FIRE IN KEY DEER HABITAT IMPROVES BROWSE, PREVENTS SUCCESSION, AND PRESERVES ENDEMIC HERBS

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Abstract: Habitat quality reduced by fire suppression may have influenced the recent decline of Key deer (*Odocoileus virginianus clavium*). A major foraging habitat for Key deer, the rockland pine community, as well as several plants endemic to this habitat, depend on periodic fires for continued existence. Refuge burning is opposed by residents of nearby urban development. To quantify effects of fire, we measured use and nutritive content of browse for the year following fire, monitored growth of the vegetation after fire, and documented succession in relation to time since the last fire. Browsing by deer was most intense early in the growing season. Deer chose species high in crude protein (CP), phosphorus (P), and in vitro digestibility (IVOMD). The 2 most heavily browsed pineland species, blackbead (*Pithecellobium keyense*) and Indian mulberry (*Morinda royoc*), were high in CP year-round. The amount of P of diet species was lower than the assumed requirement for deer but actually may be adequate. Increases in nutritive value in important dietary species lasted 6–11 months after burning. Sprout density of species in the diet was higher ($P < 0.05$) in burned than in unburned plots, providing more browse within 2 years after burning. Fruiting of diet species returned to unburned levels within 1 year after burning at most sites. Thus, burning of pineland provided temporary benefits in nutritive quality and more prolonged benefits in browse quantity. Fire's retardation of succession, however, may be of greater benefit to deer than temporary forage enhancement. Community structure was similar among pine stands on Big Pine Key. Vegetation on smaller islands was a mixture of pineland and hammock species, with few herbaceous species, including those important in the Key deer diet. A 10- to 20-year interval between fires maintains pine savanna on Big Pine Key. An interval of 10–50 years on smaller, more isolated islands arrests succession at an intermediate stage. Only a very long fire-free interval (>100 years) allows full development of a hammock community. Endemic herbaceous plants at pineland sites were generally unaffected by fire in pine savanna, whereas they were rare or absent from sites in which succession had advanced to mixed pine-hammock composition. Preventing extinction of endemic plants is a major benefit of prescribed burning. Despite the value of prescribed burning for maintaining pineland endemics and species important in the Key deer diet, management of Lower Keys vegetation should encompass other successional stages. Maintaining a diversity of stands will provide cover for deer and refuge for numerous plant species intolerant of burning. We recommend an experimental regime of replicated plots of pine savanna be burned at 5-, 15-, 25-, and 75-year intervals to document responses of plant species as well as successional shifts.

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The Key deer is the smallest subspecies of white-tailed deer in North America (Barbour and Allen 1922) and is restricted to the lower Florida Keys. The herd reached an estimated low of 25 animals in the early 1950's due to over-hunting and loss of habitat (U.S. Fish and Wildl. Serv. 1985*a*). After protection from hunting and establishment of the National Key Deer Wildlife Refuge (NKDWR) in 1957, the population grew to an estimated 400 by 1969 (Alexander and Dickson 1970). In 1978 the population was again estimated at 400, but by 1982 the number had dropped to an estimated 250–300 deer (Hardin et al. 1984). This declining trend was corroborated by Humphrey and Bell (1986).

The major factors implicated in the recent decline are road kills and loss of habitat to development of private land (U.S. Fish and Wildl. Serv. 1985*a*). Regardless of the influence of these factors, long-term maintenance of habitat quality is essential to maximize the conservation value of land owned by the U.S. Fish and Wildlife Service. Pine savanna is an important habitat for foraging Key deer (Dickson 1955, Dooley 1975), and most of NKDWR consists of pineland. Based on description of vegetation and knowledge of past burning and clearing practices, Dickson (1955) recommended burning and bulldozing to maintain food resources for deer and to prevent plant succession. Dickson (1955) recognized fire suppression as a new threat to the Key deer, yet it was the primary means of vegetation management for the first 30 years of

NKDWR stewardship. Urban development on NKDWR boundaries has heightened the need for data to determine whether burning is justified as a management practice. Thus, we determined the efficacy of maintaining food resources and preventing plant succession as mechanisms for enhancing habitat quality when prescribed burning was implemented on NKDWR in the mid-1980's. We also sought to learn how burning affected rare plants that coexist with Key deer.

Burning benefits deer by reducing plant biomass, releasing nutrients, and stimulating new growth, which may maintain important food plants, increase forage production and availability, increase palatability of food plants, and improve nutritive value (Lay 1956, Dills 1970, Thill et al. 1987). More browse becomes available because of increased sprouting within reach of deer (Alexander and Dickson 1970, Dills 1970, Halls 1978, Stransky and Harlow 1981). Fruit production of some species also may increase following fire (Lay 1956, Johnson and Landers 1978, Stransky and Halls 1979). However, all these effects of burning usually are temporary, and some do not always occur or may not always depend on fire frequency. Some studies have found little change in nutrient content on burned sites (Dills 1970, Ohmann and Grigal 1979, Wood 1988).

A second rationale for prescribed burning of the Keys pine savanna is maintenance of a suite of endemic plants considered vulnerable to extinction or extirpation. Fire is essential to maintain pine communities in the southeastern United States (Garren 1943, Bancroft 1976, Wade et al. 1980). Rockland pine forests of southern Florida support 38 endemic species of plants, of which 28 occur in no other habitat (Avery and Loope 1980, Snyder et al. 1990). This plant community requires periodic burning to prevent invasion by hardwoods (Robertson 1954, Loope and Dunevitz 1981, Snyder 1986). Succession of pineland to a hardwood community (hammock) in the absence of fire occurs within 2–3 decades on the mainland of southern Florida (Alexander 1967, Hofstetter 1984), but may take twice as long in the drier Keys (Alexander and Dixon 1972). Taylor (1980) estimated the historic natural frequency of fires in the southern Florida mainland to be about 8 years. Based on this knowledge, we sought to detect an effect of burning on maintenance of the pine savanna community of the Florida Keys by monitoring growth of the vegetation after prescribed burns and documenting succession in the pine community relative to the time since the last fire.

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STUDY AREA AND METHODS

Study Area

The NKDWR is located on Big Pine Key and nearby islands, approximately 85 km southwest of the southern tip of mainland Florida. The porous oolitic rock substrate supports a rockland pine community. Recurrent fires have removed litter, and many sites lack soil. More than 50% of the surface is a well-drained substrate of exposed limestone (Snyder et al. 1990). The climate is subtropical with an average annual rainfall of 1,113 mm, 70% falling from June to October (U.S. Fish and Wildl. Serv., Ann. Narrative, NKDWR, Big Pine Key, Fla., 1987).

Big Pine Key (approx. 2,400 ha) historically provided most of the habitat occupied by Key deer. The island is vital for the deer because it has more pineland and fresh water than other islands in the deer's range. Approximately 650 ha of Big Pine Key is pineland, including 389 ha within NKDWR boundaries (Dooley 1975). Dickson (1955) estimated 920 ha of pineland in the deer's entire range; most pineland on private lands has been or will be converted to human use.

The Florida Keys pine savanna has an overstory of southern Florida slash pine (*Pinus elliottii* var. *densa*) and a patchy understory of brittle thatch palm (*Thrinax morrisii*), silver palm (*Coccothrinax argentata*), and a mixture of tropical and temperate shrubs and trees. A diverse herbaceous groundcover, including 5 endemic species, occurs in areas with an open understory. Plant species names follow Long and Lakela (1971) and Austin et al. (1980).

Selection and Nutritive Content of Browse Species

Our study included 3 sites in pine habitat on Big Pine Key: sites A and B were burned (with prescribed backing fires) in August 1986; site D burned in a lightning fire in July 1986. Although precise fire temperatures were not recorded, scorch on pines in excess of 3 m high within all burned plots indicated the fires in 1986 to be very hot. Site A was previously burned in 1977, whereas fire histories of sites B and D are unknown. Due to temporal obligations specified in the research contract and limited availability of the U.S. Fish and Wildl. Serv. fire team, pretreatment sampling of the vegetation was not conducted. Unburned plots were established within sites A, B, and D by isolating a portion of each plot with new fire lanes.

Sampling Methods.—We monitored use of browse (woody) species by deer in 1987, after 1986 burns. The 7 species selected were: Indian mulberry, blackbead, acacia (*Acacia pinetorum*), greenbrier (*Smilax havanensis*), snowberry (*Chiococca pinetorum*), slash pine (<2 m), and locustberry (*Byrsonima lucida*). These are common pineland species often eaten by Key deer (Klimstra and Dooley 1990). Ten plants of each species were marked with a small metal tag attached at the crown in sites A, B, and D, except that site D did not contain adequate numbers of snowberry for sampling. We examined all plants monthly over 10 months for evidence and extent of browsing. Any browsing since the last examination of a plant was designated as 1 observation of use.

We collected forage samples 4 times in 1987: 1–10 March, 20–31 May, 25–31 July, and 27–28 November. At each location, 3 samples each of Indian mulberry, blackbead, greenbrier, locustberry, and pine were collected from burned sites and adjacent unburned reference areas. Acacia and snowberry were not abundant enough for sampling. Hand-plucked samples consisted of new leaves of several plants, except a few cases when older leaves (for greenbrier) or new stem growth was needed for an adequate sample.

Laboratory Methods.—Samples were dried at 65 C for 48 hours and ground in a Wiley mill to pass through a 1-mm screen. Standard analyses were run for nitrogen (N), phosphorus (P), and in vitro organic matter digestibility (IVOMD). For N and P analyses, samples were digested using a modification of the aluminum block digestion procedure of Gallaher et al. (1975). Sample mass was 0.25 g, catalyst used was 9:1 K_2SO_4:$CuSO_4$, and digestion was conducted for 4 hours at 400 C using 10 ml H_2SO_4 and 2 ml H_2O_2. Ammonia and P in the digestate were determined by semiautomatic colorimetry (Hambleton 1977). Crude protein (CP) was calculated by multiplying percent N by 6.25. IVOMD was performed by a modification of the 2-stage technique (Moore and Mott 1974), using cow rumen as the inoculum source.

Statistical Analyses.—To test for month effects on food selection, we fitted a loglinear model to the counts of grazed plants. The model included terms for species, month, and species × month effects. Only data from February through May were included in this analysis because very few plants were grazed in other months. Because there was no species × month interaction ($P = 0.13$), an analysis ignoring month was performed as follows. A given plant was scored as grazed if it had been grazed at least once within the entire study period. A Chi-square lack-of-fit test then was performed to test whether the proportions of grazed plants belonging to given species were different from the species relative abundances (10 marked plants of each species at Sites A, B, and D). Pine trees were not included in the tests because none were observed to be browsed during the study. Although pine needles were common in the Key deer diet, their contribution by volume was <0.5% (Klimstra and Dooley 1990). Given significant lack of fit, a t-test of difference between the observed species' proportion of grazed plants and the species' relative abundance was performed separately for each species. The modified Bonferroni procedure of Holms, as described in Wright (1992), was used to adjust the P-values from these t-tests.

We tested for differences between burned and unburned areas in CP, P, and digestibility of each species for sites A, B, and D (pooled) 1 year after burning using analysis of variance. Tests also were conducted among periods within each burn treatment. Differences in period means were determined using Tukey's Studentized range test (SAS Inst. 1985).

Plant Growth and Succession after Fire

We measured vegetation regrowth at sites A and B in pineland on Big Pine Key. We also used sites A and B for analyzing pineland succession. Additional pineland succession sites were located on Big Pine Key (9), including ones that burned in 1986, 1985, 1977, and 1966; No Name Key (3), 1 burned in the early 1980's and 2 last burned in the mid-1960's; and Sugarloaf Key (2), unburned for a minimum of 50 years. Two hardwood hammock sites also were used, one located on Big Pine Key and one on No Name Key. The Sugarloaf Key sites were prescribe-burned in September 1987, and the most recently burned site on No Name Key was burned by a lightning fire in October 1987. Although fire intensity was not measured or noted for any of these fires, it is assumed that very hot fires were the norm since prescribed burning has just been instigated in the recent past to reduce fuel accumulation, and as indicated by heights of scorch on pines during the most recent fires.

Sampling Methods.—We determined composition of the pine community and regrowth of plants on 14 7.2-ha plots (122 × 61 m) at sites A and B. At each site, 6 plots were prescribe-burned and one was left unburned. Four 50-m line transects were located 30 m apart within each plot; the first transect was randomly located within 15 m of a plot edge. Tree and shrub densities were determined by counting the number of individuals of all species within 1 m on each side of the line transects, noting the number in flower or fruit. We determined sprout densities by counting the number of stems of each individual. A stem was considered a sprout rather than a separate plant if it grew from below the surface litter at the base of a main stem. Foliar cover of trees and shrubs was determined by measuring the portion of each 50-m line transect intercepted by each species. Frequency of occurrence of vines, forbs, and graminoids was determined in 20 0.5-m^2 quadrats placed every 5 m on each side of the line transects. We took measurements approximately every 6 months from October 1986 through May 1988.

To document hardwood invasion and succession within the pine community, we determined frequency of woody and herbaceous species in all 18 sites during the summer of 1987. Occurrence of trees and shrubs was recorded in 30 1- × 15-m plots at each site. Three 0.5-m^2 quadrats were used in each plot to determine frequency of herbaceous plants, including endemic species. Sites were 1 ha or larger and separated by roads that may have acted as fire breaks during past fires. Each site was divided into 10- × 15-m sections and each plot was randomly located within a section, avoiding abrupt changes in vegetation such as large solution holes. The sites on No Name and Sugarloaf keys that burned in 1987 were resampled within 1 year to compare species composition before and after fire.

Statistical Analyses.—Data from sites A and B were pooled (12 burned and 2 unburned plots). We used analyses of variance with orthogonal contrasts to test for differences between burned and unburned plots within each sampling period for each of the following variables: density of sprouts and plants of woody species, cover of woody species, density of woody plants in flower or fruit, and frequency of occurrence of herbaceous species. Data were transformed to normalize distributions: log transformation for plant and sprout densities, square-root transformation for plants in flower or fruit, and arcsine transformation for frequencies and cover. We tested the following species or species groups: Big Pine partridge pea (*Cassia keyensis*), Florida five-petaled leaf flower (*Phyllanthus pentaphyllus* var. *floridanus*), Indian mulberry, blackbead, locustberry, greenbrier, snowberry, milk pea (*Galactia parvifolia*), palms (brittle thatch, silver, and cabbage [*Sabal palmetto*], saw-palmetto [*Serenoa repens*], and unidentified palm seedlings), diet species common for the Key deer (those in the top 75% by volume of Dooley's [1975] list, excluding palms), and all other species except slash pine, palms, and diet species. Only Indian mulberry, locustberry, and palms were tested for plants in flower or fruit. All tests of significance were at the $P < 0.05$ level.

We compared the species composition of the sites with principal components analysis (PCA). Species-centered PCA was performed on frequencies of woody species only and of all species (with herbaceous species occurrences combined by plot) to ordinate the sites. Analyses were run using the covariance matrix, and the scores were standardized to unit variance (SAS Inst. 1982). We multiplied the first-component scores of the analysis by all species by -1 to keep the ordering of sites on the first axis from being reversed relative to that from analysis by woody species.

RESULTS

Selection and Nutritive Content of Browse Species

Most browsing (60% of 147 observations) occurred from February through May (Fig. 1). Indian mulberry and blackbead were browsed

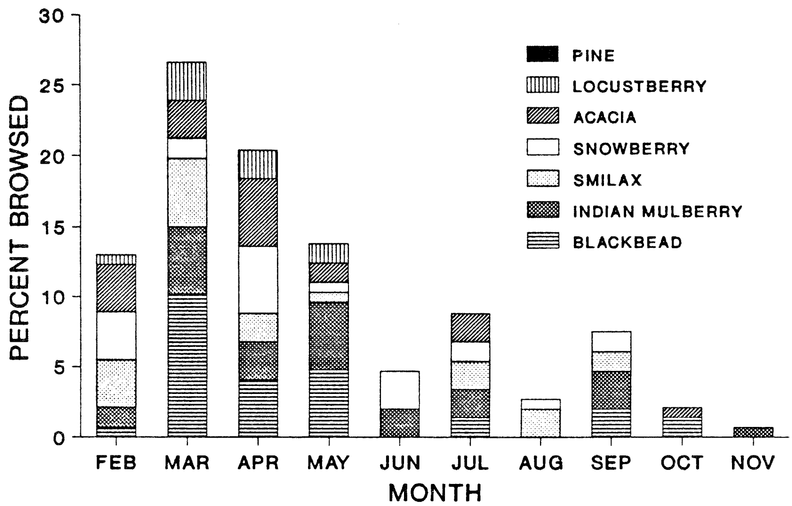

Fig. 1. Percent of marked shrubs (n = 30/species, 20 for snowberry) browsed at monthly intervals by Key deer at 3 pineland sites, Big Pine Key, Florida, 1987.

most often, and pine was not used at all. During the 11 month observation period, browsing selection differed ($\chi^2 = 11.9$, 5 df, $P = 0.04$) from expected based on relative abundance. However, confidence intervals for observed browsing included the expected values in all cases except locustberry, suggesting no selection among the other species. Locustberry was browsed less than expected ($P < 0.05$).

The CP and P concentrations in Indian mulberry were higher ($P < 0.01$) in burned than in unburned plots during March, May, and July (7 to 11 months post-burn; Table 1). The CP was higher in greenbrier and pine only during March at these sites, as was P in greenbrier and blackbead. Locustberry had less CP in burned plots during November. No response to burning occurred for P in locustberry and pine.

Burning effects on digestibility also were temporary and variable among the species sampled (Table 1). Digestibility in burned plots was higher ($P < 0.02$) than in unburned plots during March for blackbead and greenbrier and during May for blackbead and Indian mulberry. Digestibility of locustberry did not respond to burning, whereas digestibility of unburned pine was higher ($P < 0.05$) than burned in November.

Seasonal variations in nutrient concentrations generally were greater than the effects of burning (Table 1). Blackbead and greenbrier had the most temporal variation in CP and P. In May, CP was higher ($P < 0.05$) than in March or November for these 2 species. Although mean P concentrations never exceeded 0.17% among any of our samples, the P values were highest ($P < 0.05$) during May for blackbead and greenbrier. Other species had less temporal variation in CP and P content. Temporal trends in digestibility varied among the species, and no distinct time of maximum or minimum level was evident.

Plant Growth after Fire

Sprout density was generally higher ($P < 0.05$) in burned than in unburned plots, plant density differed ($P < 0.05$) between burned and unburned plots in only a few cases, and the effect of cover varied among the species (Table 2). The apparent enhancement of sprout density due to fire lasted 14 months for Indian mulberry, locustberry, and species common in the Key deer diet (diet species), but only 2 months in other species. Plant density of Indian mulberry was greater ($P < 0.05$) in burned plots by autumn 1987 (14 months). Diet species had higher plant density ($P < 0.05$) in burned plots by spring 1987 (8 months). Cover of blackbead, locustberry, palms, and diet species was less ($P < 0.05$) in the first year after burning in 1986-burn plots relative to unburned plots. In contrast, Indian mulberry cover was greater ($P < 0.05$) in burned plots 14 months after burning. Other species had lower cover values for all sample periods.

Of food plants observed in flower or fruit,

Table 1. Mean nutrient concentrations (%) and in vitro organic matter digestibility (%) at 3 pineland sites (pooled), Big Pine Key, Florida, 1987.

Species	Sampling period[a]	Crude protein			Phosphorus			Digestibility		
		Burned		Unburned	Burned		Unburned	Burned		Unburned
Blackbead	Mar	21.0 B[b]		18.9 B	0.15 B	*[c]	0.10 B	33.6 A	*	29.6 B
	May	23.4 A		26.9 A	0.17 A		0.17 A	35.2 A	*	42.3 A
	Jul	22.5 AB		21.3 B	0.15 B		0.10 B	34.3 A		33.5 B
	Nov	17.7 C		21.1 B	0.10 C		0.11 B	26.5 B		29.8 B
Indian mulberry	Mar	16.1 A	*	13.6 A	0.15 A	*	0.12 AB	51.6 A		51.7 A
	May	15.1 AB	*	13.0 AB	0.14 AB		0.12 AB	50.0 A	*	46.8 B
	Jul	14.8 B	*	12.5 B	0.14 B	*	0.11 B	50.7 A		48.0 AB
	Nov	14.1 B		13.8 A	0.13 B		0.14 A	45.2 B		45.4 B
Greenbrier	Mar	10.7 BC	*	8.2 B	0.10 BC	*	0.07 C	47.2 B	*	40.3 C
	May	13.6 A		12.7 A	0.17 A		0.17 A	57.4 A		58.2 A
	Jul	12.2 AB		11.5 A	0.14 AB		0.13 B	55.7 A		54.6 AB
	Nov	8.0 C		10.2 AB	0.07 C		0.09 C	41.6 B		43.7 BC
Locustberry	Mar	9.3 A		9.4 A	0.08 A		0.09 A	15.1 AB		15.4 AB
	May	8.5 AB		8.8 A	0.08 A		0.08 A	15.6 AB		14.8 B
	Jul	7.7 BC		7.5 B	0.06 B		0.05 B	16.0 A		16.9 A
	Nov	6.9 C	*	7.7 B	0.05 B		0.04 B	14.0 B		14.2 B
Slash pine	Mar	4.4 A	*	3.6 B	0.03 A		0.02 B	22.1 A		22.6 A
	May	4.2 AB		4.2 A	0.05 A		0.06 A	20.1 B		19.7 B
	Jul	3.7 BC		3.9 A	0.04 A		0.05 A	19.4 B		20.9 AB
	Nov	3.8 C		3.6 B	0.05 A		0.05 A	21.0 AB	*	22.9 A

[a] $n = 9$ for each sampling period/burn treatment combination.
[b] Sampling-period means for each species within a treatment followed by different letters differed ($P < 0.05$); Tukey's Studentized range test.
[c] Treatment means (burned and unburned) separated by an asterisk differed ($P < 0.05$); t-test.

excluding palms, 94% were Indian mulberry and locustberry. Density of fruiting Indian mulberry plants was greater ($P < 0.05$) in burned plots during the second spring after burning (Table 3). Locustberry had similar ($P > 0.05$) fruiting densities in burned plots as in the unburned plots during the first and second spring after burning. Density of fruiting palms did not differ ($P > 0.05$) between burned and unburned plots. During autumn 1986, more brittle thatch and silver palms were in fruit, however, at site B than at site A. Brittle thatch was the most abundant palm (Carlson 1989). The difference in spring 1987 was attributable to saw-palmetto, with many fruiting plants occurring on 1 transect.

Frequency of occurrence of diet and endemic species generally was similar ($P > 0.05$) in burned and unburned plots (Table 4), indicating rapid resprouting after burning but no enhanced recruitment. Milk pea was consistently less frequent ($P < 0.05$) in burned plots during spring samples. Snowberry frequency was lower ($P < 0.05$) on burned plots during autumn 1986 and spring 1987, and sand flax (*Linum arenicola*) was lower ($P < 0.05$) in the burned plots only during autumn 1986.

Plant Community Succession

Ordination of sites by PCA, whether with all species or with woody species only, defined the first principal component by occurrence of pine vs. hammock species (Fig. 2). Pine sites on Big Pine Key occupied 1 extreme of the first component; they were very similar in composition of woody species but varied more when herbaceous species were included. One site on No Name Key was intermediate between Big Pine sites and the other 2 No Name sites, more so considering woody species only and less so with herbaceous species included. Taken as island groups, the No Name sites and the Sugarloaf sites were intermediate between pine and hammock sites. The intermediate sites on these 2 islands had a mixture of pine and hammock species (Table 5), indicating mid-successional status. However, a paucity of herbaceous species placed most No Name sites and the Sugarloaf sites closer to the hammock sites. The 2 hammock sites occupied the opposite extreme of the first component but were somewhat different from each other.

The second component (Fig. 2) was defined

Table 2. Mean density of sprouts and woody plants and foliar cover at 2 pineland sites (pooled), Big Pine Key, Florida.

Species or group	Sampling period	Sprouts/100 m²			Plants/100 m²			Cover (%)		
		Burned		Unburned	Burned		Unburned	Burned		Unburned
Indian mulberry	Autumn 1986	21.8	*[a]	4.1	56.4		44.3	0.5		0.5
	Spring 1987	35.7	*	12.0	79.0	*	52.6	0.5		0.7
	Autumn 1987	22.7	*	4.3	59.8	*	34.8	0.8		0.4
	Spring 1988	21.5		10.4	57.2		38.1	0.9		0.4
Blackbead	Autumn 1986	49.8		6.3	32.2		23.5	0.3	*	3.0
	Spring 1987	102.9		22.1	45.6		27.9	0.5	*	5.3
	Autumn 1987	116.6		14.1	37.9		29.4	1.1	*	6.0
	Spring 1988	92.5		17.4	33.0		20.5	1.2	*	4.8
Locustberry	Autumn 1986	208.4	*	41.5	12.8		12.9	1.0	*	2.6
	Spring 1987	173.9	*	46.5	13.5		9.3	1.7		3.0
	Autumn 1987	243.0	*	33.3	11.0		10.1	2.7		2.7
	Spring 1988	242.3	*	95.4	8.9		7.4	2.9		2.7
Palms[b]	Autumn 1986	59.3		47.5	15.7	*	32.0			
	Spring 1987	72.6		74.9	23.5	*	35.8			
	Autumn 1987	57.0		49.0	29.8		32.1			
	Spring 1988	55.4		56.4	34.5		32.8			
Diet species[c]	Autumn 1986	1,352.2	*	160.3	164.3		168.3	5.3	*	12.4
	Spring 1987	996.8	*	312.0	178.0	*	120.8	7.8	*	20.3
	Autumn 1987	983.5	*	221.5	140.0		116.0	10.6	*	18.2
	Spring 1988	895.6	*	504.3	122.4		91.5	12.0		15.7
Other species[d]	Autumn 1986	434.4	*	94.9	178.0		210.3	1.4	*	14.8
	Spring 1987	405.8		405.6	196.5		183.6	2.1	*	16.5
	Autumn 1987	399.0	*	187.1	155.4		145.9	4.7	*	13.8
	Spring 1988	415.4		465.3	129.0		164.1	5.3	*	12.7

[a] Treatment means (burned and unburned) separated by an asterisk differed ($P < 0.05$); ANOVA and orthogonal contrasts.
[b] Includes silver palm, cabbage palm, saw-palmetto, and brittle thatch palm.
[c] Includes acacia, locustberry, black torch (*Erithalis fruticosa*), joewood (*Jacquinia keyensis*), wild dilly (*Manilkara bahamensis*), indian mulberry, blackbead, long-stalked stopper (*Psidium longipes*), randia (*Randia aculeata*), and tallowwood (*Ximenia americana*); all species in top 75% of the Key deer diet (Dooley 1975).
[d] Includes all woody plants except palms, diet species, and slash pine.

Table 3. Mean density (No./100 m²) of woody species in flower or fruit at 2 pineland sites (pooled), Big Pine Key, Florida.

Species	Sampling period	Treatment		
		Burned		Unburned
Indian mulberry	Autumn 1986	0.0		0.0
	Spring 1987	3.3	*[a]	7.6
	Autumn 1987	0.4		0.1
	Spring 1988	13.0	*	3.8
Locustberry	Autumn 1986	0.0		0.1
	Spring 1987	0.9		2.1
	Autumn 1987	0.0		0.1
	Spring 1988	3.5		2.4
Palms[b]	Autumn 1986	1.2		2.5
	Spring 1987	2.1		0.6
	Autumn 1987	2.6		2.1
	Spring 1988	0.6		0.1

[a] Treatment means separated by an asterisk differed ($P < 0.05$); ANOVA and orthogonal contrasts.
[b] Includes silver palm, cabbage palm, saw-palmetto, and brittle thatch palm.

by species common in the wet pine sites or hammock sites vs. other species. The first 2 components accounted for 63% (for woody species) and 57% (for all species) of the variability in the data. The analyses defined the third and fourth components as species composition of the sites on No Name and Sugarloaf keys, and of the wet and dry sites. These axes accounted for an additional 21–22% of the variability.

A total of 56 woody and 87 herbaceous species occurred in the study plots. Of these, 37 were correlated (Pearson correlation coefficients all $P < 0.01$) with the first component of either or both analyses and are therefore considered to be the most typical pine and hammock species for the region (Table 5). Pineland associates included the most common herbs, such as whitetop sedge (*Dichromena colorata*); milk pea, a common food item for deer (Klimstra and Dooley 1990); and 2 endemics, Big Pine partridge pea and Florida five-petaled leaf flower. Woody

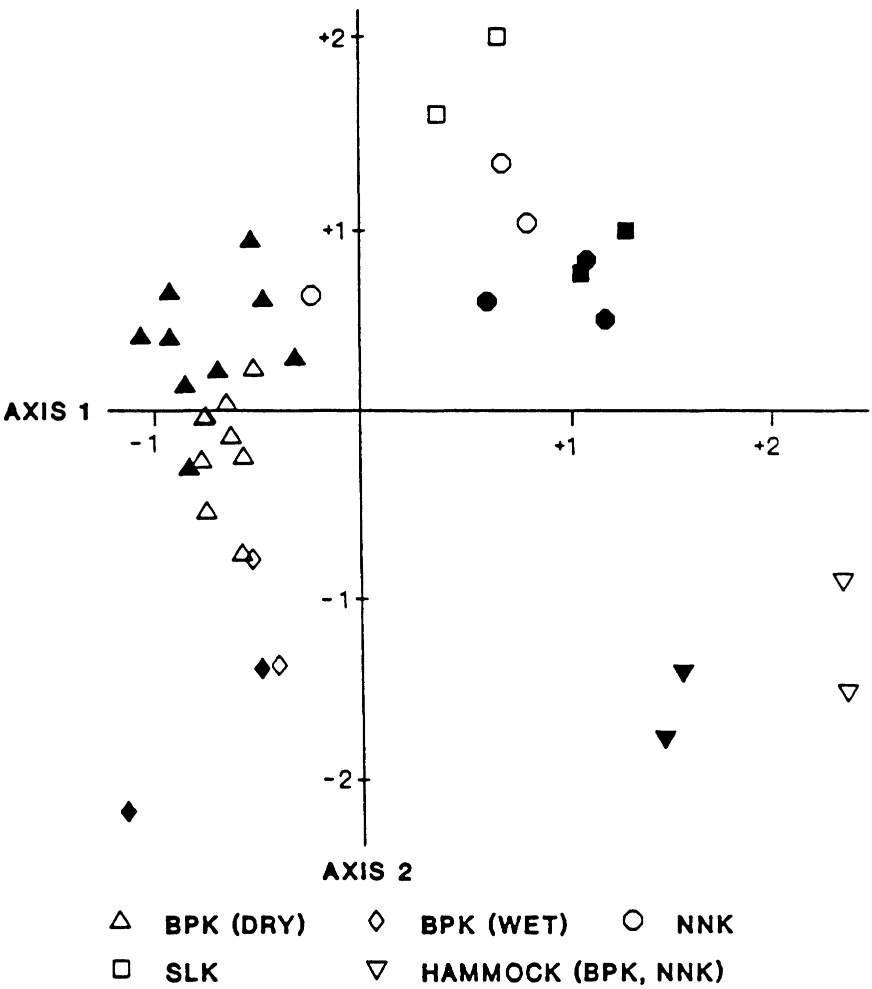

Fig. 2. Ordination by principal components analysis of sites on Big Pine Key (BPK), No Name Key (NNK), and Sugarloaf Key (SLK), Florida, 1987. Results of analyses using frequencies of woody species only and all species are indicated by open and filled symbols, respectively.

species most associated with pine stands included pisonia (*Pisonia rotundata*) and slash pine. Those associated with hammocks included white stopper (*Eugenia axillaris*), Spanish stopper (*E. foetida*), and pigeon-plum (*Coccoloba diversifolia*).

The frequencies of these 37 species illustrate the successional state of the stands and distinguish between pine, mixed, and hammock habitats (Fig. 3). Herbaceous species highly associated with pine communities began to diminish in frequency after >10 years but were still common at Big Pine sites with the longest known fire-free interval (approx. 20 yr). In contrast, those herbaceous species were virtually absent from No Name sites with fire-free intervals >10 years. Hammock species had only begun to pioneer Big Pine sites 10–20 years after fire, whereas those species at No Name sites were common 10–20 years after fire and abundant >20 years after fire. Pines persisted at these sites and at Sugarloaf sites >50 years after fire. Pines and pine-associated herbaceous species were absent from hammock sites on Big Pine Key crudely estimated as fire-free for >100 years.

Endemic Plants

Eight endemic species or varieties and two spurge species of the genus *Chamaesyce* were encountered on Big Pine Key (Table 4). At Big Pine sites, the frequency of occurrence of most of these species was unaffected by fire, although the spurges and sand flax frequencies were reduced temporarily. In contrast, none of these

Table 4. Frequency of occurrence (%) of herbaceous species and vines important in the Key deer diet or endemic to the rockland pine community at 2 sites (pooled), Big Pine Key, Florida.

Species	Sampling period	Treatment		
		Burned		Unburned
Big pine partridge pea	Autumn 1986	25.5		21.3
Cassia keyensis[abc]	Spring 1987	26.8		21.9
	Autumn 1987	30.7		23.1
	Spring 1988	31.8		22.5
Snowberry[d]	Autumn 1986	4.2	*[e]	16.8
	Spring 1987	10.3	*	20.0
	Autumn 1987	11.6		18.1
	Spring 1988	10.9		13.8
Spurges[afg]	Autumn 1986	5.3	*	17.5
	Spring 1987	7.0	*	16.9
	Autumn 1987	9.9		15.6
	Spring 1988	9.7		15.6
Milk pea[d]	Autumn 1986	12.9		19.4
	Spring 1987	15.5	*	28.8
	Autumn 1987	19.0		26.3
	Spring 1988	14.0	*	27.5
Sand flax[cfh]	Autumn 1986	0.1	*	1.3
	Spring 1987	0.6		0.6
	Autumn 1987	0.0		0.0
	Spring 1988	0.3		0.0
Fla. five-petaled leaf flower[cf]	Autumn 1986	11.5		11.9
(*Phyllanthus pentaphyllus* var.	Spring 1987	15.9		17.5
floridanus)	Autumn 1987	25.0		26.9
	Spring 1988	15.3		11.9
Poinsettia pinetorum[ch]	Autumn 1986	1.8		0.0
	Spring 1987	1.1		0.6
	Autumn 1987	3.2		1.3
	Spring 1988	2.5		0.6
Polygala boykinii var. *sparsifolia*[f]	Autumn 1986	0.7		2.5
	Spring 1987	2.2		3.8
	Autumn 1987	1.9		2.5
	Spring 1988	1.8		0.6
Schizachyrium rhizomatum[cf]	Autumn 1986	4.4		3.8
	Spring 1987	5.5		8.8
	Autumn 1987	5.1		1.9
	Spring 1988	4.7		3.1
Greenbrier[d]	Autumn 1986	24.4		23.8
	Spring 1987	26.7		31.3
	Autumn 1987	28.8		33.1
	Spring 1988	26.3		25.0
Tragia saxicola[cfh]	Autumn 1986	1.6		1.9
	Spring 1987	1.6		1.3
	Autumn 1987	3.2		1.3
	Spring 1988	2.8		0.6

[a] A candidate for federal listing, with substantial information on vulnerability and threats. Although the U.S. Fish and Wildlife Service does not protect candidates for listing under the Endangered Species Act, it "encourages their consideration in environmental planning. . ." (Federal Register 55[35]:6184–6229).

[b] Listed as threatened by the Florida Department of Agricultural and Consumer Services (list published in Preservation of Native Flora of Florida Act, Section 581.185–187, Florida Statutes).

[c] Endemic to the rockland pine community or associated habitats of southern Florida (Avery and Loope 1980).

[d] Important in the Key deer diet (Dooley 1975).

[e] Treatment means separated by an asterisk differed ($P < 0.05$); ANOVA with orthogonal contrasts.

[f] A candidate for federal listing, with some evidence of vulnerability but not enough data to support listing.

[g] Recently combined with little bluestem (*S. scoparium*). *S. rhizomatum* is no longer considered a valid species.

[h] Listed as endangered by the Florida Department of Agricultural and Consumer Services (list published in Preservation of Native Flora of Florida Act, Section 581.185–187, Florida Statutes).

Table 5. Mean frequency of occurrence (%) for plant species correlated ($P < 0.01$) with the first principal component, using woody species only or all species, Big Pine, Sugarloaf, and No Name Keys, 1987.

		Location				
Species[a]	Habitat and form[b]	Big Pine dry	Big Pine wet	No Name Key	Sugarloaf Key	Hammock
White-topped sedge (*Dichromena colorata*)	PH	64.4	76.6	0	3.3	0
Lopsided indiangrass (*Sorghastrum secundum*)	PH	64.8	65.0	0	0	0
Piriqueta caroliniana	PH	23.3	25.0	0	0	0
Milk pea (*Galactia parvifolia*)	PH	45.9	20.0	1.1	0	0
Big Pine partridge pea	PH	54.4	18.3	0	0	0
Butterfly pea (*Centrosema virginianum*)	PH	49.6	26.7	0	0	0
Fla. five-petaled leaf flower (*Phyllanthus pentaphyllus*)	PH	36.7	73.3	0	1.7	0
Greenbrier	PH	60.4	43.3	24.4	1.7	0
Ruellia caroliniensis	PH	40.4	73.3	0	0	0
Pisonia	PW	75.9	56.7	50.0	33.3	0
Cirsium horridulum	PH	13.7	16.7	0	0	0
Slash pine	PW	80.4	88.3	66.7	56.7	0
Pityopsis graminifolia	PH	13.0	23.3	0	0	0
Schizachyrium gracile	PH	47.8	5.0	6.7	5.0	0
Pineland croton (*Croton linearis*)	PH	38.9	78.3	1.1	0	0
Pteris longifolia	PH	19.6	6.7	0	0	0
Pine fern (*Anemia adiantifolia*)	PH	43.3	3.3	3.3	0	0
Crotalaria maritima	PH	22.6	11.7	0	0	0
Solidago stricta	PH	22.2	6.7	0	0	0
Silver palm	PW	81.1	81.7	90.0	5.0	18.3
Schizachyrium semiberbe	PH	37.0	3.3	0	0	0
Alternanthera ramosissima	PH	15.9	51.7	0	0	0
Indian mulberry	PW	85.6	98.3	93.3	83.3	31.7
Brittle thatch palm	PW	94.8	46.7	80.0	100.0	3.3
Locustberry	PW	55.9	65.0	45.6	58.3	3.3
Inkwood (*Exothea paniculata*)	HW	0	0	0	0	20.0
Paradise tree (*Simaruba glauca*)	HW	0	0	0	5.0	38.3
Jamaica thatch palm (*Thrinax radiata*)	HW	0	0	0	0	15.0
Leadwood (*Krugiodendron ferreum*)	HW	0	0	0	0	13.3
Gumbo-limbo (*Bursera simaruba*)	HW	0	0	0	0	36.7
Marlberry (*Ardisia escallonioides*)	HW	0	0	5.6	3.3	45.0
Jamaica dogwood (*Piscidia piscipula*)	HW	1.1	0	11.1	3.3	28.3
Wild dilly (*Manilkara bahamensis*)	HW	1.5	0	5.6	13.3	20.0
Red ironwood (*Reynosia septentrionalis*)	HW	5.2	0	60.0	38.3	31.7
Pigeon plum (*Coccoloba diversifolia*)	HW	1.5	0	41.1	13.3	66.7
Spanish stopper (*Eugenia foetida*)	HW	1.1	1.7	30.0	51.7	100.0
White stopper (*Eugenia axillaris*)	HW	3.7	0	75.6	56.7	90.0

[a] Species are ranked by coefficients of the first eigenvector for the analysis with all species.
[b] PH = pine, herbaceous; PW = pine, woody; and HW = hammock, woody.

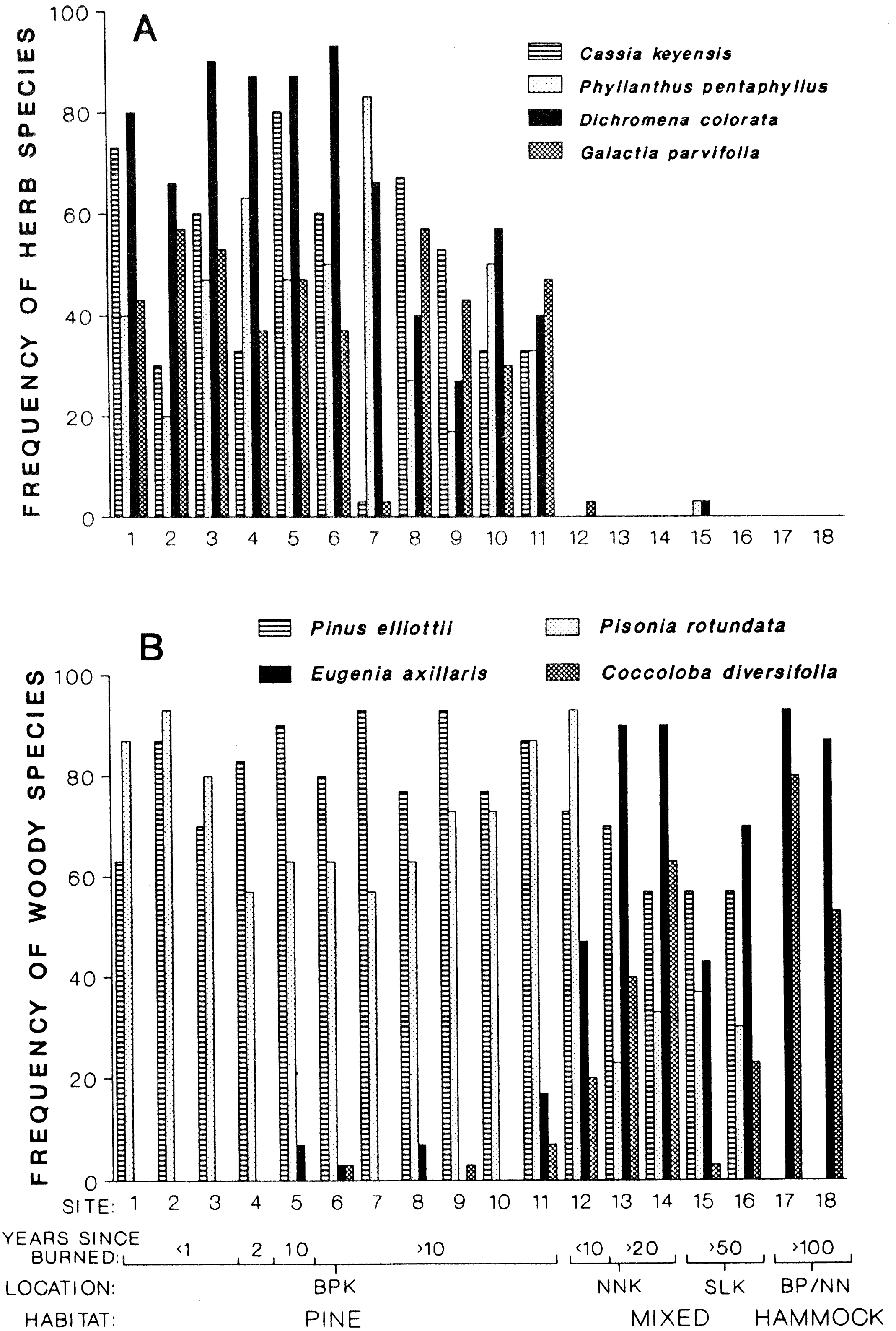

Fig. 3. Frequencies of occurrence of (A) herbaceous species and (B) woody species highly associated with pine and hammock communities in sites on Big Pine Key (BPK), No Name Key (NNK), both (BP/NN), and Sugarloaf Key (SLK), Florida, 1987.

endemic taxa was observed on No Name Key, and only two were observed in open wet areas of Sugarloaf Key (at very low frequencies, <3%).

DISCUSSION

Data describing use of browse species and their nutritive quality were collected only during the first year following fire. Although replicated in space, burn treatments were not replicated in time. Because the range of variation across years in nutritive value of browse species was not measured, the associated inferences cannot be extrapolated to other years.

Use of Browse Species

One goal of prescribed burning is the maintenance of an adequate food supply for deer. Indian mulberry and blackbead were browsed most often, confirming these as the most important pineland browse species (Klimstra and Dooley 1990). Pine was avoided. Acacia and locustberry were selected more than and the same as expected, respectively. This selectivity was associated with nutrient content and digestibility of browse, as found for white-tailed deer by others (Loveless 1959, Thill et al. 1987).

Nutritive Value of Browse Species

The CP needed for optimal deer growth is 13–14%, but the minimum requirement is estimated to range from 6–9% (French et al. 1956, McEwen et al. 1957, Holter et al. 1979). The 2 most heavily used pineland diet species, blackbead and Indian mulberry, were high in CP (>17% and >12%, respectively) throughout the year. Similarly, Sokoloff et al. (1949) found leaves of red mangrove (*Rhizophora mangle*), the top browse species of Key deer (Klimstra and Dooley 1990), to have 12–14% CP.

Although P of the diet species analyzed was lower than the assumed requirement for deer (0.25%; French et al. 1956, McEwen et al. 1957), the actual requirement is unknown (Davis and Johnson 1984). A P content >0.25% only was needed for optimal growth and antler development, whereas "deficiencies of . . . phosphorus (about 0.25 per cent) were tolerated with little or no apparent stress" (McEwen et al. 1957: 124). Body growth and general health were not affected. Furthermore, Cowan and Long (1962, cited by Davis and Johnson 1984) found that a minimum P requirement for bucks 2–3 years old was <0.2%. Thus, a minimum dietary requirement for deer is probably <0.25%, and the P levels in browse species (averaging 0.14%) may not be limiting. Cowan et al. (1970) stated that if the composite diet contained adequate CP, then other nutritional requirements are probably met.

We collected nutrition data for only the first growing season following the fire. Burning temporarily increased nutrient content and digestibility of the diet species analyzed, lasting 7–11 months. Only Indian mulberry retained heightened nutrient content in burned plots as long as 11 months post-burn. Burning often has a temporary effect on nutrient content and digestibility (e.g., Lay 1957, Springer 1977, Thill et al. 1987). Nutritive value among the species tended to be higher during March and May, corresponding to the period of maximum browse growth and use. This pattern reflects normal seasonal variation described by others (Dietz et al. 1962, Blair et al. 1977, Hanley and McKendrick 1983).

Value of Plant Growth to Key Deer

The amounts of sprouting and foliar cover in burned plots showed that browse availability had recovered or increased within 2 years after burning. Increased sprouting is the main factor in increasing browse availability (Dills 1970, Halls 1978). The temporary increase in nutritive value for diet species may partially compensate for the amount of browse removed by fire. Similarly, fruiting of diet species returned to unburned levels within 1 year after burning, except at site B (the driest site, where the effect of burning may have been compounded by water stress). Snyder (1986) also found that palm reproduction was not affected by burning and that only a few hardwoods, including Indian mulberry and locustberry, flowered in the first year post-burn. Woody species unimportant in the diet did not respond to burning as much as diet species, indicating that burning improved the understory composition for the deer.

Frequencies of diet and endemic species in the burned plots differed little from those in unburned plots within 1 year after burning. This constancy is consistent with Dickson's (1955) finding of similar frequencies and densities of greenbrier, milk pea, and partridge pea in burned and unburned pinelands on Big Pine Key by the second month post-burn. Herbaceous species generally regrow quickly after fires (Lay 1956, Lewis and Harshbarger 1976, Snyder 1986).

Plant Community Succession

Although discontinuities in the chronoseries of sites complicate their interpretation, succession of the pine community in the absence of fire appears to be a simple replacement of savanna species with forest species, with some variation in return time depending on local circumstances. At least 2 factors may be related to the similar species composition of pine stands on Big Pine Key despite differences in time since the last fire. First, none of the Big Pine savanna sites had a fire-free interval long enough to change successional state. Second, the smaller and more isolated islands other than Big Pine have less chance of being burned by fire from lightning or people, resulting in lower frequency of burning and a shorter return time to hammock after disturbance, as argued by Harper (1911). A relatively short interval between fires (on the order of 10–20 yr) on Big Pine Key should maintain savanna vegetation. An interval either the same or longer (on the order of 10–50 yr) on smaller, more isolated islands arrests succession at an intermediate stage containing both savanna and forest species. Only a very long fire-free interval (>100 yr) allows full development of a hammock community.

Herbs (milk pea and greenbrier) important in the Key deer diet (Klimstra and Dooley 1990) were highly associated with pine sites and became uncommon with hardwood succession. Milk pea only occurred once outside of pine sites on Big Pine Key, and frequency of occurrence of greenbrier was much lower on No Name and Sugarloaf Keys than on Big Pine Key. Thus, availability of herbaceous forage depends upon the amount of hardwood cover.

Higher frequencies of hammock species at two of the No Name pineland sites than in 1951–52 (Dickson 1955) reflected successional change in the intervening 35 years. In contrast, the third No Name pineland site, burned in the early 1980's, had a species composition similar to that recorded in 1951–52. Thus, for sites with a fire-free interval of approximately 10–35 years on small, isolated islands, the stoppers and pigeonplum are good indicators of successional advance. These 2 species may act as invaders and provide a shady environment needed for succession to hammock. Conversely, absence of blolly (*Guapira discolor*) may indicate successional retreat in these mixed-composition sites with intermediate fire-free intervals. Blolly occurred in 80% of Dickson's pineland plots and in 50% of his hammock plots. In the present study, blolly occurred on No Name Key only in hammock (23% frequency). Blolly was most frequent in the pineland of Sugarloaf Key (27% and 60%), but it was absent from Sugarloaf after the prescribed burn in 1987. A fire on No Name Key in the 1960's could have eliminated this species from most of the pineland, and its earlier occurrence may indicate a long absence of fire on No Name Key before 1950.

Endemic Plants

Whereas endemic herbaceous plants at pineland sites were generally unaffected by fire in pine savanna, they were rare or absent from sites in which succession had advanced to mixed pine-hammock composition. The time for endemic species to be shaded out in the pinelands of the Everglades region was estimated at 5–15 years (Robertson 1954, Snyder 1986). On Big Pine Key, endemics remained in sites unburned for at least 15 years, although their frequency of occurrence was less than in sites with a shorter fire-free interval. In Everglades National Park, Loope and Dunevitz (1981) found that a pine stand unburned for 35 years had lost all its endemic species, similar to the situation on No Name Key. These differences probably reflect both slower plant growth in the more xeric Keys relative to the mainland and the variable return time after disturbance among keys.

MANAGEMENT IMPLICATIONS

Maintenance of pine habitat of NKDWR is increasingly important to Key deer as other pinelands are lost through real-estate development. Fire probably provides a within-year increase in nutritive value of deer browse, an among-years increase in the quantity of browse, and prevents succession to hardwoods on a scale of decades. Arresting succession may be the greatest of the benefits to deer, because this prevents elimination of herbaceous species important in the deer diet. Given the relatively slow plant growth in the Lower Keys and the relatively long return time after disturbance, a fire periodicity of 5–10 years should accomplish this goal. Even the most temporary benefit, increasing nutritive value of deer browse, appears to be consequential. Maintaining prominent browse species that are particularly high in CP, such as blackbead and Indian mulberry, should become more important if deer in pineland become cut off from habitats containing other preferred browse (such as mangrove) by fencing, as has been proposed to reduce deer road-kills and conflicts with dogs. Thus, we recommend establishing a prescribed burning plan on the Refuge to provide both short- and long-term benefits for Key deer.

Preventing extinction or extirpation of endemic plants is an even stronger rationale than benefitting deer for maintaining the pine community, because the endemic herbs are more restricted to savanna conditions. Big Pine partridge pea historically occurred on at least 5 Keys, but has been extirpated from three of them by fire suppression and land development (D. F. Austin and C. E. Nauman, status report on Big Pine partridge pea, U.S. Fish and Wildlife Service, Jacksonville, Fla., 1981). One pineland endemic, Garber's spurge (*Chamaesyce garberi*), has been extirpated from Big Pine Key (U.S. Fish and Wildlife Service 1985*b*).

Management of Keys' vegetation should not focus narrowly on pineland to the exclusion of other successional stages, however. Maintaining a diversity of stands will provide cover for deer and refuge for numerous plant species intolerant of burning. Developing a prescribed fire plan for specified areas to be burned at a range of fire frequencies (e.g., 5, 15, 25, and 75 years) is necessary to maintain the natural diversity of terrestrial ecosystems in the Keys.

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