

DISTRIBUTION OF NATIVE LEGUMES (LEGUMINOSEAE) IN FREQUENTLY BURNED LONGLEAF PINE (PINACEAE)–WIREGRASS (POACEAE) ECOSYSTEMS¹

MARK J. HAINDS,² ROBERT J. MITCHELL,^{3,4} BRIAN J. PALIK,⁴
LINDSAY R. BORING,³ AND DEAN H. GJERSTAD

²School of Forestry, Auburn University, Auburn, Alabama 36849;

³Joseph W. Jones Ecological Research Center, Route 2 Box 2324, Newton, Georgia 31770; and

⁴Forestry Science, USDA Forest Service, 1831 Highway 169 East, Grand Rapids, Minnesota 55744

Legume species distribution and abundance and selected environmental variables were quantified across a complex gradient (varying in both water-holding capacity and fertility) for frequently burned longleaf pine (*Pinus palustris*)–wiregrass (*Aristida stricta*) ecosystems. Legumes were present in all months; however, abundance peaked in June and was minimal after killing frosts in October. Legume species were prominent in the flora (43 species encountered) ubiquitous (94% of 2-m² subplots had at least one legume species), and abundant (nearly 120,000 stems/ha). Although most species were widely distributed throughout the gradient, *Lespedeza angustifolia* was distinctly associated with the more hydric end of the gradient, while both *Petalostemon pinnatum* and *Galactia microphylla* were located in the more xeric extreme. The percentage variation in species that could be accounted for by environmental variation was low (27%). Of the variation that could be accounted for, a number of environmental variables were important, including soil moisture, pine basal area (i.e., light), and bivalent base cations (e.g., Ca²⁺). Although gradients in resource availability among sites did not affect the distribution of species or abundance of legumes strongly, variation in resources are likely to regulate N₂-fixation rates of the various native legume species, and thereby affect ecological functions such as maintenance of N capital and productivity.

Key words: *Aristida stricta*; fire; intermediate disturbance; Leguminosae; light; N₂ fixation; nutrients; Pinaceae; *Pinus palustris*; soil moisture.

Longleaf pine (*Pinus palustris* Mill.)–wiregrass (*Aristida stricta* Michx.) ecosystems dominated the southeastern United States prior to European settlement. These ecosystems are among the most fire-dependent in North America (Christensen, 1987). Fire occurred in longleaf ecosystems prior to European settlement (Landers, van Lear, and Boyer, 1995) with lightning as the primary ignition source supplemented by indigenous populations (Robbins and Myers, 1992). The fire return interval in the pre-European longleaf pine landscape has been estimated to vary from every year to every decade (Wahlenberg, 1946) with reports of as much as 100 g C·m⁻²·yr⁻¹, and the nutrients contained therein, consumed by fire (Olson, 1981). Fire is a major force that regulates the structure and function of these ecosystems.

Frequent fires in longleaf pine–wiregrass systems may lead to substantial nitrogen losses through volatilization, ash convection, erosion, runoff, or leaching (Raison, Khanna, and Woods, 1985). Losses of N through volatilization due to fire have been relatively well documented (Christensen, 1987; Ojima et al., 1994); however, the mechanisms that may operate to counter these losses and maintain soil N levels have not been as rigorously examined. Native legumes have been observed on frequent-

ly burned southern pine sites (Cushwa, Brender, and Cooper, 1966; Speake, 1967; Czuhai and Cushwa, 1968; Hendricks, 1989; White, Waldrop, and Jones, 1990) and may be important in replacing N losses in part or total through symbiotic N₂ fixation (Haines, 1978; Sprent, 1987; Boring, Hendricks, and Edwards, 1990; Hendricks and Boring, 1992), yet no attempt has been made to quantify the extent that these native legumes contribute to N cycling.

Longleaf pine communities span a wide ecological gradient from xeric sandhills to the edge of wetlands (Walker and Peet, 1983; Christensen, 1987). As soil resources vary across this gradient, the magnitude of N inputs from symbiotic N₂ fixation could vary due to changes in legume species composition (Hendricks and Boring, 1999), abundance of individuals, and/or the individual rate of N₂ fixation. All of these variables may be influenced by environmental constraints, particularly water stress and low P availability on sites of low resource availability or reduced light on sites of greater productivity (Dixon and Wheeler, 1983).

Little information is available on species composition of legumes and their abundance in longleaf pine ecosystems, or the factors likely to be important in regulating legume communities. The objectives of this study were to quantify spatial and temporal variation in legume composition and abundance in frequently burned longleaf pine–wiregrass communities that varied from deep sands to depressional wetlands and to determine which specific environmental variables, if any, were correlated with variation in legume composition and abundance.

MATERIALS AND METHODS

Study area—This study was conducted at the Joseph W. Jones Ecological Research Center at Ichauway, Baker County, southwest Georgia,

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⁵ Author for correspondence (phone: 912-734-4706; fax: 912-734-4707; e-mail: rmitchel@jonesctr.org).

USA. The study site has nearly 7500 ha of longleaf pine–wiregrass ecosystems that have been frequently burned (return interval varied from annual to every three years) during the dormant season for ~70 yr (Palik et al., 1997). Longleaf pine–wiregrass ecosystems at the Jones Ecological Research Center span a range in sites from deep xeric sandhills to the edges of wetlands.

Plot establishment—Eighty-five plots (five plots per site) on 17 sites were established throughout the xeric to hydric gradient on Ichauway (soil series included Bigbee, Kershaw, Lakeland, Norfolk, Orangeburg, Pelham, Troupe, Wagram, Albany, and Grady; USDA Soil Conservation Service, 1968). Initially, soil classification maps were used for transect placement within mapped soil types. Seventeen areas were selected for transect establishment based on soil drainage classes of soil mapping units (USDA Soil Conservation Service, 1968): five dry sites (excessively well drained), five wet sites (poorly drained), and seven intermediate sites (well drained to moderately drained). Each site showed evidence of frequent burning and no evidence of prior tillage (i.e., wiregrass was the dominant grass present). Plots were placed at 40-m intervals along a single transect in each soil unit parallel to the long axis of the unit. Each site had at least seven and as many as 20 plots that were initially placed on the transect depending on the size of the mapping unit. Plots falling on or near disturbed sites (i.e., wildlife food-plots, roads, firebreaks, etc.) were discarded. From the pool of plots on a transect, five were randomly selected at each of the 17 sites for a total of 85 plots. Each plot was 20 × 20 m and contained five 1 × 2 m subplots, one located at each corner and one in the center of the plot. The plot size (20 × 20 m) was based on preliminary sampling that suggested legume species vs. area was asymptotic.

Legume survey—Beginning in August 1993, plots were surveyed for the presence of legume species on a monthly basis for 1 yr. Because all study sites were burned under prescribed conditions between 15 February and 1 April 1994 the March survey was omitted. Immediately prior to the final planned survey in July 1994, southwest Georgia received heavy rains from Tropical Storm Alberto (Garza, 1995). Resultant flooding inundated 23, of the 85 plots used in this study, top-killing all legumes on several of the plots. Thus, the July survey was omitted.

Legumes were identified to species (or species complex, in the case of several hybrids within *Desmodium*, *Lespedeza*, and *Galactia* genera) in each 400-m² plot. In each subplot, the number of stems and percent cover for each species were quantified. Percent cover was determined by visual estimates for each species and assigned a value as follows: 1 = trace, 2 = < 1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, or 10 = >95% cover (Peet and Allard, 1993). Voucher specimens were collected and archived in the Jones Center herbarium. Species within *Lespedeza* were further verified by Andrew Clewell in Quincy, Florida, and *Desmodium* species identifications were confirmed by David Hall (University of Florida) in Gainesville, Florida. Nomenclature follows Clewell (1985).

Soil and site variables—In addition to legume surveys, a number of soil and site factors were quantified on each plot. Soil chemical and physical features that might influence the fertility of sites or their water relations and thereby affect legume species composition and/or abundance were analyzed. Also, basal area of pines and oaks was recorded to provide data on overstory conditions that may have affected light availability to the understory. In previous work we have shown a strong linear relationship between basal area and light reaching the understory for basal area values that we encountered in this study, while basal area was not correlated with soil moisture (Palik et al., 1997). Although this is an indirect measure of light at best, it can be quickly obtained and the impact of pine basal area on legumes is of interest to the management and restoration community.

Approximately 20 soil cores (2.5 cm diameter and 30 cm in depth) were collected from the surface horizon of each plot. The cores were

combined into one bulk sample per plot and sieved (>2 mm). Soil pH was determined from a 1:2 ratio of soil and deionized water, using a calibrated pH meter. Potential N mineralization was quantified using the methods of Wood et al. (1992). Soil was maintained at constant temperature (25°C), and moisture content was maintained at –20 kPa. Potential net mineralization was determined by the difference between extractable N (NH₄⁺ and NO₃[–]) after 30 d of incubation and initial extractable N. Extractable P was determined using the methods of Walbridge (1991). Soils treated with CHCl₃ and nonfumigated soil samples were extracted using the dilute acid-fluoride method (Olson and Sommers, 1982), and microbial P was determined as the net increase in extractable P resulting from CHCl₃ fumigation. Soil cations were quantified using the double acid extraction described by Nelson, Mehlich, and Winters (1953), coupled with atomic absorption spectroscopy.

In each plot, 1 m depth soil cores were extracted from each corner and from plot center for soil textural analysis. Depth of each horizon was recorded. A 10-g subsample of soil from each horizon was mixed in a blender with a concentration Calgon™ solution, then wet sieved through a 0.045 mm mesh sieve and dried. The fine soil fraction (silt plus clay) was estimated as mass loss following sieving. Samples were then passed through the following sieve sizes: >2, >0.5, >0.25, >0.045 mm, corresponding to coarse fragments, coarse, medium, and fine sands. Particle size was determined as a profile-weighted average as described by Day (1965). Average texture among the five cores was used to represent plot mean. In addition to texture other soil physical features were quantified. Soil moisture was determined using time domain reflectometry (Topp, Davis, and Annan, 1980). Measurements were taken at 30 and 90 cm depths at the corners and center of the plot. Depth to soil mottling and restrictive layer (clay or rock) were determined at the center of each plot using a bucket auger to a depth of 3.5 m. Landform classes were determined for each plot following the description of landforms by Jones, van Lear, and Cox (1984) and Jacquemain, Jones, and Mitchell (1999). Plot basal area was estimated using a prism (BAF = 10) with samples taken at the center and each corner of the plot.

Multivariate data analysis—Multivariate analysis provides statistical methods for study of the joint relationships of variables in data that contain intercorrelations (ter Braak, 1986). This multivariate analysis is based on ordination, by which sites and/or species are arranged along environmental gradients. Principal components analysis (PCA) was used to ordinate sites and environmental variables. Principal components analysis was run on the correlation matrix, centered, and standardized by site variables. When normality was improved, soil chemical data were log transformed and soil data were arcsine transformed before analysis. Canonical correspondence analysis (CCA) was used to proportion variance in species turnover over the gradient with variation in edaphic and site factors.

Unconstrained and constrained ordinations (ter Braak, 1987) were used to examine variation in soil physical and chemical attributes of plots, legume species composition, and the relationship between the two. Principal components analysis (PCA) was used to examine the variation in site variables among plots (Table 1). For all analyses, three wetland sites (15 plots) were deleted because no legumes were present throughout the survey. They also were inundated through much of the study period, making it impossible to collect data. The lack of complete data sets necessitated their removal. One other plot was removed due to missing data, yielding a total of 69 plots (total of 16 removed). These plots also extended beyond longleaf pine and wiregrass distribution along the gradient. Finally, canonical correspondence analysis was used to examine the variation between species composition and site factors. All analyses were conducted with CANOCO 3.10, a multivariate statistical program (ter Braak, 1990). June survey data sets were selected for analysis of legume populations because June was at or near peak abundance for legume cover values, stem densities, and species number.

TABLE 1. Landforms and soil physical measurements. Mean values (± 1 SE) are presented.

Landform	N	Soil moisture (% v:v)	Depth to mottling (cm)	Depth to restrictive layer (cm)	Coarse fragment (%)	Coarse sand (%)	Medium sand (%)	Fine sand (%)	Silt and clay (%)
Sand ridge	12	5.1 (0.33)	250 (2.0)	334 (0.69)	0.01 (0.01)	4.05 (0.89)	41.09 (3.86)	52.17 (3.55)	4.48 (0.67)
Slope	9	9.8 (1.11)	154 (3.4)	193 (3.92) ^a	9.68 (4.23)	13.87 (1.86)	29.36 (2.75)	43.62 (3.66)	8.73 (2.36)
High flat	37	8.5 (0.35)	171 (1.4)	286 (1.27)	4.86 (1.25)	21.63 (1.54)	30.41 (0.95)	34.84 (1.79)	11.35 (1.64)
Low flat	6	13.4 (1.14)	83 (0.68)	209 (2.46)	0.07 (0.04)	7.95 (0.82)	22.80 (2.36)	38.45 (3.36)	20.07 (6.80)
Pond margin	5	22.6 (2.13)	58 (0.86)	73 (0.99)	18.43 (7.36)	11.10 (2.68)	27.08 (3.46)	35.35 (4.30)	11.00 (1.06)

^a A slope plot had rock at the surface, precluding measurements of depth to mottling and restrictive layer. This plot was assigned depths of zero for these indices.

RESULTS

Soil and site variation across the longleaf pine-wiregrass gradient—Soil moisture relationships arise from complex interactions of texture and landform. From driest to wettest the landforms represented in this study were sand ridges, high flats, slopes, low flats, and pond margins. More plots were classified as high flats (37) than any other landform classification (Table 1). Successively lower numbers of plots were classified as sand ridges (12), slopes (nine), pond margins (five), and low flats (six). Landform classifications and soil texture characteristics were often related. Sand ridges had the highest sand and lowest silt-clay content, averaging 97% sand and 3% silt + clay by mass. Pond margins had the lowest sand content averaging only 73% sand by mass. Soil moisture (v:v) values were the driest on sand ridges and progressively increased on high flats, slopes, low flats, and pond margins, respectively. Soil moisture in the top 90 cm ranged from 5.1% in sand ridges to 22.6% on pond margins (Table 1).

Soil chemical composition varied considerably among plots (Table 2). Extractable Ca^{2+} exhibited the greatest range of all soil chemical variables quantified. Levels of Ca^{2+} were closely correlated with those of Mg^{2+} ($r^2 = 0.70$) and K^+ ($r^2 = 0.30$). Mineralizable N (30 d) varied from a mean of 4.2 $\mu\text{g/g}$ N on xeric sites to 1.1 $\mu\text{g/g}$ N on low flats, and, in general, mineralization rates tended to decrease from xeric to mesic sites. Phosphorus pools (extractable and microbial P) varied as much as eightfold through the study area. Extractable P was negatively correlated with soil moisture, while microbial P showed the opposite relationship (that is, greater microbial P pools on wetter sites and reduced levels in xeric sites). Soils were acidic, with pH ranging from 5.9 on sand ridges and slopes to 5.3 in pond margins.

The PCA of soil variables explained 69% of total variation, with 50% accounted for by the first two axes (Table 3). Depth to mottling, percentage medium sand, depth to restricted layer, and microbial P were the variables most closely related to axis 1. The second axis was de-

finied by Ca^{2+} , Mg^{2+} , and pH. The biplot (Fig. 1) reflects a gradient from dryer sites with lower base cation and pH values to wetter sites with greater base cations.

Seasonal patterns in legume population—Peak abundance as measured by number of stems occurred in June 1994 (Fig. 2). Cover values and legume species richness also varied in a similar pattern through time (both were at maximum in June). Forty-one of the 43 species found over the 1-yr survey period were present during the June survey (Table 4). Of the two species not found in June, *Strophostyles umbellata* first appeared in late June to early July, and *Senna obtusifolia* occurred only as a single plant on one plot in the May survey. Thus, the June survey was selected for further analysis of species distribution across complex gradients. Among the 41 species encountered during the June survey, several were indistinguishable from one another. Two species of *Galactia* (*G. mollis* and *G. volubilis*) were put in the *Galactia* species class because of insufficient taxonomic keys and resultant difficulties in determining the correct species designation (A. Gholson, personal communication). Additionally, *Desmodium marilandicum*, *D. obtusum*, and *D. ciliare* were placed in the *D. ciliare* complex (Table 4). Hybridization of *Desmodium* spp. was apparent across the environmental gradient. Similar problems with hybridization and subsequent difficulty in assigning individual species were observed for several members of the *Lespedeza* genera (A. Clewell, personal communication). Legumes not identified to a species were not included in the analysis. Thirty-seven species were used in all analyses after all ambiguous species complexes were removed.

Legume abundance was greatest in early summer, slightly lower in August, and then declined rapidly from September through November. The first frost in October 1993 top-killed most species of legumes, particularly those with erect or vine-like climbing growth forms such as *Lespedeza* spp., *Desmodium* spp., *Galactia* spp., and *Centrosema virginiana*. Legumes with prostrate or short-erect growth forms such as *Crotalaria rotundifolia*, *Des-*

TABLE 2. Landform and soil chemical measurements. Mean values (± 1 SE) are presented.

Landform	N	pH	Extractable PO_4 ($\mu\text{g/g}$)	Microbial PO_4 ($\mu\text{g/g}$)	Extractable Ca ($\mu\text{g/g}$)	Extractable K ($\mu\text{g/g}$)	Extractable Mg ($\mu\text{g/g}$)	Mineralizable N ($\mu\text{g/g}$)
Sand ridge	12	5.9 (0.08)	16.3 (2.99)	2.7 (0.31)	190 (40)	15.4 (3.13)	18 (3.7)	4.2 (0.44)
Slope	9	5.9 (0.06)	7.5 (2.25)	5.7 (0.72)	365 (75)	12.0 (1.35)	51 (7.1)	2.9 (0.74)
High flat	37	5.7 (0.04)	2.6 (0.29)	6.7 (0.55)	243 (26)	11.2 (0.76)	47 (2.8)	2.3 (0.29)
Low flat	6	5.7 (0.07)	6.9 (0.96)	5.0 (0.29)	265 (16)	13.7 (0.76)	45 (5.5)	1.1 (0.42)
Pond margin	5	5.3 (0.05)	2.8 (0.23)	8.0 (1.11)	74 (30)	13.8 (1.42)	16 (1.9)	2.8 (0.85)

TABLE 3. Principal components analysis (PCA) factor loadings for environmental variables from full data set analysis summary of eigenvalues and the cumulative percentage variance of environmental data explained, with various environmental data sets. Total variance and sum of all unconstrained eigenvalues = 1.000.

	Axis 1	Axis 2	Axis 3	Axis 4
pH	-0.3654	-0.6116	0.487	-0.0017
Extractable PO ₄	-0.4231	-0.2093	-0.5946	0.3717
Microbial PO ₄	0.7446	-0.1461	0.1038	-0.1435
Extractable Ca	-0.0317	-0.8336	0.3709	-0.0457
Extractable K	0.2209	-0.3869	-0.1786	-0.7447
Extractable Mg	0.4777	-0.7943	0.2087	0.0724
Mineralizable N	-0.5252	-0.0707	0.0776	0.0699
Depth to mottling	-0.8073	-0.0704	-0.0764	-0.1715
Depth to restr. layer	-0.5891	-0.3145	-0.2543	-0.2196
% silt and clay	0.5570	0.0701	0.0125	0.1839
% coarse sand	0.4226	-0.5398	-0.4232	-0.4830
% medium sand	-0.7204	-0.1484	-0.2205	0.1344
% fine sand	-0.5198	0.4287	0.6217	0.1484
Soil H ₂ O (May and June)	0.7915	0.3296	-0.0427	0.1395

modium lineatum, and *Rhynchosia reniformis* appeared to be more resistant to frost, perhaps due to more favorable microclimatic conditions. *Petalostemon* appears to be among the most cold-hardy legumes found in these communities. It was the only genus that persisted through repeated frosts and was present into the January and February surveys. Both *P. albidum* and *P. pinnatum* were observed in the January survey, but only *P. pinnatum* persisted until February. *Petalostemon pinnatum* was the only legume species present in every survey conducted over the 1-yr period of this study. *Petalostemon pinnatum* and *Psoralea lupinellus* were the first species to sprout on these plots in February 1994. Most legumes emerged the following March soon after dormant season burns. Stem density increased from April through June, when peak abundance was observed (Fig. 2).

Spatial distribution of legume populations—Legumes were abundant with an average of 119 stems for a 10-m² plot (119 000 stems/ha) during peak abundance (Fig. 2). An average of 3.1, 8.1, and 9.8 species were recorded for 2-, 10-, and 400-m² plot areas, respectively (Table 5). Ninety-four percent of all 2-m² subplots contained at least one legume species. A maximum of eight legume species occurred in the 2-m² subplots. Thus, the legume community is diverse and nearly ubiquitously distributed.

A plot of the sum of species cover values (using midpoint for each cover class) per plot and the PCA axis 1 scores from the full environmental data set illustrates legume cover values across the complex gradient (Fig. 3). The most xeric plots (mostly sand ridges) received the lowest PCA axis 1 scores, while the most hydric plots (mostly low flats and pond margins) received the highest PCA axis 1 scores. Legume cover was variable, but maximum at the middle portion of the gradient and declined at the more hydric and xeric extremes.

Canonical correspondence analysis, using stem density and the environmental data explained only 27% of the total variation among plots. Xeric site species (*Galactia microphylla* and *Petalostemon pinnatum*) were located in

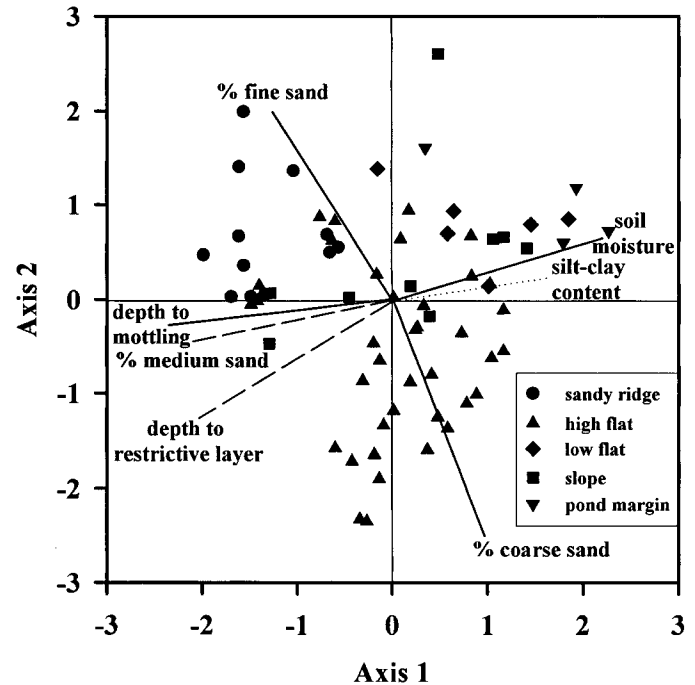


Fig. 1. Biplot of axes 1 and 2 from principal components analysis of environmental data across a gradient for a longleaf pine-wiregrass ecosystem.

the upper left quadrant, while mesic site species were found in the upper right quadrant of the biplot, with *Lespedeza angustifolia* representing species ordinated in this quadrant. When environmental factors were plotted with legume species (*Lespedeza angustifolia* removed as an outlier), axis 1 was largely defined by soil moisture and depth to a restrictive layer, while axis 2 was most strongly influenced by Ca, Mg, and pine basal area (Fig. 4).

DISCUSSION

Site variation across complex ecological gradients—References to changes in vegetation composition across environmental gradients often allude to the importance of

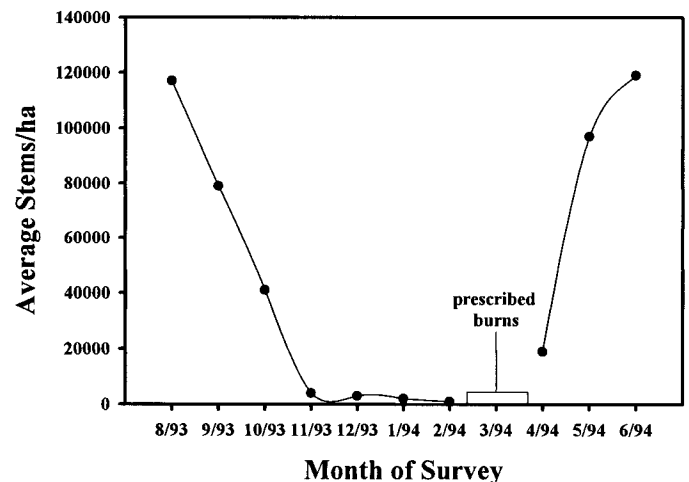


Fig. 2. Average legume stem density throughout survey period.

TABLE 4. Herbaceous legume species present across a longleaf pine-wiregrass complex gradient in June 1994.

Species	Species designation ^a	Freq. ^b (%)	Density ^c (stems/ha)
<i>Amorpha fruticosa</i> L.	AF	2.8	90
<i>Baptisia albescens</i> Small	BA	1.4	0
<i>Cassia</i>			
<i>deerengiiana</i> Macbride	CD	7.1	240
<i>fasciculata</i> Michx.	CF	2.8	10
<i>nictitans</i> L.	CN	47.1	6290
<i>Centrosema virginianum</i> (L.) Benth.	CV	80	8860
<i>Clitoria mariana</i> L.	CM	57.1	6870
<i>Crotalaria</i>			
<i>purshii</i> DC.	CP	2.8	70
<i>rotundifolia</i> Walt. ex Gmel.	CR	42.9	4500
<i>Desmodium</i>			
<i>ciliare</i> (Muhl. ex Willd.) CD.			
(<i>ciliare</i> , <i>obtusum</i> , <i>marilandicum</i>)	DC	37.1	4800
<i>flordanum</i> Chapm.	DF	1.4	0
<i>laevigatum</i> (Nutt.) DC.	DL	2.8	40
<i>lineatum</i> DC.	DX	32.9	3600
<i>paniculatum</i> (L.) DC.	DP	1.4	0
<i>strictum</i> (Pursh) DC.	DS	25.7	1010
<i>viridiflorum</i> (L.) DC.	DV	10.0	910
<i>Galactia</i>			
<i>erecta</i> (Walt) Vail	GE	44.3	2410
<i>microphylla</i>	GM	2.8	190
spp. (<i>mollis</i> , <i>volubilis</i> , other)	GZ	50.0	4130
<i>Indigofera caroliniana</i> Mill.	IC	10	190
<i>Lespedeza</i>			
<i>angustifolia</i> (Pursh) Ell.	LA	14.3	840
<i>capitata</i> Michx.	LC	1.4	70
<i>hirta</i> (L.) Hornem.-Clewel	LH	8.6	210
<i>repens</i> Michx.	LR	54.3	3590
<i>stuevei</i> Nuttall	LS	5.7	690
<i>virginica</i> (L.) Britt	LV	20.0	890
spp. (other)	LZ	8.6	490
<i>Psoralea</i>			
<i>canescens</i> Michx.	PC	8.6	10
<i>lupinellus</i> Michx.	PL	17.1	5560
<i>Petalostemom</i>			
<i>albidum</i> (T.&G.) Small	PA	15.7	2600
<i>pinnatum</i> (Walt. ex. Gmel.) Blake	PP	12.9	2740
<i>Rhynchosia</i>			
<i>reniformis</i> (Pursh) DC.	RR	70.0	5760
<i>tomentosa</i> (L.) (H.&A.	RT	5.7	190
<i>Schrankia microphylla</i> (Dry.) MacBr.	SM	70	10200
<i>Stylosanthes biflora</i> (L.) BSP	SB	92.3	17130
<i>Tephrosia</i>			
<i>florida</i> (Dietr.) Wood	TF	45.7	1140
<i>spicata</i> (Walt.) T&G	TS	15.7	390
<i>virginiana</i> (L.) Pers.	TV	2.43	14130
<i>Zornia bracteata</i> (Walt.) Gmel.	ZB	24.3	5000

^a Species designation in canonical correspondence analysis ordinations.

^b Frequency of species occurrence in 69 plots.

^c Density = average number of stems per species per hectare. [No. stems of one species counted in 350 subplots (700 m²) divided by 0.07 = stems/ha].

TABLE 5. Legume species diversity, June 1994.

Measurement	2 m ^a	10 m ^b	400 m ^c
Average no. of species	3.1	8.06	9.81
SD	1.66	2.75	2.71
Maximum	8	14	16
Minimum	0	1	1
Sample size	350	70	70
Freq. (legumes present)	94%	100%	100%

^a Average number of species found in 1 × 2 subplots.

^b Average number of species found in five 1 × 2 m subplots/plot.

^c Average number of species in each plot.

resource availability, but few data are reported that would indicate which resources are limiting and how they vary across sites (Christensen, 1981; Stout and Marion, 1993; Ware, Frost, and Doerr, 1993). Jones, van Lear, and Cox (1984) sampled vegetation and soils across a longleaf pine gradient and were able to classify sites based on depth of a sandy epipedon; however, soil moisture relations were inferred from texture and landscape position with no direct measures of soil moisture or fertility. In a recent regional study, Peet and Allard (1993) defined four major series of longleaf pine-dominated vegetation, primarily differentiated by gradients in soil moisture (xeric, subxeric, mesic, and seasonally wet); however, no soil data were reported.

Christensen (1987) suggests that moisture gradients in the Coastal Plain of the southeastern United States may be positively correlated with nutrient availability, particularly N. Generally, soils in the lower Coastal Plain physiographic region are characterized by coarse textured, highly weathered parent material with low cation exchange capacity and low fertility (Buol, 1973; Brown, Stone, and Carlisle, 1990). As soil moisture availability and productivity increase, organic matter content of soil should increase due to greater inputs to the detritus community (Christensen, 1987). Nutrient storage and availability in Coastal Plain soils have been reported to be largely dependent on the amount and type of organic matter (Gholz and Fisher, 1982; Abramson and Harnett,

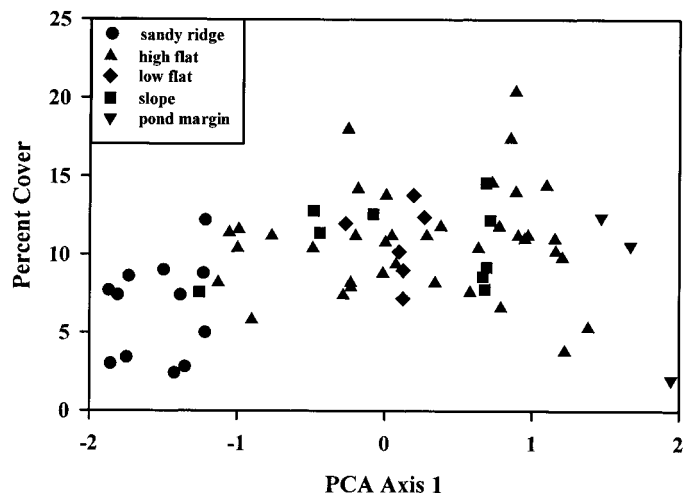


Fig. 3. Percent cover of legumes graphed across PCA scores for first axis.

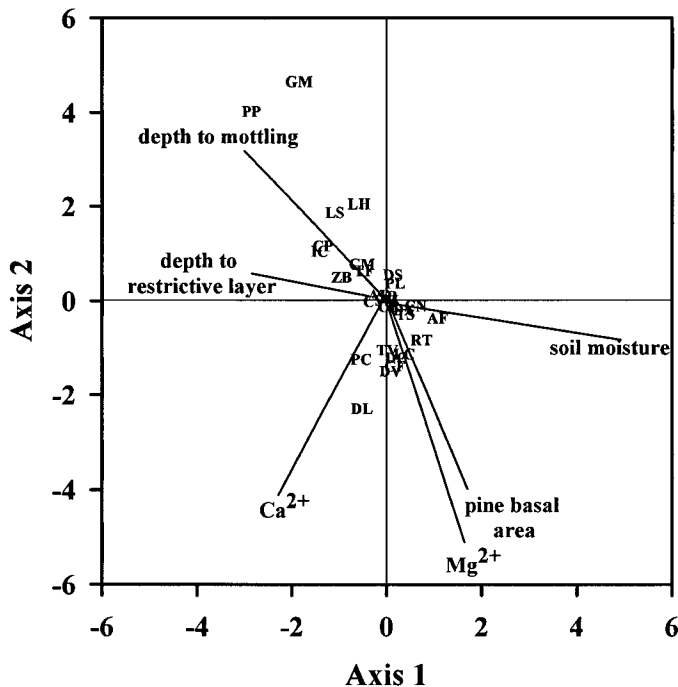


Fig. 4. Biplot of axes 1 and 2 of CCA analysis of species distribution and environmental variables across a gradient for a longleaf pine-wiregrass ecosystem.

1990; Brown, Stone, and Carlisle, 1990). Thus, increases in fertility should parallel those of moisture in the landscape (Christensen, 1987). This was evident in base cations; however, we found that potential N mineralization and extractable P were inversely related to moisture across the gradient (Tables 1, 2).

Although extractable P was greatest on xeric sites and decreased as soil moisture increased, microbial P increased with soil moisture. Apparently, microbial immobilization is limited on xeric sites. Controls on N mineralization across the gradient are perhaps related to complex feedback relationships among sites, disturbances, and vegetation. Xeric sites sampled in this study were the only sites to have an appreciable quantity of oaks in the overstory, most likely due to heterogeneity in burning patterns (Jacqmain, Jones, and Mitchell, 1999). Also, xeric sites had greater potential net mineralization. Klemmedson (1987, 1991) found that N mineralization was linearly related to gamble oak (*Quercus gambelii*) basal area. Wedin and Tilman (1990) reported that after 3 yr, the grass species that was growing on a soil was more important in regulating net mineralization of N than soil type, even though N mineralization varied more than eightfold among the three soil types at the start of the 3 yr experiment. Moreover, those grass species that were more competitive on sites of higher fertility resulted in the greatest soil N mineralization when grown for 3 yr. Perhaps oaks, which tend to be more nutrient demanding, are serving a similar function in these communities (Jacqmain, Jones, and Mitchell, 1999).

Although nutrients and soil moisture were correlated (N and P in negative ways, soil cations in positive ways), soil moisture tended to have the strongest influence on PCA ordination. Soil physical factors defined the primary

axis, while soil cations (Ca^{2+} and Mg^{2+}) were the most important factors related to the second axis. Thus, a hydrologic gradient may dominate site variation even though variation in fertility is observed.

Legume populations and site variation—Legumes were abundant (at peak almost 120 000 stems/ha), ubiquitously distributed (94% of all 2-m² subplots in uplands had at least one species of legume), and legume communities were rich in legume species (as many as 37 distinct species were found). Although legume abundance was somewhat related to site, abundance was only affected at the extremes in the gradient. Walker and Peet (1983) and Taggart (1994) reported that legume abundance was reduced in poorly drained savannas, an observation previously noted by Gano (1917) and Wells and Shrank (1931). The low population of legumes on the wet end may be related to chronic soil inundation and corresponding soil anoxic conditions, although many legume species can survive short-term inundation. At the end of this study a tropical storm inundated many of the plots and resulted in top-kill of the legumes present, however several months later legumes had resprouted and appeared healthy (M. Hains, personal observation). Thus, multiple inundations may be required to decrease legume populations. In addition to low oxygen levels associated with chronic flooded conditions, wet areas in this study were also associated with low extractable P levels, which may also serve to limit legume abundance.

Legume species turnover was low across the gradient. Three species tended to dominate ordinations; *Lespedeza angustifolia* was the dominant legume found on seasonally wet sites, and *Galactia microphylla* and *Petalostemon pinnatum* were characteristic of xeric sites, while other species tended to ordinate near the origin. The low species turnover may be a result of the perennial nature of legumes in this ecosystem, and the frequent dormant-season fire regime. Of the 37 confirmed species, all but two are perennial (two species of *Cassia* encountered, *C. fasciculata* and *C. nictitens*, are annuals). When disturbance is more frequent than the time required to competitively exclude perennials, species tend to occupy a greater diversity of sites (Huston, 1979). White, Waldrop, and Jones (1990) found that legume abundance increased with frequent winter fire in long-term study plots in southeastern Coastal Plain loblolly pine forests; however, frequent summer fire seemed to inhibit legume populations, perhaps due to depletion of carbon stores in roots, mortality of newly germinating seedlings, or fire impacts on flowering and seed production.

Only 27% of species variation across the gradient could be accounted for by environmental variables on the first four CCA axes. Soil moisture relationships appear to be the strongest variable influencing populations (i.e., it was most strongly related to species axis 1, $r^2 = 0.57$). Sprent (1985) found that N_2 fixation is strongly limited by drought, but different host species vary in their drought tolerance (Sprent, 1987). Drought tolerance and/or avoidance mechanisms of legumes in this community have not been studied, however they may be of critical importance in developing a mechanistic understanding of legume population structure and function.

Other environmental factors related to species axis

were Ca^{2+} and species axis 2, and P and species axis 3. Requirements of Ca^{2+} by legumes increases as soil pH decreases (Lowther and Lonerogan, 1968). Increased Ca^{2+} increased nodulation in acidic conditions (Munns, 1968, 1970). Perhaps variation in Ca^{2+} influences populations of legumes through regulating nodulation and N_2 fixation. Although extractable P levels varied by more than a factor of fivefold (extractable P from sand ridges was 16.3 ppm, while soils from pond margins had only 2.8 ppm P), the low level of P throughout the gradient may be strongly limiting legume abundance on all sites. Again, no study of P relations and legumes has been reported for species native to longleaf pine–wiregrass savannas. Probert and Williams (1985) report that a tropical species of *Stylosanthes* was able to grow and fix N_2 at much lower P fertility than agricultural legumes. Certainly more work is needed to understand the manner in which P may influence legume populations, their symbiotic relationships (including endomycorrhizae and *Rhizobium*), and their function within these ecosystems.

Lastly, pine basal area was related to abundance of legume species. This may be due to differential species response to pine overstory effects on light quantity and quality. Palik et al. (1997) showed light to vary in these open-canopy forests from ~25% to almost 90% full sunlight and be linearly related to basal area ($r^2 = 0.71$). In addition, we have recently measured changes in light quality, with the red:far red ratio varying from 1.2 in high-light conditions to 0.5 in woodland shade (Endlar, 1993). Although little is known with respect to the effects of light on competitive ability of these native legumes, Dixon and Wheeler (1983) report that nodule development and function were affected by changes in light (quantity, quality, and duration). Light influenced N_2 fixation not only through changes in photosynthetic rates, which would affect the supply of energy to nodules (Ching et al., 1975), but also through phytochrome-mediated mechanisms from enrichment of far red light in understory (Sprent and Silvester, 1973; Lie, 1974).

Ecological implications—The wide ecological amplitude of legumes, their abundance, and species richness undoubtedly are important in understory structure and ecosystem function for longleaf pine–wiregrass ecosystems. Legumes are common in fire-dependent communities (Leach and Givnish, 1996) and may be important in replacing N lost to fire (Hendricks and Boring, 1999). The sites studied here have received frequent (1–3 yr return fire interval) dormant-season fires, which may have promoted the establishment of legumes and decreased the competitive exclusion of legumes once established (see Huston, 1979). Legume populations were not strongly affected by site variation, except at the extremes in the gradient. However, a number of environmental variables were related to the small species turnover observed, with soil water relations being the most important factor; Ca^{2+} , P, and pine basal area (light) were also related to legume distribution.

However, the rates of fixation by individuals may be strongly affected by variation in resource availability. As sites become more stressful, photosynthetic production is likely to decline and may limit rates of fixation. No published studies have attempted to quantify fixation rates

across the environmental gradient, although Hendricks and Boring (1999) found strong variation in fixation rates among three legume species native to frequently burned Piedmont loblolly pine sites in northern Georgia. These data, however, give guidance as to which species are present in these ecosystems, their relative abundance, and their distribution. These data are important in determining which of the 37 species to prioritize for future investigations into species-specific differences in fixation and regulation of fixation rates for individuals due to variation in resource availability.

Furthermore, legumes tend to be high in protein and mineral content, thus they may be preferable forage by a number of herbivores in the longleaf pine system. For instance, juvenile gopher tortoises (*Gopherus polyphemus*) rely heavily on legumes to meet nutritional requirements (Garner and Landers, 1981; Macdonald and Mushinsky, 1988). Other herbivores such as white-tail deer (*Odocoileus virginianus*) also consume legumes preferentially (Czuhai and Cushwa, 1968), bobwhite quail (*Colinus virginianus*) and other avian species also feed heavily on legume seed (Speake, 1967). The manner in which herbivory influences legume distribution or the role that specific legumes play in maintaining herbivore populations deserve greater attention. In particular, the role of fauna in seed dispersal and the interaction of disturbances in regulating the regeneration niche of individual legume species may more clearly explain patterns of abundance and species distribution.

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