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Community composition of an old growth longleaf pine forest: relationship to soil texture

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ABSTRACT

GILLIAM, F. S., B. M. YURISH (Department of Biological Sciences, Marshall University, Huntington, WV 25755) AND L. M. GOODWIN (Weymouth Woods-Sandhills Nature Preserve, Southern Pines, NC 28387). Community composition of an old-growth longleaf pine forest: relationship to soil texture. Bull. Torrey Bot. Club 120: 287–294. 1993.—The Sandhills region of the southeastern United States is characterized as having deep, xeric, sandy soils supporting forest types comprised largely of two species, longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*). This study examined species composition with respect to elevation in the Boyd Tract, a 66 ha old growth longleaf pine forest in the North Carolina Sandhills. Sixty plots were established within two distinct site types: an atypical mesic type at higher (>165 m) elevations (uplands) and a more typical xeric type at lower (≤165 m) elevations (lowlands). Canonical discriminant analysis revealed distinct clusters of plots associated with these topographic positions on the first canonical axis. Strongest canonical correlations on this axis were found for hardwood species: negative for turkey oak; positive for black oak (*Q. velutina*), hickories (*Carya* spp.), and dogwood (*Cornus florida*). Sand content showed a significant negative relationship with clay content, representing a texture gradient between a maximum sand content of 92% in the lowland and a maximum clay content of 17% in the upland. There was a significant negative correlation between canonical axis 1 scores and sand content and a significant positive correlation between axis 1 scores and clay content. These data suggest that soil texture may be largely responsible for the distribution of hardwood species, but not longleaf pine, within this old growth forest. The higher clay content (and presumably higher moisture and fertility) of the upland soils have allowed for the development of a forest type which, with the exception of large, infrequent longleaf stems, more closely resembles the oak-hickory forests of the adjacent North Carolina Piedmont than would be expected, given its location within the Sandhills region.

Key words: longleaf pine, North Carolina Sandhills, plant-soil relationships, soil texture, old growth forests.

The Sandhills region of the southeastern United States extends somewhat continuously along the fall-line between Piedmont and Coastal Plain provinces from southern North Carolina through Georgia to northern Alabama. The soils of the region are typically deep, coarse-textured sands which, despite regionally high annual precipitation (~120–130 cm/yr), create xeric conditions for plant growth (Christensen 1988). As a result, the dominant woody species, as initially described by Wells (Wells 1928; Wells and Shunk 1931), are fairly uniform throughout true Sandhills—longleaf pine (*Pinus palustris*) in the overstory and turkey oak (*Quercus laevis*) in the understory. Present day forests within the Sandhills region are somewhat disjunct as a result of urbanization, forestry practices, and the widespread exclusion of fire, which has long been known as a requirement for successful regeneration of the dominant longleaf pine (e. g., Andrews 1917). Thus, old growth longleaf pine forests are rare and are, consequently, poorly studied.

In his classic review of southeastern U.S. Coastal Plain plant communities, Wells (1942) discussed the importance of fire in maintaining longleaf pine forests, emphasizing soil texture as a significant factor in these systems, controlling other edaphic factors (e. g., moisture and fertility) which influence the distribution of dominant tree species. He indicated that on "medium sand" longleaf pine predominates, but that in areas of finer-textured soils ("finer sands") larger oaks (e.

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Table 1. Important herbaceous layer species of upland and lowland sites of the Boyd Tract. Importance values (I.V.'s) calculated as sum of relative cover and relative frequency. Species and I.V.'s summarized from data provided by R.K. Peet and collected by the North Carolina Vegetation Survey.

Upland		Lowland	
Species	I.V.	Species	I.V.
Quercus laevis	31.0	*Quercus laevis*	23.3
Pinus palustris	22.3	*Pinus palustris*	20.6
Gaylussacia dumosa	19.6	*Nyssa sylvatica*	19.8
Sassafras albidum	17.4	*Cornus florida*	17.1
Diospyros virginiana	16.6	*Carya tomentosa*	15.6
Carya pallida	16.6	*Gaylussacia dumosa*	12.9
Nyssa sylvatica	14.4	*Diospyros virginiana*	12.2
Cornus florida	13.3	*Sassafras albidum*	11.8
Q. velutina	13.0	*Vitis rotundifolia*	11.0
Chimaphylla maculata	9.0	*Prunus serotina*	9.1
Aristida stricta	9.0	*Chimaphylla maculata*	8.3
Tephrosia virginiana	9.0	*Amphicarpa bracteata*	7.9
Vitis rotundifolia	8.8	*Ilex opaca*	7.9
		Euphorbia cordifolia	7.6
		Ipomoea pandurata	7.2
		Smilax glabra	7.2

g., black oak—*Q. velutina*), flowering dogwood (*Cornus florida*), and sweetgum (*Liquidambar styraciflua*) invade these pine forests in the absence of fire, eventually resulting in replacement of longleaf pine by hardwood species independent of site type.

The Boyd Tract in the Sandhills of the south-central part of North Carolina is unique in several ecologically important ways which permit examination of these texture-species relationships at a single site. First, it is the largest old growth stand of longleaf pine in the state of North Carolina (Muse 1975). Second, it has remained essentially unburned for >80 yr (K. L. Boyd, pers. comm.). Finally, noticeable surface soil color differences between higher elevation and lower elevation areas reveal that the higher elevations have soil with a high clay content, a condition quite atypical for a site well within the Sandhills region (Christensen 1988). Obvious vegetation differences appear to coincide with observed soil differences, suggesting a relationship between soil texture and the distribution of dominant tree species. The purpose of this study was to examine these possible relationships and to test the hypothesis of Wells (1942) that longleaf pine will be replaced by larger hardwood species under chronic fire exclusion on fine-textured soils.

Methods and Materials. STUDY SITE. Research was carried out at the Boyd Round Timber Natural Area (Boyd Tract) in Moore County, North Carolina (35°N, 79°W) within the Sandhills region of the state. The Boyd Tract is 66 ha and ranges from 137 to 180 m in elevation. Parent materials are unconsolidated Cretaceous sand and clay layers (Sechrest and Cooper 1970).

The soils of the Boyd Tract are predominantly sands of the Blaney series. Blaney soils are sandy, siliceous, thermic Arenic Fragiudults, with characteristically thick (50 to 100 cm), fairly uniform, and very strongly acid A horizons (U.S.D.A. 1972). Within the Boyd Tract, two site types were identified based on topographic position. The upland areas (>165 m) tend to have soils with higher clay content, whereas the lowland (≤165 m) soils had somewhat higher sand content. The two site types occupy approximately equal portions of the Tract.

The herbaceous layer of the Boyd Tract is sparse and relatively species-poor (R. K. Peet, pers. comm.), typical of pine forest herb layers under chronic no-fire conditions (Gilliam and Christensen 1986; Gilliam 1991). Indeed, the dominant herb layer species in both site types were seedlings of overstory tree species (Table 1). More important herbaceous species included spotted wintergreen (*Chimaphila maculata*), wiregrass (*Aristida stricta*), goat's rue (*Tephrosia virginiana*), hog peanut (*Amphicarpa bracteata*), and *Euphorbia cordifolia* (Table 1). Longleaf pine was the dominant tree species at the Boyd Tract. In addition, hardwood species included several oaks, hickories, black gum, and flowering dogwood (Table 2).

STAND HISTORY. The Boyd Tract was part of the Weymouth Estate owned by James Boyd,

Table 2. Importance values (I.V.) for tree species of the Boyd Tract as a whole ("Mean") and for upland and lowland sites separately. I.V. for each species is based on the sum of relative basal area (BA) and relative density (D). BA is expressed as m^2/ha. D is expressed as # stems/ha.

	Upland					Lowland					Mean				
Species	BA	Rel. BA	D	Rel. D	I.V.	BA	Rel. BA	D	Rel. D	I.V.	BA	Rel. BA	D	Rel. D	I.V.
Pinus palustris	15.9	43.7	74	8.2	51.9	18.5	62.9	168	10.5	73.4	17.2	52.6	121	9.7	62.3
Quercus laevis	0.8	2.2	53	5.9	8.1	6.6	22.4	1124	70.6	93.0	3.7	11.3	588	47.1	58.4
Q. velutina	11.4	31.3	151	16.8	48.1	1.2	4.1	29	1.8	5.9	6.3	19.3	90	7.2	26.5
Carya spp.	3.8	10.4	200	22.2	32.6	1.6	5.4	74	4.6	10.0	2.5	7.6	137	11.0	18.6
Cornus florida	1.4	3.8	167	18.5	22.3	0.2	0.7	33	2.1	2.8	0.8	2.4	100	8.1	10.5
Nyssa sylvatica	0.9	2.5	140	15.5	18.0	0.3	1.0	62	3.9	4.9	0.6	1.8	101	8.1	9.9
Q. marilandica	1.2	3.3	64	7.1	10.4	0.3	1.0	22	1.4	2.4	0.8	2.4	43	3.4	5.8
Diospyros virginiana	<0.1	<0.3	3	0.3	<0.6	0.2	0.7	50	3.1	3.8	0.1	0.3	27	2.2	2.5
Q. stellata	0.3	0.8	14	1.6	2.4	0.2	0.7	15	0.9	1.4	0.3	0.9	15	1.2	2.1
Q. margaretta	0.2	0.5	20	2.2	2.7	0.3	1.0	8	0.5	1.5	0.3	0.9	14	1.1	2.0
Sassafras albidum	<0.1	<0.3	3	0.3	<0.6	<0.1	<0.3	3	0.2	<0.5	<0.2	<0.3	3	0.2	<0.8
Magnolia grandiflora	<0.1	<0.3	3	0.3	<0.6	<0.1	<0.3	1	0.1	<0.4	<0.2	<0.3	2	0.2	<0.8
Ilex opaca	<0.1	<0.3	6	0.7	<0.6	—	—	—	—	—	<0.1	<0.3	3	0.2	<0.5
Acer rubrum	<0.1	<0.3	3	0.3	<0.6	—	—	—	—	—	<0.1	<0.3	2	0.2	<0.5
Oxydendron arboreum	—	—	—	—	—	<0.1	<0.3	2	0.1	<0.4	<0.1	<0.3	1	0.1	<0.4
Prunus serotina	—	—	—	—	—	<0.1	<0.3	2	0.1	<0.4	<0.1	<0.3	1	0.1	<0.4
Total	36.0	100	901	100	200	29.4	100	1593	100	200	32.7	100	1248	100	200

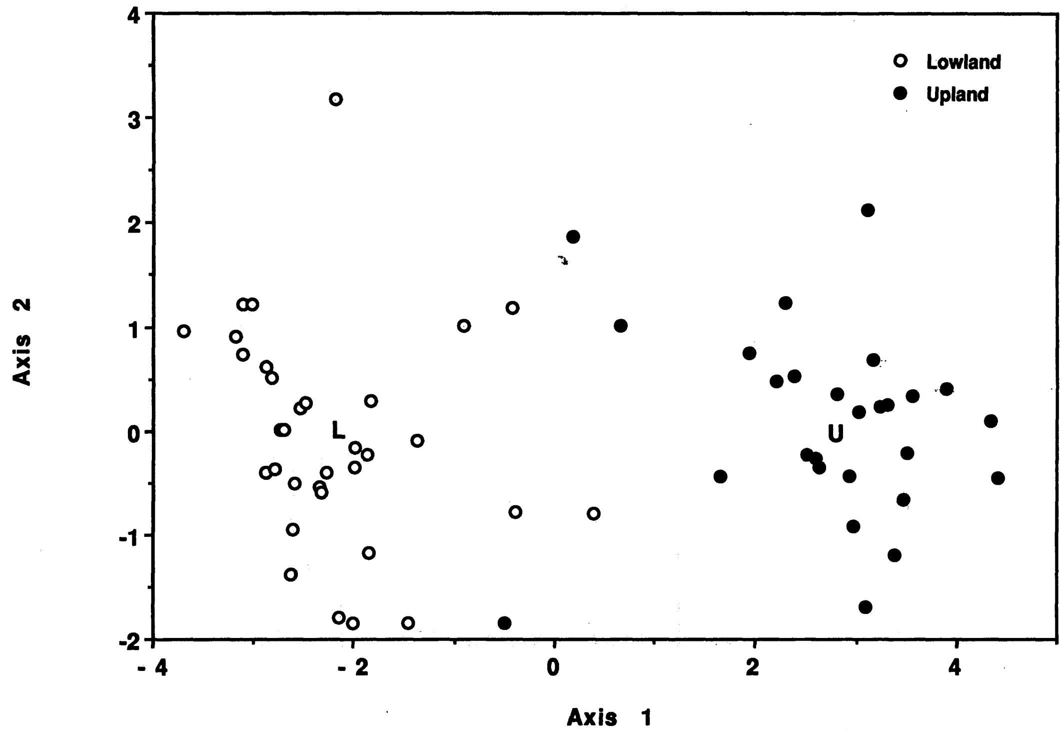

Fig. 1. Canonical discriminant ordination of 60 plots of the Boyd Tract. Plots were designated upland (closed circles) or lowland (open circles) a priori based on topographic position in the Tract. Also shown are mean score positions for upland ("U") and lowland ("L") site types.

who purchased it at the turn of this century in large part to protect the old growth longleaf pine from the extensive logging which was occurring at that time. The Tract was given to the North Carolina Division of Parks and Recreation in the 1970's and presently is managed as part of the Weymouth Woods Sandhills Nature Preserve. There has been virtually no intentional burning, and very minimal forest activity (occasional "boxing" of longleaf stems for turpentine and removal of dead longleaf pines), since the early 1900's (K. L. Boyd, pers. comm.). According to records at the Preserve, the oldest longleaf pines are >400 yr old, with stand establishment estimated at around the 1550's (E. Cook and J. Carlisle, unpubl. data).

The Boyd Tract has not experienced fire for over 80 yr. Historical records indicate that the entire Tract (and surrounding area) was burned in 1909 as a result of an intense and extensive wildfire (Huttenhauer 1980). Although this fire was reported in the popular literature (the only account of the fire) to have left "charred timber, and death, and hideous desolation," (Huttenhauer 1980), the many large pines and oaks now found on the Boyd Tract indicate that there must have been an appreciable degree of survival for these species.

SAMPLING AND ANALYSIS. A total of 60 permanent circular sample plots were established so that approximately 30 plots were located in each site type using the 165 m isocline from a topographic map: upland plots above, lowland plots below this line. Plots were located randomly within each site type. Each plot was 11.3 m in radius for a sample area of 0.04 ha. All woody stems ≥2.5 cm diameter (at 1.5 m height) within each plot were tallied, identified to species, and measured for diameter to the nearest 0.1 cm. It should be noted that not all individuals of the genus *Carya* (hickory) could be identified to species with confidence. Therefore, the hickories will be presented here as *Carya* spp. Nomenclature follows Radford et al. (1968). Importance values (I.V.'s) were calculated for each species in each plot as the sum of relative basal area and relative density (ranging from 0 to 200).

Mineral soil was taken at a 10 cm depth. Four samples were taken randomly within each sample plot and combined to yield a single composite sample; organic horizons were discarded (Gilliam 1988). Soil samples were analyzed for texture using the hydrometer method (Bouyoucos 1951), with texture data summarized as sand, silt, and clay (%).

To determine compositional variability and assess possible relationships between species composition and soil texture components, multivariate statistics were performed using canonical discriminant analysis (CDA; Proc CANDISC; SAS 1982). CDA is related to principle components analysis and canonical correlation and is particularly useful in ordinating more than a single data matrix (Pielou 1984). In this case, there were two data matrices, one for each site type. Input data for this ordination were ln-transformed species I.V.'s from each plot (Zar 1984).

CDA axis scores were compared to ln-transformed values of sand, clay, and silt content for each plot using Spearman's rank order correlation. This type of data transformation and analysis is useful when ordination scores and plot (i. e., soil) data are not normally distributed (Roberts and Christensen 1988).

Results and Discussion. COMMUNITY COMPOSITION. Although 16 woody species were tallied within the 60 sample plots, only six taxa had I.V.'s of $> \sim 10$ out of a total of 200 for all species (Table 2). Thus, this old growth forest appeared to be of a somewhat simple species composition, consistent with the observation of Christensen (1988) that Sandhills longleaf forests are generally not species-rich. The two top species suggested an overall stand structure of longleaf pine overstory and turkey oak understory, similar to that initially described by Wells (1928) for forests of this type.

Multivariate analysis, however, indicated that community composition varied substantially with elevation. Ordination with canonical discriminant analysis revealed rather distinct clusters of plots associated with topographic position along the first canonical axis (Fig. 1). Lowland plots (≤ 165 m elevation) had low axis 1 scores and upland plots (> 165 m) had high axis 1 scores. Mean scores, represented on the figure by letters, also indicate substantial overall differences in community composition between site types (Fig. 1).

To interpret the ordination pattern in Fig. 1, Table 3 presents canonical correlations between individual species I.V. data and each of the canonical variables (axes). No species was highly

Table 3. Total-sample correlation between ln-transformed species I.V.'s and first two canonical variables (CAN1 and CAN2).

Species	CAN1	CAN2
Pinus palustris	−0.33	−0.04
Quercus laevis	−0.90	−0.10
Q. velutina	0.84	0.27
Carya spp.	0.70	−0.02
Cornus florida	0.78	−0.21
Nyssa sylvatica	0.42	0.08
Q. marilandica	0.10	−0.03
Diospyros virginiana	−0.43	0.00
Q. stellata	−0.11	0.04
Q. margaretta	0.27	−0.05
Sassafras albidum	0.23	−0.01
Magnolia grandiflora	0.23	0.06
Ilex opaca	0.41	0.00
Acer rubrum	0.22	0.00
Oxydendron arboreum	−0.18	0.00
Prunus serotina	−0.12	0.04

correlated with the second canonical variable (CAN2); however, several species were highly correlated with the first canonical variable (CAN1). Among the top six important species (Table 2), longleaf pine was only weakly correlated with CAN1. Turkey oak was strongly, negatively correlated with CAN1, whereas black oak, hickories, black gum, and dogwood were strongly, positively correlated with CAN1 (Table 3). Thus, lowland plots supported woody vegetation more typical of that originally described by Wells (Wells 1928; Wells and Shunk 1931) as true Sandhills, with longleaf pine and turkey oak as sole dominants in the overstory and understory, respectively. Another frequent lowland species at this particular site was persimmon (*Diospyros virginiana*). In contrast, other than the large, sparse longleaf stems, the upland closely resembled the oak-hickory forests of the adjacent North Carolina Piedmont (Oosting 1942; Sechrest and Cooper 1970).

SOIL TEXTURE. Soil texture is an easily measured and ecologically very meaningful soil variable, integrating several other soil factors, such as fertility and moisture availability. In this study we collected soil texture data along with data on forest species composition to test the predictions of Wells (1942) that, under fire exclusion, longleaf becomes replaced by larger hardwood species (e. g., oaks and hickories) on finer-textured soils.

There was a significant negative relationship between percent clay and percent sand in the mineral soil (Fig. 2). There was a strong tendency

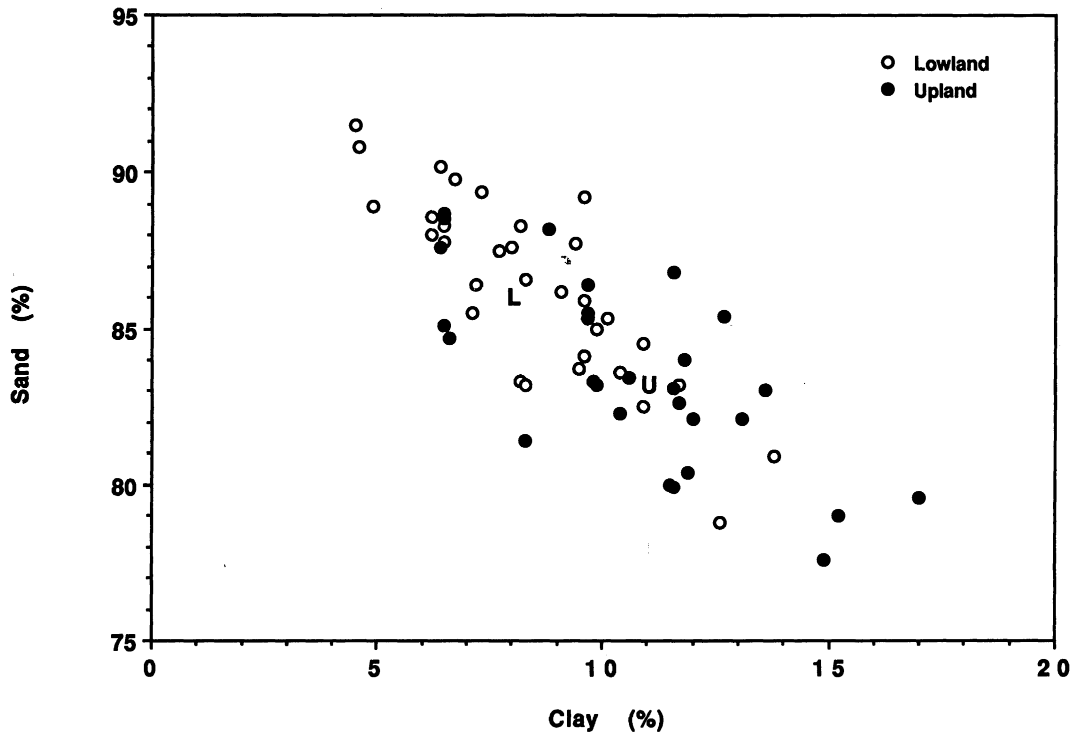

Fig. 2. Relationship of sand content to clay content of mineral soil for upland and lowland plots of the Boyd Tract. Plots were designated upland (closed circles) or lowland (open circles). Also shown are mean sand and clay values for upland ("U") and lowland ("L") site types. Equation is: $y = 94.30 - 0.98x$, $r = 0.81$, $P < 0.01$.

for lowland soils to have higher sand content and upland soils to have higher clay content, with extreme texture values ranging from a maximum sand content of 92% (with 4% each of clay and silt) in the lowland to a maximum clay content of 17% (79% sand and 4% silt) in the upland. However, based on field observations, it had been expected that soil texture values would yield somewhat tight clusters around the extremes of high sand/low clay for the lowland plots and low sand/high clay for the upland plots, assuming that silt content would not vary appreciably. Instead, although silt content varied very little between plots (~5%), soil data indicate that there was a pronounced soil texture gradient at the Boyd Tract, with many plots occupying intermediate positions along this gradient (Fig. 2).

Table 4. Spearman rank correlation coefficients between canonical discriminant analysis axis scores and texture classes for 60 plots at the Boyd Tract.

Texture class	Canonical axes: Axis 1	Canonical axes: Axis 2
Sand	−0.31*	−0.06
Clay	0.32*	−0.07
Silt	0.11	0.24**

* $P < 0.05$.
** $P < 0.10$.

COMPOSITION-TEXTURE RELATIONSHIPS. To determine how community composition might vary with respect to this soil texture gradient, Table 4 presents Spearman rank correlation coefficients between axis scores of all sample plots and corresponding ln-transformed percent sand, clay, and silt. Sand and clay were significantly ($P < 0.05$) negatively and positively correlated, respectively, with CAN1, but not with CAN2. Silt was weakly ($P < 0.10$) correlated with CAN2, but not with CAN1 (Table 4). These patterns suggest that the clusters of plots in the ordination space of Fig. 1 may be responding to soil texture, with the lowland community of longleaf pine, turkey oak, and persimmon being associated with coarse-textured, more sandy soils. The upland community of longleaf pine, black oak, hickories, dogwood, and black gum was associated with finer-textured, higher clay soils.

These results support in one respect the predictions of Wells (1942) regarding the influence of soil texture under chronic fire exclusion in longleaf pine forests. The 80-yr absence of fire indeed has resulted in differences in forest development which are related to texture, with larger hardwoods (e. g., black oak and hickories) becoming more prevalent on finer-textured soils. In contrast to the hardwoods, longleaf pine dominance appeared independent of site type; thus our data, along with size class frequency distributions for Boyd Tract tree species (Gilliam 1992), do not support the prediction that these hardwoods are replacing longleaf pine. The lack of support for this prediction may be largely a function of longevity. Longleaf pine is an extremely long-lived species (Platt et al. 1988); 80 yr is probably an insufficient period of time to see true decline in a species of this stature. This is in sharp contrast to another species of southern (yellow) pine, loblolly pine (*Pinus taeda*). If undisturbed, hardwood species will begin to replace loblolly pine in North Carolina Piedmont forests in 70–100 yr (Oosting 1942; Christensen and Peet 1984). Future studies on the Boyd Tract will focus on stand structure and longleaf seedling establishment to address this question of reproductive success of longleaf pine under chronic fire exclusion as it relates to the site-related differences in stand-texture relationships.

In conclusion, these results support earlier observations of the importance of soil texture in influencing community composition of longleaf pine forests (e. g., Wells 1942). However, in the present state of this old growth forest, soil texture appears to be influencing the distribution of hardwood species, but not that of longleaf pine. The interaction of texture differences with long-term fire exclusion has resulted in an extremely unusual condition for a Sandhills longleaf pine stand, a notable exception to the generalizations of Christensen (1988) that such fall-line Sandhills have xeric ridges comprised of longleaf pine and turkey oak and more mesic mid-slopes and bottoms with other hardwood species. At the Boyd Tract, the atypically high clay content, and presumably higher moisture and fertility (Jenny 1980), of the upland soils have allowed for the development of a forest type which, with the exception of large, but somewhat infrequent, longleaf pines, more closely resembles the oak-hickory forests of the adjacent North Carolina Piedmont than would be expected, given the location of the Boyd Tract within the Sandhills region.

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ANNOUNCEMENT

Richard and Minnie Windler Award Winner. Dr. Warren Frank Lamboy of the New York State Agricultural Experiment Station of Cornell University at Geneva, New York, was awarded the 1993 Richard and Minnie Windler Award for his paper "The taxonomic status and probable origin of *Aster chlorolepis,* a Southern Appalachian endemic," published in Castanea 57: (1): 52–65. The paper represents a portion of Dr. Lamboy's Ph.D. dissertation completed at the University of Illinois, Urbana. The Richard and Minnie Windler Award, established and endowed in 1990 by Dr. Donald R. Windler in memory of his parents, carries a $200 stipend and is awarded by the Southern Appalachian Botanical Society at its annual meeting to what is judged by the selection committee to be the best systematics paper published in Castanea during the previous year. This is the third year that the award has been given.