

Effects of prescribed burning on vegetation and soil water processes
in mixed-conifer forest stands at Boggs Mountain State Forest, California

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EFFECTS OF PRESCRIBED BURNING ON VEGETATION AND
SOIL WATER PROCESSES IN MIXED-CONIFER FOREST STANDS AT BOGGS
MOUNTAIN STATE FOREST, CALIFORNIA

Domingo Miguel Molina

Abstract

The four papers presented in this dissertation address various ecological aspects of fire effects on mixed-conifer stand sat Boggs Mountain State Forest (BMSF), north of Middletown, California. The first paper evaluates the effect of prescribed burns on water infiltration into the soil (i.e., if there is hydrophobicity) under mixed-conifer forests. The experiment followed a randomized complete block design and had three burn treatments characterized by different amounts of forest floor fuel consumption (i.e., control, low, and high consumption). Infiltration capacity was measured with 100mm-diameter ring infiltrometers in both burned and unburned conditions. The infiltration rates were not significantly changed by controlled burns of low fireline intensity and low to high fuel consumption. Therefore, we can reduce fuel accumulations, and thus wildfire hazard, using prescribed burns without significantly changing the infiltration capacity of the site.

The second paper evaluates the germination response of seeds from several hard-seeded shrubs species common to BMSF. The experimental units were sets of 25 seeds. The following species were investigated: *Arctostaphylos manzanita* C. Parry (ARMA), *Arctostaphylos canescens* Eastw. (ARCA), *Ceanothus prostratus* Benth. (CEPR), and

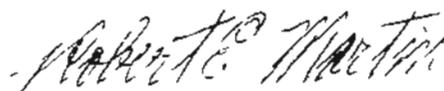
Rhamnus californica Eschsch (RHCA). Experimental investigation provided evidence into germination requirements, and interpretation of these results elucidated fire-related mechanisms associated with plant persistence. Treatments were designed to emulate, (1) fire induced scarification, (2) winter stratification, and (3) effects of leachate from burned litter. The heat treatment lasted four minutes because this is representative of the time of duff and soil heating at high temperatures during fires. RHCA seeds showed higher germination when non-stratified versus when stratified, at 80°C versus any other temperature, in moist heating treatments versus dry ones at the same temperature, and did not display differences between leachate and non-leachate treatments. CEPR and ARCA seeds showed better germination when stratified. ARMA percentage germination was negligible.

The third paper addresses short term (< 5 years) ecological effects of prescribed burns on vegetation plant diversity and spatial distribution patterns (i.e., random, uniform, and cluster) by comparing stands with different prescribed burn histories. Distance sampling techniques were used in the study of spatial distribution patterns. Results support the hypothesis that prescribed fire removes trees and shrubs preferentially from clumped areas leaving a more random distribution of individuals. Overstory trees are more sparsely distributed in underburned stands, and tended towards a sparse distribution for the understory layer. This pattern may be caused by a higher accumulation of dead and down fuels in clumps; and therefore, individual plants have a higher mortality chance in a fire event (i.e., leaving a more random distribution of individuals). No significant differences in species richness were found among treatments (i.e., control, underburned) in any strata.

Diversity indices consistently suggested that in the underburned conditions plant species diversity was lower than in controls. Evenness indices consistently suggested a more even distribution of individuals among species in the control stands versus a more clear dominance (in numbers) by one or two species in the underburned stands

The last paper examines if there are small-scale habitat differences among tree seedlings of the main tree species common to BMSF. The experimental units were randomly selected individual seedlings. There were five species (PM = *Pseudotsuga menziesii* (Mirb.) Franco, PP = *Pinus ponderosa* Dougl., PL = *Pinus lambertiana* Dougl., QK = *Quercus kelloggii* Newb., and QW = *Quercus wislizenii* A. CD.) and 26 individuals per species. Significant differences among species were only found for depth of litter and duff, and for percent plant cover ($\alpha = 0.05$). The distance to the nearest outcompeting individual yielded P-values of 0.0592 (ANOVA) and 0.0922 (nonparametric Kruskal-Wallis ANOVA). Percentage of soil covered by conifer litter and duff, light intensity (as percent of open-site light intensity), and nearest neighbor distance were nonsignificant in separating the five species of this study.

Keywords Prescribed burns, infiltration, forest floor consumption, hydrophobicity, germination, fire induced scarification, stratification, leachate, spatial distribution patterns, species diversity indices, evenness indices, mixed-conifer stands, seedling microhabitat



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PREFACE

The purpose of this research was to understand fire effects on mixed-conifer stands at Boggs Mountain State Forest (BMSF), California. This knowledge should lead to recommendations for the management prescriptions. I have examined some mechanisms relating fire and its effects on vegetation in this particular location with a given climate, topography, geomorphic processes, soil and vegetation.

The general goal is to address the following questions:

- A. How does prescribed burning affect certain physical characteristics of the soil such as infiltration rates and soil pH?
- B. How do fire-emulating treatments affect seed germination?
- C. Which are the patterns of plant species density, distribution and diversity in forest stands?
- D. Does tree seedling occurrence vary among different species in regard to operational factors of their environment?

Study site

Boggs Mountain State Forest (BMSF) is located north of Middletown, California. It is located in the east side of the North Coast Range of California and therefore coastal influence on climatic conditions is low. Yearly precipitation ranges from 560 to 2920 millimeters (California Department of Forestry and Fire Protection 1990) with hot, dry summers characteristic of a Mediterranean climate. Elevation ranges from 730 to 1150

meters. The vegetation is a mosaic of open areas with an overstory of ponderosa pine, Douglas-fir, and sugar pine, thickets of those species, and manzanita patches. The major vegetation type is a mixed conifer forest (*sensu* Barbour and Major 1977). The most common tree species in BMSF are *Pseudotsuga menziesii* (Mirb.) Franco, *Pinus ponderosa* Dougl., *Pinus lambertiana* Dougl., *Quercus kelloggii* Newb., *Quercus wislizenii* A.C.D. Recent reviews of ecophysiology and distribution for these species are found in Hermann and Lavander 1990 (*Pseudotsuga menziesii*), Oliver and Ryker 1990 (*Pinus ponderosa*), Kinloch and Scheuner 1990 (*Pinus lambertiana*), McDonald 1990 (*Quercus kelloggii*), and Pavlik et al. 1991 (*Quercus wislizenii*). The common shrub species are *Arctostaphylos manzanita* C.Parry, *Arctostaphylos canescens* Eastw., *Ceanothus prostratus* Benth., and *Rhamnus californica* Eschsch.

In 1949, the State purchased BMSF for experimental and demonstration purposes. It was to serve as an example of a recently cutover site from which all merchantable timber has been cut, except for a few seed trees and scattered patches of mature trees that were considered inaccessible by the logging company at the time of acquisition. The State Forest is open year-round for public recreational use and hunters, bikers, picnickers, and campers are frequent users of the area, and in general recreational activities are high.

Previous work

Prescribed burn research was first carried out in the Boggs Mountain area by Harold Biswell from 1951 to 1964 at Hobergs Resort (Biswell 1989). This resort is

located a few miles north of the state forest. The technique used consisted in of an initial controlled burn to reduce dead fuel and kill both shrubs and small understory trees, and next, residual large dead fuels, and shrubs and trees killed by the first burn were piled and burned (Biswell 1989) In BMSF itself, prescribed burning has been used as a management tool since February 1985. A major goal for the forest manager is wildfire hazard mitigation because of the subdivisions nearby. Prescribed burning is carried out over portions of the forest every year, preferably in winter. The forest manager expects this to reduce the number of small trees and shrub cover, and in this manner, reduce the vertical continuity of forest fuels (ladder fuels). Additionally, group selection cuts and thinning are expected to enhance the timber growth rates.

Methods

Both the experimental design and the experimental execution are explained in detail in each chapter.

The research goals were expressed as specific null hypotheses.

- 1 - The level of forest floor consumption by fire does not affect values of soil pH.
- 2 - The level of forest floor consumption does not affect infiltration rates.
- 3 - Leachate (from burned litter) treatment yield the same seed germination rates than control (clean water).
- 4.- Germination rate does not change significantly with the temperature applied in the heating treatment.

- 5.- Wet thermal treatments do not yield different germination rates than dry ones at the same temperatures.
- 6 - The different germination treatments applied do not interact.
- 7 - All the species in this study benefit equally from winter stratification (wet, cold storage for three months)
- 8.- In 1992-93, understory spatial distributions in 1988 prescribed burns are not different from controls (unburned).
- 9 - In 1992-93, overstory spatial distributions in 1988 prescribed burns are not different from controls (unburned).
- 10.- In 1992-93, understory diversity indices in 1988 prescribed burns are not different from controls (unburned)
- 11 - In 1992-93, overstory diversity indices in 1988 prescribed burns are not different from controls (unburned).
- 12.- Seedling of different species do not differ in occurrence along the gradient in litter and duff depth (microhabitat variable)
- 13.- Seedling of different species do not differ in occurrence along the gradient in distance to the nearest plant individual (microhabitat variable)
- 14 - Seedling of different species do not differ in occurrence along the gradient in distance to the nearest outcompeting plant individual (microhabitat variable)
- 15 - Seedling of different species do not differ in occurrence along the gradient in percentage of the soil surface covered by conifer litter and duff (microhabitat variable)

- 16 - Seedling of different species do not differ in occurrence along the gradient in percentage of Photosynthetic Active Radiation (PAR) reaching the seedling (microhabitat variable)
- 17.- Seedling of different species do not differ in occurrence along the gradient in total plant cover above a seedling (microhabitat variable)

Statistical analysis The SAS (Schlotzhauer and Littlell 1987) statistical package was used in the analyses of results. Linear models were used for analysis of variance (ANOVA), and orthogonal F tests (orthogonal contrasts) were used in the process of mean separation because most statisticians agree that they provide a more precise separation than multiple comparison tests (Day and Quinn 1989, Steel and Torie 1980, Little and Hills 1978). Following Little and Hills (1978), data were transformed (if necessary) to better fit the assumptions of ANOVA, continuous variables were logarithmic transformed, and percentage variable were arcsine transformed. In a like manner, the Kruskal-Wallis test (the nonparametric analog of the ANOVA F test) was used when the ANOVA assumptions were not met. Lastly, the power of the statistical test performed are reported. Power is the likelihood of the test to reject the null hypothesis when it is false.

Justification

Fire is a major form of recurrent natural disturbance in numerous terrestrial plant communities. Fire, landforms, flora, fauna, and geomorphic processes interact in different

ways causing diverse patterns of vegetation types over landscapes. Fire changes plant cover and soil properties, and can modify the hydrologic regime of a site, affecting the movement of soil and sediments within a watershed. Plant communities, through temporal and spatial patterns of fuel accumulations, affect the fire regime of a site.

From an ecological point of view, fire is neither a destructive nor a constructive factor *per se*; it simply causes change. That is, scientific investigations of fire effects on ecosystems do not involve judgment of 'good' or 'bad' outcomes. However, within the context of objectives determined by humans, outcomes may be described as desirable or non-desirable. Thus, benefits can be obtained from using prescribed burning as a forestry management tool, such as, site preparation for seeding or planting, disease control, improvement of wildlife habitat, and reduction of stand-replacing wildland fires. Martin (1981) stated that each burn should be planned to accomplish one or more well defined objectives, at the same time keeping the negative effects of burning below given levels. A single prescribed burn may achieve several benefits, e.g. a properly planned fire can reduce hazardous fuel accumulations and enhance wildland habitat. Prescribed burns are, however, not always desirable: if conditions are not carefully prescribed, burns can damage natural resources such as soils by seriously reducing soil wettability or accelerating erosional processes. Therefore, prescribed fire must be used carefully because of the multiple effects.

Additionally, fire, as a disturbance, may affect each level of organization of a given natural system. Pickett et al. (1989) state that analyses of disturbance at each level and interactions among the levels are vital to understanding the importance of disturbance

as a natural phenomenon. Thus, the principle of scale -both temporally and spatially- should be addressed.

Classification of these chapters

Chapter 1. Prescribed Burning Effects on Infiltration Capacities in Mixed-Conifer Forest Stands at Boggs Mountain Demonstration State Forest, California

Chapter 2. Seed Germination Responses to Various Thermal Regimes: Shrub Species at Boggs Mountain Demonstration State Forest, California

Chapter 3. Prescribed Burned Effects on Spatial Distribution Patterns and Plant Diversity Indices in Mixed-Conifer Stands in California

Chapter 4. Tree Seedling Microhabitat in Mixed Conifer Stands at Boggs Mountain Demonstration State Forest, California

The experiments involved in these papers (chapters) address diverse interactions among fire, flora, and soil characteristics. These experiments can be grouped as follows:

A. Spatial scale.

A 1. Microscale level

Chapter 1 Hydrologic experiments

Chapter 2. Seed germination experiments

Chapter 4. Seedling microhabitat study

A 2. Stand level

Chapter 3. Plant spatial distributions and species diversity

B. Experimental topic

B 1. Abiotic characteristics of the soil

Chapter 1. Hydrologic experiments

B.2 Community level concepts (Synecology *-sensu* Oosting 1948)

Chapter 3 Plant spatial distributions and species diversity

B 3. Organism level concepts (Autoecology *-sensu* Daubenmire 1959)

B.3 1. Chapter 4. Seedling microhabitat study (operational environment)

B 3 3. Chapter 2. Seed germination experiments

C. Category of experiments.

C.1. Manipulative experiments *sensu* Hurlbert (1984). Chapters 1 and 2

C 2. Mensurative experiments *sensu* Hurlbert (1984). Chapters 3 and 4

In summary, the purpose of this research is to understand fire effects on mixed-conifer stands at Boggs Mountain State Forest (BMSF). This knowledge should lead to recommendations for the management prescriptions. The manager of this Demonstration Forest is interested in a better understanding of vegetation dynamics, the fire effects on both soil and vegetation as well as vegetation management for growing trees (silvicultural practices). To address those needs, I have examined the mechanisms relating fire and its

effects on Douglas-fir and companion species in this particular location with a given climate, topography, geomorphic processes, soil and vegetation.

Presentation

Some replication of statements in various chapters exist because these papers are intended to stand alone (i.e., to be submitted for publication independently)

CHAPTER I

PRESCRIBED BURNING EFFECTS ON INFILTRATION CAPACITIES
IN MIXED-CONIFER FOREST STANDS
AT BOGGS MOUNTAIN STATE FOREST, CALIFORNIA

Domingo Miguel Molina

ABSTRACT: The development of a hydrophobic layer beneath the soil surface is common during wildfires. This study was aimed to evaluate the effect of prescribed burns on water infiltration into the soil (i.e., if there is hydrophobicity) under mixed-conifer forests. The experiment followed a randomized complete block design and had three burn treatments characterized by means of different amounts of forest floor consumption (i.e., control, low, and high consumption). Blocks were 50 to 100 m apart on a low gradient slope covered by Douglas-fir, (*Pseudotsuga menziesii* (Mirb.) Franco), sugar pine (*Pinus lambertiana* Dougl.), and ponderosa pine (*Pinus ponderosa* Dougl.). Infiltration capacity was measured by 100mm-diameter ring infiltrometers on both burned and unburned conditions in a mixed-conifer stand at Boggs Mountain State Forest, California. The infiltration rates were not significantly changed by controlled burns of low fireline intensity and low to high fuel consumption. Therefore, we can reduce fuel accumulations, and thus wildfire hazard, using prescribed burns without significantly changing the

infiltration capacity of the site. Similarly, soil pH was not significantly changed by the controlled burns.

KEYWORDS: Prescribed burns, infiltration, hydrophobicity, forest floor consumption, fireline intensity

INTRODUCTION

Wildfires may cause dramatic changes in soil physical and chemical properties. In particular, the development of a hydrophobic layer beneath the soil surface is common during wildfires. Within this context, how does prescribed burning affect certain physical characteristics of the soil such as infiltration rates and soil pH? In this study, our objective was to determine if infiltration capacity and soil pH are significantly changed after prescribed burns in soils under mixed-conifer stands at Boggs Mountain State Forest (BMSF), north of Middletown, California.

From an ecological point of view, fire is neither a destructive nor a constructive factor *per se*; it simply causes change. However, within the context of objectives determined by humans, outcomes may be described as desirable or non-desirable. Thus, benefits can be obtained from using prescribed burning as a forest management tool; such as, site preparation for seeding or planting, disease control, improvement of wildlife habitat, and reduction of stand-replacing wildland fires. Martin (1981) stated that each burn should be planned to accomplish one or more well defined objectives, at the same time keeping the negative effects of burning below given levels. A single prescribed burn may achieve several benefits, e.g. a properly planned fire can reduce hazardous fuel

accumulations and enhance wildlife habitat. However, if conditions are not carefully prescribed, burns can damage natural resources such as soils by seriously reducing soil wettability or accelerating erosional processes. DeBano (1989) states that fire directly affects soil structure and infiltration. DeBano (1969) found that the wettable surface layer in a soil may vary from more than a meter in depth (before burning) to a few centimeters (after burning). The hydrological characteristics of a chaparral soil change drastically, with fires allowing moderate storms to cause floods of considerable magnitude under burned conditions; and therefore, flood recurrence intervals will be much shorter (Nassieri 1989). Lastly, water repellent soils, though unlikely to be continuous over an entire catchment after a fire event, could increase the probability of overland flow and hence the amount of energy available for soil erosion (Scott and Van Wyk 1990).

Hypotheses

As stated above, our objective was to determine if infiltration capacity is significantly changed after prescribed burns in soils under mixed-conifer stands at BMSF, California. The null hypotheses (H_0) tested and the alternative hypotheses (H_1) are stated bellow:

$H_{0,1}$ = Initial (or dry-soil) infiltration rates are independent of fuel (litter and duff) consumption versus $H_{1,1}$ = initial infiltration rates are negatively correlated with fuel consumption.

$H_{0,2}$ = initial (dry-soil) infiltration rates do not change between burned and control (unburned) conditions versus $H_{1,2}$ = initial infiltration rates do change between burned and control (unburned) conditions.

$H_{0,3}$ = final (or wet-soil) infiltration rates are independent of fuel (litter and duff) consumption versus $H_{1,3}$ = final infiltration rates are negatively correlated with fuel consumption.

$H_{0,4}$ = final (wet-soil) infiltration rates do not change between burned and control (unburned) conditions versus $H_{1,4}$ = final infiltration rates do change between burned and control (unburned) conditions.

$H_{0,5}$ = within the upper 60mm, the soil pH does not change among different levels of burn treatment versus $H_{1,5}$ = within the upper 60mm, the pH does change among different levels of burn treatment

$H_{0,6}$ = within the upper 25mm, the percent of sand particles does not change between the control samples and the samples heated during 4 minutes at 100° C in moist saturated conditions versus $H_{1,6}$ = within the upper 25mm, the percent of sand particles does change between the control samples and the samples heated at during 4 minutes 100° C in moist saturated conditions.

METHODS

Study area

Boggs Mountain State Forest, north of Middletown, California, is located 39°N, 123°W, at about 730-1150 m above the mean sea level. Soils in BMSF are mapped as soil

complexes since distinct soil series are complicatedly intermingled. Parent rocks are andesite, basalt and dacite. The vegetation type is a mixed conifer forest containing the following overstory species: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* Dougl.), sugar pine (*Pinus lambertiana* Dougl.), black oak (*Quercus kelloggii* Newb.), and interior live oak (*Quercus wislizenii* A.DC.). The most common understory species are *Arctostaphylos manzanita* C.Parry, *Arctostaphylos canescens* Eastw., *Ceanothus prostratus* Benth., and *Rhamnus californica* Eschsch.

Experimental design and execution

Soil pH analyses and infiltration tests were conducted on soils from a randomized complete block design (RCBD) of burn treatments. There were four blocks, and three burn treatments characterized by means of different amounts of forest floor consumption (i.e., control, low, and high consumption). Blocks were 50 to 100 m apart in a flat, low gradient slope covered by Douglas-fir, sugar pine, and ponderosa pine.

Each block consisted of three contiguous plots (experimental units) of two meters per side. Treatments were randomly assigned to the plots. Firelines were built around the burn plots to accomplish the burn prescriptions. Firelines were approximately 0.6 m wide and cleared to bare mineral soil. There were 12 experimental units (4 blocks x 3 treatments). Flooding- or cylinder-type infiltrometers (100mm-diameter) were installed to measure: a) dry-soil infiltration capacity, and b) wet-soil infiltration capacity. While 'dry' stands for the first infiltration runs in a location, 'wet' stands for the following seven runs. Four samples were taken in each plot using four similar infiltrometers, simultaneously.

The infiltration experiments were carried out as falling head tests with the initial head of water equal to 340 mm (distance from the ground surface to the water level inside the infiltrometer) and the final water level 61 mm above the ground surface. In order to accomplish that, the infiltrometers were driven into the soil until an infiltrometer mark was even with the soil surface. They were then filled with water, and the time required to drop the water level from 340 to 61 mm was recorded. Eight runs were accomplished for every place in which the infiltrometers were located.

Fire characteristics including flame length, fireline intensity and fuel (duff + litter) consumption were measured during and after the fire. Flame length is the slant length from about the center of the base of the flame to the tip. Fireline intensity was defined by Byram (1959) as the rate of energy release per unit length of fireline; he also developed a relationship between flame length (in meters) and fireline intensity (in kiloWatts per meter).

Duff-pins were used to measure the depth of forest floor consumption. The method employed was to insert eight pins inside the plot to be burned leaving their heads level with the organic layer / air surface interface. After the burn, we were able to record the length (mm) of each pin standing above the new surface. Duff-pins were located close to the plot perimeter (buffer zone) to avoid disturbance in the area in which we would carry out the infiltration experiment. The three burn treatments were accomplished by means of a) no burn (control), b) a single head, surface fire (low consumption treatment), and c) two backing, surface fires (moderate to high consumption treatment). Note that we tried to obtain the high consumption treatment by means of backing the fireline; however, this

was not good enough and we had to burn again a week later. Lastly, a portable soil pH tester (E.W. System Soil Tester, O.S.K., Tokio, Japan) was used to measure pH in the field.

The effect of soil heating on soil texture was tested in a lab experiment. Soils were subjected to two treatments (i.e., control, and heating at 100°C during four minutes in moist saturated conditions) with three replications.

Statistical analysis

The SAS (Schlotzhauer and Littlell 1987) statistical package was used in the analyses of results. Linear models were used for analysis of variance (ANOVA). Following Little and Hills (1978), data were $\log(x+1)$ transformed to better fit the assumptions of ANOVA. The mean square of the variation in infiltration rates among locations within the same experimental unit will be referred as sampling error, and the mean square of the infiltration rates among locations in different experimental units treated alike (same burn treatment) will be called experimental error. In like manner, treatment error will be the mean square of the mean infiltration rates among experimental units treated differently. If the treatment source of variation is not real, then the last two mean squares will be of the same order of magnitude. Otherwise, the treatment error will be expected to be larger since it contains an additional source of variation. Lastly, the power of ANOVA was calculated following Zar (1984). Power is the likelihood of the test to reject the null hypothesis when it is false.

RESULTS

Mean forest floor consumption ranged from 3 mm to 19 mm in the low consumption experimental units, and from 24 to 37 mm in the moderate to high consumption experimental units. The mean forest floor depth was 45 mm before burning. Statistical analysis (t-test) of this data indicates that the different burn treatments significantly differed in consumption (P -value = 0.0081, table 1). Therefore, they were accomplished satisfactorily. Byram's (1959) equation, which relates flame length and fireline intensity, was used to calculate fireline intensity. Flame lengths were 0.5 m (or less) corresponding to fireline intensities of 60 kW/m (or less) which are quite low.

Treatment means of infiltration rates for the first run (i.e., dry condition) ranged from $1.41 (\pm 0.25) \times 10^{-3}$ to $1.62 (\pm 0.49) \times 10^{-3}$ m/s (table 2); they do not differ statistically (P -value = 0.60). Treatment means of infiltration rates for the eighth run (almost steady-state) ranged from $0.66 (\pm 0.11) \times 10^{-3}$ to $0.92 (\pm 0.20) \times 10^{-3}$ m/s (table 2). The prescribed burns conducted in this study did not change infiltration capacity significantly. The power of the tests (when specifying that the smallest difference we wish to detect between the two most different population means be equal to the value of the grand mean of infiltration rates) were low for the early infiltration runs (i.e., < 0.52). However, they were always higher than 0.62 for runs four and thereafter. It is reasonable to specify that the smallest difference we wish to detect between the two most different population means be equal to the grand mean because of the broad variability in infiltration rates reported elsewhere (Scott and Van Wyk 1990, Shakesby *et al.* 1993). Soil pH was 6.3 and did not differ statistically among treatments (P -value = 0.58, table 3). The

power of the test was very high (> 0.996) when specifying that the smallest difference we wish to detect between the two most different means be equal to 0.1 units of pH. It is reasonable to specify 0.1 units of pH as the smallest difference because it was the precision of our measurements.

The soil texture for this site, based upon the hydrometer method, is that of a loam (42% sand, 40% silt, and 18% clay). No significant differences were found between the control soil samples and the soil samples heated at 100°C in moist saturated conditions for four minutes (P-value = 0.88, 0.78, and 0.30 for percent of sand, silt and clay respectively; table 4).

Table 1. Depth in mm of Low versus High forest floor (litter + duff) consumption: Mean and standard error of the mean (SE). Randomized complete block design [4 replications and 8 samples (duff-pins)]. P-value = 0.0081. t-statistic = 3.8841.

TREATMENT	Mean (mm)	SE (mm)
High	30	3
Low	11	4

Table 2. Summary of the infiltration study: mean and standard error of the mean (SE) by consumption treatment (i.e., Control, Low, and High forest floor consumption). Infiltration rates are in 10^{-3} m/s. The first infiltration runs (i1) are the initial infiltration rates, and the eight runs (i8) are the quasi-steady-state infiltration rates.

Treatments	Control [Mean (SE)]	Low [Mean (SE)]	High [Mean (SE)]
Fuel consumption (mm)	0	11 (3)	30 (4)
Flame length ¹ (m)	0	<0.5	<0.5
Fireline intensity ² (kW/m)	0	<60	<60
i1: infiltration rate (mm/s)	1.41 (0.25)	1.46 (0.28)	1.62 (0.49)
i2: infiltration rate (mm/s)	1.06 (0.17)	1.22 (0.21)	1.39 (0.41)
i3: infiltration rate (mm/s)	0.92 (0.13)	0.99 (0.18)	1.23 (0.32)
i4: infiltration rate (mm/s)	0.84 (0.13)	0.88 (0.16)	1.15 (0.28)
i5: infiltration rate (mm/s)	0.79 (0.11)	0.81 (0.14)	1.09 (0.26)
i6: infiltration rate (mm/s)	0.74 (0.10)	0.76 (0.13)	1.02 (0.23)
i7: infiltration rate (mm/s)	0.69 (0.11)	0.72 (0.13)	0.97 (0.22)
i8: infiltration rate (mm/s)	0.66 (0.11)	0.68 (0.13)	0.92 (0.20)

¹ Flame length is the slant length from about the center of the base of the flame to the tip.

² Fireline intensity is defined as the rate of heat released across the depth of a fireline one meter wide.

Table 3. Mean and standard error of the mean (SE) of pH by consumption treatment [(i.e., Control, Low (forest floor consumption), and High (forest floor consumption)]

TREATMENT	MEAN	SE
Control	6.3	0.06
Low	6.24	0.1
High	6.24	0.11

Table 4. Percentage of sand, silt and clay by treatment. Mean and standard error of the mean (SE) in percentages. C - control, T = heated (100°C in moist conditions during 4 minutes). P-values and t-statistics from t-tests are also reported.

Treatment	% Sand [Mean (SE)]		% Silt [Mean (SE)]		% Clay [Mean (SE)]	
C	43.5	(2.5)	37	(1)	19.5	(1.5)
T	44.5	(5.5)	38.5	(4.5)	17	(1)
P-value	0.8838		0.7758		0.2999	
t-statistic	0.1655		0.3254		1.3868	

DISCUSSION

Somewhat surprisingly the prescribed burns conducted in this study did not significantly change the infiltration capacity of the soil. The mean square of treatment error and the mean square of experimental error resulted in the same order of magnitude; therefore, there is not a real source of variation due to the burn treatment. Many studies have related fires to impeded or reduced infiltration as well as increased overland flow and erosional processes (Shakesby *et al.* 1993, Scott and Van Wyk 1990, DeBano 1989). However, Sengonul (1987) found that initial infiltration rates, calculated from field infiltration trials, were increased on lightly burned areas and reduced on heavily burned areas; the slowest infiltration was recorded on unburned water-repellent soils under pine, especially *Pinus brutia* stands.

Similarly, we fail to reject the null hypothesis that soil pH does not differ among treatments (table 3). Since the power of the test was high for the pH and the latest four infiltration runs, we are confident that no differences were found among treatments. On

the other hand, for the first four infiltration runs the power was not high enough to suggest a lack of differences among treatments. Since the infiltration experiments were carried out earlier, leachate might have impaired our ability to detect changes in soil pH after the burn.

In this study, no differences were found in soil texture. In like manner Christensen (1975) did not find textural differences among burned and unburned chaparral soil samples. However, Duriscoe and Wells (1982) found significant changes in soil texture after heating soils at high temperatures (200 to 1000°C); lower clay content and higher sand content after heating. In this paper, the temperature in the heating treatment was 100°C because higher temperatures are very uncommon to last more than a few seconds in prescribed burning (Raison 1979). On the contrary, Duriscoe and Wells (1982) temperature range is adequate for wildfires

DeBano (1989) stated that predicting fire effects in soils requires: (i) characterizing fireline intensity, (ii) relating the fire regime to soil heating, and (iii) quantifying changes in chemical, physical and biological soil properties. In this study, we expanded DeBano's first condition and have considered fireline intensity as well as fuel consumption. Fuel consumption is the amount of fuel (organic matter) consumed per unit area, and is usually given in kilograms per square meter; however, in this study, it is given in millimeters (depth of forest floor removed by combustion). Finney (1991) and Woodard and Martin (1980) found that loading and depth of forest floor were linearly related for *Sequoia sempervirens* and *Pinus contorta* respectively. In this study, forest floor fuel consumption was considered to be a more important fire characteristic than fireline intensity on soil

hydraulic properties. Fireline intensity might affect the soil but only while the fireline resides at the point. On the other hand, glowing combustion may last for hours or even days transferring heat mainly by radiation and conduction. The amount of energy (heat) released to the soil is better estimated from fuel consumption (litter, duff, and vegetation) than from fireline intensity; and residual glowing combustion can account for most of the fuel consumption (Kauffman and Martin 1989). Packham (1970) found convective heat from a surface fire to be about three times that of radiated heat. As most convective heat rose, and only a portion of the radiated heat entered the soil, only about five percent of the heat from the fire heated the soil (Packham 1970). In this study, fuel (duff + litter) consumption ranged from 3 to 37 mm of depth which are considered low to moderate values (mean total depth was 45 mm). If more forest floor fuel is consumed, more heat is released which can affect both biotic and abiotic site factors as well as supply ash which may block soil pores. In addition, more fuel consumption leaves less organic material to protect the soil from raindrop impact.

A physical property quantified in the experiments reported here was the infiltration capacity. Steady-state infiltration capacity (taken as an estimation of the saturated hydraulic conductivity) fall within the range often given for a loam (e.g., Freeze and Cherry 1979). Some depth of forest floor remained after burning; therefore, soil continued to be protected from raindrop impacts. However, firelines depleted of the forest floor (this is a prescribed burn requirement) are subjected to soil erosion by means of raindrop impacts. In these small plots, the ratio of fireline area to burned area is high but in larger, management burns this ratio could be virtually negligible, and erosion minimal. However,

in locations with slope gradients higher than 20 percent. erosional processes might be important after high consumption prescribed burns.

Prescribed burns may differ from wildfires in having both lower fireline intensities and smaller forest floor consumption (Kauffman and Martin 1989, Finney 1991). Therefore, prescribed burn effects on soil water processes might be less dramatic than those from wildfires. Moreover, a given site might develop higher infiltration capacity after a prescribed burn while lower infiltration capacity after a catastrophic wildland fire (i.e., hydrophobic layer).

CONCLUSIONS

This study was designed to characterize the impacts of prescribed burns on both initial and final (steady-state) infiltration capacity. No significant differences were found in either the steady-state infiltration rates or in the early infiltration rates for loamy soils under mixed-conifer canopy after being treated with prescribed burns of low fireline intensities and low to moderate fuel consumption. There were no significant differences between burned treatment and the unburned treatment. The results presented here have implications related to cumulative watershed effects. It appears that prescribed burning does not reduce infiltration rates in loamy soils under mixed-conifer stands. In this study, small plots were used because they are easy to control and monitor. It is important, in future studies, to extrapolate (scale) the hydrological and ecological effects of controlled burns on small plots to large scales as well as to conduct experiments on a broader scale.

CHAPTER II

SEED GERMINATION RESPONSES TO VARIOUS THERMAL REGIMES: HARD-SEEDED SHRUB SPECIES AT BOGGS MOUNTAIN STATE FOREST, CALIFORNIA

Domingo Miguel Molina

ABSTRACT: Fires can affect the germination of seeds of many plant species. The objective of this research was to evaluate the germination response of seeds from several hard-seeded shrub species common to Boggs Mountain State Forest (California). The experimental units were sets of 25 seeds with four replicates. The following species were investigated: *Arctostaphylos manzanita* C. Parry (ARMA), *Arctostaphylos canescens* Eastw. (ARCA), *Ceanothus prostratus* Benth. (CEPR), *Rhamnus californica* Eschsch (RHCA). Experimental investigation provided evidence into germination requirements, and interpretation of these results elucidated fire-related mechanisms associated with plant persistence and regeneration. Treatments were designed to emulate: (1) fire induced scarification, (2) winter stratification, and (3) the effects of leachate from burned litter. RHCA seeds had higher germination when non-stratified versus when stratified, at 80°C versus any other temperature, and in moist heating treatments versus dry ones at the same temperature. Germination of ARCA and CEPR seeds is enhanced by stratification. Germination of ARCA seeds is diminished when thermal treatment levels were either 90

or 100°C. Germination of CEPR seeds is not enhanced by heating at temperatures ranging from 70 to 100°C. RHCA and ARCA seeds had similar germination rates in leachate and non-leachate treatments. ARMA percentage germination was negligible.

KEYWORDS: germination, fire induced scarification, stratification, leachate

INTRODUCTION

Historically, wildfires have burned wildlands as both headfires and backfires under a broad range of fuel and weather conditions and have resulted in diverse vegetative responses. The numerous plant adaptations to various fire regimes indicates that fire as an environmental factor has been a strong selective force in plant communities.

In particular, fires can affect the germination of seeds of many plant species. The objective of this research was to evaluate the germination response of a variety of seeds of hard-seeded shrub (early successional) species common in Boggs Mountain State Forest (BMSF), California. Specifically, how do fire-emulating treatments affect seed germination?. The term hard-seededness describes a dormant mechanism entirely controlled by the physical characteristics of the seed coat which prevents water uptake by otherwise non-dormant seed embryos (Probert 1992). Germination requirements were investigated for seeds of two species of the Ericaceae family (*Arctostaphylos manzanita* C.Parry, *Arctostaphylos canescens* Eastw.) and another two species of the Rhamnaceae family (*Ceanothus prostratus* Benth., *Rhamnus californica* Eschsch.). Germination requirements of many native plants of California are compiled in Keeley (1987) and

Emery (1988), and for woody plants growing in the United States in Schopmeyer (1974). *Arctostaphylos* is reviewed by Berg (1974), *Ceanothus* by Reed (1974), and *Rhamnus* by Hubbard (1974).

The vegetation type of BMSF is 'Ponderosa pine - Douglas fir' in Wright and Bailey (1982) classification of vegetation and fire effects. In this vegetation type, slash reduction after logging is used to reduce fuels and hence wildland fire hazard. The use of prescribed burning for slash reduction breaks the dormancy of shrub seeds in the soil. Shrubs may be very prevalent after a burn due to both sprouting and / or germination from seed. This forest has an active timber production; therefore, there is high interest in favoring conifers versus shrub species.

Hypotheses

For each of the species listed above, the following null hypotheses were studied:

$H_{0,1}$ = Leachate from burned litter does not change seed germination rates (i.e., those of clean water).

$H_{0,2}$ = Percent germination does not vary with the level of thermal treatment.

$H_{0,3}$ = Percent germination does not vary among wet and dry treatments at the same temperature.

$H_{0,4}$ = All the species in this study benefit equally from winter stratification.

$H_{0,5}$ = The different germination treatments applied do not interact.

METHODS

Study area

Boggs Mountain State Forest (BMSF), north of Middletown, California, is located 39°N, 123°W, at about 730-1150 m above the mean sea level. The vegetation type is a mixed conifer forest containing the following overstory species: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* Dougl.), sugar pine (*Pinus lambertiana* Dougl.), black oak (*Quercus kelloggii* Newb.), and interior live oak (*Quercus wislizenii* A.DC.). The most common understory species are the ones here studied.

Experimental design

This is a *manipulative* experiment (*sensu* Hurlbert 1984) and follows a randomized complete design. The experimental units (EU) are sets of 25 seeds. For each species there are 36 treatments and 4 replicates (lots of 25 seeds). Treatments were designed to emulate: (1) fire induced scarification, (2) winter stratification, and (3) leachate from burned litter.

Experimental execution

Seeds were randomly selected from Boggs Mountain. The experiment involved the following factors:

- A. scarification; a temperature treatment with six levels: 25°C, 60°C, 70°C, 80°C, 90°C, and 100°C.
- B. dry versus saturated air while scarification takes place

C. winter-stratification: control versus cold-wet-stratification (3 months at 2°C)

D. watering: clean water versus leachate from burned forest floor

Stratification treatment followed scarification. Not all A×B×C×D combinations are studied. In this manner, instead of 72 (6×2×3×2) treatments, only 36 were considered (table 1). Because of scarcity of CEPR seeds, treatments involving leachate and treatments involving heating at 60°C, and those non involving leachate were not carried out.

Table 1. Factors involved in the germination experiment by species. S = with stratification, NS = without stratification, RHCA = *Rhamnus californica*, CEPR = *Ceanothus prostratus*, ARCA = *Arctostaphylos manzanita*, ARMA = *Arctostaphylos canescens*. n/a = treatment not apply, -- = treatment with negligible germination, * = treatment with appreciable germination (used in the statistical analyses).

FACTORS				SPECIES			
heating	moisture ¹	stratification	leachate	RHCA	CEPR	ARCA	ARMA
25°C	N/A	S	L	--	n/a	*	--
25°C	N/A	S	NL	--	*	*	--
25°C	N/A	NS	L	*	n/a	--	--
25°C	N/A	NS	NL	*	--	--	--
60°C	Dry	S	NL	--	n/a	*	--
60°C	Dry	NS	NL	--	n/a	--	--
60°C	Moist	S	NL	--	n/a	*	--
60°C	Moist	NS	NL	--	n/a	--	--
70°C	Dry	S	L	--	n/a	*	--
70°C	Dry	S	NL	--	*	*	--
70°C	Dry	NS	L	*	n/a	--	--
70°C	Dry	NS	NL	*	--	--	--
70°C	Moist	S	L	--	n/a	*	--
70°C	Moist	S	NL	--	*	*	--
70°C	Moist	NS	L	*	n/a	--	--
70°C	Moist	NS	NL	*	--	--	--
80°C	Dry	S	L	--	n/a	*	--
80°C	Dry	S	NL	--	*	*	--
80°C	Dry	NS	L	*	n/a	--	--
80°C	Dry	NS	NL	*	--	--	--
80°C	Moist	S	L	--	n/a	*	--
80°C	Moist	S	NL	--	*	*	--
80°C	Moist	NS	L	*	n/a	--	--
80°C	Moist	NS	NL	*	--	--	--
90°C	Dry	S	L	--	n/a	--	--
90°C	Dry	S	NL	--	*	--	--
90°C	Dry	NS	L	--	n/a	--	--
90°C	Dry	NS	NL	--	--	--	--
90°C	Moist	S	L	--	n/a	--	--
90°C	Moist	S	NL	--	*	--	--
90°C	Moist	NS	L	--	n/a	--	--
90°C	Moist	NS	NL	--	--	--	--
100°C	Dry	S	NL	--	*	--	--
100°C	Dry	NS	NL	--	--	--	--
100°C	Moist	S	NL	--	*	--	--
100°C	Moist	NS	NL	--	--	--	--

¹ Dry and moist conditions during the heating treatment. 25°C correspond to no heating treatment and, therefore, dry and moist do not apply here.

Each heat treatment lasted four minutes because this represents the time duff and soil heats at high temperatures during fires. Once the scarification treatment was applied to the experimental units, seed germination tests were performed in Petri dishes (8 cm in diameter) on a fiber-glass paper, over a thin bed of perlite. The experimental units were regularly, slightly watered, and those involving cold stratification were placed in a refrigerator at 2°C for three months. A seed protectant agriculture fungicide (Gustafson, Gustafson Inc.) was applied evenly to all the EU. The active ingredient is Captan; this is, N-trichloromethylthio-4-cyclohexene-1-2-dicarboximide. This fungicide treatment was aimed to those pathogens most likely to cause disease development during propagation (i.e., *Phytophthora*, *Fusarium*, *Pythium*). Seed germination was recorded twice per week by presence of an emerged radicle. In this study, a seed was considered germinated when radicle was longer than half of the maximum length of the seed. After each count, the germinated seeds were discarded.

Statistical analysis

The SAS (Schlotzhauer and Littlell 1987) statistical package was used in the analyses of results. Linear models were used for analysis of variance (ANOVA), and orthogonal F tests (orthogonal contrasts) were used in the process of mean separation because most statisticians agree that they provide a more precise separation than multiple comparison tests (Day and Quinn 1989). Square root transformation of percentage germination data always improved the fulfillment of ANOVA assumptions. Therefore, statistical analysis was performed with these transformed data, and SRG stands for root

square transformation of the percent germination. However, tables report means and standard errors of the mean (SE) obtained by transforming back the SRG means and SE.

Research Hypotheses

Several specific hypotheses can be drafted to test for statistical significance (orthogonal contrasts). An estimation of the treatment mean (i.e., average of the four replicates) is denoted by μ , and subscripts identify the treatment (combination of factors) applied. C stands for control (25°C), D for dry heating, M for moist treatment, L for burned litter leachate (lack of L for clean water treatment), 70 for heating at 70°C, and other temperatures similarly.

Q1 H_0 : Seed germination by means of watering with clean water and with burned litter leachate differ only due to chance

$$H_0: \mu_C + \mu_{D70} + \mu_{D80} + \mu_{M70} + \mu_{M80} = \mu_L + \mu_{D70L} + \mu_{D80L} + \mu_{M70L} + \mu_{M80L} \text{ versus}$$

$$H_1: \mu_C + \mu_{D70} + \mu_{D80} + \mu_{M70} + \mu_{M80} \neq \mu_L + \mu_{D70L} + \mu_{D80L} + \mu_{M70L} + \mu_{M80L}$$

Q2 H_0 : Seed germination by pooling heating treatments at both 70 and 80°C versus no heating due differ only to chance

$$H_0: 4\mu_C + 4\mu_L = \mu_{D70} + \mu_{D80} + \mu_{M70} + \mu_{M80} + \mu_{D70L} + \mu_{D80L} + \mu_{M70L} + \mu_{M80L} \text{ versus}$$

$$H_1: 4\mu_C + 4\mu_L \neq \mu_{D70} + \mu_{D80} + \mu_{M70} + \mu_{M80} + \mu_{D70L} + \mu_{D80L} + \mu_{M70L} + \mu_{M80L}$$

Q3 H_0 : Seed germination by means of heating at 70°C and at 80°C differ only due to chance

$$H_0: \mu_{D70} + \mu_{M70} + \mu_{D70L} + \mu_{M70L} = \mu_{D80} + \mu_{M80} + \mu_{D80L} + \mu_{M80L} \text{ versus}$$

$$H_1: \mu_{D70} + \mu_{M70} + \mu_{D70L} + \mu_{M70L} \neq \mu_{D80} + \mu_{M80} + \mu_{D80L} + \mu_{M80L}$$

Q4 H_0 : Seed germination after dry and moist treatments differ only due to chance

$$H_0: \mu_{D70} + \mu_{D80} + \mu_{D70L} + \mu_{D80L} = \mu_{M70} + \mu_{M80} + \mu_{M70L} + \mu_{M80L} \text{ versus}$$

$$H_1: \mu_{D70} + \mu_{D80} + \mu_{D70L} + \mu_{D80L} \neq \mu_{M70} + \mu_{M80} + \mu_{M70L} + \mu_{M80L}$$

Q5 H_0 : In moist conditions, seed germination by means of watering with clean water and with burned litter leachate differ only due to chance

$$H_0: \mu_{M70} + \mu_{M80} = \mu_{M70L} + \mu_{M80L} \text{ versus } H_1: \mu_{M70} + \mu_{M80} \neq \mu_{M70L} + \mu_{M80L}$$

Q6 H_0 : Seed germination by means of heating at 80°C and no heating differ only due to chance

$$H_0: 2\mu_C + 2\mu_L = \mu_{D80} + \mu_{M80} + \mu_{D80L} + \mu_{M80L} \text{ versus } H_1: 2\mu_C + 2\mu_L \neq \mu_{D80} + \mu_{M80} + \mu_{D80L} + \mu_{M80L}$$

Q7 H_0 : When seeds are not heated, germination by means of watering with clean water and with burned litter leachate differ only due to chance

$$H_0: \mu_C = \mu_L \text{ versus } H_1: \mu_C \neq \mu_L$$

RESULTS

In RHCA seeds, temperatures others than of 25 (control), 70, and 80°C were not included in the analysis of variance because there they yielded almost no germination regardless of the levels of the other factors. RHCA seeds after stratification yielded little to none germination (9 seeds out of 1400, or 0.64%). However, RHCA without stratification treatment yielded more germination (9-31%) than with stratification and significant differences in germination among different levels of the other factors were found (table 2). Specifically, two out of the seven planned, orthogonal contrasts resulted statistically different at $\alpha = 0.05$ (table 2). From those contrasts, we inferred that i)

heating at 80°C yielded more germination than at 70°C ($23\pm 2\%$ vs. $12\pm 3\%$, P-value=0.0129) and than at 25°C ($23\pm 2\%$ vs. $15\pm 4\%$, P-value = 0.0687), and ii) leachate treatment, when no heating was involved, reduced germination rates; this is, $23\pm 5\%$ without leachate versus $9\pm 1\%$ with leachate (P-value = 0.0149). However, with heating treatment (others than the control, 25°C), germination rates were not reduced significantly by leachate treatment. Results also suggested that moist treatments yielded higher germination than dry treatment (P-value=0.1027), we could not reject the null hypothesis that seed germination by means of heating at 70 and 80°C versus no heating only differ due to chance (i.e., contrast Q2, table 2). A factorial analysis (table 3) showed that the interaction between temperature and moisture condition was highly significant (P-value=0.0001). At 70°C, dry conditions yielded lower seed germination than moist conditions. However, at 80°C the opposite was true. Similarly the interaction between temperature and water chemistry was also significant (P-value=0.0116). At 70°C, the leachate treatment yielded higher seed germination than non leachate treatment. However, at 80°C the opposite was true (table 2).

CEPR seeds without stratification treatment yielded zero germination; however, some germination occurred after the first chilling period (65 seeds out of 900, or 7.2%). ARCA seeds without stratification treatment yielded zero germination. Some germination occurred after the first stratification period (25 seeds out of 1800, or 1.4%). After the second stratification period, 52 seeds (2.9%) had germinated. Germination of ARCA and CEPR seeds is enhanced by stratification. Germination of ARCA seeds is diminished (i.e., percent germination was negligible) when thermal treatment levels were either 90 or

100°C. ARCA seeds had similar germination rates in leachate and non-leachate treatments. Germination of CEPR seeds is not enhanced by heating at temperatures ranging from 70 to 100°C. For both ARCA and CEPR seed populations, percent germination did not change significantly among the treatments that yielded appreciable germination (table 1). In those treatments, mean ARCA germination was 4.0%, ($F_{ARCA} = 0.85$, $P_{ARCA} = 0.58$) and mean CEPR germination was 6.5% ($F_{CEPR} = 0.93$, $P_{CEPR} = 0.51$). ARMA germination after one winter stratification treatment was negligible (one seed out of 1400). ©

Table 2. *Rhamnus californica* percent germination: Orthogonal contrasts and their P-values. DF = degrees of freedom, Mean = percent germination (%), SE = standard error of the mean. Statistical analyses were performed after square root transformation of the percent germination data.

Contrast	DF	P-values
Q1 all 'clean water' versus all 'leachate' treatments	1	0.3085
Q2 25°C versus a pool of 70°-80°C treatments	1	0.7226
Q3 70°C versus 80°C treatments	1	0.0129
Q4 Dry versus Moist treatments	1	0.1027
Q5 In moist conditions, leachate versus non leachate treatments	1	0.7172
Q6 25°C versus 80°C treatments	1	0.0687
Q7 Control versus leachate and no heating treatment	1	0.0149

Contrast	The two contrasting treatments	germination (%)	
		Mean	SE
Q1	clean water	18.7	0.8
	leachate	14.7	0.5
Q3	70°C	11.8	3.3
	80°C	23.1	2.5
Q4	dry	13.4	3.4
	moist	21.0	3.0
Q6	25°C	15.3	3.5
	80°C	23.1	2.5
Q7	control	23.2	5.3
	leachate and no heating	8.9	0.9

The power of tests performed were very high (> 0.99) in all cases. There was a low probability of accepting a null hypothesis when it is false or committing a type II error. The way to determine power was to specify the smallest difference we wish to detect between the two more different population means (Zar 1984). This value was set equal to 5% germination.

Table 3. *Rhamnus californica* percent germination: Factorial analysis and F- and P-values. Factors: moisture (dry and moist), temperature (70 and 80°C), and water (leachate and clean water). Mean = mean germination (%), SE = standard error of the mean. Statistical analyses were performed after square root transformation of the percent germination data.

Source	F-value	P-values
MOISTURE	9.50	0.0051
TEMPERATURE	21.39	0.0001
MOISTURE × TEMPERATURE	32.60	0.0001
WATER	0.29	0.5926
MOISTURE × WATER	0.29	0.7324
TEMPERATURE × WATER	7.47	0.0116

Interaction	germination (%)	
	Mean	SE
MOISTURE × TEMPERATURE		
Dry 70°C	4.9	1.7
Dry 80°C	26.7	2.1
Moist 70°C	22.5	4.8
Moist 80°C	19.7	4.1

TEMPERATURE × WATER	Mean		SE	
70°C Leachate	14.6	6.1		
70°C Non leachate	10.2	3.2		
80°C Leachate	19.0	3.7		
80°C Non leachate	27.7	2.4		

DISCUSSION

The purpose of this investigation was to assess the effect of heating, moisture conditions, winter stratification and leachate on germination rates of several chaparral species, as well as the possible interactions of those factors. Seed responses to daily

changes in temperature (Fenner 1985) and light (Pons 1992) were not addressed. The data suggest that germination rates were low for most species regardless of treatment.

Our results indicate that RHCA yields less germination when winter stratified than when not stratified which is in general agreement with the literature (Hubbard 1974, Emery 1988, Young and Young 1992). Then CEPR, ARCA and ARMA seed populations were dormant while RHCA seed population was mostly non-dormant. CEPR, ARCA and ARMA are obligate seeders, while RHCA do resprout after fire.

Heating at 80°C yielded the maximum germination in RHCA seeds indicating that lower temperature might not have stimulated germination, and higher temperatures might have lessened seed viability. These results highlight the fine line that exists between seed germination being enhanced by brief but intense heating and seed mortality from excessive temperature. Also in laboratory studies, Gratkowski (1965) showed that heat, applied by a variety of medium, stimulated germination of *Ceanothus* species; minimum soil temperatures inducing germination were 45-65°C, optimum were 80-105°C, and lethal temperatures were about 120°C. However, in the study presented here, *Ceanothus prostratus* germination did not differ in treatments at 25, 70, 80, 90, and 100°C. Other laboratory experiments have shown that a few minutes at high temperatures is an effective treatment to stimulate hard-seeded seeds to germinate in Chilean matorral (Muñoz and Fuentes 1989), Mediterranean shrubs (Thanos and Georghiou 1988) and in the pineywoods of SW USA (Martin *et al.* 1975). Many other studies have found heat treatment to increase germination rates of many shrub and herbaceous species (Quick 1935, Sampson 1944, Stone and Juhren 1951, Stone and Juhren 1953, Hadley 1961,

Maruyama and Uganamoto 1989). Keeley and Keeley (1987) state two theories accounting for the breaking of seed dormancy in chaparral after fire: 1) seed are inhibited from germination by the mature chaparral vegetation (allelopathy) and fire releases seeds from this inhibition, or 2) seed germination is directly stimulated by fire. Roberts (1988) found that three different seed physiological processes were affected by temperature. First, temperature and moisture content determines the rate of seed deterioration; second, temperature affects dormancy loss in dry seeds and patterns of dormancy in moist seeds; and third, temperature determines the rate of germination in non-dormant seeds.

Moist heating treatments appeared to be (P -value=0.1027) more effective in increasing RHCA germination. This may be explained by the fact that water vapor is a better heat transfer media than dry air. However, a moist treatment will be more likely to damage seed viability than dry treatment at the same temperature. In dry Mediterranean summers, seeds are in a low moisture environment and more heat resistant (Probert 1992) being less likely to be damaged by fire. In contrast, spring or fall controlled burns may favor conifer regeneration rather than germination of hard seeded species which benefit from fire induced scarification. Therefore, both spring or fall controlled burns are recommended as management tools to favor conifer regeneration in BMSF.

In this study, leachate from burned duff did not significantly reduced germination responses. However, the heating factor interacted with the leachate one (table 3) and when no heating was applied germination was diminished by leachate from burned duff. Christensen and Muller (1975) found that aqueous leaf washings from *Adenostoma fasciculatum* reduced germination and growth in ten plant species common in burned

chaparral areas in California. Similar inhibitory results were found by Keeley (1987) and by Keeley and Keeley (1987) in California chaparral. Although most organic ions do not have any specific effect on seed germination (Egley and Duke 1985), an inhibitory role is claimed for various organic substances, often involving allelopathy (Probert 1992).

In regard to ARCA and CEPR, winter stratification improved germination which is in general agreement with the literature (Berg 1974, Reed 1974). Since the power of ANOVA was high, we can infer that CEPR and ARCA germination percentages do not change within thermal treatment levels 25 to 100°C, and 25 to 80°C respectively (i.e., had differences really existed, the experiment was sensitive enough to detect them). Although, for many species, a single period of chilling is enough to overcome dormancy, a second winter doubled total germination in ARCA seeds in this study. It seems that evolution has led to slow germination rates from well stocked seed banks in the soil, in both ARCA (2.9% germination after two winters) and CEPR (7.2% after one winter). Although the power of the test was high, the low germination rates of these species might require longer spans of time to detect statistically different germination responses to the treatments studied here.

Heating lasted four minutes in all treatments because this is representative of the duration of higher temperatures at a site (in the field); however, some additional heat transfer from the glowing combustion phase (in the field) might be responsible for differences in scarification, and therefore, germination rates and percentages. Had heating treatments (in the lab) accounted for the additional heat transfer provided by the glowing combustion phase, the scope of this investigation might have been enhanced. It is

important to note, that species with a heat requirement to break dormancy might be stimulated to germinate by surface soil temperature in excess of 70°C occurring on south-facing slopes (Christensen and Muller 1975, Washitani 1988).

CONCLUSIONS

A more detailed knowledge of any given seed population of germination requirements regarding temperature, soil moisture, seed coat scarification, soil chemistry and others will provide a better understanding of patch dynamics in natural vegetation. In this study, germination responses (to the factors involved in the experiment) varied among the different shrub species. *Rhamnus californica* seeds had higher germination rates when not-stratified than when stratified, higher rates with moist heat treatment than with dry heat, and higher rates at 80°C than at 70°C. Germination of *Arctostaphylos canescens* and *Ceanothus prostratus* seeds is enhanced by stratification. Germination of *Arctostaphylos canescens* seeds is diminished at 90 and 100°C. Germination of *Ceanothus prostratus* seeds is not enhanced by temperature ranging from 70 to 100°C. RHCA and ARCA seeds had similar germination rates in leachate and non-leachate treatments. ARMA germination after one winter stratification treatment was negligible.

A sound vegetation management will result from merging this results with some studies that conclude that the present species composition may be maintained by variable burning regimes (Keeley 1987, Christensen and Muller 1975), and others state that "pyrodiversity promotes biodiversity" (Martin and Sapsis 1992). Specifically, prescribed burning provide a broad range of fire effects (i.e., some hot spots within a cool burn).

Therefore, the use of spring or fall controlled burns may favor conifer regeneration rather than germination of hard seeded shrub species (i.e., seeds in moist conditions and then non fire resistant), while providing diverse microhabitats for different species to coexist.

CHAPTER III

PRESCRIBED BURN EFFECTS ON SPATIAL DISTRIBUTION PATTERNS AND PLANT DIVERSITY INDICES IN MIXED-CONIFER STANDS IN CALIFORNIA

Domingo Miguel Molina

ABSTRACT: Species diversity and stand structure are two major attributes of vegetation important to forest management. This study addresses short term (< 5 years) ecological effects of prescribed burns on plant diversity and spatial distribution patterns (i.e., random, uniform, and cluster) by comparing stands with different prescribed burn histories (throughout Boggs Mountain State Forest, California). Distance sampling techniques were used in the study of spatial distribution patterns. Results support the hypothesis that prescribed fire removes trees and shrubs preferentially from clumped areas leaving a more random distribution of individuals. In the overstory layer study, trees are more sparsely distributed in prescribed burned stands, and this is also suggested for the understory layer. The mechanism which may explain this observation is that clumps differ from open areas by having more dead and down fuels. Therefore, individual plants in clumps have a higher probability for mortality during a fire event (i.e., leaving a more random distribution of individuals). Diversity indices suggested consistently that in the prescribed burning conditions plant species diversity was lower than in controls. Evenness indices

consistently suggested a more even distribution of individuals among species in the control stands versus a more clear dominance (in numbers) by one or two species in the prescribed burned stands.

KEYWORDS: spatial patterns, species diversity, evenness, mixed-conifer stands

INTRODUCTION

Many vegetation types are predisposed to periodic, though unpredictable, disturbance which destroys adults and creates opportunities for recruitment (Noble 1981, Pickett and White 1985). Disturbance has been defined as an event that removes biomass (Grime 1979) and modifies both community structure and resource availability (White and Pickett 1985). Silvertown (1987) states that disturbance may promote coexistence by reducing the dominant competitors. This work addresses short term (< 5 years) effects of prescribed burns on vegetation. Prescribed burns make up most of the disturbance regime of these stands and are purposely implemented to minimize the disturbance that might result from the occurrence of wildfires.

Species diversity and stand structure are two major attributes of vegetation important to forest management. In this study, our goal was to determine if the spatial distribution patterns (i.e. random, uniform, and clusters) of plant individuals vary among stands with different prescribed burn histories in mixed-conifer stands at Boggs Mountain

State Forest (BMSF), north of Middletown, California. We also compared species diversity and evenness indices among stands with different burn histories.

The first active hypothesis ($H_{1,1}$) was that prescribed burning removes trees and shrubs preferentially from clumped areas leaving a more random (i.e., less clumped) distribution of individuals. The second active hypothesis ($H_{1,2}$) was that species diversity and evenness indices are different in underburned stands compared to control stands. Underburned means that the stand was prescribed burned to consume surface litter and understory with minimum damage to the overstory vegetation. Control stands were those not subjected to underburning. Specific null hypotheses to be tested are:

$H_{0,1}$ = In a given stand, the overstory spatial distribution is random.

$H_{0,2}$ = In a given stand, the understory spatial distribution is random.

$H_{0,3}$ = Overstory spatial distributions do not change from control to underburned stands.

$H_{0,4}$ = Understory spatial distributions do not change from control to underburned stands.

$H_{0,5}$ = Overstory diversity and evenness indices do not change from control to underburned stands.

$H_{0,6}$ = Understory diversity and evenness indices do not change from control to underburned stands.

METHODS

Study site

Boggs Mountain State Forest (BMSF), north of Middletown, California, is located 39°N, 123°W, at about 730-1150 m above the mean sea level. The vegetation type is a

mixed conifer forest containing the following overstory species: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* Dougl.), sugar pine (*Pinus lambertiana* Dougl.), black oak (*Quercus kelloggii* Newb.), and interior live oak (*Quercus wislizenii* A.DC.). The most common understory species are *Arctostaphylos manzanita* C.Parry, *Arctostaphylos canescens* Eastw., *Ceanothus prostratus* Benth., and *Rhamnus californica* Eschsch.

Mensurative (*sensu* Hurlbert 1984) experiment layout

This study was carried out in different stands or mensurative experimental units (MEU) selected in different locations throughout BMSF. Different strata (i.e., overstory and understory) were studied independently. As a result of this, four different studies (table 1) are reported: overstory spatial distribution, understory spatial distribution, overstory species diversity, and understory species diversity. All them involved six stands (MEU) except overstory species diversity which consisted of only five. These stands were defined and named in terms of their locations (A, B, C, D, and E) throughout BMSF, and the burning history (X, Y, and Z) as shown in table 1. X- stands not burned for longer than five years, Y- stands last underburned in late fall 1988, and Z- stands underburned in early 1993. Statistical analyses (see below) compared X with Y stands (for the overstory study), and contrasted X with the pool of Y and Z stands (for the understory studies). No overstory data was taken for Z-stands (stands underburned in early 1993) because it was judged that a lapse of several seasons is required to assess effects on overstory vegetation.

It was assumed that *control* (X) stands and *underburned* (Y and Z) did not differ any other ecological feature than in their burn histories. Had this been a manipulative (*sensu* Hurlbert, 1984) experiment, the randomization process would have allowed us to remove the source of variability due to the *a priori* differences that might exist among experimental units.

Table 1. Mensurative experimental units (MEU or stands). These MEU were defined and named in terms of their locations (A, B, C, D, and E) throughout BMSF, and the burning history (X, Y, and Z). X- stands not burned for longer than five years, Y- stands last underburned in late fall 1988, and Z- stands underburned in early 1993.

Objective of the study	Number of MEU	MEU and their burning histories
Spatial distribution (overstory)	6	AX, BX, CX, BY, CY, DY
Spatial distribution (understory)	6	AX, CX, EX, AZ, CY, EZ
Species diversity (overstory)	5	AX, CX, EX, CY, DY
Species diversity (understory)	6	AX, CX, EX, AZ, CY, EZ

Mensurative experiment execution

Data were taken in 1992 and early 1993. For the overstory study, only trees higher than 1.3 meters were considered. For the understory study, both trees higher than 0.3 meters and smaller than 1.3 meters, and shrubs higher than 0.3 meters were considered. The analysis of different strata separately was intended to enhance the ecological meaning of counts of individuals, since most ecologists agree that the importance of a plant species in a stand should be based on such quantities as biomass or productivity rather than

counts of individuals. This segregation of individuals into two different strata was judged to accommodate, in part, that concern.

Two persons were necessary in the collection of data. To obtain the pair of distances required, random directions and distances were used to locate random points. Then (1) the distance-from the point to the nearest plant individual, and (2) the distance from the individual to its nearest neighbor were recorded. One hundred pairs of distances were recorded for each stand (MEU), and at the same time the species identity of the 200 individuals involved was recorded for the diversity analyses. Lastly, although the techniques outlined here are tedious, they are simple and nondestructive.

Statistical Analysis

From the sampling distances obtained, two indices of spatial pattern were derived for each stand: 'C' or T-square Index of Spatial Pattern (Ludwig and Reynolds 1988), and 'I' or Distance Index of dispersion (Johnson and Zimmer 1985).

$$C = (1/s) \sum_{i=1}^s [x_i^2 / (x_i^2 + 0.5y_i^2)] \quad I = (s+1) \frac{\sum_{i=1}^s x_i^4}{(\sum_{i=1}^s (x_i^2))^2}$$

where s is the total number of points (200), x_i point-to-nearest-individual distance, and y_i individual-to-the-nearest-neighbor distance. The value of C is approximately one-half for random patterns, significantly less than one-half for uniform patterns and significantly greater than one-half for clumped patterns. The value of I is approximately 2 for random

patterns, significantly less than 2 for uniform patterns and significantly greater than 2 for clumped patterns.

From the counts of individuals belonging to a given species, indices of species diversity, and species evenness were derived for each stand. The sample size (s) was always 200 to properly compare the indices below some of which are sensitive to sample size. N is the total number of species in a sample.

Diversity indices: λ or lambda (Simpson 1949 index), H' (Shannon and Weaver 1949 index), $N1$ (Hill 1973 index), and $N2$ (Hill 1973 index).

$$\lambda = \sum_{i=1}^N \frac{n_i(n_i-1)}{s(s-1)} \quad H' = -\sum_{i=1}^N (n_i/s) \ln(n_i/s) \quad N1 = e^{H'} \quad N2 = 1/\lambda$$

where s is the sample size (as above) and n_i is the number of individuals of the i th species. The higher the values of H' , $N1$ and $N2$ (and the lower the value of λ) the higher the diversity of the community. $N1$ is an exponentiated form of H' , and $N2$ is the inverse of λ . $N1$ and $N2$ are more appealing to ecologist because their units are (number of) *species*, and $N1$ represents the number of *abundant* species and $N2$, the number of *very abundant* species.

Evenness indices: $E1$ (Pileu, 1975), $E2$ (Sheldon, 1969), $E3$ (Heip, 1974), $E4$ (Hill, 1973), $E5$ (modified from Hill). Evenness refers to how species abundance are distributed among the species. The value of these indices decreases from even abundance among species to dominance by a few species.

$$E1 = \frac{H'}{\ln(N)} \quad E2 = \frac{e^{H'}}{N} = \frac{N1}{N} \quad E3 = \frac{e^{H'-1}}{N-1} = \frac{N1-1}{N-1}$$

$$E4 = \frac{1/\lambda}{e^{H'}} = \frac{N2}{N1} \quad E5 = \frac{(1/\lambda)^{-1}}{e^{H'-1}} = \frac{N2-1}{N1-1}$$

The computer programs TSQUARE.BAS and SPDIVERS.BAS (Ludwig and Reynolds 1988) were used for the statistical analysis of patterns of species distribution and species diversity, respectively. After computing these indices, t-tests were used to evaluate the existence of significant differences in indices among underburned versus control stands. Paired t-tests were used when appropriate. The SAS (Schlotzhauer and Littlell 1987) statistical package was used in these data analyses. Additionally, a test proposed by Hutchenson (1970) was used to test the null hypothesis that the diversities (H') of two sample populations (i.e., before and after burning) are equal. The power of each t-test was calculated following Zar (1984).

RESULTS

Indices of spatial distribution

Overstory layer

In regard to C or T-square index of spatial pattern (table 2). BY, CY and DY, the three burned stands, we cannot reject the underlying null hypothesis of random distribution of individuals ($H_{0,1}$). However, this is not the case in CX because its $z(C)$ statistic is too high ($z(C)=3.44$) for $\alpha = 0.05$. Therefore, for CX, I have to reject the null hypothesis, and as C equals 0.60, there is a clumped distribution of individuals. In the other unburned units, the T-square index of spatial pattern (C) resulted in failure to reject

the null hypothesis. A t-test for the C index fails to reject the null hypothesis ($H_{0,3}$) of burned and unburned conditions having a similar C mean value. However, the power of this t-test was low; therefore, we cannot accept $H_{0,3}$ (just fail to reject). With respect to the I distance index of dispersion, all units have a clumped pattern with higher values (higher clumpiness) for unburned stands (4.01, 3.43, and 3.52) versus the burned stands (2.99, 3.15, and 2.77). In a t-test, means for the I index were different for control and underburned stands (table 2). Therefore, the I index indicates us that clumpiness is higher in control than in underburned stands (reject $H_{0,3}$). XMEAN (point-to-nearest-individual distance), and YMEAN (individual-to-the-nearest-neighbor distance) resulted in significantly higher values for burned stands (table 2): this is, trees are more sparsely distributed in underburned than in control stands.

Understory layer

From data of C-index (table 2), we fail to reject the underlying null hypothesis ($H_{1,2}$) of random distribution of individuals in the understory layer in stands AX, AZ, and EZ. In the rest of the stands, we reject the null hypothesis, and as C values are greater than 0.5, we accept that the pattern of distribution of individuals is clumped. As in the overstory layers, I-index leads to the rejection of random distribution in every stand. And being I values higher than 2, clumped distribution is assumed. A t-test for the values of the I-index suggests (P-value = 0.1836) higher clumpiness in the control stands (rejection of $H_{0,4}$). Both t-tests (for C and I indices) resulted of low power. Both XMEAN and YMEAN were larger for burned stands; however, the P-values in the t-tests were relatively high

(i.e., 0.1555, 0.0734 respectively), and their power high. Therefore, although these distances appear to be larger for burned stands, results are inconclusive.

Table 2. Spatial pattern indices computed. Mean and standard error of the mean (in parenthesis) by treatment [*control* stands (N=3) and *underburned* stands (N=3)]. X- stands not burned for longer than five years, Y- stands last underburned in late fall 1988, and Z- stands underburned in early 1993.

<u>Overstory vegetation</u>				
Treatment	C ¹	I ²	XMEAN ³ (cm)	YMEAN ⁴ (cm)
X	0.564 (0.018)	3.65a (0.18)	112a (4.9)	108a (12.8)
Y ⁵	0.549 (0.002)	2.97b (0.11)	165b (13.1)	164b (10.9)
t-statistic	0.8193	3.2353	3.7825	3.3691
P-value	0.4586	0.0318	0.0194	0.0281
<u>Understory vegetation</u>				
Treatment	C ¹	I ²	XMEAN ³ (cm)	YMEAN ⁴ (cm)
X	0.569 (0.008)	3.86 (0.69)	108 (17)	110a (20)
Y and Z	0.561 (0.006)	6.72 (1.65)	166 (29)	171b (16)
t-statistic	0.7965	1.6057	1.7474	2.4114
P-value	0.4704	0.1836	0.1555	0.0734

¹ T-square index of clumping. ² Distance index of dispersion. ³ Mean point-to-nearest-individual distance. ⁴ Mean individual-to-the-nearest-neighbor distance. ⁵ Note that for the overstory study no data were taken in Z-stands. In the overstory study, a and b indicate that means are significantly different for $\alpha = 0.05$ (these t-tests address $H_{0,3}$). In the understory study, a and b indicate that means are significantly different for $\alpha = 0.10$ (these t-tests address $H_{0,4}$).

Indices of species diversity, and evenness

Overstory layer

The P-values for the diversity indices (λ , H' , $N1$, $N2$) ranged from 0.1022 to 0.1543 (table 3), and the mean values of those indices suggested consistently (in the four cases) lower diversity in the underburned conditions. The P-values for the evenness indices ($E1$, $E2$, $E3$, $E4$, and $E5$) ranged from 0.0873 to 0.1709, and the mean values of those indices consistently suggest a more even distribution of individuals among species in the control stands versus a more clear dominance (in numbers / counts) by one or two species in the underburned stands. The t-tests comparing control and underburned stands had low power. The Hutchenson (1970) test was used to test if the Shannon diversity index (H') differed in stand C among the section burned in 1988 (CY) and the unburned (CX). We reject the null hypothesis that CX and CY do not differ in regard to H' , and conclude that the unburned section is more diverse in species.

Understory layer

The same trend in mean values of the diversity indices were found in the understory layer (i.e., lower diversity in the underburned conditions). However, the P-values (>0.4495) were too large to suggest anything. The t-tests comparing control and underburned stands had low power. When comparing the paired stands, the Hutchenson (1970) test led to reject the null hypothesis (i.e., H' do not differ) for AX-AZ but failed to reject it for both CX-CY and EX-EY. There were not significant differences in evenness indices (P-value > 0.5626), although the mean values were consistently (for all

indices) higher in the control stands than in underburned (table 3). No differences were found in the number of individuals (within the 200 individual samples) of any given species between control and underburned treatments.

Table 3. Diversity and evenness indices: Mean and standard error of the mean (SE) by treatment [*control* stands (N=3) and *underburned* stands (N=2 in the overstory study, and N=3 in the understory study)]. T-statistics and P-values for the t-tests about the null hypotheses of no differences in the indices calculated here ($H_{0,5}$, and $H_{0,6}$). X= stands not burned for longer than five years, Y= stands last underburned in late fall 1988, and Z= stands underburned in early 1993.

OVERSTORY		X (control)		Y ¹ (underburned)			
INDEX	Mean	SE	Mean	SE	t-statistic	P-value	
λ	0.50	0.12	0.86	0.04	2.3292	0.1022	
H'	0.97	0.22	0.32	0.09	2.2914	0.1058	
N1	2.76	0.52	1.38	0.12	2.0333	0.1349	
N2	2.17	0.41	1.17	0.06	1.8958	0.1543	
E1	0.62	0.12	0.23	0.06	2.5049	0.0873	
E2	0.58	0.08	0.34	0.03	2.3466	0.1006	
E3	0.46	0.11	0.13	0.04	2.2906	0.1059	
E4	0.79	0.02	0.85	0.03	1.7927	0.1709	
E5	0.63	0.07	0.44	0.03	2.1759	0.1178	
UNDERSTORY		X (control)		Y and Z (underburned)			
	Mean	SE	Mean	SE	t-statistic	P-value	
λ	0.31	0.06	0.35	0.04	0.5366	0.6200	
H'	1.43	0.15	1.30	0.06	0.8215	0.4575	
N1	4.29	0.68	3.69	0.24	0.8374	0.4495	
N2	3.56	0.86	2.94	0.31	0.6814	0.5330	
E1	0.73	0.09	0.67	0.03	0.5994	0.5812	
E2	0.60	0.12	0.53	0.04	0.5368	0.6199	
E3	0.54	0.13	0.46	0.05	0.6305	0.5626	
E4	0.81	0.06	0.79	0.06	0.1773	0.8679	
E5	0.74	0.09	0.72	0.09	0.1943	0.8554	

¹ Note that for the overstory study no data were taken in Z-stands.

DISCUSSION

Our results indicate that prescribed fire removes trees and shrubs preferentially from clumped areas leaving a more random distribution of individuals. This was statistically significant in regard to the 'J' index values for both overstory and understory layers; however 'C' index was not sensitive enough yielding very close values over stands in different locations, and with different burn histories. Ludwig and Reynolds (1988) and Johnson and Zimmer (1985) also found that I-index was more powerful (sensitive) than most other indices of spatial distribution. In the overstory layer, individuals are more sparsely distributed (both XMEAN and YMEAN resulted significantly larger) in underburned stands, and this trend is also suggested in the understory layer. The underlying mechanism which is suggested to explain this observed trend is that clumps differ from open areas by having a higher accumulation of dead and down fuels which causes individual plants to have a higher probability for mortality during a fire event (i.e., leaving a more random distribution of individuals).

In the overstory analysis, the mean values of the diversity indices consistently suggested (in the four cases) that in the underburned conditions plant species diversity was lower than in controls. Similarly, the mean values of the evenness indices consistently suggested a more even distribution of individuals among species in the control stands versus a more clear dominance (in numbers) by one or two species in the underburned stands. Many recent studies relate species diversity, forestry practices and fires. Moore *et al.* (1982) found that after underburning, diversity of herbaceous species increased in a 50-year-old mixed stand of slash and longleaf pine. Suffling (1988) used historical data

(NW Ontario) to determine relations between stand replacing fires and landscape (beta) diversity in the boreal forests and his results showed that landscape diversity was greatest with intermediate amounts (i.e., intermediate frequency or intermediate burn size) of fire disturbance. Suffling *et al.* (1988) suggested that forest fire control in fire-prone (i.e., high frequency of fires) landscapes will increase landscape diversity, but that diversity is reduced by fire control in landscapes with intermediate to low disturbance. At stand scale, however, fire suppression has reduced pyrodiversity (Martin and Sapsis 1992). While fires are diverse in their nature and occurrence, fire control has established fire regimes with a narrow range but a long period between fires would have tend to exclude those plants with a short life and short propagule endurance (Martin and Sapsis 1992). Therefore, fire suppression tends to reduce biodiversity at stand level.

These studies involved few stands (3 controls and 2 or 3 underburned stands). To increase the power of our t-tests (i.e., lowering the probability of committing a Type II error), more mensurative experimental units would have helped. Moreover, different locations throughout California mixed-conifer forests would have been desirable to increase the scope of this work.

CONCLUSIONS

Prescribed fire removed trees and shrubs preferentially from clumped areas leaving a more random distribution of individuals. In the overstory vegetation, plant species diversity appeared to be lower in underburned stands than in controls. Evenness indices consistently suggested a more even distribution of individuals among species in the

control stands versus a more clear dominance (in numbers) by one or two species in the underburned stands. Prescribed burning successfully consumed surface litter and understory with minimum damage to the overstory vegetation and without causing dramatic changes in plant diversity in mixed-conifer forest stands.

CHAPTER IV

TREE SEEDLING MICROHABITAT IN MIXED CONIFER STANDS
AT BOGGS MOUNTAIN STATE FOREST, CALIFORNIA

Domingo Miguel Molina

ABSTRACT: This paper evaluates whether or not small-scale habitat (i.e., litter and duff depth, percent plant cover, light intensity, and distance to the nearest neighbor, and distance to the nearest outcompeting neighbor) differences exist among tree seedlings of species common in Boggs Mountain State Forest, California. The experimental units were randomly selected individual seedlings. There were five species (PM = *Pseudotsuga menziesii* (Mirb.) Franco, PP = *Pinus ponderosa* Dougl., PL = *Pinus lambertiana* Dougl., QK = *Quercus kelloggii* Newb., and QW = *Quercus wislizenii* A.C.D.) and 26 individuals per species. Significant differences among species were found only for depth of litter and duff (i.e., PP occurred where forest floor was deeper), and for percent plant cover (i.e., PL occurred underneath closer canopy than both QK and PP) ($\alpha=0.05$). In addition, prescribed burning experiments were carried out to monitor if fire as a disturbance modifies those microhabitat variables. Litter and duff depth decreased after burning; however, burning did not change total plant cover. Prescribed burning is likely to favor PP versus PM regeneration.

KEYWORDS: microhabitat, litter and duff depth, percentage plant cover, light intensity, nearest neighbor

INTRODUCTION

Microhabitats occupied by tree seedlings might be very different from those in which mature individuals of the same species live. Specifically, small scale mechanisms

such as litter and duff depth (Harrington and Kesley 1981), or neighborhood competition (Goldberg and Werner 1983) may differentially affect the performance of seedlings of different species. Therefore, aspects of the biotic and abiotic environment to which a seedling is exposed alter its probability of survival and recruitment into a population.

This study examines potential small-scale habitat differences among tree seedlings of species common in Boggs Mountain State Forest (BMSF), north of Middletown, California. The following species were investigated: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* Dougl.), sugar pine (*Pinus lambertiana* Dougl.), black oak (*Quercus kelloggii* Newb.), and interior live oak (*Quercus wislizenii* A.DC.). While geographical (or landscape) factors such as climate and aspect determine which kind of vegetation formations exist in a region, temperature, soil moisture, light intensity and soil nutrient availability are variables describing some features important in determining microscale patterns of distribution of tree seedlings. The general goal is to address the following question: Does tree seedling occurrence vary among different species in regard to microhabitat features of their environment? In addition, a prescribed burned was carried out to reduce forest floor fuels and some effects on microhabitat factors were studied.

Related work

Grime and Hillier (1992) emphasized that seeds and seedlings are not only involved in population processes (i.e., persistence, dispersal) but also in the distribution, dynamics and diversity of much larger units of vegetation (i.e., communities, landscapes, local floras). Willson (1992) reviews the consequences of seed dispersal at population and community levels. Much seed dispersal, at least by wind, is random with respect to the occurrence of safe sites, and the fittest seed is ultimately the one that happens by chance to fall in a favorable gap (Fenner 1992). Crawley (1992) states the importance of stochastic

variation in seed predation in permitting the coexistence of plant species. This stochastic variation prevents dominance by competitively superior species, and hence can permit coexistence. Forest and many other vegetation types are prone to periodic, though unpredictable, disturbance which kills adults and creates opportunities for recruitment (Pickett and White 1985, Ashton 1992). Silvertown (1987) states that disturbance may facilitate coexistence by reducing the dominant competitors. Nobel (1981) questions the predominant role of competition (especially in frequently disturbed environments) and emphasizes the importance of the regeneration niche in the study of vegetation replacement sequences (plant succession).

Lastly, quite complex statistical procedures are often used to determine which combination of environmental variables accounts best for the observed distribution of species (i.e., Dueser and Shugart 1979, Collins and Good 1987, and Collins 1990).

METHODS

Study site

Boggs Mountain State Forest (BMSF), north of Middletown, California, is located 39°N, 123°W, at about 730-1150 m above the mean sea level. The seedlings of this study were obtained from different gaps of various sizes in mixed conifer forest stands containing the following species: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* Dougl.), sugar pine (*Pinus lambertiana* Dougl.), black oak (*Quercus kelloggii* Newb.), and interior live oak (*Quercus wislizenii* A.DC.). Ponderosa pine and / or Douglas-fir dominate in most areas; however, there are numerous patches of sugar pine, and oaks are scattered around the forest. The most common understory species are *Arctostaphylos manzanita* C.Parry, *Arctostaphylos canescens* Eastw., *Ceanothus prostratus* Benth., and *Rhamnus californica* Eschsch.

Mensurative experiment layout

1) A first *mensurative* experiment (*sensu* Hurlbert 1984) was designed to examine several microhabitat variables around tree seedlings of species common in BMSF (California). The experimental units were randomly selected individual seedlings. There were five species and 26 individuals per species. The following species were investigated: *Pseudotsuga menziesii* (Mirb.) Franco, *Pinus ponderosa* Dougl., *Pinus lambertiana* Dougl., *Quercus kelloggii* Newb., *Quercus wislizenii* A.CD. For recent review of these species' ecophysiology and distribution see: Hermann and Lavander 1990 (*Pseudotsuga menziesii*), Oliver and Ryker 1990 (*Pinus ponderosa*), Kinloch and Scheuner 1990 (*Pinus lambertiana*), McDonald 1990 (*Quercus kelloggii*), and Pavlik *et al.* 1991 (*Quercus wislizenii*).

The experiment evaluated the microhabitat variables shown in table 1

TABLE 1. SEEDLING MICROHABITAT VARIABLES STUDIED. ACRONYMS, AND UNITS.

ACRONYMS	MICROHABITAT VARIABLES
mm -	litter and duff depth (mm)
ne -	nearest neighbor distance (cm)
nej -	nearest outcompeting neighbor distance (cm)
ld -	percentage of soil covered by conifer litter and duff (%)
li -	percentage light intensity (%)
co -	percentage of total plant cover (%)

2) A second *mensurative* experiment was carried out by means of prescribed burning (March, 1993) over a 7 ha section of the forest. Within the burn unit, four pairs of *mensurative experimental units* (MEU) were established. Each pair consisted in one MEU representing a Douglas-fir canopy with thick understory vegetation, and a close MEU representing a Douglas-fir canopy with little understory vegetation. The goal of this experiment was to determine if after crown scorch (caused by prescribed burning) total plant cover (co) decreases. Additionally, it was tested if the different vegetation structure

(i.e., thick or little understory) resulted in different effects on total plant cover changes.

Experimental execution

These variables were measured in 26 randomly selected seedlings (in a circle of a diameter of 25 cm centered around the seedling) for each of the 5 species used in this study. Three year old seedlings were selected rather than one year old ones because they had survived longer and are better indicators of the species regeneration microhabitat. The selection process involved: a) location, marking, and labeling of 90 sites (within a two hectare stand) in which, at least, one three-year-old seedling was present; b) random selection of one number from 0 to 90 (i.e., 8); and c) selection of no more than one individual seedling per species and per site beginning in site 8 until obtaining the number of seedlings needed. A wide range of both canopy cover and overstory species dominance was addressed in this study to enhance the scope of the investigation. Details of the data collection of the operational factors considered:

- 1) *mm* was obtained averaging two measurements taken consistently at 0.1 meter northwest and northeast of the seedling (NW and NE were used following a random selection). Precision was 1 mm; therefore, mean and standard error reported were rounded to the nearest millimeter.
- 2) *ne* was the distance to the nearest plant individual (i.e., herb, grass, seedling, tree). Seedlings of less than one year were not considered because they have not (yet) challenge the seedlings we were studying. Precision was 0.01 m.
- 3) *nei* was the distance to the nearest outcompeting plant individual (i.e., a seedling at least twice as tall). Precision was 0.01 m.
- 4) *ld* was the percentage of the soil surface covered by conifer litter and duff. The area considered was a square of 0.2 by 0.2 meter centered in the seedling and randomly oriented. Educated, ocular estimations were assumed to yield a precision of 5%.

- 5) *li* was the percentage of Photosynthetic Active Radiation (PAR) reaching one meter above the seedling insertion into the soil (as percent of open-site light intensity). An average of measures taken at 10am, noon, and 2pm was computed. Every five minutes a measure was taken outside the canopy (i.e., in an open site) to have data of the total PAR. A quantum sensor (Type 1905, Lo-cor Inc., Lincoln, NE) was used, and precision was assumed to be within 1%.
- 6) *co* was the total plant cover above a seedling. It was measured with a spherical densiometer which is an optical device that projects the canopy over a grid where the cover is measured. It was recorded at 1.35 meter above the seedling insertion into the soil. Four measurements (N, E, S, and W) were taken and averaged. This objective procedure was assumed to yield a 1% precision.

Lastly, although the techniques outlined here are tedious, they are simple and nondestructive.

Statistical analysis

The SAS (Schlotzhauer and Littell 1987, Cody and Smith 1987) statistical package was used in the analyses of results. Linear models were used for analysis of variance (ANOVA), and orthogonal F tests (orthogonal contrasts) were used in the process of mean separation because most statisticians agree that they provide a more precise separation than multiple comparison tests (Day and Quinn 1989, Steel and Torie 1980, Little and Hills 1978). Following Little and Hills (1978), data was transformed to better fit the assumptions of ANOVA: continuous variables were logarithmically transformed, and percentage variables were arcsine transformed. Statistical differences among species (for each habitat variable) were analyzed by one-way analysis of variance. In a like manner, the Kruskal-Wallis test (the nonparametric analog of the ANOVA F test) was used. The transformed data fitted the assumptions of ANOVA; therefore, the

Kruskal-Wallis tests have a secondary interest here. Table 2 displays an anova table for 'mm' (one of the microhabitat variables: i.e., dependent variable), and table 3 shows the orthogonal contrasts and their coefficients. The power of ANOVA was calculated following Zar (1984):

Table 2. General Anova table for an operational factor (i.e., mm). Dependent Variable: log(mm). It is a completely randomized design (CRD). DF= degrees of freedom.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	12.287	3.072	7.80	0.0001
Error	122	48.066	0.394		
Corrected Total	126	60.353			

Table 3. Orthogonal contrasts and their coefficients. PL, *Pinus lambertiana*; PM *Pseudotsuga menziesii*; PP, *Pinus ponderosa*; QK, *Quercus kelloggii*; and QW, *Quercus wislizenii*

Contrast	Species Orthogonal contrast coefficients				
	PL	PM	PP	QK	QW
q1, Conifers versus <i>Quercus spp</i>	2	2	2	-3	-3
q2, <i>Q. kelloggii</i> versus all others	1	1	1	-4	1
q3, <i>P. menziesii</i> versus all others	1	-4	1	1	1
q4, <i>P. ponderosa</i> versus all others	1	1	-4	1	1

Hypotheses

All five species listed above were investigated to test the following hypothesis:

$H_{0,1}$ = Seedling of different species do not differ in occurrence along the gradient in litter and duff depth (microhabitat variable)

$H_{0,2}$ = Seedling of different species do not differ in occurrence along the gradient in distance to the nearest plant individual (microhabitat variable)

$H_{0,3}$ = Seedling of different species do not differ in occurrence along the gradient in

distance to the nearest outcompeting plant individual (microhabitat variable)

H_{0,4}= Seedling of different species do not differ in occurrence along the gradient in percentage of the soil surface covered by conifer litter and duff (microhabitat variable)

H_{0,5}= Seedling of different species do not differ in occurrence along the gradient in percentage of Photosynthetic Active Radiation (PAR) reaching the seedling (microhabitat variable)

H_{0,6}= Seedling of different species do not differ in occurrence along the gradient in total plant cover above a seedling (microhabitat variable)

Several specific hypotheses can be drafted to test for the statistical significance of differences between groups of means (i.e., orthogonal contrasts):

q1. Conifers versus *Quercus spp*

$$H_{0,q1}: 2\mu_{PL} + 2\mu_{PM} + 2\mu_{PP} = 3\mu_{QK} + 3\mu_{QW} \text{ versus}$$

$$H_1: 2\mu_{PL} + 2\mu_{PM} + 2\mu_{PP} \neq 3\mu_{QK} + 3\mu_{QW}$$

q2. *Q. kelloggii* versus all others

$$H_{0,q2}: 4\mu_{QK} = \mu_{PL} + \mu_{PM} + \mu_{PP} + \mu_{QW} \text{ versus } H_1: 4\mu_{QK} \neq \mu_{PL} + \mu_{PM} + \mu_{PP} + \mu_{QW}$$

q3. *P. menziesii* versus all others

$$H_{0,q3}: 4\mu_{PM} = \mu_{PL} + \mu_{PP} + \mu_{QK} + \mu_{QW} \text{ versus } H_1: 4\mu_{PM} \neq \mu_{PL} + \mu_{PP} + \mu_{QK} + \mu_{QW}$$

q4. *P. ponderosa* versus all others

$$H_{0,q4}: 4\mu_{PP} = \mu_{PL} + \mu_{PM} + \mu_{QK} + \mu_{QW} \text{ versus } H_1: 4\mu_{PP} \neq \mu_{PL} + \mu_{PM} + \mu_{QK} + \mu_{QW}$$

where μ_{PL} , μ_{PM} , μ_{PP} , μ_{QK} , and μ_{QW} are the means (for a given operational factor) of the populations of seedlings of the species PL, PM, PP, QK, and QW respectively. PL, PM, PP, QK, and QW are the acronyms made using the initials of the scientific names of our tree species (i.e., PL, *Pinus lambertiana*; PM *Pseudotsuga menziesii*; PP, *Pinus ponderosa*; QK, *Quercus kelloggii*; and QW, *Quercus wislizenii*).

RESULTS

Statistical analyses showed (table 4) that variables *mm* and *co* were significant in separating the five species of this study ($\alpha=0.05$). P-values for both (parametric) ANOVA and the nonparametric Kruskal-Wallis (K-W) ANOVA are below the $\alpha=0.10$ benchmark for *nei*; however, they are not significant for $\alpha=0.05$. The remaining variables are non significant. The power of the test is important when the null hypothesis is not rejected. This is the case for variables *ld* and *li*, and as the power of the test was low in both cases, we cannot accept the null hypothesis (no differences among species in regard to light and percentage of litter cover of the soil): we just fail to reject $H_{0,3}$ and $H_{0,4}$.

Means and standard errors of the microhabitat variables by species are shown in table 4. Mean separation with orthogonal contrast is shown in table 5. *Pinus ponderosa* seedlings are distinct in occurring in sites with less depth of litter and duff than any other species (table 4, table 6, and contrast q4 in table 5). Conversely, *Pinus lambertiana* is in the other extreme occurring in sites with more depth of litter and duff than both *Quercus wislizenii* and *Quercus kelloggii* populations (tables 4 and 6). In relation to factor *nei*, two t-tests (unprotected LSD multiple comparisons) resulted significant at the 0.05 level: this is, *Quercus wislizenii* versus *Pinus ponderosa*, and *Quercus wislizenii* versus *Quercus kelloggii*. However, as stated above, the general anova and the nonparametric K-W had P-values lower than 0.10 but higher than 0.05. These results suggest that *Quercus wislizenii* seedlings which had the closest outcompeting neighbors occurred in sites that differ from those of *Pinus ponderosa* and *Quercus kelloggii* seedlings in the proximity of outcompeting neighbors (table 4). In reference to *co*, *Pinus ponderosa* seedlings are in sites with less overstory cover than *Quercus wislizenii*, *Pinus lambertiana*, and *Pseudotsuga menziesii* populations: however, they do not significantly differ from *Quercus kelloggii*. Additionally, *Quercus wislizenii* seedlings, which have the highest values of percentage plant cover, differ statistically from *Quercus kelloggii* (table 4).

In addition, the prescribed burning experiment did not decrease the total plant

cover (table 7) under any forest structure (i.e., thick or thin understory vegetation). As High P-value and high power of the t-test were obtained, the null hypothesis (H_0 = there are not differences in total plant cover either with time or among different forest structure) was accepted.

Table 4. Microhabitat variable means and standard errors by species (PL = *Pinus lambertiana*, PM = *Pseudotsuga menziesii*, PP = *Pinus ponderosa*, QK = *Quercus kelloggii*, and QW = *Quercus wislizenii*)

Variable	units	Species					Parametric P-value ¹	Nonparametric P-value ²	Power ³
		PL	PM	PP	QK	QW			
litter and duff depth ⁴	mm	49 ± 6 a	41 ± 5 a	14 ± 3 b	27 ± 6 a	30 ± 7 a	0.0001	0.0001	<0.39
nearest neighbor distance	cm	47 ± 10	55 ± 12	23 ± 8	42 ± 12	33 ± 12	0.1582	0.2859	0.96
nearest outcompeting neighbor distance	cm	174 ± 31	181 ± 20	238 ± 17	208 ± 24	146 ± 20	0.0592	0.0922	0.99
conifer litter coverage of the soil	%	99 ± 0	100 ± 0	92 ± 4	98 ± 1	96 ± 2	0.0681	0.1404	<0.39
total plant cover ⁴	%	94 ± 1 a	93 ± 1 ab	87 ± 2 b	90 ± 2 b	97 ± 1 ab	0.0030	0.0143	0.59
light intensity	%	48 ± 2	49 ± 2	55 ± 3	55 ± 3	49 ± 5	0.3014	0.3504	0.45

¹ P-value in a one way (parametric) ANOVA

² P-value in a one way nonparametric Kruskal-Wallis ANOVA

³ Power of the test (1-β) or probability of accepting the null hypothesis when it is true. β is the probability of committing a Type II error; this is, rejecting the null hypothesis when it is true. The power was calculated for α= 0.05 and for a minimum detectable difference of 0.05 times the value of the grand mean of the variable in study.

⁴ Means with the same letter are not significantly different. Mean separation was accomplished with the Ryan-Emot-Gabriel-Welsch Multiple Range Test (for transformed variables). Note that this test controls the type I experimentwise error rate.

Table 5. Mean separation with orthogonal contrasts for those significant variables ($\alpha = 0.05$).

Dependent Variable: LGMM. logarithmic transformation of *mm*

Contrast	F Value	P-values
q1. Conifers versus <i>Quercus spp</i>	0.37	0.5415
q2. <i>Q. kelloggii</i> versus all others	0.48	0.4894
q3. <i>P. menziesii</i> versus all others	4.58	0.0344
q4. <i>P. ponderosa</i> versus all others	22.03	0.0001

Dependent Variable: LGNEI. logarithmic transformation of *nei*

Contrast	F Value	P-value
q1. Conifers versus <i>Quercus spp</i>	1.09	0.2985
q2. <i>Q. kelloggii</i> versus all others	1.01	0.3161
q3. <i>P. menziesii</i> versus all others	0.08	0.7726
q4. <i>P. ponderosa</i> versus all others	4.81	0.0302

Dependent Variable: ASCO. arcsine transformation of *co*

Contrast	F Value	P-value
q1. Conifers versus <i>Quercus spp</i>	2.15	0.1453
q2. <i>Q. kelloggii</i> versus all others	1.66	0.1999
q3. <i>P. menziesii</i> versus all others	0.14	0.7135
q4. <i>P. ponderosa</i> versus all others	8.92	0.0034

Table 6. Pairs of means found to be different with LSD multiple comparisons tests (for transformed variables). Comparisons significant at the 0.05 level NOTE: This test controls the type I comparisonwise error rate; however, it does not control the type I experimentwise error rate.

depth of litter and duff	nearest outcompeting neighbor distance	total plant cover
PL versus QW	QW versus PP	PP versus QW
PL versus QK	QW versus QK	PP versus PL
PP versus PL		PP versus PM
PP versus PM		QK versus QW
PP versus QW		
PP versus QK		

Table 7. Total plant cover (%) changes either with time or among different forest structure (i.e., thin or thick understory vegetation). Mean and standard error of the mean (SE). It follows a randomized block design with four replications and four samples in each experimental unit. High P-value and high power of the t-test were obtained.

Pre-burn (28/4/93)	MEAN (%)	SE (%)
thin	87	2
thick	86	2
Post-burn (1/5/93)	MEAN (%)	SE (%)
thin	89	1
thick	86	3

DISCUSSION

The microhabitat variables shown in table 1 are not the only microhabitat features affecting the seedling performance: others might have been added to this study.

As it was anticipated, distance to the nearest outcompeting neighbor matters more than distance to the nearest neighbor: this is, nonsignificant differences were found among species in the second case. The differences found between *Pinus ponderosa* and both *Pinus lambertiana* and *Pseudotsuga menziesii* in regard to *mm* and *co* are congruent with the literature on the autoecology of these species (Hermann and Lavander 1990, Oliver and Ryker 1990, Kinloch and Scheuner 1990). Harrington and Kelsey (1979) found, from manipulative experiments (*sensu* Hurlbert 1984), that ponderosa pine seedling growth was superior in the forest openings in shoot and root length and biomass than close or beneath mature trees. Similarly, survivorship was greater in the experimental openings.

Light intensity (PAR) is easy to measure; however, is very difficult to extrapolate data from three periods of one minute in a single day to meaningful estimates of available PAR in a growing season. Additionally, sunflecks may be responsible for more than half of the productivity in understory and seedling individuals by means of a quickly opening response of stomata to bright light which is quicker in shade tolerant individuals as found in Woods and Turner (1971). However, Pereira and Kozłowski (1976) did not find

differences in stomatal response among species. In this study, the power of the test was low for both l_i and l_d ; therefore, we cannot either accept or reject the null hypothesis (i.e., H_0 = microhabitat features of any two species of seedlings do not differ with respect to l_d)

Seedling mortality is very high in the first growing season, and in this forest numerous new seedlings were recorded in early spring (1992 was a specially good year for *Pinus ponderosa* seedlings). Therefore, I hypothesize that those three or four year old seedlings outcompete their younger neighbor seedlings most of which are already gone. As Canham and Marks (1985) stated, the hypothesis that a seedling with a higher growth rate should outcompete a more slowly growing seedling established at approximately the same time makes no predictions about the (temporal and spatial) diversity in disturbance size and resource availability. The portions in the disturbance size gradient in which a species has higher growth rates than others are the portions in where the species has its highest growth efficiency (Canham and Marks, 1985). In this study, disturbance size and resource availability were quantified in terms of some operational factors investigated. This is, high resource availability may be the result of *long* distance to the nearest neighbor (ne) or *long* distance to the nearest outcompeting neighbor (nei) or *low* canopy cover (co) or *high* light availability (li).

Prescribed burning may modify the microhabitat variables here studied. It is clear with regard to mm (litter and duff depth) as reported elsewhere (Harrington and Kelsey 1979, and first chapter of this dissertation). The total plant cover (co) were not significantly changed by our controlled burn of low fireline intensity and low to moderate fuel consumption. Therefore, we can reduce fuel accumulations, and thus wildfire hazard, using prescribed burns without significantly changing the total plant cover of the site but significantly changing litter and duff depth. This has management implications such as favoring PP regeneration versus PM. There are not significant differences among these species in regard to co (table 4). However, PP seedlings were in sites more forest floor depth than PM seedling sites.

Both *ne* and *nei* are likely to increase in value after burns providing less competition for resources and more resource availability for new tree seedlings. Lastly, an increase in *li* and a decrease in *ld* might be expected after fire. The fact that *Quercus wislizenii* seedlings were present in sites with very high total plant cover, jointly with the observation that many lost their terminal shoots, may indicate that herbivory restricts them to the least exposed locations.

Examination of seedling microhabitats in different locations throughout California mixed-conifer forests would have been desirable to increase the scope of this work. Lastly, manipulative experiments are always preferable to mensurative experiments like the ones here reported.

CONCLUSIONS

Significant differences among species were only found for depth of litter and duff, and for percent plant cover ($\alpha=0.05$). Prescribed burning may modify the operational variables here studied. Litter and duff depth was changed after prescribed burns; however, the total plant cover was not significantly changed by the controlled burns of low fireline intensity and low to moderate fuel consumption. Therefore, we can reduce fuel accumulations, and thus wildfire hazard, using prescribed burns without significantly changing the total plant cover of the site but significantly changing litter and duff depth. In this manner, we can favor PP regeneration reducing litter and duff depth using prescribed fires.

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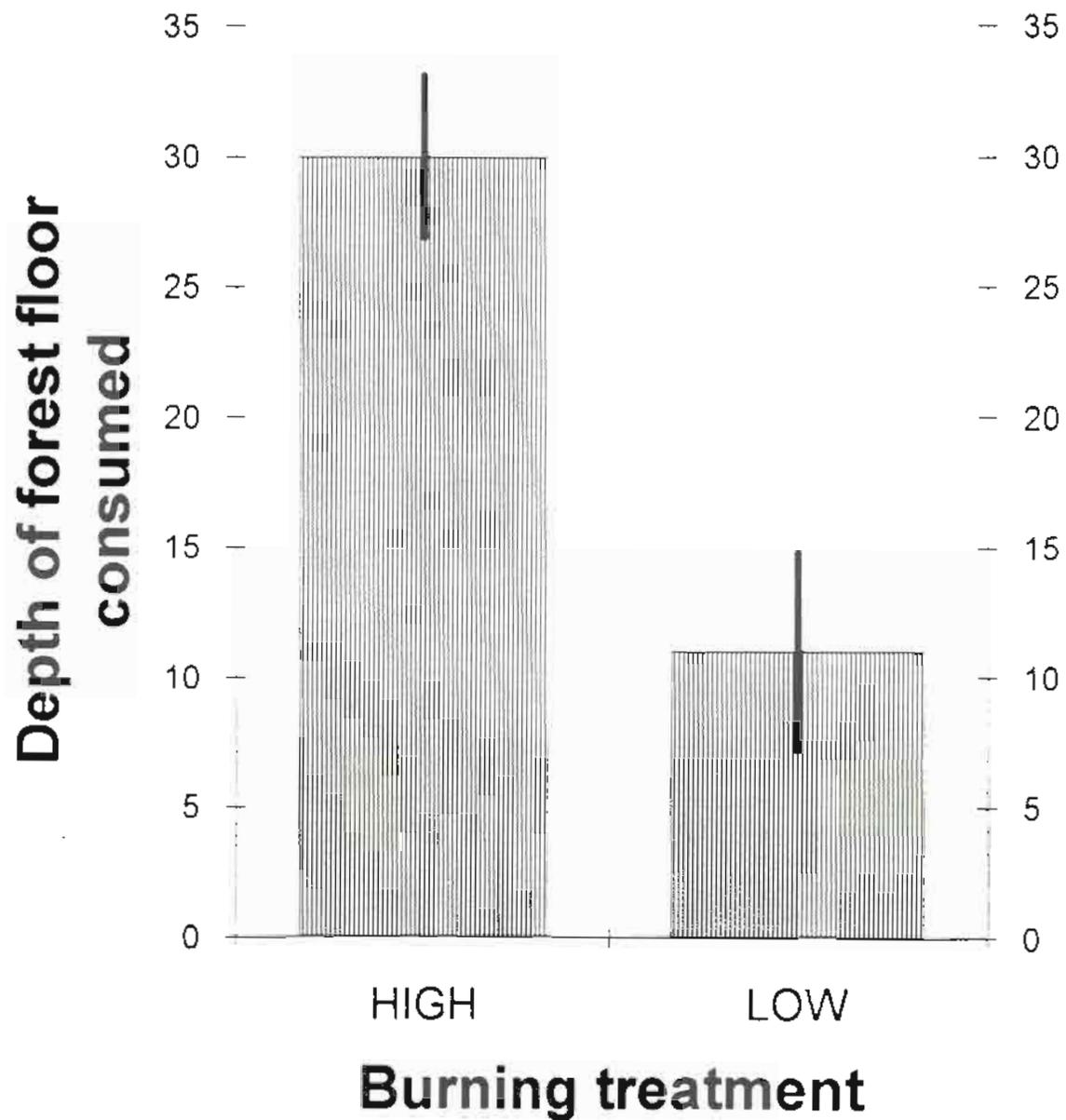
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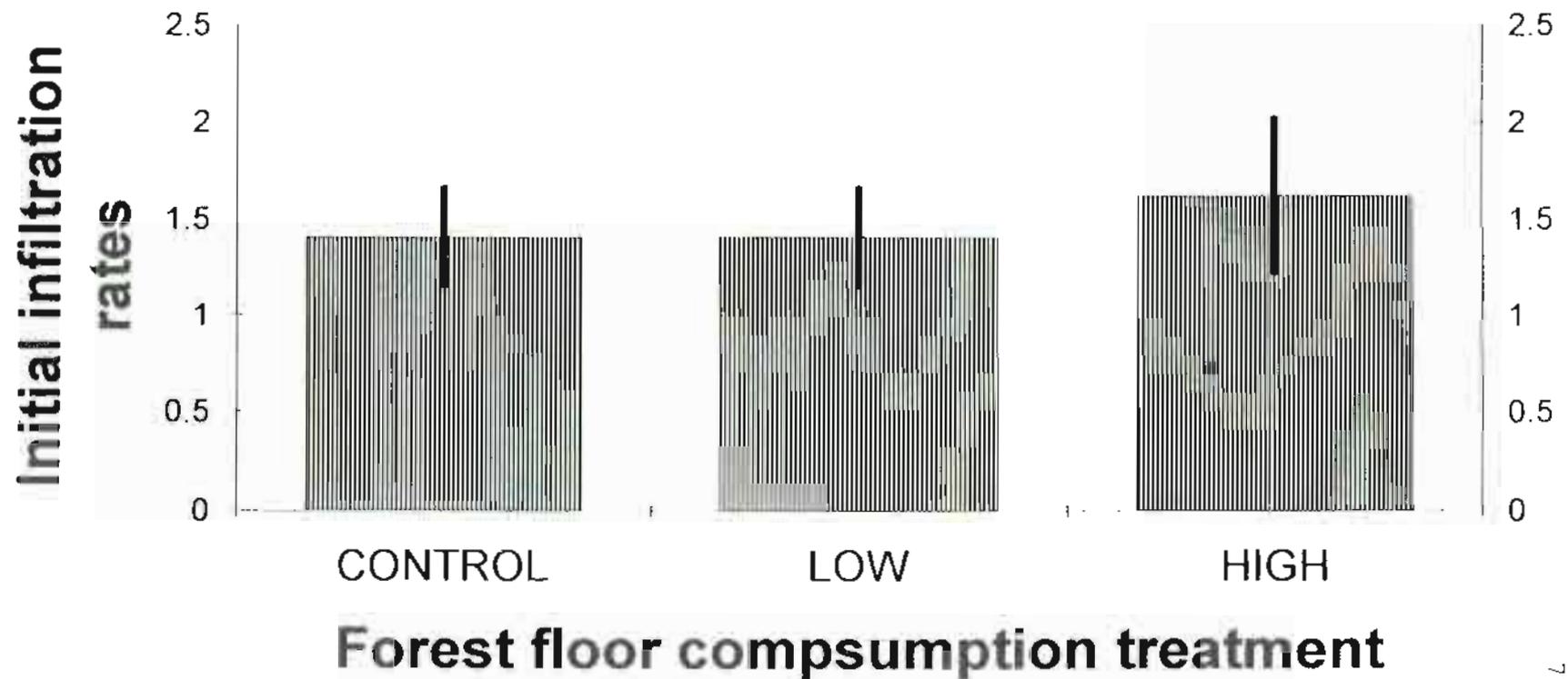
APPENDICES

APPENDIX I / CHAPTER I

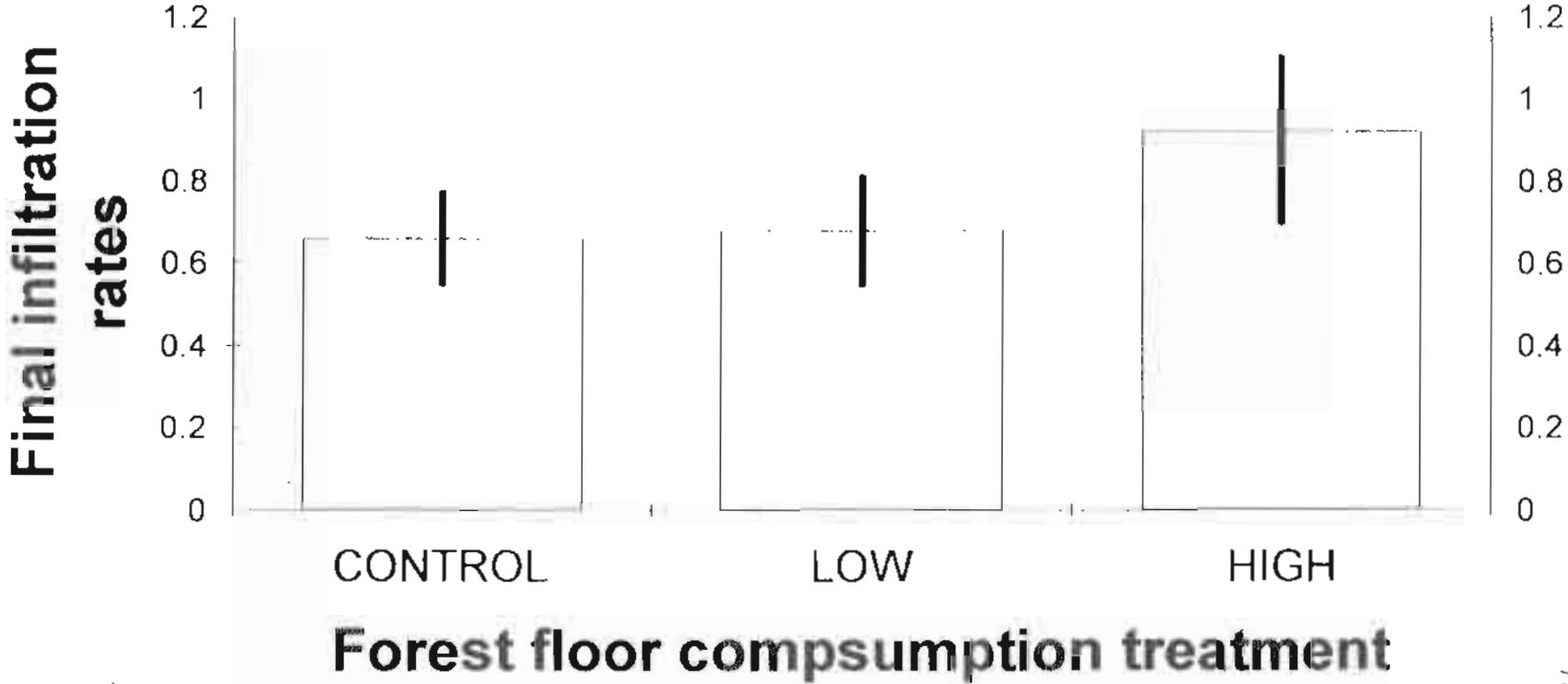
**Figure 1. Depth of forest floor consumed by treatment:
mean and standard error
P-value = 0.0081**



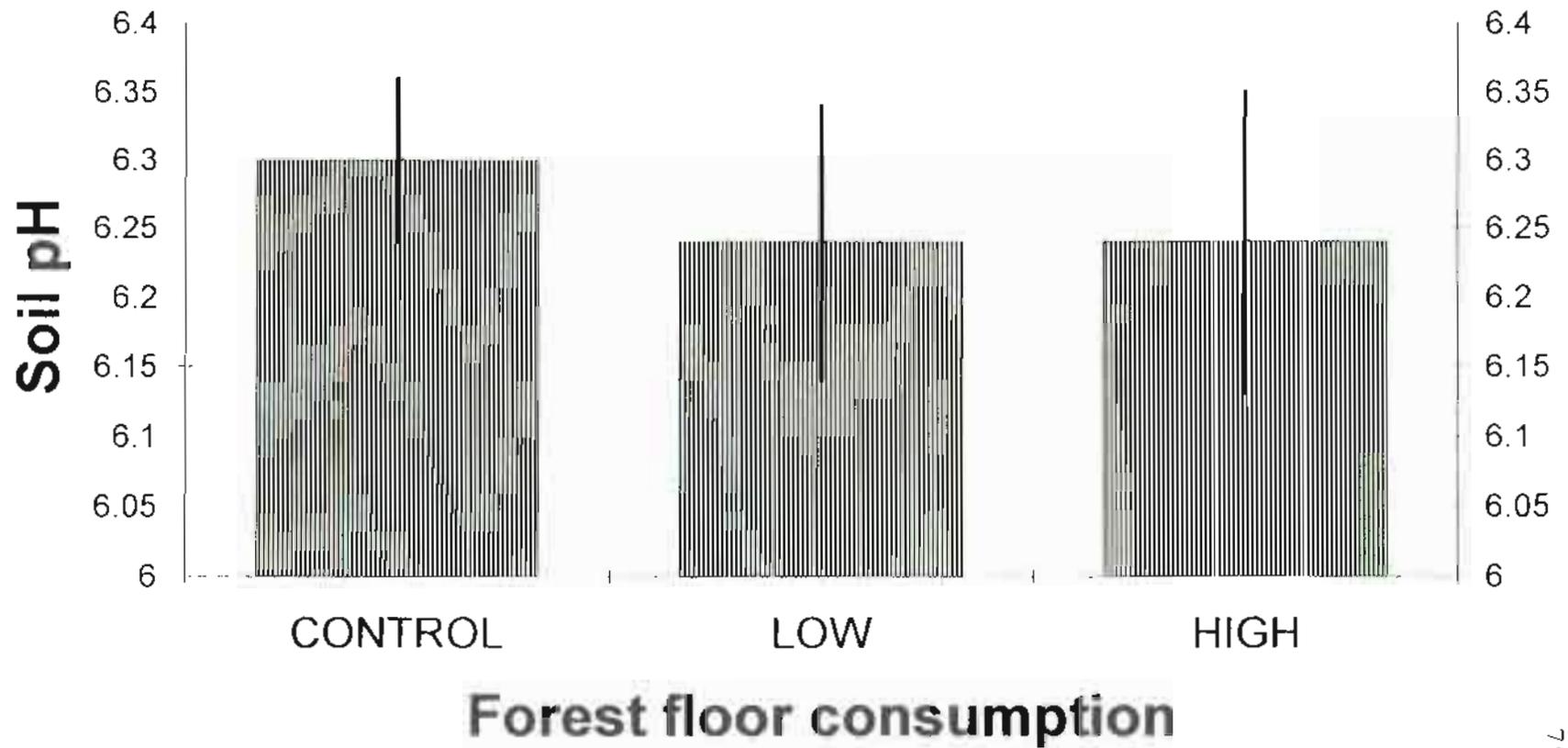
**Figure 2. Initial infiltration rates versus forest floor consumption: mean and standard error
P-value = 0.60**



**Figure 3. Final infiltration rates versus forest floor consumption: mean and standard error
P-value = 0.60**



**Figure 4. Soil pH versus forest floor consumption: mean and standard error
P-value = 0.58**



APPENDIX II / CHAPTER II

**Figure 1. *Rhamnus californica*. Contrast Q1: germination response in clean water and leachate treatments (mean and standard error)
P-value = 0.3085**

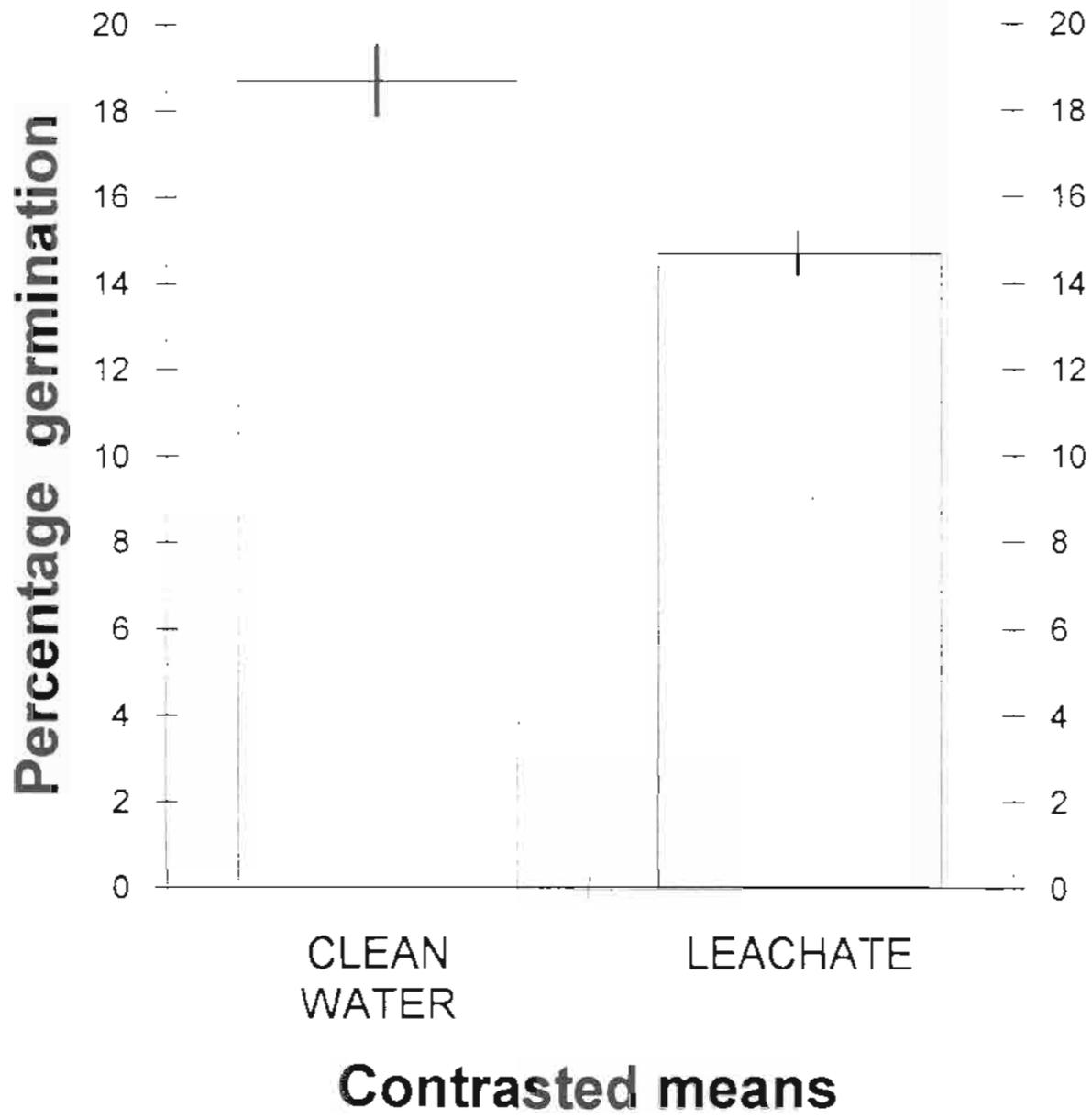


Figure 2. *Rhamnus californica*. Contrast Q3: germination response at 70°C and 80°C (mean and standard error)
P-value = 0.0129

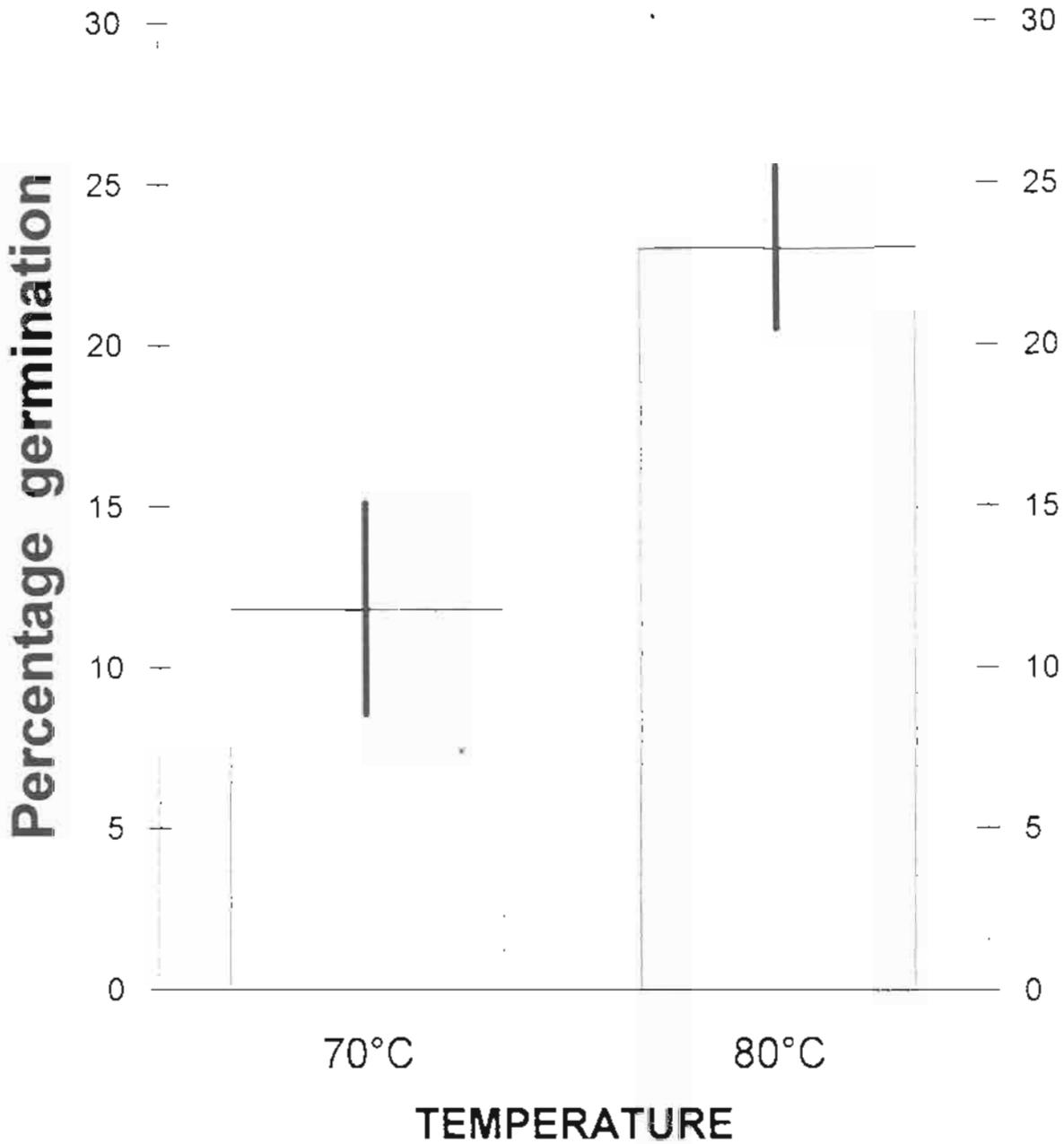
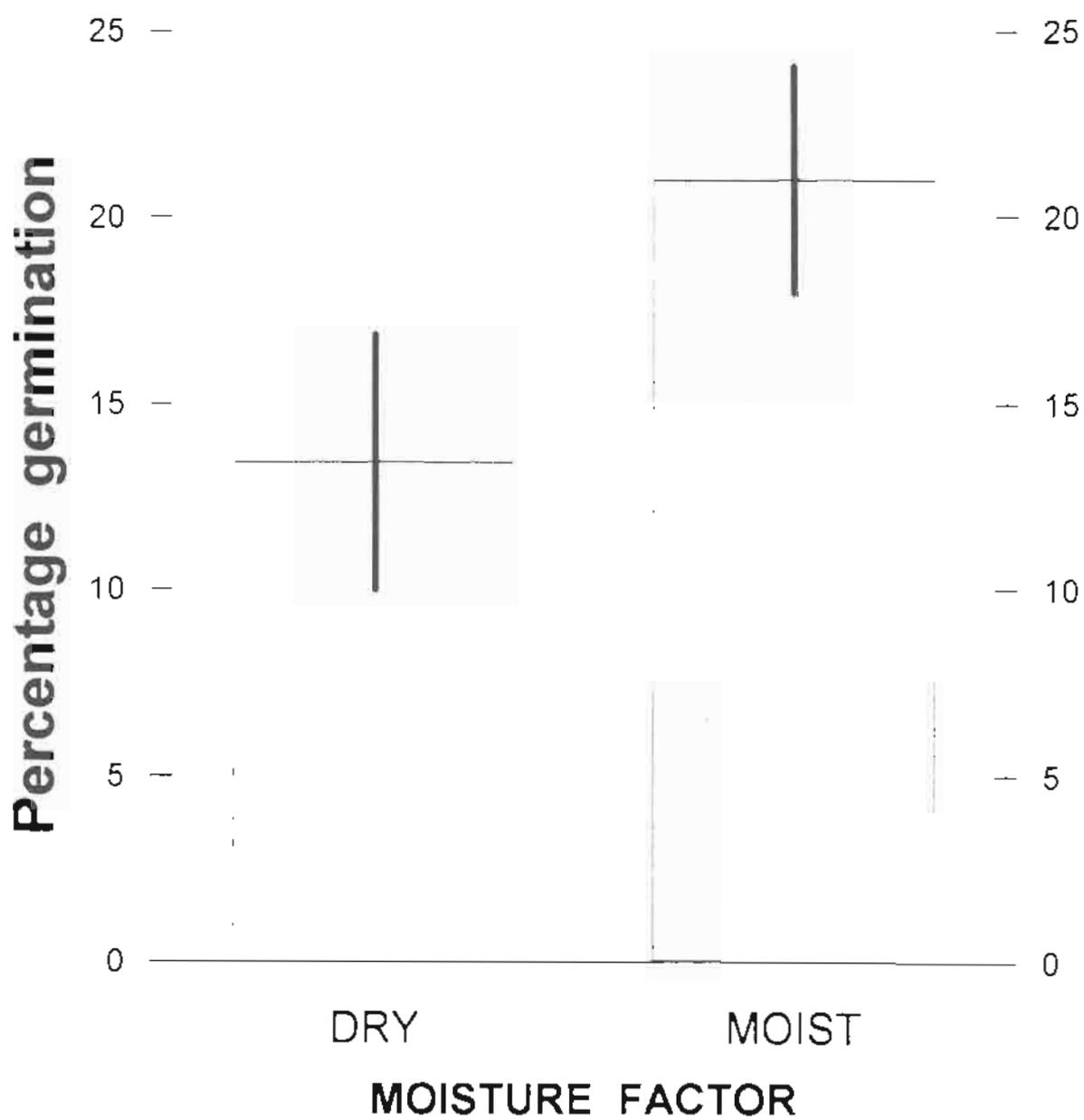


Figure 3. *Rhamnus californica*. Contrast Q4: germination response of dry versus moist heating treatments (mean and standard error)
P-value = 0.1027



**Figure 4. *Rhamnus californica*. Contrast Q6: germination response at 25°C and 80°C (mean and standard error)
P-value = 0.0687**

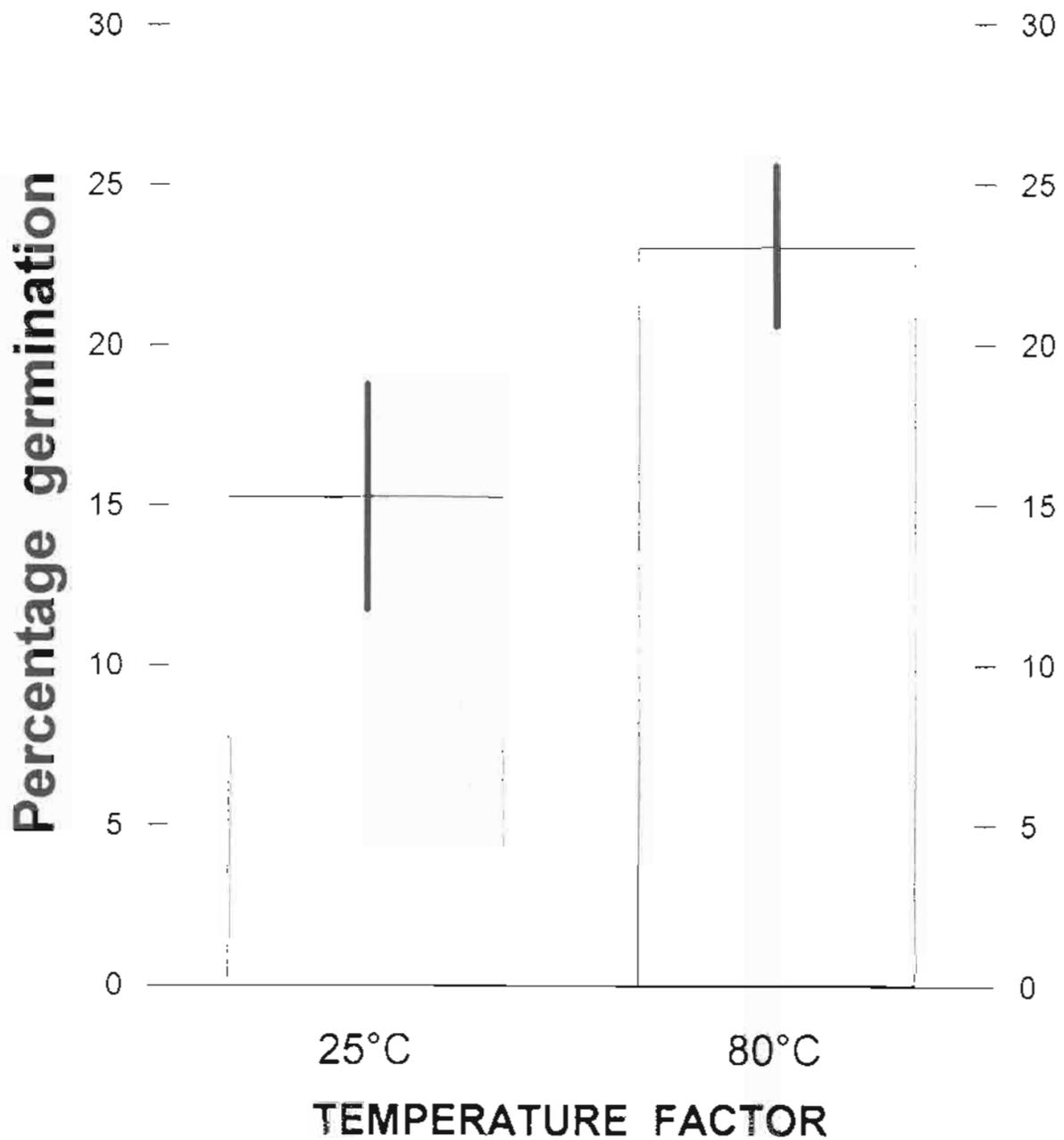
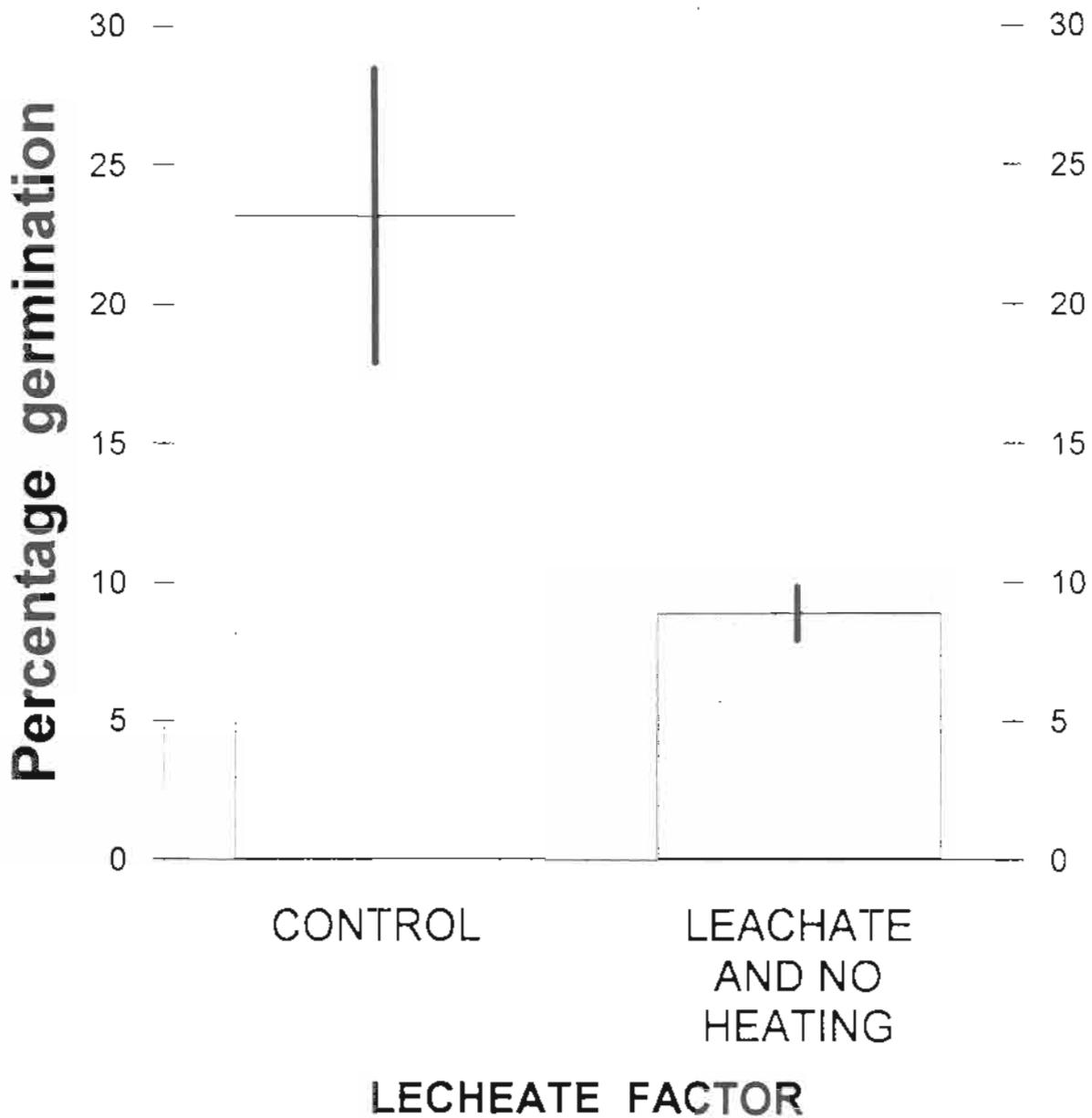
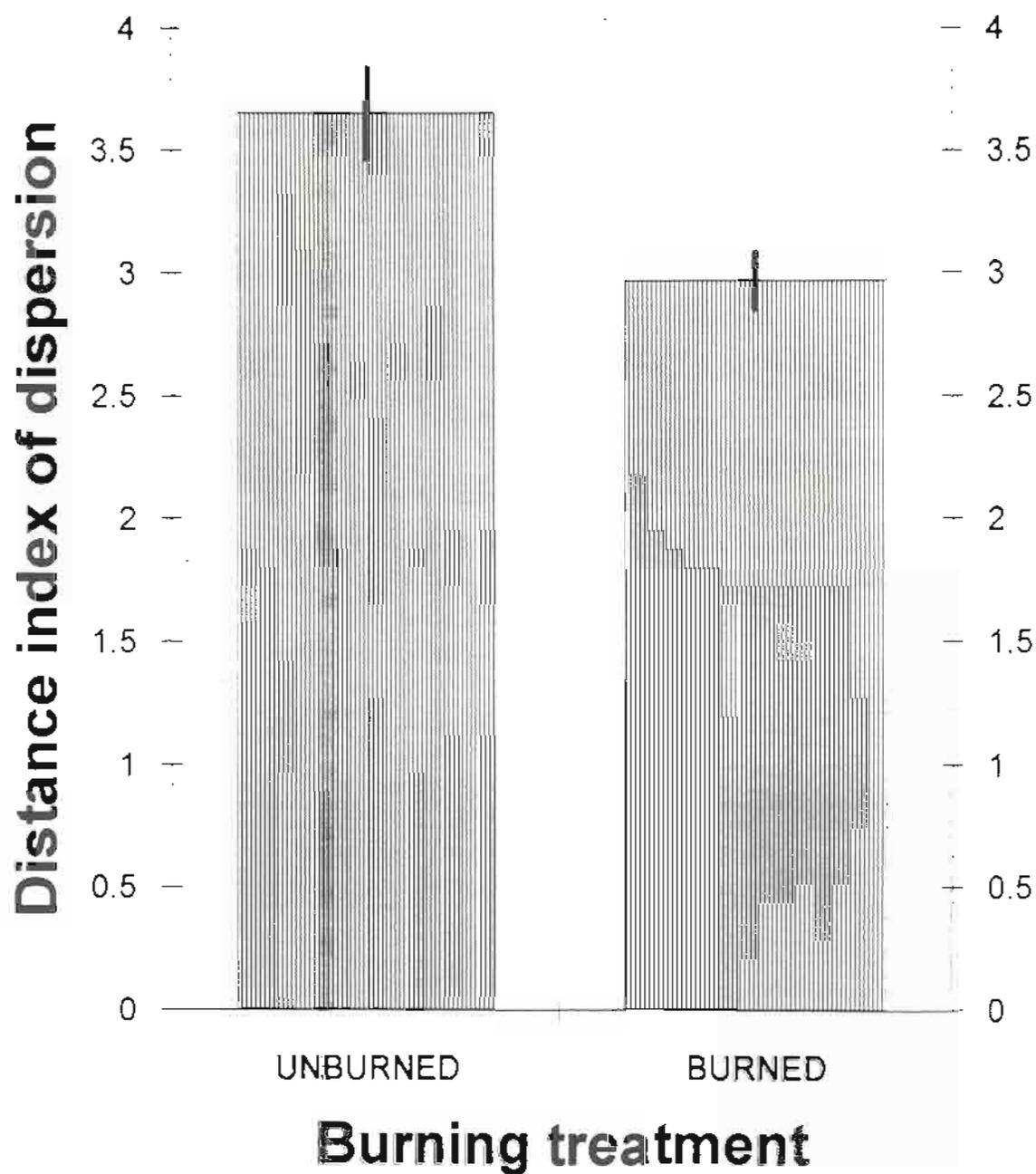


Figure 5. *Rhamnus californica*. Contrast Q7: germination response (at 25°C) in control versus leachate treatments (mean and standard error)
P-value = 0.0149



APPENDIX III /CHAPTER III

**Figure 1. Distance index of dispersion (overstory layer).
P-value= 0.0318**



**Figure 2. XMEAN or 'mean distance from a random point to the nearest individual' (overstory layer).
P-value= 0.0194**

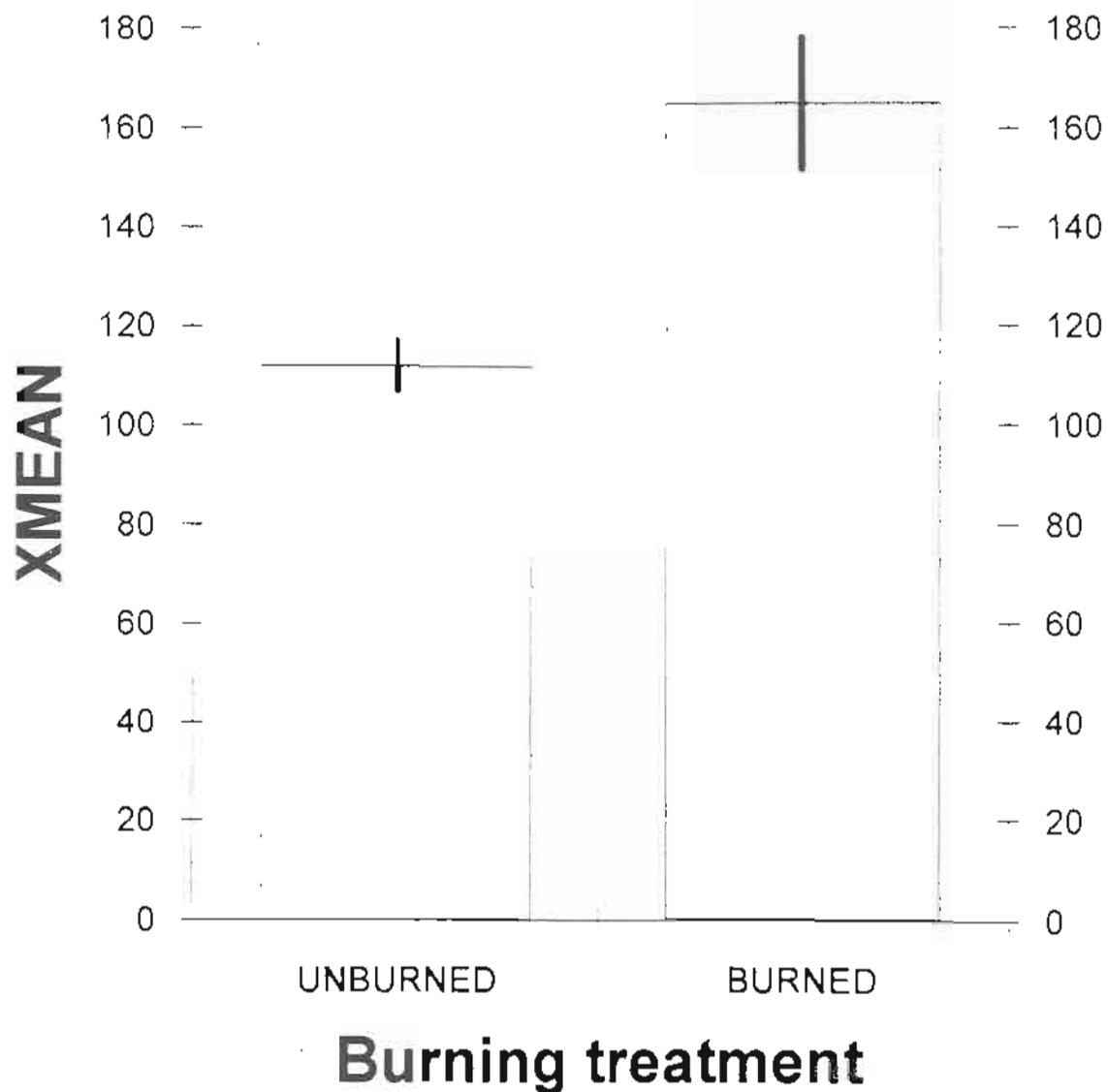
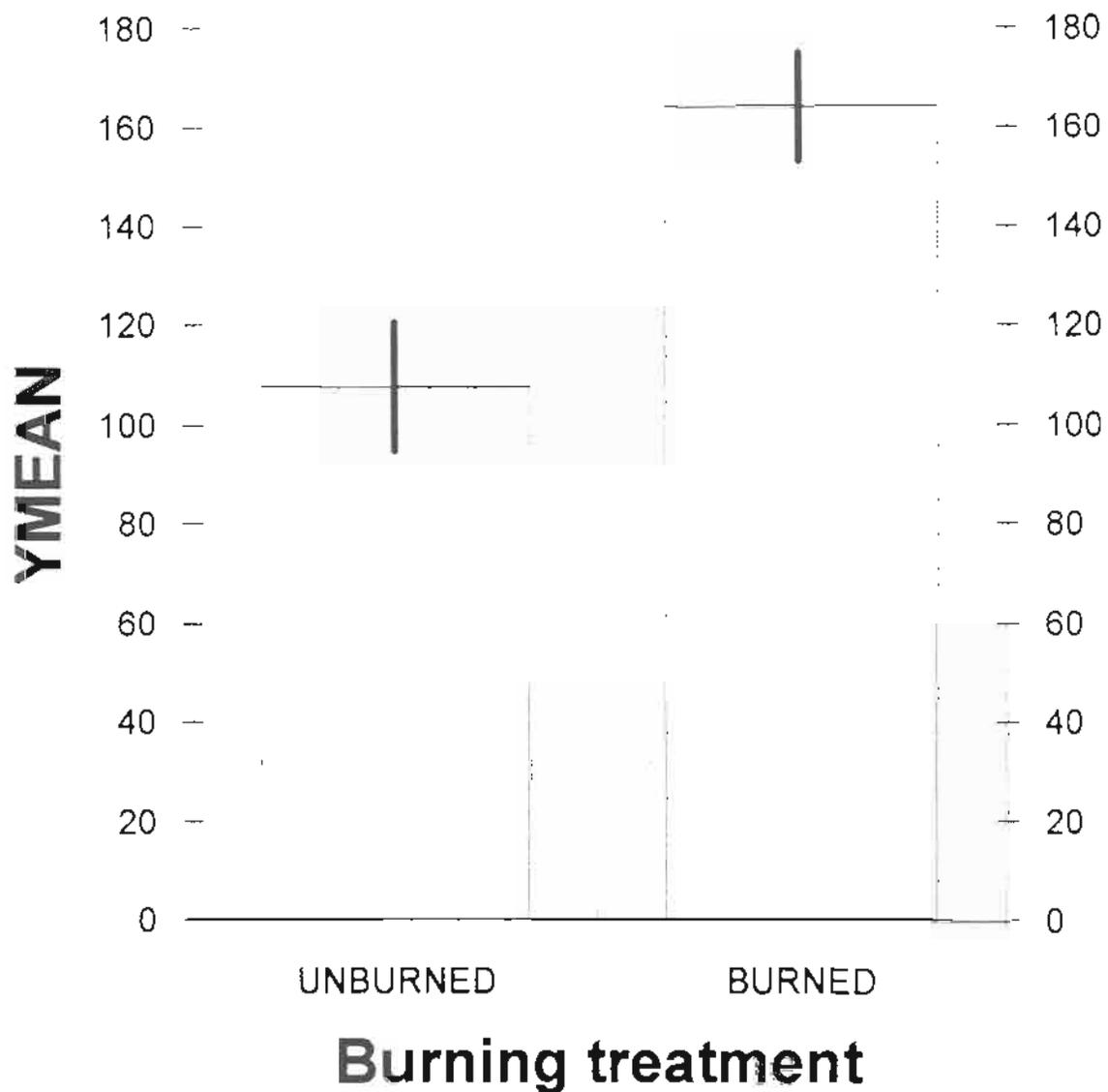


Figure 3. YMEAN or 'mean distance from an individual to its nearest neighbor' (overstory layer). P-value= 0.0281



**Figure 4. Distance index of dispersion (understory layer).
P-value= 0.1836**

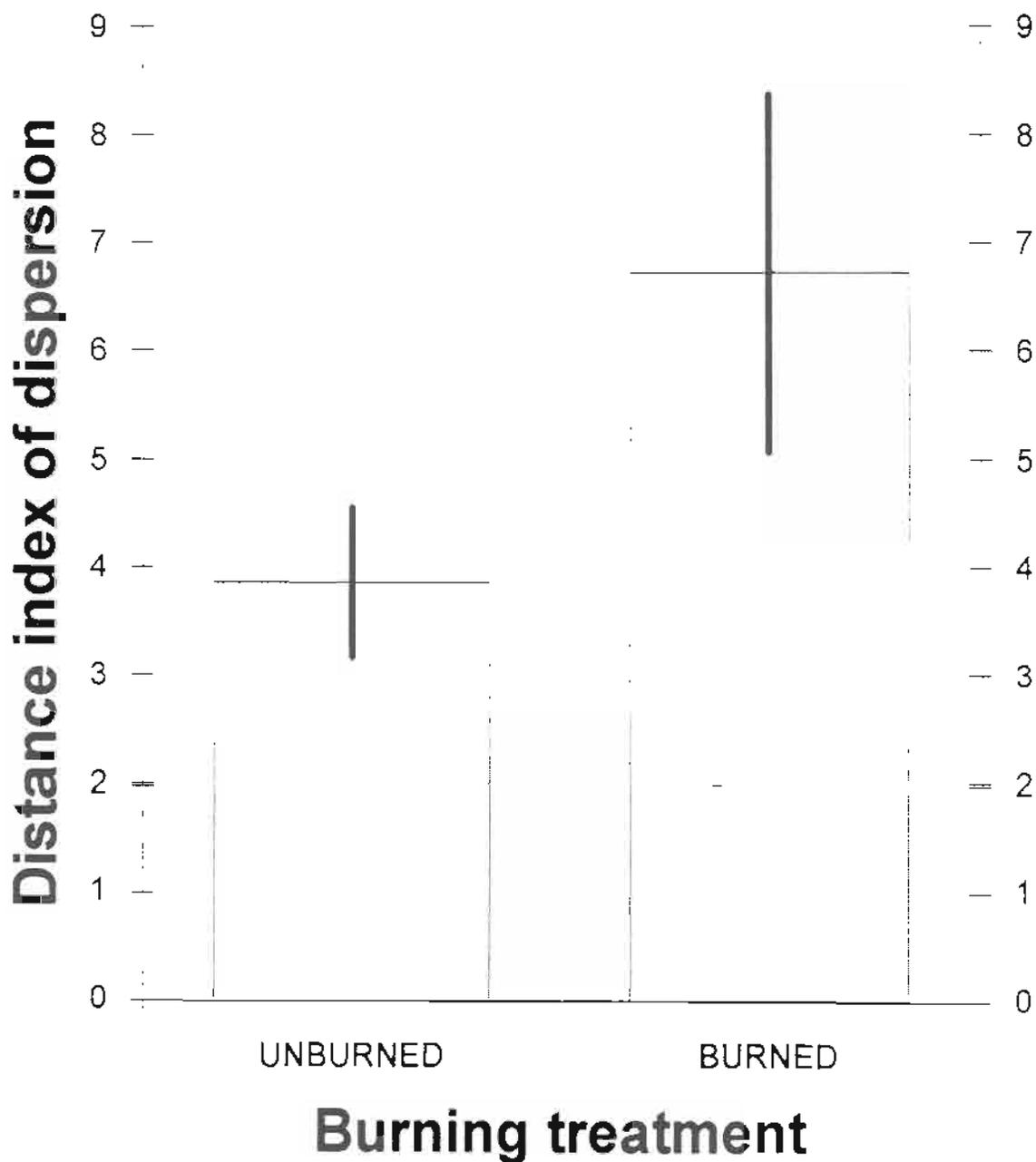
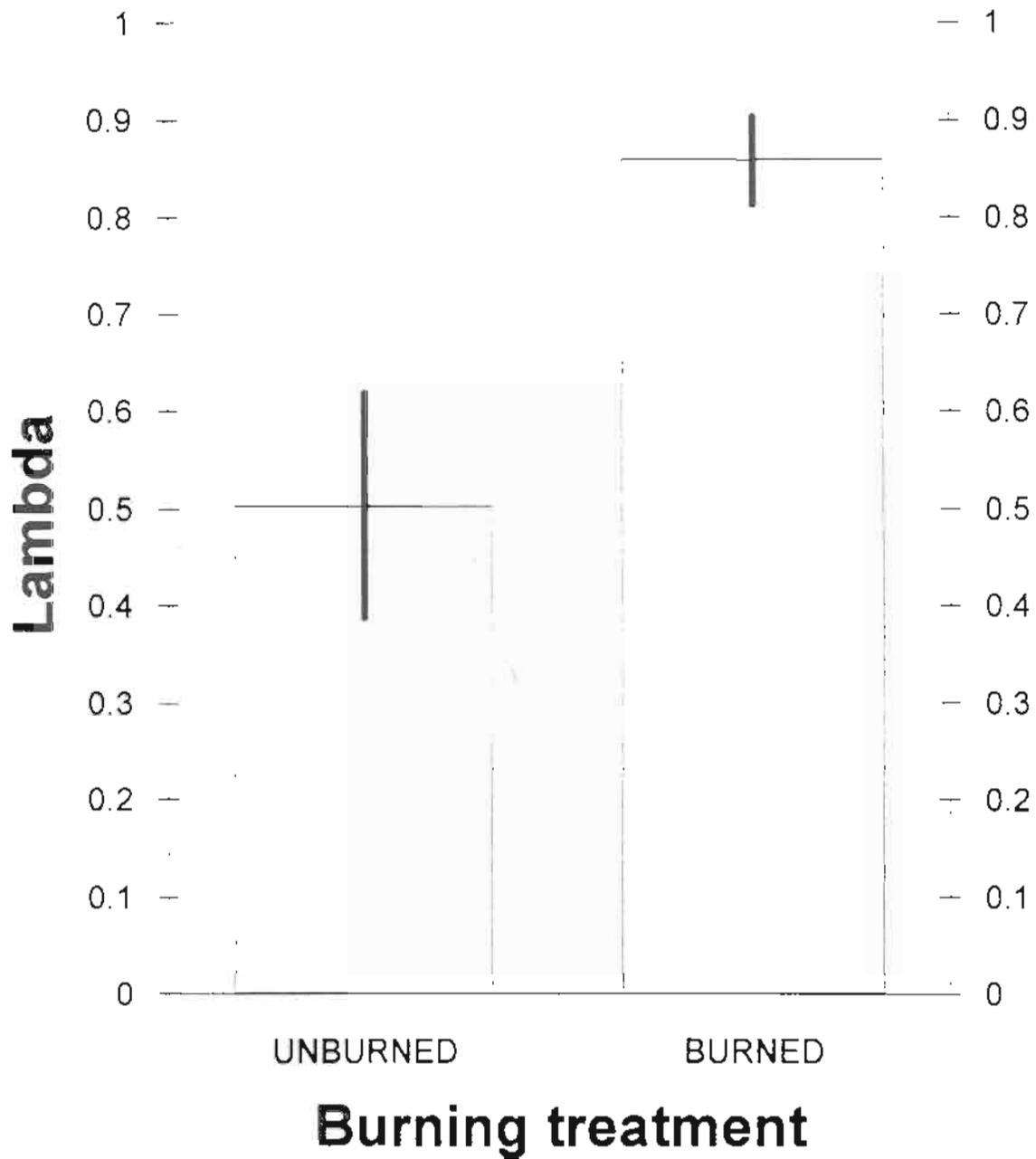
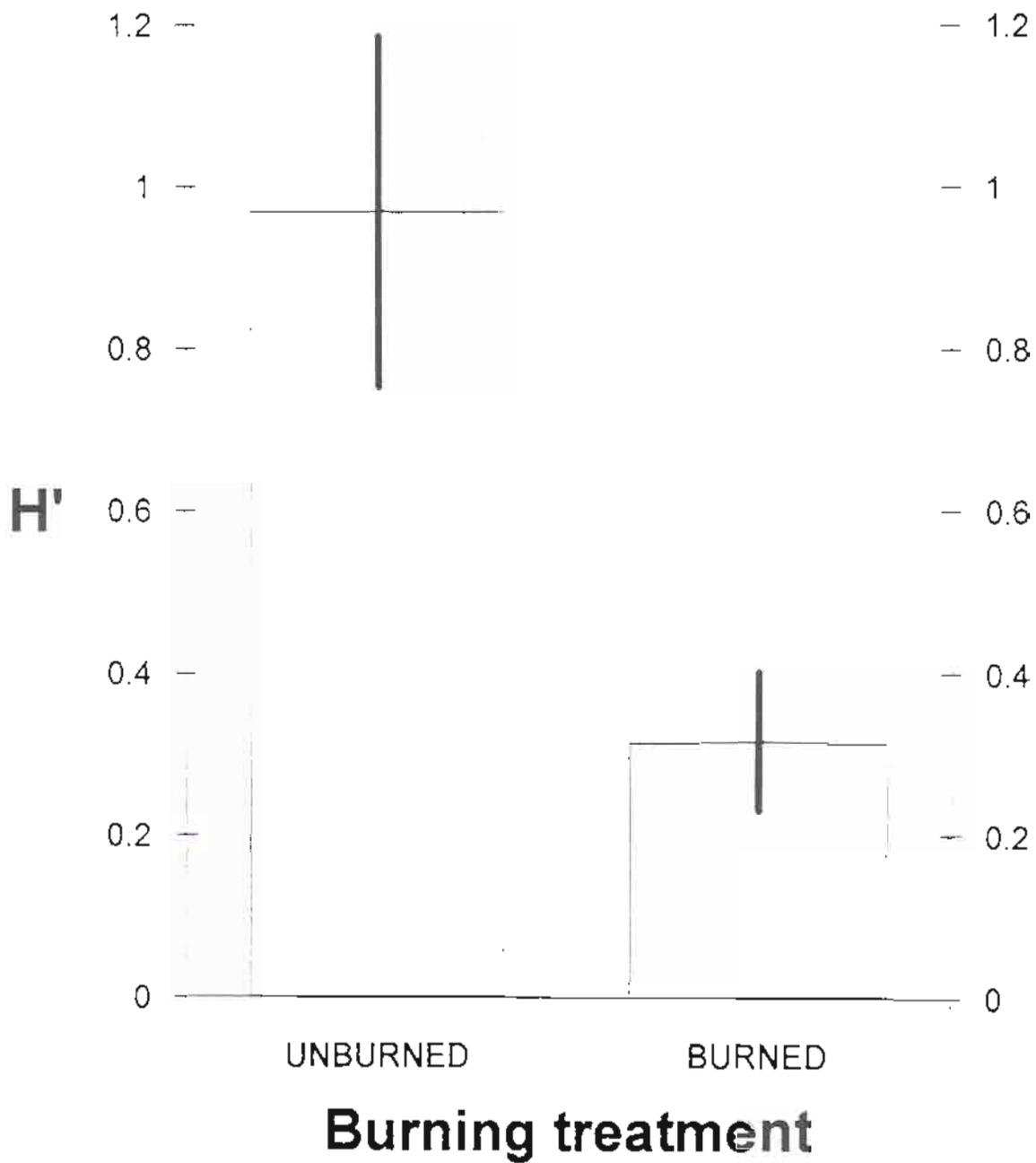


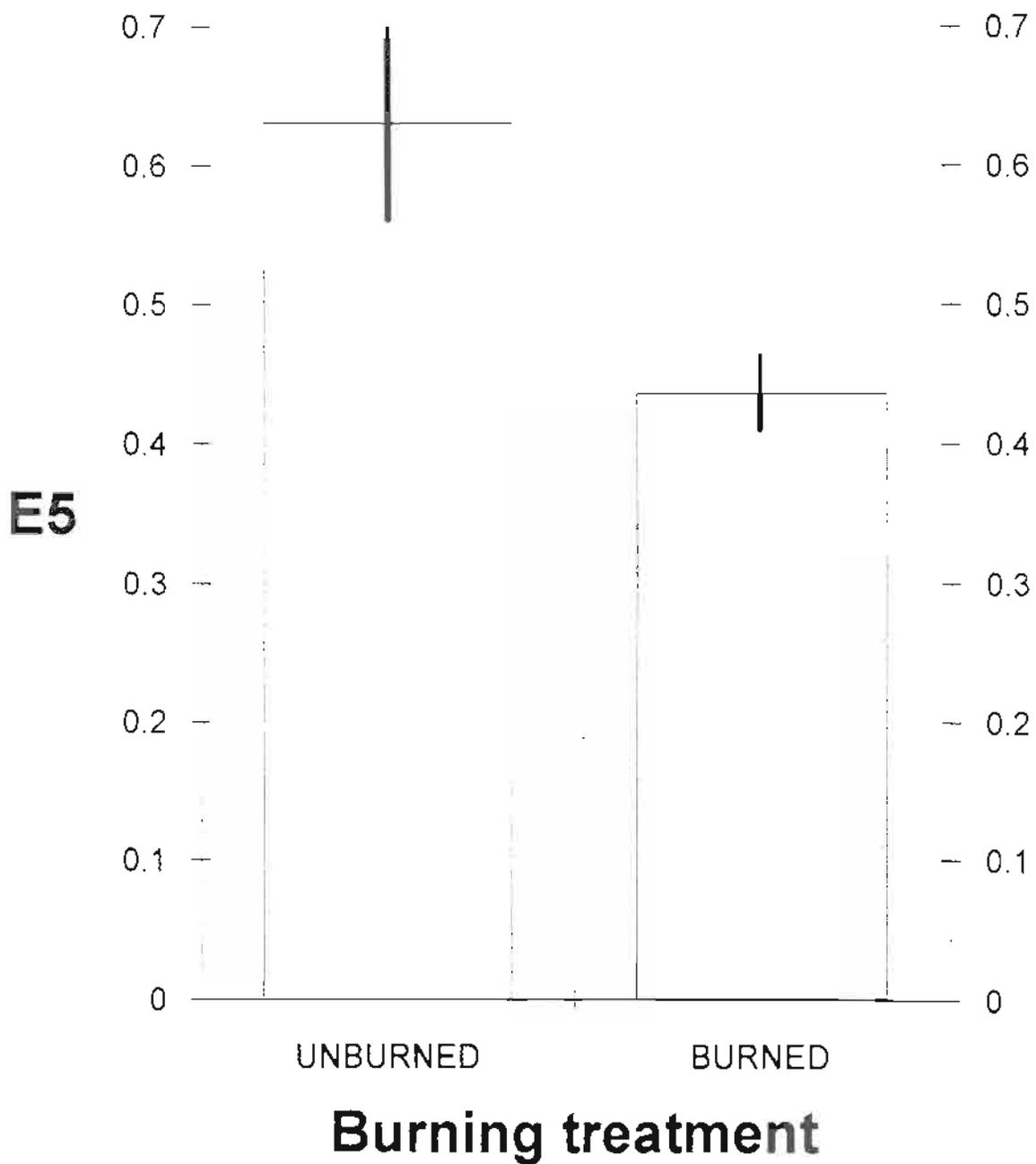
Figure 5. Lambda index of species diversity (overstory)
P-value= 0.1022



**Figure 6. H' index of species diversity (overstory layer).
P-value= 0.1058**



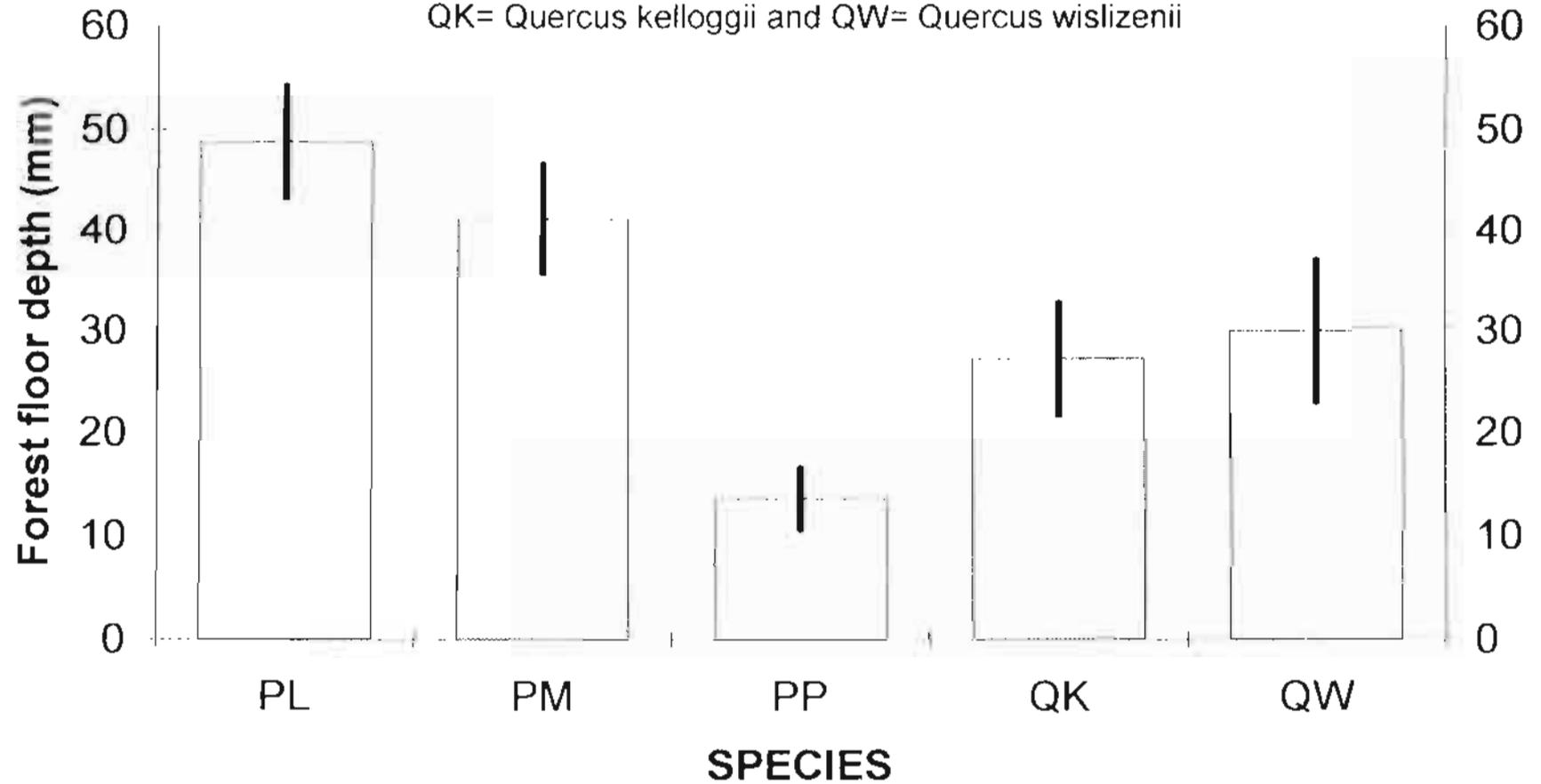
**Figure 7. E5 evenness index
(overstory layer).
P-value= 0.1178**



APPENDIX IV / CHAPTER IV

Figure 1. Forest floor depth (mm) by species: mean and standard error

PL= *Pinus lambertiana*, PM= *Pseudotsuga menziesii*, PP= *Pinus ponderosa*,
QK= *Quercus kelloggii* and QW= *Quercus wislizenii*



**Figure 2. Distance to the nearest neighbor (cm) by species:
mean and standard error**

PL= *Pinus lambertiana*, PM= *Pseudotsuga menziesii*, PP= *Pinus ponderosa*,
QK= *Quercus kelloggii* and QW= *Quercus wislizenii*

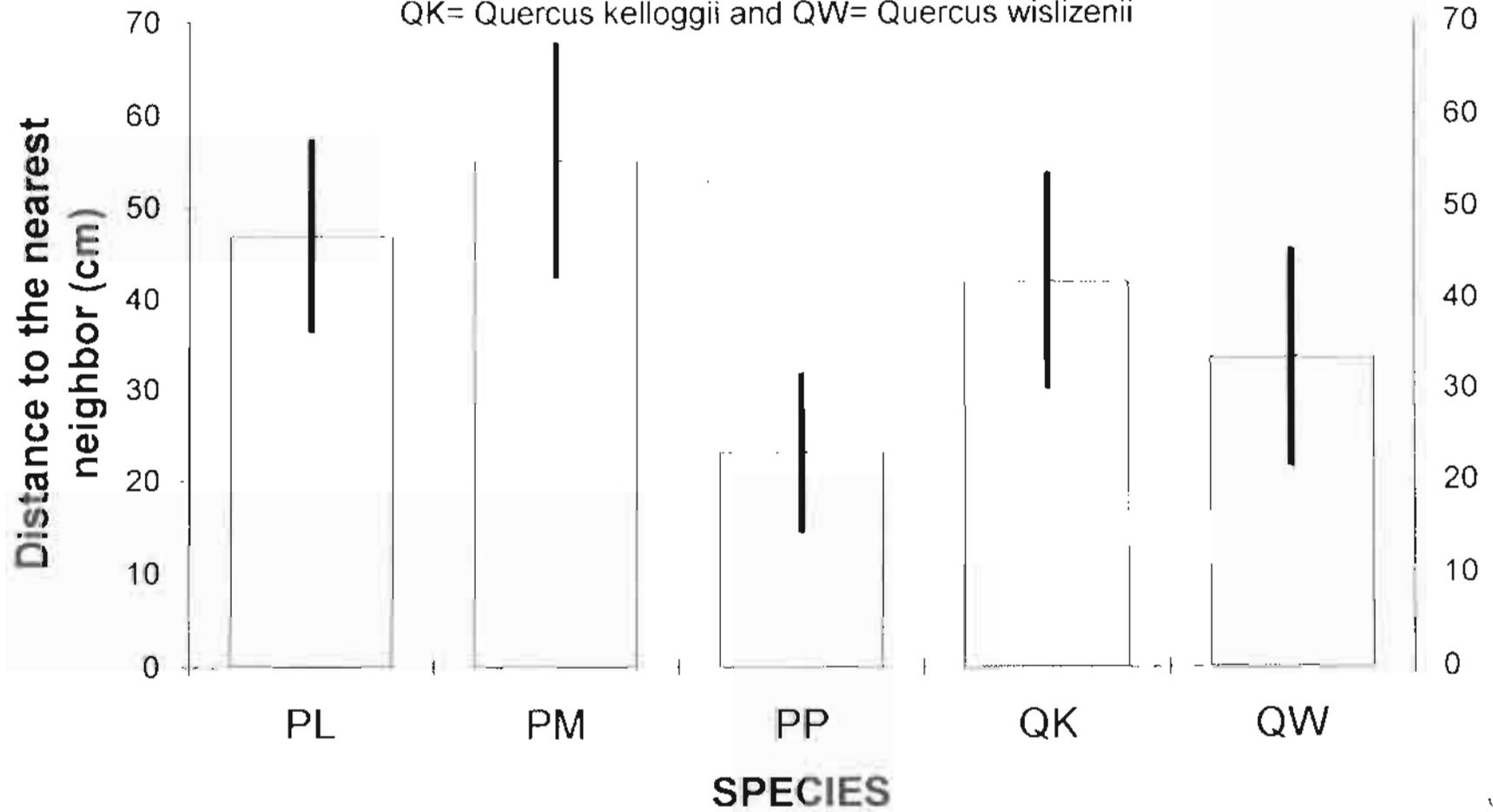
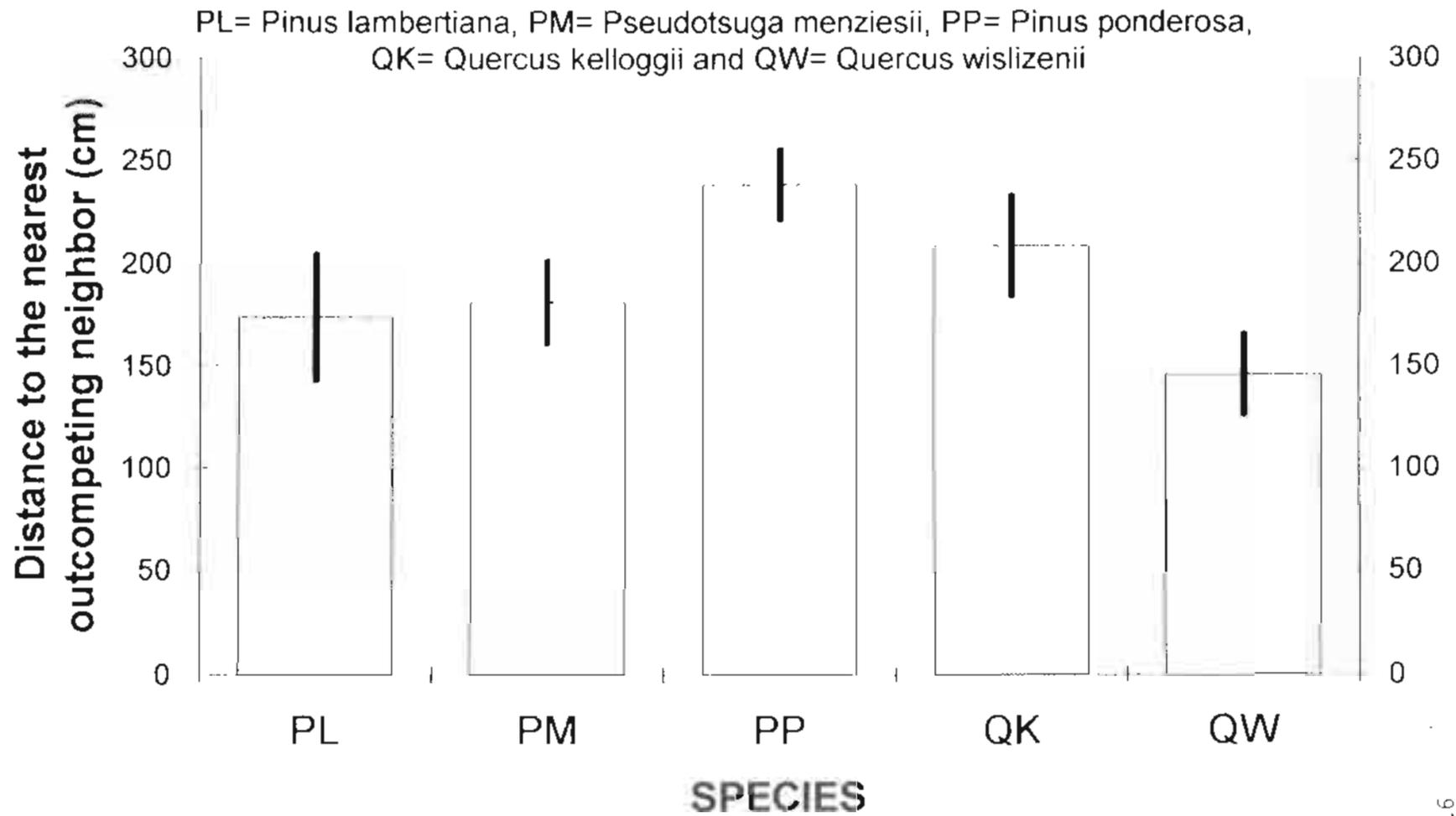


Figure 3. Distance to the nearest outcompeting neighbor (cm) by species: mean and standard error



**Figure 4. Percentage of litter cover of the soil by species:
mean and standard error**

PL= *Pinus lambertiana*, PM= *Pseudotsuga menziesii*, PP= *Pinus ponderosa*,
QK= *Quercus kelloggii* and QW= *Quercus wislizenii*

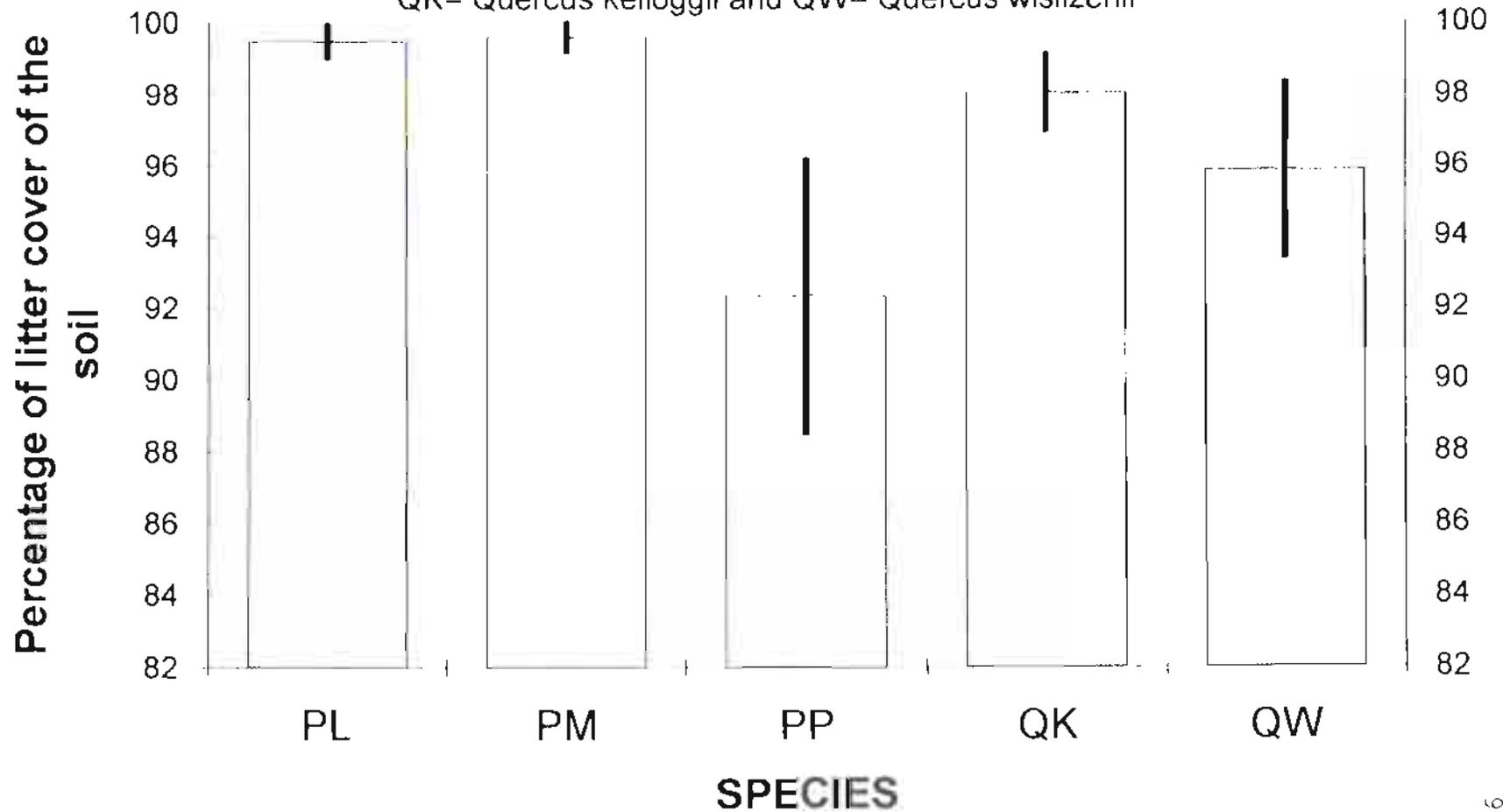


Figure 5. Percentage of total plant cover by species: mean and standard error

PL= *Pinus lambertiana*, PM= *Pseudotsuga menziesii*, PP= *Pinus ponderosa*,
QK= *Quercus kelloggii* and QW= *Quercus wislizenii*

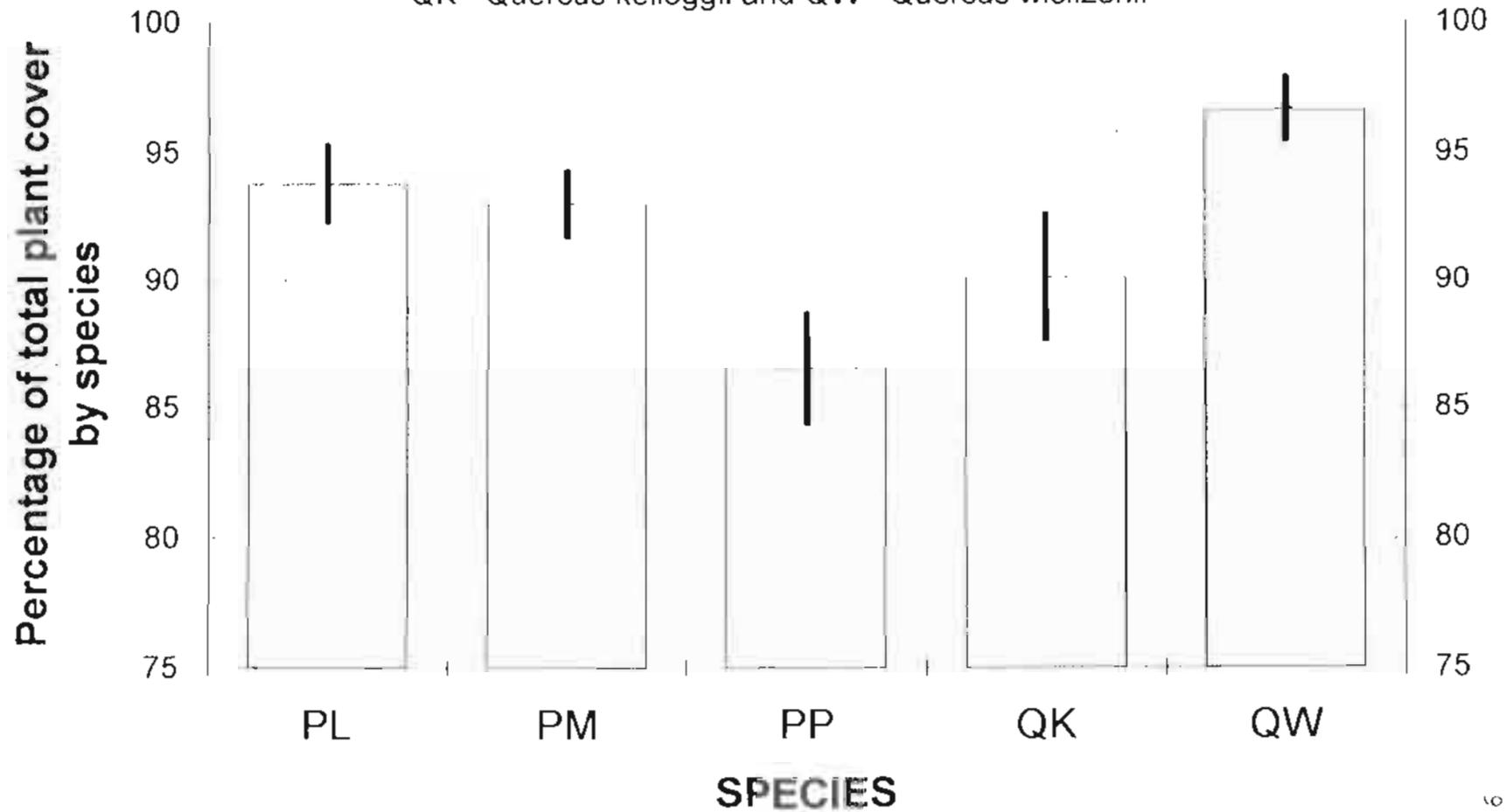


Figure 6. Percentage of light intensity by species: mean and standard error

PL= *Pinus lambertiana*, PM= *Pseudotsuga menziesii*, PP= *Pinus ponderosa*,
QK= *Quercus kelloggii* and QW= *Quercus wislizenii*

