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THE UNIVERSITY OF NEBRASKA

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## Ecological Studies in the Tension Zone between Prairie and Woodland

By J. E. WEAVER, PH. D. and ALBERT F. THIEL, A. B.

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### ECOLOGICAL STUDIES IN THE TENSION ZONE BETWEEN PRAIRIE AND WOODLAND

#### J. E. WEAVER, PH. D. AND ALBERT F. THIEL, A. B.

Upon the completion of a series of investigations in southeastern Washington and adjacent Idaho (23), in which there was found to be a direct relation between the available water content of the soil and the evaporating power of the air as succession progressed from grassland through scrub to forest, the senior writer moved to Minneapolis, Minnesota. Here such excellent conditions of prairie invaded by scrub and followed by forest offered themselves for study that the services of the junior author were enlisted and an analysis of the situation attempted. Later this study was supplemented by similar work carried on at Lincoln, Nebraska.

The time-worn controversy as to the origin of the prairies and the absence of trees from this great area of grassland has been a favorite theme for the layman and amateur as well as for the scientist. However, we need not concern ourselves here with a general discussion of the literature. A comprehensive bibliography including papers up to 1911 is given by Shimek (17); and Clements (3, 1916) summarizes the successional work in the Prairie-Plains Climax. Notwithstanding the fact that the exact methods of permanent quadrat and factor measurements of modern ecology are rapidly replacing the earlier type of observation and deduction, few quantitative data looking towards a solution of the prairie-forest problem are yet available.

Thornber (20, 1901) while studying the structure of the prairie formation at Nebraska City, Nebraska, maintained stations in prairie, *Zanthoxylum-Corylus* thicket and woodland. Since the non-available water of the soil was not determined, his moisture content readings are of little value. Numerous thermometer and psychrometer readings showed the prairie to have the highest temperature and the lowest humidity. Likewise, the soil temperature of the prairie (at 10 cm.) was always the highest and showed a greater daily range (10-20 $^{\circ}$  F.) than either of the other plant communities.

Harvey (9, 1908) working in South Dakota, summarizes the climatic and edaphic conditions during each of the seasonal aspects. Unquestionably his data on the soil moisture are the most valuable and this appears to be about the only factor reading taken in the field. The data on temperature, wind, mean relative humidity and relative evaporation, taken from the U.S. Weather Bureau at Yankton or calculated from data thus obtained, must have only a general significance as regards actual habitat conditions. The nonavailable soil moisture was determined from an experiment on the Windsor bean. Using this echard he determined the chresard repeatedly throughout the growing season. In general the soils became progressively drier with the advance of the growing season, the chresard falling to 4% in July and to 3.3% in September, but at no time was the soil moisture depleted to the non-available point. Unfortunately the depth at which the samples were taken is not indicated.

Bates (1, 1910) working in the sandhills at Halsey, Nebraska, in order to determine the qualities of various sites for tree planting, (south slope, bottom, north slope and ridge) measured the water content of the soils at 1, 2, 3, and 6 feet respectively in each of the habitats in 1909. The first measurement was made in May, another in July, and the last in September. "Soil temperatures were measured in the middle of the summer, the rate of evaporation, under typical weather conditions, was also determined by means of evaporimeters (modified Pische instruments)".

The soil moisture, which was lowest on the south slope, reached its minimum at all stations and at all depths, except at 6 feet (and at 1 foot on the ridge) in July. The writer points out a close relationship between the soil moisture conditions of the several types at the time of the July minimum and the number of dead pine transplants on the various sites, in September. The pines on the ridge, which

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owing to the almost complete absence of vegetation had rather a constant moisture supply, came through the first season without loss, although the ridge showed the highest wind velocity and the greatest evaporating power of all the habitats. The north slope showed, next to the ridge, the greatest soil water content in July (except at 6 feet) of all the habitats. Likewise, it had the lowest soil temperature and most humid air and 99% of the pine trees survived.

Shimek (17, 1911) reports the results of some experiments carried on at Missouri Valley and Council Bluffs, Iowa, and at Omaha, Nebraska, during 1908. At Missouri Valley observations in forest and prairie were made during a period of six non-consecutive days in August and September "on evaporation, temperature and relative humidity, velocity and direction of wind, clearness of sky, barometric pressure, and in a general way on rainfall". Both evaporation and psychrometer records show clearly evaporation is much more rapid in the exposed prairie areas than from areas protected by topography or forest. These data lead to the conclusion that "exposure to evaporation as determined by temperature, wind and topography is the primary cause of the treelessness of the prairies".

In 1915 the same writer reports further evaporation and humidity data taken in the Lake Okoboji Region in Iowa (18). "The region—furnishes abundant confirmation of the writer's earlier conclusions concerning the cause of the treelessness of the prairies".

The work of Gleason and Gates (7, 1912) on evaporation in central Illinois may be noted here, although as Clements (3) has pointed out it is probable the prairies of central Illinois belong to the deciduous forest climax. The writers state "most of the area was originally occupied by associations of the Prairie Province, but the climatic dominance of the associations of the Deciduous Forest Province is now gradually asserting itself wherever conditions are not interfered with by man". The evaporating power of the air was measured during June and July by means of atmometers and was found to decrease respectively in the following order of plant communities; blowout (basin); blowout (side); bunchgrass (Leptoloma consocies); bunchgrass (Eragrostis trichodes consocies); beach; Quercus velutina woods; Quercus velutina woods (typical); Quercus velutina (numerous young trees of Carya); willows (Acer saccharinum part); willows (Salix part); mixed forest (margin) and mixed forest (center).

It is interesting to note that while "the principal object of the investigation was the determination of the relative amounts of evaporation in certain well marked associations whose successional relations were clearly evident, in order to correlate the phenomena of succession and evaporation" these investigators reach a conclusion quite the converse of that determined by the extensive investigations of Fuller (5) in the Chicago region and Weaver (21) in Washington and Idaho. Gleason and Gates conclude "that successions between associations are not caused by any conditions of evaporation".

Pool (14, 1912) while carrying on his extensive investigations in the vegetation of the sandhills of Nebraska measured the wind velocity for 21 days on the rim of a large blowout, in a protected "pocket," in a pine plantation and in a river thicket. The velocity decreased progressively at the different stations in the order given. He considers the wind "by far the most important and constant climatic factor characteristic of dune regions". The evaporating power of the air measured by Livingston's standardized evaporimeters, also for a period of 21 days, was shown to decrease progressively from open hilltop, rim of blow-out, bottom of blow-out, inner slope of blow-out, protected "pocket," to pine plantation and river thicket. He also gives a table of soil temperatures taken at various depths which brings out some striking differences, and indicates much lower temperatures on north than on south exposures.

Harvey (10, 1913) reports the results of a series of evaporation and soil moisture determinations carried out

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on Chicago Lawn, an undisturbed prairie area within the city limits of Chicago. This prairie community seems to hold "the position of a very persistent stage in the succession following the sedges in the filling up of ponds and lakes" and these prairie tracts "are maintained for extended periods against the encroachment of the forests of the region". "Although it is to be considered as decidedly different in many ways from the western prairies, it gives much the same aspect" owing to the presence of numerous coarse prairie herbs characteristic also of the former region.

Evaporation was measured by Livingston's atmometers placed at a height of 30 cm. above the soil surface. The average daily evaporation graph shows the maximum for the season (1911) of 37 cc. about May 20. The seasonal maximum for 1912 was also reached in May (5) and leads the writer to the conclusion that this high rate of evaporation is probably the usual condition at the beginning of the season before vegetation becomes well developed. On the other hand the summer maximum (about 16 cc.) on the prairie is as low as the corresponding maximum of any of the forest associations yet studied in the region, excepting the beech-maple forest. An atmometer at a height of 60 cm. from the soil gave evaporation readings 25 to 30 percent higher than readings for similar periods from cups at a height of 30 cm.

Determinations of the water content of the soil were made weekly and at depths of 7.5 and 25 cm. respectively, throughout the growing season. While the soils were at or near the saturation point in April and May just before the growing season begins and again in October after it has closed, during the summer months of July and August the moisture is uniformly low. "There are times during these months that the water content of the soils at the two depths falls below the critical percentage". Periods of low water content coupled with high evaporating power of the air "may account for the xerophytic aspect of the prairie vegetation in the late summer". Fuller (5, 1914) discusses briefly the evaporation and soil moisture data obtained by Harvey in 1911 and Newlon in 1912 from the edaphic prairie in Chicago and compares these data by means of graphs with similar data from the various forest communities.

#### LOCATION OF STATIONS AND DESCRIPTIONS OF PLANT

#### COMMUNITIES

The present investigations cover a period of two years. Early in the spring of 1915 stations were established in various plant communities near Minneapolis and factor determinations were taken weekly throughout the growing season. In 1916 these determinations were continued by the junior writer and also similar studies were made at Lincoln, Nebraska.

Just south of Minneapolis in an area formed by the junction of the Minnesota and Mississippi rivers at Fort Snelling, the Federal government has a military reservation including several hundred acres of prairie, scrub and woodland. A part of the grassland covers gently rolling hills (high prairie) while other areas are flat, low and swampy. Working back from the banks of the rivers are belts of mixed forests of oak, elm, maple, etc. The border line between forest and prairie is often occupied by a fringe of shrubs, or these may occur as isolated thickets in the more moist prairie areas. In fact, conditions here presented are similar to those in Nebraska and indeed characterize the general situation all along the forest-prairie ecotone where xerophytic species of oak and other trees often invade the grassland under cover of Rhus, Corulus, Symphoricarpos or other shrubs.

The soils underlying the plant communities at Fort Snelling are somewhat variable. They may be classified in general as sandy loam. The water holding capacity



Fig. 1. Prairie and hazel thicket near Minnehaha. The crosses indicate the position of the stations. The plants in the foreground are *Stipa spartea* and *Solidago rigida*.

varies from 35% on the ridge of the high prairie to over 60% in the forest and even 80% in low, rather swampy prairie. Likewise the wilting coefficients range from 4% in the lighter sandy soils to over 16% in the loam soils.

A station in the high prairie was maintained on a low, flat-topped hill about one-half mile southwest of Minnehaha Falls. It was only 15 meters from a similar station in a hazel thicket (fig. 1). Notwithstanding the fact that these two stations represented most typically the high prairie and invading shrubs, their proximity to the city made the placing of evaporimeters there an extremely hazardous risk. However, some consecutive evaporation data were obtained.

A second group of stations including low prairie, hazel thicket and oak forest were selected about a mile west of the fort, and here soil moisture, evaporation and other data were obtained without interruption. In 1916 a fourth community, a hard maple forest at Minnetonka, 20 miles west of Minneapolis, was added to the list. A brief description of the structure of the several plant communities will be given before taking up a discussion of the habitat factors.

The prairie near Minnehaha, typical of the flora of the high rolling prairie, will first be described and contrasted with the low prairie surrounding the second group of stations. Not until the last week of April or early in May does the flora take on renewed activity. Then the blossoming of Anemone patens wolfgangiana\* in abundance everywhere, of Ranunculus ovalis, and of patches of Carex pennsylvanica, Antennaria plantaginifolia and A. canadensis change the appearance of the landscape. At the low prairie station Anemone patens wolfgangiana is absent and the prevernal aspect is poorly marked by Sisyrinchium campestre, S. angustifolium, Carex pennsylvanica and Antennaria plantaginifolia.

<sup>\*</sup> The nomenclature of Minnesota plants is according to the seventh edition of Gray's New Manual of Botany.

Late in May and extending well into June the south slope of the hill is covered with such an abundance of violets, Viola pedatifida and V. pedata, that it has received the local name of "Bluehill". Ranunculus septentrionalis, Pedicularis canadensis, Zizia cordata and Z. aurea add tone to the growing carpet of grasses, and are accompanied later by Lithospermum canescens and L. gmelini, both very abundant. Tradescantia reflexa and T. bracteata, locally abundant. with Anemone culindrica complete the list of more important vernal bloomers. Many of these species are absent on the low prairie at Fort Snelling. Here an abundance of Anemone canadensis. Zizia cordata and Z. aurea with some Anemone cylindrica. Pedicularis canadensis and Lithospermum canescens make up the list. Anemone canadensis with its large white flowers, 4 cm. in diameter, forms distinct and very conspicuous societies. Polugala senega and the stargrass, Hypoxis hirsuta, appear late in May but continue blooming in June. The latter covers the ground of the low prairie with a carpet of vellow. Its conspicuousness indicates the low stature of the grasses at this period.

During the third week in June the blossoming of Stipa spartea, and Koeleria cristata initiates the estival aspect. These are the most important early grasses. Agrostis huemalis dominates considerable areas on dry hillsides; Poa pratensis works up from the draws or outward from the scrub; while Panicum scribnerianum is more or less abundant as an interstitial. At the low prairie station neither Stipa nor Koeleria are so abundant, while here Poa plays a role of much greater importance. On the high prairie Erigeron annuus and E. philadelphicus with Achillea millefolium give tone to the landscape, which is varied in places with yellow patches of Oenothera serrulata and the showy flowers of Rosa pratincola and R. blanda. In distinct contrast the low prairies are veritable flower gardens of red and yellow Castilleja coccinea which are replaced by societies of *Phlox pilosa* in such abundance that a single square meter often reveals as many as 200 plants, each with

its large panicle of showy red flowers. A list of the more important estival bloomers on the high prairie includes:

Allium spp.	$Pentstemon\ gracilis$
Amorpha canescens	Pentstemon grandiflorus
Agropyron caninum	Physalis heterophylla
Comandra umbellata	Psoralea argophylla
Geum triflorum	Senecio balsamitae
Heuchera hispida	Steironema ciliatum
Potentilla arguta	

Late in July societies of *Coreopsis palmata* add tone for a time and with species of *Petalostemum* give the transition to the autumnal aspect. On the low prairies the plant population is esentially different. In addition to societies of Galium boreale and an abundance of Delphinium penardi and Pucnanthemum virginianum the following species, Comandra umbellata. Oxalis stricta. O. violacea. Scutellaria parvula, Vicia americana and Zugadenus chloranthus, are more or less important. In late July Lobelia spicata and Rudbeckia hirta give the prairies a distinct tone. A number of mesophytes occur along the edge of the woods and work out into the low prairie. Among these should be mentioned Geranium maculatum. Lathurus venosus. Stachus palustris. Lilium philadelphicum, L. canadense, Steironema ciliatum, Veronica virginica and Agastache scrophulariaefolia. The presence of certain distinct wet meadow and swamp species such as Valeriana edulis, Habenaria leucophaea, and Cicuta maculata indicates a high water content of the soil. In places the low prairies give way to areas dominated by Spartina cynosuroides.

Early in August the autumnal aspect begins. It is characterized by the blooming of several species of goldenrods and blazing stars as well as a number of grasses. On both the high and low prairies *Solidago canadensis*, *S. rigida*, and *S. missouriensis* are found with *Liatris scariosa*, *L. punctata* and *L. pycnostachya* in greater or lesser abundance. Andropogon scoparius and A. furcatus also occur at both stations, the former dominating high prairie while the latter is more abundant in the low prairie. Likewise Sorghastrum nutans is more abundant at the high prairie station. Panicum virgatum, Calamovilfa longifolia, Bouteloua curtipendula and Eragrostis spp. complete the list of more important autumnal grasses. The large flowers of Helianthus, Rudbeckia hirta and Heliopsis scabra give with Solidago a distinct yellow tone varied by the purple of Aster novae-angliae and blazing stars or the white flowers and fruits of Kuhnia eupatorioides. On the low prairie Monarda fistulosa forms local clans alternating with Pycnanthemum virginianum and scattered individuals of Rudbeckia hirta.

The prairies are distinctly of the sod type characteristic of the less xerophytic part of the prairie formation. Many of the more xerophytic species are absent from the low prairie while the presence of numerous mesophytes, many of which have migrated out from the wood's margin, indicate much more favorable life conditions for scrub or forest trees. Indeed, as will be shown, except for repeated mowing and fires much of the low prairie area would undoubtedly give way to woodland.

The vegetation of the scrub station at Minnehaha consists chiefly of *Corylus americana* which forms a fairly dense growth reaching a height of 3 to 5 feet (fig. 1). Intermixed with the hazel is considerable *Zanthoxylum americanum* and smaller amounts of *Rhus toxicodendron*, *Rubus* spp., *Rosa blanda* and *Viburnum*. Scattered trees and numerous seedlings of bur and red oak are found, while about 150 meters from the prairie the scrub gives way to oak forest. A light sod of *Poa pratensis* covers the ground where the shade is not too dense. Species such as *Amphicarpa monoica*, *Smilacina racemosa*, *Polygonatum commutatum* and *Geranium maculatum* indicate at least fairly mesophytic conditions.

The vegetation at the scrub station near the low prairie consists of a dense growth of *Corylus americana* with a few scattered bur oaks. In addition to a very sparse growth of

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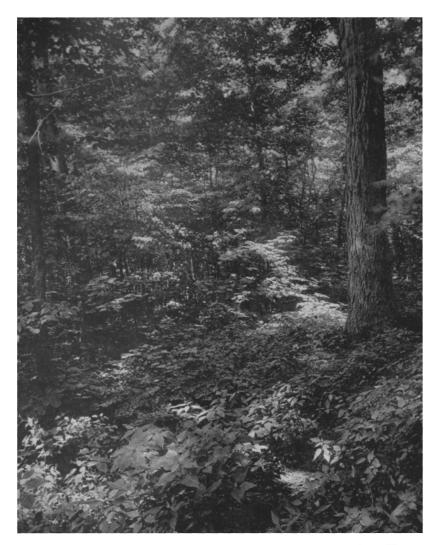


Fig. 2. Climax forest of *Acer saccharum* near Minnetonka. The chief herbs in the foreground are *Laportea canadensis*, *Phryma leptostachya*, *Adiantum pedatum* and *Circaea intermedia*.



Fig. 3. Station on ridge in the climax maple forest at Minnetonka. Ostrya virginiana is in the foreground and Quercus rubra on the right.

*Poa* some mesophytes, already mentioned as characteristic of wood's margins, occur here.

The dominant of the oak forest is *Quercus macrocarpa*. The trees vary in size from seedlings to those more than 30 cm. in diameter. Other tree species are *Quercus alba*, *Q. rubra*, *Prunus serotina*, and *Populus tremuloides*. Relict *Corylus* reaches heights of over two meters and with *Cornus paniculata* forms the scrub layer. Characteristic lianas are *Vitis vulpina*, *Psedera quinquefolia* and *Menispermum canadense*. *Poa* forms intermittent patches of sod in the open places but otherwise the ground is nearly bare. The following mesophytes occur in greater or lesser abundance:

Amphicarpa monoica	Hydrophyllum virginianum
Adiantum pedatum	Orchis spectabilis
Arisaema triphyllum	Phryma leptostachya
Circaea intermedia	Sanicula marilandica
Desmodium sp.	Smilacina racemosa
Geranium maculatum	Vicia americana

Near Minnetonka lies a small tract of climax maple This has never been cut over and, like the vegetaforest tion just described, is not pastured. It is rather typical of hundreds of square miles of former forest conditions of south-central Minnesota known as the "Big Woods". In order to determine the exact structure of this representative climax forest tract, transects including nearly a thousand square meters extending from a ridge through the center down a west slope, were selected and the vegetation charted. The dominant, Acer saccharum (fig. 2) makes up 78% of the forest; Ostrya virginiana 8%; Ulmus americana and Carya cordiformis each 4%, while Quercus rubra and *Tilia americana* complete the list of trees. On the ridge the less mesophytic and also less tolerant red oak is much more abundant than on the slope (fig. 3). Characteristic shrubs and lianas are Celastrus scandens. Menispermum canadense. Psedera quinquefolia and tree-like specimens of Rhus glabra and Ribes cynosbati. The deep, rich soil, covered with a thick layer of leaf-mould, is clothed, where the shade is not too dense, with a carpet of mesophytes. Many of these are absent or notably less abundant on the ridge than on the more moist slope. Some of the most abundant and important are:

Actaea rubra	Cryptotaenia canaden <b>sis</b>
Adiantum pedatum	Eupatorium sp.
Anemone quinquefolia	Hepatica triloba
Arisaema triphyllum	Laportea canadensis
Aralia nudicaulis	Phryma leptostachya
Asplenium filix-femina	Sanguinaria canadensis
Circaea intermedia	

A station was established on the ridge in the spring of 1916 and it was planned to maintain another on the slope. Unfortunately a lack of instruments limited the data to those taken from the ridge station and in a habitat which is less mesophytic and consequently not characteristic of the forest as a whole.

#### SOIL MOISTURE

At the various stations soil samples for moisture content determinations were taken weekly except at Minnetonka where they were taken on alternate weeks. Samples of about 100-150 grams were secured in duplicate and about one meter apart. The first series includes the soil cores representing the surface 10 cm. of soil after removing the leafmould and the second the cores from 10 to 30 cm. The soil was placed in cans with tight fitting covers, brought to the laboratory, weighed, and dried at 105° C. until it reached a constant weight. The percentage of water was calculated on the basis of the weight of the oven-dried soil. In the following figures the results are shown graphically. The weekly intervals are the abscissas, while the ordinates represent the percentage of soil moisture present at the The horizontal lines show the wiltweekly determinations. ing coefficients and these are of the same weight and character as the graph showing the water content of the same soil. Hence the intervals between the graphs and the line denoting the wilting coefficient (if this interval exists above the line) give the amount of water available for growth.\*

Figure 4 shows the moisture conditions of the soil of the high prairie at the Minnehaha station during 1915. It may be noted that notwithstanding the relatively low water content of these sandy soils, at no time during the growing season was the echard reached. An examination of the rainfall records, however, shows that June and July of 1915 were unusually wet months.

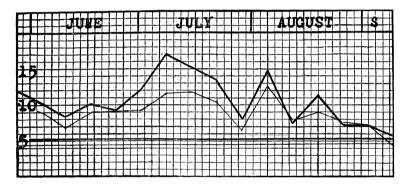


Fig. 4. Graphs showing the range of soil moisture in the high prairie at Minnehaha for 1915; the heavy line from 0-10 cm. and the light line from 10-30 cm. depth; wilting coefficients are represented by horizontal lines.

The water content of the soil in the adjacent hazel scrub is shown in figure 5. It may be noted that the wilting coefficients at both depths, 0-10 and 10-30 cm. respectively, are higher than those at the prairie station only 15 meters beyond. This is due to increased humus. While available water for growth was present throughout the season at 0-10 cm. and in much greater abundance than in the prairie, the wilting coefficient at 10-30 cm. was reached in late July.

<sup>\*</sup> The writers are deeply indebted to Dr. L. J. Briggs of the Bureau of Plant Industry for duplicate determinations of the wilting coefficients of the soils at the various stations.

On May 26th, soil samples for water content determinations were taken at these stations at intervals of 1 foot to a depth of 5 feet. The samples at the various depths, like similar ones taken late in the fall, showed in every case a higher water content in scrub than in prairie. The scrub actually receives more precipitation due to the drifting in

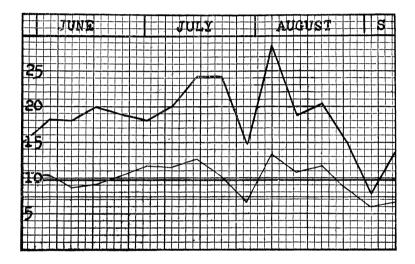


Fig. 5. Graphs showing the range of soil moisture in the hazel scrub at Minnehaha for 1915; the heavy line from 0-10 cm. and the light line from 10-30 cm. depth; wilting coefficients represented by horizontal lines.

of snow, while it conserves its moisture by shading the soil and lowering evaporation.

Trenches dug in the prairie and hazel showed that few prairie plants extend their root-systems beyond a depth of 5 feet while most of the roots were limited to the first 4 feet of soil. In the hazel the surface 8 inches of soil is a great network of roots and rhizomes, the former sometimes extending to depths of more than seven feet (cf. 19, 16, and 22).

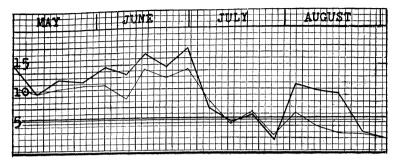


Fig. 6. Graphs showing the range of soil moisture in the high prairie at Minnehaha for 1916; the heavy line from 0-10 cm. and the light line from 10-30 cm. depth; wilting coefficients are represented by horizontal lines.

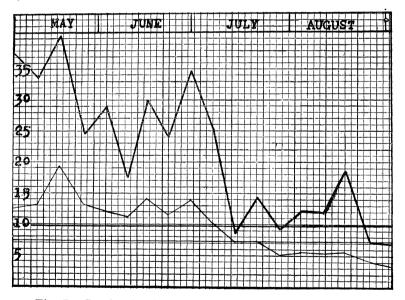


Fig. 7. Graphs showing the range of soil moisture in the hazel scrub at Minnehaha for 1916; the heavy line from 0-10 cm. and the light line from 10-30 cm. depth; wilting coefficients represented by horizontal lines.

In 1916 the soils at the prairie station after midsummer were much drier (fig. 6) and early in July the chresard was

lacking to a depth of 30 cm. In the scrub, however, (fig. 7) not only was there much more water available in the shallower soil throughout the early part of the summer but also the periods during which no chresard was available were much shorter than corresponding periods in the prairie.

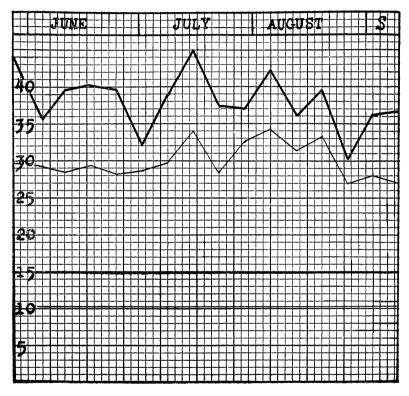


Fig. 8. Graphs showing range of soil moisture in the low prairie at Fort Snelling for 1915; the heavy line from 0-10 cm. and the light line from 10-30 cm. depth; wilting coefficients represented by horizontal lines.

Figures 8 and 9 show the march of soil water in the low prairie and scrub respectively, at Fort Snelling. A glance shows that at all times there was an abundance of water available, the prairie soil being approximately as wet as that in the scrub. During the following year, however, the soil to a depth of 10 cm. was much drier in the prairie than in the hazel (fig. 10). At 10-30 cm. there was also often less available water in the prairie than in the scrub (fig. 11).

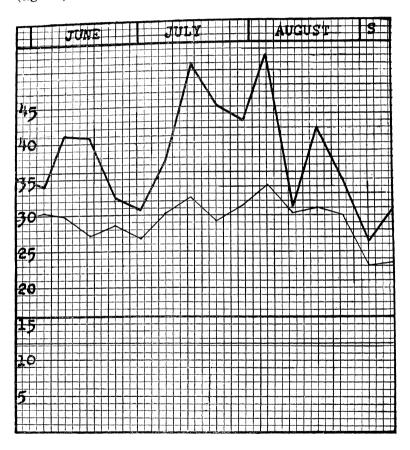


Fig. 9. Graphs showing the range of soil moisture in the hazel scrub at Fort Snelling for 1915; the heavy line from 0-10 cm. and the light line from 10-30 cm. depth; wilting coefficients are represented by horizontal lines.

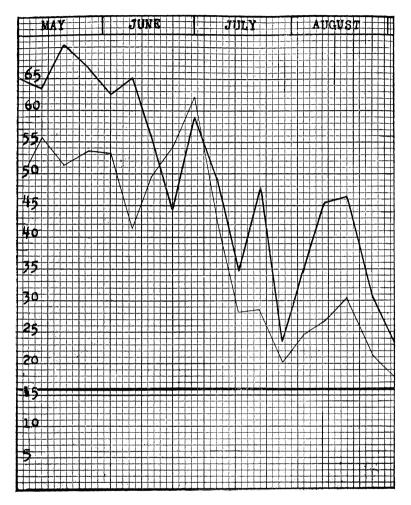


Fig. 10. Graphs showing the range of soil moisture to a depth of 10 cm. in the low prairie and hazel scrub at Fort Snelling for 1916; the heavy line indicates the soil moisture in the scrub and the light line in the prairie.

The graphs of soil moisture obtained from data taken in the oak forest bordering the prairie are shown in figure 12. This station was about one-fourth of a mile south of those in the low prairie and scrub. The sandier nature of the soil is revealed in the lower wilting coefficients. Humus content is relatively low because of occasional fires. As regards actual available water a comparison of these graphs with those in figure 8 shows that the low prairie is really the wetter of the two habitats. As far as abundance of soil

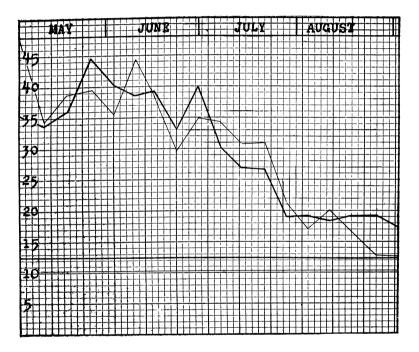


Fig 11. Graphs showing range of soil moisture at a depth of 10-30 cm. in the low prairie and hazel scrub at Fort Snelling for 1916; the heavy line indicates the soil moisture in the scrub and the light line in the prairie.

moisture is concerned there is no question that except for annual mowing and repeated fires much of the low prairie would be covered with a very mesophytic type of forest or with scrub. Rhizomes of *Corylus*, *Rhus*, and *Symphoricarpos* were found extending from 3-5 feet from the thicket borders into the grassland, while fire-scarred suckers of

various ages from charred stumps of oak and aspen tell the story of recurrent fires. As has already been pointed out, however, much of the low prairie merges into swamp where the soil is too wet for optimum forest development.

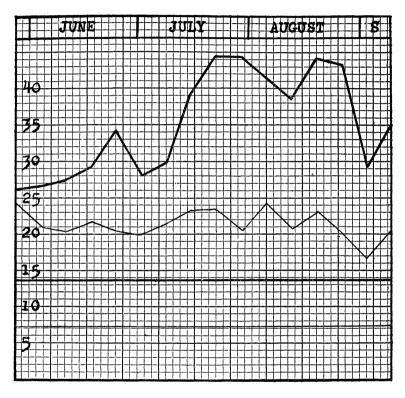


Fig 12. Graphs showing the range of soil moisture in the oak forest at Fort Snelling for 1915; the heavy line from 0-10 cm. and the light line from 10-30 cm. depth; wilting coefficients are represented by horizontal lines.

The march of soil water in the oak woods during 1916 is shown in figure 13. Data giving similar graphs were obtained from a second station in the oak woods but these need not be given here. It has been repeatedly pointed out and emphasized by ecologists that the range of soil moisture in the upper layers of the soils of various plant communities is extremely important to the plant. For it is in these layers that the roots of seedlings develop and the success or failure of these seedlings determine the character of the succeeding vegetation. In figure 14 are brought together for the sake of comparison the graphs showing soil moisture

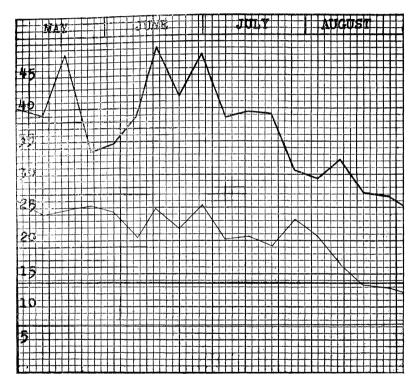


Fig 13. Graphs showing the range of soil moisture in the oak forest at Fort Snelling for 1916; the heavy line from 0-10 cm. and the light line from 10-30 cm. depth; wilting coefficients are represented by horizontal lines.

content at 0-10 cm. in typical prairie and scrub (Minnehaha stations) and oak forest (Fort Snelling) for 1915. The increasing chresard, notwithstanding the higher wilting

coefficients, as the succession advances is so evident that further discussion is unnecessary. As shown in figure 15 the same relationship held during 1916. It is interesting to note that throughout both years and even during the driest periods considerable water was available to the plants of the forest communities. The figure also gives a graph showing the march of soil moisture in the maple forest station at Minnetonka. This community representing the climax forest of the region shows the highest water content of the soil.

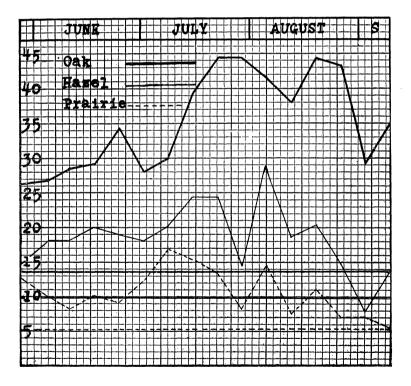


Fig. 14. Graphs showing the range of soil moisture to a depth of 10 cm. in the high prairie and hazel scrub at Minnehaha and in the oak forest at Fort Snelling for 1915; the wilting coefficients are represented by horizontal lines.

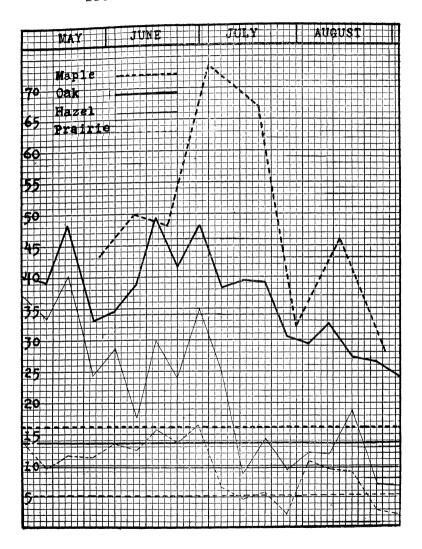


Fig. 15. Graphs showing the range of soil moisture to a depth of 10 cm. in the high prairie and hazel scrub at Minnehaha, in the oak forest at Fort Snelling and in the maple forest at Minnetonka for 1916.

Space will not permit a recapitulation of the water content data for soils at 10-30 cm. in the form of combined graphs. But a comparison of the graphs in figures 4 to 7 shows that while the soils of the hazel at 10-30 cm. depth are seldom much wetter and at times even drier than those of the prairie, as soon as the forest is reached (figs. 12 and 13) a decided increase in available water is recorded.

#### **EVAPORATION**

In analysing the water relations of plants it is not enough to know the amount of moisture available in the soil but a knowledge of the power of the air to extract water from the plant is also imperative. Consequently the evaporating power of the air in the various plant communities was measured during the same periods that data were obtained upon the available water supply.

Standardized Livingston's porous cup atmometers were used throughout, a part of them in 1916 being of the nonabsorbing type. The cups were mounted in bottles of about 300 cc. capacity, closed with tightly fitting rubber stoppers that were perforated for the atmometer tubes and for bent capillary tubes which served to equalize the atmospheric pressure within the bottles with that of the external air, without causing loss by evaporation or permitting rain to enter the reservoirs. The bottles were sunk into the soil so that the evaporating surface of the cups was in all cases 17-23 cm. above the surface of the soil. Readings were taken at weekly intervals and at each reading the bottles were refilled with distilled water from a 100 cc. graduate to a file scratch on the neck. The cups were run in duplicate, being exchanged with other newly standardized cups at the end of a 6-10 week period and at the end of each season the whole lot were restandardized.

By the coefficients thus obtained, all readings were reduced to the standard adopted by Livingston (12). To facilitate comparison of the evaporation between the various stations and to exhibit the progress of evaporation during

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the season, the average water loss per day between the readings has been calculated and shown in graphs with the ordinates representing the number of cc. lost per day by a standard atmometer; the abscissas indicate the intervals between the readings.

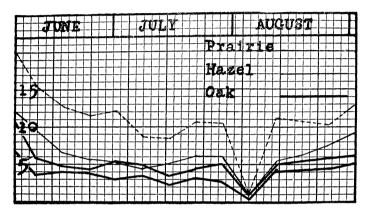


Fig. 16. Graphs showing the daily evaporation rates in the prairie, hazel scrub and oak forest at Fort Snelling for 1915.

The daily evaporation rates in the low prairie, the hazel scrub and the oak forest at Fort Snelling for 1915 are shown in figure 16. There is a rather close agreement in the weekly variations of the evaporating power of the air in the various plant communities, the prairie always being the most xerophytic. The lowest graph in the figure shows the evaporating power of the air at a station near the edge of the oak forest and in a place where as a result of recent fires dense growths of *Urtica gracilis* and *Circaea intermedia* shaded the atmometers even more than they were shaded at the station in the undisturbed part of the oak forest. During the following year evaporation readings were not taken in the burned area.

The evaporation data for 1916 are shown in fig. 17. The data from the prairie for May are missing owing to the fact that severe freezes caused the loss of the atmometers,

and consequently the readings during this period are not shown. These late frosts undoubtedly have a retarding effect upon the advance of tree seedlings into the prairie. On May 19th, 1915, oak seedlings about & inches high in the edge of the prairie at the Minnehaha station had their leaves badly frozen, some of them being entirely killed, while those under cover of the scrub were unharmed.

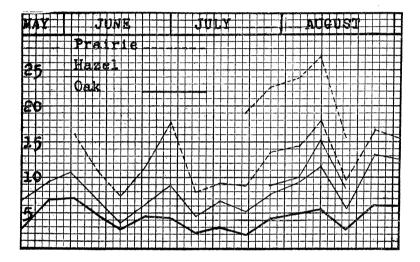


Fig. 17. Graphs showing the daily evaporation rates in the prairie, hazel scrub and oak forest at Fort Snelling for 1916. The highest graph shows evaporation rates in high prairie, and the short solid line those in the hazel at Minnehaha.

The graphs show again the same relationship between the evaporating power of the air and the stage in succession; the former decreasing as the climax community is approached. Some evaporation readings were obtained from the station on the ridge in the forest at Minnetonka, but these data are incomplete and not sufficient to warrant publication at this time.\*

<sup>\*</sup> This investigation is being continued by the junior writer and the present paper may be considered as a preliminary report.

The highest graph in figure 17 is from data taken at the Minnehaha prairie station during July and August. This shows a much higher evaporating power of the air (68% higher for the same interval) than that of the low prairie at Fort Snelling. However, the low prairie gave a higher evaporating power of the air than did the hazel at Minnehaha (light solid line) during four weeks of July and August.

We may conclude then, that as the succession advances from prairie through scrub to forest not only are plant life conditions made more favorable by an increase of available water in the soil but also by a decrease in the evaporating power of the air.

#### SOIL TEMPERATURE

In his work in Washington and Idaho, Weaver (23) found a definite relation between the temperature of the soil at various depths and the stage in the succession, the temperature decreasing as the climax community is approached. In the progress of the present investigation, a large number of soil temperature readings at depths varying from 1 inch to 3 feet were made at the same stations and at the same time that the soil samples for moisture determinations were secured. A few of these data, selected as representative, are given in the tables 1 and 2. They agree in general sequence with those taken during 1916 at Lincoln, Nebraska; the temperature becoming progressively lower at all depths from prairie through scrub to forest.

Table 1. Showing the range of soil temperature at a depth of 1 inch in the high prairie and hazel scrub at Minnehaha during 1915.

Station	June 4	June 24	July 8	July 29	Aug. 19	Sept. 9
Prairie	23.0 °C	21.9°C	23.3 °C	29.6 °C	26.7°C	25.4 °C
Scrub	15.2	15.2	16. <b>2</b>	20.5	16.6	17.6

Table 2. Showing the range of soil temperature in the prairie and scrub at Minnehaha and in the oak forest at Fort Snelling during 1916.

Depth 4 in.			Depth 12 in.			
Date	Prairie	Hazel	Oak	Prairie	Hazel	Oak
June 3	16.3 °C	13.5°C	12.1 °C			
June 23	22.4	15.0	12.8	16.3 °C	$13.3^{\circ}\mathrm{C}$	11.2 °C
July 7	29.4	18.3	17.0	25.7	17.5	15.9
July 21	30.0	21.0	18.0	27.2	19.8	17.1
Aug. 18	24.6	21.8	19.0	24.2	21.1	18.0
Sept. 2	28.1	17.3	14.9	22.0	16.6	14.5

LOCATION OF STATIONS AND DESCRIPTIONS OF PLANT COM-MUNITIES NEAR LINCOLN, NEBRASKA

During the growing season of 1916 investigations were carried on by the senior writer in several plant communities near Lincoln. In an area of about 80 acres of natural vegetation lying two miles east of Havelock and including high prairie, low prairie and stream thicket, stations were established in April. Habitat factor readings were obtained for a period of about three weeks, when the breaking of the prairie for cultivation necessitated a change. Although this move broke the continuity of the work somewhat, it was fully justifiable because of the excellent stations selected near Belmont, about three miles north of Lincoln.

The Belmont prairie covers an area of more than 100 acres of rolling hills presenting various slopes and exposures. The draws vary in degree of moisture from those clothed with ordinary low prairie vegetation to *Spartina* slough, cattail swamp and open water. On some of the slopes near the ravines scrub communities of sumac and willow have become established.

The fertile dark-colored soil is of the type known as loess,\* and is more or less intermixed with glacial drift.

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<sup>\*</sup> For a complete discussion of the physical and chemical properties of loess soils the reader is referred to a series of papers by F. J. Alway et al "The Loess Soils of the Nebraska Portion of the Transition Region". Soil Science Vol. 1, Numbers 3, 4, and 5, 1916.

Upon removal from Havelock, stations were at once established in the following locations in the several plant communities. A base station was maintained in the high prairie on a flat-topped divide having an altitude of 1230 feet and approximately 90 feet above the flood plain of Salt Creek Basin. A second base station was established in a sumac thicket on the southwest slope of the hill and about 250 meters south of the high prairie station. Α second prairie station on the same slope as the sumac and at an equal distance from the ravine (about 10 m.) was also established. This station and the one in the sumac were only 30 m. apart (fig. 18). Just across the ravine on the northeast slope and opposite the second prairie station. a third station in the prairie was maintained. As shown in fig. 18 the ravine between these stations is occupied by a Tupha community. Here also factor data were taken every week. Lastly, about a mile southeast of this group of stations another one was established in the stream-side woodland along Salt Creek. Near this last station readings of the habitat factors were obtained from time to time in a low prairie, but these data are not complete. In general the high and low prairie stations near Belmont correspond very closely to those at Havelock, while the stream-side woodland of Steven's creek, near Havelock, and that of Salt Creek are fairly typical of many similar streams in the prairie formation of eastern Nebraska. A brief statement of the vegetation in each of the various habitats will be This may help to understand better the conditions given. under which the following data were obtained and will also show how the type of vegetation indicates habitat conditions.

The prairie at Belmont, typical of the less xerophytic part of the prairie formation, is dominated by sod-forming grasses. Among these grasses grow certain legumes and composites which during part of the growing season outrank the grasses in height and degree of conspicuousness. Thus the growing season may be divided into seasonal aspects.

The earliest prevernal bloomers appear in the warmer situations early in April and about three weeks before they appear at Minneapolis. The most important are Carex penn. sulvanica\* and Antennaria campestris. Both are low perennials and they would be inconspicuous except for their gregarious habit and the fact that few other plants appear at this season upon the brown background of dry grasses and herbs. May introduces the vernal aspect and the brown tone of winter is replaced in low places especially, by the green sod of *Poa pratensis*. This is the only dominant playing a role in this aspect. Now the purple and blue patches of Astragalus crassicarpus, the massive cream-colored racemes of *Baptisia bracteata* on the slopes, and the bright vellow heads of Senecio plattensis form a pleasing sight. Sisyrinchium angustifolium may be found everywhere and intermixed are *Carex meadii*. C. festucacea, species of Lithospermum and Viola pedatifida; while Fragaria virginiana. Oxalis stricta and O. violacea are to be found near the foot of moist slopes.

Early in June the blossoming of Poa pratensis, Stipa spartea, and Psoralea floribunda introduces the estival aspect. Poa is not only dominant in many of the swales but, probably favored by repeated mowing, has become a dominant throughout much of the area. By the second week in June it is ripe and brown. Stipa is a dominant over the whole prairie and is especially abundant on the higher ridges. It, like Poa, gives a distinct tone to the landscape throughout June even after the ripening and drying up of the inflorescence. Psoralea floribunda, a large bushy plant sometimes a meter high, grows in such abundance that it gives a distinct tone to large areas. It begins flowering early in June and continues for about a month (fig. 19). Likewise the firegrass, Agrostis hyemalis, is an important species over considerable areas of high prairie, its reddish

<sup>\*</sup> The nomenclature of Nebraska plants is according to the second edition of Britton's Manual of the Flora of the Northern States and Canada.



Fig. 18. Prairie at Belmont showing the station on the southwest slope, the Rhus thicket and the Typha community.



Fig. 19. A view in the Belmont prairie in June. In the foreground are *Erigeron ramosus* and *Meriolix serrulata*; the bushy plants in the background are *Psoralea floribunda*.



Fig. 20. An area in the prairie dominated by Agrostis hyemalis. Other plants are Allium mutabile, Achillea millefolium and Stipa spartea. color making it very conspicuous (fig. 20). Koeleria cristata and Panicum scribnerianum are also abundant, the latter being a rather inconspicuous interstitial. Among the more important estival plants the following may be mentioned:

Achillea millefolium	$Erigeron \ ramosus$
Acerates spp.	Gaura coccinea
Agropyron spicatum	Glycyrrhiza lepidota
Allium mutabile	Linum sulcatum
Asclepias spp.	$Meriolix\ serrulata$
Brauneria pallida	Psoralea esculenta
Coreopsis palmata	$Psoralea \ argophylla$
Delphinium albescens	Physalis heterophylla
Eatonia obtusata	Ratibida columnaris
Elymus canadensis	Rosa arkansana
2.9	

Late in June the prairie shoestring, Amorpha canescens, begins to blossom. This shrub becomes conspicuous however before its period of anthesis, and throughout July, Poa, Stipa and Psoralea having lost their importance, its leaden color gives tone to the prairie. Near the middle of July Kuhnistera candida and K. purpurea appear in abundance and slightly earlier Meibomia illinoensis and Silphium integrifolium.

The autumnal aspect is ushered in late in July. The dominants are Andropogon scoparius, A. furcatus, especially on the low prairie and Sorghastrum avenaceum. All of these are rather tall grasses and considerably overtop most of the other vegetation. The most abundant is Andropogon scoparius. It is a sod former and only in a few places on the drier ridges does it resort to the bunch habit. Panicum virgatum and Sporobolus longifolius are also characteristic tall prairie grasses. Bouteloua oligostachya and Aristida oligantha form a carpet in places in drier soils or with Panicum capillare and Eragrostis pectinacea play a role of more or less important interstitials among the taller grasses.

Besides the grasses numerous composites,—blazing stars, sunflowers, asters and golden-rods—characterize the end of the growing season. The purple of *Lacinaria scar*-

iosa and the less abundant L. punctata is very conspicuous. Helianthus subrhomboideus, Solidago rigida, S. missouriensis and S. serotina, give eastern Nebraska prairies a tone of gold which is varied by the white flowers and fruits of Kuhnia, the abundant blossoms of Aster multiflorus and other species set against a background of the reddishbrown of drying grasses. We may now summarize by pointing out the dominant and principal species on the Belmont prairie:

## **Dominant Species**

Andropogon furcatus Andropogon scoparius Poa pratensis Sorghastrum avenaceum Stipa spartea

# Principal Species

Agrostis hyemalis	Koeleria cristata
Amorpha canescens	Liatris scariosa
Aristida oligantha	Panicum virgatum
Aster multiflorus	Kuhnistera spp.
Erigeron ramosus	Psoralea floribunda
Helianthus subrhomboideus	Solidago spp.

The Tupha community occupies an area in the ravine between the prairie stations on the two slopes. It is one of a series of hydrophytic communities watered by a small stream originating from a spring located near the base of the scrub community (fig. 18). Along this stream may be traced various stages of the hydrosere from small areas of open water, cattail swamp, *Eleocharis* slough, to wet meadows of *Phalaris arundinacea* and *Spartina* or thickets of Salix interior. The cattail swamp occupies a belt 10 meters wide and is bordered on either side by a narrow zone of Spartina cynosuroides. ...Typha is the dominant species but it is being invaded higher up the ravine and is giving way to Salix interior. A number of tall herbs such as Epilobium coloratum. Asclepias incarnata with Scirpus interior and Eleocharis palustris make up the principal species.

A thicket of *Rhus glabra* borders the edge of the *Typha* swamp and extends up the slope nearly 20 meters where it

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gives way to prairie. The instruments at this station were placed only 6 meters from the prairie's edge and 30 meters from the prairie station on the southwest slope (See fig. 18). Besides the dominants the following trees and shrubs are represented: Salix interior, Sambucus canadensis. Rosa arkansana and sparingly Acer negundo, Prunus serotina. Vitis sp., Ribes sp., and Ulmus fulva. A sod of Poa mratensis carpets the ground in places while much of the area is dominated by a weedy growth of Galium aparine and Lactuca scariola. In addition to numerous prairie relicts a number of typical mesophytes, including woodland forms. are present. Among these may be mentioned species of Muhlenbergia, Carduus altissimus, Solanum nigrum, Physalis heterophylla, Polygonum convolvulus and Teucrium canadense. Indeed it will be shown that this isolated thicket is almost as mesophytic as the woodland along Salt Creek next to be described.

The woodland station along Salt Creek consists of a belt of mixed forest about 150 meters wide. Green ash. sand-bar and peach-leaved willows intermingle with red and white elm, boxelder, choke cherry and American plum. These are flanked by patches of Symphoricarpos occidentalis. S. sumphoricarpos. Sambucus canadensis or Rhus glabra and Amorpha fruticosa. Climbing over all are Vitis vulpina, Ampelopsis cordata, Humulus lupulus and Micram*pelis lobata.* At the station, which was only a few meters from the prairie margin, the ground was rather destitute of vegetation except for a scattering growth of Sanicula marylandica, Galium aparine and Urtica gracilis. However, as is characteristic of eastern Nebraska woodland, within a short distance from the station the following mesophytes were found:

Bicuculla cucullaria Campanula americana Elymus virginicus Elymus hirsutiglumis Impatiens biflora Lappula lappula Mentha canadensis Ranunculus abortivus Thalictrum dioicum Teucrium canadense Vagnera stellata Viola papilionacea 36

At the base stations in the scrub and high prairie continuous records of air temperature and humidity at a height of 8 cm. above the soil were obtained by means of Friez's hygrothermographs. These instruments were housed in appropriate shelters consisting of well ventilated boxes with one side open. These were shaded by strips of coarse burlap about 2 feet above them and so arranged that the air could circulate freely. A continuous record of the air movement at a height of 50 cm. was obtained by frequent readings of anemometers.\* Likewise the evaporating power of the air and the water content of the soil was recorded at weekly intervals by use of similar instruments and methods already described for the work in Minnesota.

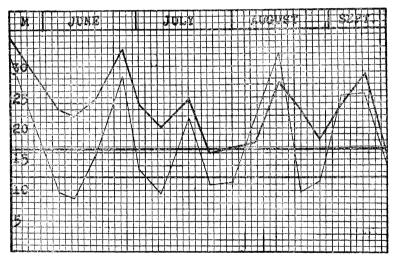


Fig. 21. Graphs showing the range of soil moisture from 0-10 cm. in the prairie on the southwest slope and in the *Rhus* thicket; the heavy line indicates the soil moisture in the scrub and the light line in the prairie. Wilting coefficients are represented by horizontal lines.

<sup>\*</sup> The writers are indebted to Mr. Clare Bradbury who during the season was in camp not far from these stations and while studying the animal ecology of the region frequently checked the hygrothermographs and read the anemometers.

# SOIL MOISTURE

The range of soil moisture at 0-10 cm. depth in the prairie and *Rhus* thicket communities on the southwest slope is shown in fig. 21. The increased humus under the scrub accounts largely for the higher wilting coefficient. While the soil moisture in the prairie repeatedly fell below the wilting coefficient, at only one determination was there no available water present in the scrub.

In figure 22 is shown the range of soil moisture at 10-30 cm. at these same stations. The graphs indicate a higher available water content in the scrub, where at no time is the wilting coefficient reached.

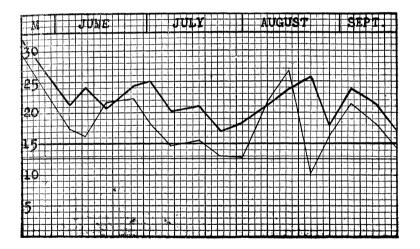


Fig 22. Graphs showing the range of soil moisture at 10-30 cm. in the prairie on the southwest slope and in the *Rhus* thicket; the heavy line indicates the soil moisture in the scrub andthe light line in the prairie. Wilting coefficients are represented by horizontal lines.

The woodland soil shows even a greater increase of available water over that of the prairie (fig. 23). It may be noted that at the high prairie station the soil moisture repeatedly fell below the wilting coefficient. The lower wilt-

ing coefficient at the woodland station is accounted for by a sandier type of soil, due in part to occasional inundations. An examination of figure 24, where the march of soil water at 10-30 cm. is given, shows the same conditions. Data obtained from the third prairie station on the northeast slope gave graphs very similar to those of the other prairie stations and need not be recorded here.

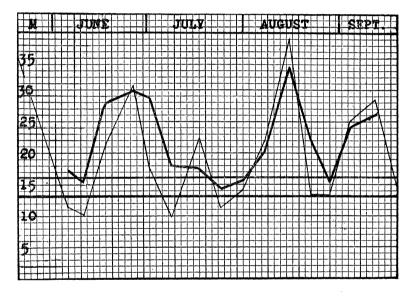


Fig. 23. Graphs showing the range of soil moisture at 0-10 cm. in the high prairie and in the woodland along Salt Creek; the heavy line indicates the soil moisture in the woodland and the light line in the prairie.

In order to show the relationship between the seasonal march of soil water and the stage in succession of the plant community even more plainly the preceding data on soil moisture (at 0-10 cm.) are replotted in figure 25, where the horizontal line passing through zero represents the limit of available water for growth at each of the stations here compared. It may be noted that in general the order of increasing water content is also that of the order of the

### STUDIES IN PRAIRIE AND WOODLAND

succession namely, prairie, scrub and woodland. Soil samples taken at depths of two and three feet at the prairie stations and in the scrub on July 24th showed a higher water content in the latter community. One of us has pointed out the necessity of deep soil moisture determinations for a complete analysis of the prairie-forest problem (23) but the press of other duties limited the determinations here to the shallower soils. However, the preceding data, which are in agreement with those obtained at Minnesota, lead us to the conclusion that in general the amount of available water in the various plant communities varies directly with the order of their occurrence in the succession, the prairie being the most xerophytic.

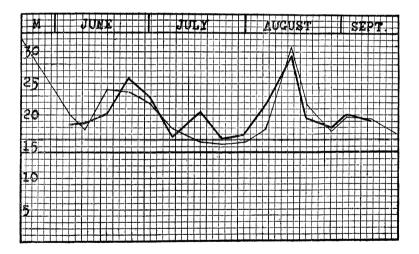


Fig. 24. Graphs showing the range of soil moisture from 10-30 cm. in the high prairie and in the woodland along Salt Creek; the heavy line indicates the soil moisture in the woodland and the light line in the prairie.

### **EVAPORATION**

The evaporating power of the air at the several stations will now be compared. These data are shown in figure 26. The station in the high prairie shows the driest aerial

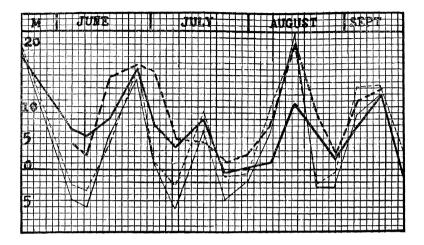


Fig. 25. Graphs showing the per cent of available soil moisture to a depth of 10 cm. in prairie, scrub, and woodland; the heavy broken line indicates soil moisture in the woodland, the heavy solid line in the *Rhus* scrub, the light broken and the light solid lines in the prairie on the southwest slope and ridge, respectively. The horizontal line indicates the limit of available water.

conditions, just as it showed the driest soil and the evaporating power decreases from prairie to scrub and woodland. While there is a marked falling off in evaporation in prairie and scrub, the aerial conditions as regards evaporation are approximately the same in scrub and woodland. It may be recalled that the available soil moisture of the woodland was only slightly greater than in the scrub. In other words, an analysis of the habitat factors show the *Rhus* thicket surrounded by prairie almost as mesophytic as the narrow belt of woodland along Salt Creek. The lowest graph (fig. 26) is from data obtained in the *Typha* community and only 20 m. from the prairie station. The early relatively high evaporation rates occurred here before *Typha* and its layer of *Epilobium* and *Asclepias* were well developed.

It is interesting to compare the average daily evaporation rates of the Minnesota prairies with those of Nebraska. The low prairie at Fort Snelling (June 3 to Sept. 2) gave an average daily loss of 12.7 cc. while the evaporation rate on the prairie at Belmont was 21.6 cc. daily. However, if we compare the midsummer evaporation rates of the high prairie at Minnehaha with those at Belmont (July 21 to Aug. 18th) we find the losses at the latter station are only slightly greater (24.5 cc.) than those at Minnehaha (21.6 cc.).

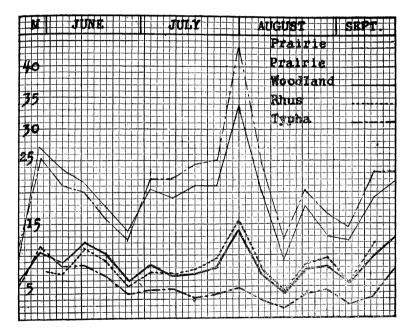


Fig. 26. Graphs showing the daily evaporation rates in the various plant communities near Belmont during 1916.

### HUMIDITY, TEMPERATURE AND WIND

A number of factors contribute to cause higher evaporation rates in the prairie; these are greater wind velocities, higher temperatures, lower humidity and greater radiant energy.

The total number of miles of wind which passed over the vegetation at a height of 0.5 m. from July 13th to Sept.

19th. 1916, at the several stations is as follows: high prairie 8.340 miles, prairie on southwest slope 4.905 miles, sumac thicket 510 miles. This gives ratios having comparative values of 100, 59 and 6 respectively. A number of investigators have pointed out the increased evaporating power of the air as the distance of the evaporimeter from the surface of the soil is increased (24, 4, 23). In prairie vegetation this increased evaporation is due in the greatest measure to increased wind velocity. Atmometers at the prairie station on the southwest slope placed at a height of 0.5 m. gave 57% greater evaporation during ten days beginning July 21st than similar instruments placed at the usual height of 17-23 cm. These differences explain to a considerable extent the habits of certain prairie plants which develop mesophytic leaves near the ground and xerophytic leaves above (cf. 6).

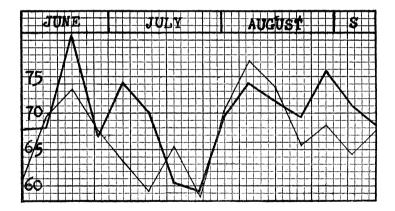


Fig. 27. Graphs showing the mean weekly humidity, based on weekly maximum and minimum humidities, in the prairie and Rhus scrub at Belmont during the season of 1916. The heavy line indicates the humidity is the scrub and the light line in the prairie.

The relative humidity, as registered by the hygrothermographs at the stations in the high prairie and scrub, shows a mean which is much lower in the latter community. The mean weekly humidity, found by averaging the

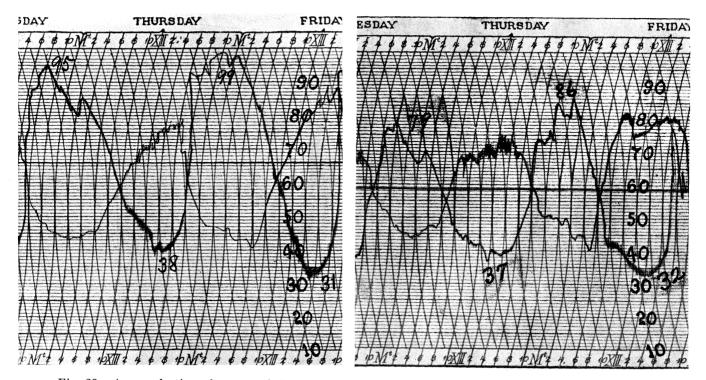


Fig. 28. A reproduction of a part of the hygrothermograph records for week ending June 12th. The one to the left from the station in the Rhus thicket and the one to the right from the station in the prairie. The graphs with the maxima and minima numbered indicate humidity. The mean humidity is represented by the horizontal line.

of the seven highest and seven lowest points sum (weekly maximum and minimum humidities) is shown in figure 27.These graphs show that the air in the scrub is often drier than that in the prairie, an entirely erroneous conclusion due to a wrong interpretation of the humidity records. An examination of figure 28 which is a reproduction of a part of these records will make the point clear. In this figure the mean humidity for the periods shown (and calculated as above indicated) is represented by the horizontal line. But it may be seen at a glance that while the air in the scrub was actually drier (on Friday) than that of the prairie, the time interval during which the humidity remained below the mean is much less (actually 1.5 hours less) than on the corresponding day in the prairie. In other words it is not the actual humidity but the low humidity multiplied by the time during which it is low that gives a real criterion of dryness. By the use of a planimeter the total areas above and below the line representing the mean were determined for each weekly record. The average of these two areas was determined and also the per cent the larger area exceeded this average. The average range (average maximum of week minus average minimum) was then multiplied by this percent and the product added to or subtracted from the mean accordingly as the greater area lay above or below the line. By means of this method it may be shown, for example, that in figure 28 the mean humidities for the prairie and scrub are not 58.5 and 66 but 57 and 70 respectively.

In figure 29 the mean humidity for the scrub and prairie calculated upon the above basis shows the prairie to be much the drier habitat. These differences are sufficient to account for much of the difference in the evaporating power of the air. These humidity graphs are inverted and plotted against evaporation in figure 30. As pointed out by Livingston (13) the cyclic factor of solar radiation is measured only in part by the white porous cup atmometers. The light values in the scrub, measured by the Clements' photometer, gave an average of 0.05.

Not only is the scrub a more favorable habitat for plant growth as regards greater available soil water, cooler soils and more moist air but the air temperatures are also lower. The mean weekly temperatures, as plotted by using maximum and minimum averages, are shown in figure 31. Here again we are led to the erroneous conclusion that the air in the scrub is hotter than that in the prairie. The mean temperature for the scrub cal-

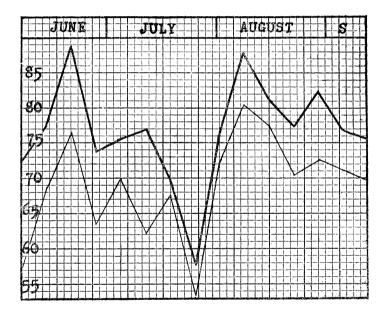


Fig. 29. Graphs showing the weekly mean humidity in the *Rhus* scrub and prairie calculated on the time-humidity basis with the aid of a planimeter The heavy line indicates the humidity in the scrub and the light line in the prairie.

culated by both methods is shown in fig. 32. It is interesting to note that the first method often gave weekly means 7% too high. An examination of figure 33 where the time-temperature method was used shows the scrub to be the cooler habitat. It seems quite probable that readings of maximum and minimum temperatures (unless these reach critical temperatures for plants) are of much less real significance than formerly supposed. Just why the air in the scrub might for a brief period each day reach a higher temperature and a lower humidity than that in the

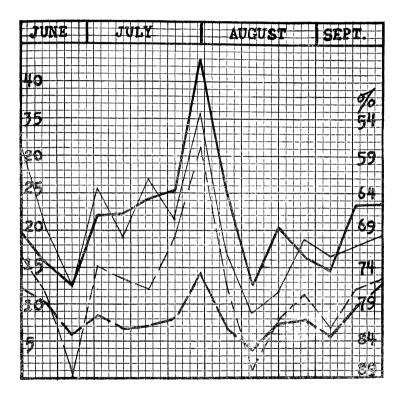


Fig. 30. Graphs showing the daily evaporation and humidity in the prairie and Rhus scrub. The heavy and light solid lines show evaporation and humidity respectively, in the prairie; the heavy and light broken lines show evaporation and humidity respectively, in the Rhus scrub.

prairie is easily explained. Any given spot in the scrub is at some period during the day entirely unshaded, and we have already noted the low wind movement. It was quite usual to find as a result of these conditions mesophytic herbs under

the scrub wilting on hot days but the period of stress is relatively short as the plants are soon shaded again. Notwithstanding the shelter, already described, afforded the hygrothermograph these normal conditions were recorded on the record sheet.

We will next consider the effect of these differences in habitat conditions upon the loss of water from the plant.

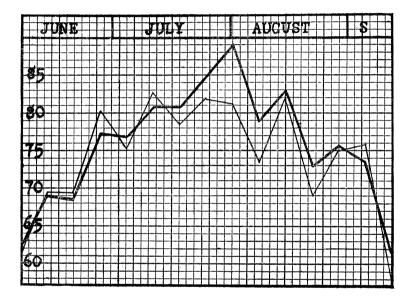


Fig. 31. Graphs showing the mean weekly temperatures, based on weekly maximum and minimum temperatures, in the prairie (light line) and scrub (heavy line) respectively.

#### TRANSPIRATION

The effect of habitat factors upon the structure and distribution of plant communities is exerted largely by a modification of the functioning of the plant. Just as too deep shade excludes intolerant species from scrub or woodland by reducing their photosynthetic activities, likewise too dry air, especially when coupled with low water content of the soil, may cause excessive water loss and permanent

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wilting followed by death. In the following experiments an attempt was made to determine the effect of the aerial factors in prairie and scrub habitats upon the transpiration of plants. Since the evaporating power of the air affords a concise expression of the combined effects of temperature, humidity, and air movement in so far as these factors effect the loss of water by plants, the ratio between transpiration and evaporation was also determined.

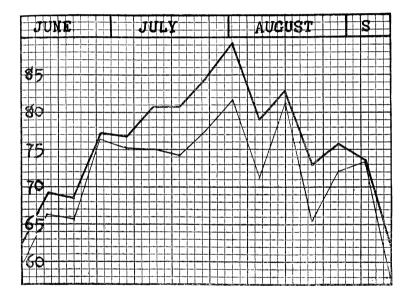


Fig. 32. Graphs showing the mean weekly temperature in the Rhus scrub based on weekly maximum and minimum temperatures (heavy line) and calculated on the time-temperature basis with the aid of the planimeter (light line).

On July 17th, 1916, nine bur oak seedlings, which had been transplanted several weeks earlier into 5 inch pots in a sandy loam soil, were taken to the Fort Snelling stations. The plants were well watered, the pots placed in Ganong's aluminum shells, the tops of which were covered with sheet rubber and sealed. Then the plants were weighed and

three of them placed in each of the following habitats, prairie, hazel scrub, and oak forest. The pots were sunk into the soil and covered in such a manner that the tree seedlings were under natural conditions as regards height from the surface of the soil and surface cover. The light value in the hazel, averaged from numerous determinations, was 0.017 while that in the oak forest was approximately the same. The plants were left in these habitats for a period of four days, until July 21st. During this time the weather

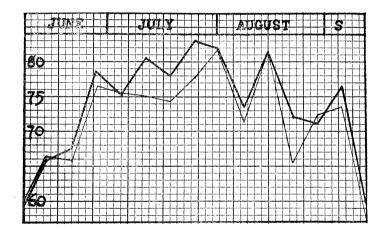


Fig. 33. Graphs showing the mean weekly temperatures in the Rhus thicket (light line) and prairie (heavy line) calculated on the time-temperature basis with the aid of the planimeter.

was favorable for maximum transpiration. The average loss of each set of three plants in grams per sq. dm. of leaf area is shown in figure 34 which also gives the evaporating power of the air in the three habitats based upon the percentage of the water lost in the prairie.

A similar experiment with six oak seedlings was conducted at Minnehaha from July 29th to August 1st, 1916. This three-day period was also favorable for high transpiration rates and the results again show a striking correlation between the transpiration of the oak seedlings and the evaporating power of the air (fig. 34). A third experiment performed in 1915, in general, confirms these results.

At Lincoln a number of experiments with one and two year old seedlings of *Acer saccharinum* placed in scrub and prairie respectively, were performed. The methods used were the same as those indicated above. The results of only two of these experiments, selected as representative, will be given.

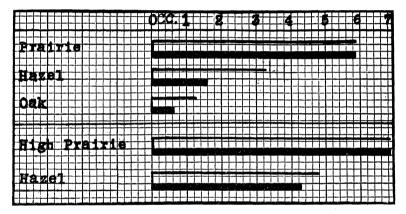


Fig. 34. Diagram showing the transpiration rates of oak seedlings in prairie, hazel thicket and oak forest at Fort Snelling (July 17-21) heavy lines; and the relative evaporation rates (light lines) based upon the percentage of water lost in the prairie. Also transpiration and evaporation rates (July 29-August 1st) in the prairie and scrub at Minnehaha.

On July 24th an experiment with four plants was begun and continued through a period of two days until July 26th. The plants were then weighed and water was added until the original weight was restored, after which those that had been in the prairie were placed in the scrub and those from the scrub were placed in the prairie. They were then allowed to transpire for a period of four days, until June 30th. Throughout the entire period fine weather prevailed. The plants in the scrub lost per unit leaf area 35% as much water as those placed in the prairie during 50

the first period, and during the second interval 26%, while the evaporimeters in the scrub lost during the whole time 41% as much as those in the prairie.

For the next experiment two maple seedlings which had grown in the shade of a large isolated parent tree were potted as usual, some weeks before they were used. These were placed in the scrub and two plants of the sun form of maple in the prairie. The experiment was conducted from July 4th to July 8th. The relative transpiration loss per unit leaf area of shade to sun form was 35%; the evaporation in the scrub was only 29% of that in the prairie. The plants were watered, reweighed and their positions exchanged. During the two days following the sun forms, now in the shade, lost only 18% as much water per unit of leaf area as the shade forms in the prairie, notwithstanding the fact that the evaporation ratio of scrub to prairie was 35:100. The results of this experiment and others to

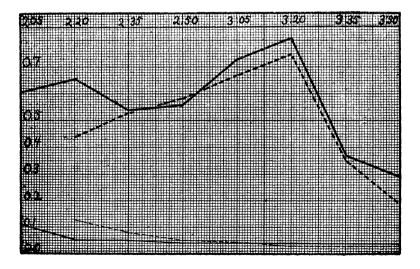


Fig. 35. Graphs showing transpiration rates in grams per sq. dm. of leaf area of branches of white elm in their natural position in the center and periphery of the crown. The shade branches gave the lower transpiration rates. be reported led the writers to compare further the transpiring power of sun and shade forms of the same species and sun and shade branches from the same plant. The following experiment is illustrative:

On July 22nd branches from an isolated white elm (*Ulmus americana*) growing on the flood plain near Salt Creek were selected from the south periphery and from the center of the crown of the tree. These were cut under water, attached to burette potometers graduated to tenths of cc. and replaced in their respective positions in the crown of the tree. After ten minutes, readings were taken at intervals of 15 minutes from 1:50 to 3:20 p. m. The losses in grams per sq. dm. of leaf area are shown in figure 35. The

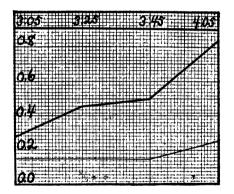


Fig. 36. Graphs showing the transpiration rates of sun and shade forms of *Rosa arkansana* in prairie and *Rhus* scrub respectively. The sun form gave the higher transpiration rate.

losses from the shade branches are only 11% of those from the sun branches. At 3:20 p. m. the branches from the periphery were hung under the crown of the tree in the shade. The graphs show a marked decrease in transpiration until 3:50 p. m. when the experiment was concluded. On this day the weather was clear and hot with only a light breeze.

Other experiments with the elm confirm the above results and still others of a similar nature performed with

Fraxinus lanceolata and Acer saccharinum lead to the conclusion that the major water losses from isolated trees are largely from a region forming a peripheral shell the topography of which is determined by the shape of the crown. The grouping of trees in forest communities must exert an enormous effect in reducing transpiration.\*

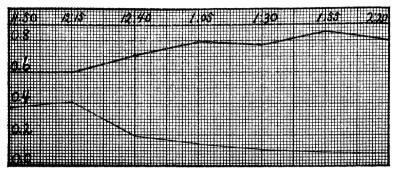


Fig. 37. Graphs showing the transpiration rates of sun and shade forms of Rosa arkansana in their natural habitats in prairie and Rhus scrub respectively. The sun form gave the higher transpiration rate.

Another group of experiments were performed with sun and shade forms of *Rosa arkansana*. The plants were growing near the prairie stations and in the *Rhus* thicket. Cut shoots and burette potometers were used and the leaf areas calculated. Transpiration losses are shown in grams per sq. dm. The results of an experiment conducted on July 15th are given in figure 36. This shows the sun form to be a much more vigorous transpirer than the shade form when they are under their natural habitat conditions. Figure 37 gives the result of a similar experiment performed July 21st. The shade form again transpires much less. At 1:05 p. m. the stomata of this plant were beginning to close.

<sup>\*</sup> The writers are indebted to Mr. H. C. Hanson for assistance in making these determinations of transpiration rates of trees. For a complete discussion of the crown of a tree as a diversified habitat see Hanson (8).

Numerous experiments performed throughout the summer showed in every case much higher transpiration rates from sun than from shade forms.

Transpiration rates from sun and shade forms both placed in the prairie are shown in figure 38. These graphs, which are typical of numerous others, show that the transpiration of the shade form of *Rosa arkansana* even when it is placed in xerophytic conditions is less than that of the sun form. On hot days, as in this experiment (July 21st), the stomata close more or less completely and although the plant may remain turgid for some time, it finally wilts.

It is interesting to note that when the sun form of Rosa is placed with the shade form in the scrub, the latter transpires as much and usually more than the sun plant (cf. 11).

Finally, the results of some experiments in which cut shoots of cherry, (*Prunus serotina*) and boxelder (*Acer negundo*), were used will be given. On June 16th two sun branches of cherry and two of boxelder, about 18 inches long, obtained from trees growing in the *Rhus* thicket were cut under water and attached by rubber tubing in the usual way to burette potometers. One of the potometers containing the boxelder and one the cherry were then placed in the prairie, and the others in the shade. After the usual time for adjustment (10 to 15 minutes) the initial readings

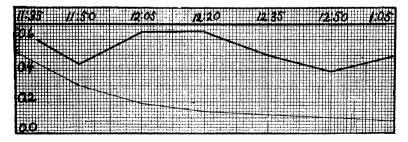


Fig. 38. Graphs showing the transpiration rates of sun and shade forms of *Rosa arkansana* both placed in the prairie. The sun form gave the higher transpiration rate.

were made and total transpiraton losses were recorded at the end of 45 minutes. Then the potometers were exchanged with those in the scrub, time again being allowed for adjustment of the plant, and the total transpiration losses recorded at the end of a period of 45 minutes. The results together with the physical factor data are shown in table 3.

Table 3, showing the transpiration rates of cut shoots of *Acer negundo* and *Prunus serotina* in prairie and *Rhus* thicket.

Habitat	Plant	Time	Trans- pira- tion Loss	Temper- ature	Hu- mid- ity	Miles Wind	Evapo- ration
Prairie	Boxelder	1:55-2:40	11.4 cc.	24.3 - 25.2	56-46	2.8	3.4 cc.
Scrub	"	"	4.4	22.2-22.8	58-48	1.3	1.4
Prairie	"	3:10-3:50	14.8	26.1 - 24.4	46 - 46	2.8	3.8
Scrub	"	"	3.9	25.4 - 23.4	48-48	1.4	1.9
Prairie	Cherry	1:55-2:40	17.2				
Scrub	"	"	8.7				
Prairie	"	3:10-3:50	27.8				
Scrub	"	"	15.8*	(*Plant j	partly i	n the su	inshine)

These results show, in the case of the boxelder, a transpiration rate in the scrub of 32% of that in the prairie, while the corresponding evaporation is 46%. The transpiration ratio in the case of the cherry is 54:100.

Another experiment with shade branches of cherry was performed on July 15th. The potometers were placed in the prairie, scrub and Typha communities. One potometer was placed in each habitat at 7:30 a. m. and after a period for the adjustment of the plant, the transpiration was measured at the end of 35 minutes. Then the potometers were shifted from prairie to scrub, scrub to Typha and Typha to prairie respectively. At the end of a second 35 minute period the potometers were again changed and in such a manner that each plant was again in a new habitat. The temperature in the various communities ranged from the beginning to the end of the experiment as follows: prairie 29.2-36.0; scrub 25.8-34.0; Typha 24.6-32.2. At 8:40 a. m. the humidity in the respective stations in the order given was 48%, 72% and 85%. The losses by transpiration are shown in the following table, where the number in parenthesis represents the period during which the plant occupied the particular habitat.

Table 4. Showing the relative transpiration of shade branches of *Prunus serotina* in various plant communities.

Plant	Prairie	Scrub	Typha
1 2 3	$5.8 (1) \\14.6 (2) \\11.2 (3)$	$\begin{array}{c} 3.7 (2) \\ 9.3 (3) \\ 3.6 (1) \end{array}$	$\begin{array}{c} \hline 2.5 & (1) \\ 0.8 & (2) \end{array}$

The results show in every case a marked falling off in transpiration when the plants are placed in the scrub and a still greater one when they are transferred to the Typhacommunity. The average loss in the prairie to that in the scrub gives the ratio of 100:53.

From these experiments it may be concluded that the aerial conditions of the habitat exert a profound effect upon the water losses of the plant. The ratio of these losses in scrub and prairie communities vary with the species of plant, and with its former environmental condition. In general there is a correlation between the transpirational losses and the aerial conditions as summed up by the evaporating power of the air.

# DISCUSSION AND CONCLUSION

The foregoing results regarding the water content of the soil and the evaporating power of the air, which are indicative in general and conclusive for the period during which the investigations were carried on, show that prairie soils to a depth of 30 cm. frequently lack available water during the growing season. This gives a clue to the absence of trees throughout the prairies except along streams or in other very favorable situations. Passing over the difficulties met by tree seeds in finding lodgement in the grasscovered prairie soils, it seems clear that even a brief period during the time of establishment, when no available water was present in the soil would prove disastrous. Exceptionally wet years might be so favorable as to permit complete establishment and sufficient root growth so that the seedling could draw upon the moisture of the deeper soil. On the other hand the usual low water content of prairie soils is coupled with high evaporating power of the air and according to the investigations of Caldwell (2) such conditions cause plants to wilt permanently long before the soil moisture is reduced to the point indicated by the calculated wilting coefficient shown in the graphs. That is, the prairie soil may be much drier physiologically than the graphs indicate.

Deep-rooted rhizome-bearing plants found in prairies are eminently adapted to withstand drought in the shallower soil while undoubtedly many shallow-rooted annuals and perennials complete their growth and reproduction before the dry midsummer. The whole question of the root distribution of prairie plants correlated with the seasonal march of soil water at different depths and extending to the lower limit of the soil occupied by roots, together with the seasonal activity of the plants, is in need of investigation.

That trees will grow in prairie soil when planted is a fact attested by thousands of groves on various types of soil throughout the prairie formation. That they will grow when the seeds are planted in furrows run at intervals of four to six feet through the native sod and that the prairie area will within a period of 30-40 years be transformed into typical woodland, is evidenced by a grove at Lincoln described by Pool (15). The fact that Rhus, Symphoricarpos. Corulus and other shrubs with rhizomes invade grassland and are then replaced by trees is familiar to all ecologists. But carefully planned quadrat studies involving quantitative measurements of the habitat factors throughout a period of years can alone satisfactorily answer the questions,—Can trees grow from seed sown in the prairie or worked into the surface soil and under what conditions can this be accomplished? Dr. R. J. Pool and the senior writer have such studies under way.

The present investigations may now be summarized. The great amount of evaporation in the prairie coupled with

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low water content of the soil is a sufficient cause for the xerophytic character of the vegetation. It shows also the difficulties met by trees in establishing themselves in grassland and may explain their absence from the prairies.

Plants placed in the more mesophytic scrub community transpire much less vigorously than others of the same species placed in the prairie. In general there is a correlation between the evaporating power of the air and the amount of transpiration.

If sufficient light is available, there is no question but that humidity of the air and the soil are the most important factors affecting the establishment of the different plant communities. The progressive increase of the humidity of the habitat causes a corresponding increase in the mesophytism of the plant community. This change of plant population from the xerophytic to the mesophytic type is a phenomenon called succession.

The evaporation rates and the amount of soil moisture in the various communities both in Minnesota and Nebraska vary in general directly with the order of their occurrence in the succession, the community nearest the climax being the most mesophytic in both respects.

The writers are indebted to Dr. R. J. Pool and Dr. F. E. Clements for suggestions in carrying on these investigations.

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The Botanical Survey of Nebraska was organized by the Botanical Seminar on August 24, 1892. The original members of the Survey were J. G. Smith, Herbert Marsland, Roscoe Pound, P. A. Rydberg, A. F. Woods and F. E. Clements with Prof. C. E. Bessey as the Botanical Adviser.

The Survey thus constituted published the following reports and papers:

- I. Preliminary: The Plan and Scope of the Survey. 1892.
- II. Report on Collections made in 1892. 1893.
- III. Report for 1893. 1894.
- IV. Report on Collections made in 1894. 1895.
  - V. Report on Recent Collections. Studies in the Vegetation of the State I. 1901.
- VI. Studies in the Vegetation of the State II. 1902.
- VII. Studies in the Vegetation of the State III. 1904.

(VIII.) The Phytogeography of Nebraska I. General

Survey. 1st Ed. 1898. 2d. Ed. 1900.

At the present time none of the original members of the survey are connected with the university, in fact none are now residents of the state. After the going away of the older members of the Survey interest in the Survey waned somewhat until three or four years ago when active work was again undertaken, but this time by a new generation of botanists.

Many plants have been collected and data have accumulated since the earlier years and since publication was suspended in 1904. It is hoped that means may be provided for the publication of further reports as well as for the continuation of the Survey.

The present paper is the first publication of the Survey under the new management. It is presented to the public as Number I of a New Series.