A PHYTOSOCIOLOGICAL STUDY OF LOWLAND HARDWOOD FORESTS IN SOUTHERN WISCONSIN

A thesis submitted to the Graduate School of the University of Wisconsin in partial fulfillmemt of the requirements for the degree of Doctor of Philosophy.

by

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Date August 1, 1955

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INTRODUCTION

"Go directly to the vegetation" is an admonition frequently expressed by those who have been confronted with decisions concerning approaches to ecological work. The impossible task of describing environmental complexes and of making habitat analyses virtually commands that the recognition and definition of plant communities take first place (Cain 1947). As long ago as 1877, T. C. Chamberlin, an eminent Wisconsin geologist, pointed out that the experiments of nature furnish us in the native vegetation a correlative index of such agricultural influences as soil, climate, topography, drainage, and underlying geologic formations. Braun Blanquet (1932) asserts that "the more sharply we have sought to delimit the problem of habitat the more complicated and involved it has become. The effective external factors are so numerous and so variable, the possible combinations so manifold, the overlappings so frequent that a clear and unequivocal delimitation of habitats according to operative external factors appears quite unattainable." By going to the vegetation itself we arrive at a logical starting point for ecological investigation.

Recent ecological studies in Wisconsin have been based on the reasoning that sociological investigations of constituent species and their numerical relations should precede autecological studies if the latter are to have maximum meaning (Curtis and McIntosh 1951). Regional quantitative studies of plant communities form a stromatal matrix to which more intensive local phytosociological studies and

autecological studies can be tied. It is, of course, a systematic approach which tends to eliminate the inefficiency of haphazard and scattered ecological work. This same approach seems to be the goal of those concerned with various phases of regional work, for frequent appeals have been made by geographers for systems which enable students to work cumulatively and to build upon what has been produced by previous workers (Russell 1949, Hartshorne 1950). Though regional work of great areal extent can often constitute scarcely more than a survey, the benefits reaped from a reasonably accurate over-all picture more than overcome the shortcomings associated with any apercu features of the work.

To date phytosociological work on a number of Wisconsin communities has been completed using quantitative methods which employ large numbers of stands. The upland hardwood forests of southern Wisconsin (McIntosh 1950), the upland conifer-hardwood forests of northern Wisconsin (Brown 1951), and the beech forests of eastern Wisconsin (Ward 1954) have been the objects of investigations which have given us regional views of upland Wisconsin forest communities. In addition Bray (1955) has recently completed a study of widespread oak opening communities in southern Wisconsin. The investigations of Christensen (1954) of the lowland areas of northern Wisconsin treat problems which are somewhat similar to those encountered in this present study. Gilbert's (1953) work on upland forest herbs, Anderson's (1954) investigation of dry lime prairies, Natelson's (1954) study of aquatic communities, Jones' (1955) work on tamarack bogs, and Goder's (1955) treatment of hemlock forests serve to demonstrate the diversity of

communities in which problems have been attacked by quantitative phyto-sociological methods.

The vegetation presently under consideration is that comprising hardwood forests of landscape features variously designated as lowlands, bottomlands, riverbottoms, swamps, floodplains, alluvial plains, and lake flats. All of these terms refer primarily to topographic features except the term "swamp" in which both topographic and vegetational characteristics are implied. A swamp is considered to be a woody community occurring in an area where the soil is inundated or saturated during part of the growing season. The term "marsh" is considered to be a general designation for a wetland grass-sedge-rush community. The accumulation of peat is a phenomenon which may occur under proper conditions regardless of the life form of the plants in the wetland community. The term "bog" implies accumulation of peat, and naturally there are transition stages between bogs and swamps (Transeau 1903, Gates 1911, Waterman 1923, Sampson 1930b, Buell 1939) and between bogs and marshes (Sears 1926, Transeau 1930 b).

Topographic features which are low and flat in comparison to surrounding terrain not only receive the rainfall runoff from higher landforms but also offer less gradient and thus tend to impede or to impound the runoff water. Any depression in the landscape whether it be presently occupied by a lake, bog, marsh, wet prairie, or swamp, is in some stage of extinction either by filling or by downcutting of its outlet. The origin of wetland features of the landscape is of secondary importance as far as the vegetation is concerned according to Clements (1928) who maintains that "deposition in the bed of a stream is very

similar to that in the bed of a lake, a similarity that becomes an identity when a stream is ponded anywhere in its course." The real factors affecting vegetational development lie in the materials and the water relations of the deposits. The origins of the lowland communities in the present study are quite diverse and in many cases somewhat obscure. The riverine or fluvial swamp origins are generally clearer than the origins of swamps now found on old lake beds, the latter here designated as lacustrine swamps (Thwaites 1950). Since there are always streams traversing extinct lake beds any distinction between fluvial swamps and lacustrine swamps can sometimes become quite meaningless. The synthesis of data from all lowland forest stands sampled is attempted in this study because separation of fluvial and lacustrine swamps is frequently not practicable and because it is felt that synthesis of all lowland forest data should precede such a separation.

The marked vicissitudes of larger streams subject fluvial swamps to moisture fluctuations of proportions scarcely equalled in swamps of lacustrine origin. Fluvial swamps owe their existence to the abandonment of channels, to frequent overflow and inundation, and to the maintenance of saturated or exceedingly moist soil for considerable periods by direct action of a stream with continuous flow. A commonly encountered floodplain feature is a slough stretching along the foot of a terrace or a bluff, separating the floodplain from the higher land. Between the slough and the main channel of the river lie relatively level alluvial deposits which are always slightly higher toward the bank of the active channel.

It has long been known that the deeper parts of lakes tend to accumulate clay sediments which may effectively seal the bottom of the lake as the clay layers grow thicker. Studies in northern Wisconsin (Broughton 1941; Juday and Meloche 1943) show that lake basin seal can be convincingly demonstrated in existing lakes. The water in certain lakes treated in these northern Wisconsin studies is significantly different chemically from the ground water of the land immediately surrounding these lakes. Lakes short distances from each other show marked differences in water level, explicable only by lake basin seal. Extinct lakes with quantities of inorganic or vegetal filling are frequently underlain by relatively impervious clay strata (Weld 1904, Pettee 1905). Even where superficial swamp characteristics are no longer apparent soil borings sometimes show a layer of clay within a few feet of the surface (Wilde 1940).

It appears that the manner in which the wetland condition is maintained is the essential difference between a fluvial swamp and a lacustrine swamp. Alluvial deposits may be deep and porous and yet inundated or saturated soil condition, attributable to activity of the nearby river, may be maintained. The maintenance of wetland conditions in a swamp of lacustrine origin can usually be ascribed only to impeded drainage. Indeed there are some swamps in eastern Wisconsin which have been called "upland swamps" (Bruncken 1902) because of the relatively elevated position of the swamp in relation to surrounding terrain. These might be described as saucer-like depressions on hills where moisture conditions are affected by a clay seal which effectively impedes drainage. A swamp of this sort will eventually become extinct by down-

cutting of the outlet; undoubtedly countless thousands of such upland depressions have already been drained.

Wisconsin swamps lie at elevations of several hundred feet above sea level and are geologically ephemeral features in comparison to swamps of the Gulf Coast region (Malott 1928) where changes are proceeding slowly at elevations near sea level in contrast to the relatively rapid downcutting and draining of the more elevated Wisconsin landscape (Braun 1950). Whereas the Gulf Coast seems to be slowly sinking (Russell 1936, Penfound 1952), there appears to be continuing natural improvement of drainage in Wisconsin and adjacent states with multitudinous gradations of drainage conditions on lowland sites (Hewes 1951, Hewes and Frandson 1952).

DESCRIPTION OF THE REGION

Location and Limits

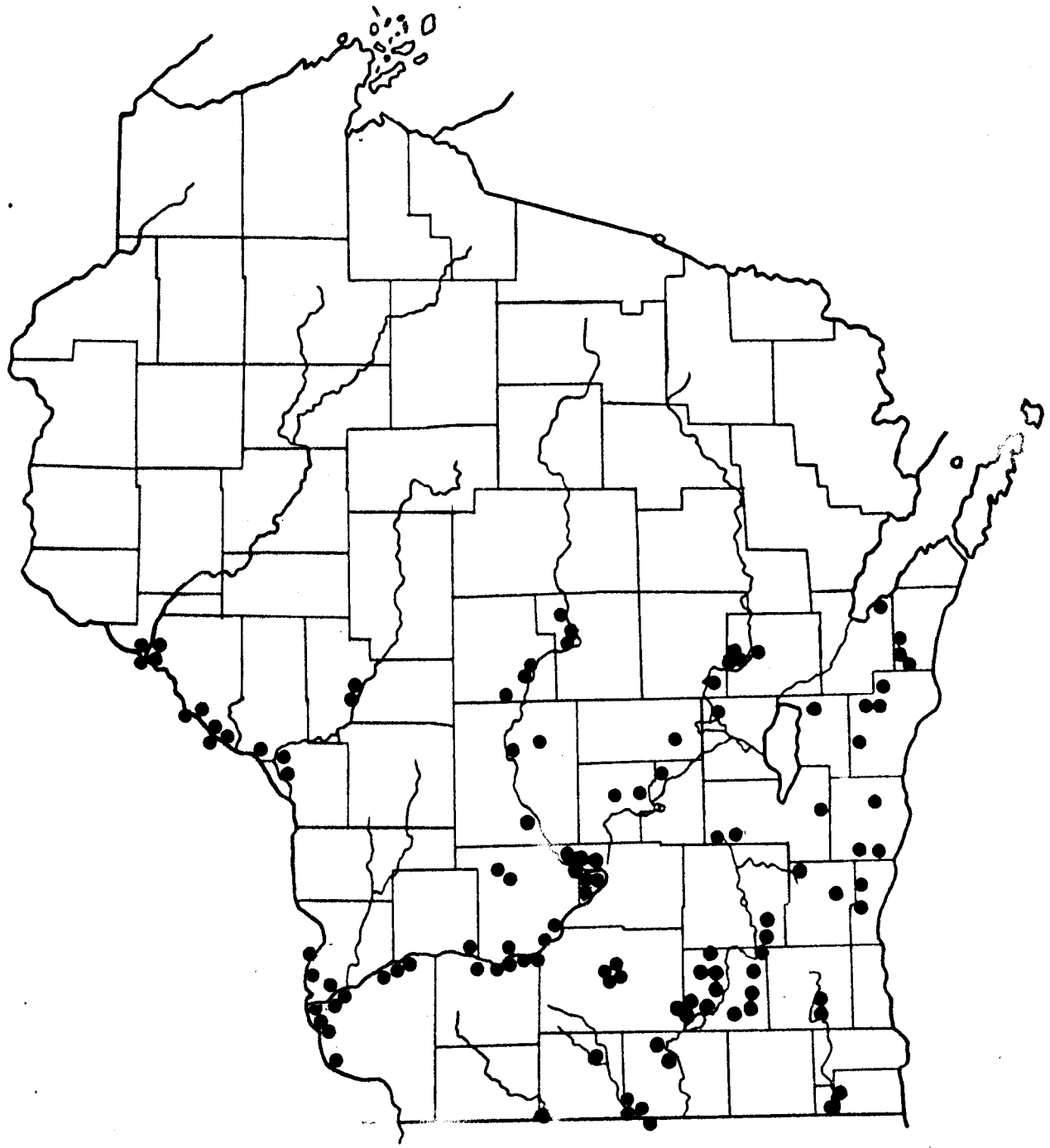
The regional extent of the study area is shown by the mapped stand locations in Figure 1. The concentrations of stands along major rivers are especially apparent as shown by the northward extensions on the map. Territory showing a paucity of stands represents country of an upland nature. The scattered stands in eastern Wisconsin are generally associated with smaller streams. A few stands in northern Illinois are included in the study since they are located on streams which also drain much of southern Wisconsin. The limits of the region studied have thus been determined more by the actual occurrence of lowland hardwood forests along drainage systems than by political boundaries.

Geology

The deposits of the various glacial advances into Wisconsin have left surficial features on which, from a geologic standpoint, erosion processes have scarcely begun to work. On the other hand, dissected Driftless Area has been subject to weathering and erosion for hundreds of thousands of years. Glaciated Wisconsin offers innumerable poorly drained places for study, the Driftless Area far fewer.

Studies of bedrock geology frequently contribute to the solution of problems concerning the nature and configurations of the vegetational substrate even when a mantle of glacial drift is present. As shown on

FIGURE 1. Map of stand locations.



the accompanying maps (Figures 2 and 3) the large area of pre-Cambrian rock in the northern part of the state constitutes the highest section in the state. The various Paleozoic strata dip generally southward from the great pre-Cambrian core of northern Wisconsin. In the vicinity of Lake Michigan the dip is both eastward and southward, and in the western part of the state the dip is somewhat westward and southward. The dip of the strata of sedimentary rocks determines the original general direction of stream flow, with modifications of drainage patterns effected by stream work on various strata with differential resistances to erosion (Durand 1925). Stream patterns shown by Figure 6 greatly modified by glacial deposition, still exhibit the general directions of flow which follow the dip of the sedimentary strata.

The sedimentary strata which underly Wisconsin are all Paleozoic in age, ranging from Cambrian sandstones to Devonian shale. The surface exposures of the strata form overlapping belts which appear as irregular V-shaped bands around the pre-Cambrian core (Figure 2). The more rapid erosion of exposures of weaker bedrock has left sharp slopes or escarpments where the visible edges of the more resistant strata overlap the weaker formations. These escarpments form in part the basis for division of the state into geographical provinces (Martin 1932).

Geographical Provinces

The geographical provinces of Martin are shown in Figure 4. The Eastern Ridges and Lowlands Province has been further divided by the indication on the map of the Niagara Escarpment. The upland belt east of the Niagara Escarpment is drained by a series of short streams which

FIGURE 2. Map showing bedrock geology of Wisconsin.

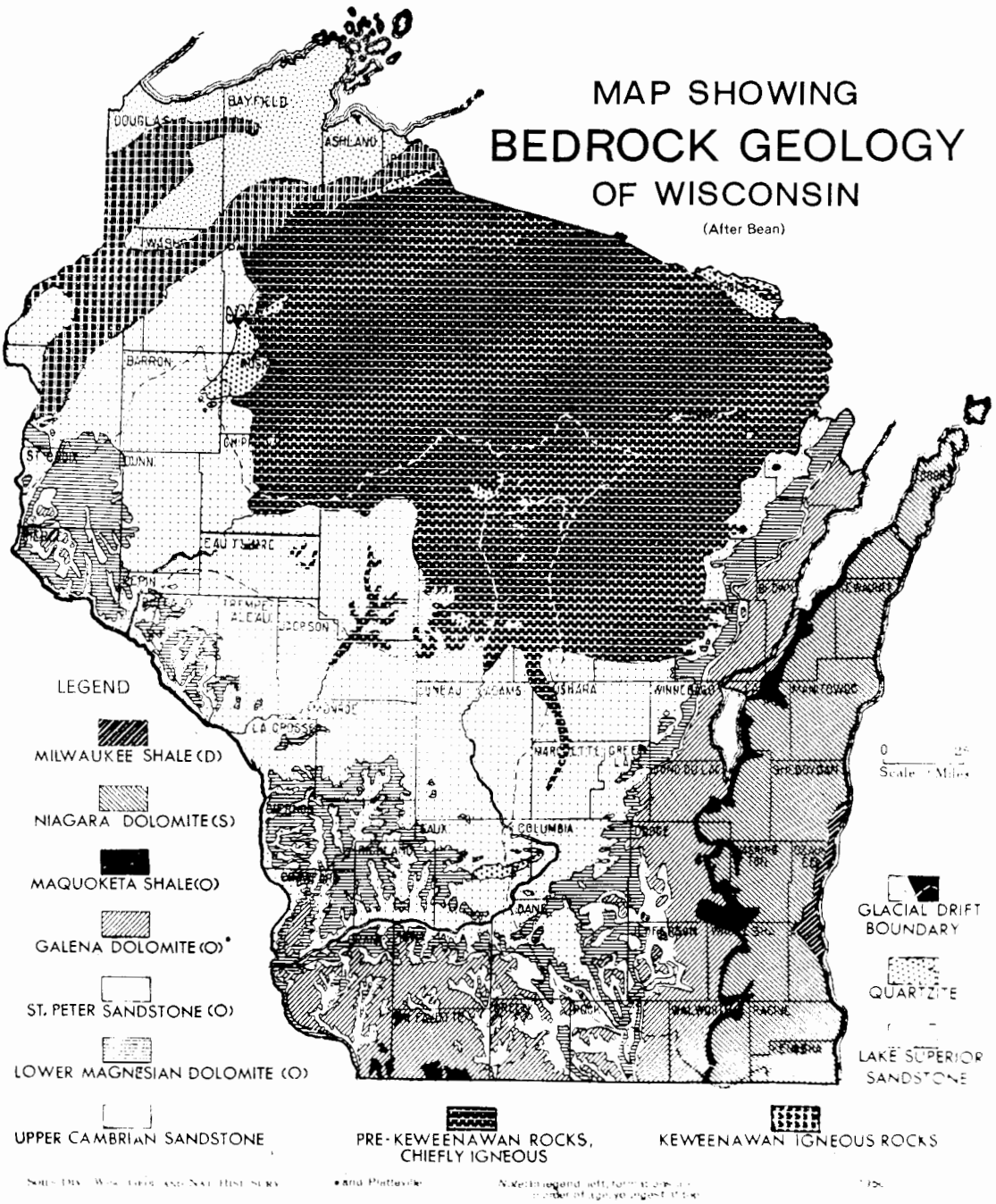

MAP SHOWING
BEDROCK GEOLOGY
OF WISCONSIN
(After Bean)
BAYFIELD
DOUGLAS
ASHLAND
BARRON
DUNN
LEGEND
MILWAUKEE SHALE (D)
NIAGARA DOLOMITE (S)
MAQUOKETA SHALE (O)
GALENA DOLOMITE (O)*
ST. PETER SANDSTONE (O)
LOWER MAGNESIAN DOLOMITE (O)
UPPER CAMBRIAN SANDSTONE
PRE-KEWEENAWAN ROCKS, CHIEFLY IGNEOUS
KEWEENAWAN IGNEOUS ROCKS
GLACIAL DRIFT BOUNDARY
QUARTZITE
LAKE SUPERIOR SANDSTONE
Scale - Miles

FIGURE 3. Contour map of Wisconsin.

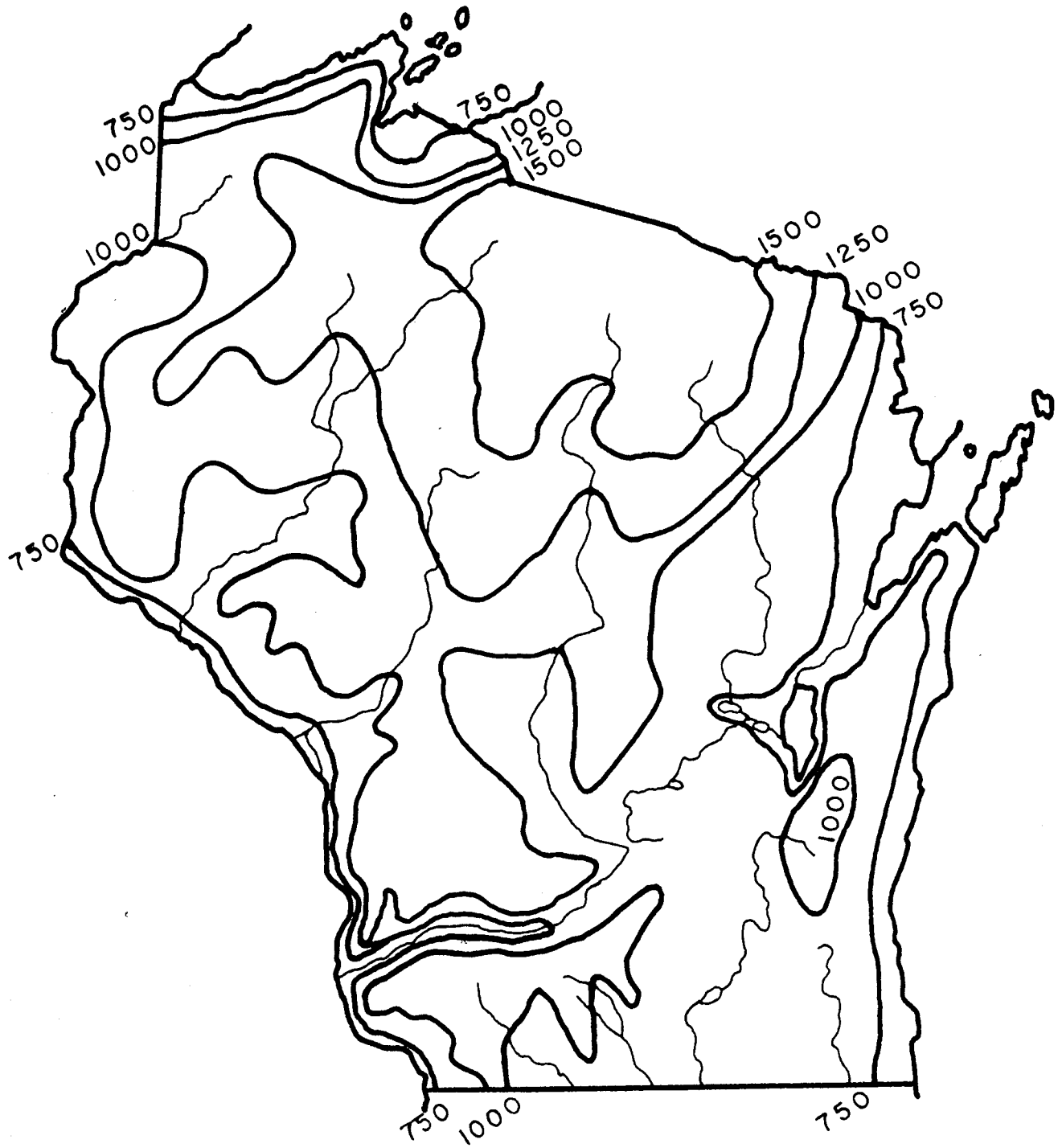
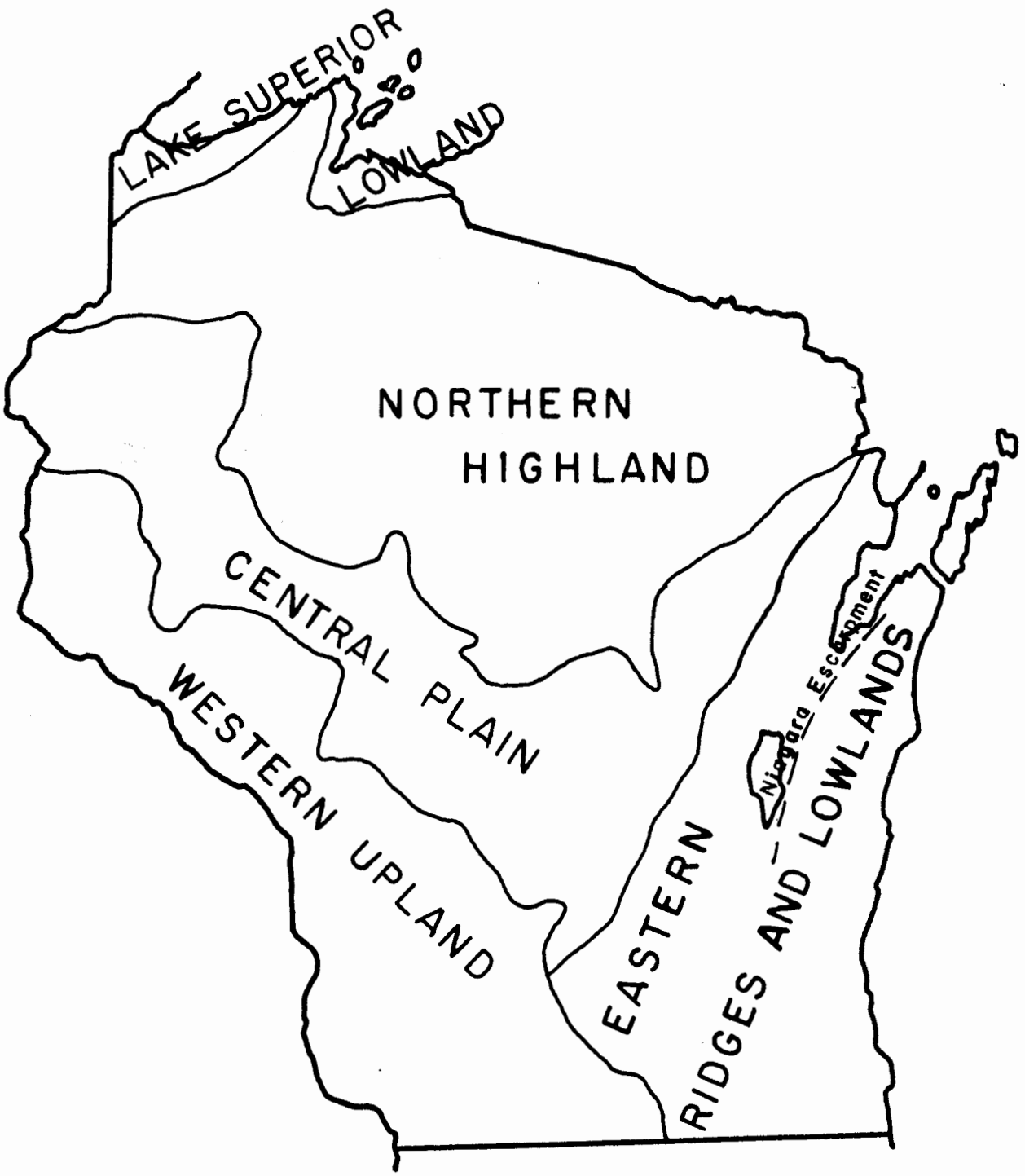

750
1000
1000
750
750
1000
1250
1500
1500
1250
1000
750
750
1000
750
1000

FIGURE 4. Geographical provinces of Wisconsin.


LAKE SUPERIOR LOWLAND
NORTHERN HIGHLAND
CENTRAL PLAIN
WESTERN UPLAND
EASTERN RIDGES AND LOWLANDS
Niagara Escarpment

flow into Lake Michigan. Immediately adjacent and to the west of the Niagara Escarpment is a belt of lowland which Martin refers to as the Rock River-Lake Winnebago-Green Bay Lowland. Still another belt of the Eastern Ridges and Lowlands Province is the Magnesian Upland belt immediately adjacent to the Central Plain, separated from the latter by an escarpment which overlooks the lowlands. This same feature, known as the Magnesian Escarpment, also separates the Central Plain from the Western Upland, where the resistant Ordovician dolomites lie high above the lowlands of the Central Plain in an exceedingly irregular line of cliffs and sheer-faced hills. Thus the Magnesian Escarpment overlooks the lowlands of the Central Plain as a huge irregular V, extending from northwestern Wisconsin southeastward to Columbia County and northeastward to the northeastern part of the state where it virtually disappears in the glacial drift.

Considerable evidence indicates that pre-glacial stream work in Wisconsin, which sculptured the topographic differences on which Martin's geographical distinctions are based, featured a series of rivers radiating outward from the Northern Highland. These rivers had greatly reduced the regional level of the Central Plain by the time that the glacial advances began to modify the bedrock topography. Pre-glacial rivers which drained the Central Plain crossed the upland belts in deep narrow valleys. Some examples are the Chippewa, Black, and Wisconsin Valleys. A pre-glacial gorge crossing the Door Peninsula at Sturgeon Bay probably represents a remnant of a former stream course flowing eastward from the Northern Highland (Martin 1932).

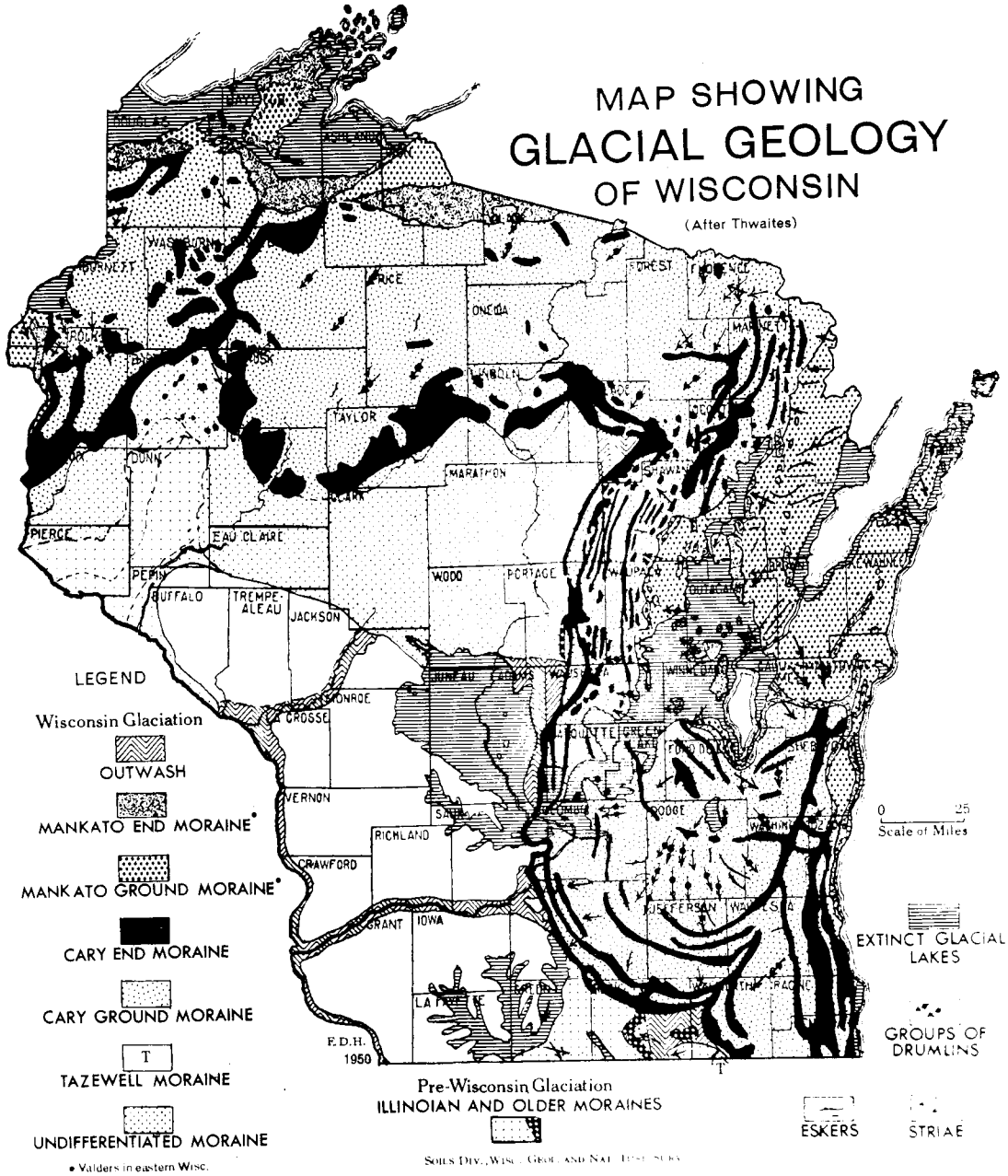
Glaciation

The various continental glaciations which have left their mark on the state are outlined in Figure 5. Thwaites (1950) lists the following classification of glaciations and interglacial intervals:

	Mankato glaciation
	Valders glaciation
	Two Creeks interstadial
Wisconsin glaciation	Cary glaciation
	Tazewell glaciation
	Peorian interstadial
	Iowan glaciation
	Sangamon interglacial interval
Illinoian glaciation	
	Yarmouth interglacial interval
Kansan glaciation	
	Aftonian interglacial interval
Nebraskan glaciation	

The subdivisions of the Wisconsin glaciation are as yet imperfectly known. The Valders and the Mankato substages may be essentially of the same age. The Valders is made up of drift left by an ice invasion which stagnated rather quickly. The high content of clay in this "red drift" came from lake clays plowed up by the glacial advance. These clays contain a high content of iron oxide originally derived from the red rocks of Lake Superior. Martin (1932) points out how topographic influences have played an important role in the direction and extent of various glacial advances. The resistant Niagara dolomite of the Door Peninsula area apparently split the advances of the Cary Substage, causing separate general movements distinguished as the Green Bay Lobe and the Lake Michigan Lobe. The Northern Highland evidently formed a

FIGURE 5. Map showing glacial geology of Wisconsin.


MAP SHOWING
GLACIAL GEOLOGY
OF WISCONSIN
(After Thwaites)
LEGEND
Wisconsin Glaciation
OUTWASH
MANKATO END MORAINE*
MANKATO GROUND MORAINE*
CARY END MORAINE
CARY GROUND MORAINE
T
TAZEWELL MORAINE
UNDIFFERENTIATED MORAINE
* Valders in eastern Wisc.
Pre-Wisconsin Glaciation
ILLINOIAN AND OLDER MORAINES
SOILS DIV., WISC. GEOL. AND NAT. HIST. SURV.
F.D.H.
1950
0 25
Scale of Miles
EXTINCT GLACIAL LAKES
GROUPS OF DRUMLINS
ESKERS
STRIAE
PIERCE
PEPIN
EAU CLAIRE
BUFFALO
TREMPE-ALEAU
JACKSON
TAYLOR
CLARK
MARATHON
WOOD
PORTAGE
PRICE
ONEIDA
FOREST
MARINETTE
VERNON
CRAWFORD
RICHLAND
GRANT
IOWA
DODGE
JEFFERSON

barrier which furnished protection to some of the region south of it so that a non-glaciated section of the state was fortuitously preserved. At the same time easier paths of movement both to the east and to the west of the Driftless Area perhaps diverted the ice from this section. The uplands of the Driftless Area display distinctive features of dissected, non-glaciated country. Such is not the case in lowlands of the Driftless Area where effects of glaciation are frequently apparent. Outwash partially filled the valleys of the major streams; an extensive glacial lake was created in non-glaciated central Wisconsin; lakes and swamps were left where tributaries were dammed by the outwash along major streams; and sheets of outwash spread out from the margins of the melting ice masses (Hansen 1933).

One of the most important aspects of glaciation and its effect on the topography of Wisconsin was the creation of several large glacial lakes. Thwaites (1943) describes two glacial lakes, existing at different times but occupying essentially the same territory, in the Fox and the Wolf Valleys (Figure 5). Concomitant with the retreat of the Cary ice, a great marginal lake was formed in the present Fox River Valley with an outlet into the Wisconsin River near Portage. As the ice of the Cary lobe melted back still farther the present Wolf River Valley became part of this great lake, known as Early Glacial Lake Oshkosh. The lake was drained when the lower Fox River area was cleared of ice. With the advance and retreat of the Valders substage, Later Glacial Lake Oshkosh was formed. The maximum determinable extent of each of these marginal lakes seems to be about the same. Expanses of flat country with numerous marshes, bogs, and swamps in the lower Wolf River Valley can be traced to the great marginal lakes discussed above.

The advance of the Cary substage filled and obliterated much of the course of the pre-glacial Wisconsin River in central Wisconsin. The melting and retreat of the Cary ice created Glacial Lake Wisconsin in the Central Plain Province. (Figure 5). The moraines left by the Cary ice continued to impound the waters of Glacial Lake Wisconsin until an outlet was carved from sandstones forming the southeastern border of the lake. The gorges formed by the river action are known as the dells of the Wisconsin River (Van Hise 1895). The poorly drained nature of vast tracts in central Wisconsin can be traced to the huge extinct glacial lake and the lake clays left by it.

In the valleys of the Sugar and the lower Pecatonica Rivers (the latter in northern Illinois) a glacial lake was formed by the Illinoian ice front blocking a common outlet of the two rivers (Thwaites 1950). Exposed sections along the Pecatonica show a deposit of block loamy alluvium underlain by several feet of bluish, laminated, non-calcareous clay. Most of the filling of the Sugar and Pecatonica Valleys has been ascribed to the work of Illinoian glaciation; however considerable silt, sand, and even outwash gravel have been washed into the valleys since the Illinoian (Alden 1918).

Drainage

The description of rivers and lakes of Wisconsin necessarily requires reference to the topographic and geologic features previously noted. Regional relief has been largely determined by pre-glacial

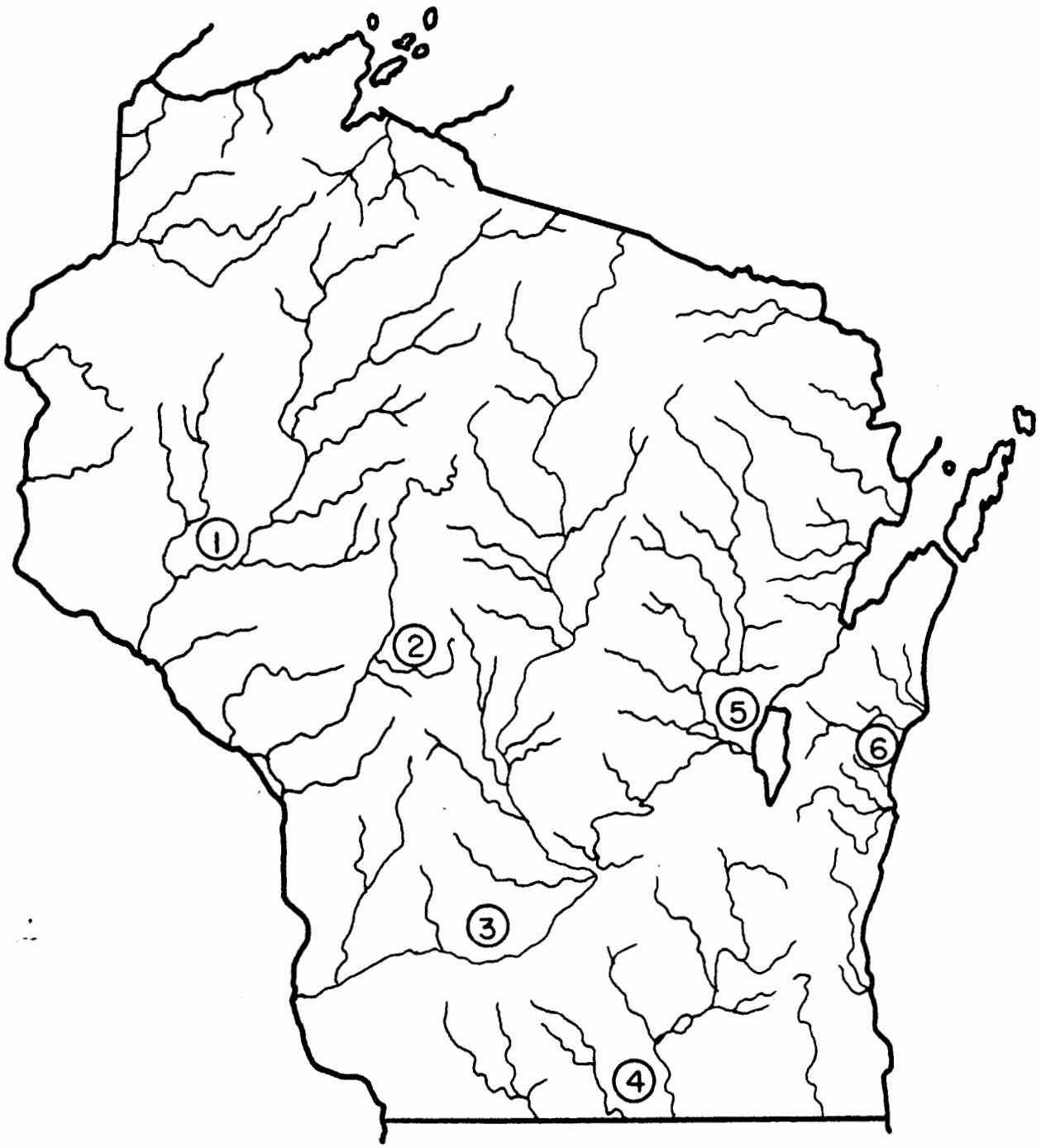
geologic sculpturing of the bedrock. The dip of the surface of the sedimentary rocks provided slopes which were modified by stream erosion. The degree of resistance of rock textures figured in the differential wearing down of surfaces. Glacial invasions markedly modified the features sculptured out of the original bedrock. Erosion and deposition scooped out basins, created lakes, filled in valleys, diverted drainage courses, and left a mildly hilly or undulating mantle of drift on which streams began working anew. On a broad regional scale the general directions of drainage have been determined by pre-glacial relief. On a more limited regional scale glacial deposits have molded a landscape with drainage patterns closely conforming to the modified surface features.

A large portion of the state lies within the Mississippi drainage system. A sizable area is drained by Lake Michigan streams while only a few Wisconsin streams empty into Lake Superior (Figure 6). The chief tributaries of the Mississippi in Wisconsin are the St. Croix, Chippewa, Black, and Wisconsin Rivers. Emptying into the Mississippi in Illinois is the Rock River which, with its tributaries, the Sugar and Pecatonica, drains a considerable section of southern Wisconsin. The Fox and Wolf Rivers comprise the chief system among the Lake Michigan streams. A number of minor Lake Michigan streams drain the easternmost counties.

Although smaller than the Mississippi, the Wisconsin River is really the master stream of the state. It rises on the Michigan boundary and flows generally southward through the heart of the state for over four-fifths of its course before turning westward toward the Mississippi.

FIGURE 6. Map showing river systems of southern Wisconsin

1. Chippewa
2. Black
3. Wisconsin
4. Rock-Sugar-Pecatonica
5. Fox-Wolf
6. Lake Michigan streams


1
2
3
4
5
6

Much of the lower course of the Wisconsin River is through the Driftless Area. The generally east to west valley of the lower course has a broad flat sandy floor with a rather marked gradient. The lower Wisconsin valley is a great gorge, partially filled with outwash sand and gravel which the streams from the glacial ice fronts deposited. The shallow Wisconsin River today is characterized by numerous sandbars and islands. The braided nature of the river is associated with its tendency to build subaqueous dunes and divide its own course into more than one channel (Fisher 1906). Natural levees are deposited during times of overflow, tending to raise the level of the floodplain immediately adjacent to the channels. The shifting of the channels leaves abandoned sloughs, known as fluves (Fidlar 1935), which become floodplain ponds or swamps.

Picturesque bluffs and canyons characterize most of the Wisconsin border portion of the Mississippi River. The floodplain of the Mississippi occupies much of the floor of the detritus-filled valley. Many of the features of the lower Wisconsin are here displayed on a grander scale; however the gradient is not so great as that of the Wisconsin nor are the sediments so coarse (McLaughlin 1932). The lower courses of the Chippewa and Black Rivers, both with valleys partially filled with glacial detritus, also resemble the lower Wisconsin (Leverett 1895). The Chippewa carried such loads of detritus supplied by glacial floods that the Mississippi was not able to remove the deposits rapidly enough. The tributary effectively built a dam, blocking the principal stream, forming Lake Pepin, which has since accumulated extensive deltaic deposits (Schwartz and Thiel 1954).

The Rock River rises among countless lakes and swamps near Lake Winnebago and flows southward in a tortuous postglacial course, draining a large section of southern Wisconsin. In crossing the beds of several former glacial lakes the Rock shows faint signs of flood-plain formation; however over most of its course in Wisconsin it wanders among drumlins, recessional moraines, and marshes, evidences of the sweeping effects of the Cary substage on the landscape. Both the Sugar and the Pecatonica Rivers drain upland sections of southwestern Wisconsin and,as previously noted, both flow in filled valleys where they traverse their lower courses (Alden 1918).

The Fox-Wolf system includes two rivers of highly different nature. The Fox resembles the Rock in that it flows through lake and marsh country, wandering from lake to lake. Its course conforms closely to the configurations left by glacial deposition. The Wolf rises in northern Wisconsin and rushes out of the pre-Cambrian upland on to the relatively flat country of Shawano and Outagamie Counties where it has built remarkable meander-scars and ox-bows along the lower part of its course. The Wolf has even formed a delta in Lake Poygan (Thwaites 1943).

Climate

General climatic differences of the eastern part of the United States have been outlined by Borchert (1950). A number of climatic regions based on their position relative to patterns of major air mass movements can be outlined. Middle-latitude westerlies descend from a major orographic barrier, the Rock Mountains, upon the great continental

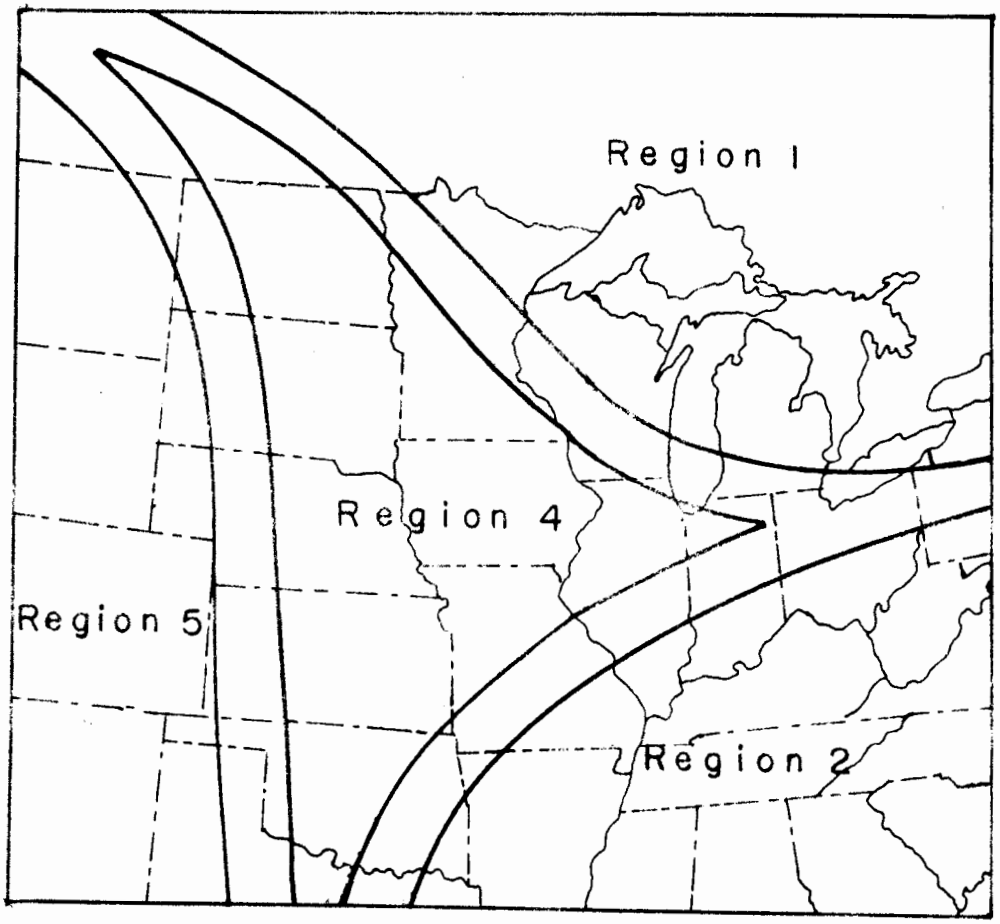
plain of North America. Tropical airstreams from the south and polar air masses from the north have access to the zone of westerlies east of the Rockies on the expanses of barrier-free interior. The stronger the westerly circulation the farther eastward the entering Arctic and tropical airstreams are carried before they converge. Consequently there exists a dry continental wedge that extends eastward from the Great Plains (Figure 7). The stronger the mean westerly circulation the more elongate the wedge-shaped area will be. During periods of drouth when low precipitation characterizes the Great Plains, it can be shown that low precipitation eastwardly correlates with the wedge-shaped area.

Wisconsin lies in the regions designated by Borchert as I and IV. Region I is characterized by snowy winters and by summers usually free from severe protracted drought. On the other hand Region IV usually has relatively dry winters and may be subject to occasional low summer rainfall. Frequent freezing and thawing conditions in southern Wisconsin are reminiscent of the winters of the Great Plains. The variability of the climate is one of its most notable features (Transeau 1935, Villmow 1952).

Soils

The soils of the lowland areas in southern Wisconsin are both fluvial and lacustrine in origin. Since the region includes sections with diverse bedrock and glacial geologic characteristics it is not surprising that a great number of different lowland soils have been

FIGURE 7. Climatic regions of the Middlewest (after Borchert).


Region 1
Region 4
Region 5
Region 2

differentiated (Whitson 1927). For example in Richland County in a recent soil survey, 13 different soil numbers were assigned to various soils classified as stream bottom and alluvial (Hole, Robinson, and Miller 1950).

Ecologists have long asserted that certain parent material influences may often be overcome by topographic conditions (Cowles 1901a, 1901b, Braun 1916, Clements 1928, Sampson 1930b, Shanks 1938). Characteristics having regional significance, yet concerned with the genetic properties of poorly drained soils, seem more meaningful in a vegetational study than an enumeration of the various soil units which have been classified. Since the degree of soil drainage is reflected by the depth of the ground water table, any method of demonstrating the depth at which soil is subject to water-logging reveals more clearly the topographic nature of the site.

Wilde (1940) has described a zone called the gley horizon which is deoxidized, often highly dispersed, sticky, and mottled with the reduced oxides of iron. His designation of a gley soil is one in which the gley layer occurs within the reach of root systems of trees or cultivated plants, which he approximates to be 7 feet. The gley layer has considerable ecological significance in that the processes of gleyization record the fluctuations of the water table in such a way that a measurement can be easily made. Furthermore the processes of gleyization may be superimposed upon soils of diverse nature. For alluvial soils of such recent origin that distinct soil horizons are not present the depth of the gley horizon maintains the same ecological significance that it does for soils with easily distinguishable A, B, and C horizons.

Considering the depth and position of the gley layer in relation to depth and to the A, B, and C horizons that characterize a mature forest soil profile, Wilde recognizes three types of gley soils.

Alpha gley soils or shallow gley soils are semi-swamp soils, more or less permanently wet, with the gley layer being within one foot of the surface, protruding up through the A_2 horizon. Alluvial stream bottom soils, soils of semi-swamp flats of lacustrine clays, and various swamp-border soils belong to this group.

Beta gley soils or mid gley soils are insufficiently drained, periodically wet soils with the gley layer superimposed upon the B horizon or about 2 to 3 feet from the surface. Shallow outwash or residual soils underlain by impervious strata, and borders of lowland prairie soils are some examples of beta gley soils. In the spring and fall the soil may be quite saturated while in summer the surface layers are usually dry.

Gamma gley soils are sufficiently drained but rather moist soils with a deep gley layer occurring in the C horizon or from about 4 to 7 feet below the surface. The composition of the soil profile may be only slightly influenced by ground water. Seasonal fluctuation of the deep ground water table is negligible in contrast to the previously discussed gley soils. Gamma gley soils may not be truly insufficiently drained soils but still must not be confused with completely well drained categories.

Soils in the lacustrine swamps of southern Wisconsin commonly display discernible profiles. Raw humus accumulations up to 6 inches in depth are not infrequent, but usually the highly organic soil of the

surface shows a gradual transition to more brownish sands or clays at a depth of 4 to 6 inches. Mucky soils associated with swamp hardwood forests were observed in only a few instances in this study and in every case the exposed roots of the trees suggested that the organic material comprising the forest floor had greatly settled during the past few decades. In a number of swamps the profile intergraded from a black loamy clay at the surface to dark brown clay at 6 inches to mottled light brown and finally to mottled yellow clay at 12 inches.

The alluvial soils of fluvial swamps mostly display poorly developed profiles. A "profile" of alluvial soil frequently shows layers of silt, sand, and clay and their order of accretion. During time of overflow the coarsest sediments are deposited near the bank of a stream. The particle size of sediments tends to decrease with increasing distance from the channel. The sediments in or near a slough at some distance from the main channel are likely to be silt or even clay. Whenever the channel of the river shifts and flows through an area where fine sediments have previously been deposited the stage is set for accretion of coarse sediments directly over fine silts and clays. Thus a "profile" of floodplain soil is likely to show a series of laminations with abrupt changes in the nature of the material comprising the layers. Where inundation has not recently disturbed the floodplain forest floor a thin layer of rapidly disintegrating leaves mixed with stems of herbaceous plants can usually be found. The surface inch of soil is sometimes so thoroughly permeated with roots that it resembles an interwoven mat. Snail shells are especially abundant on floodplain forest floors. Where overflow is

infrequent good profile development is usually apparent. The black color of the loamy soil near the surface changes gradually into the brownish color of the silty or sandy parent material.

Use of Wilde's (1940) alpha, beta, and gamma gley gives a convenient means of comparing soils regardless of origin, as well as a criterion for selecting lowland land forms. Only alpha and beta gley soils occur in the stands included in this study since all of the stands studied show a gley horizon at a depth of 3 feet or less.

Original Vegetation

Early observers describe the Wisconsin and the Mississippi Rivers with phrases which one might apply today to stretches where dams and reservoirs have not altered the water level too greatly. The journal of Father Marquette contains a splendid description of the lower Wisconsin written in 1673 and quoted by Warren (1876).

"It is very broad, with a sandy bottom, forming many shallows, which render navigation very difficult. It is full of vine-clad islets. On the banks appear fertile lands diversified with wood, prairie, and hill. Here you find oaks, walnut, whitewood, and another kind of tree armed with long thorns."

Schoolcraft (1820) pictures the Wisconsin River a short distance above Prairie du Chien in terms reminiscent of Father Marquette's account:

"It is a wide, and shallow stream, running over a bed of sand--with transparent waters--and chequered with numerous small islands, and sand bars. It has an alluvial valley, of a mile in width, bounded on each side by calcareous hills--which frequently, present naked precipices toward the river.--The dominating trees are oak, elm, and maple."

Schoolcraft also mentions the alluvial forests of the Mississippi on at least two occasions.

"The valley of the Mississippi between Prairie du Chien and the lead mines is about two miles in width, and consists of a rich deposit of alluvial soil, a part of which is prairie; and the remainder covered with a heavy forest of elm, sugar tree, black walnut, ash, and cottonwood."

In his second description Schoolcraft records impressions of an area which can be precisely delimited:

"Below the junction of this stream (the Chippewa River) the Mississippi has an increased width, and contains a great number of small willow and cottonwood islands, and the navigation is rendered more difficult, on account of the innumerable sand bars which here first make their appearance. They are attributable, in a great measure to the immense quantities of sand brought down by the Chippeway River."

The quantitative data supplied by surveyors' records of a century ago afford a more exact picture of the pre-settlement lowland forests. Broad classifications of lowland hardwood forests have been provided by Finley (1950) who mapped the original vegetation of the whole state from data supplied by surveyors' records. Finley describes as "lowland hardwoods" those forests containing silver maple, willow, elm, cottonwood, ash, river birch, and swamp white oak, which he stated occurred mainly along stream valleys in moist soils. In his "deciduous swamp forest" he lists black ash, elm, willow, and silver maple. Another category designated "basswood-oak" forest occasionally occurs along with lowland hardwood forest according to Finley. For the small portion of Dane County which borders the Wisconsin River Ellarson (1947) lists river birch, silver maple, swamp white oak, and elm as species most commonly reported by the surveyors. The relatively high percentage of river birch along the Wisconsin is especially emphasized. Elsewhere in Dane County the original survey shows swamps of black ash, oak,

maple, and willow. Relatively pure stands of black ash and willow are recorded. These latter swamps were found in protected places associated with the four lakes or with small streams flowing into the lakes.

Finley's map shows a number of places in Wisconsin where the river and swamp hardwood forests assumed sizable areal importance according to surveyors' data. The bottomlands of the Mississippi and the Wisconsin Rivers contained almost continuous woodlands, broken in places, however, by patches of grassland. The lower Wolf and lower Embarrass Rivers, especially in Outagamie County, were characterized by extensive belts of floodplain woodlands. Noteworthy tracts were also recorded for the Chippewa and Black Rivers, particularly along the lower courses of both. In eastern Wisconsin, aside from the Wolf and Embarrass Rivers, only limited floodplain forests were recorded. However, small patches of swamp forests were scattered over most of the eastern Wisconsin counties.

Post-settlement Utilization

Utilization of the wood from the floodplain forests of the Mississippi and Wisconsin Rivers seems to have been almost continuous since settlement, but generally of a local nature. Increase Lapham (1854), in describing characteristics and utilization of Wisconsin tree species, reports the use of river maple and cottonwood for steamboat fuel on the Mississippi. Martin (1932) notes that there were at least 300 steamboats plying the Wisconsin-Minnesota section of the Mississippi River in 1860. Babington (1950) recalls the operation of a charcoal

oven on one of the Wisconsin River islands below Sauk City about 1855. Telford (1926) mentions the long time use of bottomland trees of the Mississippi for making charcoal for gunpowder. Removal of river maple and elm for cordwood and swamp white oak for railroad ties occupied the winter months of many of the early settlers in the lower Wisconsin valley according to Babington. Before the passing of the steamboat era various attempts were made to control the Wisconsin channel with wing dams, into which went mostly nearby willow growth (Thwaites 1910).

Settlement of eastern Wisconsin was accompanied by the operation of numerous relatively small saw mill units which utilized the timber of the immediate vicinity (Hotchkiss 1898). The hardwood swamp woodlands of eastern Wisconsin have never been of great areal importance, nor have the hardwood species ever been in great demand for lumber. Local use for posts and cordwood accounted for the removal of much swamp forest. Lapham (1854) describes instances in which, during the earlier days of settlement in eastern Wisconsin, basswood was cut for no other reason than to provide buds for winter cattle feed. Heritage (1936) mentions the widespread use of black ash by the Indians for basketmaking. Uber (1937) discusses the use of swamp forests to supply material for corduroy and plank roads, since the swamps themselves provided the bad spots for road building. Drainage and clear cutting have made great inroads on the swamp hardwood forests of Wisconsin. Unlike the extensive floodplain forests of the larger rivers, well developed swamp hardwood forests with large trees are not easy to find today.

PHYTOGEOGRAPHY AND FLORISTICS

Floristic uniformity becomes a primary consideration in phytosociological studies of geographic areas as large as the region covered in this study. The flora of a region is the total of the species within its boundaries while the vegetation is the general effect produced by the growth of some or all of these in combination (Cowles 1926, Gleason 1939, Major 1951, Good 1953). For similar "general effect" to occur over the whole region it seems reasonable that range congruency of the species involved is an essential requisite.

A large number of similar ranges denote the existence of what have been called equiformal progressive areas (Hulten 1937), floristic areas (Egler 1947, Raup 1947), and floristic provinces (Curtis and McIntosh 1951). Transeau (1905) recognized the existence of such areas in his four great forest centers of eastern North America. It has been known for many years in Wisconsin that a rather narrow zone from northwest to southeast separated two major floristic provinces (Cheney 1893, 1894). Examples of several species of upland plants which reach the limits of their ranges along the tension zone are given by Curtis and McIntosh (1951). Strikingly correlative with the tension zone are also the northward and southward range limits of a number of weed species in Wisconsin (Lindsay 1953).

The question of floristic uniformity over a sizable geographic area poses special problems for floodplain forests. Gleason (1926) has used the alluvial forests of the Mississippi River to show, as one proceeds northward, how a gradual elimination of species ultimately leaves the

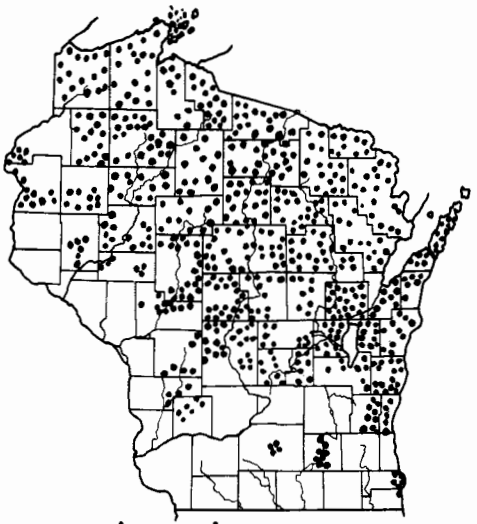
forests in the Minnesota area with a species complement quite different from Louisiana forests. Yet examination of short segments of the river discloses forests with essentially the same composition. Different ecologists making transect studies along the length of the river probably would not be able to agree on where to draw lines in an attempt to separate different forests. The floodplain forests of southern Wisconsin are composed mostly of those Mississippi Valley species which have ranges extending farthest north (Gleason 1923). Similar extensions of ranges along rivers have been recorded frequently. Cowles (1901) notes the striking collection of southern tree species on the floodplains in the Chicago area and he explains that "in such habitats are given the most congenial conditions that can be found in our area." Brown (1905) points out the southern cast of species occupying favorable places along the Huron River in eastern Michigan. Many of these species are near the northern limits of their ranges. Similar latitudinal mixing of both northern and southern species on the Dnieper system has been described by Illichevsky (1933). In the plains states forest extensions follow valleys far upstream where the woodlands gradually dwindle to narrow cottonwood and willow belts (Schaffner 1899, Kellogg 1905, Griswold 1942).

The tendency for lowland tree species to exhibit range extensions up river valleys seems to offer difficulties which can be best handled by some form of empirical delimitation of the study area. The first task was to determine the ranges of those species thought to be most common in the bottomlands. This information was gleaned from previous ecological and distributional reports on Wisconsin bottomland trees

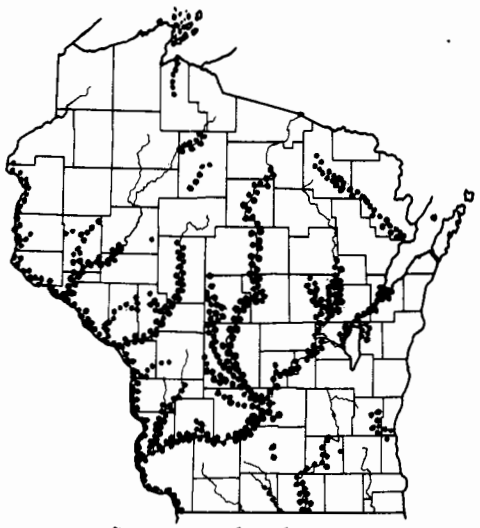
(Fassett 1930a, 1930b, 1932, Costello 1931, 1933, 1935, Hagen 1932, Leopold 1941, Seymour 1952) as well as from data from the first few stands sampled in the present survey. It was considered to be merely a tentative basis for delimitation of the area to be included in the study.

Adequate range information for most of the tree species of Wisconsin is available from the original and detailed range maps of L. S. Cheney, an early Wisconsin botanist, who covered the whole state quite thoroughly, working on barberry eradication. Cheney's work was utilized in the preparation of 24 range maps shown in Figures 8, 9, 10, and 11. It was found that the density of the distribution dots on Cheney's maps serve as a crude but satisfactory means of judging the importance of a tree species as a landscape feature. Confinement of certain species to river valleys is a distributional aspect spectacularly shown by these maps. Species with dense dot concentrations which are almost entirely associated with major stream courses are Acer saccharinum, Betula nigra, Celtis occidentalis and Quercus bicolor. All 24 species show dot concentrations along stream courses to a certain extent, but most of the species also show additional scattered dots which suggest no affinities for major streams. Fraxinus pennsylvanica and Fraxinus pennsylvanica var. subintegerrima are confined primarily to stream courses in the western part of the state but show a scattered distribution in eastern Wisconsin. The almost identical ranges of these two Fraxinus groups is particularly well demonstrated by Cheney's maps. Acer saccharum, Fraxinus nigra, Quercus rubra, Tilia americana, and Ulmus americana show statewide distribution; however in the

FIGURE 8. Range maps of Wisconsin tree species.



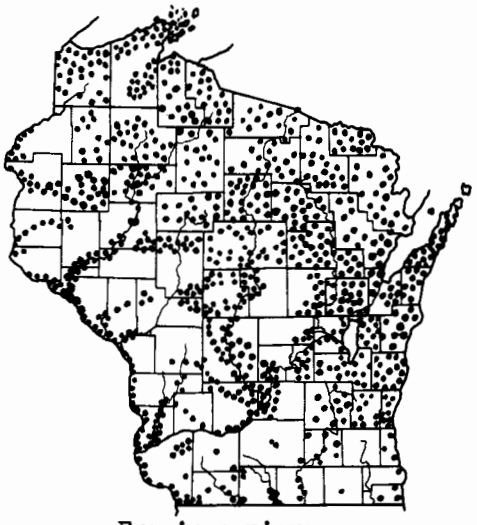
Acer rubrum



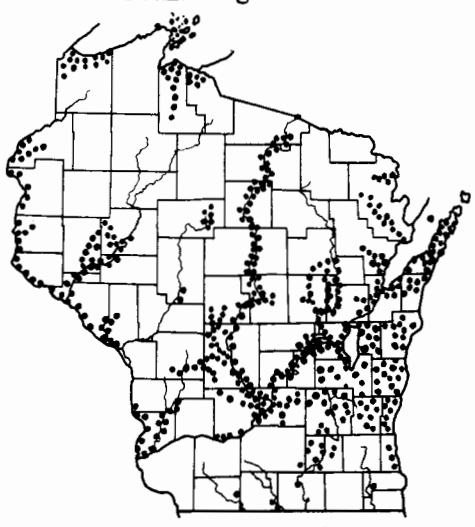
Acer saccharinum



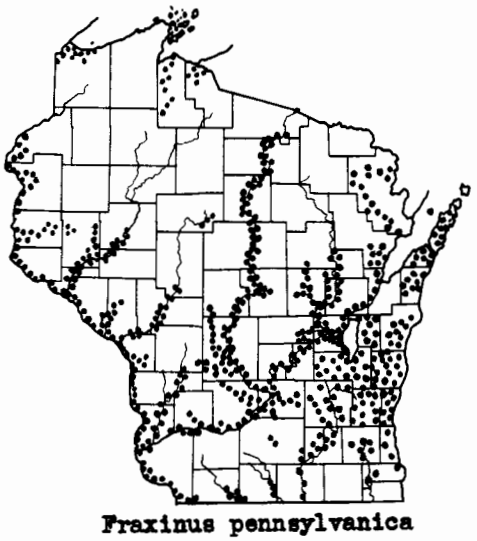
Betula nigra



Fraxinus nigra



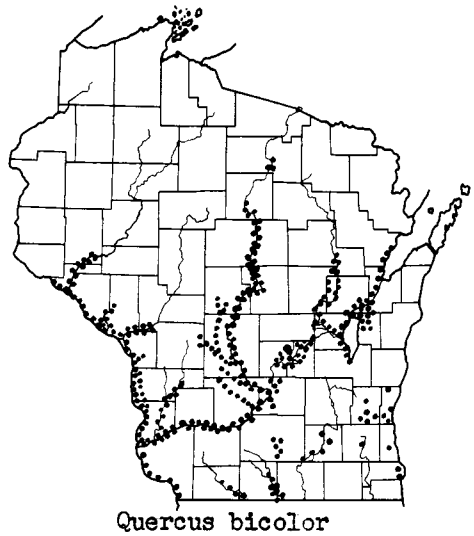
Fraxinus pennsylvanica



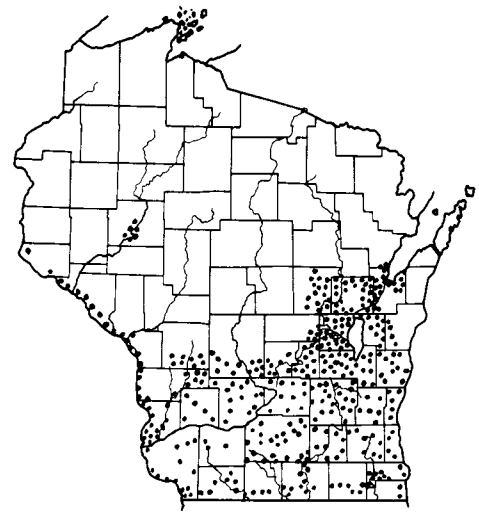
Fraxinus pennsylvanica

var. subintegerrima

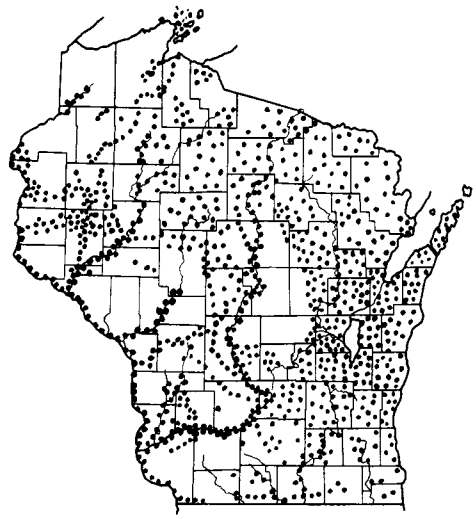
FIGURE 9. Range maps of Wisconsin tree species.



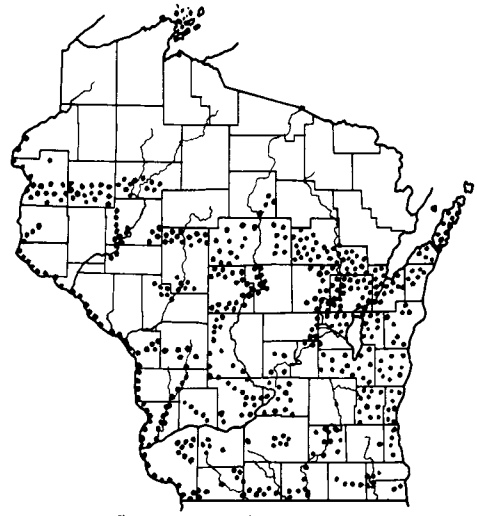
Quercus bicolor



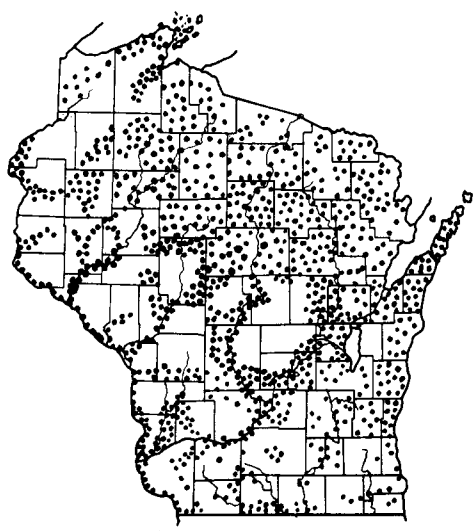
Carya ovata



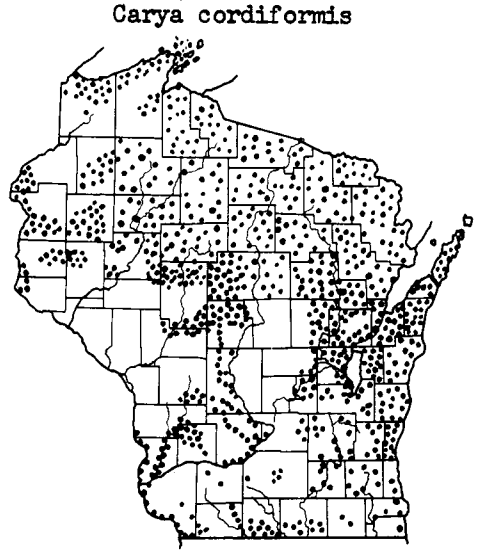
Ulmus americana



Carya cordiformis

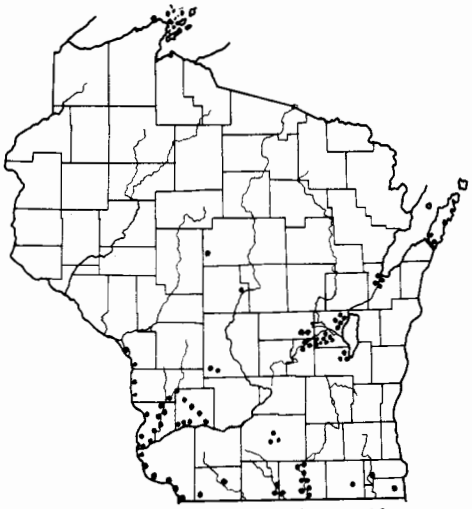


Tilia americana

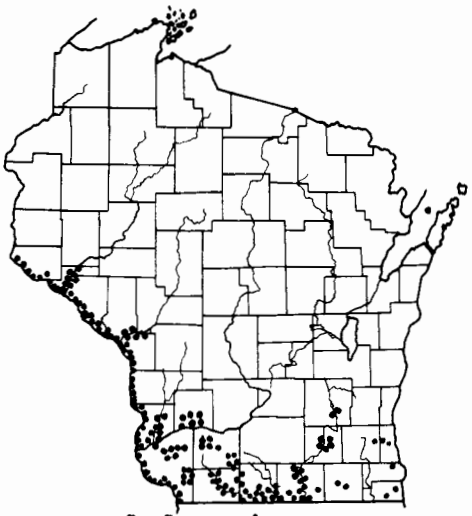


Acer saccharum

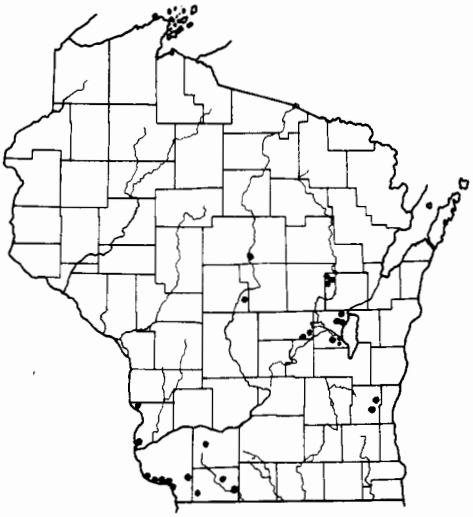
FIGURE 10. Range maps of Wisconsin tree species.



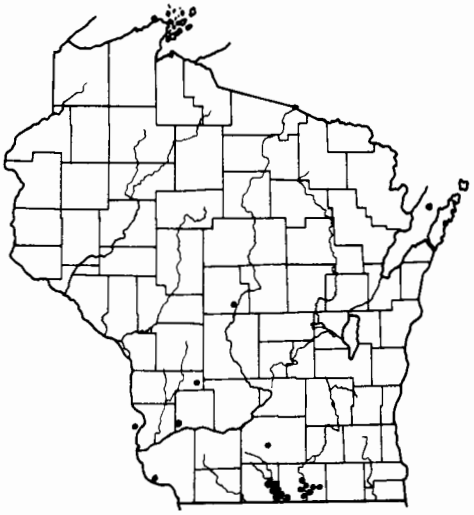
Gleditsia triacanthos



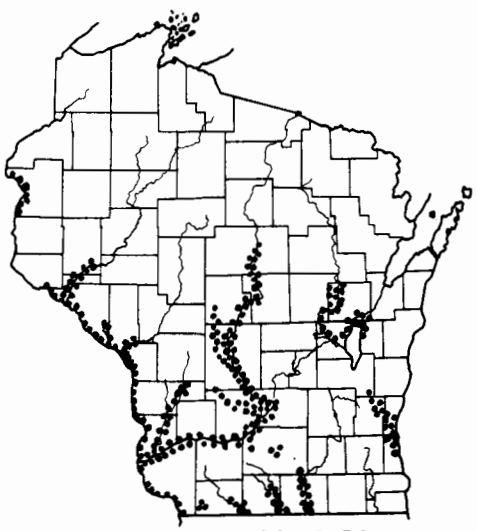
Juglans nigra



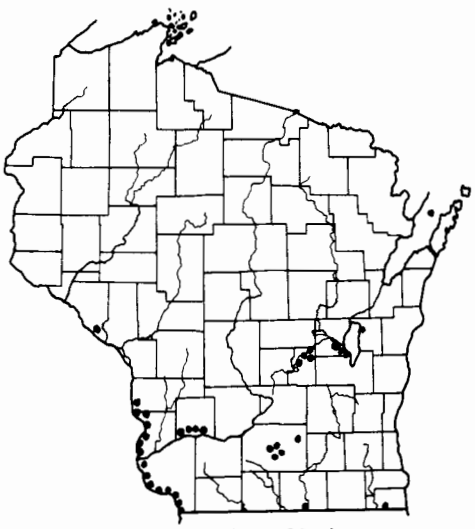
Morus rubra



Platanus occidentalis

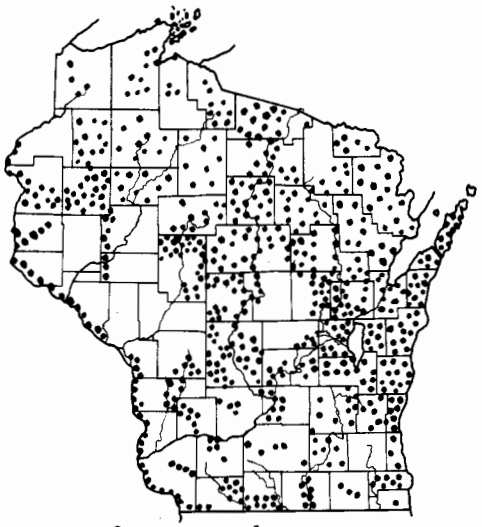


Celtis occidentalis

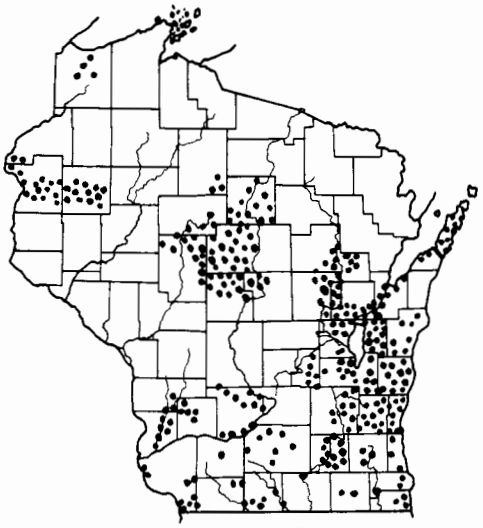


Gymnocladus dioica

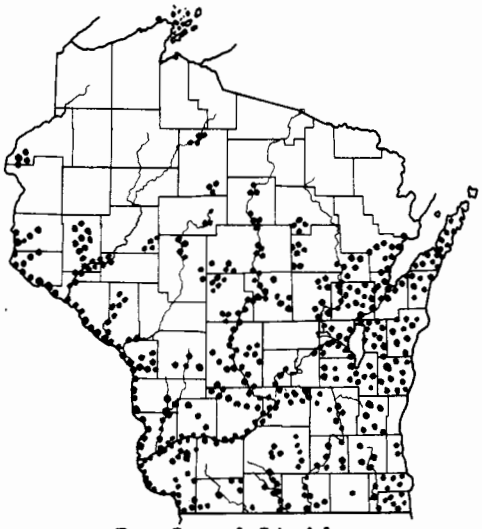
FIGURE 11. Range maps of Wisconsin tree species.



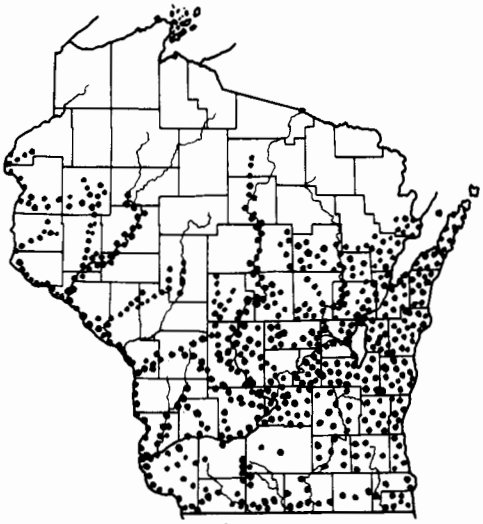
Quercus rubra



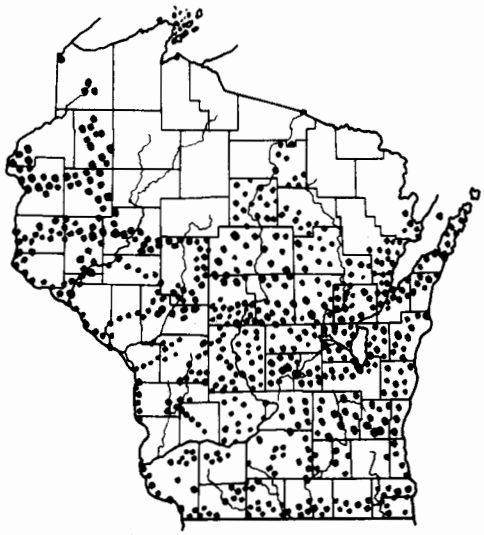
Fraxinus americana



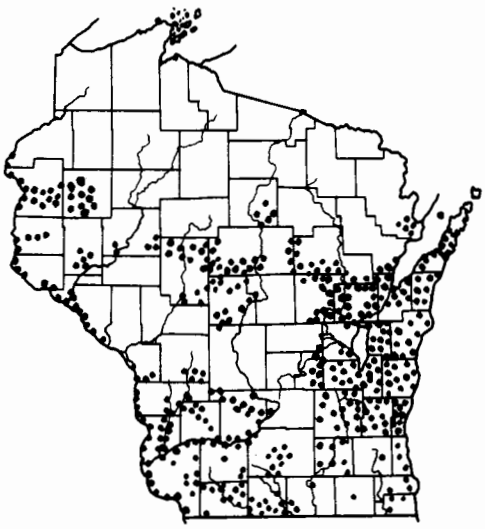
Populus deltoides



Salix nigra



Quercus macrocarpa



Ulmus rubra

southern part of the state all these species show greater tendency to follow stream courses and exhibit less uniform distribution that they do in northern Wisconsin. Of the species showing dense concentration of dots on the maps, only Betula nigra, Juglans nigra, and Acer rubrum have ranges which seem to cover only part of southern Wisconsin. While it is true that Morus rubra, Platanus occidentalis, Gleditsia triacanthos and Gymnocladus dioica also show only partial range coverage of southern Wisconsin, the sparse dots of these four species suggest far less vegetational importance than is indicated by the heavy dot concentrations of Betula nigra, Juglans nigra, and Acer rubrum. Of the 20 mapped taxa showing dense distribution dots, 17 have full range coverage of that part of Wisconsin south of the tension zone, indicating that this area indeed shows considerable range congruency of lowland species and probably sufficient on which to base a large scale phyto-sociological study. If one of the three species with only partial range coverage should prove to add a complicating factor to the treatment of the area as a unit, it was decided that the study could be regionally partitioned into two lesser studies, each new area with greater floristic uniformity and vegetational unity than that of the larger area.

Examination of species ranges and determination of floristic uniformity can precede actual ecological work. The problems of compositional homogeneity and the most effective use of taxa in the collection of data cannot be met until a considerable number of stands have been sampled. Compositional homogeneity implies similar behavior of any group of species regardless of the location of this group within the

study area. Culberson (1955) explains that if a group of species is more abundant in one part of a study area than the same group in another part of the study area, "then the over-all frequency and constancy values for these species will be manifestly influenced by the mere location of the stands sampled." Scattered and isolated swamps and linear river valleys offer formidable impediment to the free flow of species from a floristic reservoir even if theoretical floristic uniformity exists over the whole study area. Thus perfect compositional homogeneity can scarcely be expected. Since neither compositional homogeneity nor ecological usefulness of taxa can be judged until a number of stands have been sampled, these problems bear both on effective early procedure in the study and on ultimate clarification of ecological behavior. It is a situation analogous to firing the first salvo from a big gun of a ship. Careful calculations of the position and movement of the target can be made, but in most cases the initial salvo provides information for correcting the fire and finishing the task of sinking the target. A well planned first attempt is usually worth far more than the most careful calculations of problems involving elusive variables. Determining the degree of ecological variation of a particular species over all of the study area is one of the ultimate aims of such a regional undertaking, yet neglecting to make an early appraisal of the ecological usefulness of the taxa being treated can be truly as serious as disregarding the necessity for general floristic congruency.

METHODS

Criteria for Selection of Stands

The criteria used for the selection of stands for this study were the following: (1) The land form had to be low, flat, and poorly drained. (2) The stand had to be a hardwood forest of natural origin. (3) Each stand had to be at least 10 acres in extent. (4) There could be no recent disturbances such as fire, cutting, or grazing. Although the employment of these standards in the field necessarily evokes occasional subjective decisions concerning such things as landform and degree of disturbance, it is nevertheless believed that strict adherence to criteria of this nature eliminate most of the Procrustean tendencies associated with preconceived compositional notions.

Field Procedure

The location of stands for this study was accomplished mostly by reconnaissance of tracts of bottomland woods in topographically favorable areas. The location of good-sized patches of bottomland forest was not difficult, in that information was available from several sources, including aerial photographs, land inventory maps, Finley's (1950) map of the original vegetation, and numerous reports from workers who had cruised hundreds of miles of Wisconsin countryside studying other communities during previous years. All of the larger rivers of southern Wisconsin were reconnoitered. Indeed much time and energy were expended

attempting to locate stands in sections where lowland forests were scarce. Few of the stands preliminarily examined were found to be completely free from recent disturbance. Where extensive tracts of lowland forest were present in an area portions of these tracts which showed no signs of disturbance could usually be found.

The sampling methods used in this study follow those which have been applied to other woody communities in Wisconsin (Curtis and McIntosh 1951; Brown and Curtis 1952; Ward 1954). The random pairs method (Cottam and Curtis 1949) has been shown to give results comparable in accuracy to those of the quadrat method (Cottam, Curtis, and Hale 1953, Shanks 1954), while at the same time, the rapidity with which data can be collected by this plotless method makes it an indispensable device for the extensive sampling necessary for a regional survey. Arborescent species with basal area over 12 square inches at breast height were recorded by reading the basal area directly from a tape specially scaled for this purpose. Those woody stems less than 12 square inches were recorded as saplings. The four saplings nearest to each point were recorded by species count without measurement of basal area. Recording the saplings in this manner provided data from which the determination of relative density was made. In most stands the number of points taken was forty. In some stands where a single species was overwhelmingly predominant, fewer points were taken. All of the various data sheets used in the present survey are included in the Appendix.

The investigation of a stand was initiated by a reconnaissance wherein the selection criteria were applied. If the stand was found to be

acceptable, points at predetermined intervals along transects were sampled, the transects being laid out to give greatest coverage of the whole stand area. Edge effect was carefully avoided by confining points to distances at least equivalent to 2 tiers of trees or about 25 yards within the stand. Streamside trees, which often hang out over the water in crowded rows (Davis and Richards 1933), were thus entirely excluded.

Herb data were collected by sampling with 20 one square meter quadrats distributed along the transects laid out for sampling the trees. In keeping with the time and effort limitations of a forest survey encompassing many stands, the presence or absence of a species in a quadrat was the only information recorded. Herb data forms which had been prepared from preliminary presence data were used during the early part of the study. When sufficient information accumulated the herb data forms were revised and all of the herbs which had thus far been reported were listed on two data forms. On one sheet labeled "Common Species" were listed those species most frequently encountered in the survey. Less frequently encountered species were listed on the second sheet, labeled "Uncommon Species." Twenty sheets of the "Common Species" form were used for the quadrat study of each stand, the species of each quadrat being checked off on a different sheet. Tree seedlings in the quadrats were recorded with the herbs. Species found in a quadrat which were not included in the list, were written at the bottom of the sheet. A separate set of both data forms with all of the species found in the stand checked off, constituted the presence list for the stand.

For each stand a cover sheet called a "Stand Record" was prepared. Space is provided for such data as the name of the stand, date of sampling, exact location, size of stand, and other information as is indicated by the example of a "Stand Record" sheet in the Appendix.

The nature of the soil profile was determined from small soil pits. Where only alluvial laminations were found a general description of the sand, silt, and clay layers was recorded. Three samples of the A_1 horizon (or from the upper 2 inches of alluvial soil where no horizon was apparent) were pooled as a composite sample from the stand. Partch (1949) indicates that the A_1 horizon, because of its partially organic origin, shows better correlation with the canopy species than any other horizon.

The discomforts confronting the worker in lowland forests are usually a serious deterrent to effective work. Proper precautions eliminate most of the minor hazards; nevertheless the list remains impressive. The multitudinous mosquitoes necessitate liberal use of insect repellent in all stands and a head net for the more heavily infested woods. The rank growth of wood nettle (Laportea canadensis) is often head high, and progress through a bottomland forest is often seriously impeded by the forbidding sea of nettle plants; fortunately the tender succulent stems break easily, and slicing a swath with a quadrat stick is possible. Poison ivy (Rhus radicans) is an ever treacherous threat to the susceptible worker in lowland woods, but of course it does not affect the pace of sampling of the vegetation at hand. Frequently stands appear to be veritable carpets of poison ivy. The protective clothing necessary to combat the nettle and mosquito

problems only too often create further discomfort in the already warm humid atmosphere of the forest.

Condensation of Data

Laboratory treatment of data follows methods outlined by Curtis and McIntosh (1951) and Brown and Curtis (1952). Frequency in the previous studies refers to the per cent of points in which a species occurs. Relative frequency (Curtis and McIntosh 1950), which is the same as percentage sum of frequency (Raunkiaer 1934) is determined by totaling the points of occurrence and dividing the points of occurrence of each species by this total. Relative density is determined by dividing the number of trees of a species by the total number of trees, and relative dominance is found by dividing the sum of the basal areas of a species by the total sum of the basal areas for all trees in the stand. All three of these values are in terms of per cent so that when values for relative frequency, relative density, and relative dominance are totaled for all species, the sum is 300. The sum of three relative values for one particular species is called the "importance value" of the species (Brown and Curtis 1952). The various totals were transferred to a tree data summary sheet. Relative density determinations for the saplings and frequency values for the tree seedlings were also transferred to the summary sheet.

The condensation of herb data required only the determination of quadrat frequency. On the tabulation form the presence in a quadrat was recorded as a check in one of the 20 rows of spaces provided. Frequency

was quickly determined from the checked spaces. Species present in the stand but not present in quadrats were also recorded on these herb summary sheets.

The taxonomic nomenclature of all the species, both woody and herbaceous, listed in this study is based on Gray's Manual of Botany, 8th edition. Plants which could not be identified in the field were tagged for later identification. Many of these plants were subsequently deposited in the University of Wisconsin herbarium.

The soil samples were ground until all the particles passed through a 2 mm. screen. Part of the sample was sent to the State Soils Laboratory for chemical analysis and part was retained for determination of moisture-holding-capacity. Hilgard cups were used for the determination of moisture-holding-capacity by the method described by Partch (1949).

Innumerable photographs were taken throughout the course of the study. Selected views have been included to show compositional variation and seasonal differences in appearance. In addition pictures of certain phenomena unique to lowlands woods are included. A series of photographs selected to show the full range of compositional variation encountered is included in the Appendix.

Homogeneity of Stands

Judicious evaluation of the stand by application of the objective criteria set up for selection behooves the worker to neglect appraisal of compositional variation while he is actually sampling. The scheme followed in the sampling of stands for this study stressed topographical

uniformity, which was ascertained during the reconnaissance. By avoidance of abrupt topographical changes, the sampling was confined to places judged to have uniform environments. Such estimations provide no check on compositional homogeneity.

A test for homogeneity is described by Curtis and McIntosh (1951) and Brown and Curtis (1952) wherein the 40 points are treated as 4 sequential groups of 10 random pairs. The Chi Square Test (Snedecor 1946) is applied to these 4 groups. Only those stands with at least 20 individuals of one species can be tested with this method since there must be at least 5 individuals in each of 4 theoretical samples. Such an objective determination of homogeneity can only be applied after the sampling is completed. If the stand is not acceptable by this statistical test, it can be either discarded or re-studied. Using the one percent level of confidence in the test it was found that no stands showed Chi Square values exceeding the value listed in Snedecor's table. Since the stand is studied as a unit comprised of species associated with an environment favorable to the major species, it is thought that homogeneity of the major species is a manifestation of the unity and the concinnity of the whole stand.

LITERATURE REVIEW

Phytosociological studies on a quantitative basis are available from widespread points throughout the deciduous forest region though the total number of such studies is not great. For the territory encompassing neighboring states, several treatments are compared in later sections of this study. These include the studies by Telford (1926) of scattered Illinois bottomland forests and of Yeager (1949) on a large tract of floodplain forest at the mouth of the Illinois River. A series of samples along Des Moines River floodplains in Iowa by Aikman and Gilly (1948) and an investigation of the same type of the White River floodplain forests in Indiana by Lee (1945) are both later discussed. In addition, Sampson's (1930b) graphic treatment of the deciduous swamp forests of northern Ohio is used for comparative purposes. These studies are thought to be the most relevant for an attempted regional integration of lowland forest communities.

Of lesser significance to the present study because of regional dissimilarities but still meriting mention is a substantial number of quantitative studies. Oosting (1942) has presented comprehensive data on the bottomland hardwood forests of the Piedmont in North Carolina. His streamside and floodplain pioneer species data indicate similarity to more northerly communities; however his data from well established bottomland hardwood forest communities reflect the overwhelming importance of Coastal Plain species. Chittenden (1905) has presented composition data for what he terms virgin bottomland hardwood in South Carolina. Two quantitative studies of swamp forests in the Gulf Coast region have

been contributed by Penfound and Hall (1939, Hall and Penfound 1939). Penfound (1948) has also described an elm-ash floodplain community in central Oklahoma, with accompanying data. Cain, Friesner, and Potzger (1930) offer frequency data for one floodplain station in central Indiana, and Cain (1935) gives a statistical depiction of a cypress swamp in Indiana. A red maple swamp on Long Island has been treated quantitatively by Cain and Penfound (1938). Pammel (1905) lists per cent total composition for the various species of the floodplain forests of the Iowa River.

Descriptions which list various lowland forest aggregations related to Wisconsin communities are fairly common in the literature from nearby states. An organized effort in Illinois toward making ecological surveys of forestry conditions of various counties, or of even more limited areas, produced a sizable number of descriptive studies,most of which delineate some bottomland tree combinations (Fuller and Strausbaugh 1919, Schmoll 1919, Waterman 1919, Vestal 1919, Simmons 1920, DeForest 1921, Miller and Fuller 1920, 1922, Ridgway 1928, Eaton 1931, and Meyers and Wright 1948). Descriptive accounts of lowland forests in Indiana include those of Swanson (1929), Gordon (1936), McCoy (1938) and Chapman (1942). Surveys in Ohio which warrant mention include the works of Jennings (1908), Griggs (1914), Sears (1925, 1926), Sampson (1927, 1930a, 1930b, 1930c, 1930d), Braun (1928), and Shanks (1938). In Michigan,community cognizance appears in accounts by Brown (1905, 1917), Burns (1906), Davis (1906), and Kenoyer (1929, 1934, 1939). Kell (1939) has delimited the general composition of a swamp community in northern Minnesota. Reports from Iowa containing references to lowland communities include

those of MacBride (1895, 1897) Cameron (1897), and Lugn (1927).

The tendency to weave successional emphasis into investigations of lowland communities is indeed understandable since rapid vegetational change and conspicuous zonation are common phenomena among plant aggregations found along rivers and in swamps. The dynamics of river action and related plant succession on sandbars and islands have been treated in descriptive detail by a number of workers. Barclay (1924) distinguishes the different stages of pioneer vegetation developing along the Mississippi River at St. Paul, Minnesota. Gleason (1910) and Pepoon (1911) note the successional sequences of sandbar plants on the Mississippi in northern Illinois. Fitzpatrick and Fitzpatrick (1902) delineate the zones of pioneer river vegetation on the Mississippi in Iowa. Clark (1918) Aikman (1930), and Shimek and Conard (1948) give sketches of plant aggregations of river shores and sandbars in Iowa. Treatments of the successional aspects of river vegetation in Illinois include studies by Turner (1928, 1930, 1931, 1936) on the Illinois River, and by Springer (1930) on the Sangamon River. Shelford (1954) traces the origin of floodplain sites back to channel changes occurring many decades ago in his comprehensive treatment of floodplain communities in the Reelfoot Lake region of Tennessee. Shull (1922, 1944) describes the formation of an island in the Mississippi River and outlines the vegetational changes 22 years subsequent to his first report. Anderson (1948) and Dietz (1952) trace changes in topography and plant cover on gravel bars in eastern Missouri. Other discussions of pioneer vegetation along rivers include those of Brown (1929) and Penfound and Howard (1942) on the Mississippi in Louisiana; Sellards, Tharp, and Hill (1923) on the

Red River in Texas; Hefley (1937) and Ware and Penfound (1949) on the South Canadian River in Oklahoma; and McVaugh (1948) on the Hudson River.

Accounts dealing with zonation and succession in swamps and bogs are rather frequently encountered in the literature. Some of those encompass investigations in territory proximal to the study area probably cast light on the present work. Ecological relationships and complexities of geographic distribution of bogs have been discussed by Transeau (1903). Changes associated with the extinction of bogs are suggested by Gates (1911), Waterman (1922, 1923), Sears (1926), and Sampson (1927). Cain (1928) outlines some of the successional patterns of an Indiana swamp. Dachnowski (1912) notes the southern affinities of the swamp forest plants tending to move into the extinct bogs in northern Ohio. Schaffner, Jennings, and Tyler (1904) classify the zonation phenomena of Brush Lake in Ohio. They designate the swamp forest as the culmination of the vegetational changes which accompany lake filling. Sampson (1930b) sets up sequential combinations representing his interpretation of successional stages in the swamp forests of northern Ohio. Pammel (1898) and Shimek and Conard (1948) in Iowa and Baker (1910) and Schmoll (1919) in Illinois give brief sketches of swamp forest succession. Pepoon (1907) discusses the vegetation of a swamp in southwestern Michigan, incorporating comprehensive lists of plants. A series of investigations of the Huron River Valley in Michigan analyzes the swamp and bog communities. Zonation in the Huron Valley is treated in the papers of Weld (1904), Transeau (1905, 1906) and Burns (1909, 1911). Shaver (1933) and Gersbacher and Norton (1939) present swamp succession schemes for the Reelfoot Lake region.

Some of the early accounts of the floodplain forests of southern Indiana and southern Illinois contain excellent descriptions of gigantic trees as well as occasional community delimitations. The distinguished ornithologist and botanist Robert Ridgway has eloquently imparted his enthusiasm for the bottomlands of the lower Wabash Valley into flowing characterizations of the forests, punctuated with girth and height data on the "monarchs" of these forests (1872a, 1872b, 1882, 1883, 1894, 1895). The following account appeared in 1872:

"In the heavy forests of the bottom-lands, which in many places have entirely escaped the ravages of the axe, the magnitude of the timber is such as is unknown to the scant woods of the eastern states, the stiff monotonous pineries of the north, or the scrubby growth of other portions. The river flows for the greater part between dense walls of forest, which stand up to the very banks, and generally screened in front with a dense fringe of willows, with a belt of cottonwoods and sycamores behind it. Viewing this forest wall from the opposite side of the river, there is seen a compact mass of verdure, the trunks of the trees being often hidden by the fronting belt of willows, which are often overrun by luxuriant masses of wild grape or other vines, often falling down to the very water's edge, so that even the bank itself is wholly concealed. If the forest is viewed from a high bluff, it presents the appearance of a compact, level sea of green, apparently almost endless, but bounded by the line of wooded bluffs three to seven miles back from the river; the tree-tops swaying with the passing breeze, and the general level broken by occasional giant trees which rear their massive heads so as to overlook the surrounding miles of forest. The approximate height above the ground beneath of the average tree-top level is about one hundred and thirty feet--the lowest estimate after a series of careful measurements--while the occasional and by no means infrequent 'monarchs' which often tower apparently for one-third of their height above the tree-top line, attain an altitude of more than one hundred and eighty feet, or approach two hundred feet."

Brendel's (1887) paragraph concerning the bottomlands of the Illinois River furnishes excellent descriptive detail:

"The left bank of the Illinois River opposite Peoria is bottomland one mile wide, in spring inundated and for the greater part still thickly wooded. Nearest the bank we find the long-leaved and black willow, cottonwood, sycamore, soft maple and white elm. Father backward,

black walnut, butternut, pecan, ribbed hickory, blackberry, slippery elm, burr oak, swamp white oak, the five species of ash, of which the green ash is the most frequent, the coffee nut, the honey locust, mulberry, box elder, the buckeye, the paw paw, the persimmon, the elder and the false indigo. On open swampy places, the buttonbush, the osier dogwood, and species of shrubby willows."

Most of the early accounts of vegetation in Wisconsin fail to give much attention to ecological groupings of lowland species. Hoy (1852), in reporting the various species encountered in the woods of Wisconsin fails to mention such common trees as cottonwood, silver maple, green ash, river birch, and black willow. Lapham's (1854) enumeration and description of various Wisconsin tree species is replete with ecological information though no groupings are suggested. Chamberlin (1877) showed remarkable vegetational perception when he suggested intergrading groups of upland tree communities in southern Wisconsin. He lists only one hardwood swamp community however, the black ash group, which he places with the groups intermediate between upland and marsh. The areal significance of hardwood swamps was apparently not great enough to deserve recognition on his vegetation map of eastern Wisconsin. Pammel (1891) gives a short list of tree species occurring in the alluvial forests of the upper Mississippi. The work of Cheney and True (1892) in Dane County contains habitat notes on numerous swamp plants. Bruncken (1900a, 1900b) recorded observations on distribution and habitat of various tree species in the Milwaukee area and later (1902) set forth some ecologic groupings based on field observations. He states that the forests of the Milwaukee region are almost exclusively of the deciduous mesophytic association and divides this mesophytic group into three sub-associations: (1) hemi-xerophytic, (2) mesophytic, and (3) hemi-hydrophytic. The hemi-hydrophytic sub-

association is again divided into two groups, the swampy depressions of the uplands and the river bottoms. Bruncken gives excellent characterizations of these two communities, even venturing suggestions as to the dominant species of each. More recently Leopold (1941) studied a single floodplain stand on the Wisconsin River in Sauk County. By correlating growth rates of the various species, he was able to determine combinations which correspond closely to the ecological groupings independently mapped by him from direct observation. Marks (1942) cursorily mentions the former bottomland combinations of American elm, burr oak, and black maple in a primarily upland region near LaCrosse in western Wisconsin. Green (1947) records the responses of bottomland tree species to continuous inundation following the construction of dams on the upper Mississippi. Finley's (1950) map of the original vegetation of Wisconsin constructed from surveyor's records sets forth some broad categories for lowland vegetation.

RESULTS[1]

The importance values of species afford a means by which stands can be grouped for comparison. The species having the highest importance value in a stand has been designated as the leading dominant (Curtis and McIntosh 1951). When the stands of the present study were grouped on the basis of leading dominant, it was found that 15 species occur as the leading dominant in one or more stands. Eleven species occur as the leading dominant in two or more stands. These 11 species, together with the number of stands in which each occurs as the leading dominant, are listed in Table I. One or the other of the two species, Acer saccharinum or Ulmus americana, occurs as the leading dominant in a total of 70 stands, leaving only 44 stands for the other nine leading dominants. Occurring as the leading dominant in only one stand are Acer rubrum, Carya ovata, Quercus alba, and Quercus macrocarpa.

Despite the apparent predominance of Acer saccharinum and Ulmus americana, examination of the various arrangements of the first, second, third, and fourth ranking species, rankings being based on importance values, reveals great diversity in the order of species from stand to stand. There are 49 different arrangements of the top ranking pairs of species from the 114 stands. The different arrangements of the top three species number 75, and the different arrangements of the first four species total 90.

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1. All Figures to which references are made in this section are in a single group placed at the end of the section.

TABLE I. Leading dominant groups and number of stands in each group.

TABLE I

	Salix nigra	Populus deltoides	Betula nigra	Quercus bicolor	Acer saccharinum	Ulmus americana	Fraxinus pensylvanica var. subintegerrima	Fraxinus nigra	Tilia americana	Quercus rubra	Acer saccharum
Salix nigra (6)	234	46			10	1					
Populus deltoides (6)	26	168	24		57	13	9				
Betula nigra (3)	1	1	102	35	84	34	20	2	9	12	
Quercus bicolor (5)			45	127	42	26	11	22	14	2	
Acer saccharinum (38)	6	5	15	19	137	66	21	8	9	2	
Ulmus americana (32)	1	2	3	3	53	121	22	21	20	8	6
Fraxinus pensylvanica (5)	17		1		19	44	175	5	1	2	
Fraxinus nigra (2)						38	27	112	62	4	
Tilia americana (7)					1	25	6	14	86	26	10
Quercus rubra (2)						35	9	2	25	90	3
Acer saccharum (4)						43			20	4	145

The marked qualitative differences in stand composition relates to the relatively rich floristic reservoir from which the vegetational constituents of lowland forests are drawn. A total of 45 arborescent species were encountered in the present study. All but seven of these species regularly participate in canopy formation. Table II lists all 45 species and indicates the number of stands in which each occurs. Of the top ten species in Table II, only one, Carya cordiformis, was not encountered as a leading dominant. Acer saccharinum occurs as the leading dominant in far more stands than does Fraxinus pennsylvanica, yet the latter is present in more stands than is Acer saccharinum. Some additional species such as Celtis occidentalis, Ulmus rubra, and Carya cordiformis occur in a considerable number of stands, yet seldom attain a high importance value.

By following a procedure which served satisfactorily in both the studies by Curtis and McIntosh (1951) and by Brown and Curtis (1952), the stands were grouped according to leading dominant and an average importance value was obtained for each species in the group. For example the 38 stands in which Acer saccharinum was the leading dominant were considered as a group. The importance value for Acer saccharinum from every stand of the 38 was added and an average importance value was obtained. Similarly an average importance value for each of the other species in this group was obtained. Those species which have the highest importance values in this group are considered to be the closest associates of Acer saccharinum. As a tentative starting point, the group for which Salix nigra was the leading dominant was chosen, and an attempt was made to determine a phytosociological order of stands by

TABLE II. Number of stands of occurrence of 45 species.

TABLE II

1.	Ulmus americana	100
2.	Fraxinus pennsylvanica	77
3.	Acer saccharinum	75
4.	Tilia americana	58
5.	Quercus bicolor	45
6.	Fraxinus nigra	44
7.	Carya cordiformis	30
8.	Betula nigra	28
9.	Quercus rubra	27
10.	Salix nigra	27
11.	Populus deltoides	26
12.	Ulmus rubra	21
13.	Acer saccharum	20
14.	Celtis occidentalis	17
15.	Acer negundo	16
16.	Fraxinus americana	14
17.	Ostrya virginiana	14
18.	Betula lutea	13
19.	Carya ovata	13
20.	Prunus serotina	13
21.	Acer rubrum	11
22.	Quercus alba	11
23.	Quercus macrocarpa	11
24.	Juglans cinerea	9
25.	Quercus velutina	9
26.	Populus tremuloides	6
27.	Fagus grandifolia	4
28.	Tsuga canadensis	4
29.	Betula papyrifera	3
30.	Crataegus sp.	3
31.	Gymnocladus dioica	3
32.	Populus grandidentata	3
33.	Thuja occidentalis	3
34.	Juglans nigra	2
35.	Pinus strobus	2
36.	Acer spicatum	1
37.	Aesculus glabra	1
38.	Amelanchier sp.	1
39.	Carpinus caroliniana	1
40.	Gleditsia triacanthos	1
41.	Larix laricina	1
42.	Platanus occidentalis	1
43.	Prunus virginiana	1
44.	Robinia pseudoacacia	1
45.	Salix amygdaloides	1

reliance upon the importance value averages within each of the leading dominant groups. By repeated modification of the order of leading dominants the arrangement shown in Table I was accepted as the most satisfactory. Considerable reliance was placed upon the pyramidal effect displayed by the numbers in the Acer saccharinum and the Ulmus americana groups because of the large number of stands in each of these groups. Since the leading dominant method involves groups containing varying numbers of stands, some of the numbers being quite small, it is not surprising that some minor irregularities are present. Thus Table I is a tentative arrangement for ascertainment of end points of the communities under investigation and for postulation of a phytosociological order for leading dominant groups between these end points.

Grouping of the stands on the basis of leading dominant may completely separate stands which are actually very similar. If the importance values of two leading species of two stands are but slightly different, each stand may have a different leading dominant. A method by which the importance value of each species in a stand is expressed graphically was devised by Curtis and McIntosh (1951) in what is called the strip method. A modification of the strip method is employed by the use of bar diagrams in Figures 12 and 13. A bar representing the importance value of a species is placed in a symmetrical manner on the vertical line on which all importance values for that species are placed. A stand containing six species has six bars aligned horizontally, each of the bars being placed on the proper vertical species line. As a guide for the construction of the bar diagram scheme represented in Figure 12

the arrangement of the leading dominant groups in Table I was used. The stand in which the importance value of Salix nigra was found to be highest was used as the starting point and was represented by the lowermost bar on the Salix nigra vertical line. The next few stands were arranged so that the value of Salix nigra showed successive decreases. The arrangement of the bars representing importance values of Populus deltoides and the remainder of the species on the diagram is an attempt to obtain smooth and gradual increases and decreases with all of the species bar patterns, with more reliance being placed on those species which have the highest importance values. Smooth and symmetrical spindle--shaped patterns were obtained for most of the species (Figure 12); however the pattern displayed by Fraxinus pennsylvanica did not tend to widen significantly in any part of its great range.

In order to learn more about the relative behavior of Fraxinus pennsylvanica, the importance values for Acer saccharinum and Ulmus americana were removed from every stand and the summation of importance values of the remainder of the species was determined. By using this total as a basis for computation, a value in per cent for each remaining species was obtained. Stands in which the combined importance values for Acer saccharinum and Ulmus americana exceeded 240 were not used owing to the meager sample left after the removal of such overwhelmingly predominant species. By the use of these new values another series of bar diagrams was prepared (Figure 13). The bars for Fraxinus pennsylvanica exhibit a definite spindle-shaped pattern with the maximum width of the spindle covering a range of only a few stands. The addition of bars representing values for Celtis occidentalis and Quercus rubra is also shown in Figure 13.

While it is true that the number of stands employed in the construction of bar diagrams can manifestly affect the shape of the spindle patterns, the relative positions of the widest portions of the spindles will be scarcely affected by the addition of values from new stands if a sufficient number of stands of diverse composition have been used initially. Use of bar diagram representations permits more accurate comparisons of the phytosociological behavior of species than is allowed by the leading dominant groups presented in Table I in that the leading dominant groups are of vastly varying size, and some of them contain so few stands that only moderate reliance can be placed in the values recorded. The lumping of stands into leading dominant groups perhaps conveys the impression that discrete groups of stands are found; the bar diagrams demonstrate the intergradations of leading dominant groups since considerable overlap of adjacent spindles is present.

The bar diagrams indicate that a scheme in which Salix nigra is placed at one end and Acer saccharum is placed at the other end of the entire range of stands encountered does indeed fit together, and all the other species attain their highest importance values in stands located between the Salix nigra and Acer saccharum end points. By assigning Salix nigra the number 1 and Acer saccharum the number 10 it is possible to assign all of the species within this range an adaptation number in a manner similar to the assignment of such numbers in upland forest studies in Wisconsin (Curtis and McIntosh 1951, Brown and Curtis 1952). By using the bar diagrams as a basis, adaptation numbers were assigned to the 12 species for which diagrams are available. Adaptation numbers were then assigned to species of lesser importance on the basis

of their association with species for which adaptation numbers were available. Adaptation numbers are shown in Table III.

Adaptation numbers afford a means of computing weighted values for the various species included in a sample from a stand. The weighted value of a species is obtained by multiplying its importance value by its adaptation number. Since the importance values in each stand total 300 and the adaptation numbers range from 1 to 10 it is theoretically possible to have a pure Salix nigra stand with a total stand value of only 300, while a pure Acer saccharum stand would have a value of 3000. Since all of the stands in the present study were composed of more than one species, the situations suggested above were not encountered. Instead, the weighted values of several species were summed in order to obtain a stand value to which the constituent species all contributed on the basis of both importance values and adaptation numbers. Summation of weighted values for every stand and collocation of the 114 stands revealed that the stand values ranged from 321 to 2757, with reasonably good distribution of stands over the whole range. It appears that the stands constitute a compositional gradient comparable to the upland forest continuum of Curtis and McIntosh (1951) and Brown and Curtis (1952).

By plotting importance values along the compositional gradient it is possible to ascertain whether the assignment of adaptation numbers has been made properly. The location of a stand along the vegetational gradient is heavily dependent upon the adaptation numbers assigned to the dominant species of the stand. The location of a plotted point representing a high importance value is to a great extent determined by

TABLE III. Adaptation numbers of lowland tree species.

TABLE III

1.	Salix amygdaloides	1
2.	Salix nigra	1
3.	Populus deltoides	2
4.	Acer negundo	3
5.	Betula nigra	3
6.	Platanus occidentalis	3
7.	Acer saccharinum	4
8.	Gleditsia triacanthos	4
9.	Quercus bicolor	4
10.	Fraxinus pennsylvanica	5
11.	Quercus macrocarpa	5
12.	Carya ovata	6
13.	Fraxinus nigra	6
14.	Juglans nigra	6
15.	Quercus alba	6
16.	Ulmus americana	6
17.	Acer rubrum	7
18.	Betula lutea	7
19.	Carya cordiformis	7
20.	Juglans cinerea	7
21.	Quercus rubra	7
22.	Tilia americana	7
23.	Celtis occidentalis	8
24.	Fraxinus americana	8
25.	Gymnocladus dioica	8
26.	Ulmus rubra	8
27.	Carpinus caroliniana	9
28.	Ostrya virginiana	9
29.	Acer saccharum	10
30.	Fagus grandifolia	10

"feeding back" the effect of the adaptation number into the determination of the position of the stand along the gradient. The location of a plotted point representing a low importance value of a species is greatly affected by the adaptation values assigned to other species since other species will be the dominant species and will, of course, play a greater role in the determination of the position of the stand along the compositional gradient. If the assignment of adaptation numbers has been made properly the higher importance value points should be centered above a symmetrically arranged concentration of points representing lower values. The assignment of the adaptation number of 7 to Fraxinus nigra led to the arrangement of points as shown in Figure 14 in which the higher values fall somewhat too far to the right in relation to the lower points. The arrangement of plotted points when an adaptation number of 6 was used, as shown in Figure 15, displays somewhat better symmetry.

Importance values for 18 of the most common tree species were plotted along the compositional gradient in a manner illustrated by Figure 15 for Fraxinus nigra. For each species the average importance value for each 100-unit interval of the compositional gradient was calculated, and moving averages were determined from the 100-unit averages. Five species with high importance values, Salix nigra, Populus deltoides, Acer saccharinum, Ulmus americana, Tilia americana, and Acer saccharum, are placed on one graph (Figure 16). The even taper of the "tails" of every one of the curves in Figure 16 seems to indicate that the proper choice of adaptation numbers for all five species was made. Since the species with high importance values greatly

influence the position of the stand along the compositional gradient, symmetrical curves of far less influential minor species provide a somewhat separate means of confirming the propriety of assignment of adaptation numbers (Brown and Curtis 1952). Curves for tree species with lesser importance values are shown in Figures 17, 18, and 19. The scale for the importance values has been chosen to portray best the behavior of the species along the compositional gradient. The curves for Ulmus americana and Fraxinus pennsylvanica indicate strikingly great amplitudes along the compositional gradient; yet both these species have curves with definite and localized peaks. Of the 18 curves for tree species, at least one species peaks in every one of the nine 300-unit intervals of the compositional gradient. If the six "major" species are excluded from consideration there are still curves peaking in seven of the nine intervals, the two empty intervals being at the lower end of the gradient. In other words the curves of all 18 species show localized modes along the gradient, the different modes being well distributed over the whole gradient. There is somewhat greater concentration of peaking curves along the upper portion of the gradient; however there seem to be no groupings of curves which can be superimposed on one another with satisfactory agreement of lines.

Comparisons of the behavior of trees and saplings of the same species along the compositional gradient (Figures 20 to 27) indicate considerable variation inthe relative patterns and positions of the two curves. In all species except Quercus bicolor the sapling curve attains a peak at lower values on the compositional gradient than does the tree curve and the sapling curve displays a descending line at the

place where the tree curve peaks. In most of the species represented by curves, the sapling curve descends to small values somewhat lower on the gradient scale than does the tree species curve. In the cases of Betula nigra, Acer saccharinum, and Fraxinus nigra, the descending tree and sapling curves tend to converge at the higher end of the compositional gradient. The portions of the two curves of Tilia americana at the lower end of the gradient scale converge at low values; nevertheless the sapling peak of Tilia occurs somewhat lower on the gradient scale than does the tree peak.

The orderly behavior of herbs along the compositional gradient affords an independent method of corroborating the verity of the adaptation number assignments. In a forest environment highly influenced by the trees, it seems plausible that herb compositional changes, both qualitative and quantitative, should be a reflection of compositional gradations of the woody constituents. Most of the species (Figures 28-34) display symmetrical curves and easily discernible peaks along the compositional gradient. Two species, Cryptotaenia canadensis and Laportea canadensis, occur in abundance over the whole range of stands studied. Rhus radicans and Parthenocissus inserta also show large amplitudes, these latter two species being scarce at the lower end of the gradient. The behavior of five species of grasses is shown in Figure 34. The curves of all five overlap along a short segment of the gradient.

A total of 380 species of herbs and shrubs were identified in the sampling of the 114 stands. Those which were present in at least three stands have been included in the Appendix. This list, which includes 224 species, is merely an effort to indicate the more significant

bottomland species, and presence in a minimum of three stands is an arbitrary choice which tends to eliminate a host of rarely encountered species.

Some general vegetational properties which can be related to the previously established gradient are productivity and species diversity or richness. Because these features depart from considerations of behavior of individual species, they can be considered neither corroborative nor refutative with respect to merits or shortcomings of a compositional gradient. These properties are presented to show their gradual and orderly changes along the independently established gradient. What the curves indicate besides themselves is difficult to determine. The behavior of the curves showing number of species per stand (Figure 35) suggests that both herb and tree species numbers reach a maximum at the same place on the gradient, and above this point both show a similar decline. The number of tree species shows a gradual and continuous rise while the number of herb species exhibits an early drop followed by a rather sharp rise on the gradient. The curve for productivity shows an early rise on the gradient and a marked dip between 1800 and 2100 (Figure 36). In an attempt to learn more about this dip in productivity, the stands from lowlands of manifestly lacustrine origin were separated from stands from lowlands of fluvial origin, while stands from lowland areas of questionable origin were set aside and were not used. In Figure 37 the curves for productivity in both fluvial and lacustrine lowlands indicate that neither curve displays a dip in the 1800-2100 interval. A high concentration of fluvial stands in the 1200-1500 interval and a high concentration of lacustrine stands in the

1800-2100 interval creates a disparity of interval averages that is eliminated when the two groups of stands are separated. The lower productivity values of lacustrine stands over the whole gradient enables a heavy concentration of lacustrine values in any interval to lower the over-all productivity curve. The very existence of different productivity curves for the two groups of stands suggests that further study of the groups separately should be a logical continuation of the present aggregate treatment.

The curves representing values for a number of kinds of soil analyses show smooth and gradual changes along the compositional gradient. The pattern of change of calcium values (Figure 38) resembles the pattern derived from nitrate nitrogen values, (Figure 39), both curves showing rather marked dips in the 1800-2100 interval. The resemblance of the calcium curve to the productivity curve prompted the preparation of another graph on which calcium values are plotted against productivity values. Figure 40 reveals a virtually horizontal line, confirming the suspected basic concomitancy of the behavior of calcium and productivity values but indicating no direct relation of productivity to calcium. Plotted points of summarized values for ammonia nitrogen and for phosphorus disclose a noticeable downward trend along the compositional gradient (Figures 41 and 42). Marked variation in values is apparent at the lower end of the gradient, particularly in the case of phosphorus. The curve for water-holding-capacity shows a smooth and symmetrical peak in that segment of the compositional gradient where stands dominated by Ulmus americana and Fraxinus nigra are found (Figure 43). The plotted points for pH represent

median values for 300-unit classes (Figure 44). With the exception of an initially high value at the low end of the gradient (these values being obtained from fresh sediments of willow swamps), the pH medians indicate a somewhat upward trend of pH values along the compositional gradient.

DISCUSSION

The Compositional Gradient and Physiography

The compositional gradient is a representation of theoretical phytosociological relationships and has no bearing on the areal importance of the various tree species as lowland landscape features. A considerable number of species were encountered frequently enough during the course of the present work to make reliable predictions of their behavior; however in the 114 stands sampled, 70 stands have as the leading dominant either silver maple (*Acer saccharinum*) or American elm (*Ulmus americana*). Although a total of 15 leading dominants were found, a mere pair out of these 15 attain highest importance values in almost two-thirds of the stands (Table I). Occurrence of the same combinations of species in stand after stand sampled is indeed discouraging when occasional samples show combinations which clearly indicate that the range of variation is greater in lowland forests than the repeatedly encountered combinations of silver maple, green ash (*Fraxinus pennsylvanica var. subintegerrima*), and American elm seem to suggest. The explanation of the widespread predominance of a single ecological grouping of tree species can perhaps best be approached by a consideration of physiographic characteristics and dynamics of the whole range of topographic gradations occupied by lowland forests. Floodplains are treated first, followed by a briefer discussion of lacustrine sites.

Brown and Curtis (1952) have analogized the continuum concept to the visible light spectrum in which the primary colors, at least in

their midregions, can be easily located; however the boundaries between certain pairs such as blue and green or red and orange are not so readily distinguished. Conspicuous and easily named communities of lowlands such as willow-cottonwood (Salix nigra-Populus deltoides), silver maple-elm-ash, and red oak-basswood (Quercus rubra-Tilia americana) communities represent rather easily discernible bands of a lowland hardwood forest compositional spectrum. The numerous references in ecological literature to these groups attest to their relative commonness. Relating commonly occurring vegetational groupings to the compositional gradient affords a means of orienting various other treatments of lowland woody communities in relation to the current work on Wisconsin lowland hardwoods.

The willow-cottonwood community is materialization of ecesic phenomena starting from simultaneous seeding by either or both species on moist soil by tiny windborne disseminules which exhibit strikingly similar phenological and morphological characteristics (Williamson 1913). Where a receptive area is fortuitously seeded by both cottonwood and willow, the proportionate survival of each is closely related to the moisture changes of the weeks following germination. Cottonwood forms a taproot while willow roots tend to spread laterally. Any drop in the water table favors greater survival of cottonwood (Barclay 1924). The necessity for exposed moist soil for initiation is a physiographic and edaphic limitation which tends to hold willow and cottonwood occurrences together. Relative proportions of these species in various stands are legion; however since these two species are almost the only ones in Wisconsin which form forest growth on fresh

deposits of moist fluvial or lacustrine sand or silt, they form a natural grouping which has been noted frequently in ecological work (Braun 1916, Shull 1922, Barclay 1924, Hefley 1937, Little 1938, Lee 1945, McVaugh 1938, Shimek 1948). Communities of these two species can scarcely be expected to occur unless recent physiographic disturbance has occurred.

River birch (Betula nigra) and swamp white oak (Quercus bicolor) form a rather natural ecological segment of a compositional gradient because both become established best in open places which are somewhat more above the channel of the river than the bars and flats occupied by cottonwoods and willows. Both river birch and swamp white oak occur most abundantly (on the Mississippi confluents in Wisconsin) along those rivers where deposition of sand is most marked. River birch readily becomes established in grazed pastures and in abandoned fields in the bottomlands of the Wisconsin River. Swamp white oak occurs sparingly on low ridges among sloughs in dense bottomland forests, while river birch in similar forests occurs sparingly along the margins of sloughs, frequently with trunks leaning over the sloughs. The stands in which swamp white oak is most important usually occur along the borders of marshes and include open grown swamp white oak trees mixed with river birch, red ash (Fraxinus pennsylvanica) and silver maple. Swamp white oak has only a remote ecological relationship to willow or cottonwood; however river birch is found with cottonwood occasionally. Both swamp white oak and river birch initiate forest communities which are possibly later enriched with several other species. This initiation is comparable to the initiation of cottonwood or willow. It appears that any of the four species may predominate in an initial woody community.

FIGURE 12. Bar diagrams of importance values.

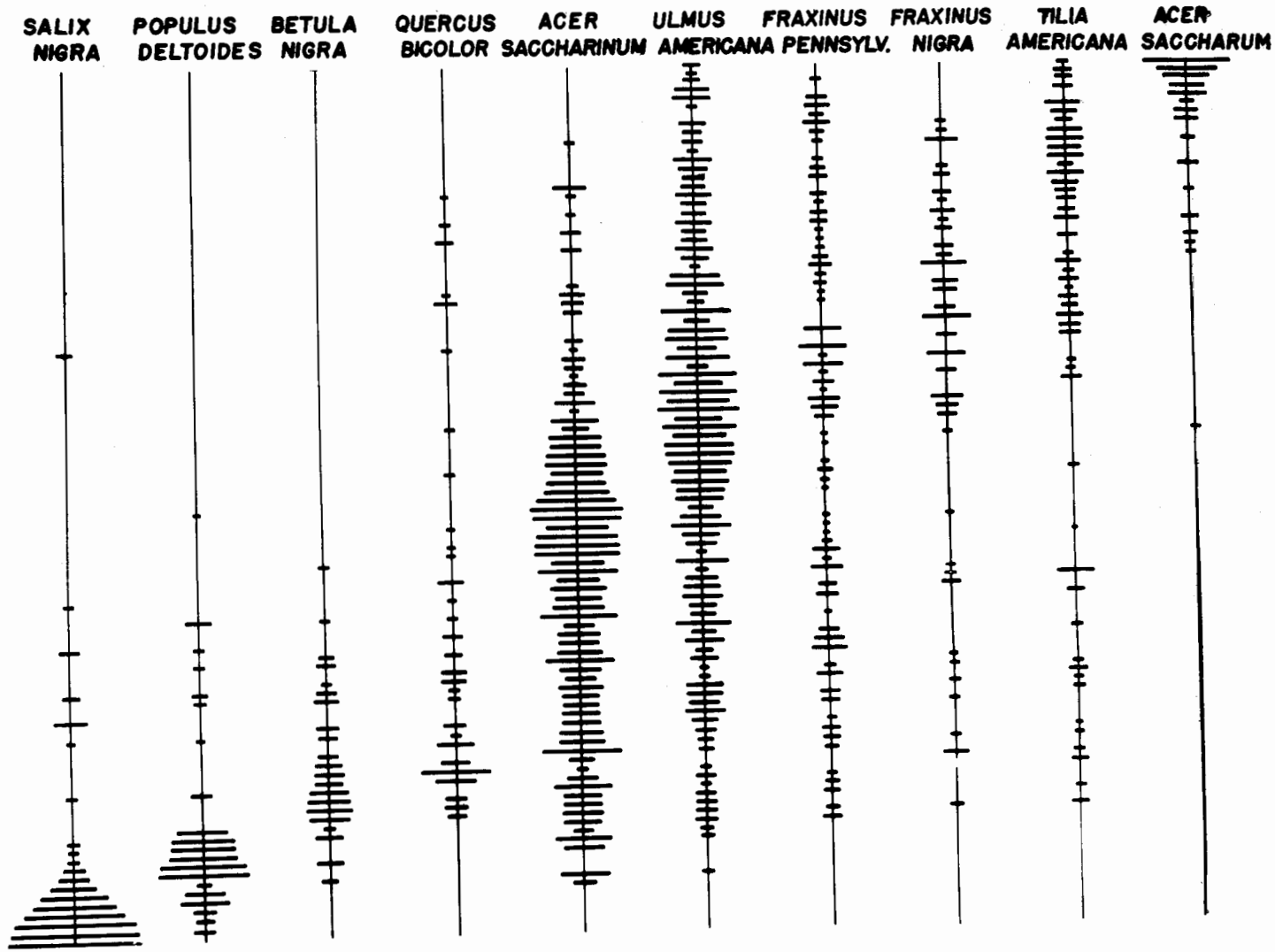

SALIX NIGRA
POPULUS DELTOIDES
BETULA NIGRA
QUERCUS BICOLOR
ACER SACCHARINUM
ULMUS AMERICANA
FRAXINUS PENNSYLV.
FRAXINUS NIGRA
TILIA AMERICANA
ACER SACCHARUM

FIGURE 13. Bar diagrams of importance values.

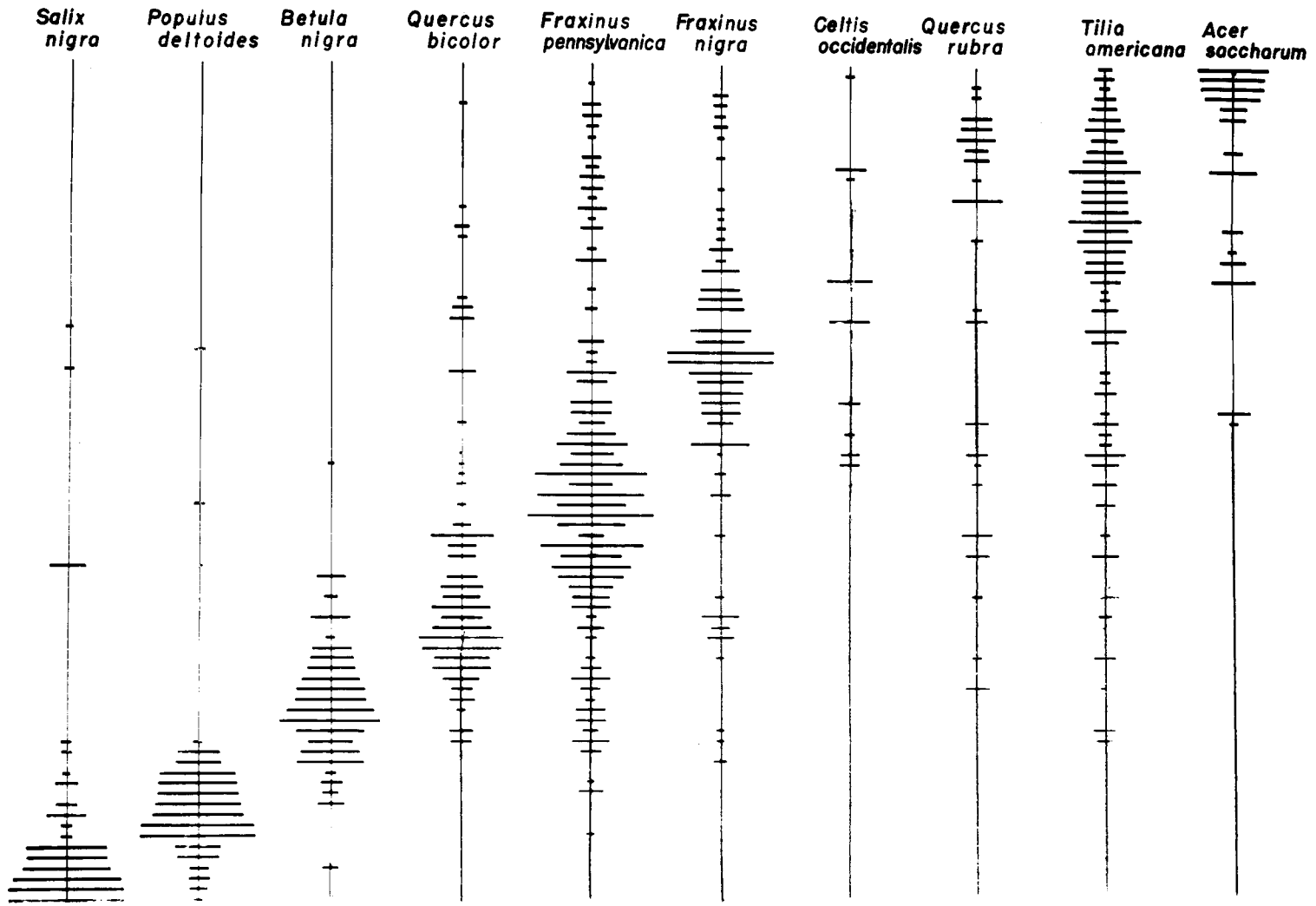

Salix nigra
Populus deltoides
Betula nigra
Quercus bicolor
Fraxinus pennsylvanica
Fraxinus nigra
Celtis occidentalis
Quercus rubra
Tilia americana
Acer saccharum

FIGURE 14. Plotted importance values of Fraxinus nigra with the assignment of an adaptation number of 7.

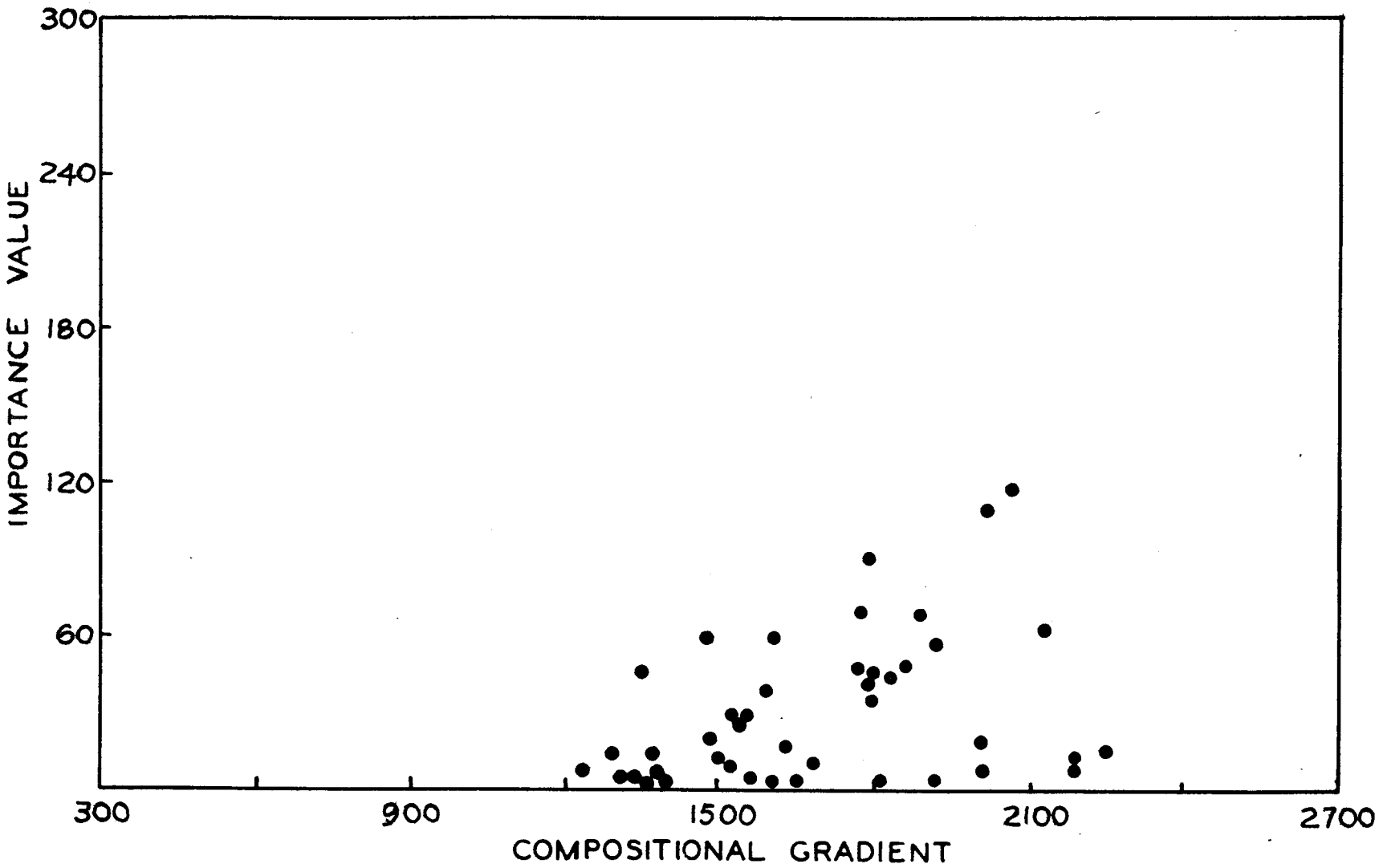

300
240
180
120
60
IMPORTANCE VALUE
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 15. Plotted importance values of Fraxinus nigra with the assignment of an adaptation number of 6.

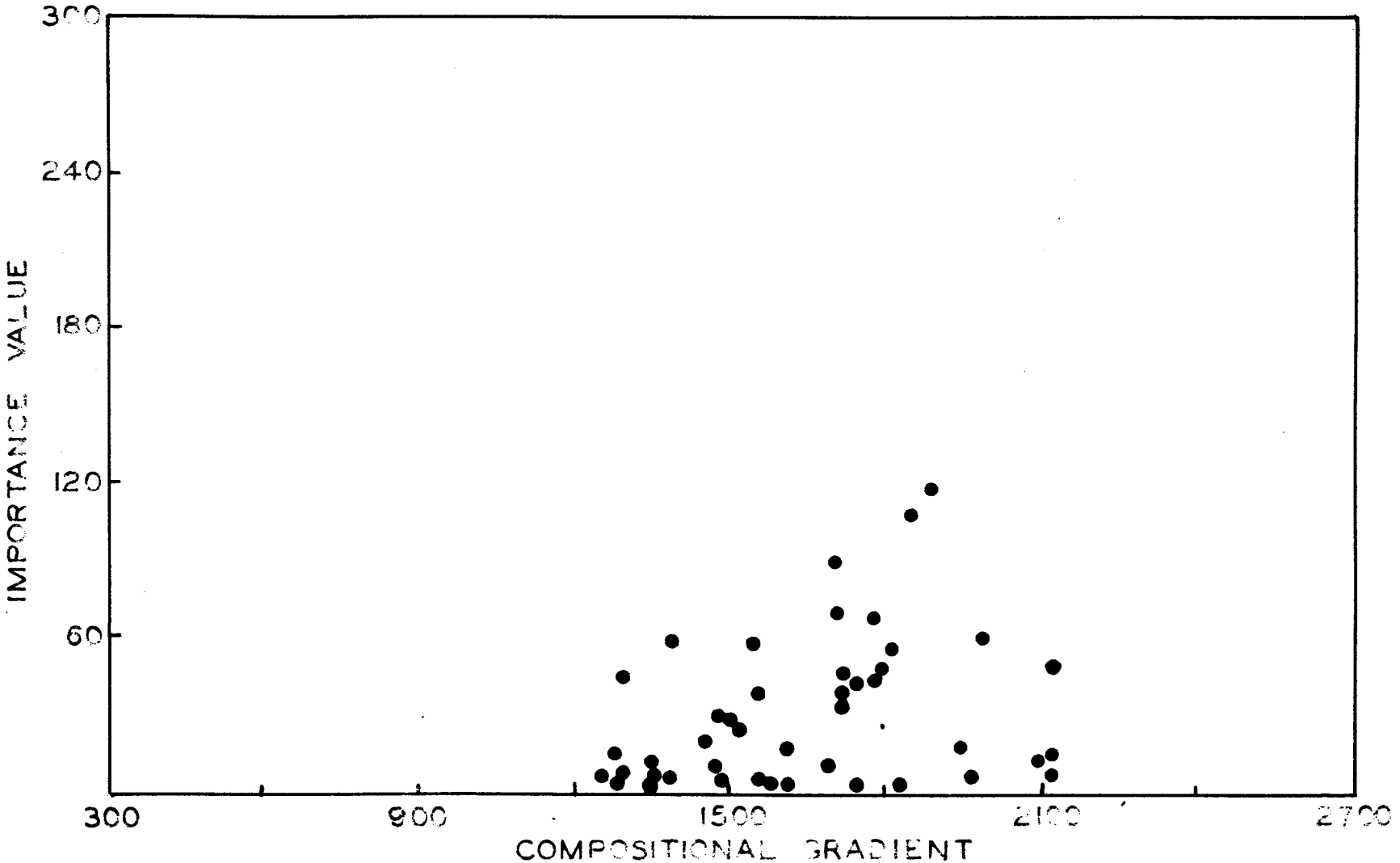

300
240
180
120
60
IMPORTANCE VALUE
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 16. Importance value curves for leading species. Curves are based on average importance values by 100-unit classes of the compositional gradient.

1. *Salix nigra*
2. *Populus deltoides*
3. *Acer saccharinum*
4. *Ulmus americana*
5. *Tilia americana*
6. *Acer saccharum*

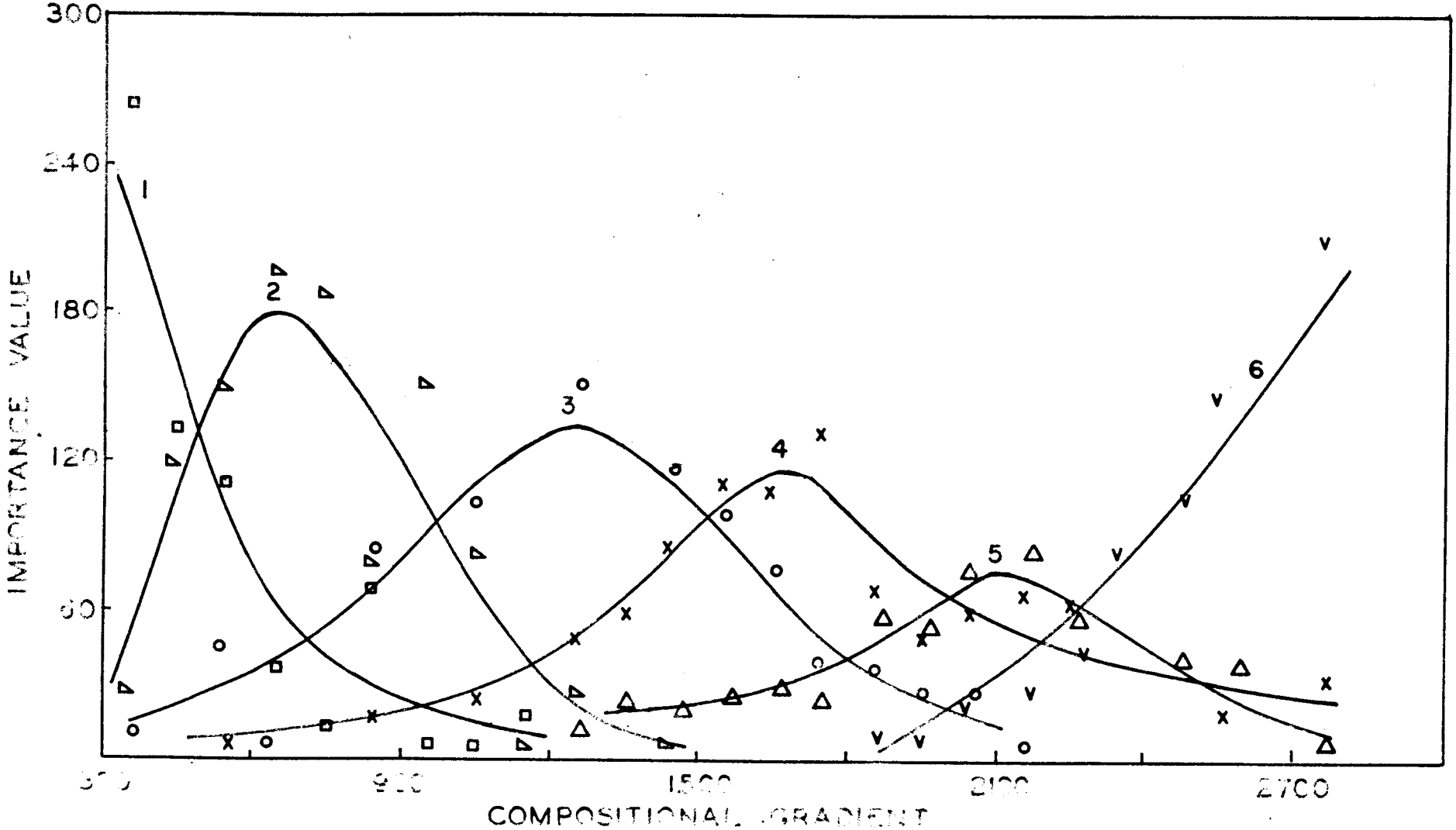

300
240
180
120
60
IMPORTANCE VALUE
1
2
3
4
5
6
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 17. Importance value curves for secondary species. Curves are based on importance value averages by 100-unit classes of the compositional gradient.

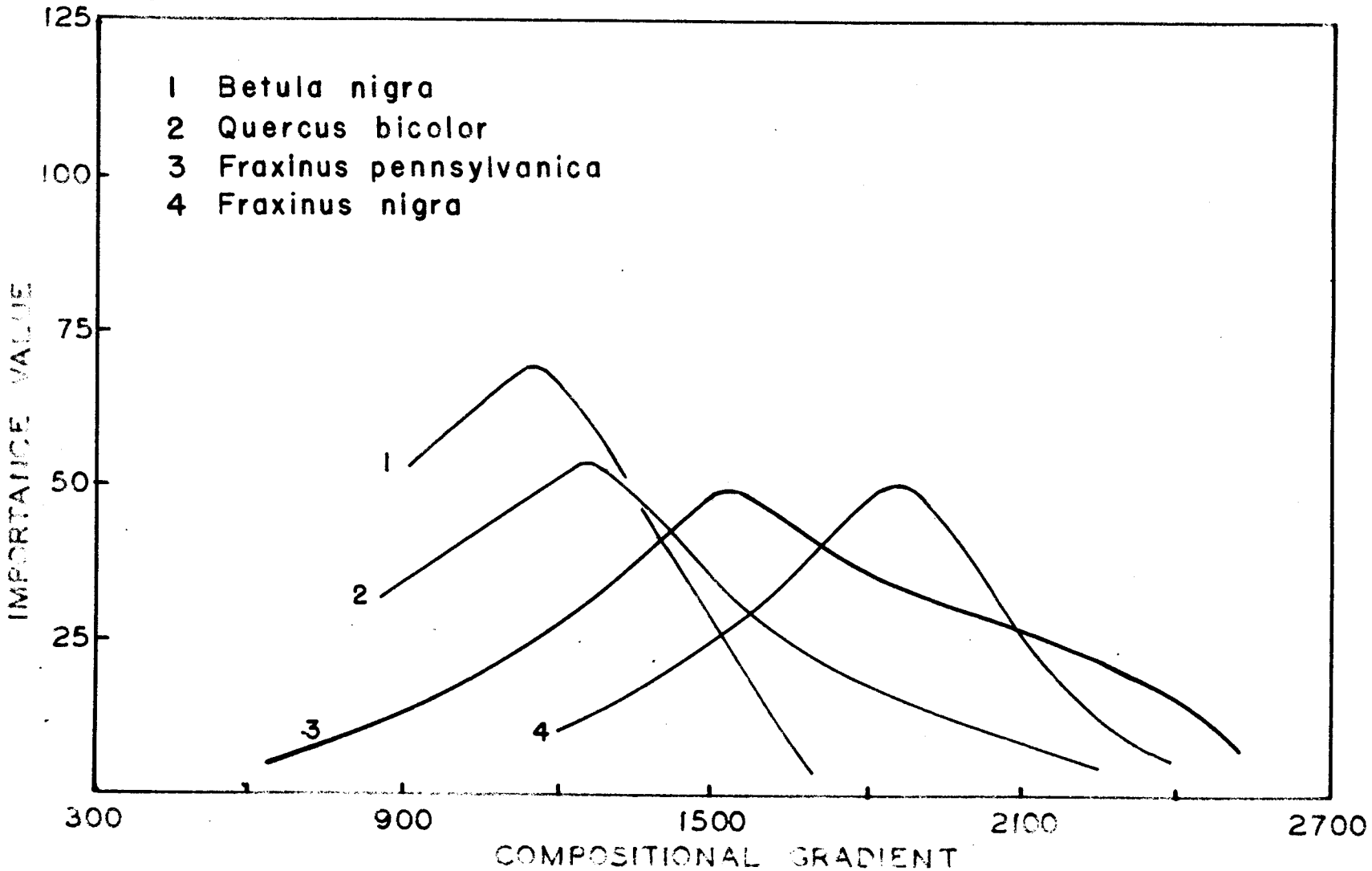

1 Betula nigra
2 Quercus bicolor
3 Fraxinus pennsylvanica
4 Fraxinus nigra
125
100
75
50
25
IMPORTANCE VALUE
1
2
3
4
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 18. Importance value curves for lesser species. Curves are based on importance value averages by 100-unit classes of the compositional gradient.

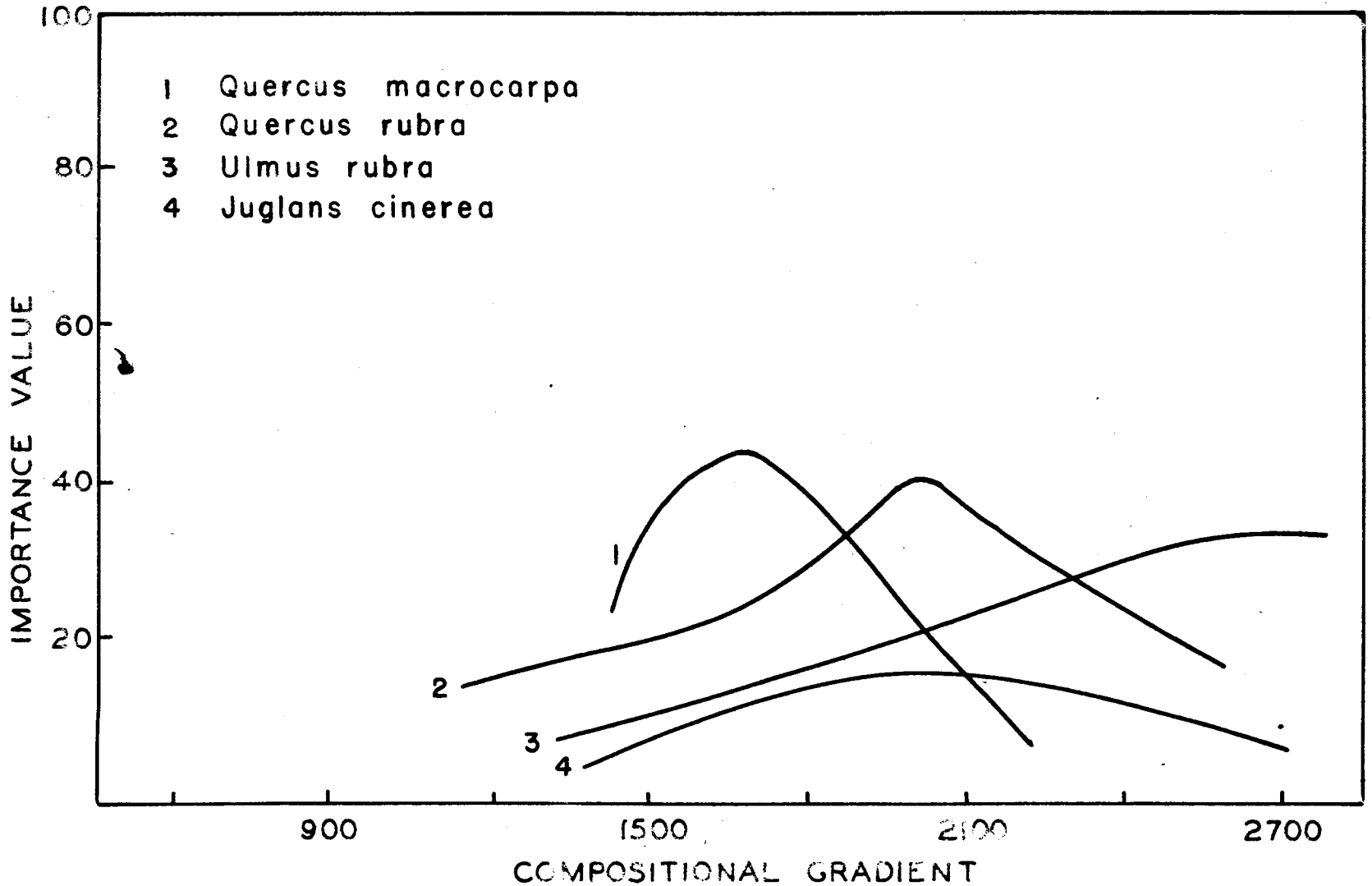

100
80
60
40
20
IMPORTANCE VALUE
1 Quercus macrocarpa
2 Quercus rubra
3 Ulmus rubra
4 Juglans cinerea
1
2
3
4
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 19. Importance value curves for secondary species. Curves are based on importance value averages by 100-unit classes on the compositional gradient.

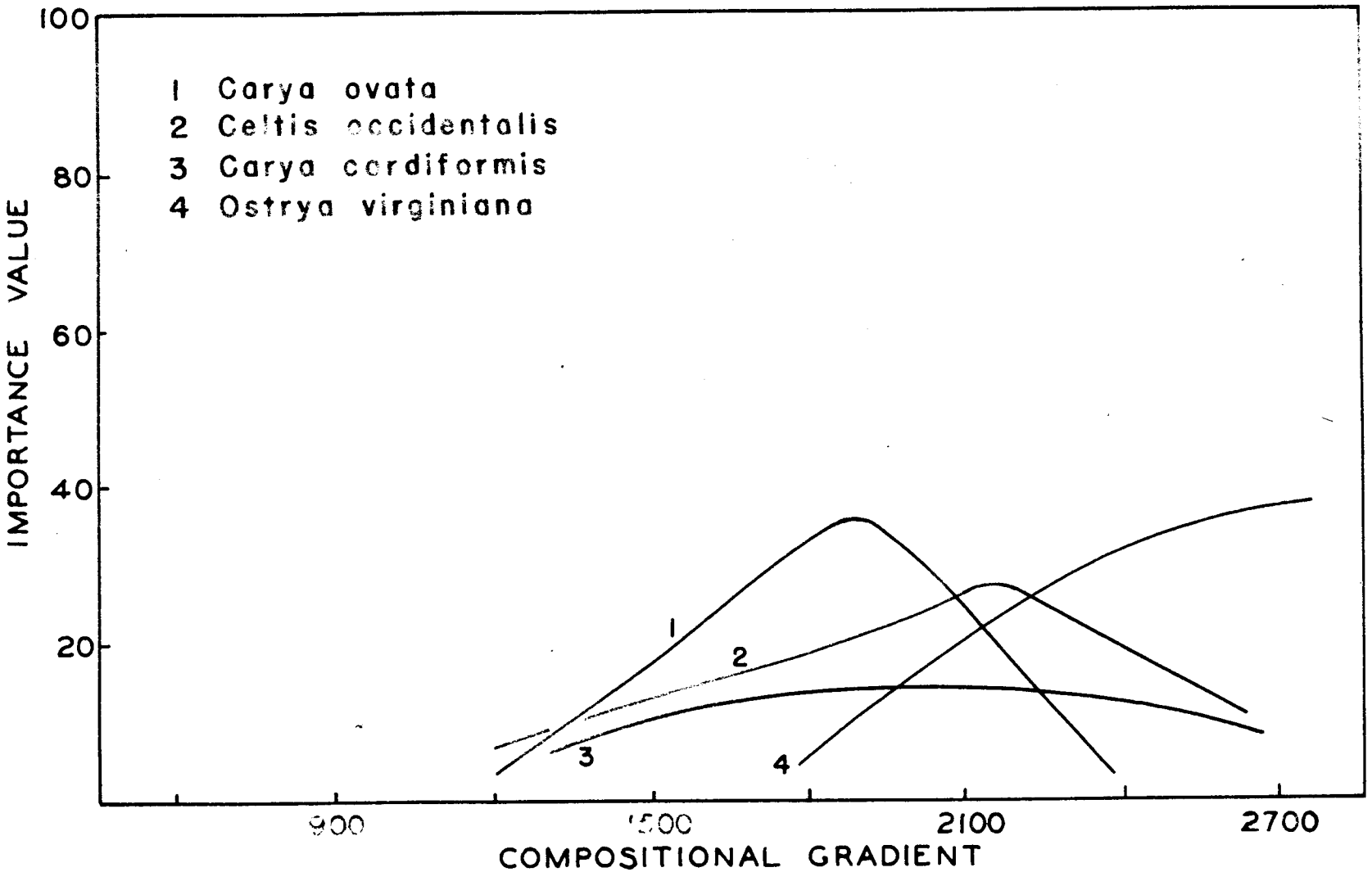

1 Carya ovata
2 Celtis occidentalis
3 Carya cordiformis
4 Ostrya virginiana
IMPORTANCE VALUE
100
80
60
40
20
900
1500
2100
2700
COMPOSITIONAL GRADIENT
1
2
3
4

FIGURE 20. Comparison of trees and saplings of Betula nigra.

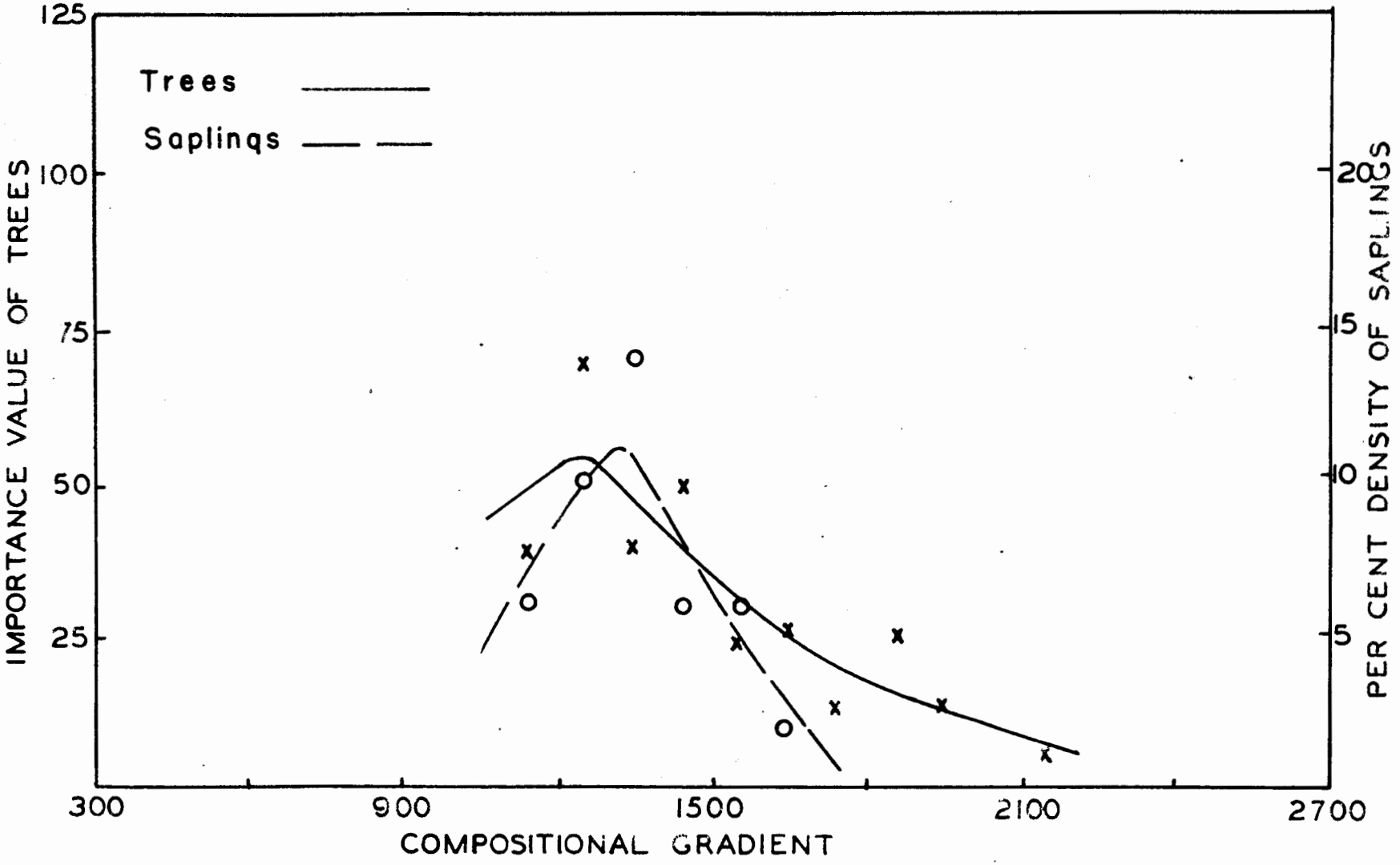

Trees
Saplings
IMPORTANCE VALUE OF TREES
PER CENT DENSITY OF SAPLINGS
125
100
75
50
25
20
15
10
5
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 21. Comparison of trees and saplings of Quercus bicolor.

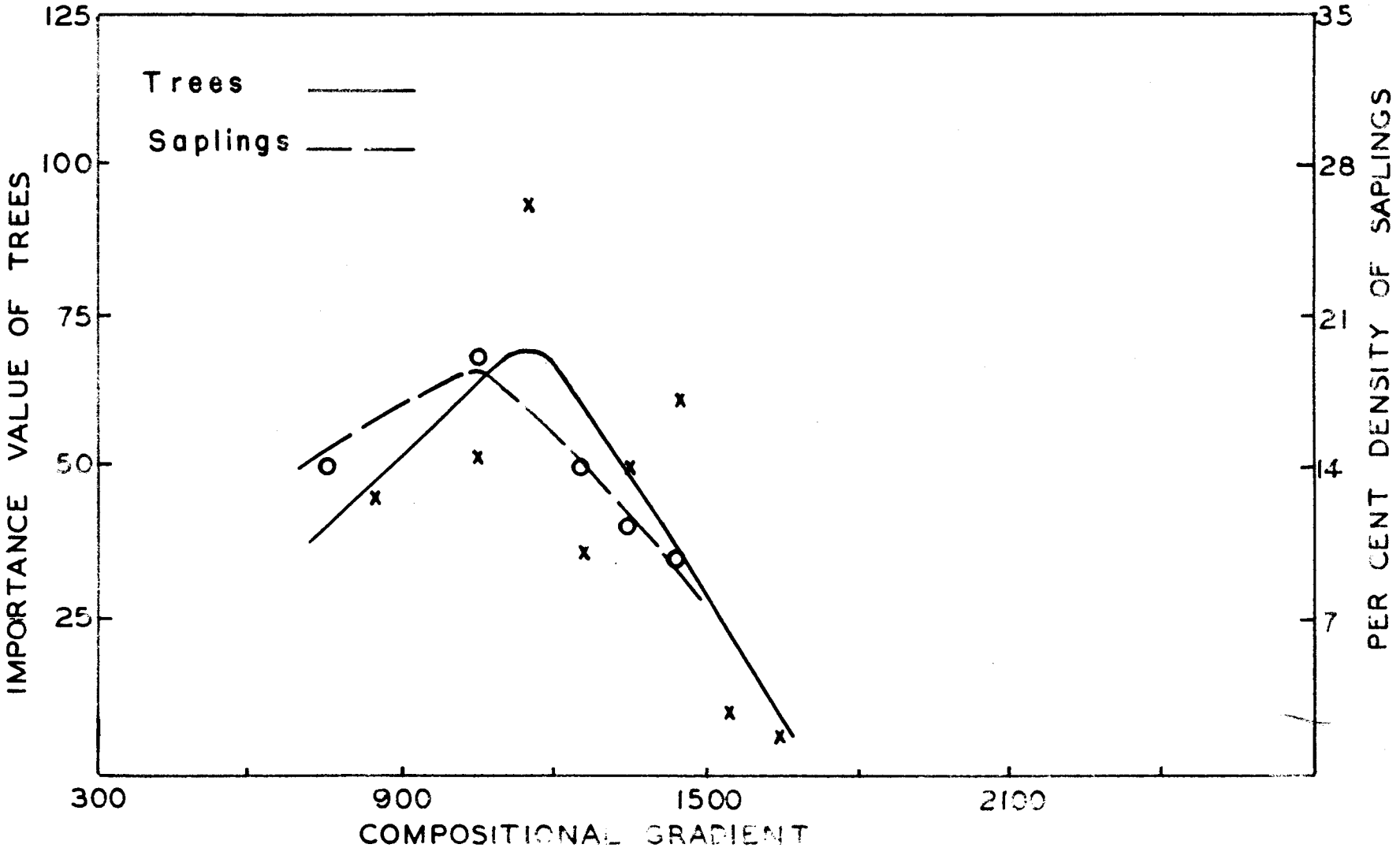

Trees
Saplings
125
100
75
50
25
IMPORTANCE VALUE OF TREES
35
28
21
14
7
PER CENT DENSITY OF SAPLINGS
300
900
1500
2100
COMPOSITIONAL GRADIENT

FIGURE 22. Comparison of trees and saplings of *Acer saccharinum*.

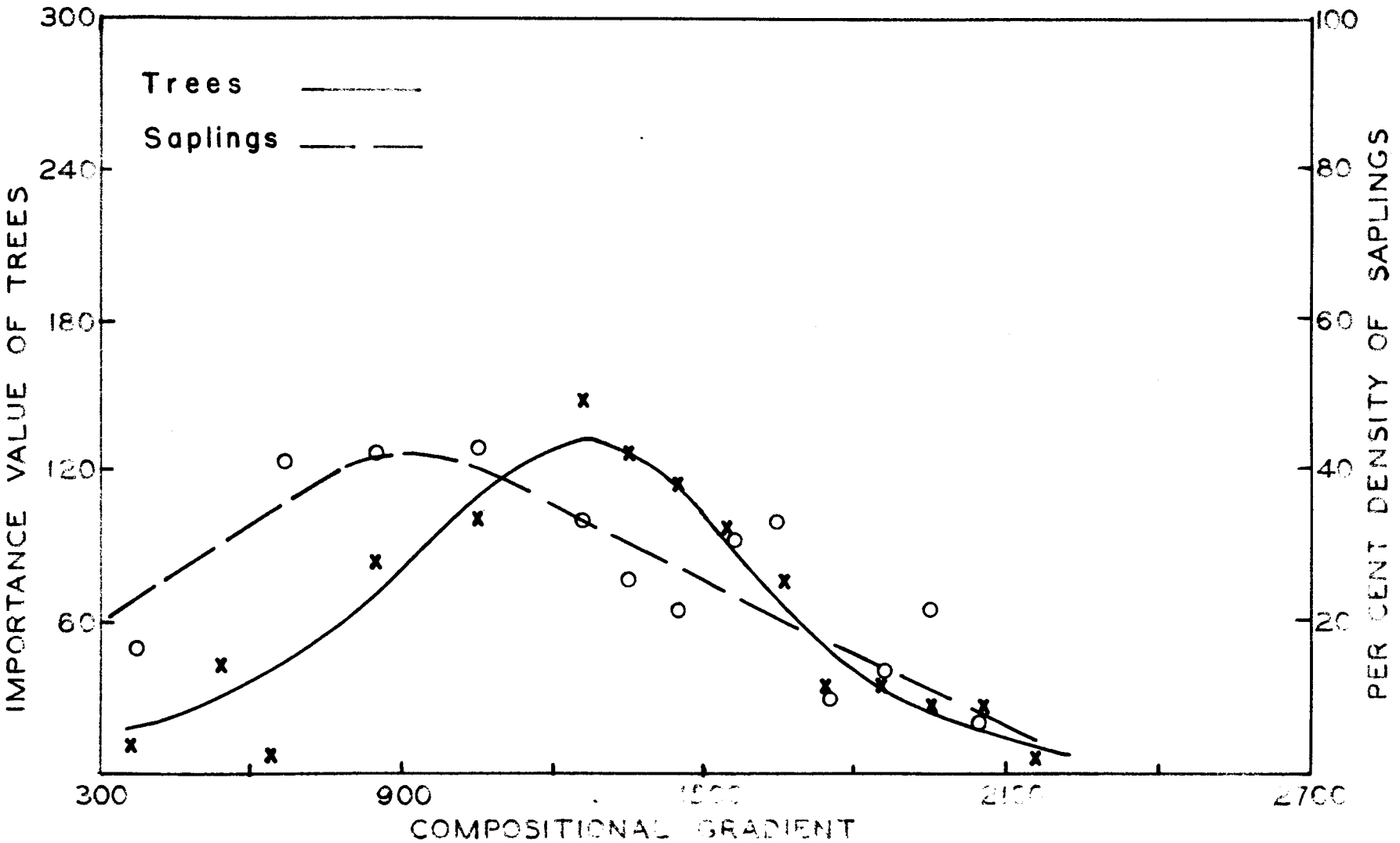

Trees
Saplings
300
240
180
120
60
100
80
60
40
20
IMPORTANCE VALUE OF TREES
PER CENT DENSITY OF SAPLINGS
300
900
2700
COMPOSITIONAL GRADIENT

FIGURE 23. Comparison of trees and saplings of Fraxinus pennsylvanica.

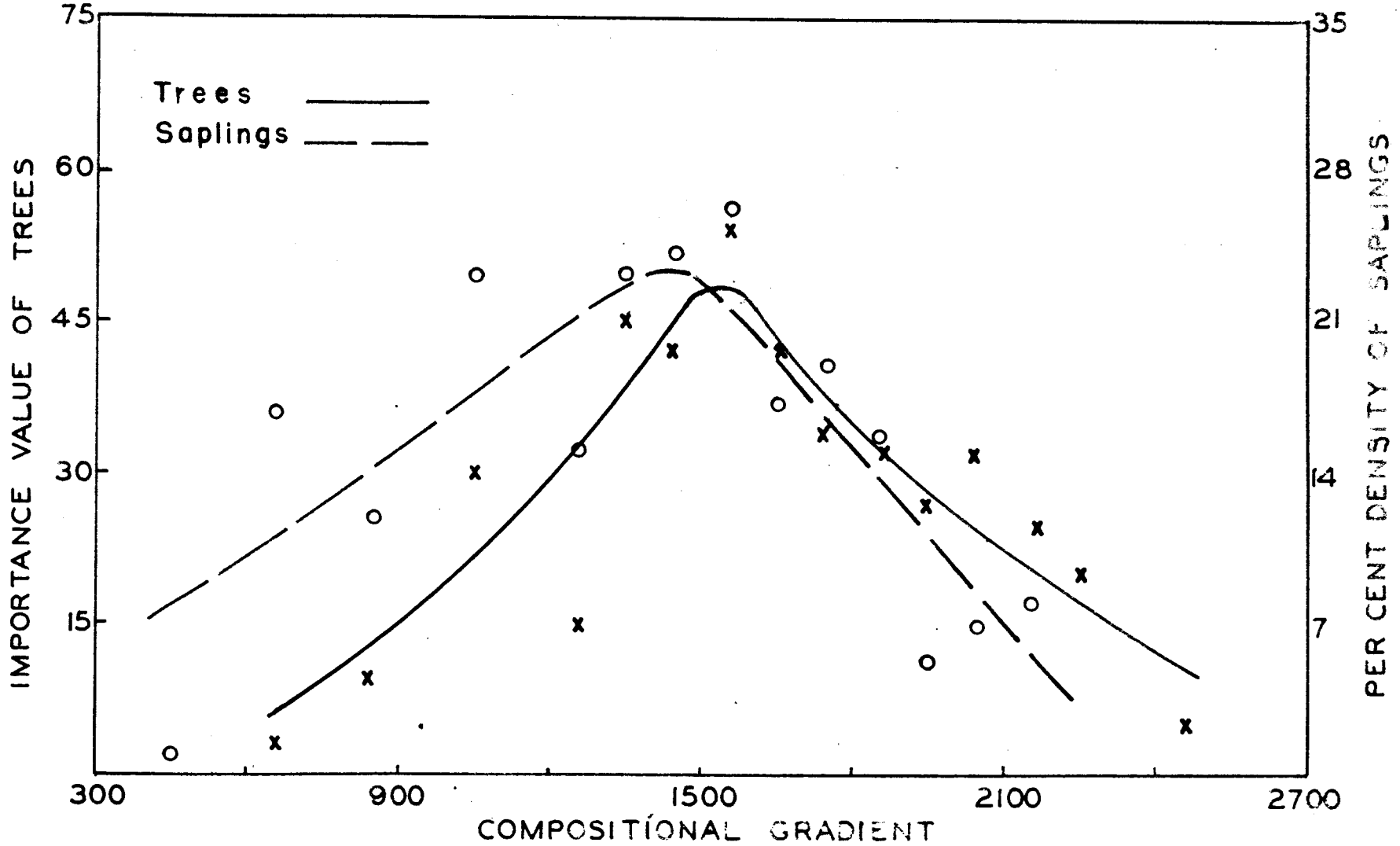

Trees
Saplings
IMPORTANCE VALUE OF TREES
PER CENT DENSITY OF SAPLINGS
75
60
45
30
15
35
28
21
14
7
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 24. Comparison of trees and saplings of Ulmus americana.

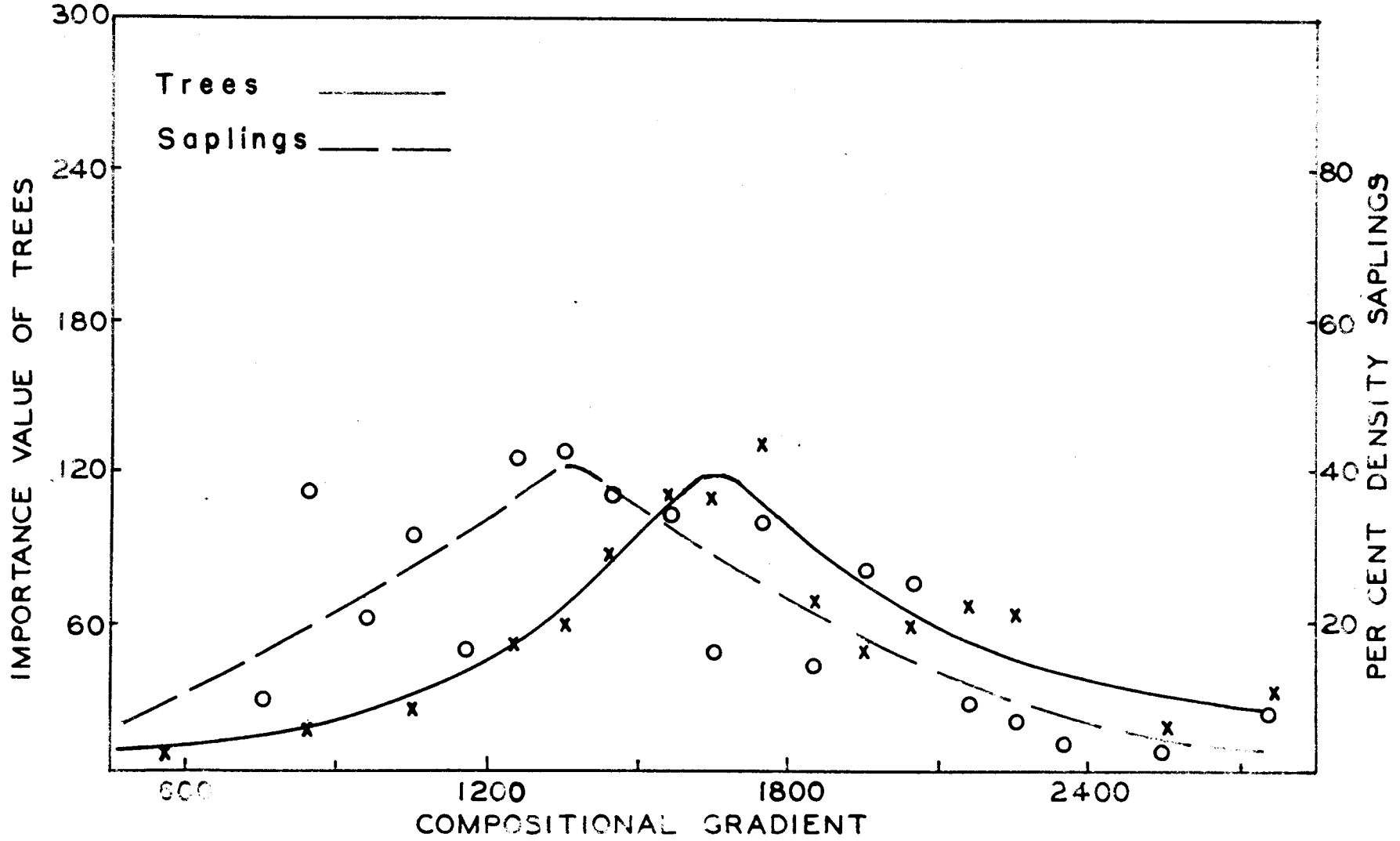

Trees
Saplings
300
240
180
120
60
80
60
40
20
IMPORTANCE VALUE OF TREES
PER CENT DENSITY SAPLINGS
600
1200
1800
2400
COMPOSITIONAL GRADIENT

FIGURE 25. Comparison of trees and saplings of *Fraxinus nigra*.

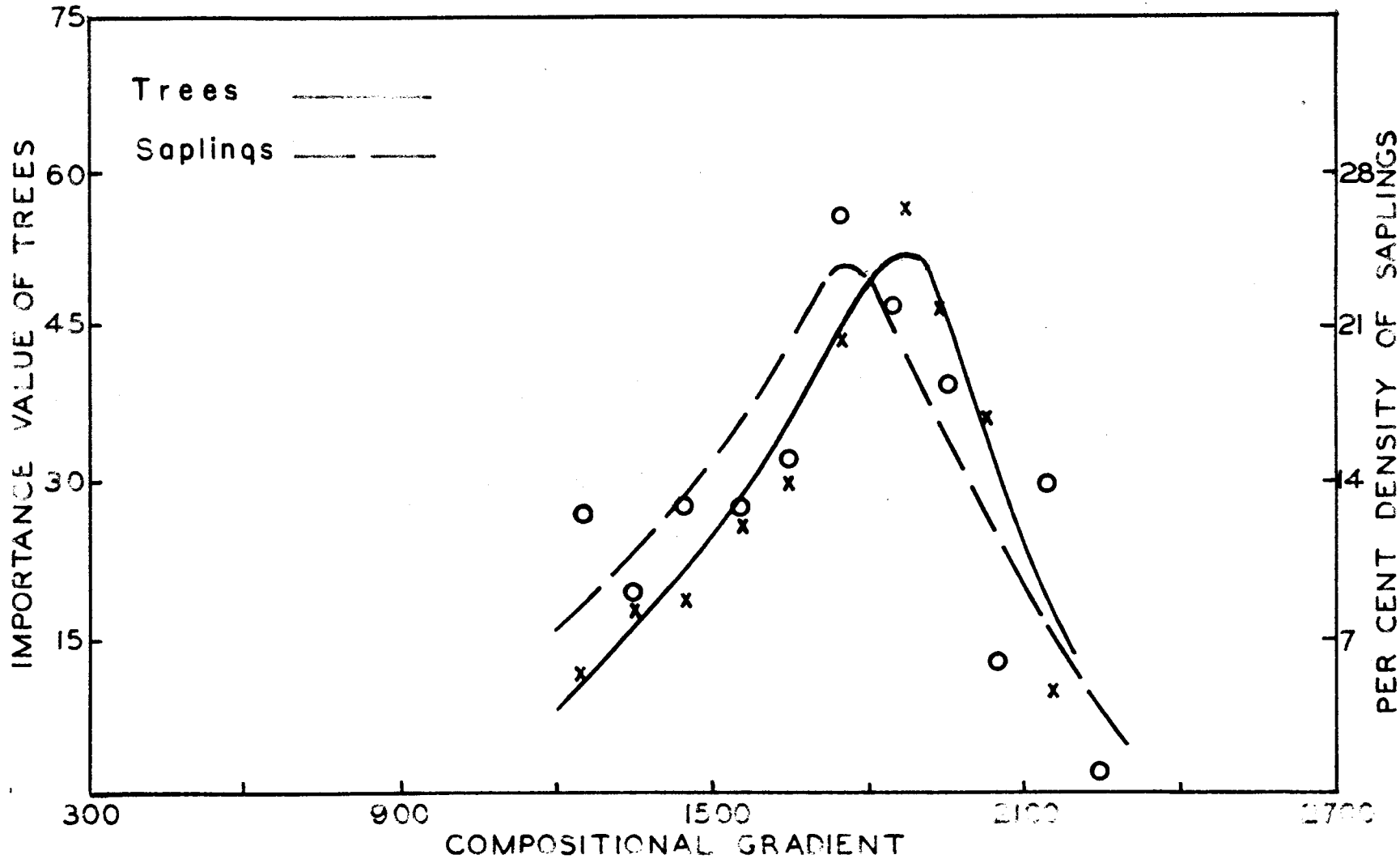

Trees
Saplings
IMPORTANCE VALUE OF TREES
PER CENT DENSITY OF SAPLINGS
COMPOSITIONAL GRADIENT
75
60
45
30
15
28
21
14
7
300
900
1500

FIGURE 26. Comparison of trees and saplings of *Tilia americana*.

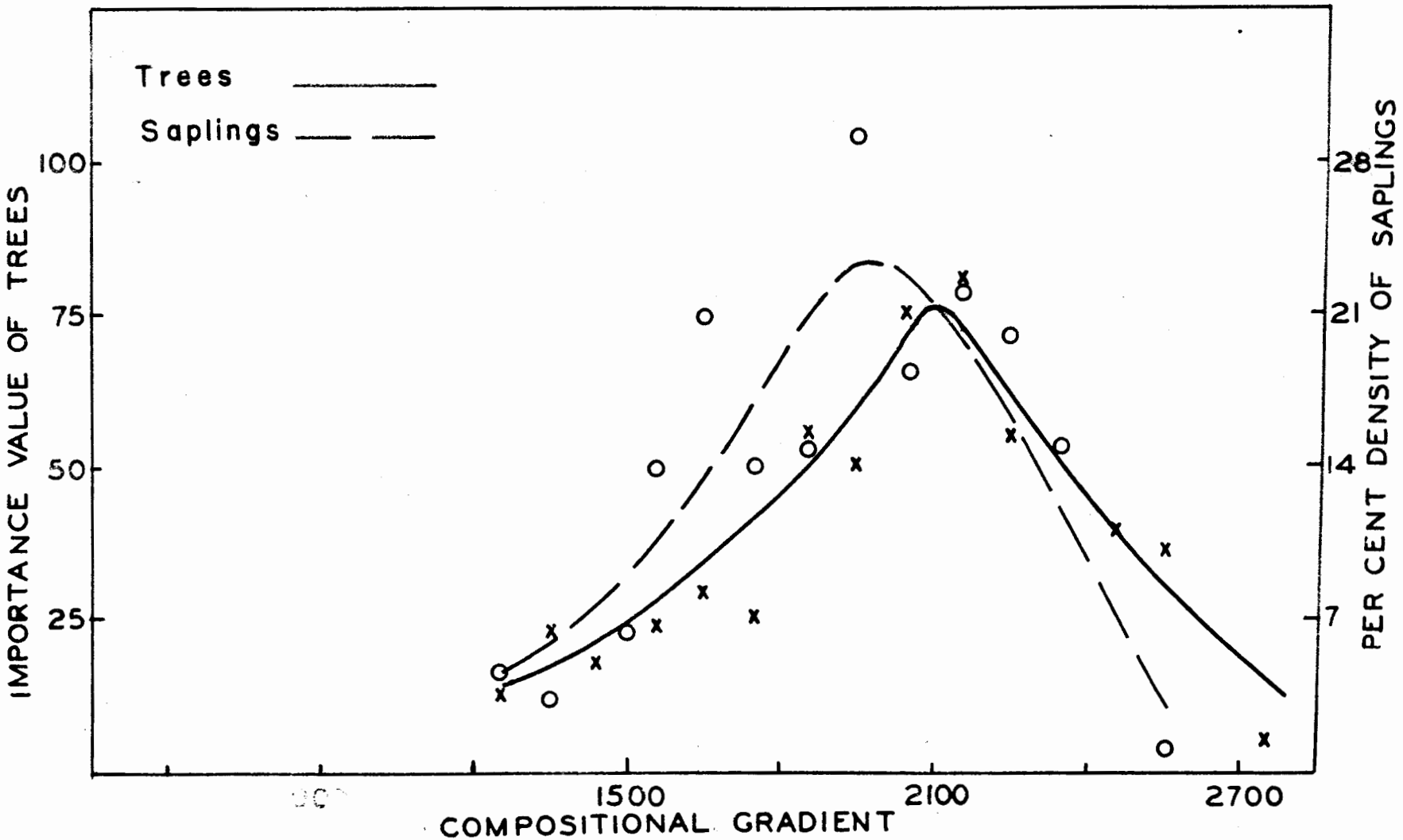

Trees
Saplings
IMPORTANCE VALUE OF TREES
100
75
50
25
PER CENT DENSITY OF SAPLINGS
28
21
14
7
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 27. Comparison of trees and saplings of Acer saccharum.

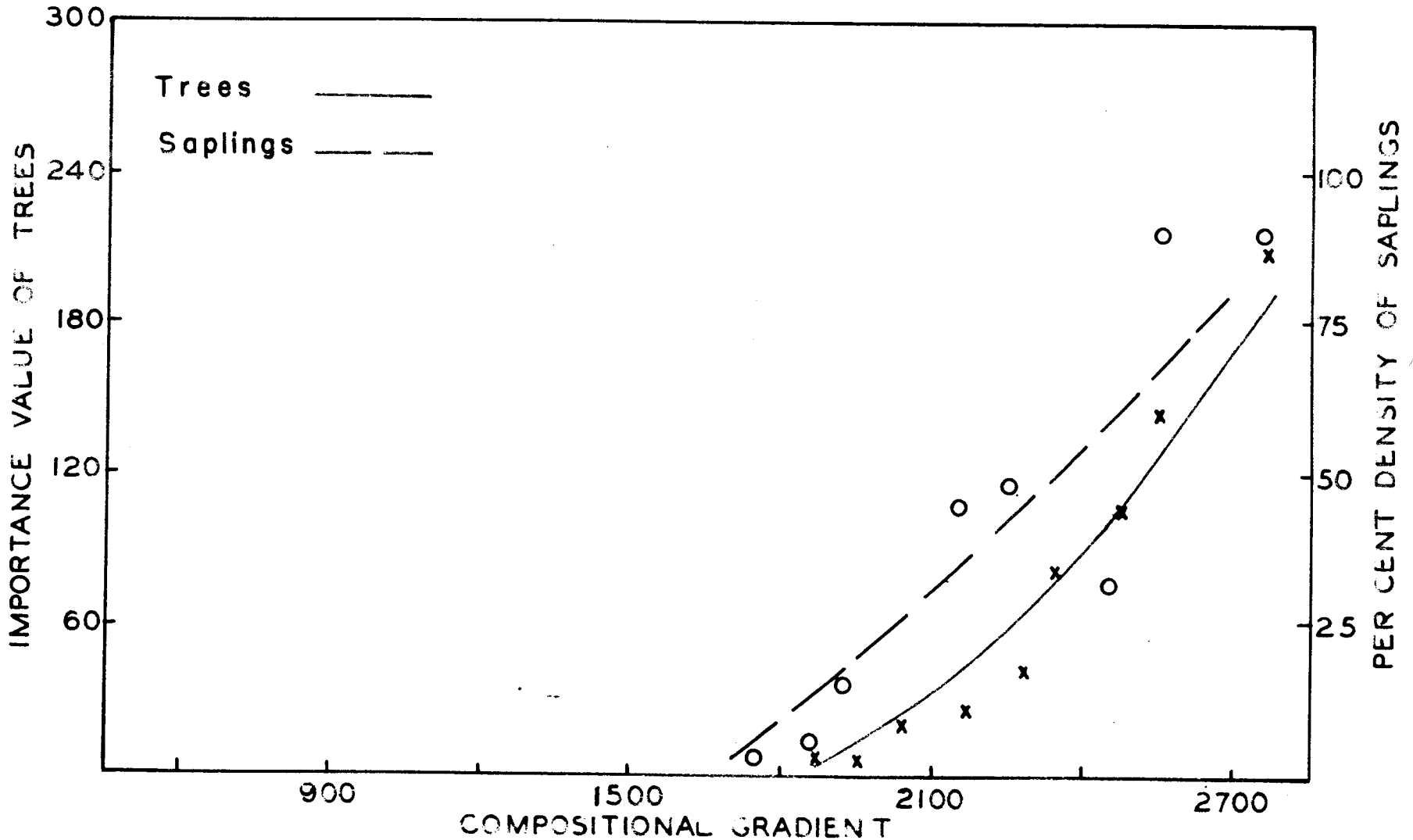

Trees
Saplings
300
240
180
120
60
IMPORTANCE VALUE OF TREES
100
75
50
25
PER CENT DENSITY OF SAPLINGS
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 28. Frequency curves of herb species. Curves are based on frequency averages by 100-unit classes of the compositional gradient.

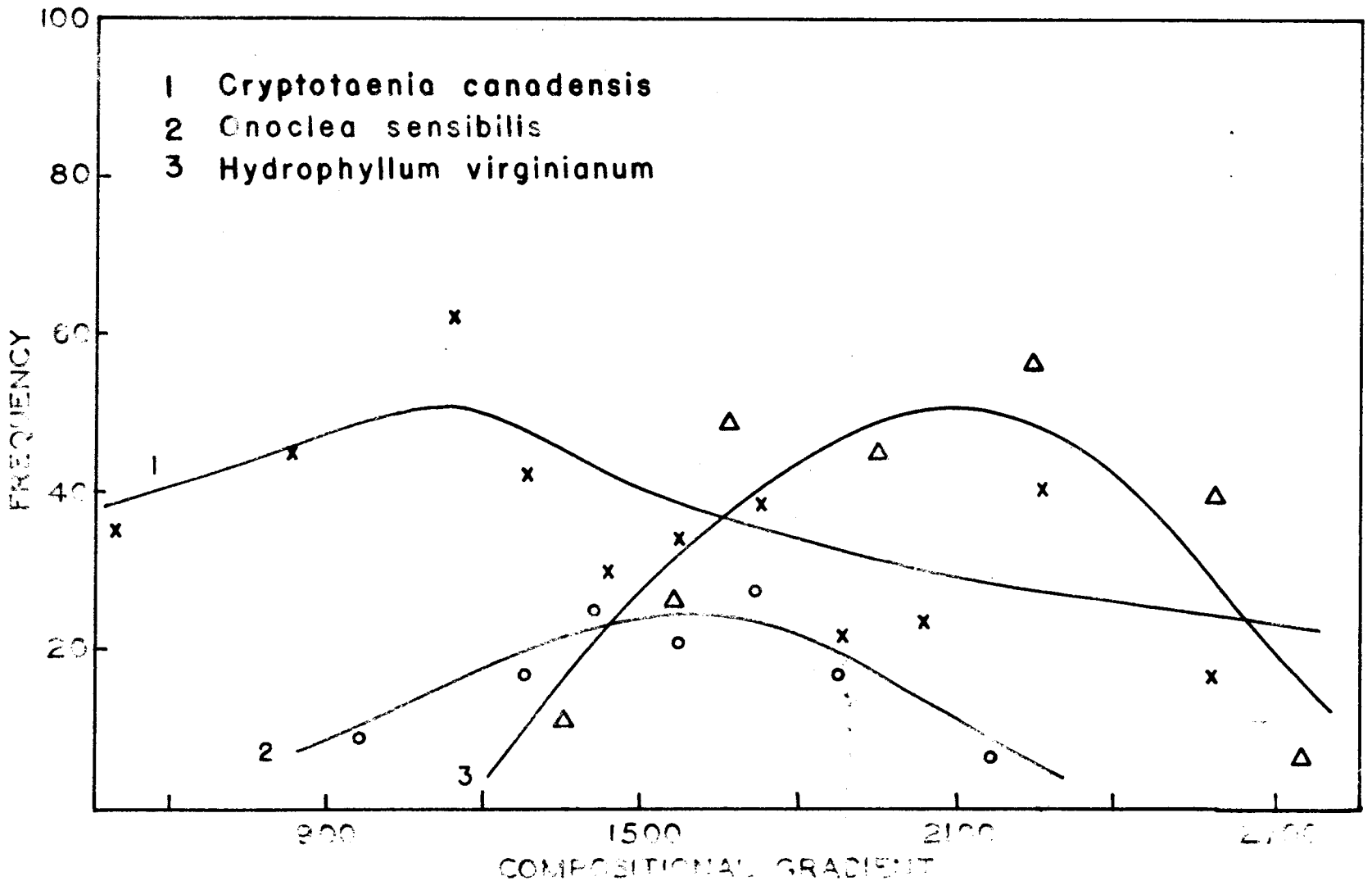

1 Cryptotaenia canadensis
2 Onoclea sensibilis
3 Hydrophyllum virginianum
100
80
60
40
20
FREQUENCY
1
2
3
900
1500
2100

FIGURE 29. Frequency curves of herb species.

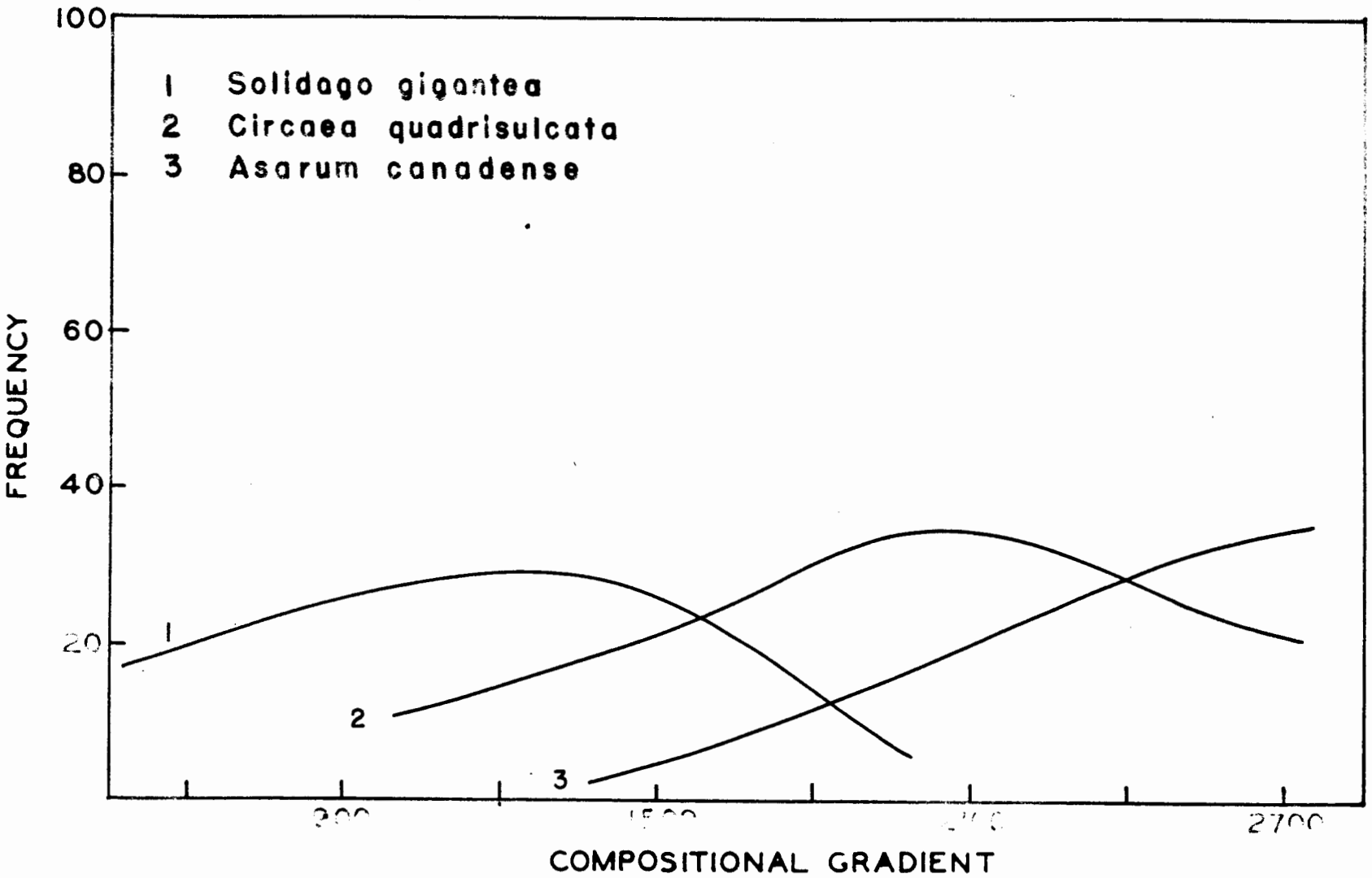

100
80
60
40
20
FREQUENCY
1 Solidago gigantea
2 Circaea quadrisulcata
3 Asarum canadense
1
2
3
2700
COMPOSITIONAL GRADIENT

FIGURE 30. Frequency curves of herb species.

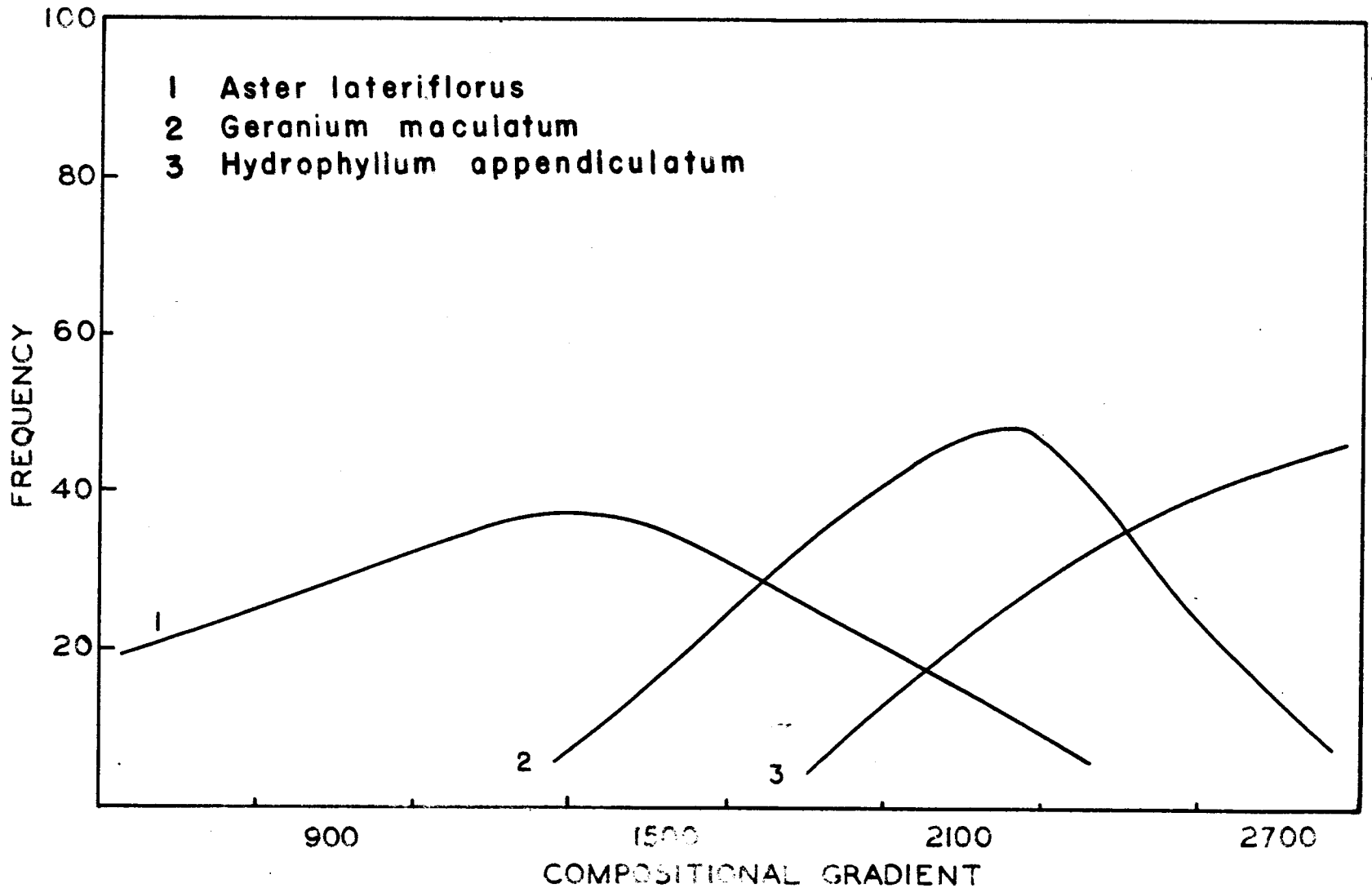

1 Aster lateriflorus
2 Geranium maculatum
3 Hydrophyllum appendiculatum
100
80
60
40
20
FREQUENCY
1
2
3
900
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 31. Frequency curves of herb species.

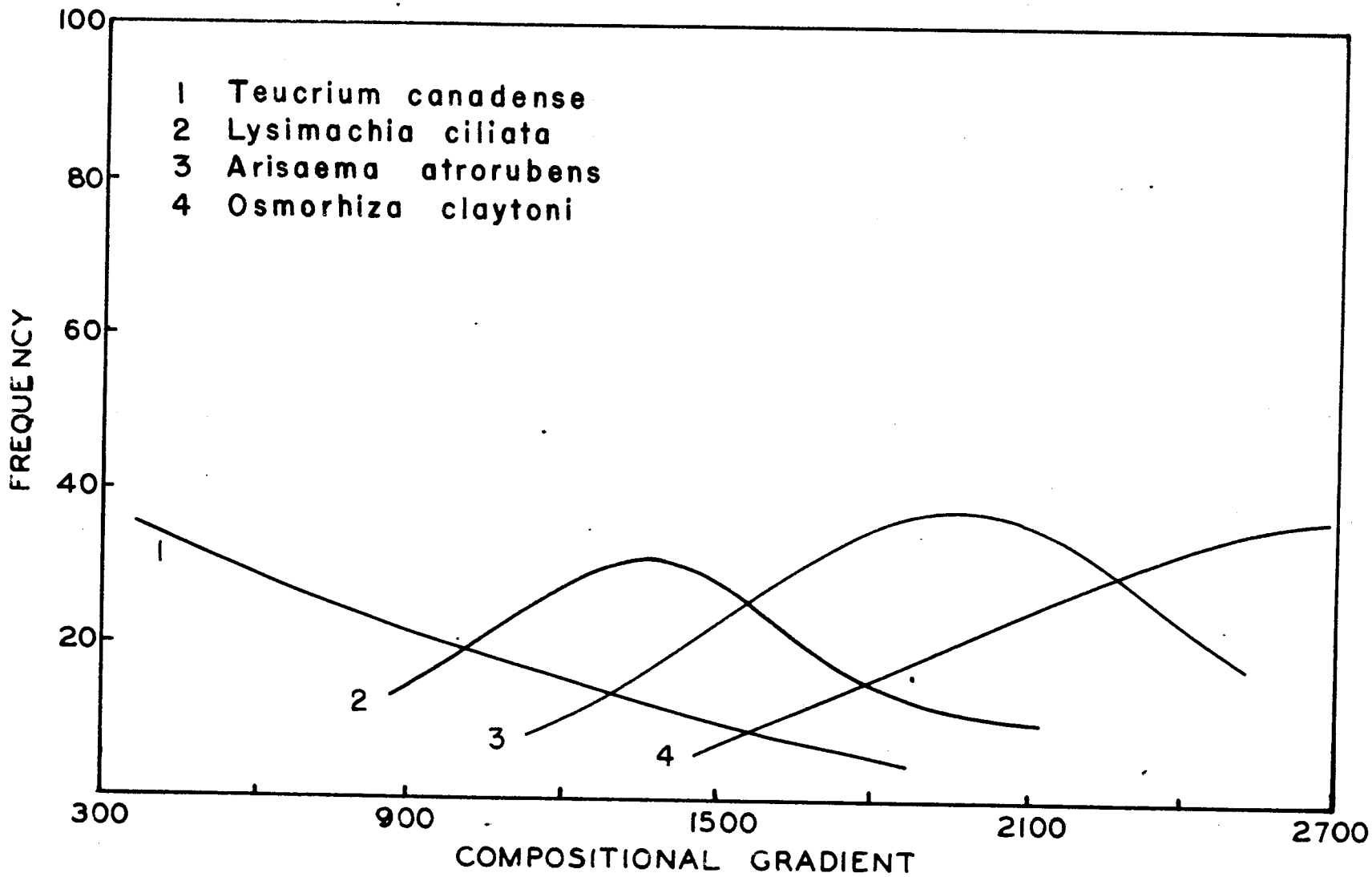

1 Teucrium canadense
2 Lysimachia ciliata
3 Arisaema atrorubens
4 Osmorhiza claytoni
FREQUENCY
100
80
60
40
20
1
2
3
4
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 32. Frequency curves of herb species.

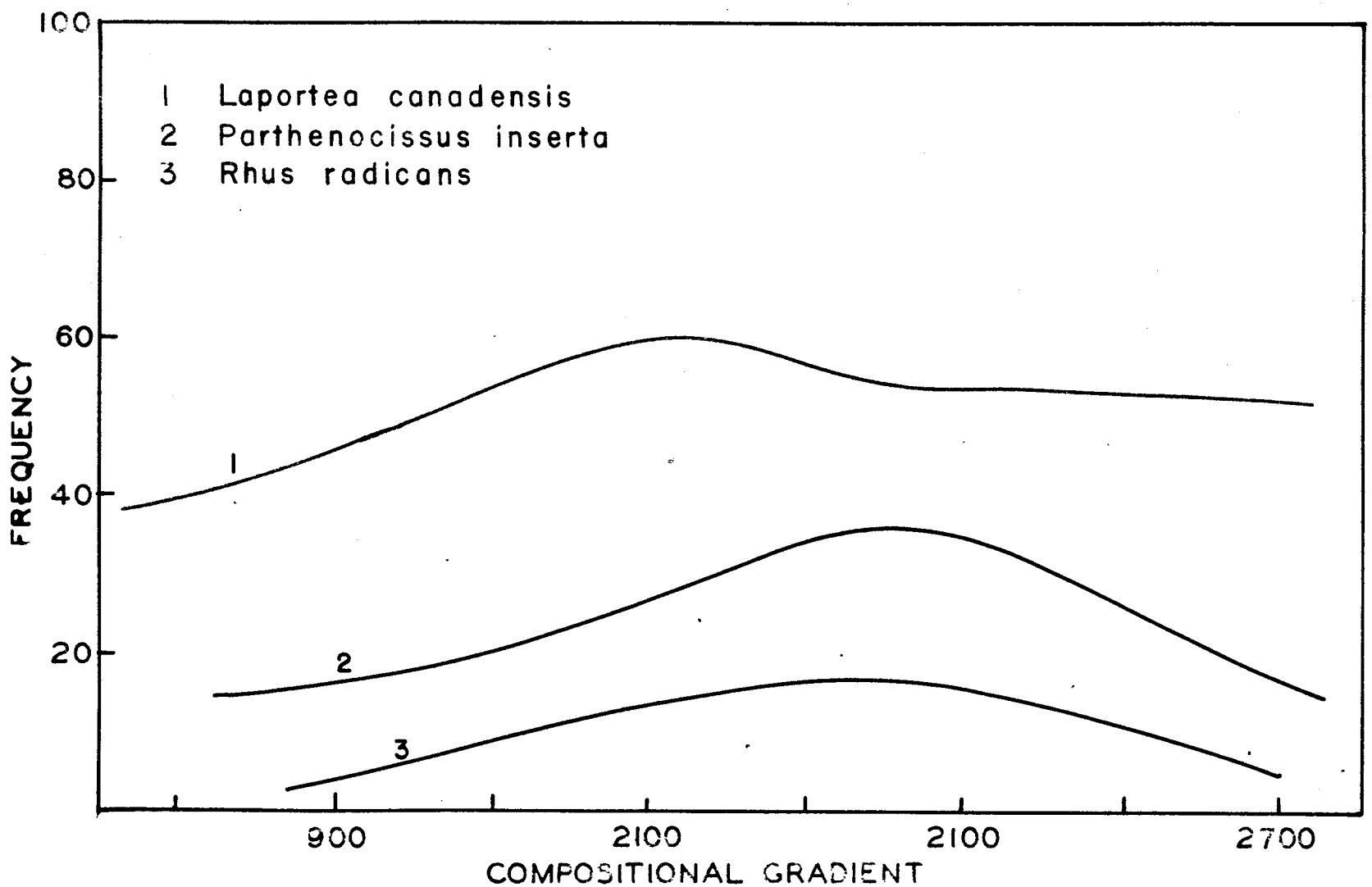

100
80
60
40
20
FREQUENCY
1 Laportea canadensis
2 Parthenocissus inserta
3 Rhus radicans
1
2
3
900
2100
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 33. Frequency curves for herb species.

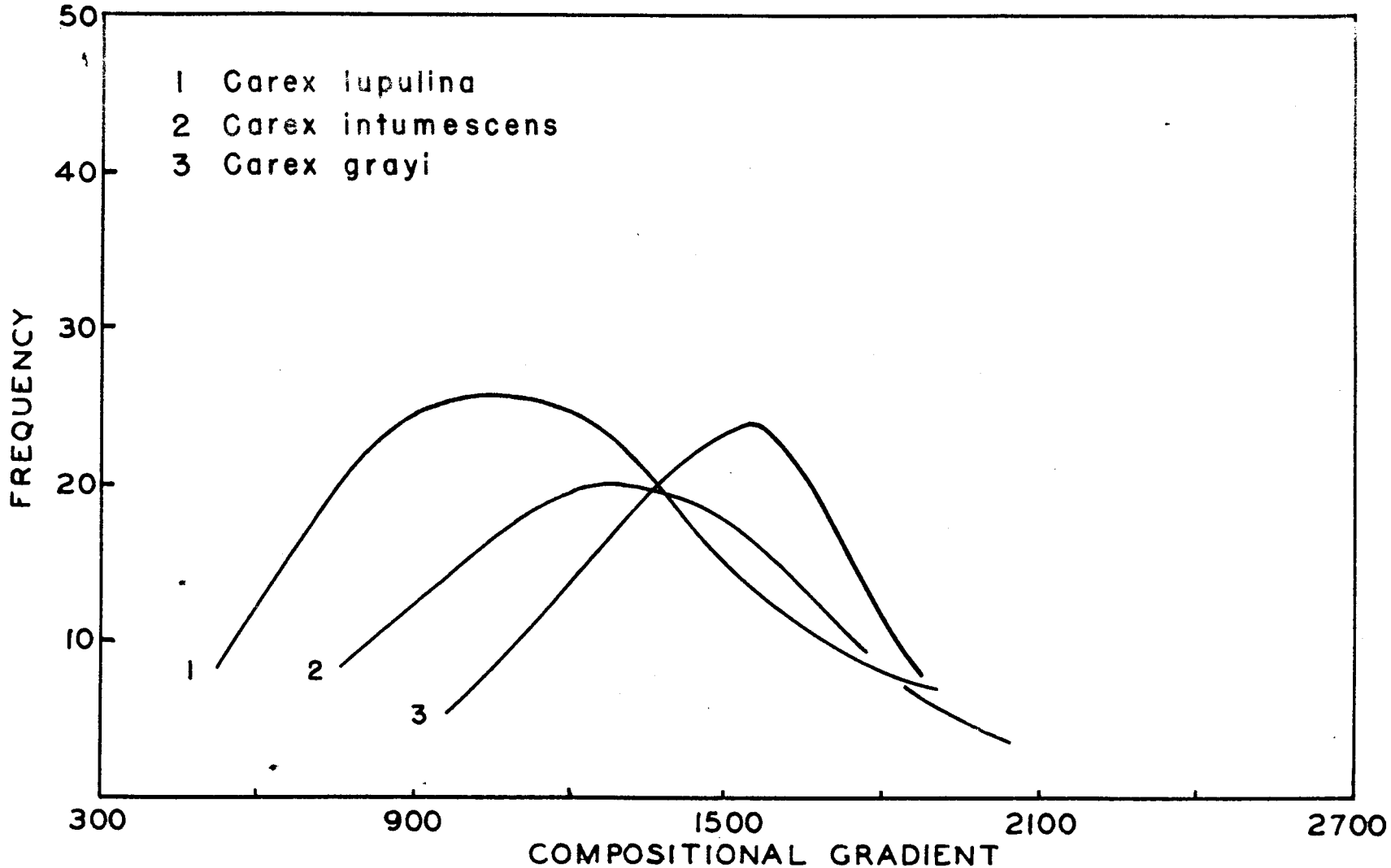

1 Carex lupulina
2 Carex intumescens
3 Carex grayi
50
40
30
20
10
FREQUENCY
1
2
3
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 34. Frequency curves for five grass species.

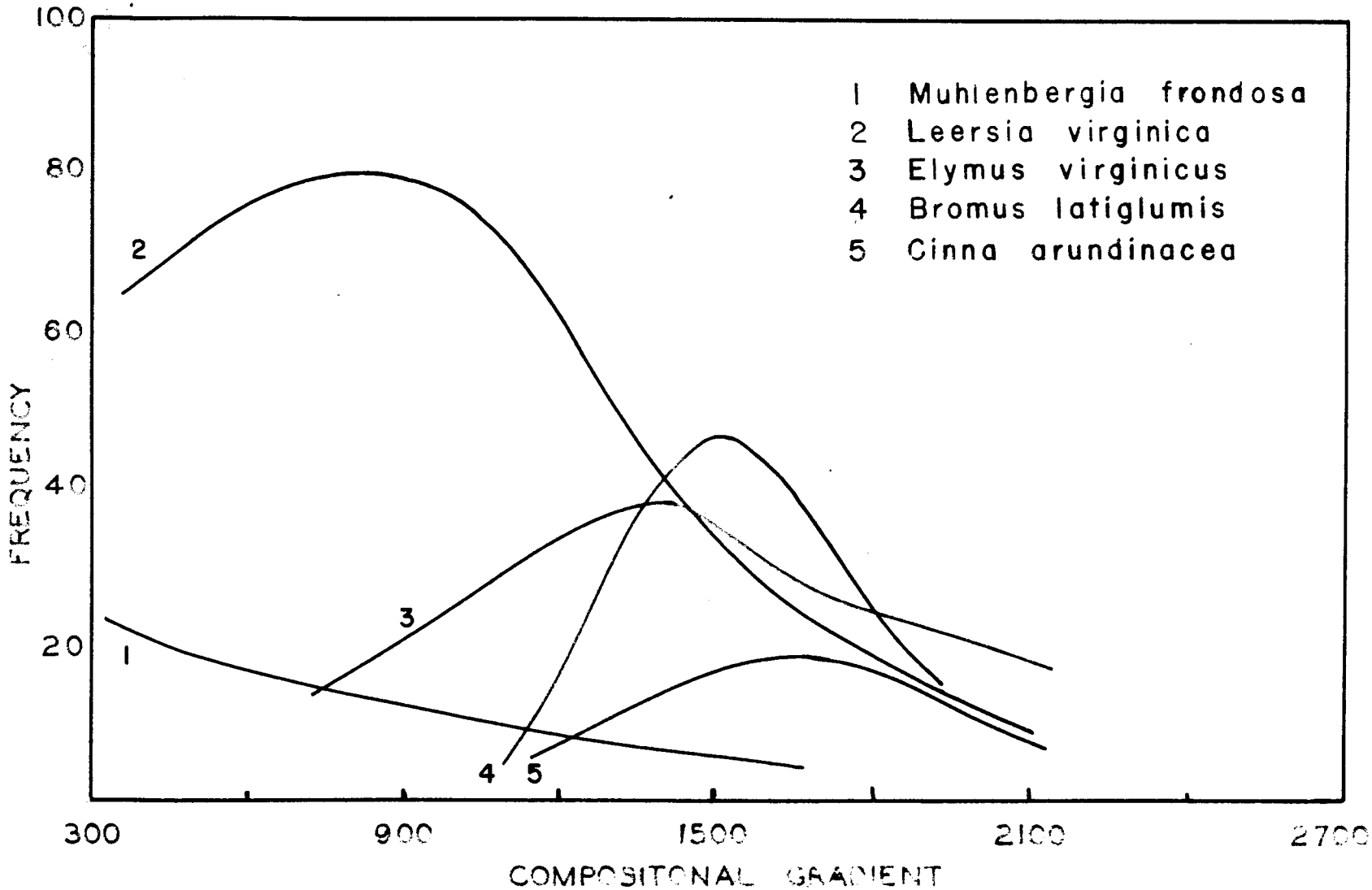

100
80
60
40
20
FREQUENCY
1 Muhlenbergia frondosa
2 Leersia virginica
3 Elymus virginicus
4 Bromus latiglumis
5 Cinna arundinacea
2
3
1
4
5
300
900
1500
2100
2700
COMPOSITONAL GRADIENT

FIGURE 35. Curves showing number of tree species and herb species per stand. Curves are based on averages of 100-unit classes of the compositional gradient.

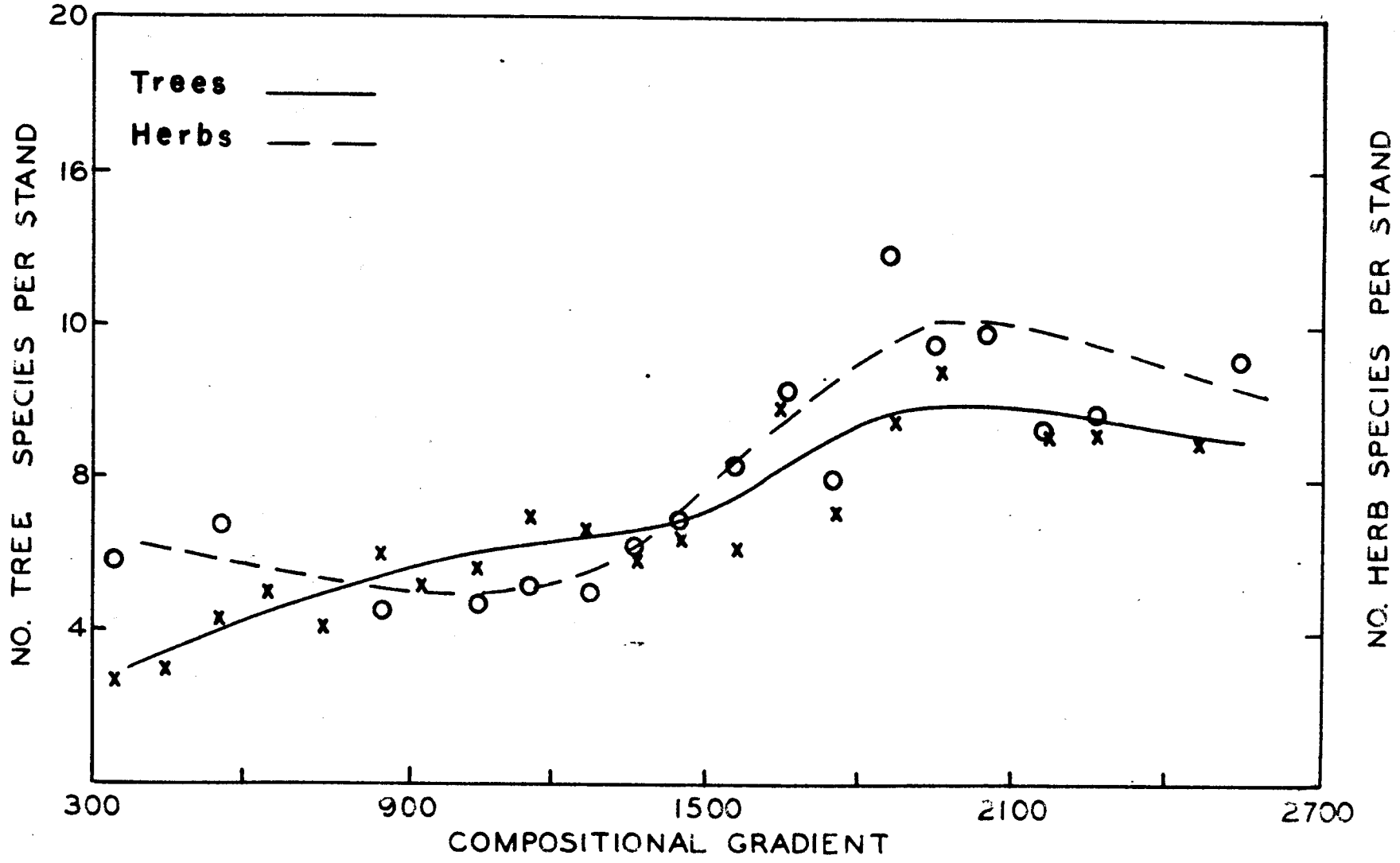

Trees
Herbs
NO. TREE SPECIES PER STAND
NO. HERB SPECIES PER STAND
20
16
10
8
4
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 36. Basal area per acre based on data from all stands.

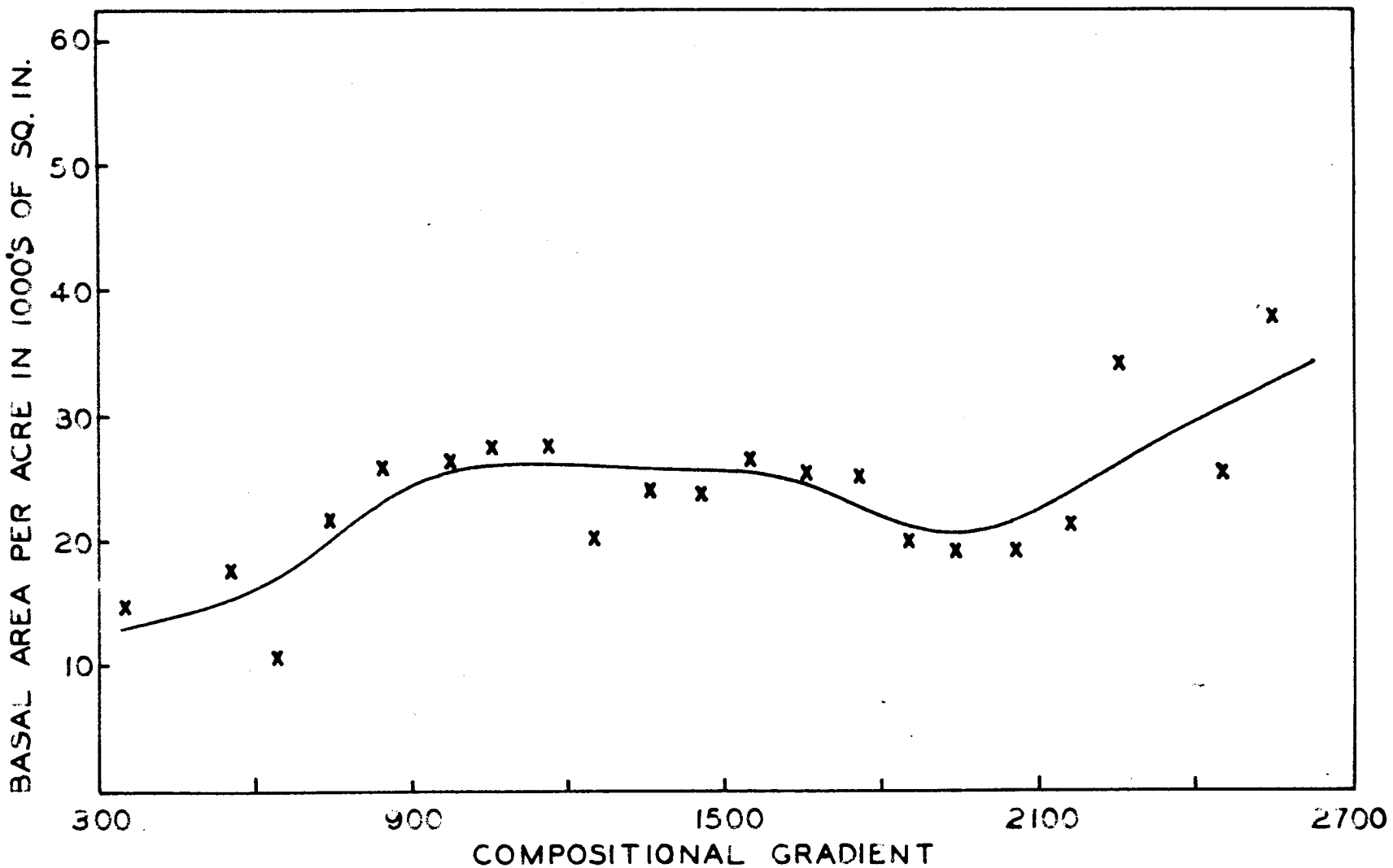

BASAL AREA PER ACRE IN 1000'S OF SQ. IN.
60
50
40
30
20
10
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 37. Basal area per acre of fluvial and lacustrine stands.

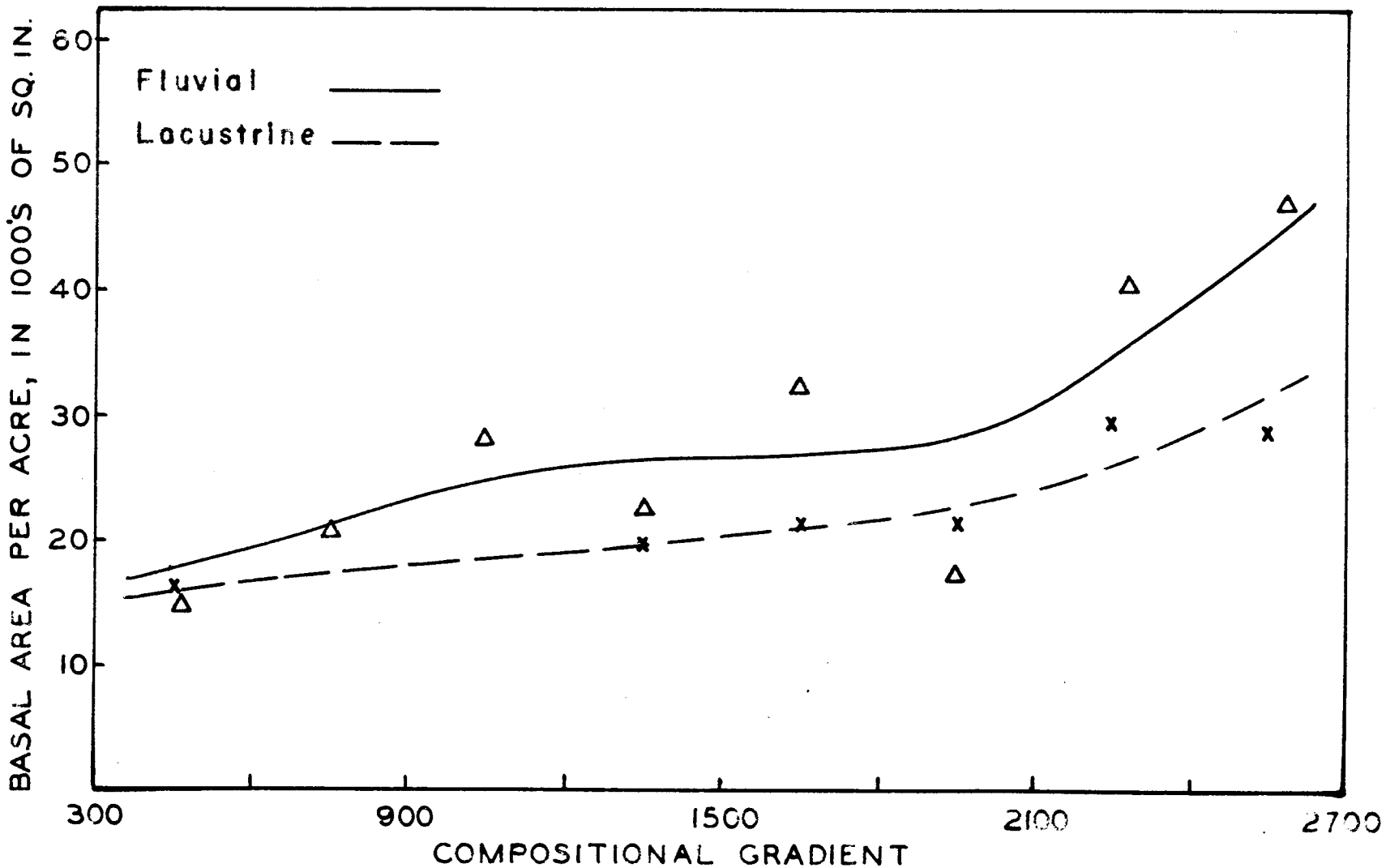

Fluvial
Lacustrine
BASAL AREA PER ACRE, IN 1000'S OF SQ. IN.
60
50
40
30
20
10
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 38. Available calcium in the surface soil.

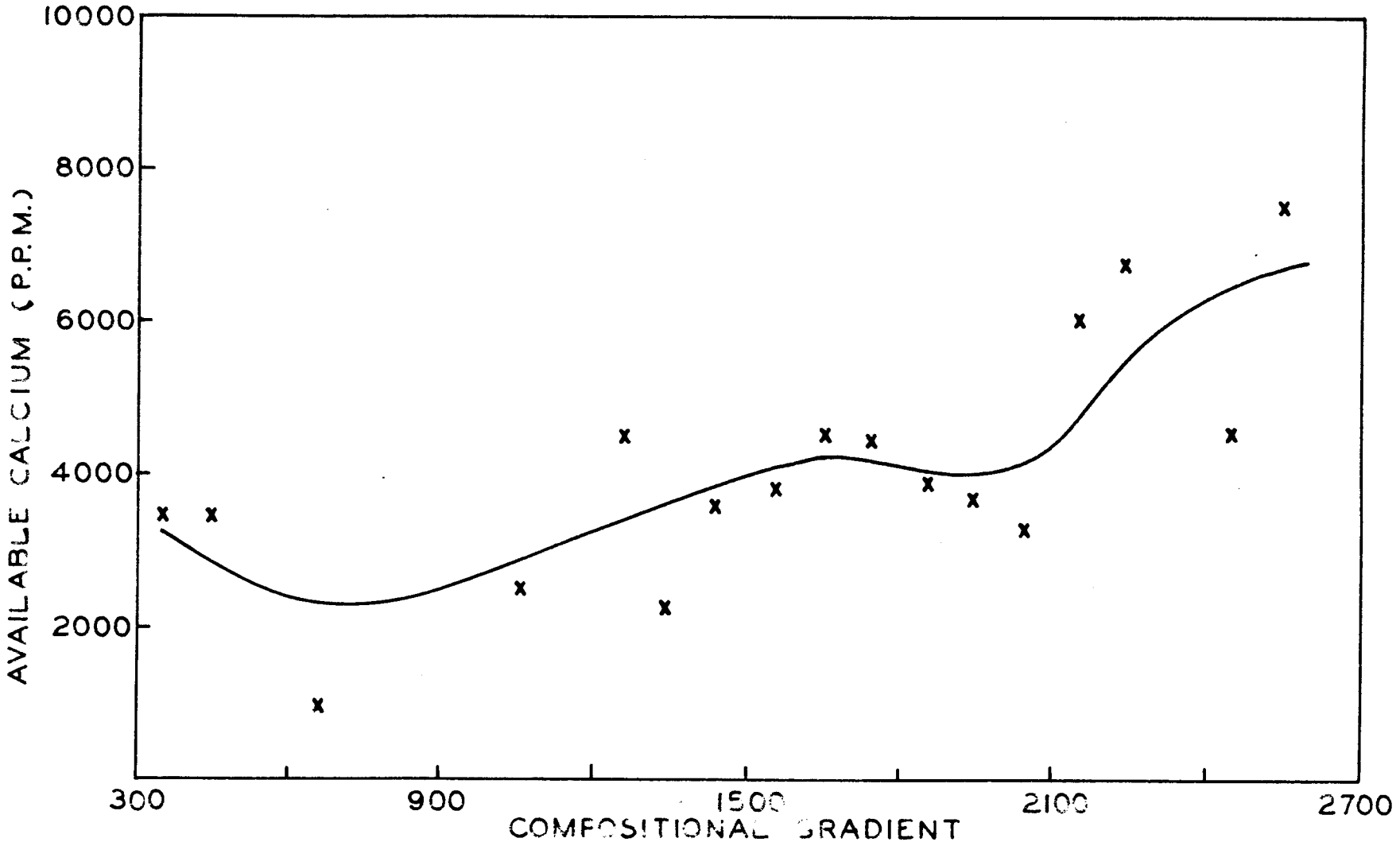

10000
8000
6000
4000
2000
AVAILABLE CALCIUM (P.P.M.)
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 39. Basal area per acre compared to calcium.

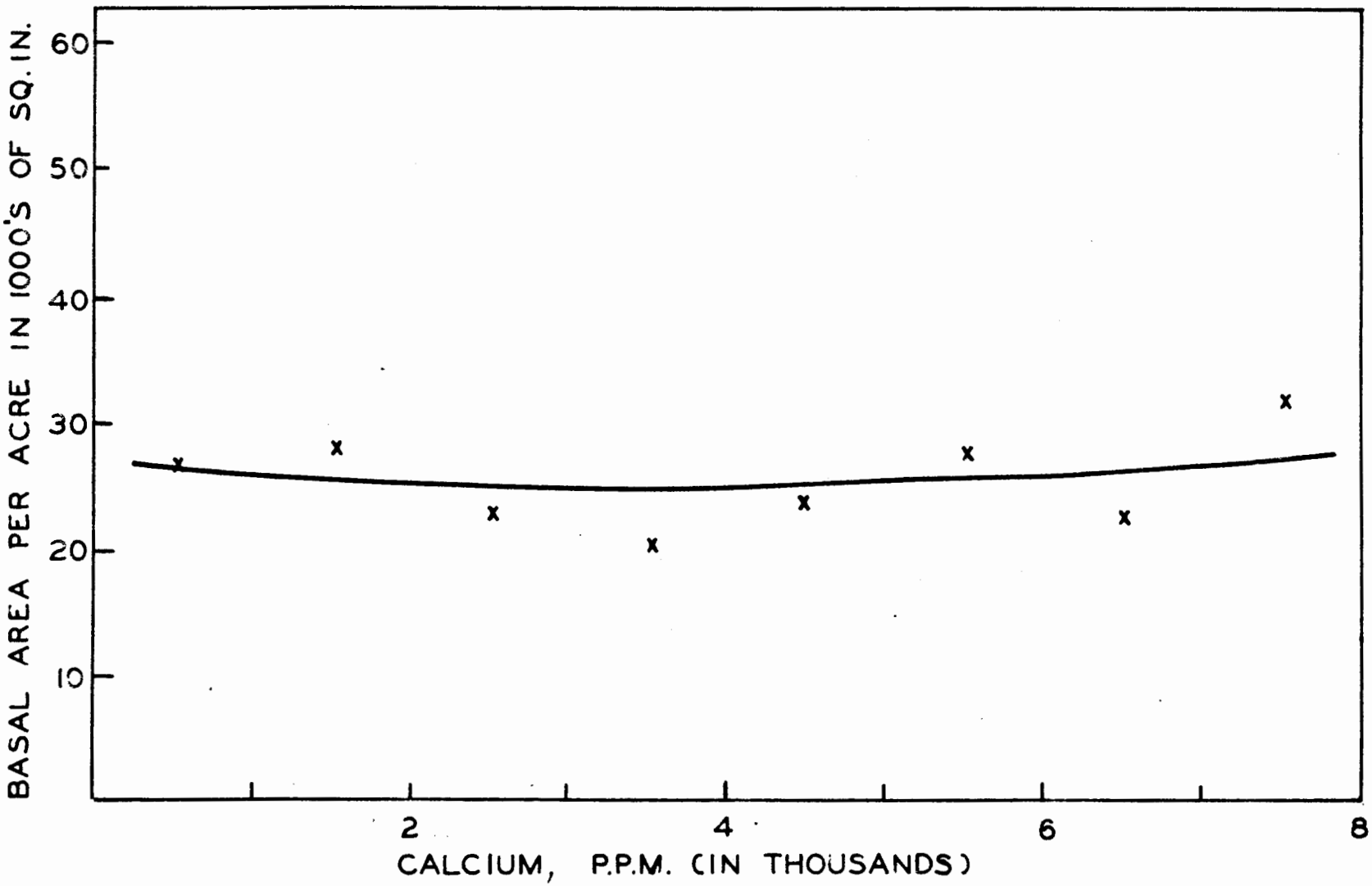

BASAL AREA PER ACRE IN 1000'S OF SQ. IN.
60
50
40
30
20
10
2
4
6
8
CALCIUM, P.P.M. (IN THOUSANDS)

FIGURE 40. Nitrate nitrogen in the surface soil.

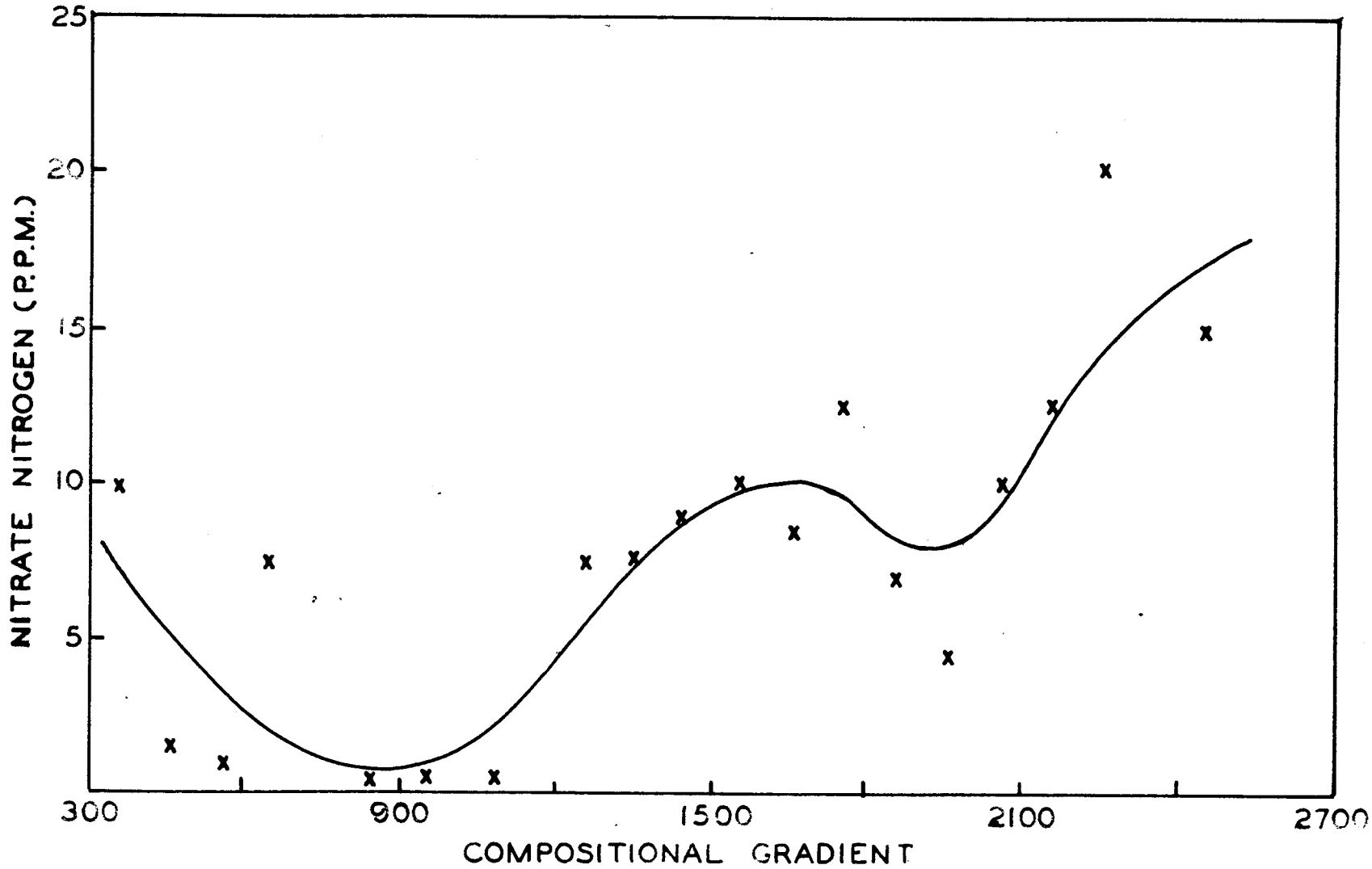

25
20
15
10
5
NITRATE NITROGEN (P.P.M.)
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

Figure 41. Ammonia nitrogen in the surface soil.

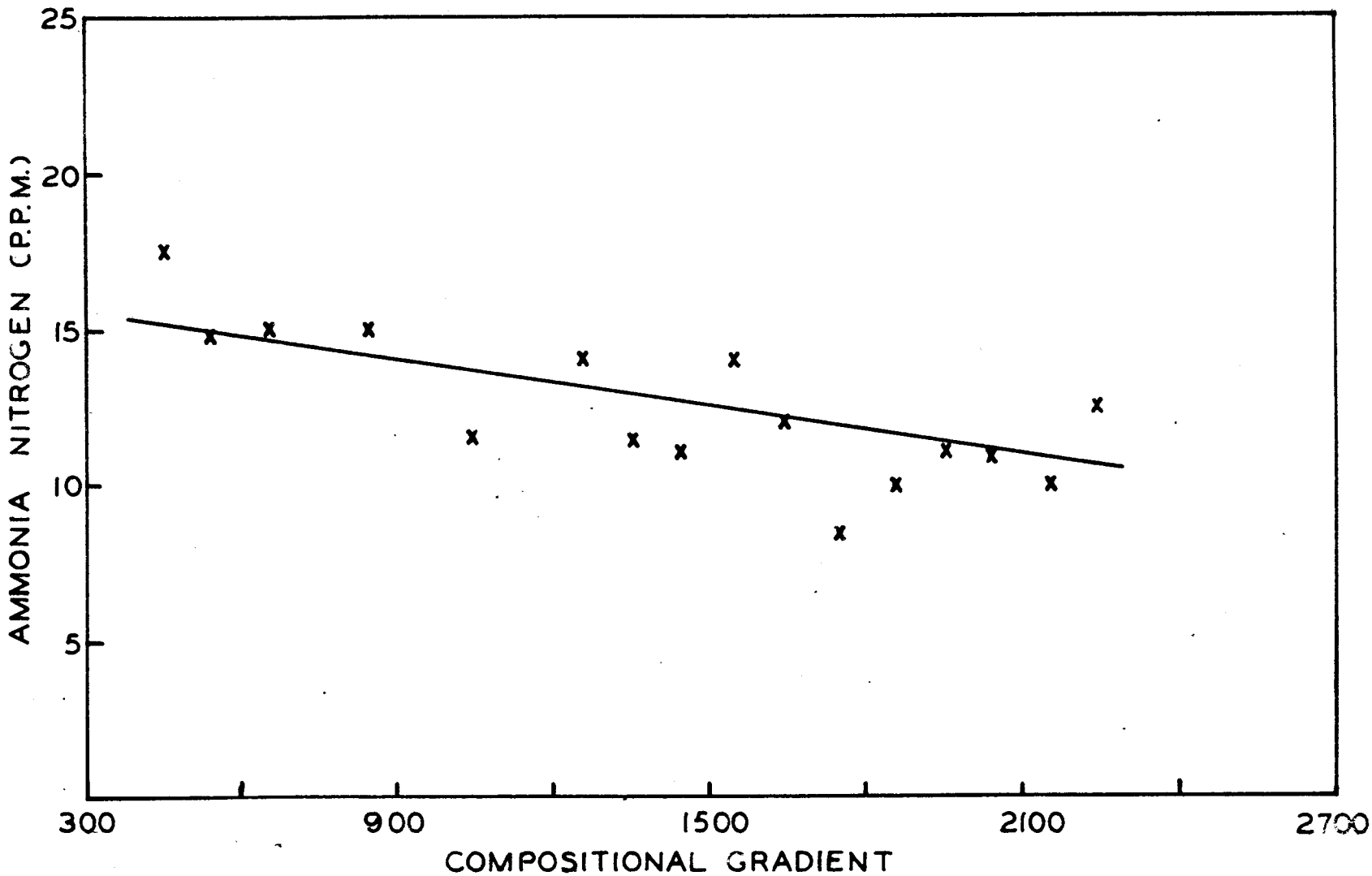

25
20
15
10
5
AMMONIA NITROGEN (P.P.M.)
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 42. Available phosphorous in the surface soil.

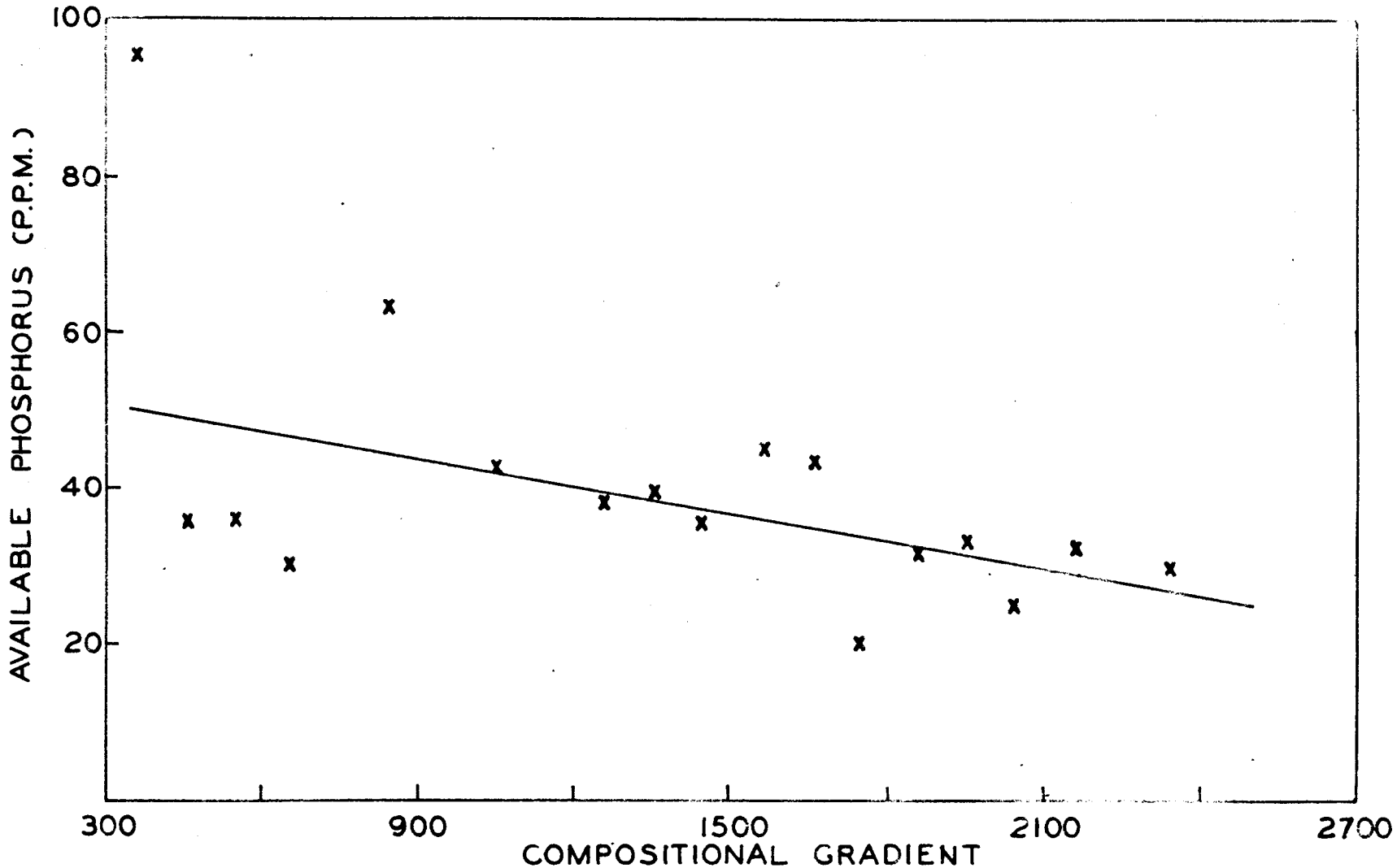

100
80
60
40
20
AVAILABLE PHOSPHORUS (P.P.M.)
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 43. Water-retaining-capacity of the surface soil.

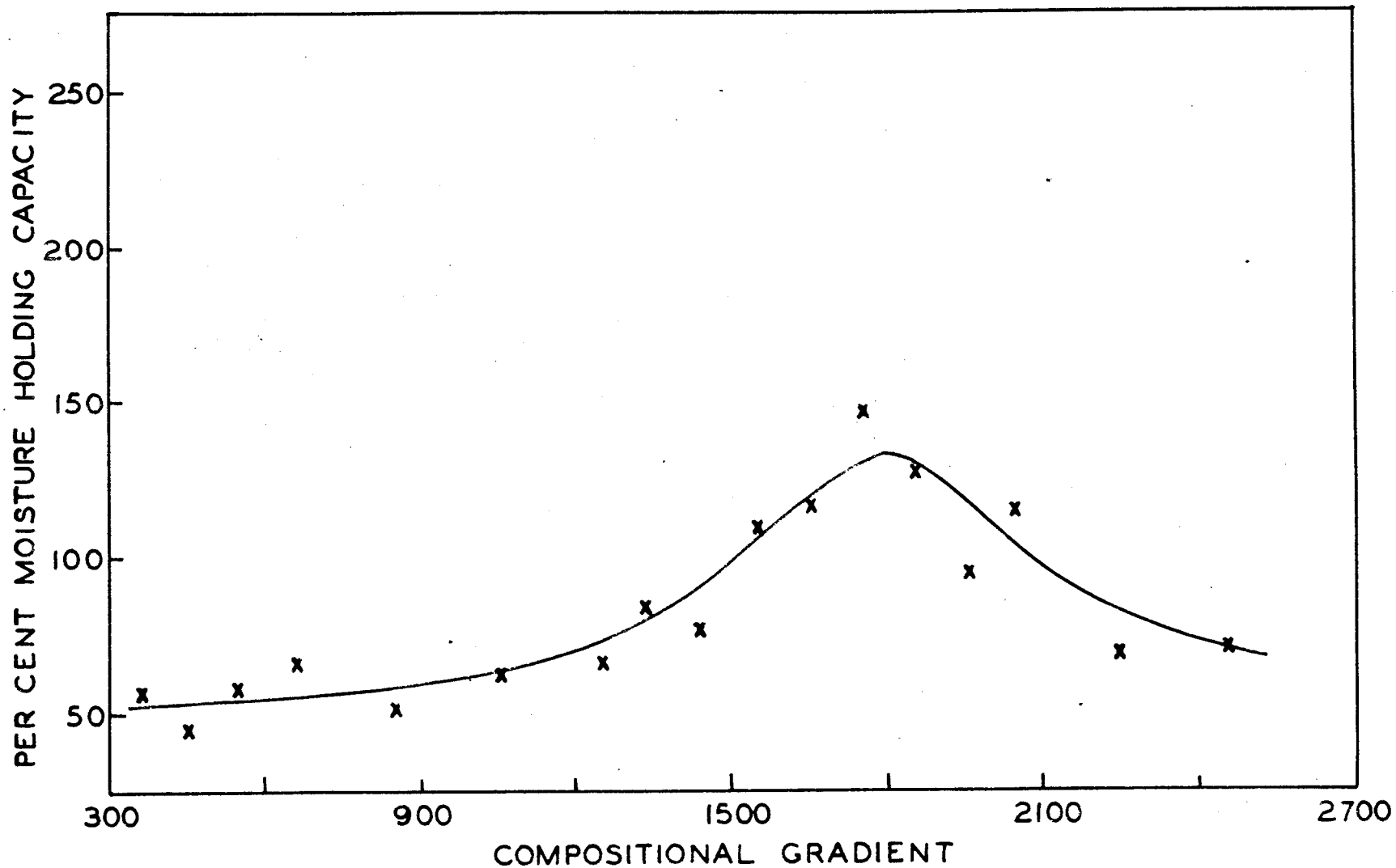
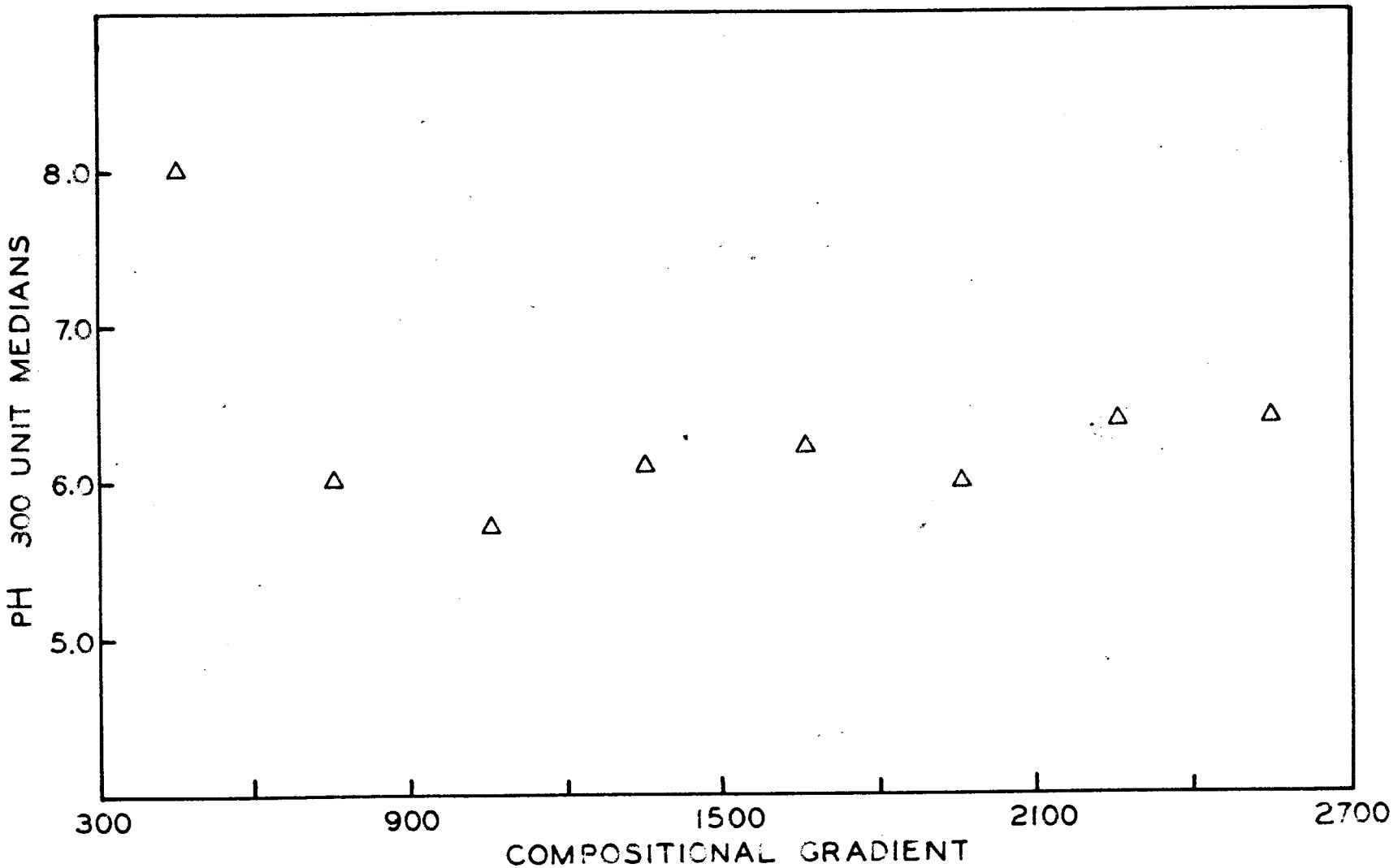

PER CENT MOISTURE HOLDING CAPACITY
250
200
150
100
50
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

FIGURE 44. Median pH values (300-unit classes).


8.0
7.0
6.0
5.0
PH 300 UNIT MEDIANS
300
900
1500
2100
2700
COMPOSITIONAL GRADIENT

Neither river birch nor swamp white oak is a true swamp tree. Both owe their success on floodplains to physiographic unevenness of the terrain and to continuing river deposition. River birch does not occur at all and swamp white oak is found rather infrequently in lacustrine swamps. The confinement of the distributions of both species to rivers is spectacularly exhibited in Figures 8 and 9. The physiographic ties of river birch and swamp white oak are thus rather pronounced.

The physiographic effects of rivers on the floodplains may frequently be rather uniform for many miles as in the case of the Wisconsin River or the Mississippi River where the latter borders Wisconsin. Floodplain forests for great distances along such courses may be subjected to similar water levels, similar frequencies of inundation, similar sedimentation, and to similar distribution of disseminules of forest trees. Those species which can best survive in such an environment of disturbance are favored on the linear and continuous floodplains. Those species combinations which occur in one place on the floodplain are likely to be found for miles along the same river because of the phenomena of similar effect. Thus in Wisconsin the overwhelming areal importance of silver maple-green ash-American elm combinations is partially explained by the homogenizing nature of the river.

A comparison of the tree and sapling curves of silver maple (Figure 22) shows that the upper limits of both on the compositional gradient tend to correspond. If the trees of silver maple are found no higher on the compositional gradient than the saplings, the explanation lies heavily in the direction of a moisture limitation rather than with a light gradient for a difference in the two curves should show clearly

if light were an important factor. Silver maple trees apparently endure regimes of high moisture which silver maple saplings similarly endure. The upper limit of the curve denoting behavior of silver maple trees probably is a noteworthy topographic demarcation on the compositional gradient. The more open initial communities of willow, cottonwood, river birch, and swamp white oak tend to be supplemented and eventually replaced by communities with various combinations of silver maple, green ash, and American elm. No other species endure the physiographic conditions ascribable to the river and no other species tend to replace the silver maple-green ash-American elm communities (though basswood, red oak, yellowbud hickory (Carya cordiformis), and hackberry (Celtis occidentalis) may occasionally occur on minor prominences) as long as physiographic conditions remain unchanged. In a stand containing only large trees, saplings are usually sparse, and saplings tend to replace trees only when openings in the canopy are created (Lee 1945). Although silver maple-green ash-American elm stands may contain magnificent trees and impressive well-developed structure and unity, moisture conditions may not greatly differ from non-woody floodplain communities because virtually all floodplain communities are equally affected by the vagaries of the nearby river and virtually all floodplain communities show immense fluctuations in soil moisture (Partch 1949). In contrast to the salubrious vegetational effect in upland forests where development is associated with improved soil moisture conditions, the effect of floodplain vegetation on the excessive soil moisture is negligible. Though many tons of water in a stand are lost by transpiration during a growing season, the forest is

just as likely to be flooded by the river whether transpiration occurs or not. Effect of organic matter on the level of the floor of a floodplain forest is also negligible. In other words, significant improvement of moisture conditions by the vegetation is trivial in floodplain forests in comparison to soil moisture improvement possible in upland forests. The lowland forest must await external or physiographic improvement of soil moisture conditions before other trees can enter the silver maple-green ash-American elm communities.

An approach in which large numbers of lowland stands are studied permits avoidance of the speculation which has plagued so many studies of lowland vegetational dynamics. If it be true that appreciable lowland forest compositional changes must await improvement of moisture conditions (drainage), then the study of a host of lowland stands is the best means of finding out actual behavior on sites presumably with slowly improving drainage. The older the stand and the fewer the disturbances the better the reflection of moisture conditions. Although an overwhelmingly large number of forest sites along rivers are subject to inundation sufficiently frequent to limit floristic diversity of the woody vegetational constituents, gradations of floodplain level above river levels do occur, ranging from flood plains which are inundated for weeks at a time, to those which are inundated for short periods infrequently, to those which are no longer flooded at all, the latter of course ceasing to be floodplains, though they display the scars of river activities occurring centuries ago. Diagrammatic cross-sections of three floodplain situations encountered in the present study (Figures 45, 46, 47) are presented to show some species groupings which occur on

FIGURE 45. Diagrammatic cross-section of the Wisconsin River.

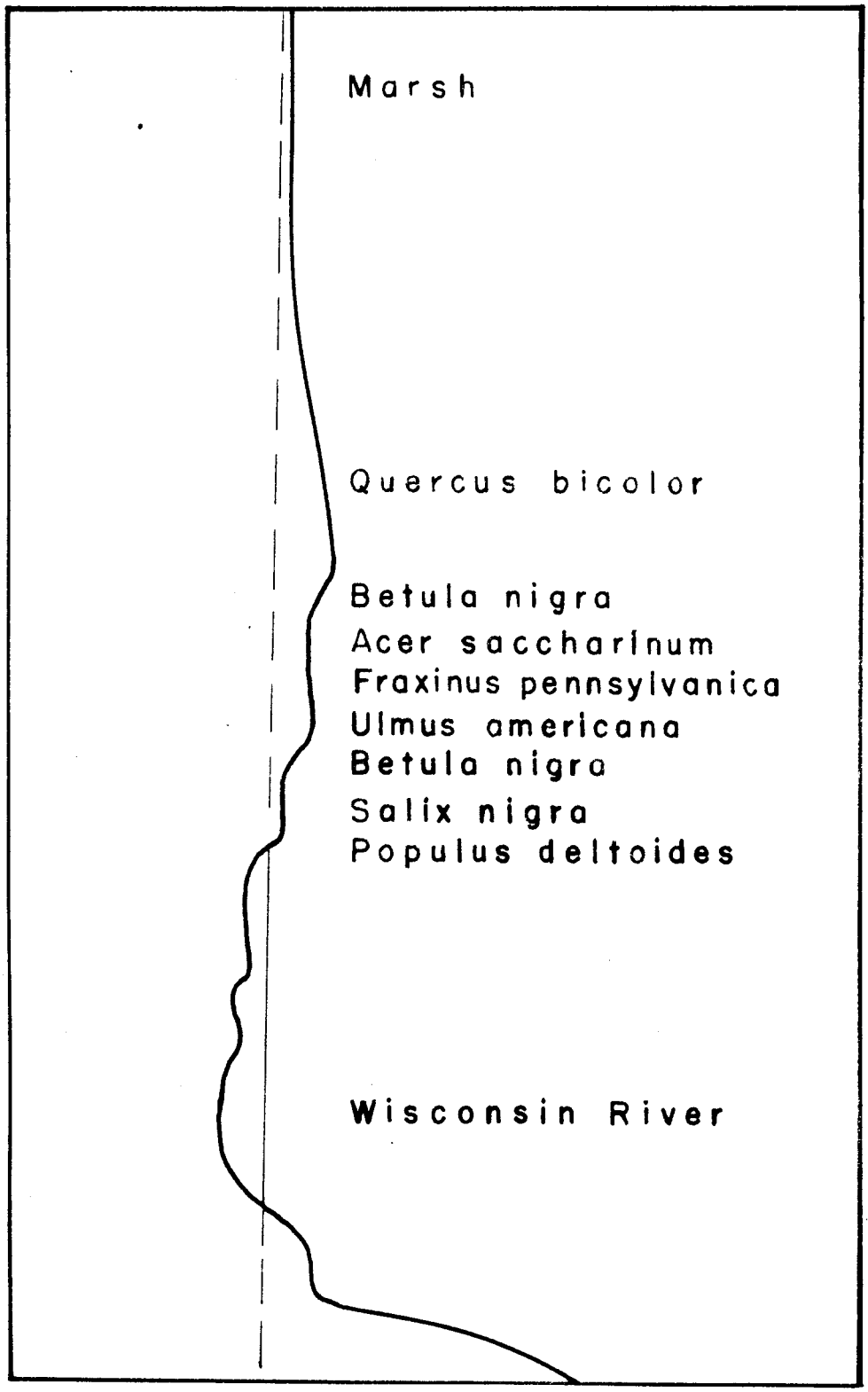

Marsh
Quercus bicolor
Betula nigra
Acer saccharinum
Fraxinus pennsylvanica
Ulmus americana
Betula nigra
Salix nigra
Populus deltoides
Wisconsin River

FIGURE 46. Diagrammatic cross-section of the Wisconsin River.

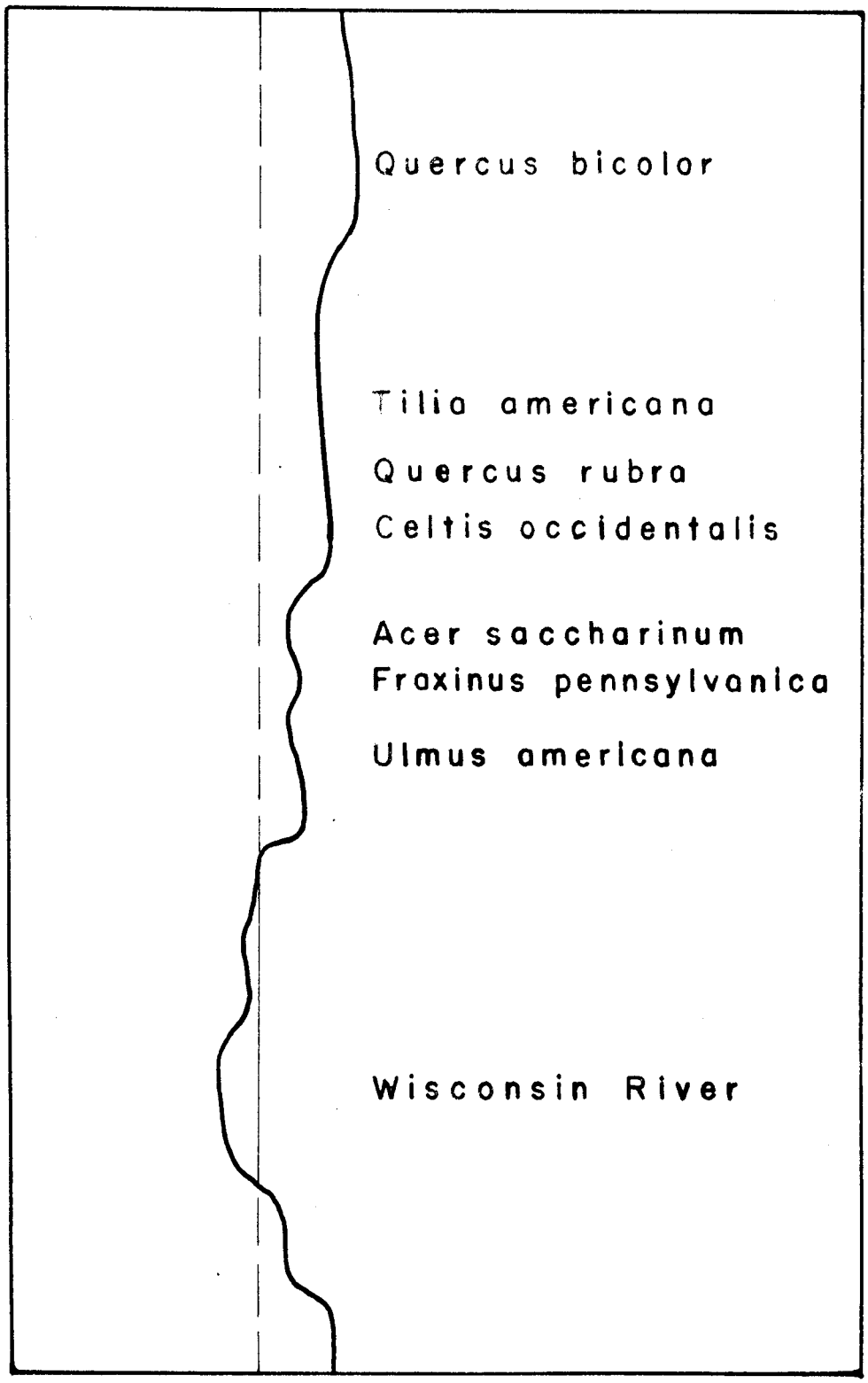
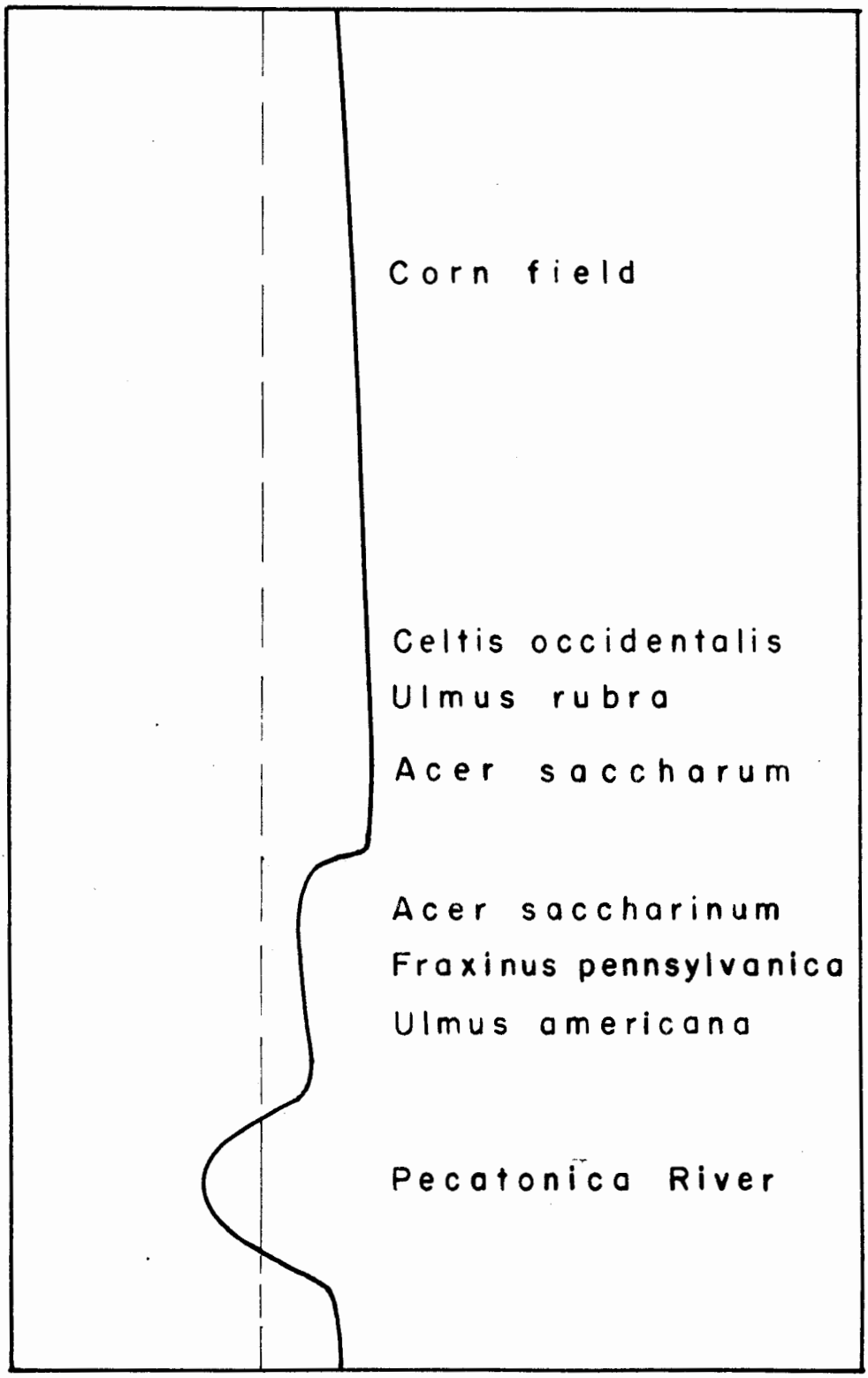

Quercus bicolor
Tilia americana
Quercus rubra
Celtis occidentalis
Acer saccharinum
Fraxinus pennsylvanica
Ulmus americana
Wisconsin River

FIGURE 47. Diagrammatic cross-section of the Pecatonica River.


Corn field
Celtis occidentalis
Ulmus rubra
Acer saccharum
Acer saccharinum
Fraxinus pennsylvanica
Ulmus americana
Pecatonica River

various floodplain levels. Figures 45 and 46 are approximations of cross-sections of floodplains observed on the Wisconsin River while Figure 47 represents a floodplain of the Pecatonica River in northern Illinois. Figure 46 shows a floodplain level on which red oak, basswood, and hackberry are the major species and Figure 47 shows a level on which sugar maple (Acer saccharum), red elm (Ulmus rubra), and hackberry are the major species. These floodplain profiles are demonstrations of the existence of species combinations other than silver maple, green ash, and American elm on floodplains at levels somewhat higher than the levels occupied by these three common species. The compositional gradient is based on gradations of composition, and gradations of composition are closely related to gradations of physiography.

The presence of well-developed sugar maple woods on the floodplain of the Pecatonica River is ample confirmation of the culmination of a commonly suggested trend of floodplain forest development (Braun 1916, Barclay 1924, Cooper 1926, Lee 1945, Braun 1950). Physiographic properties of the sugar maple forest substratum are manifestly different from physiographic properties of nearby silver maple-green ash-American elm stands on lower floodplain levels. Though abundant sugar maple seeds are distributed over the floor of the silver maple-green ash-American elm stands during years with good seed crops there is no indication whatsoever of sugar maple replacing the trees of the silver maple-green ash-American elm stands. There is very little that the vegetation can do to make the environment more suitable for sugar maple, and "floodplain succession" has apparently reached an impasse. If replacement of silver maple,green ash, and American elm by more mesic

species must await improvement of site by non-vegetational physiographic processes, then the term "floodplain succession" cannot at all imply smooth and imperceptible replacement of species within a vegetative cycle (Cowles 1911), but must be inseparably bound to gradual physiographic changes. By this reasoning two stands may appear to be related compositionally because both stands are within amplitudes of several species on a moisture gradient; yet the stands are completely separated vegetationally because of the topographic differences of site. No merging of compositional characteristics brought about by vegetational dynamics will occur, and the stands must be studied for just what they show today and nothing more. Thus in the present study successional implications are in no wise intended, and speculation on trends is certainly not in order when the spirit of the whole study lies in the presentation of a range of variations, heavily supported by actual samples from all parts of the range.

Lacustrine swamps display a stability not at all similar to the fluctuation and sedimentation phenomena of fluvial swamps. Inundation of lacustrine swamps may last for weeks, and sedimentation undoubtedly occurs, but the water quantities are usually small in comparison to overflowing river waters. The marked paucity of cottonwood, willow, river birch, and swamp white oak in lacustrine swamps is a phenomenon consistent with the disturbance demands of these four species described earlier in the discussion. It has been previously stated that the high moisture content of a lacustrine swamp is a matter of impeded drainage and that the level of the outlet of the extinct lake bed controls the water level of the swamp. Runoff water from land surrounding

the swamp cannot be retained for long at a level higher than the outlet. This regulation tends toward a maintenance of rather stable, though wet, conditions for weeks at a time. The wetter lacustrine swamps usually contain combinations of silver maple, green ash or black ash (Fraxinus nigra), and American elm. Occasional stands of cottonwood and willow may be found associated with recent changes in lake levels, but these changes are virtually always man-created. Natural shoreline changes associated with lakes are generally limited in extent; correspondingly willow and cottonwood growth near lakes is seldom very extensive. A full range of lowland physiographic gradations occupied by forest growth is available for study in Wisconsin, and stands of lacustrine origin are evenly distributed along the higher range of the compositional gradient. The blending of lowland forests into non-lowland forests is a phenomenon entirely consistent with presence of gentle slopes around lacustrine swamp areas. The use of a soil auger and the ascertainment of the depth of the gley layer (Wilde 1940) proved to be an entirely practicable and effective way of determining internal drainage conditions of the site. Only those with a gley layer of three feet or less in depth were treated as lowland sites. This is well within the limit of seven feet suggested by Wilde as indicative of impeded drainage.

The Compositional Gradient as a Viewpoint

The bar diagrams of Figures 12 and 13 are graphical representations of what appears to be an ecologically syntactical scheme for lowland hardwood forests of southern Wisconsin. The assignment of adaptation

numbers is an attempt to convert graphical information into quantitative information. The numbers assigned are naturally influenced by the floristic diversity of the community being treated. It is the weighting of relative compositional values by use of previously determined adaptation values which permits the ascertainment of differentially weighted cumulation values on which a gradient of community composition can be based. The compositional gradient thus established is a linear arrangement upon which a stand is placed on the basis of a single index number. In bottomland forests as in all forests, the composition of the natural vegetation is, in a great measure, a reflection of the complex interplay of moisture and light factors, and this interplay is inextricably interwoven into any vegetational gradient which is based only upon compositional considerations.

To better understand the relation of the light and moisture factors to a compositional gradient we may think of lowland forests as occupying sites with infinite gradations of soil moisture conditions from saturated to moderately moist. In other words, bottomland forests occur along a moisture gradient. At any one point on this gradient there may be a host of bottomland forests, all with identical moisture conditions, but no stands of this array having the same light conditions. Thus this multitude of bottomland stands occurs along a light gradient free from the complications of moisture varation. Of course there are also many other gradients of environment to which community composition can be related (Whittaker 1952, 1954, Hills 1952). If the full range of light conditions and the full range of moisture conditions in bottomland forests are given equal linear limits for plotting purposes, and moisture

values are plotted along the x-axis while light values are plotted along the y-axis, then the plotted points of a legion of stands, showing countless combinations of light and moisture values, should present the appearance of a square, very densely covered with plotted points. The consideration of varying compositional values can be done only by introducing a third dimension over the plane of the moisture-light axes. If the new dimension represents percentage composition of the species of a stand, and a theoretical example is considered in which one species occurs in pure stands, that is, one species makes up 100 per cent of every stand, and these stands correspond to all of the countless moisture-light combinations which produce the shape of a square as suggested above, then the new three-dimensional figure should present the appearance of a cube. It is not likely that any species actually will more than rarely constitue 100 per cent of any stand of Wisconsin hardwood bottomlands, but whatever the highest values are, they are likely to be localized, with decreasing composition values surrounding them. The appearance of such a three-dimensional figure can perhaps be compared to a hill, or to a mound, or to an inverted bowl, or to a bell. An attempt to present a diagrammatic depiction of the composition contours of a hypothetical species is shown in Figure 48. The solid figures may resemble halves of spheres or perhaps such objects as the elongate halves of eggs, footballs, or cucumbers, depending upon amplitudes along the moisture and light gradients. Because sufficient data are as yet not available to construct accurate representations of these three dimensional "mounds" the figures presented in Figure 49 are intended to be nothing more than tentative approximations

FIGURE 48. Diagrammatic two-dimensional compositional contours.

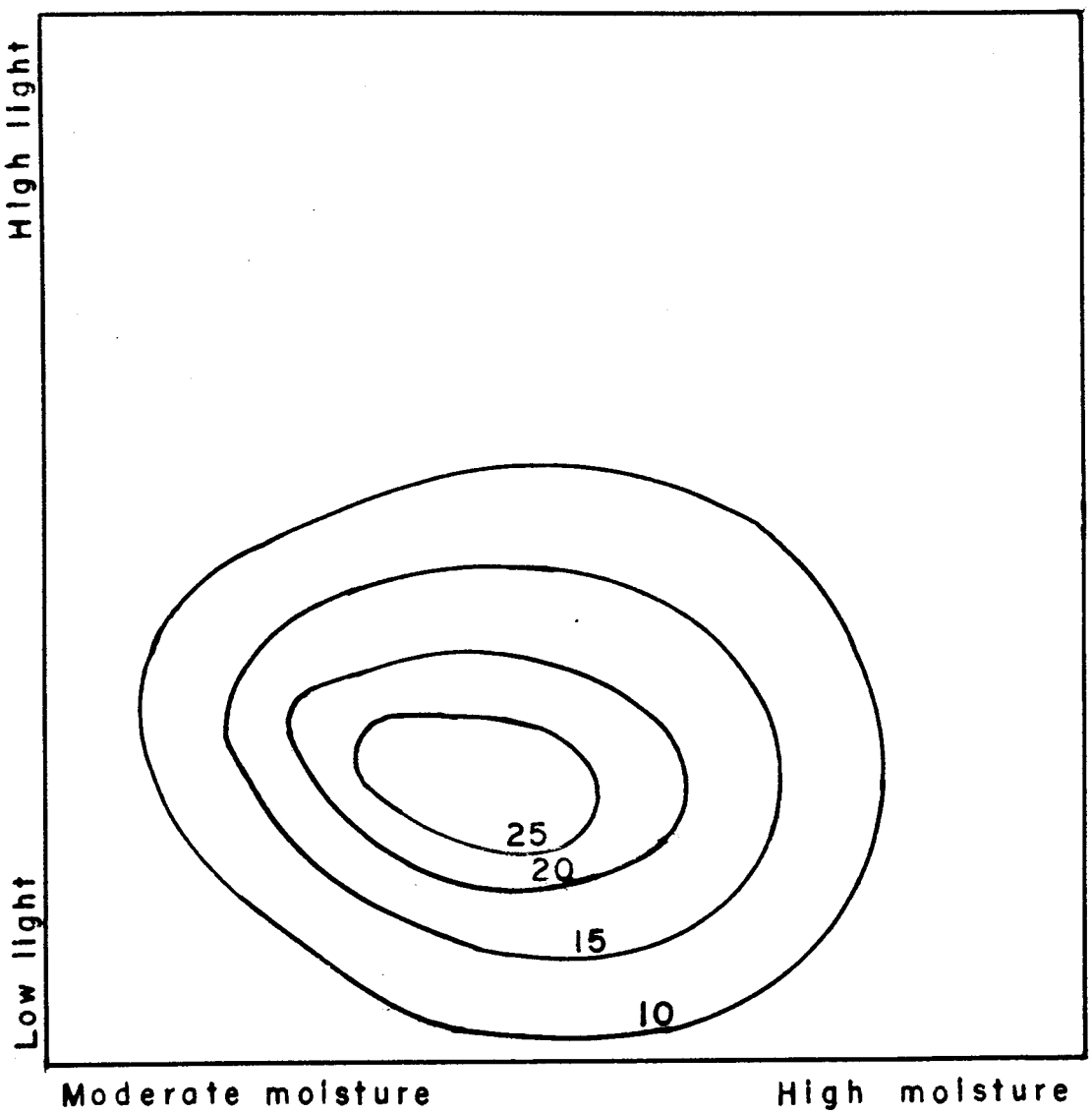
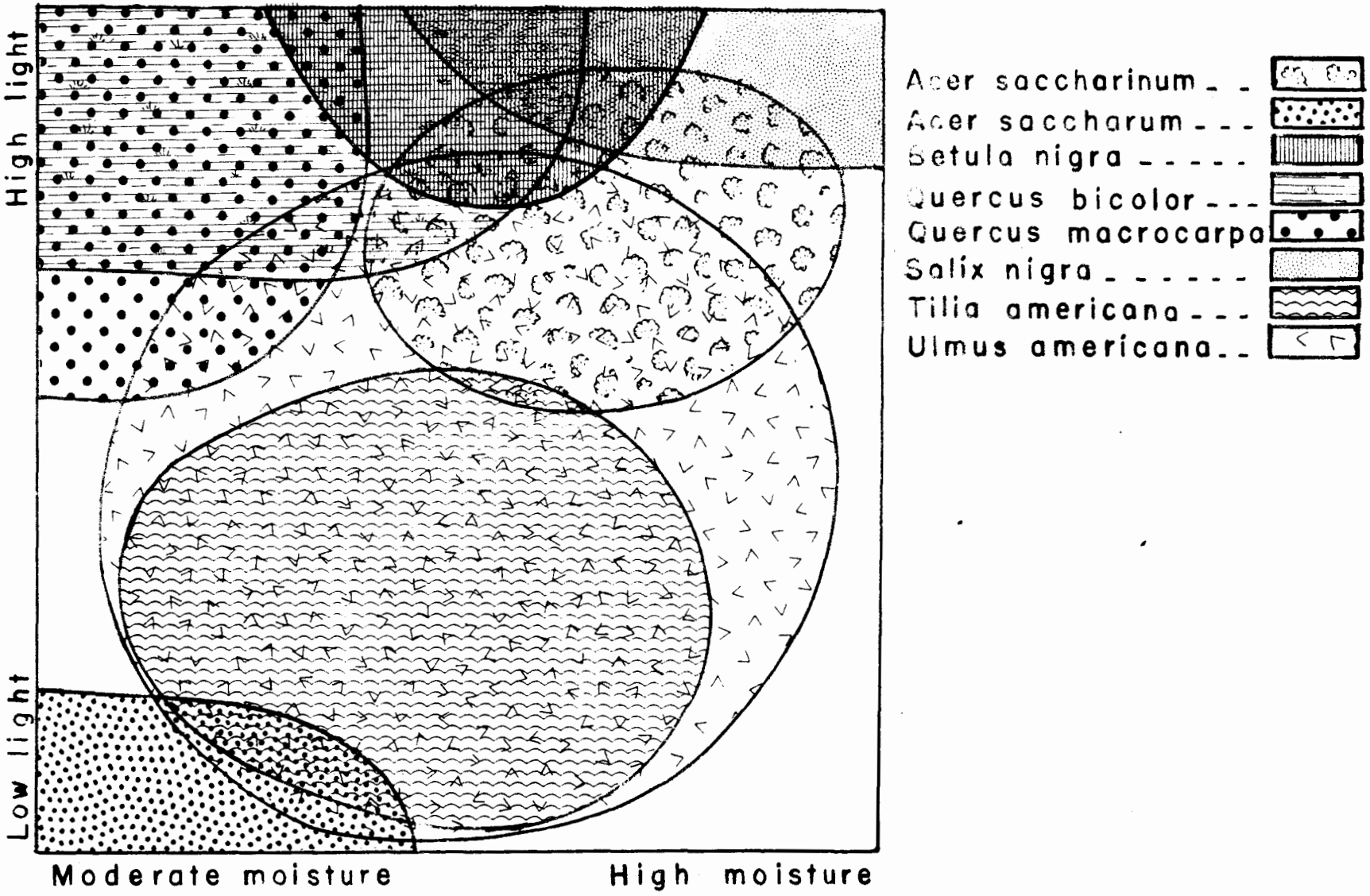

High light
Low light
25
20
15
10
Moderate moisture
High moisture

FIGURE 49. Diagrammatic two-dimensional figures for several important lowland tree species.


High light
Low light
Moderate moisture
High moisture
Acer saccharinum
Acer saccharum
Betula nigra
Quercus bicolor
Quercus macrocarpa
Salix nigra
Tilia americana
Ulmus americana

of the behavior of some common bottomland species of the current study. The mound-shaped figures diagrammed in Figure 49 may be likened to a somewhat elongated range of mountains which, if viewed from afar from a point perpendicular to the axis, appear as a series of peaks seemingly in the same plane, since depth differences are obscured owing to the distance between the viewer and the peaks. The arrangement of species along a linear compositional gradient is analogous to the view of a range of mountains from a great distance in that the peaks of the species encountered are compressed into one plane. In Figure 49 if a plane were sliced from the low light-moderate moisture corner of the figure to the high light-high moisture corner, curves for most of the species would appear on a linear compositional gradient. Curves for Betula nigra, Quercus bicolor, and Quercus macrocarpa would be completely missing because they are not bisected by the plane. In Figures 17 and 19 the curves for these three species have been "pushed" into the plane of the compositional gradient. The left portions of all three curves are partially missing. These missing portions represent compositional values not obtained in the current study for the reason that the open growths and the higher land characterizing some of the stands of these three species were features which could not qualify by the criteria set up for choice of lowland forest stands. The solid figures of these three species have centers at some distance from the plane of the vegetational gradient; however portions of the solid figures extend rather close to the plane and can be projected into the plane of compositional gradient.

Vegetational History

The ranges of a number of Wisconsin floodplain tree species (Figures 8, 9, 10, 11) show marked confinement to the valleys of the Mississippi River and its tributaries. The ranges of numerous bottomland herbs and grasses show similar river distributions (Fassett 1938, 1951). For whatever movements of river valley species might have occurred during and after the glacial periods, easy migration paths were furnished for both retreats and advances (Transeau 1905a). Gleason (1923) emphasizes the importance of the Mississippi River as a migration route for both hill and ravine species as well as bottomland species, and further stresses the importance of the route by listing it as one of two major postglacial plant migrations, one northward along the Mississippi River and tributaries, and one from the Allegheny Mountains, the latter moving first northward and thence westward, entering Michigan, Wisconsin, and Minnesota. Some species were common to both migrations so that races of similar ultimate ancestry, but of different recent history, are growing together in places where both migrations have contributed elements. Black ash and red maple (Acer rubrum) have distributions which are quite satisfactorily explained by a westward migration, while several other species such as American elm, basswood, sugar maple, and red oak are too generally distributed for any intelligent speculation concerning their recent movements.

The close ties of Wisconsin floodplain forests to Mississippi River floodplain forests farther south can be demonstrated by the use of detailed composition data from points distributed along the hundreds

of miles of the river bordering Illinois. The great floristic diversity of southern Illinois and Wabash bottomlands poses problems in that species common to both these two areas and Wisconsin can be compared on a phytosociological basis in little more than a limited way because Wisconsin species are too often eclipsed by the great assortment of more southerly species. Putnam (1951) lists at least 75 species of bottomland trees occurring on the lower Mississippi alluvial plain. Lindsey (1932) records the colossal number of 109 species of trees for the lower Wabash Valley. The disparity of these figures can be attributed to the nature of the work from which they were taken, for Putnam's work is a forestry publication, dealing primarily with timber trees and Lindsey's work is a botanical treatment with a great deal of splitting of such groups as Carya and Crataegus. The point to be emphasized is that the scope and nature of treatments frequently varies so much that community comparisons on a floristic basis are not nearly so useful as phytosociological comparisons despite the differences in species richness of different areas. The best method for actual community comparisons of floodplain forests from widely separated places, lies with the use of quantitative data encompassing comparable tracts.

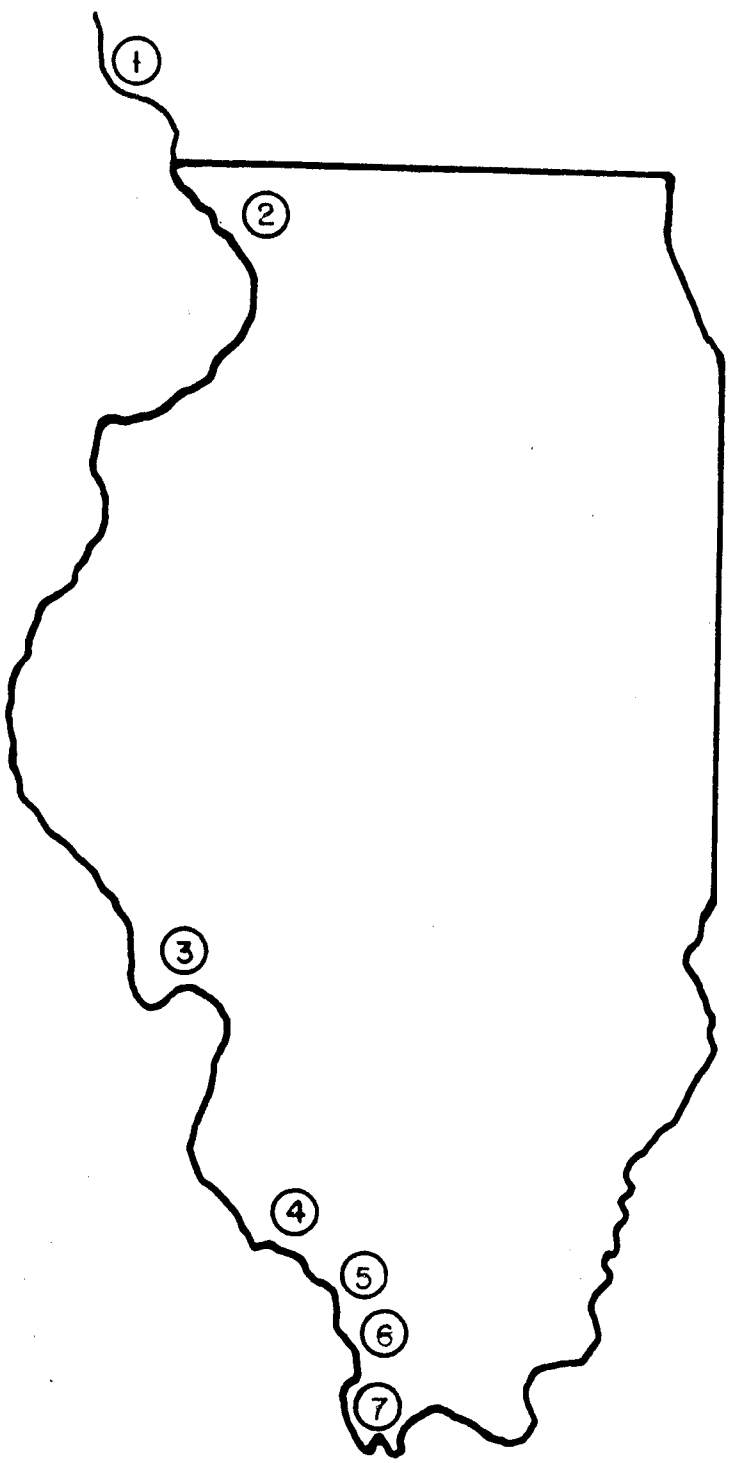
In the discussion of floristic congruency in a previous section it was pointed out that the number of species of the floodplain forests of the Mississippi River diminishes as one moves northward. Samples of floodplain forests from the upper Mississippi are presented in Table IV. The data show relative densities of floodplain forests distributed along the entire length of the state of Illinois as indicated by Figure 50.

TABLE IV. Per cent density data of floodplain forest stands of the upper Mississippi River.

TABLE IV

	Wyalusing State Park Wisconsin	Jo Daviess County, Illinois (Telford)	Mouth of Illinois River (Yeager)	Kaskaskia River (Telford)	Big Muddy River (Telford)	Mississippi River Union County, Illinois (Telford)	Cache River (Telford)
Acer saccharinum	52	39	33	13	4	33	5
Ulmus americana	24	22	17	11	12	12	10
Betula nigra	11	12	2	3	2	2	
Populus deltoides	4		1	3		14	4
Fraxinus sp.	4	6	9	25	10	18	6
Quercus bicolor	2					.6	2
Gleditsia triacanthos	1			.3	3		.1
Acer negundo	1		2				
Tilia americana	1						
Salix nigra		14	2			1	1
Quercus palustris		7	6	11	20	3	3
Celtis occidentalis			4	2		10	1
Platanus occidentalis			.5	3	2		.5
Quercus macrocarpa			.5		1		.1
Carya pecan			5			2	
Forestiera acuminata			5				
Diospyros virginiana			5				
Gleditsia aquatica			4				
Crataegus sp.			3				
Morus rubra			1				
Ulmus rubra			.1				
Gymnocladus dioica			.1				
Cercis canadensis			.1				
Quercus alba				14	12		5
Carya sp.				13	13		2
Quercus velutina				4	.6		4
Juglans nigra				3	.6		
Quercus lyrata						.6	
Liquidambar styraciflua					6	3	10
Quercus falcata					9		.3
Quercus shumardii					1		.1
Quercus prinus					.6		.1
Quercus stellata					2		
Quercus imbricaria					1		
Prunus sp.					.6		
Nyssa aquatica							20
Nyssa sylvatica						1	2
Populus heterophylla							.5
Taxodium distichum							.23
TOTAL	9	6	20	13	20	12	22

FIGURE 50. Map of Illinois showing locations of stands used for comparisons.


1
2
3
4
5
6
7

The data of five stands from Telford (1926) were obtained by complete counts of relatively small tracts. The relative density figures taken from Yeager (1949) represent data obtained by transect sampling of a 2200 acre tract, which is considerably larger than the other tracts sampled so naturally more species appear. The sample from the mouth of the Wisconsin River at Wyalusing State Park was taken from data out of the present study.

Species representation in the series of stands in Figure 50 discloses not only northward diminution in numbers (which is somewhat irregular) but also a general increase of per cent density values as progressively fewer competitors are found in the more northerly stands. The Wyalusing sample, taken from a large area of well-developed floodplain forest, is thought to be adequate to link the Wisconsin floodplain woodlands with consanguine aggregations farther south. The similarity of the composition of the Jo Daviess County stand in northern Illinois and the Wyalusing stand suggests a series of rapid compositional changes between the mouth of the Illinois River and Jo Daviess County (Telford 1926).

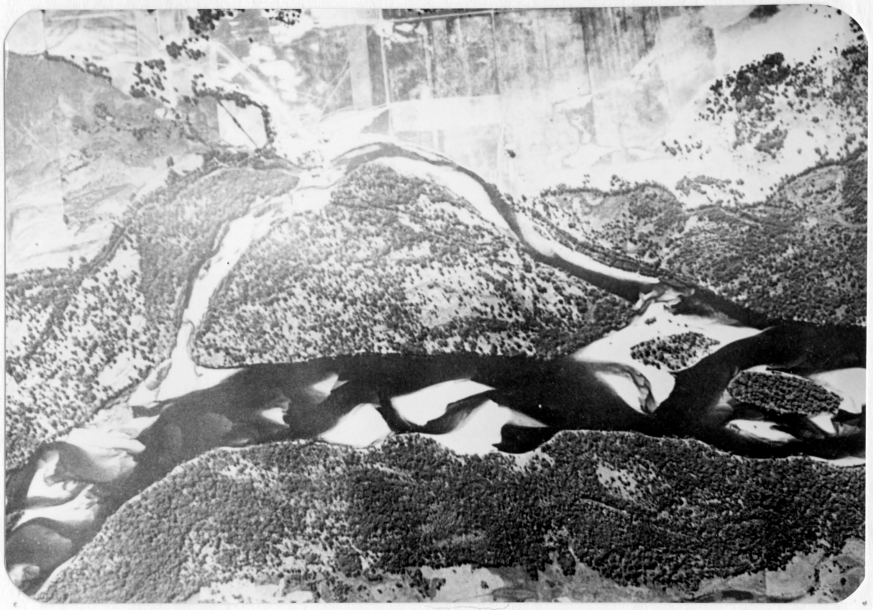
The increasing awareness of the subtle blending of both physical and cultural effects on landscape (Sauer 1925) in the prehistoric as well as historic past behooves the ecologist to beware of interpretational pitfalls. The examination of the forests of the Wisconsin River and other rivers for human disturbances or obscure indirect effects of human disturbances such as the effect of logging on the river by denudation of the watershed, should be given some consideration. The scope of agricultural activities carried on by the Indians on floodplains in Wisconsin

was quite limited when the first explorers came upon their settlements. Jonathan Carver (1767) describes a village of the Sac tribe at the present site of Sauk City near which extensive fields were under cultivation. Carver's description implies that these fields were not on the Wisconsin River floodplain but were on a flat sandy terrace above the floodplain. A few miles downstream on the Wisconsin, probably near Spring Green, Carver noted an abandoned village of the Fox tribe. Neither Father Marquette (1673) nor Father Louis Hennepin (1698) mention tribal habitations along the Wisconsin, and only a few are mentioned for the Mississippi River. Hennepin includes a specific statement emphasizing the complete absence of untilled fields on the Wisconsin. These accounts contrast to a description of the Maumee River floodplains in Ohio in 1792 (Day 1953) where the Miamis were tilling fields continuous along the Maumee from the present site of Fort Wayne to Lake Erie. Only one other account concerning a Wisconsin river was encountered in the present study. A notation by Butterfield (1880) of a large village of Foxes on the Wolf River in 1670 possibly suggests greater disturbance than that on the Wisconsin River. Whatever the effect of Indian agriculture was on floodplains during periods of higher Indian populations in the upper Mississippi Valley, agricultural disturbances on actual floodplains seem to have been rather negligible for the last three centuries.

An effort to learn more of the rate of channel changes of the Wisconsin River is illustrated by Figures 51, 52, 53, and 54. Figures 51 and 53 are maps prepared by Major G. K. Warren (1876) from a survey of the lower Wisconsin River made in 1867, The localities are Arena in

FIGURE 51. Major Warren's map of the Arena area.

FIGURE 52. Aerial photograph of the Arena area.



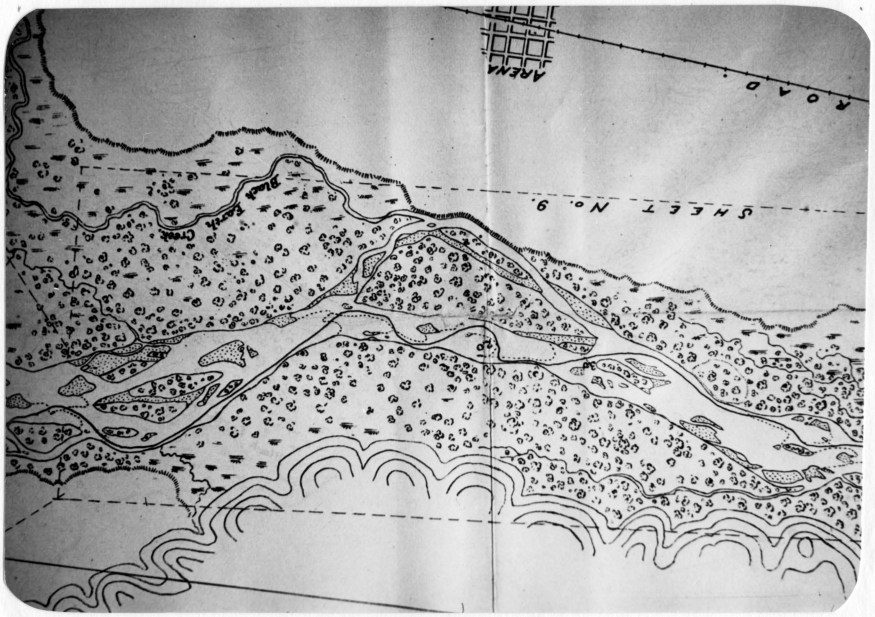
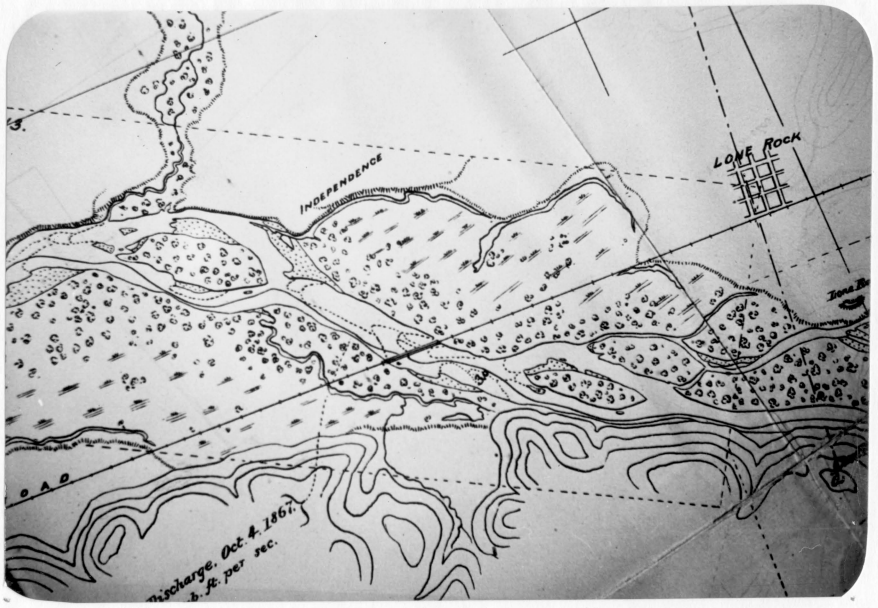

ARENA
ROAD
SHEET No. 9.
North
Creek

FIGURE 53. Major Warren's map of the Lone Rock area.

FIGURE 54. Aerial photograph of the Lone Rock area.


INDEPENDENCE
LONE ROCK
ROAD
Discharge, Oct 4, 1861
cu. ft. per sec.


FL. 6.

Iowa County and Lone Rock in Richland County. The remarkable similarity of the features outlined on Warren's maps to features shown by the aerial photographs suggests more stability for the Wisconsin River than one might guess, since exposed quantities of sand, which show so plainly on the aerial photographs, are ordinarily considered to be indicative of shifting channels. Of course numerous minor changes actually have occurred, and some rather important channel changes have been recounted by those who have lived their whole lives near the Wisconsin (Babington 1950, Derleth 1942). The map and aerial photograph comparisons seem to indicate that such features as larger islands, major sloughs, main channels, and forest-marsh transitions have retained essentially the same outlines for the past nine decades. The Wisconsin River today is a rather docile stream with its flow regulated by a series of dams. Derleth (1942) describes a post-logging, pre-dam period when the denuded watershed of the Wisconsin furnished deluges of destruction. Major Warren's maps were drawn during, or perhaps before, this period of great fluctuation; yet the major outlines of the river have remained unchanged. Comparisons of Warren's maps of other parts of the Wisconsin River to aerial photographs of these same areas seem to confirm the observation that recent vicissitudes of the Wisconsin River are of a limited nature.

The tendency for rivers to build natural levees along their channels means that lower areas, which may experience inundation for much longer periods than the natural levees, may commonly be found in bands or patches outside the natural levees. This phenomenon is particularly well

illustrated by Figure 54. Along the Wisconsin River these areas support marsh vegetation of considerable luxuriance. These marshes frequently adjoin higher sandy terraces of the Wisconsin River which support good growths of prairie grasses.

Gleason's (1923) account of the remarkable replacement of bottomland prairie by forest after settlement along the Mississippi in upper Illinois, and his attribution of this change to the cessation of fires leads to the question of possible bottomland fires on Wisconsin rivers. Examination of trees in Wisconsin bottomlands indicates a prevalence of fire scars to a surprising extent. Virtually every tree in forests proximal to marshes showed fire scars, and a remarkably large number of fire scars could be found in forests which appeared to be protected by channels or sloughs. Figures 55 and 56 show badly scarred living trees among grasses in a marsh-forest transition area. The occurrence of open grown swamp white oaks in marsh-forest transition areas is a phenomenon frequently noted along the Wisconsin River as well as on several other rivers in Wisconsin such as the Wolf, Sugar, Black, Chippewa, and Mississippi.

In a study of a Wisconsin floodplain forest in Sauk County, Leopold (1941) compared growth ring data of several common floodplain trees and found the oldest tree in the stand to be a swamp white oak, dating from 1806. In plotting average growth ring values and their trends from larger trees, he found that the maximum growth rate for swamp white oak occurred about 1870; for river birch about 1880; and for cottonwood about 1875. The maximum growth rings of silver maple were added about 1890; for red oak about 1905; and for American elm

FIGURE 55. Fire scar on the trunk of a river birch.

FIGURE 56. Fire scar on the trunk of a silver maple.





about 1915. The chronological order of the periods of most favorable growth does not agree precisely with order on the compositional gradient of the current study; however the distinct gap between the swamp white oak-river birch-cottonwood optimum and the silver maple-American elm-red oak optimum on the same site signifies a marked change of growth conditions and the apparent supplementing of swamp white oak, river birch, and cottonwood with other forest trees.

Bray (1955) shows that in stands containing open grown trees, the per cent density of swamp white oak over 100 years old among all trees over 100 years old is 33, while per cent density of swamp white oak trees less than 100 years old among all trees less than 100 years old is less than 10.

The evidences that scattered open grown swamp white oak trees are supplemented by species which ultimately form a closed canopy forest seem to be corroborated by the studies of both Bray and Leopold. The occurrence of swamp white oak as a frontier species in the marsh-forest transition of the Wisconsin River suggests that fires tend to maintain swamp white oak openings in a manner similar to the fire relationship of burr oak openings (Stout 1944, Cottam 1949). There tends to be an eating away of the floodplain forest by fire where these forests lie in juxtaposition to the highly flammable marsh, and a selective destruction of trees leaves a greater number of swamp white oaks. Large river birch, silver maple, and red ash trees seem to be moderately resistant to fire, and it is these species which occur with swamp white oak in open groves along the Wisconsin River. Younger elm, silver maple, and basswood trees may be found among the larger trees

of such open groves. The writer has observed fire moving rapidly along the floor of a well-developed floodplain forest in autumn, scarcely blackening the bark of any of the trees. On the other hand, countless destroyed trees have been observed in open forests where grasses were abundant. It may well be that certain phases of the "grass stage" mentioned earlier are completely dependent upon fire for their perpetuation. Though closer observations were made on the Wisconsin River floodplain, the swamp white oak relationship to marsh borders is just as clearly manifested on other rivers of southern Wisconsin. Figures 57 and 58 show open groves consisting primarily of swamp white oak on the Wisconsin River while Figures 59 and 60 are views of a gigantic open grown swamp white oak, which probably has the largest circumference of any swamp white oak tree in the state, measuring 14.5 feet at breast height. This tree was found on the Sugar River near Avon.

Regional Integration

Meaningful and effective colligation of vegetational studies can best be accomplished for those treatments which present some common basis for comparison. Investigations presenting positive statements on numbers and sizes of individuals as well as the space they occupy, constitute a permanent record, subject to reconsideration by other investigators, who may reinterpret the data in the light of additional experience or information (Oosting 1950). Quantitative studies thought to have significant bearing upon the lowland hardwood forests of southern Wisconsin are available from several nearby states. One study

FIGURE 57. Open groves of swamp white oak (near Arena).

FIGURE 58. Open groves of swamp white oak with abundant reproduction (near Spring Green).





FIGURE 59. Open grown swamp white oak tree (on the Sugar River near Avon).

FIGURE 60. Trunk of large swamp white oak tree of Figure 59.





which is used for comparison, that of Sampson, is not quantitative; however ecological relationships of tree species are depicted so well diagrammatically, that inclusion is considered to be essential.

The Des Moines and Missouri Rivers were studied by Aikman and Gilly (1948) by transect samples whereby nine transects were rather evenly distributed along the courses of each of the two rivers. The transect survey of the Des Moines River yielded a total of 20 woody species, of which 18 were found in the first transect, which was located near its confluence with the Mississippi. Only 14 species were found in the last transect in northwestern Iowa (Table V). Twelve species show 100 per cent constancy in both series of transects, and these 12 are also common floodplain species in Wisconsin. All but one of the 20 species encountered in the study, the exception being Salix mackenieana, occur in Wisconsin floodplain forests but not at all with the same constancies. A check of the tree species in nine stands evenly distributed along about 250 miles of the Wisconsin River discloses only 16 species (Table VI). It may well be that a transect cannot be validly compared to a stand which has been sampled as a unit, for the transect cuts across all kinds of alluvial topography. This reasoning is perhaps corroborated by the similarity of composition in so many transects in the Aikman and Gilly study; however a quantitative constancy comparison with its shortcomings, is more enlightening than a simple floristic comparison. There are rather conspicuous phytosociological differences between the Wisconsin River floodplain and the floodplains of the two Iowa rivers, a situation suggested by the data in Table IV, which treated stands along the course of the Mississippi.

TABLE V. Constancy data from transect studies on the Des Moines and Missouri Rivers by Aikman and Gilly (1948).

TABLE V

MISSOURI RIVER									SPECIES	DES MOINES RIVER								
1	2	3	4	5	6	7	8	9		1	2	3	4	5	6	7	8	9
X	X	X	X	X	X	X	X	X	Salix interior	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Salix amygdaloides	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Salix nigra	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Populus deltoides	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Acer negundo	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Gleditsia triacanthos	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Celtis occidentalis	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Fraxinus lanceolata	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Ulmus americana	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Ulmus fulva	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X	X	Juglans nigra	X	X	X	X	X	X	X	X	X
X	X	X	X	X	X	X	X		Acer saccharinum	X	X	X	X	X	X	X	X	X
				X		X	X		Salix mackenieana	X	X	X	X	X	X	X	X	X
									Salix bebbiana							X	X	X
									Juglans cinerea	X	X	X	X	X	X	X	X	
						X	X		Salix discolor	X	X	X	X	X	X	X		
X	X	X	X						Platanus occidentalis	X	X	X	X	X	X	X		
									Fraxinus nigra						X	X	X	X
									Betula nigra	X	X	X	X	X				
		X	X						Ulmus thomasi	X		X		X	X			

TABLE VI. Constancy data from nine stands of the Wisconsin River.

TABLE VI

	1	2	3	4	5	6	7	8	9
Acer saccharinum	X	X	X	X	X	X	X	X	X
Ulmus americana	X	X	X	X	X	X	X	X	X
Fraxinus pennsylvanica	X	X	X	X	X	X	X	X	X
Quercus bicolor	X	X	X	X	X	X	X	X	X
Betula nigra	X	X	X	X	X	X	X	X	
Tilia americana	X	X	X		X		X	X	X
Populus deltoides	X	X		X	X		X		
Salix nigra		X		X					
Gleditsia triacanthos	X								
Salix amygdaloides		X							
Quercus rubra							X		
Carpinus caroliniana								X	
Carya cordiformis							X	X	
Celtis occidentalis							X	X	
Fraxinus nigra							X	X	
Juglans cinerea							X	X	

The investigation of Lee (1945) on the White River system in Indiana treats 20 stands distributed along the two main branches of the stream, which flows directly into the floristically rich Wabash Valley. Of the 40 tall tree species, that is those regularly participating in canopy formation, encountered by Lee in his samples, 26 species occur on Wisconsin floodplains. Constancy data of Lee's work show that the top 16 species also occur in Wisconsin. Only one species of the remaining 24 has a constancy value more than 20 per cent. There seems to be little numerical diminution of species on the rivers studied by Lee, for species numbers in all of the 20 stands are surprisingly similar. Both Acer saccharinum and Ulmus americana have constancy values of 100 per cent. Other species in order of diminishing values are Celtis occidentalis, Platanus occidentalis, Acer negundo, Juglans nigra, Fraxinus americana, Salix nigra, Populus deltoides, and Ulmus thomasi. The agreement of this list with Table II showing constancy in Wisconsin lowland forests is fair; however it is thought that intensive studies of the Pecatonica River in northern Illinois would probably yield data quite similar to data presented by Lee.

Most of the swamps treated by Sampson (1930b) in his study of hardwood swamp forests of northern Ohio are of lacustrine origin. Of Sampson's total of 33 species, 25 are found in Wisconsin swamp forests. This suggests close ecological relationship, and this suggested close relationship seems to be borne out by the ecological relations of the swamp trees shown on Sampson's diagrams. Sampson's elm-ash-maple community may consist of either red maple or silver maple while only silver maple is present to any extent in southern Wisconsin swamps.

Sampson states that black ash or white ash (Fraxinus americana) may occur as the ash constituent of the community while in southern Wisconsin only green ash and black ash are found. His red oak-linden community represents a combination of frequent occurrence in southern Wisconsin. The burr oak-big shellbark (Quercus marcrocarpa-Carya laciniosa) hickory community has as its Wisconsin counterpart a burr oak-shagbark hickory (Carya ovata)combination of frequent occurrence. The occupation of lowland sites with sufficient drainage by a beech-sugar maple community suggests behavior similar to that of these two species in eastern Wisconsin. The similarities between northern Ohio hardwood swamps and eastern Wisconsin hardwood swamps are certainly great enough to warrant the conjecture that southern Michigan and northern Indiana areas, together with northern Ohio and eastern Wisconsin probably present enough uniformity for a fruitful regional study and synthesis of swamp forest communities.

Community Integration

Origins of lowland hardwood forests can frequently be traced from quite dissimilar communities. Transition stages from communities with unlike physiognomic properties occur over the whole range of the compositional gradient, with the exception of one segment, the willow-cottonwood end, which becomes established on open sandbars or lake shores.

The relation of lowland forest to lowland grassland or marsh has been mentioned in the discussion of the relation of fire to floodplain

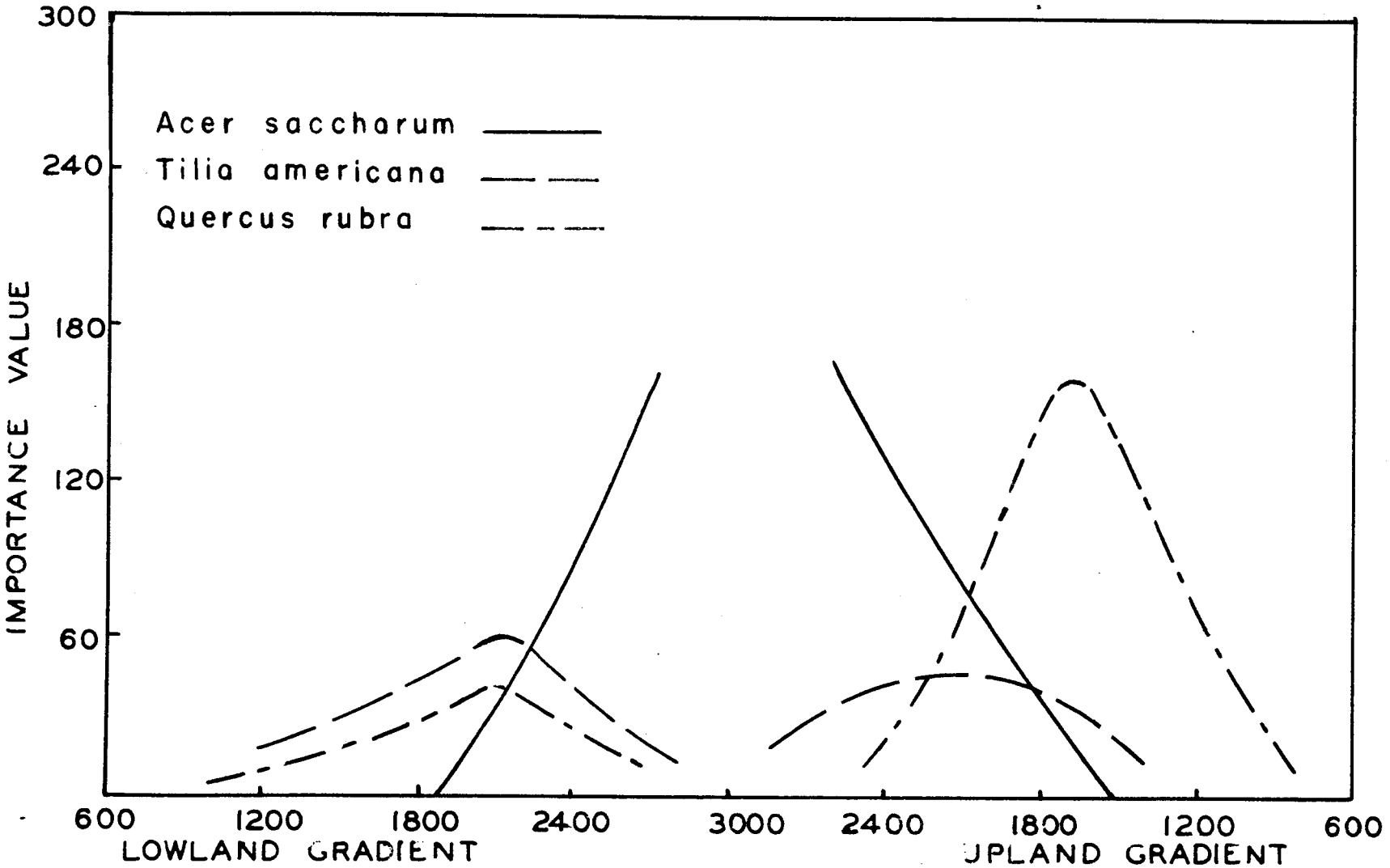
forests. There is abundant evidence that cessation of fire in lowland grasslands is followed by an increase of in the number of swamp white oak, river birch, and red ash on the sandy floodplains of western Wisconsin. Absence of fire on heavier lacustrine lowland soils favors the increase of green ash, burr oak, shagbark, hickory, and American elm. None of the tree species of Wisconsin can endure the prolonged flooding (Green 1947) which bald cypress (Taxodium distichum), tupelo gum (Nyssa aquatica), and pumpkin ash (Fraxinus tomentosa) endure in more southerly areas.

Shanks (1938) indicates for the swamps of northern Ohio a pin oak-red maple-sour gum stage replacing Carex and Calamagrostis meadows. Since these species are not represented in southern Wisconsin lowlands, the replacement of such meadows necessarily must be done by other species. Of all the tree species occurring in Wisconsin, green ash seems to possess greatest endurance of prolonged soil saturation, and pure stands of young trees have been observed in marshy areas in Jefferson County. Saturated soil for prolonged periods is very likely a limitation for tree invasion into certain swamps, particularly lacustrine swamps which are underlain by clays; however there seems to be little doubt that fire has long been an important detriment to tree survival in grassy areas, whether they are upland or lowland. Burr oak openings of lowland areas are found on poorly drained yet infrequently inundated sites, particularly in southeastern Wisconsin. A few of the lowland stands studied appear to have been former burr oak or hybrid burr--swamp white oak openings in which the canopy has been closed by the supplementing of shagbark hickory, green ash, and white oak.

One of the least known of the lowland forest transitions includes hardwood swamp stages which are replacing or have almost replaced tamarack bogs. Such transitions are rather common but have been passed up in the present study because of the physiognomic criterion which specifies that only broad leaved forests are acceptable. The only sampled stand in which any tamarack trees were found, contained a large per cent of Ulmus americana and a few trees each of Acer rubrum, Tilia americana, Fraxinus nigra, and Prunus virginiana. Sampson's (1930b) summary of the origins of swamp forests in northern Ohio agrees well with the ideas concerning community origins outlined in the present work. He states that in lake basins the antecedent communities of swamp hardwood forests are: (1) marshes and wet prairies; (2) the willow-poplar community of low sandbars and beaches; and (3) bogs. On floodplains he lists (1) the alder and willow community and (2) stream valley bogs as possible forerunners of floodplain hardwood forests.

The compositional gradient presented in the current study occupies only the high moisture portion of a moisture gradient which has at its other terminus moisture conditions too low to support tree growth. The upland gradient described by Curtis and McIntosh (1951) is compositionally characterized by burr oak-black oak forests at the drier end of the gradient and by sugar maple forests at the moderately moist or mesic end of the gradient. The lowland forests of the present work range from willow-cottonwood forests at the high moisture end of the gradient to sugar maple forests at the moderately moist or mesic end. Arranging both lowland and upland compositional gradients on a continuous linear moisture gradient should show sugar maple peaking in the

FIGURE 61. Behavior of some species common to both upland and lowland compositional gradients.


300
240
180
120
60
IMPORTANCE VALUE
Acer saccharum
Tilia americana
Quercus rubra
600
1200
1800
2400
3000
2400
1800
1200
600
LOWLAND GRADIENT
UPLAND GRADIENT

middle of the gradient. Because the two gradients are compositional gradients and because the behavior of trees on each gradient is influenced by different woody associates, the use of connected gradients to show behavior along a moisture gradient has limitations on account of the different compositional scales which determine the position of the species peaks. Curves for three species occurring on both upland and lowland gradients are presented in Figure 61. The low light values associated with the peak of sugar maple in the most mesic part of the moisture gradient are accompanied by decreased importance values of the other species which exhibit peaks on both gradients.

Genetic and Ecologic Variation

The work of the ecologist involves treatment of plant populations and their behavior. The recognition of the importance of population genetics is an unavoidable and indeed an integral part of phytosociological work. The taxa which are distinguished in taxonomic works, though ordinarily related to useful morphological discontinuities, frequently have too little relationship to ecologically useful units (Constance 1953).

Whittaker (1954) explains that a bell-shaped curve along an environmental gradient is an indication of a population which has a relatively narrow amplitude along an environmental gradient and that it is likely that the curve is an expression of the genetic range of variation which permits many individuals to survive in the middle of the curve at its mode, and only a few to complete their life-cycles away from the mode in the "tails" of the curve. From one extreme to the other, even in a

homogeneous population, there is some range of genetic variation. Where curves are much flatter without a distinct peak, the broad amplitude along the gradient is thought to imply a relatively broad range of genetic variation within the population, at least in most cases.

The curves representing behavior of tree species on the compositional gradient for the most part exhibit fairly distinct peaks. The amplitudes range from complete coverage of the gradient by American elm (Figure 16) to the relatively localized curves of cottonwood and black ash (Figures 16 and 17). The problem of the most effective use of taxa noted in an earlier section really concerns the question of the degree of heterogeneity of the population being considered as an entity. Taxa employed on the basis of descriptions in plant manuals are not only the most reliable but also quite often the only starting points for the ecologist and it is these, usually at the species level, which are most commonly used.

The extensive travel associated with the present survey brought under surveillance morphological variation of plants over considerable territory. None of the variations has been studied carefully enough yet and venturing positive explanations is not at all prudent; however it is thought that brief descriptions of some of the taxonomic and behavioral perplexities are significantly appropriate for inclusion. For instance identifications of elm in the Wisconsin River floodplains were almost always recorded as red elm for those stands which were sampled early in the study because the elms seemed to show such red elm features as scabrous upper leaf surfaces and dark cork cambium layers instead of light colored layers usually associated with American elm. Checking of herbarium specimens and flora reports (Costello 1933) disclosed that the

Wisconsin River elm is a morphologically distinct "form" of American elm. A precise ecological delimitation of this floodplain elm awaits further study.

The problem of properly handling red ash, green ash, and white ash is still far from being satisfactorily worked out, but ecological behavior of these three "entities" is much better understood in light of extensive field observation. Data sheets noting all three kinds of ashes were brought back from field trips during the early part of the study. It now seems clear that white ash in Wisconsin is not found in wet swamps, but that it does occur in lowland areas in eastern Wisconsin, exhibiting morphological characteristics that seem to intergrade with green ash. There is every reason to believe that there exists a green ash-white ash cline in the lowland areas of eastern Wisconsin with easily separable white ash occurring only in stands rarely inundated. The sizable range of variation in green ash leaves and fruits also indicate complete blending into red ash. Cheney's maps (Figure 8) show identical ranges for red ash and green ash, suggesting close relationship between the two. On this basis and because of the futility of subjective separation of so many intermediates, green and red ash were studied as an ecological group. Trees which show unquestionable red ash characters are most abundant in the Wisconsin Valley in association with fire-resistant swamp white oak. It appears that red ash is the terminus of an ash cline involving intergradation between red ash and green ash. These speculations on ashes are based on field studies of a limited area (southern Wisconsin) and are suggested for ash populations of this limited area only, with the full

realization that ash ecology and taxonony over the whole deciduous forest region is vastly more complicated. Tremendous geographic variability of ashes has been demonstrated by the studies by Wright (1944a, 1944b) for ashes of the eastern United States and by Meuli (1936) and Meuli and Shirley (1937) for ashes of the plains states.

Silver maple possesses a rather limited range of morphological variation and is usually considered to be easily distinguishable from red maple. During the course of the present study a series of stands in eastern Wisconsin was studied in which the maples were identified by some workers as silver maple while others recorded red maple. Collections of flowers showing all sorts of mixtures of floral characters indicate that these intermediates of such widespread areas are more than accidental hybrids, and represent hybridization on a vast areal scale. No references have yet been found concerning natural silver maple-red maple hybridization though Freeman (1941) has obtained artificial crosses in the vicinity of Washington, D. C. Several morphological and cytological studies of the soft maples are available (Taylor 1920, Foster 1933, Duffield 1942, Hall 1951). Foster lists the N chromosome number of silver maple as 26, and the N number of red maples as 52. Duffield concurs with Foster's finding of 52, and indicates still another red maple race with a 2N number of 78. The overlap of blooming dates of the two maples in Wisconsin (Trelease 1883, 1884) may be a favorable condition which is not present in more southerly areas such as the Wabash Valley where Schneck (1876) shows blooming dates separated by several weeks, with red maple blooming earlier than silver maple.

There seems to be, between the two maples, a compatibility which is regionally limited.

It appears that the lacustrine swamps afford hybrid habitat (Anderson 1948) between floodplains and red maple flats, the latter of which are not well drained but are higher than swamps. Deam (1921) states that the silver maple of the floodplains of southern Indiana seems to be quite different ecologically from the swamp silver maple of northern Indiana, and Wright (1949) finds striking physiological differences between silver maples from northern and southern Indiana. The disagreement in the literature concerning the ecologic roles of red maple and silver maple in southern Michigan indicates that this area may also be an area of soft maple hybridization (Veatch 1928, 1932, Kenoyer 1929, 1934, 1939). Otis (1931) mentions varation among silver maple flowers in southern Michigan, a phenomenon not reported from any other source which has been seen. Indeed confusion in soft maple taxonomy and ecology in eastern Wisconsin, southern Michigan, northern Indiana, and northern Ohio (Leue 1886, Transeau 1906) point, from a rather unusual angle, to ecological uniformity of the whole large area.

Despite the apparent hybridization of silver maple and red maple within the study area, silver maple in the present work was treated as one entity. The data of scattered stands with hybrid maples undoubtedly manifest some slight effect on the curve of silver maple on the compositional gradient. Red maple trees were encountered only rarely in the current study.

Another taxonomic and ecologic perplexity is behavior of swamp white oak, which is primarily confined to sandy floodplains in the western part of the state (Figure 9), but also occurs scatteringly over the eastern counties. It appears that swamp white oak has hybridized with burr oak, particularly on the silty and relatively stable floodplain of the Rock River and in a few other places in eastern Wisconsin. Palmer (1948) lists several reports of the occurrence of this hybrid, which in Wisconsin correlates well with the hybrid habitat in which it is found and does not have an inexplicable scattered distribution (Bray 1955).

The linear nature of floodplain vegetation strips and the tendency for floodplain species to form continuous extensions and tongues through diverse kinds of upland vegetation are phenomena which pose rigid limitations upon the gene flow with floodplain populations (S. Wright 1942, 1946; J. Wright 1952). Fassett (1949) has demonstrated a cline for two varieties of Polygonum punctatum along the Wisconsin River, and observations of the decrease of silver maple samara size as one proceeds upstream on the Wisconsin River suggest that a selection of populations occurs when species extend their ranges upstream. Species best adapted to the fluctuational environment of a floodplain must possess what might be called endurance genes, that is, endurance of vicissitudinous riverine effects such as moisture and sediment accretion. Perhaps these endurance properties relate to the great success of floodplain trees as street trees (Deam 1921). In Wisconsin the floodplain trees with their genes for endurance of a wide range of conditions, furnish a reservoir of these genes in the tension zone where the

southern limits of a number of northern species are also found. It is thought that the sharp climatic gradient of the tension zone is in some way related to the maple hybridization problems in that genes of both species are brought together under climatic conditions not perfectly suited to either species. The ecologic niches subject to occupation by hybrids are more numerous in a region with only a moderate number of species than in floristically rich areas farther south. Certain other species are believed to show limited introgression by more northerly species in the tension zone area. Unusual cottonwoods, perhaps hybrids between Populus deltoides and Populus balsamifera, such as have been reported from several places (Sargent 1933) have been observed in the Green Bay area,while considerable uncertainty as to the identification of Betula nigra in the Wisconsin Rapids area has been experienced.

While ecological studies have certainly not yet solved these problems of variation (or hybridization), it should be emphasized that it has been the familiarity gained by sampling thousands of trees which has led to the disclosure of such problems, previously overlooked or perhaps ignored by taxonomists. An ecological approach provides a pathway for the intensive work necessary for definitive studies of population behavior at the community level. Such problems are approachable in no other way than by going directly to the vegetation.

SUMMARY

1. The composition, range of variation, and ecological relationships of the lowland hardwood forests of southern Wisconsin were studied by means of quantitative information obtained by the sampling of 114 stands widely distributed over the southern half of the state. The study was restricted to forests of natural origin which displayed no indications of past disturbances such as fire, cutting, and grazing.

2. The use of the random pairs sampling method of ecologists provided data from which relative frequency, relative density, and relative dominance were obtained for each tree species in every stand. The summation of the three values yield what is known as an importance value, which was used as a quantitative basis for comparison of species behavior.

3. By representing the importance values in diagrammatic form by bars, an ecologically syntactical scheme was worked out which indicated that a relative ecological arrangement of the 12 most common species was as follows: Salix nigra, Populus deltoides, Betula nigra, Quercus bicolor, Acer saccharinum, Fraxinus pennsylvanica var. subintegerrima, Ulmus americana, Fraxinus nigra, Tilia americana, Quercus rubra, Celtis occidentalis, and Acer saccharum.

4. Adaptation numbers from 1 to 10 were assigned to species on the basis of their relative position indicated by the bar diagrams. Salix nigra was given the number 1, and Acer saccharum was given the number 10. By using both the importance values of the species of a stand and adaptation numbers of the same species; by obtaining the product of the two values for each species; and by summing the products for all species of a stand, a differentially weighted cumulation value for each stand was obtained. Stand values were used for the collocation of all 114 stands of the study along a compositional gradient.

5. Smooth and regular curves, representing the behavior of saplings, herbs, and soil properties along the compositional gradient, were found and submitted as corroborative attestation to the proper arrangement of tree species on the compositional gradient. Certain adjunctive forest properties, including water-holding-capacity of the soil, basal area per acre, available calcium, and available nitrate nitrogen, suggested that differences exist between swamps of fluvial origin and swamps of lacustrine origin which are of sufficient importance to warrant separate study of the two swamp groups.

6. Successional implications are nowise intended by the diagrammatic arrangement of tree species nor by the assignment of adaptation numbers to the tree species. There is little that the vegetation can do to make the environment of a swamp suitable for mesic species. The replacement of swamp species by more mesic species must await physiographic changes such as accretion and river deepening.

7. The expression of an ecologically syntactical scheme for lowland hardwood tree species on a linear compositional gradient is a convenient method of viewing what is well-known to be a two dimensional problem. The compressing of a number of planes into one plane is comparable to viewing an elongate range of mountains from a great distance in that the peaks blend together in what appears to be a single plane.

8. The vicissitudinous nature of swamps and floodplains seem to be related to great genetic and ecologic variability among lowland species. Knotty taxonomic and ecologic problems in the study of red, green, and white ash; red and silver maple; swamp white oak; and American elm are especially apparent in the lowland hardwood forests of southern Wisconsin.

APPENDIX

FIGURE 62. First of a series of views of representative forests arranged by numerical order on the compositional gradient. Shown is a stand predominantly composed of black willow trees, with numerous saplings and young trees of silver maple. Gradient number is 720.

FIGURE 63. Cottonwood-silver maple-American elm stand with abundant reproduction of maple and elm. Gradient number is 1274.

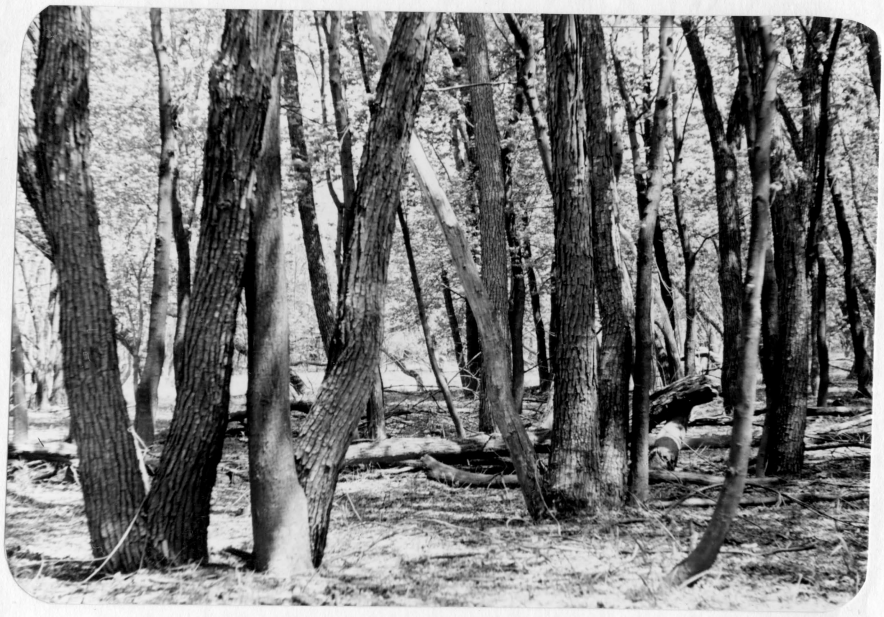




FIGURE 64. River birch-silver maple-swamp white oak-American elm stand in which overflow of Wisconsin River has left coarse sandy sediments. Grasses and Carex species constitute most of the understory. Gradient number is 1290.

FIGURE 65. Swamp white oak-silver maple-American elm stand. Large Tilia at right. Gradient number is 1293.





FIGURE 66. Silver maple-river birch-green ash-American elm stand. Understory is predominantly Laportea canadensis. Gradient number is 1323.

FIGURE 67. Silver maple-green ash-American elm stand. Gradient number is 1377.





FIGURE 68. Swamp white oak-green ash-American elm stand. Gradient number is 1447.

FIGURE 69. Silver maple-green ash-American elm stand. Understory is predominantly Laportea canadensis. Gradient number is 1510.





FIGURE 70. American elm-silver maple-green ash swamp of lacustrine origin. Understory is predominantly Laportea canadensis. Shrubs and saplings are much more conspicuous than in previous figures. Gradient number is 1746.

FIGURE 71. Red oak-red maple stand with closely grouped clean-boled trees. Gradient number is 1941.





FIGURE 72. Sugar maple stand. Associates are hackberry and red elm. Gradient number is 2757.

FIGURE 73. Sugar maple woods. Same stand as one shown in Figure 72.





FIGURE 74. First of a series of views of some interesting and unusual phenomena related to lowland hardwood forests. Recently established stand of willow on the Wisconsin River. Initial stage of a floodplain forest.

FIGURE 75. Band of willow in loop of a bend of the Sugar River.





FIGURE 76. Scattered river birch trees in sandy pasture. The pasture is located on a terrace many feet above the level of the Wisconsin River.

FIGURE 77. Largest river birch tree encountered in the study. Circumference nine and one-half feet.





FIGURE 78. Gigantic open-grown silver maple tree in the Sugar River bottomland. Circumference is 15 feet.

FIGURE 79. Sedimentation in the Sugar River bottomland. Enormous quantities of sand frequently bury trunk bases of floodplain trees.





FIGURE 80. Floodplain forest of Sugar River in winter. Fallen and leaning trees give disordered appearance to woods.

FIGURE 81. Multiple-trunked Tilia americana. Tilia with only a single trunk is rarely encountered in swamp forests.





FIGURE 82. Major Warren's sketch of the mouth of the Wisconsin River in 1867.

FIGURE 83. View of mouth of Wisconsin River today.

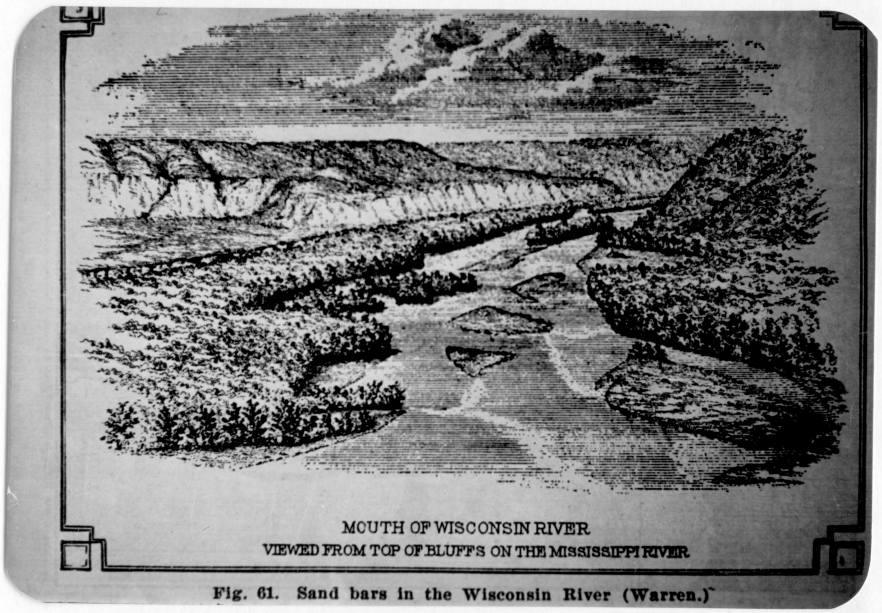


Fig. 61. Sand bars in the Wisconsin River (Warren.)



TABLE VII. List of herb and shrub species occurring in at least three stands.

TABLE VII

Actaea pachypoda
Actaea rubra
Adiantum pedatum
Agrimonia grypsosepala
Agropyron trachycaulum
Allium canadense
Allium tricoccum
Ambrosia artemisiifolia
Ambrosia trifida
Amphicarpa bracteata
Anemone canadensis
Anemone quinquefolia
Anemone virginiana
Angelica atropurpurea
Apios americana
Abrabis perstellata
Aralia nudicaulis
Aralia racemosa
Arenaria lateriflora
Arisaema atrorubens
Arisaema dracontium
Asarum canadense
Aster lateriflorus
Aster macrophyllus
Aster puniceus
Aster sagittifolius
Aster shortii
Aster simplex
Athyrium angustum
Athyrium thelypterioides
Bidens frondosa
Boehmeria cylindrica
Brachyelytrum erectum
Bromus latiglumis
Caltha palustris
Campanula americana
Carex albursina
Carex alopecoides
Carex amphibola var. turgida
Carex blanda
Carex bromoides
Carex crinita
Carex cristatella
Carex gracillima
Carex grayi
Carex intumescens
Carex laxiflora
Carex lupulina
Carex muskingumensis
Carex pensylvanica
Carex projecta
Carex retrorsa
Carex rosea
Carex stipata
Carex tuckermanni
Carex typhina
Carex vulpinoidea
Caulophyllum thalictroides
Celastrus scandens
Cephalanthus occidentalis
Chelone glabra
Cicuta maculata
Cinna arundinacea
Circaea alpina
Circaea quadrisulcata
Cirsium altissimum
Clematis virginiana
Clintonia borealis
Cornus femina
Cornus obliqua
Cornus rugosa
Corylus americana
Cryptotaenia canadensis
Cuscuta gronovii
Dentaria laciniata
Desmodium glutinosum
Dicentra cucullaria
Dioscorea villasa
Dryopteris cristata
Dryopteris spinulosa
Dryopteris thelypteris
Echinocystis lobata
Ellisia nyctelea
Elymus virginicus
Equisetum arvense
Equisetum hyemale
Erigeron annuus
Erythronium albidum
Eupatorium perfoliatum
Eupatorium purpureum
Eupatorium rugosum
Euonymus atropurpureus
Festuca obtusa
Fragaria virginiana

Galeopsis tetrahit
Galium aparine
Galium concinnum
Galium obtusum
Galium tinctorium
Galium triflorum
Geranium maculatum
Geum canadense
Geum strictum
Glyceria striata
Helianthus strumosus
Hepatica acutiloba
Heracleum maximum
Hydrophyllum appendiculatum
Hydrophyllum virginianum
Hystrix patula
Ilex verticillata
Impatiens capensis
Iris virginica
Laportea canadensis
Leersia virginica
Leonurus cardiacea
Lilium michiganense
Lilium philadelphicum
Lilum superbum
Lobelia cardinalis
Lobelia spicata
Lonicera canadensis
Lonicera prolifera
Lycopus americanus
Lycopus uniflorus
Lysimachia ciliata
Lysimachia nummularia
Lysimachia thyrsiflora
Maianthemum canadense
Menispermum canadense
Mitchella repens
Mitella diphylla
Monotropa uniflora
Muhlenbergia frondosa
Myosotis scorpioides
Nepeta hederacea
Oenothera biennis
Onoclea sensibilis
Oryzopsis racemosa
Osmorhiza claytoni
Osmorhiza longistylis
Osmunda cinnamomea
Osmunda regalis
Oxalis europaea
Parietaria pensylvanica
Parthenocissus inserta
Phalaris arundinacea
Phlox divaricata
Phryma leptostachya
Physostegia virginiana
Pilea pumila
Poa pratensis
Podophyllum peltatum
Polemonium reptans
Polygonatum canaliculatum
Polygonatum pubescens
Polygonum sagittatum
Polygonum virginianum
Prenanthes alba
Prunella vulgaris
Pteretis nodulosa
Ranunculus abortivus
Ranunculus recurvatus
Ranunculus septentrionalis
Rhus radicans
Ribes americanum
Ribes cynosbati
Ribes missouriense
Rorippa islandica
Rubus allegheniensis
Rubus occidentalis
Rubus parviflorus
Rubus pubescens
Rudbeckia laciniata
Rumex verticillatus
Sagittaria sp.
Salix amygdaloides
Salix interior
Sambucus canadensis
Sanguinaria canadensis
Sanicula gregaria
Saxifraga pensylvanica
Scutellaria lateriflora
Senecio aureus
Silphium perfoliatum
Sium suave
Smilacina racemosa
Smilacina stellata
Smilax ecirrhata
Smilax herbacea
Smilax tamnoides
Solanum dulcamara
Solidago altissima
Solidago gigantea
Solidago ulmifolia

Spartina pectinata
Spiraea alba
Stachys hispida
Stachys palustris
Staphylea trifolia
Symplocarpos foetida
Teucrium canadense
Thalictrum dasycarpum
Thalictrum dioicum
Tovara virginiana
Trientalis borealis
Trillium flexipes
Trillium grandiflorum
Trillium recurvatum
Triosteum perfoliatum
Typha latifolia
Urtica dioica
Uvularia grandiflora
Uvularia sessilifolia
Verbena urticaefolium
Veronicastrum virginianum
Viburnum acerifolium
Viburnum lentago
Viola affinis
Viola blanda
Viola conspersa
Viola cucullata
Viola pubescens
Vitis riparia
Zanthoxylum americanum

FIGURE 84. Stand Record Sheet.

Data Form No. 20 | Plant Ecology Research | Univ. of Wisconsin

STAND RECORD | FORESTS | Stand No.

Name: Locality:
County: T: R: Sec:
Date: Observers:
Size of Stand: Size of Area Sampled:
Forest Type: Soil Type:
Topography: Slope: Directions

Condition of Stand:

Open Grown Trees: % Canopy:

Stumps:

1.	4.	7.	10.
2.	5.	8.	11.
3.	6.	9.	12.

Soil Data:

	pH	N	P	K	Ca	Mg	Org. Mat.	Colloids	W.H.C.		
A_o											
A_1											
A_2											
B											

	DEPTH	CHARACTERISTICS (Color, Texture, Structure, etc.)
A_o		
A_1		
A_2		
B		

Parent Material:

Map:

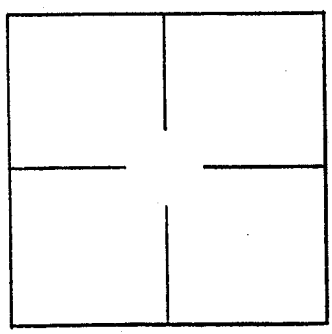


Figure 85. Point record sheet for trees.

Data Form No. 39 | Plant Ecology Research | Univ. of Wisconsin

POINT RECORD TREES | FLOOD-PLAIN HARDWOODS | Stand No.

STATION NO.	1	2	3	4	5	6	7	8	9	10
Acer negundo										
A. saccharinum										
A. saccharum										
Betula nigra										
Carya cordiformis										
Celtis occidental.										
Crataegus sp.										
Fraxinus americ.										
F. nigra										
F. pensylvanica										
Gleditsia triacan.										
Gymnocladus dioica										
Juglans cinerea										
Platanus occident.										
Populus deltoides										
P. tremuloides										
Prunus serotina										
Quercus bicolor										
Q. rubra										
Robinia pseudo.										
Salix nigra										
Tilia americana										
Ulmus americana										
U. rubra										
Distance										

FIGURE 86. Tree data summary sheet.

Data Form No. 37 | Plant Ecology Research | University of Wisconsin

Tree Data Summary

FLOOD-PLAIN HARDWOODS

Stand No.

Station Number:

TREE	# PTS	# TRS	DOM. CLASSES -80	-320	321	TOT. DOM.	# SAP	D.% SAP	F.% SDL.	F.% TRS.	% SUM F. TR.	D. % TRS.	DOM% TRS.	IMP. INDEX	C. I.
Acer negundo															
A. saccharin															
A. sacchar															
Betula nigra															
Carya cordif															
Celtis occid															
Crataegus sp															
Frax. amer.															
F. nigra															
F. pensylv															
Gleditsia tr															
Gymnocladus															
Juglans cin															
Platanus occ															
Populus delt															
P. tremulo															
Prunus serot															
Quercus bico															
Q. rubra															
Robinia pseu															
Salix nigra															
Tilia amer															
Ulmus amer															
U. rubra															

AVE. DIST. BTW'N TREES: AVE B. A.: # TREES/ACRE: DOM./ACRE:

FIGURE 87. Herb frequency sheet (common species).

Data Form No. 48

Plant Ecology Research

Univ. of Wisconsin

FLOOD-PLAIN HARDWOODS

Presence or Frequency
(Common species only)

Stand No.
Quadrat No.

Adiantum pedatum
Agrimonia grypsosepala
Allium canadense
Allium tricoccum
Amphicarpa bracteada
Anemone canadensis
Anemone virginiana
Aralia nudicaulis
Arenaria lateriflora
Arisaema atrorubens
Arisaema dracontium
Asarum canadense
Aster lateriflorus
Aster simplex
Athyrium filix-femina
Athyrium thelypterioides
Boehmeria cylindrica
Brachyelytrum erectum
Caltha palustris
Campanula americana
Carex crinita
Carex grayii
Carex intumescens
Carex lupulina
Carex normalis
Carex vupinoidea
Cephalanthus occidentalis
Cicuta maculata
Circaea quadrisulcata
Cirsium altissimum
Convolvulus sepium
Cornus femina
Cornus obliqua
Cornus rugosa
Cornus stolonifera
Corylus americana
Cryptotaenia canadensis
Desmodium glutinosum
Dioscorea villosa
Echinocystis lobata
Fragaria virginiana
Galium aparine
Galium concinnum
Galium obtusum
Galium triflorum
Geranium maculatum
Geum canadense
Glyceria striata
Hydrophyllum virginianum
Ilex verticillata
Impatiens capensis
Iris virginica
Lactuca biennis
Laportea canadensis
Leersia oryzoides
Lobelia cardinalis
Lycopus americanus
Lycopus uniflorus
Lysimachia ciliata
Lysimachia nummularia
Menispermum canadense
Onoclea sensibilis
Osmorhiza claytoni
Osmorhiza longistylis
Parthenocissus inserta
Phlox divaricata
Phryma leptostachya
Physostegia virginiana
Podophyllum peltatum
Polemonium reptans
Polygonatum canaliculatum
Prenanthes alba
Ranunculus arbortivus
Ranunculus septentrionalis
Rhus radicans
Ribes americanum
Ribes cynosbati
Ribes missouriense
Rorippa islandica
Rudbeckia laciniata
Rumex verticillatus
Sambucus canadensis
Sanguinaria canadensis
Sanicula gregaria
Smilacina racemosa
Smilacina stellata
Smilax ecirrhata
Smilax herbacea
Smilax tamnoides
Solanum dulcamara
Stachys palustris
Teucrium canadense
Thalictrum dasycarpum
Thalictrum dioicum
Tovara virginiana
Trillium flexipes
Uvularia sessilifolia
Veronicastrum virginianum
Viburnum lentago
Viola canadensis
Viola conspersa
Viola cucullata
Viola pubescens
Vitis riparia
Zanthoxylum americanum

Additional species:

FIGURE 88. Herb frequency sheet (uncommon species).

Data Form No. 49 | Plant Ecology Research | Univ. of Wisconsin

Presence List
(Uncommon species)

FLOOD-PLAIN HARDWOODS

Stand No.
Quadrat No.

Acorus calamus
Actaea pachypoda
Actaea rubra
Agastache scrophulariaefolia
Agropyron trachycaulum
Alisma subcordatum
Alnus incana
Alnus rugosa
Ambrosia trifida
Amorpha fruticosa
Anemone quinquefolia
Anemonella thalictroides
Angelica atropurpurea
Apios americana
Aralia hispida
Aralia racemosa
Asclepias incarnata
Aster cordifolius
Aster sagittifolius
Aster shortii
Bidens connata
Bidens coronata
Bidens frondosa
Bidens vulgata
Botrychium virginianum
Bromus purgans
Calamagrostis canadensis
Carex bursina
Carex alopecoidea
Carex convoluta
Carex cristata
Carex grisea
Carex laxiflora
Carex molesta
Carex muskingumensis
Carex pensylvanica
Carex projecta
Carex stipata
Carex tribuloides
Carex typhina
Carex vesicaria
Cassia marilandica
Caulophyllum thalictroides
Celastrus scandens
Chaerophyllum procumbens
Chelone glabra
Cicuta bulbifera
Circaea alpina
Clematis virginiana
Clintonia borealis
Comandra umbellata
Cornus alternifolia
Cuscuta sp.
Dentaria laciniata
Desmodium nudiflorum
Dicentra cucullaria
Diervilla lonicera
Dryopteris cristata
Dryopteris spinulosa
Dryopteris thelypteris
Ellisia nyctelea
Elymus virginicus
Epilobium palustris
Equisetum arvense
Equisetum hyemale
Erigeron philadelphicus
Erigeron pulchellus
Erythronium albidum
Eupatorium perfoliatum
Eupatorium purpureum
Eupatorium rugosum
Euonymus atropurpureus
Festuca obtusa
Fragaria vesca
Galium tinctorium
Gerardia gradiflora
Geum strictum
Hackelia virginica
Helenium autumnale
Helianthus strumosus
Hepatica acutiloba
Heracleum maximum
Hydrophyllum appendiculatum
Hypericum ascyron
Hypericum pyramidatum
Hystrix patula
Impatiens pallida
Iris versicolor
Isopyrum biternatum
Juncus tenuis
Lactuca canadensis
Lilium michiganense
Lilium philadelphicum
Lilium superbum
Lippia lanceolata
Lonicera prolifera
Maianthemum canadense
Mentha arvensis
Mertensia virginica
Mimulus ringens
Mitella diphylla
Monarda fistulosa
Muhlenbergia sp.
Napaea dioica
Nepeta hederacea
Oryzopsis racemosa
Osmunda cinnamomea
Osmunda regalis
Oxalis europaea
Oxalis stricta
Parietaria pensylvanica
Phalaris arundinacea
Phlox pilosa
Physocarpus opulifolius
Pilea pumila
Poa palustris
Polygonatum biflorum
Polygonatum pubescens
Polygonum hydropiper
Polygonum sagittatum
Pteridium aquilinum
Ranunculus recurvatus
Ratibida pinnata
Rubus allegheniensis
Rubus occidentalis
Rumex altissimus
Salix amygdaloides
Salix interior
Sanicula marilandica
Saxifraga pensylvanica
Scutellaria lateriflora
Senecio aureus
Silphium perfoliatum
Sium suave
Solidago gigantea
Solidago ulmifolia
Spiraea alba
Staphylea trifolia
Stellaria longifolia
Symplocarpus foetida
Trientalis borealis
Trillium grandiflorum
Trillium recurvatum
Triosteum perfoliatum
Urtica dioica
Uvularia grandiflora
Vernonia fasciculata
Viola renifolia
Zizia aurea

Additional Species:

FIGURE 89. Summary sheet for herb frequency.

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TABULATION FORM | FLOOD-PLAIN HARDWOODS | Stand No.

STATION NO.	p.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20		
Acorus calamus																							
Actaea pachypoda																							
Actaea rubra																							
Adiantum pedatum																							
Agastache scrophulariaefolia																							
Agrimonia grypsosepala																							
Agropyron trachycaulum																							
Alisma subcordatum																							
Allium canadense																							
Allium tricoccum																							
Alnus incana																							
Alnus rugosa																							
Ambrosia trifida																							
Amorpha fruticosa																							
Amphicarpa bracteata																							
Anemone canadensis																							
Anemone quinquefolia																							
Anemone virginiana																							
Anemonella thalictroides																							
Angelica atropurpurea																							
Apios americana																							
Aralia hispida																							
Aralia nudicaulis																							
Aralia racemosa																							
Arenaria lateriflora																							
Arisaema atrorubens																							
Arisaema dracontium																							
Asarum canadense																							
Asclepias incarnata																							
Aster cordifolius																							
Aster lateriflorus																							
Aster sagittifolius																							
Aster shortii																							
Aster simplex																							
Athyrium filix-femina																							
Athyrium thelypterioides																							
Bidens connata																							
Bidens coronata																							
Bidens frondosa																							
Bidens vulgata																							
Boehmeria cylindrica																							
Botrychium virginianum																							
Brachyelytrum erectum																							
Bromus purgans																							
Calamagrostis canadensis																							
Caltha palustris																							
Campanula americana																							
Carex albursina																							
Carex alopecoidea																							
Carex convoluta																							
Carex crinita																							
Carex cristata																							

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TITLE OF THESIS ___A PHYTOSOCIOLOGICAL STUDY OF LOWLAND HARDWOOD FORESTS IN SOUTHERN WISCONSIN

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