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Broomsedge in Illinois

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BROOMSEDGE IN ILLINOIS

(TITLE)

BY

DAVID F. KUNZ

B.A., RUTGERS UNIVERSITY, 1970

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE IN BOTANY

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

1972
YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
THIS PART OF THE GRADUATE DEGREE CITED ABOVE

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15 May 1972
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INTRODUCTION

Broomsedge, Andropogon virginicus L., Panicoideae, is a perennial bunch grass named by Linnaeus in 1753 in Species Plantarum (Hitchcock, 1951; Gould, 1968). In North America the species is found east from the 25-inch rainfall belt, as well as in California, Mexico, Central America and the West Indies (Hitchcock, 1951; Leithead et al, 1971) (Fig. I).

Broomsedge occurs mainly as an early invader of old-fields, in open woods and on sandy soil. Researchers have usually reported that broomsedge initially invades old-fields from three to five years after abandonment and remains for many years, sometimes in almost pure stands (Oosting, 1942; Keever, 1950; Bazzaz, 1968). States in which research has found broomsedge to be important in old-field succession are listed in Table I.

Many researchers have attempted to investigate old-field succession. The early studies were merely descriptive. A pioneer monograph on plant succession, which includes scientific observations, was written by Clements (1916). Clements, in discussing the causes of succession, concluded that a plant community affects the environment in such a way that it may become less favorable to the organisms responsible for the change and more favorable for other species.

Table I. States, with author citations, in which broomsedge has been reported to be important in old-field succession.

STATE	REFERENCE
Arkansas	Davis, 1967
Florida	Kurz, 1944
Illinois	Voigt, 1959 Bazzaz, 1963 Voigt and Mohlenbrock, 1964 Bazzaz, 1968 Ashby and Weaver, 1970
Kansas	Harlan, 1956
Missouri	Drew, 1942
New Jersey	Stevens, 1940 Bard, 1952 McCormick and Buell, 1957
New York	Conard, 1935
North Carolina	Crafton and Wells, 1934 Oosting, 1942 Billings, 1938 Keever, 1950
Ohio	Larsen, 1935
South Carolina	McQuilkin, 1940
Tennessee	Minckler, 1946 Quarterman, 1957
Virginia	Allard, 1942

Since Clements' studies, various mechanisms have been proposed to explain replacement of one plant population by another. The commonly cited mechanisms are: (1) life cycle including overtopping and shading, (2) soil development, (3) allelopathic effects, (4) root competition and (5) microclimatic change. Table II lists the various mechanisms with some important author citations. Animals are generally regarded as having a secondary effect on succession.

Various aspects of the life cycle, including overtopping and shading, are most frequently cited causes of plant succession. Coile (1940) ascribed the initial invasion of loblolly pine (Pinus taeda L.) on abandoned land as being related to a good seed year, while its subsequent decline was due to root competition. Keever (1950) and later Bard (1952) attributed old-field succession to aspects of the life cycle, including the time of seed maturity and germination, and to tolerances of environmental factors. Voigt (1959) has suggested that broomsedge, due to crowding and shading, eventually creates an unfavorable environment for itself, while Bazzaz (1968) suggested that it is eventually shaded out by higher vegetation.

Soil development, including physical and chemical change, is another often cited cause of succession. Changes in the physical and chemical properties of soil which increase available soil moisture might enable the invasion of the next seral stage (Warner and Aikman, 1943). Increases in soil

Table II. The most frequently cited mechanisms of plant succession, with some important author citations.

Soil Development

Physical

Crafton and Wells, 1934
Billings, 1938
McQuilkin, 1940
Smith, 1940
Werner and Aikman, 1943
Minckler, 1946

Chemical

Coile, 1940
Smith, 1940
Allard, 1942
Rice *et al*, 1960
Warren, 1965

Root Competition

Crafton and Wells, 1934
Duncan, 1935
Coile, 1940
Keever, 1950
Bazzaz, 1963

Life Cycle

Coile, 1940
Keever, 1950
Bard, 1952
Voigt, 1959
Bazzaz, 1963
Davis, 1967

Allelopathic Effects

Evenari, 1949
Bonner, 1950
Keever, 1950
Rice, 1964
Rice, 1965
Muller, 1966
Floyd and Rice, 1967
Olmsted and Rice, 1970
Rice, 1971a,b
Whittaker, 1971

Microclimatic Changes

Bryant, 1952

fertility might also allow the replacement of one plant population by another. Early studies provided little information because of attempts to compare different soil types (Bard, 1952). Some researchers deemed the observed changes in soil fertility insufficient to account for plant succession (Coile, 1940). Recent studies, however, have tended to implicate changes in soil chemistry. Rice *et al* (1960) have suggested that the relative requirements of nitrogen and phosphorus may be important in determining the order in which species invade abandoned fields. Furthermore Allard (1942) concluded that a lack of available phosphorus and nitrogen might eliminate the broomsedge stage. Smith (1940) and Bazzaz (1963) studied changes in soil characteristics and concluded that after the first two years organic matter increases, pH decreases rapidly during the first two years and then increases, and there is an improvement in moisture relations.

Recently researchers have become increasingly interested in the importance of secondary plant products. Keever (1950) has suggested that *Erigeron canadensis* in old-field succession in North Carolina rapidly loses dominance after the first year because it is stunted by its own decay products and cannot compete successfully with other invading species. Rice (1964) has shown that *Andropogon scoparius* produces substances inhibitory to nitrifying bacteria, and Muller (1966) has suggested that allelopathy, the influence of plants upon other organisms caused by products of metabolism, might be of significance in plant succession. Moreover, Warren (1965) and Rice (1971) have also investigated the possible influence on nitrifying organisms of successional species through chemical interactions. Whittaker (1971) has suggested that allelopathic effects may influence the sequence and timing of succession by, among other ways, auto-intoxication.

Root competition, which also has been proposed as a factor operating in succession, was intensively investigated by Crafton and Wells (1934). These early researchers concluded that broomsedge cannot become established until available surface soil moisture is sufficient for seedlings, and the changes in available soil moisture are brought about by tall weeds. In addition, once established the root system of the grass so thoroughly spreads throughout the soil, that weeds are eliminated. In a study of root systems in old-fields, Duncan (1935) suggested that the successful invasion by old-field species is due to efficient root systems that can compete for water and nutrients. In the Piedmont of North Carolina, loblolly pine is replaced by oak and hickory, which can penetrate below the zone of high root competition to a lower region where competition is less intense during periods of moisture stress (Coile, 1940). Keever (1950) observed that when asters and broomsedge are competing for moisture in the same soil where available water is low, broomsedge usually survives and asters eventually die. This information suggested that competition for water may be one of the controlling factors in the replacement of aster by broomsedge in old-field succession. Bazzaz (1963) also suggested that competition for soil moisture is intense between Aster and Solidago since both grow at the same time and are generally of equal height, thus eliminating shading as a factor.

Bryant (1952) investigated microclimates of three grassland plots in central Oklahoma and found the greater range of extremes in temperature under the mulch of abandoned fields might have a significant effect on succession and the general vegetative structure. The more severe and variable temperatures in the abandoned field might partly explain the long persistence of Aristida despite ample seed source from surrounding prairie grasses (Bryant, 1952). Abandoned fields were also found to have a higher evaporation rate and because a seedling is dependent on conditions within a restricted area, the severe evaporation might be a detriment to succession.

Animals generally play a role in the dissemination of propagules. With the establishment of annuals and early perennials, there is usually an increase in the animal populations of old-fields (Smith, 1940). Pearson (1959) found an increase in mammal populations in abandoned fields of New Jersey through the grass stage causing a general decrease in grass cover and subsequent increase in shrubs and trees.

In Georgia, Johnson and Odum (1959) found that bird populations increase in the grass stage, remain fairly constant during the pine stage and then increase in the deciduous understory only to decrease in climax forest. Plants with fruits eaten by animals would have a better chance of becoming established than those which do not travel long distances (Johnson and Odum, 1959; Bazzaz, 1963).

The first area of the state to be settled in the 1700's and early part of the 1800's was the Shawnee Hills of southern Illinois. Major portions of the area, which was covered with forest, were cleared for cultivation although some proved not well suited for agriculture. Rough topography, improper cutting, fire and poor agricultural practices have contributed to making erosion a major factor in the soil and vegetational history of the area. In some areas erosion has led to a decrease in soil quality and resultant poor crop yield, and portions of the area were agriculturally abandoned. Human population has decreased in the area, and Pope County has experienced the greatest loss (41.1%) (Dewey and Speers, 1949).

In an effort to salvage the productivity of the soil for timber production, watersheds and natural increase in wildlife, most of the abandoned land has been purchased by the United States Forest Service, which established the Shawnee National Forest in 1933. An extensive program of reforestation is being carried out, and in some areas pine plantations of loblolly and shortleaf pine (*Pinus echinata* Mill.) have been established. Abandoned fields, which are slowly reverting to trees of the climax forest, offer a unique opportunity to investigate old-field succession.

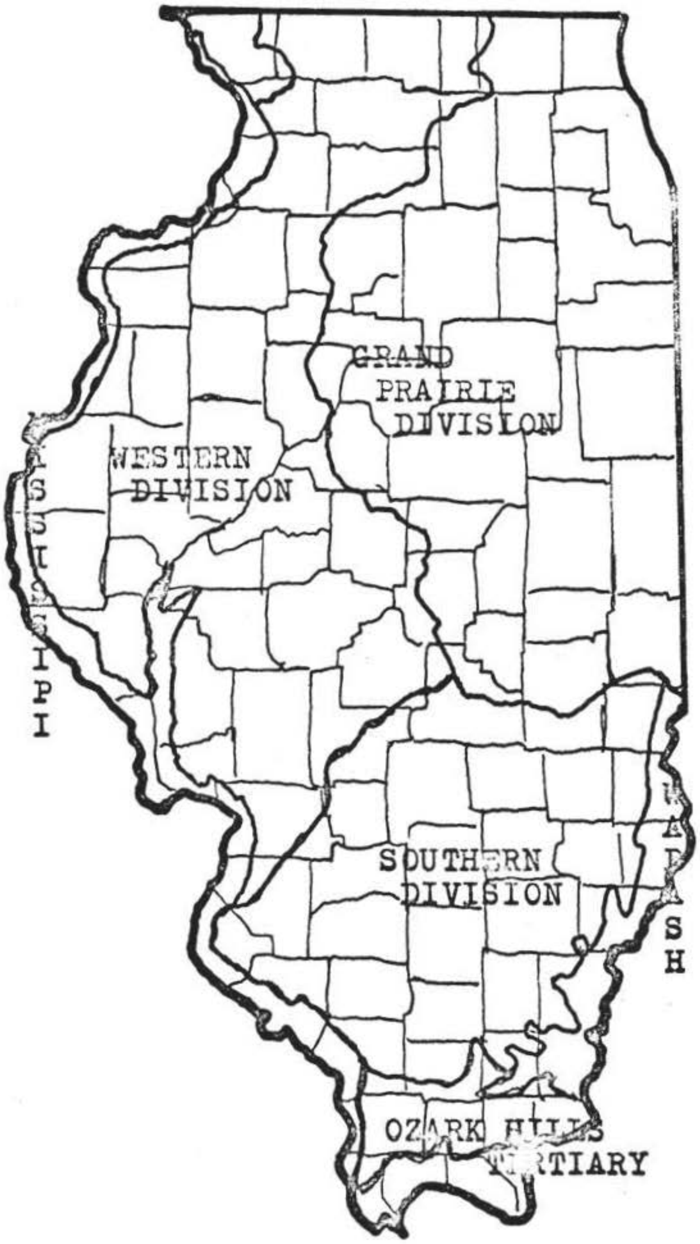
Southern Illinois, especially since the establishment of the Shawnee National Forest, has proved to be a valuable study area. The flora of the area has been extensively investigated (Gleason, 1904, 1923; Vestal, 1931; Evers, 1955; Mohlenbrock and Voigt, 1959; and Voigt and Mohlenbrock, 1964), and the process of succession documented (Voigt, 1959; Hosner and Minckler, 1963; Bazzaz, 1963, 1968; Ashby and Weaver, 1970). The soils are currently being mapped (Fehrenbacher, 1972), while past investigators have studied some of their physical and chemical properties (Boggess, 1956; Gard *et al*, 1959; Anon. 1968; Rolfe, 1968). Since broomsedge occurs in southern Illinois as a dominant of an early successional stage (Voigt and Mohlenbrock, 1964; Bazzaz, 1968), an investigation of the edaphic factors involved in the process of succession might contribute to an understanding of its distribution in Illinois. The primary objectives of this study were to accurately determine the distribution of broomsedge in Illinois, and then to evaluate and compare the physical, chemical and hydrologic characteristics of a particular soil, Grantsburg Silt Loam, as the process of succession proceeds towards climax forest. Laboratory seed germination studies aided in evaluating the field data.

DESCRIPTION OF THE STUDY AREA

Geology and Topography

The distribution of *Andropogon virginicus* L. covers the Western Division, Southern Division, Wabash Border and Shawnee Hills (Fig. II)(Vestal, 1931). The Western Division comprises most of western Illinois south of the Wisconsin line for two-thirds the length of the state. The area is covered by Illinoian glacial drift, overlayed with recent Wisconsinan loess deposits. The thickness of loess decreases with increased distance from the source, the Mississippi and lower valley of the Illinois Rivers (Fehrenbacher *et al*, 1967). The area is generally dissected since streams have been extending their tributaries more than 15,000 years. The valleys of the Green River and lower Rock River were excavated by the flood waters of the Wisconsinan ice sheet. The outwash material is coarse sandy material near the Wisconsinan moraine, and grades into finer silty material farther downstream. Extensive sand prairies have developed in the area (Evers, 1955). The area is divided into three upland districts: Freeport District, Macomb District and Springfield District. An arm of the Shelbyville Moraine separates the Springfield District from the Grand Prairie.

Figure II. Outline map of the geographic divisions of Illinois (Vestal, 1931).

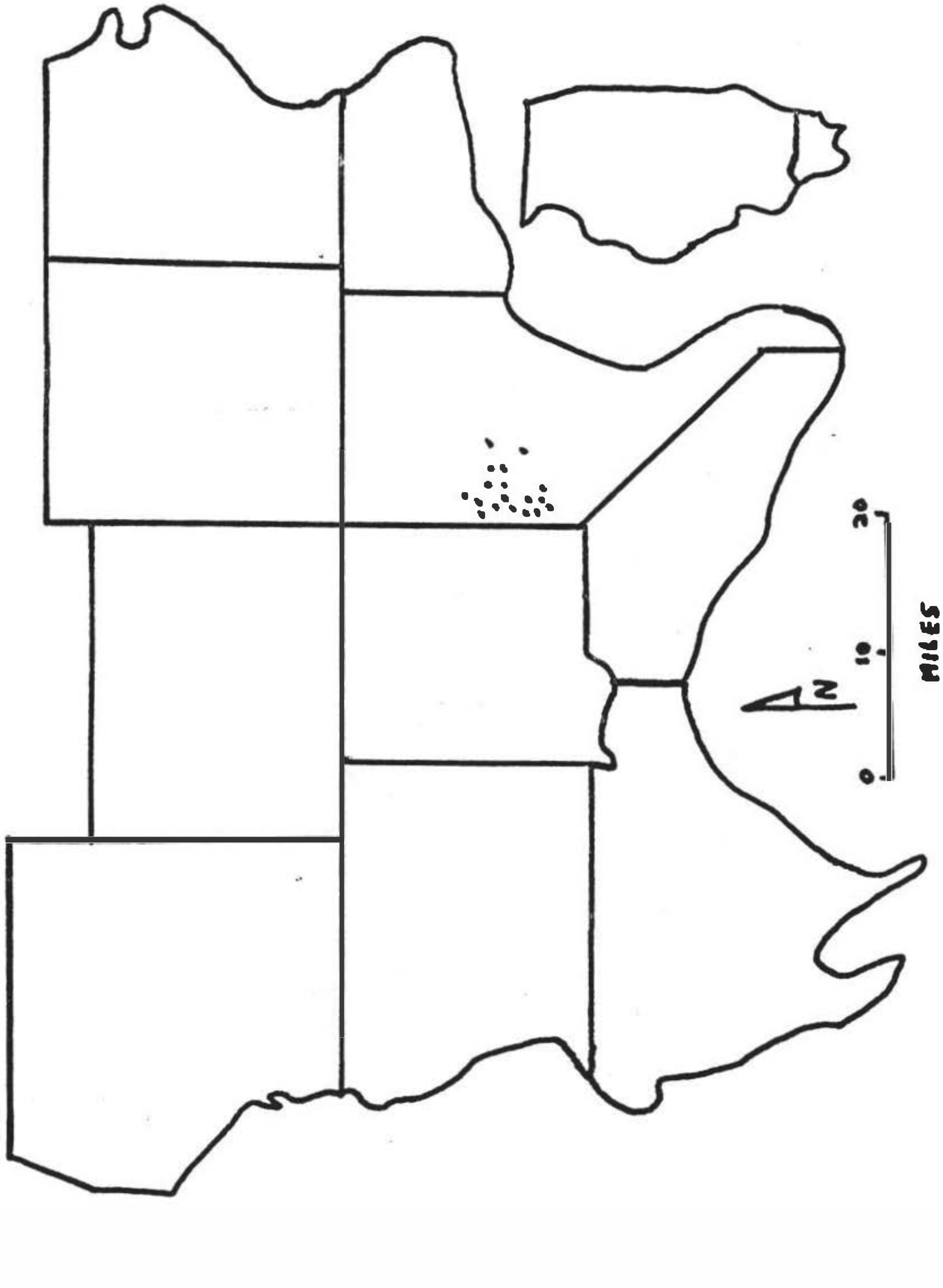


The Mississippi Border is characterized by the dry western exposed bluffs of the Mississippi River and lower Illinois River. Along the northern and central river bluffs the terrain has been eroded breaking up the loess mantle deposited since the Wisconsinan. The Wabash Border includes the bottomlands and bluffs of the Wabash and Ohio Rivers, as well as adjacent upland areas. This is a well-dissected belt of deep loess-covered hills. The bottoms of the large tributaries of the Wabash extend into the clayey uplands of the Southern Division.

The Southern Division is the oldest area of Illinoian drift exclusive of the loess-covered area along the Wabash and Mississippi borders. The area has a loess cover, which was subsequently weathered. Three districts are recognized: the relatively flat and uneroded northern part or Effingham District, the generally rolling and in places eroded southern and eastern part or the McLeansboro District, and the northwesterly zone bordering the Western Division- the old Illinoian morainal border which contains residual hills and has a deep loess cover.

The last area, the area in which broomsedge was intensively studied, is the Shawnee Hills (Ozark Hills) of southern Illinois (Fig. III). This area is south of Illinoian glaciation and is located in the Shawnee Hills Section of the Interior Low Platuea Province described by Flint (1928). Parts of Union and Pulaski counties are in the Salem Plateau Section of the same province (Leighton _et_ _al_, 1948).

Figure III. Map of the Shawnee Hills showing distribution of the experimental fields/soil test plots.


N
0
10
20
MILES

The area is an extremely dissected upland with narrow ridge tops between deeply cut valleys. It is underlain by Mississippian strata of the Chester formation, except in the northern part where some Pennsylvanian strata are present. The northern limit lies a little within the boundary of the Illinoian glaciation, while the southern boundary is the northern edge of the overlapping coastal plain sediments (Leighton _et_ _al_, 1948). A large portion of the area has been faulted and folded, especially in the eastern section, into a rugged topography with outcrops, mostly of sandstone, along the valley walls. Remnants of relatively flat uplands are preserved on narrow ridge crests throughout the region. The hills of the Ozark Uplift (Shawnee Hills) reach an average elevation of about 850 feet at their crest, and stand above the areas both to the north and south to a height of 400 to 600 feet. The uplift is generally more abrupt on the north side of the hills than on the south. The Ozark Uplift passes through the northwestern part of Jackson County, southeast across Union County, then eastward across the northern parts of Johnson, Pope and Hardin counties. The southern part of the Shawnee Hills is drained by the Cache and Big Bay Rivers which flow south into the Ohio River, while the northern part is drained to the east by the Saline River, which flows into the Ohio, and to the west by the Big Muddy, which flows into the Mississippi River.

Climate

Illinois, which occurs between 37° and 42° 5' N., is in the "Daf" and "Caf" climatic regions of Koppen as modified by Trewartha (1943). The designation "Daf" indicates a humid continental (microthermal) climate with the coldest month below 0° C., warmest month above 22° C., and precipitation throughout the year. "Caf" is the climatic designation for southern Illinois and indicates a humid subtropical (mesothermal) climate with the coldest month above 0° C., the warmest month above 22° C., and precipitation throughout the year.

The present climate is of the continental type with hot summers, the winters ranging from about -5° C. in the north to about 2° C. in the south. The mean annual biotemperature is 15° C. (Holdridge, 1947). Average annual temperatures for the state are presented in Figure IV, while average annual precipitation is presented in Figure V, and average number of frost-free days is shown in Figure VI.

The climate of Illinois during the period of soil development is difficult to characterize. The climate was probably not greatly different from the present day climate except for a general warming trend following the recession of the Wisconsinan glacial ice (Geis and Boggess, 1968) with a period of maximum warmth, the hypsithermal interval (Deevey and Flint, 1957), occurring about 5,600 to 2,500 B.C. (Flint, 1957; Dorf, 1960; Geis and Boggess, 1968). During

Figure IV. Average annual temperature (degrees Fahrenheit) in Illinois, 1931 to 1960 (Fehrenbacher _et al_, 1967).

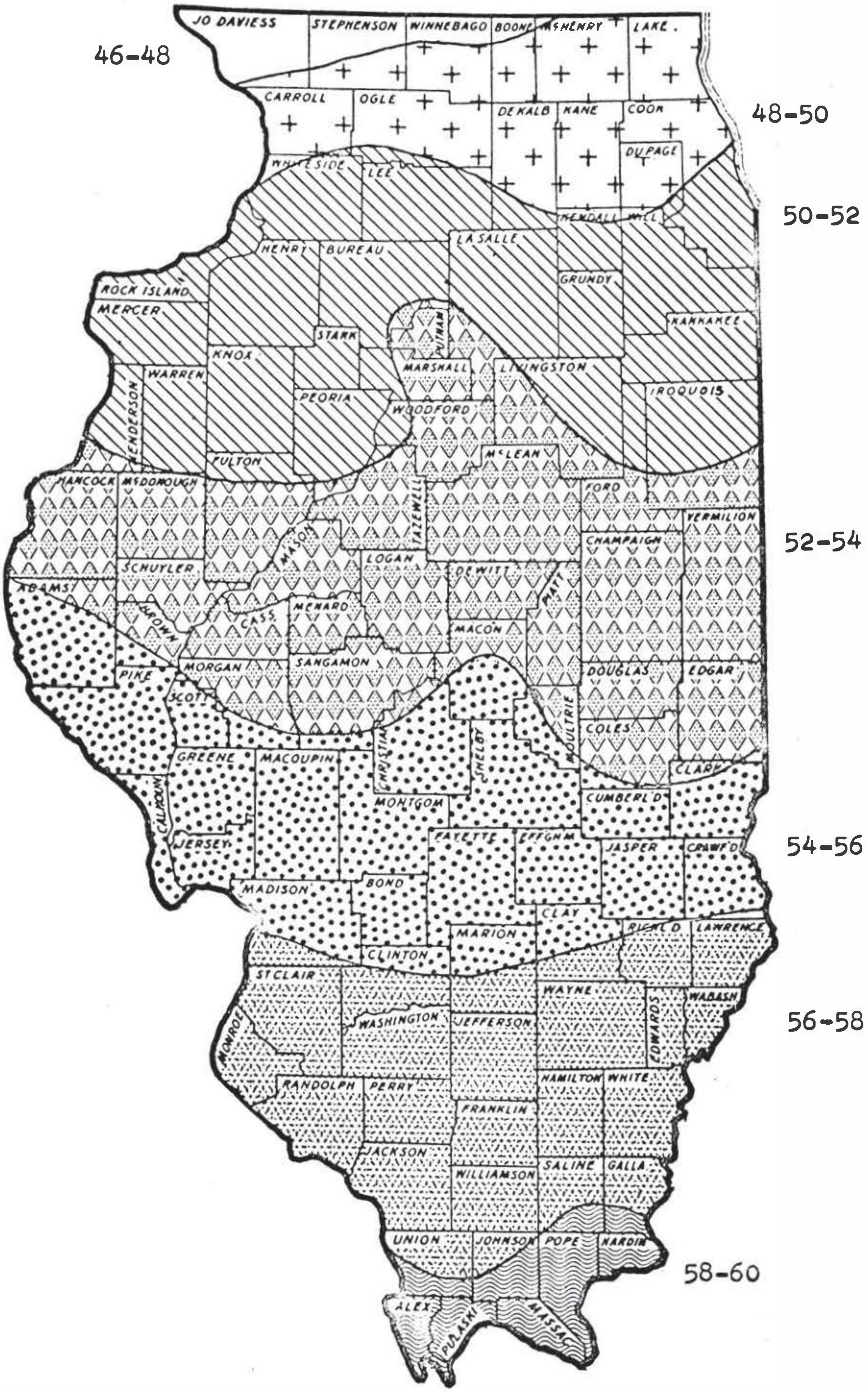
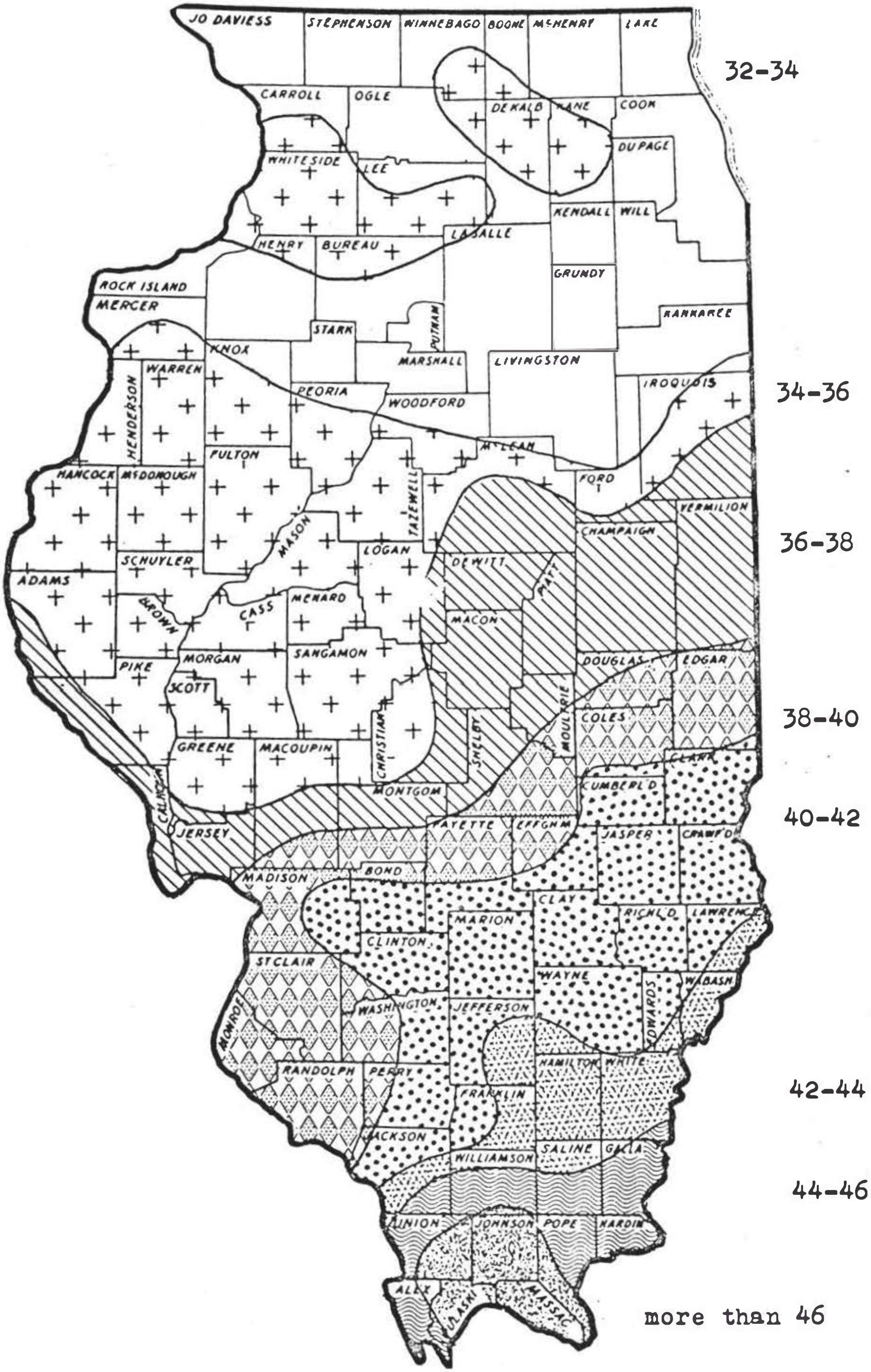

46-48
48-50
50-52
52-54
54-56
56-58
58-60
JO DAVIESS
STEPHENSON
WINNEBAGO
BOONE
McHENRY
LAKE
CARROLL
OGLE
DEKALB
KANE
COOK
DU PAGE
WHITESIDE
LEE
KENDALL
WILL
HENRY
BUREAU
LA SALLE
GRUNDY
ROCK ISLAND
MERCER
STARK
PUTNAM
KANKAKEE
KNOX
MARSHALL
LIVINGSTON
HENDERSON
WARREN
PEORIA
WOODFORD
IROQUOIS
FULTON
McLEAN
HANCOCK
McDONOUGH
TAZEWELL
FORD
VERMILION
MASON
CHAMPAIGN
SCHUYLER
LOGAN
DEWITT
PIATT
ADAMS
BROWN
CASS
MENARD
MACON
MORGAN
SANGAMON
DOUGLAS
EDGAR
PIKE
SCOTT
MOULTRIE
COLES
CHRISTIAN
SHELBY
CLARK
GREENE
MACOUPIN
MONTGOM
CUMBERL'D
CALHOUN
JERSEY
FAYETTE
EFFGHM
JASPER
CRAWF'D
MADISON
BOND
CLAY
RICHL'D
LAWRENCE
MARION
CLINTON
ST CLAIR
WAYNE
WABASH
MONROE
WASHINGTON
JEFFERSON
EDWARDS
RANDOLPH
PERRY
HAMILTON
WHITE
FRANKLIN
JACKSON
WILLIAMSON
SALINE
GALLA
UNION
JOHNSON
POPE
HARDIN
ALEX
PULASKI
MASSAC

Figure V. Average annual precipitation (inches) in Illinois, 1931-1960 (Fehrenbacher *et al*, 1967).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STEPHENSON
WINNEBAGO
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CARROLL
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DE KALB
KANE
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WHITESIDE
LEE
KENDALL
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HENRY
BUREAU
LA SALLE
GRUNDY
ROCK ISLAND
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KANKAKEE
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LIVINGSTON
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HENDERSON
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DOUGLAS
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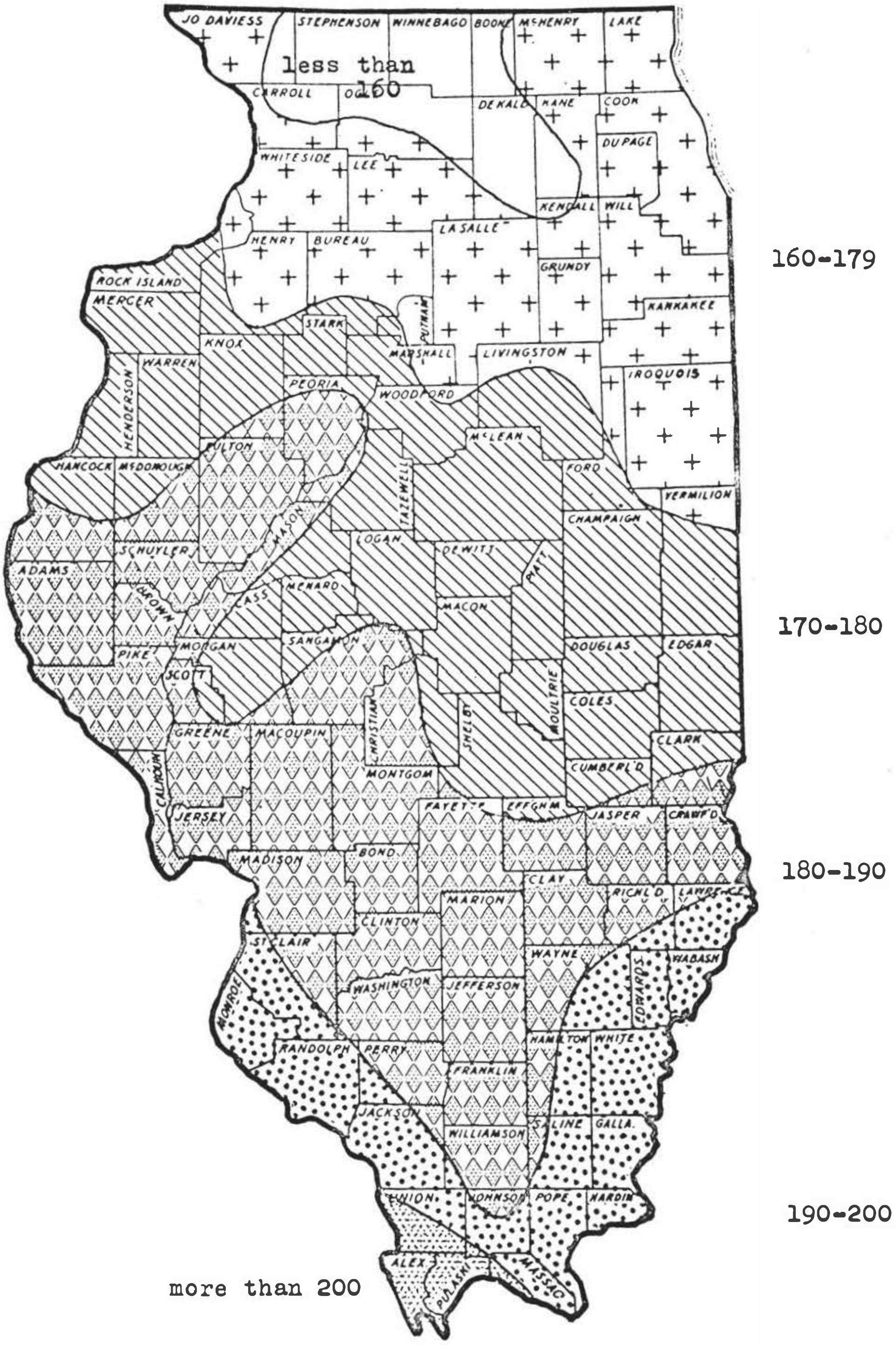
BOND
CLAY
MARION
RICHL'D
LAWRENCE
CLINTON
ST CLAIR
WAYNE
WABASH
WASHINGTON
JEFFERSON
EDWARDS
MONROE
HAMILTON
WHITE
RANDOLPH
PERRY
FRANKLIN
JACKSON
WILLIAMSON
SALINE
GALLA.
UNION
JOHNSON
POPE
HARDIN
ALEX
PULASKI
MASSAC
32-34
34-36
36-38
38-40
40-42
42-44
44-46
more than 46

Figure VI. Average number of frost free days in Illinois (Fehrenbacher *et al*, 1967).


less than 160
160-179
170-180
180-190
190-200
more than 200
JO DAVIESS
STEPHENSON
WINNEBAGO
BOONE
McHENRY
LAKE
CARROLL
OGLE
DEKALB
KANE
COOK
DUPAGE
WHITESIDE
LEE
KENDALL
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BUREAU
LASALLE
GRUNDY
ROCK ISLAND
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SALINE
GALLA.
WILLIAMSON
UNION
JOHNSON
POPE
HARDIN
ALEX
PULASKI
MASSAC

this warm period mean annual temperatures were thought to be 2° to 3° C. higher than today (Brooks, 1951), and dry conditions may have accompanied high temperatures locally but were not of global extent. (Deevey and Flint, 1957).

Vegetation

The climate of Illinois would seem to be conducive to the growth of forest, but at the time of settlement approximately 55% of the state had prairie and 45% had forest vegetation (Telford, 1926; Vestal, 1931; Fehrenbacher et al, 1967). In central and northern Illinois, in areas where prairie vegetation predominated, forests were confined to the better drained, more rolling areas bordering stream valleys (Vestal, 1931). This "Prairie Peninsula" (Transeau, 1935) probably originated with a migration of prairie grasses eastward from western centers in response to a postglacial period of warm and possibly locally dry climate (hypsithermal interval, Deevey and Flint, 1957). Once established the prairie grasses were difficult to dislodge, and many factors, including exposure to dessicating winds, seasonal extremes in soil moisture and fires, probably contributed to its persistence.

The flora of the Shawnee Hills is very old, supporting forest vegetation for thousands of years as the area was little affect-ed by the Illinoian glacial ice (Vestal, 1931). Deciduous forest vegetation during the maximum Illinoian glaciation was probably forced southward into a refuge area centered in the southern Appalachians of eastern Kentucky, Tennessee and western North Carolina. The Wisconsinan glaciation probably had a minor effect on this area for the maximum glaciation was about 150 miles to the north (Bazzaz, 1963; Gruger, 1970; Willman and Frye, 1970). Cores from three ponds near Vandalia, Fayette County, approximately 50 miles south of the Wisconsinan terminal moraine, seem to suggest that during the maximum Wisconsinan ice advance a boreal (conifer) forest did not inhabit the area. During the"most boreal" phase spruce (*Picea*) was not in all areas the dominant tree type, but in some areas based on pollen profile studies oaks (*Quercus*) dominated. Thus during the time of maximum Wisconsinan ice advance, the tundra and boreal coniferous forest did not advance into southern Illinois but were probably restricted to a strip less than 50 miles broad between the ice margin and Vandalia.

The present day flora of southern Illinois and in particular the Shawnee Hills is extremely varied and contains northern and southern elements (Voigt and Mohlenbrock,1964). American beech (*Fagus grandifolia*) shows affinities to the Mixed Mesophytic Forests of the Cumberland Mountains and may be a relict from Illinoian times (Braun, 1950). Other plants with more northern affinities may also be relicts from this period, since boreal forest may only have occupied the area in the Illinoian, and include bishop's cap (*Mitella diphylla*), nannyberry (*Viburnum lentago*) and ground pine (*Lycopodium* complanatum var. flabelliforme) (Voigt and Mohlenbrock, 1964). Some of the southern elements, for example, swamp iris (Iris fulva), show a Mississippi embayment affinity, while others, for example, shortleaf pine (Pinus echinata) and Harvey's buttercup (Ranunculus harveyi) show an Ozark distribution. A large number of weedy herbs were also able to extend their ranges north and most of these species are among the early invaders of abandoned fields (Gleason, 1923; Bazzaz, 1963). Among these species are Andropogon virginicus, and buttonweed (Diodia virginiana) (Voigt and Mohlenbrock, 1964).

The deciduous forests of southern Illinois have been divided into a lowland series and an upland series by Voigt and Mohlenbrock (1964). Table III presents the principal divisions of these series and some of their dominant species.

In recent times the forests of southern Illinois, and especially that of the Shawnee Hills, has been cleared for agricultural use or marketing of timber, pulp and other uses of forest products. The bottomlands were cleared first since the earliest pioneers settled near navigable rivers and succeeding settlers pushed farther up the smaller streams, but always settled in the forest where clear running water and material for fuel and shelter were available (Telford, 1926). Cutting and clearing increased greatly from 1800 onward, the beginning of intensive settlement. With clearing, soil erosion was initiated on the light-colored, highly weathered soils. Grazing also contributed to the reduction of

Table III. Vegetation divisions of southern Illinois (Voigt and Mohlenbrock, 1964).

	LOWLAND		UPLAND					
Species	DEEP SWAMP	BOTTOMLAND	MOIST PRAIRIE	HILL PRAIRIE	RAVINE BOTTOM	MESIC LOWLANDS	MIDSLOPE	RIDGE TOP
Bald Cyprus	X							
Black Willow		X						
Cottonwood		X						
Silver Maple		X						
Sycamore		X						
Big Bluestem			X					
Little Bluestem				X				
Side Oats Grama				X				
Beech					X	X		
Sugar Maple					X	X		
Tulip Tree					X			
White Oak						X	X	X
Red Oak							X	
Black Oak							X	
Pignut Hickory							X	
Shagbark Hickory							X	
Post Oak								X
Black Jack Oak								X

forested areas by damaging tree seedlings.

Where former vegetation in southern Illinois has been removed through drought, cultivation, fire or overgrazing, and the land subsequently abandoned, the land is repopulated by successive plant communities. On the once cultivated land of southern Illinois many of the herbaceous species with southern affinities, Andropogon virginicus, are among the early invaders of these abandoned fields (Hartley, 1958; Gould, 1967). This repopulation has been intensively studied in the Shawnee Hills and consists of a progression from an annual weed stage to a perennial weed stage which includes broomsedge, followed by a shrub or bramble stage, then a pioneer tree stage and later tree stage which approaches climax forest(Voigt and Mohlenbrock, 1964; Bazzaz, 1968). Table IV presents a list of species, and the stage in which they are present, common in old-field succession in southern Illinois. With the establishment of the Shawnee National Forest in 1933, a large portion of the abandoned land is returning to forest cover.

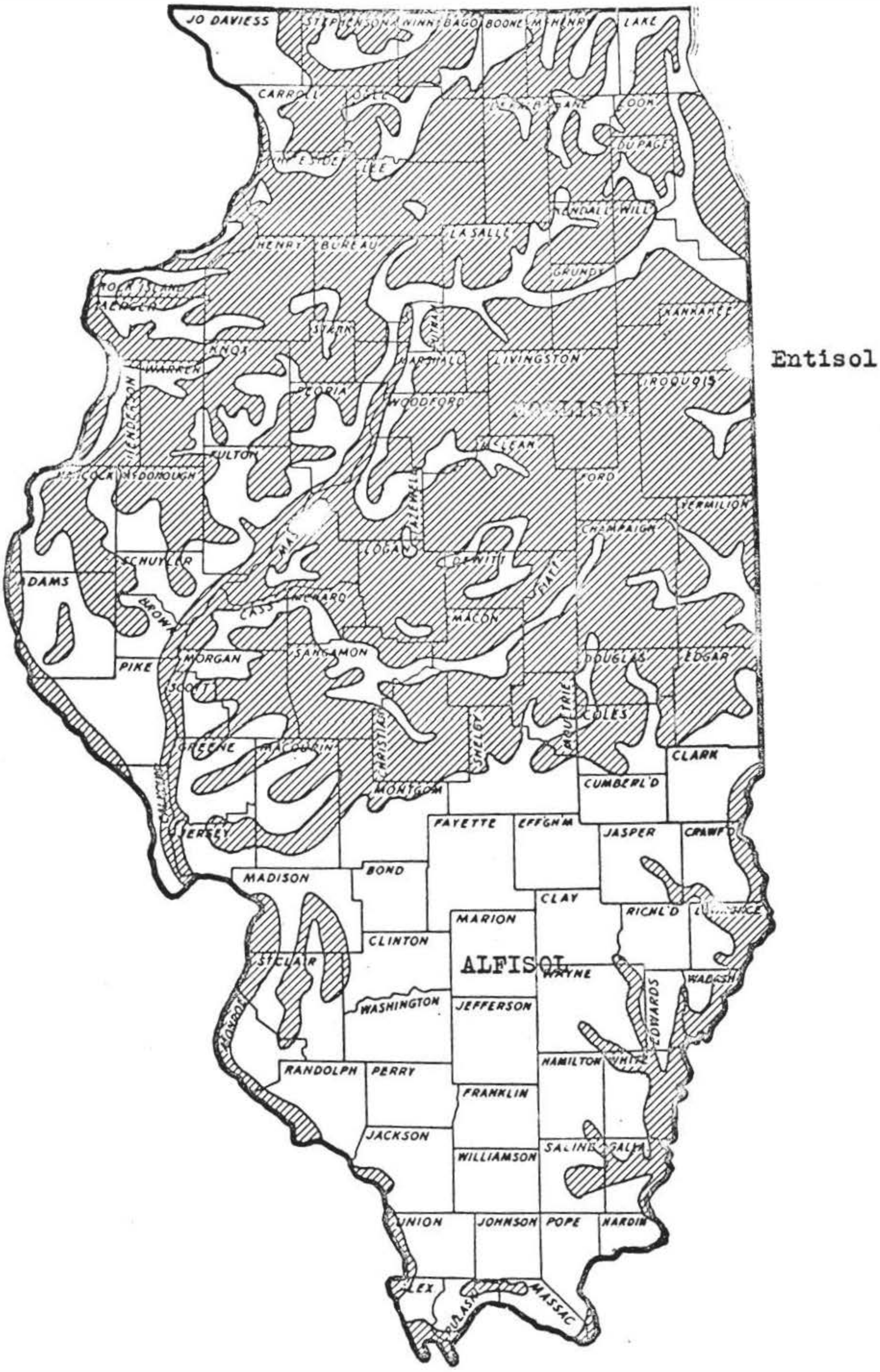
Soils

Broomsedge occurs mainly on Alfisols, which have developed over either Mississippian or Pennsylvanian strata covered by loess, and under the influence of forest vegetation. The loess cover varies from more than 20 feet in portions of the Western Division and Mississippi Border to three to five feet in southern Illinois (Fehrenbacher et al, 1965; Fehren-

Table IV. Summary of old-field succession in the Shawnee Hills, southern Illinois (Bazzaz, 1968).

	YEAR						
	1	2	5	10	25	40	100?
SPECIES							
Ragweed	X	X					
Erigeron	X	X					
Crabgrass	X	X					
Aster		X	X				
Goldenrod		X	X	X			
Diodia	X	X	X				
Broomsedge			X	X	X		
Panicum			X	X	X	X	
Juniperus					X	X	X
Juncus			X				
Potentilla				X	X	X	
Ipomoea				X	X	X	
Sassafras				X	X	X	
Persimmon				X	X	X	
Sumac				X	X	X	
Raspberry				X	X	X	
Smilax					X		
Redbud					X		
Fraxinus						X	X
Quercus						X	X
Carya						X	X

Figure VII. Major soil orders of Illinois.


Entisol
MOLLISOL
ALFISOL
JO DAVIESS
STEPHENSON
WINNEBAGO
BOONE
McHENRY
LAKE
CARROLL
OGLE
DEKALB
KANE
COOK
DU PAGE
WHITESIDE
LEE
KENDALL
WILL
HENRY
BUREAU
LA SALLE
GRUNDY
ROCK ISLAND
MERCER
STARK
PUTNAM
KANKAKEE
KNOX
WARREN
MARSHALL
LIVINGSTON
HENDERSON
PEORIA
WOODFORD
IROQUOIS
FULTON
McLEAN
HANCOCK
McDONOUGH
FORD
VERMILION
MASON
TAZEWELL
CHAMPAIGN
SCHUYLER
LOGAN
DEWITT
PIATT
ADAMS
BROWN
CASS
MENARD
MACON
PIKE
MORGAN
SANGAMON
DOUGLAS
EDGAR
SCOTT
MOULTRIE
CHRISTIAN
SHELBY
COLES
GREENE
MACOUPIN
CLARK
CALHOUN
MONTGOM
CUMBERL'D
JERSEY
FAYETTE
EFF'GH'M
JASPER
CRAWF'D
MADISON
BOND
CLAY
RICHL'D
LAWRENCE
MARION
CLINTON
ST CLAIR
WAYNE
WABASH
EDWARDS
WASHINGTON
JEFFERSON
MONROE
HAMILTON
WHITE
RANDOLPH
PERRY
FRANKLIN
JACKSON
SALINE
GALLATIN
WILLIAMSON
UNION
JOHNSON
POPE
HARDIN
ALEX
PULASKI
MASSAC

bacher et al, 1967). This soil group predominates in southern Illinois but is also present in the central, northern and western portions of the state, where Alfisols are confined largely to the more rolling, better drained sites bordering stream valleys or to the drier morainal positions. Figure VII shows the distribution of two of the major soil orders in Illinois.

Broomsedge was intensively studied in the Shawnee Hills on the Alfisol or Gray-Brown Podzol, Grantsburg Silt Loam. The type locality for Grantsburg Silt Loam is in Pope County, Illinois: T. 13S, R. 5E, Sec. 4, NW¼, NW 40, NE 10 with an oak-hickory deciduous cover having an undergrowth of small trees and shrubs (Anon., 1968). The type description and the description for the soil under cultivation is presented in Appendix I. These soils have the most highly developed fragipan of the soils of southern Illinois, and the fragipan is closer to the surface than in any other fragipan soil in the region (Grossman et al, 1959). Grantsburg is considered a highly weathered and highly leached soil (Fehrenbacher et al, 1967).

MATERIALS AND METHODS

Distribution

The previously reported distribution of Andropogon virginicus L. in Illinois was determined by consulting published reports (Evers, 1955; Jones and Fuller, 1955; Winterringer and Evers, 1960; Voigt and Mohlenbrock, 1964). Figure VIII shows the new distribution of broomsedge, and also indicates the counties in which previous workers have reported the grass. The old distribution was compared with new data obtained by examining the collections from the following herbaria (except for the first four herbaria listed abbreviations are from Lanjouw and Stafleu, 1964): Eastern Illinois University (EIU), Northern Illinois University (NIU), Western Illinois University (WIU), Illinois State University (ISU), Southern Illinois University (SIU), Illinois State Museum (ISM), Illinois State Natural History Survey (ILLS), University of Illinois at Urbana (ILL) and Chicago Circle, Field Museum of Natural History (F), Missouri Botanical Garden (MO), and the Smithsonian Institution-United States National Museum (US). Numerous broomsedge specimens on deposit in the Smithsonian were annotated. Included in the collections from the Smithsonian is a photo of Linnaeus' type specimen and a small portion of the inflorescence of that specimen. Also included are Illinois specimens from the Gray Herbarium of Harvard University (GH) and the British Museum (BM). Twenty counties from which broomsedge had not previously been collected , but which were believed to have a suitable habitat, were surveyed. Major collecting trips were made to the following areas: northwestern Illinois (September 3-5, 1971), central Illinois (various dates), southeastern Illinois (various dates), Illinois River valley (October 23-25, 1971; April 3-7, 1971; November 5-7, 1972), Sangamon River valley (numerous dates). Collections were made and deposited in the Stover Herbarium of Eastern Illinois University.

Soils

In the Ozark Hills of southern Illinois abandoned fields containing broomsedge were selected for study. In an effort to control climatic variables, all fields were located in Pope County near Dixon Springs Experiment Station, Simpson, Illinois. All fields are not more than one mile from each other. (Climatic data for Dixon Springs is presented in Table V). In addition all fields are of the same soil type-Grantsburg Silt Loam. The age of these fields was estimated to range from one to forty years, with end points in corn, pine plantation and oak-hickory climax forest. The age was determined by consulting the records of the Experiment Station And United States Forest Service District Office at Vienna, and also by using the biological criteria of Bazzaz (1968) who documented the course of succession in southern Illinois.

Samples from the top six inches of the soil profile were collected in plastic bags. The samples were dried on waxpaper and passed through a 2mm. mesh sieve and kept in plastic containers for analysis. The pH value was obtained by the glass electrode method using a 1:1 soil-water suspension (Greweling and Peech, 1965). The cation exchange capacity was determined by summation of the values for the various cations (Richards, 1969). Soil moisture both at the permanent wilting percentage (15 atmospheres) and field capacity (0.3 atmosphere) was determined (Richards, 1969). Calcium, magnesium, iron, aluminum, and manganese were first leached from the soil using 0.5 N. hydrochloric acid, filtered through one layer of Whatman No. 1 filter paper, and determined by atomic absorption spectroscopy using a Beckman Model 440 Atomic Absorption Spectrophotometer equipped with flame emission option and strip recorder read out. Sodium and potassium determination was accomplished by flame photometry with a National Instrument Laboratoriesflame photometer. Phosphorus was measured colorimetrically with a Spectronic 20 colorimeter from leachate obtained with 1 N. sodium acetate-acetic acid extracting extracting solution and molybdate and stannous chloride reagents (Greweling and Peech, 1965). Nitrate and ammonia were also determined colormetrically using a 1 N. sodium-acetate- acetic acid extracting solution and brucine, sulfuric acid and phenol-nitroprusside-tartrate and alkaline hypochlorite reagents respectively(Greweling and Peech, 1965).

Germination Experiments

Fruits of *Andropogon virginicus* were collected in November, 1971 and planted in quartz sand which had been leached for 24 hours with 0.5% hydrochloric acid (Bradshaw *et al*, 1958). The plantings were cold treated at -5° C. for one month. Following this the seeds, which were still in the quartz sand, were placed in an environmental chamber under an 18 hour photoperiod 20° C. night temperature and 25° C. day temperature (Leithead *et al*, 1971). Meyer's solution, pH $4.0 \pm .2$, consisting of 1molar soultions of KNO_3 (2 ml.), $Ca(NO_3)_2$ (3 ml.) and $MgSO_4$ (2 ml.) with 1 ml. of iron-EDTA solution and 1 ml. of a micrometabolic solution consisting of H_3BO_3 (2.5 gms./L.), $MnCl_2 \cdot 4H_2O$ (1.5 gms./L.), $ZnCl_2$ (0.10 gms./L.), $CuCl_2 \cdot 2H_2)$ (0.05 gms./L.) and MoO_3 (0.05 gms./ L.) was the basic culture solution. Experiments with various levels of micro and macronutrients were planned if initial germination studies were successful.

RESULTS AND OBSERVATIONS

Distribution

The range of broomsedge in Illinois is presented in Figure VIII. This map shows the counties from which broomsedge had not previously been reported, and indicates the counties from which broomsedge had previously been reported. Table V summarizes the collection and herbarium data.

Soils

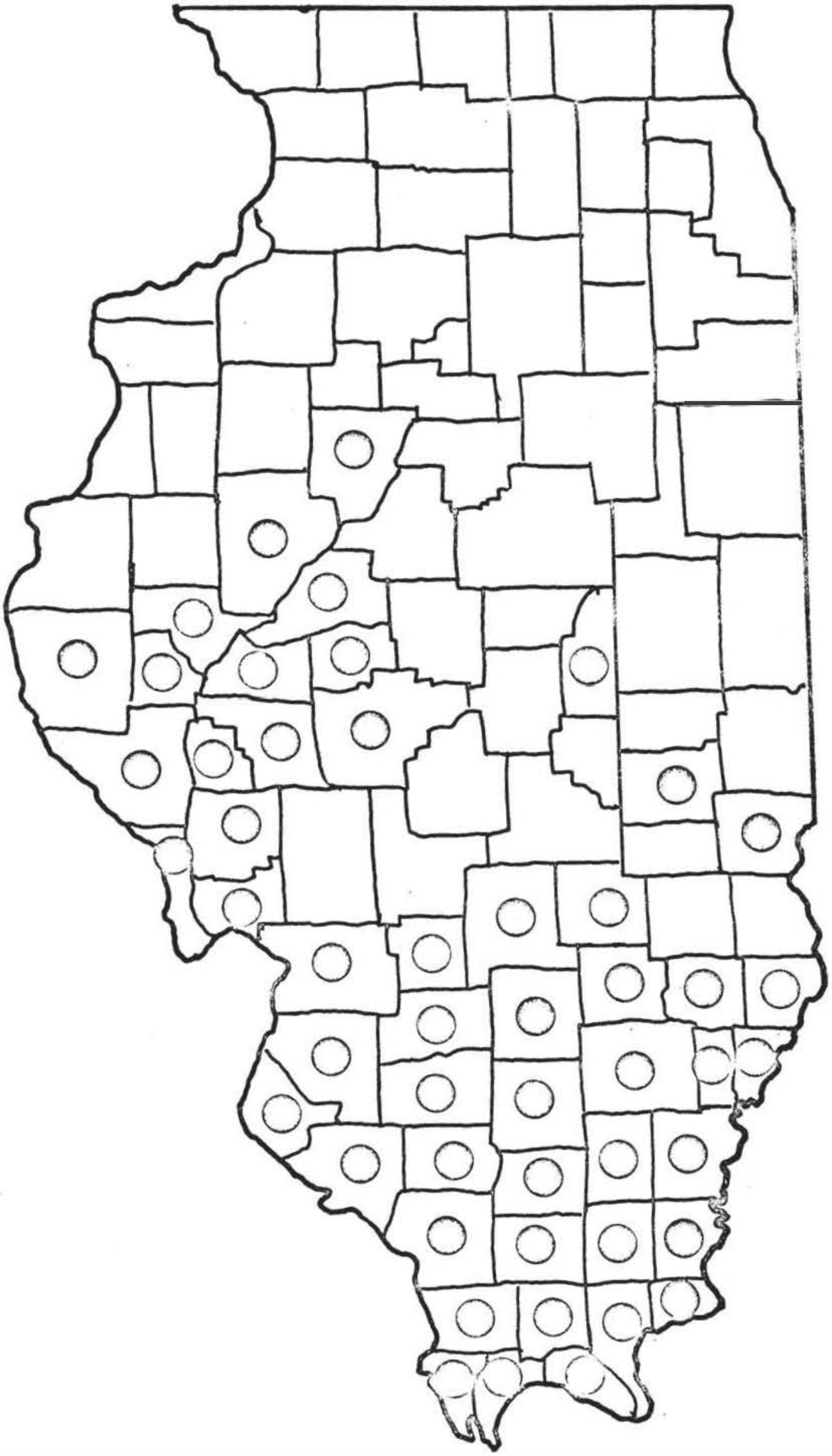
Soil characteristics studied were: soil moisture both at field capacity and permanent wilting percentage (Fig. IX), organic matter and pH (Fig. X), cation exchange capacity (Fig. XI), calcium and magnesium (Fig. XII), phosphorus (Fig. XIII), nitrate and ammonia (Fig. XIV), sodium (Fig. XV), potassium (Fig. XVI), iron and aluminum (Fig. XVII) and manganese (Fig. XVIII). Observations and climatic data for Dixon Springs Experiment Station are presented in Table VI, and observations on the flora of the abandoned fields are presented in Table VII.

Germination Experiments

Results of the germination experiments are shown in Table VIII.

Figure VIII. a Previous distribution of Illinois

b New distribution of Illinois



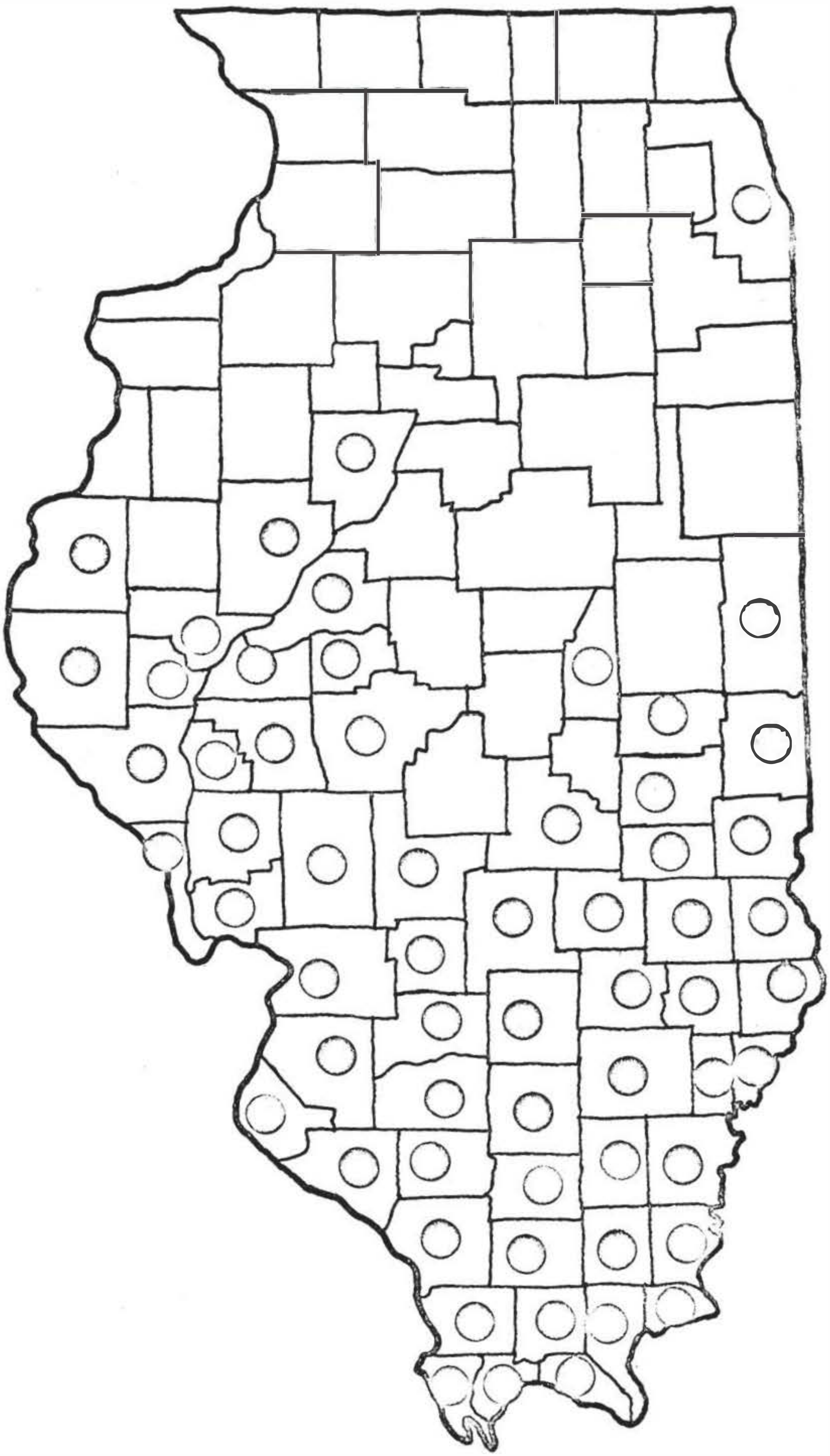


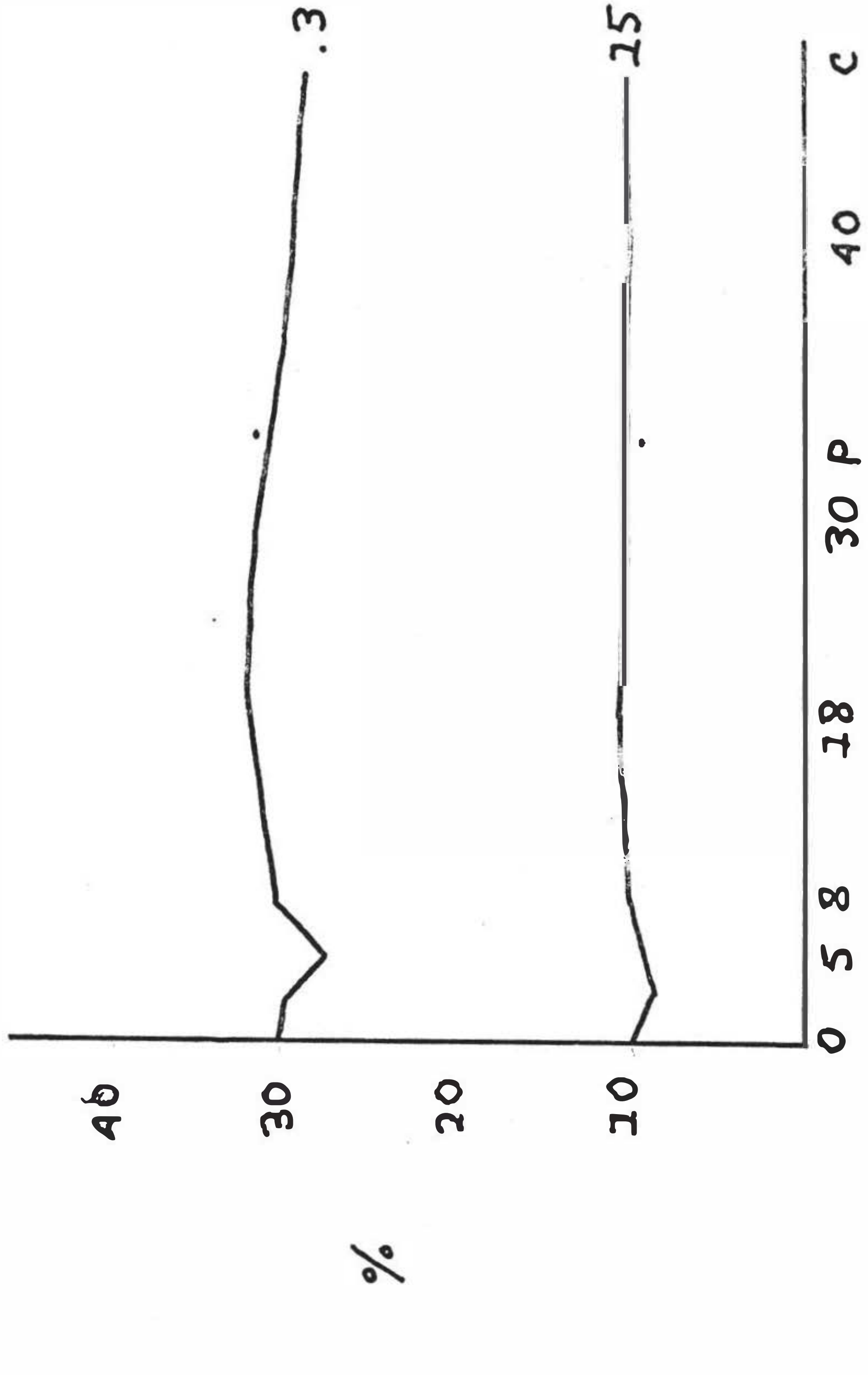
Table V. Summary of county collection records (total number of specimens examined or collected).

COUNTY	HERBARIUM SPECIMENS	PERSONAL COLLECTIONS
Adams	2	
Alexander	6	
Bond	3	
Brown	1	
Calhoun	2	
Cass	2	
Clark	2	
Clinton	1	
Coles	11	5
Cook	2	
Crawford		1
Cumberland		4
Douglas	1	1
Edgar		1
Edwards	2	
Effingham	1	1
Fayette	4	
Franklin	5	
Fulton	1	2
Gallatin	4	
Greene	2	
Hamilton	1	
Hancock	1	
Hardin	4	
Jackson	15	2
Jasper		1
Jefferson	2	
Jersey	1	
Johnson	4	
Lawrence	1	
Macoupin	1	
Madison	1	
Marion	5	
Mason	3	
Massac	4	
Menard	1	
Monroe	3	
Montgomery		3
Morgan	2	
Peoria	4	
Perry	3	
Piatt	1	
Pike	1	
Pope	4	10
Pulaski	3	
Randolph	2	
Richland	5	
Saint Clair	12	
Saline	5	

Table V. CONTINUED

COUNTY	HERBARIUM SPECIMENS	PERSONAL COLLECTIONS
Sangamon	7	
Schuyler	2	
Scott	1	
Shelby		1
Union	5	2
Vermilion		1
Wabash	5	
Washington	1	
Wayne	7	
White	2	
Williamson	8	

Figure IX. Permanent Wilting Percentage (15 atm) and Field Capacity (.3 atm.).



%
40
30
20
10
0
5
8
18
30 P
40
C
.3
15

Figure X. Organic matter and pH

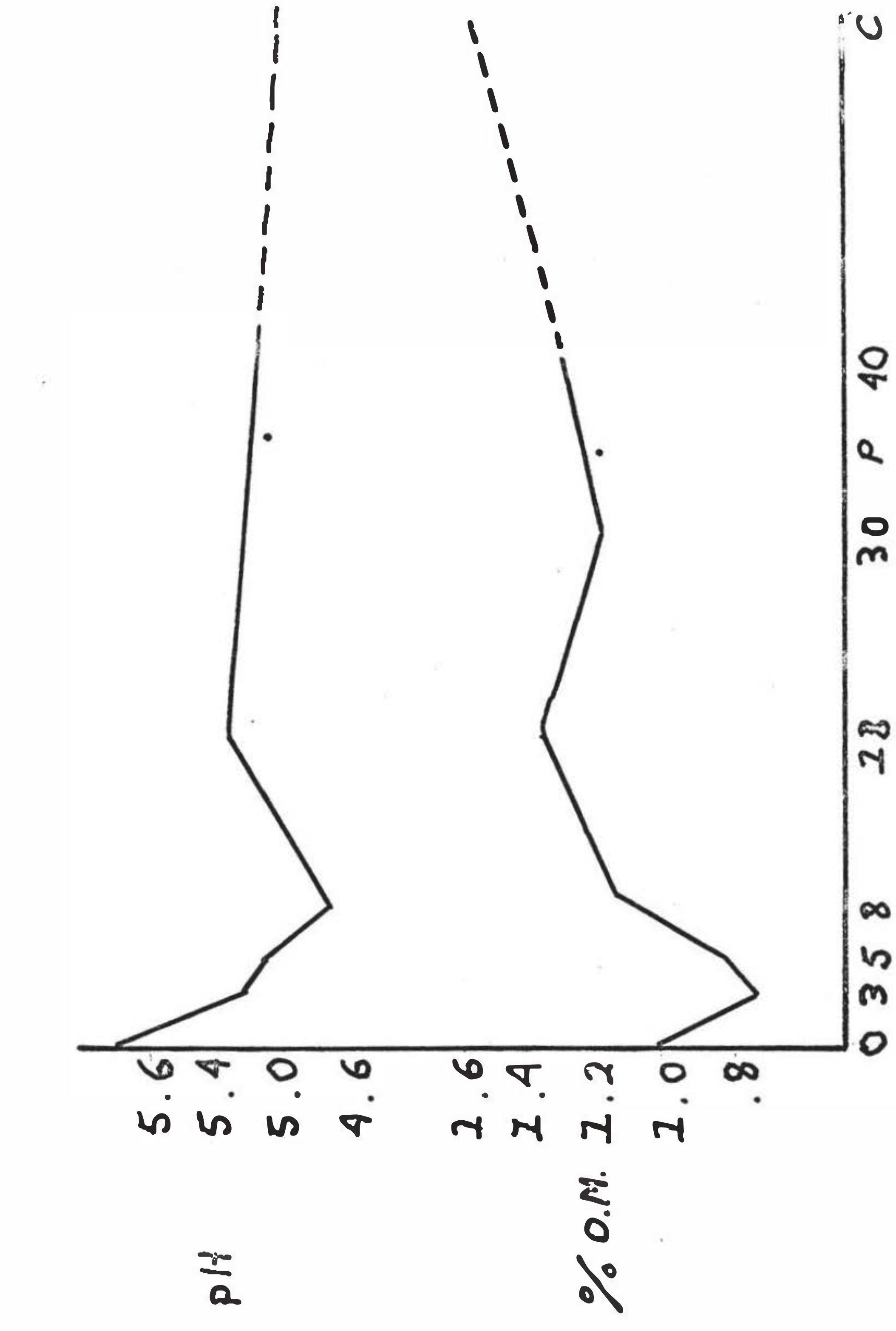

pH
% O.M.
5.6
5.4
5.0
4.6
1.6
1.4
1.2
1.0
.8
0
3
5
8
2B
30
P
40
C

Figure XI. Cation exchange capacity

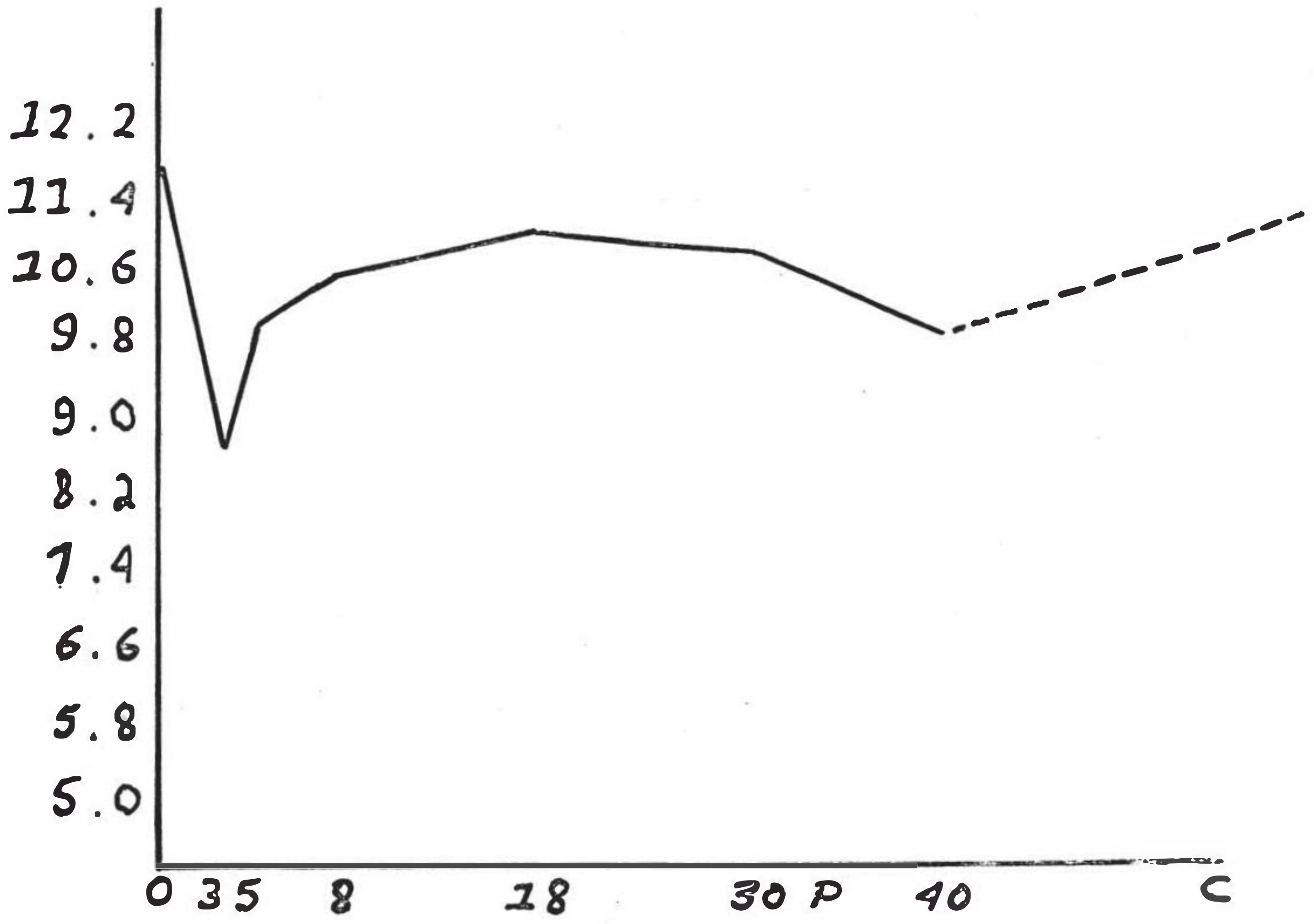

12.2
11.4
10.6
9.8
9.0
8.2
7.4
6.6
5.8
5.0
0
3
5
8
18
30
P
40
C

Figure XII. Calcium and magnesium

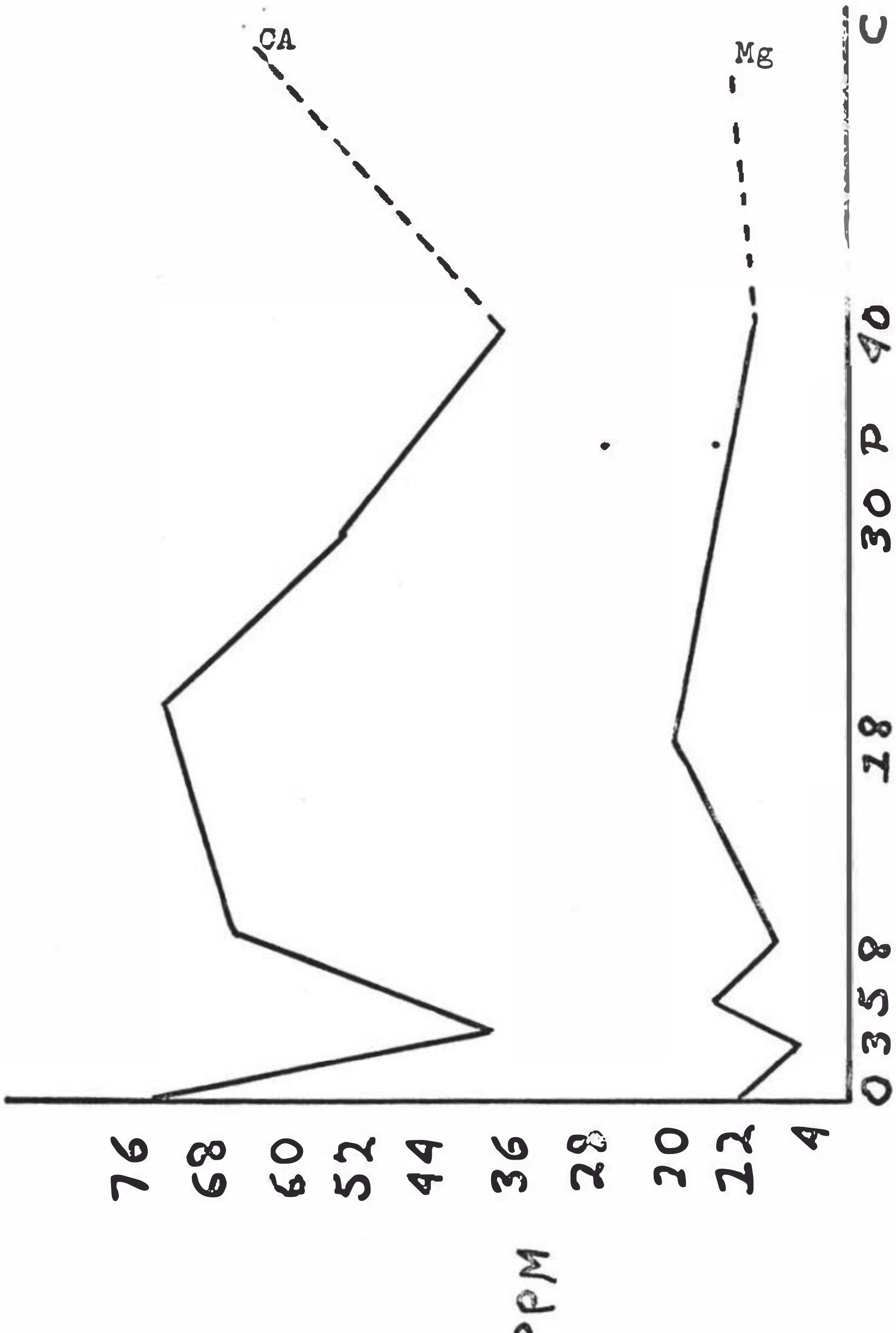

CA
Mg
PPM
76
68
60
52
44
36
28
20
12
4
0
3
5
8
18
30
P
40
C

Figure XIII. Phosphate

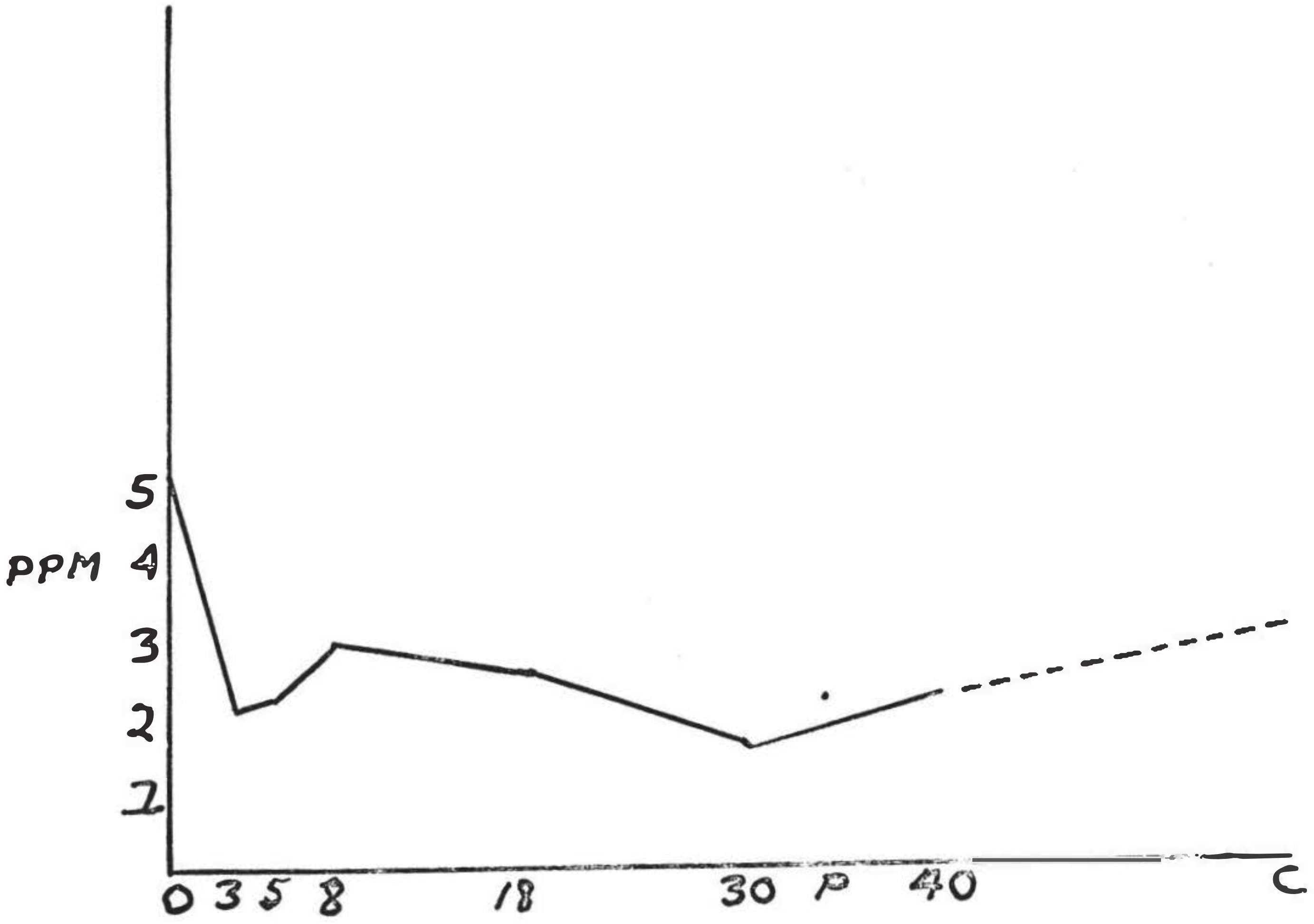

PPM
5
4
3
2
1
0
3
5
8
18
30
P
40
C

Figure XIV. Nitrate and ammonia

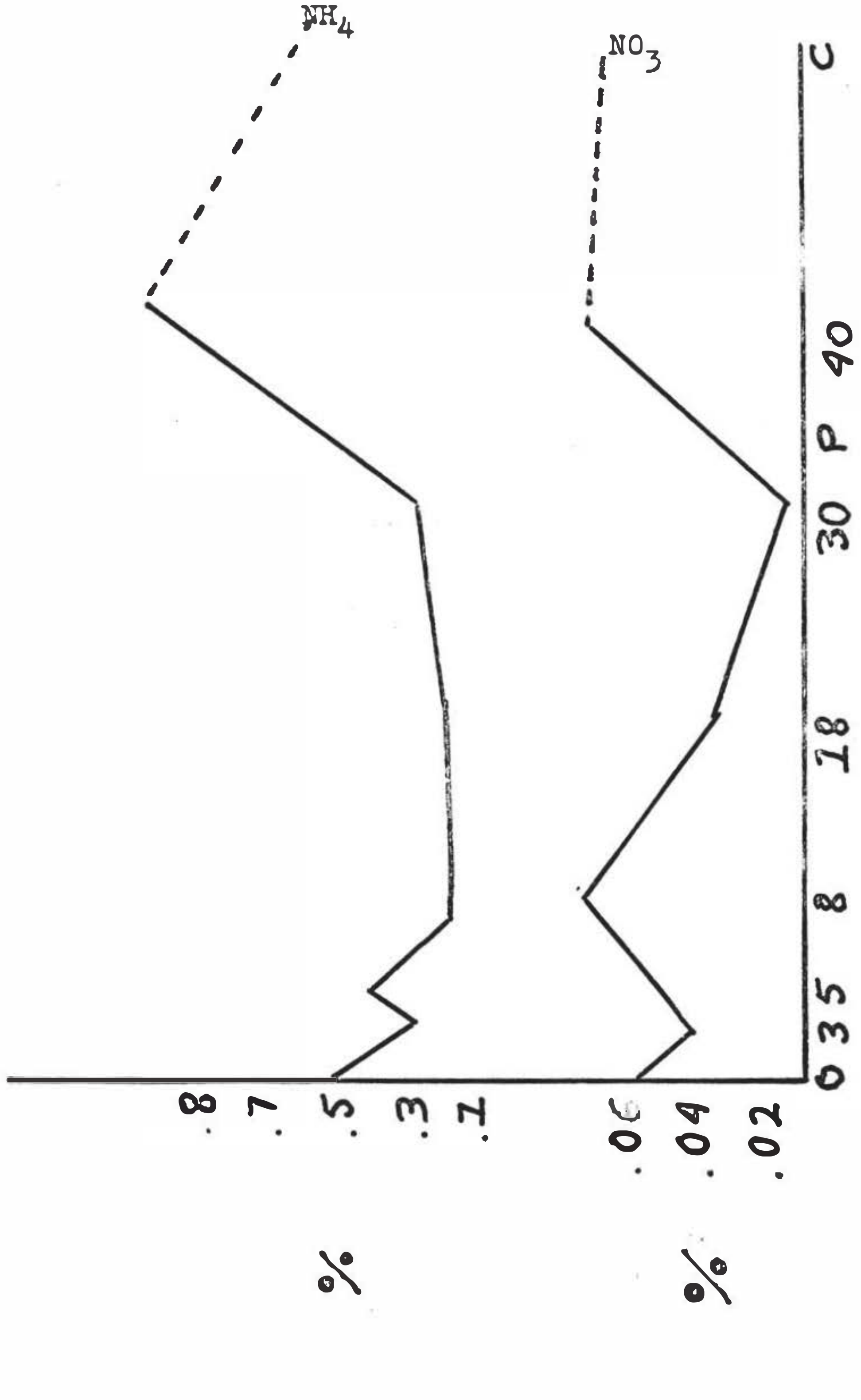

NH_4
NO_3
%
.8
.7
.5
.3
.1
%
.06
.04
.02
0
3
5
8
18
30
P
40
C

Figure XV. Sodium

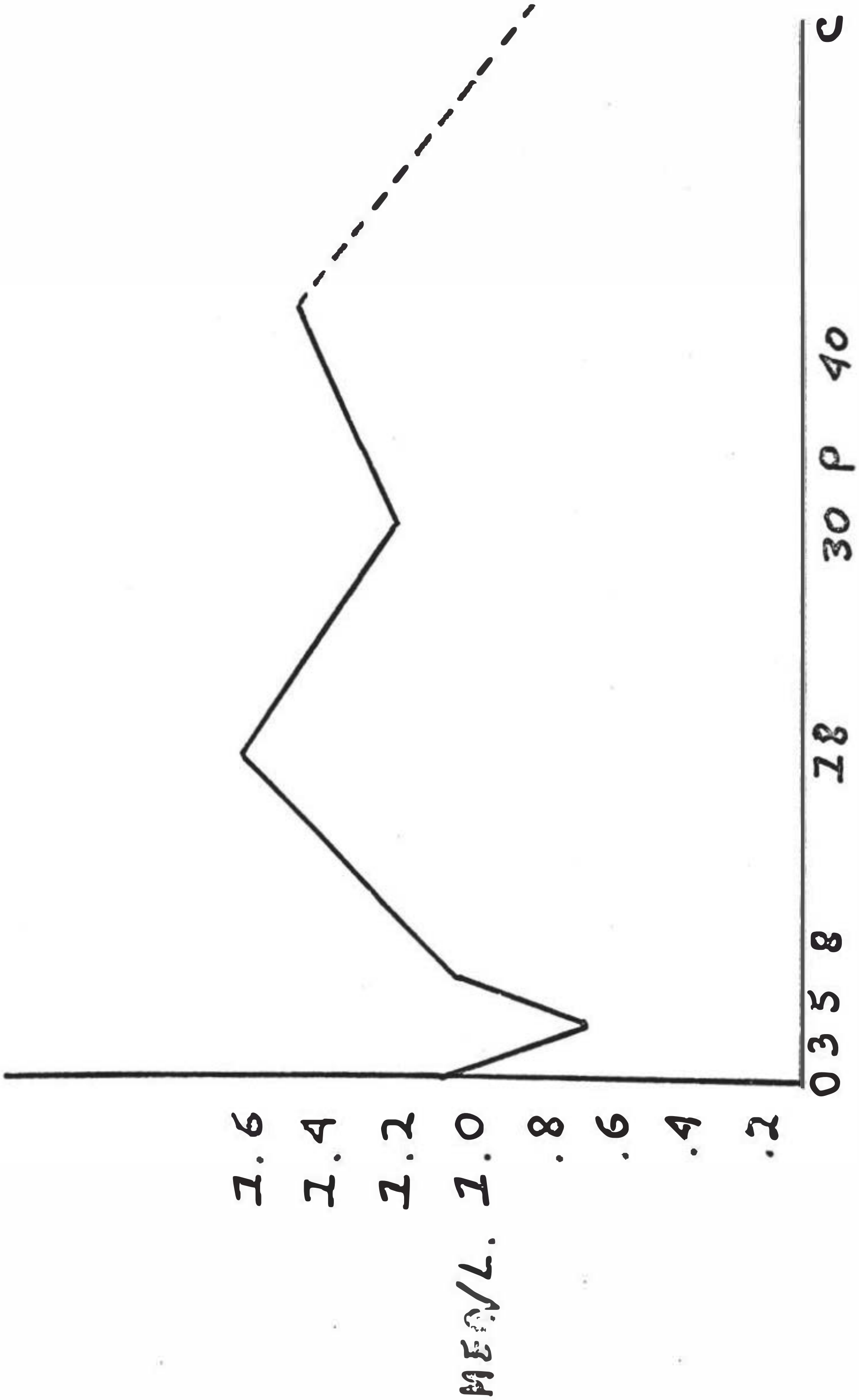

MEQ/L.
1.6
1.4
1.2
1.0
.8
.6
.4
.2
0
3
5
8
18
30
P
40
C

Figure XVI. Potassium

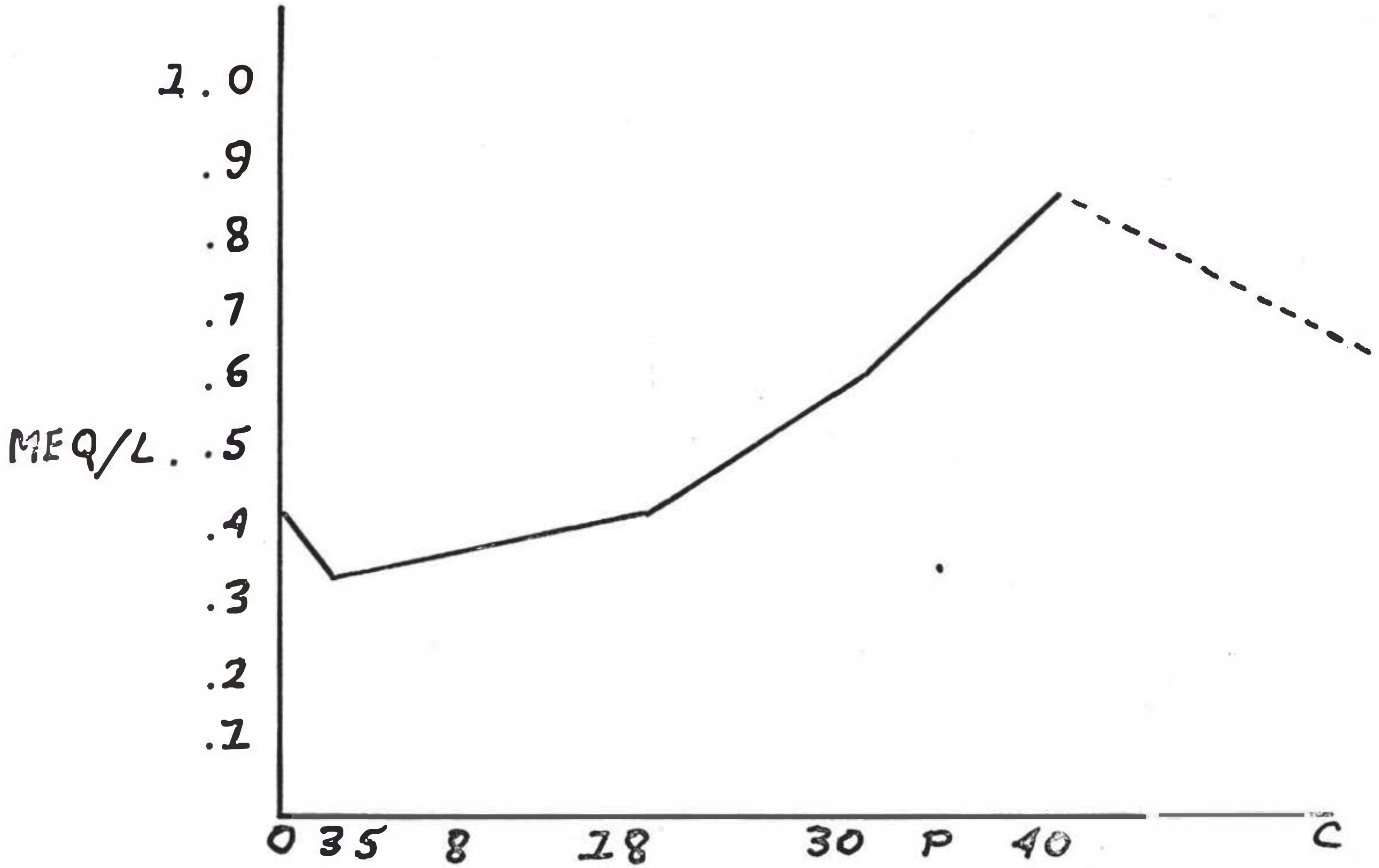

MEQ/L.
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
3
5
8
18
30
P
40
C

Figure XVII. Iron and aluminum

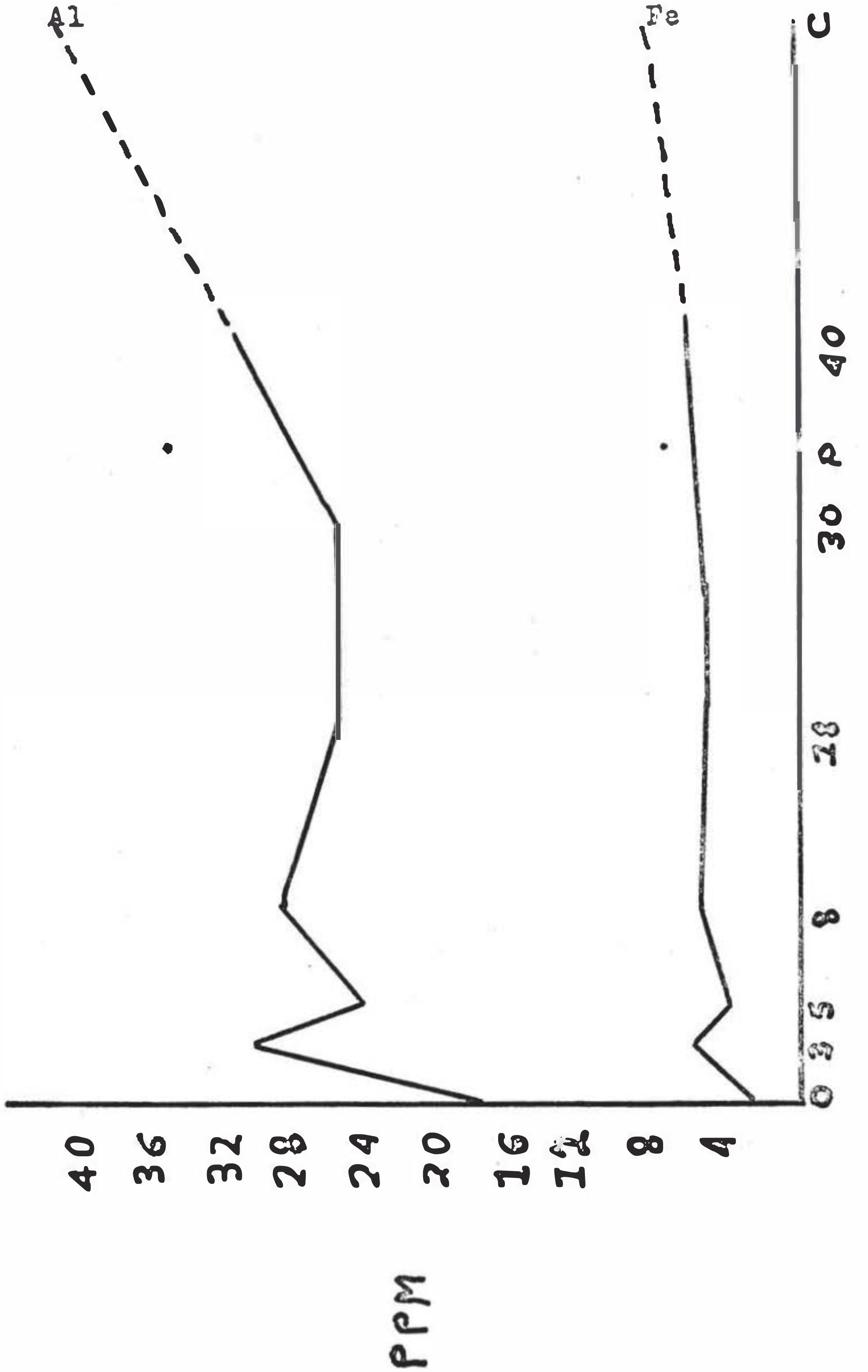

Al
Fe
PPM
40
36
32
28
24
20
16
12
8
4
0
3
5
8
18
30
P
40
C

Figure XVIII. Manganese

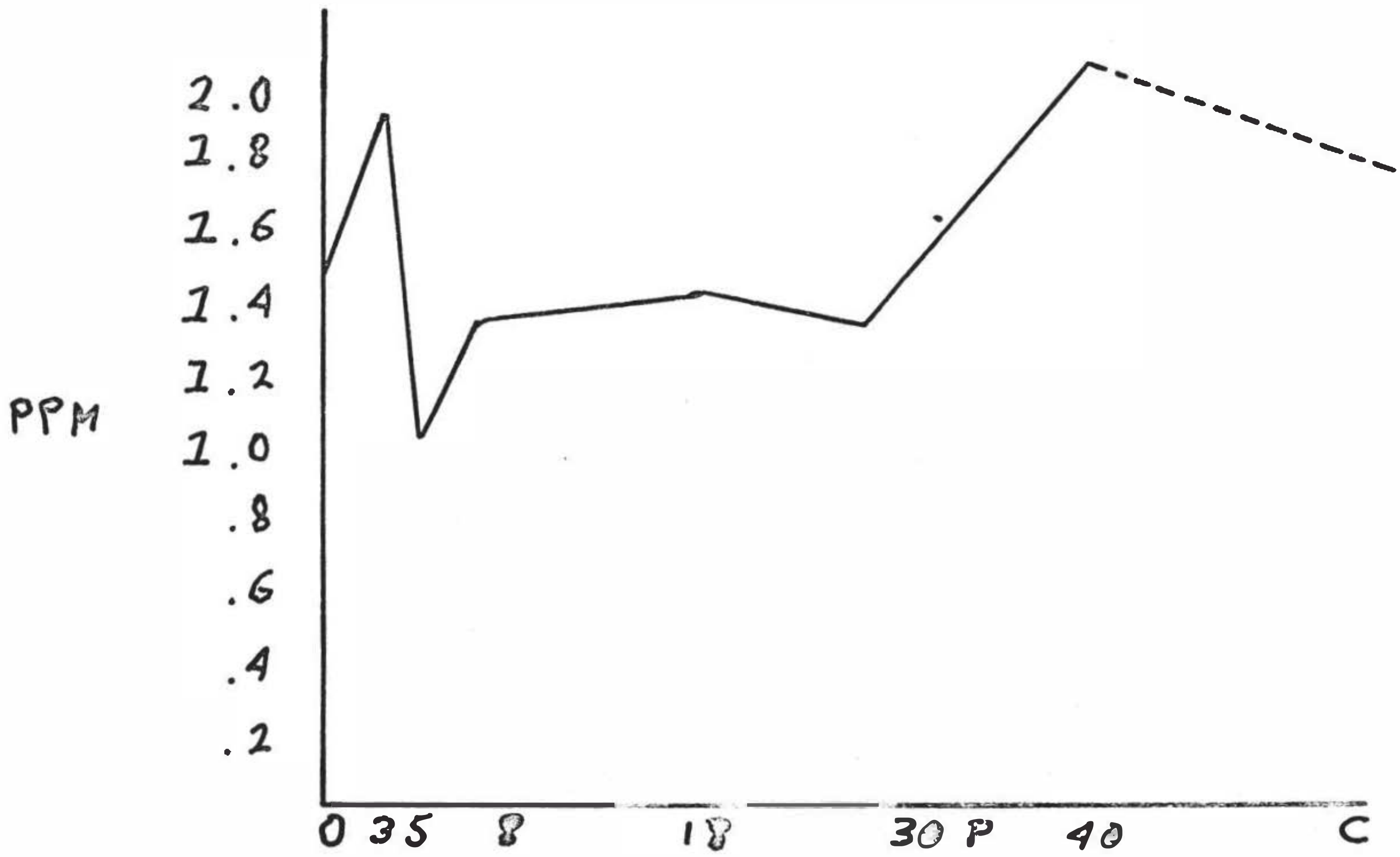

PPM
2.0
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
0
3
5
8
18
30
P
40
C

Table VI. Climatic data for 1969, 1970 and 1971 for Dixon Springs Experiment Station, Simpson, Illinois (Temperature in °F.)

TEMPERATURE

	AVERAGE MAXIMUM			AVERAGE MINIMUM			AVERAGE		
MONTH	1969	1970	1971	1969	1970	1971	1969	1970	1971
January	43	38	40	25	16	22	34	27	31
February	45	24	34	30	24	26	37	34	36
March	52	51	--	27	33	--	40	42	--
April	70	71	70	46	48	43	58	59	57
May	78	80	73	54	55	48	66	68	61
June	85	83	--	62	61	--	74	72	--
July	--	88	84	--	63	63	79	76	74
August	--	88	83	--	65	62	75	77	73
September	82	86	83	57	62	62	69	74	72
October	71	--	77	46	--	54	59	58	66
November	55	55	57	34	36	37	44	45	47
December	42	49	53	26	31	36	34	40	45

PRECIPITATION (inches)

	1969	1970	1971		1969	1970	1971
January	9.5	.8	4.2	July	3.7	.54	5.6
February	1.2	2.8	4.7	August	2.2	2.5	2.9
March	2.2	5.7	4.3	September	1.6	2.5	2.3
April	4.6	8.2	2.0	October	4.7	5.0	.97
May	2.8	8.1	4.9	November	3.2	2.3	1.7
June	9.1	5.0	--	December	4.1	2.4	4.3

Table VII. Observations on the flora of the abandoned fields.

Field	Age (Years)	Dominant Species
0	0	Corn
1	late 1	*Ambrosia artemissifolia*
2	3	*Aristida dichotoma*
3	3	*Aristida dichotoma*/ *Ambrosia*
4	5	*Andropogon virginicus*
5	5	*Andropogon virginicus*
6	8	*Andropogon virginicus*
7	15	*Andropogon virginicus*/ *Diodia*
8	18	*Andropogon virginicus*/ *Diodia*/ *Ambrosia*
9	30	*Diospyros*/ *Sassafras*/ *Andropogon*
10	35?	*Diospyros*/ *Sassafras*/ *Andropogon*
11	40	*Ulmus*/ *Quercus*/ *Solidago*
12	Pine	*Pinus echinata*
13	Pine	*Pinus echinata*
14	Climax	*Quercus*/*Carya*/ Maple (not on Grantsburg
15	Climax	*Quercus*/*Carya*
16	Climax	*Quercus*/*Carya*
17	Climax?	*Quercus*

Table VIII. Results of the germination experiments

Experiment 1.

	Meyer's Solution	Distilled/Deionized Water
Cold treatment	25--2 germinated	25--0 germinated
Control	25--0 germinated	25--0 germinated

Experiment 2.

	Meyer's Solution	Distilled/Deionized Water
Cold treatment	25--0 germinated	25--0 germinated
Cold treated on plant	25--1 germinated	25--0 germinated
Control	25--0 germinated	25--0 germinated

Experiment 3.

	Meyer's Solution	Distilled/Deionized Water
Cold Treatment	25--0 germinated	25--0 germinated
Control	25--0 germinated	25--0 germinated

Experiment 4.

	Meyer's Solution	Distilled/Deionized Water
Cold Treatment	25--0 germinated	25--0 germinated
Control	25--0 germinated	25--0 germinated

CONCLUSIONS

1. This study documents the cycling of nutrients in the annual weed, perennial grass, shrub and bramble, and early tree stage.

2. Evidence is presented which indicates an inhibition of nitrification during at least the broomsedge stage, and perhaps under climax forest. Broomsedge may secrete chemicals which, at least, inhibit nitrification.

3. Broomsedge, which seems to be an acidophilous and drought resistant species, is able to establish itself only in fields of low fertility. Furthermore there is a rapid loss of nutrients as well as organic matter in the first stage of old-field succession.

4. As broomsedge increases in dominance, there is a concomitant increase in most cations analyzed, except phosphorus, nitrate and ammonia.

5. Once established broomsedge can probably keep out invading species by limiting nitrate and ammonia levels, and possibly allelopathic effects.

6. Broomsedge is probably eliminated from succession because of the toxic effects of increased amounts of aluminum and

manganese, auto-intoxication and shading.

7. With succession from broomsedge to the shrub and bramble stage, there is a decrease in clacium, magnesium, pH, organic matter, sodium and iron.

8. The stage following broomsedge, the shrub and bramble stage, probably requires higher levels of nutrients.

9. There appears to be a correlation between increasing acidity and increased availability of metallic cations.

DISCUSSION

The range of broomsedge in Illinois has been extended, and includes: Adams, Clark, Cook, Crawford, Cumberland, Douglas, Jasper, Macoupin, Montgomery, Shelby and Vermilion counties. The Cook County populations, which may no longer be in existence, were located at "Beverly Shores, Lake Shore Drive, one block west of (Illinois?) Central." The specimens were collected by Dr. S.F. Glassman on September 5, 1956. The collections are an enigma, until one realizes that the seeds might have been dispersed by passing railroad cars or trucks from southern Illinois, and on a sandy loam soil found a habitat suitable for growth.

In the United States, broomsedge is found from the 25-inch rainfall belt eastward and also as an occasional weed in northern California. Attempts were made to correlate the distribution of broomsedge with several environmental factors. The distribution does not coincide well with mean annual temperature (Fig. IV) or average precipitation (Fig. V). The undisputed, relatively abundant distribution of the taxon does, however, somewhat coincide with the average number of frost-free days, and occurs in areas with more than 180 frost-free days. If broomsedge is assumed to have evolved in Central or South America, and is a slow growing (Crafton and

Wells, 1934), short day plant (Dale, 1971), whose seeds are not mature until late October or early November (Keever, 1950), it would seem that the plant is not yet able to extend its range throughout Illinois. Broomsedge also occurs on older Illinoian and weathered Tertiary soils possibly because it is more able to compete on soils of very low fertility. The seeds of broomsedge are not readily distributed (Rice *et al*, 1960), and extension of its range or invasion of old-fields would be a slow process.

Soil changes associated with plant succession have been documented since the early 1930's. Investigators have observed changes in physical characteristics, for example, soil moisture and bulk density, and chemical characteristics such as pH and nitrogen. Researchers have not, however, attempted to correlate these changes with the succession of seral stages. Moreover, except for the researches of R. Rose-Innes (1939), Blackman and Rutles (1947), Stiven (1957), Davidson (1962) and Bazzaz (1963), few successional studies have even attempted a thorough study of edaphic factors.

Following abandonment of fields in southern Illinois, there is a decline in soil moisture both at the permanent wilting percentage and field capacity, while available water increases slightly but later decreases. Figure IX shoes that these levels begin to increase after abandonment and level off at approximately 18 years. Bazzaz (1963) has observed similar trends on similar soils in southern Illinois. In addition to these changes in soil moisture, yearly precipitation in the Shawnee Hills is subject to fluctuations with droughts during the summer and occasional heavy rainstorms. These heavy rainstorms, however, provide little effective rainfall because of the fragipan blocking percolation of water below 60 cm. During the growing season, at least for the first few years after abandonment, there is less available water due to summer drought and a lower water supplying ability.

Crafton and Wells (1934) reported that the invasion of broomsedge depends on the establishment of more mesic conditions induced by the previous tall weed flora. The soil in closed tall weed communities does not dry out so rapidly between spring rains so that broomsedge cannot become established (Crafton and Wells, 1934). Pot experiments indicated broomsedge seedlings are very sensitive to even slightly dry soil conditions (Crafton and Wells, 1934). Keever (1950), however, stated that broomsedge seedlings are relatively drought resistant, and exhibited optimum growth in full sunlight with a seven day interval between watering. In view of the competition for soil water in the summer growing season, and the reduced water holding capacity of the fragipan soil, broomsedge, at times, would appear to be subjected to water stress. It would seem that broomsedge is indeed a drought resistant species as earlier thought. Since the germination experiments were unsuccessful, possibly because of problems with cold treatments and inviable seeds, conclusive proof is lacking.

In the Shawnee Hills erosion is a serious problem. With abandonment of fields, annuals and early perennials add some organic matter to soils (Bazzaz, 1963), but organic matter is also oxidized and lost by erosion. If the amount of organic matter oxidized exceeds that added, the result is a net loss rather than an increase. Smith (1940) and Odum (1960) reported that for areas with high temperature and precipitation, a net loss of organic matter occurs in the first few years of succession. In southern Illinois erosion as well as oxidation might be responsible for the initial loss of organic matter. Beginning with the third year (when broomsedge starts to invade abandoned fields) there is an increase in organic matter. Broomsedge not only forms a dense root system (Crafton and Wells, 1934), but its roots die and are replaced every two to three years (Rolfe, 1968). With the replacement of broomsedge by *Sassafras*, *Diospyros* and *Juniperus*, and a less dense herbaceous cover, there is again rapid oxidation and erosion of organic matter. With a buildup of surface soil litter in forest stages, the organic matter content of the top 15 cm. of soil again increases and reaches a new peak under the climax forest. Organic matter also tends to increase the amonut of water a soil can hold and the proportion of water that is available for plant growth (Buckman and Brady, 1971). With increases in the soil organic matter, there are also concomitant changes in field capacity and permanent wilting percentage, as well as available water. Broomsedge shows slightly better growth in soil containing organic matter, especially aster roots, then in soil with little organic matter (Keever, 1950).

This study confirms that the initial decrease in soil pH is the result of leaching of basic cations from the soil profile. During this pioneer stage, which is dominated by *Ambrosia artemisifolia*, *Digitaria sanguinalis*, *Erigeron canadensis*, *Aster pilosus*and *Panicum dichotomum* (Bazzaz, 1968), there is little replacement of organic matter. The forbs root fairly deeply and bring minerals from the deeper layers of the soil to the surface (Rice *et al*, 1960). The growth of these species on abandoned land probably increases the availability of mineral matter in the soil (Harper *et al*, 1934). Coile (1940) found an appreciable amount of calcium in *Aster pilosus*, but since this species is shallow rooted and dominant for only one growing season in southern Illinois (Bazzaz, 1968), there is insufficient time to bring large quantities of calcium to the surface. Eight year fields, which broomsedge dominates (Figure X), mark the lowest point in pH. Broomsedge tissues contain only traces of calcium (Durtman and Landinghans, 1930; Colie, 1940; Snider, 1946). The deeper rooted *Solidago nemoralis*, *Sassafras* and *Diospyros* may bring appreciable amounts of other basic cations to the surface, the result of which would be increases in pH (Coile, 1940; Bazzaz, 1963). Soil pH continues to increase until 18 years after abandonment, and then decreases slightly with the decrease in broomsedge.

This might be due to the invasion of trees of the climax forest, especially *Quercus* and *Carya*, and the release of organic acids by decomposition of leaf litter.

Soil pH, as an aspect of the mineral nutrition of grasses, has received only cursory attention. Bradshaw *et al* (1960) indicated that pH has a direct effect on plants, probably by affecting the ability of the plant to absorb calcium. In addition root growth of *Agrostis tenuis*was stimulated by low pH (Bradshaw *et al*, 1960). Previously Arnon and Johnson (1942) had shown a beneficial effect of high calcium in counteracting low pH. The secondary effects of high acidity or low pH in a soil are a shortage of available calcium and sometimes phosphate and molybdenum, and an excess of soluble aluminum, manganese and other metallic ions (Russell, 1968). The decomposition of the soil determines the relative importance of these factors, since it affects the level of available calcium, phosphate, aluminum or manganese (Russell, 1968).

Cation Exchange Capacity, or the total of exchangeable cations that a soil can absorb, tends to parallel changes in pH and organic matter. Leaching of exchangeable cations from the solum reaches a maximum in the three year old field (Fig. XI). Under the influence of *Aster*, *Solidago altissima* and *Solidago nemoralis* (Coile, 1940) cations are returned to the upper soil profile via the accumulation of litter. The C. E. C. continues to increase until litter from hardwood trees begins adding enough organic acids, around 40 years, to increase acidity. The result of an increase in acidity is an exchange of hydrogen ions for basic cations previously bound to the negatively charged colloidal cell micelle (Buckman and Brady, 1971), and subsequent leaching of the free cations. In later years, however, C. E. C. again rises. Ovington (1958) found that when conifer and hardwood stands are compared, the organic layers formed under conifers tend to be lower in basic cations than those under hardwoods. The litter of conifers breaks down rather slowly andthe cations are essentially lost from the mineral cycle. In addition, hardwood litter breaks down more rapidly, returning cations to the solum. Cation Exchange Capacity does not affect the distribution of plants directly since it is only an indication, one presumes, of the total quantity of elements available for plant nutrition.

Calcium and magnesium show an initial rapid decrease and begin to increase in the third year field (Fig. XII), that is, the beginning of the perennial grass stage. Succession to a shrub and bramble stage with Sassafras, Diospyros, Juniperus and sumac is marked by a decrease in calcium. The appearance of Cercis canadensis (redbud), oak and hickory, and the development of a more closed canopy and change in surface litter at about 40 to 60 years, marks the beginning of an increase in calcium. Magnesium decreases after reaching a maximum in the five year old field and varies under the influence of broomsedge, the shrub and bramble stage, and early tree stage.

Soil acidity has a pronounced affect on available calcium and magnesium. The secondary effect of increasing acidity is decreasing levels of available calcium (Russell, 1968). Following leaching of calcium (and probably magnesium) from the upper soil profile, during the annual weed stage, calcium levels again increase as Solidago, Sassafras and Diospyros return calcium and magnesium to the upper soil profile (Coile, 1940). Coile (1940) and Snider (1946) found only traces of calcium in broomsedge litter. The influence of deep rooted species such as Diospyros and Sassafras is not, however, sufficient to maintain high levels of calcium and magnesium as the cations again decline during the shrub and bramble stage. With a buildup of the litter of hardwood trees, calcium is again returned to the upper 15 cm.. Ovington (1958) concluded that afforestation increases loss of calcium from the surface mineral soil. It is generally believed that in the older climax forest, after litter has sufficient time to decompose, calcium and perhaps magnesium would tend to be higher in the forested than in unforested plots (Rolfe, 1968). The results seem to indicate this.

Low available calcium is one of the major consequences of soil acidity (Russell, 1968). Calcium and magnesium in a soil remain available until removed from the soil either by leaching or by being absorbed by the plant, and perhaps the only mechanism whereby calcium can become fixed in the soil is in combination with phosphate in mildly acid to alkaline soils (Russell, 1968). A high level of calcium depresses the uptake of magnesium and potassium (Russell, 1968). Calcium and magnesium are generally regarded as macronutrients, that is, are used by plants in relatively large amounts. Calcium acts as a cofactor in some reactions and, in addition, as calcium pectate is a major structural component of plants (Salisbury and Ross, 1969). Calcium is also essential for the growth of meristems and particularly for the proper growth and functioning of root tips (Russell, 1968). When deficient, calcium may have an indirect effect on plants by allowing other substances to accumulate in the tissues so much that they may either lower the vigor or actually harm the plant (Russell, 1968). In small quantities calcium ions antagonize the potentially toxic effects of potassium and sodium ions (Salisbury and Ross, 1968). Coile (1940) and Snider (1946) found small amounts of calcium in broomsedge. Coile (1940) noted that "broomsedge examined contained insufficient calcium for reliable quantitative measurement." In addition broomsedge is found growing on acid soils, and an acidic pH might affect plants by effecting their ability to absorb calcium (Bradshaw <u>et</u> <u>al</u>, 1960). Nixon and McMillan (1946) studied the role of soil in the distribution of <u>Andropogon</u> <u>scoparius</u>, and concluded that races of little bluestem have become physiologically differentiated in their ion uptake and/or utilization thus allowing the species to occupy bothacidic and calcareous soils. English researchers have also investigated the interaction betweeb calcium and pH. A calcoile is a plant growing in soil rich in calcium, while an acidophilous plant grows best on acid soils with relatively low levels of calcium (Clymo, 1962). Acidophilous species apparently avoid soils of neutral or basic pH and high calcium supply, but the effect of these factors is not sufficient to cause their total exclusion from calcareous soils (Steele, 1955). Broomsedge may be such an acidophilous species, which is more susceptible to the toxic effects of aluminum, manganese and sodium on root growth, since lacking sufficient calcium it cannot counteract the toxic effects of these metallic ions.

The effect of reduced levels of magnesium has not been extensively investigated. Magnesium is a constituent of chlorophyll, and also seems to be important in the transport of phosphates in the plant (Russell, 1968). Deficiencies in magnesium may seriously affect the plant's ability to synthesize chlorophyll, and in plants subjected to reduced light intensities, less than optimum chlorophyll levels may seriously effect a plant's ability to produce enough photosynthate to maintain life. Magnesium may be important as a limiting factor where increased magnesiumlevels are needed, that is, under a developing forest canopy. Reduced magnesium may therefore affect broomsedge plants growing in the shrub and bramble and tree stages.

Plants absorb phosphorusalmost exclusively as inorganic phosphate ions, probably principally as the $H_2PO_4^-$ ion (Russell, 1968). Plants are relatively inefficient users of phosphate in the field, since rarely more than 20 to 30 percent of the amount supplied as fertilizer is taken up (Russell, 1968). The remaining percentage would probably be leached from the soil since the anion is not bound to the anionic colloidal soil micelle. The field currently in corn had approximately 220 pounds/acre of 45% superphosphate and 200 pounds/acre of potash applied (McKibben, 1972). In indication that plants are inefficient users of phosphorus is that the level of the ion drops off sharply after abandonment indication that much is leached from the soil profile. Annual weeds and perennial grasses tend to return phosphorus to the upper 15 cm., thus there is still a net loss even in the broomsedge stage since the levels decline. Increasing litter from hardwood trees probably adds phosphorus to the upper horizons to a moderate degree.

With the possible exception of nitrogen no other element is as critical in the growth of plants in the field as is phosphorus. Phosphorus is important for celldivision, fat and albumin formation, flowering and fruiting, seed formation, root development, and resistance to diseases. The ion is a major constituent of phospholipids, adenosine triphosphate and nucleic acids. The availability of inorganic phosphate is determined by (1) soil pH, (2) soluble iron aluminum and manganese, (3) available calcium and other calcium minerals, and (4) amount and decomposition of organic matter. In an acid mineral soil with some soluble iron, aluminum and manganese, reactino with $H_2PO_4^-$ ions occurs, rendering the phosphorus insoluble and also unavailable for plant growth. As pH increases from 4.0 to 6.5 the amount of phosphorus available increases, that is, less phosphate is rendered insoluble as hydroxyphosphates (Buckman and Brady, 1971).

Phosphorus has often been implicated as an important factor in the timing of invasions of plants. Allard (1942) stated that the lack of essential nutrients, and particularly available phosphorus could prevent normal succession. In that study a lack of available phosphorus eliminated the broomsedge stage of succession. Allard believed that a lack of available phosphorus was even more inhibiting to the successful establishment of a closed vegeation cover than a lack of nitrogen alone. Bradshaw _et al_ (1960) showed that plants of acid, base-poor soils do respond to varying levels of phosphorus. Rice _et al_ (1960) showed that the order in which triple awn grass, little bluestem and switch grass invade abandoned fields is based on increasing requirements for nitrogen and phosphorus. In the Transvaal Highveld of South Africa, however, Roux and Warren (1963) showed that, as succession proceeds, nitrogen and phosphorus requirements decrease. The differences may be due to differences in the amount of soil remaining after abandonment. In Rice's Oklahoma study area, abandoned soils are severely leached and the uppermost horizon may even be a hardpan surface. Transvaal soils, however, usually have some topsoil left. This is a significant difference in conditions, and since invading species have had to adapt to the conditions present, this could account for the different trends in phosphorus levels.

Crafton and Wells (1934) reported that broomsedge has such a slow growth rate, that it often takes plants two years to mature. In soils with low phosphorus supplying ability, colonizers usually have an inherently slow growth rate which may be a significant adaptive feature (Clarkson, 1968). This may allow species to invade areas low in available phosphorus.

Nitrogen is essential for plant growth as it is a constituent of all proteins and hence all protoplasm. It is generally taken up by plants either as ammonium or as nitrate ions, but the absorbed nitrate is rapidly reduced, probably to ammonium, through molybdenum containing enzymes (Russell, 1968). Ammonium ions, which are positively charges, are readily held to the anionic colloidal soil micelle. Nitrate ions are negatively charged, and if not absorbed by plants, are soon lost. NH_4 shows a decrease in the first few years of succession (Fig. XIV), a small increase at about five years and then a decrease through most of the broomsedge stage of succession. With the succession to tree species, ammonium ions again increase. Nitrate (Fig. XIV) shows a similar decrease, then an increase to a maximum in the eight year old field and a steady decline while broomsedge is present. Nitrate ions increase under the influence of the shrub and bramble stage, and remain steady through climax forest.

The nitrogen cycle is an interlocking succession of biochemical reactions. Much of the nitrogen added to the soil undergoes many transformations before it is removed. Proteins and other nitrogenous compounds are converted to ammonia and ammonium compounds to nitrates and then to nitrites. The levels of nitrate and smmonium compounds have been shown to be important in plant succession. Rice *et al* (1960) showed that the order in which grasses invade abandoned fields in Oklahoma was determined by phosphorus and nitrogen. Roux and Warren (1963) and later Warren (1965) showed opposite trends, namely that the ruderal and primary grass stages are most tolerant of high nitrogen concentrations, and that nitrogen requirements decrease as succession proceeds. Warren (1965) also found that: (1) deammonifying bacteria show a decrease in numbers as succession advances, (2)nitrate oxidizing bacteria also decrease in numbers as succession advances and are almost absent in the perennial grass stage and almost completely absent in climax grassland, (3) the numbers of aerobic nitrogen-fixing bacteria increase with an advance in succession, (4) anaerobic nitrogen-fixing bacteria are more generally distributed in soils of the different stages of succession, and (5) nitrites and nitrates decrease as succession progresses toward climax and have low values in climax communities. There is also growing evidence that populations of nitrifers and nitrification may decrease as succession progresses towards climax forest (Muller et al, 1971). Low rates of nitrification may be a characteristic of some climax vegetation and may be an evolutionary response associated with a conservation of soil nitrogen since excess amounts are leached from the soil (Muller et al, 1971; Rice, 1971).

Phenolic compounds secreted by plants, which are by-products of their metabolism, seem important in inhibiting not only soil microorganisms but also inhibit other angiosperms (Rice, 1965; Bucholtz, 1971). Bucholtz has indicated that an aspect of this allelopathic response may be a reduction in plant growth. Reduction in absorbing root area, and reduction in absorptive capacity of roots for nutrients may be operative in reducing the accumulation of optimum or even adequate amounts of minerals (Bucholtz, 1971). Some phenolic compounds are also protein precipitants and may inhibit or kill microorganisms through this mechanism (Rice, 1965). It appears possible, then, that plants growing in soils already low in nutrients would be even more severely harmed if their ability to accumulate necessary nutrients was limited by allelochemics (toxic phenolic compounds produced by other plants). In view of this action of allelochemics on other plants, Whittaker (1971) has stated that allelopathic effects may influence sequence and timing of succession by: (1) the speeding of the replacement of succession of one species by the allelopathic suppression exerted by an invading species, (2) speeding replacement of one species by another through self-allelopathic effects, (3) slowing species replacement by direct allelopathic effects, by indirect effects through decay products, or by inhibition of soil organisms, and (4) influence of what species can replace a given species, by the allelopathic effects of the later on invaders.

Rice (1964) has shown that extracts of Andropogon scoparius are inhibitory chiefly to the nitrifying bacteria. Since levels of nitrate ions decrease as broomsedge assumes dominance of old fields, it seems logical that this species also produces similar allelochemics. Broomsedge may be able to assume dominance partly through the production and effects of these compounds, but increasing amounts of the chemicals may influence its ability to obtain necessary nutrients. Broomsedge may also, in part, eliminate itself through a self-allelopathic effect.

Sodium and potassium ions exhibit a decrease in newly abandoned fields (Figs. XV and XVI). Potassium increases until reaching a maximum in 40 year old fields. Sodium exhibits several oscillations but also decreases after 40 years. Potassium appears to be important in the synthesis of amino acids and proteins from ammonium compounds, while sodium does not appear to be an essential element (Russell, 1968). There is little evidence that potassium or sodium is important in plant succession. Rice et al (1960) found that potassium was not important in determining the order in which species invade abandoned fields. Usually potassium, unless a plant's ability to absorb the element is inhibited, is present in adequate quantities.

Iron, aluminum and manganese are three elements that are either needed in relatively small amounts (iron and manganese), or have no known value for plant nutrition (aluminum). Under the influence of increasing soil acidity these three metallic ions increase (Figs. XVII and XVIII). Decreasing soil acidity generally renders them less available although a lag phase may be involved. These determinations for at least aluminum and manganese show that one of the secondary effects of high acidity are an excess of iron, aluminum and manganese, as well as other metallic cations, and are in agreement with Russell (1968). Excess manganese accumulates in all tissues and interferes with their proper metabolism, while excess aluminum accumulates in the roots and may reduce very considerably their ability to translocate phosphates from the soil to the vascular system (Russell, 1968). Aluminum provides a barrier to the establishment of young seedlings in acid soils. At critical concentrations in the soil the inhibition of the root growth of seedlings makes the young plants vulnerable to desiccation (Clarkson, 1966). Calcium seems to enable a plant to withstand the toxic effects of these metallic cations (Russell, 1968). Plants, such as broomsedge, which are low in calcium may be very sensitive to increased concentrations of these ions. In the later years of the broomsedge stage of succession, especially eight through eighteen years, broomsedge seedlings may be subjected to reduced vigor through the actions of these cations.

SUMMARY

The old-field ecosystem presents an orderly sequence of changes which eventually reach a stable, self-reproducing climax. Many factors are, however, at work in producing these changes. This study has, for the first time, documented the cycling of nutrients in the annual weed, perennial grass, shrub and bramble and tree stages. Broomsedge apparentle is able to establish itself only in fields of low fertility, and the species of the annual weed stage are probably less able to survive thereafter due to reduced quantities of available nutrients. This acidophilous species is also able to gain control of the old-fields through the production of compounds inhibitory to soil microorganisms and old-field plants sensitive to their actions. Broomsedge is often eventually present in almost pure stands. The allelochemics released into the soil prevent establishment of other species, and eventually begin to exert an autotoxic effect.

Increasing levels of metallic cations probably seriously affect young broomsedge seedlings and reduce their vigor. Their effects are compounded since the plant is not able to absorb calcium in quantities sufficient to counter their toxic effects due to the allelochemics present. These allelochemics seriously impair the ability of the plants to metabolize efficiently, and the decreased amounts of other essential nutrients due to the effects of the metallic cations also adversely effect the plants. Mortality of broomsedge plants under stress increases and species which can tolerate the toxic phenolic compounds present, and probably require greater amounts of nitrogen, phosphorus, calcium and magnesium are able to invade old-fields. Once established in almost pure stands broomsedge was able to shade out seedlings of other species. With increasing numbers of taller shrubs and trees, broomsedge is now subjected to shading. Low magnesium in the upper 15 cm. of soil may effect the plant's ability to synthesize increased amounts of chlorophyll needed to utilize reduced light intensities. Broomsedge eventually disappears from the successional picture as a result of conditions in part created by itself.

The species present in the stages of succession are not just random selections of organisms that happen to be in the vicinity. Rather the stages of succession and their component species are the result of a long evolutionary process. Succession represents a series of niches into which certain species have become adapted. The adaption of a species to a particular stage of succession depends on its ability to compete with other species in regard to light, available water, soil minerals, allelochemics and also to its successful reproduction, including germination and seed availability. Even though these species are apparently well adapted to a particular stage, they eventually create changes which make the habitat less suitable for them and more suitable for

for other species. Succession is thus a dynamic process.

Broomsedge is probably slowly increasing its range in Illinois. It is not able to become a member of the successional picture, however, until it can compete successfully with other species already established. The area of Wisconsinan glaciation presents a barrier which broomsedge is not yet able to bridge since it is less able to compete with species on more fertile prairie soils.

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