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Source: *Florida Scientist*, Vol. 66, No. 2 (Spring, 2003), pp. 99-108
Published by: Florida Academy of Sciences, Inc.
Stable URL: http://www.jstor.org/stable/24321150
Accessed: 09-07-2018 17:38 UTC

HERBIVORY AND POSTGRAZING RESPONSE IN *HYPERICUM CUMULICOLA*

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Abstract: *We describe patterns of mammalian herbivory and examine possible fitness consequences of herbivory on* Hypericum cumulicola, *an herbaceous perennial endemic to Florida scrub. We noted the presence or absence of mammalian herbivory on 1841* H. cumulicola *individuals, from 23 populations in two study sites. At Archbold Biological Station, we found the presence of herbivory to be positively correlated to the number of conspecific neighbors, and negatively correlated with time-since-fire. At Arbuckle Tract of Lake Wales Ridge State Forest, presence of herbivory was affected by habitat (scrub or roadside) and negatively associated with the number of conspecific neighbors. We performed a clipping treatment on naturally occurring* H. cumulicola *individuals to simulate mammalian herbivory. The results indicated that* H. cumulicola *appears to undergo compensatory regrowth following defoliation. The one-year fitness consequences of herbivory appear to be neutral although the long-term fitness consequences of herbivory on the perennial* H. cumulicola *can not be known from this study. We hypothesize that in addition to disturbance tolerance (through increased regrowth rate), patchy distribution and low density may reduce the impact of mammalian herbivory on* H. cumulicola.

Key Words: compensatory growth, Florida scrub, herbivory, *Hypericum cumulicola*, overcompensation

Herbivory reduces plant biomass, and can affect growth and reproduction (McNaughton, 1983; Bergelson and Crawley, 1992a,b). In intensive grazing systems, selection pressure should favor plant individuals with traits allowing them to attenuate the negative effects of tissue loss. Belsky and co-workers (1993) grouped such adaptations as (1) strategies that allow the plant to avoid herbivory, such as escape from discovery through non-apparent, patchy distribution and chemical and mechanical defenses and (2) overcompensatory growth following an herbivory event. Compensatory response can be divided into three classes (Maschinski and Whitham, 1989): overcompensatory growth, compensatory growth and undercompensatory growth. In overcompensation, grazed plants produce more fruits and seeds than control plants. Compensation occurs when grazed and control plants produce similar numbers of fruits and seeds. Undercompensation occurs when grazed plants produce fewer fruits and seeds than control plants. Overcompensatory growth has been controversial, with studies in support of this phenomenon (McNaughton, 1983; Paige and Whitham, 1987; Paige, 1992, 1999) and studies

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finding no support for it (Belsky, 1986, 1987; Bergelson and Crawley, 1992a,b; Bergelson et al., 1996). An array of compensatory responses has been documented, with undercompensatory growth and overcompensatory growth at the extremes (Maschinski and Whitham, 1989). One explanation for compensatory growth is that rapid regrowth following defoliation is an evolved response of the plant to minimize the effects of structural damage, which can come from many sources including fire, trampling, and herbivory (Belsky, 1986; Belsky et al., 1993; Rosenthal and Kotanen, 1994). A meta-analysis of the impact of herbivory on plants in different resource conditions indicates that overcompensation is more likely in high resources for monocots and in low resources for dicot herbs (Hawkes and Sullivan, 2001).

This work examines mammalian herbivory on *Hypericum cumulicola*, a perennial herbaceous species restricted to sandy gaps in the Florida rosemary scrub. The study consists of two parts: (1) an observational study, relating mammalian (presumably deer *Odocoileus virginianus seminolus* and rabbit *Sylvilagus floridanus floridanus*) herbivory rates on *H. cumulicola* to demographic parameters and environmental variables, and (2) a clipping experiment testing *H. cumulicola* compensatory response to herbivory. The objectives of this study are to explore patterns of mammalian herbivory across different populations of *H. cumulicola* and to examine possible fitness consequences.

METHODS—*Study species*—*Hypericum cumulicola* ((Small) P. Adams) is a small, short-lived, perennial herb endemic to the Lake Wales Ridge of Polk and Highlands Counties in central Florida (Quintana-Ascencio et al., 1995). Though largely limited to gaps in Florida rosemary scrub, *H. cumulicola* can also be found along roads and firelanes and, infrequently, in well-drained openings in scrubby flatwoods. *H. cumulicola* branches from the base and grows to heights of 20–70 cm. Vegetative in the winter and spring, most plants become reproductive during the summer, growing reproductive stalks (1–17) with up to thousands of flowers and fruits per plant. Fire kills *H. cumulicola* individuals, but populations are able to recover through persistent seed banks and/or dispersal from nearby populations (Quintana-Ascencio et al., 1998). Fruit production, recruitment rates, and survivorship are highest for the first few years after fire, with these traits decreasing with increased time-since-fire (Quintana-Ascencio and Morales-Hernández, 1997; Quintana-Ascencio et al., 2003).

Study Sites—We conducted this study at Archbold Biological Station (Archbold) and the Arbuckle Tract of Lake Wales Ridge State Forest (Arbuckle) in south-central Florida. All study sites at Archbold were in Florida rosemary scrub. We organized the Archbold sites by time-since-fire based on records of natural, accidental, and prescribed fires kept since 1967 (Main and Menges, 1997). Study sites at Arbuckle encompassed a larger range of *H. cumulicola* habitats. These habitats included natural (rosemary scrub and oak scrub), and human disturbed (roadside and tram). The rosemary scrub and oak scrub patches in Arbuckle were within areas burned in the last decade. However, the large size of Florida rosemary (*Ceratiola ericoides*), an obligate seeder, in the Florida rosemary scrub sites indicated that fire did not reach these Florida rosemary scrub patches.

Rosemary scrub occurs on sandy, well-drained soils of ridges and knolls and is characterized by sometimes large, open gaps in the vegetation (Abrahamson et al., 1984). Florida rosemary (*Ceratiola ericoides*) often dominates the shrub layer. Other species often present include oaks (*Quercus* spp.), and palmettos (*Serenoa repens* and *Sabal etonia*). The sub-shrub *Licania michauxii*, lichens (*Cladonia* spp.), spike moss (*Selaginella arenicola*), and several herbaceous species including *H. cumulicola* grow in open gaps in the vegetation. Oaks (*Quercus* spp.), and palmettos (*Serenoa repens* and *Sabal etonia*) are dominant species in oak scrub. Though not characterized by them, oak scrub sometimes does contain scattered open gaps, which support similar vegetation as the gaps in rosemary scrub. Roadside sites were on active sand roads, which contain *H. cumulicola* populations. Tram sites lie on berms of old railroad lines. Tram sites are characterized by large gaps and a lower water table than the surrounding areas. Though the railroad tracks are no longer present, the berms now lie along side sand roads.

Fire plays a major role in determining Florida scrub community composition and dynamics (Menges and Hawkes, 1998; Menges, 1999). Fires in oak and rosemary scrub are often heterogeneous, producing gaps in the unburned vegetation. Gap specialists (such as *H. cumulicola*) are most abundant shortly after fire, but become less abundant as shrubs and lichens increase with time-since-fire. Thus, gap specialist species residing in oak and rosemary scrub depend on fire for their persistence.

Sampling methods of the observational study—At Archbold, in August 2001, we noted the mammalian herbivory on 956 *H. cumulicola* plants from 15 rosemary scrub patches, representing a gradient of time-since-fire (4 to 34 years after fire), patch size, and north-south distribution along the station. Within each patch/site, we sampled at least 70 individuals in a stratified random fashion along 1 m wide belt transects, if greater than 100 plants were present at the site. If fewer than 100, the entire population was included in the sample. At Arbuckle, we sampled 885 individuals from 8 sites: 2 oak scrub sites (n = 236), 2 rosemary scrub sites (n = 201), 2 road sites (n = 236), and 2 tram sites (n = 212). We recorded, for each plant sampled, maximum height, number of conspecifics within 15 cm, number of reproductive structures (flowering buds, flowers and fruits), and presence or absence of mammalian herbivory. Presence of mammalian herbivory was associated with complete branch removal. Insect herbivory was also present on some *H. cumulicola* individuals but was not recorded and was readily distinguished from mammalian herbivory as branches, flowers or fruits eaten by insects were not entirely removed.

We conducted forward stepwise (Wald) logistic regressions to determine the significance of the association of time-since-fire, and number of conspecific neighbors (data log-transformed) to the presence of herbivory in *H. cumulicola* at Archbold. We conducted forward stepwise (Wald) logistic regressions to determine the significance of the association of habitat, and number of conspecific neighbors (data log-transformed) to the presence of herbivory in *H. cumulicola* at Arbuckle. We then tested the significance of contrasts among habitats.

Clipping experiment—We selected three Archbold rosemary scrub patches with known populations of *H. cumulicola* and of varying time since fire (15, 8, and <1 years since fire) for the clipping experiment. Three levels of simulated herbivory were imposed on the plants between 18 and 19 August 2001, with 10 individuals sampled per treatment, per patch. Control plants had no clipping imposed, 50% treatment had one clipping made on ~half of reproductive stalks, and 100% treatment had one clipping made on each reproductive stalk. These clipping treatments mimicked the amount and type of tissue removal observed in plants with naturally occurring herbivory. We imposed clipping on a haphazardly chosen piece of stalk, at the point of the first branching event (only one stalk was present in 5 of 30 plants under the 50% herbivory treatment; clipping was imposed on this stalk). Within gaps at each scrub patch, we sampled plants along 1 m wide belt transects, running at a random distance from the edge, perpendicular to the longest axis of open sand in the gap. At 1-m increments along the belt transect, the three closest plants (without prior herbivory) were chosen for sampling. For each sampled plant, we recorded the height of the tallest stalk (pre- and post-clipping), cumulative height of the stalks (pre- and post-clipping), and the number of reproductive structures (pre- and post-clipping). Treatments were assigned left to right with respect to the tape, in a rotational fashion. At completion of sampling, plants were enclosed in cages made of wire chicken cooping, successfully preventing the subsequent occurrence of natural herbivory.

We resampled the treated plants between 15 and 17 September 2001. For each plant, height of the tallest stalk, cumulative height of stalks, and number of reproductive structures were recorded. Maschinski and Whitham's (1989) definitions of compensatory growth involve only the differences in fruit and seed production, between grazed and ungrazed plants. This study also looks at changes in plant height, as height has been found to be the best predictor of fecundity in *H. cumulicola* (Quintana-Ascencio et al., 2003).

We conducted univariate analysis of covariance to test for significance of differences among clipping treatments on *H. cumulicola*. We tested for significance of treatment, site, and their interactions

TABLE 1. Coefficients of forward (Wald) logistic regression models of presence of herbivory in *H. cumulicola* at Arbuckle State Forest, and Archbold Biological Station.

Source of variation	Beta	s.e.	df	P
Arbuckle				
Constant	−0.713	0.110	1	<0.001
Tram-Road	0.608	0.283	1	0.031
Tram-Oak scrub	3.058	0.275	1	<0.001
Oak scrub-Road	−2.450	0.234	1	<0.001
Rosemary scrub-Tram	−1.084	0.274	1	<0.001
Rosemary scrub-Road	−0.476	0.239	1	0.046
Rosemary scrub-Oak scrub	1.974	0.229	1	<0.001
Ln(neighbors)	−0.496	0.110	1	<0.001
Archbold				
Constant	1.023	0.144	1	<0.001
Years since last fire	−0.126	0.011	1	<0.001
Ln(neighbors)	0.141	0.052	1	0.007

on change in maximum height, cumulative stalk height, and number of reproductive structures over the month-long treatment. We statistically controlled for differences in initial size using original maximum height, original cumulative stalk height, and initial number of reproductive structures as covariates, respectively. We adjusted and compared linear models describing the relationship between height and number of reproductive structures for individuals with and without herbivory (or clipping). All statistical analyses were performed using SPSS 10.1.0.

RESULTS—*Observational study*—Across all rosemary scrub patches at Archbold, the presence of herbivory on *H. cumulicola* was positively correlated to number of conspecific neighbors within 15 cm, and negatively correlated with years-since-last fire (Table 1, Fig. 1). Presence of herbivory on *H. cumulicola* at Arbuckle was affected by habitat and negatively correlated to the number of conspecific neighbors within 15 cm (Table 1, Fig. 2). Presence of herbivory was significantly different among all habitats in the following descending order: oak scrub, rosemary scrub, road, and tram (Table 1, Fig. 2).

Clipping experiment—Clipped plants (at both the 50% and 100% treatments) did not differ significantly from unclipped plants with respect to final height of the tallest reproductive stalk, final accumulated height of reproductive stalks, or number of reproductive structures during the one month treatment period (Tables 2–4). Final height, when adjusted by the pre-clipping height of the tallest stalk, was still not significantly affected by clipping treatments (Table 2). Similarly, final number of reproductive structures, when statistically adjusted by the initial number of reproductive structures, was not significantly affected by clipping treatments (Table 4).

To test how closely the clipping regime mimicked natural herbivory in *H. cumulicola*, we compared growth function models describing the association between the number of reproductive structures and the height of the plant for both *H. cumulicola* individuals with natural herbivory and experimentally clipped individuals. There was a significant correlation between plant height and number of reproductive structures (logarithmic transformed), with $r^2 > 0.465$ for all curves.

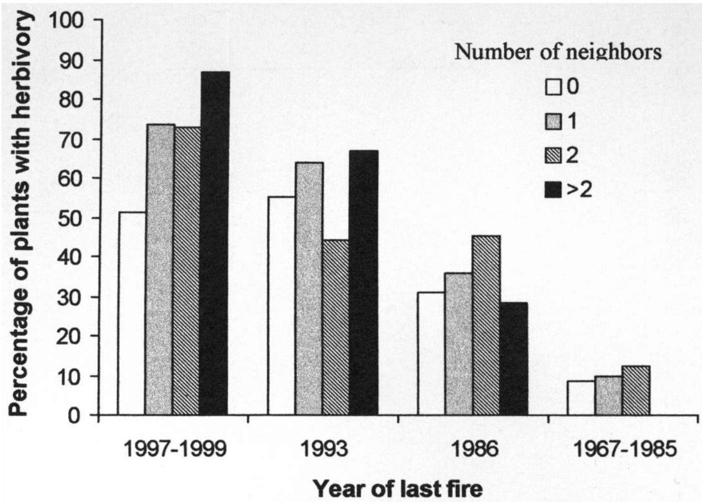

FIG. 1. Percentage of plants with herbivory in 2001 by year of last fire and number of conspecific neighbors in Rosemary scrub patches at Archbold Biological Station.

There was always overlap among standard errors of the slopes for individuals with and without herbivory or clipping (Table 5).

DISCUSSION—*Hypericum cumulicola* responded to biomass removal with compensatory growth (*sensu* Maschinski and Whitham, 1989), as experimentally grazed and ungrazed plants did not produce significantly different numbers of reproductive structures. Additionally, experimentally grazed and ungrazed plants did not show significantly different stalk heights. Although *H. cumulicola* did not exhibit overcompensatory growth, increased growth (and reproductive structure production) rate was present in clipped plants, resulting in compensatory growth. We do not see any immediate reproductive consequences of simulated herbivory on *H. cumulicola*, as clipping did not reduce or increase fruit yield. Though, as *H. cumulicola* is a perennial, the long-term fitness consequences of herbivory can not be known from this study.

In previous studies, Bergelson and Crawley (1992 a,b) and Bergelson and co-workers (1996) found no evidence for overcompensatory growth following mammalian herbivory in *Ipomopsis aggregata*, despite previous findings which supported overcompensatory growth in *I. aggregata* (Paige and Whitham, 1987; Paige, 1992; 1994; 1999). Despite the contention by Bergelson and co-workers (1996) that there is no compelling evidence for overcompensatory growth in *I. aggregata*, or any other plant species, the debate continues to rage. Hawkes' and Sullivan's (2001) review indicates that resource availability differentially affects plant recovery after herbivory in monocot and dicot herbs. These authors argue that these differences among functional groups may explain, at least in part, contradictory evidence on plant response to herbivory in the literature (Hawkes

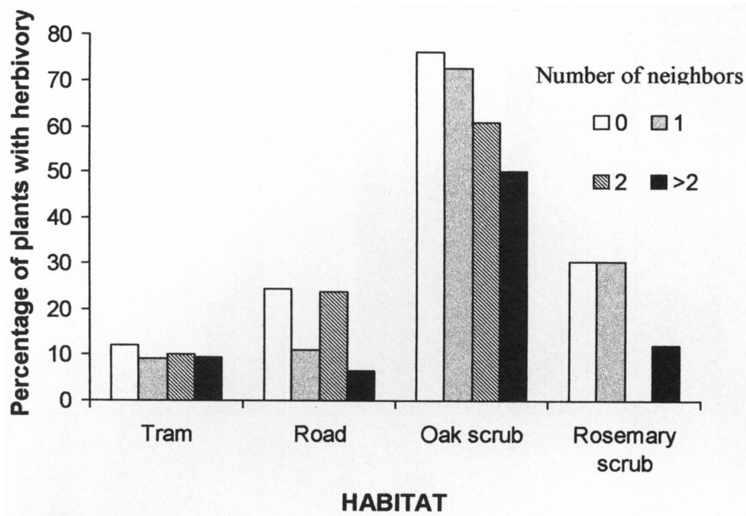

FIG. 2. Percentage of plants with herbivory in 2001 by habitat and number of conspecific neighbors at Arbuckle State Forest.

and Sullivan, 2001). Our present study lends support to those who argue for compensatory growth (Bergelson et al., 1996; for example), as we saw no evidence in support of overcompensatory growth in *H. cumulicola*.

Our study raises the question of which general anti-herbivory strategies (see Belsky et al., 1993) are employed by *H. cumulicola*, if any. These are grouped into strategies or circumstances that allow a plant to avoid herbivory and strategies that allow a plant to recover from herbivory. This study shows that *H. cumulicola* exhibits increased growth rate following an herbivory-like disturbance (clipping). Although it has been proposed that there is a resource tradeoff between herbivory tolerance and herbivory avoidance strategies (van der Meijden et al., 1988; Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999), *H. cumulicola* may avoid herbivory in addition to tolerating it. Apparency theory (Feeny, 1976) hypothesizes that if the distribution of a plant species is patchy, it can be harder for herbivores to find and plants may avoid discovery. This may explain a circumstance reducing herbivory in *H. cumulicola*, as it resides predominantly in the rosemary scrub phase of sand pine scrub, which is patchy in distribution throughout the Florida scrub ecosystem (Abrahamson et al., 1984).

The observational experiment at Archbold showed a strong correlation between herbivory rates and time-since-fire, with *H. cumulicola* receiving the highest herbivory rates in recently burned areas. Herbivory rates have been shown to be higher in woody species in recently burned areas as herbivores favor the green vegetative resprouts that woody species grow after being burned (see for example Singer and Harter, 1996). However, one might not expect a perennial herb killed by fire and that does not have large storage organs to show this trend. Why, then, would herbivory rates be higher in recently burned areas for an herbaceous species,

TABLE 2. Results of an ANCOVA of final maximum height of *Hypericum cumulicola* with clipping treatment and site as fixed factors, and initial maximum height as covariate.

Source of variance	df	Mean square	F	P
Clipping treatment	2	4.5	0.8	0.468
Site	2	2.6	0.4	0.643
Initial maximum height	1	35.5	6.1	0.016
Clipping treatment*Initial height	2	2.8	0.5	0.623
Site*Initial height	2	3.2	0.5	0.582
Clipping treatment*Site	4	10.0	1.7	0.156
Clipping treatment*Site*Initial height	4	11.8	2.0	0.099
Error	72	5.8		

which produces green shoots every year? One possibility is that *H. cumulicola* may be a focal forage species, that is, mammalian herbivores are actively seeking out *H. cumulicola* for consumption. If this were the case, plants in recently burned areas should be most highly consumed, as *H. cumulicola* individuals are most productive and most abundant in recently burned areas (Quintana-Ascencio and Morales-Hernández, 1997). Herbivores would concentrate their foraging in these areas.

However, due to the small and patchy population sizes of *H. cumulicola*, it makes more sense that *H. cumulicola* is a supplementary forage species, with the following situation taking place: In recently burned areas, most woody species rapidly resprout new shoots (Menges and Kohfeldt, 1995), which are heavily browsed by herbivores (Singer and Harter, 1996). In addition, several herbaceous species, including *H. cumulicola*, increase their densities after fire (Menges and Kimmich, 1996, Quintana-Ascencio et al., 2003). Herbivores may be attracted by all these species, but feed on *H. cumulicola*, once they have reached the site. As time-since-fire increases and woody species resume their normal aboveground vegetative state and herb abundance declines, herbivores are no longer attracted to the area and *H. cumulicola* is not consumed. A study of habitat preferences within pine flatwoods using infrared-triggered cameras indicated that white-tailed deer and all other mammals captured on film were present more frequently in a 24 months post-fire site than in an adjacent site 48 months post-fire (Main and Richardson, 2002).

TABLE 3. Results of an ANCOVA of final cumulative stalk height of *Hypericum cumulicola* with clipping treatment and site as fixed factors, and initial cumulative stalk height as covariate.

Source of variance	df	Mean square	F	P
Clipping treatment	2	26.1	0.1	0.874
Site	2	377.3	2.0	0.150
Initial stalk height	1	102.5	0.5	0.469
Clipping treatment*Initial stalk height	2	6.5	0.03	0.967
Site*Initial stalk height	2	190.7	1.0	0.379
Clipping treatment*Site	4	89.2	0.5	0.765
Clipping treatment*Site*Initial stalk height	4	66.8	0.3	0.847
Error	72	193.7		

TABLE 4. Results of an ANCOVA of final number of reproductive structures of *Hypericum cumulicola* with clipping treatment and site as fixed factors, and initial number of reproductive structures as covariate.

Source of variance	df	Mean square	F	P
Clipping treatment	2	0.2	0.6	0.527
Site	2	0.6	1.7	0.195
Initial number of reproductive structures	1	6.2	16.3	<0.001
Clipping treatment*Initial fruits	2	0.2	0.5	0.630
Site*Initial fruits	2	0.3	0.9	0.416
Clipping treatment*Site	4	0.6	1.5	0.219
Clipping treatment*Site*Initial fruits	4	0.5	1.3	0.261
Error	71	0.4		

The presence of mammals increased to levels observed in the 24 months post-fire site after 8 weeks following a prescribed fire in the site previously 48 months post-fire (Main and Richardson, 2002).

The proportion of *H. cumulicola* plants with herbivory at Arbuckle was higher in rosemary scrub and oak scrub sites than it was in road and tram sites. This can be looked at in two ways, which are difficult to distinguish since habitats are identical for each case. First, herbivory rates were higher in natural sites than in man-made sites. Second, there was more herbivory away from roads than near roads. The reason for this is unclear, but may be due to mammalian herbivores (deer and rabbits) favoring covered areas (such as scrubby sites) with places to hide, over open areas (such as roadside and tram sites).

This study has shown that herbivory is correlated to number of conspecifics. This correlation was negative at Arbuckle and positive at Archbold, in 2001. *H. cumulicola* survivorship in Florida rosemary scrub has been shown to be positively correlated to number of conspecifics (1995: $p < 0.001$ slope = 0.369, 2001: $p < 0.001$ slope = 0.185; Quintana-Ascencio and Morales-Hernández, 1997; Quintana-

TABLE 5. Parameters (and their standard error) of growth functions ($\ln y = a + b * x$) of height and number of reproductive structures (logarithmic transformed) of individuals clipped (before and after a month of treatment), untreated (control), with herbivory, and without herbivory (from the observational study, vegetative individuals not included).

Treatment	r^2	a	s.e.	b	s.e.	n
Pre-clipped (all)	0.538	1.848	0.251	0.06	0.006	90
Pre-clipped (control)	0.642	1.846	0.361	0.06	0.009	30
Post-clipped (control)	0.565	2.167	0.402	0.06	0.009	30
Post-clipped (clipped)	0.463	1.481	0.382	0.07	0.010	60
Arbuckle						
Without herbivory	0.643	1.012	0.113	0.08	0.003	557
With herbivory	0.565	0.693	0.210	0.08	0.005	238
Archbold						
Without herbivory	0.629	0.577	0.129	0.100	0.003	483
With herbivory	0.465	0.126	0.207	0.104	0.006	341

Ascencio, unpublished data). This raises a paradox, as high density areas may have higher survival despite higher herbivory. However, neither herbivory nor conspecific density have a consistent impact on *H. cumulicola* survival. Instead, it appears that other microhabitat attributes are ultimately determinant of *H. cumulicola* survival, to the point where favorable habitat allows plants to overcome the ill-effects of herbivory and competition by conspecific neighbors.

ACKNOWLEDGMENTS—We are grateful to Eric Menges for his insight and assistance throughout the course of this experiment and preparation of the manuscript. We also thank Jane Carlson, Ann Cox, Richard Lavoy, Anne Malatesta, David Matlaga, Felipe Serrano, Carl W. Weekley, and Aläa Wally for field assistance, Christine Hawkes, D. F. Martin, Joyce Maschinski and Carl W. Weekley for friendly criticism of the manuscript, and Roberta Pickert for her help with GIS. This work was supported by Archbold Biological Station, The National Science Foundation (DEB98-15370), and The Florida Division of Forestry's Plant Conservation Program.

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Florida Scient. 66(2): 99–108. 2003
Accepted: September 13, 2002