Some unsolved problems of the prairies

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Of the territory now known as Illinois, probably two thirds was originally occupied by the various plant associations constituting the type of vegetation known as prairie.* Poorly developed in southern Illinois, and extending but a short distance east into Indiana or north into Wisconsin, they swept to the west across Iowa, and in Nebraska united with the main portion of the prairie province, which extends northward from Texas on the south into the British possessions. This eastern extension has been appropriately named by Pound and Clements the eastern arm of the province, and its position is shown with considerable accuracy in their paper † on "The vegetation regions of the prairie province." The Illinois prairies alone are referred to in this paper.

Unfortunately for the ecologist, the prairies of Illinois were converted into cornfields long before the development of ecology and phytogeography in America, thus forever prohibiting the *satisfactory* investigation of some questions of the most absorbing interest and also of considerable importance in aiding a clear

*Following the stimulating and valuable example of Harper (Ann. N. Y. Acad. Sci. **17**: 25. 1906) concerning the meaning of the terms "swamp" and "branch," the use and restriction of the term "prairie" may be discussed. According to the Century Dictionary, the word is derived through the French from the Latin *pratarium* or meadow-land, and was first applied by the early French explorers to the broad expanses of grassland of Illinois, Iowa, and neighboring states. The English language, developed in a forested country, had no regular word for grassland except meadow, the meaning of which was restricted by local conditions to cultivated land or to the small strips of grassland along ponds or streams. When the word prairie was adopted from the French into the English, it was still limited to the grassland of the region mentioned above; it was and is a local term, and should be kept so. Other similar grass-covered lands in different parts of the hemisphere have received analogous names which have become more or less established in the language. Such are pampas in southern South America, llanos in northern South America, and savannas in the southeastern United States. The term prairie should be applied to none of these, nor to any other areas of grassland except those of the limited territory of the Middle West, covered by the prairie province.

† Bot. Gaz. **25**: 381–394. *pl. 21.* 1898.

understanding of American ecology and phytogeography in general. The thoroughness with which original conditions have been destroyed over central and northern Illinois is surprising to the botanists of the more densely populated, but sparsely settled East. In most of the counties of this part of the state there is absolutely no virgin prairie or forest, and in other cases the prairies are limited to narrow strips along railroads or small streams. In one case they are modified either by civilization or by burning and in the other they are not typical of the original upland prairies. Cook County, in which is located Chicago with its two million inhabitants, is mainly outside of the prairie province, but contains ten times as much unused land as do Champaign, MacLean, or Livingston counties, located in the "corn belt." On the other hand, Cook County offers poor facilities for field work in comparison with the vicinity of New York City.

The opportunity for study is, however, not entirely lost, but the investigation is made more difficult, and every succeeding season lessens the possibility of work along this line. In this paper there are merely indicated some of the particular questions that still await satisfactory solution, in the hope of awakening interest, and, if possible, stimulating research along this line. The questions are by no means entirely unanswered; every ecologist has a general idea in regard to them, but the detailed information is for the most part lacking. Our information may be drawn from a number of sources, some of which may be enumerated:

1. Books of travel and description, of which many are extant, though they are unfortunately more picturesque than scientific in their method of treatment. These begin with the published works of the early French explorers, Marquette and Hennepin, and extend to the middle of the last century. They are particularly numerous between 1810 and 1850, when the prairie country was being most rapidly settled.

2. A fairly good knowledge of the prairie flora, which we owe to Bebb, Mead, Vasey, Hall, and Brendel, of a past generation, and which may still be supplemented by direct observation along roadsides and railroads.

3. Several areas of considerable extent on which prairies are still preserved, but under abnormal conditions, such as the swampy

prairies in the Chicago area, described by Cowles,* and the sand prairies along the Illinois River,† and in other parts of northwestern Illinois.‡

4. Comparisons with the still existing prairies farther west, as described by ecologists from Iowa, South Dakota,§ and Nebraska.||

By carefully combining observations taken from as many standpoints as possible we should still be able to reconstruct for ourselves, so to speak, the prairies of the state and to solve many of the ecological questions which they call up.

Some of the questions that have occurred to me are these:

1. What were the conditions, climatic or of other nature, at the close of the glacial epoch, which led to the invasion of prairie plants from the west rather than forest plants from the southeast? Certain climatic conditions are more favorable to the growth of prairie than of forest, notably a low winter rainfall, and it is noteworthy that this type of rainfall is quite well developed in northern Illinois, and thence west, but not in Indiana, or in southern Illinois. Transeau's interesting map,¶ comparing rainfall and evaporation, is also pertinent here. Prairie plants complete their cycle of development more rapidly than forest trees, and might enter the territory sooner on that account. But if trees had migrated to the north and west ever since the glacial period at a rate equal to their present movement, the present state of Illinois would undoubtedly, by this time, have been covered entirely with forest. If the American botanists will use more geological evidence in their work, and if it can be used here as successfully as by the German phytogeographers, Schulz for example, considerable light will be thrown on this important point. The actual cause of the

* Bot. Gaz. **31**: 73–108; 145–182. *f. 1–35.* 1901.

† Gleason, Bull. Ill. State Lab. Nat. Hist. **7**: 149–194. *pl. 8–23.* 1907.

‡ A more detailed paper on other inland sand areas of the state is now in preparation.

§ Harvey, Floral succession in the prairie-grass formation of southeastern South Dakota. Bot. Gaz. **46**: 81–108; 277–298. *f. 1–4.* 1908.

|| Pound and Clements, *loc. cit.*

———. The phytogeography of Nebraska. Lincoln, 1900.

Thornber, The prairie-grass formation in region I. Bot. Surv. Nebr. **5**: 29–143. 1901.

¶ Forest centers of eastern America. Amer. Nat. **39**: 875–889. *f. 1–6.* 1905.

treelessness of the prairies, which has been so widely discussed by geologists and by a few botanists also, is not to be found in any of the present conditions, but in the accumulated effects of centuries of arid climate in the southwest, from which direction the plants of our prairies immigrated.*

2. The flora of the prairies of the Wisconsin glaciation in the northern part of Illinois is very different from that of the Illinoisian glaciation at the south, estimated to be eight times as old. Does this flora at the south indicate the survival of a pre-Wisconsin interglacial flora, which persisted during the Wisconsin period, or an invasion of prairie species from a different direction or at a different time, or merely an adaptation to different conditions of soil, temperature, or rainfall, or something else? So far as I know, no one has attempted to account for this peculiar feature of the Illinois flora. Personally, it seems that it must in some way be related to, or caused by, pre-Wisconsin conditions, although what those conditions were I have no idea. Certainly, an understanding of this question would aid in answering the first one also.

3. The aquatic plants surrounding the sloughs and ponds of the prairie were generally of broad distribution, or at least in no wise typical of the prairie province. The latter class of plants was usually semi-xerophytic, and occurred in the uplands. What is the significance of this? Does it throw any light upon the order of entrance of plants, and of western plants in particular, into this area?

4. The occurrence of scattered colonies of prairie species beyond the eastern limits of the province may indicate a former more extensive range of the prairie. A notable example of this is the colony on Cedar Point, near Sandusky, Ohio,† probably two hundred miles east of their normal limits. Will it be possible by careful search for such relict colonies in other places to determine what was the maximum extension of the prairie? This would aid in giving a good idea of the rate of invasion of the forest.

5. The isolated occurrence of the western plants on Cedar

* Cf. Harvey, *loc. cit.*, 84.

† Jennings, An ecological classification of the vegetation of Cedar Point. Ohio Nat. 8: 291–340. *f. 1–22.* 1908.

See also Bonser, Ecological study of Big Spring prairie, Wyandot County, Ohio. Ohio Acad. Sci. Special Paper 7. 1903.

Point may be compared with the presence of *Cristatella Jamesii* and *Lesquerella argentea* on the sand dunes along the Illinois and Mississippi rivers, many miles from the nearest reported station in Nebraska or Dakota, or of *Opuntia fragilis* in northwestern Illinois. A number of insects found there have also a similar distribution, as shown by Mr. C. A. Hart. Neither of the plants has any means of dispersal adequate to bridge over this gap, and we can only assume that at one time they had a distribution more nearly continuous. What have been the causes which have restricted them to these widely separated stations? Is it possible that there was a post-glacial period with so little rainfall that their distribution was continuous over the whole desert-like intervening territory? And if so, what other Neo-Sonoran plants also reached into Illinois at that time? Did we ever have *Echinocereus viridiflorus*, *Cactus missouriensis*, *Cucurbita foetidissima*, *Yucca glauca*, or other plants of similar habits in this state?

The preceding questions have been phytogeographical in nature rather than ecological and have to do mainly with the historical development of the prairies. Following are some that relate more directly to ecology:

6. What was the structure of the original prairie associations? The remnants of the prairie flora still existing along our railroad tracks give only a faint idea of the normal structure of the prairie vegetation. The older botanists neglected this matter almost entirely, although it was open to direct observation. So far as I know, but one botanist, C. W. Short, discusses the subject, in an article published in 1845. He mentions particularly the aggregation of individuals of one species and contradicts the idea given by popular, more impressionistic writers. "The flora of the prairies, the theme of so much admiration to those who view them with an ordinary eye, does not, when closely examined by the botanist, present that deep interest and attraction which he has been led to expect. Its leading feature is rather the unbounded profusion with which a few species occur in certain localities than the mixed variety of different species occurring everywhere." Probably the time has passed when this question could have been satisfactorily answered.

7. Within every complex of related plant associations there

are one or more definite orders of succession, leading from pioneer to climax associations. The steps in the succession follow each other in a regular series and constitute what may be called a normal succession. The normal succession for prairie associations has not yet been fully investigated. Cowles has described a portion of it in the pond-swamp-prairie series in the Chicago area,* and I have discussed some of the successions on prairie-covered dunes,† but this by no means exhausts the subject.

8. It is a matter of common knowledge that in this region the forest is everywhere pushing out upon the prairie. This matter has been investigated by but few, and we are still ignorant, if we may depend upon the published accounts of direct local observation, of the factors which tend to retard or accelerate the advance of the forest, or of the nature of the tension zone between the two associations, or of those particular species which may be called the pioneers in the forest advance.§ It may be said at this point that the forest undoubtedly invaded the prairie along two distinct lines, a hydrophytic to mesophytic advance longitudinally along the water courses, probably led by cottonwood, elm, maple, and ash, culminating in the climax flood-plain forest, and a xerophytic lateral advance along the bluffs, led by oak and hickory. Likewise we do not know what species, normally of the forest, migrated independently into the prairie and there, constituting the derived element of the prairie flora, possibly aided in resisting the encroachments of the forest. Neither do we know why the forest in central and southern Illinois invaded along the river courses, while in northern Illinois it advanced also along the morainic hills, nor what was the effect of prairie fires in checking the spread of the forest. Each of the points is still open to direct observation, to some extent at least; and by a careful study of the habitats of various forest species along country roadsides, at the margins of woods, along small streams, and in woodland pastures, we should still be able to get some idea of the structure of the original forest margin, and with it of the pioneer species in the forest advance.

* *Loc. cit.* 155, 156.

† *Loc. cit.* 158-171.

§ Harvey (*loc. cit.*) gives a good general summary of this subject.

For lack of a better name this type of succession may be called abnormal, to distinguish it from the normal type mentioned before.* The abnormal succession here is between Upper Austral prairies and Upper Austral forest. The prairie came in contact also with the transition zone forests at the north, and between them there is still another type of succession to be studied, even more abnormal in nature, and possibly entirely different in operation. Our Illinois prairies also approached the Lower Austral zone in southern Illinois, but there was apparently no transition between them.

These questions are by no means the only ones still awaiting investigation in the Illinois prairies. Others equally important will present themselves at once to every ecologist. Local conditions will produce local questions whose solution may throw much light on the broader problems of the prairies as a whole. Those that I have given refer entirely to the phytogeographical and associational sides of ecology. I have not touched upon any of the numerous and varied questions of individual or physiological ecology, such as light relation, water requirements, transpiration, individual or specific relations to the environment, and the like; nor have I mentioned any questions concerning the taxonomic side of the flora, which should still yield many interesting species to the modern systematist.

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* An excellent discussion of these two general types of succession has been given by Transeau in his "The bogs and bog flora of the Huron River valley," Bot. Gaz. **40**: 351–375, 418–448. 1905; **41**: 17–42. *f. 1–16.* 1906. See especially **41**: 38.