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Effects of site, landscape features, and fire regime on vegetation patterns in presettlement southern Wisconsin

Lawrence A. Leitner[1], Christopher P. Dunn[2], Glenn R. Guntenspergen[3], Forest Stearns[4] and David M. Sharpe[5]

[1]Department of Biological Sciences, University of Wisconsin, P.O. Box 413, Milwaukee, WI 53201, USA; [2]Environmental Assessment and Information Sciences Division, Argonne National Laboratory, Bldg. 301, Argonne, IL 60439, USA; [3]National Wetlands Research Center, US Fish and Wildlife Service, 1010 Gause Boulevard, Slidell, LA 70458, USA; [4]Forestry Sciences Laboratory, North Central Forest Experiment Station, Rhinelander, WI 54501, USA; [5]Geography Department, Southern Illinois University, Carbondale, IL 62901, USA

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Abstract

The presettlement tree cover (1831–33) of 3 townships in a southern Wisconsin landscape was analyzed using original survey records. Four forest types were identified: closed forest, open forest, savanna, and prairie. Comparisons of vegetation types and landscape pattern were made between the east and west sides of the Pecatonica River, which bisects the landscape and could have acted as a natural fire barrier. West of the river, presettlement tree species richness and diversity were lower and trees were smaller in diameter and less dense than to the east. The major vegetation types to the west were prairie (42% of landscape) and savanna (40%), both fire-susceptible types. Prairie was more common on gentle slopes than on other landforms. To the east, the landscape was 70% forested (closed plus open forest). Here, prairie was more frequent on steep dry sites. These vegetation differences, including the contrasting landscape placement of prairie, are attributed to distinct site characteristics and to disturbance (fire) regimes, with the west likely having more frequent fires. In terms of the four vegetation types, the east landscape was more homogeneous, being dominated by closed forest (50%). West of the Pecatonica River, the landscape was more heterogeneous because of the high proportion of both prairie and savanna; however, in terms of flammability of vegetation, the west was essentially homogeneous (82% prairie plus savanna).

Introduction

Disturbance is considered to be a major factor influencing landscape pattern and vegetation composition (Bazzaz 1983; Reiners 1983; Godron and Forman 1983; Risser *et al.* 1984; Pickett and White 1985; Forman and Godron 1986). For example, the presettlement fire regime of the midwestern United States influenced the regional distribution of plant communities (Gleason 1922; Cottam 1949; Curtis 1959; Heinselman 1973; Vogl 1974; Davis 1977; Dorney 1980; Anderson and Brown 1983, 1986; Whitford 1983; Grimm 1984; Nigh *et al.* 1985). In many instances, fires eliminated woody vegetation, while maintaining prairie. More mesic communities either survived by chance or were protected by topography or water bodies (*e.g.*, Gleason 1922; Kilburn 1959; Heinselman 1973; Grimm 1984). In other regions, the observed landscape pattern and vegetation composition are attributable more to local site conditions than to disturbance. For example, the presettlement vegetation composition of three Ohio (U.S.A) counties was controlled largely by soil texture, soil drainage, and topography rather than by disturbance (Whitney 1982). Prairie relics also existed within the forested regions occupying sites which were either poorly drained (Whitford 1958) or on droughty soils (Hanson 1922). Thus, both disturbance regime and local site conditions can explain presettlement landscape pattern.

One test of this concept of site- *vs.* disturbance-related control of landscape pattern and vegetation entails comparisons between regions of similar environment (soils, topography, glacial history, etc.) where each region apparently had equal access to plant migration. Similar sites experiencing similar fire regimes should support similar vegetation (*cf.* McCune and Allen 1985). Conversely, similar sites supporting different vegetation patterns probably experienced different disturbance regimes.

European settlers altered the natural disturbance regime directly by fire suppression and indirectly by habitat fragmentation and land-use conversion. This alteration of the fire regime was most evident in the ecotones between prairie and forest, where savanna remnants were soon converted into closed *Quercus* (oak) forest (Cottam 1949; Ward 1956; McIntosh 1957; Whitford 1983; McCune and Cottam 1985). In addition, prairie remnants were invaded by trees and shrubs. Consequently, the natural xeric vegetation changed in terms of structure rather than in species dominance. Mesic sites, having been least affected by fire, changed least when fire ceased, although, even here, stands are becoming more mesophytic as dominance by *Acer saccharurn* (sugar maple) increases (Peet and Loucks 1977; McCune and Cottam 1985; Sharpe *et al.* 1987). Thus, these mesic stands changed in dominance rather than in structure.

The extensive forest fragmentation and land-use changes that accompanied settlement of the midwestern United States (and the concomitant alteration of the fire regime) have tended to blur contemporary vegetation patterns (Host *et al.* 1987), making temporal comparisons difficult (Whitford 1983; Turner 1989; Dunn *et al.* 1990). Nonetheless, to fully appreciate the relevance of landscape pattern, a better understanding of the geographic role of disturbance is required (Turner 1989).

This study examines the roles of edaphic conditions, landscape features such as topography, and fire in contributing to (1) the abundance, spatial distribution, and size structure of forest trees and to (2) vegetation pattern in a presettlement southern Wisconsin landscape. This landscape is bisected north to south by a river which served as a fire barrier (Dorney 1980) and which therefore might have played a critical, and perhaps interactive, role with site in determining landscape pattern.

Description of the study area

Cadiz Township is located in southern Wisconsin, USA, in extreme southwestern Green County and is bordered on the south by the state of Illinois. The Pecatonica River flows north to south through the western part of the township. Cadiz Township has long been used to illustrate deforestation and landscape fragmentation in the agricultural Midwest (Shriner and Copeland 1904; Curtis 1955, 1959), and recently has been the site of a series of studies dealing with various aspects of landscape dynamics (Sharpe *et al.* 1981, 1987; Dunn *et al.* 1990).

The township lies on the eastern fringe of the Driftless Area of southwestern Wisconsin, which is part of the Western Uplands Physiographic Province (Martin 1965). The northwestern corner of the township is unglaciated, while the remainder is covered with thin, deeply weathered glacial drift of pre-Wisconsinan age. Topography is transitional – slopes tend to be longer and gentler than in the Driftless Area, but, as drainage is well established and glacial deposits are scarce, many of the features characteristic of more recently glaciated areas of Wisconsin are absent. Soils are generally good to fair for agriculture, consisting almost entirely of silt-loams (Glocker 1974).

In his map of the presettlement vegetation of Wisconsin, Finley (1976) depicted Cadiz Township as supporting primarily southern mesic forest *(A. saccharurn, Tilia arnericana, Q. rubra,* and *Q. alba)* in the east, and *Quercus* forest *(Q. alba, Q. velutina,* and *Q. rnacrocarpa)* in the west. To the northwest were found openings of *Q. macrocarpa, Q. alba* and *Q. velutina,* while prairie occupied the southeastern and southwestern corners. Lowland vegetation was found in the northwestern and north-central parts of the township, mostly bordering the Pecatonica and its tributaries.

Methodology

Presettlement vegetation

The original General Land Office surveys, which include data on trees and written descriptions of the landscape, provide a record of the presettlement vegetation and have been used by numerous researchers to reconstruct original vegetation composition and structure (Stearns **1949;** Bourdo **1956;** Lindsey *et al.* **1965;** Lorimer **1977;** Rodgers and Anderson **1979;** Leitner and Jackson **1981;** Whitney **1982;** Dunn **1987;** and many others). The surveys, conducted during the inception of settlement, used the township and range method, in which the land was divided into a grid of townships **6** miles **(9.66** km) square, with each township subdivided into **36** sections. The surveyors identified the location of each section and quarter-section corner by marking two (or, in later years, four) 'witness' trees in different quadrants, noting their identity and diameter, and distance and direction from the corner. Trees on the survey line were also recorded. Ideally, these accounts represent a random sample of the trees present at the time of the survey, though biases and inaccuracies are inevitable (Bourdo **1956).** Nevertheless, the surveys provide important insight into regional presettlement vegetation.

Species name, diameter (in inches), point-to-tree distance (in links; one link equals **20.1** cm), and location of each tree were obtained from microfilm copies of the **1831–33** surveyors' field notes. The modified quarter method of Cottam and Curtis **(1956;** Anderson and Anderson **1975;** Rodgers and Anderson **1979)** was used to determine tree densities. Normally, distance of both trees (Q1 and Q2) would be used in the calculation, but we found that placement of the second tree occurred significantly more frequently in either of the two adjacent quadrants than in the opposite quadrant ($\chi^2 = 8.65$; $p > 0.05$). It is therefore advisable to use only the shorter distance **(Q1;** Rodgers and Anderson **1979).** The mean of the shorter distances was used to calculate the number of trees for all species per acre. Multiplying this result by the relative density of each species gave the absolute density for that species. The diameters of both trees at each point, regardless of distance, were used in calculating relative basal areas. The mean of the sum of relative density and relative basal area yielded an importance value for each species. Data were calculated separately for the areas east and west of the Pecatonica River.

Tree density at each point was used to classify vegetation at the point into one of four plant community types: prairie (point-to-tree distance > **467** links **(94** m), *i.e.* = < *0.5* tree/ha); savanna **(10.0–94** m = **0.5–47** trees/ha); open forest **(6.6–10.0** m = **47–99** trees/ha); and closed forest **(< 6.6** m = > **99** trees/ha) (Anderson and Anderson **1975;** Rodgers and Anderson **1979).** Density, basal area, and importance value were calculated as before for each type.

Because most of Cadiz Township lies to the east of the Pecatonica River, there is not an equal land area on each side of the river. To produce a more balanced sample for statistical comparison between east and west, the sample was extended westward to include adjoining Wayne Township in Lafayette County. Also, the area east of the river was enlarged by about 50% by extending the sample to the western margin of the large NE to SW swath of prairie in Clarno Township, Green County. All statistical results, exclusive of tree size-class distributions, include these three townships.

Even with the addition of data from Wayne and part of Clarno Townships, the sample size seemed too small to accurately depict tree size-class distributions. Therefore, we included tree data from four complete and two partial Illinois townships (Stephenson County) to the south of, and contiguous with, Cadiz Township. This effectively doubled the total number of trees for the size-class analyses. Similar topography and soils, the north-south trend of the Pecatonica River, and a similar distribution of witness trees and vegetation types indicated that the same processes had formed the landscape there as in Cadiz Township.

Inspection of topographic and soil maps, land

Table 1. Comparison of mean (± 1 SD) total water holding capacity (TWHC) of soils for each vegetation type on the west and east of the Pecatonica River. * = significant difference ($p \leq 0.05$) in mean TWHC west *vs* east of the Pecatonica River.

	West		East	
	No. Pts.	Mean TWHC	No. Pts.	Mean TWHC
Vegetation type				
Closed forest	46	9.55 (3.85)	173	10.57 (3.88)
Open forest	31	10.19 (4.28)	54	10.64 (4.96)
Savanna	94	10.59 (3.71)	102	10.85 (4.26)
Prairie	278	11.47 (2.93)	58	9.08 (3.00)*
All points	449	11.00 (3.36)	387	10.44 (4.06)

survey data, and field observation strongly suggest that these additional areas were continuous and homologous with the areas east and west of the Pecatonica River in Cadiz Township. We are also confident that the entire landscape, regardless of east or west half, was physically homologous. Not only is glacial history identical, but the soils are very similar. To further confirm this, at each section corner and quarter-section point, we identified the soil type from the appropriate soil manuals for Green and Lafayette counties (Wisconsin) and Stephenson County (Illinois). The total area thus analyzed included five complete and four partial townships. For each soil type, the depth of the A plus **B** horizons was multiplied by the water holding capacity to give a total water holding capacity (TWHC; inches of water per inch of soil depth) for the soil profile. This TWHC was considered an index of site mesicness and was used to test for significant physical site differences between areas east and west of the river. Means of TWHC east and west of the river were compared by a two-tailed t-test ($a = 0.05$). Nomenclature follows Little (1979).

Data analysis

To test the hypothesis that forest structure did not differ significantly between east and west sides of the Pecatonica River, two-tailed t-tests were used to compare means of tree density, point-to-tree distance, and tree diameter between the two sides and between community types. The significance of differences in tree composition (rankings of species importance values) east and west of the river was tested with the White modification of the Wilcoxon rank sum test (Ambrose and Ambrose 1981). Compositional similarity of vegetation types was determined using Sorensen's Index (Mueller-Dombois and Ellenberg 1974).

Tree size-distributions were derived (using **5** cm size classes) for all trees (regardless of species) east and west of the Pecatonica River and for all trees in each vegetation type east and west of the river. Trend surface analysis maps were prepared to illustrate differences in diameter distributions across the landscape of the three most common species.

To quantify size-distributions, we used the Gini coefficient of inequality: (G; Weiner and Solbrig 1984) as a measure of tree size (here, basal area) hierarchy. By hierarchy we mean the degree to which basal area is concentrated among individuals; therefore, if all individuals in a sample or population are the same size, then inequality does not exist because all individuals are equal and there is no size hierarchy (*i.e.*, $G = 0$). Conversely, if all individuals but one (in theory, from an infinite population) approach a value of zero, then G approaches the theoretical limit of 1.0 (maximum hierarchy or inequality). The Gini limits (95%) were calculated using a bias-corrected bootstrap method (Efron and Tibshirani 1986; Dixon *et al.* 1987) with *500* bootstrap replications with replacement.

The Gini coefficient was also used to test for significant differences between size hierarchies (*e.g.*, between two plant community types or between east and west sides of the Pecatonica River). This test was achieved by drawing repeated bootstrap samples (500 samples) and calculating the difference between their *G*'s. If the confidence interval around the two *G*'s includes 0, no statistical difference ($p > .05$) exists (Dixon *et al.* 1987). Otherwise, the size hierarchies do differ significantly. These calculations were made using a Turbo-PASCAL program (P.M. Dixon pers. comm.).

Sharpe *et* al. (1987) used cluster analysis to test whether the presettlement vegetation types of Cadiz

Table 2. Vegetation types at section and quarter-section corners, west and east of the Pecatonica River, in Cadiz, Wayne, and Clarno townships. Types are based on tree density (see text) and surveyors' notes indicating absence of trees (for "prairie"). N = number of section corner and quarter-section points. Landscape diversity (H), dominance (D_o), and beta diversity (BD) were calculated using formulae in Turner (1989).

Community	West N	West %	East N	East %	Overall N	Overall %
Prairie	66	41.8	3	1.9	69	22.0
Savanna	63	39.9	44	28.4	107	34.2
Open forest	10	6.3	30	19.4	40	12.8
Closed forest	19	12.0	78	50.3	97	31.0
Total	158	100.0	155	100.0	313	100.0
H	1.160		1.097		1.326	
D_o	0.226		0.289		0.060	
BD	1.28		1.51			

Township as mapped by Finley (1976) reflected site conditions. They found that soil and topography were not the primary factors influencing vegetation type. We examined this question further with contingency-table procedures (Strahler 1977, 1978; Whitney 1982) by analyzing community type-site and witness tree species-site relationships. Each witness tree was matched with a soil type by superimposing the tree locations on U.S. Department of Agriculture soil maps of Green (Glocker 1974) and Wayne (Watson 1966) counties. Each point was coded according to several soil characteristics (drainage, texture, and % slope), with species and vegetation types being categorized as present or absent, thus providing three sets of binary data. A G-statistic (not the Gini *G*) was calculated to determine whether a species or vegetation type occurred more frequently than expected by chance on sites with particular soil characteristics. The magnitudes of the significant results were determined with standardized residuals (d-values; Haberman 1973). A positive d-value indicates a positive association with a specific site factor, while a negative value suggests a negative association.

Results

Forest types and composition

More than 50% of the section and quarter-section points east of the Pecatonica were classified as closed forest (Table 2), with open and closed forests together accounting for nearly 70% of these eastern points (Fig. 1). To the west, prairie and savanna together covered 82% of the landscape and closed forest only 12%. There was about three times as much open forest in the east as in the west (Fig. 1).

Quercus macrocarpa and *Q. albu* accounted for more than 80% of combined importance in the west, while mesic species (*e.g.*, *A. saccharum* and *Ostrya virginiana*) were completely absent (Table 3). In the east, species patterns were more complex, but *Q. alba* was consistently the single dominant species. *Quercus rubra* ranked second or third in importance. Other sub-dominants varied in ranking between communities. *Populus* spp. and *Q. macrocarpa*, present in each of the eastern types, peaked in the savanna. *Acer saccharurn*, while not a dominant species, attained its greatest importance in the eastern closed forest.

Except for the open forests, which were notably dissimilar in composition (23.7% similar; Sorensen's index), all east:west pairs ranged between 55% and 67% in similarity (Table 4). The three eastern types (savanna, open forest, and closed forest) achieved their highest similarity to the western closed forest. The eastern vegetation type most like that in the west was the savanna.

Importance value rankings by species (Table 3) indicated significant differences between the east and west savannas ($Z = 10.653$, $p < 0.05$) and east and west open forests ($Z = 8.062$, $p < 0.05$), but

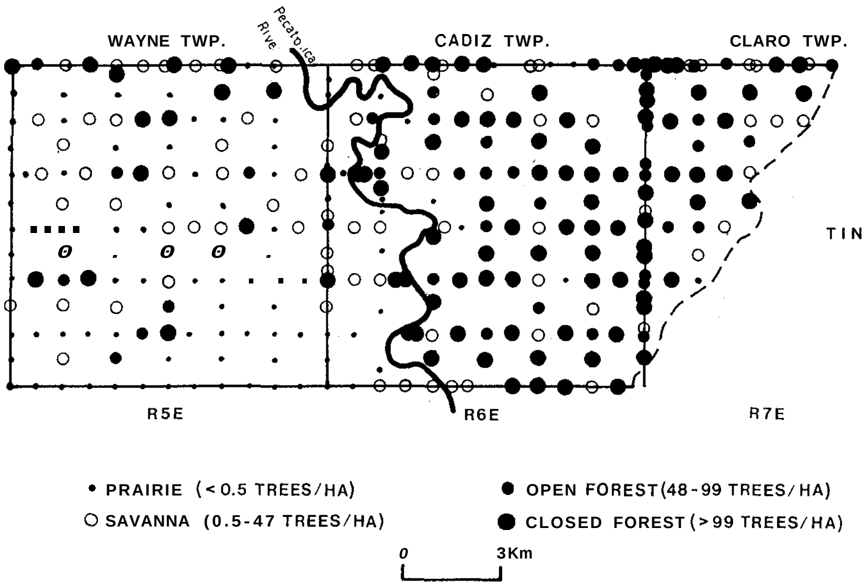

Fig. 1. Presettlement (1833) vegetation of the study area in southern Wisconsin (Wayne Township in Lafayette County and Cadiz and western Clarno Townships in Green County). Data are based on GLO surveyors' records of point to tree distances.

Table 3. Species importance values (%) and other attributes for the vegetation types east and west of the Pecatonica River in Wayne, Cadiz, and Clarno townships, based on the 1831–33 survey data.

	Savanna		Open forest		Closed forest		Overall	
Species	W	E	W	E	W	E	W	E
Quercus macrocarpa	48.2	17.6	75.1	6.7	23.4	6.8	44.8	9.2
Q. alba	37.2	40.6	12.8	42.6	55.7	29.4	39.5	34.6
Q. rubra	9.3	17.2	4.2	20.2	8.2	18.4	8.6	18.2
Q. velutina	2.4	5.3		6.0	4.1	5.3	2.8	5.4
Ulmus spp.		3.6		8.8	2.3	12.3	0.4	9.2
Populus spp.		9.0		2.7		7.1		6.3
Tilia americana		1.3		5.3	2.3	10.0	0.4	7.4
Acer saccharurn		2.3		1.3		3.1		2.8
Fraxinus spp.		0.9		1.6	4.0	2.4	0.8	2.4
Ostrya virginiana				3.7		1.8		1.5
Carya spp.	3.0		7.9			0.7	2.6	0.6
Prunus spp.				1.1		1.8		1.0
Juglans nigra		2.0						0.9
Celtis occidentalis						0.5		0.2
Salix nigra						0.4		0.2
No. of species	5	10	4	11	7	14	8	15
Mean density/ha	2.7	4.4	27.8	27.2	114.9	127.4	8.2	35.8
Mean basal area/m^2	0.3	0.6	2.3	4.5	11.8	16.3	0.6	3.4
Diversity (*H'*)	0.509	0.773	0.374	0.828	0.627	0.945	0.553	0.935

Table 4. **Matrix of similarity values (Sorensen's Index), comparing vegetation types east and west of the Pecatonica River and the entire east and west landscapes.**

	East			
	Savanna	**Open forest**	**Closed forest**	**Entire**
West				
Savanna	**66.5**	**55.6**	**48.6**	**56.1**
Open forest	**34.6**	**23.7**	**24.4**	**26.8**
Closed forest	**75.0**	**67.8**	**55.4**	**61.1**
Entire	**70.1**	**59.2**	**49.9**	**57.4**

not between closed forests (*Z* = **1.753).** Overall rankings between east and west (*Z* = 0.161) did not differ significantly.

Forest structure

Because density was used as the criterion for classifying points into vegetation types, densities for the east:west vegetation type counterparts were similar (Table **3).** Overall, tree density was over four times greater in the east than the west, and mean basal area was over five times as great. These data included only points where trees were found and densities could be calculated. If prairie points (no trees) were included, density west of the river would be far less than that calculated.

Eastern types were generally twice as species rich as their western counterparts, with the greatest richness occurring in the closed forests (Table **3).** The relative paucity of species in the west, and the dominance of the two ***Quercus*** species, is illustrated by the lower species diversity (H') in the western landscape and in each of the western vegetation types relative to their eastern counterparts (Table **3).** The two closed forests had the highest H' for their respective sides of the river. The lowest value in the west occurred in the open forest; in the east, it was in the savanna.

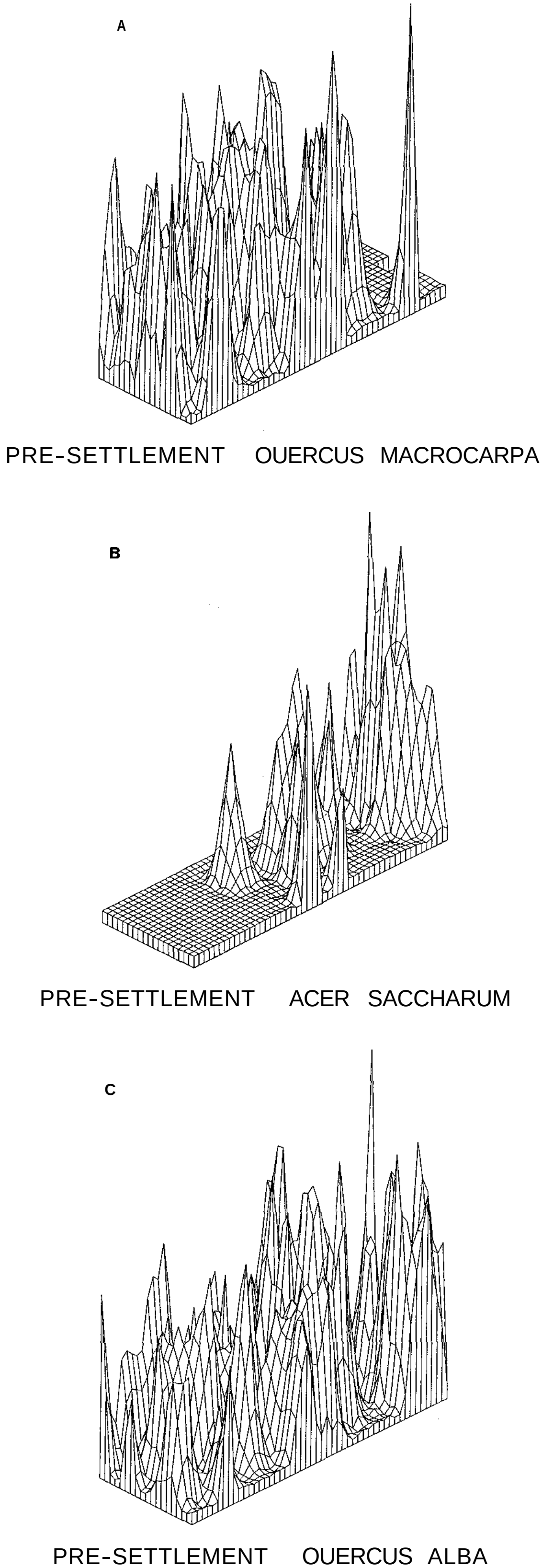

Fig. **2. Presettlement diameter distributions of three tree species across Green County, Wisconsin. (a) *Quercus macrocarpa*, (b) *Acer saccharum*, (c) *Quercus alba*.**

Table 5. Mean sizes and point-to-tree distances (± 1 SD) for the witness trees east and west of the Pecatonica River in 1831-33 in Wayne, Cadiz, and Clarno townships. Totals do not coincide because of missing or illegible survey note data, and because diameters also include line trees. N = number of trees encountered. * = difference in means between east and west is significant at $p \leq 0.05$.

Species	Diameter (cm)				Point-tree distance (m)			
	West		East		West		East	
	N	Mean	N	Mean	N	Mean	N	Mean
Q. macrocarpa	103	31.5 (10.4	42	34.2 (9.3)	89	36.9 (26.9)	35	41.4 (59.8)
Q. alba	80	38.5 (12.2)	126	41.4 (10.5)	60	28.6 (26.0)	97	12.4 (13.4)*
Q. rubra	23	28.0 (7.8)	70	40.9 (15.6)*	18	32.0 (27.0)	53	13.6 (15.8)*
Q. velutina	9	24.6 (4.7)	26	33.9 (9.6)*	7	34.1 (27.6)	19	11.6 (14.0)
Ulmus spp.	1	30.5	38	39.1 (21.0)	1	4.0	27	10.4 (12.9)
Populus spp.			28	35.0 (12.1)			23	18.9 (23.0)
Tilia americana	1	30.5	30	40.7 (15.8)	1	20.1	16	8.4 (5.5)
Acer saccharum			15	35.6 (11.8)			9	17.4 (22.3)
Fraxinus spp.	2	25.4 (0.0)	13	33.0 (5.9)	2	2.7 (1.8)	6	7.1 (4.6)
Ostrya virginiana			7	26.1 (5.4)			6	7.3 (3.8)
Carya spp.	6	29.6 (8.7)	4	29.2 (7.6)	6	24.4 (14.8)	1	23.9
Prunus			6	24.6 (5.9)			5	8.8 (7.9)
Juglans nigra			5	34.5 (8.4)			2	42.6 (46.1)
Celtis occidentalis			1	30.5			1	6.0
Salix spp.			1	20.3			1	11.9
Total	225	33.3 (11.4)	412	37.9 (15.4)*	184	32.6 (26.4)	300	16.4 (26.5)*

Tree size-classes and hierarchy

The three most common species show different diameter distributions across the landscape (Fig. 2). For instance, *Q. macrocarpa* (Fig. 2a) is virtually absent from eastern Cadiz Township, with nearly equal diameter distributions elsewhere. By contrast, *A. saccharum* (Fig. 2b) is absent west of the Pecatonica River and shows an increase in diameter towards the east. *Quercus alba* was present throughout the study area (Fig. 2c) and was the largest species on both sides of the river. Only *Q. rubra* and *Q. velutina* were significantly smaller west of the Pecatonica than east (Table 5). All trees combined, regardless of species, were significantly smaller to the west when compared to all trees in the east. Total basal area was greater in the east than in the west (Table 5).

In the east, both savanna and open forest had significantly greater mean tree diameters than their western counterparts (Table 6). Within eastern and western closed forest, tree sizes showed no significant difference (two-tailed t-test, $p > 0.05$). The largest trees were found in the eastern open forest, while the smallest trees occurred in the western open forest.

Table 6. Mean (± 1 SD) witness tree diameters (cm) by vegetation type, east and west of the Pecatonica River, for Wayne, Cadiz, and Clarno townships.

Vegetation type	N	Mean	t
Savanna east	90	39.3 (15.3)	2.16*
Savanna west	122	34.3 (12.5)	
Open forest east	57	41.8 (17.9)	3.36**
Open forest west	22	31.4 (9.2)	
Closed forest east	150	37.0 (15.6)	1.09
Closed forest west	37	34.5 (11.0)	
Entire east	412[a]	37.9 (15.4)	4.24***
Entire west	225[a]	33.3 (11.4)	

N = number of trees in each vegetation type. * = t-tests significant at $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

The most frequent stem size category in both areas was 32 cm (Fig. 3a); however, the east had a higher percentage of trees in larger classes. This comparison was also true for each vegetation type

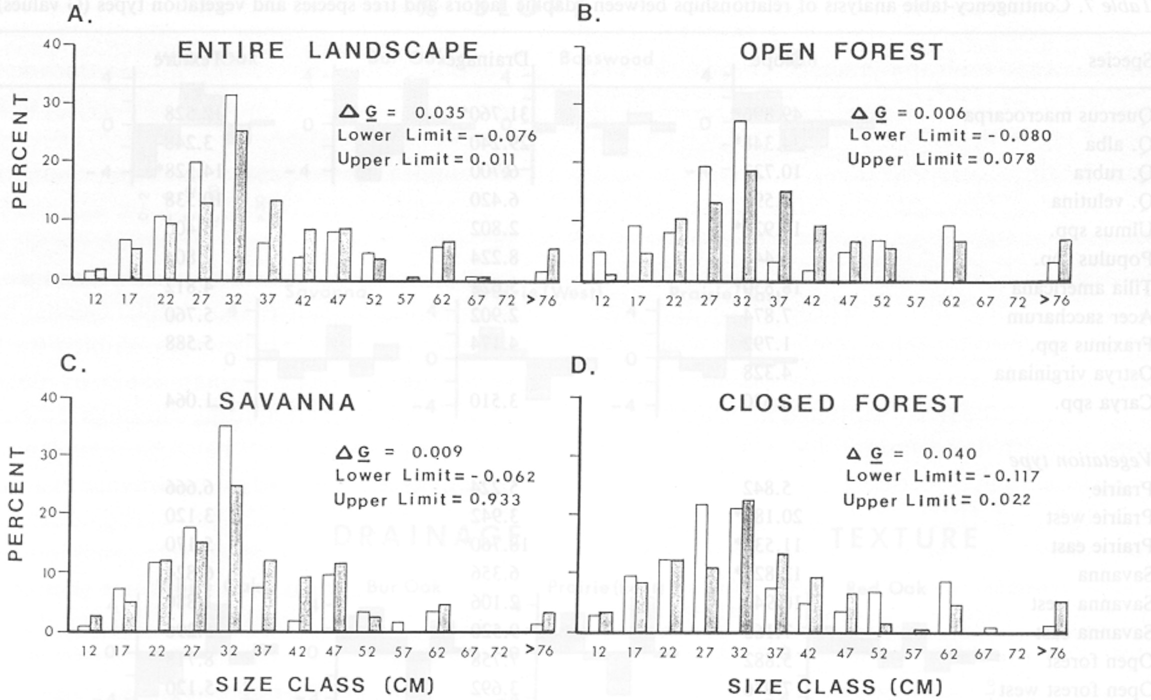

Fig. 3. Presettlement size-class distributions of witness and bearing trees in the study area (Fig. 1) plus adjacent Illinois for (a) the entire landscape, (b) open forest, (c) savanna, (d) closed forest. Open bars represent data west of the Pecatonica River; shaded bars are data east of the Pecatonica River. Within a vegetation type, no east *vs.* west distinction was significant.

individually (Figs. 3b–d). The Gini coefficients, however, indicated that neither small nor large trees (in terms of basal area) were overly represented on either side of the river. Although the two overall distributions (Fig. 3a) did not differ significantly in terms of hierarchy (based on basal area apportionment), mean tree size did differ significantly between both sides of the river. That is, the relative apportionment of basal area among individuals in a given vegetation type was similar on both sides of the Pecatonica River.

Soil and site relationships

Over 99% of the soils on each side of the Pecatonica River were classified as silt-loams. Total water holding capacity of each forest type differed little between the west and east sides of the Pecatonica River (Table 1). For only prairie was there a significant difference between east and west in the total amount of water in the soil profile available to plants, with prairie in the east being found on the driest and shallowest soils in the entire landscape.

Only seven species-site relationships and four vegetation type-site relationships were significant (Table 7), with the strengths of these significant relationships indicated by standardized residuals (Fig. 4). Among those factors tested, percent slope appeared to be the most important. The western prairie was found more frequently on areas of little relief, while the eastern prairie was more common on slopes of between 12 and 20%, either somewhat poorly or somewhat excessively drained. (For this analysis, those corner points indicated as "wet prairie" by the surveyors were eliminated.) Savanna was found more frequently on steeper slopes.

Among species, *Ulmus* was more frequent on level sites and uncommon on moderate and steep slopes (Fig. 4). Other species-site relationships were not as clear. Site preferences for *Q. alba* and *Q. macrocarpa* appeared as nearly mirror images, with the former more common on areas of moderate relief and well-drained soils, while *Q. macrocarpa*

Table 7. Contingency-table analysis of relationships between edaphic factors and tree species and vegetation types (*G* values).

Species	Slope	Drainage	Texture
Quercus macrocarpa	49.896*	31.760*	12.528
Q. alba	34.348*	29.240	3.248
Q. rubra	10.722	6.700	14.528*
Q. velutina	2.592	6.420	10.538
Ulmus spp.	18.928*	2.802	6.400
Populus spp.	6.440	8.224	7.804
Tilia americana	18.850*	5.622	4.812
Acer saccharum	7.874	2.902	5.760
Fraxinus spp.	1.792	4.174	5.588
Ostrya virginiana	4.328		
Carya spp.	2.620	3.510	1.064
Vegetation type			
Prairie	5.842	5.224	6.666
Prairie west	20.182*	3.942	3.120
Prairie east	11.538*	18.760*	5.170
Savanna	12.828*	6.356	6.824
Savanna west	10.946	2.106	1.880
Savanna east	7.168	9.520	5.296
Open forest	5.882	7.758	8.718
Open forest west	7.976	3.692	5.120
Open forest east	4.366	8.882	5.076
Closed forest	8.186	4.390	3.710
Closed forest west	10.480	5.986	3.512
Closed forest east	0.738	7.404	2.522

more often was found on poorly- or excessively-drained soils of little or high relief. The only significant association with texture was for Q. ***rubra,*** which was more often located on coarser soils or loams than on fine-textured soils (Fig. 4).

Landscape pattern

The landscapes east and west of the Pecatonica River differed in landscape diversity, dominance, and heterogeneity (Table **2).** About 50% of the east was covered by closed forest, with an additional **19%** in open forest. The extent of closed forest vegetation yielded a higher landscape dominance index (D_o; Turner **1989)** than in the west. Prairie and savanna were almost equally prevalent in the west, resulting in a lower landscape dominance. Consequently, the west landscape was more heterogeneous than the east. If prairie and savanna are combined and treated as a single fire-prone vegetation type, then the west could be considered to be more homogeneous.

Discussion

Differences in forest composition and structure evidently existed between the east and west sides of the Pecatonica River in **1831–33.** To the west, the woody vegetation types appear to be patches of the same species (primarily Q. ***macrocarpa*** and ***Q. alba*)**, but in different densities, interspersed among extensive areas of prairie. To the east, these same species were also present in lower densities and with an admixture of more mesic taxa.

Site characteristics

Physical site characteristics such as soil thickness, TWHC (drainage), and texture seem to have con-

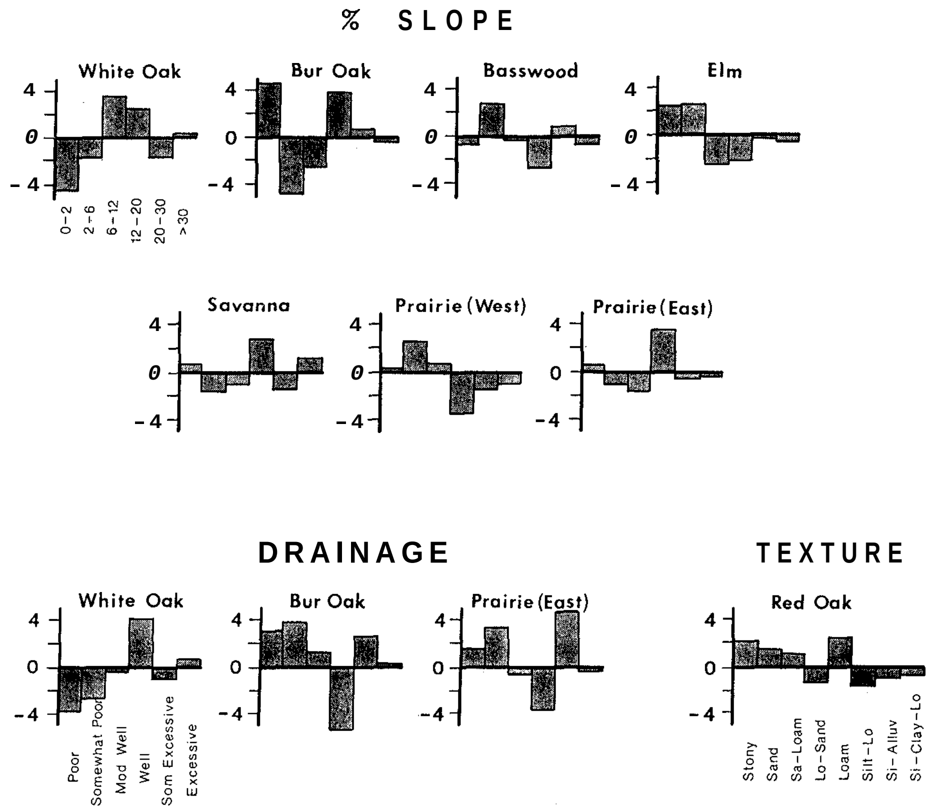

Fig. 4. **Standardized residuals of the four species-site relationships, and three vegetation type-site relationships found to be statistically significant (Haberman's *d*). Positive residuals indicate a positive association with a site characteristic, while negative residuals indicate negative associations.**

trolled the location of certain vegetation types (especially prairie and savanna) in the presettlement landscape. The west portion of the landscape was drier than the east which could have a bearing on the different fire regimes (*e.g.*, Greenlee and Langenheim **1990).** The presence of several taxa, including Q. ***macrocarpa,*** Q. ***alba, Ulmus*** spp., and ***T. americana*** was related significantly to these local site characteristics. In a similar study, Whitney **(1982)** concluded that presettlement species distributions and forest composition in northeastern Ohio (U.S.A.) were in large measure related to such site characteristics as soil texture and drainage.

Fire

In addition to some significant species-site relationships, distribution of certain species was probably controlled also by extrinsic factors such as fire at the landscape level. Thus, the presettlement pattern of vegetation (landscape scale) was likely an interactive response to site and fire (local scale). Because the original survey notes did not mention fire, this conclusion is circumstantial, but it is substantiated by documented fire regimes in prairies and savannas in other parts of southern Wisconsin (Curtis **1959;** Dorney **1980;** McCune and Cottam **1985).**

Fire return times are difficult to estimate for southern Wisconsin because of fire suppression and forest fragmentation. Dorney **(1980)** calculated an average fire return time of **16** years for areas west of major waterways in presettlement southeastern Wisconsin, compared to **112** years on the protected eastern sides. **A** similar fire return time (***i.e.***, ca. **16** years) was likely in Cadiz woodlands west of the Pecatonica. In prairies and savannas, annual fires probably occurred (Anderson and Anderson **1975;**

Anderson and Brown **1986).** It is likely that fire was more common to the west of the river because of the landscape moisture gradient (that is, the west side was drier than the east) as has been noted for some California landscapes (Greenlee and Langenheim **1990).**

Certainly, fire was not absent east of the Pecatonica, but apparently its intensity and frequency were lower. The disparity in distribution of prairie supports this conclusion. To the west, prairie occupied the long, gentle slopes where fires could progress almost unhindered. Thus, the area to the west of the river, subjected to more frequent fires, supported vegetation types (*i.e.*, prairie and *Quercus* savanna) associated with fire (Anderson and Anderson **1975).** With cessation of fire, the prairies and savannas have since been invaded by woody species (Cottam **1949;** Stewart **1951;** Daubenmire **1968;** Wells **1970;** Whitford and Whitford **1971;** Tans **1976;** Whitford **1983;** McCune and Cottam **1985).** Other studies in the midwestern United States have shown waterways to form effective firebreaks and to separate prairie and xeric woodland from more mesic forest (Heinselman **1973;** Grimm **1984;** Nigh *et al.* **1985;** Whitney and Steiger **1985).**

Less frequent fires in the east would tend to restrict prairies to the more exposed steep, dry sites with shallow soils where trees would have difficulty becoming established. Many of the taxa absent or rare to the west (*e.g.*, *A. saccharum, Ulmus* spp., *T. americana, Fraxinus* spp., ***Populus*** spp., **O.** *virginiana, Celtis occidentalis)* are fire-sensitive and could not survive frequent fires (Fowells **1965);** however, these mesic species could actually reduce the spread of fire because they are not particularly flammable (McCune and Cottam **1985;** Anderson and Brown **1986).** That fire did have some infuence on the east side of the Pecatonica is indicated by the distribution of *A. saccharum*, which, prior to settlement, existed only at low density in the landscape (but probably high density per stand). Other studies also have shown that, with cessation of fire, ***A.*** *saccharum* density increases dramatically (Peet and Loucks **1977;** McCune and Cottam **1985).**

Landscape pattern

Interaction between local site conditions and disturbance history produced measurably different landscapes on the west and east sides of the Pecatonica River. Questions remain, though, as to whether disturbance increases or decreases beta diversity, and under what circumstances. Also, how does landscape heterogeneity itself affect the spread of disturbance (Turner *et al.* 1989)**?** Greater heterogeneity is commonly believed to inhibit disturbance (Wiens *et al.* **1985;** Forman **1987)** by providing more barriers to its spread, although others have cited instances in which heterogeneous landscapes can enhance the spread of disturbance (Turner and Bratton **1987).** Generally, homogeneous landscapes provide large areas of similar site conditions, which may aid the spread of disturbance (Risser *et al.* **1984).**

Not only does the nature of the landscape affect disturbance, but the opposite is also true. Frequent and intense disturbance is generally thought to increase landscape homogeneity (Wiens *et al.* **1985).** However, because the landscape west of the Pecatonica River supported large areas of both prairie and savanna, it was more heterogeneous than the landscape east of the river. To the west of the river, greater landscape heterogeneity could have enhanced the spread of disturbance because fire can spread between the two dominant vegetation types. However, in terms of landscape flammability (prairie plus savanna), the west landscape could be considered to have been relatively uniform. This uniformity could have fostered disturbance by enabling fires to build in intensity and to travel virtually unimpeded. Thus, fire increased homogeneity (in terms of flammability) which, in turn, increased the frequency of fire – a positive feedback. As Kline and Cottam **(1979)** observed, positive feedback mechanisms favor both savanna and mesic forest, with the vegetation in part perpetuating the fire regime which helped establish it.

Although fire was important in creating and maintaining the mosaic of vegetation types in Cadiz Township, the actual effect of this disturbance depended on site conditions and geographic barriers. In the Boundary Waters Canoe Area (Minnesota, U.S.A.) for example, the physiographic location of forest stands was also shown to ameliorate fire intensity, permitting the establishment of particular vegetation types (Heinselman 1973). In the Bitterroot Canyons (Montana, U.S.A.), McCune and Allen (1985) concluded that only 10% of the compositional variation among similar sites was attributable to measured site factors. The remaining variation was a primarily a result of different fire regimes among sites. In southern Wisconsin, the legacy of this interaction between disturbance, topography, and vegetataion can be found in the scattered woodlots of today. With the cessation of fire came successional change (*e.g.*, McCune and Cottam 1985), which, with other disturbances (grazing, cutting, and forest fragmentation), have resulted in the current human-dominated landscape – a collection of scattered forest "islands" within an agricultural matrix (Sharpe et *al.* 1987). One system of patches has been replaced by a new patchy landscape.

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