

RESEARCH ARTICLE

SEED BANK CHANGES WITH TIME-SINCE-FIRE IN FLORIDA ROSEMARY SCRUB

Jennifer J. Navarra^{1,*}, Nancy Kohfeldt², Eric S. Menges², and Pedro F. Quintana-Ascencio¹

¹Department of Biology, University of Central Florida,
4000 Central Florida Boulevard, Orlando, Florida 32816, USA

²Archbold Biological Station, P.O. Box 2057, Lake Placid, Florida 33862, USA

*Corresponding author: Tel: 001-863-635-7801 ext. 102; e-mail: jnavarra@knights.ucf.edu

ABSTRACT

The soil seed bank plays a central role in the regeneration of obligate seeding species in fire-prone habitats. We evaluated how seed density and species composition changed with time-since-fire in the Florida, USA, rosemary scrub community. Because fire affects habitat availability and plant demographic variation, we predicted that soil seed density would be low in recently burned and long-unburned stands and high at intermediate time-since-fire. Seed bank soil samples were collected from a chronosequence of time-since-fire composited from two trials conducted in 1992-1993 and 2008-2009: two sites each of 3, 6, 10, and 24 years post-fire, and 3 long-unburned (~67 years) sites. The seedling emergence method was used to determine species composition of the seed bank. Across all time-since-fire age classes, herbaceous species dominated the seed bank, while long-lived subshrubs and shrubs were present in low densities. Seed banks from sites three years post-fire were distinct from the other sites. When species were sorted as functional groups, seed density was related with time-since-fire for subshrubs and ruderal herbs, but not for scrub herbs and graminoids. Subshrubs and ruderal herbs had highest seed densities in recently burned stands. Seed densities of Florida rosemary (*Ceratiola ericoides* Michx.) (the major obligate seeding shrub in this community) were associated with time-since-fire and showed highest densities at recently burned and long-unburned sites. The seed banks of two scrub herb species, paper nailwort (*Paronychia chartacea* Fernald) and nodding pinweed (*Lechea cernua* Small), were associated with time-since-fire. They reached peaks in density in the first ten years post-fire, corresponding with similar changes in their aboveground abundances with time-since-fire. Soil seed densities of several species and functional groups were associated with time-since-fire, but timing of peak seed density varied depending on species' life span and age of reproductive maturity.

Keywords: chronosequence, disturbance, fire-prone, Florida scrub, Lake Wales Ridge, obligate seeder, seed bank, seed density, shrubland, time-since-fire

Citation: Navarra, J.J., N. Kohfeldt, E.S. Menges, and P.F. Quintana-Ascencio. 2011. Seed bank changes with time-since-fire in Florida rosemary scrub. *Fire Ecology* 7(2): 17-31. doi: 10.4996/fireecology.0702017

INTRODUCTION

Fire plays a central role in shaping species life history strategies (Pickett and White 1985). Life history characteristics such as dispersal mechanisms, ability to establish and grow, and time necessary to reach critical life stages determine if a species will persist in a community during and after fire (Noble and Slatyer 1980). Species within the same ecosystem often evolve a variety of adaptive strategies to cope with frequent fire (Christensen 1985).

Fire is ubiquitous worldwide. It influences global vegetation pattern and shapes species characteristics (Bond *et al.* 2005). In fire-prone communities like African fynbos, Australian heaths, and California chaparral, species rely upon persistent soil seed banks to regenerate after fire (Keeley 1991, Auld *et al.* 2000, Holmes and Newton 2004). Recruitment from the soil seed bank is essential for obligate seeding species for which aboveground individuals are killed by fire. Fire has been found to stimulate mass recruitment events; seedling densities are generally highest in recently burned stands (Tyler 1995, Carrington and Keeley 1999, Weekley and Menges 2003). High recruitment post-fire is promoted by direct cues such as smoke, heat, or chemical leaching, which break seed dormancy, or from indirect effects such as increased light, microhabitat availability, and release from competition or allelopathic chemicals (Christensen 1985, Keeley 1991, Pierce and Cowling 1991, Tyler 1996, Keeley and Fotheringham 1998). Changes in aboveground species abundance and composition as time-since-fire increases may affect seed bank characteristics in pyrogenic communities. Available information indicates that seed bank size can be low immediately following fire when the number of seedlings is high and seed inputs are low (due to mortality of reproductive plants), peak in size at intermediate years since fire, and decline in size in long-unburned stands as aboveground populations senesce and seeds lose viability (Vaughton 1998, Clemente *et al.* 2007).

Fire is important in the Florida rosemary scrub community and likely plays a central role in determining the dynamics of the seed bank for many species, particularly those endemic to this community. Florida rosemary scrub is a xeric upland sclerophyllous shrubland found on relic sand dunes that harbor a high number of endemic plant and animals (Abrahamson *et al.* 1984, Christman and Judd 1990). Understanding how species regenerate and respond to fire is essential for proper management of plant populations (Menges 2007) because fire intervals that are either too frequent or too infrequent can lead to local population extinctions (Zedler *et al.* 1983). Species characteristics such as life span, fire sensitivity, dispersal mechanism, and timing of reproductive maturity strongly influence how species cope with fire (Keeley 1991, Ooi *et al.* 2006). One key requirement for maintaining healthy populations in fire-prone habitats is implementation of appropriate fire-return intervals. The interval for obligate seeders must be long enough to ensure that adult plants reach a reproductive life stage to replenish the seed bank; however, it should not be so long that adult life span and viability of the seed bank have been surpassed (Zammit and Zedler 1988). In Florida scrub, population viability analyses have been used to suggest fire regimes for different types of scrub vegetation (reviewed in Menges 2007), but no analyses of seed banks with varying time-since-fire have informed land managers.

In this study, we evaluated seed bank changes with time-since-fire in Florida scrub using data from a chronosequence composited from two trials conducted in 1992-1993 (trial I) and 2008-2009 (trial II). We addressed the following questions: 1) Is there an association between time-since-fire and soil seed density? 2) If so, how does this association vary among different functional groups? 3) Which rosemary scrub species form persistent soil seed banks?

METHODS

Study Site

We conducted this research at Archbold Biological Station (Archbold) located near the southern end of the Lake Wales Ridge in Highlands County, Florida, USA (Township 38S, Range 30E, Sections 5-8, 18, 19, 29-32). The station experiences mean temperatures that range from 8.33°C in winter to 34.05°C in summer and has an average annual rainfall of 1364 mm (Archbold weather data, 1932-2009). The Lake Wales Ridge is characterized by a mixture of wetlands, mesic flatwoods, and more xeric upland communities found on relic sand dunes in central Florida. Rosemary scrub is found at locally high elevations with well drained, low nutrient Archbold or St. Lucie soils (Menges 1999). This habitat is dominated by Florida rosemary (*Ceratiola ericoides* Michx.), an allelopathic shrub (Hunter and Menges 2002), but also includes patches of shrub species such as saw palmetto (*Serenoa repens* [Bartram] Small), scrub palmetto (*Sabal etonia* Swingle ex Nash), Chapman's oak (*Quercus chapmanii* Sarg.), Archbold oak (*Q. inopina* Ashe), and sand live oak (*Q. geminata* Small). Shrub patches are separated by bare sand gaps where many herbaceous endemic species grow (Menges et al. 2008). After fire, most shrub species resprout from rhizomes or roots (Menges and Kohfeldt 1995); obligate seeders such as Florida rosemary and several herbaceous species recruit from the seed banks or from nearby unburned areas (Quintana-Ascencio and Menges 2000).

Seed Bank Sampling

During trial I (1992-1993), we sampled eight rosemary scrub sites that consisted of two sites in each of four age classes of time-since-fire: 3, 6, 24 years, and long-unburned (~67 years). From each site, we collected 20 soil cores in a stratified random fashion along

a 6 m transect through the longest axis of each rosemary scrub site. Soil cores were collected in tins 10 cm in diameter × 6 cm in depth (surface area per site = 0.079 m²). We collected six samples over a one and a half year period in January, April, July, and October of 1992, and in January and April of 1993. Over this period, we collected a total of 120 soil cores per site.

During trial II (2008-2009), we established three 16 m × 16 m macroplots in three separate sites: two at ten years post-fire and one long-unburned (~67 years). Ten 2 m × 2 m subplots were randomly placed within each macroplot. Each subplot was subdivided into 40 cm × 40 cm quadrats and samples were collected in a checkerboard pattern from every other quadrat (yielding thirteen quadrats per subplot). In August 2008 and January 2009, we collected five 1.92 cm diameter by 3 cm deep soil cores from each quadrat. We aggregated the cores, yielding 130 soil samples per macroplot (surface area per plot = 0.188 m²). During both sampling periods, we collected soil cores from the quadrats in a regular coring pattern and this pattern was alternated between the two seasons to avoid coring the same locations.

We analyzed the two trials together to evaluate the effect of time-since-fire. Both trials included samples representing the gradient of time-since-fire (trial I = 3, 6, 24 and long-unburned, trial II = 10 years and long-unburned). In spite of the differences in soil depth employed during the two trials (trial I = 6 cm, trial II = 3 cm) the volume of soil per sample unit was approximately equivalent (trial I = 235.62 cm³, trial II = 217.15 cm³). Species composition has been found to be consistent within this range in soil depth (J.J. Navarra, University of Central Florida, unpublished data). Overall trends were consistent between analyses of the combined data and trial I data only (when the data of trial II, the one with the most limited time-since-fire range, was removed).

Greenhouse Monitoring

We used the seedling emergence method to determine species composition of the seed bank. During trial I, we thoroughly mixed each soil core and half the volume of soil was distributed among four separate germination trays. In trial II, we sieved each soil sample to break up soil structure and large litter and then potted the soil and litter on top of a white sand substrate. We collected the substrate from fire lanes located within Archbold Biological Station and heated it to 85°C (minimum of 8 hours) to kill any seeds that may have been present in the soil. We randomized placement of the samples within the greenhouses and the seedling flat locations were regularly changed to minimize micro-environmental effects.

For both trials, we maintained samples in unheated greenhouses and watered them regularly to keep the soil moist. Sterile soil controls were placed among the samples to detect contamination from outside seed sources and, for trial II, to also ensure that all seeds in the substrate were killed during soil heating. For trial I, we considered all seedlings in the analysis since a relatively small portion of the emerging seedlings came from the controls (~1% of the total number of seedlings emerged from the controls). For the second trial, we omitted species and seedlings from the analysis that appeared to result from contamination based on the pattern of occurrence in the samples and controls (~5% of the total number of seedlings emerged from the controls). For both trials, we monitored the soil samples for germination at monthly intervals. We removed seedlings once they had been identified to the species level; however, some seedlings died before identification was possible. Nomenclature follows the Atlas of Florida Vascular Plants online database (<http://www.florida.plantatlas.usf.edu>).

For trial I, we carried out seedling monitoring from the time of soil collection until July 1994 (minimum time = 18 months, maxi-

mum time = 30 months). For trial II, we monitored the soil samples for 8 to 12 months. Although the soil samples were monitored for different lengths of time, this variation was unlikely to bias the results of the study since the majority of seedlings emerged during the first two months after collection. For all sampling periods, germination rates reached an asymptote before germination monitoring was discontinued.

Assessing Long-Term Persistence

We determined which species form persistent seed banks using all of the data collected in trial I. Those species that continued to germinate into the second year of greenhouse monitoring and that were present in the seed bank during all six months of soil collection were considered to form persistent seed banks. This dual approach to assessing the persistent seed bank ensured that these species' seeds remained viable for at least one year and that their seeds were present in the seed bank year round (Thompson and Grime 1979, Ortega *et al.* 1997, Arroyo *et al.* 1999). This is a conservative approach to assessing seed persistence; those species that did not meet both criteria may still form persistent seed banks.

Data Analysis

We used regression to assess the association of time-since-fire with soil seed bank density (number of seedlings divided by the total surface area in m²) and species richness with the data organized by species and functional groups. For these time-since-fire analyses, we only used seed bank data collected from summer and winter seasons to combine comparable datasets from the two trials (trial I = January and July 1992, trial II = August 2008 and January 2009). We divided the species into functional groups based upon growth habit and, for herbaceous species, habitat preference. We identified the following functional

groups: 1) scrub herbs (herbaceous species found only in Florida scrub), 2) scrub subshrubs, 3) scrub shrubs, 4) graminoids (sedges, rushes, and grasses), and 5) ruderal herbs (species typical of disturbed habitats, generally not found growing aboveground in Florida scrub). We only analyzed species and functional groups that were present across at least 50% of the sites to ensure that occurrence was high enough along the time-since-fire chronosequence to reveal patterns. We averaged seed density across seasons.

We used a model selection approach for small samples (Akaike's information criterion, AIC_c) to compare linear, quadratic, and cubic models, assuming negative binomial error distribution for the seed count estimates (Venable and Brown 1988, Crawley 2007). We calculated Akaike weights for each model (Burnham and Anderson 2002) and analyses were conducted in R 2.9.1 (R Development Core Team, <http://cran.at.r-project.org/>).

We evaluated whether time-since-fire had an association with seed composition and density at the community level using Non-metric Multidimensional Scaling (NMS) ordination based on Sorensen distances (Kruskal 1964, Mather 1976). Species that occurred across less than 20% of the sites and seasons were omitted from the NMS ordination to reduce noise in the data set (McCune and Grace 2002). The data were analyzed using PC-ORD 5.0 (MjM Software Design, Sweet Home, Oregon, USA). We started with a random configuration. Dimensionality of the data was assessed using autopilot. The stability of the solution was evaluated with three repeated runs of the same data. We evaluated whether a similar final stress could be obtained by chance with Monte Carlo tests. We also tested if there were community level differences in seed density with time-since-fire with permutational multivariate analysis of variance (Permanova) (Anderson 2001). We tested for significance using F-tests developed from sequential sum of squares permutations (10000) of the raw data. The significance level was adjusted to P

≤ 0.01 after Bonnferroni correction (Sokal and Rohlf 1995). Analyses were conducted with the vegan package in R 2.9.1. We compared species richness between summer and winter seasons using a non-parametric Kruskal-Wallis one-way analysis of variance (Sokal and Rohlf 1995).

RESULTS

Species Composition

We found 3963 seedlings (trial I = 2647, trial II = 1316) belonging to 45 species in the seed banks of the two trials (summer and winter seasons only) (see Table 1). Approximately 15% of the emerging seedlings could not be identified. At all times-since-fire, the seed banks were dominated by annual and short-lived perennial herbaceous species (Figure 1). The two most abundant species in the seed bank were paper nailwort (*Paronychia chartacea* Fernald) and pineland scalypink (*Stipulicida setacea* Michx.), which comprised approximately 43% (trial I = 34%, trial II = 62%) of the emerging seedlings (Table 1). Long-lived species had fewer total seeds and species than short-lived herbs. A club moss (*Selaginella arenicola* Underw.) comprised approximately 50% of the propagules emerging from the samples collected in trial I (trial II = 1%); however, this species was not considered in the regression, NMS ordination, or Permanova analyses because it does not produce seeds. This species was observed to recruit from broken fragments and spores.

Species Richness

Across all sites and seasons, species richness ranged between 7 and 37 and had a mean of 14. We did not find evidence of association between species richness and time-since-fire. Species richness was slightly higher in winter (mean = 14.64 ± 0.47) than in summer (mean = 14.18 ± 2.38 , $df = 1$, $P = 0.026$).

Table 1. Mean seed density (m⁻²) rounded to the nearest integer (\pm standard error) for species in different time-since-fire age classes. Seed densities were calculated from seed bank soil samples collected from Archbold Biological Station in January and July 1992, August 2008, and January 2009. LU = long unburned.

Species	Time-since-fire				
	3 yrs	6 yrs	10 yrs	24 yrs	LU
Scrub herbs					
<i>Balduina angustifolia</i> (Pursh) B.L.Rob.	3 (3)	-	-	-	-
<i>Eryngium cuneifolium</i> Small	38 (38)	3 (3)	-	16 (16)	2 (2)
<i>Helianthemum nashii</i> Britton	38 (38)	-	-	-	-
<i>Hypericum cumulicola</i> (Small) W.P.Adams	3 (3)	57 (29)	3 (2)	13 (13)	86 (29)
<i>Lechea cernua</i> Small	10 (5)	70 (41)	13 (3)	-	8 (4)
<i>Lechea</i> spp. Small	13 (9)	60 (56)	-	-	2 (2)
<i>Paronychia chartacea</i> Fernald	32 (11)	395 (71)	357 (134)	99 (26)	154 (38)
<i>Polanisia tenuifolia</i> Torr. & A.Gray	-	-	3 (3)	-	1 (1)
<i>Polygonella basirama</i> (Small) G.L.Nesom& V.M.Bates	-	-	3 (2)	-	-
<i>Stipulicida setacea</i> Michx.	735 (639)	573 (135)	610 (69)	226 (56)	435 (170)
All scrub herbs	872 (611)	1159 (166)	988 (115)	353 (65)	688 (161)
Subshrubs					
<i>Calamintha ashei</i> (Weath.) Shinnars	-	-	-	-	2 (2)
<i>Lechea deckertii</i> Small	10 (3)	60 (29)	-	-	6 (6)
<i>Palafoxia feayi</i> A.Gray	41 (20)	-	5 (2)	3 (3)	4 (3)
<i>Polygonella robusta</i> (Small) G.L.Nesom& V.M.Bates	38 (38)	3 (3)	-	-	-
All subshrubs	89 (38)	64 (32)	5 (2)	3 (3)	13 (6)
Shrubs					
<i>Ceratiola ericoides</i> Michx.	67 (17)	3 (3)	-	16 (6)	28 (12)
<i>Lyonia</i> sp.	-	-	-	-	2 (2)
All shrubs	67 (17)	3 (3)	-	16 (6)	30 (13)
Graminoids					
<i>Bulbostylis warei</i> (Torr.) C.B.Clarke	3 (3)	3 (3)	-	-	-
<i>Cyperus</i> spp.	22 (10)	51 (25)	100 (38)	29 (17)	51 (18)
<i>Dichanthelium</i> spp.	3 (3)	-	-	-	-
<i>Juncus</i> sp.	-	-	8 (3)	-	2 (2)
<i>Panicum repens</i> L.	6 (6)	-	-	3 (3)	-
<i>Paspalum notatum</i> Flügge	3 (3)	-	-	-	-
<i>Paspalum setaceum</i> Michx.	10 (6)	-	-	-	-
Poaceae	45 (24)	16 (8)	7 (3)	48 (6)	45 (26)
All graminoids	92 (48)	70 (32)	114 (44)	80 (18)	98 (16)
Ruderal herbs					
<i>Conyza canadensis</i> (L.) Cronquist	10 (6)	48 (36)	-	-	4 (4)
<i>Emilia fosbergii</i> Nicolson	6 (4)	3 (3)	-	13 (13)	-
<i>Eupatorium</i> spp.	29 (11)	13 (5)	17 (13)	19 (8)	29 (10)
<i>Euthamia caroliniana</i> (L.) Greene ex Porter & Britton	10 (6)	-	-	6 (6)	2 (2)
<i>Gamochaeta purpurea</i> (L.) Cabrera	1623 (862)	-	33 (5)	-	104 (55)
<i>Houstonia procumbens</i> (J.F.Gmel.) Standl.	3 (3)	-	-	-	1 (1)
<i>Linaria floridana</i> Chapm.	54 (36)	293 (196)	43 (15)	13 (7)	92 (44)
<i>Oldenlandia corymbosa</i> L.	3 (3)	-	1 (1)	3 (3)	2 (2)
<i>Oldenlandia</i> spp.	6 (4)	57 (27)	-	-	2 (2)
<i>Oldenlandia uniflora</i> L.	10 (10)	-	3 (2)	3 (3)	2 (2)
<i>Oxalis corniculata</i> L.	67 (29)	-	-	-	17 (11)
<i>Phyllanthus tenellus</i> Roxb.	22 (11)	6 (6)	-	57 (22)	34 (31)
<i>Physalis</i> sp.	38 (38)	-	-	-	-
<i>Pilea microphylla</i> (L.) Liebm.	10 (6)	6 (4)	-	-	2 (2)
<i>Polypremum procumbens</i> L.	-	-	5 (2)	-	6 (4)
<i>Richardia scabra</i> L.	3 (3)	-	-	-	4 (4)
<i>Ruellia blechum</i> L.	6 (4)	-	-	16 (10)	8 (3)
<i>Scoparia dulcis</i> L.	-	-	4 (4)	-	4 (2)
All ruderal herbs	1900 (822)	427 (244)	106 (29)	131 (50)	314 (100)
Unknown					
Dicot - long hair	140 (56)	73 (31)	-	45 (25)	38 (15)
Solanaceae family	10 (10)	-	-	-	2 (2)
Unidentified	162 (74)	535 (194)	145 (31)	350 (47)	248 (69)
All unknowns	312 (68)	608 (224)	145 (31)	395 (45)	288 (78)
Overall total	3333 (1101)	2330 (419)	1359 (172)	977 (116)	1430 (254)

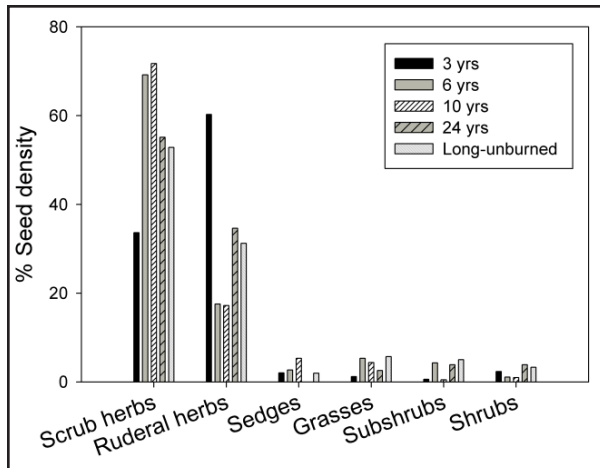


Figure 1. Percent seed density of functional groups in each time-since-fire age class. Seed density was estimated from seed bank soil samples collected from Archbold Biological Station in January and July 1992, August 2008, and January 2009.

Community Level Association with Time-since-Fire

The NMS ordination of seed density for species occurring across $\geq 20\%$ of the seasons and sites indicated that time-since-fire does explain some differences among the sites (final stress = 11.55, no. iterations = 43; axis 1 $P = 0.032$, $R^2 = 0.562$; axis 2 $P = 0.008$, $R^2 = 0.317$). The NMS ordination plot showed clear separation of sites three years time-since-fire from all other sites, particularly for the winter samples. The other time-since-fire age classes exhibited considerable overlap (Figure 2).

Permanova results revealed significant differences in seed density among the five time-since-fire age classes in both winter and summer (Table 2). Pairwise comparisons found significant differences among sites three years time-since-fire and long-unburned during the winter when seed density was at its peak, and between sites 6 and 24 years time-since-fire in the summer when seed density was lower (Table 2).

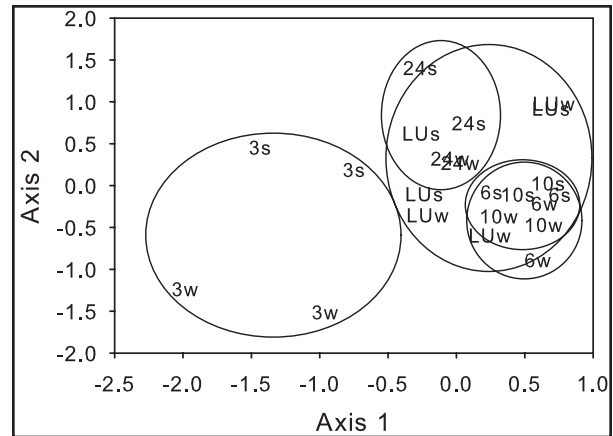


Figure 2. NMS ordination of species seed density from seed bank soil samples collected from Archbold Biological Station in January and July 1992, August 2008, and January 2009. Each number indicates time-since-fire, LU = long-unburned, s = summer, and w = winter.

Species and Functional Group Associations with Time-since-Fire

There were enough occurrences of Florida rosemary, flatsedge (*Cyperus* spp. L), boneset (*Eupatorium* spp. L), spoonleaf purple everlasting (*Gamochaeta purpurea* [L.] Cabrera), highlands scrub St. Johnswort (*Hypericum cummicola* [Small] P. Adams), nodding pinweed (*Lechea cernua* Small), Apalachicola toadflax (*Linaria floridana* Chapm.), Feay's palaflox (*Palafloxia feayi* A. Gray), paper nailwort, Mascarene Island leaf-flower (*Phyllanthus tenellus* Roxb.), Browne's blechum (*Blechum pyramidatum* [Lam.] Urb.), pineland scalypink, and four functional groups (graminoids, ruderal herbs, scrub herbs, and subshrubs) to be considered in the time-since-fire analysis. Of these, only two functional groups (ruderal herbs, subshrubs) and four species (Florida rosemary, nodding pinweed, paper nailwort, and Mascarene Island leaf-flower) had significant models predicting seed densities from time-since-fire. A quadratic model was the most informative for ruderal herbs ($P = 3.2e^{-8}$, $w_i = 0.69$) and subshrubs ($P = 0.005$, $w_i = 0.44$). Their seed densities were highest three

Table 2. PERMANOVA results for the comparison of community level differences in composition and seed density among the five age classes of time-since-fire in winter and summer. Seed densities were calculated from seed bank soil samples collected from Archbold Biological Station in January and July 1992, August 2008, and January 2009. Asterisks denote $P \leq 0.01$.

TSF (yrs)	df	Winter			Summer		
		F-ratio	R^2	P	F-ratio	R^2	P
All	4	3.32	0.69	0.012*	4.82	0.76	0.005*
3 vs. 6	1	11.45	0.85	0.25	17.11	0.90	0.24
3 vs. 10	1	7.63	0.79	0.25	6.00	0.92	0.13
3 vs. 24	1	14.12	0.88	0.25	21.18	0.91	0.26
3 vs. LU	1	2.53	0.46	0.0001*	3.40	0.77	0.15
6 vs. 10	1	9.43	0.83	0.25	96.68	0.99	0.08
6 vs. 24	1	0.83	0.29	0.66	24.54	0.92	0.0001*
6 vs. LU	1	0.77	0.20	0.40	2.42	0.71	0.38
10 vs. 24	1	17.35	0.90	0.09	1568.20	1.00	0.09
10 vs. LU	1	0.77	0.20	0.50	1.61	0.35	0.35
24 vs. LU	1	1.13	0.27	0.41	4.68	0.82	0.20

years post-fire and declined in the later time-since-fire age classes (Figure 3a and b). For scrub herbs, highest seed densities were generally observed at three to ten years post fire (Figure 3c); however, we do not have statistical evidence to reject the null model ($P = 0.008$, $w_i = 0.07$). A cubic model of time-since-fire was found to be best for Florida rosemary ($P = 0.001$, $w_i = 0.81$), nodding pin-

weed ($P = 0.0001$, $w_i = 0.92$), paper nailwort ($P = 2.1e^{-6}$, $w_i = 0.54$), and Mascarene Island leaf-flower ($P = 0.01$, $w_i = 1.0$). Florida rosemary showed highest seed density at recent and long-unburned time-since-fire (Figure 4a). Two scrub endemic herbs, nodding pinweed and paper nailwort, showed low densities in recently burned and long-unburned sites and high densities at short to intermediate (six, ten

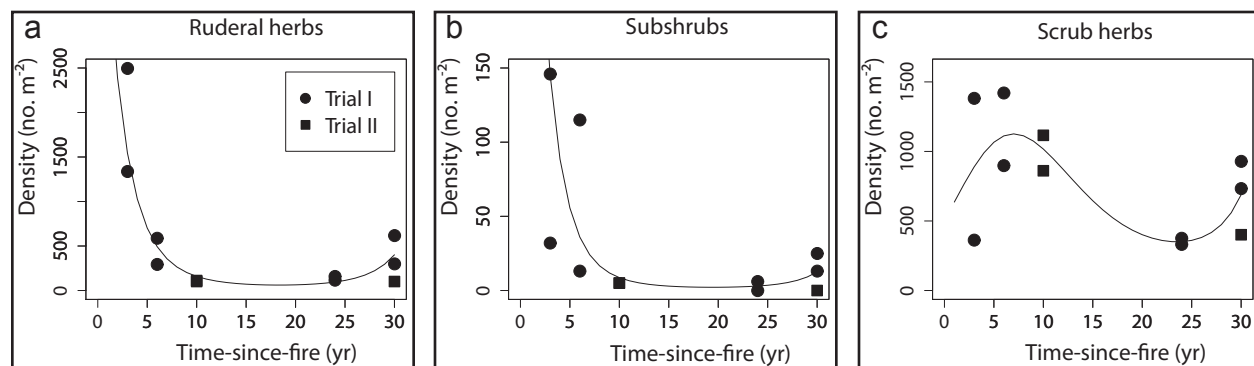


Figure 3. Negative binomial regression models for functional groups showing significant association between mean seed density (no. m^{-2}) and time-since-fire for seed bank soil samples taken from Archbold Biological Station in January and July 1992, August 2008, and January 2009. (a) Ruderal herbs, quadratic model (ratio of residual deviance over degrees of freedom = 1.4; $P = 3.2e^{-8}$; $w_i = 0.69$). (b) Subshrubs, quadratic model (ratio = 1.7; $P = 0.005$; $w_i = 0.44$). (c) Scrub herbs, cubic model (ratio = 1.6, not selected as the best model; $P = 0.008$; $w_i = 0.07$). Analyses were conducted using centered time-since-fire values but graphed using original values.

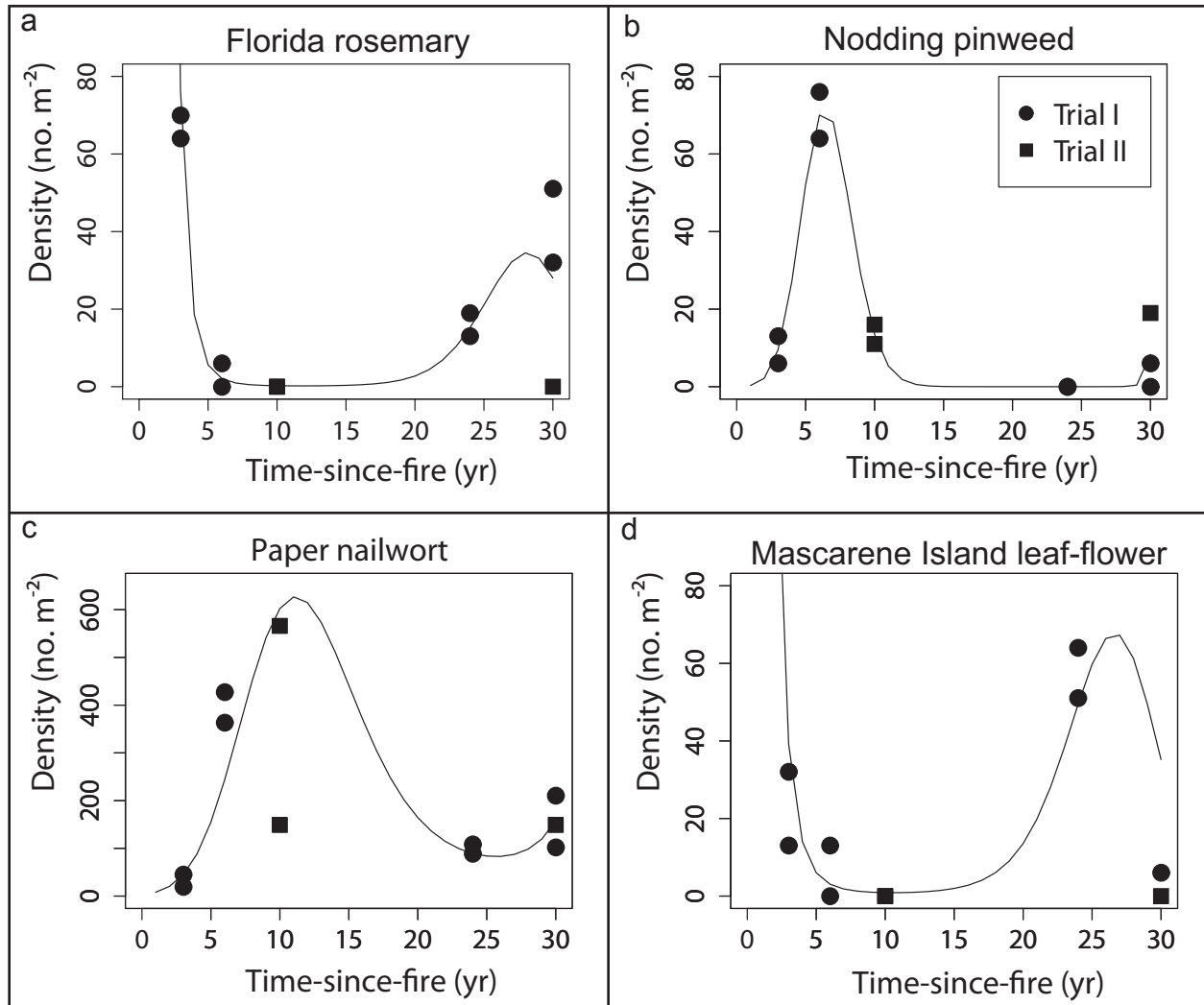


Figure 4. Cubic negative binomial regression models for species showing significant association between mean seed density (no. m⁻²) and time-since-fire from seed bank soil samples collected from Archbold Biological Station in January and July 1992, August 2008, and January 2009: (a) Florida rosemary (ratio of residual deviance over degrees of freedom = 1.8; $P = 0.001$; $w_i = 0.81$), (b) nodding pinweed (ratio = 1.9; $P = 0.0001$; $w_i = 0.92$), (c) paper nailwort (ratio = 1.6; $P = 2.1e^{-6}$; $w_i = 0.54$), and (d) Mascarene Island leaf-flower (ratio = 1.7; $P = 0.01$; $w_i = 1.0$). Analyses were conducted using centered time-since-fire values but graphed using original values.

year) times-since-fire (Figure 4b and 4c). Mascarene Island leaf-flower showed highest density in long-unburned sites (Figure 4d).

Seed Persistence

Given our conservative criteria, five scrub herbs (wedge-leaved button snakeroot [*Eryngium cuneifolium* Small], highlands scrub St. Johnswort, nodding pinweed, paper nailwort,

and pineland scalypink), one subshrub (Decker's pinweed [*Lechea deckertii* Small]), one shrub (Florida rosemary), two graminoids (flatsedge and one grass), and five ruderal herbs (slender goldentop [*Euthamia caroliniana* {L.} Greene ex Porter & Britton], bone-set, spoonleaf purple everlasting, Apalachicola toadflax, and creeping woodsorrel [*Oxalis corniculata* L.]) formed persistent soil seed banks. Several species had germinants emerging into

the third year, suggesting that the possibility of a long-term persistent seed bank (Florida rosemary, slender goldentop, boneset, highlands scrub St. Johnswort, Apalachicola toadflax, Feay's palaflox, paper nailwort, and pineland scalypink). The club moss was also found across all seasons of sampling and had propagules after the second year.

DISCUSSION

Our results indicate that fires can influence seed bank dynamics. Species composition of the seed bank was largely influenced by post-fire recovery strategies (see Menges and Kohfeldt 1995). Most species found in the seed bank were obligate seeders, or seeders and resprouters. Resprouting and clonal spreading species were virtually absent from the seed bank. Time-since-fire affected seed density for some species and functional groups. In this study, we found that association of seed density with time-since-fire varied depending on life history and timing of reproductive maturity.

Long-lived species generally showed peaks in density at recent and long-unburned time-since-fire, while short-lived scrub species reached density peaks at early to intermediate times-since fire. In other systems, life span also influences the time taken for peak seed densities to be reached following disturbance (Bekker *et al.* 1999, Clemente *et al.* 2007). For example, Clemente *et al.* (2007) compared two obligate seeding shrubs in a fire-prone Mediterranean habitat and found that the longer-lived shrub reached peak seed density later than the shorter-lived. For Florida rosemary (the major obligate seeding shrub sampled in this community), the pattern of high seed densities at recently burned and long-unburned sites and low seed densities or absence of seed at six and ten years post-fire is expected because this species takes ten years to reach reproductive maturity (Johnson 1982). The pattern observed for scrub herbs such as paper nailwort and nodding pinweed corresponds with changes in abundances of

these two species aboveground (Menges and Kohfeldt 1995) and suggests that seed densities and vegetation abundances are closely linked. These results agree well with what is already known about the demography of some scrub endemic herbs. For example, in wedge-leaved button snakeroot, seedling recruitment after fire is much higher than at other times. The plants reach maturity very quickly post-fire (Menges and Quintana-Ascencio 2004) and probably replenish the seed bank rapidly. The population declines with time-since-fire and the seed bank also likely decays fairly quickly (Menges and Kimmich 1996, Menges and Quintana-Ascencio 2004). Unfortunately, this species did not occur in enough of the sites across the time-since-fire gradient to be analyzed in this study; however, the response of this species is comparable to other scrub endemics.

The majority of herbaceous species in rosemary scrub are gap specialists, and are most abundant, have the greatest survival, and highest seed production in the years immediately following fire (Hawkes and Menges 1996, Menges and Kimmich 1996, Menges 1999). As time-since-fire increases, gaps close while shrub, litter, and lichen covers increase and herbaceous species are outcompeted (Menges and Hawkes 1998). Gap sizes are smallest in long-unburned areas and largest between six and ten years post-fire; herb cover increases with gap area (Menges *et al.* 2008). Menges *et al.* (2008) found that sites greater than ten years post-fire have a wide amount of variation in gap area. Site-to-site variation in microhabitat cover may help to explain variation in seed density among different time-since-fire age classes (Navarra, University of Central Florida, unpublished data). Environmental variables such as elevation may explain why some sites retain greater amounts of open space than others (Hawkes and Menges 1996) and thus sustain higher cover of herbs, leading to larger yearly inputs into the seed bank. Increased variability of gap area as time-since-fire increases and dominance of the seed banks by

scrub herbs may explain why, at the community level, only recently burned sites showed distinctive patterns of seed density, while sites ranging from six years post-fire to long-unburned exhibited considerable overlap.

The high seed density of ruderal herbs at recent and long-unburned sites remains unexplained as these species are not found aboveground in rosemary scrub. This pattern may be a result of location rather than response to time-since-fire. Archbold Biological Station is surrounded by a variety of human-modified habitats (primarily citrus groves and pastures). Because sites belonging to the same time-since-fire age class were generally in close proximity to each other, these sites may have also experienced similar rates of dispersal of weedy species from surrounding areas.

Seed Persistence

Seed persistence was generally well predicted by fire adaptive strategy (obligate seeders, seeders and resprouters) and seed morphology (seed size). Many of the species, particularly endemic herbs, have small seed size, which is a characteristic known to promote formation of persistent seed banks (Thompson *et al.* 1993, Funes *et al.* 1999, Moles *et al.* 2000, Thompson *et al.* 2001, Stromberg *et al.* 2008). Of the seven scrub herbs found in the seed bank, five were present year-round and germinated into the second year. While formation of a persistent seed bank is a common mechanism that species use to cope with frequent disturbance, not all obligate seeding herbs were found in the seed bank. For example, Florida jointweed (*Polygonella basiramia* [Small] G.L.Nesom and V.M.Bates) can form only a limited persistent seed bank (Maliakal-Witt *et al.* 2005) and relies primarily on dispersal from unburned areas to re-colonize post-fire (Menges 1999, Quintana-Ascencio and Menges 2000).

The seed banks were largely dominated by short-lived herbaceous species, while long-lived species were present in far fewer num-

bers of species and much lower densities. Absence of long-lived species in the seed bank is not uncommon because adult longevity has been found to be negatively correlated with seed persistence (Rees *et al.* 1996, Clemente *et al.* 2007). The majority of long-lived species in Florida scrub habitats resprout after fire and are less dependent on sexual reproduction (Menges and Kohfeldt 1995). These results contrast with most other fire-prone shrublands such as California chaparral and Australian heaths, which report higher species richness and seed densities of resprouting and obligate seeding shrubs (Zammit and Zedler 1994, Wills and Read 2007). In contrast, a study conducted in the fire-prone Mediterranean Aleppo pine forest also reported absence of long-lived species in the seed bank (Ne'eman and Izhaki 1999).

Implementation of appropriate prescribed fire regimes requires knowledge of which obligate seeding species form persistent seed banks and how seed bank densities change with time-since-fire. Applying an appropriate fire-return interval can pose one of the greatest challenges to land management. Due to differences in species' life histories, such as juvenile period, fire sensitivity and microhabitat requirements, not all species will be favored by the same fire regime (Quintana-Ascencio and Menges 2000, Ooi *et al.* 2006, Menges 2007). Endemic scrub herb persistence in the seed banks of long-unburned stands suggests that these species are able to cope with the 15 year to 30 year fire-return interval proposed for this community (Menges 2007). Implementation of patchy fires is likely the best strategy to allow for coexistence of species with varying fire requirements because smaller portions of the aboveground populations will be killed (Ooi *et al.* 2006). This fire regime is fitting for obligate seeding species that rely on dispersal for post-fire recruitment but do not form persistent seed banks, as well as for species that have long juvenile periods before they reach reproductive maturity and replenish the seed bank (e.g., Florida rosemary).

Conclusion

The results of this study support previous findings that obligate seeding species are at least indirectly affected by time-since-fire: fire opens up microhabitat, which leads to increased abundances aboveground and in the seed bank. Greatest seed densities were observed in the first ten years post-fire; however, significant site-to-site variation did occur even in recently burned stands. Many of the obligate seeding species in Florida rosemary scrub rely on persistent soil seed banks to recover af-

ter fire. Considerable variation in seed bank size in relationship to time-since-fire are likely linked to differences in life history characteristics such as plant life span, dispersal mechanism, seed size, germinability, and length of juvenile period (Pierce and Cowling 1991). Short-lived herbaceous species dominate the seed bank in Florida rosemary scrub. While these findings have broadened our understanding of how rosemary scrub changes with time-since-fire, further research is necessary to fully understand the role of the seed bank in this unique pyrogenic community.

ACKNOWLEDGMENTS

Funding and logistical support was provided by Archbold Biological Station, University of Central Florida Arboretum, the Garden Club of America, the Florida Division of Forestry, and the National Science Foundation (DEB98-15370, DEB0233899, DEB0812717). Field and greenhouse assistance was provided by A. Bernard, J.L. Garcia, L.M. Castro-Morales, M.A. Camchong, and H. McArdle. E. Stephens, L.M. Sánchez-Clavijo, J.M. Olano, A. Escudero, and J. F. Weishampel helped review this manuscript.

LITERATURE CITED

- Abrahamson, W.G., J.N. Johnson, J.N. Layne, and P.A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. *Florida Scientist* 47: 209-250.
- Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32-46.
- Arroyo, M.T.K., L.A. Cavieres, C. Castor, and A.M. Humana. 1999. Persistent soil seed bank and standing vegetation at a high alpine site in the central Chilean Andes. *Oecologia* 119: 126-132. doi: [10.1007/s004420050768](https://doi.org/10.1007/s004420050768)
- Auld, T.D., D.A. Keith, and R.A. Bradstock. 2000. Patterns of longevity of soil seedbanks in fire-prone communities of south-eastern Australia. *Australian Journal of Botany* 48: 539-548. doi: [10.1071/BT99046](https://doi.org/10.1071/BT99046)
- Bekker, R.M., E.J. Lammerts, A. Schutter, and A.P. Grootjans. 1999. Vegetation development in dune slacks: the role of persistent seed banks. *Journal of Vegetation Science* 10: 745-754. doi: [10.2307/3237090](https://doi.org/10.2307/3237090)
- Bond, W.J., F.I. Woodward, and G.F. Midgley. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525-537. doi: [10.1111/j.1469-8137.2004.01252.x](https://doi.org/10.1111/j.1469-8137.2004.01252.x)
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Carrington, M.E., and J.E. Keeley. 1999. Comparison of post-fire seedling establishment between scrub communities in Mediterranean and non-Mediterranean climate ecosystems. *Journal of Ecology* 87: 1025-1036. doi: [10.1046/j.1365-2745.1999.00419.x](https://doi.org/10.1046/j.1365-2745.1999.00419.x)

- Christensen, N.L. 1985. Shrubland fire regimes and their evolutionary consequences. Pages 86-100 in: S.T.A. Pickett and P.S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.
- Christman, S.P., and W.S. Judd. 1990. Notes on plants endemic to Florida scrub. Florida Scientist 53: 52-73.
- Clemente, A., F. Rego, and O. Correia. 2007. Seed bank dynamics of two obligate seeders, *Cistus monspeliensis* and *Rosmarinus officinalis*, in relation to time since fire. Plant Ecology 190: 175-188. doi: [10.1007/s11258-006-9199-z](https://doi.org/10.1007/s11258-006-9199-z)
- Crawley, M.J. 2007. The R book. Wiley, Chichester, United Kingdom. doi: [10.1002/9780470515075](https://doi.org/10.1002/9780470515075)
- Funes, G., S. Basconcelo, S. Diaz, and M. Cabido. 1999. Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. Seed Science Research 9: 341-345. doi: [10.1017/S0960258599000355](https://doi.org/10.1017/S0960258599000355)
- Hawkes, C.V., and E.S. Menges. 1996. The relationship between open space and fire for species in a xeric Florida shrubland. Bulletin of the Torrey Botanical Club 123: 81-92. doi: [10.2307/2996065](https://doi.org/10.2307/2996065)
- Holmes, P.M., and R.J. Newton. 2004. Patterns of seed persistence in South African fynbos. Plant Ecology 172: 143-158. doi: [10.1023/B:VEGE.0000026035.73496.34](https://doi.org/10.1023/B:VEGE.0000026035.73496.34)
- Hunter, M.E., and E.S. Menges. 2002. Allelopathic effects and root distribution of *Ceratiola ericoides* (Empetreae) on seven rosemary scrub species. American Journal of Botany 89: 1113-1118. doi: [10.3732/ajb.89.7.1113](https://doi.org/10.3732/ajb.89.7.1113)
- Johnson, A.F. 1982. Some demographic characteristics of the Florida rosemary *Ceratiola ericoides* Michx. American Midland Naturalist 108: 170-174. doi: [10.2307/2425306](https://doi.org/10.2307/2425306)
- Keeley, J.E. 1991. Seed germination and life history syndromes in the California chaparral. Botanical Review 57: 81-116. doi: [10.1007/BF02858766](https://doi.org/10.1007/BF02858766)
- Keeley, J.E., and C.J. Fotheringham. 1998. Smoke-induced seed germination in California chaparral. Ecology 79: 2320-2336. doi: [10.1890/0012-9658\(1998\)079\[2320:SISGIC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2320:SISGIC]2.0.CO;2)
- Kruskal, J.B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115-129. doi: [10.1007/BF02289694](https://doi.org/10.1007/BF02289694)
- Maliakal-Witt, S., E.S. Menges, and J.S. Denslow. 2005. Microhabitat distribution of two Florida scrub endemic plants in comparison to their habitat-generalist congeners. American Journal of Botany 92: 411-421. doi: [10.3732/ajb.92.3.411](https://doi.org/10.3732/ajb.92.3.411)
- Mather, P.M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley and Sons, London, United Kingdom.
- McCune, B., and J.B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Glenden Beach, Oregon, USA.
- Menges, E.S. 1999. Ecology and conservation of Florida scrub. Pages 7-22 in: R.C. Anderson, J.S. Fralish, and J.M. Baskin, editors. Savannas, barrens and outcrop plant communities of North America. Cambridge University Press, Massachusetts, USA.
- Menges, E.S. 2007. Integrating demography and fire management: an example from Florida scrub. Australian Journal of Botany 55: 261-272. doi: [10.1071/BT06020](https://doi.org/10.1071/BT06020)
- Menges, E.S., A. Craddock, J. Salo, R. Zinthefer, and C.W. Weekley. 2008. Gap ecology in Florida scrub: species occurrence, diversity and gap properties. Journal of Vegetation Science 19: 503-514. doi: [10.3170/2008-8-18399](https://doi.org/10.3170/2008-8-18399)
- Menges, E.S., and C.V. Hawkes. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. Ecological Applications 8: 935-946. doi: [10.1890/1051-0761\(1998\)008\[0935:IEOFAM\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)008[0935:IEOFAM]2.0.CO;2)

- Menges, E.S., and J. Kimmich. 1996. Microhabitat and time-since-fire: effects on demography of *Eryngium cuneifolium* (Apiaceae), a Florida scrub endemic plant. *American Journal of Botany* 83: 185-191. doi: [10.2307/2445937](https://doi.org/10.2307/2445937)
- Menges, E.S., and N. Kohfeldt. 1995. Life history strategies of Florida scrub plants in relation to fire. *Bulletin of the Torrey Botanical Club* 122: 282-297. doi: [10.2307/2996320](https://doi.org/10.2307/2996320)
- Menges, E.S., and P.F. Quintana-Ascencio. 2004. Population viability with fire in *Eryngium cuneifolium*: deciphering a decade of demographic data. *Ecological Monographs* 74: 79-99. doi: [10.1890/03-4029](https://doi.org/10.1890/03-4029)
- Moles, A.T., D.W. Hodson, and C.J. Webb. 2000. Seed size and shape and persistence in the soil in the New Zealand flora. *Oikos* 89: 541-545. doi: [10.1034/j.1600-0706.2000.890313.x](https://doi.org/10.1034/j.1600-0706.2000.890313.x)
- Ne'eman, G., and I. Izhaki. 1999. The effect of stand age and microhabitat on soil seed banks in Mediterranean Aleppo pine forests after fire. *Plant Ecology* 144: 115-125. doi: [10.1023/A:1009806507403](https://doi.org/10.1023/A:1009806507403)
- Noble, I.R., and R.O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21. doi: [10.1007/BF00121013](https://doi.org/10.1007/BF00121013)
- Ooi, K.J.M., R.J. Whelan, and T.D. Auld. 2006. Persistence of obligate-seeding species at the population scale: effects of fire intensity, fire patchiness and long fire-free intervals. *International Journal of Wildland Fire* 15: 261-269. doi: [10.1071/WF05024](https://doi.org/10.1071/WF05024)
- Ortega, M., C. Levassor, and B. Peco. 1997. Seasonal dynamics of Mediterranean pasture seed banks along environmental gradients. *Journal of Biogeography* 24: 177-195. doi: [10.1046/j.1365-2699.1997.00080.x](https://doi.org/10.1046/j.1365-2699.1997.00080.x)
- Pickett, S.T.A., and P.S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- Pierce, S.M., and R.M. Cowling. 1991. Dynamics of soil-stored seed banks of six shrubs in fire-prone dune fynbos. *Journal of Ecology* 79: 731-747. doi: [10.2307/2260664](https://doi.org/10.2307/2260664)
- Quintana-Ascencio, P.F., and E.S. Menges. 2000. Competitive abilities of three narrowly endemic plant species in experimental neighborhoods along a fire gradient. *American Journal of Botany* 87: 690-699. doi: [10.2307/2656855](https://doi.org/10.2307/2656855)
- Rees, M., P.J. Grubb, and D. Kelly. 1996. Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *The American Naturalist* 147: 1-32. doi: [10.1086/285837](https://doi.org/10.1086/285837)
- Sokal, R.R., and F.J. Rohlf. 1995. *Biometry*. W.H. Freeman and Company, New York, New York, USA.
- Stromberg, J.C., J.A. Boudell, and A.F. Hazelton. 2008. Differences in seed mass between hydric and xeric plants influence seed bank dynamics in a dryland riparian ecosystem. *Functional Ecology* 22: 205-212. doi: [10.1111/j.1365-2435.2007.01375.x](https://doi.org/10.1111/j.1365-2435.2007.01375.x)
- Thompson, K., S.R. Band, and J.G. Hodgson. 1993. Seed size and shape predict persistence in soil. *Functional Ecology* 7: 236-241. doi: [10.2307/2389893](https://doi.org/10.2307/2389893)
- Thompson, K., and J.P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* 67: 893-921. doi: [10.2307/2259220](https://doi.org/10.2307/2259220)
- Thompson, K., A. Jalili, J.G. Hodgson, B. Hamzeh'ee, Y. Asri, S. Shaw, A. Shirvany, S. Yazdani, M. Khoshnevis, F. Zarrinkamar, M.-A. Ghahramani, and R. Safavi. 2001. Seed size, shape and persistence in the soil in an Iranian flora. *Seed Science Research* 11: 345-355.
- Tyler, C.M. 1995. Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology* 83: 1009-1020. doi: [10.2307/2261182](https://doi.org/10.2307/2261182)

- Tyler, C.M. 1996. Relative importance of factors contributing to postfire seedling establishment in maritime chaparral. *Ecology* 77: 2182-2195. doi: [10.2307/2265711](https://doi.org/10.2307/2265711)
- Vaughton, G. 1998. Soil seed bank dynamics in the rare obligate seeding shrub, *Grevillea barklyana* (Proteaceae). *Austral Ecology* 23: 375-384. doi: [10.1111/j.1442-9993.1998.tb00742.x](https://doi.org/10.1111/j.1442-9993.1998.tb00742.x)
- Venable, D.L., and J.S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *The American Naturalist* 131: 360-384. doi: [10.1086/284795](https://doi.org/10.1086/284795)
- Weekley, C.W., and E.S. Menges. 2003. Species and vegetation responses to prescribed fire in a long-unburned, endemic-rich Lake Wales Ridge scrub. *Journal of the Torrey Botanical Society* 130: 265-282. doi: [10.2307/3557545](https://doi.org/10.2307/3557545)
- Wills, T., and J. Read. 2007. Soil seed bank dynamics in post-fire heathland succession in south-eastern Australia. *Plant Ecology* 190: 1-12. doi: [10.1007/s11258-006-9186-4](https://doi.org/10.1007/s11258-006-9186-4)
- Zammit, C., and P.H. Zedler. 1994. Organisation of the soil seed bank in mixed chaparral. *Plant Ecology* 111: 1-16.
- Zammit, C.A., and P.H. Zedler. 1988. The influence of dominant shrubs, fire, and time since fire on soil seed banks in mixed chaparral. *Plant Ecology* 75: 175-187.
- Zedler, P.H., R.G. Clayton, and G.S. McMaster. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64: 809-818. doi: [10.2307/1937204](https://doi.org/10.2307/1937204)