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Effects of repeated fire on Florida oak-saw palmetto scrub

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Abstract

Background: The dominant species of Florida oak-saw palmetto scrub sprout after burning from belowground rhizomes or fire-resistant aboveground buds with rapid reestablishment of cover. Responses to single fires are well documented; however, responses to repeated fires may differ. Fire return intervals, differences among sites, and species may influence responses. We used transect data from four sites on Kennedy Space Center/Merritt Island National Wildlife Refuge to test whether growth differed through repeated fires. Two sites burned five times in 36 years, one site burned five times in 25 years, and one burned four times in 18 years. We used linear mixed models that account for repeated measures to determine if the number of fires affected height, total cover ≥ 0.5 m and < 0.5 m, bare ground, and cover of the dominant oak (*Quercus*) ≥ 0.5 m and of saw palmetto (*Serenoa repens*) ≥ 0.5 m. We compared community composition through repeated fires using nonmetric multidimensional scaling ordination.

Results: Height, total cover ≥ 0.5 m, and cover of the dominant oak ≥ 0.5 m and of saw palmetto ≥ 0.5 m increased with time since burn; total cover < 0.5 m and bare ground decreased. A quadratic term in the growth model was significant except for total cover < 0.5 m. There were site differences for all variables except bare ground. The number of fires decreased height, total cover ≥ 0.5 m, and cover of the dominant oak ≥ 0.5 and increased total cover < 0.5 m and bare ground but had no effect on cover of *Serenoa repens* ≥ 0.5 m. Community changes after repeated fires were similar in nonmetric multidimensional ordinations with time since burn correlated to the first or second axis.

Conclusions: Scrub recovered from repeated fires at a range of intervals and seasons, but short return intervals reduced growth with responses differing among species.

Keywords: Florida, Oak-saw palmetto scrub, *Quercus*, Repeated fire, *Serenoa*

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Resumen

Antecedentes: Las especies dominantes de los arbustales de roble y palmas de Florida rebrotan luego de una quema desde rizomas subterráneos o desde meristemas resistentes con un rápido restablecimiento de la cobertura. La respuesta a fuegos individuales está bien documentada; de todas maneras, las respuestas a fuegos repetidos pueden diferir. Los intervalos de retorno del fuego, las diferencias entre sitios y entre especies pueden influenciar las respuestas. Usamos datos de cuatro sitios en el Kennedy Space Center / Refugio Nacional de Fauna de la Isla Merrit, para probar si el crecimiento difería mediante la aplicación de fuegos repetidos. Dos sitios se quemaron cinco veces en 36 años, uno se quemó cinco veces en 25 años y otro cuatro veces en 18 años. Usamos modelos lineales mixtos que tenían en cuenta medidas repetidas para determinar si el número de fuegos afectaba la altura, la cobertura total ≥ 0,5 m y ≤ 0,5 m, el suelo desnudo, la cobertura del roble dominante (*Quercus* spp.) ≥ 0,5 m y de la palma enana (*Serenoa repens*) ≥ 0,5. Comparamos la composición de la comunidad mediante fuegos repetidos usando una ordenación escalar multidimensional no-paramétrica.

Resultados: La altura, la cobertura total ≥ 0,5 m, la cobertura de los robles dominantes ≥ 0,5 m, y de la palma enana ≥ 0,5 m se incrementó en el tiempo desde la quema, y disminuyó el suelo desnudo. Un término cuadrático en el modelo de crecimiento fue significativo excepto para la cobertura < 0,5 m. Hubo diferencias en los sitios para todas las variables excepto para el suelo desnudo. El número de incendios disminuyó el crecimiento, la cobertura total ≥ 0,5 m y la cobertura de los robles dominantes ≥ 0,5 m, incrementó la cobertura total < 0,5 m y el suelo desnudo, pero no tuvo efecto sobre la cobertura de la palma enana ≥ 0,5 m. Los cambios en la comunidad luego de fuegos repetidos fueron similares en las ordenaciones multidimensionales no-paramétricas con el tiempo desde la quema correlacionada con el primero o segundo eje.

Conclusiones: Los arbustales se recuperaron después de los fuegos repetidos en un rango de intervalos y estaciones, aunque los intervalos de retorno cortos redujeron el crecimiento con respuestas diferenciales entre las distintas especies.

Background

Resprouting after fire or other disturbances is common among woody plants (Bond and van Wilgen 1996; Bond and Midgley 2001; Vesk and Westoby 2004; Clarke et al. 2013; Pausas et al. 2018) and has a long evolutionary history (Lamont et al. 2011; Pausas and Keeley 2014). In shrub vegetation that burns with intermediate frequency, sprouting allows dominant species to reestablish cover rapidly (Lamont et al. 2011). Such recovery is enhanced by bud banks (Klimesova and Klimes 2007; Klimesova et al. 2017) that are protected by being belowground in roots, rhizomes, or specialized structures such as lignotubers or aboveground but protected from fire by bark, leaf bases, or other structures (Clarke et al. 2013; Paula et al. 2016; Pausas et al. 2018).

Extensive belowground biomass and stored carbohydrate reserves are important to sprouting responses (Bond and van Wilgen 1996; Knox and Clarke 2005; Schutz et al. 2009, 2011; Paula and Ojeda 2011). Fires that are very frequent may deplete these stored reserves, banks of protected buds, or both (Iwasa and Kubo 1997; Bellingham and Sparrow 2000; Paula and Ojeda 2009; Enright et al. 2011) reducing the abundance of sprouting woody species (Prichard et al. 2017). Conversely, reduced fire frequency is related to woody invasion or expansion into formerly graminoid communities (van Auken 2009; Eldridge et al. 2011; Ratajczak et al. 2014; Yu et al. 2015; Collins et al. 2021). Thus, the recovery postfire from a series of fires over time may differ from that after a single burn (Enright et al. 2015; Prichard et al. 2017).

Increased fire frequency could reduce nutrients required for regrowth. In consuming biomass, fire also oxidizes and volatilizes carbon and nitrogen from plant tissue and litter resulting in losses of carbon and total nitrogen; however, soil cations, phosphorus, and mineralizable nitrogen frequently increase postfire (Knoepp et al. 2005). In a global analysis that included meta-analyses, field studies, and modeling, increasing fire frequency decreased soil carbon and nitrogen in broadleaf forests and savanna grasslands but not phosphorus, calcium, or potassium (Pellegrini et al. 2018).

Florida scrub

Florida scrub is a shrub community associated with former coastlines and paleo-dunes (Laessle 1967; Myers 1990) and is one of the most endangered ecosystems in the USA (Noss and Peters 1995) due to habitat loss for development and agriculture (Myers 1990; Weekley et al. 2008). It occurs on well-drained, acidic, infertile sandy soils where scrub oaks (sand live oak (*Quercus geminata* Small), myrtle oak (*Q. myrtifolia* Willd.), Chapman oak (*Q. chapmanii* Sarg.), scrub oak (*Q. inopina* Ashe)), Florida rosemary (*Ceratiola ericoides* Michx.), repent palms (saw palmetto (*Serenoa repens* (W. Bartram) Small)), scrub palmetto (*Sabal etonia* Swingle ex Nash), and ericaceous shrubs (*Lyonia* spp., *Vaccinium* spp.,) predominate (Myers 1990) with or without a pine (*Pinus* spp.) canopy. Florida scrub and the adjacent scrubby flatwoods are characterized by periodic, intense, stand replacing fire (Myers 1990; Abrahamson and Hartnett 1990) and are habitat for many rare, endemic plants (Christman and Judd 1990; Menges 1999; Stout 2001) and rare, threatened, or endangered fauna (Myers 1990; Menges 1999).

The scrub oaks, ericaceous shrubs, and repent palms in Florida scrub sprout after fire (Abrahamson 1984b) and may also spread clonally (Menges and Kohfeldt 1995). This sprouting response is supported by extensive belowground biomass (Guerin 1993; Langley et al. 2002; Saha et al. 2010; Day et al. 2013) and stored carbohydrates (Olano et al. 2006). Sprout regeneration reestablishes cover of existing species rapidly (Abrahamson 1984a; Schmalzer and Hinkle 1992a; Schmalzer 2003) though with some variation in sprouting responses (Maguire and Menges 2011). At fire return intervals of 6–15 years, scrub vegetation returns to similar structure and composition postburn within 5 years (Schmalzer 2003; Abrahamson et al. 2021). However, Menges et al. (2020) showed that very frequent (particularly annual) burning or mowing in scrub (i.e., short disturbance return intervals) reduced shrub growth. Obligate seeding species may be reduced by frequent fire; in Florida scrub, these species are of most importance on the drier sites (e.g., Florida rosemary, sand pine (*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.)) (Johnson 1982; Abrahamson 1984b) and in gaps (e.g., *Dicerandra* spp.) (Menges 1992; Evans et al. 2010; Menges et al. 2019).

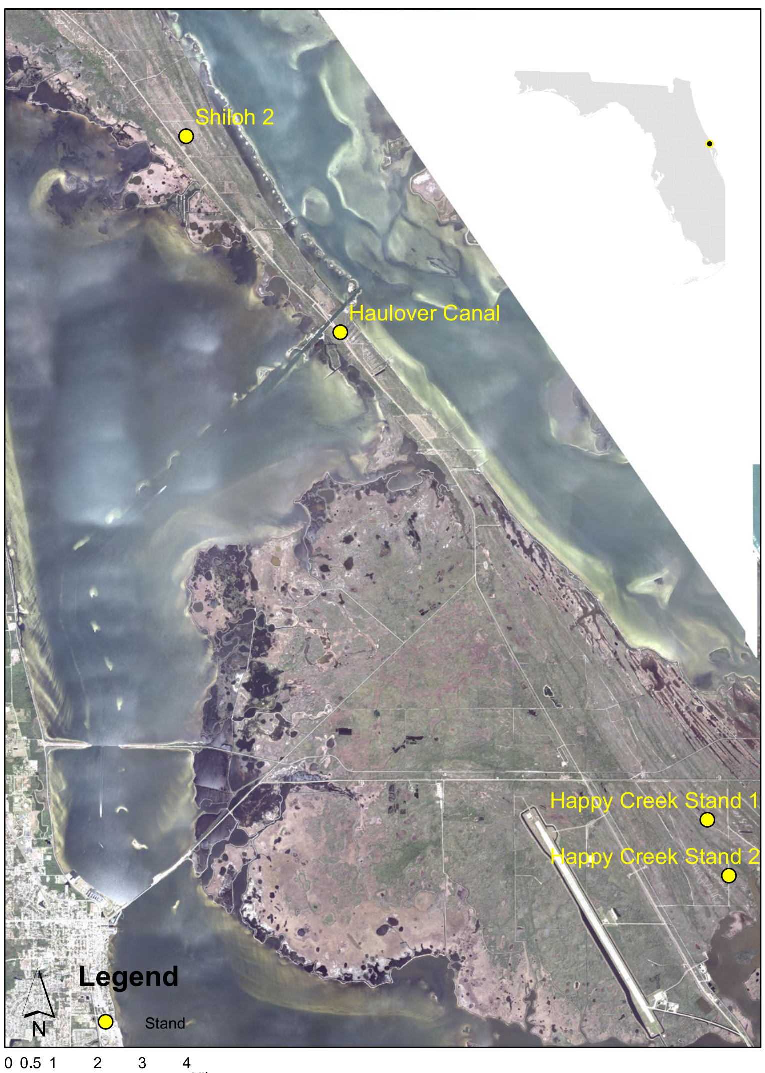

Fig. 1 Location of Happy Creek, Shiloh 2, and Haulover Canal sites on Kennedy Space Center, FL, USA

Here, we use long-term data from four scrub sites that have been burned four to five times as part of the habitat management on Kennedy Space Center/Merritt Island National Wildlife Refuge (KSC/MINWR). Fires occurred at differing return intervals, and there were some differences among sites and dominant species. These data allow comparison of responses to repeated fires under the currently prescribed fire management that includes burning for fuel reduction and managing for fire-dependent species with an overall fire return interval of 5–10 years. We address whether the growth of scrub after fire changes with increasing number of fires. Based on previous studies and observations, we expect that reestablishment of height and cover after fire will be similar after repeated fires of moderate fire return intervals. This study is unique in making these comparisons with long-term field data.

Methods

Study site

This study was conducted in the central and northern sections of KSC/MINWR located on the east coast of Central Florida (28.633333, −80.7) on the Cape Canaveral-Merritt Island barrier island complex. Specifically, we use long-term data from four sites: Happy Creek Stand 1, Happy Creek Stand 2, Shiloh 2, and Haulover Canal (Fig. 1).

The climate of KSC/MINWR is warm and humid; precipitation averages 135 cm year^{-1} (ncdc.noaa.gov/cdo-web/datasets#GSOM), but year-to-year variability is high (Mailander 1990). The wet season extends from May to October. The mean annual air temperature from 1920 to 2021 was 22.2 °C with high temperatures occurring in July (28.0 °C) and low temperatures occurring in January (15.5 °C) (ncdc.noaa.gov/cdo-web/datasets#GSOM).

Scrub vegetation occupies the well-drained ridges on the barrier island complex, pine flatwoods the more poorly drained flats, and graminoid marshes or woody swamps the lower swales (Schmalzer et al. 1999). Scrub communities on Merritt Island are primarily oak-saw palmetto scrub, a shrubland characterized by three species of oaks (Chapman oak, sand live oak, myrtle oak) along with saw palmetto and ericaceous shrubs and scrubby

Table 1 Sampling and fire history of Happy Creek Stand 1 (transects P2–P5) from 1985 through 2019, Happy Creek Stand 2 (transects P9–P12) from 1983 through 2019, Shiloh 2 (transects R53, R57, R58, and R59) from 1994 through 2019, and Haulover Canal (transects R209–R219) from 2004 through 2020, Kennedy Space Center, FL. Burn extent is the mean percent burned based on transects sampled postfire. Happy Creek Stand 1 and Stand 2 were each sampled a total of 39 times, Shiloh 2 29 times, and Haulover Canal 16 times; these totals include preburn sampling

	Happy Creek Stand 1	Happy Creek Stand 2	Shiloh 2	Haulover Canal
Preburn sampling	Jan. 1983–Jan. 1985	Jan. 1983–Jan. 1985	July 1994	
Burn 1 (extent %)	Dec. 1986 (100%)	Dec. 1986 (93.3%)	April 1995 (81.7%)	July 2004 (100%)
Sample dates (time since burn in months)	June 1987 (6)–Feb. 1997 (121)	June 1987 (6)–Jan. 1994 (84)	Oct. 1995 (6)–April 2001 (72)	Jan. 2005 (6)–Jan. 2008 (42)
Number of times sampled postburn	12	9	10	4
Burn 2 (extent %)	June 1997 (98.3%)	Nov. 1994 (35.0%)	March 2002 (72%)	May 2008 (100%)
Sample dates (time since burn in months)	Jan. 1998 (6)–May 2002 (59)	Dec. 1994 (1)–Feb. 1997 (27)	April 2002 (1)–April 2004 (25)	Jan. 2009 (8)–Jan. 2011 (32)
Number of times sampled postburn	8	3	3	3
Burn 3 (extent %)	March 2003 (75%)	June 1997 (100%)	March 2005 (87.3%)	Feb. 2011 (100%)
Sample dates (time since burn in months)	June 2003 (3)–June 2012 (110)	Jan. 1998 (6)–June 2003 (72)	April 2005 (1)–April 2008 (37)	Jan. 2012 (11)–Feb. 2017 (71)
Number of times sampled postburn	10	9	4	6
Burn 4 (extent %)	July 2012 (100%)	Marc 2004 (98.3 %)	May 2008 (88.3%)	March 2017 (100%)
Sample dates (time since burn in months)	June 2013 (11)–June 2016 (47)	June 2004 (3)–June 2008 (51)	April 2009 (11)–April 2010 (23)	Jan. 2018 (10)–Feb. 2020 (35)
Number of times sampled postburn	4	5	2	3
Burn 5 (extent %)	March 2017 (50%)	Feb. 2009 (100%)	Dec. 2010 (71.7%)	
Sample dates (time since burn in months)	June 2017 (3)–July 2019 (28)	June 2009 (4)–July 2019 (125)	April 2011 (4)–April 2019 (100)	
Number of times sampled postburn	3	11	9	

flatwoods with a similar shrub layer and scattered South Florida slash pine (*Pinus elliottii* Engelm. var. *densa* Little & K.W. Dorman) (Schmalzer and Hinkle 1992b; Schmalzer et al. 1999). Nomenclature follows Wunderlin and Hansen (2011) unless otherwise noted.

Vegetation sampling

We established and sampled line-intercept transects (15 m in length) (Mueller-Dombois and Ellenberg 1974) in each site. Cover was measured to the nearest 5 cm by species in two height strata, ≥ 0.5 m and < 0.5 m, and vegetation height was determined at four points (0, 5, 10, 15 m) along each transect. We determined the line-intercept distance burned on each transect post-fire; this is termed burn extent. Transect locations were recorded with a differentially corrected Global Positioning System (GPS).

Transects in Happy Creek Stands 1 and 2 (Fig. 1) were established in 1983 and have been sampled at least annually through 2019 (Table 1, Supplemental Tables S1 and S2). There are six transects in each of these stands, but here we use data from four transects in each stand that have burned most consistently. These transects are primarily on Pomello sand (Sandy, siliceous Oxyaquic Alorthod (Spodosol)), a moderately well to somewhat poorly drained sandy soil with a spodic (Bh) horizon at 79–157 cm (Huckle et al. 1974 and nrcs.usda.gov). Earlier publications have examined these stands as part of an age sequence (Schmalzer and Hinkle 1992b), short-term recovery from a single fire (Schmalzer and Hinkle 1992a), and recovery through 10 years from a single fire (Schmalzer 2003). Stand 1 was estimated to be 8 years postburn when established, and Stand 2 was estimated to be 4 years postburn when established (Schmalzer and Hinkle 1992b).

The Shiloh 2 site (Fig. 1) was established as part of a scrub restoration plan combining mechanical treatment and fire (Schmalzer et al. 1994). Here, we use data from four transects that have burned without mechanical treatment. We established these transects in 1994 and have sampled them at least annually through 2019 (Table 1, Supplemental Table S3). These transects are all on Paola sand (Hyperthermic, uncoated Spodic Quartzipsamment (Entisol)), an excessively drained sandy soil lacking a continuous spodic (Bh) horizon (Huckle et al. 1974 and nrcs.usda.gov).

The Haulover Canal site (Fig. 1) was established in 2004 as a burn-only comparison to nearby scrub restoration sites. We have sampled it at least annually through 2020 (Table 1, Supplemental Table S4). Transects are primarily on Cocoa sand (Siliceous, hyperthermic Psammentic Hapludalf (Alfisol)), a well-drained sandy soil underlain by coquina (Huckle et al. 1974 and nrcs.usda.gov) with one transect on Paola sand.

Fire history

Prescribed burning on KSC/MINWR is conducted by the US Fish and Wildlife Service for fuel management and for habitat management with emphasis on the restoration and management of scrub habitat for the Florida Scrub-Jay (*Aphelocoma coerulescens* Bosc, 1795) (Adrian 2006). All fires reported here were prescribed burns.

Happy Creek Stand 1 and Stand 2 have burned five times during the period of 1983–2019, but the timing of fires has differed (Table 1, Supplemental Tables S1 and S2). Fire return intervals ranged from 56 to 125 months for Stand 1 and from 31 to 94 months for Stand 2, but the short-duration fire was a partial (35%) burn (Table 1). Summary vegetation data are given in Supplemental Tables S5 and S6 (Stand 1) and Supplemental Tables S7 and S8 (Stand 2).

The Shiloh 2 stand has burned five times between 1995 and 2019, fire return intervals ranged from 31 to 83 months, and three fires occurred with return intervals of 38 months or less (Table 1, Supplemental Table S3). Summary vegetation data are given in Supplemental Tables S9 and S10. The Haulover Canal stand was 6 months postburn when established. It has burned four times between 2004 and 2020, and fire return intervals ranged from 33 to 73 months (Table 1, Supplemental Table S4). Summary vegetation data are given in Supplemental Tables S11 and S12.

Data analysis

We summarized vegetation data and used linear mixed models (IBM SPSS ver. 27, www.ibm.com) to determine effects of site, time since burn, and number of fires on response variables that included height, total cover ≥ 0.5 m, total cover < 0.5 m, bare ground, cover ≥ 0.5 m of the dominant oak (*Quercus*), and cover ≥ 0.5 m of saw palmetto. Linear mixed models account for the repeated measures structure of these data (Field 2018). Here, we specified a first order autoregressive covariance structure (AR(1)) that assumes scores become less correlated over time and heterogenous variances (Field 2018).

We conducted nonmetric multidimensional scaling (NMDS) ordination (Kruskal 1964a, b) (PCORD, ver. 7; MjM Software Design, Gleneden Beach, Oregon) of mean species cover ≥ 0.5 m of transects using the Sorenson distance measure. NMDS is considered the most generally effective method for the ordination of community data (McCune and Grace 2002). We examined relationships of sample locations on ordination axes with time since burn with Pearson correlations (IBM SPSS ver. 27).

Results

Height and cover dynamics

Height increased with time since burn across multiple fires (Fig. 2) and was best represented by a

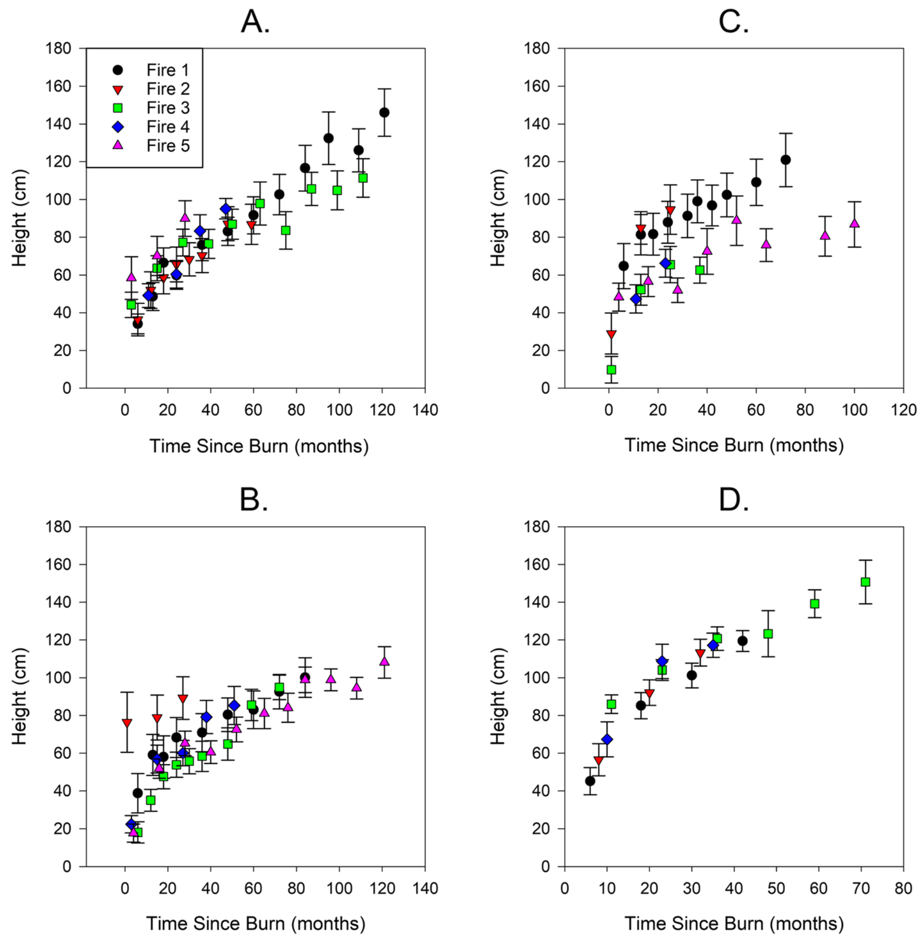

Fig. 2 Height of scrub stands through multiple fires on Kennedy Space Center, FL, USA. Transects were established beginning in 1983 and sampled through 2019–2020. The number of transects is 5 for Haulover Canal and 4 for the other sites. Data shown are means and one standard error. **A** Happy Creek Stand 1. **B** Happy Creek Stand 2. **C** Shiloh 2. **D** Haulover Canal

quadratic model with site and number of fires as significant (Table 2, Supplemental Table 13). There were differences between sites with Haulover exhibiting the greatest height and Happy Creek Stand 2 the least. The number of fires was a negative term in the model indicating a decrease in height growth by approximately 2.7 cm after each repeated fire (Fig. 2).

Total cover ≥ 0.5 m also increased with time since burn (Fig. 3) as a quadratic model with site and fire number as significant terms (Table 2, Supplemental Table 13). There were differences between sites with Haulover exhibiting the greatest cover ≥ 0.5 and Happy Creek Stand 2 the least. Repeated fires decreased total cover by 2.45% as indicated by the negative term for the number of fires (Table 2).

Total cover < 0.5 m declined with time since burn (Fig. 4); the quadratic term was not significant, but site and the number of fires were (Table 2, Supplemental Table 13). There were differences between sites with Haulover exhibiting the least cover < 0.5 and Happy Creek Stand 1 the greatest. Repeated fires increased cover < 0.5 m by 2.78% for each successive fire as indicated by its positive term in the model (Table 2). Bare ground declined with time since burn (Supplemental Fig. S1) as a quadratic model. Site differences were not significant, but the number of fires was (Table 2, Supplemental Table 13). Repeated fires increased bare ground by 0.964% for each fire, but these increases only persisted a few years (Supplemental Fig. S1).

Cover of the dominant oak ≥ 0.5 m increased with time since burn (Fig. 5) as a quadratic model with site and fire number as significant (Table 2, Supplemental Table 13). There were differences between sites with Shiloh 2 exhibiting the greatest cover of the dominant oak. Repeated fires decreased cover of the dominant oak by 2.52% for each successive fire; this included decreases in myrtle oak at Happy Creek Stands 1 and 2 and Shiloh 2 and

Table 2 Summary of linear mixed models relating response variables with site, time since burn, the quadratic term time since burn squared, and number of fires. The Shiloh site is the base for sites and is represented by the intercept. Data collected at Kennedy Space Center, FL, USA, from 1983 to 2019–2020

Response variable	Fixed effects	Estimate	Standard error	Significance
Height	Intercept	52.945	6.737	< 0.001
	Time since burn (TSB)	1.345	0.122	< 0.001
	Site = Haulover	15.297	8.805	0.099
	Site = Happy Creek 1	−8.301	8.991	0.369
	Site = Happy Creek 2	−13.808	8.975	0.143
	TSB * TSB	−0.0053	0.000904	< 0.001
	Fire number	−2.762	0.614	< 0.001
Total cover ≥ 0.5 m	Intercept	55.891	5.743	< 0.001
	Time since burn	2.096	0.122	< 0.001
	Site = Haulover	15.085	7.410	0.055
	Site = Happy Creek 1	−24.252	7.309	0.004
	Site = Happy Creek 2	−32.469	7.270	< 0.001
	TSB * TSB	−0.012	0.0011	< 0.001
	Fire number	−2.451	0.733	0.001
Total cover < 0.5 m	Intercept	33.924	2.253	< 0.001
	Time since burn	−0.378	0.033	0.06
	Site = Haulover	−8.774	2.430	0.002
	Site = Happy Creek 1	24.045	2.234	< 0.001
	Site = Happy Creek 2	11.950	2.211	< 0.001
	Fire number	2.782	0.499	< 0.001
Bare ground	Intercept	18.767	2.025	< 0.001
	Time since burn	−0.646	0.058	< 0.001
	TSB * TSB	0.0045	0.00049	< 0.001
	Fire Number	0.964	0.334	0.004
Dominant *Quercus* ≥ 0.5 m	Intercept	31.580	4.463	< 0.001
	Time since burn	0.810	0.70	<0.001
	Site = Haulover	−20.982	5.935	0.002
	Site = Happy Creek 1	−21.915	5.99	0.002
	Site = Happy Creek 2	−23.992	6.427	0.002
	TSB * TSB	−0.00457	0.00062	<0.001
	Fire number	−2.522	0.423	< 0.001
Serenoa repens ≥ 0.5 m	Intercept	8.882	3.377	0.016
	Time since burn	0.393	0.0539	< 0.001
	Site = Haulover	38.371	4.788	< 0.001
	Site = Happy Creek 1	4.846	4.570	0.304
	Site = Happy Creek 2	5.421	4.563	0.251
	TSB * TSB	−0.00206	0.000421	< 0.001

Chapman oak at Haulover Canal (Fig. 6). Saw palmetto cover ≥ 0.5 m increased with time since fire (Supplemental Fig. S2) as a quadratic model where site was significant but not the number of fires (Table 2, Supplemental Table 13). There were differences between sites with Haulover having greater saw palmetto cover than the other three sites. The increase in saw palmetto cover was similar after repeated fires (Supplemental Fig. S2).

Community dynamics

In the ordination of Happy Creek Stand 1 transects (Fig. 6), preburn samples were located to the left of the ordination. Samples taken after burning for each fire were located to the right and at subsequent times moved to the left. Transect-sample positions ($n = 146$) on the first axis were correlated to time since burn ($R_p = -0.58$, $P < 0.001$); there was no significant correlation to the second axis.

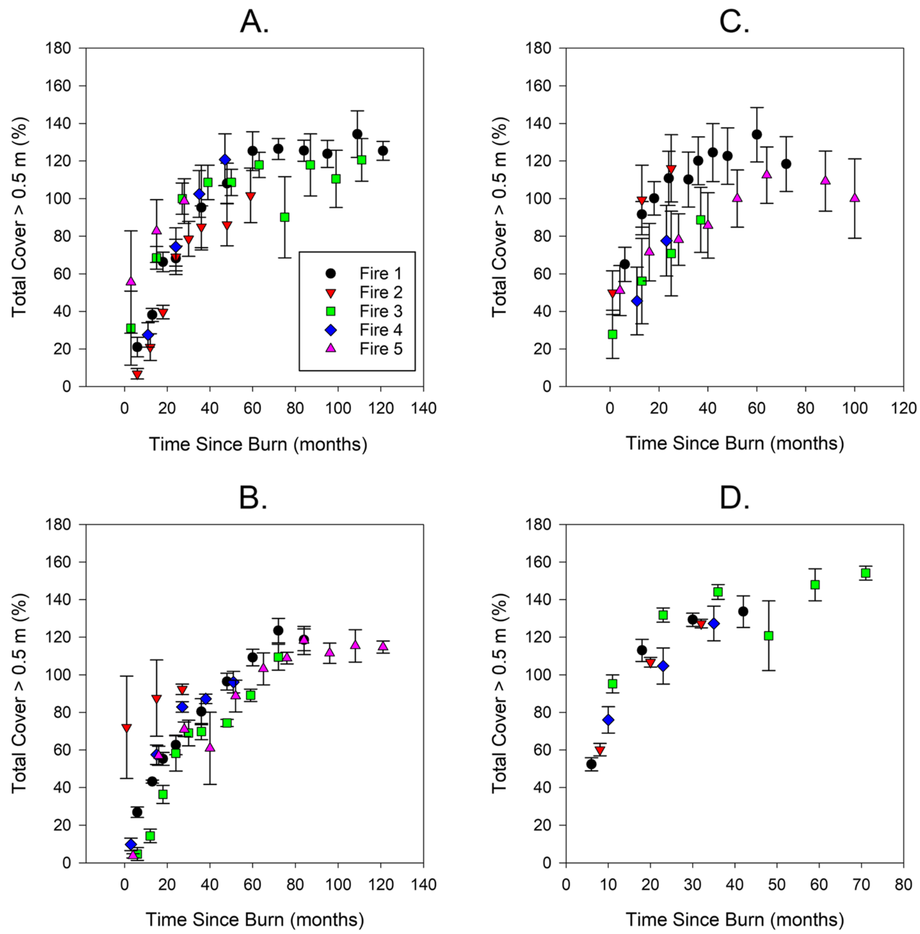

Fig. 3 Total cover ≥ 0.5 m of scrub stands through multiple fires on Kennedy Space Center, FL, USA. Transects were established beginning in 1983 and sampled through 2019–2020. The number of transects is 5 for Haulover Canal and 4 for the other sites. Data shown are means and one standard error. **A** Happy Creek Stand 1. **B** Happy Creek Stand 2. **C** Shiloh 2. **D** Haulover Canal

For the ordination of Happy Creek Stand 2 transects (Fig. 7), preburn samples were located to the lower right, while those recently postburn after each fire were to the left of the axis 1 and higher on axis 2. Transect-sample positions ($n = 146$) on the first axis were correlated positively to time since burn ($R_p = 0.51$, $P < 0.001$); on the second axis, correlations to time since burn were negative ($R_p = -0.23$, $P = 0.005$).

Preburn samples were located toward the top of the second axis in the ordination of Shiloh 2 transects, while the mostly recently burned samples were towards the bottom of this axis (Fig. 8); this was the case after each fire. Transect-sample positions on the second axis ($n = 83$) were correlated positively to time since burn ($R_p = 0.47$, $P < 0.001$); correlations on the first axis were not significant.

The initial sampling of the Haulover Canal transects was 6 months after a fire. In the ordination (Fig. 9), the most recently burned samples were to the left and those longer postburn to the right, with each fire following the same pattern. Transect-sample positions on the first axis ($n = 80$) were correlated positively to time since burn ($R_p = 0.72$, $P < 0.001$); correlations on the second and third axes were not significant.

Discussion

Scrub vegetation responded by sprouting after fire across the four sites and repeated fires. Vegetation height, cover of dominant shrubs ≥ 0.5 m, and total cover ≥ 0.5 m increased with time since burn and decreased with repeated fires. Bare ground and total cover < 0.5 m declined with time since burn but increased after repeated fires. The general pattern of revegetation after repeated fires was similar to that after a single scrub fire (Abrahamson 1984a, b; Schmalzer and Hinkle 1992a; Schmalzer 2003) and to that in other shrublands dominated by sprouting species (Bond and Midgley 2001;

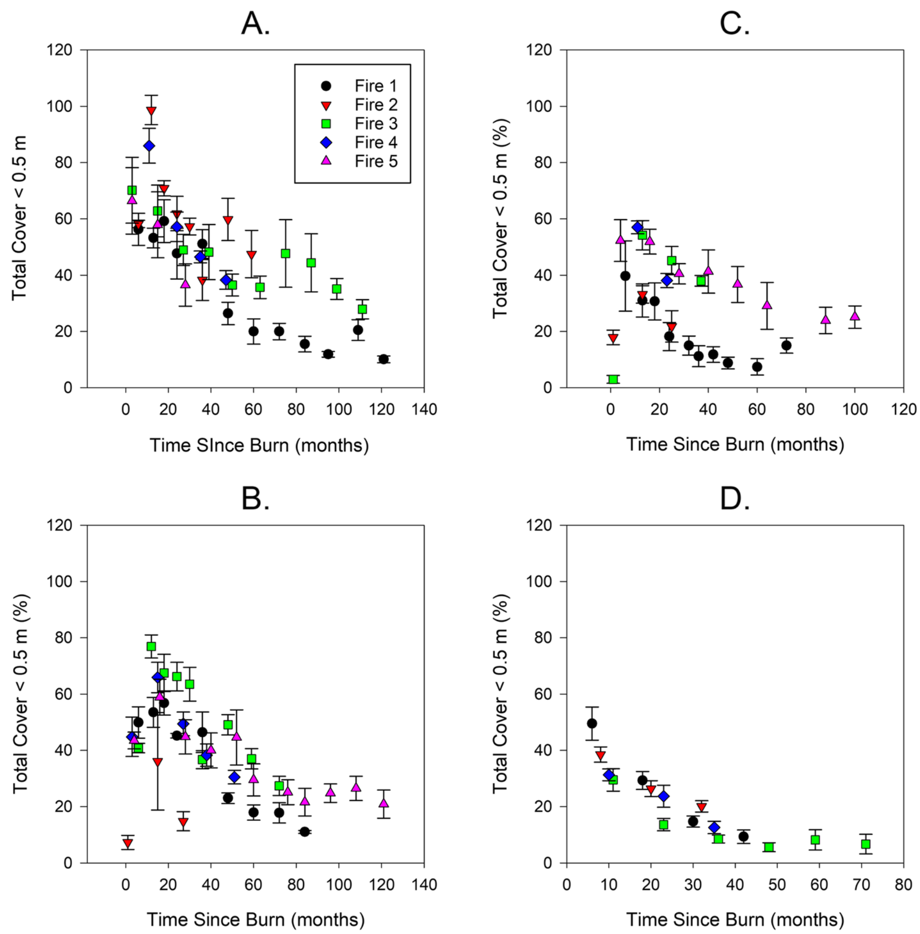

Fig. 4 Total cover < 0.5 m of scrub stands through multiple fires on Kennedy Space Center, FL, USA. Transects were established beginning in 1983 and sampled through 2019–2020. The number of transects is 5 for Haulover Canal and 4 for the other sites. Data shown are means and one standard error. **A** Happy Creek Stand 1. **B** Happy Creek Stand 2. **C** Shiloh 2. **D** Haulover Canal

Lamont et al. 2011; Clarke et al. 2013; Pausas et al. 2018). Characteristics of scrub vegetation that contribute to its ability to recover from repeated disturbance include its extensive belowground biomass with protected buds (Guerin 1993; Stover et al. 2007; Saha et al. 2010; Day et al. 2013) and clonality of its dominant species (Menges and Kohfeldt 1995; Takahashi et al. 2011).

Height and cover responses were better described by linear mixed models with a quadratic term than by linear models (Table 3). This is consistent with previous studies (Abrahamson 1984a, b; Schmalzer and Hinkle 1992b; Schmalzer 2003) that found that the rate of increase of height and cover slowed with time since burn.

Repeated fires reduced the rate of increase in height, total cover ≥ 0.5 m, and cover of the dominant oak ≥ 0.5 m and slowed the decline in total cover < 0.5 m and bare ground, but had no effect on growth of saw palmetto (Table 3). Menges et al. (2020) found that very frequent (particularly annual) fire or cutting decreased biomass and height recovery in scrub. Frequent (6-month) clipping reduced recovery of Mediterranean heathland species (Paula and Ojeda 2006). Short-interval fires (< 10 years) increased mortality but did not change growth in Australian shrublands (Enright et al. 2011). Frequent removal of aboveground vegetation could reduce rate of recovery through several mechanisms. Resprouting species mobilize stored carbohydrates for initial aboveground growth (Paula and Ojeda 2009), and frequent disturbance could reduce those reserves. In scrub, continued aboveground growth depended on new photosynthesis after fire, but roots and rhizomes were dependent longer on stored carbon, and there was a greater than 3-year lag in restoring belowground reserves (Langley et al. 2002). Non-soluble sugars and non-structural carbohydrates increased with time since fire for some scrub species including sand live oak (Olano et al. 2006). Menges et al. (2020) found a strong positive correlation

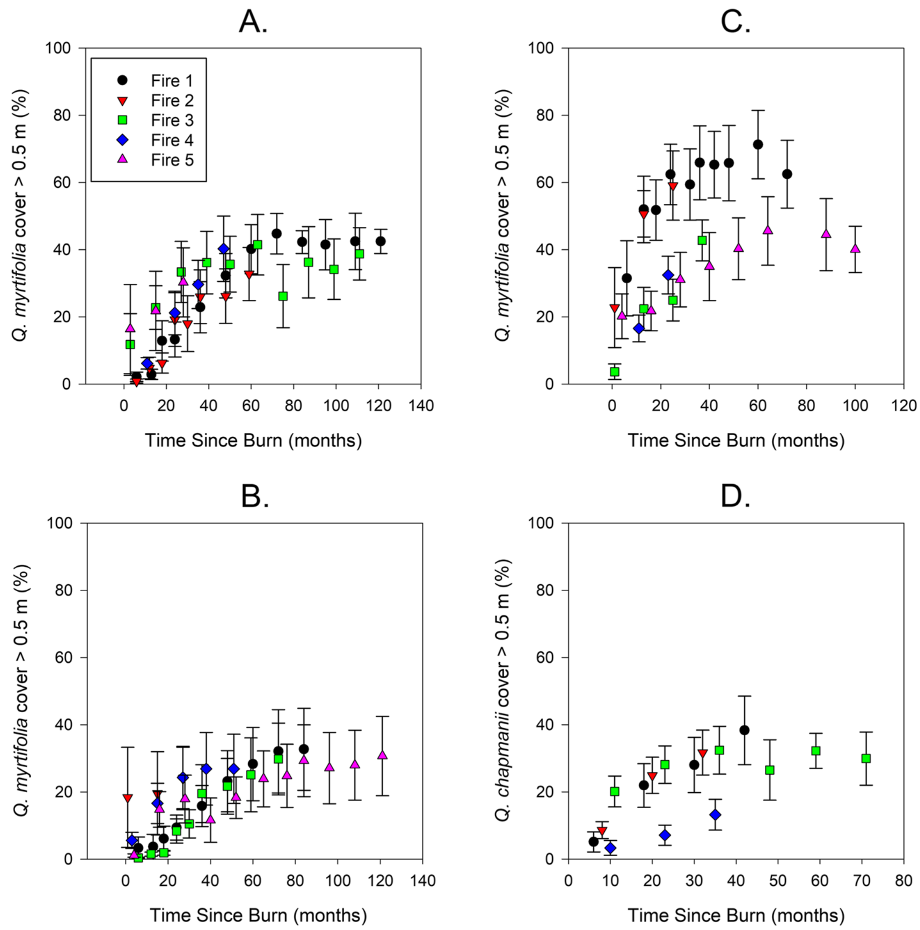

Fig. 5 Cover of dominant *Quercus* ≥ 0.5 m of scrub stands through multiple fires on Kennedy Space Center, FL, USA. Transects were established beginning in 1983 and sampled through 2019–2020. The number of transects is 5 for Haulover Canal and 4 for the other sites. Data shown are means and one standard error. **A** Happy Creek Stand 1. **B** Happy Creek Stand 2. **C** Shiloh 2. **D** Haulover Canal

between insoluble non-structural carbohydrates and biomass 6 months after treatment suggesting a role in supporting initial growth post-disturbance.

Fires may cause some mortality of buds underground or in protected structures. Menges et al. (2020) found greater densities of resprouting stems after mowing compared to burning, suggesting negative effects of burning on bud banks; however, biomass recovery was similar for most species. Resprouting in scrub is typically robust even after intense fires (Hierro and Menges 2002; Menges et al. 2021). Piled fuels that burn for extended periods and cause soil heating appear to create persisting gaps in the shrub matrix (Schmalzer and Foster 2018).

The loss of aboveground photosynthetic vegetation reduces carbohydrate supply to roots resulting in a loss of fine roots postfire, and reestablishing this fine root biomass in scrub requires about 3 years (Day et al. 2006). If disturbances occur more frequently than the recovery period, fine roots may not recover completely leading to a reduction in supply of water or mineral nutrients to aboveground vegetation. Frequent disturbance may cause a greater cumulative reduction in fine roots than do fires or cutting at longer intervals.

Scrub fires are frequently intense, volatilizing carbon and nitrogen from the system. Alexis et al. (2007) found that a prescribed scrub fire 11 years after the prior burn reduced carbon and nitrogen stocks in aboveground vegetation and litter 63.4% and 74.6%, respectively, but soil carbon and nitrogen stocks were not changed. In a prescribed fire in scrubby flatwoods, available nutrients and nitrogen mineralization rates increased immediately postfire (Dean et al. 2015), but nitrogen and phosphorus may become limiting in scrub at intermediate and longer times postfire (Schafer and Mack 2010, 2018; Hungate et al. 2013). Whether increased fire frequency in scrub could cause a cumulative reduction in nutrient stocks has not been addressed.

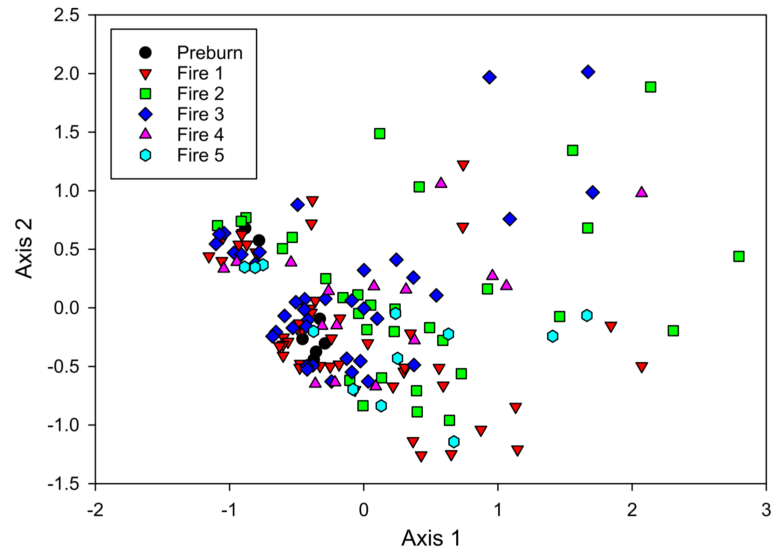

Fig. 6 Nonmetric multidimensional scaling of Happy Creek Stand 1, Kennedy Space Center, FL, USA, transects ($n = 4$) sampled preburn and repeatedly after five fires from 1983 to 2019 using mean species cover ≥ 0.5 m of 14 species present in > 1 transects-time samples. One empty sample was deleted. The final solution had 2 dimensions after 127 iterations, with a final stress of 14.01 and a final instability of less than 0.00001, and comparisons to Monte Carlo tests indicated that the reduction in stress was significant ($P = 0.02$)

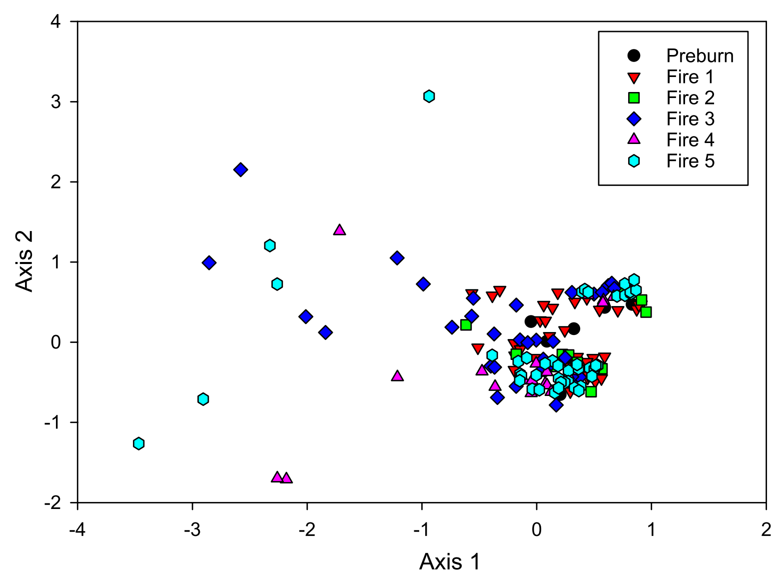

Fig. 7 Nonmetric multidimensional scaling of Happy Creek Stand 2, Kennedy Space Center, FL, USA, transects ($n = 4$) sampled preburn and repeatedly after five fires from 1983 to 2019 using mean species cover ≥ 0.5 m of 16 species present in > 1 transects-time samples. Two empty samples were deleted. The final solution had 2 dimensions after 74 iterations, with a final stress of 11.46 and a final instability of less than 0.00001, and comparisons to Monte Carlo tests indicated that the reduction in stress was significant ($P = 0.04$)

Myrtle oak was the dominant oak in three stands with Chapman oak dominant in one. Sand live oak was less abundant overall; however, it was dominant on one transect and declined in cover with repeated fires. Sand live oak is a sprouting and clonal species (Menges and Kohfeldt 1995) but appears less tolerant of repeated burning than myrtle oak or flatwoods oak species (Cavender-Bares et al. 2015). Menges et al. (2020) found that the biomass recovery of sand live oak was suppressed by frequent disturbance.

Chapman oak cover was reduced after multiple fires at the Haulover Canal site (Table 2, Fig. 6). It is

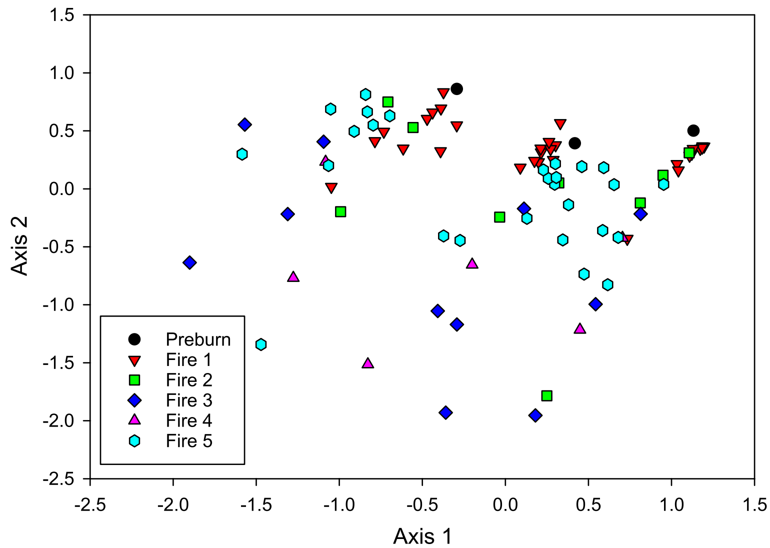

Fig. 8 Nonmetric multidimensional scaling of Shiloh 2, Kennedy Space Center, FL, USA, transects ($n = 3$) sampled repeatedly after five fires from 1994 to 2019 using mean species cover ≥ 0.5 m of 15 species present in > 1 transects-time samples. One transect with a pine overstory was excluded. One empty sample was deleted. The final solution had 2 dimensions after 66 iterations, with a final stress of 8.83 and a final instability of less than 0.00001, and comparisons to Monte Carlo tests indicated that the reduction in stress was significant ($P = 0.02$)

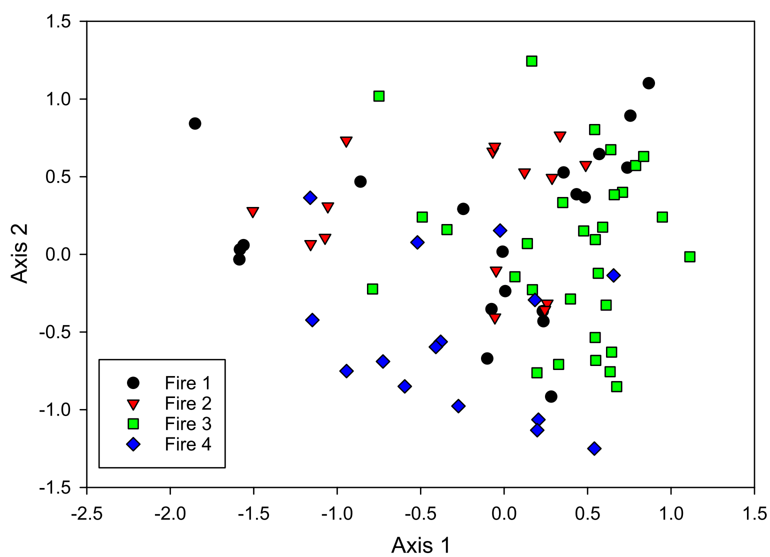

Fig. 9 Nonmetric multidimensional scaling of Haulover Canal, Kennedy Space Center, FL, USA, transects ($n = 5$) sampled repeatedly after four fires from 2004 to 2020 using mean species cover ≥ 0.5 m of 17 species present in > 1 transects-time samples. The final solution had 3 dimensions after 81 iterations, with a final stress of 12.63 and a final instability of less than 0.00001, and comparisons to Monte Carlo tests indicated that the reduction in stress was significant ($P = 0.02$)

a rhizomatous, clonal species that resprouts after fire (Menges and Kohfeldt 1995). On KSC/MINWR, it is typically less abundant than myrtle oak or sand live oak (Schmalzer and Hinkle 1992b; Schmalzer and Foster 2020). On the southern Lake Wales Ridge, Chapman oak is most abundant in scrubby flatwoods and in the scrub hickory phase of southern ridge sandhill vegetation but only dominant in occasional patches (Abrahamson et al. 1984). The reduction in cover of Chapman oak at the Haulover Canal site was not matched by a decline in increase of height or total cover ≥ 0.5 m as there was an increase in co-occurring species, saw palmetto and wax myrtle.

Table 3 Summary of effects from linear mixed models relating response variables with site, time since burn, the quadratic term time since burn squared, and number of fires. Dominant species of *Quercus* is *Q. myrtifolia* except for Haulover Canal where it is *Q. chapmanii*. Positive response is indicated by + and negative response by −. *NS* not significant. Data collected at Kennedy Space Center, FL, USA, from 1983 to 2019-2020

Response variable	Site	Time since burn (TSB)	TSB * TSB (quadratic term)	Number of fires
Height	+	+	−	−
Total cover ≥ 0.5 m	+	+	−	−
Total cover < 0.5 m	+	−	NS	+
Bare ground	NS	−	+	+
Cover of dominant *Quercus* ≥ 0.5 m	+	+	−	−
Cover of *Serenoa repens* ≥ 0.5 m	+	+	−	NS

The three co-occurring scrub oaks belong to different subgenera of *Quercus*; Chapman oak is a white oak (*Quercus* section *Quercus*), sand live oak is a live oak (*Quercus* section *Quercus* subsection *Virentes*), and *myrtle oak* is a red oak (*Quercus* section *Lobatae*) (Nixon et al. 1997). These species co-occur in our sites and elsewhere in Florida (Cavender-Bares et al. 2004a). Cavender-Bares et al. (2004b) found that Florida plant communities were more likely to contain members of different oak clades than only members of one clade (i.e., phylogenetic overdispersion).

Cover of saw palmetto was not reduced after multiple fires (Table 3). Saw palmetto is known as a very fire-tolerant species that resprouts and grows rapidly after fire, generally more rapidly than the scrub oaks (Abrahamson 1984b; Schmalzer and Hinkle 1992a; Abrahamson and Abrahamson 2006; Maguire and Menges 2011; Menges et al. 2020).

Cover < 0.5 m increased immediately after fire and then declined across sites and repeated fires; this is the same pattern seen after single fires in this system (Schmalzer and Hinkle 1992a; Schmalzer 2003). Cover < 0.5 m is expected to decline as species grow into the ≥ 0.5-m strata and shading increases. As repeated fires slowed height growth and increase of cover ≥ 0.5 m, cover < 0.5 m declined more slowly.

Bare ground declined rapidly across sites; repeated fires increased bare ground, but this increase did not persist after about 24 months postburn. 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). Gaps in the more xeric Florida rosemary scrub may persist for long periods after fire (Hawkes and Menges 1996; Menges et al. 2008; Menges et al. 2017). In contrast, gaps in oak-saw palmetto scrub or scrubby flatwoods close more rapidly after fire (Abrahamson 1984a; Schmalzer and Hinkle 1992a; Young and Menges 1999; Schmalzer 2003; Dee and Menges 2014). However, burning piled fuels produced gaps in oak-saw palmetto scrub that persisted for > 10 years (Schmalzer and Foster 2018).

Ordination analyses indicated movement toward composition similar to preburn in the three sites with preburn data and a similar pattern in the Haulover Canal site where sampling began at 6 months postfire. Trajectories of recovery were similar, and repeated fires did not shift overall community composition to any major degree. There are compositional and environmental gradients within scrub sites that relate to depth to water table (Abrahamson et al. 1984; Schmalzer and Hinkle 1992b; Boughton et al. 2006), soil differences (Menges et al. 2007; Schmalzer and Foster 2020), and other factors, but time since fire is a major factor here and in other scrub sites (Menges et al. 1993; Abrahamson et al. 2021).

Conclusions

Our data indicated that scrub vegetation recovers from repeated fires that occurred at a range of recurrence intervals and different times of the year. Repeated fires particularly at short return intervals reduced height and cover ≥ 0.5 m similar to the results of Menges et al. (2020). Although all scrub oaks are resprouting, clonal species, their growth can be slowed by repeated frequent fire. Saw palmetto tolerates a range of fire return intervals. As natural fire regimes in scrub landscapes varied in time and space (Duncan et al. 2010, 2011), such differences may contribute to the coexistence of these species (Menges 2007).

Management implications

Management of scrub vegetation often focuses on maintaining habitat conditions for threatened and endangered fauna, including the Florida scrub jay (Breininger et al. 2014), and for rare scrub flora (Menges 2007). Fire frequency and return interval can be varied to modify height and cover so that they fall within the requirements of habitat-specific species while not exceeding the tolerances of the dominant scrub species. Resprouting scrub species recover from fires of varying intensities and residence times common to prescribed fires (Menges et al. 2021) as well as varying frequencies. Climate change in the Southeast is expected to increase fire frequencies through higher temperatures, increased variability in precipitation, increased evapotranspiration, and a longer dry season (Bedel et al. 2013; Mitchell et al. 2014; Prestemon et al. 2016; Fill et al. 2019). Drought, particularly in spring, reduces growth of scrub oaks (Foster et al. 2014, 2015). The projected changes do not appear likely to exceed the ability of the dominant scrub species to persist although some shifts in abundance may occur. Maintaining populations of rare, fire-dependent fauna and flora remains challenging (Cox et al. 2020) in requiring suitable conditions at landscape scales (Breininger et al. 2014; Kelly et al. 2018; Quintana-Ascencio et al. 2018; Mason and Lashley 2021). Integrating management and monitoring in an adaptive management framework (e.g., Eaton et al. 2021) will be increasingly important.

Abbreviations

GPS: Global Positioning System; KSC/MINWR: Kennedy Space Center/Merritt Island National Wildlife Refuge; NMDS: Nonmetric multidimensional scaling; TSB: Time since burn.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-022-00140-9.

Additional file 1: Table S1. Sampling and fire history of Happy Creek Stand 1, Kennedy Space Center, Florida USA (Transects P2-P5) from 1983 through 2019. **Table S2**. Sampling and fire history of Happy Creek Stand 2, Kennedy Space Center, Florida USA (Transects P9-P12) from 1983 through 2019. **Table S3**. Sampling and fire history the Shiloh 2 stand, Kennedy Space Center, Florida USA (Transects R53, R57, R58, R59) from 1994 through 2019. **Table S4**. Sampling and fire history of the Haulover Canal stand, Kennedy Space Center, Florida USA (Transects R209 – R213) from 2004 through 2020. **Table S5**. Mean species cover ≥ 0.5 m in repeatedly burned transects of the Happy Creek Stand 1, Kennedy Space Center, Florida, USA study site ($n = 4$). **Table S6**. Mean species cover < 0.5 m in repeatedly burned transects of the Happy Creek Stand 1, Kennedy Space Center, Florida, USA study site ($n = 4$). **Table S7**. Mean species cover ≥ 0.5 m in repeatedly burned transects of the Happy Creek Stand 2, Kennedy Space Center, Florida, USA study site ($n = 4$). **Table S8**. Mean species cover < 0.5 m in repeatedly burned transects of the Happy Creek Stand 2, Kennedy Space Center, Florida, USA study site ($n = 4$). **Table S9**. Mean species cover ≥ 0.5 m (%) in repeatedly burned transects of the Shiloh 2, Kennedy Space Center, Florida, USA study site ($n = 4$). **Table S10**. Mean species cover < 0.5 m (%) in repeatedly burned transects of the Shiloh 2, Kennedy Space Center, Florida, USA study site ($n = 4$). **Table S11**. Mean species cover (%) ≥ 0.5 m in repeatedly burned transects of the Haulover Canal, Kennedy Space Center, Florida, USA study site ($n = 5$). **Table S12**. Mean species cover (%) < 0.5 m in repeatedly burned transects of the Haulover Canal, Kennedy Space Center, Florida, USA study site ($n = 5$). **Table S13**. Model selection of linear mixed models for height, total cover ≥ 0.5 m, total cover < 0.5 m, bare ground, cover of the dominant oak ≥ 0.5 m, and cover of *Serenoa repens* ≥ 0.5 m with time since burn (TSB, months) and number of fires (NFires) for all sites.

Additional file 2: Fig. S1. Bare ground of scrub stands through multiple fire on Kennedy Space Center, Florida, USA. Transects were established beginning in 1983 and sampled through 2019-2020. Number of transects is 5 for Haulover Canal and 4 for the other sites. Data shown are means and one standard error. A. Happy Creek Stand 1. B. Happy Creek Stand 2. C. Shiloh 2. D. Haulover Canal.

Additional file 3: Fig. S2. Cover of *Serenoa repens* ≥ 0.5 m of scrub stands through multiple fire on Kennedy Space Center, Florida, USA. Transects were established beginning in 1983 and sampled through 2019-2020. Number of transects is 5 for Haulover Canal and 4 for the other sites. Data shown are means and one standard error. A. Happy Creek Stand 1. B. Happy Creek Stand 2. C. Shiloh 2. D. Haulover Canal.

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Authors' contributions

PAS initiated the study. PAS and TEF collected and analyzed the data. PAS drafted the manuscript with input from TEF. Both authors edited and revised the manuscript and approved the final version.

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Availability of data and materials

Summary data are provided in the Supplemental Information. Original data are NASA property and may be obtained through a Freedom of Information Act request as detailed at https://www.nasa.gov/centers/kennedy/about/foia/guide.html#.YHnPDx1KhPY.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interests.

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