RESEARCH ARTICLE

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Fire Frequency Effects on Longleaf Pine (*Pinus palustris* P. Miller) Vegetation in South Carolina and Northeast Florida, USA

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ABSTRACT: Southeastern United States habitats dominated by longleaf pine (*Pinus palustris* P. Miller) have declined precipitously in area and extent. Conservation of diverse ground-layer vegetation in these endangered habitats depends on prescribed fire. While the need for prescribed fire is now generally accepted, there is disagreement concerning the most appropriate fire regime. One of the more important variables is frequency of fire. Several hypothetical relationships between fire frequency and vascular plant richness and composition are suggested by the existing literature. Results of two long-term prescribed fire studies support the hypothesis that burning as frequently as fuels permit is optimal for maintaining the largest number of native ground-layer plant species. However, fire frequency effects on species composition differed between the two studies. Increasing fire frequency in South Carolina Ultisol flatwoods and wet savannas was associated with a distinct shift from woody to herbaceous-dominated communities. Herbs, particularly bunchgrasses and perennial forbs, dominated annual- and biennial-burn treatment plots, whereas triennial- and quadrennial-burn plots were shrub-dominated. In contrast, annual and biennial fires did not produce herbaceous dominated ground-layer vegetation in North Florida Spodosol flatwoods. Reduced dominance of saw palmetto and somewhat increased importance of forbs and grasses, particularly rhizomatous grasses, distinguished the annually burned plots. However, biennial- and quadrennial-burn plots were similar in composition and did not differ significantly in species richness at the largest spatial scale.

Efectos de la Frecuencia del Fuego en la Vegetación de Pino de Hoja Larga (*Pinus palustris* P. Miller) en Carolina de Sur y el Noreste de Florida, USA

RESUMEN: Los hábitats del Sur de USA, dominados por el pino de hoja larga (*Pinus palustris* P. Miller) han declinado drásticamente en área y extensión. La conservación de capas diversas de vegetación en esos hábitats amenazados dependen del fuego recetado. Mientras la necesidad del fuego recetado está ahora generalmente aceptada, hay un desacuerdo acerca del régimen de fuego más apropiado. Una de las variables más importantes es la frecuencia del fuego. En la literatura existente se sugieren muchas relaciones hipotéticas entre la frecuencia del fuego y la riqueza de plantas vasculares y la composición. Resultados de dos estudios de largo término de fuego recetado, apoyan la hipótesis que la quema tan frecuente como sea posible es el óptimo para mantener el mayor número de plantas de especies nativas. No obstante, el efecto de la frecuencia del fuego en la composición de especies varió entre los dos estudios. El aumento de la frecuencia del fuego en los bosques de llanura Ultisol de Carolina del Sur y en las savanas húmedas estuvo asociado con un cambio distinto desde comunidades dominadas por leñosas a herbáceas. Las hierbas, particularmente pastos asociados ('bunchgrasses'), un 'forb' perenne, dominó las lotes tratados con fuego anual y bienal, mientras que los plots tratados con fuegos trienales y cuadrienales estuvieron dominados por arbustos. En contrate, los fuegos anuales y bienales no produjeron una vegetación dominada por herbáceas en los bosques llanos Spodosoles en el Norte de Florida. La disminución de la dominancia de 'saw palmetto' y el aumento de la importancia de 'forbs' y pastos, particularmente los rizomatosos, distinguieron los plots anualmente quemados. No obstante, los plots bienales y los cuadrienales fueron similares en composición y no difirieron significativamente en riqueza de especies a una gran escala espacial.

Index terms: fire frequency, fire regime, longleaf pine, *Pinus palustris*, prescribed burning

INTRODUCTION

Longleaf pine (*Pinus palustris* P. Miller) dominated woodlands and savannas are among the most species rich plant communities in North America (Bridges and Orzell 1989, Peet and Allard 1993). Unfortunately, these habitats are also highly endangered. Of an estimated 36 million ha of presettlement old-growth habitat, only about 3% remains in anything close to the original condition (Frost 1993). Fire exclusion is the primary factor responsible for the loss of longleaf pine habitat (Brockway and Lewis 1997). Historically, recurring low-intensity fires perpetuated longleaf pine savannas. In the absence of fire the diverse longleaf ground-layer vegetation, characterized by numerous grasses, forbs, and low shrubs, is replaced by a depauperate understory dominated by hardwood trees and large shrubs (Heyward 1939, Lemon 1949, Komarek 1974, Abrahamson and Hartnett 1990, Waldrop et al. 1992, Brockway and Lewis 1997).

The need for prescribed fire in management of longleaf pine dominated habitats

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is well established. However, numerous questions remain concerning the most appropriate burn regime and how that might vary among habitats and along environmental gradients. One important question concerns frequency of fire. Field observations and some experimental data tend to suggest that very short fire return times, that is, 1 to 3 y, are necessary to maintain species richness of longleaf ground-layer vegetation (Lewis and Harshbarger 1976, Komarek 1974, Walker and Peet 1983, Peet et al. 1983, Waldrop et al. 1992; see also Tester 1989, 1996 for similar results obtained in midwestern oak savannas). These studies also documented strong effects of fire frequency on vegetation composition. Generally, annual or biennial burning resulted in ground-layer communities dominated by grasses, albeit often with small shrubs and some forbs in a subdominant position. In contrast, less frequent or periodic fires tended to favor shrubs and woody sprouts, with reduced importance of grasses and forbs.

The studies cited above support what we will henceforth refer to as the "Most Frequent Fire Hypothesis" (MFFH) of longleaf pine ground-layer community management. This hypothesis suggests that burning as frequently as fuels will allow is the best strategy for maintaining species richness and composition of the native longleaf ground layer. At present, the MFFH forms the scientific basis of most current fire management in longleaf pine stands. It is, however, at variance with results of several recent publications as well as a popular hypothesis from plant community ecology theory. The "Intermediate Disturbance Hypothesis" (IDH; Connell 1978) postulates that highest levels of species richness in plant communities should occur at "intermediate" disturbance frequencies that allow persistence of both "early" and "late" successional species. Testing the IDH is difficult because of the difficulty of defining an "intermediate" fire frequency. From the theoretical point of view, an intermediate fire return interval would be defined relative to the extremes of fire return times naturally occurring in a particular habitat (Connell 1978). However, investigators attempting to test the IDH have generally defined "intermediate" relative to the range of fire frequencies that happened to be encompassed by their own studies (Collins et al. 1995, Beckage and Stout 2000).

Several recent prescribed fire studies, including three in southeastern pinelands, have challenged the validity of both the MFFH and IDH. Mehlman (1992), in a long-term study of old field loblolly pine (*Pinus taeda* L.) stands in north Florida (the Stoddard Fire Plots at Tall Timbers Research Station), found that increases in fire frequency were associated with increased species richness but only up to some threshold level. Additional analysis of Mehlman's (1992) data suggested that fire return intervals of about six years would be sufficient to maintain maximal levels of species richness in the Stoddard Plots and that more frequent burning would have little additional effect (Beckage and Stout 2000). We will henceforth refer to the hypothesis that fire effects tend to plateau or "saturate" as the Saturation Hypothesis (SH).

In addition to reanalyzing Mehlman's (1992) data, Beckage and Stout (2000) presented results of their own study of frequency of burning in central Florida sandhills. They were unable to detect a statistically significant effect of fire history on either species composition or species richness in these sandhill plots. Beckage and Stout (2000) acknowledged that this study, which was observational rather than experimental, lacked replication and statistical power, and therefore did not constitute a strong test of the IDH or the MFFH. The authors concluded that at least three treatment replicates would be needed to have at least a 50% probability of detecting a real fire frequency effect, whereas six replicates would be required for a statistical power of 0.8. As Beckage and Stout (2000) pointed out, few fire experiments, or observational studies, have anywhere close to this level of replication.

Brockway and Lewis (1997), in an experiment carried out in south Georgia longleaf pine–*Ilex glabra*–*Aristida beyrichiana* Trinius & Ruprecht–*Sporobolus curtissii* flatwoods (nomenclature follows Kartesz 1994 unless otherwise indicated), demonstrated major differences in composition and vascular plant species richness between burned and long-term unburned plots. However, differences among three fire frequency treatments, that is, annual, biennial, and triennial dormant-season burning, were relatively minor and, for the most part, not statistically significant ($P > 0.05$). An important point is that the fire frequency treatments in this study were carried out from 1942 to 1954 and that a period of 24 y elapsed between the termination of treatments and data collection in 1980. During the interval all the plots went unburned for 9 y and, when burning was resumed, the former annual, biennial, and triennial plots were all burned on a biennial schedule. There may well have been clear effects of the different frequency of burn treatments in 1954 that disappeared during the long interval prior to collection of data. This study was further hampered by low replication (n=2), making it even more difficult to detect a treatment effect.

Two recent studies in tallgrass prairie also challenged the MFFH and IDH. Collins et al. (1995) demonstrated a negative correlation between fire frequency and species richness. They suggested that too frequent burning might enhance the competitiveness of dominant grasses at the expense of forbs, thereby reducing rather than enhancing species richness. We will refer to this suggestion as the "Frequent Fire Species Loss Hypothesis" (FFSLH). Engle et al. (2000) did not, however, find this effect in "highly disturbed early successional prairie communities" in Oklahoma. In their experiment, differences in species composition and richness among treatment plots were related to edaphic factors and time since the last burn rather than the fire frequency treatments.

One problem in comparing results of these various studies is scale. For example, Mehlman (1992) and Beckage and Stout (2000) measured species richness on a relatively large scale, while Walker and Peet (1983) and Brockway and Lewis (1997) made their observations on a much smaller scale. Sampling over a range of spatial scales might help to resolve some inconsistencies.

We present results from two ongoing long-term studies that constitute a strong test of the MFFH and the various alternative hypotheses. The two studies were carried out in longleaf pine-dominated flatwoods (wet savannas were admixed at one of the locations), albeit in different geographic locations and with very different species compositions. Both studies were experiments with random treatment assignment and adequate replication (n=4 in one study, n=6 in the other) to detect any meaningful effects. The range of fire frequency treatments in these experiments (1- to 4-y fire return intervals) was not sufficient to elucidate the full relationship between fire frequency and species richness. However, it probably was sufficient to allow us to test for a "saturation" effect of the sort found in Mehlman's (1992) data or a negative effect of very frequent fire as found by Collins et al. (1995). Our sampling and analytical techniques also allowed for a test of scale effects on species richness.

METHODS

Tiger Corner Study

Francis Marion National Forest (FMNF) is located in the Atlantic Coastal Plain, just northeast of Charleston, South Carolina. In addition to the Tiger Corner Study, to be discussed herein, FMNF was the site of another long-term fire study, the well-known Santee Fire Study located at the Santee Experiment Station near Cordesville (Waldrop et al. 1992 and earlier publications cited therein). The Santee Study, which spanned the 43-y period between 1946 and 1989, was discontinued following Hurricane Hugo, a category 4 storm that came ashore in September 1989 and caused substantial canopy damage throughout much of the national forest.

The Tiger Corner study site is located approximately 4 km southeast of Jamestown, South Carolina, and 15 km northeast of the old Santee Fire Study plots. The experiment, ongoing since 1958, originally consisted of 20 0.8-ha plots arranged into four blocks of five plots each. Five experimental treatments were randomly assigned to plots within blocks. The treatments included fire frequencies ranging from annual to quadrennial as well as an unburned "control." One control and one triennial plot were lost to salvage operations following Hurricane Hugo in 1989. One plot assigned an annual burn treatment was so wet that it rarely burned; it was consequently excluded from the study. Numbers of treatment fires applied during the study period ranged from 44 for the annual plots to 11 for the quadrennials. Biennial plots burned 22 times and triennials were burned 14 times. Fires were generally administered in late winter, usually in February or early March. Wade et al. (1993) documented post-Hugo fire behavior in the plots.

The vegetation in the Tiger Corner plots can be classified according to Peet and Allard (1993) as Atlantic Longleaf Flatwoods with inclusions of Atlantic Mesic Longleaf Woodland, Atlantic Longleaf Savanna, and Longleaf Seepage Bog (see Peet and Allard 1993 for lists of species associated with each of these community types). Dominant Atlantic Longleaf Flatwoods species cited by Peet and Allard (1993) include *Pinus palustris, P. elliottii, P. serotina, Ilex glabra, Serenoa repens, Quercus pumila, Ilex coriacea, Cyrilla racemiflora, Myrica cerifera, Gaylussacia frondosa, Lyonia mariana, Pteridium aquilinum*, and *Aristida stricta*, "although not all the species occur throughout the range." In central South Carolina where our plots are located, *Pinus elliottii* is rare except in maritime vegetation and *Aristida stricta/beyrichiana* and *Serenoa repens* are absent. Instead, *Pinus taeda, Aristida virgata, Clethra alnifolia, Schizachyrium scoparium, Andropogon virginicus* var. *decipiens, Andropogon glomeratus, Vaccinium tenellum, Lyonia lucida, Lyonia ligustrina*, and *Arundinaria tecta* (Walt.) Muhl. are characteristic, dominant, or subdominant, flatwoods plants (Komarek 1974; Porcher 1995; E. Kjellmark, P. McMillan, R.K. Peet, J.S. Glitzenstein, D.R. Streng, unpubl. data). The combination of the lack of wiregrass and the admixture of bog and cane-break type shrubs within flatwoods is apparently unique to the outer Coastal Plain of central South Carolina. The Nature Conservancy (TNC) recognizes three globally rare South Carolina variants (i.e., associations in TNC terminology) of Atlantic Longleaf Flatwoods that are common in FMNF and comprise the majority of the vegetation in our Tiger Corner study plots (NatureServe Explorer 2001). These include (1) *Pinus palustris–Arundinaria gigantea* ssp. *tecta–Liquidambar styraciflua–Andropogon glomeratus–Sarracenia minor* Woodland (G1 global ranking), (2) *Pinus palustris–Clethra alnifolia–Gaylussacia frondosa–Quercus pumila–Schizachyrium scoparium* Woodland (G1 global ranking), and (3) *Pinus palustris–P. serotina–Ilex glabra–Lyonia lucida* Woodland (G3-G4 global ranking). Maintaining these globally rare associations could be considered a management priority despite their local abundance.

In the Tiger Corner study plots, longleaf pine is the dominant canopy tree in only one of the four blocks (mean canopy cover approximately 18%, vegetation sampling methods are discussed below). In the other blocks loblolly pine was the canopy dominant prior to Hurricane Hugo (in fact, that was one reason for blocking), but the hurricane decimated loblolly pine throughout much of FMNF (Sheffield and Thompson 1992), including at Tiger Corner. Presently, loblolly pine still dominates the canopy in a single block, though mean canopy cover is less than 10%. In one block loblolly and longleaf pines now co-dominate, each with less than 5% mean cover, and in the remaining block canopy dominance is split equivalently between longleaf, loblolly, and pond pines, all with less than 5% canopy cover. Despite these differences in pine species dominance, now much reduced due to Hurricane Hugo, similar mixtures of ground-layer communities occur in each of the blocks. This is indicated by the fact that Redundancy Analysis (RDA) ordination (this analytical technique will be discussed in detail below) failed to detect any statistically significant differences in species composition related to blocking ($F = 1.06$, $P = 0.46$, Monte-Carlo $n = 99$). The conclusion seems to be that current differences in pine species dominance among blocks are most likely related to logging history and perhaps fire history during the early phases of post-logging stand regeneration and do not indicate significant environmental differences. In all probability, longleaf pine was historically the dominant canopy tree on all the sites (Frost 1993). We therefore feel justified in classifying the plots as longleaf woodlands whether or not longleaf pine is presently the dominant canopy tree.

Soils in the Tiger Corner plots are Ultisols, primarily of the Lynchburg series (fine loamy, siliceous, thermic Aeric Paleaquult; see Binkley et al. 1992). Ultisols are soils characterized by a sandy surface soil overlying a loamy or clayey subsoil (i.e., an argillic horizon). Aquults are "Ultisols that occur in wet places where groundwater approaches the soil surface for large parts of most years" (Brown et al. 1990: 50). The clayey subsoil tends to retain moisture and nutrients during dry periods to a larger extent than in Spodosols where the argillic horizon is lacking (see discussion of Osceola study site soils below). This may account for the greater frequency of bog-type shrubs in Ultisol Flatwoods (Taggart 1990). A detailed study of soil nutrients at Tiger Corner found little effect of fire frequency treatments except in the control plots. In these plots only the fine fraction of the forest floor (Oe+, Oa horizons) was significantly enriched in carbon and nitrogen (Binkley et al. 1992).

We collected two types of data in the Tiger Corner plots. During 1992–1993 we sampled plant biomass from eight 0.25-m^2 locations within each of the 14 fire treatment plots (the "controls" were not sampled). Prior to sampling, we laid out a grid of 10-m x 10-m cells in each plot and measured elevation at each grid intersection using a laser-plane. This was done in an effort to control for the effect of elevation, which was assumed to be a surrogate for hydrology. Biomass was sampled in each plot from eight grid cell intersections randomly located within the same relatively narrow range of elevations (approximately 0.2 m). Biomass samples were sorted to species, dried, and weighed. Biomass was sampled in each plot at the end of the first growing season after burning so that results would not be confounded by time-since-burn effects.

During 2000–2001 we used the North Carolina Vegetation Survey (NCVS) (Peet et al. 1998) methodology to sample vegetation in the annual, biennial, and quadriennial burn plots (11 total plots). All plots but one were sampled during the first growing season after burning and the other plot was sampled early in the following growing season. Triennial plots were not sampled since they were not due to burn again until late winter 2002 (they will be sampled during the 2002-growing season). Controls also have not yet been sampled for either biomass or NCVS data. The negative consequence of long-term fire exclusion, that is, almost complete loss of characteristic longleaf ground-layer vegetation, is clearly evident in these plots even in the absence of data. Furthermore, effects of not burning are already well established by other studies, and lack of burning is not considered to be a valid management strategy in southeastern pinelands (see Introduction above; also Komarek 1974, Bridges and Orzell 1989, FNAI-FDNR 1990, Taggart 1990, Frost 1993, Peet and Allard 1993, Platt 1999). Lastly, fire frequency and time since burn effects are unavoidably confounded in the control plots. Thus sampling those plots has thus far been a low priority.

Fire treatment plots were subdivided into 20-m x 50-m (the size of an NCVS plot) sections and one section was randomly selected for sampling. NCVS data were collected following the procedures of Peet et al. (1998). The NCVS plot was itself subdivided into 10 10-m x 10-m "modules," and 4 contiguous modules in predetermined locations (the so-called "intensive modules") were sampled for cover and "level" data. Cover was estimated according to a semi-quantitative scale ranging from 1 (trace) to 10 (95%–100% cover). "Level" referred to the scale at which a species was first encountered. A series of nested plots was searched, beginning with the smallest (10 cm x 10 cm) and ending with the largest (10 m x 10 m). Species were assigned scores as follows depending on the scale at which they were first encountered: (5) 10 cm x 10 cm, (4) 32 cm x 32 cm, (3) 1 m x 1 m, (2) 3.16 m x 3.16, (1) 10 m x 10 m. Level data were collected at two of the corners of each intensive module. We summed the level data to provide an overall measure of abundance. Species not present in the intensive modules but present elsewhere in the 20-m x 50-m sample plot were assigned a total score of 0.5. For these "residual" species only, cover was estimated across the entire 20-m x 50-m plot.

A list of all the vascular plant species encountered in the Tiger Corner NCVS study plots is provided in Appendix A, available online at <http://www.talltimbers.org/research.html>. All plant species encountered in both long-term studies discussed herein were natives, with the exception of *Lespedeza cuneata*, which occurred at trace levels in a single Tiger Corner plot.

Osceola Study

Osceola National Forest (ONF) is in the Coastal Plain of eastern Florida, approximately 65 km west of Jacksonville. The long-term study plots are located along County Road 250A, about 6 km northeast of Olustee, Florida. This experiment consisted of 24 0.8-ha plots arranged in six blocks of four plots each. Treatments were the same as in the Tiger Corner study, except that there was no triennial burn treatment. The Osceola experiment was initiated simultaneously with the Tiger Corner experiment, and numbers of treatment fires were equivalent at the two sites. As at Tiger Corner, burns were typically carried out in late winter.

Vegetation in the Osceola plots can be classified primarily as Southern Longleaf Flatwoods (Peet and Allard 1993) with small inclusions of Southern Mesic Longleaf Woodland (see Peet and Allard 1993 for lists of indicator species characteristic of these communities). Using the FNAI-FDNR (1990) system, the prevailing vegetation would be classified as Mesic Flatwoods. *Serenoa repens* was the dominant understory species in all plots, with cover values generally exceeding 50%. The tree stratum was composed almost entirely of longleaf pine (mean canopy cover = 35%). Other common species in the plots considered characteristic of Southern Longleaf Flatwoods (Peet and Allard 1993) included *Myrica cerifera, Ilex glabra, Kalmia hirsuta, Vaccinium myrsinites,* and *Aristida beyrichiana*. *Quercus minima* and *Sporobolus curtissii*, two other common species in our Osceola plots, are important species of longleaf flatwoods communities in the north Florida–south Georgia region (FNAI-FDNR 1990; Streng et al. 1993; Brockway and Lewis 1997; E. Kjellmark, P. McMillan, and R.K. Peet, unpubl. data).

Soils in the Osceola study plots are Spodosols, primarily Leon sands (sandy siliceous thermic Aeric Haplaquod; see McKee 1982). Spodosols are sandy soils distinguished by a "spodic horizon", that is, "a subsurface zone in which organic matter in combination with aluminum and/or iron has accumulated due to downward leaching." Spodosols lack the clayey subsoil that is characteristic of Ultisols and consequently have somewhat poorer moisture and nutrient retention during dry periods. "Aquods are spodosols that are wet for extended periods in most years" (Brown et al. 1990). Perhaps due to the difference in soil orders, soil nutrient responses to fire appeared to differ between the two study areas. McKee (1982) reported generally higher soil nutrient concentrations in burned as compared to unburned plots at a variety of Coastal Plain locations, including our ONF study plots.

We did not collect biomass data from ONF. However, NCVS data were collected using the same methods as in the Tiger Corner Study. Once again, all burn treatment plots were sampled in the growing season following burns the previous winter. Controls were not sampled. A vascular plant species list for the ONF experiment is provided in Appendix B, available online at <http://www.talltimbers.org/research.html>.

Analyses

Effects of fire frequency on abundance of individual species (cover, level data) were analyzed using model I, two-way ANOVA as appropriate for a randomized blocks design (see Sokal and Rohlf 1969: 325). As it turned out, the two measures of abundance were highly correlated (Tiger Corner $r = 0.81$, $P = .000$, n = 1230; Osceola $r = 0.79$, $P = .000$, n= 787) and results of analyses were similar. Consequently, only the cover results will be presented herein.

Block and fire effects on species composition data were analyzed using redundancy analysis (RDA), available through the CANOCO software package (Ter Braak 1987-1992). RDA is closely related to PCA, a commonly used multivariate technique (Ter Braak 1995). Like PCA, RDA assumes linear relationships between species abundances and environmental gradients. Unlike PCA and other indirect ordination techniques, the ordination axes in RDA and other types of direct ordinations are "constrained" (this term will be explained below) to be linear functions of the independent variable(s). When combined with the Monte-Carlo randomization test included with CANOCO, RDA permits a direct statistical test of the effect of the independent variables on species composition. RDA is particularly useful for analyses of experimental data because experimental treatments typically produce unidirectional response patterns that meet the required assumptions of linearity. It is therefore recommended for analysis of vegetation experiments with large numbers of species (Ter Braak 1987-1992, 1995). MANOVA, the multivariate extension of ANOVA that would generally be used for such analyses, is useless when the number of dependent variables (species in an ordination analysis) exceeds the number of experimental units. Thus RDA can be viewed as a replacement for MANOVA when the limitations of the latter are exceeded (Ter Braak 1987-1992).

Since readers may be unfamiliar with PCA and RDA we will attempt a brief summary of the mathematical concepts underpinning these techniques. Readers wishing a fuller understanding of this topic are urged to consult Ter Braak (1995) or some other text in quantitative plant ecology.

PCA is easiest to conceptualize using a simple two-species system. Imagine a number of sites that are inhabited by two species that differ in abundance among the sites. If the x-axis represents the abundance of species-A and the y-axis represents the abundance of species-B then one can plot the location of each site using the abundance values for the two species. One can then draw a line through the cloud of data points in the direction of the greatest scatter or variance among the points (see Figure 5.13 in Ter Braak 1995). This line is the first principal component, or first "PCA axis" in ordination terminology. The first axis site scores are determined by extending a perpendicular from each point to the line. The two-dimensional variability among sites has now been reduced to a single dimension, albeit with some loss of information. If instead of two species we have many species, the concept is the same although impossible to visualize graphically. A single ordination axis will generally be inadequate to describe the variation in a multidimensional system and it will consequently be necessary to extract additional axes. The second and higher axes are located analogously to the first, except that they are oriented in the direction of the highest amount of residual variance that is orthogonal to (i.e., not correlated with) the axes already derived.

A PCA ordination axis, like any indirect ordination axis, is a purely mathematical entity that must be interpreted with reference to external data. For those of us who like to think in terms of real environmental effects, it is convenient to think of an indirect ordination axis as an underlying, but unknown, environmental gradient that influences species composition in some important way (Ter Braak 1995). Once the ordination is completed one is still, however, left with the task of determining which, if any, actual environmental gradients are represented by a particular ordination axis. RDA is an extension of PCA that attempts to circumvent this problem. It does so by inserting a regression step into the weighted summation iterative algorithm by which PCA attempts to extract the ordination axes (we will not attempt to explain how this algorithm works; interested readers are referred to Ter Braak 1995). In each cycle of the iteration, the site scores are regressed on the environmental (i.e., independent) variables and the predicted values from the regression are taken as the new site scores for the next iteration. Instead of searching for an axis associated with the maximal amount of remaining unexplained variance, this additional step forces the ordination solution to converge on an axis that is already related to the pre-selected independent variables.

In the case of our study, the only independent variable was fire frequency, that is, time between fires, so we were certain that the first ordination axis extracted by RDA would be related to this variable. Since the second and higher axes were not constrained by any independent variables, these axes were the same as would be derived through PCA with the qualification that they must be orthogonal to the first constrained axis. At this point there still remained the issue of statistical significance. As noted above, this is solved in CANOCO through a Monte-Carlo randomization procedure. The observed eigenvalue, a measure of the amount of explained variance for the first (i.e., constrained) axis was compared to eigenvalues obtained by ordinating artificially generated data wherein species and associated abundance data were randomly assigned to experimental treatments. If eigenvalues from 5 or fewer in 100 random permutations exceed the actual observed eigenvalue, the experimental treatment effect is considered to be significant at the 0.05 level.

Blocking in experiments can be accommodated in the CANOCO Monte-Carlo test by restricting permutations to plots within blocks (Ter Braak 1987-1992 refers to this sort of restricted permutation test as partial RDA). Altering the permutation test in this fashion is only justified if the block effect has been previously demonstrated to be statistically significant in its own right. As we noted above, this was not the case for the Tiger Corner Study, so the full or unrestricted Monte-Carlo test was employed for that study. In contrast, the block effect was significant for the Osceola plots (F = 2.15, P = 0.04, number of permutations = 99); thus the partial or restricted permutation test was justified for that analysis. Incidentally, the analysis of block effects at Osceola identified two groups of plots corresponding to different sections within the overall study area. Basically, the three southern blocks appeared to be compositionally distinct from the three northern blocks, for reasons that were not apparent but may have been related to some aspect of management history.

In summary, ordination output from CANOCO includes two sets of scores, site scores and species scores. Site scores were discussed above. Species scores are related to site scores and essentially indicate the contribution of each species to the placement of the ordination axis. Thus species with high scores on a particular axis are those that are strongly positively correlated with that axis. Treatment means, referred to as centroids, can be displayed in ordination space by averaging across sites receiving the same experimental treatments.

When interpreting ordinations, one ordinarily graphs the site and species scores onto the coordinate space defined by the major axes (Ter Braak 1995). Because of the large numbers of species at our two sites (Tiger Corner n = 278, Osceola n = 110), displaying ordination results of individual species was confusing and uninformative. Consequently, we divided species into 32 groups (see figure legends for Figures 1 and 4 and the appendices <http://www.talltimbers.org/research.html>) and averaged the species scores. Groups were based mostly on life form, life history (Godfrey and Wooten 1979, 1981), and comparative ecology (Taggart 1990, Peet and Allard 1993), but two families, Fabaceae and Orchidaceae, were recognized as separate groups due to their unique forms of nutrient acquisition and reproductive biology. Some groups consisted of only single species or genera—for example, PV = parastic vine (*Cuscuta compacta*), SP = shrubby palm (*Serenoa repens*), SG = shrubby grass (*Arundinaria tecta* [Walt.] Muhl.), TG = shade-tolerant grass (*Chasmanthium laxum*), SF = shrubby forb (*Baptisia tinctoria*), and BS = biennial shrub (*Rubus* spp.). Some species were included in more than one group (e.g., Herbaceous Vine + Fabaceae). Decisions about groupings and, to some extent, assignment of species to groups inevitably involved a certain amount of subjectivity. Readers wishing to display the results using their own groupings may do so by consulting the RDA species scores provided in Appendices A (Tiger Corner) and B (Osceola NF), available online at <http://www.talltimbers.org/research.html>.

Species richness data from NCVS plots were analyzed with model I two-way ANOVA appropriate for a randomized blocks experiment (see Sokal and Rohlf 1969: 325). Single degree of freedom polynomial contrasts were used to test for linear and second order trends, thereby evaluating the hypotheses discussed in the introduction. A significant increasing linear trend coupled with a nonsignificant second-order term would be consistent with the MFFH but not with any other hypothesis. In contrast, a significant quadratic contrast coupled with an insignificant linear contrast would be consistent with the IDH. Support for the FFSLH would come from a negative linear contrast. A complete lack of significance (i.e., no significant contrasts) might indicate the absence of any meaningful effect of frequency of burn on species richness. However, such an outcome might also be consistent with "saturation" at a longer fire return interval than the range encompassed by our studies. A final possibility, "saturation" at very short fire return times, would show up in our analyses as the combination of significant linear and quadratic contrasts.

RESULTS AND DISCUSSION

Species Composition

Tiger Corner Experiment

Significant ($P \leq 0.05$) effects of fire frequency on vegetation composition were evident at both study sites. However, the dominant mode of species composition variation in the cover data (2nd RDA axis, 1st unconstrained axis, 28.4% explained variance in the Tiger Corner RDA) was not a function of fire frequency. Instead, this axis (henceforth referred to as the "moisture axis") was clearly associated with soil moisture/hydrology. Species group FA (Fabaceae) was a good indicator. Almost without exception, ground-layer species in this family occur in mesic to dry habitats and not in wetter longleaf habitats (Taggart 1990, Peet and Allard 1993). In the Tiger Corner ordination, FA was located close to the lower end of the moisture axis (i.e., the left side of Figure 1C, henceforth referred to as the "dry end"). Other groups with a predominance of legumes—for example, HV (herbaceous vine), PF (prostrate forb), and SF (*Baptisia tinctoria*)—were also found toward the dry end of this axis. In contrast, SG (*Arun-*

dinaria tecta, switchcane) a dominant species of wet flatwoods and swamp ecotones in the outer South Carolina Coastal Plain (Komarek 1974), was a good indicator for the wet end of the moisture axis (right side of Figure 1C). Group GM (non-Poaceae graminoids, particularly wet savanna *Carex* and *Rhynchospora*) was another good wet end indicator.

The first RDA cover axis (y-axis in Figure 1), constrained to be a function of fire frequency, was the second most important in terms of percent of explained cover variance (17.7%). This axis clearly separated the Tiger Corner plots according to frequency of burn treatments. Quadrennial-burn plots were located toward the top of this axis and annual-burn plots were at the bottom. Biennial-burn plots occupied an intermediate position between the other two treatments, but tended to be more closely associated with the annual-burns than the quadrennial-burns (Figure 1A, note the locations of treatment centroids). According to the CANOCO Monte-Carlo test, the frequency of burn effect was marginally significant (F = 1.96, P = 0.06, n = 99 permutations).

The most obvious change in vegetation composition across the Tiger Corner fire frequency gradient was in the relative dominance of woody and herbaceous plants (Figure 1B). Woody species were clustered toward the low fire end of the gradient while herbaceous species predominated at the high end. This trend was evident in the biomass data as well (Figure 2B). Ordination trends may sometimes reflect relative rather than absolute changes for certain groups, but that was not the case for Tiger Corner. Absolute cover and biomass of woody plants declined substantially with increases in fire frequency while herbaceous species showed the opposite trend (Figures 2A, 3). Within the woody and herbaceous categories, most dominant

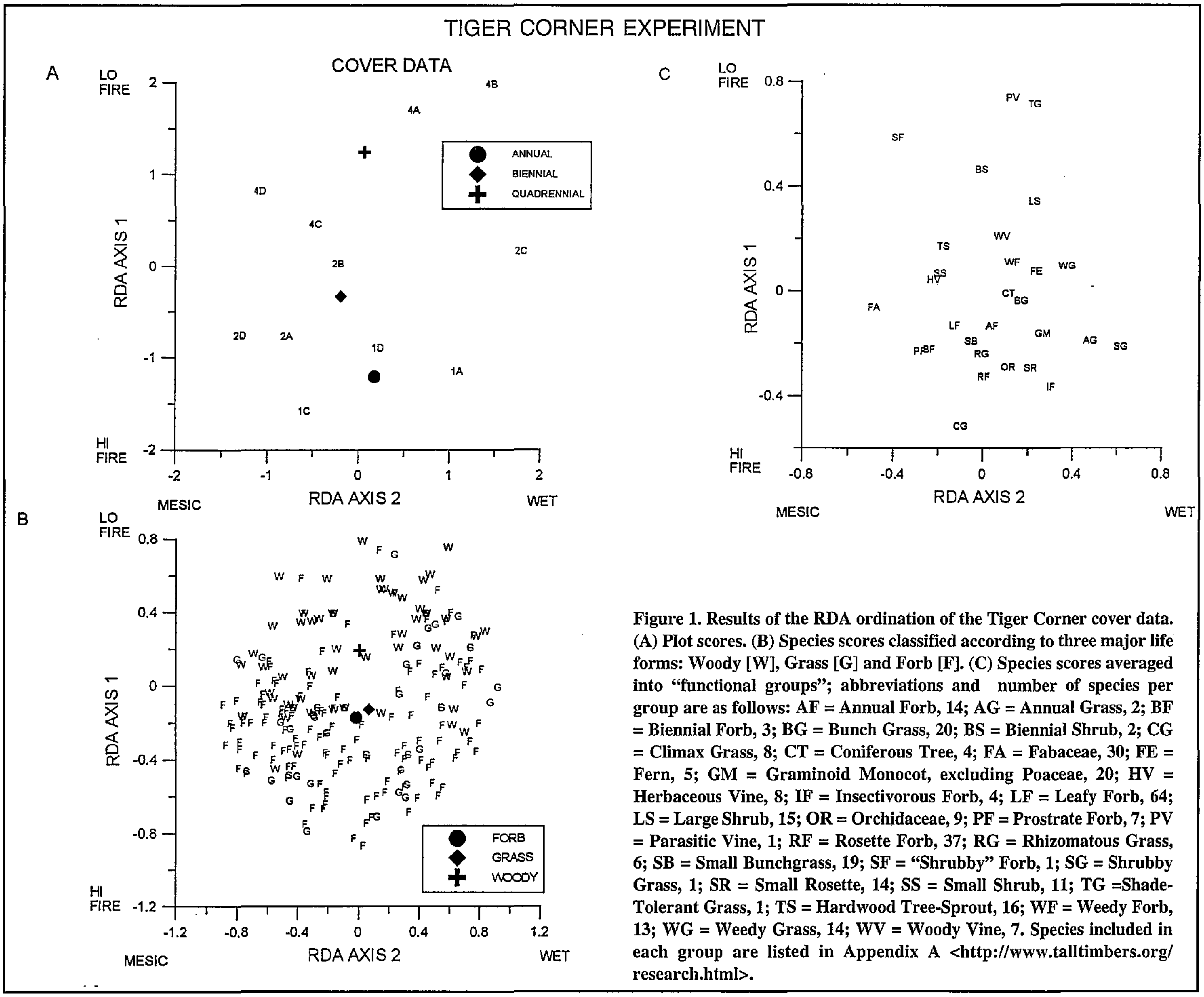

Figure 1. Results of the RDA ordination of the Tiger Corner cover data. (A) Plot scores. (B) Species scores classified according to three major life forms: Woody [W], Grass [G] and Forb [F]. (C) Species scores averaged into "functional groups"; abbreviations and number of species per group are as follows: AF = Annual Forb, 14; AG = Annual Grass, 2; BF = Biennial Forb, 3; BG = Bunch Grass, 20; BS = Biennial Shrub, 2; CG = Climax Grass, 8; CT = Coniferous Tree, 4; FA = Fabaceae, 30; FE = Fern, 5; GM = Graminoid Monocot, excluding Poaceae, 20; HV = Herbaceous Vine, 8; IF = Insectivorous Forb, 4; LF = Leafy Forb, 64; LS = Large Shrub, 15; OR = Orchidaceae, 9; PF = Prostrate Forb, 7; PV = Parasitic Vine, 1; RF = Rosette Forb, 37; RG = Rhizomatous Grass, 6; SB = Small Bunchgrass, 19; SF = "Shrubby" Forb, 1; SG = Shrubby Grass, 1; SR = Small Rosette, 14; SS = Small Shrub, 11; TG =Shade-Tolerant Grass, 1; TS = Hardwood Tree-Sprout, 16; WF = Weedy Forb, 13; WG = Weedy Grass, 14; WV = Woody Vine, 7. Species included in each group are listed in Appendix A <http://www.talltimbers.org/research.html>.

species showed similar, and statistically significant, trends (Figure 3).

In contrast to the different responses of woody plants and herbs, grass and forb species were distributed similarly with respect to fire frequency (Figure 1B). In fact, the centroids of these groups were in almost the same location in the ordination scatterplot.

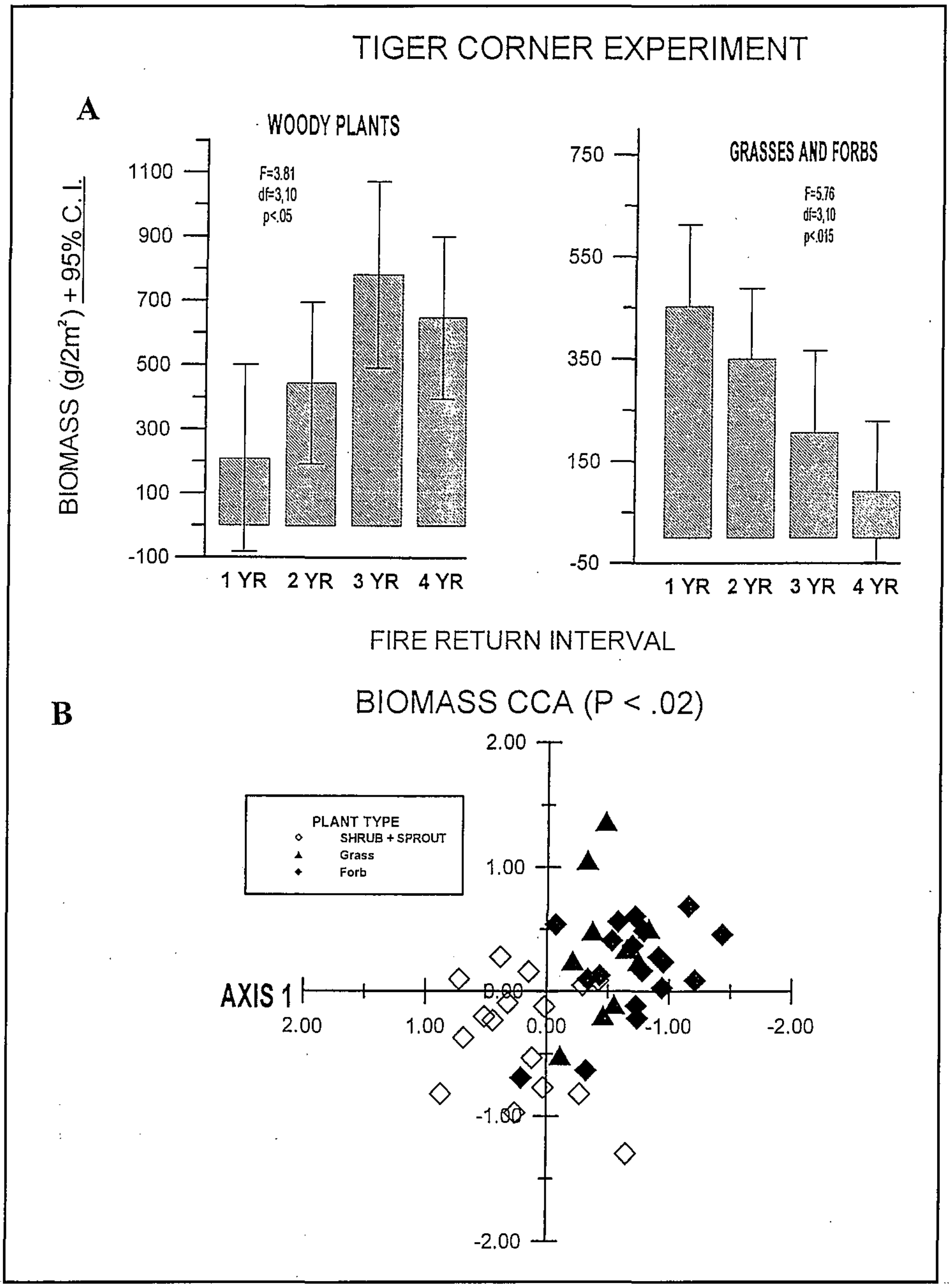

Figure 2. Effects of fire frequency on biomass composition in the Tiger Corner Study plots. (A) Absolute differences in woody and herbaceous biomass. ANOVAs include a block and treatment effect. Error degrees of freedom were reduced by two to account for two missing observations (Sokal and Rohlf 1969: 338): the annual plot that was too wet to burn and a triennial plot excluded due to salvage damage (see text). (B) CCA ordination scatterplot. Each symbol represents a single species. First axis is constrained to be a function of fire frequency. Moisture effects are reduced in this ordination because elevation, presumed to be a surrogate for hydrology, was explicitly controlled for when collecting the data (see text). CCA ordination is similar to RDA ordination discussed in the text but assumes unimodal rather than linear species responses to treatments. Similar results for the two types of ordinations and input data (i.e. biomass and cover) provide confidence that the fire treatment effect is indeed meaningful.

Centroid plots of finer groupings were a bit more interesting (Figure 1C). As would be expected, most of the woody plant groups occurred near the low fire frequency end of the fire axis (upper half of Figure 1C). *Rubus* spp. (group BS, biennial shrub) responded as typical for woody plants. In contrast, *Arundinaria tecta* (SG, shrubby grass) did not. This species occurred close to the high fire end of the fire frequency axis (bottom right of Figure 1C), suggesting considerable tolerance for even very frequent fires. This result is consistent with the observation that *Arundinaria* is, and was even in presettlement times, an important dominant of wetter fire-maintained pinelands in the Carolinas (Lawson 1709, Hughes 1966, Komarek 1974). Another interesting observation was the tendency for small shrubs (group SS), such as *Gaylussacia* spp., *Hypericum crux-andreae*, *H. galioides*, *Quercus pumila*, *Vaccinium tenellum*, to occur closer than the other woody plant groups (TS, LS, WV) to the high fire frequency end of the gradient. This finding is consistent with plant community surveys (Peet and Allard 1993) and results of other fire studies (e.g., Abrahamson 1984, Waldrop et al. 1992, Streng et al. 1993) in demonstrating that these small, mostly rhizomatous shrubs can be important components of frequently burned pinelands.

Most herbaceous groups were closely associated with the high end of the fire frequency gradient (Figure 1C). Group CG was particularly favored by very frequent fire. This group included "climax" or matrix grasses *Schizachyrium scoparium*, *Ctenium aromaticum*, *Muhlenbergia expansa* (Poir.) Trin., *Andropogon gerardii*, *Sorghastrum nutans*, *Andropogon virginicus* var. *decipiens*, and *Panicum virgatum*. These grasses are collectively characteristic of pristine soils in the outer Coastal Plain region of central South Carolina (Peet and Allard 1993; Porcher 1995; P. McMillan, J.S. Glitzenstein, D.R. Streng, and R.K. Peet, unpubl. data). Other groups appearing to be exceptionally favored by, or dependent on, frequent fire included rosette forbs (group RF), small rosettes (group SR; e.g., *Lachnocaulon anceps, Rhynchospora chapmanii*), insectivorous forbs (group IF, including *Sarracenia* spp., *Drosera* spp., *Pinguicula lutea)*, and Orchidaceae (group OR).

All herbaceous groups were not associated with frequent burning, however. One curious example was the parasitic forb *Cuscuta compacta* (PV = parasitic vine in the RDA ordination scatterplot). This genus lacks roots as mature plants and derives nutrition through haustorial connections with host plants. According to Godfrey and Wooten (1981), *C. compacta* has been shown to parasitize a fairly large number of host plants, many of which are common hardwood trees and shrubs of flatwoods and swamp ecotones (e.g., *Magnolia virginiana, Cyrilla racemiflora, Clethra alnifolia, Rubus* spp., *Myrica* spp.). We have observed it to be particularly abundant on sprouts 1–2 y after fire. Apparently it was favored in the quadrennial-burn plots by the greater density and vigor of hardwood sprouting.

Another herb associated with lower fire frequencies was the shade-tolerant grass *Chasmanthium laxum* (TG). This grass is found in a wide range of habitats from pine savannas and flatwoods through various types of closed woodlands and even hardwood bottomlands (Godfrey and Wooten 1979, Weakley 1999). Compared to most other Poaceae it appeared to tolerate and perhaps even prefer longer fire return intervals. On the drier end of the moisture gradient, the same could perhaps be said for (SF) *Baptisia tinctoria*. Based on its position in ordination space, this robust forb appeared to be more tolerant of less frequent fire than most other legumes. Ferns (group FE, including *Pteridium aquilinum, Osmunda* spp., and *Woodwardia* spp.), another shade-tolerant herbaceous group (Grime et al. 1988), also appeared to tolerate a somewhat reduced frequency of fire.

Last, and perhaps most unexpectedly, the groups WG (weedy perennial grasses) and WF (weedy forbs) were also associated, at least to a greater extent than most other herb groups, with the low end of the fire frequency axis. We hypothesize that these

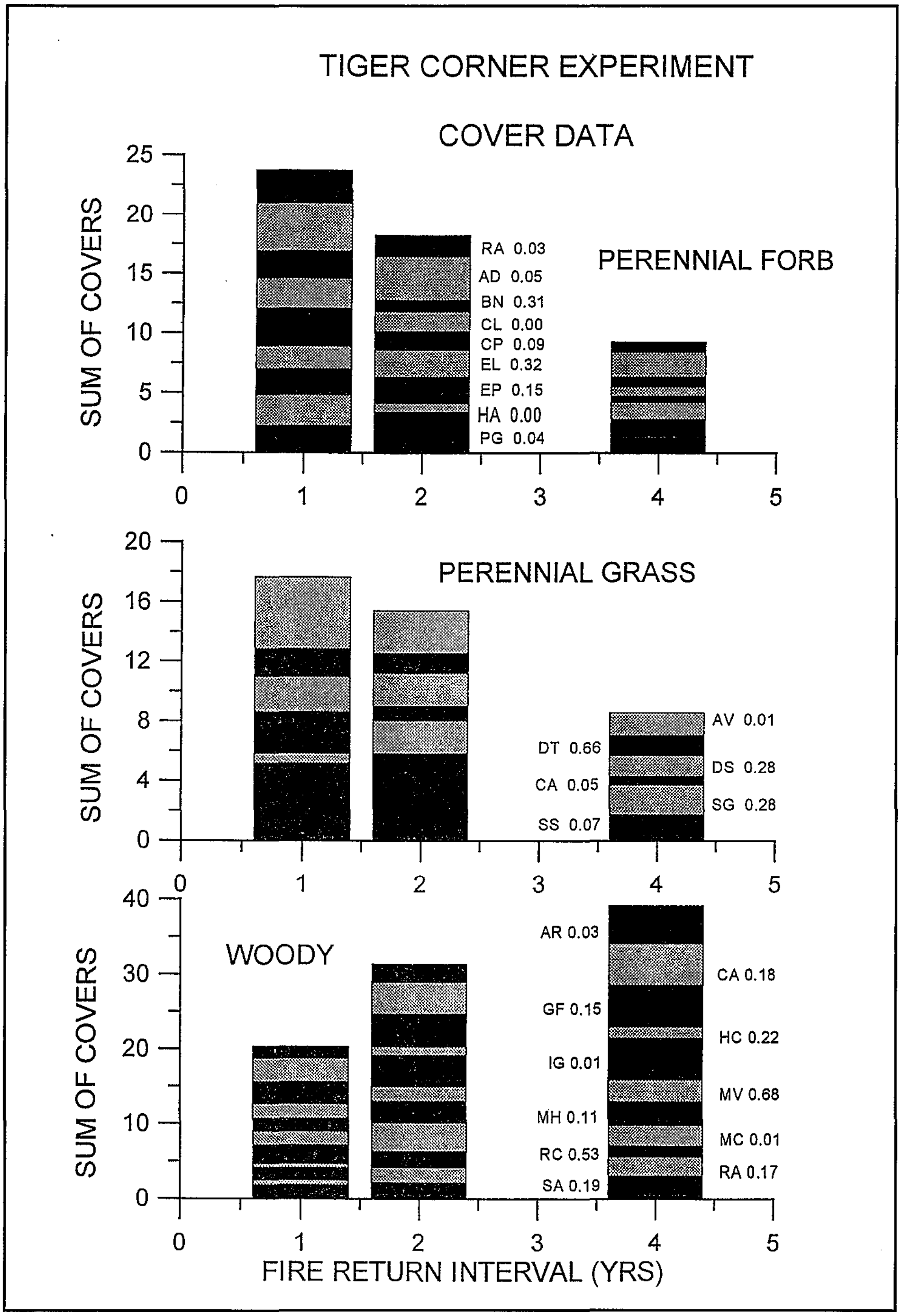

Figure 3. Effects fire frequency on individual and cumulative species cover scores in the Tiger Corner study plots. All species occurring in at least ten plots were included. Cover scores and associated cover ranges are as follows: 1 = trace, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, 10 = 95–100%. Note that the sum of cover scores for a particular plant category is not equivalent to plot cover for that category (e.g., sum of cover scores for woody plants is not equivalent to woody plant cover). Nevertheless, the sum of scores does represent an alternative unbiased indicator of the importance of a particular group in a plot. Species abbreviations: Woody: SA = *Sorbus arbutifolia* (L.) Heynh., RA = *Rubus argutus*, RC= *Rhus copallinum*, MC = *Myrica cerifera*, MH = *Myrica heterophylla*, MV = *Magnolia virginiana*, IG = *Ilex glabra*, HC = *Hypericum crux-andreae*, GF = *Gaylussacia frondosa*, CA = *Clethra alnifolia*, AR = *Acer rubrum;* Grasses: SS = *Schizachyrium scoparium*, SG = *Saccharum giganteum*, CA = *Ctenium aromaticum*, DS = *Dichanthelium strigosum*, DT = *Dichanthelium dichotomum* var. *tenue*, AV = *Andropogon virginicus* var. *decipiens;* Forbs: PG = *Pityopsis graminifolia*, HA = *Helianthus angustifolius*, EP = *Eupatorium pilosum*, EL = *Eupatorium leucolepis*, CP = *Carphephorus paniculatus*, CL = *Coreopsis linifolia*, BN = *Bigelowia nudata*, AD = *Aster dumosus*, RA = *Rhexia alifanus*. *P*-values from ANOVA tests are listed next to the species codes.

ruderal species may benefit from temporary windows of reduced competition in the less frequently burned plots. Such "windows" may open briefly when shrubs are temporarily damaged following higher intensity fires resulting from excessive fuel accumulations and less weedy herbs have been reduced or eliminated during several fire-free years.

A final interesting pattern in the Tiger Corner ordination data concerned a possible interaction between soil moisture and fire frequency. Moving from wet to dry across the moisture axis, there was some suggestion of increasing similarity in species composition between quadrennial and more frequently burned plots (Figure 1A). This may reflect the fact that most of the larger shrubs (e.g., *Lyonia lucida, Ilex glabra, Clethra alnifolia, Myrica cerifera*) were more prevalent toward the wetter end of the moisture gradient. With even minor reductions in burn frequency—for example, from biennial to quadrennial burning—these wet flatwoods shrubs increase greatly in cover (Figure 3) and biomass (Figure 2), in the process competitively excluding grasses and forbs. Toward the drier end of the moisture gradient, where large shrubs are less important due to edaphic restrictions, the ground-layer community may be able to tolerate longer intervals between fires without loss of species. Plant community differences related to fire history did appear to be more distinct in the wetter Tiger Corner plots. Annually and biennially burned plots on the "wet" end of the soil moisture gradient encompass some of the finest wet savannas in the FMNF while the less frequently burned triennial and quadrennial plots on similarly moist soils are shrub-dominated flatwoods.

Osceola Experiment

The dominant mode of variation in the

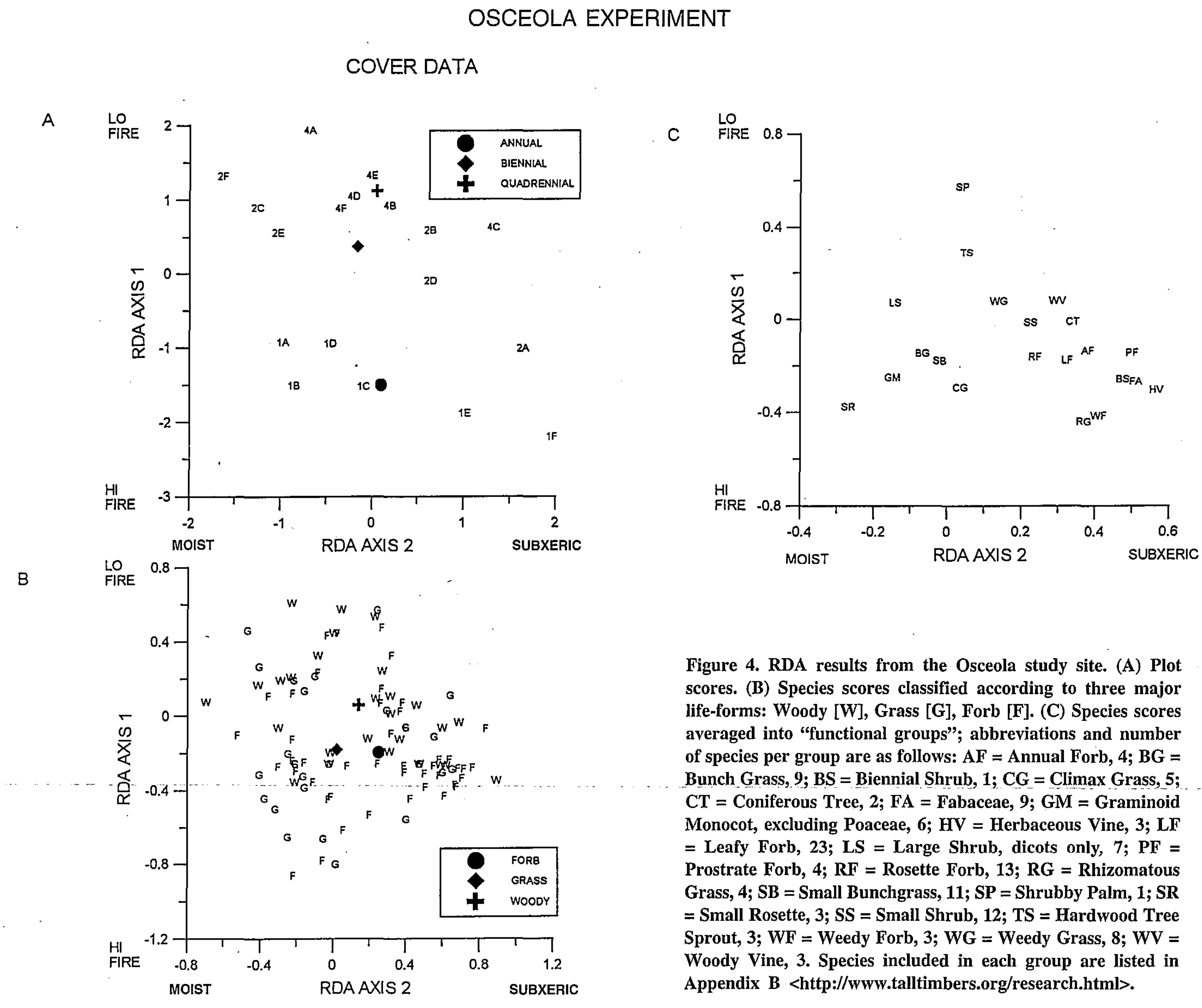

Figure 4. RDA results from the Osceola study site. (A) Plot scores. (B) Species scores classified according to three major life-forms: Woody [W], Grass [G], Forb [F]. (C) Species scores averaged into "functional groups"; abbreviations and number of species per group are as follows: AF = Annual Forb, 4; BG = Bunch Grass, 9; BS = Biennial Shrub, 1; CG = Climax Grass, 5; CT = Coniferous Tree, 2; FA = Fabaceae, 9; GM = Graminoid Monocot, excluding Poaceae, 6; HV = Herbaceous Vine, 3; LF = Leafy Forb, 23; LS = Large Shrub, dicots only, 7; PF = Prostrate Forb, 4; RF = Rosette Forb, 13; RG = Rhizomatous Grass, 4; SB = Small Bunchgrass, 11; SP = Shrubby Palm, 1; SR = Small Rosette, 3; SS = Small Shrub, 12; TS = Hardwood Tree Sprout, 3; WF = Weedy Forb, 3; WG = Weedy Grass, 8; WV = Woody Vine, 3. Species included in each group are listed in Appendix B <http://www.talltimbers.org/research.html>.

Osceola cover data (RDA axis 2, 1st unconstrained axis, 30.9% explained variance, x-axis in Figure 4) was again related to soil moisture rather than fire frequency. Again, groups FA (Fabaceae), HV (herbaceous vine), and PF (prostrate forb) were good indicators for the dry end of the moisture gradient (right side of Figure 4), while SR (small rosette) and GM (non-Poaceae graminoid monocot) helped to identify the wetter end. Group LS (large shrub), including moist flatwoods dominants *Ilex glabra* and *Lyonia fruticosa,* as well as shrub bog species *Ilex coriacea* and *Ilex myrtifolia,* also occurred close to the wet end of the Osceola moisture gradient. In addition to the group means, the identities of individual species found at the opposite ends of the gradient suggested moisture differences as the explanation. The six species with the lowest RDA second axis scores included moist/mesic flatwoods indicators *Ilex glabra, Rhynchospora plumosa, Aristida spiciformis,* and *Andropogon glaucopsis* Elliott (Godfrey and Wooten 1979, 1981; FNAI-FDNR 1990; Peet and Allard 1993; Streng et al. 1993). At the other extreme, the six species with the highest scores on this axis included dry flatwoods/sandhill species *Quercus minima, Cnidoscolus stimulosus, Elephantopus elatus, Aster walteri, Sericocarpus tortifolius* (Michx.) Nees, and *Tephrosia hispidula* (FNAI-FDNR 1990, Peet and Allard 1993, Streng et al. 1993).

The RDA ordination identified frequency of burn as the second most important influence on vegetation composition in the Osceola study plots. Axis 1 (y-axis in Figure 4), constrained to be a function of fire frequency, accounted for 21.8% of the species variance and was statistically significant (Monte-Carlo F = 3.07, $P = 0.02$). As at Tiger Corner, quadrennial-burn and annual-burn plots were at opposite ends of the fire frequency axis. Biennial-burn plots again occupied an intermediate position, but here, unlike the Tiger Corner ordination, they were more closely associated with, and tended to overlap, the quadrennial-burn plots (Figure 4A).

Distributions of species groups across the Osceola fire frequency axis were perhaps deceptively similar to Tiger Corner. Woody

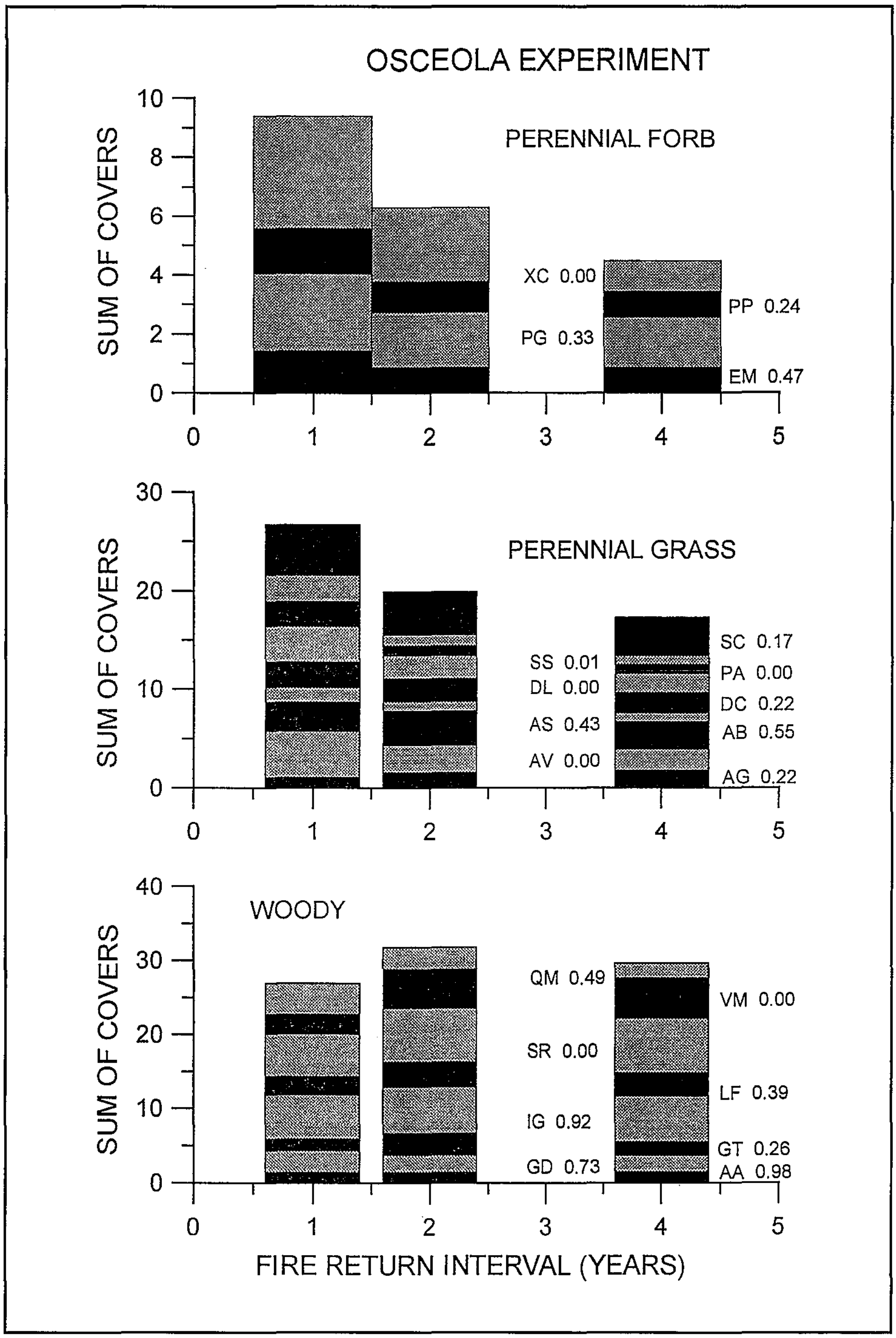

Figure 5. Effects of frequency of fire on individual and cumulative species cover scores in the Osceola study plots. All species occurring in at least 16 plots were included. Cover scores and associated cover ranges are as follows: 1 = trace, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, 10 = 95–100%. See note in the legend for Figure 3 concerning interpretation of sum of cover score measurements. Species abbreviations: Woody: AA = *Asimina angustifolia*, GD = *Gaylussacia dumosa*, GT = *Gaylussacia tomentosa* (Gray) Pursh *ex* Small, IG = *Ilex glabra*, LF = *Lyonia fruticosa*, SR = *Serenoa repens*, VM = *Vaccinium myrsinites*, QM = *Quercus minima;* Grasses: AG = *Andropogon glaucopsis* Elliott, AV = *Andropogon virginicus* var. *decipiens*, AB = *Aristida beyrichiana* Trinius & Ruprecht, AS = *Aristida spiciformis*, DC = *Dichanthelium chamaelonche (=Panicum chamaelonche* Trin.), DL = *Dichanthelium portoricense* (Desv. *ex* Ham.) B. F. Hansen & Wunderlin, PA = *Panicum anceps* var. *rhizomatum* (A. S. Hitchc. & Chase) Fern., SS = *Schizachyrium stoloniferum*, SC = *Sporobolus curtissii*; Forbs: EM = *Eupatorium mohrii*, PG = *Pityopsis graminifolia*, PP = *Pterocaulon pycnostachyum* (Michx.) Ell., XC = *Xyris caroliniana*. *P*-values from ANOVA tests are listed next to the species codes.

plants and herbs were again clustered in opposite halves of the ordination graph, woody plants associated with less frequent fire, herbs the reverse (Figure 4B). However, an examination of absolute cover values revealed an important difference between the two sites. At Tiger Corner, changes in fire frequency were associated with absolute changes in cover and biomass of both woody and herbaceous species. At Osceola, in contrast, total woody cover and mean cover values for dominant woody species were relatively unaffected by frequency of fire (Figure 5). The one exception was *Serenoa repens*, which had significantly lower cover scores in the annually burned plots. Overall, however, differences in relative abundance of woody and herbaceous species suggested by the ordination results were due primarily to effects of fire frequency treatments on herbaceous cover. Furthermore, increases in herbaceous cover were most evident in the annually burned plots. The obvious inference is that decreased saw palmetto cover associated with annual burning opened up space for herbs.

Differing responses of plant groups to fire frequency are indicated by the graph of group centroids in RDA ordination space (Figure 4C). Herbaceous groups that appeared to benefit especially from high fire frequencies included rhizomatous grasses (group RG), such as *Panicum anceps* var. *rhizomatum* (A. S. Hitchc. & Chase) Fern., *Schizachyrium stoloniferum*, and *Ctenium floridanum*; small rosettes (group SR, this group included some sedge species that were technically small bunches rather than true rosettes), *Hypoxis juncea, Rhynchospora plumosa*, and *Lachnocaulon anceps*; and, in contrast to Tiger Corner, weedy forbs (group WF), such as *Diodia teres, Euthamia minor* (Michaux) Greene. Climax grasses (group CG, defined in this context as matrix grasses of high quality East Gulf Coastal Plain flatwoods; Peet and Allard 1993) were also favored by frequent fire, but not to the same extent as at Tiger Corner. Wiregrass (*Aristida beyrichiana*), expected to dominate the herbaceous layer in eastern Florida longleaf pine woodlands (Peet and Allard 1993), showed little response to frequency of burning (Figure 5). A possible explanation may be that sexual reproduction and hence population growth of this important grass may have been limited by the lack of growing-season fires (see Streng et al. 1993).

As expected from mean cover scores (Figure 5), *Serenoa repens* (group SP) was closely associated with the low fire end of the Osceola burn frequency axis. Other woody plant groups were also associated with this end of the fire gradient, though to a lesser extent than *Serenoa*. Small shrubs (group SS, e.g., *Quercus minima, Q. pumila, Vaccinium myrsinites, V. stamineum, Hypericum microsepalum, Gaylussacia* spp.) once again appeared to be more tolerant of closely spaced fires than did other groups of woody plants, but the difference between LS and SS was narrower than at Tiger Corner. A similarity with Tiger Corner was the relative proximity of WG (weedy bunchgrasses) to the low fire frequency end of the gradient, a result that was discussed earlier.

Finally, there was some indication of the same sort of interaction between fire frequency and soil moisture noted earlier in the Tiger Corner ordination results. Once again, species composition of plots burned at different frequencies appeared to converge to some extent at the dry end of the soil moisture gradient (Figure 4A).

Rare Species

Effects of fire frequency on globally rare plants or endangered species are of special interest to conservation. Two such species occurred in our study plots. *Pteroglossaspis ecristata* (spiked-medusa orchid, Nature Conservancy G-Rank = 2) was confined to a single biennial burn plot in the Tiger Corner Study. During the survey of this plot in autumn 2000 we observed seven flowering stems of this plant in or around the NCVS plot located within burn treatment plot 2A. Though small, this is one of the largest concentrations of this species in the FMNF (J. Glitzenstein, pers. obs.; also J. Townsend, former curator of Clemson Herbarium, pers. com.). Presence of a species in a single plot is not an adequate sample with which to speculate about fire frequency effects. However, most observations of this species range-wide are consistent with its occurrence in frequently burned flatwoods or mesic savannas (Weakley 1999).

Asclepias pedicellata (stalked milkweed), another globally rare plant (Nature Conservancy G-Rank = 3) occurred in all annual and quadrennial NCVS sample plots at the Osceola study site. However, the species was present in only three of six biennial burn plots. Given the sparse distribution of this plant (overall mean cover < 1%), lower occurrence rates in the biennial-burn treatment plots are probably of little consequence. However, its occurrence in all of the quadrennial plots suggests that it may be more tolerant of longer interval fires than many forb species (Appendix B <http://www.talltimbers.org/research.html>). Careful demographic monitoring is needed to better document responses to variable fire regimes of these and many other rare plants (e.g., Kirkman et al. 1998).

Species Richness

Plots of species richness versus fire frequency were, for the most part, consistent with the MFFH (Figures 6A, B). At both sites, species richness tended to increase linearly with decreasing fire return times, and this pattern was observed across a variety of spatial scales. Predictions of the other hypotheses were not supported. Species richness did not peak at intermediate fire frequencies as predicted by the IDH, there was no evidence of a "saturation effect," and species richness was not highest at the longest fire return interval as predicted by the FFSLH. Our results were, however, consistent with the observations of Beckage and Stout (2000) in one important respect. At both Tiger Corner and Osceola the *P*-value indicating the strength of the statistical relationship between fire frequency and species richness decreased noticeably with spatial scale (Figures 6A, B). In fact, at both sites, the linear contrast for the largest plot size (1000 m^2) fell short of significance at the 0.05 level (Tiger Corner $P = 0.11$, Osceola $P = 0.29$). Thus, our results at this largest scale of measurement were similar to Beckage and Stout's (2000) findings for their sandhill study, which were based on a similarly large plot size (500 m^2).

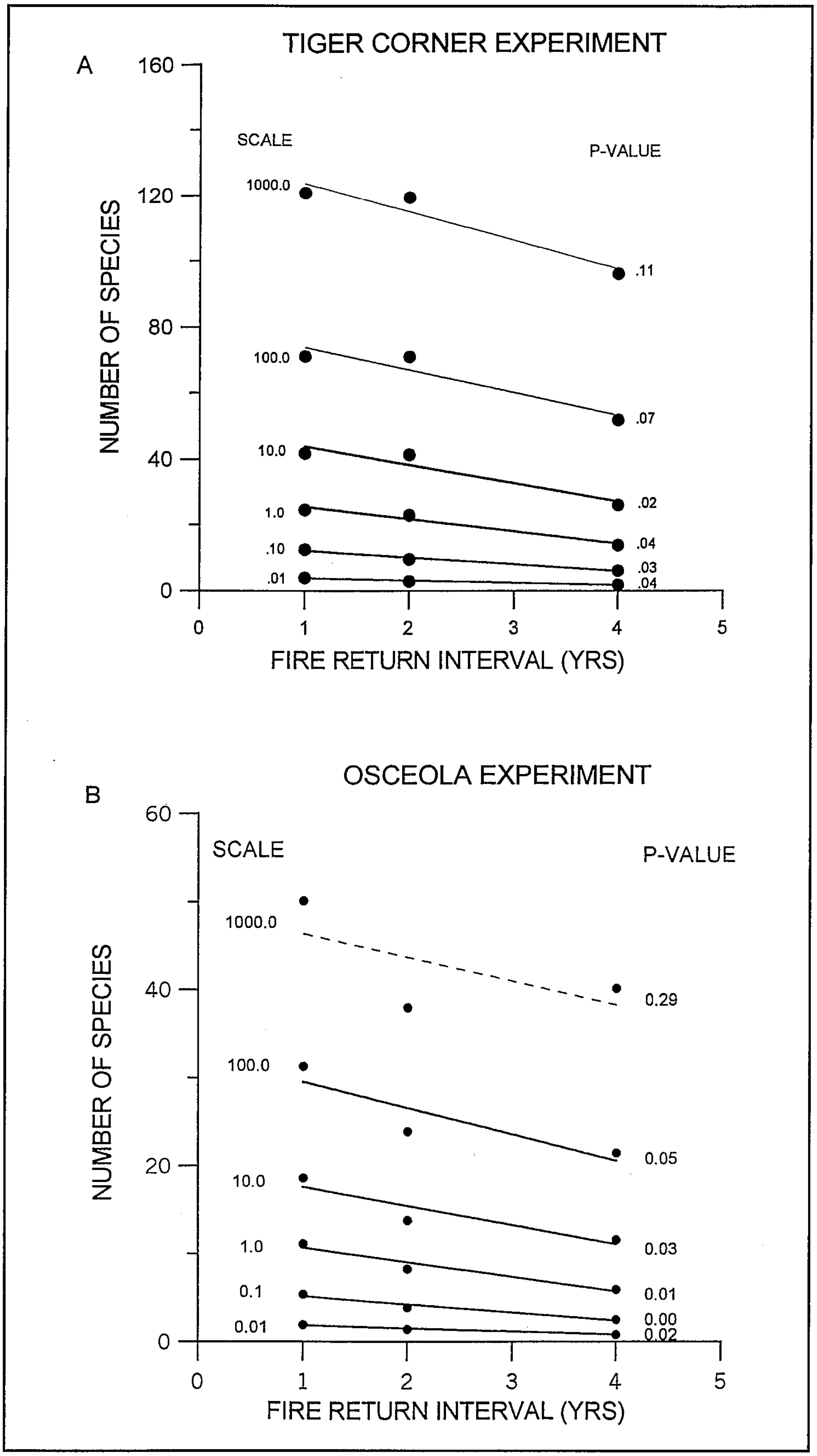

Figure 6. Species richness curves for the (A) Tiger Corner and (B) Osceola studies. *P*-values of single degree of freedom linear contrasts are shown to the right of each fitted line. Each point represents an average of all data collected at the scale in square meters indicated to the left of the line.

We tentatively conclude, therefore, that decreases in longleaf ground-layer species richness with less frequent burning are more evident at smaller spatial scales. A critical issue is therefore whether this buffering capacity, as we might refer to it, at a large scale is likely to be a stable feature of these habitats or represents instead an ephemeral condition. We suspect that it is ephemeral and is due to patchiness in the rate at which large woody species become established and displace other ground-layer plants. Thus, we hypothesize that reductions in species richness related to reductions in fire frequency appear first at small scales and are then translated to increasingly larger scales, leading ultimately to community scale and even landscape scale declines in biodiversity. An alternative hypothesis is that patches of habitat suitable for herbs and small shrubs may be consistently generated at longer fire return intervals, though these patches may make up a smaller proportion of the total area then would be the case with more frequent burning. Repeated sampling over time in the same plots will be necessary to discriminate between these two hypotheses.

DISCUSSION AND CONCLUSIONS

Our results overall strongly supported the MFFH and will perhaps serve to further emphasize to ecologically oriented land managers the need for short interval burns in southern pinelands. This conclusion is consistent with the findings of the Santee Study (Waldrop et al. 1992) which, together with our own results, would appear to constitute the best available information on this topic. Annual and biennial burns also produced the finest quality, most species-rich wet savanna communities in the renowned Green Swamp area of North Carolina (Walker and Peet 1983) and in numerous sites sampled by Taggart (1990). Our ONF results suggest that long-term annual burning, particularly during restoration, may be necessary in systems dominated by highly fire-tolerant shrubs such as *Serenoa repens*.

Before concluding, however, we would like to advance a few caveats and suggestions for future research. Perhaps the most important caveat is that before prescribing any particular fire regime, managers need to consider the conservation priorities at their own site. For example, if one is managing a rare shrub (e.g., *Elliottia racemosa, Stachydeoma graveolens, Fothergilla gardenii, Lindera melissifolia*), quadrennial burning in late winter may be a perfectly appropriate management strategy. The same may apply to rare shrub-dominated communities. For example, two locally abundant but globally rare FMNF flatwoods communities (*Pinus palustris–Clethra alnifolia–Gaylussacia frondosa–Quercus pumila–Schizachyrium scoparium* Woodland Association and *Pinus palustris–P. serotina–Ilex glabra–Lyonia lucida* Woodland Association) in the Tiger Corner plots may be threatened over the long term by long-term annual and biennial fires. If maintaining these shrub-dominated associations is considered to be an important management priority, it might be helpful to set aside certain sections of FMNF for slightly longer interval burns.

A second important caveat is that we need to recognize that most fire frequency experiments in longleaf pine communities, including our own, have been carried out in flatwoods. Flatwoods, by definition, are communities with a strong shrub component or, at least, environmental conditions conducive to shrub invasion (Abrahamson and Hartnett 1990). Reducing fire frequency, even slightly, stimulates sprouting and vegetative proliferation of shrubs, reducing space available for herbaceous plants and decreasing species richness (Waldrop et al. 1992, Brockway and Lewis 1997). It is therefore not surprising that data collected in flatwoods are consistent with the MFFH.

In contrast to the various studies of flatwoods, Beckage and Stout (2000) is the only fire frequency study that we know of that focused on drier longleaf pine habitats. Despite the limitations of that study, straightforwardly acknowledged by the authors themselves, the results are interesting. In contrast to flatwoods, sandhill longleaf pine forests typically lack an understory of dense shrubs, although an understory-midcanopy layer of "scrub" oaks (e.g., *Quercus laevis, Q. incana*) is present either as sprouts or small trees. With reductions in fire frequency the scrub oaks get larger but, being more widely spaced, they may not be as effective as flatwoods shrubs in competitively excluding herbs. Based on our own field experience, and results from the dry end Tiger Corner and Osceola plots, we tend to agree with Beckage and Stout (2000) that sandhills may be less sensitive to variations in fire return intervals than are flatwoods.

In addition to drier longleaf pine sites, some studies have suggested that wet savanna sites and the species therein may also be less sensitive than flatwoods to longer fire return intervals (Streng and Harcombe 1982, Brewer 1999). The data from this study, however, do not support this hypothesis. Most groups of wet savanna indicator species, such as small rosette forbs and sedges, Orchidaceae, and insectivorous plants, were amongst the most sensitive to reductions in fire frequency. Brewer (1999) criticized previous studies as not providing truly conclusive evidence of the need for annual or biennial fires for maintenance of *Sarracenia* populations. Our results, involving long-term randomly applied burn treatments and observations standardized for time-since-burn effects, appear to avoid most of Brewer's (1999) criticisms. Perhaps our disagreement can be resolved when we consider that Brewer's (1998, 2002) own studies indicate that dominant flatwoods shrubs such as *Ilex glabra* can invade pine savanna habitats under certain circumstances. Furthermore, Brewer (2002) acknowledged that reduced fire frequency is one of several factors that may facilitate invasion of flatwoods shrubs into bogs and wet savannas. It therefore seems reasonable to hypothesize that lower fire frequencies maintained over several decades, as in our study, might gradually lead to conversion of wet grass-dominated savannas into wet shrub-dominated flatwoods. This is a likely scenario in our Tiger Corner study plots since most of the wet savanna patches occur along ecotones or in small inclusions within the flatwoods. Hurricanes such as Hugo might accelerate the conversion of savannas to flatwoods by increasing the area and rate of natural soil disturbances including tip up mounds and high intensity fires associated with fuel accumulations (Wade et al. 1993). Brewer (2002) experimentally demonstrated increased rates of *Ilex glabra* seedling appearance in small artificially generated soil disturbances, and the same phenomenon presumably occurs in natural disturbances. Thus hurricanes and reductions in fire frequency may interact to promote establishment and growth of shrubs in wet savanna habitats. Increasing competition from shrubs might then lead to substantial reductions in abundance and diversity of wet savanna herbs, such as we observed at Tiger Corner.

One conclusion from the above discussion is that cross-habitat comparisons of fire frequency treatments would appear to be a profitable area for future research (see also Liu et al. 1997). Even within flatwoods communities, comparisons across geography and soil formations may be of interest. Comparisons of Tiger Corner and Osceola data, along with results of other studies, strongly suggest that Spodosol Flatwoods and Ultisol Flatwoods respond differently to the same fire frequency treatments. Fire frequencies (i.e., annual, biennial burns) that produced herbaceous dominated communities in Ultisol flatwoods (Santee Study, Tiger Corner Study, Brockway-Lewis Study) had little effect on shrub cover in Spodosol flatwoods (Osceola Study). Biennial burning, regardless of burn season, has also not reduced biomass of dominant flatwoods shrubs in the long-term St. Marks season-of-burn study (J.S. Glitzenstein, D.R. Streng, unpubl. data). Flatwoods plots in the St. Marks Study are also located on Spodosols. It would appear that, on the whole, shrubs on Spodosols are more tolerant of closely spaced fires (see also Taggart 1990). This hypothesis is consistent with other observations that woody plants on coarser textured soils are generally more resistant to stress. For example, as climate becomes limiting in Oklahoma and central Texas, eastern trees and shrubs become restricted almost entirely to sandy soils (Costello 1969).

Given that we accept the MFFH, a related issue concerns fire season. Prior to the arrival of humans in North America it is probable that most fires in southeastern longleaf pine woodlands, ignited by lightning associated with thunderstorms, occurred during the growing season (May–September; Komarek 1968). Thus, the growing season is the "natural" fire season to which, presumably, most native plants have adapted. It is also true that humans have been burning during the fall and winter for hundreds, if not thousands of years, and that these human-started fires covered large areas of the landscape (Lawson 1709, Elliott 1816-1824). Plants not also adapted to this anthropogenic fire season would long since have been selected out of existence. It is not within the scope of this paper to take sides in the issue of growing- versus dormant-season fire (see Streng et al. 1993). We merely note, as has been noted previously by others (Waldrop et al. 1992, Brockway and Lewis 1997), that frequent dormant-season fires can be used to maintain species-rich and apparently high quality longleaf pine ground-layer in a variety of habitat types. Of this there is no doubt. It may be desirable to switch from dormant-season burning to growing-season burning while maintaining an equally high fire frequency (e.g., growing-season burns may have more effectively promoted establishment of wiregrass and other dominant bunchgrasses in our Osceola plots). However, managers should be aware that reducing fire frequency or area burned in order to burn at a more "natural" season is likely to be a risky strategy.

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