

PRODUCTIVITY AND SPECIES RICHNESS ACROSS AN ENVIRONMENTAL GRADIENT IN A FIRE-DEPENDENT ECOSYSTEM¹

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The fire-dependent longleaf pine–wiregrass (*Pinus palustris* Mill.–*Aristida beyrichiana* Trin. & Rupr.) savannas of the southeastern United States provide a unique opportunity to examine the relationship between productivity and species richness in a natural ecosystem because of the extremely high number of species and their range across a wide ecological amplitude (sandhills to edges of wetlands). We used a natural gradient to examine how plant species richness and plant community structure vary with standing crop biomass (which in this system is proportional to annual net productivity) as a function of soil moisture and nitrogen mineralization rates in a frequently burned longleaf pine–wiregrass savanna. Highest ground cover biomass and highest species richness were found at the same position along the gradient, the wet-mesic sites. Relative differences in species richness among site types were independent of scale, ranging from 0.01 m² to 100 m². Nitrogen availability was negatively correlated with species richness. Dominance of wiregrass (in terms of biomass) was consistent across the gradient and not correlated with species richness. Regardless of site type, the community structure of the savannas was characterized by many perennial species with infrequent occurrences, a factor in the low temporal heterogeneity (percent similarity between seasons and years) and high within-site spatial heterogeneity (percent dissimilarity of vegetation composition). The coexistence of numerous species is likely due to the high frequency of fire that removes competing hardwood vegetation and litter and to the suite of fire-adapted perennial species that, once established, are able to persist. Our results suggest that soil moisture is an important factor regulating both the number of species present and community production within the defined gradient of this study.

Key words: *Aristida beyrichiana*; *Aristida stricta*; longleaf pine; *Pinus palustris*; plant diversity; productivity; resource gradient; species richness; wiregrass.

Mechanistic explanations of the relationship between species richness and productivity have been controversial, and predictions of conditions that produce monotonic or unimodal patterns remain unresolved (see reviews in Huston, 1994; Abrams, 1995; Waide et al., 1999). Although numerous empirical studies have been conducted to examine the effects of resource additions or disturbance regimes on species richness (Laves, Gilbert, and Masters, 1882; Milton, 1940; Silvertown, 1980; Wilson and Tilman, 1991; Collins and Steinauer, 1998; and many others; see Huston, 1994), difficulties arise in applying generalized theoretical models to patterns in natural environments because patterns may be scale-dependent (Waide et al., 1999). Few studies of productivity–species richness patterns in extremely species-rich communities have been conducted across natural resource gradients, particularly at scales intermediate between small plots and continents or within vegetation types (Abrams, 1995). Weiner (1995) has argued that examination of patterns at a local level is an essential first step

in generating testable hypotheses regarding the basis of a species diversity gradient. In this study, we examine the productivity–species richness relationship and spatial heterogeneity of species distributions in one of the most diverse temperate ecosystems (Peet and Allard, 1993): the *Pinus palustris* Mill.–*Aristida beyrichiana* Trin. and Rupr. (longleaf pine–wiregrass) savanna.

The fire-dependent longleaf pine–wiregrass savannas of the southeastern USA provide a unique opportunity to examine the relationship between productivity and species richness in a natural ecosystem, not only because of the extremely high number of species in the ground cover (Drew, Kirkman, and Gholson, 1998), but also because of its wide ecological amplitude (sandhills to edges of wetlands). In this system, prescribed fire every 2–3 yr is a large-scale disturbance that decreases the abundance of competing hardwoods and removes litter accumulations.

Although longleaf pine–wiregrass communities may have greater annual net aboveground productivity and an obvious difference in biomass partitioning (canopy vs. groundcover) than tallgrass prairies do (Mitchell et al., 1999), structural similarities suggest that patterns of species richness in these grasslands can help provide the framework for hypotheses regarding diversity–fertility relationships in longleaf pine communities. Similar structural features among these ecosystems include (a) a high number of groundcover species that coexist within a matrix of dominant grass species and (b) a decline in groundcover species richness in the absence of fire with increased presence of hardwoods. For both ecosystems, the relationship between fire and species richness is consistent with an assumption of the intermediate disturbance hypothesis in

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that there is a trade-off between the ability of a plant to tolerate disturbance and its ability to compete. Within tallgrass prairies, species richness decreases with increasing standing crop biomass (Barnes, Tieszen, and Ode, 1983; Abrams and Hulbert, 1987; Gibson and Hulbert, 1987; Collins, 1992), and in other North American prairies, intermediate biomass has been reported as more favorable to high species richness than the extremes (Dix and Smeins, 1967). Interpreted in the context of theoretical models of species richness (Grime, 1979; Huston, 1979; Huston and DeAngelis, 1994), the decline in species richness in more productive sites is due to higher rates of extinction of less common species as dominance of competitors increases with increasing soil fertility. Disturbances that alter the dominance of matrix species play an integral role in this relationship (Huston, 1979, 1994; Guo and Berry, 1998).

Even though tallgrass prairies are considered to be primarily nitrogen (N)-limited (Seastedt, Briggs, and Gibson, 1991), Turner et al. (1997) reported a surprising inverse relationship of productivity to direct measures of N availability. This pattern suggests that factors controlling productivity and nitrogen mineralization differ (Turner et al., 1997), and nitrogen availability may not necessarily be a reliable predictor of site fertility.

Temporal and spatial heterogeneity appear to contribute to species coexistence in the tallgrass prairie. For example, species richness increases throughout the growing season (Collins, 1987), and a maximum number of species occurs the second year following fire (Collins and Steinauer, 1998) even though frequent fire increases dominance of large clonal grasses (Hulbert, 1988; Seastedt and Ramundo, 1990). Community heterogeneity (mean percent dissimilarity in species composition) is scale dependent, with increases in heterogeneity in areas where the size of the disturbance is small relative to the size of the community sampled (Collins, 1992). Across landscape scales in this prairie system, differences in heterogeneity of species composition (between plots within a site) may be attributable to site productivity. Heterogeneity as used in this paper will refer to mean percent dissimilarity in plots within a site or sites, as opposed to other measures of ecological diversity. Heterogeneity is negatively related to the cover of the dominant C_4 grasses and positively related to species richness (Collins, 1992). In contrast to a monotonic relationship, a bimodal distribution of species abundances occurs at both the level of local assemblages of species as well as at the regional level, suggesting that similar mechanisms associated with coexistence are operating at both scales (Collins and Glenn, 1990).

Thus, based on patterns in prairies, across a net productivity gradient varying nearly two-fold (proportionally equivalent range to that of tallgrass prairies), a unimodal or monotonic relationship of groundcover biomass (which is proportional to productivity in this system) and species richness might be predicted for the *Pinus palustris*-*Aristida beyrichiana* ecosystem. Such a relationship has been suggested for closely related *Pinus palustris*-*Aristida stricta* sites (Walker and Peet, 1983). Further, we predict that heterogeneity of species composition will decrease with increasing soil moisture in the *Pinus palustris*-*Aristida beyrichiana* (referred to here as longleaf pine-wiregrass) ecosystem, along with increased dominance of wiregrass. We used a natural gradient approach to examine how patterns of plant species richness and plant community structure vary with productivity (standing crop biomass) as a function of soil moisture and nitrogen mineralization rates in

a frequently burned longleaf pine-wiregrass savanna. Specifically, we addressed the following questions: (1) Does groundcover species richness vary unimodally across the complex resource-productivity gradient, and is the dominance of wiregrass correlated with species richness? (2) Do these relationships vary temporally (phenologically or within the 2-yr burn cycle)? (3) Are species abundance distributions and patterns of heterogeneity scale-dependent, and do they vary with site types along the gradient?

MATERIALS AND METHODS

Study site—Physiography, geology, and soils—The study site is located at Ichauway, a 115-km² reserve located in the Coastal Plain of southwestern Georgia. The climate for this region is characterized as humid subtropical (Christensen, 1981), with an average annual precipitation of 131 cm evenly distributed throughout the year. Mean daily temperatures range between 21°–34°C in summer and 5°–17°C in winter (Goebel et al., 2001). Ichauway is located within the Dougherty Plain physiographic region in the Gulf Coastal Plain Province of Walker and Coleman (1987) or the Lower Coastal Plain and Flatwoods (LCPF) section (Plains and Wiregrass Plains subsections) of McNab and Avers (1994). The LCPF Province is a karst landscape characterized by flat, weakly dissected alluvial deposits over Ocala Limestone (Hodler and Schretter, 1986). Parent materials are marine and continental sand and clay deposits formed during the Mesozoic (65–225 million years BP) and Cenozoic eras (present to 65 million years BP) (Keys et al., 1995).

We selected study sites with soils of the following three drainage classes, encompassing the range of soil moisture conditions of longleaf pine-wiregrass ecosystem types at Ichauway: (1) excessively well drained, (2) somewhat excessively drained, and (3) somewhat poorly drained. The excessively well drained sites occur on upland sand ridges of undulating slopes of 3–4% and have deep, sandy soils, often with no argillic horizon (i.e., no significant accumulation of clay) within 300 cm. These soils are Typic Quartzipsamments with a water-holding capacity (in the upper 300 cm) of ~18 cm water (Goebel et al., 2001). The somewhat excessively drained sites occur on upland terraces with undulating slopes of 2% and have soils classified as Psammentic Kandiodults or Grossarenic Kandiodults. These soils are loamy sands over sandy loams, with a depth to argillic horizon between 150 and 200 cm. The water-holding capacity of these sites is 28 cm water (in the upper 300 cm) (Goebel et al., 2001). The somewhat poorly drained sites occur on upland terraces with soils classified as Aquic Arenic Kandiodults. These soils are sandy loam over sandy clay loam or clay on nearly level slopes with a water-holding capacity of 40 cm water (in the upper 300 cm) (Goebel et al., 2001). An argillic horizon is present within 50 cm of the soil surface.

Vegetation and ecological site classification—The three soil drainage classes correspond to ecosystem types identified by a recent site classification of Ichauway based on landscape position, soil type, and vegetation (Goebel et al., 2001). We refer to these types as xeric, intermediate, and wet-mesic in the remainder of the text. The vegetation of all site types has been maintained with frequent dormant season prescribed fire (return interval of 2–5 yr for over seven decades, depending on moisture conditions and fuel accumulation) for bobwhite quail (*Colinus virginianus*) habitat. The xeric sites are dominated by open stands of *Pinus palustris* Mill., *Quercus laevis* Walt., and *Q. margaretta* Ashe in the overstory (>10 cm diameter at breast height [dbh]), mid-story (2.5–10 cm dbh), and understory (<2.5 cm dbh and <30 cm tall). Intermediate sites are characterized by *Pinus palustris* Mill. as a dominant overstory species and by *Q. incana* Bartr. and *Q. margaretta* Ashe occurring only as a midstory or understory component. The wet-mesic sites are characterized by the single dominant *Pinus palustris* in the overstory and mid-story, with *Diospyros virginiana* L. occurring frequently in the understory. Dense groundcover at all sites is dominated by the perennial grass *Aristida beyrichiana* Trin. and Rupr. with numerous species of other perennial grasses and forbs also present (Goebel et al., 2001).

Study design—This study was designed as a component of a multidisciplinary

plinary investigation that focuses on vegetation–resource interactions of the longleaf pine–wiregrass ecosystem across a landscape gradient (see also Mitchell et al., 1999; Wilson et al., 1999). The three longleaf pine ecological site types are similar to the range of site conditions that occurs throughout southwestern Georgia and northern Florida. We selected three replicate sites with a similar disturbance history in each of the three ecological site types (for a total of nine sites). Due to few potential sites with xeric soils and similar disturbance history and to their inherently clustered spatial distribution, the xeric sites were closer to each other than the mesic sites. Sites (replicates of a site type) were ~ 0.25 ha in size (50×50 m). Plots ($\sim 4 \times 13$ m) for resource measurements and vegetation sampling were randomly located within each site and stratified by longleaf pine basal area distribution. To stratify plot locations, a 5-m grid was established across each site and longleaf pine basal area measurements (using a hand-held prism, basal area factor 5) were made at the intersection of the grids. The distribution of pine basal area was then divided in 20 percentile rankings, and two randomly selected locations were chosen from each percentile ranking, yielding ten plots per site (total of 90 plots). All sites were burned in March 1995.

Vegetation sampling—A 1×3 m vegetation composition sampling quadrat was established at each plot, and vegetation was sampled in June and October 1995 and October 1996. Because of the high number of species per quadrat, the following measure of species abundance was used for greater precision in detecting change than visual estimates of cover (Critchley, Nigel, and Simon, 1998). Each vegetation sampling quadrat was gridded into 0.3×1 m units and species abundance was determined as frequency of occurrence within the 10 grid units of the 3-m^2 quadrat. Adjacent to each vegetation sampling quadrat, a circular frame (0.75 m^2) was randomly located for aboveground biomass clipping. Groundcover vegetation was clipped two times annually (in June and October) for two consecutive years (1995 and 1996). All herbaceous vegetation and all woody vegetation with stem diameter < 1 cm was harvested at ground level. Plant material was sorted into six classes (wiregrass, other grasses, legumes, other forbs, woody plants, ferns, and dead plants and litter), dried, and weighed. Randomly located quadrats with disturbed soil, such as pocket gopher mounds or gopher tortoise burrows, were eliminated from the pool of potential sampling units for vegetation composition or biomass sampling.

To examine how species richness patterns varied with scale across the gradient, we also sampled species richness in hierarchically nested quadrats (Peet, Wentworth, and White, 1998). At each site, we established a 20×20 -m quadrat, which was subdivided into four modules (10×10 m). Species presence was determined for a \log_{10} series of nested subquadrats (e.g., 0.01, 0.1, 1.0, and 10 m^2) within a corner of each 100-m^2 module.

Net N mineralization—Nitrogen availability was estimated monthly for a 12-mo period, beginning June 1995, using in situ buried bag incubations of the mineral soil in each of the ten plots (Eno, 1960). Inorganic nitrogen represents the standing nitrogen pool after release, leaching, and plant uptake, whereas nitrogen mineralization represents nitrogen flux and supply. In each of two soil sampling quadrats (1×4 m quadrats, located within the 4×13 m plots outside of the vegetation quadrats) per plot, ten soil samples were obtained with a push probe (which sampled the top 10 cm). Soil samples were composited for each plot, sieved at the laboratory, and subsampled for estimation of initial pools of inorganic nitrogen as well as soil moisture content. Four 50-g dry mass aliquots were drawn from each composite soil sample and placed in gas-permeable plastic bags. Two bags were buried at 10 cm depth into their original plot location within a 24-h period. After an incubation cycle of 4–5 wk (28–35 d) these samples were retrieved, composited within plot, and analyzed for final nitrogen content. Inorganic nitrogen in the initial and incubated soil samples were extracted with 2 mol/L KCl (10 g : 25 mL) by vigorous agitation on a mechanical shaker for 15 min, followed by centrifugation for an additional 15-min period. The supernatant for each sample was then drawn off and stored frozen until analysis. Ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were analyzed colorimetrically on a Lachat Flow Injection analyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). Ammonium-N was analyzed by the indophenol-blue method, and nitrate-N

was reduced to nitrite using a Cd (Cadmium) column and then determined by diazotiation (Keeney and Nelson, 1982; Lachat Instruments, 1992). Net nitrogen mineralization was then calculated by subtracting the initial from the final pools of extractable inorganic N. Monthly N mineralization was summed for the year (Wilson et al., 1999).

Soil moisture measurements—Percent volumetric soil moisture was measured using time domain reflectometry (Topp, Davis, and Annan, 1982; Baker and Allmaras, 1990). A pair of 30-cm stainless steel rods was inserted vertically in the soil in each of the sampling plots at all sites. Soil moisture was quantified every 2 wk throughout the study period (June 1995–June 1997) and percent volumetric soil moisture was averaged over the sampling period. We determined soil water potential values from water retention tables for each site based on soil classification (Dane et al., 1983; Quisenberry et al., 1987).

Data analysis—Analysis of variance of species richness (3-m^2 plots) and biomass among site types were analyzed as a completely randomized design via PROC GLM (SAS, 1990). Jaccard's index of similarity (JI) was used to compare vegetation by site types (Ludwig and Reynolds, 1988). To assess temporal change in composition, we also used JI to examine changes in presence and absence between seasons and between years. Differences among site types in mean values of JI were examined via PROC GLM (SAS, 1990). Mean comparisons were made using Tukey's procedure (SAS, 1990). The relationship of species richness to area sampled was determined by examining differences in species richness values between site types for each of the nested quadrats via PROC GLM (SAS, 1990). Comparisons of mean values between site types were made using Tukey's procedure (SAS, 1990).

Distribution of species abundances were examined by site type (within each site type, $n = 30$ vegetation sampling quadrats) and across the gradient (all site types, $n = 90$ vegetation sampling quadrats) by plotting the frequency of quadrats occurring with a given number of species following Collins (1992). We also examined average spatial heterogeneity in species composition by site type, defined as mean dissimilarity in species composition among samples at a site within a given year following Collins (1992) and based on Whittaker (1975). We made computations at two scales for each site type: (1) the site replicate level (all possible $[n(n - 1)/2]$ pair-wise quadrat : quadrat comparisons within a site; 10 quadrats per site resulting in a matrix of 45 values per site type, i.e., within-site type heterogeneity is the mean of 135 values); and (2) the pooled site level (all possible pair-wise quadrat : quadrat comparisons pooled by site types; 30 quadrats resulting in a matrix of 435 values for each site type, i.e., within-site type heterogeneity is the mean of a subset composed of 33% randomly selected values from the matrix of 435 values). Differences in mean heterogeneity values between site types were analyzed separately at both scales via PROC GLM (SAS, 1990).

Species richness values (3-m^2 quadrats) were tested for correlation with water and nitrogen availability, groundcover standing crop, and wiregrass percent of total groundcover standing crop using site means of ten plots. Within site types, species richness values were also tested for correlation with overstory basal area. Differences between site types for in situ inorganic nitrogen and nitrogen mineralization rates were determined with PROC GLM (SAS, 1990). Comparisons of means between site types were made using Tukey's procedure ($P < 0.05$) (SAS, 1990).

RESULTS

Aboveground biomass and vegetation structure—Total aboveground standing crop biomass (live and dead) of the groundcover did not differ among site types at the initial sampling date of spring 1995 following the prescribed burn ($F = 1.32$, $P = 0.33$, $df = 2$) (Fig. 1). However, in subsequent sampling periods, groundcover biomass was consistently greater in the wet-mesic sites (fall 1995, 246 g/m^2 ; spring 1996, 233 g/m^2 ; fall 1996, 269 g/m^2) than in the xeric sites (fall 1995, 145 g/m^2 , $F = 5.89$, $P = 0.04$, $df = 2$; spring 1996, 130 g/m^2 , $F = 3.49$, $P = 0.1$, $df = 2$; fall 1996, 143 g/m^2 , $F = 7.27$, $P = 0.02$, $df = 2$). No significant differences

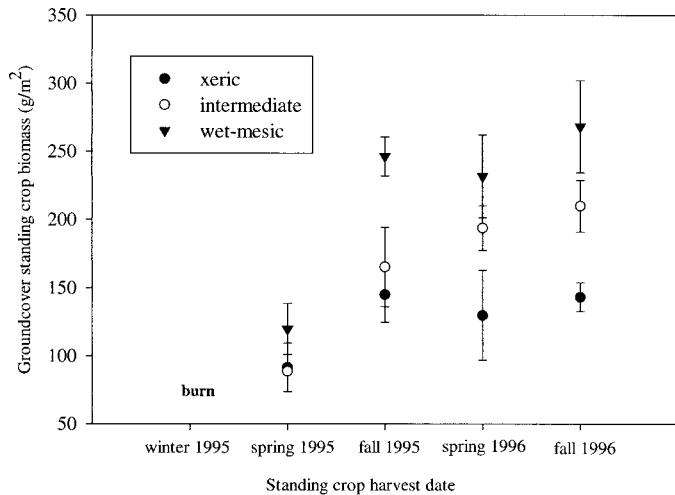


Fig. 1. Standing crop biomass (means ± 1 SE) of groundcover vegetation by sites (1995 and 1996).

were detectable between the intermediate site and either of the other sites ($P > 0.05$).

At the end of the first growing season following fire, the relative proportion of wiregrass (live and dead) biomass to total aboveground groundcover biomass was similar ($F = 0.72$, $P = 0.52$, $df = 2$) across the gradient (ranging from 40 to 51%) (Fig. 2). By fall 1996, the end of the second growing season following fire, the standing crop biomass of wiregrass in the wet-mesic sites was twice that of the xeric site ($F = 5.71$, $P = 0.04$, $df = 2$); however, the percentage of total groundcover standing crop still did not differ among sites (ranging from 54 to 71%) ($F = 3.25$, $P = 0.11$, $df = 2$).

The mean basal area of overstory trees (primarily *Pinus palustris* and *Quercus laevis*) was lower in the xeric sites than that of the other two soil drainage sites ($F = 14.5$, $P < 0.01$). Approximately half of the total basal area in this soil drainage class was composed of oaks, primarily *Quercus laevis*, whereas few oaks were found in the overstory of other sites. We did not detect a consistent pattern between overstory basal area and species richness within site types (R^2 ranging from 0.006 to 0.12) suggesting that neither canopy basal area nor tree density were strongly controlling species richness at the scale at which we sampled in our study areas.

Relationship of environmental variables with patterns of species richness—Floristic diversity (203 species) was unevenly distributed across the gradient, with 78% of the total species pool occurring in the wet-mesic sites, 55% in the intermediate sites, and 30% in the xeric sites (Table 1). Perennials accounted for >90% of total species in all site types. At the scale of sampling quadrats (3 m²), mean species richness also differed among all site types ($F = 33.6$, $P < 0.01$). The highest mean number of species (36) per quadrat occurred in

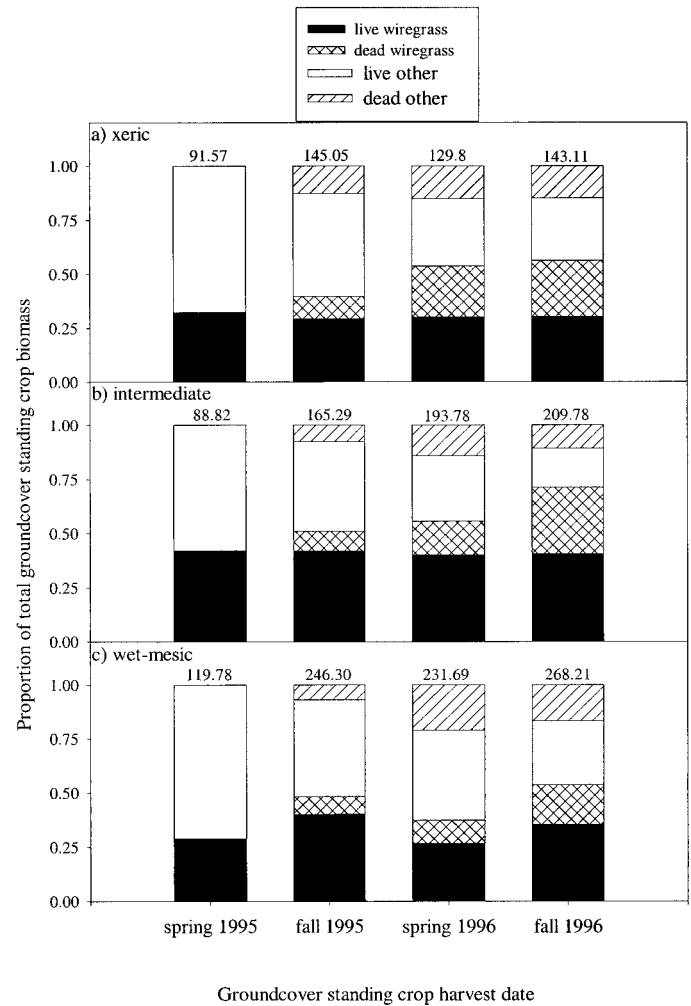


Fig. 2. Percentage of total aboveground standing crop groundcover biomass for spring and fall harvests 1995 and 1996. (a) Xeric sites. (b) Intermediate sites. (c) Wet-mesic sites.

the wet-mesic sites and was more than twice that of the xeric sites. Intermediate values of species richness values occurred in the intermediate sites. Mean species richness per plot was strongly correlated with an increasing standing crop biomass (Fig. 3) and with soil moisture (Fig. 4a). Species richness was not correlated with wiregrass percent of total standing crop biomass for either year (fall 1995, $R^2 = -0.08$, $P = 0.54$; fall 1996, $R^2 = -0.14$, $P = 0.99$). Nitrogen mineralization was significantly and inversely related to species richness (Fig. 4b, Table 2).

Spatial and temporal heterogeneity—Regardless of site type, the majority of species occurred infrequently (Fig. 5).

TABLE 1. Species richness among site types (means ± 1 SE, $n = 3$). Means with different superscripts are significantly different in species richness per 3-m² plot for the sampling date ($P < 0.05$, Tukey's procedure for multiple comparisons).

	1995			1996		
	Xeric	Intermediate	Wet-mesic	Xeric	Intermediate	Wet-mesic
Species number per plot	15.2 ± 0.83 ^A	24.4 ± 0.93 ^B	35.3 ± 1.08 ^C	15.63 ± 0.90 ^A	26.53 ± 0.94 ^B	36.57 ± 1.31 ^C
Total species in site type	62	113	162	66	119	156

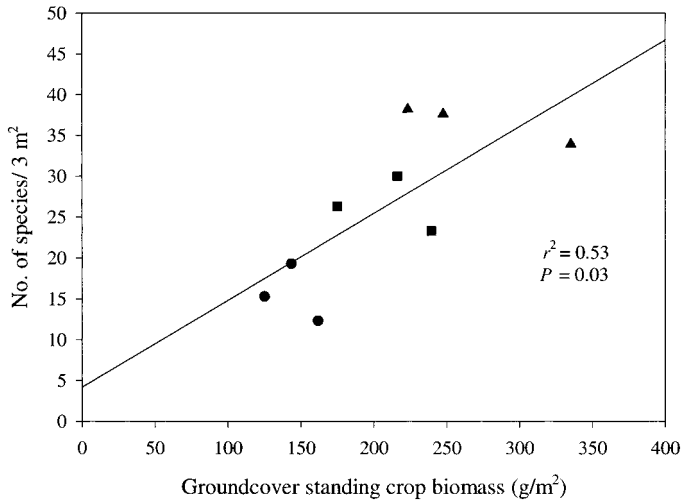


Fig. 3. Relationship between species richness (fall 1996) and aboveground groundcover standing crop biomass (in grams per square meter). Xeric sites = ●, intermediate sites = ■, wet-mesic sites = ▲.

However, for each site type, at least three species occurring within that site type occurred in 90% (27 out of 30) or more of the quadrats. At the 3-m² quadrat scale, there were ~0.25–0.30 species per total number of species per site type across all soil types.

As indicated by percentage similarity, species presence or absence was highly consistent between spring and fall within a year for all sites, and similarly, between years (Table 3). The wet-mesic site had a slightly greater change in species both seasonally and yearly (Table 3).

Low floristic similarity occurred between site types. A slightly greater affinity existed between the wet-mesic site type and intermediate site type than between the xeric site type and either of the other site types (Table 3). Of the total species, 26 were common to all site types. There were some species that were uniquely present at each site type (xeric = 16 species, intermediate = 22 species, wet-mesic = 69 species).

Average spatial heterogeneity was site dependent. Heterogeneity within site replicates was least for the xeric site type, and no differences in heterogeneity occurred between intermediate and wet-mesic site types ($F = 18.63, P < 0.01$) (Table 4). However, for comparisons across all plots within site types, heterogeneity among all site types differed, the intermediate with greater heterogeneity than that of the xeric or wet-mesic site types ($F = 31.16, P < 0.0001$) (Table 4).

Species richness varied consistently with area (ranging from 0.01 to 100 m²) regardless of site type. At all scales the xeric site type had approximately half the number of species of the wet-mesic site. Differences in species richness between the xeric and intermediate site types emerged at the 100-m² level (Table 5).

DISCUSSION

Species richness and standing crop relationship—Our findings of a positive correlation of species richness with groundcover standing crop demonstrate no unimodal pattern of species richness across the moisture and groundcover aboveground biomass gradient in our longleaf pine–wiregrass study area. As in other fire-dependent systems, fire plays a major role in maintaining high species richness in longleaf

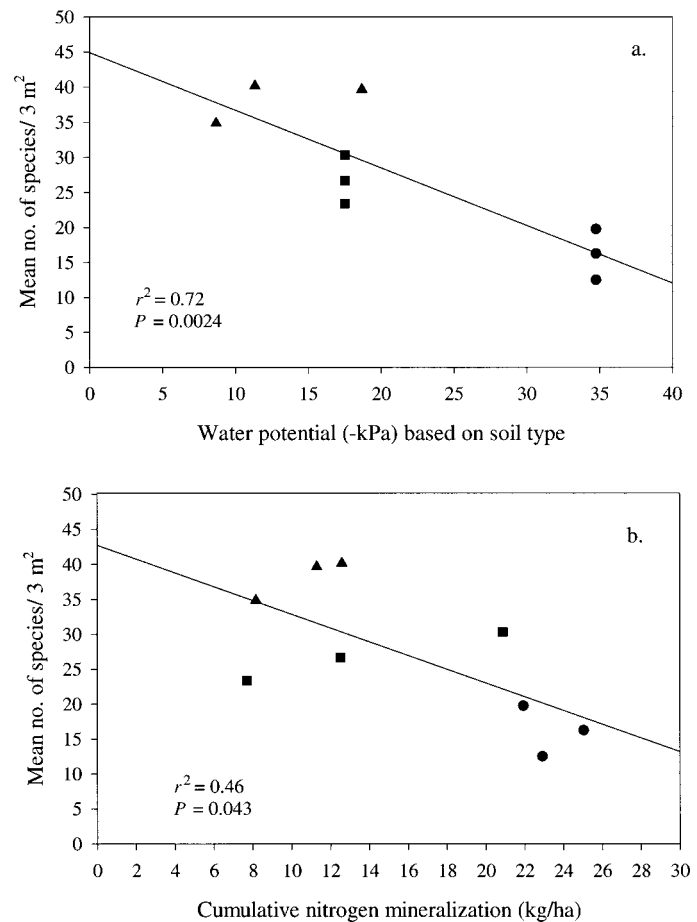


Fig. 4. Relationship between species richness (fall 1996) and resources. (a) Soil moisture. (b) Nitrogen availability. Xeric sites = ●, intermediate sites = ■, wet-mesic sites = ▲.

pine–wiregrass savannas (Leach and Givnish, 1996). The extremely high number of species in longleaf pine savannas has been interpreted as evidence of a long evolutionary history of selection in a relatively infertile and frequently disturbed environment (Walker and Peet, 1983). In the absence of fire, hardwoods dominate the vegetation, competition among forbs and grasses for light increases, and in turn, species richness declines (Lemon, 1949; Myers, 1990). Thus, because fire is a large-scale disturbance that reduces aboveground competition for light in the longleaf pine–wiregrass ecosystem, and because species numbers are not reduced with increasing groundcover standing crop as reported in other grassland ecosystems, factors other than competitive exclusion appear to structure patterns of species richness across the productivity gradient of

TABLE 2. In situ N pools and flux rates for a 12-mo period starting June 1995. Mean differences analyzed using Tukey’s procedure; values followed by different superscripts within a given pool are significantly different ($\alpha = 0.05$).

Site type	In situ inorganic N (kg/ha)	Net N mineralization (kg/ha)
Xeric	8.6 ^A	13.0 ^A
Intermediate	6.5 ^A	7.1 ^B
Wet-mesic	4.6 ^A	3.8 ^B

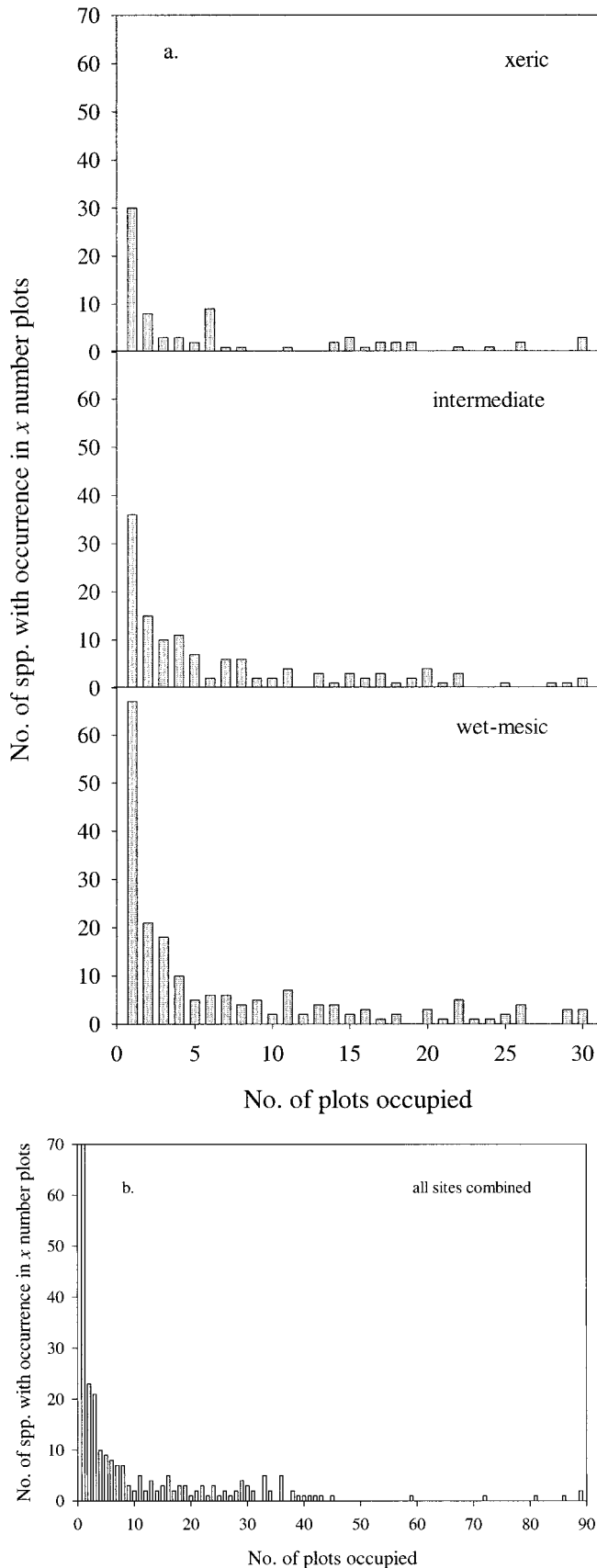


Fig. 5. Frequency of plots occurring with given number of species (fall 1996). (a) By site type. (b) Across the moisture gradient.

TABLE 3. (I) Jaccards' Index (JI) of percent similarity between site types and (II) contrasts between site types for (mean \pm 1 SE) season-to-season and year-to-year similarity. Differences between site types for similarity are indicated by superscript ($P < 0.05$, using Tukey's procedure for means comparisons).

I) Site type	Spring vs. fall 1995 (mean \pm SE)	1995 vs. 1996 fall (mean \pm SE)
Xeric	90.7 \pm 2.0 ^A	89.7 \pm 0.0 ^A
Intermediate	91.3 \pm 1.0 ^A	87.5 \pm 1.6 ^A
Wet-mesic	79.0 \pm 1.0 ^B	80.7 \pm 1.9 ^B
II) Site type comparison	Similarity	
Xeric vs. wet-mesic	24.1%	
Intermediate vs. wet-mesic	42.8%	
Xeric vs. intermediate	30.2%	

Note: $JI = a/(a + b + c)$ where a = the number of species in common between two samples (A, B), b = the number of species in sample A not in sample B, and c = the number of species in sample B not in sample A.

this study. This pattern not only differs from findings by Walker and Peet (1983), but also that of fire-dependent North American prairies (Collins, Glenn, and Gibson, 1995; Collins and Steinauer, 1998).

Arguments that patterns without humps (i.e., monotonic) are a result of studies with insufficient ranges of productivity have been frequently presented (see review in Waide et al., 1999). The range of standing crop biomass values for maximum species richness reported in many tallgrass prairies (Risser et al., 1981; Towne and Owensby, 1984; Abrams, Knapp, and Hulbert, 1986) and European grasslands (Al-Mufti et al., 1977; Grime, 1979; Vermeer and Berendse, 1983) is >400 g/m² and exceeds that for groundcover standing crop at our site. However, the total annual net productivity (ANNP, groundcover plus overstory) of our study sites (391–743 g/m²) is within the range of ANNP of those reported above (Knapp et al., 1993; Mitchell et al., 1999). Productivity represents an overall demand on resources, regardless of whether or not trees are present. The productivity range of the longleaf pine-wiregrass savannas is, in fact, great enough for competitive exclusion by hardwoods to occur in the absence of fire, even though the

TABLE 4. Spatial heterogeneity (mean percent dissimilarity [PD] in species composition among samples) among site types. (I). Contrasts among all possible sampling quadrat pairs within site (10 sampling quadrats; $n = 45$ contrasts within site; $n = 135$ contrasts within site type) by site type. (II). Contrasts among all possible sampling quadrat pairs within site type (30 sampling quadrats; $n = 33\%$ randomly selected contrasts from 435 possible contrasts within site type). Within a sampling period, means with the same superscript are not significantly different ($P < 0.05$, using Tukey's procedure for mean comparisons).

Site type	Spring 1995	Fall 1995	Fall 1996
(I) PD (mean \pm 1 SE) contrasts within site			
Xeric	45.3 \pm 0.01 ^A	43.8 \pm 0.01 ^A	45.3 \pm 0.01 ^A
Intermediate	50.2 \pm 0.01 ^B	48.4 \pm 0.01 ^B	51.1 \pm 0.01 ^B
Wet-mesic	51.6 \pm 0.01 ^B	46.5 \pm 0.01 ^B	49.1 \pm 0.01 ^B
(II) PD (mean \pm 1 SE) contrasts within site type			
Xeric	48.0 \pm 0.0 ^A	47.3 \pm 0.0 ^A	47.4 \pm 0.0 ^A
Intermediate	57.2 \pm 0.0 ^B	55.4 \pm 0.0 ^B	56.0 \pm 0.0 ^B
Wet-mesic	55.4 \pm 0.0 ^C	52.5 \pm 0.0 ^C	52.6 \pm 0.0 ^C

Note: $(PD = 1 - (1 - 0.5 \sum |\rho_a - \rho_b|))$; where ρ_a = the proportional abundance of species ρ in sample A and ρ_b = the proportional abundance of species ρ in sample B).

TABLE 5. Species richness–area relationship. Values reported are number of species per sampling quadrat by site type (means \pm 1 SE; $n = 3$). Within each area, means with different superscripts are significantly different using Tukey's procedure for multiple comparisons ($P < 0.05$).

Site type	Area (m ²)				
	0.01	0.1	1.0	10	100
Xeric	1.0 \pm 1.0	4.0 \pm 1.5 ^A	8.3 \pm 1.8 ^A	16.3 \pm 3.2 ^A	25.0 \pm 3.6 ^A
Intermediate	3.3 \pm 0.3	8.0 \pm 2.1 ^{AB}	14.3 \pm 1.7 ^{AB}	28.0 \pm 1.0 ^{AB}	48.7 \pm 3.5 ^B
Wet-mesic	3.3 \pm 0.9	7.0 \pm 1.5 ^B	20.3 \pm 2.7 ^B	35.3 \pm 3.7 ^B	55.7 \pm 3.2 ^B

inherent productivity of the sites are not increased by fire exclusion. In the absence of fire, a decline in species richness is general across all longleaf pine–wiregrass soil types, including low productivity sandhill sites (Heyward, 1939). While fire exclusion also reduces species richness in tallgrass prairies, competitive exclusion, in addition to disturbance, appears to be a factor regulating species richness (Abrams and Hulbert, 1987; Gibson and Hulbert, 1987; Hartnett and Fay, 1998). In contrast, the relationship between species richness and productivity of longleaf pine–wiregrass ecosystems appears to be merely correlative rather than causal, while disturbance and species richness appear to be mechanistically related.

Although the intrinsic structural differences in carbon allocation in grasslands and longleaf pine–wiregrass ecosystems may be a factor explaining why competitive exclusion by wiregrass was not observed, structural and life-form differences between groundcover vegetation of longleaf pine–wiregrass savannas and prairies suggest some additional factors that may influence patterns of species richness. In this study, the relative dominance of wiregrass in the ground cover remained consistent across the resource gradient, differing from that of fire-maintained prairies, where perennial grasses increased in dominance with increasing productivity and excluded other life forms that contribute disproportionately to species richness (Dix and Smeins, 1967; Barnes, Tieszen, and Ode, 1983; Abrams and Hulbert, 1987; Gibson and Hulbert, 1987). This uniformity in dominance may be attributable to the fact that wiregrass is not rhizomatous and consequently does not rapidly expand, in contrast to that of many dominant prairie species (Freeman, 1998; Hartnett and Fay, 1998). Although characteristically similar to tallgrass prairies in having many species with infrequent occurrence, longleaf pine–wiregrass savannas differ in having only a few widely occurring matrix species, as opposed to a bimodal distribution of species. In other words, a lower percentage of the flora occurs frequently and is less likely to codominate in the longleaf pine–wiregrass savanna (Collins and Glenn, 1990).

Our findings may have differed with that of Walker and Peet (1983) because of possible differences in the realized habitat breadth of the two species of wiregrass (*Aristida stricta* and *A. beyrichiana*). *Aristida stricta* does not dominate in somewhat poorly drained or wetter sites in North Carolina; other grasses assume dominance in such sites (Kologiski, 1977). In contrast, in the Gulf Coast region, *A. beyrichiana* occurs and dominates in very wet sites (Abrahamson and Hartnett, 1990). Although the Green Swamp savannas (Walker and Peet, 1983) and Ichauway savannas of this study may be comparable moisture gradients, a direct comparison of the two gradients is not possible with the data available.

Our results suggest that soil moisture is an important factor regulating both the number of species present and community production within the defined gradient of this study. Water is likely a limiting resource and fewer species are adapted to the

more drought-prone end of the gradient, although numerous species span the entire gradient. Truncated distribution patterns for many plants in conditions of lower resource availability have been reported (Ellenberg, 1953; Werner and Platt, 1976; Austin, 1987; Mueller-Dombois and Ellenberg, 1974) and modeled by Smith and Huston (1989). Water limitation across the longleaf pine–wiregrass gradient could also imply that the environment might be particularly stressful for seedling establishment. Thus, variation among species in their regeneration niche, stress tolerance during establishment (Grubb, 1977), traits that encourage persistence and resilience to disturbance (Grime, 1974), and perhaps facilitation of establishment (Goldberg and Miller, 1990; DeSteven, 1991; Greenlee and Callaway, 1996; Kelly and Burke, 1997) are potentially more important than those related to competitive abilities in ordering plant species distribution patterns in this landscape.

Although species richness was negatively correlated with N mineralization, this relationship is an artifact of a negative correlation of N availability and soil type, rather than representative of a causal factor. A negative relationship between N availability and species richness is a pattern that has been reported for other experimental studies with N additions, but where standing crop biomass is positively correlated with nitrogen levels (Lawes, Gilbert, and Masters, 1882; Milton, 1940; Silvertown, 1980; Tilman, 1996; and many others, see Huston, 1994). Our results are strikingly similar to the relationships of N mineralization and productivity for the Konza prairie, both in magnitude and direction (Turner et al., 1997). Because nitrogen availability is negatively correlated with standing crop biomass (and ANNP, Mitchell et al., 1999) and species richness in our site, we propose that the processes that result in this correlation differ from those suggested by conventional models of resource supply and competitive relations (Tilman, 1988, 1990, 1996). Although N mineralization rates of surface soils in savannas were low compared to other North American forests, productivity in this ecosystem appears to be more moisture limited than nitrogen limited (Mitchell et al., 1999; Wilson et al., 1999).

The low N mineralization in surface soil layers is due to inherently low soil organic matter, as well as to fire, which eliminates formation of a decomposing litter layer. Thus, root turnover is the major addition to the detritus pool. Soil incubations to 1 m in depth show that although significant N mineralization occurs at greater depths than that of our study, the N mineralization rates at this depth relative to the surface are proportionally similar among sites (Mitchell et al., unpublished data). Soil nitrogen availability appears to be mediated through soil organic matter quality (lignin content) and microclimatic variations (Turner et al., 1997; Wilson et al., 1999). Resource manipulations coupled with demographic studies are needed over multiple fire cycles to reveal mechanisms that regulate species richness in longleaf pine–wiregrass savannas.

Temporal and spatial heterogeneity of vegetation composition—The consistent year-to-year and season-to-season species richness values can be attributed to the predominantly perennial composition of this system. Once established, individuals of many fire-adapted perennials may persist for several years, although precise turnover rates of individual plants in this system are unknown. Walker and Peet (1983) did not find a change in species richness among seasons, but they noted that maximum standing crop peaked early in the season for some species such as sedges. The decrease in species richness throughout the season in prairies could be due to the large percentage of annual species (nearly 30%) reported in tallgrass prairies (Freeman, 1998). Spatial heterogeneity in our study falls within the upper range of that of the Konza Prairie (Collins, 1992). However, in our study it appears to be decoupled from species richness regardless of spatial extent of comparisons. Greater spatial heterogeneity in the wet-mesic relative to the intermediate and xeric site might be expected because the probability of variations in species composition would be greater with a larger number of rarely occurring species, as well as a greater distance between sites for the wet-mesic site type (White and Walker, 1997). While the range of edaphic parameters we used to artificially segment the intermediate zone perhaps was greater than for other site types, a similar trend (albeit, not significant) of high within-site heterogeneity of the intermediate site type is also present. Localized disturbance patterns (i.e., fossorial animal soil mounds) (W. Michener, University of New Mexico, unpublished data) or historical legacies (timber harvest or grazing) that are associated with particular physical soil characteristics, such as soil texture or frequency of soil saturation, are potential factors that could differentially influence species patterns along the environmental gradient.

Implications for conservation and restoration of longleaf pine-wiregrass savannas—The longleaf pine ecosystem was once the dominant vegetation of the southeastern Coastal Plain (Ware, Frost, and Doerr, 1993). Because of the wide ecological amplitude of the original extent of the longleaf pine ecosystem and the scarcity of extant stands today, knowledge of structure and functional processes has been largely anecdotal or applicable to site-specific environmental conditions. The paucity of information is partly due to the fact that only remnants of longleaf pine-wiregrass savannas remain, and these primarily occur on soils that are either too wet or too dry for agricultural or silvicultural conversion (Peet and Allard, 1993). Consequently, few examples of longleaf pine-wiregrass remain on sites that are similar to our intermediate site type (Drew, Kirkman, and Gholson, 1998).

We recognize that our study represents only a portion of the range of this once extensive ecosystem (Kologiski, 1977; Walker and Peet, 1983; Bridges and Orzell, 1989; Clewell, 1989; Noss, 1989) and that many other factors such as variations in flora, soil types, geomorphology, disturbance regimes, and landscape contexts could have distinct effects on patterns of species richness across the region. However, the results of this study provide information about patterns of species richness and resource availability across an intact longleaf pine-wiregrass landscape that can help guide restoration of similar sites (Aronson, Dhillion, and LeFloc'h, 1995; Hobbs and Norton, 1996; Fulé, Covington, and Moore, 1997), particularly when coupled with multiple sources of reference information to produce a description of potential ecological varia-

tion (White and Walker, 1997; Braakhekke and Hooftman, 1999).

A key finding in this study is that the highest aboveground groundcover biomass and highest diversity were found at the same position along the gradient (i.e., the wet-mesic sites). This evidence indicates that local diversity would not be maximized by restoring intermediate sites. Rather, the presence of unique species sets for each site type, as well as low site-site similarity, suggests that regional diversity would be best captured by preserving a range of site types in the landscape.

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