# POPULATION ECOLOGY OF FENDLER CEANOTHUS: RESPONSES TO HERBIVORY AND FOREST RESTORATION TREATMENTS

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# ABSTRACT

## POPULATION ECOLOGY OF FENDLER CEANOTHUS: RESPONSES TO HERBIVORY AND FOREST RESTORATION TREATMENTS

### DAVID W. HUFFMAN

To understand responses of Fendler ceanothus to forest restoration treatments and large ungulate herbivory, I focused research on four areas: 1) effects of large ungulate herbivores on Fendler ceanothus stem size, morphology, and flower production, 2) production, fate, and germination of Fendler ceanothus seeds, 3) importance of overstory density, ungulate herbivory, prescribed fire, and drought for Fendler ceanothus growth and regeneration, and 4) simulation of population dynamics under various management scenarios.

After two seasons (1999, 2000), plants protected from large ungulate herbivores were larger and produced greater biomass, leaf area, and flowering stems than plants that were not protected. These results showed that large herbivores such as mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus*) constrained growth and reproduction of Fendler ceanothus in thinned forest units.

Fendler ceanothus stems that were not protected from large herbivores did not produce fruit over the four-year study (1999-2002). Seed production (2000-2001) was affected by stem size and probably drought. Predispersal seed parasites and post-dispersal predators were important sources of ovule loss. Seed germination after exposure to 90ºC (10-minute duration) was greater than without heat treatment. These results increase our understanding of Fendler ceanothus seed production and losses.

Stand density index (SDI) and browsing by ungulates were negatively related to Fendler ceanothus growth. Prediction of growth from SDI and browsing was poor in years of drought. Plant mortality was positively related to depth of forest floor consumed in experimental burning. Fendler ceanothus seedlings emerged on burned plots but not on unburned plots. These results indicate that overstory tree thinning and prescribed fire can increase growth and reproduction of Fendler ceanothus but responses are constrained by herbivory and drought.

Simulation of Fendler ceanothus population dynamics suggested that restoration treatments and herbivory interact to affect long-term persistence and population structure. Populations that did not experience fire were generally dominated by dormant seeds whereas burned populations had relatively even life stage structures at the end of the 25-year simulation. Frequent fire (2-5 yr) stimulated growth of protected populations but negatively affected populations exposed to intense herbivory.

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# PREFACE

The following dissertation was written in journal format and main chapters were meant as stand-alone manuscripts for publication.  For this reason, there are some redundancies among chapters, particularly in Methods sections where the study area and experimental designs are described.  I have attempted to reduce these redundancies in later chapters by referencing the earlier ones.

For all the studies presented, I received generous help from my major professor, Dr. Margaret Moore, as well as, students, staff, and faculty in the Ecological Restoration Institute and School of Forestry at Northern Arizona University.  I have used a first-person, active voice throughout this dissertation with no intention of ignoring this much appreciated assistance.

# CHAPTER 1: INTRODUCTION

*"One for the rook, one for the crow, one to rot, and one to grow"*

The research presented in this dissertation was conducted within a larger experiment designed to study ecological restoration of ponderosa pine (*Pinus ponderosa* Laws.) forests of northern Arizona. Ecological restoration is defined as, "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2002). Whether or not an ecosystem has been degraded or damaged, and therefore is in need of restoration, is determined through analysis of present conditions and comparison with the system's historical range of natural variation (Landres et al. 1999, Moore et al. 1999, Allen et al. 2002). In ponderosa pine ecosystems of northern Arizona, historical range of natural variation for overstory structure has been described as open stands of mainly ponderosa pine and Gambel oak (*Quercus gambelii* Nutt.) with densities of 7-116 trees per hectare (Covington and Moore 1994a) distributed in scattered, uneven-aged groups (White 1985, Mast et al. 1999). Fire was a dominant disturbance process in the evolutionary environment of species in these forests and burned through fine fuels of herbaceous and shrubby understories at intervals of 3-6 years (Fulé et al. 1997). Surprisingly, very few details are available concerning predegradation composition or structure of understory plant communities in this area. These communities, however, are thought to have been much more diverse and productive than they are today (Covington and Moore 1994b, Covington et al. 1997).

Degradation of ponderosa pine ecosystems in northern Arizona began with the onset of Euro-American settlement around 1870 and industrial exploitation of forest resources (Cooper 1960, Covington and Moore 1994b, Kolb et al. 1994, Covington et al. 1997, Allen et al. 2002). Dense forest overstories developing from these land use practices create critical problems with respect to biological diversity and an increased risk of large, stand-replacing, crown fires. Forest restoration treatments presently underway in ponderosa pine forests are aimed at reestablishing more natural overstory density and spatial patterns, increasing native plant diversity and productivity, and assisting successional trajectories (Covington et al. 1997, Allen et al. 2002, SER 2002). The most basic of these treatments include thinning of young, small-diameter trees and application of surface fire.

Monitoring protocols and adaptive feedback mechanisms are critical in any effective land management practice (Walters and Holling 1990). Restoration ecology provides restoration programs with theoretical frameworks, practical tools, and methodologies for implementing and monitoring activities (SER 2002). Restoration science is conducted at various levels of biological organization and spatial and temporal scales. It can focus on ecosystem structure, process, or function. Ideally, restoration programs should make use of a diverse array of studies at various scales to gain the most complete understanding of ecosystem recovery.

This dissertation presents four ecological studies of the shrub, Fendler ceanothus (*Ceanothus fendleri* Gray: Rhamnaceae), which is common in ponderosa pine forests of western North America from Mexico to South Dakota (Conard et al. 1985). The four studies focus on autecological and population responses to forest restoration treatments. Autecological and population research can provide insight into patterns of ecosystem development and dynamics (Whittaker 1975, Harper 1977). For example, research at this scale of biological organization can reveal species' life history traits and mechanisms for persistence, population dynamics and constraints to population growth, morphological responses to changing environmental conditions, and trophic interactions important in food web dynamics. By providing this type of information, population-level studies can link to broader scales of investigation such as community ecology (Montalvo 1997). These studies are central to monitoring programs and evaluation of ecological restoration projects (Clewell and Rieger 1997, Montalvo et al. 1997). Further, it should be noted that ecological restoration projects, in turn, provide experiments within which to test hypotheses and theoretical models.

Fendler's ceanothus was selected for study due to its importance and uniqueness in ponderosa pine forests as well as its heuristic potential. Few studies of this species have been conducted (but see Vose and White 1987 and 1991) although the importance of this genus in other western ecosystems is widely recognized (Conard et al. 1985). Overall study of Fendler ceanothus provides basic information regarding its growth characteristics and strategies for regeneration and persistence. Further, detailed examination of this species provides information regarding the nature and magnitude of constraints to understory development after forest restoration treatments. Central objectives in this research were: 1) quantify growth potential and constraints imposed by large herbivores after restoration thinning; 2) quantify and describe seed production and fate of seeds in restoration treatment units; 3) compare regeneration and growth of plants under restoration thinning and prescribed fire treatments; and 4) model population dynamics and compare restoration management scenarios in terms of population abundance and structure.

The four studies presented in this dissertation correspond to these objectives, respectively. Chapter two quantifies the impacts of large herbivores on Fendler ceanothus growth and potential reproduction. Chapter three quantifies seed production and describes losses from development through dispersal. Chapter four describes growth across a gradient of overstory density and demographic responses to prescribed fire. Chapter five reports results from 25-year simulation modeling of populations under a set of restoration management alternatives. Finally, Chapter six summarizes some important results from the preceding chapters and explores questions in need of future research.

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# CHAPTER 2: UNGULATE HERBIVORY ON FENDLER CEANOTHUS IN AN ARIZONA PONDEROSA PINE FOREST

## Abstract

Monitoring processes that affect plant population dynamics and community structure is central in forest restoration ecology. To study effects of mule deer (*Odocoileus hemionus)* and elk (*Cervus elaphus*) on Fendler ceanothus (*Ceanothus fendleri* Gray), I built 90 exclosures in 3 ponderosa pine (*Pinus ponderosa* Laws.) forest restoration management units and compared vegetative and flowering characteristics with unprotected plots for 2 years. On unprotected plots, 69% of current-year branches were browsed the first year and 44% were browsed the second year; 2-3% of stems on protected plots had terminal buds removed, apparently by invertebrates, over the two years, respectively. There was no difference in number of aerial stems or current-year branches between protected and unprotected plots in the first year, yet stems on protected plots were longer (24.1 cm; $p<0.01$) and retained more than 4 times the current-year biomass (1.4 g stem$^{-1}$; $p<0.01$) than stems on unprotected plots (12.9 cm and 0.3 g stem$^{-1}$, respectively). Stem number, length and diameter, number of current-year branches, and current-year biomass on protected plots were all greater ($p<0.01$) than on unprotected plots in the second year. Stems on protected plots had significantly higher ($p<0.01$) length-diameter ratios and had fewer ($p<0.05$) current-year branches per unit length than unprotected stems. Flowering stems were found on significantly ($p<0.05$) more protected plots (55%) than unprotected plots (8%) in the second year. Ungulate herbivory is an

important constraint to early understory development and restoration of Fendler ceanothus in this Southwest ponderosa pine forest.

## Introduction

It is widely recognized that large mammalian herbivores, through selective grazing and site disturbance, often play key roles in ecosystems and affect community composition, structure, and development as well as various ecological processes (Anderson and Loucks 1979, Naiman 1988, Augustine and McNaughton 1998). Under episodic or light herbivory, browsed plants may compensate for tissue loss by increasing production of biomass or reproductive structures (Paige and Whitham 1987, Rosenthal and Kotanen 1994, Augustine and McNaughton 1998, Throop and Fay 1999). Intense herbivory can lead to decreased stature and reproductive output, regeneration failure, and population decline (Strohmeyer and Maschinski 1996, Kay 1997, Augustine and Frelich 1998, Augustine and McNaughton 1998, Suzuki et al. 1999, Opperman and Merenlender 2000). Through direct competition with other herbivores and indirect effects such as changes in plant phenological characteristics or site modification, large herbivores can affect population dynamics and distribution of other members of the food web (Baines et al. 1994, Rooney 2001, Stewart 2001). The array of potential ecosystem-level consequences makes assessment and monitoring of herbivore impacts particularly important for ecological restoration programs and forest management in general.

An extraordinary increase in tree density over the last century has led to critical conservation problems in ponderosa pine (*Pinus ponderosa* Laws.) ecosystems of the southwestern United States (Arnold 1950, Covington and Moore 1994a, 1994b, Kolb et al. 1994, Biondi 1996, Savage et al. 1996, Fulé et al. 1997, Mast et al. 1999). Among other effects, dense forest conditions have reduced forage abundance and habitat quality for wildlife that rely on understory vegetation (Covington and Moore 1994a). In concert with forest structural changes, Rocky Mountain elk (*Cervus elaphus nelsonii*) were introduced to the region in the early 1900s to replace the extirpated Merriam's elk (*C. e. merriami).* Numbers of elk have increased over the last 100 years to around 30,000 animals in Arizona and 40,000-50,000 animals in New Mexico (Truett 1996). Although restoration treatments such as thinning small diameter trees and reintroducing low-intensity surface fires have been suggested to restore ecological structure and function to these forests (Kolb et al. 1994, Covington et al. 1997, Moore et al. 1999), research on the impacts of herbivory on plant species' response to restoration thinning is presently lacking.

Fendler ceanothus (*Ceanothus fendleri* Gray), is a semi-evergreen, nitrogen-fixing shrub common in ponderosa pine forest understories of the Southwest (Story 1974, Conard et al. 1985). As a shrub species in primarily herbaceous understory communities, Fendler ceanothus can provide structural heterogeneity and enhance ecological diversity. Although Fendler ceanothus has been reported as an important browse plant for mule deer (*Odocoileus hemionus*), and other animals including elk consume its leaves, stems, fruit, and seeds (Urness et al. 1975, Epple 1995, Allen 1996, Huffman 2002), effects of herbivory on Fendler ceanothus growth and reproduction have not been studied. Information concerning intensity of wild ungulate herbivory and its effects on important understory species can help land managers interpret trends in community development and better understand processes constraining restoration of ecosystems. My objectives in this study were to: 1) quantify the effects of large ungulate herbivory on Fendler ceanothus vegetative characteristics such as size, production, and morphology; and 2) examine herbivory effects on Fendler ceanothus potential reproduction.

## Methods

### Study Site

I conducted my study from 1999-2000 on the Fort Valley Experimental Forest (35° 16' N, 111° 41' W) in Coconino County approximately 10 km northwest of Flagstaff, Arizona. The area receives around 52 cm of precipitation annually with a distinct dry period in May and June. Precipitation falls in late summer as rain from monsoonal thunderstorms and in winter as snow. The study area was located from 2225 to 2380 m above mean sea level. Aspect was generally southern and the topography was gentle with average slopes of approximately 5-10%. Soils are classified as Brolliar clay loams (fine, smectitic, mesic Typic Argiustolls) developed on tertiary basalt parent material and are moderately well drained (Covington et al. 1997).

Overstory vegetation was nearly pure ponderosa pine less than 120-years-old with scattered old-growth trees. Common understory species included the grasses Arizona fescue (*Festuca arizonica* Vasey), mountain muhly (*Muhlenbergia montana* (Nutt.) A.S. Hitchc.), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) and pine dropseed (*Blepharoneuron tricholepis* (Torr.) Nash); forbs such as lupine (*Lupinus* spp.), fleabane (*Erigeron* spp.), buckwheat (*Eriogonum* spp.), yarrow (*Achillea millifolium* L.), and pussytoes (*Antennaria* spp.); and shrubs Fendler ceanothus and woods rose (*Rosa woodsii*

Lindl.). Large mammalian herbivores present on the site included mule deer and elk. Cattle were excluded from the study site.

## Experimental Design

In late winter 1998, tree thinning was initiated on the study site in forest units of 14-16 hectares each. Thinning reduced tree density by about 80%. Trees retained in thinning included large (≥41 cm at breast height) and old (> about 130 years) trees, as well as, smaller, younger trees that were left to replace evidence of presettlement trees such as dead and downed logs, snags, and stumps (see Fulé et al. 2001 for restoration guidelines). Residual tree densities in forest units varied with presettlement forest structure (live trees plus dead evidence) and number of trees left as presettlement evidence replacement. I selected three of these forest units for my study and each represented a different rate of presettlement replacement (1.5-6 replacement trees per evidence; see Fulé 2001). Across the three selected units, overstory density was approximately 111-210 trees per hectare. Units were separated by at least one kilometer.

In early spring 1999, I located 60 Fendler ceanothus clonal assemblages in each of the three units (180 total). Circular plots, 1 $m^2$, were established around one or more existing stems and contained 1-25 Fendler ceanothus stems. Fendler ceanothus can expand vegetatively (Vose and White 1987) and sprouting occurs from belowground branches and a pronounced root crown (Huffman pers. obs.). Thus, it is not known how many clones produced the aerial stems I sampled. Selected stem assemblages were spatially discrete and generally covered an area less than 2 $m^2$. Hereafter, I refer to stem assemblages within plots as “plants.” Stems on plots were counted, average stem height was estimated, and notes were collected regarding signs of previous herbivory.

Herbivore protection treatment (exclosure) was randomized assigned to plots within each unit.Herbivore exclosures 4 $m^2$ in area and 1.4 m in height were constructed around plots receiving the protection treatment. Mesh size used for fencing exclosures was 5 x 10 cm. This allowed entry of small mammalian and invertebrate herbivores but excluded large ungulates.

In each of the 2 study years, I collected data on flower production and vegetative characteristics. In June of each year, I examined stems in all plots for production of inflorescences. For stems producing flowers or flower buds, I measured total stem length and basal diameter. I also counted number of inflorescences on flowering stems. In September, measurements collected for flowering stems were taken for all stems on the plots. I classified stems into 4 relative age groups according to stem base characteristics as follows: Class-1) first-year stems, not suberized, generally supple, gray-green pubescence at stem base; Class-2) bright green, not suberized, previous year’s growth of lateral branches present, generally lacked pubescence; Class-3) similar to Class-2 with bark developing in patches at stem base; Class-4) stem bases dark brown to black, fully suberized, bark often furrowed. Although Fendler ceanothus plants monitored on long-term plots at other sites appear to follow a similar developmental sequence (Moore pers. obs.), I was not able to confirm actual stem ages through ring counts or meristem scars. Additionally, number of current-year branches, average length of current-year branches, and longest current-year branch were measured.

For all stems, biomass and leaf area (LA) of current-year branches were estimated using predictive relationships developed from separate sampling in the study units. Forty-five to 50 current-year stems were collected from clonal assemblages outside the experimental plots. For biomass determination, length of current-year stems ($n = 50$) was measured, oven-dried (70° C for 48 h), and weighed to the nearest 0.01 g. For LA determination, length of current-year stems ($n = 45$) was measured, leaves were removed, and projected leaf area for each stem was measured using a video projection system (AgVision™, Ankeny, IA). The equation to predict current-branch biomass was: Ln Biomass = -4.919 + 1.395(Ln Branch Length) ($r^2=0.94$, $p<0.001$) (Fig. 2.1a). The equation to predict current-branch LA was: Ln LA = 0.663 + 0.827(Ln Branch Length) ($r^2=0.91$, $p<0.001$) (Fig. 2.1b).

## Data Analyses

One-way analysis of variance (ANOVA) was used to test for effects of protection on vegetative characteristics of Fendler ceanothus plants within study years (1999 and 2000). Overstory unit was included in the ANOVA model as a blocking factor. Paired t-tests were used to test ($p<0.10$) between-year differences in vegetative parameters within treatment (protected and unprotected) groups. Data for individual stems (i.e., length, number of current-year branches, length of current-year branches, biomass and leaf area per stem) were averaged at the plot level and analyses were performed on these values. Additionally, stem diameter, current year biomass, and current-year leaf area were summed at the plot level prior to analysis. Two morphological characteristics, "branchiness" and stem height-diameter ratio, were also compared between treatments with ANOVA. Branchiness was calculated as the number of current-year branches divided by stem length. Data met distribution and variance assumptions for ANOVA tests and were not transformed. In April 2000, 24 of the plots were burned as part of another experiment. These plots were excluded from analysis in year 2000.

A Mantel-Haenszel test was used to compare ($p<0.05$) proportions of unprotected and protected plots with flower-producing stems. Mann-Whitney nonparametric tests were used to compare ($p<0.05$) differences in number of stems and current-branches between treatments.

## Results

### Plant Size and Current-Year Biomass

Analysis of pretreatment data indicated no difference in stem length or number of stems between treatments. Stem height averaged 7.6 cm (SE=0.30) and number of stems per plot averaged 4.9 (SE=0.31) in May, 1999, before exclosures were erected.

By the end of the first growing season (September, 1999) after treatment, 69% of the current-year branches on unprotected plots had been browsed. Two percent of the new branches inside exclosures had terminal buds removed, apparently by invertebrates. I did not observe signs of small rodent herbivory inside exclosures although mesh size permitted rodent access. Herbivory on unprotected plants appeared consistent with browsing from large ungulates; current-year branches were nipped roughly, often near their bases, and I did not find discarded shoots or leaves that might suggest herbivory by rodents (Bullock 1991, Balgooyen and Waller 1995). In addition, deer and elk were frequently observed on the study site and their tracks and scat were noted near experimental plots.

One growing season after installing the herbivore exclosures, plant size was significantly different between protected and unprotected treatments. Lengths of stems and current-year branches of protected plants were from 1.9 to 2.8-fold greater than those of unprotected plants (Table 2.1). Average stem diameter was also greater for protected plants than unprotected plants. Differences in current-year branch lengths between protected and unprotected plots translated directly to differences in biomass and leaf area (Table 2.1). Individual stems on protected plots had more current-year biomass by a factor of 4.7, and leaf area by a factor of 2.5, compared to stems on unprotected plots. No difference was found in average number of stems on plots or the number of new branches produced by stems on protected and unprotected plots in 1999. All stems produced an average of 5.3 (SE=0.2) new branches during the first growing season.

In 2000, growing season precipitation (20.4 cm; March-September) was about 66% of the 91-year average (31.0 cm; Western Regional Climate Center 2000) and both protected and unprotected Fendler ceanothus plants showed varying degrees of stem dieback. In September 2000, 44% of current-year branches had been browsed on unprotected plots whereas terminal buds had been removed on 3% of the protected stems. Average total stem length on protected plots increased ($p=0.05$) slightly from the previous year and was significantly greater than that of unprotected plots, which decreased ($p=0.06$) (Table 2.1). Similarly, average stem diameter was greater on protected plots than unprotected plots. Although current-year branch lengths on both protected and unprotected plots decreased ($p<0.001$ for both treatments) in 2000 from

1999, number of current-year branches increased (p<0.001 and p=0.003 for protected and unprotected plots, respectively). Average number of current-year branches produced by stems on protected plots nearly tripled in 2000 from 1999 and was significantly greater than the number produced by stems on unprotected plots (Table 2.1). Both average length and length of the longest current-year branch were greater on protected plots than unprotected plots by a factor of 2 or greater. Individual stems on protected plots comprised significantly more current-year biomass than stems on unprotected plots by a factor of 8 (Table 2.1). Large differences also existed between protected and unprotected stems for current-year leaf area.

Average number of stems did not change significantly (p=0.31) from 1999 to 2000 on protected plots, but decreased on unprotected plots (p=0.002). More stems of larger average diameter led to significantly greater sum stem diameter (sum of all stems on a plot) on protected than unprotected plots in 2000 (Table 2.1). Similarly, sum current-year biomass on protected plots in 2000 did not change from 1999 (p=0.81), whereas biomass decreased significantly (p<0.001) on unprotected plots. In 2000, current-year biomass summed on protected plots was greater than that on unprotected plots by a factor of 12 (Table 2.1). Similar patterns existed between protected and unprotected plots for sum current-year leaf area (Table 2.1). Sum leaf area significantly increased (p=0.014) from 1999 to 2000 on protected plots but decreased (p<0.001) on unprotected plots.

## Stem Morphology

Herbivory of current-year branches on Fendler ceanothus stems led to noticeable differences in stem morphology. Stem height-diameter ratio was significantly greater for plants on protected plots than for plants on unprotected plots (Table 2.2). Stems within herbivore exclosures typically appeared long and drooping whereas stems exposed to herbivores were most often short and stubby in appearance. Although protected plants produced more current-year branches than unprotected plants in 2000, the number of branches relative to stem length was significantly greater for stems on unprotected plants in both 1999 and 2000 (Table 2.2).

## Flower Production

In June 1999, three months after exclosures were established, no difference in flower production was found between protected and unprotected Fendler ceanothus plots. Stems produced flowers on just 2 of 180 total plots (1.1% overall).

In June 2000, flowering stems were found in a significantly greater proportion of protected plots (55%) than unprotected plots (8%). On average, 22% (SE=3.6) of stems on protected plots produced flowers whereas 0.8% (SE=0.4) of stems produced flowers on unprotected plots. In protected plots, up to 11 (maximum) stems produced flowers whereas no more than 1 stem flowered in any unprotected plot.

Stems that produced flowers tended to be the larger and apparently older stems on plots (Fig. 2.2). No stems under 20 cm in length produced flowers and 85% of the flowering stems were greater than 30 cm in length. Similarly, 82% of the flowering stems were greater than 4 mm in diameter. No current-year stems flowered and more than 90% of the flowering stems had suberized bases (age classes 3 and 4). The mean number of inflorescences (panicles) produced per flowering stem was 7.3. Inflorescences were comprised of many individual flowers although these were not counted. An average of 2 branches per stem flowered; the maximum number of flowering branches was 9 per stem.

## Discussion

Mule deer and Rocky Mountain elk appeared to be the primary large herbivores of Fendler ceanothus and caused significant reduction of current-year biomass in both study years. Plants that were not protected from large herbivores had small, branchy stems, decreased aerial stem survival, and limited flowering compared with protected plants. Reduced flowering and stem survival could in turn lead to declines in local Fendler ceanothus abundance, affect community successional dynamics, and have indirect effects on other ecosystem components (Baines et al. 1994, Augustine and Frelich 1998). It is clear that herbivory by deer and elk is limiting development of understory structural diversity by constraining Fendler ceanothus growth and flower production. I did not examine interactions of herbivory and low-intensity fire, although prescribed burning is an important component of Southwest ponderosa pine restoration programs (Covington et al. 1997). Fire often leads to increases in vegetative and sexual regeneration through sprout production and seed germination, however, it can also increase palatability of plant tissues and create conditions that attract herbivores (Whelan 1995). My results indicate that deer and elk herbivory after forest thinning should be considered an important constraint to the ecological restoration of these ecosystems.

Intensity of deer and elk herbivory on Fendler ceanothus and other species varies with season, site conditions, and ungulate population characteristics (Reynolds 1964, Patton 1974, Urness et al. 1975, Furniss et al. 1978, Allen 1996, Throop and Fay 1999). For example, Urness et al. (1975) found that Fendler ceanothus comprised up to 6.9% of mule deer summer diet and was a consistently important browse species throughout the year at Beaver Creek, a site located around 55 km south of ours. Other woody species preferred by mule deer at Beaver Creek were Gambel oak (*Quercus gambelii* Nutt.), mountain mahogany (*Cercocarpus breviflorus* Gray), and Utah serviceberry (*Amelanchier utahensis* Koehne). These species are not commonly found on my study site and thus preference for Fendler ceanothus may be greater at Fort Valley than reported by Urness et al. (1975). Allen (1996) noted severe browsing of Fendler ceanothus 15 years after an extensive wildfire in New Mexico and related intensity of herbivory to a dramatic elk population increase. Patton (1974) found that mule deer use increased in ponderosa pine forests after overstory thinning. Thus, in my study, deer and elk may have been attracted to the open conditions created by forest thinning treatments.

Levels of herbivory that stimulate flower production or enhance plant growth may positively contribute to ecological restoration goals by increasing plant resources for various organisms in the food web (Jackson et al. 1995). Paige and Whitham (1987) reported increased flower production after experimental clipping as well as natural herbivory by deer and elk for a northern Arizona forb, scarlet gilia (*Ipomopsis aggregata* (Pursh) V. Grant). Similarly, Throop and Fay (1999) found that browsed New Jersey tea (*Ceanothus herbaceous* Raf. var. *pubescens* (T. & G.) Shinners) produced a greater number of inflorescences than unbrowsed plants on a tallgrass prairie site. In contrast, by reducing plant biomass, production of reproductive structures, and fitness, intense herbivory may be a constraint to ecosystem restoration. Stein et al. (1992) noted that elk completely consumed arroyo willow (*Salix lasiolepis* Benth.) resprouts after experimental burning in northern Arizona. Similarly, Strohmeyer and Maschinski (1996) reported both wild and domestic herbivores reduced total shoot length and number of branches of Arizona willow (*Salix arizonica* Dorn). Intense herbivory by deer and elk is known to limit production of flowers, seeds, and vegetative regeneration of various plant species in other western ecosystems (DeByle 1985, Dunlap 1988, Mitchell and Freeman 1993, Hoffman and Wambolt 1996, Kay 1997, Opperman and Merenlender 2000). In my study, Fendler ceanothus flowers were observed on less than 10% of the unprotected plots. Low flower production may affect populations of species, such as *Eurytoma squamosa* Bugbee (Hymenoptera) that feed on seeds of Fendler ceanothus (Huffman 2002). This suggests that ungulate herbivory may affect diversity and composition of invertebrate communities through direct competition and/or indirect effects (e.g., reduced production of seeds, alteration of microsite characteristics, etc.) (Baines et al. 1994, Rambo and Faeth 1999, Rooney 2001, Stewart 2001).

Further research is needed to explore the roles of wild ungulate herbivory in conservation and ecological restoration of Southwest ponderosa pine ecosystems. Current understanding of presettlement conditions – attributes that provide baselines to guide ecological restoration – is greatest for overstory characteristics and fire regimes (Covington and Moore 1994a, Covington et al. 1997, Fulé et al. 1997, Mast et al. 1999). Little is known regarding presettlement understory composition and diversity (but see Kerns et al. 2001). Moreover, information concerning population dynamics and spatial distribution of large herbivores or the range of historical variability for their effects in Southwest forest ecosystems is lacking (but see Truett 1996). On some landscapes, including that of my study area, elk are thought to be more abundant and distributed more evenly than they were for possibly the last 800 years (Allen 1996, Truett 1996, Kay 1997). Indeed, ungulate herbivory in combination with forest structural changes appears to be exacerbating conservation problems in these ecosystems. For ecological restoration activities that seek to reestablish ecosystem integrity and function, it is important to understand evolutionary environments of native species and emulate historical conditions of landscape-scale processes that include herbivory by large, wild ungulates.

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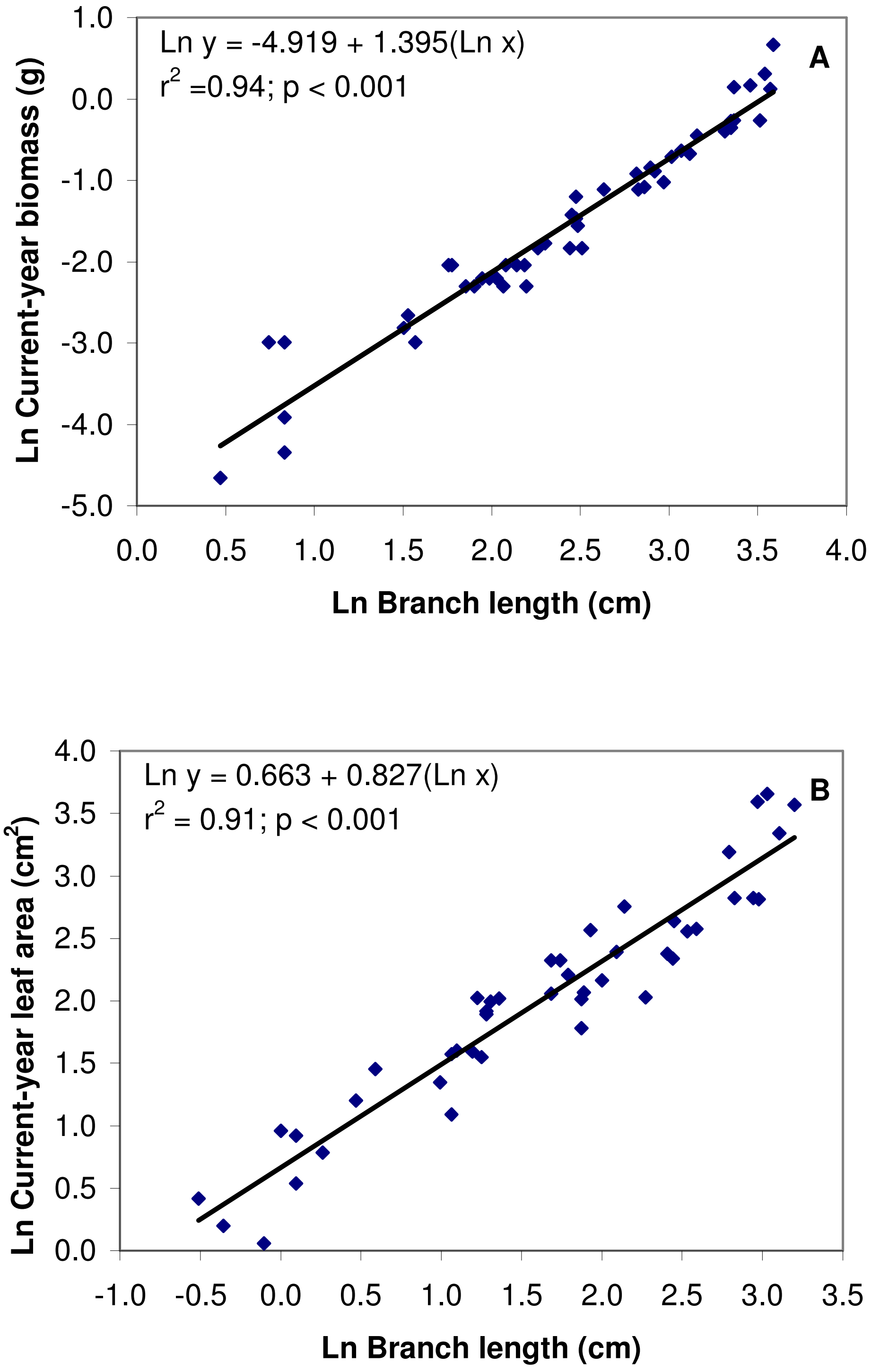

Figure 2.1. Relationships used to estimate biomass (A) and leaf area (B) of current-year branches on Fendler ceanothus plants.

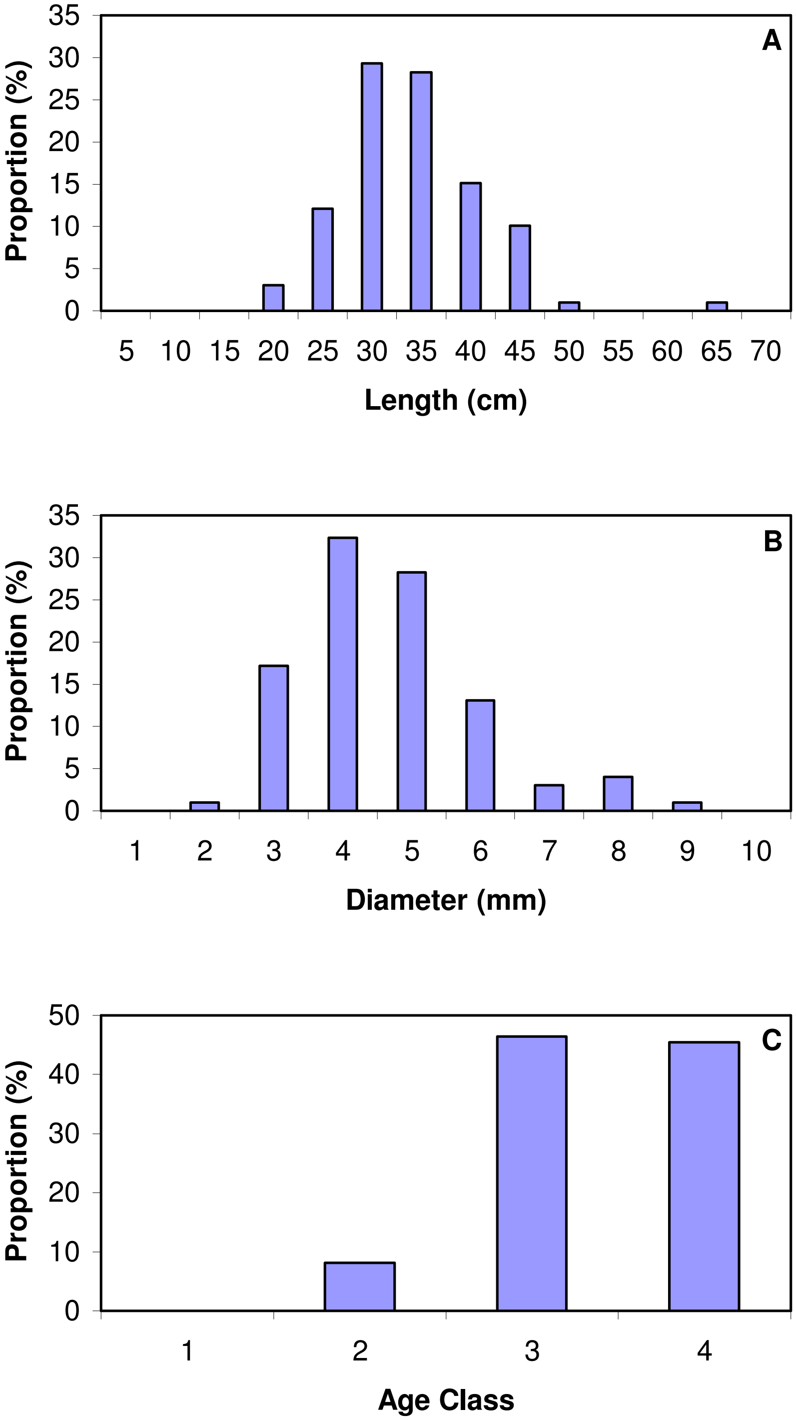

Figure 2.1. Proportion of Fendler ceanothus stems that produced flowers by length (A), diameter (B), and age class (C).

Table 2.1. Means (standard errors) of Fendler ceanothus vegetative characteristics on plots protected from large herbivores and on unprotected plots in 1999 and 2000.

| | 1999 | | 2000 | |
|---|---|---|---|---|
| Variable | Protected | Unprotected | Protected | Unprotected |
| Stems | | | | |
| Number | 8.1 (1.0) | 6.9 (0.6) | 9.1 (1.2) * | 5.4 (0.5) |
| Length (cm) | 24.1 (0.8) **[1] | 12.9 (0.7) | 25.9 (1.0) ** | 11.2 (0.8) |
| Diameter (mm) | 3.5 (0.1) † | 3.1 (0.1) | 4.1 (0.2) * | 3.5 (0.1) |
| Current-Year Branches | | | | |
| Number | 5.3 (0.3) | 5.3 (0.3) | 15.3 (1.5) ** | 7.1 (0.6) |
| Length (cm) | 13.1 (0.4) ** | 4.7 (0.4) | 5.8 (0.4) ** | 2.5 (0.2) |
| Longest (cm) | 19.5 (0.6) ** | 7.7 (0.5) | 9.7 (0.6) ** | 4.5 (0.4) |
| Biomass (g) | 1.4 (0.1) ** | 0.3 (< 0.1) | 1.6 (0.5) ** | 0.2 (< 0.1) |
| Leaf Area (cm$^2$) | 83.9 (6.3) ** | 33.5 (3.3) | 132.4 (26.4) ** | 27.4 (3.1) |
| Plot | | | | |
| Sum Diameter (mm m$^{-2}$) | 24.5 (3.0) * | 18.5 (1.5) | 30.4 (3.4) ** | 17.1 (1.5) |
| Sum Current-Year Biomass (g m$^{-2}$) | 8.1 (0.9) ** | 1.7 (0.2) | 8.7 (1.7) ** | 0.7 (< 0.1) |
| Sum Current-Year Leaf Area (cm$^2$ m$^{-2}$) | 492.0 (55.0) ** | 177.5 (16.3) | 739.1 (95.1) ** | 109.5 (9.7) |

[1] Symbols indicate significant difference between treatments within years († $P < 0.10$; * $P < 0.05$; ** $P < 0.01$)

Table 2.2. Means (standard errors) of morphological characteristics of Fendler ceanothus stems on protected and unprotected plots.

| | 1999 | | 2000 | |
|---|---|---|---|---|
| Variable | Protected | Unprotected | Protected | Unprotected |
| Height-Diameter Ratio ($cm\ cm^{-1}$) | 73.5 (1.9) **[1] | 42.3 (1.8) | 68.3 (2.1) ** | 32.6 (1.8) |
| Branchiness[2] ($N\ cm^{-1}$) | 0.2 (<0.1) ** | 0.4 (<0.1) | 0.5 (<0.1) * | 0.7 (<0.1) |

[1] Symbols indicate significant difference between treatments within years (* P<0.05; ** P<0.01).

[2] Branchiness=Number Current-year Branches ÷ Stem Length

# CHAPTER 3: SEED ECOLOGY OF FENDLER CEANOTHUS: IMPLICATIONS FOR FOREST RESTORATION

## Abstract

In the initial stages of ponderosa pine (*Pinus ponderosa* Laws.) forest restoration in the Southwest, understory environments are typically characterized by: 1) low plant abundance due to previously dense overstory conditions; and 2) highly disturbed forest floors due to mechanical tree thinning and application of prescribed fire. Herbaceous and shrub understory recovery on these sites appears to be limited, in part, by propagule abundance. To quantify flower, fruit, and seed production for an important shrub, I monitored Fendler ceanothus (*Ceanothus fendleri* Gray) plants for four years on 90 plots in three forest units undergoing restoration treatments in northern Arizona. I examined ovule and seed losses in predispersal and post-dispersal stages. I also conducted seed germination tests and examined effects of heat, heat duration, and cold stratification. Fendler ceanothus flowering generally increased over the four study years although fruit production appeared to be related to precipitation. Mean fruit production varied from 7 to 39 fruits per stem. In a year of high fruit production, distributions of fruiting stem sizes significantly ($p<0.001$) deviated from those of the overall stem population and were shifted toward larger length and diameter classes. A weak ($p<0.05$) positive relationship was found between fruit and seed production and stem diameter. Ovule losses during fruit set were 23-35%. Of the total number of seeds produced, 50-58% were undeveloped. Of seeds that appeared normally developed, 7-71% were parasitized by a seed chalcid (*Eurytoma squamosa* Bugbee). An additional 1-3% of seeds were otherwise hollow.

Post-dispersal seed predation varied from 2-24 % and predation was significantly ($p<0.05$) greater on charred forest floor substrate from prescribed fire than on unburned ponderosa pine litter. Laboratory tests showed significantly ($p<0.05$) higher germination for seeds exposed to 90ºC compared to no-heat treatment (~20ºC). Seeds exposed to temperatures greater than 120ºC did not germinate. Information from this study can help managers determine strategies for increasing Fendler ceanothus seed production and regeneration while providing for ecosystem diversity and function.

## Introduction

One of the primary goals of ponderosa pine (*Pinus ponderosa* Laws.) forest restoration in the southwestern United States is to increase understory plant community productivity and diversity to levels more closely reflecting conditions that existed prior to ecosystem degradation (Covington and Moore 1994, Kolb et al. 1994, Covington et al. 1997, Moore et al. 1999). Plant phytolith analyses revealed that an abundant understory of grasses, forbs, and shrubs associated with open forest conditions likely prevailed before ca 1870 (Kerns et al. 2001). These communities have been severely reduced over the last ~130 years by population irruptions of ponderosa pine trees that resulted from overgrazing, exclusion of natural surface fires, and selective timber harvesting associated with EuroAmerican settlement of the region (Arnold 1950, Cooper 1960, Fulé et al. 1997, Mast et al. 1999). Treatments to restore these forests include: 1) thinning of young (postsettlement) trees to emulate pre-degradation density and spatial pattern or to recreate more open conditions; and 2) application of low-intensity fire to reduce accumulated woody fuels and reintroduce a critical ecosystem process (Covington et al 1997, Moore et al. 1999). Remnant populations of plants, dormant seeds stored in soil, and wind-blown seed serve as propagule sources for understory recovery after restoration activities. Disturbances associated with mechanical thinning and reintroduction of fire, in combination with low understory plant abundance before treatment, result in an abundance of safe sites (sensu Harper 1977) and population recruitment of individuals and maintenance of soil seed banks appear to be limited by seed supply (Springer et al. 2000). Under these conditions, seed production, fate, and viability are important determinants of population growth, replacement of individuals, and colonization of new sites (Andersen 1989).

Fendler ceanothus (*Ceanothus fendleri* Gray) is a small shrub common to ponderosa pine forests in the Southwest (Epple 1995). Like other species in its genus, Fendler ceanothus is a nitrogen-fixer (Story 1974, Conard et al. 1985) and provides various important structural and habitat elements to understory communities. In particular, its values as wildlife browse and woody growth in predominantly herbaceous understories make it a key species in these ecosystems.

Fendler ceanothus flowering can occur April-October but tends to peak in late June (Kearney and Peebles 1964, Epple 1995, Huffman pers. obs.). Flowers are small (~2 mm), borne in panicles, and can be prolific; many species in the genus are cultivated for ornamental purposes and some are commonly referred to as "mountain lilac" (Kearney and Peebles 1964, Epple 1995). In a previous study (Chapter 2 this dissertation), I reported that flowering stems tended to be larger and older members of stem populations.

Fendler ceanothus fruits are 3-celled capsules (Kearney and Peebles 1964) that ripen August-September. At present, I am not aware of any fruit or seed production data for Fendler ceanothus. Predispersal seed parasitism by a chalcidoid wasp (*Eurytoma squamosa* Bugbee) can destroy as much as 71% of developed seeds (Huffman 2002). At full development, seeds are dark brown in color and about 2 mm diameter.

Seeds are dispersed by ballistic expulsion as fruits dehisce (Kearney and Peebles 1964). Although Fendler ceanothus stems and leaves are eaten by large ungulates such as mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus*) (Urness 1975, Conard et al. 1985, Allen 1996, see also Chapter 2 this dissertation), no information is currently available regarding rates of post-dispersal seed predation.

After fire, Fendler ceanothus utilizes a dual regeneration strategy consisting of sprout production and seedling establishment (Pearson et al. 1972, Vose and White 1987, Vose and White 1991). Seed germination requirements of Fendler ceanothus have not been studied in detail (Story 1974, Krishnan 1989), although heat treatments and cold stratification have been found to improve germination of several other *Ceanothus* species (Hadley 1961, Quick and Quick 1961, Gratkowski 1974).

The main objectives of my study were to: 1) quantify Fendler ceanothus flower, fruit, and seed production in forest stands undergoing ecological restoration treatments; 2) quantify ovule and seed losses during development and dispersal; and 3) evaluate germination characteristics of Fendler ceanothus seeds. Information concerning seed output, relative importance and variability of seed losses, and seed dormancy traits can help ecologists and resource managers understand successional trends manifested on sites for which ecological restoration is a goal. Further, this information can help managers formulate prescriptions aimed at manipulating Fendler ceanothus population characteristics.

## Methods

### Study Site

The area used for studies of Fendler ceanothus reproductive capacity (flower, fruit, and seed production), seed parasitism, and seed predation was the Fort Valley Experimental Forest about 10 km northwest of Flagstaff, AZ. This study site was previously described in detail in Chapter 2 of this dissertation.

Flower, fruit, and seed production were measured on Fendler 180 plots, 1 $m^2$ in size, in three experimental forest restoration units 1999-2002. Plot establishment and design are described in detail in Chapter 2. In each forest unit, plots were randomly assigned to herbivore protection and experimental burning treatments in a 2x2 factorial design. Plots selected for herbivore protection were surrounded by wire mesh exclosures ("cages") (see Chapter 2 this dissertation). Herbivore protection and burning treatment combinations resulted in four treatments hereafter referred to as NCNB (no cage, no burn), NCB (no cage, burn), CNB (cage, no burn) and CB (cage, burn). Experimental burning of plots was conducted in April of 2000 (24 plots) and May of 2001 (65 plots) when U.S. Forest Service staff implemented prescribed fire within the forest units. More detail regarding experimental burning is given in Chapter 3, this dissertation.

Germination experiments were done using seeds collected from four sites near Flagstaff, Arizona: 1) Bear Jaw Canyon (BJ); 2) Dutton Hill (DH); 3) Fort Valley (FV); and 4) Obsidian Tank (OT). All sites had large ($\geq$1 ha) populations of Fendler ceanothus that produced abundant seeds. The sites were separated by at least 21 km and represented a range of management histories and stand structure (Table 3.1). Four sites were selected to provide a general description of Fendler ceanothus seed germination characteristics.

## Sampling and Laboratory Procedures

### *Flower, Fruit, and Seed Production*

Fendler ceanothus plants plots were examined in June 1999-2002 for flowering stems. Length, diameter, and age class were recorded for flowering stems found on these plots each year (see Chapter 2 this dissertation). In July, I identified all stems with fruits. In 1999 and 2002, fruits were found on less than 0.05 stems per plot and seed production was not sampled. Fruit and seed production was intensively sampled in 2000 and 2001 when fruits were produced in greater abundance. In 2000, all stems bearing fruit were sampled. In 2001, fruit production was prolific and fruiting stems were randomly sampled at a rate of 43%. For each sampled stem, number of fruits and empty receptacles were counted. In 2001, I also recorded length, diameter, and age class on fruiting stems.

To estimate seed production, fruits were surrounding with nylon mesh (mesh size < 2 mm) "traps" that caught seeds as they were dispersed. In 2000, all stems bearing fruit were sampled and fitted with seed traps. In 2001, stems randomly selected for sampling (see above) were fitted with seed traps.

In late August of both sample years, seed trap contents (seeds, debris, and fruit remaining on stems) were collected and taken to the laboratory for analysis. Seeds collected from traps were separated from plant debris and counted. Seeds were classified as "developed" or "undeveloped". Developed seeds were approximately 2 mm diameter with smooth, full seed coats and glossy brown in appearance (Fig. 3.1a). In contrast, undeveloped seeds were typically smaller than 2 mm, flattened, and had wrinkled, yellowish appearing seed coats (Fig. 3.1b). Number of seeds per hectare (SPH) was calculated using the following:

$$\text{SPH} = (\text{seed producing stems} \cdot \text{m}^{-2}) * (\text{seeds} \cdot \text{stem}^{-1}) * 10{,}000\ \text{m}^{2} \cdot \text{ha}^{-1}$$

### *Seed Parasitism*

Developed seeds collected in traps were examined under a dissecting scope (10-20 power) for parasite emergence holes or other signs of damage. Seeds were dissected to determine embryo condition and presence of parasite larvae/pupae. A small sample (n=10) of undeveloped seeds also were dissected. To identify seed parasites, I monitored (1999-2001) seeds collected from Fendler ceanothus shrubs growing on microsites adjacent to the restoration units. Adult parasites emerging from seeds were captured and preserved in 70% isopropyl alcohol. Specimens were sent to Dr. Robert Zuparko at the California Academy of Science (CAS), San Francisco, CA, USA, and to the USDA Systematic Entomology Laboratory (SEL) (specimens identified by E. Eric Grissell, Research Entomologist), Bethesda, MD, USA for identification.

### *Seed Predation*

To study rates of post-dispersal seed predation, removal of Fendler ceanothus seeds (collected 1999) from experimental seed depots at the Fort Valley site was quantified in September 2000 and 2001. Seed predation transects, 250 m in length, were systematically established in the three forest restoration units used for herbivory studies (see Chapter 2 this dissertation). Transects were located near Fendler ceanothus plots used for herbivory studies and systematically oriented in directions that assured they remained within the forest restoration units (i.e., transects did not extend into adjacent forest areas). At 50-m intervals (five points) along transects, seed depots were established and Fendler ceanothus seeds were placed on substrate-filled Petri dishes. Because I wanted to understand how seed predation varied with substrate, 2 dishes at each seed depot were filled with charred forest floor or unburned ponderosa pine needles substrates. Charred forest floor substrate was collected on-site from forest units that had been burned with prescribed fire. Ten Fendler ceanothus seeds were placed on the substrate surface of each dish. In 2001, an additional dish of each substrate was added to randomly selected points along each transect and sunflower (*Helianthus* sp.) seeds were placed on these. Sunflower seeds were added to provide an indication of seed predator activity and relative preference for Fendler ceanothus seeds; sunflower seeds were presumed to be preferred by many generalist seed predators (C. Chambers pers. comm.).

Seed depots were left in place for 8-10 days. At collection, Petri dishes were covered and transported to the laboratory for analysis. Seeds remaining in dishes were sieved from substrate and counted to determine the number removed at depots.

### *Seed Germination*

Fendler ceanothus capsules were collected in late August 2001 from each of the four sites described in Table 3.1. Capsules from at least 5 shrub patches per site collected and stored in paper bags until processed. In the laboratory, seeds were separated from capsules by gently grinding with a mortar and pestle.

To broadly identify requirements for Fendler ceanothus seed germination, I conducted a pilot experiment in 2001. The objectives of the experiment were to examine the effects of heat and heat duration on seed germination. Five samples of 9-17 seeds each were separated from each of the four seed collection sites (BJ, DH, FV, OT) and dissected as described above (see Methods: *Seed Production and Parasitism*). Dissections allowed me to select a collection with a relatively high proportion of filled seeds. Based on these dissections, seeds from the DH site (87% filled) were used. Seeds (n=10-21) were randomly assigned to one of 18 treatments in a factorial temperature (6 levels) x duration (3 levels) design. Seeds were placed in shallow aluminum pans and heated in an electric drying oven at one of six temperatures: 60, 90, 120, 150, 180, or 210ºC. The duration of heating was: 1, 10, or 20 minutes. Each temperature x duration combination was replicated twice with separate applications of heat. Four seed samples were left unheated as controls. Seeds were germinated on moistened filter paper in Petri dishes in a controlled incubation chamber (Percival Scientific Inc., model 1500). Day length and temperature in the chamber were set to 14 hours, and 30ºC, respectively. Full-spectrum, fluorescent lighting was provided during day periods. Night length and temperature were 10 hours and 20ºC, respectively. Seeds were examined approximately every two days until germination was completed (about 24 days). Germination was defined as successful if radicals extended beyond the seed coat by at least 2 mm.

Based on pilot study findings (see Results), a germination experiment was designed with better understanding of heat duration effects and effective temperature range. In this study, I tested a narrower temperature range and also examined effects of cold stratification on seed germination. Seed samples (n = 10) were separated from each of the four collection sites and randomly assigned to one treatment using a 6 (temperature) x 2 (cold stratification) factorial design. Each treatment was replicated three times for each site by separate applications of heat. Temperatures tested were the following: no heat, 50, 70, 90, 110, and 130ºC. Seeds were heated for 10 minutes in an electric drying oven following the procedures described above. Similar methods have been used to test fire-related germination cues for seeds of other shrub species (Kenny 2000). Seeds were then either cold-stratified or left unstratified. Stratified seeds were placed between moistened filter papers in Petri dishes and allowed to imbibe water at room temperature (~ 20ºC) for 24 hours. Petri dishes were then sealed in black plastic and placed in a cooler at approximately 4ºC for 60 days. Seeds were germinated in a controlled incubation chamber as described above.

To test their germinability, 100 undeveloped seeds were separated from each of the DH and FV collections. Lots of 50 seeds each were randomly assigned to either heat treatment (90ºC) or control (no heat). Germination tests followed the procedures described above.

### Data Analysis

Proportion of stems producing flowers and fruits was calculated for individual plots within herbivore protection x burning treatments. Chi-squared tests were used to analyze distributions of fruiting stem sizes versus sizes of all stems in the population (all stems on protected, unburned plots) (Devore and Peck 1986). Normality of stem size distributions was assessed using normal probability plots. Stem length data were separated into 5-cm classes (df = 12) and stem diameters were placed in 0.1-mm ($\log_{10}$-

transformed to approximate normality) classes (df = 12) for analysis. A 0.05 probability level was used to determine significant deviation from chi-squared critical values.

Linear regression was used to examine relationships between fruit and seed production in 2001 and stem length and diameter. Data were natural-log transformed when residual plots showed increasing variance with increasing values of the independent variable. Relationships were considered significant at a 0.05 probability level.

Mann-Whitney nonparametric tests were used to test differences in number of seeds removed from charred forest floor and unburned pine litter substrates in the post-dispersal seed predation experiments. A 0.05 probability level was used for tests of statistical significance.

Analysis of variance (ANOVA) was used to test effects of heat duration (3 levels) and temperature (6 levels) on seed germination in the pilot study. A probability level of 0.05 was used for significance tests of main effects and temperature x duration interaction. One-way ANOVA was also used to test for main effects of temperature alone on germination. Bonferroni post-hoc tests were used to compare mean differences between temperatures (Kuehl 1994). Germination values (proportions of seeds germinating) were arcsine-transformed to stabilize variances and allow values of observations to more closely conform to assumptions of the linear model (Kuehl 1994).

ANOVA was used to test for effects of cold stratification (2 levels) and temperature (6 levels) on seed germination. Collection site was used as a blocking factor in the ANOVA model. Seed germination values were square-root, arcsine-transformed and a probability level of 0.05 was used to determine significance of main effects. One-way ANOVA was used to test for main effects of temperature alone. Bonferroni post-hoc tests were used to compare mean differences between temperatures (Kuehl 1994).

## Results

### Flower, Fruit, and Seed Production

Fendler ceanothus flower production generally increased over the four study years although herbivory and burning affected the proportion of stems on plots that flowered (Fig. 3.2). In 1999, approximately three months after overstories in the forest units had been thinned, only two stems on 180 plots (less than 0.05 stems/plot) were found with flowers. In 2000, mean proportion of stems producing flowers varied with treatment (Fig. 3.2). First-year resprouts arising on plots that were burned in spring of 2000 did not produce flowers. Flowering occurred on 14.6-28.8% of stems on protected plots and 1.3-2.3% of stem on unprotected plots that were not burned (Fig. 3.2). Flowering in 2001 showed a similar pattern as observed in 2000; no first-year resprouts and very few (0-2.3%) stems not protected from herbivores produced flowers (Fig. 3.2). In 2002, 0.8-8.9% of stems on unprotected plots and 7.8-52.4% of stems on protected plots produced flowers.

In 1999, I observed empty receptacles on the two stems that had produced flowers earlier in the spring. Thus, it appeared that one or more fruits had been produced (Fig. 3.3). In the following three years (2000-2002) no fruit were found on stems that were not protected from large herbivores. Field observations suggested that lack of fruiting on unprotected plots was primarily due to direct herbivory of inflorescences as well as fruit-set failure. Proportion of stems that produced fruit on unburned, protected plots ranged from 2.4 to 5.6% in 2000 and from 11.2 to 20.9% in 2001 (Fig 3.3).

Across all treatments, from 1 to 28 fruits per stem were produced in 2000 (mean=7.4; SE=3.2). This amount represented 3-84 potential seeds per stem (mean=22.2; SE=9.6) as based on 3 ovules per fruit (Kearney and Peebles 1964). In 2001, fruit production increased and from 1 to 408 fruits per stem were observed (mean=39.4; SE=7.4). This amount represented 3-1,224 potential seeds per stem (mean=118.2; SE=22.2). In 2002, I recorded what appeared to be near complete failure of Fendler ceanothus fruit set (Fig. 3.3). Although not statistically analyzed, fruit production appeared to be positively related to winter plus growing season (Jan.-Sept.) precipitation. In the last three years of study (2000-2002), growing season precipitation was 60, 93, and 50% of the long-term average for the site, respectively (Western Regional Climate Center 2003). Flower production appeared to be independent of growing season precipitation (Fig. 3.4).

Fruiting stem sizes (2001) were large relative to the total population of stems on plots (Fig. 3.5). Distributions of fruiting stem length and diameter were shifted towards the larger size classes in the population. No stems less than 20 cm in length produced fruit, although these sizes comprised approximately 15 % of the total population. Similarly, no fruit was found on stems less than 3 mm basal diameter, although these stems comprised just over 28% of the total population. Although fruiting stems were relatively large, number of fruits produced per stem was not significantly ($p>0.05$) related to stem length. A weak positive relationship ($r^2=0.06$; $p=0.02$) existed between fruit production and stem diameter.

Patterns of seed production followed patterns for fruiting. In 2000, seed-bearing stems produced 14.4 (SE=7.8) total seeds per stem on average. This represented a 35% ovule loss from the potential number of seeds (Table 3.2). Of the total seeds produced in 2000, 50.0% were undeveloped. Dissections of undeveloped seeds typically showed no embryo present (i.e., hollow seed) or small flattened embryos that were apparently not viable (see **Seed Germination** below). More than one-third (35.4%) were parasitized by a chalcidoid wasp (Eurytomidae: *Eurytoma squamosa* Bugbee). Parasitized seeds from which adults wasps had emerged were always found to be hollow. Diagnostic emergence holes were evident on many parasitized seeds although immature (larvae or pupae) wasps were also found during seed dissections. Seeds housing immature wasps showed no visible signs of infestation without dissection, suggesting that oviposition occurred during early stages of seed ripening. Loss of otherwise normally developed seeds (i.e., excluding undeveloped seeds) due to parasitism was 70.8%. Hollow seeds comprised 1.3% of all seeds produced. Filled seeds with apparently healthy embryos comprised 13.2% of all seeds collected (Huffman 2002). On average, 1.9 (SE=1.6) sound seeds were produced per stem in 2000, an amount that represented an ovule loss of 91.4% based on seed production potential (Table 3.2). Number of sounds seed per hectare in 2000 was approximately 3,410.

In 2001, an average of 90.9 (SE=26.8) total seeds per stem were produced. Similar to 2000 patterns, this number represented a 23% ovule loss from the potential seed number based on fruit production (Table 3.2). Undeveloped, parasitized, hollow, and filled seeds comprised 58.1, 3.1, 0.7, and 38.0%, respectively, of the total number produced in 2001. Loss of otherwise normally developed seeds due to parasites was

7.5%. Number of sound seeds produced in 2001 averaged 34.6 per stem (SE=11.6), an amount that represented a loss of 70.4% based on seed production potential (Table 3.2). Number of sound seeds per hectare in 2001 was approximately $9.04 \times 10^5$.

Similar to fruit production, linear regression analysis showed no significant ($p>0.05$) relationship between total number of seeds produced and stem length. A weak ($r^2=0.09$; $p=0.005$) positive relationship was found between number of seeds produced per stem and stem diameter.

### Post-Dispersal Seed Predation

In 2000, few Fendler ceanothus seeds were removed from seed depots in the three experimental restoration units. I found no significant ($p>0.05$) difference in counts of seeds removed from charred forest floor or unburned litter substrate (Table 3.3). Seed removal averaged 1.0% (SE=1.0) across all samples.

Significantly ($p<0.05$) more seeds were removed from dishes containing charred forest floor substrate than those with unburned litter in 2001 (Table 3.3). On charred forest floor substrate, nearly one-quarter of Fendler ceanothus seeds were removed whereas removal on unburned litter was less than 3%. Discarded Fendler ceanothus seed coats at depots indicated that predators, probably rodents, immediately consumed seeds as they found them. Although low sample size made sunflower seed removal patterns difficult to assess, trends similar to those observed for Fendler ceanothus occurred. No sunflower seeds remained in charred forest floor dishes (n=3), whereas all 10 seeds remained in one dish (n=3; removal=66.7%) containing unburned litter.

Accounting for post-dispersal losses, estimates of Fendler ceanothus seed inputs to soil seed banks were approximately 3,329-3,410 and $6.9 \times 10^5$-$8.9 \times 10^5$ seeds per hectare in 2000 and 2001, respectively. These values represent cumulative ovules losses of 71.2-91.6% from the number of seeds potentially produced based on mean number of fruit per stem (Table 3.2).

## Seed Germination

Condition of seeds from the four collection sites was dramatically different as demonstrated by dissection of random samples (Table 3.4). For example, parasitism and otherwise unfilled seeds comprised 57-84 % of the total number of seeds from BJ and OT sites. In contrast, over 75 % of the seeds from DH and FV sites were sound.

The pilot study using seeds from the DH site indicated that temperatures of 150ºC or greater were lethal to Fendler ceanothus seeds (Table 3.5). Effect of heat duration on germination was not significant ($p>0.05$). Interestingly, a temperature effect was apparent when seeds were exposed to heat for just one minute. Across all durations, germination was significantly ($p<0.05$) affected by temperature and significantly ($p<0.05$) more seeds germinated when heated to 90ºC than all other treatments (Table 3.5). Undeveloped seeds (FV and DH collection sites) did not germinate regardless of whether they were subjected to heat treatment or not.

No effect ($p > 0.05$) of cold stratification on Fendler ceanothus germination was found in the larger experiment using seeds from all four collection sites. For cold-stratified and not stratified seeds combined, heat (10 minute duration) significantly ($p<0.05$) affected germination (Fig. 3.6). Seeds exposed to 90º C had higher germination rates than seeds receiving no heat, or those exposed to 50, 110, or 130º C. Temperatures of 70 and 90ºC had a similar effect on germination. No seeds germinated after exposure to 130ºC.

## Discussion

### Herbivory and Fire Effects on Flower and Fruit Production

Reduced flower production associated with intense herbivory by large mammals, such as mule deer and Rocky Mountain elk, during the first two years after restoration tree thinning was described earlier (Chapter 2 this dissertation). This trend continued into the third and fourth years of observation. Although flower production appeared to increase slightly over the four years on unprotected plots, mean proportion of stems producing flowers was never greater than about 9%. This contrasted sharply with protected plots where mean proportion of stems producing flowers reached about 52% on unburned plots in 2002 (Fig. 3.2). Intense herbivory on other woody plants has been shown to decrease flower production and stem recruitment in Southwest and other ecosystems (Stein et al. 1992, Hoffman and Wambolt 1996, Strohmeyer and Maschinski 1996, Opperman and Merelender).

Experimentally burned plants produced resprouts that did not flower during their first growing season. Flower production on these stems appeared to recover to unburned levels within one to two years. I did not observe patterns that suggested that flower production was enhanced by fire although other studies have shown this to be common (Miller 2000). Season of burning may play a large role in determining whether fire enhances flower production. For example, Platt et al. (1988) found fires during the growing season increased flowering synchronization and decreased flowering duration for understory species in longleaf pine (*Pinus palustris* Mill.) forests. Burning in my study was done in the dormant season (spring) and thus may not have coincided with phenological or environmental cues that affect flowering. In addition to release of dormant buds that may be stimulated to flower, production may increase after fire due to changes in microclimate (e.g., increased light and soil temperature) or soil properties (e.g., increased soil moisture and soluble nutrients) (Miller 2000).

## Reproductive Capacity and Ovule Losses

Large differences in flower, fruit and seed production between the two study years (2000 and 2001) likely reflected combined influences of release from overstory tree competition and drought. For example, flower production generally increased for four years since time of overstory thinning in 1998-1999, likely because of improved microsite conditions such as increased light, soil moisture, and nutrient availability (Covington et al. 1997, Kaye and Hart 1998, Meyer et al. 2001). For example, negative relationships between vegetative production of understory plants and ponderosa pine overstory density have been widely reported (Ffolliott and Clary 1975, Ursek and Severson 1989, Tapia et al. 1990 Moore and Deiter 1992). Further, precipitation (Jan.-Sept.) in 2002, a year of abundant flower production but massive fruiting failure, was about 50% of the sites long-term average (Western Regional Climate Center 2003). In 2001, precipitation was nearly (91%) normal and both flower and fruit production were relatively high. Variability in fruit production has been linked to previous-year precipitation for other species of *Ceanothus* in chaparral ecosystems (Keeley 1977, Keeley 1987, Zammit and Zedler 1992). For these chaparral species, floral buds are produced in the year prior to flowering. Although my four-year study was not long enough to clearly assess effects of precipitation on fruit and seed production, my results did show that widespread fruit failure can occur in an extremely droughty year even though rates of flower production in that year were similar to the previous year when precipitation was closer to normal (Fig. 3.4). In years of adequate precipitation, fruiting appeared to be related to stem size. Although I found only a weak relationship between number of fruits produced and stem diameter, fruit production was observed on only the largest stems (both length and diameter) of the overall population. Similarly, Zammit and Zedler (1992) found that shrub size was the primary determinant of seed production for *C. greggii* plants that ranged from about 50-300 cm in height.

Differences between potential and actual seed production indicated that about 1 ovule per fruit failed. Causes for ovule loss in this study are not known. In general, ovule losses are thought to be linked to lack of pollination, resource limitation, fruit abortion, and/or predation (Stephenson 1981). In 2001 and 2002, I observed flower visitation by various adult insects (Huffman unpublished data) in the Lepidoptera and *Apidae* (Hymenoptera); both groups are potential pollinators (Borror et al. 1989). Number and diversity of adult Lepidoptera have been found to increase after restoration treatments in ponderosa pine forests (Waltz 2001). I also observed species of *Chrysomelidae*, insects that often feed on flowers and pollen (Huffman unpublished data). Furniss et al. (1978) speculated that psyllids may have contributed to ovules losses of redstem ceanothus (*Ceanothus sanguineus*).

Incomplete seed ripening was another consistently important (50-58% loss of total seeds) source of seed loss in 2000 and 2001. Dissection and germination tests confirmed that seeds classified as undeveloped were not viable. Abnormal seeds with shriveled seed coats have been classified for other *Ceanothus* species as “unsound” (Furniss et al. 1978) and “aborted” (Zammit and Zedler 1992). Additionally, Keeley (1977) scored *Ceanothus* sp. seeds as “inviable” if embryos were shrunken or discolored as indicated by seed dissection. For redstem ceanothus, unsound seeds comprised 52-86% of the total crop over a three-year period at three sites in Idaho (Furniss et al. 1978). Zammit and Zedler (1992) reported that from 1 to 2 seeds per capsule were aborted for *C. greggii* over five study years; fewer seeds were aborted in stands of young (6-32 years) shrubs. Similarly, Keeley (1977) found that at least half the seeds produced by both *Ceanothus greggii* and *C. leucodermis* were not viable over three study years on a chaparral site in California. Causes for undeveloped seeds in my study are not known although other authors hypothesize that interactions of precipitation and plant carbohydrate stores determine seed outputs for *Ceanothus* species in chaparral (Keely 1977, Zammit and Zedler 1992).

Predispersal parasitism was variably important (7-71 % loss of developed seeds) in further reducing number of viable seeds. The chalcidoid wasp, *Eurytoma squamosa*, was the only predispersal seed parasite found. In an early note, Huffman (2002) documented Fendler ceanothus in Arizona as an extension of the known host and range record for this insect. Parasitic wasps of the *Eurytoma* genus have been reported feed on seeds of several *Ceanothus* species and members of the *Rhamnaceae* family (Bugbee 1967, 1971, Furniss and Krebill 1972, Furniss et al. 1978, M. Gates pers. comm.). A lack of ceanothus congeners on my site suggests an important linkage between Fendler ceanothus and *Eurytoma squamosa*. Further research is needed to describe temporal and spatial dynamics of this host-parasite system and the importance of seed parasitism in population dynamics of Fendler ceanothus. My data indicate that more than two-thirds of otherwise normally developing seeds can be consumed in a given year by this insect.

Similar to predispersal seed parasitism, post-dispersal seed predation was a variably (2-24% of dispersed seeds) important source of seed loss. Although I did not attempt to determine identities of seed predators, discarded seed coats left at depots suggested that rodents were responsible for some predation. Rodents such as *Tamias cinericolis*, *T. dorsalis*, *Peromyscus maniculatus*, and *Neotoma* spp. are common in these forests and have been implicated in high (~80% removal) rates of seed predation in other studies (Compton unpublished data). In chaparral, harvester ants were found to be more important than vertebrates in removing *Ceanothus* seeds from experimental depots in nighttime hours. Further, vertebrate predators were poor at locating seeds buried under plant litter (Mills and Kummerow 1989). My results corroborate these findings and suggest that risks of predation are lowest when seeds disperse onto pine litter. Seeds rapidly percolate into this coarse substrate whereas on charred forest floor seeds are more exposed to predators.

### Seed Germination

Results from laboratory experiments showed that application of moderate heat (70-110ºC) for periods of 1-20 minutes stimulated Fendler ceanothus seed germination. Many *Ceanothus* species require heat to allow opening of seed coats, although a few show adverse response to heating (Hadley 1961, Quick and Quick 1961, Reed 1974). I found 90ºC to be optimal for stimulating germination regardless of duration of heat (up to 20 minutes) or cold stratification, whereas temperatures greater than 120ºC caused seed mortality. These results indicate that Fendler ceanothus utilizes a dormant-seed regeneration strategy. This is a common trait of the *Ceanothus* genus in ecosystems ranging from coastal chaparral to ponderosa pine forests of the northwestern United States (Gratkowski 1974, Keeley 1977, Conard et al. 1985). The dormant-seed strategy is advantageous for recolonizing sites after severe disturbances such as infrequent fire. Temperatures in soil environments during fire vary greatly depending on fuel conditions, fire behavior, and depth in profile (Whelan 1995). Although Fendler ceanothus has been reported to increase after prescribed burns and wildfires in ponderosa pine forests of the Southwest (Pearson et al. 1972, Ffolliott et al. 1977), few studies have documented germination and seedling emergence from seed banks (but see Vose and White 1987). In other ecosystems, *Ceanothus* seeds are thought to remain viable in soil for decades (Gratkowski 1974, Keeley 1977). In this way, ceanothus can persist in the seed bank through periods of potentially high levels of competition from full understory communities or dense overstory conditions (Gratkowski 1974). Fire or other disturbances that stimulate germination also can create favorable microsites for seedling establishment (Keeley 1977). Long-term seed viability of Fendler ceanothus seeds is unclear although 40-year-old seeds can be successfully germinated (Huffman unpublished data). In the present study, a fraction (20%) of seeds germinated without being heated and thus these seeds may have short-term residence in seed banks. Findings from these germination tests suggest that Fendler ceanothus regeneration strategies allow for both immediate colonization of microsites and simultaneous development of a dormant seed bank.

## Management Implications

Management activities that facilitate growth and retention of large Fendler ceanothus stems can increase seed inputs to soil seed banks. Protecting plants from intense ungulate herbivory may allow rapid development of large fruit-producing stems (see Chapter 2 this dissertation). Although not tested in this study, operational approaches to herbivore protection may include strategic piling of thinning slash, modification of hunting regulations, or use of commercially available ungulate deterrent.

Gross fruit production as an indicator of viable seed inputs may be misleading since ovule and seed losses from abortion and predispersal parasitism can be high. Rapid estimates of viable seeds can be made by examination of mature fruit contents before dehiscence. A subsample of normal-appearing seeds should be dissected to determine degree of parasitism. Managers also should note that seed predators may consume a significant proportion of dispersed seeds and predation can vary widely among years. Fendler ceanothus flower, fruit, and seed use by various organisms demonstrates the importance of each of this species' reproductive stages in contributing to overall ecosystem function.

Germination of Fendler ceanothus seeds can be accomplished using heat treatments of temperatures between 70 and 90ºC. Assessments of seed bank composition for these forests should include heating as a germination cue or otherwise risk underestimating Fendler ceanothus viable seed abundance. Managers wishing to increase

Fendler ceanothus on sites can pre-treat seeds before sowing, or use low severity prescribed fire to stimulate natural seedling emergence (Vose and White 1987).

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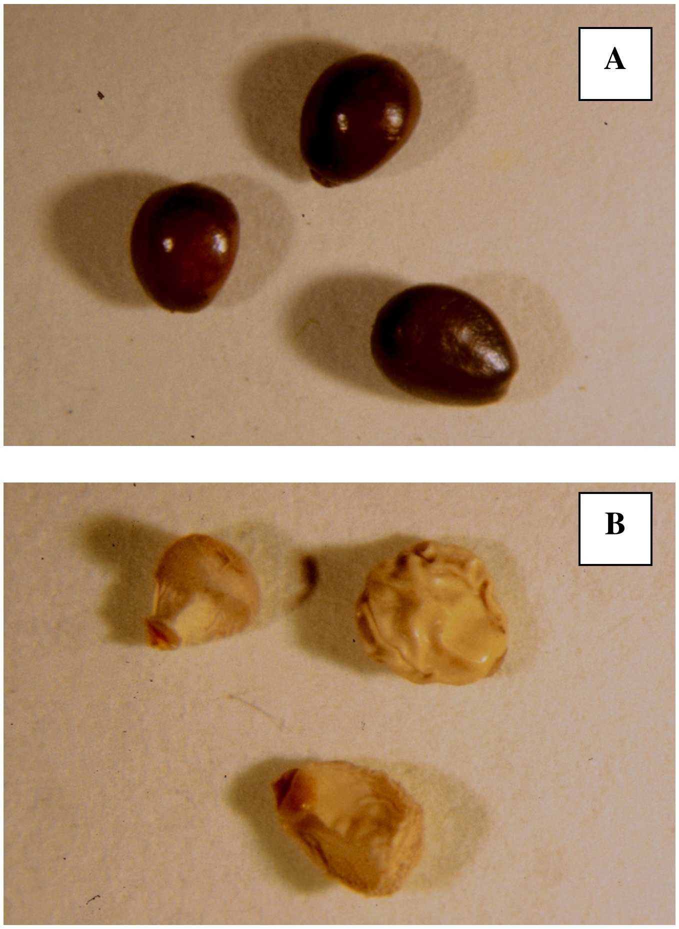

Figure 3.1. Fendler ceanothus seeds were classified as developed (A) or undeveloped (B) based on seed coat appearance and seed size.

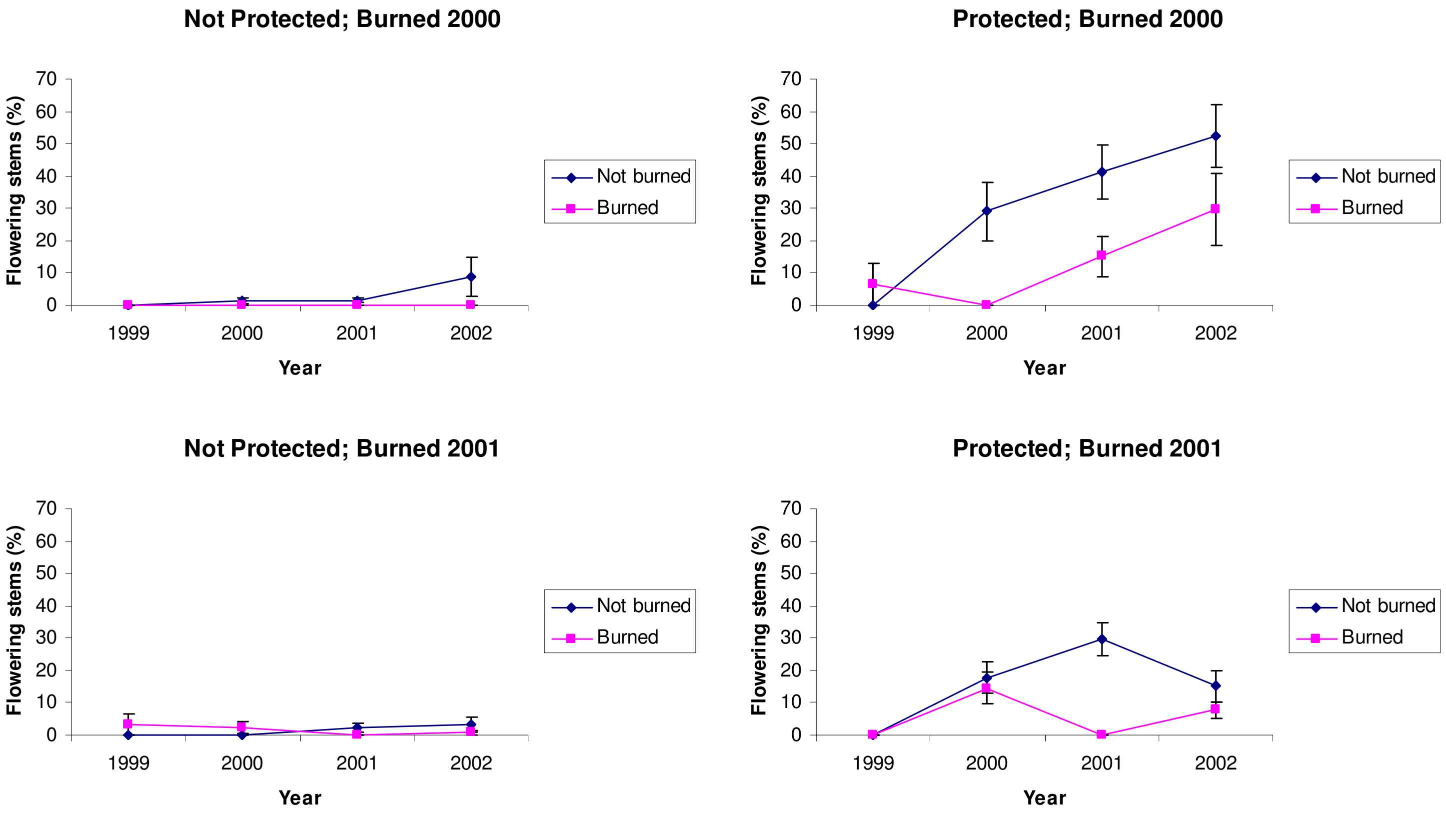

Figure 3.2. Mean proportion of stems producing flowers 1999-2002 on plots in overstory units burned in 2000 or 2001. Shown are trends for plots protected and not protected from large herbivores. Bars around means are standard errors.

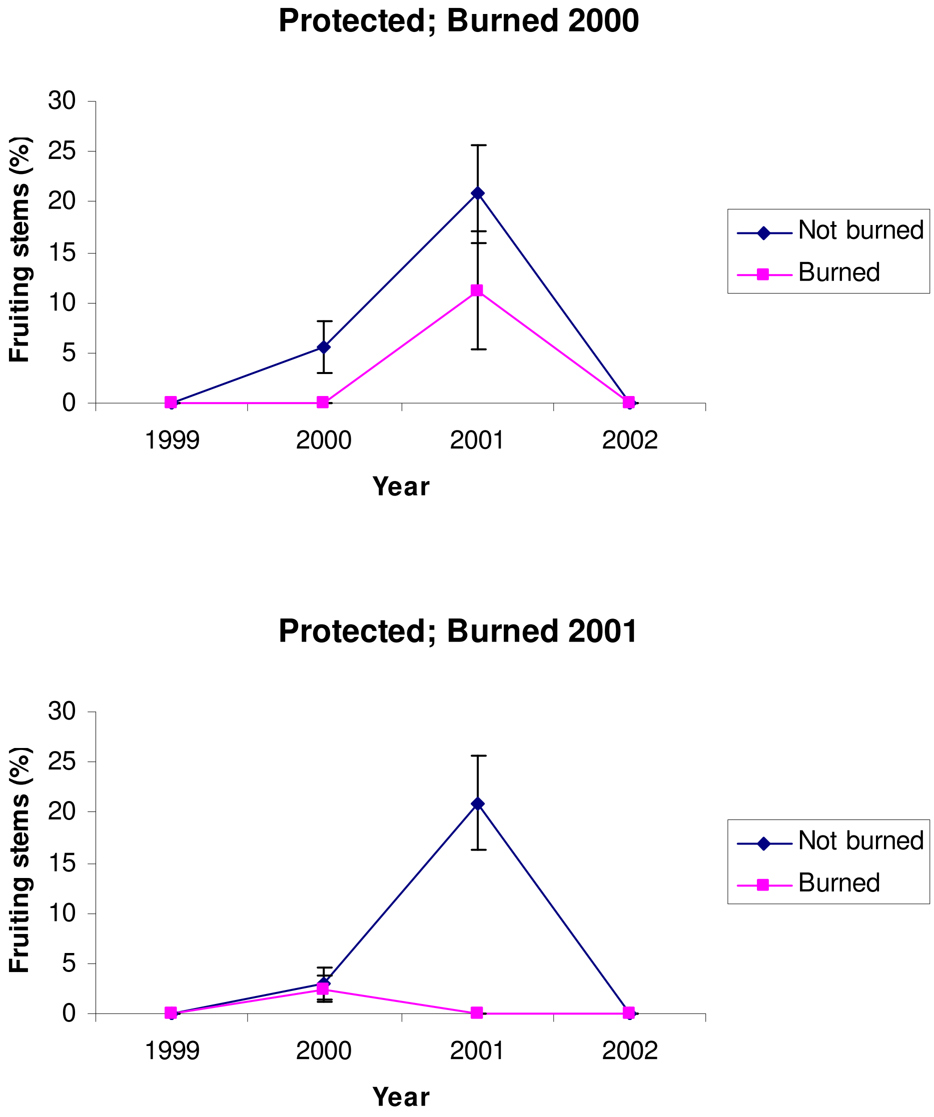

Figure 3.3. Mean proportion of stems producing fruit 1999-2002 for plots protected from large herbivores in overstory units burned in 2000 and 2001. No stems on unprotected plots produced fruit in any year. Shown are trends for plots protected from large herbivores; no stems that were not protected produced fruit in any year. Bars around means are standard errors.

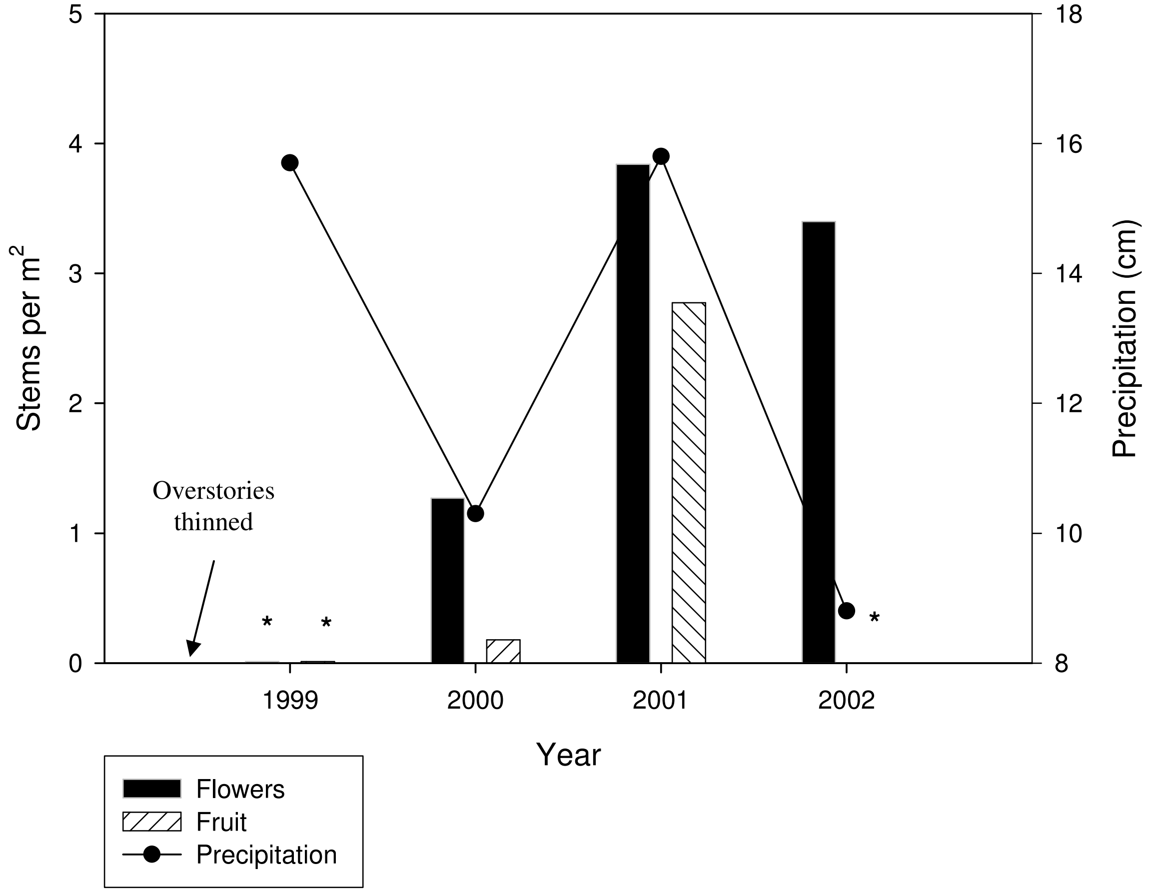

Figure 3.4. Number of fruiting and flowering buckbrush stems per plot and precipitation (Jan.-Sept.) over four study years. Asterisks indicate less than 0.05 stems per plot. Arrow indicates time of forest overstory thinning in late 1998.

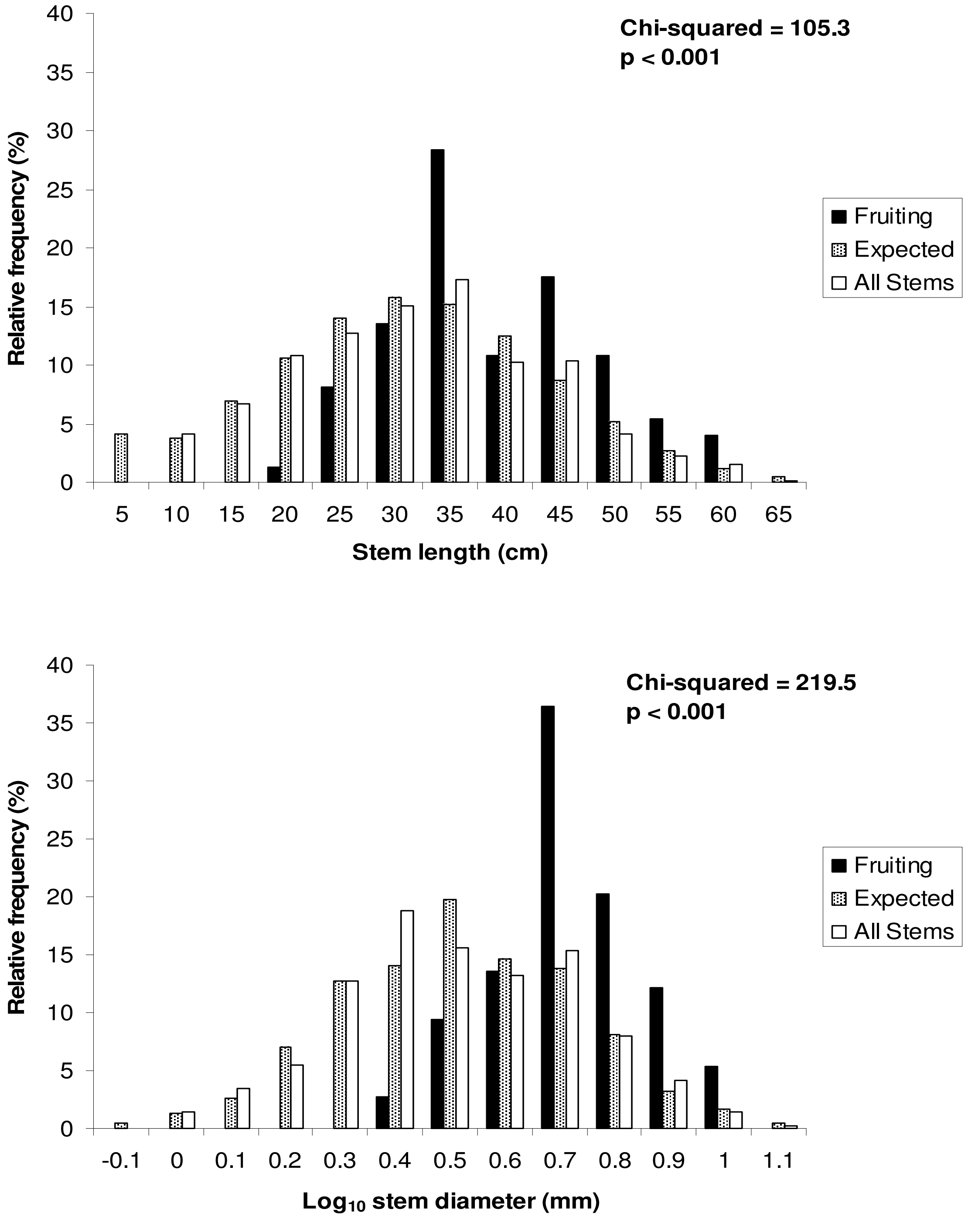

Figure 3.5. Comparison of fruiting stem length and diameter distributions versus expected values based on standard normal (z) curve areas. Normal curves constructed from means and standard deviations for all stems in Fendler ceanothus population.

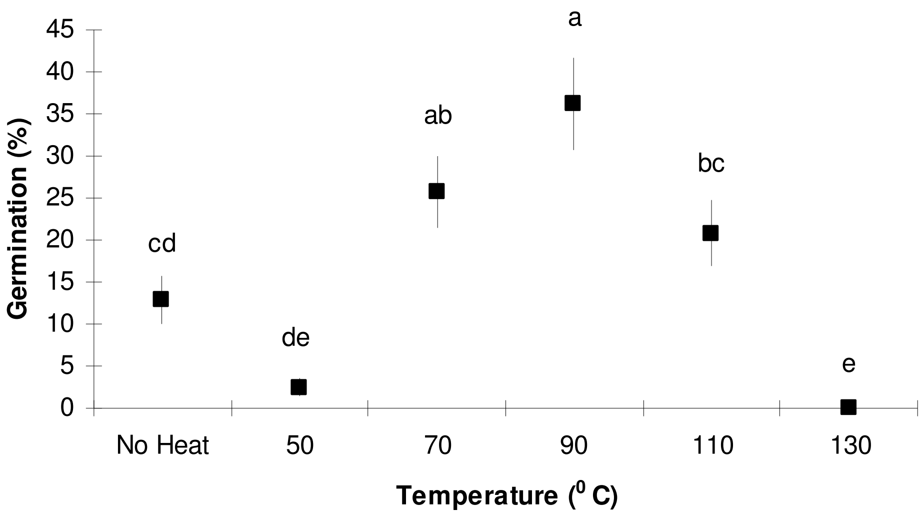

Figure 3.6. Effect of temperature on Fendler ceanothus seed germination. Seeds were exposed to the given temperatures for 10 minutes. Means are for cold-stratified and not stratified seeds combined and bars represent standard errors. Similar letters indicate statistically similar means at alpha = 0.05.

Table 3.1. Descriptions of sites where Fendler ceanothus seeds were collected for germination experiments.

| Site | Elevation (m) | Aspect | Overstory Canopy | History | Latitude/Longitude |
|---|---|---|---|---|---|
| BJ | 2290 | NE | Open pine | Thinned and burned mid 1980s | 35N 24'/111W 38' |
| DH | 2219 | SE | None | Wildfire early 1980s | 35N 07'/111W 49' |
| FV | 2255 | SW | Open pine-pine/oak | No recent thinning or burning | 35N 16'/111W 41' |
| OT | 2306 | N | None | Wildfire late 1970s | 35N 20'/111W 56' |

Table 3.2. Mean number of seeds per stem and incremental losses for Fendler ceanothus during developmental stages associated with predispersal and post-dispersal periods.

| | | 2000 | | 2001 | |
|---|---|---|---|---|---|
| | Stage | Number | Loss (%) | Number | Loss (%) |
| Predispersal | Potential[1] | 22.2 | | 118.2 | |
| | | | 35.0 | | 23.0 |
| | Produced[2] | 14.4 | | 90.9 | |
| | | | 50.0 | | 58.1 |
| | Developed[3] | 7.2 | | 38.1 | |
| | | | 73.6 | | 9.2 |
| | Sound[4] | 1.9 | | 34.6 | |
| | | | 0.0-2.0 | | 2.7-24.0 |
| Post-dispersal | Escaped[5] | 1.9 | | 26.6-34.0 | |
| *Predispersal Loss (%)* | | | *91.4* | | *70.7* |
| *Cumulative loss* (%) | | | *91.6* | | *71.2-77.5* |

[1] “Potential” is the number of fruit per stem x three potential ovules per fruit.

[2] “Produced” is the number of seeds caught per stem in traps. Values include undeveloped, parasitized, hollow, and filled seeds.

[3] “Developed” is the number of developed seeds per stem – see text and Figure 3.1 for description.

[4] “Sound” is the number of seeds per stem with apparently healthy embryos, based on seed dissections. that

[5] “Escaped is the number of seeds that escape post-dispersal predation. Values are based on field removal rates.

Table 3.3. Mean removal (%) of Fendler ceanothus seeds from charred forest floor and unburned ponderosa pine litter substrates at seed depots in 2000 and 2001 (standard error in parentheses).

| | Year | | | |
|---|---|---|---|---|
| | 2000 | | 2001 | |
| Species | Charred | Litter | Charred | Litter |
| Fendler ceanothus (n=15) | 2.0<br>(2.0) | 0.0<br>(0.0) | 24.3*<br>(6.3) | 2.7<br>(1.2) |
| Sunflower (n=3) | | | 100.0<br>(0.0) | 66.7<br>(33.3) |

* Mean Fendler ceanothus seed removal significantly ($p < 0.01$) greater on charred forest floor than on unburned litter in 2001.

Table 3.4. Condition of Fendler ceanothus seeds used for germination experiments.

| | Seed Condition (%) | | |
|---|---|---|---|
| Site | Hollow | Parasitized | Filled |
| BJ | 44.2 | 12.9 | 42.9 |
| DH | 1.3 | 11.6 | 87.1 |
| FV | 21 | 1.2 | 77.8 |
| OT | 60.2 | 23.8 | 15.9 |

Table 3.5. Effects of temperature and heat duration on Fendler ceanothus seed germination (%). Seeds used in these tests were from the DH site.

| Duration (min.) | Temperature (º C) | | | | | | |
|---|---|---|---|---|---|---|---|
| | No Heat | 60 | 90 | 120 | 150 | 180 | 210 |
| 0 | 18.2 | - | - | - | - | - | - |
| 1 | - | 25.0 | 60.0 | 30.0 | 0 | 0 | 0 |
| 10 | - | 4.8 | 69.0 | 2.4 | 0 | 0 | 0 |
| 20 | - | 9.5 | 30.9 | 7.1 | 0 | 0 | 0 |
| ***Average*** | *18.2b* | *13.1b* | *53.3a* | *13.2b* | *0b* | *0b* | *0b* |

* Similar lowercase letters indicate statistically similar means at $p \geq 0.05$.

# CHAPTER 4: RESPONSE OF FENDLER CEANOTHUS TO FOREST THINNING, PRESCRIBED FIRE, AND DROUGHT

## Abstract

Overstory tree thinning and prescribed fire are used to restore ecosystem structure and function in ponderosa pine (*Pinus ponderosa* Laws.) forests of the Southwest. In order to examine the effects of these restoration treatments on growth and reproduction of a common shrub species, I monitored Fendler ceanothus (*Ceanothus fendleri* Gray) plants from 1999 to 2002 in thinned and unthinned forest restoration units. I evaluated the importance of stand density (Reineke's SDI) and ungulate herbivory in predicting current-year branch length, number of branches, biomass, and leaf area. I also experimentally burned plants and studied mortality, seedling emergence, and growth response. SDI was negatively ($p<0.05$) correlated with current-year branch length, branch number, biomass, and leaf area but explained only up to 23% of variation in simple linear regressions. Proportion of current-year branches browsed improved models and r-squared values increased to 0.47. Model predictions of growth were highest in years with near normal precipitation and lowest in drought years. Mortality was 17-32% and 0-5% for burned and unburned plants, respectively. Mortality was significantly ($p<0.05$) related to amount (cm) of forest floor consumed. Surviving burned plants responded by producing long resprouts and current-year branches were significantly ($p<0.05$) longer than unburned plants although fewer in number. Unburned plants had greater current-year biomass and leaf area than burned plants one growing season after fire, but differences were short-lived. Seedlings emerged on 44% of burned plots and a

quadratic relationship ($p<0.05$) represented the relationship between emergence and forest floor consumption. No seedlings were observed on unburned plots. Results indicate that forest restoration treatments can help increase abundance of *Ceanothus fendleri* but growth responses are constrained by ungulate herbivory and severity of prescribed fires.

## Introduction

It is well known that tree thinning and opening of dense overstory canopies alters understory microclimate by allowing greater light transmission and increasing throughfall precipitation and soil temperatures (Anderson et al. 1969, McLaughlin 1978, Vales and Bunnell 1988, Groot and Carlson 1996). Reduction of overstory density can also increase available soil moisture and nutrients (Covington et al. 1997, Kaye and Hart 1998). These changes can be beneficial to understory plants and increased community production is commonly observed after overstory thinning (Jameson 1967, Ffolliott and Clary 1975, Uresk and Severson 1989). Response of understory communities to changes in overstory density can be expressed by negative linear or curvilinear functions (Ffolliott and Clary 1975). For example, in northern Arizona ponderosa pine (*Pinus ponderosa* Laws.) forests, forage production increased linearly as values of Reineke's stand density index (SDI; Reineke 1933) decreased below 400-550 (Moore and Deiter 1992). At higher SDI values, understory production responses to variations in stand density were minimal.

Quantification of overstory-understory relationships allows forest managers to predict outcomes of ecological restoration treatments that use thinning to reduce overstory densities to levels more like those of presettlement forests (Covington and Moore 1994, Covington et al. 1997, Moore et al. 1999). In some cases, however, other interactions may be as important as stand density in constraining understory plant growth and reproduction. For example, I previously showed that Fendler ceanothus (*Ceanothus fendleri* Gray) not protected from browsing mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus*) had around one-fourth the current-year biomass as protected plants in ponderosa pine stands that had been thinned as part of an ecological restoration experiment (see Chapter 2 this dissertation). Additionally, severe drought may override potential benefits of forest thinning in these semi-arid ecosystems (Fulé et al. 2002). Finally, seeds of plants with seedbank strategies often require scarification or other cues to initiate germination (Harper 1977). For these species, recruitment of new genets into populations may not occur as a result of overstory thinning alone.

Prescribed fire is often used with thinning as an ecological restoration tool in ponderosa pine forests of the Southwest (Covington et al. 1997, Moore et al. 1999, Allen et al. 2002). Low intensity fire can mineralize accumulated forest floor litter layers, release nutrients bound in detritus, reduce slash fuel loads that are created from tree thinning, and stimulate plant sprouting and germination of dormant seeds (Whelan 1995). Importantly, low-intensity fire was common in presettlement ponderosa pine forests of the Southwest, returning at mean intervals ranging from 2 to 20 years (Fulé et al. 1997) Thus, fire is a critical process to be reintroduced when restoration of functional attributes in these ecosystems is a goal (Kauffmann et al.1994, Covington et al. 1999).

Presettlement fires likely burned quickly through abundant grassy fuels and transferred little heat to soil systems in Southwest ponderosa pine forests. Low fuel loads, high fuel moistures, high relative humidity, low daytime temperatures, and low wind speed are needed to safely reintroduce fire in these forests where it has been excluded for nearly 130 years (Sackett et al. 1996, Fulé et al. 1997). These initial fires can smolder in slash and deep layers of accumulated forest floor debris and release lethal levels of heat into soils (Covington and Sackett 1990, Sackett et al. 1996). Thus, fire behavior and severity may be important determinants of successional trajectories for understory communities after prescribed burning. Development of easily measured fire behavior variables predictive of effects on understory species can help land managers prescribe burns that both reduce accumulated fuels and accomplish ecological objectives related to vegetation structure and composition.

My objective in this study was to quantify the effects of overstory density and prescribed fire on Fendler ceanothus, a semi-evergreen, nitrogen-fixing shrub common in understories of ponderosa pine forests throughout the Southwest (Story 1974, Conard et al. 1985). Scattered populations of Fendler ceanothus provide structural heterogeneity and wildlife habitat particularly browse for mule deer and elk, in these plant communities (see Chapter 2 this dissertation). Resprouting of Fendler ceanothus after disturbances such as fire appears to be common (Pearson et al. 1972, Ffolliott et al. 1977, Vose and White 1991) although detailed descriptions of vegetative characteristics and variation of response to fire behavior is presently lacking. Its seeds are forcibly ejected from dehiscing capsules and likely remain in forest floor seed banks for years until stimulated by heat from fire to germinate similar to congeneric species (Kearney and Peebles 1951, Quick and Quick 1961, Reed 1974, Krishnan 1989). Here I report Fendler ceanothus growth and reproduction under various forest stand densities and the importance of herbivory and drought in constraining response. I also describe mortality, production, and seedling recruitment on experimentally burned plots.

## Methods

### Study Site

I conducted my study 1999-2002 on the Fort Valley Experimental Forest (35° 16' N, 111° 41' W) in Coconino County approximately 10 km northwest of Flagstaff, Arizona. Elevation of the study area was around 2300 m above mean sea level. Aspect of the site was generally southern and the topography was gentle with average slopes of approximately 5-10%. Soils are developed on tertiary basalt parent material and are moderately well drained. Annual precipitation at the site averages around 52 cm and is typically bimodal in distribution with July-September rain and December-March snow. In 1999, precipitation was 96% of the long-term (51 y) average of 41.3 cm for January-September (Western Regional Climate Center 2003). In 2000, 63% of the long-term average fell in these months. In 2001, precipitation was 91%, but in 2002 only 54% of the long-term average for January-September occurred. Thus, 1999 and 2001 had near average precipitation whereas 2000 and 2002 were droughts.

Forest overstories were comprised of ponderosa pine and common understory species included the grasses Arizona fescue (*Festuca arizonica* Vasey), mountain muhly (*Muhlenbergia montana* (Nutt.) A.S. Hitchc.), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) and pine dropseed (*Blepharoneuron tricholepis* (Torr.) Nash); the forbs lupine (*Lupinus* spp.), fleabane (*Erigeron* spp.), buckwheat (*Eriogonum* spp.), yarrow (*Achillea millifolium* L.), and pussytoes (*Antennaria* spp.); and shrubs Fendler ceanothus and woods rose (*Rosa woodsii* Lindl.). No domestic livestock were present at the study site and primary large herbivores were mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus*).

## Design

Fendler ceanothus patches were located in three forest units undergoing ecological restoration treatments and three adjacent untreated (control) units in March 1999. Forest restoration units were 14-16 hectares in size and were thinned in late winter 1998. Before thinning, basal area was 34-38 $m^2$/ha and density was 955-1492 trees/ha. Thinning from below reduced basal area by 35-56% and left 140-243 trees/ha in scattered groups to emulate presettlement spatial structure (Fulé et al. 2001).

Ten discrete patches of Fendler ceanothus were found in each of the forest restoration and control units (N =60). Patches were generally no more than 2 m in area and comprised 1-15 Fendler ceanothus stems. Fendler ceanothus can expand vegetatively and sprout from belowground branches and root crowns (Vose and White 1987, Huffman pers. obs.). It is not known whether patches comprised more than one clone. Hereafter, I refer to stems populations in these patches as Fendler ceanothus “plants”. Circular plots (1 $m^2$) were established at the center of Fendler ceanothus patches and metal rebar was used to mark plot centers for relocation. These plots were used to examine effects of overstory density on Fendler ceanothus growth and reproduction.

I established an additional 50 Fendler ceanothus plots in each of the restoration units and used these to study effects of prescribed fire (N=150) and interactions with herbivory on growth and reproduction. Effects of prescribed fire could only be examined within the thinned forest units due to extreme fuel hazard in control units. Forest floor depth was estimated to the nearest 0.1 cm at plot center. In restoration units, plots were randomly assigned to herbivore protection and experimental burning treatments in a 2x2 factorial design.

### Herbivore Protection

Fenced exclosures, 2x2 m in area and 1.4 m in height, were constructed in spring 1999 around plots selected for herbivore protection. Exclosures were made of wire fence (5x10 cm mesh) and T-bar posts. The small size of the fenced area discouraged deer and elk from jumping over the fencing and large mammal herbivory was effectively eliminated within exclosures. From 0.6-5% of terminal buds on current-year branches were damaged or removed, apparently by invertebrates, within exclosures across the four study years.

### Experimental Burning

In order to burn selected plants, fire lines were constructed around all Fendler ceanothus plots in restoration units. Fire lines were continuous fuel breaks approximately 25-50 cm in width wherein all vegetation and forest floor material was removed exposing the mineral soil. The area protected by fire lines, and which encompassed each Fendler ceanothus plot, was approximately 4 $m^2$. Additionally, all downed woody debris larger than 5 cm in diameter was removed from plots in order to control fire behavior and severity.

Fendler ceanothus plots were experimentally burned in April 2000 and May 2001 in coordination with United States Forest Service's (USFS) broadcast burning of the larger forest units. In April 2000, 24 Fendler ceanothus plots (12 protected from herbivores, 12 unprotected) were burned in one of the restoration units (called unit 3T). Drip-torches filled with a diesel-gasoline mixture were used to ignite forest floor material around edges of the plots and fires were allowed to burn until naturally extinguished. Due to extreme fire danger in spring 2000, the USFS halted all prescribed fires before I could complete treatments and no other plots were burned in this year. I was able to resume experimental burning in May 2001. At this time, sixty-five additional plots (33 protected from large herbivores, 32 unprotected) were burned in the two remaining restoration units (called units 1T and 2T).

Average and maximum flame lengths on plots were estimated during burning. To assess fire behavior, forest floor depth on plots was measured within 2 months of burning following methods used at plot establishment. Additionally, burn severity for vegetation and substrate was categorized using a 5-class rating system (USDI 1992; e.g., 1 = most severe, 5 = unburned).

### Fendler ceanothus Measurements

Length and number of Fendler ceanothus stems on plots were measured in March 1999 (pretreatment). Subsequently, Fendler ceanothus stems were measured annually in September each year from 1999 to 2002. Stem length, basal diameter, current-year branch length (estimated average and longest), and number of current-year branches were measured. Stems were classified into relative age groups according to stem base characteristics (see Chapter 2 this dissertation). First-year stems (Class-1) lacked dark patches of bark, were gray-green, and pubescent at the base. Class-2 stems also lacked bark patches, were bright green, and generally lacked pubescence at base. Class-3 stems were similar in color to Class-2 stems, or yellowish, with bark patches noticeable at the base. Class-4 stems were dark brown to black and were fully surrounded by bark at the base. Age classification allowed me to identify current-year stems and estimate stem recruitment. Current-year biomass and leaf area (LA) were estimated from stem length relationships developed from separate destructive sampling (see Chapter 2 this dissertation).

Fendler ceanothus seedling recruitment was assessed twice per year (July and September) and emerging seedlings were counted at each plot within the 2x2-m areas encompassed by fire lines and herbivore exclosures. Emergent seedlings were identified by their small stature (stem diameter<0.5 mm, length<5 cm) and the presence of cotyledons.

Overstory density was measured in 2001 at each plot using point sampling (Avery and Burkhart 1983). Wedge prisms of 20 basal area factor (BAF) were used for tree tallies. All tally trees were measured for diameter at breast height (1.37 m) and recorded in 4-cm diameter classes.

## Data Analyses

Linear regression was used to analyze relationships between Fendler ceanothus growth variables and overstory density and browsing. Significance level selected for regressions was 0.05. Fendler ceanothus growth variables analyzed were stem number, current-year branch length (average and longest), current-year biomass, and current-year leaf area for each of the four years of the study. Overstory density values were derived using Reineke's stand density index (SDI; Reineke 1933) and tree diameters from point samples. Browsing values were calculated as the number of current-year branches browsed divided by the total number of current-year branches counted on each plot. Additionally, relationships between SDI and net change in Fendler ceanothus aerial stem density (number of 2002 stems ÷ number of 1999 stems) were tested (alpha=0.05). Data were natural log-transformed when examination of residual plots indicated increasing variance with increasing estimated values.

One-way analysis of variance (ANOVA) was used to test for effects of prescribed burning within restoration units (no plots were burned in untreated units). Since significant differences in stem number, size, and current-year biomass and leaf area had developed between protected and unprotected plots by the time they were burned (see Chapter 2 this dissertation), effects of burning were analyzed for these two groups separately. Further, effects of burning were analyzed separately for the two burn years (2000 and 2001). To analyze fire effects in 2000, data from burned and unburned plots in unit 3T were used. To analyze fire effects in 2001, data from burned and unburned plots in units 1T and 2T were used. In ANOVA tests for burn-year 2001 plots, overstory unit was included as a blocking factor. Fendler ceanothus response variables analyzed were stem number, population change, current-year branch number and length (average and longest), current-year biomass, and current-year leaf area. Data were natural-log transformed when necessary to normalize data distributions and homogenize variances. Significance level for tests was 0.05.

Logistic regression was used to test for relationships between Fendler ceanothus mortality (categorical) and flame length and amount (cm) of forest floor consumed in burning. Linear regression was used to analyze the relationship between seedling emergence and forest floor consumption.

Seedling establishment was assessed by evaluating: (1) emergence, defined as the number of first-year seedlings counted on a plot. Such seedlings typically had cotyledons and one or more true leaves; (2) one-year survival, defined and the number of seedlings counted for emergence divided by the number of seedlings remaining on the same plot after the next growing season multiplied by 100 (e.g., [emergence 2000/remaining 2001] * 100); (3) two-year survival, defined as the number of seedlings counted for emergence divided by the number remaining on the same plot after two growing seasons multiplied by 100 (e.g., [emergence 2000/remaining 2002] * 100). Two-year survival assessment only applied to plots in the unit (3T) that was burned in 2000.

## Results

### Overstory Density, Herbivory, and Drought

Values for SDI ranged from 124 to 1754 across all plots (thinned and control forest units) sampled. Although SDI contributed significantly ($p<0.05$) to models and was negatively related to Fendler ceanothus growth, its importance was generally low compared to that of Browse (proportion of current-year stems browsed) (Table 4.1). In 1999, a year of near normal (96%) precipitation January-September, the full model (both SDI and Browse included as predictors of growth) explained up to 60% of data variation. Neither SDI nor Browse was significantly related to number of current-year branches in

1999 (Table 4.1). In 2000, a drought year (63% normal precipitation January-September) SDI was only significantly ($p<0.05$) related to current-year biomass and leaf area on plots. Browse in 2000 was significantly ($p<0.05$) related to all growth variables except longest current-year branch length, number of current-year branches, and current-year leaf area on plots (Table 4.1). In 2001, a year of near normal (91%) precipitation, results were similar to those of 1999 and the full model generally provided the best predictions of growth (Table 4.1). In 2002, a year of extreme drought (54% normal precipitation January-September) SDI was significantly related to number of current-year branches and current-year biomass and leaf area on plots. Browse was not significantly ($p \geq 0.05$) related to any growth variable in 2002.

Values of r-squared for growth models were generally higher in years 1999 and 2001 than in 2000 and 2002. Annual precipitation played a significant role in determining the importance of overstory tree density and browsing on Fendler ceanothus growth parameters. Although only four growing seasons were available to assess the relationship, a significant ($p<0.05$) positive trend was observed between correlation coefficients of Fendler ceanothus growth models (current-year branch length response variable) and percent of average long-term precipitation for the months January-September (Fig. 4.1).

## Experimental Burning

In general, fire behavior and severity were similar on plots burned in 2000 and 2001 (Table 4.2). In 2000, burning resulted in morality of 17% (4 of 24 burned) of ceanothus plants whereas no plants died that were not burned in forest unit 3T. In 2001, 32% (21 of 65) of the burned plants died whereas 5% of plants died that were not burned in units 1T and 2T. For all burned plots combined, probability of mortality was significantly ($p<0.001$) related to amount of forest floor consumed (Fig. 4.2). Probability of plant death increased dramatically after about 3 cm of forest floor consumption and no plants survived on plots where more than 6 cm of forest floor was consumed. Mean amount of forest floor consumption that resulted in mortality was 4.7 cm (SE = 0.4).

Fendler ceanothus plants died on 6 of 37 (16%) plots for which vegetation burn severity was rated as "scorched" (vegetation burn severity class 4; USDI 1992). Depth of forest floor consumption on these plots averaged 1.3 cm (SE=0.2). On plots for which vegetation burned severity was rated as "lightly burned" (vegetation burn severity class = 3), plants died on 12 plots (28%). On lightly burned plots, depth of forest floor consumption averaged 2.6 cm (SE=0.3). Fendler ceanothus plants died on 8 of 9 (89%) plots for which vegetation burn severity was rated as "moderately burned" or "heavily burned (vegetation burn severity classes 2 and 1, respectively). On plots for which vegetation burn severity was rated as class 2, mean depth of forest floor consumption was 4.2 cm (SE=0.7) and for severity class 1, consumption averaged 5.5 cm (SE=0.5). Average and maximum flame lengths observed during experimental burning were not significantly related to Fendler ceanothus mortality. Maximum flame lengths recorded were 91 and 117 cm on plots burned in 2000 and 2001, respectively. Mean flame length in the two burn years ranged from 13 to 19 cm.

Across all burned plots, 66-96% of the aerial stems died back to ground level (4-34% escaped fire-related mortality). On plots where burning did not result in Fendler ceanothus mortality, plants resprouted from aerial stem bases or belowground structures within about 60 days from burning. In general, burning converted Fendler ceanothus patches from all-aged stem assemblages to those dominated by first-year sprouts (Figs. 4.3 and 4.4).

***Protected Plots***

Experimental burning did not significantly ($p \geq 0.05$) affect number of stems on plots protected from large herbivores. Similarly, burning did not affect net change in stem populations for protected plots. Mean stem number generally increased on protected plots from 1999 to 2002 regardless of burning and net change ranged from 140 to 300% across burned and unburned plots (Fig. 4.3).

Burned Fendler ceanothus plants produced longer current-year branches than unburned plants one growing season after treatment (Fig. 4.5). Current-year branches of burned plants were mainly sprouts originating from stem bases or belowground structures. These were long stems with relatively few lateral shoots. On protected plots burned in 2000, I measured current-year branches up to 43 cm in length.

Stems of unburned plants had significantly ($p<0.05$) more current-year branches than those of burned plants one growing season after burning (Fig. 4.5). For plots burned in 2000, differences in current-year branch number persisted for two growing seasons. More current-year branches on stems of unburned plants translated to significantly ($p<0.05$) greater current-year biomass and leaf area than on burned plants (Fig. 4.5). No significant difference in current-year stem biomass was found between burned and unburned plants for those burned in 2000 (Fig. 4.5). Current-year leaf area on stems was significantly ($p<0.05$) greater on unburned (95.8-138.0 $cm^2$) than burned (40.1-59.4 $cm^2$)

plants one growing season after burning for both years (2000 and 2001 burns). In 2002, no significant differences were found between protected burned and unburned plots for any variable analyzed (Fig. 4.5).

### *Unprotected Plots*

On plots that were not protected from large herbivores, stem number was significantly greater in 2000 (pre-burn; $p<0.05$) and 2001 (first-year post-burn; $p<0.01$) for plots burned in 2001 (Fig. 4.4). Although pretreatment (2000) differences were present, paired t-tests showed a significant ($p<0.05$) increase in number of stems on burned plots whereas stem number did not significantly ($p\geq0.05$) change on unburned plots in 2001. Stem number was not significantly ($p\geq0.05$) different between unprotected burned and unburned plots in any of the four years for those burned in 2000 (Fig.4.4). Similar to protected plots, net change in stem populations on unprotected plots was not affected ($p\geq0.05$) by burning and ranged from 120 to 140% across all unprotected burned and unburned plots.

One growing season after burning, mean current-year branch length was significantly greater on plants burned in 2000 than unburned (Fig. 4.6). In units burned in 2001, there were no significant differences in current-year branch length between burned and unburned plants (Fig. 4.6). Similar to protected plots, branch number on unprotected plots was greater on unburned plants than burned plants one growing season after burning for both burn years (Fig. 4.6). Pretreatment (1999) differences for current-year branch number existed for those burned in 2000, however, branch number significantly (Mann-Whitney test; $p<0.05$) decreased on these burned plots but did not significantly change on unburned plots one growing season after prescribed fire. Current-year biomass was significantly ($p<0.05$) greater on unburned stems than burned stems one growing season after burning for those burned in 2001 (Fig. 4.6). For plots burned in 2000, burning had no significant effect on current-year stem biomass after one growing season. Current-year stem biomass was, however, significantly ($p<0.05$) greater on unburned than burned stems two growing seasons after burning (Fig. 4.6). In 2002, no differences in current-year stem biomass were found between burned and unburned plots for either burn year. Current-year leaf area on Fendler ceanothus stems followed a similar pattern as biomass showing lower values on burned stems one growing season after burning with no differences between burned and unburned stems in 2002. Current-year leaf area on unprotected stems that were not burned ranged from 3.1 to 73.2 $cm^2$ across the four study years.

### *Seedling Establishment*

No seedlings emerged on unburned plots in any of the four study years. On plots burned in 2000, seedlings emerged on nearly half (45.8%) the plots and a mean of 1.0 (SE=0.3) seedlings per plot (2,500 seedlings per ha) occurred. Seedlings were found on 55% of plots burned in 2001 and emergence averaged 5.1 (SE=1.4) seedlings per plot (12,750 per ha). The maximum seedling emergence occurred on a plot burned (in 2002 where 53 seedlings (132,500 per ha) occurred. Protection from large herbivores did not significantly (Mann-Whitney; $p\geq0.05$) affect the number of seedlings per plot for either burn year. Therefore, summaries for seedling emergence and survival are given for protected and unprotected plots combined (N=89).

Number of seedlings emerging on plots was not significantly related to amount of forest floor consumed. However, a significant ($p<0.05$) relationship was found between probability of seedling emergence on plots (proportion of plots on which seedlings emerged) and amount of forest floor consumed in 0.5-cm classes (Fig. 4.7). The form of the relationship was quadratic (i.e., $y_i = b_0 - b_1x_i^2 + b_{11}x_i$); seedlings were observed on a relatively small proportion (0-45%) of plots with either low (<2 cm) or high (>7 cm) amounts of forest floor consumed. Probability of emergence was greatest (45-100%) on plots with moderate (2.5-6.5 cm) amounts consumed.

Fire severity rating also corresponded to probability of emergence. Seedlings emerged on 18% (5 of 27) of the plots were rated as “scorched” (substrate burn severity class 4; USDI 1992). On these plots, mean depth of forest floor consumption was 0.8 cm (SE=0.1). On plots rated as “lightly burned” (severity class 3), seedlings emerged on 66% (37 of 56) of the plots. Mean amount of forest consumed on substrate burn severity class 3 plots was 2.5 cm (SE=0.2). Seedlings emerged on 83% (5 of 6) the plots rated as “moderately” or “heavily burned” (severity classes 2 and 1, respectively). On these plots, forest floor consumption averaged 5.6 cm (SE=0.3).

One-year seedling survival was 26.7% (SE=9.4) on plots burned in 2000. Live seedlings were found on 45% (5 of 11) of plots on which emergence was observed the previous year. Mean seedling density was 0.4 per plot (SE = 0.2) (1000 per ha).

One-year survival on plots burned in 2001 was 11.0% (SE=4.7). Seedlings were found on 55% (20 of 36) of the plots where they emerged and mean density was 0.5 per plot (SE=0.3) (1250 per ha). Mean first-year survival was not significantly ($p \geq 0.05$) affected by protection from large herbivores for plots in either burn year.

Two-year seedling survival on plots burned in 2000 was 3.6% (SE=3.6). In 2002, two seedlings remained on just one plot. Average number of seedlings per plot was 0.08 (SE=0.08) (200 per ha).

## Discussion

### Fendler ceanothus Growth as Related to Overstory Density

Growth of Fendler ceanothus, in terms of current-year branch length and number and current-year stem biomass and leaf area, was inversely related to overstory stand density and browsing. Similar results relating understory production to overstory structure have been reported for Arizona ponderosa pine forests (Arnold 1950, Ffolliott and Clary 1975, Tapia et al. 1990). Values of SDI in this study were within the range reported by Moore and Deiter (1992) who found a slight negative relationship between Fendler ceanothus growth and overstory density in ponderosa pine forests of the North Kaibab National Forest in Arizona. In my study, browsing was generally more important than SDI in explaining variations in Fendler ceanothus growth on plots. In other studies, shrubs have been found to respond weakly to changes in ponderosa pine forest density. For example, Moore and Deiter (1992) found that understory response was dependent on functional group (i.e., grass, forb, shrub, etc.) but it was not clear if this was due to factors related to plant physiological characteristics or extrinsic factors such as species interactions. The authors implied that domestic grazers were not present on their study site and elk were likely absent from their site on the North Kaibab National Forest in the early 1990s. In a study of ponderosa pine stands in South Dakota, 6-8 shrub species were present yet only bearberry (*Arctostaphylos uva-ursi*), a species unavailable to browsers in winter due to snow cover, made significant contributions to production differences between overstory growing stock levels (Ursek and Severson 1989). Patton (1974) reported that grass and forb production, numbers of browse plants (woody sprouts 30-137 cm in height), and large ungulate use all increased after harvesting ponderosa pine in patches 2-32 acres in size. I previously reported that Fendler ceanothus plants protected from large herbivores retained nearly five times more current-year biomass than plants exposed to browsing by mule deer and elk (Chapter 2 this dissertation). Allen (1996) speculated that severely browsed Fendler ceanothus plants on a large wildfire site in New Mexico were the result of rapid post-fire increases in elk populations. These results suggest that restoration thinning of dense forests has the potential to enhance growth of Fendler ceanothus plants; however, response is constrained by large ungulate herbivory. Herbivore preferences and changes in use patterns can result in minimal benefit from changes in stand density for some understory species, especially shrubs.

Climate affected relationships between Fendler ceanothus growth, overstory stand density, and browsing. In drought years, models were insignificant or explained no more than 14% of the variation in Fendler ceanothus growth (Table 4.1). A positive linear association between model correlation coefficients and percent of normal precipitation for important months showed that effects of overstory stand density and browsing were muted by severe droughts in 2000 and 2002. Similarly, Fulé et al. (2002) suggested that droughty conditions in 2000 could have been, in part, responsible for no differences in understory cover between thinned and unthinned forests at Grand Canyon National Park.

## Vegetative Response to Prescribed Fire

More than one-fourth of all Fendler ceanothus plants experimentally burned in my study did not resprout and mortality was positively related to amount of forest floor consumed. Although maximum flame length was never greater than 117 cm, which indicated relatively low fire intensity (Pyne et al. 1996), lethal temperatures were apparently generated belowground by smoldering combustion in deep forest floor layers. On a similar site, Vose and White (1987, 1991) reported substantial Fendler ceanothus mortality (55-67%) when consumption of heavy (46.2-145.9 Mg/ha) forest floor fuel loads during prescribed fire was 55-95%. Smoldering combustion in duff layers during prescribed fires has also been indicated as the cause of mortality for presettlement-age ponderosa pine trees (Covington and Sackett 1984, 1990). Subsequently, land managers interested in forest restoration rake forest floor debris away from bases of presettlement trees before burning to reduce heat-related mortality (Fulé et al. 2001, 2002). To reduce severe effects on the entire understory community, complete removal of the duff layer prior to initial reintroduction of surface fire has been tested (Covington et al. 1997). It is clear that initial reintroductions of fire in these ponderosa pine forests with deep forest floor fuel accumulations can be detrimental to remnant plant communities if burn conditions allow high rates of fuel consumption. Activities that result in high mortality of existing native plants, particularly for species that are not overabundant, may be counter to most ecosystem restoration goals.

Fendler ceanothus plants that survived prescribed fires resprouted readily and aerial stem populations were converted from all-age to even-age structures. Unburned populations remained all-age and stem number appeared to be stable over the four years of study. Annual recruitment of new stems in burned and unburned plots appeared to allow persistence by replacing stems lost to mortality. After two growing seasons, burned plants appeared to be regaining an all-age population structure. Sprouting and annual stem recruitment are important strategies for persistence in other competitive plant communities (Keeley 1977, Kurmis and Sucoff 1989, Huffman et al. 1994, Tappeiner et al. 2001). Keely (1992) identified various vegetative strategies for shrubs after fires in chaparral including pulse recruitment of stems immediately after fire, continual turnover of stems through time similar to my findings for Fendler ceanothus, and continual stem recruitment with little mortality. In general, sprout production after disturbance may be a viable strategy for persistence when safe sites for seedling regeneration are rare (Keeley 1977).

Persistence of Fendler ceanothus in understories may be further accomplished by production of long, unbranched sprouts after fire. Vigorous production of long sprouts may allow plants to quickly occupy growing space. Vose and White (1987) reported burned Fendler ceanothus plants were similar in size to unburned plants one year after fire. In the present study, I found longer current-year branches on burned plants than unburned plants. Sprouts arising from belowground buds were up to 43 cm in length. Throop and Fay (1999) hypothesized that long sprouts produced after fire by New Jersey Tea (*Ceanothus herbaceous*) could confer reproductive advantage over seedling establishment since stem size is often positively related to flowering. Indeed, in Chapter 2 of this dissertation, I found that more than 80% of Fendler ceanothus stems producing flowers were relatively large (>30 cm length; >4 mm diameter). In the present study, there were fewer current-year branches and less biomass and leaf area on burned plants than unburned plants but these differences were short-lived. Rapid recovery of Fendler ceanothus to pre-burn size and production may allow this species to persist in understory communities that naturally burned at intervals less than 20 years before Euro-American settlement of the region.

## Regeneration from Seed

Similar to plant survival, probability of Fendler ceanothus seedling emergence was related to depth of forest floor consumed during experimental burns. Probability of emergence was greatest at moderate depths (>2 and <7 cm) of consumption. Dormant Fendler ceanothus seeds in soil seed banks were apparently stimulated to germinate after exposure to heat from fire (Story 1974, Krishnan 1989). Although no attempt was made to correlate fire behavior and emergence, Vose and White (1991) reported fewer Fendler ceanothus seedlings on plots where fire intensities were low (open sawtimber) than on plots with high fuel loads and heat yield (below canopy sawtimber and pole). Other *Ceanothus* species utilize a similar buried seed strategy and can form extensive brush fields on severely burned sites (Gratkowski 1974, Keeley 1977, Noste 1985, Conard et al. 1985, Keeley 1992).

I did not measure temperature profiles in forest floor and soils, although temperature required to break seed coat dormancy and stimulate germination is around 90°C (see Chapter 3 this dissertation. Story (1974) reported germination of Fendler ceanothus seeds after treating with boiling water (100°C). Quick (1935) found temperature and cold stratification requirements varied for several *Ceanothus* species; some species showed negative responses to low (>70°C) levels of heat. Gratkowski

(1974) found optimal temperatures for germination of mountain whitethorn (*Ceanothus cordulatus*) ranged between 90 and 105ºC. Conard et al. (1985) generalized that temperatures greater than 120ºC are lethal to *Ceanothus* seeds, which is supported by my research with Fendler ceanothus (see Chapter 3 this dissertation).

### Management Implications

My results indicate that tree reduction and prescribed fire treatments used to restore ponderosa pine forest ecosystems have potential to increase Fendler ceanothus growth and reproduction. Large herbivores, however, such as mule deer and Rocky Mountain elk, and drought limit Fendler ceanothus response to forest treatments. Protection of understory plants against large herbivores could allow plants to retain greater current-season production and accelerate understory development. Although my study did not address operational-scale herbivore protection, use of logging slash (e.g. tree limbs and tops) to influence ungulate movement patterns and browse availability could be tested where desired or sensitive understory species are present.

Effects of fire on demographic structure of Fendler ceanothus populations depend on depth of forest floor consumed during burning. Preburn fuel measurements can be used to develop burn plans that encourage Fendler ceanothus sprouting and seeding establishment and limit detrimental effects. As additional programs are established to restore ecological function in ponderosa pine forest ecosystems, further research should examine response patterns for other important understory species.

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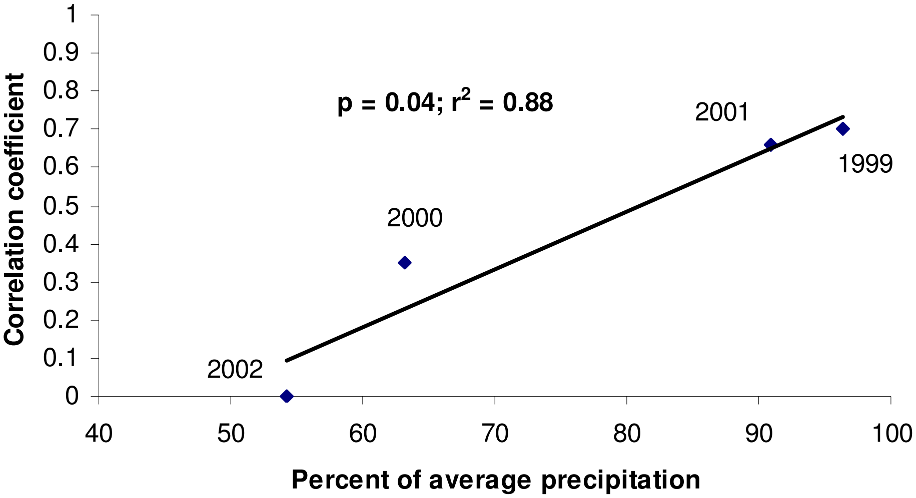

Figure 4.1. Relationship of Fendler ceanothus growth model correlation coefficient and percent of average precipitation for months of January-September. Model is: Ln(current-year branch length)= B0+B1(SDI)+B2(Browse); where *SDI* is Reineke's (1933) stand density index, and *Browse* is percent current-year branches browsed by large ungulates (see Table 4.1).

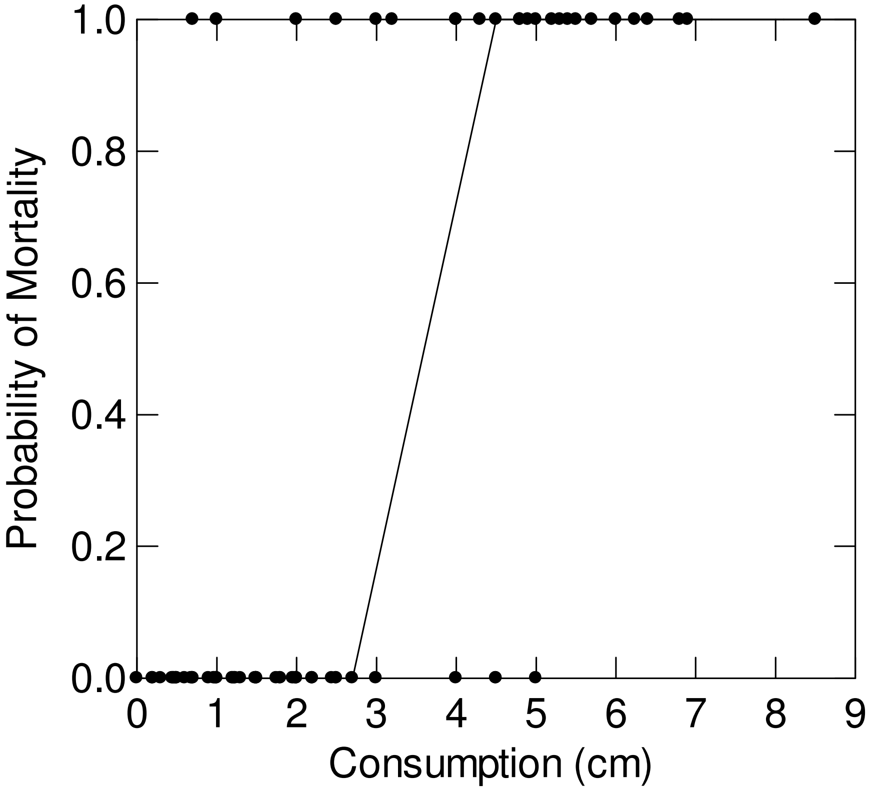

Figure 4.2. Probability of Fendler ceanothus mortality as related (p<0.001) to amount (cm) of forest floor consumed in experimental burns. Data are for plots burned in 2000 and 2001 pooled.

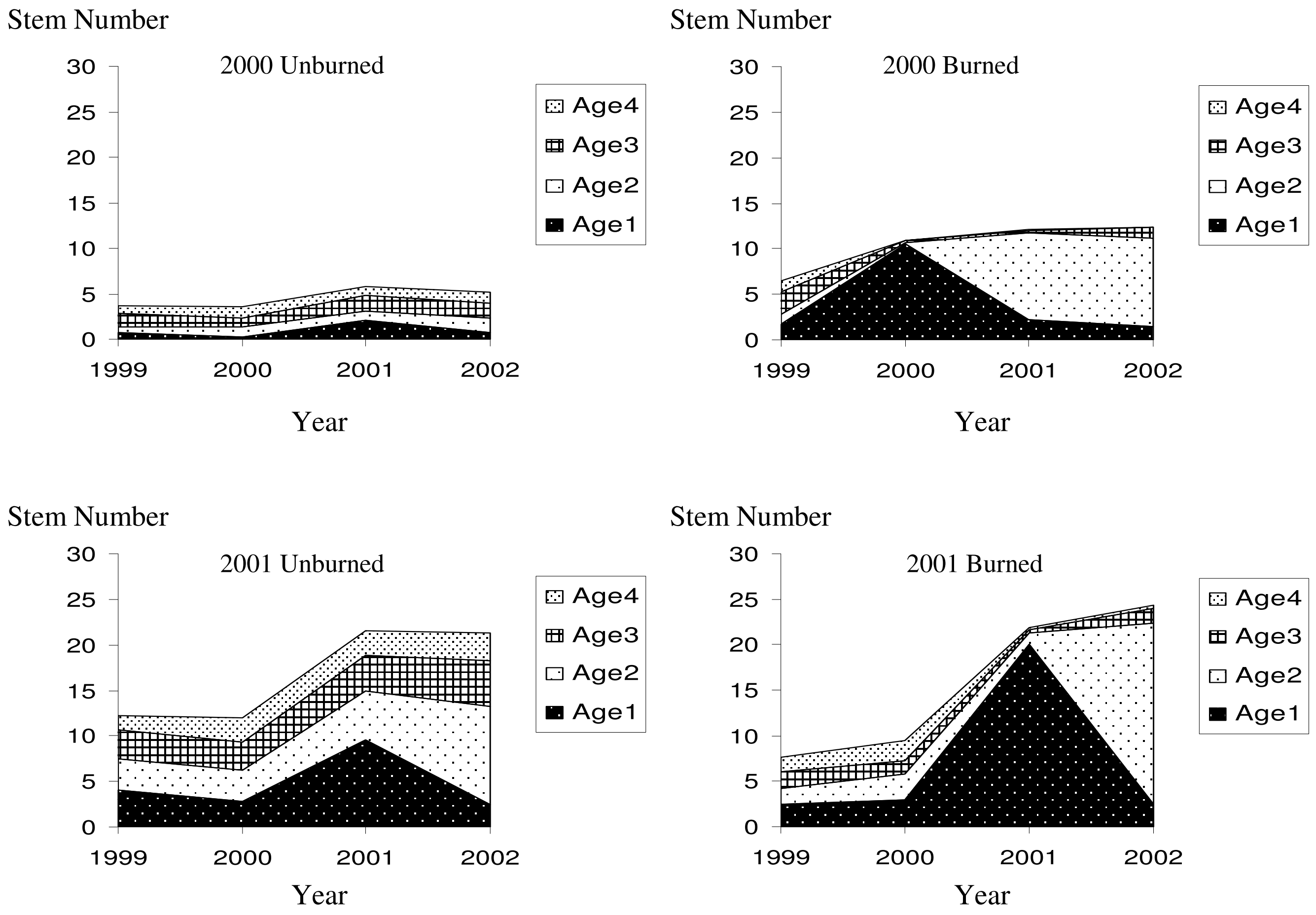

Figure 4.3. Distribution of mean number of stems by age class for plots protected from large herbivores. Shown are plots in the overstory unit burned in 2000 (unburned and burned plots) and those in overstory units burned in 2001 (unburned and burned plots).

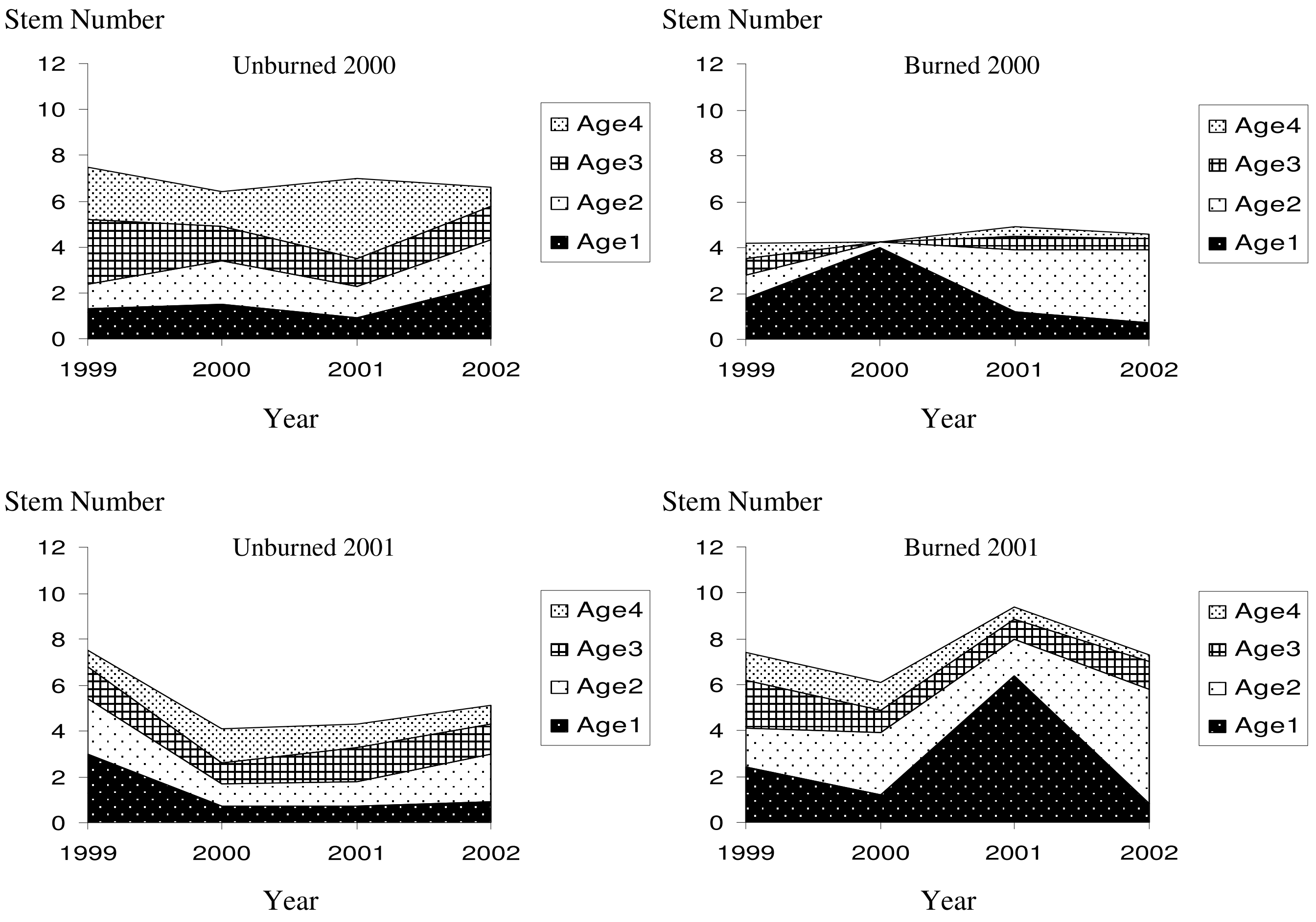

Figure 4.4. Distribution of mean number of stems by age class for plots not protected from large herbivores. Shown are plots in overstory unit burned in 2000 (unburned and burned plots) and those in overstory units burned in 2001 (unburned and burned plots).

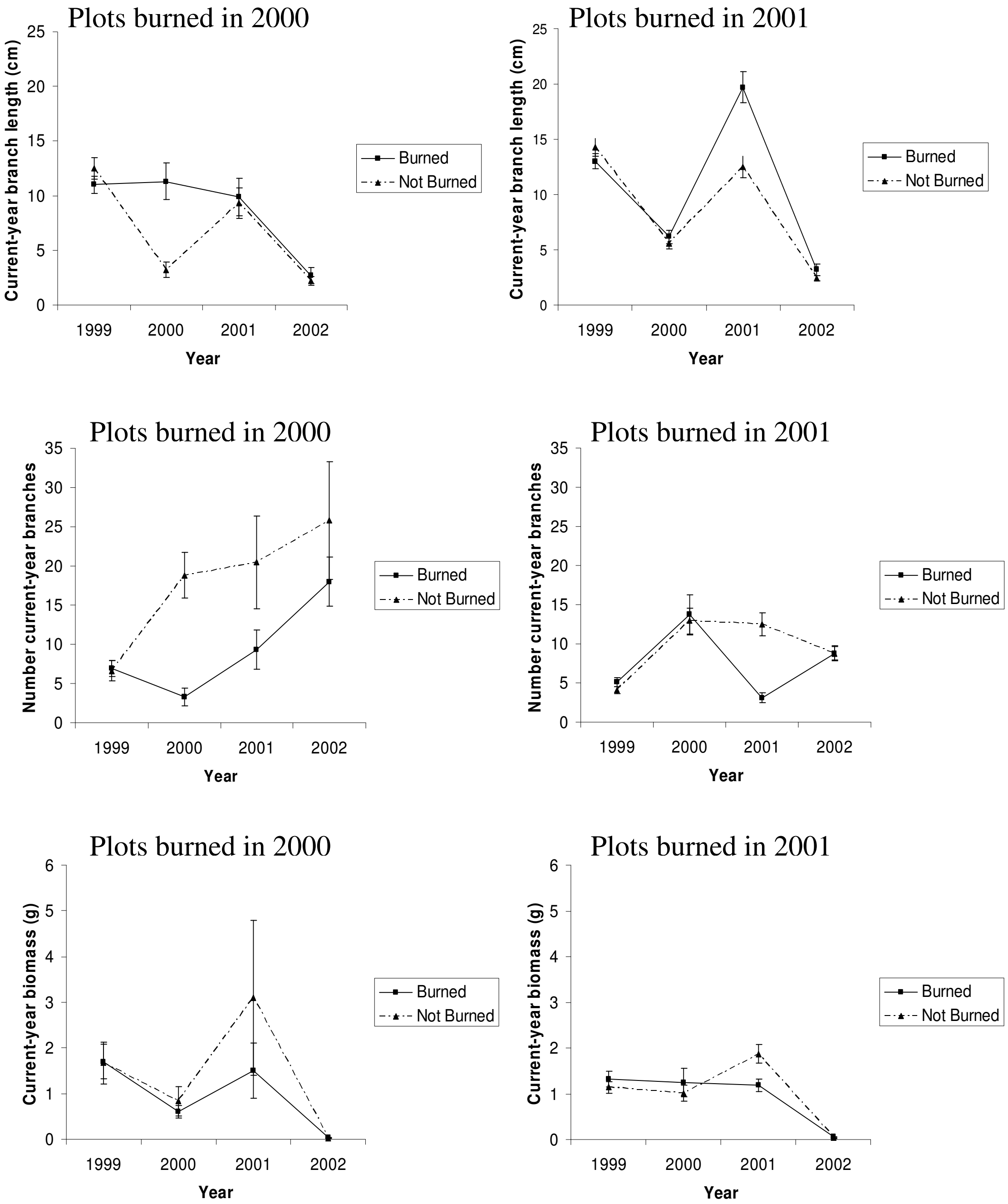

Figure 4.5. Average current-year branch length, number, and biomass of Fendler ceanothus stems on plots protected from large herbivores. Shown are plots in overstory unit burned in 2000 and those in overstory units burned in 2001. Bars standard errors.

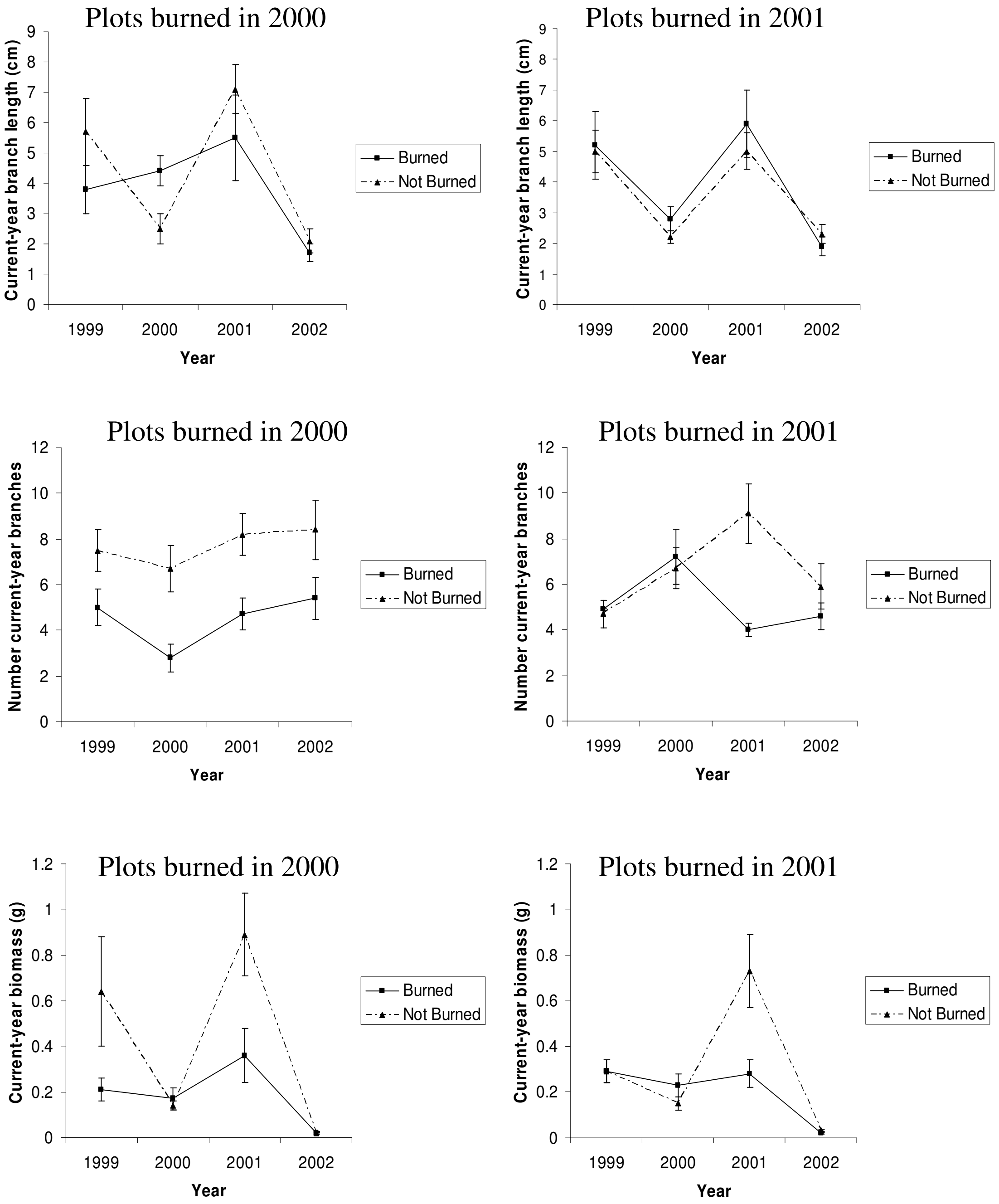

Figure 4.6. Average current-year branch length, number, and biomass of Fendler ceanothus stems on plots not protected from large herbivores. Shown are plots in overstory unit burned in 2000 and those in overstory units burned in 2001. Bars are standard errors.

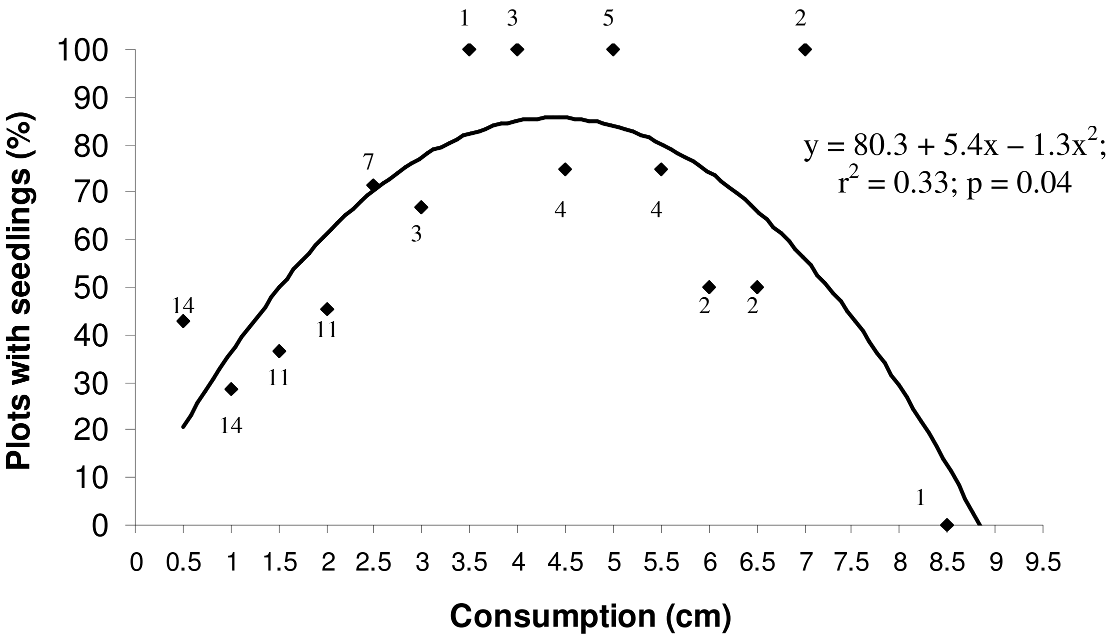

Figure 4.7. Relationship between proportion of plots on which Fendler ceanothus seedlings emerged and forest floor consumption during experimental burning. Values shown in association with data points are number of plots in forest floor consumption classes.

Table 4.1. R-squared, regression coefficients, and P-values for models of Fendler ceanothus current-year growth (Y,) on plots not protected from large herbivores and not burned, as related to ponderosa pine stand density (SDI[1]) and proportion of current-year branches browsed (Browse). When both SDI and Browse were significant ($p<0.05$) in the regression, statistics for the full model[2] are presented. When either SDI or Browse was not significant ($p\geq0.05$) in the regression, statistics for the partial model[3] are given.

| | Year | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1999 | | | | 2000 | | | | 2001 | | | | 2002 | | | |
| Variable (Y) | $r^2$ | $X_1$ | $X_2$ | *p* | $r^2$ | $X_1$ | $X_2$ | *p* | $r^2$ | $X_1$ | $X_2$ | *P* | $r^2$ | $X_1$ | $X_2$ | *p* |
| Mean branch length (cm) | 0.47 | -0.001 | -0.014 | <0.001 | 0.11 | ns | -0.008 | 0.008 | 0.42 | -0.002 | -0.011 | <0.001 | ns | ns | ns | ns |
| Longest branch (cm) | 0.47 | -0.001 | -0.014 | <0.001 | ns | ns | ns | ns | 0.34 | -0.002 | -0.010 | <0.001 | ns | ns | ns | ns |
| Number of branches[4] | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns | 0.01 | -0.002 | ns | 0.018 |
| Stem biomass (g) | 0.60 | -0.002 | -0.018 | <0.001 | 0.13 | ns | -0.015 | 0.003 | 0.24 | -0.003 | -0.017 | <0.001 | ns | ns | ns | ns |
| Stem leaf area (cm2) | 0.19 | -0.001 | -0.010 | 0.001 | 0.08 | ns | -0.009 | 0.022 | 0.14 | -0.002 | -0.011 | 0.008 | ns | ns | ns | ns |
| Plot biomass ($g/m^2$) | 0.27 | -0.004 | -0.012 | <0.001 | 0.14 | -0.002 | -0.015 | 0.007 | 0.16 | -0.004 | ns | 0.002 | 0.12 | -0.004 | ns | 0.008 |
| Plot leaf area ($cm^2/m^2$) | 0.18 | -0.003 | -0.005 | 0.001 | 0.09 | -0.002 | ns | 0.046 | 0.10 | -0.003 | ns | 0.012 | 0.14 | -0.003 | ns | 0.005 |

[1] SDI: Reineke's (1933) stand density index
[2] Full model in the form: $\mathrm{Ln}(Y)=ß_0+ß_1(X_1)+ß_2(X_2)$; where $X_1$=SDI and $X_2$=Browse
[3] Partial model in the form: $\mathrm{Ln}(Y)=ß_0+ß_1(X_1)$ *or* $\mathrm{Ln}(Y)=ß_0+ß_2(X_2)$; where $X_1$=SDI and $X_2$=Browse
[4] Square-root transformed

Table 4.2. Means (standard error) for fire behavior and severity characteristics on Fendler ceanothus plots burned in 2000 and 2001.

| | | Flame Length (cm) | | Severity Rating | | Forest Floor Consumption | |
|---|---|---|---|---|---|---|---|
| Year | N | Average | Max | Substrate | Vegetation | Percent | Depth (cm) |
| 2000 | 24 | 18.7 (1.5) | 48.7 (5.7) | 3.1 (0.1) | 3.0 (0.1) | 50.0 (5.7) | 2.7 (0.4) |
| 2001 | 65 | 12.6 (0.6) | 36.8 (2.3) | 3.2 (0.1) | 3.3 (0.1) | 52.0 (4.0) | 2.3 (0.2) |

# CHAPTER 5: POPULATION DYNAMICS OF FENDLER CEANOTHUS: SIMULATION OF FOREST RESTORATION SCENARIOS

## Abstract

Plant population models provide insight concerning plant life history patterns and life stage transitions important for persistence and recovery in changing environments and are valuable tools for assessing ecological tradeoffs between forest management approaches. In order to evaluate a set of ecological restoration alternatives, I constructed simple stage-based models and simulated 25-year dynamics for Fendler ceanothus (*Ceanothus fendleri* Gray), a shrub common in understories of ponderosa pine (*Pinus ponderosa* Laws.) forests of the southwestern United States. I tested the following management scenarios: 1) control (no forest or shrub treatments); 2) overstory thinning (NCNB); 3) overstory thinning plus prescribed fire (NCB); 4) overstory thinning plus protection from large herbivores (CNB); and 5) overstory thinning, prescribed fire, and protection from large herbivores (CB). I also analyzed effects of fire return intervals (2-, 5-, 10-, and 25-year) on protected and not protected populations. Results showed that CB populations had more than 20-times the abundance of aerial stems and more even life stage distribution (J′=0.657) than control (J′=0.105) populations. Elasticity analyses indicated that vegetative stem recruitment was most important for growth of CB populations whereas seed survival was most important for persistence of control populations. Populations in management scenarios that did not include protection from herbivores did not differ in abundance from control populations although burning resulted in greater life stage evenness due to emergence of seedlings from dormant seed banks. For protected populations, burning at 2-year frequencies increased abundance and life stage evenness compared with longer return intervals. For populations not protected from herbivores, high fire frequency resulted in population decline. These results suggest that forest restoration treatments and herbivory interact to affect long-term population dynamics of Fendler ceanothus.

## Introduction

Life history traits help determine plant survival, growth, and reproduction in changing environments. In particular, regeneration strategies, such as resprouting and seed production, play a large role in determining plant population dynamics and structure after disturbances or for persistence in highly competitive environments (Bellingham and Sparrow 2000). For example, shrubs in fire-prone environments are commonly classified by regeneration response after fire (Keeley 1977, 1998). Although life history traits are of primary importance in dictating population dynamics, demographic patterns are often affected by disturbances such as herbivory (Bullock 1991). Herbivory can affect (both positively and negatively) plant flowering, seed production, and vegetative recruitment (Paige and Whitham 1987, Stein et al. 1992, Augustine and Frelich 1998, Throop and Fay 1999, Ch 2 this dissertation). Because herbivory often affects reproductive processes, assessment of population-level effects of herbivory is best conducted over multiple generations (Verkaar 1987). Understanding regeneration strategies and long-term population dynamics of key species in changing environments is of special importance to ecologists and land managers engaged in forest restoration programs. In ponderosa pine (*Pinus ponderosa* Laws.) forests, where ecological restoration treatments are urgently needed (Covington and Moore 1994, Moore et al. 1999), population modeling may be a valuable tool for assessing long-term effects of management alternatives.

Treatments aimed at restoring more natural conditions to ponderosa forests are underway on many sites in the southwestern United States (Covington et al. 1997, Fulé et al. 2002, Allen et al. 2002). Forest tree densities in this forest type have increased by an order of magnitude or more over the last century due to harvesting of large trees, intensive livestock grazing, and elimination of frequent surface fires (Covington and Moore 1994, Fulé et al. 1997, Mast et al. 1999, Allen et al. 2002, Moore et al. in press). Dense forests and exclusion of surface fire have reduced understory plant community diversity and abundance, slowed nutrient cycles, lowered habitat quality for various wildlife species, and created an environment ripe for occurrence of devastating crownfires (Covington and Moore 1994, Covington et al. 1997, Kaye and Hart 1998, Covington et al. 2001, Fulé et al. 2001). Thus primary goals for restoration programs are to reverse these trends and reestablish forest structural attributes and process that are more like those that prevailed prior to degradation (Moore et al. 1999).

Although debate continues regarding details of treatment implementation, most ecological restoration approaches call for decreasing tree density, usually by thinning trees in younger age classes, and reintroduction of surface fire (Allen et al. 2002). Treatment options that have been tested include overstory thinning alone, use of fire alone, and combinations of thinning intensities and prescribed fire (Sackett et al. 1996, Covington et al. 1997, Allen et al. 2002, Fulé et al. 2002). In general, understory communities in these forests increase production after overstory thinning and low-intensity fire (Jameson 1967, Ffolliott and Clary 1975, Uresk and Severson 1989, Moore and Deiter 1992, Covington et al. 1997). Little is known, however, concerning the long-term dynamics of plant populations in response to these management activities.

## Ecology of Fendler ceanothus

Fendler ceanothus (*Ceanothus fendleri* Gray) is a common shrub found throughout northern Arizona ponderosa pine forests. It is an important species in understory communities; it is actinorhizal and capable of nitrogen-fixation (Story 1974), provides important browse for ungulates such as mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) (Urness et al. 1975, Allen 1996, Ch 2 this dissertation), and provides structural heterogeneity in the predominantly herbaceous understories of these forests.

Fendler ceanothus is a small shrub that grows up to 1.5 m in height. It forms discrete patches of up to 104 aerial stems $m^{-2}$. Aerial stems are produced annually or semiannually from belowground buds on branches and root crowns. Fendler ceanothus also resprouts after fire from these belowground buds and from stem bases (Vose and White 1987, Chapter 4 this dissertation). Undisturbed patches of aerial stems are typically all-aged whereas populations produced from resprouting after low-severity fire or similar disturbances are even-aged for at least the first year (Chapter 4 this dissertation). Fendler ceanothus is somewhat sensitive to heat and moderate-intensity fire can cause mortality (Chapter 4 this dissertation). Sprouting after low-severity fire can be prolific and stem populations can increase in density compared with pre-fire stem numbers (Chapter 4 this dissertation). Sprouts produced after fire are typically long and generally unbranched, often reaching lengths similar to undisturbed stems within one growing season (Chapter 4 this dissertation). Intense herbivory can dramatically reduce stem length, current-year branch production, and recruitment of new vegetative stems (Chapter 2). Overstory density also negatively affects aerial stem density in Fendler ceanothus patches.

Flowering of Fendler ceanothus begins in mid June. Flowers are borne in panicles on stems usually greater than 20 cm in length (Chapter 2 this dissertation). Flower production appears to depend on stem age and size (Chapter 2 this dissertation). Small, browsed stems, and resprouts arising immediately after fire, have not been observed to flower (Chapter 4 this dissertation). Fruit set typical occurs in Mid July to early August. Like flowering, fruit production is positively related to stem size. Fruits are 3-celled capsules and seed dispersal is by ballistic expulsion as fruits dehisce in late August to early September.

Fendler ceanothus appears to utilize a dormant seed strategy and seedling emergence is often observed after fire (Vose and White 1991, Chapter 4 this dissertation). Seeds are ~ 2 mm in diameter and a dark, glossy brown when fully developed. Most seeds in an annual cohort require heat to germinate although some seeds can germinate without heat (Ch 3 this dissertation). Seeds enter the soil seed bank and apparently remain dormant until moderate-intensity fire allows germination (Huffman unpublished data). Seed germination is enhanced by exposure to temperatures of 70-100º C (Story 1974, Krishnan 1989, Chapter 3 this dissertation). After low-severity fire, seedlings emerge with the onset of seasonal monsoon rains in late July or August. Seed longevity under field conditions is not known. Specific microsite characteristics that affect seedling survival have not been studied. Seedlings can reach heights of 20 cm by their second growing season (Huffman unpublished data) although time or size required for seedlings to attain sexual maturity is not known.

My objectives in this study were the following: 1) construct stage-based population models for Fendler ceanothus from demographic field data collected 1999-2002 (Chapters 2, 3, and 4 this dissertation); and 2) analyze relative effects of forest restoration alternatives (i.e., overstory thinning and prescribed fire), and interactions with ungulate herbivory, on long-term population dynamics. Analysis of effects of restoration treatment on plant population dynamics can help resource managers refine management approaches and better understand community patterns. Further, these studies can illuminate important life history traits and stage transitions that facilitate population persistence under varying environmental conditions.

## Methods

### Demographic and Life Stage Data

I collected demographic and life stage data 1999-2002 on field plots and in laboratory studies for modeling Fendler ceanothus population dynamics. These studies were described in earlier chapters (Chapters 2, 3, and 4) of this dissertation. Field plots were located on the Fort Valley Experimental Forest in northern Arizona (35º 16’ N, 111º 41’ W). Overstories of forest units were comprised of nearly pure stands of ponderosa pine. Understories were sparse and comprised of mainly the grasses (e.g., *Festuca arizonica*, *Muhlenbergia montana*, and *Elymus elymoides*) and the forbs (e.g., *Lupinus* spp., *Antenaria* spp., and *Erigeron* spp.). Scattered populations of shrubs included mainly Fendler ceanothus, and woods rose *Rosa woodsii*.

Sixty plots (1 $m^2$) centered on patches of Fendler ceanothus stems were established in three forest units (~14 ha in size) in 1999. Overstory trees in these units were thinned from below 1998-1999 as part of a larger forest restoration experiment (see Fulé et al. 2001). Overstory density after thinning ranged from 177 to 310 trees per hectare (TPH) (tree quadratic mean diameter (QMD) was 36-45 cm at 1.37 m height above ground). Thinned units were broadcast burned by the U.S. Forest Service in spring (April-May) 2000 and 2001.

Fendler ceanothus plots in the thinned units were randomly assigned to one of four treatments in a 2x2 factorial design. Treatments were protection from large herbivores (exclosures), and experimental burning. Treatments were applied on 2x2-m areas centered on Fendler ceanothus plots. Large ungulate exclosures were built around 30 plots per unit (N=90) in spring 1999. Experimental burning of plots (24-35 plots per unit) was done in spring 2000 and 2001 (see Chapter 4 this dissertation).

I also established 10 plots in each of three forest units that were not thinned ("Control"). Overstory densities in Control units ranged from 984-3450 TPH (QMD=19-26 cm). Control units were not burned and Fendler ceanothus plots in these units were neither protected from large herbivores nor experimentally burned.

Demographic characteristics of Fendler ceanothus stem populations were measured on plots 1999-2002. In June each year, I visited plots and tallied flowering stems (Chapter 2 this dissertation). I returned to plots in July to assess fruit production and install seed traps around fruiting stems to estimate seed production (Chapter 3 this dissertation). In September, I tallied total number of stems on plots and collected seed traps. At each field measurement throughout the growing season, I searched plots for seedlings. Seedlings were identified by their size at emergence (<4 cm height) and presence of cotyledons. When found, seedlings on plots were mapped to allow subsequent assessment of survival (see Chapter 4 this dissertation).

Viable seed production per stem was estimated in the laboratory by dissecting seeds from seed traps and tallying the number filled. To estimate the number of seeds successfully dispersed, I experimentally tested post-dispersal seed predation (Chapter 3 this dissertation). Ten seed depots were installed along one 250-m transect in each treated (thinned and burned) forest unit (2000 and 2001). Fendler ceanothus seeds were placed in Petri dishes and left at depots for 8-10 days. At the end of this period, dishes were collected and seed removal was assessed. Seed germination characteristics, including response to heat and cold stratification, were determined in the laboratory (Chapter 3 this dissertation).

Treatment combinations imposed on Fendler ceanothus plots allowed me to model population dynamics for five distinct management scenarios. Scenarios were the following: 1) no thinning, no herbivore protection, and no burning (Control); 2) overstory thinning, no herbivore protection, and no burning (no cage, no burn; NCNB), 3) overstory thinning, no herbivore protection, and experimental burning (no cage, burn; NCB); 4) overstory thinning, herbivore protection, and no burning (cage, no burn; CNB); and 5) overstory thinning, herbivore protection, and experimental burning (cage, burn; CB).

## Simulation Models

### *Transition Matrices*

To model management effects on population dynamics, the life cycle of Fendler ceanothus was simplified into four discrete stages: seed, seedling, vegetative adult, and reproductive adult (Fig. 5.1). Since the species sprouts from belowground branches and identification of individual plants was problematic without excavation, aerial stems were selected as the unit of analysis for population modeling. Stage-based transition matrices (Caswell 2001) were built from 1999-2002 field and laboratory data (Table 5.1).

### *Vital Rates*

Vital rates are probabilities for survival and transition into subsequent life stages. I calculated vital rates for stage elements as the average of the annual changes for each life stage transition over the four years of field study (Table 5.2). Each forest unit was treated as a separate and independent population. Vital rates for stage transitions were determined by analyzing changes in total numbers of seedlings and aerial stems within forest units. Calculations and assumptions are described as follows:

1) Seed germination of Fendler ceanothus is facilitated by heat (~70-100ºC; see Chapter 3 this dissertation). In field studies (see Chapter 4 this dissertation), I observed no seedlings over four years on unburned plots and I assumed that seed dormancy was high in seed banks. Seeds of other ceanothus species are thought to remain viable in seed banks for decades (Conard et al. 1985). Thus, I assumed little seed mortality over 25 years for seed banks and set seed

survival rate ($P_1$) for no-burn scenarios to 0.99. Further, I set seed-seedling transition ($G_1$) for no-burn scenarios (i.e., Control, NCNB, and CNB) to 0.01 (non-zero vital rates allowed a somewhat conservative approach to projection of population dynamics). Seed-seedling vital rate for scenarios that included prescribed fire (i.e., CNB, CB) was set to 0.60. This value was the average germination rate found for seeds from the Fort Valley site exposed to 90ºC heat (10 minute duration) in laboratory studies (Chapter 3 this dissertation). Seed survival ($P_1$) for prescribed fire scenarios, was set to 0.10.

2) Probability for seedling-seedling ($P_2$) transitions was average one-year survival observed in the field (Chapter 4 this dissertation). Although survival was nil in one unit, I set the minimum probability for $P_2$ to 0.01. The highest one-year survival was 0.267. I did not have two-year survival rates for two forest units where plots were burned in 2001. Therefore, I used average 2-year seedling survival from one unit as the best approximation of transition vital rate (0.061) for seedling-vegetative adult ($G_2$) for all units. I did not observe flower production for any seedlings over the study period although seedlings can begin to develop adult-like morphological characteristics, such as thick (>2 mm) stem bases and heights of up to 20 cm, within two years of emergence (Huffman pers. obs.). There is evidence that seedlings of at least one species of ceanothus (*Ceanothus integerrimus* H. & A.) can produce flowers within three growing seasons and new vegetative stems and root crowns within one growing season (McDonald et al. 1998). In my model, I

assumed very few seedlings transitioned to reproductive stems ($G_4$) in two years and thus set $G_4$ values to 0.01 for simulations.

3) Probability of vegetative stem survival ($P_3$) was calculated as $Vt_{i+1}$/ $Vt_i$; where $Vt_i$ = number of non-flowering stems tallied on plots in year i. Range of values for $P_3$ was 0.44-2.53 (vegetative regeneration allowed $P_3 > 1.0$).
4) Transition from vegetative to reproductive adult stem ($G_3$) was calculated as $Rt_{i+1}/Vt_i$; where $Rt_{i+1}$ = number of flower-producing stems in year i + 1. No flowering stems were observed in Control units in any of the four study years (Chapter 4 this dissertation). Similar to other low vital rates, I set $G_3$ for Control units to 0.01. Survival of reproductive stems ($P_4$) was calculated as $Rt_{i+1}/Rt_i$. Since previous studies indicated that flowering and fruit production was related to stem size and age, I assumed that, once stems were observed flowering, little retrogression ($G_5$) to vegetative stage occurred. Thus, I set $G_5$ values to 0.01 for all simulations.
5) Fendler ceanothus fertility ($F_1$; the number of seeds successfully dispersed) was estimated from previously described studies of seed production. Values used in matrices for this study reflected production of developed seeds minus losses due to predispersal parasitism and post-dispersal predation (Chapter 3 this dissertation). The number of seeds per stem used to estimate fertility was 16.1 (Table 5.2).

## Model Projections

Population dynamics of Fendler ceanothus were modeled for the five management scenarios using the computer software RAMAS Metapop (Akçakaya 1998). Transition matrices were projected using the general population growth model:

$$N_{t+1} = A(N_t)$$

where: N = population size; t = time, and A = matrix of vital rates. Time step used was one year and duration (time period of projection) modeled was 25 years. For each population, 1,000 model simulations were run.

Environmental stochasticity was incorporated into model projections by inputting matrices of vital rate standard deviations (Akçakaya 1998). For invariable vital rates (e.g., $P_1$ and $G_1$) standard deviations were set to 0.01.

Populations among field units varied in size (25-218 aerial stems) and were initially (1999) dominated by vegetative stems (i.e., no seedlings or reproductive stems. Thus, in order to make reasonable comparisons between management scenarios a hypothetical population structure was constructed and used for all projections. This initial population represented a diverse structure with all life stages in the following abundances: seeds=500; seedlings=100; vegetative stems=50; reproductive stems=25. This starting point allowed me to fairly judge effects of management scenarios on population characteristics such as relative abundance of life stages. It should be noted that initial population structure does not affect estimates of finite rate of increase ($\lambda$) (Silvertown and Charlesworth 2001),

A carrying capacity (K) value of 2500 was used as a population "ceiling" to simulate density-dependent effects. Although population responses of Fendler ceanothus to increasing density are not known, this ceiling roughly allowed a quadrupling of population size from initial conditions. Density dependence affected all vital rates as population size approached K (Akçakaya 1998).

Prescribed burning scenarios were modeled by treating fire as a "catastrophe" (Akçakaya 1998). For comparisons of management scenarios, probability of fire was set to 0.20 to simulate a five-year burn interval. This probability corresponded with presettlement fire return intervals found on nearby sites and restoration management alternatives that include frequent application of prescribed fire (Covington et al. 1997). In years when fire occurred, matrix element multipliers were used to adjust vital rates to reflect values derived from field and laboratory observations of fire response (Chapters 3 and 4 this dissertation). Important fire effects included increased seed germination from seed banks ($G_1$), reduced survival of seedlings ($P_2$), and reduced probability of transition from vegetative to reproductive stems ($G_3$). Since my field studies indicated that these fire effects were short-lived and observable in the growing season immediately after burning, vital rates in years without fire remained the same as for unburned plots.

In addition to modeling population dynamics within the five basic management scenarios, I also examined effects of fire frequency and herbivory on population structure and abundance. Model parameters described above were held constant for NCB and CB scenarios while probability of fire was varied. Fire probabilities (Pr=0.5, 0.2, 0.1, and 0.04) simulated burn frequencies of 2, 5, 10, and 25 years. Population dynamics were simulated as described above for other scenarios.

### Statistical Analysis

Analysis of variance (ANOVA) was used to evaluate differences in population characteristics resulting from management scenarios. Model output averages for populations in each forest unit were used as replicates (n=3) for each management scenario. Parameters tested were: 1) finite rate of increase (λ); 2) population size (i.e., sum abundance of all stages); 3) total number of plants (i.e., sum all stages minus abundance of seeds); and 4) relative abundance of each life stage in modeled populations (i.e., number of individuals in a given life stage divided by total number of individuals in the population). Additionally, I tested effects of management scenarios on evenness of life stage distribution. Evenness was calculated as: $J'=H'/H'max$; where: $H'$=Shannon's Index of Diversity, and $H'max$=maximum value for $H'$ (Hunter 1990). When main effects ($p<0.05$) were found in ANOVAs, Bonferroni adjusted pairwise comparisons were used to test for differences among management scenario means (Kuehl 1994).

Similar analyses were conducted to test effects of fire frequency and herbivory on population dynamics. ANOVA was used to examine main effects ($p<0.05$) of fire frequency on population size, relative abundance of life stages within populations, and life stage evenness. Post-hoc tests of mean differences were conducted using Bonferroni adjusted pairwise comparisons.

## Results

### Effects of Forest Thinning, Fire, and Herbivory on Population Structure

Mean finite rate of increase (λ) was significantly ($p<0.05$) greater for scenarios that included protection from large herbivores (CNB, CB; $\lambda=1.33$) than those that did not include protection (Control, NCNB, NCB). There was no significant ($p>0.05$) difference in $\lambda$ between Control ($\lambda=0.99$) and NCNB (or NCB) scenarios ($\lambda=1.06$) (Table 5.3). Prescribed fire was modeled as a probabilistic event that only affected vital rates during the year of occurrence. Furthermore, $\lambda$ was calculated using vital rate matrices and calculations did not include matrices used to adjust vital rates for simulation of fire effects. Therefore, adding fire to a management scenario (i.e., protection and no protection from herbivores) did not change model estimates of $\lambda$ relative to those that did not include burning. Population trajectories, however, showed considerably different patterns among the five management scenarios (Fig. 5.2).

At the end of the 25-year duration, abundance was greater ($p<0.05$) for populations with herbivore protection with no burning (CNB) than Control and no herbivore protection with burning (NCB) scenarios (Table 5.4). Similarly, CB (protection and burning) and NCNB (no protection, no burning) had significantly ($p<0.05$) greater total abundance than NCB. Scenarios NCNB, CNB, and CB generally increased population abundance over the 25-year simulation whereas populations in Control and NCB scenarios declined (Fig. 5.2). Population size of NCNB, CNB, and CB doubled in roughly 2-5 years. Mean size of CNB populations tripled in about 3 years.

Relative abundance of life stages in populations was also affected by management scenarios. Although most populations were dominated by dormant seeds, NCB populations had significantly ($p<0.05$) fewer seeds than all other scenarios with the exception of Control (Fig. 5.3). Relative to total population size, NCB and CB populations had significantly ($p<0.05$) fewer seeds in comparison with other scenarios (Fig. 5.3). Control populations had less than 3% of their total abundance comprised by life stages other than seeds. Significantly ($p<0.05$) more seedlings were found for CB populations than all other scenarios, which were statistically similar (Fig. 5.3). Populations of NCB and CB scenarios had a significantly ($p<0.05$) greater proportion of their total abundance comprised of seedlings than other scenarios (Table 5.4). Similar ($p>0.05$) numbers of vegetative stems were found for all scenarios (Fig. 5.3). As a proportion of total population size, however, NCB had significantly ($p<0.05$) greater relative abundance of vegetative stems than Control and CNB populations (Table 5.4). Populations in the CB scenario had a significantly greater mean number of reproductive stems than all other scenarios (Fig. 5.3). Additionally, populations in the CNB scenario had significantly more reproductive stems than other scenarios with the exception of CB. A significantly ($p<0.05$) greater relative abundance of reproductive stems was present in CB populations than those of other scenarios (Table 5.4).

Structural diversity differed among the five management scenarios showed (Table 5.4). Evenness of life stages among the populations was greatest for NCB and CB scenarios. These two scenarios showed evenness values greater than 65% of the theoretical maximum ($H'$ max; see Hunter 1990) for a completely even population. In contrast, evenness for Control, NCNB, and CNB scenarios showed values 10.5-24.5% of $H'$ max.

Proportional sensitivity of $\lambda$ to small changes in life stage vital rates is expressed as model elasticities (Caswell 2001). Examination of elasticities suggested differences among management scenarios for model sensitivity to life stage transitions (Table 5.5). For example, $\lambda$ for the Control scenario was nearly completely dependent on transition values for $P_1$ (seed survival) whereas other matrix elements made relatively small contributions to $\lambda$. In contrast, $\lambda$ for the other management scenarios was relatively less sensitive to changes in $P_1$ than the Control scenario and more sensitive to changes in $P_3$ (vegetative stem survival and recruitment).

## Fire Frequency and Herbivory

Fire frequency and protection from herbivores interacted to affect Fendler ceanothus population size and structure. Total population abundance of both protected and not protected populations was significantly ($p<0.05$) greater for the lowest probability of fire (Pr=0.04; i.e., 25-year simulated frequency) than for the highest probability (Pr=0.50; i.e., 2-year simulated frequency) (Table 5.6). Population trajectories, however, showed different patterns for protected and not-protected plots within the four fire frequencies (Fig. 5.4). Protected populations increased from initial size over the 25-year simulation for all fire frequencies simulated. Populations that were not protected from herbivores generally decreased in abundance for simulations of 2-year and 5-year fire frequencies. A fire probability of 0.50 (i.e., 2-year frequency) was associated with a drastic population decline (Fig. 5.4). For longer fire return periods (i.e., 10-year and 25-year frequencies), populations that were not protected increased in abundance.

In addition to patterns observed for population trajectories, interactions between fire frequency and protection from herbivores were observed in life stage abundances (Fig. 5.5). Both protected and not-protected populations showed a pattern of increasing seed abundance with decreasing fire frequency. Protected populations had significantly ($p<0.05$) more seeds than not-protected populations at fire frequencies of 2 and 5 years

(Fig. 5.5). Similarly, relative abundance of dormant seeds in populations decreased with increasing fire frequency (Table 5.6). Seedling abundance tended to decline for protected populations as fire frequency decreased (Fig. 5.5). In contrast, seedling abundance increased with decreasing fire frequency for populations that were not protected from herbivores. Significantly ($p<0.05$) more seedlings were present in protected populations than not-protected populations for 2-year fire frequencies but there were no differences when fire was less frequent (Fig. 5.5). Similarly, relative abundance of seedlings of protected populations was significantly ($p<0.05$) greater for a frequency of 2 years than for a 25-year frequency (Table 5.6). No significant ($p\geq0.05$) differences were found among fire frequencies for relative abundance of seedlings in populations not protected from herbivores (Table 5.6). Similar interactions between herbivore protection and fire frequency were found for abundance of vegetative and reproductive stems (Fig. 5.5). Abundance of these stages tended to decrease with decreasing fire frequency for protected populations whereas, for not-protected populations, abundance increased as fire frequency decreased (Fig. 5.5).

Evenness of life stages decreased with decreasing fire frequencies for populations protected from herbivores (Table 5.6). Evenness was significantly greater for frequencies of 2 and 5 years than for a 25 year frequency. No differences were found for population evenness among fire frequencies for populations not protected from herbivores (Table 5.6).

# Discussion

## Management Alternatives

My results suggest that Fendler ceanothus populations benefit from restoration treatments that include overstory thinning, prescribed fire, and protection from large mammal herbivory. In CB populations burned at 5-year frequency, more than 20 times more aerial stems were present at the end of the 25-year simulation than in Control populations. The aboveground fraction of CB populations was even larger when burn frequency was two years. For CB populations burned at 2-5-year frequencies, aerial stems were distributed evenly among life stages compared with Control populations. Large populations of aerial stems in CB populations resulted from three main processes: 1) seedling emergence ($G_1$=0.60) in years of fire; 2) recruitment of vegetative stems from belowground buds in years without fire ($P_3$=1.11-1.37) and increased recruitment from resprouts in years with fire ($P_3$=1.40-2.50); and 3) recruitment of reproductive stems ($G_3$=0.18-0.80) in years without fire. Elasticity analysis showed that recruitment of vegetative stems was most important in affecting finite rate of increase for CB populations. These patterns differed substantially from those of Control populations, which had little seedling emergence, declining vegetative stem numbers, and little reproductive stem recruitment. Elasticity analysis for Control populations showed that seed survival in seed banks was most important for population persistence.

Although increased abundance of Fendler ceanothus after fire has been previously reported (Pearson et al. 1972), effects of disturbance and forest management practices on population structure has been minimally researched. After thinning, increased aerial stem recruitment might be expected since other studies in ponderosa pine forests have shown negative relationships between overstory density and understory production (Arnold 1950, Ffolloitt and Clary 1975, Tapia et al. 1990, Moore and Deiter 1992). Similarly, aerial stem density in clonal shrub patches of other ecosystems has been shown to be greater in thinned forests than in unthinned forests (Tappeiner et al. 1991, Huffman et al. 1994, Huffman and Tappeiner 1997, Tappeiner et al. 2001). Tappeiner et al. (2001) hypothesized that reduced annual production of aerial stems in populations of salmonberry (*Rubus spectabilis* Pursh) and salal (*Gaultheria shallon* Pursh) growing in dense coastal Northwest forests of was likely due to low levels of nonstructural carbohydrates in rhizome and low rhizome density as compared with thinned forests. In forests that have been burned, seedling recruitment might be expected since seed germination is stimulated by heat (Chapter 3 this dissertation). Vose and White (1991) found both resprouts and seedlings of Fendler ceanothus after prescribed burning in ponderosa pine forests that had not been thinned, although in their study population abundance generally decreased. In my study, low rates of aerial stem survival and reproductive stem recruitment in Control (not thinned) units were likely due to competitive and amensalistic effects of dense forest overstories. I was not able to evaluate effects of fire in unthinned forests.

In my study, populations that were not protected from large herbivores showed no difference in aerial stem or seed abundance after 25-year simulations than populations in the Control scenario. Other studies in southwestern ponderosa pine forests have shown that intense deer and elk herbivory can lead to decreased stem recruitment and flower production for various woody species (Stein et al. 1992, Strohmeyer and Maschinski 1996, Ch 2 this dissertation). It is clear that selective browsing by ungulates can limit stem size, reduce leaf area, remove floral buds, and constrain vegetative regeneration of plants in many western ecosystems (Debyle 1985, Dunlap 1988, Hoffman and Wambolt, Kay 1997, Oppermann and Merenlender 2000). These results suggest that intense herbivory can limit any beneficial effects that may be associated with overstory thinning and prescribed burning. Further, populations not protected from herbivores may, in fact decline, if fire is applied frequently (2-5 yr) as a management alternative. Protecting Fendler ceanothus from herbivores allowed plants to complete life cycles whereas populations not protected had low recruitment of reproductive stems, which apparently lead to depletion of seed banks in frequent fire scenarios.

## Life History Strategies

Analysis of population dynamics under simulated management scenarios provided insight regarding Fendler ceanothus' life history and strategies for persistence. Sprouting and seedling establishment from a dormant seed bank appears to allow this species to persist under a wide range of overstory and disturbance conditions. For example, under dense overstory conditions with infrequent disturbance (e.g., Control scenario), aboveground stems decline yet dormant seeds provide potential for site recolonization. This strategy is known for other species of ceanothus in ecosystems characterized by infrequent and/or high intensity fire regimes (Gratkowski 1974, Keeley 1977, Noste 1985, Montygierd-Loyba and Keeley 1987, Morgan and Neuenschwander 1988, Keeley 1992). For example, Gratkowski (1974) described dense stands of *ceanothus cordulatus* that develop after overstory cutting and slash burning in mixed conifer forests of the Pacific Northwest. In these forests, reproductive plants are typically absent from understories before disturbance. Similarly, post-fire seedling emergence of Fendler ceanothus has been noted on sites where adult plants were scarce before fire (Vose and White 1987, Huffman pers. obs.).

In addition to a dormant seed strategy, Fendler ceanothus can persist under open overstories in the absence of disturbance (e.g., NCNB and CNB scenarios). This appears to be facilitated by two processes: 1) frequent vegetative production of aerial stems from belowground buds (Chapter 4 this dissertation), and 2) stems that can live for four years or more (Huffman unpublished data). Similarly, *Ceanothus spinosus* periodically recruits aerial stems in chaparral communities and stem populations are uneven-aged more than 50 years after fire (Keeley 1992). *Ceanothus greggii* establishes from dormant seed after fire and its stems can persist for at least 90 years in the absence of disturbance (Keeley 1977). In contrast, *Ceanothus megacarpus* stands develop after fire from dormant seed banks yet, in the absence of fire, populations of this species apparently decline from density dependent competition and infrequent vegetative stem recruitment (Montygierd-Loyba and Keeley 1987). Annual stem production in clonal shrub populations has been described as a means of persistence for various other species such as hazel (*Corylus cornuta*) in Minnesota (e.g., Balogh and Grigal 1987, Kurmis and Sucoff 1989) and salal (*Gaultheria shallon*) in the Pacific Northwest (e.g., Huffman and Tappeiner 1997, Tappeiner et al. 2001). After low severity fire (e.g., NCB and CB scenarios), Fendler ceanothus can produce abundant sprouts from belowground branches or root crowns (Vose and White 1987, 1991, Chapter 4 this dissertation).

Based on work with shrubs (including *Ceanothus* spp.) in chaparral ecosystems, Keeley (1977, 1992, 1998) has described four "evolutionary options" related to life history traits and recovery from disturbance: 1) sprout and seedling production (i.e., facultative seeders; 2) abundant seedling production ("obligate seeders"); 3) low seedling production but high seedling survival; and 4) predominantly sprouting ("obligate resprouters"). Obligate seeding species are likely to have evolved in environments characterized by infrequent, intense fire. These species (e.g., *Ceanothus greggii*) cannot resprout and must recolonize sites through seedling establishment. Obligate resprouting species are likely to have evolved in frequent, low intensity fire environments. These species recruit few seedlings and persist on sites through vegetative regeneration (Keeley 1977). The two opposing strategies theoretically confer unique ecological advantages; obligate seeders can recolonize a site after an intense disturbance that produces high mortality in the vegetative community. Seedling recruitment can also increase genetic variability in populations and allow maximum potential for adaptation. Conversely, sprouting allows rapid reestablishment in competitive communities and can decrease time to reproduction relative to seedling development (Keeley 1977, Throop and Fay 1999). Fendler ceanothus appears to behave as a facultative resprouter; seedling establishment as well as resprouting can occur after fire (Chapter 4 this dissertation). This dual strategy allows the species to persist under a range of conditions including frequent and infrequent fire.

## Ecological Restoration Implications

A basic goal in ecological restoration is to enhance native biodiversity (Allen et al. 2002). Biodiversity includes not only richness of species but also of structural attributes and genotypes (Spies and Franklin 1996). My study suggests that ponderosa pine restoration treatments are likely to achieve biodiversity goals with respect to Fendler ceanothus population abundance and population structure if plants are protected from herbivory, at least for the first few years after thinning and burning. For Fendler ceanothus, as well as other plant species, treatments that initiate establishment of seedlings, and thus increase genetic diversity, are likely to enhance the ability of populations to adapt to changing environments (Keeley 1977). Further, treatments that allow full expression of plant life cycles may benefit other species in these ecosystems. For example, in early studies I documented seed parasitism on Fendler ceanothus by a chalcidoid wasp (*Eurytoma squamosa*) (Huffman 2002). The host-parasite linkage appeared to be relatively tight as this wasp parasitizes seeds of a limited number of plants species, mainly those in the family Rhamnaceae (M. Gates pers. comm.). Studies in progress indicate that herbivory of Fendler ceanothus may reduce diversity of other arthropods (Huffman unpublished data). More studies are needed to describe ecosystem-level effects of changes in population dynamics for important understory plant species. Population analyses, such as those presented in my study, are good starting points for understanding ecological tradeoffs associated with various restoration treatments and dissecting complex community response patterns as ecosystems are assisted in recovery from processes of degradation.

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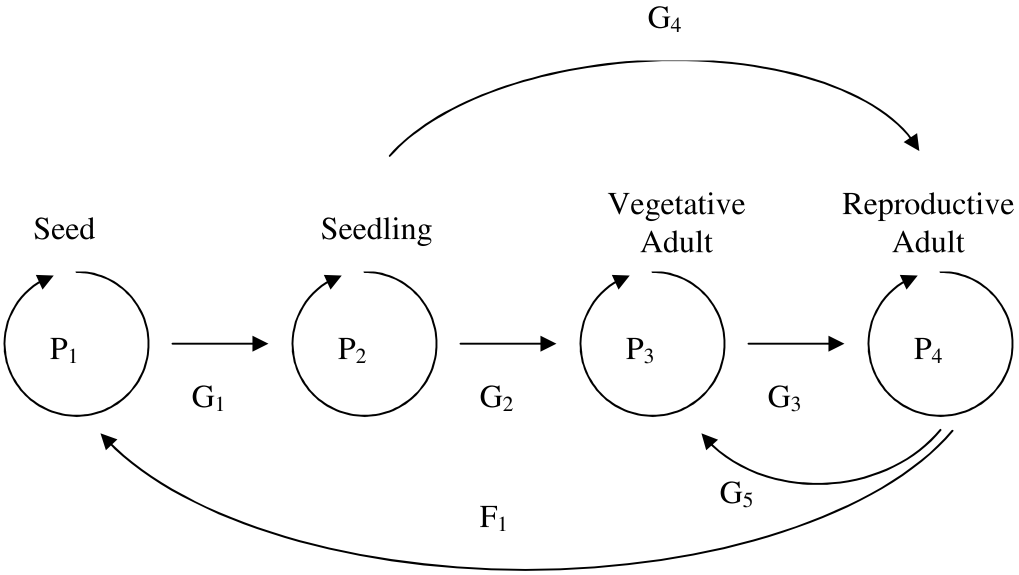


Figure 5.1. Simplified life cycle of Fendler ceanothus.

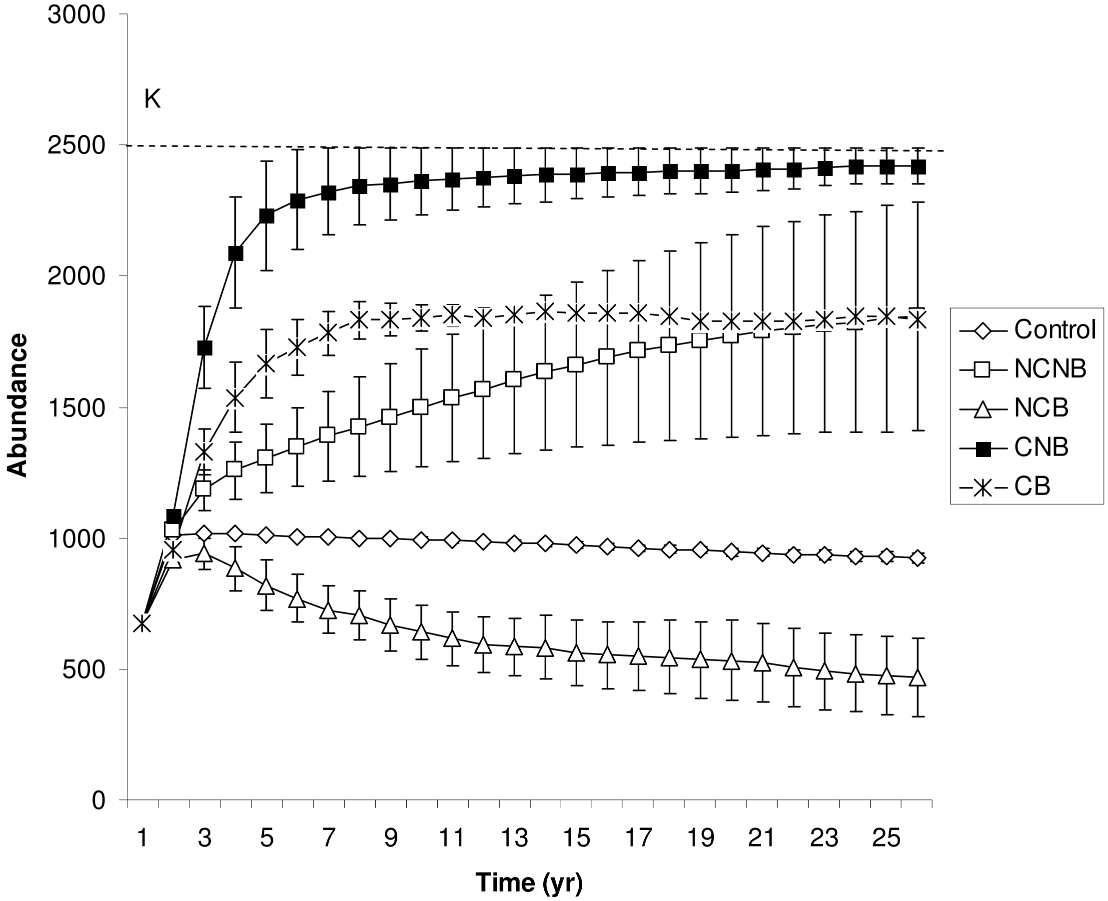
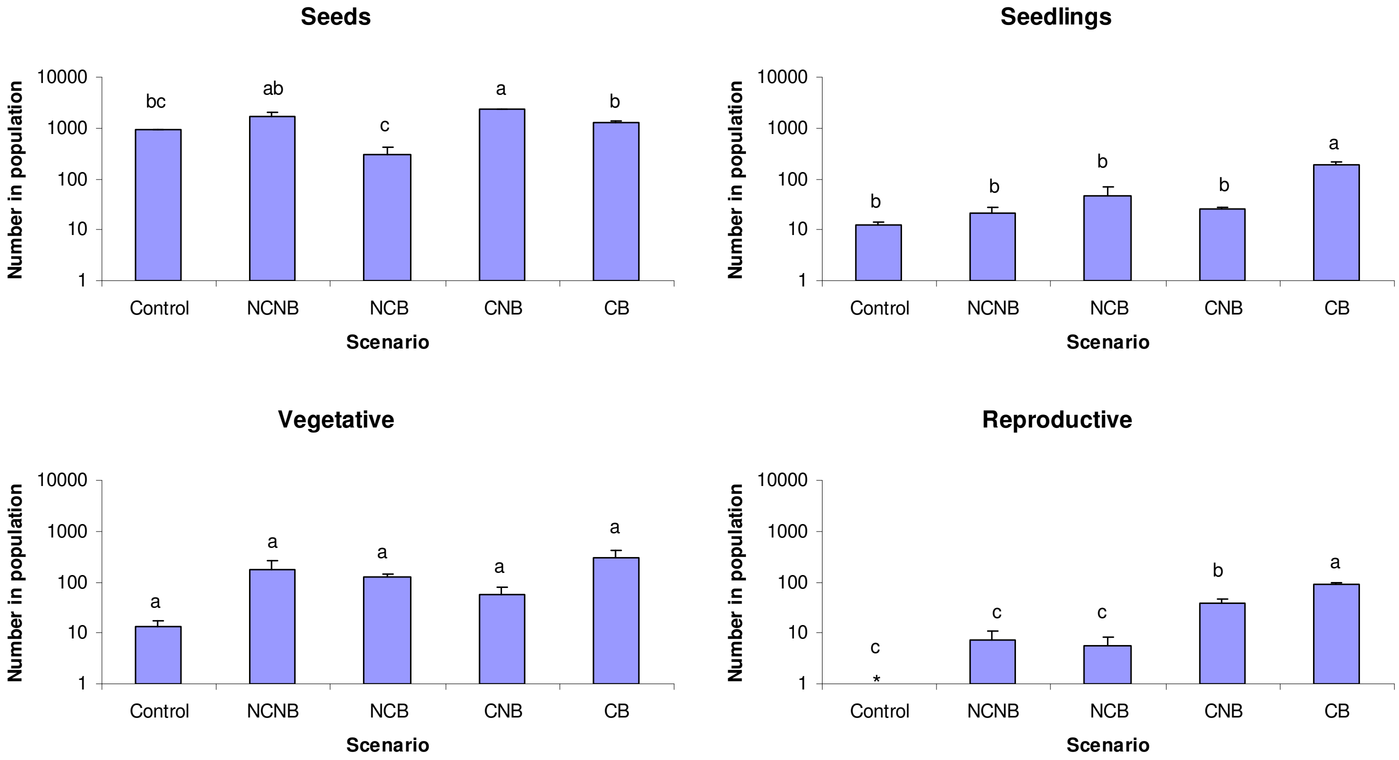


Figure 5.2. Fendler ceanothus population trajectories for five restoration management scenarios. Scenarios were Control: no overstory thinning, no protection from large herbivores, and no prescribed fire, NCNB: overstory thinning, no protection from large herbivores, no prescribed fire, NCB: overstory thinning, no protection from large herbivore, prescribed fire, CNB: overstory thinning, protection from large herbivores, no prescribed fire, CB: overstory thinning, protection from large herbivores, prescribed fire. Carrying capacity (K) was used in model simulations as a ceiling for population growth.

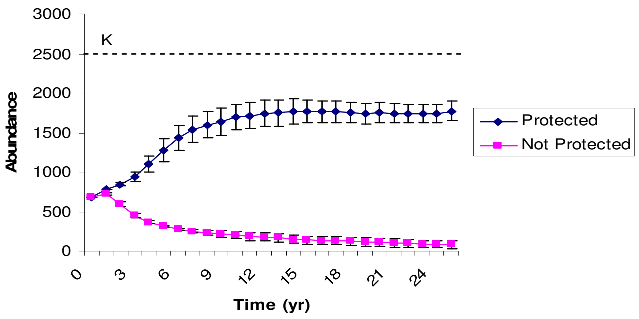

Seeds

Seedlings

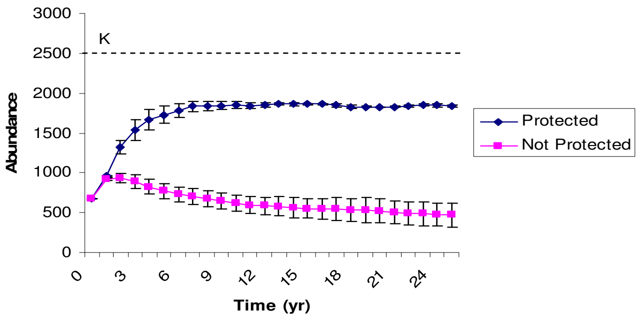
Vegetative

Reproductive

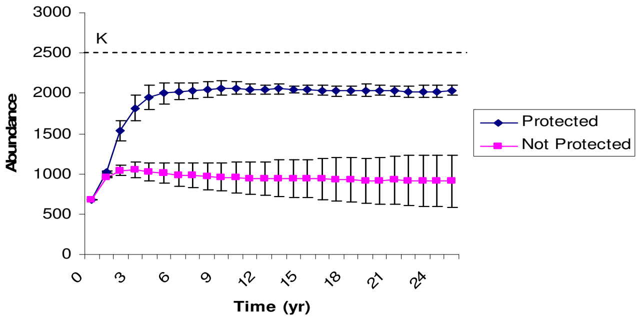
Figure 5.3. Life stage abundances for Fendler ceanothus in five restoration management scenarios. Scenarios were Control: no overstory thinning, no protection from large herbivores, and no prescribed fire, NCNB: overstory thinning, no protection from large herbivores, no prescribed fire, NCB: overstory thinning, no protection from large herbivore, prescribed fire, CNB: overstory thinning, protection from large herbivores, no prescribed fire, CB: overstory thinning, protection from large herbivores, prescribed fire.



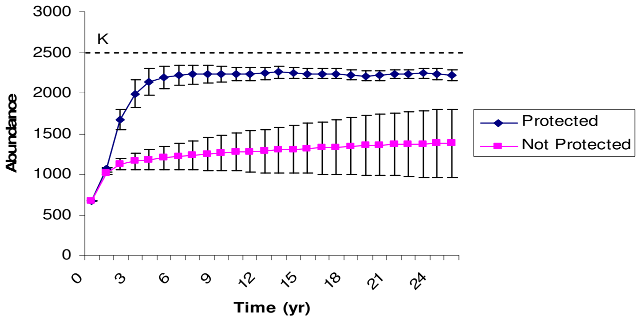
2-Year Fire Cycle



5-Year Fire Cycle



10-Year Fire Cycle



25-Year Fire Cycle

Figure 5.4. Fendler ceanothus population trajectories for four simulated fire frequencies.

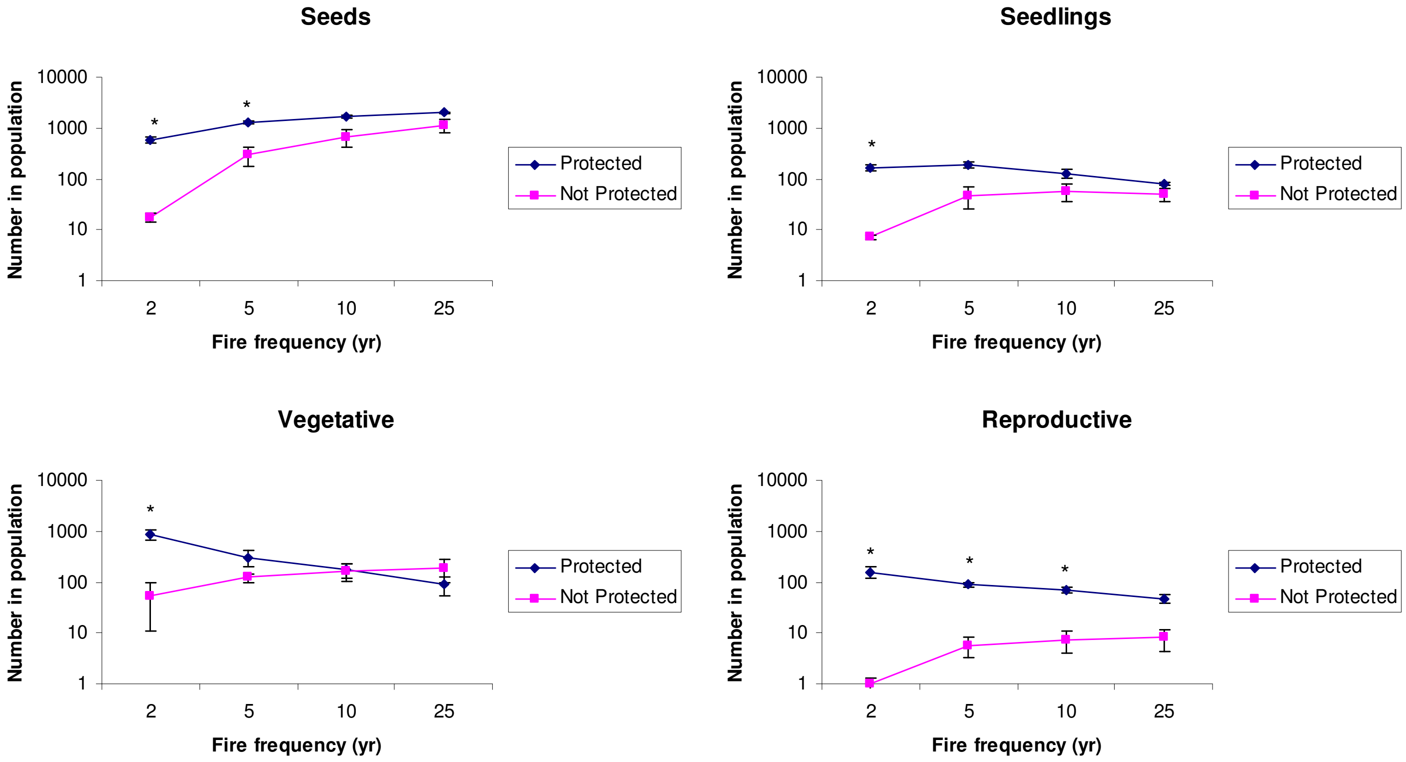


Figure 5.5. Life stage abundances for Fendler ceanothus populations in four simulated fire frequencies. Asterisks indicate statistically ($p<0.05$) different means between protected and not protected populations within fire frequencies.

Table 5.1. Life stage matrix constructed to model population dynamics of Fendler ceanothus.

| | Stage t | | | |
|---|---|---|---|---|
| Stage t+1 | Seed | Seedling | Vegetative | Reproductive |
| Seed | $P_1$ | - | - | $F_1$ |
| Seedling | $G_1$ | $P_2$ | - | - |
| Vegetative | - | $G_2$ | $P_3$ | $G_5$ |
| Reproductive | - | $G_4$ | $G_3$ | $P_4$ |

Table 5.2. Ranges of vital rates applied to models of Fendler ceanothus population dynamics in five ponderosa pine forest management scenarios1. Values represent average vital rates for four years of study (1999-2002). Ranges are from three replicates of each management scenario.

| | | | Stage | | Management |
|---|---|---|---|---|---|
| Stage (t+1) | Seed | Seedling | Vegetative | Reproductive | Scenario |
| Seed | 0.99 | - | - | 16.1 | Control |
| | 0.99 | - | - | 16.1 | NCNB |
| | 0.10 | - | - | 16.1 | NCB$^2$ |
| | 0.99 | - | - | 16.1 | CNB |
| | 0.10 | - | - | 16.1 | CB$^2$ |
| Seedling | 0.01 | 0.01 | - | - | Control |
| | 0.01 | 0.01-0.27 | - | - | NCNB |
| | 0.60 | 0.01 | - | - | NCB$^2$ |
| | 0.01 | 0.01-0.27 | - | - | CNB |
| | 0.60 | 0.01 | - | - | CB$^2$ |
| Vegetative | - | 0.061 | 0.81-0.90 | 0.01 | Control |
| | - | 0.061 | 0.97-1.12 | 0.01 | NCNB |
| | - | 0.061 | 0.57-1.25 | 0.01 | NCB$^2$ |
| | - | 0.061 | 1.11-1.37 | 0.01 | CNB |
| | - | 0.061 | 1.40-2.50 | 0.01 | CB$^2$ |
| Reproductive | - | 0.01 | 0.01 | 0.01 | Control |
| | - | 0.01 | 0.01-0.04 | 0.01-0.99 | NCNB |
| | - | 0.01 | 0.01 | 0.01 | NCB$^2$ |
| | - | 0.01 | 0.18-0.80 | 0.99 | CNB |
| | - | 0.01 | 0.01 | 0.01 | CB$^2$ |

[1] Management scenarios:

Control: No overstory thinning, no protection from large herbivores, and no prescribed fire

NCNB: Overstory thinning, no protection from large herbivores, no prescribed fire

NCB: Overstory thinning, no protection from large herbivore, prescribed fire

CNB: Overstory thinning, protection from large herbivores, no prescribed fire

CB: Overstory thinning, protection from large herbivores, prescribed fire

[2] For management scenarios that included prescribed fire, vital rates in year of fire occurrence (fire probability = 0.20) were adjusted to values shown in table. In years when fire did not occur, vital rates were same as scenarios that did not include prescribed fire.

Table 5.3. Mean values and standard error (SE) of finite rate of increase (λ) for 25-year simulations of management scenarios1. Prescribed fire (CB, NCB) did not affect values of λ. The same lowercase letters associated with values denote statistically similar means at alpha = 0.05.

| Mgt. Scenario | λ | SE |
|---|---|---|
| Control | 0.99b | 0.001 |
| Protected (CNB, CB) | 1.33a | 0.044 |
| Not Protected (NCNB, NCB) | 1.06b | 0.036 |

[1] Management scenarios:

Control: No overstory thinning, no protection from large herbivores, and no prescribed fire
NCNB: Overstory thinning, no protection from large herbivores, no prescribed fire
NCB: Overstory thinning, no protection from large herbivore, prescribed fire
CNB: Overstory thinning, protection from large herbivores, no prescribed fire
CB: Overstory thinning, protection from large herbivores, prescribed fire

Table 5.4. Mean characteristics of Fendler ceanothus populations under five simulated management scenarios1. The same lowercase letters read across management scenarios denote statistically similar means at alpha = 0.05.

| | Management Scenario | | | | |
|---|---|---|---|---|---|
| Characteristic | Control | NCNB | NCB | CNB | CB |
| Number in Population: | | | | | |
| Aerial stems[2] | 25.6b | 198.4b | 175.9b | 119.4b | 575.8a |
| Total[3] | 922.3bc | 1847.1ab | 468.2c | 2420.0a | 1832.4ab |
| Relative Abundance in Population (%): | | | | | |
| Seeds | 97.2a | 90.6a | 58.3b | 95.0a | 68.6b |
| Seedlings | 1.3b | 1.1b | 8.9a | 1.0b | 10.3a |
| Vegetative | 1.4b | 8.0ab | 31.8a | 2.4b | 16.3ab |
| Reproductive | <0.01c | 0.3bc | 1.1bc | 1.6b | 5.8a |
| Life Stage Diversity: | | | | | |
| Evenness[4] | 0.105b | 0.245b | 0.652a | 0.176b | 0.657a |

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[1] Management scenarios:

Control: No overstory thinning, no protection from large herbivores, and no prescribed fire

NCNB: Overstory thinning, no protection from large herbivores, no prescribed fire

NCB: Overstory thinning, no protection from large herbivore, prescribed fire

CNB: Overstory thinning, protection from large herbivores, no prescribed fire

CB: Overstory thinning, protection from large herbivores, prescribed fire

[2] Number of aerial stems in population - does not include seeds

[3] Number in population; total aerial stems plus seeds

[4] Evenness: J′ = H′/H′max (Hunter 1990)

Table 5.5. Elasticities for matrix elements by management scenario. Prescribed fire (NCB, CB) did not affect calculations of elasticities.

| | Stage | | | | |
|---|---|---|---|---|---|
| Stage (t+1) | Seed | Seedling | Vegetative | Reproductive | Management Scenario[1] |
| Seed | 0.983 | 0.000 | 0.000 | 0.003 | Control |
| | 0.326 | 0.000 | 0.000 | 0.005 | NCNB, NCB |
| | 0.068 | 0.000 | 0.000 | 0.020 | CNB, CB |
| Seedling | 0.003 | 0.001 | 0.000 | 0.000 | Control |
| | 0.005 | 0.001 | 0.000 | 0.000 | NCNB, NCB |
| | 0.020 | 0.004 | 0.000 | 0.000 | CNB, CB |
| Vegetative | 0.000 | 0.001 | 0.007 | 0.000 | Control |
| | 0.000 | 0.004 | 0.651 | 0.000 | NCNB, NCB |
| | 0.000 | 0.019 | 0.751 | 0.006 | CNB, CB |
| Reproductive | 0.000 | 0.002 | 0.001 | 0.000 | Control |
| | 0.000 | 0.001 | 0.005 | 0.002 | NCNB, NCB |
| | 0.000 | 0.000 | 0.026 | 0.085 | CNB, CB |

[1] Management scenarios:

Control: No overstory thinning, no protection from large herbivores, and no prescribed fire

NCNB: Overstory thinning, no protection from large herbivores, no prescribed fire

NCB: Overstory thinning, no protection from large herbivore, prescribed fire

CNB: Overstory thinning, protection from large herbivores, no prescribed fire

CB: Overstory thinning, protection from large herbivores, prescribed fire

Table 5.6. Mean characteristics of Fendler ceanothus populations protected and not protected from large herbivores under four simulated fire frequencies. The same lowercase letters, read for individual characteristics across fire frequencies, denote statistically similar means at alpha = 0.05.

| | Fire Frequency (years) | | | |
|---|---|---|---|---|
| Characteristic | 2 | 5 | 10 | 25 |
| ***Protected*** | | | | |
| Number in Population: | | | | |
| Aerial stems[1] | 1200.3a | 575.8b | 370.1bc | 215.1c |
| Total[2] | 1773.9b | 1832.4ab | 2035.8ab | 2222.2a |
| Relative Abundance in Population (%): | | | | |
| Seeds | 32.7c | 68.6b | 81.7ab | 90.2a |
| Seedlings | 9.6a | 10.3a | 6.1ab | 3.5b |
| Vegetative | 48.7a | 16.3b | 8.6b | 4.1b |
| Reproductive | 9.0a | 5.8ab | 3.5b | 2.1b |
| Life Stage Diversity: | | | | |
| Evenness[3] | 0.815a | 0.657ab | 0.470bc | 0.299c |
| ***Not Protected*** | | | | |
| Number in Population: | | | | |
| Aerial stems[1] | 63.1a | 175.7a | 233.2a | 242.6a |
| Total[2] | 80.6b | 468.2ab | 908.2a | 1378.7a |
| Relative Abundance in Population (%): | | | | |
| Seeds | 33.5b | 58.3ab | 73.8a | 83.6a |
| Seedlings | 15.3a | 8.9a | 6.1a | 3.7a |
| Vegetative | 49.6a | 31.8a | 19.4a | 12.2a |
| Reproductive | 1.6a | 1.1a | 0.7a | 0.2a |
| Life Stage Diversity: | | | | |
| Evenness[3] | 0.687a | 0.652a | 0.533a | 0.390a |

[1] Number of aerial stems in population - does not include seeds
[2] Number in population; total aerial stems plus seeds
[3] Evenness: J′ = H′/H′ max (Hunter 1990)

# CHAPTER 6: FUTURE RESEARCH NEEDS

As is often the case, the research conducted for this dissertation was effective in answering a predefined set of questions but, in the process, also uncovered questions beyond the scope of the project's objectives. Unanswered questions related to population ecology of Fendler ceanothus and study approaches that may be used to address these questions are discussed in this chapter. Studies addressing these questions would provide new information for land managers and forest ecologists and improve our understanding of Fendler ceanothus autecological characteristics and long-term population dynamics. Moreover, these studies could better elucidate linkages among species and increase understanding of processes occurring in ponderosa pine ecosystems undergoing ecological restoration treatments.

## Herbivory: Spatial and Temporal Considerations

Growth, stem recruitment, and flower production of Fendler ceanothus were negatively affected by large mammal herbivory in forest units thinned for ecological restoration (Chapter 2). Simulation modeling indicated that intense herbivory adversely impacted long-term population abundance of Fendler ceanothus, particularly when prescribed fire was applied frequently (Chapter 5). Herbivore effects on population growth appeared to be due to a combination of stem mortality and reduced flowering. Several spatial and temporal questions arose from these results.

**Q1: Are ungulate herbivory effects dependent on forest treatment unit size or distance to the forest edge?** The relatively small size (~14 ha) of the treated forest units provided a large amount of edge relative to interior habitat and were likely attractive to mule deer and elk (Patton 1974, Clary and Larson 1971, Severson and Medina 1983). Reynolds (1962) noted that mule deer use in natural forest openings was generally similar across a distance of about 200 m from the forest edge. From these results, he concluded that mule deer use in forest openings of about 14 ha would be evenly distributed. Both mule deer and elk use generally declined past distances greater than 200 m from the forest edge (Reynolds 1962). Thus, browse plants located toward the interior of treated forest areas larger than 14 ha may experience less herbivory than those near the forest edge. Less herbivory may allow plants to complete their life cycle or even enhance flower production (Paige and Whitham 1987, Throop and Fay 1999). Plants located farther from the forest edge may therefore function as sources for population growth and persistence.

Experiments to examine spatial patterns of herbivory and effects on plant life cycles and population dynamics could be tested at the Fort Valley study area. For example, the Greater Flagstaff Forests Partnership (GFFP) is continuing to treat forest areas near and adjacent to the experimental units described in this dissertation (GFFP 2003). These treatment areas create larger forest openings, which may be used to study spatial questions related to herbivory of Fendler ceanothus. Answers to these questions could help land mangers determine minimum size of treatment areas needed to reduce herbivore effects and promote development of Fendler ceanothus populations.

**Q2: Does intensity of herbivory decrease over time as understory communities develop?** Fendler ceanothus plants I examined in this dissertation research were remnants from depauperate understory communities existing before forest treatment. The studies were conducted during the early stages of understory recovery after treatments and, in the first two years after overstory thinning, understory community structure was similar between treated and untreated forest units (Korb 2001). Under these conditions, large herbivores may have been initially attracted to openings created by forest thinning and preferential selection of Fendler ceanothus plants may have resulted from low availability of other forage. In studies of mule deer diets in the Southwest, several other browse species have been reported to be higher in importance than Fendler ceanothus (Hungerford 1970, Neff 1974, Urness et al. 1975, McCulloch 1978). Although surprisingly few studies have documented elk diets in the Southwest, examination of rumen contents indicate similar patterns with respect to Fendler ceanothus use (i.e., elk select other plants more frequently) (Severson and Medina 1983). Highly preferred species, such as aspen (*Populus tremuloides* Michx.), mountain mahogany (*Cercocarpus* spp.), cliffrose (*Purshia* spp.), and oak (*Quercus* spp.) are infrequent or nonexistent at the Fort Valley study site. Thus, although Fendler ceanothus is an important browse plant, intense herbivory at my study site may reflect necessity rather than herbivore preference as other foods were scarce (e.g., McCulloch 1978).

Various research approaches might be used to address temporal questions related to herbivory on Fendler ceanothus. The most obvious of these would be to study herbivore effects over a longer (e.g., more than four years) period of time and test relationships between herbivory and understory community characteristics. Alternatively, one might introduce preferred browse plants in arrays of varying density and diversity near Fendler ceanothus plants in order to test selection patterns and resulting effects on growth and reproduction. Information provided by these studies could help land mangers determine time frames required for protection of key browse species if these actions were deemed necessary. Additionally, such information could alert land managers to habitat deficiencies and supplemental treatments needed, such as seeding or transplanting of important browse species, to support local populations of large ungulate herbivores.

## Herbivory: Indirect Effects

Reduced flowering was found in all years (1999-2002) for Fendler ceanothus plants not protected from large herbivores (Chapter 3). For stems that were reproductive, parasitism of seeds by the chalcidoid wasp, *Eurytoma squamosa*, accounted for varying amounts of ovule loss and over two-thirds of the developed seeds produced in a given year could be eaten by this invertebrate. Experiments of post-dispersal predation indicated that other organisms, such as birds and rodents, could remove about one-quarter of the annual cohort of seeds dispersed to the forest floor. These interactions raise questions regarding direct and indirect competition among various species for Fendler ceanothus reproductive structures.

**Q3: What are the effects of intense ungulate herbivory on food web dynamics?** Research in other ecosystems has indicated that activity of large herbivores such as deer and elk can have significant effects on invertebrate communities (Baines et al. 1994, Rooney 2001, Stewart 2001). These effects can be in the form of direct competition for plant resources such as biomass, pollen, nectar, or seeds (e.g., Baines et al. 1994). Interactions can also impact species composition in plant communities, predator-prey relationships, or microclimate conditions (e.g., Rooney 2001). Changes in invertebrate communities can further cascade through higher trophic levels in the ecosystem (Stewart 2001).

Studies to examine effects of herbivory on invertebrate communities could be easily conducted on experimental plots established for research presented in this dissertation. Various sampling techniques would likely be needed in order to gain a comprehensive inventory of species associated with Fendler ceanothus plants. All sampling techniques, when used independent of complimentary methods, are likely to miss some invertebrate species due to the great variety of behavioral characteristics found in insect communities (Borror et al. 1989). Other temporal constraints (e.g., ontological, seasonal, diurnal, etc.) affect the compositional fraction of insect communities sampled with any given technique (Southwood and Henderson 2000). In northern Arizona, Rambo and Faeth (1999) sampled insect communities inside and outside grazing exclosures using sweep netting and found greater insect abundance associated with areas that had been excluded from livestock and wild ungulate use. This technique was also used successfully to sample insects associated with flowers, fruit and seeds of *Ceanothus sanguineus* (Furniss et al. 1978). Other techniques that may be used to increase sampling depth for invertebrates associated with Fendler ceanothus include seed dissection and rearing insects from tissues such as galls formed on leaves and stems.

Information provided by such studies is particularly relevant for restoration programs attempting to increase sources of native biodiversity on degraded sites. Additionally, basic information can be gained related to species interactions and food web structure. This type of information is exemplified by initial investigations of seed parasitism that revealed a close linkage between Fendler ceanothus and *Eurytoma* *squamosa*, a species not previously reported in Arizona or associated with this host species (Huffman 2002).

## Seed Production

In studies of seed production, variation appeared to be related to stem size and annual precipitation (Chapter 3). Although seed production varied substantially, the proportion of seeds that were undeveloped varied relatively little and accounted for 50-58% of the total yield from fruits in the two years when samples were collected. Little is known regarding causes of ovule failure for Fendler ceanothus. Fruit predation and seed parasitism are important factors to which ovule loss can be attributed; however, further research is needed to identify the importance of pollinators and abiotic resources in determining fruit and seed development (e.g., Stephenson 1981).

**Q4: Are Fendler ceanothus plants pollinator-limited at the Fort Valley restoration site?** Few studies have been undertaken to describe pollinator distribution in southwestern ponderosa pine forests or invertebrate responses to ecological restoration treatments. Waltz and Covington (2001) showed that butterfly (Lepidoptera) species richness and abundance increased after restoration treatments comprised of thinning and burning. Further, microclimatic changes associated with ponderosa pine restoration treatments increase activity of butterflies (Meyer and Sisk 2001). Information concerning restoration treatment effects on abundance and richness of other pollinators, such as species of Hymenoptera, Diptera, and Coleoptera, is presently lacking.

Experiments could be designed to examine relative importance of pollination versus resources in affecting Fendler ceanothus seed production. These studies could test treatment combinations of pollinator exclusion, hand pollination, and supplementation of resources such as water and nutrients. Information gained from such research could help restoration practitioners identify constraints to Fendler ceanothus population growth as well as general processes that may be lacking on restoration sites. Assessment of mutualistic interactions is critically important in evaluation of restoration success (e.g., Korb et al. 2003).

## Regeneration Niche

Fendler ceanothus seedlings emerged on 46-55% of the plots that were experimentally burned at the Fort Valley study site in 2000 and 2001, respectively (Chapter 4). No seedlings emerged in any of the four years on plots that were not burned. Seedling emergence was related to depth of forest floor consumed in burning and seedlings occurred most frequently on plots with moderate burn depths (3.5-5.0 cm). Extreme drought in 2002 made analysis of microsite effects on seedling survival difficult; mortality of seedlings that emerged on sample plots in 2001 averaged 89%. Although drought (i.e., soil moisture) obviously plays a large role in affecting seedling survival, other microsite characteristics may assume pivotal roles in years of adequate precipitation. Presently, microsite characteristics that affect survival of Fendler ceanothus are not known.

**Q5: What microsite factors are important in affecting Fendler ceanothus seedling establishment?** Grubb (1977) described the importance of species' "regeneration niches" in determining diversity and persistence in plant communities. A species' regeneration niche includes important influences on seedling emergence and survival such as microclimatic characteristics (e.g., light, temperature, moisture), substrate, and predators. Similarly, Harper (1977) described “safe sites” as microsites with conditions conducive to germination and establishment and thus lacking mortality agents. For some species, narrow environmental parameters associated with germination and establishment suggests high levels of specialization (e.g., Harmon 1987, Huffman et al. 1994, Keeley and Fotheringham 1998). This in turn suggests that seed germination and establishment characteristics are commonly traits that experience a high degree of selection pressure (Silvertown and Charlesworth 2001). Little information is presently available concerning seedling establishment of species common in ponderosa pine forests of the Southwest. Korb (2001) found that emergence of several grass and forb species was higher on native soil than on soils that experienced severe heat from burning of logging slash. Vose and White (1987) noted emergence of Fendler ceanothus seedlings after prescribed fire in northern Arizona but did not present data on seedling survival.

Studies to examine conditions influencing Fendler ceanothus seedling survival could be conducted using several approaches. Field studies could be designed such that Fendler ceanothus seeds (pretreated – see Chapter 3) could be sowed on various microsites. Microsite characteristics that might be varied include overstory density and substrate conditions. Since seeds of this species have higher rates of germination when they are exposed to heat such as that from fire (Chapter 3), microsite conditions that include ash and charred litter from forest floor burning or mineral soil substrate might be of particular interest. Controlled experiments to examine environmental conditions that influence survival could be conducted in a greenhouse or outdoor nursery beds.

Information regarding Fendler ceanothus seedling establishment would help land managers predict development of local populations on sites for which environmental conditions are known. In turn, these predictions could provide insight regarding understory community development and long-term patterns.

## Mechanisms of Resprouting

Mortality of Fendler ceanothus plants after fire was positively related to depth of forest floor consumed in burning. Probability of resprouting was near 1.0 when less than about 3 cm of forest floor was consumed during burning. Resprouting decreased to zero when burn depth on plots was 5 cm or greater (Chapter 4). Fire converted patches of Fendler ceanothus stem from all-aged to even-aged. Resprouts on plots protected from large herbivores were typically long and unbranched. This research suggested that burn severity can be high when prescribed fire is applied in forests having over 100 years of forest floor fuel accumulation (Fulé et al. 1997). Also, vigorous resprouting after fire allows Fendler ceanothus to rapidly reoccupy space and quickly regain reproductive potential. Greater understanding of Fendler Ceanothus response to disturbance could be gained by posing questions related to pre-burn conditions that may influence resprouting.

**Q6: What site and/or plant characteristics determine production of new sprouts after fire?** Little research has been done to quantify resprouting of Fendler ceanothus after fire. Pearson et al. (1972) reported increases in abundance of this species after wildfire but did not describe whether changes were due to seedling emergence or resprouting. Vose and White (1991) found vigorous resprouting of Fendler ceanothus after prescribed fire but no attempt was made to correlate response to pre-burn plant characteristics. In other species, resprouting can be related to plant age, size, and carbohydrate reserves in belowground structures (Zasada et al. 1994, Landhäusser and Lieffers 1997, Hodgkinson 1998, Bellingham and Sparrow 2000).

Studies to examine relationships between pre-burn plant characteristics and resprouting after fire might be simple to design. In the field, a range of plant sizes and ages could be selected and fire behavior could be controlled by limiting the amount of fuel consumed during burning. To examine effects of available resources on repsprouting, a subset of the selected plants could be restricted in access to light (e.g., by using shade cloth) or moisture. Samples of belowground tissue could be carefully collected before burning to quantify carbohydrate reserves in belowground branches or root crowns. More complicated experimental designs would include variation in season of burn to determine phenological effects that might interact with resource availability and plant age.

Information concerning mechanisms that control resprouting of Fendler ceanothus could help land managers formulate restoration burns plans that encourage population growth through vegetative recruitment. Additionally, better understanding of resprouting mechanisms for Fendler ceanothus could help generate hypotheses related to recovery strategies for other species in these plant communities.

## Population Dynamics

Simulated growth of Fendler ceanothus populations was significantly affected by management alternative; growth was highest for populations burned and protected from large herbivores in thinned forest units (Chapter 5). These populations had relatively even distribution of life stages and represented the greatest potential for persistence and adaptation to environmental changes. Size of populations that were not protected from herbivores and burned frequently (e.g., every 2-5 years) declined dramatically. Herbivory dramatically lowered probability of stem transition to the reproductive stage and this disruption of Fendler ceanothus' life cycle inhibited population recovery after fire.

In simulation models, one-year-old Fendler ceanothus seedlings were assumed to suffer high rates of mortality ($P_2 = 0.01$; Chapter 5) when fire occurred. Seedlings could potentially transition to a vegetative adult stage ($G_2$) in their second growing season and to reproductive adults ($G_3$) in their third year. These assumptions were based on limited observations of Fendler ceanothus seedlings in greenhouse and field studies as well as research of *Ceanothus integerrimus* (McDonald et al. 1998), a species common in mixed conifer forests of California. Faster or slower rates of transition to a reproductive stage may affect population structure and long-term dynamics.

**Q7: What is the maximum rate of transition from seedling to reproductive life stage?** McDonald et al. (1998) found that out-planted seedlings of *C. integerrimus* produced multiple stems from incipient root crowns during their first growing season. By the third year, 42% of the plants produced flowers. Large herbivores were excluded from the study site, most competing vegetation was removed, and seedlings were given supplemental water and nutrients during the first six weeks of the study. Thus, these results likely represent the maximum rate at which young plants of this species develop adult characteristics. For salal (*Gaultheria shallon* Pursh.), a clonal shrub species of the Pacific Northwest, production of rhizomes and vegetative expansion can occur within about six years of seedling emergence (Huffman et al. 1994). Flowering of this species can occur within four years of emergence (Bunnell 1990). Such information is not available for Fendler ceanothus.

Field and laboratory studies could be designed to test the maximum rate (i.e. minimum age) at which young Fendler ceanothus plants could attain adult characteristics such as root crowns, flowers, and the ability to expand vegetatively. Seedlings could be grown in nursery beds under controlled conditions and effects of constraints to development, such as resource availability, herbivory, or disturbance such as fire, could be assessed. These results could be compared with those from studies of field grown seedlings to generate further hypotheses concerning constraints and rate of plant development. Information from this research could help land managers better predict changes and growth of Fendler ceanothus populations given known environmental conditions. Monitoring plan development and testing predictions related to population dynamics could be used to evaluate management strategies.

Another assumption used in simulation models was related to density-dependent effects on vital rates. A “ceiling” carrying capacity (K) was set at 2500 individuals (aerial stems and seeds), roughly four-times the initial population size (Chapter 5). The value for K and the type of density-dependence were arbitrarily selected since no information was available on true density-dependent relationships for Fendler ceanothus. Further, since forest units were in early stages of development, population growth was assumed to be unaffected by interspecific competition. Potential for Fendler ceanothus density in these forests and intra-specific density regulation mechanisms are not known.

**Q8: Do Fendler ceanothus populations exhibit density-dependence as population size approaches carrying capacity?** Maximum aerial stem density on any sample plot studied was 104 per square meter (Chapter 4). This represented 1.04 x $10^6$ stems per hectare. Whether or not this was a "crowded" condition is not known; longer-term data are needed to assess stem recruitment in this patch. Crowding in populations can affect plant growth, which in turn can affect size, mortality, and fecundity (Silvertown and Charlesworth 2001). Further, whether the stem density observed represented one or more clones (or clonal fragments) is not known. It is generally thought that intra-clonal competition is rare and cooperative integration among ramets might be typical for clonal plants, even in stressful environments (Pitelka and Ashman 1985). Thus, whether an stem populations are comprised of one or several clones may affect maximum density and density-dependent processes. Information concerning maximum densities for other understory species in ponderosa pine forests is not available.

Studies to determine maximum density and density-dependent effects on population dynamics are most easily done by experimentally controlling population density (Silvertown and Charlesworth 2001). Fendler ceanothus seedlings could be planted in a common garden at different densities and monitored over a period of years. A common garden study would allow control over other, density-independent processes that affect population growth. Further, experiments could be designed to test maximum stem density attained by individual clones versus clonal assemblages. Information from these studies could help land managers determine potential forage and habitat resources for wildlife as well as assess condition of local Fendler ceanothus populations.

Information concerning density dependent effect could also help ecologists develop more precise population models and better predict population dynamics.

## Conclusion

The research presented in this dissertation answered several questions related to Fendler ceanothus autecology and population dynamics in ponderosa pine forests treated for ecological restoration. Several new questions were generated from this research and most could be addressed experimentally. Answers to these questions would increase our basic understanding of Fendler ceanothus as well as provide details concerning processes important in ponderosa pine ecosystems. Information generated by these studies would help land managers make more informed decisions and evaluate techniques designed to restore ecological diversity to understory plant communities in these forests.

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