Responses of the Clonal Florida Endemic Shrub Polygonella myriophylla to Fire and Mechanical Disturbance

Author(s): Kristina D. Horn, Eric S. Menges, and Pedro F. Quintana-Ascencio

Source: The American Midland Naturalist, 180(2):175-188.
Published By: University of Notre Dame
https://doi.org/10.1674/0003-0031-180.2.175
URL: http://www.bioone.org/doi/full/10.1674/0003-0031-180.2.175

Am. Midl. Nat. (2018) 180:175–188

Responses of the Clonal Florida Endemic Shrub Polygonella myriophylla to Fire and Mechanical Disturbance

KRISTINA D. HORN[1]
Department of Biology, University of Central Florida, Orlando, 32611

ERIC S. MENGES
Plant Ecology Program, Archbold Biological Station, Venus, Florida, 33862

AND

PEDRO F. QUINTANA-ASCENCIO[2]
Department of Biology, University of Central Florida, Orlando, 32611

Plant Ecology Program, Archbold Biological Station, Venus, Florida, 33862

ABSTRACT.—There is an unsettled debate on the benefits of mechanical disturbance for native species in fire-prone habitats. We compared the demographic effects of fire and mechanical treatments (Gyro-tracing) on *Polygonella myriophylla,* a prostrate clonal shrub listed as endangered and narrowly endemic to pyrogenic scrub ecosystems in south-central Florida. This species is commonly found in gaps within a matrix dominated by resprouting shrubs, but also occurs under other shrubs and along the shoulders of adjacent road-side habitats. We designed and executed a replicated (that plots per treatment, 1 ha per plot; total 147 initial plants) experiment including plots burned, mechanically chopped, with both treatments and without treatments at the Lake Wales Ridge Wildlife and Environmental Area - Carter Creek in Highlands County, central Florida (2005-2008; treated in summer of 2005). Cumulative mortality of standing *P. myriophylla* after 3 y was higher in burned plots (> 80%) than in chopped-only and untreated plots (~ 50 % and ~ 40 % respectively). Post disturbance growth in canopy area among the surviving plants was consistently higher in mechanically disturbed plots compared to untreated plots and intermediate burned conditions. We found three putative seedlings, accounting for less than 3% of the initial genets, before treatment application, but many seedlings after treatments. Seedling recruitment (~ 90) post-treatment was higher in disturbed plots, highest when both treatments occurred together, and almost null in untreated plots. Recruitment was highest in the first-year post disturbance (70%), decreasing in subsequent years. Disturbances may improve the persistence of *P. myriophylla* by increasing recruitment and individual growth, however; fire and mechanical disturbance should be used with caution for this species given many plants died during treatment.

INTRODUCTION

Fire is a widespread disturbance worldwide, and many species are likely adapted to this disturbance (Bond and Keeley, 2005; Pausas and Keeley, 2009). Lighting ignitions and human-caused fires are regular disturbances in vast regions of the world. Fires have strong effects on composition and structural attributes of many ecosystems (*e.g.*, Lehmann *et al.*, 2014; Pausas and Dantas, 2017) and are essential to maintain viable populations of many species (Bonebrake *et al.*, 2014; Bowles *et al.*, 2015). Prescribed fire is also a tool for

[1] Current address: Hoover Middle School, Indialantic, Florida 32903
[2] Corresponding author: e-mail: pedro.quintana-ascencio@ucf.edu

decreasing fuel loadings (Fernandes and Botelho, 2003) and to improve forage quality (Augustine *et al.*, 2010). Notwithstanding the benefits of fire, there is pressure to reduce fire risks associated with escaped fires and smoke, particularly in areas encroached by human sprawl (Agee and Skinner, 2005; Menges and Gordon, 2010). Fire suppression creates higher risks and complicates future management. Because of growing concerns on risks associated with fire, such as smoke exposure and property damage, managers are increasingly applying alternatives or pretreatments to fire (Schwilk *et al.*, 2009; Menges and Gordon, 2010).

Roller-chopping, mowing, logging, and herbicide applications are now extensively used by land managers, particularly to reduce fuel loads and the impact of wildfires (Menges and Gordon, 2010). However, these mechanical treatments may not necessarily benefit ecosystems (Reinhardt *et al.,* 2008). Mechanical treatments and herbicides work best in combinations with fire but can have many potential detrimental effects (Schwilk *et al.*, 2009; Stephens *et al.*, 2009). Prefire mechanical treatments can more effectively consume fuels, but they change fire intensities, alter habitat heterogeneity, and may increase soil compaction (Busse *et al.*, 2005; Rickey *et al.*, 2007). Mechanical disturbance is associated with higher nonnative invasions in the western U.S. (Keeley, 2001). Additional unintended negative effects include alteration of carbon, nutrient, and microbial dynamics (Gundale *et al.*, 2005; Giai and Boerner, 2007; Boerner *et al.,* 2008) and failure to provide direct fire germination cues such as heat or smoke (*e.g.*, Rokich and Dixon, 2007; Lindon and Menges, 2008; Reyes and Trabaud, 2009).

Fire is an important disturbance agent in the southeastern United States (Noss, 2013), especially in Florida (Platt *et al.*, 1988; Menges *et al.,* 2007), affecting vegetation dynamics (Duncan *et al.*, 1999; Ruth *et al.,* 2007) and the demography of many Florida endemics (Breininger and Schmalzer, 1990; Menges and Hawkes, 1998; Slapcinsky *et al.*, 2009). In contrast with scrub oaks and palms, which survive fire, plants killed by fire depend on seed recruitment after fire for population persistence (Menges and Kohfeldt, 1995; Weekley and Menges, 2003). For these obligate seeders, the duration of fire return intervals can determine the viability of populations due to the strong dependence of seedling establishment on open spaces created by fire (*e.g.;* Quintana-Ascencio and Morales-Hernandez, 1997; Menges and Quintana-Ascencio, 2004). Mechanical treatments are currently being tested as surrogates for fire in managing ecosystems in the southeastern United States, including Florida scrub (Menges and Gordon, 2010). However, limited data are available on how native species are affected by fire or mechanical disturbance.

Here, we present the results of an experiment evaluating these effects on a Florida scrub endemic plant. Sandlace, *Polygonella myriophylla* (Small) Horton (Polygonaceae), is a clonal, hermaphroditic, perennial shrub, listed as endangered, and narrowly endemic to pyrogenic Florida scrub ecosystems of the Lake Wales Ridge (USFWS, 1993; Chafin, 2000). Although numerous studies have shown the importance of fire to Florida scrub plants (*e.g.*, Menges and N. Kohfeldt, 1995), none of these species has the prostrate woody growth form as *P. myriophylla.*

Fire effects on clonal plants differ from those seen on nonclonal species. Clonal plants will resprout after fire (Menges and Kohfeldt, 1995), affecting the numbers and sizes of resulting ramets. For example fires at certain seasons may dramatically increase shoot densities (Brewer and Platt, 1994; Cirne and Scarano, 2001). Post-fire clones can have larger numbers of smaller ramets, with no reductions in seed production (Hartnett, 1987). It has also been shown that post-fire clones can have size-independent growth for a time, shifting later to size-dependent growth as clones grew (Cirne and Scarano, 2001). Fires, more than windstorms, accelerated post-disturbance ramet population growth rates in a bamboo species (Gagnon and Platt, 2008).

We predict because *P. myriophylla* is a prostrate shrub, it may be less affected by gyro-tracing (chopping), a common method to remove vegetation, than by fire. We also expect this species to show different responses than many other co- occurring species. Although fire is expected to kill some existing plants, we hypothesize the post-disturbance survival, growth, and recruitment of *P. myriophylla* to increase in response to both fire and mechanical disturbance, likely due to reduction in competition with other shrubs and release of nutrients and space.

Habitat loss and alteration threaten the persistence of scrub species such as *P. myriophylla*. Between 1945 and 1990, approximately 83% of the native scrub habitat in the Lake Wales Ridge in Central Florida was lost to agricultural, commercial, or residential development, resulting in a fragmented scrub archipelago (Turner *et al.*, 2006; Weekley *et al.,* 2008a). In 1988 *P. myriophylla* was found in Orange, Polk, Highlands, and Osceola Counties in 118 scrub sites covering approximately 10,000 ha and protected in eight sites covering less than 300 ha (Christman, 1988). More recently, the loss of habitat due to development has continued, although more areas are now protected. By 2005 *P. myriophylla* presence was reduced to 96 scrub sites, only 40 of them protected (Christman, 2006). Better understanding of the management needs for this endemic species will be critical for its persistence in the remnant scrub.

METHODS

STUDY COMMUNITY AND SPECIES

The Lake Wales Ridge is a 160 km long, 30 km wide sandy upland situated within Polk, Orange, Highlands, and Osceola counties in south-central Florida (Weekley *et al.*, 2008b). Florida scrub is a subtropical shrubland dominated by scrub oaks (*Quercus spp.*) and palmettos (*Serenoa repens, Sabal etonia*), often with ericads, pines, grasses, and other shrubs such as Florida rosemary (*Ceratiola ericoides*) (Abrahamson *et al.*, 1984; Menges, 1999). Rosemary-dominated scrub occurs characterized by open gaps usually covering 10-40% of the ground area (Menges and Hawkes, 1998). These gaps are rich in endemic plant species (Menges *et al.,* 2008, 2017). Patches of rosemary scrub often function as islands, with some species showing metapopulation dynamics (Miller *et al.*, 2012). The fire regime of Florida scrub includes high intensity crown fires moving through shrub canopies, historically ignited by lightning fires occurring during the growing season, especially in late spring. Fires can be patchy, especially in rosemary scrub. Unlike co- occurring shrubs which are strong resprouters (Maguire and Menges, 2011; Schafer and Mack, 2014), Florida rosemary is killed by fire and recovers by recruiting from a soil seedbank (Johnson, 1982). Because Florida rosemary seedlings grow more slowly than the resprouting shrubs, gaps often persist in rosemary scrub for several years following fire. The fire return interval for rosemary scrub is longer (15-25 y) than fire return intervals for scrub dominated by resprouting shrubs (Menges *et al.*, 2017). Florida rosemary produces allelochemicals (Williamson *et al.*, 1992) that suppress seed germination of co- occurring plants (Hunter and Menges, 2002; Hewitt and Menges, 2008). However, after fires that remove Florida rosemary, many species will recruit seedlings (Menges and Quintana-Ascencio, 2004).

Polygonella myriophylla is found on both white and yellow sands and in a variety of Florida scrub types (Menges *et al.,* 2008). It also prospers along some roadsides where periodic

TABLE 1.—Number of *P. myriophylla* subplots per macroplot, initial genets and ramets per macroplot (summed over *P. myriophylla* subplots), percent ramets alive in July 2006 a year after treatment, and number of seedlings per macroplot pretreatment (in 2005), and 1, 2 and 3 y after treatment

Treatment	Sub-Plots	Genets In 2005	Ramets In 2005	% alive post treatment	Seedlings 2005	2006	2007	2008	Total seedlings
Untreated	12	15	197	72.6	0	0	0	0	0
Untreated	12	22	221	73.3	0	0	1	0	1
Chop only	12	21	217	63.6	0	11	0	0	11
Chop only	12	21	326	52.1	0	16	5	0	21
Burn only	11	19	156	16.7	0	2	7	0	9
Burn only	10	15	338	13.0	0	0	1	0	1
Chop&Burn	10	14	189	0	0	28	3	0	31
Chop&Burn	11	20	243	18.5	0	4	8	2	14
					0	61	25	2	88

mowing eliminates taller shrubs. Our study sites at Lake Wales Ridge National Wildlife Refuge Carter Creek (27°32′10″N, 81°24′5″W), were on white sands (Archbold and Satellite soils) supporting a mixture of rosemary scrub and oak-dominated scrub. Eight listed plant species were found in our plots (Weekley *et al.*, 2008a). Although we do not have exact information on the fire history at the start of the study, the sites appeared to have last burned 20-30 y ago.

FIELD METHODS

In January 2005, using ArcView, we randomly selected eight macroplots at Lake Wales Ridge National Wildlife Refuge Carter Creek. The macroplot criteria were: (1) edge >10 m from any road; (2) 1 ha in size; (3) dominated by oak-rosemary scrub; (4) *Polygonella myriophylla* present through the macroplot; and (4) largely undisturbed by trails. We intended to have 12 random circular vegetation subplots and 12 *P. myriophylla* subplots within each macroplot. Vegetation subplot centers were at least 10 m apart, 5 m from the macroplot border, and 4 m in diameter. Plot criteria were that vegetation subplots were not on a trail and should not have a downed tree covering more than 50% of the subplot. Vegetation subplots were marked with a short aluminum stake with a tag wired on. Tag numbers indicate the management unit and the plot number. To characterize the vegetation and ground cover in each plot, we recorded number of independent clumps/stems for each shrub species present within each vegetation subplot and the proportion of bare sand and litter cover estimated as increments of 10 (anything less than 5% was recorded as 1%, trace). Vegetation nomenclature followed Wunderlin and Hansen (2011).

Polygonella myriophylla subplots were located using random directions starting from the center of the vegetation plots and no farther than 5 m from their border. Polygonella subplots could be contiguous but always nonoverlapping with the vegetation plots (even if these contained *P. myriophylla*). In many cases several random directions were selected before one plant of this species was found. If no *P. myriophylla* plant was found within this neighborhood the subplot was not included. We located 96 *P. myriophylla* subplots within all macroplots, 10-12 subplots per vegetation plot (Table 1). *Polygonella myriophylla* subplots were marked with rebar and a blue flag with a tag. In March 2005 we located and marked with a flag and an aluminum tag every *P. myriophylla* putative plant (thereafter genet) with rooted branches (thereafter ramet) lying inside each plot. Due to the clonal nature of *P. myriophylla,* it was not feasible to define independent plants without genetic information. There is evidence of groups of intermingling ramets of this species with mixed genetic identity (Metzger, 2010). We used an operational criterion of $>$ 30 cm distance between ramets to categorize putative independent genets. To evaluate changes in growth, survival, and recruitment associated with the disturbance treatments, we collected data on number of ramets, and putative genets, canopy area, mortality and recruitment of *P. myriophylla* within these subplots. We recorded the length and perpendicular width for every genet (including canopy outside the plot) and measured with calipers the diameter of the main axis (the thickest visible branch) and all rooted ramets $>$0.3 cm inside the plot. Ramet diameter measurements were taken at the point where the ramet met the ground. A colored wire was loosely attached at this point for identification purposes. Some ramets rooted multiple times. We measured and marked every rooting location independently.

Mechanical treatments (gyro-tracing [chopping], Gyro-Trac Co.) were applied in July 2005, followed by prescribed burns in August and September 2005, all accomplished by staff from the Florida Fish and Wildlife Conservation Commission. Two plots were untreated, two plots were prescribed burned, two plots were roller chopped and burned, and two plots only roller chopped (Table 1). We revisited every plot in September 2005 to relocate and reflag every plot. Plots were revisited in July 2006, July 2007, and May 2008, when we recorded *P. myriophylla* survival and took the same measurements as in the pretreatment visit. We also searched for *P. myriophylla* seedlings in each plot and measured and marked them.

STATISTICAL ANALYSES

We evaluated the heterogeneity in the abundance of shrub species among macroplots prior to the application of the different management treatments (using the R library vegan; Oksanen *et al.,* 2018). We used linear mixed models (using the R library lme4; Bates *et al.*, 2015) to account for the hierarchical nature of data within plots (random effect of subplots within macroplots and macroplots within treatments) and evaluate percent ground cover of litter and bare sand as a function of management and subplot type (vegetation or *P. myriophylla*). We also used generalized mixed models (using the R library lme4 Bates *et al.*, 2015) to evaluate genet survival and individual plant growth by the end of the study as a function of treatment and initial plant canopy area (with random effects of macroplot within treatment). Binomial distribution and logit link was used for survival and normal errors and identity link for change in plant size. A generalized linear model with logarithm link and negative binomial distribution was used to assess number of seedlings recruited among treatments. Counts were pooled within treatments.

RESULTS

Prior to the application of the treatments, we found 14 species of shrubs within our study plots (Table 2). The palms *Serenoa repens* and *Sabal etonia,* and the oaks *Quercus inopina* and *Q. myrtifolia* were the most abundant. Only 2.93 % of all randomly chosen vegetation subplots were occupied by *Polygonella myriophylla.* Prior to the treatments, there was significant heterogeneity in the abundance of several shrub species and on the shrub composition within macroplots with different treatments (Table 2; Permanova $MS_3 = 0.69$, $Residual_{86} = 0.22$, $F = 3.05$, $P = 0.01$, $r^2 = 0.09$). Pretreatment ground cover, as defined by

TABLE 2.—Average number of stems per shrub species as function of treatment allocation over vegetation subplots per macroplot prior to the application of the treatment. The statistical significance of the contrasts with the untreated treatment are indicated. Those contrasts with significantly different numbers between treated (b = burn, ch = chopped, ch&b = chopped and burned) and untreated (c) are in bold. β_0 = model intercept. NA = species with too small sample sizes. $\bar{x}$ = mean number of stems

						P *(contrast)*			
	untreated	burn	chop	ch & bu	$\bar{x}$	β_0	c-b	c-ch	c-ch&b
Serenoa repens	3.09	2.54	3.68	2.00	2.83	0.000	0.494	0.471	0.180
Quercus inopina	0.50	4.04	2.14	0.65	1.83	0.645	**0.020**	0.288	0.920
Sabal etonia	2.23	0.25	1.18	1.61	1.32	0.000	**0.004**	0.131	0.364
Quecus myrtifolia	0.45	0.96	0.41	0.65	0.62	0.055	0.124	0.891	0.548
Quercus geminata	0.27	0.00	0.82	0.30	0.35	0.071	0.190	**0.011**	0.880
Lyonia ferruginia	0.45	0.12	0.55	0.04	0.29	0.000	**0.018**	0.515	**0.004**
Ceratiola ericoides	0.00	0.50	0.09	0.57	0.29	NA	NA	NA	NA
Garberia heterophylla	0.14	0.12	0.09	0.39	0.19	NA	NA	NA	NA
Persea humilis	0.05	0.08	0.14	0.04	0.08	NA	NA	NA	NA
Asimina reticulata	0.05	0.04	0.05	0.04	0.05	NA	NA	NA	NA
Calamintha ashei	0.00	0.00	0.00	0.17	0.04	NA	NA	NA	NA
Opuntia humifusa	0.05	0.04	0.00	0.00	0.02	NA	NA	NA	NA
Ilex opaca	0.00	0.04	0.00	0.00	0.01	NA	NA	NA	NA
Polygonella myriophylla	0.00	0.04	0.00	0.00	0.01	NA	NA	NA	NA

proportion of bare sand and litter cover, was also heterogeneous among treatments and between vegetation subplots randomly chosen and those occupied by *P. myriophylla* (Table 3, Fig. 1). Subplot bare sand cover prior to the treatment was higher in untreated plots and varied 5-40 % among macroplots. Pretreatment ground litter cover was > 70% in random vegetation subplots but only 40 - 60 % in subplots with *P. myriophylla.*

There was no evidence of significant differences before disturbances among treatment plots in number of *P. myriophylla* genets (overall mean: 18.4 + 0.4 SE; P = 0.67), average genet canopy cover (P = 0.47), and number of ramets (235.9 + 8.1 SE; P = 0.84). After application, fire and mechanical disturbance killed many standing *P. myriophylla* (Tables 4, 5). Mortality after 4 y was highest in burned plots (> 80%), lowest in untreated plots (>40 %), and

TABLE 3.—Analysis of pretreated ground cover (litter and bare sand) at vegetation subplots within macroplots with different management

Variable		Litter			Bare sand	
Random effects		Std.Dev.			Std.Dev.	
Subplot /macroplot		0.83			1.30	
Macroplot		0.0001			0.23	
Fixed effects	Estimate	SE	P	Estimate	SE	P
Intercept	2.18	0.17	<0.001	-0.57	0.31	0.07
Chop	-1.26	0.24	<0.001	-0.78	0.38	0.04
Burn	-0.59	0.24	0.01	-1.54	0.38	<0.001
Chop & Burn	-0.60	0.24	0.01	-2.22	0.39	<0.001
Presence of *P. myriophylla*	-1.02	0.03	<0.001	-0.44	0.06	<0.001

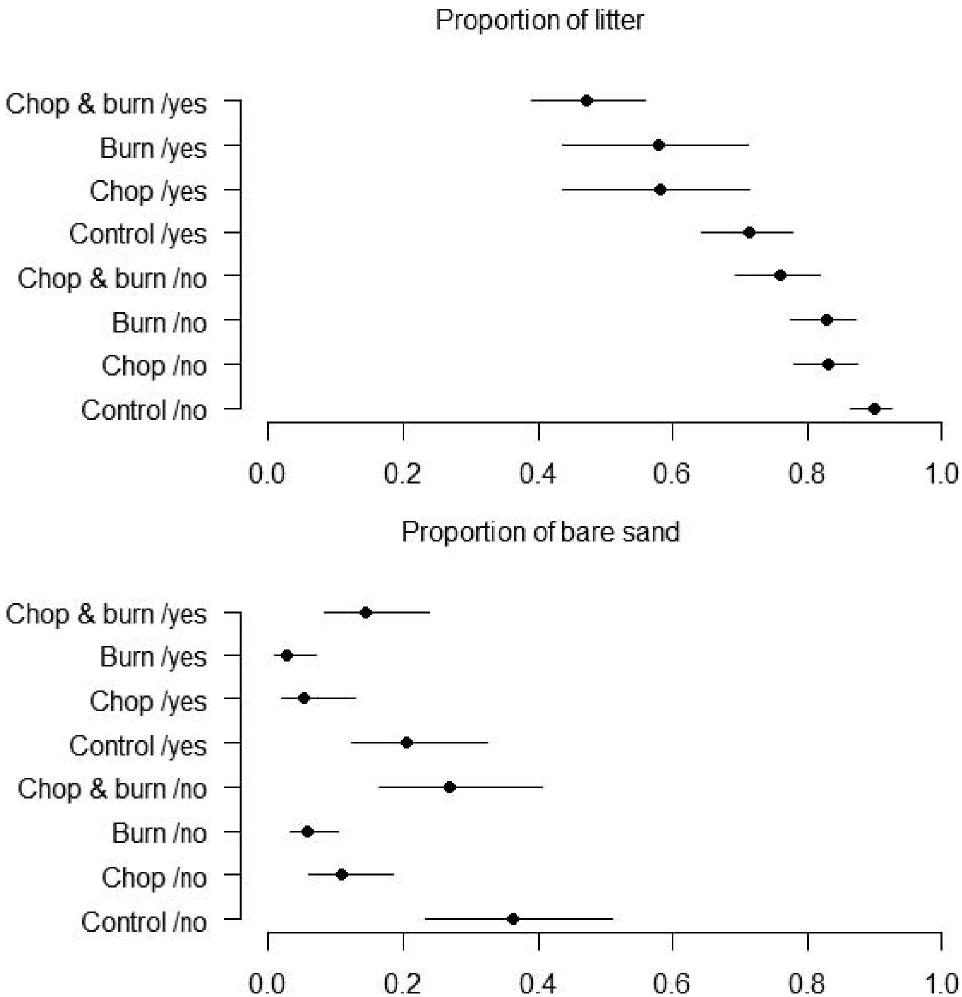


FIG. 1.—Percent cover of bare sand and litter prior to the application of the treatments (in 2005) in random vegetation subplots per treatment level without (no) and with (yes) presence of *Polygonella myriophylla*. Mean + 95 % CI estimated from fixed effect coefficients of the mixed model in Table 3

intermediate in chop-only plots (Table 4). Survivors in burned plots were in open sandy patches that failed to burn.

Polygonella myriophylla canopy area varied among genets and affected subsequent change in size. Post treatment canopy area was positively related to pretreatment area (Table 6). Growth in canopy area was consistently highest in chop-only plots compared to untreated plots and intermediate in burned conditions (Fig. 2). The chop-only plots had significantly greater growth than other treatments (chop*time interaction, Table 6).

We found three putative seedlings (cover < 0.00004 m^{-2}), accounting for less than 3 % of the initial genets before treatment application. Seedling recruitment ($\sim$ 90 seedlings) post

TABLE 4.—Post-treatment genet survival (nonseedlings)

Treatment	Macroplot id	Subplots	# Initial genets	# Survivors post fire	% alive genets post-treatment 2008
Untreated	2	12	15	13	86.7
Untreated	4	12	22	13	59.1
Chop only	3	12	21	10	47.6
Chop only	7	12	21	12	57.1
Burn only	6	11	19	2	10.5
Burn only	8	10	15	2	13.0
Chop&Burn	1	10	14	0	0
Chop&Burn	5	11	20	4	20.0

treatment was higher in mechanically disturbed plots, highest in plots where both treatments occurred (0.002 seedlings m^{-2}), and almost null in untreated macroplots (0.00005 seedlings m^{-2}; Table 7). Recruitment was highest in the first year post-disturbance (70%), decreasing in the subsequent years.

DISCUSSION

Our results indicate disturbances will be necessary to increase chances of persistence of *P. myriophylla*. Although burning and chopping both increased mortality, post-disturbance growth was highest in chopped treatments and also increased in burned treatments. In addition seedling recruitment was highest with a combination of chopping and burning. However, these results do not mean chopping and fire should be used indiscriminately, even if the goal were to manage this single species. Too frequent disturbance is likely to create high mortality but insufficient time for population recovery. Importantly, the patchy nature of the treatments in this study allowed some plants to survive treatments, which may have helped the population recover. In a more complete fire studied by Weekley and Menges (2003), no *P. myriophylla* plants survived.

Recovery of *P. myriophylla* populations when most plants are killed by fire or other disturbances will depend on seedling recruitment. It is not known whether this species has a persistent seed bank, but *P. basiramia*, an herbaceous plant that co- occurs in Florida scrub, does not form a persistent seed bank and recolonizes from dispersed seed from unburned patches. Land management will need enough time between disturbances to allow

TABLE 5.—Mixed generalized linear model of genet survival by disturbance treatment (untreated as a reference) with replicate as random effect by with initial size as covariate (random effects of macroplot within treatment). Random effects by group as standard deviation by replicate = 0.27

Fixed effects	Estimate	SE	z value	P-value
(Intercept)	3.117	1.069	2.916	0.004
Initial canopy area	0.111	0.102	1.095	0.273
Burn only	-4.989	1.294	-3.856	<0.001
Chop only	-0.221	1.473	-0.150	0.881
Chop Burn	-4.922	1.246	-3.950	<0.001

TABLE 6.—Mixed linear model of canopy size by year with individual and replicate as random effects by disturbance treatment (untreated as a reference) with initial size as covariate. Random effects by group as standard deviation by replicate = 0.55, and as standard deviation by individual = 2.81. Residual random variation = 4.25

Fixed effects	Estimate	SE	d.f.	*t*-value	P-value
(Intercept)	129.9	745.5	168	0.174	0.862
Initial canopy area	1.4	0.1	85	14.335	<0.001
time	-0.1	0.4	168	-0.175	0.861
Burn only	-1604.5	1768.8	4	-0.907	0.416
Chop only	-8059.2	1087.6	4	-7.410	0.002
Chop Burn	-2642.1	1758.3	4	-1.503	0.207
time: Burn only	0.8	0.9	168	0.907	0.366
time: Chop only	4.0	0.5	168	7.414	<0.001
time: Chop Burn	1.3	0.9	168	1.503	0.135

populations of *P. myriophylla* to recover. Patchy burns will be particularly useful if *P. myriophylla* requires seed dispersal from unburned patches to recruit post-disturbance. Because fire reduces aboveground biomass and releases subdominant herbaceous and shrub species from competition (*e.g.*, Quintana-Ascencio and Morales-Hernández, 1997), these post-burn sites may be particularly beneficial for seedling recruitment and growth.

Polygonella myriophylla benefited from chopping with a gyrotrac, a mechanical disturbance that reduced other woody cover. This may be because *P. myriophylla* is closer to the ground than the surrounding shrubs and trees. This prostrate shrub species suffers less damage during mechanical chopping than upright shrubs. Abundant patches of this species along regularly mown highways are consistent with the ability of this prostrate shrub to deal with frequent mechanical disturbance. A combination of mechanical treatment followed by fire may be a good way of favoring *P. myriophylla* when restoring overgrown Florida scrub. However, we are not suggesting this as a management strategy, because *P. myriophylla* co-occurs with many other rare and common species that may have negative responses to mechanical treatments.

Scrub restoration using mechanical treatments, either alone or preceding fire, and in comparison, with fire, have been assessed on the Lake Wales Ridge (LWR) in central peninsular Florida (Weekley *et al.*, 2008a; Rickey *et al.*, 2007). In these studies all treatments dramatically reduced canopy pine and subcanopy hardwood densities, but no mechanical treatment was successful in significantly reducing stem densities in the shrub layer (Weekley

TABLE 7.—Generalized linear model with logarithm link and negative binomial errors of seedling counts as a function of disturbance treatment. Data pooled by year to allow enough sample size

Treatment	Estimate	SE	z value	P
(Intercept)	-2.1	1.206	-1.7	0.085
Burn	2.3	1.418	1.6	0.104
Chop	3.5	1.394	2.5	0.013
Chop & Burn	3.8	1.390	2.7	0.006
Theta = 0.27				

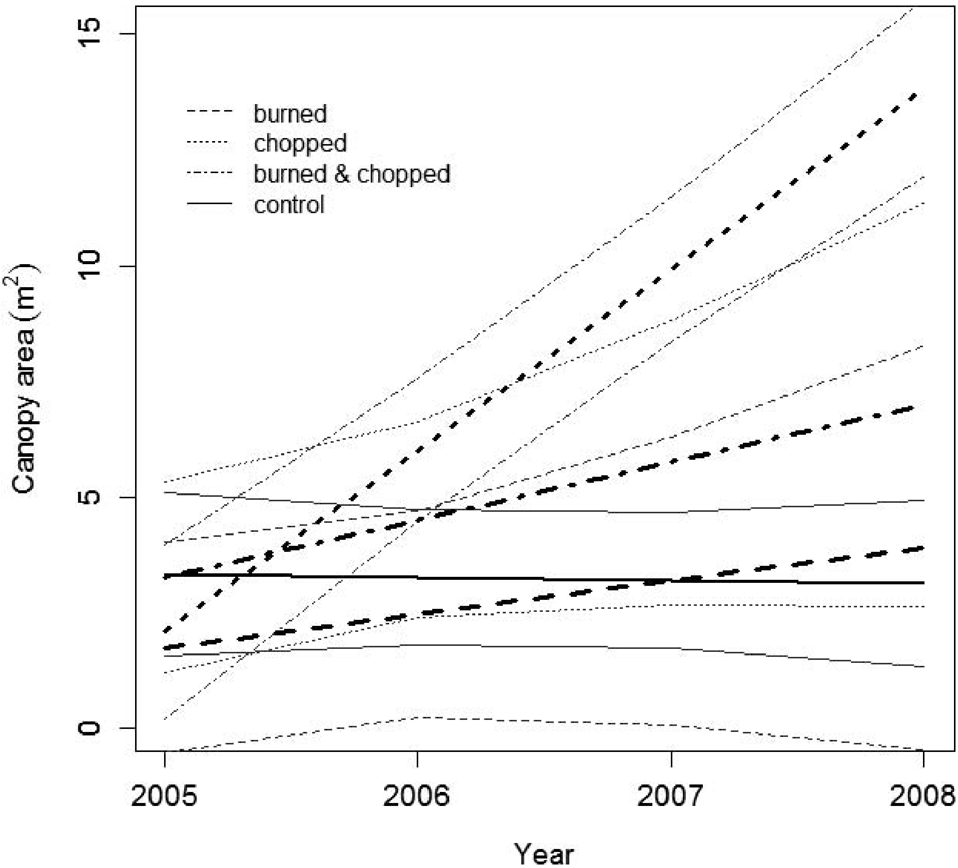


FIG. 2.—*Polygonella myriophylla* canopy cover (m^2 + 95% CI) between 2005 and 2008. Treatments were applied in summer 2005 after the initial measurement. Mean + 95 % CI estimated for the fixed effect coefficients of the mixed model in Table 6

et al., 2008a). Burning (with or without prior chopping) was more effective than chopping alone in promoting conditions required for the recruitment of many rare and imperiled Florida scrub herbs (Weekley *et al.*, 2008a). While all three management treatments reduced woody cover relative to the untreated site, only the burn-only and chop and burn treatments increased bare sand and reduced litter and lichen cover, encouraging herb recruitment (Weekley *et al.*, 2008a).

Since mechanical treatments alone do not restore favorable conditions for many native species and carry risks of excessive soil disturbance and facilitation of invasive species, they should be used in combination with fire (Menges and Gordon, 2010). Management aimed to maintain biodiversity will require the consideration of the simultaneous and potentially conflicting requirements of multiple species and the consequences of alternative management strategies. Understanding the evolutionary history of these species should be fundamental to identify the best management combinations.

Acknowledgments.—The staff from Florida Fish and Wildlife Conservation Commission performed the mechanical treatments and burns. We thank David Martin at US Fish and Wildlife Service for his continuous support. C. Weekley, K. Clanton, A. Feliciano, M. Ford, B. Kotlyar, and T. N. Thirer (UCF), A. Quintana-Morales and E. Quintana-Morales, M.C. Morales-Hernández and B. Ochocki contributed with field work. We received a research-collecting permit from the Florida Department of Environmental Protection and Division of Recreation and Parks, Permit Number 11-24-04-0, (11/24/04 - 11/24/05). We received harvesting permits from the Florida Department of Agriculture and Consumer Services, Permit Number 636 (January 2006 - January 2007), and Permit Number 683 (January 2007 - January 2008). S. Koontz' comments improved the manuscript.

LITERATURE CITED

ABRAHAMSON, W.G., A.F. JOHNSON, J.N. LAYNE, AND P.A. PERONI. 1984. Vegetation of the Archbold Biological Station, Florida: An example of the southern Lake Wales Ridge. *Fl. Sci.*, **47**:209–251.

AGEE, J.K. AND C.N. SKINNER. 2005. Basic principles of forest fuel reduction treatments. *For. Ecol. Manage.,* **211**:83–96.

AUGUSTINE, D.J., J.D. DERNER, AND D.G. MILCHUNAS. 2010. Prescribed fire, grazing, and herbaceous plant production in shortgrass steppe. *Rangeland Ecol. Manage.,* **63**:317–323.

BATES, D., M. MÄCHLER, B.M. BOLKER, AND S.C. WALKER. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Soft.,* DOI 10.18637/jss.v067.i01

BOERNER, R. E. J., J. HUANG, AND S. C. HART. 2008. Fire, thinning, and the carbon economy: effects of fire and fire surrogate treatments on estimated carbon storage and sequestration rate. *For. Ecol. Manag.,* **255**:3081–3097.

BREININGER, D. R. AND P. A. SCHMALZER. 1990. Effects of fire and disturbance of plants and birds in a Florida oak/palmetto scrub community. *Am. Midl. Nat.,* **123**:64–74.

BREWER, J.S. AND W.J. PLATT. Effects of fire season and soil fertility on clonal growth in a pyrophilic forb, *Pityopsis graminifolia* (Asteraceae). *Am. J. Bot.* **81**:805–814.

BOND, W.J. AND J.E. KEELEY. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.,* **20**:387–394.

BONEBREAK, T.C., A.D. SYPHARD, J. FRANKLIN, K.E. ANDERSON, H.R. AKCAKAYA, T. MIZEREK, C. WINCHELL, AND H.M. REGAN. 2014. Fire management, managed relocation, and land conservation options for long-lived obligate seeding plants under global changes in climate, urbanization, and fire regime. *Cons. Biol.,* **28**:1057–1067.

BOWLES, M.L., J.L. MCBRIDE, AND T.J. BELL. 2015. Long-term processes affecting restoration and viability of the federal threatened Mead's milkweed. *Ecosphere,* **6**:1–22.

BUSSE, M. D., K. R. HUBBERT, G. O. FIDDLER, C. J. SHESTAK, AND R. F. POWERS. 2005. Lethal soil temperatures during burning of masticated forest residues. *Inter. J. Wild Fire,* **14**:267–273.

CHAFIN, L. C. 2000. Field guide to the rare plants of Florida. In: Florida Natural Areas Inventory. Available via DIALOG. http://www.fnai.org/fieldguide/ Accessed 23 Feb 2008

CHRISTMAN, S. P. 1988. Endemism in Florida's interior sand pine scrub. Technical Report, Project Number GFC 84-101. Florida Nongame Wildlife Program. Tallahassee, Florida, U.S.A.

———. 2006. Distribution and status of three endemic Lake Wales Ridge scrub plants, rangewide status surveys for *Polygonella basiramia, Polygonella myriophylla and Liatris ohlingerae.* Final report, Part 2 to U.S. Fish and Wildlife Service.

——— AND W.S. JUDD. 1990. Notes on plants endemic to Florida scrub. *Fl. Sci.,* **53**:52–73

CIRNE, P. AND F.R. SCARANO. 2001. Resprouting and growth dynamics after fire of the clonal shrub *Andira legalis* (Leguminosae) in a sandy coastal plain in southeastern Brazil. *J. Ecol.* **89**:351–357.

DUNCAN, B. W., S. BOYLE, D. R. BREININGER, AND P. A. SCHMALZER. 1999. Coupling past management practice and historic landscape structure on John F. Kennedy Space Center, Florida. *Land. Ecol.,* **14**:291–309.

FERNANDES, P.M. AND H.S. BOTELHO. 2003. A review of prescribed burning effectiveness in fire hazard reduction. *Int. J. Wildland Fire,* **12**:117–128.

GAGNON, P.R. AND W.J. PLATT. 2008. Multiple disturbances accelerate clonal growth in a potentially monodominant bamboo. *Ecology* **89**:612–618.

GUNDALE, M. J., T. H. DELUCA, C. E. FIEDLER, P. W. RAMSEY, M. G. HARRINGTON, AND J. E. GANNON. 2005. Restoration treatments in a Montana ponderosa pine forest: effects on soil physical, chemical, and biological properties. *For. Ecol. and Manag.,* **213**:25–38.

GIAI, C. AND R. E. J. BOERNER. 2007. Effects of ecological restoration on microbial activity, microbial functional diversity, and soil organic matter in mixed-oak forests of southern Ohio, USA. *App. Soil Ecol.,* **35**:281–290.

HARTNETT, D.C. 1987. Effects of fire on clonal growth and dynamics of *Pityopsis graminifolia Am. J. Bot.* **74**:1737–1743.

HEWITT, R. E. AND E. S. MENGES. 2008. Allelopathic effects of *Ceratiola ericoides* (Empetraceae) on germination and survival of six Florida scrub species. *Plant Ecol,* **198**:47–59.

HUNTER, M.E. AND E. S. MENGES. 2002. Allelopathic effects and root distribution of *Ceratiola ericoides* (Empetraceae) on seven rosemary scrub species. *Am. J. Bot.*, **89**:1113–1118.

JOHNSON, A. F. 1982. Some demographic characteristics of the Florida rosemary *Ceratiola ericoides* Michx. *Am. Midl. Nat.*, **108**:170–174.

KEELEY, J. E. 2001. Fire and invasive species in Mediterranean-climate ecosystems of California. p. 81–94. *In:* K.E.M. Galley. and T.P. Wilson (eds.), Proc. Invasive Species Workshop: the Role of Fire in the Untreated and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Misc. Pub. No. 11. Tall Timbers Research Station, Tallahassee, FL.

LEHMANN, C.E.R., T.M. ANDERSON, M. SANKARAN, S.I. HIGGINS, S. ARCHIBALD, W.A. HOFFMAN, N.P. HANAN, R.J. WILLIAMS, R.J FENSHAM, J. FELFILI, L.B. HUTLEY, J. RATNAM, J. SAN JOSE, R. MONTES, D. FRANKLIN, J. RUSSELL-SMITH, C.M. RYAN, G. DURIGAN, P. HIERNAUX, R. HAIDAR, D.M.J.S. BOWMAN, AND W.J. BOND. 2014. Savanna vegetation-fire-climate relationships differ among continents. *Science,* **343**:548–552.

LINDON, H. L. AND E. S. MENGES. 2008. Effects of smoke on seed germination of twenty species of fire-prone habitats in Florida. *Castanea,* **73**:106–110.

MAGUIRE, A.J. AND E.S. MENGES. 2011. Post-fire growth strategies of resprouting Florida scrub species. *Fire Ecol.,* **7**:12–25.

MENGES, E.S. 1999. Ecology and conservation of Florida scrub. p. 7–22. *In:* R.C. Anderson, J.S. Fralish, and J. Baskin (eds). The savanna, barren, and rock outcrop communities of North America. Cambridge University Press, Cambridge, UK.

——— AND D. R. GORDON. 2010. Should mechanical treatments and herbicides be used as fire surrogates to manage Florida's uplands: a review. *FL. Sci.,* **73**:145–172

——— AND N. KOHFELDT. 1995. Life history strategies of Florida scrub plants in relation to fire. *Bull. Torrey Bot. Club,* **122**:282–297.

——— AND C.V. HAWKES. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. *Ecol. Appl.*, **8**:935–946.

——— AND P. F. QUINTANA-ASCENCIO. 2004. Evaluating population viability analysis with fire in *Eryngium cuneifolium*: deciphering a decade of demographic data. *Ecol. Monog.,* **74**:79–100.

———, A. WALLY, J. SALO, R. ZINTHEFER, AND C.W. WEEKLEY. 2008. Gap ecology in Florida scrub: species occurrence, diversity, and gap properties. *J. Veg. Sci.,* **19**:503–514.

———, S. J. H. CRATE, AND P. F. QUINTANA-ASCENCIO. 2017. Dynamics of gaps, vegetation, and plant species with and without fire. *Am. J. Bot.*, **104**:1825–1836.

METZGER, G. A. 2010. Clonality and genetic diversity in *Polygonella myriophylla*, a Lake Wales Ridge endemic plant. Master thesis. Department of Biology. University of Central Florida, Orlando, Florida.

MILLER, T., P.F. QUINTANA-ASCENCIO, S. MALIAKAL-WITT, AND E.S. MENGES. 2012. Metacommunity dynamics over 16 years in a pyrogenic shrubland. *Con. Bio.,* **26**:357–366.

NOSS, R.F. 2013. Forgotten grasslands of the south: natural history and conservation. Island Press, Washington, DC. 320 pp.

PAUSAS, J.G. AND V.D.L. DANTAS. 2017. Scale matters: fire-vegetation feedbacks are needed to explain tropical tree cover at the local scale. *Global Ecol. Biogeog.,* **26**:385–399.

——— AND J.E. KEELEY. 2009. A burning story: the role of fire in the history of life. *BioScience,* **59**:593–601.

PLATT, W. J., G. W. EVANS, AND S. L. RATHBURN. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *Am. Nat.,* **131**:491–525.

OKSANEN, J., F. G. BLANCHET, M. FRIENDLY, R. KINDT, P. LEGENDRE, D. MCGLINN, P. R. MINCHIN, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. HENRY, H. STEVENS, E. SZOECS, AND H. WAGNER. 2018. vegan: Community Ecology Package. R package version 2.4-6. https://CRAN.R-project.org/package=vegan.

QUINTANA-ASCENCIO, P. F., AND M. MORALES-HERNÁNDEZ. 1997. Fire-mediated effects of shrubs, lichens, and herbs on the demography of *Hypericum cumulicola* in patchy Florida scrub. *Oecologia,* **112**:263–271.

REINHARDT, E. D., R. E. KEANE, D. E. CALKIN, AND J. D. COHEN. 2008. Objectives and considerations for wildland fuel treatment in forested ecosystems of the interior western United States. *For. Ecol. Manag.,* **256**:1997–2006.

REYES, O. AND L. TRABAUD. 2009. Germination behavior of 14 Mediterranean species in relation to fire factors: smoke and heat. *Plant Ecol.,* **202**:113–121.

RICKEY, M. A., E. S. MENGES, AND C. W. WEEKLEY. 2007. Effects of mechanical treatments and fire on litter reduction in Florida scrub and sandhill. p. 104–108. *In:* R.E. Masters and K. E. M. Galley (eds.), Proc. of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems. Tall Timbers Research Station, Tallahassee, FL.

ROKICH, D.P. AND K.W. DIXON. 2007. Recent advances in restoration ecology, with a focus on the Banksia woodland and the smoke germination tool. *Aust. J. Bot.,* **55**:375–389.

RUTH, A. D., D. L. MILLER, S. JOSE, AND A. LONG. 2007. Effects of reintroduction of fire into fire suppressed coastal scrub and longleaf pine communities along the lower Gulf coastal plain. *Nat. Areas J.,* **27**:332–344.

SLAPCINSKY, J. L., D. R. GORDON, AND E. S. MENGES. 2009. Responses of rare plant species to fire across Florida's fire-adapted communities. *Nat. Areas J.,* **30**:4–19.

SCHAFER, J.L. AND M.C. MACK. 2014. Growth, biomass, and allometry of resprouting shrubs after fire in scrubby flatwoods. *Am. Midl. Nat.,* **172**:266–284.

SCHWILK, D. W., J. E. KEELEY, E. E. KNAPP, J. MCIVER, J. D. BAILEY, C. J. FETTIG, C. E. FIEDLER, R. J. HARROD, J. J. MOGHADDAS, K. W. OUTCALT, C.N. SKINNER, S. L. STEPHENS, T. Q. WALDROP, D. A. YAUSSY, AND A. YOUNGBLOOD. 2009. The national fire and fire surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. *Ecol. Appl.,* **19**:285–304.

STEPHENS, S. L., J. J. MOGHADDAS, C. EDMINSTER, C. E. FIEDLER, S. HAASE, M. HARRINGTON, J. E. KEELEY, E. E. KNAPP, J.D. MCIVER, K. METLEN, C.N. SKINNER, AND A. YOUNGBLOOD. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. Forests. *Ecol. Appl.,* **19**:305–320.

TURNER, W. R., D. S. WILCOVE, AND H. M. SWAIN. 2006. State of the Scrub. Conservation progress, management responsibilities, and land acquisition priorities for imperiled species of Florida's Lake Wales Ridge. Archbold Biological Station, Lake Placid, FL.

USFWS. 1993. Endangered and threatened wildlife and plants: endangered of threatened status for seven central Florida plants. United States Fish and Wildlife Service. *Federal register* **58**(79):25746–25755.

WEEKLEY, C.W. AND E.S. MENGES. 2003. Species and vegetation responses to prescribed fire in a long-unburned, endemic-rich Lake Wales Ridge scrub. *J. Torrey Bot. Soc.,* **130**:265–282.

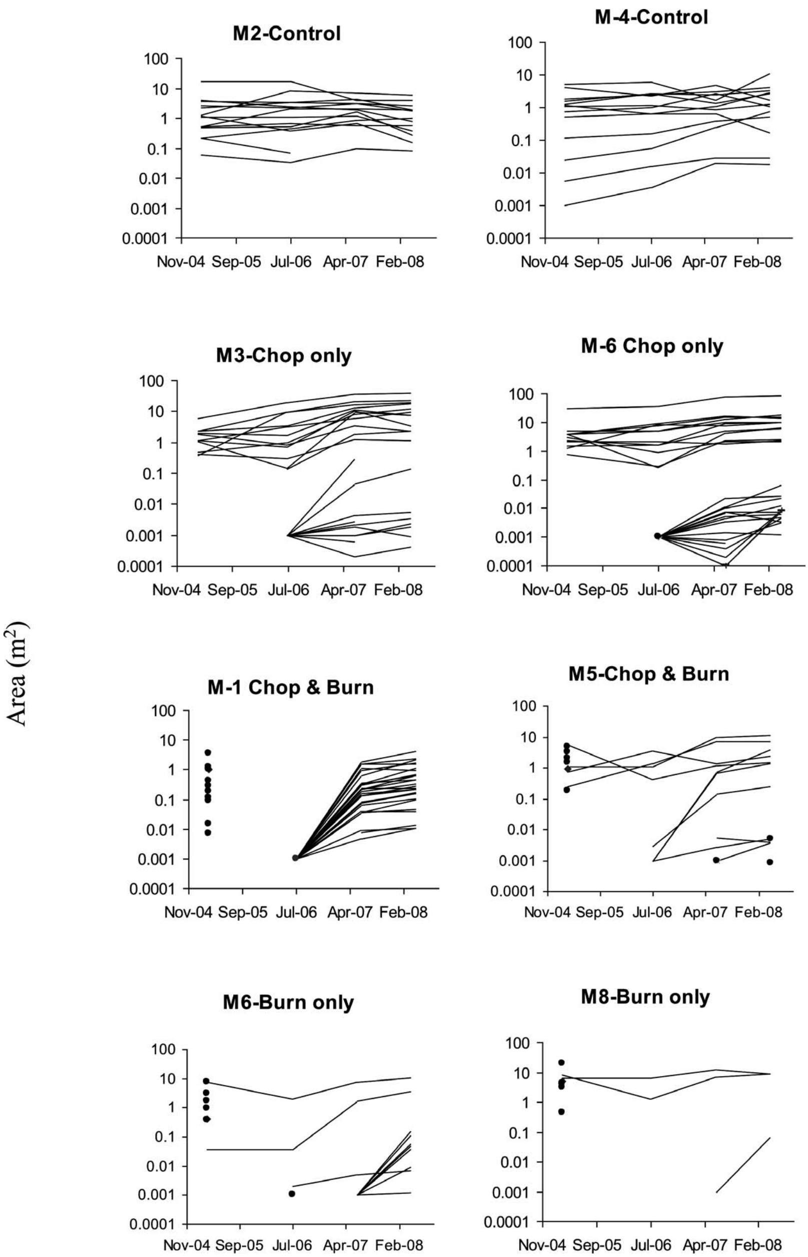
———, ———, M. A. RICKEY, G. CLARKE, AND S. A. SMITH. 2008a. Effects of mechanical treatments and fire on Florida scrub vegetation. Final Report to U.S. Fish and Wildlife Service, Vero Beach Office, Vero Beach, FL.

———, ———, AND R.L. PICKERT. 2008b. An ecological map of Florida's Lake Wales Ridge: A new boundary delineation and an assessment of post-Columbian habitat loss. *Fl. Sci.,* **71**:45–64.

WILLIAMSON, G. B., E. M. OBEE, AND J. D. WEIDENHAMER, 1992. Inhibition of *Schizachyrium scoparium* (Poaceae) by the allelochemical hydrocinnamic acid. *J. Chem. Ecol.,* **18**:2095–2105.

WUNDERLIN, R.P., AND B.F. HANSEN, 2011. Guide to the vascular plants of Florida, 3rd ed. University Presses of Florida, Gainesville, FL, US.

SUBMITTED 3 JAN 2018 ACCEPTED 20 APRIL 2018



APPENDIX FIG. A1.—Plant cover per genet (m^2). Notice new seedlings (smaller plants that started later) and the initial size of non-surviving plants (single points) in some Macroplots (M). Treatments were applied in summer 2005 after the initial measurement