The Prairie Peninsula as a Filter Barrier to Postglacial Plant Migration

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The wedge of persistent grassland plants and plant communities that extends into the deciduous forest eastward across Illinois and into parts of Indiana, Michigan, Ohio, and Kentucky is still poorly known with respect to its time of origin and its phytogeographic history. This study is an attempt to apply some evidence from pollen diagrams to these problems.

It appears that Gleason (6) was the first to identify the Prairie Peninsula, although it was Transeau (23) who gave it this name and defined its geographic boundaries (shown in generalized form in Figure 1) and climatic characteristics. Gleason showed remarkable insight in identifying this feature from floristic evidence. In the arguments by which he laid down the outlines of post-glacial history of vegetation in the Middle West, Gleason ascribed the origin of this eastward extension of grassland vegetation to an earlier period of greater dryness. He believed that the regional climate was drier during the Wisconsin glaciation, but that the eastward penetration of grassland probably occurred in the wake of northward migrating conifer forests and before the deciduous forests entered the deglaciated region from the south and southeast. He envisaged the grassland elements occupying dry hilltops and other xeric sites, mesophytic and hydrophytic forest pushing into the deglaciated region along stream valleys, and oak-hickory forest resulting from xerarch succession on the intermediate sites. He postulated two avenues of deciduous forest invasion from a "southern Alleghenies" (Central Appalachian) origin: one extending westward as far as the Ozarks, the other passing northwestward to Minnesota, with more recent general northward and westward advance between these two routes in response to a later post-glacial gradual increase in rainfall. Two deciduous elements were involved: ". . . one moving from the Ohio valley and one from the Allegheny Mountains." Gleason believed that Indian-set prairie fires then reduced the extent of deciduous forest to the condition found at the beginning of European settlement early in the nineteenth century, when afforestation again took place until checked by cultivation of the land.

About 1930 a post-glacial climatic optimum was being confirmed in Europe through studies of peat deposits and their fossil pollen. This concept was soon brought to North America, and was subsequently developed (19) into an explanation for expansion of grasslands at the expense of forests in the Interior of North America, including the eastward extension of grassland that is the subject of this discussion. Transeau (23) presented the most informative single account of this feature he called the Prairie Peninsula. He was convinced, on the basis of evidence from fossil pollen and other sources of "a late postglacial

prehistoric dry period with more wide spread drought conditions and more prolonged droughts than at present." He thought that, "If pollen studies of the upper layers of peat within the Peninsular region fail to show a period of this kind either the methods of pollen analysis or the assumptions upon which they are based need further investigation." However, all subsequently published pollen diagrams from Ohio, Indiana, and southern Michigan have failed to produce such evidence, at least that we have been able to recognize. Transeau's distribution maps for tree species such as *Fagus grandifolia* (beech), *Tsuga canadensis* (Canadian hemlock), *Pinus strobus* (white pine), *Liriodendron tulipifera* (tulip poplar), and *Thuja occidentalis* (arbor vitae) could as well suggest that these species were obstructed in crossing the Prairie Peninsula in early post-glacial time as that they were driven back in more recent time.

In 1957 I discussed ambiguities of Prairie Peninsula pollen diagrams with the late Theodore Just, who agreed that we might well look for evidence of an earlier post-ice origin of the feature. We took the problem to Karl P. Schmidt, who has also since died, and found he continued firm in his belief that most of the evidence pointed to an early post-ice origin. He had concluded that at least 11 species of amphibians and reptiles (no less than 6 of which are endemic to this "steppe peninsula") achieved their present ranges by reason of eastward development of the peninsula in the earlier postglacial when "the area was for a time relatively empty of animal life, so that the normal barrier of a saturated fauna was temporarily absent" (17). Philip W. Smith (21) made an extensive review of terrestrial vertebrate distributions related to the Prairie Peninsula, using the range patterns and trends in geographic variation as evidence to support his postulated changes in climate and shift in the eastward extent of the Peninsula. He distinguishes the postglacial Climatic Optimum (warm, humid, with mesophytic trees predominant in pollen spectra) from a subsequent Xerothermic interval, "during which time mesic forest habitats shrank to the east, north, and south of encroaching oak-hickory forest and expanding grassland habitats." This relatively recent dry interval, he believes, can account for disjunct populations of several grassland vertebrates now isolated on the Atlantic Coast. Schmidt had called this route to the Atlantic coast watershed the "steppe corridor" but implied it was early post-ice in age.

Potzger, with his colleagues and students, made a series of studies that established the composition and extent of the pre-settlement and modern forest types in Indiana and especially in the seven northwestern "prairie counties" (14). These studies revealed the predominance of beech forests in central and south-central areas, of oak-hickory forest in northern, northwestern, and southwestern areas, and oak openings with prairie stands only in the northwestern corner and on the western boundaries of Indiana.

Potzger and Friesner (13) made an early and revealing analysis of post-glacial forest history in Indiana by comparing the stratigraphic appearance and disappearance of 11 tree genera in pollen records of 7 bogs in central Indiana (Marion County north to southern Cass County).

It is of interest here that *Fagus* was not recorded at all from 3 of the bogs, appeared well after *Acer* in 3, and appeared before *Carya* only in 1 (Emporia, Madison County), where there was the oldest and longest record for *Fagus*. *Tsuga* was not treated in this study, probably because of its extremely weak representation in the fossil pollen records of the area considered.

Analysis of Fossil Pollen Records

Recently Mrs. Darlene (Helmich) Southworth and I completed a re-analysis of Third Sister Lake sediments from Washtenaw County, Michigan particularly to determine the non-arboreal pollen. We confirmed the earlier analysis of these sediments (15) with respect to the late arrival and weak expression of *Fagus* and *Tsuga*. Those genera are similarly expressed in the diagram for Sodon Lake in Oakland County (2) about 40 miles to the northeast, except that *Fagus* arrived there earlier. These facts and the above-mentioned findings of Potzger and Friesner (13) led me to inquire into the records of *Fagus* and *Tsuga* in pollen diagrams from the Prairie Peninsula region in general. These two kinds of pollen grains provide suitable evidence because each represents only one species in this region, they are readily identified with certainty, and they are not likely to be overlooked or confused with other kinds.

From approximately 100 pollen diagrams from Ohio, Indiana, Michigan, and Illinois, 15 of the longest and most detailed records were selected as representative with respect to *Fagus* and *Tsuga*, one being a composite diagram of 5 bogs in north-central Ohio (Table 1, Figure 1). One diagram from Hancock County in north-central Iowa was included as an example of the record near the western margin of the Prairie. In each diagram the mean percentages (of total tree pollen) for *Fagus* and *Tsuga* were estimated for each of the vegetation sequence stages, which were expanded from the 5 post-glacial periods of Sears (20), as indicated in the heading of Table 1. Localities 3 to 15 in Table 1 are arranged in essentially a north-to-south order but with minor rearrangement to establish order in the times of appearance of the two genera. The Iowa record indicates the weak and brief appearance of *Fagus* in the Pine-Oak stage and the complete absence of *Tsuga* pollen in the post-glacial of the western part of the prairie. It must be kept in mind that the columns (stages of different predominant tree pollen) are not time units but stages in the succession of gross kinds of vegetation as indicated by fossil pollen. If time were indicated from left to right in Table 1, the columns successively to the left of Period III would be increasingly narrowed and displaced toward the right from the southernmost locality (15) to the northernmost (3). Therefore, Table 1 compares the appearance and relative dominance of *Fagus* and *Tsuga* pollen with the developmental stages of post-glacial vegetation in the selected localities. With increased numbers of radiocarbon dates and detailed pollen diagrams we can look forward to the day when it will be practicable to make these correlations on an absolute time scale.

TABLE 1. Occurrences of *Tsuga* (T) and *Fagus* (F) pollen in selected pollen diagrams from Late-glacial to near-modern time. Symbol "t" signifies presence generally less than 1% of total tree pollen; 1, 2, 3, etc. are approximate mean percentages during the vegetation stage indicated in heading. The total time span for the southernmost localities approaches 16,000 years, but for the northernmost is less than 11,000 years. At southern localities 10, 14, and 15, an extra vegetation stage of Pine-Oak-Hardwoods occurs between two Pine maxima and possibly represents the Two Creeks Interval as expressed in this region (Engelhardt, 1960; Frey, 1959).

Period (after Sears, 1942b) Vegetation stage (based on predominant tree pollen)	I Spruce-Fir	Pine-Spruce	II Pine	Pine-Oak	III Hdwds-Oak	IV Oak-Hickory	V Oak-Hdwds
1. Iowa, Hancock Co., Lane, 1931		---/ /--	----------	F1	---	--Steppe--	-----
2. Illinois, Lake Co., Voss, 1934						Tt	T2
3. Michigan, Cheboygan Co., Potzger, 1946	---/ /--	T1		Tt	T15 F4	T12 F10 Pine	T7 F7
4. Michigan, Clare Co., Potzger, 1948	Tt	Tt F1	T2 Ft	T2	T10 F10	T15 F3	T20 F12
5. Michigan, Berrien Co., Houdek, 1935	F1	F1	F1	F1	Tt F2	T3 F3	T2 F3
6. Michigan, Allegan Co., Potzger, 1948		F3	F1	T3 F10	T2 F20	T1 F15	T7 F10
7. Michigan, Oakland Co., Cain & Slater, 1948		F2	F1	Tt F1	Tt F3	T1 F3	Tt F2
8. Michigan, Washtenaw Co., Potzger & Wilson, 1941		T1		F1	F2	Tt F2	T1 F8
9. Indiana, Steuben Co., Houdek, 1933		Tt Ft	F1	F1	F4	Tt F3	Tt F3
10. Indiana, Marshall Co., Frey, 1959		F1	Ft	Ft	F3	F2	F10
11. Indiana, Lagrange Co., Potzger, 1946				F1	Tt F11	Tt F5	F8
12. Indiana, Kosciusko Co., Potzger, 1946					F2	F3	Tt F6
13. Indiana, Adams Co., Potzger, 1946					Tt F10	T2 F5	F8
14. Indiana, Hamilton Co., Engelhardt, 1960			T1			F3	F4
15. Indiana, Marion Co., Engelhardt, 1960		Tt	F3 Tt Ft	T2 F1	F3	F4	F6
16. Ohio, N. Central, 5 bogs, Potter, 1947			T1 F1	T2 F10	T1 F40	Tt F2	F5

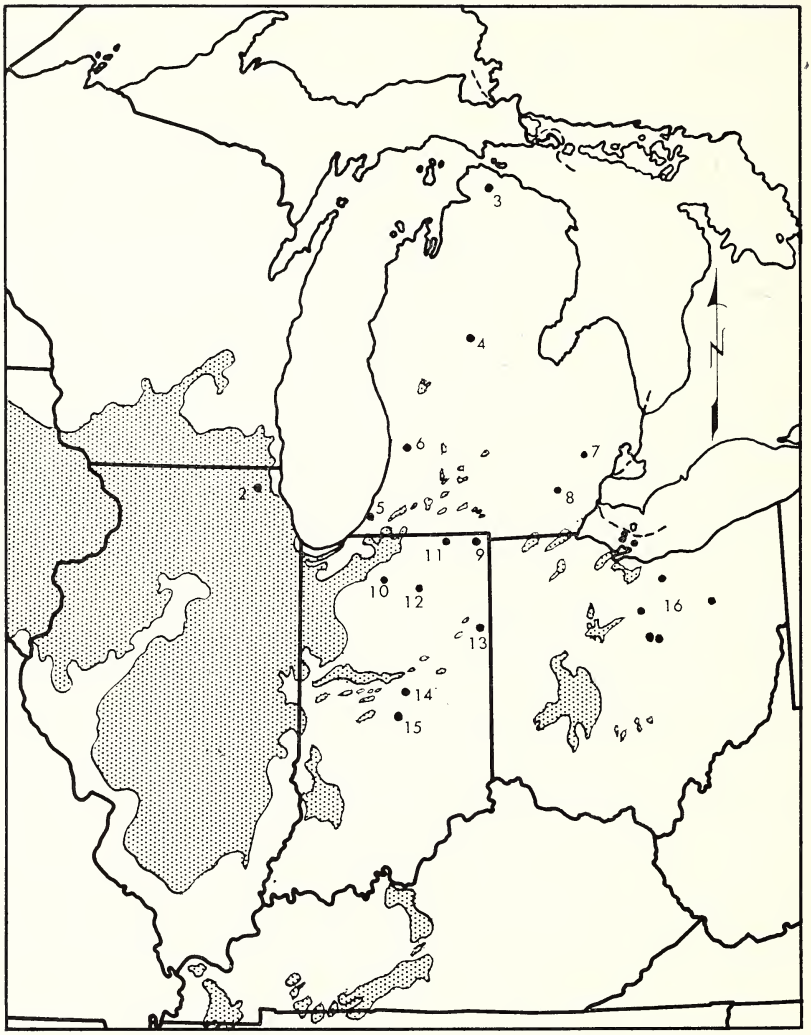

Figure 1. The Prairie Peninsula. Stippling represents areas containing concentrations of characteristic plant communities generalized and redrawn from detailed map by Transeau (23). Black dots mark localities of pollen diagrams 2 through 15, and five localities for composite diagram 16, all of which are listed in Table 1.

Discussion

We can be reasonably certain that both *Fagus* and *Tsuga* persisted in the southern Appalachians, probably even on parts of the Cumberland Plateau, during the Wisconsin glaciation of the area under discussion. *Tsuga* wood has been found in north-central Iowa and dated by radiocarbon in years B.P. as >17,000, 16,367±1000, 13,300±900, and

12,120±539 (16), although *Tsuga* does not appear in the post-glacial pollen record for Hancock County (Table 1, no. 1). By the Pine stage both *Fagus* and *Tsuga* were represented in the pollen record of Marion County, Indiana (locality 15) and north-central Ohio (localities in the area of 16). However, except for the brief appearance of *Tsuga* at locality 14 in the Pine stage, both genera failed to appear at localities 11 to 14 until the Pine-Oak stage or later. On the other hand, at localities 4 through 7 in Lower Michigan *Fagus* appeared not later than the Pine-Spruce stage. *Tsuga* appeared in the Spruce-Fir or Pine-Spruce stage at localities 4 and 3; *Fagus* appeared in the Pine-Spruce stage at 4, and in the Hardwoods-Oak stage at 3. It appears that *Tsuga* and *Fagus* began moving northward from their full-glacial refuges along with oaks and other hardwoods, following the retreat of spruce; but they were delayed in entering the northern half of Indiana and southeastern Michigan. The earlier appearance of *Tsuga* and *Fagus* in Steuben and Marshall Counties, Indiana (9, 10) than in surrounding localities is not understood. In general, it appears that the Prairie Peninsula served as a barrier to *Tsuga* and *Fagus* migration in early post-glacial time.

Another line of evidence in support of early post-ice invasion of grassland elements into the Prairie Peninsula region is to be found in the more recently described Late-glacial pollen spectra in which the non-arboreal pollen has been identified as far as possible. The early Spruce-Fir stage usually has a large component (20 to 100% based on total arboreal pollen) of non-arboreal pollen. For example, the spruce-dominated spectrum associated with woodland musk ox skeletal material in Kalamazoo County, Michigan, 13,000±600 B.P. in C^{14} years has a total NAP of 22.8% (1). Another spruce-dominated spectrum associated with a mastodon skull in Oakand County, Michigan, 11,900±350 B.P. in C^{14} years, has 85% NAP (22). The earliest organic sediments in Third Sister Lake (locality 8 in Figure 1 and Table 1), dominated by spruce pollen, also have more than 80% nonarboreal pollen (Benninghoff and Southworth, manuscript), but before pine dominance is attained in this diagram the total non-arboreal percentage drops to about 5%. This high proportion of non-arboreal percentage in the Late-glacial exceeds the proportion of non-arboreal pollen in many post-agricultural settlement spectra in this forest region. Common to both the Late-glacial and modern NAP maxima are *Ambrosia*, other Compositae, Cyperaceae, Gramineae, Chenopodiaceae-Amaranthaceae, and *Plantago*. *Artemisia* and Caryophyllaceae were more common in the Late-glacial spectra. These are evidences in support of earliest Late-glacial invasion by grassland elements, under conditions which, as Schmidt said (17), offered least resistance from competition. We must then reject Gleason's hypothesis that the grassland elements intruded between the northward retreating pines of the Pine stage and the invading hardwoods.

It is interesting that *Fagus*, and to some extent *Tsuga*, appear for the first time (localities 11 to 13) or attain strong positions (7, 8, 9, 10, and 14) just before or during the Oak-Hickory maximum. This appears to be evidence contrary to the concept of maximum warmth and dryness during the Oak-Hickory stage and contrary to the belief that the Prairie Peninsula either originated or expanded during this time, which is

usually taken to be about 3500 years ago. On the other hand, where *Fagus* and *Tsuga* were already well represented in the pollen diagram, they showed decreased dominance during the Oak-Hickory stage (and in some localities did not recover their previous status), evidence in support of the "Xerothermic" maximum. Obviously we need more evidence, and in greater variety, to indicate in more detail the nature of this fluctuation and associated climatic changes.

If we accept the premise that the Prairie Peninsula acted as a barrier to the northward migration of *Fagus* and *Tsuga*, then it remains to be explained how those genera reached the central, western, and northern parts of Lower Michigan, and the central and western parts before the attainment of Hardwoods-Oak dominance. The most logical solution is to postulate invasion from the east north of Lake Erie. This is the northern of the two migration routes postulated by Gleason (6, pp. 73-75), the other being a northward and westward route from the forests along the southern edge of the prairies. From comparisons of the records for localities 4 to 8 in Table 1, it appears that *Fagus* reached Berrien County (5) before it reached Clare County (4), Allegan County (6), and Oakland County (7). On the other hand, *Tsuga* appears in Clare County (4) well before it appears in any of the other three. There is no obvious explanation of these records; but they do suggest that *Fagus* and *Tsuga* entered Lower Michigan from the east and spread northwestward and westward, somehow bypassing Oakland County (7) at first and *Tsuga* spreading southward somewhat later than *Fagus*. These two forest trees occur in stands having the aspect of Hemlock—White Pine—Northern Hardwoods along the eastern shore of Lake Michigan almost to the extreme southwestern corner of Lower Michigan. Some stands of this kind in Allegan and Berrien Counties have reminded me very much of the "Transition Hardwoods" in Massachusetts, between the Oak-Mixed Hardwoods ("Central Hardwoods") and the Hemlock—White Pine—Northern Hardwoods to the south and north respectively. The Transition Hardwoods parallel in southwesternmost Lower Michigan is made the more impressive when one recalls the remarkable disjunct population of *Betula populifolia*, the gray birch, a prominent successional tree in the Transition Hardwoods of New England, formerly known from two very small areas in Lake County in the extreme northwest corner of Indiana (3). There is much to be investigated in connection with the post-glacial forest history of the southern shores of Lake Michigan.

If the Prairie Peninsula did exert a filter barrier effect on northward migration of tree species and did stall the direct northward migration of beech and hemlock from refugia south of the Ohio River, we have a plausible explanation of the absence of pollen spectra indicating Hemlock—White Pine—Northern Hardwoods between the Pine stage and the Hardwoods—Oak or Oak-Hickory stages in pollen diagrams from northern Indiana and southern Michigan. The Hemlock—White Pine—Northern Hardwoods in northern Lower Michigan and in the eastern Upper Peninsula must have formed from species that came from different source areas and that arrived at different times. This forest type probably originated in more or less its present range within this region,

rather than having migrated northward as a unit during post-glacial time.

It seems likely that the beech forests over northern Indiana and southeastern Michigan are not more than 5,000 or 6,000 years old, perhaps in places only about 3,000 years old. The markedly different characters of the beech forests and beech-maple forests of southern Indiana and southern Ohio, as compared with those of northern Indiana, northwestern Ohio, and southeastern Michigan, and these in turn with beech-maple forests of southwestern Michigan, are at least in part attributable to the effects of the Prairie Peninsula on post-glacial plant migration. We need more floristic phytosociological surveys of existing forest stands and detailed pollen analytical investigations at many more sites in this region to reconstruct properly the post-glacial history of this complicated phytogeographical region.

Summary

The Prairie Peninsula was identified by Gleason, and delineated and named by Transeau, on floristic evidence; it was subsequently shown by Schmidt, Smith, and others to have significance zoogeographically as well as phytogeographically. Gleason believed this feature developed eastward between the post-glacial Pine stage and the invasion of Hardwoods, and was intensified and extended by pre-settlement Indian fires; but Transeau ascribed its origin to a late post-glacial period of prolonged droughts.

A study of selected pollen diagrams from the Prairie Peninsula region demonstrates that *Fagus* (beech), although an early (Pine stage) migrant into central Indiana, failed to enter the Prairie Peninsula until 5,000 or 6,000 years ago, some time after this tree had migrated from an eastern source into the central and southwestern parts of Lower Michigan. *Tsuga* (hemlock) did not enter the Prairie Peninsula at any time during the post-glacial, and was slower than beech in migrating from an eastern source into central and southwestern Michigan. This evidence is interpreted to mean that the Prairie Peninsula is older than the Pine stage in central Indiana; and high percentages of grassland elements in the earliest Spruce-Fir stage in southern Michigan pollen diagrams is regarded as evidence that the Peninsula was established shortly after glacial retreat. At some localities within the Peninsula beech, and in a few instances hemlock, first appear in the pollen diagrams or attain strong positions just before or during the Oak-Hickory stage, which is usually accepted as the "Xerothermic interval"; obviously there is some inconsistency here.

It can be shown that the Hemlock—White Pine—Northern Hardwoods forest type of northern Michigan must have formed within its present range. Thus we can account for lack of evidence for this forest tpye between the Pine stage and Hardwoods stages in pollen diagrams from the Prairie Peninsula and somewhat farther south.

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