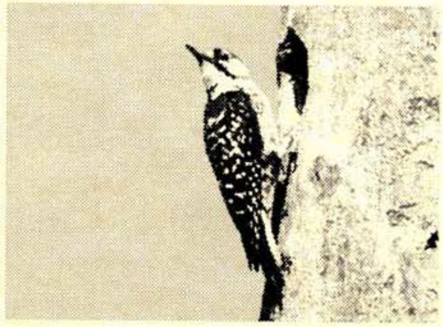
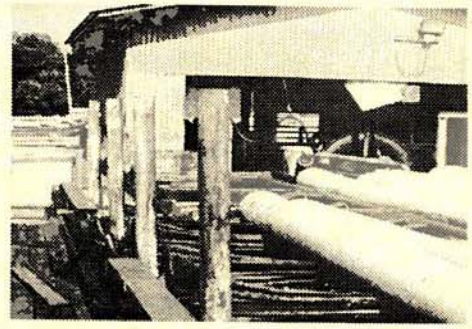
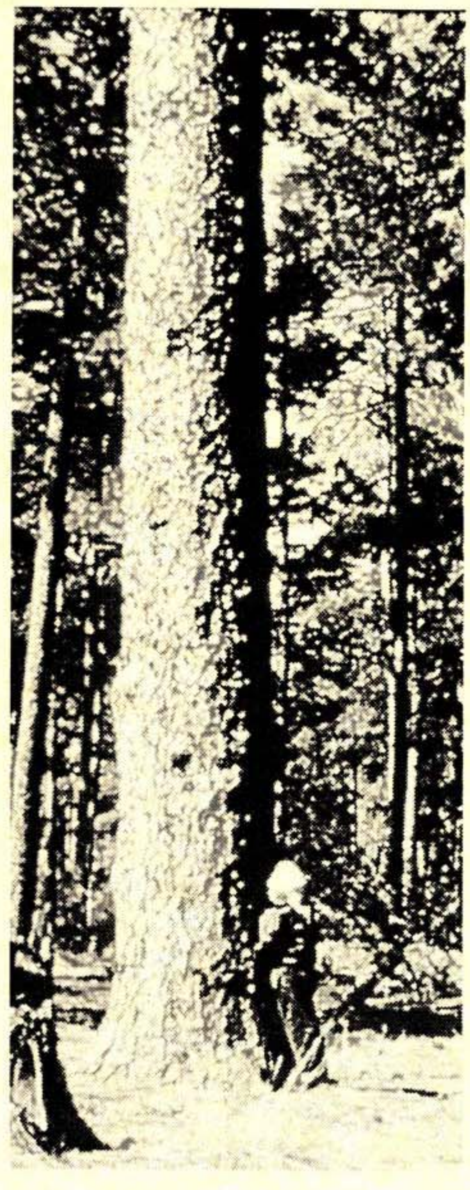




PROCEEDINGS



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Legume Population Dynamics in a Frequently Burned Longleaf Pine-Wiregrass Fire Ecosystem

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ABSTRACT - Longleaf pine-wiregrass ecosystems once covered most of the southeastern Coastal Plain, but this ecosystem type has been greatly reduced in range and extent. Fire has historically played an important role in species distributions and soil chemical dynamics of this diminished longleaf pine-wiregrass ecosystem. This frequently burned ecosystem may sustain large losses of N through volatilization by fire. Through symbiotic N-fixation, legumes may play an important role in sustaining N levels. However, the temporal and spatial distribution of legumes in longleaf pine-wiregrass ecosystems has been little studied. A series of plots were established across a frequently burned-complex gradient in a longleaf pine-wiregrass ecosystem, and surveyed monthly over a one year period to assess temporal variation. Legumes were surveyed by species for presence, cover class, and stem density. The peak month in species richness was selected for further multivariate statistical analysis to assess spatial variation in relation to several environmental variables measured across the complex environmental gradient. The number of legume species reported here is much greater than other reports from the southeastern Coastal Plains. Legume populations decreased slightly at the xeric end of the environmental gradient, and decreased steeply at the hydric end of the gradient, with virtually no legumes being found in the wetlands sampled. Some species appeared more tolerant of periodically inundated soil conditions (i.e. *Lespedeza angustifolia*), while others occurred most frequently on very xeric soils (i.e. *Petalostemon pinnatum*). Legume stem densities and cover class values appeared to be correlated with soil moisture, pH, extractable PO_4, extractable Ca, extractable Mg, and extractable K. From this study, it appears that legume populations in undisturbed, fire maintained, longleaf-wiregrass ecosystems, are larger and more divers than previously documented. The large number of species (43), high stem densities (119,460 legume stems ha^{-1}), and large cover classes, indicate that legumes may play important roles as faunal food sources. From the large number of legumes found across the complex gradient, there is the potential for these legumes to fix a large amount of N in this system. Furthermore, this study is the first to document the spatial and temporal distributions of many of these species across a complex environmental gradient.

INTRODUCTION

Frequent fires in longleaf pine-wiregrass systems may lead to substantial nutrient losses through volatilization, ash convection, erosion, runoff, or leaching. Losses of N through volatilization in fire dominated communities have been relatively well documented (see Christensen 1987). However, mechanisms that maintain soil N levels have not been as rigorously examined. Large populations of herbaceous legumes have been observed on frequently burned southern pine sites. Through long term inputs, biological fixation may replace N losses in part or total due to burning (Boring et al. 1990). While it is generally accepted that legume populations increase with increasing fire frequency and can be an important source for N inputs, quantifying the functional control that legumes exert on maintenance of nitrogen in frequently burned longleaf pine ecosystems has not been attempted.

Longleaf pine communities span a wide ecological amplitude from xeric sandhill communities to the edge of wetlands. As soil resources vary across sites, the magnitude of N inputs from symbiotic fixation could vary due to changes in population (both changes in species and abundance of individuals), or as resources become limiting, the individual rate of N fixation may decline. No estimates of fixation from native legumes in longleaf ecosystems have been published. Before this type of investigation can be conducted, more information is needed on the species of legumes present and their abundance throughout the longleaf pine landscape, as well as the factors that are likely to be important in regulating legume populations. The objective of this study was to quantify variation in legume populations in frequently burned longleaf pine-wiregrass communities that varied from deep sands to depressional wetlands, and determine which specific environmental variables were correlated with variation in legume populations.

METHODS

This study was conducted at the Joseph W. Jones Ecological Research Center at Ichauway in southwest Georgia. The study site has nearly 6,000 hectares (about 15,000 acres) of longleaf pine-wiregrass savannas that have been frequently burned (return interval varied from annual to every three years) during the dormant season for approximately 70 years. Longleaf pine wiregrass sites at Ichauway span the range from deep sandhills, to the edge of wetlands in which standing water is present throughout much of the year.

Eighty-five plots were established throughout a xeric to seasonally hydric gradient. Initially, soil classification maps were used for transect placement within mapped soil types. Seventeen areas were selected for transect establishment: 4 dry sites, 4 wet sites, and 9 intermediate site. Each site showed evidence of frequent burning and no evidence of prior tillage (i.e. wiregrass was the dominant grass present). Of the remaining plots, five were randomly selected at each of the 17 sites for a total of 85 plots. Each plot was 20x20m and had five 1x2m nested subplots, four located in each corner, and one in the center of the plot.

Beginning in August 1993, all 85 plots were surveyed for legumes. Surveys continued on a monthly basis for one year. The March 1994 survey was omitted while the plots were prescribed burned and the July 1994 survey was omitted due to floods from Tropical Storm Alberto.

Legumes were identified to genus and species, or to a species complex in the case of some *Desmodiums*. The number of species present in each 400 m^2 plot was recorded. In addition, the presence of gopher tortoises (*Gopherus polyphemus)*, and important legume herbivore, was estimated by quantifying the number of burrows and distance of burrows form sub-plots (to a maximum distance of 10m). Lastly, basal area of pines and oaks were recorded to provide some data on relative openness and light availability to the understory.

To assess soil fertility, fifteen to twenty soil cores (2.5 cm diameter) were collected from the surface horizon of each plot. The cores were combined into one bulk sample per plot and sieved (<2mm). Subsamples of soil were dried at 100^{o}C for 48 hours to determine percent moisture content. Soil samples at field moisture content were used for chemical analysis, and the quantity of soil was converted to dry weight from the subsample as described above. Soil analysis followed standard methods. Gopher tortoise abundance and activity were measured on all plots.

All analyses were conducted with CANOCO 3.10, a multivariate statistical package (ter Braak 1987). 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. Fifteen plots from the three wetland sites thrown out of the analysis because there were no legumes present in the wetlands. Legume diversity and abundance was analyzed using stem density, percent cover, and presence/absence (PA) data.

Multivariate analysis provides statistical methods for study of the joint relationships of variables in data that contain intercorrelations. This multivariate analysis is based on ordination, by which sites and/or species are arranged along environmental gradients. Principle components analysis (PCA) was used to ordinate sites and environmental variables. Correspondence analysis (CA) was used to determine species turnover across complex environmental gradients, and canonical correspondence analysis (CCA) was used to proportion variance in species turnover over the gradient with variation in edaphic site factors.

RESULTS

The peak abundance as measured by number of stems occurred in June 1994. Of these 41 species, several were indistinguishable from one another. Two species of *Galactia* were put in the *Galactia spp*. class because of insufficient taxonomic keys and resultant difficulties in determining the correct species designation (*G. mollis* and *G. volubilis*). Additionally, *Desmodium marilandicum, D. obtusum*, and *D. ciliare* were placed in the D. ciliare complex. Hybridization of *Desmodiums* was apparent across the environmental gradient sampled. Similar problems with hybridization and subsequent difficulty in assigning individual species were observed for several members of the *Lespedeza* genera (personal communication with A. Clewell, and *Galactias* personal communication with A. Gholson). Legumes not identified to a specific species were not included in the analysis. Thirty-seven species were used in all analyses after all ambiguous species were removed.

Some genera were notably more abundant in cover values, stem values, and numbers of species present. The two genera with the largest number of species encountered during the June survey were *Desmodium* (7) and *Lespedeza* (6). Several measures of abundance (species presence/absence, stems per plot, and mean cover class) were used in assessing legume distributions.

Within the complex gradient sampled, an average of 119 stems for a 10-m^2 plot (119,000/ha) were found during peak abundance. Legume abundance was distributed across a wide range of species with 3.1 species found in 2-m^2 subplot, and 8.1 and 9.8 for 10-m^2 and 400-m^2 plot areas. Ninety four percent of all 2-m^2 subplots contained at least one legume species and up to eight legume species were found in individual 2-m^2 subplots. Thus, legumes were both diverse and widely distributed.

In addition to variable soil moisture relations, soils were quite variable in their chemical composition. Extractable Ca^{+2} exhibited the greatest range of all soil chemical variables quantified. Levels of Mg^{+2} were closely correlated to those of Ca^{+2}. Furthermore, K^+ levels were correlated (r^2=0.30) with extractable Ca^{+2}, heavier textured soils with greater CEC tended to have greater cation concentration than deep sands with low organic matter and clay content. Mineralizable N varied from a mean of 4.2 ppm N on xeric sites to 1.1 ppm N on low flats, and in general mineralization rates tended to decrease from xeric to mesic sites. Phosphorus pool (extractable and microbial P) varied as much as 8-fold through the study area with greater extractable P in xeric sand ridges and declines in extractable P as sites became more mesic; however, microbial P showed the opposite relationship (greater microbial P pools on wetter sites and declines as sites became more xeric). Soils were uniformly acidic with pH ranges from 5.9 on sand ridges and slopes to 5.3 in pond margins.

Principal Components Analysis (PCA) was run with three sets of environmental variables: physical soil variables, chemical soil variables, and both data sets. The physical soil data set yielded the highest eigen values and percent variance explained: 87.6% of the variance was accounted for by axes 1-4 of the PCA analysis. Depth-to-mottling and soil moisture were the most important environmental variables defining axis 1, while percent coarse-sand and fine-sand were the most important variables defining axis 2. Wet-mesic plots ordinated to the right side of the graph and xeric plots ordinated to the left. Percent silt and clay predominantly influenced axis 3, and axis 4 was largely defined by percent medium sand.

The PCA summary analysis of the chemical soil data set resulted in a slightly smaller cumulative variance (85.1%) explained by axes 1-4 than for the physical soil variables. Axes 1 and 2 of the physical soil data set explained more variance (66.9%) and had higher eigen values than axes 1 and 2 of the chemical soil data set. Mg and Ca were the most important variables defining axes 3 while mineralizable N was them most important variable in defining axis 4. When chemical and physical soil variables were combined, the total percent of variation explained among plots on the first four axes dropped to 68.5%. Ordination of the combined data set (soil physical and chemical variables) was similar to the ordination of the physical data set in that xeric plots were ordered to the left and mesic plots were found to the right on Axes 1 and 2.

A plot of the sum of species cover values per plot and the PCA axis 1 scores from the full environmental data set illustrates legume cover values across the complex gradient. The most xeric plots (mostly sand ridges) received the lowest PCA axis 1 scores, illustrating a hydrological and extractable P gradient. Legume cover was variable across the gradient but appeared to increase slightly as sites became more mesic, then decline rapidly at the more hydric end of the gradient.

The legume species distribution was ordinated using correspondence analysis (CA). Three legume species data sets were analyzed with CA: species present, cover class by species, and stem density of each species. The stem density data set yielded the highest cumulative unconstrained eigenvalue (5.91) and percent variation of species data explained (41.3%) on the first four axes. Ordination of legume species by stem density (axes 1 & 2) resulted in three species outliers strongly influencing the ordination and obscuring most species in the plot origin. The three species were *Lespedeza angustifolia*, *Galactia microphylla*, and *Petalostemon pinnautum*. *L. angustifolia* was one of the few legumes, in some cases the only legume found on the frequently inundated pond margin sites. On the opposite extreme *G. microphylla*, and *P. pinnautum* occurred nearly exclusively on the most xeric sites. While these species were segregated along the gradient, most of the other species encountered were not as strongly influenced by site variation. The ordination of species located near the origin of the above mentioned plots became more discernible when the outliers are excluded. There was a more continuous gradient of species turnover across the environmental gradient: xeric site species were in the lower right (i.e., *Psoralea lupinellus*, *Tephrosia florida*, *Lespedeza hirta*, and *Cassia deeringiana*) quadrant: mesic site species (*Lespedeza capitata* and *Cassia fasciculata*) ordinating in the upper left quadrant: and intermediate site species *Tephrosia virginiana, Psoralea canescens,* and *Desmodium laevigatum* found in the lower left quadrant of the plot of axis 1 and 2.

Canonical Correspondence Analysis (CCA) with the stem density data set and the full environmental data set yielded the highest unconstrained (5.91) and constrained eigenvalues (2.61), and the greatest total species variation explained (27.5%) , as compared to the cover class and species presence data sets. Similar to the cover and species presence ordinations, xeric site species (*G. microphylla* and *P. pinnautum*) were located in the upper left quadrant while mesic site species were found in the upper right quadrant of the bi-plot, with *L. angustifolia* removed as an outlier) axis one was largely defined by soil moisture and depth to mottling, while axis 2 was most strongly influenced by Ca, Mg, and pine basal area.

DISCUSSION

Legumes are rich in species, ubiquitous in abundance, and are widely distributed throughout the complex gradient inhabited by longleaf pine-wiregrass ecosystems. The number of species reported in this work (43) is much greater than reported by Walker and Peet (1983): they reported eight species of legumes encountered throughout a xeric to hydric gradient in longleaf wiregrass savannas in the Green Swamp. In fact, the number of legume species reported for this study rivals that reported by Peet and Allard (1993) in a regional study of longleaf pine savannas east of the Mississippi in which they report only 42 legume species.

One reason for the high degree of species richness may be the wide ecological gradient sampled and the frequent dormant season burning that occurred on the study site. Although large variation in sites were documented, abundance of legumes and species distributions of legumes were not very sensitive to site variation, except at the extremes of the gradient. Legume abundance increased from xeric sites and decreased rapidly at the hydric extreme in the gradient. In addition, most species ordinated near the origin of CA and CCA analysis with the exception of three species *L. angustifolia* on the wet end and G. microphylla and P. pinnatum on the dry end. Savannas in this study were burned frequently during the dormant season (return intervals varying from 1-3 years). White et. al. (1990) reported that frequent dormant season burning increased legume populations in southern pine forests, although fires during the growing season at the same frequency tended to reduce legume abundance. They reported as many as 28,000 legume plants per plot (.1ha^{-1}) in the annual dormant season burning treatment. Although we were unable to clearly identify individual plants due to the clonal nature of many of the legumes encountered, the 119,000 stems ha^{-1} average across the entire gradient suggests similar abundance to that reported by White et. al. (1990). In addition to generally increasing abundance of legumes, frequent fires may increase the ecological amplitude of legumes by precluding competitive exclusion. In addition, legumes are preferred forage for many herbivores in this ecosystem. Herbivory may be acting to reduce abundance and presence of species on sites that are capable of supporting that species. Thus disturbance may be acting in diametrically opposite ways; fire increasing the range of sites occupied, and herbivory reducing presence on particular sites, but both acting in concert to reduce the coupling between variation in site factors and population characteristics.

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