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Further Studies in the Ecotone between Prairie and Woodland

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II.—FURTHER STUDIES IN THE ECOTONE BETWEEN PRAIRIE AND WOODLAND

BY R. J. POOL, J. E. WEAVER AND F. C. JEAN

A series of intensive investigations of the ecological features of the tension zone between prairie and woodland in the Mississippi valley was begun by Weaver and Thiel in 1915. These studies were continued for two seasons in Minnesota and were also extended to the prairies of eastern Nebraska in 1916. These investigations represent the first attempt to attack the prairie-forest problem on a comprehensive scale by means of the quantitative methods of modern ecology.

Some of the results secured from these studies have been published as the first paper of a series planned to deal with critical investigations in the ecology of the prairie province. The above studies were continued and considerably extended in the Nebraska area by the authors of the present paper during the year 1917.

The object of the present paper is to record the results and conclusions derived from another season's investigations of some of the fundamental problems connected with the ecology of the areas lying within the vegetative borderlands between the prairies and the woodlands of the Missouri valley in Nebraska. This contribution is a natural sequel to the paper¹ by Weaver and Thiel noted in a previous paragraph.

Results are here recorded from our old stations in the prairie and woodland in the vicinity of Lincoln and also many additional data and materials are presented from a new series of stations established in 1917 near Peru, on the Missouri River. It has been demonstrated that the latter stations exhibit conditions which are

¹ "Ecological Studies in the Tension Zone between Prairie and Woodland," J. E. Weaver and A. F. Thiel, *The Bot. Surv. Nebr.*, N. S., No. 1, 1917.

in all cases much more mesophilous than obtain at our corresponding Lincoln stations. Contrasts between the vegetative conditions characteristic of the two areas are remarkable and ecologically very significant although the areas are only about 60 miles apart. These contrasts are clearly shown to be due to striking differences in both edaphic and climatic factors in the two series of stations. This paper also contains many experimental data bearing upon the successional sequence of the various woodland types as commonly developed in the region about Peru.

LOCATION OF STATIONS AND DESCRIPTIONS OF PLANT COMMUNITIES

The descriptions of our stations and of the plant communities prevailing therein have been adequately presented by Weaver and Thiel in the above publication in so far as they pertain to the prairie near Lincoln. The situation is quite different, however, for the woodland habitat at Lincoln and for all of the stations at Peru. Descriptions of these stations and of the plant communities concerned are not incorporated in the former paper hence they must be treated as a portion of the present report. A description of the woodlands at Lincoln follows immediately, while that of the various stations at Peru will be found in the latter portion of the paper, which deals in particular with the investigations in that part of the state.

The station in the woodlands near Lincoln is located in a typical habitat well within the broad-leaved, fringing forest along Salt creek about two miles southwest of the city. Salt creek is a shallow, sluggish stream which drains the broad Lincoln basin, through which it flows in a generally north or northeasterly direction until it enters the Platte river near Ashland about 20 miles northeast of Lincoln.

The soil along the stream is a fine, dark silt-loam, varying in depth, and in sand and humus content away from the stream banks to the uplands. There is considerable leaf litter covering the surface in the higher, denser woods, while in many low-lying areas practically all surface litter is removed annually during periods of high water. The surface in such periodically flooded

areas is covered by a layer of very fine silt containing considerable organic matter.

The vegetation in general is characteristically that described by Pound and Clements² under "The Bur Oak-Elm-Walnut Formation." The woodlands in question are, however, not perfectly typical of this type as the above authors described it for farther eastward in the state, but they are clearly derived from that "formation" as delineated by them. These woodlands exhibit some of the usual well-known variations of the type as it is seen nearer the main body of forest along the Missouri river farther to the eastward. The principal differences most noticeable are a more open stand and fewer dominant and secondary species as compared with the typical "formation" in its optimum expression. This vegetation is fairly typical of areas found as tongues of woods following up the numerous stream courses from the Missouri river in eastern Nebraska. More or less similar communities may be seen along such streams as Weeping Water creek and the Nemaha river. Such belts of timber vary from a few rods in width to a mile or more wide along their easternmost limits where they merge insensibly into the main body of timber on the Missouri river bluffs and along the valleys to complete disappearance at the headwaters of the streams far back in the prairies. Frequently the trees are found only in the immediate proximity of the streams. Such linear belts of woods are clearly the fingered extensions of the great main broadleaf forest complex whose center lies in the Ohio valley.

The most striking floristic contrast among the dominant species of the Salt creek woods as compared with those farther eastward in the state, as at Peru, is seen in the absence of *Quercus rubra* and *Hicoria ovata* which Pound and Clements included among the dominants of their "Red Oak-Hickory formation" so well developed in southeastern Nebraska. The red oak-hickory formation is not represented at all in the woods about Lincoln. Bur oak, *Quercus macrocarpa*, and the Bitternut hickory, *Hicoria minima*, are the only representatives of those important genera

² *Phytogeography of Nebraska*. 1898.

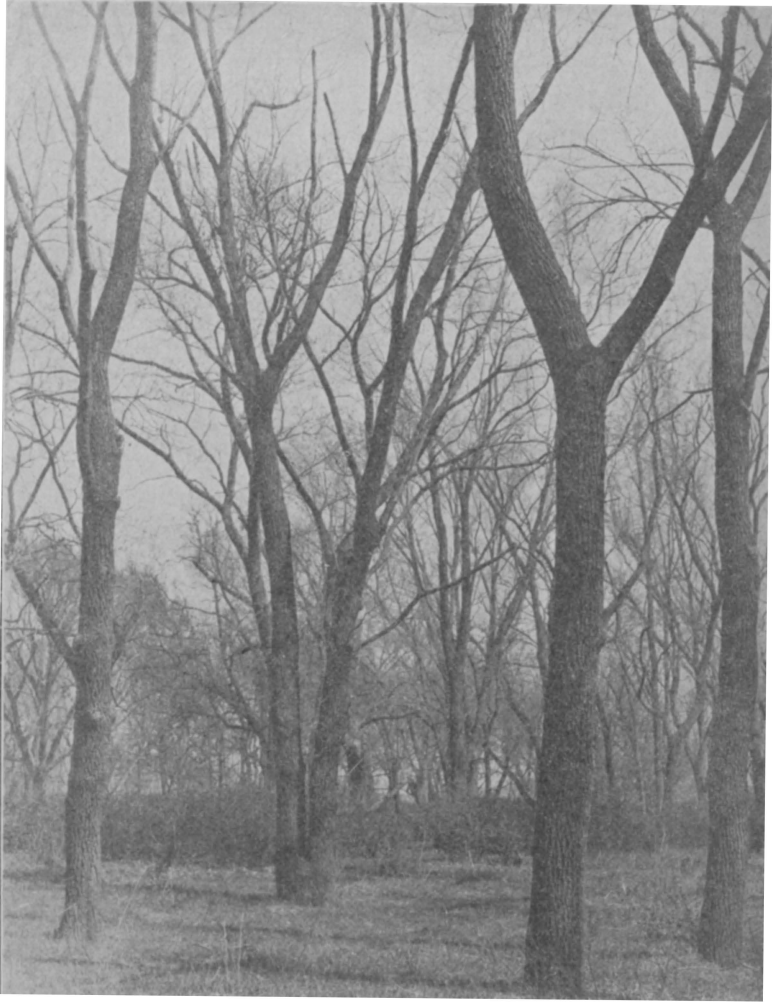


FIGURE 1. The location of the woodland station at Lincoln.

which have migrated this far westward from the main body of broadleaved forest farther southeastward, as about Peru.

Numerous species of eastern trees, shrubs and herbs that are common a few miles farther east are also missing from the wood-

lands along Salt creek at Lincoln. This fact serves to intensify the floral contrast all the more as we compare the two areas included in these studies.

Besides the common oaks and hickories the following are among the more conspicuous ligneous species absent from the Lincoln woodlands: *Amelanchier canadensis*; *Aesculus glabra*, *Asimina triloba*, *Cercis canadensis*, *Crataegus mollis*, *Prunus sero-*



FIGURE 2. The location of the sumac station at Lincoln.

tina, *Tilia americana*, *Ostrya virginiana*, *Xanthoxylum americanum* and *Corylus americana*. The absence of such species as these means that the woody plants that have succeeded in invading this more xerophilous area have assumed a more decidedly dominant rank than is the regular feature of their distribution in the woodlands along the Missouri. Hence *Quercus macrocarpa*, *Fraxinus pennsylvanica*, *Ulmus fulva*, *Celtis occidentalis*, *Acer negundo*, *Acer saccharinum*, and *Juglans nigra* have become the decidedly dominant forms along Salt Creek. Associated with these trees are the infrequent and unusually widely scattered

individuals of *Gymnocladus dioicus*, *Hicoria minima*, *Juniperu. virginiana*, *Ulmus americana*, *Gleditsia triacanthos*, and *Salix nigra*. The juniper is very rarely noted.

The individuals of the dominant species as well as of the secondary species range in diameter from four to twenty-four inches and in height from twenty to forty feet. The trees are usually much branched and the crowns tend to become bushy and widely spreading because of the relatively open nature of the woods. The light intensity beneath the trees as determined by the Clements actinometer ranges from 0.112 to 0.058, a fact which quite clearly pictures the relative openness of the stand.

The ground cover is poorly developed in so far as shrubs are concerned but is rich in perennial herbs. *Ribes missouriensis* and *Symphoricarpos symphoricarpos* are the only conspicuous shrubs although occasional individuals of *Cornus asperifolia* and patches of *Prunus americana* and *Sambucus canadensis* are seen in the more open places or along the border of the woods. The wild grape, *Vitis vulpina*, *Smilax hispida*, and *Celastrus scandens* are infrequent vines.

The principal herbaceous species are as follows:

<i>Geum canadense</i> (f)*	<i>Fragaria virginiana</i> (f)
<i>Viola papilionacea</i> (va)	<i>Arisaema triphyllum</i> (i)
<i>Elymus virginicus</i> (a)	<i>Eupatorium ageratoides</i> (i)
<i>Oxalis corniculata</i> (i)	<i>Sanicula marylandica</i> (f)
<i>Erythronium albidum</i> (va)	<i>Impatiens biflora</i> (i)
<i>Poa pratensis</i> (va)	<i>Teucrium canadense</i> (r)
<i>Ranunculus abortivus</i> (f)	<i>Aster salicifolius</i> (i)
<i>Muhlenbergia tenuiflora</i> (a)	<i>Verbesina alternifolia</i> (f)
<i>Urtica dioica</i> (f)	<i>Urticastrum divaricatum</i> (f)
<i>Eragrostis hypnoides</i> (i)	<i>Viola rafinesquii</i> (i)
<i>Agastache nepetoides</i> (i)	<i>Parietaria pennsylvanica</i> (f)
<i>Bicuculla cucullaria</i> (r)	<i>Galium aparine</i> (f)

Characteristic dense communities of *Ambrosia trifida*, *Polygonum pennsylvanicum* and *Mentha canadensis* are frequently noted in moist depressions or flattish, more or less marshy areas close to the stream.

* va=very abundant, a=abundant, f=frequent, i=infrequent, r=rare.

SOIL MOISTURE

Soil samples for moisture content determination were taken at stations in the above woodland area and also in the regular stations in the prairie and thicket areas as previously described by Weaver and Thiel. The usual technique was followed in securing these samples, in drying them in electric ovens and in computing the percentage of moisture present. The samples were always taken in duplicate, or in triplicate and the average percentage obtained in this manner was used as the water content for each class. The depth classes were 0-6 in., 6-12 in., 12-24 in., 24-36 in., 36-48 in. and 48-60 in. Samples were taken at these depths in all of the stations and at frequent intervals, although the deeper series were taken only at monthly intervals beginning in April and ending in September. Samples were taken at certain depths as often as once a week. Weather conditions frequently interrupt any set program for soil sampling routine.

The salient features of soil moisture conditions at the various depths in the above woodland habitat, in the sumac thicket on the prairie, and in the typical prairie station at Lincoln (the latter two stations previously described by Weaver and Thiel) for the vegetative season of April to September, 1917, may be readily portrayed by a series of graphs. These graphs indicate at a glance the fluctuations in water content for each depth and station and also the march of soil moisture for the whole season.

Figure 3 shows the moisture conditions of the soil at the woodland station for the 0-6 in., 6-12 in., and 12-24 in. depth classes. The horizontal lines in the figure represent the wilting coefficients for the soil at 0-12 in. and 12-24 in., the lower line being that for the second foot of soil. It will be noted that the percentage of moisture in the second foot of the woodland soil was considerably lower than that in the first foot throughout the season of 1917. Also that the wilting coefficient was reached for only a brief period during the latter part of July and continuing into the fore part of August for the second foot. This period coincides fairly closely with the maturation of the greater number of species whose root systems probably secure water supplies from the upper two feet of soil. The fluctuations of soil moisture

at this station for the 3-4 ft. and 4-5 ft. classes are not shown in this figure but it may be stated in general that the water content

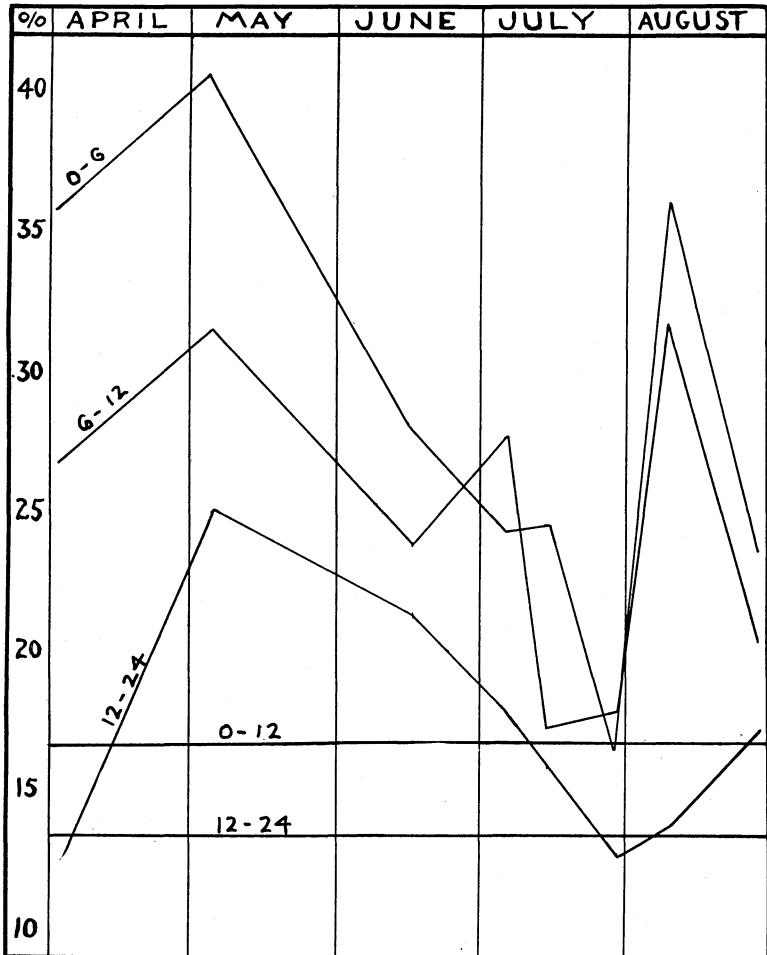


FIGURE 3. Soil moisture at 0-6 in., 6-12 in., and 12-24 in. at the woodland station, Lincoln, 1917.

at those levels was still lower than that in the second foot as indicated in the graph. For instance, the maximum for the fourth

foot was 15.7 per cent. on June 19 and the minimum at the same level was 9.8 per cent. on April 2. The percentages of available

TABLE 1
SHOWING THE PER CENT. OF AVAILABLE SOIL MOISTURE IN THE PRAIRIE AND
WOODLAND STATIONS AT VARIOUS DEPTHS DURING THE SEASON
OF 1917, AT LINCOLN

Wilting Coef.....	13.4	16.6	13.4	16.6	15.4	13.4	14.5	12.6	16.1	11.4
Station,	Prairie	Woods	Prairie	Woods	Prairie	Woods	Prairie	Woods	Prairie	Woods
Depth.....	0-6 in.		6-12 in.		1-2 ft.		2-3 ft.		3-4 ft.	
April 2.....	4.3	19.1	4.3	10.3	-2.6	-1.0	-1.6	-1.1	-2.9	-2.3
May 5.....	9.4	13.9	6.7	14.9	2.2	11.5	-1.4			
June 19.....	4.9	11.4	10.8	7.3	8.1	7.7	8.4	4.9	6.1	8.1
July 9.....	-1.9	7.7	2.0	10.9						
July 16.....	-1.7	7.9	0.7	0.8	2.1	2.5	1.8	0.6		
July 23.....	-3.1	2.5	-1.7	-1.3						
July 30.....	-5.3	-0.4	-2.4	1.2	-4.0	-0.8				
August 6.....	1.6	16.9	-1.3	5.0	-2.0	-1.2				
August 13.....	7.0	19.5	0.5	5.0	-3.2	15.1				
August 28.....	2.1	7.1	1.7	3.6	-2.1	3.6	-1.3	11.8	-4.5	3.9

TABLE 2
SHOWING THE TOTAL WATER CONTENT OF THE SOIL IN THE PRAIRIE AND
WOODLAND STATIONS AT VARIOUS DEPTHS IN 1917, AT LINCOLN

Depth..	0-6 in.		6-12 in.		1-2 ft.		2-3 ft.		3-4 ft.		4-5 ft.	
Station....	Prairie	Woods	Prairie	Woods	Prairie	Woods	Prairie	Woods	Prairie	Woods	Prairie	Woods
April 2...	17.7	35.7	17.7	13.5	12.8	12.4	12.9	10.5	13.2	9.1	15.7	9.8
May 5...	28.8	40.5	20.1	31.5	17.6	24.9	13.3					
June 19...	18.3	28.0	23.2	23.9	23.5	21.1	22.9	17.5	22.2	19.5	20.4	15.7
July 9....	11.5	24.3	15.4	27.5								
July 16...	11.7	24.5	14.1	17.4	17.5	15.9	16.2	13.2				
July 23...	10.3	19.1	11.7	15.3								
July 30...	8.1	16.2	11.5	17.8	11.4	12.6						
Aug. 6...	15.0	33.5	12.1	21.6	13.4	13.8						
Aug. 13...	20.4	36.1	13.9	31.6	12.2	28.3						
Aug. 28...	15.4	23.7	15.1	20.2	13.3	17.0	13.2	24.4	11.6	15.3	14.2	10.8

soil moisture for the prairie and woodland sites at all depths are shown in table 1. The total water contents are shown in table 2.

Considerable fluctuation in water content in the first foot of soil during July at this station is explained by frequent local showers. The effect of such precipitation is, however, seldom felt by the lower soil layers.

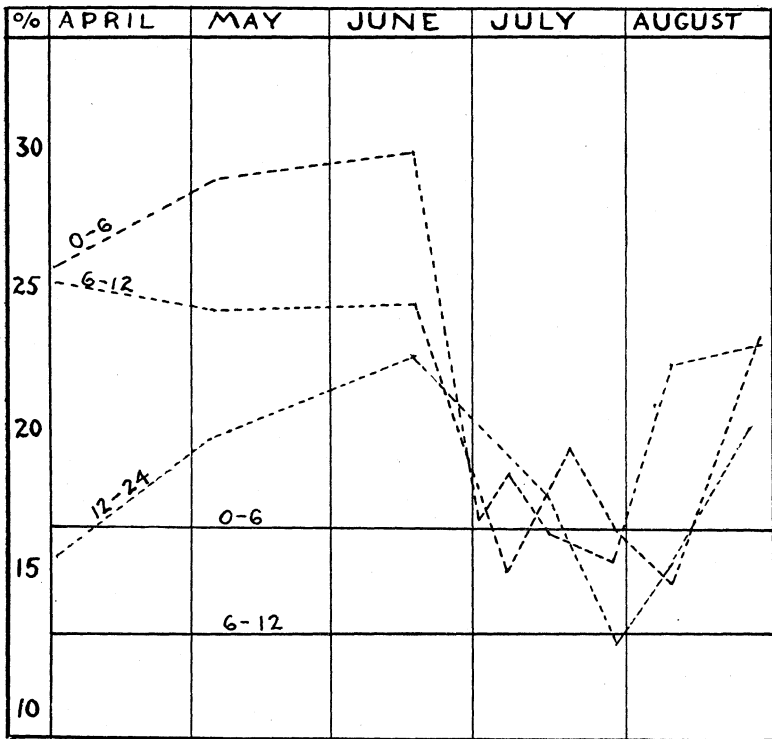


FIGURE 4. Soil moisture at 0-6 in., 6-12 in., and 12-24 in. at the sumac station, Lincoln, 1917.

Figure 4 indicates the soil moisture conditions which prevailed in the sumac thicket on the prairie during the season of 1917. The most significant fact revealed by these graphs is that there was no available moisture in the upper two feet of the soil for considerable periods during the latter part of the growing season and that there was considerable fluctuation of the water content

of the first foot in July because of local showers. By comparing this graph with figure 22 of Weaver and Thiel, it will be seen that the sumac station was characterized by considerably less available water in the upper layers of soil during the season of 1917 than in 1916. However, there was an abundance of moisture at the lower depths in the sumac thicket throughout the summer, ranging from a minimum at 4-5 feet of 21.0 per cent. to a maximum of 27.0 per cent. for the same level. This is a significant fact in connection with the possibility of colonization of such stations by the deeper rooted shrubs and later, by trees. The ecological position and possibilities of the sumac thicket as compared with adjacent prairie habitats in so far as soil moisture is concerned is strikingly illustrated by the fact that the water content of the 4-5 ft. level in the prairie was barely one half that of the same depth in the sumac. And, furthermore, it was found that this contrast in the two sites continued throughout the vegetative season. These facts are of utmost importance when considering the possibility of the invasion of the prairie by any but the most deeply rooted species and consequently also when considering the successional relations involved.

Figure 5 portrays the march of soil moisture in the prairie station at depths of 0-6 in., 6-12 in., and 12-24 in. from April to September, 1917. The horizontal lines represent the wilting coefficient, the upper being that for the 12-24 in. layer and the lower that for the 0-12 in. layer.

The rapid depletion of soil moisture from about June 15 until late in August is the striking feature of the conditions which this graph represents. Available soil moisture was completely exhausted by late June or early July and the depression of the moisture content continued rapidly until late July. The wilting coefficient was not again exceeded until August 7 for the 0-6 in. level and August 28 for the 6-12 in. level. The moisture content in the second foot of soil was still below the wilting coefficient at the close of August. Thus during practically the entire latter half of the vegetative period very little or no soil moisture was available for those plants whose root systems are confined to the upper two feet of the soil. Determinations which are not re-

corded on the graph show also that there was little moisture available at the 3-4 ft. and 4-5 ft. levels in this prairie station.

On the whole our data indicate that the prairie was a considerably drier habitat, in so far as soil moisture is concerned, during the summer of 1917 than in 1916. The after-summer period was

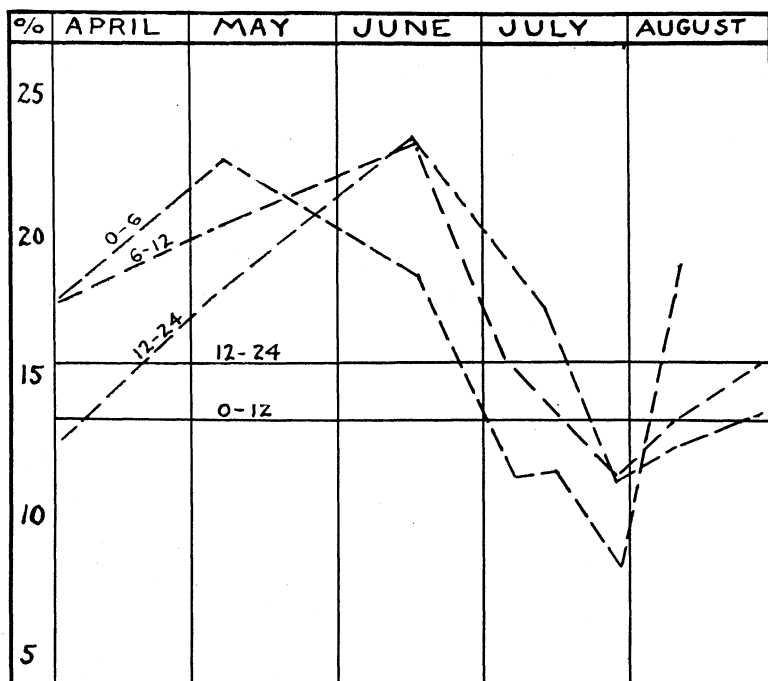


FIGURE 5. Soil moisture at 0-6 in., 6-12 in., 12-24 in. in the prairie station, Lincoln, 1917.

particularly dry in all three of the stations and this condition was strikingly indicated by the relatively early maturation of aestival and serotinal species, especially upon the prairie.

Figure 6 shows the march of soil moisture at the 0-6 in. depth in all three of the stations for 1917. The wilting coefficients of the soils for the different stations are indicated by the horizontal lines. The xerophytism of the prairies is nicely illustrated in this

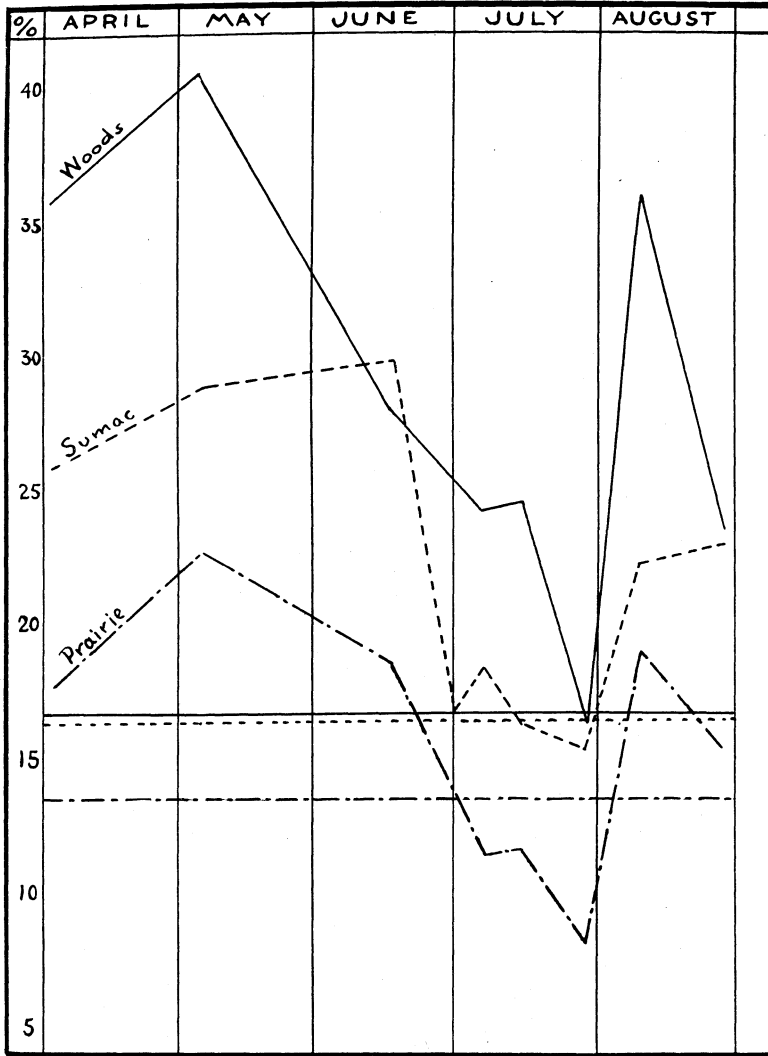


FIGURE 6. The march of soil moisture in the three stations at Lincoln, 1917, at 0-6 inches.

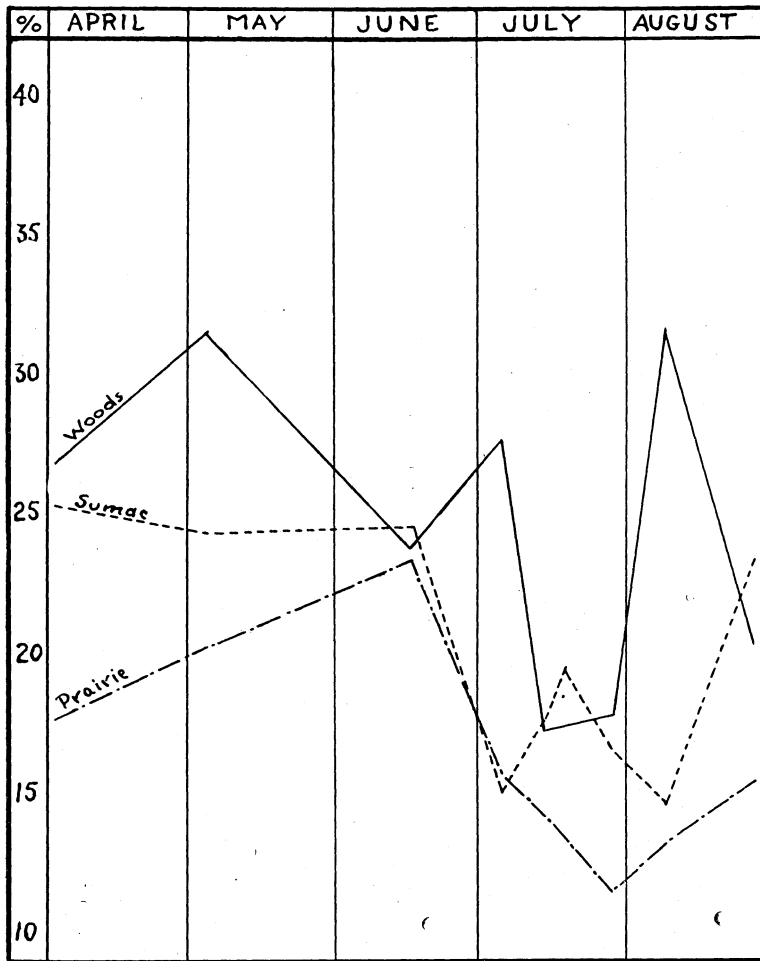


FIGURE 7. The march of soil moisture in the three stations at Lincoln, 1917, at 6-12 inches.

contrasty graph as compared to the conditions existing in the woodland habitat and even in the small sumac thicket completely circumscribed by the prairie.

The march of soil moisture at 6-12 in. for the three stations is

contrasted in figure 7 in which the xerophilous nature of the prairie soil is again conspicuous.

In figure 8 the range of moisture content for the three stations at a depth of 12-24 inches indicates that at this depth there is not so great a divergence as in the shallower levels. Even at this depth, however, the prairie is still the driest habitat. Determinations at still lower levels, as 3-4 ft. and 4-5 ft. show that this relation still

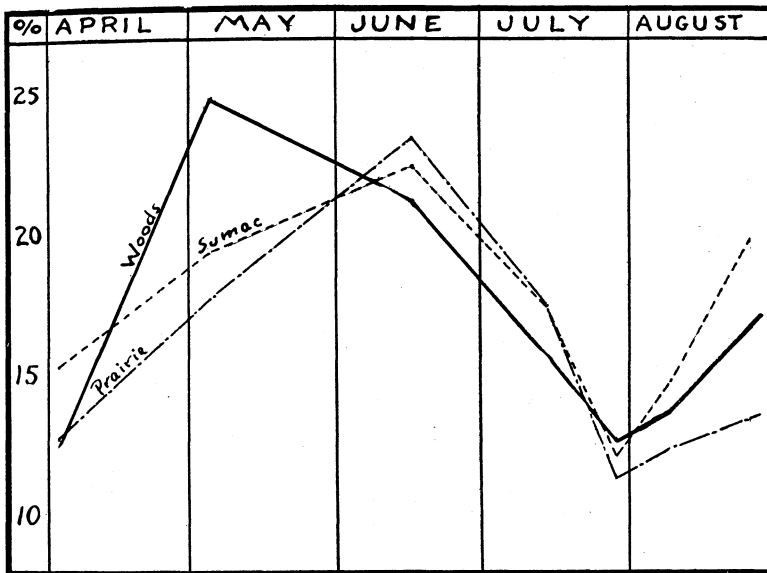


FIGURE 8. The march of soil moisture in the three stations at Lincoln, 1917, at 12-24 inches.

holds true and that in general there is a more rapidly diminishing water residue in prairie soils at depths of 4 and 5 ft. than in either of the two other stations under investigation.

These soil moisture studies, now covering three entire seasons of vegetational activity, abundantly prove the importance of soil moisture as a factor in plant succession as between prairies on one hand and forest on the other. All of the data from the three summers' work are in agreement in that the percentages of avail-

able moisture in the various plant communities vary directly with the order of those communities in succession. Long periods during which there is a deficiency of available moisture in the upper two or three feet of prairie soil are efficient barriers in the way of a general invasion of prairies by trees in the absence of the usual intermediary and ameliorating successional stages. Even an infrequent depletion of soil moisture at the depths from which trees obtain their water supplies is a factor powerfully opposing the success of forest growth in a prairie soil and climate.

The severe winter droughts of 1916-17 and 1917-18 and the extensive winter killing resulting therefrom throughout the central portion of the prairie province are particularly illuminating in this connection especially in view of the fact that the deep-rooted perennials so characteristic of our prairie associations were not noticeably affected by those exceedingly xerophilous periods. Such extreme limits of environmental factors are likely to prove peculiarly fatal to vegetation not possessed of the full complement of anatomical and physiological peculiarities necessary to cope with these extremes.

SOIL TEMPERATURE

Soil temperature is probably an important factor in the development of vegetation in the prairies, especially during the earlier ecesic phenomena. The precise rôle performed by soil temperature in ecology will not be clearly understood until much more investigation has been conducted with reference to that particular factor. However, it is doubtless safe to state that the temperature of the soil, especially at the surface, is actually the determining factor in the failure or success of many very young seedlings, and it may, indeed, inhibit germination itself. This is particularly true in the case of arid and semi-arid habitats. The period during which soil temperature extremes may prove fatal to the establishment of plants in the field, and the relative resistance of species to soil temperature extremes are problems that should be investigated in connection with all studies of succession.

Soil thermographs were operated continuously at the prairie

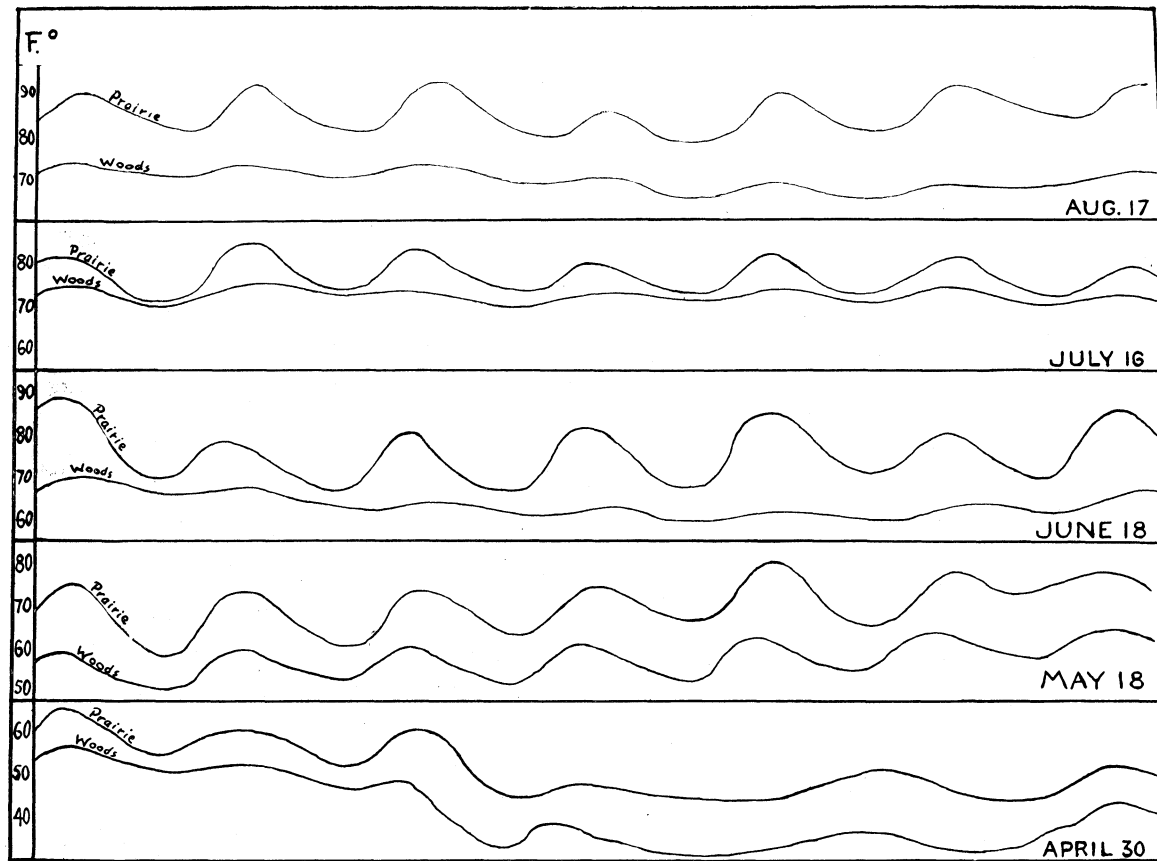


FIGURE 9. Selected weekly records of soil temperature at a depth of 2 inches in the prairie and woodland stations at Lincoln during the season of 1917.

and woodland stations throughout the vegetative season of 1917, beginning early in April and closing in September. Figure 9 shows the weekly march of soil temperature at a depth of 2 inches in the prairie and woodland for selected weeks during the months of April, May, June, July and August. The depth of 2 inches was selected because it was thought that temperature conditions within that portion of the soil are particularly important and significant as related to germination and ecesis and consequently to the whole problem of succession. Sufficient equipment was not at hand to enable us to secure temperature data for other depth classes simultaneously with these secured at a depth of 2 inches.

The curves in figure 9 show a number of interesting facts about the soil temperature in our two extreme stations. The curves are direct copies of the graphs traced by the thermograph pens upon the record sheets for the weeks ending on the dates indicated. The only change that was allowed in making such transcripts was a slight rounding-off of the original graphs to make somewhat smoother curves. This method does not affect the value of the transposed graphs in any significant manner because those irregularities were merely sharp angular fluctuations with only slight amplitude, such as may be caused by cloudiness.

The general and gradual rise of temperature in the two stations is nicely demonstrated by the graphs. The lower graph in all cases is that from the woodland station, the upper one is from the prairie. A striking difference in the amplitude of the two curves is noted after the month of May, the daily extremes being much farther apart at the prairie station, as might be expected. During the month of April the amplitude of the two curves is practically the same, even during the last three days of the month when the sky was generally clouded, but all through the month the temperature in the woods was approximately ten degrees lower than that in the prairie. The soil of the prairie warms up much sooner than that in the woods, but the rate of change is about the same during this vernal period.

The most nearly coincident range of temperature in the two habitats is seen in May as illustrated by the curves for the week

ending May 18. The difference between the two curves is slightly in excess of ten degrees, but the daily fluctuations of the two curves are practically of the same amplitude, the two being in general, of course, higher than in April. This interesting correlation is probably due to the fact that at that time the trees and other species in the woods were not yet leaved out sufficiently to shade the soil to any great extent. The soil in the woods was exposed to nearly full insolation during mid-day almost as in the prairie, but the period of maximum temperature occurs at a slightly earlier time of day and does not last quite so long as in the prairie.

The curves for the week ending on June 18 show some very striking differences as compared for the week in May. In the first place both curves show the expected elevation, being on the average about ten degrees higher than the respective curves in the middle of May. But the June curves exhibit a great difference in amplitude or fluctuation. The curve from the woods is almost flat, due to the fact that the soil was completely shaded and although the temperature is considerably higher the fluctuations from day to day and from day to night are relatively slight. The curve from the prairie, on the other hand, shows great diurnal and nocturnal variations. These conditions continue into July, but with the temperature in the woodland soil approaching more nearly that of the prairie. During the week ending July 16 the nocturnal minima shown by the two curves very nearly coincided, but the maxima were still far apart due to obvious reasons. The soil temperature at the woodland station remained about the same in August as it was in July varying through only about five degrees about 70° from day to day, but the soil temperature at the prairie station reached a point nearly ten degrees higher than in July with about the same daily fluctuation.

The most significant features exhibited by the march of soil temperature at a depth of 2 in. for the entire season in the two sites are the greater amplitude and the higher extremes of temperature in the prairie station. The graphs clearly portray the temperature relations surrounding germination or other growth

phenomena in the first two inches of soil in the two habitats. The high temperature of the soil and its fluctuations coupled with a relatively high saturation deficit of the air, and these two conditions frequently coincident with a deficiency of soil moisture in the first 2 inches clearly present a difficult situation for the vanguard of invaders to solve. A frequently fluctuating soil temperature coupled with occasional, dangerously high extremes are probably of considerable significance in determining the direction of succession as has been indicated by Weaver's investigations in Washington.³

EVAPORATION

Studies of the evaporating power of the air at the various stations were also continued in connection with the quantitative determination of the other environmental factors. It has already been conclusively shown by Weaver and others that evaporation plays a very important rôle in the determination of the course of succession and in the composition of plant communities. The data herewith presented still further support and corroborate the conclusions drawn from earlier investigations in this regard.

The data on evaporation were secured by the now well-known Livingston porous-cup atmometer method. Standardized cylindrical cups were used and these were fitted to containers both with and without the greatly improved rain-correcting type of apparatus. Thus the cups were run in duplicate, but everything surrounding the work pointed conclusively to the greater reliability of the data secured from the rain-correcting instruments and so these are the only data considered in this discussion. The authors feel that data secured by means of the older type of apparatus without the rain-correcting features are at best poor approximations of the actual evaporating power of the air in the habitats in question. The rain-correcting instrument should certainly be used in all investigative work of this sort. All other apparatus for the study of evaporation based upon the principle of the porous-cup should be abandoned for investigative work.

³ "A Study of the Vegetation of Southeastern Washington and Adjacent Idaho," J. E. Weaver, Univ. Nebr. Studies, XVII., No. 1, 1917.

Readings were made and the water replenished from time to time according to the best technique which has now become so nearly standardized as to require no detailed description here. Suffice it to say that the data here considered are all from standardized rain-correcting instruments to which the proper corrections have been applied. The porous cups were run for periods of 5-6 weeks after which they were replaced by newly standardized cups and the whole apparatus cleaned and started afresh.

The graphs on evaporation have been drawn by first computing the average water loss in cubic centimeters per day between the successive readings and then these data are plotted as the ordinates while the intervals between the readings are indicated by the abscissae. This method facilitates the comparison of evaporation quantities from the various stations and it also depicts in a graphic manner the march of evaporation for each of the respective stations throughout the season.

Some striking facts are disclosed by a comparison of the 1917 evaporation graphs with those for the 1916 season. In the first place it is seen that the season of 1917 was marked by a very much higher evaporation rate which began in early spring and continued practically throughout the summer. The maximum evaporation in the prairie station in 1916 came during the latter portion of July and the fore part of August when the extreme of 43 c.c. was reached. The next highest figure was late in May when the evaporation was slightly above 25 c.c. In comparison with these figures we see that the highest maximum for the season of 1917 was 47 c.c. (Fig. 10) and this occurred the latter part of April. But there were also three other secondary maxima, one of 45 c.c. during May, another in the middle of June of 39 c.c. and another near the close of July of 35 c.c. All of these are high as compared with the evaporation rates for the season of 1916. Correspondingly higher evaporation rates were also recorded for the thicket and woodland stations in 1917 as is readily noted by comparing the march of evaporation in those two stations as depicted in the two sets of graphs.

Our data concerning the evaporating power of the air thus indicate that aerial conditions in all of our stations were very much

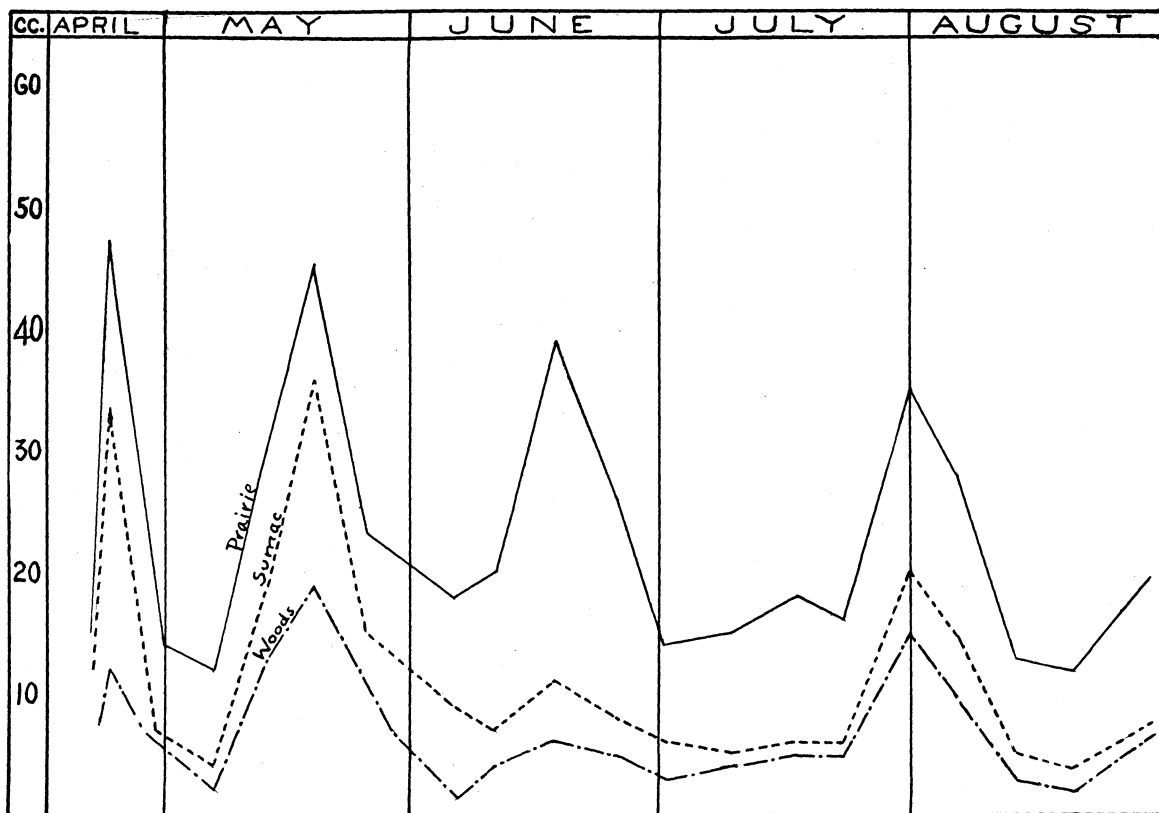


FIGURE 10. The seasonal march of evaporation in the prairie, sumac, and woodland stations at Lincoln for the season of 1957.

more xerophilous during the summer of 1917 than in 1916. But nevertheless they also indicate a close correlation between the evaporating power of the air and the stage in the succession. This relation was even more emphatically demonstrated in 1917 than in 1916.

Our data for 1917 also corroborate in an interesting and conclusive degree the really quite close approach of the conditions in the *Rhus* thicket to the mesophilous conditions of the woodland, a fact that appeared during our 1916 studies. This is particularly significant when we remember that the *Rhus* thicket is but a very small area on a southwest slope and completely surrounded by typical prairie, the xerophilous conditions of which have been already pointed out.

The course of evaporation upon the prairie during the season of 1917 doubtless indicates some of the peculiarly trying conditions experienced by the propagules of shrubs and trees, and in fact of whatever plants may have found their way there, in becoming established in such a habitat which, at best, is a real test of the amplitude of physiological response possessed by the plants in question. The relations of these extreme conditions of the prairie to the possibility of tree establishment have been investigated by a series of studies conducted in 1917, the results of which will appear in another paper.

The monthly recurrence of relatively high evaporation maxima recorded for the season of 1917, especially during the physiologically important fore-summer, are doubtless of great significance in the maintenance of the typical xerophily of the prairies. If such seasons occur in fairly close succession we have much added light upon the reasons for the very slow invasion of prairie by woodland species. Such would also go far toward showing why trees probably never become directly established upon the prairies. Because of these and other important relations we ought to secure data to show the march of evaporation for a long period of years in such stations as we have established.

HUMIDITY AND TEMPERATURE

In the first paper in this series Weaver and Thiel have shown how relatively low humidities, high temperatures, and high wind velocities contribute to maintaining the higher evaporating power of the air in the prairie as compared to that in the thicket and woodland station.

The general trend of evaporation in the three stations was considerably higher during the season of 1917 than in 1916, as has already been noted. This difference is significant as to the relative dryness of the air for the several stations and for the two seasons because in 1917 the atmometers were run at a lower level than in 1916. The porous, evaporating surfaces were more or less protected by the surrounding vegetation from the full effect of the wind. This was particularly true, of course, for the prairie station.

An examination of our humidity-temperature records reveals the fact that the minimum humidities recorded in the prairie are almost without exception lower than those in the shrub or woodland stations. The minimum humidity in the prairie and shrub communities approached each other rather closely on a number of days during the early part of the summer, but these were infrequent and for only relatively brief periods. These facts are shown on the graphs for the week of April 25, and they are in general true only for that period of spring and early summer before the plants of the shrub habitat have developed their full foliage density. Other series of records show considerable differences in the minimum humidities of the three stations, and these are to be taken as illustrative of the greater portion of the growing season. But naturally the relatively low minimum humidity of the shrub community during the physiologically important fore-summer may be very significant as contributing to the difficulties of ecesis therein. A period of low relative humidity of late May, 1917, was reflected in a striking manner by a great increase in evaporation in all of the stations.

For a very short period during the driest time of the day the humidity in the shrub station was occasionally slightly lower than that for the same day in the prairie, but as in 1916, such minima

were recorded for a considerably shorter period of time in the sumac thicket than in the prairie. Even under these brief periods of greatest stress some of the more typical mesophytes in the thicket were noticeably wilted. The duration of the periods of stress was so short, however, that no permanent injury resulted to the vegetation of the thicket. As Weaver and Thiel have already pointed out it is the humidity-time relation that is critical here, *i.e.*, the minimum humidity multiplied by the time of duration of that minimum. This renders the true physiological criterion for the air-drought of a plant habitat.

The same relations also hold for the temperature conditions in our series of stations. The mean weekly temperatures computed upon the weekly maximum and minimum temperatures are unsafe in yielding a true criterion of temperature as an ecological factor. The maximum temperature for the shrub community may be, and actually was, sometimes slightly above that for the prairie station, but the duration of the maximum temperatures in the shrub was nearly uniformly less than that in the prairie. Frequently, even when there was considerable difference in the maximum temperatures in the prairie and shrub communities, the prairie maximum was sustained for a considerably longer period.

A point of considerable interest comes from a comparative examination of all of the hygrothermograph records for the three stations for the entire season. This may not be, probably is not, significant ecologically, and it may be due to poor technique in the operation of the instruments, but we speak of it at this point. The reference is to the fact that our hygrothermographs frequently recorded the highest maximum humidity for certain days at the station in the high prairie and the lowest maximum in the woodland. Also during some periods of several days duration the night air of the prairie was recorded as containing several per cent. more moisture than was present in the shrub or in the woodland; or the air in the shrub may be more moist at night than that of the prairie, but very much more moist than that of the woods. Rather frequently also the minimum temperature for corresponding days was lower in the prairie than in the shrub community. These points are shown in the records for several days.

During the mid-summer weeks the maximum humidities were recorded as a rule between 2 o'clock and 4 o'clock a.m.

One would be inclined to interpret such records as these to mean that upon frequent occasions during the night combined influences of habitat conditions produce a higher relative humidity in the habitat that is naturally the most xerophilous. As to the cause of this interesting feature of our records we can scarcely guess at present in the absence of extensive data from a careful investigation of that particular point. Possibly the prairie community transpires more moisture at night than the shrub or woodland communities. If that is true then one can readily understand why the hygrometer should read higher in the prairie, especially during a still night, than in the other habitats. It may be pointed out in connection with this matter that as a rule there is usually much more dew in evidence in grassland vegetation than in forest or shrub vegetation in our climate. However, knowing full well of the unreliability of the common types of hygrometers especially with the higher humidities, we are not inclined to place too much confidence in the value of these particular data unless perhaps the readings should be checked hourly during the night. The whole matter may simply represent a trick of the instrument. Nevertheless there is need for a careful investigation of the whole problem of the relative water loss from these types of vegetation and the conditions which determine the same during the night.

STUDIES IN SUBCLIMAX PRAIRIE, SCRUB, AND FOREST NEAR PERU

Considerable quantitative evidence has already been given by one of us (Weaver, 1919⁴) to show that the prairies of southeastern Nebraska, particularly about Nebraska City and Peru, are subclimax in nature. This is indicated in a number of ways. Although the floristic composition in general is very similar to the prairies at the stations already described, yet a number of herbaceous, half-shrubby and shrubby species which are elements proper to the woodland flora, occur here only or at least occur much more abundantly than in the prairies westward. Moreover, the actually more favorable climatic complex for plant

⁴ "The Ecological Relations of Roots," Carnegie Inst. Wash. Pub. 286, 1919.

growth at Peru is shown in the much more luxuriant development of many of the prairie species growing at both of our prairie stations. For example, at Peru *Andropogon furcatus* extends to the very crests of the steepest ridges where it grows to a height of 5 or 6 feet, while its roots extend to a depth of over 9 feet into the moist loess soil. The excellent growth made by other prairie species even upon the drier ridges indicates conditions very favorable for chaparral growth, and indeed, thickets of *Corylus americana*, *Rhus glabra*, and *Symphoricarpos* spp. are very frequent in the grassland. Nor is it uncommon to find the seedlings of elm and oak near the edges of these thickets. Except for fires, grazing or other disturbance much of this subclimax grassland would undoubtedly pass through a scrub stage in succession and culminate in forest while still other extensive areas would probably remain covered with chaparral. It will be shown that habitat conditions are actually much less xerophilous as regards both moisture of the air and soil than at the Lincoln station. While the precipitation at Lincoln is only 28 inches, that at Peru is 34 inches.

While the flood plain forest station at Lincoln represents, as already pointed out, the "bur oak-elm-walnut formation" of Clements and Pound, the forests about Peru are of the more mesophytic "red oak-hickory type." *Quercus rubra*, *Hicoria ovata*, *Ulmus americana*, *Fraxinus lanceolata*, *Juglans nigra* and *Tilia americana* are all dominants in the best developed forests, although many other trees play important rôles in the various stages of succession. Among those occupying the drier soils and with the chaparral, under favorable conditions gradually encroaching upon the prairie, are such species as *Quercus macrocarpa* and *Quercus velutina*. On the other extreme, such species as *Platanus occidentalis*, *Gleditsia triacanthos* and *Gymnocladus dioicus* occupy the rich moist soils of the ravines as well as the slopes of the bluffs. Indeed a large number of eastern trees of considerable frequency but limited abundance are striking features of these rich woodlands. Many of these, having entered the state from the southeast along the Missouri, soon reach their westward limit and drop out as one proceeds northward or west-

ward. Even the dominant red oak and shell-bark hickory lose their importance near the mouth of the Platte and are replaced by the bur oak-elm-walnut type.

In contrast to the open forest canopy with its development of layers of vegetation as found at the Salt creek station, the forest types at Peru in general and in the better developed red oak-hickory associates or linden consocieties in particular, present a very distinct difference. Here the trees stand closer together with tall straight trunks and rather narrow compact tops. The crowns normally touch each other thus giving continuous shade beneath. Not only are the dominants better developed, reaching greater heights and much greater trunk diameters than the dominants along Salt creek at Lincoln, but where the latter occur as secondary species in the forest about Peru they respond to the more favorable environmental conditions by a much more sturdy growth.

Owing to low light intensities the secondary layer of small trees and shrubs is never well-developed in this woodland. *Asimina triloba*, *Euonymus atropurpureus*, *Rhamnus lanceolata*, *Staphylea trifoliata*, *Cornus asperifolia* with *Cercis canadensis* are the most important species. They occur frequently but seldom very abundantly. In the more open bur oak-black oak forests, and especially on the forest borders, they find greater expression and together with certain other species frequently are components of thickets or extensive bushland. However, the chief components of the latter are usually *Corylus americana*, *Xanthoxylum americanum* (both of which are less xerophytic than the following and consequently do not reach the Lincoln station) *Rhus glabra*, *Symphoricarpos symphoricarpos*, *Prunus americana* and *Prunus virginiana*.

Thus the woodland proper, whether occupying the lowlands and steep bluffs along the Missouri river or following one of its many tributaries far into the prairie region, but always with a decreasing number of both species and individuals, is usually separated from the grassland by a bordering fringe or zone of chaparral. This may be composed almost wholly of a single

species forming a socies or it may be represented by a mictium of several species.

Certain other species of low shrubs such as *Ribes gracile*, *Rubus strigosus*, and *Ribes occidentalis* together with various lianas such as *Smilax hispida*, *Rhus toxicodendron* and *Clematis virginiana* are more or less regular components of the more open forests and often occur abundantly in the scrub mictium. However, it would take us quite beyond the limits of this paper to give a thorough floristic description of the very interesting and diverse developmental vegetational complex found in this portion of our state. Details of the structure of the vegetation at each station will be shown by means of quadrats and transects. Therefore, suffice it to say that the mesophytism of these forests and their approach to the more typical Ohio-Missouri parent complex is indicated by the growth in the herbaceous layer of such species as *Podophyllum peltatum*, *Impatiens biflora*, *Sanguinaria canadensis*, *Orchis spectabilis*, *Trillium nivale*, and *Claytonia virginica*.

LOCATION AND DESCRIPTION OF STATIONS

In the spring of 1917 a station was selected in the prairie about half way up a rather steep hillside and on a slope somewhat east of south, figure 11. A second station was located in the *Corylus* thicket which occupied the north and west slopes of the same hill. A third station was chosen on a typically wooded north slope at a distance of about one and one-half miles from the prairie and shrub stations. This last station was in the linden forest, figure 12.

At each station frequent soil moisture determinations were made, some to a depth of 5 feet, while a continuous record of the evaporating power of the air was obtained throughout the growing season. Also certain other factor determinations together with a careful study of the structure of the vegetation were made.

The prairie vegetation previous to these investigations had not been disturbed for several years either by fires, mowing or by grazing. But early in the spring of 1917 a prairie fire swept over the hillside burning off the grasses and herbaceous vegetation and

killing back many of the shrubs, especially *Rhus glabra* which was encroaching upon the grassland from the shelter of the more moist ravines and protected slopes. The dominance of *Andropogon scoparius* and the general structure of the prairie vegetation is shown in the following list quadrats carefully selected near the station and listed in September. It is clear that at this time certain prevernal and vernal blooming species had disappeared.

Species	Quadrat				Remarks
	1	2	3	4	
<i>Andropogon scoparius</i>					
individuals.....	217	73	213	83	Bunches 1 to 6 inches in diam.
bunches.....	28	35	28	27	
<i>Andropogon furcatus</i>		7			Bunches 2 to 4 inches in diam.
individuals.....				40	
bunches.....	3	3			
<i>Bouteloua curtipendula</i>	45				Bunches from 2 to 6 inches in diam.
individuals.....		19		23	
bunches.....		4	2	14	
<i>Eragrostis pectinacea</i>					Bunches from 1 to 4 inches in diam.
individuals.....	5	126	136	101	
bunches.....		16	18	6	
<i>Sorghastrum avenaceum</i>					Bunches only 1 to 2 inches in diam.
individuals.....	2		3	4	
bunches.....				3	
<i>Amorpha canescens</i>	4	2	3	1	
<i>Brauneria pallida</i>		3	1	1	
<i>Ceanothus ovatus pubescens</i>	7	2			
<i>Euphorbia corollata</i>	1		2	3	
<i>Kuhnia eupatorioides</i>			1		
<i>Lygodesmia juncea</i>				17	
<i>Lespedeza capitata</i>			4		
<i>Liatris punctata</i>	2			1	
<i>Petalostemon purpurea</i>	20	17	19	18	
<i>Rosa arkansana</i>	2		1	3	
<i>Ulmus americana</i> (seedling)		1			

The shrub station is dominated by *Corylus americana* and *Rhus glabra*. These with *Symphoricarpos symphoricarpos*, small trees of *Cercis canadensis* and *Prunus americana* form rather dense thickets from 5 to 8 feet in height. Several woody lianas such as *Celastrus scandens*, *Vitis vulpina*, and *Ampelopsis quinquefolia* are present in sufficient numbers to add considerably to the mass of vegetation. The following list, tabulated in September, shows the variety and abundance of species of shrubs, small

trees, lianas and herbs occurring in an area of 16 square meters surrounding the station where the factor readings were made. The shade cast by the shrubs was so dense that most of the annuals as well as the herbaceous perennials were extremely small.

The vegetation in an area of 16 square meters at the shrub station:

Woody Plants

<i>Ampelopsis quinquefolia</i>	6	<i>Quercus macrocarpa</i> (seedlings)	2
<i>Celastrus scandens</i>	2	<i>Rhus glabra</i>	26
<i>Corylus americana</i>	34	<i>Symphoricarpos symphoricarpos</i>	7
<i>Fraxinus lanceolata</i> (seedlings)	6	<i>Ulmus fulva</i> (seedlings)	7
<i>Morus rubra</i> (seedling)	1	<i>Vitis vulpina</i>	6
<i>Prunus americana</i>	4		

Herbs

<i>Amphicarpa comosa</i>	38	<i>Humulus lupulus</i>	2
<i>Amaranthus retroflexus</i> (ruderal)	1	<i>Lactuca scariola</i> (ruderal)	9
<i>Ambrosia trifida</i> (ruderal)	8	<i>Leptilon canadense</i> (ruderal)	522
<i>Acalypha virginica</i>	16	<i>Melolitus officinale</i> (ruderal)	1
<i>Andropogon scoparius</i>	19	<i>Monarda fistulosa</i>	26
<i>Aster drummondii</i> }		<i>Muhlenbergia</i> sp.	14
<i>Aster novae-angliae</i> }	71	<i>Onagra biennis</i>	6
<i>Carex</i> sp.	25	<i>Panicum capillare</i> (ruderal)	2
<i>Carduus altissimus</i> (ruderal)	8	<i>Setaria viridis</i> (ruderal)	3
<i>Chenopodium album</i> (ruderal)	27	<i>Solanum nigrum</i>	14
<i>Eragrostis pectinacea</i>	6	<i>Trifolium pratense</i>	1
<i>Euphorbia preslii</i>	1	<i>Verbena stricta</i> (ruderal)	9
<i>Fragaria virginiana</i>	27	<i>Vernonia fasciculata</i>	1
<i>Geum canadensis</i>	30	<i>Viola sororia</i>	49
<i>Helianthus hirsutus</i>	108		

The station in the linden wood was located on a north slope in a growth of virgin forest on the campus of the Peru State Normal School, figure 12. A good idea of the composition of this forest together with the dominance of *Tilia americana* may be gained by a study of the accompanying belt transect. This extends up from the dry creek at the base of the slope 34 meters to the station and thence onward toward the crest of the hill, figure 13. The iron-

wood, *Ostrya virginiana*, although even much more abundant than the linden; is a small tree which does not reach the level of the general forest canopy and hence plays only a rôle of minor importance. It survives only because of its very great tolerance, enduring a degree of shading to which many other trees succumb. Most of the dead or fallen trees in figure 12 are *Cercis canadensis*. Indeed in this community the light values are so low that



FIGURE 11. Location of the station in the prairie at Peru. The flood plain of the Missouri river is shown at the right.

a layer of either well developed shrubs or of herbs is entirely lacking. Some eke out an existence for a period as relicts, many trees grow for a time, and with certain tolerant herbs make up the scant vegetation. But except in favorably lighted places the moss-covered ground is predominately in evidence. A major quadrat (4 m. square) made in October, 1917, showed the following plants growing at this forest station:

Woody Species

<i>Ampelopsis quinquefolia</i>	9	<i>Rhus toxicodendron</i>	2
<i>Cercis canadensis</i> (seedlings)*..	7	<i>Tilia americana</i> (16 inches diam.)	1
<i>Cornus asperifolia</i>	16	<i>Tilia americana</i> (seedling).....	1
<i>Fraxinus lanceolata</i> (seedlings). 12		<i>Ulmus fulva</i> (seedlings).....	7
<i>Hicoria ovata</i> (seedlings).....	4	<i>Vitis vulpina</i>	10
<i>Ostrya virginiana</i> (seedlings)...	6	<i>Xanthoxylum americanum</i> (seed-	
<i>Prunus serotina</i> (seedlings)....	2	lings)	3
<i>Quercus rubra</i> (seedling).....	10		

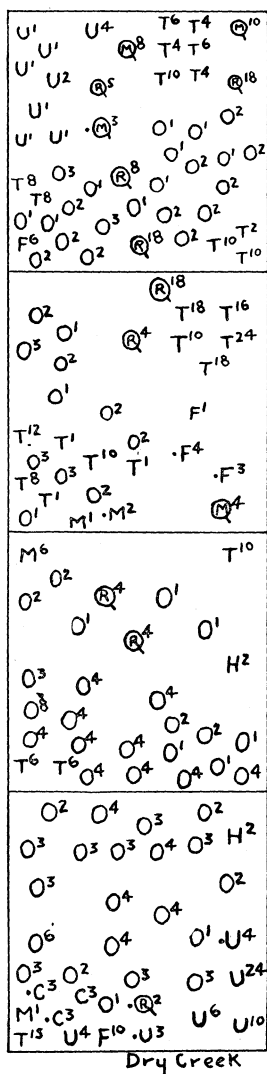
Herbs

<i>Acalypha virginica</i>	27	<i>Leptilon canadense</i> (ruderal)...	9
<i>Aster</i> sp.	1	<i>Meibomia grandiflora</i>	46
<i>Carex</i> sp.	34	<i>Menispermum canadense</i>	27
<i>Chenopodium album</i> (ruderal)..	1	<i>Muhlenbergia racemosa</i>	1
<i>Circaea lutetiana</i>	42	<i>Muhlenbergia tenuiflora</i>	26
<i>Eupatorium ageratoides</i>	68	<i>Potentilla monspeliensis</i>	9
<i>Galium tinctorium</i>	31	<i>Smilax hispida</i>	1
<i>Geum canadense</i>	8	<i>Viola sororia</i>	3

* All of the tree seedlings as well as the herbs were of small size and showed plainly the effects of poor photosynthetic conditions.



FIGURE 12. Location of the station in the linden forest at Peru.



Legend:

T = *Tilia americana*Q = *Quercus rubra*O = *Ostrya virginiana*H = *Hicoria minima*U = *Ulmus fulva*M = *Morus rubra*C = *Cercis canadensis*F = *Fraxinus lanceolata*Q = *Quercus macrocarpa*

•F, •U, etc. = Dead trees

Large areas of the ground are
covered with moss

Belt transect 16 meters long
in the linden station

FIGURE 13. A belt transect 10 meters wide extending up the slope through the linden station at Peru.

Soil Moisture

Soil moisture determinations were made by means of a Briggs geotome at somewhat irregular intervals from April 5 to September 22, 1917. In taking samples in the shrub and especially in the forest the practice was followed of removing the leaf mould or duff before inserting the soil tube. Samples to a depth of 5 feet were taken only four times during the season, those from 2 to 3 feet in depth somewhat oftener, while soil moisture in the first 2 feet of soil, that portion which shows the greatest variation, was determined 14 times during the growing season. These data for prairie, shrub and woodland are shown in the following tables:

TABLE 3

THE AVAILABLE WATER CONTENT OF THE SOIL IN THE PRAIRIE, SHRUB AND FOREST COMMUNITIES AT DEPTHS OF 0 TO 6 AND 6 TO 12 INCHES AT PERU IN 1917

Station	Depth	Wilt- ing Co- effi- cient	Apr. 5	May 15	June 30	July 9	July 14	July 24	July 28	Aug. 6	Aug. 11	Aug. 18	Aug. 25	Sept. 8	Sept. 22
Prairie.	0"-6"	11.5	13.4	13.0	13.9	6.5	9.5	0.9	-1.4	4.0	8.4	2.3	1.3	6.2	-1.2
Shrub..	"	13.7	21.4	14.7	20.8	3.9	11.5	4.6	-1.7	6.6	12.6	7.6	6.4	10.2	-1.6
Forest .	"	14.7	32.9	20.3	21.6	12.1	13.6	3.9	3.0	7.9	14.3	12.6	4.6	13.0	3.0
Prairie.	6"-12"	10.5	12.2	12.0	11.8	7.3	7.4	2.5	0.4	-0.5	1.5	1.9	0.2	-0.8	-1.7
Shrub..	"	12.0	18.0	14.1	17.1	7.4	5.1	3.4	-0.4	2.6	5.7	1.5	1.8	2.4	0.5
Forest .	"	12.7	26.1	15.0	20.2	12.2	7.9	5.2	2.5	3.9	2.7	6.5	1.1	6.0	-0.3

An examination of table 3 reveals several interesting facts. It may be seen that the wilting coefficient of the soil at depths of 0-6 and 6-12 inches respectively, increases progressively from prairie to forest. This is undoubtedly due to the increase in the humus content of the soil. Further it may be seen that the water available for plant growth also increases as we go from prairie through scrub to forest, and this notwithstanding the greater progressive increase of non-available water. In other words the water holding capacity of the humus enriched soil is increased much more rapidly than its corresponding ability to withhold water from the plant. Comparing the available water of grass-

land and shrub habitats we find that the latter, with very few exceptions, has the greater amount. A comparison of that between shrub and forest further illustrates the law of succession determined by Fuller in Illinois and Weaver in Washington, Idaho and Minnesota, that as the xerosere progresses toward the climax stages there is a continuous increase in the water content of the soil.

Periods when no water was available for plant growth in the first six inches of soil occurred twice in the prairie and scrub; while the non-available point in the second six inch soil layer was reached three times in the prairie, only once in the scrub, but also once in the forest.

However, as our knowledge of the greater extent of root systems of prairie plants grows and we find how even seedlings of grasses and trees rapidly reach soil depths greater than a foot, we can more clearly understand why drought in the surface soil layers even through extended intervals is not necessarily fatal.

The following table shows the total soil moisture at depths of 1 to 5 feet.

TABLE 4

TOTAL WATER CONTENT OF THE SOIL IN THE PRAIRIE, SHRUB AND FOREST AT DEPTHS OF 1 TO 2, 2 TO 3, 3 TO 4 AND 4 TO 5 FEET IN THE PRAIRIE, SHRUB AND FOREST AT PERU IN 1917

Station	Depth	Wilt- ing Coeffi- cient	Apr. 5	May 15	June 30	July 24	July 28	Aug. 6	Aug. 25	Sept. 8	Sept. 22
Prairie.....	1'-2'	10.4	18.9	20.8	22.7	13.5	12.6	9.4	10.1	11.2	9.4
Shrub.....	"	12.5	24.6	24.1	25.6	15.5	13.7	13.1	12.4	12.1	11.8
Forest.....	"		25.6	25.9	27.0	21.2	16.3	17.0	13.3	14.6	13.7
Prairie.....	2'-3'	9.9	14.9	18.0	22.5	15.0	14.4	11.8	10.8	11.5	9.7
Shrub.....	"	11.3	19.3		24.2	16.8	15.7	13.8	12.5	10.3	11.8
Forest.....	"		18.5		25.7	21.6	19.5	18.3	14.5	15.8	16.8
Prairie.....	3'-4'		15.9		20.5			15.5			12.2
Shrub.....	"		16.6		24.7			15.4			12.1
Forest.....	"										
Prairie.....	4'-5'		13.0		21.4			16.9			11.9
Shrub.....	"		16.1		24.9			16.7			13.0
Forest.....	"										

Even a casual examination of these data reveals a higher water content of the soil in the thicket than in the prairie, or in the forest than in the shrub. Although wilting coefficient determinations were not made for all the soils at these depths, it seems probable that water was available for plant growth at all times in the forest. In the shrub it was exhausted to a depth of 3 feet in September, beyond which depth the roots of hazel, sumac, grape coral berry and other shrubs in this community were found to extend. No water was available to prairie plants in the 6-24 inch soil stratum on August 6 nor again on August 25, while on September 26 all available moisture had been used to a depth of 3 feet. Whether prairie vegetation occupying a unit area of soil surface gives off more water by transpiration than is lost in a similar manner from woody plants occupying an equal soil area, or whether the greater water content of forest soils is due entirely to their greater water-holding capacity and lower soil surface evaporation remains to be determined. The writers are inclined strongly toward the view that increased transpiration from grassland plays an important rôle.

A comparison of the soil moisture conditions at Lincoln with those at Peru may be found interesting. The following table shows the number of times during the growing season during which the soil moisture had reached the non-available point at the various depths.

TABLE 5

A COMPARISON OF THE PERIODS DURING WHICH WATER WAS NON-AVAILABLE FOR PLANT GROWTH IN THE PRAIRIES AT LINCOLN AND AT PERU

Soil Depth	Lincoln	Peru
0''-6''	May 6, July 9, 16, 23, 30	July 28
6''-12''	July 23, 30, August 6	August 6
1'-2'	April 3, July 30, August 28	August 6, 25
2'-3'	April 3, May 6, August 28	*
3'-4'	April 3, August 28	*
4'-5'	April 3, August 28	*

* Assuming that the wilting coefficients which were not determined at these depths are no greater than at a depth of 1 or 2 feet.

An examination of these data shows that plants at Peru grow under a much more favorable condition of soil moisture.

It has already been pointed out that below a depth of 12 inches the soil of the linden forest always had water available for plant growth. That at the Salt Creek station had no available moisture at depths of 1-4 feet on April 2 and again at 2 feet on July 30 and August 6 respectively. Such differences in the distribution of soil moisture coupled with corresponding differences in evaporation readily account for the variations in the structure of the vegetation.

EVAPORATION

The evaporating power of the air at the different stations was measured from June 1 to September 22, 1917. The atmometers were placed in duplicate at the various stations and at a height of about 17 cm. above the soil surface. The data are shown in the form of graphs in figure 14.

The marked parallelism among the graphs is no more striking than the differences in the average daily evaporation, the latter always being least in the forest and highest in the prairie community.

Wind movement exerts a profound effect in accelerating transpiration and evaporation. During the interval from June 29 to July 28, 3,900 miles of wind, as measured by a standard anemometer, passed over the prairie vegetation at a height of one-half meter; while only about 6 per cent. as much (250 miles) was recorded by an anemometer similarly placed in the scrub. Again from July 28 to September 22, 4,077 miles of wind were recorded by the instrument in the prairie and only 666 miles (16 per cent.) in the thicket.

A comparison of the average daily evaporating power of the air obtained from the readings of the atmometers at Peru, which were not fitted with the rain correcting device, and similar instruments at Lincoln operated beside the rain correctors, gives the following comparison: in the prairie at Lincoln the average daily evaporation from June 4 to August 27 was 19.5 c.c. At Peru it was about 2 c.c. less, *i.e.*, 17.6 c.c. This reduction in the

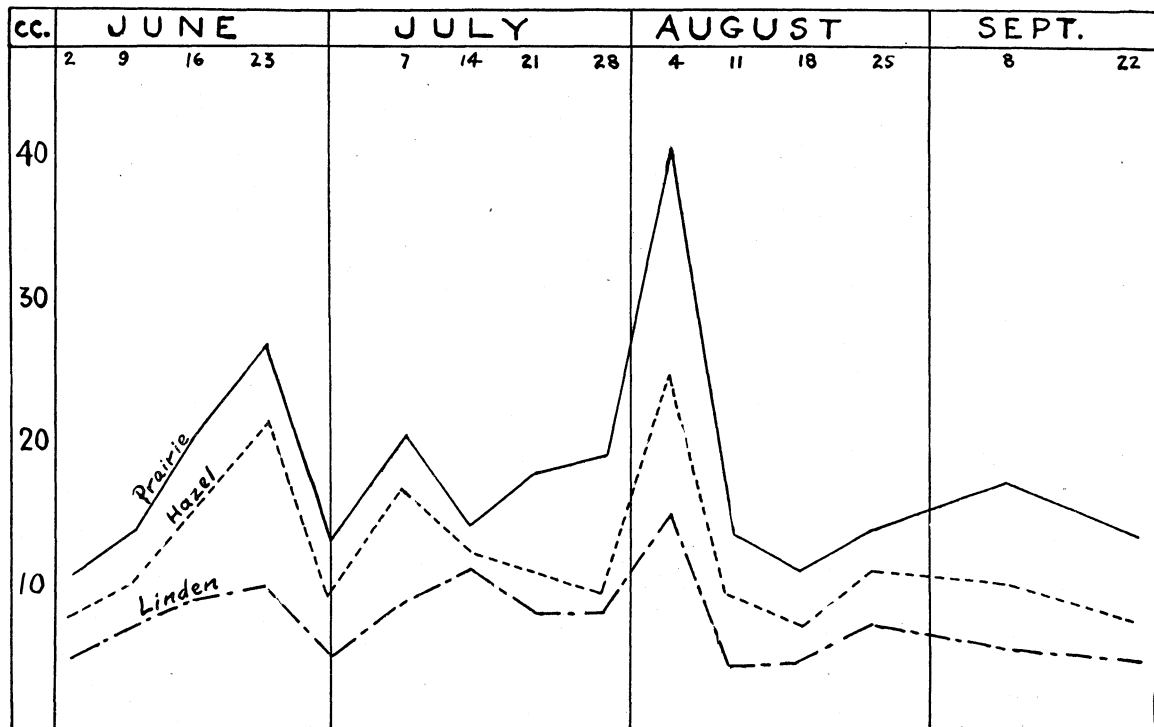


FIGURE 14. Graphs showing the seasonal march of the evaporating power of the air in forest, shrub, and prairie at Peru in 1917.

average daily rate of evaporation is an important factor where high water losses are concerned.

FURTHER STUDIES IN THE FOREST COMMUNITIES

It has already been pointed out that the different forest dominants, although frequently occurring in apparent mixtures, usually are grouped in more or less distinct communities. Even casual observation shows the dominance of *Tilia americana* and *Quercus rubra* in the ravines at the bases of the moist slopes; of *Quercus macrocarpa* on the drier crests, with *Quercus velutina*, *Hicoria ovata*, and other trees occupying intermediate positions.

Belt transects 10 meters wide were run from the crest to the foot of several slopes. At intervals of 8 meters cross tapes were inserted and in the areas thus delimited a census was taken of the tree population together with their diameter B. H. Each tree was charted in its relative position in the area. One of these transects showing the height and slope of the hill, the charted areas and the plant communities they pass through is shown in figure 15.

This figure is very illuminating and worth careful consideration. The transect at the foot of the chart shows the exact number, diameter and position of every woody plant (exclusive of seedlings) growing on the area. The transect at the top of the chart is merely a summary statement of the corresponding areas shown below. In every case the dominants have been placed first. They are preceded by numbers which indicate their abundance in the area and are followed by an exponent which gives the average diameter in inches. In a similar manner the other trees in the particular area are summarized. For example, an examination of the area (10 × 8 meters) on the extreme right at the foot of the figure shows that *Tilia* is dominant, that seven trees of this species occur in the area and that they have an average diameter of 7 inches. Also one *Quercus rubra* with a diameter of 4 inches occurs here. This is summarized in the corresponding area at the upper right corner of the figure.

From these summaries it is relatively easy to delimit in a quantitative manner and with a considerable degree of accuracy the

extent of an area occupied by a certain dominant or by ecologically equivalent dominants. Thus beginning with the slope on the extreme left we find the upper portion occupied by a community in which *Quercus macrocarpa* and *Quercus velutina* are dominant (27 large trees). Two red oaks and three red elms are also present and with several saplings of red elm, an ironwood and a mulberry, make up the forest.

On the steeper slopes near the base of the ravine this forest type gives way abruptly to one dominated by *Tilia*. Here occur 36 large linden trees, a few red oaks, considerable green ash, a few elms and a number of the very tolerant ironwoods. It should be noted that a number of trees, especially black oaks, have died.

Proceeding up the slope we enter the *Quercus macrocarpa-Quercus acuminata* community. The entire absence of the linden here as on the corresponding opposite slope should be noted. Proceeding once more down the gentle westward slope we pass through a narrow belt of timber dominated by the red oak; the transition being one through the black oak stage. The dead bur and black oaks indicate a rather unsuitable habitat for these species, probably due to the shading by the red oaks. The appearance of linden indicates greater mesophytism, and indeed lower down the slope this species becomes dominant.

From this transect it appears that the bur oak, yellow oak or black oak communities occupy the higher ridges; that they give way on the lower slopes to red oak, which is in turn replaced near the foot of the slopes and in the ravines by a community dominated by linden.

We will next examine a transect starting at the top of a ridge 91 feet above the ravine and proceeding down a long gentle northeast slope; figure 16.

The sharp top of this ridge (as is frequently the case on the bluffs) is clothed with grassland. This gives way, through a narrow belt of *Rhus glabra* and *Cornus asperifolia*, to a mixed forest community of black, yellow and bur oak. There are a number of representatives of green ash, red elm (mostly small trees) and an occasional shag-bark hickory, which has migrated up from lower down the slope.

The transition to the mixed hickory-oak community is rather gradual. The community is marked by the presence of a number of large hickories, by the increasing abundance of red oak in the lower portion and by the appearance of the ironwood,—trees entirely absent from the preceding community. However, bur and especially yellow oak occur throughout, the former disappearing entirely and the latter being much less abundant in the red oak community.

The red oak community is characterized not only by the abundance of the dominant, but also by the dropping out of the less mesophytic and less tolerant yellow, bur, and black oaks on the one hand and the increasing abundance of ironwood on the other. The red oak gives way lower down the slope to a well developed linden-ironwood community. Here only an occasional oak is to be found. These are invariably red oak. A few trees of black walnut, swamp hickory and a few other species (not found in this transect) complete the list.

The preceding examples of the community arrangement of tree dominants are typical for the forest in this portion of the formation. Grassland is replaced, usually through a chaparral stage, by forest of the more xerophilous trees,—*Quercus macrocarpa* and *Q. acuminata* followed by *Q. velutina*. In more mesophytic situations *Q. rubra* and *Hicoria ovata* dominate, while a community of *Tilia americana* with *Ostrya virginiana* hold possession of the more moist and richer slopes and ravines.

Three primary habitat factors are concerned in this tree distribution. They are soil moisture, atmospheric humidity and light. The pioneer tree associates invading situations quite too extreme for their more exacting successors, react upon the habitat in such a manner as to make it more moist as regards both soil and air. These reactions, likewise favorable to the early tree occupants, make possible the invasion of the area by more tolerant species. For a time the area is covered with a mixture of the members of the two associates. But gradually, because of the unfavorable light reaction, the species of the earlier woody community largely or entirely disappear. Change of dominants in an area is usually characterized by striking changes in the shrubby

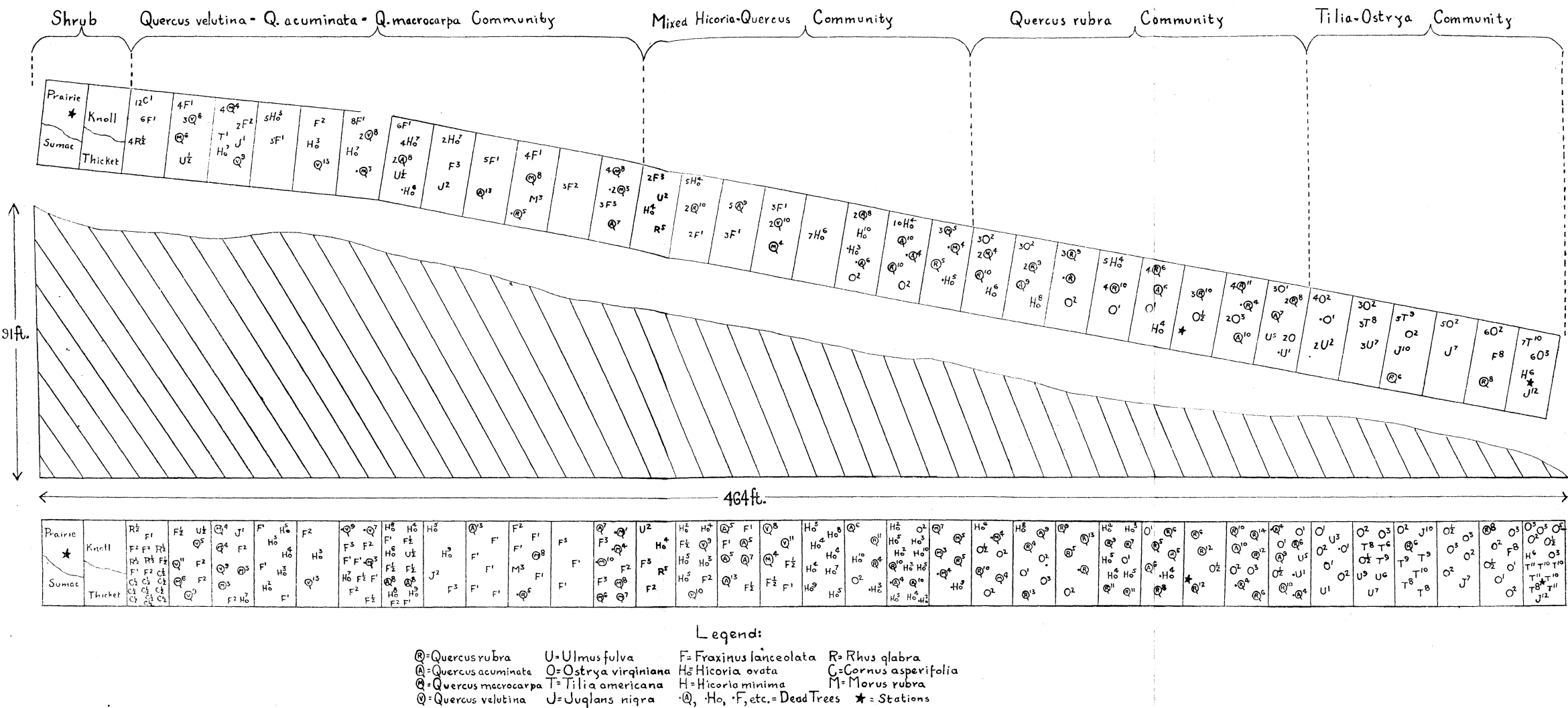


FIGURE 16. Transect 2. Belt transect 10 meters wide showing the composition of the plant communities from the Tilia-Ostrya combination to the shrub community of a prairie knoll, Peru, 1917.

and herbaceous as well as in the fungus flora, each community as it becomes temporarily stabilized sorting out the particular population best adjusted to the particular set of environmental conditions.

Repeated light determinations at the several stations showed a diminution in the following sequence: prairie 1.00; bur oak 0.06; black oak 0.05; red oak 0.028; linden 0.02.

SOIL MOISTURE

Typical stations were selected in each of the preceding communities and in that portion of the area included in the transects as follows:

Prairie station; in the prairie on the knoll shown in figure 2: bur oak station; at the crest of the hill on the right shown in figure 1: black oak station; near the top of the slope shown at the left in figure 1: red oak and linden stations were selected in their respective communities as shown in figure 2.

At each of these stations soil moisture was determined at the intervals and to the depths indicated respectively in the following tables:

TABLE 6
THE AVAILABLE WATER CONTENT TO A DEPTH OF 12 INCHES IN THE SEVERAL
FOREST COMMUNITIES AT PERU, 1917

Station	Depth	Wilting Coefficient	July 19	July 31	Aug. 18	Sept. 5
Bur oak.....	0"-6"	10.5	8.3	2.2	2.9	0.9
Black oak.....	0"-6"	10.8	3.6	1.1	6.7	2.0
Red oak.....	0"-6"	11.4	11.5	3.4	5.5	1.5
Linden.....	0"-6"	11.0	19.6	8.8	16.8	8.7
Bur oak.....	6"-12"	10.2	6.0	2.2	3.0	0.3
Black oak.....	6"-12"	10.5	2.7	3.0	1.2	0.5
Red oak.....	6"-12"	11.4	9.0	3.0	0.1	0.1
Linden.....	6"-12"	10.8	15.0	5.8	7.0	4.7

An examination of these data reveals the fact, that with the exception of the black oak habitat which is almost throughout uniformly drier, that in the main there is an increasingly available soil moisture parallel with the direction of the succession.

As has been shown conclusively for plains and prairie plants (and investigation will probably show the same holds true for many forest trees) root systems are so much more extensive than heretofore supposed that too much emphasis should not be placed upon the water content of the surface layers of soil, and certainly not to the degree of neglecting the deeper substrata. Soil moisture of the deeper soils is given in the following table.

TABLE 7

TOTAL WATER CONTENT OF THE SOIL IN THE SEVERAL FOREST COMMUNITIES AT DEPTHS OF 1 TO 2, 2 TO 3 AND 3 TO 4 FEET, AT PERU, 1917

Station	Depth	July 19	July 31	August 18	Sept. 5
Bur oak.....	1'-2'	18.9	15.8	12.4	14.9
Black oak.....	1'-2'	14.4	13.6	11.4	10.4
Red oak.....	1'-2'	22.6	16.3	15.1	12.7
Linden.....	1'-2'	22.8	18.2	16.0	13.7
Bur oak.....	2'-3'	17.7	12.9	10.7	12.8
Black oak.....	2'-3'	15.6	14.1	11.1	9.6
Red oak.....	2'-3'	20.7	16.7	15.9	13.0
Linden.....	2'-3'	23.8	19.3	16.1	14.9

Station	July 31	
	3'-4'	4'-5'
Bur oak.....	12.9	10.7
Black oak.....	15.1	13.4
Red oak.....	15.4	15.8
Linden.....	19.9	18.7

At depths of 3 to 5 feet the soil moisture increases gradually but directly from bur oak to linden forest. Indeed this holds true throughout every determination and at all depths indicated except in the case of the black oak at depths of 1 to 3 feet, where the soil is usually of lower moisture content than in the bur oak forest. Indeed this may be the prevailing condition, and only further soil sampling can determine this point. However, from all other evidence the writers feel quite certain that future determination will show this consocieties to conform to the general law of increasing soil moisture content as succession progresses.

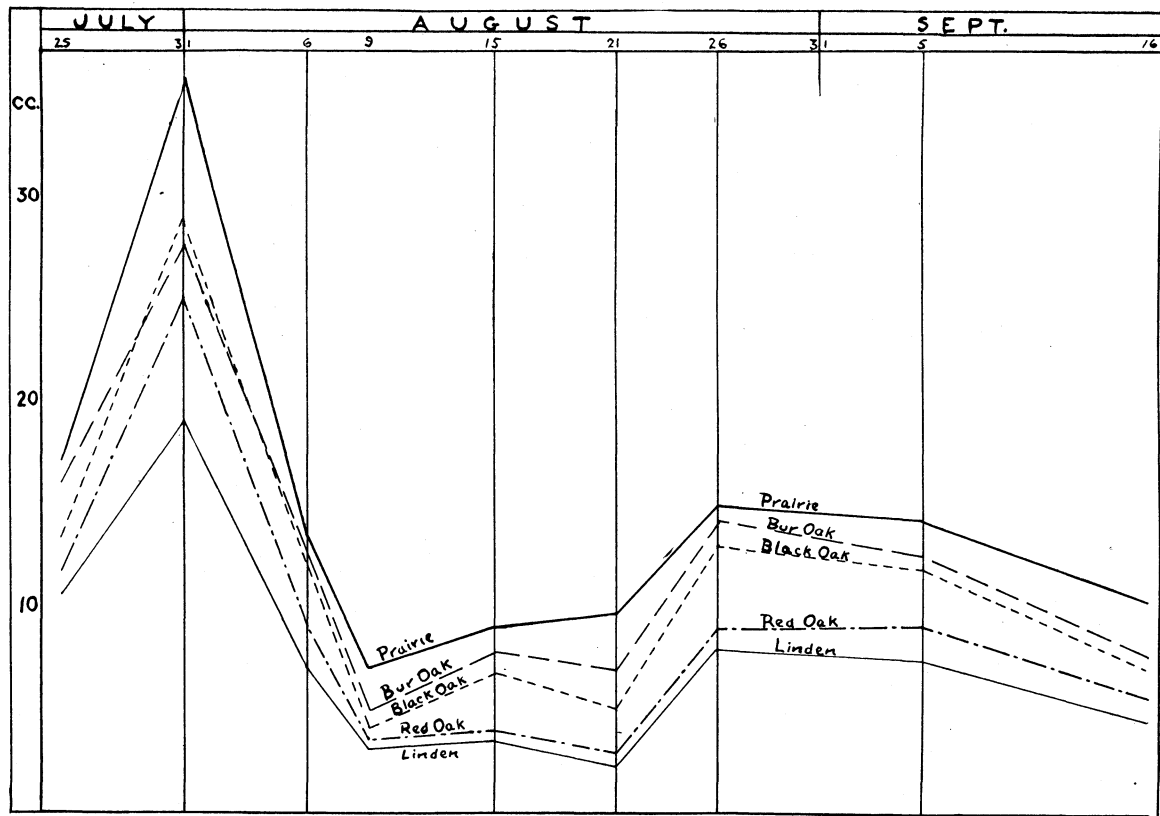


FIGURE 17. Graphs showing the evaporating power of the air in the several forest types at Peru during the season of 1917.

EVAPORATION

A continuous record of the evaporating power of the air was obtained from July 25 to September 16, in all of the forest stations and also in the prairie on the knoll shown in the transect, figure 16. The atmometers were placed as usual at a height of only 15-17 cm. above the soil surface and in that portion of the aerial stratum occupied by the leaves of tree seedlings. The data are shown in figure 17. An examination of these data shows a remarkable uniformity in the general trend of the graphs which also point out plainly the decreasing evaporating power of the air which reaches its minimum in the linden consocieties.

SUMMARY

1. This paper contributes data which still further substantiate the conclusions drawn from previous investigations that evaporation rates and soil moisture conditions in the various plant communities studied vary in general directly with the order of the communities in succession, the communities nearest the climax being the most mesophytic in both respects.

2. The prairies and woodlands in the vicinity of Lincoln are considerably more xerophytic than those in the neighborhood of Peru. This fact is strikingly revealed in a comparison of the ecological factor data from the two areas, and it is also strongly reflected in the composition of the plant communities in the two places, although the two areas are only about 60 miles apart. Available soil moisture was exhausted in the prairie station at various depths in the vicinity of Lincoln on eighteen different dates in 1917, from May to September, while the same condition was recorded for only four dates, late in July and August, in the prairie station at Peru.

3. Ecological conditions are shown to change rapidly as the forest-prairie ecotone is traversed in Nebraska. Habitats rapidly become more xerophilous and many of the more mesophytic species drop out entirely between Peru and Lincoln. It is thus shown that the natural extension of our native woodlands is greatly hindered, possibly altogether prevented in so far as any

significant permanent extension is concerned, by the increasing severity of natural environmental conditions as we move westward away from the woodland types of southeastern Nebraska.

4. The high saturation deficit and the low soil moisture content (often reaching the non-available point) of the prairie sites in eastern Nebraska constitute barriers over which forest trees can scarcely pass. We probably have herein the most ready explanation as to why our natural Nebraska woodlands are confined to the moist slopes of rather narrow valleys, and also the most probable answer to the oft-repeated question as to the treelessness of the prairies in general.

5. The common forest types or communities of the region about Peru in the order of their place in succession are as follows, beginning with the most mesophytic: The linden-ironwood type, the red oak type, the black oak-hickory type, the bur oak-yellow oak type. A bur oak-yellow oak-black oak combination is also quite common. The common forest type near Lincoln is the bur oak-hickory type, often mixed with elm and black walnut.