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COMPETITION STUDIES IN THE ECOTONE BETWEEN PRAIRIE AND WOODLAND

J. M. AIKMAN

The tall grass prairie forms a belt across the United States from Canada to Mexico. This belt lies between the deciduous forest on the east and the plains association on the west. It is approximately 250 miles wide except at a point slightly above the middle where it extends to about three times this width from eastern Nebraska across Iowa and northern Missouri, Illinois and Indiana into western Ohio.

The deciduous forest is represented in Iowa and in eastern Nebraska almost exclusively along stream courses. Missouri river and its tributaries have cut bluff-rimmed depressions below the wind-swept prairie level. Here soil moisture and humidity are increased to such an extent that forests develop in an otherwise prairie region.

The chief forest communities, in order of increasing mesophytism, are as follows: bur oak-bitter nut hickory (*Quercus macrocarpa*¹-*Hicoria cordiformis*) associates; black oak-shellbark hickory (*Q. velutina*-*H. ovata*) associates and red oak-linden (*Q. rubra*-*Tilia americana*) association.²

The sumac-hazel (*Rhus-Corylus*) associates borders the bur-oak forest on its more xerophytic edge. This zone of chaparral varies in width 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 coral berry (*Symphoricarpos orbiculatus*) and wolf berry (*S. occidentalis*).

Corylus americana, with other more mesophytic shrubs, grows in close proximity to forests.

Averages are taken of the factor data from several stations along lower Missouri River in Nebraska. The shrub zone as developed along the river bluffs from Omaha to the Kansas line will be considered as typical. This type will later be compared with shrub development along the upper Missouri in Nebraska.

¹ Nomenclature is according to Gray's New Manual of Botany.

² Aikman, J. M. Distribution and structure of the forests of eastern Nebraska. (In press). University (Nebraska) Studies, Lincoln, Neb.

Water content determinations showed available water in the shrub and forest stations during the growing seasons of 1924, 1926 and 1927. Several times during the three growing seasons prairie soil was reduced to near the nonavailable mark. At all times, except at the beginning of the season, water content of the soil was lower in the prairie soil than in that of the shrub and forest. Soil acidity is slightly lower in the prairie than in the forest. The following are averages of determinations at several points: prairie 7.2; shrub 7, bur oak 6.8. These changes correlate with the increase of humus in the soil as shown by the total nitrogen determinations: prairie 0.162 per cent, shrub 0.197 per cent and bur oak 0.253 per cent.

Humidity is higher in the shrub zone than in the prairie. This is caused by the greater height of vegetation in this zone and in turn reacts as protection to a more luxuriant mesophytic type of vegetation. During the warmer part of the growing season from 10 a.m. to 2 p.m. the prairie had an average air temperature of over 98 degrees Fahrenheit compared to 87.2 degrees in the chaparral and 77.5 in the bur oak associates. The differences in soil temperatures of the three stations were: prairie 79.8 degrees, shrub 74.5 degrees and bur oak 70.6 degrees. The great difference in air temperature is an important factor in the invasion of the prairie by trees and shrubs since increased temperature greatly accelerates water loss by lowering the humidity. Wind as a factor in the development of the shrub zone is also important principally as it increases evaporation. At three inches above the ground Keuffel and Esser hand anemometers gave readings of 22 feet per second in the prairie, 14 feet per second in the sumac-coral berry shrub and 2.5 feet in the bur oak. These are averages of results taken in many situations. Average daily evaporation from standardized atmometer cups was 14.1 c.c. in the prairie, 11.2 c.c. in the hazel shrub, 10.2 c.c. in the bur oak and 8.2 c.c. in the red oak. Less complete data from other stations indicate a greater difference between evaporation of the prairie and the shrub communities.

Light is an important factor in forest development. In the tension zone between the woodland and the prairie, the shading of the grasses is one of the outstanding features of the invasion of the grassland by the shrubs. Light intensities in different shrub communities vary with the density of the canopy. The average illumination at noonday in the upland prairie was 56 per cent as compared to only 27.5 per cent in the *Rhus-Symphoricarpos* shrub. It was 10 per cent in an average bur oak community. Such a strik-

ing difference explains the reason for the elimination of prairie species under the cover of an invading shrub.

Within the shrub zone 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 rocky hills; species of *Symphoricarpos* usually gain dominance in less exposed situations and *Corylus americana* is the least xerophytic of all. This is shown by their zonal distribution where the three species are found in common, by the relative distances they extend from the protection of the forest and especially by their behavior in post-climax areas. Sumac is the first to disappear before the invading hazelnut and is followed by the coral berry which is somewhat more tolerant. Where hazelnut has become fully established, light values are too low for these other shrubs to carry on sufficient photosynthesis to maintain life. There is also intense root competition.

These three shrubs invade the grassland both by rhizomes and seeds. *Symphoricarpos* also invades, but usually ineffectively, by stolons. The measurement from year to year of clumps formed from isolated shrub seedlings gives interesting data on the advance of shrubs into the grassland. The area covered by such clumps is increased from 10 to 50 per cent in a period of three to five years.³ Mass invasion at a level above most of the prairie grasses is most effective. The area dominated extends one to two feet beyond that which the stems of the clump occupy due to the shade cast by the plants leaning far out toward the light.

In this shaded area, prairie grasses first cease to form seed and later disappear. Root competition seems to favor the shrubs because of their more widespread root systems and the increased absorbing efficiency of their roots. Blue grass (*Poa pratensis*) can grow for a time in this disturbed area. As new plants invade this marginal territory, a thick mulch of leaves together with the increased shade causes the disappearance of the blue grass. The invasion of the shrubs is followed by the bur oak, under the shade of which the more tolerant shrubs can survive.

This advance is taking place only in the subclimax prairie. Extensive planting experiments at Lincoln, Nebraska, have shown that trees cannot successfully invade the true prairies.

The following is a list of important species of the shrub associates in southeastern Nebraska in order of decreasing tolerance and mesophytism.

³ Clements, F. E., J. E. Weaver and H. C. Hanson. Carnegie Inst. Wash. Pub. (In press).

<i>Corylus americana</i>	<i>Psedera quinquefolia</i>
<i>Lonicera dioica</i>	<i>Ribes gracile</i>
<i>Lonicera glaucescens</i>	<i>Symphoricarpos orbiculatus</i>
<i>Rubus allegheniensis</i>	<i>Smilax hispida</i>
<i>Zanthoxylum americanum</i>	<i>Rosa setigera</i>
<i>Rhamnus lanceolata</i>	<i>Rhus toxicodendron</i>
<i>Cornus stolonifera</i>	<i>Celastrus scandens</i>
<i>Cornus amomum</i>	<i>Vitis vulpina</i>
<i>Cephalanthus occidentalis</i>	<i>Sambucus canadensis</i>
<i>Staphylea trifolia</i>	<i>Amorpha fruticosa</i>
<i>Amelanchier canadensis</i>	<i>Prunus americana</i>
<i>Evonymus atropurpureus</i>	<i>Rhus glabra</i>
<i>Rubus strigosus</i>	<i>Ceanothus americanus</i>
<i>Rubus occidentalis</i>	<i>Rosa pratincola</i>
<i>Cornus asperifolia</i>	<i>Amorpha canescens</i>

In general shrubs occupying the district along Missouri river in northeastern Nebraska play more of a pioneer role than do those in the southeastern district. The habitat is less mesophytic so the shrubs meet the competition of the grasses under conditions more favorable to the latter. Annual rainfall is as low as 23 inches compared to 32.5 inches in the southeast. Water content is much lower in the prairie bordering the woodland in the northeast district, often being reduced below the point of availability for much of the growing season. There is a slight reduction in total soil nitrogen as one proceeds along the river and a marked increase in rate of evaporation. The most important temperature difference between the two regions is the decrease in the length of the growing season from 180 days in the south to 150 days in the north.

In the northeastern district entire summits of bluffs bordering forested areas along the upper Missouri are covered with *Rhus glabra*. The covering of the perfect leaf mosaics of the sumac reduces the light. The typical prairie grasses such as *Stipa spartea*, *Koeleria cristata*, *Andropogon scoparius* and *Bouteloua curtipendula* are shaded out under this canopy. Because of a climate less favorable to forest development, the invasion of the subclimax grassland by the shrubs proceeds from the woodland outward along the gullies which extend into the grassland. The first shrub development in these ravines is sumac followed by coral berry, but, as development proceeds, the latter retains its hold and becomes the dominant of the shrub layer under the succeeding bur oak forest. Rough-leaf dogwood (*Cornus asperifolia*) follows the sumac and *Symphoricarpos* in the shrub succession. It is a tall sturdy plant which helps make a suitable nursery for seedling bur oaks, giving way to them after they have attained a height of 10 to 14 feet. These well developed shrub communities shade the soil, lessen evaporation and promote the accumulation of debris. Near the western limit of the northeastern district, shrub and tree develop-

ment often starts in advance of other forest species with the establishment of buffalo berry (*Shepherdia argentea*) and western choke cherry (*Prunus melanocarpa*) in small protected pockets in the grassland. Wolfberry (*Symphoricarpos occidentalis*) enters and is followed by these shrubs introduced from the north and west: *Physocarpus opulifolius*, *Cercocarpus montanus*, *Cornus baileyi* and *Amelanchier humilis* Wiegand, as well as *Cornus stolonifera*, *Rubus occidentalis*, *Rhus strigosus*, *Evonymus atropurpureus* and *Zanthoxylum americanum*.

In the subclimax region bordering the forest area along Missouri river shrubs and trees are invading the grassland and, where not hindered by fires, cuttings 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. At any place within this area where the conditions in the grassland are altered to considerably increase soil moisture and decrease evaporation, invasion by the chaparral is possible.

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