EFFECTS OF FIRE SEASON AND POSTFIRE HERBIVORY ON THE CYCAD ZAMIA PUMILA (ZAMIACEAE) IN SLASH PINE SAVANNA, EVERGLADES NATIONAL PARK, FLORIDA

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We investigated the effect of prescribed wet-season fire on the demography of Zamia pumila L. (Zamiaceae) in slash pine savanna of Everglades National Park, Florida. We monitored survival, coning, leaf production, and herbivore damage on two plots burned during the wet season of 1995 and on two unburned plots. Fire killed all leaves and promoted the flushing of new leaves but caused minimal mortality of adults and seedlings. Seeds within cones were killed, but some dispersed seeds survived. Coning, particularly of females, was enhanced in the plot that burned earlier and hotter. Larvae of Seirarctia echo appeared on new leaves within 1 mo postfire and were present at higher density on burned plots. Herbivore damage was significantly greater on burned plots for the first wet season following the fire, with many plants completely defoliated. This defoliation, which was more frequent in the plot burned late in the wet season, resulted in mortality of some adults but promoted greater leaf production in the remainder. Seirarctia echo consumed some Zamia cones, cancelling the positive effect of fire on reproduction. Overall, the combined direct and indirect effects of wet-season fires on Zamia was positive for the early wet-season fire but negative for the late wet-season fire because of reduced coning and increased mortality following herbivory.

Keywords: cycad, demography, Everglades, prescribed fire, herbivory, reproductive effort, population structure, Seirarctia echo, Zamia.

Introduction

Fire frequency, intensity, duration, and timing influence plant life histories and demographic traits (Bazzaz 1984). This kind of disturbance can change the population size and structure of many long-lived plant species by affecting survival, fecundity, growth, and morphology (e.g., Ahlgren and Kozlowski 1974; Whelan 1995). Many plants survive fire via resprouting of foliage and small stems (Viera et al. 1996). Other plants require fire for reproduction, seed release, and germination and/or vegetative growth (Gill 1975). For instance, fire stimulated new foliar growth and clonal stem production and induced changes in seed bank dynamics of a rare herb, Bonamia grandiflora (Convolvulaceae; Hartnett and Richardson 1989); stimulated the occurrence of flowering in pyrogenic grassland and savannas (Gill 1981) and in species such as Pityopsis graminifolia (Asteraceae; Brewer and Platt 1994) and Jacquinonia curtisii (Convolvulaceae; Spier and Snyder 1998); promoted seed germination in some savanna species (Christensen 1977); and promoted seedling recruitment in Silene regia (Caryophyllaceae; Menges 1995). In pine forests, the time of year when fire occurs (Platt et al. 1988; Spier and Snyder 1998) and the local temperature achieved (Gibson et al. 1990) are among the variables influencing demographic responses of plants.

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Encephalartos transvenosus in South Africa (Grobbelaar et al. 1989). For Zamia pumila (hereafter referred to as Zamia), the only cycad native to the United States, Tang (1990) attributed a gradual decrease in cone production during 4 yr following a wet-season fire to greater shading from shrubs.

In Florida, Zamia occurs in habitats characterized by both frequent fire (pine flatwoods and rockland pine forest) and infrequent fire (hardwood hammocks) (Long and Lakela 1976; Olmsted et al. 1983). Previous research on fire in south Florida rockland pine forest (hereafter “slash pine savanna”) focused on hardwood trees and some understory plants (e.g., Taylor and Herndon 1981; Gunderson et al. 1983), but there are no reports of the effects on Zamia demography. The Everglades National Park Fire Management Plan (1991) states that Zamia “requires fire” and “frequent fire may be damaging” but provided no evidence.

In Everglades National Park (ENP) slash pine savannas, fires were suppressed from the establishment of the park in 1947 until 1958, when prescribed burning was initiated to suppress invasion by hardwood trees and shrubs (Taylor 1981). The slash pine savannas of Long Pine Key (LPK) were divided into invasion by hardwood trees and shrubs (Taylor 1981). The slash pine in LPK was 1147 trees ha

Material and Methods

Species Description and Study Site

Zamia pumila L. occurs in southern Georgia, Florida, and the Greater Antilles (Stevenson et al. 1990; Jones 1993). Plants are small and fernlike and are dioecious, with a subterranean tuberous stem and a basal rosette of compound leaves (Norstog and Nicholls 1997). Cones are formed during the wet season at ground level and thus, like the leaves, cannot escape the effects of ground fires. Males produce cones more frequently than females (Tang 1990). Larger plants have several rosettes of leaves resulting from branching of the stem, but the proximate causes of this branching are unknown. Seeds are sometimes dispersed short distances by animals and remain dormant for several months before germinating (Negrón-Ortiz and Breckon 1989; Tang 1989). Seedlings produce coralloid roots, which are eventually infected with a cyanobacterium that fixes atmospheric nitrogen (Stevenson 1990).

The study was conducted in slash pine savannas of LPK and ENP, Florida. South Florida has a subtropical climate with wet summers and dry winters. Average annual rainfall among five of the six Everglades stations ranged from 1190 to 1570 mm (Duever et al. 1994). Slash pine savanna is a fire-dependent vegetation with slash pine, Pinus elliotti var. densa, dominant in the overstory and the palms Serenoa repens and Sabal palmetto dominant in the understory (Snyder et al. 1990; Platt 1999). The density of slash pine in LPK was 1147 trees ha

Experimental Design

We studied Zamia in four adjacent fire blocks: H, I-1, I-2, and J (25°22′–24°N, 80°37′–38°W). The distance between plots ranged from 1.0 to 2.6 km. Block I-1 was burned in the early wet season of a wet year (June 10, 1995) and again on June 26, 1997; block J was burned in the late wet season of the same years (July 23, 1995, and September 9, 1997). The unburned plots, H and I-2, serve as controls relative to plots in burned fire blocks with respect to immediate fire effects, but they are not true controls since they are plots in which fires have occurred and will occur in the future (Platt et al. 1988).

Within each fire block, we selected a study plot in an area of high Zamia density. Plots ranged in size from 56 m² (I-2) to 780 m² (J) and contained 51–52 adult Zamia, for a density of 0.07–0.93 plants m⁻². The plots were established in 1995 before fires, and Zamia individuals were monitored over a 2.5 yr period. Individuals were considered seedlings if they had one or two leaves, each ≤12 cm long, with ≤6 leaflets. All other individuals were considered adults (we did not discriminate between juveniles and adults sensu Negrón-Ortiz et al. 1996). Within each plot, all Zamia adults were marked and censused biweekly for the 4 mo postfire and monthly for 1.5
yr for the number of new and mature leaves, number of branches, the stage and sex of each cone, and mortality. Adults and branches of multistemmed adults were considered dead if they remained leafless >12 mo. This is based on our finding that no plant or branch that was leafless for >10 mo subsequently produced a leaf during the 2.5-yr study. At each census we also scored each leaf on each adult into one of seven categories to reflect the loss of leaflets or entire leaves to herbivory and counted the number of seedlings near each adult. Censuses began on May 5, 1995, in plot I-1; on May 9, 1995, in plot J; on October 1, 1995, in plot I-2; and on November 1, 1995, in plot H.

To determine the effect of local fire temperature, we chose five areas of high Zamia density within each plot to be burned in 1995, and in the center of each we designated a “temperature station.” At each temperature station we placed a set of Tempil pellets (Tempil, South Plainfield, N.J.) wrapped in aluminum foil and strung on a wire at ground level, one pellet of each of the following critical temperatures: 48°, 132°, 212°, 302°, 371°C (the 48°C pellet was omitted in J). Tempil pellets are manufactured to melt when the critical temperature is reached; wrapping ensures recovery but increases the melting temperature. We use the calibration equation derived by Platt et al. (1991) in muffle oven experiments: $Y = 1.21X + 42.8$, where $X =$ manufacturer’s rating and $Y =$ actual melting temperature. In plot I-1, the pellets were placed on the day of the fire and recovered the next day between 10:00 and 11:00 AM. In plot J, fire pellets were placed on the day before the fire between 9:30 and 11:30 AM and were collected the day after the fire between 10:00 and 11:00 AM. If one pellet was partly melted, we used its calibrated melting point as the maximum fire temperature at that station. Otherwise, we report the range between the melted pellet with the highest critical temperature and the unmelted pellet with the lowest critical temperature and use the midpoint in the calculation of plot average.

To test the effect of fire on seed germination, we placed 15–20 mature Zamia seeds within 50 cm of each of two temperature stations in each plot. These seeds were collected from five female cones that were beginning to disarticulate on May 12, 1995, and that were from pinelands at Charles Deering Estate, ca. 45 km NE of LPK. We checked these seeds biweekly for 4 mo postfire and monthly through 1.5 yr; then all the seeds were removed at the end of the study.

**Statistical Analyses**

Data were analyzed separately for the wet and dry seasons. New leaves were considered to have been produced in the wet season if they were first censused between June and November and in the dry season if they were first censused between December and May.

The relationship between prefire and postfire leaf number was explored using Pearson correlation. To determine whether the proportion of Zamia adults producing ≥1 new leaf in a season differed among treatments or plots, we used the G-test of independence (Sokal and Rohlf 1995), using Statview 4.5 (df = 1 except where indicated). Where appropriate, the two plots of the same treatment (burned and unburned) were first compared. If these were not significantly different, then data were pooled to allow comparison of the two treatments.

For those adults that produced at least one new leaf in a given season, we tested whether the number of new leaves per adult produced each season differed between burned and unburned plots. This was done by nested ANOVA using PROC GLM in SAS (version 6.12), where the plot was nested within the treatment (burned vs. unburned), after confirming that residuals did not deviate greatly from the normal distribution. For the 1995 wet season we had complete data only for the two burned plots, and we compared their postfire new leaf production by one way ANOVA.

To test whether the proportions of adults or leaves that were subjected to different levels of herbivory differed among treatments or plots, we used G-tests of independence, as above.

To explore the effect of herbivory in the 1995 wet season on leaf production in the following dry season, we first tested whether dry season leaf production in plot I-1 differed between plants that had leaves eaten before maturation versus those that suffered herbivory only after leaf maturation by using a Student t-test. Because nearly all plants in plot J had leaves eaten before maturation, we could not carry out the same contrast, but we compared their dry season leaf production to that of I-1 plants that had suffered comparable levels of herbivory by using a Student t-test.

**Results**

**Fire Temperature and Direct Effect of Fire**

Maximum fire temperatures reached in the Zamia plots in block I-1 were between 299° and 492°C ($X = 422°C$), while those in the plot in block J ranged from <202° to 408°C ($X = 273°C$; table 1). All Zamia leaves in plot I-1 were consumed in the prescribed fire (fig. 1). In plot J, most leaves were consumed, but some were only singed and, subsequently, were abscised, indicating that lower temperatures were associated with less complete combustion of leaves.

Postfire mortality of adult Zamia was very low, despite the high temperature recorded at ground level, where apical meristems are located. In plot I-1, one plant never leafed out after the 1995 fire. In plot J, fire killed the initial stem of one plant, but two new branches leafed out 8 mo later. No adults died in either the J plot or in the control plots.

Of the 56 seedlings recorded next to five females in plot I-1,

<table>
<thead>
<tr>
<th>Fire station</th>
<th>Plot I-1</th>
<th>Plot J</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>408–492</td>
<td>299–408</td>
</tr>
<tr>
<td>2</td>
<td>408–492</td>
<td>408</td>
</tr>
<tr>
<td>3</td>
<td>408</td>
<td>&lt;202</td>
</tr>
<tr>
<td>4</td>
<td>299–408</td>
<td>&lt;202</td>
</tr>
<tr>
<td>5</td>
<td>408–492</td>
<td>299</td>
</tr>
</tbody>
</table>

Note. If one pellet was partly melted, we used its calibrated melting point (Platt et al. 1991); otherwise, we report the range between the melted pellet with the highest critical temperature and the unmelted pellet with the lowest critical temperature. Where no pellet melted, we report <202.
Figs. 1, 2 Habitat and growth habit of *Zamia pumila*. Fig. 1, Plot I-1 on Long Pine Key, Everglades National Park, 1 d after prescribed burn, June 1995. Fig. 2, *Zamia pumila* adult with a flush of numerous new leaves within the first 2 mo after prescribed fire.

1 before the burn, at most 30 (54%) survived the fire. Eleven of these seedlings produced their first postfire leaves between July and August 1995, and two more produced leaves at the end of the wet season (November 1995). Twenty-five of these were still alive in early 1997, for a 2-yr survival rate of 45%. An additional 14 seedlings were first observed in leaf some time in the year following the fire; these were still alive in February 1997, but we do not know if these were new recruits or established seedlings that lacked leaves before the burn. All five seedlings censused in plot J survived the fire. One had new leaves 2 mo postfire, four had new leaves by November 1995, and all five had new leaves by 1996. All seedlings were still alive in 1997. Of 25 seedlings recorded in the control plots at the end of the wet season (November 1995), 64% survived to early 1997 (plot H = 7 of 8; plot I-2 = 9 of 17). In addition, two new seedlings were recruited in H during the 1996 wet season.

Female cones with developing seeds survived the fires, except for one cone that ceased to develop (plot J). On three of seven female cones, some sporophylls were completely burned (dark black) after the fire and opened between 1 and 4 mm. The sarcotesta (outer fleshy layer) of the more exposed seeds in these cones was consumed by the fire, whereas the sarcotesta of the less exposed seeds was burned black but remained surrounding the seeds; the sclerotesta (inner hard layer) of a few seeds was found burned. The seeds from these cones were released between August 1995 and January 1996. None of these seeds germinated; they were found eaten (empty sclerotesta) by unknown animals between March and July 1996.

There was no germination of the seeds that were placed in cages before the fire (I-1 = 30 seeds; J = 38 seeds). Some seeds that had matured and had been released naturally in the year preceding the fire did germinate. Of ≥30 seeds total released by three plants in I-1, at least 13 germinated and produced a leaf within a year after the fire. In plot J, no seeds were observed before the fire.

**Fire Effect in Leaf Production**

Most adults flushed new leaves within 2 mo of the fire, with a big pulse of new leaves ca. 1 mo postfire during the first wet season (June–November 1995; figs. 2, 3). The proportion of adults flushing leaves within 2 mo postfire was significantly greater in I-1 (92%) than in J (75%; $G = 6.2$, $P < 0.05$). Leaf production was lower in the 1995 wet season, but by the end of the season, all surviving adults in I-1 had flushed new leaves versus 84% of surviving adults in J (Fisher’s exact $P = 0.0058$). For those plants that did flush new leaves, the average number of new leaves per plant in I-1 was more than double that in J (fig. 4; table 2).

In plot I-1, the number of new leaves produced per plant in the 1995 wet season was correlated with the number of leaves on the plant before fire (May 5, 1995; $n = 52$ plants, $r =$
Fig. 4  Mean + SE number of new leaves per Zamia pumila adult during each wet and dry season, for the burned and control plots; F = fire. Only plants with one or more new leaves produced that season were included. In each plot, 51 live adults were monitored, except for plot J during and after the 1995–1996 dry season in which 52 adults were monitored. The percentages of adults producing one or more new leaves each season were pre-fire: I-1 = 22%; wet 1995: I-1 = 100, J = 84; dry 1996: I-1 = 57, J = 90, I-2 = 20, H = 14; wet 1996: I-1 = 94, J = 92, I-2 = 84, H = 82; dry 1997: I-1 = 12, J = 10, I-2 = 10, H = 16.

0.684, $P < 0.0001$). In plot J, the number of new leaves produced after fire in the 1995 wet season was also correlated with the number of leaves on the plant at the beginning of the wet season (May 9, 1995; $n = 49$ plants; $r = 0.373$, $P = 0.0079$). In plot J, however, some new leaves were produced in the 2.5 mo preceding the fire, and there was a negative correlation between prefire and postfire wet season leaf production ($r = -0.292$, $P = 0.0413$).

During the first dry season after fire (December 1995–May 1996), the proportion of adults producing at least one new leaf was greater in plot J (90%; $G = 15.85$, $P < 0.0001$) than in plot I-1 (57%). The two unburned plots were similar to each other ($G = 0.64$, $P = 0.42$), with only 17% of adults producing new leaves, which was significantly fewer than in J ($G = 82.24$, $P < 0.0001$) or I-1 ($G = 25.44$, $P < 0.0001$). Furthermore, for those adults that did produce new leaves, average leaf production was significantly greater on the burned plots (fig. 4; table 2).

Differences in leaf production between burned and unburned plots extended into the second year following the fire, but only for the first half of this year. During the wet season (June–November 1996), the proportion of adults producing new leaves was greater in the burned plots (93%) than in the unburned plots (83%; $G = 4.96$ $P = 0.0259$; no difference between plots in the same treatment). For those plants producing leaves, the number of leaves produced per plant did not differ between burned and unburned plots (fig. 4; table 2). The proportion of adults producing new leaves during the subsequent (1997) dry season was very low and did not differ between burned (11%) and unburned plots (13%; $G = 0.21$, $P = 0.65$). For those plants with new leaves, the average did not differ between burned and unburned plots (fig. 4; table 2).
Reproduction

New cones were visible 16 d postfire in plot J and 59 d postfire in plot I-1. In both plots, cone production peaked in October, and cones reached the pollination stage between January and March. The four plots differed in the number of adults bearing cones in this first year following the fire (table 3). The numbers of adults coning in plot I-1 (35%) were significantly greater than in plot J (18%; $G = 4.14, P = 0.0419$) and in the two control plots (16%; $G = 7.24, P = 0.0071$), which did not differ from each other. Plot J did not differ from the pooled controls ($G = 0.10, P = 0.76$). The same pattern was evident in reproductive effort, whether it was expressed as the number of initiated cones divided by the number of branches of adults in the plot or as initiated cones divided by the number of leaves that expanded on adults during the wet season (table 4).

All plots had more male than female cones, but the ratio of male to female cones was lower in the burned plots in the first year postfire than it was in the unburned plots that year or in any of the plots in the second year (table 3). In the second year following fire (1996–1997 pollination season), cones were produced and pollinated in the same months as in the first year postfire, but cone production and reproductive effort in the burned plots were much reduced (table 3). In the control plots there were only slight decreases in cone production and reproductive effort in the second year as compared with the first (table 3). The proportion of coning adults was very low in plot J (2% of adults), which was significantly lower than in plot I-1 (12%; $G = 4.33, P = 0.0375$). The two unburned plots did not differ from each other, with 11% of adults coning, which was significantly more than in plot J ($G = 4.64, P = 0.0312$) but the same as in plot I-1 ($G = 0.03, P = 0.8562$). Both measures of reproductive effort showed this same pattern (table 3).

In the third year, coning was infrequent in all plots. Through November 1997, only one plant in plots H and J and two plants in plot I-1 had initiated cones (one male cone in each case). We cannot rule out the possibility that some cones initiated after that date.

<table>
<thead>
<tr>
<th>Year and plot</th>
<th>Plants with cones</th>
<th>Total cones</th>
<th>Reproductive effort</th>
<th>Cones maturing (MM : FF)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Cones/branch</td>
<td>Cones/leaf</td>
</tr>
<tr>
<td>1995–1996:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I-1</td>
<td>18</td>
<td>30</td>
<td>23 : 6</td>
<td>0.37</td>
</tr>
<tr>
<td>J</td>
<td>9</td>
<td>10</td>
<td>6 : 3</td>
<td>0.14</td>
</tr>
<tr>
<td>H</td>
<td>9</td>
<td>10</td>
<td>9 : 1</td>
<td>0.17</td>
</tr>
<tr>
<td>I-2</td>
<td>7</td>
<td>7</td>
<td>6 : 1</td>
<td>0.12</td>
</tr>
<tr>
<td>1996–1997:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I-1</td>
<td>6</td>
<td>7</td>
<td>6 : 1</td>
<td>0.08</td>
</tr>
<tr>
<td>J</td>
<td>1</td>
<td>1</td>
<td>1 : 0</td>
<td>0.01</td>
</tr>
<tr>
<td>H</td>
<td>6</td>
<td>6</td>
<td>6 : 0</td>
<td>0.10</td>
</tr>
<tr>
<td>I-2</td>
<td>5</td>
<td>6</td>
<td>5 : 1</td>
<td>0.09</td>
</tr>
</tbody>
</table>

Note. Maturation is pollen release (males) or seed initiation (females). Each plot contained 51 adults, except plot J during 1995–1996 pollination season, which contained 52 adults. One cone each in plots I-1 and in J was eaten before sexed. Reproductive effort = total cones divided by the number of branches and total cones divided by the number of leaves produced in the wet season. n.d. = no data because leaf production was not quantified in plot H and I-2 in 1995 wet season.

² Includes two male cones and one female cone with partial herbivory; the male cones matured.

² Female cone with partial herbivory that later matured.

Table 2

ANOVAs of Number of New Leaves Produced per Adult in Each 6-mo Season

<table>
<thead>
<tr>
<th>Season, year, and effect</th>
<th>df</th>
<th>Mean square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet 1995:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot</td>
<td>1</td>
<td>540.14</td>
<td>22.80</td>
<td>0.0001</td>
</tr>
<tr>
<td>Error</td>
<td>92</td>
<td>23.69</td>
<td>22.80</td>
<td>0.0001</td>
</tr>
<tr>
<td>Dry 1995–1996:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>1</td>
<td>84.53</td>
<td>305.90</td>
<td>0.0033</td>
</tr>
<tr>
<td>Plot (treatment)</td>
<td>2</td>
<td>0.27</td>
<td>0.03</td>
<td>0.9742</td>
</tr>
<tr>
<td>Error</td>
<td>89</td>
<td>10.14</td>
<td>0.03</td>
<td>0.9742</td>
</tr>
<tr>
<td>Wet 1996:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>1</td>
<td>111.09</td>
<td>9.94</td>
<td>0.0876</td>
</tr>
<tr>
<td>Plot (treatment)</td>
<td>2</td>
<td>11.20</td>
<td>1.04</td>
<td>0.3552</td>
</tr>
<tr>
<td>Error</td>
<td>177</td>
<td>10.75</td>
<td>1.04</td>
<td>0.3552</td>
</tr>
<tr>
<td>Dry 1996–1997:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>1</td>
<td>2.60</td>
<td>1.03</td>
<td>0.4176</td>
</tr>
<tr>
<td>Plot (treatment)</td>
<td>2</td>
<td>2.54</td>
<td>1.14</td>
<td>0.3408</td>
</tr>
<tr>
<td>Error</td>
<td>20</td>
<td>2.23</td>
<td>1.14</td>
<td>0.3408</td>
</tr>
</tbody>
</table>

Note. Only plants with one or more new leaves produced that season were included. For the 1995 wet season, only data from the two burned plots were available. For all other seasons, leaf production was analyzed by nested ANOVA with plot nested within treatment, where treatment refers to burned or not in the 1995 wet season.
Herbivory by Seirarctia echo

Larvae of Seirarctia echo, the echo moth, were more common on plants growing in areas that were recently burned (fig. 5). Larvae of echo moths were found on new leaves in both burned plots within 4 wk of the fire, and they completely consumed many of these new leaves. Plot J had the highest number of larvae and plot I-1 had the second highest. The unburned control plots never had more than two larvae per census (fig. 5).

Early instar larvae were frequently observed on immature leaves, whereas late instar larvae (>3 cm long) were often found on older leaves and cones (table 4). If seedlings are grouped with immature leaves and stems, cones, and seeds are grouped with mature leaves, the preference was significant (Fisher’s Exact \( P = 0.0443 \)).

First Wet Season

Nearly all of the adult Zamia on the burned plots that flushed new leaves within 2 mo postfire were subjected to partial or complete herbivory by S. echo larvae during the wet season (98% in I-1, 95% in J). The proportion of these plants that were completely defoliated before leaves matured was greater in J (77%) than in I-1 (44%; \( G = 10.1, P = 0.0015 \)). Of 30 defoliated plants in plot J, 18 were defoliated twice and three were defoliated three times during the wet season. Of 21 defoliated plants in plot I-1, nine plants were defoliated twice and two were defoliated three times during this wet season.

Was this more severe wet-season herbivory in plot J (vs. I-1) responsible for the greater leaf production in this plot during the following dry season (reported above), or was the later date of the fire directly responsible? To test this, we compared the dry season leaf production of plants subjected to different levels of herbivory in the month immediately following the fire. In plot I-1 there was only one plant that escaped herbivory, but plants that had some or all of their new leaves eaten while they were still expanding produced significantly more new leaves \( (X = 3.1, n = 32) \) in the following dry season than plants that had all of their leaves mature and only suffered herbivory on the mature leaves \( (X = 0.4 \text{ new leaves}, n = 15; \ t = 2.723, \ df = 45, P = 0.0092) \). Leaf production in this latter group of plants was the same as that in the unburned plot I-2 (0.4 new leaves per adult) where plants had older leaves and suffered less herbivory (table 5). In plot J, 92% of the plants that produced leaves in the months following the fire had all or some of these leaves eaten while still expanding. These 36 defoliated plants averaged 4.1 new leaves in the next dry season, which was not significantly greater than comparable plants in I-1 \( (t = 1.242, df = 66, P = 0.2187) \). Taken together, these data indicate that enhanced leaf production in the dry season resulted from herbivory on young leaves in the months following the fire, rather than being a direct effect of fire.

Following defoliation, three adults in plot J died, as did one branch of each of four other adults (two in J and two in I-1). Another adult plant composed of three branches flushed new leaves after the fire, and immediately all were consumed; in the dry season all branches leaved out again, and one branch was defoliated again and it died. In one case in plot J, two last-instar larvae were observed eating the exposed above-ground portion of two branches of a single plant; however, a few months later these branches flushed new leaves. No plants or branches died in either control plot.

Dry Season

During the first dry season following the fire, the proportions of both mature and new leaves damaged by herbivores differed significantly among the four plots (mature leaves: \( G = 83.0, df = 6, P < 0.0001 \); new: \( G = 20.3, df = 6, P = 0.0024 \); table 6). For both categories of leaves, herbivory was greatest in one of the burned plots (J) and lowest in one of the unburned plots (H).

Leaves produced early in the dry season in plots H and I-2 were, in general, defoliated, whereas fewer of those leaves produced late in the season were eaten.

Table 4

<table>
<thead>
<tr>
<th>LARVAE SIZE</th>
<th>SEEDS</th>
<th>SEEDLINGS</th>
<th>IMMATURE LEAVES</th>
<th>MATURE LEAVES</th>
<th>STEM</th>
<th>CONE</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMALL (&lt;3 CM)</td>
<td>0</td>
<td>2</td>
<td>29</td>
<td>31</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>LARGE (≥3 CM)</td>
<td>1</td>
<td>0</td>
<td>5</td>
<td>12</td>
<td>1</td>
<td>3</td>
</tr>
</tbody>
</table>

Fig. 5 Number of Seirarctia echo observed at each census of Zamia pumila in burned (I-1 and J) and unburned (H and I-2) plots.
Table 5
Herbivory on Adult Zamia in the 1995 Wet Season: Number of Adults with Herbivore Damage as Censused on November 1, 1995

<table>
<thead>
<tr>
<th>Herbivory category</th>
<th>Plots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I-1 (burned)</td>
</tr>
<tr>
<td>Defoliated</td>
<td>14</td>
</tr>
<tr>
<td>Half or more of leaves with herbivore damage</td>
<td>29</td>
</tr>
<tr>
<td>Less than half of leaves with herbivore damage</td>
<td>3</td>
</tr>
<tr>
<td>No herbivore damage</td>
<td>6</td>
</tr>
<tr>
<td>Total number of plants</td>
<td>52</td>
</tr>
</tbody>
</table>

Note. No data are reported for plot H because leaf damage was not scored on this date.

Table 6
Herbivory on Adult Zamia during the 1995±1996 Dry Season: Number of Mature and New Leaves That Received Different Levels of Damage from Herbivores

<table>
<thead>
<tr>
<th>Plot</th>
<th>Mature leaves</th>
<th>New leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No additional damage</td>
<td>Minor damage</td>
</tr>
<tr>
<td>I-1</td>
<td>91</td>
<td>77</td>
</tr>
<tr>
<td>J</td>
<td>6</td>
<td>30</td>
</tr>
<tr>
<td>I-2</td>
<td>65</td>
<td>107</td>
</tr>
<tr>
<td>H</td>
<td>111</td>
<td>33</td>
</tr>
</tbody>
</table>

Note. For mature leaves, “minor damage” = some or all leaflets partly eaten or less than half of leaflets completely eaten. “Severe damage” = most or all leaflets completely eaten, including leaves with all but proximal portion of rachis eaten. For new leaves, “completely defoliated” = all leaflets consumed. Numbers in parentheses are percentages.

Second Wet Season

Although most plants on each plot produced new leaves during the second wet season following fire, ca. half of these plants had some or all of these leaves eaten by larvae before maturation (table 7). Plots differed significantly in the proportion of plants subjected to each level of herbivore damage on new leaves ($G = 32.2$, df = 9, $P = 0.0002$; plants without new leaves excluded from analysis). This herbivory was most severe in one of the unburned plots (I-2) and least severe in one of the burned plots (J). Plots H and I-1 suffered intermediate levels of herbivory and were the only two plots not significantly different from each other based on contingency tests using the four herbivory categories.

Cone Predation

Cones of both sexes in early stages of development were subjected to predation by S. echo larvae. In one case, a last-instar larva consumed an entire male cone within 2 h (V. Negrón-Ortiz, personal observation). Most cones with partial herbivory subsequently matured to the pollination stage (table 3). Cone predation was much lower in control plots and in the second year following fire (table 3).

Discussion

Fire Intensity

The maximum fire temperatures recorded at ground level in the earlier fire (plot I-1) were similar to those recorded by W. J. Platt (personal communication) for prescribed summer burns in ENP pinelands and for summer burns in annually and biennially burned longleaf pine (Pinus palustris) savannas in northern Florida (Platt et al. 1991). The cooler temperatures we recorded for the later fire (plot J) were more similar to those recorded for fall and winter burns in longleaf pine (Platt et al. 1991). Much cooler temperatures were reported for both wet- and dry-season burns in slash pine forests at another south Florida site (Spier and Snyder 1998). While these studies used the same method of determining fire temperature as we did, a study using tiles painted with temperature-indicating paint (Gibson et al. 1990) reported much lower temperatures in annually and biennially burned P. palustris savanna in southwest Florida. In savannas that were burned in late spring every 5 yr, maximum temperatures were similar to those we report for block J (Gibson et al. 1990).

Fire Effects on Demography

The aboveground parts of Zamia, leaves and cones, did not survive either fire despite the thick cuticle and epidermis of leaves and the thick sporophylls of cones. Mortality of individual plants was very low, probably because the stems and roots are subterranean and are insulated by the soil.

We attribute the greater frequency of branching on the burned plots to a wound response to heat damage of the exposed portion of the underground stem, including the apical meristem. Branching is an uncommon phenomenon in cycads, but the formation of adventitious buds, which eventually give rise to branches, can be stimulated by mechanical injury to the stem (Stevenson 1990; Jones 1993; Norstog and Nicholls 1997). The tendency for more branching following the later
The rapid refilling of leaves occurred when the environment was most open and light intensities were highest. The flush of new leaves within 2 mo of the fire may result from the death of the old leaves or from heat-stimulated leaf initiation. The thick underground stem has a high proportion of storage tissue, thus providing energy as starch reserves that are required for sprouting after fire. Postfire changes in soil chemistry or nutrient availability might also influence leaf production. In both burned and unburned plots, new leaf production occurred mostly in the wet season. However, the combination of fire and postfire herbivory resulted in high levels of leaf production in the first dry season following fire. Enhanced leaf production in burned plots was still apparent in the second wet season following fire. The thick underground stem has a high proportion of storage tissue, thus providing energy as starch reserves that are required for sprouting after fire. Postfire changes in soil chemistry or nutrient availability might also influence leaf production. In both burned and unburned plots, new leaf production occurred mostly in the wet season. However, the combination of fire and postfire herbivory resulted in high levels of leaf production in the first dry season following fire. Enhanced leaf production in burned plots was still apparent in the second wet season following fire.

Table 7

| Herbivory on Adult Zamia during the 1996 Wet Season: Number of Adults with Different Levels of Herbivore Damage on New Leaves over the 6 mo Season |
|-----------------|-----------------|-----------------|-----------------|-----------------|
|                 | Burned I-1 | J | Control I-2 | H |
| All completely eaten before maturation | 6 | 2 | 6 | 9 |
| Some completely eaten before maturation | 15 | 14 | 27 | 13 |
| None eaten before maturation, but some leaflets eaten after maturation | 19 | 12 | 3 | 11 |
| No herbivory | 8 | 20 | 8 | 9 |
| No new leaves produced | 3 | 3 | 7 | 9 |

Fecundity. Many plants in fire-prone habitats show increased reproduction in the year following a fire (Menges 1995; Whelan 1995; Spier and Snyder 1998). We found enhanced coning in burned plots only in the plot subjected to the hotter fire and only in the first year following the fire. In the other burned plot, coning in the second year was actually reduced below the level of the control plots. Production of female cones appears to be particularly stimulated by fire. Only 11 female cones were produced on >200 monitored adults over the 3 yr of this study, but nine of these were on the burned plots during the first year postfire. These findings are consistent with Tang's (1990) observations that females cone less frequently than males in the absence of fire, and that coning frequency, especially for male plants, declines after 4 yr postfire. However, greater predation on cones by late instar Seirarctia echo larvae in the burned plots reduced the positive effect of fire on reproduction.

We do not know if enhanced coning following fire is a direct developmental response to heat or if it results from enhanced mineral nutrition or decreased shading following fire. Beaton (1982) suggested that the stress induced by the fire to Macrozamia communis and the nutrients returned to the soil stimulate this cycad to allocate energy into reproduction, accounting for a postfire increase in seed yield. In addition, production of coralloid roots was prominent in Macrozamia riedlei plants in recently burned habitats (Halliday and Pate 1976). Nutrients such as phosphorus, potassium, and zinc reported in coralloid roots of M. riedlei were highest on recently burned sites, indicating that these nutrients are more available in the soil after a fire (Grove et al. 1980). Although Zamia has coralloid roots, we did not quantify these in our study.

Seeds and seedlings. The seed was the only life-history stage where we found that fire reduced survival. Whelan (1995) stated that for seeds to tolerate fire, they must be protected from direct fire and be tolerant of high temperatures. Zamia seeds placed in cages before the fire did not survive; however, some naturally dispersed seeds apparently germinated within the first year postfire. These may have been in microsites subjected to relatively low fire temperature. There is no evidence of seed burial by animals (Tang 1989), which might protect seeds from heat. Seeds that were within cones at the time of the fire were subsequently dispersed but failed to germinate, indicating that they too were killed by the fire. The sporophylls of these cones, which enclose the seeds, are not insulating structures. Thus, high mortality of seeds may be attributed to their lack of protective structures against high temperatures and fire intensity.

Although seedlings also lost their leaves in the fire, many were able to produce new leaves and survive. These seedlings were already established in the soil, presumably with a well-developed underground stem, indicating that a seedling bank contributes to the persistence of Zamia populations. Seedling survival was similar in burned and control plots.

Herbivory. There are important effects of fire season that are indirectly manifested through herbivory, specifically the repeated defoliations that kill some adults and cone predation. There is a strong interaction between fire and herbivory on Zamia populations. Herbivory was caused by only one Lepidopteran, E. echo. A second Lepidopteran, Eumaeus atala, a specialist on Zamia, was never observed during this study. Tang (1990), however, observed an outbreak of herbivory by E. atala 4 yr postfire at a shadier site within ENP. Perhaps the absence of the latter herbivore in our plots results from its preference for shadier environments. In the coastal dunes of Veracruz, Mexico, Castillo Guevara and Torres Hernández (1995) observed that younger leaves of Zamia furfuracea were highly damaged by Eumaeus spp. Other herbivores presumably avoid Zamia because all parts are toxic to nonspecialists, as is the case with all cycads (Rothschild et al. 1986; Jones 1993). The two best-studied toxins in Zamia and most cycads are cycasin and a related compound, methylazoxymethanol (MAM) (Nash et al. 1992). Seirarctia echo sequesters cycasin and converts MAM into cycasin, which is less toxic (Rothschild et al. 1986). However, this moth apparently is not an
obligate herbivore of *Zamia*. We also observed the larvae feeding on *Ruellia carolinensis* (Acanthaceae) and *Quercus* sp. (Fagaceae).

Why was herbivory much greater on burned plots? According to Ohgushi (1992), nitrogen is the key limiting nutrient for many herbivorous insects, and nitrogen content correlates with larval survival, growth rate, and female pupal weight and fecundity. In *M. riedlei*, nitrogen and phosphorus concentrations were highest in new leaves from recently burned sites (Grove et al. 1980), and colonization and herbivory by a specialist mealv bug increased after fire (Dolva and Scott 1982). Similarly, colonization of *Palicourea rigid*a (Rubiaceae) by leaf-galling midges in cerrado savanna, Brazil, was greater on burned sites where new leaves were more frequent (Viera et al. 1996). Thus, the high density of *S. echo* larvae we documented after fire may have been caused by higher larval survival as a consequence of the abundance of young leaves (and hence high nitrogen content) and/or to greater oviposition in burned plots (supported by the association of young larvae with young leaves). Oviposition would be enhanced if female *S. echo* preferentially search in burned or open habitats and/or preferentially deposit eggs in *Zamia* with new leaves. Also, new leaves may be more easily consumed by these larvae; they appear to be preferred by early instars. Preference of *S. echo* for the rapidly expanding young leaves of *Zamia* support the plant vigor hypothesis, in which rapidly growing modules are favorable to herbivores (Price 1991).

Importance of Prescribed Fire Regime for Persistence of *Zamia* Population

*Zamia pumila* was resistant to low-intensity prescribed fires and also responded to those fires. The wet-season prescribed fires studied did not cause decreases in the number of *Zamia* present in ENP pine savannas. Adult mortality from fires was minimal, and seedling mortality was not different in burned and unburned plots. Leaf production of established plants was higher in burned than unburned plots for 1.5 yr postfire. Early wet-season fire also appeared to stimulate coning during the year after fire, but no increase in coning occurred following late wet-season fire. However, fires resulted in an increase in the density of the specialist herbivore, *S. echo*. Larvae of this moth often defoliated refusllogging *Zamia*, causing some mortality of repeatedly defoliated plants. This indirect effect was more pronounced in the plot burned late in the wet season. Overall, populations of *Zamia pumila* appear to benefit from early wet-season fires as a result of reproduction being stimulated and greater survival of established plants following postfire herbivory. These findings indicate that this slash pine savanna *Zamia* population is adapted to early wet-season fire, supporting the hypothesis that this was the common presettlement fire regime (Snyder et al. 1990).

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