

**PONDEROSA PINE DISPERSAL AND RECRUITMENT:
THE ROLE OF SEED-CACHING RODENTS**

By Lee Ann Compton

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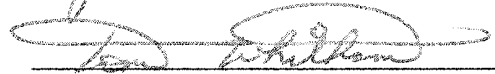
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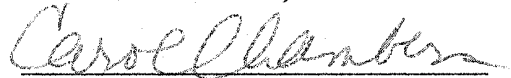
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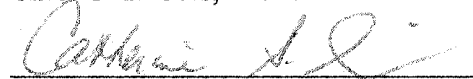
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ABSTRACT

PINE DISPERSAL AND RECRUITMENT: THE ROLE OF SEED-CACHING RODENTS

Lee Ann Compton

Seed-caching rodents are important agents of dispersal for many plant species and understanding the factors that determine spatial patterns of seed dispersal are critical for understanding plant recruitment and demographics. Although ponderosa pine has traditionally been viewed as a wind dispersed pine, I found that rodent seed-caching behavior could be advantageous to ponderosa pine for several reasons. First, rodents cached seeds in contact with mineral soil which enhances germination. Second, rodents covered caches with a layer of litter that may protect seedlings from mortality due to frost heaving by acting as insulation. Third, rodents doubled the dispersal distance (compared to wind) of ponderosa pine seeds which could increase escape from distance-dependent mortality, increase the probability of colonizing open habitats, and increase the probability that seeds arrive in suitable microsites. Finally, rodents non-randomly placed seed caches near rocks, where seedlings had higher survival, and near downed wood, where seedlings may benefit from fire-resistant "hot beds" following surface burns. Taken together these data suggest that rodents may act as directed dispersers of ponderosa pine seed and could enhance germination and recruitment above background levels.

Fire is a key disturbance process in the ponderosa pine forests of the southwestern United States but little is known about how fire impact seed-caching behavior of rodents. Using seed-dish lines and exclosures that selectively excluded birds and rodents, I

documented that seed removal rates were two times higher in burned areas than in unburned areas and that most removal could be attributed to rodents. I then followed the fate of radioactively (Scandium-46) labeled seeds placed at the boundary between burned and unburned habitat and found that 1) rodents preferentially moved seeds into burned areas and 2) seed caches were preferentially placed in charred substrate within the burned areas. Finally, I experimentally documented that seed caches lasted longer when placed in charred substrate, suggesting that burned substrate affected the ability of rodents to find caches that were not their own. The net movement of seeds into burned areas and into charred substrate, where caches have a higher potential for germination and survival, suggests that rodents could have a positive influence on post-fire ponderosa pine regeneration.

Finally, I examined patterns of seedling establishment and survivorship of pinyon pine in microsites that included open areas, areas adjacent to tree and shrub canopies and under the canopies of trees and shrubs for a cohort of seedling produced during the mast year of 1999 in northern Arizona. I found that seedlings were more prevalent under tree canopies than expected based on the abundance of these microsites and less prevalent in other microsites. The number of seedlings under juniper increased relative to availability over time while the number under pinyon decreased, suggesting enhanced survivorship in the microsite under juniper. I tested several hypotheses that could potentially explain differences using both marked and collected subsets of seedlings. Although survivorship was significantly higher under juniper nurses (44%) compared to pinyon (14%), no significant differences among surviving seedling in shoot length, shoot/root ratio, number of lateral roots, or mycorrhizal development were found. In the pinyon-juniper

woodlands of northern Arizona, junipers appear to be an important nurse for pinyon during early seedling development. Rodent dispersal of seeds to these sites could act as a form of directed dispersal.

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I would like to extend thanks to my committee for their valuable contributions to this work. I am thankful to Dr. Kitty Gehring for her enormous contribution to chapter four of this dissertation from its conception through design and completion and for her willingness to join the committee later in the process and provide excellent advice and critical review of the project. I thank Dr. Carol Chambers for her support throughout the entire dissertation including her willingness to stay on the committee when the original project had to be abandoned. Her additions to the design of this project were critical and her leadership as a successful woman in science was appreciated. Dr. Tom Whitham was instrumental in shaping my view of ecology through multiple courses and his interaction on this project. A special thanks to Dr. Syl Allred for bringing me to NAU and for supporting me in numerous ways throughout the process. Dr. Allred's commitment to teaching and mentorship has been inspirational to me.

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PREFACE

This dissertation is organized as three chapters representing three manuscripts prepared for publication. They appear in the appropriate format for the journal they have been or in which they will be submitted. Please excuse any redundancy this format provides. The three chapters, their respective titles and outlines for submission are listed below:

Chapter 2..... Seed caching behavior of nocturnal and diurnal rodents in southwestern ponderosa pine forests.

To be submitted to Journal of Mammalogy.

Chapter 3..... Effect of nurse type on pinyon pine (*Pinus edulis*) seedling germination, survival, growth and mycorrhizal relationships.

To be submitted to Southwest Naturalist.

Chapter 4..... Effect of fire on seed removal and seed caching behavior of rodents in ponderosa pine forests.

To be submitted to Forest Ecology and Management.

CHAPTER 1

INTRODUCTION

Understanding the factors that determine spatial patterns of seed dispersal are critical for understanding plant recruitment and demographics (Nathan and Muller-Landau 2000). Animals may play an important role in creating the spatial pattern of seeds by dispersing seeds directly from the plant (primary dispersal) or by moving seeds to new locations after initial dispersal by some other mechanism (secondary dispersal). Several species of birds and mammals store seeds in shallow, scattered caches and may act as agents of either primary or secondary seed dispersal when those caches are not recovered (Vander Wall 1992). Because of the high cost of seeds eaten by these animals, their effectiveness as dispersers depends upon the advantage seeds experience by being placed in those microsites animals choose as cache sites. Plant dependence on animal-chosen microsites will depend, in part, on the abiotic challenges seeds and seedlings face.

Recent studies have indicated that tree species that traditionally have been viewed as "wind-dispersed" may be strongly impacted by seed-caching rodents (Vander Wall 2002). In chapter two, I address the interaction of rodents with ponderosa pine (*Pinus ponderosa*), the dominant wind-dispersed pine of northern Arizona, and compare the fate of seeds initially removed by either nocturnal or diurnal rodents in terms of cache spatial distribution, cache characteristics and the spatial distribution of naturally occurring seedlings. Using scandium-46 I was able to follow the fate of seeds handled by rodents and examine the pattern of dispersal and specific caching behavior. Several lines of evidence suggest that ponderosa pine, occurring in the arid southwest, may be microsite limited (Biswell et al. 1953, Heidmann 1974, Pearson 1950). This plant animal

interaction could be particularly important if the microsites selected for caching are favorable for ponderosa pine germination. This chapter specifically addresses three aspects of the interactions between seed caching rodents and ponderosa pine regeneration: 1) seed fate and rodent caching behavior, 2) microsites selection, and 3) comparison of nocturnal and diurnal rodent caching behavior.

In chapter three, I expand the study of rodent-ponderosa pine interactions to investigate the role of fire. Low intensity ground fires have been hypothesized to have been an important ecological factor shaping ponderosa pine forests in the past, and recent forest management based on ecological restoration have emphasized the re-introduction of fire after a century of fire suppression (Bailey and Covington 2002). Given this history and the current practices of prescribed burning, it is important to understand how fire affects the potential role of seed caching rodent as dispersers. This chapter specifically addresses 1) the effect of fire on seed removal by rodents, 2) the movement of seeds across a burn boundary, and 3) the effect of burned substrate on caching a pilfering behavior.

In chapter four of this dissertation, I shift focus to a different vertebrate-dispersed pine species, pinyon pine (*Pinus edulis*). Pinyon pine is highly dependent on vertebrates for dispersal and this plant-animal interaction effects the arrival of seed to microsites. However, because pinyon seedlings require nurses for successful germination (Charters 1997), the suitability of the microsite is likely a result of the plant-plant interaction. Because nurse plant relations are often a balance between facilitation and competition, different species of nurse plant could have different impacts on seedling germination and survival. Differences in canopy structure of the nurses, root architecture (Callaway et al.

1991) and mycorrhizal symbionts (Amaranthus et al. 1990) could all impact the relative effect of the nurse. This study took advantage of a cohort of seedlings produced from a mast seed crop that occurred in northern Arizona in 1999, to examine how arrival under the canopies of different species of nurse plants could potentially affect the germination, early survival, growth and mycorrhizal relationships of pinyon pine seedlings.

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CHAPTER 2

SEED-CACHING BEHAVIOR OF NOCTURNAL AND DIURNAL RODENTS IN SOUTHWESTERN PONDEROSA PINE FORESTS

ABSTRACT

Seed caching vertebrates have been shown to be important agents of dispersal for many plant species including some “wind-dispersed” pines. However, how rodents influence seed dispersal of ponderosa pine in the southwestern United States remains relatively unknown. I address three aspects of the interactions between seed caching rodents and ponderosa pine regeneration: 1) seed fate and rodent caching behavior, 2) microsite selection, and 3) comparison of nocturnal and diurnal rodent caching behavior. I found that rodents a) doubled the dispersal distance of ponderosa pine seeds compared to wind, b) placed seeds in contact with mineral soil, and c) covered the seeds with a layer of litter, all of which are likely to enhance seed germination and seedling survivorship. Additionally, rodents non-randomly placed seeds near rocks, where seedlings showed higher survivorship, and near downed wood, where seedlings may be protected after fires. Finally, seeds initially cached by nocturnal and diurnal cachers differed in cache depth and seed number. Therefore, these two groups likely have differential impacts on patterns of plant recruitment. Although these classes of rodents generally occur sympatrically, abiotic factors such as fire may effect their populations or behavior differently, in turn altering dispersal in the system. Overall, rodents altered the spatial pattern of seed distribution and may serve as directed dispersers by non-randomly selecting cache sites that enhance germination. Taken together, these findings suggest that the interaction of rodent seed cachers and ponderosa pine is an important part of the process of natural regeneration in forests.

INTRODUCTION

A fundamental goal of plant ecology is to understand effects of specific seed dispersers on plant fitness (Wenny and Levey 1998). Several species of birds and mammals store seeds in shallow, scattered caches and have been shown to be important agents of dispersal for plants (Vander Wall 1995a, Adler and Kestell 1998, Forget et al. 1999, Stapanian and Smith 1978). Even those plant species with seeds apparently adapted for other dispersal modes, such as many “wind-dispersed” pines, may have spatial patterns of seed and seedling distribution altered through the action of seed caching rodents (Vander Wall 1992, 2003).

Ponderosa pine (*Pinus ponderosa*) is a tree species with relatively small, winged seeds that traditionally has been viewed as primarily wind-dispersed. Rodents have been shown to cache ponderosa pine seeds in a mixed conifer forest in Nevada where ponderosa pine did not naturally occur but its seed was introduced as a novel food resource (Vander Wall 2003). However, how rodents influence seed dispersal of this tree species in other areas, especially in the southwestern United States, remains relatively unknown. Ponderosa pine forests of the southwest occupy relatively arid areas and evolved with short (2-8 year) fire intervals (Fulé et al. 1996). Under these conditions, ponderosa pine faces several unique challenges to regeneration. This study focused on the interaction of seed caching rodents and ponderosa pine regeneration in Northern Arizona. This paper addresses three important aspects of that interaction: seed fate and rodent caching behavior, microsite selection, and comparison of nocturnal and diurnal rodent caching behavior.

Scatter-hoarding rodents can return to and redistribute their caches multiple times and cache characteristics can potentially change through this process. For example, Vander Wall (1995b) documented that yellow pine chipmunks (*Tamias amoenus*) re-cached about 30% of the antelope bitterbrush (*Purshia tridentata*) seeds that they recovered from primary caches and that the secondary and tertiary caches were moved further from the source and had fewer number of seeds per cache. More recently, Vander Wall and Joyner (1998) demonstrated that yellow pine chipmunks move Jeffrey pine (*Pinus jeffreyi*) seeds up to five times and that 31% (4 of 13) of these quintic (fifth order) caches germinated. These studies demonstrate that cache management can influence the

ultimate microsite that germinating seeds experience. Using Scandium-46 (a radioactive isotope), I was able to follow the fate of seeds from removal through several subsequent movements during this study.

The second objective of this study was to document the microsites rodents selected as cache sites to determine the potential for these animals to place seeds in sites suitable for germination. Studies in the early 1900's identified several challenges for ponderosa pine regeneration that suggest that these plants could be microsite limited. Seedlings must grow to a significant size to survive low-intensity fires, seedlings must obtain sufficient water as their root systems are developing, and they must avoid frost heaving and herbivory (Biswell et al. 1953, Heidmann 1974, Pearson 1950). Microsites that offer these characteristics are likely to be limiting, and movement to them via rodent seed-cachers could enhance seedling recruitment. I specifically documented the distribution of cache sites relative to environmental features such as downed wood, rocks and mature trees (all structures that could ultimately affect seedling survival), and compared cache spatial distribution to that of naturally occurring ponderosa pine seedlings.

Much of the previous work investigating the role of seed caching rodents has examined the rodent community as a whole (Abbott and Quink 1969, Edwards and Crawley 1999, Forget 1990, Vander Wall 1992, 1997, 2003, West 1968). The design of this study allowed me to independently examine the fate of seeds removed by nocturnal and diurnal cachers and determine if differences in seed fate resulted. The nocturnal rodent community in ponderosa pine forests includes primarily two species of *Peromyscus* (*P. maniculatus* and *P. boylii*). *Peromyscus* species rely heavily on seeds, including conifer seeds, as a food source (Smith and Aldous 1947, Williams 1959) and have been known to cache those seeds (Sanchez and Reichman 1987, Vander Wall et al. 2003, Vander Wall 2003). *P. boylii* has been shown to cache pinyon pine seeds (Pearson and Theimer, *in press*, Vander Wall 1997) but no studies have examined this species' interaction with ponderosa pine seeds. *P. maniculatus* has been hypothesized to act primarily as a seed predator by hoarding the majority of its seeds in deep larders where seeds are unlikely to germinate (Vander Wall 1992). However, field experiments in Nevada have shown that *P. maniculatus* scatter-hoard Jeffrey pine seeds in shallow (2-12

mm deep) caches of 1-2 seeds (Vander Wall 2000). The diurnal rodent seed-caching community of southwestern ponderosa pine forests includes three species. Two species of *Tamias* (*T. cinereicollis* and *T. dorsalis*) are known to rely heavily on seeds (Hart 1971). Vander Wall (2003) demonstrated that a closely related species (*T. amoenus*) cached several species of seeds, including conifer seeds, and that they contributed strongly to plant establishment. However, no studies have followed the fate of ponderosa pine seeds handled by *T. cinereicollis* and *T. dorsalis* or described their cache characteristics. Elsewhere, golden-mantled ground squirrels (*Spermophilus lateralis*) cached large numbers of seeds in deep caches where they were unlikely to germinate and thus probably served primarily as a seed predator (Vander Wall 1992). Because any one, or several, of these species of rodents may interact with seeds in the ponderosa pine system, it is important to understand similarities and differences among species in seed handling behaviors. I was interested in determining the characteristics of caches made by these two classes of rodent seed-cachers. Based on home range sizes, I predicted the diurnal species, *Tamias* and *Spermophilus*, would move seeds a greater distance from the source compared to the nocturnal, *Peromyscus*, species. Additionally, I predicted the diurnal species would store a greater number of seeds per cache and at greater depths because of their digging morphology and larger body size.

MATERIALS AND METHODS

Study Site and Rodent Community

This study was conducted in a monodominant ponderosa pine forest located approximately 35 miles south of Flagstaff, Arizona near Morman Lake. Understory perennial grasses included; Arizona fescue (*Festuca arizonicus*), mountain muhly (*Muhlenbergia montana*), and squirrel tail (*Sitanion hystrix*). Herbaceous dicots included; silver lupine (*Lupinus argenteus*), American vetch (*Vicia americana*), and common thistle (*Cirsium wheeleri*) (Mast 1998). Ponderosa pine in the area produced a mast crop in 2001 and the majority of the seeds used in these experiments were collected from trees less than 10 kilometers from the study site. I selected two forested areas that were separated by an open meadow approximately 200 m wide. Each site had a mixture of large yellow pines (dbh > 30cm) and areas of small diameter (dbh < 20 cm) trees.

Both areas were similar in canopy structure and understory vegetation and both sites had a slight east-west slope.

Thirty Sherman live traps baited with rolled oats and bird seed were placed across each of the sites described above in May, 2002. Traps were opened for 6 consecutive nights and 3 days. Trapping was repeated for 3 nights just prior to offering the seed source in July. Results indicated that *P. maniculatus*, *P. boylii*, *T. cinereicollis* and *T. dorsalis* were present at both sites. On at least one night, a maximum of 7 unique individuals were captured on each site suggesting that multiple animals could potentially interact with the seeds. Both video and still cameras, triggered by an infra-red sensor (Trailmaster, Inc), were also used to confirm the identity of animals that interacted with the seeds.

Seed Fate and Caching Behavior

To follow the fate of seeds handled by rodents, ponderosa pine seeds were labeled with Scandium-46, a radioactive isotope that emits high-energy gamma radiation (1.12 x 10⁶ electron volts) and has a short half-life of 84.5 days. The decay product, titanium-46, is stable and inert. Additionally, seeds were uniquely numbered in order to follow multiple movements of individual seeds. I tracked movements of these seeds after rodents had handled them using a portable Geiger counter. The signal produced by labeled seeds could be detected from about 50 cm through the air and 30 cm through the soil. In addition to finding seeds buried in caches, I was also able to locate discarded shells of eaten seeds.

In July 2002, ponderosa pine seeds were placed at the base of two simulated source trees within each of two 60 x 90 meter grids. Source trees were mature ponderosa pine trees with DBH \geq 50cm. Seeds were placed in wire mesh cages to exclude birds and ensure that seeds were only taken by the rodent community. Grids were separated by at least 200 m of open field to assure that no single animal influenced more than one grid. Because I was interested in examining difference between the handling behaviors of nocturnal cachers and diurnal cachers, I monitored seed removal from each source tree at dawn and dusk and noted the individual identity numbers of seeds that had been

removed. I continued to put out seeds and monitor them until at least 50 seeds were removed from each source tree at each grid in both nocturnal and diurnal periods.

A complete search of the grid was performed in late July (one week after seeds had been taken). Additional searches were performed in August, September, October, and in March of the following spring. When seeds were located I examined three levels of seed dynamics. First, seeds were categorized into a seed fate category: 1) eaten at source, 2) eaten at a feeding station (on top of rock or log), 3) scatter-hoarded in a shallow cache, 4) eaten at a cache site, 5) placed in a relatively deep larder containing many seeds or 6) unknown. Second, cache sites were mapped using Cartesian coordinates and carefully excavated to record total cache depth, depth of soil, depth of litter, number of seeds cached and distance to the source tree. After these parameters were measured, individual identities of each seed were recorded and the cache site was reburied. This allowed me to examine a third level of seed dynamics: cache recovery and management. For example, a seed might initially be found in a cache with five other seeds, then, during a subsequent search, found in a cache with the same five seeds and two additional seeds, and finally, the shell might be found at a feeding station on a log. These secondary movements were monitored because they influence the final fate of the seed and thus influence the potential for successful seed germination. Independent t-tests were used to compare cache characteristics of seeds initially handled by nocturnal versus diurnal cachers. This analysis only included those caches that I was able to unquestionably assign to one or the other category. This was not always possible because, for example, some seeds lost their individual identifications and some caches contained seeds from both categories.

To determine whether seed caches were placed non-randomly with reference to environmental structures, distance to nearest rock, log, or standing tree was recorded. I then compared these distances to those obtained at 100 random points at each site. Finally, to determine how seed cache locations compared to the distribution of naturally occurring ponderosa pine seedlings, I surveyed both 60 x 90 m grids for naturally occurring seedlings (less than 2 yrs old) and compared that distribution to the cache sites. That survey was conducted in August 2002 and repeated in September 2003.

RESULTS

Seed Fate

A total of 463 seeds were taken by rodents over the course of the study. Of these, I was able to track and recover 86% (Fig. 1). Sixty-seven percent (312) of the seeds were initially cached, 19% (86) were eaten before caching and I was unable to relocate the remaining 13% (60) of the seeds. Of the cached seeds, 39% (121) were found in two independent caches, 13% (41) were found in three or more caches, 21% (57) were eaten after being cached and 10% (31) survived over-winter in caches. These are conservative estimates of the amount of seed movement as a result of cache management as it was only possible to determine the minimum number of movements for each seed.

Microsites Selected by Rodents and Seedling Distribution

Rodent seed caches were significantly closer to both rocks (Fig. 2) and downed logs (Fig. 3) than randomly selected locations. However, caches were not nearer to standing trees than randomly selected points. I found that 61% of caches were less than 0.5 m from downed wood compared to only 2% of random points. Fifty-four percent of caches (N = 74) were less than 2 cm from a rock, while only 5% of the random points were less than 2 cm from rocks. In August 2002, 87% of ponderosa pine seedlings (N= 375) were located less than 2 cm from a rock. The seedling survey conducted in September 2003 demonstrated 61% survival of seedlings located less than 2 cm from a rock and only 37% survival of all other seedlings.

Nocturnal versus Diurnal Cachers

Cache characteristics differed between seeds that were initially handled by nocturnal and diurnal cachers, however, they did not consistently follow the predictions (Table 1). Seeds that were initially available to the nocturnal rodent community were moved a slight but significantly greater distance from the source tree, were placed in more shallow caches and contained significantly fewer seeds (N = 38 caches) compared to those initially handled by diurnal cachers (N = 36 caches)(Table 2). Depth of cache and number of seeds per cache were consistent with the predictions that *Tamias* and *Spermophilus* species make larger and deeper caches. However, photographs obtained

from automatically triggered cameras documented nocturnal species pilfering caches made by diurnal cachers and vice versa. Despite the potential interaction of the two classes of seed cachers via pilfering and re-caching, the results indicate that the identity of the initial cacher affects the ultimate seed fate.

DISCUSSION

Rodents removed 100% of the seeds offered during this study suggesting that they interact with a large number of seeds. They initially cached 67% of those seeds and ultimately 3% of those cached seeds germinated. This is a conservative estimate of the amount of germinants resulting from rodent caches because the strength of the radioactive label used here deteriorates over time resulting in limited ability to locate cache sites the following spring. Despite the small percentage of germinants, their presence indicated that rodents cached seeds in a manner conducive to germination.

I suggest that rodent seed caching behavior could be advantageous to ponderosa pine for several reasons. First, rodents often cached seeds in contact with mineral soil and then covered caches with a layer of litter. Ponderosa pine seeds experience higher germination rates when in contact with mineral soil (Pearson 1950) and litter may protect soil from frost heaving by acting as additional insulation (Heidmann 1974).

Second, rodents are essentially doubling the dispersal distance of ponderosa pine seeds. In the absence of rodents, ponderosa pine seeds are primarily dispersed by wind, and Barrett (1979) demonstrated that most wind dispersed seeds fall less than 10 m from the parent. After reaching the ground, ponderosa pine seeds move less than 5 cm per day for a total of only 8 days (Vander Wall and Joyner 1998). Comparatively, rodents moved seeds an average of 19.32 m from the source tree. As a result, seed movement by rodents could potentially increase escape from distance-dependent mortality (Janzen 1970, Connell 1971), increase the probability of colonizing open habitats (Howe and Smallwood 1982), and increase the probability that seeds arrive in suitable microsites (Wenny and Levey 1998).

Because earlier studies suggested that ponderosa pine could be microsite limited (Biswell et al. 1953, Heidmann 1974, Pearson 1950), the sites that rodents select for caching could enhance germination. Rodents non-randomly placed seeds near rocks and

downed wood. Fifty-four percent of caches were placed less than 2 cm from a rock. The possibility that rocks could be important in influencing seedling germination and early survival is consistent with the distribution of naturally germinating ponderosa seedlings. Eighty-seven percent of these seedlings were also located near rocks. However, although this similarity in the distribution of rodent caches and naturally germinating seedlings could indicate that many seedlings arise from rodent caches, the pattern could also be due to the ability of rocks to concentrate wind blown seeds, or to increase germination of wind-blown seeds in these microsites. Given that some rodent-cached seeds followed in this study did germinate, at least some of this regeneration is likely to be from rodent caches. Additionally, the higher survivorship of seedlings less than 2 cm from a rock (61%) compared to other seedlings (37%), indicates that seedlings located near rocks have some advantage during early stages of growth.

Rodents also cached seeds near downed wood. In the presence of fire, downed wood could burn hotly enough to create fire-resistant “hot beds” as described by White (1985). Fire has been called a “key disturbance process” in ponderosa pine forests (Covington and Moore 1994) and based on dendrochronology, Swetnam and Baisan (1996) concluded that ponderosa pine forests of the southwest have experienced high-frequency, low-intensity surface fires over the last 500 years (excluding areas where fire suppression was practiced over the last century). Fulé et al. (1996) suggested that, in northern Arizona, the historical fire interval was 2-8 years. Under natural fire conditions these “hot beds” could eliminate potential competitors for ponderosa seedlings such as grasses, and provide protection from subsequent fires by removing fuel.

The fate of seeds removed by nocturnal versus diurnal seed cachers showed significant differences, however, they did not consistently follow the predictions (Table 1). Diurnal caches tended to be larger and deeper, consistent with the hypothesis that *Tamias* and *Spermophilus* species make larger and deeper caches. In contrast, nocturnal caches tended to be shallower, with fewer seeds. Additionally, seeds initially cached by nocturnal rodents moved a significantly greater distance from the source. These differences could be a result of different caching behaviors of the two classes of cacher. It is also possible that these differences were the result of interactions between the two cachers. For example, Vander Wall et al. (2003) demonstrated that, under wet

conditions, *P. maniculatus* was able to recover more experimentally buried ponderosa pine caches than *T. amoenus*. However, under dry conditions, *T. amoenus* was the superior pilferer. If the conditions were such that nocturnal cachers were superior pilferers, then the greater distance of nocturnal caches from the source could, in part, be a result of more numbers of movements per seed.

Despite the potential interaction of the two classes of seed cachers via pilfering and re-caching, my results indicate that the identity of the initial cacher affects the ultimate seed fate and these differences could influence germination potential. The depth of caches resulting from seeds initially removed by diurnal cachers (2.3 cm) may be too deep for germination. Mean depth of the few caches that germinated during this study (0.75 cm) is consistent with the recommended burial depth (0.60 cm) for ponderosa pine found in much of the silvicultural literature (Hainds 2003) and more closely matches the depth of caches resulting from seeds initially removed by nocturnal cachers (0.96 cm). Additionally, other *Pinus* species for which germination depth profiles have been completed have very narrow ranges of optimal germination (Hadas 1982, Jones 1947, Duchensne et al. 2000) suggesting that even small differences in cache depth may have large impacts on the germination potential.

The higher number of seeds/cache resulting from seeds initially removed by diurnal cachers (12.5) could also influence the spatial distribution of seeds and seedling fate. Given a limited number of seeds, animals that place more seeds in each cache lower the overall number of caches. If all seeds germinated from these larger caches, seedling competition would also be higher, especially when seed numbers approach the maximum number of seeds found in a diurnal cache (47). However, seedling competition could be avoided if few seedlings actually germinate from an entire cache and more often result from caches that have been revisited and partially recovered. On several occasions I observed caches that were revisited and all seeds but one were recovered. I suspect that these single seed caches are less likely to be revisited or pilfered and thus have a much greater chance of surviving to germination. In fact, 2 of the 6 germinating caches followed in this study fit this description.

Given the differences in seed fate for seeds initially cached by nocturnal and diurnal rodents, any factors that differentially affect these classes of cachers could alter

germination patterns. One factor that is likely of importance in the arid ponderosa pine forests of the southwest United States is fire. The Southwestern ponderosa pine system evolved with high-frequency, low-intensity surface fires. Studies have shown that population densities of *P. maniculatus* are often higher after prescribed burns (Ahlgren 1966, Fala 1975, Goodwin and Hungerford 1979, Irvine 1991, Kaufman et al. 1983, Lawrence 1966, Marell 1984,) but this is not always true (Halford 1981). Similarly, *Tamias* spp. also respond unpredictably to fires (Marell 1984, Halford 1981). Ultimately, the relative abundance of these rodent groups could shift the role of rodents from seed disperser to seed predator.

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TABLE 2-1--Cache characteristics averaged over the entire rodent community present at two grids in a ponderosa pine forest in northern Arizona.

Parameter	N	Mean	Range	Std Error
Distance (m)	86	19.32	0 - 48.00	2.19
Total Depth (cm)	79	1.73	0 - 6.80	0.26
Soil (cm)	75	0.82	0 - 4.00	0.08
Leaf Litter (cm)	74	0.99	0 - 5.00	0.18

TABLE 2-2—Comparison of cache characteristics for seeds initially handled by nocturnal (N = 38) versus diurnal (N = 36) rodent seed cachers combined across two grids in a northern Arizona ponderosa pine forest.

	Nocturnal	Diurnal	<i>t</i>	<i>p</i>	Std Error
Distance from source (m)	21.6	19.5	2.6	0.046	1.2
Cache depth (cm)	0.96	2.3	-3.7	0.001	0.24
Seeds/ cache	4.1	12.5	-3.7	0.001	0.15

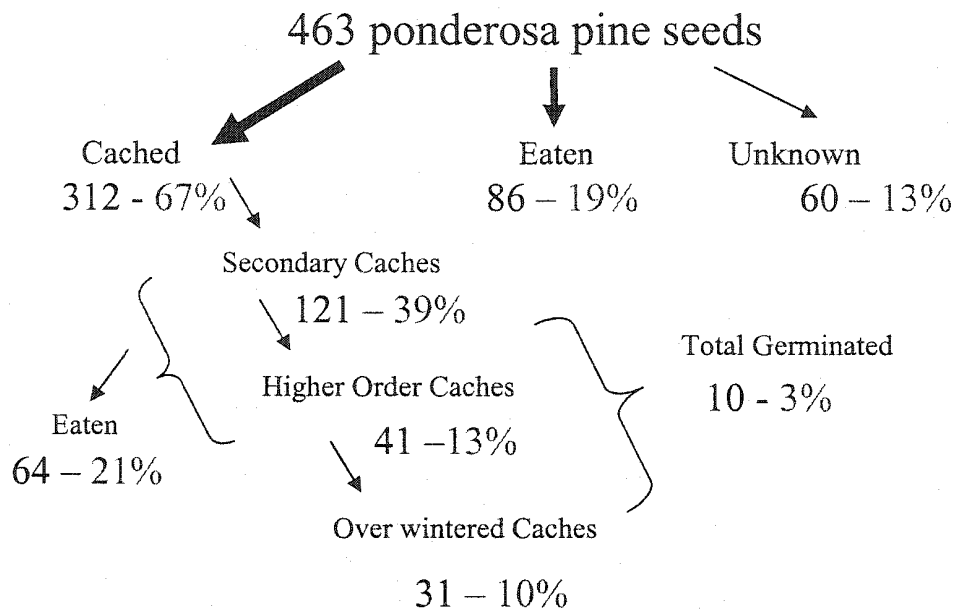


FIG. 2-1-- Seed fate diagram for ponderosa pine seeds removed by rodents at two sites in northern Arizona.

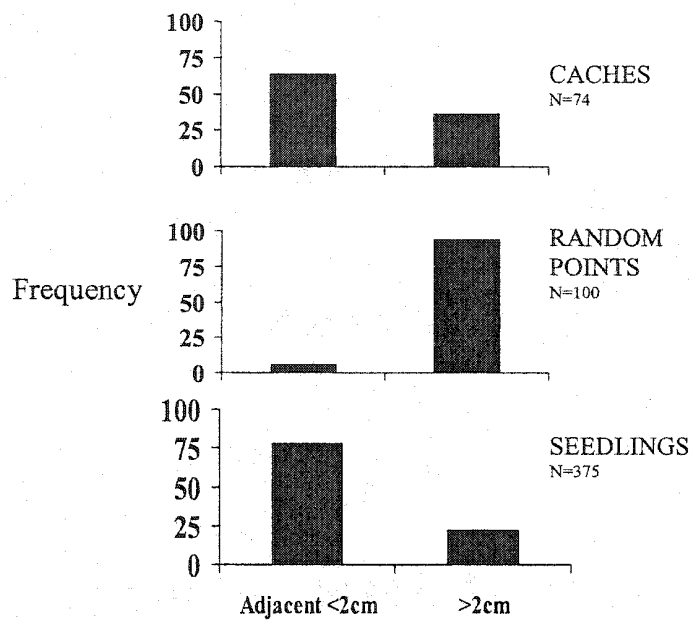


FIG. 2-2 -- Percentage of caches, ponderosa pine seedlings and randomly chosen points that were within 2 cm of rocks or were greater than 2 cm from rocks.

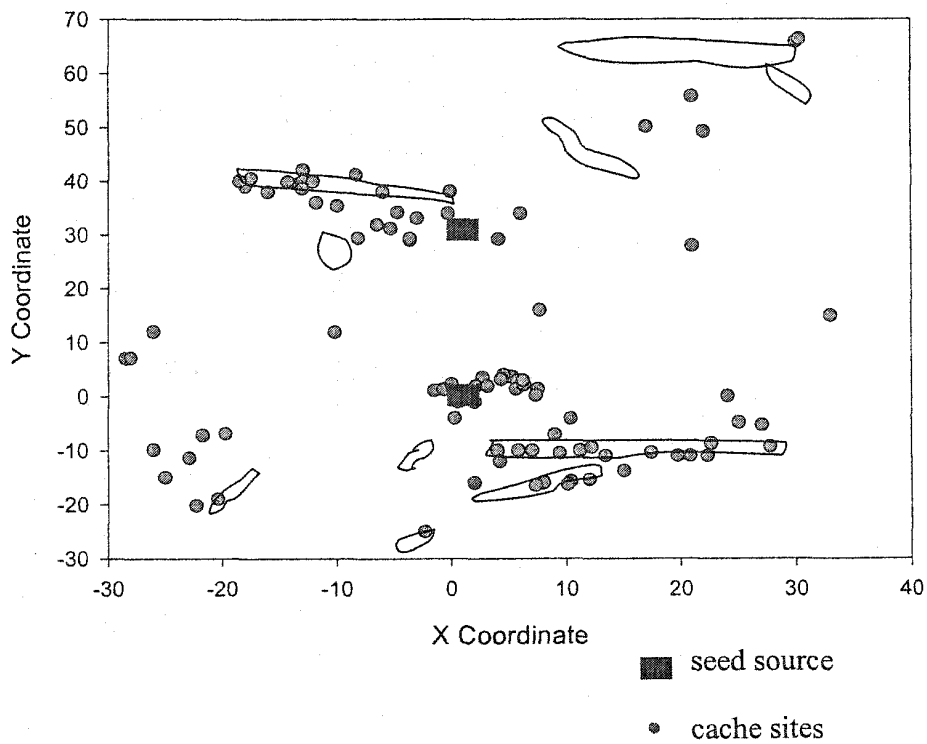


FIG. 2-3 – Map of rodent seed caches relative to downed logs on one of the grids studied in a ponderosa pine forest of northern Arizona.

CHAPTER 3

EFFECT OF FIRE ON SEED REMOVAL AND SEED CACHING BEHAVIOR OF RODENTS IN PONDEROSA PINE FORESTS.

ABSTRACT

I investigated the interaction between rodent seed dispersal and fire in ponderosa pine forests of northern Arizona. Based on ponderosa pine seed removal rates from seed-dish lines and from exclosures that selectively excluded birds and rodents, I documented that seed removal rates were two times higher in burned areas than in unburned areas and that most removal could be attributed to rodents. I then followed the fate of radioactively labeled ponderosa pine seeds placed at the boundary between burned and unburned habitat and found that 1) rodents preferentially moved seeds into burned areas and 2) seed caches were preferentially placed in charred substrate within the burned areas. Finally, I examined whether substrate affected the ability of rodents to find caches that were not their own and documented that seed caches lasted longer when placed in charred substrate. The net movement of seeds into burned areas and into charred substrate, where caches have a higher potential for germination and survival, suggests that rodents could have a positive influence on post-fire ponderosa pine regeneration.

INTRODUCTION

The importance of rodents in affecting seed dynamics by acting as seed dispersers has been demonstrated in a growing number of systems, from the tropics to temperate zones (Price and Jenkins, 1986; Vander Wall and Forget, 2001), but the potential importance of rodent seed dispersal in ponderosa pine systems of the American southwest

is still unknown. Even though ponderosa pine is one of the most widespread pine species in the western US, currently little is known about regeneration of this species under natural fire regimes, the role that small mammals may play in dispersing its seeds, or how that role may be altered by fire. Although ponderosa pine has traditionally been viewed as a wind-dispersed species, McGuinn-Robbins (1998) documented higher germination of ponderosa pine seeds that were placed in simulated caches compared to wind dispersal. Additionally, recent studies have shown that rodents can have significant impacts on the ultimate pattern of seed dispersal in a number of other "wind-dispersed" pines (Vander Wall, 1992, 1994, 2003).

Several lines of evidence suggest that, under natural fire regimes, ponderosa pine seedlings may be microsite dependent, a characteristic that could make directed seed dispersal to these microsites an important factor influencing regeneration. Studies in the early 1900's identified several challenges for ponderosa pine regeneration. Seedlings must grow to a significant size to survive low-intensity fire, they must obtain adequate water to survive prolonged periods between rains, and they must avoid frost heaving and herbivory (Pearson, 1950; Biswell et al., 1953; Heidmann, 1974). If rodents moved seeds to microsites where seeds and seedlings would have a higher probability of overcoming these challenges, they could act as directed seed dispersers and positively impact regeneration. Wenny and Levey (1998) defined directed dispersal as, "non-random placement of seeds in sites predictably favorable for seedling establishment." Previous studies (Compton and Theimer, 2004) in northern Arizona have demonstrated that rodents in unburned ponderosa pine forest cached seeds non-randomly in microsites that may be conducive to ponderosa pine germination in several ways. First, seeds were

cached in contact with mineral soil, a factor that increases ponderosa pine seed germination (Pearson, 1950). Second, rodents replaced the overlying litter after making caches, thereby leaving an insulative litter layer that could protect young seedlings from mortality due to frost heaving of soil (Heidmann, 1974). Third, caches were placed near rocks where seedlings have higher survivorship over the first two years. Finally, many caches were placed near downed wood. In the presence of fire, downed wood could burn hotly enough to create the fire-resistant “hot beds” important for seedling survival as suggested by White (1985). When rodents move seeds to these areas near downed wood after fire they experience the benefit of increased germination in burned soil (Schultz and Biswell 1959), increased survivorship of seedlings (McGuinn-Robbins 1998), and protection from future burns as a result of elimination of fuels from the surrounding area. Taken together, these data suggest that rodents may act as directed dispersers of ponderosa pine seeds and could enhance germination and recruitment above background levels.

Several seed-caching rodent species that may influence seed dispersal are common in the ponderosa pine forests of northern Arizona. Two species of *Peromyscus* (*P. maniculatus* and *P. boylii*) rely heavily on seeds, including conifer seeds, as a food source (Smith and Aldous, 1947; Williams, 1959) and sometimes cache those seeds (Sanchez and Reichman, 1987; Vander Wall, 2003; Compton and Theimer, 2004). Two chipmunks (*Tamias cinereicollis* and *T. dorsalis*) and the golden-mantled ground squirrel (*Spermophilus lateralis*) also feed on seeds. In Nevada conifer forests, a congeneric chipmunk (*T. amoenus*) has been shown to cache seeds of several pine species in shallow, scattered caches and has been argued to be an important factor in pine establishment

(Vander Wall, 1995a, 1995b). In contrast, the golden-mantled ground squirrel tends to cache large numbers of seeds together in caches buried too deep to allow germination (Vander Wall, 1992) and thus probably acts primarily as a seed predator.

Fire has been called a “key disturbance process” in ponderosa pine forests (Covington and Moore, 1994). Pines have a collection of evolutionary traits, such as protected buds, thick bark, prolific seed production, rapid seedling growth, long resinous needles, and highly flammable litter, all of which are interpreted as adaptations to frequent, low-intensity surface fires (Barton, 1993; Moore and Covington, 1999). Based on dendrochronology, Swetnam and Baisan (1996) concluded that ponderosa pine forests of the southwest have experienced high-frequency, low-intensity surface fires over the last 500 years (excluding areas where fire suppression was practiced over the last century) and that stand replacement fires were rare or nonexistent. Fulé et al. (1996) suggested that in northern Arizona the historical fire interval was 2-8 years.

Understanding the ecological process of seed dispersal via seed-caching rodents becomes more important in light of recent changes in management strategies for ponderosa pine forests of the southwestern United States. Over the past century, fire suppression has led to highly altered stand structure and increased fuel loads. As a result of this altered forest structure, this area has experienced several of the largest stand-replacing forest fires in recorded history during the last eight years (Fulé et al., 2001). Because these stand-replacing fires are costly and can have devastating impacts on the human communities affected by them, there has been increasing emphasis on management to return forests to fire regimes more similar to those that existed before fire suppression. Ecological restoration is emerging as a dominant management objective for

ponderosa pine forests of the southwest (Bailey and Covington, 2002). Recently, Allen et al. (2002) called for ecological restoration to “reset ecosystem trends toward an envelope of natural variability, including the reestablishment of natural processes.” Much of the research regarding ecological restoration in ponderosa pine forests has focused on the removal of ponderosa pines to lower stand density and fuel loads (Griffis et al., 2001). However, the natural process of regeneration of ponderosa pine has received less attention (Heidmann et al., 1982) and given the suggestions that rodents may play an important role in the natural process of regeneration, it is important to understand how fire will effect this interaction

Fire could affect the interaction between seed caching rodents and ponderosa pine by altering the abundance and/or community of rodents present or by altering the seed caching behavior of rodents. *P. maniculatus* abundances have been documented to increase after prescribed fire in a number of studies across a range of plant communities (Tester, 1965; Ahlgren, 1966; Lawrence, 1966; Fala, 1975; Kaufman et al., 1983;) including in ponderosa pine forests (Goodwin and Hungerford, 1979; Irvine, 1991; Reading, 2001; Roberts, 2003). *Tamias* spp response to fire generally depends upon the severity (Halford, 1981; Marell, 1984; Lowe et al., 1978; Kyle, 2000). In addition to altering foraging behavior, fire could alter the caching behavior of rodents. Substrate type can influence rodents caching preference (Pearson and Theimer, 2004) and fires often create a patchy distribution of burned and unburned soil that could interact with substrate preferences. If rodents prefer to initially cache seeds in either burned or unburned substrate, this could result in a net movement of seeds into or out of burned areas. However, because rodents subsequently return to and recache previously cached

seeds, however, the ultimate disposition of seeds may vary from initial cache site patterns. Chambers and MacMahon (1994) define two phases of seed dispersal. Phase I consists of movement of the seed from the parent plant and phase II is defined as any subsequent movement of the seed before germination. Studies have demonstrated that cache management may influence the ultimate microsite that germinating seeds may experience and thus the importance of phase II dispersal (Vander Wall, 1995b; Vander Wall and Joyner, 1998). The second phase of dispersal is also likely to be influenced by burning of the substrate. Evidence indicates that rodents use both spatial memory and olfaction when recovering their own caches and pilfering (stealing) caches made by other members of the community (Howard and Cole, 1967; Vander Wall, 2003). It has been suggested that seeds buried in the soils of burned areas are more difficult for rodents to detect (Vander Wall 2003); therefore, caches made in burned soil may have a higher probability of escaping subsequent recovery than those cached in unburned sites.

In this study, I addressed three main questions about how fire could influence the potential for seed dispersal by seed-caching rodents in southwestern ponderosa pine forests. First, I compared seed removal rates in burned and unburned sites at three locations to determine whether seed removal rates differed as a result of fire. Second, I followed the fate of radioactively-labeled seeds at one site to determine a) if there was net movement of seeds toward or away from a burned area, and b) if rodents cached seeds preferentially with respect to burned versus unburned substrate. Third, I experimentally tested the hypothesis that caches made in burned substrate would have a lower rate of pilferage than those placed in unburned substrate due to differences in the ability of rodents to locate caches in those two substrate types.

METHODS AND MATERIALS

Seed Removal Study

To compare seed removal in burned and adjacent unburned areas, I used three different mid-elevation ponderosa pine sites located near Flagstaff, Arizona that were subjected to prescribed burning during August and September of 2001. These prescribed burns mimicked the low-intensity ground fires that have been hypothesized to have been a regular feature of these forests historically. The Mint burn was located approximately 35 miles south of Flagstaff, Arizona near Mormon Lake. The Peaks burn site was approximately 15 miles north of Flagstaff at the base of the San Francisco Peaks. The Mars Hill burn site was located four miles northwest of Flagstaff near Lowell Observatory. The fires at all sites were patchy surface burns with no tree mortality. Small mammal live-trapping was conducted in the fall of 2001, spring and fall of 2002, and spring and fall of 2004. Four trap lines of 10 traps each, spaced 10 m apart, were placed in each of the three burn areas and two similar lines were placed in adjacent unburned plots. Traps were open for one day and three nights during each trapping session. Additionally, understory plants were censused in two 1 x 1 m plots at each burn site. Two replicate seed dish lines, containing 10 dishes, were placed in each burn site and paired with two lines in the adjacent unburned area for a total of six burn lines and six non-burn lines. Dishes contained sand (used as a substrate to lower seed loss to wind and rain) and 10 ponderosa pine seeds. Dishes were collected after two weeks and the percentage of seed removal per dish was measured. Data collection began in October 2001 (1-2 months post burn) and the process was repeated every two months for the

following 18 months. A repeated measures ANOVA was used to analyze seed removal for the effect of time, site, and treatment.

In burned areas of these same sites, semi-permeable exclosures were erected to differentiate the effects of rodent seed removal from that of birds. At each site, two replicate sets of five 2 x 2 m plots were established. Four of these plots were fenced, while the fifth acted as an unfenced control. Exclosures were of four types. Rodent exclosures had wire mesh (1 cm diameter) sides supported by metal posts. Sides were 1 m tall with the bottom edge staked into the soil to prevent access by rodents from below. In addition, a 15 cm strip of metal flashing encircled the top to prevent rodents from climbing over the top. The top was open so that birds had access. Bird exclosures were constructed as for rodents, except that poultry netting was wired across the top of the exclosure to prevent access by birds. Small holes were cut at ground level into the wire mesh sides at eight locations and a 30 cm long piece of 5 cm diameter PVC pipe was placed in each hole. These "tunnels" allowed rodent access but prevented bird access. Exclosures that excluded both rodents and birds were constructed as for bird exclosures but without the "tunnels" that allowed rodent access. Finally, a control for potential fence-effects was erected that had wire mesh sides but no top and with 10 cm x 10 cm holes cut in the wire at ground level. Dishes containing *Pinus ponderosa*, *Lupinus argenteus*, *Vicia americana*, and *Sitanion hystrix* seeds mixed with sand were placed in each plot and the number of seeds removed monitored after two weeks. This was repeated at two month intervals.

Caching and Pilfering Study

I examined caching and pilfering behavior of rodents at a fourth burn site on the NAU Centennial Forest, where I was able to obtain approval for the use of Scandium-46 to track the movements of seeds. This site is located approximately six miles southwest of Flagstaff, Arizona and is a monospecific, mid-elevation ponderosa pine forest. The control burn, conducted in the fall of 2002, was one year old at the time of the study. A 60 x 60 m grid was laid out with half of the grid placed on burn and half on unburned substrate (Fig. 3-1). Within the burned area, substrate varied due to the patchy nature of low-intensity ground fires. Some areas had all of the overlying litter burned away leaving only charred soil and woody debris. Other areas showed little effects of fire, with the overlying unburned litter still in place. A trap line was set up along the perimeter of the grid with a total of 42 traps and the traps were monitored for six nights prior to the experiment.

I used radioactively labeled ponderosa pine seeds to examine the caching behavior of rodents at this site. The seeds were labeled with Scandium-46, a radioactive isotope that emits high-energy gamma radiation (1.12×10^6 electron volts) and has a relatively short half-life of 84.5 days. The decay product is titanium-46 which is stable and inert. I was able to track the movements of these seeds after rodents handled them using a portable Geiger counter. I also uniquely numbered each seed so that I could examine multiple movements of individual seeds. Ponderosa pine seeds were placed in a wire mesh cage located at the center of a 60 x 60 m grid. The wire mesh cage had entry holes cut to a size that prevented access to the seeds by other seed predators (Abert squirrels, foxes, etc) or potential dispersers (Steller's jays). To increase the likelihood

that multiple animals were interacting with the seeds, they were placed out in lots of 500 over several nights. Removal of seeds was monitored daily and when all of the seeds from the lot were removed an additional lot was placed in the cage. The process was repeated until 1000 seeds were removed.

I began searching the grid for caches the day after all seeds were removed and continued periodic searches (completing at least one search of the grid every two weeks) through the end of September. When seeds were located they were categorized into one of six seed fate categories: 1) eaten at source, 2) eaten at a feeding station (on top of a rock or log), 3) cached, 4) eaten at a cache site, 5) larder hoarded or 6) unknown. They were also categorized depending upon the area and substrate in which they were found: 1) burn/char (in the burned area and on charred soil), 2) burn/non-char (within the burned area but on unburned soil), and 3) non-burn (in the unburned area and therefore on unburned soil). Cache sites were mapped using Cartesian coordinates and carefully excavated. I recorded cache depth (including overlying litter as well as soil), depth of soil only, number of seeds cached, distance to nearest rocks and/or log, and distance from source. I estimated the proportion of charred soil and unburned soil in each 10 x 10 m section of the grid in the burned area to obtain an estimate of the proportional availability of each substrate type. A Chi-square goodness of fit test was performed to compare substrate selected for caching, larder hoarding, and seed eating to substrate available.

To examine the effect of burned substrate on pilfering behavior, I placed 15 simulated caches, each containing five ponderosa pine seeds buried at a depth of 1 cm in each of the substrate types (burn/char, burn/non-char, and unburned) in the area around the grid. All experimental caches were at least 10 m apart to reduce the effects of area-

restricted search by animals discovering one cache type. At least two seeds from each cache were radiolabeled allowing the fate of the caches to be checked daily without further disturbance to the soil. In addition to checking the simulated cache sites, an area within a 10 m radius of each site was scanned after the cache had been pilfered. When seeds from these caches were found, they were categorized as above by seed fate, substrate type, and distance moved from original cache site. ANOVA was used to examine differences in the cache site characteristics for the three substrate types.

RESULTS

Seed Removal in Burned and Unburned Areas

Live trapping and understory plant surveys suggested that similar plant and rodent species were present at all three study sites (Table 3-1).

The mean percent removal of ponderosa pine seeds averaged over two years was two times higher in burned areas (32%) compared to the non-burned areas (16%) when removal at all three sites was combined. There was a significant effect of burn ($F = 3.22$, $p = .001$) and a marginally significant effect of time ($F = 3.86$, $p = 0.091$). The interaction of time x burn ($F = 1.96$, $p = .086$) indicated a trend and was also marginally significant. This trend was further supported by post hoc analysis indicating that the difference between burn and non-burn was significant ($p < 0.05$) for the first four sample periods or ~ 1 year post burn. There was no significant effect of burn site ($F = 1.87$, $p = 0.635$; Fig. 3-2), indicating similarity in the results obtained from each of the different burns.

Seed removal was ten times higher in those enclosures that allowed rodent access than in treatments that excluded them, with very low removal rates from enclosures that selectively allowed birds access ($F = 26.86, p = 0.001$; Fig 3-3). Post hoc analysis indicated that there was no significant difference between seed removal by birds and the amount of seed lost due to experimental error in the control enclosure that excluded both birds and rodents ($p < 0.05$)

Movement of Seeds Across a Burn Boundary

Live trapping indicated that *P. maniculatus*, *P. boylii* and *T. cinereicollis* were present at the site used for this experiment. On one night, a total of nine different individuals were captured, indicating that multiple animals used the area that the grid encompassed and thus could potentially interact with the seeds. Seed removal occurred over a nine day period from July 29 through August 6, 2003. Of the 1000 ponderosa pine seeds taken by rodents, 698 were moved into the burned area of the grid while 441 were moved into the unburned area. The relative proportions of substrate available within the grid were 21% burn/char, 29% burn/non-char and 50% not burned. Based on expected values calculated from these proportions, more seeds were moved into the burn/char area than expected and less seeds moved into the burn/non-char and into the unburned area ($\chi^2 = 450.73, p < 0.001$; Table 3-2).

Seed Fate and Substrate Types

A total of 193 seeds were cached and 112 (58%) of those were cached in charred substrate within the burn, 53 (27%) in burn/non-char substrate within burned areas, and

28 (15%) in the unburned areas ($X^2 = 169.18, p < 0.001$). The number of seeds larder hoarded and eaten in the three substrate types showed the same pattern (Table 3-2).

Because the number of seeds per cache varied, I examined the number of caches in each substrate type and the characteristics of caches within each substrate (Table 3-3). Consistent with the pattern of seed movement discussed above, more caches were made in the burn/char (29) followed by burn/non-char (10) and non-burn (7) ($X^2 = 11.37, p = 0.003$). Seeds cached in charred soil in burned areas were moved a greater distance from the source (17.9 m) compared to those found in non-charred substrates in the burned area (11.2 m) and in the unburned area (8.7 m) ($F = 8.7, p = 0.001$). However, there were no other differences for the three substrate types in cache depth, depth of soil, and number of seeds/cache (Table 3). I also found no difference in the relationship between caches and standing trees ($F = 7.2, p = 0.21$) or rocks ($F = 5.2, p = 0.96$) for any substrate type.

Seed pilfering from burned and unburned soils in burned and unburned areas

Seeds placed in simulated caches in burn/char substrate survived 2 times longer (3.06 days) than those in burn/non-char (1.67 days) or unburned (1.43 days) areas ($F = 4.900, p = 0.014$). Additionally, when the fate of these seeds was followed, 19 of the 21 that were recached were found in the charred substrate of the burned area, while only 2 were re-cached in the unburned area. No re-caching was documented in non-charred soil in the burned area.

DISCUSSION

Directed seed movement

Removal of ponderosa pine seeds was two fold higher in burned areas than in unburned areas and seed removal from semi-permeable exclosures at the same sites indicated that rodent removal of ponderosa pine seeds was nine times greater than bird removal. Taken together, these results indicate that fire increased seed removal rates by rodents. This increase in seed removal could be the result of changes in rodent population numbers, altered foraging patterns, or both. *P. maniculatus* abundances have been documented to increase after prescribed fire in a number of studies across a range of plant communities (Tester, 1965; Lawrence, 1966; Ahlgren, 1974; Fala, 1975; Kaufman et al., 1983;) including in ponderosa pine forests (Goodwin and Hungerford, 1979; Irvine, 1991; Reading, 2001; Roberts, 2003). A single study that documented a negative response of *P. maniculatus* to fire also examined the diet of the rodents at the site, indicating that 0% of the *P. maniculatus* diet was comprised of seeds (Halford, 1981). This finding is unusual for this species, as seeds generally comprise a relatively large percentage of the diet (Abbot, 1961; Smith and Aldous, 1947; Williams, 1959). This suggests that the positive responses of *P. maniculatus* to fire may be contingent on their seed foraging behavior.

It has been shown that burned substrate affects the foraging success of both birds (Nystrand and Granstroem, 1997) and rodents (Hufmann, 2003). In the ponderosa pine system, seeds may become more visible on the dark background and are less likely to filter through the litter and become buried. Less is known about *Tamias* spp response to prescribed fire. Lowe et al. (1978) demonstrated that *T. cinereicollis* abundances

dropped after a severe wildfire in a northern Arizona ponderosa pine forest. Kyle (2000) confirmed that severe wildfire had a negative impact on *T. cinereicollis* but found no change in abundance after a moderate fire. Marell (1984) documented that *Tamias minimus* increased after a low severity wildfire in a mixed wood forest in Ontario. This response is consistent with the hypothesis that seed foraging is facilitated by prescribed fire (which is generally of low severity) that leaves a charred substrate but suggests that higher severity fires likely destroy other necessary resources. Regardless of the mechanism, this study indicates that fire increases ponderosa pine seed removal.

Two major patterns emerged from following seed fate along a burn edge: 1) rodents preferentially moved seeds into the burned area and 2) within the burn, they preferentially moved seeds into patches that had charred soil over areas that showed little impact of the burn. Although more seeds than expected were larder-hoarded and eaten (two seed fates with no potential for germination) on the burned substrate, this behavior would not likely lower the total number of seeds available for germination in the burn compared to the other substrate types due to the substantially larger number of seeds that were initially moved to the burn area. This net movement of seeds into the burned area suggests that rodents could be important agents for moving seeds into burned areas, at least along burn perimeters. An important caveat is that these conclusions are based on results at a single site, and whether net movements into burned areas are a general phenomenon remains to be verified. Although one animal with a den site or home range centered in the burn could have cached a large percentage of seeds, thus biasing these results, this seems unlikely for several reasons. First, trapping at the site indicated a minimum of at least nine individuals that could have interacted with seeds. Second, it

took nine days for all seeds to be removed, and seeds were available both day and night, increasing the probability that seeds were taken by multiple individuals.

The preference of rodents for charred substrate may have been due to differences in the effect of substrate type on cache survivorship. Rodents use both spatial memory and olfaction when recovering their own caches and pilfering (stealing) caches made by other members of the community (Vander Wall, 2003; Howard and Cole, 1967). Seeds buried in charred soils may be more difficult for rodents to detect if burning alters the ability of seed odors to penetrate the overlying soil. For example, in his model of how environmental conditions could influence odors used by rodents to detect seeds, Vander Wall (2003) argued that “soils with high levels of organic material (including...charcoal from a fire) have a lower flux of odorant molecules when moistened than do mineral soils”. As a result, caches made in burned soil may have a higher probability of escaping subsequent recovery by animals other than the original cacher. Rodents in our study may have responded to this by preferentially caching in this substrate to avoid pilferage, behaviors consistent with the “pilfering avoidance hypothesis” (MacDonald, 1976).

Pine regeneration

The net movement of seeds into the burned area and the higher number of caches in the charred substrate could have important implications for ponderosa pine regeneration. Several studies have demonstrated higher germination and survival of ponderosa pine seedlings on burned areas (Schultz and Biswell 1959; Taylor and Wendel, 1964; Ffolliott et al., 1977; Haase 1981; McGuinn-Robbins 1998). This enhanced germination is likely due to exposed mineral soil, higher soil moisture, and increased

nutrients in the soil by conversion of aboveground fuels into mineralized components in burned areas (Haase, 1981; Covington and Sackett, 1984; Ryan and Covington, 1986).

Control of rodent populations has been suggested as a means to enhance regeneration of ponderosa pine after fire (Schubert and Adams, 1971; Heidmann et al., 1982; Weaver 1943). In this study, I documented higher removal of seeds in burned areas consistent with an overall negative impact of rodents on seeds. However, I also documented net movement of seeds into burned areas where rates of germination are higher (Schultz and Biswell 1959; Ffolliott et al., 1977; Haase 1981; McGuinn-Robbins 1998). This study also documented preferential caching of seeds in charred substrate where seeds experience longer survivorship in caches and thus higher germination potential. Several studies have shown that cache survival to germination is typically low, and in fact, it may be so low that any benefits of seed caching by rodents may appear too small to be important. However, as pointed out by Chambers and McMahon (1994), “many of the seeds that are harvested are killed, but those that survive may exhibit substantial benefit. The tendency is often to classify interaction between seeds and animals based on the most common outcome, even though the least common outcome may be of greatest importance to the plant.” In this regard, the action of rodents as seed dispersers could act as an important mechanism for seed arrival into burned areas after low-intensity fire.

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Table 3-1. Rodent and understory plant communities at three seed removal study sites.

	Mint Burn	Peaks Burn	Mars Hill Burn
Fire Size (Acres)	30	30	15
Rodents in Burn	<i>P. maniculatus</i> <i>T. cinericollis</i> <i>T. dorsalis</i>	<i>P. maniculatus</i> <i>T. cinericollis</i> <i>T. dorsalis</i> <i>Neotoma spp</i>	<i>P. maniculatus</i> <i>T. cinericollis</i> <i>T. dorsalis</i>
Rodents in Non-burn	<i>P. maniculatus</i> <i>T. dorsalis</i>	<i>P. maniculatus</i> <i>T. cinericollis</i> <i>T. dorsalis</i>	<i>P. maniculatus</i> <i>T. cinericollis</i> <i>Neotoma spp</i>
Understory Plants	<i>Elymus elymoides</i> (18%) <i>Rosa woodsii</i> (9%) <i>Lupinus argenteus</i> (8%) <i>Vica americana</i> (7%) <i>Dactylis glomerata</i> (4%)	<i>Elymus elymoides</i> (13%) <i>Lupinus argenteus</i> (9%) <i>Vica americana</i> (8%) <i>Poa fendleriana</i> (7%) <i>Cirsium wheeleri</i> (6%)	<i>Elymus elymoides</i> (10%) <i>Lupinus argenteus</i> (7%) <i>Vica americana</i> (8%) <i>Cirsium wheeleri</i> (8%) <i>Erigeron divergens</i> (8%)

Table 3-2. The relationship between seed fate and substrate type*

	Total	Burn/char		Burn/Non-char		Non-burn		χ^2	<i>p</i>
		Obs	Exp	Obs	Exp	OBS	Exp		
% Substrate Availability		21%		29%		50%			
seeds moved to substrate	882	442	186	186	256	254	441	450.73	<0.001
seeds cached in substrate	193	112	41	53	56	28	97	169.18	<0.001
seeds larder in substrate	465	165	106	75	135	32	233	232.90	<0.001
Seeds eaten on substrate	418	166	88	58	121	194	209	103.02	<0.001

* The observed (Obs) values of each parameter are shown and the expected (Exp) values are calculated based on the availability of each substrate.

Table 3. Comparison of characteristics of caches placed in the three substrate types

	Burn/char	Burn/ Non-char	Non-burn	Test statistic	<i>p</i>
N	29	10	7	$\chi^2 = 11.37$	0.003
Distance from source (m)	17.9	11.2	7.5	$F = 8.7$	0.001
Total depth (cm)	1.0	1.4	1.6	$F = 3.6$	0.087
Soil depth (cm)	.9	.8	.6	$F = 8.4$	0.687
Distance to rock (m)	4.8	5.2	3.9	$F = 7.2$	0.956
Distance to tree (m)	6.6	5.4	5.1	$F = 5.2$	0.206
Seeds / cache	4.3	5.1	4.2	$F = 7.7$	0.775

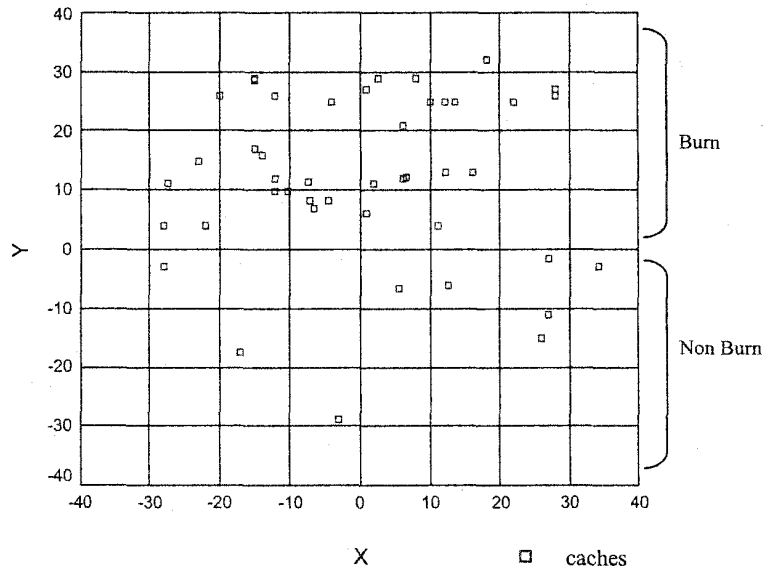


Fig 1. Seed fate grid showing the location of all cache sites. All seeds were initially removed from the center of the grid (0,0).

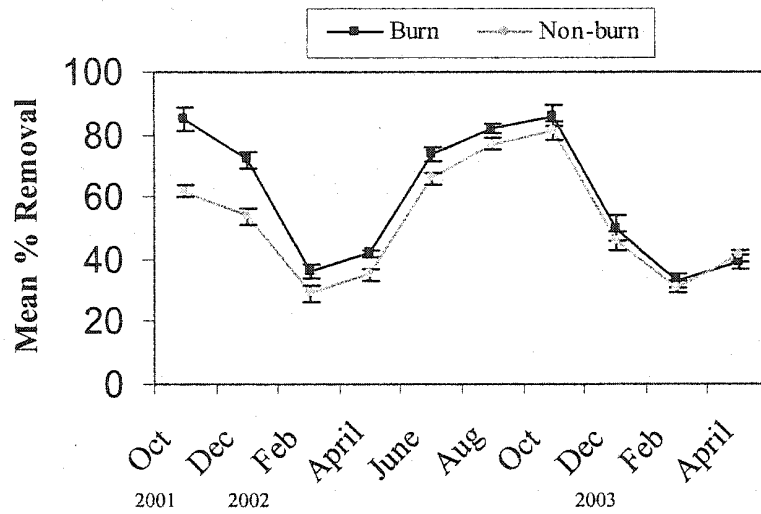


Fig 2. Mean percent removal of ponderosa pine seeds in the burn area compared to the non-burn ($\pm 1SE$). There was a significant effect of time ($F = 3.856, p = 0.091$) and burn ($F = 3.22, p = .001$) and an interaction of time x burn ($F = 1.96, p = .086$) but no significant effect of burn site ($F = 1.87, p = 0.635$). Post hoc analysis indicated that the difference between burn and non-burn was significant ($p < 0.05$) for the first four sample periods or ~ 1 year post burn.

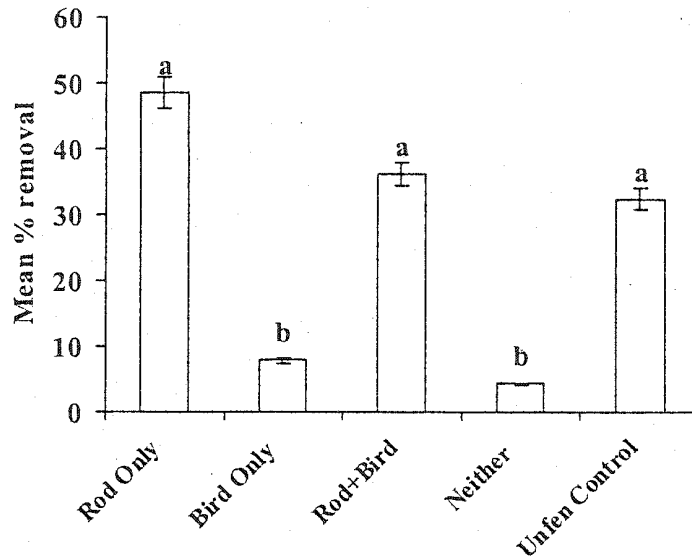


Fig 3. Mean (\pm SE) number of ponderosa pine seeds removed from semi-permeable exclosures at four locations in northern Arizona ($F = 26.854, p = 0.001$). Exclosures allowed access 1) by rodents only, 2) by birds only, 3) by both birds and rodents, 4) by neither birds nor rodents or 5) were unfenced and allowed access by both. Results from post hoc analysis are indicated above bars ($p < 0.05$).

CHAPTER 4

EFFECT OF NURSE TYPE ON PINYON PINE (*PINUS EDULIS*) SEEDLING GERMINATION, SURVIVAL, GROWTH AND MYCORRHIZAL RELATIONSHIPS.

ABSTRACT

The establishment of young conifer seedlings is difficult to estimate in the field due to their patchy distribution in space and time. I examined patterns of seedling establishment and survivorship in microsites that included open areas, areas adjacent to tree and shrub canopies and under the canopies of trees and shrubs for a cohort of *Pinus edulis* seedlings produced during the mast year of 1999 in northern Arizona. I surveyed seedling distribution in microsites in the fall of 2000, and again in the spring and fall of 2002. Seedlings were more prevalent under pinyon and under juniper canopy than expected based on the abundance of these microsites and less prevalent in the open. These trends were the same for each sample period; however, the number of seedlings under juniper canopy increased relative to availability over time while the number under pinyon decreased, suggesting enhanced survivorship in the microsite under juniper. I then tested several hypotheses that could potentially explain differences in seedling survival under juniper versus pinyon nurses using both marked and collected subsets of seedlings. Although survivorship was significantly higher under juniper nurses (44%) compared to pinyons (14%), no significant differences among surviving seedlings in shoot length, shoot/root ratio, number of lateral roots, or mycorrhizal development were found. In the pinyon-juniper woodlands of northern Arizona, junipers appear to be an important nurse for pinyon during early seedling development.

INTRODUCTION

Pinyon-juniper woodland is the third largest vegetation type in North America, covering approximately 42 million acres of the southwestern United States, and has almost doubled in the last decade (Laycock, 1999). Several explanations have been offered for the expansion of this habitat type including: changing fire regimes, global climatic changes, and shifting agricultural practices (Tausch et al., 1981; West and Van

Pelt, 1987). Regardless of the driving force, an understanding of seedling germination patterns is fundamental to identifying the mechanism(s) for this expansion.

Although relatively little is known about the germination requirements of *Pinus edulis* (Chambers, 2001), the existing research suggests that germination is microsite-limited, that is, germination may not be directly proportional to seed production, but instead may be limited by availability of suitable microsites and/or mechanism(s) necessary for dispersal of seeds to those microsites. Differential success among the microsites could be the result of many factors. In the arid and semi-arid areas that *Pinus edulis* occupies, shrubs and trees have been described as “islands of fertility.” The microhabitat beneath these canopies often has higher organic matter and total nitrogen, lower bulk densities, higher infiltration and soil water holding capacities, as well as higher rates of nutrient cycling (Evert et al., 1986). Additionally, these microhabitats experience lower irradiance and lower soil temperatures (Stark, 1994), which may be especially important for pinyon establishment. For example, pinyon seedlings have higher survival rates in the presence of artificial shade and supplemental watering (Meagher, 1943) and establishment appears to be sensitive to variations in soil temperature and moisture (Chambers, 2001; Drivas and Evertt, 1988).

Because nurse plant relations are often a balance between facilitation and competition, different species of nurse plants could have different impacts on seedling germination and survival. As pointed out by Callaway (1995) “the overall effect of one species on another may be the cumulative effect of multiple, complex interactions.” Differences in canopy structure of the nurses, root architecture (Callaway et al., 1991), and mycorrhizal symbionts (Amaranthus et al., 1990) could all impact the relative effect of the nurse on germinating seedlings. For example, Chambers (2001) demonstrated that mean growing season temperature is higher under juniper (*Juniperus osteosperma*) compared to pinyon (*P. monophylla*), suggesting that seedlings under juniper should experience increased shoot growth if other resources are not limiting. However, the root architecture of juniper allows it to capture more shallow inter-canopy water (Breshears et al., 1997), while adult pinyon roots access water from deeper soil depths (Breshears, 1993). Haskins (2003) investigated belowground competition in pinyon juniper woodlands and showed that juniper roots are more abundant than pinyon roots in the top

30 cm of soil. As a result, because young pinyon seedlings' roots occupy these upper layers of soil, seedlings nursed by junipers could encounter higher competition for water and thus experience higher mortality or have characteristics associated with low water availability such as higher root to shoot ratios and more lateral root development. Nurse plants also may affect seedlings differentially via the mycorrhizal community (Dickie et al., 2002). For example, Kranabetter (1999) showed that seedlings dependent on ectomycorrhiza had increased ectomycorrhizal infection rates when planted near ectomycorrhizal birch trees. Because junipers are arbuscular mycorrhizal (endomycorrhizal) and pinyons are primarily ectomycorrhizal, pinyon nurses could provide higher densities of ectomycorrhizal inoculum than juniper for mycorrhizal development.

This study took advantage of a cohort of seedlings produced from a mast seed crop that occurred in northern Arizona in 1999, to determine patterns of seedling establishment and survivorship in six microsites: under pinyon canopy, near pinyon but beyond the canopy, under juniper canopy, near juniper but beyond the canopy, under/near shrubs, and in the open. I followed survivorship of a subset of these seedlings to determine if nurse species varied in their effect on seedlings. In addition to survival, I analyzed seedling differences in shoot length, shoot/root ratio, and number of lateral roots to determine if seedling growth varied among microsites. I also examined levels of mycorrhizal colonization on seedling roots to determine if areas under pinyon or juniper canopies varied in the amount of inoculum available to establishing pinyon seedlings. I predicted that differences among nurses would lead to differential success among seedlings as a result of variable seedling growth and/or mycorrhizal development.

METHODS AND MATERIALS—

Study Site--

Seedling survivorship was monitored in a pinyon-juniper woodland north of Flagstaff, Arizona near Red Mountain at 2031 m elevation. Pinyon and juniper trees occurred in approximately equal abundance and dominated the site, with relatively few shrubs including: *Pursia tridentate*, *Artemisia tridentate*, and *Chrysothamnus nauseosus*.

The patchy clumps of grasses and forbs that are typical of pinyon-juniper woodlands in semi-arid areas were also present.

Distribution of seedlings among microsites--

I determined patterns of seedling establishment and distribution for a cohort of seedlings produced from a regional pinyon mast in 1999. In October 2000, fifteen random 10 x 1 m² transects were searched and all seedlings from the 1999 cohort were placed into one of the six microsite categories described above. The availability of each microsite was calculated as the percentage of the transect falling into each microsite category and chi-square analysis was used to compare the frequency of seedlings observed to the expected frequencies based on the availability of each microsite. To examine survivorship in each category, this procedure was repeated with independently selected transects in April 2002 and October 2002.

To test for the possibility that more seedlings were found under trees with larger canopy areas, fifteen pinyon and fifteen juniper nurses were paired by canopy size. A t-test was performed to compare number of seedlings per tree.

Marked pinyon seedlings: pinyon vs. juniper nurses--

To further investigate survivorship of seedlings in the two most common microsites, under pinyon canopy and under juniper canopy, 100 seedlings (from the 1999 cohort) were marked with individual numbers. Fifty of those were under adult pinyon nurses and 50 were under adult juniper nurses. In May 2002 an initial height was collected for all marked seedlings and a t-test was used to compare the height of those seedlings being nursed by pinyons versus junipers.

These seedlings were re-visited in August 2002, after the summer growing season. During this second survey I examined total number of needles, needle length (mean of 5 randomly selected needles for each seedling), new growth (growth occurring between the initial survey in May 2002 until August 2003) and total height of all living seedlings. T-tests were used to compare these response variables between the two nurse types.

Collected seedlings--

To examine differences in growth characteristics, overall biomass, root/shoot ratio, root development, and mycorrhizal associations, one seedling from under 15 trees of each nurse type was collected in August 2002. Seedlings were removed by digging holes large enough to encompass all of the root system. Excess soil was removed by hand and seedlings were placed in plastic bags with water for transport to the lab. In the lab seedlings were placed in a water bath to remove soil and refrigerated for no more than 3 days before processing. I measured shoot length, length of longest root, and number of lateral roots. I distinguished between first year and second year growth by identifying the constriction scar in the shoot resulting from overwintering. Roots were examined for ectomycorrhizae and a percentage of mycorrhizal colonization was calculated as described by Gehring and Whitham (1991). Finally, seedlings were dried at 60° C to measure total plant biomass and shoot/root biomass ratio. T-tests were used to compare these response variables between the two nurse types.

RESULTS

Distribution of seedlings among microsites--

Seedlings were more prevalent under pinyon and under juniper canopy than expected based on their abundance and less prevalent in the open (Fall 2000 $X^2 = 156.8$, $p < 0.05$; Spring 2002 $X^2 = 130.7$, $p < 0.05$; Fall 2002 $X^2 = 252.5$, $p < 0.05$; Fig. 4-1). These trends were the same for each sample period; however, relative abundance changed over time in the two most common microsites. The number of seedlings under juniper canopy increased relative to availability while the number under pinyon decreased, suggesting differential survivorship in these two microsites. In fall 2000, there was more than four-fold the number of seedlings observed than would be expected under pinyon canopy. However, by fall 2002 there was less than two-fold the number of seedlings observed than would be expected. Conversely, the number of seedlings observed under juniper canopy increased from less than three times to greater than six times than expected (Fig. 4-1).

When canopy area was held constant by comparing trees paired for canopy size, there was almost twice the number of seedlings under juniper canopies compared to

pinyons (paired t: $t = -2.728, p = .016$). This result suggests that the higher number of seedlings surviving under juniper canopy was not a result of larger overall canopy size.

Marked seedling survivorship: pinyon vs. juniper nurses--

When I marked and followed survivorship of seedlings in the two most common microsites (under pinyon canopy and under juniper canopy), I confirmed that nurse type affected survivorship. Forty-four percent (22/50) of seedlings nursed by junipers survived until August 2002, while only fourteen percent (7/50) of those under pinyons survived ($X^2 = 3.88, p < 0.05$). Despite the difference in survivorship, no differences were found in any of the measured parameters; total number of needles, needle length, new growth and total height (Table 4-1).

Collected seedlings--

Because I were unable to identify any above ground differences in seedlings nursed by pinyon versus juniper, I collected seedlings and compared water content, root development, mycorrhizal associations, and a suite of growth characteristics. I found no significant differences between seedlings nursed by pinyons and junipers in shoot length, first year growth, second year growth, total plant biomass, shoot/root biomass ratio, number of lateral roots, length of the longest root, and the percent of mycorrhizal colonization (Table 4-2).

DISCUSSION

Patterns of seedling occurrence and survivorship--

Pinyon seedlings were more prevalent under pinyon and under juniper canopy than expected based on their abundance and less prevalent under shrubs and in open areas. The importance of shrubs as nurses for pinyons has been suggested by several other studies (Blackburn and Tueller, 1970; Callaway et al., 1996; Charters, 1997) and it is possible that the importance of the shrub microsite was underestimated simply because shrubs were relatively rare at our site (6% of the available microsites). However, those studies that suggested the importance of shrubs examined juvenile pinyons rather than seedlings, while two studies that examined pinyon seedlings also found a higher number

of seedlings under trees than under shrubs (Evert et al., 1986; Chambers, 2001). Although this could indicate that the benefit of shrub versus tree nurses may differ throughout the life stages of the seedling, it is more likely that this difference was due to differences in the availability of these microsites. As pinyon-juniper woodlands expand into shrub environments, the percentage of shrub microsites declines (Eddleman, 1987) and in later successional stage pinyon-juniper woodlands, higher numbers of seedlings typically occur under trees compared to under shrubs (Chambers et al., 1999).

The increased abundance of seedlings found under tree canopies in this study and others could be a result of either enhanced germination in these microsites or arrival of a larger number of seeds to these microsites via abiotic or biotic seed dispersal mechanisms. Due to the large, wingless nature of pinyon seeds it is unlikely that they would be dispersed very far from the canopy of the parent without animals acting as vectors. In fact, Lanner (1972) estimated that a wind of 160 km/h would be needed to move a pinyon seed 10 m if it fell from a height of 10 m. Therefore, in the absence of seed dispersal by vertebrates, most seeds should fall to the ground and rest below the canopy of the parent. In contrast, this study demonstrated a seedling distribution nearly equal under pinyon (43 %) and juniper (37%) canopies for the first year after germination. These data are consistent with the hypothesis that seedlings arise from seeds moved to these microsites by vertebrates, a hypothesis supported by several other studies that have demonstrated that vertebrates remove a large percentage (80-100%) of seeds from the ground below pinyons (Christensen and Whitham, 1993; Martinez-Delgado et al., 1996; Vander Wall, 1997,). Both rodents and birds cache seeds in open microsites as well as under tree canopies (Vander Wall, 1997; Vander Wall and Balda, 1981), thus differential abundance of seedlings between open and canopy sites is most likely a combination of vertebrate dispersal and reduced germination and survival in open microsites.

Effects of juniper and pinyon nurses on survival, growth and mycorrhizal development--

In the pinyon-juniper system, the two dominant trees could represent very different nurse environments. I demonstrated that abundance of seedlings under junipers increased over time while relative abundance under pinyon canopy decreased. Likewise,

the cohort of marked seedlings showed the same pattern, with seedlings under junipers showing higher survivorship (14%) compared to those under pinyons (7%). These data suggest that seedlings nursed by junipers experienced some advantage. Chambers (2001) demonstrated that mean growing season temperature was higher under juniper (*J. osteosperma*) compared to pinyon (*P. monophylla*), therefore, I predicted increased shoot growth of seedlings under juniper. However, I found no significant differences in shoot growth between seedlings under junipers compared to pinyons. It is possible that higher temperatures under junipers may only have a positive effect on growth when water is not limited. I independently examined the growth for each of the growing seasons (2000, 2001) and did not find any significant differences. Although average precipitation differed between 2000 and 2001, both of these years were classified as drought conditions by NOAA.

I predicted lower seedling survival under junipers and that seedling nursed by junipers would have characteristics associated with low water availability such as higher root-to-shoot ratios and more lateral root development. However, I found higher survival under junipers and no difference in either of the two latter characteristics between seedlings under the two nurse types. This result is surprising in light of the different root systems of pinyon and juniper. Breshears et al. (1997) demonstrated that, in response to experimental watering, adult juniper acquired more of the water in the shallow layers of soil than adult pinyon. I expected the difference in water availability for the seedlings to be particularly influential given the drought conditions our study site experienced.

The lower water availability under junipers may also create a greater need for mycorrhizal associations. However, because junipers are endomycorrhizal (arbuscular mycorrhizal) and pinyons are primarily ectomycorrhizal, the lower inoculum potential for seedlings nursed by junipers could result in less mycorrhizal development. In spite of this, I found no differences in ability of pinyon seedlings to acquire ectomycorrhizae between the two nurse types. It is possible that pinyon may be abundant enough at the site that most pinyon seedlings encounter pinyon roots or hyphae even when under a juniper. In a recent study at another site in northern Arizona, Haskins (2003) grew pinyon seedlings in soil collected from pinyon dominated, juniper-dominated and pinyon-juniper areas. She demonstrated that levels of ectomycorrhizal colonization of seedlings

were 12 times greater when soils were taken from areas of pinyon dominance compared to juniper-dominated areas. She also demonstrated no difference in colonization rates between pinyon dominated and pinyon juniper areas, indicating that the presence of pinyon, regardless of its abundance, increases the ectomycorrhizal fungal inoculum potential for pinyon seedlings. Because ectomycorrhizal abundance has been shown to be positively and linearly correlated with pinyon seedling growth (Gehring and Whitham, 1994), it seems likely that juniper is only a better nurse when pinyons are also present at the site.

Although I did not see any differences in seedling growth or mycorrhizal associations between the two nurse types, both the change in distribution of seedlings over time and the results from our marked seedlings demonstrated higher survival under junipers. Chambers (2001) investigated *P. monophylla* seedlings and also demonstrated the highest survival in the microsite under junipers when seedlings were exposed to natural vertebrate herbivory. In contrast, seedlings that were protected from herbivory by cages survived equally well under pinyon. This suggests that the major advantage provided by juniper nurses may be better protection from herbivory. It is likely that this protection is provided by the overall lower canopy of juniper compared to pinyon at our site. I randomly sampled 25 trees of each species at our study site and found a significantly higher mean canopy height (distance from ground to lowest portion of the canopy) for pinyon (0.51 m) compared to juniper (0.09 m) ($t = 4.732, p < 0.001$). Callaway et al. (1996) found that 68-92% of *P. monophylla* seedling mortality was due to animal predation when nurse shrubs were removed compared to only 20% when shrubs were left intact. They also reported frequent observations of chewed stems and cut shoots indicating larger predators rather than pathogen or insects. Potential predators of seedlings included jackrabbits (*Lepus californicus*), mule deer (*Odocoileus hemionus*), yellow pine chipmunks (*Tamias amoenus*), woodrats (*Neotoma spp.*) and deer mice (*Peromyscus spp.*). All of these seedling predators occur on our study site and may have influenced survival rates via predation.

In pinyon-juniper woodlands of northern Arizona, junipers appear to be an important nurse plant for pinyon pine during the earliest stages of seedling development. The advantage of juniper nurses does not appear to be any factor that influences growth

or mycorrhizal colonization. Rather, I hypothesize that survival under juniper at our site was higher primarily as a result of the lower canopy of junipers nurses offering better protection from mammal herbivory.

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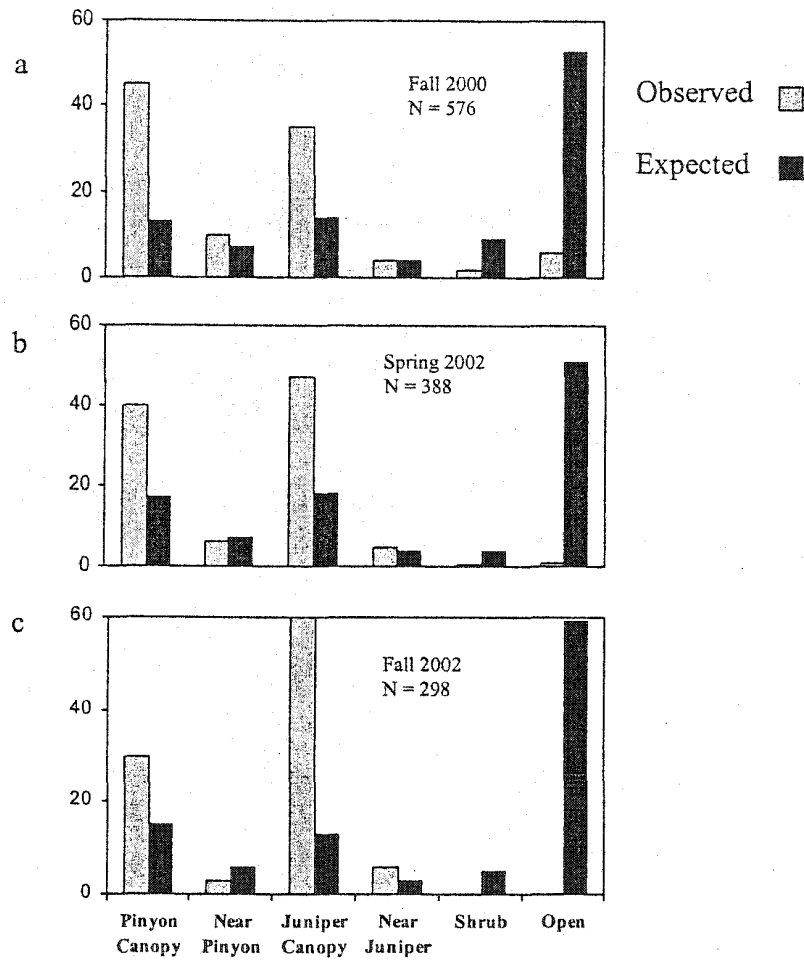
TABLE 4-1--Comparison of growth parameters measured in the field for *Pinus edulis* seedlings being nursed by pinyon versus juniper.

	PINYON (SD)	N	JUNIPER (SD)	N	<i>t</i>	<i>p</i>
Total Height (cm)	2.79 (0.7)	23	2.98 (0.9)	31	-1.069	.290
New Growth (cm)	0.86 (0.06)	19	0.92 (0.09)	24	-0.592	.558
Needle Length (cm)	1.58 (0.38)	20	1.53 (0.35)	23	0.439	.663
Number of Needles	25.2 (11.2)	20	25.6 (8.6)	24	-0.138	.891

TABLE 4-2--Comparison of growth and mycorrhizal development (mean (SD)) for *Pinus edulis* seedlings collected under pinyon (N = 15) versus juniper (N = 15) nurses.

	PINYON (SD)	JUNIPER (SD)	<i>t</i>	<i>p</i>
Shoot length (cm)	2.39 (0.52)	2.33 (0.67)	0.358	.722
Year 1 growth (cm)	1.01 (0.30)	1.02 (0.22)	-0.240	.812
Year 2 growth (cm)	1.39 (0.54)	1.32 (0.38)	0.506	.616
Total dry biomass (g)	0.37 (0.02)	0.38 (0.01)	0.822	.952
Root/Shoot biomass	0.15 (0.01)	0.16 (0.01)	0.612	.912
Number of lateral roots	8.60 (5.92)	7.05 (3.71)	0.992	.327
Length of longest root (cm)	14.5 (4.09)	15.2 (2.34)	-0.611	.545
% Mycorrhizal colonization	53	65	0.875	.523

FIG. 4-1--Distribution of pinyon seedlings among microsites relative to that expected based on availability of that microsite in a) Fall 2000, b) Spring 2002, and c) Fall 2002.



CHAPTER 5

CONCLUSIONS

The study of plant dispersal is important because it is the only mobile stage of the plant life cycle and because it creates a template for all subsequent population demographic processes. Although dispersal via seed-caching can have very high cost resulting from seeds being eaten, it often carries the advantage of seeds being dispersed to non-random sites. When these non random sites are favorable for germination this type of dispersal can be advantageous. In chapters two and three of this document I discussed the behavior of seed-caching rodents, the implications of that behavior for ponderosa pine dispersal, and the effect of fire on that plant animal interaction. In the fourth chapter I examined a plant-animals interaction from the perspective of the germination requirements of a vertebrate dispersed plant, pinyon pine.

The data presented here suggests that rodents non-randomly select sites favorable for germination and thus serve as directed dispersers of ponderosa pine seeds. I also presented evidence that, in burned forests, rodents preferentially move seeds into burned areas and specifically into burned substrate where seeds have increased germination and higher seedling survival. Taken together, these data suggest that rodents are important dispersers of ponderosa pine and that they enhance post-burn recruitment.

In chapter four I demonstrated that pinyon pine seeds dispersed to the microsite under juniper canopy have higher survivorship compared to other microsites. Although there were no differences in growth or mycorrhizal relationships that may account for the differences in survivorship, both transect studies and marked seedlings demonstrated that seedlings experience higher survivorship under juniper canopies. Because juniper canopies at the study site had significantly lower canopies, it is possible that junipers provided better protection from herbivory. Therefore, animal dispersers that select this microsite for caching could act as a form of directed dispersal in this system.