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Research Article

Effects of Soil Temperature during Fire on Seed Survival in Florida Sand Pine Scrub

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Soil temperatures recorded with thermocouples and temperature-sensitive paints were quantified during Florida sand pine scrub prescribed fires at Ocala National Forest and Archbold Biological Station in May 1993. Thermocouples and glass petri dishes painted with temperature-sensitive paints and containing seeds of *Eriogonum floridanum* were placed at 0 cm and 2 cm depth, and in vegetated and open microsites. Maximum temperatures were higher and peak temperature durations shorter at 0 cm than at 2 cm depth. Temperatures did not differ between microsites during the Ocala fire, but were higher in open microsites during the Archbold fire, probably due to combustion of well-aerated litter. Maximum temperatures of petri dishes were lower than those of adjacent thermocouples due to time required to melt paints. All *Eriogonum* seeds recovered from petri dishes after the Archbold fire failed to germinate. Germination was quantified for *Eriogonum floridanum* and *Garberia heterophylla* seeds heated to 100°C and 60°C under laboratory conditions. Seeds failed to germinate at 100°C, while germination was similar to controls for seeds exposed to 60°C. Results from this study suggest that small-scale spatial variation temperatures at the soil surface during fires is essential for seed survival and subsequent post-fire recruitment.

1. Introduction

Seeds that survive fires in the soil contribute to postfire recruitment to varying degrees among fire-influenced communities [1, 2]. The capacity of species in these communities to establish seedlings after fire from seeds in a soil seed bank should be influenced by several factors including (1) magnitude and duration of high or elevated temperatures during fire at soil depths and in microsites where viable seeds are located, and (2) seed germination responses to elevated temperatures.

A large volume of field research and laboratory research has been conducted on temperatures reached during natural fires [3–24], and on seed germination responses to elevated temperatures [4, 6, 9, 13, 16, 25–35]. These two lines of research usually have been mutually exclusive, and have concentrated largely on Mediterranean-climate ecosystems and their species.

Researchers generally have used either temperature-sensitive paints or thermocouples to quantify soil temperatures reached during fires. Although recorded temperatures have varied among ecosystems and with differences in burning conditions, several patterns have been consistent across studies. Maximum soil temperatures generally decrease as depth in the soil increases, but durations of elevated temperatures increase [3, 6, 9, 12, 13, 16–19]. Soil temperatures reached during fires also tend to vary with microsites, with temperatures in open microsites lower than temperatures in microsites with higher fuel accumulations [12, 15].

In laboratory germination studies, plant species from several ecosystems have demonstrated positive germination responses after being exposed to temperatures typically reached during fires. Taxa or functional groups with this response include legumes in the southeastern United States, California, and Australia [9, 13, 17, 25, 28, 29, 32]; obligately seeding shrubs in California chaparral and in southern France [25, 27, 30, 34], and annual species in California chaparral [25, 29]. Other species, however, have responded to elevated temperatures with decreased or no germination. Some functional groups that have demonstrated this response are herbaceous perennials [29] and other species that do not establish seedlings after fires [30].

This study documents soil temperatures during fires, and seed germination responses to elevated temperatures in sand pine scrub, a community occurring primarily in Florida on well-drained sandy soils of former Miocene to Pleistocene dunes. Sand pine scrub is dominated by woody shrubs including several oak species (*Quercus* spp.), rusty lyonia (*Lyonia ferruginea*), Florida rosemary (*Ceratiola ericoides*), and occasionally scrub hickory (*Carya floridana*); often an overstory of sand pine (*Pinus clausa*) is present [36]. Small-statured (<2 m tall) perennial species are usually sparse, and annual species are virtually absent.

Natural fires are lightning-initiated, and usually occur during the wet growing season during the months of April through July. Although frequency of lightning strikes is extremely high in Florida [37], sand pine scrub fires occur infrequently, approximately every 10 to 100 years. A combination of fuel characteristics and season of burning influences fire frequency—ground litter and other fine fuels are often sparse, most living vegetation is neither highly flammable nor easily ignited, and fuels are rarely dry during the lightning season. Consequently, fires tend to occur under extreme conditions of high fuel buildup, dry weather, or high winds, and often are intense [36].

As in other fire-influenced communities, plant species in sand pine scrub vary in their responses to fire. Most woody shrub species resprout and do not establish seedlings immediately following fires. In contrast, seedling establishment occurs primarily or exclusively after fire for some plant species that are killed by fire (e.g., *Pinus clausa, Ceratiola ericoides, Dicerandra frutescens, Calamintha ashei* [36, 38–40]), as well as for some small-statured species that resprout following fire (e.g., *Eriogonum floridanum, Garberia heterophylla* [41, 42]).

Although heat- and smoke-induced germination have not been documented in sand pine scrub as in some other fire-influenced communities [33, 43], seeds of some sand pine scrub species germinate after surviving fire in a soil seed bank [39, 44]. In a recent study conducted at Archbold Biological Station, viable seeds were present in soil samples collected less than three months after fires, from 0–7 cm depth in the soil (Kohfeldt *personal communication*).

Temperatures reached during fires and germination responses to those temperatures are relatively unknown for sand pine scrub. Only one other study has measured temperatures at the soil surface during a sand pine scrub fire [24], and germination responses to high temperatures of most species have not been studied. Additional information on soil temperatures during fires and germination responses after fires should further elucidate the plant community response to fire in sand pine scrub, and could potentially increase effectiveness of rare species conservation through use of fire.

The first of two objectives of this study was to measure soil temperatures at different depths and in different microsites during fires in sand pine scrub. Lower peak soil temperatures and longer temperature durations were expected with increasing depth in the soil, as documented in other studies. Spatial patterns of combustible fuel in sand pine scrub are defined primarily by a widespread matrix of woody shrub vegetation underlain by moderate amounts of ground litter, interspersed with canopy openings with little or no litter. In this study, soil temperatures in microsites under vegetation (e.g., shrubs) were expected to be higher than those in openings.

The second objective of this study was to quantify germination responses of two small-statured perennial species after exposing the seeds to temperatures typically reached during sand pine scrub fires. Small-statured perennial species were chosen for study because much of the postfire seedling establishment response in sand pine scrub is attributable to species from this general group [42]. The two study species (hereafter referred to by their generic names), *Eriogonum floridanum* (Polygonaceae; Reveal 1981) and *Garberia heterophylla* (Asteraceae), were chosen because (1) both species establish seedlings primarily after fire; (2) although both species are relatively common locally, they are endemic to Florida, occur primarily in sand pine scrub, and are subjects of conservation concern (*Eriogonum floridanum* is federally listed as threatened).

Eriogonum is an herbaceous perennial and *Garberia* a woody shrub; both species have strong postfire resprouting and flowering responses [42]. As documented for other herbaceous perennials, germination was expected to decrease for *Eriogonum* seeds after exposure to an elevated temperature at any depth in the soil. Seeds of resprouting shrub species have exhibited a variety of responses to high temperatures and to high temperatures in combination with smoke [45, 46], making the *Garberia* germination response in this study potentially less predictable. Consequently, in this study *Garberia* seed germination was expected to decrease, remain unchanged, or possibly increase after exposure to an elevated temperature at any depth in the soil.

2. Materials and Methods

2.1. Field Experiments. Study areas were sand pine scrub sites at Ocala National Forest in Marion County, Florida (29° 08′, 81° 45′) and Archbold Biological Station in Highlands County, Florida (27° 15′, 81° 15′). The Ocala site and Archbold site last burned in 1935 and 1927, respectively. Both sites had a dense shrub layer consisting primarily of several species of oaks (*Quercus* spp.). Overstories differed in the two sites, however; sand pine was the only species in the overstory at Ocala, while at Archbold sand pines were interspersed with south Florida slash pines (*Pinus elliottii* var. *densa*).

Controlled burns were conducted at the Ocala and Archbold sites on May 10, 1993 and May 25, 1993, respectively. Before each fire, a datalogger (21X Micrologger, Campbell Scientific, Inc.) connected to 16 copper-constantan, 0.51 mm diameter thermocouples via insulated leads was buried in the site to be burned. The thermocouple leads were 1.5–4 m long, and were buried approximately 2 cm deep; the datalogger was placed in a fiberglass case and buried approximately 50 cm deep.

Each thermocouple was placed either at the soil surface or at 2 cm depth, and either in an open microsite or under vegetation. The 2 cm depth was chosen because seeds typically are

found at this depth [47, Kohfeldt *personal communication*], yet were expected to be relatively insulated from high surface temperatures reached during a fire. Each depth-microsite combination was replicated four times through placement of individual thermocouples. Adjacent to each thermocouple, a glass petri dish containing 10 *Eriogonum* seeds was placed at the same soil depth and microsite. In each petri dish, *Eriogonum* seeds were placed on top of a layer of sand completely covering the bottom of the petri dish. Six petri dishes with *Eriogonum* seeds also were placed at a nearby control site that did not burn.

At Archbold the sides of each petri dish were painted with 19 temperature-sensitive paints (Tempilaq, Tempil Division, Big Three Industries, Inc.). Manufacturer-specified melting temperatures of paints ranged from 37.8°C to 815.6°C. In addition to petri dishes adjacent to thermocouples, petri dishes also were placed throughout the site so that each depth-microsite combination was replicated eight additional times.

During each fire, the datalogger recorded thermocouple temperatures every five seconds. Temperature recording occurred from 90 minutes before the fire until 90 minutes after the flame front went through at the Ocala site, and from 90 minutes before the fire to 60 minutes after the flame front went through at Archbold.

After each fire, the datalogger and all petri dishes were recovered. Intact seeds were extracted from soil in the petri dishes, and were classified as charred or noncharred. All noncharred seeds were placed on moist filter paper in clean petri dishes, and observed for germination for one month. Viability of non-germinated seeds was assayed with a tetrazolium test [48]. At Archbold, maximum temperature reached during the fire was quantified for each petri dish by determining which temperature-sensitive paints melted.

Data on thermocouple maximum temperatures and temperature durations were analyzed separately for the Archbold and Ocala fires. Analyses of variance were conducted on rank-transformed maximum thermocouple temperatures to detect differences due to depth in the soil and microsite [49]. Temperature duration was defined for each thermocouple as the length of time that 75% of the maximum thermocouple temperature was maintained or exceeded. Kolmogorov-Smirnov tests were used to compare median temperature durations between thermocouples placed at the soil surface and those placed at 2 cm depth [50].

Maximum temperatures during the Archbold fire of petri dishes placed at the soil surface and at 2 cm depth were compared using a chi-square test, and a *t*-test was used to compare maximum temperatures of petri dishes and adjacent thermocouples. Data from both fires on *Eriogonum* seeds recovered from petri dishes were combined to determine the immediate fire effect on the seeds. Numbers of petri dishes with charred *Eriogonum* seeds at the soil surface and at 2 cm depth were compared using a linear model analysis (Proc CATMOD in SAS) [51].

2.2. Laboratory Experiments. Seeds of *Eriogonum* and *Garberia* were observed for germination after being exposed to a control temperature (25°C) and elevated temperatures and durations representative of those sustained at the soil surface and at 2 cm depth during the experimental fires. Elevated temperatures used were 100°C (commonly sustained at the soil surface for 4–6 minutes, but usually not reached at 2 cm depth) and 60°C (commonly sustained at 2 cm depth for 4 to >91 minutes).

Experiments were conducted from December 8–17, 1993, and from December 14, 1995 to January 7, 1996 for *Eriogonum* and *Garberia* seeds, respectively. Separate experiments, using 160 seeds in each, were conducted for each species and for each elevated temperature. Half of the seeds were placed in a drying oven and exposed to the elevated temperature for five minutes or 30 minutes in the experiments using 100°C and 60°C, respectively. The remaining seeds in each experiment were kept at room temperature. Then seeds were placed on moist filter paper in petri dishes and observed for germination. Seed germination responses were compared between 25°C and 100°C treatments using Fisher exact tests [48]; *t*-tests were used to compare germination responses between 25°C and 60°C treatments.

To determine times required to melt temperature-sensitive paints on petri dishes, trials were conducted in which a petri dish painted with a temperature-sensitive paint was placed in a muffle furnace (Thermolyne, Sybron Corporation) with the door open, and timed until the paint melted. A minimum of five trials was conducted for each of 13 paints, with manufacturer-specified melting temperatures ranging from 37.8°C to 704.4°C. After five trials, if the coefficient of variation was >0.25, additional trials were conducted. Up to 14 trials were conducted to record times required to melt paints with melting temperatures between 50°C and 125°C, the temperature range likely relevant to seed survival versus mortality during fires.

Table 1: Weather conditions and fire characteristics for Florida sand pine scrub fires at Ocala National Forest and Archbold Biological Station during May 1993.

	Ocala	Archbold
Date of fire	May 10, 1993	May 25, 1993
Time of measurements	1150–1205	1259–1305
Air temperature	28°C	29°C
Relative humidity	46%	52%
Wind speed	0.89 m/s	0.54 m/s
Wind direction	SE	SE
Flame length	3–5 m	6–15 m
Rate of spread	12 m/min	12 m/min

3. Results

3.1. Field Experiments. Weather conditions and fire characteristics were similar for the two fires, but flame lengths in the Archbold fire were greater than those in the Ocala fire (Table 1). Although soil temperatures quantified with thermocouples and their temporal patterns varied widely

Table 2: ANOVA of the effects of soil depth and microsite on maximum temperatures recorded during a controlled burn in sand pine scrub at Ocala National Forest, Florida. Temperatures were recorded with copper-constantan thermocouples placed at the soil surface and at 2 cm depth, and in open and vegetated microsites. Data were rank-transformed prior to the ANOVA.

Source	SS	*df*	*F* ratio	*P*
Depth	182.3	1	19.5	$P < .005$
Microsite	25.0	1	2.7	$P > .10$
Depth × microsite	20.3	1	2.2	$P > .10$
Error	112.5	12		

Table 3: ANOVA of the effects of soil depth and microsite on maximum temperatures recorded during a controlled burn in sand pine scrub at Archbold Biological Station, Florida. Temperatures were recorded with copper-constantan thermocouples placed at the soil surface and at 2 cm depth, and in open and vegetated microsites. Data were rank-transformed prior to the ANOVA.

Source	SS	*df*	*F* ratio	*P*
Depth	121.0	1	11.2	$.005 < P < .01$
Microsite	64.0	1	5.9	$.025 < P < .05$
Depth × microsite	25.0	1	2.3	$P > .10$
Error	130.0	12		

Table 4: Temperature durations of copper-constantan thermocouples placed at the soil surface and at 2 cm depth in the soil. Temperatures were quantified during prescribed fires conducted during May 1993 at Ocala National Forest and Archbold Biological Station, Florida. Temperature duration was defined as length of time that (0.75 × maximum thermocouple temperature) was maintained or exceeded.

Site	Depth in soil (cm) ($n = 4$)	Temperature duration (s) (median (range))
Archbold	0	105 (20–>3260)
	2	2020 (160–>3250)[(a)]
Ocala	0	80 (65–1555)
	2	2918 (675–>4625)[(a)]

[(a)]Separate Kolmogorov-Smirnov tests were conducted for Archbold ($P = .05$) and Ocala ($P < .01$) sites to test for difference in temperature durations with depth in soil.

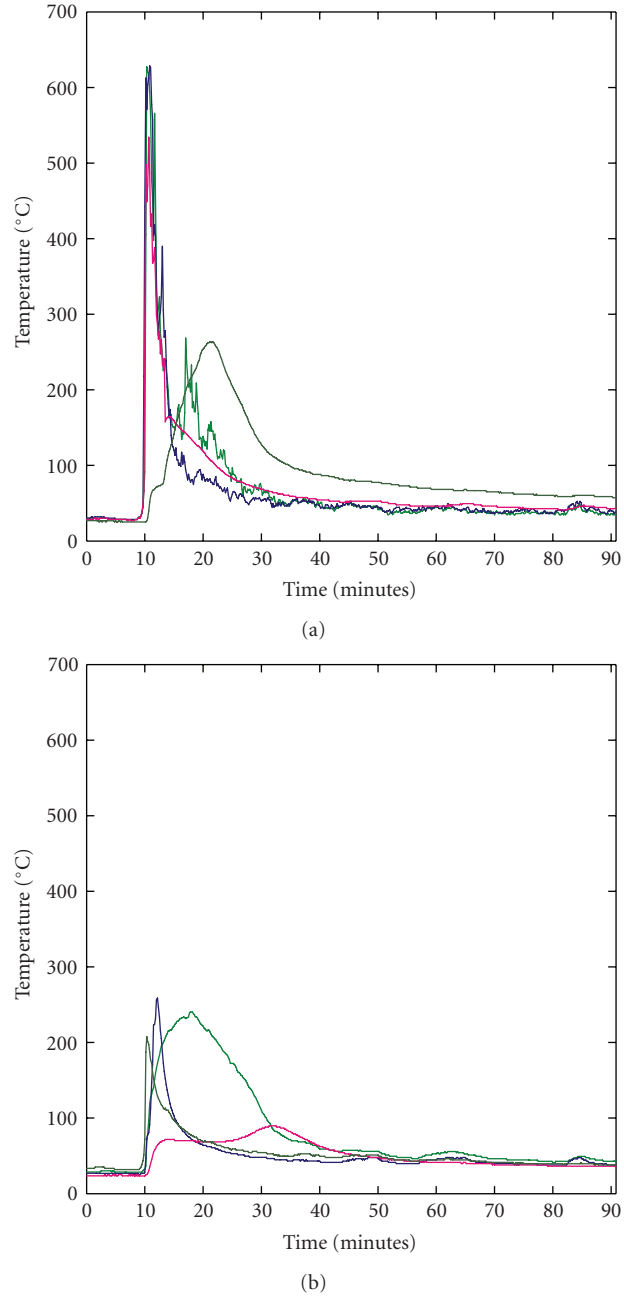


Figure 1: Soil temperatures at the soil surface during a prescribed sand pine scrub fire at Ocala National Forest, Florida on May 10, 1993. Temperatures were recorded with copper-constantan thermocouples placed in vegetated (a) and open (b) microsites. Each microsite location was replicated four times.

both within and between microsite treatment combinations during both fires (Figures 1, 2, 3, and 4), temperatures were higher at the soil surface than at 2 cm depth as expected (Ocala: $F_{1,12} = 19.5$, $P < .005$; Archbold: $F_{1,12} = 11.2$, $.005 < P < .01$), (Tables 2 and 3). Temperatures at the soil surface reached maxima of 628.8°C and 621.7°C during the Ocala and Archbold fires, respectively; in contrast, maximum temperatures at 2 cm depth were less than half those at the surface (Figures 1–4). The higher temperatures at the soil surface also had shorter durations than temperatures at 2 cm depth (Kolmogorov-Smirnov test; Ocala: $P < .01$; Archbold: $P = .05$) (Table 4).

Temperatures in vegetated versus open microsites differed from predicted patterns, however. Although temperatures during the Ocala fire tended to be higher in vegetated than in open microsites, a large range of temperatures within microsites resulted in no statistically significant difference in temperatures between microsites (Table 2). Temperatures during the Archbold fire were higher in open microsites than in vegetated microsites ($F_{1,12} = 5.9$, $.025 < P < .05$; Table 3), in contrast to the expected trend.

As with thermocouple-quantified temperatures, patterns of melted paints on petri dishes at the Archbold site showed

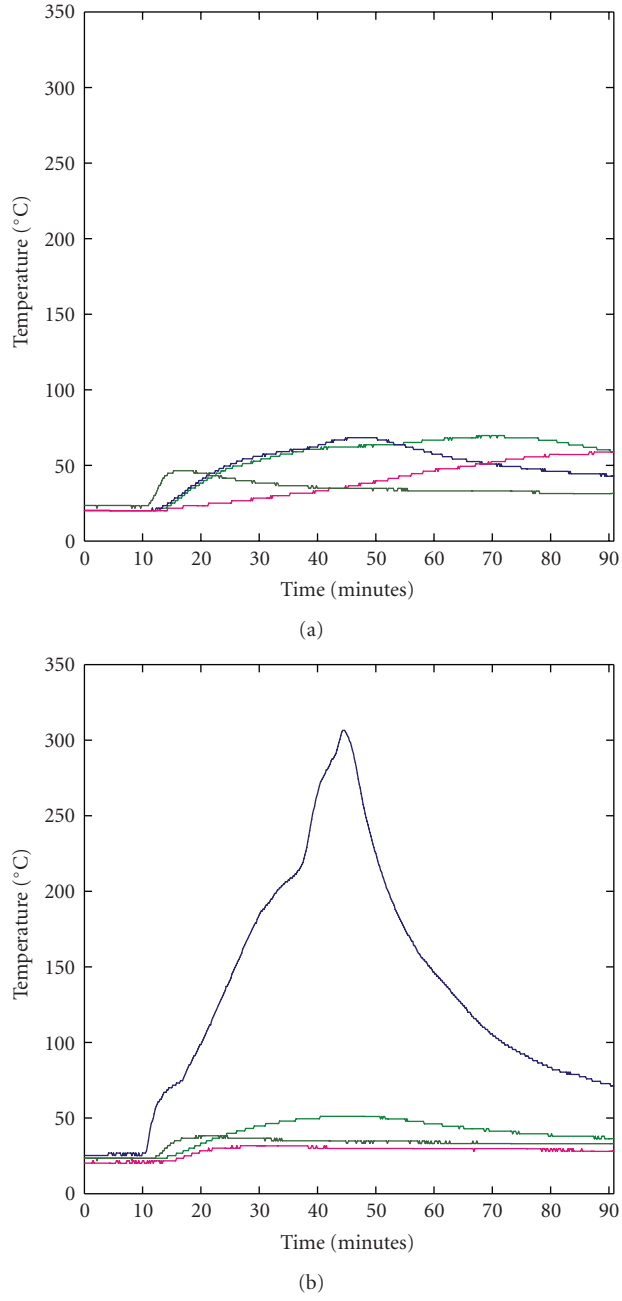


Figure 2: Soil temperatures at 2 cm depth during a prescribed sand pine scrub fire at Ocala National Forest, Florida on May 10, 1993. Temperatures were recorded with copper-constantan thermocouples placed in vegetated (a) and open (b) microsites. Each microsite location was replicated four times.

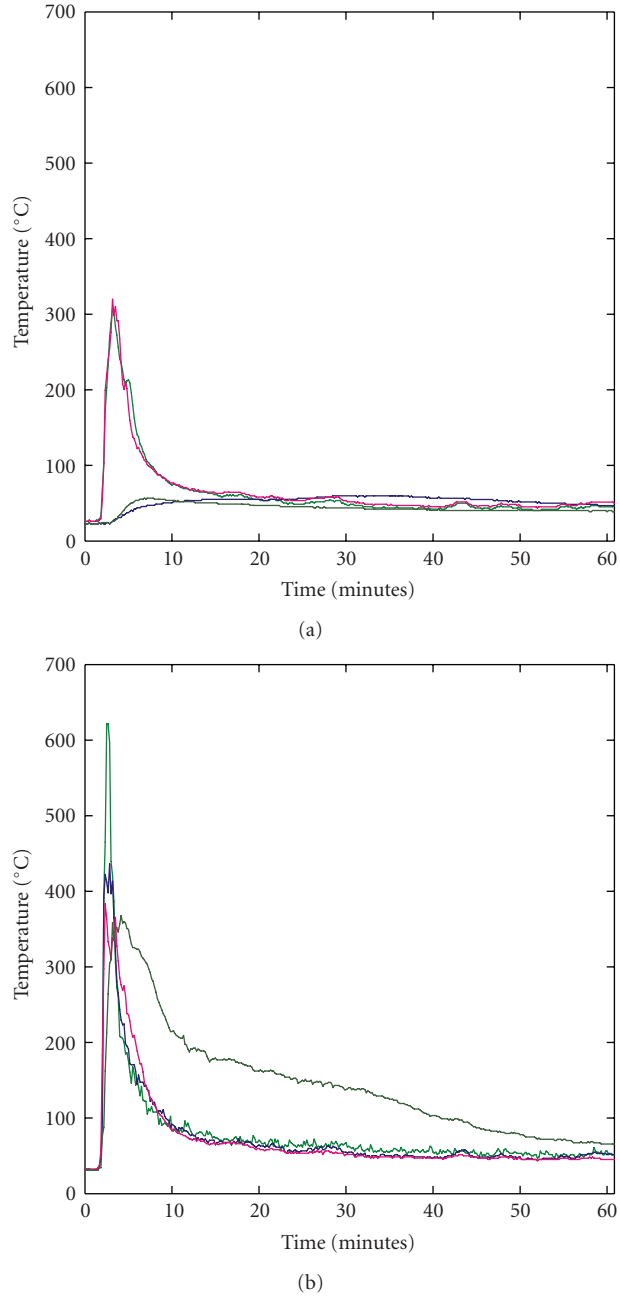


Figure 3: Soil temperatures at the soil surface during a prescribed sand pine scrub fire at Archbold Biological Station, Florida on May 25, 1993. Temperatures were recorded with copper-constantan thermocouples placed in vegetated (a) and open (b) microsites. Each microsite location was replicated four times.

that maximum soil temperatures were higher at the surface than at 2 cm depth ($\chi^2 = 33.6$, $P < .001$). Maximum temperatures of petri dishes placed at the soil surface varied widely. Most temperatures ranged from 93°C to 315°C, but 4 of 24 surface petri dishes reached temperatures >343°C, while 2 surface/open petri dish temperatures were <37.8°C (Figure 5). In contrast, maximum temperatures of petri dishes placed at 2 cm depth were more similar; only 1 of 24 petri dishes placed at 2 cm depth exceeded 100°C (Figure 5). Although differences between temperatures of petri dishes in open versus vegetated microsites were not tested statistically due to small sample sizes, temperatures appeared similar among microsites (Figure 5). Comparison of thermocouple maximum temperatures with maximum temperatures of adjacent petri dishes showed that temperatures quantified via the two methods differed ($t = 25.0$, $.02 < P < .05$)

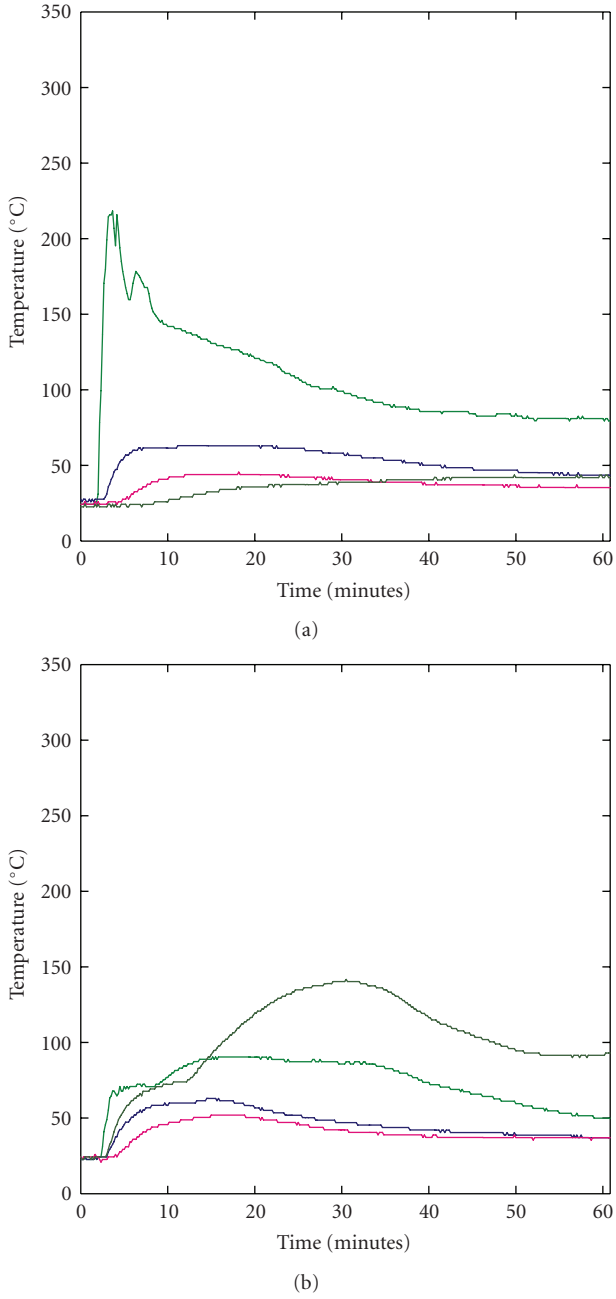


Figure 4: Soil temperatures at 2 cm depth during a prescribed sand pine scrub fire at Archbold Biological Station, Florida on May 25, 1993. Temperatures were recorded with copper-constantan thermocouples placed in vegetated (a) and open (b) microsites. Each microsite location was replicated four times.

Table 5: Maximum temperatures at 0 cm and 2 cm soil depth, and in open and vegetated microsites, during a prescribed fire in sand pine scrub at Archbold Biological Station, Florida. Temperatures were quantified with copper-constantan thermocouples and with temperature-sensitive paints placed on adjacent glass petri dishes.

Depth	Microsite	Maximum Temperature	
		Thermocouple	Paint[(a)]
0 cm	open	621.7	163.7
0 cm	open	436.2	107.2
0 cm	open	383.5	289.8
0 cm	open	367.8	<37.8
0 cm	vegetated	308.1	260.0
0 cm	vegetated	59.8	287.8
0 cm	vegetated	319.8	232.2
0 cm	vegetated	56.9	162.8
2 cm	open	63.0	<37.8
2 cm	open	90.4	<37.8
2 cm	open	52.0	<37.8
2 cm	open	141.7	<37.8
2 cm	vegetated	218.3	<37.8
2 cm	vegetated	63.0	<37.8
2 cm	vegetated	45.6	<37.8
2 cm	vegetated	43.6	<37.8

[(a)]Temperatures represent the manufacturer-specified melting temperatures of the paints that melted.

Table 6: Number of petri dishes from which charred *Eriogonum floridanum* seeds were recovered after controlled burns in sand pine scrub at Archbold Biological Station and at Ocala National Forest, Florida, versus number of petri dishes from which all seeds were recovered non-charred; and total number of non-charred seeds recovered. Petri dishes were placed at 0 cm and 2 cm depth in the soil, and in open and vegetated (from 0–2 m vegetation height) microsites. Each petri dish contained ten seeds.

Soil depth/microsite	Petri dishes with charred seeds	Petri dishes without charred seeds[(a)]	Total non-charred seeds
0 cm/open	17	0	0
0 cm/vegetated	16	1	10
2 cm/open	3	14	154
2 cm/vegetated	3	14	156

[(a)]More petri dishes with non-charred seeds were recovered from 2 cm depth ($\chi^2 = 43.95$, $P < .001$).

(Table 5), presumably due to time required to melt paints on petri dishes (Figure 6).

Most non-charred *Eriogonum* seeds recovered after both fires were from petri dishes placed at 2 cm depth ($\chi = 43.95$, $P < .001$). Of a total of 34 petri dishes recovered from the soil surface after the fires, only one dish contained non-charred seeds. Numbers of petri dishes with charred seeds did not appear to differ between open and vegetated microsites, although differences were not tested statistically due to small sample sizes (Table 6).

No seeds germinated during trials using non-charred seeds recovered after the fires. Tetrazolium tests on seeds that were collected at the same time as seeds used in the experimental fires indicated that viability was 34 ± 4%.

3.2. Laboratory Experiments. In both *Eriogonum* and *Garberia* experiments 100°C was lethal to seeds; no seeds exposed

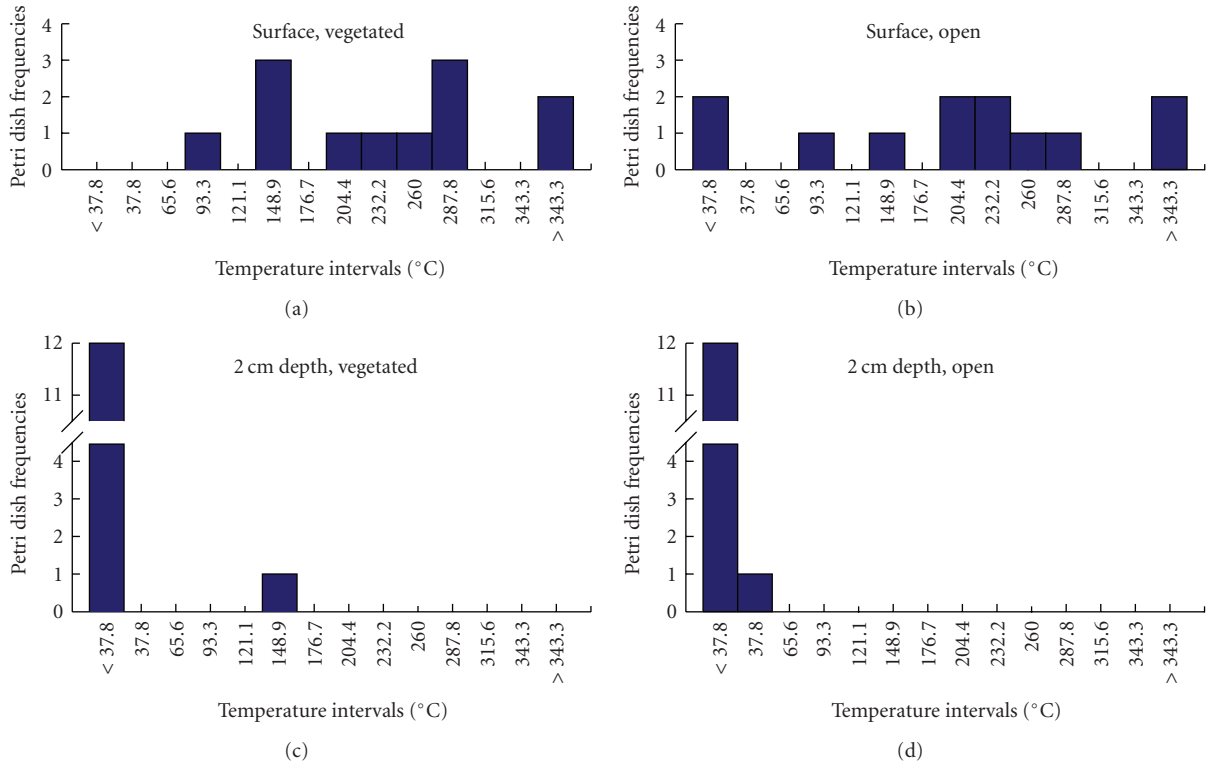


Figure 5: Frequency distributions of maximum petri dish temperatures during a prescribed sand pine scrub fire at Archbold Biological Station, Florida on May 25, 1993. Temperatures were quantified with temperature-sensitive paints on the petri dishes; temperature intervals for the frequency distributions represent melting points of the paints. Petri dishes were placed at the soil surface in vegetated (a) and open (b) microsites, and at 2 cm depth in vegetated (c) and open (d) microsites; each depth-microsite combination was replicated 12 times.

Table 7: Number of petri dishes from which *Eriogonum floridanum* (Polygonaceae) and *Garberia heterophylla* (Asteraceae) seeds germinated after being exposed to 100°C or 25°C for 5 minutes. Germination trials were conducted from December 8–17, 1993, and from December 14, 1995 to January 2, 1996 for *Eriogonum* and *Garberia*, respectively.

Seed species	Temperature (°C)	Number of petri dishes[(a)] ($n = 4$)
Eriogonum	25	4
	100	0[(b)]
Garberia	25	4
	100	0[(b)]

[(a)] Each petri dish contained 20 seeds.
[(b)] Fisher exact test showed a reduction in germination ($P = .0143$).

Table 8: Number (mean ± S.E.) of *Eriogonum floridanum* (Polygonaceae) and *Garberia heterophylla* (Asteraceae) seeds that germinated after being exposed to 60°C or 25°C for 30 minutes. Germination trials were conducted from December 8–17, 1993, and from December 30, 1995 to January 7, 1996 for *Eriogonum* and *Garberia*, respectively. Identical superscripts within the same species indicate no difference in germination between temperature treatments (t-test, $P > .05$).

Seed species	Temperature (°C)[†]	Germinated seeds (mean ± S.E.)
Eriogonum	25	$15.0 \pm 1.6^{(a)}$
	60	$11.5 \pm 2.3^{(a)}$
Garberia	25	$19.0 \pm 0.4^{(a)}$
	60	$19.3 \pm 0.5^{(a)}$

[†] $n = 4$ petri dishes, each with 20 seeds.

to 100°C for five minutes germinated, while seeds exposed to room temperature germinated in all petri dishes (Fisher exact test, $P = .0143$ for both species, Table 7). Seeds of both species also behaved similarly when exposed to 60°C for 30 minutes; seeds germinated from all petri dishes in both experiments, with no differences in numbers germinating between seeds exposed to 60°C and seeds exposed to room temperature (*Eriogonum*: $t = 1.27$, $P = .25$; *Garberia*: $t = 0.397$, $.5 < P < .9$; Table 8).

4. Discussion

4.1. Soil Temperatures during Fires. Depth in the soil has a strong influence on magnitude and variability of temperatures during Florida sand pine scrub fires, and thus influences seed survival during fires. As expected, maximum temperatures at the soil surface were higher and peak temperature durations were shorter than at 2 cm depth. Less predictable, however, were (1) effects of microsites at the soil surface on maximum temperatures; and (2) detailed

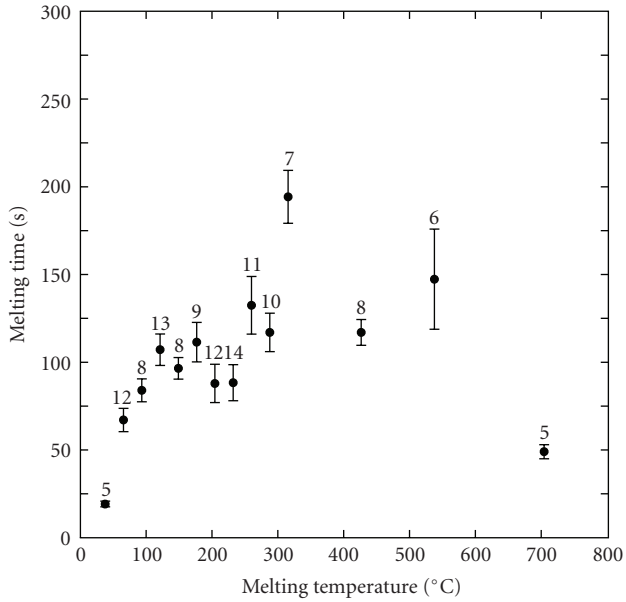


Figure 6: Melting times (mean ± S.E.) of temperature-sensitive paints (Tempilaq, Tempil Division, Big Three Industries, Inc.) on glass petri dishes. The number above each symbol represents the number of melting trials conducted for that paint. In each trial a petri dish was placed in a muffle furnace set at the melting temperature of the paint on the dish, and melting time was quantified.

spatial patterns of temperatures at the soil surface, and their implications for seed survival.

The effect of microsites on soil temperatures was different from that predicted, and was different between the two fires. Differences in overstory pine species and resulting litter characteristics between the sites contributed to the different microsite effects. Sand pine, the only tree species at Ocala, produces sparse litter consisting of short needles, but south Florida slash pine has much longer and more flammable needles than sand pine, and produces more litter. Because south Florida slash pine was present only at Archbold, different types and amounts of pine litter had accumulated in open microsites at the two sites; litter in vegetated microsites consisted primarily of sclerophyllous leaves with comparatively low flammability.

During the Ocala fire, a high variance in temperatures within microsites precluded detection of a microsite effect. During the Archbold fire a microsite effect was detected, but the pattern of temperatures between open and vegetated microsites was the reverse of the expected pattern. Higher maximum temperatures in open microsites were probably due to the well-aerated, relatively flammable slash pine litter in open microsites burning more completely and at higher temperatures than the more compacted, less flammable oak and hickory litter in vegetated microsites [50]. As reported in other studies [12, 14, 15], patterns of soil temperatures during fires appear to be related more directly to litter (i.e., fuel) type and amount than to microsites defined in this study.

Not only was the effect of microsites on soil temperature unpredictable, but temperatures at the soil surface in general were variable when compared to temperatures at 2 cm depth. Soil surface temperatures, in addition to having greater variation among experimental locations than at 2 cm depth, varied widely both in time and in space within experimental locations, as demonstrated by temperatures recorded with thermocouples and with temperature-sensitive paints. Temperatures recorded by thermocouples at the soil surface generally increased to extremely high, brief maxima, thereby producing many within-location combinations of temperatures and temperature durations. As a consequence of this high variation in temperatures over time, temperature-sensitive paints on petri dishes usually underestimated maximum temperatures of adjacent thermocouples at the soil surface. The maximum temperatures recorded by temperature-sensitive paints apparently were the highest temperatures that persisted long enough to melt the corresponding paints. As might be predicted by the variation in patterns of thermocouple temperatures versus time, differences between maximum temperatures of petri dishes and adjacent thermocouples varied widely.

Differences between petri dish and adjacent thermocouple temperatures at Archbold also indicated that soil temperatures varied spatially within experimental locations. Because maximum temperatures recorded by temperature-sensitive paints often differed from those expected based on temperature patterns of adjacent thermocouples (Table 4, Figures 3 and 4), temperatures and temperature durations must have varied over a very small spatial scale.

4.2. Seed Survival during Fires. Because virtually all maximum temperatures at the soil surface were >100°C and lethal to *Eriogonum* and *Garberia* seeds, much of the variation in soil surface temperatures during fires was irrelevant to seed survival for these species. Such extremely variable but high temperatures also should be lethal to most other species of seeds; in other studies, even seeds for which germination increased after exposure to high temperatures were usually killed by temperatures between 120–150°C [32]. Nevertheless, a fraction of seeds at the soil surface may survive fires in sand pine scrub, because *Eriogonum* seeds in one petri dish at the soil surface remained non-charred, and soil surface temperatures presumably were heterogeneous at a very small scale.

Seed survival is more likely and more predictable at 2 cm depth in the soil, because soil temperatures during fires were relatively low, and varied little from site to site. Although higher proportions of seeds should survive through fire at this depth in the soil, some seed mortality must occur, because lethal temperatures were occasionally reached. Surprisingly, in this study all *Eriogonum* seeds recovered after the Archbold fire from petri dishes placed at the surface and at 2 cm depth failed to germinate, even though seeds subjected to temperatures lower than 100°C in the laboratory germinated. Perhaps an unanticipated factor, possibly related to the glass petri dishes, prevented germination after the fire.

For species that rely on recruitment from seeds that survive through fire, a tradeoff exists between higher probability of survival and increasing difficulty of seedling emergence with increasing depth in the soil. Seedlings from larger seeds should emerge from 2 cm depth with little difficulty, as has been demonstrated for several legume species with seed masses near 30 mg [9, 13, 32]. *Eriogonum* and *Garberia* seeds, however, are much smaller, having an average mass of 3.7 ± 0.1 mg. Their seeds may be incapable of germination and seedling emergence from 2 cm depth, especially because litter apparently acted as a mechanical barrier to *Eriogonum* seedling emergence in another experiment [52, 53].

The extremely limited capacities for *Eriogonum* and *Garberia* seed survival through fires are consistent with postfire recruitment characteristics for these species. In a concurrent study of seedling recruitment following the experimental fires, *Eriogonum* and *Garberia* seedlings germinated from seeds produced after the fires by resprouting adults. Seeds of some species quantified as seedlings after the fires (e.g., *Calamintha ashei, Lupinus diffusus, Tephrosia chrysophylla*), however, presumably germinated after surviving the fires, as adults of the species were killed by the fires and seeds had no obvious long-distance dispersal mechanisms [51]. Although seed germination characteristics for these adult-killed species are unknown, seeds probably were capable of germinating after exposure to elevated temperatures (i.e., −60–100°C). Seeds germinated either at the soil surface in microsites that failed to reach lethal temperatures, or at depths beneath the soil surface from which seedlings could emerge.

This study not only showed that patterns of temperatures differ between the soil surface and 2 cm depth, but also demonstrated differences in relative strengths and weaknesses of two temperature quantification methods. Temperature-sensitive paints on petri dishes were much less precise than thermocouples in quantifying maximum temperatures; therefore, results from temperature-sensitive paints were reliable only at 2 cm depth, where temperature durations were long. Nevertheless, temperature-sensitive paints are adequate for documenting large differences in temperatures between depths in the soil, and for recording maximum temperatures beneath the soil surface, where relatively large proportions of seeds should survive fires.

In addition to maximum temperatures, temperature duration influences seed survival through fires. Since (1) variation in temperature duration and spatial variation in maximum temperatures at the soil surface are potentially relevant to seed survival and (2) thermocouples can quantify temperature duration and complex spatial patterns in temperatures, thermocouples should be used in studies of temperatures relevant to seed survival during fires to quantify temperature patterns at the soil surface.

Results from this study suggest that small-scale spatial variation in temperature exists at the soil surface during fires, and that low-temperature patches are essential for seed survival on the soil surface. Additional studies are needed to document small-scale patterns of temperatures, temperature durations, and seed survival at the soil surface during fires. Seed survival through fire and germination after fire, however, are only a small part of the process of postfire recruitment. Future research on topics such as effects of postfire microsite conditions on seedling establishment, and the relevance of postfire microsite conditions to the evolution of seed germination characteristics, will contribute to a comprehensive characterization of postfire recruitment.

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