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AFFINITIES OF THE FLORA OF THE ILLINOIAN TILL PLAIN OF SOUTHWESTERN OHIO¹

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THE Illinoian till plain of southwestern Ohio² is a more or less delimited floristic district distinguished from adjacent areas by the presence of a group of characteristic species, by the occurrence of a number of species not in adjacent areas, by the greater abundance or even dominance of certain species rare or absent in either of the adjacent areas, and by the pronounced northern affinity of its flora. It is further marked by the paucity of its flora and by the absence of most of the showy spring flowers abundant in hillier sections of southern and southwestern Ohio, as *Erythronium*, *Trillium*, *Camassia*, *Anemonella*, *Isopyrum*, *Hepatica*, *Delphinium*, *Aquilegia*, *Jeffersonia*, *Sanguinaria*, *Stylophorum*, *Dicentra*, *Erigenia*, *Hydrophyllum*, *Mertensia*, *Senecio* and others.

Eastward, the till plain is separated by but a short distance from the eastern margin of the Interior Low Plateau with its prairie relic communities with rich mid-western flora, and from the Allegheny Plateau with its distinctly Alleghenian flora. (Braun, 1928a.) Westward, it overlaps the Cincinnati region, a dissected limestone and

¹ The reproduction of the maps in this paper is made possible through aid to RHO-DORA from the National Academy of Sciences.

² This area covers approximately 1500 square miles to the east of the Little Miami River (FIGS. 4 and 5). Topographically, it is a flat or nearly flat upland, in places as yet little dissected by stream valleys, and covered by a mantle of glacial drift of Illinoian age. Due to the youthful topography of parts of the area, certain habitats have remained relatively unchanged since the Pleistocene. Acid soils prevail in the area; the Clermont silt loam or "white clay" is the most characteristic, and has developed on all the flattest portions of the area. Because of poor drainage, hydromesophytes find favorable habitats. The plant ecology of this region is treated in "Forests of the Illinoian till plain of Southwestern Ohio," Ecological Monographs, in press.

drift area (Braun, 1916). Northward, it is bounded by the rolling

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Wisconsin glacial plains which comprise a large section of western Ohio. In number of species it is much poorer than the regions to east or west, though it contains some found neither to east or west.

PLANTS OF ILLINOIAN TILL PLAIN NOT FOUND IN ADJACENT AREAS, OR ABUNDANT OR CHARACTERISTIC IN THE TILL PLAIN AND RARE OR ABSENT IN EITHER OF THE ADJACENT AREAS. PRESENCE PERCENTAGE INDICATED BY THE 1 TO 5 SCALE; ABSENCE BY X.

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Aspidium noveboracense*23Viola lanceolataX1XLophotocarpus calycinusX1 -XNeksia virginicaX1 -XLuzula campestris var. bulbosaX11Cornus racemosaX3XLuzula campestris var. bulbosaX1XYaccinium stamineumX14Uvularia perfoliataX12Yaccinium stamineumX14Uvularia perfoliataX12Yaccinium stamineumX14Smilax Bona-noxX24Gentiana SaponariaX1-2XHabenaria peramoena1-3XPhlox maculata1-2XTipularia discolorX1-1var. odorataX2-3XPolygonum arifolium1-2Xvar. macrospermaX1XRanunculus pusillusX1XGerardia flava4X1XRanunculus hispidus var. falsusX11XGelaium tinctorium*2XSpiraea tomentosa Spiraea alba (Rosa palustris)X1X11X11Lobelia cardinalis (Rosa palustris)14X1112XSpiraea alba (Rosa palustris)14X1111XIbubs hispidus (Rosa palustris)14<		Cincinnati Region	Illinoian Till Plain	Mineral Springs Reg.		Cincinnati Region	Illinoian Till Plain	Mineral Springs Reg.
	Aspidium noveboracense Lophotocarpus calycinus Juncus bufonius Luzula campestris var. bulbosa Uvularia perfoliata Smilax Bona-nox Habenaria peramoena Tipularia discolor Salix discolor Polygonum arifolium Polygonum arifolium Polygonum sagittatum Stellaria longifolia Ranunculus laxicaulis Ranunculus laxicaulis Ranunculus pusillus Ranunculus hispidus var. falsus Anemone quinquefolia Cardamine bulbosa Spiraea tomentosa Spiraea alba Spiraea latifolia Pyrus melanocarpa Rubus hispidus Rosa carolina (Rosa palustris) Baptisia leucantha Linum striatum Callitriche heterophylla Ilex verticillata Vitis labrusca Viola cucullata	* XX XXX1-X1-1-1-1 * XX XX1 XXXXX 1 + 1 X* *	$\begin{array}{c} 2\\ 1 \\ -1\\ 1\\ 1\\ 2\\ 3\\ 1 \\ -3\\ 2\\ 3\\ 2\\ 1\\ 1 \\ -3\\ 2\\ 3\\ 2\\ 1\\ 1 \\ -2\\ -3\\ 1\\ 4\\ 1 \\ -2\\ -3\\ 1\\ 4\\ 1 \\ -1\\ 1\\ 4 \\ +4\\ 3\end{array}$	3 X 1 X 2 4 X 1 X X 1 X X X X X X X X X X X X X X	Viola lanceolata Viola pallens Viola sagittata Rhexia virginica Cornus racemosa Chimaphila maculata Vaccinium stamineum Vaccinium vacillans Gentiana Saponaria Phlox maculata var. odorata Myosotis virginica var. macrosperma Verbena hastata Trichostema dichotomum Pentstemon calycosus Pentstemon digitalis Gerardia flava (Aureolaria flava) Galium tinctorium Mitchella repens Viburnum pubescens var. indianense Viburnum Lentago Lobelia puberula Lobelia cardinalis Vernonia noveboracensis Solidago rugosa Aster umbellatus Solidago serotina Pluchea petiolata Hieracium marianum	XXXXXX [†] XXXX X X X X ¹ ¹ X X [*] ¹ X X [*] X X X X [*] X X X X X X X X X X X X X X X	$\begin{array}{c} 1\\1\\-1\\1\\3\\2\\1\\1\\-2\\-3\\1\\1\\-\\1\\-\\1\\-\\1\\-\\1\\-\\1\\-\\1\\-\\1\\-\\1\\$	XX3 1-X1 4 4 X X X X X X X X X X X X X X X X X

* Only in flat upland areas of the Cincinnati region, and hence in habitats which are western outliers of the till plain.

† Present in one station only.

‡ Reported nearly 100 years ago from one station which was ecologically similar to the till plain; now extinct (Braun, 1934).

Of approximately 200 species (exclusive of trees, grasses and sedges) of the till plain communities, 35 do not occur in the dissected Cincinnati region or even in dissected areas in the counties in which the till plain is most extensive and 39 do not occur in the Mineral Springs region of Adams County which is but a short distance to the east. Of these, 23 occur in neither region. The occurrence of 51 species absent in adjacent regions to east or west or both, emphasizes the floristic distinctness of the till plain. These species and six additional which are very rare to east or west are listed in the accompanying table, together with presence percentage (Pr %) of each.¹ Grasses and sedges are not included because of incomplete records.

The geographical distribution of the eight species of trees of highest percentage occurrence (Pr %) in the till plain is shown in the map, FIG. 1. Of these trees, only *Liquidambar styraciflua*² is floristically distinctive; the rest are general in Ohio. It is not found west of the till plain in southwestern Ohio, though it is abundant in the "Flats" of southeastern Indiana. Eastward, in the Allegheny region, it is a tree of alluvial flats. In the till plain, it is general only in the southern half (FIG. 2A) and scattered in the northern part. North of the till plain it is known in only a few stations. Similarly in Indiana, Liquidambar extends just north of the Illinoian drift area (Lindsey, 1932). Its known distribution in Ohio, Indiana and Kentucky is such as to suggest a relation to preglacial drainage patterns (FIG. 2B); due to post-glacial migration it has extended its range slightly into adjacent favorable territory. Fraxinus profunda, a distinctly southern species of the Mississippi embayment, is present in two stations in the till plain and not elsewhere in Ohio. Cow oak (Q. Michauxii Nutt. or Q. Prinus L), one of the characteristic trees of the Indiana "Flats" (Lindsey, 1932) does not enter our area.

Certain of the shrubs are very characteristic of this area. A larger number of shrubs is present than in the adjacent dissected areas. All except those of late successional stages are species requiring abundant soil moisture or acid soil or both. The widespread species are best represented by *Cephalanthus occidentalis*, which is transcontinental in range and reaches from the Gulf of Mexico to Canada. This species

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¹ "By presence is meant the more or less persistent occurrence of a species in all the stands of a certain community." (Braun-Blanquet, 1932). As defined by Cain (1932). "Presence concerns the degree of regularity with which species reoccur in different examples of an association." This may be expressed in percentage, or less exactly, in the 1 to 5 scale suggested by both Braun-Blanquet and Cain.

² Nomenclature according to Gray's New Manual of Botany, 7th edit., 1908, except as noted.

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is generally distributed in the wettest places in the till plain. Alleghenian species of acid soils are represented by *Vaccinium stamineum* (FIG. 4A) and *V. vacillans*, both of which are rare and local in the till plain. *Smilax glauca* (FIG. 4B), of southern range, is common, though



FIG. 1. Geographic distribution of eight trees of highest percentage occurrence in the till plain. Spokes of wheel in lower right-hand corner give direction of lines used for species indicated by numbers at ends of spokes:

1.	FAGUS GRANDIFOLIA	4.	ACER RUBRUM	7.	LIQUIDAMBAR
2.	QUERCUS ALBA	5.	ULMUS AMERICANA		STYRACIFLUA
3.	QUERCUS PALUSTRIS	6.	CARYA OVATA	8.	NYSSA SYLVATICA

southern species are on the whole few and unimportant in the area. Northern and northeastern species, as Vitis labrusca, Spiraea tomentosa (FIG. 4C), Spiraea alba, Ilex verticillata, Pyrus melanocarpa, Rubus hispidus, Salix discolor and Viburnum Lentago, prevail. The map, FIG. 3, of the superimposed ranges of these eight species emphasizes

the general northeasterly range of the shrub flora of initial and intermediate successional stages. *Viburnum pubescens* var. *indianense* Rehder, is an endemic of the Illinoian till plain of Indiana and Ohio;



FIG. 2A. Distribution of LIQUIDAMBAR STYRACIFLUA in the Illinoian till plain (See FIG. 5).

the species from which it is isolated is of northern distribution. This is in contrast to that of the trees, which is to be expected, as the trees entered later with the advance of forest after Illinoian glaciation. *Rosa setigera* and *Hypericum prolificum* are more central in range.

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As the later successional stages are reached and the vegetation approaches the climatic climax, shrubs of more southerly or wider range enter, as *Benzoin aestivale*, *Asimina triloba* and *Sambucus canadensis*.

Among the herbaceous plants, great variety is exhibited in types of geographic ranges. Species whose general range is comparable to that of deciduous forest prevail; this distribution is illustrated by *Medeola virginica*, *Polygonum sagittatum*, *Chelone glabra*, *Lobelia*



FIG. 2B. Distribution of LIQUIDAMBAR STYRACIFLUA in the Ohio Valley region (Data by courtesy of E. N. TRANSEAU).

cardinalis and Solidago rugosa of pin oak openings and secondary meadows and by *Pedicularis canadensis* and *Mitchella repens* of initial and intermediate forest stages of succession. All of these occur on the Illinoian till plain of Ohio and Indiana and are more or less generally distributed in these states.

Certain species, as Aspidium noveboracense, Polygonum arifolium, and Chimaphila maculata (FIG. 4D) are somewhat more eastern in range. Such species are general in eastern (Alleghenian) Ohio and more local westward in Ohio and Indiana.

Hierochloë odorata (FIG. 4E), Anemone quinquefolia, Viola cucullata, Viola lanceolata and Viola pallens are the most northern in range of

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the plants of the till plain. The distribution displayed by these species in Ohio and Indiana is of particular interest. All occur in the northern, particularly lake counties, of these states, and in certain southern counties, particularly those affected by Illinoian glaciation. *Hiero*-



FIG. 3. Geographic distribution of eight characteristic shrubs of the till plain; pronounced northerly range evident:

- 1. VITIS LABRUSCA
- 4. ILEX VERTICILLATA 7. SALIX DISCOLOR
- 2. Spiraea tomentosa 5.
- 5. Pyrus melanocarpa 8. Viburnum Lentago
- 3. SPIRAEA ALBA
- 6. Rubus hispidus.

chloë in Indiana is confined to the north. The gap between northern and southern stations is pronounced in all except Anemone quinquefolia, a more mesophytic species than the others. This distribution appears to be related to glacial and post-glacial migrations; in the southern stations the species are relics (Braun, 1928b). Their absence from intermediate stations may be due to the Wisconsin xerothermic period.

Lilium canadense, Houstonia caerulea and Aster umbellatus are intermediate in range between the northern species and species of deciduous forest range. They display more general distribution in Ohio and Indiana than the more northern species. However, in Indiana there is some evidence of disruption in range between the "Flats" and other more northern stations for these species. This is to be expected if the peculiarity of ranges of these and the group of more northern species is a result of glacial migrations and climatic restrictions. *Phlox maculata* var. odorata (Sweet) Wherry and *Ra*nunculus hispidus var. falsus Fernald are northern varieties of more widely distributed species. Both are common on the till plain. The distribution of the former is mapped by Wherry (1932).

Only one herbaceous plant of the till plain (an amphibious plant) is extremely southern in distribution, namely Ranunculus pusillus, a plant of the Atlantic and Gulf Coastal Plain and Mississippi embayment. It is known from only one county in Ohio and one county in Indiana, both stations in the Illinoian till plain. Lobelia puberula, Rhexia virginica (FIG. 4G), Tipularia discolor (FIG. 4H), Pluchea petiolata and Lophotocarpus calycinus (FIG. 4I) are southern plants, all more or less rare and local on the Illinoian till plain of Ohio. Lobelia is somewhat scattered in both Ohio and Indiana; Rhexia and Tipularia occur in the south and in the Lake counties in Ohio, Tipularia only in the south in Indiana. Rhexia displays a type of distribution common to many migrating southern plants-stations in unglaciated and adjacent glaciated territory, and along the Great Lakes whither they may have entered by Mississippi valley routes or eastern routes during or following the last or marine substage of the Pleistocene. These southern plants are, in contrast to the northern ones, regarded as relatively recent entrants in the till plain. Lophotocarpus is an example of a southern plant which is much more general in southern Indiana than in Ohio.

Habenaria peramoena (FIG. 4J), Coreopsis tripteris and Baptisia leucantha (FIG. 4K) are central in range, the first with most restricted range but very general in the till plain, the last more western in range and very local in the till plain. The distribution of Baptisia in Ohio (the western half of the state) and its distribution in Indiana (represented in all quarters) is in keeping with its usual community affiliations (prairie) and post-Wisconsin eastward migration. Habenaria, south-central in range, is in both states confined to southern stations, unglaciated and glaciated.

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Wides, as is to be expected, are best represented among the aquatic and amphibous species, though the most widespread and cosmopolitan of such species as *Typha latifolia*, *Spirodela polyrhiza*, *Lemna minor*, *Ceratophyllum demersum*, etc., are absent or rare in the till plain.

Representative examples of the distribution displayed in Ohio and Indiana¹ by plants of the several distribution types are shown in FIG. 4, A to K. To show relation of ranges to age areas of the states, a glacial map, FIG. 4L, is included.

To summarize, the flora of the Illinoian till plain, though composed largely of intraneous species, nevertheless contains a considerable percentage of forms which, if not actually extraneous, have somewhat discontinuous ranges as demonstrated by their absence from adjacent areas. Its species are derived from different floristic regions: species of the deciduous forest region prevail; western species are poorly represented; a few Alleghenian species from the nearby Allegheny Plateau are present; the southern element is represented by tree, shrub and herb species; the strong northern affinity of the flora is demonstrated by a considerable group of species of north-northeastern range. This northern affinity is also indicated by the "life form spectrum" of the younger successional communities (Withrow, 1932).

The explanation of the ranges of species which occur on the till plain is to be found in post-Illinoian and recent migrations; post-Wisconsin movements seem inadequate to explain the distribution of the group of northern species. The absence of western species, other than the mid-western *Baptisia leucantha* (FIG. 4K), is in contrast to areas to east and west where relic prairie species do occur. The prairie relics to the west in the Cincinnati region are certainly of Wisconsin age; those to the east in Adams County have been interpreted in a previous paper (Braun, 1928b) as of pre-Illinoian age. The absence of true loess in the region to the east of the Little Miami River—in the area of the Illinoian till plain—is evidence that the Wisconsin xerothermic period was not extreme in this area and hence that occupying vegetation was not displaced by more xeric types. The lack of disturbance to vegetation in southern Ohio by the Wis-

¹Ohio distributions are taken from Schaffner, Revised Catalog of Ohio Vascular Plants, 1932; and from Transeau and Williams, 1929. The distribution of Indiana shrubs from Deam, 1932; of grasses, Deam, 1929. For other distributions, the writer is indebted to Miss Dorothy Parker who has secured the data from distribution records filed at Butler University.

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consin xerothermic period is further attested by the boreal relics along the nearby glacial border to the east, and by the many Tertiary relics, as Styrax, Calycanthus, Halesia, in unglaciated territory not far from the glacial boundary, and by the marked contrast between the vege-



FIG. 4. Examples of types of distribution in Ohio and Indiana displayed by plants of the Illinoian till plain:

- A. VACCINIUM STAMINEUM E. HIEROCHLOË ODORATA I. LOPHOTOCARPUS
- B. SMILAX GLAUCA
- F. VIOLA CUCULLATA
- C. Spiraea tomentosa D. CHIMAPHILA MACULATA H. TIPULARIA DISCOLOR
- G. RHEXIA VIRGINICA
- CALYCINUS
- J. HABENARIA PERA-MOENA
- K. BAPTISIA LEUCANTHA
- L. Glacial map of Ohio and Indiana (after LEVERETT): EW. Early Wisconsin.
- U. Unglaciated area. I. Illinoian drift.
- LW. Late Wisconsin.
- LP. Lake plains of glacial Lakes Maumee and Chicago.



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tions of map, south of Wisconsin drift boundary, are areas of Clermont silt loam-the flattest portions of the till plain.

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tation, generally, of glaciated and unglaciated areas of Ohio. Boreal hydro-mesophytic species were able to persist on the Illinoian till plain throughout the period of Wisconsin glaciation and are represented today by the many plants of northern distribution. If they did later move across the Wisconsin drift area they were eliminated by the increasing aridity. Hence their ranges are remarkably dis-The occurrence of a young endemic of northern relationrupted. ship-Viburnum pubescens var. indianense-is further evidence of the long isolation of the northern relics on the till plain. The same climatic condition which appears to be responsible for the disrupted ranges of the northern species made possible marked eastward movement of prairie. But, to the migrating prairie species the Illinoian till plain was unfavorable and few species were able to invade it. The long period of conifer dominance on the youngest glaciated land (the Wisconsin drift area) which is so amply demonstrated by pollen studies of Sears (1930, 1931) seems never to have affected this area, or any of the great southern lobe of the Illinoian glacier. That migratory movements of species are still in progress is indicated by the presence and behavior of southern species in the area (FIG. 2A). This element is relatively new. Though numerically few and for the most part found in but few stations, these species are important in pointing to the ultimate displacement of the northern relics.

The more general distribution and greater abundance of the characteristic species in the northeastern and eastern part of the till plain (Brown, Highland, Clinton counties), their greater rarity in the western part (Clermont County) and almost complete absence in the northwestern part (Warren County) raises some question as to the factors which may have affected the distribution of species within the area of the till plain (FIG. 5A, B). Certainly the effects of the Wisconsin xerothermic period would have been more pronounced in the western and northwestern parts of the area than elsewhere. Present unequal distribution of summer rainfall in the area, resulting in "dry islands," at least one of which is in an area of lesser abundance of characteristic species-the middle western part-coupled with the lowering of the water table by man's interference may have been detrimental to these species, all of which are hydro-mesophytes. The topography of the northwestern part of the area (Warren County) differs slightly from the rest of the plain; its ridges and depressions are longitudinal, lying in a northeast-southwest direction, instead of irregular, and the plain here tips southwestward. This part, too, is

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partly surrounded by the Earlier Wisconsin drift. Position and topography suggest the possibility of some Wisconsin wash across this part of the plain. Thus all post-Illinoian vegetation would have been destroyed in that area, which then would have been occupied by invasion from the south. Here are two of the southern tree species-Liquidambar styraciflua and Fraxinus profunda. Rosa setigera, of midwestern range, is more abundant here and in the middle western part of the Illinoian till plain than elsewhere.

The floristic distinctness of the Illinoian till plain is due to the prevalence of the hydric or hydro-mesic environment favoring a group of species which find few possible habitats either to east or west; to the prevailingly acid soil, which may account for the absence or rarity of many of the species common in adjacent areas and for the presence of certain Alleghenian acid soil species; and to the glacial and post-glacial history of the area which favors the persistence of many northern species.

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