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Dynamics of gaps created by burning in Florida oak–saw palmetto (*Quercus*, Fagaceae–*Serenoa repens*, Arecaceae) scrub[1,2]

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Abstract. Sandy gaps in the shrub matrix of oak (*Quercus* L.)–saw palmetto (*Serenoa repens* (W. Bartram) Small) scrub are created by fire but typically close quickly because of rapid regrowth. Such gaps are important habitat features for rare scrub flora and fauna and appear to have been more common in the historical landscape. We followed, from 1993 to 2016, the dynamics of 12 gaps (32.2–98.1 m^2) created by burning slash piles as part of restoration of long-unburned scrub. Gaps closed slowly, primarily by canopy spread of oaks around the gaps. In the absence of subsequent fire, gaps closed within approximately 12 yr. When burned a second or third time, gap area increased to near the initial after-burn size but then declined in area more rapidly than after the initial fire. Vegetation that reestablished in gaps differed from that of the scrub matrix in having less cover of scrub oaks, less cover of *S. repens* > 0.5 m, greater cover of native shrubs and forbs > 0.5 m, and more bare ground. Soil heating from slash-pile burning killed the roots and rhizomes from which scrub oaks, *Serenoa*, and ericaceous shrubs sprout; this altered and slowed the after-fire recovery.

Key words: *Quercus*, restoration, scrub oaks, *Serenoa*, slash pile, sprouting

Natural disturbance, such as fires, windstorms, and floods, affects vegetation structure and composition at multiple spatial and temporal scales (White 1979, Pickett and White 1985, Mitchell 2013). Disturbance regimes are integral to the survival of many species and the maintenance of diversity (Gardner and Engelhardt 2008). Gaps—openings in a forest canopy where one tree died and recruitment of new individuals occurs (Watt 1947)—are disturbances that are small, relative to the vegetation matrix. Canopy gaps influence regeneration and species diversity in temperate, tropical, and boreal forests (Brokaw 1985, Runkle 1985, Platt and Strong 1989, Denslow and Spies 1990, Spies *et al*. 1990, Yamamoto 1992, Brokaw and Busing 2000, McCarthy 2001, Martins and Rodrigues 2002, Rantis and Johnson 2002, Kwit and Platt 2003); they are recognized as important in forest systems worldwide (Muscolo *et al*. 2014, Zhu *et al*. 2014, Buettel *et al*. 2017). Gaps contribute to greater herbaceous diversity in forested wetlands (Anderson and Leopold 2002) and herbaceous-layer composition and diversity in tropical forests (Dirzo *et al*. 1992). Gap formation may be the primary disturbance (Runkle 1998) or may interact with more-widespread disturbances, such as typhoons (Yao *et al*. 2015), ice storms (Nagel *et al*. 2017), or fire (Cannon *et al*. 2017). Fire is an important disturbance in vegetation worldwide (Bond and van Wilgen 1996, Bond and Keeley 2005).

Gaps in the prevailing vegetation matrix also influence vegetation in nonforested systems, including shrublands (Dickinson *et al*. 1993), woodlands (Pecot *et al*. 2007), and grasslands (Tozer *et al*. 2008, Franzese *et al*. 2009). Crawford and Young (1998) found species richness to be greater in gaps than it was in a shrub thicket. Mounds created by badgers in a prairie supported fugitive plants (Platt and Weis 1977). Patches of bare ground influenced herb and shrub establishment in subalpine heathland and grassland (Williams 1992). Oak survival and growth in an oak savanna–dry forest matrix was influenced by the interaction between gaps and fire (Rebertus and Burns 1997), and pine growth increased in gaps in a pine savanna (McGuire *et al*. 2001). In California

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chaparral, Keeley *et al*. (2016) found obligate-seeding species favored by large gaps.

Disturbance of belowground biomass can lead to the formation of aboveground gaps. In an old field, Cahill and Casper (2002) found that canopy gaps corresponded to gaps in belowground biomass. Persistent openings in New Jersey pinelands formed where disturbance, probably fire, removed the organic horizon and the dense roots and rhizomes contained in it (Ehrenfeld *et al*. 1995).

Florida Scrub. Florida scrub is a shrub community on well-drained, infertile, sandy soils, in which scrub oaks (*Quercus geminata* Small, *Quercus myrtifolia* Willd., *Quercus chapmanii* Sarg., *Quercus inopina* Ashe), Florida rosemary (*Ceratiola ericoides* Michx.), repent palms (*Serenoa repens* (W. Bartram) Small, *Sabal etonia* Swingle ex Nash), and ericaceous shrubs predominate (Myers 1990). Florida scrub is known for the number of rare, endemic plants it contains (Christman and Judd 1990, Menges 1999, Stout 2001), and it is habitat for a number of rare, threatened, or endangered fauna (Myers 1990, Menges 1999).

Florida scrub is characterized by periodic, intense fire (Abrahamson and Hartnett 1990, Myers 1990). Fire is an important disturbance in scrub; vegetation composition in scrub is influenced by fire, depth to water table, and soils (Myers 1990, Menges 1999). Fire behavior and effects are heterogeneous at the landscape scale (Turner *et al*. 1994, 2003) within stands of vegetation (Odion and Davis 2000) and at fine spatial scales of $\leq$ 1 m (Thaxton and Platt 2006, O'Brien *et al*. 2016). Variation in fuels contributes to heterogeneity in fire behavior and effects (Mitchell *et al*. 2009).

Gaps—open, sandy areas—are critical microhabitat features for many of the rare scrub plants (Menges and Hawkes 1998, Menges 1999, Menges *et al*. 2008) and scrub fauna (Greenberg *et al*. 1994, Hokit *et al*. 1999, Carrel 2003, Breininger *et al*. 2014). The microclimate of those gaps may differ from the surrounding scrub matrix; for example, Weekley *et al*. (2007) found soil moisture to be greater in gaps than it was in the scrub matrix in several scrub types.

Gaps in Florida rosemary scrub may persist for long periods after fire (Hawkes and Menges 1996, Menges *et al*. 2008). *Ceratiola ericoides* is killed by fire, reestablishes by seed, and grows more slowly than sprouting scrub oaks (Johnson 1982, Menges *et al*. 2008). In addition, *Ceratiola* sp. produces allelochemicals that depress germination of co-occurring plant species (Hunter and Menges 2002, Hewitt and Menges 2008). In contrast, gaps in oak–saw palmetto scrub or scrubby flatwoods, close more rapidly after fire, where postfire regeneration is primarily by sprouting of clonal species (Abrahamson 1984a, b; Schmalzer and Hinkle 1992; Young and Menges 1999; Schmalzer 2003; Dee and Menges 2014). However, gaps in scrubby flatwoods are important for regeneration and persistence of some species (Young and Menges 1999, Dee and Menges 2014).

At the landscape scale, gaps in Florida scrub were historically more abundant before landscape fragmentation and fire suppression; prescribed fire management has restored gaps in some sites but not others (Duncan *et al*. 1999).

Here, we examined the dynamics of aboveground gaps in oak–saw palmetto scrub that were established by burning of piles during restoration of long-unburned scrub to restore habitat for the threatened Florida scrub-jay (*Aphelocoma coerulescens*; Schmalzer *et al*. 1994, Breininger *et al*. 2014). Our objectives were (a) to determine the persistence of these created gaps, (b) to identify the vegetation composition within the gaps, and (c) to compare the vegetation composition in the gaps to vegetation in the surrounding scrub matrix. We followed the extent and vegetation composition of a set of 12 of these gaps through an unburned recovery period of 10 yr. We also observed how gaps changed after second and third fires up until 2016. Because gaps are a critical habitat feature for many scrub species, it is important to understand how gaps created by management practices change over time.

Materials and Methods. This study was conducted in the northern section of the Kennedy Space Center/Merritt Island National Wildlife Refuge (KSC/MINWR) in the Shiloh area (28°38′N, 80°42′W). Two adjacent stands of long-unburned oak–saw palmetto scrub, separated by a sand road, were selected for restoration as part of the scrub-habitat compensation plan for KSC/MINWR (Schmalzer *et al*. 1994). The northern stand was about 12.1 ha, and the southern stand was 9.1 ha.

Before mechanical treatment, 20 line-intercept transects (15 m long; Mueller-Dombois and Ellenberg 1974) were established and sampled in

Table 1. History of the Shiloh scrub restoration site.

Year	Event
1992–1993	Transects ($N = 20$) established and sampled before treatment (1992). Scrub cut and piled. Burned in November 1993. Dimensions of 12 gaps delimitated.
1994–2002	Transects (matrix) resampled 7, 16, 24, 30, 36, 48, 60, 72, 84, 96, and 108 mo after the burn.
1995–2003	Gaps sampled annually in June ($N = 12$).
May 2004	Prescribed burn: seven gaps burned, four not burned, one cut and not burned; eight transects in north section burned, two not burned, south section not burned.
2004–2007	Gaps sampled annually in June ($N = 11$).
May 2005	Prescribed burn of southern section: four transects burned, six not burned, no gaps burned.
2005–2007	Transects in northern section sampled annually in May.
May 2008	Prescribed burn: six gaps burned (two partially), five not burned; eight transects in northern section burned at least partially, seven transects in southern section burned at least partially.
2008–2012	Gaps sampled annually in June ($N = 11$).
2009–2012	Transects in both section sampled annually in May.
January 2013	Prescribed burn: five gaps burned (four partially), six not burned; two transects in northern section burned partially.
2013–2016	Gaps sampled annually in June ($N = 11$). Transects in both sections sampled annually in May.

the scrub matrix in 1992; 10 transects were north and 10 south of the sand road. Cover was measured to the nearest 5 cm by species in two height strata, > 0.5 m and < 0.5 m. Vegetation transects in the scrub matrix were sampled from 1994 through 2016 (Table 1).

The scrub matrix was dominated by scrub oaks (*Q. geminata*, *Q. myrtifolia*, and *Q. chapmanii*), *Serenoa repens*, and ericaceous shrubs, before treatment (Schmalzer *et al.* 1994). Initial vegetation height was 4.2 m north and 3.8 m south of the sand road. Soils were mapped as Paola fine sand, a Spodic Quartzipsamments (Huckle *et al.* 1974). The vegetation height and structure were indicative of scrub long unburned because of a combination of landscape fragmentation and fire suppression (Schmalzer *et al.* 1994). Subsequent dating of basal sections of *Q. myrtifolia* cut during sampling in 1992, before treatment, gave an age range of 22–53 yr north and 13–33 yr south of the sand road.

Because of the large stature of the scrub oaks at this site, a D6 tractor (Caterpillar, Peoria, IL) with a V-blade was used to cut the trees between January and March 1993. The resulting fuel bed had a high percentage of heavy fuels consisting of oak stems with basal diameters of 12–20 cm. These were left scattered to dry, then some of the heavy fuels were piled to enhance complete burning. Prescribed burns were conducted in early November 1993. The prescribed burn of the northern section was less complete (60–70%, November 1, 1993) than the southern section (95%, November 3, 1993), but the slash piles burned completely in both fires (Schmalzer *et al.* 1994).

The areas in which the slash piles burned completely left behind aboveground gaps in the scrub-vegetation matrix. The dimensions of 12 gaps were delineated after the fire, 8 in the northern section and 4 in the southern section. We sampled the gaps annually from 1995 to 2016. Gaps were approximately elliptical in shape, and area was estimated based on the lengths of the major and minor axes (Runkle 1992, Schliemann and Bockheim 2011). At each sampling, we determined the length of each axis that remained open (defined as not covered by continuous woody vegetation). The major axis of each gap was used as a line-intercept transect (Mueller-Dombois and Ellenberg 1974), and vegetation cover was determined by species each year in two height strata, $>$ 0.5 m and $<$ 0.5 m.

The northern section of the site burned again in May 2004 (Table 1) when seven gaps burned. One gap in the southern section of the site was disturbed by roller-chopping but not burned and was dropped from further sampling. Prescribed fires in 2008 and 2013 burned some gaps (Table 1). Some scrub-matrix transects were burned in 2004, 2005, 2008, or 2013 (Table 1).

Native and introduced species of similar life forms were classified into six plant groups (Table 2) to follow dynamics of vegetation change over time and to compare the vegetation composition of the gaps to the scrub matrix. That grouping was necessary because of the large number of individual species. Taxonomic nomenclature follows Wunderlin and Hansen (2011). We used linear models to determine how gaps and time-since-fire affected the percentage of cover for plant groups in

Table 2. Plant groups in the Shiloh scrub matrix and gaps.

Group	Taxa
Scrub oaks (ScrubOak)	*Quercus chapmanii*, *Q. geminata*, *Q. myrtifolia*
Woody vines (WoodVine)	*Smilax auriculata*, *Vitis rotundifolia*
Native shrubs (NatShrub) (not scrub oaks or *Serenoa*)	*Asimina obovata*, *Baccharis halimifolia*, *Bejaria racemosa*, *Callicarpa americana*, *Carya floridana*, *Diospyros virginiana*, *Gaylussacia dumosa*, *Hypericum tetrapetalum*, *Ilex glabra*, *Licania michauxii*, *Lyonia ferruginea*, *L. fruticosa*, *L. lucida*, *Myrica cerifera*, *Osmanthus americanus*, *Persea borbonia*, *Quercus laurifolia*, *Rhus copallinum*, *Rubus* spp., *Sambucus nigra* subsp. *canadensis*, *Vaccinium myrsinites*, *V. stamineum*, *Ximenia americana*, *Zanthoxylum clava-herculis*
Exotic grasses (ExoGrass)	*Melinis repens*, *Panicum maximum*, *Paspalum urvillei*
Native grasses (NatGrass)	*Andropogon* spp., *Dichanthelium* ssp., *Digitaria ciliaris*, *Eustachys petraea*, *Paspalum* spp., *Setaria parviflora*
Native forbs (NatForb)	*Ambrosia artemisiifolia*, *Bulbostylis* spp., *Chamaecrista fasciculata*, *Chamaecrista* spp., *Chamaesyce maculata*, *Clitoria mariana*, *Conyza canadensis*, *Cyperus ovatus*, *Erechtites hieracifolia*, *Eupatorium capillifolium*, *Galactia elliottii*, *G. volubilis*, *Gamochaeta antillana*, *Heterotheca subaxillaris*, *Linaria canadensis*, *Lupinus diffusus*, *Mikania* spp., *Opuntia humifusa*, *Passiflora incarnata*, *Phoradendron leucarpum*, *Physalis walteri*, *Phytolacca americana*, *Pteridium aquilinum*, *Scleria triglomerata*, *Seymeria pectinata*, *Solidago odora* var. *chapmanii*, *Stillingia sylvatica*, *Tillandsia recurvata*, *Tillandsia usneoides*

both strata (> 0.5 m and < 0.5 m) and how gaps, time-since-fire, and strata affected total cover using R software (R Foundation for Statistical Computing, Vienna, Austria). Because of the large number of zeros in the data set, the residuals of the models were not normal; the model point estimates should still be unbiased, but the variance may be underestimated. We used linear regression to examine changes in opening area over time (SPSS Statistics, version 24; IBM, Armonk, NY).

Results. RESPONSES AFTER FIRST BURN. The initial area of gaps ranged from 32.2 to 98.1 m^2, with a mean of 55.6 m^2. The area remaining open declined to a mean of 14.9 m^2 by June 2003, which was 116 mo after the burn (Fig. 1). For gaps that did not burn a second time, the area that remained open declined to < 3 m^2 by 140 mo after the fire (Fig. 1).

Within gaps, total cover > 0.5 m increased from 1995 (20 mo after the burn) to 2003 (116 mo after the burn; Fig. 2A; Table 3). Cover of scrub oaks, *Serenoa*, woody vines, and native shrubs > 0.5 m increased through that period (Table 4, S1). Cover of native forbs > 0.5 m increased after burning but then declined by the end of the period (Table 4, S1). Total cover < 0.5 m within gaps increased after burning and then declined (Fig. 2B; Table 3), as did native forbs and scrub oaks < 0.5 m (Table 5, S2). Bare ground within gaps declined from 1995 to 2003 (Fig. 2C; Table 5).

Table 3. Estimates and standard errors for the general linear model showing effects of gaps, time since fire, and strata (< 0.5 m and > 0.5 m) on total vegetation cover; > 0.5 m was the base strata. Adjusted R^2 was 0.6327; $P < 0.001$. TSF = time since fire. Regression models for each strata are provided in the last rows of the table.

Predictor	Estimate	SE	*t*	*P*
Intercept	55.2274	3.01399	18.324	< 0.001
GAP	−49.06451	3.21298	−15.271	< 0.001
LessThan	−19.69996	4.26242	−4.622	< 0.001
TSF	0.73836	0.04674	15.797	< 0.001
GAP:LessThan	74.15088	4.54384	16.319	< 0.001
LessThan:TSF	−1.01643	0.0661	−15.377	< 0.001

Response variable	Scrub matrix	Gap
< 0.5 cover	35.52744 − 0.27807 × TSF	60.61381 − 0.27807 × TSF
> 0.5 cover	55.2274 + 0.73836 × TSF	6.16283 + 0.73836 × TSF

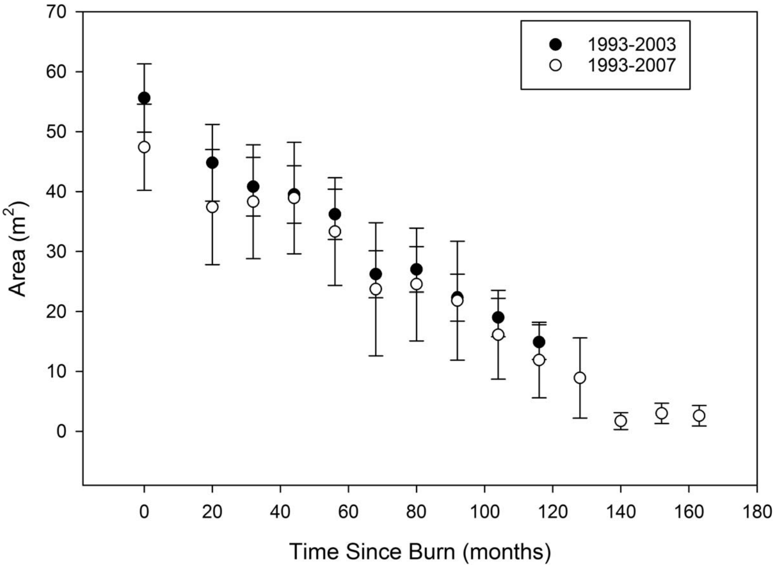

FIG. 1. Change in area of scrub gaps after creation by burn piles. Area of scrub gaps ($N = 12$) from 1993 to 2003 (116 mo after the burn). Area remaining open declined as Area = 53.209–0.337 (time), $r = -0.626$, $P < 0.001$. Seven of these gaps burned in 2004. Area of four scrub gaps from 1993 to 2007 (163 mo after the burn). Area remaining open declined as Area = 47.782–0.304 (time), $r = -0.70$, $P < 0.001$. These gaps did not burn in 2004. Error bars indicate 1 SE.

In the scrub matrix, total cover > 0.5 m decreased immediately after the burn and then increased (Fig. 2A; Table 3) as did cover > 0.5 m of scrub oaks and *Serenoa* species (Table 4, S5). Woody vines and native shrubs > 0.5 m (Table 4, S5) increased from preburn values after the burn. Native forbs > 0.5 m increased after the burn and then decreased to low values (Table 4, S5). Total cover < 0.5 m in the scrub matrix (Fig. 2B, Table 3) increased after the burn and then declined, as did the cover of scrub oaks and native forbs < 0.5 m (Table 5, S6). Bare ground increased after the burn and then declined (Fig. 2C; Table 5). Native grasses had low cover values > 0.5 m and < 0.5 m in the scrub matrix and gaps (Table 4, 5, S1, S2, S5, S6).

Cover of plant groups differed in the gaps, compared with the scrub matrix, with the exceptions of woody vines > 0.5 m and native shrubs < 0.5 m (Table 4, 5). Gaps had less total cover > 0.5 m (Fig. 2A; Table 3) and less cover of scrub oaks and saw palmetto > 0.5 m. (Table 4, S1, S5). Gaps had greater total cover < 0.5 m than the scrub matrix had (Fig. 2B; Table 3) and greater cover of native forbs < 0.5 m (Table 5, S2, S6) but less cover of scrub oaks < 0.5 m (Table 5, S2, S6). Gaps retained greater bare ground than the scrub matrix (Fig. 2C; Table 5).

No rare or gap-specialist plants established in the gaps (Table S3, S4). Invasive, exotic plants also did not establish and persist in the gaps, with only transitory occurrences of *Melinis repens* (Willd.) Zizka and *Lantana camara* L. (Table S3, S4). Specifically, *Melinis* occurred twice at 20 and 32 mo after the burn at 0.2–0.3% mean cover (Table S3, S4). *Lantana* occurred once at 68 mo after the burn at 0.2% cover (Table S3). In the scrub matrix, *Melinis* occurred at 0.2% or less mean cover at 7, 24, and 30 mo after the burn, but not subsequently, whereas *Lantana* did not occur (P.A.S. and T.E.F., unpublished data).

RESPONSES AFTER SUBSEQUENT BURNS. Seven gaps burned for a second time in May 2004 (Table 1). Gap area increased immediately after the burn to close to the initial size (Fig. 3A). However, gap area declined more rapidly after the second burn than after the original treatment (Fig. 3A). Four gaps burned again in both 2004 and 2008 (Table 1). After both subsequent burns, gap area increased to close to the original size (Fig. 3B). Gap area declined more rapidly after the second and third burns than after the initial treatment, with expected closure at about 5 yr after the burn (Fig 3B). Responses after the second and third burns were similar (Fig. 3B).

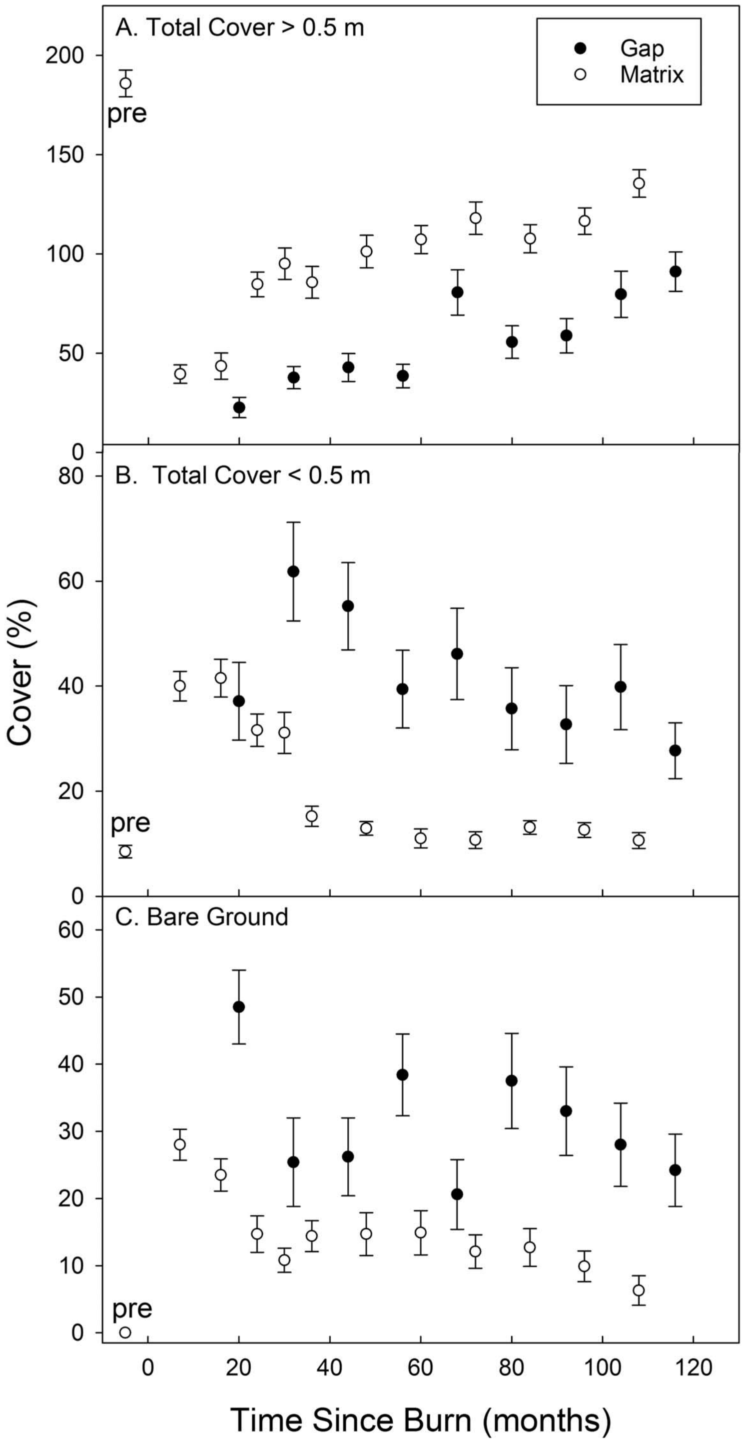

FIG. 2. Comparison of total cover and bare ground in gaps and scrub matrix through 10 yr after the burn. (A) Total cover > 0.5 m in gaps ($N = 12$) created by burning and in the scrub matrix ($N = 20$) from 1993 to 2003. Error bars indicate 1 SE. After the burn, cover differed between gaps and matrix. (B) Total cover < 0.5 m in gaps ($N = 12$) and in the scrub matrix ($N = 20$) created by burning from 1993 to 2003. After the burn, cover differed between gaps and matrix. (C) Bare ground in gaps ($N = 12$) and in the scrub matrix ($N = 20$) created by burning from 1993 to 2003. After the burn, cover differed between gaps and matrix.

Table 4. Estimates and standard errors for the general linear model showing effects of gaps, time since fire, and plant group cover in the > 0.5 m strata. Native Forb is the base plant group. Adjusted R^2 was 0.6491; $P <$ 0.001. Plant groups follow Table 2. TSF = time since fire. Regression models for each plant group are provided in the last rows of the table.

Predictor	Estimate	SE	*t*	*P*
(Intercept)	5.97747	1.39045	4.299	< 0.001
GAP	5.71374	1.48225	3.855	< 0.001
NatGrass	−4.26575	1.96639	−2.169	0.030
NatShrub	2.60089	1.96639	1.323	0.186
ScrubOak	19.42187	1.96639	9.877	< 0.001
Serenoa	3.75808	1.96639	1.911	0.056
WoodVine	−2.28823	1.96639	−1.164	0.245
TSF	−0.05901	0.02156	−2.737	0.006
GAP:NatGrass	−5.19702	2.09622	−2.479	0.013
GAP:NatShrub	−12.115	2.09622	−5.779	< 0.001
GAP:ScrubOak	−46.8026	2.09622	−22.327	< 0.001
GAP:*Serenoa*	−13.4831	2.09622	−6.432	< 0.001
GAP:WoodVine	−5.96444	2.09622	−2.845	0.004
NatGrass:TSF	0.04292	0.03049	1.407	0.159
NatShrub:TSF	0.20262	0.03049	6.644	< 0.001
ScrubOak:TSF	0.58384	0.03049	19.146	< 0.001
Serrep:TSF	0.17183	0.03049	5.635	< 0.001
WoodVine:TSF	0.08924	0.03049	2.926	0.003

Response variable	Scrub matrix	Gap
Native forb cover	5.97747 − 0.059 × TSF	11.69121 − 0.059 × TSF
Native grass cover	1.71167 − 0.01608 × TSF	2.22841 − 0.01608 × TSF
Native shrub cover	8.57836 + 0.14362 × TSF	2.1771 + 0.14362 × TSF
Scrub oak cover	25.39937 + 0.52484 × TSF	−15.6899 + 0.52484 × TSF
Serenoa cover	9.7355 + 0.11283 × TSF	1.96629 + 0.11283 × TSF
Woody vine cover	3.68927 + 0.03024 × TSF	3.43861 + 0.03024 × TSF

Discussion. Burning piled fuels produced gaps in the scrub matrix that persisted for > 10 yr. Increased and longer-duration soil heating appeared to kill the roots and rhizomes of scrub oaks, ericads, and *Serenoa* that resprout under typical fire conditions. These gaps retained greater cover of bare ground and forbs but less cover of scrub oaks and *Serenoa* compared with the scrub matrix. After second and third burns, gap areas initially expanded but closed more rapidly than after the original treatment. This suggests that relatively frequent fire might maintain more gap area. It is also possible that if the second burn had occurred earlier than 10 yr after the original treatment, more of the gap area would have remained open. In rosemary scrub, the gap area declined for 10 yr after the burn but then plateaued in the absence of a second fire (Menges *et al.* 2017). In our study, gap area continued to decline. However, when partially closed gaps burned, the open areas increased in our study, as it did in the rosemary scrub (Menges *et al.* 2017).

Scrub fires are intense stand-replacing fires that typically kill aboveground stems of oaks, ericads, and *Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg. (Myers 1990). The pulse of heat from those fires may exceed 700 °C (Wally *et al.* 2006) but is of short duration. The rapid movement of the flame front and the insulating properties of soil limits heating of the soil (DeBano *et al.* 2005), such that temperatures are not lethal to roots and rhizomes in the soil (Whelan 1995, Busse and DeBano 2005). Alexis *et al.* (2007) found that soil temperatures at 2–3 cm depth remained < 100 °C, litter surface temperatures ranged from 371 to 760 °C, and temperature in the vegetation ranged from 260 to 816 °C in the 2004 prescribed burn of this site.

Scrub oaks have extensive belowground roots and rhizomes (Guerin 1993, Day *et al.* 2013), as do ericads. Belowground biomass of scrub at KSC/MINWR makes up approximately 85% of total biomass (Stover *et al.* 2007). Under normal fire conditions, the belowground roots and rhizomes survive, and after fire, carbon stored belowground is used for sprouting (Stover *et al.* 2007). Sprouting is rapid and scrub vegetation reestablishes cover quickly (Abrahamson 1984a, 1984b, Schmalzer and Hinkle 1992, Schmalzer 2003).

Table 5. Estimates and standard errors for the general linear model showing effects of gaps, time since fire, and plant group cover in the < 0.5 m strata. Bare ground is the base plant group. Adjusted R^2 was 0.5276, $P <$ 0.001. Plant groups follow Table 2. TSF = time since fire. Regression models for each plant group are provided in the last rows of the table.

Predictor	Estimate	SE	*t*	*P*
(Intercept)	21.63817	1.01927	21.229	< 0.001
GAP	18.58707	1.08656	17.106	< 0.001
NatForb	−12.67067	1.44146	−8.79	< 0.001
NatGrass	−19.54104	1.44146	−13.556	< 0.001
NatShrub	−16.35234	1.44146	−11.344	< 0.001
ScrubOak	−7.00084	1.44146	−4.857	< 0.001
Serenoa	−19.56103	1.44146	−13.57	< 0.001
WoodVine	−20.26708	1.44146	−14.06	< 0.001
TSF	−0.13142	0.01581	−8.314	< 0.001
GAP:NatForb	12.57063	1.53663	8.181	< 0.001
GAP:NatGrass	−16.78667	1.53663	−10.924	< 0.001
GAP:NatShrub	−17.62012	1.53663	−11.467	< 0.001
GAP:ScrubOak	−26.15951	1.53663	−17.024	< 0.001
GAP:*Serenoa*	−19.67787	1.53663	−12.806	< 0.001
GAP:WoodVine	−18.63449	1.53663	−12.127	< 0.001
NatForb:TSF	0.01671	0.02235	0.747	0.455
NatGrass:TSF	0.11759	0.02235	5.26	< 0.001
NatShrub:TSF	0.09686	0.02235	4.333	< 0.001
ScrubOak:TSF	0.04299	0.02235	1.923	0.055
Serrep:TSF	0.12885	0.02235	5.764	< 0.001
WoodVine:TSF	0.11964	0.02235	5.352	< 0.001

Response Variable	Scrub Matrix	Gap
Bare ground cover	21.6382 − 0.1314 × TSF	40.2253 − 0.1314 × TSF
Native forb cover	8.9672 − 0.11469 × TSF	40.1249 − 0.11469 × TSF
Native grass cover	2.09716 − 0.01381 × TSF	3.89726 − 0.01381 × TSF
Native shrub cover	5.28496 − 0.03454 × TSF	6.25194 − 0.03454 × TSF
Scrub oak cover	14.63736 − 0.08841 × TSF	7.06495 − 0.08841 × TSF
Serenoa cover	2.07717 − 0.00255 × TSF	0.9864 − 0.00255 × TSF
Woody vine cover	1.37112 − 0.01176 × TSF	1.32373 − 0.01176 × TSF

Fine roots also recover rapidly after fire (Day *et al.* 2013). Oak cover returns to preburn values usually within 5 yr (Schmalzer 2003). The aboveground buds of *Serenoa* are well-protected, resulting in little fire-related morality (Abrahamson and Abrahamson 2002). Saw palmetto leaves regenerate rapidly after fire (Abrahamson and Abrahamson 2006), and cover returns to preburn levels usually within 1 yr.

Hence, prescribed burns do not generally lead to the creation of persistent gaps in oak–saw palmetto scrub because of the lack of soil heating. Where logging has produced greater fuels on the ground, residence times of elevated temperatures are longer (Wally *et al.* 2006). Adding fuel elevated the soil temperatures significantly in prescribed burns in flatwoods but did not change shrub regeneration (Hierro and Menges 2002). In maritime chaparral fires, variation in fuel distribution caused spatial variation in surface heating that affected both seed and sprout regeneration (Odion and Davis 2000). Prolonged heating from burning slash piles or masticated fuels can cause soil heating to depths lethal to soil organisms, plant roots and rhizomes, and seeds (Whelan 1995, Korb *et al.* 2004, Busse *et al.* 2005, DeBano *et al.* 2005). Our data indicate that burning of piled oak stems killed most or all of the roots and rhizomes of oaks, ericads, and *Serenoa* within the pile area, resulting in gaps that persisted for > 10 yr. This differed from the scrub matrix where the percentage bare ground decreased rapidly postfire.

Closure of the gaps that formed was slow, with much of the cover of scrub oaks developing from branches arching over the gap as oaks rooted outside the gap grew in height; this is reflected in the scrub oak cover increasing in > 0.5 m oaks, without first increasing in < 0.5 m scrub oaks, in contrast to the scrub matrix. When subsequent fires top-killed oaks surrounding the gaps, gap area increased. Some clonal spread of oaks, and perhaps *Serenoa*, into gaps was occurring; seedling

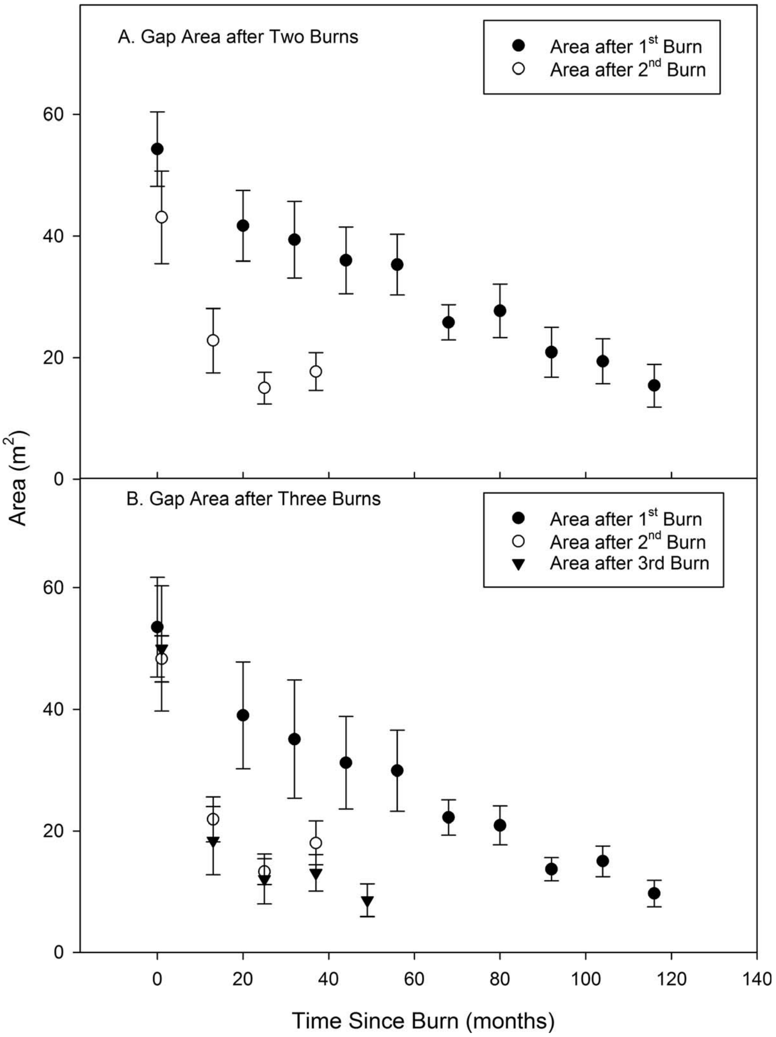

Fig. 3. Changes in area of gaps burned a second and third time. (A) Area of seven gaps created in 1993 and burned again in 2004. Error bars indicate 1 SE. After the first burn, gap area declined as Area = 50.624–0.311 (time), $r = -0.678$, $P < 0.001$; after the second burn gap area declined as Area = 37.919–0.699 (time), $r = -0.565$, $P = 0.002$. (B) Area of four gaps created in 1993 and burned in 2004 and 2008. After the first burn, gap area declined as Area = 48.330–0.348 (time), $r = -0.752$, $P < 0.001$; after the second burn, gap area declined as Area = 41.101–0.828 (time), $r = -0.752$, $P = 0.001$; after the third burn, gap area declined as Area = 38.805–0.734 (time), $r = -0.686$, $P = 0.001$.

establishment of oaks and *Serenoa* can occur but appears infrequently in the study area. Recovery of belowground biomass is slow compared with the rapid recovery of aboveground biomass by sprouting when the roots and rhizomes remain intact. Other systems that typically recover from disturbance by sprouting show much slower or altered recovery when belowground roots and rhizomes are killed (*e.g.*, Matlack *et al.* 1993, Ehrenfeld *et al.*1995).

The more-open conditions in the gaps favored herbaceous species. *Galactia elliottii* Nutt. The most abundant herbaceous species in the gaps, also occurs in the surrounding scrub matrix. Whether it established from seed in the soil or dispersed from the adjacent matrix is not known. Invasive, exotic species did not establish persisting populations in the gaps, although old fields with populations of exotic grasses (Schmalzer *et al.* 2002) occurred within < 100 m of some of the gaps.

Gaps in scrub are important for rare scrub plants (Menges and Hawkes 1998, Menges 1999, Menges *et al*. 2008, 2017), but none established in these created gaps. The long period of fire exclusion before restoration began in 1993 probably contributed to the lack of any gap-dependent rare plants in the surrounding scrub matrix. Scrub on KSC/MINWR has fewer rare scrub plants than that of the Lake Wales Ridge (Schmalzer *et al*. 1999), but some gap-dependent scrub plants do occur. Known populations of gap-dependent species, such as *Lechea divaricata* Shuttlw. ex Britton occur approximately 5 km from the study site (Schmalzer and Foster 2016), limiting potential dispersal.

Recovery after burning of slash piles in a restoration project differs from recovery after typical scrub fires, confirming the suggestion of Hierro and Menges (2002) that only very intense fires would alter postfire responses. Are there natural analogs that could produce similar results? Hurricanes or other severe windstorms could produce additional, concentrated fuels that could subsequently burn (Myers and van Lear 1998). Wind and fire may have amplified effects under some circumstances (Cannon *et al*. 2017). Liu *et al*. (2008) presented paleoecological data suggesting that intense hurricanes reduced populations of pines and were followed by intense fires.

The shrub layer of scrub vegetation is relatively resistant to hurricane winds with short-term defoliation and reduction in photosynthesis (Li *et al*. 2007) but little to no damage to rare scrub plants (Menges *et al*. 2011). Of the pines that occur associated with scrub vegetation, *Pinus clausa* is the most vulnerable to hurricane damage that produces debris (Myers 1990, Parker *et al*. 2001, Drewa *et al*. 2008, Menges *et al*. 2011). *Pinus elliottii* Engelm. var. *densa* Little & K.W. Dorman is relatively resistant to hurricane winds (Platt *et al*. 2000), but some damage and mortality does occur. *Pinus palustris* Mill. is also relatively resistant (Provencher *et al*. 2001) but can suffer damage (Kleinman and Hart 2017). We have observed gaps of varying sizes around burned pine stumps, branches, or boles in scrubby flatwoods. Scattered *P. elliottii* var. *densa* occurred in the study site but did not occur on the transects.

There is some potential for hurricanes or similar winds to produce concentrated fuels that, when burned, form gaps. Subsequent, normal fires, if frequent enough, could maintain at least parts of those gaps by limiting the height and canopy spread of shrubs that would close gaps from the sides because the reestablishment by seed or clonal spread into gaps is slow compared with sprouting from underground rhizomes. This may represent one mechanism by which gaps can form in oak–saw palmetto scrub and scrubby flatwoods that persist for more than a few years after a fire.

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