

## COMPETITIVE ABILITIES OF THREE NARROWLY ENDEMIC PLANT SPECIES IN EXPERIMENTAL NEIGHBORHOODS ALONG A FIRE GRADIENT<sup>1</sup>

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We conducted field experiments manipulating lichens, shrubs, and herbs along a time-since-fire gradient and assessing effects on three endemic herbaceous species of Florida scrub: *Eryngium cuneifolium*, *Hypericum cumulicola*, and *Polygonella basiramia*. Responses included seed germination, survival, biomass, and fecundity. Transplants into recently burned patches generally had higher survival, larger biomass, and greater reproductive output than transplants into long-unburned patches. Open areas and sites near oaks frequently were more favorable than sites near Florida rosemary. Ground lichens did not affect germination but increased mortality rate of seedlings. Neighboring small shrubby and herbaceous species did not affect the performance of these species. Of the three species, naturally occurring *E. cuneifolium* were farthest from large shrubs, and their microhabitats had the least ground lichens and shrubs. *Eryngium cuneifolium* and *H. cumulicola* are capable of forming persistent seed banks and their recruitment after fire depends mostly on these dormant seeds. *Polygonella basiramia* relies on seed dispersal and immediate seed germination to colonize recently burned patches. Management for these species should involve variable fire regimes to allow all three species to persist along with many other scrub endemics.

**Key words:** competition; disturbance; *Eryngium cuneifolium*; Florida scrub; *Hypericum cumulicola*; lichens; *Polygonella basiramia*; seed banks.

Fire is a major evolutionary and ecological force in many plant communities (e.g., Gill, 1975; Forman and Boerner, 1981; Christensen, 1985; Abrams, 1992; Whelan, 1995). The mechanisms proposed to explain fire effects on plant species include soil heating and burning, removal of competitors, and elimination of predators and herbivores (Tyler, 1996, and references therein). Short-term effects of fire on seed dormancy, germination, and establishment promote emergence because of changes in soil structure, nutrient levels, or allelochemicals. Long-term effects of fire on resource availability and aboveground biomass create opportunities for recruitment and growth (Tyler and D'Antonio, 1995; Tyler, 1995, 1996).

Understanding life history traits and ecological attributes limiting species abundance and range is necessary for improved land management. Comparative approaches

among co-occurring or related species can offer insights on limiting factors (e.g., Rabinowitz and Rapp, 1981; Fiedler, 1987; Prober, 1992; Byers and Meagher, 1997). Fire return intervals, fire intensity, and seasons of burn may affect species viability (Burgman and Lamont, 1992; Bradstock et al., 1996; Menges and Dolan, 1998; Enright et al., 1998). If species respond differentially to changes produced by different fire regimes, then trade-offs among species should be considered in management decisions. Land managers need to discern these trade-offs and make decisions to manage for mixtures of species or for particularly critical species.

The Florida scrub is a fire-maintained, shrubby association ranging from open communities dominated by Florida rosemary (*Ceratiola ericoides*) to dense stands of dwarf oaks (e.g., *Quercus inopina*, *Q. chapmanii*, and *Q. geminata*; Abrahamson and Abrahamson, 1996; Menges, 1998; nomenclature follows Wunderlin, 1998). *Eryngium cuneifolium*, *Hypericum cumulicola*, and *Polygonella basiramia* are perennial herbs nearly restricted to this community (Menges, 1998). These and other herbaceous species concentrate in gaps among shrubs where their density decreases with ground lichen cover (Abrahamson et al., 1984; Hawkes and Menges, 1996). Preliminary evidence suggests that their population dynamics is associated with periodic fires and the subsequent availability of open space that may reduce competition (Abrahamson, 1984; Johnson and Abrahamson, 1990; Hawkes and Menges, 1995; Menges and Kimmich, 1996; Quintana-Ascencio and Morales-Hernández, 1997). The distribution and demography of these species in different habitats suggest that they may have contrasting competitive abilities and gap size requirements. *Eryngium cuneifolium* has the most limited range and is restricted to large openings between shrubs (Menges and Kimmich, 1996). *Hy-*

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TABLE 1. Summary of experiments involving three herbaceous species in experimental competitive neighborhoods with different time-since-fire at Archbold Biological Station (ABS) and Lake Apthorpe Preserve (APT) in central Florida.

Expt.	Life stage	Caged	Sites	Treatments	Response variables
1	seed, seedlings	Yes	ABS, APT	(1) burned/not burned (2) lichens absent/present	germination, survival
2a	transplants <sup>a</sup>	No	ABS <sup>b</sup> , APT	(1) burned <sup>c</sup> /not burned (2) near rosemary/near oak/ open habitat	survival, biomass, fecundity
2b	transplants	Yes	ABS	burned-open habitat/not burned- near rosemary	survival, biomass, fecundity
3	established plants	No	ABS, APT	(1) burned/not burned (2) neighbor removal/no removal	survival, fecundity

<sup>a</sup> *H. cumulicola* and *E. cuneifolium* only in recently burned at Archbold.

<sup>b</sup> See Fig. 1 for treatment combinations.

<sup>c</sup> Recently burned patches did not contain large Florida rosemary, only near oak and open habitat.

*pericum cumulicola* has a wider distribution and can be found in intermediate size gaps. Their demographic performance is best shortly after fire (Menges and Kimmich, 1996; Quintana-Ascencio and Morales-Hernández, 1997). The higher incidence of *E. cuneifolium* and *H. cumulicola* in larger and more aggregated Florida rosemary scrub patches suggests their limited dispersal (Quintana-Ascencio and Menges, 1996). *Polygonella basiramia*, the most widespread species, grows in both large and small gaps in Florida scrub patches.

This study compares the effects of competition and fire on demographic responses of these three perennial herb species. The responses of seeds, seedlings, transplants, and established focal plants were examined in relation to variation in time since fire, lichen cover, and the importance of co-occurring herbs and shrubs, through a series of field experiments (Table 1).

## MATERIALS AND METHODS

**Study species**—The snakeroot *E. cuneifolium* Small (Apiaceae), The Highlands scrub hypericum *H. cumulicola* (Small) P. Adams (Hypericaceae), and the wireweed *P. basiramia* (Small) Nesom and Bates (Polygonaceae) are narrowly endemic to central Florida (Christman and Judd, 1990). These are short-lived, nonclonal, perennial herbaceous species with basal vegetative stems. All develop erect and branched reproductive stalks. *Eryngium cuneifolium* and *H. cumulicola* are bisexual and self compatible, and *P. basiramia* is gynodioecious (Menges and Yahr, 1998). *Hypericum cumulicola* and *P. basiramia* are obligate seeders, while *E. cuneifolium* can rarely resprout after fire (Menges and Kohfeldt, 1995). Seeds of *E. cuneifolium* (~1–2 mm wide) are at least 2–4 times larger than *H. cumulicola* seeds or *P. basiramia* achenes. *Eryngium cuneifolium* and *H. cumulicola* appear to disperse by gravity and have limited dispersal distances (<2 m; Menges et al., 1998). In contrast, the persistent calyxes of the achenes of *P. basiramia* appear to be adapted for wind dispersal.

**Study sites**—We established field experiments at The Nature Conservancy's Lake Apthorpe Preserve (Apthorpe) and at Archbold Biological Station (Archbold). Both sites are located in the southern part of the Lake Wales Ridge, Florida, and are characterized by a mosaic of Florida scrub, flatwoods, and seasonal ponds (Abrahamson et al., 1984; Menges, 1998; Menges and Hawkes, 1998). Our study sites included three recently burned and three long-unburned rosemary scrub patches. This is a particularly open and xeric type of Florida scrub restricted to well-drained white sands (Abrahamson et al., 1984; Menges and Hawkes, 1998; Menges, 1998). Prescribed fires were applied in April 1994

at Apthorpe, and in September 1993 and May 1995 at Archbold (Kevin Main and Steve Shatler, personal communication). The three long unburned scrub patches have been without fire for at least 20 yr, but include some large openings of bare sand.

**Seed germination, fire, and lichens (experiment 1)**—We sowed seeds of the focal species with and without ground lichens in recently and long-unburned patches. We collected up to four mature fruits of *E. cuneifolium*, *H. cumulicola*, and *P. basiramia* from individual plants. Fruits were opened in the laboratory and examined under the microscope to select seeds without signs of damage or deformation. The seeds were temporarily stored in aluminum foil within labeled paper bags.

We placed 20 triplets of wire mesh cages (one cage per species; 20 × 20 × 4 cm with 0.6 cm mesh) every 5 m along random transects in recently burned rosemary scrub and in available gaps at least 1 m from the closest Florida rosemary in long-unburned rosemary scrub. Within each triplet, seeds of each species were placed in their own cage (*E. cuneifolium*, 20 fruits, November 1995; *H. cumulicola*, 80 seeds, July and September 1995, sown twice to mimic its longer fruiting season; *P. basiramia*, 40 fruits, December 1995). In half of the cages, we added a 3 cm width thallus fragment from each of the two most common ground lichen genera at the study sites, *Cladonia* spp. (mostly *C. leporina*) and *Cladina* spp. (mostly *C. evansii*). Seeds were deposited on the ground inside partially buried dark green plastic pots (13 × 11 × 5 cm pots without bottoms for drainage) within the cages, and watered once. We also placed two control groups of each species outdoors on filter paper within a petri dish and followed their germination for 4 mo. Seeds, seedlings, and other biological material for all our experiments were not transferred among sites. Response variables were percentage germination and subsequent seedling survival.

Log-linear models were employed to compare differences in the proportion of cages with germinated seeds (P) among sites (S), fire (B), and lichen treatments (L). The significance of an interaction was measured relative to the model to which it was added. We used BLS,P as "null model," assuming that this table reflects treatment distribution of the cages and the frequency of cages with seedlings, but this frequency is independent of site, fire, and lichens (Fienberg, 1987). We used Mann-Whitney *U* tests to examine seedling number variation among the same treatments.

**Effects of shrubs on transplanted plants (experiment 2)**—We transplanted *E. cuneifolium*, *H. cumulicola*, and *P. basiramia* to microsites in the center of open sandy areas and in the proximity of dominant shrub species. We used Florida rosemary scrub patches with different fire histories and protected some plants from large herbivores.

**Culture, transplantation, and plant measurements**—We germinated *E. cuneifolium*, *H. cumulicola*, and *P. basiramia* seeds on humid filter

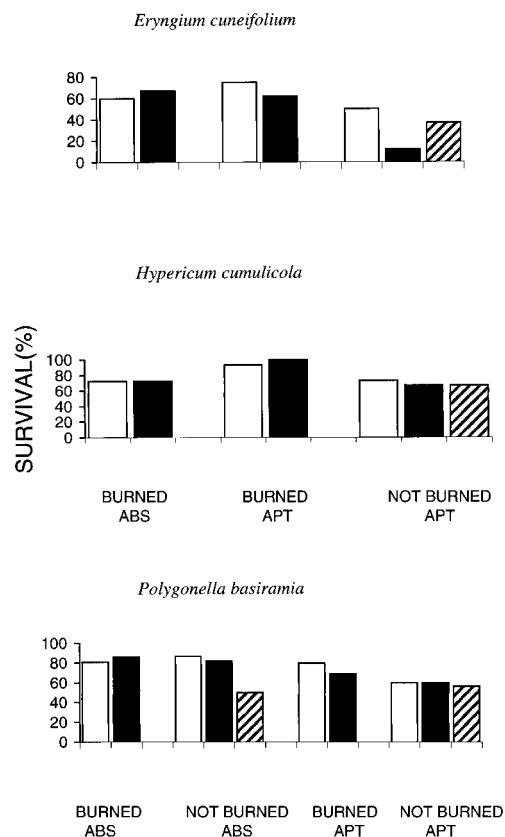


Fig. 1. Survival of transplanted *Eryngium cuneifolium*, *Hypericum cumulicola*, and *Polygonella basiramia* into open habitat (open bars), near oak (dark bars), and near Florida rosemary (hatched bars) in burned and unburned scrub patches at Archbold (ABS) and Apthorpe (APT).

paper in petri dishes and transplanted 2–5 d old seedlings to plastic bags (~250 mL [8 oz] disposable baby feeding bottles) with local soil (see Table 1). The seedlings were watered as needed, kept under 40 W fluorescent lamps (F40 agrolite, 1600 lumens) in a unheated greenhouse, and later transplanted to the field. We also excavated 100 *P. basiramia* juveniles (before they developed reproductive stems) from each site between 26 September and 2 October 1995. We used a 20 × 6 cm PVC (polyvinyl chloride) tube and a mallet to unearth the plants. The sand cylinder with the plant was transferred to a plastic bag (~250 mL disposable baby feeding bottles), watered, and kept in a greenhouse until transplanting. All plants were transplanted to the field in April 1996 except *P. basiramia* juveniles in February 1996. We made holes with a soil auger (8 cm wide) to receive the transplants and removed litter, ground lichens, and plants within a 10 cm radius. Plants were watered once after transplant (~0.5 L).

We measured height and branch length (or cover) at the time of transplanting and height, branch length (or cover), reproductive status, survival, and damage by large herbivores monthly until November 1996. Fecundity (number of flowers and fruits for *H. cumulicola* and number of clusters for *P. basiramia*) was evaluated in July, October, and November 1996. Plants were removed from the soil in November 1996, dried (Fisher Isotemp Oven Senior Model/Forced draft, Göttingen, Germany) for 48 h, and weighed (Sartorius scale model 1264; 0.01 g). There were no significant differences in height and branch length (or cover) at transplant time among individuals of the same species in contrasting microhabitats within sites, except for the height of *H. cumulicola* transplanted in Apthorpe ( $F = 2.62$ ,  $P = 0.043$ , df 4, 68).

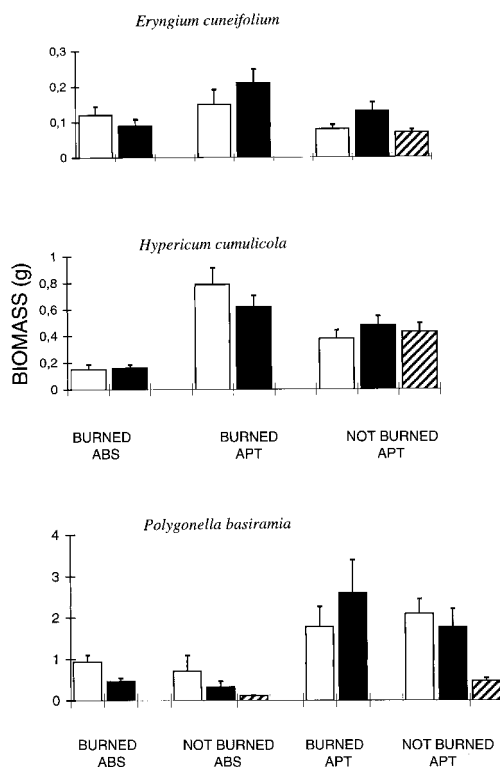


Fig. 2. Final biomass (mean and SE) of transplanted *E. cuneifolium*, *H. cumulicola*, and *P. basiramia* into open habitat (open bars), near oak (dark bars) and near Florida rosemary (hatched bars) in burned and unburned scrub patches at Archbold (ABS) and Apthorpe (APT).

**Experiment 2a: plants without cages**—We transplanted *E. cuneifolium* ( $N = 6, 5, 7, 8, 7, 6, 7$ , habitat order as in Figs. 1 and 2), and *H. cumulicola* ( $N = 17, 18, 15, 13, 15, 15, 15$ ) seedlings and *P. basiramia* juveniles ( $N = 16, 18, 15, 13, 8, 8, 11, 15, 15, 16$ ) unprotected from large herbivores to five experimental microsites resulting from combinations of two different levels of time-since-fire (recently burned and long-unburned patches) and three microhabitats defined by shrub distance and shrub species (Florida rosemary height =  $119.9 \pm 46.4$  cm [mean and standard deviation]; *Quercus* spp. height =  $78.8 \pm 29.6$  cm, and  $97.3 \pm 39.6$  cm in time since fire, respectively). Microhabitats adjacent to shrubs were shaded part of the day. We used three microsites near the southern end of natural gaps: (1) open habitat—1 m away from any oak canopy and 2 m from any Florida rosemary canopy; (2) near oak—below the drip line of the northern margin of an oak canopy bordering an open area; and (3) near Florida rosemary—below the drip line of the northern margin of the canopy of a Florida rosemary bordering an open area. These three treatments were not applied to *E. cuneifolium* and *H. cumulicola* in the long-unburned area at Archbold. We used only two microsites in recently burned patches: (1) open sites; (2) near oak. Recently burned patches contained only seedlings of Florida rosemary. We distributed transplants randomly among treatments within sites. One individual of each species was included in a replicated triplet (except as indicated), 20 cm apart from each other focal plant in each microhabitat studied. Final sample size was reduced by exclusion of plants disturbed by animals (probably raccoons).

**Experiment 2b: seedlings inside cages**—We transplanted seedlings of *E. cuneifolium* ( $N = 13, 14$ , habitat order as in Fig. 4), *H. cumulicola* ( $N = 14, 13$ ), and *P. basiramia* ( $N = 10, 13$ ) into microsites protected from large herbivores. We chose two microhabitats in Florida rosemary scrub patches at Archbold: (1) open habitat in a recently burned patch,

TABLE 2. (A) Estimates of germination and seedling dynamics at two sites, Archbold and Apthorpe, for the three study species. G = proportion of cages with seedlings ( $N = 10$  cages per species per treatment); M = mean proportion of seeds germinated in cages with seedlings; and F = mean proportion of seedlings remaining at the end of the experiment in November 1996 (within cages with seedlings). (B) Log-linear tests of cage number with seedlings among treatments. B = burn condition, L = lichen treatment, S = site, P = seedling presence (\* =  $P < 0.003$ , NS = not significant, NA = not analyzed).

Fire history	Lichen presence	Species								
		<i>E. cuneifolium</i>			<i>H. cumulicola</i>			<i>P. basiramia</i>		
		G	M	F	G	M	F	G	M	F
<b>A)</b>										
<b>Archbold</b>										
Burned	no	0.20	0.20	0.62	0.20	0.05	0	0.80	0.29	0.13
	yes	0.10	0.05	0	0.20	0.02	0	0.80	0.26	0.12
Unburned	no	0	0	0	0.10	0.04	0	0.60	0.32	0.37
	yes	0.20	0.08	0	0.20	0.06	0	0.90	0.42	0.15
<b>Apthorpe</b>										
Burned	no	0	0	0	0.30	0.03	0.48	1.00	0.60	0.45
	yes	0	0	0	0.30	0.01	0	1.00	0.50	0.25
Unburned	no	0	0	0	0	0	0	1.00	0.53	0.21
	yes	0	0	0	0	0	0	1.00	0.45	0.13
<b>B)</b>										
BLS, P		NA			NS			14.1		
BLS, PS					NS			4.4		
PS					NS			9.7*		
BLS, BLP		NA			NS			12.9		
BLS, BLP, PS					NS			3.1		
PS					NS			9.9*		

approximately every 5 m along two random transects, at least 2 m from the nearest oak; and (2) near Florida rosemary in a long-unburned patch, below the drip line of the northern margin of the shrub canopy bordering an open area. We distributed transplants randomly (one individual of each species per group) and 20 cm from every other focal plant. Each group of plants was enclosed in a wire mesh cage (46 × 46 × 40 cm and 0.6 cm mesh).

Contingency tables and *G* tests were used to compare differences in survival of transplants between shrub treatments. We described growth variation within species only in terms of biomass because of the high correlation between size variables ( $r^2 = 0.63-0.82$ ,  $P < 0.001$  in every case). The significance of differences in final aboveground biomass (natural-log transformed) among transplants in different microhabitats was evaluated with analysis of variance for *H. cumulicola* and *P. basiramia*. An exact randomization test was employed for *E. cuneifolium* biomass data because of its small sample sizes (Sokal and Rohlf, 1981). The effect of fire and microhabitat on total number of reproductive structures (using height as a covariate) was assessed using analysis of covariance.

**Effect of experimental removal of neighbors (experiment 3)**—We evaluated the effect of neighboring herbaceous and small shrub species around 20 naturally occurring focal individuals of each of our study species per site. Plants were selected in a stratified random fashion, along the center of randomly located 2 m wide belt transects. We compared naturally occurring *H. cumulicola* individuals in a recently burned rosemary scrub patch with those in a long-unburned scrub patch, at Archbold and Apthorpe. We studied *P. basiramia* from the same long-unburned scrub patches, but this species was not present in recently burned patches. *Eryngium cuneifolium* was examined in the same recently burned scrub at Apthorpe and at the border of a rosemary scrub at Archbold. We removed all plants and ground lichens within 30 cm of half of all focal plants in June 1995 and January and June 1996. We counted number of stems and total number of reproductive structures (flowering stalks of *P. basiramia*) and measured height and total branch length of each focal *H. cumulicola* and *P. basiramia*, and maximum width and its perpendicular width for each *E. cuneifolium*.

We counted and identified all rooted plant species, recorded the pres-

ence of ground lichens within 15 cm of studied individuals, measured the distance of every individual to the nearest oak and Florida rosemary, and measured the height of these shrubs. We used Detrended Correspondence Analysis in PC-ORD (McCune, 1993) to depict multivariate changes in dominance of species neighborhoods for each focal species in recently burned and long-unburned sites.

RESULTS

**Seed germination, fire, and lichens (experiment 1)**—Germination and soil seed dynamics were different among the three study species. Seed germination was highest for *P. basiramia*. Most (>95%) seeds of *P. basiramia* in the control petri dishes germinated during the first 4 d following their placement outdoors. However, after ~120 d, only 20–40% *H. cumulicola* seeds and 5–20% *E. cuneifolium* seeds in the petri dishes germinated. In the field, seeds started germinating by December 1995. *Polygonella basiramia* seedlings were present in most of the cages within 1 mo of sowing, and between 12 and 45% of them remained alive after 14 mo (Table 2). By January 1996, *H. cumulicola* seedlings occurred in <30% of cages and no more new seedlings of these species were found after March 1996. *Hypericum cumulicola* seedling survival was generally low. We did not find any seedlings of *E. cuneifolium* during the first 9 mo, but a few seedlings germinated between December 1996 and January 1997, a year after sowing (Table 2).

Site and lichen presence affected *P. basiramia*. The proportion of cages with *P. basiramia* seeds germinated (Table 2) and final seedling number per cage ( $z = -2.11$ ;  $P = 0.03$ ) were higher in Apthorpe than Archbold. Neither fire history nor presence of ground lichens affected the proportion of cages with *P. basiramia* seeds germinated. Final seedling number was higher in cages without lichens than with lichens in both sites but only statisti-

TABLE 3. Results of analysis of variance of biomass (log-transformed) and analysis of covariance for fecundity of transplanted-uncaged *Hypericum cumulicola* and *Polygonella basiramia* in different microhabitats in burned and unburned scrub patches.

Source	<i>H. cumulicola</i> , Apthorpe				<i>P. basiramia</i> , both sites			
	df	MS	F	P	df	MS	F	P
<b>Biomass</b>								
Site (S)					1	24.97	21.91	>0.001
Fire (F)	1	2.97	5.77	0.02	1	2.76	2.45	0.12
Microhabitat (M)	2	0.16	0.30	0.74	2	4.26	3.73	0.03
S × F	1				1	4.47	3.92	0.05
S × M	2				2	2.17	1.91	0.15
M × F	1	0.84	1.63	0.21	1	1.04	0.91	0.34
S × F × M	1				1	1.24	1.09	0.30
Error	56	0.51			81	1.14		
<b>Fecundity</b>								
Height, Nov96	1	61 756	14.90	0.001	1	300 816	39.12	>0.001
Site (S)					1	3674	0.48	0.49
Fire (F)	1	26 187	6.32	0.018	1	27 244	3.54	0.06
Microhabitat (M)	2	27 545	6.64	0.004	2	2141	0.28	0.76
S × F	1				1	50 386	6.55	0.01
S × M	2				2	244	0.32	0.97
M × F	1	24 443	5.90	0.022	1	4828	0.63	0.43
S × F × M	1				1	389	0.05	0.82
Error	56	4146			81	7693		

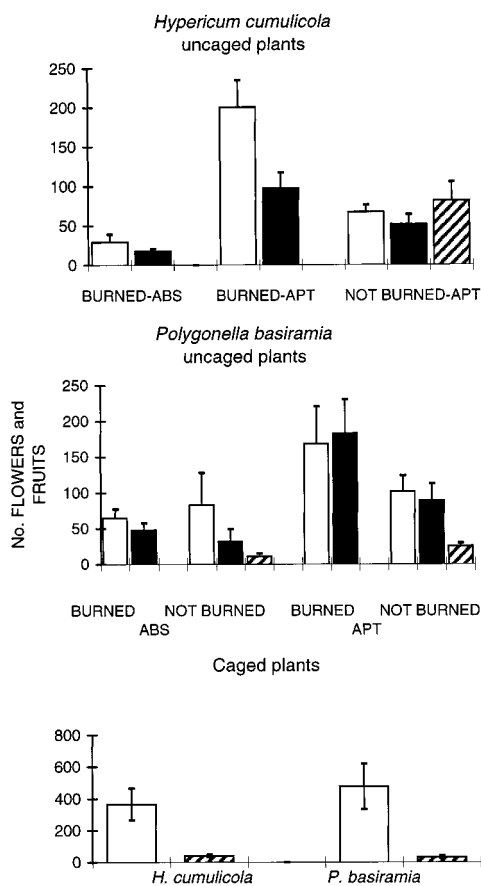


Fig. 3. Reproductive output of *H. cumulicola* and *P. basiramia* transplanted into open habitat (open bars), near oaks (dark bars), and near Florida rosemary (hatched bars) in burned and unburned scrub patches at Archbold (ABS) and Apthorpe (APT) unprotected and protected by cages.

cally significant in Archbold ( $z = -2.185$  and  $P = 0.03$  for Archbold;  $z = -1.779$  and  $P = 0.07$  for Apthorpe). We could not analyze the responses of *E. cuneifolium* and *H. cumulicola* seeds and seedlings to the presence of ground lichens, fire history, or site because of their low germination rates (Table 2).

**Effects of shrubs on transplanted plants (experiments 2a and 2b)**—The effects of fire and shrub presence on survival differed among the three study species. Survival of *E. cuneifolium* and *H. cumulicola* transplanted without cages was significantly higher in recently burned patches than in long-unburned patches at Apthorpe (Fig. 1;  $G = 3.94$ , 1 df,  $P = 0.047$  for *E. cuneifolium*;  $G = 9.73$ , 1 df,  $P = 0.002$  for *H. cumulicola*). We found no significant survival differences for *E. cuneifolium* and *H. cumulicola* transplanted to different microhabitats (oak, rosemary, or open), nor any significant effects of fire or microhabitat on *P. basiramia* survival in either site (Fig. 1;  $P > 0.15$  for any test). Survival rates were fairly high for transplants in most treatments (Fig. 1).

Fire or shrub presence differentially affected final biomass of all three study species. Final biomass of surviving *E. cuneifolium* transplants in Apthorpe was higher near oaks in recently burned patches than in any other microhabitat (Fig. 2;  $P = 0.028$ , randomization test). Final biomass of surviving *H. cumulicola* transplants was higher in the burned area at Apthorpe, but no significant differences were found due to shrub microhabitat (Fig. 2; Table 3). *Polygonella basiramia* transplants in Apthorpe and near oaks and in open habitats had higher final biomass (Fig. 2; Table 3).

Fecundity also varied by treatment. The number of reproductive structures was larger in open burned habitats for *H. cumulicola* in Apthorpe (Fig. 3; Table 3). *Polygonella basiramia* transplanted to the recently burned patch in Apthorpe had higher fecundity than those transplanted to the long-unburned patch (Fig. 3; significant interaction  $S \times F$  in Table 3) but we did not find any

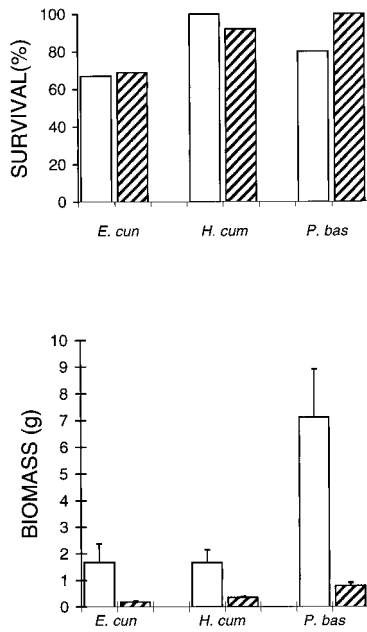


Fig. 4. Survival and final biomass (mean and SE) of *E. cuneifolium*, *H. cumulicola*, and *P. basiramia* transplanted protected by cages into open-burned habitat (open bars) and near Florida rosemary (hatched bars) in Archbold.

significant differences in Archbold (Fig. 3). The *Polygonella basiramia* gender ratio was not significantly heterogeneous inside treatments (39 females and 32 hermaphrodites;  $G = 1.47$ , 4 df,  $P = 0.831$ ). Transplanted *E. cuneifolium* did not flower during the study interval.

We found evidence of herbivory on *E. cuneifolium*, *H. cumulicola*, and *P. basiramia* throughout the study period. Many damaged plants were clipped to the base.

After 7 mo, the three species protected inside cages had lower performance when transplanted near Florida rosemary in the long-unburned patch than in the open habitat of the recently burned patch, but they varied in the strength of their response. Survival of *E. cuneifolium* was significantly lower than that of *P. basiramia* and *H. cumulicola* in both patch types (Fig. 4;  $G = 7.60$ , 2 df,  $P = 0.022$  and  $G = 7.52$ , 2 df,  $P = 0.023$  in recently and long-unburned patches, respectively). Survival within species was not significantly different among patches. Final biomass was lower near rosemary in the long-unburned patch than in the open area of the recently burned patch for each of the three species (Fig. 4; Table 4). By the end of the trial *P. basiramia* reached higher biomass than *H. cumulicola*, which was heavier than *E. cuneifolium* (Fig. 4; Table 4). *Hypericum cumulicola* and *P. basiramia* transplanted near rosemary in the long-unburned patch flowered later and had lower reproductive output and reproductive effort than those in the recently burned patch (Figs. 3, 5; Table 4). *Eryngium cuneifolium* did not flower during the experiment.

**Effect of experimental removal of neighbors (experiment 3)**—After 12 mo, <20% of target *H. cumulicola* and *E. cuneifolium* died, but 50–80% (by site and microhabitat combination) of *P. basiramia* perished. Reproductive effort (number of flowers and fruits/height)

TABLE 4. Results of analysis of variance of biomass (log-transformed) and covariance of fecundity of *Eryngium cuneifolium*, *Hypericum cumulicola*, and *Polygonella basiramia* transplanted caged to open habitat in a burned patch and near Florida rosemary in an unburned patch at Archbold.

Source	df	MS	F	P
<b>Biomass</b>				
Species (S)	2	15.47	19.98	<0.001
Microhabitat (M)	1	36.88	47.63	<0.001
S × M	2	0.76	0.99	0.378
Error	62	0.77		
<b>Fecundity of <i>H. cumulicola</i></b>				
Height in October (H)	1	367 472	7.83	0.012
Microhabitat (M)	1	231 731	4.93	0.040
H × M	1	330 199	7.03	0.017
Error	17	46 953		
<b>Fecundity of <i>P. basiramia</i></b>				
Height in October (H)	1	548 776	12.83	0.002
Microhabitat (M)	1	274 234	6.41	0.019
H × M	1	470 843	11.01	0.003
Error	22	42 769		

of focal *H. cumulicola* in June 1996 (the beginning of reproductive season) was not significantly different between site, time since fire, or removal treatments (any  $P > 0.166$ ). In June 1996, there were no reproductive structures on any focal *E. cuneifolium* or *P. basiramia*.

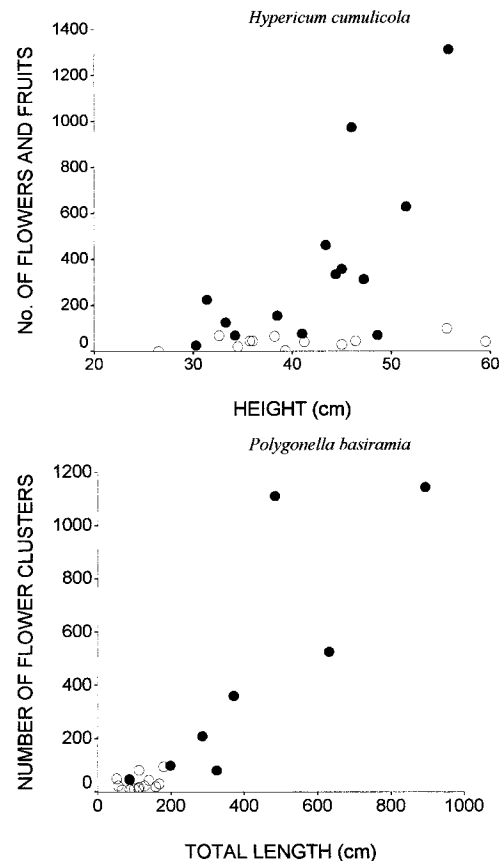


Fig. 5. Reproductive effort of *H. cumulicola* and *P. basiramia* transplanted protected by cages into open-burned habitat (closed circles) and near Florida rosemary (open circles) in Archbold.

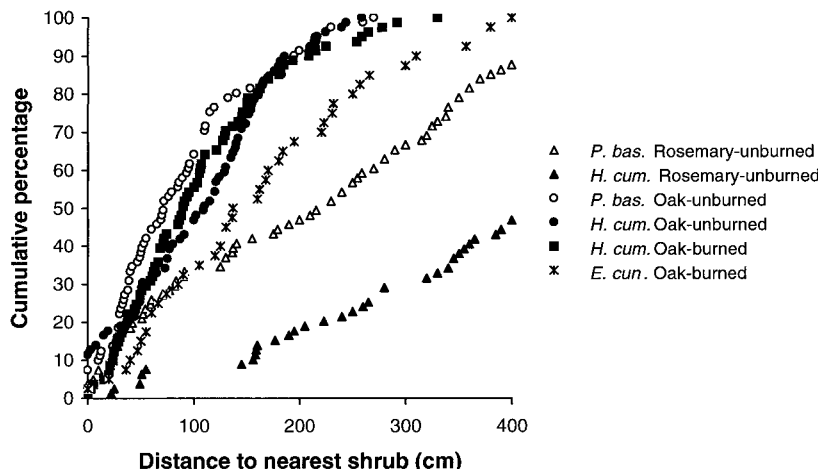


Fig. 6. Plot of cumulative percentage of individuals of naturally established individuals by distance to nearest shrub (sites pooled).

*Analysis of microhabitat characteristics*—We found *E. cuneifolium*, *H. cumulicola*, and *P. basiramia* in contrasting locations on gradients of distance to shrubs, presence of lichens, and neighbor floristic composition and abundance. In long-unburned patches, *P. basiramia* occurred closer to oaks and rosemary than *H. cumulicola* (Fig. 6). In recently burned patches (which lacked *P. basiramia*), *H. cumulicola* occurred closer to oaks than *E. cuneifolium* (Fig. 6).

Ground lichens were present in 60–75% of the neighborhoods of *P. basiramia* and *H. cumulicola* in long unburned patches, but in <20% of *E. cuneifolium*. Fewer than 30% of the neighborhoods of *H. cumulicola* and *E. cuneifolium* had ground lichens in the patches 2–3 yr postfire.

We found >30 species in the study species' neighborhoods, including grasses, forbs, and shrubs. Conspecifics were frequent in the neighborhoods of the focal species. *Paronychia chartacea* and *Stipulicida setacea*, two small

herbaceous species common in open areas, were the most frequent neighbor species. Neighborhood species richness and abundance were highest for *E. cuneifolium* and lowest for *P. basiramia*.

There were significant effects of study site and focal species on scores of the first axes of the neighbor floristic gradients detected by DECORANA ordination (eigenvalue 0.817,  $N = 294$ ; Table 5). The neighborhoods of *E. cuneifolium* were subsets of the neighborhoods for the other two species and grouped in the lower left portion of the cloud of points in the space defined by the first two axes of the ordination (Fig. 7). This portion of the graph was mostly characterized by herbaceous species and a few common shrubs (*Opuntia humifusa* and *Palafoxia feayii*). The neighbors of *P. basiramia* and *H. cumulicola* overlapped considerably and had a wider distribution in the ordination space.

DISCUSSION

Understanding the relative importance of direct and indirect fire effects on postfire responses of herbaceous species is central for wise management (e.g., Tyler, 1996, and references therein). Demographic variation in response to changes in shrub and lichen cover importance may help to explain the contrasting distribution of *Eryngium cuneifolium*, *Hypericum cumulicola* and *Polygonella basiramia* along a time-since-fire gradient. Observed species patterns were concordant with their differential

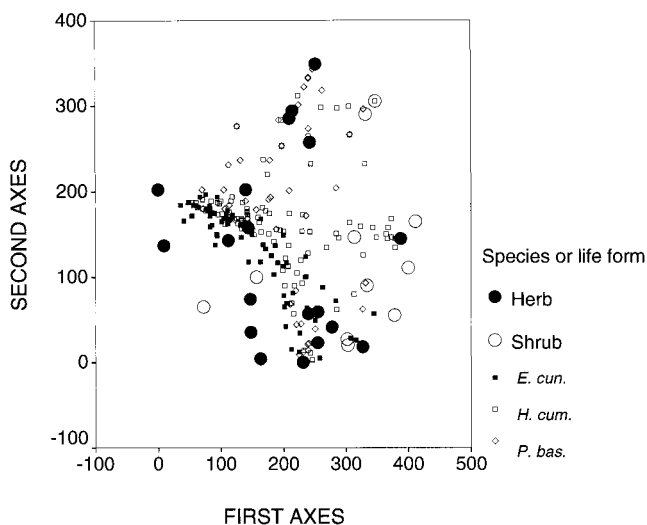


Fig. 7. Plot of the first two axes of a DECORANA ordination of species' neighborhoods for the three focal species (*E. cuneifolium*, *H. cumulicola*, and *P. basiramia*; shown by small symbols). Locations of the neighbor species are shown by large symbols.

TABLE 5. Results of analysis of variance of the effects of focal species, removal treatment, and study site on scores of the first axes of the neighbor floristic gradients detected by DECORANA ordination.

Source	df	MS	F	P
SPECIES (P)	2	44 424	11.377	<0.001
REMOVAL (R)	1	194	0.050	0.824
SITE (S)	1	818 383	209.594	<0.001
S × R	1	3169	0.812	0.368
S × P	2	7922	2.029	0.133
R × P	2	1520	0.389	0.678
S × R × S	2	8921	2.285	0.104
Error	282	3905		

sensitivity to fire, presence or absence of gaps and patch size. *Polygonella basiramia* survival and biomass were least affected by time since fire, but its seedlings showed increasing mortality near ground lichens. Previous work found *P. basiramia* natural densities were unrelated to time since fire but sensitive to the amount of open sand (Hawkes and Menges, 1995). The lower survival and biomass of transplanted *H. cumulicola* and *E. cuneifolium* in long-unburned patches were similar to that found in naturally occurring populations (Menges and Kimmich, 1996; Quintana-Ascencio and Morales Hernández, 1997). A 10-yr study of *E. cuneifolium* populations documented their extinction in Florida rosemary scrub patches between 20 and 30 yr postfire (Menges and Yahr, 1998). Mortality in *H. cumulicola* is lowest shortly after fire, although subsequent patterns are more complex (Quintana-Ascencio, 1997). Overall mortality rates were higher for *P. basiramia* than for the other species, consistent with demographic differences seen in long-term studies (Menges and Kimmich, 1996; Quintana-Ascencio and Morales-Hernández, 1997; Menges, unpublished data).

The analysis of microhabitats that is part of this study provides additional detail on the microsites within gaps where these three species can grow. *Eryngium cuneifolium* appears more sensitive to gaps (Menges and Kimmich, 1996), its microhabitats were farther from large shrubs, less covered by lichens, and floristically characterized by more herbaceous and fewer shrub species than the other two species. *Polygonella basiramia* requires only small gaps and can even persist in the small, rather ephemeral gaps of scrubby flatwoods (Young and Menges, 1999).

Because there are predictable changes in rosemary community structure as the sites age between fires (Hawkes and Menges, 1996), the explanations based on fire and gaps are complementary. As rosemary sites age, the cover of lichens and the abundance of large shrubs increase (Menges and Kohlfeldt, 1995). Growth of shrubs, especially Florida rosemary, decreases gap sizes and area (Hawkes and Menges, 1996). As gaps shrink, microhabitats become less favorable first for *E. cuneifolium*, later for *H. cumulicola*, and finally for *P. basiramia*.

What makes postfire environments and open gaps so critical for *E. cuneifolium* and *H. cumulicola*? There are at least seven possible and nonmutually exclusive hypotheses (modified from Sousa, 1984). These involve competition from large shrubs, competition from small shrubs and herbs, competition from ground lichens, competition from the cryptobiotic soil crust, direct effects of fire, differential herbivory, and seed dormancy and germination.

This study addresses many of these hypotheses, although not all the answers are clear. Herbaceous species in unburned sites often survive at higher rates after shrub removal or trenching to reduce their root competition (e.g., Swank and Oechel, 1991; Tyler, 1996). In our study, large shrubs that border the gap appear to have differential effects depending on the shrub species. Neighboring oaks in recently burned patches facilitate the growth of transplants. However, neighboring rosemary shrubs often were associated with the slowest growth rates of our study species. Since Florida rosemary is killed by fire and has only small seedlings in recently

burned sites, its effects are difficult to completely separate from the effects of fire per se. In natural populations, rosemary shrub presence, size, and distance proved to be among the most important factors predicting demographic performance of *E. cuneifolium* (Menges and Kimmich, 1996) and *H. cumulicola* (Quintana-Ascencio and Morales-Hernández, 1997). The mechanisms could involve allelochemicals that affect germination of other species (Williamson, Obee, and Weidenhamer, 1992).

On the other hand, there were no significant effects of small shrubs and herbs within the gaps on the performance of transplants in this study. This is consistent with their lack of effects on naturally occurring *E. cuneifolium* (Menges and Kimmich, 1996), *H. cumulicola* (Quintana-Ascencio and Morales-Hernández, 1997), and *P. basiramia* (Hawkes and Menges, 1995).

This study provides some weak evidence that ground lichens can affect the early stages in the life cycle of herbaceous species. Lichens increased seedling mortality in *P. basiramia* and resulted in lower seedling densities in *H. cumulicola* in these experiments. In community plots in rosemary scrub, seedling recruitment was increased by lichen removal (Menges and Hawkes, unpublished data). Biotic soil crusts could also affect germination and nutrient cycling and may interact with lichens as well (Lawrey, 1986; Bever, Westover and Antonovics, 1997; Hawkes, unpublished data).

Fire may have direct effects that are not reflected in changes in community structure, including heating of the soil, release or combustion of nutrients, smoke production, and volatilization of allelochemicals (McPherson and Muller, 1969; Christensen and Muller, 1975b; Keeley and Keeley, 1987; Tyler, 1996; Keeley and Fotheringham, 1998). Nutrient addition experiments at Archbold suggest that community responses in scrubby flatwoods are not strongly tied to any postfire nutrient flush (Dawn Berry, unpublished data), but phosphorus fertilization mimicked fire effects on flowering for one of two populations of an herb growing on xeric sandhill soils in Florida (Brewer, 1995). Nutrient addition alone did not affect survival of herbs in an unburned chaparral (Swank and Oechel, 1991). Heating experiments on seeds of some scrub species have not demonstrated any significant effects on germination percentages (Menges, unpublished data). The fact that the transplant experiments in this study occurred after fires, yet had qualitatively similar patterns to natural populations affected by fire, suggests that direct effects of fire do not account for most of the postfire patterns seen.

Herbivores can affect postfire plant survival (Christensen and Muller, 1975a; Swank and Oechel, 1991; Tyler, 1996). In this study, herbivory was quite variable in space and time and does not seem consistent with being the major force differentiating early postfire and unburned environments, nor explaining the different positions of the three study species on a postfire gradient. However, herbivory in Florida scrub remains little studied.

Seed dormancy and germination are clearly important components of these species' life histories, and our studies have garnered some important information in this regard. *Polygonella basiramia* is the only one of these three species not to possess a persistent seed bank, according to our experiments. These results are consistent with its



lack of germination from rosemary scrub soil samples (Kohfeldt and Menges, unpublished data). In contrast, *E. cuneifolium* and *H. cumulicola* delay some seed germination and are capable of forming a persistent seed bank, with germination occurring after fire. Again, this is consistent with a community seed bank survey (Kohfeldt and Menges, unpublished data) and results of experimental burial of *H. cumulicola* seeds (Quintana-Ascencio, Dolan and Menges, 1998).

Patterns of natural seedling appearance in relation to fire are also consistent with our experiments. Seedlings of *H. cumulicola* and *E. cuneifolium* appear within a year of fire, sometimes in large numbers. *Polygonella basiramia* seedlings appear more gradually within a few years of fire. This species must be recruiting from seeds dispersed from unburned patches, which are common in rosemary scrub (Main and Menges, 1997). Of the three species, *P. basiramia* appears best dispersed. Perhaps as a consequence of this better dispersal as well as the ability to use small patches in the surrounding scrubby flatwoods matrix, *P. basiramia* is the only species of the three not to exhibit patterns of site occupancy consistent with metapopulation dynamics (Quintana-Ascencio and Menges, 1996).

These results have several implications for management. First, prescribed fire is a useful tool in controlling the competitive effects of large shrubs and lichens on these herbaceous plants and in providing opportunities for seedling recruitment. Since each species differs from the others in its range of postfire tolerance, microsite preferences, and tolerance to competition, variable fire frequencies and spatially patchy fire intensities are most likely to retain all three species in the landscape. Variable fire frequencies will also benefit other endangered species with different requirements. Patchy fires will benefit *P. basiramia* in particular, since it requires dispersal from unburned patches. However, patchy fires may also be an advantage to the other two species by allowing recolonization of gaps from small, unburned patches. Variable and patchy fires are the environmental milieu within which these scrub species evolved and are likely the best conditions for maintenance of biodiversity and population viability.

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