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## Fire-mediated effects of shrubs, lichens and herbs on the demography of *Hypericum cumulicola* in patchy Florida scrub

Received: 4 December 1996 / Accepted: 5 June 1997

**Abstract** Understanding the effect of disturbance and interspecific interactions on population dynamics and availability of suitable habitats for colonization and growth is critical for conservation and management of endangered species. *Hypericum cumulicola* is a narrowly endemic, small perennial herb virtually restricted to open areas of well-drained white sand in Florida rosemary scrub, a naturally patchy community that burns about every 20–80 years. Over 1 year (September 1994 to September 1995) we evaluated variation in survival, growth and fecundity among 1214 individuals in 14 rosemary scrub patches of different sizes (0.09–1.85 ha) and fire histories (2, 8–10, and >20 years since the last fire). Fire kills aboveground individuals of *H. cumulicola*, but new individuals were present a year after fire. Recruitment decreased in patches more than a decade post-fire. Survival, annual height growth rate, and fecundity (number of flowers and fruits) were higher in recently burned patches. Scrub patch size did not affect these demographic variables. Survival was positively associated with the presence of conspecifics and negatively related to proximity to the dominant shrub Florida rosemary (*Ceratiola ericoides*), prior reproductive output, and ground lichen cover. Since *H. cumulicola* and other herbaceous species in the rosemary scrub depend on sporadic fires to decrease interference of shrubs and ground lichens, its persistence may be threatened by fire suppression.

**Key words** Competition · Endangered species · Florida rosemary · Disturbance · Management

### Introduction

Recurrent disturbance is widespread and common in nature (Pickett and White 1985). In transient communities, disturbance and interspecific interactions may determine local rates of extinction and the availability of suitable habitats for colonization and growth (Caswell and Cohen 1991). Different temporal and spatial disturbance regimes create habitat gradients and mosaic-landscapes that provide favorable habitats for species with contrasting microhabitat requirements, life history traits and colonization abilities (Christensen 1985; Runkle 1985; Connell and Keough 1985). Models of patch dynamics predict that habitat subdivision, disturbance and dispersal can promote coexistence (Levin and Paine 1974; Pickett 1980; Shmida and Ellner 1984; Kareiva 1990). However, anthropogenic alteration of natural disturbance regimes may threaten species that are dependent on habitat conditions created during community recovery.

Understanding the mechanisms determining persistence of plant populations is critical for conservation and management of endangered species (Synge 1985). In many communities, the spatial structure and population dynamics of herbaceous species are affected by asymmetric interactions with shrubs (Knoop and Walker 1985; Tielbörger and Kadmon 1995; Menges and Kimnich 1996). For example, shrub shade and interference limit the access of herbs to light, soil moisture, and nutrients (Adams et al. 1970; Belsky 1994; Roux et al. 1995). Allelopathic agents released from some shrubs may inhibit seed germination and decrease growth (Tanrisever et al. 1988; Williamson 1990; but see Keeley and Keeley 1989). The presence of shrubs also modifies the interactions of herbs with mycorrhizal fungi, herbivores, and seed predators and dispersers (Bartholomew 1970; Jaksic and Fuentes 1980; Keeley and Keeley 1989; Brundrett and Abbott 1991; Vargas-Mendoza and González-Espinosa 1992). Beside shrubs, other factors commonly decreasing the distribution and abundance of

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herbaceous species include litter and lichen cover, and the presence of other small plants (Goldberg and Werner 1983a; Lawrey 1986; Facelli and Pickett 1991; Rusch and Fernández-Palacios 1995).

The rosemary phase of sand pine scrub is a naturally fragmented community sporadically disturbed by fire, almost entirely restricted to central and coastal Florida (Abrahamson et al. 1984). In central Florida, this community is characterized by stands of the shrub Florida rosemary (*Ceratiola ericoides*), with scattered clumps of dwarf sclerophyllous oaks (*Quercus* spp.) and palmettos (*Serenoa repens* and *Sabal etonia*; Abrahamson et al. 1984a; Gibson and Menges 1994). In the areas between shrubs, several lichens in the genera *Cladonia* and *Cladina* frequently account for more ground cover than herbaceous plants, particularly in long-unburned stands, where they can form almost continuous carpets (Abrahamson et al. 1984). Occasional high-intensity fires kill standing Florida rosemary individuals, enlarge open sand areas and decrease lichen cover (Johnson 1982; Abrahamson et al. 1984; Abrahamson 1984a, b; Myers 1985, 1990; Menges and Kohfeldt 1995; Hawkes and Menges 1996). The slow recovery growth rate of Florida rosemary and lichens, and limited colonization of available space by other woody species, allow large openings to persist in the rosemary scrub for decades after a fire (Johnson et al. 1986; Hawkes and Menges 1996). These sandy open areas in the rosemary scrub provide microhabitats for a large group of endangered and endemic herb species (Abrahamson et al. 1984a; Christman and Judd 1990; Hawkes and Menges 1995, 1996; Menges and Kimmich 1996), many of which are killed by fire and regenerate from seeds (Abrahamson 1984a; Johnson and Abrahamson 1990; Hawkes and Menges 1995; Menges and Kohfeldt 1995; Menges and Kimmich 1996).

This work examines the effect of shrubs, lichens, and herbs along gradients of time since the last fire and community patch size on the demography of *Hypericum cumulicola*, a perennial herbaceous species restricted to open sandy habitats in rosemary scrub. We tested the hypothesis that fire affects survival, growth and fecundity of open habitat specialists like *H. cumulicola* through its effect on aboveground distribution and abundance of woody species, lichens and other herb species. Characteristics of microhabitat surrounding *H. cumulicola* were compared with those of random points in the communities. Associations between *H. cumulicola* individual survival, height growth rate and fecundity, and parameters describing structure and composition of surrounding vegetation, were analyzed using existing variation in patch size and time since fire in rosemary scrub patches at Archbold Biological Station, in south-central Florida.

## Methods

### Study species

The Highlands scrub hypericum [*Hypericum cumulicola* (Small) P. Adams] is a small perennial herb, branched from the base. Its

distribution is limited to the southern half of the Lake Wales Ridge, in south-central Florida. Within a narrow east-west range of nearly 14 km and a north-south range of approximately 70 km, this rare species is virtually restricted to open areas of well-drained white sand in rosemary scrub and along adjacent roads and firelanes, but also occurs infrequently in large openings in scrubby flatwoods where soil drainage is good (Christman and Judd 1990; Quintana-Ascencio et al. 1995). Reproduction of this iteroparous species takes place between April and October, but most flowering and fruiting occurs between June and September (Menges and Salzman 1992). *H. cumulicola* individuals do not survive burning. Buried seeds in the soil and dispersal from nearby populations provide new recruits for population recovery (Menges and Kohfeldt 1995; P.F. Quintana-Ascencio, R.W. Dolan and E.S. Menges unpublished work).

### Archbold Biological Station

This study was carried out in the western section of Archbold Biological Station (Archbold) in south-central Florida. This 1075-ha area is characterized by a mosaic of scrubby flatwoods, flatwoods, and seasonal ponds with scattered patches of the rosemary phase of sand pine scrub (Abrahamson et al. 1984a; Quintana-Ascencio and Menges 1996). The regional climate has hot, wet summers and mild, dry winters. Weather conditions during the period of study (September 1994–September 1995) were slightly wetter than average (1724 mm of precipitation vs. 1546 mm for the same 13-month interval, based on a 43-year period 1952–1995, data from Archbold Biological Station). Rainfall was higher than average, particularly in November and December of 1994, but significantly lower in May 1995, the last month of the dry season. Most rosemary scrub occurs on sandy, acidic, and nutrient-poor St. Lucie, Archbold, and Satellite soils on scattered ancient sand dunes (Abrahamson et al. 1984; Carter et al. 1989; Brown et al. 1990). Local variation in vegetation structure and composition is associated with fire regime and drainage (Abrahamson et al. 1984).

### Fire history and rosemary scrub patch size

In September 1994, *H. cumulicola* occurred in 52 of 89 rosemary scrub patches in the west section of Archbold (Quintana-Ascencio and Menges 1996). We used a factorial design with two levels of rosemary scrub patch size (<0.5 ha and >0.5 ha) combined with three levels of time since fire (>20 years, 8–10 years, and <2 years; Table 1) to choose 14 rosemary scrub patches with *H. cumulicola* populations. Long-term records at Archbold Biological Station were used to determine the fire history of each rosemary scrub patch (K. Main, unpublished work). Rosemary scrub patches that experienced patchy fire during the last burn were avoided. Available maps were used to determine rosemary scrub patch size (Abrahamson et al. 1984; Quintana-Ascencio and Menges 1996). We found three replicates for half of the combinations of treatments. Only two long-unburned rosemary scrub patches smaller than 0.5 ha were included and only one patch larger than 0.5 ha and two smaller than 0.5 ha were recently burned.

### Individual sampling and microhabitat characterization

In September of 1994 we sampled at least 64 individuals of *H. cumulicola* in every patch, but most samples included 80 or more plants ( $n = 1214$ , Table 1). A sample of individuals occurring along a former road was included in the analysis of *H. cumulicola* microhabitat (site 38, Table 1). Sample size in 1995 was smaller because of disturbance by animals ( $n = 1130$ ). Individuals were sampled in a stratified random fashion along 1-m-wide belt transects parallel to the longest axis of open sand gaps supporting *H. cumulicola*. The closest individual, if present, for every meter along the center of each transect was included in the study. A flag with a numbered aluminum tag was placed near each individual.

**Table 1** Rosemary scrub patch identification number (*ID*), patch size (*ha*), date of last fire, number of gaps and their area (*m*<sup>2</sup>), number of plants and points (*point*), and percent number of random quadrats without shrubs or lichens (*open*)

Patch ID	Patch size	Date of last fire	Gaps <sup>1</sup>	Area	Plants	Points	% Open
1	1.85	< 1967	10	318	90 (69)	50	12
62	0.70	< 1967	3	282	80 (47)	50	14
93	0.57	1972	9	336	90 (90)	48	19
59	0.37	1968	7	189	80 (76)	45	36
32	0.17	< 1967	1	183	80 (80)	33	30
29	1.26	January 1985	1	300	80 (55)	50	40
91	0.81	June 1986	1	960	80 (75)	48	81
67	0.60	June 1986	6	220	79 (74)	49	41
88	0.27	June 1986	1	272	80 (80)	38	68
45	0.25	July 1986	2	345	80 (79)	47	21
87	0.17	June 1986	1	1260	80 (76)	50	56
42	1.69	August 1993	3	335	80 (80)	51	55
50	0.40	August 1993	1	180	101 (99)	48	50
57	0.09	August 1993	2	142	64 (62)	50	76
38 <sup>2</sup>	NA	< 1967	2	219	70 (69)	NA	83

<sup>1</sup> Plot sampling was limited to intershrub areas (gaps) occupied by *Hypericum cumulicola*. Random sampling was based on points placed throughout all the area of the patch. Sample size for logistic regression of survival was smaller (in parentheses); *n* plants = 1214 (1111), *n* points = 657

<sup>2</sup> Site 38 was a primitive road

In September of 1994 and 1995, we measured maximum height and counted the total number of flowers, fruits and reproductive buds for each individual previously marked. Total length of reproductive stalks for every individual was also measured in September 1995. During this time, the two most apical, mature fruits of randomly selected individuals in every rosemary patch were collected (range per patch, 5–11 plants; total 120 plants). Ten damaged fruits without seeds were eliminated from the sample.

Between January and February of 1995, we measured the distance from every marked *H. cumulicola* to the nearest Florida rosemary and oak (mostly *Quercus inopina*, but also *Q. geminata* and *Q. chapmanii*) within a 4-m radius. Maximum height of each of these dominant shrubs was also measured. We used a 30-cm diameter wood frame centered over every marked individual to determine frequency, density and floristic composition of neighboring plants. Ramets of clonal species were counted independently. Relative frequency plus relative abundance were used to determine importance values for each neighbor species. Percent cover of ground lichens, litter, and *Selaginella arenicola* within the frame area were also recorded by categories of 0, 1–25%, and 25–100% cover. Vascular plant species were identified following Wunderlin (1982) and Kartesz (1994).

In November 1995, we measured the distance from stratified random points to the nearest Florida rosemary and oak every 5 m along the center of 1-m wide random belt transects in each patch (Table 1). Percent lichen ground cover around these random points was estimated using the same method described for the plants.

#### Analysis

Differences between variables describing microhabitat surrounding random points and *H. cumulicola* individuals were assessed with multiple *G*-tests of contingency tables, adjusted with the Bonferroni correction (Sokal and Rohlf 1981). We tested for significant differences in the proportion of *H. cumulicola* individuals surviving (data arcsine-transformed) among Florida rosemary scrub patches with variable time-since-fire and area using an analysis of variance (but see Sheil et al. 1995; Sheil and May 1996 for the limitations of this approach). The relationships of time-since-fire and patch size to annual height growth rate and fecundity were tested with analyses of covariance (Sokal and Rohlf 1981). Initial height of *H. cumulicola* (1994) was used as a covariate in the analysis of annual height growth rate. Current height and total branch length in 1995 were used as covariates in the analysis of the number of flowers and fruits (natural logarithmic-transformed). Slopes of the linear relationships between number of reproductive structures and height and branch length were considered to be rough indicators of reproductive effort. Individuals without reproductive structures were not included in the analysis of reproductive effort across treatments. We tested for significant differences between the slopes of the linear relationships of these variables and their covariates among different time-since-fire and patch-size treatments.

We used stepwise logistic regression (Fienberg 1987) to examine the association of survival with 15 variables describing characteristics of *H. cumulicola* and its microhabitat (19 plants with dry reproductive stalks were not included in this analysis, Table 2). We

**Table 2** Microhabitat and individual variables tested for association with *Hypericum cumulicola* survival. Values show upper limits except as indicated

Variable	Type	Observations
Distance to nearest rosemary (cm)	Categorical	0–50, 100, 200, 300, > 300
Distance to nearest oak (cm)	Categorical	0–50, 100, 200, 300, > 300
Ground lichen cover (%)	Categorical	0, 1–25, 100
Initial height (cm)	Continuous	
Litter cover (%)	Categorical	0, 1–25, 100
Presence of conspecifics <sup>1</sup>	Categorical	0, 1
Presence of <i>Paronychia chartacea</i> <sup>1</sup>	Categorical	0, 1
Presence of <i>Polygonalla basiramia</i> <sup>1</sup>	Categorical	0, 1
Presence of <i>Aristida gyrans</i> <sup>1</sup>	Categorical	0, 1
Presence of <i>Lycania michauxii</i> <sup>1</sup>	Categorical	0, 1
Buds, flowers and fruits (1994)	Continuous	
<i>Selaginella arenicola</i> cover (%)	Categorical	0, 25, 100
Size of nearest Florida rosemary (cm)	Categorical	0, 50, 250
Size of nearest oak (cm)	Categorical	0, 50, 250
Total neighbor plant density	Continuous	

<sup>1</sup>Species with average importance value higher than 10

also tested for significant effects of two-way interactions of independent variables with size and distance from nearest Florida rosemary and oak, ground lichen cover, and initial height and prior reproductive output of *H. cumulicola* (see Hosmer and Lemeshow 1989 for model-building strategies). Significance limits of the forward selection model were set at  $P < 0.05$  to enter variables and at  $P > 0.10$  to remove them. Coefficients of the logistic model provide an estimate of the logarithmic change in the odds of an event occurring (the ratio of the probability that it will occur to the probability that it will not occur) associated with a one-unit change in the independent variable (Fienberg 1987). The goodness-of-fit of the model was assessed by comparing predicted and observed outcomes, and calculating the likelihood of the observed results, given the parameter estimates (Norusis 1992). We used deviation coding schemes to obtain coefficients involving categorical variables with significant interactions (size of Florida rosemary, presence of *Paronychia chartacea*, and ground lichen categories), and each predictor category was compared to the overall effect, except the last category. We used simple coding schemes for presence of conspecifics and classes of distance to nearest Florida rosemary, and each category was compared to the first one (Norusis 1992). All statistical tests were done using SPSS version 5.0 (Norusis 1992).

**Results**

Time-since-fire, patch size and microhabitat

The occurrence of *H. cumulicola* was strongly associated with open sandy microhabitats. Nearly 85% of the individuals were found in microsites with  $\leq 25\%$  ground lichen cover and  $\geq 0.5$  m from Florida rosemary and oaks (Fig. 1). Most *H. cumulicola* were further from Florida rosemary and oaks than were random points in the same rosemary scrub patches (Fig. 1). There were significant differences ( $P < 0.004$ ) between *H. cumulicola* and random point distances to Florida rosemary and oaks in two of three recently burned patches, three of six patches that were previously burned 8–10 years ago and in four of five with more than 20 years since the last fire. We found significant differences between *H. cumulicola* and random point distances to Florida rosemary but not to oaks in one recently burned patch, and to oaks but not to Florida rosemary in two patches a decade after postfire, and one patch more than 20 years postfire.

The distance between Florida rosemary and *H. cumulicola* decreased (Fig. 1B and C) while the size of the nearest Florida rosemary increased with time-since-fire (mean height + standard error was  $7.9 + 2.05$  cm for  $< 2$  years since the last fire;  $29.8 + 0.75$  cm after 8–10 years; and  $80.3 + 2.89$  cm in patches  $> 20$  years postfire). *Q. inopina*, *Q. geminata* and *Q. chapmanii* are able to resprout after fire and changes in oak size ( $46.1 + 1.66$  cm,  $72.5 + 2.13$  cm, and  $79.7 + 1.97$  cm for oak height, respectively, for the same intervals after fire) and distance to *H. cumulicola* were less marked (Fig. 1).

Presence of ground lichens in the vicinity of study plants increased from approximately 20% of the neighborhoods in recently burned patches, to 30–60% a decade postfire, and 70–80% in patches more than 20 years

postfire. More *H. cumulicola* neighborhoods had lower lichen cover compared to random points in two of three recently burned patches, one of six patches a decade postfire and four of five patches more than 20 years postfire.

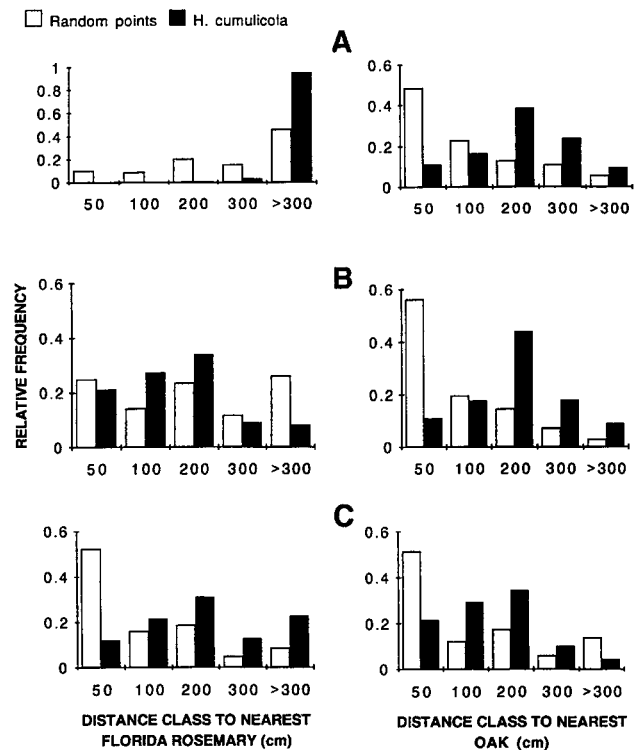


Fig. 1A–C Frequency distribution (data pooled across patches) of distance classes of random points (open bars) and *Hypericum cumulicola* (filled bars) to nearest Florida rosemary, and to oaks in patches: A 2 years after fire; B 8–10 years; and C  $> 20$  years. Values along the ordinate are upper limits for each class, except for the last distance class which shows the lower limit and is open on its right side

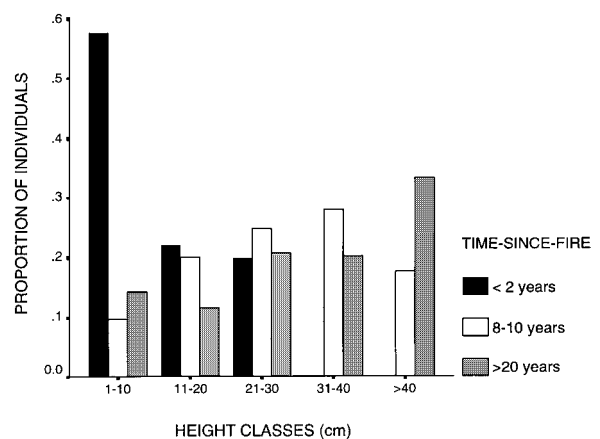


Fig. 2 Proportion of *H. cumulicola* individuals by height classes in Florida rosemary scrub patches with different time-since-fire (data pooled across patches 1994)

### Demographic variation with patch size, time-since-fire and microhabitat

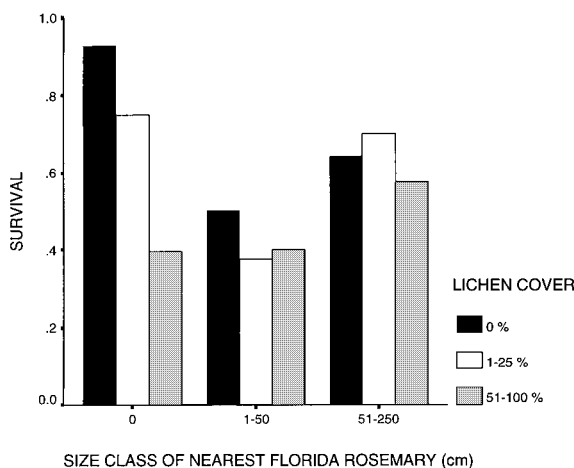
Small non-reproductive stages (< 10 cm height) of the life history of *H. cumulicola* accounted for more than 80% of the individuals in scrub patches one year after fire (Fig. 2). The proportion of small plants decreased with time since last fire, and the proportion of tall, often multiple branched adult plants increased in long-unburned patches (Fig. 2).

The proportion of *H. cumulicola* surviving was greatest in recently burned rosemary patches ( $F = 7.81$ ,  $n = 14$ ,  $P = 0.01$ ). No significant effects on the pro-

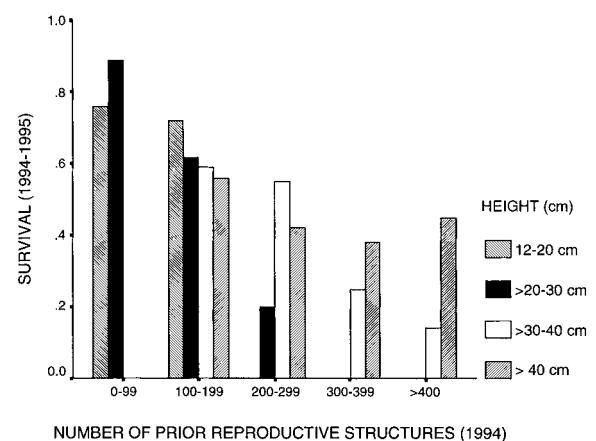
portion of surviving plants were found for patch size or its interaction with time-since-fire. At the individual level, survival of *H. cumulicola* in rosemary scrub was primarily affected by the presence of Florida rosemary and ground lichens, the main species determining the availability of open space (Table 3). Survival increased with distance from Florida rosemary (40 vs. 80% survival for 1 and > 3 m respectively). There was a significant interaction between the effects of the size of the nearest Florida rosemary and ground lichen cover on survival (Fig. 3; Table 3). The lowest mortality of *H. cumulicola* was associated with absence of shrubs and ground lichens, but lichen cover had little effect when the

**Table 3** Results of a forward stepwise logistic regression analysis of *H. cumulicola* survival in Florida rosemary scrub patches (correctly classified by the logistic model: overall 73.7%, alive 84.3%, dead 55.2%;  $n = 1111$ ; model  $\chi^2 = 281.9$ , 19 *df*,  $P < 0.001$ . *A* Variables are shown in the order they were entered into the stepwise regression model (*Imp.* improvement; *P(i)*: level of significance). *B* Logistic regression coefficients for variables in the final model (*B* coefficient value, *SE* standard error of coefficient; *P(W)*, significance level for the Wald statistic). See Table 2 for a full list of variables

Variable	(a) Model history			(b) Coefficients		
	Imp.	<i>df</i>	<i>P(i)</i>	<i>B</i>	<i>SE</i>	<i>P(W)</i>
Constant		1	< 0.001	1.28	0.23	< 0.001
Initial height (1994)	79.5	1	< 0.001	-0.01	0.01	0.04
Height of nearest F. rosemary	105.6	2	< 0.001			0.08
(1) No Florida rosemary				0.33	0.26	0.19
(2) 1–50 cm height				-0.58	0.26	0.03
Presence of conspecifics	22.5	1	< 0.001	0.63	0.16	< 0.001
Distance to nearest F. rosemary	17.6	4	0.0015			0.005
(2) 51–100 cm distance				0.10	0.25	0.68
(3) 100–200 cm distance				0.52	0.23	0.02
(4) 200–300 cm distance				0.88	0.30	0.004
(5) > 300 cm distance class				0.92	0.38	0.02
Ground lichen cover	12.6	2	0.0018			0.28
(1) 0% Lichen cover				0.004	0.17	0.98
(2) 1–25% Lichen cover				-0.25	0.28	0.38
Prior reproductive output	7.1	1	0.0075	-0.008	0.002	< 0.001
Presence of <i>Paronychia chartacea</i>	3.4	1	0.06	0.004	0.12	0.97
Ground lichens × Height of F. ros.	16.9	4	0.005			< 0.001
(1, 1) 0% lichen – no F. rosemary				0.73	0.21	< 0.001
(1, 2) 0% lichen – 1–50 cm height				-0.21	0.27	0.43
(2, 1) 1–25% lichen – no F. ros.				0.17	0.20	0.39
(2, 2) 1–25% lichen – 1–50 cm				-0.28	0.27	0.30
Prior rep. output × Initial height	9.9	1	0.005	0.0001	0.00003	< 0.001
<i>P. chartacea</i> × lichens	6.51	2	0.04			0.04
No <i>P. chartacea</i> – 0% lichens				0.33	0.13	0.01
No <i>P. chartacea</i> – 1–25% lichens				0.08	0.14	0.53



**Fig. 3** Survival of *H. cumulicola* individuals sorted by size of nearest Florida rosemary and percent ground lichen cover



**Fig. 4** Survival (1994–1995) of *H. cumulicola* individuals sorted by classes of prior reproductive output (1994) and initial height

nearby Florida rosemary was large (Fig. 3). Several other variables affected *H. cumulicola* survival. The amount of prior reproductive output was negatively associated with survival, and its effect depended on initial size of the individuals (Fig. 4). Annual and perennial herbs were the most frequent immediate plant neighbors of *H. cumulicola*, and conspecifics had the highest neighbor importance value. Presence of conspecifics was positively associated with survival of *H. cumulicola*. The interaction of presence of *Paronychia chartacea* with ground lichen cover accounted for only a minor amount of *H. cumulicola* survival variation. No other microhabitat variables significantly affected individual survival.

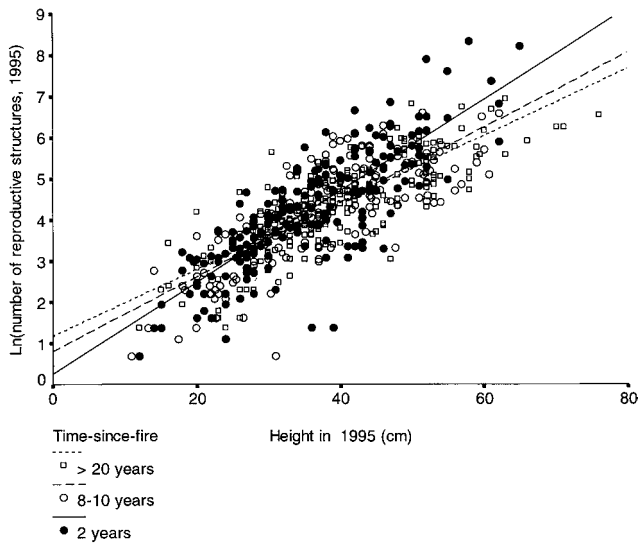
There was a significant effect of time-since-fire and its interaction with initial height (1994) on *H. cumulicola* growth rate (Table 4, Fig. 5). The different elevations and slopes of the linear relationships between initial height and growth rate across different time-since-fire

classes indicate that the smallest individuals (< 20 cm) in recently burned patches had the highest growth rates (Fig. 5). Growth rate was higher in large patches, but there was no significant interaction between patch size and initial height for this variable.

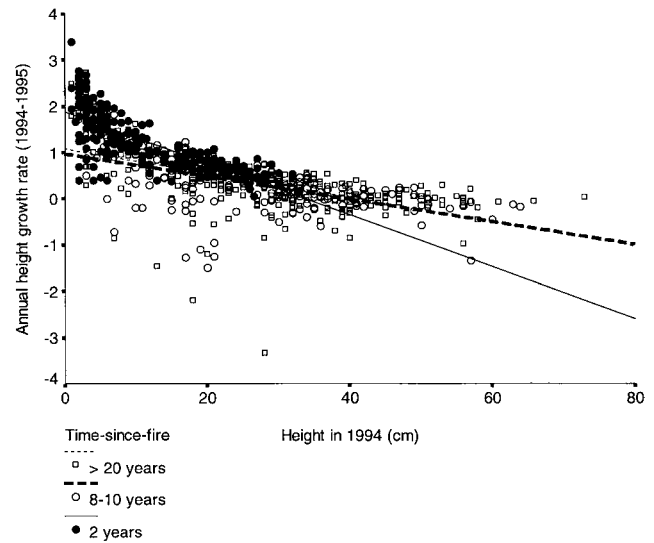
Reproductive effort, represented by the increase in number of reproductive structures with height varied across patches with different time-since-fire (Table 4, Fig. 6). The shortest individuals (< 30 cm) in recently burned patches invested less in reproduction than did similarly sized individuals in patches with longer intervals after fire, but this relationship was reversed for tall plants. These results indicate that fast growing young plants may reach large sizes before reproducing in recently burned patches while short older plants in older patches had slower growth rates but larger reproductive outputs compared to same size plants in young patches. Neither patch size, nor its interaction with current height

**Table 4** Analysis of covariance of height growth rate and *H. cumulicola* number of reproductive structures in Florida rosemary scrub patches with different times-since-fire and patch size

Source of variation	Growth rate			Flowers and fruits		
	F	df	P	F	df	P
Fire	62.55	2	< 0.001	6.02	2	0.003
Patch size	5.65	1	0.018	1.83	1	0.18
Fire × patch size	1.14	2	0.31	5.83	2	0.003
Covariates						
Initial height (1994)	440.19	1	< 0.001			
Fire × initial height	28.02	2	< 0.001			
Patch × initial height	0.75	1	0.38			
Current height (1995)				400.83	1	< 0.001
Length (1995)				89.89	1	< 0.001
Fire × height (1995)				6.38	2	0.002
Fire × length				4.12	2	0.017
Patch × height (1995)				2.44	1	0.119
Patch × length				4.14	1	0.042
Error		644			563	



**Fig. 5** Plot of annual height growth rate with initial height in 1994 for *H. cumulicola* in patches with different time-since-fire: 2 years,  $r^2 = 0.33$ ; 8–10 years,  $r^2 = 0.33$ ; > 20 years,  $r^2 = 0.59$



**Fig. 6** Plot of number of flowers and fruits (logarithmic-transformed) with current height in 1995 for *H. cumulicola* in patches with different time-since-fire: 2 years,  $r^2 = 0.65$ ; 8–10 years,  $r^2 = 0.61$ ; > 20 years,  $r^2 = 0.68$ . Only plants with reproductive structures were included

affected the number of reproductive structures, but there was a significant interaction between patch size and total branch length and patch size and time-since-fire on the number of reproductive structures. Average number of reproductive structures was higher in small recently burned and long-unburned patches than in large patches with similar time-since-fire, but no difference in average number of flowers and fruits was found between large and small patches a decade after fire.

Ripe, dark red fruits accounted for 5–25% of total number of reproductive structures at any given time (range 0–45%). Seed number per fruit ( $15 + 0.4$  SE, maximum 30, aborted seeds not included) did not vary significantly among patches with contrasting patch size and time since fire ( $P > 0.50$ ).

## Discussion

Fire creates opportunities for recruitment and growth of herbaceous species like *H. cumulicola* in rosemary scrub patches because of its long-term effect on resource availability and aboveground biomass (see Zedler and Zammit 1989; Tyler and D'Antonio 1995). *H. cumulicola* is virtually absent in the dense and shrub-dominated scrubby flatwoods and flatwoods that are more common in the regional landscape. Rapid recovery from fire of resprouting shrubs in these less xeric communities quickly fills in ephemeral openings (Menges and Kohfeldt 1995). Survival and growth of *H. cumulicola*, and other herbaceous species in rosemary scrub, are higher in recently burned patches, and decline with time-since-fire, as open habitat decreases with shrub and ground lichen recovery (Menges and Kohfeldt, 1995, Menges and Kimmich, 1996; Hawkes and Menges, 1996).

Several mechanisms may explain the interacting effects of shrubs and lichens on *H. cumulicola*. Florida rosemary has dense foliage which may limit access to light for herbaceous species. Additionally, allelopathy and belowground interference constraining nutrient and water availability may influence the performance of herbaceous species in this shrubby and relative open community. The compound ceratiolin, released from the leaves of *Ceratiola ericoides*, yields hydrocinnamic acid in the soil, an agent with detrimental effects on germination and growth of plants (Richardson and Williamson 1988; Williamson et al. 1992; Fischer et al. 1994). Ground lichen thalli could affect *H. cumulicola* through light limitation or mechanical interference with its seedlings, but here too, chemical substances may also mediate their interaction. Several phenolic substances produced by lichens suppress seed germination, reduce plant growth and inhibit bacteria and mycorrhizal fungi (Lawrey 1986 and references cited therein).

Diverse competitive interactions may occur among herbaceous species with outcomes largely depending on local abundance and the size asymmetries of interacting individuals (Goldberg and Werner 1983b). The positive association between survival of *H. cumulicola* and

presence of conspecifics may indicate that the variation in microsite quality overrides low levels of intraspecific competition. Among other herbaceous species, only *Paronychia chartacea* had a significant effect on *H. cumulicola* survival, but these interactions were dependent on the presence of ground lichens. *Paronychia chartacea* is an annual herb that recovers in large numbers from a soil seed bank after fire (Johnson and Abrahamson 1990; Menges and Kohfeldt 1995). This species was among the most common neighbors of *H. cumulicola* and showed significant changes in importance with time since fire.

The absence of consistent, significant effects of rosemary scrub patch size on *H. cumulicola* survival and fecundity suggests that for this species, there is no significant association of habitat quality with patch size variation in the range studied (0.09–1.85 ha). Patch size variation may alter habitat quality because of the occurrence of edge effects (Laurence and Yensen 1991; Saunders et al. 1991). Non-significant floristic differences between the edge and the center of scrub vegetation (scrubby flatwoods and flatwoods) adjacent to planted pastures and orange groves suggest that their borders effectively define the extent of these communities (S. Halpern and E.S. Menges unpublished work). Incidence-based metapopulation models indicated that *H. cumulicola* has lower risks of extinction and higher colonization rates in large and aggregated rosemary scrub patches (Quintana-Ascencio and Menges 1996). From the lack of association between survival and fecundity of *H. cumulicola* and patch size seen in this study, we infer that its patterns of distribution at a regional scale are more likely explained by other demographic factors determining patch extinction and colonization probabilities, such as local abundance and dispersal.

The negative association of prior reproductive output and individual survival of *H. cumulicola*, especially among small plants, suggests a physiological trade-off between these life history traits. A trade-off between reproduction and survival has been associated with unfavorable conditions near species tolerances (Stearns 1992, and references therein). Limited resource acquisition may be common for rosemary scrub plants, inasmuch as soils are poor in nutrients and drought occurs periodically (Abrahamson 1984b; Menges and Gallo 1991; Menges 1994). Vegetative and reproductive growth in *H. cumulicola* occur during different seasons, and reproduction and survival may rely on reserves accumulated during favorable periods of vegetative growth. Shorter and more numerous vegetative stems occur in winter, when lower temperatures may induce only mild water restriction, and before reproductive stalks are differentiated. Growth of reproductive stalks (mean stem number = 3, range 1–17) coincides with the driest months (March–May). With the beginning of winter, reproductive stalks die back.

This study provides general recommendations for the management of populations of *H. cumulicola* and other herbaceous species in Florida scrub. However, they must

be considered with caution since we do not have estimates of the temporal variation of the population demographic parameters and we have not yet analyzed other important demographic factors (e.g., seed dispersal, seed dormancy, seedling recruitment). Fire suppression may hinder the persistence of *H. cumulicola*. Very long fire intervals may expose remnant populations to higher extinction risks associated with demographic and environmental stochasticity characteristic of small populations with slow growth rates (Menges 1992). Local disturbances, including mechanical disturbance, may maintain some *H. cumulicola* in areas where burning is not possible. Managers, however, need also to be aware of the requirements of other species with contrasting disturbance requirements.

Fire has a major role in the population dynamics of many plant species in Florida scrub (Abrahamson 1984a, b; Johnson and Abrahamson 1990; Menges and Kohfeldt 1995; Menges and Kimmich 1996). During the last three decades, human dwellings, orange groves and ranches have replaced large portions of the original Florida scrub in central Florida (Peroni and Abrahamson 1985a, b). Fire suppression and changes in fire pattern due to loss and isolation of fire-prone habitats may have profound effects on population dynamics of scrub species. Contemporary human-modified landscapes may not provide conditions for the maintenance of suitable disturbance regimes (see Oostermeijer 1996). Active management therefore may be necessary for the conservation of species requiring habitats shaped by historic disturbance regimes.

**Acknowledgements** We thank Eric S. Menges for his invaluable advice on many aspects of this work. Rebecca Yahr kindly identified several plant species. Ted Batley, Christine V. Hawkes, Margaret E.K. Evans, Doria Gordon, Jessica Gurevitch, Charles H. Janson, Eric S. Menges, Maureen Stanton, Keith A. Tarvin, James D. Thomson, Rebecca Yahr and two anonymous reviewers offered very useful comments on the manuscript. We appreciate the field assistance of Dawn M. Berry, Margaret E.K. Evans, Deborah H. Graves, Stacey L. Halpern, George Landman, Amarantha Z. Quintana-Morales, Eréndira M. Quintana-Morales, Joyce Vonegan, and Rebecca Yahr. This work was supported by Archbold Biological Station, Lake Placid, Florida; El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, Mexico, and Fulbright and the Consejo Nacional de Ciencia y Tecnología, Mexican Government through a fellowship for P.F.Q.-A. (46610).

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