Journal of Vegetation Science 11: 113-122, 2000
© IAVS; Opulus Press Uppsala. Printed in Sweden

Effects of repeated burning on species richness in a Florida pine savanna: A test of the intermediate disturbance hypothesis

Beckage, Brian[1] & **Stout, I. Jack**

Department of Biology, University of Central Florida, Orlando, Fl 32816, USA;
[1]*Current address: Botany Department, Duke University, Durham, NC 27708, USA;*
Fax +1 919 660 7293; E-mail bb2@duke.edu

Abstract. We studied the effect of burning frequency on the density and species richness of understory flowering stems in a Florida sandhill. Flowering stems were censused weekly for 54 weeks in six sites that had been burned one to six times in the previous 16 years. We concurrently measured overstory characteristics such as species composition, density and basal area. We used maximum likelihood and Akaike's Information Criterion to compare linear, quadratic, saturating, and null models of community response to repeating burning. We did not find a relationship between species richness, diversity or flowering stem density and fire frequency. Tree density was related to fire frequency and may represent an indirect pathway for fire effects on understory characteristics. While we found no support for the Intermediate Disturbance Hypothesis, an analysis of our experimental design indicated that we had low statistical power. We develop the hypothesis that a saturating model of response to fire best describes understory species richness in our system. We test this hypothesis using the most extensive published fire data set we are aware of and find support for a saturating model.

Keywords: Fire frequency; Florida sandhill.

Nomenclature: Wunderlin (1982) except for *Aristida beyrichiana,* which follows Peet (1993). Vouchers for each species were collected and deposited at the University of Central Florida herbarium.

Abbreviations: AIC = Akaike's Information Criterion; IDH = Intermediate Disturbance Hypothesis.

Introduction

Many communities in nature never achieve a state of equilibrium but are in some stage of recovery following disturbance (e.g. Reice 1994; Bergeron et al. 1998). The species richness of these communities represents a balance between colonization and competitive displacement (Huston 1979). Disturbance frequency mediates this balance because of a hypothesized tradeoff between competitive ability and dispersal (Werner & Platt 1976; Gleeson & Tilman 1990; Tilman 1990). High disturbance frequencies do not afford competitively superior (but poorly dispersed) species sufficient time to become established prior to the next disturbance. In contrast, well dispersed species are eliminated at low disturbance frequencies by competitive displacement. Highest community diversity is hypothesized to occur at intermediate disturbance regimes (Intermediate Disturbance Hypothesis or IDH) where species from both groups exist together (Connell 1978; Huston 1979).

Studies have examined the IDH in relation to fire with mixed results. Some studies have found species richness to increase with fire frequency without a subsequent decline in species richness at higher burn frequencies (Tester 1989; Mehlman 1992; Nuzzo et al. 1996). Others have found species richness to decline with increasing fire frequency (Collins et al. 1995) or lowest species richness at intermediately disturbed sites (Schwilk et al. 1997). The inconsistent nature of these results may be partly attributable to differing times since last fire (known to affect species diversity, Gibson & Hulbert 1987; Mehlman 1992) and inclusion of dormant season burns which may impact flora differently than growing season fires (e.g. Platt et al. 1991; Streng et al. 1993; Sparks et al. 1998).

The abundance of species may be more sensitive to fire frequency than is species richness. Since fire-sensitive species may decline prior to their elimination, measures of abundance may indicate the effects of fire before species richness changes. In contrast, fire-adapted species increase in abundance with burning (Hartnett 1987; Tester 1989; Waldrop et al. 1992; Tester 1996; Nuzzo et al. 1996). Fire-adapted species not only benefit from reduced competition with fire sensitive species but also from increased seed production and seed viability (Lemon 1967; Vogl 1972; Abrahamson 1984; Snyder & Ward 1987; Platt et al. 1988; Myers 1990; Ostertag & Menges 1994; Outcalt 1994) and increased vegetative production following fire (Hartnett 1987). Differential success over many fires may result in a community dominated by fire-adapted species (Lemon 1967; Waldrop et al. 1992) but without actual elimination of other species.

Our objective was to ascertain the effects of repeated burning on richness, abundance, and diversity of understory species at a uniform time following fire. We intensively sampled species abundance through weekly surveys of flowering stems as opposed to less intense sampling of more sites. We also measured overstory characteristics, e.g. density and basal area, to identify overstory response to fire and to assess its influence on understory species patterns.

Study area

This study was conducted in an upland longleaf pine savanna, or sandhill community, in Wekiwa Springs State Park (WSSP), Florida, USA. Sandhill communities are located on sandy, well-drained, infertile Entisols and occur from Virginia south to Florida and west into Texas (Myers 1990; Stout & Marion 1993). They are characterized by an open overstory of *Pinus palustris* and *Quercus laevis*, with a diverse ground cover of grasses, particularly wire grasses, and herbaceous species (Myers 1990; Brockway et al. 1998). The structure of these communities depends on low intensity surface fires, occurring at intervals as short as 1 to 3 years (Christensen 1981; Myers 1990; Stout & Marion 1993). Historically, most of these fires were started by lightning and occurred naturally during the growing season from about March through September in Florida (Myers 1985).

Methods

We selected six study sites (referred to as burn zones) which were burned from 1 - 6 × in the 16 yr prior to this study (Table 1). All sites were last burned at the same time, avoiding the confounding effect of variation in time since last fire and concomitant effects on species richness (Gibson & Hurbert 1987; Mehlman 1992; Collins et al. 1995). Burns were administered from April to October, within the range of natural fire events. Since season of burn has little effect on which species flower (Platt et al. 1988), the variation in timing of fires within the growing season does not bias our results. Limited burning may have been done in the park prior to 1977, but there is no documentation (Rosi Mulholland, Park Biologist, pers. comm.). All six burn zones were located on Candler fine sands (Doolittle & Schellentrager 1989), with a maximum distance of 0.8 km between any of the sites, thus minimizing local variations in rainfall, seed sources and past land use. Throughout the paper we refer to the sites with a number that corresponds to the number of burns each site received, e.g., burn zone 3 was burned three times in the previous 16 years.

Table 1. The burn histories of the six study sites. Note that the burn zone number equals the total number of burns received in the 16 years prior to this study.

Burn zone	Burn history: dates of controlled burns (month/year)					
1	8/90					
2	8/90	4/87				
3	4/90	6/86	4/79			
4	5/90	4/88	5/85	4/80		
5	4/90	6/86	4/83	4/80	4/77	
6	4/90	10/87	10/85	4/83	9/81	9/78

We used periodic flowering stem counts to measure species richness and abundance in the understory. We choose this methodology because many ground layer species in our study system are impossible to identify when not in flower or are ephemeral and only obvious when in flower. The limitation of this method is that species that did not flower were not included. We are aware of only one species, *Aristida beyrichiana*, that typically flowers only following a burn and would be largely absent from our flowering stem counts. Otherwise, our flowering stem surveys included all species that we observed (regardless of flowering status) occurring in our study areas without any bias associated with prior burn history (personal observation). This is supported by the fact that the species richness in our study (89) was slightly greater than that reported by Brockway et al. (1998) for a north Florida sandhill (87).

Flowering stem counts of all understory vascular plants (grasses, sedges and forbs) were made in a single 2.5 m × 200 m (500 m^2) belt transect. Transects were randomly located in each burn zone, except to avoid a 10 m wide buffer strip around burn zone boundaries. Each transect was divided into eight sequential 25 m sections, with flowering stem censuses completed weekly in every other section so that each burn zone was completely censused every 2 weeks. Censuses were done for 54 weeks beginning in April 1993. A stem was recorded as flowering if at least one flower had a receptive stigma and/or anthers shedding pollen. The total number of flowering stems was recorded by species without regard to whether the stems were found on the same or on multiple individuals.

We used the flowering stem counts to compute several metrics of community and species response to fire. Species richness was the number of understory species observed over the course of the study with at least one flowering stem. Abundance of individual species was equated to their total number of flowering stems. There is some evidence that the number of flowering stems is related to plant basal area (Canfield & Tanner 1997), loosely linking it to more traditional measures of plant abundance. Shannon-Wiener diversity of the understory was calculated from these measures of species richness and abundance. Finally, the frequency of individual species was the number of subplots within a burn zone that contained the species.

As species' responses to fire were likely to be related to life history traits, we examined the flowering stem abundance of five major plant families (Zomlefer 1991), *Asteraceae*, *Cyperaceae*, *Euphorbiaceae*, *Fabaceae* and *Poaceae*, as a surrogate for life history. While the life history characteristics of species within some of these families vary widely, they were relatively similar in our study system. The *Asteraceae* were mostly perennial, often rhizomatous, with corm-like or tuberous root systems and leaves in basal rosettes. The *Cyperaceae* were largely rhizomatous perennials, often with a cespitose habit. The *Euphorbiaceae* were all perennials with three seeded schizocarp fruits that may be dispersed several meters upon dehiscence. The *Fabaceae* were largely characterized by a perennial habit (some with taproots) and an association with nitrogen fixing bacteria (Zomlefer 1991; Hendricks & Boring 1999). The seed of some species of *Fabaceae* was dispersed through explosive dehiscence of their pods. The *Poaceae* were mostly perennial bunch grasses with wind dispersed seed.

To assess overstory characteristics, we recorded the species and diameter at breast height (DBH) of all trees over 2.5 cm DBH in a single 50 m × 50 m quadrat placed in each burn zone. The quadrats were placed adjacent to the belt transects and partially overlapped them.

Analysis

We analysed community, individual species, and family responses to fire frequency. Community-level metrics for the understory were species richness, total flowering stem abundance, and Shannon-Wiener diversity. In addition, we calculated Sørensen's similarity index (Pielou 1984) for all pair-wise comparisons among burn zones. Species-level metrics were abundance and frequency within burn zones. Finally, we compared overstory density to fire frequency as well as to understory diversity. In all analyses, the burn zone was the experimental unit avoiding the problem of pseudoreplication (Hurlbert 1984).

We compared four alternative models of response to fire frequency: (1) a null model, (2) a linear model, (3) a quadratic model and (4) a saturating model. The null model (1) was simply a mean response, independent of fire, plus error:

$$\hat{Y} = \hat{\beta}_0 + \varepsilon \cdot \tag{1}$$

In the linear model (2), the mean was a monotonically increasing function of fire, i.e.

$$\hat{Y} = \hat{\beta}_0 + \hat{\beta}_1 \times \text{Burns} + \varepsilon \text{,} \tag{2}$$

where 'Burns' refers to the number of burns a plot received. Model 3 allowed for a unimodal curve; the mean was a quadratic function of burns, e.g.

$$\hat{Y} = \hat{\beta}_0 + \hat{\beta}_1 \times \text{Burns} + \hat{\beta}_2 \times \text{Burns}^2 + \varepsilon \cdot \tag{3}$$

In model (4), the mean was a saturating function of burns:

$$\hat{Y} = \hat{\beta}_0 + \hat{\beta}_1 \times \left(\frac{\exp\left[\hat{\beta}_2 \times \text{Burns}\right]}{\left(1 + \exp\left[\hat{\beta}_2 \times \text{Burns}\right]\right)} \right) + \varepsilon \,. \tag{4}$$

This allowed the response variable to initially increase with burning but then to level off at an asymptote. The intermediate disturbance hypothesis would predict a unimodal relationship with disturbance (Model 3).

We fit these four models using maximum likelihood. Since the species richness and flowering stem data are counts, we initially used a Poisson likelihood with a log link (Gelman et al. 1997). However, inspection of the fitted model indicated that the data were probably overdispersed. We chose a negative binomial likelihood as a robust alternative to the Poisson for overdispersed data (Gelman et al. 1997). We used the parameterization given in Hillborn & Mangel (1997) with a log link:

$$\mathcal{L}\{X|\hat{Y},\ \hat{k}\}\ \prod_{i=1}^{n} \frac{\Gamma\left(\hat{k} + x_i\right)}{\Gamma\left(\hat{k}\right) x_i!} \left(\frac{\hat{k}}{\hat{k} + \exp\left(\hat{Y}_i\right)} \right)^{\hat{k}} \left(\frac{\exp\left(\hat{Y}_i\right)}{\hat{k} + \exp\left(\hat{Y}_i\right)} \right)^{x_i} \tag{5}$$

where $\hat{k}$ is an overdispersion parameter, exp($\hat{Y}$) is the mean (where $\hat{Y}$ is given by the models above) and the x_i's (i = 1 to n) are the observations. To avoid numerical underflow when computing the likelihood, we minimized the negative log-likelihood as is customary. The negative log-likelihood is given by:

$$L\left\{X \mid \hat{Y}, \hat{k}\right\} = \sum_{i=1}^{n} -\log\Gamma\left(\hat{k} + x_i\right) + n\log\Gamma\left(\hat{k}\right) + \sum_{i=1}^{n} \log\left(x_i!\right) - \sum_{i=1}^{n} x_i \log\left(\frac{\exp\left(\hat{Y}_i\right)}{\hat{k} + \exp\left(\hat{Y}_i\right)} \right) - \hat{k} \sum_{i=1}^{n} \log\left(\frac{\hat{k}}{\hat{k} + \exp\left(\hat{Y}_i\right)} \right) \tag{6}$$

For the species diversity data, which are continuous, we used a normal likelihood for model fitting. The normal likelihood is

$$\mathcal{L}\left\{Y \middle| \hat{Y}, \hat{\sigma}^2\right\} = \prod_{i=1}^{n} \frac{1}{\hat{\sigma}\sqrt{2\pi}} \exp\left(-\frac{\left(x_i - \hat{Y}_i\right)^2}{2\hat{\sigma}^2} \right) \tag{7}$$

where $\hat{Y}$ is the mean (as given above), the x_i's are the observations and $\hat{\sigma}^2$ is the maximum likelihood estimate of the variance (Burnham & Anderson 1998). We again obtained maximum likelihood estimates for parameters by minimizing the negative log-likelihood:

$$\mathrm{L}\left\{\mathrm{X} \mid \hat{\mathrm{Y}}, \hat{\sigma}^{2}\right\} = n\left[\log(\hat{\sigma}) + \frac{1}{2}\log(2\pi)\right] + \sum_{i=1}^{n}\left(\frac{\left(x_i - \hat{\mathrm{Y}}_i\right)^{2}}{2\hat{\sigma}^{2}}\right) \qquad (8)$$

We analysed the frequency data, which described the occurrence of species in subplots within burn zones, using the binomial likelihood. The logit, i.e. log (Y/1–Y), of the probability that a species occurred in a subplot was described by the four models described above, e.g. for model (1) logit($\hat{\mathrm{Y}}$) = $\hat{\beta}_0$ +ε. This yielded the following likelihood:

$$\mathcal{L}\ \{\mathrm{X}|\ \hat{\mathrm{Y}}\ \} = \prod_{i=1}^{n}\binom{8}{x_i}\left(\frac{\exp\left(\hat{\mathrm{Y}}_i\right)}{1+\exp\left(\hat{\mathrm{Y}}_i\right)}\right)^{x_i}\left(\frac{\exp\left(\hat{\mathrm{Y}}_i\right)}{1+\exp\left(\hat{\mathrm{Y}}_i\right)}\right)^{8-x_i} \qquad (9)$$

where 8 was the number of subplots in each burn zone, x_i is the number of subplots in burn zone *i* in which a given species was found. We minimized the negative log-likelihood:

$$L\left\{\mathrm{X}\middle|\hat{\mathrm{Y}}\right\} = \sum_{i=1}^{n} -\log\binom{8}{x_i} - \sum_{i=1}^{n} x_i \log\left(\frac{\exp\left(\hat{\mathrm{Y}}_i\right)}{1+\exp\left(\hat{\mathrm{Y}}_i\right)}\right) -$$

$$\sum_{i=1}^{n}\left(8 - x_i\right)\log\left(1 - \frac{\exp\left(\hat{\mathrm{Y}}_{\mathrm{i}}\right)}{1+\exp\left(\hat{\mathrm{Y}}_{\mathrm{i}}\right)}\right) \qquad (10)$$

For the overstory data, we fit the four models described above to both tree density and basal area. We also fit models where understory species richness, flowering stems, and diversity were functions of tree density, basal area, or tree density and basal area. We compared these models to those that were a function of burn frequency only. We used a negative binomial likelihood for count data and a normal likelihood for continuous data.

We compared models using Akaike's Information Criterion (AIC) (Burnham & Anderson 1998). The AIC allows direct comparison of both nested and non-nested models (e.g., the saturating model in our study) rather than testing of individual null hypotheses (e.g., that a parameter in a model is not different from 0) or the direct comparison of only nested models (likelihood ratio tests). This provided a consistent, easily interpreted method of model comparison independent of nesting status or the probability distribution used to calculate the likelihood. Because the ratio of data points to parameters in our models was less than 40, we used the small sample AIC or $\mathrm{AIC_c}$ for model comparison (Burnham & Anderson 1998):

$$\mathrm{AIC}_c = 2\mathrm{L}(\mathrm{X} \mid \Theta) + 2p\left(\frac{n}{n-p-1}\right) \qquad (11)$$

where *n* is the number of data points, *p* is the number of model parameters and L(X|Θ) is the negative log likelihood of the data X given the set of estimated parameter values Θ. The model with the lowest $\mathrm{AIC_c}$ is considered the 'best' model given the data. The second term is a penalty for additional parameters. In the limit as *n* goes to infinity, the second term goes to 2*p* so that the addition of a parameter must lower the negative log likelihood by one to offset the penalty.

Table 2. Model fitting results for species richness, flowering stems, and Shannon-Wiener Diversity. A negative binomial likelihood was used for the species richness and flowering stem data while a normal likelihood was used for the diversity data. Bold indicates the best model for the data.

	Parameters	–log likelihood	$\mathrm{AIC_c}$
Species richness			
Null	2	21.59	**51.18**
Linear	3	20.85	59.70
Saturating	4	19.97	87.95
Quadratic	4	19.99	87.99
Flowering stems			
Null	2	49.25	**106.50**
Linear	3	49.04	116.07
Saturating	4	46.60	141.20
Quadratic	4	42.45	132.90
Diversity (*H'*)			
Null	2	–2.22	**3.56**
Linear	3	–2.35	13.30
Saturating	4	–3.73	40.54
Quadratic	4	–4.90	38.20

Results

We found no relationship between species richness, flowering stems, or diversity of the understory and number of fires (Figs. 1a-c). The null model had the lowest $\mathrm{AIC_c}$ in all cases (Table 2). Furthermore, overall similarity of burn zones was not related to burn frequency, e.g. Sørensen's similarity index indicated that burn zones 1 and 6 were more similar than burn zones 1 and 2 (Table 3).

Table 3. Sørensen's similarity index (as a percent) for all pairwise comparisons. BZ 1 refers to the burn zone with 1 burn, BZ 2 the burn zone with 2 burns, etc.

	BZ 1	BZ 2	BZ 3	BZ 4	BZ 5	BZ 6
BZ 1	100					
BZ 2	32	100				
BZ 3	37	38	100			
BZ 4	39	38	53	100		
BZ 5	37	47	53	41	100	
BZ 6	42	53	39	51	57	100

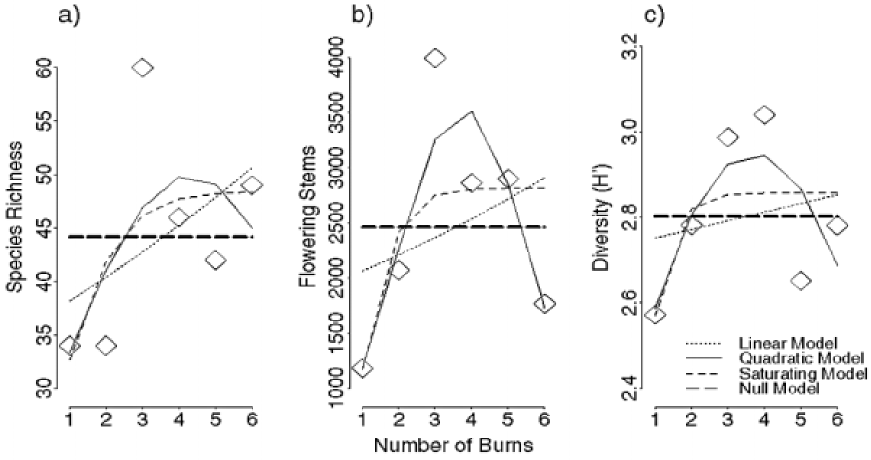

Fig. 1. **a.** Species richness; **b.** flowering stems; **c.** Shannon-Wiener diversity as a function of burn treatment. Curves represent maximum likelihood fits for linear, quadratic, saturating, and null models. Species richness and flowering stem data were modeled using a negative binomial likelihood, while a normal likelihood was used for the diversity data. The bold line represents the best fit as judged by AIC$_c$.

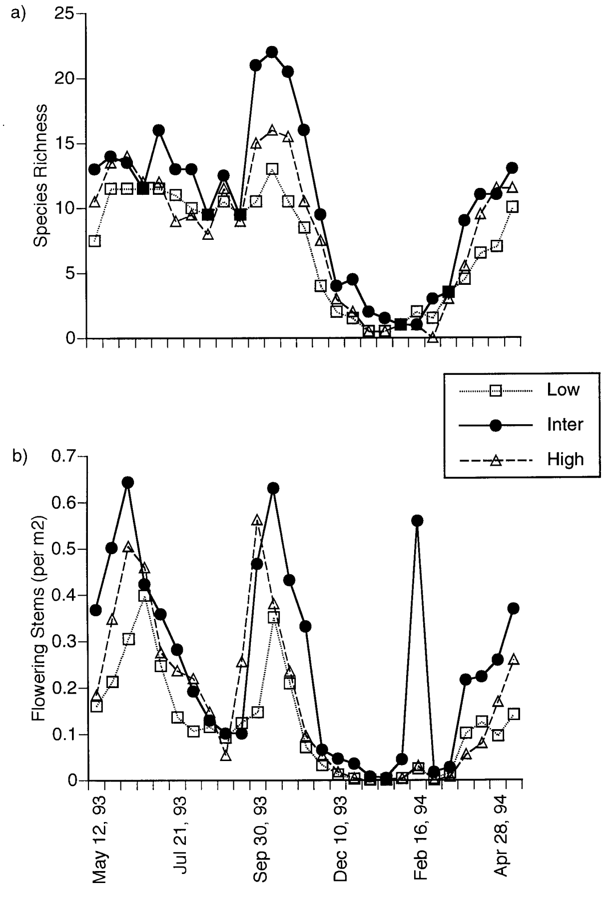

Fig. 2. **a.** Species richness; **b.** Flowering stem density by census date for the low (1 or 2 burns), intermediate (3 or 4 burns), and high (5 or 6 burns) fire frequencies.

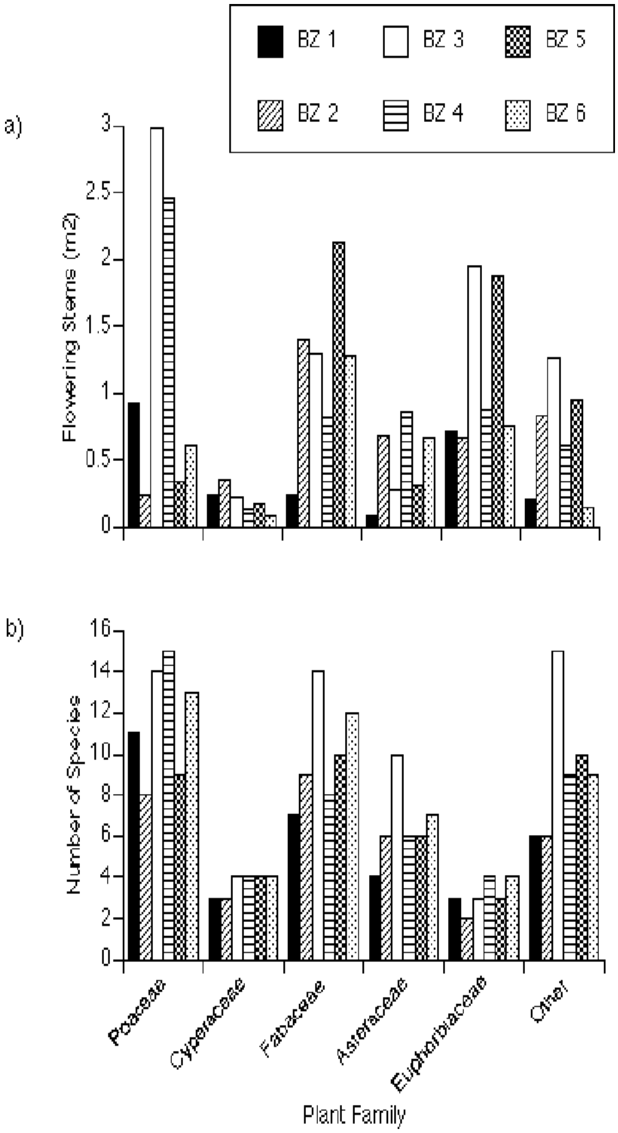

Fig. 3. Contributions of specific plant families to (**a**) flowering stem density and (**b**) species richness.

Patterns of species richness and flowering stem abundance varied across burn zones throughout the year, with the intermediately burned zones, i.e., burn zones 3 and 4, tending to have higher species richness and flowering stem densities (Fig. 2). This was particularly pronounced in the fall, which is a period of intense flowering in sandhill communities. There were two additional flowering peaks; one occurred across all sites early in the summer, while the other occurred in the winter but only in the intermediately burned zones. This latter flowering peak was composed largely of a single species, *Hedyotis procumbens* (*Rubiaceae*) but made a substantial contribution to the higher flowering stem counts found at intermediate burn frequencies (Fig. 1b).

In the species-level analyses, neither flowering stem density nor the frequency of species within burn zones was related to burn frequency for any species, i.e., the null was consistently selected using the AIC_c. But overall, flowering maxima (i.e. species' peak abundances) were not evenly distributed across the six burn zones ($\chi^2 = 45.86$, df = 5; $P < 0.01$); more species (~50) than expected showed flowering maxima in the intermediately burned zones 3 and 4.

At the family level, flowering density was not related to number of burns for any of the five families examined. However, the null and linear models explained the abundance of *Cyperaceae* nearly equally well (AIC_c = 72.79 and 72.94, respectively) indicating that there may be a negative linear relationship between burning and *Cyperaceae* abundance (Fig. 3a). Nevertheless, *Euphorbiaceae* and *Poaceae* did account for much of the increased flowering stem response in intermediately burned sites (Fig. 3a). In contrast, changes in species richness in the intermediately burned sites (Fig. 3b) resulted from a general increase in the number of species across families rather than pronounced increases in particular families.

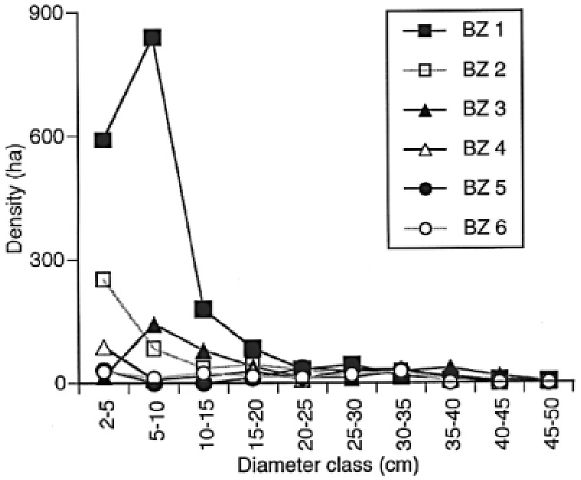

Fig. 4. Tree diameter distributions by burn treatment. All stems greater than 2.5 cm DBH were censused. Burn zone (BZ) numbers correspond to number of times the site was burned in the previous 16 years.

Table 4. Overstory characteristics of the burn zones. All trees which were ≥ 2.5 cm DBH were measured.

	Burn treatment					
	1	2	3	4	5	6
Trees per ha	1808	496	388	224	156	140
Basal area (m^2/ha)	15.7	7.0	13.5	6.1	8.0	4.9
	Dominance as % of basal area					
	1	2	3	4	5	6
Pinus clausa	30	0	0	0	0	0
Pinus palustris	25	61	81	94	100	84
Quercus geminata	23	1	1	4	0	11
Quercus incana	0	0	0	0	0	0
Quercus laevis	21	38	15	1	0	5
Quercus laurifolia	0	0	3	0	0	0
Quercus stellata var. *margarita*	< 1	< 1	< 1	0	0	< 1
	Dominance as % of stems					
	1	2	3	4	5	6
Pinus clausa	6	0	0	0	0	0
Pinus palustris	5	52	37	79	100	63
Quercus geminata	69	3	2	4	0	17
Quercus incana	0	0	1	0	0	0
Quercus laevis	20	42	56	18	0	17
Quercus laurifolia	0	0	2	0	0	0
Quercus stellata var. *margarita*	< 1	2	2	0	0	3

Overstory density and composition were related to burn history. Tree density decreased linearly with fire frequency (Table 4, AIC_c= 90.4 compared to 95.2, 112.2, and 135.2 for null, quadratic or saturating models, respectively). Basal area was not related to fire frequency, e.g. the null model had the lowest AIC_c. While the dominance of the fire-tolerant *Pinus palustris* increased with burn frequency (Table 4), the null model was selected over other models (AIC_c= 72.9 for the null compared to 82.4, 107.8, 112.9, for the linear, quadratic, and saturating models). The density of the relatively fire-intolerant *Quercus laevis* decreased with burning, but the null was again selected over other models (AIC_c = 77.1 for the null model compared to 82.8, 112.8, and 117.1 for the linear, quadratic, and saturating models). In general, less-burned sites were dominated by fire-intolerant tree species, whose large numbers and small diameters suggest that they became established in the absence of fire (Fig. 4, Table 4).

Neither species richness, diversity, nor flowering stem density of the understory was a function of tree density or basal area, i.e. the null model was selected over the linear, quadratic or saturating models. In all cases, models with only fire frequency as a predictor had lower AIC$_c$'s than models with both tree density and basal area.

Discussion

We did not find a relationship between understory species richness, diversity, or flowering stem abundance and number of burns. While fire appeared to result in increased species richness (Fig. 1a) and an unimodal increase in flowering stem abundance (Fig. 1b) and diversity (Fig. 1c), our model selection criterion (AIC$_c$) favored the null model (a single mean plus error) over linear, quadratic, or saturating models. The greater similarity among burn zones 1 and 6 than burn zones experiencing similar number of burns (Sørensen's similarity index, Table 3) further supports this interpretation.

Failure to support the IDH could result from three causes: (1) the IDH is, in fact, not operating in our system, (2) an inadequate range of burn frequencies was used or (3) the relationship between fire and response variables was too subtle to detect with our experimental design (Toft & Shea 1983). The highest fire frequency in our study was 2-3 years, within the natural range for sandhills but short of the annual burning reported for some sandhill communities (Stout & Marion 1993). However, we believe that a wider range of fire frequencies would be unlikely to change our results because overstory composition and structure had already changed dramatically across our fire frequencies (Fig. 4, Table 4). The possibility of low power seemed reasonable given our relatively small sample size.

If the quadratic model was the 'true' model, how much replication would be needed before it would be selected? We addressed this question by using Monte Carlo simulations to generate power curves. First, we assumed that the true relationship between the response variables and fire was the quadratic model fit to the data. Then, we simulated a given number of data points, N, from the appropriate probability density (e.g., negative binomial or normal) for each burn frequency with mean and variance given by the model fit. We compared the four models of response (described in methods) and selected the 'best' one using the AIC$_c$. We repeated this process 1000 × and recorded the percentage of times that the 'true' model was selected. We continued this process for increasing N until the true model was selected $\geq 80\%$ of the time. The resulting power curves are shown in Fig. 5.

If the quadratic model was the 'true' model, then we had low statistical power for detecting this relationship (Fig. 5). With one replicate per treatment, the 'true' model won <1% of the time for species richness, species diversity, and flowering stem abundance. 80% power would require five replicates per burn treatment for species richness, three replicates per treatment for species diversity, and two replicates per treatment for flowering stem abundance. The first case would necessitate a total sample of 30, a sample size larger than most experiments in the fire literature. We examined 12 papers that addressed the relationship between fire and species richness and found the median sample size to be 10 with only three of the 12 papers having samples sizes ≥ 30. If such studies generally suffer from power problems then it is not surprising that their results are often inconsistent; ranging from increased species richness with burning (Lewis & Harshbarger 1976; Allen & Wyleto 1983; White 1983; Walker & Peet 1983; Gilliam & Christensen

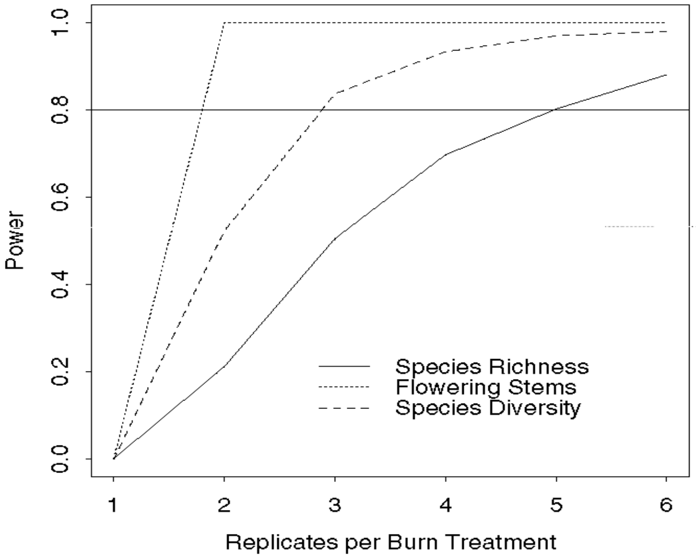

Fig. 5. Experimental power for increasing levels of replication. Curves are based on Monte Carlo simulations. Species richness and flowering stem data were modeled using a negative binomial distribution, while diversity data was assumed to follow a normal distribution. Distribution parameters were estimated from our data.

1986; Gibson & Hulbert 1987; Tester 1989; Mehlman 1992; Nuzzo et al. 1996; Arthur et al. 1998) to decreased species richness with burning (Collins et al. 1995; Schwilk et al. 1997) with varying degrees of certainty. This result suggests the need for a global or meta-analysis of the fire literature.

We found no evidence for a relationship between flowering stem density and fire frequency for any understory species. In contrast, some previous studies have linked fire frequency to abundance of individual species (Lewis & Harshbarger 1976; White 1983; Harnett 1987; Tester 1989; Anderson & Menges 1997). Similarly, the frequency (within burn zones) of understory species was not related to the number of burns. Failure to find stronger support for relationships between particular species and fire frequency could be due to lack of replication.

Aggregating species into families as a surrogate for life history did not change this result – we still did not find any relationships between flowering stem density and number of burns for the five families examined. However, for *Cyperaceae*, a negative linear model essentially tied with the null model. *Poaceae* and *Euphorbiaceae* contributed much of the flowering response in the intermediately burned sites despite being best described by the null model (Fig. 3a). This is consistent with the strong association of these families with sandhill communities (Platt et al. 1988; Myers 1990; Hendricks & Boring 1999) and with their reported responses to fire (Waldrop et al. 1992).

Tree density and composition were closely tied to fire history. Overstory density was inversely related to fire frequency; the density of our least burned site was 13 × that of our most burned site (Table 4). Most stems in the infrequently burned sites were in the smallest size classes (Fig. 4) and were comprised of fire sensitive hardwoods (nearly 90%). In contrast, the most burned sites contained a few, large individuals of the fire tolerant longleaf pine. While there were large longleaf pines in the least burned sites, they were in a 'sea' of small hardwoods. The invasion of pinelands in the absence of fire *Pinus clausa* and hardwoods has also been documented by others (Veno 1976; Givens et al. 1984), and is consistent with decreased tree densities following fire in oak savannas (White 1983; Tester 1989) and changes in tree size class distributions in pinelands following fire (Rebertus et al. 1989; Waldrop et al. 1992). Once these changes in overstory structure occur, they are difficult to reverse; large hardwoods are not easily eliminated using fire (Ferguson 1957; Grano 1970; Rebertus et al. 1989; Cole et al. 1992).

Previous studies have explained changes in understory communities in response to fire by primarily focusing on the direct effects of fire on herbaceous species, such as increased numbers of ramets (Hartnett 1987; Platt et al. 1988; Brewer & Platt 1994) and increased germination of seeds following fire (Whelan 1986). We found that the strongest effects of varied fire frequency were on overstory density and composition, which may, in turn, impact the composition and abundance of understory species. This suggests that the primary effect of fire may simply be the maintenance of an open overstory, minimizing competition for light and soil resources among understory species, and, thereby allowing rich understories to develop. Reduced burn frequencies allow dense stands of fire-intolerant tree species to establish in the open sandhill physiognomy, ultimately resulting in declines in understory species richness. This would led us to expect species richness to follow a saturating model; initial increases in species richness with burning would be followed by little additional increase in richness as continued burning only maintains overstory openness. Because of the low power of our study, and likely of most fire studies, we tested

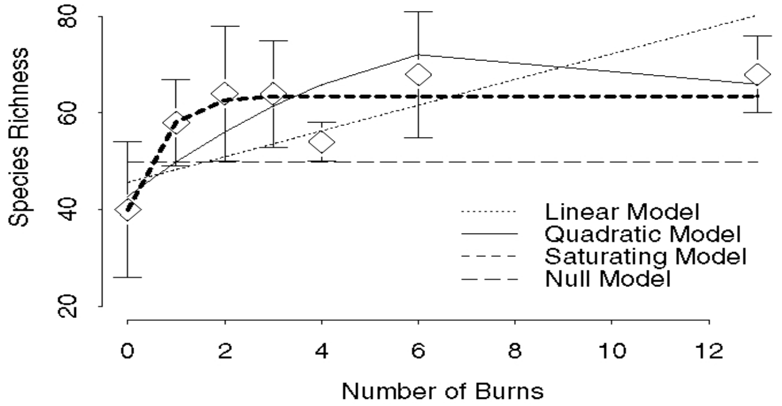

Fig. 6. Species richness as a function of burn treatment for data from Mehlman (1992). Curves represent maximum likelihood fits for linear, quadratic, saturating, and null models using a normal likelihood. The bold line represents the best fit as judged by AIC$_c$.

this hypothesis by fitting our four models to the most extensive set of species richness data (as a function of fire frequency) that we are aware of. Mehlman (1992) published the species richness of 70 plots in Florida pinelands that had been burned 0 to 13 × in the previous 13 yr – although it should be cautioned that fires were administered in the winter and number of burns is confounded with time since last fire. We visually estimated the mean and standard deviation from the seven treatments in Mehlman's Fig. 1a, computed the sufficient statistics from this information (DeGroot 1989), which then allowed us to fit our four models using a normal likelihood. A saturating model of species richness was supported, i.e., had the lowest AIC_c (Fig. 6; $AIC_c = 554.7$ for saturating vs. 574.6, 565.2, and 591.3 for linear, quadratic, and null models, respectively). Additional support for this hypothesis is provided by Brockway et al. (1998); they eliminated overstory oaks from a sandhill community using herbicides only and found resultant increases in species richness and cover of graminoids and forbs in the absence of fire.

Acknowledgements. We thank John Wilder, David Hanf, and Parks Small for assistance with field work. We thank the staff of Wekiwa Springs State Park for access to and background data on the study sites. We thank Dave Higdon and Michael Lavine for statistical advice. We also thank Phil Camill, Jim Clark, Phil Dixon, Deborah Goldberg, Paul Harcombe, Jackie Mohan, and two anonymous reviewers for their helpful comments.

References

Abrahamson, W.G. 1984. Species responses to fire on Florida Lake Wales Ridge. *Am. J. Bot.* 71: 35-43.

Allen, T.F.H. & Wyleto, E.P. 1983. A hierarchical model for the complexity of plant communities. *J. Theor. Biol.* 101: 529-540.

Anderson, R.C. & Menges, E.S. 1997. Effects of fire on sandhill herbs; nutrients, mycorrihizae, and biomass allocation. *Am. J. Bot.* 84: 938-948.

Arthur, M.A., Paratley, R.D. & Blankenship, B.A. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. *Bull. Torrey Bot. Club* 125: 225-236.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H. & Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests – Special Feature. *J. Veg. Sci*. 9: 463-468.

Brewer, J.S. & Platt, W.J. 1994. Effects of fire season and soil fertility on clonal growth in a pyrophilic forb, *Pityopsis graminifolia* (Asteraceae). *Am. J. Bot.* 81: 805-814.

Brockway, D.G., Outcalt, K.W. & Wilkins, R.N. 1998. Restoring longleaf pine wiregrass ecosystems: plant cover, diversity and biomass following low-rate hexazinone application on Florida sandhills. *For. Ecol. Manage*. 103: 159-175.

Burnham, K.P. & Anderson, D.R. 1998. *Model selection and inference, A practical information-theoretic approach.* Springer, New York, NY.

Canfield, S.L. & Tanner, G.W. 1997. Observations of pineywoods dropseed (*Sporobolus junceus*) phenological development following fire in a sandhill community. *Florida Sci.* 60: 69-72.

Christensen, N.L. 1981. Fire regimes in southeastern ecosystems. In: Mooney, H.A., Bonnickson, J.M., Christensen, N.L., Lotan, J.E. & Reiners, W.A. (eds.) *Fire regimes and ecosystem properties*, pp. 112-136. USDA Forest Service General Technical Report, Washington, DC.

Cole, K.L., Klick, K.F. & Pavlovic, N.B. 1992. Fire temperature monitoring during experimental burns at Indiana Dunes National Lakeshore. *Nat. Areas J.* 12: 177-183.

Collins, S.L., Glenn, S.M. & Gibson, D.J. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* 76: 486-492.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

DeGroot, M.H. 1989. *Probability and statistics.* Addison-Wesley Publishing Company, Reading, MA.

Doolittle, J.A. & Schellentrager, G. 1989. *Soil survey of Orange County, Florida.* U.S. Department of Agriculture, Soil Conservation Service.

Ferguson, E.R. 1957. Stem-kill and sprouting following prescribed fires in a pine-hardwood stand in Texas. *J. For.* 55: 426-429.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. 1997. *Bayesian data analysis.* Chapman and Hall, New York, NY.

Gibson, D.J. & Hulbert, L.C. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72: 175-185.

Gilliam, F.S. & Christensen, N.L. 1986. Herb-layer response to burning in pine flatwoods of the lower Coastal Plain of South Carolina. *Bull. Torrey Bot. Club* 113: 42-45.

Givens, K.T., Layne, J.N., Abrahamson, W.G. & White-Schuler, S.C. 1984. Structural changes and successional relationships of five Florida Lake Wales Ridge plant communities. *Bull. Torrey Bot. Club* 111: 8-18.

Gleeson, S.K. & Tilman, D. 1990. Allocation and the transient dynamics of succession on poor soils. *Ecology* 71: 1144-1155.

Grano, C.X. 1970. *Eradicating understory hardwoods by repeated prescribed burning.* U.S. Forest Service Southern Forest Experiment Station Resource Paper SO-56, New Orleans, LA.

Hartnett, D.C. 1987. Effects of fire on clonal growth and dynamics of *Pityopsis graminifolia* (Asteraceae). *Am. J. Bot.* 74: 1737-1743.

Hendricks, J.J. & Boring, L.R. 1999. N_2-fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *For. Ecol. Manage*. 113: 167-177.

Hillborn, R. & Mangel, M. 1997. *The ecological detective:*

confronting models with data. Princeton University Press, Princeton, NJ.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54: 187-211.

Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.* 113: 81-101.

Lemon, P.C. 1967. Effects of fire on herbs of the southeastern United States and Central Africa. *Proc. Tall Timbers Fire Ecol. Conf.* 6: 112-127.

Lewis, C.E. & Harshbarger, T.J. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina coastal plain. *J. Range Manage.* 29: 13-18.

Mehlman, D.W. 1992. Effects of fire on plant community composition of North Florida second growth pineland. *Bull. Torrey Bot. Club* 119: 376-383.

Myers, R.L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. *Bull. Torrey Bot. Club* 112: 241-252.

Myers, R.L. 1990. Scrub and high pine. In: Myers, R.L. & Ewel, J.J. (eds.) *Ecosystems of Florida*, pp. 150-193. University of Central Florida Press, Orlando, FL.

Nuzzo, V.A., McClain, W. & Strole, T. 1996. Fire impact on groundlayer flora in a sand forest 1990-1994. *Am. Midl. Nat.* 136: 207-221.

Ostertag, R. & Menges, E.S. 1994. Patterns of reproductive effort with time since last fire in Florida scrub plants. *J. Veg. Sci.* 5: 303-310.

Outcalt, K.W. 1994. Seed production of wiregrass in central Florida following growing season prescribed burns. *Int. J. Wildland Fire* 4: 123-125.

Peet, R.K. 1993. A taxonomic study of *Aristida stricta* and *Aristida beyrichiana*. *Rhodora* 95: 25-37.

Pielou, E.C. 1984. *The interpretation of eological data: A primer on classification and ordination.* John Wiley and Sons, New York, NY.

Platt, W.J., Evans, G.W. & Davis, M.M. 1988. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. *Oecologia* (*Berl*.) 76: 353-363.

Platt, W.J., Glitzenstein, J.S. & Streng, D.R. 1991. Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. *Proc. Tall Timbers Fire Ecol. Conf.* 1G: 143-161.

Rebertus, A.J., Williamson, G.B. & Moser, E.B. 1989. Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. *Ecology* 70: 60-70.

Reice, S.R. 1994. Nonequilibrium determinants of biological community structure. *Am. Sci.* 82: 424-435.

Schwilk, D.W., Keeley, J.E. & Bond, W.J. 1997. The intermediate disturbance hypothesis does not explain fire and diversity patterns in fynbos. *Plant Ecol.* 132: 77-84.

Snyder, J.R. & Ward, G. 1987. Effect of season of burning on the flowering response of subtropical prairie plants. *Bull. Ecol. Soc. Am.* 68: 419.

Sparks, J.C., Masters, R.E., Engle, D.M., Palmer, M.W. & Bukenhofer, G.A. 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. *J. Veg. Sci.* 9: 133-142.

Stout, I.J. & Marion, W.R. 1993. Pine flatwoods and xeric pine forests of the southern (lower) coastal plain. In: Martin, W.H., Boyce, S.G. & Echternacht, A.C. (eds.) *Biodiversity of the southeastern United States / Lowland terrestrial communities*, pp. 373-446. John Wiley and Sons, New York, NY.

Streng, D.R., Glitzenstein, J.S. & Platt, W.J. 1993. Evaluating effects of season of burn in longleaf pine forests: a critical review and some results from an ongoing long term study. *Proc. Tall Timbers Fire Ecol. Conf.* 18: 227-259.

Tester, J.R. 1989. Effect of fire frequency on plant species in oak savanna in east-central Minnesota. *Bull. Torrey Bot. Club* 123: 304-308.

Tester, J.R. 1996. Effect of fire frequency on oak savanna in east-central Minnesota. *Bull. Torrey Bot. Club* 116: 134-144.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58: 3-15.

Toft, C.A. & Shea, P.J. 1983. Detecting community-wide patterns: estimating power strengthens statistical inference. *Am. Nat.* 122: 618-625.

Veno, P.A. 1976. Successional relationships of five Florida plant communities. *Ecology* 57: 498-508.

Vogl, R.J. 1972. Fire in the southeastern grasslands. *Proc. Tall Timbers Fire Ecol. Conf.* 12: 175-198.

Waldrop, T.A., White, D.L. & Jones, S.M. 1992. Fire regimes for pine-grassland communities in the southeastern United States. *For. Ecol. Manage.* 47: 195-210.

Walker, J. & Peet, R.K. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55: 163-179.

Werner, P.A. & Platt, W.J. 1976. Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *Am. Nat.* 110: 959-971.

Whelan, R.J. 1986. Seed dispersal in relation to fire. In: Murray, D.R. (ed.) *Seed dispersal*, pp. 237-271. Academic Press, San Diego, CA.

White, A.S. 1983. The effects of thirteen years of annual prescribed burning on a *Quercus ellipsoidalis* community in Minnesota. *Ecology* 64: 1081-1085.

Wunderlin, R.P. 1982. *Guide to the vascular plants of central Florida.* University Presses of Florida, Tampa, FL.

Zomlefer, W.B. 1991. *Flowering plants of Florida: a guide to common families.* Biological Illustrations, Inc. Gainesville, FL.

Received 7 January 1998;
Revision received 26 October 1998;
Accepted 13 June 1999.
Coordinating Editor: D.E. Goldberg.