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Secondary Seed Dispersal of Longleaf Pine, *Pinus palustris*, and Sand Live Oak,
Quercus geminata, in Florida Sandhill

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Biology
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infestation

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Dedicated to my mother, Janice Ansley, for encouraging me to pursue my dreams and enabling me to do so, and to my daughter, Sophie Ansley, that I can give her the same opportunities.

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Secondary Seed Dispersal of Longleaf Pine, *Pinus Palustris*, and Sand Live Oak, *Quercus Geminata*, in Florida Sandhill

Shannon Elizabeth Ansley

ABSTRACT

Studies of secondary seed dispersal by small mammals have largely been focused on the interaction between nut-bearing tree species and sciurid rodents such as squirrels, and on heteromyid rodents in the southwestern United States. However, there is now evidence that wind-dispersed tree species such as pines also undergo a process of secondary seed dispersal, where animals redistribute (cache) seeds that have already fallen to the ground, often in microhabitats more suitable for successful seed germination. In Florida sandhill, where fire suppression has threatened wind-dispersed longleaf pine (*Pinus palustris*) by encouraging the encroachment of hardwoods such as sand live oak (*Quercus geminata*), secondary seed dispersal may be an important factor in determining community composition and persistence of longleaf pine systems. Using a combination of seed depots and seed predator exclosures, I looked at both longleaf pine and sand live oak in terms of whether small animals such as squirrels (*Sciurus carolinensis*) and cotton mice (*Peromyscus gossypinus*) cache the seeds, and where the seeds of these two tree species best germinate. Since sand live oak acorns are prone to infestation by weevils (*Curculio* spp.), I also examined whether nut condition affects acorn germination potential. I found that longleaf pine seeds are cached by small mammals to a small degree. While these seeds are not moved great distances from where they originate, they

are often redistributed into microhabitats that promote successful seed germination. Caging experiments indicated that seeds were most likely to germinate when buried in open areas between adult trees, and to some degree, under shrub cover. On the other hand, sand live oak acorns appear to face heavy predation by large seed predators such as raccoons (*Procyon lotor*) and wild pigs (*Sus scrofa*). Those acorns that do escape predation, including weevil-infested acorns, may provide an opportunity for seedling establishment. However, it appears that sand live oak depends heavily on vegetative sprouting for regeneration. This suggests that even in the absence of fire, longleaf pines in Florida sandhill are able to persist through secondary seed dispersal by small animals coupled with heavy seed predation on competing sand live oak.

INTRODUCTION

Diplochory

Diplochory is defined as being two or more seed dispersal phases with a different dispersal mechanism in each phase. This multi-step dispersal process is thought to increase the probability of seedlings establishing from just one phase alone (Vander Wall and Longland, 2004). Phase one occurs when the seeds are moved away from the parent in an attempt to decrease competition with, and predation under, the parent tree. Phase one is random with respect to where seeds land, often depositing the seeds in clumps which can increase predation risk, or in sites that decrease germination probabilities, such as into dense litter or on the soil surface (Vander Wall and Longland, 2004). For species such as pines, wind dispersal would be phase one; the gravitational drop of acorns from oaks is also an example of this phase.

Phase two concerns the movement of the seeds from their initial landing spot to “safe” sites, where they are somewhat protected from predation and environmental effects, and where there is an increased chance of seed germination. Often termed “directed dispersal” or “secondary dispersal”, this phase is seen as a higher quality dispersal process that redistributes seeds into sites that are usually favorable for seedling establishment (Lanner 1998). A small mammal scatterhoarding seeds that it has harvested from the ground would represent phase two of diplochory.

Seed Caching and Secondary Seed Dispersal by Small Mammals

As far back as the 1940s, studies have documented animals storing seeds for future use (Hatt, 1943; Spencer, 1941). Despite the importance of animal seed dispersal and the interaction between small mammals and plants, however, investigators have largely ignored this stage of seed dispersal except with respect to the general interaction between squirrels and acorns (Plucinski and Hunter, 2001; Steele et al., 2001; Steele et al., 1996; Weckerly et al., 1989; Stapanian and Smith, 1984) and heteromyid rodents in the southwestern United States (Longland et al., 2001; Price et al., 2000; Longland and Clements, 1995; Reichman, 1979; but see: Wang et al., 2004; Manson et al., 1999; Vander Wall, 1994; Price and Jenkins, 1986). As Vander Wall (1992) suggested, a tendency exists to focus on the first stage of dispersal, from parent plant to contact with soil. Generally, where small mammals have been investigated, the studies have usually been directed toward their roles as seed predators (Wenny, 2000; DeSimone and Zedler, 1999). Although most rodents are indeed seed predators, they also tend to be seed dispersers (Brewer, 2001; Price and Jenkins, 1986), when a proportion of their seed caches are not consumed.

Seed caching can potentially be beneficial to the plant species, the mammals that cache them, or both. Seed caching allows small mammals to guard against food scarcity and compete for limiting resources (Vander Wall, 1990; Jensen and Nielsen, 1986; Price and Jenkins, 1986), while the seeds may benefit through decreased predation by non-caching animals, decreased intraspecific competition with larger plants, and the potential for being buried in favorable germination sites (Forget et al., 2000; Vander Wall, 1990; Jensen and Nielsen, 1986; Price and Jenkins 1986). In fact, recolonization of cleared

sites has (in some cases) been attributed to mammal seed caches—in these cases, caching in open sites decreases chance of cache robbery, and simultaneously increases germination and survival probabilities (Kollmann and Poschlod, 1997; Dickman and Doncaster, 1989). Borchert and Jain (1978) found that in experimental sites in California grassland where rodents were present, recruitment of both small and large-seeded grass species was enhanced, while in sites where rodents were excluded, there was a negative effect on the abundance of small-seeded species because of interspecific competition with the larger-seeded species. Therefore, it appears that rodent seed-cachers may have an important role in the establishment of plant populations, especially in cleared sites. However, animals may cache seeds in sites that are not necessarily favorable for germination. Animals that cache seeds in these “bad” sites thus have a negative effect on seedling establishment (Hollander and Vander Wall, 2004). Directed seed dispersal by animals is not always towards the best germination sites, but it may be more likely to occur than with “random” wind dispersal (Purves and Dushoff, 2005).

The proportion of cached seeds that survive to germination is unknown, although estimates have ranged from 2.2% (Guariguata et al., 2000) to 15% (West, 1968), and as high as 99% (Vander Wall, 1994). However, Vander Wall (1990) argued that although only a small proportion of seeds may escape predation through caching, this dispersal method is so effective that some plants are primarily dependent on small mammals for seed dispersal. Indeed, nut morphology (i.e. being large and nutritious) and the fact that nuts and seed fall to the ground appear to be adaptations for dispersal by ground-dwelling small mammals (Vander Wall, 1990).

Probability of germination is likely a function of a number of factors such as plant species (Vander Wall 1990), seed size (Brewer, 2001; Price and Jenkins, 1986), and whether it is a masting year, where an increase in the seed crop can lead to an increase in the number and size of caches, as well as a higher probability of cached seeds going unrecovered (Vander Wall, 1992; Price and Jenkins, 1986), although high year-to-year variability in annual seed production (Herrera et al., 1998) may render this effect highly unpredictable. In addition to environmental stochasticity, however, microsite appears to be the single most important factor in determining whether a seed will germinate into a seedling (Xiao et al., 2005; Hollander and Vander Wall, 2004; Kollman and Pochslo, 1997).

Increasingly, researchers are looking at the interactions between seeds and animals beyond seed predation, to secondary seed dispersal and the processes involved in diplochory (Vander Wall et al., 2005; Brewer, 2001). The study of secondary seed dispersal allows a better understanding of plant population biology and the ultimate fate of seeds.

The Sandhill Community

Sandhill vegetation is a fire-adapted system of longleaf pine (*Pinus palustris*) over an understory of wiregrass (*Aristida stricta*) and scattered oaks, including turkey oak (*Quercus laevis*), and sand live oak (*Q. geminata*) (Myers and Ewel, 1990). The sandhill ecosystem occurs on the xeric, well-drained soils of the southeastern coastal plain of the United States, into the Florida panhandle and northern and central peninsular Florida. Sandhill vegetation is dependent on frequent fires; in fact, many of the vegetation species

have life cycles that are intrinsically linked with fire (Platt, 1998; Myers and Ewel, 1990; Rebertus, 1988).

Because of its long association with sandhill, fire is an important component of the disturbance regime. Historically, sandhill probably burned every 2-5 years in the early summer (May-June), when there is the highest probability of afternoon thunderstorms (Mushinsky and Gibson, 1991; Myers and Ewel, 1990; Rebertus, 1988). Fire is necessary to maintain the stability of the system, by decreasing canopy cover and litter, and increasing wiregrass and herbaceous plant densities (Streng et al., 1993; Mushinsky and Gibson, 1991). As well, if fires are frequent and low-intensity during the growing season, there is a higher probability of oak mortality, slowing hardwood invasion of sandhill. On the other hand, if the natural fire regime is interrupted and time between burns increases, there is increased canopy closure, greater litter depth, and an increase in the number of hardwood species (Mushinsky and Gibson, 1991; Rebertus, 1988). For example, Mushinsky and Gibson (1991) found that an annual burn plot had only 4% canopy cover, while an unburned plot had 45-60% canopy cover. In the absence of fire, hardwoods such as oaks quickly invade the ecosystem (Myers and Ewel, 1990; Humphrey, 1982).

The sandhill ecosystem is now considered endangered over much of its range. About 75-95% of the original 24 million hectares has been exploited for citrus culture, urban, and commercial development, reflecting the suitability of its well-drained soils for anthropogenic purposes (Richardson and Rundel, 1998; Myers and Ewel, 1990; Rebertus, 1988; Humphrey, 1982). Most of the remaining sandhill vegetation has been highly disturbed. In fact, even with the return of prescribed burns aimed toward restoring

longleaf pine and wiregrass, turkey oaks tend to dominate the system, and wiregrass populations are slow to regenerate (Rebertus, 1988). A number of hardwood species present in sandhill have seeds that are mainly mammal-dispersed, including oaks, hickory, dogwood, black cherry, southern Magnolia, and American holly (Myers and Ewel, 1990), which has implications for hardwood encroachment of sandhill in the absence of fire.

Objectives

1. To determine the extent to which diplochory occurs in the major sandhill tree species (longleaf pine, *Pinus palustris*) and an associated hardwood species, sand live oak (*Quercus geminata*). I examined whether secondary seed dispersal occurs with respect to both of these tree species, and the implications of diplochory on the composition of sandhill. No data exist on secondary seed dispersal of longleaf pine, but since mammals have been known to cache seeds of wind-dispersed species (Thayer and Vander Wall, 2005; Vander Wall, 1992), I felt that it was likely that longleaf pine, too, is secondarily dispersed. Small mammals readily cache acorns (Smallwood et al., 2001; Steele et al., 2001) and thus I hypothesized that mammals would cache sand live oak acorns (Abrahamson and Layne, 2003), which could lead to oak establishment in unoccupied patches.
2. To examine what factors affect germination probabilities of longleaf pine seeds and sand live oak acorns. Whether seeds are actively cached by animals or not, which microsites are most favourable to seedling establishment, and what are the consequences of these factors? With longleaf pine, it has been suggested that seeds

germinate best when in contact with soil (Boyer, 1990) in open areas (Platt et al., 1988). I hypothesized that longleaf pine seeds were more likely to germinate in open sites, and that burial would enhance germination. Estimates of seedling establishment for sand live oak are difficult to obtain, but other oak species germinate well when buried (Price and Jenkins, 1986) in open sites (Abrams, 1996), and I felt that this too would be the case for sand live oak.

Study Site

This study took place at the University of South Florida's Ecological Research Area (Eco Area) (28°05'N, 82°20'W) located in Tampa, Florida. The EcoArea is a one square mile tract of land that consists of sandhill, flatwoods, and swamps. In the southern portion of the tract, the Eco Area is divided into experimental burn plots of 6000m² to 20000m² in size. The vegetation in the Eco Area burn plots, as well as in patches north of these plots, is typical of the southern sandhill association found in xeric upland areas with sandy, fairly infertile soil. An open canopy is dominated by longleaf pine interspersed with turkey oak and sand live oak. The ground cover consists of various grasses (*Andropogon* spp., *Aristida stricta*), herbaceous plants (*Pityopsis* spp., *Liatris* spp., *Eupatorium* spp., *Aster* spp.), and saw palmetto (*Serenoa repens*).

The Eco Area is home to a number of seed predators and potential seed dispersers, including grey squirrels (*Sciurus carolinensis*), cotton mice (*Peromyscus gossypinus*), cotton rats (*Sigmodon hispidus*), wild pigs (*Sus scrofa*), raccoons (*Procyon lotor*), white-tailed deer (*Odocoileus virginianus*), and wild turkey (*Meleagris gallopavo osceola*).

CHAPTER ONE

SECONDARY SEED DISPERSAL OF LONGLEAF PINE

Introduction

Longleaf pine, of the Family Pinaceae, is found in the upland sandy soils of the United States coastal plain, from Virginia to Texas and into south-central Florida. Longleaf pine is extremely drought-tolerant, because of a large taproot, but is also quite shade-intolerant, preferring open canopies maintained by frequent fires in order for its seedlings to flourish (Fralish and Franklin, 2002), although seedlings and juveniles can persist in the shade (Gordon Fox, pers. comm.). Its entire lifecycle is intrinsically linked to fire. Where fire is suppressed by humans or does not occur naturally, hardwood species are able to invade into open areas, decreasing the number of patches available for colonization by longleaf pine seedlings. Only 5% of the original longleaf pine woodlands still remain, reflecting fire suppression and agricultural practices (Richardson and Rundel, 1998).

Longleaf pine masts every 7-10 years, producing winged seeds that are dispersed primarily by wind. Longleaf pine releases its seeds in the fall, and germination occurs during the relatively dry winter (Whitney et al., 2004). Longleaf pine recruits mostly into open spaces between adult trees; seeds do not germinate well if shaded by adult trees or if under heavy litter (Platt et al., 1988), or if there is no contact between seed and soil

(Boyer, 1990). Early growth of the seedlings is heavily weighted toward the development of a deep taproot that reaches far into the soil to maximize uptake of nutrients and water (Whitney et al., 2004). In xeric sandhill, water limitation may strongly affect the distribution of longleaf pine seedlings if they are competing with neighboring seedlings for limited soil nutrients and moisture. It is also likely that seedlings compete strongly for light. Whitney et al. (2004) argued that any aggregation of seedlings that occurs as a result of dispersal eventually shifts to a more diffuse distribution as a result of this competition, but it may depend more on the amount of light available, as many open spaces in longleaf pine woodlands are occupied by clusters of pine seedlings.

Longleaf pine seedling biology is largely unknown. Seedlings are thought to spend the first 2 to 12-15 years in what is known as the “grass stage” (Burns and Honkala, 1990a), where a grass-like bunch of needles surrounds the fire-resistant apical bud. After accumulating sufficient carbohydrate stores, the seedling “bolts” in a rapid growth phase that takes the apical meristem out of the range of most fires within 2-3 years (Keeley and Zedler, 1998). Because longleaf pine self-prunes its lower branches, once a tree is above the critical height of approximately 1.5m, it increases its odds of escaping major damage from the low-intensity ground fires that naturally occur in longleaf pine stands (Agee, 1998), although trees at least twice this height can be killed by fire (Gordon Fox, pers. comm.).

Recruitment of longleaf pine is highly episodic and is most likely to occur during mast years (Platt et al., 1988). Wind causes the seeds to fall randomly with respect to site from the source tree. The openness of longleaf pine stands makes it likely that some

seeds fall into open spaces, but many more fall into less suitable germination sites, such as into shrubs or in areas of dense litter. The majority of seeds on the ground likely are subject to predation by animals. Also likely, some proportion of these seeds is carried away by scatterhoarding animals into ground caches (Lanner, 1998). Seeds in caches that are unrecovered by the animal that cached them or by a naïve forager, if placed in suitable microsites, can germinate, adding to the existing pine population. Several studies have documented small mammals actively caching wind-dispersed pine seeds (Thayer and Vander Wall, 2005; Vander Wall, 2002; Abbott and Quink, 1970). In fact, caching may be extremely important where seeds and seedlings are faced with moisture limitation, as buried seeds are less likely to dehydrate than are seeds on the soil surface (Vander Wall, 1990). In sandhill, caching of longleaf pine seeds may be advantageous in promoting seedling establishment, especially in open sites.

The traditional forestry theory is that wind-dispersed seeds fall into cracks and depressions in the soil in order to reach safe sites for germination (Lanner, 1998). Lanner (1998) points out that because there is no evidence for this theory, it is most likely based on the reasoning that seeds would not be able to survive on the soil surface because of high levels of dehydration and because of predation. While it is possible that seeds could be dispersed into soil cracks, it would be hard to gather evidence confirming this, and it seems more likely that many seeds are actively carried away by small animals and buried in sites that may be favorable for germination, in the second phase of diplochory. As diplochory in wind-dispersed pines has not been well-documented, my first objective was to determine to what extent diplochory occurs in longleaf pine.

Regardless of how a seed arrives at a potential germination site, environmental factors play an important role in determining the likelihood that the seed will be able to germinate (Xiao et al., 2005). My second objective was to determine how much more likely longleaf pine seeds are able to germinate in “ideal” open areas as opposed to under shrub cover, and the differences that result from being buried (as in an animal cache) as to lying on the soil surface (as in random wind dispersal).

Methods

Caching By Small Mammals

In October 2005, I chose five mature longleaf pines within the study area. At each tree, I set up 20 seed depots (a Petri dish glued to a 30.5cm x 35.6cm tray) in a pattern that simulated wind dispersal (Table 1). This “wind dispersal” pattern was adapted from Greene and Johnson’s (1989) conifer seed wind dispersal model and corresponding experimental results. The seeds at each depot were marked with fluorescent powder (Radiant Color, Richmond, CA); each tray was filled with fluorescent powder to mark the feet of any animals visiting the depots.

Table 1. Number and density of seeds at varying distances of depots from source tree to simulate a wind-dispersed seed shadow.

Distance From Tree (m)	Number of Depots	Number of Seeds/Depot	Density (Seeds/m ²)
4	8	55	8.75
8	8	58	3.08
12	4	25	0.40

I checked the depots every two days and counted the number of seeds removed: “eaten” (empty hulls) or “gone” (completely eaten or carried away from the depot). I also went out at night on days 5 and 10 with a handheld ultraviolet light to track powder trails and find cache sites. I marked each cache site with a flag, and returned the next day to measure the following cache characteristics, after checking that the cache was still present: cache size, distance from depot, and distance from tree.

I measured percent cover of grass and shrubs to use in my statistical analyses as measures of vegetation structure. I walked four 24m transects in an area that encompassed the seed depots around each tree. At 8m intervals along each transect, I determined the percent cover of grass and the percent cover of shrubs. I did this by estimating the amount of ground covered by grass and shrubs in a 1m² quadrat and converting my estimates into percent cover.

Germination Success by Microhabitat and Presence of Small Mammals

This experiment took place in the winter months, from December 2005 to March 2006. I established a 3-way factorial design with the following levels: open ground vs. under shrub canopy, caged vs. uncaged, and buried vs. unburied seeds. Each cage measured 0.5m x 1.0m x 0.3m and was made of fiberglass screening stapled to wooden stakes. The screening was buried > 5cm into the ground at the bottom of the cages to prevent animals from burrowing under the edges.

Fifteen cages were placed in “open” habitats (open canopy with a mixture of sandy/grassy soil surface). The other 15 cages were placed in “shrub” habitats (in shrubby stands of bushes/oak trees). One half of each cage was randomly assigned

“buried” and the other half was designated as “unburied”. Twenty-five longleaf pine seeds were placed within each of these treatments (50 total per cage) in a 5 x 5 pattern, with the “buried” seeds being buried 1 cm in the ground and covered with a light layer of topsoil, and the “unburied” seeds being placed directly on the soil surface. Fiberglass screening was stapled over the top of the cages to prevent birds and other seed predators from removing the seeds. This screening caused minimal shading effects. Controls (uncaged treatments) were established within 1m of each of the cages. Cages were monitored every few days for evidence of germination.

Statistical Analyses

Statistical analyses were performed in SAS (v9.1) and SigmaStat (v3.1). For the seed depot and caching data, I examined seed removal rates via life table analyses of survival probability and hazard functions. Thompson’s chi-square test for spatial patterning using nearest-neighbor methods was used to determine the spatial distribution of cache sites (Thompson, 1956). The observed χ^2 value is tested against two alternative hypotheses, where a significantly small value of χ^2 (i.e. less than $\chi^2_{0.975}$ at $\alpha = 0.05$) signifies an aggregated pattern, and a significantly large value of χ^2 (i.e. more than $\chi^2_{0.025}$ at $\alpha = 0.05$) implies uniform patterning. Any χ^2 values that fall within this range indicate that the data is randomly patterned. I used both nearest-neighbor and second-nearest neighbor methods to analyze spatial pattern, as both can provide information on spatial distribution. For example, if there is an office building with two people in each office, using nearest-neighbor methods would likely indicate that individuals are in a clumped pattern. Using second-nearest-neighbor distances would likely show a more uniform

pattern. Increasing levels of nearest-neighbor distances would probably not add much more information with respect to spatial pattern. In the case of seed caches, nearest-neighbors may be clumped, but on the scale of second-nearest-neighbor mean distances, caches may demonstrate a more regular pattern as a whole. A one-way ANOVA and Holm-Sidak pairwise comparisons were used to determine whether caches were made disproportionately with respect to habitat. I used logistic regression to relate seed fate to vegetation cover.

A log-linear model for count data, assuming a Poisson distribution and utilizing a log link function, was used to examine the effects of protection level (caged or uncaged), habitat (open site or under shrub cover), and microsite (buried or on top of soil) on germination of longleaf pine seeds. The model tested the individual effects and their interactions on the fate (i.e. germination or not) of pine seeds.

Results

Caching By Small Mammals

Within 10 days, $98.9 \pm 1.37\%$ (mean \pm 1 SD) (97.21-99.9%) of longleaf pine seeds were removed, with a mean removal rate of 99.94 seeds per day. Empty hulls indicated that $5.57 \pm 6.79\%$ (0.60-17.13%) of the seeds were eaten at the depots. Life table survival estimates indicate that there was a short delay immediately following the placement of the seeds in the depots, followed by a rapid but steady decrease in survival of the seeds over time (Figure 1). The hazard function, which is the per capita probability of death at any one time given survival up to that time, increased sharply after an initially steady rate (Figure 1).

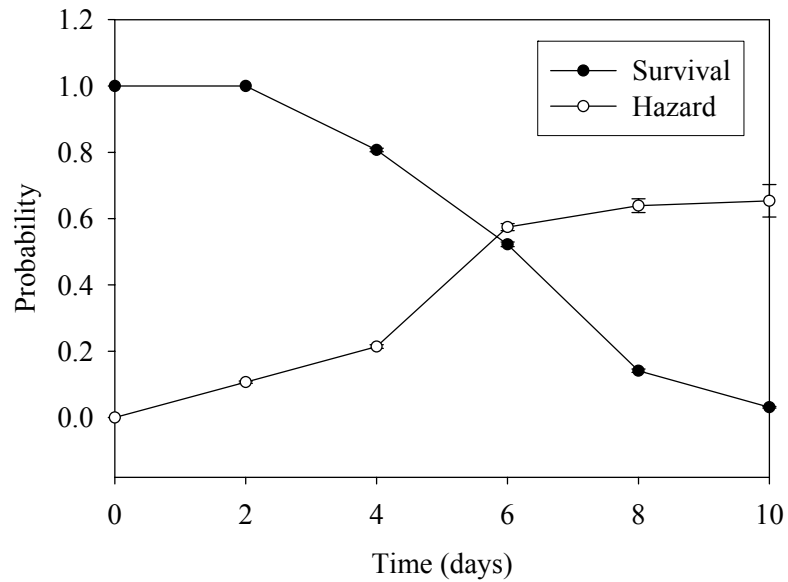


Figure 1. Survival distribution and hazard functions (± 1 S.E.) for longleaf pine seeds. Error bars are not always visually apparent because sample size is on the order of 5000.

I was able to track $1.91 \pm 0.34\%$ (1.39-2.29%) of the seeds to caches made by small animals. Figure 2 shows the location of these caches relative to each individual tree.

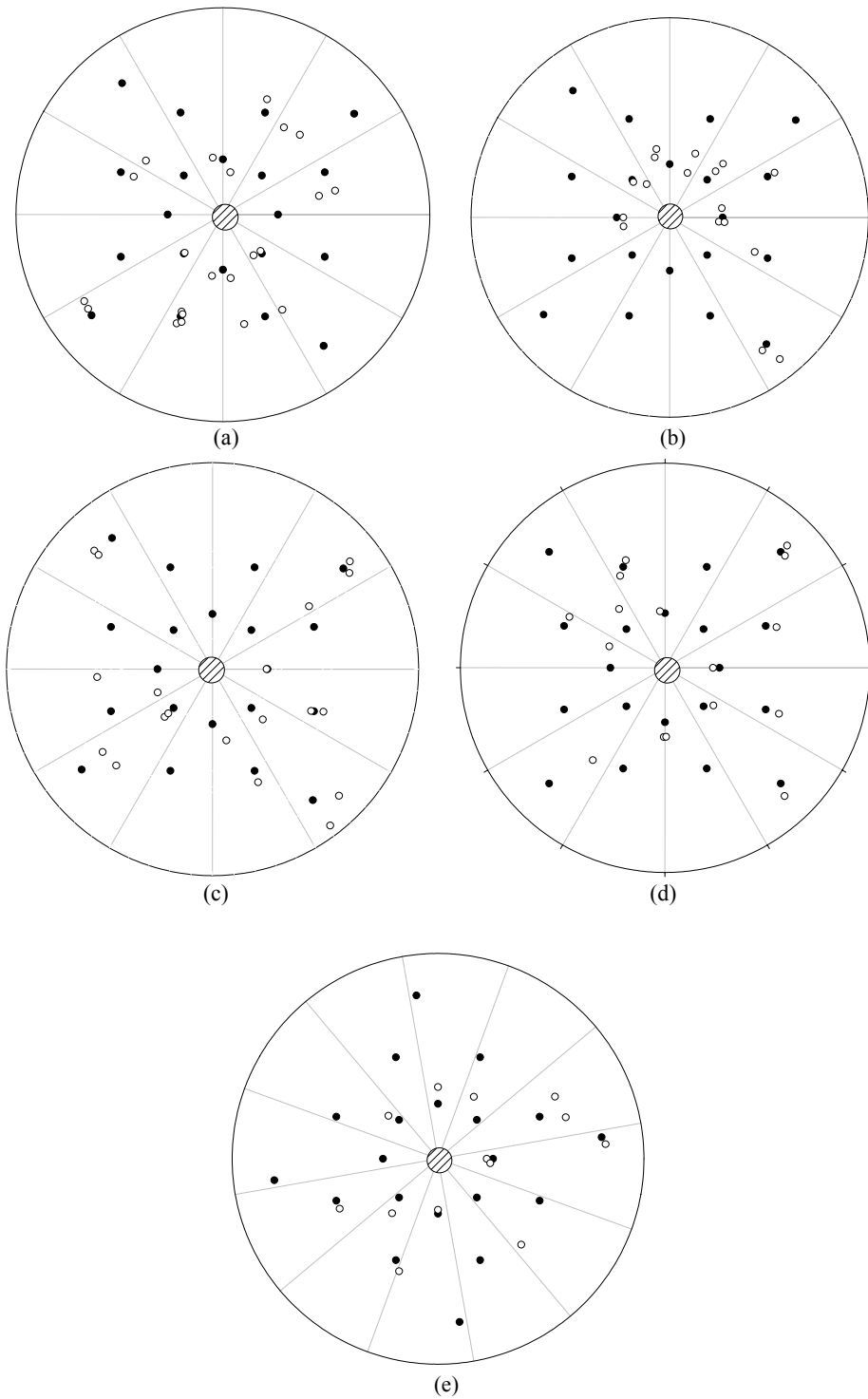


Figure 2. The locations of longleaf pine seed caches made by small mammals around each of five source trees, (a) tree one, (b) tree two, (c) tree three, (d) tree four, and (e) tree five. Source tree is represented by the cross-hatched circle. Filled circles represent locations of seed depots. Open circles represent locations of caches.

Using nearest-neighbor data, I determined that caches around trees one and two were distributed in a clumped pattern ($\chi^2_{44} = 22.65$, $p < 0.05$ and $\chi^2_{34} = 14.01$, $p < 0.05$ respectively; Table 2). Caches around tree three were randomly distributed ($\chi^2_{38} = 39.84$, $p = 0.388$; Table 2). Trees four and five had caches that were uniformly distributed ($\chi^2_{32} = 59.37$, $p < 0.05$ and $\chi^2_{26} = 38.33$, $p < 0.05$ respectively; Table 2).

Table 2. Spatial pattern of longleaf pine seed caches around source trees as a function of nearest-neighbor distances.

Tree	df	χ^2	p	Spatial Pattern
1	44	22.65	0.0032	Clumped
2	34	14.01	0.001	Clumped
3	38	39.84	0.3882	Random
4	32	59.37	0.0023	Uniform
5	26	38.22	0.0578	Uniform

When second-nearest-neighbor data were used, the distribution of caches were uniformly distributed around trees one, three, four and five (Table 3). Tree two had randomly distributed cache sites (Table 3).

Table 3. Spatial pattern of longleaf pine seed caches around source trees as a function of second-nearest-neighbor distances.

Tree	df	χ^2	p	Spatial Pattern
1	88	160.53	<0.0001	Uniform
2	68	74.89	0.2648	Random
3	76	181.05	<0.0001	Uniform
4	64	122.83	<0.0001	Uniform
5	52	88.47	0.0012	Uniform

I analyzed third-nearest-neighbor data for tree two, and found that on this scale, caches were distributed in a random pattern around the tree ($\chi^2_{102} = 125.73$, $p = 0.0555$).

Although this p value is not quite significant, it indicates that as higher-level nearest-neighbor distances are used, caches show a more uniform distribution.

The number of seeds cached per tree ranged from 13 to 22 seeds (mean = 17.4 ± 3.36 seeds) (Table 4). The majority of these caches had one seed in them (mean = 1.09 ± 0.03 seeds/cache; range 1-2) (Table 4).

Table 4. Number and size of longleaf pine seed caches made by small mammals. No significant difference exists among trees.

Tree	Number of Caches Made	Number of Seeds Cached	Cache Size	
			Mean	SD
1	22	23	1.05	0.21
2	17	20	1.12	0.33
3	19	21	1.11	0.32
4	16	18	1.13	0.34
5	13	14	1.08	0.28

Seeds were not moved very far from their originating depots (mean = 0.93 ± 0.29 m), but were generally moved away from the trees toward the canopy edges (a mean net distance of 0.33 ± 0.28 m away from the tree) (Table 5). Seed caches appeared to be somewhat clustered in distribution.

Table 5. Longleaf pine seed movements and dispersal distances.

Tree	Seed Movements Relative To Their Origin		Secondary Dispersal Distance (m)			
	Toward source tree	Away from source tree	Mean*	SD	Shortest	Longest
1	12	10	-0.084	0.56	0.08	3.59
2	7	10	0.25	0.84	0.07	2.55
3	5	14	0.33	1.02	0.08	2.96
4	3	13	0.49	0.56	0.20	1.45
5	3	10	0.65	0.74	0.26	1.82

* A negative dispersal distance indicates that seeds were moved toward the source tree.

When cache sites were characterized by microhabitat, I found that 48.28% of the caches were made in open, grassy sites, 33.33% were made in bare sandy soil, and 18.39% were made under shrubs and dense vegetation. Numbers of caches made were significantly different as a function of microhabitat, as shown by both a χ^2 test and a one-way ANOVA ($F_{2,12} = 4.105$, $p < 0.05$). Holm-Sidak pairwise multiple comparison procedures showed a significant difference between the number of caches made in grass as opposed to in shrub microhabitats ($p < 0.05$).

Grass cover among sites ranged from 60.31-86.63% (mean = $69.39 \pm 10.70\%$), while shrub cover was 9.94-39.69% (mean = $29.18 \pm 11.61\%$) (Figure 3). A generalized logistic model indicated that grass cover, shrub cover, and the interaction between the two types of cover, all had significant effects ($p < 0.05$) on the fate of seeds, i.e. whether seeds were eaten immediately or cached (Table 6).

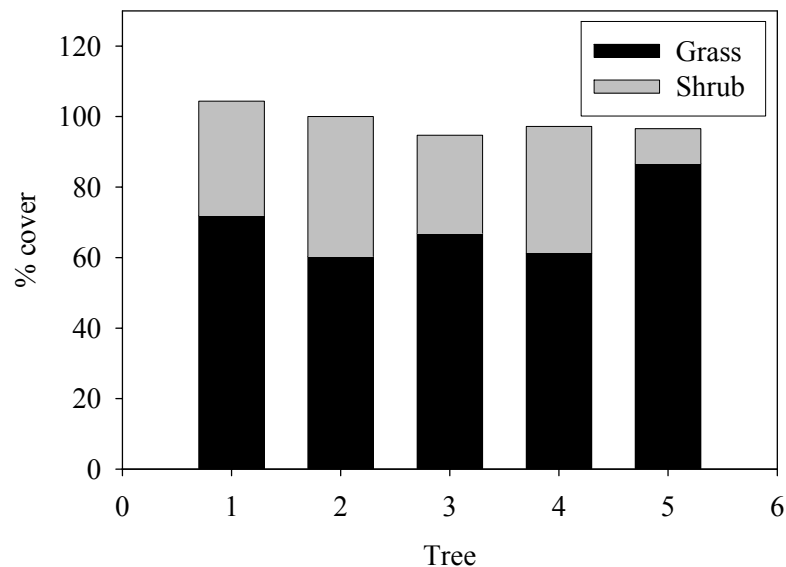


Figure 3. Percent cover of grass and shrubs around source longleaf pines. Grass cover and shrub cover are not mutually exclusive as both can be present in a given location.

Table 6. The effects of grass cover and shrub cover on the fate of longleaf pine seeds.

Source	df	χ^2	p
Grass cover	1	4.11	0.0426
Shrub cover	1	12.93	< 0.001
Grass cover x shrub cover	1	20.45	< 0.001

Germination Success by Microhabitat and Presence of Small Mammals

The mean number of germinated seeds for each main effect of protection, habitat, and microsite are shown in Figure 4.

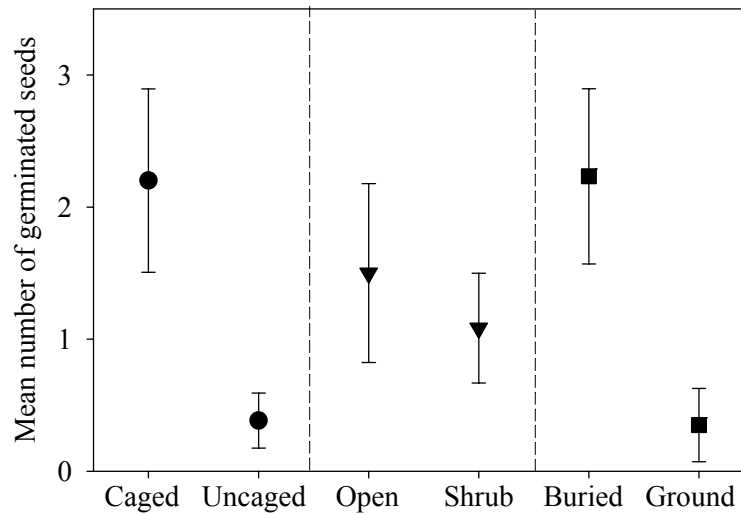


Figure 4. The separate effects of protection, habitat, and microsite on the germination of longleaf pine seeds. Error bars represent standard error.

The combined effects of protection and habitat on the mean number of longleaf pine seeds that germinated when either buried or on soil surface are shown in Figure 5.

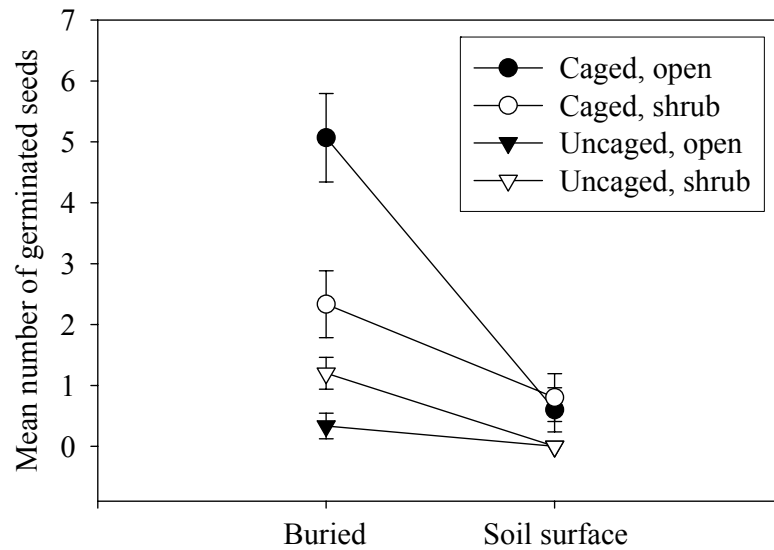


Figure 5. The effects of habitat (open areas vs. under shrub cover) and protection (uncaged controls vs. caged treatments) on germination of buried and ground-surface longleaf pine seeds. Error bars represent standard error.

A log-linear model (a generalized linear model assuming a Poisson distribution and utilizing a log link function) tested the main effects “protection”, “habitat”, and “microsite”, the three two-way interactions, and the three-way interaction, in relation to pine seed germination.

Protection: Caged vs. Uncaged

When caged, 2.20 ± 2.69 seeds germinated, while only 0.38 ± 0.80 uncaged seeds germinated. Protection from predation significantly affected germination probabilities ($\chi^2 = 57.03, p < 0.05$; Table 7).

Habitat: Open Ground vs. Under Shrub Cover

More seeds germinated in open areas (1.50 ± 2.62 seeds) than did under shrub cover (1.08 ± 1.61 seeds), but not significantly so (Table 7).

Microsite: Buried vs. Soil Surface

Seeds germinated in significantly higher proportions ($\chi^2 = 47.70$, $p < 0.05$; Table 7) when buried (2.23 ± 2.57 seeds) than when on the soil surface (0.35 ± 1.07 seeds).

The Effects of Habitat and Protection

The effect of caging was greater in open areas (2.83 ± 3.15 seeds germinated) than in shrubby areas (1.57 ± 1.98 seeds germinated), but not significantly (Table 7). Interestingly, the opposite was true in the uncaged controls, where more seeds germinated in shrubby sites than in open sites (0.60 ± 0.93 and 0.17 ± 0.59 seeds, respectively).

The Effects of Habitat and Microsite

The difference between the number of buried seeds that germinated and those on soil was greater in open areas (2.7 ± 3.15 buried, 0.30 ± 1.02 on the ground) than in shrubby areas (1.77 ± 1.74 buried, 0.40 ± 1.13 on the ground), but not significantly so (Table 7).

The Effects of Protection and Microsite

The effect of caging was greater for buried seeds than for those on the ground, but not significantly so (Table 7). When seeds were buried, 3.7 ± 2.82 caged and 0.77 ± 1.01 uncaged seedlings arose, while 0.70 ± 1.44 caged seedlings came from seeds on the soil surface. No uncaged seeds on the soil surface survived to produce seedlings.

The Effects of Habitat, Protection, and Microsite

The effects of protection and microsite (i.e. buried vs. soil surface) were more prominent with seeds that were in open areas. With open areas, the difference between caged and uncaged seeds was much larger for buried seeds than for those on the ground. Under shrub cover, the difference between caged and uncaged seeds was only slightly

higher with buried seeds. There was basically no difference in germination proportions between protection levels with seeds placed on the soil surface, whereas there was a large difference between protection levels for buried seeds.

Table 7. Likelihood ratio statistics for Type III analysis of the effects of fate, habitat, protection, and microsite on germination of longleaf pine seeds.

Source	df	χ^2	p
Fate	2	24983.10	< 0.001
Protection x fate	2	57.03	< 0.001
Habitat x fate	2	0.49	0.783
Microsite x fate	2	47.70	< 0.001
Protection x habitat x fate	2	2.13	0.345
Protection x microsite x fate	2	3.23	0.199
Habitat x microsite x fate	2	0.46	0.796
Protection x habitat x microsite x fate	2	3.07	0.216

Discussion

Evidence exists that diplochory does occur in longleaf pine, and that small animals do cache wind-dispersed seeds. While only a small percentage of seeds were found in caches, these seeds have the potential to add to the existing pine population. Regardless of how seeds arrive in a potential germination site, those that are in open areas have a better chance of surviving to seedlings. Burial also enhances germination success by offering more protection from both predation and dehydration than is afforded those that are lying on the soil surface.

Seeds in depots were removed rapidly after an initial delay, indicating that seeds lie on the soil surface for a short period before being found by animals. After seeds were discovered, hazard for an individual seed increased substantially. It appears that animals have the potential to remove an entire seed crop within a few weeks, eating some and caching others. More than 90% of the seeds in the depots were unaccounted for, so those seeds not immediately eaten appear to have been transported away from their origin. While the fate of these seeds is not known, seed removal does not necessarily imply seed predation (Vander Wall et al., 2005; Brewer, 2001). Perhaps some of these seeds also were cached. Vander Wall (1993) stressed that misinterpretation of seed removal results can lead to an overestimation of seed predation rates, especially in cases such as this where secondary seed dispersal through caching occurs.

Less than two percent of pine seeds were located in caches. This number seems small until longleaf pine life history is taken into consideration. Longleaf pines produce their first cones in about their thirtieth year, and depending on the size of an adult, pines can produce between 15 and 65 cones annually, with an average of 35 seeds per cone (Boyer, 1990). Over a lifetime of 70 years, two percent of an individual tree's seed yield could potentially result in anywhere from 700 to several thousand pine seeds being cached. The number of seedlings resulting from these caches would of course depend on successful germination and seedling survival. However, as longleaf pines can live several hundred years (Boyer, 1990), recruitment could likely be quite significant.

Seeds were not moved great distances, but secondary dispersal does not necessarily mean that there is any advantage to the seed in terms of increasing dispersal distances. Instead, seeds are redistributed around the source with an emphasis on

directed dispersal, often toward favorable germination sites (Vander Wall and Longland, 2004). Caches close to other caches tended to be aggregated or uniformly distributed. However, second-nearest-neighbor caches were regularly spaced. This suggests that animals rearrange wind-dispersed seed shadows into a more uniform distribution, although individual caches may be clumped together to a small degree. In this case, the process of caching actually redistributed the seeds in a more evenly-spaced distribution than that displayed by wind dispersal (Vander Wall and Longland, 2004).

The majority of seeds were cached in open sandy and grassy areas, while only a small proportion were cached under shrubs. While directed dispersal does not always favor the species being dispersed, in this case, the seeds were placed in sites where longleaf pine seeds do better: in open areas between adult trees (Platt et al, 1988). The animals largely avoided caching pine seeds under the shade of shrubs where pine seeds often fail to germinate. Thus, directed dispersal of longleaf pine by small animals may be toward advantageous microsites, which may be important in maintaining the current longleaf pine population and in colonizing open spaces.

The caging experiment demonstrated that buried seeds are far more likely to germinate than are seeds placed on the soil surface. Wang et al. (2004) found that seeds of oil tea (*Camellia oleifera*) germinated significantly more when buried than when left on the soil surface. Burial of seeds both enhances germination and decreases predation rates (Guariguata et al., 2000; Crawley, 1997). All of the uncaged seeds on the soil surface and many of the caged ground-surface seeds were removed by animals; some may have been cached but it is likely that many were eaten. Most of the seedlings originated from buried treatments, especially those protected from animals. Also, it is

likely that seeds on the soil surface are subject to dehydration over hot, dry winters, which may decrease the likelihood of germination (Lanner, 1998).

Those seeds in open habitats were also more likely to survive to germination than those under shrub cover. This is most likely due to the fact that small mammals prefer some degree of cover to decrease predation risk (Vander Wall, 1990), and seeds under shrubs are more accessible than those in the open. Kollman and Poschlod (1997) suggest that seed survival increases with openness because less cover is available as protection for small seed predators. Many animals also cache their seeds in open areas to decrease cache pilferage (Vander Wall, 2000; Vander Wall, 1990), so these seeds are less prone to a naïve animal locating them. However, a number of seeds did germinate under shrub cover. Because the literature strongly suggests that pine seedlings in the shade do not survive as well as those in open areas (Keeley and Zedler, 1998), further study on first and second year seedling survival would help to determine the importance of habitat in seed germination.

Both Price and Jenkins (1986) and Shaw (1968) found that seeds protected from mammals were better able to germinate. However, even without caging, a small proportion of seeds, both buried and on the soil surface germinated (Shaw, 1968). In my study, all of the seeds that were uncaged and on the soil surface were removed. This suggests that seeds on the ground are prone to heavy predation and are not likely to survive to germination. This also suggests that longleaf pine seedlings most likely arise from animal seed caches, since some that were buried were able to establish, regardless of protection level.

Thus, diplochory does occur in longleaf pine, with a proportion of the seed crop being cached by small animals. Those cached seeds that go unrecovered, if buried in suitable sites such as open areas, and to some degree under shrub cover, are able to germinate. These seeds that germinate into seedlings are the ones that will contribute to the existing pine population.

CHAPTER TWO

SECONDARY SEED DISPERSAL OF SAND LIVE OAK

Introduction

Sand live oak (*Quercus geminata* Small) is a white oak in the Family Fagaceae. It is a semi-evergreen broadleaf shrubby tree that is found in the lower coastal plain of the United States, from Louisiana to North Carolina and stretching into Florida. Sand live oak is usually found in xeric to mesic sites subject to nutrient and water limitations, such as sandhill (Fralish and Franklin, 2002). While sand live oak does respond to fire by vegetative resprouting, it actually invades more readily as fire intervals increase (Menges and Kohfeldt, 1995). In the absence of fire, sand live oak, along with other hardwood species such as turkey oak (*Q. laevis*), has the tendency to replace longleaf pine (*Pinus palustris*) in the southeastern pine-hardwood associations (Fralish and Franklin, 2002).

Sand live oak produces acorns every year, and most trees in a given population mast every 2-6 years. These acorns mature and drop in the fall and, like other white oak acorns, germinate shortly after landing on the ground. This lack of dormancy, coupled with a large amount of stored carbohydrates, makes the acorns highly palatable to seed consumers (Abrahamson and Abrahamson, 1989).

In northern temperate forests, squirrels and other small mammals readily cache vast quantities of acorns (Smallwood et al., 2001; Steele et al., 2001; Barnett, 1977).

However, the amount of acorn caching that occurs in southern sandhill is not known. While resprouting of sand live oak may aid in local population maintenance, secondary dispersal via small animals may allow colonization of new patches within the open sandhill system, allowing sand live oak to more easily invade and replace longleaf pine stands. Therefore, my first objective was to determine if secondary dispersal of sand live oak acorns occurs in Florida sandhill. I hypothesized that since acorns of other oak species are secondarily dispersed by small mammals, it is likely that sand live oak acorns will undergo a similar process.

Although oak species do not tend to be light-limited, oaks readily establish large numbers of seedlings with rapid growth rates in high light environments (Abrams, 1996). In characteristically-open sandhill, fast growth rates offer many opportunities for sand live oak to rapidly regenerate. The amount of light available to sand live oak may affect the success of acorn germination. As well, although white oak acorns do tend to germinate shortly after seed drop, some species of oak are unable to germinate on the soil surface (Price and Jenkins, 1986). Thus, my second objective was to determine the microsite that best enhances sand live oak acorn germination. I hypothesized that burial in open sites would enhance germination of sand live oak acorns.

Weevils of the Family Curculionidae attack acorns of different species to varying degrees (Branco et al., 2002; Steele et al., 1996; Andersson, 1992). The adult female oviposits eggs into maturing acorns. These eggs hatch within 1-2 weeks, and the larvae dwell inside the acorn, feeding on the endosperm for at least two weeks before chewing an exit hole and leaving the acorn to continue development underground. Weevil larvae can infest up to 70% of an acorn crop in a given year (Steele et al., 1996). Animals are

known to actively select seeds and manage their caches, often rejecting weevil-infested seeds (Crawley and Long, 1995; Vander Wall, 1990). Roth and Vander Wall (2005) observed a chipmunk picking out infested bush chinquapin seeds while carrying away sound seeds. Rejected weevil-infested acorns have the potential to germinate and provide a means of seedling establishment for an oak population, if the acorn embryo is not damaged and if enough of the endosperm remains (Branco et al., 2002). My third objective was to determine whether uninfested acorns are preferred over weevil-infested acorns, and to what extent weevil-infested acorns are able to germinate. I felt that sound acorns would be taken preferentially over infested acorns, and that infested acorns would be able to germinate despite damage to the endosperm.

Methods

Removal and Caching By Small Mammals

This experiment took place in October and November 2005, during natural seed fall. I chose five mature sand live oak (*Q. geminata*) trees within the study area. At each tree, I set up 10 seed depots (a Petri dish glued to a 30.5cm x 35.6cm tray) in a circle around the tree. The radius of this circle was 5m; the trays were approximately 3.14m apart. This circular pattern is similar to that shown by gravitational dispersal of acorns.

At each depot, I placed 80 acorns marked with fluorescent powder (Radiant Color, Richmond, CA). I also filled each tray with fluorescent powder in order to mark the feet of any animals visiting the depots. I checked the depots every other day and counted the number of acorns removed from each depot. Removed acorns were further categorized as “eaten” (empty acorn hulls present at or around depot) or “gone” (either

completely eaten or carried away from the depot). On day 6 of this experiment, I went out at night with a handheld ultraviolet light to track any fluorescent powder trails.

Germination Success by Microhabitat and Presence of Small Mammals

This experiment took place over the winter, from December 2005 to March 2006. I established a 3-way factorial design with the following levels: caged vs. uncaged, open ground vs. under shrub canopy, and buried vs. unburied. Each cage measured 0.5m x 1.0m x 0.3m and was made of fiberglass screening stapled to wooden stakes. The screening was buried > 5cm into the ground at the bottom of the cages to prevent animals from burrowing under the edges.

Fifteen cages were placed in “open” habitats (open canopy with a mixture of sandy/grassy soil surface). The other 15 cages were placed in “shrub” habitats (in shrubby stands of bushes/oak trees). One half of each cage was randomly assigned “buried” and the other half was designated as “unburied”. Twenty-five acorns were placed within each of these treatments (50 total per cage) in a 5 x 5 pattern, with the “buried” acorn being buried 3-4 cm in the ground and covered with a light layer of topsoil, and the “unburied” acorns being placed directly on top of the soil surface. Fiberglass screening was stapled over the top of the cages to prevent birds and other seed predators from removing the seeds. This screening caused minimal shading effects. Controls (uncaged treatments) were established within 1m of each of the cages. Cages were monitored every few days for evidence of germination.

The Effects of Weevil Infestation on Removal and Germination

To determine infestation rates of a typical crop of acorns, I counted the number of acorns with weevil holes from a sample of 1000 acorns. Acorns were collected in October 2005, at the time of natural seed fall. I used the presence or absence of weevil holes as an estimate of the maximum amount of damage that a weevil larva could inflict before exiting an acorn.

Transect Experiment

In November 2005, I established ten 120m transects throughout the study area. Each transect consisted of 24 stations placed 5m apart, with one acorn per station. On each transect, half of the acorns were sound (intact nut with no weevil holes) and half of the acorns were infested (visible weevil hole), and I assigned their positions randomly. Transects were monitored daily to determine removal rates.

Greenhouse Experiment

This part of the study took place at the greenhouse in the University of South Florida's Botanical Gardens from November 2005 to March 2006. I randomly assigned 120 sound and 120 infested acorns to 240 pots in the greenhouse. I planted individual acorns at a depth of 2.5 times the width of the acorn in potting soil within these pots, and watered them every other day. I monitored these acorns every few days for emergence and germination proportions and rates.

Statistical Analyses

Statistical analyses were performed in SAS (v9.1) and SigmaStat (v3.1). I used life table analyses to examine removal rates for both acorns from depots, and for acorns

from transects. Logistic regression was used to determine the effect of nut condition on germination in the greenhouse.

Results

Removal and Caching By Small Mammals

Within 16 days, $99.58 \pm 0.61\%$ (mean \pm 1 SD) (98.5-100%) of the acorns were removed, with a mean removal rate of 49.79 acorns per day. $15.6 \pm 12.22\%$ (3.25-29.63%) of the acorns were eaten at the depots (shown by empty hulls at or around the depot). Life table survival estimates indicate that survival probabilities initially remain high, then begin to steadily decrease (Figure 6). Hazard, the probability of non-survival at a time x given survival until time x , increases gradually before suddenly peaking, and then declines sharply before increasing quickly again (Figure 6).

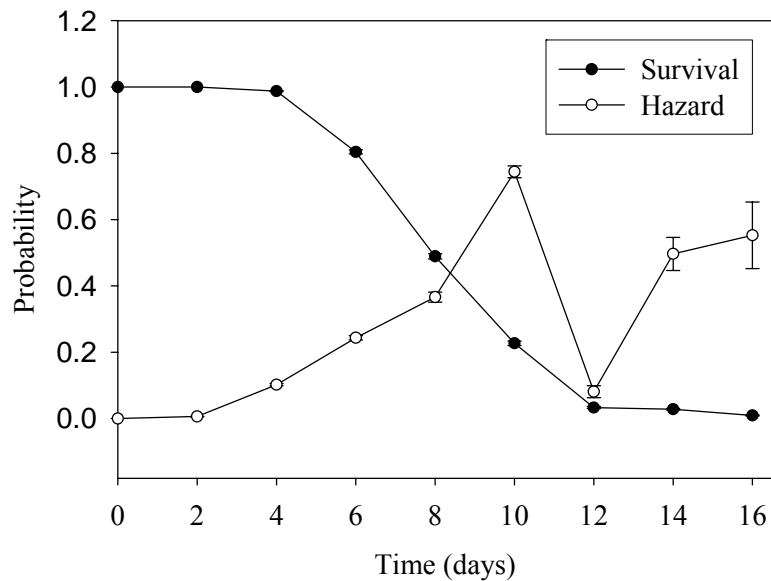


Figure 6. Survival distribution and hazard functions (± 1 S.E.) for sand live oak acorns.

It was impossible to tell, however, if any acorns were carried away by small animals, because one or more raccoons visited each depot at all 5 trees, strewing the fluorescent powder around and making it difficult to track anything other than raccoon prints, which are easily identifiable in the field.

Germination Success by Microhabitat and Presence of Small Mammals

Only 0.23% of the acorns survived to germination. Twenty-eight of the thirty cages were knocked over and uprooted by what looked like wild pigs and raccoons. As well, more than 90% of the acorns that were used in this experiment were removed.

Of the seven acorns that germinated, 100% of them had been buried. Six acorns (85.7%) were in open sites, while the remaining acorn was under shrub cover. Four of the seven seedlings (57%) came from caged treatments, and the other three (43%) from uncaged controls.

The Effects of Weevil Infestation on Removal and Germination

3.6% of the acorns that I surveyed for weevil infestation had weevil holes.

Transect Experiment

Within 8 days, 94.2% of sound acorns and 77.5% of infested acorns were removed. Both sound and infested acorns were removed at a steady rate after the first day (Figure 7). Nut condition significantly affected daily removal rates (Wilcoxon chi-square, $p < 0.05$). The mean survival time of sound acorns was 3.54 ± 2.14 days, while the mean survival time of infested acorns was 4.78 ± 2.38 days. A Wilcoxon test indicated that nut condition had a significant effect on mean survival time between the

two groups ($p < 0.05$). The hazard function, which estimates the probability of death given survival up to that time, indicates that while infested acorns are prone to a slight increase in removal over time, sound acorns are much more at risk, with a large increase in the probability of being eaten the longer that they remain on the ground (Figure 8).

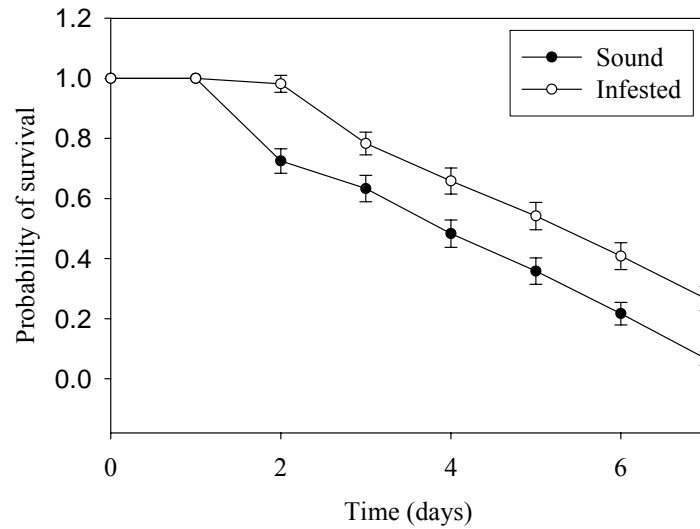


Figure 7. Survival probabilities (± 1 S.E.) of sound and weevil-infested sand live oak acorns from transects.

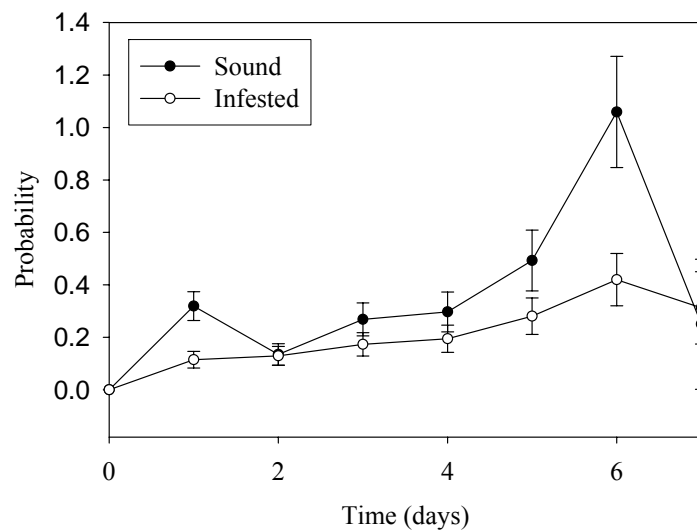


Figure 8. Hazard function (± 1 S.E.) for sound and weevil-infested sand live oak acorns from transects.

Greenhouse Experiment

Within 118 days, 35.8% of sound acorns and 12.5% of infested acorns germinated. Type III analysis through logistic regression indicated that nut condition significantly affected the number of acorns that germinated ($p < 0.05$).

However, the mean time to germination did not differ significantly with respect to nut condition (Mann-Whitney rank-sum test, $p = 0.797$) (Figure 9). Sound acorns germinated in 75.2 ± 16.0 days, while infested acorns germinated in 78.3 ± 22.3 days.

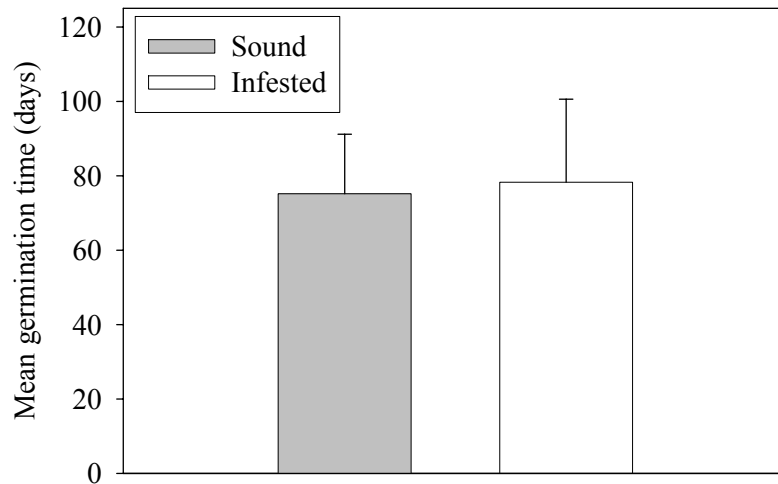


Figure 9. Mean (± 1 S.E.) germination times of sound and infested sand live oak acorns.

The probability of a weevil-infested acorn surviving to germination is 0.0281, while the probability of a sound acorn surviving to germination is 0.0208 (Figure 10).

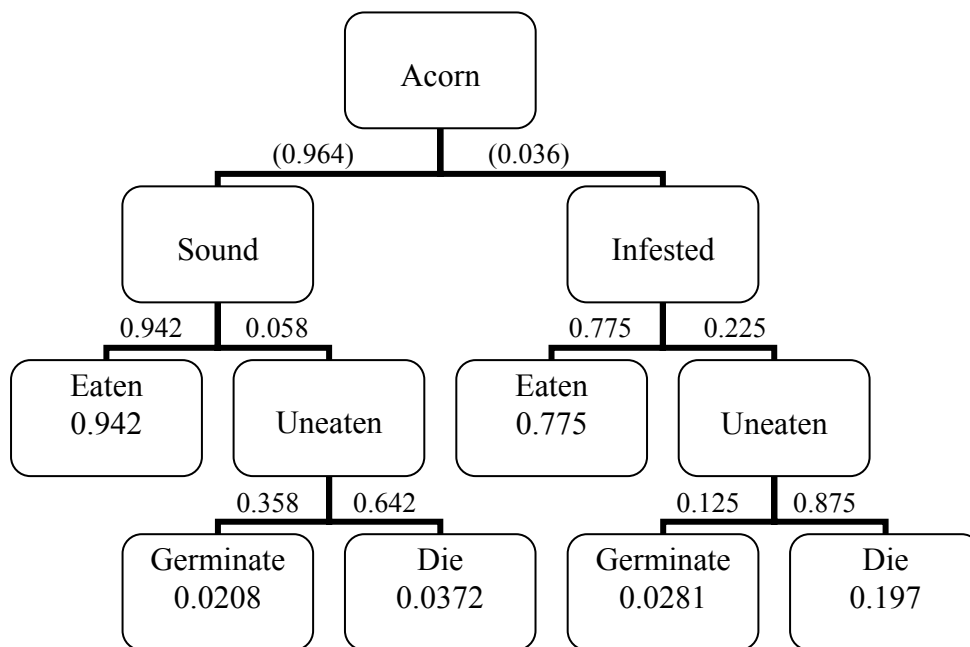


Figure 10. The cumulative probability of survival to germination for sound and weevil-infested acorns. Numbers on branches indicate conditional survival probabilities. Numbers in brackets indicate the probability of nut condition and are not included in survival probability calculations.

Discussion

It is evident that sand live oak acorns are subject to extremely high levels of predation in Florida sandhill. However, those acorns that do manage to escape predation, including weevil-infested ones, may provide a means of seedling establishment.

Acorns from seed depots were removed fairly quickly from seed depots. There was a delay between when the depots were put out and when raccoons found the seeds. There was then another delay, which might be explained as a period where the raccoons ate to satiation, rested for a day or so, and then returned to finish eating the seeds. While the depots may have attracted the animals by promising a concentration of food, I feel that this is unlikely, as there were many acorns on the ground around the source trees as

well. There is the potential that other small animals may have had brief opportunities to move acorns into caches, but unfortunately there is no evidence of such. Large mammal exclusion experiments may help determine if small mammals are actually caching acorns, but they would most likely give an overestimate of seed caching proportions. While raccoons can be seed dispersers of various types of fruit (LoGiudice and Ostfeld, 2002; Cypher and Cypher, 1999), it is unlikely that they are dispersers of acorns. The only exception would be if acorns were only partially consumed, and if the embryo was still intact. In this case, the acorns may still be able to germinate (Branco et al., 2002).

The caging experiment again points to high levels of acorn predation. Uncaged acorns were found almost immediately; even buried acorns were dug up. Cages were destroyed by large seed predators (most likely wild pigs and raccoons). It is important to note that the animals were not cueing into the cages themselves; pine seed cages close by were not destroyed or even touched. While further study is required, it is likely that these large seed predators are attracted to the odor and relatively high nutritional value of the acorns; it is unlikely, however, that these animals provide much in the way of secondary seed dispersal. The mechanical disturbance of the soil caused by these large animals digging around in the soil may cause some seeds to become inadvertently buried and perhaps escape predation (Thayer and Vander Wall, 2005; Alexander et al., 1986), but it appears that most acorns are eaten. The seven seedlings that were found to originate from my cages represent a very small (<1%) proportion of the original number of acorns that I put out. While the fact that all of them emerged from burial sites points to animal caching as providing a means of germination, without further testing it is almost impossible to speculate on the implications of this seedling establishment.

However, while only a small proportion of acorns were able to germinate, one must consider the implications of long-term acorn production by sand live oak. Sand live oak can produce acorns within the first year (Carey, 1992). While estimates of annual sand live oak acorn production are vague, other white oaks can produce from 200 to over 2000 acorns annually (Stransky, 1990). Oaks are long-lived species (Fralish and Franklin, 2002), and an estimate of 70 acorn-producing years is conservative, but even over this time period, a sand live oak could potentially produce 14,000 to several hundred thousand acorns. While less than 1% of these acorns may survive to germination, they represent an addition of 20 to several hundred oak seedlings to the understory, per adult oak.

Interestingly, animals were less likely to remove weevil-infested acorns than they were to remove sound acorns. Transect experiments showed that infested acorns were more likely to spend more time on the ground, offering possibilities for both germination and for small animals to eventually carry off and cache. Weevil-infested acorns clearly are able to germinate, although less so than sound acorns (Branco et al., 2002; Fukumoto and Kajimura, 2000; Andersson, 1992). However, when the probability of an acorn surviving predation is taken into account with the probability of germination, there is very little difference between sound and infested acorns; in fact, an infested acorn has a slightly higher probability of surviving to germinate. If infested acorns are rejected by seed-eating animals, it may provide a way for acorns to escape predation and produce viable seedlings (Weckerly, 1989). Since white oak acorns germinate so soon after seed drop, those weevil-infested acorns that are left behind, if able to germinate on the soil surface, may enhance that escape mechanism. While less than 5% of the acorns that I

surveyed were weevil-infested, that proportion most likely increases over time (Steele et al., 1996), suggesting that infested acorns may make up a significant proportion of those seedlings that originate from acorns. Further study on seedling viability over time would be useful in determining the extent to which infested acorns contribute to a standing oak population.

However, despite the large acorn crops that can result from sand live oaks, seed germination and seedling establishment appears to be relatively rare in the upland sandhill habitats (Abrahamson and Layne, 2003). Sand live oak depends heavily on clonal expansion for population maintenance, which most likely counteracts the incredibly high levels of predation to which sand live oak acorns are subject. Sprouting likely allows the persistence of sand live oak in sandhill systems. However, while acorn escape and survival to germination may be rare, it is probably still important in oak recruitment in the long-term (Clark and Hallgren, 2003), contributing to the presence of sand live oak in the sandhill understory.

DISCUSSION

Secondary seed dispersal does occur in Florida sandhill, at least with respect to longleaf pine. Sand live oak, and most likely other oak species such as turkey oak (*Q.laevis*), appear much more at risk of seed predation, and secondary seed dispersal is likely rare.

During the caging experiments, large seed predators (most likely wild pigs, deer, and raccoons) knocked down cages to get to the acorns. Pine seed cages in close proximity to the destroyed acorn cages were untouched. Large seed predators were probably attracted by the odor of the acorns (Vander Wall, 2000). While a majority of uncaged pine seeds were eaten, the results of the caging experiments indicate that when a higher quality food is available, animals will opt for those, affording the other seeds an opportunity to escape predation and germinate. In sandhill, where acorns of several oak species are readily available, pine seeds stand a relatively good chance of surviving to establish seedlings.

Acorns are more desirable food sources than are wind-dispersed pine seeds because of their higher moisture and nutrient content (Fornara and Dalling, 2005). Larger seeds such as acorns are also prone to higher predation risk than are smaller seeds, especially with large seed predators that have large energy needs (Taulman and Williamson, 1994; Price and Jenkins, 1986); acorns, with their high levels of fat,

digestible carbohydrates, and other nutrients, fulfill these energy needs more than smaller, drier wind-dispersed seeds (Abrahamson and Abrahamson, 1989). Alternate sources of food may cause differences in foraging and caching behavior. Thus, when evaluating the fate of seeds, it is important to consider all of the food sources available to seed predators and potential seed dispersers (Roth and Vander Wall, 2005).

The sandhill system may be somewhat self-sustaining, even in the absence of frequent fire. Longleaf pine has the ability to regenerate through both random wind dispersal events and through the secondary dispersal of seeds via animal caching. It is also likely that large seed predators such as wild pigs, deer, and raccoons, may be indirectly aiding in burying wind-dispersed seeds through the disturbance of soil caused by foraging for larger seeds (Thayer and Vander Wall, 2005; Alexander et al., 1986). Sand live oak seedling establishment, on the other hand, appears to be suppressed by the presence of these large seed predators. It is likely that the oak species in sandhill counteract the lack of secondary seed dispersal by vegetatively sprouting (Abrahamson and Layne, 2003).

Regardless, a very complex interaction exists in the sandhill. Although even without frequent fires, longleaf pine appears to be persisting (at least in this study area), sand live oak has a propensity to invade as fire intervals increase. Frequent fires likely keep the oak population somewhat under control while creating the open spaces necessary for pine seedlings to establish. With widespread fire suppression in sandhill, the ability of longleaf pine to continue to colonize open patches may depend to quite some extent on mammalian seed dispersers.

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