RESEARCH ARTICLE

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Restoration of Florida Pine Savanna: Flowering Response *of Lilium catesbaei* to Fire and Roller-Chopping

Jean M. Huffman'

Patricia A. Werner

Department of Wildlife Ecology
and Conservation
University of Florida
Gainesville, Florida 32611 USA

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Current address: Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803 USA

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ABSTRACT: The reduced frequency of fire in southeastern pine savannas over the past six decades has caused increases in woody species cover and decreases in herbaceous species cover. Although fire and restoration roller-chopping (chopping using techniques adapted for restoration) are established management techniques used to restore herbaceous cover to these savannas, little is known of the effects of roller-chopping on sparsely distributed herbaceous species. In an experimental field study we examined the response of *Lilium catesbaei* Walt. (pine lily), a species that is widespread in southeastern pine savannas but always a minor element of the flora, to fire and roller-chopping in saw-palmetto *(Serenoa repens* [Bartr.])-dominated Florida dry prairie (a type of pine savanna). The study included three treatments: burn-only, chop-only, and chop-and-burn. Marked subplots were monitored for numbers of flowering *L. catesbaei* plants during five separate years following treatments. Significant differences in flowering response were documented. In plots treated with fire only, flowering response of *L. catesbaei* was low. Plots treated with roller-chopping only produced significantly greater numbers of flowering plants. When both fire and roller-chopping were used in combination by applying fire three years after a roller-chopping treatment, the numbers of flowering lilies declined to levels not significantly different from those in burn-only plots. Restoration roller-chopping is well suited to sites with a history of fire-exclusion that have become dominated by saw-palmetto; it effectively reduced the cover of this highly fire-resistant woody species and also caused no declines in numbers of flowering *L. catesbaei* plants.

Index terms: fire, *Lilium catesbaei,* restoration, southeastern pine savanna. *Serenoa repens*

INTRODUCTION

Southeastern **Pine Savannas and Fire Exclusion**

Pine savannas, a variety of habitats containing scattered pines as overstory trees and warm season, C4 grasses in the under-story, were once the most prominent up-land plant communities in the landscape of the southeastern United States (Means 1996, Platt 1998). Currently, less than three percent of the original extent of pine savannas remain, mostly as highly degraded fragments (Outcalt and Outcalt 1994, Means 1996). Often, the degraded state of these remaining savannas is attributed to alterations in fire regime. Frequent fire is essential to maintain the structure and highly diverse herbaceous cover of these savannas (Abrahamson and Hartnett 1990, Platt 1998). In the absence of frequent fires, especially during the lightning sea-son, woody species become dominant (Glitzenstein et al. 1995). The rich layer of herbaceous species declines in cover, and may eventually disappear under the dense canopy of woody species (Wade et al. 1980, Platt 1998).

Throughout the Southeast, human-caused alterations of fire regimes (fire-exclusion, reduced fire frequency, and shifts in sea-son of fire) in these fire-dependent savannas have resulted in widespread and dramatic increases in woody species cover and declines in herbaceous cover. Because these changes have occurred so extensively throughout the Southeast (Noss 1989, Means 1996), nearly all managers of south-eastern savannas today are faced with the challenge of restoration.

Methods for Restoration

Restoring frequent fire, particularly during the early lightning season, is sufficient to reduce hardwood species, especially oaks, that are widespread invaders during fire-free intervals in some southeastern pine savanna communities (Glitzenstein et al. 1995). However, in most cases the reintroduction of fire alone has not been successful in reducing the cover of saw-palmetto *(Serenoa repens* [Bartr.] Small; hereafter, palmetto) a low-growing, woody, native palm that is common in pine flatwoods and dry prairie, two types of savannas that occur in Florida.

Expansion of the cover of palmetto and changes in its growth form can occur during periods of fire exclusion. Palmetto appears to be maintained in a small, low-growing state (<0.5 m tall) in savannas when fires are frequent. But when fire is excluded palmetto can develop extensive recumbent trunks and long petioles, gaining both cover and height (to 2 m or more) and often forming a dense "canopy" in these habitats. Although some re-searchers have documented slow growth in palmetto (Hilmon 1968, Abrahamson 1995), plants have been observed in fire-excluded populations to grow and expand in cover quite rapidly, as can be seen through a time series of aerial photo-graphs in mesic pine savannas in south-west Florida. These tall, extremely dense stands of palmetto regain their stature and cover very rapidly following a fire (Schmalzer and Hinkle 1992, Fitzgerald 1995) and are extremely tolerant of frequent burning.

Roller-chopping is a technique used to reduce the cover of palmetto and other woody vegetation by cutting it with multiple blades mounted on metal drums pulled behind a tractor. Roller chopping has been employed over the past 50 years for range management and silvicultural site-preparation (Moore 1974, Moore et al. 1982, Tanner et al. 1988), sometimes with devastating effects on the native vegetation. However, over the past decade natural area managers have also begun to use roller chopping to reduce palmetto cover in areas where it has increased as a result of fire exclusion (Huffman and Dye 1994, Perry 1997).

Commercial and restoration roller-chopping differ in technique and in the intensity of disturbance of the ground cover vegetation (Table 1). For restoration purposes, only a single pass is made with the chopper, rather than double or triple passes, and the chopper drums are kept relatively light by not weighting them with large quantities of water. These practices produce less soil disturbance while still reducing woody species cover. Restoration roller-chopping is usually followed by prescribed fire within one to three years, preferably in the early lightning season, to maintain woody species cover reduction (Huffman and Dye 1994).

Timing of the application of restoration and management treatments is also of concern to natural area managers. Season of fire is known to influence species composition, physiognomy, and phenology of southeast-ern pine savannas (Platt et al. 1988, 1991; Streng et al. 1993; Glitzenstein et al. 1995). Fires that occur early in the growing season kill or suppress the growth of most woody species and favor many herbaceous species, whereas winter, dormant-season fires have the opposite effect, stimulating the growth of woody species and disfavoring herbaceous species (Platt et al. 1991, Robbins and Myers 1992, Streng et al. 1993, Glitzenstein et al. 1995). Even though the spring growing season is now generally recognized as the season of "natural" lightning-initiated fires (April–June), most prescribed burning in Florida is still applied in the winter dormant season (October–February) (Robbins and Myers 1992). Season of application may be an important consideration for roller-chopping as well. Experimental stud-ies where vegetation was clipped or mowed in different seasons generally report that responses of herbaceous vegetation are very similar to burning and that the responses vary with the season of treatment (e.g., Aus-tralia: Gill 1981; Florida: Myers and Boet-tcher 1987; Brewer and Platt 1994).

Study Objectives

Although the use of restoration roller-chopping is increasing in Florida, there are few scientific studies of its effects. Most studies of roller-chopping have examined the effects of more intensive forestry site-preparation chopping treat-ments (e.g., Moore et al. 1982, Swindel et al. 1983). One of the few exceptions is Fitzgerald et al. (1995), who examined the short-term effects of fire and restoration roller-chopping on small mammals, birds, and dominant vegetation in Florida dry prairie. They found that chopping de-creased palmetto and other woody species cover substantially while burning alone reduced shrub cover but had little effect on palmetto. While Fitzgerald et al. reported on the short-term response of dominant species of vegetation, little is known of the effect of restoration roller-chopping on uncommon herbaceous species. Glitzenstein et al. (1993) examined the short-term effects of two intensities of commercial chop-ping on three rare herbaceous species in north Florida with mixed results: by the end of the second year after treatment one species recovered to pretreatment levels,

Table 1. A simplified comparison of alternate methods of roller-chopping. Methods of roller-chopping application for silviculture and range-management ("traditional") are variable and depend on management goals, which may range from land-clearing for the elimination of native vegetation to range-improvement (where both goals and methods may be very similar to restoration roller-chopping).

Method of Roller-Chopping Application	
Traditional Roller-Chopping	**Restoration Roller-Chopping**
More than one pass of chopper (usually 2–3 passes)	Only one pass of chopper
Chopper-drum heavily weighted	Chopper-drum not heavily weighted
Maximum reduction in woody species	Moderate reduction in woody species
Usually much soil disturbance. Blades cut into and turn over soil.	Very little soil disturbance. Blades usually do not reach surface of soil, or only cut but do not turn over soil.
Usually much loss of existing herbaceous vegetation	Very little loss of existing herbaceous vegetation

one species declined significantly, and one increased in numbers of clumps but de-creased in numbers of stems.

We chose to focus on the flowering response to restoration treatments of *Lilium catesbaei* Walt. (pine lily) (Figure 1), a sparsely distributed herbaceous perennial restricted to the savannas of the Southeast. Although flowering of *L. catesbaei* has been observed after fire (Abrahamson 1984, Abrahamson and Harnett 1990), no studies have systematically evaluated this species' response to fire. Similarly, nothing is known of the flowering response of this species to chopping, although Kral (1983) indicated that roller-chopping is suspected of destroying endangered *Lilium* species. Finally, it is not known if varying the season of treatment may affect this species, as it does other species of Liliaceae that flower only after fire in a particular season—for example, spectacular postfire blooms of geophytic lilies in South Africa (Kruger and Bilgalke 1984, Le Maitre and Brown 1992).

Figure I. ***Lilium catesbaei*** **plant flowering in dry prairie of Myakka River State Park, Florida.**

This experimental study was conducted over a period of nine years in Florida dry prairie. We compared the flowering response of *L. catesbaei* to three types of treatments (burn-only, chop-only, and chop-and-burn) applied in two seasons (growing season and dormant season). We then analyzed how changes in palmetto cover in response to the various treatments may relate to differences in flowering responses, and considered several hypotheses that might explain these responses. Any differences in the effects of these treatments on *L. catesbaei* would not only be relevant to the management of this species but might also be relevant to other herbaceous species and therefore to wider at-tempts to restore and manage southeastern pine savannas.

METHODS

Biology of *Lilium catesbaei*

Lilium catesbaei, a relatively uncommon but widely distributed species, is indigenous to fire-dependent southeastern coast-al plain savannas. Where fire has been excluded for some time, lilies are known to decrease in number and eventually to disappear. Like many plants of fire-prone areas, individual plants of *L. catesbaei* can survive with little or no aboveground foliage in a nonreproductive state until light levels increase, such as occurs after fire (Abrahamson and Hartnett 1990).

Historically, pine lilies were reported as abundant. In the early part of this century the botanist Henry Nehrling (1933) wrote that "[pine lilies] grow abundantly in the flatwoods of Florida. In September, their large, orange-red, upright flower-chalices, spotted with deep brown, form glorious masses of rich color." He reported seeing the pine flatwoods "ablaze with hundreds of thousands of Catesby's lilies *[Lilium catesbaei]"* (Nehrling 1933). Today, pine lilies usually are not found in large numbers and are listed as threatened by the state of Florida (Wood 1996).

Pine lilies are perennial, growing from a 1.5- to 3-cm, multisectioned bulb. They have 5- to 7-cm-long basal leaves and numerous cauline leaves on the flowering stem. In southwest Florida, flowering occurs between early September and mid-November (Huffman 1997). Each plant produces a single flower stem with one bright, orange-red flower (Figure 1). After pollination, a single, three-parted, loculicidal capsule develops. Seeds have high viability (90–95%) immediately after release (J. Huffman and B. Perry, unpubl. data). In cultivation under ideal conditions, plants may be grown from seed to flower in one year, but typically they grow from seed to flower in two to three years (J. Durando, nurseryman, Alachua, Fla., and J. Beckner, horticulturist, Selby Botanical Gardens, Sarasota, Fla., pers. corn.).

Lilium catesbaei plants have somewhat unpredictable periods of dormancy. In cultivation lilies become dormant after cold weather, extreme drought, or when subjected to competition with other plants (J. Durando, pers. corn.). In the wild some individual plants may become dormant in November or December after they have completed flowering, and plants frequently become dormant when shaded. It is unknown exactly how long pine lilies can survive as dormant bulbs.

Study Area

Myakka River State Park, in southwest Florida (Sarasota and Manatee Counties) provided an ideal location to study the response of *L. catesbaei* to restoration techniques. A long history of fire set by lightning and indigenous peoples followed by almost a century of frequent burning for range cattle preceded the establishment of the park in 1934. In the 1930s park management adopted a policy of complete fire-suppression, nearly excluding fire for 40 years in spite of the fire-prone nature of the vegetation and the occurrence of periodic lightning-ignited fires and runaway fires from adjacent ranches. Over the decades of fire suppression, most of the dry prairie was transformed from a grassland, that in the 1940s was reportedly so low, open, and grassy that a horse and rider could cross it at a gallop (P. Benshoff, Myakka River State Park, Sarasota, Fla., historic interviews) into a tall, dense thick-et of shrubs and palmetto (aerial photo documentation, Huffman and Blanchard 1991). Currently, restoration of dry prairie is a management priority at Myakka. In an attempt to reduce the cover of palmetto and to restore herbaceous dominance in the dry prairie, park management staff have used prescribed fire since the 1970s and roller-chopping since 1987.

The predominant terrestrial communities of the 11,686-ha park are pine flatwoods and dry prairie (Huffman and Judd 1998); the latter is one of the rarest and most threatened plant communities in Florida (Florida Natural Areas Inventory 1995). Myakka dry prairies are open areas with widely scattered clusters of pines *(Pinus elliotii* var. *densa* Little & Dorman) and sabal palms *(Saba/ palmetto* [Walt.] Lodd. ex Schultes) and a wide variety of herbaceous species including an abundance of C4 perennial grasses (e.g., *Aristida beyrichiana* Trin & Rupr., *Schizachyrium stoloniferum* Nash., and *Sorghastrum secundum* [Ell.] Nash), various low shrubs (e.g., *Quercus minima* (Sarg.) Small, *Lyonia lucida* [Lam.] D. Don., *Lyonia fruticosa* [Michx.] G.S. Ton.), and the recumbent palm, palmetto (Huffman and Judd 1998).

Experimental Design

The fire and roller-chopping experiments for the current study are subsets of a larger long-term field study initiated in 1986 by Dr. George Tanner, University of Florida, of the effects of roller-chopping and fire on small mammal and bird populations and on wildlife habitat (vegetation) of dry prairie. The design of Tanner's long-term study consists of two replicate blocks (North and South) each with plots of approximately 6 ha, for six treatment combi-:7ations (summer burn, winter burn, summer chop, winter chop, summer chop/burn, and winter chop/burn). The treatments were randomly assigned to plots within the two blocks (Fitzgerald et al. 1995, Huffman 1997). Each plot also contains two sub-plots, each 0.21 ha, marked with rebar for relocation, wherein flowering of *Lilium catesbaei* was monitored.

Treatments were applied as follows. In 1988, the burn treatments were first applied and were then repeated every three years (1991 and 1994). On separate plots, roller-chopping treatments were applied in 1988. In 1991 one-half of those chopped plots remained as chop-only plots (on a six-year cycle) (1994) and one-half were designated as chop-and-burn plots with the original chop of 1988 followed by burns on a three-year cycle (1991, 1994) ()Figure 2). In the spring of 1986, two years prior to the application of any treatments, a wildfire burned the entire study area and consequently established equal times-since-last-burn for all plots.

The overall design included three treatments: burn-only (burned in 1988, 1991, and 1994), chop-only (chopped in 1988 and 1994), and chop-and-burn (chopped in 1988 only and burned in 1991 and 1994). Half of all plots in each block were treated in the summer growing season (June) and half in the winter dormant season (January). The season of treatment on each plot was maintained throughout the study (Figure 2). One winter chop-only plot was burned by a lightning-ignited fire in July 1989; these data were excluded from analysis.

Censusing of *Lilium catesbaei*

Pretreatment censuses of *L. catesbaei* populations were not conducted because these lilies usually exist in a dormant or vegetative state, making visibility and counting virtually impossible. Thus, even though all treatment plots had similar histories, an assumption of our study is that pretreatment populations were equivalent among plots. Because the effects of different treatments in different plots were very similar, any pretreatment differences appeared to have been minor relative to the treatment effects.

Flowering lilies were surveyed in two time intervals, each following an experimental treatment. After the 1988 treatments lilies

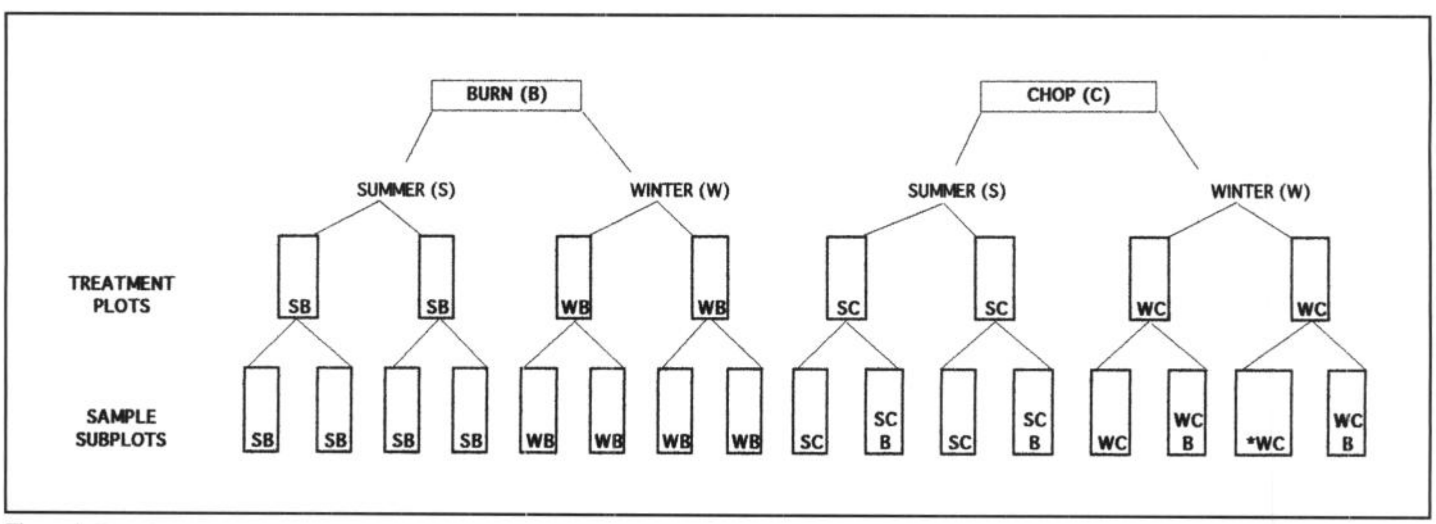


Figure 2. Experimental design; B=burn, C=chop, S=summer, and W=winter. Full plots are indicated with 1988 treatments, subplots with subsequent (1991, 1994) treatments. All burn-only plots were burned in 1988, 1991, and 1994. All chop-only plots were roller-chopped in 1988 and 1994. Chop-and-burn plots were chopped in 1988 and burned in 1991 and 1994. * indicates plot designated as winter chop-only that was burned by a lightning fire in 1989 and excluded from the analysis.

Table 2. Number of flowering Gillum *catesbaei* plants in burn-only, chop-only, and chop-and-burn treatment subplots (mean and standard error).

	Burn-Only		Chop-Only		Chop & Burn	
Year	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
1989	5.50	1.87	47.00	25.59		
1990	0.50	0.25	28.00	9.93		
(1989-1990)	3.00	1.17	38.00	10.31		
N	**8**		7			
1994	2.75	1.32	24.67	11.89	5.50	2.72
1995	1.63	0.87	40.67	37.71	4.00	2.48
1996	0.13	0.12	2.33	1.45	0.50	0.29
(1994-1996)	1.50	0.58	22.56	12.70	3.33	1.28
N	**8**		**3**		**4**	

were surveyed in 1989 and 1990, and after the 1994 treatments lilies were surveyed in 1994, 1995, and 1996. No surveys were conducted in 1991-1993, following the 1991 treatments. These flowering surveys were conducted every 7 to 10 days in the permanent subplots throughout the flowering season of mid-September through middle to late November. During each survey flowering plants in all subplots were counted and marked for relocation with numbered survey flags. Because of the experimental design (Figure 2), the number of subplots during the first time interval was eight burn-only and eight chop-only (less one lightning-burned sub-plot); whereas the number of subplots during the second time interval was eight burn-only, four chop-only (minus lightning burned subplot), and four chop-and-burn (1994, 1995, and 1996) (Figure 2).

Analyses

The numbers of flowering *L. catesbaei* plants (flowering abundance) were analyzed statistically for the two time intervals, each following a treatment application: (a) the grouped 1989 and 1990 data, and (b) the grouped 1994 and 1995 data. Data from 1996 are presented in tables and descriptive figures, but were not used for statistical analyses because very few subplots contained any flowering plants. Field data consisting of numbers of flowering plants were not normally distributed, so log transformations were used to reduce heteroscedasticity prior to applying ANOVA tests in a repeated measures design where whole plots are represented by treatment type and season, while successive measures are repeated each year. There were two types of treatments in the first sampling interval (1989-1990), three types of treatments in the second sampling interval (1994-1995), and two seasons of treatments in each time interval.

To compare one treatment type to another, when significant differences were indicated by the ANOVA, we used comparisons of means. Because of unequal sample sizes, the expected mean squares in the second time interval were adjusted using Satterthwaite's approximation before performing an F-test (Snedecor and Cochran 1980). A correlation analysis was used to test for a significant relationship between the numbers of flowering *L. catesbaei* plants and percent cover of palmetto.

RESULTS

Response to Type and Season of Treatment

In both time intervals the absolute numbers of flowering *L. catesbaei* plants were several times greater in chop-only sub-plots than in burn-only subplots (Table 2). Considering only the second time interval, the chop-and-burn subplots had slightly larger numbers of flowering plants than burn-only subplots (Figure 3).

The ANOVA for the second sampling interval (1994-1995) indicated no significant difference in numbers of flowering plants between seasons of treatment (win-ter vs. summer), nor any significant inter-action between treatment type and season. Among the three types of treatments, how-ever, flowering abundance was significantly different ($P=0.043$). Therefore, further analysis focused on type of treatment, pooling data for season of treatment. When comparing the three treatments for the second time period, the number of flowering lily plants in chop-only subplots was significantly different from both the number in burn-only subplots ($P=<0.001$) and the number in chop-and-burn subplots ($P=0.003$). There was, however, no significant difference in flowering abundance between the burn-only treatment and the chop-and-burn treatment ($P=0.113$).

Lily flowering response to treatments in the first sampling interval (1989-1990) mirrored the second time interval. That is, there was no significant difference in numbers of flowering plants in response to season of treatments ($P=0.548$) nor was there any significant interaction between season and type of treatment ($P=0.922$, Table 3). However, there was a significant difference in lily flowering abundance between the two types of treatments ($P=0.009$, Table 3), with much greater numbers of flowering plants in the chop-only plots.

Saw-Palmetto Cover in Experimental Plots

To explore possible mechanisms underlying flowering responses of *L. catesbaei,* we examined changes in cover of palmetto following different treatments, analyzing unpublished field data generously provided by Dr. George W. Tanner (for 1988-1990 and 1994-1996, Figure 4). Before treatments began in 1988, palmetto cover was about 60%, whereas cover of all other

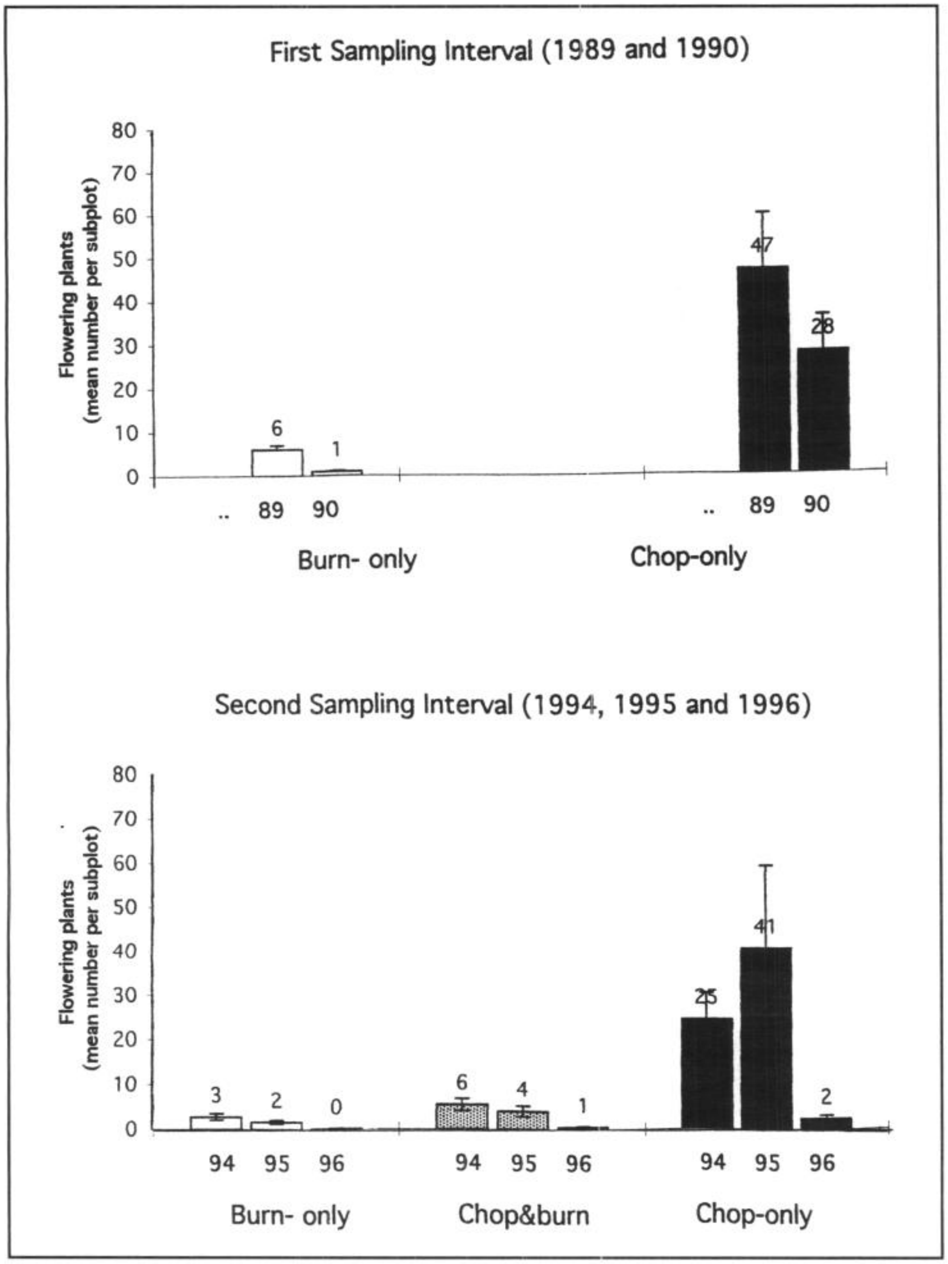


Figure 3. Number of flowering *Lilium catesbaei* plants in burn-only, chop-only, and chop-and-burn treatments. Plots that were chop-only treatments during the first sampling interval were divided into chop-only and chop-and-burn treatments during the second interval. Numbers on top of bars are average number of flowering lily plants per subplot. Error bars indicate S.E.

Table 3. Summary of ANOVA, first time interval **(1989 and 1990), testing the effects** of **season and type of treatment on number (log)** of **flowering plants** of *Lilium catesbaei*. **Significance indicated by** ** (p < **0.01).**

Source	DF	MS	F	P
Treatment Type: Burn vs. Chop	1	7.790	22.480	0.009**
Treatment time (Season): Winter vs. Summer	1	0.149	0.430	0.549
Treatment Type x Season	1	0.004	0.010	0.922

shrubs combined was less than 20% (Fitzgerald et al. 1995).

Roller-chopping reduced palmetto cover by 65% the first year after treatment, while burned plots had only a 35% reduction. The reduction lasted much longer in chopped plots: three years after treatment, chopped plots sustained a 45% reduction, but there was little or no reduction of cover in burned plots (Figure 4). Burning after restoration chopping maintained the lower palmetto cover produced by chopping. In plots treated with a combination of chop and burn (chopped in 1988, burned in 1991 and 1994), palmetto cover was almost identical to those plots that were chopped-only (in 1988 and 1994) (Figure 4).

Because of the reduction of palmetto and shrubs in the chopped plots, there were large areas of open ground for the first several years after treatment. In contrast, the vegetation in burn-only plots grew back to preburn cover levels so rapidly that there was very little open ground visible by the second growing season after fire. Initially (e.g.,1988), in chop treatment plots, there was much surface mulch from the cut vegetation, and herbaceous vegetation was relatively sparse until the mulch had decayed, up to two growing seasons later. Tall grasses and other herbaceous plants had started to cover the open spaces as the mulch decayed, and by the second round of surveys (1994–1996) almost no open ground remained (G. Tanner and J. Huff-man, pers. obs.).

Correlation of Flowering with Saw-Palmetto Cover

There was a strong negative correlation between palmetto cover and lily flowering response in chop-only and in burn-only treatments (r = -0.92 for the first time interval, -0.87 for the second time interval). When palmetto cover was greater than 35% (six of the type x season subplots), there were fewer than five flowering L. *catesbaei* plants per subplot. In contrast, when palmetto cover was less than 35% (as in three of the type x season subplots), there were more than 25 flowering plants per subplot. However, palmetto cover in bum-only plots was never below 35%, and

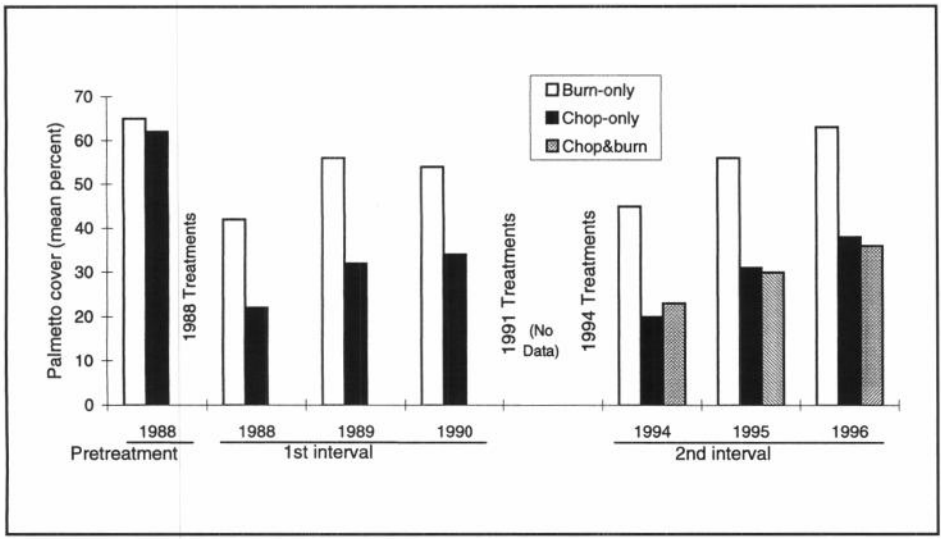


Figure 4. Saw-palmetto cover in burn, chop, and chop-and-burn treatment plots (from data of G.W. **Tanner).**

it is not possible to clearly separate the potential effects of palmetto cover from the effects of treatment. In addition, when chop-and-burn plots were included in the overall analysis, the correlation between palmetto cover and the number of flowering lily plants was no longer statistically significant (r = -0.60). Even though the chop-and-burn plots had a low cover of palmetto, similar to that in the chop-only plots (cf. Figure 4), there was little flowering of *L. catesbaei,* not unlike the low number in burn-only plots (Table 2).

DISCUSSION

Flowering Response to Treatments

Flowering of *Lilium catesbaei* in the dry prairie savanna habitats at Myakka River State Park was stimulated by both fire and roller-chopping. Flowering of many other herbaceous species occurs following fire or the removal of canopy vegetation (Curtis and Partch 1950; Hulbert 1969, 1988; Old 1969; Gill 1981; Myers and Boettcher 1987; Le Maitre and Brown 1992; Brewer and Platt 1994).

Pine lily responded very differently to burning and to roller-chopping. Chopping stimulated more flowering than burning did, and lilies in chopped plots flowered for a longer duration. Lilies were still flowering three years after treatment in the chopped plots, but very rarely flowered in burn plots.

Increased flowering in chopped plots may be due to the substantial and long-term reduction in canopy cover of palmetto and other woody species. The sustained canopy reduction after chopping, relative to fire, increased the amount of light reaching ground level for a longer period of time, which may have stimulated the flowering of lily plants or dormant bulbs that were already present at the time of canopy removal. In many other grassland plants, increased light is a key stimulus for flowering (Old 1969, Hulbert 1988).

Palmetto-canopy reductions also may have provided opportunities for recruitment of new *L. catesbaei* plants by opening up space for colonization. Openings that pro-vide spaces for colonization are generally rare in perennial grassland communities (Platt and Weis 1985, Streng et al. 1993). However, the sustained reduction of palmetto in chop treatment plots produced much unoccupied, open ground that persisted for the first few years after the initial chop treatment in 1988. And, indeed, numerous *L. catesbaei* seedlings were observed in chopped plots during the first two years of the study. *Lilium catesbaei* seedlings have the capacity to flower after a year and commonly flower after two years in cultivation (J. Durando and J. Beckner, pers. ohs.). It is likely that a portion of surveyed *L. catesbaei* flowers in the study came from new seedlings rather than from existing plants or previously dormant bulbs.

However, roller-chopping did not contribute to the enhanced flowering response by physically spreading existing *L. catesbaei* plants, or by opening a "seed bank." Be-cause *L. catesbaei is* not rhizomatous and has small, sparsely distributed bulbs, roller-chopping does not initiate clonal growth. In addition, because of the density of vegetation and palmetto trunks, chop-per blades often do not reach the soil's surface. When blades do reach the surface they tend to make vertical cuts into the soil that would not cause the break up and spread of lily bulbs. Neither does roller-chopping open a seed bank of lily seeds; lily seeds are nearly paper thin, flammable, and germinate soon after being moistened.

Although the correlation between palmetto cover and number of flowering lilies was strong in chop-only and burn-only plots, in the chop-and-burn plots palmetto cover was low, but number of flowering lily plants was also low. This indicates that although canopy cover may have an important influence on flowering, reasons for flowering are more complex than the simple absence or presence of canopy cover. Several factors may have contributed to the reduced flowering in chop-and-burn treatments. First, an increase in competition occurred during the second sampling period. After the initial chop treatment, reduced palmetto cover produced open space, minimizing competition for light and nutrient resources for lilies during the first sampling interval. By the second sampling interval these open areas had become densely colonized, mostly by grasses, increasing competition for resources. When fire was applied to lilies already subjected to in-creased competition, the additional loss of aboveground foliage may have prevented many lily plants in the chop-and-burn plots and the burn-only plots from accumulating the reserves necessary for flowering. In contrast, declines were less severe for the plants in the chop-only plots that were not exposed to the additional stress of loss of above-ground foliage by fire.

Fire may also have direct effects on lily seedlings. Possibly, the *L. catesbaei* seedlings could survive in the chop-only plots where there was no fire, but not in the chop-and-burn plots where fire occurred every three years. Seedlings that may have established from plants that flowered in the fall of 1989 or 1990 had a maximum of one growing season to become established be-fore fire in 1991. Bulbs of young plants may not yet have been developed enough to be fire-resistant. The period of time required for *L. catesbaei* seedlings to become established sufficiently to be able to withstand fire is currently unknown; such information would allow us to determine the fire-return intervals that allow for the establishment of new plants in restoration efforts. It is important to learn more about the establishment requirements and life history of *L. catesbaei* and similar herbaceous perennial species of Florida savannas to discern the longer term effects of various alternative management decisions in restoration efforts.

Flowering Response to Season of Treatment

The amount of flowering by *L. catesbaei* was not different over the two- to three-year periods following dormant and growing-season treatments (chopping or fire). There was, however, a difference in the length of time it took lily plants to flower, and the difference was related to season of treatment (Huffman 1997). Following dormant-season treatments, the greatest flowering response occurred during the first flowering season after treatment. In contrast, following growing-season treatments, flowering peaked during the second flowering season after treatment. These differences in timing of flowering are probably related to the amount of time a plant requires to recover reserves adequate to initiate flowering. Although there might be differences in flowering for a single year related to season of treatment, when we examined the total flowering of more than one year following treatment we found similar total numbers of flowering plants following both dormant-and growing-season treatments.

Increased flowering responses following growing-season treatments may be most apparent for plants that have an apical meristem that is killed by fire. Fire-related damage appears to release dormant buds that then grow and flower the same season (Platt et al. 1988). Some southeastern pine savanna grasses and forbs have been shown to produce many more flowering stems following growing-season fires than they do following dormant-season fires (e.g., *Aristida beyrichiana, Panicum abscissum*, and *Pityopsis graminifolia;* Myers and Boettcher 1987, Platt et al. 1988, Streng et al. 1993, Brewer and Platt 1994). These responses may not occur in plants such as lilies with below-surface perennating organs and a solitary flowering stem.

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

Frequent fire is essential to maintain the savanna habitats in which pine lilies occur (Platt 1998). Following long-term fire suppression, pine lilies and other species in the herbaceous ground cover perish in the shade of a canopy of woody shrubs and trees. Nonetheless, our data indicate that once fire is excluded for long periods of time, it cannot always be used as the sole agent of restoration.

We found that restoration roller-chopping, when used to reduce the cover of fire-tolerant palmetto, does not appear to have negative effects on *L. catesbaei.* Pine lily flowering was much greater after roller-chopping than after burning alone. This suggests that chop treatments can produce reductions in the canopy, especially of palmetto, and can result in in-creased flowering and increased opportunities for recruitment in pine lily populations.

After restoration roller-chopping, woody plant reductions can be maintained by frequent fire; however, further investigation is necessary to determine the appropriate time interval between chopping and the application of fire. We need to investigate possible reasons for the decline in number of flowering lilies in chop treatments after the application of fire, such as the interval necessary for fire-survival by juvenile pine lilies.

Management and restoration actions appropriate for pine lily habitats depend on the existing condition of the particular habitat. A summary of predicted responses of pine lily flowering and palmetto cover to various management treatments is presented in Figure 5. Good condition prairie is maintained by frequent fire (Figure 6a). In areas where palmetto cover has increased during extended periods of fire exclusion (degraded condition dry prairie, Figure 6b), fire alone is unlikely to reduce palmetto cover or restore prefire exclusion levels of herbaceous cover and flowering lily plants. Roller-chopping, however, is predicted to reduce palmetto canopy and increase the numbers of flowering lilies, as well as other original herbaceous species, shifting the system toward healthy, restored prairie (Figure 6a).

If palmetto and other woody plants be-come dominant for a long period of time with prolonged fire suppression, lilies are expected to disappear (highly degraded prairie, Figure 6c). Eventually, an under-story of tall, dense shrubs and palmetto, followed in some cases by an oak overstory *(Quercus virginiana* Mill. and *Q. laurifolia* Michx.) (Figure 6d), is predicted to replace open prairie (see Huffman and Blanchard 1991). If restoration roller-chopping occurs after dry prairie reaches this highly degraded state, dense palmetto is predicted to be replaced by weedy colonizing species such as *Andropogon glomeratus* and *A. virginicus*, rather than the original prairie species, including *L. catesbaei*, that have been lost (weedy dry prairie, Figure 6e). Therefore, restoration activities are most effective if they occur before the habitat becomes extremely de-graded, and certainly before the species becomes extinct locally.

In summary, *Lilium catesbaei* and associated pine savanna species can be maintained or increased in sites where they naturally occur if proper fire management and, where appropriate, restoration roller-chopping are applied. The prescription is two fold: use prescribed fire to reduce woody competition and to stimulate herbaceous flowering (Platt et al. 1988, 1991; Streng et al. 1993; Glitzenstein et al. 1995) and, when appropriate, use the care-

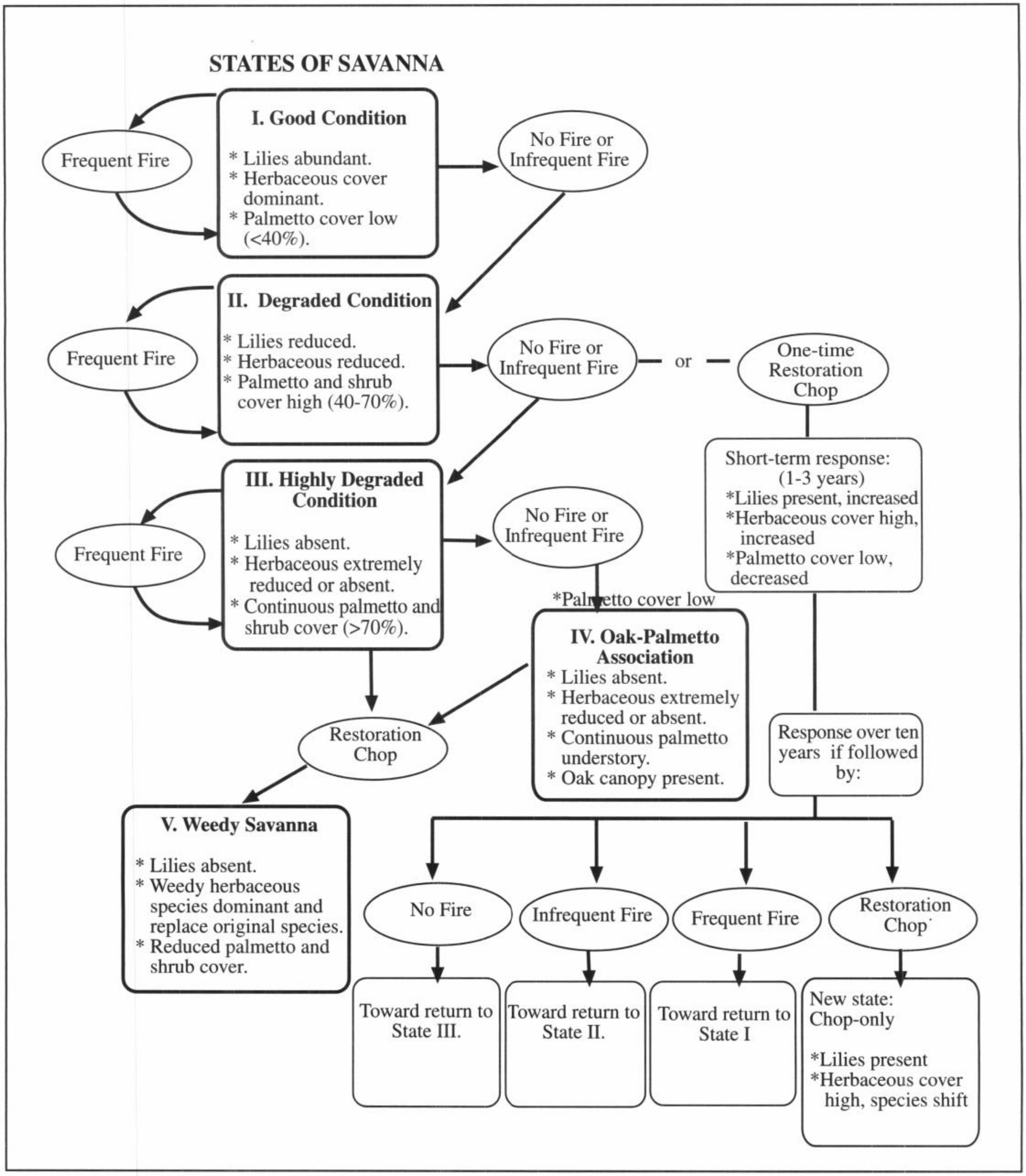
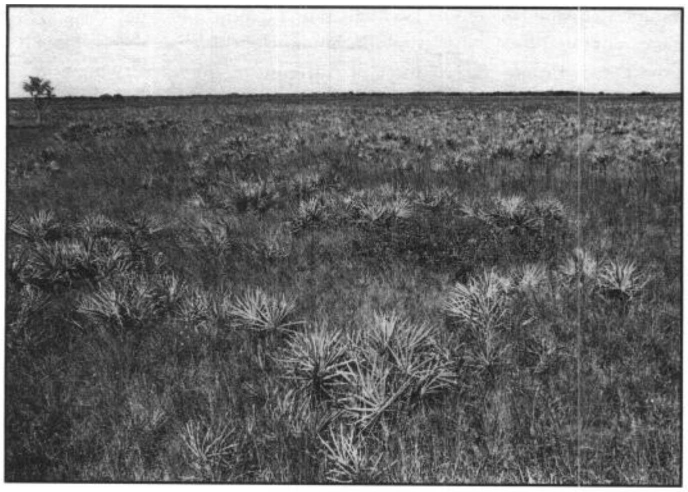
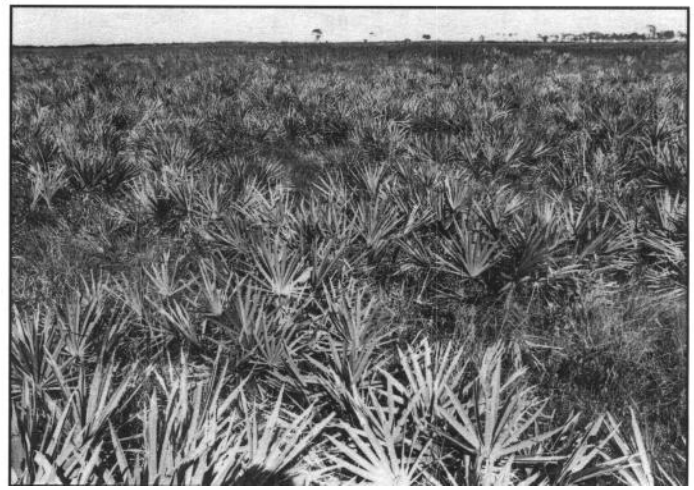


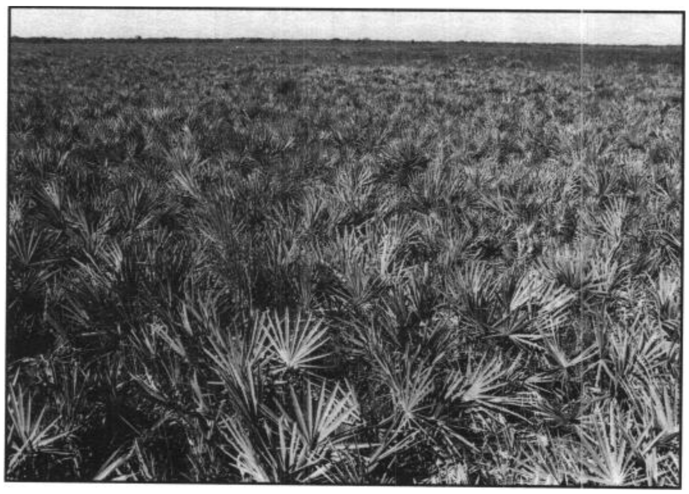
Figure 5. Florida savanna (pine flatwoods and dry prairie) management and restoration for pine lily. Various states of savanna are indicated by bold-outline boxes. Ovals indicate management actions. "Frequent fire" is defined as less than a four-year inter-fire interval; "infrequent fire" is defined as a greater than a four-year interval. More than a decade is **involved** in transitions from one savanna state to another when fire is involved, and there is great variability that is dependent on specific site conditions. In contrast, roller-chopping initiates immediate change.



(a)

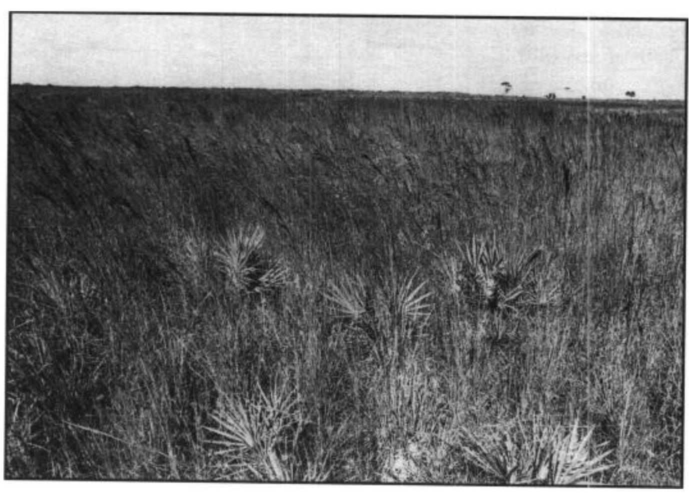


(b)



(c)

(d)



(e)

Figure 6. The "states of savanna" (Figure 5) illustrated by the various states of dry prairie at Myakka River State Park, Florida. (a) Good **Condition** Dry Prairie: **good condition,** restored **dry prairie with** low-growing saw-palmetto and abundant herbaceous cover of typical dry prairie species such as wiregrass *(Aristida beyrichiana).* This is after **the one application** of **restoration-roller-chopping** and two burn treatments **(photograph** taken six years after the original chop treatment). (b) Degraded Condition Dry Prairie: the high saw-palmetto and shrub cover here is brought about by a history of fire exclusion or long fire-free intervals. Original herbaceous species are reduced from pre-fire-exclusion levels but are still present in patches and as suppressed plants below the saw-palmetto. Degraded dry prairie responds most favorably to restoration roller-chopping since the remaining herbaceous species increase when saw-palmetto is reduced. This is the same area shown in Figure 6a, before the application of **roller-chopping** restoration treatment. (c) Highly Degraded Dry Prairie: Note the extremely high cover of tall, dense saw-palmetto and the lack of herbaceous cover. (d) Oak-invaded Dry Prairie: Where a seed source is available, oaks can move into fire-excluded dry prairie areas that have a dense cover of saw-palmetto. When fire is reintroduced oaks may die but palmetto remains. (e) Weedy Dry Prairie: When highly degraded dry prairie is roller-chopped, weedy **species, predominantly *Andropogon glomeratus,* colonize after chopping reduces the dense saw-palmetto cover.**

ful application of roller-chopping to in-crease the ratio of herbaceous species to palmetto and other shrubs in the ground-cover vegetation.

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A doctoral candidate at Louisiana State University, Jean Huffman is studying landscape-level fire effects in south-central Florida. This paper is based on work done while she was staff Biologist at Myakka River State Park. Her interests include fire ecology and management and the restora-tion of fire-dependent plant communities.

Patricia A. Werner is a Professor of Wild-life Ecology and Conservation at the University of Florida, where she teaches Savanna Ecology and Biogeography. Her lifelong interest in plant populations in-cludes a decade of research on the effects of fire on the savannas of northern Austra-lia.

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