THE LOWLAND HARDWOOD FORESTS OF INGHAM COUNTY, MICHIGAN: THEIR STRUCTURE AND ECOLOGY

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THESIS

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ABSTRACT

THE LOWLAND-HARDWOOD FORESTS OF INGHAM COUNTY, MICHIGAN; THEIR STRUCTURE AND ECOLOGY

by Robert Louis Bryant

A considerable acreage occupied by lowland-hardwood forests in southern Michigan is considered to have a storage and stabilizing influence on ground water supplies. Since little is known about the composition, ground water hydrology, successional relationships, and general ecology of these forests the present study is an attempt to provide preliminary information on these subjects.

Measurement of the number, size, and distribution of tree species in the lowland-hardwood stands was accomplished using four sampling methods. A plot method was used as a standard for the study against which data were compared from the other methods. Non-areal methods included random pairs, the point-centered quarter, and the variable plot-radius methods.

In order to determine the relative reliability of the various sampling methods, simple correlations (r), were calculated between three parameters (basal area, frequency, and density), as determined from each of the methods. The relationships indicated by the use of coefficients of determination (r^2) showed that any of the four sampling methods gave almost as much information about the three parameters as did the best method.

The same measures (basal area, frequency, and density) were used in describing the composition of the stands selected for the study. Continuum indices were calculated for all lowland-hardwood stands. These indices indicated a rather complete coverage for the spectrum of lowland sites. Importance values calculated from the three parameters proved to

give the best measure of species dominance.

The effects of fire and pathogenic influences, windthrow and rooting systems on community structure of lowland-hardwood stands were discussed. Windthrow and rooting habits of certain lowland tree species served to influence the eventual stand-age-structure of lacustrine forests.

An examination of the soil profiles showed that the majority of soil types were alpha-gleys which were poorly drained.

Soils were analysed for total sand, silt, and clay content. Other analyses included moisture equivalent, loss on ignition, and pH. Differences in soil characteristics between the stands were evaluated statistically.

Simple correlations were calculated between the importance values and basal areas of the ten most abundant species and soil physical properties. Two species showed a tendency to be found on soils with certain physical characteristics--black cherry and slippery elm. Because the presence of non-significant correlations between soil characteristics in different horizons was great, it was suggested that future vegetation studies in the lowland-hardwood land type should ignore the measurement of physical soil parameters.

Weekly measurements of water table levels during the 1961 growing season were recorded for 72 ground water wells. Differences in water table depths between the stands were evaluated statistically. The greatest changes in true water levels occurred in beta-gley and certain alpha-gley soils. Actual water table variation was least in poorly-drained mucks.

Simple correlations which were calculated between the importance values and basal areas of the ten most abundant species and ground water depths during the growing season involved two species--sugar maple and American basswood. Additional statistical analyses were performed between water table depths and the date of measurement. It was suggested that a subsequent series of ground water measurements to give maximum information on water table depth could be substantially reduced.

As a means of depicting the behavioral pattern of lowland-hardwood forests, the stand to stand relationships based on vegetation similarities and environmental measures were included in a series of graphs. Using the continuum as an index of similarity was not unlike the figures derived from a formula method. Succession in lowland-hardwood stands implied by the most significant environmental measurements was represented in a dimensional figure.

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Introduction

In recent years the use of quantitative measurements in phytosociological studies has been devoted largely to upland forest communities (130, 2?, 157,132,60,28,53). Fewer phytosociological studies have been carried out exclusively in lowland hardwood forests probably because of the numerous discomforts which are always present, including boggy terrain, irritating insects and obnoxious plants, which usually impede progress in the collection of quantitative information. Those studies carried out in spite of these difficulties, include the efforts of Christensen, Clausen and Curtis (40), Ware (150), Lindsey (102), and Wistendahl (167).

The lowland hardwood forests of southern Michigan are of considerable importance. Although they occupy only six to ten percent of the commercial forest land throughout the region, this amounts to about 750,000 acres in the lower peninsula of the state.[1] The considerable acerage occupied by lowland hardwoods makes it one of the major forest types in Michigan, whose future economic potential as a source of forest products may be great. Such a large forested area, occupying sites which are so poorly drained, serves as a catchment basin for precipitation and runoff and acts as a storage and stabilizing influence on the ground water supplies in this section of the state.

The present condition of the majority of stands in this type consists of overmature, defective and cull specimens left after cutting and utilization practices which removed only the most valuable trees. Lowland hardwoods usually have been bypassed as an area of research in southern

[1]Unpublished information, Lake States Forest Experiment Station.

Michigan and most of the research effort requiring detailed investigations has been devoted to the more valuable oak, oak-hickory, and sugar maple-beech forests on upland soils.

The lowlands in hardwood forests are primarily of glacio-lacustrine or fluvial origin, occupying such depressional features as elongated glacial drainageways, swales and basins of till plains, ground moraines, and shallow muck swamps. In addition, these forests are often found along the borders of many lakes and streams, small tributaries, and enclosed upland depressions and bogs.

The major tree species of these forests in the northern part of the lower peninsula consists of pure conifers to mixed conifers and hardwoods, while the southern part consists of nearly pure hardwoods.

The primary objective of the present study was to describe and compare the structure and several environmental characteristics of a series of stands in this poorly known lowland forest type. The environmental parameters were mechanical analyses of soils and the changes occurring in water table levels. Basic information on the ground water hydrology for this section of the state consists only of information on representative wells influenced by pumping. A second objective was to construct estimates of the successional relationships among the lowland forest types.

Because the collection of hydrologic data requires a definite schedule of observations in wells, the area within which the stands were chosen was kept small. Ingham County, in which the study was made, is considered reasonably representative of the 13 other counties in southern Lower Michigan. It contains 13,200 acres (11%) of lowland hardwoods, a rather large portion of the type occurring in the 13 county area.

Description and Early History of the Area

Ingham county, the area in which this study was made, is located in the south-central part of the lower peninsula of Michigan. The county is roughly square in outline, composed of four tiers of townships, and includes an area of approximately 550 square miles within its limits.

Several hundred Indians were the first known human inhabitants of Ingham County (63). Since they relied heavily on water as their principal means of transportation, it is only natural that the first dwellings were established along the few waterways that exist in the county. The largest Indian village in the county was established at Okemos, beside a clear shallow river called the Red Cedar. Early surveyor's notes also indicated the presence of two smaller villages. One was located beside a small lake in the northern part of Stockbridge township and the other along the Grand River in Onondaga township (63).

Overland trails used by the Indians usually followed established water routes. Away from the rivers, trails were established on higher ground, usually along the tops of winding eskers and ridges of the larger moraines. Two large eskers, running from the northeastern to the southwestern part of the country, were used rather extensively as travel routes.

According to Fuller (63), the tribes depended heavily upon upland beech-maple and oak-hickory forests, as well as floodplain forests for food, shelter, and clothing. No mention was made, however, of the extensive lowland hardwood forests, in old glacial drainageways and lowland basins, being used for any purpose. It is possible that these areas were avoided because of fear of sickness, fever and pestilence, bred by the hordes of mosquitoes which inhabit such places. Small open areas of wet marshes were mentioned as being extensively used for trapping purposes.

At the time that permanent settlement by white men began, during the 1830's, the entire county was covered by dense hardwood forests. Little pine was present, except for the area around Lake Lansing. Tamarack, however, was prevalent in the swamps and drains of the watersheds. The early settlers immigrating into the southeastern part of the county, in Stockbridge township, testified to the fact that dense forests ranged to the west and north.

Initial purchases of land for timber and minerals were made in the northern part of the county. It was here, and in the western sections of the county, that the greatest variety of timber species was found (63). The principal species found on the well drained mesic sites were beech and sugar maple, which are considered climax for this region. Originally, the heaviest timbered sugar maple stands were found in Vevay township. Maple trees were tapped in these early days for the sap, which was made into syrup and together with venison served as items of trade between the Indians and pioneer settlers. It was reported by Fuller (63), that the most heavily stocked lowland hardwood stands were found in Meridian, Leslie, Wheatfield, Alaiedon, Onondaga, Stockbridge and Vevay townships.

Toward the south and east, homesteads were established on the well drained and intermediate textured soils. Oak stands were found on the deeper sands and somewhat drier upland soils. It appears from the early records that oak timber was very abundant on these soils, and was the most valuable forest asset in the country. According to the early lumbermen, Ingham County produced the greatest quantity and some of the finest quality oak timber found in the state (63). Before the 1860's, over 21 small sawmills had been established throughout the county. The largest mills were located in Wheatfield, Onondaga, and Stockbridge townships.

During this time, millions of feet of oak timber were cut to supply local and regional markets to the west. Oak was used for practically everything, including shingles and flooring, staves for barrels and casks, wheelbarrows and hand trucks, bridges, corduroy roads, and railroad ties. After the railroads were built, oak lumber was sent to the shipyards of the eastern markets. Waste slabs and cull lumber were made into charcoal, shipped to the northern part of the state and used for smelting iron.

In these early days the timber on upland areas was also cleared for agriculture. Plowing and planting these lands to various crops reduced the natural fertility of the soil, and more land was cleared as yields became progressively lower. Little was done by the landowners to protect the soil from erosion or to increase its fertility. As a result of this treatment, a great amount of soil material washed into and filled the natural drains. In a very few years competition for finer textured soils increased as marginal droughty uplands were abandoned and eventually some of the poorly drained mineral soils and mucks were placed under cultivation.

In earlier times, these poorly drained areas were considered unfavorable for the production of crops and continued to support lowland hardwood forests. Since the cost of drainage is high many areas have remained relatively undisturbed until the present time. It appears from the early records, that lowland hardwood forests were not generally exploited for their timbers, at least to the extent which occurred in the oak forests of the county. One exception to this situation occurred in lowland floodplain forests, which favored the development of sycamore, cottonwood, yellowpoplar, black cherry, butternut and black walnut. It appears that the walnuts, prized for their use in furniture and cabinet making, and black cherry, a fine wood used in the manufacture of coffins, were subjected to such destructive cutting that they were practically obliterated on floodplain soils.

In the early days of pioneer settlement, tamarack was cut rather extensively on the wet organic soils and hewn into ship timbers (63).

The agricultural potential of the lowland soils was found to be high under conditions of proper drainage and in recent years some of the better lowland hardwood stands have been cut. Original forest growth on fine textured soils of imperfect and poor drainage, including the wet organic peats and mucks, favored a development of large individual trees. Elms, ashes, soft maples, basswood, and swamp white oak were the principal species according to Veatch, et al. (147). Tamarack, quaking and bigtooth aspen, white and paper birch, willows and an occasional black spruce were also present.

The neutral to basic organic soils also supported a lush growth of shrubs, sedges, and grasses, in addition to the previously mentioned species of trees. On highly acid bogs, the vegetation was shrublike consisting mostly of leatherleaf, dogwoods, and winterberries.

At the present time about 80 percent of the total land area in Ingham County has been cleared for agricultural purposes, leaving about 15 percent in forests. Although the greater portion of the forested terrain is characterized by rather good natural drainage, about 30 percent of the forested area has soils which are imperfectly or poorly drained. Alluvial and organic soils comprise about 17 percent of the lands classified as wet or in a permanently swampy condition. The mineral soils are rather dark in color and have developed on glacial till from calcareous gray and yellow loam to clay loam. Where drainage is feasible, most of the organic soils at the present time are very valuable for agricultural purposes.

Climate

Generally the climate of Ingham County may be characterized as continental in nature, with extremes in temperature, humidity and precipitation rather uncommon. Owing to the interior location of the county in the southern peninsula, considerable variation may be found in meteorological conditions. At times, moisture-laden winds carried inland from the surrounding Great Lakes produce a semi-marine influence, with accompanying moderately high humidities.

Low wind velocities and evaporation rates are the norm for this section of Michigan. Prevailing wind movement in the county is from the southwest, averaging 8.2 miles per hour, except for the month of March, when wind direction from the northwest has an average velocity of 10.2 miles per hour. The highest wind velocities have been recorded from the northwest compared to other directions (45).

The average annual precipitation in the county amounts to about 31.1 inches. The driest year for 60 years of weather records occurred in 1958 with an annual rainfall of 21.8 inches, while the wettest year, with an annual rainfall of 39.7 inches occurred in 1947. Most of the precipitation is from storms which are cyclonic in origin, producing less than .25 inches of rainfall per storm.(45).

A fairly recent classification of rainfall patterns for the East Lansing area shows that most of these storms are of low intensity, and that most of them occur during the month of November every year (137). The major part of the annual precipitation falls during the mid-part of the growing season, from May until August, a product of high intensity convectional storms.

Water losses due to runoff from storms are usually low, except when the soil surface is frozen or not protected by a cover of vegetation. Nevertheless, through percolation, infiltration, and subterranean transfer of unconfined ground water, about 30 percent of the annual precipitation appears as stream flow in the creeks and rivers of the local watersheds (137). In addition, melting of accumulated snow cover contributes to runoff during the late spring months. The heaviest blanket of snow cover on record occurred during the winter of 1951-1952, with a mean depth of 88.8 inches.

The average length of the growing season for the county varies from 154 to 158 days (165). Although the state of Michigan is noted for some of the greatest extremes in temperature within the continental limits of the country, such is not the case for Ingham County. The 60-year record indicates a mean annual average temperature of 46.7°F. with a mean deviation of 19.8°F. between maximum and minimum means. The highest temperatures usually occur during the month of July and the lowest during the month of February. Average dates of the last killing frost in spring and first killing frost in autumn occur in early May and late October, respectively.

A brief resume of normal climatological data by months of the year is compared to the values for the 1961 growing season in Table I. It may be observed from the tabular values that mean monthly temperatures for the present year were approximately normal.

The rainfall pattern, however, was definitely abnormal. As shown, the total annual accumulation was far below the normal trend, making 1961 one of the driest years on record. Although not indicated in the table, the accumulated departure from normal for each succeeding month was negative for the entire year, primarily because the initial deficit during the early winter months was large.

TABLE.- 1. Mean monthly temperature precipitation data for a 60-year record and the 1961 growing season for Ingham County, Michigan

Month	Temperature		Precipitation		
	60-year mean	1961	60-year mean	1961	Departure from normal
	°F.	°F.	inches	inches	inches
January	23.8	19.9	1.87	0.45	-1.42
February	24.2	27.8	1.81	1.60	-0.21
March	33.2	37.0	2.57	2.87	0.30
April	45.3	41.8	2.83	3.45	0.62
May	56.5	52.9	3.75	1.00	-2.75
June	67.4	64.8	3.37	2.97	-0.40
July	71.1	69.8	2.28	2.28	0.00
August	69.0	68.7	2.68	3.33	0.65
September	61.8	66.4	3.05	4.61	1.56
October	50.5	52.2	2.45	1.58	-0.87
November	37.9	39.0	2.30	1.77	-0.53
December	27.1	26.3	2.12	1.44	-0.68
Average or Total	47.3	47.2	31.08	27.35	-3.73

Physiography, Soils and Geology

The major portion of the county is part of a broad glaciated plain known as the "Thumb Upland." This elevated plain is typical of an area having been recently glaciated, whose topographic features have been affected by advances and subsequent retreats of the ice fronts, during Pleistocene time. In Inhgam county the plain rises from 200 to 600 feet above the level of the Great Lakes and is bordered on the north by a flat lowland plain, which crosses the state from Saginaw Bay to Lake Michigan. The lowland plain lies 200 to 400 feet below the "Thumb Upland" (99).

The higest elevations in Inhgam county are found in the four southeastern townships, where the first permanent settlement of the county took place. The average elevation in this area is about 990 feet above sea level. The surrounding countryside gradually slopes away from this area in the four cardinal directions. Differences in elevation between the high and low points in the county are not great, averaging about 300 feet. Between lowland swamps and adjacent higher ground, differences average about 100 feet (147).

During the late Wisconsin Age, the ice sheet of the Cary substage covered earlier Pleistocene features, by depositing an unstratified drift mantle of varying thickness over the county. The soils of Ingham county have developed from this drift and belong to the Gray-Brown Podzolic and Humic-Gley great soil groups. Unweathered glacial materials of these soil groups are usually strong calcareous mixtures of sorted and unassorted deposits. This history of glacial activity in Ingham county has been described in detail by Leverett and Taylor (99, 100). The physiography of the county may best be described as one of smoothly or gently undulating ground moraines and nearly level clayey and sandy outwash plains, which are interrupted by old glacial drainageways and closed basin depressions. A map illustrating the basic geologic formations of the county is shown in Figure 1.

In the northern part of the county, a low upland called the "Lansing Moraine , travels eastward from Lansing township into Wheatfield township. The topography along this moraine varies from flat to undulating, and tends to become less pronounced in the northeastern part of the county. South of this area, the Kalamazoo and Charlotte till plains are found, which gradually slope southward at the rate of six to ten feet to the mile. Along the southern part of the Charlotte moraine, the topography again becomes rather hilly. These two moraines, averaging 40 to 75 feet in depth, form a rather thin drift layer in Ingham County, compared to adjoining counties, where the drift mantle averages from 300 to 400 feet in depth (99, 100).

Although a system of slender sub-moraines oriented in an east-west direction are apparent on the surface of the larger till plains, the most striking surface features are the numerous eskers. The majority of these glacial features are oriented in a north-south direction and appear to be strongly associated with elongated glacio-fluvial basins. An examination of the differentiation of materials in these formations indicated that they were probably produced by streams under the glacier, sweeping from side to side in a serpentine manner as the stratified deposits were laid down. Thus, confined and elongated lowlands would have eventually resulted from this type of activity under a rapidly retreating ice front.

The Mason esker system, one of the largest in the state, and referred to previously as an ancient Indian trail, does not show as strong a relationship to the elongated basin depressions, as the Dansville and Williamston esker systems in the eastern part of the county. At the present time, these esker systems are discontinuous, with several small creeks winding through openings created by stream dissection.

Accompanying natural land divisions, produced by the retreating ice masses of the Cary substage, include shallow potholes and swales, shallow and deep muck swamps and bogs widely distributed throughout the county. Additional depressional features include irregularly shaped shallow basins, variable in size and created by sheet flow from glacial melt-waters. It appears that lowland hardwood forests were predominant in the remains of these glacial drainageways at the time of settlement of the county by the white man (63).

All of the features previously described are strongly related to conformations of glacial origin rather than erosion or stream dissection. Erosion since the last glacial retreat has produced a modified dentritic drainage pattern. Since stream dissection is not prevalent, water tables remain close to the ground surface in lowlands for the major part of the year, and flooding occurs rather frequently during the spring season.

Literature Review

Ecology in General -- Pre-history

In the field of ecology concerned with the organization and sociological relationships of plants, probably no question has been more argued than "What constitutes climax?" Although early workers in the field recognized and described patterns of easily discernable changes in vegetation, Clements (44) contributed most to the concepts of climax and succession. The principal concept in his writings was expressed in the unity of the climax and climate. The two were considered inseparable and all successional stages in the development of vegetation pointed toward a single climax.

Thus, the monclimax theory evolved, a concept long accepted by many workers in the field. According to this theory, all vegetation, regardless of its starting point in development, would eventually reach theoretical equilibrium under the general control of climate. The visible unity of the climax was expressed in the "formation," a unit having similarities between the life forms of the dominant species. In this sense, it would be expected that all vegetation within a given region, given a sufficient period of time, would be uniform regardless of habitat.

If the effects of climate were eventually made manifest in producing stabilization of the vegetation, then a true climax would prevail. In this respect, climate, climax, and geologic time would be inseparable. The probability for either of the foregoing siuations taking place, however, would be quite low in the natural sequence of events. The specialized often complex terminology used by Clements (44) in his descriptions of vegetation obscured the time element, which was largely ignored as an associational identity with the climax.

While most ecologists have, at one time or another, stressed the spatial concept in plant succession, time as an indispensable element in interpreting successional patterns of change has been emphasized by Gleason (68). Gleason (67) stressed the difficulties of attempting to define variation in plant communities. While the writings of other ecologists at this time were concerned with the use of suitable terms to describe communities, Gleason's (67) main purpose was to understand the causes bringing about the complexity in the expression of vegetation.

It was during this period that Clements (44) proposed the use of many terms to describe the various developmental stages in plant succession.

Phillips (118) was a devoted advocate of the theses and nomenclature postulated by Clements. His analyses of concepts regarding succession and the climax were succinctly presented in several papers. Tansley (143,144) and Phillips (118,119) clarified some of the principles and modified some of the terminology set forth in the Clementsian system.

Tansley (144), recognizing that certain biotic and edaphic influences would limit changes in vegetation often for an indefinite period of time, suggested that a series of stable climaxes would be produced. Thus, the polyclimax theory suggests that succession progresses to a stage of development where a series of terminal communities are produced and controlled by factors other than climate. The regional control of climate, of course, is not completely divorced from this theory but is simply not given exclusive control. The polyclimax theory stresses the termination of succession by local factors of the environment, such as topography, drainage, and soil conditions. Phillips (118,119), however, suggested that such factors may deflect, accelerate, or retard succession only on a temporary basis, and believed these so-called climaxes could be explained in terms of the "climatic climax," or monoclimax theory.

The principal difficulty of accepting monoclimax lies in its application on a regional basis. Recently, Whittaker (158), in a consideration of climax concepts, stressed the complexity of species-environment relationships and emphasized the acceptance of "gradient analysis." The distribution and organization of plant communities is obviously influenced by a multiplicity of factors, inherent and environmental. Under natural and undisturbed conditions, the ranges of plants are limited by tolerances which are genetically controlled.

Each species population, subject to ramifications within the environment, has a particular genetic endowment which more or less restricts the population to the particular site on which it is found. This, of course, depends upon the ecological amplitude within the species population --its adjustment to climatic, edaphic, and physiographic variation. Micro-variation occurs over relatively short distances which eventually produces physiological and ecological differences in species populations. Differences in temperature, precipitation, light, humidity, soil chemical and textural constituents, amount of organic matter present, depth and fluctuation of water tables, aspect, slope, etc., bring about physiological responses which show up as morphological variation (148).

Considering the passage of time there must be a genetic adjustment of the species complement to the effects of the environment. In other words, the introduction of environmental extremes results in a change of selective pressures which increases the mechanism by which surviving individuals perpetuate the species. Therefore, the expression of vegetation is a result of an almost infinite series of interactions between the inherent potential of the species and the biotic potential of the environment. In this sense, Gleason's (67) individualistic concept that each plant community differs from every other plant community becomes tenable.

The use of gradient analysis techniques advocated by Whittaker (158) for describing the vegetation as a whole has found wide acceptance in the continuum approach developed by Curtis (53,54). Although the continuum reflects the un-interrupted development of the vegetation, representing pioneer and the present terminal stages of succession, it does not describe the vegetation in terms of environmental parameters. The continuum expresses the progression of vegetation change toward a type of climax, as the expansion of a point into a sphere having a diameter which pulsates. At the same time it rejects the recognition of the absolute unit in vegetation.

Whittaker (158) has defined "climax" as, "the average population of mature self-sustaining stands on a type of site as defined and limited." In this respect, old, mature, self-sustaining lowland hardwood stands can be considered climax for those areas in which they are found. Since recurrent high ground water produces the most conspicuous influences on the composition of forest stands occupying such sites, the climax condition is dependent upon maintaining this physiographically controlled condition.

Lowland Hardwood Types in the Eastern United States

Distribution.--The Society of American Foresters has published a classification of the forest types of the United States, based on varying combinations of tree cover (139). Four distinctive forest types occurring along floodplains and enclosed swamp depressions have been described for the northern forest region. Three of these types are typical of northern coniferous swamp. The remaining black ash-American elm-red maple type (Type 39) has been found to occur extensively throughout the Lake States region, and northward into the Canadian boreal forests. This types also extends southward into the central forest region in Indiana (122).

Varying combinations of at least two of the type species are often found in association with balsam fir, (*Abies balsamea*), balsam poplar (*Populus balsamifera*), tamarack, (*Larix laricina*), and northern white cedar (*Thuja occidentalis*) in northern Michigan.[1] In this area, black ash becomes increasingly abundant. Southward throughout Ohio and Indiana, hardwoods are more prevalent in the type. Pin oak (*Quercus palustris*), blackgum (*Nyssa silvatica*), silver maple, (*Acer saccharinum*), swamp white oak (*Quercus bicolor*) and sweetgum (*Liquidambar styraciflua*) are common associates.

Two species, American elm (*Ulmus americana*) and red maple (*Acer rubrum*) appear to be ubiquitous on lowland sites throughout the eastern deciduous forest region.

Other mixed types containing the major species found in lowland forests which have been classified as common species on wet flats and bottomlands,

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[1]Scientific names follow Fernald for herbs and shrubs and Little for trees (61, 105).

are the silver maple-American elm type (Type 62), extending throughout the central forest region northward into Canada, and the pin oak-sweetgum type (Type 65) , in the Ohio Valley area. The sugarberry-American elm-green ash type (Type 93), sycamore-pecan-American elm type (Type 94), and sweetbay-swamp tupelo-red maple type (Type 104) , are found in the southern forest region.

In these lowland forest types the major canopy species are shown in Table 2.

It is common knowledge that floristic dissimilarities exist in northern versus southern lowland forests. The difficulty of defining distinct and separable units of vegetation within lowland forests of the major streams and tributaries has been stressed by Curtis (54). Some variation in species complement, however, is found from stand to stand within any continuous forest type whether it be located on a floodplain or farther inland. One stand at a particular point along the major streams, tributaries, and adjacent lowlands may be characterized as being homogenous. However, progressive floristic differences may be observed as an increase in both woody and herbaceous species occurs toward southerly latitudes. This becomes especially noticeable in the lowland forests.

South of Michigan through the forests of Indiana and Ohio, an increase in the number of tree species on lowland sites may be noted. The rich complex of southern bottomland hardwood species provides a forest reserve, from which lowland species must have advanced along rivers, streams and smaller tributaries toward more northerly latitudes in post-Wisconsin time.

The tree composition of river fronts, battures, ridges, and terraces of the complex bottomland hardwood region of the southern United States has been described by Putnam and Bull (125) and Sternitzke and Putnam(141).

TABLE.- 2 . Major canopy species in the lowland-hardwood types of the eastern United States (Types 39, 62, 63, 93, 94, and 104).[a]

Species		Lowland type
Common name	Scientific name	----number----
Black ash	Fraxinus nigra	39
Green ash	Fraxinus pennsylvanica	62,93,94
American basswood	Tilia americana	39
Blackgum	Nyssa sylvatica	39,104
Cottonwood	Populus deltoides	63,94
American elm	Ulmus americana	39,62,93,94,104
Slippery elm	Ulmus rubra	39,62
Hackberry	Celtis occidentalis	93
Water hickory	Carya aquatica	93
Honeylocust	Gleditsia triacanthos	93
Red maple	Acer rubrum	39,62,93,104
Bur oak	Quercus macrocarpa	39
Over cup oak	Quercus lyrata	93
Swamp white oak	Quercus bicolor	39,62
Water oak	Quercus nigra	93,94
Willow oak	Quercus phellos	93
Bitter pecan	Carya illinoensis	94
Sugar berry	Celtis laevigata	94
Sweetbay	Magnolia virginiana	93,94
Sycamore	Platanus occidentalis	62,94
Swamp tupelo	Nyssa sylvatica var. biflora	104
Silver maple	Acer saccharinum	39,62,94

[a] Report of the committee on forest types (129).

in contrast to the few lowland forest types of the central and northern hardwood forest regions, Putnam (122) described eight important forest type combinations, containing over 75 tree species of which 55 were of commercial value.

Second bottoms and high terrace flats in the bottomland hardwood region permit the invasion and ecesis of certain oaks and hickories. Increasing topographic gradation, the depression of the water table and resulting better drainage, allow the establishment of other oaks, which eventually give way to southern magnolia (Magnolia grandiflora L.), basswood, and American beech (Fagus grandifolia), (98,135).

Conducting a survey of stands found on coastal and alluvial floodplains throughout the southeastern United States, Penfound and Hall (78,79,115), included comprehensive lists of lowland tree species. Among the dominants were bald-cypress (Taxodium distichum), swamp black gum, red maple, tupelo gum (Nyssa aquatica), green ash and sweetbay.

While climate is often considered as the primary influence controlling regional floristic composition, auxiliary factors such as physiography, soils, and ground water are considered to be the primary factors, which limit the local ranges of plants (35,36,69,70).

Hydromorphic Soils and Ground Water.--Basically, the sites occupied by lowland hardwood forests in the eastern United States may be classified into two origins: floodplain and lacustrine. Since characteristic differences exist in the forest vegetation occupying such sites it is important to consider the conditions causing these differences.

Alluvial soils of streamside forests are frequently subjected to periods of overflow. Sediments in the overflow are usually deposited within a spectrum of fanlike patterns. The coarsest sandy materials, owing to their greater specific gravity, are deposited near the origin of overflow, while fine-textured silts and clays are carried further inland. The latter materials are deposited as the turbulence of flowing water decreases. With periodic innundations, subsequent deposition of additional sediments results in a series of laminations of varying width. Thus, soils of floodplains are stratified azonal deposits.

It may be recognized by the most casual observer that the effect of stream overflow in floodplain forests is one of extreme disturbance to the ecesis of most lowland tree species. Not only does a disturbance to the edaphic medium take place, but the depth and duration of surface water on the site has a detrimental effect on seed, young seedlings, and low plants. The effect is complex, probably involving low oxygen levels as well as silt deposition on plant surfaces.

Lacustrine forests in enclosed depressions, on the other hand, are not equally subject to the homogenizing influence of deposition by flowing water, since these areas are commonly innundated by rising ground water tables. Ground water movement, although affected by infiltration and percolation of soil water, is principally controlled by the hydro-geologic characteristics of the watersheds in which these forests are found. Direct water effects are also present here, but the sedimentation and silt deposition on plant surfaces as well as erosive forces are minor.

Lowland Hardwood Types in the Lake States and Central States

Distribution.-- Studies associated with the classification of lowland communities in the Lake States and Central States have been numerous (33,27, 17,57,159,19,79,80,44,93,94).

In describing the lowland forests of the Illinoian till plains in southwestern Ohio, Braun (19) observed certain forest groups, which she termed "association segregates". These forests were composed of varying combinations of pin oak, red maple, American elm and sweetgum. Using graphic methods, Sampson (128,129) presented a sequence of patterns in the swamp forests of northern Ohio. Three phases of the widespread elm-ash-maple communities on lowland soils were designated as transitional, throughout which American elm white ash, and red maple were dominant.

A study of the floodplain forests along the White River system in Indiana, showed that the most characteristic riverfront species were silver maple, red maple, and elms (97). In New Jersey, the most prevalent species found on the Raritan River floodplain were red maple and American elm (167). Along the outer floodplains an increase in the abundance of sugar maple, American beech, yellowpoplar (*Liriodendron tulipifera*), slippery elm, and basswood were recorded.

Speaking of river-swamp communities in southern Michigan, Braun (20) noted that American elm, silver maple, and black ash dominated along the borders of streams.

In southern Wisconsin, Wilde et al. (163) suggested that the principal sub-climax species on floodplains were American elm, slippery elm, black ash, and red maple. In the northern part of the state, white spruce (*Picea glauca* var. *glauca*), black spruce (*Picea mariana*), tamarack, and northern white cedar are the most important constituents of lowland stands as the hardwoods begin to diminish. In the lowlands of Wisconsin, Clausen (43) determined the main species in transition between northern and southern coniferous swamps to be tamarack, northern white cedar, paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), red maple, American elm, and black ash.

While estimating the average tree composition of 106 lowland stands in southern Wisconsin, Curtis (54) reported the dominant species to be silver maple, American elm, green ash, basswood, swamp white oak, red maple, and black ash. Silver maple and American elm were the first invaders of willow and cottonwood stands. In southern Wisconsin floodplain and lacustrine forests, Ware (156) found that American elm, green ash, and red maple were the leading dominants. Swamp white oak and silver maple were concentrated along stream bottoms, rather than deep swamps.

In many cases certain dominants of lowland forests have formed a consistent component of upland forest communities. A study of upland conifer-hardwood forests in northeastern Wisconsin showed that lowland dominants such as American elm and basswood were common in climax stands dominated by sugar maple and American beech (Brown and Curtis 28). A study of a virgin stand in Michigan by Donahue (59) supports this evidence as well as other studies by Graham (71), and Stearns (140).

Working in 98 stands of upland second-growth hardwoods in Missaukee County, Michigan, Elliot (60) found that American elm and basswood were consistently represented in all size classes. Examining the species composition of 110 stands in the Lake States region and southern Canada, Maycock and Curtis (110), found American elm attained a leading dominant position in only one stand but was present to some degree in 32 stands. Studying the species-soils relationships of hardwoods in northern Michigan, Westveld (153) found that most of the basal area for several upland stands was devoted to sugar maple, where American beech was also an important stand component. If American elm or basswood was present, the proportion of basal area for sugar maple was reduced even though the density of the latter species remained quite high.

Hydromorphic soils-lake States and Central States.-- The hydromorphic soils developed under hardwood forest vegetation in this region include the imperfectly-drained members of the light colored Grey-Brown Podzolic soils (155). These are soils underlain by a true or phreatic water table and are found in nearly level to slightly undulating landscapes. Poorly-drained or very poorly-drained soils found in depressions and swampy areas are dark colored soils and are commonly referred to as Humic-Gleys. These soils are periodically flooded by ground water especially throughout the winter season until late spring. Alluvial soils are those found in bottomlands which are constantly subject to periodic inundation from nearby streams.

Previous Studies--Hydromorphic Soils and Lowland Hardwoods.-- The importance of soils to the growth and development of forest vegetation has been known for many years. In the past few decades, however, significant advances in understanding the processes by which soils influence forest growth and development have been added to our store of knowledge (107,82,86,91, 159,153,161,162,163). In many of these studies relationships between soil characteristics and certain lowland hardwood species have been suggested.

Relating certain soil characteristics to forest composition in northern Michigan, Westveld (153) found that American elm and basswood were present to some extent on 15 of 25 soil types while red maple was present on 11 types. An absence of American elm on loamy sands and fine sandy loam soils have cementations in the subsoil horizons was reported.

A study in Illinois showed that American elm was widely distributed on a coarse textured floodplain, underlain by fine textured clays. This species, however, was not present on a sandy loam upland 100 feet away and

20 feet above the floodplain. The dominant species on the upland were basswood, white, and northern red oaks (96). Another study in Minnesota by Kell (86), showed that American elm was second in importance on peats. Black ash and balsam fir were the first and third in importance, respectively.

Using the moisture equivalent as a measure of soil preferences for several species of upland trees, Daubenmire (55) found that American elm preferred fine textured soils having moisture retentive capacities from 8 to 28 percent. Several species of oaks in this study were characteristic of soils which were coarser in texture.

On the floodplain and organic soils, including wood peats of the northern podzol region in Wisconsin, Wilde, Wilson, and White (163) showed that red maple forms a definite part of communities containing American elm, slippery elm, black ash, willows, speckled alder (Alnus rugosa), and several coniferous species. Although this species occurs as one of the principal invaders on sandy podzols, gley-podzolic sands, and melanized loams, along with such species as quaking aspen, bigtooth aspen (Populus grandidentata) paper birch, mountain maple (Acer spicatum), and mountain ash (Sorbus americana), it was not reported on lacustrine clay and clay loam mucks in Wisconsin. The dominant species on these soils were American elm, slippery elm, black ash, bur oak, American hornbeam (Ostrya virginiana).

The ubiquity of red maple as a species able to survive throughout a wide range of soil texture and moisture conditions has been reported by several authors (54,59,84,111,154,163). The bimodal distribution of red maple has been demonstrated by Curtis (54), while studying the species-stand-structure of lowland and upland vegetation types. The importance value of this species actually increases along the environmental gradient, at two definite ordinates within the range of the continuum. Donahue (59) found red maple and paper birch co-existent with spruce in swamps and flats in the state of New York.

(?) 30

Working in Minnesota, Buell and Cantlon (29) and Kittredge (91) suggested that green ash was a common species on soils of alluvial origin in the northern part of its range. The occurence of this species appears to be correlated with those soils having a consistently high moisture content (Shear and Stewart (134)).

Swamp white oak has been described, however, as one of the major associate species on shallow wet mucks and peats in swamps and ponded flats of the lowland hardwood types (38,154). It has also been reported by Aldrich (3), Sampson (129), and Braun (19) as a typical species on poorly drained soils in Indiana and Ohio which are normally subject to flooding. The affinity of this species for soils of fluvial origin in southern Wisconsin has been confirmed by Ware (150).

American basswood is another species reported able to exist throughout a wide range of soil textural classes in situations similar to those for American elm, red maple, and American beech. The occurrence of basswood on extremely coarse textured sands and sandy sites has been described by Harlow and Harrar (81) and Betts (11). In Minnesota, Keil (86) suggested that basswood was more restricted to fine textured soils than sugar maple, while Daubenmire (55) found the opposite condition in the same state. Although this species may be found in association with sugar maple on coarse textured soils, including sandy loams and loams, it is usually found in smaller numbers. The presence of basswood being closely associated with those soils possessing a high degree of moisture retentiveness, especially silt loams, has been suggested by Westveld (153). The presence of this species on coarse textured soils, therefore, may actually be due to the presence of fine textured bands of silty or clayey materials in the subsoils. Such soils

as these would be capable of retaining additional moisture during periods of drought.

Several investigators have attempted to map the distribution of swamp forest types, using as a basis original survey notes, and soil maps (128, 129, 87,88,146).

Recently Elliot (60), using up-to-date soil survey maps and early survey records, mapped the original vegetation of north-central Michigan. Shanks (132), studying the percentage composition of original forests and forest remnants of Shelby County, Ohio, showed that American beech, elms, white oak (Quercus alba)., and hickories were the dominant species on the poorly drained soils.

Ground water-Lake States and Central States-- At the present time information on ground water and its effects on lowland-hardwood forest development is inadaquate for this region. No really detailed studies, other than simple reconaissance, related to the development and distribution of lowland hardwood species with respect to ground water changes have been made. References to the basic hydrology of ground water, however, are numerous (120,104,85,166 66).

Previous Studies--Ground Water and Lowland Hardwoods-- A review of the literature shows that several studies have established stand and tree distribution relationships based on inference or general conclusions regarding average water table depths (3,17,27,50,65,102,129,160,164).

In the Lake States region, Wilde (159) established certain relationships between the types of forest species associated with soils having poor and adequate internal drainage and aeration. In northern Michigan, Westveld (153) placed less emphasis on soil texture than the soil moisture regime as one of the major factors influencing the growth and survival of American elm.

Describing the original vegetation on seasonally ponded soils in seven Indiana counties, Lindsey (102) found that American beech, swamp white oak, and American elm were the three leading species in the early 19th century. In a study of lowland hardwood types in central Indiana, Potzger (122) determined that American beech enters lowlands as soon as the water table drops a few inches below the soil surface. Similar evidence has been reported by other investigators (80,20).

In another study, Potzger (122) pointed out that red maple, American elm, and sweetgum, were the dominant species in Indiana on wet soils.

A study of bogs and swamps in Ohio by Aldrich (3) showed that red maple, silver maple, American elm, black ash, white ash, swamp white oak, and pin oak were the leading dominants. Conducting successional studies in Cheboygan County, Michigan, Gates (64) suggested that lowland forests of elms, ashes, and maples were the typical vegetation phase on drier sites not subject to spring flooding.

Lowland Hardwood Types in Southern Michigan

Distribution--The lowland hardwood forests of southern Michigan and Ingham County closely correspond to the black ash-American elm-red maple type (Type 39), described by the report of the committee on forest types (139). The indicator species for this type is black ash since it is not as common as the other two species. Black ash, however, has been recorded as a common to abundant tree in bogs, swamps, and river valleys in Minnesota, Ohio, and Wisconsin (3,86,129,150). In Ingham County, it is found rather infrequently and occurs most often in small openings created by the windthrow of other species.

A comparative study of the climax association on mesic sites was made by Quick (126) in southern Michigan, where the leading dominants of the southeastern lake-plain forests were also described. The most abundant dominants in these stands, which lie eastward of Ingham County, were American elm, sugar maple, American beech, American basswood, and white ash. In addition, red maple, silver maple, hackberry, green ash, blackgum, and yellowpoplar were characteristic of lowland areas. Black ash was not mentioned as a dominant species in these lowland forests.

On the lowland soils to the north of Ingham County, the leading dominants were essentially the same species with the addition of swamp white oak, and slippery elm. Black walnut, butternut (Juglans cinerea), yellowpoplar, sweet birch (Betula lenta), and chinkapin oak (Quercus muehlenbergii) were also mentioned (125).

The swamp forests to the west of Ingham County were characterized as containing large amounts of tamarack, yellow birch (Betula alleghaniensis), red maple, black ash, swamp oaks, American elm, silver maple, sycamore, and honeylocust (Kenoyer 86).

Hydromorphic Soils in Southern Michigan.--Relief and drainage conditions dominate the development of hydromorphic soils. Imperfectly drained mineral soils occupy an intermediate position between well-drained and poorly drained mineral soils. High water tables, fluctuating throughout the profiles, have caused strongly mottled subsoils. Wilde (160), in a discussion of hydromorphic soils refers to this condition, typical of soils which are periodically wet or insufficiently drained, as the mid-gley or beta-gley type of development. The gley layers in these soils are superimposed on the profiles at depths of two to three feet. The most common soil series with imperfect drainage in Ingham County are the Blount, Conover, Locke, Matherton and Brady series.

Poorly drained mineral soils were formed in low areas of glaciofluvial outwash and lacustrine plains which were swampy or permanently wet with the water tables remaining continuously at or near the surface. Wilde (160) calls these soils alpha-gleys, owing to the presence of high water tables producing intense gleization of the profiles, except for the immediate surface horizons. In Ingham County the most common soil series with poor drainage are the Brookston, Sebewa, and Gilford series.

Alluvial soils, or those found on the floodplains of streams, consist of recently deposited sediments and may be classified as either beta or alpha-gleys depending on the intensity of gleization in the profiles. Since alluvium is composed mainly of stratified deposits, which continue to be disturbed by seasonal flooding and deposition, clear differentiation of the profiles is difficult.

Organic soils consisting of peats and mucks were developed from accumulations of vegetation in shallow lakes, marshes, swamps, or old glacial drainageways. The thickness of the organic deposits overlying the mineral base varies according to the duration of suitable accumulation conditions, post-accumulation, drainage and nature of the plant material deposited. Linnwood and Carlisle mucks are the most common organic soils in Ingham County.

Previous studies--hydromorphic soils and lowland hardwoods-- While attempting to establish area correlations between closely related groups of soil types and pre-settlement vegetation, Veatch (145,146) described several mixed types of swamp forest in Ingham County. On acid peats tamarack was dominant. This species gave way to silver maple, ashes, and elms on the deeper mucks. Shallow mucks underlain by mineral materials were not differentiated during the study, hence differences in the forest vegetation on these soils compared to that found on deep mucks were not discussed. The studies of Veatch also showed that American elm was well distributed, not only on mucks, but also on alpha and beta-gley soils.

Surveying lowland hardwood forests in 13 southern Michigan counties, Bouglirner (15), found American elm, red maple, silver maple, and black ash were the species most often encountered on organic soils. Other species included slippery elm, swamp white oak, willow, and river birch (Betula nigra).

Ground water in southern Michigan.-- Since the lowland hardwood stands in southern Michigan occupy depressional areas in natural drainageways, this forest type serves to store, transpire, and otherwise regulate ground water supplies within the mantle of glacial drift. The 14 stands selected for the ground water study in Ingham County lie in the basins of the Sloan, Deer, and Sycamore Creek watersheds. Alpha, beta-gley, and organic soils, with seasonally high water tables and poor drainage, are the principal soils of these watersheds.

The aquifers enclosed by the shales and sandstone of the Saginaw formation, lying at a depth of 200 to 300 feet over consolidated bedrock provide most of the commercial and domestic water used in this country, while only a few wells obtain water from the glacial mantle (66). The overlying sorted and unassorted glacial drift is relatively thin in the basin areas and does not provide an adequate supply of water for the needs of the populace (66,100). With the ever-increasing demands being made on our water resources, it is likely that additional numbers of shallow wells will be placed in the glacial drift mantle to serve local domestic needs in the future. In this sense, undisturbed lowland hardwood stands may ameliorate losses due to runoff by retarding the flow of rainwater to natural and artificial drainage channels.

Previous studies - Ground water and Lowland Hardwoods.-- Contrasting the plant societies of drained and undrained swamps in Kent County, Michigan, Livingston (106) suggested that the lack of oxygen in organic soils caused by high water tables was the principal factor precluding the invasion of species from mesophytic areas.

It has also been suggested by Kenoyer (87) from a comparison of early surveyors notes with present vegetation, that the swamp forest compostion in Kalamazoo County, Michigan, has remained essentially the same over the past century, even though the drainage of lowland areas has been rather extensive.

Studying the growth rates of lowland-hardwood species in southern Michigan, Boughner (15) suggested that the effect of water table depth was more important than soil texture. On the better lowland sites where water tables during the summer season dropped eight to ten feet below the surface of the soil, American elm and red maple were the dominant species. Summer water tables within four to eight feet of the soil surface were classified as medium sites. Here, American elm, red maple, white ash, silver maple, swamp white oak, and American basswood became important components of the stands. On the poorest sites, having water tables at or near the soil surface, black ash and silver maple increased in importance although the other species listed were dominant with the exception of basswood.

Plots.--In past ecological studies, considerable variation in number, size, and location of plots has been employed (14,26,103,114,133). Many ecologists in this country have preferred using a standard 10 x 10 meter quadrat for sampling trees, a 4 x 4 meter quadrat for sampling shrubs, and a 1 x 1 meter quadrat for sampling lesser vegetation. Foresters have, for many years, used circular plots of various sizes in their inventories of coniferous and hardwood stands. The 1/10 or 1/5 acre circular plot is the standard size used for most estimates of timber volume.

The use of some form of rectangular plot to increase the sampling precision in natural plant populations was recommended by Bormann (14). The use of square plots rather than circular plots has been suggested by Cain (37), since one cannot rotate with a tape about plot centers in forests. In most studies plots are located in a systematic manner. The use of random rather than systematic sampling in ecological studies has been suggested by Bordeau (16) and Borman (14). Random rather than systematic placement of sample plots has also been advocated by Cain (37), and Greig-Smith (72,73) where the investigator is concerned with establishing confidence limits for quantitative statements concerning the various species. Although random sampling may require more field time, the gain in being able to use a number of statistical tools for evaluating confidence limits of mean values, significance of differences, etc., justifies its use.

Since the use of plots regardless of their size is laborious and time consuming, new methods of sampling forest vegetation have recently received wide recognition. One of the most widely used is the technique developed by Bitterlich (13), called point-sampling.[1] The expansion of this method

[1]All trees are selected through the use of a 3 diopter prism.

into a useful system for the inventory of stands and volume estimations can be attributed to Grosenbaugh (74,75,76). Several other investigators have used this method for similar purposes (1,5,9,24,51,83).

Other "plotless" methods, which have been recently developed for rapid sampling in forest ecological studies, are the nearest-neighbor method of Clark and Evans (42), and the random pairs and quarter methods of Cottom and Curtis (46,47,48).[1] These methods have been tested in various forest types against complete forest inventories, using standard plot methods (101,103,127,133,142). The majority of these studies, however, were performed in individual woodlots or stands rather small in size.

Sampling Efficiency-Time--In recent years, a considerable amount of attention has been devoted to ascertaining differences in field efficiencies of vegetation sampling. It has been suggested that the random pairs method is the most rapid procedure in making forest surveys (Cottom and Curtis (47)). A later study (Cottom and Curtis (49)), showed that the point-centered quarter method resulted in a savings of time over other point methods which required more samples to yield equivalent information.

The variable plot-radius method was chosen by Shanks (133) in preference to other methods for yielding more information with the least investment of time in field and office computations. The field efficiencies of several forest sampling methods, including square plots, circular plots, strips, the quarter method, and two modifications of the variable plot-radius method were compared by Lindsey, Barton, and Miles (103). Although the range-finder Bitterlich method was the fastest in terms of field time, this

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[1]Random pair method-after choosing the first tree, a second tree is chosen which lies outside of a 180° sector.

Quarter method-the nearest tree in each of four quadrants is chosen.

advantage was offset to some extent by subsequent office calculations.

Sampling Efficiency-Information--Although efficiency studies such as those made by the above investigators are significant to the fields of forestry and plant ecology, it must be understood that information contributed by each method is of greater importance.

One of the first ecologists to study variance in plant populations when the data were gathered by different methods was Clapham (41). The need to increase sampling size to estimate accurately the amount of variability inherent in plant communities has been repeatedly stressed by Cottom, Curtis, and Hale (46). In a comparison of methods, using five different sized quadrats and two point methods, the variability of density was reduced by increasing the number of sampling units. Exclusive of the method used, Cottom et. al. recommended that at least 30 individuals of any species must be present in the sample in order to estimate with reasonable accuracy species density. A sample range of 25 to 100 quadrats (10 x 10 meters) was considered sufficient to determine average tree composition in northern deciduous forests(46).

To secure adaquate sample size, Curtis (54) and Ware (150) used the Chi-square test of homogeneity for sampling lowland hardwood stands in Wisconsin.

Several other studies in the field of quantitative ecology, more concerned with information than efficiencies in terms of the amount of time invested, are worthy of mention. Using colored card aggregations in varying combinations, Penfound (11c) sampled frequency, density, and cover relationships with three quadrat sizes.[1] Working in two upland forest communities in New Jersey, Buell and Cantlon (29) compared frequency, density, and basal area, using transects and quadrats. They found that transects resulted in better estimates of cover for large crowned species. The value of cover in characterizing community dominance has also been emphasized by Bauer (8) and other authors (44,103).

Line strips and quadrat methods in coniferous and hardwood stands were compared by Lindsey (101). He found that eight line-strip sampling units 24 feet wide and 600 feet long were adequate to estimate the major tree species, with an acceptable sampling error. Using four distance methods, Cottom and Curtis (49) mapped artificial populations and compared the results with a quadrat method. With know population parameters, extreme variability was found between the methods with inadequate sample sizes. The random pairs method was found to be less variable than the other methods. The quarter method was recommended as superior to other methods because of several advantages including the use of fewer sampling points, more data per point, and less computation to determine relative quantitative values.

Working with two plot sizes, random pairs, and variable plot-radius samples, in the coniferous and hardwood forest types of Tennessee, Shanks (133) described several important differences between the methods. Information derived from relative frequency calculations was comparable between the variable plot-radius and conventional plot methods. Relative frequency data for random pairs was lower than the other methods, and a skewed distribution

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[1]Frequency -- a measure of dispersion expressed as the percentage of quadrats in which a given species occurs.

Density -- a quantitative measure of the number of individuals per unit of area.

Cover -- the use of crown area rather than basal area as the measure of dominance.

of basal area data was apparent. The skewed results were attributed to the effect of small sample size in the use of random pairs.

In Shank's study (133), calculations of density and basal area for the most important species were comparable between plots and point samples, except for random pairs. This latter method, under-represented density and over-represented basal area for species which sprout prolifically. American basswood, a species widely known as a sprout producer, was one of the leading dominants in the study. Thus both it and associated species were subject to error as the data were expressed on a relative basis.

Relative frequency as determined by random pairs was affected by tree size in a southern oak forest (Rice and Penfound (127)). Differences were also apparent in the determination of basal area by this method and others.

In Oklahoma, an arms length rectangle method was tested against a complete census of a floodplain forest and discrepancies were found for frequency, but not density and basal area for the majority of species (Penfound and Rice (117)). In a comparison of variable radius and plot sampling estimates by Grosenbaugh and Stover (76) in southeastern Texas differences in mean basal area values by the two methods were not statistically significant. This was true even though the variable plot-radius method sampled trees of one inch d.b.h. and larger, and the plot method excluded trees smaller than five inches d.b.h.

Stand Similarities

A considerable amount of information is available in the literature regarding pattern and internal spatial arrangement of the species, when the stand is taken as an individual unit (5,24,67,72,73,89,90,113,118,119,143, 144,156). Poore (121) suggested that with large quantities of data, a statistical form of multi-variance analyses might be used in the study of phytosociological methods. Recognizing the multitude of variables present in the environment, Cain (36) suggests that interaction would produce some problems that are unanswerable. Ashby (5) contended that the value of statistical procedures lies in analysing the distribution of individual species within the community.

Using abundance-frequency ratios Whitford (156) studied the relative dispersion of species found in quadrats, which were randomly located in 26 stands. To determine pattern in plant communities of several types, Kershaw (89) used cover and frequency and Greig-Smith (72,73) used differences in abundance.

The occurrence of a particular species on a particular site, whether it be upland or lowland, is not necessarily due to any single cause but rather is a complex interaction of many factors, including all the environmental changes that have acted on the species during its life history. That each species in various plant communities possesses specific amplitudes of tolerance, which are reflected in its abundance along an environmental gradient was pointed out by Curtis (54) and Whittaker (158). The species which make up these communities form a continuous series of mosaics with an array of ecotopic overlap taking place on the slope of changing environment.

There is definite organization to communities expressed as departures from randomness which at least in the initial stages become more and more evident with increasing amounts of time for community development (Kershaw (89)).

Moreover, interactions between species further increase the complexities of community patterns (Margalef (109), Hairston (77), Kershaw (90)). Discontinuities in the environment generally result in changing rates of vegetational development, as well as differences in composition, and the series of mosaics along the gradient of environment appears to be continous rather than abrupt (54).

Recently, various methods have been used by ecologists to show the variability which occurs in the distribution of both woody and herbaceous vegetation along environmental gradients (21,22,53,54,67,11,158). The synecological requirements of a number of trees, shrubs, and herbs in the forests of Minnesota was outlined by Bakuzis and Hansen (6). In a later study a frequency-countour scheme was used to show the edaphic and climatic complexes affecting the distribution of forest communities in the state (7).

A dimensional approach can also be used in conjunction with community coefficients to show not only stand to stand relationships, but the species arrangement and reaction to vicissitudes of environment within the community complex (23,43,110). A gradient analysis of the conifer-swamps of Wisconsin based on the similarities of ground flora was constructed by Clausen (43). Bray and Curtis (23) described a method of multi-dimensional treatment in the ordination of forests in southern Wisconsin. Dimensional relationships were also used to pictorialize the ecotopic sphere of influence for a number of tree species in southern Ontario, Minnesota, Wisconsin, and northern Michigan (Maycock and Curtis (110)). The use of this type of representation shows the over-all influence of interaction-complexity within the environment upon the species. If the ecotopic sphere encompassing certain important timber species could be delimited, the management problems of foresters would become less complicated. In addition, ecologists are interested in defining the ecotopic amplitudes or tolerances that each species possesses.

METHODS

Stand Survey

A general reconnaissance of the lowland hardwood stands in Ingham County was started during the summer of 1960. The vegetation in representative portions of many of these stands was sampled between the summer of 1960 and the fall of 1961. The selection of stands for the study was made with the criteria that the stands were of natural origin, relatively undisturbed and representative of lowland-hardwoods. The location of the stands sampled is shown in Figure 1.

Stands which had been recently subject to disturbance from fire, grazing or extensive cutting were rejected, and only 19 of 37 stands visited met the criteria set forth for selection. Eight stands varied in size from 129 to 302 acres. The remaining 11 stands included in the survey were smaller, ranging from 22 to 98 acres, while the total area of all stands chosen for sampling was 1,300 acres.

Plot Selection

A starting point for sampling each stand was randomly chosen from a grid of coordinates. Depending upon the starting point chosen, a corresponding random plot pattern was then selected from a group of patterns, which had been previously constructed. In the field the location of the plots was predetermined by the selected grid pattern, however, distances between plots were adjusted according to the size of each stand. The pattern was expanded for large stands and contracted for small stands, providing for an equal number of randomly located plots regardless of stand size. In addition, the sum of the sample areas was the same for each stand.

Since one of the major interests of the study concerned quantitative descriptions of lowland-hardwoods, it was decided that for such purposes, ten plots (5 x 20 meters) per stand would be sufficient. Owing to the extre-

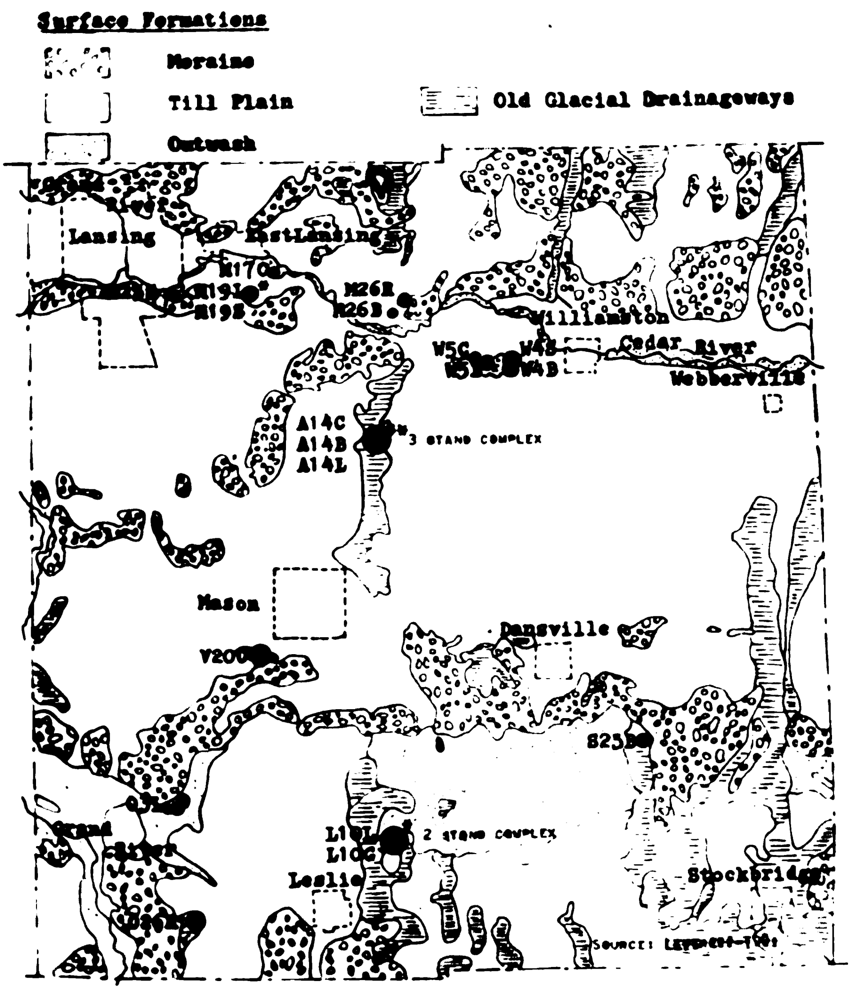

Fig. 1 . Map of Ingham county showing the surface geology after Leverett (1915) and location of the lowland hardwood stands selected for the vegetation study.

variability in the sizes of selected stands, any type of partial cruising would have resulted in varying numbers of plots per stand, and the resultant use of unwieldy conversion factors for the treatment of quantitative data.

All stands were assigned a letter-number designation referring to its location and predominant soil series. For example: W4B refers to Wheatfield township, Section 4, Brookston series.

Sampling Methods

Measurement of the number, size, and distribution of each tree species to determine the present composition of lowland-hardwood stands was accomplished using four sampling methods. The first of these was a standard 5 x 20 meter plot for recording tree data for the calculation of frequency, density, and dominance. For sampling shrub and herb data, nested 2x8 meter and .5 x 2 meter plots were placed in the southeast corner of the larger plot. In the field, plots were oriented alternately in two directions.

The three other methods used in the present study (Figure 2) were non-areal point samples and included the random pairs and point-centered quarter methods (47, 48, 49) and the variable plot-radius method (13, 74).

The point methods are briefly described as follows:

1. Random pair method. After choosing the first tree a second tree is chosen which lies outside of a 180° sector.
2. Quarter method. The nearest tree in each of four quadrats is chosen.
3. Full Bitterlich method. All trees are selected through the use of a 3 diopter prism.

The latter method was modified by actual measurement of the tree diameters within the sample area (103). The plot method was used as a standard for the study, and point samples were obtained concentrically from points located in the geometric center of each plot. All four methods were used in only 15 of the 19 stands investigated. In the remaining stands, only the

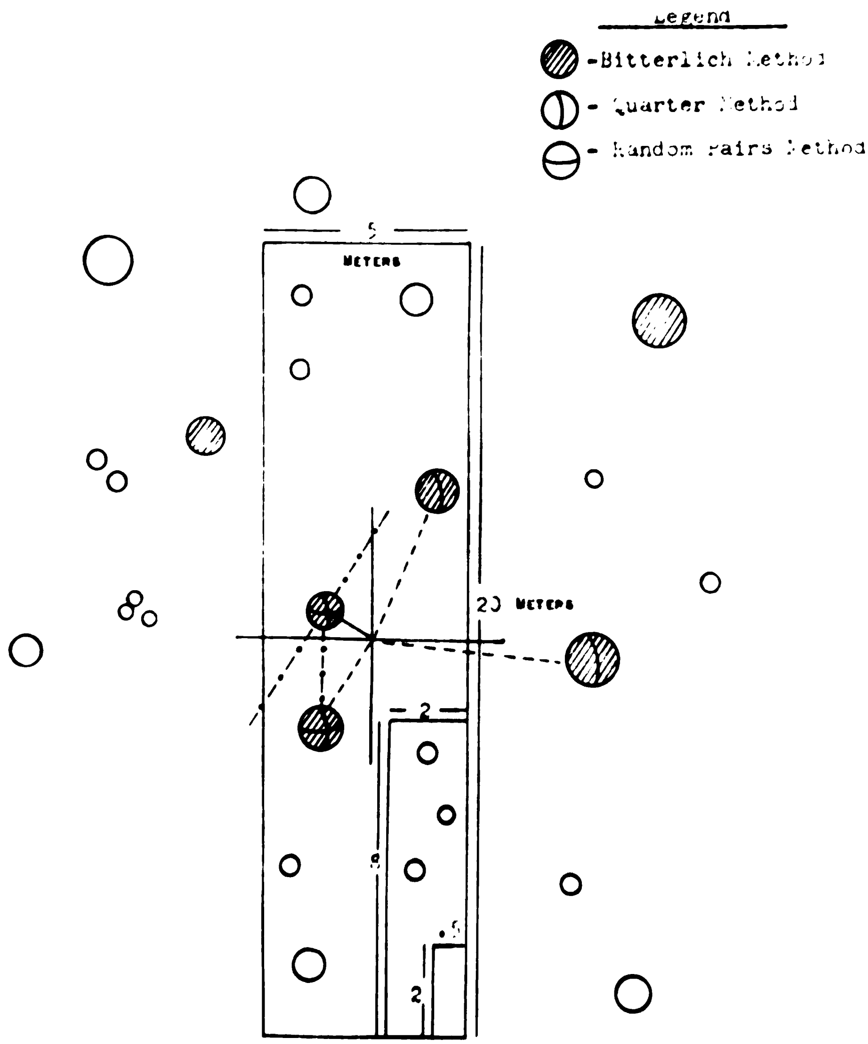

Fig. 2 . Sampling methods used in lowland hardwood forest survey.

Random pairs method. Second tree is chosen outside of 180° sector.

Quarter method. Nearest tree in each of four quadrants is chosen.

Full Bitterlich method. Trees are selected with a prism.

plot method was used.

Stand Characterization

The field data for all tree species were calculated in terms of relative: frequency, density, and dominance. All three of these indices expressed on a relative basis have been described in the literature (34, 52). For the plot method, the lower diameter limit for trees was one inch d.b.h. In a comparison of methods, four inches d.b.h. was selected as the lower diameter limit. Density per 1.9 hectares and percent frequency determinations were made for seedlings and saplings less than an inch in diameter. Percent frequency on .5 by 2 meter nested plots was determined for herbs. The sum of the relative values, having a single total of 300 is referred to as the importance value.

The "importance value" denotes a species' importance in a particular stand, high values being assigned to the dominant species (53). Importance value is defined mathmatically as the sum of relative basal area, relative density, and relative frequency. Or, stated in algebraic terms.

$$I = B + D + F$$

where I = importance value

B = relative basal area

D = relative density = percentage of individuals/stand in which species occurs.

F = relative frequency = percentage of stands in which species occurs

Since a few species having high importance values usually characterize stand composition, and since differences in the importance values of two or even three dominant species may be slight, it appears appropriate to characterize a stand on the basis of more than a single species. In describing the stands selected for study, at least three species with the highest importance values were used to indicate dominance within each stand.

Importance values of the tree species in each stand were multiplied by climax adaptation numbers appropriate for southern Michigan hardwoods. A climax-adaptation number is a subjectively determined number which indicates the relative position of a species in succession. The coefficients are usually defined on a scale of 0 to 10, the lowest numbers being assigned to species which occur earliest in succession and often on the more extreme sites. In this paper, the Michigan modification of the climax-adaptation coefficients recommended by Curtis and McIntosh for Wisconsin are used (52). They are given in Table 3.

A continuum index is a number which shows relative position of a plot or stand to the average species composition of an old forest on a mesic site in the same region. It is computed from the data for all tree species by summing the products of climax-adaptation numbers X importance values. The relation can be expressed mathematically as follows:

$$CI = \sum (CA)\ (I)$$

where CI = continuum index for a stand

CA and I = climax-adaptation number and importance values, respectively, for the species in the stand.

Continuum indices may vary from 0 for stands on severe sites in very early successional stages to less than 3000 for old stands on mesic sites. The continuum indices were calculated for all lowland hardwood stands in the survey (Table 10 and 11).

Soil Measurements

An intensive survey of the soils found in 15 of the 19 stands revealed the presence of 11 mineral and three organic soil series.

TABLE -3 Climax adaptation numbers used for lowland hardwood tree species found in Ingham County, Michigan.[a]

Species	Climax adaptation numbers
Acer saccharum	10
Fagus grandifolia	10
Tilia americana	9
Hamamelis virginiana	9
Ostrya virginiana	9
Carpinus caroliniana	8
Carya cordiformia	8
Ulmus americana	8
Acer rubrum	7
Quercus rubra	7
Nyssa sylvatica	7
Fraxinus americana	6
Quercus alba	6
Ulmus rubra	6
Carya ovata	6
Carya ovalis	6
Fraxinus pennsylvanica	5
Quercus bicolor	5
Prunus serotina	4
Acer saccharinum	4
Celtis occidentalis	4
Crataegus spp.	3
Platanus occidentalis	3
Sassafras albidum	2
Fraxinus nigra	2
Populus deltoides	2
Larix laricina	1
Salix nigra	0
Betula X purpusii	0
Populus tremloides	0

[a]Modified after Curtis (52).

Soil profiles were exposed by digging shallow pits with a spade, and samples from each horizon were extracted with a bucket auger. A soil series may contain more than one type depending on the texture of the surface soil, and among the 14 series examined, 15 soil types were identified. Samples were taken from horizon midpoints of each soil type within a series, regardless of the depth at which the horizon was located. A total of 320 samples, consisting of four sample replicates from five horizons in each soil type were collected. All physical determinations followed the proceedures outlined in the standard methods of analysis for forest soils by the Forest Soils Committee of the Douglas-Fir region (62). Only mineral soils in the stands where water tables were to be observed were completely analyzed for physical characteristics. One soil, an alpha-gley Brookston series, was excluded from the analysis because of its small areal extent and marginalposition in one of the stands.

Horizon samples of the mineral soils and the mineral materials underlying the organic soils were analyzed for total sand, silt, and clay content by the Bouyoucos hydrometer method. Samples were screened through a 2 mm. sieve prior to analysis. The determination of moisture equivalent was accomplished with an International centrifuge, equipped with an automatic controlling rheostat. Soil organic matter content was approximated with a pyrometer controlled Temco muffle furnace and is reported as loss on ignition. Finally, soil pH was determined by the glass electrode method, using a Beckman (Zeromatic), pH meter.

Groundwater and Precipitation Measurement

A preliminary traverse of a proposed route showed that 12 hours was the minimum time needed to make a complete circuit of several tentatively selected stands. It was suspected that some difficulty might be encountered in excavating to the true water table, due to perching of tables in the

finer textured soils. In addition, it was desirable to record water table depths within a reasonable time period to minimize observational errors in well drawdown. Owing to these factors, and because of excessive distance from Lansing, Michigan, five stands were eliminated from the ground water study.

During the month of March, 1961, before the start of the growing season, 72 ground water wells were installed in 14 of the 19 stands selected for the vegetation study. Four wells, located at random, were drilled on each of 14 soil series using a five-foot bucket auger equipped with a $3\frac{1}{2}$ inch barrel. A resultant drop in water tables, as the growing seeson progressed, required the addition of five-foot extensions on the auger. This was necessary in order to reach the true water tables on beta-gley soils during the summer and fall of 1961.

If a perched water table was suspected in a particular well, additional excavations were made with the auger until no further drop could be detected and the water level stabilized. It is obvious that confounding of the records on true well levels would have occurred, if the possibility of perching had not been taken into account. Many times sloughing and caving of the excavations between sucessive reading occurred, superimposing a false water level within the wells. However, the possibility of reading false well levels was minimized by re-drilling each well, each week.

The detection of perched water tables was also accomplished by observing whether or not lateral seepage occurred from the profile into the well excavation, as drilling proceeded to the phreatic surface. The depth at which notable seepage occurred was defined as a perched table.

The largest number of wells was installed on alpha-gley soils and the organic mucks. These soils contained the greatest segment of the study area in lowland hardwoods. The location and number of wells in the stands selected for ground water studies are indicated in Figure 3.

Weekly measurements of the water levels, beginning two weeks before and ending three weeks after the 1961 growing season, were recorded for all wells. (Figures 19-24) The fluctuations of the water tables were measured with a nylon line, marked at one-foot intervals and attached to a 12-ounce plumbing weight (Figure 4). A flashlight was used as an aid in determining when the weight reached the water table. Readings between the marks designated for feet were taken to the nearest inch with a ruler. Although the wells were not capped, the probability of precipitation or surface runoff influencing the water levels in the wells was slight, owing to the small diameter of the aperture and the level topography surrounding well locations. In addition, the wells were further protected from surface water influences, by elevating the soil around the aperture after each measurement.

Statistics

MISTIC. All statistical analyses were performed on Michigan State's tape input digital electronic computer, MISTIC.

Analysis of Variance. Analyses of variance were performed to determine the significance of differences for soils and water table measurements (Appendix and Tables 15-19). All statistical determinations followed the standard methods and procedures described by Snedecor (138).

Correlation Analyses. Correlation analyses were performed to show the degree of association between plot versus point samples for use in forest surveys (Table 8,9). Additonal analyses were performed to determine correlations between species distribution and soil characteristics, and species distribution and depth of ground water (Table 13,20,21).

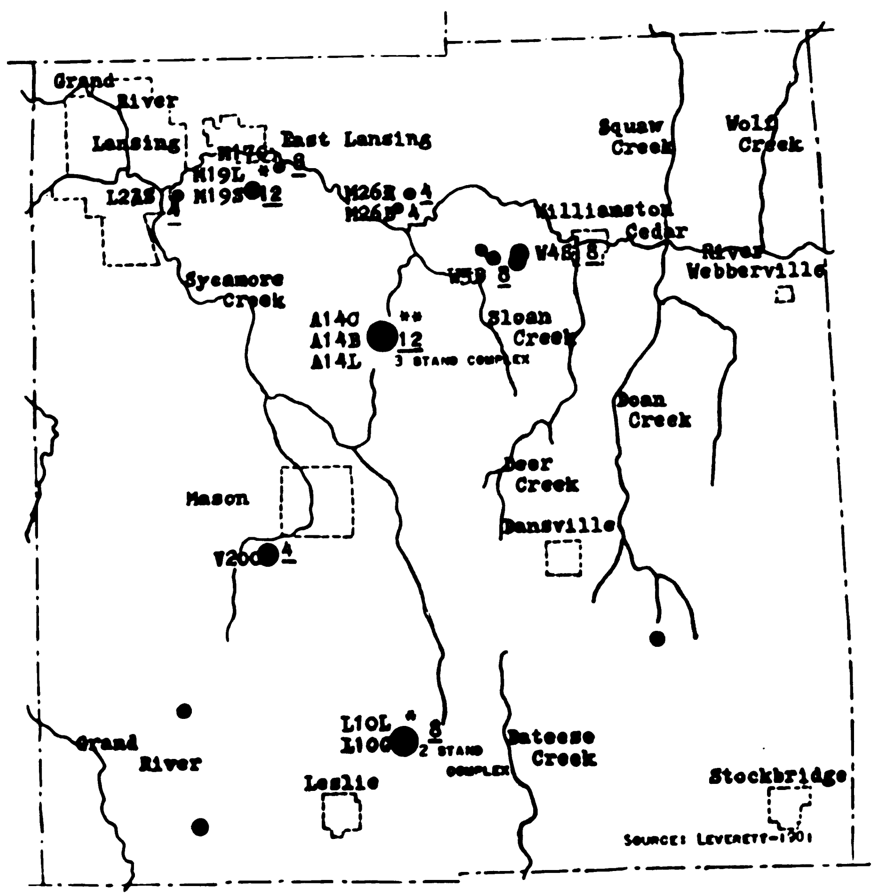

Fig. 3 . Map of Ingham county showing the drainage system, location and number of ground-water wells in stands selected for the ground water study.

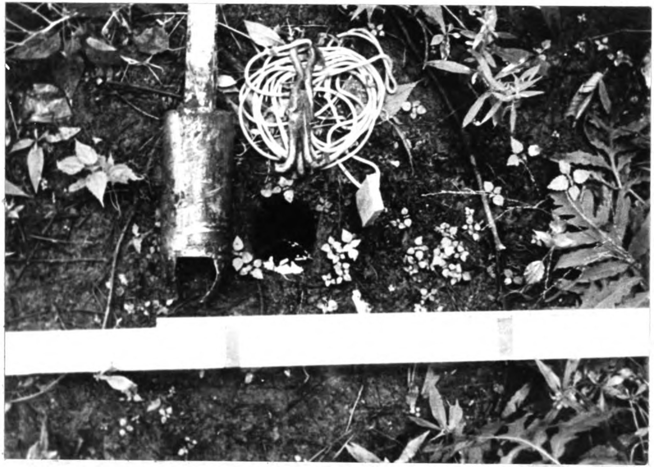

Fig. 4 . A ground water observation well in the shallow Linwood muck of the stand L10L. Note the lack of ground cover on this site. At the time this photograph was taken, during the first week in July, the mean ground water depth was 13 inches below the soil surface.

Stand Similarities. As a means of showing the behavioral pattern of the dominant species of the study area in relation to the environmental parameters investigated, a table of community coefficients was constructed (Table 28). The importance values of all tree species, calculated for each stand, were used in place of frequency or frequency percent advocated by Gleason (68) and Kulczynski (95).

The basic formula used by these authors may be expressed in algebraic terms as:

$$C = 2W/a+b$$

where C = the community coefficient

W = the sum of the lower importance values for each species in the stands being compared.[1]

a = the sum of the importance values of the first stand selected.

b = the sum of the importance values for the second stand selected to be compared to the first stand.

A common early technique for representing similarities between forest stands is the use of a herbaceous indicator species (Cajander (38)). Herbaceous plants are also used in ordination techniques because of their greater numbers and sensitivity to differences in environmental conditions. However, their use in the present study was undesirable from two points of view. First of all, many areas in which the quadrats were located were devoid of, or contained only a partial herbaceous cover. Secondly, herbaceous vegetation is often reflective of temporal changes in lowland stands and may be indicative only of a particular year or time of year in which the study is made.

Trees, on the other hand, reflect relatively long term changes in the edaphic environment; the individual having weathered the vicissitudes of

[1] Importance values used in place of frequency or frequency percent.

environmental pressures for many years. The similarity techniques in the present study were based on stand composition of the major and minor tree species present in 19 lowland-hardwood stands.

Since three measures rather than one measure are included in the importance value, it was selected as the most worthwhile indicator of community composition. Using the importance values of the tree species, the mathematical expression of community similarity is in algebraic terms:

$$C = \frac{2W \times 100}{600}$$

since a+b = 600 in all cases, which will further simplify to C = 1/3W. Expressed in terms of W : W = 3C.

When all of the stands were arranged according to their continuum index placement and the table of community coefficients was constructed, it was apparent that some difficulty would be experienced in explaining its content. In addition, the evidence indicated that within the compiled table, a further separation was needed to arrange the stands in an orderly sequence for comparisons. To accomplish this, a gradient analysis procedure advocated by Bray (23) was used.

An arrangement of values was compiled using two stands as reference points at opposite ends in the segment of the continuum covered by the study. When the community coefficients for all other stands were arranged in descending order, in relation to the reference stands, a complete table could then be constructed. The rearranged table of community coefficents for the 19 stands indicated the relationship of each stand to every other stand (Table [illegible]). High community coefficients near the 300 value indicate stands which are very similar in tree composition. Low values indicate stands having little similarity to other stands.

RESULTS

Sampling Methods

The five leading dominants of the lowland hardwood forests in Ingham County, recorded by the plot methods, were American elm, red maple, green ash, swamp white oak, and silver maple. Dominance was based on the importance values of the species recorded on 150 plots or point samples in 15 stands (Tables 4, 5, 6, 7). The same sequence of dominance was evident in the random pairs method.

In the quarter and bull Bitterlich methods, swamp white oak the fifth leading dominant, was replaced by silver maple. For the complete survey of 15 stands, American elm and red maple had the highest frequency, density, and basal area values, compared to the other species.[1] Although green ash had a greater importance value than either swamp white oak or silver maple, this could be attributed to the species being observed more frequenctly in each sample, with a greater density in the smaller size classes.

Considering the number of species recorded by the plot methods as a standard, three additional species were tallied by the quarter and full Biterlich methods. They were American hornbeam (*Carpinus caroliniana*), bur oak, and butternut. All other species tallied by the plot method were also tallied by the quarter method and the full Bitterlich method. No additional species were found using random pairs, and this method also failed to tally red hickory (*Carya ovalis*), black gum, or hackberry. All additional species, or species missed by other methods in comparison to the plot method, had an importance value of two or lower, and an average basal area per acre of less than one square foot.

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[1] In percent.

TABLE .-4 A summary of forest survey tree data for 15 lowland hardwood forests of Ingham County, based on the 100 meter plot method.

Species	relative frequency	relative density	relative basal area	basal area per acre	importance value
	----percent-----			square feet	---percent---
Acer rubrum	12.3	16.1	12.3	18.5	40.7
Acer saccharinum	8.3	6.7	9.5	14.1	24.5
Acer saccharum	7.0	8.3	4.4	6.7	19.7
Betula X purpusii	.3	1.5	.8	1.2	2.6
Carya cordiformis	.5	.3	.1	.1	.9
Carya ovalis	.5	1.2	.6	.8	2.3
Carya ovata	1.9	1.3	1.1	1.6	4.3
Celtis occidentalis	.3	.1	.2	.2	.6
Fagus grandifolia	1.9	1.1	.7	1.0	3.7
Fraxinus americana	1.1	.9	1.1	1.6	3.1
Fraxinus nigra	1.1	1.2	1.2	1.8	3.5
Fraxinus pennsylvanica	10.8	9.0	8.8	13.2	28.6
Larix laricina	.3	.8	.5	.8	2.1
Nyssa sylvatica	.5	.5	.3	.3	1.1
Ostrya virginiana	.5	.3	----	.1	.8
Platanus occidentalis	.5	.4	.5	.8	1.4
Populus deltoides	1.6	1.3	5.2	7.7	8.1
Populus tremuloides	1.6	1.8	1.2	1.8	4.6
Prunus serotina	4.0	3.1	1.5	2.3	8.6
Quercus alba	.5	.3	.7	1.0	1.5
Quercus bicolor	7.8	7.5	12.3	18.4	27.6
Quercus rubra	3.8	3.4	3.8	5.7	11.0
Salix nigra	.5	.5	.6	.9	1.6
Tilia americana	5.1	4.4	4.1	6.2	13.6
Ulmus americana	20.9	23.4	26.7	40.0	71.0
Ulmus rubra	5.9	4.8	1.8	2.7	12.5

TABLE.- 5 A summary of forest survey tree data for 15 lowland hardwood forests of Ingham County, based on the random pairs method.

	relative				
	frequency	density	basal area	basal area per acre	importance value
	----percent-----			square feet	---percent---
Acer rubrum	13.3	14.0	11.1	26.2	38.4
Acer saccharinum	6.5	8.0	10.6	25.0	25.1
Acer saccharum	7.3	7.7	5.1	12.0	20.1
Betula X purpusii	.4	.7	.5	1.2	1.6
Carya cordiformis	.4	.3	.1	.2	.8
Carya ovalis	----	----	----	----	----
Carya ovata	1.7	1.3	1.5	3.6	4.5
Celtis occidentalis	----	----	----	----	----
Fagus grandifolia	2.4	2.0	1.8	4.3	6.2
Fraxinus americana	1.2	1.0	1.8	4.3	4.0
Fraxinus nigra	.8	.7	.1	.2	1.6
Fraxinus pennsylvanica	12.1	11.7	8.9	21.0	32.7
Larix laricina	1.2	1.0	.4	1.0	2.6
Nyssa sylvatica	----	----	----	----	----
Ostrya virginiana	.4	.3	.2	.5	.9
Platanus occidentalis	.4	.3	.3	.7	1.0
Populus deltoides	1.7	1.7	4.5	10.6	7.9
Populus tremuloides	2.4	2.3	1.3	3.1	6.0
Prunus serotina	1.7	1.3	.6	1.4	3.6
Quercus alba	.4	.3	1.1	2.6	1.8
Quercus bicolor	9.7	8.4	12.9	30.4	31.0
Quercus rubra	3.2	3.0	4.8	11.3	11.0
Salix nigra	.4	.3	.1	.2	.8
Tilia americana	4.4	3.7	6.7	15.8	14.8
Ulmus americana	22.3	24.0	22.9	54.0	69.2
Ulmus rubra	5.7	6.0	2.7	6.4	14.4

TABLE .-6 A summary of forest survey tree data for 15 lowland hardwood forests of Ingham County, based on the quarter method.

Species	relative frequency	relative density	relative basal area	basal area per acre	importance value
	-----percent----			square feet	--percent--
Acer rubrum	13.2	15.2	13.3	19.7	41.7
Acer saccharinum	7.6	7.7	9.3	13.8	24.6
Acer saccharum	6.8	7.5	4.4	6.5	18.7
Betula X purpusii	.3	.5	.4	.6	1.2
Carya cordiformis	.3	.2	.1	.2	.6
Carya ovalis	.3	.2	.1	.2	.6
Carya ovata	1.3	1.2	1.2	1.8	3.7
Celtis occidentalis	----	----	----	----	----
Fagus grandifolia	1.9	1.2	3.2	4.7	6.3
Fraxinus americana	.8	.5	1.0	1.5	2.3
Fraxinus nigra	1.9	1.3	.6	.9	3.8
Fraxinus pennsylvanica	11.9	12.0	9.7	14.4	33.6
Larix laricina	1.1	.8	.3	.4	2.2
Nyssa sylvatica	.5	.3	.3	.4	1.1
Ostrya virginiana	.5	.3	.2	.3	1.0
Plantanus occidentalis	.3	.2	.1	.1	.6
Populus deltoides	1.3	1.5	3.7	5.5	6.5
Populus tremuloides	2.9	3.3	1.7	2.5	7.9
Prunus serotina	3.2	2.2	1.3	1.9	6.7
Quercus alba	.8	.8	.6	.9	2.2
Quercus bicolor	8.0	5.8	9.5	14.1	23.3
Quercus rubra	3.5	3.0	3.2	4.7	9.7
Salix nigra	.8	.8	.9	1.3	2.5
Tilia americana	5.6	5.5	6.9	10.2	18.0
Ulmus americana	19.6	22.8	25.8	38.2	68.2
Ulmus rubra	4.8	4.7	2.0	3.0	11.5
Carpinua caroliniana[a]	.5	.3	.1	.2	.9
Quercus macrocarpa	.3	.2	.1	.2	.6

[a] additional species recorded compared to the plot method.

[illegible] A summary of forest survey tree data for 15 lowland hardwood forests of Ingham County, based on the Full Bitterlich method.

Species	relative frequency	relative density	relative basal area	basal area per acre	importance value
	-----percent----			square feet	---Percent---
Acer rubrum	13.3	16.5	13.6	15.6	43.4
Acer saccharinum	7.8	8.8	12.6	15.5	29.2
Acer saccharum	5.5	6.2	4.4	5.4	16.1
Betula X purpusii	.2	.5	.2	.3	.9
Carya cordiformis	.2	.1	----	----	.3
Carya ovalis	.2	.4	.3	.4	.9
Carya ovata	2.1	1.2	1.1	1.3	4.4
Celtis occidentalis	.2	.1	----	.1	.3
Fagus grandifolia	1.4	.6	.5	.6	2.5
Fraxinus americana	1.4	.7	.8	.9	2.9
Fraxinus nigra	1.5	1.2	.6	.7	3.3
Fraxinus pennsylvanica	11.1	10.2	8.3	10.1	29.6
Larix laricina	.6	.4	.2	.2	1.2
Nyssa sylvatica	.6	.2	.1	.2	.9
Ostrya virginiana	.2	.1	----	.1	.3
Platanus occidentalis	.4	.2	.1	.2	.7
Populus deltoides	2.0	2.3	4.4	5.4	8.7
Populus tremuloides	2.5	2.5	1.2	1.4	6.2
Prunus serotina	2.9	2.2	.9	1.1	6.0
Quercus alba	.6	.7	.6	.8	1.9
Quercus bicolor	9.5	6.6	9.1	11.2	25.2
Quercus rubra	4.3	3.1	3.3	4.0	10.7
Salix nigra	1.2	.8	.9	1.1	2.9
Tilia americana	7.0	6.0	6.0	7.4	19.0
Ulmus americana	18.1	24.3	29.1	35.7	71.5
Ulmus rubra	4.9	3.9	1.6	1.9	10.4
Juglans cinerea [a]	.4	.2	.1	.1	.7

[a] additional species recorded compared to the plot method.

The results for frequency and density calculated from the random pairs method, do not agree with the results of Shanks (133), even though species which typically regenerate by sprouts are abundant in lowland hardwood stands.

Part of the difference in results between these two studies might be explained on the basis of a 20-degree difference in the exclusion angle used by Shanks (133), and the present 180° sector used in this study. The projection of basal area per acre figures for the leading dominant species were comparable between all methods except random pairs, for which substantially higher values were caluclated. An explantation for this discrepancy may lie in summing individual basal area records, and the assignment of an average basal area per tree for conversion to an acre basis.

Stand Characterization

The hardwood stands sampled in Ingham County were spread over the lower two-thirds of the continuum, indicating a rather complete coverage for the spectrum of lowland sites. The range of stand continuum values varied from a low of 684 for a stand in which tamarack, black cherry, and red maple predominated, to a high of 2429 for a stand composed mainly of sugar maple, northern red oak, American elm, and basswood. The majority of lowland stands were clustered within a segment of the continuum range from 1800 to 2200 (Figures 5-17). Such high values for these stands are derived from the contribution to frequency, density and basal area made by American elm and the effect of a corresponding high climax adaptation number (8) for this species (Tables 8 and 9).

Comparison of Quantitative Measurements and Species Dominance. The use of basal area per acre, as a measure of species dominance, is one of significant value. When frequency and density are ignored, basal area as a single index merits use, because of its strong relationsip to cover, and the overwhelming effect of those species capable of attaining large diameters. It is these species which lend character to any stand. Because of the importance placed on certain pioneer species such as cottonwood, which easily attain large girth in the early stages of succession, the sole use of basal area as an index for successional changes may be somewhat undesirable.

A review of the average basal area per acre values, for all stands in the survey, shows that the eight leading species in descending order were: American elm, red maple, swamp white oak, green ash, silver maple, basswood, cottonwood, and sugar maple. When basal area rather than the importance value was selected as the criterion of dominance, green ash, and slippery elm were replaced by swamp white oak, basswood, and cottonwood.

The calculation of the importance value appears to be the most worthy

Fig. 5 . Interior view of stand W4S on poorly drained Sebewa loam, continuum index 1394. Leading dominants in importance value: slippery elm, cottonwood, red maple; and in basal area: cottonwood, American elm, and slippery elm.

Fig. 6 . Interior view of stand M26k on poorly drained Rifle peat, continuum index 1408. Leading dominants in importance values and in basal area: red maple, black cherry, and quaking aspen.

Fig. 7 . Interior view of stand M22S on poorly drained Sloan loam, continuum index 1453. Leading dominants in importance values and in basal area: green ash, silver maple, and slippery elm.

Fig. 8 . Interior view of stand M17C on poorly drained Cohoctah sandy loam, continuum index 1540. Leading dominants in importance values and in basal area: American elm, silver maple, and cottonwood.

Fig. 9 . Interior view of stand M26B on a poorly drained Brookston soil, continuum index 1659. Leading dominants in importance value: swamp white oak, northern red oak, and American elm.

TABLE.-8 Importance values of tree species found in 19 lowland-hardwood stands in Ingham County.[a]

Species[b] / Stand	O26R	W4S	M26R	M22S	M17C	M26B	W4B	V20C	S23B	L10L	A14L	S5B	L10C	A14B	O3L	A14C	W5C	M19S	M19L
	percent																		
Acer saccharum	---	--	---	--	--	--	21	---	--	---	---	20	--	11	---	78	36	48	100
Fagus grandifolia	---	--	---	--	--	--	5	---	--	---	---	5	--	--	---	4	11	30	35
Tilia americana	---	10	---	9	15	--	26	---	--	15	---	---	22	27	---	30	24	25	2[illegible]
Ostrya virginiana	---	--	---	--	--	--	10	---	7	---	---	5	10	5	---	--	--	11	---
Carpinus caroliniana	---	--	---	--	--	--	3	---	--	---	---	4	19	--	---	7	--	--	10
Carya cordiformis	---	--	---	--	6	--	7	---	--	---	---	---	--	--	---	9	--	4	10
Ulmus americana	---	--	---	15	77	41	38	133	25	105	53	115	90	78	153	40	74	39	23
Acer rubrum	32	35	117	--	--	38	--	18	91	61	140	6	41	48	4[illegible]	11	6	12	4
Quercus rubra	---	--	14	--	--	42	18	---	17	---	---	---	--	13	---	10	8	--	37
Nyssa sylvatica	---	--	---	--	--	--	--	---	13	---	---	---	--	--	---	--	--	--	---
Fraxinus americana	---	--	---	--	--	7	14	---	--	---	---	---	--	5	---	9	10	--	4
Quercus alba	---	--	---	--	--	16	--	---	--	---	---	---	--	--	---	--	--	--	---
Ulmus rubra	---	47	17	70	20	--	25	---	12	9	14	---	14	17	---	11	15	14	5
Carya ovata	---	13	---	--	--	4	19	---	29	---	---	5	--	--	---	--	--	--	---
Carya ovalis	---	--	---	--	--	--	11	---	--	---	---	14	--	--	---	--	--	--	---
Fraxinus pennsylvanica	---	11	---	9[illegible]	18	37	31	104	17	45	27	11	31	43	45	40	15	21	10
Quercus bicolor	---	16	---	14	11	56	40	49	51	12	6	42	45	22	36	--	21	37	10
Prunus serotina	63	18	92	--	--	19	6	---	15	10	6	7	--	18	---	19	18	--	---
Acer saccharinum	---	29	---	81	74	15	7	26	--	---	38	53	--	--	---	--	26	53	6
Celtis occidentalis	---	--	---	--	8	--	--	---	--	---	---	---	--	--	---	--	--	--	---
Crataegus spp.	---	--	---	--	--	4	--	---	--	---	---	4	--	--	---	--	--	--	---
Platanus occidentalis	---	--	---	--	18	--	--	---	--	---	---	---	--	--	---	--	--	--	---
Sassafras albidum	---	--	---	--	--	9	--	---	--	---	---	---	6	--	---	--	--	--	7
Fraxinus nigra	---	--	---	--	6	6	--	---	19	---	---	---	20	6	---	--	--	--	---
Populus deltoides	---	45	---	--	40	--	11	---	--	---	---	---	--	4	---	--	--	--	---
Larix laricina	205	--	---	--	--	--	--	---	--	5	---	---	--	--	---	--	--	--	---
Salix nigra	---	19	---	13	--	--	--	---	--	---	---	---	--	--	---	--	--	--	---
Betula X purpusii	---	--	---	--	--	--	--	---	--	26	---	---	--	--	---	--	--	--	---
Populus tremuloides	---	8	47	--	--	--	--	---	--	---	---	---	--	--	7	--	--	--	---
others	---	15	14	7	6	4	8	---	4	10	16	9	5	3	8	13	17	6	4
total	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300	300

[a] Stands arranged in ascending order in continuum.
[b] [illegible] in descending order of [illegible] numbers.

TABLE.-9 Basal area per acre for tree species found in 10 lowland-hardwood stands in Ingham County. [a]

Species[b] / Stand	O26R	W4S	M26R	M22S	M17C	M26B	W4B	V20C	S23B	L10L	A14L	W5B	L10G	A14B	O3L	A14C	W5C	M19S	M19L
	square feet																		
Acer saccharum	--	--	--	--	--	--	8	--	--	--	---	3	--	1	--	27	28	4	34
Fagus grandifolia	--	--	--	--	--	--	1	--	--	--	---	1	--	--	--	--	--	10	5
Tilia americana	--	1	--	3	8	--	18	--	--	5	---	---	11	27	--	12	37	14	12
Ostrya virginiana	--	--	--	--	--	--	1	--	--	--	---	---	--	--	--	--	--	--	--
Carpinus caroliniana	--	--	--	--	--	--	--	--	--	--	---	---	1	--	--	--	--	--	--
Carya cordiformis	--	--	--	--	--	--	2	--	--	--	---	---	--	--	--	--	--	--	--
Ulmus americana	--	27	--	4	70	27	23	35	15	95	26	115	90	84	64	18	60	18	19
Acer rubrum	2	11	34	--	--	17	--	6	49	36	102	3	25	24	17	6	2	10	--
Quercus rubra	--	--	2	--	--	10	17	--	13	--	---	---	--	14	--	6	6	--	19
Nyssa sylvatica	--	--	--	--	--	--	--	--	7	--	---	---	--	--	--	--	--	--	--
Fraxinus americana	--	--	--	--	--	--	11	--	--	--	---	---	--	--	--	4	10	--	--
Quercus alba	--	--	--	--	--	15	--	--	--	--	---	---	--	--	--	--	--	--	--
Ulmus rubra	--	20	--	27	5	--	9	--	1	2	2	---	12	1	--	1	4	8	--
Carya ovata	--	--	--	--	--	--	8	--	15	--	---	---	--	--	--	--	--	--	--
Carya ovalis	--	--	--	--	--	--	6	--	--	--	---	6	--	--	--	--	--	--	--
Fraxinus pennsylvanica	--	4	--	45	1	25	17	35	5	15	3	4	18	43	15	23	6	7	--
Quercus bicolor	--	4	--	8	6	63	29	30	40	--	2	31	38	15	10	--	19	21	4
Prunus serotina	4	11	30	--	--	1	2	--	5	4	2	4	--	4	--	3	4	--	--
Acer saccharinum	--	23	--	31	51	21	4	15	--	--	23	26	--	--	--	--	13	38	1
Celtis occidentalis	--	--	--	--	4	--	--	--	--	--	---	---	--	--	--	--	--	--	--
Crataegus spp.	--	--	--	--	--	--	--	--	--	--	---	---	--	--	--	--	--	--	--
Platanus occidentalis	--	--	--	--	11	--	--	--	--	--	---	---	--	--	--	--	--	--	--
Sassafras albidum	--	--	--	--	--	--	--	--	--	--	---	---	3	--	--	--	--	--	1
Fraxinus nigra	--	--	--	--	1	1	--	--	14	--	---	---	--	3	--	--	--	--	--
Populus deltoides	--	59	--	--	45	4	12	--	--	--	---	---	--	--	--	--	--	--	--
Larix laricina	22	--	--	--	--	--	--	--	--	2	---	---	--	--	--	--	--	--	--
Salix nigra	--	14	--	10	--	--	--	--	--	--	---	---	--	--	--	--	--	--	--
Betula X purpusii	--	--	--	--	--	--	--	--	--	19	---	---	--	--	--	--	--	--	--
Populus tremuloides	--	4	10	--	--	--	--	--	--	--	---	---	--	--	2	7	--	--	--
others	--	1	--	--	--	--		--	--	--	8	---	--	--	1	1	--	--	--
total	28	179	76	128	222	184	160	121	164	178	168	193	198	216	169	108	189	130	95

[a] stands arranged in ascending order in continuum

[b] species arranged in descending order of climax-adaptation numbers

Fig. 10 . Interior view of stand V20C, on poorly drained Carlisle muck, continuum index 1818. Leading dominants in importance values and in basal area: green ash, American elm, and swamp white oak.

Fig. 11 . Interior view of stand S23B on poorly drained Brookston soil, continuum index 1827. Leading dominants in importance values and in basal area: red maple, swamp white oak, and shagbark hickory.

measure of expressing species dominance, since three direct field measurements are used. Nevertheless, as a measure of dominance in relation to stand-age structure, its use has a repressive effect on those species which are large in diameter, but occur at infrequent intervals with low density. The eight leading species in over-all importance values for the entire study area in descending order were: American elm, red maple, green ash, swamp white oak, silver maple, sugar maple, slippery elm and basswood.

Within the boundaries of the study area, 12 species occurred as a leading dominant in at least one stand. American elm was the leading dominant in 35 and 40 percent of the stands, based on importance value and basal area, respectively. Green ash, swamp white oak, and sugar maple were the leading dominants in 10 percent of the stands, considering their importance values, and basal areas, while red maple occurred as the leading dominant in 16 percent of the stands. Silver maple, slippery elm, and tamarack each attained a leading dominant position in a single stand.

On the basis of importance values, American elm was the leading or second place dominant in stands ranging from 1832 to 2035 along the continuum. In stands falling outside this range, it occurred as a leading dominant only twice: once in a stand of floodplain origin and once in a stand located on glacial till. This species was a third place dominant in at least four stands, mostly located at the upper end of the continuum. It did not attain a dominant position in three stands found at the lower end of the continuum.

Red maple occurred as a leading dominant in a rather narrow range of the continuum, within the spectrum dominated by American elm. At the lower end of the continuum, this species led in either importance value or basal area in closed basin depressions. It was absent as a dominant species in stands on materials of fluvial origin. In addition, it did not attain dominance in four stands at the upper end of the continuum although its presence was recorded in these stands.

Fig. 12 . Interior view of stand L10L on shallow Linwood muck continuum index 1832. Leading dominants in importance values and in basal area: American elm, red maple, and green ash.

Fig. 13 . Interior view of stand W5B on poorly drained Pewamo loam, continuum index 1920. Leading dominants in importance value: American elm, silver maple, swamp white oak: and in basal area: American elm, swamp white oak, and silver maple.

Fig. 14 . Interior view of stand A14B on poorly drained Brookston sandy loam, continuum index 1989. Leading dominants in importance value: American elm, red maple, green ash; and in basal area: American elm, green ash, and basswood.

Green ash was a second or third place dominant across the upper two-thirds of the continuum. Where the basal area of American elm was great, green ash although frequently encountered, contributed little to total basal area. One exception occurred in a stand found on deep muck, were the basal area of both species was approximately equal. Besides the stand just mentioned, green ash appeared as a leading dominant in two other stands: one located on a floodplain of the Red Cedar River and another on a poorly drained glacial-till. It did not attain a dominant position in three stands in the upper part of the continuum.

Swamp white oak, attained its greatest dominance in stands within the continuum spectrum from 1540 to 1830. This species was present to some degree in all but two of the stands. Sugar maple was the leading or second placed dominant in importance value within the upper third of the continuum from 2110 to 2430. In two stands within this range, it also had the highest per acre values for basal area. Basswood appeared as a weak leading dominant associated with sugar maple in the upper portion of the continuum. It also appeared as a dominant species in the continuum around a value of 1800.

Slippery elm was strongly represented as a dominant component of the stands in the lower third of the continuum. This was attributed to its high frequency and density, rather than basal area. Northern red oak was intermittently dominant throughout and appeared to increase in dominance at the upper end of the continuum.

Fig. 15 . Interior view of stand W5C on imperfectly drained Conover soil, continuum index 2155. Leading dominants in importance value: American elm, sugar maple, silver maple, and in basal area: American elm, basswood, and sugar maple.

Fig. 16 . Interior view of stand M19S on imperfectly drained Spinks loamy sand, continuum index 2160. Leading dominants in importance value: silver maple, and American elm. Leading dominants in basal area are: silver maple, swamp white oak, and American elm.

Fig. 17 . Interior view of stand M19L on imperfectly drained Locke sandy loam, continuum index 2429. Leading dominants in importance values and in basal area: sugar maple, northern red oak, and American elm.

Determination of Soil Properties

The stands selected for this study occurred on a rather wide variety of hydromorphic soils, including imperfectly and poorly drained mineral soils, alluvial soils, and organic soils. These were distinguished according to the classification proposed for hydromorphic forest soils by Wilde (160), and by the Michigan State University Soil Science Department and U. S. Soil Conservation Service. The toposequence of drainage conditions and parent material relationships for mineral soils is shown in Table 10. The relationships of underlying materials and thickness of the organic soils is also included. The results of the field survey and laboratory analyses showed that four of the mineral series were beta-gley soils, three of which (Conover, Locke, and Spinks series) were formed from coarse to moderately coarse textured glacial drift. The other soil was a moderately coarse textured alluvial soil, the Ceresco series.

The remaining seven mineral series were alpha-gley soils, five of which developed from glacial till of stratified sands and gravel to non-stratified fine textured loams, silt loams, or light clay loams. Included in this group were the Barry, Pewamo, Brookston, Gilford, and Sebewa series. Two of the series, Sloan and Cohoctah, were fine textured alluvial soils. The three organic series were Carlisle muck, Linnwood muck and Rifle peat.

Beta-Gley Soils.- The imperfectly drained Conover, Locke, and Spinks series are non-stratified Gray-Brown Podzolic soils, which formed from calcareous parent materials of loam, sandy loam, and loamy sand respectively, and are similar in morphological drainage and color characteristics, when compared to the associated members of their respective catenas. The Ceresco series is an alluvial soil, developed from loamy fine sand.

The A_0 horizons consist of partially decomposed forest litter, varying from one to three inches in thickness. It was absent in some places on the

TABLE.- 10 Soil series in the area covered by the soil survey arranged to show the parent materials and catenal relationships.[a]

Parent materials	Soil group			
Texture	Gray-Brown Podzolic soils	Humic-Gley soils	Organic Soils	
	---BETA-GLEY---	---ALPHA-GLEY---	Very poorly-drained	
Clay loam to silty clay loam	Blount	Pewamo*	Shallow	Deep
Loams	Conover*	Brookston*	less than 42 inches thick	over 42 inches thick
Sandy loam	Locke*	Barry*		
Loamy sands	E-13*	I-13	over loam	over sands or loams
Sandy loam to silt loam overlying sand and gravel at depths of 24 to 42 inches	Matherton Brady	Sebewa* Gilford*	Linnwood*	Carlisle* Rifle*
Texture	Alluvial soils			
	---BETA-GLEY---	---ALPHA-GLEY---		
Loam to silt loam	Shoals	Sloan*		
Loamy fine sand to fine sandy loam	Ceresco*	Cohoctah*		

[a]Information furnished by I.F. Schneider, Soil Science Department, Michigan State University.
*series on the study areas.

Ceresco series, due to periodic removal of the material by seasonal flooding.

The A_{11} and A_{12} horizons of this group are dark grayish-brown loams to loamy fine sands of friable to weak granular structure, which broke sharply into the subsoil at depths of nine to fifteen inches. Thickness of the mineral surface horizons varied from two to nine inches.

Locke, Spinks, and Ceresco soils differed from Conover soils in having coarser textured subsoils. In the Spinks series, the textural subsoil horizons were thin, wavy and discontinuous layers of sandy loam and loamy sand. Subsoils of the Conover series consisted of mottled, gray, and yellowish-brown loams of medium nuciform structure, which became coarser in depth. The B_1 and B_2 horizons, or the A_2 and B_t arrangement in the Spinks series, were approximately 20 inches in thickness. Corresponding C_{1g} and C_{2g} horizons of the Ceresco series were somewhat thinner.

Mottling of the subsoils, associated with the presence of organic matter under imperfectly drained conditions and insufficient aeration, was strongest in Ceresco, Conover, and Locke soils, respectively. Owing to the low organic matter content and coarse nature of the materials, only slight evidence of mottling was apparent in the Spinks soils. The parent materials, although differing in texture, were strongly mottled gray and yellowish-brown strata, descending in this study to an undisclosed depth.

Alpha-Gley soils.- Soils of the Barry, Pewamo, Brookston, Gilford, and Sebewa series, are poorly or very poorly drained medium dark Humic-Gleys found in depressions or flats. The first three series are formed in non-stratified highly calcareous glacial till, consisting of sandy loam, silt loam or clay loam. The latter series are two-storied soils, developed in loamy materials overlying calcareous sand and gravel.

Barry soils occupy small depressions or pockets within a broader mapping unit, and are in a permanently ponded condition most of the time. These soils, owing to their wetness, represent the lower limits of invasion by higher vegetation.

Two alluvial soils, the Sloan and Cohoctah series, occurring in nearly level old stream channels, were formed from materials of varying texture, usually sandy loam to loams. The A_0 horizons of these soils were somewhat thinner than those of the beta-gleys, and on the alluvial series were often absent due to flooding which exposes bare mineral soil. Owing to better preservation and mixing of organic matter under poor aeration and drainage, the A_{11} and A_{12} horizons of this group were a very dark brown, gray, or black color, considerably darker when compared with surface horizons of the beta-gleys. Texture in these soils ranged from sandy loams to loams of weak, fine to moderately fine granular structure. Thickness of the surface horizons varied from six to thirteen inches.

Subsoil horizons designated GB_1, GB_{21}, and GB_{22}, of the Gilford and Sebewa series, differed from the other alpha-gleys in having coarser textured materials of moderate sub-angular blocky structure containing few, weak, light olive to yellowish-brown mottles. In the alpha-gley non-stratified series, mottling in the B_{21g} and B_{22g} horizons was common, of medium intensity and distinct. Dark olive and dark brown to gray, grayish-brown, and black coatings appeared on many ped faces of firm sub-angular to fine angular blocky structure.

Alluvial soils of this group contained strongly mottled light gray and weak yellow subsoils; however, the granular structure was generally pervious and friable. Horizons in alluvial soils are often designated by numbers, where they are obscure or diffuse within the profiles. Average thickness of the subsoils varied from 20 to 25, and from 30 to 40 inches in the stratified and non-stratified alpha-gley tills, respectively. Owing to the irregularity of stream flow at the time of deposition, subsoil depths in the stratified alluvial soils varies according to the manner in which the materials were sorted, rearranged, and deposited.

The till materials of the Pewamo and Brookston soils and the structureless parent materials of the Gilford and Sebewa soils contained many olive, grayish, and yellowish-brown mottles. Parent materials of the alluvial soils were similar in coloration, but mottling was weaker and the stratified deposits were single grained.

Organic Soils.- Very poorly drained organic soils, derived principally from decomposing plant remains, varied considerably in reaction, texture, structure, and thickness of the deposits. Rifle peat was over 42 inches thick and was derived from coniferous and deciduous woody and fibrous materials, in which the plant structures could still be identified. Two mucks, the Carlisle and Linnwood series, derived from decidous woody materials, are the products of peat decomposition, in which few of the plant structures could be recognized. Linnwood mucks are shallow organic soils, 12 to 42 inches in thickness, overlying medium textured sandy loam to sandy clay loam materials, and differ from Carlisle mucks, which are over 42 inches thick.

The O_1 horizons of these soils consist of very dark brown to black peat or muck containing few to numerous woody fragments, with disintegrated materials being of moderate, fine to medium, granular structure. Surface horizons were in descending order: thinnest in the Rifle peat, next in Linnwood, and thickest in Carlisle mucks. The range for the group was four to twenty-four inches. Although Carlisle muck and Rifle peat may vary in depth from 42 inches to 10 feet or more, this was not the case for the two series examined. Sandy clay loam and loamy sand materials were found for Rifle peat and Carlisle muck at depths of 50 and 70 inches, respectively.

Soil Properties and Species Development

American Elm.- American elm attained its highest importance value on a Linnwood muck underlain by materials containing 80 percent sand. This species, however, was most strongly developed on a Pewamo loam. In this stand (W58) American elm was second in importance value but highest in basal area for all of the stands in the study area.

The Pewamo loam of this stand had a mean sand, silt, and clay content of 45,24,and 31 percent, respectively. Mean values for loss on ignition and moisture equivalent were correspondingly 10 and 30 percent. In addition, this soil had a higher clay content than any of the soils analyzed and compared to other soils was second from the lowest in sand content.

American elm, however, was low in importance on an alluvial Sloan soil (stand M22S). This soil was also a loam, and its values for the aforementioned parameters were not significantly different from Pewamo loam at either the .05 or.01 level.

Although American elm decreased in importance in the present study on certain other lowland mineral soils, it was rather strongly represented on most Brookston sandy loams and loams. In addition, this species was well represented on Conover loams, which were not significantly different in soil texture from Brookston soils. On the Spinks soils, it was about as well represented as on Locke soils, even though the two soils were significantly different from each other in sand content at the .01 level.

Considering the distribution of American elm within the other stands of the study area, this species was best developed on certain organic soils. Those stands having shallow Linnwood or deep Carlisle mucks, underlain by coarse textured materials with more than 70 percent sand, contained the greater proportion of this species.

American elm did not appear at all on deep Rifle peats and decreased in importance on shallow Linwood muck (20 to 30 inches), having 50 percent sand with approximately equal proportions of silt and clay in the underlying mineral materials.

A review of the horizon and profile values for the most coarse to fine textured mineral soils did not indicate strong trends associated with the presence or absence of American elm. The complete range of textural variation for the soil types within the study area was rather narrow. None of the soils were coarser than sandy loams or finer than loams, therefore the fiducial limits of textural variation affecting the development of this species could not be established.

Red Maple.-- Red maple, on the average, attained its highest importance values and basal area in stands on the deeper Linnwood mucks, although it was still well represented on shallow mucks of the same type. Unlike American elm, this species was not as well represented on Carlisle muck, which was lowest in loss on ignition and highest in soil reaction for organic soils. In addition, it appeared to be quite tolerant of the acidic conditions in the fibrous materials of Rifle peats.

Within the remaining stands of the study area, red maple was fairly well represented in those stands located on Brookston sandy clay loam, loams, and Gilford sandy loams. In textural variation, these soils had mean horizon values of 47 to 72 percent sand, 14 to 32 percent silt, and 13 to 21 percent clay. This species was rather poorly represented on Conover, Spinks, and Locke soils, which reflects the decline in importance value found by previous investigators within this segment of the continuum (54,110).

Among the stands located on organic soils, red maple had the lowest importance in a stand on Carlisle muck. The materials underlying this muck corresponded very closely to the textural classification of the previous soil.

Green Ash.-- Green ash, the third leading species in importance on the entire study was represented to some extent on all soils except Rifle peats. In this respect, it appears to follow the sequence of stands in which American elm appeared. Green ash was most strongly represented on the soils in stands where red maple was low in importance, especially the floodplain soils and mucks. It may be noted that green ash was the leading species on Sloan soils, which contained the greatest proportion of combined silt and clay for any of the soils analyzed. A relationship for the occurrence of this species with fine textured soils could not be substantiated from the data, however, because this tand was one of the lowest in total basal area. On shallow Linnwood mucks this species was generally overshadowed by the importance value contributed to stand structure by red maple. Most of the shallow and deep mucks in the study area were underlain by rather sandy materials, and no apparent connection with coarse textures was evident, since this species attained high importance values on mucks which were significantly different from each other at the .01 level. In addition, green ash declined in importance on the coarse textured Conover, Spinks, and Locke soils in the upper portion of the continuum. Thus, because of conflicting evidence regarding textural variation, no convincing data appeared from which to suggest major soil properties governing the development of this species on lowland sites.

Swamp White Oak.--Swamp white oak was another major tree species of high importance in this study. Because of the rather large average diameters attained by this species, its basal area contribution to stand structure was impressive.

In the present study swamp white oak was better represented on mucks of the Linnwood and Carlisle series than on alluvial soils. Like green ash and American elm, this species was not found at all on Rifle peats. Moreover, swamp white oak contributed strongly to the vegetation of stands found on Brookston loam, Pewamo loam, and Spinks sandy loam. The range of variation covered by the textural limits of all soils on which the species occurred, was over 90 percent for sand and silt, and 100 percent for clays. Thus, it appears that swamp white oak was quite adaptable to lowland soils, at least within the limits of textural variation found in this county.

Silver Maple.-- Of all the species tallied in the study area, silver maple showed the strongest affinity for flood plain soils. In the present study, it was best represented on the Ceresco and Sloan soils of the Red Cedar floodplain. This species also appeared on Cohoctah soils of the same stands, which were not significantly different from Ceresco soils in sand and clay content at the .01 level.

Strangely enough, silver maple was outstandingly represented on the Spinks soils of a ground moraine. This soil was far removed from the homogenizing effects of streamside inundation.

Sugar Maple and American Beech.-- Although sugar maple and American beech are often thought of as the dominant species growing on upland till plains, they are also important species on lowland soils in Ingham County. This is especially true for stands found on beta-gley soils. These two species were consistently represented in stands on Conover loams, Spinks, and Locke sandy loam. The mean sand, silt and clay content of the profiles of these three soils accounted for a considerable portion of the variation in textural conditions. Sand content ranged from 50 to 77 percent, silt content from 13 to 33 percent, and clay content from 10 to 18 percent.

On these soils, however, sugar maple importance value and basal area far outweighed the contribution to stand character added by American beech. In addition, the former species was found on several alpha-gley Brookston loams and sandy clay loams, which were intermediate in textural variation to the beta-gley soils. American beech was absent from the alpha-gley soils.

American Basswood.--American basswood was especially well represented in those stands found on the same soils as sugar maple and American beech. Although the Spinks soils contained increasing amounts of silt and clay in the A_{2Bt} horizons and underlying materials; for similar horizons, both the Conover and Locke soils were significantly higher in fine textured materials. The Spinks soil was peculiar in having alternate layers of fine textured materials in the subsoils, even though the percentages were quite low compared to other beta-gleys.

American basswood contributed heavily to the importance of stands located on certain Brookston loams and Gilford sandy loam. It also appeared to some extent on alpha and beta-gley soils of floodplain origin, and was represented on one Linnwood muck containing 77 percent sand, 12 percent silt, and 10 percent clay in the underlying materials.

Lesser Species.--Other species occurring throughout the study area, which contributed to the important vegetation of several lowland stands, included black cherry, slippery elm, and northern red oak.

Slippery Elm.--Slippery elm appeared as the leading dominant on Sebewa and Gilford sandy loams. The range of textural variation for these two soils is rather narrow for sand and silt; however, the range for clay was about 70 percent of the total for all soils analyzed.

Like green ash, slippery elm was strongly represented on floodplain soils of the Sloan, Cohoctah, and Ceresco series. It was also an important species on Linwood mucks, Brookston sandy clay loam, Conover loam, and Spinks sandy loam.

Northern Red Oak.-- In the present study, northern red oak was well represented on Brookston loams and Conover loam. It was best developed toward the upper portion of the continuum on Locke soils. This soil was not significantly different from the Brookston and Conover soils in sand and clay content at the .01 level.

This species was also important on mineral soils containing as much as 20 percent clay in the profile, and oddly enough appeared as a weak component of a stand on Rifle peat (M26R). It is interesting to note that the Rifle peat upon which this species was growing contained greater percentages of silt and clay in the underlying mineral materials compared to other organic soils. Evidently this species has a rather wide ecologic amplitude to acid conditions similar to that of red maple.

Black Cherry.-- Black cherry was one of the major species associated with red maple on Rifle peats, Brookston sandy clay loam, and Conover loams. It was not very well represented with red maple in those stands located on shallow Linnwood mucks.

Ground Water and Precipitation Measurement

During the period from April 22 to December 3, 1961, a total of 2,376 water table measurements were made. In Figures 18 through 24, hydrographs of the well records and histograms of the precipitation records are shown. Rainfall information for the year was obtained from four automatic recording stations closest to the well locations. This information was available from the U. W. Weather Bureau records in East Lansing, Michigan.

Perched water tables, distinct from the main water tables, were noticed during the third week of observations and were most pronounced in the Brookston, Conover and Locke soils. The main cause of perched water tables lies in the presence of a clay pickup in the loam B_{21g}, B_{22g}, and B_1, B_2 horizons of these soils, respectively. The relationship between the depth to and intensity of mottling and the duration of perched water tables has been discussed by Diebold (58). In the present study, mottling was strongest and most distinct in the upper profiles of alpha-gley soils compared to the profiles of the two other soil groups. This condition could not be attributed to perched water remaining in the profiles for any considerable length of time. Therefore, it seems reasonable to attribute the mottling intensity in these soils to the long period in which the true water table is near the surface, especially during the winter season. Perched water tables were observed throughout the spring, summer, and early fall, but not after the 22nd week of the study.

The true water level in alpha and beta-gley sandy loams stabilized in less than ten minutes, after drilling the well while the flow to the cone of depression created by the excavations in alpha and beta-gley loams took ten to twenty minutes longer. Owing to the loose consolidation of materials and the nearness to the surface of the ground water in organic soils, little difficulty was experienced in recording water table depths.

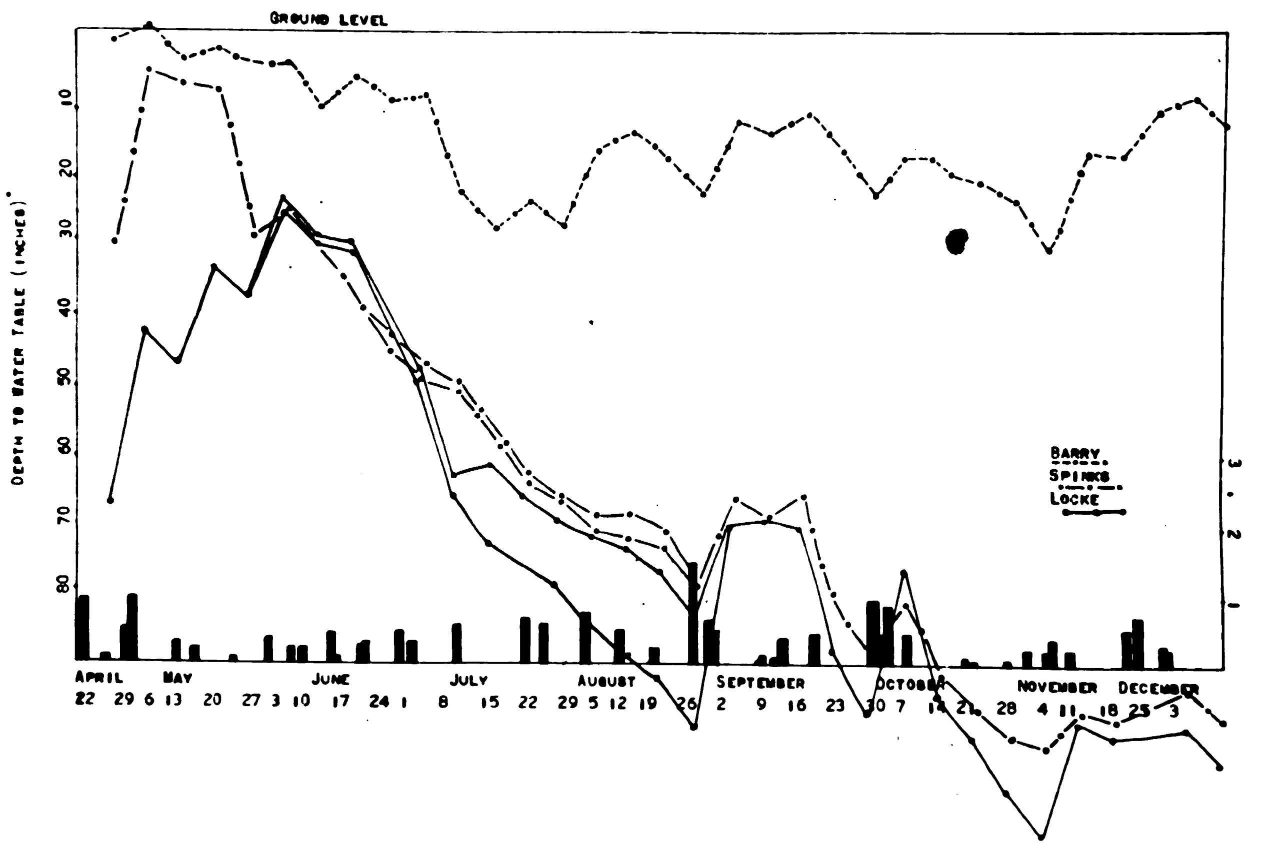

Fig. 13 . Hydrographs of true and perched water tables in moisture regime A (stands M19S and M19L). The upper hydrograph represents water table fluctuations occurring in a permanently ponded soil. The 1961 rainfall histogram located 1/4 mile to the N is also shown.

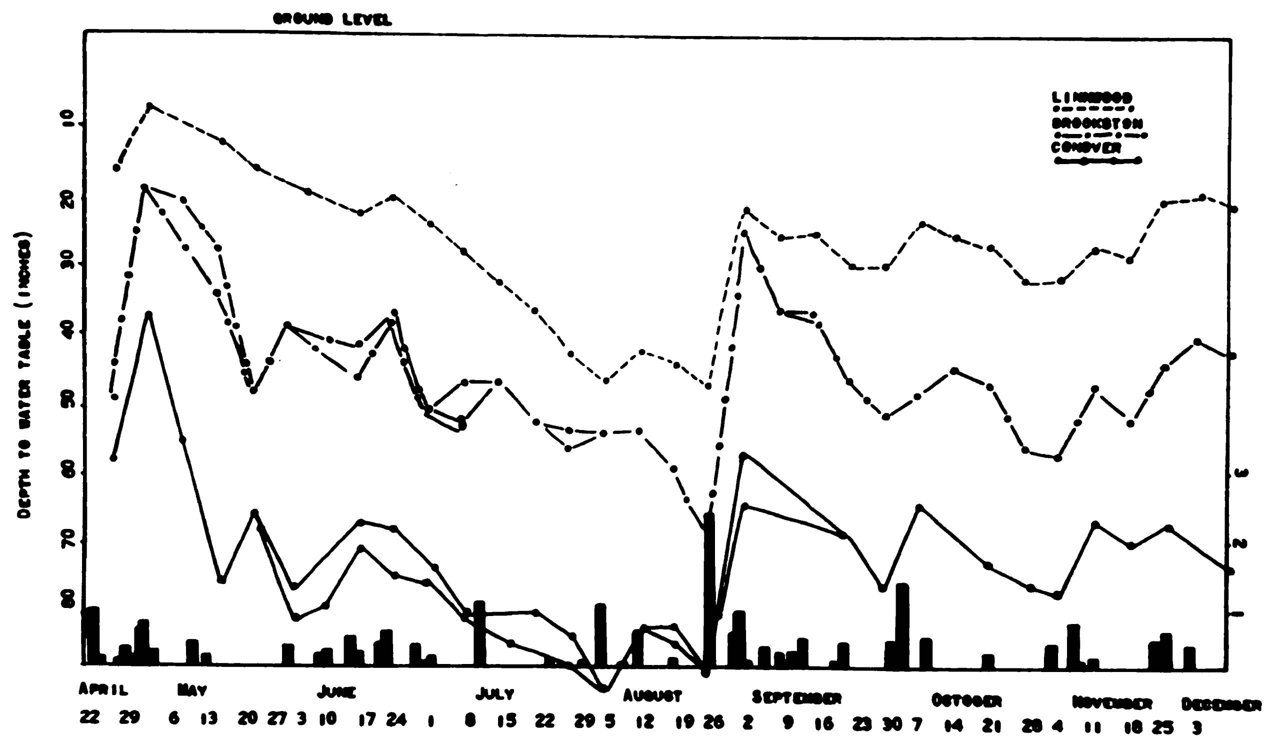

Fig. 19 . Hydrographs of true and perched water tables in moisture regime B (stands A14C, A14B, and A14L). The 1961 rainfall histogram for the precipitation station located one mile to the SE is also shown.

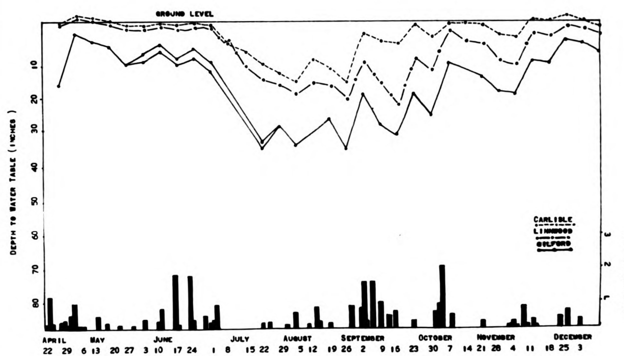

Fig. 20. Hydrographs of true and perched water tables in moisture regime C (stands L10G, L10L, and V20C). The 1961 rainfall histogram for the precipitation station located three miles to the NE is also shown.

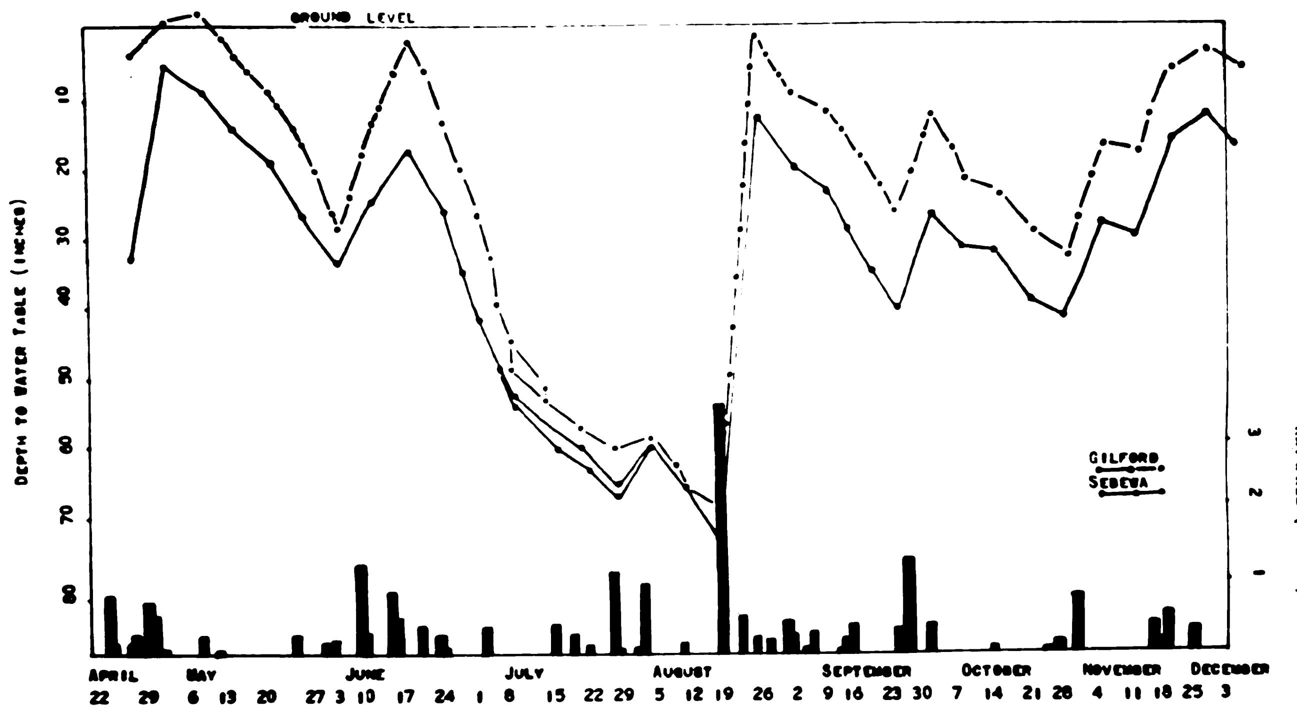

Fig. 21 . Hydrographs of true and perched water tables in moisture regime D (stand W4S). The 1961 rainfall histogram for the precipitation station located 1/2 mile to the NW is also shown.

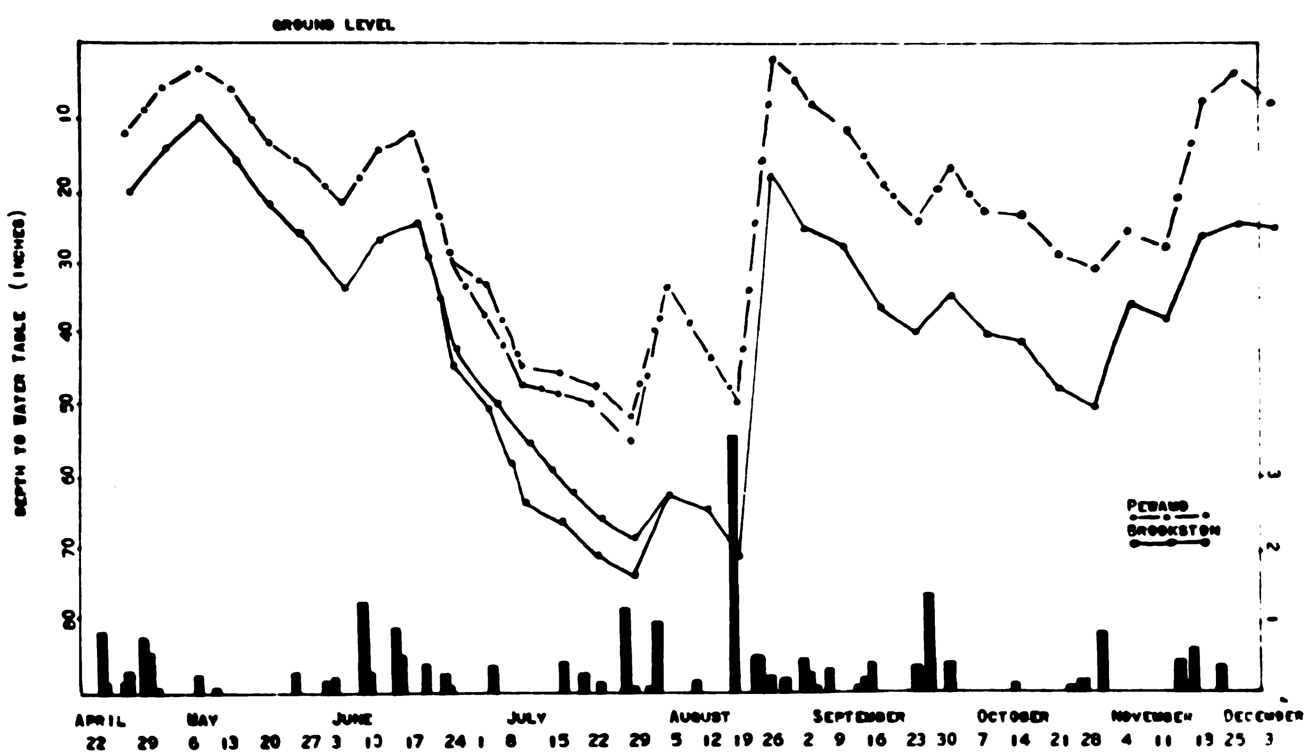

Fig. 22 . Hydrographs of true and perched water tables in moisture regime D (stand W58). The 1961 rainfall histogram for the precipitation station located 3/4 mile to the NE is also shown.

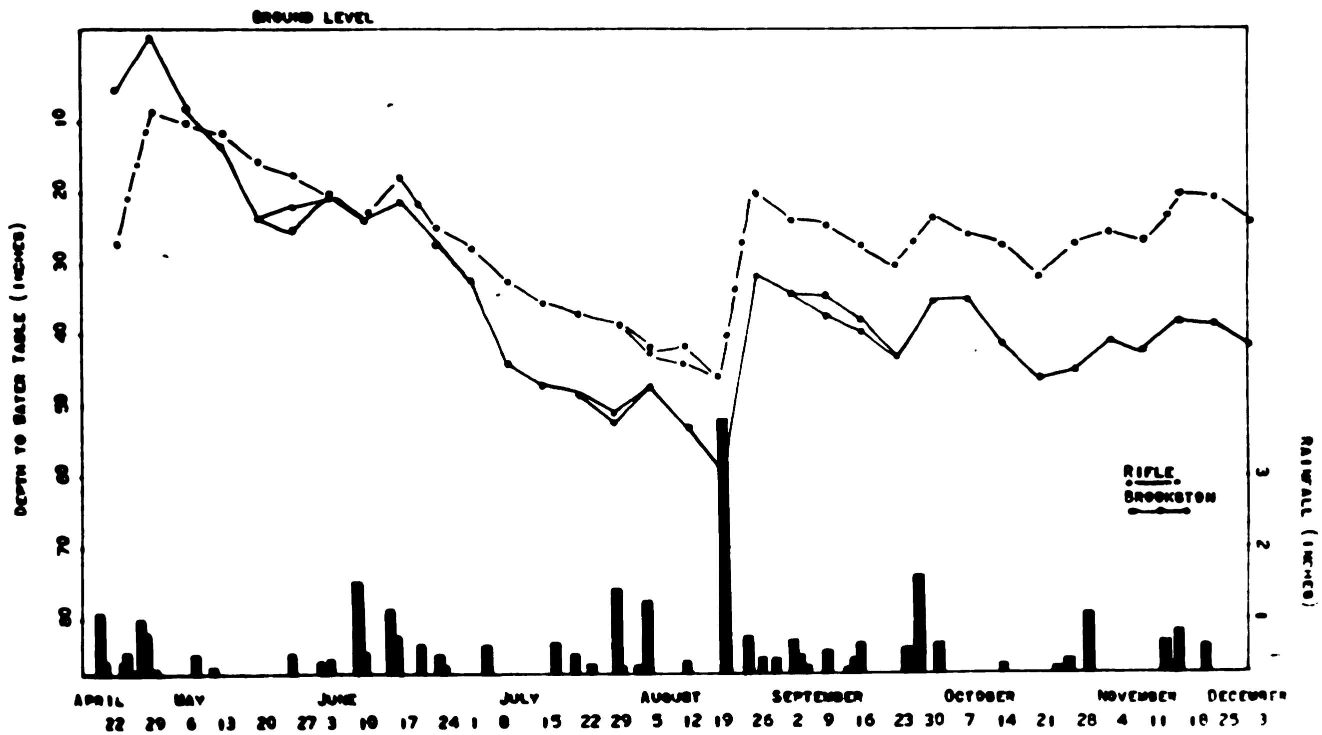

Fig 23. Hydrographs of true and perched water tables in moisture regime E (stands M26B and M26R). The 1961 rainfall histogram for the precipitation station located three miles to the NW is also shown.

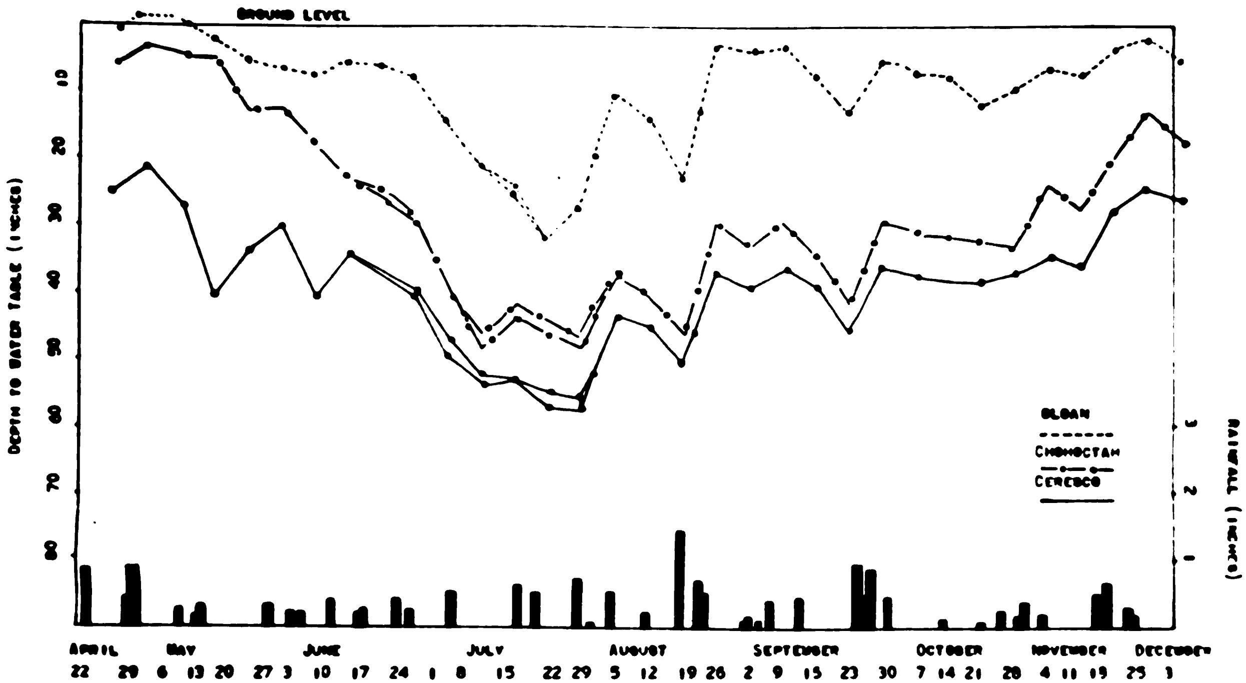

Fig. 24. Hydrographs of true and perched water tables in moisture regime F (stands M22S and M17C). The 1961 rainfall histogram for the precipitation station located 3/4 mile SW is also shown.

A review of the contour elevations for the Deer, Sloan, and Sycamore Creek watersheds, and an evaluation of the hydrographs revealed that the water tables under investigation were being influenced by at least six different recharge patterns.

The relative position of the water table for any period of the year in these stands is obviously being governed by the amount of runoff and unconfined seepage which occurs. This in turn is determined by contour elevations, drainage outlets, permeability of the lower subsoils, glacial drift mantle, and underlying rock formations. In this respect it was practically impossible to evaluate losses due to these factors, since the discharge patterns in these stands were not monitored hydrologically. The hydrographs for the current year, however, can be consider representative of water table conditions and changes for lowland soils which have existed for a considerable period of time. This in itself is evident in the age of the stands located on such areas.

Spring water tables were at the highest level in all soils during the second week of the study. Saturated soil conditions immediately after the spring thaw, the lack of transpirational draft, and the amount of rainfall which occurred prior to this time were contributing factors producing high water table regimes.

A general lowering of the water tables occurred in all stands, except those located on alluvial soils, during the period from April 29 to August 19. Water tables in the alluvial alpha and beta-gley soils were being influenced during this period by the rise and fall of the Red Cedar River, which drains all basins in which the stands are located.

Minor fluctuations (1-10 inches) caused by precipitation from Class 2 uniform storms (Smith and Crabb (137)), affected the position of spring and summer water tables in all stands during the same period. Several Class 4 advanced storms occurred during the month of June with little effect on most water tables, except those of the poorly or very poorly drained Sebewa, Gilford, Brookston, and Pewamo soils (stands W4S and W5B). Most of these storms produced a total rainfall of less than one inch, which apparently was not sufficient to satisfy the total interception loss plus existing soil moisture deficits in the profiles.

Maximum depths of water tables occurred in most stands during the last two weeks of July and the first two weeks of August. Mean depths recorded were greatest in the Conover, Locke, and Spinks soils (stands A14C, M19L and M19S). Maximum fluctuations in water table levels occurred in the latter stands throught the growing season. However, a comparable amount of fluctuation was observed in the Sebewa and Gilford soils of stand W4S. The Ceresco soils, one of the alluvial beta-gleys, had a shallower depth to the mean water table than several of the alpha-gley soils.

Water tables throughout the growing season fluctuated least and were most frequently within ten (10) inches of the surface in organic soils. This was especially true for Linnwood muck (stand L10L) and Carlisle muck. The other Linnwood muck (stand A14L) and the Rifle peat, however, had deeper water tables on the average than the Pewamo soils, Gilford soils (stand L10G), and the alluvial Sloan soils.

Even though the growing season during which the study was made was one of the driest in 21 years (Figure 25), ending with a minus 3.73 inches deficit in rainfall, it appears that some Class 6 and 4 advanced storms were of sufficient intensity and duration to produce some recharge of the phreatic water tables.[1] Storms of these two classes, normally producing

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[1]See Table 1, total departure from normal rainfall.

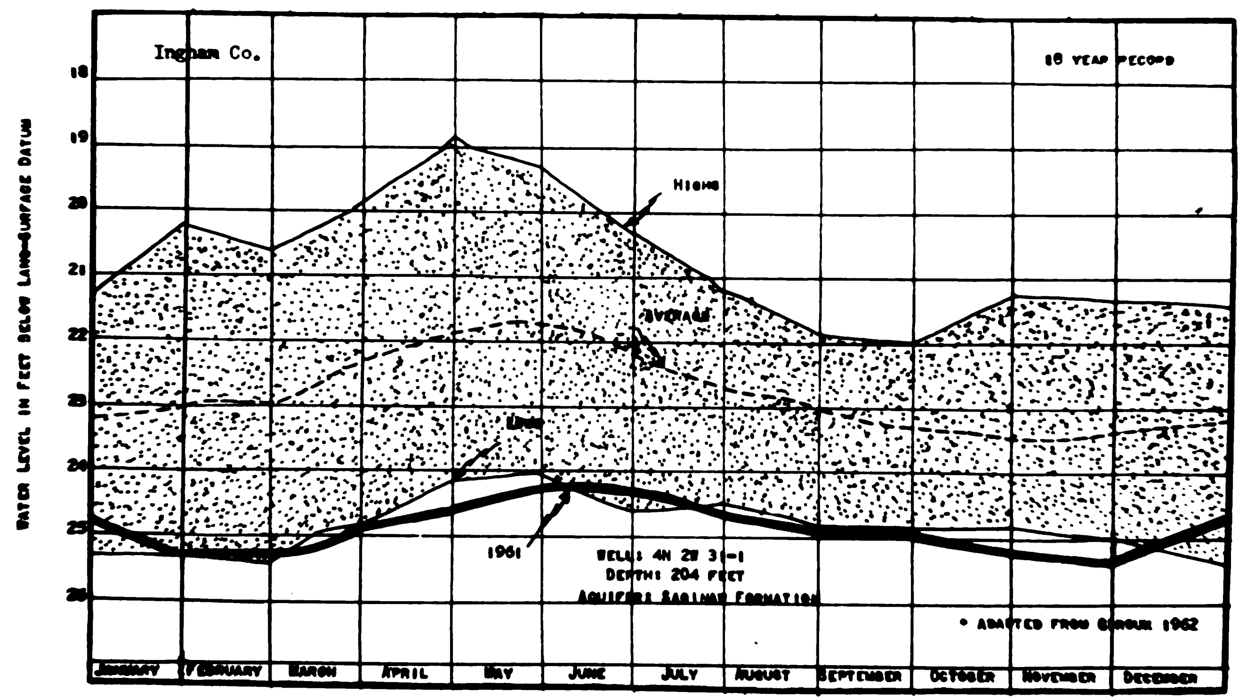

Fig. 25 . An 18-year record of mean water levels for the only observation well in the Lansing area glacial drift. Note that the 1961 water level in this well established a new record low during the entire growing season, except for the period from mid-June until mid-July.

rainfall intensities exceeding .5 or .7 inches per hour, respectively, will produce a partial recharge of subsurface waters in lowland hardwood stands.

Regardless of whether or not the soil was an alpha-gley or beta-gley, recharge of the phreatic water tables occurred quite soon; a matter of several hours after a convectional storm of these intensities. The duration of storms of these classes must necessarily be longer than an hour. Such rapid recharging of the water tables could not be attributed to flow of water into the well aperture, since proper precautions were taken to prevent errors of this type, In addition, a vist to the well locations immediately after several storms of these classes did not show disturbances around the well openings due to runoff.

It was surmised that this situation was not brought about by saturation of the soil profiles immediately above the water tables at any given point, since some of the tables were 80 to 100 inches deep at the time that rapid recharge took place. On some of the poorly or very poorly drained sites direct recharge was probable. However, the evidence in the present study . gathered from numerous observations, indicates that recharge of the phreatic surface may result from gradient flowage. This would be dependent upon the slope of the underlying strata and the permeability of these materials. The upward movement of water tables in these low areas, however, does not necessarily mean recharge from gradient flowage. If the water table is in a steady state relationship with gradient flow from above and local evapotranspiration, any reduction in the intensity of evapotranspiration (in situ) would reduce the drain on the local ground water. Further, a reduction of evapotranspiration upwatershed would increase the gradient flow and a rise in water table level would occur.

A strong recharge pattern began in the third week of August, 1961, after a Class 6 advanced storm which registered 3.56 inches of rainfall at one of the recording stations. The total rainfall from this storm at the gauges of the other stations were 2.[illegible]0, 1.48, and .96 inches. Gradual recharge of the ground water continued after this storm in most soils for the remainder of the growing season. Two exceptions were noted in the Locke and Spinks soils. These two soils, during the third week of August, had water tables 80 to 100 inches deep at the time this storm occurred. After this period, their water tables continued to drop until the third week of October when recharge to the surface began.

At the termination of the study on December 3, only the water tables in mucks and alpha-gley soils of stands V20C, L10L, L10C, and W4S were fully recharged. The Brookston soils (stand W53) and the Locke and Spinks soils (stand M19L and M19S), were considerably different, being 26, 35, and 67 inches respectively below the measurements taken the first week of the growing season. All other water tables were within three to sixteen inches of the level observed when the study was first initiated.

Ground Water and Species Development

Depression storage from precipitation, or a rise in the ground water table from beneath during the winter season and early spring, usually reaches a sufficient depth to preclude the survival of all young plant growth. This condition was evident not only on floodplain soils, but also on several of the lacustrine soils. Therefore, the current vegetation of several lowland stands was subjected to a natural annual disturbance. Only during those seasons which would be fairly but not uncommonly dry, could woody and herbaceous species develop sufficient root systems and shoot growth to survive the effects of seasonal flooding.

Of the dominant tree species which appeared throughout the lowland stands in the county only four: siver maple, red maple, sugar maple, and basswood showed a tendency to be associated with rapid changes in water table levels.

Silver Maple.--The occurrence of silver maple along small streams and on soils proximate to major streams has been reported extensively (124,150,16[illegible]). The reproduction of this species is very pronounced on bare mineral soil alongside such waterways (124). This condition was apparent on the floodplain soils of Ingham County, where the reproduction was abundant but segregated into groups. Little competition was present from other plants, and the distributional pattern of the reproduction appeared to be associated with overflow depth from the Red Cedar River (Figure 26).

In reviewing the apportionment of basal area for the canopy members within all stands, it would appear that a relationship existed between the development of silver maple and the rapidity with which drainage occurs. This was apparent not only for floodplain soils but also lacustrine soils. Among floodplain soils all, except the Sloan soils, exhibited the maximum variation

Fig. 26 . A layer of silver maple (Acer saccharinum) seedlings on the Cohoctah sandy loam of stand M17C. The mean water table depth at this stage of seedling development was 47 inches. This particular spot will be completely innundated during the winter months to a depth of 18 inches. The tall seedling at the left will probably survive the effects of backwater overflow to this depth.

in water table depth and fluctuation. The development of silver maple on Sebewa sandy loam and those Linnwood mucks of similar hydrologic characteristics also support this contention.

Red Maple.--Of interest was the conspicuous absence of all but seedlings of red maple on the fast draining alluvial soils. The lack of this species on soils of floodplain origin could not be attributed to variations in soil texture. It appeared that the occurrence of this species was somewhat sensitive to alluvial sites which drain rapidly after flooding.

American Basswood.--American basswood appeared to possess a wider ecological amplitude than sugar maple on lacustrine soils where the drainage was poor. Possibly, catenal positions of the soils on which it was found was more important in influencing the presence of basswood than their textural attributes. The presence of large individual specimens of basswood in the lowlands of the county could be a stand-age-structure relationship associated with the interval in time since these stands first became established.

Understory Vegetation and Ground Flora in Lowland Hardwoods.

The woody and herbaceous understory vegetation, tallied during the collection of tree data, attained various degrees of importance along a gradient of changing moisture conditions. The species in most lowland hardwood stands showed considerable variation in density within stands, as well as between stands. Although a considerable number of medium and low shrubs were recorded on soils of the beta-gley type, the opposite condition was apparent on the more poorly drained alpha-gley and organic soils.

Open areas on Rifle peats showed the greatest development of high and medium shrubs, including highbush blueberry (Vaccinium corymbosum), red osier (Cornus stolonifera), and small cranberry (Vaccinium Oxycocos).[1] In these large openings, herbaceous plants were mostly representative of the Composite family, especially goldenrods. Where tree shade was present, shrub development was absent or greatly curtailed.

On the other organic soils of the Linnwood and Carlisle series the cover of understory vegetation was discontinuous. Possibly, this condition was due to the controlling influence of dominant canopy species allowing little light to reach the forest floor. Moreover, the phreatic water tables in these soils often flood the soil surface or remain close to it during the major part of the growing season. Such a combination of factors is obviously not favorable to the ecesis of most perennial shrubs. The principal shrubs present, however, included strawberry bush, (Euonymus obovatus), wild black currant (Ribes americanum), and winterberry (Ilex verticillata).

In many situations the ground layer of plants was complete. The leading species present for the very wet segment on lowland organic soils were: pale touch-me-not, a seasonal indicator of disturbance by flooding;

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[1] Subsequent listings in decreasing order of frequency.

stinging and wood nettles, sweet scented bedstraw, bog hemp, and quicksilver weed. Of lesser importance in frequency and density were the ferns: sensitive fern, spinulose shield fern cinnamon fern and royal fern.

Herbaceous plants of lesser frequencies included: black snakeroot, miterwort, and fowl-meadow grass. Of interest was the appearance in spring of pitcher plant (Sarrancenia purpurea) on shallow circumneutral mucks.

The numbers of understory saplings, seedlings, shrubs, and the development of the ground flora, ranged from one extreme to the other on alpha-gley soils. The frequency as well as density values for tree species of size class two is shown in Tables 11 and 12.[1] It appeared that frequency and density of saplings increased as drainage conditions became better. The peak in frequency and ensity, as well as variety of sapling tree species, was found on soils of the Brookston series.

On some of these soils, few shrubs and very little herbaceous undergrowth was present, while others contained an abundance of species. Such differences might be attributed to the effects of seasonal flooding which prevented the survival of many herbaceous and woody plants. The main seedling species present on mineral soils of the Brookston, Sebewa, Pewamo, and Gilford series were: sugar maple, slippery elm, green ash, red maple, and black cherry. The major shrubs and vines included green osier (Cornus alternifolia), gray dogwood (Cornus racemosa) shadbush (Amelanchier aborea), common elder, (Sambucus canadensis), maple-leaved viburnum (Virburnum acerifolium), woodbine (Parthenocissus quinquefolia), poison ivy (Rhus radicans), and winterberry.

Amon the herbaceous plants, sweet cicely, honewort, purple meadow rue, sweet-scented bedstraw, black snakeroot, quicksilver weed, pale

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[1]Saplings 1.1 to 4.0 inches d.b.h.

TABLE 11 . Species frequencies in 19 lowland-hardwood stands in Ingham County based on saplings 1.1 to 4 inches in diameter.[a]

Species[b] / Stand	O26P	W4S	M26R	M22S	M17C	M26B	W4B	W20C	S23B	L10L	A14L	W5B	L10G	A14B	O3L	A14C	W5C	M19S	M19L
	percent																		
Acer saccharum	--	--	--	--	--	--	10	--	--	--	--	10	--	30	--	20	30	40	50
Fagus grandifolia	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	10	20	10	30
Tilia americana	--	[illegible]	--	--	--	--	10	--	--	[illegible]	--	--	10	--	--	10	--	--	20
Ostrya virginiana	--	--	--	--	--	--	20	--	10	--	--	--	10	20	--	--	20	20	20
Carpinus caroliniana	--	--	--	--	--	--	10	--	--	--	--	10	30	--	--	10	--	--	20
Carya cordiformis	--	--	--	--	10	--	--	--	--	--	--	--	--	--	--	10	--	10	20
Ulmus americana	--	--	--	--	--	[illegible]	10	20	10	20	10	--	--	10	10	--	10	--	--
Acer rubrum	--	30	20	--	10	20	--	--	20	10	10	--	--	20	10	10	--	--	10
Quercus rubra	--	--	--	--	--	50	--	--	--	--	--	--	--	10	--	--	--	--	10
Nyssa sylvatica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fraxinus americana	--	--	--	--	--	10	--	--	--	--	--	--	--	10	--	--	--	--	10
Quercus alba	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ulmus rubra	--	20	10	10	20	--	10	--	20	10	10	--	--	20	--	10	10	--	--
Carya ovata	--	20	--	--	--	10	10	--	10	--	--	--	--	--	--	--	--	--	--
Carya ovalis	--	--	--	--	--	--	10	--	--	--	--	--	--	--	--	--	--	--	--
Fraxinus pennsylvanica	--	--	--	10	20	20	20	30	20	50	10	--	20	--	10	20	10	20	20
Quercus bicolor	--	10	--	--	--	--	20	10	20	10	--	10	30	10	20	--	10	10	--
Prunus serotina	10	--	10	--	--	30	--	--	--	--	--	10	--	--	--	10	20	--	--
Acer saccarinum	--	--	--	10	30	--	--	--	--	20	--	10	--	--	--	10	10	--	--
Celtis occidentalis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Crataegus spp.	--	--	--	--	--	10	--	--	--	--	--	10	--	--	--	10	--	--	--
Platanus occidentalis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sassafras albidum	--	--	--	--	--	10	--	--	--	--	--	--	--	--	--	--	--	--	--
Fraxinus nigra	--	--	--	--	--	--	--	--	--	--	--	10	--	--	--	--	--	--	--
Populus deltoides	--	--	--	--	--	--	--	--	--	--	--	--	--	10	--	--	--	--	--
Larix laricinia	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Salix nigra	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Betula X purpusii	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Populus tremuloides	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
others	--	10	10	--	--	--	--	--	--	--	--	10	--	--	--	--	--	--	10
total	10	100	50	30	90	190	130	60	110	140	40	80	100	140	50	130	140	110	220

[a] stands arranged in ascending order in continuum

[b] species arranged in descending order of climax-adaptation numbers

TABLE.- 12. Species density in 19 lowland-hardwood stands in Ingham County based on saplings 1.1 to 4 inches in diameter.[a]

Species[b] / Stand	O26R	W4S	M26R	M22S	M17C	M26B	W4B	V20C	S23B	L10L	A14L	W5B	L10G	A14B	O3L	A14C	W5C	M19S	M19L
	--------	--------	--------	--------	--------	--------	--------	--------	number	--------	--------	--------	--------	--------	--------	--------	--------	--------	--------
Acer saccharum	--	--	--	--	--	--	17	--	--	--	--	[illegible]	--	23	--	10	29	64	28
Fagus grandifolia	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3	9	4	20
Tilia americana	--	15	--	--	--	--	4	--	--	[illegible]	--	--	5	--	--	7	--	--	6
Ostrya virginiana	--	--	--	--	--	--	8	--	19	--	--	--	20	9	--	--	--	9	9
Carpinus caroliniana	--	--	--	--	--	--	4	--	--	--	--	11	35	--	--	10	--	--	9
Carya cordiformis	--	--	--	--	6	--	--	--	--	--	--	--	--	--	--	7	--	4	6
Ulmus americana	--	--	--	--	--	12	4	33	12	11	10	--	--	4	25	--	5	--	--
Acer rubrum	--	31	27	--	8	9	--	--	19	8	50	--	--	7	12	3	--	--	3
Quercus rubra	--	--	--	--	--	26	--	--	--	--	--	--	--	4	--	--	--	--	3
Nyssa sylvatica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fraxinus americana	--	--	--	--	--	7	--	--	--	--	--	--	--	4	--	--	--	--	--
Quercus alba	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ulmus rubra	--	15	27	7	12	--	12	--	12	12	8	--	--	20	--	32	13	--	--
Carya ovata	--	8	--	--	--	2	12	--	6	--	--	--	--	--	--	--	--	--	--
Carya ovalis	--	--	--	--	--	--	4	--	--	--	--	--	--	--	--	--	--	--	--
Fraxinus pennsylvanica	--	--	--	27	38	7	12	50	12	30	20	--	15	--	12	20	9	9	9
Quercus bicolor	--	8	--	--	--	--	8	17	12	8	--	11	15	4	37	--	5	4	--
Prunus serotina	10	--	7	--	--	19	--	--	--	--	--	11	--	--	--	3	9	--	--
Acer saccharinum	--	--	--	53	31	--	--	--	--	2	--	11	--	--	--	1	5	--	--
Celtis occidentalis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Crataegus spp.	--	--	--	--	--	2	--	--	--	--	--	--	--	--	--	--	--	--	--
Platanus occidentalis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sassafras albidum	--	--	--	--	--	12	--	--	--	--	--	--	--	--	--	--	--	--	--
Fraxinus nigra	--	--	--	--	--	--	--	--	--	--	--	5	--	--	--	--	--	--	--
Populus deltoides	--	--	--	--	--	--	--	--	--	--	--	--	--	4	--	--	--	--	--
Larix laricina	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Salix nigra	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Betula X purpusii	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Populus tremuloides	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
others	--	19	2	--	--	--	--	--	--	--	--	11	--	--	--	--	--	--	--
total/1.9 hectares	10	96	63	87	95	96	85	100	92	86	88	85	90	79	86	96	84	94	93

[a] Stands arranged in ascending order in continuum

[b] Species arranged in descending order of climax-adaptation numbers

touch-me-not, and cinquefoil were quite common. Some rather infrequent plants included: white baneberry, mandrake, anise root, miterwort, Indian turnip, pretty bedstraw, and the true and false Solomon's seals. Sensitive fern was the most common pteridophyte on these soils.

Alpha-gley soils of floodplain origin, exhibited a broken mosaic of groundcover. Within this patchwork, in addition to some of the plants previously mentioned, a variety of species was present. Silver maple, slippery elm and green ash were the main seedling species. Along the margins of permanently wet depressions buttonbush (Cephalanthus occidentalis) was a common shrub. Other shrubs and vines included wild black current, prickley gooseberry (Ribes cynosbati), woodbine, poison ivy, and frost grape (Vitis riparia).

Of common occurrence in the ground flora were such plants as bugleweed, tufted loosestrife, wild ginger, bog hemp, stinging nettles, arrow-leaved aster, and swamp milkweed. Rather uncommon were bottlebrush grass and Cardinal flower.

Under conditions of better aeration and drainage, the most abundant herbaceous plants were: bloodroot or red puccoon, spotted cranesbill, and swamp buttercup.

Understory plants on the soils of mid-gley development, not subject to the effects of streamside innundation, showed an increase in numbers as well as dispersion of ground cover species. Of interest was the abundance of dog's tooth violet and spring beauty in the springtime. With the gradual disappearance of these species in the very late weeks of spring, the wake-robin or large flowered trillium becomes quite conspicuous, together with scattered colonies of mandrake.

Other herbaceous species common to the beta-gley soils of the wet-mesic environment included: sweet cicely, spotted cranesbill, sweet-scented bedstraw, several species of violets, including downy blue violet, black snakeroot, cinquefoil, wild ginger, horse-balm, wild leek, white avens, bloodroot, the spikenards, true and false Solomon's seals, blue-stem goldenrod, bellwort, blue cohosh, and lopseed.

Shrubs and vines of rather common occurrence on these soils included: strawberry bush, common elder, shadbush, woodbine, poison ivy, the currants and gooseberries, green osier, sweet viburnum (*Viburnum Lentago*), and button-bush.

A complete list of the lesser species found in lowland-hardwood stands indicating changes in species importance along a gradient of changing moisture conditions is shown in Table 13.

TABLE -13 A species list of the ground flora common to the lowland hardwood stands of Ingham County showing the degree of importance attained by each species.

Species	Very wet Organic soils	Wet Alpha-gley soils	Wet-mesic Beta-gley soils[b]
	Soils and moisture regime[a]		
	number		
Actaea pachypoda	-	1	2
Actaea rubra	-	0	-
Allium canadense	-	0	-
Allium tricoccum	-	1	3
Anemone canadensis	-	2	-
Aralia racemosa	-	0	-
Arisaema atrorubens	-	1	1
Asarum canadense	-	4	3
Asclepias incarnata	-	3	-
Aster sagittifolius	[illegible]	3	-
Boehmeria cylindrica	3	5	3
Cardamine pratensis	2	-	-
Caulophyllum thalictroides	-	-	3
Collinsonia canadensis	-	-	3
Cicuta maculata	-	3	-
Cryptotaenia canadensis	-	3	2
Erythronium americanum	-	-	5
Galium concinnum	-	2	1
Galium triflorum	4	4	2
Geranium maculatum	-	3	4
Geum canadense	-	2	3
Glyceria striata	3	3	-
Hystrix patula	2	2	1
Impatiens capensis	2	1	-
Impatiens pallida	5	2	-
Lobelia cardinalis	-	0	-
Lycopus americanus	-	3	-
Lysimachia thyrsiflora	-	3	-
Lysimachia ciliata	-	2	-
Lysimachia quadrifolia	-	2	-
Lythrum salicaria	-	0	-
Mitella diphylla	3	3	-
Nasturtium officinale	2	-	-
Osmorhiza Claytoni	[illegible]	3	4
Osmorhiza longistylis	-	2	1
Phryma longistylis	-	0	2
Podophyllum peltatum	-	2	3

TABLE.-13.. continued

Potentilla palustris	2	1	-
Potentilla recta	-	3	3
Polygonum natans	2	-	-
Polygonatum caniculatum	-	2	2
Ranunculus recurvatus	-	2	3
Ranunculus septentrionalis	-	3	-
Sanguinaria canadensis	-	2	4
Sanicula gregaria	-	1	2
Sanicula marilandica	3	4	4
Smilacina racemosa	-	3	4
Smilacina stellata	-	2	3
Sarracenia purpurea	2	-	-
Solidago caesia	-	3	3
Sodidago graminifolia	4	-	-
Thalictrum dasycarpum	-	2	3
Thalictrum dioicum	-	3	3
Urtica gracilis	3	4	-
Urticastrum divaricatum	5	4	-
Uvularia grandiflora	-	2	2
Viola sororia	-	2	3
Viola spp.	-	2	3
<u>Pteridophytes</u>			
Adiantum pedatum	-	-	3
Dryopteris spinulosa	3	4	-
Equisetum Hymale	-	-	3
Onoclea sensibilis	4	4	-
Osmunda cinnamonea	4	2	-
Osmunda regalis	3	-	-

[a]arranged according to a gradient of decreasing moisture.
[b]numbers refer to the following scale of occurrence.

0-present
1-scarce
2-uncommon
3-infrequent
4-common
5-very common

Biotic Factors and Their Effects on Community Structure

Evidence of the destruction of natural vegetation by biotic influences is visible thoughout the Lake States region. Ravages caused by insects, diseases, fires, animals, and especially man has seriously altered natural succession in many types of vegetation. These changes, principally by man, were most evident during the early days of logging.

Fire Influences.--The role of fire as a factor in the ecology of lowland hardwood forests in Ingham County has been of little consequence in determining its vegetation. Although extensive fires have played an important part in forest succession, evident in the record for the state's fire history, fires of natural origin in this county have been more or less confined to upland sites. Lowland hardwood forests probably escaped the clear cutting practices that prevailed in the coniferous and hardwood forests of upland sites and the ensuing fires that took place after such devastation. On occasion, fires have occurred on the sparsely forested deep peat soils of the county during periods of extremly dry weather. For the most part, however, the destruction of these primarily deciduous lowland forests by fire would indeed be a rare event since the ground water is so close to the soil surface.

Although the soils of most lowland stands are not permanently saturated with ground water, the extent of the capillary fringe above the phreatic surface serves to keep most lowlands from reaching a highly combustible state. Moreover, periodic saturation of the soil profiles by convectional storms and resultant ground water fluctuations occurs often enough and with sufficient magnitude to effectively reduce the likelihood of serious fires.

During the ten-month period that the ground water study was being conducted, the route of the survey was tantamount to a series of random road counts used often in wildlife studies. Although debris burning on land being cleared was seen rather frequently, not a single wildfire was observed in the lowland hardwood land type for the entire year.

From the voluminous literature concerning the effects of forest fires on soils and living organisms, very few studies have reviewed the effects of post-fire succession on lowland soils (2,31,32,108,136). The majority of references on this subject have discussed the use of fire as a silvicultural tool in the management of coniferous forest stands. The practice of setting fires by the indigenous tribes of Indians for purposes of communication or hunting game was never mentioned in the early history of Ingham County (63). It is not here inferred, however, that fires of low intensity have never occurred. On fallow and ungrazed land, where herbaceous vegetation continually adds to the bulk of potential fuel, the probability of fires whatever the cause is enhanced (Figure 27).

Buell and Borman (31) found that paper birch stands sometimes directly reseed to a mesic species such as basswood. Quaking aspen, black cherry, and northern prickly ash (*Zanthoxylum americanum*), however, are the most likely species to reseed lowland soils in Ingham County following fires. (Figure 28). Quaking aspen, however, is not necessarily linked to post-fire sucession. In this study it was most prevalent on Rifle peats, which showed no evidence of a prior fire history. Likewise, its presence on mineral soils in the study area appeared to be correlated with natural disturbance factors, especially windthrow of other species.

Windthrow, Rooting Systems and Community Structure.--The importance of root systems and their development, as a prime factor affecting species density and eventually stand composition in lowland forests, has been largely ignored in past ecological studies. The tremendous amount of labor and time involved in the excavation of large root systems, not to mention the difficulty of identification while keeping smaller roots intact,

Fig. 27. A fire scar gives mute testimony to the fact that this area was swept by a low intensity fire ten years previously. Such man made objects not only give proof of fire occurrence, but the fire may be dated by the landowner. In addition, fences act as systematic detectors to the occurrence of fires over large land areas. No evidence of this fire having occurred was apparent from examining the soil surface.

Fig. 28. A young stand of quaking aspen (Populus tremuloides) on the alpha-gley Sebewa loam adjacent to stand W4S. Note the presence of bur oak (Quercus macrocarpa) and northern prickly ash (Zanthoxylum americanum) . This stand resulted from the fire, which swept through the area indicated by the previous photograph.

constitutes a major problem. The majority of root system stratification and development studies on hydromorphic soils has been devoted to seedlings or shrublike plants (10,12,56,152). Nevertheless, a reasonable degree of confidence on probable root system extension may be established by observing the rooting habit on windthrown trees and trees with partially exposed root systems.

While the soils of lacustrine forests in this county are not affected by the homogenizing effects of floodwaters as in floodplain stands, windthrow as a mortality factor serves to influence stand-age-structure during later stages of succession.

This condition is most evident in stands found on organic soils. The loose consolidation of granular or peaty materials was not only subject to being blown away from the forest floor by unusually high winds, but a collapse of the organic matter has occurred with the passage of time (Figure 29). The extensive system of storm drainage outlets installed in Ingham County over the past 20 years may be partially responsible for this collapse. Alternate wetting and drying within the soil profiles, from precipitation and fluctuating water tables, however, also produces this result. Eventually the supporting medium for larger trees is weakened. Moreover, a periodic re-assortment and deposition of lighter materials caused by wind and wave action occurs when the stands are flooded. In many cases, the major portion of the anchor roots of dominant species are partially or almost completely exposed. Root growth, however, probably keeps pace unless decline of the water table is rapid.

During the earlier stages of succession, cottonwood plays an important part in lowland stands. Because of its perpendicular taproot or heartroot development, this species is better able to gain a foothold on sites having substantial fluctuation in ground water levels. On the other hand.

Fig. 29. A silver maple (Acer saccharinum) located on the deep Carlisle muck of stand V20C. The system of anchor roots is almost completely exposed, due to collapse of the supporting materials and periodic washing from the floodwaters of Sycamore creek. Windthrow on these sites is a noteworthy factor contributing to the mortality of the leading dominants.

black willow is confined to those depressional areas which remain more or less permanently wet. Because of the plate-like development of the root system in the latter species, withering of the fibrous root system is common. Black willow is soon replaced by cottonwood, especially after a series of droughty seasons.

The plate-shaped development of the root system characteristic of certain lowland tree species, such as red and silver maple, also contributes to the seriousness of windthrow on organic as well as mineral soils. The system of heartroot development in swamp white oak and American elm is somewhat flattened on soils with shallow water tables. Windthrow does not seem to be of serious consequence, however, inhibiting the eventual dominance of these two species. American elm seems to possess great stability on such sites, due to its widespread and fluted rooting habit as shown in Figure 30.

The rooting system of green ash appears to be intermediate between the strongly flattened heartroots of the maples and the deeper penetrating systems of other species such as elms and oaks. The mortality of this species in lowland hardwood stands was quite noticeable although this condition could not altogether be attributed to windthrow. Green ash, a prolific seeder, easily becomes established in small openings created by the windfall of other species. The resultant closure of adjoining canopy species around such openings acts as the main factor in later eliminating this species from most stands.

A summary of the mortality for the major and minor tree species recorded by the plot method is shown in Table 14. As indicated in the table, green ash is quite frequently represented. However, most of the mortality for this species occurring in the four to eight inch diameter classes was related to canopy closure. The mortality values for quaking aspen and black willow were also related to stand closure. Windthrow,

Fig. 30. An American elm (Ulmus americana) growing on the Pewamo loam of stand W4B. Notice the fluted arrangement of the anchor roots. This is partially due to wind and wave action on the mineral materials surrounding the base of the root system, during the winter season.

TABLE.- 14 . Species mortality (basal area) in 19 lowland-hardwood stands in Ingham County.[a]

Species[b] Stand	O26R	W4S	M26R	M22S	M17C	M26B	W4B	V20C	S32B	L10L	A14L	W5B	L10C	A14C	W5C	M19S	M19L		
	-----square feet-----																		
Acer saccharum	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fagus grandifolia	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Tilia americana	--	--	--	4	3	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ostrya virginiana	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Carya cordiformis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ulmus americana	--	--	--	--	22	--	--	--	8	--	1	11	3	4	4	12	1	--	--
Acer rubrum	--	--	--	--	--	--	--	--	--	1	1	--	3	--	--	--	--	--	--
Quercus rubra	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Nyssa sylvatica	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fraxinus americana	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Quercus alba	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ulmus rubra	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Carya ovalis	--	--	--	--	--	--	3	--	--	--	--	--	--	--	--	--	--	--	--
Carya ovalis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fraxinus pennsylvanica	--	--	--	5	--	--	--	--	--	--	--	2	--	1	--	--	1	--	--
Quercus bicolor	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Prunus serotina	--	--	--	--	--	--	--	--	4	--	--	--	--	--	--	--	--	--	--
Acer saccharinum	--	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Celtis occidentalis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Crataegus spp.	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Platanus occidentalis	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sassafras albidum	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fraxinus nigra	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--	--	--	--
Populus deltoides	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Larix laricina	--	--	--	--	--	--	--	--	--	--	1	--	--	--	--	--	--	--	--
Salix nigra	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Betula X purpusii	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Populus tremuloides	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	--	--	--	--
others	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
total	--	1	--	9	26	--	3	--	12	1	3	13	8	5	6	12	2	--	--

[a]stands arranged in ascending order in continuum

[b]species arranged in descending order of climax-adaptation numbers

however, was the major factor causing mortality for the maples and black cherry, especially on organic soils.

<u>Pathogenic Influences and Community Structure</u>.-- Of all the species recorded in the study, American elm had the highest mortality rate. Over 95 percent of the mortality for this important lowland hardwood appeared to be attributable to the Dutch elm fungus (<u>Ceratostomella ulmi</u> (Schwartz) Busiman). The spores of this fungus are carried to the trees by the elm bark beetles (<u>Hylurgopinus rufipes</u> (Eichh.) and (<u>Scolytus multistriatus</u> Marsh.). It was not unusual to find some of the finest, largest specimens of American elm suffering from the ravages of this disease. No size class appeared to be immune, but total mortality was more evident in clustered groups of trees smaller than ten inches in diameter.

The number of dead or dying trees appeared to be highest along the periphery of most stands on organic as well as mineral soils. Moreover, the incidence of attack was practically complete where American elm had attained dominance at the edges of stands. Within most stands, however, the number of trees being attacked was low, and the prevalence of the disease seemed to increase with a corresponding decrease in stand density. Isolated groups and individual trees in open fields or along fence rows were almost always dead or in the process of dying at the time of the survey.

Since no cheap effective control has as yet been developed to combat this disease in natural stands, it would appear that an extremely high loss of American elm is to be anticipated in the lowland hardwood land type. Although American elm has low commercial value at the present time, the importance of this species as a stand component of considerable worth cannot be ignored. Should the disease continue to extend its influence in geometric proportions, American elm may soon become a rather infrequent species.

The vacancies created by the loss of this species at the present time are most likely to be filled by increasing amounts of green ash and swamp white oak on mineral soils. On organic soils and in the later stages of succession red maple is the most likely species to fill the void, replacing green ash and to some extent swamp white oak. The loss of American elm on wet-mesic sites, where it decreases in frequency as well as density, is not as great a loss to the character of lowland stands as on the very wet to wet areas where it is strongly dominant.

Statistics

Correlations between sampling methods.-- In order to determine the relative reliability of the various sampling methods, simple correlations were calculated between three parameters (basal area, density, and frequency) as determined from each of the sampling methods. These calculations involved all possible combinations among the 12 parameter-method measurements. The means for 23 species were used as items.

The correlation coefficients (= r) are presented in Table 15. The coefficients of determination (= r^2), which provide better estimates of the information provided by one method relative to another, are presented in Table 16.

The smallest coefficient of determination between any two methods used to determine relative basal area of different species was.95. This was for the comparison between the random pairs and the full Bitterlich methods. In effect, such a value means that the random pairs method gave 95 percent as much information about the Bitterlich-determined basal areas as did the Bitterlich method. The coefficients of determination were all .97 when basal areas determined by the plot method were compared with those determined by any of the other three methods.

Similarly , any of the four sampling methods gave 96 to 98 percent as much information about relative density of the 23 species as did the best method. And each method gave 95 to 98 percent as much information about relative frequency as did sampling of ten 5 x 20-meter plots in each stand.

The coefficients of determination between relative density and relative frequency were also high, all being greater than .92. Thus, by whatever method determined, the data on density gave 92 to 99 percent as much information about frequency as did a direct determination of frequency. The coefficients of determination between basal area and the other two parameters were lower -- between .84 and .95 for density and between .87 and .92 for frequency.

TABLE.- 15 . Correlations between species' basal area, frequency, and density as measured by four sampling methods.[a]

Parameter	Method	Basal area as measured by ----method----				Density as measured by ----method----				Frequency as measured by ----method----		
		random pairs	quarter	Bitterlich	plot	random pairs	quarter	Bitterlich	plot	random pairs	quarter	Biterlich
Basal area	quarter method	.98										
" "	Bitterlich method	.97	.99									
" "	plot method	.98	.98	.98								
Density	random pairs method	.94	.96	.95	.95							
"	quarter method	.92	.96	.94	.93	.99						
"	Bitterlich method	.94	.98	.97	.95	.98	.92					
"	plot method	.92	.96	.94	.94	.98	.98	.99				
Frequency	random pairs method	.94	.96	.94	.95	.99	.98	.97	.98			
"	quarter method	.93	.96	.93	.93	.99	.99	.98	.98	.99		
"	Bitterlich method	.95	.96	.93	.94	.97	.97	.97	.96	.98	.99	
"	plot method	.94	.96	.95	.94	.99	.98	.98	.98	.99	.99	.98

a All correlations were greater than the value of r= .641 needed for significance at the .01 level with 21 degrees of freedom.

TABLE.- 16. Coefficients of determination (r^2) for species' basal area, frequency, and density as measured by four sampling methods.

Parameter	Method	Basal area as measured by ----method----				Density as measured by ----method----				Frequency as measured by ----method----			
		random pairs	quarter	Bitterlich	plot	random pairs	quarter	Bitterlich	plot	random pairs	quarter	Bitterlich	plot
Basal area	quarter method	.96											
" "	Bitterlich method	.95	.97										
" "	plot method	.97	.97	.97									
Density	random pairs method	.88	.93	.90	.90								
"	quarter method	.84	.92	.88	.86	.98							
"	Bitterlich method	.88	.95	.93	.90	.96	.98						
"	plot method	.85	.91	.89	.88	.97	.97	.98					
Frequency	random pairs method	.89	.92	.87	.90	.99	.96	.94	.96				
"	quarter method	.87	.92	.87	.87	.97	.98	.96	.95	.98			
"	Bitterlich method	.90	.92	.87	.88	.94	.94	.94	.92	.95	.98		
"	plot method	.89	.92	.89	.89	.98	.96	.96	.96	.97	.98	.96	

Improvements in methodology--sampling lowland vegetation.--The relationships indicated by the results from the correlations between sampling methods indicate that for all practical purposes one can determine density or frequency by any of the methods tested with little loss of important information. They indicate also that species density and frequency were so nearly synonymous that only one needed to be measured. Thus, if one were content to accept a possible 13 to 16 percent loss in information he could estimate relative basal area from either frequency or density and avoid the necessity for detailed measurements. If one needs greater accuracy than this, he must measure basal area. Esitmates of basal area are, of course, more difficult to gather than estimates of either frequency or density.

Although the main goal of the present comparison of methods was information yield from a forest survey standpoint, it was obvious in collecting field data that the most rapid method was random pairs. This was evident since an equal number of sampling points was taken by each method. No other estimate can be made as to the order of aggregate time in the field by the other methods.

On the basis of the procedures used for the methods in the present study, the quarter method shows the most promise for use in lowland ecological surveys. It is recommended for the following reasons:

a. the yield in information content was higher than the other methods used, when basal area and frequency was considered.

b. the number of plots used in the analyses was great, compared to other analyses of a similar nature (102,133,142).

c. the loss of field time in measuring twice as many trees as in the random pairs method is offset by more rapid office computations.

In using the quarter method, the greatest amount of time spent at each sampling point lies in measuring single tree distances from the point center. It appears that these distances can be rather accurately determined with the use of a simple rangefinder. Although rounding-off errors will be introduced, they should be compensating errors with a small sacrifice in precision. The increased speed of data collection, reducing the cumulative man hours spent at sampling points, further justifies the use of this method in the field.

Soil Measurements.--Computer analysis of the samples taken from the 15 randomly located soil profiles indicated that the various soil types differed significantly (F test .01 level) in all analyses except sand content. Profile means, horizon means, and least significant differences are shown in Tables 29, 30, 31, 32, 33, and 34 in the Appendix.

Profiles and Horizons of Beta-Gley Soils.--Ceresco and Spinks soils were significantly higher in sand content and lower in silt and clay content than Conover and Locke soils at the .01 level. Sand content of the Ceresco and Conover soils increased at depth in all horizons, while the silt content decreased from a maximum at the surface. The percentage of clay was highest at mid-horizons levels. Sand was highest, and silt content and moisture retaining capacity lowest in the mid-horizons of the Locke and Spinks soils.

Differences in reaction and loss on ignition for this group were not significant. Moisture equivalent for Ceresco was significantly different from Locke and Spinks soils at the .01 level, while Conover, Locke, and Spinks soils showed no significant differences from each other.

Relative organic matter decreased rapidly in all beta-gley soils, from a maximum in the surface horizons. Reaction was neutral to slightly acid, becoming akaline in the lower horizons.

Profiles and Horizons of Alpha-Gley Soils.--Sloan, Pewamo, Brookston, and Sebewa profiles were significantly lower in sand content than Gilford soils at the .01 level.

Although sand content by horizons, for alpha-gley and beta-gley soils, were not significantly different from each other, coarse textured materials were highest in most horizons of the Gilford soils.

Significant differences in reaction were not apparent between soil profiles in this group. Moisture equivalents of the surface horizon were significantly different from other horizons in most cases (.01 level). Loss on ignition was greatest in those soils containing a higher proportion of finer textured materials. It was lowest in the parent materials, owing to the often saturated conditions which exist, decreasing quite rapidly from the surface mineral horizons. The decrease in loss on ignition, with increasing depth from the soil surface, was proportionately greater in the alpha-gleys compared to beta-gleys. .

Profile and Horizons of the Organic Soils--The profiles of the poorly drained organic soils varied considerably in relative organic matter content. Carlisle muck showed the lowest loss on ignition and was significantly different from Linnwood mucks and Rifle peat at the .01 level. This condition might possibly be attributed to an incorporation of mineral sediments into the profile during periods of overflow from a neighboring creek. No significant differences in loss on ignition were apparent for the materials underlying the organic deposits (.01 level).

Rifle peat was the most acid organic soil and was significantly different from Carlisle muck and one Linnwood muck (.01 level). All profiles of the muck soils were not significantly different in reaction from alpha and beta-gleys.

Underlying Materials of the Beta-Gley, Alpha-Gley, and Organic Soils--
The underlying materials of the Ceresco soils, Gilford soils, Carlisle muck, and one of the shallow Linnwood mucks were highest in sand and lowest in silt and clay content. Differences were significant from all other soils at the .01 level.

Mineral materials underlying one of the deeper Linnwood mucks and the Rifle peat showed evidence of shallow lake depressions; being significantly different in sand, silt and clay content from the other organic soils at both levels of the test. Alpha-gley parent materials were not significantly different from each other in sand content; however, Sebewa soils were lower in silt and clay content at both levels of significance.

Correlations between species distribution and soil characteristics-- In order to study the relationships between species distribution and various soil characteristics simple correlations were calculated between the importance values of the 10 most abundant species and soil physical properties in different horizons. Similar analyses were calculated between species' basal areas and soil properties. The species were: American elm, red maple, green ash, swamp white oak, silver maple, sugar maple, American basswood, slippery elm, northern red oak, and black cherry. The analyses were made on the data from 10 stands (numbers M19L, M19S, A14C, A14B, L10G, W5B, M26B, M17C, M22S, and W4S), in which complete soils analyses were made.

To make these analyses stand means were used as items, giving 10 degrees of freedom for each correlation. Although statistical significance at the .05 level is commonly accepted as meaningful, those correlations which fell between $r_{.05}$ and $r_{.02}$ were disregarded. They were felt to be essentially meaningless because they occurred with about the same frequency as would have been expected due to chance.

The correlations as calculated apply to stands only because they are based on stand means. Thus, from them one might say that a stand with high factor X also has high factor Y, but he could not necessarily say that the same relationship applies to small areas within the stands. The correlations as calculated also apply to soils as horizon 1, 2, 3, 4, and 5 because names between horizons do not have the same designation in all stands.

Distribution of One Species Not Related to That of Another-- Neither the importance value nor the basal area of a species was related to that of the other species. Of 90 correlations which were calculated to test such relationships, only one approached significance at the 5 percent level.

Ther are two probable reasons for the lack of significant species interrelationships. First the 12 stands were all in the middle stages of secondary succession; the situation may have been different if some pioneer and some late-succession stands had been considered. Secondly, most species have a rather limited dispersion distance. Stand 026R (see Table 10) contains only one pioneer species, tamarack, probably because that was the only pioneer species which could seed the area. Lack of seed supply might have prevented invasion by other species even though site conditions might have been right.

Species Distribution Slightly Related to Soil Physical Properties--The importance of the 10 species in each of the 12 stands was slightly related to the 5 physical characteristics of the soils which were measured. In fact no relationships were apparent when species' importance value was compared with the soil characteristics. When basal areas were used in the calculations, some evidence of association between kind of tree and soil could be noted for two species--black cherry and slippery elm. The statistically significant correlations are presented in table 17.

Two species showed some tendency to be found on soils with certain physical characteristics. Slippery elm and black cherry had high basal areas in stands in which the soil was characterized by high loss on ignition and high moisture equivalent. Black cherry was also most prevalent on soils with a low sand content.

Black cherry has been reported to grow on a variety of soil textural classes including gravelly and sandy loams with fine textured silt and clayey subsoils (Hough and Forbes 82). It has also been reported as a definite component in forests on melanized gley loams, embryonic and leached grood soils (Wilde et al. 163).

It has been suggested that slippery elm is more closely associated with soil moisture conditions than any particular soil characteristic (Scholz 131). Black cherry, however, showed a somewhat stronger relationship than

TABLE.- 17 . Relation between some physical characteristics of soils and species importance. Only those correlations of statistical and possible biological significance are shown. (An additional 216 correlations calculated for 8 other species were not significant).

If there was high	The basal area of Slippery elm was	The basal area of Black cherry was
Sand in horizons 2 and 3	NS	Low*
" " " 4 " 5	NS	Low**
Clay in horizon 5	Low**	NS
Loss on ignition in horizon 1	High*	High*
" " " " " 2	NS	High***
" " " " " 3, 4, 5	High**	High**
Moisture equivalent in horizon 1	High*	NS
" " " " 2	NS	High*
" " " " 3	High**	High**
" " " " 4	High***	High**

NS = Non-significant relationship
* = r greater than .658, significant at 2 percent level
** = r greater than .708, significant at 1 percent level
*** = r greater than .823, significant at 0.1 percent level

slippery elm for mineral soils having a high loss on ignition.

The other eight species for which importance value--soil or basal area--soil correlations were calculated are: American elm, red maple, green ash, swamp white oak, silver maple, sugar maple, American basswood, and northern red oak. In none of them were the relations between species' abundance and soil characteristics significant.

Correlations Between Soil Characteristics in Different Horizons.--The correlations between soil characters for 12 stands are shown in Table 18.

Some of the relations were expected and need no explanation. Such is the case for the high correlations between sand contents of the A and B horizons; also for the correlations between silt content in the A and B horizons and between clay content in the upper soil layers. Also, it was expected that there should be strong negative correlations between sand and silt contents and sand and clay contents.

It is interesting to note the very low degree of correlation between the upper soil and the "parent" material in any of the five characteristics. Evidently, in most of these stands the upper soil was not derived from the so-called "C" or parent material and it is in effect an underlying stratum of different origin, i.e.a "D" horizon.

The losses on ignition of the various horizons were not correlated with each other, either. This is due to the fact that in the A horizon the loss represents the decomposition of organic matter, whereas in the lower layers it may be confounded be a loss of water of hydration of clays, decomposition of carbonates, etc. The loss on ignition therefore cannot be taken as an indicator of organic matter content on subsoil horizons. The same reasoning explains the general lack of correlations between loss on ignition and sand, silt, or clay contents.

Although the presence of significant correlations was by no means universal, there was a general and expected direct relationship between moisture equivalent and silt or clay content. The relationship to sand content is obviously inverse.

TABLE.- 18 . Correlations between various soil characteristics in 10 stands of lowland hardwoods. All possible correlations were calculated but only those significant at the 2 percent level are noted.

Parameter	Soil horizon	Sand content in horizon					Silt content in horizon				
		1	2	3	4	5	1	2	3	4	5
Sand content	2	***									
" "	3	***	***								
" "	4	***	***	***							
" "	5	NS	NS	NS	*						
Silt content	1	-***	-***	-***	-**	NS					
" "	2	-**	-***	-**	-**	NS	***				
" "	3	-***	-***	-***	-**	NS	***	***			
" "	4	-***	-***	-***	-***	NS	***	***	***		
" "	5	Ns	NS	NS	-*	-***	NS	NS	NS	*	
Clay content	1	-***	-*	-**	-*	NS	**	NS	NS	*	NS
" "	2	-**	-*	-**	-*	NS	*	NS	NS	*	NS
" "	3	-***	-**	-***	-**	NS	**	NS	*	**	NS
" "	4	NS	NS	NS	-**	-*	*	NS	NS	*	NS
" "	5	NS	NS	NS	NS	-***	NS	NS	NS	NS	NS
Ignition loss	1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
" "	2	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
" "	3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
" "	4	NS	NS	NS	-***	NS	NS	NS	NS	**	NS
" "	5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Moisture equivalent	1	NS	NS	-**	-*	NS	NS	NS	NS	NS	NS
" "	2	NS	-*	NS	NS	NS	NS	NS	*	NS	NS
" "	3	-***	-**	-**	NS	NS	**	NS	**	NS	NS
" "	4	-**	NS	-**	-*	NS	*	NS	*	NS	NS
" "	5	NS	NS	NS	NS	-***	NS	NS	NS	NS	***

NS = Not significant
* = r greater than .715, significant at 2 percent level
** = r greater than .765, significant at 1 percent level
*** = r greater than .872, significant at 0.1 percent level

TABLE.- 18 . continued.

Parameter	Soil horizon	Clay content in horizon					Ignition loss in horizon					Moisture equivalent in horizon			
		1	2	3	4	5	1	2	3	4	5	1	2	3	4
Sand content	2														
" "	3														
" "	4														
" "	5														
Silt content	1														
" "	2														
" "	3														
" "	4														
" "	5														
Clay content	1														
" "	2	**													
" "	3	***	***												
" "	4	NS	NS	NS											
" "	5	NS	NS	NS	NS										
Ignition loss	1	NS	NS	NS	NS	NS									
" "	2	NS	NS	NS	NS	NS	NS								
" "	3	NS	NS	**	NS	NS	NS	NS							
" "	4	NS	NS	*	NS	NS	NS	NS	NS						
" "	5	NS	NS	NS	NS	NS	NS	NS	NS	NS					
Moisture equivalent	1	NS	NS	NS	NS	NS	*	NS	NS	NS	NS				
" "	2	NS	NS	NS	NS	NS	NS	**	NS	NS	NS	NS			
" "	3	**	***	***	NS	NS	NS	NS	NS	NS	NS	NS	**		
" "	4	**	*	**	*	NS	NS	NS	**	NS	NS	NS	NS	**	
" "	5	NS	NS	NS	NS	**	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS = Not significant
* = r greater than .715, significant at 2 percent level
** = r greater than .765, significant at 1 percent level
*** = r greater than .872, significant at 0.1 percent level

Improvements in Methodology - Sampling Lowland Soils--The presence of non- significant correlations between soil characteristics in different horizons was great, as indicated by the results from Table 18. It is therefore suggested that future vegetation studies in the lowland-hardwood land type should ignore the measurement of physical soil parameters at least to the extent of those included in this study. Among the chemical measurements organic matter, expressed as loss on ignition, and reaction (pH) can also be eliminated from studies of this type.

The lack of significant correlations for the soil physical determinations can only be attributed to the lowland nature of the sites with high water tables. The effects of sand, silt, and clay content, loss on ignition, and reaction on lowland-hardwood vegetation is probably being masked by the selective pressures exerted by recurrent high ground water. This would be especially true for stands found in a very wet or wet environment. It would be true to a lesser extent for stands found in the wet-mesic segment of the environment.

Ground Water and Precipitation Measurement.--Analyses of variance were performed to show the significance of differences for water tables throughout the growing season. Summaries of the problems for the analysis of variance of perched and actual water table levels are shown in tables 19 through 22.

All tabled F values were highly significant at the .01 level. Mean depths of the ground water levels within soils for the entire growing season and least significant differences are shown in table 23.

Fluctuations of the Water Tables Within Soils.--The greatest amount of variance in actual water table levels within soils occurred at opposite ends of the continuum placement of lowland hardwood stands (1394-2429). A partitioning of the variances indicated that over 96 percent of the changes in water table levels occurred within the Locke and Spinks soils, and the Sebewa and Gilford soils of stands M19L, M19S, and W4S, respectively.

For example, the partitioning of variance for Spinks soils is as follows:[1]

(a)

$$240.26 = V_e^2 \quad V_s^2$$

$$\text{error} = 1 = V_e^2$$

$$240.26 = 1 - 4V_s^2$$

$$V_s^2 = 14.10, \text{ therefore}$$

(b)

$$\frac{V_s^2}{V_s^2 \quad V_e^2} = 98 \text{ percent}$$

where

V_s = variance due to soils, and

V_e = variance due to error

1 See Table 20, for values used in the sample calculation..

TABLE.- 19. Summary of the analyses of variance showing the differences in perched water tables due to week of measurement throughout the 1961 growing season.

Soil series	Stand	Source of variation: Weeks	Source of variation: Error	F(a)
Locke	M19L	153.37	5.37	28.58
Spinks	M19S	190.26	2.22	85.61
Conover	A14C	33.24	8.04	4.13
Brookston	A14B	56.12	5.56	10.10
Gilford	L10G	54.45	2.70	20.19
Brookston	W5B	166.29	2.86	58.14
Pewama	W5B	115.25	3.57	32.21
Linnwood	A14L	51.02	1.26	40.34
Linnwood	L10L	26.31	.51	52.13
Carlisle	V20C	15.54	.10	161.50
Brookston	M26B	75.97	7.22	10.53
Ceresco	M17C	29.56	4.16	7.11
Cohoctah	M17C	75.23	2.12	35.49
Sloan	M22S	36.55	.88	41.33
Rifle	M26R	44.51	1.05	42.44
Sebewa	W4S	17.40	1.94	98.65
Gilford	W4S	23.69	1.06	233.39
Barry	M19L	26.05	.56	46.45
	Degrees of freedom	19	57	

[a]all were significant at the .01 level

TABLE.- 20 . Summary of the analyses of variance showing the differences in phreatic water tables due to week of measurement throughout the 1961 growing season.

Soil series	Stand	Source of variation: Weeks	Source of variation: Error	F(a)
		---Mean squares---		
Locke	M19L	2727.24	28.18	96.79
Spinks	M19S	3388.63	14.10	240.26
Conover	A14C	467.83	43.03	10.87
Brookston	A14B	442.23	50.53	8.75
Gilford	L10G	422.11	22.30	18.93
Brookston	W5B	1341.63	23.29	57.60
Pewamo	W5B	934.92	28.90	32.35
Linnwood	A14L	404.18	9.47	42.69
Linnwood	L10L	220.17	5.16	42.66
Carlisle	V20C	119.52	.89	134.06
Brookston	M26B	807.24	97.45	8.28
Ceresco	M17C	348.20	54.80	6.35
Cohoctah	M17C	709.08	23.02	30.80
Sloan	M22S	260.73	4.48	58.23
Rifle	M26R	331.13	7.01	47.21
Sebewa	W4S	1357.92	13.47	100.80
Gilford	W4S	1750.62	8.59	203.71
Barry	M19L	270.59	4.26	63.54
		Degrees of freedom		
		32	96	

a all were significant at the .01 level

TABLE.- 21 . Summary of the analyses of variance showing the differences in perched water tables between stands throughout the 1961 growing season.

Date of measurement	Source of variation: Stand	Source of variation: Error	F(a)
	---Mean squares---		
May 6	108.64	4.75	22.87
" 13	143.02	6.22	23.01
" 20	124.28	11.38	10.92
" 27	129.49	7.88	16.43
June 3	126.[illegible]	13.33	9.46
" 10	115.40	10.31	11.19
" 17	135.12	14.08	9.60
" 24	156.22	16.70	9.36
July 1	139.91	14.45	9.68
" 8	141.73	12.71	11.15
" 15	138.02	12.19	11.33
" 22	139.76	12.64	11.06
" 29	161.08	11.89	13.55
August 5	190.91	11.99	15.92
" 12	196.16	15.10	12.99
" 19	206.34	11.08	18.61
" 26	188.74	16.20	11.65
September 2	177.52	13.02	13.63
" 9	165.61	13.57	12.20
" 16	240.52	10.21	23.57
	Degrees of freedom		
	17	51	

a all were significant at the .01 level

TABLE.- 22. Summary of the analysis of variance showing the difference in phreatic water tables between stands throughout the 1961 growing season.

Date of measurement	Source of variation: Stand	Source of variation: Error	F[(a)]
	---Mean squares---		
April 22	172.37	1.67	103.44
" 29	67.14	1.02	66.05
May 6	112.60	4.28	26.32
" 13	151.96	4.96	30.66
" 20	122.30	11.12	11.00
" 27	138.20	7.82	17.68
June 3	143.47	11.26	12.75
" 10	128.21	10.66	12.03
" 17	154.34	11.38	13.56
" 24	166.55	16.40	10.15
July 1	165.87	13.61	12.19
" 8	163.50	11.18	14.63
" 15	160.58	9.48	16.95
" 22	165.50	10.76	15.38
" 29	98.09	10.15	19.52
August 5	222.28	11.80	18.83
" 12	228.68	12.52	18.26
" 19	227.12	10.75	21.12
" 26	201.80	14.29	14.12
September 2	178.28	13.22	13.49
" 9	170.06	13.31	12.78
" 16	241.44	10.96	22.03
" 23	257.09	10.73	23.97
" 30	228.76	11.96	19.13
October 7	290.05	11.07	26.21
" 14	314.31	10.28	30.57
" 21	332.72	9.22	36.08
" 28	356.94	9.19	38.85
November 4	317.51	7.72	41.13
" 11	327.10	7.21	45.34
" 18	376.15	7.08	51.83
" 25	379.19	6.66	56.98
December 3	382.21	6.41	59.66
	Degrees of freedom: 17	51	

[a] all were significant at the .01 level

Table 23-. Mean depth of water tables in soils for the 1961 growing season.[a]

Stand	W19L	W19S	A14C	A14B	L13B	W5B	W5B	A14L	L10L	V20C	W26B	W17C	W17C	W22S	W25R	W4S	W4S	W19S
Soil Series	Locke	Spinks	Conover	Brookston	Gilford	Brookston	Pewamo	Linwood	Linwood	Carlisle	Brookston	Ceresco	Cohoctah	Sloan	Rifle	Sebewa	Gilford	Barry
Weeks	Mean Depth (inches)																	
1	68	31	60	51	19	20	12	19	1	1	8	25	6	0	30	33	4	2
2	43	7	39	21	5	14	6	10	0	0	1	21	3	0	11	5	0	0
3	48	8	60	29	6	10	3	12	0	0	10	27	5	0	13	9	0	4
4	34	9	78	36	7	16	6	15	1	0	16	41	5	3	14	15	4	3
5	38	30	67	51	12	23	13	18	2	1	26	34	12	5	18	19	9	5
6	26	26	83	41	12	26	16	21	2	1	28	30	12	7	20	27	17	5
7	30	32	81	45	9	34	22	23	1	0	23	41	18	8	23	34	29	11
8	31	39	74	49	12	27	14	23	2	1	26	34	23	6	27	24	14	7
9	42	46	77	41	11	25	12	22	2	0	24	37	26	6	20	17	2	10
10	50	50	78	54	14	44	29	26	2	1	30	40	29	8	28	27	13	10
11	67	52	83	56	20	51	37	31	6	6	35	49	39	15	30	42	26	24
12	73	57	86	50	29	64	46	35	13	9	47	54	48	21	35	54	49	29
13	76	65	88	55	37	66	48	40	17	12	50	53	43	25	39	59	52	25
14	79	67	90	57	31	71	50	45	18	15	51	57	47	32	40	62	57	28
15	85	72	94	59	36	74	54	50	21	17	55	58	48	27	42	67	60	17
16	89	73	84	57	34	62	33	43	18	11	50	43	38	11	45	60	58	15
17	93	74	87	63	28	65	41	46	19	13	55	45	41	15	46	66	65	19
18	100	80	92	72	38	72	49	50	23	18	61	51	47	24	49	74	69	24
19	71	67	67	28	21	18	1	25	12	3	34	36	30	3	23	13	1	13
20	70	70	69	40	30	26	8	29	18	6	37	39	34	4	27	20	9	15
21	71	66	70	42	33	29	11	28	20	6	40	36	30	4	27	24	11	12
22	88	82	72	50	21	36	19	33	11	1	42	39	35	8	30	32	15	17
23	97	89	80	55	28	41	25	34	14	4	46	46	42	13	33	40	25	24
24	76	81	67	42	12	35	17	28	3	1	38	36	30	6	26	26	11	16
25	95	92	72	48	15	41	23	30	6	0	38	38	31	7	28	31	21	20
26	101	96	76	51	16	42	24	30	7	1	44	39	32	8	30	31	23	21
27	108	100	78	60	21	48	30	35	11	4	49	39	33	12	34	38	28	24
28	114	102	80	61	22	51	32	36	13	4	48	38	33	10	30	41	32	30
29	98	96	70	51	12	36	26	32	3	0	44	35	24	7	28	27	16	16
30	100	98	72	56	12	39	29	33	4	0	45	37	28	8	29	29	17	17
31	99	96	70	48	6	27	9	24	1	0	41	28	20	4	22	15	6	11
32	98	94	74	43	7	25	5	24	2	0	41	25	14	2	23	11	3	8
33	103	98	76	47	9	26	9	25	3	1	44	27	18	5	27	16	6	12
L.S.D. .05	9	7	12	12	8	4	10	6	4	1	17	13	9	4	5	7	5	4
L.S.D. .01	12	9	15	16	11	11	12	7	5	2	22	17	11	5	6	8	7	5
Recharge Pattern	A	A	B	B	C	D	D	B	C	C	E	F	F	F	E	D	D	A

[a] Arranged according to soil series and the continuum placement of lowland hardwood stands.

The previous sample calculation shows that 98 percent of the changes in water table depth of this soil could be attributed to time.

Error variance due to local differences between wells within these stands was correspondingly high when compared with other soils, except for the poorly drained Gilford soils. Only four percent of the variance was due to differences between well locations within a particular stand.[1]

High variances indicated by rapidly changing water levels were also noted for the perched water tables in stands of the beta-gley soils; however, this was not true for those stands found on two-storied alpha-gleys. Differences in variation between actual and perched water tables could not be entirely explained on the basis of existing differences in horizon textural characteristics, or the presence of impermeable layers in the profiles of these soils. Apparently the ground water level is being determined by topographic and subterranean drainage controls, which would be indeed difficult to investigate without calibration of the watersheds in which these stands are located. The soils of these stands were subject to the influences of two different topographical recharge patterns (water regimes A and D) of the Sycamore and Sloan Creek watersheds.

Such high seasonal variation and similarity in water table levels of stands so different in species complement would seem to indicate that the arbitrary assignment of stands to a particular moisture regime may be weak when a single observation is made on water table depth. This would be especially true for any ecological study concerned with determining the rate of successional change.

---

[1]An average value for all stands.

Actual water table variation within soils was least in the very poorly drained mucks and certain soils of the alpha-gley type. An analysis of the components of variance showed that over 90 percent of the fluctuations within water tables of the Linnwood and Carlisle mucks (stands A14L, L10L, and V20C), Rifle peat, ponded Barry soils, and the alluvial Sloan soils could be attributed to time. The remaining variance could be allocated to differences between well locations of the respective stands.

In the remaining alpha-gleys, the variances, due to time, were greatest in the Brookston and Pewamo soils of stand W5B. This was evident for perched as well as the true water table depths recorded during the course of the study. Although the soils in the stands W4S and W5B are under the influence of the same physiographic recharge pattern (water regime D) , the higher clay content in the deeper lying horizons of Pewamo soils is evidently responsible for greater variances in perched tables. Both stands are situated in closed basin depressions and receive little water from adjacent areas.

Actual water table levels for the complex of stands in water regime B showed that approximately 70 percent of the variances could be attributed to time. The Conover soils had variances only slightly greater than the more poorly drained alpha-gley and organic soils. Approximately 30 percent of the variances were due to differences between well location within each stand.

Weekly variances in perched water tables were greater in the latter soils. This condition might be attributed to an increasing clay content at lower depths for Brookston soils (stands A14B) and the clayey parent materials underneath the Linnwood muck of stand A14L. The high silt content of the Conover profile (stand A14C) was apparently not influential in causing greater variance in perched water tables when compared to other beta-gley soils, or even some of the alpha-gleys.

Although perched water tables were not frequent in shallow or deep organic soils, their occurrence was observed when the well boring penetrated into the underlying materials. Thus, differences in variance in actual and perched water tables of Linnwood muck (stand A14L) and Rifle peat, compared to other Linnwood and Carlisle mucks, could be attributed to the significantly higher clay content of the underlying materials. Differences between the wells of these stands due to local variation was insignificant.

Local variation in actual water table levels (over 35 percent) attributable to physiographic differences in well location within each stand was greatest in the Brookston soils of stand M26B and the floodplain Ceresco soils of stand M17C. Variance in the Cohoctah soils and Gilford soils (stand L10G) was intermediate compared to other soils having poor drainage. In these alpha-gleys, approximately 80 percent of the variance was accountable to water level fluctuations throughout the spring, summer, and fall seasons, while the remaining 20 percent was due to variance between wells.

Fluctuation of the Water Tables Between Soils.--The largest amount of variation in actual water table levels between soils occurred during the first week of the study.[1] Variance partitioning revealed that over 90 percent of the variance in actual water levels for the entire growing season took place from April 22 to April 29, and from October 7, until the end of the study on December 3, 1961.

After May 6, when a general downward trend in the actual water table levels was observed, these analyses showed an increasing amount of variance between all soil types. This trend continued until the termination of the study, except for some minor and expected reduction in variances due to

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[1]See Table 22; column of values for F.

partial recharge of the phreatic surface from rainfall. Partitioning of the variance also showed that the lowest amount of variability (71 to 78 percent) between the water tables of all soils occurred during the summer season from June 7 until July 12, and from August 19 until the beginning of fall on September 21, 1961. This could be largely attributed to the effects from convectional Class 4 advanced storms, which were insufficient to satisfy soil moisture profile deficits.

Increasing variances, between soil water tables toward the end of the growing season, might be accounted for in the continuing drop of water levels in the beta-gley Locke and Spinks soils, which was directly opposite to the trend of levels observed in other soils during the latter part of the study.

Correlations Between Species Distribution and Ground Water.-- In order to study the relationships between species distribution and water tables simple correlations were calculated between the importance values of the ten most abundant species and ground water depths during the growing season. Similar analyses were also calculated between species' basal area and ground water depths. The species were: American elm, red maple, green ash, swamp white oak, silver maple, sugar maple, American basswood, slippery elm, northern red oak, and black cherry. Data were available from 14 stands. The stands were (M19L, M19S, A14C, A14B, L10G, W5B, A14L, L10L, V20C, M26B, M17C, M22S, M26R, and W4S), in which water tables were measured.

Stands means were used in the analyses. The items entering into the input were:

1. importance value of each of the ten (10) species.
2. basal area of each of the ten (10) species, and
3. water table depth for each of 28 weeks.

There were 12 degrees of freedom for each correlation. Correlations which fell between $r_{.05}$ and $r_{.02}$ were disregarded. The correlations as calculated apply to the period April 29 until November 4, 1961. This period was considered to be the most important hydro-ecologic segment of the study.

Species Distribution Related to Ground Water Depths.--The correlations of biological significance between ground water depth and species importance involved two species-- sugar maple and American basswood (Table 24.) When basal areas were used in the calculations, the same type of association was noted. It may be observed from the correlations and ground water depths in tables 20 and 21 respectively, that American basswood was more tolerant of shallow water tables and poor aeration than was sugar maple. For instance: the water tables in the stands where basswood was present was within one inch

TABLE.- 24 . Correlations between ground water depth and importance of sugar maple and American basswood. (An additional 224 correlations for 8 other species were not significant.)

Date of measurement	Correlations between depth of water table and			
	Sugar maple		American basswood	
	importance value	basal area	importance value	basal area
between May 6 and June 17	NS	NS	NS	NS
between June 17 and August 19	High**	High**	NS	NS
between August 19 and September 2	High***	High**	NS	NS
between September 2 and September 9	High***	High**	High*	NS
between September 9 and November 4	High***	High**	NS	NS

NS = Non-significant relationship
* = r greater than .612, significant at 2 percent level
** = r greater than .661, significant at 1 percent level
*** = r greater than .780, significant at .01 percent level

TABLE.- 25 . Relationship between the range of ground water depth and importance of sugar maple and American basswood.

Date of measurement	Water table depth in stands in which			
	Sugar maple was		American basswood was	
	present	absent	present	absent
between May 6 and June 17	9-83	0-41	2-83	0-41
between June 17 and August 19	29-100	1-74	1-100	1-74
between August 19 and September 2	18-71	1-39	1-71	1-39
between September 2 and September 9	29-71	4-40	4-71	4-33
between September 9 and November 4	35-114	0-46	6-114	0-46

of the soil surface between August 19 and September 2 (Table 25). During this same period, water tables were at least 17 inches deeper in those stands where sugar maple was important. Such factual evidence reaffirms the known silvical characteristics of these species (Braun 20, Bray and Curtis 23, Maycock and Curtis 110).

Correlations Between Water Table Depth and Date of Measurement.--It was noted during the measurement of water tables that both the drop and recharge in ground water was approximately equal between similar stands for each week of measurement. Presumably this situation was brought about by the effects of local evapo-transpiration and recharge by rainfall. Such a condition was most evident on muck soils which were least affected by gradient differences.

In order to study the relationships between water table depth and date of measurement simple correlations were calculated between the dates on which water tables were measured and their recorded depth. The periods of observation on successive weeks were from April 29 until November 4, 1961. Water tables were measured in stands (M19L, M19S, A14C, L10G, W5B, A14L, L10L, V20C, M26B, M22S, M26R, and W4S).

Stand means were used in the analyses. The items entered on the tape-input were inches of depth recorded below surface datum for each of 28 weeks.

There were 12 degrees of freedom for each correlation. The correlations which fell below $r=.78$ were disregarded. The results of the analyses are shown in table 26.

The results of the data suggest that a strong association existed between water tables in stands from September 16 until the end of the period entered for the analyses. Stabilized ground water levels could be partially attributed to a reduction in the amounts of local evapo-transpiration within stands and the surrounding areas. In addition, most of the precipitation during this part of the year is produced from Class 4 storms of cyclonic origin (Smith and Crabb 137). Such storms became prevalent during the latter weeks in October and the early weeks of November. This type of storm is of low intensity and serves to satisfy existing soil moisture deficits. Throughout the winter season, of course, storms of this type will produce recharge of the ground water after profile moisture deficits cease to exist.

Table . Correlations between water table depth and date of measurement.[a]

Date of measurement	Month: April date 29	May date 6	13	20	27	June date 3	10	17	24	July date 1	8	15	22	29
May 6	.97													
" 13	.86	.94												
" 20	.82	.90	.93											
" 27	NS	.84	.94	.94										
June 3	NS	.84	.93	.94	.98									
" 10	NS	.84	.90	.97	.90	.97								
" 17	.81	.88	.90	.96	.92	.93	.97							
" 24	.81	.86	.86	.97	.91	.94	.97	.97						
July 1	.86	.88	.86	.94	.88	.92	.92	.94	.98					
" 8	.80	.84	.81	.88	.85	.89	.85	.90	.94	.98				
" 15	.78	.81	.78	.87	.84	.88	.87	.90	.94	.97	.99			
" 22	.79	.82	.78	.87	.84	.88	.86	.90	.94	.98	.99	.99		
" 29	.78	.80	NS	.85	.82	.86	.85	.88	.93	.97	1.00	.99	.99	
August 5	.78	.79	NS	.84	.75	NS	.81	.86	.89	.92	.93	.95	.93	.96
" 12	NS	.78	NS	.83	.75	.78	.82	.85	.89	.93	.94	.96	.95	.97
" 19	NS	NS	NS	.83	.75	.78	.81	.84	.89	.93	.95	.96	.96	.97
" 26	NS	NS	NS	NS	.66	NS	NS	NS	.81	.81	.80	.82	.80	.81
September 2	NS	NS	NS	.80	.68	NS	.78	.88	.84	.83	.81	.83	.81	.82
" 9	NS	.78	NS	.81	.70	NS	.79	.88	.84	.84	.83	.85	.82	.84
" 16	NS	NS	NS	.80	.66	NS	.78	.87	.87	.88	.87	.89	.88	.90
" 23	NS	NS	NS	.80	.67	NS	.78	.87	.87	.89	.88	.91	.90	.91
" 30	NS	NS	NS	.80	.67	NS	.79	.87	.87	.88	.87	.88	.88	.89
October 7	NS	NS	NS	NS	NS	NS	NS	.84	.85	.86	.86	.88	.89	.89
" 14	NS	NS	NS	NS	NS	NS	NS	.84	.84	.86	.85	.87	.87	.88
" 21	NS	NS	NS	NS	NS	NS	NS	.82	.84	.86	.85	.87	.87	.88
" 28	NS	NS	NS	NS	NS	NS	NS	.81	.83	.85	.85	.87	.87	.88
November 4	NS	NS	NS	NS	NS	NS	NS	.82	.84	.85	.84	.86	.86	.87

NS= Not significant

[a]All correlations (r greater than .78), which were significant at the .01 level are shown.

TAPLE.-26 . continued.

Date of measurement	Month												
	August				September					October			
	date				date					date			
	5	12	19	26	2	9	16	23	30	7	14	21	28
May 6													
" 13													
" 20													
" 27													
June 3													
" 10													
" 17													
" 24													
July 1													
" 8													
" 15													
" 22													
" 29													
August 5													
" 12	.99												
" 19	.99	1.00											
" 26	.88	.84	.83										
September 2	.90	.96	.85	.99									
" 9	.92	.88	.87	.98	.99								
" 16	.95	.94	.93	.96	.96	.96							
" 23	.96	.94	.94	.95	.96	.96	.99						
" 30	.93	.92	.91	.95	.95	.94	.99	.99					
October 7	.93	.92	.92	.94	.94	.94	.99	.99	.99				
" 14	.93	.92	.92	.94	.94	.94	.99	.99	.99	1.00			
" 21	.94	.93	.93	.93	.93	.93	.99	.99	.99	1.00	1.00		
" 28	.94	.93	.93	.92	.93	.93	.98	.99	.98	.99	.99	.99	
November 4	.92	.92	.91	.93	.93	.92	.99	.98	.99	1.00	1.00	1.00	.99

NS = Not significant

[a] All correlations (r greater than .78), which were significant at the .01 level are shown.

During the period from August 5 until September 16 relatively slight changes in water tables occurred as indicated by the correlations in the table. These slight changes could be partially attributed to the effect of increasing or decreasing evapo-transpiration locally as well as in the surrounding watersheds. The ground water depth was also affected by convectional storms of moderate to severe intensities during this part of the year. Changes in water tables for the period June 17 to August 5 were also complicated by storms of this type (Class 6 storms, Smith and Crabb 137).

Non-significant relationships between the water tables in all stands occurred from about May 6 until June 10 when water tables were decreasing or increasing differentially. These changes were most strongly at variance during the earlier weeks of this period as a result of thawing and freezing of soil water which caused differential recharge of the phreatic surfaces. Immediate and continuing effects from precipitation, intermittent changes in the amounts of water being transpired by trees, and temperature differences probably added to confusion of ground water levels during the early part of the year.

Since 2376 measurements of water tables were made during the present study a subsequent series of measurements with a minimum effort should yield similar trends of fluctuation. In addition, a series of yearly trends could be established in ground water levels for subsequent studies in lowland hardwood areas.

Improvements in Methodology - Sampling Ground Water.--The relationships indicated by the results from the correlations between water table depths and the date of measurement suggested that precise data may be gathered by intermittent sampling of ground water depths during the growing season. Considering the amount of time and effort expended in collecting such information, a reduction in the number of field measurements would indeed be desirable.

From the analyses of the ground water correlations for 1961 the following information was derived:

a. If one could afford to sample ground water depth only once during the growing season the best time to sample would have been between June 17 and July 15. The lowest correlations between samples taken on any of these dates was between $r = .78$ and $r = .81$

b. Sampling twice during the growing season would not have given more information on water table depths than sampling once.

c. If one could afford to sample ground water depth three times during the growing season the best time to sample would have been on May 20, July 29, and August 19. The lowest correlations between water table data taken on those dates and intervening weeks was .83.

Correlations for additional samples taken on ground water depth are shown in table 27.

TABLE.- 27 . Optimum sampling data in 1961 to give maximum information on water table depth at minimum effort.

if one could afford: to sample this many times	the best time to sample was	the lowest correlation between measured water table depths in intervening weeks was (a)
number	--------date-------	
1	between June 17 and July 15	.78 to .81
2 (b)	------------------	----------
3	May 20, July 29 and August 19	.83
4	May 20, July 29, August 19, and August 26	.85
5 (c)	-----------------------	----------
6	May 6, May 20, June 10, July1, August 19, and August 26	.90
10 (d)	April 29 and May 27-then on June 17, July 1, August 5, August 26, and September 30	.95

(a) All correlations were significant at the 0.1 percent level.
(b) No combination of two dates gave better results than the best sampling on one date.
(c) No combination of five dates gave better results than the best sampling on four dates.
(d) If one desired 90 percent (r^2) information on water table depth, sampling would have been made on these dates.

Stand Similarities

From the values within the table of community coefficients, (Table 28) several relationships are suggested. It is evident that on peat soils the tree composition is quite dissimilar to that found on mucks and mineral soils. In addition, the canopy vegetation may be just as dissimilar between peat soils. The strongest disparity is indicated, however, between the vegetation types found on peats and alluvial soils as shown by the extremely low values at the base of Table 28. A comparison of the remaining community coefficients indicated that no other abberations were present within the table. Since 23 different hardwood species were used in the construction of the table, the continuing homogeneity of lowland hardwood stands is demonstrated by the small differences between most values.

As has been previously mentioned, an attempt to show stand similarities through the use of the basic community coefficients proved that the stand aligament was distorted. The use of the gradient treatment suggested by Bray gave a better perspective of the spatial relationships between stands. The spatial separations along a single axis actually represents the compression of a two dimensional relationship into one dimension (23, 43). The points at which each stand is located along the two-dimensional axis is commonly referred to as its W value.[1]

An attempt to portray relationships based on stand to stand similarities and the data for the environmental measurements were included in a series of graphs. It was decided that the best method of representing the continuous nature of the gradient would not require any additional or arbitrary segmentation of the data. Since the water tables of the stands were actually measured, rather than inferred, the arbitrary division of moisture classes would be presumptuous.

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[1] a coefficient of community similarity.

TABLE.-28 . Community coefficients (W= 3C) based on the importance values of tree species in the 19 lowland-hardwood stands of Ingham County.

Stand	Stand	M19L	M19S	A14C	W5C	W5B	A14B	W4B	M22S	V20C	O3L	M26B	L10G	A14L	L10L	S23B	W4S	M17C	M26R
		number																	
M19S		277	275																
A14C		274	222	182															
W5C		271	274	266	183														
W5B		266	254	257	255	247													
A14B		256	248	267	275	250	213												
W4B		255	270	223	265	251	238	226											
M22S		210	252	133	248	238	219	233	243										
V20C		207	250	181	242	218	252	275	257	233									
O3L		203	220	216	235	222	265	248	240	286	212								
M26B		202	233	245	245	221	256	248	203	260	248	138							
L10G		200	226	198	159	224	270	236	223	257	268	237	212						
A14L		199	247	208	249	167	254	266	229	288	276	256	248	112					
L10L		196	224	226	223	203	270	232	221	265	275	226	261	270	129				
S23B		181	196	164	213	200	266	235	177	248	261	267	253	248	248	164			
W4S		175	217	209	230	244	254	233	248	235	246	214	225	255	238	230	176		
M17C		173	207	258	203	212	200	199	250	222	189	165	181	186	180	121	299	225	
M26R		122	204	203	174	148	196	140	6	91	150	191	120	219	193	213	217	3	103
C26R		2	3	86	82	49	107	75	0	37	55	102	52	250	215	130	100	0	182

The relationships of lowland hardwood stands based on their W values and the various soil measurements are shown in Figures 31 through 40. Mean values of the edaphic parameters are indicated along the ordinates, while W values for stand arrangement are shown along the abscissas. At each stand position changes in the importance values for four of the leading dominant species are also shown. This was accomplished by using single lines scaled to actual importance values at the cardinal points of stand position.

Any attempt to represent a species pattern through the use of line diagrams was not suitable for the following reasons:

a. the number of stands used in the ordination was small, and lines connecting stand positions to show species changes would have resulted in identical patterns.

b. the use of actual importance values attained by the species appeared to be greater value in gradient treatments, than the selection of an average importance value to define species pattern.

Stand Shift Related to the Number of Stands Sampled.-- The spatial distribution of the stands along the abscissa, representing similarities in tree composition between stands, is a resultant of the number of stands sampled. It is apparent that the inclusion of additional stands in the present technique would produce an entirely different distribution on the gradient. Likewise, this condition would be equally true for stands which were omitted from the technique. The shift in spatial relationships which occurs when a different stand is selected as a base of reference is shown in Figure 31.

It may be observed that the magnitude of shift is least for those stands containing large amounts of silver maple and small amounts of red maple. Since an index of similarity formed the basis of the gradient treatment, stands most unlike the reference stands would be displaced the least.

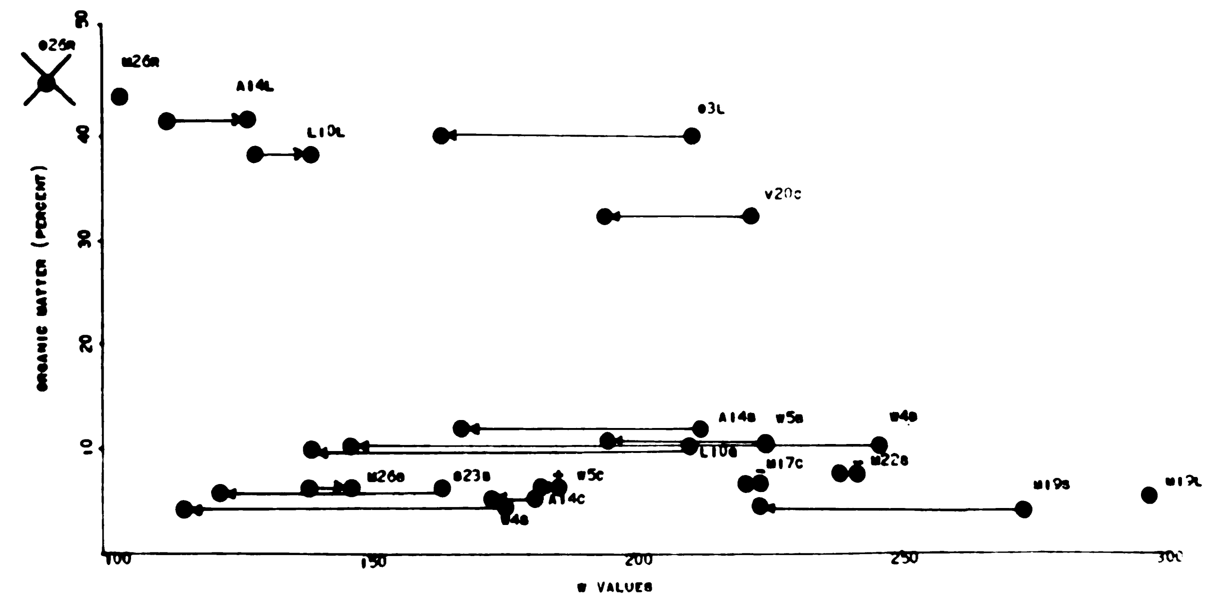

Fig. 31 . The shift in spatial relationships of lowland hardwood stands, which occurs when stand M26R is selected in place of stand O26R as a base of reference.

Although most of the stands located on mineral soils were shifted downward, all stands located on mucks were shifted closer to each other.

The remaining graphs were constructed on the basis of the original gradient technique since many combinations of reference points could be included in a treatment of this type.

Stand Shift With Changes in Organic Matter (loss on ignition).--A comparison of the changes between stands with changes in organic matter, or loss on ignition from the soils, shows a distinct separation of the stands into mutual groups (Figure 32). It may be noted that red maple is most strongly represented at the left of the gradient on peat and muck soils. An analogous situation prevails for this species on the mineral alpha-gley soils. Although this species decreases in importance as the W values increase, it is most weakly represented on the right side of the gradient.

The three other species green ash, American elm, and swamp white oak, enter the gradient on Linnwood muck soils. Swamp white oak is somewhat better represented than green ash on Linnwood mucks. However, green ash usurps the importance of the former species on alpha-gley soils in this section of the gradient. The synecological requirements of these two species for sites possessing high amounts of light and moisture is rather well known.(125, 150, 154) Although the two species occur at about the same stage in sucession, green ash appears to be more tolerant of wet extremes in moisture and full sunlight than does swamp white oak. The differences in amplitude between the two species in this segment of the gradient may be due to differences in such conditions between the stands. The trends for these species are uncertain toward the right as both species continue to be approximately equal in importance along the remainder of the gradient.

Although American elm attained a high level of importance in the majority of stands, it reached its maximum development toward the right of the gradient.

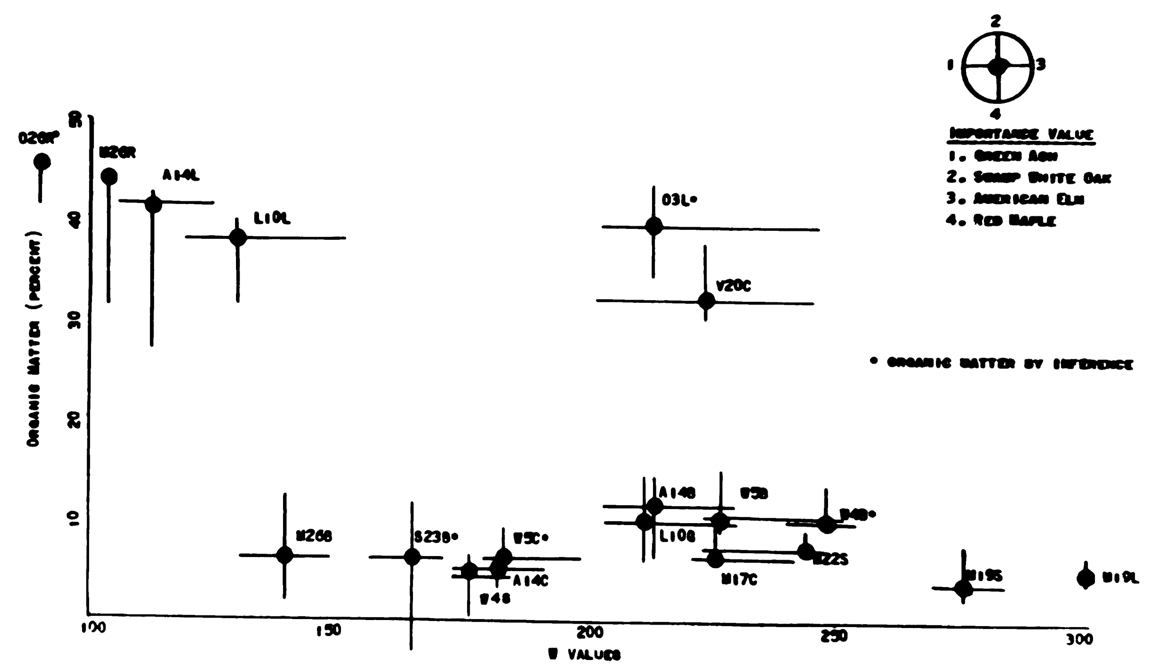

Fig. 32. Relationship of lowland hardwood stands based on the organic matter content of the soils (loss on ignition) and W values. Changes in the importance values for four dominant species are also shown along the gradient.

The fact that this species did not show up as a major species at either end of the gradient satisfies the assertion that the gamut of lowland hardwood stands within the country had been sampled.

Stand Shift with Changes in pH-- The use of mean soil reaction as a parameter showed a strong rise to the right from about 4.5 to 6.2 on the acid peats to mucks. Slight increases toward the right were more oe less continuous in a band of values from 6.7 to 7.9 for most of the remaining stands eventually becoming asymptotical at the end of the gradient (Figure 33).

Of the four species plotted for this ordination, only red maple appeared to be tolerant of extreme acid conditions below a mean soil reaction of 4.5. The vacillating decline of this species toward the right of the gradient may represent the initial side of the bimodal curve reported by other authors (54, 110). Likewise, its entrance at the extreme right may reflect the initial upswing of the second peak. These changes are not necessarily the effects of soil reaction, except where this species exhibits a clear tendency to attain optimum importance at the lower end of the gradient. Even so, red maple may simply possess a wider ecotopic amplitude for acidic peat soils compared to other lowland hardwood species.

Stand Shift with Changes in Sand, Silt, and Clay Content-- The distribution of the stands also showed noteworthy patterns of change when mean values for textural variation within the soils were plotted (Figures 34, 35, and 36). The bands of vertical separation decreased proportionately in width, from sand to silt to clay, between the 12 stands sampled for soil texture. The coarse sand fraction, beginning at 47 percent at the left of the gradient, showed an increasing width in the band of values of approximately 25 percent. A median value value of 57 percent was reached on the far right.

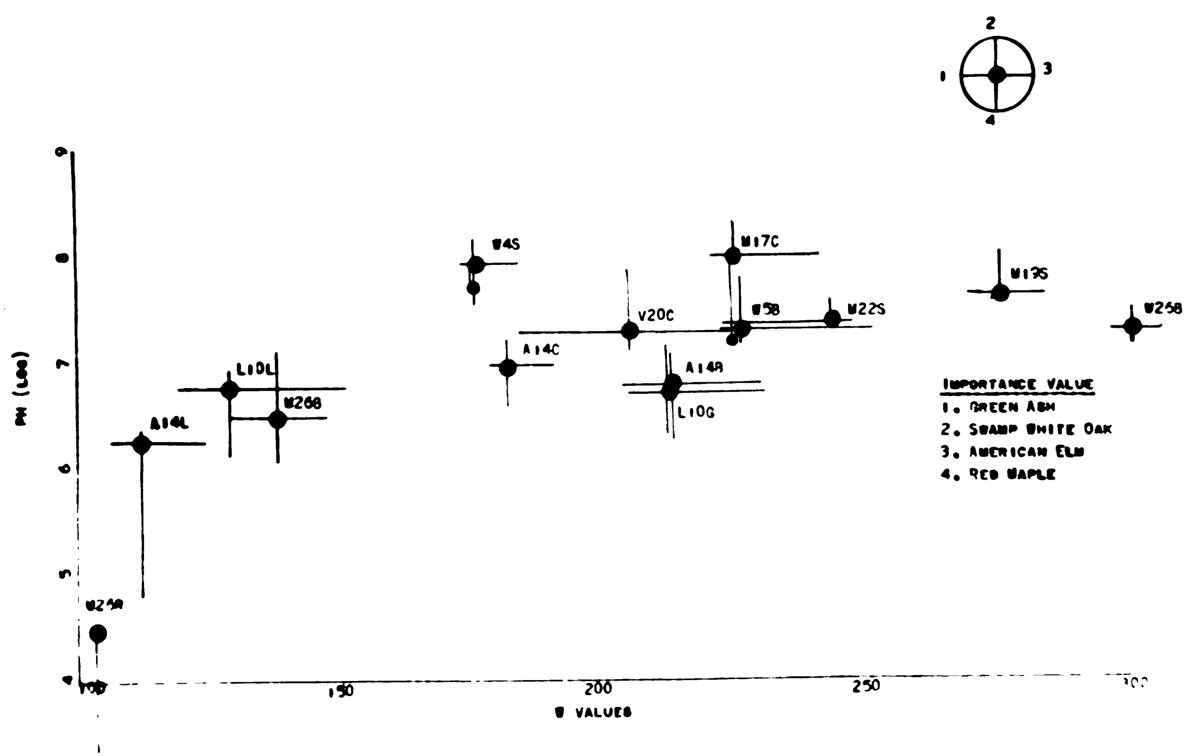

Fig.33. Relationship of lowland-hardwood stands based on on the pH of the soils and W values.

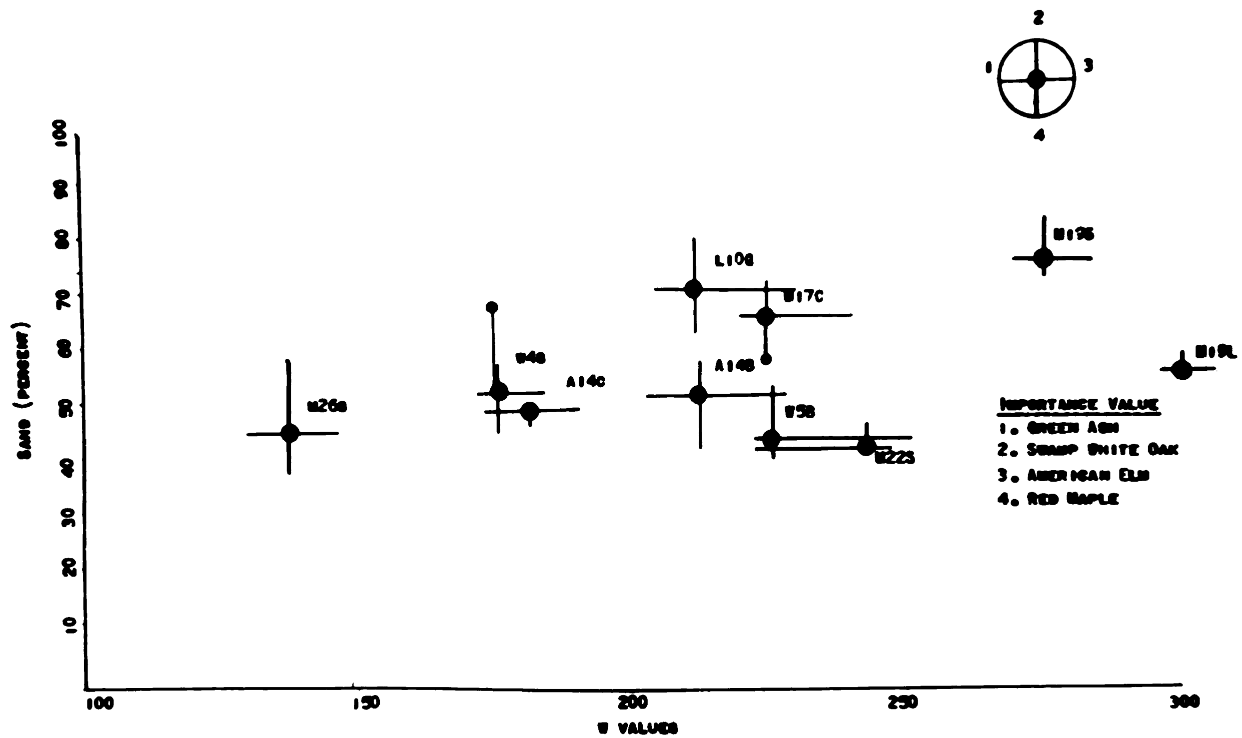

Fig. 34. Relationship of lowland-hardwood stands based on the percent sand in the soil and W values.

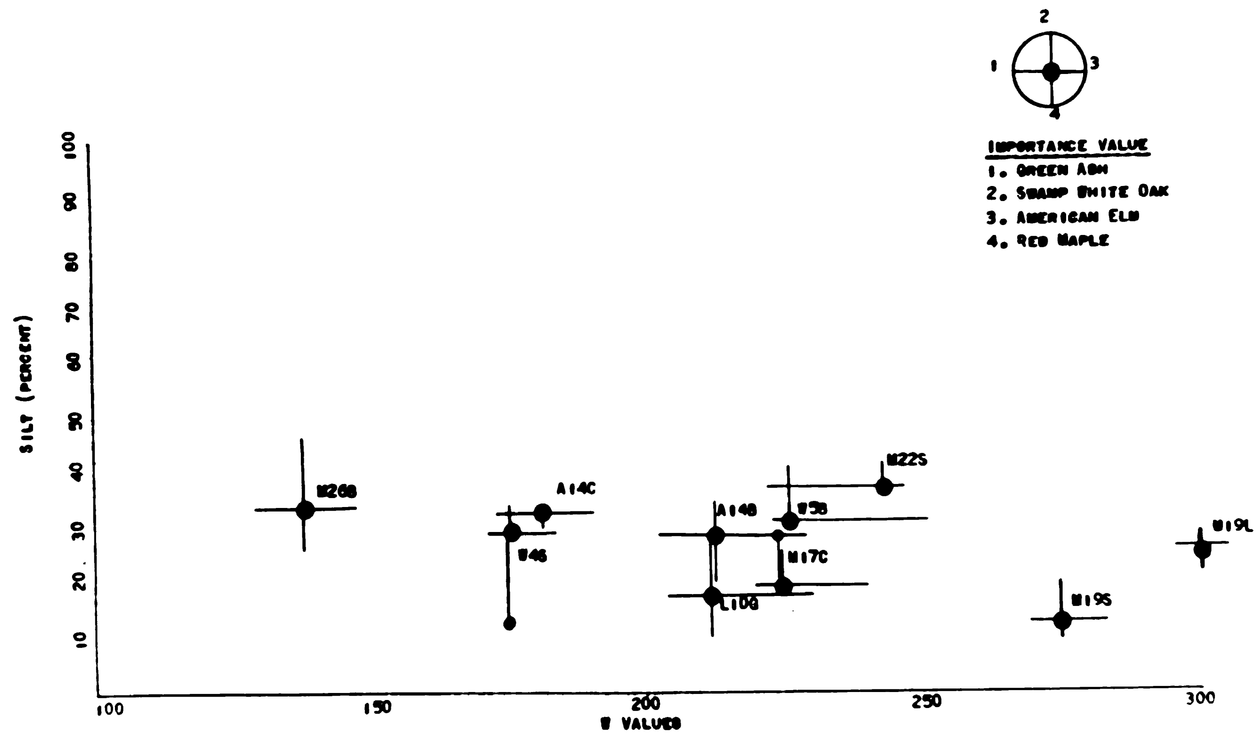

Fig. 35. Relationship of lowland-hardwood stands based on the percent silt in the soils and W values.

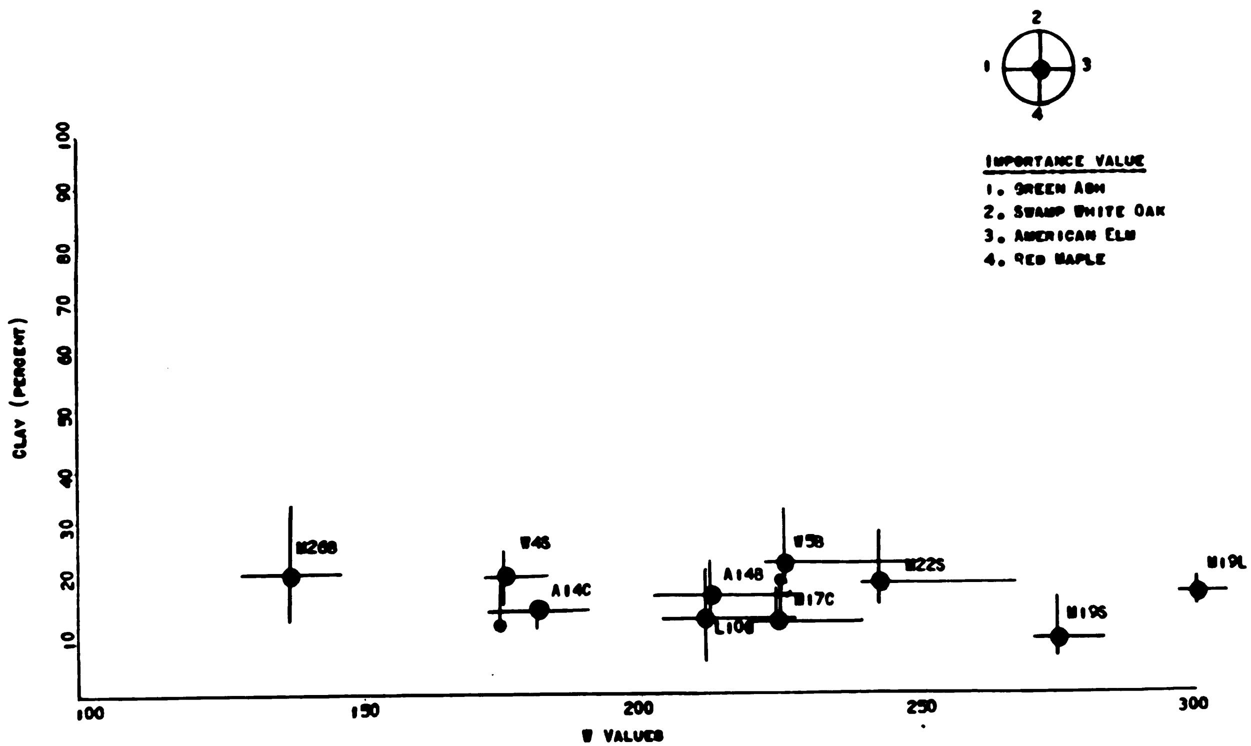

Fig. 36. Relationship of lowland-hardwood stands based on the percent clay in the soils and W values.

The intermediate soil fraction, or silt content, showed a slight decrease from 32 percent on the left to 25 percent on the right along the entire gradient. The widest part of the silt band was coincident with the range of W values for sand but was somewhat narrower having a width of 23 percent. The trend of change for the fine fraction or clay content of soils deviated least showing only a slight increase from 18 percent on the left to 21 percent on the right. The maximum width of the band, only four (4) percent, was considerably less than that of the other soil fractions.

Within the stands sampled for soil texture, three species increased in importance toward the right between W values from 200 to 250. American elm and swamp white oak showed stronger importance values than green ash, while red maple declined in importance for this portion of the gradient.

Stand Shift with Changes in Moisture Equivalent-- The use of the moisture equivalent in the treatment (Figure 37) showed a continuous rise from 25 to 32 percent, which was proportionately opposite to the trend observed for the intermediate soil fraction. An abrupt break, unlike the trend for silt content occurred at a W value above 250, which corresponded to the two stands found on sandy soils in the upper segment of the continuum. Changes in the importance values for the four species plotted in the graph followed the patterns described for soil texture.

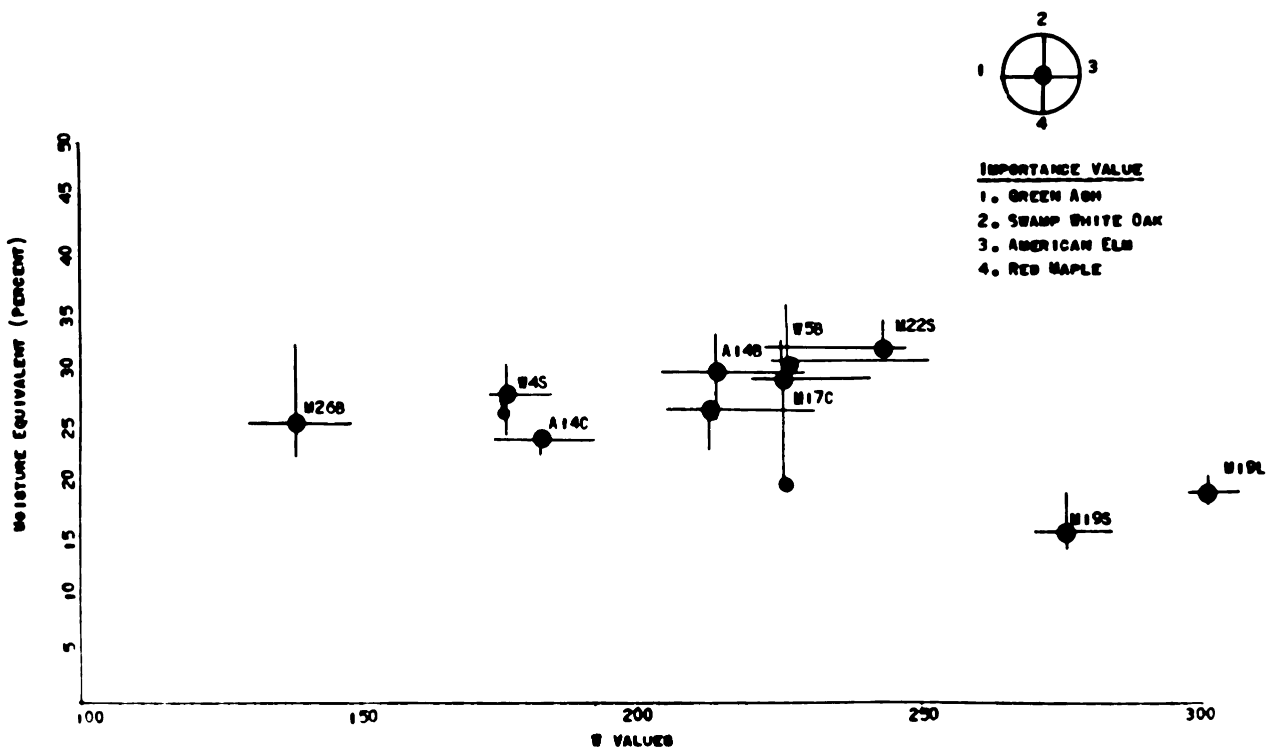

Fig. 37. Relationship of lowland-hardwood stands based on the moisture equivalent of the soils and W values.

Stand Shift with Changes in Water Tables-- A graph of the lowland hardwood stands based on mean water table depth and similarities of tree composition is shown in Figures 38 and 39. The catenal relationships of water tables between the soils in the stands is also shown. A distinct separation of the stands was again indicated by using this parameter which was similar to that shown by using loss on ignition. The stands on both alpha-gley and beta- gley soils are arranged into a paracentrical figure resembling a paraboloid which points downward toward the right of the gradient. The toposequence of water tables indicated by the directional lines connecting the stands serves to confirm the segregation of moisture regimes by soil profile examination.

Within the stands located on mineral soils, American elm increased toward the center of the figure decreasing on either side of the gradient. This species also showed a general increase in importance with a rise in average depth of the ground water to within 20 inches of the surface. Red maple, with the exception of alluvial soils, was better represented within the area having decreasing ground water depth from 55 to 23 inches. Swamp white oak increased in importance within an area from 24 to 38 inches in average depth. Green ash was best represented along the gradient when the ground water came closest to the soil surface. Although this species was almost as well represented as swamp white oak in several stands, it increased in importance on either side of the vertical axis where swamp white oak was absent or deficient.

The stands on organic soils are clustered into an elliptical shaped group in the figure. The ellipse or band, which tapers to zero, is 25 percent wider on the left of the gradient than on the right. Within these stands the importance of red maple decreased from the left to the right of

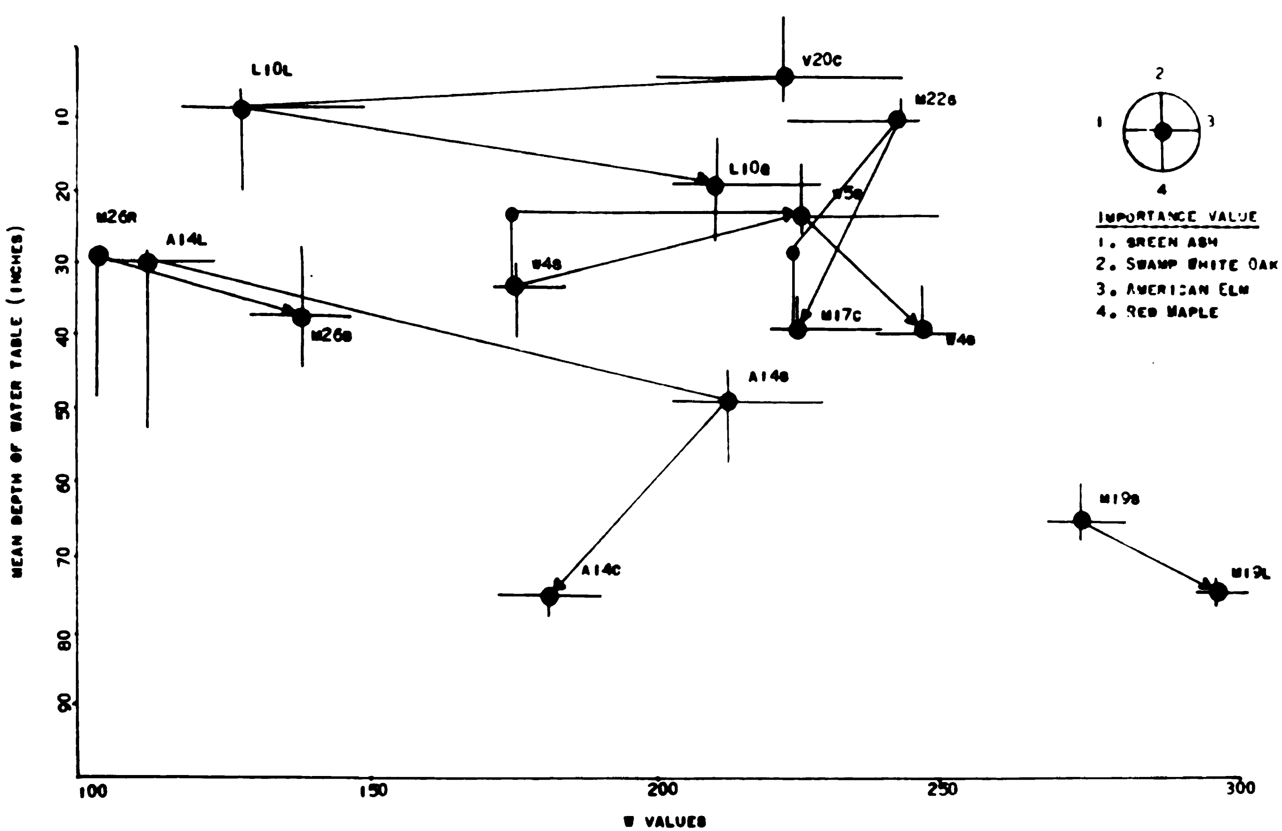

Fig. 38. Relationship of lowland-hardwood stands based on mean water table depth and W values showing the toposequence of water tables within the soils.

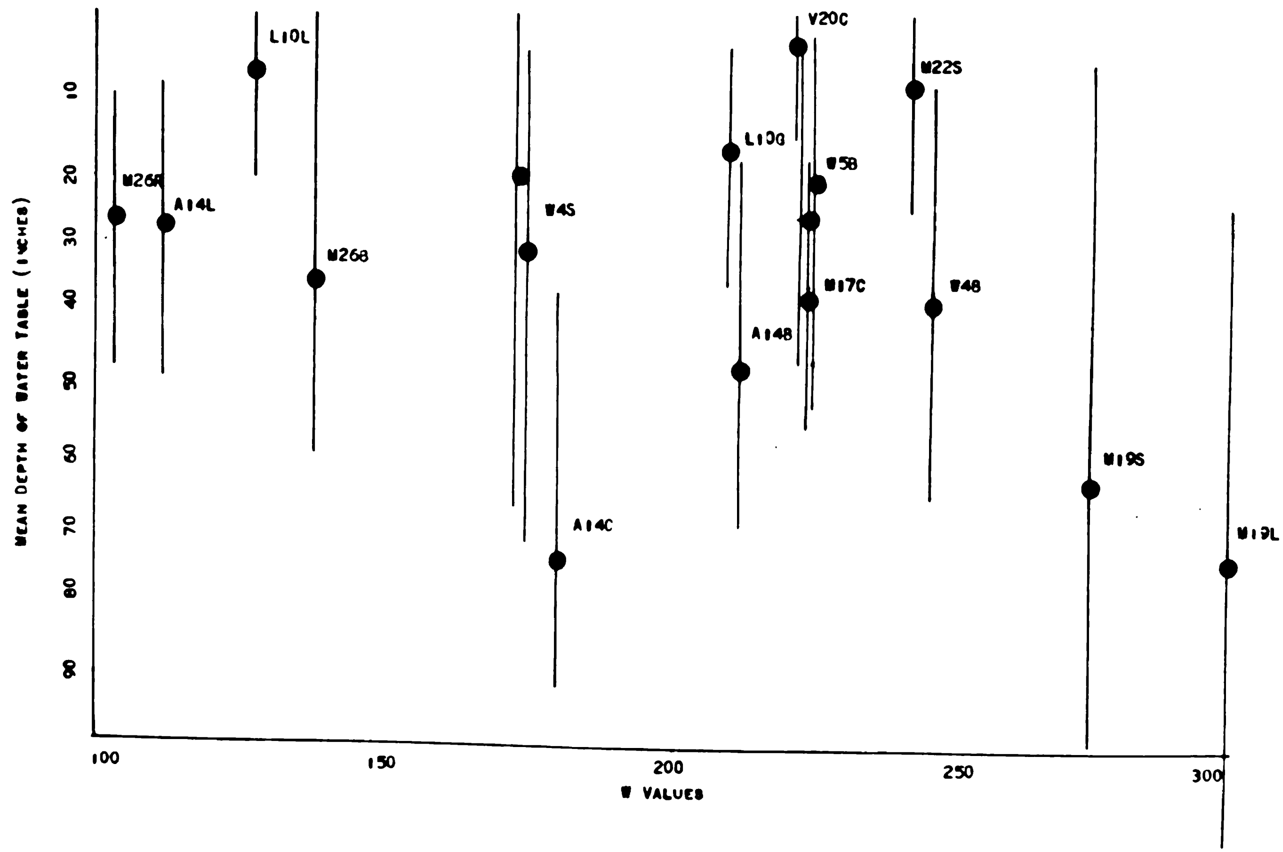

Fig. 39. Relationship of lowland-hardwood stands based on mean water table depth and W values showing the range of water table fluctuation during the growing season.

the gradient while green ash and swamp white oak increased in this direction.

Changes in the importance of American elm, even on some of the mineral soils, were inconsistent with changes in the importance of the other three species. This could be attributed to the fact that the graph shows only present day community conditions. All stands within the study area were not at the same developmental stage in succession. The degree of importance attained by American elm, within any stand must necessarily be due to the amount of elapsed time since the species became important in the intermediate phases of secondary succession. Because of its terminal position in lowland succession, a nearly pure stand of American elm would represent the finite stage of development on very poorly drained soils.

A graph based on mean water table depth and the continuum placement of lowland-hardwood stands (Figure 40) was constructed for comparison with the values derived from the formula method. By referring to the respective figures, several similarities as well as differences are apparent. It may be noted that the paracentrical figures derived from using the continuum as an index of similarity are not greatly unlike the figures derived by the formula method. This is evident for stands found on organic as well as mineral soils. Within this representation four additional stands, each located on contrasting soil types and moisture regimes, were plotted from several observations of ground water depths during the course of the study.

The chief distinction between the two graphic treatments is that the continuum does not represent a two-dimensional compression of similarities in vegetation but rather one dimension. Even so, the use of the continuum values along the abscissa lends credence to the thesis that a strong correlation exists between tree composition in lowland-hardwood stands and the mean depth of their respective water tables. Evidence in support of this thesis is shown in the continuing decline of stand position with increasing

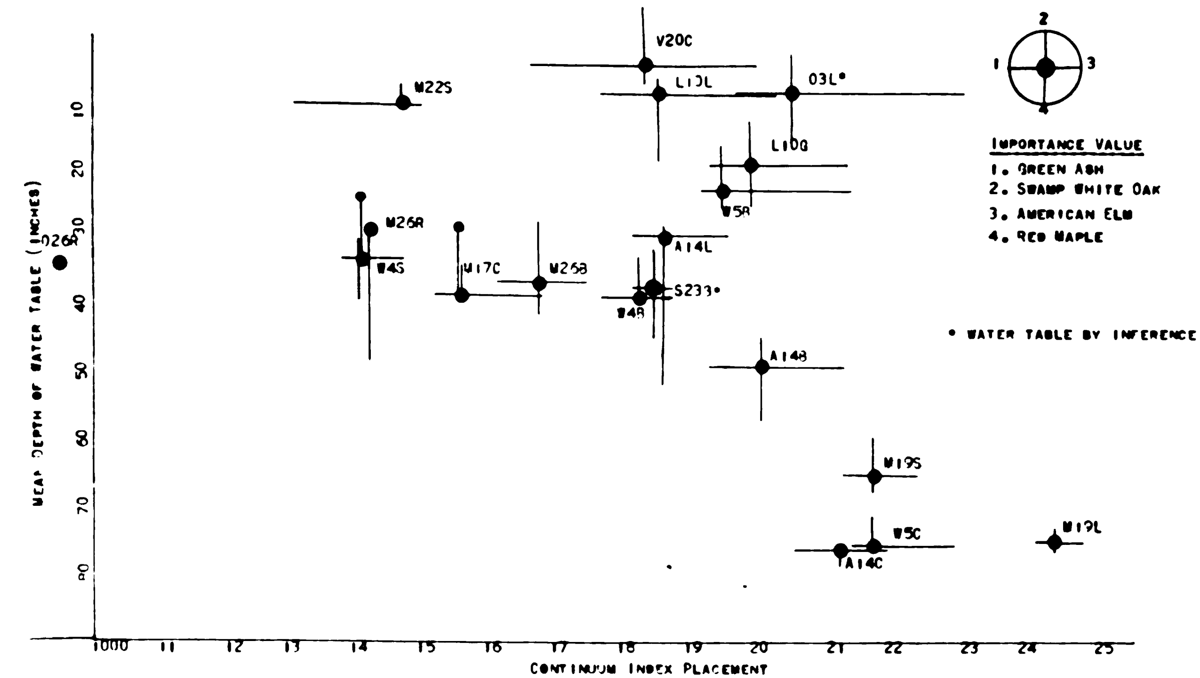

Fig. 40. Relationship of lowland-hardwood stands based on their continuum index placement and average water table depth during the growing season.

ground water depth toward the lower right. Of some importance is the fact that the use of the continuum failed to show dissimilarities between stand composition on alluvial soils compared to peats.

As a means of strengthening the ordination by the formula method, an additional calculation was performed resulting in a change of stand order along the abscissa. This procedure involved the integration of units in ground water depth and fluctuation with the W values obtained from the table. The multiplication of respective values resulted in an increasing spatial assignment for stand position which could be best represented on a logarithmic scale. The abscissa, or original W values axis, was expanded to 5.77 times the original range. An example of the construction using percent organic matter or loss on ignition is shown in Figure 41. The catenal relationships of water tables are also indicated.

Although a strong separation of the stands is again evident, the principal distinction lies in the shifting of stand position. Compared to the former technique, where the position of each stand along the axis was based solely on vegetation similarities, a more logical sequence with respect to the continuum is now indicated. This is most obvious for stands on mineral soils. Those stands on alluvial and beta-gleys have been shifted considerably toward the left side of the gradient. Stands found on the alpha-gleys of ground moraines and basin depressions have brought closer together. Stands located on beta-gley tills having better drainage conditions have moved upward toward the right edge of the gradient.

It may be noted that some stands on organic soils have been shifted downward a considerable distance while others have moved upward on the gradient. Within the organic soil group, red maple is now somewhat better represented to the right of those stands containing American elm, swamp white oak, and green ash as the major species. Such evidence would appear

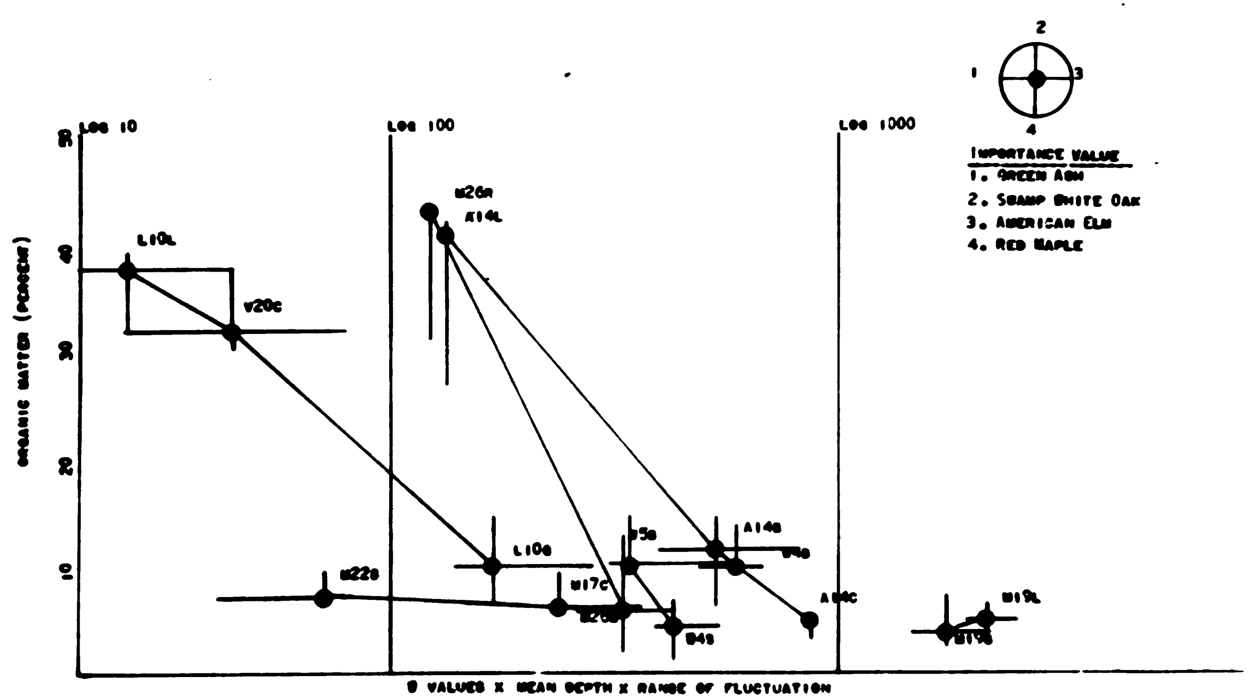

Fig. 41. Relationship of lowland-hardwood stands based on the organic matter content of the soils (loss on ignition) and a logarithmic scale of W values X mean water table depth X range of water table fluctuation.

to be in conflict with the expected ordering of stands on the basis of community resemblances. The positions of the stands along the gradient, however, are being influenced mainly by the water table regimes within the stands. The entire spatial displacement between stand points is indicative, therefore, of a compromise between the present composition of lowland hardwood stands and the trends of gradual or rapid alteration in composition to be expected over a period of years. Relatively rapid changes in tree composition would be indicated by a substantial displacement along the horizontal axis while stands in juxtaposition would be similar in their trends of change.

Succession in the Lowland Hardwood Complex-- It is obvious that certain difficulties are inherent in trying to portray community relationships brought out by the foregoing techniques. The rise or fall of stand position along the ordinate is entirely dependent upon the changing values in a selected parameter of the environment. The position of each standpoint, is actually within a sphere of values within the environment and each stand point is a result of sample size. Such relationships especially those concerning succession may be more easily visualized through the construction of a three-dimensional model.

Succession in hardwood stands of the lowland survey, implied by the most significant variables of the environment, is represented in Figure 42. The construction is based on present stand positions in the continuum, depth of the organic mantle in organic soils, mean moisture equivalent of the alpha and beta-gley soils, and mean water table depths and fluctuations which occurred during the 1961 growing season. The figure in its entirety indicates a probable succession of 15 lowland hardwood stands. Five of these stands are located on organic soils, six on alpha-gleys, and four on beta-gley soils. The soil types are represented by three colors; red for organic soils, green for alpha-gleys, and orange for beta-gleys.

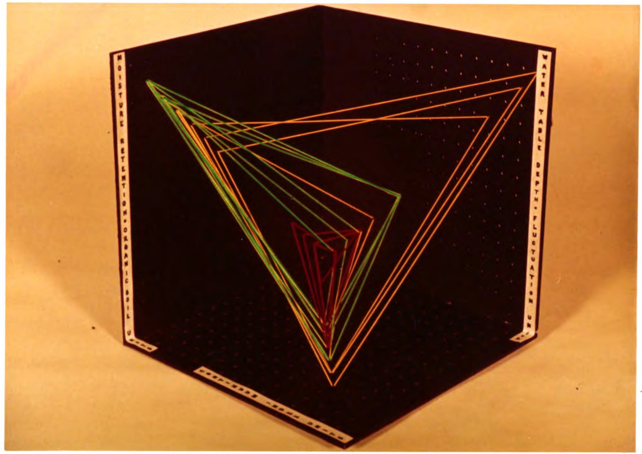

Fig. 42. A construction for 15 lowland hardwood-stands based on their present continuum position, organic matter and moisture equivalent units, and units of mean water table depth and fluctuation.

The construction may be envisaged as proceeding from the center of a vortex outward along three axes. The stands are represented as a series of interlocking triangles which by definition are either isosceles, equilateral, or oblique. Each stand or triangle is tilted at a slightly different angle depending on the plane from which it is viewed. The three axes have each been divided into comparative units of 30 parts as follows:

a. axis 0-X, proceeding along a line from the geometric center of the construction to the foreground and representing the present position of each stand in the continuum (range 300-3000).

b. axis 0-Y, proceeding along a line from the geometric center of the construction to the upper left and representing:

aa. depth of the organic mantle in organic soils (lower third of the axis, 1-3 levels or units)

bb. mean moisture equivalent of the alpha and beta-gley soils (upper two-thirds of the axis, 3-30 units), and

c. axis 0-Z, proceeding along a line from the geometric center of the construction to the upper right and representing units of mean water table depths times range of fluctuation (0-30 units in logarithmic scale).

The position of each stand along the continuum (axis 0-X) reflects the progression of successional change through time to the present, as defined by stand-species composition. Along this axis the penetration of planes, representing stands on organic soils, into the segment of the continuum occupied by stands on alpha-gleys is attributable to the elapsed time since the origin of each stand. It may be noted that all stands on organic soils are represented by a cluster of red triangles having their furthest extension along this axis. The group as a whole resembles a small pyramidal viewed from the terminal position in the continuum. The diminutive base of each triangle is caused from two repressive factors, which may be considered inseparable and essential to the subjugation of lowland hardwood succession on organic soils. Most important are the suppressing effects of ground water remaining close to the soil surface. Of secondary importance is the curbing effect of increased depth to the mantle of organic matter inherent in such stands.

Those stands growing on alpha-gley soils, represented by a cluster of green triangles, are tilted toward the upper left (axis 0-Y) and become almost congruent when viewed from the terminal position of maximum moisture equivalent. The fact that alpha-gley soils possess higher moisture equivalents than beta-gley soils indicates that conditions should be quite favorable for the advance of lowland succession toward a mesophytic climax. This is dependent of course upon the trend of future drainage patterns. Such a situation could only be brought about by increased ditching of adjacent wetlands, or a series of droughty years causing a general lowering of phreatic water levels. At the present time, however, changes in the species complement of this particular group of stands is subservient to the smothering effects of high ground water. It may be observed that the planes representing certain stands on alpha-gley soils are interlaced with stands on organic soils, while others are intermediate along the 0-Z axis. The fact that the pyramidal figure representing stands on alpha-gley soils appears to tilt upward to the left is a result of the continuing pressure exerted by recurrent periods of innundation. This condition of course serves to limit further extension along the 0-Z axis.

Those stands growing on beta-gley soils are represented by a cluster of orange triangles having their furthest extension along two axes (0-X and 0-Z). This results from the fact that phreatic water tables were much deeper in these stands compared to others and the nearly terminal position occupied by these stands along the continuum. The intermediate extension along axis O-Y is indirectly a result of coarser textured materials in the soil profiles, compared to the alpha-gley group. When projecting the line of sight to the focal center of the figure, it may be observed that between stand separation is greatest on the beta-gley soils. In addition, the narrow base pyramid representing this group appears to be falling into the center of the figure. This is an optical illusion created by the crossing of planes at the top of the figure and the lower position of stand M17C along the O-Z axis.

As a whole, stands of the beta-gley group are actually tilted upward to the right, a result of greater fluctuation and depth in ground water. The degree of spatial separation along the O-Z axis, between this group and the others, is indicative of a somewhat faster rate in progressive successional change for stands on these soils.

A review of comparative values between the present position of each stand in the continuum based on its present vegetation, with a projection of probable successional changes indicates the following:

a. stand W4S will proceed toward some point close to a mesophytic climax at the fastest rate.

b. stands M17C and M26B will proceed at about two-thirds the rate of the preceeding stand, but one-third more rapidly than stands M22S, W4B, and A14C.

c. stand M26R will proceed most rapidly toward the stand character represented at the present time by stand A14L.

d. stand A14L will show the smallest rate of progressive change, together with stand V20C.

e. stands L10L and L10G will continue to progress very slowly from their present stand character. They may or may not be dominated by American elm, depending upon the eventual progress of the Dutch elm disease. If this species gives way to the disease, the stands will be dominated by red maple.

f. since stands O26R and M19L form the reference stands, a shift from one direction to the other is not apparent. It would be expected, however, that stand M26R will progress rather slowly to the stage of vegetation now exemplified by stand M26R. Stand M19L should continue toward the mesophytic climax at a slightly faster pace than either stand M19S or A14C.

Discussion-- In most cases, the lowland hardwood stands represented by the trend lines of succession in the ordination are relatively stable communities. The host of extremely complex interactions, within the sequence of generations that produced these stands, has been instrumental in determining the character of the stands. The stands represented by the cluster of green triangles in the center of the construction are probably the most stable of any group, because of the greater numbers of species present within their boundaries. By the very nature of their age-structure, these forested communities are practically immune to invasion by other species. In general, the continuing pressures exerted by high ground water serves to set the limits within which the composition and structure of the stands can vary. Although these communities are by no means as diverse in species composition as their counterparts on upland soils, they are diverse within their own realm.

Outside and below this area of green triangles in the ordination diagram, the group of stands represented by the set of red triangles are less diverse forested communities with few species. In these stands the more rigorous environment, deep organic mantle, low pH, and high ground water, are probably instrumental in maintaining a lower species diversity than in the stands on alpha and beta-gleys.

The area in the ordination occupied by the series of orange triangles presents a somewhat different picture. Since this zone forms an area of ecological overlap between mesic and wet-mesic sites, it contains numerous species from both lowland and upland areas. With this resultant increase in diversity the variability from place to place is greater. Although the normal development of these sites is not expected to bring about drastic changes within the immediate future, water table fluctuations control the wealth of species. These communities are therefore seasonably unstable and subject to the periodicity of continual or irregular hydrologic variation.

Taken as a unit, the lowland hardwood complex represents a relatively homeostatic situation. The successional changes outlined in the preceeding are dependent, therefore, upon an assumption that future land use and drainage patterns will remain essentially unchanged.

SUMMARY

A considerable acreage occupied by lowland-hardwood forests in southern Michigan is considered to have a storage and stabilizing influence on ground water supplies. Since little is known about the composition, ground water hydrology, successional relationships, and general ecology of these forests the present study is an attempt to provide preliminary information on these subjects.

Measurement of the number, size and distribution of tree species in the lowland-hardwood stands was accomplished using four sampling methods. A plot method was used as a standard for the study against which data were compared from other methods. Non-areal methods included random pairs, the point-centered quarter, and the variable plot-radius methods.

In order to determine the relative reliability of the various sampling methods, simple correlations (r), were calculated between three parameters (basal area, frequency, and density), as determined from each of the methods. The relationships indicated by the use of coefficients of determination (r^2) showed that any of the four sampling methods gave almost as much information about the three parameters as did the best method. The quarter method was recommended for further use in lowland-hardwood ecological surveys.

The same measures (basal area, frequency, and density) were used in describing the composition of the stands selected for the study. Continuum indices were calculated for all lowland-hardwood stands. These indices indicated a rather complete coverage for the spectrum of lowland sites. The range of continuum values varied from a low 680 to a high 2430. Most of the stands were clustered within a segment of the range from 1800 to 2200.

Importance values calculated from the three parameters proved to give the best measure of species dominance. The leading dominants in the study were American elm, red maple, green ash, swamp white oak, silver maple, slippery elm, and American basswood.

The effects of fire and pathogenic influences, windthrow and rooting systems on community structure of lowland-hardwood stands were discussed. The role of fire in the ecology of these forests appeared not to be of consequence in determining its vegetation. Windthrow and rooting of certain lowland tree species served to influence the eventual stand-age-structure of lacustrine forests. This condition was most evident in stands found on organic soils. Thedevelopment of the understory and ground flora ranged from one extreme to the other on poorly-drained soils. As drainage conditions became more favorable the density of the flora increased. Differences in frequency and density of the ground flora could be partially attributed to the effects of seasonal flooding.

An examination of the soil profiles showed that the majority of soil types were alpha-gleys which were poorly drained.

Soils were analysed for total sand, silt, and clay content. Other analyses included moisture equivalent, loss on ignition, and pH. Differences in soil characteristics between the stands were evaluated statistically.

Simple correlations were calculated between the importance values and basal areas of the ten most abundant species and soil physical properties. Two species showed some tendency to be found on soils with certain physical characteristics--black cherry and slippery elm. Because the presence of non-significant correlations between soil characteristics in different horizons was great, it was suggested that future vegetation studies in the lowland-hardwood land type should ignore the measurement of physical soil parameters.

Weekly measurements of water table levels during the 1961 growing season were recorded for 72 ground water wells. Differences in water table depths between the stands were evaluated statistically. The greatest changes in true water levels occurred in beta-gley and certain alpha-gley soils. Actual water table variation was least in poorly-drained mucks. Maximum depths of water tables occurred in most stands during the last two weeks of the growing season. At the termination of the study only the water tables in organic soils and the alpha-gley soils of four stands were fully recharged. All other water tables were within 3 to 16 inches of the level observed when the study began. Recharge of the true water tables occurred within a few hours after convectional storms. Advanced storms producing rainfall intensities exceeding .5 and .9 inches/hour caused a partial recharge of subsurface waters.

Simple correlations which were calculated between the importance values and basal areas of the ten most abundant species and ground water depths during the growing season involved two species--sugar maple and American basswood. Additional statistical analyses were performed between water table depths and the date of measurement. It was suggested that a subsequent series of ground water measurements to give maximum information on water table depth could be substantially reduced.

As a means of depicting the behavioral pattern of lowland-hardwood forests the stand to stand relationships based on vegetation similarities and environmental measures were included in a series of graphs. Using the continuum as an index of similarity was not unlike the figures derived from a formula method. Succession in lowland-hardwood stands implied by the most significant environmental measurements was represented in a dimensional figure.

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APPENDIX I

TABLE.-29 Profile means for alpha-gley and beta-bley soils, showing differences between soil texture, moisture equivalent, loss on ignition and reaction.[a]

Soil group Soil series, and stand	Physical and chemical parameters Content of sand	silt	clay	Moisture equivalent	Loss on ignition	pH
	percent					number
BETA-GLEYS						
Locke M10L	57.15	24.95	17.90	18.12	5.53	7.29
[illegible]ks [illegible]	77.3[illegible]	12.85	9.80	14.93	4.19	7.13
[illegible]over [illegible]4C	50.7[illegible]	33.05	16.25	23.49	5.18	6.98
Ceresco M17C	67.75	19.00	12.75	25.48	4.81	7.98
ALPHA-GLEYS						
Brookston A14B	52.60	29.20	17.65	29.35	11.66	6.77
Gilford L10G	72.25	13.96	13.55	26.10	10.63	6.71
Pewamo W5B	45.05	31.35	23.60	30.12	10.74	7.29
Brookston M26B	47.15	31.95	20.90	25.10	6.52	6.49
Cohoctah M17C	58.30	29.10	12.60	19.43	6.66	7.12
Sloan M33S	43.50	36.85	19.65	31.60	7.80	7.32
Sebewa W4S	54.00	29.55	20.45	27.74	4.76	7.93
Gilford W4S	68.75	20.20	10.95	15.89	4.41	7.73
L.S.D. .05	8.70	5.33	5.02	7.23	2.98	1.63
L.S.D. .01	11.60	7.08	6.66	9.58	3.96	2.15

[a] arranged according to soil group and the continuum placement of lowland hardwood stands.

TABLE.- 30. Horizon means for beta-gley soils developed from glacial drift, showing differences in soil texture, moisture equivalent, loss on ignition, and reaction.[a]

Soil type, stand	Soil horizon	Content of sand	Content of silt	Content of clay	Moisture equivalent	Loss on ignition	pH
		percent	percent	percent	percent	percent	number
Locke	A_1	57.0	29.2	13.8	23.7	11.0	7.0
[illegible]y loam	A_2	53.7	[illegible]	14.6	[illegible]	8.5	6.7
[illegible]	B_1	[illegible]	[illegible]	18.0	[illegible]	3.1	[illegible]
	B_2	56.2	[illegible]	21.8	[illegible]	2.8	[illegible]
	C	[illegible]	[illegible]	21.3	[illegible]	2.4	[illegible]
[illegible]inks	A_1	81.8	[illegible]	6.2	[illegible]	10.7	6.7
[illegible] sand	A_2	[illegible]	[illegible]	7.2	[illegible]	6.2	6.9
[illegible]	B_t	85.5	9.0	5.5	5.0	1.4	7.4
	A_{2Bt}	79.3	9.5	11.2	10.5	1.0	7.3
	C	61.3	19.7	19.0	16.2	1.8	7.5
Conover loam	A_{11}	45.5	40.0	12.5	36.6	11.3	6.7
[illegible]	A_{12}	48.0	38.8	13.2	30.0	7.2	6.7
	B_1	48.4	32.3	19.3	19.4	2.6	6.9
	B_2	50.3	30.5	19.2	18.2	2.1	6.7
	C	59.3	23.7	17.0	13.3	2.7	7.8
L.S.D. .05		NS	8.8	8.4	10.6	6.8	.6
L.S.D. .01		NS	11.2	10.7	13.4	9.0	.7

[a] arranged according to soil type and the continuum placement of lowland hardwood stands.

Table.- 31. Horizon means for alpha-gley soils developed from glacial drift, showing differences in soil texture, moisture equivalent, loss on ignition and reaction.[a]

Soil type, stand	Soil horizon	Content of sand	Content of silt	Content of clay	Moisture equivalent	Loss on ignition	pH
		percent					number
Brookston sandy loam A14B	A_{11}	56.7	31.8	11.5	47.3	29.6	6.3
	A_{12}	51.5	34.5	14.0	49.2	19.6	6.2
	B_{21g}	50.6	31.2	18.2	16.6	3.5	6.7
	B_{22g}	54.8	24.7	20.5	17.2	1.9	7.0
	C_g	52.0	23.8	24.2	16.4	3.7	7.7
Gilford sandy loam L10G	A_1	66.7	24.3	9.0	66.2	35.9	6.0
	GB_1	79.4	12.6	8.0	17.9	6.8	6.3
	GB_2	76.7	10.3	13.0	13.2	3.8	7.0
	GB_3	66.1	11.1	21.8	20.2	4.3	6.9
	D_g	72.1	11.6	16.0	13.0	2.4	7.5
Pewamo loam W5B	A_{11}	74.5	36.3	16.2	46.4	23.0	7.1
	A_{12}	43.8	33.0	18.7	36.4	15.9	7.2
	B_{21g}	48.0	28.3	23.7	23.3	7.1	7.4
	B_{22g}	35.8	32.0	32.2	25.8	4.7	7.3
	C_g	45.5	27.3	27.2	18.9	3.1	7.5
Brookston loam M26B	A_{11}	49.0	39.0	12.0	36.8	12.4	6.2
	A_{12}	74.5	36.0	16.5	28.2	8.6	6.0
	B_{21g}	48.5	31.5	20.0	22.0	5.9	6.5
	B_{22g}	4.15	30.7	27.8	21.3	3.7	7.7
	C_g	49.5	22.4	28.1	17.3	2.0	7.1
Sebewa loam W4S	A_1	51.6	33.2	15.2	49.9	13.2	7.5
	GB_1	54.6	24.0	21.4	28.2	2.8	8.0
	GB_{21}	45.6	26.7	27.7	26.7	3.1	7.9
	GB_{22}	52.6	24.2	23.2	23.2	1.1	8.1
	D_g	65.8	19.5	14.7	10.8	3.7	8.3
Gilford sandy loam W4S	A_1	66.8	25.2	8.0	29.4	11.9	7.5
	GB_1	66.1	22.1	11.8	15.3	3.7	7.6
	GB_2	67.5	18.5	14.0	15.1	2.6	7.7
	GB_3	66.2	20.0	13.8	12.5	1.8	7.7
	D_g	77.0	15.2	7.8	7.1	2.1	8.2
L.S.D..05		NS	8.8	8.4	10.6	6.8	.6
L.S.D..01		NS	11.2	11.2	13.4	9.0	.7

[a] arranged according to soil type and the continuum placement of lowland hardwood stands.

Table.-32. Horizon means for alluvial soils showing differences in soil texture, moisture equivalent, loss on ignition, and reaction.[a]

Soil type, stand	Soil horizon	Physical and chemical parameters					
		Content of sand	Content of silt	Content of clay	Moisture equivalent	Loss on ignition	pH
		percent	percent	percent	percent	percent	number
Ceresco sandy loam M19L	A_1	56.0	30.0	14.0	43.2	10.5	7.5
	C_{1g}	60.2	25.5	14.3	32.9	7.1	8.0
	C_{2g}	62.7	21.0	16.3	24.4	3.8	8.0
	C_{3g}	73.0	14.6	12.4	19.7	1.5	8.1
	C_{4g}	78.0	6.3	6.7	7.3	1.2	8.4
Cohoctah sandy loam M17C	A_1	61.1	30.4	8.5	29.7	16.5	6.6
	G_1	57.8	32.9	9.3	23.1	8.5	6.7
	G_2	55.6	29.7	14.7	15.6	4.1	7.5
	G_3	55.6	28.9	15.5	15.4	2.6	7.4
	C_g	61.4	23.6	15.0	13.5	1.6	7.4
Sloan loam M22S	A_1	42.4	42.0	15.6	51.4	17.1	7.1
	C_{1g}	43.4	413	15.3	37.0	12.3	7.2
	C_{2g}	43.4	34.5	22.1	23.4	4.5	7.5
	C_{3g}	41.7	34.5	23.8	24.1	1.5	7.5
	C_{4g}	46.7	32.0	21.3	22.1	3.6	7.4
L.S.D. .05		NS	8.8	8.4	10.6	6.8	.6
L.S.D. .01		NS	11.2	10.7	13.4	9.0	.7

[a] arranged according to soil type and the continuum placement of lowland hardwood stands.

TABLE.- 35. Profile and horizon means for organic soils, showing differences in loss on ignition and reaction.[a]

Soil type, stand	Soil horizon	Chemical parameters: Loss on ignition		pH	
		profile	horizon	profile	horizon
Linnwood muck A14L	O_1		59.4		5.6
	O_2		62.1		6.1
	O_3	41.7	54.8	6.24	6.3
	O_4		29.2		6.4
	D_g		3.1		6.0
Linnwood muck L10L	O_1		52.3		6.4
	O_2		59.6		6.6
	O_3	38.77	54.5	6.76	5.6
	O_4		25.2		7.6
	D_g		2.2		7.7
Carlisle muck V20C	O_1		42.1		6.9
	O_2		58.2		6.7
	O_3	32.58	51.8	7.27	7.0
	O_4		7.0		7.8
	O_5		4.0		8.0
Rifle peat M26R	O_1		63.6		4.5
	O_2		73.6		3.9
	O_3	44.15	71.5	4.50	3.8
	O_4		9.3		5.0
	D_g		2.8		5.2
L.S.D. .05		3.34	13.2	1.63	.6
L.S.D. .01		4.47	17.4	2.15	.7

[a] arranged according to soil type and the continuum placement of lowland hardwood stands.

TABLE.-[illegible]. Horizon means of underlying materials of the beta-gley, alpha-gley, and organic soils showing differences in texture.[a]

Soil group Soil series, and stand	Soil horizon	Content of sand	Content of silt	Content of clay
		-----percent	---------	
BETA-GLEYS				
Locke M19L	C	50.7	28.0	21.3
Spinks M19S	C	61.3	19.7	19.0
Conover A14C	C	59.3	23.7	17.0
Ceresco M17C	C_{4g}	87,0	6.3	6.7
ALPHA-GLEYS				
Brookston A14B	C_g	52.0	52.0	24.2
Gilford L10G	D_g	72.1	11.6	16.0
Pewamo W5B	C_g	45.5	27.3	27.2
Brookston M26B	C_g	49.5	22.4	28.1
Cohoctah M17C	C_g	61.4	23.6	15.0
Sloan M22S	C_{4g}	46.7	32.0	21.3
Sebewa W4S	D_g	65.8	19.5	14.7
Gilford W4S	D_g	77.0	15.2	7.8
ORGANIC SOILS				
Linwood A14L	D_g	53.4	23.0	23.9

TABLE -3a. Continued

Linnwood L10L	D_g	77.1	12.0	10.9
Carlisle V20C	D_g	81.0	13.0	6.0
Rifle M26R	D_g	43.9	25.5	25.6
L.S.D. .05		17.6	9.1	11.3
L.S.D. .01		23.3	12.0	15.0

[a] arranged according to soil group and the continuum placement of lowland hardwood stands.

VITA

Robert Louis Bryant

Candidate for the Degree of

Doctor of Philosophy

Dissertation: The Lowland Hardwood Forests of Ingham County, Michigan: their Structure and Ecology.

Major studies: Forestry
Minor studies: Soils and Statistics

Biographical Data:

Birthdate: January 3, 1928, New York N.Y.

Undergraduate studies:

McNeese State College, 1949,-1950.
Louisiana State University, Forestry Dept., 1950-1953.
B.S. 1953.

Graduate studies:

Louisiana State University, Forestry Dept,, 1954.
M. S. 1954.
Michigan State University, Forestry Dept., 1959-1962.

Experience:

Research biologist, Louisiana Wildlife and Fisheries Commission-Fish and Game Section., 1952-1953.

Refuge biologist, Rockefeller Refuge, Grand Chenier, La., 1954.

Assistant Professor of Forestry., McNeese State College, Dept. of Plant Science, 1954-1959.

Graduate Teaching Assistant., Michigan State University, Forestry Dept., 1959-1962.

Assistant Professor of Forestry., McNeese State College, Dept. of Agriculture, 1962 to present.

Member:

Alpha-Zeta
XI Sigma Pi
Society of American Foresters

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