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RESEARCH ARTICLE

Responses of Rare Plant Species to Fire in Florida's Pyrogenic Communities

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ABSTRACT: Lightning- and human-ignited fires have shaped many of Florida's natural communities. Plant persistence in these habitats requires adaptation to survive high temperatures, ability to respond to aboveground tissue loss, or avoidance of these conditions through survival in unburned patches or in the soil seed bank. Limited distribution of many rare species in increasingly fragmented habitats and uncertainty of whether rare species tolerate, require, or persist through avoidance of fire hampers fire management when it is possible and threatens long-term viability of plants. We review up to 14 years of monitoring data for 18 rare plant species from 14 families occurring on sandhill, scrub, pine rockland, and mixed deciduous hardwood communities across Florida. For a number of variables measured, including density, frequency, flowering, and recruitment, 50% of the species showed significant positive responses to burning and 50% of the species showed a neutral or no response. None of the species were unable to recover post-burn. These results suggest that prescribed fire in these pyrogenic habitats need not be delayed until species-specific responses to fire are understood.

Index terms: fire, Florida, Florida scrub, pine rocklands, pyrogenic, sandhill

INTRODUCTION

Recent hypotheses suggest that fire plays an important role in shaping the characteristics of many of the world's biomes (Bond and Keeley 2005). Fire-adapted or pyrogenic ecosystems have been estimated to cover 40% of the world's land surface (Chapin et al 2002), and it is the fire regime (fire intensity, severity, frequency, and season) that has created some of the most biodiverse habitats. Fire-adapted habitats include tropical systems that burn in the dry season, like savanna woodlands, monsoon forests and tropical pine forests (Nasi et al. 2002), Mediterranean climate regions of the world that include habitats of the Mediterranean basin, California chaparral, South African fynbos and Australian heathlands (Cowling et al. 1996; Bond and Keeley 2005), and circumpolar boreal forests, taiga and tundra habitats with permafrost (Nasi et al. 2002).

Among North American fire-maintained ecosystems are grasslands, prairies, and pine forests that represent over 90% of the southeastern United States (Frost 1995). These systems are substantially influenced by lightning- and human-ignited fire and tropical storms (Brockway and Lewis 1997). Peninsular Florida has one of the highest incidences of lightning strikes in the world (Goodman and Christian 1993). Lightning flash densities are greater than 30 fl km $^{-2}$ yr $^{-1}$, second only to the world "hotspot" in the equatorial Congo Basin (Christian et al. 2003). Historically, most fires were caused by lightning, which was most prevalent during the convective storm events of the growing season (Huffman 2006). Past fire regimes were augmented by native American-ignited fires (Brown 2004) often set during times other than the lightning fire season (Snyder 1991). Today, prescribed fire for conservation and agricultural purposes now generally replaces these natural and historic sources of fires (Robbins and Myers 1992).

As a consequence of fire's consistent presence on the Florida landscape, approximately 70% percent of the terrestrial natural plant communities and nearly 100% of the palustrine natural plant communities described by the Florida Natural Areas Inventory (1990) are considered fire-dependent or fire-adapted. Both wide-ranging and geographically restricted species in these communities have developed life history strategies in response to fire (Menges and Kohfeldt 1995).

Years of fire-suppression and loss of habitat due to land development and conversion (Brockway and Lewis 1997) have led to declining distributions of Florida's rare species, especially in Florida scrub (Hall et al. 2002), pine rocklands (U.S. Fish and Wildlife Service 1999), and sandhill (Noss 1989; Frost 1993). Land managers are often reluctant to use fire as a management tool unless there are assurances that fire will not threaten imperiled species. Fire return intervals, identified as the number of years between two successive fire events at a specific site, are currently increasing even where fire management does occur (Hardin 2002; Mulholland et al. 2003). In 1926, the Florida Department of Forestry and Parks estimated that roughly 5,260,921 hectares, or approximately 75% of the pinelands in

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Florida, burned annually (Baker 1926). From 1995 to 2003, the average annual number of hectares that burned in Florida was estimated to be 76,486, or less than 1% of the state (Florida Division of Forestry 2005).

Given the importance of fire to rare species in upland Florida ecosystems, and the likely negative impacts of fire suppression, more information on fire responses of Florida's rare plants is essential. Here, we integrate post-burn data on rare species abundances and vital rates (e.g., survivorship and reproduction), focusing on data collected by The Nature Conservancy (TNC) and Archbold Biological Station (ABS). Over the past 15 years, both organizations have implemented monitoring and management programs of the rare plant species that occur on their, and some publicly owned, properties. The plant species in both monitoring programs are globally (ranked G1-G3) and locally rare. Nearly every natural upland community maintained by fire in Florida is represented within these preserves and both organizations manage their properties with fire (among other methods) at frequencies depending on vegetation type (Robbins and Myers 1992). We summarize the responses of 18 rare plants to fire.

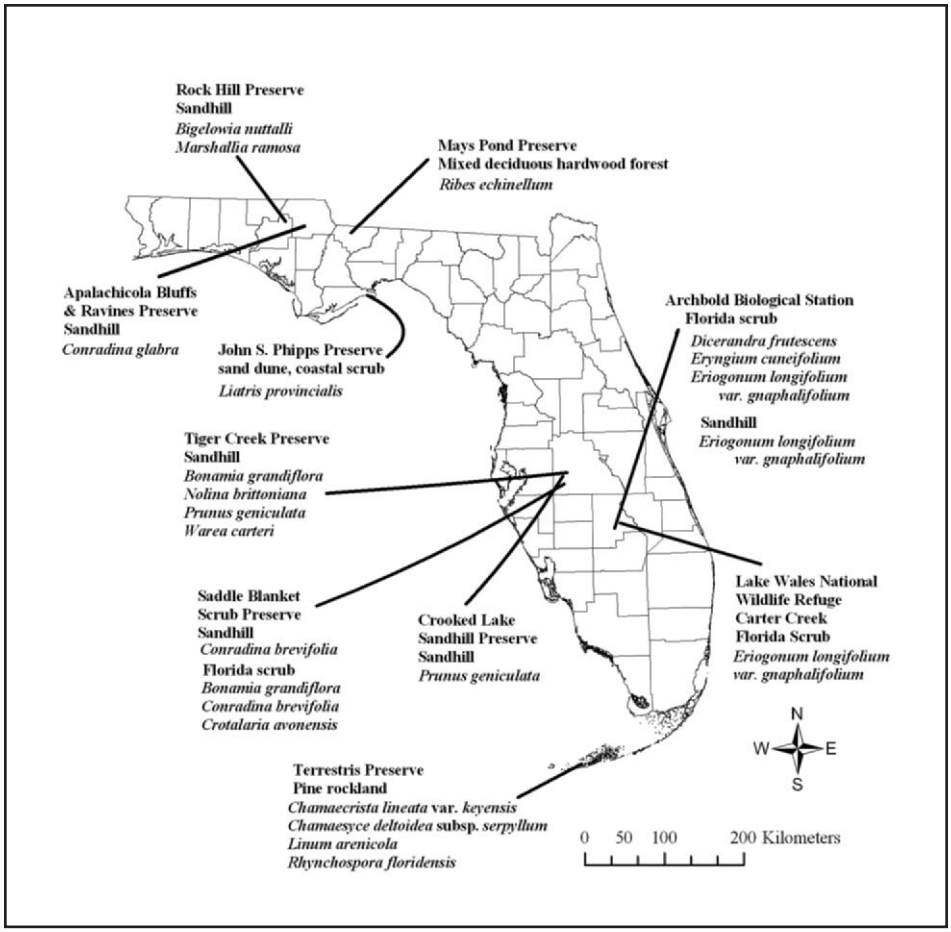


Figure 1. Ten preserves, their associated habitat(s) and 18 species monitored in Florida.

METHODS

Populations of 15 of the 18 rare plant species have been monitored annually on 10 preserves previously or currently owned by TNC in Florida (Figure 1). The remaining three species were monitored on property owned and managed by ABS or monitored by ABS on public conservation areas. All species are monitored on habitats that burn periodically either naturally by lightning-caused fires or by prescribed fire at hypothesized natural intervals (Table 1).

Six of the rare species are found in one of more than seven types of scrub habitats (e.g., scrubby flatwoods, white sand scrub, oak scrub; see Abrahamson et al, 1984, Menges 1999, and Schmalzer 2003 for descriptions) on the preserves where they were monitored (Figure 1). For the purposes of this paper, "Florida scrub" will be used for all Florida scrub-types. This habitat is found on ABS (Highlands County) and Saddle Blanket Scrub Preserve (Polk County) located on the Lake Wales Ridge (LWR). This relict shoreline and dune system is characterized by relatively high elevation and excessively draining sandy soils, and dates back to at least the Pleistocene (White 1970; Myers 1990; Webb 1990). Florida scrub is maintained by recurrent disturbances including fire (Myers 1990; Gibson and Menges 1994; Menges 1999) at intervals of every 8-16 years for scrubby flatwoods, every 5-12 years for oak-hickory scrub, and every 15-30 years for rosemary scrub (Menges 2007). For our purposes, we define the fire return interval as a range from 5-30 years (Table 1).

Six species were monitored in sandhill at Tiger Creek Preserve (Polk County), Crooked Lake Sandhill Preserve (Volusia County), Rock Hill Preserve (Washington County), Apalachicola Bluffs and Ravines Preserve (Liberty County), and ABS (Table 1). In Florida, longleaf pine systems occur mostly in the north and central parts of the state, on gently rolling terrain on deep, excessively drained, mostly yellow, oligotrophic sands. These systems are characterized by frequent, low intensity lightning-caused fires that occur with return intervals of one to five years (Table 1) (Christensen 1981; Means and Grow 1985; Noss 1989; Glitzenstein et al. 1995).

Three of the six species that were monitored in scrub were also monitored in sandhill habitats (Table 1). *Bonamia grandiflora* (A. Gray) Hallier f. was monitored in sandhill at both Saddle Blanket Scrub Preserve and Tiger Creek Preserve. *Eriogonum longifolium* Nutt. var. *gnaphalifolium* Gandog. was monitored in both scrub and sandhill at Archbold Biological Station, and *Conradina brevifolia* Shinners was monitored on both habitats at Saddle Blanket Scrub

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Table 1. Species and variables used in this study. "Monitored habitat(s)" is the habitat in which the species was monitored. Variables that were tested are listed with the number of preserves or populations (# Pop), number of management areas, burn units or baselines (# BU), the number of sampling units (# SU), their sizes (SU size), and the number of years pre- and post-burn that were analyzed.

Species	Monitored habitat(s)	Habitat fire interval (years)	Variable(s)	# Pop	# BU	# SU	SU size	Years pre- and post-burn analyzed
Bigelowia nuttallii	sandhill	1-5[a]	% flowering, density	1	7	20	30 x 1 m	0, 2, 4, 6
Bonamia grandiflora	sandhill, Florida scrub	1-5[a], 5-30[b]	total density, recruit density, % reproduction	2	4	-	-	1-10, 21-25
Chamaecrista lineata var. *keyensis*	pine rockland	2-15[c]	density	1	2	26	50 x 2 m	0-6
Chamaesyce deltoidea subsp. *serpyllum*	pine rockland	2-15[c]	frequency	1	2	21	50 x 2 m	0-6
Conradina brevifolia	sandhill, Florida scrub	1-5[a], 5-30[b]	density	1	2	36	1 x 2 m	0-5
Conradina glabra	sandhill	1-5[a]	density	1	2	79	3 x 3 m	0-3
Crotalaria avonensis	Florida scrub	5-30[b]	% flowering, density	1	5	8	10 x 10m, 10 x 15 m	0-2
Dicerandra frutescens	Florida scrub	5-30[b]	density	3	-	29	1 x 1m	0-2
Eriogonum longifolium var. *gnaphalifolium*	sandhill, Florida scrub	1-5[a], 5-30[b]	density	5	-	15	10 x 10 m	1-7
Eryngium cuneifolium	Florida scrub	5-30[b]	# plants	1	7	12	-	1-18
Liatris provincialis	sand dune, coastal scrub	under 20 years	density	1	2	-	-	1-3, 10
Linum arenicola	pine rockland	2-15[c]	density	1	3	25	50 x 2 m	0-8
Marshallia ramosa	sandhill	1-5[a]	# flowering plants	1	9	-	-	0-4
Nolina brittoniana	sandhill	1-5[a]	% flowering	2	4	16	10 x 10, 5 x 5 m	1-6
Nolina brittoniana	sandhill	1-5[a]	density	2	5	10	10 x 10, 5 x 5 m	0-4
Prunus geniculata	sandhill	1-5[a]	# plants	2	21	-	-	1-10
Rhynchospora floridensis	pine rockland	2-15[c]	frequency	1	3	24	50 x 2 m	0-8
Ribes echinellum	mixed deciduous hardwood forest	under 20 years	density, % reproduction	1	3	13	30 x 1 m, 50 x 1 m	1-3
Warea carteri	sandhill	1-5[a]	# plants	1	39	-	-	0-3

[a]Glitzenstein et al. 1995, [b]Menges 2007, [c]Snyder et al. 1990. The burn interval for Florida scrub (5-30 years) includes all scrub types described by Menges (2007).

Preserve (Figure 1).

Four of the monitored species are endemic to south Florida pine rockland, which has a limestone substrate with shallow, droughty, and sandy soils (Table 1). The habitat is fire maintained with an historic frequency of either every two to three years (based on the time it takes for fuels to accumulate) or every 10 to 15 years, an estimate of the time it takes for herbaceous endemics to be shaded by a closed canopy (Table 1) (Snyder et al. 1990). Terrestris Preserve is an 8 ha pine rockland habitat in a freshwater marsh community on central Big Pine Key, Monroe County, Florida.

Finally, we use data from two rare species occurring in hardwood forests and in coastal habitats (Table 1). The Mays Pond conservation easement site, Jefferson County, is a deciduous, mixed hardwood forest in proximity to the northeast shore of Lake Miccosukee that burns infrequently (G. Seamon, Fire Training Specialist, the Nature Conservancy, pers. comm. 2007) and contains the rare *Ribes echinellum* (Coville) Rehder. The Nature Conservancy's John H. Phipps Preserve is on the easternmost coastal barrier shoreline in Franklin County where *Liatris provincialis* R.K. Godfrey occurs. This species was monitored on sand dunes and adjacent coastal scrub habitat (Figure 1). The habitat is further described as evergreen oak-sand pine scrub by Godfrey and Ward (1979). These coastal scrub habitats are subjected to frequent storm activity (flooding and winds) and have hypothesized modal historical burn frequencies of under 20 years (Schmalzer 2003).

Species and Data Collection Methods

All of the 18 species, except for *Rhynchospora floridensis* (Britton ex Small) H. Pfeiff, are state listed as endangered in Florida (Table 1) and all but four species (*Bigelowia nuttallii* L.C. Anderson, *Marshallia ramosa* Beadle and F.E. Boynton, *Ribes echinellum* (Coville) Rehder, and *Rhynchospora floridensis* (Britton ex Small) H. Pfeiff are Florida endemics. Species were monitored for different traits with varying population and plot sizes and were subjected to one or more prescribed burns at various times during monitoring. Monitoring site locations are in Figure 1.

Bigelowia nuttallii L.C. Anderson, Nuttall's rayless goldenrod, is an herbaceous perennial found on the coastal plain and piedmont of Georgia and Florida, the Cumberland Plateau of Alabama, and in central and western Louisiana and eastern Texas. The species is found in four localized patches in sandhill at TNC's Rock Hill Preserve (RHP). We used restricted random sampling in seven sub-populations to place three 30-m x 1-m belt transects within each sub-population. We then counted reproductive and non-reproductive plants each September annually from 1992 to 1995 and thereafter biennially to 2001.

Bonamia grandiflora (A. Gray) Hallier f., Florida bonamia, is an endemic to Florida and a perennial herbaceous vine. We annually censused two sub-populations in sandhill at TNC's Tiger Creek Preserve (TCP) and two sub-populations at Saddle Blanket Scrub Preserve (SBSP) from 1991-1997 and tagged each plant. Every year we re-located each individual and tagged new individuals to derive survival and recruitment rates.

Chamaecrista lineata (Sw.) Greene var. *keyensis* (Pennell) H.S. Irwin and Barneby, Big Pine partridge pea, is an herbaceous perennial endemic to Florida's pine rockland habitat. We used restricted random sampling to establish multiple 2-m wide permanent belt transects in each of three burn units on TNC's Terrestris Preserve on Big Pine Key. Starting in 1993, we counted individuals annually along the 2-m wide belt transects so that average density per m^2 could be determined.

Chamaesyce deltoidea (Engelm. Ex Chapm.) Small subsp. *serpyllum* (Small) D.G. Burch, wedge spurge, is an herbaceous perennial endemic to Florida. We used restricted random sampling to establish multiple 2-m wide permanent belt transects in each of three burn units on TNC's Terrestris Preserve on Big Pine Key. Starting in 1993, we recorded frequency of this species in continuous 2-m x 1-m plots.

Conradina brevifolia Shinners, short-leaved rosemary, is a shrub endemic to Florida scrub. In 1999 at TNC's Saddle Blanket Scrub Preserve, we estimated density annually in three permanent 15-m x 2-m plots randomly located within the population in each of four burn units. An additional five plots on the Preserve were added and sampled annually from 2000-2003.

Conradina glabra Shinners, Apalachicola rosemary, a mint, is an endangered shrub endemic to north Florida sandhill. We set up three permanent burn units at TNC's Apalachicola Bluffs and Ravines Preserve into which we translocated propagated cuttings in 1991 (Gordon 1994). Beginning in 1992, we found and tagged naturally establishing seedlings in 45 of the experimentally located 3-m x 3-m plots in each burn unit annually. We stopped tagging new recruits after 1995, but we continued to census all tagged plants until 2002 to determine survival rates.

Crotalaria avonensis Delaney and Wunderlin, tortoise bells, is an herbaceous perennial, endemic to Florida scrub. From 1992 to 2005, we sampled all plants within randomly located permanent 10-m x 10-m or 10-m x 15-m plots in each of five sub-populations at SBSP. We mapped individual plants annually to track recruitment and flowering condition.

Dicerandra frutescens Shinners, scrub balm, is a shrub endemic to Florida scrub. We marked all individual plants at 11 sites at ABS and have followed plant survival, growth, and recruitment since 1988, which has led to a recent assessment of population viability (Menges et al. 2006).

Eriogonum longifolium Nutt. var. *gnaphalifolium* Gandog., scrub buckwheat, is an herbaceous perennial endemic to Florida scrub. From 1989 to the present, we monitored six sub-populations in four burn units at ABS, leading to an assessment of population viability (Satterthwaite et al. 2002). Within each sub-population, we established between four and 14 permanent 10-m x 10-m plots, in which all scrub buckwheat plants were tagged and censused annually. One additional population

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has been monitored in circular permanent quadrats (3 m radius) at the Lake Wales National Wildlife Refuge (Carter Creek tract) since 2001.

Eryngium cuneifolium Small, wedge-leaved button-snakeroot, is an herbaceous perennial endemic to Highlands County in Florida scrub. We have censused 11 sub-populations and marked all individuals at ABS annually since 1988, leading to an assessment of population viability (Menges and Quintana-Ascencio 2004).

Linum arenicola (Small) H.J.P. Winkler, or sand flax, is an herbaceous perennial endemic to southern Florida pine rockland. We used restricted random sampling to establish multiple 2-m wide permanent belt transects in each of three burn units on TNC's Terrestris Preserve on Big Pine Key. Starting in 1993, we counted individuals along the 2-m wide belt transects annually so that average density per m^2 could be determined.

Liatris provincialis R.K. Godfrey, Godfrey's blazing star, is an herbaceous perennial, endemic to the Florida panhandle. From 1996-2002, we censused two coastal sandhill burn units at John S. Phipps Preserve in the fall of each year (except 1998) to track population size.

Marshallia ramosa Beadle and F.E. Boynton, pineland Barbara buttons, is a perennial herb known from 20-30 sites in south central Georgia and northwestern Florida. We annually censused all *Marshallia ramosa* individuals and the number of flowering individuals in eight sandhill burn units from 1992-2002 at Rock Hill Preserve.

Nolina brittoniana Nash, Britton's beargrass, is an herbaceous perennial, endemic to Florida that occurs in scrub and sandhills (Menges et al. 2006). From 1991 to 2001, we haphazardly set up five permanent 10-m x 10-m monitoring plots in burn units at Tiger Creek Preserve and tagged plants annually (except 2000) to track recruitment and flowering.

Prunus geniculata R.M. Harper, scrub plum, is a shrub endemic to sandhill on Florida's Lake Wales Ridge. From 1991 to 1996, we tagged all individual plants annually to track population size at the Tiger Creek and Crooked Lake Sandhill Preserves. We also recorded the presence of reproductive structures for each plant.

Rhynchospora floridensis (Britton ex Small) H. Pfeiff, Florida white-top, is an herbaceous perennial found in about 49 pine rockland sites in Florida (NatureServe 2006) and otherwise known only from the Bahamas (Godfrey and Wooten 1981). We used restricted random sampling to establish multiple 2-m wide permanent belt transects in each of three burn units on TNC's Terrestris Preserve on Big Pine Key. Starting in 1993, we recorded frequency of this species in continuous 2-m x 1-m plots.

Ribes echinellum (Coville) Rehder, Miccosukee gooseberry, is a woody sub-shrub known from two mixed hardwood sites in Jefferson County, Florida, and from one site in McCormick County, South Carolina. We annually monitored plant density from 1992-2001 in eighteen 50-m x 1-m and two 30-m x 1-m permanent belt transects located through a restricted randomization process at the May's Pond site in north Florida.

Warea carteri Small, Carter's mustard, a sandhill and Florida scrub endemic found on the Lake Wales Ridge, is an annual. Previous work on this species demonstrated that populations are released from the seed bank following fire, and decline precipitously thereafter (Menges and Gordon 1996). We annually censused this species during peak flowering in Tiger Creek Preserve sandhill. Starting in 1991, we recorded the total number of plants per sub-population. Sites were carefully searched each year and all new sub-populations were mapped. A total of 66 sub-populations have been monitored at Tiger Creek Preserve.

Data Analysis

A total of 24 variables for 18 species were tested. Twelve variables were tested with repeated measures analysis of covariance (RM ANCOVA) and 12 were tested with analysis of variance (ANOVA). Multiple variables were tested for five species (Table 1). RM ANCOVA was used to examine the relationship between time since fire and abundance or vital rates (e.g., survivorship and reproduction) of 10 of the species (Figures 2 and 3). Where available, a covariate was used to examine the variation explained by pre-burn (sometimes long-unburned, defined as > 10 years since fire) conditions. Covariate data was expressed as density, plant numbers, frequency, or percent flowering (depending on the trait(s) measured for each species). All assumptions associated with RM ANCOVA were tested and were met. Data were transformed as necessary to meet the assumption of normality. Graphs for variables tested with RM ANCOVA show the response variable on the y-axis, with the covariate at zero year since burn (Figures 2 and 3).

Where we had insufficient post- or pre-burn data to run RM ANCOVA (12 variables of eight species), we used ANOVA. We transformed the 12 response variables to a percentage by calculating the percent change from one year to the next, starting from zero year since burn. The percent change for the variable is again graphed starting with one year since burn on the y axis (Figures 4 and 5). Using the percent change of the response variable from one year to the next reduces the potential effects of pseudoreplication (Wiens and Parker 1995).

Significance was determined at the $P < 0.05$ level for all statistical tests. The monitoring site, population, or quadrat (if applicable) were included as fixed effects for all tests. A positive response was identified by either a significant initial increase in the response variable after fire that may or may not be followed by a decline or an initial decline after fire followed by a longer-term increase. A neutral response to fire was determined if response was independent of time since fire ($P > 0.05$), and a negative response occurred where populations declined significantly after prescribed fire and showed no recovery.

We had no pre-fire data for three species: *Bonamia grandiflora*, *Eryngium cuneifolium,* and *Prunus geniculata* (Table 1). Monitoring for these species started one

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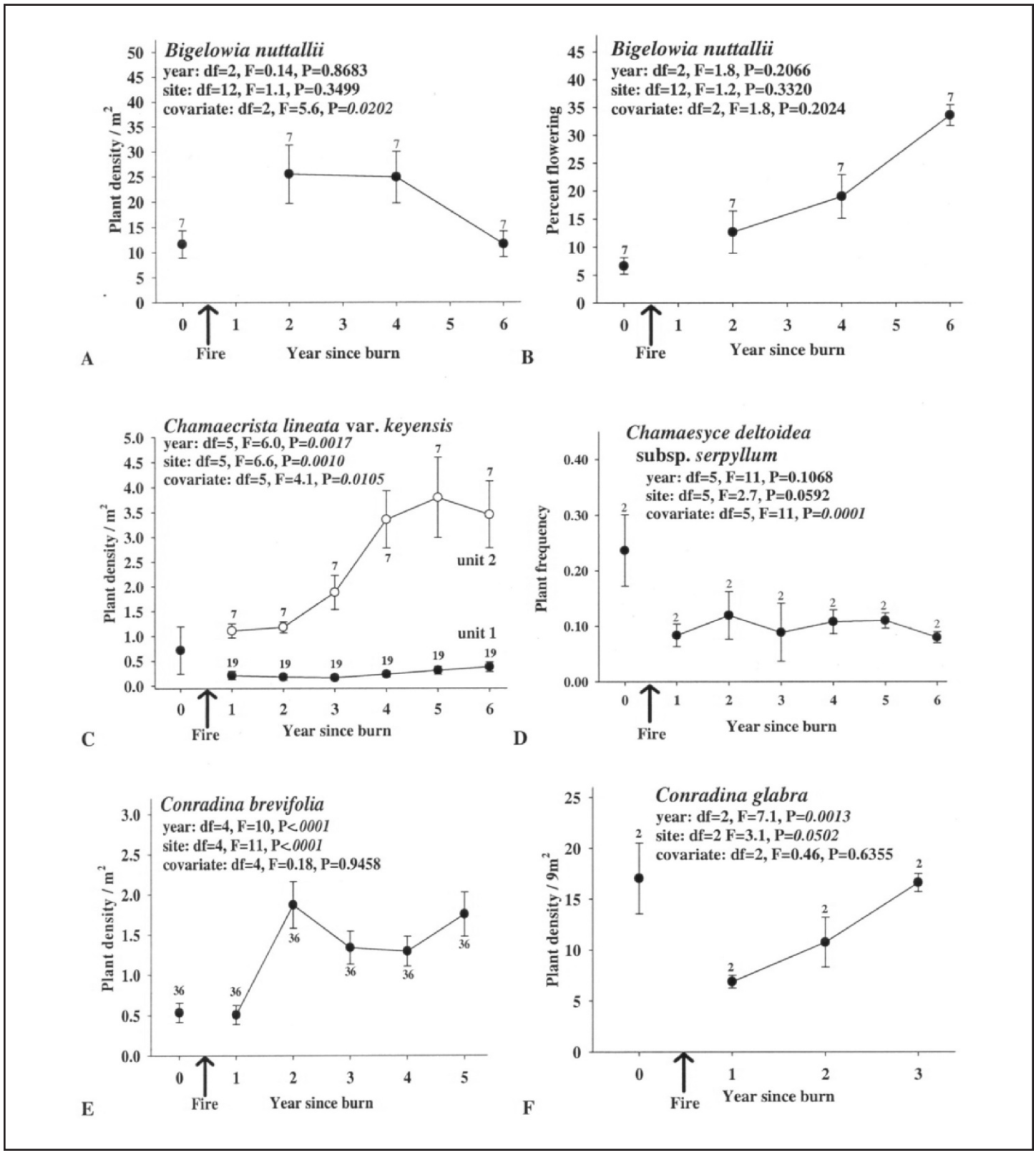


Figure 2. Species whose variables (A through F) were analyzed with repeated measures analysis of covariance (P < 0.05). The value separated from the line at 0 year since burn represents the covariate value: the pre-burn or long-unburned population condition. All graphs shown are ± 1 SE. Number above or below error bar denotes sample size. Where mean change obscures significant trends, population responses are shown separately. Significant p-values are italicized. Variable A = *Bigelowia nuttallii* density, B = B. *nuttallii* percent flowering, C = *Chamaecrista lineata* var. *keyensis* density, D = *Chamaesyce deltoidea* subsp. *serpyllum* frequency, E = *Conradina brevifolia* density, F = C. *glabra* density.

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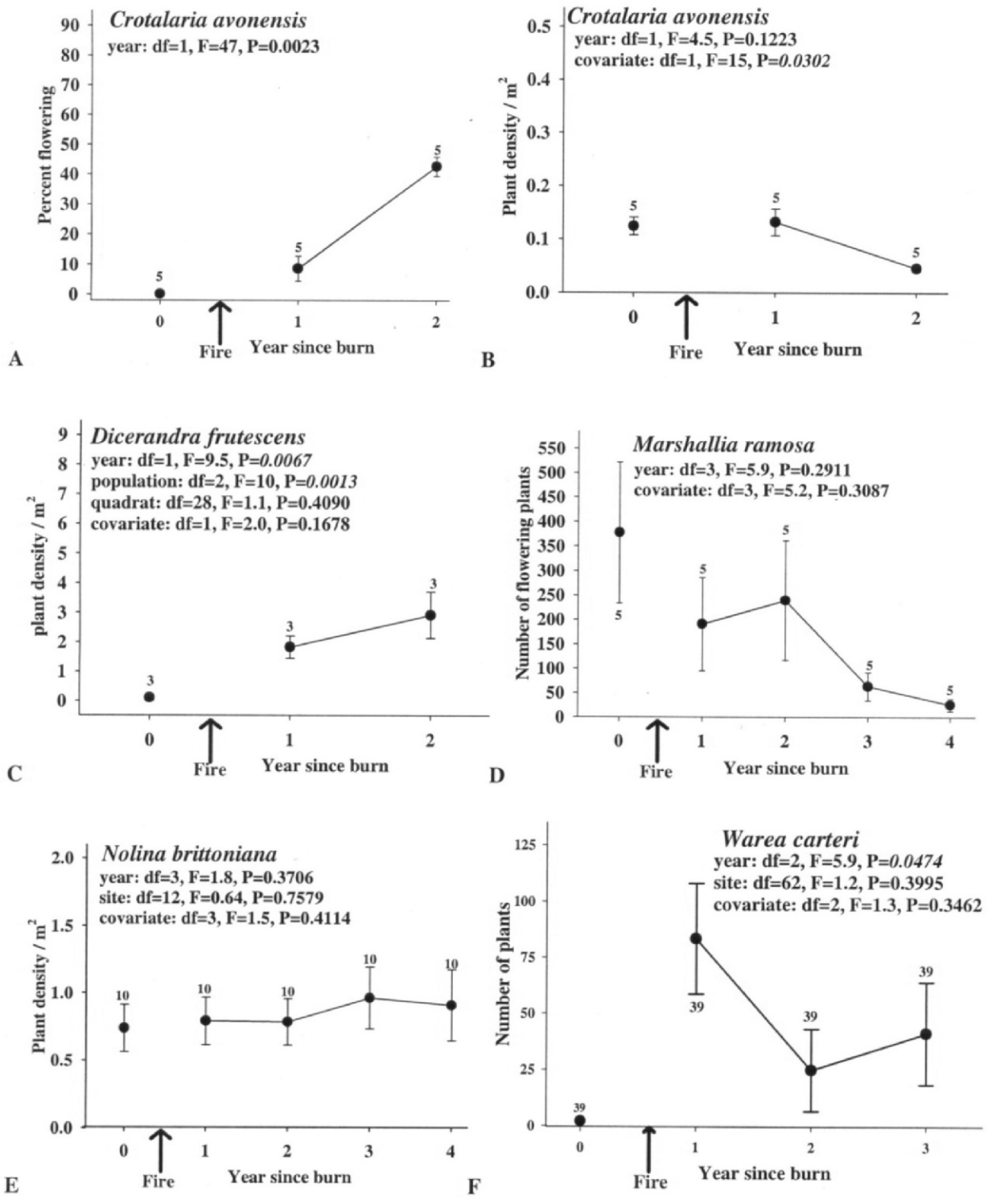


Figure 3. Species whose variables (A through F) were analyzed with repeated measures analysis of covariance (P < 0.05). The value separated from the line at 0 year since burn represents the covariate value: the pre-burn or long-unburned population condition. All graphs shown are ± 1 SE. Number above or below error bar denotes sample size. Significant p-values are italicized. Variable A = *Crotalaria avonensis* percent flowering, B = *C. avonensis* density, C = *Dicerandra frutescens* density, D = *Marshallia ramosa* number of flowering plants, E = *Nolina brittoniana* density, and F = *Warea carteri* number of plants.

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year after prescribed burn. Therefore, for these three species, a positive response was statistically significant at $P < 0.05$ where the population(s) showed an increasing trend since the burn.

RESULTS

RM ANCOVA Results

Chamaecrista lineata var. *keyensis* density significantly increased after fire, with significant site and covariate effects. The site effect ($P = 0.0017$) (Figure 2C) resulted from increased density of the population in unit 2 from the third through the fifth year after burning, while unit 1 showed no change over time.

Data were limited to the first two years after burning for two scrub species that exhibited significant and positive responses to fire. *Crotalaria avonensis* flowering ($P = 0.0023$) (Figure 3A) and *Dicerandra frutescens* density ($P = 0.0067$) (Figure 3C) increased the second year after burning. We had three years of post-burn data for *Conradina glabra*, which showed density increases in years two and three after fire ($P = 0.0013$) (Figure 2F). This response varied among the sites ($P = 0.05$) (Figure 2F). Three years of post-burn data for *Warea carteri* numbers showed a dramatic increase one year post-burn followed by a sharp decline in the second year ($P = 0.0474$) (Figure 3F). Species for which we had longer post-burn intervals included *Conradina brevifolia,* which showed dramatic increases in plant density the second year after burning and continued to increase through five years after fire ($P < 0$ .0001) (Figure 2E).

Traits of three species showed a significant dependence on time since fire ($P < 0.05$), but had non-significant overall models. These were frequency of *Chamaesyce deltoidea* subsp. *serpyllum* ($P = 0.1068$) (Figure 2D), density of *Bigelowia nuttallii* ($P = 0.8683$) (Figure 2A), and density of *Crotalaria avonensis* ($P = 0.1223$) (Figure 3B). Neither year since burn nor any other model variable significantly affected the percent flowering of *Bigelowia nuttallii* ($P = 0.2066$) (Figure 2B), number of flowering plants of *Marshallia ramosa* ($P = 0.2911$) (Figure 3D), or density of *Nolina brittoniana* ($P = 0.3708$) (Figure 3E).

ANOVA Results

Three of the nine species showed significant positive dependence of percent change in vital rates or abundance traits on fire. *Eryngium cuneifolium* density increased ($P = <0.0001$) (Figure 4E) gradually up to six years post-burn and remained at high population numbers for about six to nine years post-burn, before gradually declining. *Eriogonum longifolium* var. *gnaphalifolium* density increased significantly ($P <0.0001$) (Figure 4D) one year post-burn, followed by a sharp decline thereafter. Although site factors were significant for both traits measured for *Ribes echinellum*, percent reproduction increased the second year after burning ($P = 0.0096$) (Figure 5F); density increased steadily for three years after burn although no significant fire-dependence was found ($P = 0.2182$) (Figure 5E).

Six of the species showed no statistically significant response to year since fire. Traits followed for all these species were stable or showed some recovery after prescribed burns. Number of plants ($P = 0.4916$) (Figure 4A), percent reproduction ($P = 0.1018$) (Figure 4B), and number of recruits ($P = 0.0699$) (Figure 4C) of *Bonamia grandiflora* were independent of fire management. Responses were also not significant for density of *Liatris provincialis* ($P = 0.6716$) (Figure 4F), percent flowering of *Nolina brittoniana* ($P = 0.3371$) (Figure 5B), or number of plants of *Prunus geniculata* ($P = 0.6091$) (Figure 5C). Finally, two pine rockland species showed no statistically significant trends; neither *Linum arenicola* density ($P = 0.0968$) (Figure 5A) nor *Rhynchospora floridensis* frequency ($P = 0.3790$) (Figure 5D) changed over the duration monitored.

DISCUSSION

Across all species and life history traits, variables for nine of the 18 species (50%) showed statistically significant positive responses to fire, and variables for nine species (50%) showed neutral responses to fire. Responses varied across species, traits, and sites (Figures 2, 3, 4 and 5). No species showed a significantly negative response to fire.

Plant Adaptations to Fire

This work contributes to the growing documentation of fire requirements for viability of species. Post-burn resprouting and obligate seeding in other fire-dependent communities have been well documented, including the Mediterranean Basin (Canadell et al. 1991; Lloret and López-Soria 1993; Pausas 1997; Quintana et al. 2004), Australia (Zammit and Westoby 1987; Benwell 1998), southern California (Keeley and Zedler 1978; Moreno and Oechel 1993), the southern Andes (Burns 1993), southeastern Brazil (Cirne and Scarano 2001), in circum-boreal forests (Rowe 1983; Goto et al. 1996), and in South Africa (Holmes and Newton 2004). However, such mechanisms of fire adaptation have received less attention in Florida's pyrogenic habitats.

Recent work has documented mechanisms that contribute to species survival and viability in Florida scrub (Menges and Kohfeldt 1995; Carrington 1999; Weekley and Menges 2003; Menges 2007), sandhill (Menges and Deyrup 2001; Mulligan and Kirkman 2002), and pine rockland (Liu et al. 2005; Liu and Menges 2005). Adaptations that allow species to persist in habitats that burn include the ability to survive high temperatures and resprout after tissue loss. For example, the predominant pines of sandhills and pine rocklands, *Pinus palustris* P. Miller (longleaf pine) and *Pinus elliottii* var. *densa* Little and Dorman (Florida slash pine), respectively, have morphological adaptations that confer resistance to frequent, low intensity fires (Menges and Deyrup 2001). The growing meristems of seedlings of both species are protected close to the ground within a dense cluster of needles. As adults, both also shed lower branches and develop thick layers of bark.

Three species we document with significant responses to burning have been demonstrated to resprout after tissue loss from fire or other disturbance. One plant species native

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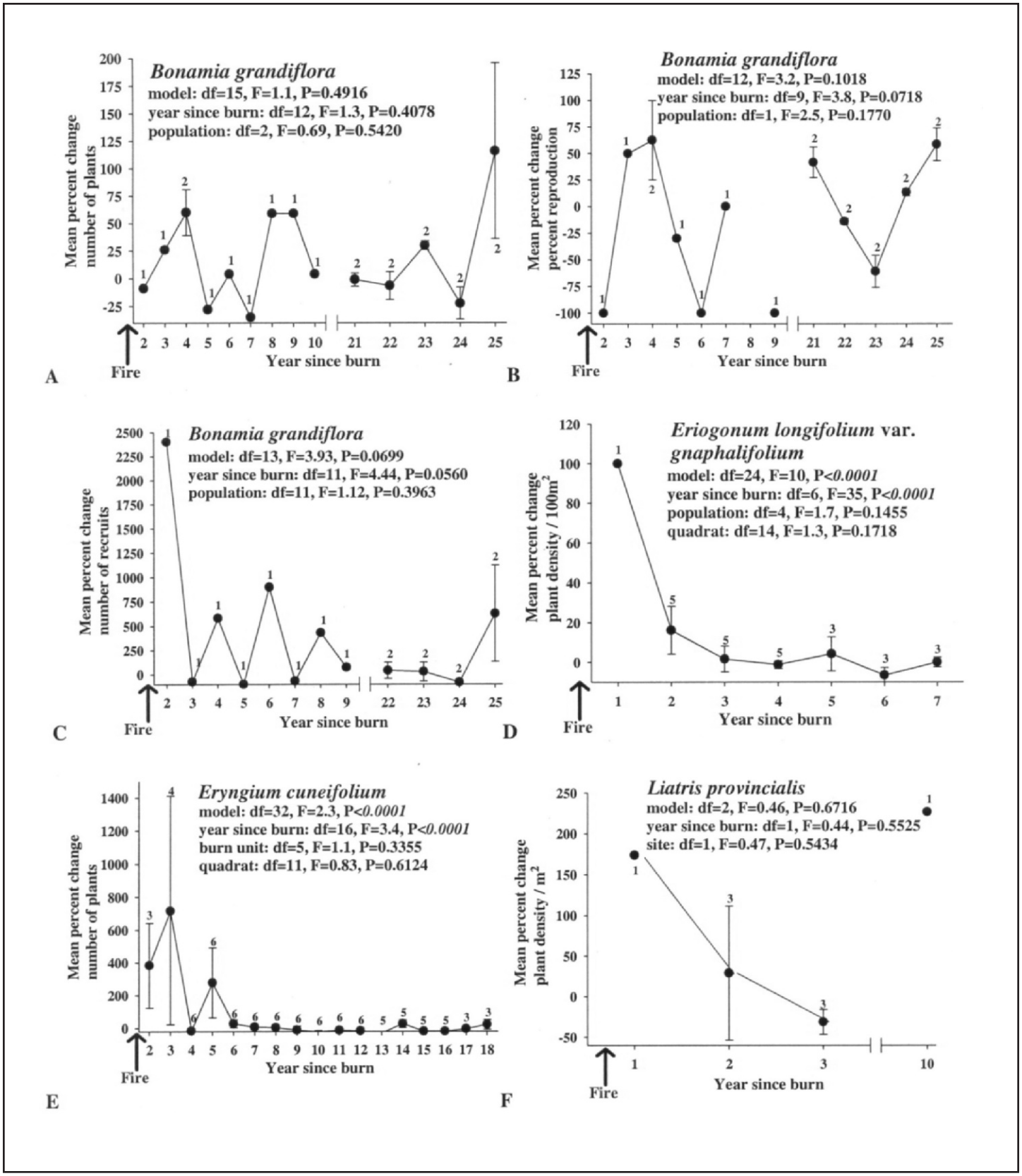


Figure 4. Species whose variables (A through F) were analyzed with analysis of variance using percent change data ($P < 0.05$). All graphs shown are ± 1 SE. Number above or below error bar denotes sample size. Significant p-values are italicized. Variable A = *Bonamia grandiflora* number of plants, B = *B. grandiflora* percent reproduction, C = *B. grandiflora* number of recruits, D = *Eriogonum longifolium* var. *gnaphalifolium* density, E = *Eryngium cuneifolium* number of plants, and F = *Liatris provincialis* density.

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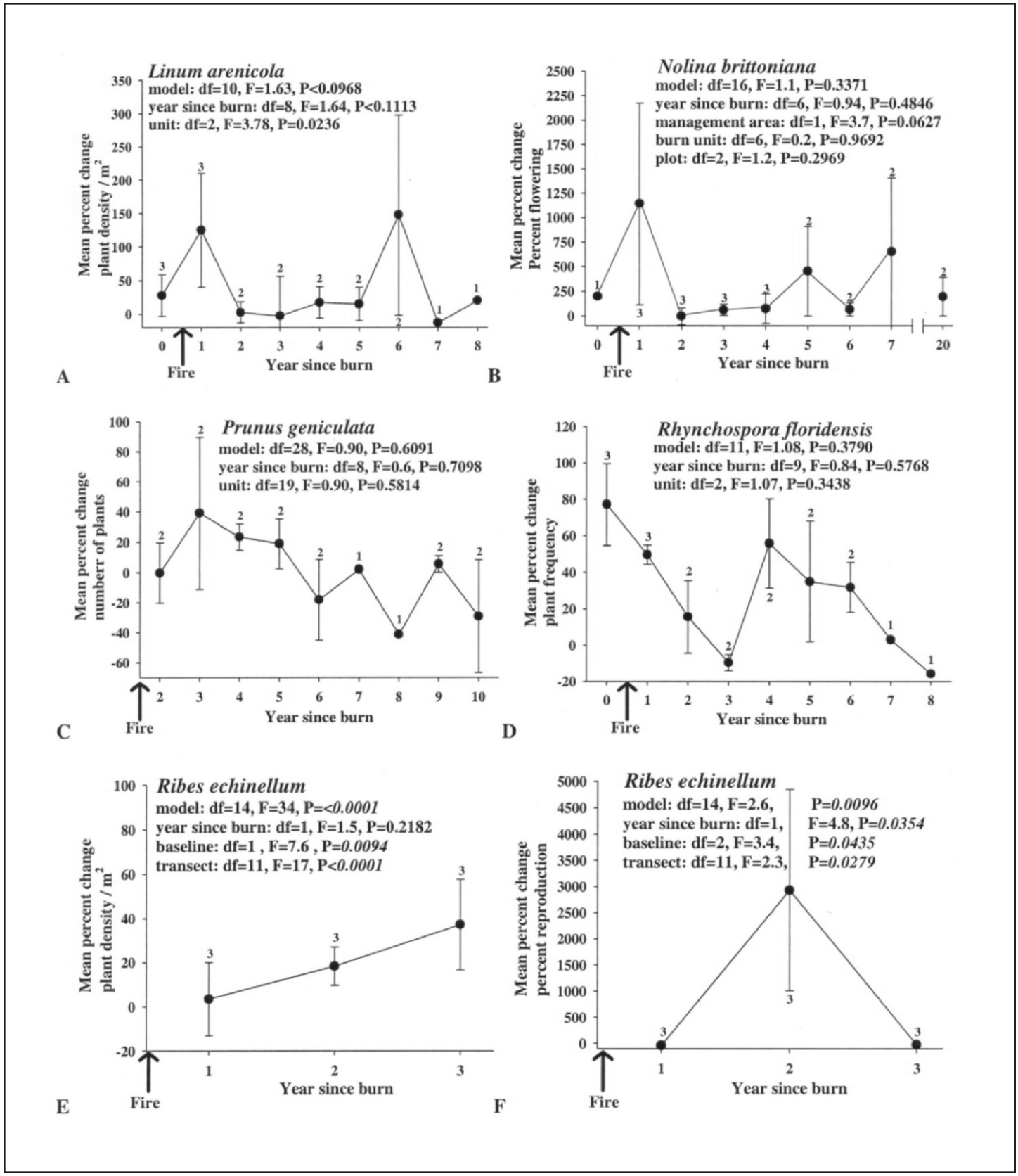


Figure 5. Species whose variables (A through E) were analyzed with analysis of variance using percent change data ($P < 0.05$). All graphs shown are ± 1 SE. Number above or below error bar denotes sample size. Significant p-values are italicized. Variable A = *Linum arenicola* density, B = *Nolina brittoniana* percent flowering, C = *Prunus geniculata* number of plants, D = *Rhynchospora floridensis* frequency, E = *Ribes echinellum* density, and F = *R. echinellum* percent reproduction.

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to sandhills, *Conradina glabra,* responds to frequent fire by resprouting and recruiting from seed after fire and is resilient to a range of fire return intervals (Gordon 1994; Menges 2007). Carrington (1999) reported that *Eriogonum longifolium* var. *gnaphalifolium* resprouts and flowers in response to fire and has strong post-burn seedling establishment responses within 19 months post-burn. Increases in reproductive output of this species result from increased flowering following fire (Satterthwaite et al. 2002). McConnell and Menges (2002) noted that seedling establishment of *E. longifolium* var. *gnaphalifolium* increases in burned areas due to litter removal as a result of burning. *Crotalaria avonensis* can resprout after low intensity fire (B. Pace-Aldana, Monitoring Biologist, The Nature Conservancy, pers. comm. 2008). This work demonstrates significant increases in flowering of *C. avonensis* the second year after burning. More post-burn data would be ideal for documenting further trends.

Species seen here to have neutral responses to fire have been documented to resprout in other studies. Weekley and Menges (2003) described *Bonamia grandiflora* as a strong resprouter with no significant differences in recruitment pre- or post-burn. Hartnett and Richardson (1989) reported increased reproduction and plant density of *Bonamia grandiflora* in recently burned plots via seedling recruitment and resprouting. We found no significant recruitment of *Bonamia grandiflora* after burning, although our low sample size may have influenced the result. We also found non-significant change in both plant density and flowering of *Nolina brittoniana* and number of plants of *Prunus geniculata* with time since burn. Weekley and Menges (2003) reported 98% survival of tagged *Nolina brittoniana* individuals and significantly higher post-burn stem densities of *Prunus geniculata*. As seen in this study, fire did not result in increased mortality in either species (Weekley and Menges 2003).

Other species in these pyrogenic habitats respond similarly to fire (Table 2), which can stimulate resprouting and flowering (Abrahamson 1984a; Kirkman et al. 1998; Carrington 1999; Yahr et al. 2000; Norman 2003), especially after cooler fires (Spier and Snyder 1998), increase cover (Reinhart and Menges 2004), and increase root and rhizome to shoot ratios (Hartnett 1987). Post-burn stimulation of flowering in some species may be delayed for several years (Ostertag and Menges 1994).

Other species are post-burn obligate seeders that are killed by fire but recruit from seed banks (Table 2). Demography of these species can provide information about likely natural fire return intervals (Menges 2007). Longer-lived species that recover from seed banks following fire should be better adapted to systems with longer fire intervals than should relatively short-lived perennials. Johnson (1982) hypothesized that fire return intervals shorter than about 10 years may eliminate *Ceratiola ericoides* Michx. (Florida rosemary) from scrub sites. Additionally, demographic transitions of some species are affected by time since fire (Evans et al. 2008). Multiple matrix population models, deterministic analyses, and stochastic simulations of *Chamaecrista lineata* var. *keyensi*s demonstrated that recently burned sites (1–2 years post-burn) had the highest finite population growth rates in this species of all sites (Liu et al. 2005).

Fire Management Implications

Habitat needs of wildlife species in Florida also suggest the historical frequency of fire for associated plant communities. *Aphelocoma coerulescens* (Bosc, 1795), or Florida Scrub Jay, often abandons habitat after scrub vegetation exceeds three meters in height (Woolfenden and Fitzpatrick 1984; Schmalzer et al. 1994; Breininger et al. 1999; Duncan et al. 1999) or if sand pine invades the site (Woolfenden and Fitzpatrick 1984). Species found in sandhill and flatwoods require groundcover and open midstories maintained within relatively frequent fire. Examples include *Gopherus polyphemus* (Daudin, 1802), or Gopher Tortoise, which requires sufficient cover of herbaceous forage found in open pinelands (Breininger et al. 1994; Hermann et al. 2002), and *Picoides borealis* (Vieillot, 1809), the Red-cockaded Woodpecker, which also requires an open midstory (Hovis and Labisky 1985; Kelly et al. 1994; James et al. 1997). Several species occur in habitats with significant cover of bare soil, including Florida Scrub Jay (Woolfenden and Fitzpatrick, 1984), *Sceloporus woodi* Stejneger, 1918, or Florida Scrub Lizard, and *Neoseps reynoldsi* Stejneger, 1910, or Sand Skink (Greenberg et al. 1994; Branch et al. 1999; Gianopulos 2001; Greenberg 2002).

Even where fire management remains an active practice, providing a variable or diverse fire regime may help benefit conservation of ecosystems in Florida (Abrahamson 1984b; Robbins and Myers 1992; Spier and Snyder 1998; Liu et al. 2005). In the last century, prescribed burners, especially those burning with silvicultural or rangeland goals, concentrated on winter burns to facilitate fire management and rejuvenate spring forage (Robbins and Myers 1992; Miller and Wade 2003). However, more natural growing season burns are essential for certain plant species. Several of those species showing neutral responses to prescribed fire management in this study were burned mainly in the winter or early spring (*Bigelowia nuttallii* was burned in February, *Marshallia ramosa* was burned in February and March, and *Nolina brittoniana* was burned from October through March). The timing of these fires may have been insufficient to stimulate the responses described above that should have facilitated positive responses to fire.

Fire Surrogates

Today, prescribed fire for conservation and agricultural purposes now generally replaces the natural and historic sources of fire (Robbins and Myers 1992). A recent analysis by the Florida Division of Forestry and the Florida Park Service identified as much as 40% (104,836 hectares of 262,090 managed hectares) of fire-dependant habitats managed by Florida state agencies to be fire suppressed (Hardin 2002). Difficulty of fire management in an increasingly developed landscape is resulting in substitution of mechanical (mowing, chopping, disking) and herbicide approaches for vegetation management.

These fire surrogates have been used to prepare sites for prescribed burns or replace burning entirely when it is considered no

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Table 2. Examples of plant species responses to fire in Florida's pyrogenic habitats from the literature.

Species	Response to fire	Habitat	Reference
Aristida stricta Michx.	Viable seed production	Sandhill, flatwoods	Duever 1989; Outcalt 1994; Mulligan and Kirkman 2002
Calamintha ashei (Weath.) Shinners	Increased seedling recruitment		Carrington 1999
Ceratiola ericoides Michx.	Obligate post-burn seed bank	Florida scrub	Johnson 1982
Chamaecrista lineata var. *keyensi* s	Obligate post-burn seed bank	Pine rockland	Liu and Menges 2005
Conradina brevifolia	Obligate post-burn seedbank	Florida scrub	B. Pace-Aldana pers. comm. 2008
Dicerandra frutescens	Obligate post-burn seed bank	Florida scrub	Quintana-Ascencio et al. 2003; Menges and Quintana-Ascencio 2004; Menges, unpublished data
Eryngium cuneifolium	Obligate post-burn seed bank	Florida scrub	Quintana-Ascencio et al. 2003; Menges and Quintana-Ascencio 2004; Menges, unpublished data
Garberia heterophylla (W. Bartram) Merr. and F. Harper	Resprout, stimulated flowering and recruitment	Florida scrub	Carrington 1999
Hypericum cumulicola (Small) P. Adams	Obligate post-burn seed bank	Florida scrub	Quintana-Ascencio et al. 2003
Lechea deckertii Small	Increased seedling recruitment	Florida scrub	Johnson and Abrahamson 1990
Lechea cernua Small	Increased seedling recruitment	Florida scrub	Johnson and Abrahamson 1990
Palafoxia feayi A. Gray	Resprout, stimulated flowering	Florida scrub	Ostertag and Menges 2004
Paronychia chartacea Fern	Increased seedling recruitment	Florida scrub	Johnson and Abrahamson 1990
Pinus clausa (Chapman ex Engelm.) Vasey ex Sarg.	Obligate post-burn seed bank, serotinous cones	Florida scrub	Outcalt and Greenberg 1998
Polygala lewtonii Small	Increased seedling recruitment	Sandhill	U.S. Fish and Wildlife Service 1999; Weekley and Menges unpublished data
Warea carteri	Obligate post-burn seed bank	Scrub, sandhill	Menges and Gordon 1996

longer feasible. Clear-cutting and salvage logging of *Pinus clausa* (Chapman ex Engelmann) Sargent (sand pine) in scrub (Greenberg et al. 1996; Provencher et al. 2000), hardwood reduction using herbicides and chain-saws in sandhills (Provencher et al. 2001), stand thinning in pine rocklands in southern Florida (Maschinski et al. 2005), and chopping or mowing in habitats from flatwoods to dry prairie to scrub (Watts et al. 2006; Williges et al. 2006) have all been used to mimic the structural and fuel reduction impacts of fire with some measure of success for some species. However, these approaches appear not to substitute for fire for some species considered keystone to these habitats. For example, *Aristida stricta* Michx. (pineland threeawn or wiregrass) will flower in response to various stresses like defoliation and soil disturbance (Parrott 1967); however, it needs a summer burn to produce viable seed (Duever 1989; Outcalt 1994). Mechanical treatments that are not

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followed by fire fail to allow recruitment of endemic Florida scrub herbs (Rickey et al. 2007), which is probably due to persistent litter that would otherwise be consumed by fire. Without understanding of the mechanisms behind responses of species like the ones examined here, we cannot be confident that these alternative approaches will have the desired effects on all components of the community.

Implications for Future Research and Monitoring

The duration of these monitoring projects, even those continued for over 10 years, may be insufficient to fully clarify patterns of response to fire. The lag time observed for positive responses, especially in the scrub species whose individuals initially die after burning, represents the time needed for seed germination and seedling growth. Longer monitoring and autoecological studies may clarify patterns for those species that had insignificantly positive responses to fire in this study. Alternatively, chronosequence studies that monitor populations at multiple sites with a range of times post-burn may be used to infer post-burn patterns (Menges 2007).

While these results cannot be used to identify life-history traits that are more closely associated with significant positive response to fire (reproductive traits were measured for six of the 18 species), several lines of evidence suggest that the absence of fire poses a more critical threat to persistence of these rare species than does its presence. Fire exclusion is predicted to cause local extinction of Florida scrub plants (Menges and Quintana-Ascencio 2004; Menges et al. 2006). With increased time since fire, rare and common species associated with longleaf pine-wiregrass habitats may decline (Provencher et al. 2001; Gray et al. 2003). Without fire, changes in community structure of sandhills will occur (Menges et al. 1993); such changes can be reversed if fire is re-introduced, potentially following fuel reduction treatments (Provencher et al. 2001; Reinhart and Menges 2004). While, more studies measuring multiple population variables in addition to abundance may help define associations of certain variables to fire and possibly provide future datasets for a more complex meta-analysis, lack of data on specific responses of individual rare species to fire in pyrogenic natural communities should not preclude fire management.

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