A Phytosociological Study of the Woody Plants Constituting Twenty-five Type Forests of the Illinoian Till Plain in Indiana

SCOTT McCOY, Arsenal Technical H. S., Indianapolis

Introduction

Plant sociological studies have held the attention of European students of plant life for many years but have had little consideration in the United States until recent times when H. S. Conard and Stanley A. Cain gave this study of plant life impetus.

Many of American studies of the relationship of plants to their habitat were published under generalized headings of ecological survey; and they were usually extensive rather than intensive, empirical rather than quantitative, and so were not very analytical. This is especially true for Indiana, which Friesner (1937) has aptly called "a critical botanical area." For here are limits of extension of plants from every cardinal point of the compass. It was frequently assumed that because Indiana is a more or less uniform till plain, especially when viewed on a map, the plant cover should also be more or less homogeneous and uniform. That is, however, an erroneous conception, especially when forest types within the deciduous forests are involved. Potzger (1937) has shown that microclimate or local climate is sufficiently important to vary expression in oak-hickory or beech-maple type by the small difference of north or south exposures of ridges.

The present study is concerned with the forests on the topographically uniform Illinoian till plain which has an eastern and western lobe extending southward beyond the later-deposited Wisconsin glacial till. A considerable portion of the eastern lobe is known as the "flats" area. The soil is more or less uniform, and so one might expect a striking uniformity in forest type.

Various plant geographers of the past apparently considered such an assumption the true status.

Weaver and Clements (1929) give two particular climax forest types as applicable to the general region under study, these being the beech-maple and oak-hickory types.

A committee of the Society of American Foresters (1932) places the "flats" of Indiana into the beech type of forest, the beech being pure or predominating.

Zon (1924) placed practically all of Indiana into the oak-hickory type of forest. Such a classification was based on little field study and so has given an incomplete picture of our Indiana forest climaxes.

Gordon (1936) states that the north-central part of Sullivan County, where three of the western lobe forests under study are located, has pure stands of beech, beech-sugar maple, and beech-sugar maple-yellow popular types. Practically all the forests on the eastern lobe, considered in this paper, fall into his beech-sweet gum district. All of these classifications are incorrect, as subsequent data will show.

It is, thus, apparently assumed that the homogeneous Illinoian till plain is characterized by a homogeneous vegetation cover. Investigation of the concepts frequency, density, and fidelity promised most information on the true relationships with respect to the woody species constituting the forests on the Illinoian till plain in Indiana; and so these concepts were stressed in the present study.

The concept fidelity is used here in a modified sense from that given it by Braun-Blanquet and Pavillard. It is used as referring to the regularity of occurrence of a species in twenty-five similar habitat sites but not necessarily with similar vegetation complex, and its degree is expressed in percentage. It is thus, a modification of the diagram presentation of the same concept by Sampson (1930).

Geologic and Physiographic History

The two regions under study are located on the Illinoian till plain, one on the eastern side of the state comprising most of Jackson, Jefferson, Jennings, and Ripley counties and the other on the western side in Davies, Greene, Sullivan, and Vigo counties (Figure 1).

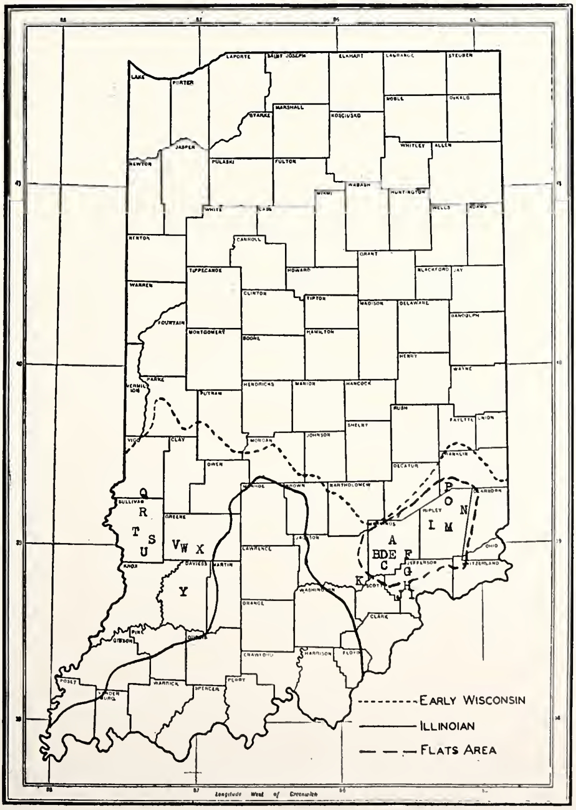

Fig. 1. Glacial boundaries, extent of the "flats" area, and locations of the forest sites studied.

The geologic and physiographic history of Indiana is probably more diverse and complex than one might assume from casual observation and is due to a number of significant geological phenomena of the past, such as series of uplifts and subsequent levelings and periodic crustal stability during which time denudation took place. During Pleistocene times continental glaciation modified most of Indiana and obliterated much of the erosional surface features formed after the Cincinnati Arch uplift. Three glacial invasions are recognized, *viz.*, the Illinoian, Early, and Late Wisconsin. Of these, the Illinoian was the most extensive, reaching the Ohio River but leaving a large triangular area in the south-central part comprising approximately 6,250 acres unglaciated. Most of the surface evidence of the Illinoian glaciation was covered by the moraines and till of the two Wisconsin ice sheets. The two lobes of the Illinoian till plain which are still exposed comprise 3,100 square miles in the eastern lobe and 4,100 square miles in the western lobe (Malott 1922). The soil is extremely leached, consisting chiefly of a whitish clay with usual poor drainage. The monotonously featureless plain of the eastern lobe has coined for it the term "flats" area. Although, as a whole, the western area has a somewhat better drainage, it has essentially the same soil characteristics so that one might suggest a western "flats" area.

Climatic Factors

The climate always presents an important group of factors affecting vegetation, and the areas under study are no exception. The precipitation and temperature data for the areas under study were compiled from the work of Martin (1933), data taken from weather bureau stations nearest a respective group of forests.

Edaphic Factors

The typical soil structure of the Illinoian glacial drift is a compact whitish clay, and most of the soil where the twenty-five forests under study were located was of this type. Variants of other soil types were a yellowish clay, sandy clay mixture, grayish clay, and a black loam.

This whitish clay soil has a tendency to become rather compact at the surface and to form a hardpan layer beneath. The very fine texture of the soil and the presence of the hardpan layer permit only a limited amount of subsoil drainage.

There was very little surface drainage in most of the twenty-five forests. The rather level topography and the compactness of the soil are pertinent factors in making the soil water-logged. In general, roadside and other drainage ditches have had some effect on the water table level.

Methods and Type Forest Locations

Twenty-five forests, sixteen on the eastern lobe and nine on the western lobe, were selected for this study. It was attempted to select the most representative and least disturbed forests of the Illinoian till plain which could be found.

Twenty quadrats, ten by ten meters, were run in each of these forests. Usually two lines of ten quadrats each were run. All woody stems one inch and over DBH. were measured. All stems three feet and over in height were included in the density tabulation. The shrubs were tabulated for frequency but not for density. Deam's books (1924, 1931) on Indiana shrubs and trees were the chief sources of the nomenclature used.

All the forests on the eastern lobe of the till plain, with the exception of forests J and P, are on very level lands with practically no surface drainage. Most of these are in the so-called "flats" area of eastern Indiana. Here the glacial drift (Malott, 1922) varies in depth from practically nothing, where it has been removed by subsequent erosion, to over 100 feet. On the average it is less than 25 feet in depth. Much of the drift-covered portion of southeastern Indiana is exceptionally flat, still exhibiting the characteristics of a featureless ground moraine. The deeper drift occupies the pre-glacial valleys.

Topography where the forests on the western lobe are located is similar to that of the eastern lobe with the exception of forest R, which has rather good surface drainage, and X, which has excellent surface drainage.

Fig. 2. Some of the few beech present in forest T, Sullivan County. (All photographs by Dr. J. E. Potzger, Jan. 31, 1938.)

Fig. 3. Open park-like area in Forest T, Sullivan County. Pasturing has reduced the number of young stems.

Observations and Results

Precipitation and temperature.—The records which were consulted for these two areas covered, in most cases, more than 30 years and in some cases up to 45 years, all terminating with the year 1930. These records show very little difference in the average monthly and annual precipitation for the two areas. The average annual precipitation for the eastern lobe is 42.95 inches and that for the western lobe 39.10 inches, a difference of 3.85 inches in the annual precipitation; however, for the growing season from April to September, inclusive, there is a difference of only 0.83 inches, this in favor of the eastern lobe.

The records for average temperature show even less difference between the two areas. For March, May, and September it is the same for both lobes for the months February, April, June, July, August, and November there is a difference of only .3 of a degree or less.

Soil.—County location (Fig. 1) and brief description of the 25 type forests follow:

Forest	County	Soil	Surface Drainage	Disturbance
A	Jennings	fine light clay	little	none
B	Jennings	fine whitish clay	good	none
C	Jennings	fine whitish clay	poor	severe pasturing
D	Jennings	fine whitish clay	fair	very little
E	Jennings	fine whitish clay	very little	none noticed
F	Jennings	fine whitish clay	very little	some, years ago
G	Jefferson	fine whitish clay	good	very little
H	Jefferson	fine whitish clay	very poor	very little
I	Jefferson	fine whitish clay	very poor	completely cut over 28 years ago, now cattle range
J	Jefferson	yellow clay type	very good	none
K	Jackson	fine whitish clay	none	slight cutting
L	Ripley	fine whitish clay	some	pasturing and cutting
M	Ripley	fine whitish clay	very little	years ago, cutting
N	Ripley	fine whitish clay	fair	pasturing and cutting
O	Ripley	fine whitish clay	very little	some recent cutting
P	Franklin	yellow clay	very good	cutting, years ago
Q	Vigo	gray clay	very little	some cutting
R	Sullivan	gray clay	rather good	cutting, years ago
S	Sullivan	light gray clay	very little	very little
T	Sullivan	light gray clay	rather good	pasturing
U	Sullivan	gray clay	fair	pasturing
V	Greene	black loam	none	very young forest, no recent disturbance
W	Greene	light clay	none	pasturing and cutting
X	Greene	sand clay mixture	good	pasturing
Y	Daviess	black loam	fair	by flood waters

The soil, with the exception of that in forest J on the eastern lobe and probably V and X on the western lobe, is practically of the same whitish texture, which in level uneroded sites makes for water-logged conditions. That the soil is water-logged at times is shown by the shallow root systems of such trees as beech and elm, many of their roots having their upper surfaces above the ground for some distance from the tree trunks (Fig. 4). Braun (1936) reports this same condition in certain forests on the Illinoian till plain in Ohio.

No tests were made for soil acidity on the western lobe, but the author (1937) found that the acidity for the soil in forest F on the eastern lobe ranged from pH 4.8 to 5.6 at the surface, 4.8 to 5.4 at

Fig. 4. Showing exposure of beech roots in forest T, Sullivan County.

the three-inch level, and 4.5 to 5.2 for the twelve-inch level. Braun (1936) reported practically the same acidity range for the soil in similar areas in Ohio.

Size classes of the woody plants; frequency, fidelity, density.—The results of the field study relative density, DBH., and subsequent division into size classes are given in Tables I to V, inclusive. The frequency and density of species in the large tree class for both lobes are shown in Table VI. The fidelity of the species in the large tree class for both lobes is shown in Table VII. The frequency and fidelity of species occurring in areas with good and poor surface drainage on both the eastern and western lobes are shown in Table VIII.

TABLE I.—Size Classes, Forests A to E

Species	A						B						C						D						E					
	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f
Acer rubrum	202	132												1	1	1									2	3	9	8	2	
A. saccharum							584	63		1									96	56	6	1		1	31	10				
Carya cordiformis																									6					
C. glabra																									2		1			
C. laciniosa	6						3													1										
C. ovata	16	7					5	3						3		2	2	1	14						113	25	5	1		
Fagus grandifolia							153	16		1	9	3		5	2	24	22		77	21	1	2	6	2	73					
Fraxinus americana							1	1		1															15	1				
F. biltmoreana							50	4					1						17	22										
F. lanceolata							35	7											15	14					95					
F. nigra		1																												
Juglans nigra								1		1																				
Liquidambar Styraciflua	16	110	9				72	3			1	1	5	6	1	1	6		9	3		1			4	2	5	8	1	
Liriodendron Tulipifera							18	15				1								5										
Nyssa sylvatica	29	66					1	1						1						1	1				13	6	7	1		
Platanus occidentalis		2					1				1																			
Prunus serotina	1						3												3	2										
Quercus alba		5	2				1																		48	3				
Q. bicolor																									2					
Q. borealis maxima																				1										
Q. palustris	9	60	54	2																										
Q. velutina	1	4																												
Ulmus americana							9	1																						
U. racemosa	210	109											5	2					3	9	2	1			18				1	

a—under 1 inch DBH.
b—1 to 5 inches DBH.
c—6 to 10 inches DBH.
d—11 to 15 inches DBH.
e—16 to 25 inches DBH.
f—over 25 inches DBH.

TABLE II.—Size Classes, Forests F to J

Species	F						G						H						I						J					
	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f
Acer rubrum	91	112	4	1			19	9					19	26	9	8			1	6	7				7	5				
A. saccharum		2					30	1																	121	102	2	1	1	
Carya cordiformis																									2	1				
C. glabra																				3					23	28	5	4		
C. laciniosa							1						4							6	1									
C. ovata	24	19					76	41					8							3					10	10	3			
C. tomentosa																									2		1			
Fagus grandifolia	6	16	2				305	51		1	12	1	163	30	1	1	8	1							27	36	2	2		1
Fraxinus americana							2																							
F. biltmoreana							3						6	1	1										16	3			1	
F. lanceolata	3	7																							12					
F. nigra													1																	
F. profunda	1																													
Juglans nigra																												1		
Liquidambar Styraciflua	32	104	3	2			421	130		2	2		12	3	7	3	1	1	9	164	75	1								
Liriodendron Tulipifera	33	63	1	1			10	18	6	3		1	8	1	1														2	
Nyssa sylvatica	45	34	2				7	3					35	13	5	1	1	1	34	216	6				4	2	2			
Platanus occidentalis		2																				1								
Prunus serotina	3	2					31	9	1				1												8	1				
Quercus alba		3					14	8	3				17	7			1			22	20				9	21	6	2	3	
Q. bicolor							4													9	11									
Q. borealis maxima	2	3					2	1					8	1	2					3	1				1	4				
Q. palustris	7	36							1				1		1	1				1	6									
Q. Prinus	1	1					8	4			1			2	1															
Q. velutina																									9	1	1	2	3	
Ulmus americana	19	16	1											1												3				
U. fulva													1												3	1				
U. racemosa	5	9	1	1			35	26	2				12	9	1				5	3	1									

a—under 1 inch DBH. c—6 to 10 inches DBH. e—16 to 25 inches DBH.
b—1 to 5 inches DBH. d—11 to 15 inches DBH. f—over 25 inches DBH.

TABLE III.—Size Classes, Forests K to O

Species	K						L						M						N						O					
	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f
Acer rubrum	284	5	5		1			1	3	4	3		6	7	9	6			1		4	2			16	6	2	1	3	
Carya laciniosa	10	2																												
C. ovata	11	2					2			1	1			5		1	3		36	5	1		4		43	8				
Fagus grandifolia			1	5	7			2	2	10	10		12	38	1	7	12		37	7	2	6	19	3	70	12	11	15	4	
Fraxinus americana																			6	2					38	8		1	1	
F. lanceolata							1																							
F. profunda														3	1															
Liquidambar Styraciflua	115	14	3	2					1					5	3				26	7	4	8	1	2	61	4	2	7	1	1
Liriodendron Tulipifera															1	1			1		2	6					1	2		
Nyssa sylvatica	77	10	1	2				3	1	1				4	1	1	1		8	4			4		36	12	4	1		
Prunus serotina	9																						1		3					
Quercus alba	30	42		2				4	4	4	2			1	1	1	1				2			1	2			1	1	5
Q. bicolor		7																												
Q. borealis maxima	16	10	1		1					2				3						1					3	1	1		2	2
Q. palustris	14	13	2	2	1					2	2	6		2	1	1	2	2												
Q. velutina																							1							
Ulmus americana																				1		2			39	21	2		1	2
U. racemosa	2	6							2					6	1	1			3	1										

a—under 1 inch DBH. c—6 to 10 inches DBH. e—16 to 25 inches DBH.
b—1 to 5 inches DBH. d—11 to 15 inches DBH. f—over 25 inches DBH.

TABLE IV.—Size Classes, Forests P to T

Species	P						Q						R						S						T					
	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f
Acer rubrum											1		4		1		5	1											1	
A. saccharum	227	82	2	1			2												1						59	5	1	2	2	
Carya cordiformis	1																1				1									
C. glabra	2	2	2	1	3																									
C. laciniosa							11			2			15	18			1		5	1					6					
C. ovalis								1		1				1							2	3	2							
C. ovata	4	2					23	3	5	1	1		16	8			1		4	21	2	4			8	9	7	3	1	
C. tomentosa		9	4	3	1		23	1	5	7	1	2	2			1														
Celtis occidentalis							12																							
Fagus grandifolia	22	8	1	3	10	1																			3	1	1	1	8	
Fraxinus americana	19	7	1	1			17	1					25	34	1				1	2	1									
F. lanceolata							25	5	1				3	1					24	2					54	5	3	1	1	
F. profunda													22	5																
Gleditsia triacanthos																2														
Juglans nigra							7	3						5		2										2	1	2		
Liquidambar Styraciflua						1																				3	3	4	8	
Liriodendron Tulipifera		3	6		1	1	11					1																4	2	
Nyssa sylvatica	56	25	4	1	5	1	8	2							1				32	21	5									
Prunus serotina	14	15					30	13					32	19					5											
Quercus alba													13	2	1	2	2	1		3	6	7	6			2	1			1
Q. bicolor													2	2			1			4	1	3	1							
Q. borealis maxima		2		2	1											2	4	1												
Q. imbricaria																				8	2	2	3							
Q. palustris																		1		2		2	3							
Q. velutina		1		3			2	1	2	2	8	1	3			2	5			5								1	4	
Ulmus americana			1	1			13	2					66	12					2											
U. fulva		2											56	10		2	1		3						5				1	
U. racemosa							3	2					37	40					2	2	1				29	6	2	3		

a—under 1 inch DBH.
b—1 to 5 inches DBH.
c—6 to 10 inches DBH.
d—11 to 15 inches DBH.
e—16 to 25 inches DBH.
f—over 25 inches DBH.

TABLE V.—Size Classes, Forests U to Y

Species	U						V						W						X						Y					
	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f	a	b	c	d	e	f
Acer rubrum			1								1		4	5											61	26	4	3		
A. saccharinum							72	55	21	2	3																			
A. saccharum	4			1															103	49	1	1								
Carya cordiformis							4												5	3										
C. glabra																			7	9	5									
C. ovata	52	76	19				2	1					93	21		1	5	1	12	46	6	1			2			1		
C. tomentosa				1									1	1						8	1									
Fagus grandifolia		2	1																	1										
Fraxinus americana		2																	23	11	16	2	2							
F. biltmoreana																			1											
F. lanceolata														1					3	3		1								
F. profunda							56	54	4	2															93	24	15	3		
F. quadrangulata							1																							
Gleditsia triacanthos								4	2																1					
Liquidambar Styraciflua																									2		1	1		
Nyssa sylvatica	38	15	6	1															1	2	2									
Platanus occidentalis							1																		1				1	
Populus heterophylla										1																1		1		
Prunus serotina	28	5											42	11						1										
Quercus alba			1	1																3	2	3	6	1						
Q. bicolor													18	7	5	11	1	1								1	5	4	8	
Q. borealis maxima													1														2			
Q. imbricaria				12	5								34	19		5	4			1										
Q. Muhlenbergii																						1								
Q. palustris							45	99	18		1		24	32			2	1							11	5	8	11	2	1
Q. stellata	1		1	2																										
Q. velutina				1	15	1																	1							
Ulmus fulva													1						24	30	1									
U. racemosa	38	3					19	29	5	1	1		18	21					2	7	1				33	31	4	1	2	
U. americana																			3	4										

a—under 1 inch DBH.
b—1 to 5 inches DBH.
c—6 to 10 inches DBH.
d—11 to 15 inches DBH.
e—16 to 25 inches DBH.
f—over 25 inches DBH.

TABLE VI.—Frequency and Density of Species in the Large Tree Class Occurring in 16 Type Forests (Eastern Lobe) and 9 (Western Lobe) of the Illinoian Till Plain in Indiana.

Species	Eastern Lobe		Western Lobe		Total Both Areas	
	F. I.	Density	F. I.	Density	F. I.	Density
Acer rubrum	43.8	1,054	16.7	118	34.0	1,172
A. saccharinum	....	....	8.9	156	3.2	156
A. saccharum	30.6	1,412	15.0	240	25.6	1,652
Carya cordiformis	2.2	9	5.0	15	3.2	24
C. glabra	9.7	75	6.1	22	8.4	97
C. laciniosa	5.6	34	10.0	59	7.2	93
C. ovalis	....	....	3.3	10	1.2	10
C. ovata	41.6	569	53.9	407	46.0	976
C. tomentosa	.6	9	9.5	65	3.8	74
Celtis occidentalis	....	....	2.2	12	.8	12
Fagus grandifolia	71.9	1,421	6.1	18	48.2	1,439
Fraxinus americana	13.8	115	17.8	128	15.2	243
F. biltmoreana	12.5	125	.6	1	8.2	126
F. lanceolata	17.0	267	22.2	55	18.6	322
F. nigra	1.6	5	....	....	2.8	5
F. profunda	1.3	5	22.8	278	9.0	283
F. quadrangulata	.3	1	.6	1	.4	2
Gleditsia triacanthos	....	....	1.7	9	.6	9
Juglans nigra	1.0	3	2.2	22	1.4	25
Liquidambar Styraciflua	55.6	1,506	9.5	22	39.0	1,528
Liriodendron Tulipifera	20.9	212	4.4	18	15.0	230
Nyssa sylvatica	46.3	704	16.7	130	35.8	734
Platanus occidentalis	1.6	5	2.2	5	1.8	10
Populus heterophylla	....	....	1.7	3	.6	3
Prunus serotina	16.6	120	17.8	173	17.0	293
Quercus alba	33.1	238	26.1	137	30.6	375
Q. bicolor	3.4	49	17.2	60	8.4	109
Q. borealis maxima	17.5	75	6.1	12	13.4	87
Q. imbricaria	....	....	18.0	95	6.4	95
Q. Muhlenbergii	....	....	.6	1	.2	1
Q. palustris	19.1	229	26.6	268	21.8	497
Q. Prinus	3.8	18	....	....	2.4	18
Q. stellata	....	....	1.7	4	.6	4
Q. velutina	4.1	26	17.2	54	8.8	80
Ulmus americana	7.5	120	9.4	102	8.2	222
U. fulva	1.9	8	15.0	134	6.6	142
U. racemosa	36.2	491	45.5	341	39.6	832
Total Density	....	8,805	....	3,175	....	11,980

TABLE VII.—Fidelity (in per cent) of Woody Species, Large Tree Class, Constituting 25 Type Forests of Illinoian Till Plain in Indiana.

Species	Eastern Lobe	Western Lobe	All Areas
Acer rubrum	81	77	80
A. saccharinum	....	11	4
A. saccharum	44	55	48
Carya cordiformis	19	44	28
C. glabra	25	11	20
C. laciniosa	44	44	44
C. ovalis	....	33	12
C. ovata	100	100	100
C. tomentosa	6	44	20
Celtis occidentalis	....	11	4
Fagus grandifolia	88	33	68
Fraxinus americana	38	55	44
F. biltmoreana	50	11	36
F. lanceolata	38	66	48
F. nigra	19	....	12
F. profunda	12	33	20
F. quadrangulata	6	11	8
Gleditsia triacanthos	....	33	12
Juglans nigra	12	33	20
Liquidambar Styraciflua	94	22	68
Liriodendron Tulipifera	69	22	52
Nyssa sylvatica	100	55	84
Platanus occidentalis	25	33	28
Populus heterophylla	....	22	8
Prunus serotina	75	77	76
Quercus alba	88	88	88
Q. bicolor	25	44	32
Q. borealis maxima	81	33	64
Q. imbricaria	....	44	16
Q. Muhlenbergii	....	11	4
Q. palustris	50	55	52
Q. Prinus	19	....	12
Q. stellata	....	11	4
Q. velutina	25	66	40
Ulmus americana	44	44	44
U. fulva	25	55	36
U. racemosa	75	100	84

Analysis of Table II shows that forest A, evidently a comparatively young forest, has 986 stems ranging in size up to 5 inches DBH., 67 between 6 and 15 inches, 65 of these being 10 inches or under. Forest B has 1,051 stems in the two lower size classes and only 20 stems above 5 inches DBH. In this forest the surface drainage is rather good. No pasturing has occurred in both of these forests so that reproduction is unhampered by cultural influences. Forest C is subjected to almost continual pasturing. Here are only 29 stems in the two lower size-classes and 63 in the upper classes, the majority being above 15 inches DBH. Forest E is a mature stand on rather level land. It has 472 stems in the two lower size-classes. Seventy-three of these are beech, indicating that beech is just coming in. Forest I was completely cut over 28 years ago, but the beech has not as yet come in although it is present in the older forests in the vicinity. Here the oaks and sweet and sour gums are the dominant species. Forest J has excellent surface drainage, and here white and black oak and four species of Carya, namely *C. cordiformis*, *C. tomentosa*, *C. ovata*, and particularly *C. glabra*, are giving the beech and sugar maple serious competition. On the western lobe beech is poorly represented; the dominant species seem to be beech, oak, and hickory, with considerable sugar maple in a few forests. On the drier sites red elm may be found.

TABLE VIII.—The Frequency and Fidelity of Species Occurring in Areas with Good and Poor Surface Drainage on the Eastern and Western Lobes of the Illinoian Till Plain.

Species	Eastern Lobe				Western Lobe			
	Frequency Gullying		Fidelity Gullying		Frequency Gullying		Fidelity Gullying	
	Yes	No	Yes	No	Yes	No	Yes	No
Acer rubrum	16.7	60.5	50	100	8.3	20.8	66	83
A. saccharinum	......	......	......	......	......	13.3	......	17
A. saccharum	69.2	7.5	83	20	38.3	3.3	66	50
Carya cordiformis	3.3	1.5	33	10	11.7	1.7	66	33
C. glabra	22.5	2.0	33	20	18.3	......	33	......
C. laciniosa	3.3	7.0	50	40	13.3	8.3	66	33
C. ovalis	......	......	......	......	1.7	4.2	33	33
C. ovata	41.7	41.5	100	100	63.3	49.2	100	100
C. tomentosa	1.7	......	17	......	10.0	9.2	66	33
Celtis occidentalis	......	......	......	......	......	3.3	......	33
Fagus grandifolia	85.0	64.0	100	80	15.0	1.7	66	17
Fraxinus americana	19.2	11.5	68	20	36.6	8.3	66	50
Fraxinus biltmoreana	27.5	3.5	68	30	1.7	......	33	......
F. lanceolata	23.3	12.5	50	30	41.6	12.5	100	50
F. nigra	......	2.5	......	30	6.7	4.2	33	17
F. profunda	......	2.0	......	20	5.0	31.7	33	33
F. quadrangulata	......	.5	......	10	......	.8	......	17
Gleditsia triacanthos	......	......	......	......	1.7	1.7	33	33
Juglans nigra	2.5	......	33	......	6.6	1.7	33	33
LiquidambarStyraciflua	39.2	65.5	83	100	21.7	3.3	33	17
Liriodendron Tulipifera	27.5	17.0	100	50	5.0	4.2	33	17
Nyssa sylvatica	32.5	55.0	100	100	5.0	22.5	66	50
Platanus occidentalis	.8	2.0	17	30	1.7	2.5	33	33
Populus heterophylla	......	......	......	......	......	2.5	......	33
Prunus serotina	29.2	9.0	100	60	16.7	26.7	66	68
Quercus alba	26.7	32.0	83	90	33.3	22.5	100	83
Q. bicolor	.8	5.0	17	30	3.3	24.2	33	50
Q. borealis maxima	9.2	22.5	83	80	13.3	2.5	66	33
Q. imbricaria	......	......	......	......	1.6	25.8	33	50
Q. Muhlenbergii	......	......	......	......	1.6	......	33	......
Q. palustris	.8	30.0	17	70	1.6	39.2	33	68
Q. Prinus	5.8	2.5	17	20	......	......	......	......
Q. stellata	......	......	......	......	......	2.5	......	17
Q. velutina	10.0	1.5	33	20	30.0	18.3	100	50
Ulmus americana	10.0	6.5	87	10	20.0	4.2	66	33
Ulmus fulva	3.3	1.0	33	20	33.3	5.8	100	50
U. racemosa	21.7	44.0	50	100	41.6	47.5	100	83

A comparison of the frequency, density, and fidelity of the ten leading species on the two lobes is shown in Table IX.

TABLE IX.—Showing 10 Species Highest in Frequency, Density, and Fidelity.

FREQUENCY

	Eastern Lobe	Per cent	Western Lobe	Per cent
1	Fagus grandifolia	71.9	Carya ovata	53.9
2	Liquidambar Styraciflua	55.6	Ulmus racemosa	45.5
3	Nyssa sylvatica	46.3	Quercus palustris	26.6
4	Acer rubrum	43.8	Quercus alba	26.1
5	Carya ovata	41.6	Fraxinus profunda	22.8
6	Ulmus racemosa	36.2	Fraxinus lanceolata	22.2
7	Quercus alba	33.1	Quercus imbricaria	18.0
8	Acer saccharum	30.6	Prunus serotina	17.8
9	Liriodendron Tulipifera	20.9	Fraxinus americana	17.8
10	Quercus palustris	19.1	Quercus velutina	17.2

DENSITY

1	Liquidambar Styraciflua	1,506	Carya ovata	407
2	Fagus grandifolia	1,421	Ulmus racemosa	341
3	Acer saccharum	1,412	Fraxinus profunda	278
4	Acer rubrum	1,054	Quercus parlustris	268
5	Nyssa sylvatica	704	Acer saccharum	240
6	Carya ovata	569	Prunus serotina	173
7	Ulmus racemosa	491	Acer saccharinum	156
8	Fraxinus lanceolata	267	Quercus alba	137
9	Quercus alba	238	Ulmus fulva	134
10	Quercus palustris	229	Nyssa sylvatica	130

FIDELITY

1	Carya ovata	100	Carya ovata	100
2	Nyssa sylvatica	100	Ulmus racemosa	100
3	Liquidambar Styaciflua	94	Quercus alba	88
4	Quercus alba	88	Acer rubrum	77
5	Fagus grandifolia	88	Prunus serotina	77
6	Acer rubrum	81	Fraxinus lanceolata	66
7	Quercus borealis maxima	81	Quercus velutina	66
8	Ulmus racemosa	75	Nyssa sylvatica	55
9	Prunus serotina	75	Quercus palustris	55
10	Liriodendron Tulipifera	69	Acer saccharum	55

With conclusions based on data from forests A, B, and D, it would seem that sweet gum and pin oak are the first to invade level, water-logged land. Pin oak shows greatest dominance with 56 of the 67 stems over five inches DBH. Later red maple, sour gum, cork elm, and shellbark hickory come in. In forest D surface drainage is better than in Forest A and the stand is more mature. Here pin oak has passed out completely, cork elm is very much reduced in density, sweet gum, red maple, sour gum, and shellbark hickory are remaining but with a much reduced frequency on the part of the first three mentioned, inasmuch as white oak, certain ashes, and hickories, as well as beech, are just coming in along with the sugar maple. In forest B, a rather mature forest with good surface drainage, beech is clearly the dominant tree; however, sugar maple has by far the greater reproduction. Red maple and cork elm have disappeared, and white elm and tulip poplar have come in.

Discussion

Most investigators associated with the geographically delimited "flats" region of southeastern Indiana a beech-sweet gum forest cover. This is a generalized statement on plant sociology for a highly indefinite area as far as plant habitat is concerned. Quantitative field data are almost a necessity for a fairly accurate analysis of the conditions which control and the expression of forest which they induce. The best quantitative data were expected from an analysis of the combination study of frequency, density, and fidelity, especially to ascertain whether or not the more or less uniform Illinoian till plain region had a corresponding homogeneous forest cover; and for this reason these sociological concepts were stressed in the present study.

In a general way we might say beech-sweet gum make up much of the crown cover of the forests on the Illinoian till plain in southeastern Indiana; but micro-climate here imposes striking variations, too. As shown by Table IV, beech shows only a frequency index of 71.9 and sweet gum one of 55.6. In fidelity in appearance in the different forest stands (Table VII), beech shows only 88% and sweet gum 94%. That means that even in three stands or forests in this region beech and sweet gum were not present in the forest cover. In density (Tables I, II, VI) both of these two species are prominent in large size-classes, as well as in the younger growth. Beech with 1,421 stems and sweet gum with 1,506 stems in 16 stands considered control much of the crown cover.

It is at once quite evident, when considering the nine forests on the western lobe of the Illinoian till plain, that the habitat here must be strikingly different from that on the eastern lobe. Beech has a frequency of only 6.1% and sweet gum 9.5%. Density also drops into insignificance. Fidelity is a little higher than frequency, but both of the above named species are present only in less than one-third of the nine stands. This clearly shows that the two lobes are strikingly different as habitat sites. Gordon (1936) classifies the typical forest of this region (western lobe) as beech-sugar maple or beech-sugar maple-yellow poplar. The present study shows that all of these species are in the lowest frequency, density, and fidelity classes (Table VI) and thus play a secondary role in the crown cover of these forests. A study of Table VI will show that the forests are outstanding by heterogeneity, no few species controlling dominance over crown cover as in the forests on the eastern lobe. This at once indicates a heterogeneous habitat. In the highest frequency classes are *Ulmus racemosa* (45%), *Carya ovata* (53.9%), and several species of ash and oak with a F. I. in the lower twenties. Sugar maple has a F. I. of 15% and tulip poplar only 4.4%. With such low frequency, fidelity, and density we would hardly be justified to consider them as key species typifying forest cover. *Carya ovata* has the greatest density of any species (407 stems), and *Ulmus racemosa* is second with a total of 341 stems (Table IX). These same two species have a 100% fidelity; *Quercus alba* has a fidelity of 88%. As a whole, the forests on the western lobe are more of the oak-hickory-elm type; but as previously stated, the region as a whole is marked by a heterogeneous crown control. So these two topographically similar regions are not in the least similar in plant cover.

There are, of course, various other comparisons that could be made between the forest complexes of these two regions, notably among them the fact that *Nyssa sylvatica* and *Acer rubrum* play an important part in the forests on the eastern lobe but are unimportant in forests on the western lobe, the tables on density, frequency, and fidelity showing these differences to full advantage. Note especially the summary presentation in Table IX.

Considering the 25 forests, we find that the only species with 100% fidelity is *Carya ovata* (Table VII); nearest this species is *Quercus alba* (84%), which indicates a greater potentiality for habitats in these species and suggests at the same time that the more localized dominants like beech, sugar maple, and sweet gum may represent more closely confined sere dominants in a succession cycle with optimum conditions pictured where density is high in both mature growth and reproduction. One of the environmental controls of this variation in forest type is indicated in the comparison of sites with and without gullying shown in Table VIII; but we must admit that, when considering the problem of plant sociology on the 25 sites of the Illinoian till plain in Indiana as a whole, we are confronted by a number of situations which are not easily explained by mere data from the vegetational complex. The habitats to all appearances are very much alike. Macroclimatic factors are similar for the whole season, and for this reason temperature and precipitation *per se* are probably not the primary cause of variation in forest types in these Illinoian till plain areas. The real cause must be sought for in edaphic factors. Soil texture, too, is rather uniform, and topography shows little variation; but the forest associations vary considerably on the different sites. Especially baffling is the distribution of beech. It may be a prominent dominant in water-logged sites as in forest F, associated there with sweet gum, sour gum, pin oak, and red maple, occupying the slightly elevated hummocks; or it may be co-dominant with sugar maple and white oak on well-drained mesophytic sites, as in forest B. This greater potentiality for habitat variation in beech was described by Potzger (1933) for the flood-plain and north-facing slopes of flanking uplands in the Salt Creek Valley in Monroe County, Indiana.

Pin oak and sweet gum are limited to wet sites, although sour gum and red maple have such a wide range of adaptability to habitat that they might be expected in any habitat, as Sampson (1930) also shows for northeastern Ohio.

The quantitative data collected during the present investigation do not support entirely the classifications by a Committee of the Society of American Foresters (1932) and Weaver and Clements (1929), and they do not agree at all with the classifications by Gordon (1936) and Zon (1924).

As already pointed out, variation in forest association is especially marked on the western lobe, for no one species here shows a high per cent fidelity. Even though advantage of centers from which migration might take place can account for some heterogeneity in forest associations, it does not solve the whole problem, for time must eventually have modified such advantages. The real cause must be sought in hidden microclimatic differences in the habitat. If exposure of slope may initiate a sharp dividing line between beech-maple and oak-hickory in central Indiana, slight variations in edaphic or meteorological conditions may well account for the differences in the forests on the western lobe. This region is nearer the prairie influences so that the similarity in precipitation between the two lobes may well be eliminated by higher evaporation on the western lobe. Evaporation differences make beech-maple forests possible in northern Michigan with a rainfall of 25 inches and in Indiana with 40 to 45 inches. Rainfall in the uniform prairie formation ranges from 20 to 40 inches (Weaver and Clements, 1929). Yet in the end, evaporation difference unifies the effect on the plant cover.

Physiographic characteristics, such as the regional slope of the strata to the southwest and the proximity of the Wabash river drainage, might have developed better subsoil drainage in this western region than exists on the eastern lobe. Borings in Sullivan county disclosed sand and gravel in the lower layers of the soil and this would favor efficient subsoil drainage.

It appears that it is not the soil texture which exerts a selective influence on species and associations but rather the water relationship of the soil; and the associations will vary as sites vary in degree of drainage, approximating, thus, forest types controlled by physiography and topography in the unglaciated section of Indiana.

Taking the Illinoian till plain as a whole, there is no one species nor association of species which by their fidelity might be termed indicators of Illinoian till plain habitat sites. On the contrary, even though the two lobes are marked by topographic uniformity, vegetationally they present a series of habitat sites which range from late stages of a hydrosere to late stages of a xerosere. Results shown in Tables VIII and XI on frequency, density, and fidelity of the dominant species of the 16 forests on the eastern lobe indicate that pin oak, sweet gum, sour gum, cork elm, and red maple are early invaders of the level, poorly drained, undissected lands. As soon as hummocks raise the soil ten to twelve inches above the water table, beech, white oak, and shellbark hickory invade; and, with increasing drainage, sugar maple, tulip poplar, hickories, and oaks initiate the succession to a typical mixed mesophytic forest.

The forests on the western lobe can hardly be compared with those of the eastern lobe as to phytosociological complex unless they are considered an indication of succession from mesophytic to the drier site oak-hickory type of forest cover, for they are already expressions of such forest type.

Completing the indicated succession of the forests on the Illinoian till plain, we would have, beginning with undrained areas, invasion by pin oak, sweet gum, sour gum, cork elm, red maple to beech, white oak, and shellbark hickory, associated with the former species, to beech, maple, hickories, and mesophytic oaks, to typical oak-hickory dominance, initiated and maintained by degree of drainage of the soil. The shrub layer is poorly expressed in all stages of succession. Thus, when the vegetation of the Illinoian till plain as a whole is in question, all the various stages and forest types may be encountered.

Here, too, applies the statement by Nichols (1929) "It should be borne in mind that in attempting to classify the facts of nature, we are dealing with merging phenomena."

Summary and Conclusions

1. A phytosociological study was made of the woody species in 25 forests on the Illinoian till plain in Indiana. Sixteen of these were located on the eastern lobe and nine on the western lobe.

2. The topography of the sites ranged from a very level surface without much surface drainage to areas with good surface drainage.

3. Habitat sites on both lobes are very similar as to soil texture, temperature, and precipitation factors.

4. The fine texture of the whitish clay soil is conducive to water-logged conditions where drainage is poor.

5. Forest types differ markedly in the various sites, especially with respect to eastern and western lobes.

6. Beech and sweet gum are in low frequency and density classes on the western lobe.

7. Shellbark hickory is the only species with 100% fidelity in the 25 forest sites.

8. Controlling factor in the selection of forest type appeared to be degree of drainage of the soil.

9. Dominant species in the water-logged sites were pin oak, sweet gum, red maple, sour gum, cork elm, and beech.

10. Beech showed a wide range preference with respect to available water in the soil. It invaded the higher hummocks in wet sites and continued as dominant into mesophytic beech-maple sites.

11. Dominants on the mesophytic sites are sugar maple, tulip poplar, pignut hickory, red oak, and beech.

12. With continued dissection of the site, mixed hardwoods gave way to oak-hickory.

13. Forests on the western lobe were predominatingly of the oak-hickory elm type.

14. Species showing greatest fidelity on the eastern lobe were: shellbark hickory 100%, sour gum 100%, sweet gum 94%, beech 88%,

white oak 88%, red maple 81%, red oak 81%, cork elm 75%, black cherry 75%, black oak 66%.

16. Species with highest F.I. on the eastern lobe were: beech 71.9%, sweet gum 55.6%, sour gum 46.3%, red maple 43.8%, shellbark hickory 41.6%.

17. Species with highest F.I. on the western lobe were: shellbark hickory 53.9%, cork elm 45.5%, pin oak 26.6%.

18. It is suggested that less soil water, because of greater evaporation stresses and better subsoil drainage, may account for low frequency and fidelity of beech, sweet gum, and sugar maple in the forests on the western lobe, with resultant oak-hickory-elm control.

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