Journal of the Torrey Botanical Society 132(4), 2005, pp. 551–560

A three-year demographic study of Harper's Beauty (*Harperocallis flava* McDaniel), an endangered Florida endemic[1]

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WALKER, J. L. AND A. M. SILLETTI (USDA Forest Service, Southern Research Station, 233 Lehotsky Hall, Clemson University, Clemson, SC 29634). A three-year demographic study of Harper's Beauty (*Harperocallis flava* McDaniel), an endangered Florida endemic. J. Torrey Bot. Soc. 132: 551–560. 2005.—*Harperocallis flava* is a federally listed endangered plant narrowly endemic to the Florida panhandle. A lack of knowledge about *Harperocallis* population dynamics currently hinders conservation planning. Our objectives included describing ramet size, reproductive status, and mortality and recruitment rates in natural populations of *H. flava*. In 1998, we established permanent plots and marked individual ramets at six sites representing two habitat types in Apalachicola National Forest. At each site, we established ≥ 3 plots of varying size (0.12–1.8 m^2) to include ~300 ramets / site. In the first year we tagged, recorded reproductive status of, and measured individual ramets (# of leaves, longest leaf length). In 1999 and 2000, new ramets were tagged and all tagged ramets were re-measured. Analysis of variance methods were used to detect site, year, and habitat effects on response variables. Total number of ramets sampled varied between sites and declined from year to year. The proportion of ramets bearing reproductive structures was low (0.01 to 0.10) and varied with site and year. Logistic regression indicated that larger ramets were more likely to produce reproductive structures, and that smaller ramets suffered higher mortality. There were significant habitat and year effects on mortality; recruitment differed between years. The relatively short duration of this study precluded examination of potentially important fire effects. A rhizomatous habit and unexpected levels of crayfish-induced mortality suggest that knowledge of population structure and processes at larger scales is needed to develop effective monitoring and management strategies for *H. flava*.

Key words: demography, endangered species, Florida, *Harperocallis flava*, Harper's beauty, longleaf pine, seepage bogs.

The longleaf pine ecosystem has high plant species richness, especially at small scales (Walker and Peet 1983, Peet and Allard 1993), and is characterized by a large number of narrowly endemic (Estill and Cruzan 2001, LeBlonde 2001, Sorrie and Weakley 2001) and rare species (Hardin and White 1989, Peet and Allard 1993, Walker 1993). Because of habitat loss and changes, especially those produced by fire exclusion, dozens of longleaf pine associated plants are listed as threatened or endangered under the Endangered Species Act. Many others are ranked as G1-G3 species by The Nature Conservancy or are given special conservation status by various state governments (NatureServe 2005). Conservation efforts have focused on habitat management with particular emphasis on prescribed burning during the growing season, because such burning results in reduced woody plant cover and abundant flowering of herbaceous ground-layer species at many sites (Platt et al. 1991, Robbins and Myers 1992, Glitzenstein et al. 1995, Glitzenstein et al. 2003). However, species in these habitats vary considerably in life history, growth form, and phenology (Hardin and White 1989, Walker 1993), and thus are likely to respond in different ways to management actions. Although a few of these species have been studied intensively (e.g., Kirkman et al. 1998), remarkably little is known about individual rare species in the longleaf pine ecosystem, and there is a clear need for species-specific data on more of these populations to enhance conservation and management.

Like many rare longleaf pine associates, *Harperocallis flava* McDaniel (Tofieldiaceae) is an herbaceous perennial typically found in wetter habitats such as depressions, ditches, and seepage bogs (Walker 1993). *Harperocallis flava*

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[1] Funding was provided by the USDA Forest Service Southern Research Station, Clemson, SC.

[2] This study would not have been possible without the help of Louise Kirn and other personnel at the Apalachicola National Forest in Bristol, FL. We also thank Dana Madsen Schulze, Molly Middlebrook, and Tina Kessler for data collection. Stanley J. Zarnoch of the Southern Research Station assisted with statistical analysis. Mary Carrington, Joseph O'Brien, Peter S. White, and two anonymous reviewers provided reviews that markedly improved this manuscript.

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Received for publication September 24, 2004, and in revised form August 5, 2005.

was first described by McDaniel in 1968 and was listed as endangered under the Endangered Species Act in 1979 (U. S. Fish and Wildlife Service 1983). This species is known only from Franklin, Liberty, and Bay Counties in the Florida panhandle, with most known populations occurring inside the Apalachicola National Forest. McDaniel described the species from a bog adjacent to a state highway, and early surveys suggested that the species was restricted to roadside locations and a few isolated "natural" off-road sites. With subsequent increases in prescribed burning and intensified survey activities in the 1990s, additional off-road sites were located (L. Kirn, personal communication). Although there are preliminary studies of *H. flava*'s insect pollinators (Pitts-Singer et al. 2002), breeding system, seed viability and germination (Wagner and Spira 1996), and genetic diversity (which is extraordinarily low; Godt et al. 1997), there is very little information on population structure and dynamics of this species. Demographic studies have been very useful in anticipating trends in plant population size and detecting response to disturbance in rare species (Menges and Gordon 1996, Byers and Meagher 1997), and, therefore, may be an important tool for increasing understanding of *H. flava*.

Ultimately, we would like to understand the population dynamics of *H. flava* and use this knowledge to determine how this species should be protected and managed. As a first step, we examined the spatial and temporal variation in selected populations to determine whether the populations were stable and reproducing. We did this by monitoring individual ramets of *H. flava* in six sites in the Apalachicola National Forest. Specifically, we addressed the following questions: 1) How do ramet size and flowering vary among sites, habitat types, and years? 2) How do recruitment and mortality vary across sites, habitat types, and years? Because the number of ramets sampled in a fixed area declined markedly in most of our locations over the course of the study, which we think may have been due to precipitation patterns, we present data on precipitation during the study period.

Methods. STUDY SPECIES. *Harperocallis flava* represents a monotypic genus recently transferred from the Liliaceae to the Tofieldiaceae (Zomlefer 1997). *Harperocallis* is most closely related to *Narthecium*, *Pleea*, and *Tofeldia*, the latter two of which are morphologically similar to *Harperocallis* and are often found in its vicinity. As described by McDaniel (1968), each ramet has 2–5 basal, linear leaves that range from 5–21 cm long and from 2–3 mm wide. The stems are short and usually sheathed at the base with fibrous old leaf bases. The plant increases vegetatively by shallow rhizomes that produce new ramets at their tips, and forms small-to-large dense clumps (< 5 to > 100 ramets). A ramet of Harper's Beauty can produce a single yellow flower borne on a scape much longer than the leaves, up to 55 cm tall. A three-carpel capsule encloses many fusiform seeds 2–3 mm long. Flowering occurs in mid-April through early May; fruits develop through July; and old fruits can persist on the scape for more than one growing season.

STUDY AREA. This study was conducted on the Apalachicola Ranger District of the Apalachicola National Forest near Sumatra and Wilma, Florida. Previous observations indicated that *H. flava* grows in two types of habitat differentiated here by the plant community. Populations of *H. flava* are most commonly found in open seepage bogs dominated by herbaceous species (including small *Dichanthelium* spp., *Rhynchospora* spp., *Drosera* spp., *Pinguicula* spp., *Bigelowii nudata*, and *Carphephorus pseudoliatris*) and generally lacking cover by woody species. Less commonly, *H. flava* is found growing at the base of evergreen shrubs (*Cliftonia monophylla*, *Myrica inodora*) in areas with much less herbaceous cover. Both habitats are located in the ecotone between upland pine communities and *Taxodium ascendens* or evergreen shrub communities.

We chose four study sites from bog habitats (Sites 1–4) and two from shrub habitats (Sites 5 and 6). All six sites were burned in prescribed fires within six months prior to plot establishment, one (site 1) in December 1997 and five in February 1998. Although unplanned, site 1 was burned again in February 2000.

SAMPLING METHODS. The overall sampling goal was to mark and measure approximately 300 ramets at each site. Because the within-site distribution was patchy and the ramets were very difficult to locate, it was not feasible to select individual ramets randomly. Instead, we established the following sampling strategy. Within each site, marked ramets were to be distributed in at least 3 discrete patches, each with about 100 ramets. Patches to be sampled were chosen non-randomly from among areas where the *H. flava* density appeared to be the highest

Table 1. Number of *Harperocallis flava* ramets tagged in the first year of the study, the number of sample units, and the total area sampled at each of six sites in the Apalachicola National Forest.

Site	Habitat	Number of ramets tagged in 1998	Number of sample units	Total area sampled (m^2)
1	bog	390	4	4.32
2	bog	360	7	4.45
3	bog	293	5	5.20
4	bog	193	3	2.84
5	shrub	341	7	3.84
6	shrub	293	5	3.15

within each site. The actual area that was to be re-sampled and examined for recruitment was defined by sample units. Two kinds of sampling units were used. In areas where ramets occurred in small patches of very high density, we used 30 cm × 30 cm quadrats as sample units. In areas with sparser patches, 40 cm wide transects of varying length (0.4–4.4 m long) were used. The length of each transect was extended in 20 cm increments as needed to locate about 100 individual ramets, or until no more ramets could be found. A minimum of 3 units per site (quadrats, transects, or a combination of the two) were established for re-sampling; in some sites more units (up to 7) were needed to achieve the overall goal of 300 ramets. The total number of ramets sampled, the resulting number of sample units at each site and the total area ultimately sampled is given in Table 1. This sampling strategy, with its use of unequal sample unit sizes, precluded a direct comparison of ramet density. We acknowledge that the results of our study relate only to the high density patches within sites, and not to the entire population of *H. flava* at the site. Additionally, it is possible that patterns in reproduction, recruitment, and mortality observed in high density patches may not be applicable to lower density patches of *H. flava*.

In early June 1998, all ramets within each sample unit were identified and marked with numbered aluminum bands. The bands enclosed the base of the ramet and were anchored in the ground by florists' greening pins painted with rust-resistant paint. The ramets at each sample point were numbered as systematically as possible to make re-locating individual ramets easier. In the first year, we recorded the total number of marked ramets per sample unit, the number of leaves of each ramet, the length of the longest leaf on each ramet, and the presence of any current-year (green) reproductive structures (scapes, flowers, or capsules). In June of the second and third years, we returned to the marked sample units, relocated marked individuals, and re-measured them. In years two and three we also measured and tagged any new individuals that were found within each sample area. Tagged ramets that could not be located were classed as missing, and explanatory notes were made (e.g., "buried by a crayfish", "no plant in tag"). In years two and three we encountered many instances where tagged plants had been buried under mounds built by crayfish during the previous year.

Recruitment of individuals into each sample area was calculated on a per ramet (ramets recruited / total ramets) basis for the first (1998–1999) and second (1999–2000) between-sample intervals. The number of new, unmarked ramets recorded in a sample unit in years two (1999) and three (2000) was divided by the total number of ramets recorded for that unit in the previous year. In the same way, ramet mortality (ramets lost / total ramets) was calculated by dividing the number of individuals lost (i.e., those classified as missing) between sample periods by the number of ramets in the unit in the previous year.

Values for all parameters were calculated on the sample unit level and statistical analyses were performed with mean sample unit as the subject.

PRECIPITATION DATA. We acquired monthly precipitation totals for the Apalachicola Municipal Airport, Apalachicola, FL from the National Climate Data Center (http://www.ncdc.noaa.gov/oa/ncdc) and calculated total precipitation for the 12 months preceding each sample date. To examine season trends in precipitation, we also calculated departures from long-term (30 year) averages on a monthly basis by subtracting each monthly precipitation value from the long-term average precipitation for that month. Deviation from the long-term average was also calculated for total annual precipitation (the 12 months preceding each sample date) by adding the monthly values.

Statistical Analysis. To examine plant size, proportion of individuals bearing reproductive structures, recruitment of ramets into the sampled plots, and loss of ramets from the sampled plots we used a mixed model analysis of variance (ANOVA) with repeated measures, testing the main effects of site and year and the site × year interaction (PROC MIXED; SAS/STAT™ software, Release 8.1 for WINDOWS; Copyright©2000, SAS Institute Inc. Cary, NC, USA). For recruitment and mortality analyses, year referred to between-sample intervals (1998 represented recruitment of individuals during the 1998–99 interval, and 1999, during the 1999–2000 interval). We used a completely randomized design in which site and year were fixed factors and sample unit within site was a random factor. When $P < 0.05$ for an effect in the ANOVA, least-squares means analysis was used to compare all possible pairwise comparisons of treatment means at a 0.05 experimentwise alpha error rate. In addition, linear contrasts were used within this analysis to determine if there were significant differences between bog and shrub habitats for each response variable by testing the difference between the means of Sites 1–4 and Sites 5–6. If initial analyses indicated that there was a significant site × year interaction, we also used contrast statements to test for a habitat × year interaction on the response variable. Mortality (ramets lost / total ramets) and recruitment (new ramets / total ramets) values were square root transformed prior to analysis to meet ANOVA assumptions; all other analyses were performed on raw data and untransformed data are presented in all figures.

To examine the importance of crayfish burial at each site, we calculated the proportion of plants buried during our study by tallying the total number of ramets lost to crayfish burial in 1999 and 2000 in each plot and dividing by the total number of ramets at the beginning of the study in 1998. After square root transformation, we analyzed this data in a mixed-model ANOVA testing the effect of site, with a contrast statement to test for differences between bog and shrub habitats.

To examine the relationship between ramet size and reproductive status, we used logistic regression analysis. We performed a separate analysis for each year of the study. We employed maximum likelihood procedures in SAS/STAT software (PROC GENMOD) to build regression equations with reproductive status (reproductive structures present or not present) as the response variable and ramet size (number of leaves) as the explanatory variable. Pearson's chi-square test was used to check equations for goodness of fit (equations were considered to fit the data if $P < 0.15$; Ramsey and Schafer 2002). Significance of leaf number as a factor in predicting the presence of reproductive structures was determined by examining Wald's statistic and the chi-squared test from the maximum likelihood statistics. Estimates from the logistic regression were used to calculate the predicted logit for each leaf number, which was then used to calculate the probability of observing reproductive structures on an individual ramet in a given year.

We used similar methods to evaluate the relationship between ramet size and survival from one sample date to the next. We removed ramets that were known to be buried by crayfish from this analysis, as we judged that this process would not have been related to ramet size. We then determined whether individual ramets were lost from the population in each of the two between-sample intervals (1998–1999 and 1999–2000). Plants that were observed to be present in two successive years were considered to have survived. Those that were observed to be present in one year but were not recorded in the next year were considered to have died. Separate logistic regression analyses were performed for each between-sample interval. Survival status (survived or died between years) was the response variable and ramet size (leaf number) the explanatory variable. Logistic regression analysis was performed as described above and logits from the analysis were again used to calculate the probability that a ramet would be lost from the population between sample dates at each given leaf number.

Results. Number of Ramets. Although we were unable to use statistical analysis to examine changes in total number of ramets sampled, our data show that the number of ramets was highest in 1998 and declined through 1999 to its lowest point in 2000 (Fig. 1a). We note that this pattern held across all sites except Site 5 (Fig. 1b).

Ramet Size. There were significant effects of sample site ($F_{5,24.7} = 2.91$, $P = 0.034$), year ($F_{2,31.7} = 99.5$, $P < 0.0001$), and the site × year interaction ($F_{10,37.3} = 17.2$, $P < 0.0001$) on the average number of leaves / ramet. Average num-

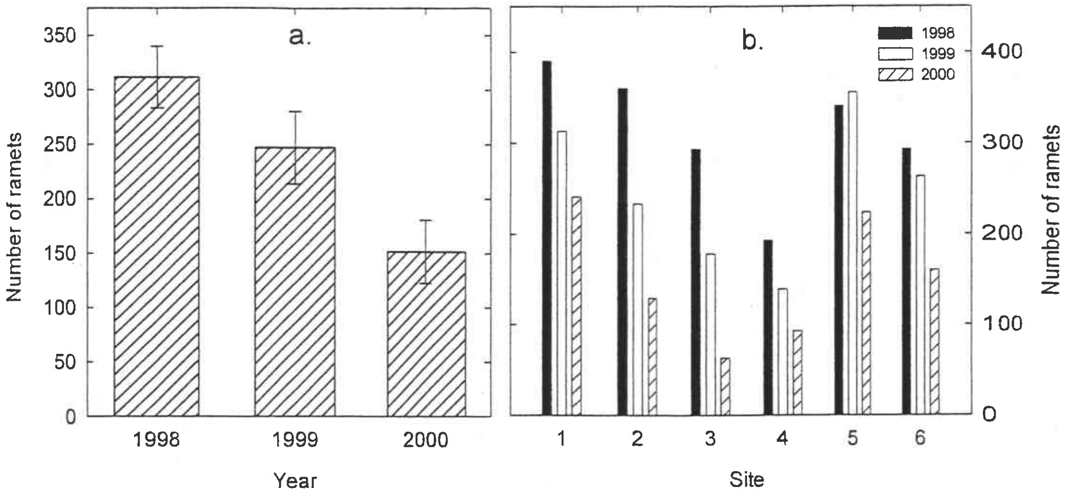

FIG. 1. (a.) Mean number of *H. flava* ramets sampled for all sites combined for the three years of the study. Error bars represent ±1 SE. (b.) Total number of *H. flava* ramets sampled at six sites in Apalachicola National Forest from 1998–2000.

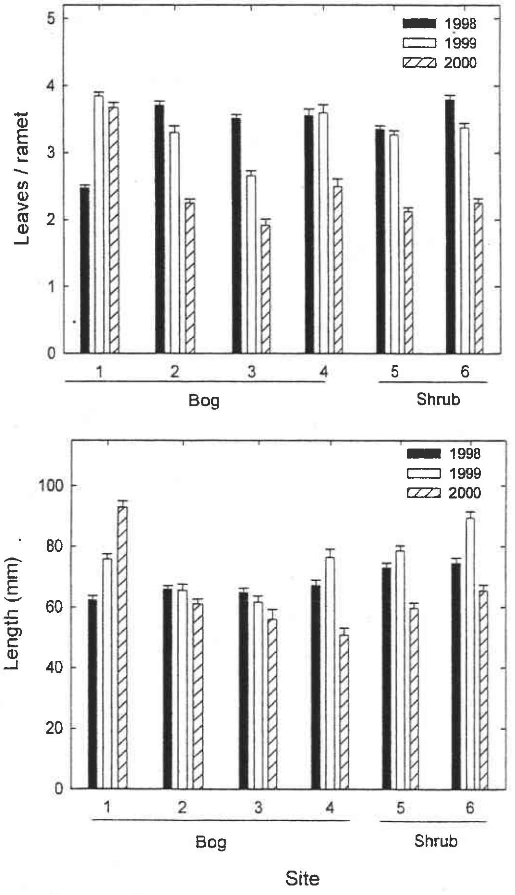

FIG. 2. Mean number of leaves / ramet (top) and mean length of the longest leaf on the ramet (bottom) of *H. flava* at six sites from 1998–2000. Error bars represent + 1 SE for both panels.

ber of leaves / ramet decreased in four of the six sites over the course of the study (Fig. 2, top), whereas two sites had the greatest number of leaves in 1999. Average number of leaves / ramet did not differ significantly by habitat type ($F_{1,24.5} = 0.09$, $P = 0.763$), but the habitat × year interaction was significant ($F_{2,31.6} = 13.4$, $P < 0.0001$).

Although site had no significant effect on the average length of the longest leaf of a ramet ($F_{5,25.6} = 1.76$, $P = 0.156$), there was a significant year effect ($F_{2,47.4} = 31.3$, $P < 0.0001$) and site × year interaction ($F_{10,47.4} = 11.9$, $P < 0.0001$). Mean leaf length was shortest in 2000 except in Site 1, where the mean length of the longest leaf increased through time (Fig. 2, bottom). Length of the longest leaf did not differ significantly by habitat type ($F_{5,25.6} = 2.01$, $P = 0.168$), but there was a significant habitat × year interaction ($F_{2,47.4} = 17.4$, $P < 0.0001$).

REPRODUCTION. Overall, the proportion of ramets bearing evidence of reproductive structures (scapes, flowers, and/or capsules) was very low. Across all sites, the proportion was 0.109 ± 0.018 ramets / ramet in 1998, 0.017 ± 0.005 ramets / ramet in 1999, and 0.036 ± 0.014 ramets / ramet in 2000. Site averages across years ranged from 0.012 to 0.100. Site ($F_{5,20.9} = 3.52$, $P = 0.018$), year ($F_{2,34.9} = 24.5$, $P < 0.0001$), and the site × year interaction ($F_{10,38.3} = 3.95$, $P = 0.001$) were all significant in the ANOVA. Because the number of ramets exhibiting evidence of reproductive structures was extremely

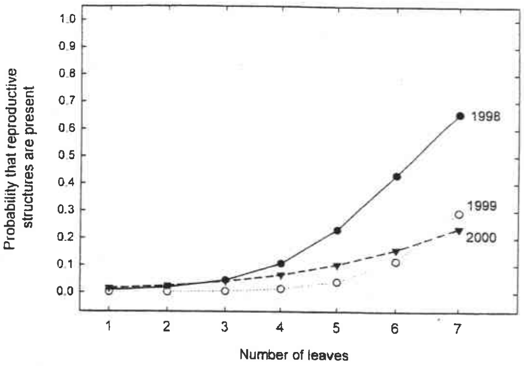

FIG. 3. Predicted probability that an individual ramet of a given size (leaf number) bears reproductive structures (scape, flower, or fruit). Probabilities were calculated using logistic regression. Separate analyses were done for each year of the study.

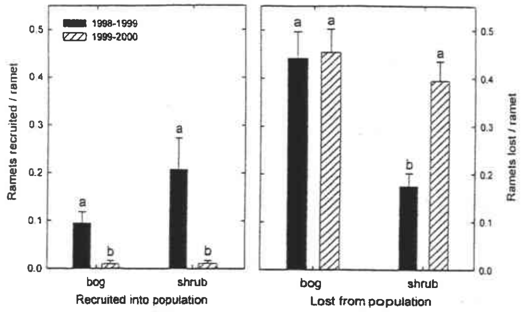

FIG. 4. The mean recruitment (left) and loss of ramets (right) from sample locations by habitat type. Bars show means by habitat type ($n = 4$, bog habitats; $n = 2$, shrub habitats). Error bars represent + 1 SE for both panels. Within a panel, different letters above bars indicate significant differences ($P < 0.05$) between time periods.

low, results of means separation tests are not clearly interpretable; that is, apparent site-to-site differences may be a result of small sample size. The difference between habitats in the proportion of ramets with reproductive structures (bog = 0.058 ± 0.01 ramets / ramet; shrub = 0.049 ± 0.017) was not significant ($F_{1,20.9} = 0.12$, $P = 0.734$). Additionally, the number of ramets bearing flowers or fruits (rather than scapes only) at the time of sampling was so small (1998 = 67 ramets, 1999 = 10 ramets, 2000 = 29 ramets) that statistical analysis of this measure was not possible.

The probability that an individual ramet would produce reproductive structures increased with increasing number of leaves (Fig. 3), although the exact relationship between leaf number and probability changed from year to year. The overall probability that reproductive structures were present was higher in 1998 than in 1999 or 2000, especially at higher leaf numbers. Leaf number was significant in predicting the presence of reproductive structures (as determined by Wald's statistic) in 1998 ($P < 0.0001$), 1999 ($P < 0.0001$), and 2000 ($P = 0.0006$).

RECRUITMENT AND MORTALITY. Recruitment of new individuals into the population was very low in both the first and second between-sample intervals (Fig. 4). Year had a significant effect on recruitment of individual ramets into the sampled population ($F_{1,25} = 43.9$, $P < 0.0001$), with the1998–99 interval having a higher rate of recruitment than 1999–2000 (Fig. 4). Neither the site main effect ($F_{5,25} = 1.83$, $P = 0.143$), nor the site × year interaction ($F_{5,25} = 1.34$, $P = 0.282$) was significant. There was not a significant habitat effect ($F_{1,25} = 1.32$, $P = 0.261$) on recruitment.

Analysis of mortality showed that there were significant effects of year ($F_{1,22.4} = 6.83$, $P = 0.016$) and site ($F_{5,22.9} = 3.84$, $P = 0.011$) and a significant site × year interaction ($F_{5,22.4} = 2.90$, $P = 0.036$). Contrasts indicated that habitat ($F_{1,23} = 8.81$, $P = 0.007$) and the habitat* year interaction ($F_{1,22.6} = 11.3$, $P = 0.003$) were significant as well. Overall, the rate of loss of ramets was greater in the bog habitats than the shrub habitats. The loss of ramets from the population between sample years was constant in the bog habitat, but mortality in the shrub habitat was higher in the second inter-sample period (1999–2000) than in the first (1998–1999) (Fig. 4).

Crayfish mounds and chimneys buried many of the ramets that were lost from the sample locations. Of the ramets initially observed in 1998, significantly more were buried in bog sites (22.2%) than in shrub sites (3.6%) by the end of the study ($F_{1,17.3} = 9.43$, $P = 0.007$). The percentage of ramets in each site buried by crayfish by the end of the study ranged from 0–36%, resulting in a significant site effect ($F_{5,18} = 4.11$, $P = 0.012$).

Ramets that had more leaves were less likely to be lost from the population between sampling periods (Fig. 5). Number of leaves was significant in predicting between-sample ramet mortality for both intervals (1998–1999, $P < 0.0001$; 1999–2000, $P < 0.0001$; Wald's statistic). The pattern of decline in probability of mortality with leaf size was different for the two intervals.

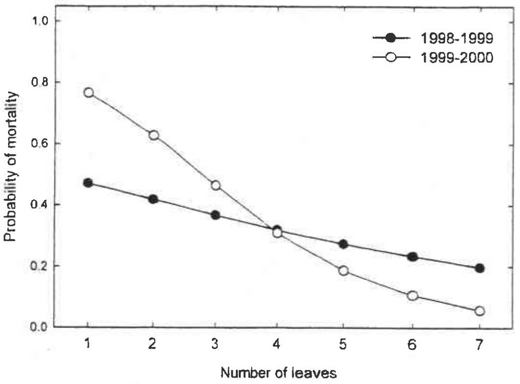

FIG. 5. Predicted probability that an individual ramet of a given size (number of leaves) is lost from the sample location from one sample year to the next, excluding those ramets observed to have been buried by crayfish. Separate logistic regression analyses for each between-sample interval were used to calculate probabilities.

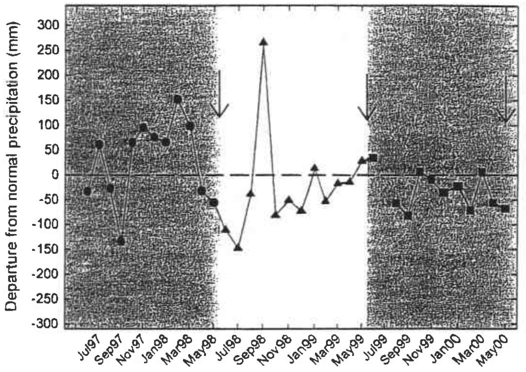

FIG. 6. Monthly departure of precipitation from long-term monthly average from July 1997–May 2000. Dashed line at zero indicates long term (30 year) averages. Arrows in graph represent the three times the plants were sampled. Different symbols indicate different sample years (sample year consists of the 12 months [June–May] preceding a sample date). Breaks in the line indicate that data are unavailable for that month.

PRECIPITATION. Total precipitation during the 12 months preceding each sample date declined through the three years of the study (June 1997–May 1998 = 173.40 cm; June 1998–May 1999 = 111.78 cm; June 1999–May 2000 = 91.41 cm). These represented departures from the 30-year average of +33.83 cm, −27.79 cm, and −48.16 cm, respectively. Both the number of ramets sampled and the size of individual ramets (Fig. 1, 2) decreased with decreasing annual rainfall.

Precipitation fluctuated above and below the long-term averages for each month during the study (Fig. 6). In the first year of the study, precipitation was well above average in the fall and early spring before our measurements were made but was slightly below average in the two months immediately preceding our measurements. In contrast, the second year of our study had a relatively dry fall and early spring (other than a pulse of precipitation from Hurricane Georges in September 1998). In the last year, precipitation was generally at or below average prior to our June measurements.

Early spring (February–March) is a period of aboveground growth, and possibly flower initiation, in *H. flava*, and may be a critical period for the species. The amount of precipitation in the spring before our first year's observations was above the long-term average, but pre-measurement spring precipitation fell well below the 30-year average in the second and third years.

Discussion. Low recruitment and high mortality together suggest that the *Harperocallis* populations we studied are not growing vigorously, and that they may be declining. Very low numbers of ramets with reproductive structures, potentially limiting opportunities for population growth via sexual reproduction, add to concern for the stability of *Harperocallis* in our study area. However, because our study was of relatively short duration and focused on only a few locations, we cannot conclude at this time that Harper's Beauty populations are at risk. Our results do provide insights into population processes and factors that may influence them, and suggest the importance of continued research.

The declining number of *Harpercallis* during our study is consistent with previous reports of reductions in herbaceous species' abundance and reproductive effort with increased time since burning (Lemon 1949, Walker and Peet 1983, Kirkman et al. 1998, Glitzenstein et al. 2003), possibly as a result of increased competition for light or nutrients. However, we observed the same declines at Site 1, even though it was burned in February 2000. We think it is more likely that this strong pattern of decline reflects the trend of decreasing precipitation over the study period. *Harperocallis flava* occupies wet habitats, and it seems likely that moisture conditions would be critical to the species' success. The observed declines in number of ramets would occur if the amount or timing of rains were critical to the survival of individual *H. flava* ramets in a single year, and would likely be cumulative with consecutive dry years or dry springs.

The size-dependence of mortality (i.e., small ramets are more likely than large ramets to be missing the following season; Fig. 5) and of sexual reproduction (i.e., larger ramets are more likely to exhibit evidence of reproductive structures; Fig. 3) seem to indicate that ramet size reflects ramet health or vigor. In this study, the increase in the number of small ramets during the driest year (Fig. 2, top) supports the hypothesis of negative drought impacts. The exception to this pattern was Site 1, which produced its largest ramets in 2000 (as defined by leaf length; Fig. 2, bottom) and was the only site burned in February 2000. The Site 1 response suggests that increasing competition for resources with increasing time since burning may also limit growth of *H. flava*. We hypothesize that fire during the early spring may promote growth by increasing available nutrients or light. Our study has shown that increased size makes both survival and sexual reproduction more likely, and thus suggests that fire may be important in this species' management.

Bog and shrub populations differed only in total mortality and mortality resulting from crayfish activity. Although there are reports of crayfish activity in similar Florida seepage bogs (Folkerts 1982, Brewer 1999), we were surprised by the extent of crayfish influence at our study sites. While this activity caused little mortality at shrub sites, up to 35% of ramets at bog sites were buried by the chimneys and mounds formed by crayfish burrowing. Differences in soil depth and moisture status likely accounted for the differences in crayfish activity in the two habitats. As is the case with other small-scale animal disturbances in longleaf pine systems (Hermann 1993), these mounds could be important functional components of pineland bog habitats. Burrowing crayfish may bring leached nutrients to the soil surface (Folkerts 1982), and this movement could be vital in these nutrient-poor bog soils (Plummer 1963). In addition, crayfish mounds may provide short-lived bare-soil microsites favorable for seedling establishment by burying established plants and litter (Brewer 1999). The effects of these mounds on established *H. flava* plants and *H. flava* seedling recruitment merit further investigation.

Habitat differences in ramet mortality from undetermined causes in the interval between the 1998 and 1999 samples is striking and suggests habitat differences in limiting resources, especially water. It is possible that there was greater or more sustained water flow in shrub habitats, and that this delayed mortality caused by increasingly dry conditions. Also, the post-fire recovery of competing shrubby vegetation may have been slower than that of competing herbaceous vegetation, thus delaying competition-related *Harperocallis* mortality. The critical habitat requirements for *Harperocallis* are not known, and this knowledge is needed to predict population performance with changing management and climate patterns.

The consistently low proportion of ramets with reproductive structures may be either typical of *H. flava* or contingent on environmental conditions. Life history theory suggests that species adapted to habitats in which nutrient availability is extremely low, such as the soils of seepage bogs, will flower at low rates and rely primarily on vegetative reproduction for population growth (Grime 2001). Changing resource availability would not be expected to change reproductive effort proportionally. Alternatively, flowering rates may be controlled by resource availability and thus vary from year to year (Waller 1988, Weiner 1988). Where this is the case, observed low rates of sexual reproduction would represent a direct response to water and nutrient limitations, or perhaps an indirect response mediated by limitation on plant growth and would increase with increasing resources. The observed relationship between ramet size and the development of reproductive structures was as would be expected (Weiner 1988), and is consistent with resource availability controls on flowering in *H. flava*.

The burn history of our study sites may also play a role in the flowering response. Many species of longleaf pine flatwoods and sandhills flower vigorously after spring and early summer (April–May) fires (Platt et al. 1988), and given similar exposures to fire through evolutionary time, bog species may be expected to respond in the same way. Our sites were burned in February, and this timing may not have been optimal for floral initiation. Although the timing of fire may be critical for abundant flowering, we note that roadside populations and greenhouse populations of *H. flava* regularly flower without burning at any time (J. L. Walker, personal observation). Thus, if fire is critical to flowering in natural settings, we suspect it results from an indirect mechanism, such as increasing availability of or reducing competition for limiting resources such as nutrients or light.

In conclusion, our results suggest two broad areas for continued research. The low recruitment rates observed, together with low numbers of reproductive individuals, appear to limit population growth and may threaten population persistence in *H. flava*. We need a better understanding of the role of, and the processes that affect, sexual reproduction in natural populations of this species, including studies of reproductive, seed, and seedling ecology. It is also evident that we have only a limited understanding of habitat requirements for growth and persistence of individuals. Apparent responses to drought conditions, differences between mortality patterns in different habitat types, and possible effects of burning all suggest environmental controls on reproduction and growth.

We hypothesize that resource availability and competition, influenced by small-scale variations in topography and hydrology, fire, and climate, are likely to be the most important determinants of population trends in this species. For this reason, we believe that research on habitat requirements is more critical than detailed work on reproductive biology at this time. In addition, it may be possible to manipulate resource availability through management, especially through prescribed burning. An understanding of habitat requirements could be used to devise management to benefit the species.

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