

Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina*

Joan Walker & Robert K. Peet**

Department of Biology 010A, University of North Carolina, Chapel Hill, NC 27514, U. S. A.

Keywords: Biomass, Coastal plain, Fire, Grassland, North Carolina, Phenology, *Pinus palustris*, Primary production, Savanna

Abstract

Fire-maintained, species-rich pine-wiregrass savannas in the Green Swamp, North Carolina were sampled over their natural range of environmental conditions and fire frequencies. Species composition, species richness, diversity (Exp H' , $1/C$), and aboveground production were documented and fertilization experiments conducted to assess possible mechanisms for the maintenance of high species diversity in these communities.

Although savanna composition varies continuously, DECORANA ordination and TWINSPLAN classification of 21 sites facilitated recognition of 3 community types: dry, mesic, and wet savannas. These savannas are remarkably species-rich with up to 42 species/0.25 m² and 84 species/625 m². Maximum richness occurred on mesic, annually burned sites. Aboveground production, reported as peak standing crop, was only 293 g . m⁻² on a frequently burned mesic savanna but was significantly higher (375 g . m⁻²) on an infrequently burned mesic site. Production values from fertilized high and low fire frequency sites were equivalent. Monthly harvest samples showed that savanna biomass composition by species groups did not vary seasonally, but within groups the relative importance of species showed clear phenological progressions.

The variation in species richness with fire frequency is consistent with non-equilibrium theories of species diversity, while phenological variation in production among similar species and the changing species composition across the moisture gradient suggest the importance of equilibrium processes for maintenance of savanna diversity.

Introduction

The savannas or grass sedge bogs of the coastal plain of the southeastern United States are characterized by scattered pines with an understory sward of mixed graminoids and forbs. These savannas are

well known for their floristic richness and especially their numerous orchids, insectivorous plants and regional endemics (e.g. Wells, 1928; Wells & Shunk, 1928; Lemon, 1949). The descriptive reports of Wells and others prompted our study of the diversity of these communities in the Green Swamp of North Carolina where the most extensive and best preserved mesic savannas on the Atlantic coast are located.

Initial results showed that vascular plant species richness was often near 40/m², a level of small-scale species diversity higher than any previously reported for North America and roughly equivalent to the highest values reported in the world literature

* Botanical nomenclature follows Radford, Ahles & Bell (1968). See footnotes to Appendix for details.

** We thank the Federal Paper Board Co., Inc. and the North Carolina Nature Conservancy for permission to work on their lands. Support for this work was provided by the National Science Foundation and the University of North Carolina. Helpful comments on the manuscript were offered by N. L. Christensen, J. D. Doyle, M. A. Huston & W. H. Schlesinger.

(Whittaker, 1977b; Grime, 1979; Peet *et al.*, 1983). The Green Swamp savannas, however, are unique among communities reported to have high small-scale species diversity. Other equivalently species-rich communities have long histories of chronic grazing or mowing. Although neither grazed nor mowed, these savannas have a long history of regular burning. In addition, many of the species encountered in the savannas are specific to this habitat and many are endemic to southeastern North America. Few annuals and no adventives were encountered. In contrast, previously described areas of high small-scale species diversity often contain many non-habitat-specific species (e.g. many species of the species-rich pastures in Britain and chalk grasslands in Holland are described as also inhabiting roadsides and waste places; see Clapham *et al.*, 1962; Bowen, 1968) and sometimes numerous annuals (Naveh & Whittaker, 1979; Shmida & Ellner, 1984).

Many papers present theories to explain the maintenance of high species diversity (see reviews in Whittaker, 1977a; Tilman, 1982; Peet *et al.*, 1983; Shmida & Ellner, 1984). These theories are often divided into two classes: equilibrium and non-equilibrium. Equilibrium theories derive from the competitive exclusion principle and require that species have significant differences in their ecological niches if they are to co-exist indefinitely (Schoener, 1974, 1982; Grubb, 1977). Non-equilibrium theories invoke external factors which interrupt competitive interactions and thereby allow co-existence of species that might otherwise be unable to persist together (Paine, 1966; Connell, 1978, 1980; Grime, 1979; Huston, 1979; Peet *et al.*, 1983; Shmida & Ellner, 1984).

Published evidence suggests that both types of mechanisms might be important in maintaining high species diversity in coastal plain savannas. Numerous studies have contrasted low diversity unburned savannas with more diverse burned sites (e.g. Heyward & Barnette, 1934; Stoddard, 1931; Lemon, 1949, 1967; Eleuterius & Jones, 1969; Vogl, 1973). The maintenance of species diversity by fire, especially on low production sites, is consistent with non-equilibrium theories (e.g. Grime, 1979; Huston, 1979). Other papers describe a striking phenological variation among savanna species (Wells & Shunk, 1928; Folkerts, 1982; Gaddy, 1982). Such differentiation may represent a form of

niche-partitioning consistent with equilibrium theories.

Our discovery of the extraordinary small-scale diversity of the Green Swamp savannas motivated! the research reported here. In this paper we first document the variation in species composition and high species diversity of the Green Swamp savannas. We then examine evidence for two commonly suggested mechanisms for maintenance of high diversity in savannas: high fire frequency coupled with low primary production – a non-equilibrium mechanism, and phenological differentiation an equilibrium mechanism.

Study area

At the time of European settlement mesic pine wiregrass savanna was widely distributed on fine, poorly drained, oligotrophic sands of the coastal plain from roughly the James River in Virginia south to Florida and then west to the Mississippi River (Harper, 1906, 1914, 1943; Gano, 1917; Wells, 1932; Fernald, 1937; Wharton, 1978; Folkerts, 1982). Outlying communities floristically similar to savannas could be found north into the New Jersey pine barrens (Olsson, 1979) and west to eastern Texas (Streng & Harcombe, 1982). Regionally, savannas can be viewed as communities occupying the center of a soil moisture gradient along which vegetation ranges from shrub bog through savannas and pine flatwoods to dry sandhills (see Wells, 1932; Christensen, 1979). Small pockets of savanna-like vegetation can be found in depressions and sinks within the flatwoods, and in seeps where clay layers surface in the sandhill regions of the uppermost coastal plain (Wells & Shunk, 1931). All of these savanna habitats have a fire cycle typically of less than eight years (Christensen, 1981).

The Green Swamp, originally an area of roughly 80 000 ha, is primarily an ombrotrophic peatland with elevation ranging from 12 to 18 m above sea level. Emerging from the matrix of peat are low islands of mineral soil on which savanna vegetation frequently occurs. The islands vary in convexity, height, and drainage, though most rise less than 1.5 m above the surrounding peat surface. Island size ranges from 1 to 20 ha. The more isolated islands generally have lower fire frequencies and consequently are often overgrown with shrubs. The

more species-rich areas are flat and poorly drained with the water table within a few centimeters of the surface during spring and after heavy rains.

The mineral soils of the savannas developed from Pleistocene deposits of fine to coarse sand and clay. The most frequently encountered savanna soils are of the Leon (Aeric Haplaquod), Rains (Typic Paleaquult), Lynchburg (Aeric Paleaquult), and Foreston and Wrightsboro (Aquic Paleudult) series. All of these soils are notably acidic and low in nutrients, particularly nitrogen and phosphorus (Metz *et al.*, 1961; Plummer, 1963; Buol, 1973).

Climatological records are available for Southport, NC, approximately 35 km southeast of the study area. There the average annual precipitation of 1318 mm is distributed fairly evenly throughout the year with the highest precipitation occurring from June through September. Mean annual temperature is 16.8 °C with the July mean 26 °C and the January mean 8 °C. Precipitation data from a U.S. Forest Service station 2.5 km north of the study site (1600 mm/yr) indicate that annual precipitation in the Green Swamp might be slightly higher than in Southport.

Like virtually all of the coastal plain of the southeastern United States, the Green Swamp has been significantly modified by man. Large areas of original *Taxodium*, *Nyssa*, *Chamaecyparis* swamp forest were converted to pocosin by cutting and burning in the late 19th century. Subsequently large areas of pocosins and original savannas have been converted to commercial pine plantations.

The remaining undeveloped savannas have also been influenced by man, who, as archeological evidence suggests, has inhabited the Green Swamp savannas for at least 3000 yr (Rights, 1947; Ward, 1979). Burning was widely used by aboriginal peoples throughout the southeastern United States to improve hunting (Lawson, 1714; Bartram, 1791; Maxwell, 1910; Vogl, 1973), and it is almost certain that the early inhabitants burned these savannas regularly. Burning was continued by the European settlers who burned the savannas to keep the land open and to improve grazing conditions. (Our limited information about early land use by the European settlers in the study area comes from historical records and anecdotal sources compiled by H. McIver and R. Kologiski.) Although European settlements were already established near the Cape Fear River in the 1660's, it was not until the 19th

century that the Green Swamp savanna lands were variously exploited for grazing and for tar, turpentine and timber production. Today, probably as a result of these operations, few pines over 40 cm dbh remain in the Swamp. Grazing by domestic stock ended by the late 1930's and turpentine by the late 1940's. Fire has continued on a 1 to 4 year cycle as a management tool to control fuel accumulation and to minimize growth of broadleaved trees.

Methods

The multiplicity of the questions to be addressed required that a variety of methods be used. It was necessary to sample both species composition and aboveground production of the savannas over the range of environmental conditions. Sampling with a series of nested quadrats provided data to describe species diversity at different size scales. Harvest data were collected to test the hypothesis that there is phenological variation in aboveground primary production. Biomass data also provide a more effective measure of species importance in these complex communities than does frequency, and they provide a basis for comparison with other studies which relate diversity to standing crop (e.g. Grime, 1973, 1979; Al-Mufti *et al.*, 1977; Willems, 1980). Fertilization experiments were used to examine the interaction between increased site production and diversity. Because fire history has been shown to affect both diversity and site production (Parrot, 1967; Christensen, 1977), harvesting and fertilization experiments were conducted in sites with histories of both annual burning and infrequent burning.

Composition

Twenty-one savanna sites were selected to represent a range of environmental conditions and fire frequencies. At each site species presence was recorded in nested quadrats including 10 contiguous square 0.25 m² quadrats (= 1 x 2.5 m quadrat), a 25 m², and a 625 m² quadrat. In each large quadrat five soil samples were collected from the top 10 cm of mineral soil. Soils were analyzed by the North Carolina State Soils Laboratory for exchangeable phosphate, potassium, calcium and magnesium, organic matter content, cation exchange capacity,

percent base saturation and pH. Topographic position scores were assigned, ranging from I for dry ridges to 4 for depressions. Soil drainage was scored with 0.5 for well-drained sites and 2.5 for the poorly drained extreme. These two subjective scores were summed to produce a single site moisture scalar. The length of the fire cycle during the last two decades for each savanna was estimated based on fire records of the Nature Conservancy and Federal Paper Board Company, Inc., the degree of isolation of the site, and the age of woody growth since the last fire.

Aboveground production

Six rectangular 12 x 24 m permanent plots were established for measurement of net aboveground production. Three plots were set up in an annually burned mesic savanna. One of these plots was fertilized two weeks after the burn with 5.4 g/m² N, 1.3 g/m² P and 2.7 g/m² K. Paired control and fertilized plots were established on a mesic savanna with a 3-4 year fire cycle. A final control plot was established on a drier, annually burned site. All sites were burned in February, 6 weeks before data collection was initiated.

Net aboveground production was estimated by harvesting biomass in 10 square 0.5 X 0.5 m quadrats at 2 to 4 week intervals from April 7 through September 2. Five regularly spaced quadrats were centered in alternating meters along each of two transects. This design provided buffer strips between sampled quadrats, minimized trampling damage, and ensured sampling across any within-plot variation. Aboveground biomass was cut to within 0.5 cm of the soil, placed in plastic bags, and stored at 4 °C until sorting. Samples were sorted into live and dead parts by species, dried at 60-65 °C for 4 hr, and weighed. Production is reported as maximum standing crop biomass, a measure which underestimates site production. In this report we do not account for asynchrony among species biomass peaks, nor do we estimate belowground production.

From mid-1979 through 1981 a major drought occurred on the North Carolina coastal plain (U.S. Dept. Commerce, 1977-83). During this period many of the savanna forbs did not flower, which suggested a decline in vigor and may also have led to a decline in the available seed pool. In a season of

normal precipitation immediately following the drought (1982), we resampled a control plot (Plot 3) to assess year to year consistency of our results and the possible impact of the drought.

Data analysis

The 21 stand x 151 species data matrix was ordinated using Detrended Correspondence Analysis (DCA: Hill, 1979a; Hill & Gauch, 1980). DCA ordination of both presence/absence and frequency data, both with and without woody species, produced similar arrangements of stands and species. The effects of fire history on the ordination were minimized by using only herbaceous species and presence/absence data in the final analysis. In addition to helping identify environmental factors highly correlated with major trends in species composition, the ordination provided the species order for a phytosociological summary table (see Appendix).

The stands were divided into three community types based on position on the first DCA axis. TWINSpan (Hill, 1979b), a polythetic divisive clustering program (see Gauch & Whittaker, 1981; Gauch, 1982) was used to further examine possible groupings of stands.

Among methods for quantifying species diversity, species richness, measured as species per unit area, is probably the most computationally simple and easily interpretable (Peet, 1974; Whittaker, 1977a). The nested quadrat sampling scheme allowed determination of species richness at several size scales. Two dominance-weighted indices of species diversity, Simpson's index ($C = \sum p_i^2$) and the Shannon-Wiener index ($H' = -\sum p_i \log p_i$), were calculated. Importance values (p_i) were measured as relative aboveground biomass for harvested plots and relative frequency of occurrence in 10 0.5 x 0.5 m quadrats for nested-quadrat samples. While C is strongly affected by the importance of the most abundant species, H' gives more weight to species of intermediate importance. We use the reciprocal form of C (Hill's N_2) and the exponentiated form of H' (Hill's N_1) which are interpretable as the number of equally common species that will produce the observed heterogeneity (see Hill, 1973; Peet, 1974). Evenness was calculated as $(N_2-1)/(N_1-1)$ which is Alatalo's (1981) revision of Hill's (1973) ratio $E_{1,2}$.

Results

Community composition

The DCA ordination of the twenty-one 625 m² plots is shown in Figure 1. Values of the moisture scalar strongly correlate with the first axis (Spearman rank correlation = 0.80, $p < 0.001$), which can be interpreted as a moisture gradient from wet to dry sites (see ordered species list in Appendix). The second ordination axis varies with fire frequency such that the annually burned sites are consistently located above the infrequently burned sites.

Soil pH is negatively correlated with the first axis score (Spearman rank correlation = 0.44). Among environmental parameters soil pH is negatively correlated with the estimated length of the fire cycle, while percent organic matter, CEC, K, and Ca are positively correlated with fire cycle length. These correlations were significant at the $p < 0.05$ level.

The distributions of some groups of ecologically related species are strongly correlated with the first DCA axis moisture gradient (Table 1). The mean DCA positions of species within a group, which indicate the centers of distribution for the groups along the moisture gradient, vary markedly and corroborate the direct correlations with the axis scores. The percentages of the flora composed of

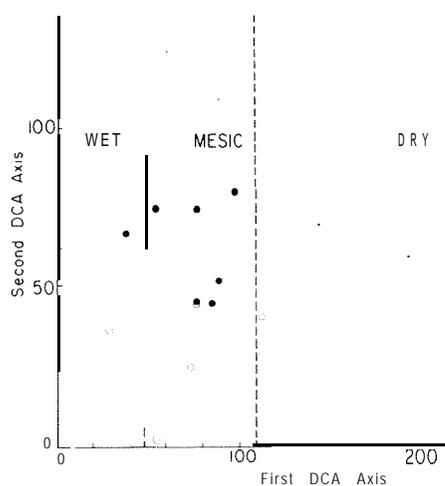


Fig. 1. DCA ordination of presence/absence data for non-woody species in 625 m² quadrats. Open symbols indicate sites with infrequent fires and filled symbols sites with annual fires.

Table 1. Distributions of species groups along the DCA ordination axes. The first 2 columns show Spearman rank correlations between percentages of all species in the 625 m² quadrats which belong to the group and the position of the stand on the DCA axis (* = $p < 0.05$, ** = $p < 0.001$). The final columns show mean species positions on the axes. The ranges of species positions on the two axes are 205 to 473 and -229 to 418 respectively. Axis 1 is a gradient from wet to dry savannas; Axis 2 is correlated with fire frequency.

Species group	Spearman rank correlation		Species mean DCA position	
	1	2	1	2
Grasses	0.018	0.068	79.79	61.05
Sedges	0.413*	0.004	58.14	113.57
Other monocots	0.612*	0.318	45.52	66.43
Composites	0.758**	0.599*	196.96	103.50
Legumes	0.855**	0.040	332.80	35.00
Other herbaceous dicots	0.423*	0.137	18.45	78.94
Ferns and lycopods	0.118	0.140	186.00	84.17
Woody species	0.024	0.191	151.23	115.26

sedges, monocots (excluding grasses and sedges), and herbaceous dicots (excluding legumes and composites) decrease from wet to dry sites, whereas composite and legume importances increase along the gradient. The relative importance of composites also increases along the second axis suggesting an increase with frequent burning. Of the species which occurred in at least 2 high and 2 low fire frequency mesic sites, 5 were significantly more abundant (frequency in 0.5 x 0.5 m quadrats; Student's *t*-test, $p < 0.05$) in annually burned sites than in less frequently burned sites (*Helianthus heterophyllus*, *Marshallia graminifolia*, *Polygala hookeri*, *Tofieldia racemosa*, *Trilisa paniculata*). No species showed the opposite trend at a statistically significant level. Of the 46 species which occurred in only high or low fire frequency sites, 36 were found in the high frequency type.

We recognize wet, mesic, and dry savanna types. The somewhat arbitrary divisions of the DCA axis are consistent with the TWINSpan results. The first TWINSpan division separated 1 very dry site (#11). Subsequent divisions segregated first the wet sites, and then mesic from dry savannas.

All of the Green Swamp savannas have a sparse pine canopy (0-150 stems/ha) and a grass-dominated understory. Shrubs up to 1.5 m tall, the real-

ized height depending on the length of time since the last fire, can be present under all moisture conditions. The bunch-forming grasses grow up to 50 cm in height and are largely responsible for creating microtopographic variation within the communities. Grass clump size varies inversely with fire frequency from 5–15 cm basal diameter in annually burned sites to 35–40 cm. Wet sites along with low fire frequency sites have relatively pronounced vertical relief, up to 10 cm difference between the tops of grass hummocks and the hollows between them.

Wet savannas

Wet savannas are found in shallow depressions and as ecotones between mesic savanna vegetation and the shrub-dominated pocosins. In particular, wet savannas are likely to be found where fires on mesic savannas have spread into the adjacent pocosin eliminating the dominant shrubs.

Dominant grasses of wet savannas include *Ctenium aromaticum*, *Muhlenbergia expansa* and *Sporobolus teretifolius*, all of which are also dominants in mesic savannas. *Dichromena latifolia* and *Carex verrucosa* are sedges restricted to these communities or found only rarely in wet microsites on drier savannas. Other species which are apparently specific to wet savannas in the Green Swamp include *Drosera intermedia*, *Coreopsis falcata*, *Rhynchospora chalarocephala*, *Oxypolis filiformis*, *Iris tridentata*, *Aristida affinis*, *Anthaenantia rufa*, and the shrubs *Vaccinium corymbosum* and *Cyrilla racemiflora*. In contrast to drier savannas where *Pinus palustris* is the only tree species present, wet savannas support occasional individuals of *Pinus serotina*, *Taxodium ascendens* and *Nyssa sylvatica* var. *biflora*.

Most species in wet savannas are confined to the grass hummocks; the low depressions are typically devoid of vegetation. The extended period of winter and spring inundation in these microsites, coupled with incomplete combustion of wet litter restricts the growth of small plants and inhibits most seedling establishment.

Dry savannas

Dry savannas typically occur on the high, central portion of the more dome-shaped islands (up to 1.5 m above the surrounding pocosin), or where the soil is coarse textured and well drained. Total plant cover ranges between 50 and 70% compared to over

100% cover in the other savanna communities. The open tree canopy contains only *Pinus palustris*, and the grass *Aristida stricta* dominates the field layer. Although relatively uncommon on mesic and wet sites, legumes are well represented in dry savannas (Table 1, Appendix). Legumes that are apparently confined to drier sites in the study area include *Cassia fasciculata*, *Lespedeza capitata*, *Clitoria muniuna*, and *Amorpha herbacea*. Other characteristic species (100% constancy) are the woody *Myrica cerifera* and *Smilax glauca*, and the forbs *Euphorbia curtisii* and *Viola septemloba*. Sedges, where present, are restricted to wet microsites.

Mesic savannas

Mesic savannas occupy an intermediate position on the moisture gradient and are especially rich in species. Where present, the tree canopy consists almost exclusively of *Pinus palustris*, though rarely does it exceed 40% cover. The few species that are restricted to mesic savannas include *Polygala cruciata*, *Pinguicula* spp., *Lachnocaulon anceps*, *Lilium catesbei* and *Xyris smalliana*. The only species with 100% constancy is the endemic Venus' flytrap, *Dionaea muscipula*. A large group of species with high constancy in mesic savannas can be identified in the Appendix.

Although hummock and hollow microtopography occurs on these mesic sites, the relief is less pronounced than in wet savannas. Graminoids, the most important of which are *Sporobolus teretifolius*, *Muhlenbergia expansa*, *Ctenium aromaticum*, *Andropogon* spp. and *Rhynchospora plumosa*, form the hummocks and dominate the herbaceous layer. Most of the hollows are litter free and are important microhabitats occupied by species such as *Lycopodium carolinianum*, the sedges *Rhynchospora breviseta* and *Rhynchospora chapmanii*, the insectivorous *Dionaea muscipula* and *Drosera capillaris*, and many species of composites. Frequently burned sites are dominated by numerous, small interdigitating hummocks. As litter accumulates in the absence of fire, plants which typically grow between the hummocks and even the small hummocks largely disappear.

Diversity patterns

Species richness

Species richness in savannas ranges up to 42 spe-

Table 2. Species richness statistics for wet, mesic and dry savannas under annual and infrequent fire regimes. Mean (s.d.) species counts are shown for quadrats of 0.25, 1, 2.5, 25 and 625 m².

Quadrat size (m ²)	Wet		Mesic		Dry	
	High	Low	High	Low	High	Low
Number of sites:	2	2	8	3	3	3
0.25	19.5 (0.5)	20.8 (1.7)	22.2 (3.6)	14.0 (3.2)	13.2 (4.9)	11.0 (5.X)
1.0 ^a	32.2 (2.3)	33.6 (2.4)	35.2 (4.X)	25.9 (7.3)	24.3 (X.X)	22.4 (9.1)
2.5	43.5 (4.9)	44.5 (2.1)	46.5 (6.3)	34.7 (3.2)	33.7 (12.7)	31.7 (12.9)
25	53.5 (2.1)	54.0 (5.7)	57.3 (X.6)	50.3 (1.1)	43.0 (14.4)	43.3 (11.1)
625	73.5 (3.5)	6X.0 (5.7)	79.3 (5.3)	71.2 (2.9)	58.0 (13.0)	54.3 (8.1)

^a Calculated from species-area curves obtained by regression. Species richness = $A + B(\log \text{area})$.

cies per 0.25 m² quadrat, to over 50 per m², and from 63 to 84 (43 in site 1) species in 625 m² plots. For all quadrat sizes maximum richness is found in annually burned, mesic savannas (Table 2, Fig. 2). Richness for both 0.25 and 625 m² samples increases with site moisture (decreasing axis 1 score) to a peak in mesic savannas, and levels off or decreases slightly in wet sites. At the 0.25 m² scale the dry sites are only 60% as rich as annually burned, mesic savannas. This in part reflects the smaller plant size in mesic savannas, but at the 625 m² scale richness in dry savannas is still only 73% of that on mesic sites.

Annually burned mesic savannas average 26% more species per m² than less frequently burned savannas. In wet and dry savannas, however, differences in richness with fire frequency are not significant.

Table 3. Diversity indices calculated using frequency in ten 0.5 x 0.5 m quadrats per stand in the 2 1 plots sampled using nested quadrats. Values are means (s.d.).

Number plots	Moisture class	Fire frequency	Spp., 0.25 m ²	Hill's N_2 (1/C)	Hill's N_1 (Exp(H'))	Alatalo's $E_{1,2}$ ((N_2-1)/(N_1-1))
2	wet	high	19.5 (0.5)	2X.01 (2.12)	32.14 (2.71)	0.87 (.01)
2	wet	low	20.8 (1.7)	29.95 (0.89)	33.96 (0.08)	0.88 (.03)
8	mesic	high	22.2 (3.6)	31.05 (0.27)	35.44 (4.74)	0.87 (.03)
3	mesic	low	14.0 (3.3)	21.24 (4.58)	25.14 (4.65)	0.83 (.03)
3	dry	high	13.2 (4.9)	20.99 (X.X7)	25.00 (10.52)	0.83 (.03)
3	dry	low	11.0 (5.X)	18.73 (9.4X)	22.90 (10.52)	0.80 (.04)

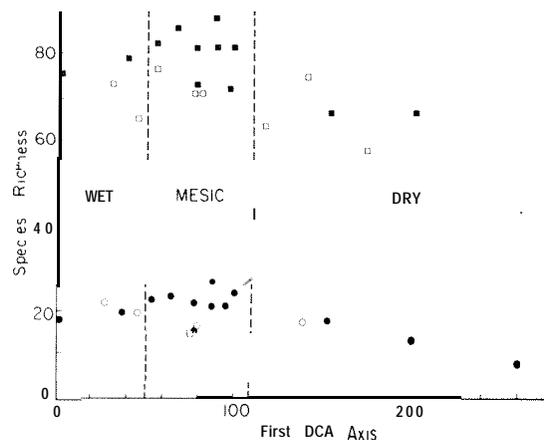


Fig. 3. Species richness as a function of fire frequency and position on the DCA Axis 1. Open symbols indicate infrequently burned sites and filled symbols annually burned sites. Squares indicate richness for 625 m² quadrats and circles the mean richness in ten 0.25 m² quadrats.

Diversity indices

Frequency data were used to calculate dominance-weighted diversity statistics for the 6 classes of savannas (3 moisture classes under 2 fire regimes; Table 3). Consistent with the observations on species richness, the highest diversity values (1/C; Exp N') occurred in the frequently burned mesic savannas. The mesic savannas also showed the greatest drop in diversity with a shift to low fire frequency. Among infrequently burned savannas diversity was highest in wet sites. No clear differences were apparent in Alatalo's evenness index. Biomass data were used to calculate diversity indices for the six harvested sample sites (Table 4). Results for 1979 from sites 1 and 3 (selected as replicates) are nearly identical.

Diversity (1/C; Exp W') appeared notably higher in 1982 while at the same time the number of species

Table 4. Diversity indices calculated using aboveground biomass in 6 100.25 m² plots. Values for richness are means (s.d.).

Plot/year	Moisture class	Fire frequency	Spp./0.25 m ²	Hill's N_2 ($1jC$)	Hill's N_1 ($\text{Exp}(H')$)	Alatalo's $E_{1,2}$ ($(N_2-1)/(N_1-1)$)
<i>Control</i>						
1/79	mesic	high	33.1 (4.0)	7.45	13.76	0.51
3/79	mesic	high	31.4 (1.8)	8.18	13.41	0.58
3/82	mesic	high	26.0 (6.1)	10.36	15.59	0.64
2/79	dry	high	24.0 (3.3)	5.00	8.04	0.54
5/79	mesic	low	11.5 (3.2)	2.43	4.51	0.49
<i>Fertilized (1 season)</i>						
4/79	mesic	high	32.9 (4.9)	10.00	14.41	0.67
6/79	mesic	low	13.3 (2.4)	4.02	6.26	0.57
<i>Fertilized (4 seasons)</i>						
4/82	mesic	high	29.0 (5.7)	7.40	12.36	0.56

per 0.25 m² plot had dropped markedly. The data suggest a post-drought decline in the abundance of the typical dominants leading to lower concentration of dominance (note the decline in importance of grasses shown in Table 6), but also a decline in the average number of species per plot.

Fertilization resulted in no decrease in species per 0.25 m² during the first year. After four years the drop in richness was no more than on the control plot where drought apparently caused a modest decline.

Spatial homogeneity

We have observed conspicuous spatial heterogeneity in savannas. On particularly wet or dry sites, or on sites with only infrequent fire, the dominant grasses form large, discrete tussocks. In contrast, frequently burned mesic sites are characterized by small, anastomosing clumps of grasses and sedges. We attempted to quantify this difference in homogeneity by calculating the mean pairwise coefficient of community (see Whittaker & Gauch, 1973) between the ten 0.25 m² quadrats for each plot. As shown in Figure 3, the mesic, frequently burned sites had the highest homogeneities and the dry sites (with one exception notable for its low diversity) had low values. Thus, on mesic sites with frequent fires, the between-patch diversity at the 0.25 m² scale is small relative to that of other savanna types.

Aboveground production

Peak aboveground biomass

Peak live, aboveground biomass for the six harv-

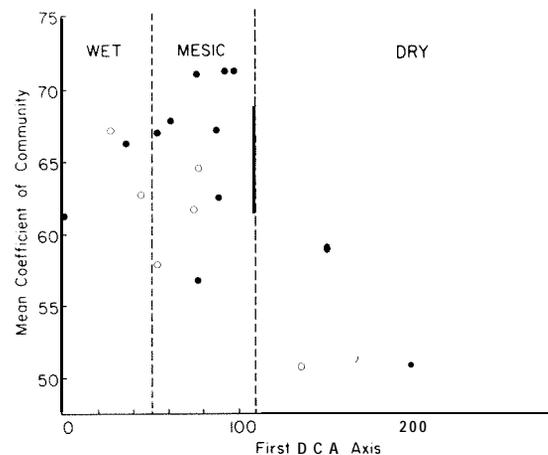


Fig. 3. Within-community homogeneity as a function of fire frequency and position on the DCA Axis 1. Homogeneity is represented by the mean pairwise similarity of ten 0.25 m² quadrats. Open symbols indicate in frequently burned sites and filled symbols annually burned sites.

ested savanna plots is shown in Table 5. Peak standing crop in the two annually burned mesic savannas was estimated at 293 and 236 g/m² for 1979, while the dry site had a lower value of 216 g/m². The mesic, low fire frequency site supported a significantly greater living biomass than the mesic sites that were annually burned.

Grasses contributed about 70% of the biomass on all sites, whereas the importance of other groups varied with moisture and fire frequency (Table 6). With low fire frequency, sedges, other monocots, and composites declined in relative biomass, while other dicot herbs and shrubs increased. Differences

Table 5. Peak aboveground living biomass on control and fertilized sites. Values are means (s.d.) of 6–10 0.25 m² quadrats per site.

Year	Plot	Moisture class: Mesic		Dry		
		Biomass	Plot	Biomass	Plot	
		Fire frequency: Annual		Annual		
<i>Control</i>						
1979	1	73.15 (11.5)	5	94.18 (35.4)	2	54.00 (17.2)
1979	3	58.99 (44.9)				
1982	3	75.08 (06.7)				
<i>Fertilized (one season)</i>						
1979	4	10.36 (27.4)	6	113.13 (24.2)		
<i>Fertilized (four seasons)</i>						
1982	4	93.74 (5.2)				

in shrub biomass were particularly dramatic, shifting from 1% to 15% of the standing crop with decreased fire frequency.

Changes following fertilization

Fertilization of an annually burned mesic savanna nearly doubled peak standing crop the following summer (264 vs 441 g/m²), though no further increase was observed after four seasons of fertilization (Table 5). In contrast, fertilization of a low fire frequency mesic site resulted in a much smaller increase in production. Biomass production values from the fertilized, high and low fire frequency sites were almost identical.

Seasonal variation in production

Throughout the sampling season the relative contribution of species groups to standing crop remained nearly constant, but production associated with various species within groups showed considerable seasonal variation. These seasonal differences were examined for three important groups: composites, grasses, and sedges. Figure 4 shows the seasonal progression in standing crop for selected members of these groups as measured for plot 1, an annually burned mesic savanna.

Numerous species of composites were present and they varied markedly in flowering phenology as well as production. In general, peak aboveground biomass coincided with bolting and flowering. Early season species, not shown because of their infrequent occurrence, include *Chaptalia tomentosa* and *Erigeron verna*, both of which flower March through April. Several species flower mid-season while most species flower in late summer or autumn.

Grasses, which form the dominant species group both in biomass and in contribution to community structure, generally accumulate aboveground biomass through the spring and summer and then bloom in late summer or fall. (Figure 4 shows standing live biomass and does not include senescent leaves which begin to accumulate by midsummer.) Although phenologies are similar, periods of maximum growth rates are different among the grass species. For example, *Ctenium aromaticum*, the most abundant species in this plot, grows rapidly as early as 6 weeks after fire, and reaches maximum biomass in July coincident with its maximum flow-

Table 6. Percent contributions of species groups to peak biomass in control and fertilized plots. Group codes: G = grasses, S = sedges, M = other monocots, C = composites, D = other herbaceous dicots, F = ferns and lycopods, W = woody dicots.

Plot	Moisture class	Fire frequency	Year	Species group						
				G	S	M	C	D	F	W
<i>Control</i>										
1	mesic	high	1979	72.0	8.0	5.4	12.4	0.6	0.05	1.6
3	mesic	high	1979	74.4	8.1	1.3	12.8	0.3	0.0	1.3
3	mesic	high	1982	63.8	14.3	3.9	14.2	2.7	0.1	0.9
2	dry	high	1979	74.2	6.9	1.3	16.8	0.4	0.0	0.4
5	mesic	low	1979	75.1	1.8	0.6	1.2	2.3	0.0	19.0
<i>Fertilized (1 season)</i>										
4	mesic	high	1979	72.5	5.9	3.0	15.4	0.5	1.7	1.0
6	mesic	low	1979	62.5	0.8	1.6	0.9	1.5	3.3	29.4
<i>Fertilized (4 seasons)</i>										
4	mesic	high	1982	71.4	8.7	3.5	11.1	3.0	0.02	1.4

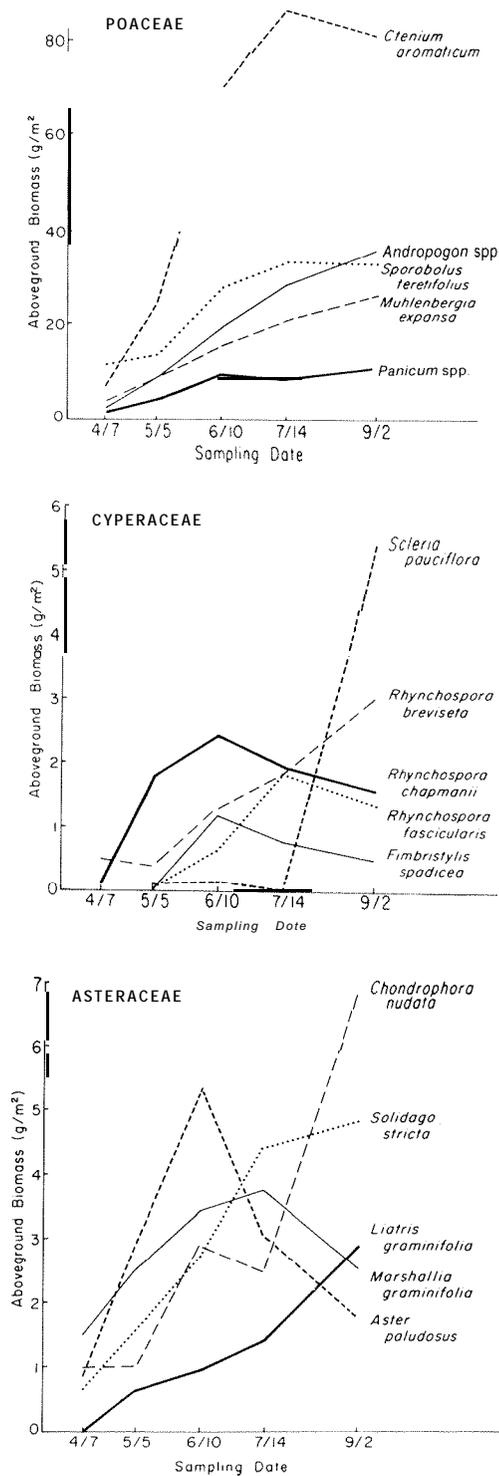


Fig. 4. Seasonal trends in aboveground living biomass of selected individual species of (a) grasses, (b) sedges, and (c) composites. Data show biomass in Plot I, a mesic annually burned site.

ering but ahead of the peak for most species. *Panicum chamaelonche*, which flowers twice each season, similarly peaks early.

Sedges also show variable seasonal patterns of growth, but generally peak before the dominant grasses. For these species flowering and the associated peak biomass proceeds from the small statured species like *Rhynchospora chapmanii* early in the season to the taller canopy species like *R. breviseta* and *R. plumosa* in the autumn.

Discussion

Savanna composition

Published descriptions of savanna vegetation include the physiognomic sketches provided by early botanical explorers (Bartram, 1791; Elliot, 1821–1824; Nash, 1895), as well as floristic analyses featuring species lists (e.g. Thorne, 1954; Pullen & Plummer, 1964; Eleuterius & Jones, 1969; Gaddy, 1982). Only a few studies systematically describe savannas in the context of regional vegetation or interpret variation in savanna vegetation relative to environmental gradients. Among these few reports, all suggest the importance of a moisture gradient and several also emphasize the significance of fire frequency (e.g. Lemon, 1949, 1967; Vogl, 1973).

Woodwell (1956) described savannas as coastal plain wetland communities. He recognized three distinct herbaceous components which he found associated with *Pinus palustris* or *P. serotina* on wetter sites. His *Pinus*/*Aristida* communities, which were found on sandy flats and ridges, overlap with the dry savannas described here. He reported herb layers dominated by *Muhlenbergia* and *Andropogon*, and compositionally similar to mesic and wet savannas occurring on clay substrates.

Both Snyder (1980) and Kologiski (1977) described geographically more restricted vegetation units. It is clear that the sites Snyder studied in the Croatan National Forest (150 km northeast of the Green Swamp) were not as species-rich as the Green Swamp counterparts, resulting perhaps from drier conditions at his sites, and in part from the lack of propagules of typical savanna species, many of which reach their northern limits in the area. Kologiski's Green Swamp *P. palustris*/*Aristida stricta*/*Rhynchospora* community covers the range of

mesic and dry sites in our study. His *P. serotina-Aristida stricta-Rhynchospora* type generally coincides with our wet sites, but the name is somewhat misleading considering that *Aristida stricta* dominates only on dry sites in the study area.

Wells & Shunk (1928) related species composition to habitat factors such as seasonal variation in the water table, soil aeration, and soil nutrient status. They described *Campulosus (Ctenium)*, *Panicum*, and *Andropogon* consocieties which represent a gradient from the wet to the dry-mesic savannas of our study. Our dry savannas correspond closely with a hydric or *Aristida* semi-bog phase of Wells' *Quercus-Aristida* associates (Wells & Shunk, 1931).

Species richness

The Green Swamp savannas are remarkable for their high species diversity. At a 625 m² scale, the range of 70 to 84 species places mesic savannas among the more species-rich communities in temperate North America (see Peet, 1978). At the 1 m² and 0.25 m² scales, however, the Green Swamp savannas appear to surpass all other North American plant communities. In over 20 000 1 m² plots examined for temperate North American woodlands and forests, species richness never exceeded 17 species, and in extensive studies of North American tall-grass prairie, richness averaged 18 m² and never exceeded 28 m² (Peet *et al.*, 1983). The average richness of 35 m² in frequently burned mesic savannas of the Green Swamp provides a striking contrast that begs explanation.

Species richness on a 1.0 or 0.25 m² scale equal to that in the Green Swamp savannas has been reported in the world literature only in areas chronically grazed by domestic stock or wildlife, or regularly mowed for long periods. These communities include chalk grasslands in Britain (Rorison, 1971; Grime, 1973; 1979), oligotrophic grasslands in Japan (Itow, 1963) and in the Netherlands (van den Bergh, 1979), the alvars of Sweden (Sjögren, 1971; Rosen & Sjögren, 1973), dune slacks in Holland (van der Maarel, 1971; van der Maarel & Leertouwer, 1967; Thalen, 1971), Mediterranean scrub in Israel (Whittaker, 1977b; Naveh & Whittaker, 1979; Shmida & Ellner, 1984), calcareous fens in Sweden (Regnéll, 1980), and wildlife-grazed grassland in Sri Lanka (Mueller-Dombois, 1977). All of the examples appear to be from communities where

soil conditions are less than optimal for plant growth.

Non-equilibrium theories of species diversity

Several authors have advanced non-equilibrium theories of species diversity which predict that a moderate amount of disturbance maximizes species diversity (e.g. Loucks, 1970; Grime, 1973; 1979; Whittaker, 1977b; Connell, 1978; Huston, 1979; Abugov, 1982). Grime (1973; 1979) proposed that species richness can be interpreted as a function of 'environmental stress' and/ or intensity of management 'such as grazing, mowing, burning and trampling, which tend to prevent potentially competitive species from attaining maximum size and vigor'. He hypothesized that species richness will peak at some intermediate value of these two factors. He attributed low species richness in environmentally stressful or frequently disturbed sites to the small number of species adapted to the imposed stress, and he hypothesized that low richness in stable and/or highly productive sites results from the ability of a few species to pre-empt resources, thereby suppressing richness by competitive exclusion.

A refinement of Grime's model has been proposed by Huston (1979). Huston's model differs in that he explicitly described an interaction between disturbance and rate of competitive exclusion. In Huston's view, the frequency of population reduction or disturbance which maximizes richness in a particular community is dependent on potential growth rate and thus competitive exclusion by the potential dominants. The rate of competitive displacement is correlated with site favorability: good sites yield more rapid growth and consequently have more rapid extinction of competitors. Thus, rather than a single, complex gradient, Huston proposed that two gradients are necessary to determine a richness response surface.

Our observations on species richness in the Green Swamp savannas are consistent with the Grime and Huston models. Mesic, annually burned sites typically have higher species richness than less frequently burned sites (Fig. 2), a result consistent with the prediction that when the disturbance regime is relaxed, richness will drop. As would be predicted from Huston's model, the influence of fire is less pronounced at the extremes of the moisture gradient where the potential for competitive exclusion

is lower. None of the savannas burn with less than a 1-year cycle, so we cannot directly assess the impact of more frequent disturbance. The frequency of disturbance in savannas contrasts with the continual biomass reduction typical of most other species-rich communities. The low fertility of savanna soils enforces a slow recovery from disturbance and it is thus likely that any increase in frequency or intensity of disturbance would lead to a reduction in species richness.

Al-Mufti *et al.* (1977) scaled Grime's one-dimensional gradient of stress and disturbance using aboveground standing crop. Among a variety of herbaceous communities, they found maximum richness to be limited to sites supporting biomass in the range of 350 to 750 g . m². in the Green Swamp savannas maximum richness occurs at roughly 280 g . m² with high values occurring when standing crop is as low as 165 g . m² (dry sites). Similarly, Willems (1980) reported richness to peak in north-western European chalk grasslands with biomass values between 150 and 350 g . m². Willems attributed this deviation from the Al-Mufti *et al.* results to his own harvesting at 2 cm rather than ground level.

The high savanna diversity at a somewhat lower biomass than observed by Al-Mufti *et al.* can be interpreted in an evolutionary context. Evolutionary history should lead to a local pool of species adapted to prevailing ecological conditions (see Terborgh, 1973). The savanna flora evolved under conditions of lower fertility than did the British communities where Al-Mufti *et al.* worked. Whittaker (1977b; Naveh & Whittaker, 1980) proposed a similar explanation when confronted with differing richness responses to grazing intensity in different ecosystems.

The role of fire

The species-rich savannas of the Green Swamp appear distinctive among communities currently known to have species richness greater than 35 m² in that the only chronic disturbance is fire. This association with fire is an ancient one. It is likely that man has burned the savannas of southeastern North America for more than 3 000 years (Rights, 1947; Vogl, 1973; Christensen, 1981), and lightning is likely to have ignited savanna fires long before the first human occupation (Vogl, 1973). The large

number of species endemic to these communities attests to the antiquity of the assemblage.

Fire can function in several ways to enhance savanna diversity. The most conspicuous effect is the reduction in woody plants which would otherwise increase in size and density until the savannas were replaced by forest or shrubland (Wells & Shunk, 1928; Lemon, 1949; Eleuterius & Jones, 1969; Wells & Whitford, 1976; Christensen, 1981; Folkerts, 1982). Fire also removes grass and sedge foliage which casts a heavy shade and which can lead to a loss of the smaller grasses and forbs which grow between the clumps. As many savanna species grow under the grass canopy and conduct much of their photosynthesis by means of rosettes of leaves, failure to burn the litter layer for more than one or two seasons may contribute to a decline in the number of species occupying a typical 1 m² area. Low light levels as found under heavy litter accumulations have been implicated in the loss of *Dionaea muscipula* from such communities (Roberts & Oosting, 1958).

In addition to stimulating flower and seed production in many savanna species (Greene, 1935; Lemon, 1949; Parrot, 1967; Vogl, 1973), fire also opens microsites in which new seedlings can become established (Grubb, 1977). The importance of fire for seedling establishment in the Green Swamp savannas has not yet been ascertained, but Lemon (1949) has described a group of readily dispersed species which colonize savanna sites made available by fire.

Species which become established following disturbance are likely to experience less rigorous competition than might otherwise be the case. Consequently, species typically found in adjacent habitats may develop substantial populations in communities which they could not invade without periodic fire. Peet *et al.* (1983) used this argument to predict that average niche breadth along the moisture gradient should be greater in annually burned savannas than in the less frequently burned savannas. By similar reasoning beta diversity, compositional changes along the gradient, should decrease with increased fire frequency. Our observation that many species common on annually burned savannas appear confined to mesic ecotones between savanna and shrub bog in the absence of fire is consistent with this prediction.

Equilibrium theories of species richness

According to equilibrium theories, species should co-exist in a community only if significant differences exist in their use of resources such that competitive exclusion does not occur. Niche differentiation among species should be the rule.

The phenological patterns in savannas, in both flowering (Wells & Shunk, 1928; Gaddy, 1982) and aboveground growth (Fig. 5), may represent a form of niche differentiation resulting in reduced competition. It has been suggested that in a similar way seasonal partitioning of primary production serves to maintain species richness in North American prairies (Williams & Markley, 1973).

Seasonal differences in aboveground growth are particularly pronounced among the sedges. This observation could be interpreted to be the result of competition, with the remaining sedges having divergent phenologies. However, coupling these observations with species morphological data suggests an alternative interpretation. The sedges appear to have adopted different strategies for co-existence with the dominant grasses. Small-statured sedges which are likely to be overtopped by grasses grow rapidly early in the season thus avoiding competition (e.g. *Rhynchospora chapmanii*, *R. ciliaris*), whereas larger species which effectively compete with the grasses for canopy space (e.g. *Rhynchospora breviseta*), peak concurrently with the grasses.

Marked phenological variation in production can also be seen among the composites, but this is largely due to timing of bolting and may be unrelated to photosynthesis, much of which could take place during the winter months in the basal rosette leaves.

A second likely form of species differentiation is in response to soil moisture. Our ordination analysis of the Green Swamp savannas shows a compositional gradient correlated with soil moisture. Significant species turnover occurs along this gradient as indicated in the Appendix. In addition, the relative contributions of various species groups show pronounced trends (Table 1).

We have reported only the most prominent mechanisms of potential species differentiation in savannas. Numerous other factors are likely to be important, some perhaps peculiar to one or a few species. For example, a number of woody species

appear largely confined to growth on old, rotting pine logs, and *Carduus virginiana* has a conspicuous affinity for ant hills (Wells & Shunk, 1928). Other possible factors such as root distribution and adaptations for uptake of scarce nutrients and differing nutrient requirements (see Tilman, 1982) still need to be examined.

Conclusions

Our investigations confirm that the Green Swamp savannas are remarkably species-rich, especially at small scales, and that this richness is maximal in sites with high fire frequency near the middle of the moisture gradient. Both non-equilibrium and equilibrium processes appear to contribute to the establishment and maintenance of high species diversity in these savannas.

Appendix

Constancy of species in wet, mesic and dry savannas

Herbaceous species which occur in more than one and less than 17 of the 21 stands are ordered by increasing DCA first axis scores.

Species	Savanna type:		
	wet Number of stands: 4	Mesic 11	Dry 6
<i>Dichromena latifolia</i>	75	09	00
<i>Drosera intermedia</i>	50	00	00
<i>Coreopsis falcata</i>	50	00	00
<i>Eragrostis refracta</i>	25	09	00
<i>Pilea tenuifolia</i>	50	09	00
<i>Sarracenia flava</i>	100	18	00
<i>Sarracenia purpurea</i>	100	36	00
<i>Scleria reticularis</i>	50	09	17
<i>Sarracenia rubra</i>	100	45	00
<i>Eriocaulon decangulare</i>	100	45	00
<i>Spiranthes praecox</i>	00	18	00
<i>Lachnanthes caroliniana</i>	50	45	00
<i>Smilax walteri</i>	25	18	00
<i>Calopogon</i> spp. ¹	100	73	00
<i>Xyris ambigua</i>	75	82	00
<i>Oxypolis ternata</i>	25	64	00
<i>Bartonia virginica</i>	75	73	00
<i>Arundinaria gigantea</i>	75	82	00
<i>Rhexia lutea</i>	100	55	33
<i>Polygala hookeri</i>	75	75	00
<i>Polygala cruciata</i>	75	27	17

Appendix (Continued)

Species	Savanna type:	Wet	Mesic	Dry
	Number of stands:	4	11	6
<i>Rhexia mariana</i>		00	IX	00
<i>Eryngium integrifolium</i>		75	91	17
<i>Osmunda cinnamomea</i>		00	27	00
<i>Dionaea muscipula</i>		50	100	17
<i>Carphephorus tomentosus</i>		100	x2	33
<i>Cleistes divaricata</i>		25	36	17
<i>Pinguicula</i> spp. ²		00	45	00
<i>Lachnocaulon anceps</i>		00	75	00
<i>Sabatia difformis</i>		50	36	17
<i>Solidago stricta</i>		75	82	33
<i>Polygala ramosa</i>		25	36	17
<i>Carex verrucosa</i>		100	09	17
<i>Erigeron verna</i>		100	55	50
<i>Seymeria cassioides</i>		25	91	17
<i>Lilium catesbaei</i>		00	18	00
<i>Viola primulaefolia</i>		50	73	33
<i>Smilax laurifolia</i>		100	64	67
<i>Helianthus angustifolius</i>		25	36	17
<i>Aristida virgata</i>		50	45	17
<i>Xyris smalliana</i>		00	45	00
<i>Lycopodium alopecuroides</i>		50	55	17
<i>Woodwardia virginica</i>		50	21	50
<i>Helianthus heterophyllus</i>		100	82	17
<i>Scleria pauciflora</i>		25	82	50
<i>Fimbristylis spadicea</i>		00	36	17
<i>Agalinis aphylla</i>		25	64	17
<i>Polygala lutea</i>		75	73	x3
<i>Rhynchospora ciliaris</i>		00	x2	33
<i>Sisyrinchium arenicola</i>		100	64	67
<i>Rhynchospora plumosa</i>		75	73	67
<i>Hypoxis micrantha</i>		00	45	50
<i>Carduus virginiana</i>		00	45	50
<i>Lobelia nuttallii</i>		25	55	50
<i>Panicum</i> spp. ³		50	36	x3
<i>Linum virginianum</i>		00	18	17
<i>Liatris graminifolia</i>		100	45	67
<i>Agalinis obtusifolia</i>		00	36	50
<i>Trilisa paniculata</i>		00	82	67
<i>Prenanthes autumnalis</i>		00	36	50
<i>Baptisia tinctoria</i>		00	09	50
<i>Desmodium tenuifolium</i>		00	36	67
<i>Smilax glauca</i>		00	27	50
<i>Gymnopogon brevisetia</i>		00	55	33
<i>Andropogon virginicus glom.</i> ⁴		50	09	16
<i>Ludwigia virgata</i>		00	27	67
<i>Panicum ciliatum</i> ³		00	73	100
<i>Desmodium lineatum</i>		00	27	83
<i>Aster squarrosus</i>		00	27	67
<i>Eupatorium rotundifolium</i>		25	55	83
<i>Pteridium aquilinum</i>		25	45	67
<i>Chaptalia tomentosa</i>		25	00	50
<i>Euphorbia curtisii</i>		00	55	100
<i>Amorpha herbacea</i>		00	45	100
<i>Chamaelirium luteum</i>		00	00	33

Appendix (Continued).

Species	Savanna type:	Wet	Mesic	Dry
	Number of stands:	4	11	6
<i>Rhynchospora</i> sp.		00	09	17
<i>Viola septemloba</i>		00	18	100
<i>Stylosanthes biflora</i>		00	18	67
<i>Crotalaria purshii</i>		00	00	67
<i>Tephrosia hispidula</i>		00	18	83
<i>Lespedeza capitata</i>		00	00	50
<i>Cassia fasciculata</i>		00	00	33
<i>Eryngium yuccafolium</i>		00	09	33
<i>Anthraenantia villosa</i>		00	09	17
<i>Pterocaulon pycnostachyum</i>		00	00	33
<i>Heterotheca mariana</i>		00	00	33
<i>Elephantopus nudatus</i>		00	00	33
<i>Aster pilosus</i>		00	00	33

Additional herbaceous species occurring in >80% of all stands (ordered by first DCA axis score): *Rhynchospora chapmanii*, *Ctenium aromaticum*, *Tofieldia racemosa*, *Habernaria* spp.⁵, *Drosera capillaris*, *Rhynchospora fascicularis*, *Marshallia graminifolia*, *Lycopodium carolinianum*, *Rhynchospora brevisetata*⁶, *Rhexia petiolata*, *Panicum chamaelonche*³, *Coreopsis gladiata*, *Eupatorium leucolepis*, *Chondrophaera nudata*, *Aster paludosus*, *Aster dumosus*, *Aletris farinosa*, *Sporobolus teretifolius*, *Rhexia alifanus*, *Andropogon* spp.⁴, *Aristida stricta*, *Xyris caroliniana*, *Heterotheca graminifolia*.

Herbaceous species occurring in only one stand (ordered by first DCA axis score): *Utricularia subulata*, *Rhynchospora chalerocephala*, *Oxypolis filiformis*, *Erianthus* sp., *Aristida affinis*, *Anthraenantia rufa*, *Iris tridentata*, *Scleria minor*, *Paspalum laeve*, *Sabatia gentiana*, *Hypoxis hirsuta*, *Asclepias longifolia*, *Spiranthes longilabris*, *Rhynchospora torreyana*, *Osmunda regalis*, *Balduina uniflora*, *Solidago odora*, *Clitoria mariana*.

Woody species (ordered by first DCA axis score): *Taxodium ascendens*, *Vaccinium corymbosum*, *Cyrilla racemiflora*, *Symplocos tinctoria*, *Ilex cassine*, *Pinus serotina*, *Nyssa sylvatica* var. *biflora*, *Myrica heterophylla*, *Ilex coriacea*, *Rhododendron* sp.⁷, *Hypericum stans*, *Lyonia mariana*, *Vaccinium atrococcum*, *Hypericum reductum*, *Gaylussacia dumosa*, *Vaccinium crassifolium*, *Pinus palustris*, *Vaccinium staminium*, *Vaccinium tenellum*, *Diospyros virginiana*, *Rubus* sp.

¹ *Calopogon* spp. includes *C. barbatus*, *C. pallidus* and *C. pulchellus*.

² *Pinguicula* spp. includes *P. caerulea* and *P. lutea*.

³ *Panicum* is divided into three groups: *P. chamaelonche* (which includes some *P. portoricense* and *P. longiligulatum*), *P. ciliatum* (which includes some *P. strigosum*) and *Panicum* sp. (which includes all other small stature *Panicum* species).

⁴ Two groups of vegetative *Andropogon* are recognized: *A. virginicus* (which includes some *A. scoparius* and possibly *A. tenarius*) and *A. virginicus* var. *glomeratus* which in the study area is vegetatively and ecologically distinct, but is variously recognized in manuals as a synonym of *A. virginicus* (Radford *et al.*, 1968) and as a separate species (Hitchcock, 1950).

- ⁵ *Habenaria* spp. includes, in order of decreasing abundance, *H. cristata*, *H. integra*, *H. ciliaris*, *H. nivea* and possibly *H. blephariglottis*.
- ⁶ *Rhynchospora brevisetata* includes some *R. oligantha*.
- ⁷ *Rhododendron* spp. includes *R. atlanticum* and *R. viscosum*.

References

- Abugov, R., 1982. Species diversity and phasing of disturbance. *Ecology* 63: 2X9 293.
- Alatalo, R.V., 1981. Problems in the measurement of evenness in ecology. *Oikos* 37: 199 204.
- Al-Mufti, M. M., Sydes, C. L., Furness, S. B., Grime, J. P. & Band, S. R., 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* 65: 759 791.
- Barnes, P. W., Tieszen, L. L. & Ode, D. J., 1983. Distribution, production, and diversity of C₃- and C₄-dominated communities in a mixed prairie. *Can. J. Bot.* 61: 741 751
- Bartram, W., 1791. Travels through North and South Carolina, Georgia, East and West Florida, etc., Facsimile ed., Dover Publ., Inc., New York.
- Bergh, J. P. van den. 1979. Changes in the composition of mixed populations of grassland species. In: M. J. A. Werger (ed.). *The Study of Vegetation*, pp. 59 80. Junk, The Hague.
- Bowen, H. J. M., 1968. *The Flora of Berkshire*, Holywell Press, Oxford. 389 pp.
- Buol, S. W., 1973. Soils of the Southern States and Puerto Rico. USDA South. Coop. Ser. Bull. 174. 105 pp.
- Christensen, N. L., 1977. Fire and soil-plant nutrient relations in a pine wiregrass savanna on the coastal plain of North Carolina. *Oecologia* 31: 27 44.
- Christensen, N. L., 1979. The xeric sandhill and savanna ecosystems of the southeastern Atlantic Coastal Plain, U.S.A. In: H. Lieth & E. Landolt (eds.). *Contributions to the Knowledge of Flora and Vegetation in the Carolinas*. Vol. 68, pp. 246-262. *Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich*.
- Christensen, N. L., 1981. Fire regimes in southeastern ecosystems. In: H. A. Mooney *et al.* (eds.). *Fire Regimes and Ecosystem Properties*, pp. 112 136. USDA For. Ser. Gen. Tech. Rpt. WO-26.
- Clapham, A. R., Tutin, T. G. & Warburg, E. F., 1962. *Flora of the British Isles*, 2nd ed. Cambridge Univ. Press, Cambridge. 1269 pp.
- Connell, J. H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302 1310.
- Connell, J. H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35: 131 138.
- Eleuterius, L. N. & Jones, S. B., 1969. A floristic and ecological study of pitcher plant bogs in south Mississippi. *Rhodora* 71: 29 34.
- Elliot, S., 1821 1824. *A Sketch of the Botany of South-Carolina and Georgia*. J. R. Schenk, Charleston. S. C.
- Fernald, M. L., 1937. Local plants of the inner coastal plain of southeastern Virginia. III. Phytogeographical considerations. *Biologia* 39: 465 491
- Folkerts, G. W., 1982. The Gulf coast pitcher plant bogs. *Am. Sci.* 70: 260 267.
- Caddy, L. L., 1982. The floristics of three South Carolina pine savannahs. *Castanea* 47: 393 402.
- Gano, L., 1917. A study in physiographic ecology in northern Florida. *Bot. Gaz.* 63: 337 372.
- Gauch, H. G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge Univ. Press, Cambridge. 29X pp.
- Gauch, H. G. & Whittaker, R. H., [1981], Hierarchical classification of community data. *J. Ecol.* 69: 537 557.
- Greene, S. W., 1935. Relation between winter grass fires and cattle grazing in the longleaf pine belt. *J. For.* 33: 339 341.
- Grime, J. P., 1973. Control of species density in herbaceous vegetation. *J. Environ. Manage.* 1: 151-167.
- Grime, J. P., 1979. *Plant Strategies and Vegetation Processes*. Wiley, New York. 222 pp.
- Grubb, P. J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107 145.
- Harper, R. M., 1906. A phytogeographical sketch of the Altamaha Grit Region of the Coastal Plain of Georgia. *Ann. N.Y. Acad. Sci.* 1: 415.
- Harper, R. M., 1914. Geography and vegetation of northern Florida. *Ann. Rep. Florida State Geol. Surv.* 6: 167 451.
- Harper, R. M., 1943. *Forests of Alabama*. Geol. Survey of Alabama Monogr. 10. Univ. of Alabama.
- Heyward, F. & Barnette, R. M., 1934. Effect of frequent fires on chemical composition of forest soils in the longleaf pine region. *Florida Ag. Expt. Sta. Tech. Bull.* 265.
- Hill, M. O., 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427 432.
- Hill, M. O., 1979a. DECORANA. Cornell Ecology Program, Cornell Univ., Ithaca, New York.
- Hill, M. O., 1979b. TWINSPLAN. Cornell Ecology Program, Cornell Univ., Ithaca, New York.
- Hill, M. O. & Gauch, H. G., 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47 58.
- Huston, M., 1979. A general hypothesis of species diversity. *Am. Nat.* 113: 81 101.
- Itow, S., 1963. Grassland vegetation in uplands of western Honshu, Japan. Part II. Succession and grazing indicators. *Jap. J. Bot.* IX: 133 167.
- Kologiski, R. L., 1977. The phytosociology of the Green Swamp, North Carolina. N.C. Ag. Expt. Sta. Tech. Bull. No. 250. 100 pp.
- Lawson, J., 1714. *Lawson's history of North Carolina*. Garrett and Massie, Inc., Richmond, VA. 259 pp. (2nd ed. printed 1952.)
- Lemon, P. C., 1949. Successional responses of herbs in longleaf-slash pine forest after fire. *Ecology* 30: 135 145.
- Lemon, P. C., 1967. Effects of fire on herbs of the southeastern United States and central Africa. *Proc. Tall Timbers Ecol. Conf.* 6: 112 127.
- Loucks, O. L., 1970. Evolution of diversity, efficiency, and community stability. *Am. Zool.* 10: 17 25.
- Maarel, E. van der, 1971. Plant species diversity in relation to management. In: E. Duffey & A. S. Watt (eds.). *The Scientific Management of Animal and Plant Communities for Conservation*. Symp. Brit. Ecol. Soc. 11: 45 63.
- Maarel, E. van der & Leertouwer, J., 1967. Variation in vegetation and species diversity along a local environmental gra-

- dient. *Acta Bot. Neerl.* 16: 211-221.
- Maxwell, H., 1910. The use and abuse of forests by the Virginia Indians. *William & Mary Coll. Q. Hist. Mag.* 19: 73-103.
- Metz, L. J., Lotti, T. & Klawitter, R. A., 1961. Some effects of prescribed burning on Coastal Plain forest soil. *USDA For. Ser. Res. Pap. SE-113*, Asheville, N.C. 10 pp.
- Mueller-Dombois, D., 1977. Comment on Whittaker's paper. In: R. Tüxen (ed.). *Vegetation und Fauna*. pp. 421-422. J. Cramer, Vaduz.
- Nash, G. V., 1895. Notes on some Florida plants. *Bull. Torrey Bot. Club* 2: 141-161.
- Naveh, Z. & Whittaker, R. H., 1979. Measurements and relationships of plant species diversity in Mediterranean shrublands and woodlands. In: F. Grassle, G. P. Patil, W. Smith & C. Taillee (eds.). *Ecological Diversity in Theory and Practice*, Statistical Ecol. Vol. S6, pp. 219-239. Internat. Coop. Publ. House, Fairland, Md.
- Naveh, Z. & Whittaker, R. H., 1980. Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. *Vegetatio* 41: 171-190.
- Ode, D. J., Tieszen, L. L. & Lerman, J. C., 1980. The seasonal contribution of C₃ and C₄ plant species to primary production in a mixed prairie. *Ecology* 61: 1304-1311.
- Olsson, H., 1979. Vegetation of the New Jersey pine barrens: a phytosociological classification. In: R. T. T. Forman (ed.). *Pine Barrens Ecosystem and Landscape*, pp. 245-263. Academic Press, New York.
- Paine, R. T., 1966. Food web complexity and species diversity. *Am. Nat.* 100: 65-75.
- Parrot, R. T., 1967. A study of wiregrass (*Aristida stricta* Michx.) with particular reference to fire. M.A. Thesis, Duke Univ., Durham, N.C. 137 pp.
- Peet, R. K., 1974. The measurement of species diversity. *Ann. Rev. Ecol. Sys.* 5: 285-307.
- Peet, R. K., 1978. Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio* 37: 65-78.
- Peet, R. K., Glenn-Lewin, D. C. & Wolf, J. W., 1983. Prediction of man's impact on plant species diversity. In: W. Holzner, M. J. A. Werger & I. Ikusima (eds.). *Man's Impact on Vegetation*, pp. 41-54. Junk, The Hague.
- Plummer, G. L., 1963. Soils of the pitcher plant habitats in the Georgia coastal plain. *Ecology* 44: 727-734.
- Pullen, T. & Plummer, G. L., 1964. Floristic changes within pitcher plant habitats in Georgia. *Rhodora* 66: 375-381.
- Radford, A. E., Ahles, H. E. & Bell, C. R., 1968. *Manual of the Vascular Flora of the Carolinas*. Univ. N.C. Press, Chapel Hill. 1183 pp.
- Regnéll, G., 1980. A numerical study of successions in an abandoned, damp calcareous meadow in South Sweden. *Vegetatio* 43: 123-130.
- Rights, D. L., 1947. *The American Indian in North Carolina*. Duke Univ. Press, Durham, N.C.
- Roberts, P. R. & Oosting, H. J., 1958. Responses of Venus' flytrap (*Dionaea muscipula*) to factors involved in its endemism. *Ecol. Monogr.* 28: 193-218.
- Rorison, I. H., 1971. The use of nutrients in the control of the floristic composition of grassland. In: E. Duffey & A. S. Watt (eds.). *The Scientific Management of Animal and Plant Communities for Conservation*. Symp. Brit. Ecol. Soc. 11: 65-7X.
- Rosén, E. & Sjögren, E., 1973. Sheep grazing and changes of vegetation on the limestone heath of Öland. *Zoon, suppl.* 1: 137-151.
- Schoener, T. W., 1974. Resource partitioning in ecological communities. *Science* 185: 27-39.
- Schoener, T. W., 1982. The controversy over interspecific competition. *Am. Sci.* 70: 5X7-595.
- Shmida, A. & Ellner, S. P., 1984. Coexistence of plant species with similar niches. *Vegetatio* (in press).
- Sjögren, E., 1971. The influence of sheep grazing on limestone heath vegetation on the Baltic island of Öland. In: E. Duffey & A. S. Watt (eds.). *The Scientific Management of Animal and Plant Communities for Conservation*. Symp. Brit. Ecol. Soc. 11: 487-495.
- Snyder, J. R., 1980. Analysis of coastal plain vegetation, Croatan National Forest, North Carolina. In: H. Lieth & E. Landolt (eds.). *Contributions to the Knowledge of Flora and Vegetation in the Carolinas*, Vol. 69, pp. 40-113. Veröff. Gebot. Inst. ETH, Stiftung, Rübel, Zürich.
- Stoddard, H. L., 1931. *The Bobwhite Quail, Its Habits, Preservation and Increase*. Charles Scribner's Sons, New York.
- Streng, D. R. & Harcombe, P. A., 1982. Why don't Texas savannas grow up to forest? *Am. Mid. Nat.* 108: 278-294.
- Terborgh, J., 1973. On the notion of favorableness in plant ecology. *Am. Nat.* 107: 481-501.
- Thalen, D. C. P., 1971. Variation in some saltmarsh and dune vegetations in the Netherlands with special reference to gradient situations. *Acta Bot. Neerl.* 20: 327-342.
- Thorne, R. F., 1954. The vascular plants of southwestern Georgia. *Am. Mid. Nat.* 52: 257-327.
- Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton Monogr. Pop. Biol. 17, Princeton Univ. Press, Princeton, New Jersey. 296 pp.
- U.S. Dept. Commerce, National Oceanic and Atmospheric Adm., 1977. *Climatological Data North Carolina*, Vol. X2 8X. National Climatic Data Center, Asheville, N.C.
- Vogl, R. J., 1973. Fire in the southeastern grasslands. *Tall Timbers Fire Ecol. Conf. Proc.* 12: 175-198.
- Ward, T., 1979. Memo to Thomas Massengale, North Carolina Nature Conservancy, Chapel Hill, N.C. April 13, 1979.
- Wells, B. W., 1928. Plant communities of the coastal plain of North Carolina and their successional relations. *Ecology* 9: 230-242.
- Wells, B. W., 1932. *The Natural Gardens of North Carolina*. Univ. of N.C. Press, Chapel Hill. 458 pp.
- Wells, B. W. & Shunk, I. V., 1928. A southern upland grass-sedge bog: an ecological study. *N.C. Ag. Expt. Sta. Tech. Bull.* 32.
- Wells, B. W. & Shunk, I. V., 1931. The vegetation and habitat factors of the coarser sands of the North Carolina coastal plain: an ecological study. *Ecol. Monogr.* 1: 465-520.
- Wells, B. W. & Whitford, L. A., 1976. History of stream-head swamp forests, pocosins, and savannas in the southeast. *J. Elisha Mitchell Sci. Soc.* 92: 148-150.
- Wharton, C. H., 1978. *The Natural Environments of Georgia*. Off. of Planning and Res., Ga. Dept. Natl. Resources, Atlanta. 227 pp.
- Whittaker, R. H., 1977a. Evolution of species diversity in land communities. In: M. K. Hecht, W. C. Steere & B. Wallace (eds.). *Evolutionary Biology*, Vol. 10, pp. 1-67. Plenum

- Publ. Corp., New York.
- Whittaker, R. H., 1977b. Animal effects on plant species diversity. In: R. Tüxen (ed.), *Vegetation und Fauna*, pp. 409.-425. J. Cramer, Vaduz.
- Whittaker, R. H. & Gauch, H. G., 1973. Evaluation of ordination techniques. In: R. H. Whittaker (ed.), *Ordination and Classification of Communities*, Hndbk. of Veg. Sci. 5, pp. 287-321. Junk, The Hague.
- Willems, J. H., 1980. Observations on north-west European limestone grassland and communities. *Proc. K. Ned. Akad. Wet. Series C* 83: 279-306.
- Williams, G. J. & Markley, J. I., 1973. The photosynthetic pathway type of North American shortgrass prairie species and some ecological implications. *Photosynthetica* 7: 262-270.
- Woodwell, G. M., 1956. *Phytosociology of coastal plain wetlands of the Carolinas*. M.A. Thesis, Duke Univ., Durham, N.C. 51 pp.

Accepted 17.10.1983.