Population Status and Demography of the Endangered *Harrisia fragrans* (Cactaceae) at Savannas Preserve State Park

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Abstract

Harrisia fragrans is an endemic shrubby cactus listed as endangered by the U.S. Fish and Wildlife Service and the State of Florida. Its current distribution is limited to the Savannas Preserve State Park, an area approximately 13 km long by 0.5 km wide. A previous study conducted between 1988 and 1996 indicated that the population was rapidly declining and would possibly go extinct within 30 years. The goals of this study were to monitor the population status of *H. fragrans* and to examine whether there were any temporal or spatial population dynamics. We tagged and mapped all plants, following their fates and estimating recruitment, mortality and fruit production. The population size of *H. fragrans* remained relatively stable over the three-year study (1999 – 2002) and increased slightly during the last year. At the end of the study, 2150 plants were alive and distributed among nine subpopulations in the park. For a shrub species, the population was relatively dynamic with approximately 10% of the plants dying each year and another 10% recruiting. The data suggest that the discrepancy in population trend between the previous study of *H. fragrans* and this one was due principally to lower recruitment estimates in the previous study. Because recruitment appears to be more variable than mortality, future studies should address the processes that affect recruitment so that biologists can manage the population for favorable recruitment rates. No single microhabitat type was ideal for *H. fragrans*, suggesting that managers should maintain habitat patchiness and remove invasive exotics species that would homogenize environmental conditions. Given the dynamic nature of *H. fragrans*, it will be necessary to continue monitoring its status to ensure long-term species viability.

Cover image by M.E. Eaton, 1912, from the archives of the Smithsonian Institution

Introduction

Harrisia fragrans Small ex Britton & Rose is a shrubby cactus endemic to Florida, which is listed as endangered by the U.S. Fish and Wildlife Service and the State of Florida. It has been reported from several central-eastern coastal, Florida counties including Brevard, Indian River, St. Lucie and Volusia, (Wunderlin & Hansen 2002). It has also been reported for Big Pine Key and the Flamingo area of Monroe County (Benson 1982). However, reports outside of St. Lucie County may be in error (Austin 1984; Bradley et al. 2002; Gann et al. 2002). Today, all known occurrences of *H. fragrans* are in southeastern St. Lucie County (Rae 1995; FNAI 1997). According to Small (1933), this species was historically found in hammocks on high sand dunes, kitchen middens and coquina ledges; although he may have mistaken the similar *H. simpsonii* for *H. fragrans* in some cases. Small's specimens of *H. fragrans* (8457 NY, 8459 FLAS) are from "Hammock on Sand Dunes" in or near what is now the Savannas Preserve State Park (Savannas PSP). The Institute for Regional Conservation (IRC) reported *H. fragrans* as being frequent at Savannas PSP (Bradley et al. 1999), based on surveys conducted in 1998.

Between 1988 and 1993, and then again in 1996, two subpopulations of *H. fragrans* in and around the Savannas PSP were monitored by Rae (1996). Each summer between 1988 and 1993, Rae recorded mortality, plant size and fruit and flower production for all plants in the two subpopulations. His results showed that both subpopulations suffered serious decline (41.8% & 41.3%) between 1988 and 1993. Later, using a matrix model of population dynamics based on five years of data, Rae & Ebert (2002) predicted the decline and eventual extinction of *H. fragrans* by 2022. They hypothesized that excessive shading as well as overexposure were responsible for such a rapid decline, theorizing that *H. fragrans* prefers partially shaded conditions.

In 1998, preliminary monitoring of the entire population of *H. fragrans* at the Savannas PSP was initiated by IRC and the Florida Department of Environmental Protection (FDEP). During that survey, 802 plants were identified and mapped (Bradley et al. 1999). Although IRC surveyed a slightly larger area than Rae (1996), IRC discovered more plants in Rae's study area than were indicated or predicted by Rae.

The main goal of this study was to continue the monitoring program initiated by the IRC in 1998 (Bradley et al. 1999) and to examine whether there was any temporal or spatial variation due to light environment in the population dynamics of *H. fragrans*. Of particular interest was an evaluation of whether the population size of *H. fragrans* was continuing to decline. To help accomplish this goal, we used Rae & Ebert's (2002) matrix model of population dynamics to evaluate the long-term trend of the population given recent environmental conditions (1999-2002).

Methods

Study Site. *H. fragrans* is presently known from a 13 km by 0.5 km section of the Atlantic Coastal Ridge between the cities of Ft. Pierce and Jensen Beach, and between the Indian River and a large swale known as the Savannas (Figure 1). Most of the undeveloped area in this region is now located within the Savannas PSP. This section of the Atlantic Coastal Ridge is transected by the Florida East Coast (FEC) Railway from north to south. The Savannas PSP, and the bulk of the *H. fragrans* population, is on the west side of these tracks. To the east of the tracks, extensive development has occurred and little is in public ownership. An undetermined number of *H. fragrans* occur on private lands east of the

tracks. *H. fragrans* is found on St. Lucie sand with 0-8 percent slopes, at elevations between approximately 8 and12 meters (Watts & Stankey 1980). The area receives 140 cm rainfall/year, with about 62% occurring from June to October (Watts & Stankey 1980).

Before human alteration, the vegetation along the ridge was primarily scrub, dominated by a sand pine (*Pinus clausa*) canopy with an understory of *Quercus* spp., *Ceratiola ericoides*, *Carya floridana*, and *Ximenia americana*, and a sparse forb layer. Xeric hammocks were located primarily on the slopes of the ridge and were dominated by *Quercus* spp., *Carya floridana, Ximenia americana,* and *Sideroxylon tenax*. Much of this scrub community is intact along the western edge of the ridge, although those on the eastern edge have been mostly developed. Extensive clearing for pineapple farms occurred from the 19th century through the 1920s (Watts & Stankey 1980; Rae & Ebert 2002). This farming included the use of fertilizers (Watts & Stankey 1980) that may have altered soil properties. Little scrub has regenerated in areas previously farmed; these areas are now dominated by fields of *Aristida gyrans* and *Polygonella robusta,* open sand, isolated or clumped *Sabal palmetto* stands associated with vines (especially *Smilax auriculata*) and stands of *Quercus* spp. and *Carya floridana.*

H. fragrans rarely occupies areas of *Pinus clausa* scrub that do remain at the Savannas PSP. We have found that the species is intolerant of fire, an important component of the scrub ecosystem. It is likely that plants were formerly restricted to the eastern and western edges of this ridge in areas of xeric to mesic hammock where fires rarely occur. *H. fragrans* frequently grows along the edges of *Sabal palmetto* or *Quercus* stands or in the shade beneath them; plants are rarely found in open sun. Given, its current distribution, *H. fragrans* may have colonized abandoned pineapple plantations in areas where plants did not formerly occur.

Study Species. *H. fragrans* is a columnar cactus with multiple stems reaching 4 meters. Stems may be 5 cm in diameter and are armed with gray spines that are 2-4 cm long. Branches arise from both the base of the plant and laterally from other stems. White to pink fragrant flowers that are ca. 20 cm long open at night and are presumably moth pollinated (Ted Fleming pers. comm.). The red fruits are globose and 5-6 cm in diameter and can contain ca. 1400 seeds (Rae 1995). Plants may live at least 14 years, as we have monitored plant that were tagged by John Rae in 1988. Few interactions with animal have been observed. A scale insect, *Diaspis echinocati* (Diaspididae) is frequently observed on plants. Birds, gopher tortoises, and raccoons may play a role in dispersal, although this has not been observed.

Sampling. In October and November of 1999-2002, the coastal ridge of the Savannas PSP was surveyed for *H. fragrans*. Plant locations were recorded using Trimble GPS units that were accurate to within a few decimeters. All plants were individually tagged and their fates followed for the remainder of the study. For each plant, the number of stem tips, length of the longest stem, number of fruits (mature and immature), number of flowers (mature and immature) and light microhabitat (sun, partial-shade, shade) were recorded. During each census, newly discovered plants were tagged and mapped using the GPS unit as well. It was noted whether new plants represented sexual or asexual recruits or whether they represented older plants that were not seen in previous censuses. Approximately 300 person hours were devoted during each census towards the survey and monitoring of *H. fragrans*. Plants that could not be located using maps and the GPS unit were recorded as missing. If they were not found again in the subsequent year, they were assumed to have died. The number of basal

stems and length of the longest stem were used to estimate the total length of all stems using an allometric model (Koop and Bradley unpub. data).

Analysis. The current population status of *H. fragrans* was evaluated by examining the change in number of individuals over time. However, because the change in population size of *H. fragrans* was confounded due to the addition of new plants that were previously undiscovered, an unbiased examination of population trend must exclude plants that do not represent new sexual or asexual recruits. Consequently, change in population size due to recruitment and mortality was examined for each cohort of plants that were alive during the 1999, 2000, and 2001 censuses. Mortality and recruitment rates were calculated for each of the three census periods and examined for temporal variability.

Recruitment due to sexual and asexual reproduction was estimated for each of the three census periods. Chi-square goodness of fit tests were used to determine whether one form of recruitment was more frequent than the other for each census period, while a chi-square test of independence was used to determine whether the relative contribution of both recruitment types changed during the study. Even if one type of recruitment may be more frequent than the other, it may not necessarily be more important for population growth if those recruits suffer a higher rate of mortality. To determine whether first year mortality for newly recruited plants is different between sexual and asexual recruits, a chi-square test of independence was performed on the number of surviving and dying plants of both recruitment types.

Plant Growth and Reproduction. The effect of microhabitat and year on the relative growth rate of plants was analyzed using a two-way Kruskal-Wallis test (Sokal and Rohlf 1995). Relative growth rate was calculated as the difference between total plant length in year 1 and year 2, divided by total plant length in year 1. Relative growth rates standardize the increase in plant size by the original size of a plant. The effect of microhabitat and year on relative growth rates was calculated for six different size classes of plants. These six size classes follow that of Rae & Ebert (2002) and are described in Table 1. The effect of microhabitat and year on fruit production was analyzed with a two-way Kruskal-Wallis test for each of the size classes as well.

Fates of Vegetative Plants. To determine whether there was any temporal or spatial variation in fates of vegetative plants, a series of log-linear analyses were performed on each size class (Proc CATMOD, LOGLIN option, SAS v. 8). Plants were first cross-classified into a three-way frequency table with year (3 levels), microhabitat (3 levels) and fate (4 levels) as the three factors. To minimize the number of cells with zero observations, the seven categories of plant fate (transitions to all six size classes and death) were collapsed into four fates (regression, stasis, growth and death). To allow parameter estimation, 0.5 was added to all cells (Fingleton 1984). Use of log-linear analyses to examine variation in demographic fate have been described elsewhere, including choice of the appropriate null model (Caswell 2001; Horvitz and Schemske 1995). Analysis and notation of the hierarchical log-linear models followed that of Caswell (2001).

Projection Matrix Analysis. The pattern of survival, growth, and reproduction of plants within populations is very important in determining population dynamics. Using estimates of these three demographic parameters, a matrix model of population dynamics can be created and used to calculate the asymptotic (long-term) growth rate of the population (λ). A λ of one indicates that the population size is not changing, while lambdas greater than one and less than one indicate that the population is growing or decreasing, respectively. Note

that lambda predicts the long-term behavior of a population given current conditions. Often times, short-term dynamics (known as transient dynamics) will differ from the long-term dynamics of the population (see Caswell 2001 for a description).

A matrix model is given by the following formula,

$$\mathbf{n}_{(t+1)} = \mathbf{A} \times \mathbf{n}_t$$

where $\mathbf{n}_t$ is a column vector of all the individuals within the population at time t (classified by stage or size); $\mathbf{n}_{(t+1)}$ is a similar vector that describes the distribution of individuals at time t+1; and $\mathbf{A}$ is a matrix (size n X n) with elements a_{ij} that describe the transitions from stage j at time t to stage i at time t + 1. Elements in the diagonal of the matrix ($a_{11},…,a_{88}$) represent the proportion of individuals that survive but do not change stage class. Elements above the diagonal represent regression to a smaller stage class while those below the diagonal represent growth to a larger stage class. Generally, except for a_{11}, all elements in the first row of the matrix ($a_{21},…a_{61}$) give the fertility rates for individuals in stage j, while all elements in the first column give recruitment rates of vegetative classes from seeds.

For *H. fragrans*, population projection matrices were constructed for three census periods using the available data (1999-2000, 2000-2001 and 2001-2002). The methods used in this study to generate the projection matrices follow that of Rae & Ebert (2002) for comparative purposes. For *H. fragrans*, elements in the first row of the matrix include regression probabilities and size-class fertilities. Although it is unclear whether Rae & Ebert (2002) included asexual recruitment in their fertility estimates, we included it in this analysis since it does represent a type of recruitment and it does contribute to population growth. Projection matrix analysis was conducted using Matlab (v. 6.1).

Results
Short-term Population Status
Over the five-year study period, we tagged 2,633 plants across the study area. The plants were subdivided into nine populations (Fig. 1 and Appendices A-I). Plants occurred over a wide range of microhabitats varying from full sun to almost full shade. Plants were located in areas composed of mostly native vegetation to areas dominated by invasive exotic species such as *Schinus terebinthifolius* and *Callitris glaucophylla*. In some cases, plants were covered by vine blankets of *Smilax auriculata* and/or the invasive exotic *Abrus precatorius*.

The total number of *H. fragrans* plants that were tagged increased with each census, not only due to recruitment, but also due to previously undiscovered plants. These plants contributed an additional 344, 662, and 256 plants in 2000, 2001, and 2002 respectively. The majority of the previously undiscovered plants (68.0%) that were mapped in 2001 were due to the addition of a new site to the Savannas Preserve State Park (Colony 1; Fig. 1).

The population size of *H. fragrans* remained relatively constant between 1999 and 2001 and then experienced a noticeable increase between 2001 and 2002 (Fig. 2). The pattern of increase and decrease was due to the relative magnitude of mortality and recruitment. During two years, 1999-2000 and 2001-2002, recruitment rates were greater than mortality rates (12.1% vs. 8.0% and 20.1% vs. 11.8%, respectively, Fig. 3.), while between 2000 and 2001, recruitment was less than mortality (5.8% vs. 11.1%). Over the study period, recruitment was more variable than mortality (Coefficient of Variation: 56.8% vs. 19.6%, respectively; Fig. 3).

Sexual and Asexual Recruitment

The number of plants recruiting from seeds was significantly greater than the number of plants recruiting from broken or fallen stems in 2000 and 2002 (chi-square goodness of fit tests: χ^2=6.19, P=0.0129, DF=1; χ^2=56.97, P<0.0001, DF=1; respectively), but not in 2001 (χ^2=0.06, P=0.8111, DF=1). The relative contribution of seedling recruitment to total recruitment varied from 2000 to 2002 (chi-square test of independence: χ^2=9.52, P=0.0085, DF=2), suggesting that there may be different processes contributing to these two types of recruitment. Across study years, the frequency of recruitment events for sexually- and asexually-derived recruits differed among light microenvironments (chi-square test of independence: χ^2=40.33, P<0.0001; DF=2; Fig. 4). Seedlings recruited more frequently in shady microenvironments (79.8%) relative to asexually derived recruits, which more evenly distributed between shady (53.0%) and partial-light (43.2%) microenvironments. Chi-square analysis of the survival of first year recruits demonstrated that a greater proportion of asexual recruits died than did sexually produced recruits (2000-2001: χ^2=35.52, P<0.05, DF=1; 2001-2002: χ^2=4.30, P<0.05, DF=1; Fig. 5). Mortality of recruits produced from stems remained constant during the two years (60.5% and 60.0%), while that of seedling recruits increased (6.3% to 34.3%).

Growth & Reproduction

The mean relative growth rates for the six size classes of *H. fragrans* decreased steadily from 0.51 for the smallest stage class to –0.05 for the largest stage class (Fig. 6). This pattern was probably due to greater resource allocation to reproduction than growth for larger plants. A negative growth rate for the largest size class (-0.05) indicates that large plants on average tend to decrease in total plant length. Large plants typically have long stems that readily break off. Kruskal-Wallis tests indicated that year and microhabitat do not have a strong effect on relative plant growth (Table 2). Across all size classes, both factors resulted in only one significant effect each (Table 2).

Except for the smallest size class, all size classes of *H. fragrans* bore fruit. The number of fruits per plant increased with increasing size class (Table 3; Fig. 7A) and was positively associated with total plant length (r = 0.55, P < 0.0001; N = 5901). However, this increase was due mostly to an increased probability of fruiting for plants (Fig. 7B), rather than an increase in the number of fruits per fruiting plant (Fig. 7C). Total fruit production increased with increasing size class as well (Fig. 7D).

Microhabitat consistently had a significant effect on mean fruit production (Table 3). Plants growing in sunny conditions produced more fruits per plant than plants growing in partial-shade conditions, while those in partial-shade conditions produced more fruits than those in shady conditions (Fig. 7). However, because plants in partial-shade were more frequent than plants sun, plants in partial-shade made the greatest contributions to total fruit production across all size classes (Fig. 7D).

Variation in Vegetative Fates and Matrix Analysis

Log-linear analysis revealed a relatively strong effect of year and microhabitat on plant fate for the smallest and second-to-largest size class, and weak to no-effects for the other four size classes (Table 4). Summing DF and G^2 values across stage classes produced tests of the effect of site and year on plant fate, given the effect of plant size class (Table 4). All four tests were significant, supporting the overall importance of year and microhabitat on

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plant fate. Examination of the relative magnitudes of the G^2 values, indicates that variation in light environment had a stronger effect than did variation in year. Plant mortality was greatest in shady and sunny microhabitats (Fig. 8).

Over the four-year study period, we noted several causes of plant mortality. Between 2001 and 2002 thirteen plants died due to fire. Careful examination of the remains suggested that plants would not resprout from underground roots or stems. Other plants died due to falling debris from the canopy. This was particularly frequent for small plants growing underneath *Sabal palmetto*. Finally, some plants appear to have died due to overshading from canopy trees.

Summarizing the overall pattern of survival, growth and reproduction for plants, population projection matrices showed that for all six size classes, over 25% of the plant transitions involved either a growth or regression event to another stage class. This pattern is consistent with that reported in Rae & Ebert (2002). Estimates of long-term population growth rates obtained from the projection matrices were 0.9921 (1999), 0.9386 (2000) and 0.9902 (2001; Fig. 9). The first and last estimates were very similar to 1.0, suggesting that population size will remain constant; while, the estimate obtained from 2000 suggests that the population will eventually decline. It is important to realize that environmental conditions vary yearly and that these estimates of population growth are based on the environmental conditions experienced by plants in any given year. An accurate understanding of the long-term trend for any population should be based on more than five years of data (Menges 2000).

Discussion

During the last census of this study there were approximately 2100 extant plants across the study area. Approximately 63% of these plants occur in the Savannas PSP with the remainder in unposted inholdings or in the FEC easement. We estimate that the total population size may be as high as 3000 with a smaller number on private lands in the area, east of the FEC railroad tracks and on posted inholdings west of the FEC tracks.

Direct observations of the population size of *H. fragrans* during this study period suggest that the population is not declining, but has remained relatively stable with a slight increase in the last year. Results from projection matrix analysis were similar to those from direct observations of population size; however, they suggest there may be long-term population decline. Estimates of population growth rate from the first and last years were just below 1.0 while that for the second year was 0.94, which suggests population decline. Even though results from these two types of analyses seem slightly contradictory, it is possible for populations to exhibit transient dynamics that differ from long-term dynamics.

Rae & Ebert (2002) predicted the rapid extinction of *H. fragrans* based on population size trends and projection matrix models. Between 1988 and 1996, they found that two sub-populations declined by 55.3% and 59.8%. They attributed the decline to high mortality and low recruitment. The mean mortality rate obtained in our study (10.37%) was very similar to the mean mortality rate (11.75%) obtained by Rae & Ebert (2002). However, recruitment rates were higher in our study. Thus, the difference in long-term predictions between both studies is due to higher estimates of recruitment in our study.

The population of *H. fragrans* is very dynamic, with a relatively large percentage of individuals dying and recruiting each year. A change in any of the processes that influence mortality or recruitment will have a substantial effect on population size in the short term.

Because mortality rates have been shown to be relatively consistent both within this study period and between this study and Rae & Ebert's (2002) study, yearly variation in recruitment rates appears to have a strong and direct influence on short-term changes in population size. However, the effect of these short-term population dynamics is difficult to assess without a longer study.

Although light microhabitat had a significant effect on recruitment, survival and reproductive output, no single microhabitat was best all around. Shady habitats favored recruitment for both asexual and sexual recruits, presumably due to low water stress; sunny habitats were best for reproduction due to high light resource availability; and partial-shade habitats were best for survival. These results suggest that the long-term survival of *H. fragrans* depends on the maintenance of a spatially and temporally patchy light environment. We have observed that *H. fragrans* sometimes recruits under small thickets of *Smilax* and later emerges through the short canopy (usually < 1.0 meters) or is exposed when the *Smilax* dies back. These types of microhabitats are probably ideal in that they provide adequate protection for recruitment and early growth and then allow for future reproduction.

Recommendations for Research

- Because of the high, yearly turnover rate of plants, a negative change in any ecological process that affects mortality or recruitment would result in a substantial decline of *H. fragrans*. We recommend that researchers continue monitoring the population status of *H. fragrans* so that a change in dynamics can be detected early. However, the entire distribution of *H. fragrans* does not need to be monitored every year. Instead, one third of the area could be monitored every three years, so that the entire area is monitored once every three years. All plants should be tagged, located with a GPS unit and then relocated in subsequent years.

- Matrix models of population dynamics are powerful and useful tools to use in the conservation and management of endangered species due to the wide array of analytical results they provide (Menges 1990; Nault & Gagnon 1993; Caswell 2001; Rae & Ebert 2002). We recommend that a detailed demographic study of three subpopulations of *H. fragrans* be conducted annually to provide a thorough understanding of ongoing spatial and temporal variation in population dynamics. These studies should also include quarterly surveys of flower and fruit production to detect long term changes in reproduction. A new matrix model that incorporates habitat structure (i.e., shade, partial-shade, and sun habitats) can be developed to analyze how the different microhabitats contribute to long-term population growth of *H. fragrans*. Habitat-structured matrix models of other species have shown the importance of particular habitats (Pascarella and Horvitz 1998).

- Our study showed that recruitment was more variable than mortality and accounted for the differences in population trend reported between our study and Rae & Ebert's (2002) study. The processes contributing to variability in recruitment need to be determined. The presence of a seed bank, which can potentially buffer a population from environmental variation, should also be determined. A series of field germination experiments can address these questions. Furthermore, it is unclear whether sexual or asexual recruitment is ultimately more important for population maintenance and growth.

Even though this study discovered that sexual recruitment was more prevalent and that sexually derived plants survived better during their first year, asexually derived plants may still be important if they contribute more to population growth. Only a population projection matrix analysis that takes into account contributions from these types of recruitment separately can address this issue adequately. Rae & Ebert's (2002) model did not tease apart these two processes.

- An understanding of the causes of plant mortality would also be of benefit for management of *H. fragrans*, especially if the factor affecting recruitment can not be altered. We observed some plants die due to fire, shading and others due to physical damage from falling debris. Some dying stems have been heavily infested by the scale insect *Diaspis echinocacti*. These insects may cause stem dieback, ultimately killing the plant, although it is also possible that the insects colonize plants already under stress. We do not know the causes of mortality for the majority of plants. Future studies that revisit populations frequently (several times a year) may be able to catch more plants in the process of dying and thereby identify their cause of mortality. Analysis of dying tissues may reveal unknown pathogens. Austin (1984) reported that a disease, possibly bacterial, turned the stems of the related *H. aboriginum* to "slush."

- The coastal ridge that runs through the Savannas PSP was historically dominated by *Pinus clausa* community. With one exception *H. fragrans* is not associated with *Pinus clausa*. One of the subpopulations of *H. fragrans* has a remnant stand in an open sand pine community that contains only 14 plants, while a larger population of approximately 75 plants is located 75 meters down slope in xeric hammock . Whether *H. fragrans* is unable to establish in sand pine community due to differences in environmental conditions (e.g., soil or moisture) or a lack of recruitment opportunities should be determined.

- Nothing is known about the pollination biology of *H. fragrans*. Although plants have flowers that are characteristically moth-pollinated, the specific pollinator(s) has not been identified. Furthermore, it is unknown whether plants are predominantly selfing or outcrossing. The type of mating system and breeding system of population will have important consequences for population genetic diversity and structure.

- Finally, some insight into the biology and management of *H. fragrans* may be gained by studying Florida's other two species of *Harrisia*. Located on the southwest coast of peninsular Florida, *H. aboriginum* is critically imperiled (Gann et al. 2002) with population sizes estimated at fewer than 500. *H. simpsonii,* also endangered, is found in hardwood communities throughout coastal southeastern Florida. Considerable insight may be gained if parallel studies and experiments were conducted simultaneously on all three species.

Recommendations for Management
- Continued acquisition of private inholdings in the Savannas PSP should be a high priority for managers. Unposted inholdings contained 37% of the plants that were monitored in this study and additional plants are known from posted inholdings that we

did not access. The FEC easement contains about 200 plants that were included in our surveys as well as others along the east side of the tracks. A change in management of this easement could impact these plants. A cooperative agreement should be developed with FEC to ensure the protection of *H. fragrans* along the easement.

- Over the course of this study, we encountered numerous invasive exotic species that may have affected the population dynamics of *H. fragrans*. The most common species were *Abrus precatorius, Allamanda cathartica, Callitris glaucophylla, Kalanchoe* spp., and *Schinus terebinthifolius*. Management of invasive species needs to be conducted in a manner that will not increase *H. fragrans* mortality. Mechanical removal of exotics may be detrimental for plants that are established underneath the exotics' canopies. Although *H. fragrans* can recruit from broken stems, survival is not high.

- Prescribed burning is a critical form of management in many habitats in Florida (Myers and Ewel 1990). In fire-climax communities, it restores habitat structure and maintains community diversity. The importance of fire in the area of the Savannas PSP with *H. fragrans* is unknown due to the unusual post-farming ecosystem that has formed there. Large-scale fires would be detrimental for *H. fragrans* since it is sensitive to fire and may experience 100% mortality. Fire management that maximizes the number of burn units with the Savannas PSP is recommended. Maximizing the number of burn units would minimize mortality of *H. fragrans* at any given time and would promote habitat patchiness which may be important for its biology.

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Table 1. Classification of six size classes of *H. fragrans* (follows that of Rae & Ebert (2002)).

Size Class	Total Length (cm)
1	< 10
2	10 - 39
3	40 - 79
4	80 - 159
5	160 - 319
6	>= 320

Table 2. Two-way Kruskal-Wallis test for the effect of year and microenvironment on the relative growth rates of *H. fragrans*. Values in bold represent a significant effect at $P < 0.05$. Effect for year and microhabitat were tested with two DF, while that of the interaction was test with 4 DF.

| Size Class | Relative Growth Rate | | | | | | | | | Effect | | | | | |
| | 1999-2000 | | | 2000-2001 | | | 2001-2002 | | | Year | Micro-Habitat | Inter-action | Mean | N | SE |
	Shade	Partial	Sun	Shade	Partial	Sun	Shade	Partial	Sun						
1	0.44	0.36	1.00	0.53	0.52	0.19	0.44	0.68	1.33	1.09	**6.83**	6.50	0.51	331	0.046
2	0.41	0.50	0.34	0.41	0.45	0.76	0.35	0.35	0.72	1.35	1.84	1.15	0.41	677	0.028
3	0.26	0.43	0.30	0.16	0.21	0.23	0.29	0.28	0.29	1.28	1.18	1.09	0.27	530	0.029
4	0.23	0.18	0.34	0.25	0.07	0.19	0.21	0.30	0.14	3.14	1.27	7.55	0.21	647	0.025
5	0.04	0.04	0.19	-0.04	0.00	0.05	-0.02	0.09	-0.08	3.27	1.71	4.91	0.03	695	0.016
6	0.02	-0.04	-0.19	-0.13	-0.08	0.06	-0.04	-0.02	0.05	**8.97**	3.99	6.80	-0.05	493	0.014

[1]Size classes follow that of Rae & Ebert (2002)

Table 3. Two-way Kruskal-Wallis test for the effect of year and microenvironment on the number of fruits produced by *H. fragrans*. Values in bold represent a significant effect at $P < 0.05$. Effect for year and microhabitat were tested with two DF, while that of the interaction was test with four DF.

| Size Class | Mean Number of Fruits | | | | | | | | | | | | Chi-square Values | | |
| | 1999 | | | 2000 | | | 2001 | | | 2002 | | | Year | Micro-Habitat | Inter-action |
	Shade	Partial	Sun	Shade	Partial	Sun	Shade	Partial	Sun	Shade	Partial	Sun			
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	NA	NA	NA
2	0.04	0.01	0.00	0.01	0.03	0.05	0.00	0.02	0.00	0.00	0.06	0.03	2.33	**7.45**	4.21
3	0.07	0.06	0.26	0.04	0.05	0.12	0.04	0.08	0.13	0.01	0.03	0.08	**10.10**	**21.27**	6.17
4	0.14	0.16	0.30	0.16	0.15	0.24	0.16	0.22	0.32	0.07	0.18	0.11	6.93	**8.62**	2.86
5	0.42	0.68	1.17	0.28	0.48	0.62	0.43	0.66	0.97	0.17	0.71	1.18	7.01	**50.45**	10.00
6	1.30	1.73	2.00	1.40	1.68	4.00	1.18	2.88	4.89	1.00	2.40	3.63	1.90	**38.26**	9.77

[1]Size classes follow that of Rae & Ebert (2002)

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Table 4. Log-linear analysis of the effect of year (Y) and Microhabitat © on fate (F) of *H. fragrans* plants for six size classes. Five different analyses are shown. Model notation follows a hierarchical approach and is described in Caswell (2001). The test of an effect is performed when the effect is isolated through subtraction from two other models. Summed values in the right-hand column test for the presence of an overall effect across all size classes. Values marked with * are significantly different at P<0.05.

| | | G^2 | | | | | | | |
Model	DF	Size Class 1	Size Class 2	Size Class 3	Size Class 4	Size Class 5	Size Class 6	df	Sum
Analysis 1: Marginal test of the effect of year on fate									
YC, F	24	66.14	29.52	35.36	40.86	47.2	20.05	144	239.13
YC, YF	18	44.87	20.66	26.87	32.27	30.55	14.27	108	169.49
YF	6	21.27*	8.86	8.49	8.59	16.65*	5.78	36	69.64*
Analysis 2: Marginal test of the effect of microhabitat on fate									
YC, F	24	66.14	29.52	35.36	40.86	47.2	20.05	144	239.13
YC, CF	18	22.6	17.36	31.41	25.71	34	15.47	108	146.55
CF	6	43.54*	12.16	3.95	15.15*	13.2*	4.58	36	92.58*
Analysis 3: Conditional test of the effect of year on fate									
YC, CF	18	22.6	17.36	31.41	25.71	34	15.47	108	146.55
YC, YF, CF	12	5.61	8.87	23.21	16.12	17	9.52	72	80.33
YF (given CF)	6	16.99*	8.49	8.2	9.59	17*	5.95	36	66.22*
Analysis 4: Conditional test of the effect of microhabitat on fate									
YC, YF	18	44.87	20.66	26.87	32.27	30.55	14.27	108	169.49
YC, YF, CF	12	5.61	8.87	23.21	16.12	17	9.52	72	80.33
CF (given YF)	6	39.26*	11.79	3.66	16.15*	13.55*	4.75	36	89.16*
Analysis 5: Test of the three-way interaction term									
YC, YF, CF	12	5.61	8.87	23.21	16.12	17	9.52	72	80.33
YCF	0	0	0	0	0	0	0	0	0
YCF	12	5.61	8.87	23.21*	16.12	17	9.52	72	80.33

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Figure 1. Distribution of nine populations of *H. fragrans* across the Savannas PSP. Dots represent individual plants.
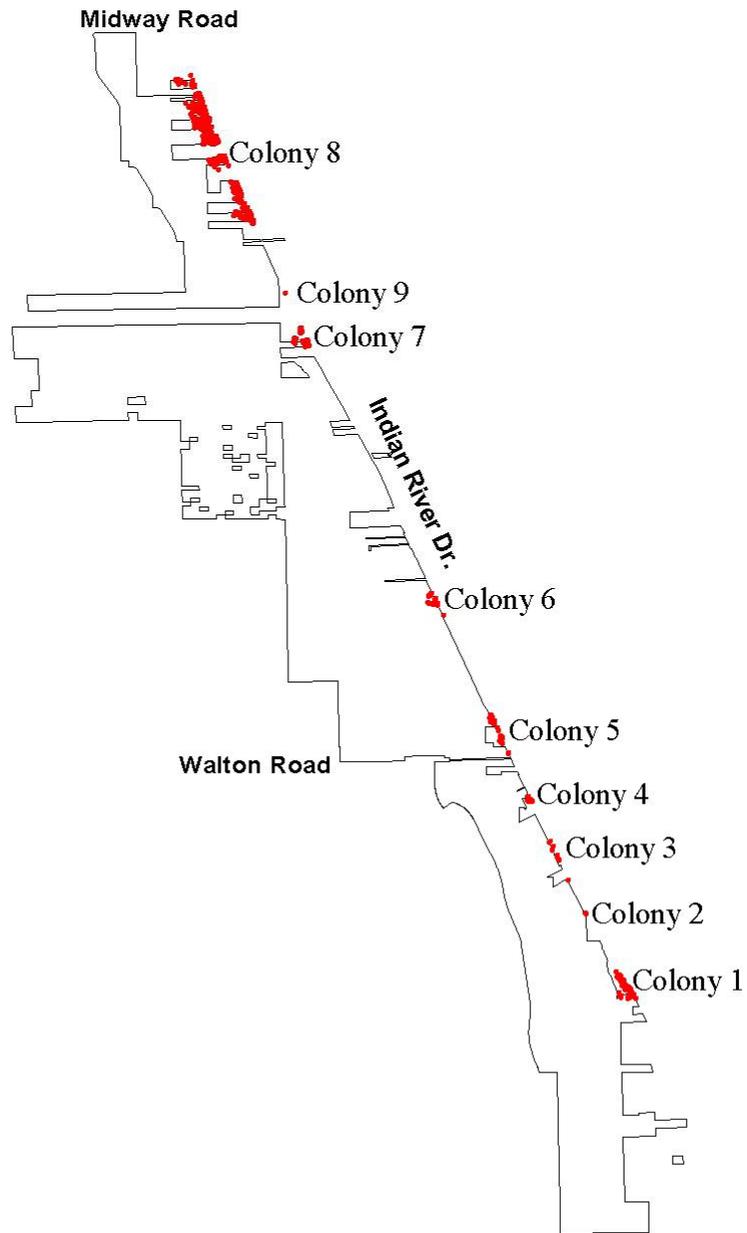
Figure 2. Population size of *H. fragrans* for four cohorts. Population sizes of cohorts
increase from the first year due to the location of additional plants that were missed in
previous censuses.
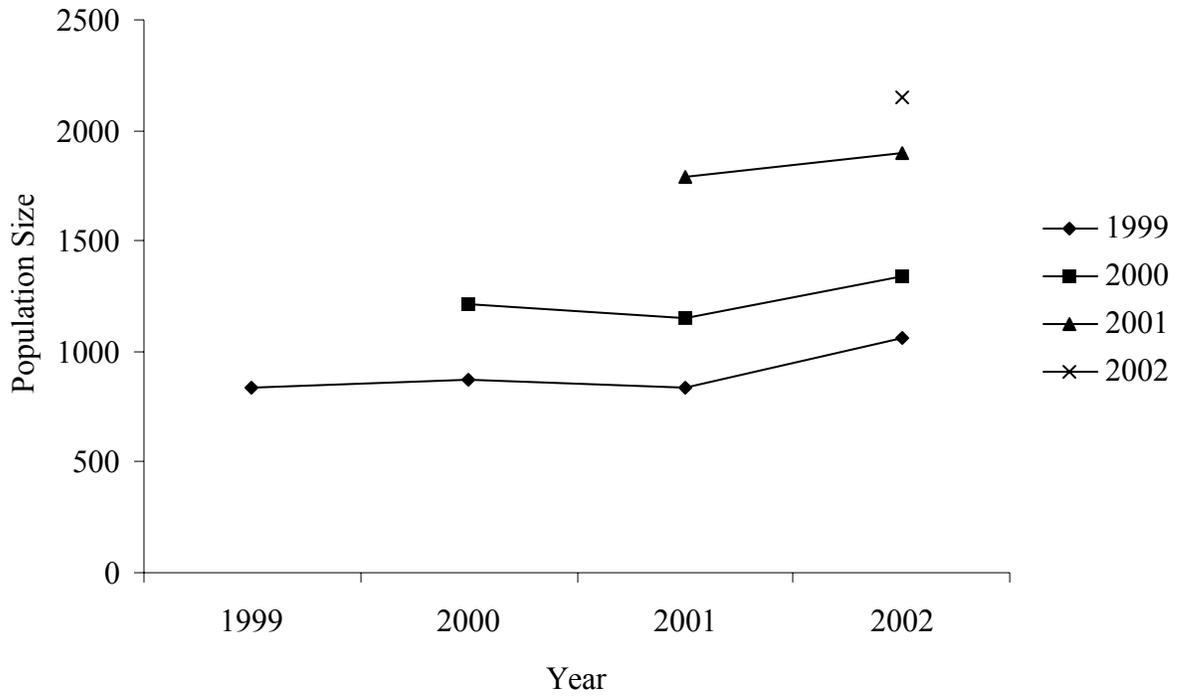
Figure 3. Temporal variation in mortality and recruitment of *H. fragrans*. Recruitment
includes sexual and asexual recruitment.
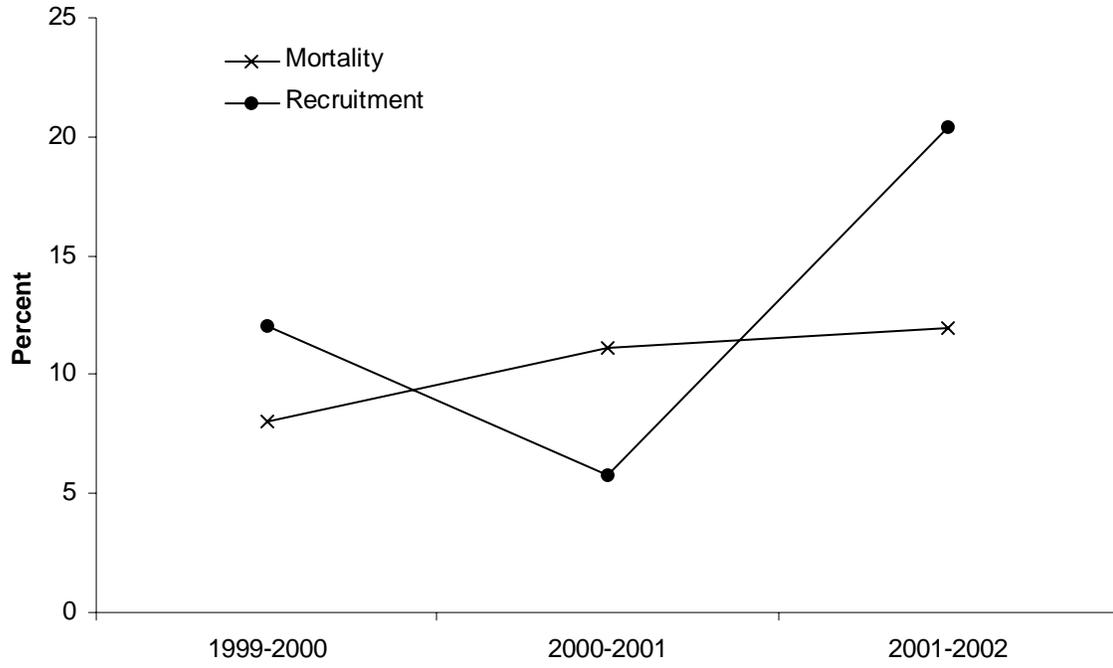
Figure 4. Pattern of recruitment of sexually and asexually derived *H. fragrans* plants across three different light environments. Data were pooled across all census periods.
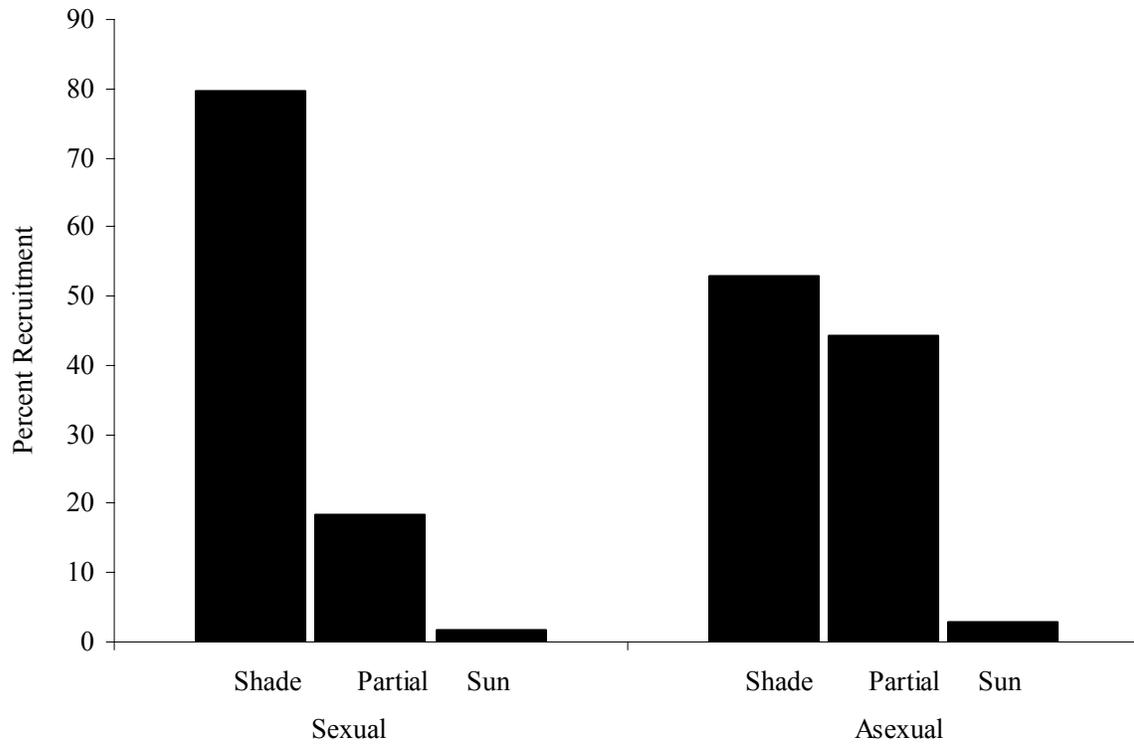
Figure 5. Percent mortality of asexually and sexually derived *H. fragrans* plants during their
first year.
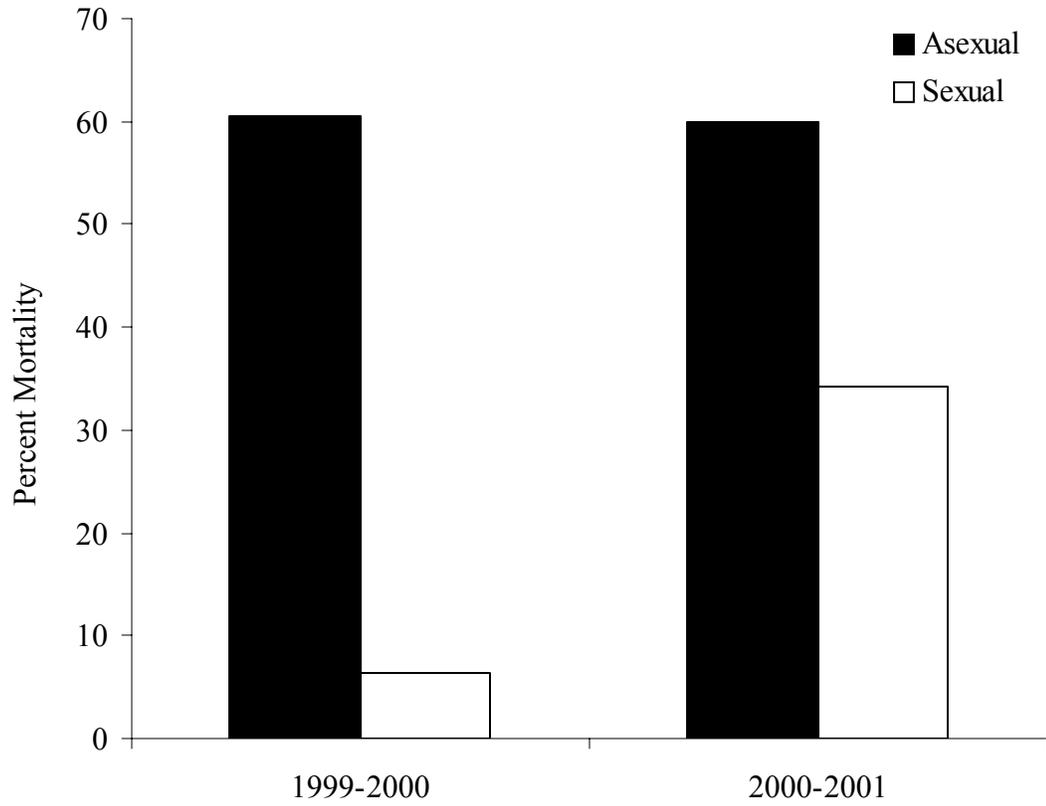
Figure 6. Relative growth rates calculated for six size classes of *H. fragrans*. Relative growth rates were calculated as (year 2 height – year 1 height) / year 1 height. Data were pooled across censuses.
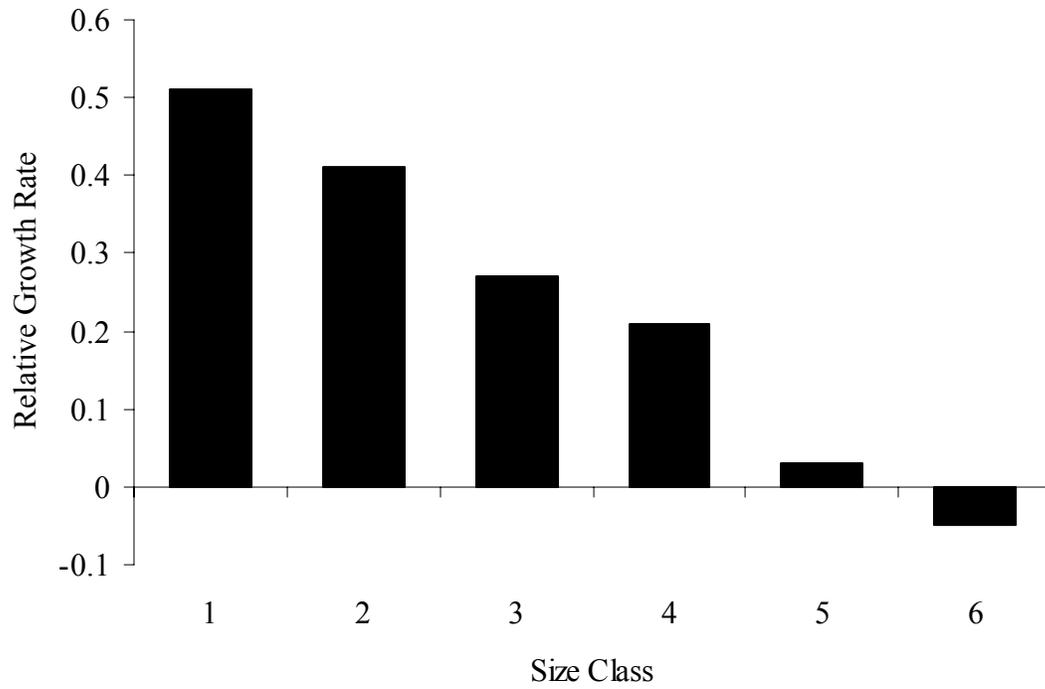
Figure 7. Pattern of fruit production for six size classes of *H. fragrans*: (A) mean number of fruits (includes fruiting and non-fruiting plants); (B) Percent of plants producing fruits; (C) mean number of fruits produced for only fruiting plants; and (D) total fruit production. Bars represent means across light microhabitats and years. Note that none of the plants in the smallest size class produced fruits.
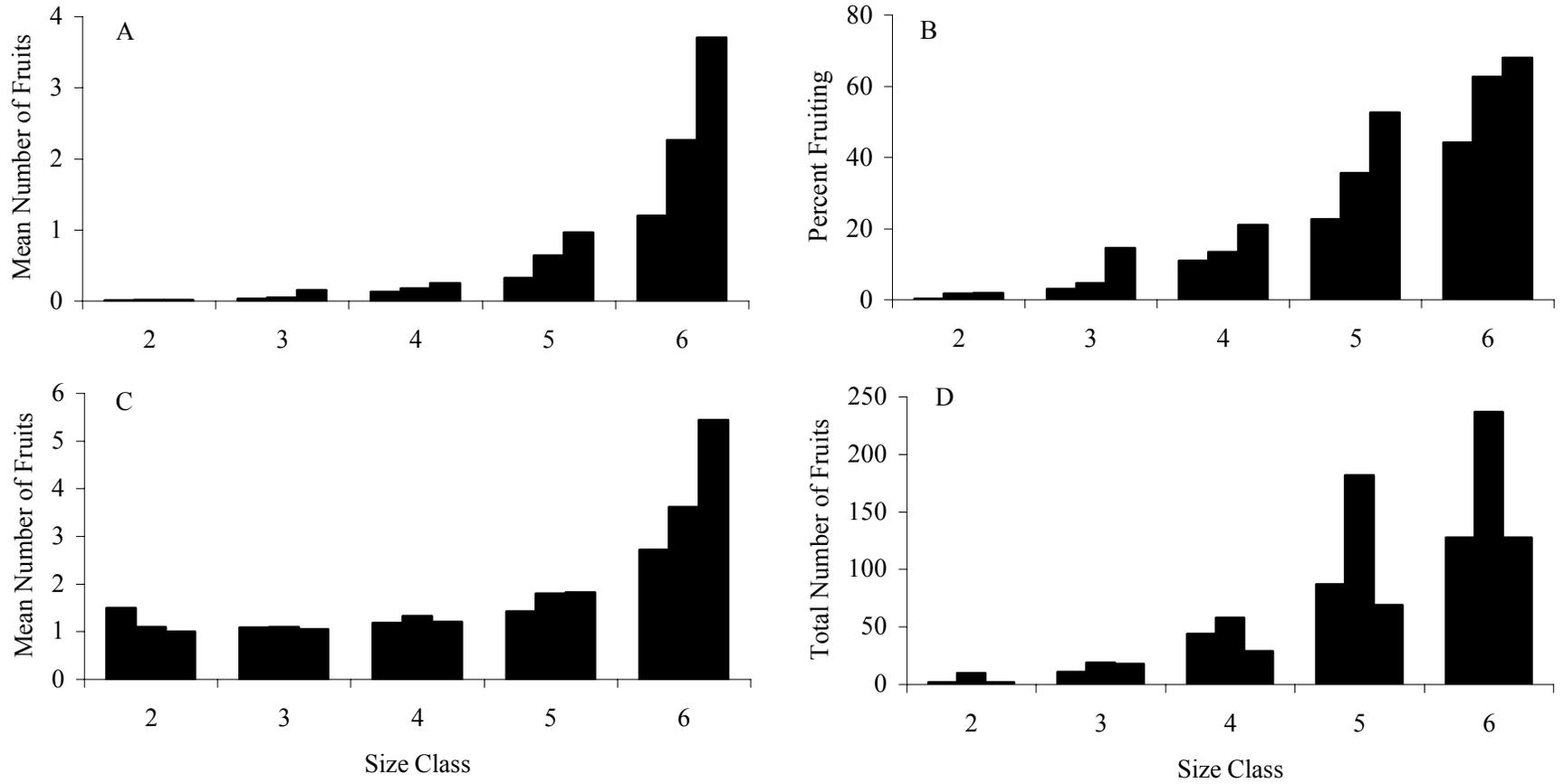
Figure 8. Effect of light microhabitat on plant mortality. Data were pooled across all years.
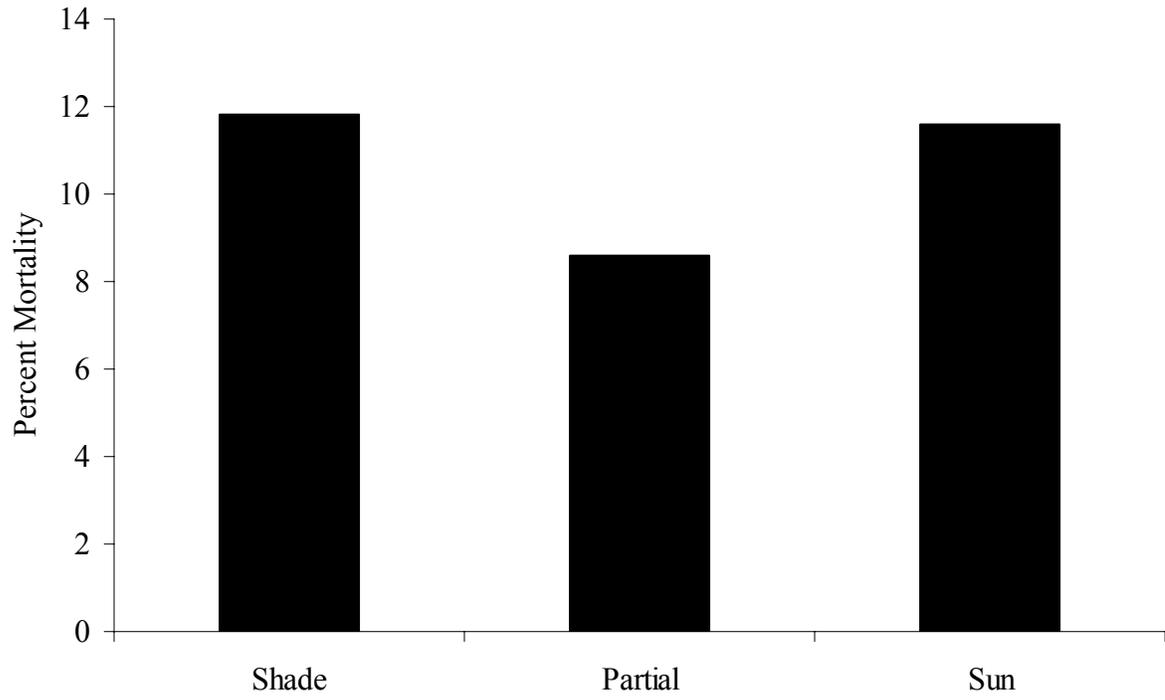
Figure 9. Population growth rates (lambda) estimated from projection matrix analysis. Note that a growth rate of 1.0 indicates a stable population size.
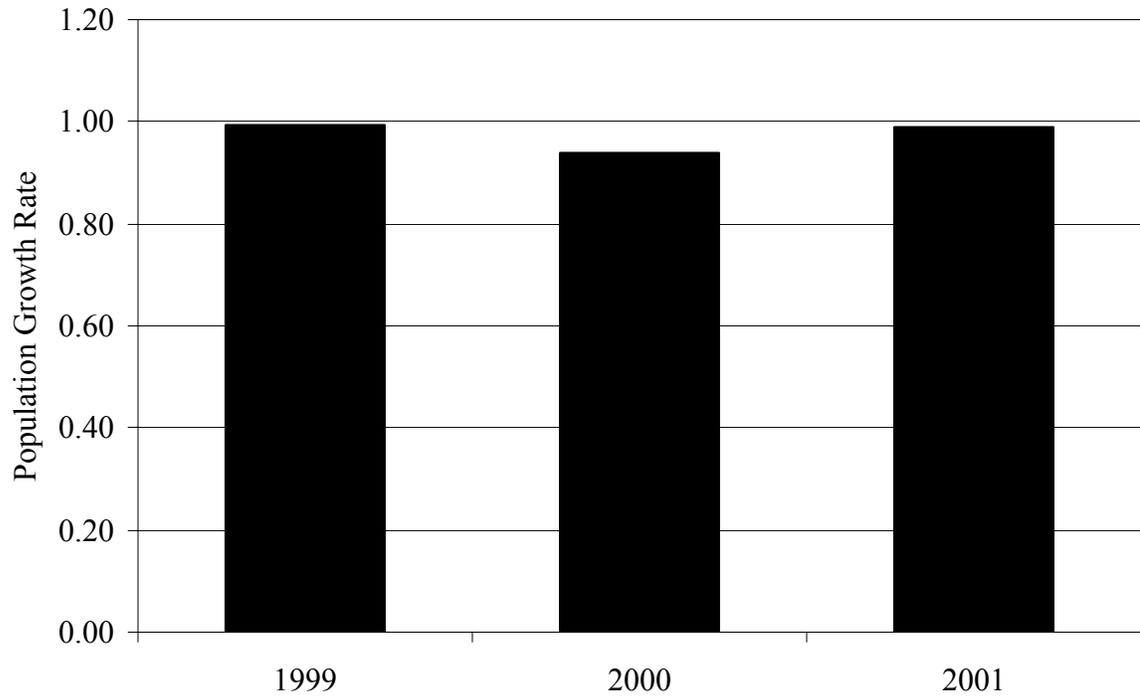
Appendix A. Map of subpopulation 1 of *H. fragrans* showing location of all individuals alive in the Fall of 2002.
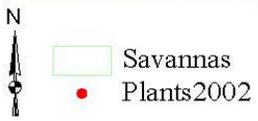
Appendix B. Map of subpopulation 2 of *H. fragrans* showing location of all individuals
     alive in the Fall of 2002.
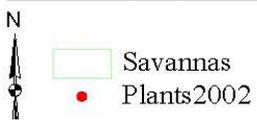
Appendix C. Map of subpopulation 3 of *H. fragrans* showing location of all individuals
alive in the Fall of 2002.
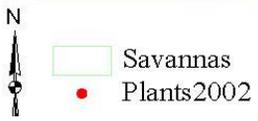
Appendix D. Map of subpopulation 4 of *H. fragrans* showing location of all individuals
    alive in the Fall of 2002.

Appendix E. Map of subpopulation 5 of *H. fragrans* showing location of all individuals alive in the Fall of 2002.
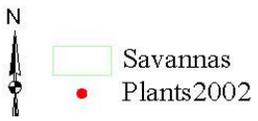
Appendix F. Map of subpopulation 6 of *H. fragrans* showing location of all individuals alive
in the Fall of 2002.

Appendix G. Map of subpopulation 7 of *H. fragrans* showing location of all individuals
    alive in the Fall of 2002.

Appendix H. Map of subpopulation 8 of *H. fragrans* showing location of all individuals alive in the Fall of 2002.

Appendix I. Map of subpopulation 9 of *H. fragrans* showing location of all individuals alive
in the Fall of 2002.

Appendix J. Lateral and front view of a flower of *H. fragrans*.