Historical development of gallery forests in northeast Kansas*

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Abstract

Woody vegetation, soils, age-diameter relationships and historical development are described for 18 gallery forest stands on Konza Prairie, a tallgrass prairie reserve in northeast Kansas. Detrended correspondence analysis (DCA) coupled with the importance values of dominant species was used to identify four stand types in these forests: Quercus muehlenbergii, Q. muehlenbergii – Q. macrocarpa, Q. macrocarpa – Q. muehlenbergii, and Celtis occidentalis – Q. macrocarpa. Location of these groups on the first DCA axis was correlated with decreasing slope and increasing percent silt (i.e. a moisture gradient from xeric to mesic). Shrub cover increased with droughtiness and decreased with both stand basal area and total reproduction.

Original Land Office Survey suggest a dramatic expansion of gallery forests along the stream channels and ravines during the period from 1859–1939. Further expansion occurred through 1978. Increases in woody vegetation were attributed to decreased fire intensity and frequency since European settlement. Q. macrocarpa and/or Q. muehlenbergii were the oldest and largest trees in each stand, but were poorly represented as young trees and seedlings. In contrast, Celtis occidentalis, Cercis canadensis and Ulmus spp. were well represented as young trees and were vigorously reproducing singly or in combination in all stands. The growth of these species into trees occurred 10 to 30 years after the major recruitment of Q. macrocarpa and Q. muehlenbergii into the tree size class. It is suggested that the oaks will be replaced by C. occidentalis on the more mesic sites and by C. canadensis on the more xeric sites. The potential of Ulmus spp. as an overstory dominant is probably limited by the Dutch Elm Disease.

Introduction

Woody vegetation has expanded throughout much of the Great Plains of North America since European settlement (Kucera, 1960; Bragg & Hultbert, 1976; Pyne, 1983), which has been attributed to decreased fire frequency and intensity (Sauer, 1950; Penfound, 1962). Many researchers believe that the near-complete domination of much of the Great Plains by grassland was due to frequent burning by Indians (Gleason, 1913; Sauer, 1950; Pyne, 1983), although lightning-caused fires were probably also important (Komarek, 1968; Higgins, 1984). The importance of fire in maintaining prai-
rie and checking woody-plant invasion is well documented by Kucera (1960) and Bragg & Hubert (1976) who showed how quickly certain grasslands are converted to woody vegetation when fire is excluded.

Not only have woodlands increased throughout the Great Plains but succession has occurred. This frequently involved oak (Quercus spp.) replacement by more shade tolerant hardwoods. For example, Pool et al. (1918) described a succession for the lowlands of the Missouri River going from grassland to mesophytic forest in the following stages: shrub, Q. macrocarpa - Q. muehlenbergii, Q. velutina, Q. rubra - Carya ovata, and the final stage, Tilia americana - Ostrya virginiana.

The gallery forests on Konza Prairie are dominated by Quercus species and have dramatically expanded since European settlement in the mid-1800’s. A study of these forests was initiated during the spring and summer of 1983 to characterize: 1) woody species distribution in relation to soil and topographic parameters, 2) stand structure and successional dynamics, and 3) historical development.

Study area and methods

Konza Prairie is a 3,487 ha tallgrass (Andropogon-Panicum-Sorghastrum) prairie reserve located in the Flint Hills in northeast Kansas, and was once a cattle ranch acquired piecemeal during the late 1800’s and early 1900’s. The gallery forests present are relatively thin bands of woodlands (ranging from about 10 to 300 m wide) that are more or less continuous along stream channels and ravines in the prairie interior.

Climate

The climate of the study area is continental, characterized by hot summers, cold winters, moderately strong surface winds and relatively low humidities (Brown & Bark, 1971). The average length of the frost-free season is 180 days. Mean annual temperature was 12.8°C (range = -2.7 to 26.6°C) and mean annual precipitation was 835 mm based on a 30 year record (1951-1980). Precipitation ranges from 21 to 134 mm per month with May and June being the wettest and December-February being the driest months. Annual precipitation varies greatly and droughts occur frequently. In northeast Kansas, drought occurred during 38% of the months between 1931 and 1968 and of these 11% were rated severe or extreme (Brown & Bark, 1971).

Field methods

During the spring and summer of 1983, 18 gallery forest stands were surveyed, which represented nearly all of the stands in a ‘natural condition’ on Konza Prairie. The natural condition of these gallery forests was difficult to define because of past fires (Abrams, 1985), selective logging, cattle grazing and herbicide spraying. If an area showed evidence of heavy logging or herbicide mortality it was not surveyed. However, areas in which only a few trees had been killed were considered acceptable, but potential plots containing stumps or dead trees were excluded.

All woody vegetation in the gallery forests was surveyed and divided into trees (≥ 10 cm diameter breast height, dbh), saplings (tree species <10 cm dbh and taller than 1.5 m), seedlings (tree species <1.5 m tall) and shrubs. Trees were surveyed using the point-quarter method, in which the closest tree in each of four quadrants was measured (Cottam & Curtis, 1956). Species name, dbh and distance to point center of each tree were recorded. Two arbitrary trees at each point were bored at 1.2 m for age determination and ring counts were made in the field with the aid of a magnifying lens.

Points were located at 20 m intervals along transects through the approximate middle portion of the forest (e.g., the midpoint between the forest edge and the stream or ravine bottom which typically bisected the forest). Ten points were generally surveyed on each side of the stream and a stand was defined as a relatively homogeneous forest unit large enough to contain 20 sample points. Because of the difficulty in distinguishing between Ulmus americana and U. rubra, these species were identified by genus, only. Saplings, seedlings and shrubs were recorded by species in a 10 m² circular plot at each point used for the tree survey and cover of each shrub species was estimated into cover classes established by Daubenmire (1959).

In July and August 1983, 20 soil samples were collected from each gallery forest stand along the
same approximate transects used in the vegetation survey. A 47 cm³ sample of the top 15 cm of mineral soil was taken at each point and grouped in order of collection into four equal composite samples. Also measured was percent slope at each sampling point. Soil samples were air dried and analyzed for texture, pH, organic matter, NH₄, NO₃, extractable P, Mn, Cu, Zn and Fe, and exchangeable K, Mg and Ca using standard procedures (Dahnke, 1980) at the soil testing lab at Kansas State University.

Historical development of gallery forests on Konza Prairie

To reconstruct the development of gallery forests on Konza Prairie, the extent of these forests as mapped during the Original Land Office Survey (1855–56) was compared to that in U.S.D.A. aerial photographs taken in 1939 and 1978. When the original survey of the Kansas Territory was conducted, every section line (N-S and E-W) was surveyed for construction material (e.g. timber and rock), vegetation type and quality of land. Witness trees that were often used to mark quarter and section corners in other regions were generally unavailable in this part of Kansas, but surveyors noted the points along section lines when timber was entered and left. The original township maps drawn in 1858 indicated the boundaries of wooded areas, but the location of forest not on or close to section lines was typically inaccurate or not recorded.

Numerical analyses

Importance values were calculated from the tree data in each stand as outlined by Cottam & Curtis (1956). These values (15 species × 18 stands) were subjected to detrended correspondence analysis (DCA) using DECORANA (Hill, 1979; Hill & Gauch, 1980; Gauch, 1982).

Statistical analyses used were simple correlation, multiple stepwise regression and test of significance (F-test), which were computed using SAS (SAS Institute Inc., 1982).

Results

Stand classification and ordination

The stands were arbitrarily divided into four ecological groups along DCA axes 1 and 3 according to the importance values of the three dominant species (Table 1, Fig. 1). Group 1 (stands 1, 2, 6, 18) includes Celtis occidentalis – Quercus macrocarpa dominated stands, with Q. muehlenbergii and Ulmus spp. as subdominants. Group 2 stands are dominated by Q. macrocarpa (stands 3, 9, 10) or Q. macrocarpa and Q. muehlenbergii (stands 4, 7) with lesser amounts of C. occidentalis and Ulmus. Q. muehlenbergii and Q. macrocarpa are the dominants and Ulmus and Cercis canadensis the subdominants in group 3 (stands 5, 8, 11, 12, 14, 16). Q. muehlenbergii dominated stands in group 4 (stands 13, 15, 17), with Q. macrocarpa, C. canadensis and Ulmus as subdominants. The density of C. canadensis increased in these stands with increasing density of Q. muehlenbergii (p<0.05, r=0.77). Significant relationships between other dominant and subdominant species were not observed.

Relationship of vegetation to soil and topographic factors.

Simple correlations of DCA axis 1 position with all 15 soil parameters and slope for the 18 stands were significant (p<0.05) for percent silt, percent clay, extractable P, exchangeable Ca, slope and organic matter. From this group, clay was negatively correlated with silt (p<0.05, r=-0.085). Clay was therefore deleted leaving silt, P, Ca, slope and or-
Table 1. Importance values of tree species in 18 gallery forest stands on Konza Prairie. Stands are organized into groups identified by detrended correspondence analysis.

<table>
<thead>
<tr>
<th>Species</th>
<th>Group 1</th>
<th></th>
<th>Group 2</th>
<th></th>
<th>Group 3</th>
<th></th>
<th>Group 4</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>6</td>
<td>1</td>
<td>2</td>
<td>18</td>
<td>9</td>
<td>3</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>Quercus muehlenbergii</td>
<td>17.5</td>
<td>11.4</td>
<td>51.1</td>
<td>72.4</td>
<td>38.8</td>
<td>40.6</td>
<td>72.9</td>
<td>76.7</td>
</tr>
<tr>
<td>Quercus macrocarpa</td>
<td>69.3</td>
<td>121.8</td>
<td>100.2</td>
<td>38.9</td>
<td>211.3</td>
<td>243.1</td>
<td>148.9</td>
<td>180.2</td>
</tr>
<tr>
<td>Celtis occidentalis</td>
<td>149.8</td>
<td>148.7</td>
<td>118.2</td>
<td>142.5</td>
<td>4.6</td>
<td>53.6</td>
<td>31.7</td>
<td>5.3</td>
</tr>
<tr>
<td>Ulmus spp.</td>
<td>34.3</td>
<td>13.3</td>
<td>17.1</td>
<td>20.6</td>
<td>25.6</td>
<td>6.9</td>
<td>5.2</td>
<td>45.6</td>
</tr>
<tr>
<td>Cercis canadensis</td>
<td>4.2</td>
<td>4.0</td>
<td>5.1</td>
<td>8.5</td>
<td>4.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morus rubra</td>
<td>5.0</td>
<td>4.8</td>
<td>9.1</td>
<td>4.4</td>
<td>5.1</td>
<td>4.2</td>
<td>25.7</td>
<td>4.8</td>
</tr>
<tr>
<td>Gleditsia triacanthos</td>
<td>19.9</td>
<td>17.6</td>
<td>11.2</td>
<td>6.2</td>
<td>4.6</td>
<td>9.9</td>
<td>25.7</td>
<td>4.8</td>
</tr>
<tr>
<td>Juglans nigra</td>
<td>6.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fraxinus pennsylvanica</td>
<td>4.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juniperus virginiana</td>
<td>25.7</td>
<td>4.8</td>
<td>9.1</td>
<td>4.4</td>
<td>6.9</td>
<td>4.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gymnocladus dioica</td>
<td>16.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aesculus glabra</td>
<td>738</td>
<td>271</td>
<td>311</td>
<td>530</td>
<td>266</td>
<td>146</td>
<td>254</td>
<td>243</td>
</tr>
<tr>
<td>Platanus occidentalis</td>
<td>49.2</td>
<td>28.4</td>
<td>37.9</td>
<td>36.6</td>
<td>34.9</td>
<td>36.6</td>
<td>28.3</td>
<td>52.3</td>
</tr>
</tbody>
</table>

Density/ha: 738 271 311 530 266 146 254 243 250 207 250 404 402 505 319 407 927 583

Basal area (m²/ha): 49.2 28.4 37.9 36.6 34.9 36.6 28.3 52.3 17.8 14.1 31.6 16.2 26.4 23.6 17.2 13.4 23.2 18.7
ganic matter as the variables used in a multiple stepwise regression analysis. The results showed that slope ($r=1.8\pm 3.6\%$) and $27.8\pm 1.3\%$ in groups 1 and 4, respectively) accounted for most of the variance in DCA axis 1 position ($r^2 = 0.67$), followed by silt ($46.0\pm 2.6\%$ and $38.7\pm 0.2\%$ in groups 1 and 4, respectively); these were the only variables that significantly (multiple $r^2 = 0.75$, $p < 0.05$) improved the regression model.

Sand, pH, K and Mn were significantly correlated ($p < 0.05$) with stand DCA axis 3 position. Potassium followed by Mn were the significant variables ($p < 0.05$) identified by multiple stepwise regression analysis ($r^2 = 0.36$, multiple $r^2 = 0.65$).

**Reproduction data**

No significant relationship existed between total reproduction and stand DCA axis 1 position (Table 2). However, the dominant species reproducing in each stand varies among groups. Most noteworthy is the decrease in *Celtis occidentalis* reproduction going from group 1 (*C. occidentalis* – *Q. macrocarpa* stands) to group 4 (*Q. muehlenbergii* stands) and the corresponding increase in *Cercis canadensis* reproduction. Variation in *Celtis* reproduction was significantly correlated ($p < 0.05$, $r = 0.83$) with its overstory importance values; this relationship was not found in *Cercis*.

*Ulmus* spp. was dominant in reproduction in 14 of the 18 stands (Table 3), in spite of it only having an average importance value of $10.7\pm 17.4$ (range 0–74.6). *Q. macrocarpa* was reproducing poorly or not at all in these stands. *Q. muehlenbergii* reproduction was present at somewhat higher frequency than that of *Q. macrocarpa*, but was underrepresented in most stands. *Q. muehlenbergii* reproduction was significantly correlated with its overstory density ($p < 0.05$, $r = 0.83$).

**Shrub data**

Total shrub cover, which ranged from 14.1–55.3%, was significantly correlated with stand DCA axis 1 position ($p < 0.05$, $r = 0.74$). The increase in shrub cover going from wet to dry (group 1 to group 4) was due to increases in *Cornus drummondi* (roughleaf dogwood) and low cover of *Symphoricarpos orbiculatus* (buckbrush) in group 1. A likely explanation for this trend is that basal shrub area decreased significantly ($p < 0.05$) from group 1 to group 4 (Table 1). Shrub cover was, in fact, negatively correlated with stand basal area and total reproduction ($p < 0.05$, $r = -0.57$ and -0.55, respectively).

**Table 2.** Reproduction data (± S.D.) by species for the four gallery forest stand groups on Konza Prairie. Values equal seedlings + saplings in number/ha.

<table>
<thead>
<tr>
<th>Species</th>
<th>Group 1</th>
<th>Group 2</th>
<th>Group 3</th>
<th>Group 4</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ulmus</em> spp.</td>
<td>7950 ± 6408</td>
<td>10352 ± 2315</td>
<td>11517 ± 4418</td>
<td>7683 ± 2599</td>
</tr>
<tr>
<td><em>Celtis occidentalis</em></td>
<td>14975 ± 7684</td>
<td>2787 ± 3651</td>
<td>517 ± 584</td>
<td>66 ± 47</td>
</tr>
<tr>
<td><em>Cercis canadensis</em></td>
<td>1087 ± 970</td>
<td>1037 ± 1279</td>
<td>4483 ± 2746</td>
<td>4867 ± 1074</td>
</tr>
<tr>
<td><em>Quercus macrocarpa</em></td>
<td>187 ± 129</td>
<td>200 ± 195</td>
<td>17 ± 24</td>
<td>17 ± 24</td>
</tr>
<tr>
<td><em>Quercus muehlenbergii</em></td>
<td>375 ± 470</td>
<td>502 ± 520</td>
<td>892 ± 406</td>
<td>2117 ± 995</td>
</tr>
<tr>
<td><em>Gleditsia triacanthos</em></td>
<td>25 ± 25</td>
<td>366 ± 483</td>
<td>50 ± 58</td>
<td>–</td>
</tr>
<tr>
<td><em>Fraxinus pennsylvanica</em></td>
<td>388 ± 152</td>
<td>259 ± 264</td>
<td>333 ± 702</td>
<td>–</td>
</tr>
<tr>
<td><em>Juniperus virginiana</em></td>
<td>75 ± 56</td>
<td>32 ± 27</td>
<td>125 ± 149</td>
<td>100 ± 41</td>
</tr>
<tr>
<td><em>Morus alba</em></td>
<td>12 ± 22</td>
<td>140 ± 280</td>
<td>192 ± 197</td>
<td>467 ± 557</td>
</tr>
<tr>
<td><em>Carya cordiformis</em></td>
<td>62 ± 52</td>
<td>32 ± 41</td>
<td>8 ± 19</td>
<td>–</td>
</tr>
<tr>
<td><em>Gymnocladus dioica</em></td>
<td>–</td>
<td>10 ± 20</td>
<td>17 ± 37</td>
<td>–</td>
</tr>
<tr>
<td><em>Juglans nigra</em></td>
<td>12 ± 22</td>
<td>10 ± 20</td>
<td>42 ± 93</td>
<td>50 ± 71</td>
</tr>
<tr>
<td><em>Aesculus glabra</em></td>
<td>25 ± 43</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Tilia americana</em></td>
<td>25 ± 43</td>
<td>–</td>
<td>125 ± 279</td>
<td>–</td>
</tr>
<tr>
<td><em>Asimina triloba</em></td>
<td>–</td>
<td>–</td>
<td>83 ± 186</td>
<td>–</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>25200 ± 7777</td>
<td>15604 ± 3230</td>
<td>18400 ± 6993</td>
<td>15367 ± 2697</td>
</tr>
</tbody>
</table>
Age-diameter data

Species age-diameter and diameter class frequency data from a representative stand for each of the four stand-types is shown in Figures 2–5. Stand 1 (Fig. 2a) is a C. occidentalis – Q. macrocarpa stand in which Q. macrocarpa stems were the largest and oldest present; most Q. macrocarpa were over 40 cm diameter and 70 years old. The size and age of Q. macrocarpa was distinct from that of Celtis, which generally ranged from 10–40 cm diameter and 23–53 years old. Diameter class frequency data for stand 1 (Fig. 2b) showed that Celtis dominated the smaller diameter classes and Q. macrocarpa dominated the larger.

Stand 7 is representative of Q. macrocarpa – Q. muehlenbergii stands (Fig. 3a). Q. macrocarpa was the largest and oldest species surveyed with most individuals over 40 cm diameter and 75 years old, while Q. muehlenbergii was mostly between 20–35 cm diameter and 65–75 years old. Celtis and others (Ulmus, Cercis and Morus rubra) dominated the smallest and youngest diameter and age classes.

![Fig. 2. Age-diameter data and diameter size class distribution for gallery forest stand 1 on Konza Prairie.](image1)

![Fig. 3. Age-diameter data and diameter size class distribution for gallery forest stand 7 on Konza Prairie.](image2)

![Fig. 4. Age-diameter data and diameter size class distribution for gallery forest stand 8 on Konza Prairie.](image3)
Fig. 5. Age-diameter data and diameter size class distribution for gallery forest stand 17 on Konza Prairie.

(Fig. 3b). A large gap between ages 39 to 57 separated the oaks from the other species.

In stand 8, a *Q. muehlenbergii*—*Q. macrocarpa* stand, *Quercus* species dominated the larger and older diameter and age classes, whereas *Cercis, Ulmus* and, to a lesser extent, *Celtis* dominated the smaller and younger classes (Fig. 4). A predominant age gap between 34 and 69 years separated these species groups. Both *Quercus* species showed a peak frequency in the 20–30 cm diameter class.

Stand 17 was dominated by *Q. muehlenbergii* and showed a fairly distinct age separation between that species and the younger class of *Cercis* and *Ulmus* (Fig. 5a). Most of the *Q. muehlenbergii* and all the *Q. macrocarpa* aged were over 52 years, whereas *Ulmus* and *Cercis* were generally under 38 years. Because of the slow growth of *Q. muehlenbergii* in this stand it dominated the smaller diameter classes, despite its relatively high age (Fig. 5b).

**Historical development of gallery forests on Konza Prairie**

Using data from the 1858 Original Land Office Survey of Konza Prairie and aerial photographs taken in 1939 and 1978, it was possible to determine changes in the extent of gallery forests during that 120 year period. In 1858 only two areas of continuous forest comprising about 5 ha were noted; however, the extent of gallery forests away from the section lines is not known. Occasionally, a few trees or scrubby timber and shrubs were recorded in other areas of Konza Prairie, especially along the stream channels and ravine bottoms, but in general this area was described as rolling prairie devoid of woody vegetation. The aerial photographs of Konza Prairie taken in 1939 and 1978 were in marked contrast to that described in 1858. During those periods a large expansion of the gallery forests to approximately 111 and 206 ha occurred, respectively, with widespread invasion of shrublands and forests onto the prairie and development of shrublands into forests.

**Discussion**

Ordination of the gallery forests on Konza Prairie indicated four stand-types ranging from *Celtis*—*Q. macrocarpa* to *Q. muehlenbergii* stands. These stands followed an environmental gradient from low slope and soils with high silt content to steep slope and soils with less silt, which may be interpreted as a moisture gradient from mesic to xeric.

The distribution and overall ecology of the gallery forests on Konza Prairie has been greatly affected by anthropogenic factors. The limited extent of the gallery forests in 1858 was probably due to higher fire intensity and frequency prior to European settlement, which started about 1840 (cf. Pendfound, 1962). Following settlement, the number, extent and intensity of fire most likely decreased in the Flint Hills due to road construction, expansion of towns, agriculture, continuous cattle grazing, suppression of wildfire and recommendations against burning during the mid-1900's (Bragg & Hulbert, 1976). Therefore, after settlement forests increased rapidly, which suggests that fire, rather than low precipitation, limited growth of woody vegetation in northeast Kansas.
Since settlement, the gallery forests have been affected by other disturbance factors such as logging and cattle grazing. Konza Prairie was grazed by cattle since the late 1800's until 1977, which would prevent normal reproduction in woodlands by packing the soil, browsing and breakage of seedlings and consumption of seeds (Ware & Smith, 1939). It can also be assumed that early settlers cut wood from these forests, which was scarce in Kansas and indispensable for construction material and as fuel. Insects, disease, drought, and more recently herbicide spraying have also influenced these forests.

Because of the disturbance oriented history of the gallery forests on Konza Prairie, care must be taken when discussing succession or species replacement in these stands. From the data presented, however, it appears that a succession from shade intolerant Quercus species to the more tolerant Celtis or Cercis is taking place. Quercus macrocarpa and/or Q. muehlenbergii, which represented the largest and oldest species in each stand, showed very little recruitment into the tree size class for over half a century. In contrast, numerous Celtis, Ulmus and Cercis trees younger than 50 years old were present in these stands. On the more mesic sites Celtis may be the future sole dominant, which is in agreement with Bellah & Hulbert (1974) who felt that Celtis would be the climax species in floodplain forests in an adjacent county in northeast Kansas. Already in group 1 stands (1, 2, 6, 18) Celtis is the dominant in spite of it being younger and smaller than Q. macrocarpa. Celtis, in addition, is reproducing vigorously in these stands, which suggests increased dominance by this species in the future and less by Quercus. Even though Ulmus is a dominant reproducer in nearly all stands, its potential as an overstory dominant is probably limited by the Dutch Elm Disease. This blight was discovered in Kansas in 1937 and has depleted many area forests of mature elms (Thompson et al., 1978).

On the steeper, drier sites on Konza Prairie, where Celtis was rare, it is more difficult to speculate about future stand composition. Reproduction and young trees of Q. muehlenbergii were scarce in these stands, whereas Cercis and Ulmus saturated the understory with reproduction and were well represented as young trees. Considering again that Ulmus potential may be limited by the Dutch Elm Disease, this leaves Cercis as the species most likely to replace Q. muehlenbergii. Cercis' small stature as a tree did not rule it out as a potential replacement species here because the size of Q. muehlenbergii is limited on these harsh sites. Further evidence that Cercis can function as an overstory species on these sites comes from its ability to invade prairie slopes in this region along with Juniperus virginiana and form mixed stands with that species.

A successional sequence involving Quercus replacement by more tolerant hardwoods has been documented in other prairies and prairie-forest ecotones. For example, in the central Missouri valley, Weaver (1960) noted that blue stem prairie gave way to Q. macrocarpa in the ravines, which was soon replaced by either Q. velutina, Q. rubra or Tilia. In a study of Quercus woodlands in southwestern Wisconsin, Cottam (1949) reported Q. macrocarpa occurred almost exclusively in the largest diameter classes, with very few in the smallest diameter class (2.5-10.0 cm), and a lack of Q. macrocarpa reproduction. Cottam hypothesized that the protected portions of these forests will be one generation stand of Quercus, which will be replaced by Ulmus rubra and Osytra, then eventually Acer saccharum and Tilia. More recently, Grimm (1983) outlined a similar sequence occurring in the prairie woodland region of southern Minnesota. Both authors believed that the change from prairie or Q. macrocarpa savanna to Quercus woodlands to Acer-Tilia forests required a reduction in fire frequency.

While I recognize that other factors such as grazing, drought, logging and herbicides have affected the spread of these forests and the succession occurring, I think that cessation of burning is the major factor driving the changes observed. I conclude that the reduction of fire frequency and/or intensity following European settlement allowed invasion of prairie lands by Quercus to form open savannas. The Quercus species continued to reproduce and grow into the canopy until about 50 years ago, at which time factors such as a thick organic seedbed and low light may have inhibited Quercus establishment and growth. After a period of ten to 30 years, more shade tolerant species became established and grew vigorously under the oak canopy. If the present management continues, Quercus may be replaced by Celtis forests in moister areas and by Cercis forests in the drier areas.
References


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