of less than 75 percent in upper horizons of mineral soil, indicative of an Ultic subgroup, was assumed based on the soils being forested. This assumption, based on laboratory data, has been used to classify similar soils in the region. These soils were placed in the xeric soil moisture regime.

Serpentine Soils

Serpentine soils are derived from ultramafic parent materials (rock with >90% magnesium-ferrous silicate composition) primarily composed of peridotite or serpentinite. Although mineralogically different, peridotite minerals include olivine

and pyroxene while chrysotile, lizardite, and antigorite comprise the serpentine mineral group, the two are related as serpentinite is a product of peridotite weathering (Brooks 1987).

The primary sources of terrestrial ultramafic rocks are layered complexes of ocean crust accreted during subduction zone geological processes (Coleman and Jove 1992, and Alexander et al. 2007). These ophiolitic complexes form as molten mantle rock rises and cools along ridges near spreading centers in the ocean floor. Differential cooling of the mantle material creates a new ocean crust comprised of a layered sequence of pillow lava, diabase dikes, and gabbro resting atop the ultramafic peridotite basement material (Alexander et al. 2007).

Ultramafic rocks exhibit high concentrations of iron, magnesium, cobalt, chromium, and nickel and low concentrations of aluminum, calcium, potassium, and sodium (Brooks 1987 and Alexander et al. 2007). The variability associated with soil development processes makes it difficult to generalize about soils formed from ultramafic materials, however, serpentine soils do appear to exhibit similar elemental patterns as described for the parent material (Rai et al. 1970, Brooks 1987 and Alexander et al. 2007). Brooks (1987) described 4 common attributes of serpentine soils: 1) high concentrations of iron, cobalt, nickel, and chromium; 2) low concentrations of nitrogen, phosphorous, and potassium; 3) low calcium : magnesium ratio, and; 4) low clay content.

The unique chemical and physical properties of serpentine soils exert significant influence over the vegetation that inhabits serpentine environments. Generally the vegetation growing on serpentine soils is characterized as shorter statured, less dense, less vigorous, more xeric in nature, and in stark contrast to adjacent non-serpentine vegetation (Rai et al. 1970, Brooks 1987, and Alexander et al. 2007). The variable conditions for plant growth across all serpentine soils, however, makes it unlikely that one factor associated with serpentine can be isolated as the cause of the distinctive vegetation.

It is apparent that the relationship between calcium and magnesium plays a significant role in limiting the vegetation on serpentine sites. Earlier suggestions that

calcium limitation was the primary factor related to reduced plant performance (eg. Rai et al. 1970) have been rejected in favor of the Ca:Mg ratio (Proctor and Nagy 1992 and Alexander et al. 2007). A clear understanding of the mechanisms associated with calcium and magnesium is lacking but may be related to the magnesium toxicity, magnesium interference in calcium availability, and the absence of calcium moderated amelioration of magnesium toxicity (Proctor and Nagy 1992).

High nickel concentrations in serpentine soils have also been highlighted as limiting factor for vegetation growth. It is unclear how nickel toxicity manifests in serpentine soils and given the confounding interactions among nickel, calcium, and magnesium it is unclear if elevated concentrations of nickel really have an impact (Proctor and Nagy 1992 and Alexander et al. 2007). Earlier indications of toxic levels of chromium and cobalt associated with serpentine soils (eg. Rai et al. 1970 and Brooks 1987) have been similarly modified as there has been relatively little evidence to suggest a major involvement in serpentine soil-plant interactions (Proctor and Nagy 1992).

Low levels of soil nitrogen, phosphorous, and potassium in serpentine soils appear related to plant species composition and vigor (Alexander et al. 2007). Experiments reviewed by Brooks (1987), Proctor and Nagy (1992) and Alexander et al. (2007) indicated positive responses in plant growth and in some cases changes in species composition with the addition of various combinations of nitrogen, phosphorous, and potassium.

The high rock content and shallowness of some serpentine soils have also been cited as a factor in reducing soil moisture availability and consequently limiting plant growth (Rai 1970 and Proctor and Nagy 1992). Although the droughtiness associated with skeletal or shallow soils is assured, Alexander et al. (2007) noted that low water availability is not a common feature of serpentine soils and that the drought resistant morphology of many serpentine plant species can not be attributed to reduced water availability unless the inability to obtain water is related to some other characteristic of serpentine ecosystems.

It is conceivable that the ash deposition in our area, particularly the deep ash mantels, has mitigated much of the serpentine influence that would have otherwise existed. Bulmer et al. (1992), investigating the potential for polygenesis of serpentine soils overlain by tephra deposits, found that sites appeared to exhibit more moderate growing conditions after the ash depositions and indicated that the tephra may effect a buffering capacity on the toxic weathering products of serpentine based parent materials. The authors did indicate a serpentine influence in the ash-based horizons, however the serpentinitic additions were colluvial and aeolian in nature, not the result of the integration with genetic material from the serpentine layers below. Although our soils were shallower than some of those reported by Bulmer et al. (1992), there was little evidence of active serpentine erosion/deposition processes that would influence the ash horizons of our soils.

Vegetation

The vegetation of the study area is a climax ponderosa pine (*Pinus ponderosa* (Dougl.)) forest with an understory herbaceous layer dominated by Idaho fescue (*Festuca idahoensis* Elmer). This kind of vegetation has been classified by Johnson and Clausnitzer (1992) as a Ponderosa pine / Idaho fescue plant association (PIPO/FEID).

The forested vegetation consisted of large-diameter ponderosa pine trees scattered across a landscape dominated primarily by patches of smaller pines. Over 90% of the trees in the study area are less than 100 years old while approximately 3% are over 250 years old (see Appendix A for ponderosa pine age distribution in the study area). The understory vegetation was clearly dominated by Idaho fescue with lesser amounts of other grasses including pine bluegrass (*Poa scabrella* (Thurb.) Benth.), Prairie junegrass (*Koeleria macrantha* (Ledeb.) J.A. Schultes), Squirrel Tail (*Sitanion hystrix* (Nutt.) Smith), Western Needlegrass (*Stipa occidentalis* Thurb. var. *occidentalis*), Wheelers bluegrass (*Poa nervosa* (Hook.) Vasey var *wheeleri* (Vasey) Hitchc.), and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scrib. & Smith).

In some of the denser pine patches, pinegrass (*Calamagrostis rubescens* Buckl.) and ross sedge (*Carex rossii* Boot) were observed. The most common forbs were Yarrow (*Achillea millefolium* L.) and hood's phlox (*Phlox hoodii* Rich.) although an increase in forb diversity was associated with site conditions that favor higher spring soil moisture. This vegetation type is relatively shrub-free, however sporadic occurrences of Grey rabbit brush (*Chrysothamnus nauseosus* (Pall.) Britt. var. *nauseosus*), antelope bitterbrush (*Purshia tridentate* (Pursh)), big sagebrush (*Artimisia tridentate* Nutt.), green rabbit brush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), and mountain mahogany (*Cercocarpus ledifolius* Nutt.) occur.

Johnson and Clausnitzer (1992) reported that the average aboveground air dry biomass of herbaceous species, total stand basal area, and total tree canopy cover for PIPO/FEID plant associations in the Blue and Ochoco mountains were 407 kg / ha, 18.8 m² / ha and 33%, respectively.

Disturbance

Disturbance has played a significant role in the development of the vegetation as it exists today and includes agents such as fire, insect and disease, wind-throw, logging and grazing.

The area was historically grazed by sheep and cattle, however, since the 1960s it has been grazed primarily by cattle in the summer from July to October (C. McArthur, Personal Communication). No evidence of recent fire or logging activity was apparent in the study plots, however the area was logged in 1978 and a variety of silvicultural activities have occurred in the general vicinity. The abundance of fire scarred trees found throughout the area is indicative of the stand maintaining fire regime typical of ponderosa pine forests. There are several recorded fire spots in the area (L. Stokes, Personal Communication) but none existed within our study plots. Additionally, the study sites are within the general perimeter of a prescription burn carried out in the spring of 1999, however, our specific study plots did not appear to have been impacted; an assessment supported by U.S. Forest Service information that

suggested not all areas within the perimeter burned in that fire (L. Stokes, Personal Communication).

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CHAPTER 3: HERBACEOUS UNDERSTORY SPECIES ABUNDANCE IN RELATION TO PONDEROSA PINE (*Pinus ponderosa* Dougl.) SITE OCCUPANCY

Abstract

Lengthened fire return intervals in contemporary ponderosa pine forests have altered vegetation structure and ecosystem processes and in many cases have triggered a transition away from the historic range of variability. Management prescriptions for these forests often incorporate restoration to a structure that more closely resembles pre-European contact forests. Successful restoration programs must also incorporate the herbaceous understory component and published research specifically addressing changes in understory species composition is minimal. Ponderosa pine influence on the under-canopy environment may be an important driver of understory vegetation distribution, thus this study was initiated to elucidate relationships among ponderosa pine abundance, under-canopy environment and understory species composition and to make inferences with respect to restoration potential. Data representing vegetation, soil, and environmental attributes were measured in 28 plots in a eastern Oregon ponderosa pine forest. Relationships among the parameters measured were evaluated using cluster analysis, indicator species analysis and ordination. Increased ponderosa pine occupancy was related to reductions in understory perennial bunchgrass abundance and diminished species diversity and appeared to regulate the under-canopy environment through alterations in light and nitrogen availability and soil temperature. Light availability was the most significant driver with respect to understory vegetation distribution. Alterations to ecosystem processes associated with increased pine abundance appear minimal and restoration practices that reduce pine occupancy should enhance the conditions for perennial bunchgrass growth, however this is constrained by the potential for understory species loss from stands with excessive pine in growth.

Introduction

Contemporary ponderosa pine forests are generally thought to exist outside their historic range of variability (Covington and Moore 1994, Tiedemann et al. 2000 and Allen et al. 2002). Activities associated with European settlement in the late 1800s including road and trail development, intensive livestock grazing, and active fire suppression triggered a substantial increase in the fire return interval, and combined with favorable conditions for ponderosa pine seed germination and seedling establishment, effected unprecedented changes in the fire regime and vegetation structure in ponderosa pine forests (Covington and Moore 1994, Johnson 1994).

Increased fire return intervals have generated a greater probability and existence of severe stand-replacing wildfires in what was historically an ecosystem dominated by a low severity – high frequency fire pattern (Agee 1993). Coupled with this change in disturbance regime are altered vegetation patterns across stand and landscape levels, tending toward a more homogeneous single-aged high-density forest susceptible to insect and disease outbreak and severe wildfire behavior, and diminished in wildlife habitat, forage production, and species diversity (Covington et al. 1987 and Allen et al. 2002).

In established ponderosa pine forests, overstory pine trees are favored in competitive interactions with the understory herbaceous and shrubby components. By eliminating the majority of pine regeneration, fire, in a low-intensity high frequency regime, confers a competitive advantage to understory herbs and shrubs. Over time and in the absence of fire, increased pine stem density, canopy cover, and/or root density effects an increasing level of stress on understory species by reducing available light, water and nutrient resources (Krueger 1981 and Riegel et al. 1991, 1992, and 1995) and may eventually lead to localized extirpation of understory species (Moore et al. 1999 and Stephenson 1999). Relative to open pre-settlement forest stands, dense stands of ponderosa pine show significant limitations in many

understory attributes including diversity, density, and vigor (Clary et al. 1975, Uresk and Severson 1998, Naumberg and DeWald 1999, and Naumberg et al. 2001). In some of the densest stands, the understory component is replaced by a thick mat of pine needle litter (Moir 1966 and Wienk et al. 2004). Overstory – understory interactions are well documented for ponderosa pine forests and herbaceous production, and the general trend is one of decreasing understory production associated with increasing overstory pine canopy (Ffolliot and Clary 1982, and Riegel et al. 1991 and 1992). However, the relationship between ponderosa pine abundance and understory species composition and the associated causes are generally not well understood.

Riegel et al. (1995) found that understory species composition in a seral ponderosa pine forest in northeastern Oregon was variously influenced by light availability, soil moisture availability and soil nutrient availability. The differences in individual species responses to imposed environmental conditions were related to species physiological tolerances to resource limitation or morphological adaptations for resource capture. In Arizona ponderosa pine forests, Naumberg and DeWald (1999) found that plots with diminished overstories were associated with increased graminoid species presence and abundance, and that species presence was primarily associated with tree diameter while light availability was the strongest predictor of species abundance. Tree diameter, however, was linked to understory light conditions (Naumberg and DeWald 1999). The effects of variable light intensity treatments on several common Arizona ponderosa pine understory species also identified light as an important parameter with respect to understory species compositional persistence in a changing understory environment (Naumberg et al. 2001).

Management of ponderosa pine forests toward a structure that more closely resembles pre-settlement conditions is often prescribed and is desirable from many perspectives. Most restoration programs focus on recent alterations to overstory structure, however understory species have also been impacted. Knowledge of understory species compositional dynamics associated with overstory structural and

consequent under-canopy environmental changes should therefore be an integral component of any ponderosa pine restoration program (Moore et al. 2006).

However, the bulk of the published research on ponderosa pine ecology has occurred in Southwestern Pine types that exist in a different climatic regime than the Pacific Northwest and have understories comprised of both C3 and C4 species while Pacific Northwest understories have only C3 species. Research on these issues is needed in Pacific Northwest forests to assist in developing appropriate management strategies.

Study Objectives

This study was initiated in the Blue Mountains of eastern Oregon to evaluate the relationships among ponderosa pine, under-canopy environment, and understory species composition. Specifically, the objectives of this study were to: 1) evaluate the variability in understory species composition along an increasing gradient of ponderosa pine abundance; 2) evaluate the variability in understory growing environment (i.e. soil moisture availability, nutrient availability, and light availability) along an increasing gradient of ponderosa pine abundance; 3) elucidate relationships among ponderosa pine abundance, understory environment, and understory species composition, and; 4) make inferences with respect to management strategies and restoration potential of similar ponderosa pine stands.

Methods

Study Area

The study area was located in eastern Oregon (44°12'52" N latitude, 118°59'16" W longitude) in a Ponderosa pine / Idaho fescue plant association (Johnson and Clausnitzer 1992) and within the John Day ecological province (Anderson et al. 1998) and the Continental Zone Highlands sub-region of the Blue Mountains Ecoregion (Bryce and Omernik 1997). The area ranges from 1500 m to 1560 m in elevation and is situated in an area of gently sloping (~ 8% slope gradient) north-facing hillsides. The average daily high and low summer and winter

temperatures, recorded between 1971 and 2000 at Seneca (~ 8 km south of the study area) were 24°C and 1.5°C and 4°C and -9°C respectively (Oregon Climate Service 2007). Approximately 35 cm of precipitation is received annually, most occurring in the winter months and primarily in the form of snow (Oregon Climate Service 2007). Seneca is approximately 100m lower in elevation than the sites used in this research project and exists in a relatively broad non-forested valley. Thus, it is expected that the study area receives slightly more precipitation than that recorded at Seneca and that the temperature regimes differ slightly between the two areas.

Soils of the study area are composed of a variable thickness ash mantle associated with the eruption of Mt. Mazama 6000 – 7000 years ago (Klimasauskas et al. 2002), overlaying serpentinite gravel and cobble. Soils were classified as either a fine-loamy, mixed, superactive, frigid Vitrandic Haploxerolls or a clayey-skeletal, smectitic, Lithic Ultic Argixerolls (Carr 2007a). Thickness of the ash-influenced mantle is a distinguishing feature of these soil types; Vitrandic Haploxerolls having an ash-influenced layer that is 20 to 30 cm thicker. Both soils are classified in a xeric soil moisture regime and frigid soil temperature regime.

The study area is a climax ponderosa pine forest consisting of large-diameter ponderosa pine trees scattered across a landscape dominated primarily by patches of smaller pines. Over 90% of the trees in the study area are less than 100 years old while approximately 3% have survived for more than 250 years (see Appendix A for ponderosa pine age distribution in the study area). The area was historically grazed by sheep and cattle, however, since the 1960s it has been grazed primarily by cattle in the summer from July to October. No evidence of recent fire or logging activity was apparent in the study plots, however the area was logged in 1978 and a variety of silvicultural activities have occurred in the general vicinity (Carr 2007a).

Data Collection

Twenty-eight 15m x 15m permanent plots representing a gradient of ponderosa pine density were established in the summer of 2005. Several plots were selected to fit each of 4 broad density categories (Table 2) ensuring adequate

representation of stands along the gradient. To reduce extraneous variability and avoid potentially confounding factors, the plots selected for study were limited to those with similar site characteristics including slope, aspect, elevation, and soils and had no obvious evidence of recent logging or fire activity. The site characteristics of each of the 28 plots used in this study are displayed in Appendix A.

Table 2. Average and range of ponderosa pine densities in groups from the initial plot selection

	Density Category			
	Low	Low-Moderate	Moderate-High	High
Stems/Ha	311	667	1778	3244
Range	133 – 756	356 – 1200	1333 – 2400	2267 – 4800

Vegetation Characteristics

In each plot, trees >1.4 m in height were tallied and their diameters at breast height (dbh = 1.4m) recorded. Individual tree basal area (BA) was calculated from the dbh using the following equation,

$$BA = \pi \left(\frac{dbh}{2} \right)^2 \quad (\text{Equation 1})$$

and tallied across all trees in the plot to generate a plot-level basal area value.

Canopy closure was evaluated from 3 randomly located upward looking hemispherical photographs using HemiView image analysis software (HemiView Version 2.1, Delta T Devices Ltd.). Canopy closure was calculated as 100 - % visible sky.

In each plot, understory species cover and density were subsampled in 0.5 m² (1 m x 0.5 m) and 0.125 m² (0.25 m x 0.50 m) quadrats respectively. Vegetation sampling occurred through the first 3 weeks of July 2006. Quadrats were

systematically positioned from a random starting point along transects placed randomly along the north baseline of each plot. The number of transects and quadrats differed by plot in accordance with plant community heterogeneity. Percent cover was estimated using cover classes modified from Daubenmire (1959) and are shown in Table 3.

Table 3. Cover classes and associated ranges of % cover and midpoints used in assessing cover of understory species.

cover class	% cover range	mid-point
1	0 – 1	0.5
2	1 – 5	3.5
3	5 – 25	15
4	25 – 50	37.5
5	50 – 75	62.5
6	75 – 95	85
7	95 – 100	97.5

Under-Canopy Environment

Under-canopy light conditions were modeled in each plot from 3 randomly positioned upward looking hemispherical photographs using the HemiView image analysis software (HemiView version 2.1, Delta T Devices Ltd.). The total below canopy radiation ($\text{MJ m}^{-2}\text{yr}^{-1}$) is the sum of the under-canopy direct and diffuse radiation. Plot values were averages of the 3 subsamples and provide a relative comparison among plots rather than a quantitative assessment of insolation occurring during the study period.

Gravimetric soil moisture integrated over the top 15 cm of the soil was determined for each plot by averaging 4 randomly located soil samples removed by auger to a depth of 15cm. Fifteen centimeter depth was selected as it represented the general rooting depth of understory species in the study area. Soil moisture was sampled bi-weekly throughout the growing season.

Plant available nitrogen ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) was evaluated using PST-1 ion exchange resin capsules (UNIBEST Inc.). PST-1 capsules are ion exchange resin beads used in a mixed bed format that provides both cation and anion adsorption (Skogley et al. 1990). PST-1 capsules indicate nutrient availability by relying on diffusion and massflow mechanisms of ion transport and accumulation and respond to nutrient variability in a similar manner as plants and thus provide an indicator of nutrient phytoavailability (Skogley et al. 1990). Four capsules were placed at 15cm depth in the soil at each of 4 randomly selected locations in each plot. One capsule from each sampling location was removed at 4 different times throughout the growing season (June 11, July 12, August 12, and September 9, 2006). Samples at each removal date were composited within the plot to provide a plot level value of N availability. Capsules were stored in labeled plastic bags and refrigerated until desorption. Capsules were desorped with 2M KCl and the resultant solution analyzed for $\text{NO}_3 - \text{N}$ and $\text{NH}_4 - \text{N}$ using an Astoria Pacific auto analyzer at the Central Analytical Lab at Oregon State University.

Soil temperature was measured at 5cm depth in 3 randomly selected locations in each plot using Stowaway® XTI thermistors (Onset Computer Corporation) programmed to log temperature every 2 hours. To characterize soil temperature in each plot, the daily maximum and minimum temperature for 5 randomly selected days (July 5, July 16, July 26, August 21, and August 26) were averaged among each thermister in each plot provide a plot level value for the average daily maximum and minimum soil temperature.

Data Analyses

Understory species density and cover data sets were converted into plot (row) by species (columns) matrices consisting of 28 plots and 63 species and 28 plots and 62 species for density and cover, respectively. Although beta diversity (β_w) was moderate for both matrices (Table 4), cover and density values were log transformed ($b_{ij} = \log(x_{ij} + 0.1) - (-1)$) to account for approximately 4 orders of magnitude difference between the smallest and largest values in each data set. This approach to

log transformation was used to maintain the original orders of magnitude while ensuring zeros from the untransformed data remained once transformed (McCune and Grace 2002). Species density and cover values were relativized by species maxima to moderate the influence of dominant species. McCune and Grace (2002) suggested this is an effective transformation for community data as it tends to equalize the influence of abundant and uncommon species. To reduce the bulk and noise in these data, species occurring in fewer than 4 plots were excluded from the analyses (McCune and Grace 2002).

Table 4. Alpha, beta and gamma diversity values for untransformed understory species density and cover data sets.

	α	β_w	γ
Density Matrix	21.3	2.0	63
Cover Matrix	21.0	2.0	62

The data were evaluated for outliers by comparing the average distance between each plot and all the other plots to the overall mean distance between all plots. Plots 6-4 and 7-4 were 2.4 and 2.8 standard deviations away from the mean Sørensen distance between all plots in the density data set while plot 4-4, 6-4, and 7-4 were 2.4, 2.2, and 2.1 standard deviations away from the mean Sørensen distance in the cover data. Although these plots were identified as moderate outliers, they appeared to accurately represent the data and were in response to high abundance of species unique to the stand conditions represented by the plots and were considered an important part of the data structure. Thus, these plots were not excluded from these analyses.

Hierarchical agglomerative cluster analysis with Sørensen distance and flexible beta linkage ($\beta = -0.25$) was used to group plots based on understory species abundance. One cluster analysis was performed for each data set using PC-ORD

version 4.39 (McCune and Mefford 1999). Indicator species analysis (ISA) (Dufrene and Legendre 1997) was used to describe species relationships to the groups formed through cluster analysis. ISA evaluates the faithfulness and exclusivity of a species to a particular group against a perfect indicator species which would always and only be present in sample units that represent a particular grouping (McCune and Grace 2002). ISAs were performed with PC-ORD version 4.39 (McCune and Mefford 1999) using 1000 randomizations in the Monte Carlo tests of indicator significance.

Non-metric multidimensional scaling ordination (NMS) (Kruskal 1964 and Mather 1976) of plots in species space was used to display compositional differences in understory species among the groups identified through cluster analysis. NMS iteratively searches for the best positioning of plots in k dimensions (axes) by minimizing stress (departure from monotonicity) in the relationship between ranked interplot distances in species space and ordination space (McCune and Grace 2002). NMS analyses were based on Sørensen distance measure and utilized 40 runs with real data from a randomized starting configuration, a maximum of 400 iterations and an instability criterion of 0.00001. Fifty runs with randomized data were used in a Monte Carlo test to evaluate if the reduction in stress achieved was lower than expected by chance. NMS is particularly useful for community data as it is well suited to non-multivariate normal data (McCune and Grace 2002). NMS ordinations were performed with PC-ORD version 4.39 (McCune and Mefford 1999). Joint plot overlays of understory species functional groups and diversity indices were used to illustrate understory species variability among the groups identified through cluster analysis.

To evaluate relationships between understory species composition and under-canopy growing conditions, joint plots of soil moisture, soil temperature, soil nitrogen availability, and under-canopy light conditions were overlaid on the NMS ordinations of understory species density and cover. Synthetic variables representing soil moisture and soil nitrogen were created from the strongest principle components generated from principle components analyses (PCA). PCA is a multivariate normal ordination technique that seeks to maximize the variation in responses explained

sequentially by axes (components) placed orthogonally through the data (McCune and Grace 2002). The first few components tend to explain the strongest co-variation among variables (McCune and Grace 2002). PCA were performed using correlation matrices in PC-ORD version 4.39 (McCune and Mefford 1999). PCA is based on assumptions of multivariate normality and linear relationships among variables. Linearity was evaluated through bivariate scatter plots (Appendix B) while multivariate normality was accepted based on the low skewness (<1) associated with these data. McCune and Grace (2002) suggested that data with a skewness <1 will exhibit a similarly low kurtosis and provide a reasonable approximation a multivariate normal distribution.

$\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ were combined to represent total mineral N availability. The PST-1 capsules were not effective in maintaining a continuous ion sink over time. Rather, NH_4 and NO_3 were lost from the capsules likely in response to competition for N from plants or microbes or increased accumulation and exchange of higher valency ions (e.g. Ca^{2+} or Mg^{2+}) for which the PST-1 has a greater affinity (Earl Skogley, 2007, personal communication). It is unclear which of these mechanisms was most important in the loss of N from the PST-1 capsules, however it is likely that both were playing a role. Fungal hyphae were observed inside several of the PST-1 capsules during field removal suggesting that fungal competition for mineral N was occurring. In addition, elevated concentrations of higher valency cations (e.g. Fe, Co, Ni, and Mg) apparent in serpentine influenced soils and the abundance of NH_4 , a cation, in the soil mineral N pool ($\sim 57\%$ of the N across all plots and dates was NH_4) suggested that opportunities existed for cation exchange between higher valency ions and NH_4 . Nevertheless, the dynamic exchange of mineral N reflects the nature of N availability in the study plots as the variability created by the lack of continuous ionic sink was experienced across plots. Increased microbial or plant competition for mineral N is a reflection of plot conditions and if uniform across similar plots, the pattern will be revealed in the analyses. Although a complete chemical evaluation of the study area soils was not performed, we assume that ion exchange between N and higher valency ions was uniformly experienced

across all plots because site selection was restricted by the requirement of uniform site characteristics.

A synthetic variable of pine occupancy that integrated basal area, density, and canopy closure was similarly created using PCA. The relationships among pine occupancy, understory species composition, and understory growing conditions were evaluating using joint plot overlays on NMS ordination of plots in species density and cover space.

Results

Understory Density

The hierarchical cluster analysis used to evaluate plot groupings based on understory species density was pruned at 4 groups (38.6% information remaining; Wishart's objective function; Figure 9). Indicator species analysis (Table 5) identified perennial bunchgrasses, including *Festuca idahoensis* Elmer, *Poa scabrella* (Thurb.) Benth, and *Agropyron spicatum* (Pursh) Scrib. & Smith, as indicators of plots in group A. Group B plots were indicated by the presence of the perennial bunchgrasses *Koeleria macrantha* (Ledeb.) J.A. Schultes and *Sitanion hystrix* (Nutt.) Smith and by the presence of a variety of forb species. Seven forb species expressed significant indicator values for this group. The presence of *Poa nervosa* (Hook.) Vasey var. *wheeler* (Vasey) Hitchc. appeared to characterize plots in group C while group D plots were identified by the presence of *Berberis repens* Lindl., *Silene menziesii* Hook. var. *menziesii*, and *Calamagrostis rubescens* Buckl..

A two dimensional solution to NMS ordination of plots in species density space was the best fit for these data (Figure 10; final stress = 13.053, final instability = 0.00001). The accumulated proportion of variance represented by the 2 axes in this ordination was 90.2%.

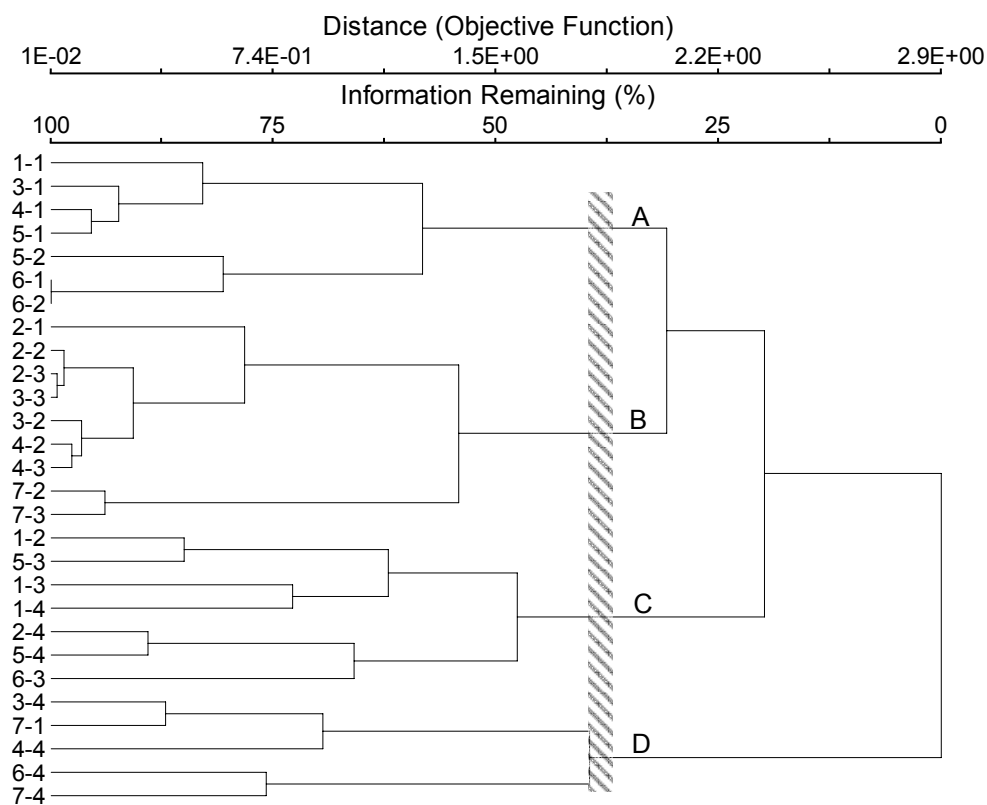


Figure 9. Hierarchical cluster analysis of understory species density. Numbers along the left edge of the dendrogram identify plots. The hashed column identifies the pruning location and letters identify plots groups as described in the text.

Table 5. Significant indicator values for the 4 understory density groups identified through cluster analysis. Indicator values and associated p-values represent the ability of a particular species to indicate the associated plot group.

	Group	Indicator Value	p value
<i>Festuca idahoensis</i>	A	32.6	0.001
<i>Phlox hoodii</i>	A	49.0	0.001
<i>Lomatium triternatum</i>	A	52.4	0.001
<i>Poa scabrella</i>	A	40.5	0.005
<i>Astragulis purshii</i>	A	54.6	0.005
<i>Calochortus macrocarpa</i>	A	50.0	0.009
<i>Agropyron spicatum</i>	A	50.7	0.012
<i>Chrysothamnus nauseosus</i>	A	51.8	0.013
<i>Lupinus</i> sp.	B	67.0	0.001
<i>Lupinus argenteus</i>	B	72.2	0.001
<i>Helianthella uniflora</i>	B	69.2	0.001
<i>Castilleja miniata</i>	B	71.5	0.001
<i>Koeleria macrantha</i>	B	36.2	0.002
<i>Eriophyllum lanatum</i>	B	67.1	0.002
<i>Sitanion hystrix</i>	B	42.0	0.003
<i>Achillea millifolium</i>	B	32.2	0.004
<i>Carex rossii</i>	B	38.8	0.015
<i>Antennaria geyeri</i>	B	41.5	0.04
<i>Poa nervosa</i> var <i>wheeleri</i>	C	43.0	0.036
<i>Berberis repens</i>	D	97.0	0.001
<i>Silene menziesii</i>	D	75.0	0.001
<i>Calamagrostis rubescens</i>	D	59.1	0.002

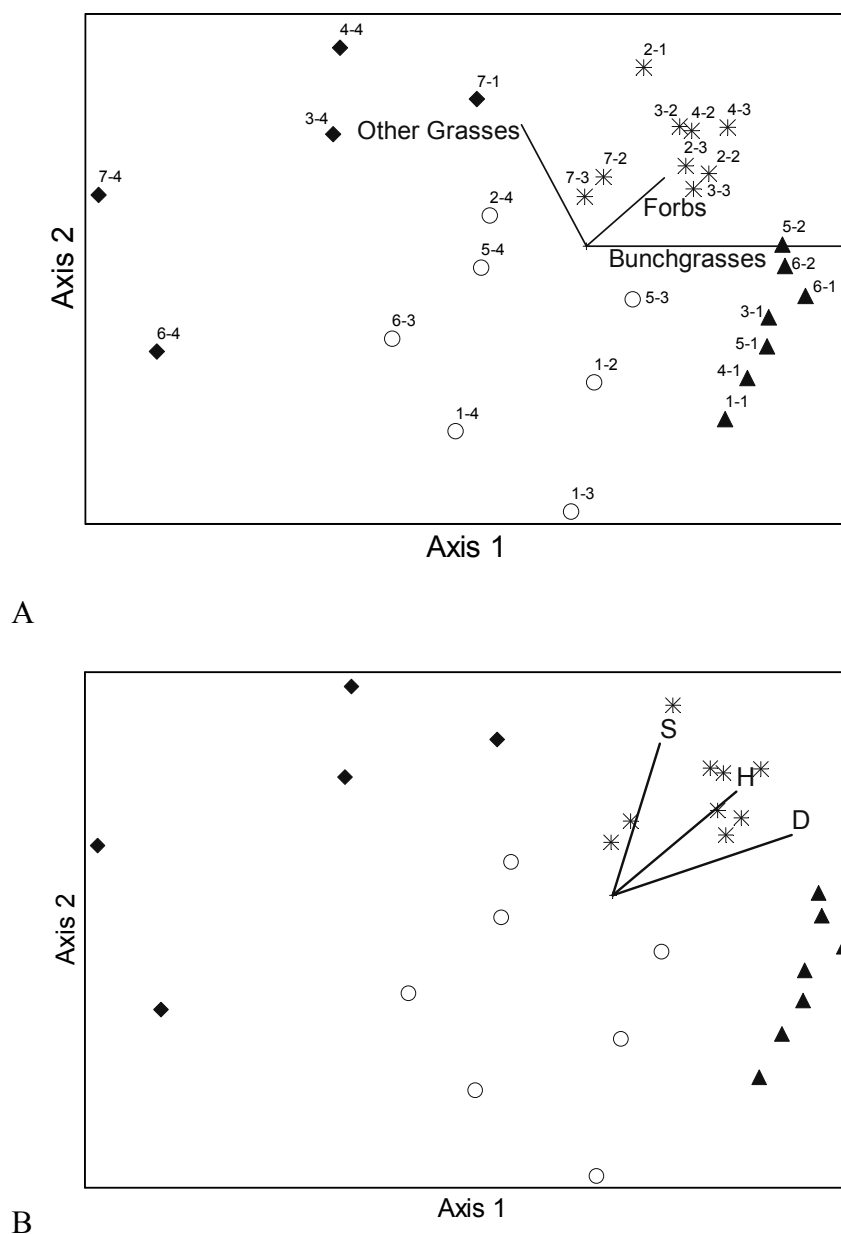


Figure 10. NMS ordination of understory species density data showing plots in species space. Symbols represent plot groups identified through cluster analysis (group A (▲), group B (*), group C (○), and group D (◆)). Joint plots represent correlations with ordination axes. Correlation strength and direction are represented by line length and angle. Panel A displays the relationships among plot groups and understory plant functional groups while panel B identifies patterns in diversity indices (D = Simpson's, H = Shannon's, S = species richness). Plot numbers are identified in panel A.

Plant functional group overlays correspond well with the indicator species analyses on cluster generated groupings (Figure 10). The presence or absence of perennial bunchgrasses was associated with the gradient represented by axis 1 while the occurrence of forbs and other grasses (predominantly the rhizomatous species *C. rubescens*) were associated with axis 2 (Table 6). Plot groups A and B existed at higher values (to the right) along the axis 1 gradient, while groups C and D existed at lower values, corroborating the significance of perennial bunchgrasses to the understory species composition of groups A and B identified through ISA. Group B plots associated with high forb diversity in the cluster analysis occupied the upper portions of the axis 2 gradient also related to the presence of forbs. Although uniform in the absence of perennial bunchgrasses, some plots in group D were higher in other-grass abundance, primarily associated with very high densities of *C. rubescens*.

Table 6. Pearson correlations between ordination axes and understory species functional groups for the NMS ordination of understory species density as presented in Figure 10.

	Axis 1	Axis 2
Perennial Bunchgrasses	0.872	-0.023
Other Grasses	-0.425	0.596
Forbs	0.475	0.428

The strongest correlations of perennial bunchgrass species to axis 1 were *F. idahoensis*, *P. scabrella*, and *K. macrantha* (Table 7), indicating that plots in groups A and B had high densities of these species while plots in groups C and D were lacking. As suggested by the diagonal trend of the forb joint plot, numerous forbs shared correlations with both axes (Table 7), however *Phlox hoodii* Rich., *Achillea millifolium* L., and *Lomatium triternatum*(Pursh) Coult & Rose expressed a substantially stronger alliance with axis 1 (Table 7). *B. repens* and *S. mensiezii* both

expressed strong negative correlations with axis 1 confirming the indicator species analysis which identified these two species as indicators of group D plots. *C. rubescens* expressed a strong correlation with axis 2 and a weaker negative correlation with axis 1, corroborating the earlier suggestion of the significance of *C. rubescens* in the other grasses functional group. *Carex rossii* Boot exhibited a similar relationship among axes, however only contributed ~8% of the total other grasses density. In contrast, the relative density of *C. rubescens* was 71%. The density of *Lupinus argenteus* Pursh showed the strongest correlations with axis 2 (Table 7).

Table 7. Pearson correlations between ordination axes and understory species density for the NMS ordination of understory species density as presented in Figure 10.

	Axis 1	Axis 2
<i>Festuca idahoensis</i>	0.907	-0.139
<i>Koeleria macrantha</i>	0.78	0.326
<i>Poa scabrella</i>	0.83	0.04
<i>Agropyron spicatum</i>	0.423	-0.599
<i>Phlox hoodii</i>	0.838	-0.285
<i>Achillea millifolium</i>	0.776	0.373
<i>Agoseris glauca</i>	0.521	0.52
<i>Lomatium triternatum</i>	0.849	-0.149
<i>Calochortus macrocarpa</i>	0.608	0.114
<i>Carex rossii</i>	-0.21	0.679
<i>Sitanion hystrix</i>	0.568	0.356
<i>Aster occidentalis</i>	0.025	0.509
<i>Berberis repens</i>	-0.756	0.235
<i>Stipa occidentale</i>	0.511	0.245
<i>Lupinus sp.</i>	0.12	0.72
<i>Lupinus argenteus</i>	0.207	0.732
<i>Helianthella uniflora</i>	0.22	0.564
<i>Castilleja miniata</i>	0.336	0.519
<i>Silene mensiezii</i>	-0.756	0.342
<i>Calamagrostis rubescens</i>	-0.397	0.661

Overlaying indices of species diversity (Figure 10) suggested that plots in groups A and B, trending to the right along axis 1, were higher in species diversity relative to groups C and D. Although Simpson's (D) and Shannon's (H) diversity values integrate different aspects of community structure, both incorporate species richness and evenness and higher values suggest greater diversity (McCune and Grace 2002). Group B plots, in the upper right of the ordination space had higher species richness than the remaining plots, likely a reflection of substantial increase in forb abundance evident in this group. Similar results were obtained when the ordination was rotated to maximize the correlation between Shannon's and Simpson's diversity values and axis 1.

The results of the principal components analyses of soil moisture, soil nitrogen availability and tree occupancy are presented in Tables 8 and 9. The first 2 components from the PCA on soil moisture were used for the synthetic soil moisture variables. The first component clearly represented the absence of late season moisture, showing very high negative correlations with July 22, August 3, and August 15 soil moisture measurements (Table 9). Principle component 2 was highly correlated with June 1 and July 4 soil moisture and was interpreted to represent early season soil moisture. To aid in display and interpretation, the PCA coordinates of the first component were multiplied by (-1) creating a variable that represented higher late season soil moisture rather than lower late season soil moisture.

The first component of the PCA on mineral N availability accounted ~51% of the variation in the data and represented a general index of inorganic N availability (Table 8 and 9). Plots with higher scores on component 1 generally had more nitrogen available than plots with low scores. The second component represented September nitrogen availability and higher PCA scores were associated with higher September nitrogen availability.

The synthetic variable of pine occupancy incorporated only the first principle component of the PCA on basal area, density and canopy closure, and owing to the negative association between the component and tree occupancy variables,

represented a lack of pine occupancy. No single variable emerged as a dominant indicator of tree presence rather the first principal component essentially integrated all three tree occupancy measures (Table 9). To aid in display and interpretation the PCA coordinates of the first component were multiplied by (-1) creating a variable that represented pine occupancy rather than pine vacancy.

Table 8. Percent of variance explained by axes interpreted in principle components analyses of soil moisture, nitrogen availability and pine occupancy.

Component	% of Variance Explained	Cumulative % of Variance
Soil Moisture		
1	55.063	55.063
2	19.593	74.656
Nitrogen Availability		
1	51.409	51.409
2	24.001	75.410
Pine Occupancy		
1	85.175	85.175

Early summer soil moisture displayed a strong relationship with the gradient represented by axis 2 of the NMS ordination, indicating that the plots in group B and most of the group D plots experienced higher early season soil moisture (Figure 11 and Table 10). Plots to the right on axis 1 tended to have higher soil temperatures with both daily maximum and minimum soil temperatures showing relatively strong correlations with this gradient (Figure 11; Table 10).

Under-canopy radiation was strongly aligned with axis 1, evidence of substantially higher light intensity in plots associated with groups A and B (Figure 11 and Table 10).

Table 9. Correlations between variables and principal components from PCA analyses of soil moisture, nitrogen availability and pine occupancy.

	Principal Component	
	1	2
Soil Moisture		
June 1 Soil Moisture	-0.5163	0.7238
June 20 Soil Moisture	-0.2683	-0.0666
July 4 Soil Moisture	-0.5806	0.6411
July 22 Soil Moisture	-0.9564	-0.1213
August 3 Soil Moisture	-0.9378	-0.2973
August 1 Soil Moisture	-0.9132	-0.3648
Nitrogen Availability		
June 11 Nitrogen	0.8009	-0.0232
July 12 Nitrogen	0.8825	-0.0951
August 12 Nitrogen	0.7365	-0.2520
September 9 Nitrogen	0.3060	0.9418
Pine Occupancy		
Basal Area	-0.8927	-
Density	-0.9360	-
Canopy Closure	-0.9393	-

Note: Dashes indicate components that were not interpreted.

Of the nitrogen availability variables generated, pooled N showed the strongest relationship with the distribution of plots associated with understory species density (Figure 11 and Table 10). Pooled nitrogen is a reflection of the overall nitrogen availability across dates and represents an index of the general availability of nitrogen in each plot. Plots with higher pooled N values had more available N.

Accordingly, groups A and B were higher in nitrogen availability compared to plots from the other groups.

Ponderosa pine occupancy was strongly correlated to axis 1, indicating that plots in groups A and B and existed in stands of low pine occupancy while plots in Group D generally existed in high pine occupancy stands.

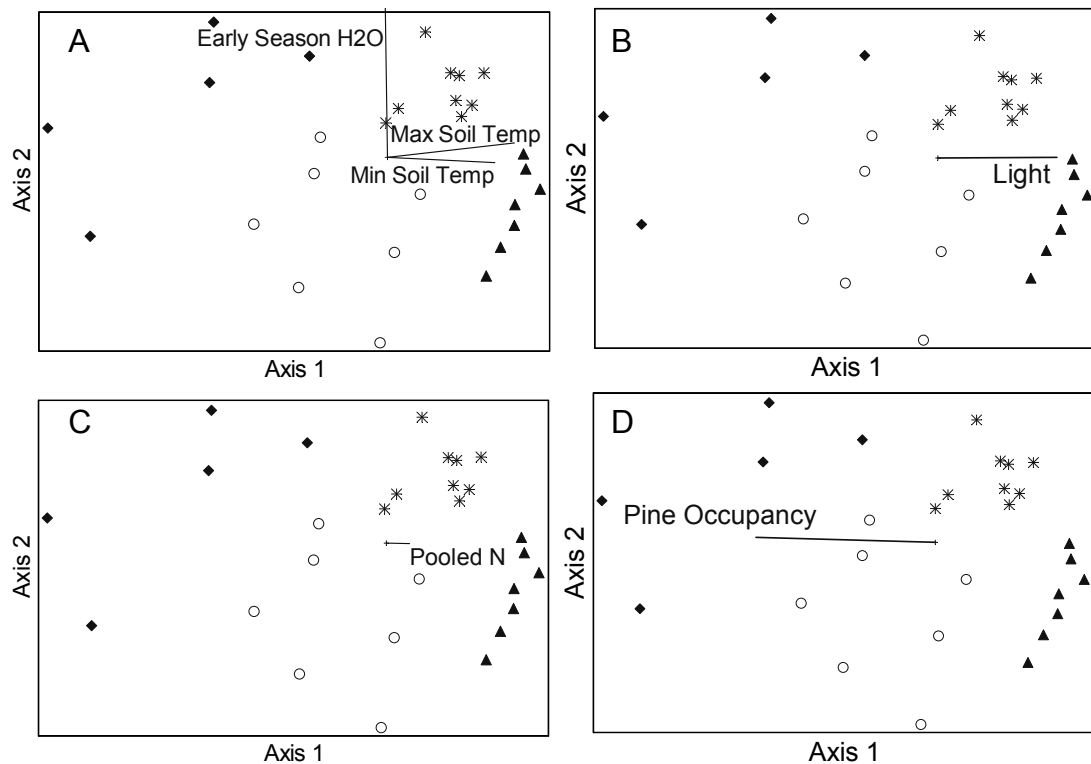


Figure 11. NMS ordination of understory species density data showing plots in species space. Symbols represent plot groups identified through cluster analysis (group A (▲), group B (*), group C (○), and group D (◆)). Joint plots represent correlations with ordination axes. Correlation strength and direction are represented by line length and angle. Panels display the relationships among plot groups and soil moisture and temperature (A), under-canopy light (B), nitrogen availability (C), and pine occupancy (D).

Table 10. Pearson correlations between ordination axes and understory growing conditions for the NMS ordination of understory species density as presented in Figure 11.

	Axis 1	Axis 2
Early Summer H ₂ O	-0.068	0.792
Maximum Soil Temperature	0.727	0.178
Minimum Soil Temperature	0.656	-0.201
Light Availability	0.703	0.026
Pooled N	0.309	-0.037
Pine Occupancy	-0.864	0.068

Understory Cover

The hierarchical cluster analysis used to evaluate plot groupings based on understory species cover was pruned at 5 groups (44.3% information remaining; Wishart's objective function; Figure 12). Species with significant indicator values are presented in Table 11. Plots in group A were indicated by *F. idahoensis* and *P. hoodii* along with *L. triternatum* and *Astragalus purshii* Dougl.. Group B plots were indicated by perennial bunchgrasses *K. macrantha*, *S. hystrix*, and *P. scabrella* and were high in forb diversity with 9 different forbs expressing significant indicator values for this group. Only *Silene douglasii* Hook. var. *douglasii* provided a significant indicator for group C. The presence and cover of *Erigeron gracilis* Rydb. and *P. ponderosa* saplings identified those plots in group D, while *S. menziesii*, *B. repens*, and *C. rubescens* provided significant indicators of group E.

A two dimensional solution to NMS ordination of plots in species cover space was the best fit to these data (Figure 13; final stress = 13.38, final instability = 0.00001). The accumulated proportion of variance represented by the 2 axes in this ordination was 87.4%.

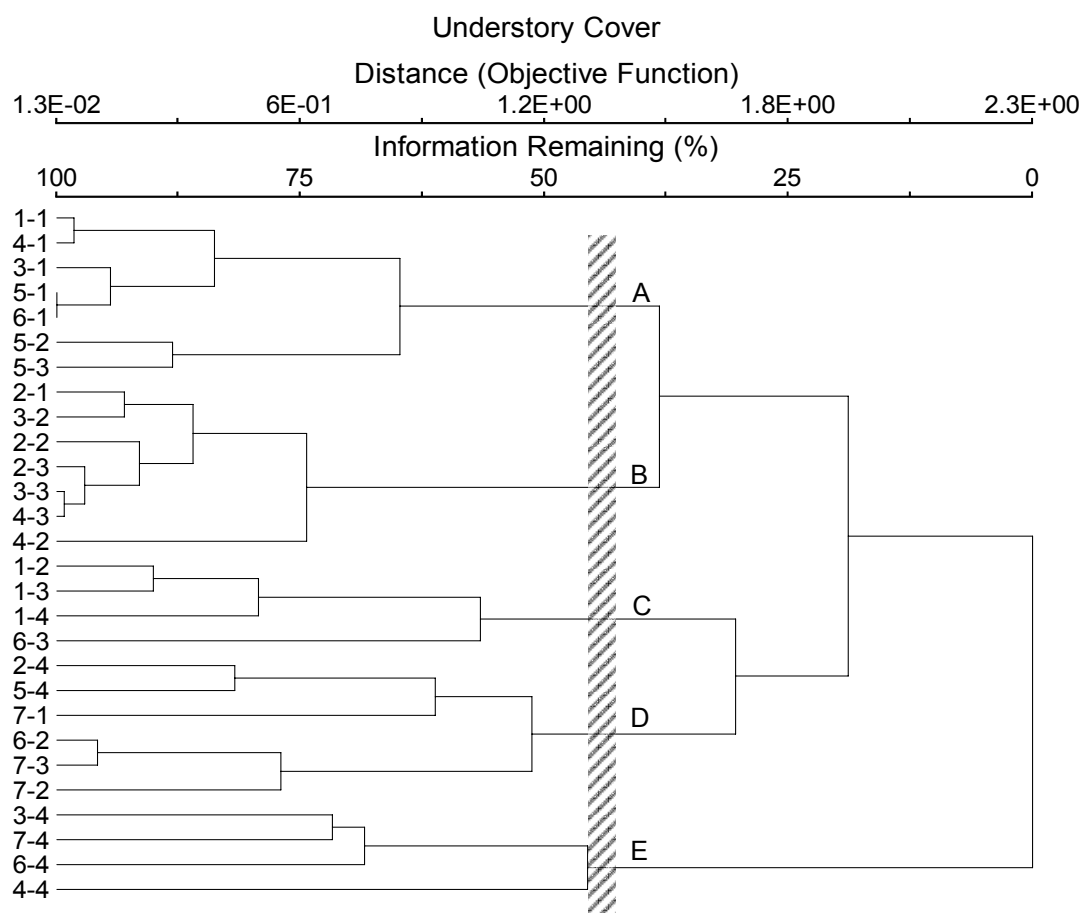


Figure 12. Hierarchical cluster analysis of understory species cover. Numbers along the left edge of the dendrogram identify plots. The hashed column identifies the pruning location and letters identify plots groups as described in the text.

Table 11. Significant indicator values for the 5 understory cover groups identified through cluster analysis. Indicator values and associated p-values represent the ability of a particular species to indicate the associated plot group.

	Group	Indicator Value	P value
<i>Festuca idahoensis</i>	A	24.9	0.001
<i>Phlox hoodii</i>	A	34.0	0.003
<i>Lomatium triternatum</i>	A	46.6	0.005
<i>Astragalus purshii</i>	A	57.1	0.012
<i>Achillea millifolium</i>	B	26.6	0.001
<i>Koeleria macrantha</i>	B	33.6	0.001
<i>Helianthella uniflora</i>	B	66.8	0.001
<i>Lupinus argenteus</i>	B	80.2	0.001
<i>Lupine sp.</i>	B	82.0	0.001
<i>Agoseris glauca</i>	B	42.0	0.002
<i>Castilleja miniata</i>	B	71.4	0.002
<i>Sitanion hystrix</i>	B	38.5	0.003
<i>Poa scabrella</i>	B	37.2	0.004
<i>Eriophyllum lanatum</i>	B	56.4	0.006
<i>Antennaria geyeri</i>	B	45.9	0.023
<i>Calochortus macrocarpum</i>	B	40.6	0.048
<i>Silene douglasii</i>	C	48.2	0.014
<i>Erigeron gracilis</i>	D	63.7	0.003
<i>Pinus ponderosa</i> sapling	D	31.8	0.034
<i>Silene mensiezii</i>	E	75.5	0.001
<i>Berberis repens</i>	E	62.2	0.003
<i>Calamagrostis rubescens</i>	E	43.3	0.023

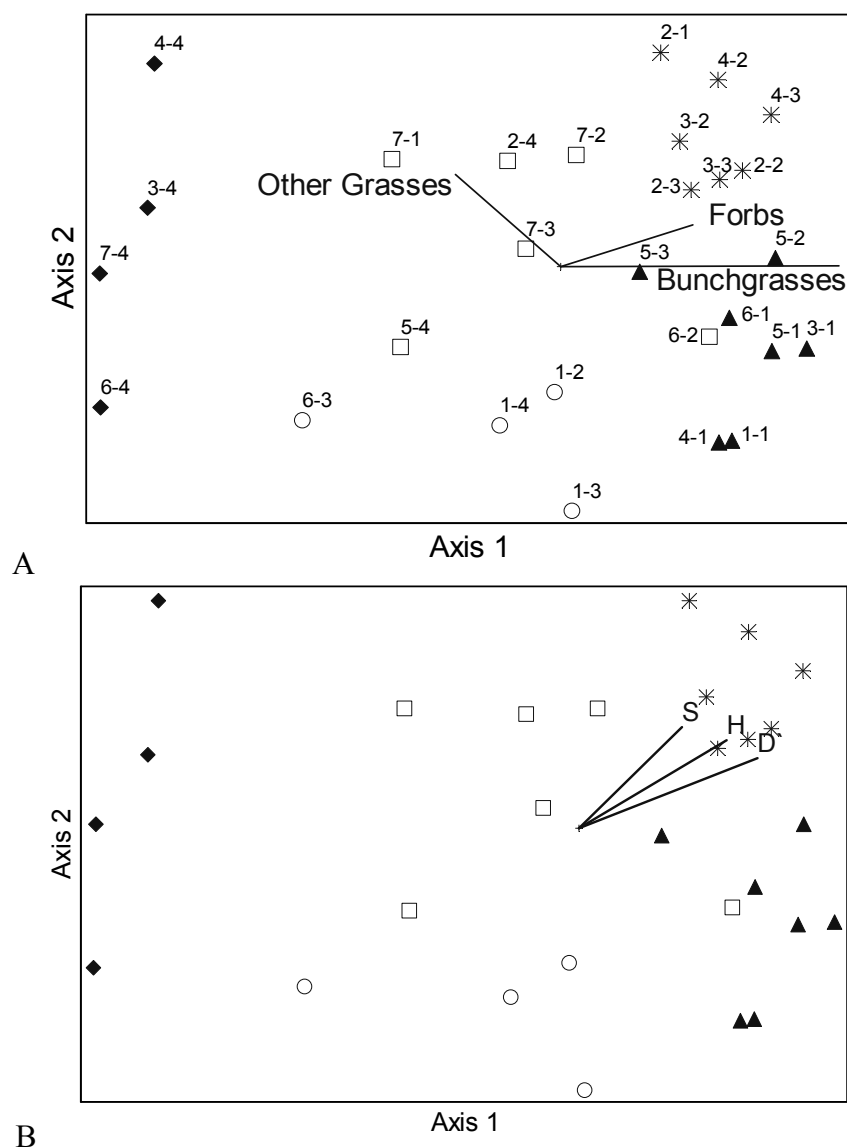


Figure 13. NMS ordination of understory species cover data showing plots in species space. Symbols represent plot groups identified through cluster analysis (group A (▲), group B (*), group C (○), group D (□), and group E (◆)). Overlays represent correlation with ordination axes. Correlation strength and direction are represented by line length and angle. Panel A displays the relationships among plot groups and understory plant functional groups while panel B identifies patterns in diversity indices (D = Simpson's, H = Shannon's, S = richness). Individual plots are identified in panel A.

Overlays of understory species functional groups corresponded well with the indicator species analysis. Axis 1 clearly described a gradient in perennial bunchgrass cover (Figure 13 and Table 12) indicating that groups A and B were substantially higher in perennial bunchgrass cover than plots in group E. The other grasses functional group, including rhizomatous species such as *C. rubescens*, *P. nervosa* var. *wheeleri*, and *C. rossii*, accounted for gradients on both axes and it was clear that plots in the upper left region of the ordination space possessed higher abundances of these species. Forb species were also represented by both axes, and identified plots in the upper right of the ordination space as those having high forb abundances. Specifically, group B plots, as demonstrated by ISA, were high in forb diversity and abundance.

Table 12. Pearson correlations between ordination axes and understory species functional groups for the NMS ordination of understory species cover as presented in Figure 13.

	Axis 1	Axis 2
Perennial Bunchgrasses	0.888	0.023
Other Grasses	-0.539	0.536
Forbs	0.617	0.323

F. idahoensis, *K. macrantha*, and *P. scabrella*, all had strong correlations with axis 1 of the NMS ordination indicating their significance in determining the relationship between groups A and B and the abundance of perennial bunchgrasses (Table 13). As suggested by the diagonal trend in the forb joint plot, a variety of forb species, including *Antennaria geyeri* Gray, *L. argenteus*, *Agoseris glauca* (Pursh) Raf. var. *glauca*, *Helianthella uniflora* (Nutt.) T. & G. var. *douglasii* (T.&G.) Weber and *Lupinus* sp., were correlated to both axis 1 and axis 2, however *P. hoodii*, *A.*

millifolium, and *S. menziesii* showed much stronger relationships with axis 1 (Table 13). The negative correlation of *S. menziesii* affirmed the ISA which identified this species as an indicator of plots in group E. Similarly, the negative correlation between *B. repens* and axis 2 was also in agreement with the ISA of these data. Of the other grass species both *C. rubescens* and *C. rossii* corresponded with the position of the joint plot representing this functional group showing similar negative and positive associations with axis 1 and axis 2, respectively (Table 13). The cover of *L. argenteus* expressed the strongest correlation with axis 2.

Table 13. Pearson correlations between ordination axes and understory species cover for the NMS ordination of understory species cover as presented in Figure 13.

	Axis 1	Axis 2
<i>Festuca idahoensis</i>	0.871	-0.143
<i>Koeleria macrantha</i>	0.798	0.438
<i>Poa scabrella</i>	0.788	0.272
<i>Agropyron spicatum</i>	0.296	-0.675
<i>Phlox hoodii</i>	0.867	-0.244
<i>Achillea millifolium</i>	0.770	0.422
<i>Agoseris glauca</i>	0.483	0.511
<i>Lomatium triternatum</i>	0.667	0.069
<i>Calochortus macrocarpa</i>	0.521	0.198
<i>Carex rossii</i>	-0.340	0.567
<i>Sitanion hystrix</i>	0.636	0.456
<i>Aster occidentalis</i>	-0.046	0.570
<i>Berberis repens</i>	-0.727	0.040
<i>Stipa occidentale</i>	0.574	0.418
<i>Lupinus sp.</i>	0.261	0.570
<i>Lupins argenteus</i>	0.345	0.690
<i>Helianthella uniflora</i>	0.335	0.546
<i>Silene mensiezii</i>	-0.815	0.210
<i>Calamagrostis rubescens</i>	-0.446	0.592
<i>Antennaria geyerii</i>	0.225	0.658

Under the rotation imposed on the ordination in Figure 13, the distribution of plots with respect to species diversity followed a diagonal pattern from the lower left to upper right corners of the ordination space with plots becoming more diverse along this gradient. Plots in Group B, owing to the higher diversity of forbs, were more diverse than the remaining plots, however, Group A plots also possessed relatively high diversity. Plots in groups E and C possessed the lowest species diversity.

Early summer soil moisture displayed a strong relationship with the gradient represented by axis 2, indicating that the plots in group B, most of the plots in group D, and some of the group E plots experienced higher early season soil moisture (Figure 14 and Table 14). Plots to the right along axis 1 experienced higher soil temperatures as indicated by the strong association between daily maximum and minimum soil temperature and the axis 1 gradient (Figure 14 and Table 14).

Under-canopy radiation was strongly related to the gradient represented by axis 1, indicating a substantially higher light intensity in plots associated with groups A and B (Figure 14; Table 14).

Both late season and pooled nitrogen availability appeared to have a relationship with the distribution of plots (Figure 14; Table 14). The PCA derived pooled N variable represents an index of the general availability of mineral nitrogen, and it appears from these analyses that plots along the right side of axis 1 (groups A and B) generally possessed higher mineral nitrogen availabilities compared to the other plot groups. Similarly, plots in the upper portions appeared to have greater abundance of plant available nitrogen later in the growing season.

Pine occupancy was also highly correlated to the gradient represented by axis 1 (Figure 14; Table 14). Plots on the left side of the ordination space existed in stands of high pine occupancy while plots to the right occupied stands with relatively low pine occupancy.

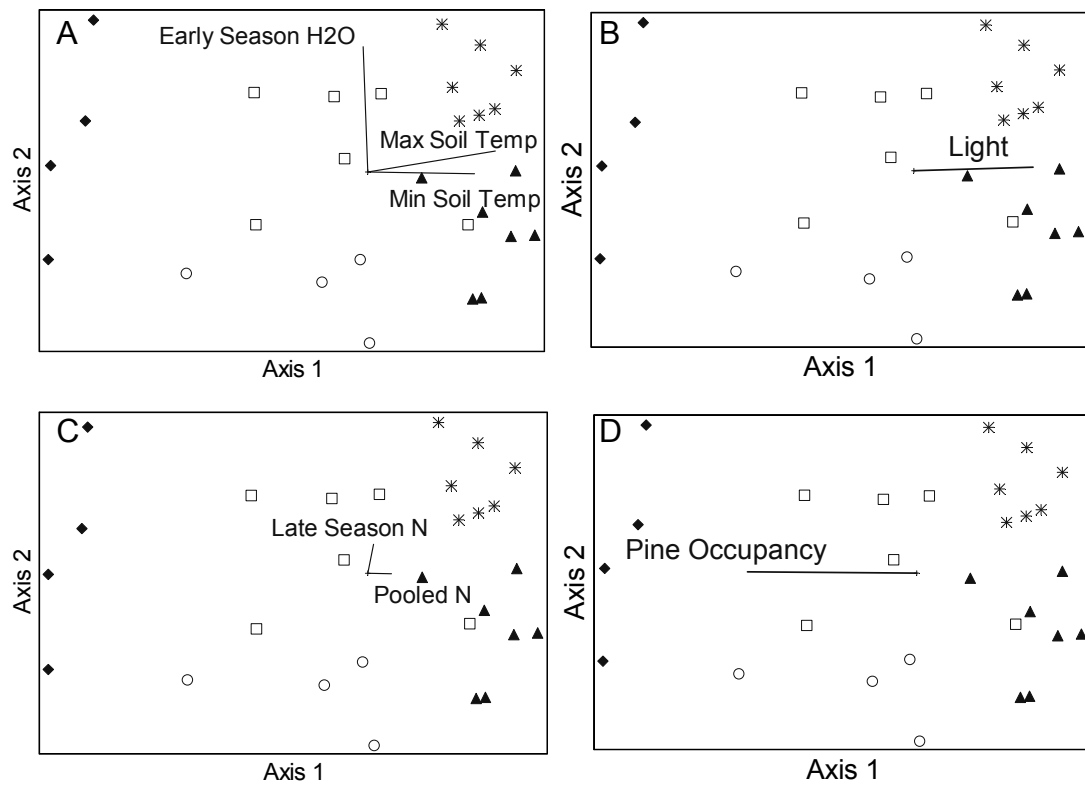


Figure 14. NMS ordination of understory species cover data showing plots in species space. Symbols represent plot groups identified through cluster analysis (group A (▲), group B (*), group C (○), group D (□), and group E (◆)). Overlays represent correlation with ordination axes. Correlation strength and direction are represented by line length and angle. Panels display the relationships among plot groups and soil moisture and temperature (A), under-canopy light (B), nitrogen availability (C), and pine occupancy (D).

Table 14. Pearson correlations between ordination axes and understory growing conditions for the NMS ordination of understory species cover as presented in figure 14.

	Axis 1	Axis 2
Early Summer H ₂ O	-0.147	0.715
Maximum Soil Temperature	0.726	0.294
Minimum Soil Temperature	0.662	-0.091
Light Availability	0.705	0.130
Pooled N	0.312	-0.056
Late Season N	0.153	0.345
Pine Occupancy	-0.842	0.028

Discussion

The results from analyses of the understory species density and cover data sets, although incorporating different response variables, provided similar interpretations of the relationships among plots with respect to understory species composition. NMS ordination axis 1 from both analyses represented a gradient in perennial bunchgrass abundance. Groups A and B in both cover and density analyses were identified as having high abundances of perennial bunchgrasses while density group C and D and cover groups C, D, and E had relatively small or absent perennial bunchgrass component. *Festuca. idahoensis* was the dominant perennial bunchgrass in both data sets and expressed a relative cover of 81% and relative density of 61% within the perennial bunchgrass functional group comprised of *F. idahoensis*, *A. spicatum*, *S. hystrix*, *Elymus cinereus* Scrib. & Merr., *K. macrantha*, and *P. scabrella*. Group B in both analyses also represented plots with high diversity and abundance of forb species.

The analyses of the 2 data sets did alter the classification of several plots (Table 15). Plots 2-4 and 5-4 were identified by the presence of *P. nervosa* var. *wheeleri* in the density analysis and by *P. ponderosa* saplings and *E. gracilis* in the

cover analyses. Although *P. nervosa* can reach high densities, its cover at any particular location is generally low as it often exists as a 1 or 2 leaved single tiller. The opposite pattern is often true of sapling *P. ponderosa* as single stems can provide a significant cover. Plot 7-1 was classified in the D group in both analyses, however cover group D was identified by the presence of *P. ponderosa* saplings and *E. gracilis* while *C. rubescens*, *S. menziesii*, and *B. repens* identified density group D. The other grasses functional group appeared to adequately characterize the plot location in both analyses and this was likely in response to the high abundance of rhizomatous species, particularly *C. rubescens*. Similar to *P. nervosa*, *C. rubescens* often exists as single tillers with few leaves that do not provide high cover values relative to density. Plots 2-4, 5-4, and 7-1 remained appropriately classified within the overarching perennial bunchgrass gradient and were identified in both analyses as plots exhibiting relatively low perennial bunchgrass abundance.

Table 15. Cluster analysis derived plot groupings associated with analyses of understory density and understory cover data sets.

Plot	Density	Cover	Plot	Density	Cover
1-1	A	A	4-3	B	B
1-2	C	C	4-4	D	E
1-3	C	C	5-1	A	A
1-4	C	C	5-2	A	A
2-1	B	B	5-3	C	A
2-2	B	B	5-4	C	D
2-3	B	B	6-1	A	A
2-4	C	D	6-2	A	D
3-1	A	A	6-3	C	C
3-2	B	B	6-4	D	E
3-3	B	B	7-1	D	D
3-4	D	E	7-2	B	D
4-1	A	A	7-3	B	D
4-2	B	B	7-4	D	E

Interestingly, several plots were classified as low perennial bunchgrass plots in one analysis and high perennial bunchgrass plots in the other analysis. Plot 5-3 was classified to group C in the density analysis and group A in the cover analysis. However, classification as a process attempts to fit a line through a gradient of change, and plot 5-3 existed in the high perennial bunchgrass abundances associated with density group C and low perennial bunchgrass abundance associated with cover group A. As described previously, *P. nervosa* tends to express higher density relative to cover and it is likely that the high densities overshadowed the presence of perennial bunchgrasses in the density analyses, although perennial bunchgrass presence was indicated in the relative positioning of the plot in the ordination space.

An interesting shift in classification saw plot 6-2 classified as a perennial bunchgrass plot in the density analysis (group A) and a pine sapling plot in the cover analysis (Group C). This plot appeared more similar to the cover group A plots based on its location in the ordination space but was classified as a cover group C. This plot was one of the few plots that had *E. gracilis* present and along with a relatively high abundance of pine saplings, this resulted in its classification as a cover group C plot. However, from a perennial bunchgrass cover perspective this plot effectively remained a high perennial bunchgrass abundance plot based on its position along the NMS axis 1 gradient. Much like several of the other plots within density group C and cover groups C and D other plant species present in the plot apparently provided more distinguishable characteristics upon which to classify.

Although plots 7-2 and 7-3 were classified as density group B and cover group D, both plots exist in similar spaces with respect to the perennial bunchgrass gradient in the analyses. These plots were positioned in the lower perennial bunchgrass abundance in the density group B while they were located in regions of high perennial bunchgrass cover relative to the remaining plots in cover group D. The relatively high cover of pine saplings and the exclusive nature of *E. gracilis* in these plots likely contributed to the difference in classification.

Plot 7-1 was classified as group D in both analyses, however the two group D's were not identified by the same species. Regardless, this plot appeared in similar regions of NMS ordination space and existed toward the low end of perennial bunchgrass abundance for cover group D and the high end of perennial bunchgrass abundance for density group D. In both situations, however, this plot existed in NMS region of high abundance of other grasses functional group, likely in response to the high abundance of *C. rubescens* observed in this plot.

Several plots were grouped as density group D and cover group E, however both groups were indicated by a similar suite of species and were representing similar understory conditions and were identified by a lack of perennial bunchgrasses and the presence of *C. rubescens*, *B. repens* and *S. mezesii*.

A distillation of the group similarities across both analyses is presented in Table 16. Plots were identified as high perennial bunchgrass (PBG), high perennial bunchgrass with forbs (PBG/Forb), low perennial bunchgrass (low PBG) or no perennial bunchgrass (no PBG).

Table 16. Plot group identifier based on combined results of the analyses of understory density and cover data sets. PBG = perennial bunchgrass.

Combined Group ID	Density Grouping	Cover Grouping
PBG	A	A
PBG/Forb	B	B
Low PBG	C	C & D
No PBG	D	E

Ponderosa pine can influence the understory environment and growing conditions for understory species by altering soil moisture (Barrett 1970 and Helvey 1975), light availability (Naumberg and DeWald 1999) and nutrient cycling and availability (Kay and Hart 1998). The results presented in this report indicate that

ponderosa pine site occupancy was inversely related to light and nitrogen availability and soil temperature but was unrelated to the dominant soil moisture gradient.

Under-canopy light availability increased as tree occupancy decreased reaching a maximum in those plots least influenced by ponderosa pine (Figure 15). A similar pattern can be observed when representing light availability categorized by the understory plot groups identified through cluster analyses and indicator species analyses (Figure 16). Plots identified as perennial bunchgrass abundant plots experienced very similar light conditions and were present under the highest light availability conditions encountered in the study. Plots classified as low perennial bunchgrass abundance and those categorized as no perennial bunchgrass existed at sequentially lower light availability and higher pine occupancies.

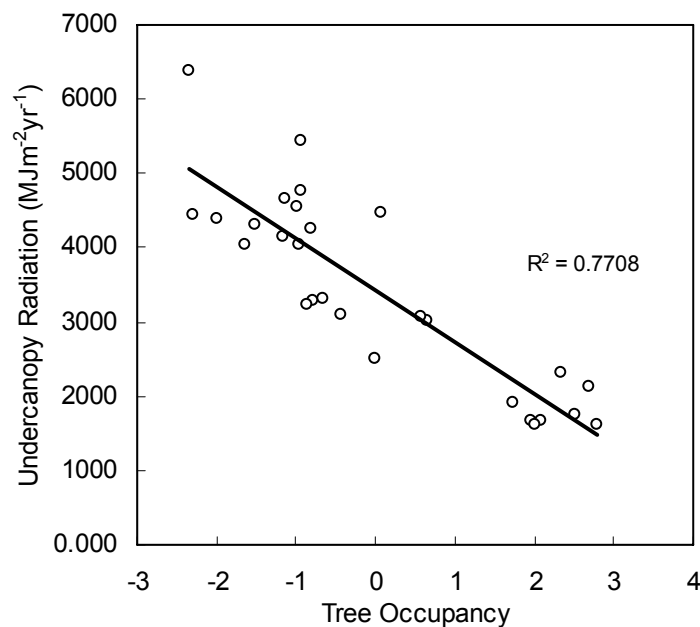


Figure 15. Relationship between under-canopy light availability and tree occupancy. Tree occupancy represents the first component of a principal components analysis incorporating tree basal area, density, and canopy closure.

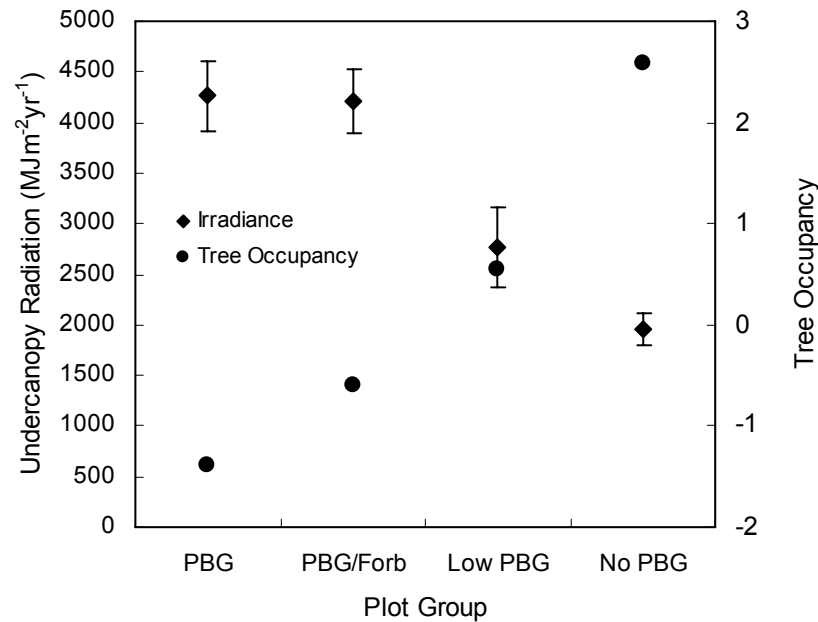


Figure 16. Relationships between plot groupings, under-canopy light availability and tree occupancy. Tree occupancy is the first component of a principal components analysis incorporating tree basal area, density, and canopy closure.

Naumburg and DeWald (1999) identified *P. ponderosa* forest structural attributes, in particular tree diameter, as significant with respect to graminoid species presence, however the authors further elucidated the relationship between tree diameter and light intensity and suggested that variable light intensity associated with differing pine diameters may be a mechanism responsible for the observed relationship. Riegel et al. (1995) observed an effect of canopy reduction on some species and indicated that species composition within life forms differed in response to canopy manipulation. The authors suggested that species that changed in density or cover in response to canopy reduction did so because of increase light availability (Riegel et al. 1995). Interestingly, Riegel et al. (1992) reporting on the same study as their 1995 paper referenced above, indicated that light had no impact on understory plant production. Although plant biomass was not measured in our study the positive association between biomass and vigor would suggest that the biomass of perennial

bunchgrasses was lower in plots with reduced cover and density of these species. The species encountered in the Riegel et al. (1992 and 1995) studies are species generally better adapted to grow under-canopy cover (e.g. according to Stubbendieck et al. (2003), *C. rubescens* preferred habitat is open to dense pine woods and it will not persist in open sunlight) than the perennial bunchgrasses encountered in the open stands in our study. It is probable that species better suited for under-canopy growth possess a lower light saturation point which, if the pre-treatment light conditions were above, would indicate that light was not limiting; as was concluded by Riegel et al. (1992). The area studied in Riegel et al. (1992) was a mesic seral ponderosa pine stand which suggests that the results of our study, in more arid climax ponderosa pine forests may not apply to ponderosa pine types functioning under different environmental conditions.

Festuca idahoensis was the dominant understory species in plots associated with high light environments (Figure 17). A significant loss in fescue abundance was evident between high perennial bunchgrass groups and low perennial bunchgrass groups which mirrored the pattern observed in light intensity (Figure 17). Moreover, *F. idahoensis* was essentially absent in plots within the lowest light intensity group. Moir (1966) investigated the influence of shading on *F. idahoensis* growth and found that plants grown in lower light environments produced significantly less biomass than those grown in full sunlight. Similarly, Carr (2007b) observed smaller values for root and shoot biomass, lower foliar cover and described reduced overall vigor for *F. idahoensis* plants grown under 80% shade treatment when compared to those grown in maximal light conditions. Carr (2007b) attributed this effect to reduced photosynthetic activity and an associated decline in carbon fixation. Thus, reduced light environments may influence plant vigor and growth to the extent that it limits the persistence of populations of species like *F. idahoensis* whose habitat preference is for higher light intensities.

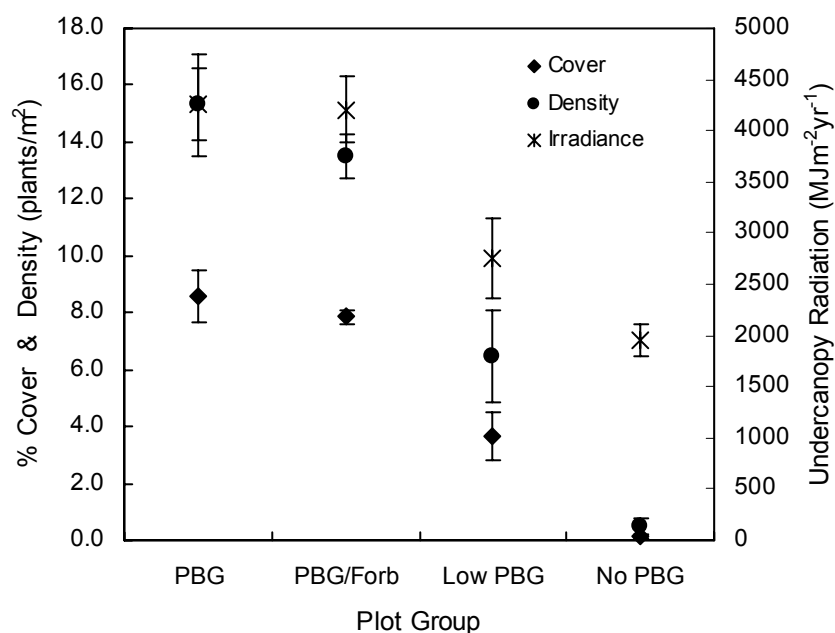


Figure 17. Relationships among average density and cover of *F. idahoensis* plants and under-canopy light intensity.

Soil temperatures exhibited moderately strong relationships with tree occupancy (Figure 18) indicating that soils were cooler under increasing canopy conditions. Similarly, plots in high perennial bunchgrass groups tended to exhibit hotter temperatures compared to those with low or no perennial bunchgrasses (Figure 19). Lower soil temperatures in high pine occupancy stands are likely due to the interactive effect of increased insulation from the thick mat of pine needle litter on the forest floor and the reduced radiation intensity associated with elevated canopy closure. Soil temperature can influence plant growth and is a major driver of plant distribution (Lambers et al. 1998). However, it is unclear what role, if any, soil temperature plays in the observed differences in understory plant species composition along the pine occupancy gradient. The optimum temperature for root growth of plants in temperate regions is between 10 and 30°C (Bowen 1991 and Lambers et al. 1998), within the range of temperatures encountered in the present analyses. Furthermore, Nasri and Doescher (1995), who evaluated the growth response of *F.*

idahoensis to experimentally controlled temperature variation, found very few differences among fescue plants grown at 5, 10, or 15°C. As the coolest temperatures on our sites were around 13°C, it is unlikely that the temperatures associated with higher pine occupancy played a major role in the associated decline in perennial bunchgrass abundance.

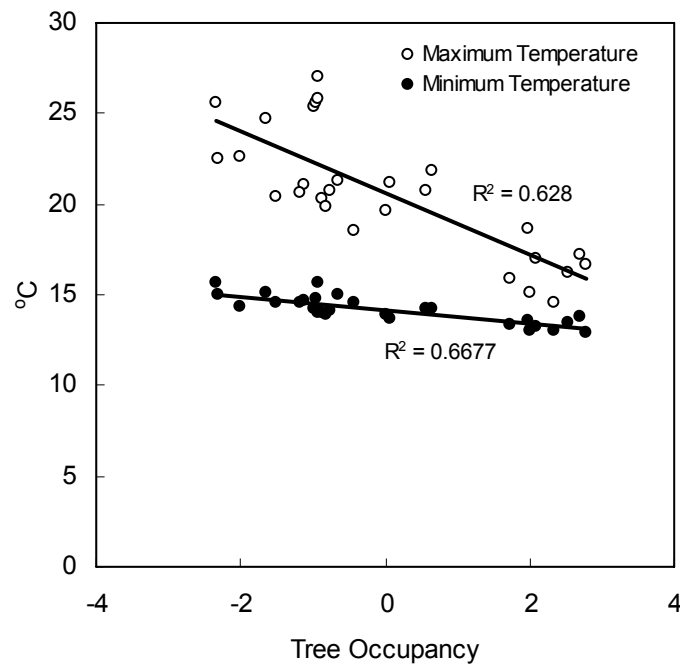


Figure 18. Relationship between tree occupancy and average daily minimum and maximum soil temperatures. Tree occupancy is a synthetic variable generated through principal components analyses and incorporates basal area, density and canopy closure.

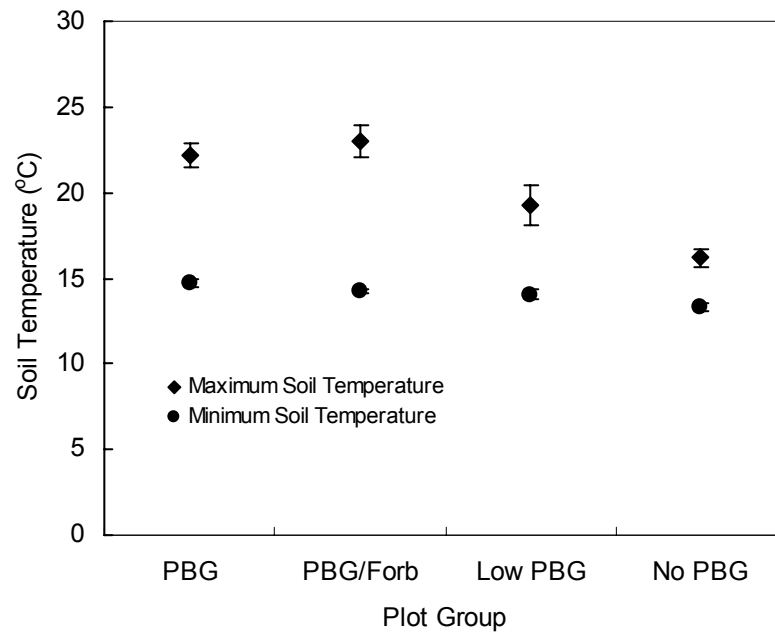


Figure 19. Relationships among average daily minimum and maximum soil temperatures and plot group.

Only pooled mineral nitrogen varied along the gradient of ponderosa pine occupancy and it displayed a relatively weak inverse relationship with tree abundance (Figure 20). The non-linear pattern apparent in nitrogen availability across the pine occupancy gradient (Figure 21) was likely responsible for the weakness observed in the correlation based joint plot overlay. A substantial reduction in mineral nitrogen availability was observed between plot groups with high perennial bunchgrass abundance and low tree occupancy and those with low perennial bunchgrass abundance and higher tree occupancy (Figure 21). Although it is often speculated that increasing pine abundance can decrease nutrient cycling (e.g. Covington and Sackett 1984) very few studies have examined this relationship. Kaye and Hart (1998) compared nitrogen transformation rates between relict openings and dense pole-sized ponderosa pine patches and found that the net rate of nitrogen mineralization in the grassy openings was nearly twice that of the pine patches. The authors suggested that this difference was related to substrate quality as grass litter is

typically low in lignin and high in nitrogen and as a result decomposes more rapidly than pine needle litter. Others have also identified the relatively recalcitrant nature of ponderosa pine needles (e.g. Klemmedson et al. 1985) and it is possible that this is a similar mechanism for the pattern in nitrogen availability observed in our data. Rates of decomposition are also influenced by soil temperature (Wolf and Wagner 2005) and it is likely that the observed differences in soil temperature contributed to the variability evident in plant available nitrogen. Warmer soil temperatures associated with increased fine-leaved grass substrate probably worked synergistically in producing increased rates of decomposition and nitrogen mineralization which contributed to higher values of nitrogen availability.

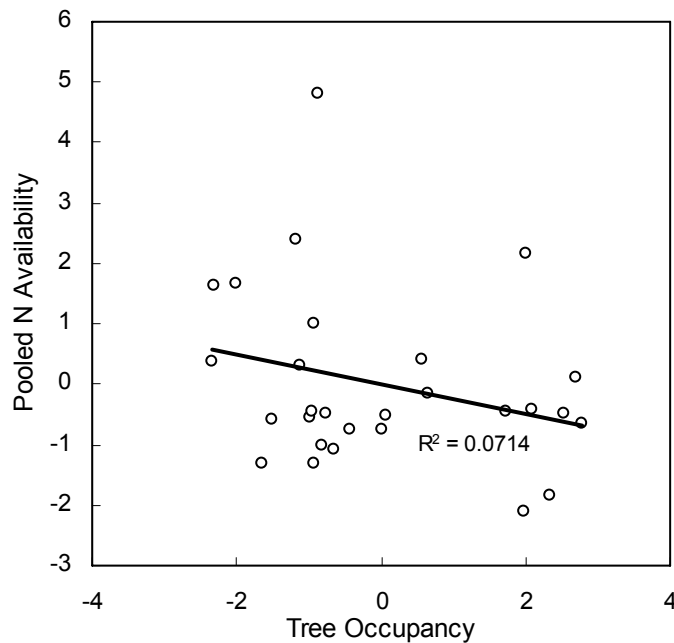


Figure 20. Relationship between tree occupancy and pooled nitrogen availability. Both parameters are synthetic variables generated through principal components analyses. Pooled N represents general trend in nitrogen availability across the season while tree occupancy incorporates basal area, density and canopy closure.

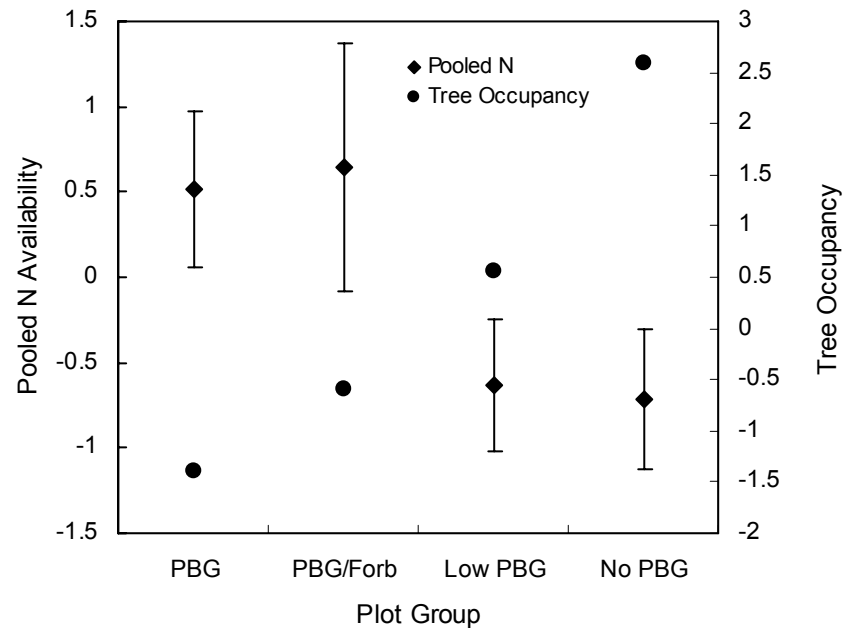


Figure 21. Relationships among tree occupancy, pooled mineral nitrogen availability and plot group. Tree occupancy and pooled N are synthetic variables generated through principal components analyses. Pooled N represents general trend in nitrogen availability across the season while tree occupancy incorporates basal area, density and canopy closure.

The large drop in *F. idahoensis* abundance evident between perennial bunchgrass dominated plots and low bunchgrass abundance plots corresponded to a similar reduction in nitrogen availability (Figure 22). Although the pattern in Figure 22 is intriguing and suggests a fairly rapid decline in nitrogen availability associated with moderate increases in tree occupancy, the influence of nitrogen availability on the distribution of perennial bunchgrasses is uncertain. Kaye et al. (2005) reported increased rates of net nitrogen mineralization in ponderosa pine plots that had been subjected to restoration thinning treatments (removal of >2000 *P. ponderosa* / ha), however they did not find a corresponding increase in total plant nitrogen uptake. They concluded that nutrients did not appear to be major drivers of post-treatment plant growth because stands with different net N mineralization had similar production and plant nitrogen uptake (Kaye et al. 2005). Similarly, Carr (2007b),

found no effect of increased nitrogen availability on root biomass, shoot biomass, or foliar cover of *F. idahoensis* plants grown under two nitrogen levels. Although nitrogen availability was higher in the fertilized treatments, Carr (2007b) suggested that *F. idahoensis* plants were not limited by available nitrogen as plant growth and vigor were similar for both nitrogen treatments. Riegel et al. (1991 and 1992) evaluating understory responses to increased resource availability in mesic *P. ponderosa* forests of northeast Oregon, found that understory production was greater under conditions of elevated moisture and nitrogen availability. Although the two factors probably function synergistically, the authors contend that improved soil moisture availability was likely the most influential factor in the observed increased production, and that understory species were not limited with respect to nitrogen as the increases in growth did not correspond to the observed increases in plant nitrogen uptake (Riegel et al. 1992).

The weak relationship between nitrogen availability and the abundance of perennial bunchgrasses observed in our study may also reflect a relative lack of nitrogen limitation along the gradient in perennial bunchgrass abundance. Thus, nitrogen availability may not be a major driver of the understory vegetation dynamics observed along the gradient in ponderosa pine site occupancy.

Although ponderosa pine forest structural changes have been shown to generate differences in soil moisture status (e.g. Barrett 1970 and Helvey 1975), soil moisture did not appear correlated with the gradient of tree occupancy identified in the present study (Figure 23). The strongest relationship between soil moisture and understory plant species composition was observed for early season soil moisture and this relationship was nearly orthogonal to the gradient exhibited in tree occupancy. Elevated early season soil moisture was associated with high diversity and abundance of forb species, most notably associated with plots classified as perennial bunchgrass/Forb and with the presence of other grass species, led primarily by the abundance of *C. rubescens*.

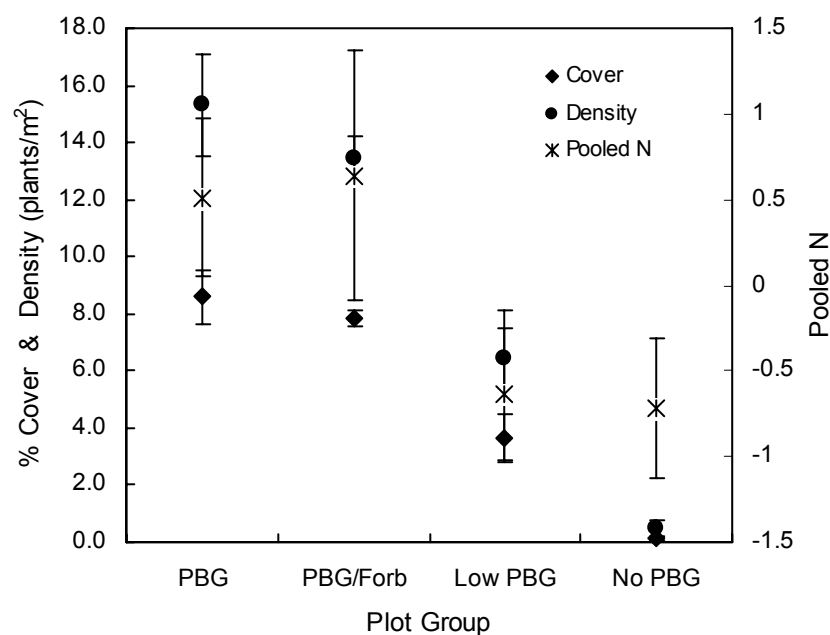
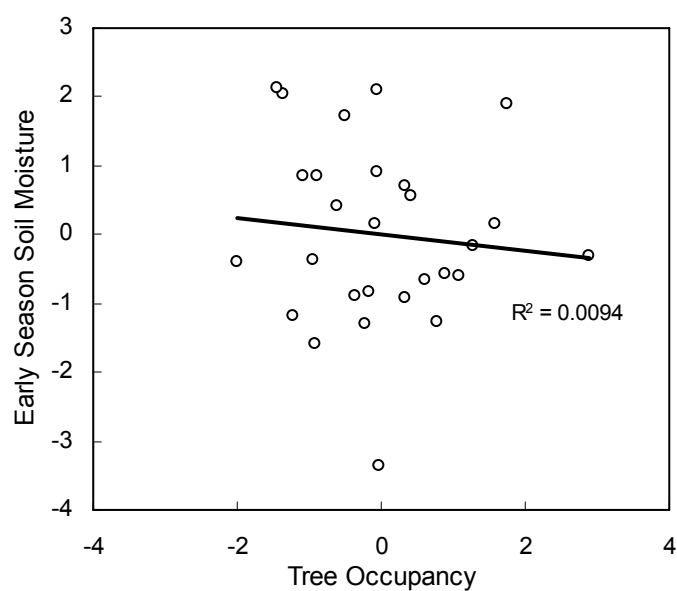


Figure 22. Relationship among *F. idahoensis* cover and density and pooled mineral nitrogen availability. Pooled N is a synthetic variable generated through principal components analyses and represents the general trend in nitrogen availability across the season.



The lack of a consistent trend in soil moisture along the gradient of tree occupancy is not surprising as several authors have observed only a short-term fluctuation in soil moisture status associated with stand manipulations.

Evapotranspiration is the major driver of soil moisture flux in semi-arid environments (Brandes and Wilcox 2000), and increased tree densities are generally associated with elevated transpirational demands. However, increased understory plant growth under conditions of low tree occupancy can also provide adequate leaf area to rival the transpirational demand observed in more dense pine types (Barrett and Youngberg 1965, Helvey 1975 and Baker 1986).

Differences in snow interception and accumulation among dense and open ponderosa pine stands have also been reported. Haupt (1951) observed lower levels of snow accumulation in dense pole sized ponderosa pine stands relative to more open or sapling forest structures. Variability in snow accumulation relative to stand density was observed on our sites (no quantitative data was recorded), however it is expected that the relatively small patch sizes, saturated soil conditions, and generally sloping nature of the sites limited the potential for differences in snow accumulation to effect similar differences in soil moisture.

Although changes in forest structure did not appear to influence soil moisture status competition for soil moisture between overstory trees and understory vegetation may additionally influence understory vegetation dynamics. Riegel et al. (1991, 1992, and 1995), through root trenching and resource addition experiments, concluded that understory vegetation production and species composition were influenced by tree mediated water availability. In our study, it is probable that the increased abundance of understory vegetation associated with lower *P. ponderosa* presence and diminished understory vegetation associated with high *P. ponderosa* abundance balanced the ecosystem level transpirational demands across the gradient of tree occupancy by partitioning soil water use relative to the abundance of the vegetation strata (i.e. overstory or understory). If understory plants are water limited

in higher pine occupancy sites, this limitation would likely be caused by competitive interactions with overstory pine trees.

Summary and Conclusions

The results of this study demonstrated contagion among plots based on understory species abundance. Whether measured by understory plant cover or density, plots with high species diversity and an abundance of perennial bunchgrasses, predominantly *F. idahoensis*, existed in stands of relatively low *P. ponderosa* occupancy and high light availability. On the opposing end of the pine occupancy gradient were plots exhibiting low species diversity, low light intensity and devoid of the perennial bunchgrasses common in more open canopies. A group of plots were also observed that possessed high understory forb diversity and abundance, however these unique associations were un-related to the variability in ponderosa pine occupancy.

Elevated ponderosa pine abundance appeared to influence the under-canopy environment primarily through alterations in available light. Although mineral nitrogen availability was higher in plots associated with lower pine abundance, no clear evidence of a nitrogen limitation in understory species emerged. Higher pine abundances also related to lower soil temperatures, however the range of temperatures observed even in the coolest plots appears within the range of tolerance of Idaho fescue. No pattern in soil moisture was evident that corresponded to the gradient in pine occupancy or the abundance of perennial bunchgrasses. However, given the similarity in soil moisture along the pine gradient, it is likely that competition for moisture among overstory and understory vegetation could influence understory species distribution in spite of the apparent lack of ponderosa pine modified soil moisture status.

Increased pine abundance associated with many contemporary ponderosa pine forests can result in a significant loss of dominant understory species. Fortunately, alterations to ecosystem processes, including hydrology and nutrient cycling, appear

minimal and restoration practices that reduce pine occupancy should promote understory growth through increased light and moisture availability. However, if pine abundance has proceeded to the point of perennial bunchgrass loss, recovery of the dominant understory physiognomy is unlikely without the re-introduction of desired species either through manual seeding or immigration from off-site sources.

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CHAPTER 4: IDAHO FESCUE (*Festuca idahoensis* Elmer) RESPONSE TO VARIABLE LIGHT AND NITROGEN AVAILABILITY

Abstract

Elevated ponderosa pine (*Pinus ponderosa* Dougl.) abundance associated with lengthened fire return intervals can alter the under-canopy environment and may influence understory species composition and distribution. Experimental evidence linking under-canopy resource alteration to changes in understory vegetation is scarce yet an understanding of the mechanisms associated with understory vegetation dynamics corresponding to increased ponderosa pine occupancy would be beneficial in developing appropriate restoration and management strategies. We initiated a greenhouse experiment designed to investigate the effect of various levels of nitrogen and light availability on the growth and vigor of *Festuca idahoensis* Elmer, a dominant perennial bunchgrass found in eastern Oregon ponderosa pine forests. Two levels of nitrogen (50kg N/ha and no N addition) and shade (80% shade and no shade) were applied in a split plot design to *F. idahoensis* plants growing individually in 3.98 L pots. Shoot length was measured weekly and foliar cover bi-weekly throughout the course of the experiment while shoot biomass, root biomass, final shoot length, and final foliar cover were recorded at the end of the experiment. The data were analyzed using ANOVA for split plot designs and included a covariance structure appropriate for repeated measures where required. Plants grown in unshaded conditions produced greater root and shoot biomass and higher cover values compared to those in the shaded treatments. The addition of nitrogen, however, had little effect on plant growth, suggesting that soils from dense ponderosa pine stands depauperate in understory were not nitrogen deficient and *F. idahoensis* plants grown in these soils not nitrogen limited. Ponderosa pine ecosystem restoration initiatives should incorporate understory species. Restoration activities that promote increased under-canopy light availability will similarly promote understory recovery, however

this is constrained by the potential loss of understory species associated with excessive ponderosa pine in growth.

Introduction

Contemporary ponderosa pine forests are generally thought to exist outside their historic range of variability (Covington and Moore 1994, Tiedemann et al. 2000 and Allen et al. 2002). Activities associated with European settlement in the late 1800s including road and trail development, intensive livestock grazing, and active fire suppression triggered a substantial increase in the fire return interval, and combined with favorable conditions for ponderosa pine seed germination and seedling establishment, effected unprecedented changes in the fire regime and vegetation structure in ponderosa pine forests (Covington and Moore 1994, Johnson 1994).

In established ponderosa pine forests, overstory pine trees are favored in competitive interactions with the understory herbaceous and shrubby components. By eliminating the majority of pine regeneration, fire, in a low-intensity high frequency regime, confers a competitive advantage to understory herbs and shrubs. Over time and in the absence of fire, increased pine stem density, canopy cover, and/or root density effects an increasing level of stress on understory species by reducing available light, water and nutrient resources (Krueger 1981, Riegel et al. 1991, 1992, and 1995) and may eventually lead to localized extirpation of understory species (Moore et al. 1999 and Stephenson 1999). Relative to open pre-settlement forest stands, dense stands of ponderosa pine show significant limitations in many understory attributes including diversity, density, and vigor (Clary et al. 1975, Uresk and Severson 1998, Naumberg and DeWald 1999, and Naumberg et al. 2001). In some of the densest stands, the understory component is replaced by a thick mat of pine needle litter (Wienk et al. 2004).

The increased density, canopy cover and basal area of pine trees common in contemporary ponderosa pine forests has impacted the growing conditions of

understory species through alteration in above ground (light) and below ground (moisture and nutrient availability) resources.

Variability in evapotranspiration dominates the water budget in arid and semi-arid environments (Brandes and Wilcox 2000). In ponderosa pine forests of the Pacific Northwest, increased tree densities are generally associated with increased transpirational demands which can result in higher growing season water use. In Oregon, plots with lower ponderosa pine density tended to exhibit lower moisture use (Barrett and Youngberg 1965, Barrett 1970 and Helvey 1975). Differences in evapotranspiration associated with varying pine density may be muted over time, however, as a vigorous understory can also provide adequate leaf area to rival the evapotranspirational demands observed in more dense stand types (Barrett and Youngberg 1965, Helvey 1975 and Baker 1986). Increasing pine densities may also influence patterns of snow accumulation, the primary source of soil moisture, groundwater recharge, and stream flow in Pacific Northwest ponderosa pine watersheds. It has been widely reported for a variety of forest types, that dense stand conditions promote snow interception and subsequent ablation and reduce the quantity of snow accumulation (e.g. Gary and Troendle 1982, Toews and Gluns 1986 and Moore and McCaughey 1997). Haupt (1951) observed lower levels of snow accumulation in dense pole sized ponderosa pine stands relative to more open or sapling structures.

Nutrient cycling processes may also be disrupted under contemporary ponderosa pine forest structures. The steady increase of recalcitrant pine needle litter and reduction in soil temperature and moisture may stagnate nutrient cycling under dense ponderosa pine canopies (Covington and Sackett 1984, Covington and Sackett 1990, Kaye and Hart 1998 and Selmanns et al. 2003). Kaye and Hart (1998) found approximately double the rate of net N mineralization in pre-settlement openings when compared to post-settlement pole-sized ponderosa pine patches. An additional threat to ecosystem nutrient status in contemporary ponderosa pine forests is the increasing abundance of nutrients stored in standing live and dead trees, down trees and litter. These nutrient reserves are unavailable for plant growth and are extremely

vulnerable to loss through fire, particularly within the context of modern fire regimes (Klemmedson 1975, Covington and Sackett 1984, Covington and Sackett 1990 and Tiedemann et al. 2000).

Changes in understory light conditions associated with increasing ponderosa pine canopy closure have been identified as contributing to observed alterations in understory species diversity, vigor and composition. Naumberg et al. (2001) and Naumberg and DeWald (1999) found light availability to be the strongest predictor of understory graminoid species cover and density and implied that high light availability was an important habitat feature of graminoid species in Arizona ponderosa pine forests. Riegel et al. (1995) also identified light, along with nitrogen and water availability, as influential in determining understory species composition.

In a companion study, Carr (2007b) found ponderosa pine stands with higher pine occupancy had substantially diminished understories and obvious lack of perennial bunchgrasses (i.e. *Festuca idahoensis*, *Koeleria macrantha* (Ledeb.) J.A. Schultes, and *Poa scabrella* (Thurb.) Benth.) that were dominant in more open canopy environments. Associated measurements of understory environmental attributes along the gradient of ponderosa pine site occupancy identified a strong relationship between the presence of perennial bunchgrasses and understory light availability and a weaker association with nitrogen availability. No association between soil moisture and perennial bunchgrass presence was observed.

Experimental evidence linking understory resource limitation to changes in understory vegetation is scarce. Although Riegel et al. (1991, 1992, and 1995), Naumberg and DeWald (1999) and Naumberg et al. (2001) provide some insight into the mechanisms associated with understory response to increasing pine occupancy, the results are variable and neither consider pure ponderosa pine forests of the Pacific Northwest. Thus, experimental research corroborating ecological relationships ascertained through field observations is needed for Pacific Northwest ponderosa pine forests. An understanding of the mechanisms associated with understory vegetation dynamics corresponding to increased ponderosa pine site occupancy will be beneficial in developing appropriate restoration and management strategies.

Study Objectives

This study was designed to corroborate field-based observational relationships among understory species, resource availability and ponderosa pine site occupancy. Specifically, we investigated the effect of various levels of nitrogen and light availability on the growth, vigor, and biomass of the dominant understory species (*F. idahoensis*) found in intact understories of Ponderosa Pine / Idaho Fescue plant associations (Johnson and Clausnitzer 1992) of eastern Oregon. Our objectives were to 1) evaluate if understory resource limitations apparent under dense ponderosa pine stands influence the growth and vigor of *F. idahoensis*, and 2) assess and discuss the implications for restoration of altered understory environments associated with increased ponderosa pine abundance.

Methods

A green house study with two levels of shade and nitrogen was conducted to test for differences in *F. idahoensis* growth rate, biomass and vigor. *Festuca idahoensis* was selected because it is the dominant understory species in Ponderosa Pine / Idaho Fescue plant associations in eastern Oregon (Johnson and Clausnitzer 1992). *Festuca idahoensis* is a native, C3, perennial bunchgrass that initiates growth in early spring. It occurs across much of western North America from 300 m to 4000 m in elevation and often in open woodlands and foothill rangelands (Stubbendieck et al. 2003).

Field Protocol

Festuca idahoensis plants were collected in early April from a ponderosa pine stand in northeast Oregon (44°12'52" N latitude, 118°59'16" W longitude). The site was located at 1500m elevation and situated in an area of gently sloping (~8% slope gradient) north-facing hillsides. The average daily high and low summer and winter temperatures, recorded between 1971 and 2000 at Seneca (~ 8 km south of the study

area) were 24°C and 1.5°C and 4°C and -9°C respectively (Oregon Climate Service 2007). Approximately 35 cm of precipitation is received annually, most occurring in the winter months and primarily in the form of snow (Oregon Climate Service 2007). Seneca is approximately 100m lower in elevation than the sites used in this research project and exists in a relatively broad non-forested valley. Thus, it is expected that the study area receives slightly more precipitation than that recorded at Seneca and that the temperature regimes differ slightly between the two areas.

Soils of the study area are composed of an ash mantle overlaying serpentinite gravel and cobble. Soils were classified as a fine-loamy, mixed, superactive, frigid Vitrandic Haploxerolls and in a xeric soil moisture regime and frigid soil temperature regime (Carr 2007a).

The site has an open canopy structure relatively free of trees. The adjacent forest was composed primarily of small-diameter ponderosa pine trees (15 - 20 cm diameter) growing at a density of approximately 260 trees / ha.

Festuca idahoensis plants (2 – 3 cm basal diameter) were removed to a depth of 10 cm using a 5.08 cm diameter soil core centered on the plant. Fescue plugs were placed in a container of native soil for transportation to the greenhouse where they were replanted into 3.79 L pots. Prior to replanting each fescue plug was clipped at a height of 5 cm and the soil below 5 cm depth was removed. Soil from a dense ponderosa pine stand (2800 trees / ha) adjacent to the location of fescue harvest was used for potting media. This soil was selected because it represented the soil conditions of ponderosa pine forests encumbered by increased pine occupancy and significantly lacking the characteristic perennial bunchgrass dominated understory. It was expected that this soil would provide the baseline soil conditions from which increasing resource availability would provide insight into soil components that are lacking in depauperate understory environments. The soil was harvested to a depth of 10 cm (mineral soil) and prior to potting was passed through a 7 mm screen to remove rocks, litter, and root fragments.

Greenhouse Protocol

Potted fescue plants were grown in a greenhouse located on the Oregon State University campus at Corvallis, Oregon (44°34'12" N latitude, 123°16'48" W longitude). The average daytime (06:00 – 20:00) temperature of the greenhouse throughout the study was 23.7°C (standard deviation = 2.19) (Appendix C). Shade treatments were applied using tents made of 80% shade cloth draped over a PVC pipe frame. Each shade tent measured approximately 76 x 76 x 76 cm and the entire area was covered by shade cloth. Eighty percent shade represented the average canopy closure observed (average canopy closure = 79.14%) in the dense ponderosa pine stands used in the field based companion study (Carr 2007b). Urea (46-0-0) was applied at 50 kg N / ha to each pot selected for nitrogen treatment. Urea pellets were covered with soil and watered-in to prevent nitrogen loss through ammonia (NH₃) volatilization. 50 kg N / ha was deemed adequate to meet the needs of eastern Oregon Idaho fescue growth. A plant tissue nitrogen content of 2-5% (dry weight) is required for optimal plant growth (Marschner 1995) and the average dry weight biomass of *F. idahoensis* in ponderosa pine / Idaho fescue plant associations is 365 kg/ha (Johnson and Clasunitzer 1992), thus, approximately 7.3 – 18.25 kg N/ha was needed to support typical growth of Idaho fescue in the region of our field sites. We used 50 kg N / ha to ensure that nitrogen supply was not limiting and to allow for some N loss through leaching. As a significant relationship between water availability and the presence of perennial bunchgrasses in the understory did not emerge in our field studies, it was not included as a treatment in this experiment. However, all pots were kept moist throughout the experiment with regular watering.

Experimental Design

Two levels of shade and nitrogen were applied in a split plot design. Whole plots (80% shade or no shade) were randomly assigned to greenhouse bench location (replications) and subplots (50 kg N / ha or 0 kg N / ha) were randomly assigned to 2 pots randomly allocated within each whole plot. Five replications of each treatment

combination were performed ($N = 5 \times 2 \times 2 = 20$). The experiment was run for 83 days from April 11 through to July 3.

Data Collection

To evaluate differences in mineral nitrogen associated with treatment effects, soil samples were taken from each pot prior to and at the conclusion of the experiment. Samples were tested for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ at the Oregon State University Central Analytical Lab using an Astoria Pacific auto analyzer at the Central Analytical Lab at Oregon State University. To evaluate the shading efficiency of the shade tents, photosynthetically active radiation (PAR) was measured in each whole plot using a LI-190S-1 quantum sensor (LI-COR, Inc. Lincoln, Nebraska). Pre-treatment fescue size, indexed by the product of the length of the longest axis through the base of the plant and the axis perpendicular to the longest axis, was measured for use as a co-variate in the analyses. Measurements of plant height and foliar cover were performed weekly. Plant height values used in the analyses are averages of the shortest, tallest and two intermediate length leaves. Foliar cover was evaluated using downward looking digital photographs of each plant. A digital grid of 3400 uniformly spaced dots was overlaid on each digital photo in ArcMap version 9.1 (ESRI 2005). The number of points touching leaf material was tallied for each plant and used as an index of foliar cover. Images were acquired using a Nikon Coolpix 950 digital camera mounted 1 m above the ground on a PVC frame modified from Louhaichi et al. (2003). This set up along with uniform focal length (7.2 mm) and resolution (1200 x 1600 pixels) for each photo provided standard image dimensions of 89 x 67cm with a pixel size of 0.56mm. At the end of the experiment shoot and root biomass were measured. Plants were clipped at ground level and all leaf material weighed after drying for 48 hours at 60°C. Root material was collected by passing the potting media through a 7 mm screen and then washing the remaining material through a 0.59 mm (#30) sieve. The residual root material was dried for 48 hours at 60°C and then weighed. Three shoot

biomass samples measured below the resolution of the scale used to weigh the samples (0.1g). To provide a value for trace biomass, 0.09g was used in the analyses.

Data Analysis

PAR values were log transformed for analyses to meet the assumptions of equal variance (Appendix B). These data were analyzed as a two sample t-test using PROC TTEST in SAS version 9.1 (SAS Institute 2003).

Analyses of shoot biomass, root biomass, final shoot length, final cover, and mineral nitrogen concentration were performed using PROC MIXED in SAS version 9.1 (SAS Institute 2003). Random effects for replication and whole plot were included in the model along with the fixed effects of shade, nitrogen and their interaction.

Values for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ were evaluated separately and in combination representing total mineral nitrogen. Pre-treatment N quantities were subtracted from corresponding post-treatment values to provide a measure of the net change in NH_4 , NO_3 , and total mineral N over the course of the experiment.

Root and shoot biomass along with all mineral nitrogen values expressed substantial heterogeneity in the variability among treatment groups, a violation of the assumptions associated with ANOVA based analyses. Thus, these data were log transformed prior to analysis. See Appendix B for exploratory plots of these data sets. To account for negative data values a constant was added to each change in total mineral N value prior to log transforming (Johnson and Wichern 2002 and Sheskin 2004). The log transformation of this variable took the form of: $y = [\log(x + 0.7)]$, where y = the transformed value of x .

Foliar cover and leaf length over time were evaluated using proc MIXED in SAS version 9.1 (SAS Inc. 2003). The models included fixed effects for shade, nitrogen, date, and their interactions and random effects for replication, whole plot and subplot. To account for the repeated measures nature of the experiment a covariance structure appropriate for modeling the within plant variability was included in each model. Several covariance structures were evaluated prior to

selecting one for incorporation into a model. The successful covariance structure generally exhibited low fit statistic values (-2 Residual Log Likelihood, AIC, AICC, and BIC) and relatively few covariance parameters. Compound symmetry and first-order autoregressive were the covariance structures used to model the within plant variability in analyses of leaf length and plant cover data sets respectively. Because of a consistent lack of significance of the 3-way and shade X nitrogen interactions, models for both responses were reduced to the main effects of shade, nitrogen and time and the interactions of shade X time and nitrogen X time. To meet the assumptions of equal variance both the cover and leaf length data were log transformed prior to analyses (see Appendix B for exploratory plots and covariance structure evaluation).

The initial size of each fescue plant was recorded prior to the start of the experiment for use as a covariate in future analyses. As no relationship between pre-treatment plant initial size and shoot biomass, root biomass, leaf length, or cover was evident (Appendix B), the variable was not included in any subsequent analyses.

Results

Light Intensity and Mineral Nitrogen Pool Sizes

The use of shade tents to apply the shade treatments significantly reduced the PAR intensity ($p < 0.0001$). The average intensity of PAR in the unshaded treatments was $409.96 \mu\text{molm}^{-2}\text{s}^{-1}$ while shaded treatments averaged $88.99 \mu\text{molm}^{-2}\text{s}^{-1}$.

All pre-treatment mineral nitrogen concentrations ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and total mineral N) were similar across pots assigned to the two shade treatments while $\text{NH}_4\text{-N}$ and total mineral N differed between pots assigned to the nitrogen treatments (Table 17). Pots assigned to the nitrogen addition treatment had higher background $\text{NH}_4\text{-N}$ levels which translated into higher pre-treatment total mineral nitrogen (Figure 24).

Table 17. P values associated with tests for differences in pre-treatment mineral nitrogen concentration between pots assigned to nitrogen and shade treatments.

	Treatment Group P-values	
	Shade	Nitrogen
NO ₃	1.0000	0.3434
NH ₄	0.3164	0.0268
Total mineral N	0.3608	0.0145

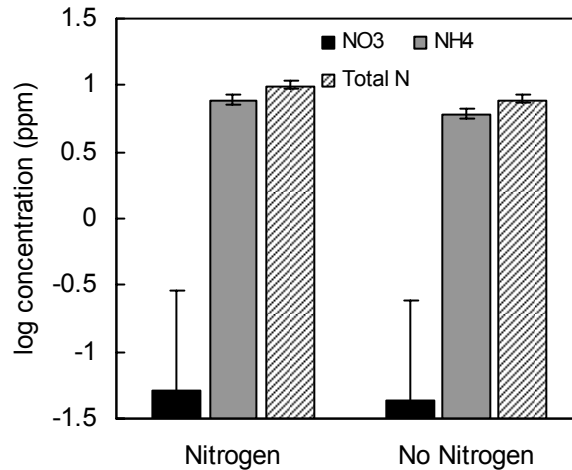


Figure 24. Mean pre-treatment log soil mineral nitrogen concentration from pots assigned to either the Nitrogen or No Nitrogen treatments. Error bars represent standard error.

The net change in total mineral N concentration, indicated by the difference between the post-and pre-treatment total mineral nitrogen concentrations, varied by both shade and nitrogen treatments although the response to one treatment appeared to depend on the level of the other as the interaction term was also significant (Table 18). Soil in pots assigned to the shade treatment and pots assigned to the nitrogen addition treatment both exhibited higher net accumulation of total mineral N at the end of the experiment compared to the alternative treatment in each treatment group

(Figure 25). These effects appear driven primarily by the large post-treatment increase in the $\text{NO}_3\text{-N}$ pool observed in both shade and nitrogen addition treatments (Figure 26).

Differences in the net change in NO_3 concentration were evident among the shade treatments and among the nitrogen treatments (Table 18). An interaction term was significant in the NO_3 analyses indicating that the difference in NO_3 accumulation between shade treatments varied by nitrogen treatment. (Figure 25)

Table 18. P values from type III tests of fixed effects from analyses evaluating differences in the net change of soil mineral nitrogen pools ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and total mineral N) between pots assigned to Nitrogen and Shade treatments.

	Treatment Group P-values		
	Shade	Nitrogen	Shade X Nitrogen
$\text{NH}_4\text{-N}$	0.2510	0.0973	0.9509
$\text{NO}_3\text{-N}$	0.0025	<0.0001	0.0067
Total mineral N	0.0058	<0.0001	0.0357

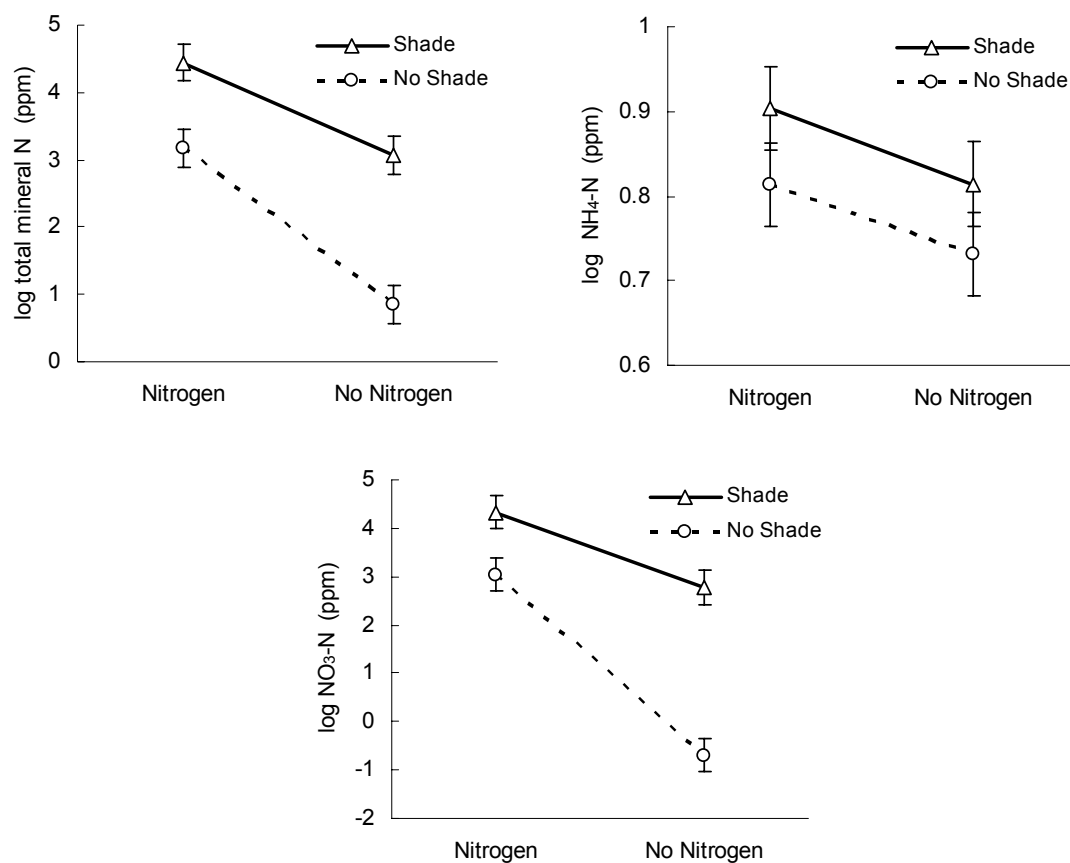


Figure 25. Main effects and interactions of nitrogen and shade treatments on the average log net change in soil nitrogen pool size (total mineral N, NO₃-N and NH₄-N). Note the different scale associated with NH₄-N. Error bars represent standard error.

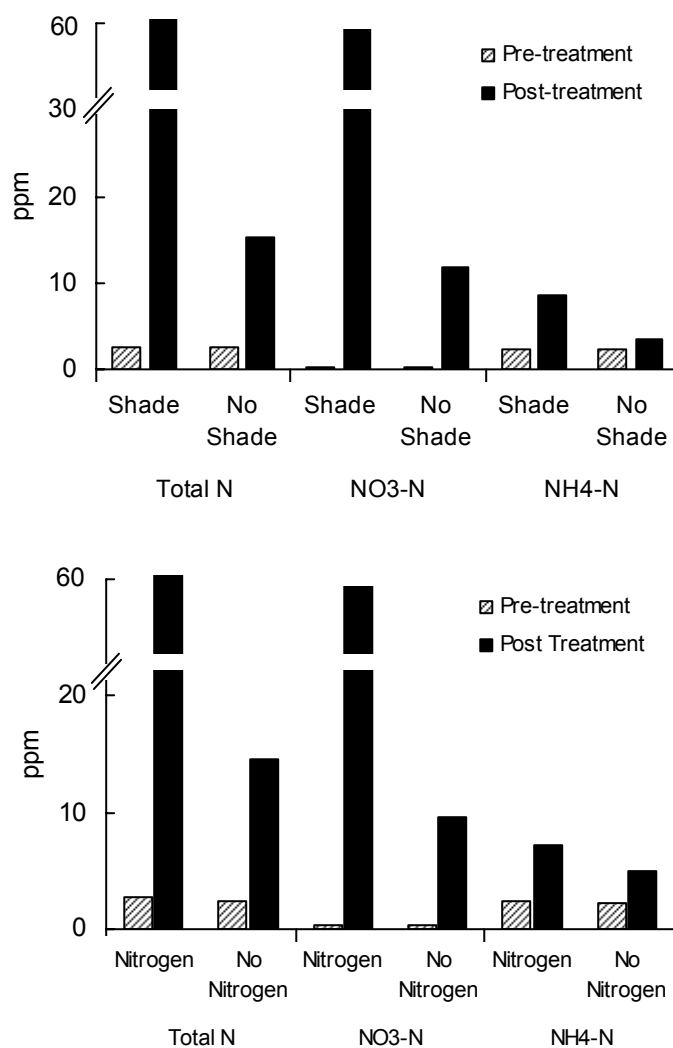


Figure 26. Mean pre- and post-treatment mineral nitrogen pools referenced by shade (top panel) and nitrogen (lower panel) treatment levels.

No differences in the net change in the NH₄-N pool were apparent among treatment groups (Table 18). Although a similar pattern to that observed in total mineral N and NO₃-N pools was present, higher net accumulation under shade and under fertilized treatments, the differences were very small and non-significant (Figure 25).

The results obtained from the analyses of the net change in $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$ and total mineral N data were generated from a data set with one fescue plant removed because of its significant influence on the results. The inclusion of this plant masked the relationships observed among treatment groups and net mineral N pool accumulation. This plant was fertilized and un-shaded, had the lowest recorded post-treatment pool sizes for $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and total mineral N and expressed a net decrease in total mineral N. Removal of this individual from these analyses was justified based on its obfuscation of otherwise apparent patterns, particularly with respect to nitrogen treatment groups, and its substantial difference in plant size compared to other individuals. This was a large plant that produced substantially more biomass than any other plant and the lack of mineral N pool typically observed for plants in the un-fertilized treatment group may have been related to this accumulation of plant biomass.

Shoot and Root Biomass

The only statistically significant effect in the analysis of shoot biomass was associated with the shade treatment (Table 19). Plants growing under shade had lower shoot biomass compared to those growing in the un-shaded conditions (Figure 27). Although nitrogen addition appeared to show a positive trend in shoot weight (Figure 27), this was not statistically significant. The lack of a significant interaction term is illustrated in Figure 27.

The shade treatment produced the only significant effect on Idaho fescue root biomass (Table 20). Implementing the 80% shade treatment caused a significant reduction in the total root biomass (Figure 28). A positive trend in the effect of nitrogen addition was also evident (Figure 28), but non-significant. Lack of interaction between nitrogen and shade can be observed in Figure 28.

Mean root and shoot biomass values for the main effects of the shade and nitrogen treatments are presented in Table 21.

Table 19. Significance values from Type III test of the fixed effects of shade, nitrogen and shade X nitrogen interaction from the analyses of Idaho fescue shoot weight.

	F statistic	P value
Shade	56.61	0.0017
Nitrogen	2.40	0.1602
Shade x Nitrogen	1.10	0.3244

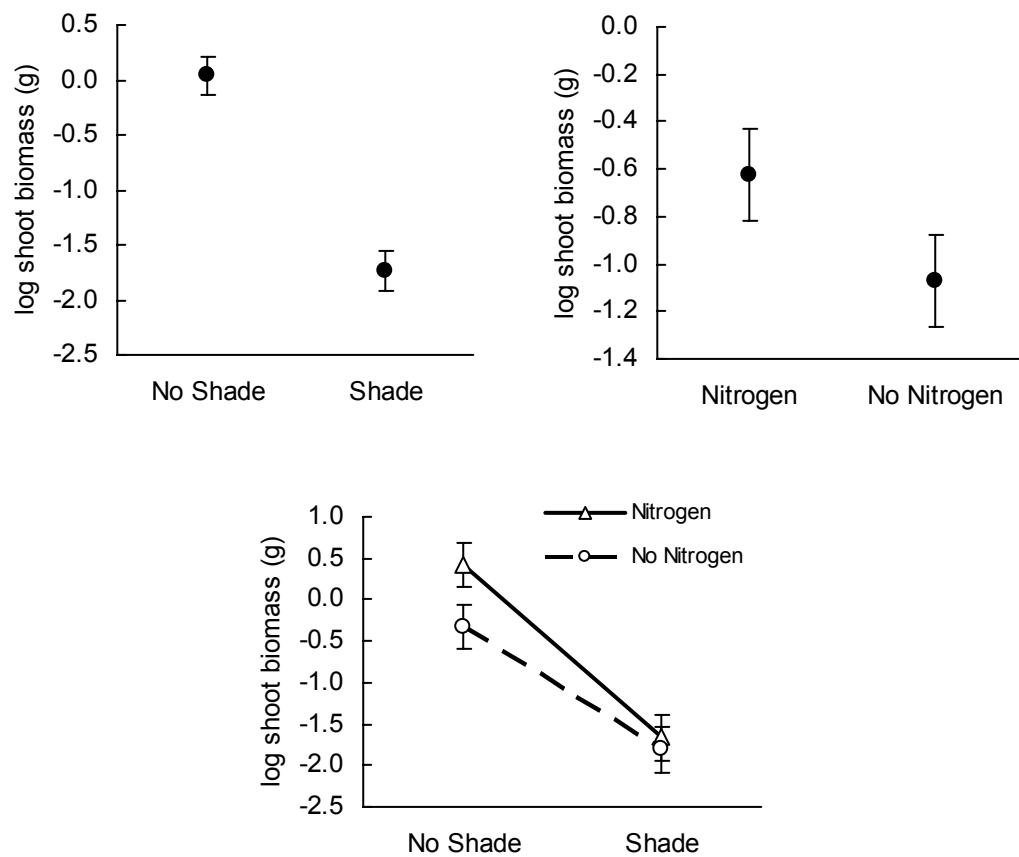


Figure 27. Main effects and interaction of shade and nitrogen treatments on Idaho fescue shoot biomass. Dots represent the associated group mean while error bars are ± 1 standard error.

Table 20. Significance values from Type III test of the fixed effects of shade, nitrogen and shade x nitrogen interaction from the analyses of Idaho fescue root weight.

	F statistic	P value
Shade	433.46	0.0027
Nitrogen	0.47	0.5129
Shade x Nitrogen	0.10	0.7567

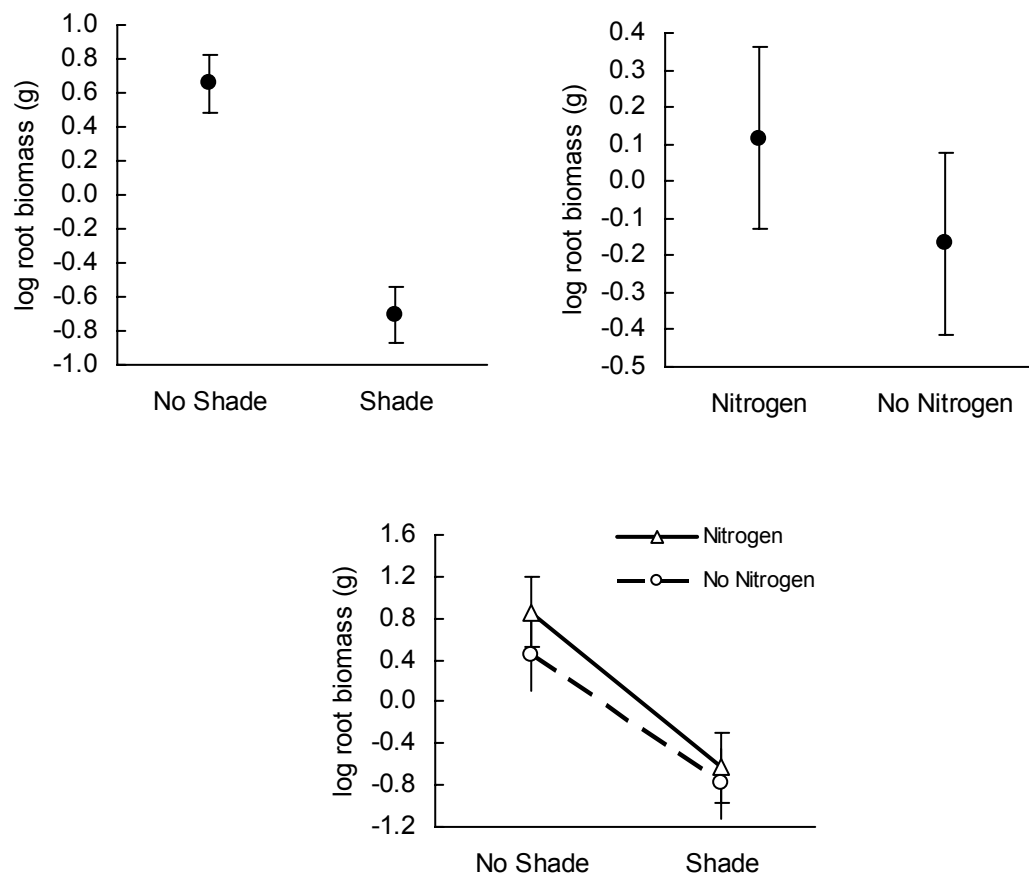


Figure 28. Main effects and interaction of shade and nitrogen treatments on Idaho fescue root biomass. Dots represent the associated group mean while error bars are ± 1 standard error.

Table 21. Table of means associated with the main effects of the shade and nitrogen treatments on the responses of shoot biomass, root biomass, final cover, and final length. Standard deviations are in parentheses.

	Treatment			
	Shade	No Shade	Nitrogen	No Nitrogen
Shoot Biomass	0.19 (0.17)	1.21 (0.74)	0.93 (0.92)	0.47 (0.43)
Root Biomass	0.68 (0.59)	2.20 (1.30)	1.75 (1.55)	1.13 (0.82)
Final Cover	29.70 (12.80)	55.80 (27.40)	49.40 (29.76)	36.10 (17.56)
Final Length	14.62 (0.79)	11.57 (1.14)	13.38 (1.86)	12.81 (1.86)

Shoot Length

The only statistically significant effect on the final shoot length of Idaho fescue plants was the shade treatment (Table 22). Plants subjected to the 80% shade treatment were longer than plants grown in maximal light conditions (Figure 29). A trend towards longer shoots on plants with the addition of nitrogen was apparent in Figure 29, however this effect was not significant. The lack of an interaction can also be observed in Figure 29.

When including time as a factor in the analyses of shoot length, the main effect of shade remained significant while differences in shoot length over time in response to nitrogen addition were also apparent (Table 23). No shade X nitrogen interaction was evident however significant interactions between shade and time and nitrogen and time were also apparent (Table 23).

Table 22. Significance values from Type III test of the fixed effects of shade, nitrogen and shade X nitrogen interaction from the analyses of Idaho fescue final shoot length.

	F statistic	P value
Shade	50.19	0.0021
Nitrogen	2.57	0.1478
Shade x Nitrogen	0.03	0.8596

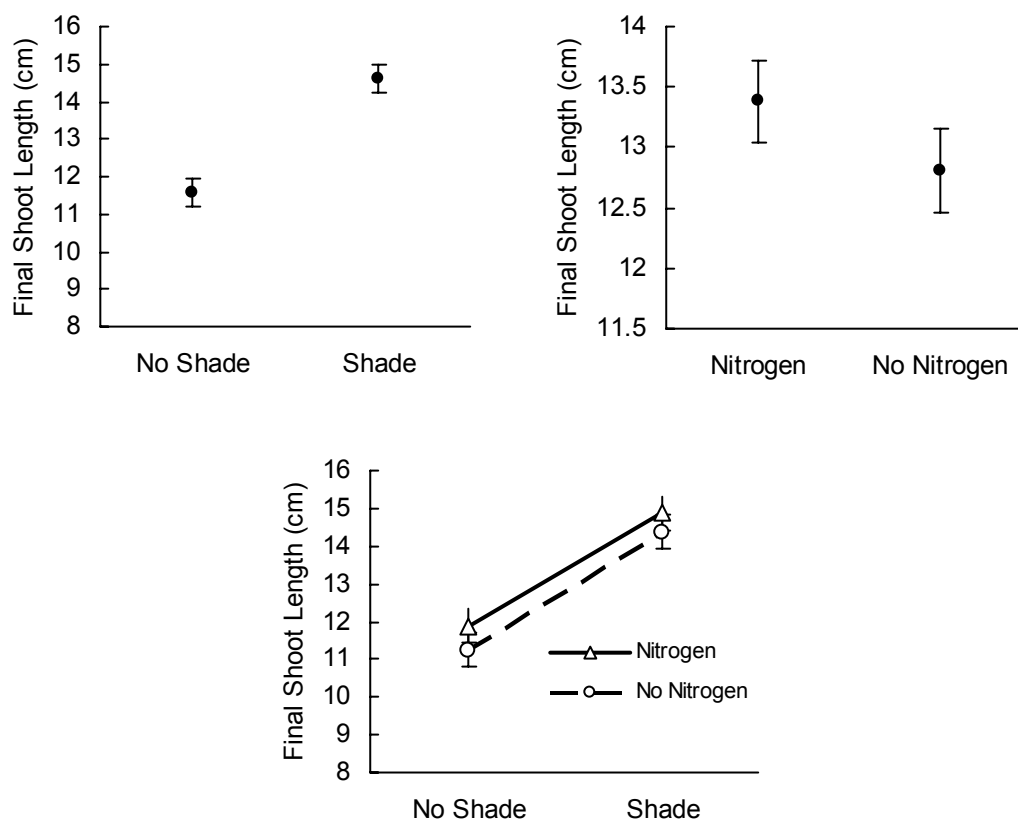


Figure 29. Main effects and interaction of the shade and nitrogen treatments on the final shoot length of Idaho fescue. Dots represent the associated group mean while error bars are ± 1 standard error.

Table 23. Significance values from Type III test of the fixed effects of shade, nitrogen, time, shade X time and nitrogen X time from the analyses of Idaho fescue shoot length over time.

	F statistic	P value
Shade	29.19	0.0001
Nitrogen	7.50	0.0169
Time	295.16	<0.0001
Shade X Time	10.36	<0.0001
Nitrogen X Time	3.50	0.0006

The change in shoot length over time tended to follow a curvilinear pattern showing rapid elongation in early growth and stabilizing as maximum shoot length was approached in the later weeks of the experiment (Figure 30). Differences in shoot length among shade treatment groups were not evident in the first 2 weeks of growth, however the subsequent time periods showed successive increases in shoot length in the shaded treatment (Figure 30). The addition of nitrogen stimulated an increase in the early rate of leaf elongation as significant differences among nitrogen treatment groups occurred in weeks 2 through 5, however, by the end of the study plants in the un-fertilized treatment had shoot lengths that equaled that of the fertilized plants (Figure 30 and Table 23). Significance tests of the shade and nitrogen effects at each time period are presented in Table 24.

Mean final shoot length values for the main effects of the shade and nitrogen treatments are presented in Table 21 while mean length values for the shade and nitrogen effects at each time interval are presented in Table 25.

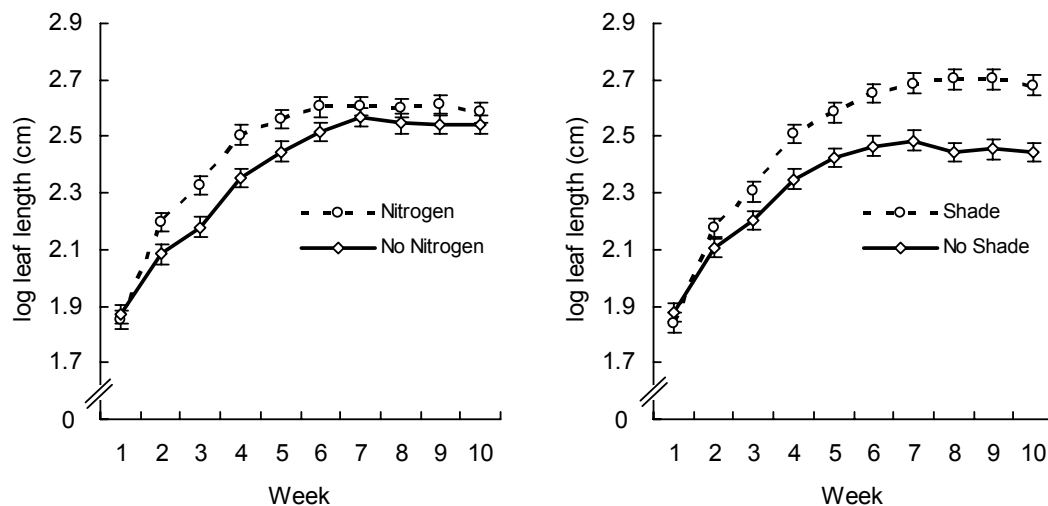


Figure 30. Nitrogen and shade treatment effects on Idaho fescue leaf length measured weekly throughout the experiment. Dots represent group means while error bars are ± 1 standard error.

Table 24. P-values from F tests of the fixed effects of shade and nitrogen on leaf length within each time step performed using the slice option of proc MIXED in SAS version 9.1 (SAS Inc 2003).

Week	Shade Effect P-value	Nitrogen Effect P-value
1	0.3559	0.6274
2	0.0870	0.0068
3	0.0138	0.0007
4	0.0003	0.0004
5	0.0002	0.0068
6	<0.0001	0.0321
7	<0.0001	0.3071
8	<0.0001	0.1907
9	<0.0001	0.0846
10	<0.0001	0.2782

Table 25 Table of shoot length and foliar cover means associated with the main effects of the shade and nitrogen treatments at each time interval measured. Standard deviations are below and in parentheses. Dashes represent weeks when foliar cover was not measured.

	Week									
	1	2	3	4	5	6	7	8	9	10
Mean Shoot Length										
No Shade	6.56 (0.38)	8.26 (0.86)	9.12 (1.25)	10.59 (1.67)	11.34 (1.13)	11.84 (1.28)	12.08 (1.33)	11.58 (1.22)	11.72 (1.33)	11.57 (1.14)
Shade	6.33 (0.57)	8.86 (0.92)	10.07 (1.06)	12.41 (1.83)	13.36 (1.69)	14.29 (1.65)	14.76 (1.33)	14.96 (1.31)	14.95 (1.20)	14.62 (0.79)
Nitrogen	6.39 (0.59)	9.03 (0.72)	10.29 (0.97)	12.35 (1.64)	13.04 (1.59)	13.64 (1.93)	13.69 (1.95)	13.62 (2.19)	13.79 (2.06)	13.38 (1.86)
No Nitrogen	6.50 (0.38)	8.08 (0.87)	8.91 (1.10)	10.65 (1.92)	11.66 (1.68)	12.49 (1.80)	13.15 (1.88)	12.92 (2.12)	12.87 (2.07)	12.81 (1.86)
Mean Foliar Cover										
No Shade	6.50 (2.46)	-	13.1 (7.23)	-	33.70 (20.01)	-	48.50 (25.22)	-	55.80 (27.39)	-
Shade	5.80 (1.68)	-	13.40 (5.72)	-	23.40 (8.10)	-	29.80 (13.85)	-	29.70 (12.79)	-
Nitrogen	6.40 (2.55)	-	16.50 (6.77)	-	34.80 (18.03)	-	44.80 (27.21)	-	49.40 (29.76)	-
No Nitrogen	5.90 (1.60)	-	10.00 (3.97)	-	22.30 (10.64)	-	33.50 (14.52)	-	36.10 (17.56)	-

Cover

As reported for shoot and root biomass and final shoot length, shade provided the only significant effect on final cover of the Idaho fescue plants (Table 26). Plants grown under the 80% shade treatment produced less overall foliar cover compared to those grown in maximal light conditions (Figure 31). Although not statistically significant, the addition of nitrogen showed an increasing trend in foliar cover (Figure 31). The lack of a significant interaction term can also be observed in Figure 31.

Including time in the analysis of the cover index data set produced significant effects of the nitrogen X time and shade X time interaction terms. The main effect of nitrogen was weak while the main effect of shade was non-significant (Table 27).

Plant cover change over time generally followed a curvilinear pattern with rapid increase in foliar cover through the early portion of the experiment followed by a much reduced rate of increase toward the end of the trial (Figure 32). Differences in fescue cover among shade treatment groups were not evident in the first 6 weeks of the experiment, however the subsequent 2 measurements, in week 8 and week 10, indicated successive increases in plant cover and identified un-shaded plants as eventually accumulating greater plant cover compared to shaded individuals (Figure 32). The addition of nitrogen stimulated an increase in foliar cover earlier in the experiment as significant differences among nitrogen treatment groups occurred in weeks 4 and 6. However, by the end of the experiment, plants in the un-fertilized treatment had foliar cover values that rivaled that of the fertilized plants (figure 32).

Significant tests of the shade and nitrogen effects on foliar cover at each time period are presented in Table 28. Mean final foliar cover values for the main effects of the shade and nitrogen treatments are presented in Table 21 while mean foliar cover values for the shade and nitrogen effects at each time interval are presented in Table 25.

Table 26. Significance values from Type III tests of the fixed effects of shade, nitrogen and shade \times nitrogen interaction from the analyses of Idaho fescue final cover.

	F statistic	P value
Shade	9.35	0.0378
Nitrogen	3.85	0.0853
Shade x Nitrogen	0.02	0.8932

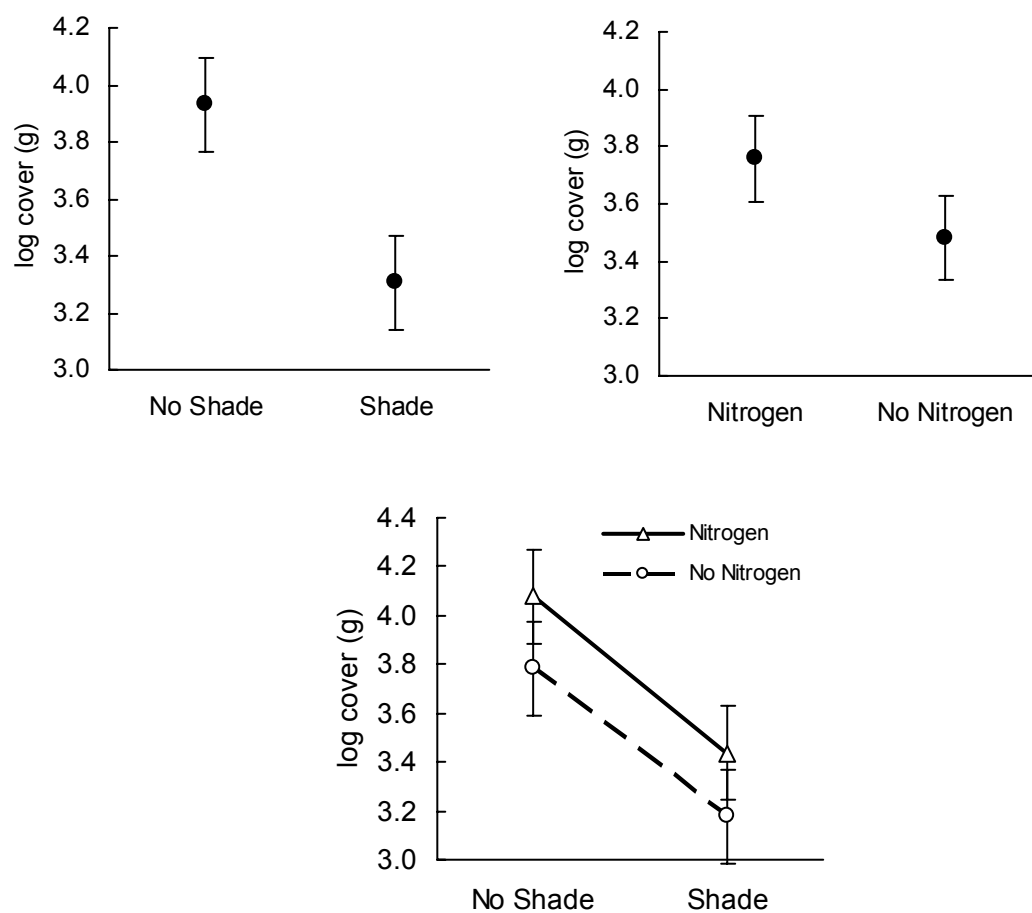


Figure 31. Main effects and interaction of the shade and nitrogen treatments on the foliar cover of Idaho fescue. Dots represent the associated group mean while error bars are ± 1 standard error.

Table 27. Significance values from Type III test of the fixed effects of shade, nitrogen, time, shade x time and nitrogen x time from the analyses of Idaho fescue cover over time.

	F statistic	P value
Shade	3.57	0.1309
Nitrogen	5.61	0.0422
Time	183.57	<0.0001
Shade X Time	5.63	0.0009
Nitrogen X Time	4.13	0.0059

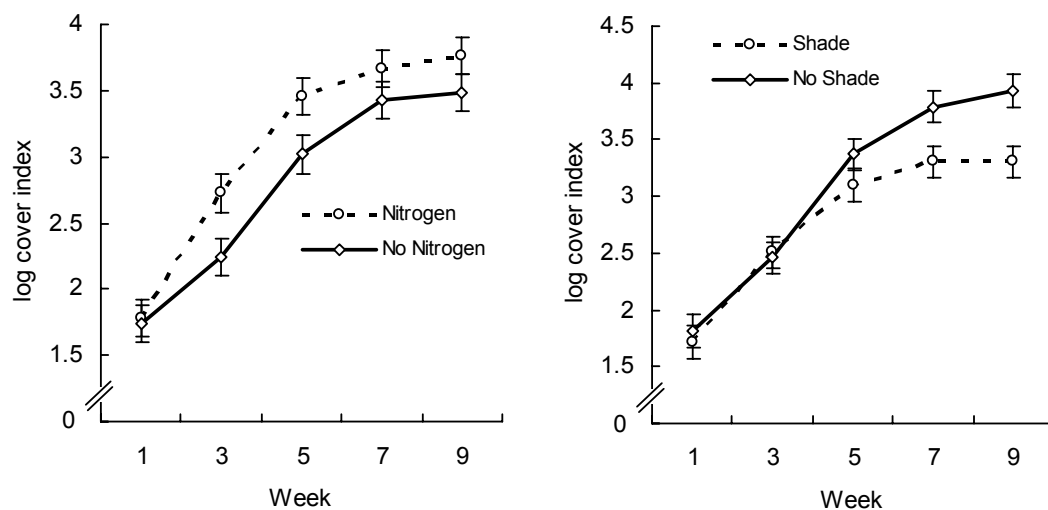


Figure 32. Nitrogen and shade treatment effects on Idaho fescue index of foliar cover measured bi-weekly throughout the experiment. Dots represent group means while error bars are ± 1 standard error.

Table 28. P-values from F tests of the fixed effects of shade and nitrogen on foliar cover within each time step performed using the slice option of proc MIXED in SAS version 9.1 (SAS Inc 2003).

Week	Shade Effect P-value	Nitrogen Effect P-value
1	0.5860	0.7651
2	0.7720	0.0051
3	0.1609	0.0099
4	0.0290	0.1318
5	0.0101	0.0817

Discussion

The higher pre-treatment levels of mineral nitrogen observed in the nitrogen addition treatment could have created a spurious fertilizer effect. However, fertilizer effects on the Idaho fescue growth and vigor responses that were measured were not evident. Any effect generated by this chance elevation in pre-treatment N level would have simply been construed as a fertilizer effect and as we were not specifically interested in quantifying the amount of N required to generate an effect this would not have altered the interpretation of the results.

Upon application to the soil, urea rapidly hydrolyzes to form ammonium (NH_4^+) which can subsequently follow several potential pathways in the soil; the most common are nitrification and subsequent production of NO_3 , immobilization, and plant uptake (Havlin et al. 2005 and Myrold 2005). It is expected that the nitrification of NH_4 derived through urea hydrolysis was the primary agent for the large increase in post-treatment NO_3 observed in the fertilized pots in this study. Increases in post-treatment mineral N pools associated with the shade treatments also incorporated differential nitrogen uptake associated with shade treatment effects on plant biomass production. Larger Idaho fescue plants found in the un-shaded treatment groups necessarily removed greater quantities of nitrogen from the soil than the smaller plants in the shaded treatment. These treatment effects on net mineral N

accumulation can be envisioned as superimposed upon the baseline nitrogen cycling that occurred in the absence of these modifying influences. Thus, the general pattern that emerged across all groups was an increase in mineral nitrogen pool sizes regardless of treatment combination.

The differential influence that the two treatment groups had on the net mineral nitrogen accumulation may also help explain the significant interactions observed in the net change in the $\text{NO}_3\text{-N}$ and total mineral N pool sizes. These interactions appear to exist primarily because of the extreme low net change in $\text{NO}_3\text{-N}$ associated with the no shade / no nitrogen treatment combination (Figure 25). This group was composed of high biomass plants that would have removed a substantial amount of nitrogen from the soil to support their size. The nutrient depletion associated with growth likely intensified the low soil N concentrations that would have been observed in these pots because of their selection for the no nitrogen addition treatment.

It is apparent from these analyses that Idaho fescue plants grow larger in higher light intensity environments. Plants in the un-shaded treatments exhibited higher shoot and root biomass and larger cover indices than those in the shaded environments. Plants commonly exhibit greater biomass and growth when developed at high irradiance (Boardman 1977 and Allard et al. 1991). Similar results have been observed previously for Idaho fescue where Moir (1966) observed a significant decrease in total plant dry weight for plants grown under 36% daylight compared to full sunlight. Naumberg et al. (2001) also reported a uniform decrease in total biomass for several common Arizona ponderosa pine forest grass species that were grown under densely shaded conditions.

Approximately 40% of plant dry matter comes from carbon fixed through photosynthesis (Lambers et al. 1998) thus changes in plant biomass may be attributed to changes in the photosynthetic activity of the plant. Although numerous factors can affect photosynthesis including light, temperature, water, CO_2 availability and plant health and age (Coyne et al. 1995) it is evident that light availability influenced the photosynthetic ability of the Idaho fescue plants used in this experiment. The light

saturation point for a plant is reached at a light intensity where carbon fixation and photosynthetic activity is maximized and further increases in light intensity do not confer attendant increases in photosynthetic activity. Coyne et al. (1995) indicated the light saturation point for C₃ species, like Idaho fescue, is around 50% of full sunlight. Our 80% shade treatment corresponded to a PAR intensity approximately 22% of that experienced in the un-shaded treatments and thus substantially lower than the light saturation point.

The increase in leaf length observed in the shaded treatments is also a common response of plants grown in low irradiance environments (Boardman 1977 and Allard et al. 1991). Moir (1966) suggested that Idaho fescue foliar length was greater under a shaded treatment compared to natural daylight conditions, although this response was not actually measured. Increased leaf length effects an increase in leaf area which has also been identified as a leaf level response to growth under shaded conditions (e.g. Murchie and Horton 1997 and Allard et al. 1991). Leaf elongation is part of a shade tolerance response associated with more conservative resource use that is related to reduced growth rates and other morphological and physiological changes (see Bjorkman 1989 for list of potential changes) that promote efficient light energy capture while reducing respiratory losses (Boardman 1977, Smith 1982 and Bjorkman 1989). These changes enable plants to maintain a net carbon balance under conditions of limited carbon input brought on by the diminished availability of light energy (Bjorkman 1989).

The shade effect on leaf length was consistent over time with the exception of the first 2 measurement periods, although divergence in leaf length was evident by week 2. As described for final leaf length, plants in the shaded treatment exhibited longer leaf lengths over weeks 3 through 10. The lack of a significant shade effect over the first 2 weeks likely reflected a growth initiation and environmental equilibration period.

Longer leaves were evident in plants subjected to the nitrogen addition treatment during weeks 2 through 6, indicating that leaf growth rate was higher under the nitrogen treatment during this time period. As this was not a persistent effect and

final leaf length did not differ among nitrogen treatment groups, it is likely that this temporal effect was related to increased mineral N supply to the plants in the fertilized treatments. Mechanisms associated with root-nutrient contact including mass transport, diffusion and root interception are enhanced under conditions of higher soil nutrient concentrations (Havlin et al. 1999). Thus, plants in the fertilized treatment were able to acquire the nitrogen needed to meet their growth needs at a faster rate than those in the un-fertilized treatments simply as a function of increased nitrogen availability associated with higher soil concentrations.

As described for the shading influence on leaf length, there was also a lag period prior to observing a significant difference in foliar cover between plants in the two shade treatment groups. It appears as though initial rates of increase in foliar cover were similar, however at around 5 weeks, the plants in the shaded treatment substantially reduced the rate of increase in cover while those in the un-shaded group continued with a strong growth rate. The decline in the growth rate of shaded plants was likely related to the inability of these plants to fix carbon at a rate required to support further growth because they were limited by the availability of light energy needed for carbon fixation (Lambers et al. 1998).

Nitrogen addition also appeared to stimulate a short term increase in the growth rate, as indexed by cover, of Idaho fescue plants. Plants in the nitrogen addition treatment expressed larger foliar cover values than those in the un-fertilized group during weeks 3, 5 and 7. Cover values from the two groups were statistically similar in early growth (i.e. week 1) and later growth (week 9). This pattern was also apparent in the growth rate indexed by leaf elongation, and as explained, this was likely in response to increased availability of mineral nitrogen at the root-soil interface associated with elevated soil nitrogen concentrations in the fertilized treatment. The unfertilized plants were eventually able to accumulate enough nitrogen to meet their growth requirements as foliage cover values for both nitrogen treatment groups were similar by the end of the experiment.

The general lack of a lasting nitrogen effect on Idaho fescue growth indicates that soils from dense ponderosa pine forests were not nitrogen deficient and Idaho

fescue plants grown in these soils were not nitrogen limited. Although others have reported decreases in net nitrogen mineralization associated with increasing ponderosa pine abundance (e.g. Moir 1966, Kaye and Hart 1998 and Carr 2007b), the reduction may not have a substantial effect on the growth of desired understory species. Moir's data were suggestive of a decreasing trend in Idaho fescue dry weight biomass associated with soils from an increasing gradient of ponderosa pine occupancy (Moir 1966). However this relationship was not statistically verified and it is unclear how the soils used in this study were handled prior to the experiment. In our study, soils were sieved prior to use to remove all litter and coarse organic material which likely reduced the potential for nitrogen immobilization and this may explain why nitrogen mineralization rates were high enough to support vigorous plant growth, even in un-fertilized treatments. Kaye et al. (2005) reported similar findings to ours where increased net nitrogen mineralization associated with restoration treatments in formerly dense ponderosa pine stands did not correspond to increased total plant biomass or total plant N uptake. Rather, plant biomass and N uptake were similar across dense pine control stands and the two restoration treatments applied, however the vegetation components involved in nitrogen cycling varied (i.e. greater abundance of herbaceous species which accounted for a larger proportion of the total N budget) (Kaye et al. 2005).

Caution is recommended in directly applying these results to field situations, however, as other factors including pine needle litter accumulation and reduced soil temperatures under dense ponderosa pine stands may alternatively influence Idaho fescue growth patterns from what was observed in this greenhouse experiment.

Summary and Conclusions

Although Idaho fescue vigor was not a measured variable in these analyses, it was apparent the plants grown in un-shaded conditions were more vigorous individuals. Plants in un-shaded treatment groups produced greater root biomass, shoot biomass and expressed larger indices of foliar cover. The 80% shade treatment

did stimulate an increase in leaf length, a common response to growth in low irradiance environments. After an initial growth and environmental equilibration period, the rate of growth, as indexed by foliar cover, was also higher for un-shaded Idaho fescue plants. Interestingly, nitrogen addition had little effect on plant growth and vigor, but did provide a short-term increase in growth rate measured by leaf elongation and foliar cover, however this was not a persistent effect.

As observed in the companion field study (Carr 2007b), light availability and its influence on carbon fixation appears to be strongly related to the vigor and growth of Idaho fescue, the dominant perennial bunchgrass of open ponderosa pine stands in the Ponderosa pine / Idaho fescue plant association of eastern Oregon (Johnson and Clausnitzer 1992).

Carr (2007b) also observed a low correlation between total mineral nitrogen availability and the presence of perennial bunchgrasses, a functional group that was dominated by Idaho fescue. A weak, non-statistically significant relationship between Idaho fescue and the nitrogen treatments was also present in this greenhouse study. The responses of shoot biomass, root biomass, leaf length, and foliar cover all suggested increases associated with the nitrogen addition treatment and this may be an avenue for further analyses.

Restoration efforts that promote an increase in understory light availability should be a critical component of restoration programs aimed at directing ponderosa pine forests toward that which more closely resembles pre-settlement forests. However, natural recruitment of herbaceous understory plants may require long periods of time or may not occur at all if a viable seed source is not available within the dispersal limits of the target species (Carr 2007c and Korb et al. 2005) or thick litter layer remains after canopy treatment (Laughlin et al. 2006).

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**CHAPTER 5: UTILITY OF THE SOIL SEED BANK IN THE RECOVERY
OF UNDERSTORY HERBACEOUS SPECIES IN A PONDEROSA PINE
(*Pinus ponderosa* Dougl.) ECOSYSTEM**

Abstract

Elevated ponderosa pine (*Pinus ponderosa* Dougl.) abundance associated with lengthened fire return intervals can alter the under-canopy environment and substantially diminish or even eliminate the herbaceous understory component. Recovery of the herbaceous understory following ponderosa pine structural restoration requires an available and germinable propagule source. The objective of this study was to evaluate the soil seed bank as a source for recovery of herbaceous understory species within ponderosa pine ecosystems stressed by increased tree abundance. Seed bank samples were collected from 7 ponderosa pine stands with an intact perennial bunchgrass dominated understory and 7 ponderosa pine stands with little or no understory component. Both stand types existed on similar sites and were assumed to possess comparable ecological potential. The seed bank was evaluated using the seedling emergence method and seed bank density and diversity comparisons made using the Wilcoxon rank-sum test while seed bank species composition was compared using multiple response permutation procedures and indicator species analysis. Comparisons were also made between seed bank and understory vegetation species composition. No statistical differences were present in seed density or seed bank species diversity measures, although the intact seed bank trended higher in both accounts. The intact understory seed bank represented the dominant physiognomy of the intact vegetation, primarily as a result of the abundance of perennial bunchgrass seeds. The seed bank of depauperate understories, however, did not possess species that characterized the intact understory vegetation indicating that the propagules required for recovery of intact vegetation must come from off-site sources. Restoration initiatives in ponderosa pine ecosystems should include the seeding of desired herbaceous understory species.

Introduction

Vegetation recovery on sites where species loss has occurred requires a plant propagule source. Plant propagules are either stored onsite in the seed bank - reserves of viable seeds present in and on the soil (Roberts 1981) - or immigrate from off site sources. Desirable native perennial species often have poor dispersal mechanisms (Marlette and Anderson 1986) making the re-establishment of these species on sites previously occupied reliant on stored propagules in the seedbank. An understanding of the characteristics of the seedbank is important for predicting the potential vegetation following natural or management induced perturbation (Roberts 1981).

Contemporary ponderosa pine forests are generally thought to exist outside their historic range of variability (Covington and Moore 1994, Tiedemann et al. 2000 and Allen et al. 2004). Activities associated with European settlement in the late 1800s including road and trail development, intensive livestock grazing, and active fire suppression triggered a substantial increase in the fire return interval, and combined with favorable conditions for ponderosa pine seed germination and seedling establishment, effected unprecedented changes in the fire regime and vegetation structure in ponderosa pine forests (Covington and Moore 1994, Johnson 1994).

In established ponderosa pine forests, overstory pine trees are favored in competitive interactions with the understory herbaceous and shrubby components. By eliminating the majority of pine regeneration, fire, in a low-intensity high frequency regime, confers a competitive advantage to understory herbs and shrubs, however, over time and in the absence of fire, increased pine stem density, canopy cover, and/or root density effects an increasing level of stress on understory species by reducing available light, water and nutrient resources (Krueger 1981 and Riegel et al. 1991, 1992, and 1995) and may eventually lead to localized extirpation of understory species (Moore et al. 1999 and Stephenson 1999). Relative to open pre-

settlement forest stands, dense stands of ponderosa pine show significant limitations in many understory attributes including diversity, density, and vigor (Clary et al. 1975, Uresk and Severson 1998, Naumberg and DeWald 1999, and Naumberg et al. 2001). In some of the densest stands, the understory component is replaced by a thick mat of pine needle litter (Moir 1966 and Wienk et al. 2004).

In a study evaluating herbaceous understory species abundance along a gradient of ponderosa pine occupancy, Carr (2007b) characterized open stands as perennial bunchgrass dominated understories, represented primarily by high abundances of Idaho fescue (*Festuca idahoensis* Elmer), while high pine occupancy stands were devoid of perennial bunchgrasses and exhibited low diversity understories of few forbs and rhizomatous grasses. The absence of a perennial bunchgrass understory in high pine occupancy stands restricts the plant propagule source for recovery following removal of overstory competition, a function ostensibly performed by fire although may be achieved through other manipulations (i.e. timber harvest), to the soil seed bank. Although seed immigration from off-site sources is an avenue for understory re-establishment, distance to nearest seed source and lack of dispersal mechanisms can hinder successful recovery of desired species (Whisenant 1999). Relatively little is known about the understory recovery potential from the soil seedbank in ponderosa pine forests (Korb and Springer 2003 and Korb et al. 2005).

Strickler and Edgerton (1976) found 38 species in the seed bank of a mixed conifer forest in northeast Oregon. Most of the seedlings emerged from the litter layer and many were species with effective wind-borne dispersal mechanisms, likely representing recent arrivals from off site sources. Thirteen of the 38 species (~34%) that germinated were also found in the associated vegetation and 7 of them accounted for 44% of the total cover (Strickler and Edgerton 1976).

Pratt et al. (1984) realized the importance of the soil seed bank to understanding the composition of post-disturbance vegetation and endeavored to describe the species composition of the seed bank in a Ponderosa pine / *Symphoricarpos albus* habitat type in eastern Washington. They found very high

densities of viable seed, reporting 14463 ± 1356 seeds/m² in their fall samples. Although species dominance in the vegetation of the study area was not comparable to dominance in the seed bank, species composition was more alike with 63% of the species germinating from the seed bank also present in the vegetation.

Vose and White (1987) found very few germinable seeds in the soil under ponderosa pine forest in Arizona. They reported 8.4 seeds/m² and 22.1 seeds/m² in burned and unburned plots respectively. Wienk et al. (2004) also reported low germinable seed densities, 78 seeds/m² before burning and 186 seeds/m² post-fire, from seed banks in a dense ponderosa pine forest in North Dakota.

Arbella (2005) described 66 different species contributing an average of 2500 seeds/m² (0-10 cm depth) in seed banks from Arizona ponderosa pine forests. Arbella (2005) suggested a stronger correlation existed between extant vegetation and seed bank species than is generally reported in the literature. Species found in the seed bank were generally present in the associated vegetation, however it was not clear if the reciprocal relationship was also present.

Korb et al. (2005) reported between 275 and 1560 seeds/m² in seed banks from Arizona ponderosa pine stands varying in historical disturbance regime. None of the seed banks correlated well with the vegetation present at the seed bank sampling locations and most of the species that germinated were annuals, ruderals, and non-natives causing the authors to question the reliability of seed banks as a source for the re-introduction of native perennials to sites where past land use changes have caused localized extirpations (Korb et al. 2005).

Management of ponderosa pine forests toward a structure that more closely resembles pre-settlement forests is often prescribed and is desirable from many perspectives. However, a clear understanding of the seed bank's role in understory species recovery associated with overstory structural and attendant understory environmental change is lacking. Moreover, published research reporting on ponderosa pine seed bank composition and utility in restoration is scarce and of those reports that do describe pine seed banks, only 1 is from the Pacific Northwest. Research on these issues is needed in Pacific Northwest ponderosa pine forests to

assist in understanding potential vegetation dynamics in response to natural or management induced perturbations and in developing appropriate management strategies for ponderosa pine forests stressed by uncharacteristically high pine abundance.

Study Objectives

This study was designed to develop an increased understanding of ponderosa pine seed bank composition and to evaluate the feasibility of the soil seed bank as a propagule source for vegetation recovery from depauperate understory conditions. Specifically, the objectives of this study were to: 1) evaluate and compare the seed banks from ponderosa pine stands with either depauperate or intact herbaceous understories; and, 2) assess the implications of seed bank compositional variation for understory restoration.

Methods

Study Area

The study area is located in eastern Oregon (44°12'52" N latitude, 118°59'16" W) in a Ponderosa pine / Idaho fescue plant association (Johnson and Clausnitzer 1992) and within the John Day ecological province (Anderson et al. 1998) and the Continental Zone Highlands sub-region of the Blue Mountains Ecoregion (Bryce and Omernik 1997). The area ranges from 1500 m to 1560 m in elevation and is situated in an area of gently sloping (~ 8% slope gradient) north-facing hillsides. The average daily high and low summer and winter temperatures, recorded between 1971 and 2000 at Seneca (~ 8 km south of the study area) were 24°C and 1.5°C and 4°C and -9°C respectively (Oregon Climate Service 2007). Approximately 35 cm of precipitation is received annually, most occurring in the winter months and primarily in the form of snow (Oregon Climate Service 2007). Seneca is approximately 100m lower in elevation than the sites used in this research project and exists in a relatively broad non-forested valley. Thus, it is expected that the study area receives slightly

more precipitation than that recorded at Seneca and that the temperature regimes differ slightly between the two areas.

Soils of the study area are composed of a variable thickness ash mantle associated with the eruption of Mt. Mazama 6000 – 7000 years ago (Klimasauskas et al. 2002), overlaying serpentinite gravel and cobble. Soils were classified as either a fine-loamy, mixed, superactive, frigid Vitrandic Haploxerolls or a clayey-skeletal, smectitic, Lithic Ultic Argixerolls (Carr 2007a). Thickness of the ash-influenced mantle is a distinguishing feature of these soil types; Vitrandic Haploxerolls having an ash-influenced layer that is 20 to 30 cm thicker. Both soils are classified in a xeric soil moisture regime and frigid soil temperature regime.

The study area is a climax ponderosa pine forest consisting of large-diameter ponderosa pine trees scattered across a landscape dominated primarily by patches of smaller pines. Over 90% of the trees in the study area are less than 100 years old while approximately 3% have survived for more than 250 years (see Appendix A for ponderosa pine age distribution in the study area). The area was historically grazed by sheep and cattle, however, since the 1960s it has been grazed primarily by cattle in the summer from July to October. No evidence of recent fire or logging activity was apparent in the study plots, however the area was logged in 1978 and a variety of silvicultural activities have occurred in the general vicinity (Carr 2007a).

Data Collection

Seven 15m x 15m plots were located in each of two ponderosa pine stand types (N = 14 plots) representing intact and depauperate understory conditions. Plots exhibiting a robust herbaceous understory dominated primarily by the perennial bunchgrass *F. idahoensis* were identified as intact understories while depauperate understory conditions were identified by the absence perennial bunchgrasses and general paucity in understory species. Understory conditions were not quantified prior to the study. Pine canopy conditions of each group are presented in Table 29.

Table 29. Overstory conditions associated with intact and depauperate understory groups. Standard errors are presented in parentheses.

	Intact Understory	Depauperate Understory
Pine Density (stems/ha)	679 (110)	3244 (316)
Pine Basal Area (m ² /ha)	15.97 (6.04)	41.32 (15.62)
Canopy Closure (%)	56.76 (21.45)	79.14 (29.91)
Under-canopy Radiation (MJ/m ² /yr)	4369 (253.87)	1869 (100.28)

In each plot, understory species cover and density were subsampled in 0.5 m² (1 m x 0.5 m) and 0.125 m² (0.25 m x 0.50 m) quadrats respectively. Quadrats were systematically positioned from a random starting point along transects placed randomly along the north baseline of each plot. The number of transects and quadrats differed by plot in accordance with plant community heterogeneity. Percent cover was estimated using cover classes modified from Daubenmire (1959) (Table 30).

Table 30 Cover classes and associated ranges of % cover and midpoints used in assessing cover of understory species.

cover class	% cover range	mid-point
1	0 – 1	0.5
2	1 – 5	3.5
3	5 – 25	15
4	25 – 50	37.5
5	50 – 75	62.5
6	75 – 95	85
7	95 – 100	97.5

Soil samples were collected from each plot in October, 2005. Thirty 25.3 cm^3 soil cores incorporating the litter layer through to 5 cm depth in the mineral soil were collected in each plot, resulting in an aggregate plot sample volume of 759 cm^3 . Six cores were removed from random locations along each of 5 transects in each plot and composited to provide 5 samples for each plot. When more than 5 transects were present in a plot, 5 were selected at random. Samples were placed in plastic bags, labeled and stored in darkness for ~6 months at approximately 2.7°C (see Appendix C for seed bank sample storage temperature regime).

Seed bank composition was evaluated using the seedling emergence method. Although this approach to characterizing the seed bank may underestimate total composition if germination requirements for all species are not met (Roberts 1981 and Baskin and Baskin 1989), it does provide a good estimate of the readily germinable fraction of the seed bank (Gross 1990). Each sample was washed through a 4 mm (# 5) and then through a $180 \mu\text{m}$ (# 80) sieve removing litter and large soil particles and concentrating the seed sample (Wienk et al. 2004). Concentrating the seed samples can significantly increase the number of individuals and species found through emergence methods (Ter Heerdt et al. 1996 and Bossuyt et al. 2000). The concentrated samples were spread in a thin layer, approximately 1 cm deep, over potting soil (Sunshine Grower's Mix A) in $10.2 \times 10.2 \times 8.9 \text{ cm}$ pots. Pots were then placed in a growth chamber (Hoffman Manufacturing SG 30) programmed for 14 hours of light at 20°C and 10 hours dark at 5°C . Light and temperature settings were selected to represent average late spring day length and temperature for the study area. Pots were kept moist and seedlings grown until they could be positively identified. In this study no differentiation was made between seed, rhizomes or other below ground plant propagules as they equally represented sources of future plant material.

Data Analysis

Although t-tests are relatively robust to departures from normality, the small sample size and apparent violations of the assumptions of normality and equal

variance in the seedling density data and diversity indices (Appendix B) suggested that a non-parametric approach was better suited for characterizing differences between groups (Ramsey and Schafer 1997). The Wilcoxon rank-sum test was used to evaluate differences in seed bank seed density and diversity indices between the intact and depauperate understory groups. The Wilcoxon rank-sum test employs a ranking transformation that organizes the data by rank within the combined sample and evaluates the likelihood of obtaining as small a rank sum of the first group against the sum of ranks for this group from a randomization of the data (Ramsey and Schafer 1997). Analyses were performed using SPLUS 7.0 (Insightful Corp., 2005).

Differences in seedbank species composition were tested using Multi-Response Permutation Procedures (MRPP). MRPP is a non-parametric analytical tool for multivariate data that does not rely on assumptions of multivariate normality or equal variances, and is particularly useful in evaluating group differences in ecological community data (McCune and Grace 2002). MRPP evaluates the within group similarity by comparing the average within group distance to that expected by chance; groups that occupy different regions of multidimensional space will have smaller within group distances than expected, as evaluated through multiple randomized permutations of the data (Mielke 1984, Mielke and Berry 2001 and McCune and Grace 2002). MRPP analysis was performed in PC-ORD version 4.39 (McCune and Mefford 1999) using the Sørensen distance measure. Indicator species analysis was used to evaluate species relationships with understory group seed bank. ISA evaluates the faithfulness and exclusivity of a species to a particular group against a perfect indicator which would always and only be present in sample units that represent a particular grouping (McCune and Grace 2002). ISA was performed with PC-ORD version 4.39 (McCune and Mefford 1999) using 1000 randomizations in the Monte Carlo tests of indicator significance.

Because of the high overall heterogeneity of the seed bank seed density data ($\beta_w = 7.5$) they were transformed to presence – absence. This is a useful transformation as the majority of the information present in heterogeneous data exists in the presence or absence of species (McCune and Grace 2002). Although the

coefficient of variation of the species totals in the transformed data set remained moderately high ($CV = 90.70\%$), it was substantially lower than the untransformed data and no further transformations or relativizations were applied. MRPP and ISA were performed on the presence-absence transformed data set.

ISA was also used to identify relationships among understory vegetation and the intact and depauperate groups. Although beta diversity was relatively low ($\beta_w = 1.6$), the data were relativized by species maximum to reduce the influence of very abundant species. McCune and Grace (2002) suggested this as an effective transformation for community data as it tends to equalize the influence of abundant and rare species. To reduce noise and improve signal strength, species occurring in fewer than 2 plots were removed from the data set (McCune and Grace 2002). Because of the inherent variability associated with seed bank data (Baskin and Baskin 2001), interesting trends observed in these analyses were also described even when not statistically significant (Arbella 2005).

Results

Seed Bank

A total of 20 different species, comprised of 15 forbs, 3 grasses, 1 sedge, and 1 tree, germinated across both understory groups. Several seeds germinated during the storage period and were not included in these analyses. Two forb species in the depauperate seed bank and 3 forb species in the intact seed bank germinated but did not survive long enough to allow identification. They were apparently different species and were included in the analyses as unknown forbs. In both groups, forbs expressed the highest frequency and density, occurring in the seedbank of every plot in the intact group, while grasses, followed by the lone tree species, *P. ponderosa*, exhibited sequentially lower densities and frequencies (Table 31).

The seed density in the intact understory group was 555 seeds/m² while 207 seeds/m² were recorded in the depauperate group. Grasses were 2.4 and forbs 2.7-times more abundant in the intact seed bank compared to the depauperate (Table 31).

The frequency of occurrence, relative abundance and density of the more common species in each group are presented in Table 31.

Table 31. Frequency, relative abundance and density of common species and functional groups found in the seed bank of intact and depauperate understories.

	Frequency (%)	Relative Abundance (%)	Density (seeds/m ²)
Intact Understory			
<i>Lithophragma parviflora</i>	85.71	62.71	348
<i>Festuca idahoensis</i>	42.86	11.86	66
<i>Carex rossii</i>	28.57	5.08	28
Grasses	71.43	23.73	132
Forbs	100.00	74.58	414
Tree / Shrub	14.28	1.69	9
Depauperate Understory			
<i>Lithophragma parviflora</i>	14.28	27.27	56
<i>Carex rossii</i>	28.57	18.18	38
<i>Silene menziesii</i>	14.28	13.64	28
<i>Poa nervosa</i> var. <i>wheeleri</i>	14.28	9.09	19
<i>Epilobium watsonii</i>	28.57	9.09	19
Grasses	42.86	27.27	56
Forbs	85.71	72.73	151
Tree / Shrub	0	0	0

Note: Grass functional group includes the sedge *C. rossii*.

Across both understory groups, *Lithophragma parviflora* (Hook.) Nutt. ex Torr. & Gray was the most common and abundant species comprising 53% of the overall abundance, and 63% and 27% of the abundance in the intact and depauperate understory groups respectively. This species occurred in almost 86% of the plots in the intact understory while its presence was recorded in only 14% of the depauperate plots. Other dominant species in the intact understory group include *F. idahoensis*, *Koeleria macrantha* (Ledeb.) J.A. Schultes, and *Carex rossii* Boot, while *Carex rossii*, *Silene mensiezii* Hook., *Epilobium watsonii* (Barbey), and *Poa nervosa* (Hook.)

Vasey var. *wheeleri* (Vasey) Hitchc. were common in the depauperate group (Table 31 and Figure 33).

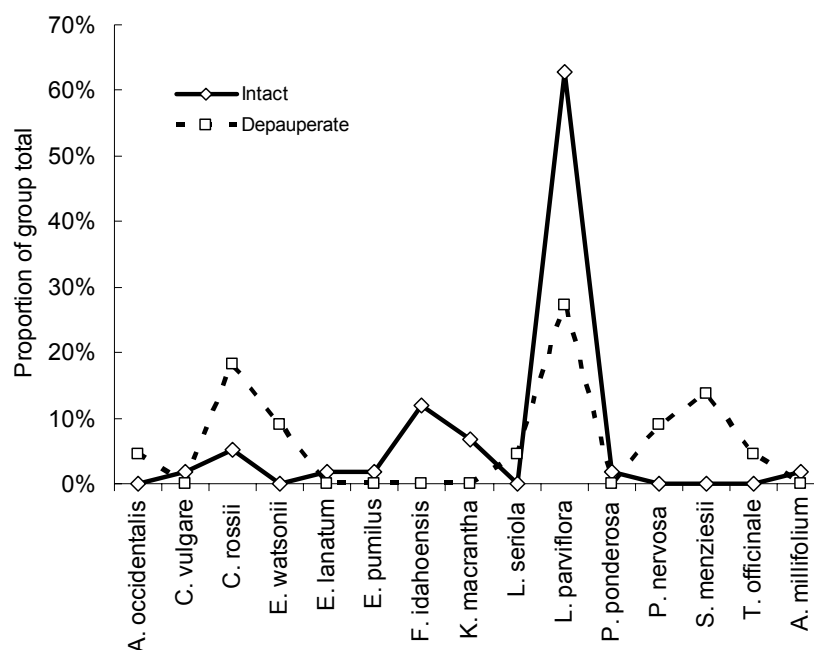


Figure 33. Relative seedling density by understory group.

Although the intact group was higher in seed density, species richness and Simpson's and Shannon's diversity indices (Figures 34 and 35), no statistically significant differences were detected. The p-values from a Wilcoxon rank-sum test of the hypothesis of equal group means were 0.0721, 0.2118, 0.2874, and 0.2874 for density, species richness, Simpson's index, and Shannon's index, respectively.

There was evidence of a difference in the species composition of the germinable seed bank between the two understory conditions ($A = 0.07896$, $p = 0.00516$, MRPP). This difference was primarily related to the presence of *L. parviflora* in the intact group (Indicator value for intact group = 73.5, $p = 0.0350$). The next largest indicator values for the intact group were *F. idahoensis* (IV = 42.9, $p = 0.1750$) and *K. macrantha* (IV = 28.6, $p = 0.4620$) although neither were

significant. No significant indicator values emerged for the depauperate understory group, however *E. watsonii* did express the largest indicator value for this group (IV = 28.6, $p = 0.4740$).

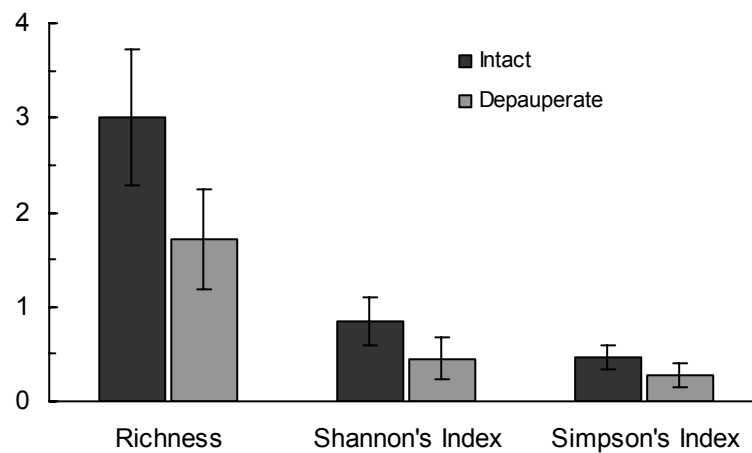


Figure 34. Seed bank diversity indices. Error bars are ± 1 Standard Error.

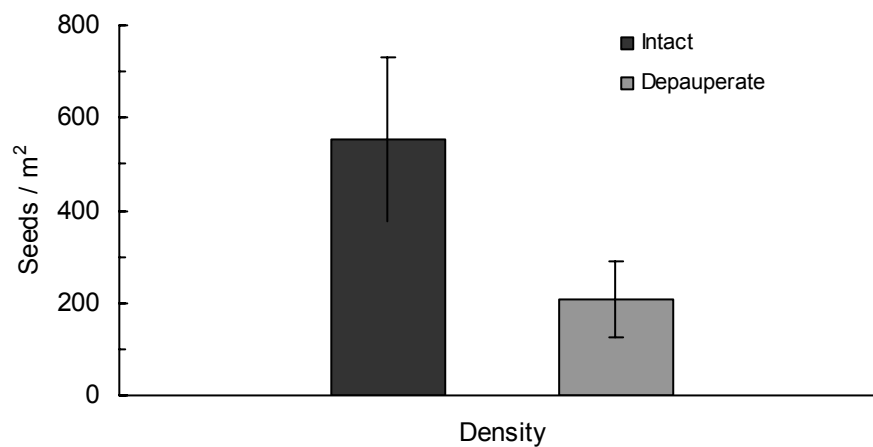


Figure 35. Seed bank seed density. Error bars are ± 1 Standard Error.

Understory Vegetation

The understory vegetation of the intact group was best described as a perennial bunchgrass plant community dominated primarily by *F. idahoensis* with smaller components of *K. macrantha* and *Poa scabrella* (Thrub.) Benth. and a forb component dominated by *Achillea millifolium* L. and *Phlox hoodii* Rich.. Large indicator values for the intact group were observed for each of these species from indicator species analyses of the understory density and cover data sets (Table 32).

The density of the depauperate understory group was dominated by the rhizomatous species *Calamagrostis rubescens* Buckl. and *P. nervosa* along with the forb *S. menziesii*. Combined, these three species contributed 82% of the density and 47% of the cover observed in the depauperate plots. Several species, including *C. rossii*, *Berberis repens* Lindl., and *F. idahoensis* contributed little in terms of density but were more prominent when measured by cover.

The understory vegetation of the intact group had 123% higher total density and 325% more total plant cover than the depauperate group, illustrating the relative paucity of vegetation in the depauperate plots. Moreover, no species exhibited statistically significant or large indicator values for the depauperate group, reflecting the relatively large proportion of plots with few species present which impaired the ability of any particular species to be faithful (always present) to a particular group; a component of a strong indicator. Table 33 shows the relative abundances of the common species found in each understory type.

Table 32. Indicator values for 5 common species in the understory vegetation of the intact group. Density and cover represent indicator values from ISAs of the respective data sets.

	Group	Density		Cover	
		IV	P value	IV	P value
<i>Festuca idahoensis</i>	Intact	91.4	0.0030	92.9	0.0020
<i>Koeleria macrantha</i>	Intact	89.2	0.0050	93.6	0.0030
<i>Poa scabrella</i>	Intact	93.4	0.0030	95.1	0.0020
<i>Achillea millifolium</i>	Intact	93.2	0.0060	90.7	0.0030
<i>Phlox hoodii</i>	Intact	99.0	0.0030	96.7	0.0040

Discussion

Published reports of ponderosa pine seed bank densities vary from a low of 8.4 seeds/m² (Vose and White 1987) to upwards of 14000 seeds/m² reported by Pratt et al. (1984). The high densities observed by Pratt et al. (1984), however, were attributed to the highly diverse and abundant understory associated with the transitional community that was sampled, grading from steppe to forest vegetation. The seed density reported in our study for the depauperate understory group ($\bar{x} = 207$ seeds/m²) correspond well with Wienk et al. (2004) who reported 78 and 186 seeds/m² in dense ponderosa pine stands in South Dakota. The understories of these stands were described as “sparsely vegetated” (Wienk et al. 2004) and would likely fit within our depauperate designation. The 200 – 400 seeds/m² observed by Korb et al (2005) in the seed bank of near reference Arizona ponderosa pine stands is slightly lower than the 555 seeds/m² average density recorded in our intact understory group. However our intact stands have experienced past disturbances including logging and grazing, and as indicated by Korb et al. (2005), seed bank seed

density appears to follow a disturbance gradient and this may explain why our results indicated higher seed densities in our intact understory plots. Moreover, our estimates of seed density are conservative as we likely did not meet the germination requirements of all species and several seeds germinated during cold storage and were not included in the analyses.

No differences in seed density or seed bank species diversity were observed between the seed banks of depauperate and intact understories. Although trends were particularly apparent in seed density and species richness, indicating that the intact group may have higher values of these parameters, differences were not statistically significant. The large mean seed density observed in the intact group was strongly influenced by the presence of *L. parviflora*, contributing over 60% of the total seed density (Figure 33). This species was also dominant in the depauperate group although not to the same extent. Other researchers have also reported a substantial dominance in the seed bank of one or a few species. Pratt et al. (1984) found that 3 species (*Poa pratensis*, *Stellaria media* and *Cerastium vulgatum*) comprised over 50% of the seeds in their samples. Similarly, Korb et al. (2005) observed that 60% of the seed bank in high disturbance stands was comprised of *Verbascum thapsus*, while Wienk et al (2004) reported 54% of seedlings germinated were to *Rumex* sp. In our case, because *L. parviflora* exhibits rhizomatous growth behavior (Parish et al. 1999), it is possible that >1 seedling emerged from the same rhizome piece inflating the reported propagule density of this species.

The high mean seed bank species richness of the intact group was influenced by elevated richness values observed in several of the intact plots. Five species were observed in one intact plot while 6 species germinated in another. The most species observed in any of the depauperate plots, however, was four. Figure 36 displays the raw species richness values for each of the plots used in these analyses.

Table 33. Relative density and cover of common species in the understory vegetation of the intact and depauperate understory groups. Relative values are a measure of the cover or density of a species relative to the total for that group. Total group abundance (density or cover) is given in the last line of the table.

Species	Relative Density (%)	Relative Cover (%)
Intact Group		
<i>Festuca idahoensis</i>	17.12	40.91
<i>Poa scabrella</i>	5.24	3.61
<i>Koeleria macrantha</i>	3.63	5.63
<i>Achillea millifolium</i>	33.03	12.16
<i>Carex rossii</i>	3.95	5.10
<i>Calamagrostis rubescens</i>	12.62	2.28
<i>Phlox hoodii</i>	4.20	14.21
Total Group Abundance	532.86	128.10
Depauperate Group		
<i>Calamagrostis rubescens</i>	61.36	27.40
<i>Poa nervosa</i> var. <i>wheeleri</i>	12.53	6.51
<i>Silene menziesii</i>	7.96	13.09
<i>Achillea millifolium</i>	2.99	4.07
<i>Carex rossii</i>	2.49	11.65
<i>Berberis repens</i>	1.20	11.79
<i>Festuca idahoensis</i>	1.98	10.11
Total Group Abundance	431.64	39.37

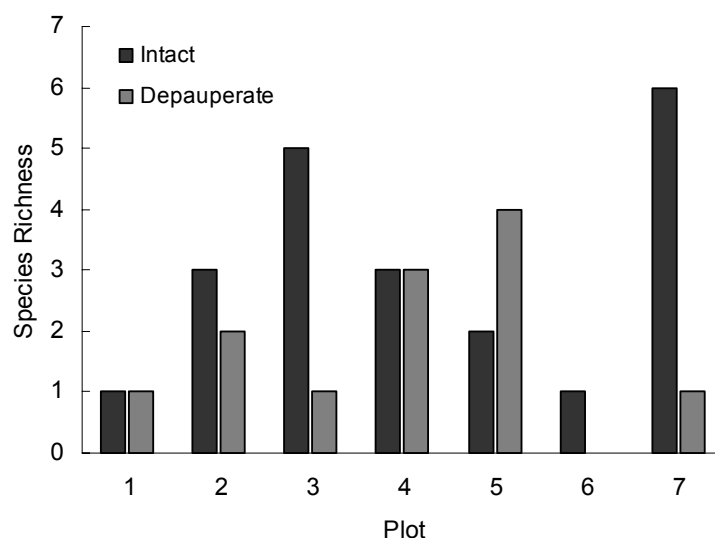


Figure 36. Species richness values for the seven plots in each of the understory condition groups.

Differences in seed bank species composition between the two understory condition groups were attributed primarily to the presence of *L. parviflora* in the intact group. Although this species also contributed a significant proportion of the density in the depauperate group, its occurrence was documented in only one plot. Conversely, *L. parviflora* was present in 6 of the 7 plots in the intact group and combined with the consistent occurrence in intact plots generated the strong indicator value for the intact group observed for this species. No other species provided a significant indicator value for either group, however this is not surprising given the sparseness of the data set (88.2% zeros) and the relatively high frequency of species with 1 or 2 occurrences (17 of the 20 species (85%) occurred in 2 or fewer plots). Sparse data sets preclude the achievement of large indicator values because the faithfulness component required for a strong indicator is restricted when species tend to occur in few plots. Moreover, species with low occurrences will not generate an indicator value greater than expected by chance because the observed indicator value will also be common in the randomized data (McCune and Grace 2002).

Aside from the obvious peaks associated with the abundance of *L. parviflora* in both groups, several patterns in seed bank species composition emerged that appeared to differentiate between the two groups (Figure 33) and substantiate the difference identified through MRPP. Generally, when there was a peak in abundance of a particular species for one group, there was a trough in the other (Figure 33). With the exception of *L. parviflora*, this pattern can be observed for *Poa nervosa* and *S. menziesii*, *F. idahoensis* and *K. macrantha*, and *C. rossii* and *E. watsonii*.

In addition to *L. parviflora*, depauperate seed banks were also comprised of *S. menziesii*, *P. nervosa* var. *wheeleri*, and *C. rossii*, species, that in the study region, are often found under the canopy of ponderosa pine trees, and *E. watsonii* a herbaceous dicot with windborne seeds that has been shown to be a significant component of seed banks in other eastern Oregon forests (Strickler and Edgerton 1976).

The intact seed bank, in addition to the obvious contribution of *L. parviflora*, was also characterized by the presence and abundance of two perennial bunchgrass species, *F. idahoensis* and *K. macrantha*. A peak associated with *C. rossii* was also evident but not to the extent of the depauperate group.

Seven species from the intact seed bank were also present and relatively abundant in the intact understory vegetation (Table 34). The three most common species in this group, *F. idahoensis*, *K. macrantha*, and *C. rossii* comprised almost 24% of the total seed density and approximately 64% of the remaining intact seed density after accounting for the contribution of *L. parviflora*. These same species were also heavily represented in the understory vegetation of the intact groups. Combined, they accounted for approximately 25% of the total density and almost 52% of the total cover in the intact understory vegetation (Table 33). *Achillea millefolium* was also present in both the seed bank and vegetation, and when included in the comparison above, augmented the total standing vegetation density accounted for by species that were also found in the seed bank to almost 60%. Thus, understory vegetation species that are a substantial component of the intact vegetation were accounted for in the soil seed bank. However, the relative proportions of species in

their respective strata differed and only 17% of the species present in the standing vegetation were accounted for in the seed bank.

Table 34. Relative densities (%) of seed bank species that were also present in the associated understory. Relative density is a measure of the density of a species relative to the total seed density.

Intact		Depauperate	
<i>Festuca idahoensis</i>	11.9	<i>Carex rossii</i>	18.2
<i>Koeleria macrantha</i>	6.8	<i>Silene menziesii</i>	13.6
<i>Carex rossii</i>	5.1	<i>Poa nervosa</i> var. <i>wheeleri</i>	9.1
<i>Pinus ponderosa</i>	1.7	<i>Aster occidentalis</i>	4.5
<i>Eriophyllum lanatum</i>	1.7		
<i>Erigeron pumilus</i>	1.7		
<i>Achillea millifolium</i>	1.7		

Four species from the depauperate seed bank were also present in the standing understory vegetation in plots from this group (Table 34). Combined, *C. rossii*, *S. menziesii*, and *P. nervosa* contributed 41% of the total seed density in the depauperate seed bank. In the depauperate understory vegetation, these three species contributed approximately 23% and 31% of the total density and cover respectively (Table 33). Compared to the intact seed bank, a smaller proportion of the understory vegetation was accounted for in the depauperate group. The relative proportions of the species in their respective strata differed, and only 9% of the species found in the depauperate standing vegetation were observed in the seed bank. With the exception of *C. rossii*, which occurred in limited abundances in the pre-threshold vegetation, none of the species common in the depauperate seed bank were present in any abundance in the pre-threshold vegetation (Tables 31 and 33).

Interestingly, the most common species in the seed bank, *L. parviflora*, was not accounted for in the vegetation, however, it is an early spring species that quickly disappears (Parish et al. 1999) and may have senesced prior to sampling as our

sampling scheme was designed to occur during maximal vegetation expression, later in the growing season.

Arbella (2005) found that species detected in the seed bank were almost always present in the above ground vegetation and suggested this as evidence against the commonly reported lack of correlation between seed bank and standing vegetation in forested systems (Roberts 1981). The inverse of this relationship differed as only ~37% of the above ground species were accounted for in the seed bank (Arbella 2005), implying perhaps a weaker correspondence among the two strata.

Other studies in ponderosa pine forests have indicated a low correspondence between seed bank and standing vegetation (e.g. Pratt et al. 1984 and Korb et al. 2005). Interestingly, Korb et al. (2005) found an increased similarity in species composition between seed bank and vegetation in plots recently exposed to soil disturbance through logging. The seed bank was primarily composed of ruderals, annuals, and non-natives and the authors attributed the observed increase in similarity between seed bank and vegetation to an increase in the abundance of ruderal and annual species in the vegetation associated with the disturbance (Korb et al. 2005).

Our data did not suggest an overly strong association between the seed bank and standing vegetation. However, the intact seed bank species composition did represent the dominant vegetation found in intact understories. The lack of representation of rarer species may simply be related to the correspondingly rare occurrences of the propagules of these species.

Restoration programs in ponderosa pine forests often involve partial removal of the pine overstory in an attempt to mimic tree density, basal area and canopy closure conditions of pre-settlement forests (e.g. Covington et al. 1997). A major component of restoration is to restore the native herbaceous vegetation and as such, the soil seed bank should be considered when developing restoration programs (Korb et al. 2005). Perennial species tend not to develop a persistent seed bank (Rees 1994) and may instead rely on vegetative persistence as a mechanism to maintain site occupancy (Parker et al. 1989, Korb et al. 2005). A significant lack of perennial

bunchgrasses in the vegetation and absence in the seed bank of depauperate understories suggests that propagules for the dominant vegetation of intact understories are not available in depauperate sites and can not be relied upon for their recovery (Halpern et al. 1999 and Korb et al. 2005).

Idaho fescue, the dominant understory species in the intact vegetation, does show some evidence of seed banking ability as it was present in the seed bank of the intact group, however the persistence of this propagule source is unclear from the data in this study. The soil seed bank of *F. idahoensis* is likely not long-lived given its absence from the depauperate stands. Other studies in arid and semi arid ecosystems have also shown a scarcity of perennial grasses in the seed bank (e.g. Koniak and Everret 1982, Hassan and West 1986 and Rice 1989).

Festuca idahoensis exhibits high variability in seed production and viability (USDA 1937 and Ensign et al. 1984) and seed dispersal is limited primarily to the immediate vicinity of the plant (Marlette and Anderson 1986, Goodwin et al. 1996 and Zouhar 2000). Thus, the absence of *F. idahoensis* in the seed bank and vegetation of depauperate understories combined with a lack of effective seed dispersal will likely result in extended periods of time of *F. idahoensis* absence from understories of ponderosa pine forests restored from high pine occupancy and depauperate understory conditions through treatments focused on pine occupancy reduction (Korb et al. 2005). Direct seeding of understory species should be considered as part of any restoration activities.

Summary

Seed bank species composition differed between seed banks from intact and depauperate understory conditions. Seed bank species composition did not correspond well to understory standing vegetation, however intact understory seed bank represented the dominant physiognomy of the intact vegetation, primarily in the abundance of *F. idahoensis* and the presence of *K. macrantha* and *A. millifolium*. The lack of perennial bunchgrasses in the vegetation and seed bank in depauperate

understories indicated that the propagules required for the reintroduction of intact understory vegetation during restoration activities must come from off-site sources. Given the general lack of seed dispersal mechanisms of most native perennial bunchgrass species, which in the present study included *F. idahoensis*, long periods of time without intact vegetation structure or species composition should be expected unless the seeding of desired herbaceous understory species are included in restoration initiatives.

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CHAPTER 6: ECOSYSTEM RESILIENCE AND THRESHOLDS IN CONTEMPORARY PONDEROSA PINE ECOSYSTEMS

Abstract

State and transition models of ecosystem dynamics are becoming more prevalent in the ecological literature. Although the potential for non-equilibrium behavior in ponderosa pine (*Pinus ponderosa* Dougl.) forests has been recognized for some time and many ecologists accept the existence of a threshold triggered by the loss of frequent low-intensity surface fire, state and transition models have not previously been used to describe ponderosa pine ecosystem dynamics. Here we propose a state and transition model for a ponderosa pine forest in eastern Oregon and describe the results of 3 separate research projects that provided evidence in support of the hypothesized model. Specifically we address the existence of a post-threshold irreversible transition to an alternative stable state characterized by a dense ponderosa pine forest with depauperate understory conditions. Understanding this trajectory of ecosystem change is important for recognizing and evaluating the constraints to successful ecological restoration. Increased ponderosa pine abundance, evident in many contemporary ponderosa pine forests can alter the under-canopy environment and effectively eliminate understory species otherwise dominant in more open canopy structures. Although increased ponderosa pine abundance negatively influenced nitrogen availability and soil temperature, reductions in light availability appeared to be the major pine mediated driver of understory species compositional loss. Understory species common in pine stands functioning within the normal range of variability do not form a persistent seed bank thus, seeds of these species are not available in post-threshold depauperate sites and can not be relied upon as a tool for their recovery. Ponderosa pine ecosystem restoration activities directed at returning ecosystems to pre-threshold structure and function should

consider understory species loss and the need for seed or other viable plant materials to ensure the components associated with system stability are re-introduced.

Introduction

Non-equilibrium approaches to describing ecosystem dynamics are established within the ecological literature and have been applied to a variety of ecosystems and ecosystem components (e.g. Holling 1973 and May 1977). Researchers have recognized that traditional linear succession approaches to ecosystem change inadequately characterized the observed vegetation dynamics in arid and semi-arid ecosystems (West et al. 1984, Westoby et al. 1989, Laycock 1991 and Svejcar and Brown 1991). Emerging ecological concepts provide for multiple stable states, multiple successional pathways, and thresholds of ecosystem change (Westoby et al. 1989, Friedel 1991, George et al. 1992, West 1999, Stringham et al. 2003, and Briske et al. 2006) and describe ecosystem dynamics in terms of the range of natural variability (Fulé et al. 1997, Moore et al. 1999, Landres et al. 1999 and Fulé et al. 2002). State and transition ecosystem dynamics incorporate non-equilibrium concepts in an ecosystem resilience based framework of multiple stable states, ecological thresholds and multiple successional pathways (Stringham et al. 2003, Briske et al. 2005, 2006 and 2007).

Stringham et al. (2003) developed an approach to state and transition modeling that provided needed consistency in the definition and interpretation of model components and application. Their approach, based on initial state and transition concepts (eg. Westoby et al. 1989, West 1999 and Friedel 1991) provided a framework for organizing complex ecological relationships into a model that predicts ecosystem response to natural disturbances or management actions (Stringham et al. 2003). The state and transition model proposed by Stringham et al. (2003) (Figure 37) incorporated an ecosystem processes approach whereby thresholds and transitions were defined by changes to one or more of the primary ecological processes (energy flow, nutrient cycling, and hydrology).

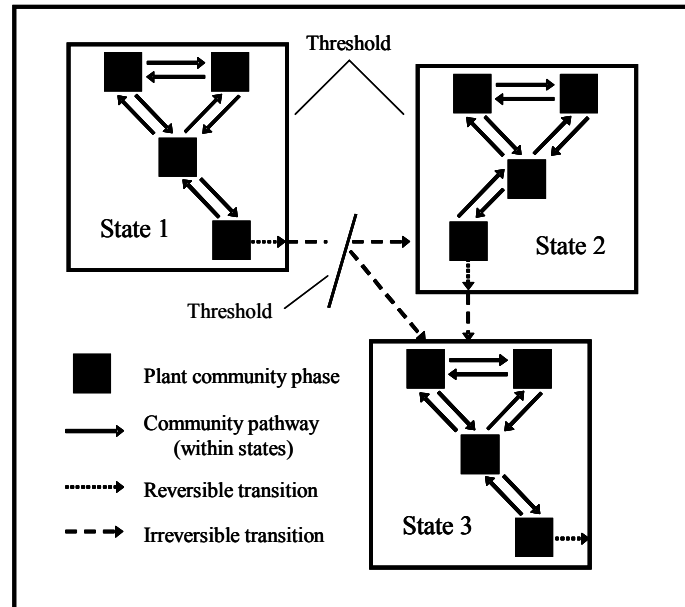


Figure 37. Conceptual state and transition model showing multiple stable states, transitions, and thresholds. Modified from Stringham et al. (2003).

Stringham et al. (2003) defined the components of their model as follows. A state is a recognizable, resistant and resilient complex of soil and vegetation components and is bound by a threshold. Within a state, ecosystem structure and function are thought to exist within the range of natural variability. Plant community phases can shift along community pathways in response to natural and/or management pressures whose impacts on the primary ecological processes are within the recovery capacity (resistance and resilience) of the state. Thresholds are defined as a boundary in space and time between any and all states, or along irreversible transitions, such that one or more of the primary ecological processes has been irreversibly changed and must be actively restored before return to a previous state is possible. Reversible transitions exist within the confines of a state (i.e. system has not crossed a threshold) and are characterized by autogenic system recovery of

degraded processes upon removal of the associated stress. Alternatively, a threshold is crossed when a system is unable to recover damaged processes.

Thresholds are a fundamental component of state and transition models; they define the existence of multiple stable states and describe the mechanisms by which the resilience of the initial state is lost. The concept of an ecological threshold, although not always termed so, has been used variously throughout the literature (e.g. Holling 1973, May 1977, Westoby et al. 1989, Archer 1989, Friedel 1991, Laycock 1991, Tausch et al. 1999, Brown et al. 1999 and Bestelmeyer et al. 2003). Most recently, Briske et al. (2006 and 2007) have proposed a unifying framework for the assessment and application of ecological thresholds based on ecosystem resilience. In this application thresholds describe ecological conditions where ecosystem resilience limits have been exceeded and system structure and function are altered beyond the capacity for self repair (Briske et al. 2007). Ecological resilience is defined by the ecosystem's ability to tolerate disturbance or stress and is described as the amount of change or disruption required to facilitate the alteration of ecosystem stability from one suite of mutually reinforcing feedbacks to another (Peterson et al. 1998 and Briske et al. 2007). Thresholds are breached when stabilizing forces associated with negative feedbacks are diminished in favor of destabilizing positive feedbacks and this feedback switch can be triggered by alterations to biotic or abiotic system components, individually or in combination (Briske et al. 2007). The positive feedback driven trajectory of change along the post-threshold irreversible transition (Stringham 2003) promotes continued degradation of the properties associated with the pre-threshold state until a stable alternative state is created and maintained by a new suite of structural and functional components that define an alternative ecological resiliency. Progression along the post-threshold irreversible transition corresponds to an increasing difficulty in restoration.

State and transition models may be an appropriate tool for modeling contemporary ponderosa pine ecosystem dynamics (Arno et al. 1985, Johnson 1994, Johnson et al. 1994, Stephenson 1999, Tiedemann et al. 2000, Griffis et al. 2001, Allen et al. 2002 and Kaye et al. 2005). In the time since European settlement,

grazing, logging, and active fire suppression practices have combined to effect a substantial increase in the fire return interval and, along with favorable conditions for ponderosa pine seedling establishment, have generated substantial increases in pine density and canopy cover, reductions in understory growth and vigor, and have altered hydrologic and nutrient cycling processes and understory species composition. These alterations have lead to increased insect and disease outbreaks, limitations on available wildlife habitat, reduced forage production, and an increased risk and occurrence of severe stand-replacing wildfires (Weaver 1943, Dickman 1978, Covington and Moore 1994, Covington et al. 1997, Tiedemann et al. 2000, and Allen et al. 2002).

Recognition of the unhealthy status of many arid forest systems and concern over the risk of stand-replacing wildfire has lead to increased implementation of forest thinning and under-burning and has also generated significant interest in system restoration through the reintroduction of historic fire patterns. However, in many cases the stabilizing negative feedback mechanisms associated with fire maintained open ponderosa pine stands (i.e. fire promoted open stand structures favor abundant herbaceous understories which in turn provide the fine fuels required for frequent low-intensity stand maintaining surface fire) are no longer functioning and it is unlikely that simply re-introducing a more natural fire regime will initiate system self recovery.

Although a threshold triggered by the loss of frequent low-intensity surface fire is commonly alluded to in the literature, further alterations to residual pre-threshold state properties are likely which present additional constraints to restoration activities. In particular, the potential loss of understory species associated with increasing ponderosa pine abundance represents an additional progression along the post-threshold transition. However, relatively little research is available that has explicitly evaluated understory species compositional changes associated with contemporary ponderosa pine forest structural alterations. Moreover, state and transition models have not previously been used to describe ponderosa pine dynamics, thus, we posited a state and transition model for an eastern Oregon

ponderosa pine forest and developed a research program designed to assess the proposed model with specific focus on the potential loss of understory species.

Hypothesized State and Transition Model

A state and transition model for an eastern Oregon ponderosa pine ecosystem is presented in Figure 38. This model is based on the framework of Stringham et al. (2003) and the resilience-based threshold approach of Briske et al. (2007). State 1 represents a system dominated by large well-spaced ponderosa pine trees and a vigorous understory of perennial bunchgrasses that is maintained structurally and functionally by periodic low-intensity surface fire. Several community phases are identified that differ primarily in the abundance of small-diameter ponderosa pine reproduction which varies in concordance with the time since the last fire event. Localized variability in understory species abundance occurs in association with pine density where understory components are diminished under more dense pine canopies. At the landscape scale the relative abundance of plant community phases remains comparatively stable with a preponderance of large-size patches of widely spaced mature pine trees with low sapling densities and vigorous perennial bunchgrass understory and few smaller-sized patches of dense younger trees with diminished understory components. Fluctuation among these community phases, driven by periodic low-intensity surface fire, is represented conceptually by plant community phases (PIPO/PBG) that cycle along community phase shifts (Figure 38). The negative feedback associated with State 1 stability is related primarily to fire maintained open stand conditions that promote the vigor of understory herbaceous species. The herbaceous understory in turn provides the necessary fuel conditions (i.e. type and continuity) to support frequent low-intensity surface fire, the characteristic fire regime that maintains the open nature of ponderosa pine forests.

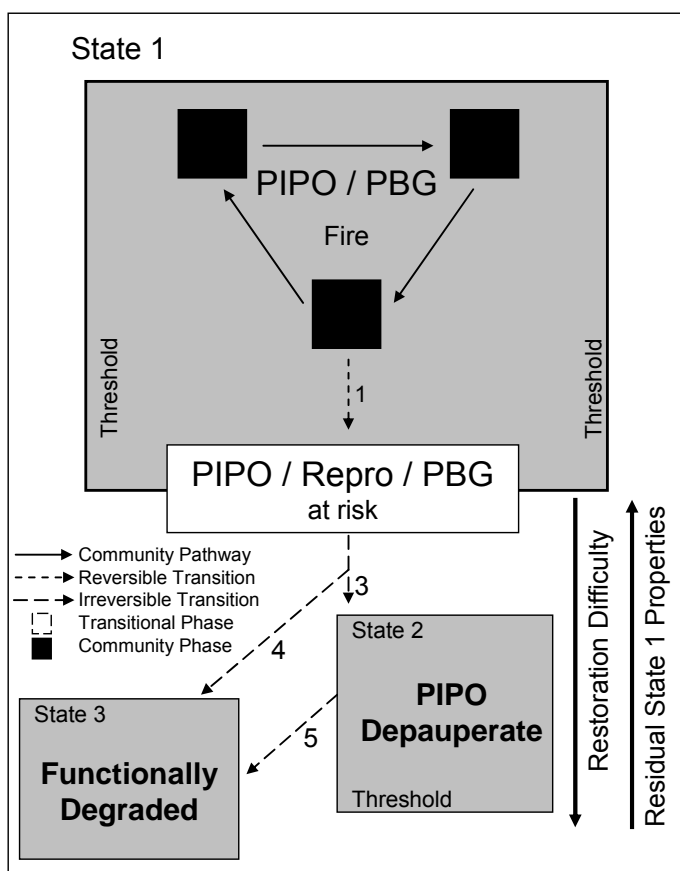


Figure 38. Proposed state and transition model for an eastern Oregon ponderosa pine ecosystem. The general framework including plant community phases, community shifts and reversible and irreversible transitions follows Stringham et al. (2003). PIPO/PBG identifies community phases of ponderosa pine forests that possess a robust perennial bunchgrass understory and whose function and structure are maintained by frequent fire and exist within the range of natural variability of State 1. PIPO/Repro/PBG at-risk phase represents ponderosa pine forests with a high abundance of small-diameter trees and pine reproduction along with residual perennial bunchgrass understory components. This phase exists at the end of reversible transition 1 and along a threshold which is triggered by a reduction in periodic low-intensity surface fire. PIPO depauperate state (State 2) represents ponderosa pine stands with very high pine abundance and depauperate understory conditions, while the functionally degraded state (State 3) identifies ponderosa pine stands that have undergone high severity stand replacement fires, indicated by irreversible transitions 4 and 5, and are subjected to diminished ecosystem function which substantially increases the risk of soil erosion. Irreversible transition 3 is an extension of reversible transition 1 but represents sequentially greater ecosystem degradation from which system self recovery is not possible.

The prolonged absence of fire (i.e. fire return intervals that exceed the normal range of variability - in eastern Oregon ponderosa pine forests, the mean fire return interval typically ranges between 10 and 17 years; Weaver 1943, Hall 1973, Bork 1984, and Heyerdahl et al. 2001) results in increased abundance of understory pine regeneration, decreased areal extent of open ponderosa pine patches and reduced perennial bunchgrass understory. This trajectory is represented by reversible transition 1 culminating in the PIPO/Repr/PBG at-risk phase (Briske et al. 2007) (Figure 38). Many of the structural and functional properties associated with State 1 remain within the at-risk phase and the reversibility property of transition 1 is related to the retention of system stability upon the subsequent fire event. Fire behavior that maintains the essence of State 1 canopy structure while substantially thinning the sapling and pole sized patches, would favor understory re-establishment from residual populations and together with fire-based fuel reductions would contribute to the maintenance of the negative feedback and system stability. However, the reversibility of transition 1 is constrained by burn conditions (i.e. temperature, relative humidity, wind, and fuel conditions) and post-fire residual tree and understory plant and propagule availability. Consequently, the at-risk community phase is positioned along the threshold (Figure 38) to capture the tenuous nature of residual ecosystem resilience associated with at-risk communities.

The absence of a fire that initiates recovery along reversible transition 1 will trigger a threshold defined by the loss of the negative feedback associated with frequent fire, and result in structural and functional conditions external to the natural range of variability (Weaver 1943, Covington et al. 1997 and Tiedemann et al. 2000). In systems that have crossed this threshold, the next fire may be a destabilizing high severity stand replacement fire that does not promote the maintenance of an open ponderosa pine forest. Furthermore, increasing pine occupancy alters the under-canopy growing environment and effects increased competitive interactions with understory species which combine to diminish the understory component and eliminate the fine fuel source that is critical to the stabilizing feedback that functions within State 1.

In the absence of post-threshold fire, ponderosa pine continue to invade open patches and fill-in patches already subjected to increased pine density. This trajectory is represented by irreversible transition 3 (Figure 38). The spatial pattern of pine patches across the landscape is altered as the size of the dense patches increase at the expense of the open mature pine patches prevalent in the pre-threshold system. Competition for soil moisture and nutrients and reductions in the under-canopy light, soil nutrient and soil moisture availability eventually eliminate the perennial bunchgrass understory characteristic of the pre-threshold vegetation. The remaining dense ponderosa pine monoculture is represented by a new state, PIPO depauperate (State 2, Figure 38). Autogenic recovery from these conditions through natural fire is not probable (i.e. irreversibility) as fuel loads and fuel continuity nearly assure high severity stand replacement fire (transition 5) and the loss of understory species combined with relatively poor seed banking abilities of many perennial herbaceous plants (Rees 1994) effectively precludes understory recovery from on-site resources.

Irreversible transition 4 represents a high severity stand replacement fire event that removes most if not all pre-threshold structural properties resulting in a functionally degraded state (Figure 38). Similarly, irreversible transition 5 is associated with a breach of the threshold surrounding State 2 and triggered by a stand-replacing fire event. Severe stand replacement wildfire can result in excessive soil exposure which increases the risk of soil erosion, reduces hydrologic function and nutrient cycling, and limits plant growth. The probability of excessive soil loss associated with the functionally degraded state varies with slope steepness, precipitation, and rate of vegetative colonization. The approach to transition 5 flows through the PIPO depauperate state and is largely a function of vegetation dynamics over time in the absence of fire.

The existence of a threshold triggered by a reduction in the occurrence of low-intensity surface fire and a trajectory along irreversible transition 4 toward a functionally degraded condition is commonly addressed in the scientific literature (e.g. Covington and Moore 1994, Johnson 1994, and Allen et al. 2002). However,

relatively few have assessed understory species loss through irreversible transition 3 and its existence is important with respect to restoration activities on sites that have yet to progress along irreversible transitions 4 or 5 in response to stand replacement fire.

Research Protocols

We developed three separate research components designed to test for the existence of transition 3 (Figure 38) and to elucidate the associated mechanisms. We initiated a field-based observational study to assess understory species distribution along a gradient of ponderosa pine site occupancy and incorporated parameters representing under-canopy growing conditions to evaluate relationships among understory species composition, under-canopy environment, and ponderosa pine abundance (Carr 2007b). Data from 28 plots were grouped according to similarities in understory species composition using hierarchical cluster analysis and specific plant species affinity for the environmental conditions associated with each group was evaluated through indicator species analysis (ISA). Non-metric multidimensional scaling ordination (NMS) was employed to evaluate relationship among understory species composition, ponderosa pine occupancy and under-canopy environmental parameters.

A greenhouse experiment testing the effects of variable light and nitrogen treatments on the growth and vigor of *Festuca idahoensis* Elmer, the dominant understory perennial bunchgrass in the pre-threshold state, was conducted to corroborate field assessments of ponderosa pine influence on under-canopy growing conditions and the associated effect on perennial bunchgrass abundance (Carr 2007c). *Festuca idahoensis* shoot biomass, root biomass, foliar cover, and shoot length were measured at the end of 83 days while foliar cover and shoot length were also evaluated bi-weekly throughout the experiment. Two levels of shade (80% and no shade) and 2 levels of nitrogen (50kg N/ha as urea and no nitrogen) were applied in a split plot arrangement to *F. idahoensis* plugs (~2 cm basal diameter) potted in 3.98

liter containers filled with soil from a ponderosa pine stand with a depauperate understory.

To test the irreversibility property of transition 3, a seed bank analysis was performed on soils from high ponderosa pine abundance stands with depauperate understories and relatively open canopy stands with intact perennial bunchgrass understories. Seed bank composition was evaluated with the seedling emergence method on samples grown in a growth chamber programmed with temperature and light settings selected to represent average late spring day length and temperature for the eastern Oregon study area (Carr 2007d). Differences in seed bank species composition were evaluated with multiple response permutation procedures (MRPP).

Study Area

The field based study was performed, and *F. idahoensis* plant materials and seed bank samples were collected from plots established in a Ponderosa pine / Idaho fescue plant association (Johnson and Clausnitzer 1992) in eastern Oregon (44°12'52" N Latitude; 118°59'16" W Longitude). The plots were in an area of gently sloping north facing hillsides ranging between 1500 and 1560 meters in elevation. The average daily high and low summer and winter temperatures, recorded between 1971 and 2000 at Seneca (~ 8 km south of the study area) were 24°C and 1.5°C and 4°C and -9°C respectively (Oregon Climate Service 2007). Approximately 35 cm of precipitation is received annually, most occurring in the winter months and primarily in the form of snow (Oregon Climate Service 2007). Soils of the study area are composed of a variable thickness ash mantle associated with the eruption of Mt. Mazama 6000 – 7000 years ago (Klimasauskas et al. 2002), overlaying serpentinite gravel and cobble. Soils were classified as either a fine-loamy, mixed, superactive, Vitrandic Haploxeroll or a clayey-skeletal, smectitic, lithic Ultic Argixeroll (Carr 2007a). The depth of the ash mantle is a distinguishing feature of these soil types; the Haploxeroll has a much deeper ash layer. Both soils exhibit a xeric soil moisture regime and frigid soil temperature regime.

The study area is a climax ponderosa pine forest consisting of large-diameter ponderosa pine trees scattered across a landscape dominated primarily by patches of smaller pines. Over 90% of the trees in the study area are less than 100 years old while approximately 3% have survived for more than 250 years (see Appendix A for ponderosa pine age distribution in the study area). The area was historically grazed by sheep and cattle, however, since the 1960s it has been grazed primarily by cattle in the summer from July to October. No evidence of recent fire or logging activity was apparent in the study plots, however the area was logged in 1978 and a variety of silvicultural activities have occurred in the general vicinity (Carr 2007a).

The greenhouse experiment and the seed bank analysis were performed on the Oregon State University campus in Corvallis, Oregon (44°34'12" N Latitude; 123°16'48" W Longitude).

Evidence in Support of the Existence of Transition 3

Cluster analysis identified 4 general plot groupings that were characterized by understories with high abundance of perennial bunchgrasses, high abundance of perennial bunchgrass and elevated forb diversity, low abundance of perennial bunchgrass, or no perennial bunchgrass. The perennial bunchgrass functional group was comprised of *F. idahoensis*, *Agropyron spicatum* (Pursh.) Scrib. & Smith, *Sitanion hystrix* (Nutt.) Smith, *Elymus cinereus* Scribn. & Merr., *Koeleria macrantha* (Ladeb.) J.A. Schultes, and *Poa scabrella* (Thurb.) Benth., however, 81% of the total cover and 61% of the total density for this functional group was attributed solely to *F. idahoensis*.

Results from NMS ordination indicated that understory species groups were distributed along a gradient of pine occupancy (Figure 39). Plots with abundant perennial bunchgrass understories were found in stands with low pine stem density, canopy closure and basal area while those without perennial bunchgrasses were found under closed canopy conditions with elevated stem densities and high basal areas (Table 35).

The patterns observed in the cover and density of the dominant perennial bunchgrass, *F. idahoensis*, also showed significant reductions associated with increasing ponderosa pine occupancy (Figure 39). High ponderosa pine occupancy stands were essentially void of *F. idahoensis* plants while more open stands exhibited very high abundances of this species.

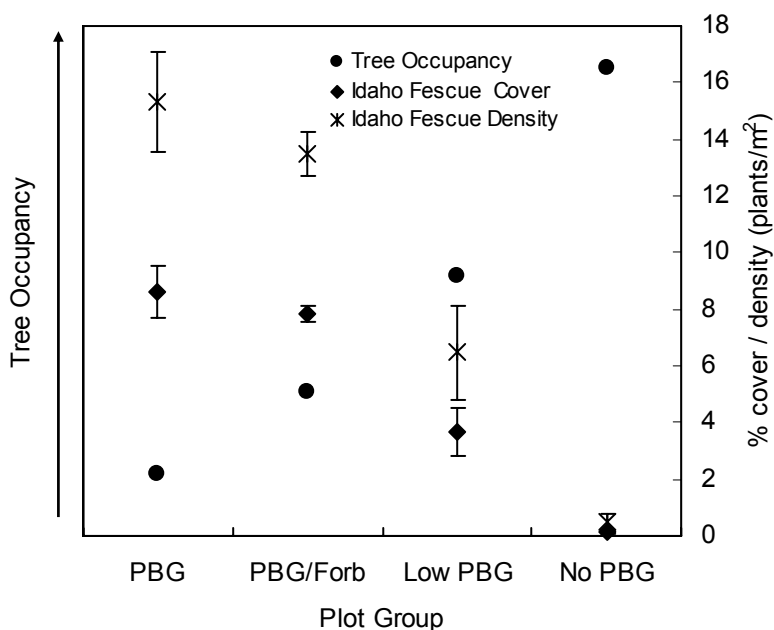


Figure 39. Relationships among tree occupancy, Idaho fescue abundance and understory species groups identified through cluster analyses. Tree occupancy is the first component of a principal components analysis incorporating tree basal area, density and canopy closure. PBG = perennial bunchgrass. Error bars represent the stand error.

Table 35. Average overstory ponderosa pine conditions in the understory species composition based groups identified through cluster analyses.

	Density (stems/ha)	Canopy Closure (%)	Basal Area (m ²)
PBG	422	55.62	0.30
PBG/Forb	1130	59.54	0.44
Low PBG	3021	67.97	0.66
No PBG	3656	78.87	0.98

These data provide evidence in support of the trajectory of vegetation change posited in the state and transition model in Figure 38. The abundance of understory perennial bunchgrasses appears to be related to the profusion of ponderosa pine associated with longer time since fire. In the absence of fire, ponderosa pine stands tend to shift toward a structure of increased pine density, canopy closure and basal area and diminished perennial bunchgrass cover and density. Plots within the group identified by high abundance of perennial bunchgrasses (PBG and PBG/Forb) likely exist within the range of variability associated with the normal fire cycle of these ponderosa pine forests. These stands are resilient and possess the structural characteristics that support the stabilizing feedback associated with frequent low-intensity surface fire. Plots identified as low perennial bunchgrass abundance plots, and associated with intermediate pine occupancy are thought to exist along the reversible transition 1 or in the at-risk phase, with the specific stand location dependent on the juxtaposition of pine and understory abundances. Plots from high pine occupancy stands and lacking a perennial bunchgrass understory were positioned in the PIPO depauperate state and are plots that have crossed the threshold triggered by the loss of low-intensity surface fire as pine abundance was elevated enough to effectively remove the dominant understory physiognomy and create a fuel structure that eliminated the probability of low-intensity surface fire. Plot group locations have been incorporated in the state and transition model in Figure 40 and the structural attributes associated with each group are presented in Table 36.

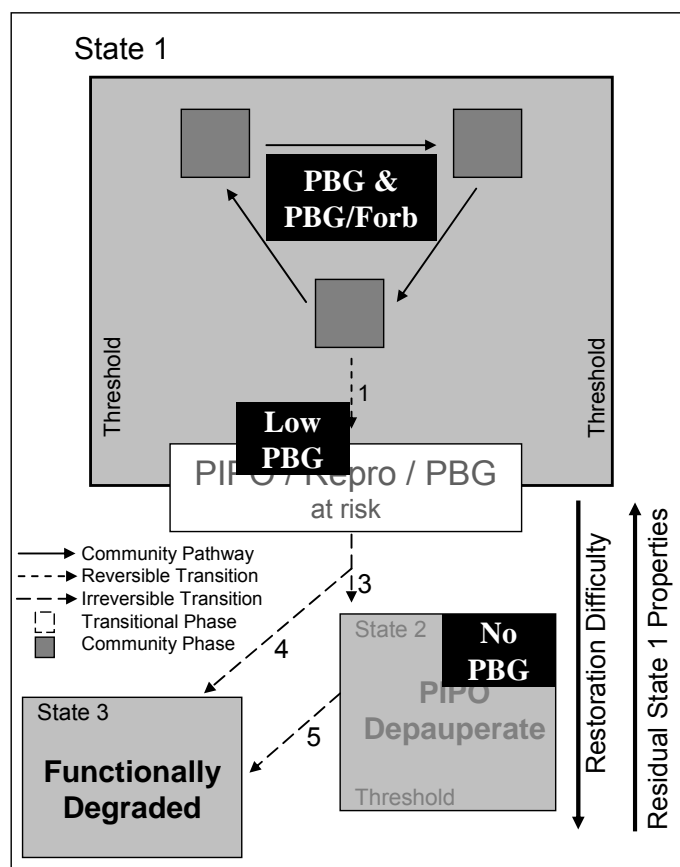


Figure 40. Proposed state and transition model for an eastern Oregon ponderosa pine ecosystem. The general framework including plant community phases, community shifts and reversible and irreversible transitions follow Stringham et al. (2003). Groups identified by cluster analysis of understory species data are identified and placed within the state and transition framework based on ecosystem resiliency and degradation in pre-threshold properties. PBG & PBG/Forb represent ponderosa pine stands with low pine abundance and understories dominated by perennial bunchgrasses or perennial bunchgrasses combined with high forb abundance and diversity. Low PBG identifies ponderosa pine stands with a high abundance of smaller diameter pine trees and a meager expression of perennial bunchgrasses in the understory. No PBG indicates ponderosa pine stands with very high pine occupancy (density, basal area, and canopy closure) and no perennial bunchgrasses in the understory. The remaining model components are as described for Figure 38.

Table 36. Ponderosa pine stand structural properties associated with plot group position within the state and transition framework presented in Figure 40. PBG refers to perennial bunchgrasses.

	Density (stems/ha)	Canopy Closure (%)	Basal Area (m ²)	Under-Canopy Light intensity (MJ/m ² /yr)	<i>Festuca idahoensis</i> density (#/m ²)	<i>Festuca idahoensis</i> cover (%)
PBG	422	55.62	0.30	4259.4	15.3	8.6
PBG/Forb	1130	59.54	0.44	4206.0	13.5	7.8
Low PBG	3021	67.97	0.66	2759.9	6.5	3.6
No PBG	3656	78.87	0.98	1955.0	0.5	0.1

We did not explicitly evaluate the fire chronology of the ponderosa pine stands used in this study. We can not say for certain whether the perennial bunchgrass - low pine occupancy plots were a result of a more frequent fire regime relative to those plots with elevated pine and lower bunchgrass abundances, however there was no obvious evidence of recent fire in any of the plots evaluated in this study. Although tree densities differed among groups (Table 36), the dominant age of trees was similar (94%, 95%, 90%, and 96% of the trees sampled were ≤ 100 years of age in group PBG, PBG/Forb, Low PBG, and No PBG respectively; see Appendix A for tree age distribution by group), suggesting that differing fire regimes were not the cause of the structural patterns. The lack of recent fire across all sites combined with their similar site potentials suggests that the more open stands in this study had not yet been invaded by ponderosa pine trees (Laughlin et al. 2006) and over time and in the absence of future fire it is likely that these stands too will be subjected to excess pine abundance.

Mechanisms Associated with the Progression of Transition 3

Ponderosa pine ingress may influence understory growing conditions through alterations in light availability (Riegel 1995 and Naumberg and DeWald 1999), hydrology (Barrett and Youngberg 1965, Helvey 1975, and Baker 1986) and nutrient cycling (Kaye and Hart 1998 and Selmants et al. 2003). These changes can diminish understory growth and promote site progression along irreversible transition 3 (Figure 40). To evaluate the mechanisms associated with transition 3 progression, we compared understory species distribution with patterns evident in resource availability (light, water, nitrogen) along the gradient of ponderosa pine occupancy sampled as part of the field based component of this research program (Carr 2007b) and experimentally tested the effects of differing nitrogen and light regimes on the growth and vigor of *F. idahoensis* plants (Carr 2007c).

Under-Canopy Light Availability

The results of NMS ordination and joint plot overlays displaying correlations between environmental parameters and the ordination axes indicated that ponderosa pine site occupancy was related to light and nitrogen availability and soil temperature but was unrelated to the dominant soil moisture gradient.

As would be expected, increased canopy closure associated with high pine occupancy effected a substantial decrease in under-canopy light availability (Figure 41). Plots with high perennial bunchgrass abundances (PBG and PBG/Forb) experienced very similar light conditions and were present under the highest light availability conditions encountered in the study. Low abundance perennial bunchgrass and plots with no perennial bunchgrasses existed in sequentially lower light environments (Figure 41).

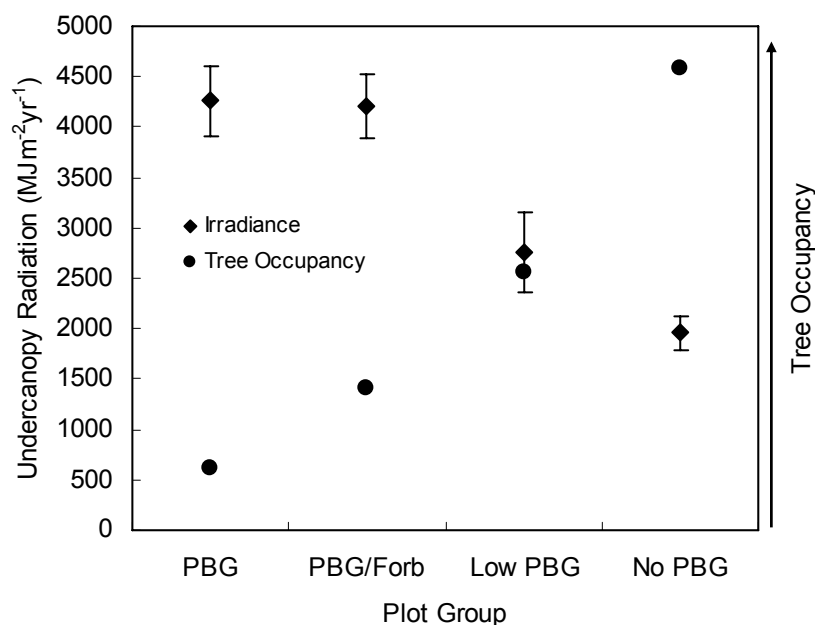


Figure 41. Relationship between plot groupings, under-canopy light availability and tree occupancy. Tree occupancy is the first component of a principal components analysis incorporating tree basal area, density, and canopy closure. Error bars represent \pm standard error.

Similar results were attained when experimentally testing the influence of light availability on the vigor of *F. idahoensis* where a significant shade effect ($p < 0.05$) was observed for root biomass, shoot biomass, foliar cover, and growth rate of *F. idahoensis* (Carr 2007c). Plants in the shaded treatment group had lower shoot biomass, root biomass, foliar cover, and a reduced growth rate over time as indexed by foliar cover (Figure 42), indicating that *F. idahoensis* preferred high light environments.

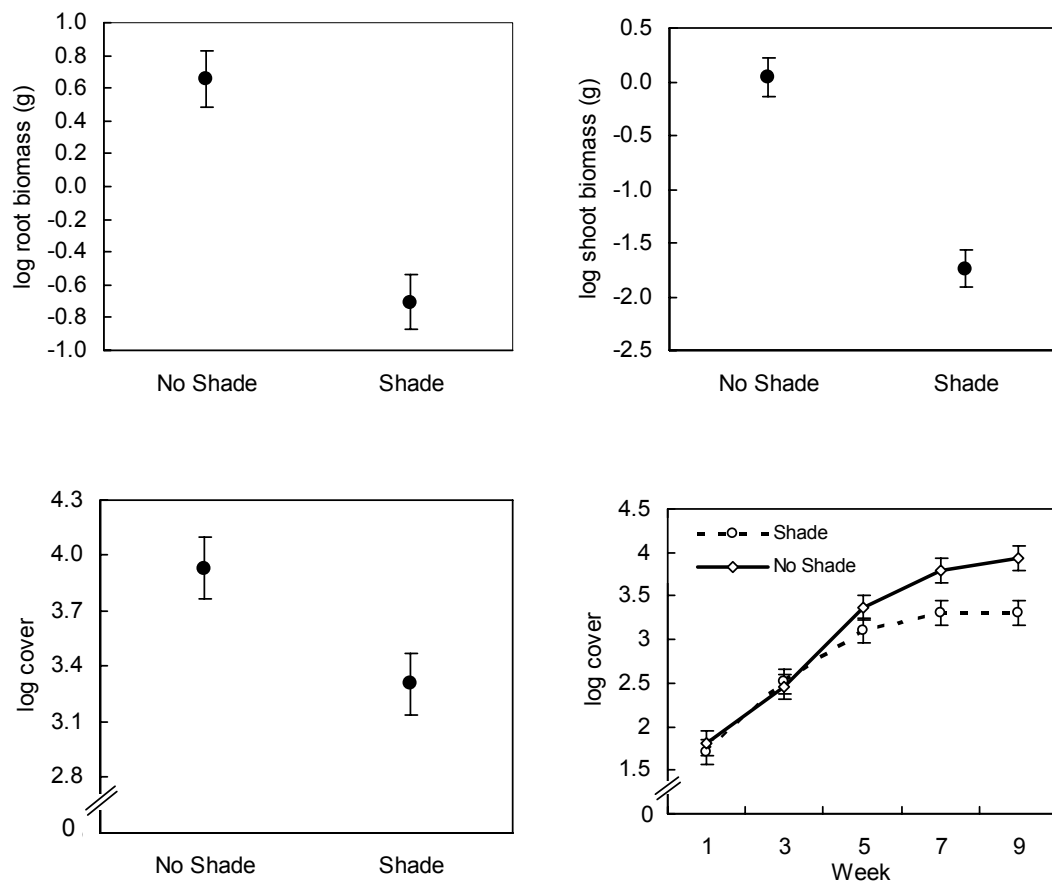


Figure 42. Clockwise from top left are charts displaying the shade effect on root biomass, shoot biomass, foliar cover, and foliar cover over time. Error bars are \pm standard error. Data are presented in the log transformed form.

Mineral Nitrogen Availability

Plots with lower pine occupancy and increased abundance of perennial bunchgrasses exhibited higher mineral nitrogen availability. The correlation between nitrogen availability and the gradient in tree occupancy was weak, however, owing to the strong non-linearity in the pattern of nitrogen availability (Figure 43). Mineral nitrogen availability was relatively similar for the two plots on each end of the pine occupancy gradient, however a large drop in nitrogen availability was evident associated with the transition from perennial bunchgrass dominated plots to those with a limited bunchgrass component (Figure 43).

Experimental nitrogen addition stimulated a short term increase in the growth rate of Idaho fescue plants, indexed by cover and leaf length, however unfertilized plants eventually accumulated enough nitrogen to meet their growth requirements as foliar cover values and leaf length values were similar in both nitrogen levels by the end of the experiment. No nitrogen effect was evident on root biomass, shoot biomass, final leaf length, or final foliar cover and the general lack of a lasting nitrogen effect indicated that soils from dense ponderosa pine forests and lacking understory were not nitrogen deficient.

Although ponderosa pine ingress did influence mineral nitrogen availability, the experimental addition of nitrogen to soils from sites with reduced mineral nitrogen did not stimulate *F. idahoensis* growth. These soils, although diminished in nitrogen availability, were apparently not nitrogen limited with respect to Idaho fescue growth.

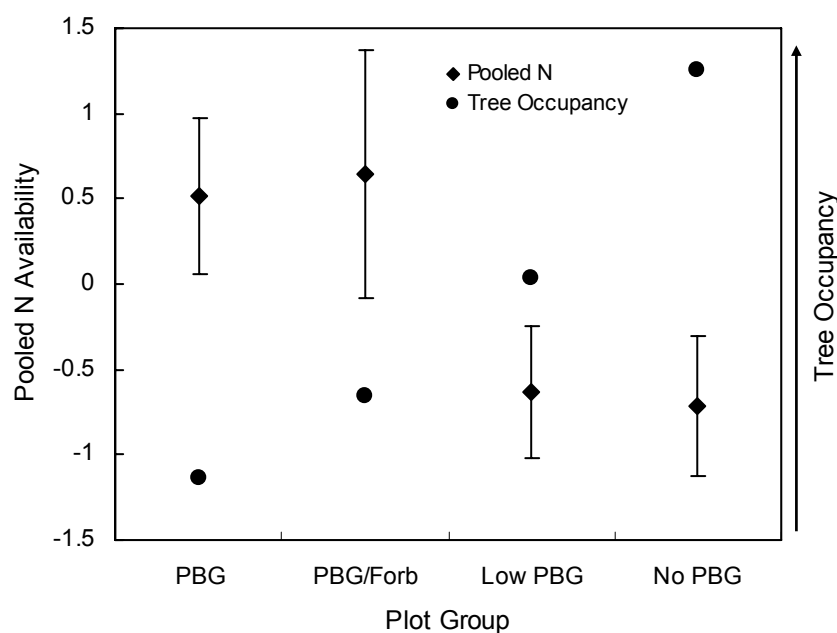


Figure 43. Relationships among tree occupancy, pooled mineral nitrogen availability and plot group. Error bars represent \pm standard error.

Soil Temperature

Soil temperatures exhibited moderately strong relationships with tree occupancy indicating that soils were cooler under increasing canopy conditions. Similarly, plots in high perennial bunchgrass groups tended to exhibit hotter temperatures compared to those with low or no perennial bunchgrasses (Figure 44). Lower temperatures in high pine occupancy stands were likely due to the interactive effect of increased insulation by the thick mat of pine needles on the forest floor and reduced radiation intensity associated with elevated canopy closure.

Soil Moisture

Gravimetric soil moisture was not correlated to the gradient in ponderosa pine occupancy (Carr 2007b). The strongest relationship between soil moisture and understory species distribution was observed for early season soil moisture and this relationship was nearly orthogonal to the gradient exhibited in tree occupancy. Elevated early season soil moisture was associated with high diversity and abundance of forb species, most notably associated with plots classified in the PBG/Forb group.

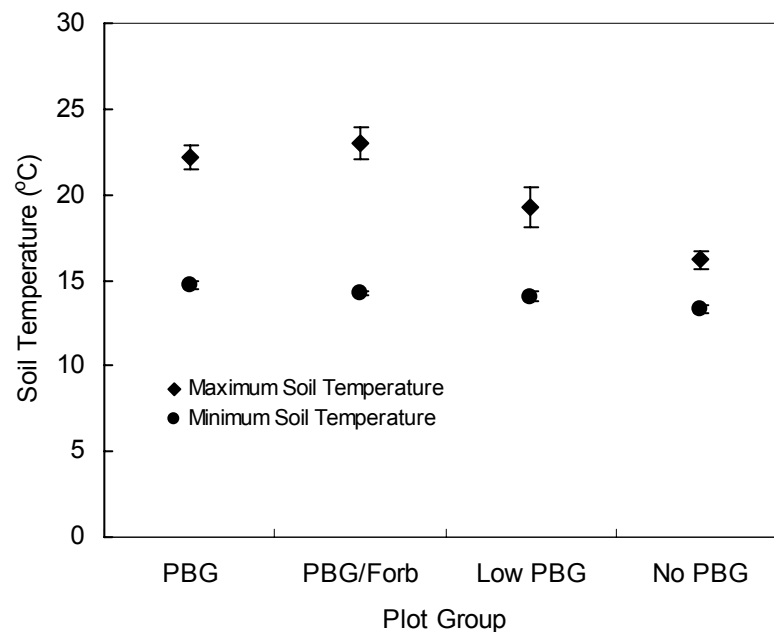


Figure 44. Relationships among average daily minimum and maximum soil temperatures and plot group.

The preceding data support the contention that ponderosa pine ingress modifies the under-canopy environment and this modification may influence understory species composition promoting the loss of perennial bunchgrass species. Increased pine abundance reduced under-canopy light and soil nitrogen availability and soil temperature but did not influence soil moisture status. Reduced light availability negatively influences plant photosynthetic capacity and carbon fixation (Coyne et al. 1995 and Lambers et al. 1998) and is a likely mechanism associated with perennial bunchgrass reduction under low light conditions (Carr 2007c).

Decreased nitrogen mineralization associated with increased pine occupancy has been attributed to associated changes in substrate quality, as grass litter is typically low in lignin and high in nitrogen and as a result decomposes more rapidly than pine needle litter (Klemmedson et al. 1985 and Kaye and Hart 1998). Moreover, soil temperature also plays a significant role in decomposition dynamics (Wolf and Wagner 2005) and soil temperatures in plots with reduced nitrogen availability also

experienced lower temperatures. Interestingly, the soils in dense pine stands did not appear to be nitrogen limited with respect to *F. idahoensis*, the dominant understory species in the perennial bunchgrass dominated understory. Although increased pine density does appear to effect a change in the nitrogen availability of the site, this change is apparently not sufficient enough to limit plant growth (Kaye et al. 2005).

Soil temperature can also influence plant growth and is a major driver of plant distribution (Lambers et al. 1998). However, it is unclear what role soil temperature plays in the observed differences in understory plant species composition along the pine occupancy gradient. The optimum temperature for root growth of plants in temperate regions is between 10°C and 30°C (Bowen 1991 and Lambers et al. 1998), within the range of temperatures encountered in the present analyses. Furthermore, Nasri and Doescher (1995), who evaluated the growth response of *F. idahoensis* to experimentally controlled temperature variation, found very few differences among fescue plants grown at 5°C, 10°C, or 15°C. As the coolest temperatures on our sites were around 13°C, it is unlikely that the temperatures associated with higher pine occupancy played a major role in the associated decline in perennial bunchgrass abundance.

From these analyses, it appears the ponderosa pine influenced alterations to under-canopy light availability is a major environmental driver of perennial bunchgrass loss along irreversible transition 3 (Figure 38). Although pine influenced alterations to the under-canopy environment that negatively impact understory species appear limited to above ground resources, interspecific competition for soil moisture and nutrients may additionally influence understory species distribution (Riegel et al. 1991, 1992, and 1995), however our data did not explicitly evaluate competitive relationships.

Materials for Restoration

Recovery of system stability from post- threshold conditions becomes increasingly difficult as pre-threshold properties are lost (Briske et al. 2006). The trajectory of vegetation change along the path of irreversible transition 3 resulting in State 2(Figure 38) is associated with the loss of perennial bunchgrasses and their recovery is reliant on an available plant propagule source. A source for plant species recovery from degraded conditions is the soil seed bank, however plant species vary in their seed banking ability and many perennial species do not form a persistent soil seed bank (Parker et al. 1989 and Rees 1994).

MRPP analysis indicated that seed bank species composition differed ($A = 0.07896$, $p = 0.00516$, MRPP) between pre-threshold ponderosa pine stands and those with a deficiency in the understory component (i.e. sites that have crossed the threshold triggered by the loss of low-intensity surface fire and progressed along irreversible transition 3). The seed bank species composition of pre-threshold stands effectively represented the understory vegetation. *F. idahoensis*, *K. macrantha* and *Carex rossi* Boot, comprised 25% of the total understory vegetation density and 52% of the total understory cover and were also present in the seed bank of pre-threshold communities (Table 37). Together these species contributed approximately 24% of the total seed density and after accounting for the extremely high abundance of *Lithophragma parviflora* (Hook.) Nutt. ex Torr. & Gray, they contributed 64% of the remaining seed density. Moreover, when including *Achillea millifolium* L., present in both seed bank and vegetation, the seed bank species composition included species that contributed almost 60% of the understory plant density. In contrast, the seed bank of the post-threshold understory depauperate stands did not provide species that represented the dominant vegetation of the pre-threshold understories. With the exception of *C. rossi*, which occurred in limited abundances in the pre-threshold vegetation, none of the species common in the depauperate seed bank were present in any abundance in the pre-threshold vegetation (Tables 37 and 38).

From these data it appears that propagules of the dominant understory vegetation of State 1 communities are not available in State 2 depauperate understory sites and can not be relied upon as a tool for their recovery. Ecosystem recovery along restoration pathway R3 (Briske et al. 2007) (Figure 45) will require a reduction in the ponderosa pine abundance to release pine control over the under-canopy environment and the addition of desired understory perennial bunchgrass seeds or other viable plant material.

Table 37 Frequency, relative abundance and density of common species and functional groups found in the seed bank of pre-threshold and post-threshold depauperate understories. Relative abundance is the proportion of total density represented by that species or functional group.

	Frequency (%)	Relative Abundance (%)	Density (seeds/m ²)
Pre-Threshold Understory			
<i>Lithophragma parviflora</i>	85.71	62.71	348
<i>Festuca idahoensis</i>	42.86	11.86	66
<i>Carex rossii</i>	28.57	5.08	28
Grasses	71.43	23.73	132
Forbs	100.00	74.58	414
Tree / Shrub	14.28	1.69	9
Post-Threshold Depauperate Understory			
<i>Lithophragma parviflora</i>	14.28	27.27	56
<i>Carex rossii</i>	28.57	18.18	38
<i>Silene menziesii</i>	14.28	13.64	28
<i>Poa nervosa</i> var. <i>wheeleri</i>	14.28	9.09	19
<i>Epilobium watsonii</i>	28.57	9.09	19
Grasses	42.86	27.27	56
Forbs	85.71	72.73	151
Tree / Shrub	0	0	0

Note: Grass functional group includes the sedge *C. rossii*.

Table 38 Relative density and cover of common species in the understory vegetation of pre-threshold and post-threshold depauperate understory ponderosa pine stands. Relative density and relative cover are measures of the proportion of total abundance represented by a particular species. Total cover and total density in each group are identified in the table by Group Total.

Species	Density	Cover
Pre-Threshold Stands		
<i>Festuca idahoensis</i>	17.12	40.91
<i>Poa scabrella</i>	5.24	3.61
<i>Koeleria macrantha</i>	3.63	5.63
<i>Achillea millifolium</i>	33.03	12.16
<i>Carex rossii</i>	3.95	5.10
<i>Calamagrostis rubescens</i>	12.62	2.28
<i>Phlox hoodii</i>	4.20	14.21
Group Total	532.86	128.10
Post-Threshold Depauperate Stands		
<i>Calamagrostis rubescens</i>	61.36	27.40
<i>Poa nervosa</i> var <i>wheeleri</i>	12.53	6.51
<i>Silene menziesii</i>	7.96	13.09
<i>Achillea millifolium</i>	2.99	4.07
<i>Carex rossii</i>	2.49	11.65
<i>Berberis repens</i>	1.20	11.79
<i>Festuca idahoensis</i>	1.98	10.11
Group Total	431.64	39.37

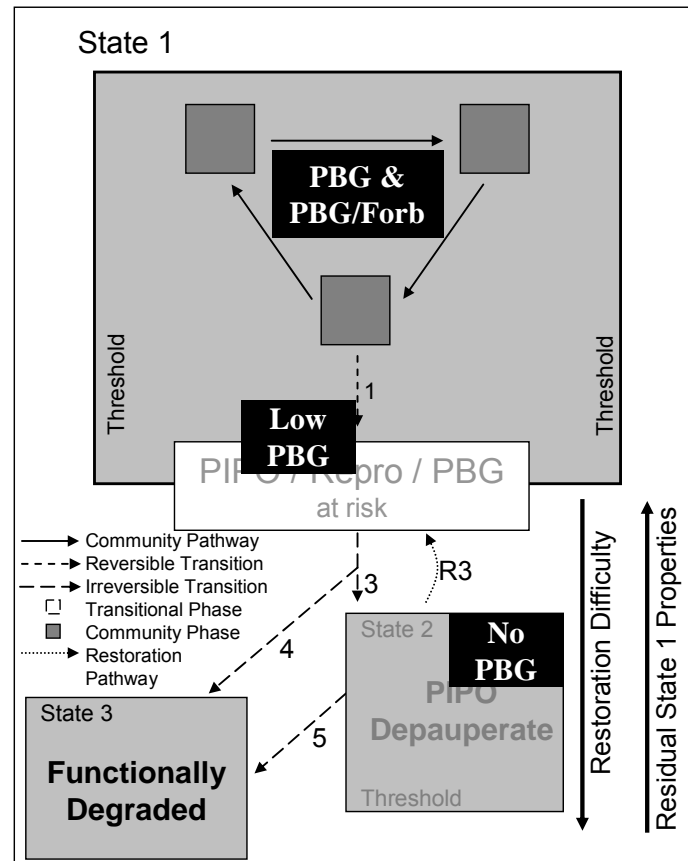


Figure 45. Proposed state and transition model for an eastern Oregon ponderosa pine ecosystem. The general framework including plant community phases, community shifts and reversible and irreversible transitions follow Stringham et al. (2003). R3 identifies the restoration pathway associated with the manipulation of ponderosa pine structure and related alterations in fuel conditions and the reintroduction of herbaceous understory species propagules or other viable plant material. The remaining model components are as identified in Figures 38 and 40.

Summary and Conclusion

The data considered in this paper represent the results of 3 separate studies designed to evaluate the effectiveness of state and transition models at describing ecosystem dynamics in ponderosa pine forests and test for the existence of additional ecosystem change beyond the threshold triggered by the loss of frequent low-

intensity surface fire commonly described in the literature. The data effectively described ecosystem dynamics in accordance with the hypothesized state and transition model presented in Figure 38.

In the absence of stand maintaining frequent surface fire events, increased ponderosa pine abundance can effect a significant loss in understory species. Increased pine abundance was related to substantially diminished understory conditions that were devoid of perennial caespitose grasses, the dominant understory physiognomy within the natural range of variability of this ponderosa pine forest. Depauperate understory conditions were represented as a new state surrounded by a threshold whose breach can be triggered by a subsequent stand replacement fire. The resultant irreversible transition (transition 4) leads to a functionally degraded state related to reduced hydrologic function and increased rates of soil erosion both of which function in a positive feedback (a cycle of increasing degradation) with reductions in vegetative cover.

The transition to the depauperate understory condition was related to ponderosa pine influenced moderations of the under-canopy environment that are detrimental to the persistence of understory species more common in open canopy situations. Evidence from these analyses indicated that alterations in under-canopy light availability is a major driver of understory species distribution. High light environments were positively correlated with the abundance of perennial bunchgrass species. Experimental manipulation of light availability also produced significant effects on the growth and vigor of *F. idahoensis*, the dominant understory perennial bunchgrass present on the study area, indicating that this species preferred high light environments.

Ponderosa pine restoration programs should include as a major focus of their activities, the re-introduction of understory species (Moore et al. 2006). In stands that have not experienced stand replacement fire events, ponderosa pine driven alterations to ecosystem processes (i.e. hydrology and nutrient cycling) do not appear irreparably damaged and restoration programs that reduce pine occupancy should promote conditions favorable for understory growth by increasing resource

availability. However, ecosystem restoration appears constrained by a lack of perennial bunchgrass plant and propagule availability and the restoration of depauperate understory pine stands will require the addition of desired understory perennial bunchgrass seeds or other viable plant materials as well as the reduction in ponderosa pine abundance.

The hypothesized state and transition model (Figure 45) adequately captured ecosystem dynamics in the eastern Oregon ponderosa pine forest evaluated in this study. An assessment of community phases, transitions and thresholds and evaluation of ecosystem dynamics within the framework of ecological resilience provided useful information for understanding potential ecosystem response to management activities (i.e. ecological restoration) or natural events (i.e. fire).

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CHAPTER 7: GENERAL CONCLUSIONS

The general objectives of the research program described in this thesis were to develop an improved understanding of herbaceous understory dynamics in Pacific Northwest ponderosa pine (*Pinus ponderosa* Dougl.) forests and to develop a state and transition model that adequately described ponderosa pine ecosystem dynamics and provided informative predictions of ecosystem response to natural (i.e. wildfire) or management induced (i.e. restoration) events. We developed 3 separate studies designed to: 1) evaluate understory differences along a gradient of ponderosa pine occupancy and to elucidate relationships with associated under-canopy environmental differences; 2) experimentally corroborate the relationships observed in the field based case study by testing the effects of variable light and nitrogen availability on the growth and vigor of *Festuca idahoensis* Elmer, the dominant understory species in open ponderosa pine stands of the study area; and, 3) to assess the understory recovery potential in stands that have lost their understory due to increased pine abundance. These data were combined to evaluate the utility of a hypothesized state and transition model in characterizing ecosystem dynamics and to elucidate restoration activities required to ensure successful recovery of understory species.

Differences in understory species composition associated with the gradient in ponderosa pine abundance were apparent. A major shift in understory character away from perennial bunchgrasses was evident in high pine occupancy stands. Plots with high understory species diversity and an abundance of perennial bunchgrasses, predominantly *F. idahoensis*, existed in stands of relatively low ponderosa pine occupancy. Elevated ponderosa pine abundance was related to under-canopy environmental differences including available light and nitrogen as well as soil temperature, however only light availability was identified as a potentially significant driver of understory vegetation dynamics. Study plots that existed in low ponderosa pine occupancy sites experienced relatively high under-canopy light intensity and possessed understories dominated by perennial bunchgrasses. Although mineral

nitrogen availability was higher in plots associated with lower pine abundance, no clear evidence of a nitrogen limitation in understory species was present.

Similarly, in a greenhouse experiment that tested the effects of variable light and nitrogen availability on *F. idahoensis* plants grown in soil from stands with depauperate understory conditions, light availability emerged as a significant parameter in determining plant growth and vigor. Plants grown in un-shaded conditions produced greater root biomass and shoot biomass, expressed larger indices of foliar cover, and possessed higher growth rates. Interestingly, nitrogen addition had very little effect on plant growth indicating that soils from dense ponderosa pine stands were not deficient in nitrogen and *F. idahoensis* plants grown in these soils were not nitrogen limited.

Although the seed bank species composition of intact stands represented the dominant character of the understory vegetation in these stands the seed bank from stands with depauperate understory conditions did not provide species that corresponded to the vegetation of intact understories. The lack of perennial bunchgrasses in the vegetation and seed bank of high occupancy ponderosa pine stands indicated that the plant materials required for the re-introduction of perennial bunchgrasses characteristic of the intact ponderosa pine stands must come from off-site sources and should be incorporated in restoration initiatives.

The results of these experiments provided evidence in support of the hypothesized state and transition model, particularly related to the progressive degradation of ecosystem structure along the post- threshold irreversible transition that culminated in a transitional phase characterized by high pine abundance stands lacking an herbaceous understory. The transition to the depauperate understory condition was related to ponderosa pine influenced moderations of the under-canopy environment that are detrimental to the persistence of understory species more common in open canopy situations. Evidence from these analyses indicated that alterations to under-canopy light availability is a major driver of understory species distribution. High light environments were positively correlated with the abundance of perennial bunchgrass species. As perennial bunchgrass species did not form a

persistent seed bank the seed bank can not be relied on for the recovery of perennial bunchgrasses from depauperate understory conditions.

Successful ecological restoration of ponderosa pine forests must also incorporate the herbaceous understory component. Restoration initiatives in Pacific Northwest ponderosa pine forests should consider that: 1) elevated ponderosa pine abundance associated with lengthened fire return intervals appears to modify the under-canopy environment and alter understory species composition; 2) the changes in under-canopy environment are not irreparable and restoration activities that modify pine canopy structure will improve conditions for understory growth, as light availability appears to be a significant driver of under story species distribution; and, 3) restoration is constrained by a lack of perennial bunchgrass seed availability in depauperate sites and successful recovery will likely require the introduction of seeds or other viable plant materials.

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APPENDICIES

APPENDIX A

Pedon Description: Vitrandic Haploxerolls

Location:	Grant County, Oregon; Malheur National Forest; Blue Mountain Ranger District; 10 km north of the town of Seneca on Hwy 395; Pedon is east of Hwy 395 3.5 km along Forest Road 3925 and 200m up the hill on the south side of the road; 44.217° N, 118.989° W.
Classification:	fine-loamy, mixed, superactive, frigid Vitrandic Haploxerolls
Vegetation:	Ponderosa pine / Idaho fescue plant association (Johnson and Clausnitzer 1992)
Parent Materials:	Volcanic ash deposition over fractured ultramafic (serpentine) rock
Landform:	Linear contour and linear slope
Physiography:	Mid/backslope
Land Use:	Forestry, grazing, recreation
Elevation:	1500 m
Slope Gradient:	8%
Slope Azimuth:	358°

Described and Sampled in the field by Duane Lammers, Jamie Kienzle, Cici Brooks, Bill Krueger, and Craig Carr on August 25, 2005, and in the lab by Duane Lammers and Craig Carr on October 12, 2006. (Colors are for moist soil unless stated otherwise.)

- A1** 0 – 9 cm; very dark grayish brown (10YR 3/2) ashy sandy loam, grayish brown (10YR 5/2) dry; weak coarse subangular blocky structure parting to moderate medium granular; many very fine and fine roots; many very fine and fine pores; clear wavy boundary.
- A2** 9 – 21 cm; very dark grayish brown (10YR 3/2) ashy sandy loam, light brownish gray (10YR 6/2) and grayish brown (10YR 5/2) dry; weak fine platy structure parting to weak fine granular; common very fine and fine, and few medium and coarse roots; many fine, common medium and few coarse pores; clear wavy boundary.

- AB** 21 – 32 cm; dark brown (10YR 3/3) ashy loam, brown (10YR 5/3) dry; weak coarse platy structure parting to weak medium subangular blocky; few very fine, fine, medium, coarse and very coarse roots; common fine, medium, and coarse pores; 3 percent serpentine gravel; clear wavy boundary.
- Bw1** 32 – 37 cm; brown (10YR 4/3) ashy loam, very pale brown (10YR 7/3) dry; weak coarse angular blocky structure; few very fine, fine, and medium roots; common very fine and fine pores; abrupt wavy boundary.
- 2Bw2** 37 – 49 cm; very dark grayish brown (10YR 3/2) sandy clay loam, light brownish gray (10YR 6/2) dry; moderate medium subangular blocky structure; few very fine, fine and medium roots; few very fine and fine irregular pores; clear wavy boundary.
- 2Bw3** 49 – 60 cm; dark grayish brown (10YR 4/2) clay loam, light gray (10YR 7/2) dry; moderate medium subangular blocky structure parting to moderate fine subangular blocky; slightly brittle; few very fine and common fine roots; few very fine and common fine irregular pores; 10 percent serpentine gravel; clear wavy boundary.
- 3 Bw4** 60 – 75 cm; dark olive gray (5Y 3/2) extremely gravelly sandy clay loam, olive (5Y 5/3) dry; moderate medium subangular blocky structure; few very fine and fine roots; many very fine, common fine and few medium pores; 65 percent gravel and 10 percent serpentine cobbles; gradual irregular boundary.
- 3 Cr** 75 cm; unconsolidated serpentine rock

Diagnostic Horizons and Features:

Mollic epipedon (0 – 32 cm)
 Vitrandic subgroup properties (0 – 37 cm)
 Cambic horizon (32 – 75 cm)
 Xeric soil moisture regime
 Frigid soil temperature regime

Comments:

This describes a typical soil that represents moderately deep, ash-over-serpentine soils found throughout the study area. Although, variability in the thickness of the ash mantel and clay content of subsoil horizons was observed throughout the area this description characterizes well the ash dominated soils of this area.

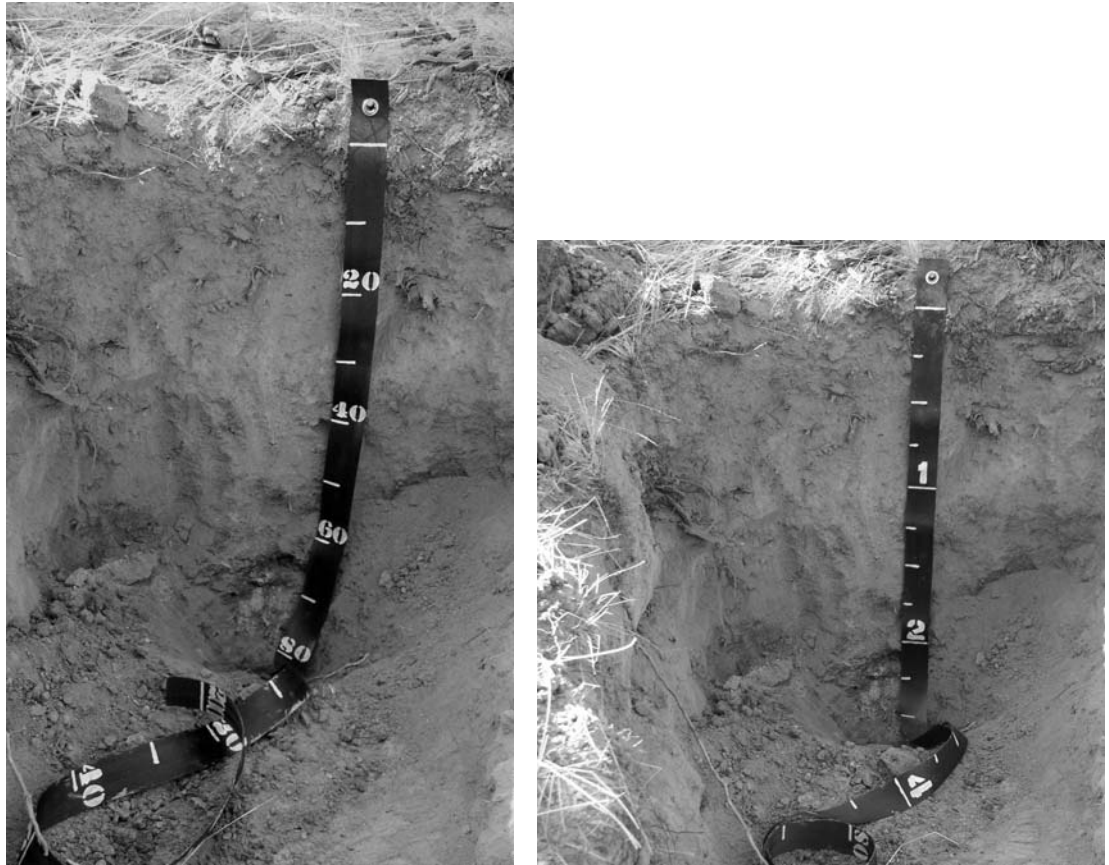


Figure A1. fine-loamy, mixed, superactive, frigid Vitrandic Haploxerolls from area northeast of Seneca, Oregon. The measuring tape in the left photo refers to centimeters while the photo on the right photo indicates feet.

Pedon Description: Lithic Ultic Argixerolls

Location: Grant County, Oregon; Malheur National Forest; Blue Mountain Ranger District; 10 km north of the town of Seneca on Hwy 395; Pedon is east of Hwy 395 4.0 km along Forest Road 3925 and 500m up the hill on the south side of the road; 44.214° N, 118.988° W.

Classification: C\clayey-skeletal, S\smectitic, frigid Lithic Ultic Argixerolls

Vegetation: Ponderosa pine / Idaho fescue plant association (Johnson and Clausnitzer 1992)

Parent Materials: Volcanic ash deposition over fractured ultramafic (serpentine) rock

Landform: Convex contour and linear slope

Physiography: Mid/backslope

Land Use: Forestry, grazing, recreation

Elevation: 1520 m

Slope Gradient: 8%

Slope Azimuth: 340°

Described and Sampled in the field by Duane Lammers, Jamie Kienzle, Cici Brooks, Bill Krueger, and Craig Carr on August 25, 2005, and in the lab by Duane Lammers and Craig Carr on October 12, 2006. (Colors are for moist soil unless stated otherwise.)

- A** 0 – 8 cm; very dark grayish brown (10YR 3/2) ashy loam, grayish brown (10YR 5/2) dry; weak medium platy structure parting to moderate fine granular; many very fine and fine roots; many fine, common medium and few coarse pores; 5 percent serpentine gravel; clear smooth boundary.
- Bt1** 8 – 19 cm; very dark grayish brown (10YR 3/2) clay loam, yellowish brown (10YR 5/4) and brown (10YR 5/3) dry ; moderate coarse platy structure parting to moderate fine granular; few very fine, fine and medium roots; few very fine and fine irregular pores; few thin clay films lining pores and on ped faces; 10 percent serpentine gravel; clear smooth boundary.

- Bt2** 19 – 29 cm; very dark grayish brown (10YR 3/2) very gravelly clay loam, dark grayish brown (10YR 4/2) dry; moderate coarse angular blocky structure parting to moderate medium subangular blocky; few very fine, fine, medium and coarse roots; common very fine and many fine pores; common moderately thick clay films in root channels and on ped faces; 45 percent gravel and 10 percent serpentine cobbles; gradual wavy boundary.
- Bt3** 29 – 40 cm; brown (10YR 4/3) extremely cobbly sandy clay, pale olive (5Y 6/4) dry; moderate medium subangular blocky structure parting to moderate fine granular structure; few fine pores; common moderate thick clay films on ped faces; 35 percent gravel and 30 percent serpentine cobbles; abrupt irregular boundary.
- R** 40 cm; serpentine bedrock

Diagnostic Horizons and Features:

Mollic epipedon (0 – 19 cm)
 Argillic horizon (8 – 40 cm)
 Lithic contact (40 cm)
 Xeric soil moisture regime
 Frigid soil temperature regime

Comments:

This soil description characterizes area soils that have experienced erosional losses to a significant proportion of the overlaying ash mantel. Generally these soils were found on areas likely to have experienced soil or ash entrainment in wind, such as ridge tops or locations of convex landform features.

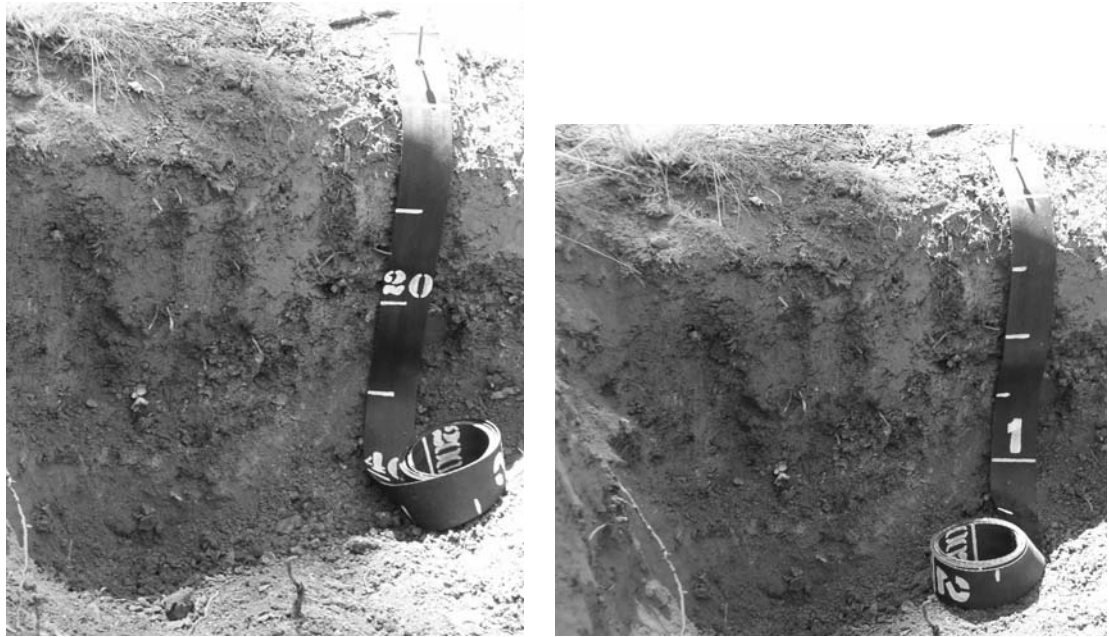


Figure A2 clayey-skeletal, smectitic, frigid Lithic Ultic Argixerolls from area northeast of Seneca, Oregon. The measuring tape in the left photo refers to centimeters while the photo on the right indicates feet.

Age Distribution of Ponderosa Pine Trees

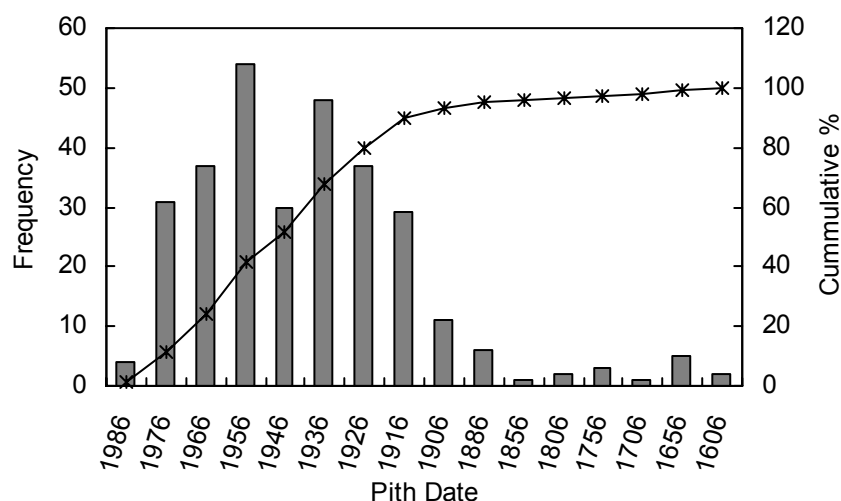


Figure A3. Age distribution of ponderosa pine trees from the eastern Oregon study area. Columns represent the number of trees with pith dates that fall within the associated date increment. The cumulative percent frequency is indicated by the trend line. Data are presented in 10, 20, 30 and 50 year increments between 1986 and 1906, 1906 and 1886, 1886 and 1856, and 1806 and 1606, respectively. 301 trees from the study area were cored in the summer of 2006.

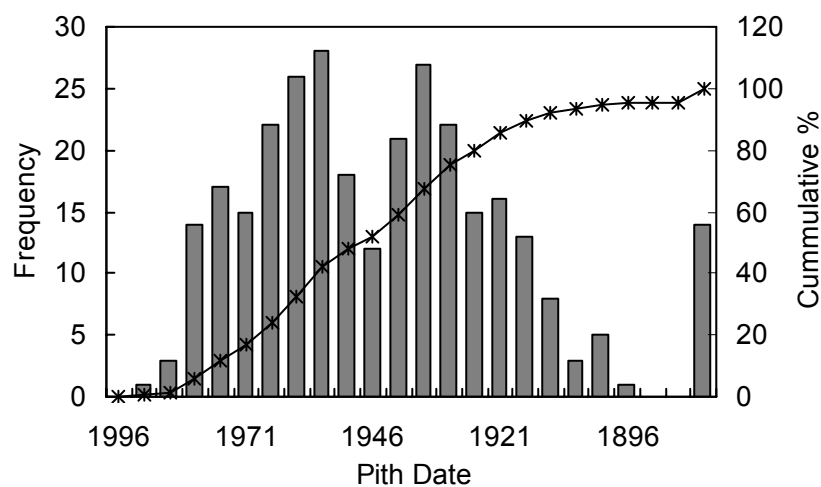


Figure A4. Post-settlement era age distribution of ponderosa pine trees from the eastern Oregon study area magnified across the post-settlement time span. Columns represent the number of trees with pith dates that fall within the date increment. The cumulative percent frequency is indicated by the trend line. Data are presented in 5 year increments between 1996 and 1886, while trees with pith dates older than 1886 are incorporated within the final column. 301 trees from the study area were cored in the summer of 2006.

Site Characteristics

Table A1. Site characteristics of each plot used in the study.

Plot	Elevation (m)	Aspect (°)	Slope (%)	Soil Type ¹	Pine density (trees/ha)
1-1	1520	348	8	a	178
1-2	1520	340	8	b	889
1-3	1520	320	8	b	1333
1-4	1520	4	13	a	2222
2-1	1500	343	12	a	800
2-2	1500	358	8	a	756
2-3	1500	352	6	a	2133
2-4	1500	354	8	a	2800
3-1	1510	27	2	a	356
3-2	1500	350	10	a	356
3-3	1500	354	9	a	1556
3-4	1480	350	10	a	4800
4-1	1520	340	12	b	133
4-2	1500	8	8	a	889
4-3	1500	352	5	a	1422
4-4	1500	9	6	a	3822
5-1	1500	28	11	a	178
5-2	1500	354	3	a	444
5-3	1500	350	3	a	1511
5-4	1510	356	19	a	3067
6-1	1560	347	5	a	222
6-2	1560	328	7	a	356
6-3	1550	358	11	a	2400
6-4	1540	354	17	a	2844
7-1	1530	20	15	a	489
7-2	1530	18	12	a	1067
7-3	1540	357	12	a	1911
7-4	1540	10	9	a	3156

¹Soil Type a: Fine-loamy, Mixed, Superactive, Vitrandic Haploxeroll
 Soil Type b: Clayey-skeletal, Smectitic, Lithic Ultic Argixeroll

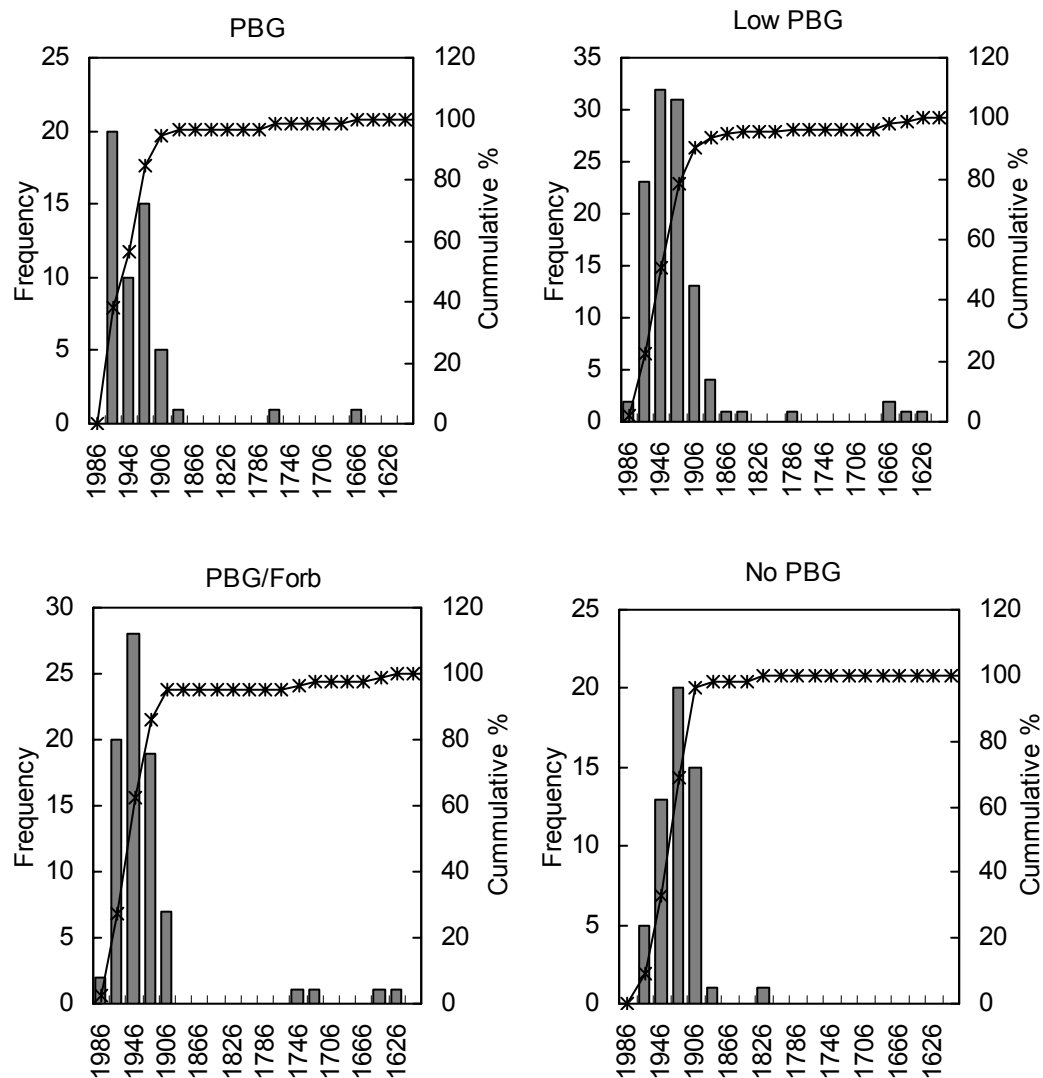


Figure A5. Age distribution of ponderosa pine trees within the 4 understory species composition based groups. Columns represent the number of trees with pith dates that fall within the date increment. Data are represented in 20 year date increments going backward from 2006.

APPENDIX B

Scatter Plots of Variables Used in PCA

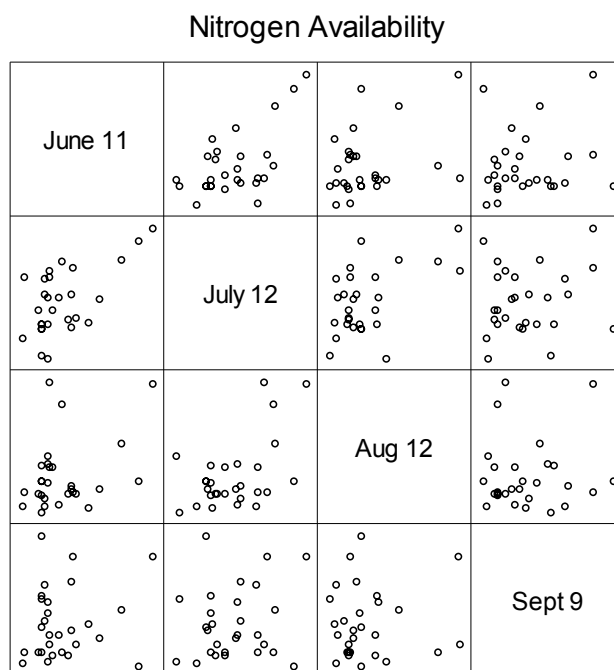


Figure A6. Bivariate scatter plots of raw mineral N availability (ppm) used in evaluating the appropriateness of PCA as an analytical tool for these data.

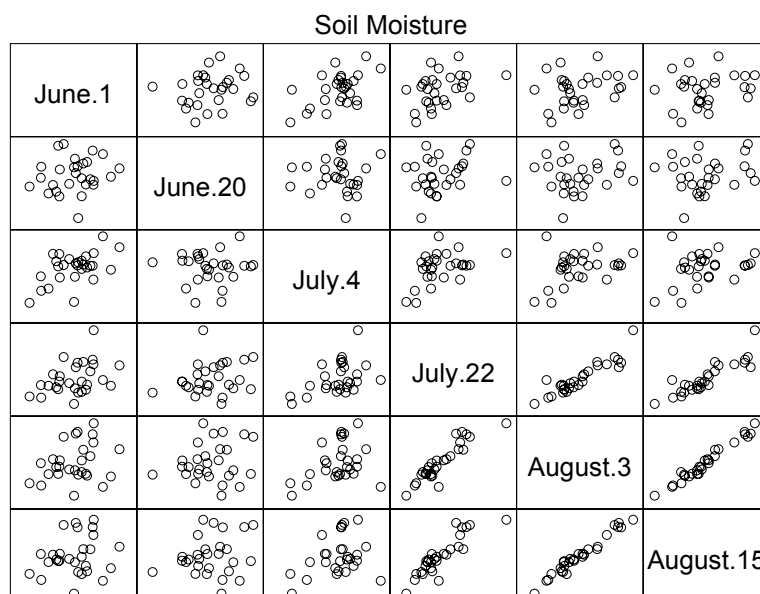


Figure A7. Bivariate scatter plot of gravimetric soil moisture (%) used to evaluate the appropriateness of PCA as an analytical tool for these data.

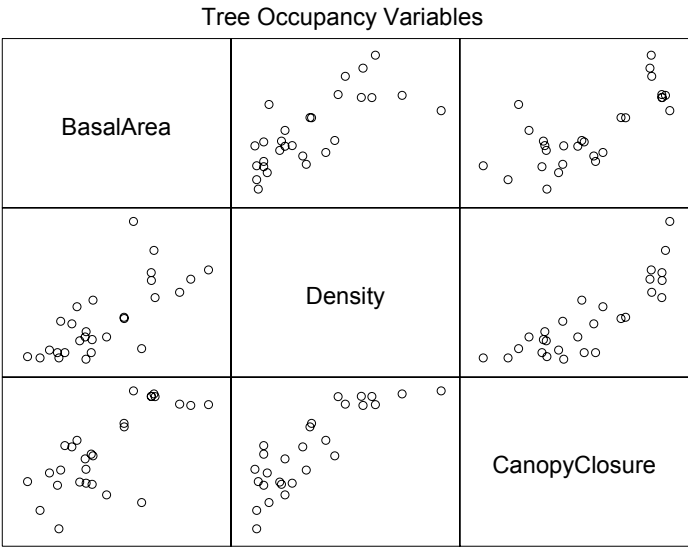


Figure A8 Bivariate scatter plot of tree basal area (m^2), tree density (stems/ha), and canopy closure (%) used to evaluate the appropriateness of PCA as an analytical tool for these data.

Distributional Exploration of Data used in Greenhouse Study

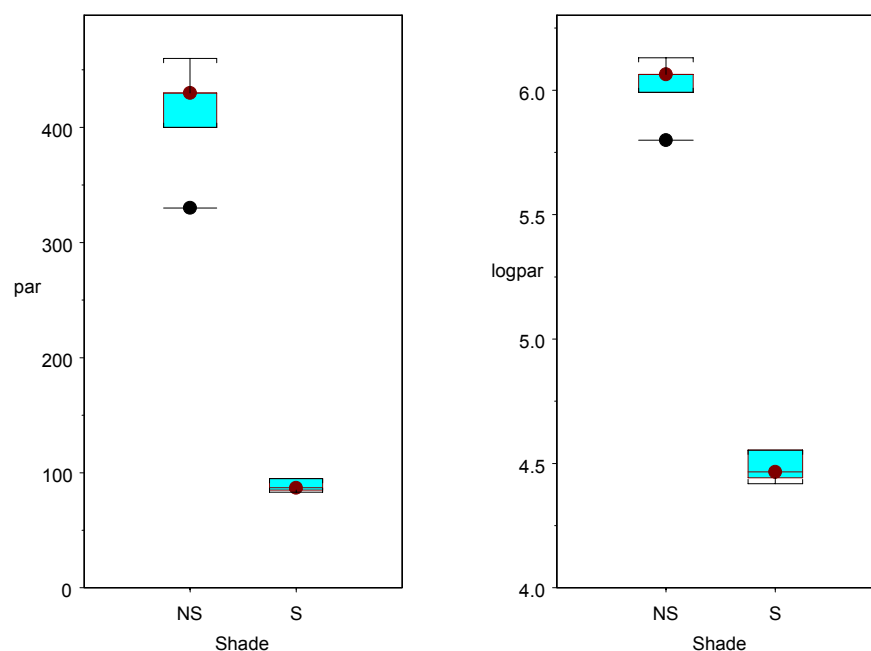


Figure A9. Box plots showing raw (left) and log transformed (right) distributions of the PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) data. (S=80% Shade; NS=No Shade). Dots inside the boxes indicate the median value while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

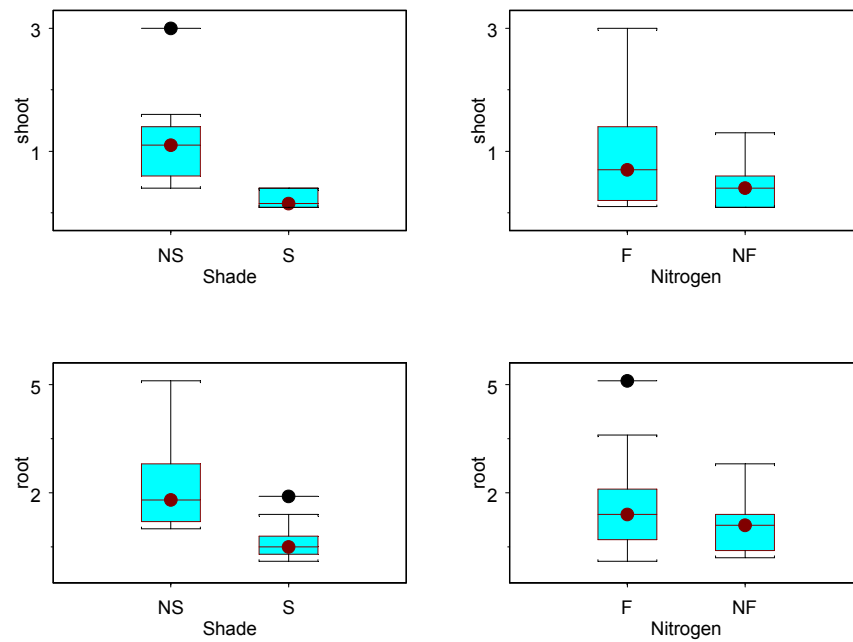


Figure A10. Box plots showing untransformed distributions of shoot (top) and root (bottom) biomass (g) data sets. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

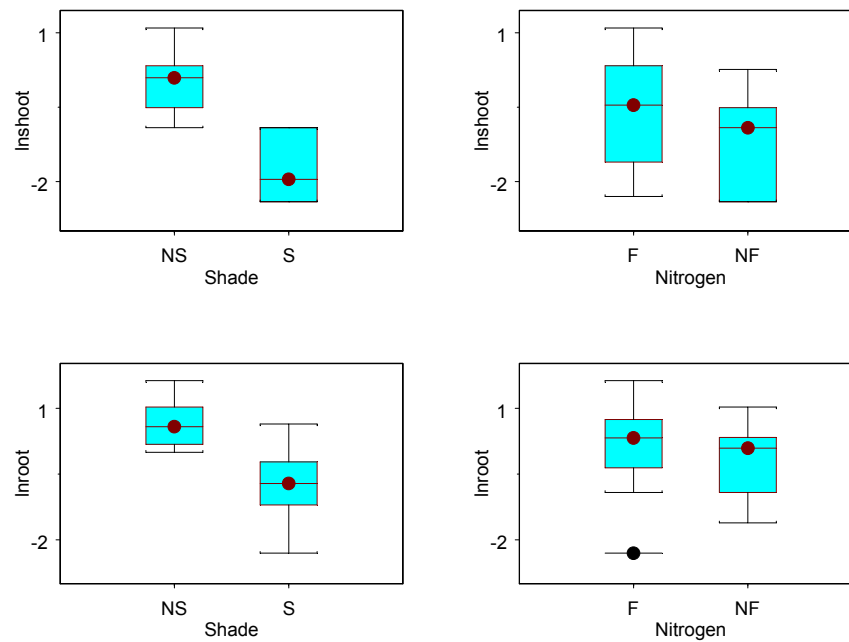


Figure A11. Box plots showing log transformed distribution of shoot (top) and root (bottom) biomass (g) data sets. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

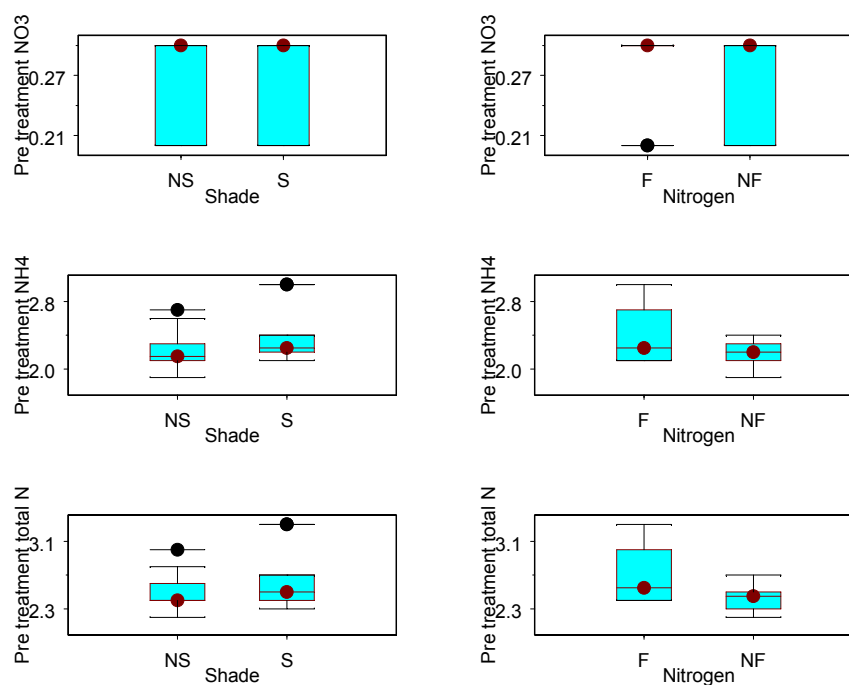


Figure A12. Box plots showing the distributions of pre-treatment potting media nitrogen concentrations (ppm). Plots are arranged by shade (left) and nitrogen (right) treatments. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

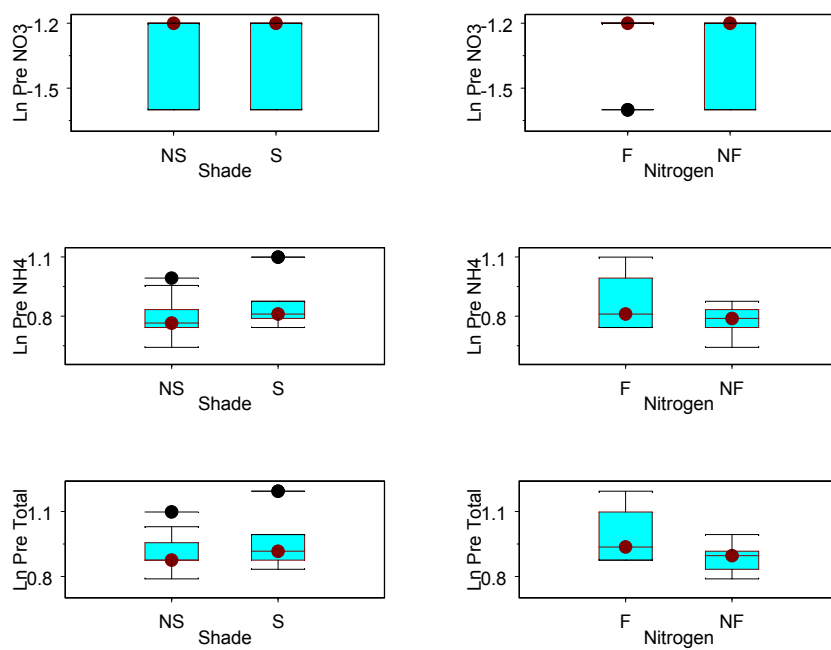


Figure A13. Box plots showing the log transformed distributions of pre-treatment potting media nitrogen concentrations (ppm). Plots are arranged by shade (left) and nitrogen (right) treatments. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

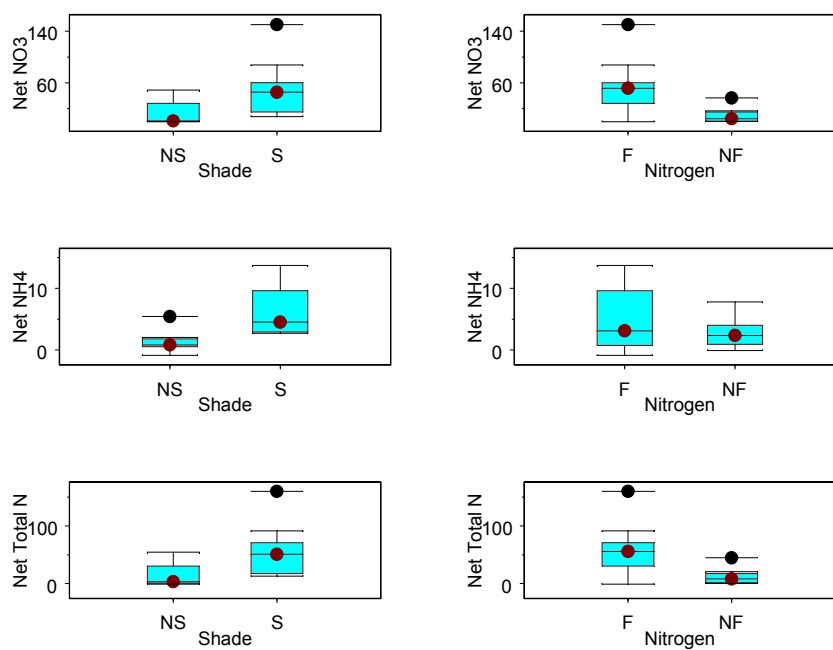


Figure A14. Box plots showing the distributions of the net change in potting media nitrogen concentrations (ppm). Plots are arranged by shade (left) and nitrogen (right) treatments. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

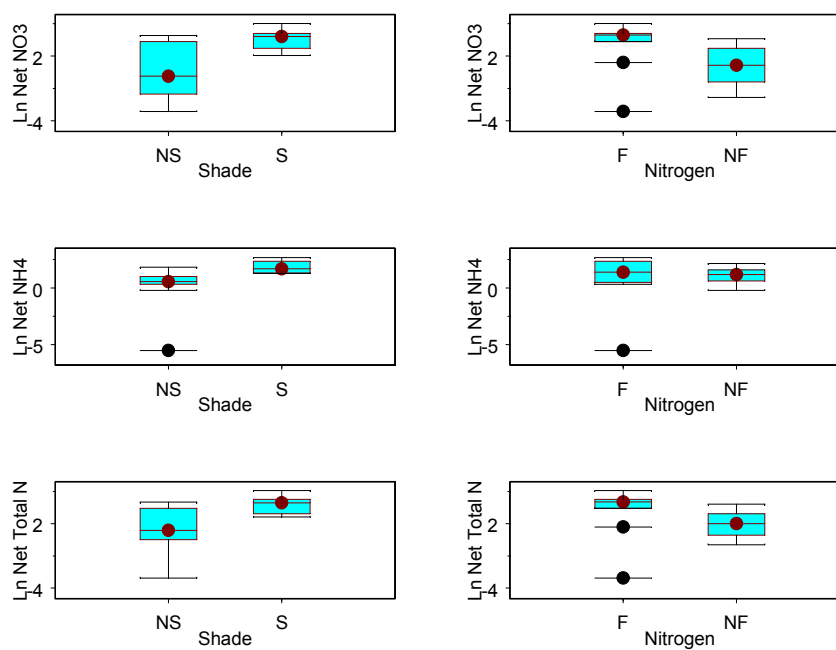


Figure A15. Box plots showing the log transformed distributions of the net change in potting media nitrogen concentrations (ppm). Plots are arranged by shade (left) and nitrogen (right) treatments. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

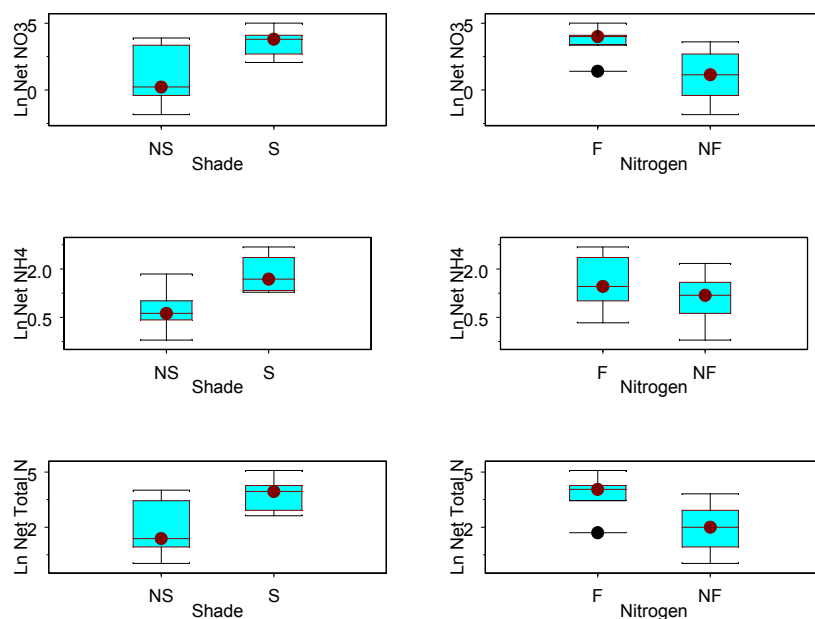


Figure A16. Box plots showing the log transformed distributions of the net change in potting media nitrogen concentrations (ppm). Plots are arranged by shade (left) and nitrogen (right) treatments. Pot 18, identified as an outlier was removed from the data set used to generate these charts. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

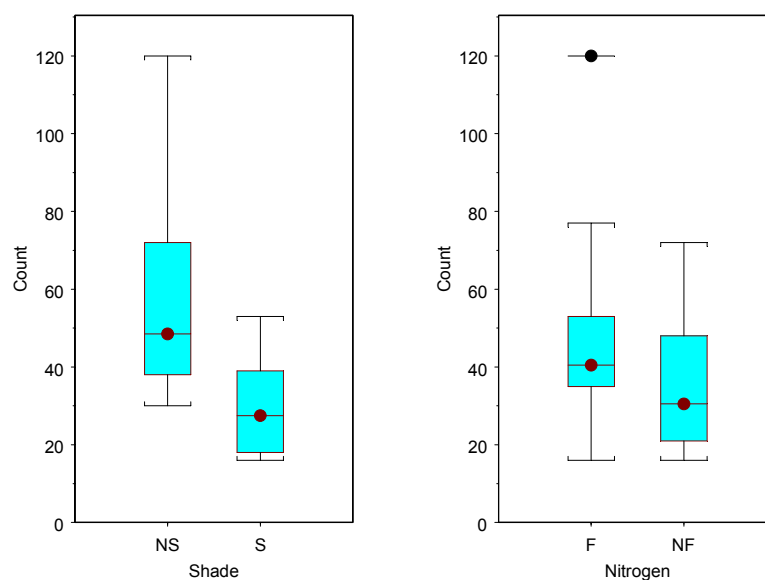


Figure A17. Box plots showing the distributions the foliar cover index data. Plots are arranged by shade (left) and nitrogen (right) treatments. Count represents the number of grid points that contacted vegetation in the evaluation of the digital photographs and is an index of foliar cover. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

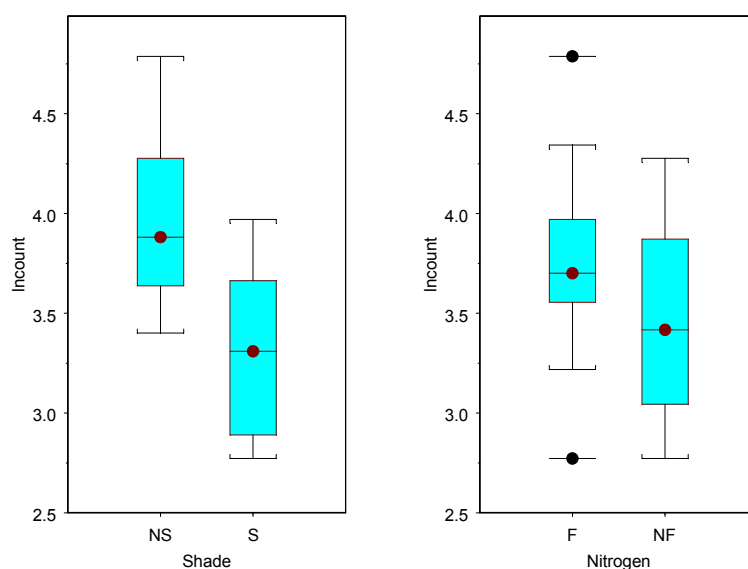


Figure A18. Box plots showing the log transformed distributions the foliar cover index data. Plots are arranged by shade (left) and nitrogen (right) treatments. Count represents the number of grid points that contacted vegetation in the evaluation of the digital photographs and is an index of foliar cover. Lncount represents log transformed count data. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

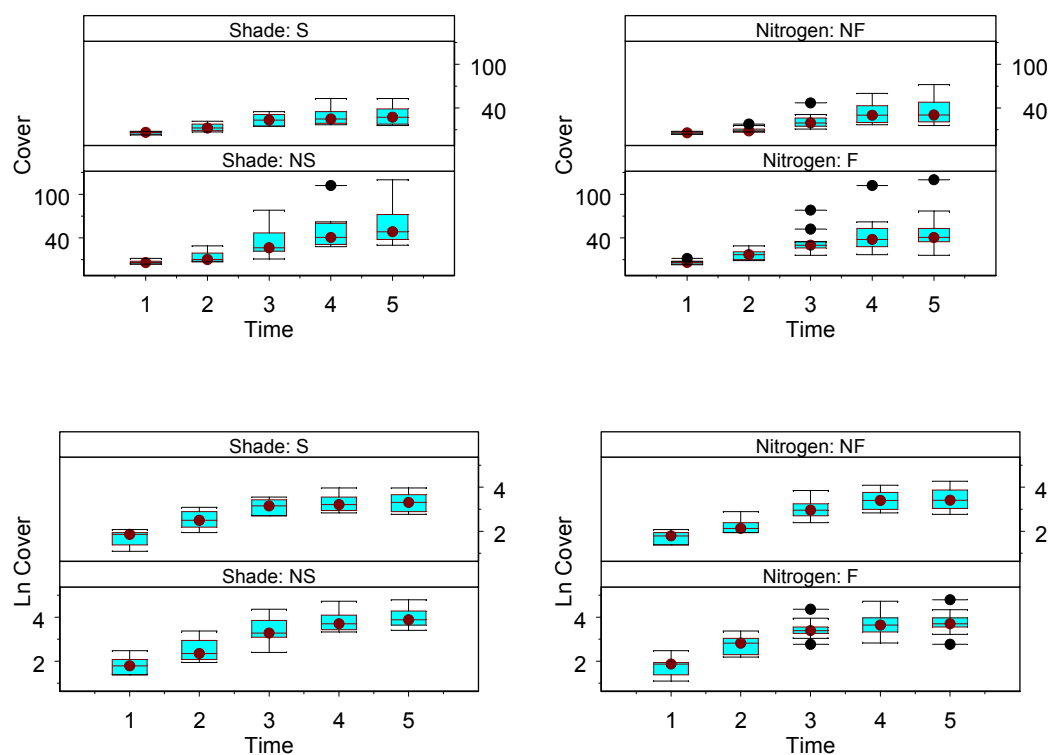


Figure A19. Box plots showing the raw (top) and log transformed (bottom) distributions the foliar cover index data over time (number of weeks). Plots are arranged by shade (left) and nitrogen (right) treatments. Cover data represent the number of grid points that contacted vegetation in the evaluation of the digital photographs and are an index of foliar cover. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

Table A2. Fit statistics for the evaluation of correlation structure efficiency in modeling data covariance from the repeated measures experiment of foliar cover over time.

	Unstructured	Compound Symmetry	AR(1)	TOEP	ANTE(1)
-2LL	20.0	40.4	34.5	33.7	22.5
AIC	52.0	48.4	44.5	47.7	44.5
AICC	60.6	48.9	45.3	49.3	48.4
BIC	45.8	46.8	42.6	45.0	40.2
Parameters	17	4	5	7	11

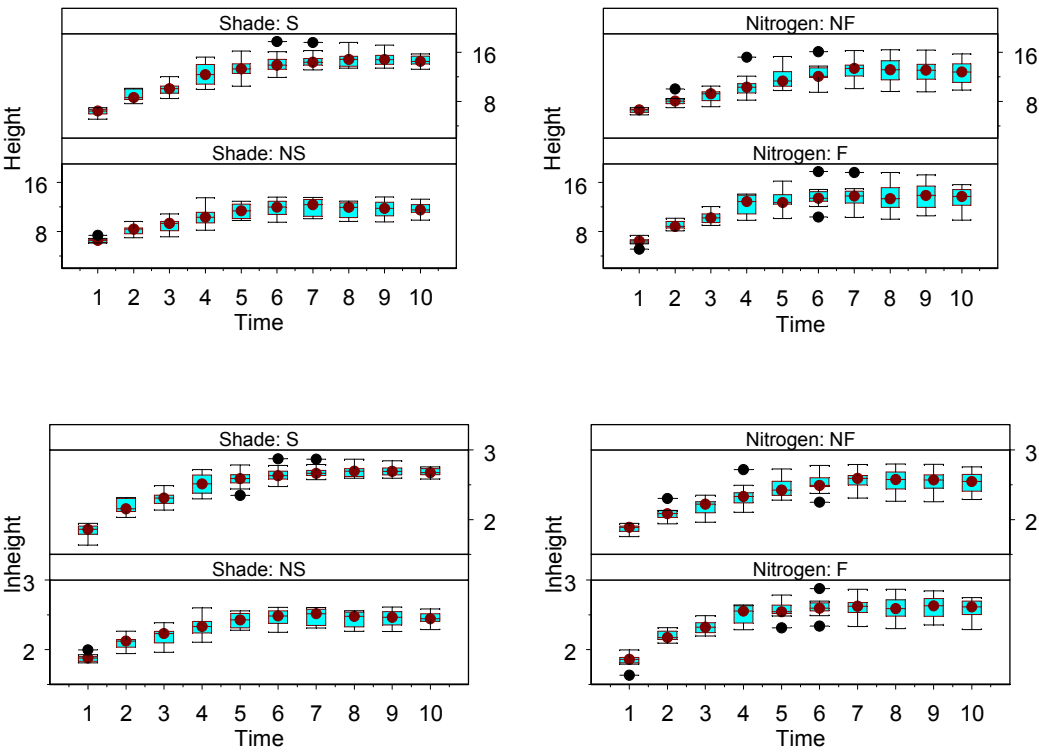


Figure A20 Box plots showing the raw (top) and log transformed (bottom) distributions of leaf height (cm) over time (weeks). Plots are arranged by shade (left) and nitrogen (right) treatments. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

Table A3. Fit statistics for the evaluation of correlation structure efficiency in modeling data covariance from the repeated measures experiment of shoot length over time.

	Unstructured	Compound Symmetry	AR(1)	TOEP	ANTE(1)
-2LL	-443.4	-316.6	-347.3	-365.0	-375.6
AIC	-333.4	-310.6	-339.3	-343.0	-335.6
AICC	-274.2	-310.6	-339.3	-341.2	-329.5
BIC	-354.9	-311.8	-340.9	-347.3	-343.4
Parameters	57	4	5	12	21

Relationships Between Shoot Biomass, Root Biomass, Foliar Cover and Shoot Length and Initial Idaho Fescue Plant Size

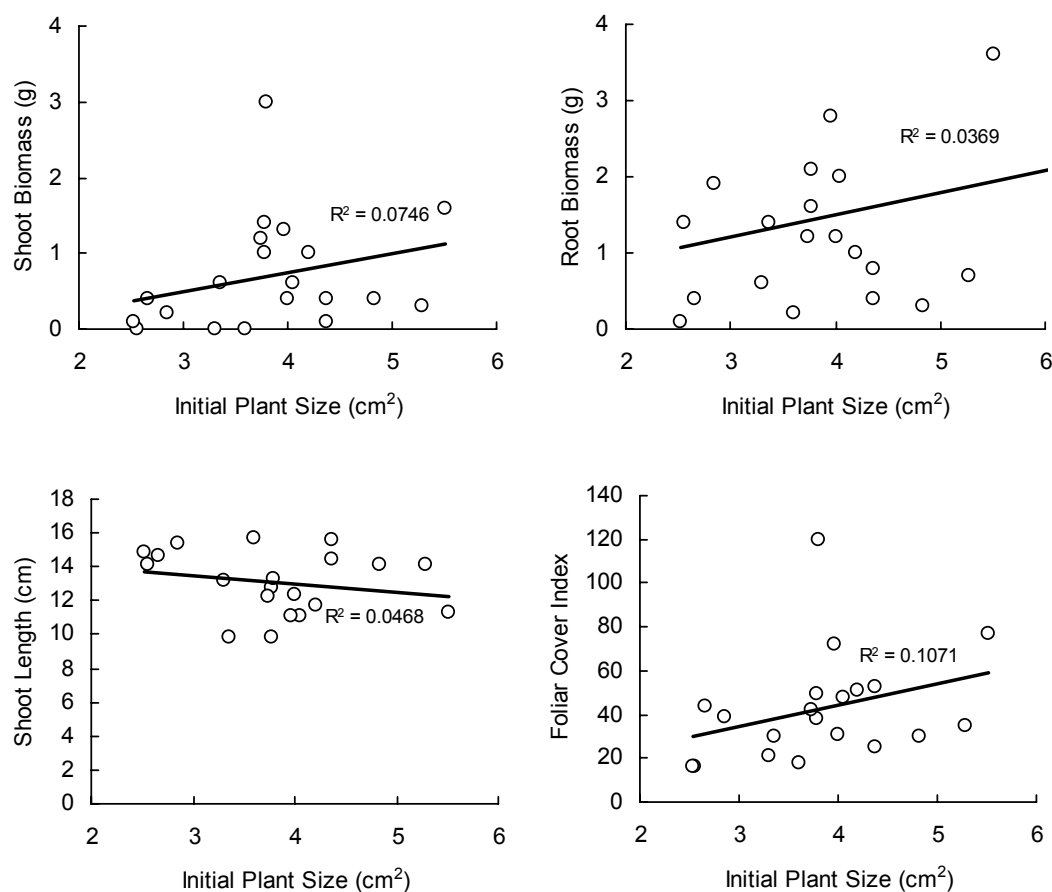


Figure A21. Charts showing the relationship between shoot biomass (g), root biomass (g), shoot length (cm) and foliar cover index and the initial pre-treatment Idaho fescue size. Cover data represent the number of grid points that contacted vegetation in the evaluation of the digital photographs and are an index of foliar cover.

Distributional Exploration of Seedling Density and Diversity Measures

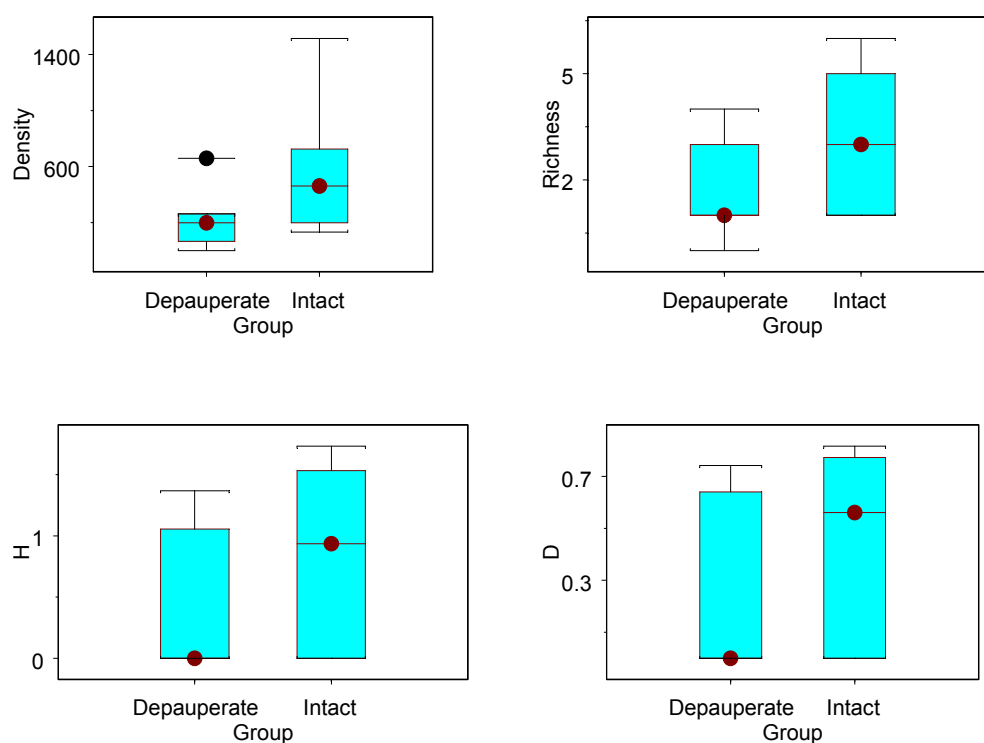


Figure A22. Box plots exploring the distribution of seed bank density (seeds/m²) and diversity data sets. Richness is species richness, H refers to Shannon's diversity index and D refers to Simpson's diversity index. Dots inside the boxes indicate the median while dots external to the box represent outliers. Outliers were data points with values greater than 1.5-times the inter-quartile range.

APPENDIX C

Temperature Regime for Seed bank Sample Storage

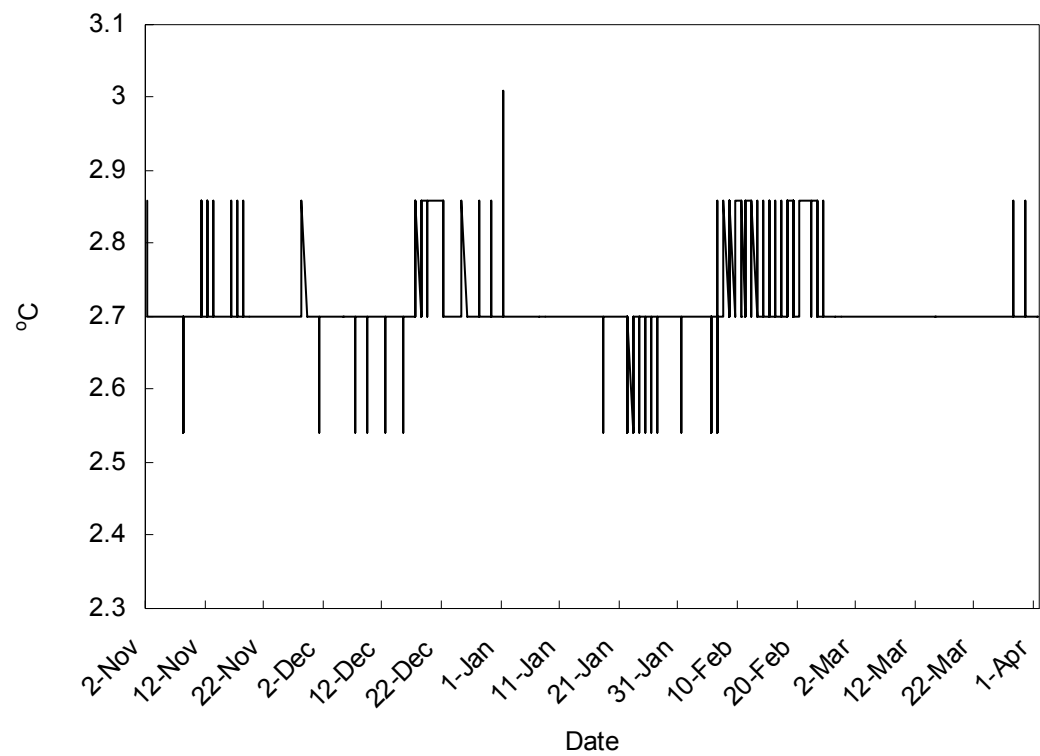


Figure A23. Storage Temperatures for seed bank samples.

Average Daytime Temperatures Inside Greenhouse

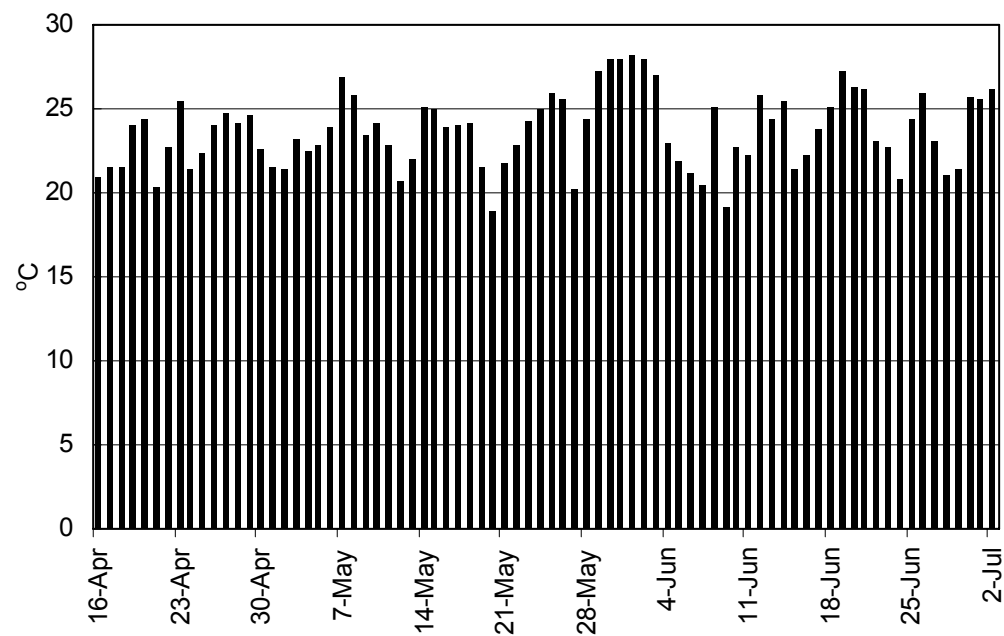


Figure A24. Average daytime (06:00 – 20:00) temperatures inside the greenhouse for each day of the resource limitation experiment.