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Distribution and Structure of the Forests of Eastern Nebraska

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DISTRIBUTION AND STRUCTURE OF THE FORESTS OF EASTERN NEBRASKA

INTRODUCTION

This paper is a study of the distribution and structure of the forests of extreme eastern Nebraska. The Missouri river, which forms the eastern boundary of the state, has so greatly modified the climate, that along its course an arm of the deciduous forest extends far into the grassland. Most of the trees and shrubs composing this forest are at the extreme western limit of their range. The range, grouping, and behavior of the several dominants and subdominants, under the environmental conditions imposed upon them, and the transition of forest to grassland are the subjects of this investigation.

This region has been of interest to botanists since the time of the earliest explorations of the nineteenth century. The explorers (Lewis and Clark, 1803-1806; Nuttall and Bradbury, 1808; the Nicollet expedition, 1843; Warren, 1857) usually confined their activities to the woodlands along the natural highways, the streams; excursions into the prairie beyond being infrequent.

Systematic investigation of the flora of Nebraska was begun in 1884 by Bessey. This resulted in the publication of numerous preliminary papers. Of these there may be mentioned the studies of the distribution of certain woody species (1887) and notes on the age and circumference of different trees planted in the prairie. A final list of the forest trees of Nebraska based on herbarium specimens was published in 1898. Bates (1894) in his notes on trees and shrubs of northern Nebraska discussed their distribution, and Pool (1919) in his handbook of Nebraska trees also gives their distribution in the state. Pound and Clements (1900) divided the state into regions based upon the natural vegetation. The woodlands were subdivided into "types."

The formulation of the developmental system of classification of plant communities and an increased knowledge of plant succession (Clements, 1916), together with the development of modern methods of quantitative ecology, make possible a thorough and exact study of the environment and the distribution of forest communities.

Weaver and Thiel (1917) conducted in Minnesota and in eastern Nebraska a series of intensive investigations in the tension zone between prairie and woodland. This was the first attempt to attack the prairie-forest problem on a comprehensive scale by means of the quantitative methods of modern ecology. In Nebraska, stations for the determination of environmental factors were located in prairie, chaparral, and woodland near Lincoln. These studies were continued in Nebraska (Pool, Weaver, and Jean, 1918) and extended to include subclimax prairie, chaparral, and several forest communities at Peru in the southeastern part of the state. The findings of these investigators will be later compared with those of the writer.

Detailed studies of the root distribution of subclimax prairie and chaparral dominants of this area have been made by Weaver (1918). In 1925, Weaver, Hanson, and Aikman traced the distribution of trees and shrubs and the development of forest communities from the headwaters of the Weeping Water and the Little Nemaha rivers to their junction with the Missouri. The nature and results of competition between important prairie, shrub, and tree species in several communities in eastern Nebraska have been studied intensively by Clements, Weaver, and Hanson (1929). Their results have thrown much light upon many problems of community structure and forest distribution.

This investigation was undertaken on the suggestion of Dr. J. E. Weaver. To him the writer is indebted for outlining the problem and for direction throughout the period of field work and in the preparation of the manuscript. He is also indebted to Dr. R. J. Pool for helpful advice. Certain factor data from Peru and Bristow were available only

through the kindness of Prof. A. E. Holch and the assistance of Mr. M. G. Anderson to whom acknowledgments are made. For the analyses of soils the writer is under obligation to the Department of Agronomy of the University of Nebraska. Finally thanks are due to Prof. T. J. Fitzpatrick for helpful criticism in reading the manuscript and proof.

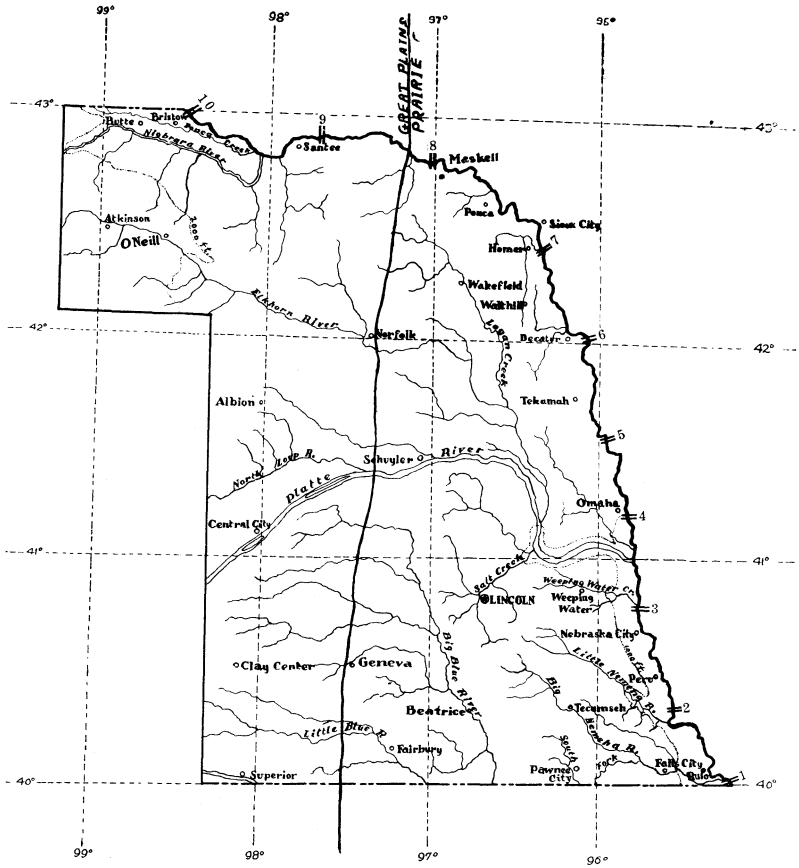

FIGURE 1. Map of eastern Nebraska showing the location of rivers, stations, transects, elevation lines, and the approximate boundary line between the prairie and the great plains.

EXTENT AND POSITION OF THE AREA

The area under consideration is bounded on the east by the Missouri river and on the north by the river and 43° latitude. It is bounded on the south by 40° latitude. The western boundary is less definite. Woodland extends westward along the tributaries of the Missouri river for many miles but much of it is postclimax. Even along the Missouri the belt of deciduous forest becomes very narrow northward. A line limiting the western extent of the area investigated lies somewhat parallel to the Missouri but closer to it in the northeastern than in the southeastern part of the state. In the north, the western boundary of Boyd and Holt counties, 30 miles west of the Missouri river on the South Dakota line, forms the western boundary. This, with a line running south parallel to the eastern boundaries of these counties, delimits the area on the west (Fig. 1). The distribution of forest communities along the streams is shown in Figures 13, 14, and 15. The approximate width of the woodland areas along the streams was determined by measurements at variable intervals. In numerous places along many of the streams the land has been cleared of trees and shrubs except in ravines or other areas of irregular topography.

GEOLOGY AND SOILS

The soils of eastern Nebraska are underlaid by a series of geological formations which are continuous beneath the greater part of the area (Condra, 1920). Since drainage in the state is toward the southeast, the oldest geological formation exposed (Pennsylvanian) is in the southeastern corner of the area. This thick series of limestones and shales is overlaid by a thin bed of Jura-Trias which in turn is covered by a thick stratum of rusty-red Dakota (Cretaceous) sandstone. Above the sandstone, in regular order, come the Graneros shale, the Greenhorn limestone, the Carlisle shale, the Niobrara chalk, and the Pierre shale. Exposures of these different strata are not extensive and in general the lowest ones are exposed in the southeastern part of the area and the

upper ones toward the north and west. Practically all of the soils except very local rock outcrops are derived from transported materials.

The first transported material was brought in by two glacial invasions. Approximately the eastern two-thirds of the area was covered. The Kansan drift constitutes the upper part of the glacial deposit. It consists of a heterogeneous covering of clay, silt, sand, gravel, and boulders. Below the Kansan drift lies the Aftonian material which consists largely of stratified sand and gravel with a few boulders. The Nebraskan, the lowest drift sheet, consists of blue clay, containing small pebbles and a large number of boulders.

Later the entire area was covered by a second layer of transported material, a thick mantle of loess. The time of deposition of the loess is presumed by some geologists to be closely connected with later glacial advances which did not reach Nebraska.

At present the soil of the area south of the Platte river consists of loess except in the eastern part where the loess

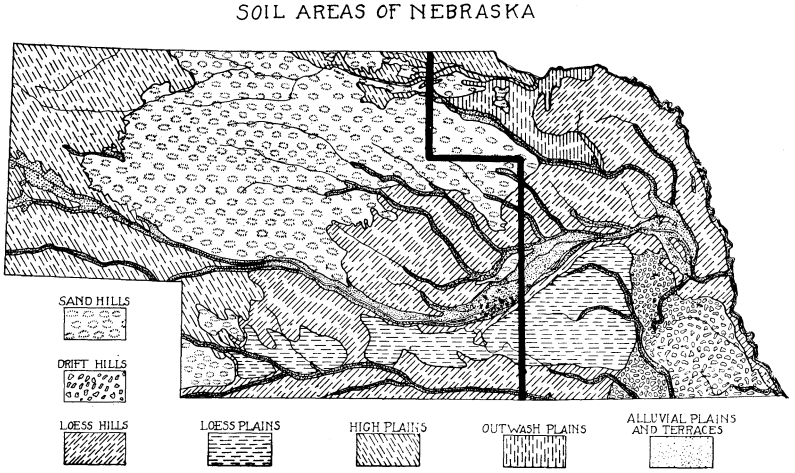

FIGURE 2. Soil map of Nebraska (courtesy of the Department of Agronomy, University of Nebraska). Note the great extent of alluvial plains along the Platte river and its tributaries compared to that of the Missouri.

covering has been eroded, leaving exposed the original deposit of glacial drift. The latter has been worn into drift hills (Fig. 2). Most of the drift-hill soils are quite heavy and clayey with a somewhat heavy subsoil but gravel and more or less rounded glacial boulders or "niggerheads" are also common. North of the Platte river occur the loess hills. These stand in striking contrast to the area south of the Platte where the wide floor-like expanse of loess is broken only here and there by immature streams. The loess soil is finer grained and has a less compact structure than that of the glacial soil. It retains a columnar structure when exposed, as along stream banks or railway cuts, whereas the soil of glacial origin tends to crumble.

Although only two of the seven general glaciers of North America entered Nebraska, some of the others advanced nearly to its northeastern border and the soils of this part of the state have been derived from the outflow of gravel, sand, and finer materials. These outwash plains soils are heterogeneous mixtures forming a number of different soil types often in close juxtaposition.

The soils of the bench and bottom lands throughout the entire area form alluvial plains and terraces. They are composed of the materials eroded from the uplands and their deposition is by stream overflows. They are the youngest soils and are still being formed at a rapid rate. Because of the diversity of their origin and the sorting action of water, a great variety is found.

A very small portion of the sandhills of the state occur in the northwestern part of the area.

The map (Fig. 2) shows the narrow strip of high plains in the extreme north. Southward lie the outwash plains bounded on the southwest by sandhills and on the south and east by the wide expanse of loess. In the southeast the drift hills are left exposed. The alluvial plains lie along the rivers and are especially extensive along the Platte and its tributaries.

TOPOGRAPHY AND DRAINAGE

The surface of eastern Nebraska is little diversified. Drainage is from an elevation of about 2,000 feet in the northwestern part of the area studied to 850 feet in the southeastern. From the north and west to the southeast, the descent is at the rate of about 1 foot per 1,000 feet (Condra, 1912). Thousand foot contour lines are shown on the map (Fig. 1).

The valley of the Missouri river lies along the eastern boundary of the state. This river has an average width of about 2,500 feet at Bristow near the South Dakota line, and a valley varying from one-half to one and one-half miles in width. It has a slightly greater width and depth and a valley 8 to 14 miles wide at Rulo, near the Kansas line. It borders the state on the east and northeast for approximately 360 miles but its actual length along this border is about 500 miles. It has an average fall of a little less than one foot per mile for this entire distance. The valley is bounded on the west by rather steep and broken bluffs. Near the Dakota line it is young and U-shaped and on an average is 150 feet below the summit of the first row of bluffs. Near the Kansas line it is broad and rather mature and is about 100 feet below the bluffs.

The area is drained principally by the Missouri river and its tributaries. The largest of these, the Platte, which divides the area into almost equal northern and southern portions, is a broad shallow stream with low banks, except the last 20 miles of its course where it becomes narrower and the slopes steeper. The Elkhorn, the main tributary of the Platte, arises in small, sandhill lakes just beyond the northwestern border of the area and flows in a southeasternly direction. It is a shallow river with gradual valley slopes cut into the loess plains. Sandhills border the valley on the south to a point a few miles east of Norfolk (Fig. 1). The Niobrara, flowing across the northern part of the area, is a shallow but swift river with steep, well protected bluffs. Ponca creek, a shallow meandering stream with practically

no tributaries, drains the extreme northern strip of territory north of the Niobrara. The southeastern corner of the area is drained into the Missouri by the Weeping Water, the Big Nemaha, and the Little Nemaha. In their lower courses, these streams have eroded the drift material to a depth that affords considerable protection to tree vegetation. The Big Blue and Little Blue rivers drain the southern portion of the area from close to the southern bank of the Platte southeastward. The Little Blue, to the west, is a swift stream in a sandy channel but the Big Blue is a more sluggish stream with muddy beds and banks. Of the two, the Little Blue cuts the deeper channel and offers protection to tree growth for a greater distance into the flat prairie of the southwestern part of the area.

Except for the presence of the Missouri river and the profound influence exerted by it upon the climate, eastern Nebraska would probably be destitute of forests. This mighty stream has not only eroded a great bluff-rimmed depression but numerous tributaries and their branches have also cut canyons below the general wind-swept prairie level. The physiography of the region is such as to afford protection to forests. The rivers and streams increase soil moisture and humidity and forests develop in an otherwise prairie region.

GENERAL DISTRIBUTION OF THE VEGETATION AND PLANT-LIFE CONDITIONS

METHOD OF STUDY

In dealing with this subject it was necessary to use a method of study which would enable a single investigator to obtain a first-hand knowledge of the forest vegetation along all of the more important streams. The transect method as employed by Weaver, Hanson, and Aikman (1925) was used. From the roads near the different stream courses, it was possible to locate the best forested situations. North slopes were found to be especially favorable. As progress was made up or down a given stream, transects about a mile wide were

selected at intervals to include these sites. The distance between the transects was determined by the amount of remaining forest and the rapidity of change of the vegetation. Along all of the important streams, except the Missouri, the intervals average about 6 miles. Figure 1 shows the location of ten transects along the Missouri river. More than 40 were located and studied along this river alone and from data thus obtained it was possible to map the various communities and define the limits of species distribution.

The area studied in each transect extended about a mile along the river and entirely across the belt of woodland. Trees, shrubs, and lianas were listed. Size and density of stand of the different tree and shrub species were recorded as well as their location in the transect, and the amount of reproduction and branching habit. A study of the sequence of the appearance of trees and shrubs proceeding down a river course and the manner in which they segregate into communities throws much light upon invasion and ability to tolerate unfavorable growth conditions. Rate of growth in selected transects along certain streams, as revealed by width of annual rings, adds much to the story of adaptation to habitat and forms an excellent measure of growth conditions in the several transects as integrated by the living plant. Methods of detailed investigation in the several communities are discussed elsewhere (page 16).

OUTLINE OF PLANT COMMUNITIES

The main body of the deciduous forest of North America covers a large part of the United States east of the Mississippi river. It extends somewhat west of the river in the north and south and in the center is encroached upon as far east as Ohio by the prairie. Conditions most favorable to the development of deciduous forest occur in the Ohio valley. Both the size of trees and number of species decrease westward as one proceeds toward the great prairie area.

The deciduous forest is represented in Nebraska almost exclusively along the Missouri river and its tributaries. The Grassland Formation bounds the woodland on the west.

Where aided by prairie fires and timber cuttings, grasses are making inroads upon the forest.

The mean annual precipitation in southern Ohio and eastern Kentucky is 42 inches compared to 32.5 inches in extreme southeastern Nebraska, which is the best watered portion of the state. This difference in precipitation is an index of the difference in general plant-life conditions between the two regions. The number of woody species of ecological importance is over 200 near the center of the deciduous forest which number is reduced to about 80 in southeastern Nebraska. Of those at the center, two widely ranging dominants, *Fagus grandifolia* [1] and *Acer saccharum*, have dropped out along with many others such as the white, pin, post, and laurel oaks, chestnut, magnolia, tulip-tree, sassafras, and flowering dogwood. Red oak and linden are climax dominants in this western arm of the formation. These two species are reduced in size, however, due to the decreased water content of soil.

The limited distribution of forests to the most sheltered sites in northeastern Nebraska is shown in Plate 1. Their further extension from the protecting Missouri river bluffs in the central portion of the state may be seen in Plate 2. Plate 3, from southeastern Nebraska, shows woodland extending uninterruptedly (except for clearings) over the hilltops several miles from the Missouri river.

The chief forest communities are, in order of increasing mesophytism, as follows: the bur oak-bitternut hickory (*Quercus macrocarpa-Hicoria cordiformis*) associes (Plates 4A, 5A); black oak-shagbark hickory (*Q. velutina-H. ovata*) associes (Plates 5B, 6A, and 7A); and red oak-linden (*Q. maxima-Tilia americana*) (Plates 6B, 7B, 8, and 9). The various stages of forest development on sandbars and sandy banks cover considerable areas (Plates 10 and 11) as do also the various types of flood-plain forest along most of the streams (Plates 12B, 13, and 14).

[1] The nomenclature is mostly according to the second edition of Britton and Brown's *Illustrated Flora of the Northern United States, Canada, and the British Possessions.* New York. 1913.

The red oak-linden association [1] is best developed in the southeastern part of Nebraska but extends up the river from the Kansas line to beyond transect 7 near Ponca (Figs. 1 and 15). The average width of the general potential forest area which is dominated only in the more protected parts by red oak and linden, is about 25 miles in the south but only 2.5 miles in the north. A consociation of linden occurs from Ponca to Bristow, this being beyond the range of the red oak. The width of the forest strip dominated by the linden is reduced gradually from about 2.5 miles in transect 7 to the side of the bluff next to the river or to about one-fourth mile, as an average, in transect 10. The forest is continuous in the red oak-linden association except where it has been cut. Except in the better watered soils of the southeastern portion, however, red oak and linden dominate only on the more mesophytic north slopes and in protected ravines. The height of the trees in the best situations southeastward is 80 to 90 feet but they decrease to an average height of 25 feet in the northwestern part of the area.

The number of species is also reduced northwestward. This reduction is very marked even under the more favorable conditions along the course of the Missouri river. The number of upland, woody species of ecological importance is 62 in transect 1 but only 31 in transect 10. The number of floodplain species is likewise reduced from 16 in transect 1 to 12 in transect 10. This computation includes the addition of those species which have migrated from the west and are found only along the upper Missouri.

In southeastern Nebraska, on sites where conditions are slightly less mesophytic, the *Quercus velutina-Hicoria ovata* associes is found. This is more limited in extent than the preceding. It occupies a narrow strip along the Missouri river for only about one-third of its length (Fig. 14). On

[1] It has been found expedient in describing the most mesophytic forests of Nebraska to group the linden and the red oak because of their close topographical association notwithstanding the fact that eastward the former is often a dominant in the *Acer-Fagus* association and the latter in the *Quercus-Hicoria* association.

gentle slopes in this part of the area, it occupies the zone between the *Quercus maxima-Tilia americana* and the *Quercus macrocarpa-Hicoria cordiformis* communities. The height of the trees varies from about 75 feet in the more favorable situations in the extreme southeast to about 30 feet in the less favorable places near the limits of their range.

Hicoria ovata is more xerophytic than *Quercus velutina.* It is often found in pure stands on gentle, well-drained slopes, above the site occupied by the latter. It extends farther into the area along some of the streams than does the black oak. Less shade under this associes makes possible a somewhat scattered shrub layer of gooseberry *(Grossularia missouriensis),* raspberry *(Rubus* spp.), blackberry *(Rubus alleghenienses)*, and hazelnut (*Corylus americana*) as well as an herbaceous layer both of which are much more poorly developed or absent in the red oak-linden community.

The *Quercus macrocarpa-Hicoria cordiformis* associes is found on the more xerophytic slopes and tops of hills. Its extent is shown in Figure 13. It occupies a position between the tension zone of shrubs and the more mesophytic tree communities. The width of this xerophytic-tree zone varies from a few feet in less favorable situations to a mile or more on gentle, well-drained slopes in favorable locations. The average height of the trees in this association is reduced from about 70 feet to 20 feet. In the northern and western part of the area there is no distinct community of bur oak on the hills bordering the small streams but a mictium of bur oak and flood-plain species occurs on the hillsides facing the stream as well as on the flood-plain.

The stand in a typical bur-oak community is somewhat sparse and light values are relatively high, averaging about 10 per cent. Hence there is often a well developed layer of shrubs. The distribution of this associes is far more extensive than any of the preceding. *Hicoria cordiformis* does not reach the northern nor the extreme western part of the area but *Quercus macrocarpa* extends westward along the larger streams beyond the limits of the region studied. The

bur oak is the only upland tree which is widely distributed over the entire area and it is the only one which is able to establish itself in the outlying *Rhus-Corylus* chaparral.

The bur-oak forest is rather regularly bordered on its more xerophytic outer edge by a fringe of shrubby species of the *Rhus-Corylus* associes. The width of this zone of chaparral varies from a very few feet on dry ridges to a mile or more in gullies or where trees have been suppressed by fires and cuttings. *Rhus glabra* extends farthest into the grassland and is followed by *Symphoricarpos orbiculatus* and *S. occidentalis. Corylus americana,* with other more mesophytic shrubs, grows in closer proximity to forests. Light values in general are higher at the outer margin of the shrub zone and lower at the inner one near the forest where the growth is denser. Determinations in many situations give the following: *Rhus* 32 per cent, *Symphoricarpos* 23 per cent, *Corylus* 5 per cent.

The flood-plain forest associes is very important because, in some stage of its development, it is found along all of the streams of the area, many of which have no other tree growth. Thousands of small gullies and hollows at the sources of streams are in the first stage of forest development, i.e., that represented by the willow (*Salix* spp.). Farther down the stream the willows are associated with the invading cottonwood (*Populus deltoides*) and boxelder (*Acer negundo*). This early stage of development is represented for considerable distances along the small streams in the western part of the area, especially the smaller tributaries of the Big and Little Blue, the Elkhorn, and the Loup rivers, which extend far into the plains. The next stage, resulting from the invasion of ash *(Fraxinus pennsylvanica)* and elms *(Ulmus americana* and *U. fulva)* and followed somewhat later by the walnut *(Juglans nigra)* and certain other species, constitutes the typical flood-plain forest which is found on all of the more mature flood-plains. In the southeastern part of the area the ash-elm-walnut flood-plain forest is, on an average, developed within 2 to 4 miles of the sources of the streams.

Flood-plain forests are best developed where protected by upland forest communities. In the western part of the area, the bur-oak consocies is especially important along the streams. Figure 13 shows the extent to which the development of the flood-plain forest is accompanied by the development of the bur oak on the bordering slopes and on the flood-plain. Near the mouths of the larger streams, in practically all cases, only the width of the flood-plain itself limits the width of the flood-plain forest. Toward the north and west the flood-plain species gradually become confined to the banks of the streams.

Along the larger rivers, as the Missouri, the Platte, and the Niobrara, a short hydrosere develops on sandbars and on low sandy banks. The first woody invaders, and in fact usually the pioneers, are *Salix interior, S. nigra,* and *S. amygdaloides,* followed or often accompanied by *Populus deltoides.* A later development is shown by the growth of such species as *Acer negundo, Ulmus americana, U. fulva, Fraxinus pennsylvanica,* and *Juglans nigra.* These in turn may finally be replaced by *Tilia americana,* the elms often remaining as codominants.

ENVIRONMENTAL FACTORS

The most important factors affecting the distribution and structure of forest communities are water content of soil and light. Water content directly affects absorption, and humidity of the air has a profound influence upon transpiration. Both must be taken into account in a study of the moisture relations. Light is important in determining what species may grow in a forest community, although where moisture and other conditions are favorable trees can endure more shading. A knowledge of precipitation, evaporation, temperature, and wind movement is also important since they affect the water relations.

LOCATION OF STATIONS

One series of stations was maintained along the Weeping Water creek near Weeping Water, 30 miles east of Lincoln

and 14 miles west of the Missouri river (Fig. 1). Four stages of development between grassland and climax forest were represented here within a distance of one-fourth mile. Although the forest communities were not so extensive nor mature as those in the southeastern corner of the state, (in fact they are young and of recent development) still they were typical of many similar situations in the area.

A station was located on the top of a high hill in the subclimax prairie. Here the soil had a depth of only 10 to 12 inches and was underlain with limestone. The upper portion of the soil consisted of a dark-colored loam, but below six inches it became lighter and somewhat yellow in color and was filled with rock fragments.

A station in the chaparral was located about one hundred feet from the grassland station in an area of hazelnut which formed a tension zone between the grassland and the forest. The soil was only slightly deeper than that in the prairie.

The station in the bur oak was located below the crest of a hill on a gentle south slope. The bur-oak trees, which were 20 to 35 feet high, together with a scattered growth of hazelnut, gooseberry, and *Symphoricarpos,* constituted a rather open cover. The soil from the disintegrated limestone had a thickness of about two feet.

The red-oak station was situated on a gentle north slope and was protected by the surrounding low hills. The stand was much thicker than that of the bur oak and because of the dense shade there was no shrub layer. The red-oak trees were 50 to 55 feet tall and had a trunk diameter of 10 to 12 inches. Continuous records of humidity, temperature, and evaporation were obtained and frequent determinations of water content of soil and light were also made.

In order to compare factors within similar communities in different parts of the state, stations were also maintained at Tecumseh, 40 miles south of Weeping Water. Here the rate of evaporation and soil and air temperatures were measured in the prairie and in a bur-oak ravine. During the summer of 1926, stations were also maintained at Peru, about 40

miles from the southeastern corner of the state, and at Bristow, 10 miles from the Missouri river where it enters South Dakota. At the latter stations temperature, humidity, and evaporation in the most mesophytic and the most xerophytic habitats of the two localities respectively, were obtained. At both Peru and Bristow one station was located in the most mesophytic forest community. The other, at Bristow, was on a hilltop in the grassland; that at Peru, on a hilltop from which the forest had been cleared.

Other studies were carried on in the Nehawka forests, 8 miles east of the Weeping Water station. Here the several communities were quite extensive. Measurements of light intensity were made over a period of weeks by means of Clements' photometer. Soil and air temperatures and wind velocity were measured in three forest communities and in the chaparral and prairie.

PRECIPITATION

A knowledge of precipitation is of primary importance in a study of the distribution of plant communities. Not only the amount but also the manner in which it occurs and its distribution throughout the year are of great significance. Luxuriant forests are characteristic of temperate regions having abundant winter and summer precipitation. Grasslands are found in similar temperate regions with moderate rainfall which occurs mostly during the growing season. In eastern Nebraska, where the soils are not widely divergent in type, precipitation affords a general index to forest distribution. The best developed forests are found in the southeast where the precipitation is greatest.

Records of precipitation have been kept by the U. S. Weather Bureau at various stations in eastern Nebraska over an average period of about 30 years. These data show about 32.5 inches annual precipitation in the southeastern corner of the area as compared with only 23 inches in the northwest (Fig. 3). The decrease in the mean annual amount from south to north is shown in Figure 4 (see Fig. 1 for location of stations).

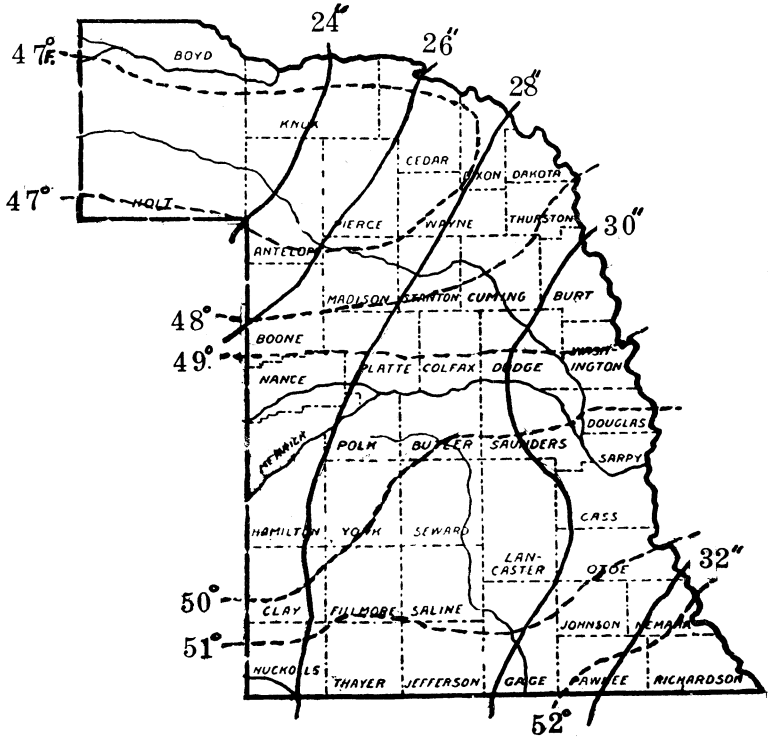

FIGURE 3. Mean annual precipitation in inches (solid lines) and isotherms (broken lines).

Distribution of the mean annual precipitation at four stations along the Missouri river from the Kansas to the South Dakota line is shown in Fig. 5. At all stations, the distribution is of the Great-Plains type. There is one period of heavy precipitation during the growing season. It may be noted, however, that at the most southerly station, Falls City, this period covers five months of almost equal rainfall whereas at Santee, near the South Dakota line, the period of high rainfall is maintained for only two months. The rainfall at Falls City is also more evenly distributed throughout the year, being about the same in amount as at the other stations during midsummer and greater for the remaining months of the year. This distribution is more favorable to the growth of trees.

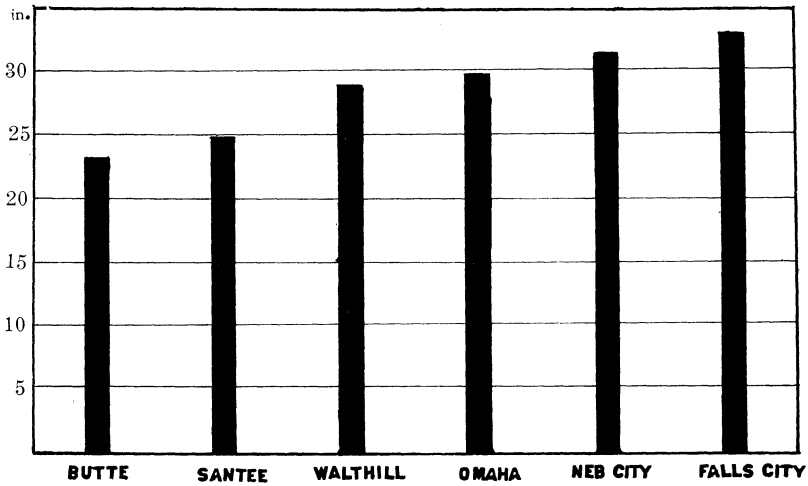

FIGURE 4. Mean annual precipitation in inches at stations along the Missouri river from north to south (reading from left to right). Averages for 20 years.

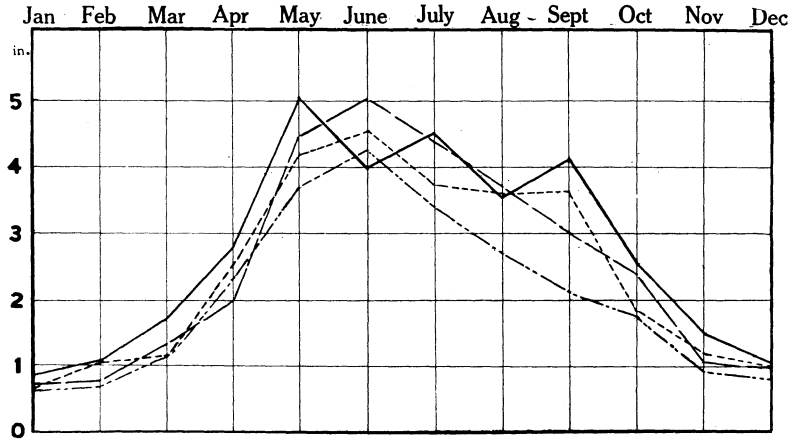

FIGURE 5. Mean annual (25 years) precipitation in inches at Falls City in the southeastern corner of the state (solid line), Omaha (long broken lines), Walthill (short broken lines), and Santee in the northeastern corner of the area (mixed broken lines).

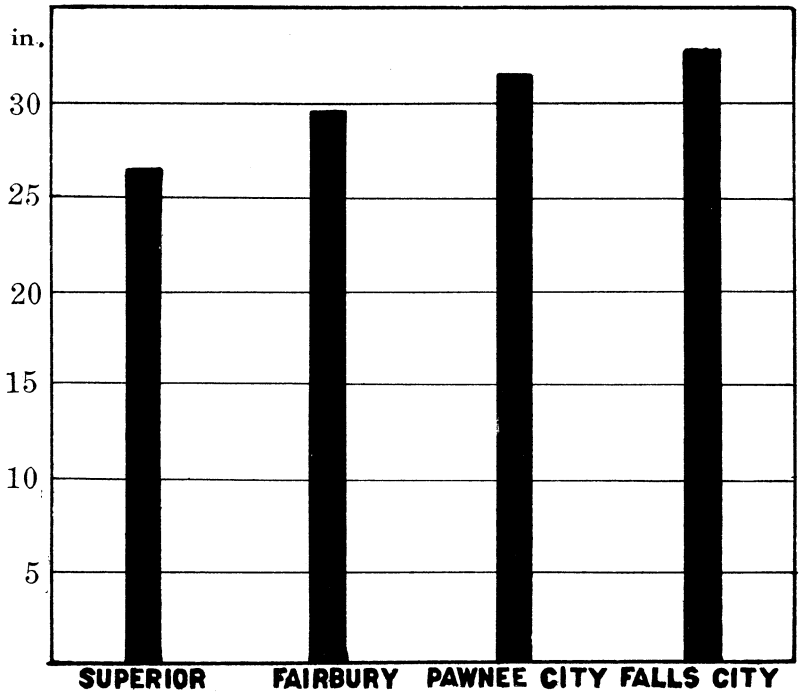

FIGURE 6. Mean annual precipitation in inches at stations along the southern border of the area from west to east (reading from left to right). Averages for 25 years.

The decrease in precipitation westward is even more rapid than it is northward (Fig. 6). The average decrease from east to west across the state has been computed at one inch for each 25 miles. Although many other factors such as evaporation, run-off, percolation, etc., affect efficient rainfall, but in this region none of these differences are so pronounced as to overshadow the effects of the marked differences in precipitation.

SOILS

Along the Missouri river the soil of the lower bordering bluffs has been derived from loess and is classified as Knox silt loam and Marshall silt loam. There appears to be greater

variation in the physical than in the chemical composition of these exposed soils. Their differing structure and texture affect their ability to hold water.

Soil texture is important in a consideration of soil in relation to forest distribution since it affects both water-holding capacity and aeration. The hygroscopic coefficient of a soil is an index of its texture. A comparison of the hygroscopic coefficients of soils of approximately equal organic content from bur-oak forests, throughout the area, shows that the hygroscopic coefficients are lower, as one progresses from the drift soils in the southeast to the loess soils in the north and west. The coefficients are 14.5 near transect 3, 11.2 near transect 7, 6.9 near transect 10, and 12.0 near Central City in the western part of the area. Since the coarser-textured soils holds less water, conditions for tree growth are more favorable in the southeastern part.

The reaction of the forest soils from the several communities throughout the area ranges from pH 7.2 to 6.5. Soil acidity increases slightly from the prairie through the pioneer woodland communities to the climax forest. An average of determinations at several points in the area gave the following: prairie 7.2, shrub 7.0, bur oak 6.8, and red oak-linden 6.5. These changes correlate with the increase of humus in the soil.

Forests add nitrogen to the soil by the accumulation and decay of much vegetable material. Averages of the per cent of total nitrogen for stations in transects 1, 7, and 10 are as follows: prairie .162 per cent, shrub .197 per cent, bur oak .253 per cent, and linden .488 per cent.

Russel and McRuer (1928) have shown that the relative magnitude of the nitrogen content of soil is best shown by a calculation of the ratio of hygroscopic coefficients to nitrogen (Hc/N). They report Hc/N ratios of the first six-inch section of stabilized grassland soils of southeastern Nebraska. On the rolling type of soils average values are about 44:1 and on level types 40:1.

Ratios calculated for bur-oak forest are 49.9 for shagbark hickory 46.6, and for red oak-linden 34.6. When more

extensive sampling is done it may be necessary to change these ratios somewhat, but at any rate they give an idea of the increase in nutrients caused by the development of forests on the soils of eastern Nebraska. There is little difference in the total nitrogen in the soil of the same community in different parts of the state, although there is a slight decrease from southeast to northwest. For example, soil from bur-oak communities in several localities gave the following total nitrogen contents: .292 per cent near transect 1, .287 per cent near transect 3, .265 per cent near transect 7, and .206 per cent near transect 10.

In addition to physical and chemical analyses of the soils, planting experiments were made to determine the ability of certain seeds to germinate and the seedlings to establish themselves in soils from extreme parts of the area. *Quercus maxima, Q. velutina, Hicoria ovata,* and *H. glabra* are among the species which are not found along the upper Missouri river in Nebraska. *Hicoria glabra* does not occur in Nebraska, *Quercus velutina* and *Hicoria ovata* are absent from and beyond the fifth transect, and *Quercus maxima* from and beyond the eighth. The aim of the experiment was to ascertain if seeds of these species would germinate and grow in soil from the vicinity of transect 10 as well as in soil from transect 1. The best developed soil was selected from the wooded bluff bordering the Missouri at Niobrara and north of Lynch in the northeastern corner of the area. Soil was also secured from the bordering bluff of the river at Rulo in the southeastern corner of the state. The soil from these two extremes of the area was shipped to the greenhouse at Lincoln and placed in galvanized iron containers, one foot square and two feet deep. Twelve of these containers were employed. The soil was watered and tamped in the containers into as nearly its original condition as possible, after which the seeds were planted. The four species germinated and grew in the soil from both parts of the area and there was no perceptible difference (Plate 18B). Linden, green ash, elm, and walnut also grew equally well in both soils. These

results show that other factors than the kind of soil limit the extent of certain woody species along the Missouri river in northeastern Nebraska. The controlling factor is soil moisture.

WATER CONTENT OF SOIL

Various species of trees and shrubs differ greatly in their ability to survive under conditions of limited soil moisture. The amount of available water is the most important factor in determining whether or not forests become the dominant vegetation of a region.

Simpson (1927) measured the total effect of the forest upon soil moisture by comparing a forested site with a bare one, similar in all other respects. The average amount of soil moisture in the latter during the summer exceeded that in the forest by 55 per cent. The forest conserves soil moisture because both the living and dead ground cover retains precipitation and decreases evaporation from the soil surface. It decreases soil moisture by the interception of large amounts of the precipitation by the forest canopy and the transpiration of large quantities of water from the extensive above-ground parts of the trees. Several investigators (Weaver and Thiel, 1917; Pool, Weaver, and Jean, 1918; Weaver, 1919) have shown that in Nebraska soil moisture is usually higher in chaparral and woodland than in the prairie.

Soil samples were taken at the four stations at Weeping Water during the summer of 1924 (Table 1). Although the surface soil in the prairie had the greatest amount of available water at the beginning of the growing season and the second six-inch layer also a large amount, yet this soil was driest at the end of the summer. Because of the rocky nature of the soil in the prairie, soil samples at greater depths had to be secured from the crevices where run-in usually kept the soil more moist than that of the forest communities.

Water-content determinations were made during the growing season of 1927 in the prairie and in the bur-oak forest

TABLE 1.—*Available soil moisture (i.e., amount above the hygroscopic coefficient) in the several stations at Weeping Water during 1924*

	0-6 inches				6-12 inches				12-24 inches			
Week ending	Prairie	Hazel	Bur oak	Red oak	Prairie	Hazel	Bur oak	Red oak	Prairie	Hazel	Bur oak	Red oak
May 3	33.3	23.0	16.8	28.9	18.8	27.4	16.4	15.4	9.1	19.4	12.4	10.1
May 17	16.3	12.3	16.9	18.6	18.2	11.5	10.7	12.4	10.7	10.1	11.0	8.1
June 14	20.8	23.4	14.2	23.5	17.5	16.8	18.1	11.7	19.6		7.0	9.5
July 4	15.6		8.9	18.3	18.2		8.8	10.4	17.8		9.5	7.8
July 26	18.0	13.4	14.7	18.1	19.5	9.9	10.1	11.2	16.4		11.1	11.4
August 9	5.3		1.9	5.2	11.3		6.4	3.7			4.0	5.5
September 6	1.1		2.1	1.0	1.1		1.2	1.4	0.2		1.4	2.5
Hygroscopic Coefficient	14.0	14.0	14.6	7.2	15.1	15.1	14.3	6.3	14.5	14.5	15.8	8.9

at Bristow and also in the several communities at Nehawka. Soil water was available throughout the season at all of the Nehawka stations as well as in the bur-oak station at Bristow. Available soil moisture increased in amount, proceeding in the order of succession, from the prairie to the linden forest. Soil moisture was available in the two upper soil layers (i.e., 0-6 and 6-12 inches) in the prairie station at Bristow for only a few days following each period of rainfall, in spite of the unusually large amount of rainfall and the favorable growing season. There was no available soil moisture during the growing season after July 10 at 2-3 and the 3-4 feet levels.

Water-content determinations in prairie, chaparral, and forest at Peru and at Lincoln (Pool, Weaver, and Jean, 1918) also show that the amount of available water decreases from the forest to the prairie. In the forest at Peru, with the exception of the black oak which was drier, the available water increased with the progressive stages in the succession. At depths of 3 to 5 feet, however, the black-oak station was not an exception and the soil moisture increased progressively from the bur oak to the linden.

In general, the water content of the soil in comparable situations decreases toward the north and west. The available water content of the prairie soil is greater in practically all depths at Peru than at Lincoln. The same is true in prairie and bur-oak areas at Nehawka as compared with Bristow. There is a marked difference between the available water content of soils in prairie and bur oak at Nehawka and at Bristow, the amount being much lower at the latter station.

ATMOSPHERIC HUMIDITY

Records of relative humidity and temperature were obtained by the use of Friez and Sons' hygrothermographs. Well ventilated, water-proof shelter houses were used to protect the instruments which were checked every week. Mean day humidity was secured by taking the average of the seven readings at the two-hour intervals beginning with 6 A. M.

The night humidity was secured by averaging the five readings, beginning at 8 P. M. These were then averaged for day and night during weekly periods. In addition to the data from the stations at Weeping Water, humidity was determined during the summer of 1926 at Peru and Bristow. The seasonal average of relative humidity in the bur oak at Weeping Water was but little higher than in the adjoining subclimax prairie. The small extent of the prairie (only a few acres at this station) and its protection by the surrounding woodland raised the humidity nearly to that of the woodland.

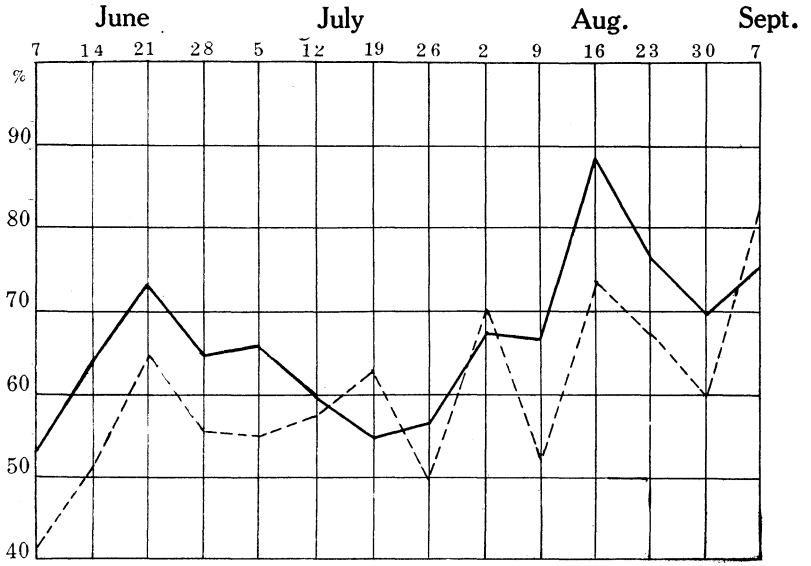

FIGURE 7. Average daily humidity by weeks in the prairie (broken line) and in a bur-oak ravine (solid line) at Bristow, 1926.

Humidity at Bristow during 1926 was greater with two exceptions in the bur oak than in the prairie (Fig. 7). Humidity is an important factor in the distribution of bur oak in the ravines of the northeastern part of the state (Plate 1B). The air in such sheltered areas averages several per cent more humid than on the wind-swept hills. Figure 8 shows the difference between the humidity of a well protected

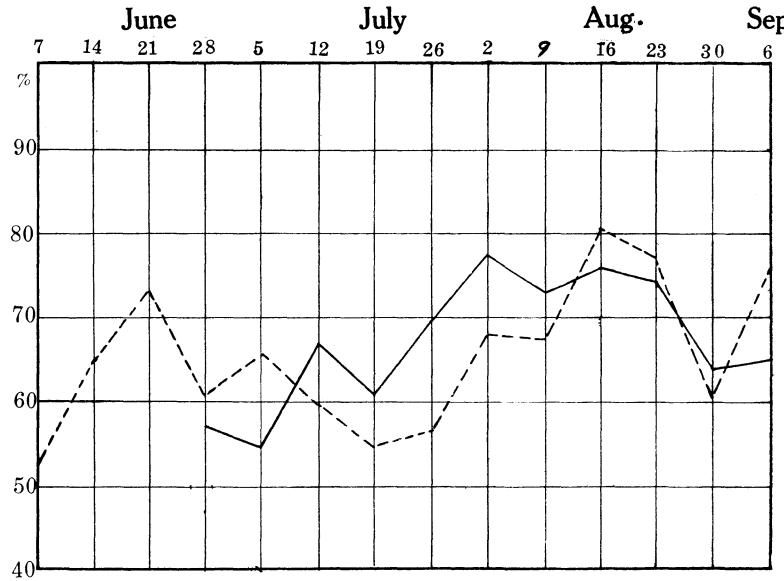

FIGURE 8. Average daily humidity by weeks in the linden station at Peru (solid line) and in a sheltered bur-oak ravine at Bristow (broken line), 1926.

area of climax vegetation at Peru and a similar area at Bristow in the Ponca district. The stations were selected in the most mesophytic areas in the respective localities. The station at Peru was located in a linden woods and at Bristow in a sheltered ravine filled with bur oak. The marked differences in humidity in comparable situations of these two localities must be considered in explaining the differences in the vegetation of these two widely separated parts of the state.

AIR AND SOIL TEMPERATURE

The area under consideration lies between the isotherms of 53° and 47° F. (Fig. 3). It may be noted that near the eastern border the lines turn northward along the river, indicating the higher temperature of this more protected region. The average monthly temperature from the U. S. Weather Bureau records, obtained for the three stations nearest the Missouri river, shows a gradual decrease northward (Table 2).

TABLE 2.—*Average monthly temperature at the three stations nearest the Missouri river (Cf. Fig. 2)*

Stations	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Ann.
Butte	21.6	22.0	35.2	48.5	59.6	69.6	73.6	72.0	62.0	51.2	36.2	23.7	47.9
Omaha	21.3	24.8	37.0	51.2	62.3	71.6	76.6	74.6	66.1	54.4	39.0	27.1	50.5
Falls City	27.8	27.8	42.1	53.7	63.6	72.7	77.9	76.9	68.7	57.3	43.6	29.1	53.4

The average winter temperature varies from 37.9° in the southeast to 35.2° in the southwest, and 30.6° in the northwest. The average summer temperatures at the same places are 68.9°, 67.9°, and 63.8° F., respectively.

Figure 9 shows the difference in temperature in the most mesophytic areas in the vicinity of Peru and of Bristow. The average for the growing season is 69.1° F. at the latter station and 73.4° F. at Peru.

Seasonal temperature extremes are great. At Butte, in the northwestern part of the area, variations from –30° F. in winter to 102° in summer are not uncommon. An extreme daily variation of 40° (from 64° to 104° F.) was found in the prairie station at Bristow during the summer of 1926.

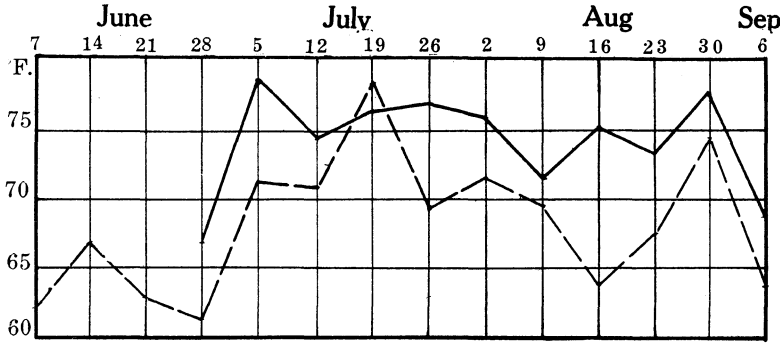

FIGURE 9. Average daily (24 hour) temperature in a mesophytic linden station at Peru (solid line) and in a protected bur-oak ravine at Bristow (broken line).

Winter temperatures also have an influence on the development of seedlings. Extremely low winter temperatures tend to reduce the number of seedlings due to soil heaving as well as to winterkilling resulting from drought in the frozen soil.

Another factor affecting the composition of the vegetation is the length of the frost-free season. At the southern border of the area this season extends over a period of 180 days compared with 150 days at the northern border. The mean date of the last killing frost in spring is April 21 in the southeastern corner of the area and May 6 in the northwestern. This difference is reflected in the development of

forest species as well as of crops. The average date of cutting the first crop of alfalfa (1927) was May 30 in the vicinity of transect 1 as compared with June 15 near transect 10. The average date of blooming of *Vitis vulpina* was May 25 in transect 1 and June 10 in transect 10. This difference in the length of the growing season has a very noticeable effect on the development of seedlings. A thirty-day shortening of the growing season and a proportionate delay of favorable temperatures for growth in spring retards the development of certain seedlings to such an extent that it is extremely difficult or impossible for them to establish themselves in the north before the advent of summer drought. It would seem that temperature acts directly in excluding the growth of certain species of southern origin such as *Asimina triloba, Aesculus glabra,* and others from the northern part of the area.

A comparison of the temperatures at the several stations at Weeping Water, during the middle of the growing season, shows that they were lowest in the red oak, intermediate in the bur oak, and highest in the prairie (Fig. 10). In the

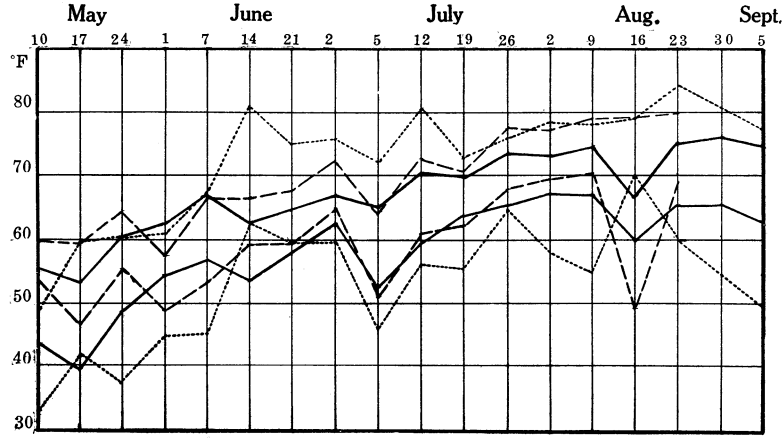

FIGURE 10. Average day temperatures (three upper lines) and average night temperatures (three lower lines) in the linden forest (solid lines), in bur-oak forest (broken lines), and in prairie (dotted lines) at Weeping Water.

early part of the season, before the leaves were fully grown, the temperature of the woodland was higher than that of the prairie. At Tecumseh the average air and soil temperatures (the latter taken at a depth of 3 inches) for the growing season were 82.3° and 73.1° respectively in the prairie as compared to 70.5° and 48.3° F. in a bur-oak ravine.

The influence of the forest on temperature has been studied by Ebermayer (1873), Pearson (1920), Li (1926), and others. All agree that the forest lowers the daily mean temperature in spring and summer and raises it in autumn and winter and that, especially in the summer, the forest lowers the daily maximum temperature and raises the daily minimum.

Temperature readings were also taken in the forested area along the Weeping Water creek at Nehawka. Non-recording instruments were used. The air temperatures were recorded at the surface of the ground, the bulb of the thermometer being protected from the sun. Readings taken at different times of the day for 15 days, between June 20 and August 20, (1927), were averaged. The results are shown in Table 3. Soil temperature readings were made at the same time with Tycos soil thermometers (Table 4).

TABLE 3.—*Average air temperature in degrees Fahrenheit from readings taken at Nehawka for fifteen days during the growing season of 1927*

Station	7AM	9AM	10AM	11AM	12M	1PM	2PM	3PM	5PM
Prairie	71.3	91.0	98.2	104.5	108.6	107.2	102.0	95.0	82.4
Shrub	69.5	77.9	82.4	88.3	90.1	89.2	86.0	82.4	77.0
Bur oak	68.0	72.1	75.7	76.6	79.3	78.4	77.7	76.6	73.4
Shagbark hickory	68.0	71.3	73.0	74.3	77.5	77.0	76.1	75.2	73.4
Red oak-Linden	66.2	71.3	72.5	73.9	75.6	75.2	75.2	74.8	73.4

From 10 A. M. to 2 P. M. the prairie had an average air temperature of over 98° F. during the warmer part of the growing season. The bur oak, in the same locality, had an average temperature ranging from 75° to 78° F. The difference between the soil temperatures of the two localities was only 10° F. The great difference in air temperature is a factor of importance in the extension of trees into prairie since increased temperature by lowering the humidity, greatly accelerates water loss. Air temperatures of 110° and surface soil temperatures of 140° F. are sometimes attained in the prairie.

TABLE 4.—*Average surface soil temperature in degree Fahrenheit. The readings were taken at Nehawka throughout the growing season of 1927*

Station	7AM	9AM	10AM	11AM	12M	1PM	2PM	3PM	5PM
Prairie	70.5	74.0	76.0	77.5	81.0	82.0	83.5	85.0	82.5
Shrub	69.5	71.8	72.5	74.0	75.3	75.3	75.3	76.0	75.0
Bur oak	67.0	67.8	68.5	70.0	71.5	71.5	71.5	72.0	72.0
Shagbark hickory	66.5	67.0	67.5	67.8	69.5	70.0	70.0	70.3	70.0
Red oak-Linden	66.5	67.3	68.0	68.0	69.3	69.3	69.5	70.0	70.0

WIND

Wind has considerable influence on forest development in eastern Nebraska. This is exerted chiefly through its effect upon lowering the humidity. Records from sixteen stations selected within or near the borders of the area show that the wind blows almost equally from the south and the northwest. The wind is prevailingly from the south at the four southernmost stations along the Missouri. Even at these most mesophytic points the south winds are usually hot and dry

for at least a few days in summer. In a typical prairie region these are very trying times for forest vegetation. The drying winds in the western and northwestern parts of the area blow for a greater length of time and increase evaporation in a marked degree. Here the growth of trees and shrubs is limited to the more protected banks of streams and ravines. The rate of movement of the wind is greater for the western than for the eastern part of the area. Government records at Omaha, covering a period of 48 years, show an average hourly wind movement of 8.6 miles; those at Lincoln, covering a period of 26 years, give an hourly average of 10.7 miles.

Wind velocity in the prairie was compared with that in the forest communities at Nehawka. Keuffel and Esser hand anemometers were employed. For comparison of wind velocity between prairie and oak the Robinson type of anemometer was used. The average of several readings at a height of 3 feet, taken during the growing season of 1927, gave the following results: prairie 46.5 feet per second, bur oak 6.8 feet, shellbark hickory 3.8 feet, red oak-linden 3.2 feet. Attempts to measure the wind velocity at 3 inches above the ground in all stations were unsuccessful because of the stillness of the air in the more dense forest communities. The average of readings at 3 inches are: prairie 22 feet per second, *Rhus-Symphoricarpos* shrub 14 feet, and bur oak 2.5 feet. The anemometers, placed at a height of 14 inches, gave a weekly total of 171.3 miles in the prairie but only 21.4 miles in the bur-oak forest.

EVAPORATION

White, cylindrical, standardized atmometers, equipped with a non-absorbing device, were operated in pairs at each station. Average daily evaporation in the four stations at Weeping Water during the growing season of 1924 are as follows: prairie 14.1 c.c., hazelnut 11.2 c.c., bur oak 10.2 c.c., and red oak 8.2 c.c. Figure 11 gives the weekly averages at the four stations. These data show a higher rate of water loss in the prairie than in the shrub and forest-covered areas.

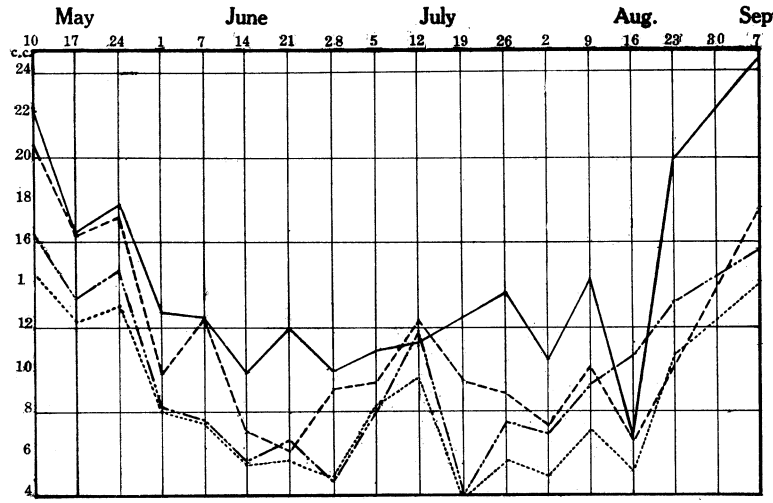

FIGURE 11. Average daily evaporation at Weeping Water: prairie (solid line), shrub (short broken lines), bur oak (mixed broken lines), and linden (dotted line), 1924.

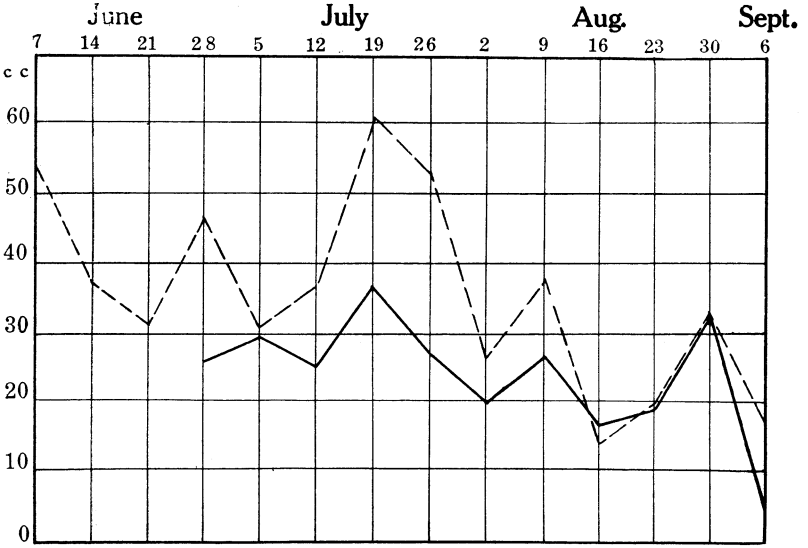

FIGURE 12. Average daily evaporation by weeks in the prairie at Bristow (broken line), and on a cleared hilltop at Peru (solid line), 1926.

At Tecumseh, toward the southeastern corner of the area, the average daily evaporation for 1924 was 28.9 c.c. in the prairie and 13.8 c.c. in a bur-oak ravine. In general, aerial factors (except light) are much less favorable to plant growth in the prairie than in the shrub and woodland.

The difference in evaporation at Peru and Bristow (1926) is shown in Figure 12. The daily averages for the season of 1925 (June 21 to September 6) were 23.8 c.c. at Peru and 33.1 c.c. at Bristow. These data were obtained in comparable habitats in the two localities, i.e., the broad flat summits of hills above streams. Hills of this type are covered with bur oak at Peru and with mixed prairie at Bristow. At Peru the bur oak had been cleared from the summit of the hill where the station was located. In general, evaporation rates are lower as one proceeds from the northwestern to the southeastern part of the area and from the grassland, through the several chaparral and forest communities to the red oak-linden association.

LIGHT

Nebraska is a region usually with clear skies. The thirty-year average of all of the weather bureau stations of the state gives 192 clear, 92 partly cloudy, and 81 cloudy days. Light is an important factor in forest development. In the tension zone between the woodland and the prairie, the shading of the grasses by the shrubs is one of the outstanding features of the invasion of the grassland. In the bur oak-bitternut hickory associes the shade is dense enough to make the habitat unfavorable for prairie grasses but most of the more tolerant shrubs can thrive. In the black oak-shagbark hickory associes shade is denser and shrubs occur in less abundance along with more tolerant trees. In the red oak-linden association light values are lowest.

Readings of light intensity in typical communities at Nehawka gave results which, in general, agree with those taken in similar communities by Pool, Weaver, and Jean (1918) at Peru. The figures in Table 5 are averages of many readings.

Light intensity under dense *Corylus* may be as low as 1 per cent and under a "canopy" of *Rhus* only 1.5 per cent as compared to 10 per cent under a sparse stand of *Quercus macrocarpa.* The following readings, taken at a height of 3 inches, represent average conditions.

TABLE 5.—*Average light intensity on clear days in the different forest communities at Nehawka. (June 20–August 20, 1927)*

Station	8AM	9AM	10AM	11AM	12M	1PM	2PM	3PM	4PM	5PM
Upland prairie	33.2	36.6	47.3	54.0	56.0	53.0	48.1	39.2	35.0	31.5
Sumac-Symphoricarpos	5.0	9.3	12.0	23.0	27.5	24.8	24.0	17.0	10.4	4.3
Bur oak.....	3.0	3.7	7.1	8.8	10.0	9.0	6.6	4.8	4.0	2.8
Shagbark hickory	1.4	2.2	2.6	3.5	4.5	3.8	3.3	2.5	2.5	1.1
Red oak-linden	0.3	0.5	0.6	0.9	1.3	1.0	0.8	0.7	0.4	0.3

The average illumination at noonday (Table 5) in the upland prairie is 56 per cent as compared to only 27.5 per cent in the *Rhus-Symphoricarpos* community. Such a striking difference explains the reason for the elimination of prairie species under the cover of an invading shrub.

Within the chaparral and woodland the light changes are also marked. The greatest difference is between the *Rhus-Symphoricarpos* chaparral (27.5 per cent) and the bur oak (10 per cent). More tolerant shrubs following *Rhus* and *Symphoricarpos* in the succession may reduce the light intensity to 15 per cent or less. This is the case with well developed *Corylus.* The *Hicoria ovata* consocies, with an average noonday illumination of 4.5 per cent and the *Quercus maxima-Tilia americana* association with an illumination of 1.1 per cent, mark a reduction in light intensity to a point which excludes the growth of most species of trees. There are only remnants of a shrub layer and practically all but vernal herbs are excluded.

In summarizing the environmental factors it may be said that eastern Nebraska offers widely different conditions for forest growth. The precipitation is heaviest in the southeast and decreases northward and even more rapidly westward. The soils are all very rich and well drained and have a high water retaining power. The latter is greatest in the south and southeast where the texture is somewhat finer. Both soil and air moisture also decrease somewhat in direct proportion to the decrease of precipitation so that near the Dakota line conditions favorable for forest growth are found only along the river bluffs and in well sheltered ravines. Temperature decreases with latitude as does also the length of the growing season. Wind velocity is greater westward and evaporation becomes higher as the humidity becomes lower and air movement greater.

Light is an important factor within the forest communities. Proceeding from the prairie, through chaparral and from the more xerophytic to the climax mesophytic forest, light, wind, evaporation, and (summer) day temperatures all decrease but water content and humidity become greater. These changes are brought about largely by the development of the forest communities themselves, the structure of which will be considered.

THE PLANT COMMUNITIES

Even casual examination of the forests of eastern Nebraska shows that they are composed of a number of different communities. Extensive study throughout the area reveals the following units which will be described beginning with the most xerophytic.

RHUS GLABRA-CORYLUS AMERICANA ASSOCIES

Along the border of the woodland in eastern Nebraska, chaparral occupies the tension zone separating forested areas from prairie. As to number of species this associes is better developed in the southeastern part of the state but it is more extensive in the northeastern portion where the climate is drier and there is less competition with trees for favorable

sites. Extension of forests into subclimax prairie is nearly always preceded by chaparral.

Intensive investigations by Weaver (1927), extending through a period of years, have thrown much light upon the invasion of shrubs into grassland and the climax or postclimax nature of forest communities in Nebraska. The disappearance of prairie grasses before invading shrubs at Weeping Water and the establishment of trees has been fully studied. As regards the shrubs, the sequence of xerophytism is in close accord with that of their tolerance to shade. *Rhus glabra* usually pioneers in grassland, often on the driest slopes of the rocky hills; species of *Symphoricarpos* usually gain dominance in less exposed situations; and *Corylus americana* is least xerophytic of all. This is shown not only in zonal distribution where the three species are found in common, but also in the relative distances they extend from the protection of the forest, and especially by their behavior in postclimax areas. Here *Corylus* is usually absent, *Symphoricarpos* occurs typically along streams and on floodplains, but *Rhus glabra* extends into much more xerophytic situations.

Sumac is the first to disappear before the invading hazelnut. *Symphoricarpos* is more tolerant, but likewise succumbs to the overtopping hazelnut. Experiments have shown that where the hazelnut is dense, light values are too low for these other shrubby species to carry on sufficient photosynthesis to maintain life. Intense root competition is also an important contributing factor.

All of these shrubs invade the grassland both by rhizomes and seeds. *Symphoricarpos* also invades, but usually ineffectively, by stolons. The development of isolated seedlings of hazelnut and other shrubs into clumps of sufficient size to cast effective shade and form a center for further invasion has been followed in the subclimax prairie at Weeping Water. Such chaparral areas develop slowly, increasing their territory sometimes only 10 per cent but often over 50 per cent in a period of 3 to 5 years (Clements, Weaver, and Hanson,

1929). Mass invasion is most effective. This occurs at a level above most of the prairie grasses. Clumps of hazelnut especially dominate an area 1 to 2 feet beyond that which the stems actually occupy. This is due to the shade cast by the peripheral plants leaning far outward toward the light. In this marginal territory, prairie grasses first cease to form seed and later disappear. The process, which has been followed in detail, seems to be hastened by root competition, the absorbing efficiency of the shrubs being very high. Bluegrass (*Poa pratensis*) being more tolerant of shade, occupies the area for a time. As new plants invade by rhizomes, a thick mulch of leaves is held among the stems, and this, with increased shade, causes in turn the disappearance of the bluegrass (Plate 15B).

Not only shrubs but also the more xerophytic oaks as well, especially bur oak, are able to compete successfully with the grasses. This is probably due in part to the rocky nature of the substratum at this station which will not permit of a continuous sod, but the oaks are also favored by the rich, moist soil in the rock crevices. Even on the most exposed slopes seedling trees, which have been followed from year to year, make a steady although sometimes a slow growth, withstanding even the driest summers.

These facts indicate the subclimax nature of the prairie along the Missouri river while other experimental data quite as clearly show the postclimax nature of certain shrub and forest areas farther westward.

Continued planting experiments of tree seeds and seedlings at Lincoln have conclusively shown that trees cannot successfully invade true prairie. Similarly extended studies with quadrat, bisect, and other exact ecological methods have shown that communities of shrubs, gaining a foothold in mesophytic ravines, are not extending their territory and evidently are giving way to the climax grassland vegetation. Conditions on low prairie are unfavorable for tree and shrub seedlings because of the dense shade cast by the tall overtopping grasses. The seedlings cannot invade such sites.

Soil moisture on the uplands is insufficient to sustain their growth in competition with the grasses under the prevailing dry grassland climate.

In the subclimax region bordering the forest area along the Missouri river shrubs and trees, however, are invading the grassland and, where not hindered by fires, cutting, or grazing, are establishing forest conditions. This area of potential forest has a width of several miles in the extreme southeastern part of the state but is gradually reduced to a very narrow strip along the river in the north. In fact, the fertile upland farms in the southeast area are on land which is potentially forest (Plate 3). Evidence of this fact is the presence of shrubs and often tree stumps in the fields throughout the region.

A line drawn from the Platte river through the western extent of the red oak along the Weeping Water and the Nemaha rivers approximately delimits this potential forest area south of the Platte (Fig. 15). North of the Platte it is much less definite.

The following list gives the important species of the chaparral associes. Each group is listed in the approximate order of increasing xerophytism.

Dominants (Consocies)

Corylus americana	Symphoricarpos occidentalis
Symphoricarpos orbiculatus	Rhus glabra

Subdominants

Lonicera dioica	Amelanchier canadensis
Lonicera glaucescens	Euonymus atropurpureus
Rubus allegheniensis	Ribes americanum
Zanthoxylum americanum	Rubus strigosus
Rhamnus caroliniana	Rubus occidentalis
Rhamnus lanceolata	Cornus asperifolia
Cornus stolonifera	Cornus baileyi
Cornus amomum	Parthenocissus quinquefolia
Cephalanthus occidentalis	Grossularia missouriensis
Staphylea trifolia	Smilax hispida

Rosa setigera	Vitis vulpina
Amelanchier humilis	Sambucus canadensis
Padus melanocarpa	Amorpha fruticosa
Lepargyraea argentea	Amorpha nana
Opulaster opulifolius	Prunus americana
Cercocarpus montanus	Ceanothus americanus
Toxicodendron radicans	Ceanothus ovatus
Padus nana	Rosa pratincola
Celastrus scandens	Amorpha canescens

The *Rhus-Corylus* associes may be divided into three districts. The southeastern district includes approximately the area along the Missouri from the Kansas line to Decatur (transect 6) and extends west to beyond the region drained by the tributaries except the Platte (Fig. 1). The northern district extends along the Missouri river from Decatur to the South Dakota line and along the Niobrara to the western extent of the area including the strip of territory drained by the tributaries of these two rivers. The remainder of the area, including the region drained by the Big and the Little Blue rivers and portions of the Platte, Loup, and Elkhorn rivers, makes up the western district.

In general shrubs in the north and the west districts play more of a pioneer rôle than do those in the southeastern district (Plates 1B, 1C, and 16). The habitat is less mesophytic so they must meet the competition of the grasses under conditions more favorable to the latter. *Symphoricarpos occidentalis* and *Rhus glabra* dominate the shrub zone in these districts. *Rhus glabra* is essentially the pioneer because it is more xerophytic and less tolerant of shade than *Symphoricarpos*. Under very slightly more favorable climatic or edaphic conditions these shrubs are able to compete successfully with the grasses.

In the northern district entire summits of bluffs, bordering forested areas along the upper Missouri, are covered with *Rhus glabra*. The cover afforded by the leaf mosaics of *Rhus glabra* reduces the light for the grasses very materially. The typical prairie grasses such as *Stipa spartea, Koeleria*

cristata, Schizachyrium scoparium, and *Atheropogon curtipendula* disappear under such conditions.

The invasion of the subclimax grassland by the chaparral proceeds from the woodland outward along the gullies which extend into the grassland (Figure 1). These more mesophytic gullies might be called strategic lines of attack. The more xerophytic ones are filled with *Rhus glabra* and often contain some *Symphoricarpos.* As development proceeds *Symphoricarpos* becomes more important and occupies larger areas at the expense of the sumac. The former retains its hold and becomes the dominant of the shrub layer under the succeeding bur-oak forest. The next important shrub to follow *Symphoricarpos* is *Cornus asperifolia.* It is a tall, sturdy plant which helps make a suitable nursery for seedling bur oaks which, under these conditions, are able to establish themselves. The shrubs shade the soil and lessen evaporation. The thick growth of vegetation retards the force of the wind and promotes the accumulation of debris. This upon decay becomes incorporated in the soil making it light and mellow. Where the shrubs are not too thick they form a natural nursery for tree seedlings.

The dogwood is able to grow among the sumac and the developing bur-oak trees. It follows the sumac in its advance upon the prairie and gives way to the bur oak after the latter obtains a height of 10 to 14 feet.

Numerous prairie shrubs are associated with the sumac as it first advances into the grassland. Among these are *Rosa pratincola, Amorpha canescens,* and *Ceanothus ovatus.*

Besides the three dominants, shrubs of ecological importance found in these areas are, in order of appearance, *Prunus americana* (replaced by *Padus melanocarpa* in the western part). *Lepargyraea argentea, Amelanchier humilis, Grossularia missouriensis, Opulaster opulifolius, Cercocarpus montanus, Cornus baileyi, C. stolonifera, Rubus occidentalis, R. strigosus, Euonymus atropurpureus,* and *Zanthoxylum americanum. Lepargyraea, Padus melanocarpa, Opulaster,* and *Cercocarpus* have come in from the west. The first two are

especially important in the northwestern part of the district. Associated with the trees and in the more dense chaparral areas the following lianas are found in considerable abundance: *Parthenocissus quinquefolia, Celestrus scandens, Toxicodendron radicans,* and *Vitis vulpina. Corylus americana* is of ecological importance in the area for only a short distance above transect 6 on the Missouri river where it is found bordering well established woodland.

Shrub and tree development near the western limit of the north district often starts in advance of other forest species with the establishment of *Lepargyraea argentea* or *Padus melanocarpa* or an associes of the two in small protected pockets situated in the grassland. *Symphoricarpos* then enters and is followed by many of the shrubs previously listed. *Rhus* is usually lacking, its pioneer rôle having been taken by *Lepargyraea* and *Padus melanocarpa. Fraxinus pennsylvanica* is associated with *Quercus macrocarpa,* as a pioneer tree, in many of these pockets and gullies.

The western district as a whole has a prairie climax. The postclimax nature of the shrubs and trees makes the existence of the shrub associes along the streams a temporary one. Recession may be detected, however, only with the aid of exact experimental methods. *Symphoricarpos orbiculatus, S. occidentalis,* and *Rhus glabra* are dominants. The list of shrubs of ecological importance in this district is somewhat reduced compared with that for the southeastern district. Besides the dominants, important species found along the streams and in the canyons are as follows:

Zanthoxylum americanum
Cornus stolonifera
Euonymus atropurpureus
Ribes americanum
Rubus occidentalis
Rubus strigosus
Cornus asperifolia
Cornus baileyi
Parthenocissus quinquefolia
Cercocarpus montanus
Smilax hispida
Amelanchier humilis
Padus melanocarpa
Lepargyraea argentea
Opulaster opulifolius
Grossularia missouriensis
Toxicodendron radicans
Celastrus scandens

Vitis vulpina	Ceanothus americanus
Sambucus canadensis	Ceanothus ovatus
Amorpha fruticosa	Rosa pratincola
Prunus americana	Amorpha canescens

The dominants of the southeastern district are *Corylus americana, Symphoricarpos orbiculatus,* and *Rhus glabra.* The place of each of these in the succession has already been discussed. The greater rainfall and lower evaporation have likewise been pointed out (Figs. 3 and 12). Owing to the more mesophytic conditions and the introduction from the Missouri forests of several additional species, the chaparral is much better developed in this district than elsewhere. Most of the new species are of the shade tolerant type. They are more closely associated with the forests beyond which, making contact with the grasses, are the more xerophytic, less tolerant *Symphoricarpos* and *Rhus.* All of the dominant and secondary species listed for the shrub associes (page 41) are of ecological importance in this district except the western species, viz.: *Lepargyraea argentea, Amelanchier humilis, Opulaster opulifolius, Padus melanocarpa,* and *Cercocarpus montanus.*

QUERCUS MACROCARPA-HICORIA CORDIFORMIS ASSOCIES

The most xerophytic forest associes in eastern Nebraska is *Quercus macrocarpa-Hicoria cordiformis.* In the succession it follows the shrub associes and in the more mesophytic situations is, in turn, replaced by *Quercus velutina* and *Hicoria ovata.* It is found along the Missouri river in the more xerophytic situations and also extends out along the tributaries beyond the boundary of the area studied (Fig. 13). This associes is not continuous along any of the streams to great distances. Breaks occur where cuttings have been made for timber or the land cleared for farming and where edaphic or climatic conditions are such as to favor more mesophytic types of woodland. In the distributional maps the original location of the associes is shown as nearly as possible and no account is taken of the disturbances mentioned.

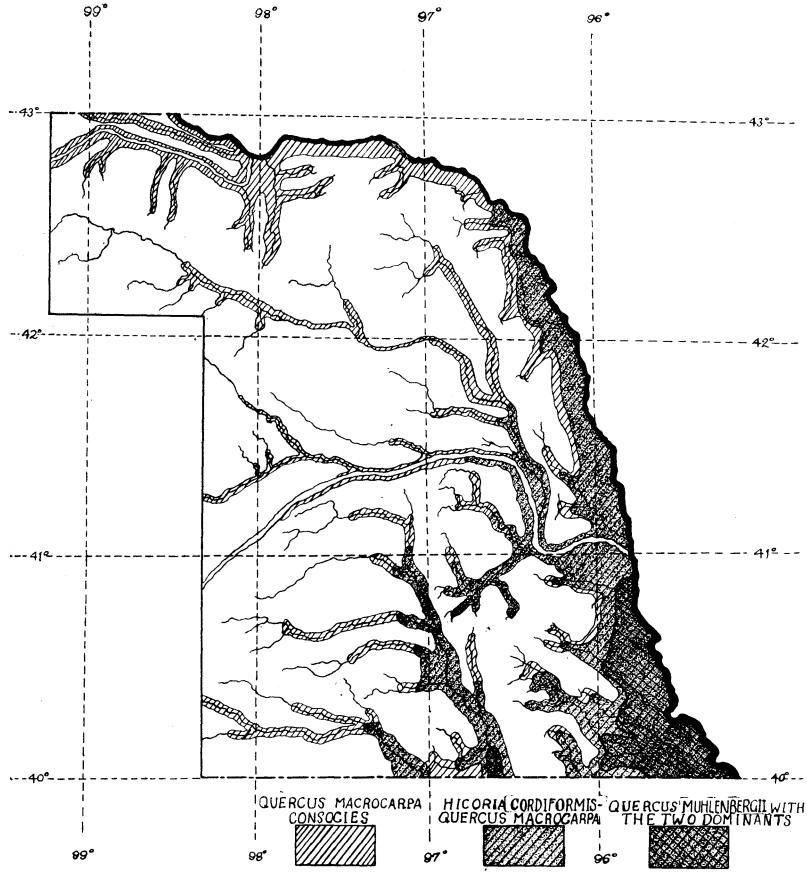

FIGURE 13. Map showing the distribution of the *Quercus macrocarpa-Hicoria cordiformis* associes. The distribution of a nearly ecologically equivalent species, *Quercus muhlenbergii*, is also shown.

Dominants (Consocies)

Quercus macrocarpa	Hicoria cordiformis

Subdominants

Trees

Quercus maxima	Hicoria ovata
Tilia americana	Quercus muhlenbergii
Quercus velutina	Cercis canadensis

Padus virginiana
Juglans nigra
Ulmus fulva
Ulmus americana
Fraxinus pennsylvanica
Celtis occidentalis
Gleditsia triacanthos
Crataegus mollis
Morus rubra
Malus ioensis
Juniperus virginiana

Shrubs

Corylus americana
Zanthoxylum americanum
Rhamnus lanceolata
Cornus stolonifera
Cornus amomum
Amelanchier canadensis
Euonymus atropurpureus
Rubus strigosus
Rubus occidentalis
Cornus asperifolia
Parthenocissus quinquefolia
Grossularia missouriensis
Smilax hispida
Rosa setigera
Toxicodendron radicans
Celastrus scandens
Vitis vulpina
Symphoricarpos orbiculatus
Symphoricarpos occidentalis
Prunus americana
Rhus glabra

The dominants of this associes are fairly well adapted to the climate of eastern Nebraska. *Quercus macrocarpa* at the center of its range in southern Indiana and Illinois attains a height of 170 feet and a trunk diameter of 7 feet. Here it is associated with *Quercus bicolor, Ulmus fulva, U. americana,* and *Celtis occidentalis* on rich bottom lands. It is tolerant, however, to much less favorable climatic conditions. In the better protected localities of southeastern Nebraska it grows to a height of 85 feet and attains a diameter of 30 inches. The age of a tree of this size varies according to the habitat but the average is about 100 years.

Bur oak is also found surviving under conditions which would seem too severe for tree growth. In poorly protected situations along the smaller streams in the western part of the area many communities of bur oak are making a "last stand" against the rigors of a prairie climate. A community of this kind may be found on the upland bordering the Elkhorn river about 6 miles southeast of Norfolk. Bur

oak cannot grow on the low sandhills on the south side of the river. But on the north side in a soil with higher water content a shallow ravine is filled with small, scrubby bur oak. Table 6 gives the size and the age of four of the smaller specimens, selected at random, in this locality and four found in contact with the prairie near transect 10. They are contrasted with the size and age of four of the most rapidly growing bur oaks in the vicinity of Rulo in the southeastern corner of the state. These data show the ability of the bur oak to grow under very diverse conditions. It may grow an inch in diameter in only 2.5 years or, if the environment is extremely unfavorable, the same diameter growth may require 12 years.

The bur oak in Nebraska is a sturdy tree with large branches and stout, somewhat sparse branchlets. In close stands the trees are irregular in shape and have fewer and smaller branches. Isolated trees develop a more rounded top and produce more shade. The bark on large trees is about 1.5 inches thick, deeply furrowed and grayish-brown in color. The large acorns are produced in abundance. Its distribution along practically all of the larger streams of the state is attributed to the fact that the fruits are carried and stored for food by squirrels and other animals. The roots of the bur oak are deep and widely spreading thus coming in contact with large volumes of soil. This characteristic makes ecesis possible in a soil which has very little more moisture than that of true prairie.

Hicoria cordiformis, like the oak, has the center of its range in southern Indiana, which is somewhat west of that of the deciduous forest complex. It is a good pioneer tree because of its means of distribution, a thin-shelled nut, which although bitter, is used as food by several rodents. This species has a much smaller range in the state than does the bur oak, a fact due, in part, to its lesser tolerance to unfavorable conditions and in part to a fungus disease which causes the death of the trees after they have become fully established and often fully grown. Near Lincoln, for example,

TABLE 6.—*Variation in rate of growth of bur oak*

Criteria	Poorly protected gullies								Protected ravines				Mesophytic situation			
	Norfolk				Bristow				Bristow				Rulo			
Height, feet	2	4	3	7	12	10	12	3	15	18	18	22	70	60	60	65
Diameter, inches	1.5	2.5	1.7	3.5	2.5	2.5	3	1	4	5	6	6	30	17	24	26
Age, years	20	32	26	28	28	30	33	17	32	38	40	36	85	50	60	80
Number of years for 1 inch growth	13	13	15	8	11	12	11	17	8	7.5	6.5	6	2.5	3	2.5	3
Average No. years for 1 inch growth	12.25				12.75				7.0				2.75			

bitternut hickory trees have practically disappeared from the bur oak-bitternut hickory community on the flood-plain of Salt creek. The hickory does not seem able to reduce its size and live as a shrub at the border of its range to a degree equal to that of the bur oak.

The typical bur oak-bitternut hickory community is made up of a somewhat sparse stand of trees. The bur oak outnumbers the bitternut hickory about three to one. The height of the hickory trees in a typical community is about 35 feet, but varies from 20 to 70 feet, depending upon the location in the area, the amount of protection, and water content.

The bitternut hickory is usually a more slender tree than the bur oak and slightly taller. Nor are its branches as long as those of the bur oak. The lower ones occur at a height of 12 to 18 feet from the ground. The sparse arrangement of the branches enables the light to enter to such an extent that light values are high, averaging about 10 per cent of noonday illumination compared to 3.5 in the black oak-shagbark hickory community and 1.1 per cent among the red oak and linden.

The diameter of bur oaks in the typical community is 6 to 14 inches, that of the bitternut hickory, 4 to 10 inches. The average in several quadrats (100 by 100 feet) of typical bur oak-bitternut hickory gave 48 of the former and 15 of the latter per unit area. The average diameter of the trees in these quadrats was 9 and 5 inches respectively.

Of the secondary species *Quercus muhlenbergii* is most nearly the ecological equivalent of the dominants. The remainder is made up of flood-plain species which have migrated to the upland, and of members of other associes.

In the mesophytic southeastern corner of the area the bur oak-bitternut hickory community is found only on the more xerophytic hilltops and southwestern slopes. It lies in close contact with the chaparral. Invasion of the bur oak and bitternut hickory into the chaparral in this part of the state is possible where the chaparral has obtained a good foothold

in subclimax prairie. The hickory follows the bur oak in this advance. *Corylus americana, Zanthoxylum americanum, Amelanchier canadensis, Rubus strigosus, Grossularia missouriensis,* and similar mesophytic shrubs afford the necessary protection for the development of xerophytic trees. Under conditions of this kind the typical bur oak-bitternut hickory community develops. As it approaches maturity the shrubs are reduced in size and number but all members of the shrub associes listed for this community (page 41) can grow under this sparse forest cover. Openings among the trees are soon occupied by the suppressed shrubs which respond quickly to the increased light and moisture.

The bur oak consocies is far more extensive than that of the bitternut hickory. Not only does it frequently occupy rather extensive areas in the south and east but extends far beyond the range of the hickory which drops out along the Missouri near Maskell (transect 8), near Firth along the Big Nemaha, near Palmyra along the Little Nemaha, at Elmwood along the Weeping Water, and at Morse Bluffs along the Platte (Figs. 1 and 13). Beyond the range of its codominant it covers the more xerophytic upland areas westward and extends beyond the boundaries of the area under consideration. The individual trees become smaller westward along the streams. The relation of this consocies to chaparral has already been pointed out. Scrubby bur oaks are common in ravines near the source of many small streams. These scrubby specimens are often many years old.

The bur oak consocies is also found on the flood-plains of smaller streams throughout the area. In the western part it is also able to compete with the flood-plain species along the larger streams as the upper Missouri, the Platte, the Elkhorn, the Niobrara, and the Blue rivers.

QUERCUS VELUTINA-HICORIA OVATA ASSOCIES

This associes occupies areas in southeastern Nebraska which are midway in mesophytism between the *Quercus macrocarpa-Hicoria cordiformis* and the *Quercus maxima-*

Tilia americana associes. It is not as widely distributed as are the other two (Fig. 14) nor is it as important within the area of its distribution. The map shows the extreme location of the associes but not its continuous distribution. Cutting has been so extensive that at the present time there are comparatively few black oak-shagbark hickory communities in the state.

Along the larger streams in the southeastern corner, where the communities, responding to differences in water content,

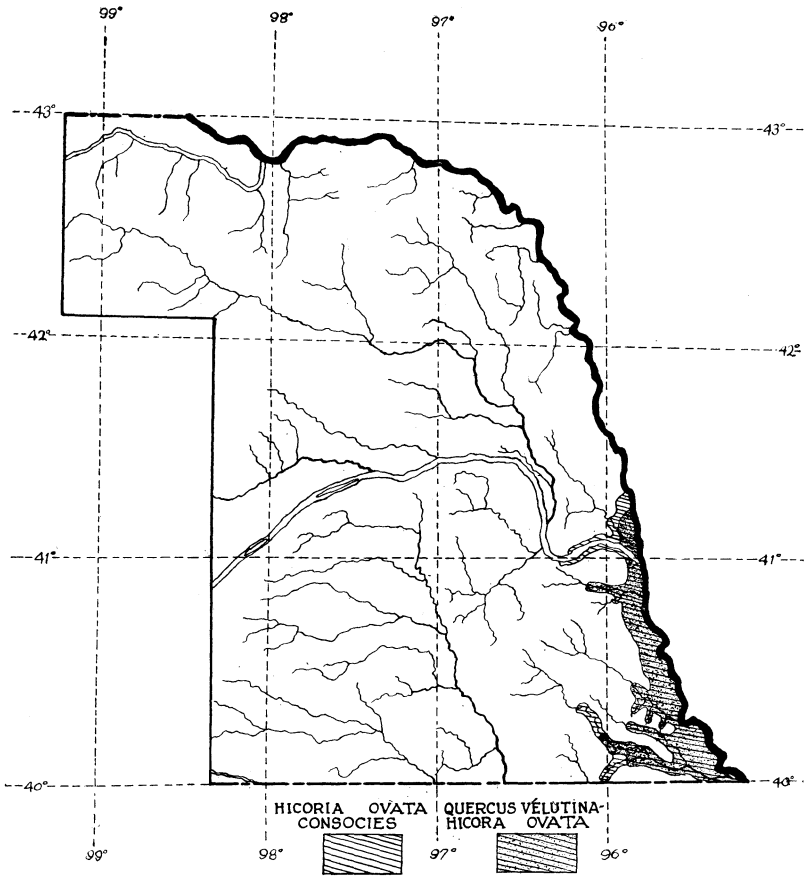

FIGURE 14. Map showing the distribution of the *Quercus velutina-Hicoria ovata* associes.

form zones on the hillsides, the zone of black oak and shagbark hickory occurs above that of red oak-linden on better drained slopes. There is a tendency, where these slopes are gentle and quite extensive, for the two species to be separated; the shagbark hickory on the upper, drier part of the slope and the black oak on the lower part.

The more important subdominant tree species are *Quercus muhlenbergii, Gymnocladus dioica, Tilia americana,* and *Quercus maxima.* There is no true shrub layer. The following species are frequently found under the trees but they are very sparse and are poorly developed: *Zanthoxylum americanum, Lonicera dioica, Rubus allegheniensis, Euonymus atropurpureus, Grossularia missouriensis, Rubus occidentalis, R. strigosus, Rosa setigera, Parthenocissus quinquefolia, Cornus stolonifera, Staphylea trifolia,* and *Smilax hispida.* More often, however, almost pure stands of one or both of the dominants occur. At the border of the range of the associes where the zoning is not distinct, many species from the bur oak-bitternut hickory and the red oak-linden communities are found within the black oak-shagbark hickory associes.

Quercus velutina attains its greatest size in the valley of the lower Ohio river. Here trees 70 to 100 feet high and 3 to 4 feet in diameter are found. It is less mesophytic than the red and white oaks. In southeastern Nebraska the black oak rarely exceeds 75 feet in height and 20 inches in diameter. The age of a tree of this type averages 100 years. The typical community is made up of trees about a foot in diameter, mostly 35 to 50 feet in height and growing about 10 to 15 feet apart. An area 100 by 100 feet contains an average of 60 trees. A narrow open crown is formed of slender somewhat spreading branches. Old, pioneer specimens, growing on the upper slopes with the bur oak, are short and have many crooked branches and roughened bark (Plate 17). Since the black oak follows the bur oak in the succession, it is not found in pioneer situations in as close contact with the grasses as is the latter. The black oak accom-

panies the bur oak and bitternut hickory along the Missouri river and its tributaries, growing in situations where the light and moisture conditions have been made suitable by the growth of these species.

Hicoria ovata is a tall forest tree with a straight, columnar trunk. The bark, which exfoliates in long, hard, plate-like strips hanging attached at the upper end, gives it the appearance of shagginess. In the lower Ohio valley it grows to be 100 feet high and is often free from branches to more than half of this distance. This is especially true when growing in close stands as is the habit of the species.

The height of the best developed shagbark hickory trees in the area is about 70 feet and the diameter of the individuals 12 inches. Under more xerophytic conditions they may not exceed 35 or 40 feet. The typical shagbark hickory consocies is composed of a pure stand of closely growing trees (Plate 6A). In a community with a height of 60 feet, the lowest branches are 30 to 40 feet from the ground. As the height of the entire forest increases, the lower branches die and become broken. An average quadrat (100 by 100 feet) contains about 80 trees. The density of the upper crown produces a canopy effect under which a sparse layer of shrubs may grow. Light averages 3.5 per cent as compared with 10 per cent under the bur oak. Smaller trees in more scattered stands may be seen advancing into the bur oak with the bitternut hickory but the shagbark hickory remains far behind the bur oak in its advance into the chaparral. This slow advance is not due to poor distribution because the hickory nuts are readily eaten by rodents or stored in large numbers. Instead it must be due to the factors affecting ecesis.

QUERCUS MAXIMA-TILIA AMERICANA ASSOCIATION

The climax forest of the region is that dominated by the red oak and the linden. It clothes the best protected slopes and ravines along the rivers in the eastern part of the state and in the southeast all of the lower slopes and the north exposures of higher ones (Plates 3, 6B, 7B, 8, and 9). Pro-

ceeding north and west, soil and air moisture is so reduced that at the extreme limit of its range, this climax vegetation covers only the foot of north slopes.

The climax forest has a very mesophytic aspect in comparison with the other forest communities. It has the highest water content of soil, the highest humidity and lowest evaporation, and the lowest light intensity. Light readings averaged 1.1 per cent at noonday as compared with 3.5 per cent in the black oak-shagbark hickory, and 10 per cent in the bur oak-bitternut hickory. A comparison of soil temperatures during the day at different periods in the various communities gave the following averages in degrees Fahrenheit: prairie 76.9, shrub 73.8, bur oak 70.2, black oak-shagbark hickory 69.6, and red oak-linden 68.6. Air temperatures, taken at the surface of the soil, gave the following daily averages: prairie 95.6, shrub 82.5, bur oak 75.4, black oak-shagbark hickory 73.9, and red oak-linden 72.2.

The stand is not so dense as in the shagbark hickory community but the increased size of the trees and the closed canopy contribute to make a much better protected community and one in which the dominants of the preceding associes cannot thrive. The ironwood, *Ostrya virginiana,* is a rather constant component, but because of its small stature it is a subdominant under the red oak and linden. The average stand in a typical area of 100 by 100 feet is 28 linden (6-16 inches in diameter), 22 red oak (8-14 inches in diameter), and 25 ironwood (2-6 inches in diameter). Where the stand is densest there are no shrubs but a few of the more mesophytic shrubs are usually found scattered throughout. There is, however, no distinct shrub layer as in the better lighted communities preceding it in the successional sequence, and even the herbaceous layer is mostly prevernal and vernal. In the southeast, where the forest canopy is best developed and densest the following are found: *Lonicera dioica, Rubus occidentalis, Zanthoxylum americanum, Parthenocissus quinquefolia,* and *Rosa setigera.* But along the upper Missouri, beyond the range of the red oak, most of the shrubs listed for

the northeastern district occur under the linden and ironwood.

The number of tree species of this association is much greater toward the southeast. The following are of ecological importance:

Dominants (Consociations)	
Quercus maxima	Tilia americana
Subdominants	
Ostrya virginiana	Gymnocladus dioica
Asimina triloba	Aesculus glabra
Quercus velutina	Padus virginiana
Hicoria ovata	Cercis canadensis
Hicoria cordiformis	Juglans nigra
Quercus muhlenbergii	Ulmus americana
Quercus macrocarpa	Ulmus fulva
Fraxinus pennsylvanica	Celtis occidentalis

The red oak extends up the Missouri river to transect 8 (Fig. 1) and the linden occurs along both the Missouri and the Niobrara far beyond the area investigated. The farthest westward extent of red oak is about 40 miles along the Big Nemaha and the Platte, but the linden is found farther west on these streams and also along the Blue rivers and their larger tributaries (Fig. 15). Where the two are associated, the linden occurs on the lower slopes which are of higher water content and the red oak is found in the better drained areas. Although there is a considerable mingling of the two dominants the lines of demarcation are often quite distinct. It is of interest to note that in the southeast the mesophytic linden on moist, rich slopes is widely separated from the drier habitat of the bur oak usually by a zone of oaks and hickory of intermediate water relations. Just as it is possible for the bur oak to find sufficient water in sheltered ravines and bluffs even in the far north, so too the lower slopes of the bluffs afford a suitable site for the growth of linden. Slopes of intermediate mesophytism do not occur and the other oaks

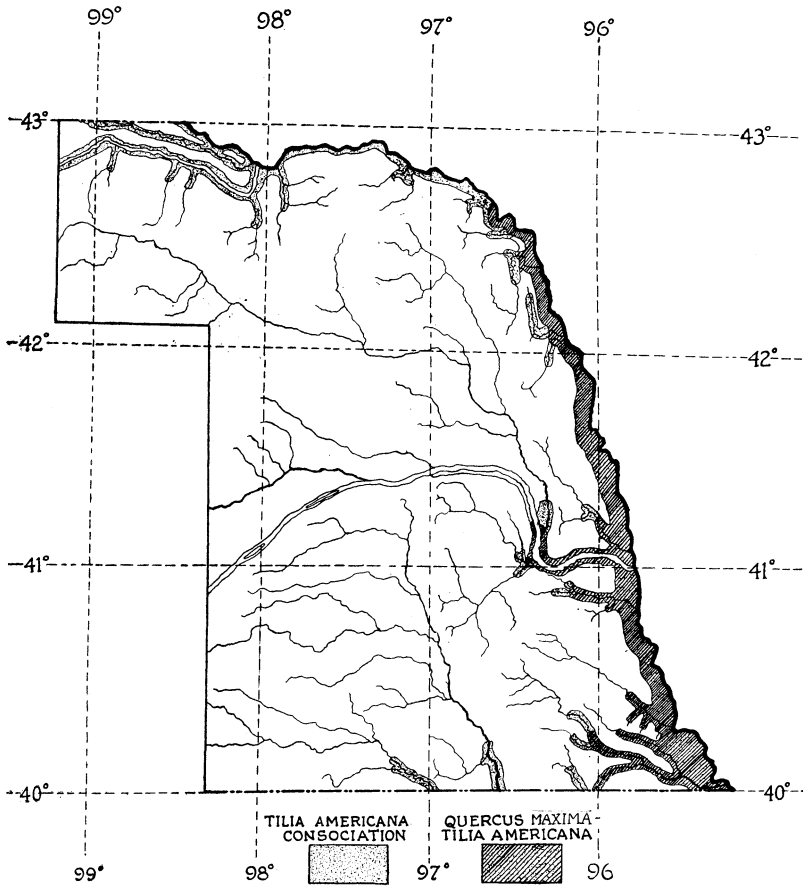

FIGURE 15. Map showing the distribution of the *Quercus maxima-Tilia americana* association.

and hickories are excluded. The bur oak thus grows in juxtaposition to the linden, both finding growth conditions less favorable than farther southward and their ranges within a given area are very limited.

Quercus maxima in the valley of the Ohio river grows to a height of more than 100 feet and has a trunk diameter of 3.5 feet. It is a hardy tree, growing farther northward than any other oak and farther westward than any except the bur

oak. In close stands it has a somewhat narrow, rounded top but when growing alone the branches are usually at right angles to the trunk and the crown is broader. The bark on young stems and on the upper part of the limbs of large trees is smooth and light gray in color. On the older trunks it is about an inch thick and grayish brown tinged with red. It is divided into appressed plates. In Nebraska, near the limit of its western range, it is much reduced in size. The heights of the larger trees range from about 75 feet in transect 1 to about 28 feet in transect 8 and in trunk diameter from 24 inches to 8 inches in the two transects respectively.

Tilia americana is a little less than 100 feet tall in the center of its range with a trunk diameter of 3 to 4 feet. Its greatest size in Nebraska varies from about 80 feet in height and 33 inches in diameter in transect 1 to a height of about 22 feet and a diameter of 8 inches in transect 10. The crown is broad and rounded but in close stands it adapts itself to less space and becomes taller and more columnar. The branches are small, weak, and often pendulous. The bark is light grayish brown and about an inch thick near the base of the trunk.

Ostrya virginiana is a subdominant of importance because of its association with the dominants in the red oak-linden associes. It would probably be a dominant except for its small size. In Nebraska its greatest height is about 30 feet and its greatest diameter about 10 inches. Its average height throughout the area is about 18 feet and it has an average diameter of about 4 inches. Unlike the two dominants, it is not reduced in size northward along the Missouri, but rather it becomes a little larger due to better lighting resulting from the reduced size of the linden and the gradual disappearance of the red oak. It is closely associated with the linden both along the Missouri and the Niobrara. It occurs along the Niobrara, beyond the range of the linden, and, in fact, extends into the Black Hills. From transect 8 to the South Dakota line, it might be said to dominate the climax com-

munity together with the linden which here it practically equals in size and number.

Secondary species are of very little importance in this association because of their limited number. *Aesculus glabra* is not found beyond transect 2. *Asimina triloba* and *Quercus muhlenbergii* do not occur beyond transect 3, and *Q. velutina, Hicoria ovata,* and *Fraxinus americana* are not found above transect 5. Of the tree species listed, ironwood alone is tolerant enough to grow in a dense stand of red oak and linden.

In the area along the Missouri river covered by transects 6 to 10, ironwood is the chief secondary species. Bur oak increases in importance in the upper transects due to the disappearance of other species except in the most favorable sites. The Kentucky coffee tree (*Gymnocladus dioica*) is also of some importance. Above transect 5 there are only 4 upland secondary species of any ecological significance, viz.: ironwood, Kentucky coffee tree, bitternut hickory, and bur oak. Species of flood-plain trees migrate up the slopes in the upper transects and take their place among the upland trees on the bordering bluffs. This is especially true above transect 8 in the linden consociation.

FRAXINUS PENNSYLVANICA-ULMUS AMERICANA ASSOCIES

The flood-plain forest associes is represented along all of the streams of the state. The development of this associes has been studied along typical streams in the eastern part of the area by Weaver, Hanson, and Aikman (1925). The stages in the development of the flood-plain are practically the same throughout the area.

The first stage in development is seen where the prairie slopes gently to form a broad valley and in the lower part of which an intermittent stream runs and furnishes enough moisture to support growth of trees. Here, isolated individuals of *Salix nigra, Salix amygdaloides,* and *Populus deltoides* are found. Small groups of all of these species may occur at intervals but the black willow predominates. Usually there are no shrubs in this early stage although *Amorpha*

fruticosa and *Sambucus canadensis* soon appear. When the stream begins to cut a channel, protected banks or low areas in its meandering course afford sufficient moisture for the growth of *Symphoricarpos orbiculatus, S. occidentalis,* and *Prunus americana.*

In the next stage of development *Acer negundo* appears with willows and cottonwood. The stream is no longer intermittent and is usually from 1 to 10 feet wide and has a width of 15 to 50 feet between sloping banks and at least the beginnings of a flood-plain. The trees often spread from the stream banks onto the flood-plain for a distance of a few yards. Shrubs grow along the banks and on the flood-plain beyond the trees. The shrub dominants are *Symphoricarpos orbiculatus* and *S. occidentalis.* Other shrubs and lianas associated with these are *Rubus occidentalis, R. strigosus, Cornus asperifolia, Rhamnus lanceolata, Vitis vulpina, Celastrus scandens, Smilax hispida,* and *Toxicodendron radicans.* In low places on the banks of the stream *Sambucus canadensis* and *Amorpha fruticosa* are found. *Rhus glabra* and *Prunus americana* fringe the flood-plain forest and extend into the prairie. In the western and northern parts of the area the vegetation along most of the small streams is in this stage of development.

A third stage in development is found along small streams in the eastern part of the area and in better protected situations in the western part where *Ulmus americana, U. fulva,* and *Fraxinus pennsylvanica* are the dominants. As they increase in number and size the willows first disappear and are followed by the cottonwood and boxelder. Subdominants associated with the elm and ash are *Platanus occidentalis, Acer saccharinum, Padus virginiana,* and *Celtis occidentalis.* At Fremont and a few other points along the Platte river, red cedar (*Juniperus virginiana*) has invaded the lower flood-plain and islands in the river. They have followed a poor development of the willow-cottonwood stage (Plate 12A). Light relations are not so good for the development of shrubs as in the open flood-plain but the mesophytic growth condi-

tions more than overbalance this factor. *Grossularia missouriensis* is the most typical flood-plain shrub. In addition to those listed above, the following are typical on the flood-plains: *Zanthoxylum americanum, Cornus stolonifera, Rubus allegheniensis,* and *Parthenocissus quinquefolia.*

The flood-plain associes reaches its best development along the larger streams in the southeastern part of the area. Black walnut (*Juglans nigra*) takes its place as a dominant with the red and white elms and green ash. Since the shade is denser, fewer of the less tolerant species are found. The individual trees are much larger and in every way the flood-plain forest is better developed. Secondary species are *Fraxinus americana, Padus virginiana, Gymnocladus dioica, Aesculus glabra, Celtis occidentalis,* and *Platanus occidentalis.* The shrub layer is not as prominent as in the previous stage because of the reduced light. In addition to the species listed, *Corylus americana* and *Cornus amomum* are sparingly found.

The flood-plain may finally be built up to a place where the soil becomes sufficiently well drained and aerated to permit the growth of the climax dominants. When flooding ceases, the accumulation of forest litter adds year by year to the richness and water-holding capacity of the soil and also improves its structure. The advance of red oak and especially of linden into such areas has been repeatedly observed and sufficiently studied to show the trend of development towards this climax.

CORRELATION OF VEGETATION WITH ENVIRONMENT

The vegetation of the area is mostly grassland with forests principally along the streams. The forests decrease in mesophytism northward and westward. The subclimax nature of a small portion of the grassland bordering the Missouri in the southeast has been shown. Trees and shrubs are advancing into the prairie in this area, since the cessation of prairie fires. A study of the factors and of the vegetation beyond this narrow strip of potential forest land, however,

shows that the climatic climax is true prairie. Forests bordering the streams in true prairie are postclimax; they forecast the general advance of woodland should the climate become wetter, but hold their present place only because of the locally more moist habitat due to the presence of the streams. The tension line between the woodland along the streams and the prairie is not stationary. Fires, cuttings, protective plantings, and cycles of climatic variations tend to change its position.

The most important factor influencing the development of forest communities in Nebraska is water content of soil. The amount of soil water in turn depends upon precipitation, drainage, and soil structure. Humidity, which is modified by both temperature and wind movement, is also important, and within the community the factor of light. All data on water content are in agreement that available soil moisture in the different plant communities increases directly with the order of development, i.e., chaparral, bur oak-bitternut hickory, black oak-shagbark hickory, and red oak-linden. In the prairie, soil moisture, especially in the surface layers, is frequently reduced almost or quite to the point of non-availability for plant growth. Since soil moisture is directly dependent upon precipitation, the rainfall is extremely important. There is, for example, a direct correlation between the rainfall at Nehawka and Bristow and the soil moisture of the prairie at the two stations. Both are lower northward. Drainage has a marked influence on the amount of soil moisture. Steep slopes along the streams increase the run-off but in most cases the amount is much reduced by the forest cover which intercepts the rain and by the humus covering of the soil under the trees which retards surface water movement. Shrubs are especially effective in reducing run-off and preventing erosion on the sides of ravines and gullies.

The composition of the soil usually favors mesophytic vegetation in the southeastern part of the area and more xerophytic types in the west and northwest. This is due to

the fact that the soils formed from the glacial material exposed in the southeast are quite heavy and have a higher content of clay than the finer-grained but more porous loess soils to the west and northwest. Water content in the southeast is usually sufficient to produce a mesophytic forest association of red oak and linden. As the soil moisture decreases less mesophytic communities occur. From east to west the transition is more rapid than from south to northwest along the Missouri river.

Just as the amount of available moisture determines in a large measure the rate of absorption, so too the humidity of the air has a pronounced effect upon transpiration. In general the humidity is greater in the area of higher rainfall and maximum water content of soil, all of which decrease northward and westward.

The course of evaporation shows great variation from year to year but it is often high during periods in spring or early summer. During the summer of 1924, for example, evaporation was extremely high at the beginning of the season and again near its close. The occurrence of high evaporation during the important foresummer is very significant. Woodland species have great difficulty in establishing themselves in the border of the prairie under such conditions. In 1926, conditions for ecesis in the prairie were even more unfavorable. Evaporation was very high with a daily maximum of 73 c.c. in the prairie at Bristow during the first week in June. A second period of high evaporation throughout the area occurred in the middle of July. The extreme xerophytism of the northeastern part of the state and the inability of trees and shrubs to invade the hilltops bordering the river may be understood when these high evaporation rates are taken into account. Evaporation during 1917 (Pool, Weaver, and Jean) was even greater than in 1924 and 1926. In every case the evaporation was much less in the southeast than in the northwest. This increase in the dryness of the air and the frequent lack of available water in the areas westward and northward in contrast to the lower evaporation combined

with moist soils in the southeast explain the presence of the red oak-linden and the black oak-shagbark hickory forest in the latter locality and their absence in the drier areas.

The wind is an important factor in increasing transpiration and evaporation. It is especially strong during the early spring but the hot winds of summer are more effective in lowering the humidity and drying the vegetation. Probably no other factor, aside from water content, has so much to do with limiting tree and shrub growth as the disastrous effects of hot, southwest winds. Even where soil moisture is sufficient for the growth of plants under ordinary conditions, hot winds increase the rate of transpiration to such a degree that death may result. Wind is also an important factor in the dispersal of the seeds of woodland plants. The distribution of all species of trees in Nebraska has probably been affected somewhat by wind. Fifteen important trees of the area, including such pioneers as the willows, boxelder, cottonwood, ashes, and elms, have modifications for dispersal by wind. Carriage by wind of the linden has been very favorable to its wide distribution. The effect of topography and resulting protection from the drying effect of the wind is shown by the well developed vegetation on the bluffs of the Missouri river and in many similar places along its tributaries.

The temperature of eastern Nebraska is lower than that at the center of the deciduous forest. The area in Nebraska lies between the isotherms of 47° and 53° F. but the forest area of southern Ohio, northern Kentucky, and West Virginia lies between the isotherms of 53° and 58° F. Temperature as such appears to be a rather unimportant factor in distribution of species in Nebraska. Moisture is of much greater importance. This is illustrated elsewhere by the fact that southern species such as *Magnolia acuminata* and *Liriodendron tulipifera* extend to Lake Erie (Hough, 1907; Sargent, 1922) in the east where moisture conditions are favorable but range no farther than southeastern Missouri since moisture conditions westward are not favorable to growth. The length of the frost-free season, 180 days in the southeast and 150 days

in the northeast, however, is a factor in the establishment of species. Seedlings in the northern part of the area germinate later and have a much shorter time for establishment and consequently have less chance of living through the first winter. It clearly seems that moisture and not temperature is the limiting factor to the westward extension of such trees as bitternut and shagbark hickory, black walnut, red, black, and yellow oaks, and many other trees and shrubs since they are found in much colder climates in eastern North America where soil water is abundant. The following species extend as far northward in Nebraska as they do farther eastward: *Asimina triloba, Cercis canadensis, Gymnocladus dioica, Aesculus glabra,* and *Rhamnus caroliniana.* It may be that both low temperature and low water content contribute in limiting their range.

Fire has been important in limiting distribution of forests in the state. Within the memory of early settlers, red oak and linden have migrated up the Weeping Water and the Nemahas and replaced the chaparral and scrubby bur oaks. Several tracts within the area delimited as potential forest, which are known to have been subclimax prairie fifty years ago, are now covered with a good growth of bur oak and hickory. The comparative absence of fire during the last half century has contributed much to the present development of forests in Nebraska. On the other hand, there has been constant cutting of timber during this period. Most of the flood-plains of the Missouri and its tributaries have been cleared for farming. Furthermore, drainage projects along many of the streams have made the entire flood-plain, to the very edge of the old channel, suitable for farming and have entirely eliminated the flood-plain forest. The clearings have spread to the upland until there are in many places practically no upland forests remaining except in sheltered ravines and on other rough land unsuitable for farming. The distance between these remnants of the deciduous forest makes migration difficult and uncertain.

The rate of growth of forest trees in different parts of the

area furnishes data which are important in attempting to correlate the development of vegetation with the environment. For this purpose upland and flood-plain species, growing naturally in the several localities, were used. *Populus deltoides* was also studied where it had been grown on the upland. This species has been especially useful since it is generally grown throughout the entire area.

The rate of growth of bur oak in six transects along the Missouri river is shown in Table 7. The most favorable upland site in each transect was selected and the average rate of growth of 20 typical trees was taken in each.

TABLE 7.—*Variation in rate of growth of Quercus macrocarpa in six transects along the Missouri river*

Criteria	I	III	V	VIII	IX	X
Ave. height of trees, ft.	70	55	45	35	25	18
Ave. diam. of 6 largest trees	28	20	16	14	11	8
No. of yrs. for 1 in. diam. growth	3.9	4.4	5.0	5.8	6.7	7.5

In transect 1, near the Kansas state line, it required about 4 years for one inch of growth. This period increased to 7.5 years in transect 10 near the South Dakota state line. This decrease indicates the effect of the total change in environment as one proceeds northward along the river. Plate 19A was made from specimens selected to show approximately these averages. It may be seen from the table that the average height of stand decreases more rapidly than does the rate of diameter growth. The small size of the trees in transect 10 indicates that the climate of the region is that of prairie. Even along the bluffs bordering the river, this most xerophytic species of tree has difficulty in growing.

Table 8 gives a summary of data on the average size and

TABLE 8.—*Average size and rate of growth of well developed trees in four transects*

Transect	1			4			7			10		
Species	Diam., inches	Ht., feet	Growth rate, Yrs. per inch	Diam., inches	Ht., feet	Growth rate, Yrs. per inch	Diam., inches	Ht., feet	Growth rate, Yrs. per inch	Diam., inches	Ht., feet	Growth rate, Yrs. per inch
Linden	16.0	70	4.5	14	55	5.0	10.0	45	5.4	8	25	5.4
Red oak	13.0	75	5.0	12	60	5.4	8.5	45	6.0			
Black oak	11.6	65	5.1									
Shagbark hickory	9.0	65	6.5	6	45	10.0						
Elm	26.0	80	2.5	21	65	2.8	16.0	50	3.6	14	45	4.2
Walnut	21.0	75	3.0	20	70	3.8	14.0	50	4.2	11	45	4.7

rate of growth of four species of the upland and of two species of the flood-plain. For each transect at least 12 typical but not the largest specimens were used. Of the species of the upland listed only the linden is found in transect 10 where it grows only in the better protected areas where conditions are not so unfavorable as to materially reduce its rate of growth. The species of the flood-plain also show less increase in rate of growth than that ascertained for bur oak. However, there is more variation in the rate of growth of the species of the flood-plain within a given transect than there is in the species of the upland, hence the results are not so definite. This is probably due to the greater variation in water content of flood-plain soils in a given situation.

It has been shown that change in plant-life conditions is much more rapid from the Missouri river westward along its several tributaries than northward along the river. On the Weeping Water creek the average rate of growth of 20 walnut trees was 1 inch each 4.3 years as compared to an inch each 3.8 years at Nehawka, 8 miles east. This rapid increase of xerophytic conditions westward along the small streams is also shown by the increase in rate of growth of the green ash. It requires 3.1 years for an increment of one inch on the flood-plain of the Missouri river and 3.7 years on the flood-plain of the Big Nemaha river near Tecumseh, about 75 miles west.

TABLE 9.—*Number of years for one inch of diameter growth in 30 specimens of cottonwood and of ash at each of four stations from the Missouri river westward*

Species	Flood-plain, Rulo	Upland, Pawnee City	Upland, Fairbury	Upland, Clay Center
Cottonwood	1.1	2.2	2.7	3.4
Green ash	3.1	5.2	6.8	7.4

The differences in plant-life conditions as indicated by the growth of cottonwoods planted on the upland is shown in Table 9 where the rate of growth of green ash is also given.

The rate is 1.1 years for one inch in diameter growth at Rulo on the flood-plain of the Missouri river as compared to 2.2 on the upland near Pawnee City, 2.7 on the upland near Fairbury, and 3.4 on the upland near Clay Center. These data on growth show the effect of the climate favorable to grasses in the western part of the area on forest trees. It may be seen that the rate of growth of the cottonwood is over 3 times as great at Rulo as at Clay Center. In the case of the ash the rate is more than twice.

SUMMARY

A study was made of the present distribution and structure of the forests of eastern Nebraska. The portion of the deciduous forest formation which extends into the state from the southeast is found mainly in this area. Forests chiefly occur along the Missouri river and its tributaries; hence most of the area involved in this study lies in the Grassland Formation. It includes about 26,000 square miles between the Missouri river on the east and northeast and approximately the 98th meridian on the west.

The soil is of transported material and does not come from the underlying rocks; it is largely glacial drift in the southeast and loess in the remainder of the area. Extensive alluvial plains include the flood-plain of the Missouri river and especially that of the Platte. The soil is fine in texture, has a high water-holding capacity, is very fertile, and usually neutral in reaction.

The elevation ranges from 850 feet in the southeast to about 2,000 feet in the northwest, hence drainage is towards the east and southeast to the Missouri river. The loess north of the Platte and the glacial drift material in the eastern part of the area southward are eroded into hills. Otherwise the surface is almost wholly flat. The valley of the Missouri river, varying in width from one-half to one and one-half

miles near the South Dakota state line and from eight to fourteen miles near the Kansas state line, is bordered on the west by rather steep and broken bluffs. Similar bluffs border many of the larger streams in part but often the broad flood-plains are merely bordered by hills.

The mean annual precipitation varies from 32.5 inches in the southeastern part of the area to 23 inches in the northwestern portion. Likewise water content of soil is higher and less variable southeastward. In the northwestern portion the entire available supply may be exhausted during periods of drougth. The growing season is 30 days shorter, temperatures are lower, and there is slightly greater temperature variation in the northern and western parts than in the southeastern. Wind velocity is also greater and humidities lower in the northwestern than in the southeastern part. Average daily evaporation ranges from 24 c.c. or less in the southeast to 33 c.c. or more in the northwest. In general the climate of the northern and western parts of the area is of the drier and more variable prairie type but that of the southeastern part is more nearly the type suitable to woodland vegetation.

There are two climax formations in the area: the Grassland Formation and the Deciduous Forest Formation. This study is chiefly concerned with the Deciduous Forest Formation, but its relation to grassland also has been taken into account. In the main, forests occur only along the Missouri river and its tributaries although in the southeast they extend several miles from the river into the uplands. The Grassland Formation bounds the forests along a transition line which lies slightly west of the Missouri river and somewhat parallel to it. Tongues of forest extend into the grassland climax, bordering the several tributaries of the Missouri river and their branches. The forests have been cut except on the rougher land but the area of potential woodland bordering the Missouri river has a width of approximately 25 miles in the extreme southeast, 5 miles in the vicinity of Omaha, but often less than one-half mile in the extreme northwestern part of the area.

Immediately bordering the streams, flood-plain communities dominated by *Fraxinus pennsylvanica* and *Ulmus americana* are well developed along the larger streams. Toward the sources of these and along smaller streams the flood-plain forest largely consists of species of *Salix* and *Populus deltoides.*

Adjoining the flood-plain, on the better protected slopes, occurs the climax forest association dominated by *Quercus maxima* and *Tilia americana.* This association is found in protected sites from the Kansas border northward along the Missouri river nearly to Sioux City. It extends back from the river about 10 miles in the south, but only about one mile in the north. Along the tributaries of the lower Missouri it extends westward for a distance of about 30 miles. The *Tilia americana* consociation extends far beyond the range of *Quercus maxima* both northwestward and westward.

The *Quercus velutina-Hicoria ovata* associes dominates areas which are slightly less mesophytic than the preceding but its extent is more limited. It does not occur farther north than Omaha and its westward distribution is slightly less than that of *Quercus maxima.*

An associes of *Quercus macrocarpa* and *Hicoria cordiformis* is found on the more xerophytic slopes and tops of hills. The northward extent of the hickory in this associes is about the same as that of the red oak but its westward extent is slightly greater. The bur-oak consocies occurs along the larger streams often far beyond the western extent of the area.

After a preliminary survey along each stream, transects about a mile wide were selected at intervals of about 8 miles. These extended across the best developed bordering woodland. Investigation of the transects disclosed the structure, extent, and environmental conditions of the forest communities.

The red oak-linden community is the most mesophytic. Here water content and humidity are highest but evaporation and light intensity are lowest. Favorable water relations make possible the growth of a dense stand of trees which are larger than those of any other community. Poor light re-

lations practically eliminate the shrubs and all but prevernal and vernal herbs. *Ostrya virginiana* is the only tree that is sufficiently tolerant of shade to make a good growth under this cover. An average stand in a typical area 100 by 100 feet consists of about 28 linden, 24 red oak, and 25 ironwood.

The typical black oak-shagbark hickory associes is intermediate in mesophytism between the red oak-linden association and the bur oak-bitternut hickory associes. It is less widely distributed and less important in the area than are the other communities. These two dominants have a tendency to form consocies, the hickory being found in the drier, higher parts of the slopes. Light relations are such as to make possible the development of a sparse layer of shrubs.

The most xerophytic forest community is the bur oak-bitternut hickory consocies. Moisture conditions are less favorable but light relations are more congenial to the growth of subdominants. Rather well developed layers of shrubs and herbs are found under the typical open stand of bur oak and bitternut hickory. The trees are usually 6 to 8 inches in diameter and about 30 to 35 feet high. There are about 48 bur oaks and 15 bitternut hickories in an area of 100 by 100 feet. This forest has direct contacts with the chaparral which the bur oak, especially, can successfully invade. The shrubs usually form an understory in the forest.

A transition zone of chaparral (*Rhus-Corylus* associes) occurs between the forests proper and the grassland. This associes borders the woodland throughout the area. It has a width varying from a few feet to one-half mile or more in gullies or where forest extension has been retarded by fires or cuttings. Although it is more extensive northward, it is represented by fewer species. Where the conditions in the grassland are in any way altered so as to considerably increase soil moisture and decrease evaporation, invasion by the chaparral is possible. Measurements in numerous chaparral and prairie areas show that the former are characterized by an increased water content, higher humidity, lower (summer) soil and air temperatures, decreased wind velocity, reduced

evaporation, and decreased light intensity. There are marked differences in plant-life conditions in the chaparral as compared to those of the forest proper although they are not so great as between the prairie and the chaparral.

Prairie fires have been an extremely important factor in the past in checking the extension of the forest over the subclimax prairie area of southeastern Nebraska and generally along stream courses. Cutting of the forest in late years has greatly limited their distribution. The effect of the climate favorable to grasses in retarding tree development has been strikingly shown by measuring the annual increment of the common species.

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