THE WOODY VEGETATION OF LITTLE BLACK SLOUGH: AN UNDISTURBED UPLAND-SWAMP FOREST IN SOUTHERN ILLINOIS1/

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Abstract.--A study was conducted in Little Black Slough and relatively undisturbed uplands (Boulder Slope Woods), Johnson County, Illinois to analyze the woody vegetation in relation to several soil-site characteristics and to describe community types and diameter-class structure. Vegetation was sampled in 290 0.04 ha plots located throughout the area. Soil-site variables including maximum depth of flooding and soil texture were measured in 181 of the vegetation plots located along the upland to swamp gradient in Boulder Slope Woods and adjacent lowlands. Gradient analysis and classification techniques were used to elucidate vegetation-environment relationships. Vegetation was found to vary along a complex flooding-soil texture (ie. drainage-aeration) gradient. Seven dominance types were identified in the study area, most of which correlate with vegetation types found elsewhere in the Southern Floodplain Forest Region. Diameter-class analysis was done on trees growing on four site types found in the study area using both the negative exponential and the negative power models. The diameter-class stucture in the four site types, including the upper slope, lower slope-floodplain contact, floodplain and swamp, showed a significant fit to both models but the goodness of fit declined from upland to swamp. If current regeneration patterns persist, the stand will perpetuate itself but with some change in composition.

Keywords: Bottomland Hardwoods, Classification, Floodplain, Indirect Gradient Analysis, Ordination, Diameter-class Analysis, Soil-site Variables, Swamp

INTRODUCTION

Southern floodplain forests extend northward along the Mississippi River to the southern tip of Illinois and into the lower portions of the Wabash and Ohio Rivers (Kuchler 1964). Braun (1950) includes the bottomland forests of this region in the Southeastern Evergreen Forest Region and the upland forests in the Western Mesophytic Forest Region. Both of these forest types, as she describes them, occur in Southern Illinois and in the area defined in this study. Lowland forests range from swamps dominated by *Taxodium distichum* and *Nyssa aquatica* to floodplains dominated by bottomland hardwoods. Uplands in the region are characterized by species of *Quercus* and *Carya* which may dominate the forest stands.

From data presented by Telford (1926), it is estimated that the bottomland forests of Illinois have been reduced in area by over 90% as a result of clearing and draining. Consequently,

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few sites remain from which baseline information about natural or 'near pristine' bottomland forests can be obtained.

With this in mind, the least disturbed portions of Little Black Slough and adjacent uplands (Boulder Slope Woods) were sampled to describe the composition and structure of the woody vegetation in relation to selected soil-site variables along an upland to swamp gradient. Also, the entire lowland portion of Little Black Slough along with Boulder Slope Woods was studied to describe the woody vegetation and the diameter-class structure on major site types occurring within the area.

DESCRIPTION OF STUDY AREA

The Little Black Slough Natural Area comprises about 1,100 ha along the Cache River floodplain, backwater lowlands and adjacent uplands in Johnson County, Illinois (Figure 1). Little Black Slough is located in the Shawnee Hills Section of the Interior Low Plateaus Province. The lowlands in Johnson County are in the Coastal Plain Province and interface with the uplands in the study area.

The region has mild winters, warm summers and abundant rainfall. At New Burnside, the nearest long-term reporting station, the mean January temperature is 1.44 C and the mean July temperature is 25.9 C. Average annual precipitation of the nearest reporting weather station ranges from 1050-1150 mm (Page 1949). Precipitation is fairly evenly distributed throughout the year with some dry periods occurring in July and August. The area has a frost-free period of 190-213 days from about April 17 to October 21 (Page 1949, Fehrenbacher and Walker 1964). River discharges in the area peak in March and April and decline throughout the growing season to a minimum in September (USDI Geological Survey Water Resources Division, file data).

Soils of the study area range from very rocky on the slopes to very clayey in the lowlands. The soils of Little Black Slough and Boulder Slope Woods include Hosmer silt loam on upper slopes and ridges, Wellston-Muskingum complex on mid to lower slopes, and Bonnie silt loam and Karnak clay in the bottoms (Fehrenbacher and Walker 1964). The Hosmer silt loam is a fine-silty, well drained, mixed mesic Typic Fragiudalf. It is derived from loess and has a slightly to well developed fragipan which may impede drainage (Fehrenbacher and Walker 1964). The Wellston-Muskingum complex occurs throughout the area on slopes ranging from 7-30%. The Wellston series is a fine-silty, mixed mesic Ultic Hapludalf while the Muskingum series is a loamy skeletal, mixed mesic Lithic Dystrochrept.

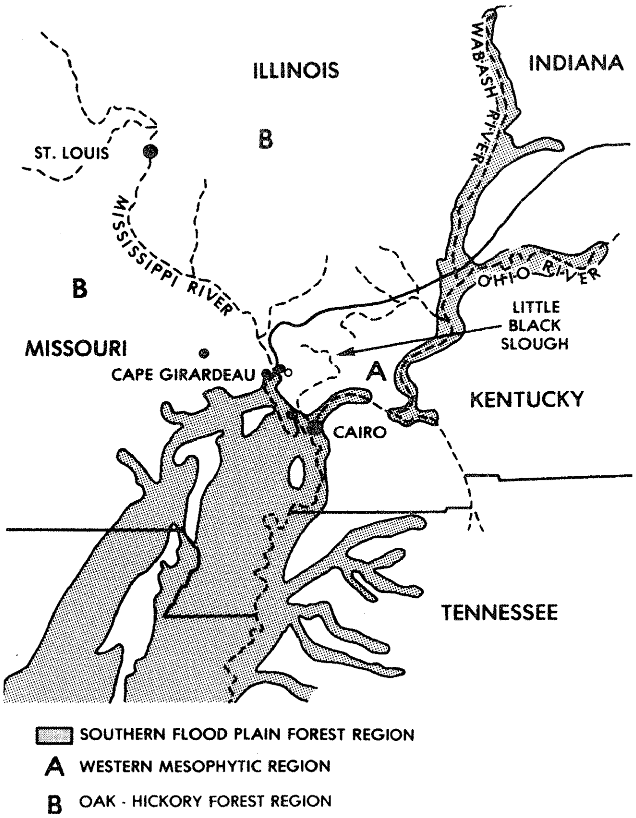

Figure 1. Location of Little Black Slough, Johnson County, Illinois.

The Karnak clay, which occurs in the slough below Boulder Slope Woods, is a silty clay which is a poorly drained, fine montmorillonitic, nonacid mesic Vertic Haplaquept. Bonnie silt loam occurs primarily in the northern end of the Slough and is a poorly drained moderately slowly permeable soil of floodplains (Fehrenbacker and Walker 1964). It is fine silty, mixed, acid, mesic Typic Fluvaquent.

Maximum relief of Little Black Slough and Boulder Slope woods is about 60 m. Slope gradients are level in the

Slough and up to 70% in Boulder Slope Woods. Boulder Slope Woods is located down slope from outcrops of Cypress Sandstone that are common in the area.

Little Black Slough and Boulder Slope Woods are owned by the Illinois Department of Conservation with the latter designated as a Natural Preserve. Little Black Slough has had light selective logging in the past and is experiencing substantial sedimentation from erosion of the cultivated land on the uplands surrounding the study area (Max Hutchinson, Ill. Nat. Heritage Program, pers. comm.). Along the southern edge of Little Black Slough is the 100 ha Boulder Slope Woods which is the least disturbed part of the study area. Because of a relatively low amount of disturbance throughout Little Black Slough and the continuity of the upland to swamp gradient in Boulder Slope Woods, an excellent opportunity exists to develop a better understanding of the upland to lowland forests near the northern terminus of the Southern Floodplain Region (Braun 1950).

METHODS AND MATERIALS

In Boulder Slope Woods and adjacent lowlands of Little Black Slough, 181 plots were sampled for both vegetation and soil-site data (intensive plots). The assumption was that vegetation and soil-site relationships would be best expressed where disturbance was minimal. In addition, 109 plots were sampled randomly throughout the remaining portion of Little Black Slough for vegetation data only (extensive plots). The extensive plots plus the intensive plots were used to describe the vegetation of Little Black Slough and provide the data for the diameter-class analysis. Sampling of the intensive plots occurred along transects which began at the base of the sandstone bluffs or on undisturbed ridgetops in Boulder Slope Woods. Transects, located about 100-150 m apart, were established perpendicular to the predominant topographic gradient and extended through the floodplain to the swamp until the entire gradient was sampled. The length of the transects varied depending on the distance from the bluff or ridge to the swamp. Additional samples were taken along the upland-floodplain contact to more evenly sample all site types along the topographic gradient. Along each transect, 0.04 ha rectangular plots (66.6 X 6.0 m) were placed 15-30 m apart. Distance between plots depended on topography. When topographic change was rapid (ie. steep slopes), plots were close together and when topography was level plots were farther apart. On slopes, the long axis of the plot was oriented parallel to the contour to maximize between-plot variance and minimize within-plot variance. The extensive vegetation plots were located by the use of random numbers to determine direction and distance along a pace transect originating from a predetermined starting point on each sampling day.

Within each plot, the diameter at breast height (dbh) or diameter above the buttress (dab) was measured for all trees > 6.6 cm and recorded by species. Shrubs and saplings (understory) with a dbh of 2.54 $\leq$ 6.6 cm were counted and recorded by species in a 0.004 ha rectangular plot nested on the center of the larger plot.

Because of funding limitations, soil-site estimates had to be made expediently and quickly in the field and, therefore would not be considered 'standard'. Environmental measurements made in each of the 181 plots included depth to and texture of the least and most permeable layers and maximum depth of flooding. Flooding was determined by measuring the high water mark on 5 trees in each plot and averaging. Soils were sampled using a 2.54 cm tube sampler and texture was determined following methods presented in Robertson et al. (1978). To minimize compaction, cores were extracted in increments of at least 0.3 m to a depth of about 1 m. Along the core, texture was estimated by the 'feel' method and the most and least permeable layers were determined. Once those layers were defined, texture of each was estimated and depth to the least permeable layer was measured. Soil samples from 20 plots were analyzed in the laboratory for texture (Bouycous 1927, 1951) to provide data for checking field determinations.

Understory, overstory and soil-site data from the intensive plots were combined into three separate matrices for analysis. The understory matrix was edited to include only those species with more than 10 occurrences, square-root transformed and relativized (sample totals equal 100) to remove the effects of a wide variation in density and possible outliers. Basal area (and, when needed for scaling purposes, relative basal area) was chosen as the tree species-response measure since basal area is related to biomass (Reiners 1972, Skeen 1973) and, to a lesser extent, canopy cover. The overstory basal area matrix for the intensive plots was screened to eliminate the 15 rarest species.

Both the overstory and understory matrices were ordinated separately by DECORANA or Detrended Correspondence Analysis (Hill 1979a, Hill and Gauch 1980), an improved version of reciprocal averaging ordination. Reciprocal averaging has been shown to be an effective technique for identifying major environmental gradients in bottomland forests (Robertson 1978, Robertson et al. 1978, Robertson et al. 1984).

Stepwise multiple regression was used to relate soil-site variables to the ordinations from both the overstory and understory data. Soil-site variables including depth of flooding, clay and sand in the most and least permeable layers and depth to the least permeable layer were used as the independent variables and the ordination score was the dependent variable. The best model was that which had the maximum R2 and the minimum C(p) value. C(p) is an expression of the size of the total squared error component for each set of independent variables and can be used as a criterion for model selection (Neter and Wasserman 1974).

TWINSPAN (two-way indicator species analysis, Hill 1979b) was used to classify the overstory vegetation using a data set comprised of both the extensive and intensive plots and a data set comprising only the intensive plots. TWINSPAN, a divisive classification technique, dichotomizes samples repeatedly using reciprocal averaging ordination of species' presence or importance.

Diameter-class analysis was performed on the total stand and on groups defined from the TWINSPAN classification of the full data set. Diameter classes were from 2.54 $\leq$ 6.6 cm as class 1 and the remaining classes increasing in 5.0 cm increments from 6.6 cm dbh. Both the negative exponential and negative power models were fit to the diameter-class data using all stems in both the understory and canopy and stems of species with only canopy potential to quantify the diameter-class distribution of the entire stand and of various site-types within the area. These models have been shown to express the diameter-class distributions of some forests (Schmelz and Lindsey 1965, Hett and Loucks 1976, and Robertson et al. 1978).

RESULTS

Vegetation structure and composition

Sixty tree species (Table 1) were encountered in the 290 samples and average species richness per 0.04 ha sample was 7.14. Total number of species encountered in the understory plots was 41; 6 of which were true shrubs and 4 were subcanopy tree species.

Table 1.--Structural characteristics of the woody vegetation in Little Black Slough and adjacent uplands, Johnson County, Illinois.

Parameter	Tree1/ Density	Tree Basal Area2/	Understory Density1/
Range	100-2625	7.6-105.4	0-2750
Mean	486.3	33.9	849.5
Standard Deviation	242.8	16.9	2588.7
N	290	290	191
Species	60	60	41
Species/ plot	7.1	7.1	2.1

1/ Stems/ha, dbh > 6.6 cm
2/ m2/ha

Average species richness per sample was 2.1 (Table 1). Species occurring in the study area but not encountered in the samples included *Carya aquatica*, *C. illinoensis*, *Quercus bicolor*, *Juglans cinerea*, *Viburnum dentatum*, and *Planera aquatica*. Nomenclature follows Mohlenbrock (1975).

Structural characteristics of the forest are presented in Table 1. Basal area ranged from 7.6 to 105.4 m2/ha ($\bar{x}$ = 33.9) and tree density ranged from 100.0 to 2625.0 stems/ha ($\bar{x}$ = 486.3). Understory density ranged from 250.0 to 2750.0 stems/ha ($\bar{x}$ = 849.5).

Soil-site characteristics varied along the topographic gradient (Table 2). Silt content in both the most and least permeable layers was highest on the slopes while clay content of both layers was highest in the lowlands. Maximum depth of flooding ranged from none on the slopes to a maximum of 185 cm in the lowest portion of the intensively sampled area.

Table 2.--Soil-site characteristics (means and standard deviation) in 181 plots from Boulder Slope Woods and adjacent lowlands, Little Black Slough, Johnson County, Illinois.

Soil-site Characteristics	Slope N=59 Mean	Slope N=59 Std	Lowlands N=122 Mean	Lowlands N=122 Std
Most permeable layer (%)				
Clay	15.3	13.1	37.4	21.8
Silt	63.4	15.9	45.5	20.4
Sand	21.4	16.4	16.5	8.3
Least permeable layer (%)				
Clay	28.9	13.8	43.6	18.9
Silt	55.8	10.8	42.1	18.7
Sand	15.3	6.5	14.4	6.2
Depth to least permeable layer, cm	29.9	21.7	12.4	19.0
Maximum depth of flooding, cm	0.6	4.2	61.0	51.9

Gradient Analysis

The overstory DECORANA ordination of both the full data set (extensive) and the environmental (intensive) plots resulted in scattergrams in which the samples were well dispersed along the first axis, indicating that no outlier samples occurred (Figures 2 and 3). Swamp and upper slope samples characterized opposite ends of the first axis. Multiple regression analysis of the environmental variables on the first DECORANA axis revealed that variation in the overstory ordination is strongly related to, in order of decreasing importance, maximum depth of flooding, clay in the most permeable layer and sand in the most permeable layer. Seventy nine percent of the variation in the ordination scores was explained by the regression model (Table 3).

A similar analysis of the second DECORANA axis indicated that no

Table 3.--Parameters for reg models relating first axis ord scores to soil-site variable overstory and understory dat Little Black Slough, Johnson Illinois.

Parameter	B value	Std. Error	F
Overstory N=180			
Clay most permeable layer	3.33	0.743	20.13
Sand most permeable layer	-3.67	0.950	14.88
Maximum depth of flooding	2.00	0.293	46.72
R-Square	0.7933		
C(p)	4.69		
Understory N=129			
Clay most permeable layer	4.69	1.28	13.46
Clay least permeable layer	2.53	1.05	5.81
Sand least permeable layer	-5.12	1.74	9.02
Maximum depth of flooding	1.13	0.47	5.80
R Square	0.4714		
C(p)	3.55		

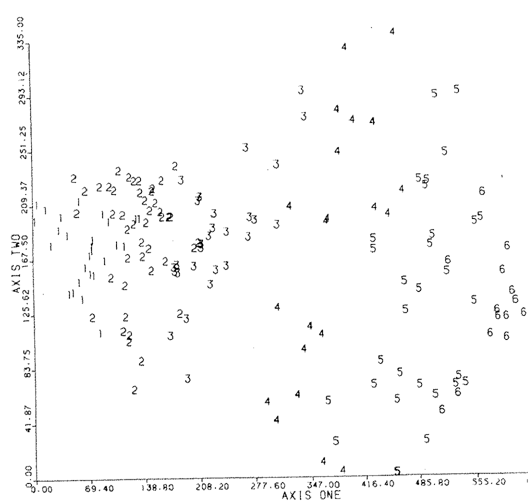

Figure 2.--Overstory ordination plots from Boulder Slope Wo adjacent lowlands, Little Black Johnson County, Illinois. reference TWINSPAN types: 1 = m 2 = lower slope, 3 = lower floodplain, 4 = shallow floodpl deep floodplain and 6 = swamp.

significant relationships occurred between the environmental variables and the ordination ($R2 < 0.03$).

The understory DECORANA first axis ordination revealed a strong gradient similar to that observed for the overstory. Plots containing swamp species ordinated on one end while plots with mesic upland species ordinated on the opposite end of the axis. Forty seven percent of the variation in the first axis was accounted for, in descending order, by clay in the most permeable layer, followed by sand in the least permeable layer, clay in the least permeable layer and maximum depth of flooding (Table 3). Second or higher axes were not significantly related to any of the measured environmental variables ($R2 < 0.04$).

Classification

TWINSPAN classification of the 290 vegetation plots and the 181 intensive plots from Boulder Slope Woods and adjacent lowlands delineated 7 and 6 groups, respectively (Tables 4 and 5). In both classifications, two swamp groups were combined because of small sample size and similarity of dominant species. A vegetation type dominated by Liquidambar styraciflua, Carya laciniosa, Quercus pagodaefolia and Acer rubrum was defined from classification of the full data set but was not identified in the portion of Little Black Slough sampled by the intensive plots (Table 4).

TWINSPAN groups from Boulder Slope Woods and adjacent lowlands included the following dominance types (sensu Whittaker 1978); 1) Quercus alba-Q. rubra-Carya spp., 2) Quercus rubra-Liriodendron tulipifera-Liquidambar styraciflua, 3) Liquidambar styraciflua-Quercus michauxii-Acer saccharum, 4) Acer rubrum-Quercus palustris-Liquidambar styraciflua, 5) Acer rubrum-Quercus lyrata-Fraxinus tomentosa, and 6) Nyssa aquatica-Taxodium distichum (Table 4). These types are ordered in sequence from upland-mesic sites with no flooding and relatively low clay content to swamp sites with deep flooding and fine textured soils (Table 5). Species richness (S) generally decreases and dominance, as indicated by the basal area of the dominant species, increases from mesic uplands to wet conditions (Tables 4 and 5).

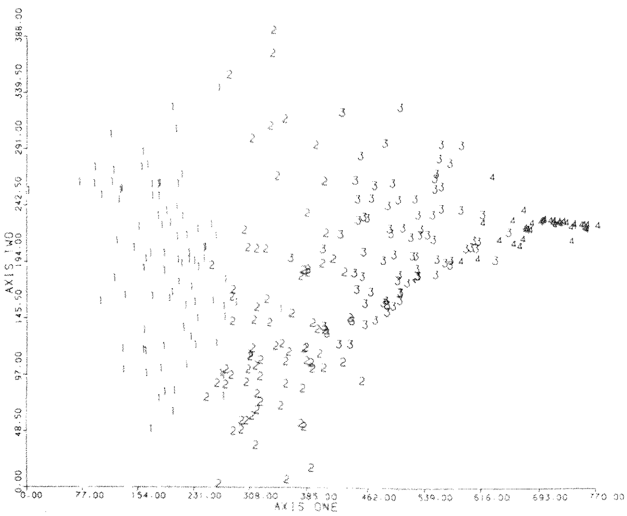

Figure 3.--Overstory ordination of 290 plots from throughout Little Black Slough, Johnson County, Illinois. Plotted numerals designate the vegetation types used in the diameter-class analysis. They are 1) a Quercus rubra-Q. alba-Liriodendron tulipifera type located on mid to upper slopes, 2) a Liquidambar styraciflua-Quercus michauxii-Acer saccharum type located along the lower slope-floodplain contact, 3) an Acer rubrum-Quercus lyrata-Q. palustris floodplain type and 4) a Nyssa aquatica-Taxodium distichum swamp.

Diameter-class analysis

The diameter distribution of the entire stand (extensive plots) displayed a significant fit to both the negative exponential ($R2 = 0.94$) and the negative power ($R2 = 0.97$) models (Table 6, Figure 4). When only canopy species were included, the fit to both models remained significant. Four dominance types identified from TWINSPAN (Figure 3), which occur on different sites, were used in the analysis following Harcombe and Marks (1978) and Whipple and Dix (1981) whereby the diameter-class structure is examined at different points along an environmental gradient. These four dominance types were derived (from TWINSPAN) by essentially combining the two Quercus types, the two Liquidambar styraciflua types and the two Acer rubrum types presented in Table 4 for the full data set (extensive plots).

These four types were redefined in terms of topographic position and are the mesic upland, lower slope-floodplain, floodplain and swamp. Diameter-class distributions for these types are presented in Figure 5. The diameter distribution of trees on the mesic slope displayed the best fit to the negative exponential model. The R2 ranged from 0.95 for the mesic upland type to 0.74 for the swamp (Table 6). When only species with only canopy potential were included, R2 values ranged from 0.95 for the mesic upland to 0.92 for the swamp. When the diameter-class distributions for all species and only canopy species were fit to the negative power model, R2 values were lower for all site types (Table 6).

Subcanopy species that contributed individuals to the smaller size classes in the mesic upland included *Asimina triloba*, *Cercis canadensis* and *Ostrya virginiana*. Canopy species with individuals in the smaller diameter-classes included *Acer saccharum*, *Carya* spp., *Quercus alba* and *Ulmus rubra*. Canopy species typical of this type which had no individuals in the smallest diameter-class include *Carya cordiformis*, *C. tomentosa*, *Juglans nigra*, and *Prunus serotina*. *Liriodendron tulipifera* displayed a bimodal diameter-class distribution with maximum numbers of individuals in the smallest (2.54 $\leq$ 6.6 cm dbh) and in the 50 cm diameter-class. In the lower slope-floodplain type, *Acer saccharum*, *Carya laciniosa*, *Fraxinus pennsylvanica*, *Morus rubra*, *Quercus michauxii*, *Ulmus americana* and *U. rubra* along with such subcanopy species as *Asimina triloba*, *Carpinus caroliniana*, and *Ilex decidua* contributed in excess of 50 stems each to the smallest diameter-class (2.54 $\leq$ 6.6 cm dbh). Canopy species in this type with no individuals in the smallest diameter-class included *Quercus pagodaefolia*, *Q. palustris* and *Platanus occidentalis*.

Abundant canopy species in the smallest diameter-class in the floodplain type included *Acer rubrum*, *A. negundo*, *Liquidambar styraciflua*, *Fraxinus tomentosa*, *Nyssa aquatica* and *Ulmus americana*. Subcanopy species contributing 50 or more individuals to the smallest diameter-class included *Carpinus caroliniana*, *Cornus foemina* and *Ilex decidua*. *Betula nigra*, *Diospyros virginiana*, and *Salix nigra*, species typical of this type, had no individuals in the smallest diameter-class. Species in the two smallest size classes in the swamp included *Nyssa aquatica* with 70% of stems and *Taxodium distichum* with 13%. The only subcanopy species with abundant regeneration in the small diameter-class was *Cornus foemina*. The only major canopy species in the swamp that had no individuals in the smallest diameter-class was *Populus heterophylla*.

Throughout the slough several species had so few stems that no statement could be made about their diameter-class distribution. These species generally had no individuals in the small diameter-class and only scattered individuals in the remaining diameter classes and, as examples, include *Acer saccharinum*, *Gleditsia aquatica*, *G. triacanthos*, *Q. macrocarpa*, *Q. shumardii*, *Q. stellata* and *Tilia americana*.

Table 6.--Negative exponential (upper) and negative power model (lower) parameters of size-class structure in four TWINSPAN derived segments of an upland-swamp gradient in Little Black Slough, Johnson County, Illinois.

	All Species			Canopy Species			
Segment	R2	a	b	R2	a	b	N
Mesic-upland	0.95	1091.6	-0.07	0.95	942.2	-0.07	91
	0.91	159097.1	-2.28	0.89	106062.7	-2.18	
Lower Slope	0.95	887.8	-0.07	0.95	783.0	-0.06	78
Floodplain	0.87	84822.0	-2.14	0.85	60222.9	-2.05	
Floodplain	0.94	810.1	-0.06	0.94	777.4	-0.06	82
	0.82	117260.5	-2.23	0.81	103568.3	-2.19	
Swamp	0.74	214.1	-2.69	0.92	544.0	-0.06	39
	0.72	202.2	-1.82	0.71	20640.7	-1.79	
Stand	0.94	2732.3	-0.07	0.97	3880.4	-0.07	290
	0.81	1451975.7	-2.62	0.80	1127807.5	-2.54	

Table 4.--Dominance types derived from TWINSPAN classification of full data set (290 plots) and environmental-vegetation subset (181 plots) from Little Black Slough, Johnson County, Illinois.

Full Data Set Species	Basal Area m2/ha	Vegetation-Environment Subset Species	Basal Area m2/ha
Quercus alba	6.5	Q. alba	6.4
Carya ovalis	3.7	Q. rubra	3.4
Q. rubra	3.7	Carya glabra	3.4
C. glabra	3.6	Acer saccharum	2.1
N = 25 S = 30		N = 27 S = 30	
Quercus rubra	4.9	Q. rubra	5.4
Liriodendron tulipifera	3.1	L. tulipifera	3.2
Quercus alba	2.1	Liquidambar styraciflua	2.1
Acer saccharum	1.7	F. pennsylvanica	2.0
N = 66 S = 39		N = 48 S = 34	
Liquidambar styraciflua	5.7	L. styraciflua	6.8
Quercus michauxii	4.9	Q. michauxii	4.7
Acer saccharum	3.5	A. saccharum	2.5
A. negundo	1.7	Ulmus americana	1.2
N = 48 S = 44		N = 25 S = 34	
Liquidambar styraciflua	5.7	No equivalent	
Carya laciniosa	3.6		
Quercus pagodaefolia	3.0		
Acer rubrum	2.7		
N = 30 S = 34			
Acer rubrum	11.5	Acer rubrum	6.6
Quercus palustris	4.8	Q. palustris	5.8
Fraxinus pennsylvanica	4.0	Liquidambar styraciflua	4.6
Liquidambar styraciflua	3.7	Quercus lyrata	3.6
N = 51 S = 33		N = 22 S = 28	
Acer rubrum	9.7	Acer rubrum	13.4
Quercus lyrata	7.9	Quercus lyrata	9.3
Fraxinus tomentosa	6.5	Fraxinus tomentosa	4.9
Nyssa aquatica	5.8	Nyssa aquatica	3.9
N = 29 S = 22		N = 30 S = 19	
Nyssa aquatica	35.3	Nyssa aquatica	31.6
Taxodium distichum	16.5	Taxodium distichum	19.70
Populus heterophylla	2.2	Populus heterophylla	2.0
Acer rubrum	2.1	Acer rubrum	2.4
N = 39 S = 18		N = 29 S = 18	

Table 5. Average basal area (m2/ha) and environmental variables for six species groupings derived from TWINSPAN classification of 181 plots from Boulder Slope Woods, Little Black Slough, Johnson County, Illinois.

Species	Mid-slope N=27	Lower slope N=48	Lower slope-Floodplain Contact N=25	Shallow Floodplain N=22	Deep Floodplain N=30	Swamp N=29
Acer negundo	0.01	0.03	0.37	3.45	0.66	0.0
A. rubrum	0.00	0.00	0.14	6.59	13.4	2.85
A. saccharum	2.10	1.41	2.50	1.43	0.00	0.00
Asimina triloba	0.01	0.01	0.01	0.00	0.00	0.00
Betula nigra	0.00	0.00	0.39	0.65	0.00	0.13
Carpinus caroliniana	0.00	0.03	0.28	0.22	0.00	0.00
Carya cordiformis	0.60	1.41	0.84	0.00	0.00	0.00
C. glabra	3.40	0.45	0.56	0.00	0.00	0.00
C. laciniosa	0.01	0.14	0.91	0.38	0.00	0.00
C. ovalis	2.19	1.28	0.63	0.00	0.00	0.00
C. ovata	1.01	0.65	0.31	0.00	0.00	0.00
C. tomentosa	0.36	0.17	0.30	0.00	0.00	0.00
Cercis canadensis	0.09	0.19	0.16	0.00	0.00	0.00
Celtis laevigata	0.00	0.07	0.08	0.00	0.06	0.00
C. occidentalis	0.05	0.01	0.32	0.32	0.00	0.00
Diospyros virginiana	0.00	0.00	0.00	0.13	0.00	0.00
Fraxinus americana	0.39	0.84	1.14	0.01	0.00	0.00
F. pennsylvanica	0.12	2.01	0.72	1.56	0.49	0.60
F. tomentosa	0.00	0.00	0.03	0.04	4.90	0.89
Juglans nigra	0.11	0.59	0.05	0.00	0.00	0.03
Liquidambar styraciflua	0.14	2.13	6.76	4.64	0.39	0.00
Liriodendron tulipifera	1.07	3.22	1.32	0.02	0.00	0.00
Morus rubra	0.04	0.11	0.04	0.01	0.00	0.00
Nyssa aquatica	0.00	0.00	0.00	0.00	3.88	31.57
Ostrya virginiana	0.15	0.16	0.01	0.01	0.00	0.00
Platanus occidentalis	0.00	0.09	0.12	0.14	0.13	0.00
Populus heterophylla	0.00	0.00	0.00	0.09	0.00	2.03
Prunus serotina	0.01	0.15	0.09	0.42	0.00	0.00
Quercus alba	6.36	1.39	0.37	0.00	0.00	0.00
Q. lyrata	0.00	0.00	0.00	3.61	9.25	0.76
Q. michauxii	0.14	1.16	4.68	0.58	0.15	0.00
Q. muehlenbergii	1.01	0.02	0.07	0.00	0.00	0.00
Q. pagodaefolia	0.59	0.05	0.10	0.00	0.36	0.00
Q. palustris	0.00	0.00	0.70	5.82	0.64	0.24
Q. rubra	3.35	5.42	0.71	0.00	0.00	0.00
Q. velutina	1.32	0.11	0.00	0.00	0.00	0.00
Sassafras albidum	0.20	0.58	0.26	0.00	0.00	0.00
Salix nigra	0.00	0.00	0.00	0.09	0.07	0.82
Taxodium distichum	0.00	0.00	0.00	1.28	0.34	19.7
Ulmus alata	0.09	0.01	0.00	0.00	0.00	0.00
Ulmus americana	0.21	0.54	1.18	1.54	2.30	0.12
U. rubra	0.41	0.78	0.97	0.00	0.00	0.00
Clay Most Permeable	14.6	15.4	20.1	29.5	49.0	61.3
Silt Most Permeable	64.1	62.8	60.6	53.2	38.6	24.3
Sand Most Permeable	21.3	21.8	19.3	17.3	12.4	14.3
Clay Least Permeable	22.8	31.3	31.0	37.3	50.1	62.1
Silt Least Permeable	59.9	54.6	53.1	49.0	37.4	23.2
Sand Least Permeable	17.4	14.4	15.9	13.7	12.5	14.7
Depth Least Permeable	19.2	30.6	24.5	12.7	4.1	1.4
Depth of flooding, cm	0.0	0.0	26.4	50.5	76.1	118.2

DISCUSSION

The structure and composition of the vegetation in Little Black Slough and adjacent uplands is representative of relatively undisturbed forests of this region (Robertson et al. 1978, Mackenzie 1980, Elliott 1981, Robertson et al. 1984). The composition is a mixture of northern, central and southern deciduous species, and many of the southern species reach their northern-most distribution in this area (Voigt and Mohlenbrock 1964, Fowells 1965). The relatively high basal area and density values reflect favorable site conditions, ie. mesic slopes and lowland sites with adequate moisture and nutrient inputs from flooding (Mitsch 1978). In addition, the high basal area reflects the lack of recent severe man-caused disturbance. These conditions have resulted in a stand structure that exceeds the 30 m2/ha that Held and Winstead (1975) propose as an upper limit for mature mesic forests in this region. Basal area of the upland site is similar to or greater than values reported for other mesic stands in the Oak-Hickory or Western Mesophytic forest types (Rochow 1979, Kilkus 1977, Adams and Anderson 1980, Shotola 1985). In the lowlands, basal area is likewise similar to other forests in the eastern United States (Lindsey et al. 1961, Anderson and White 1970, Schlesinger 1978, Marks and Harcombe 1981), although basal areas of lowland ecosystems north and east of the Southern Floodplain Forest region are generally lower than those reported in this study (Wikum and Wali 1974, Johnson et al. 1976, Frye and Quinn 1979).

Ordination of the understory and the overstory indicates that the major variation in the vegetation is associated with the topographic-moisture gradient. Regression analysis of the first axis ordination suggests a complex flooding-soil texture gradient is strongly related to variation in vegetation. This relationship has been demonstrated in other studies of similar vegetation types in the region (Broadfoot and Williston 1973, Robertson et al. 1978, Mackenzie 1980, Elliott 1981, Robertson et al. 1984). Both flooding (Putnam and Bull 1932, Hosner and Boyce 1962, Bell 1974, Bedinger 1979, McNight 1981, Huffman and Forsythe 1981, Parsons and Ware 1982) and soil texture (Brady 1974, Fralish 1976, Frye and Quinn 1979, Adams and Anderson 1980, Golden 1981) have been shown to be important in affecting species distributions. In the lowlands, fine soil texture and flooding result in limited oxygen in the soil which may limit species distributions (Wharton et al. 1982).

Variation in the understory seems to be less sensitive to the environmental factors measured in this study as indicated by the regression analysis of the ordination. This may be, in part, because of shading by the overstory. Bell (1974) suggested that modification of the light regime influenced the distribution of understory along an upland to stream gradient in central Illinois. Although flooding was relatively unimportant in the regression equation explaining variation in the understory ordination, it would appear that it may be a significant environmental factor affecting understory patterns as 37 of the 181 plots supported no understory individuals. In addition, 62 percent of the plots containing understory were on non-flooded sites. Thus, the greater importance of soil textural variables in explaining variation in the understory suggests that this stratum is responding differently than the overstory to the soil-site variables measured in this study.

Classification of the plots from Little Black Slough defined dominance types that are common in the region and throughout the Southern Floodplain Forest type. All types defined in this study can be placed in the classification scheme presented by Larson et al. (1981) for bottomland hardwood forests (BLH zones). The *Quercus rubra-Q. alba* type is similar to a *Q. rubra* type identified by Fralish (1976) in the Shawnee Hills of southern Illinois, a type which is widespread (see SAF description for type 55, Society of American Foresters, Eyre 1980, BLH zone VI). This type occurs on mesic, well drained sites and *Quercus rubra* is probably successional as it is shade intolerant (Peet and Loucks 1977) and is not reproducing well in the study area or throughout this region (Shotola 1985).

The *Quercus rubra-Liriodendron tulipifera-Liquidambar styraciflua-Fraxinus pennsylvanica* type is found on the lower slope and slightly into the floodplain and may be considered a successional-transitional type. It may be successional in that many of the dominants are species that respond to disturbance. This type may be considered transitional as both mesic upland and floodplain species are important (BLH zone V and VI). Also, the *Liquidambar styraciflua-Quercus michauxii-Acer*

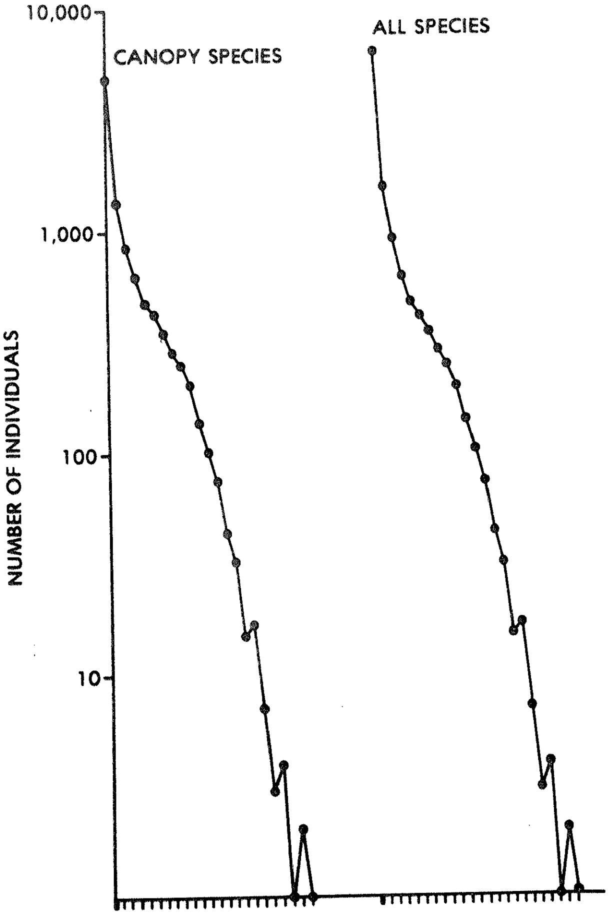

Figure 4.--Diameter-class distribution for canopy species and all species from Little Black Slough, Johnson County, Illinois. N = 290 plots.

saccharum-Ulmus americana type appears to be a similarly transitional type. In Little Black Slough, these two types occur where the lower slope is in contact with the floodplain. Here, apparently site conditions are optimal for Q. michauxii which attains greatest dominance in this zone. Quercus michauxii is only weakly flood tolerant and grows best in bottoms that have hummocks or well drained loamy ridges (McNight et al. 1981).

The amount of small diameter Acer saccharum occurring in the shallow reaches of the floodplain is significant indicating that 1) A. saccharum is able to become established on the floodplain where sedimentation has formed topographic highs which results in less flooding stress or 2) it is more tolerant of flooding than previously believed. Wharton et al. (1982) indicate that the mere presence of a species may not be related to the current local topography. Consequently, because of sedimentation at the base of the slopes, small Acer saccharum may be associated with larger, older individuals of typical floodplain species which became established before excessive sediment deposition occurred. Acer saccharum is generally reported to typify well-drained upland sites (Hough 1924, Fowells 1965). Perhaps Acer saccharum will persist on these depositional sites until an extremely large flood event occurs which may eliminate it if, in fact, Acer saccharum is flood intolerant. If Acer saccharum is more flood tolerant than previously believed, it will likely persist on these floodplain sites.

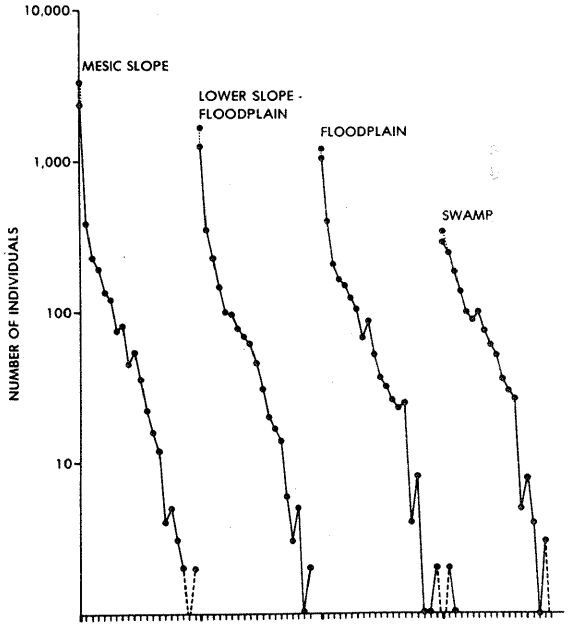

Figure 5.--Diameter-class distribution of all species (solid with dotted lines) and canopy species (solid lines) for trees on four site-types derived from TWINSPAN classification of 290 plots from Little Black Slough and adjacent uplands, Johnson County, Illinois.

The *Acer rubrum*-*Quercus palustris*-*Liquidambar styraciflua*-*Quercus lyrata* type and the *Liquidambar styraciflua*-*Carya laciniosa*-*Quercus pagodaefolia*-*Acer rubrum* type may be variants of the Sweetgum bottomland oak type defined by Shelford (1954) and the *Rufacer-Liquidambar-Quercus* type of Penfound (1952) (BLH zone IV). In Little Black Slough, the type co-dominated by *Carya laciniosa* formed park-like stands in areas that appeared to be shallowly flooded. This type occurred in the northern part of Little Black Slough and was sampled only by the extensive plots.

The *Acer rubrum*-*Quercus lyrata*-*Fraxinus tomentosa*-*Nyssa aquatica* type is similar to the SAF *Quercus lyrata*-*Acer rubrum* type number 96 (Eyre 1981, BLH zone III). Again, it may be a successional type in the swamp. *Acer rubrum* is a species found in many forest types and is considered to be successional. Perhaps, as the stand matures, *Acer rubrum* will decrease and *Quercus lyrata* will become dominant.

The *Nyssa aquatica*-*Taxodium distichum* swamp (BLH zone II) is one of the most characteristic forest types in the southern Floodplain Forest Region (Braun 1950) and, because of its low diversity, is not highly variable. The dominance of *Nyssa aquatica* in Little Black Slough stands may be due to some selective harvesting of *Taxodium distichum* in the 1940's and 1950's. Putnam et al. (1960) indicate that logging may enhance dominance of *Nyssa aquatica*.

The diameter-class analysis of individual woody stems from each of the four major site types as well as from the entire study area indicates that the stand is all-sized (aged). Although a number of stems in the smallest (2.54 $\leq$ 6.6 cm dbh) diameter-class are understory, canopy species, for the most part, are reproducing, particularly those that are shade tolerant. Eliminating the subcanopy species from the diameter-class analysis did not significantly change the fit to the regression models, further substantiating the all-sized (aged) nature of the stand. As a result of some canopy species reproducing in different proportions from the abundance in the overstory, composition of the stands along the topographic gradient will likely shift. For example, on the mesic slope, 37% of the individuals in the smallest diameter class are *Acer saccharum* while it is not dominant in the overstory. Shotola (1985) and others (Boggess 1964, Ebinger and Parker 1969, Abrell and Jackson 1974, Miceli 1977) have shown evidence of increasing *A. saccharum* reproduction elsewhere in the region.

The bimodal diameter-class distribution of *Liriodendron tulipifera* occurs in other old-growth stands in southern Illinois (Shotola 1985) and most likely reflects past disturbances in those stands. The stems in the small diameter-class seem to be regenerating in gaps created when large trees fall. It is common throughout Boulder Slope Woods to encounter 'groves' of large *Liriodendron tulipifera* that became established in a former opening in the canopy. Patchy distributions of successional tree species have been documented in other undisturbed stands in the region (Robertson et al. 1978, Shotola 1985). Continued gap-phase regeneration will be necessary to maintain these successional species.

If current regeneration patterns prevail, *Quercus pagodaefolia* may be lost from the lower slope-floodplain type. Perhaps one of the reasons why *Quercus pagodaefolia* is not reproducing in the stand is because the seeds are a favored food for wildlife (Fowells 1965). *Diospyros virginiana* and *Salix nigra* may also be lost from the floodplain. *Salix nigra* is most likely not reproducing because of the closed canopy and extreme shade intolerance. In the swamp, *Populus heterophylla* may be lost and a shift toward more *Nyssa aquatica* may occur. Harcombe and Marks (1978) found that mortality of understory, and therefore underrepresentation of some canopy species, increased along an upland to lowland gradient. They attributed this increase in mortality to increased competition in lowland areas. In this study area, reduction in number of individuals in the understory may be due to harsh conditions such as flooding and poor drainage as well as to competition from the overstory.

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