FLORIDA INTERNATIONAL UNIVERSITY

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SOIL SEED STOCKS OF TROPICAL HARDWOOD HAMMOCKS IN SOUTHERN FLORIDA : IMPLICATIONS FOR RESTORATION

A thesis submitted in partial satisfaction

of the requirements of the degree of

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by

Laura J. Flynn

1998

To: Dean Arthur W. Herriott
College of Arts and Sciences

This thesis, written by Laura J. Flynn, and entitled Soil Seed Stocks of Tropical Hardwood Hammocks in Southern Florida: Implications for Restoration, having been approved in respect to style and content, is referred to you for judgement.

We have read this thesis and recommend that it be approved.

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The thesis of Laura J. Flynn is approved.

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Florida International University, 1998

I dedicate this thesis to my husband Joe

for his guidance, support , and most of all, patience.

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ABSTRACT OF THE THESIS

SOIL SEED STOCKS OF TROPICAL HARDWOOD HAMMOCKS IN SOUTHERN FLORIDA : IMPLICATIONS FOR RESTORATION

by

Laura J. Flynn

Florida International University, 1998

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Professor Bradley Bennett, Major Professor

Tropical hardwood hammocks are evergreen, broad-leaved forests occurring in southern Florida and throughout the Caribbean basin. I examined the soil seed stocks of hardwood hammocks in six south Florida sites. Three sites represent urban, fragmented forests situated along coastal uplands of mainland Florida and three sites are located in relatively undisturbed forests in northern Key Largo. The purpose of my research was to determine the species composition and abundance of seeds in the soil, and to determine the abundance and distribution of exotic seeds in this community. Seed bank characteristics were determined by collecting soil samples every 5 m along two 50 m transects at each site. A total of 1970 seedlings, representing 64 species emerged from all combined soil samples. Approximately, 4% of the seedlings were exotic. Sites differed in total seed density and in species composition of the seed bank. Detrended Correspondence Analysis showed distinct species composition patterns from mainland and Keys seed banks. Based on seed bank patterns and phenological data, I classified seed bank strategies for hardwood hammock species.

To understand the potential role of a soil seed bank in restoration of hardwood hammocks, I examined how buried seeds corresponded to the vegetation. Importance values, based on relative basal area, relative frequency, and relative cover were calculated for trees and shrubs. I compared these importance values with species percentages of seeds recovered in the soil. Similarity of buried seeds to the vegetation was low, using Jaccard's coefficient. Detrended Correspondence Analysis showed distinct seed bank and vegetation associations. A comparison of successional stages represented in the vegetation and the seed bank shows that there are consistent ratios between early, mid and late successional species among the sites. Based on these results, I recommend that the seed bank be considered when restoring tropical hardwood forests.

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INTRODUCTION

Fragmentation and exotic species alter ecosystem processes and confound management of natural areas. In fragmented forests, the influence of adjacent ecosystems often become more ecologically significant than internal processes (Saunders et al. 1991). To manage natural systems effectively, it is necessary to understand how ecological processes have been altered. Common changes include edge effects, which influence microclimate, wildlife composition and plant population processes, such as seed dispersal. In some cases, fragmented forests are more susceptible to the establishment of exotic plants (Hobbs and Huenneke 1992, Brothers and Spingarn 1992). Exotics compete with natives, often changing forest structure, and patterns of forest regeneration. Yet, there is little understanding of how exotics establish within natural systems (Thompson 1991).

There were more than 500 hammocks ranging in size from 0.1 ha to over 40 ha, totaling approximately 4,573 ha, at the turn of the century in Dade County, Florida (Craighead 1974, Davis 1943). Today, less than 5% of the original hammock area remains (Shaw 1975, R. Hammer personal communication).

Nearly 1/3 of the species are exotic (Horvitz 1995). To understand the role of these species, Horvitz et al. (in press) examined the influence of exotic plants on forest regeneration following Hurricane Andrew (August 1992). They concluded that the abundance or persistence of exotic seeds in the soil may also play an important role in post-disturbance successional dynamics in hardwood hammocks.

Recent studies suggest that modification of the landscape around fragments affects soil seed bank characteristics (Quintana-Ascencio et al. 1996). Previous research in tropical forests shows that soil seed banks account for much regeneration following disturbance, and composition and abundance of seeds affect regeneration in various ways (Garwood 1989). A seed bank in tropical forests has been defined to include all seed buried in the soil and those on the surface, and several strategies relating to dormancy and regeneration have been identified for tropical seed banks (Garwood 1989). However few tropical species have persistent seed banks.

Because seed banking can be an important aspect of plant life cycles and forest regeneration, I examined the abundance and composition of both exotic and native seeds in the soil to determine the role of seed banks in southern Florida tropical hardwood forests. I measured species composition and densities, and examined the differences in these characeristics among three seasons. My objective was to provide information on the potential role of native seed banks in restoration efforts and to quantify exotic seeds in the soil. I hypothesized that the species composition of seeds in the soil of fragmented hammocks would differ from that of less disturbed, continuous forests. Based on previous seed bank studies in tropical forests, I anticipated that most seeds would represent early successional species, and that there would be seasonal patterns in the composition and abundance of seeds recovered in soil samples related to the fruiting phenology of banking species (Garwood 1989, Guerva and Gomez-Pompa 1972). I predicted that the number of exotic seeds in the soil would be higher in areas of heavy exotic vegetation cover. High densities of exotic seeds in the soil would indicate the regenerative advantage of exotic species, perpetuating their detrimental role in this community. I also expected that some very widespread exotic species would occur in soils of hammocks that have low exotic cover, and that widely dispersed exotic seeds would play a role in establishment of these particular species.

STUDY SITES AND METHODS

Sites description

Rockland tropical hammocks occur at relatively high elevations (1.5 m to 4 m) of the Miami rock ridge, on the Keys, and in eastern Big Cypress swamp (Snyder et al. 1990). The flora includes approximately 150 species of semideciduous and evergreen trees and shrubs that form a closed canopy forest. Most are common in the West Indies, reaching their northern range limits in Florida (Craighead 1971, Little 1978, and Long & Lakela 1971). The hammocks of the Keys are included in Holdrige's (1967) Tropical Dry Forest Life Zone and Walter's (1985) Zonobiome II (tropical with summer rains) (Ross et al. 1992). The southern portion of mainland Florida borders on a subtropical classification due to slightly lower average temperatures (Holdridge 1967).

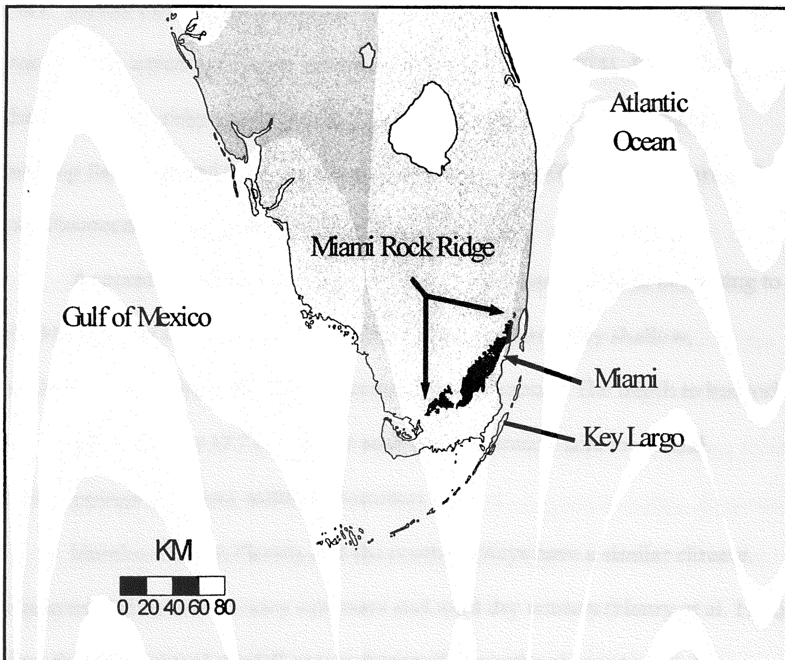


Figure 1. Map of study area. Three sites are located in the vicinity of Miami, FL. Three sites are also located in northern Key Largo.

To determine variation in hammock seed banks, I selected six study sites, three on the eastern mainland, and three in North Key Largo (Figure 1). Mainland sites for this study include, Matheson Hammock (135.9 ha), Simpson Hammock (17.8 ha), and Addison Hammock (296.5 ha) at the Deering Estate.

These three hammocks represent remnants along the Miami rock ridge, a limestone outcrop extending from downtown Miami to Everglades National Park. Miami Limestone, is a soft oolitic limestone formed approximately 130,000 years ago in a shallow marine environment (Hoffmeister 1974). Elevations along the Miami rock ridge never exceed 7 m (Snyder et al. 1990). This limestone outcrop first emerged from the sea approximately 120,000 years ago during the late Pleistocene (Hearty and Kindler 1995).

A recent soil survey assigns soils in mainland hammocks as belonging to the Matecumbe series (Noble et al. 1996). These soils are very shallow, moderately well drained, rapidly permeable and organic. The depth to bedrock is typically 5.1 cm to 12.7 cm. These soils are moderately acid to neutral. Outcroppings of Miami oolite are common.

Mainland South Florida and the northern Keys have a similar climate, characterized by warm, rainy summers and mild dry winters (Henry et al. 1994). Two thirds of annual rainfall occurs during the months of June to October. Rainfall is greater on the mainland, where wet season conditions typically begin earlier in late April (Henry et al. 1994). The northern portions of the Miami rock ridge receives an average of 1,525 to 1,650 mm a year. Rainfall diminishes south in the Keys, with the upper Keys receiving an average of 1,015 to 1,145 mm (MacVicar and Lin 1984). Frosts occur occasionally on the mainland and less frequently in North Key Largo (Henry et. al. 1994). The effect of climate on hammock vegetation is apparent in the drought deciduous nature of many of the species.

I also selected 3 sites in North Key Largo. These sites are part of a contiguous forest that is approximately 3,800 hectares (Strong et al. 1994). One site occurs in the Crocodile Lakes National Wildlife Refuge, and two occur within Key Largo Botanical Preserve. The hammocks in this area are largely intact, though State Road 905 bisects the island near its highest elevation. Early aerial photos (1926) show much of this area in cultivation (M. Ross, personal communication). At this time, northern Key Largo was extensively cleared for agriculture, including pineapple (*Ananas comosus* (L.) Merr), Key lime (*Citrus aurantifolia* (Christm.) Sw.), and sapodilla (*Manilkara zapota* (L.) van Royen) (Viele 1996). Both Key lime and sapodilla are found in the vegetation today. Over the last 50 years, the area was largely abandoned and allowed to recover to native forest.

The surface rock in the Upper Keys belongs to the Key Largo Limestone, which comprises fossil coral reef materials. Soils here are classified as

Pennekamp gravelly muck and Matecumbe muck (Hurt et al. 1995), these are mildly to moderately alkaline organic soils. Depth to the bedrock is typically 4 to 16 inches (Hurt et al. 1995).

Soil samples

At each site, I established two transects 50 m in length. Along these transects, I collected soil in ten 625 cm^2 plots to a depth of 3 cm at 5 m intervals. I constructed a frame from galvanized steel to collect the specified area of top soil. Preliminary data collected in June 1994 at Matheson Hammock provided me with an estimate of the appropriate sample size. I collected soil three times between late April 1995 to mid-March 1996. These sampling periods coincided with early wet season (late April and early June), late wet season (mid-November) and late dry season (mid-March). Because the beginning of the rainy season typically occurs slightly later in North Key Largo, my first sampling period in this area was approximately one and a half months after samples were collected on the mainland. Late wet season and mid-dry season samples were all collected during a one week time period.

Immediately after collecting samples, I spread the soil into 27 cm x 35 cm flats containing a base layer of sterilized germination mix. Soil depth was 5.5 cm. I placed the samples in full sunlight. To provide regular irrigation, the flats were watered for 15 minutes, once a day in the late evening. This watering schedule ensured that the soil became saturated once a day, while allowing it to dry in the late afternoon. I adjusted the irrigation system as needed during the wet season by lengthening or shortening the duration of watering. Germination slowed after 4 weeks. At this time, I stirred the soil and continued to monitor germination for an additional 12 weeks. Twenty control flats contained only sterilized soil. I maintained each of the sampling sessions for 16 weeks.

Seeds typically began to germinate within two weeks. Using plastic toothpicks, I marked emerging cotyledons, allowing seedlings to remain in the flats until they could be accurately identified. North American taxonomy described here follow Kartesz (1994). When seedlings could not be readily identified, I transplanted all unknown species and grew them until I could identify them. I inspected flats at least 2 times a week, often 3 or 4 times.

Vegetation sampling

Around each transect, I established vegetation plots within a 20 m x 55 m plot. I measured all tree species with a dbh 7.5 cm and greater. I selected this plot size to represent the vegetation that was most likely the source of seed rain in the soil samples. I recorded dbh, and estimated crown diameter. To facilitate measurement of trees less than 7.5 cm, and at least 2 m tall, I established a 5 m x 55 m subplot nested within the larger plot. In this case, I assumed that the smaller canopy trees would not disperse seeds as far as larger trees.

Species Composition

I used Detrended Correspondence Analysis to summarize the species composition data for all of the sites. Site scores were generated from the species percentages of all seeds germinating from the three sample periods.

Soil Sieving

Following the first sampling period, I sieved soil samples using a 0.1 mm to 4 mm sieve to recover seeds that had not germinated under the conditions specified above. I assumed that seeds that were intact, and did not float in water were viable. I was able to identify seeds to species from herbarium specimens and a seed collection.

Phenological surveys

Once a month I recorded stages of flowering, and the presence of immature and mature fruit in each of the vegetation plots. I also surveyed areas adjacent to the plots. I collected these data to correlate phenological patterns to seeds recovered from the soil at any one sampling period. As herbarium specimens are typically collected when species are flowering or fruiting, I used herbarium specimens for those species that were recovered in the germination trials, but had not been observed in the phenological surveys to supplement these surveys. I also referred to the literature, most specifically to Tomlinson (1980) and Loope (1980).

Other seed and species parameters

I recorded habit, species origin, fruit type, dispersal mechanisms and approximate seed size, referring to the literature as needed (Long and Lakela 1971, Tomlinson 1980, and Scurlock 1992). To supplement estimates of seed sizes in the literature, I measured seed size of several species from herbarium specimens.

Based on my field observations, I categorized species into early, mid-, and late successional. For the purposes of this analysis, I define early successional species as those that can germinate under high light conditions and with the exception of vines, these species do not persist in the vegetation once the canopy re-establishes (e.g., *Trema micranthum* (L.) Blume). Seeds of these species are relatively small, typically less than 5 mm. Mid-successional species germinate under both full sun and shade and may persist in later seral stages (i.e *Bourreria ovata* Miers). Late successional species included those species that are found predominantly in mature forests.

Seed Longevity of Exotic Species

To test persistence of two abundant invasive species in mainland hammocks, I collected and buried seeds of *Jasminum fluminense* Vell. and *Jasminum dichotomum* Vahl. I buried 100 seeds in 5 mesh boxes (20 per box) at each of the mainland sites. I selected heavily shaded microsites with at least 5 cm of soil.

RESULTS

Composition and abundance

At total of 1,970 seeds representing 64 species emerged from soil samples (Table 1). The most abundant families of seeds from soil in Key Largo included: 1. Boraginaceae (32% of seeds germinating, one species); 2. Fabaceae (24.5%, two species); and 3. Rubiaceae (8.9%, one species). The most abundant species of seeds germinating from the mainland hammocks included: 1. Moraceae (31.8%, one species); 2. Solanaceae (13.3%, two species); and 3. Phytolacaceae (8.0%, one species) (Table 1). Table 2 shows each species percentage of the total number of seeds germinating from all three sampling periods, numbers in parentheses indicate number of species occuring in each family.

Table 1. Most common plant families of seeds recovered in soil samples.

Keys		Mainland	
Family	**% seeds**	**Family**	**% seeds**
Boraginaceae	32 (1)	Moraceae	31.8 (1)
Fabaceae	24.5 (2)	Solanaceae	13.3 (2)
Rubiaceae	8.9 (1)	Phytolacaceae	8.0 (1)
Moraceae	8.4 (1)	Ulmaceae	7.8 (1)
Solanaceae	4.0 (1)	Vitaceae	5.2 (2)
Rhamnaceae	3.1 (1)	Caricaceae	4.6 (1)
Poaceae	3.0 (1)	Rubiaceae	3.1 (1)
Rutaceae	2.2 (1)	Myrtaceae	2.9 (1)
Ulmaceae	1.8 (1)	Dioscoreaceae	2.7 (1)
Caricaceae	1.3 (1)	Rhamnaceae	2.7 (1)
Vitaceae	0.6 (2)	Asteraceae	2.0 (1)
TOTAL	89.78	Poaceae	1.9 (1)
		Sapotaceae	1.9 (1)
		Rutaceae	1.9 (1)
		Fabaceae	1.1 (1)
		TOTAL	90.9

Most germination from soil samples occurred within the first 8 weeks for all three sampling periods (Figure 2). There were some exceptions. Neither *Eugenia axillaris* (Sw.) Willd., nor *Sideroxylon foetidissimum* Jacq., in mainland samples, germinated until after the first 8 weeks, suggesting physical or physiological dormancy. In all 3 sampling periods, *Piscidia piscipula* (L.) Sarg, *Bourreria ovata* Miers, *Guettarda elliptica* Sw, *Lysiloma latisiliquum* (Benth). L. and *Gouannia lupuloides* (L.) Urb., continued emerging from Keys soil samples until week 16. From mainland sites, *Ficus* spp., and *Zanthoxyllum fagara* (L.) Sarg. continued to germinate late into the trials.

Unlike the early and late wet season samples, the dry season germination trials had two germination peaks late in the trial (week 11 and 14). In particular, *Ficus* spp. and *Piscidia piscipula* germinated during these periods. *Piscidia* is a legume, and like many legumes may have recalcitrant seeds (Garwood 1989). Though *Ficus* spp. germinated throughout the trial, day length may affect germination. Day length was longer towards the end of the dry season trials and may have triggered the additional germination of *Ficus* seeds.

I extracted several seeds through sieving the soil after the first germination trial. Seeds of five species were found, including *Piscidia piscipula* (26 seeds), *Sideroxylon foetidissimum* (5 seeds), *Coccoloba diversifolia* Jacq. (1 seed), *Bourreria ovata* (12 seeds) and unknown (2 seeds). I did not recover any seeds of species that had not emerged in the previous germination trials.

Based on the number of seedlings that germinated, I calculated mean number of seeds per m^2 at each site for 3 sampling periods. Means are plotted by site and sample period in Figure 3. I used a fixed-effects two-way ANOVA to test significant differences between sites and sampling periods (Table 3). To perform this analysis, I applied a square-root (x+1) transformation to correct violations of the normality assumptions for an analysis of variance.

Table 2. Seed bank species abundances. Percentage of total seeds germinating from three sample periods.

Sites: D= Deering, M= Matheson, S= Simpson. N-1 - N-3 are North Key Largo sites.

	Sites					
SPECIES	**D**	**M**	**S**	**N-1**	**N-2**	**N-3**
Amyris elemifera					1.26	0.61
Ardisia elliptica	0.23					
Ardisia escallonioides						0.2
Argemone mexicana		0.56				
Berlandiera subacaulis	0.23					
Bidens alba	3.01					
Bischophia javanica		3.35				
Bourreria ovata				45.07	6.03	48.89
Bumelia salicifolia				0.35	0.25	0.2
Bursera simaruba	0.23	1.68	1.06			
Capparis flexuosa					0.5	
Cardiospermum halicacabum					1.76	
Carica papaya	6.26	4.47	1.06		3.01	0.4
Coccoloba diversifolia	2.55		1.06	0.35	1	0.81
Colubrina elliptica				0.35		1.23
Dioscorea bulbifera	3.24	5.03				
Emilia fosbergii	0.23					
Eugenia axillaris		12.29	0.53	0.7	1.26	
Eupatorium capillifolium	0.46					
Exothea paniculata					1.26	
Ficus spp	20.18	34.08	56.08	11.26	8.79	5.93
Grass	0.69	6.15	0.53	0.35		
Gouania lupuloides	1.86		4.76		9.04	0.2
Guapira discolor					0.5	
Guettarda elliptica				19.71	2.01	8.59
Gymnathes lucida				0.7		0.2
Hamelia patens	5.33		0.53	0.35		0.2
Ipomea indica	0.23	0.56			0.5	0.61
Lasiacis divaricata					3.01	4.07
Ludwigia spp	0.23					
Lysiloma latisiliquum					4.77	0.41
Melothria pendula	0.46		1.59		1.76	
Metopium toxiferum				0.35		
Morinda royoc		0.56				0.82
Ocotea coriacea				0.35	0.25	
Oplismenus setarius	0.23	3.35		0.7	0.5	0.2
Oeceoclades maculata				2.46		0.61
Parthenocissus quinquefolia	0.69	3.91	1.59	0.35		0.2
Petivaria alliacea	4.17	0.56				
Piscidia piscipula			4.76	4.23	41.46	19.01
Psychotria nervosa					0.25	0.82

SPECIES	D	M	S	N-1	N-2	N-3
Reynosia septentrionalis				0.35		
Ricinus communis	1.39					
Rivina humilis	8.12	5.03				
Scleria spp		1.67				
Sideroxylon foetidissimum	1.16	2.79	1.59			
Solanum erianthum	0.23	1.67	6.35	4.93	5.52	2.04
Solanum nigrum	16.47	1.67	15.87			
Trema micranthum	12.99	4.47	0.53	3.17	1.76	0.2
Vitis rotundifolia	6.72			1.06		0.2
Zanthoxyllum fagara		5.59	2.11	0.7	2.01	1.64

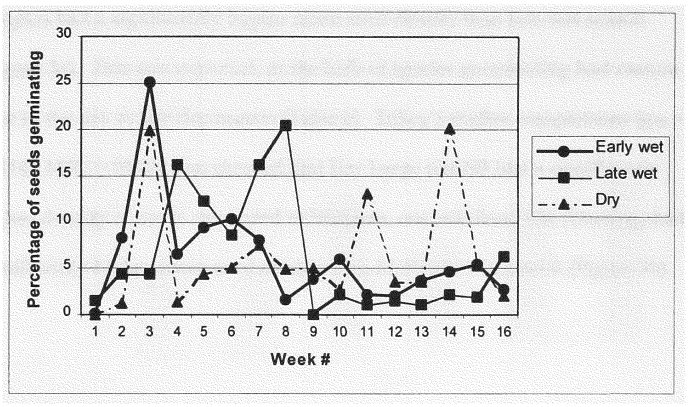


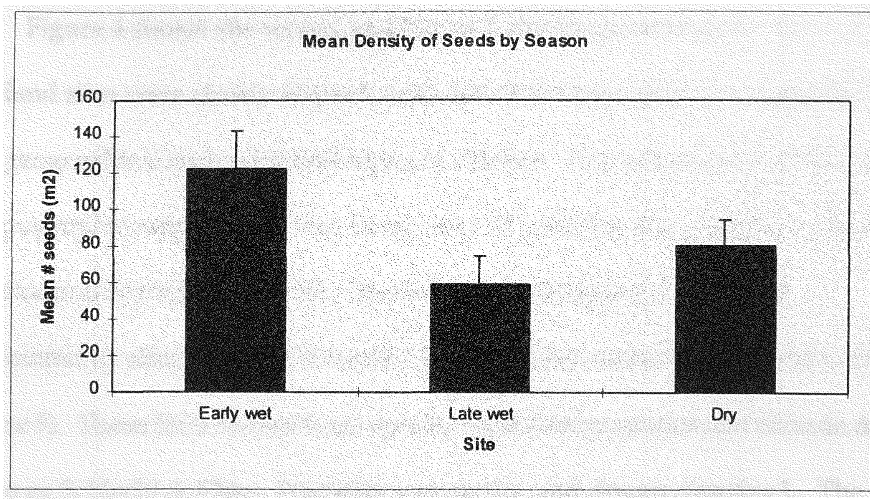
Figure 2. Germination trends. Percentage of seeds germinating per week of germination trials for three sampling periods, early wet, late wet and dry season for combined samples.

Table 3. Summary of two-way ANOVA on mean number of seeds per m^2 and season of soil sample. A square root transformation was applied to the data set.

Effects	Mean Square Effects	Mean Square Error	F	*p*-level
Season	121920.7	10248.46	11.896	.000
Site	72437.2	10248.46	7.068	.000
Interaction	12521.7	10248.46	1.222	.276

There were no significant interactions between the factors. Tukey's *post hoc* pairwise comparison ($q_{.05}$ = {3,117}; HSD = 54.10) showed that early-wet season samples had a significantly higher mean seed density than late-wet season (Figure 3a). This was expected, as the bulk of species germinating had mature fruit in the dry to late dry-season (Table 8). Tukey's *posthoc* comparisons ($q_{.05}$ = {6,114}; HSD = 93.26) also showed that Key Largo site N3 had a significantly higher density of seeds compared to Simpson, one mainland site (Deering) had a significantly higher mean seed density than Matheson Hammock (Figure 3b).

3a)



3b)

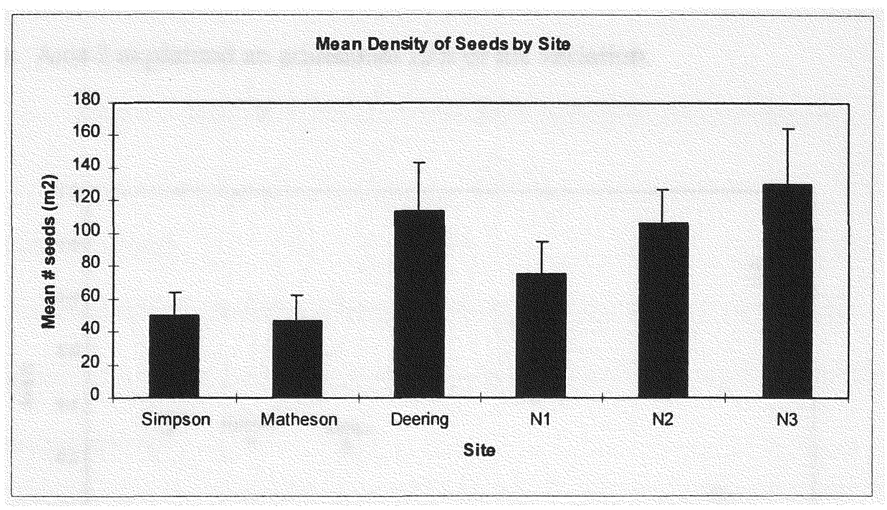


Figure 3. a) Mean number of seeds per m^2 recovered from germination trials for each season, early wet (EW), late-wet (LW) and dry. b) Mean number of seeds per m^2 recovered from germination trials for each site.

Community Ordination

Figure 4 shows site scores, and Figure 5 shows species scores. Each of the mainland sites were closely aligned, and each of the Keys sites were aligned, but each geographical region formed separate clusters. Axis one explained 62% of this geographic range. North Key Largo sites N2 and N3, were relatively distant in ordination space from site N1. Species scores in regions of the graph represented by sites N2 and N3 tended to be later successional compared to N1 (Figure 5). These later successional species were *Ardisia escallinoides* Schiede & Deppe ex Schlecht & Chan, *Psychotria nervosa* Sw, and *Amyris elemifera* L. The seed bank in mainland sites were predominantly of weeds and early successional species. Axis 2 explained an additional 23% of the variation.

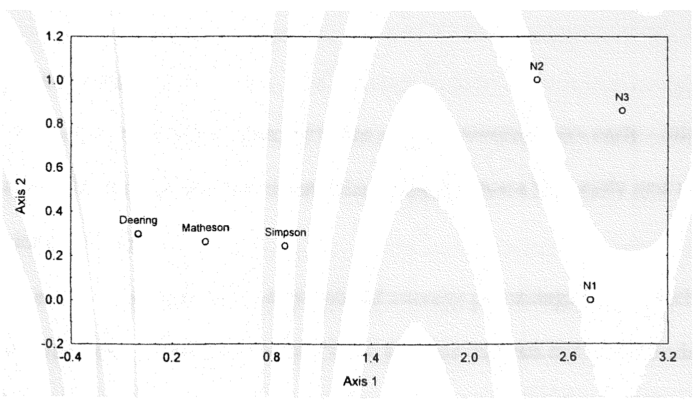


Figure 4. Site scores for Detrended Correspondence Analysis

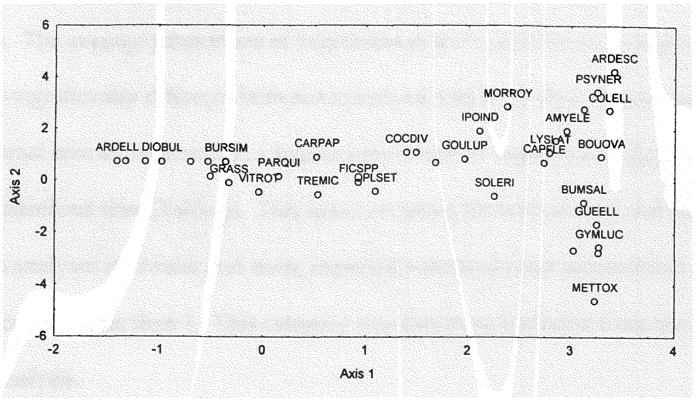


Figure 5. Species scores for Detrended Correspondence Analysis.

Successional stages

In the Keys' sites, 94% percent of the seeds recovered were early - mid successional (Figure 6). Seeds from mainland samples were 92% early and mid-successional species.

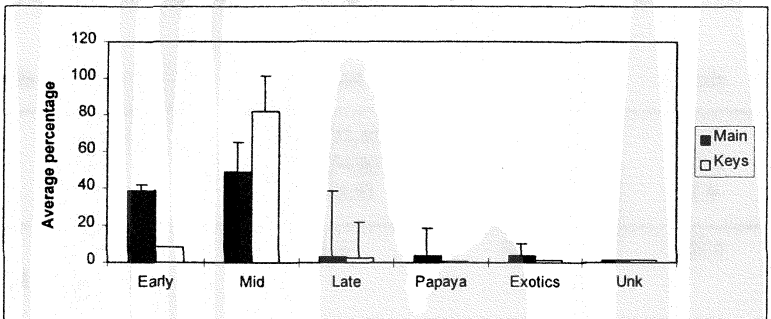
I used a chi-square test to determine if average percentage within each category was independent of location (Table 4). This analysis did not include the proportion of papaya seeds and other exotics. There were significant differences between the average proportions of early, mid-, and late successional seeds recovered in the soil of mainland and Keys sites. The greatest difference occurred between the average proportion of mid-successional seeds, with Keys sites having a higher proportion of mid-successional seeds germinating in soil samples. The average proportion of vegetation in each successional category was also significantly different between mainland and Keys sites. Again, mid-successional species represented a higher proportion of vegetation at Keys sites than at mainland sites (Table 4). This trend occurred for both shrubs and trees. For both analyses of shrubs and trees, expected values of early successional vegetation were less than 5. This category was therefore excluded from the chi-square analysis.

Life form

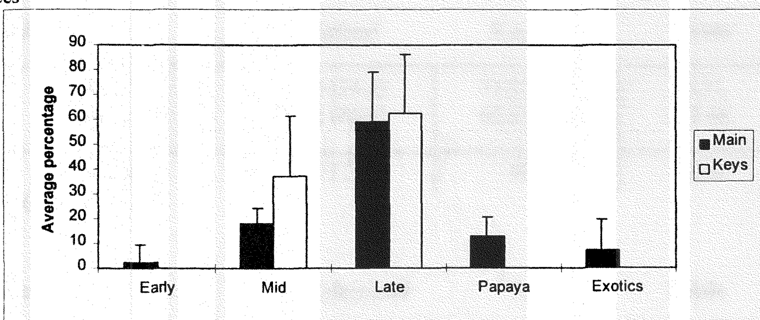
Trees were the dominant life form of most seeds germinating in this study (Figure 7 and 8). However, in one mainland site, Addison Hammock, a slightly higher proportion of herbaceous species germinated. As a group, mainland sites had a higher proportion of herbaceous weedy species than Keys sites (Figure 7). I defined weeds as being species that are native but generally found in disturbed sites, such as roadsides. Samples from the mainland had high proportions of such species as *Solanum nigrum* L. and *Bidens alba* (L.) DC. In all, Addison Hammock had 7 weedy herbaceous species, Matheson 2 and Simpson 1 weedy species. *Solanum nigrum* L. was common at all three mainland sites.

Figure 6. Average percentage of seeds, shrubs, and trees in three successional categories from mainland and Keys sites. Average percentage of *Carica papaya*, and other exotics are also included. Below are the following: a) average number of seeds in each category based on germination trials; b) average percentage of trees, measured in vegetation plots; and c) average percentage of shrubs, measured in vegetation plots.

a) Seeds



b) Trees



c) Shrubs

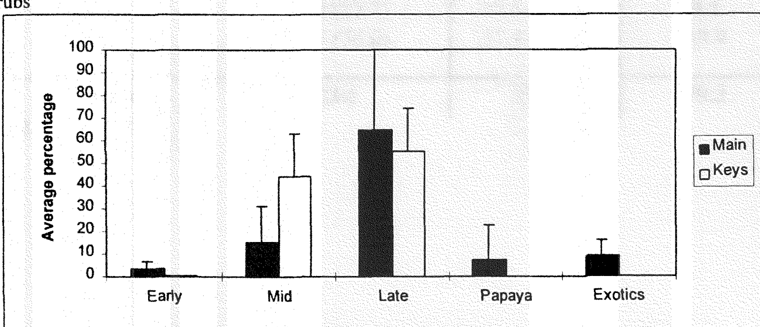


Table 4. Contingency tables of average proportion of seeds, shrubs and trees in each successional category from mainland and Keys sites. Below are the following contingency tables: a) average number of seeds in each category based on germination trials; b) average number of trees, measured in vegetation plots; and c) average number of shrubs, measured in vegetation plots. Expected values are in parentheses.

a) Seeds

	Mainland	Keys	Totals
Early	38.9 (31.4)	8.6 (32.2)	75.2
Mid	49.3 (54.8)	82.1 (56.2)	131.4
Late	3.0 (4.9)	2.7 (5.0)	11.8
Totals	91.2	93.4	218.4

$\chi^2 = 33.37,\ p < .05$

b) Shrubs

	Mainland	Keys	Totals
Mid	18.0 (24.2)	37.3 (31.2)	55.31
Late	59.2 (60.9)	62.3 (68.4)	121.46
Totals	77.2	99.6	176.8

$\chi^2 = 4.05, p < .05$

c) Trees

	Mainland	Keys	Totals
Mid	15.2 (27.7)	37.3 (33.0)	59.3
Late	64.5 (56.0)	55.4 (66.6)	119.9
Totals	83.6	99.6	179.2

$\chi^2 = 12.61,\ p < .05$

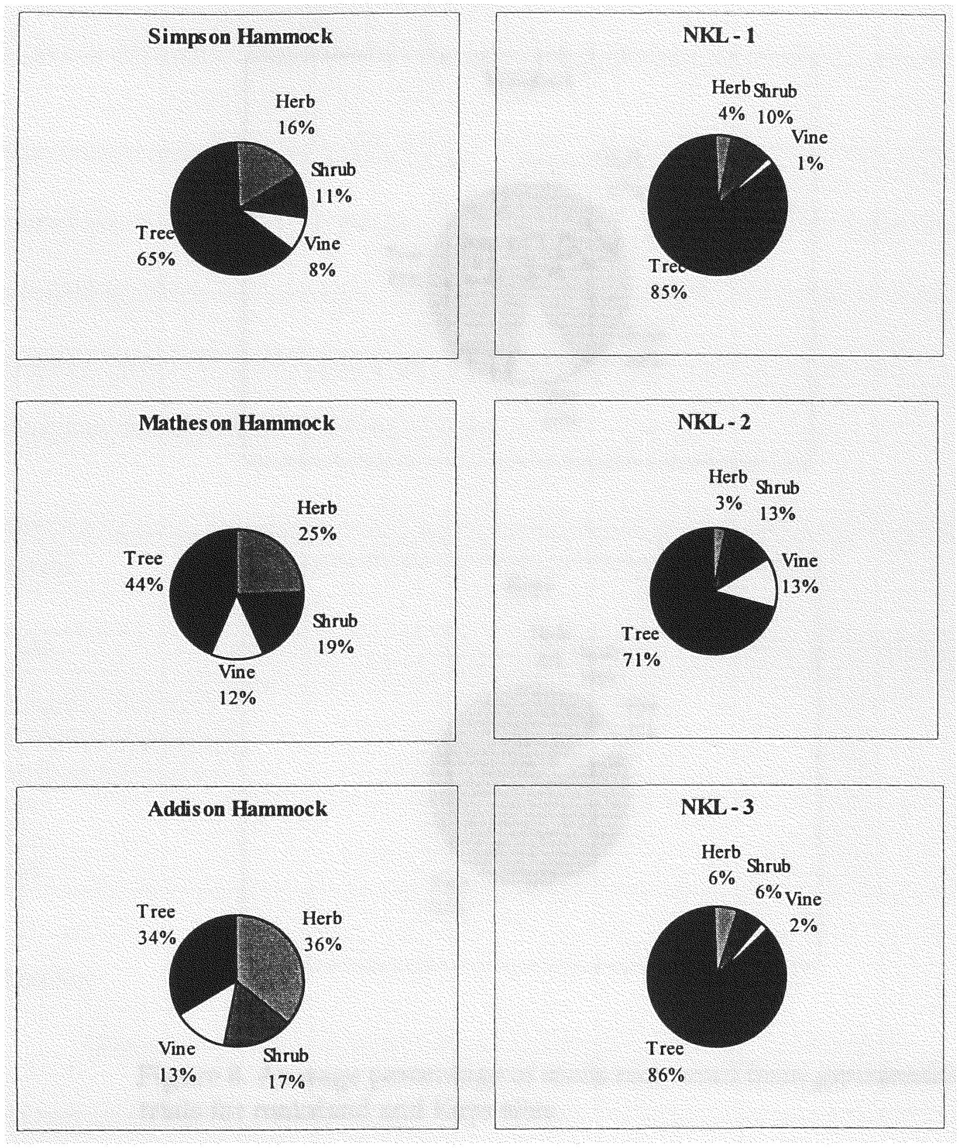


Figure 7. Mean percentage of life forms represented by seeds recovered in germination trials.

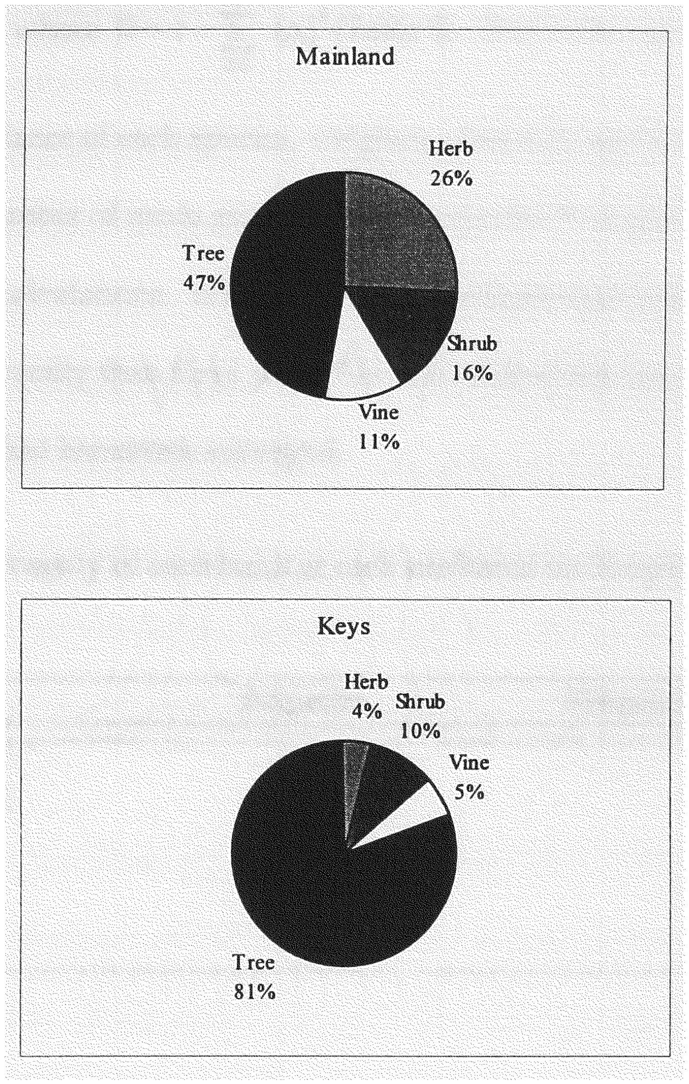


Figure 8. Average percentage of seeds recovered from germination trials for mainland and Keys sites.

Species Diversity

I calculated species diversity of the seed bank at all sites using Simpson' s index of diversity where $D = 1 - \sum_{i=1}^{s} (p_i)^2$ (Table 5). This index takes into account the relative abundance of each species, weighing abundant species more heavily. I used the total number of seeds germinating per species throughout the three seasons for these calculations. With this index, mainland sites tended to have a slightly higher diversity than Keys sites. The lowest diversity occurred at Simpson the smallest hammock surveyed.

Table 5. Species diversity of seed bank at each site based on Simpson's diversity index.

Site	# Species	Simpson's Diversity
Simpson Hammock	16	.65
Matheson Hammock	22	.85
Addison Hammock	28	.89
N-1	23	.73
N-2	29	.79
N-3	27	.71

Exotics

There were approximately 40 exotic species growing in mainland hammocks (Table 6). Compared to the diversity of exotic species at mainland sites, there was far less species diversity of exotic seeds in the soil. The most abundant exotic seeds were those of *Carica papaya* L., a short-lived early successional species. This species occurred at nearly all sample sites (Table 2).

The highest percentages of papaya seeds occurred at sites that sustained substantial damage from Hurricane Andrew, and where papaya was present in the vegetation. This also included the most northern Key Largo site (N2) where 3.01% of the seeds recovered were papaya. Interestingly, at the southernmost Key Largo site, apparently the youngest on the basis of species composition of the vegetation, I did not recover any papaya seeds.

Many of the most invasive species, including *Jasminum fluminense* and *J. dichotomum, Schinus terebinthifolius* Raddi, *Casuarina equisetifolia* L. and *C. glauca* Sieber ex Spring ,and *Neyraudia reynaudiana* (Kunth) Keng ex A.S. Hitche, did not occur in soil samples. *Bischophia javanica* Blume, occurred in soil samples at one mainland site. One exotic species, *Dioscorea bulbifera* L., which does not appear to produce viable seed in south Florida, produces bulbils that did occur in soil samples.

Problem exotics found on North Key Largo include *Manilkara zapota, Leucaena leucocephala* (Lam.) de Wit, *Schinus terebinthifolius, Casuarina* spp., and *Neyraudia reynaudiana.* None of these species were found in vegetation plots adjacent to soil sampling transects. Currently, these species do not seem to be widely dispersed in the seed bank. Other exotic species that occur in Keys' samples, were *Cardiospermum halicacabum* L., and *Oeceoclades maculata* (Lindl.) Lindl. , a terrestrial ground orchid.

Table 6. Exotic species recorded by Natural Areas Management, MetroParks Department in Dade County.

Species	Family	Origin
Abrus precatorius	Fabaceae	India
Agave sisalana	Agavaceae	Bahamas, Mexico
Albizia lebbeck	Fabaceae	Africa, Carribean
Antigonon leptopus	Polygonaceae	Mexico
Ardisia ellipitica	Myrsinaceae	Africa
Bambusa sp.	Poaceae	India, China
Bischophia javanica	Euphorbiaceae	China
Schefflera actinophylla	Araliaceae	Australia
Kalanchoe pinnatum	Crassulaceae	E. Africa
Canavalia brasiliensis	Fabaceae	Tropical Americas
Carica papaya	Caricaceae	Tropical Americas
Casuarina equisitifolia	Casuarinaceae	Old world tropics
Selenicereus pteranthus	Cactaceae	West Indies
Cereus undatus	Cactaceae	West Indies
Citrus spp.	Rutaceae	S & S.E Asia
Clerodendrum speciossimum	Verbenaceae	S.E Asia
Colubrina asiatica	Rhamnaceae	Asia
Cupaniopsis anacardiodes	Sapindaceae	New Guinea
Delonix regia	Fabaceae	Madagascar
Dioscoriea bulbifera	Dioscoreaceae	Tropical Americas
Diospyros ebenaster	Ebenaceae	Tropical Americas
Encephalartos spp	Zamiaceae	S. Africa
Epipremnum pinnatum	Araceae	W. Pacific
Eriobotrya japonica	Rosaceae	China
Eugenia uniflora	Myrtaceae	Tropical Americas
Harpullia arborea	Sapindaceae	Australia
Jasminum dichotomum	Oleaceae	Old world tropics
Jasminum fluminense	Oleaceae	Old world tropics
Leucaena leucocephala	Fabaceae	Tropical Americas
Malvaviscus arboreus	Malvaceae	Tropical Americas
Manilkara zapota	Sapotaceae	Mexico, C. Amer.
Melaleuca quinquenervia	Myrtaceae	Australia
Merremia dissecta	Convolvulaceae	Tropical Americas
Merremia tuberosa	Convolvulaceae	Tropical Americas
Momordica charantia	Cucurbitaceae	Old world tropics
Mucuna sloanei	Fabaceae	Tropical Americas
Neyraudia reynaudiana	Poaceae	Old world tropics
Oxalis corniculata	Oxalidaceae	Tropical Americas
Paederia foetida	Rubiaceae	S.E. Asia
Panicum maximum	Poaceae	Old world tropics
Passiflora edulis	Passifloraceae	Tropical Americas
Pennisteum purpureum	Poaceae	Old world tropics
Phoenix spp.	Palmae	Old world tropics

Species	Family	Origin
Pilea herniaroides	Urticaceae	Old world tropics
Pithecoctineum crucigenum	Bignoniaceae	Tropical Americas
Pouteria campechiana	Sapotaceae	C. Amer, W. Indies
Premna gaudachaudi	Verbenaceae	Old world tropics
Psidium guajava	Myrtaceae	Tropical Americas
Psychotria punctata	Rubiaceae	Tropical Americas
Ptychosperma spp	Palmaceae	Australia
Rhoeo spathacea	Commelinaceae	Tropical Americas
Ricinus communis	Euphorbiaceae	Old world tropics
Russelia equisetiformis	Scrophulariaceae	Tropical Americas
Sansevieria thyrsiflora	Agavaceae	S. Africa
Sarcostemma clausum	Asclepiadaceae	Old world tropics
Sorghum bicolor	Poaceae	Old world tropics
Syngonium podophyllum	Araceae	Tropical Americas
Syzygium jambos	Myrtaceae	Tropical Americas
Syzygium cumini	Myrtaceae	Tropical Americas
Urena lobata	Malvaceae	Tropical Americas
Complaya trilobata	Compositae	Tropical Americas

Phenology

Results of phenological surveys are presented in Table 7. Estimates of seed size, determined from field observations and herbarium specimens, are also presented. Due to Hurricane Andrew, there were fewer large reproductive trees on the mainland. More ruderal species were abundant and phenologically active on the mainland.

Many of the most common species found in soil samples were fruiting in dry (winter), and late-dry (spring) seasons. These species included *Bourreria ovata* (winter), *Lysiloma latisliquum* (winter), and *Piscidia piscipula* (late-spring). Ruderal species, such as *Rivina humilis* L., and early successional species, such as *Hamelia patens* Jacq., have mature fruit throughout wet and dry seasons.

Table 7. a) Phenology of species represented in soil samples.b) Phenology of species represented in vegetation, but did not appear in soil samples. Habit, H = herb, S= shrub, T = tree, V = vine; successional stage, for native species only, E = early, M = mid-successional, L = late-successional; origin N = native, X = exotic; dispersal, A = animal, W = wind; Fruit season, P = persistent, fruit is present at any given time throughout the year, SP = spring, S = summer, F = fall; W = winter.

a).

Species	Habit	Successional stage	Origin	Fruit	Dispersal	Fruiting season	Seed size (mm)
Rivina humilis	H	E	N	berry	A	P	3
Solanum nigrum	H	E	N	berry	A	P	1 - 1.5
Scleria spp.	H	E	N	achene	W	SP-S	2.5
Petivaria alliacea	H	E	N	achene	W	P	7
Oeceoclades spp	H		X	capsule	W	P	*
Lasiacis divaricata	H	E	N	caryopsis	W	F,W	3
Argemone mexicana	H	E	N	capsule	W	W,SP	25
Cenchrus spp	H	E	N	achene	W	P	*
Bidens alba	H	E	N	achene	A, W	W	*
Berlandiera subacaulis	H	E	N	achene	W	SP-F	4
Oplismenus setarius	H	E	N	caryopsis	W	F,W	5
Eugenia axillaris	S	M	N	berry	A	P	7.5
Carica papaya	S		X	berry	A	W -S	3.5
Zanthoxyllum fagara	S	M	N	berry	A	S	1.5 - 2
Ricinus communis	S	E	X	capsule	E	P	7 - 9
Hamelia patens	S	E	N	berry	A	P	5.5
Ateramnus lucidus	S	L	N	capsule	A	S	4.5
Psychotria nervosa	S	L	N	drupe	A	S,F,W	6
Capparis flexuosa	S	M	N	pod	A	S,F	4-6
Ardisia elliptica	S		X	drupe	A	F,W	6
Solanum erianthum	S	E	N	berry	A	P	10.5
Bursera simaruba	T	M	N	drupe	A	LF-W	8.5
Ficus spp	T	M	N	multiple	A	W, S, F	*
Bishophia javanica	T		X	capsule	A	Sp - F	9
Sideroxylon foetidissium	T	L	N	berry	A	Sp	20
Coccoloba diversifolia	T	L	N	berry	A	LS	9-11
Piscidia piscipula	T	M	N	winged legume	W	LSp-S	4.5
Guettarda elliptica	T	M	N	drupe	A	F	9
Bumelia salicifolia	T	M	N	berry	A	S	7
Bourreria ovata	T	M	N	berry	A	W	5 - 6
Colubrina elliptica	T	M	N	capsule	A	W	7

Species	Habit	Successional stage	Origin	Fruit	Dispersal	Fruiting season	Seed size (mm)
Ocotea coriacea	T	L	N	drupe	A	F-W	9
Exothea paniculata	T	L	N	berry	A	S	7
Lysiloma latisliquum	T	M	N	legume	W	W	6
Guapira discolor	T	M	N	drupe	A	F-W	7.5
Metopium toxiferum	T	M	N	drupe	A	S-F	10-15
Amyris elemifera	T	L	N	drupe	A	F-W	5 - 8
Morinda royoc	V	E	N	drupe	A	P	3 - 5
Dioscorea bulbifera	V		X	bulbil	A	Sp-S	*
Gouania lupuloides	V	M	N	samara	W	F	6-10
Vitis rotundifolia	V	E	N	berry	A	Sp-S	3 - 5
Melothria pendula	V	E	N	berry	A	Sp-S	2 - 3
Ipomea indica	V	E	N	capsule	W	P	1-2
Parthenocissus quinquefolia	V	E	N	berry	A	Sp-S	3 - 5
Ampelopsis arborea	V	E	N	berry	A	Sp-S	8

b.)

Species	Habit	Successional stage	Origin	Fruit	Dispersal	Fruiting season	Seed size (mm)
Adenanthera pavonia	T		X	legume	A	*	*
Calyptranthes pallens	T	L	N	berry	A	F	5 - 8
Canella winterana	T	L	N	berry	A	W	2-3
Celtis laevigata	T	*	N	berry	A	Sp-S	*
Chrysophyllum oliviforme	T	L	N	berry	A	S	10
Citrus spp.	T	*	X	hesperi dium	A	Sp-S	*
Drypetes diversifolia	T	L	N	drupe	A	S	10 -12
Drypetes lateriflora	T	L	N	drupe	A	S	5 - 8
Eugenia confusa	T	L	N	berry	A	*	3 - 5
Exostema caribaeum	T	L	N	capsule	W	LSp	3 - 5
Krugiodendron ferreum	T	L	N	drupe	A	LSp	5 - 8
Manilkara zapota	T		X	berry	A	S	5 -8
Persea borbonia	T	*	N	drupe	A	S	10 - 12
Picramnia pentandra	T	L	N	berry	A	LS -F	5 - 8
Prunus myrtifolia	T	L	N	drupe	A	LSp -ES	5 - 8
Quercus virginiana	T	*	N	acorn	A	*	10 - 15
Schefflera actinophylla	T		X	*	*	*	*
Simarouba glauca	T	L	N	drupe	A	LSp	10 - 12
Swietnia mahagoni	T	M	N	capsule	W	LF	3 - 5
Ximenia americana	T	*	N	drupe	A	P	15 - 25

* Missing values indicate insufficient data.

Seed Bank Patterns

Based on phenology of hammock species, and the seasonal occurrence of seeds from soil samples, I identified five types of seed bank patterns (Table 8). These strategies were based largely on those described by Garwood (1989) for tropical forests. I was unable to test the persistence of seeds of all species; therefore, in developing these strategies, I assumed that seeds in soil samples were from the most recent phenological event. Appendix A. provides examples of these strategies found in the flora of hardwood hammocks.

Table 8. Seed bank patterns for hardwood hammocks of southern Florida

1. Semi-persistent seeds: species produce fruit once a year, and have seeds that appear to be stored in the soil for at least one year. The seeds are very abundant to moderately abundant in the soil of hammocks where these species occur in the vegetation.
2. Transient seeds: species fruit in the late-spring through summer. The seeds of these species are not viable in the soil after this season.
3. Safe-keeping seeds: species fruit in late-fall to early winter. Seeds persist through the dry season. They are not viable at the end of the rainy season.
4. Opportunistic seeds: species have mature fruit that persists on the tree, often for an entire year. Seeds of these species are found in the soil throughout the year.
5. Gap colonizing seeds (long-lived): species are classified as gap colonizers. When these species are present in the vegetation, fruit may be produced throughout the year. Seeds may persist for more than one year. Seeds of these species are common throughout all of the hammocks, and are moderately abundant though they have low importance values in the vegetation.

DISCUSSION

Previous research from wet and dry tropical forests (Cheke et al. 1979, Ewel and Conde 1979, Guerva and Gomez-Pompa 1972, Hall and Swaine 1980, Hopkins and Graham 1983, Garwood 1989, Putz 1983, Putz and Appanah 1987, and Horvitz, unpublished data) show that seed densities from mature forests range from 25 - 3,350 seeds per m^2, representing 4 - 79 species. Pioneer species dominate these seed banks. In south Florida hardwood hammocks, seed densities average 104 seeds per m^2, representing 44 species for Upper Keys hammocks, and 71 seeds per m^2, representing 36 species for mainland hammocks. A closely related study of seed banks in Caribbean dry forests of the Virgin Islands found, on average in mature forests, 151.5 seeds/m^2, representing 19.5 tree species, 3.5 shrub species, 2 vine species, and 3.5 herbaceous species (Ray and Brown, 1994). Soil samples in the Virgin Island study were collected only during the end of the summer dry season.

Garwood (1989) generalizes several seed bank strategies for tropical forests based on seed bank data. Tropical seed banks are generally transient. Transient seeds have no dormancy and germinate immediately, or remain in the soil for short periods of time less than one year. Weedy species and short-lived pioneers have persistent seed banks, with seeds remaining viable for more than one year. Other seeds, such as long-lived pioneers and primary species, have seasonally-transient seed banks. Here, seeds remain dormant through an adverse period such as a dry season. Garwood (1989) also suggests that average seed density, within-year variances in density, and the abundance of species with seasonal-transient seed banks should increase as the length of the dry season increases.

Since southern Florida has a distinct dry season of approximately six months, many of the species recovered in soil samples belong to what I have classified as semi-persistent seeds. This classification corresponds closely to Garwood's (1989) description of seasonal-transient seed banks. This seed bank type is composed of seasonally dormant seeds with intermediate longevity that are dispersed for short or long periods.

As the data here shows, several of the most abundant seeds recovered from soil samples throughout the year belonged to mid-successional species (e.g. *Bourreria ovata, Piscidia piscipula, Guettarda elliptica, Bursera simaruba*). The seed bank strategy of all of these species is seasonally-transient or semi-persistent as described in this paper. These species generally have mature fruit in the fall through late winter. The seed bank strategy for these species may be an effective means of regeneration in these seasonally dry forests, and where periodic hurricanes create scattered, smaller light gap conditions.

Recent seed storage longevity studies in Caribbean dry forests have shown that species of *Coccoloba* and *Guettarda* maintained moderate germination percentages (35-55%) for at least five months, and germination of *Bursera* *simaruba* seeds diminished to 2% in five months (Ray and Brown 1994). This study in the Virgin Islands also found that a *Piscidia* species was among several species that exhibited the greatest seed longevity.

Previous studies have shown short longevities of late successional tropical tree species (Vazquez-Yanes & Orozco-Segovia 1984). For my study, I recovered very few late sucessional seeds (e.g. *Sideroxylon foetidissimum, Ateramnus lucida*). Many late successional species in the vegetation did not occur in my soil samples (Table 4b). Monthly soil sampling may help to better detect the abundance of seeds in the soil of these species.

I recovered far fewer exotic seeds than I expected, given relatively high (30%) exotic vegetation cover. Many of the exotic species invading south Florida communities are tropical in origin, and have larger seeds adapted to germinate under low light conditions (Horvitz in press). As a trade-off, these larger seeded species may be more prone to predation (Thompson 1993).

As this data shows, there are no hidden costs for managing exotic species in these preserves. Once exotic vegetation is removed, exotics probably arrive from outside the preserve, rather than from a persistent seed bank. Elsewhere, exotic species seem to germinate and persist in a seedling bank. One exception is *Carica papaya*, an early successional exotic species with persistent, small seeds. Following Hurricane Andrew, this species became prevalent in the vegetation in Dade County hammocks. Compared to native early-successional species, papaya is very short-lived in the vegetative phase. It is not clear how an over-abundance of papaya seeds in a seed bank may affect natural regeneration dynamics (Horvitz 1996).

The community ordination shows that seed bank species composition of mainland and Keys sites are distinctly different. This analysis also shows that Key Largo sites are less congruent. Garwood (1989) suggests that seed bank change during succession. Differences among Key Largo sites may be due to the successional stage of the vegetation. Much of Key Largo was cleared at various points in time during the early part of the 20th century. However, one site, N3, is thought to have never been cleared (W. Hoffman, personal communication). The most southern site, N1, is also the youngest stand of the three in Key Largo and has the lowest mean of all Key Largo sites. This difference in stand age may contribute to species composition of the seed bank. For example, in examining the proportion of species that are late-successional at Key Largo sites, there is a pattern consistent with stand age. At N1, the youngest site, approximately 1.4% of the seeds recovered were late-successional. While in more mature stands 4.5% and 2.0% were seeds of later successional species. This pattern is less distinct for early successional species which had approximately the same relative abundance throughout the sites.

It is also likely that the separation between mainland and Keys sites is due to differences in the composition of the vegetation. Disturbance from Hurricane

Andrew in 1992, which had a greater impact on the southern mainland of Florida than the Keys, may also contribute to the results of the ordination.

A significant difference between fragmented (mainland) and less fragmented (Keys) sites is the average proportion of seeds that are herbaceous. The abundance of seeds representing herbaceous species may be explained, in part by Hurricane Andrew. Several early successional species, such as *Rivina humilis* and *Petivaria alliacea* germinated following the storm and continued to be reproductive for a period thereafter. However, one weedy, herbaceous species, *Solanum nigrum* was commonly found in soil samples at mainland sites, though it was not abundant in the vegetation. Additionally, *Carica papaya* is an exotic, herbaceous shrub, which rapidly dies as the upper canopy re-establishes after disturbance. The most northern Keys site sustained similar hurricane force winds to those at the two northern-most mainland sites, yet, with the exception of papaya, none of these herbaceous species occurred in Keys' soil samples or vegetation. In previous studies, weeds have been shown to interfere with tree seedlings and saplings during early stages of forest regeneration (Kellman 1974 and Ewel 1986). The abundance of weedy, and exotic species, particularly those with long-lived seeds may ultimately have an effect on forest structure and composition. However, there does not seem to be an effect on species diversity of the seed bank.

Carica papaya may be assuming the role of early and mid-successional species. These native early-successional species provide necessary microhabitat conditions for the establishment of late-successional species. As hurricane damage in fragmented forests tends to be exacerbated, due to edge effects, large gaps resulted. Papaya germinated and fruited widely throughout mainland sites. In the Keys, hurricane damage resulted in interspersed large and small gaps, and papaya emerged intermittently throughout the forest. Papaya seems to have seeds that persist for many years. This may have a significant impact on the structure of mainland hammock preserves with each significant disturbance, as papaya seeds are deposited into a seed bank. Presumably, with an abundance of papaya in the vegetation, fewer native early successional species will be able to compete.

Quintana-Ascencio et al. (1996) have shown that the current expansion of pastures and agricultural fields in Mexico modify the seed bank of tropical forests in this region. This suggests that this resultant change in seed deposition and storage in the soil alters processes of secondary succession. Similar trends seem to occur in South Florida mainland hammocks examined here, in that a larger percentage of herbaceous species, typically found along edges of forests and disturbed sites, were found in soil samples.

This study provides a framework for more specific experimental studies pertaining to seed longevities, and the role of these persistent seeds throughout seral stages. The role of persistent seed banks may be an important consideration for restoration of hardwood hammocks. This study also provides a basis from which seed banks in fragmented forests can be monitored.

LITERATURE CITED

Brothers, T. S. and A. Springarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology 6: 91-100.

Cheke, A. S., W. Nanakorn, and C. Yankoses. 1979. Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rainforest in northern Thailand. Biotropica. 11(2): 88-85.

Craighead, F.C. 1974. Hammocks of South Florida. Pages 53-60 *in* P.J. Gleason, editor. Environments of South Florida: Present and Past. Miami Geological Society, Miami Florida, USA.

Davis, J.H. 1943. The natural features of southern Florida, especially the vegetation and the Everglades. Geol. Bull No. 25. Florida Dept. of Cons. Geol. Survey.

Ewel and Conde. 1979. Seeds in the soil of former Everglades farmlands. Pages 225-234 *in* R.M. Linn, editor. Proceedings of the First Conference on Scientific Research in the National Parks. Vol. 1, Trans. Proc. Ser. No. 5. Natl. Park Service, U.S. Dept. Int., Washington, D.C.

Ewel, J.J. 1986. Designing agricultural ecosystems for the humid tropics. Ann. Rev. Ecol. Syst. 17: 245-271.

Garwood, N. 1989. Pages 149-204 *in* M.A. Leck, V.T. Parker, and R.L. Simpson, editors. Ecology of Soil Seed Banks. Academic Press, Inc., San Diego, CA.

Guerva, S. and A. Gomez-Pompa. 1972. Seeds from the surface soils in a tropical region of Veracruz, Mexico. Journal Arnold Arboreteum 53: 312-335.

Hall, J.B. and M.D. Swaine. 1980. Seed stocks in Ghanaian Forest Soils. Biotropica. 12(4): 256-263.

Hearty, P.J. and P. Kindler. 1995. Sea-level high stand chronology from stable carbonate Platforms (Burmuda and the Bahamas). Journal of Coastal Research. 11(3):675-689.

Henry, H.A., K.M. Portier and J.M. Coyne. 1994. The Climate and Weather of Florida. Pineapple Press, Sarasota, Florida

Hobbs, R.J. and L. Huenneke. 1992. Disturbance, Diversity, and Invasion: Implications for Conservation. Conservation Biology. 6(3): 324-337.

Hoffmeister, J.E. 1974. Land From the Sea: The Geologic Story of South Florida. University of Miami Press, Coral Gables, Florida.

Holdridge, L.R. 1967. Life Zone Ecology. Tropical Science Center, San Jose , Costa Rica.

Hopkins, M.S. and A.W. Graham. 1983. The species composition of soil seed banks beneath lowland tropical rainforest in North Queensland, Australia. Biotropica. 15(2): 90-99.

Horvitz, C., S. McMann, and A. Freedman. 1995. Exotics and hurricane damage in three hardwood hammocks in Dade County Parks, Florida.

Horvitz, C., J.P. Pascarella, S. McMann, A. Freedman, and R. Hofstetter. (in press) Invasive exotic plants and regeneration niches: subtropical hardwood forests after hurricanes as a model system. Ecological Applications.

Hurt, G.W., Noble, C.V., and R. W. Drew. 1995. Soil Survey of Monroe County Area, Florida Keys Area, Florida. Natural Resources Conservation Service, US Dept. of Agriculture; 72 p. Available from: US Government Printing Office, Washington, D.C.

Kartez, J.T. 1994. A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland. 2nd edition. Timber Press, Portland, Oregon.

Kellman, M.C. 1974. The viable weed seed content of some tropical agricultural soils. Journal of Applied Ecology 11: 669-677

Little, E.L. 1978. Atlas of United States Trees. Volume. 5: Florida. U.S. Forest Service Misc. Publ. No. 1361. U.S. Government Print. Office, Washington, D.C.

Loope, L.L. 1980. Phenolgy of flowering and fruiting in plant communities of Everlades National Park and Biscayne National Monument. Florida Everglades National Park. South Florida. Research Center Report T-593.

Long, R.W. and O. Lakela. 1971. A Flora of Tropical Florida. Univ. of Miami Press, Coral Gables, Florida.

Macvir, T.K., and S. T. Lin. 1984. Pages 477-509. *In* P.J. Gleason, editor. Environments of South Florida: Present and Past II. University of Miami Press. Coral Gables, Florida.

Noble, C.V., R.W. Drew, and J.D. Slabaugh. 1996. Soil Survey of Dade County Area, Florida. Natural Resources Conservation Service, US Dept. of Agriculture; 116 p. Available from: US Government Printing Office, Washington D.C.

Putz, F. and S. Appanah. 1987. Buried seeds, newly dispersed seeds and the dynamics of a lowland forest in Malaysia. Biotropica. 19(4): 326-333.

Putz, F.E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees in Barro Colorado Island Panama. Ecology 64: 1069-1074.

Quintana, P.F., M. Gonzalez, N. Ramirez-Marcial, G. Dominquez-Vasquez, and M. Martinez-Ico. 1996. Soil seed banks and regeneration of tropical rain forest from milpa fields at the Selva Lacandona, Chiapas, Mexico. Biotropica. 28(2): 192-209.

Ray, G. and B. Brown. 1994. Seed ecology of woody species in a Caribbean Dry Forest. Restoration Ecology. 2(3): 156-163.

Ross, M.S., J.J. O'Brien, and L.J. Flynn. 1992. Ecological site classification of the Florida Keys terrestrial habitats. Biotropica 24(4): 488-502

Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1990. Biological consequences of ecosytem fragmentation a review. Conservation Biology 5: 18-32.

Scurlock , J.P. 1992. Native Trees and Shrubs of the Florida Keys. 2nd edition Laurel Press, Pittsburgh, Pennsylvania

Shaw, Clifford. 1975. The pine and hammock forestlands of Dade County. Report by Metro-Dade Urban Forestry, Florida Division of Forestry.

Snyder, J.R., A. Herdon, and W.B. Robertson. 1990. Pages 230-247 *in* R.L. Myers and J.J. Ewel, editors. Ecosystems of Florida. Univ. of Central Florida Press, Orlando, Florida.

Strong, A.M. and G.T. Bancroft. 1994. Patterns of deforestation and fragmentation of mangrove and deciduous seasonal forests in the upper Florida Keys. Bulletin of Marine Science. 54(3): 795-804.

Thompson, K., S.R. Band, and J.G. Hodgson. 1993. Seed size and shape predict persistence in soil. Functional Ecology 7: 236-241.

Tomlinson, P.B. 1980. The Biology of Trees Native to Tropical Florida. Harvard University Printing, Allston, Mass.

Vazquez-Yanes, C. and A. Orozco-Segovia. 1984. Ecophysiology of seed germination in the tropical humid forests of the world. Pages 37-50 *in* E. Medina, H.A. Mooney, and C. Vasquez-Yanes, editors. Physiological Ecology of Plants in the Wet Tropics. Junk, Hague, Netherlands.

Viele, J. 1996. The Florida Keys: A History of the Pioneers. Pineapple Press, Sarasota, Florida

Walters, H. 1985. Vegetation of the Earth and Ecological Systems of the Geo-biosphere. Springer-Verlag, New York Inc., Secaucus, New Jersey.

APPENDIX A: Seed bank strategies by species.

ED= Early dry season, D= dry season, LD= late dry season, EW= early wet season, W= wet season, LW= late wet season
******* = mature fruits occurring, —— germination occurred from soil samples.

Type : Semi-persistent seeds

Species	Seed size (mm)	Dispersal mode		ED	D	LD	EW	W	LW
Piscidia piscipula	4.5	Anemochory	Mature fruit				*******		
			Soil samples		--------		--------		--------
				ED	D	LD	EW	W	LW
Guettarda elliptica	9.0	Endozoochory	Mature fruit						*******
			Soil samples		--------		--------		--------
				ED	D	LD	EW	W	LW
Bouerria ovata		Endozoochory	Mature fruit	*******					*******
			Soil samples		--------		--------		--------
				ED	D	LD	EW	W	LW
Sideroxylon foetidissimum	17.0	Endozoochory	Mature fruit			*******			
			Soil samples		--------		--------		--------

Type: Semi-persistet seeds (cont.)

Species	Seed Size (mm)	Dispersal mode		ED	D	LD	EW	W	LW
Capparis flexuosa		Endozoochory	Mature fruit					********	
			Soil samples		--------		--------		
				ED	D	LD	EW	W	LW
Zanthoxylum fagara	2.5	Endozoochory	Mature fruit					********	
			Soil samples		--------		--------		--------
				ED	D	LD	EW	W	LW
Coccoloba diversifolia	10.0	Endozoochory	Mature fruit			*******			
			Soil samples		--------		--------		

Type: Transient seeds

Species	Seed size (mm)	Dispersal mode		ED	D	LD	EW	W	LW
Sideroxylon salicifolia	7.0	Endozoochory	Mature fruit			*******	****		
			Soil samples				--------		
				ED	D	LD	EW	W	LW
Nectandra coriacea	9.0	Endozoochory	Mature fruit			*******	****		
			Soil samples				--------		
				ED	D	LD	EW	W	LW
Exothea paniculata	9.5	Endozoochory	Mature fruit			*******	****		
			Soil samples				--------		
				ED	D	LD	EW	W	LW
Gymanthes lucida	5.0	Endozoochory	Mature fruit				*******		
			Soil samples				--------		
				ED	D	LD	EW	W	LW
Guapira discolor		Endozoochory	Mature fruit				*******	********	
			Soil samples				--------		

Type: Safe-keeping seeds

Species	Seed size (mm)	Dispersal mode		ED	D	LD	EW	W	LW
Colubrina elliptica	4.5	Anemochory	Mature fruit	*******					
			Soil samples		--------		--------		
				ED	D	LD	EW	W	LW
Metopium toxiferum		Endozoochory	Mature fruit	*******					
			Soil samples		--------				
				ED	D	LD	EW	W	LW
Amyris elemifera		Endozoochory	Mature fruit	****	*******				****
			Soil samples		--------				--------

Type: Opportunistic seeds

Species	Seed size (mm)	Dispersal mode		ED	D	LD	EW	W	LW
Lysiloma latisilquum	6.0	Anemochory	Mature fruit	********	*******	*********	*******	*********	*******
			Soil samples		-------		-------		--------
				ED	**D**	**LD**	**EW**	**W**	**LW**
Eugenia axillaris	7.5	Endozoochory	Mature fruit	********	*******	*********	*******	*********	********
			Soil samples		-------		-------		--------

Type: Gap colonizing seeds

Species	Seed size (mm)	Dispersal mode		ED	D	LD	EW	W	LW
Carica papaya		Endozoochory	Mature fruit	*********	********	**********	********	**********	*********
			Soil samples		--------		--------		---------
				ED	D	LD	EW	W	LW
Solanum erianthum		Endozoochory	Mature fruit	*********	********	**********	********	**********	*********
			Soil samples		--------		--------		---------
				ED	D	LD	EW	W	LW
Trema micrantha		Endozoochory	Mature fruit	*********	********	**********	********	**********	*********
			Soil samples		--------		--------		---------
				ED	D	LD	EW	W	LW
Petivaria alliaceae		Anemochory	Mature fruit	*********	********	**********	********	**********	*********
			Soil samples		--------		--------		---------
				ED	D	LD	EW	W	LW
Rivina humilis		Endozoochory	Mature fruit	*********	********	**********	********	**********	*********
			Soil samples		--------		--------		---------
				ED	D	LD	EW	W	LW
Hamelia patens		Endozoochory	Mature fruit	*********	********	**********	********	**********	*********
			Soil samples		--------		--------		---------

Buried seeds in tropical hardwood hammocks: a role in restoration

INTRODUCTION

Restoration of degraded habitats may be a true test of ecological theory and understanding (Bradshaw 1987, Ewel 1987). The objectives in recreating natural forest systems are to build a semblance of representative species associations, and restoring the processes associated with a particular seral stage. There are many factors and questions to consider when restoring ecological processes including soil development, nutrient cycling, species composition, and the facilitative role of succession. One question restorationists should consider when attempting to recreate a forest type is, "What is the role of a seed bank in hardwood hammocks?"

My examination of the soil seed bank of southern Florida's dry tropical forests prompted a consideration of the role of seed banks in restoration efforts. One of the challenges of effective restoration projects is understanding how the restored system maintains itself over time and disturbance.

Fragmentation, clearing, and invasion have degraded dry tropical forests of southern Florida. In Central and South America, and throughout the Caribbean, it is the most threatened of all major lowland tropical forest types (Janzen 1988a). Fortunately, opportunities to restore natural systems are available, though much information is still needed to optimize restoration activities.

Resource managers seek to mimic natural regeneration strategies in forest restoration projects. The efficacy of forest restoration depends on recreating various regeneration stages and strategies. Oftentimes, in facilitating the regeneration of dry tropical forests, seeds may be dispersed on site, or seedlings may be planted (Ray & Brown 1995, Gerhardt 1992a ,1993b). This approach may be suited for situations where time is not a limiting factor to recreate a closed canopy system. More often, the objective of restoration is to recreate a mature forest quickly, therefore a diversity of mature forest species are planted.

Restoration ecology is beginning to consider the role of seed banks and seed dispersal in temperate forests (Bakker et.al 1996). Seed banks play an important role in regeneration of several early and mid-successional species in dry tropical forests of southern Florida (see chapter one). Restoration of dry tropical forests should incorporate species that contribute substantially to a seed bank. This approach develops a seed bank for future regeneration following disturbance.

In this chapter, I examine relationships between buried seeds and the vegetation of dry tropical forests in southern Florida to understand the role of seed banks in restoring this forest type. The following questions will be addressed: 1. How does the vegetation of dry tropical forests in southern Florida correspond to the abundance and species composition of the seed bank? 2. What role do species with long-lived seeds play? 3. For dominant species, what are the relationships between different life stages? 4. What is the role of exotic seeds in restoration of hardwood hammocks?

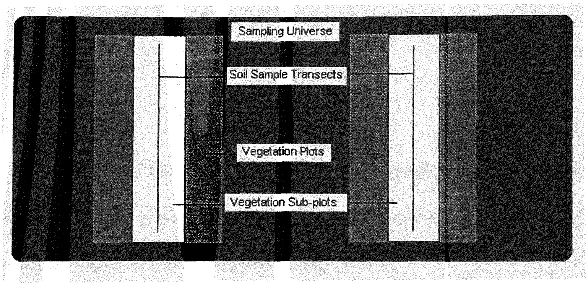
STUDY SITES AND METHODS

I selected six hardwood hammock sites, three fragmented sites in Dade County and three protected sites within a large continuous tract in northern Key Largo. The methodology for determining species composition and abundance of seeds in the soil at each site is described in chapter one of this thesis.

Vegetation sampling and analysis

Around each transect, I established plots to measure the vegetation (Fig 1). I used a 20m x 55m plot to measure all tree species with a dbh 7.5 cm and greater. I selected this plot size to represent the vegetation that was most likely the source of seed rain in the soil samples. To measure species less than 7.5 cm, and at least 2m tall, I established a 5 m x 55 m subplot.

Figure 1. Sampling diagram.



I calculated importance values for tree and shrub species based on relative density, basal area and frequency for each site. North American taxonomy here follow Kartesz (1994).

Analysis

I calculated the mean number of seeds for each species at each site (chapter one, Figure 3). In addition, I calculated importance values for species in the vegetation. To examine the relationship between the seed bank and vegetation communities, I used Detrended Correspondence Analysis. As species abundance for vegetation and seeds are not at the same scale, I used importance values calculated (represented as a percentage) for the vegetation and percentage of total seeds by species recovered for this analysis. I also used Jaccard coefficient of similarity to compare the seed bank with above-ground communities.

RESULTS

Seed bank analysis

Results of seed bank composition and average abundance for each site are presented in Table 2 of chapter one. In addition, general seed bank strategies for hardwood hammocks are described in chapter one.

Vegetation analysis

Importance values for tree and shrub species are presented in Tables 1 and 2. Because Hurricane Andrew affected mainland sites more directly in 1992, the importance values for some early successional species tended to be greater than those found in northern Key Largo. These species included *Carica papaya, Trema micranthum, Hamelia patens,* and *Solanum erianthum.*

Table 1. Species importance values for shrub species. Importance values calculated from relative frequency and relative cover of trees less 7.5cm dbh. D = Deering Estate; M = Matheson Hammock; S = Simpson Hammock; N1, N2, and N3 are sites in North Key Largo.

Species	D	M	S	N-1	N-2	N-3
Adenanthera pavonia		2.27				
Amyris elemifera				4.57	3.27	7.08
Ardisia elliptica	3.89	1.58				
Ardisia escallonioides	4.71	5.06		5.38	1.72	5.13
Bishophia javanica	3.89	1.42				
Bourreria ovata				6.77	1.78	
Sideroxylon salicifolia		1.33		4.88		
Bursera simaruba		2.9		4.44	1.9	15.74
Calyptranthes pallens	7.65	3.13	5.89		5.48	2.44
Calyptranthes zuzygium					5.01	
Canella winterana				2.06	1.69	
Capparis flexuosa						2.35
Carica papaya	16.24	25.11	2.46		2.18	
Caryota spp.						
Celtis laevigata	3.48					
Chioccoca alba		1.28		1.63		
Chrysophyllum oliviforme		1.39				
Citris spp.	2.35	1.43				
Clerodendrum spp.		1.28				
Coccoloba diversifolia	7.74	6.72	14	12.01	17.28	7.49
Colubrina elliptica						
Cupaniopsis anacardioides		1.28				
Diospyros ebenaster		1.57				
Drypetes diversifolia					2.21	2.57
Drypetes lateriflora		3.19		1.7	1.8	2.69
Eugenia axillaris	7.25	13.45	6.9	20.78	12.58	6.03
Eugenia confusa			35.31			
Eugenia foetida			2.42	4.29	2.05	
Erythrina herbacea		1.64				
Exostema caribaeum						2.38
Exothea paniculata		1.29		1.69		
Guapira discolor					2.23	
Guettarda elliptica				7.1		
Gymnanthes lucida			5.72	3.76	15.24	30.17
Hamelia patens	2.12					
Krugiodendron ferreum		1.29	2.85	7.69	5.49	8.97
Lysiloma latisiliquum						
Manilkara zapota		1.69		1.73		
Metopium toxiferum		1.28		4.62	1.88	
Morus rubra	1.86					
Ocotea coriacea	9.1	3.27	5.67	1.68	3.8	

Species	D	M	S	N-1	N-2	N-3
Phoenix spp.	1.82	3.41				
Picramnia pentandra			5.93			
Piscidia piscipula			2.32	1.9	3.53	4.68
Prunus myrtifolia		1.9				
Psychotria nervosa	3.64	1.32				
Schaefferia fructescens					1.82	
Schefflera actinophylla		1.4				
Schinus terebinthifolius	3.59					
Sideroxylon foetidisssimum	6.93	1.78	5.45			
Simarouba glauca	6.01	1.87	2.53			
Solanum erianthum		1.28	2.95			
Swietenia mahagoni				1.82	2.09	
Trema micranthum	7.46					
Ximenia americana					2.12	
Zanthoxylum fagara		1.38			1.89	2.86

Table 2. Species importance values for tree species. Importance values calculated from relative basal area, relative frequency and relative cover of trees equal to and greater than 7.5cm dbh. D = Deering Estate; M = Matheson Hammock; S = Simpson Hammock; N1, N2, and N3 are sites in North Key Largo.

Species	D	M	S	N-1	N-2	N-3
Adenanthera pavonia		1.61				
Amyris elemifera					3.31	6.3
Ardisia escallonioides	1.58		1.12			
Bishophia javanica	6.67					
Bouerria ovata				4.03	1.29	3.03
Bumelia salicifolia		1.99	3	8.24		6.68
Bursera simaruba	9.64	7.13	8.8	14.01	11.09	10.98
Calyptranthes pallens		2.87	2.5		1.59	1.2
Canella winterana					1.29	
Carica papaya	5.85	8.34	2.13			
Celtis laevigata	3.12					
Chrysophyllum oliviforme			2.13			
Citrus spp.	1.66					
Coccoloba diversifolia	15.01	14.05	20.18	16.68	22.63	16.77
Colubrina elliptica						7.37
Drypetes diversifolia					3.3	3.17
Drypetes lateriflora		5.29			1.32	
Eugenia axillaris			1.23	1.8		
Eugenia confusa			11.49			
Exostema caribaeum						2.63
Exothea paniculata		4.43	1.41		1.52	1.32

Species	D	M	S	N-1	N-2	N-3
Ficus aurea	3.51	9.34	3.44			4.68
Ficus citrifolia	12.1		2.01			
Guapira discolor					2.85	1.39
Guettarda elliptica			1.3	2.18	1.44	2.8
Gymnanthes lucida			2.41		4.16	8.43
Krugiodendron ferreum		3.96	4.28	4.27	12.38	7.43
Lysiloma latisiliquum					10.35	
Manilkara zapota		3.36				
Metopium toxiferum				34.17	7.64	2.31
Ocotea coriacea	3.95	5.07	4.3			1.06
Persea borbonia	1.77					
Piscidia piscipula			9.86	5.06	4.35	7
Prunus myrtifolia		1.43				
Quercus virginiana	8.07					
Sabal palmetto	7.25					
Schefflera actinophylla		1.42				
Sideroxylon foetidisssimum	5.07	24.31	13.74	4.13		
Simarouba glauca	7.25	5.19	3.59		2.6	
Swietnia mahagoni				5.41	6.11	
Trema micrantha	6.14					
Ximenia americana						2.09
Zanthoxylum fagara	1.61		1.32			1.05

Vegetation and seed bank communities

Results of the Detrended Correspondence Analysis showed that major groupings based on site scores are apparent, including scores for seed bank, trees and shrubs. There was a distinct separation between mainland and Keys seed bank composition. The same distinction occurred for both site scores for tree species and shrub species. There was a greater disparity between shrub site scores for mainland sites and the Keys. Shrub site scores were more closely aligned with tree site scores for the Keys. This relationship was less clear for mainland sites.

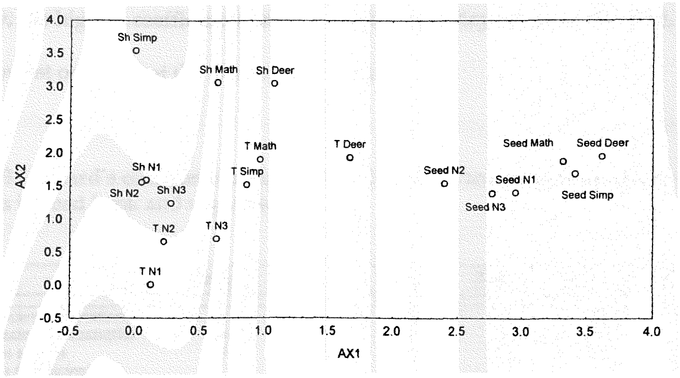


Figure 2. DCA site scores for tree (T), shrub (Sh), and seed assemblages in six southern Florida hardwood hammcocks.

Vegetation and Seed Bank Similarity

I used Jaccard's similarity coefficient to determine the similarity of the soil seed composition to vegetation. Coefficient values were calculated as the number of species present in both the soil and the vegetation divided by the total number of species in the soil and vegetation at each site (Table 3). Coefficient values can range from 0%, no species in common, to 100%, identical sets of species. I pooled species from both transects and calculated the coefficient for each site. Additionally, as Jaccard's coefficient is based on presence/absence of species, I included vines and herbs although these were not quantified. In this study, the highest coefficient occurred at one North Key Largo site (47.5%), and the lowest occurred at the Deering site (32%).

Table 3. Jaccard's coefficient of similarity. Calculated to compare similarity of species in seed bank and vegetation.

	Simp	Math	Deer	N-2	N-3	N-1
Total species- Vegetation	28	43	38	34	33	24
Total species- Soil samples	16	22	28	24	26	21
Common species	13	16	16	16	19	21
Jaccard's Coefficient of Community (%)	41.9%	32.7%	32.0%	38.1%	47.5%	45.2%

Dominant Species

Several species were relatively abundant in the seed bank (Chp. 1, Table 2). These species included *Piscidia piscipula, Bourreria ovata, Guettarda elliptica, Ficus* spp, *Solanum erianthum, Carica papaya,* and to a lesser extent *Lysiloma latisiliquum, Eugenia axillaris, Sideroxylon foetidissimum, Coccoloba diversifolia,* and *Bursera simaruba.*

In several cases, dominant seed bank species were also dominant in the vegetation (Table 1 & 2). Several canopy tree species occurred at all sites. These included, across all of the sites, *Coccoloba diversifolia* and *Bursera simaruba*. In mainland hammocks, *Sideroxylon foetidissimum* and *Ficus* spp were common; while in the Keys, *Metopium toxiferum* and *Krugiodendron ferreum* occurred frequently.

Coccoloba diversifolia saplings also occurred throughout all of the sites. In the Keys, *Bursera simaruba* saplings occurred in the shrub stratum. *Eugenia axillaris*, a sub-canopy species, was abundant throughout all of the sites. I graphed three life stages: trees greater than or equal to 7.5 cm; saplings less than 7.5 cm; and seeds, to show the relative importance of common species throughout these stages (Figures 3 - 6). Figure 3 shows the three common species throughout all of the sites. The importance of *Coccoloba diversifolia* saplings closely paralleled that of trees at all of the sites. Though seeds of this species were not abundant, they were recovered at nearly all of the sites. Similar patterns occurred for *Bursera simaruba*.

Carica papaya seeds occurred at nearly all of the sites (Figure 3). Densities of trees and shrubs of this species at mainland sites increased following Hurricane Andrew. It is unknown if higher seed densities were a result of recent inputs from new recruits or if densities were greater at these sites prior to the disturbance. Of the Keys sites, N2 sustained the greatest damage, with papaya recruiting in large gaps. Very few papaya seeds were recovered from North Key Largo sites.

At Keys sites, several species (*Bourreria ovata, Piscidia piscipula, Guettarda elliptica*) that were relatively dominant in the seed bank, were not dominant in the vegetation, but had consistent importance values for trees and shrubs throughout all three sites (Figure 4). There was considerable variation in seed densities of dominant species throughout these sites. In other cases at Keys sites, several dominant tree and shrub species had no seeds in the soil, or relatively low numbers (Figure 5).

Both *Ficus citrifolia* and *Ficus aurea* occurred in the canopy at mainland sites (Figure 6). Densities of *Ficus* seeds were also very high (20% to 56% of seeds germinating) for mainland sites. As I was unable to discern the difference between the two species at the seedling level, I consolidated the importance values of trees and shrubs to graph relationships. No *Ficus* saplings occurred at any of the sites.

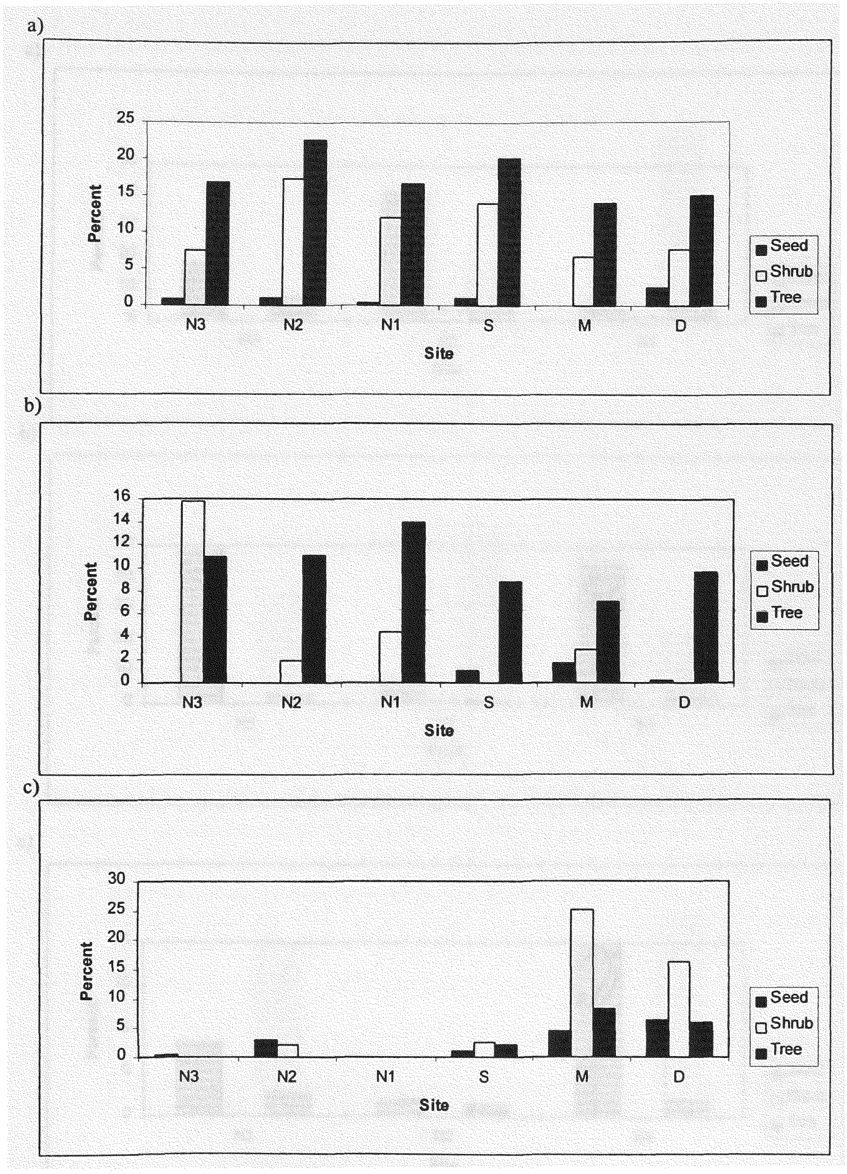


Figure 3. Percentage of total density of vegetation in quadrants and percentage of seeds recovered for a) *Coccoloba diversifolia*; b) *Bursera simarouba*; and c) *Carica papaya* at all sites.

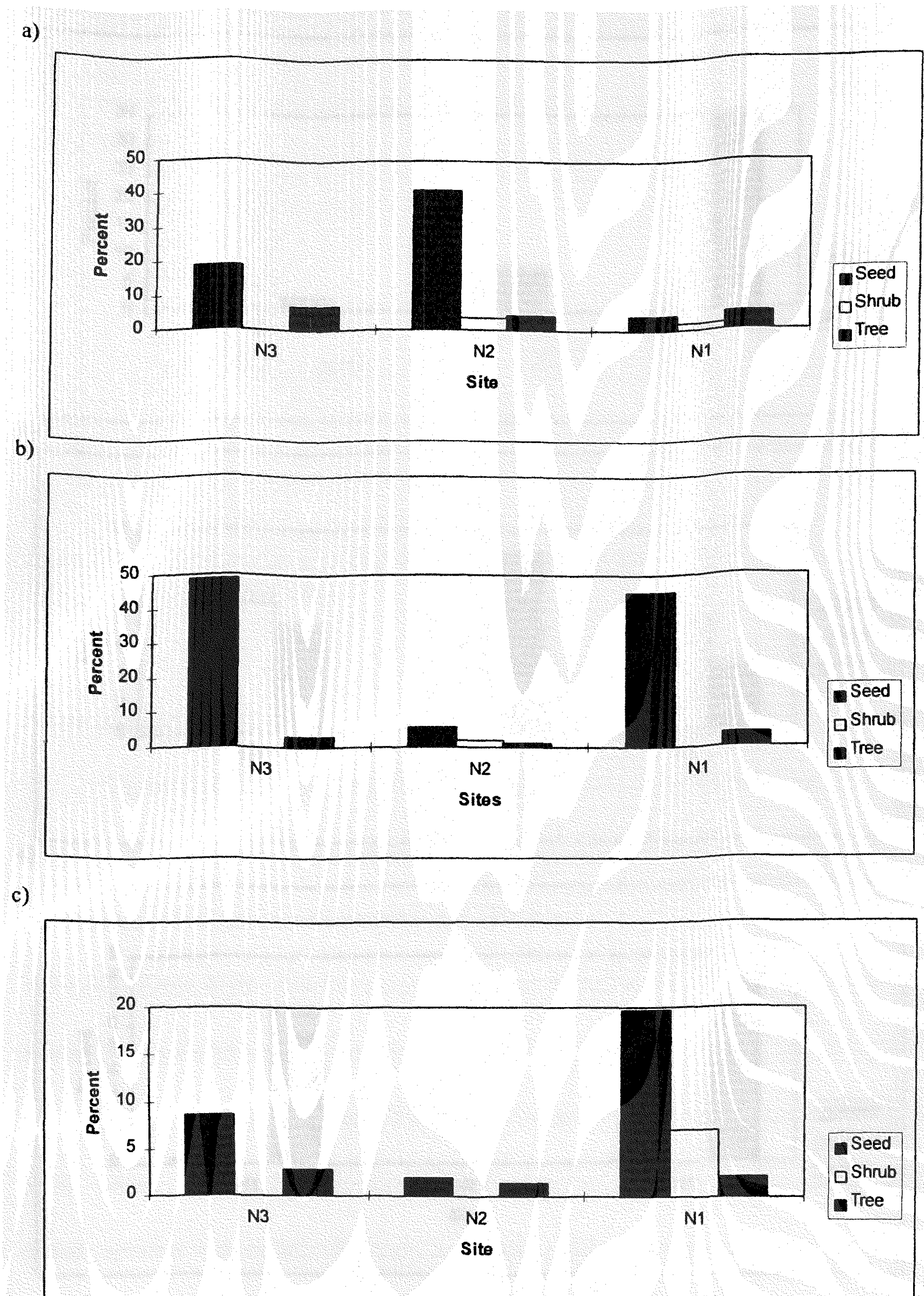


Figure 4. Percentage of total density of vegetation and percentage of seeds recovered for a) *Piscidia piscipula*; b) *Guettarda elliptica*; and c) *Bourreria ovata* at Key Largo sites.

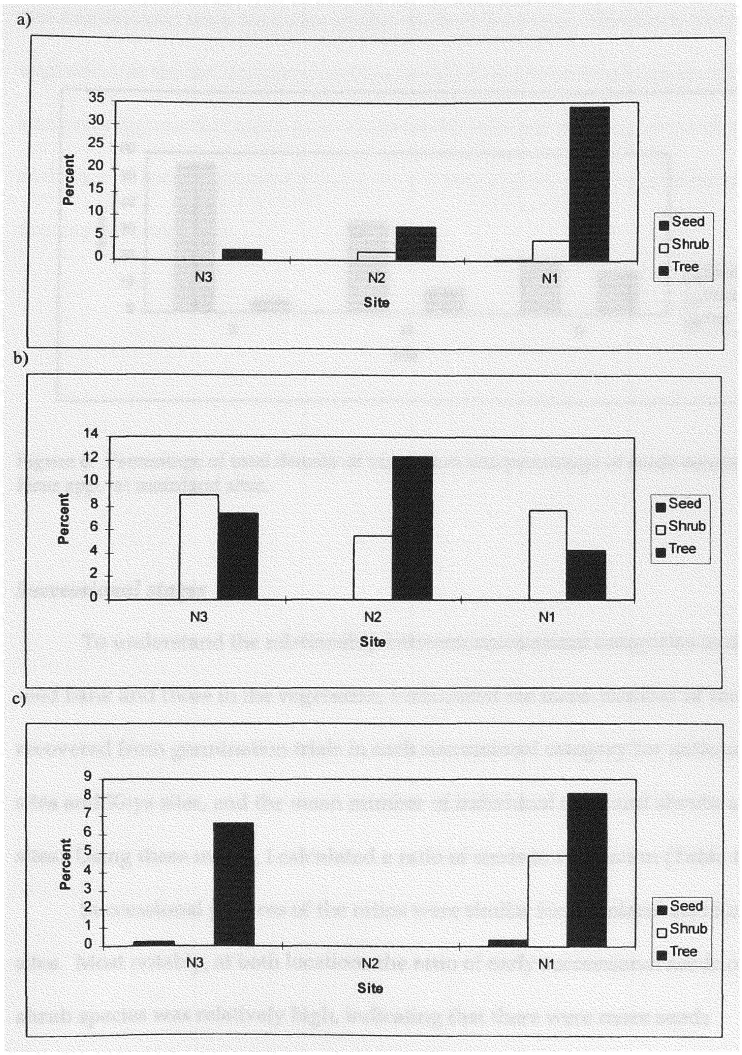


Figure 5. Percentage of total density of vegetation and percentage of seeds recovered for a) *Metopium toxiferum*; b) *Krugiodendron ferreum*; and c) *Bumelia salicifolia* at Key Largo sites.

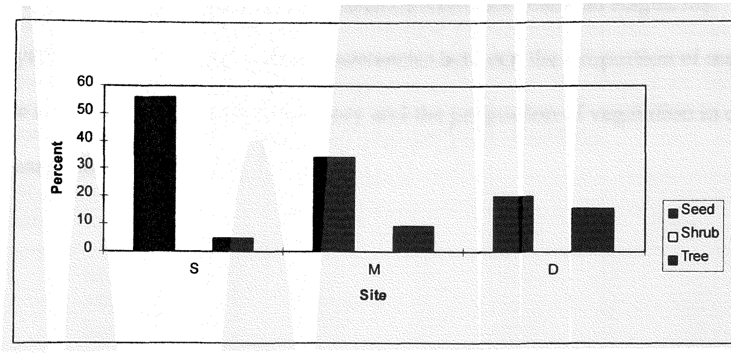


Figure 6. Percentage of total density of vegetation and percentage of seeds recovered for *Ficus* spp. at mainland sites.

Successional stages

To understand the relationship between successional categories in the seed bank and those in the vegetation, I calculated the mean number of seeds recovered from germination trials in each successional category for mainland sites and Keys sites, and the mean number of individual trees and shrubs at all sites. Using these means, I calculated a ratio of seeds to vegetation (Table 4).

Successional patterns of the ratios were similar for mainland and Keys sites. Most notably, at both locations the ratio of early successional seeds of shrub species was relatively high, indicating that there were more seeds recovered than shrubs present at the sites. The trends for mid-successional and late successional trees were also similar for both locations. Therefore, though the vegetation at the two locations represents different successional stages, my analysis suggests that there were consistencies between the proportion of seeds in the soil in each successional category and the proportion of vegetation in each successional category.

Table 4. Mean number of a) seeds of tree species recovered from germination trials versus trees, and b) seeds of shrub species recovered from germination trials versus shrubs in each successional category for mainland and Keys sites. Ratio shows relationship between seed bank and vegetation in successional categories. Low ratios indicate high representation in vegetation, with few seeds in the soil. Higher ratios indicate greater representation in the seed bank than in the vegetation.

MAINLAND SITES

a) Seeds vs Trees	Seeds	Trees	Ratio
Early	0	3.9	0
Mid	94.3	15.2	6.2
Late	8.7	64.5	.13

b) Seeds vs shrubs	Seeds	Shrubs	Ratio
Early	86.3	2.5	34.5
Mid	8	18.0	.44
Late	0	59.2	0

KEYS SITES

a) Seeds vs Trees	Seeds	Trees	Ratio
Early	0	0.03	0
Mid	305	44.1	6.9
Late	10	55.4	.18

b) Seeds vs shrubs	Seeds	Shrubs	Ratio
Early	21.7	0	21.7
Mid	3	37.3	.08
Late	1.7	62.3	.03

DISCUSSION

The results of this study show that the community of buried seeds differs from the vegetative community in hardwood hammocks. Although there is much variation among the sites sampled, several patterns emerge. There are widespread species (e.g. *Coccoloba diversifolia* , *Bursera simaruba*) that are consistently found in hardwood hammocks, and have buried seeds, though these seeds are not abundant and are sparsely distributed. *Coccoloba diversifolia* and *Bursera simaruba* both s have large seeds, suggesting the ability to germinate under lower light conditions and are thus less likely to be incorporated in the soil (Thompson 1993). There is a close relationship between adult individuals and saplings, suggesting that these species are well dispersed and recruit readily in the hammocks sampled. Because the density of seeds was low, it may be that these species have a seedling bank where seeds germinate and remain as seedlings until appropriate environmental conditions allow them to grow to maturity.

Though a mature forest structure may be the primary goal of restoration, in recreating a hammock it is important to incorporate earlier and mid-successional species even though these species will be replaced as the forest matures. A common restoration strategy is to plant late-successional saplings or mature trees, I recommend including individuals that will contribute to a seed bank. As this study shows, some mid-successional species, *Bourreria ovata, Piscidia piscipula*, and *Guettarda elliptica*, contribute substantially to buried seeds. No long-term longevity studies have been conducted on these species, but it has been suggested that *Guettarda* and *Piscidia* have relatively long-lived seeds of at least 5 months (Ray and Brown 1994). At many cleared sites in the Keys, these have been some of the earliest colonizers. Most likely very early recruitment is from a seed bank, rather than from recently dispersed seeds.

Previous studies show that, for tropical forests, extensive deforestation that alters seed-rain regimes may cause local extinctions of pioneer species (Alvarez-Buylla and Gracia-Barrios 1991). In hardwood hammocks, these pioneer species include *Hamelia patens* and *Solanum erianthum*. Incorporating these plants along with later successional species will allow some seeds to become incorporated into the soil as the forest develops. This approach also applies to mid-successional species. Birds likely disperse some of these species (e.g. *Bourreria ovata, Guettarda elliptica*), but in the case of isolated projects seed dispersal by natural vectors may be ineffective. *Piscidia piscipula* , a wind dispersed species, also played an important role in the seed bank and may also be limited by its dispersal mechanism. The nitrogen-fixing capabilities of this important legume may play a significant role in forest regeneration of scarified sites.

Very little is known about dispersal distances and important dispersal agents of many hammock species. It is commonly thought, however, that seed rain density decreases with distance from the parent plant, and seed survival increases (Janzen 1970, Hubbel 1980). Both dispersal in space and time (with the incorporation of seeds into a seed bank) of individual species may determine the success of management aimed at restoration of a target vegetation. Many species in temperate zones tend to be specialized on either good dispersal capacity or building a persistent seed bank (Bakker et al. 1996). In the Keys, nearly 75% of the species in hardwood hammocks are dispersed by birds (Tomlinson 1980). There is evidence that white-crowned pigeons are a principal dispersers (Strong et al. 1994). Because so many of the species in this forest type are animal dispersed, and many species do not have long-lived seed banks, including bird perches may facilitate dispersal to the site (Robinson 1993, Slocum 1997). Other studies have shown limited movement of birds in fragmented tropical forests (Silva et al. 1996). More information needs to be documented concerning the biology of important seed dispersers in this habitat. For example birds may prefer cover in small forest "islands" within degraded sites to move into and disperse seeds (Gerhardt 1993).

Mainland hammocks lack both *Piscidia* and *Guettarda,* which historically were found in these hammocks, but at unknown densities. Except for Simpson hammock, where *Piscidia* occurs in the vegetation, seeds of these species were not recovered in soil samples at the other two sites. There seems to be an absence of species that fill the same regenerative niche at mainland sites. For example, many of the seeds recovered from mainland sites belonged to native vines, early successional shrubs, and weedy herbs. It may be important to monitor recruitment in restoration sites in fragmented urban settings, particularly following a major disturbance, and potentially enhancing seed dispersal of important species by hand.

Buried exotic seeds are not a significant problem in intact hammocks (see chapter one). However, cleared sites that have been left fallow for a period of time may support weedy herbaceous and invasive exotic plants. This leads to an increase in buried seeds of weedy species, and pose problems in the development of a hardwood hammock.

Hammock restoration provides opportunities to investigate and address questions regarding important ecological processes. There are important processes to mimic in creating effectively restored forests. As this research shows, seed banks play an important role in regeneration of dry tropical forests in southern Florida. Species in this forest type have developed strategies for regeneration given such selective pressures as seasonal dry periods and hurricanes. I encourage restorationists to consider the implications of developing a seed bank, as well as planting mature trees in restoration projects. This approach is intended to mimic the natural regeneration strategies of early and mid- successional species in hardwood hammocks. Many restoration sites have been severely fragmented and scarified. Seeds of important early hammock colonizers may therefore be absent. Without a significant seed rain, either from species within the site or from dispersal agents, large scale disturbances such as hurricanes, may significantly impact a project. I would also suggest that soil samples be collected and monitored to determine if a seed bank is developing. It would be interesting to investigate how the composition and abundance of buried seeds change over time. For example, in this study, the greatest mean density of seeds occurred at one site that was suspected to have never been cleared in the Keys (N3). In this site, the distribution of dominant buried seeds was also more consistent within the transects. This may be closely related to stand age. Young et al. (1987) showed that as the vegetation grew in a Costa Rican tropical forest the soil seed bank increased to a peak after 4 to 7 years.

LITERATURE CITED

Alvarez-Buylla, E.R., and R. Garcia- Barrios. 1991. Seed and forest dynamics: a theoretical framework and an example from the neotropics. American Naturalist 137: 133-154.

Bakker, J.P., P. Poschlod, R.J. Strykstra, R.M. Bekker and K. Thompson. 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Bot. Neerl. 45 (4): 461-490.

Bradshaw, A.D. 1987. Pages 23 - 29. *in* W.R. Jordan, M.E. Gilpin and J.D. Aber editors. Restoration ecology: A synthetic approach to ecological research. Cambridge University Press, New York

Ewel, J.J. 1987. Pages 31 - 33. *in* W.R. Jordan, M.E. Gilpin and J.D. Aber editors. Restoration ecology: A synthetic approach to ecological research. Cambridge University Press, New York

Gerhardt, K. 1993a. Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. Journal of Vegetation Science 4: 95-102.

Gerhardt, K. and H. Hakan. 1992b. Natural dynamics and regeneration methods in tropical dry forests- an introduction. Journal of Vegetation Science 3: 361-364.

Hubbell, S.P. 1980. Seed predation and the coexistence of tree species in tropical forests. Oikos 35: 214-229.

Janzen, D.H. 1988a. Tropical dry forests: the most endangered major tropical ecosystem. Pages 130-137 *in* E.O. Wilson (ed.) Biodiversity. National Academic Press, Washington D.C.

Janzen, D.H. 1970b. Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501-528.

Kartesz, J.T. 1994. A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland, 2nd edition. Timber Press, Portland, Oregon.

Ray, G. and B. Brown. 1994. Seed ecology of woody species in a Caribbean Dry Forest. Restoration Ecology 2(3): 156-163.

Ray, G. and B. Brown.1995. Restoring Caribbean Dry Forests: evaluation of tree propagation techniques. Restoration Ecology 3(2):86-94.

Robinson, G.R., and S.N. Handel. 1993. Forest regeneration on a closed landfill: rapid addition of new species by bird dispersal. Conservation Biology 7(2):271-278.

Silva, J.M., C. Uhl, and G. Murray. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abancdoned amazonian pastures. Conservation Biology 10(2):491-503.

Strong, A.M., R.J Sawicki,. and G.T. Bancroft. 1994. Estimating white crowned pigeon population size from flight-line counts. Journal of Wildlife Management 58(1):156-161.

Tomlinson, P.B. 1980. The Biology of Trees Native to Tropical Florida. Harvard University Printing, Allston, Mass.

Thompson, K., S.R. Band, and J.G. Hodgson. 1993. Seed size and shape predict persistence in soil. Functional Ecology 7: 236-241.

Young K.R., J.J. Ewel, and B.J. Brown. 1987. Seed dynamics during forest succession in Costa Rica. Vegetatio 71: 157-173.