TREE SPATIAL PATTERNS IN AN OLD-GROWTH FOREST IN EAST-CENTRAL INDIANA[1]

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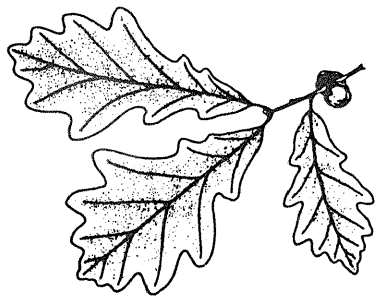

ABSTRACT.--Tree spatial patterns were determined from the 1981 locations of all trees, ≥ 10.0 cm dbh, within the central 8.5 ha of a 20.6 ha old-growth forest in east-central Indiana. Four spatial indices: variance-to-mean ratio, Morisita's index of dispersion, Clark-Evans nearest neighbor index, and Pielou's nonrandomness index, were used to determine the degree of dispersion for each species (i.e., whether the population is uniform, random or aggregated). All four indices suggest that most species are aggregated to various degrees. Causes of aggregation include gap colonization, impeded soil drainage (Acer saccharinum, Fraxinus nigra, and Quercus macrocarpa), vegetative reproduction (Aesculus glabra, Fagus grandifolia, and Gleditsia triacanthos), and historical factors (cutting and grazing). Only Quercus rubra has a uniform pattern; Acer saccharum and Ulmus americana have the most random dispersion. Suggestions for the use of spatial data are given.

INTRODUCTION

Forest compositional and structural attributes provide the species abundance, size, age, etc., but do not reveal how individuals are distributed within the forest relative to conspecifics and other species. Spatial distributions are more indicative of dynamic forest processes than simple population parameters. Three broad types of spatial patterns are possible: (1) regular or uniform, in which a species is distributed as trees might be arranged in an orchard; (2) clumped or aggregated, in which a species occurs in scattered discrete groups; and (3) random, in which a species appears to be distributed haphazardly. Furthermore, there are two components of any pattern: intensity and grain (Pielou 1974, p. 147). Intensity is the extent to which density changes throughout a community; grain is the scale of patch size within the community. Spatial indices represent these components to various degrees, or not at all. Of the many indices employed to elucidate spatial patterns (e.g., see Grieg-Smith 1983; Pielou 1969, 1974; Poole 1974) two general methodologies are used: distance measurements or quadrat (area) analyses (Goodall and West 1979).

Such indices have been used to describe tree spatial patterns in temperate pine (Cooper 1961, Laessle 1965, West 1969, Daniels 1978, Yeaton 1978), mixed hardwood (Williamson 1975, Whipple 1980), and mixed hardwood-conifer (Payandeh 1974, Gill 1975, Christensen 1977, Squiers and Klosterman 1981, Good and Whipple 1982) forests. Their applicability has also been demonstrated for tropical forests (Richards and Williamson 1975, Hubbell 1979, Veblen et al. 1979, Forman and Hahn 1980, Abbott 1984).

Four indices were selected to describe tree species patterns in an old-growth oak-hickory forest in east-central Indiana. These indices were the Clark-Evans nearest neighbor index and Pielou's point-to-nearest neighbor plant index (both distance based); and Morisita's index of dispersion and the variance-to-mean ratio (both quadrant based). The present study is unique because: (1) only one spatial analysis has been published for central hardwood forests (Williamson 1975), and for fewer species; (2) four indices were calculated for each species, rather than one or two; (3) the study area has long been relatively undisturbed; and, (4) the sample area is relatively large.

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Assumptions, advantages, limitations, and applications of each spatial index are addressed in this paper. Possible reasons for indicated patterns are also discussed.

STUDY AREA

The 20.6 ha Davis-Purdue Research Forest (fig. 1) is located in Randolph County in east-central Indiana 24 km northeast of Muncie (Section 23, T 21 N, R 12 E). It is one of the best examples of relatively undisturbed forest remaining on the intensively farmed Tipton Till Plain which covers most of central Illinois, Indiana and Ohio. Details on the history, topography and soils of this stand are given in Parker and Leopold (1983) and Parker et al. (1985). The forest was apparently subject to livestock grazing prior to Purdue ownership in 1917. Limited cutting of dead or dying trees was made in the 1940s and 50s for local farm use. A small surface fire occurred in the western portion in 1972.

METHODS

Field Measurements

All stems $\geq$ 4.0 in (10.2 cm) dbh (diameter at breast height, 1.37 m aboveground) were measured, tagged and mapped on the entire 20.6 ha forest in 1926. In 1976, all trees $\geq$ 10.0 cm dbh in the central 21 plots (0.4 ha each, 8.5 ha total; fig. 1) were again measured, tagged and mapped. Ingrowth trees (those $\geq$ 10.0 cm not tallied in the 1976 inventory) in the central 21 plots were measured and mapped in 1981, and mortality for each species was updated. Tree locations were described as east-west and north-south coordinates (nearest 1 m) for computer analyses. Thorough descriptions of the field aspects of this study are described elsewhere (Parker and Leopold 1983, Parker et al. 1985). Population parameters of tree species are shown in table 1.

Spatial indices were calculated for trees $\geq$ 10.0 cm dbh that were alive in 1981. Since only the central portion of the forest was analyzed, spatial patterns were not influenced by forest edge effects.

Descriptions of Indices

CLARK-EVANS NEAREST NEIGHBOR INDEX.--The Clark-Evans nearest neighbor index (R) expresses nonrandomness on a relatively small scale because conspecific distances are determined from individuals which are usually part of a local patch. Therefore only the intensity of the pattern is measured (Pielou 1969). The mathematical derivation of this index is shown in Clark and Evans (1954); it is calculated by:

$$R = \bar{r}_a/\bar{r}_e = ((\Sigma r)(2\sqrt{\rho}))/N$$

where $\bar{r}_a$ equals the mean observed nearest neighbor distance ($\Sigma r/N$); $\bar{r}_e$ is the expected mean nearest neighbor distance given random dispersion; r is the measured distance to the nearest neighbor; ρ equals the density expressed as individuals per unit area; and N is the number of measurements. The significance level is calculated using the standard variate of the normal curve (Clark and Evans 1954, p. 447-448). If values are not significantly different from 1.0, then the population has a random dispersion. Values greater than 1.0 suggest a uniform distribution; those less than 1.0, an aggregated pattern. An independent estimate of population density is required unless it is known, as it is for this study. If only a subsample of trees is taken then such sampling must be random (Pielou 1959). In this study nearest neighbor distances were calculated for all individuals of each species within the study area. The Clark-Evans index may be the best method to measure pattern intensity of smaller patches (Pielou 1969).

PIELOU'S POINT-TO-PLANT INDEX.--Pielou's point-to-plant index α describes nonrandomness at small to large scales since tree distances are determined from random points throughout the forest. Consequently, this index reflects both the intensity and grain of species patterns (Pielou 1969). It is represented by:

$$\alpha = \pi D\bar{\omega}$$

where D is the number of individuals per unit area; and $\bar{\omega}$ is the mean of the squared distances from randomly located points to the nearest individuals of a particular species. In a randomly dispersed population the expected value of α equals (n-1)/n where n is the number of random points. Calculated values significantly greater than the expected suggest that the population is aggregated. Those less than the expected value imply a uniform distribution, and those not significantly different from the expected values indicate random dispersion. Significance levels are determined from the table of confidence intervals in Pielou (1959, p. 609); the derivation of this index is also presented there. This index requires that points be randomly located throughout the area; and, as for the Clark-Evans index, an independent estimate of population density is required, unless population density is known.

MORISITA'S INDEX OF DISPERSION.--Morisita's index of dispersion (I_δ) is given by:

$$I_\delta = q\Sigma n_i\ (n_i-1)/N(N-1)$$

where q is the number of quadrats, n_i is the number of individuals of the species in the ith quadrat and N is the total number of individuals in all q quadrats. While significance levels can be determined as shown by Brower and Zar (1977, p. 122); Stiteler and Patil (1969) have questioned the validity of the significance levels. I_δ equals 1.0 if the species is randomly distributed, is greater than 1.0 for aggregated patterns, and is less than 1.0 for uniform distributions. Values of I_δ at various quadrat sizes suggest the size of natural patches (Morisita 1959, Williamson 1975).

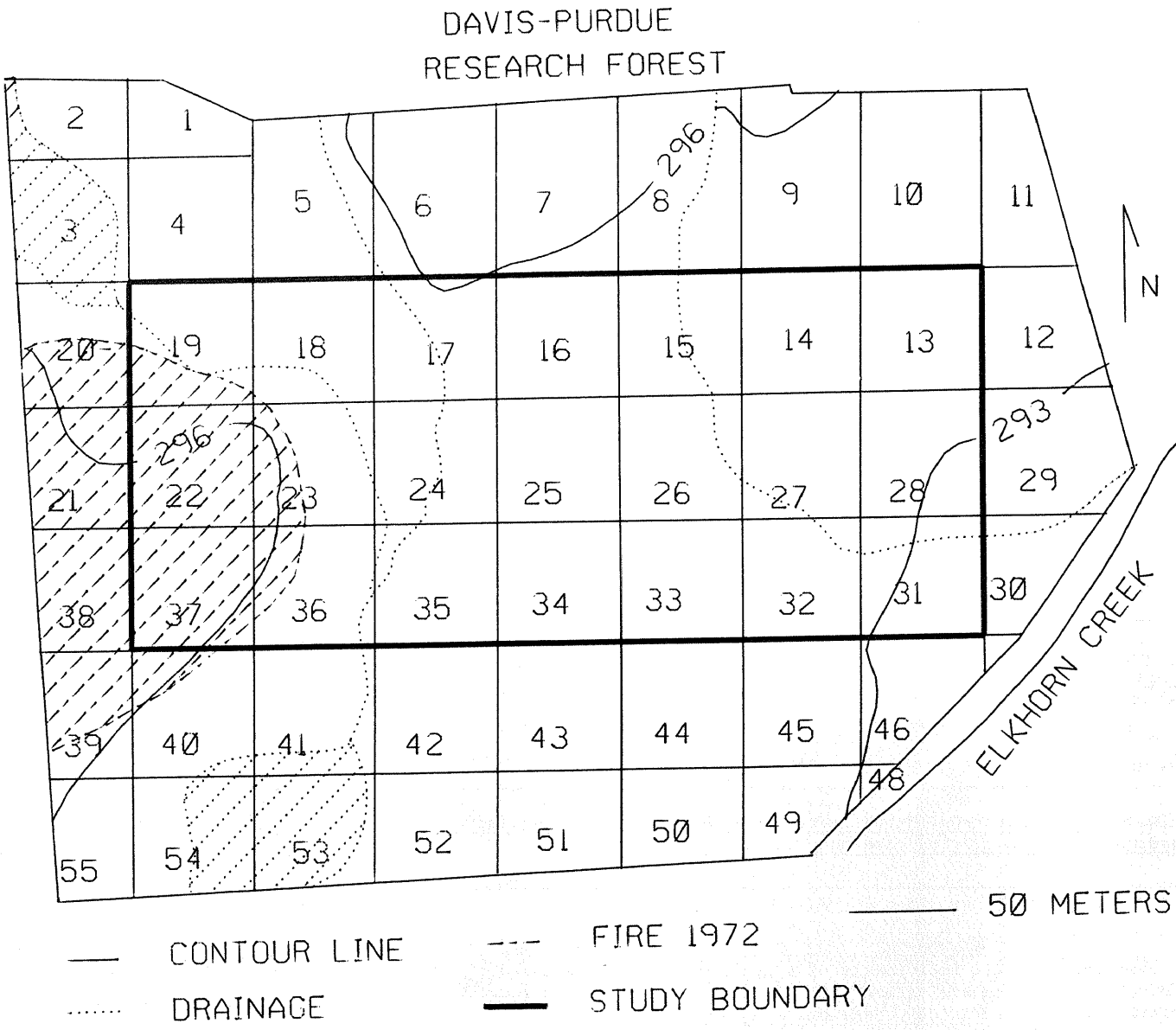


FIGURE 1.--Map of Davis-Purdue Research Forest with study area delineated.

Therefore both intensity and grain of pattern are indicated by Morisita's index. Additional details on the derivation and use of this index are in Morisita (1959, 1962, 1971).

VARIANCE-TO-MEAN RATIO.--The variance-to-mean ratio is based on the assumption that a randomly dispersed population has a Poisson distribution, i.e., the population mean μ equals the population variance σ^2. Frequencies of species densities in randomly placed unit areas are determined. A randomly dispersed population has a variance to mean ratio of 1.0. Ratios significantly greater than 1.0 denote a clumped pattern whereas ratios less than 1.0 imply a uniform pattern (Greig-Smith 1983, p. 61-63). Significance is determined by multiplying the variance-to-mean ratio by (n-1) where n equals the number of observations. The resulting value is known as the "index of dispersion", and it is compared to χ^2 values with (n-1) degrees of freedom.

Computer Analyses

The Clark-Evans and Pielou indices were calculated over the entire 8.5 ha for species with 10 or more individuals. For the Clark-Evans index, distance to the nearest conspecific neighbor

TABLE 1.--Density (D), relative density (RD), basal area (BA), relative basal area (RBA), and Importance Values (IV=(RD + RBA)/2) by species, of trees ≥ 10.0 cm dbh in the central 8.5 ha of Davis-Purdue Research Forest in 1976 (modified from Parker and Leopold 1983).

Species	D (no. of trees)	RD	BA(m^2)	RBA	IV
Quercus rubra	195	7.2	76.4	29.0	18.1
Ulmus americana	633	23.3	12.7	4.8	14.1
Acer saccharum	481	17.7	11.9	4.5	11.1
Quercus alba	92	3.4	34.0	12.9	8.2
Fraxinus americana	165	6.1	25.6	9.7	7.9
Quercus macrocarpa	69	2.5	31.4	11.9	7.2
Carya ovata	214	7.9	8.4	3.2	5.6
Quercus bicolor	43	1.6	13.7	5.2	3.4
Aesculus glabra	138	5.1	2.6	1.0	3.0
Juglans nigra	69	2.5	8.4	3.2	2.9
Quercus muehlenbergii	29	1.1	8.4	3.2	2.2
Quercus palustris	27	1.0	8.4	3.2	2.1
Carpinus caroliniana	103	3.8	0.8	0.3	2.0
Celtis occidentalis	78	2.9	1.6	0.6	1.8
Fagus grandifolia	74	2.7	2.6	1.0	1.8
Ulmus rubra	43	1.6	1.6	0.6	1.1
Carya cordiformis	44	1.6	0.8	0.3	1.0
Crataegus spp.	43	1.6	0.8	0.3	1.0
Ostrya virginiana	39	1.4	0.8	0.3	0.9
Prunus serotina	37	1.4	0.8	0.3	0.9
Acer saccharinum	18	0.7	1.6	0.6	0.7
Fraxinus nigra	15	0.6	1.6	0.6	0.6
Gleditsia triacanthos	12	0.4	1.6	0.6	0.5
Acer negundo	18	0.7	0.3	0.1	0.4
Platanus occidentalis	4	0.1	0.8	0.3	0.2
Other species[a]	39	1.4	5.8	2.2	1.8
Total, 8.5 ha.	2722	100.0	263.5	100.0	100.0
Total ha^{-1}	320		31.0		

[a]Includes Tilia americana, Morus rubra, Fraxinus quadrangulata, Carya glabra, Populus deltoides, Cercis canadensis, Cornus florida, Amelanchier arborea

was determined for all individuals of a species. Therefore, sample numbers varied with species densities, from 10 (Fraxinus quadrangulata) to 626 (Ulmus americana). For Pielou's nonrandomness index, 200 points were randomly located throughout the forest for each species, and the distance to the nearest individual of that species from each point was determined.

For each species, the Morisita index of dispersion and the variance-to-mean ratio were computed on the one 0.4 ha plot that had the most trees of that species. Analyses were done only on species that had at least 7 individuals on any of the 21 plots. Quadrat sizes for both indices began at 1x1 m and increased by 1 m increments up to 12x12 m and thereafter, usually by 2x2 m increments up to 30x30 m. For Morisita's index the number of quadrats used for a given quadrat size equals 60x60 m (~ dimension of each plot) divided by the area of the quadrat size (e.g., 3600 1x1 m quadrats, 144 5x5 m quadrats, 9 20x20 m quadrats). Variance-to-mean ratio values are based on 100 randomly placed quadrats of each size for each species. Only the results for 5x5, 10x10, and 15x15 m quadrats are presented here.

RESULTS

CLARK-EVANS INDEX.--Average distances to the nearest conspecific individual vary substantially among species (table 2). This distance was shortest for Acer saccharinum (4.8 m), longest for Tilia americana (56.5 m).

The Clark-Evans index indicates that over half of the tree species at the Davis-Purdue Research Forest are aggregated within small patches (table 2). By this index, ten species are randomly distributed and two are uniformly distributed.

PIELOU'S NONRANDOMNESS INDEX.--This index suggests that all species are aggregated at a scale wider than that found by the Clark-Evans index, (table 2). Disparities between the two distance-based indices are due to differences in scale that each index encompasses. For example, many species

TABLE 2.--Clark-Evans nearest neighbor index (R) and Pielou's nonrandomness index (α) for each species (10 or more individuals in forest) at the Davis-Purdue Research Forest.

Species	Density[a]	r_e[b]	r_a[c]	R	Pattern[d]	α	Pattern
Acer negundo	21	31.50	14.81	0.47**[e]	A	4.60**	A
A. saccharinum	18	34.02	4.76	0.14**	A	40.15**	A
A. saccharum	600	5.89	5.54	0.94**	A	2.62**	A
Aesculus glabra	150	11.79	10.25	0.87**	A	2.16**	A
Amelanchier arborea	13	40.43	41.64	1.03	R	1.92**	A
Carpinus caroliniana	93	14.97	11.08	0.74**	A	3.95**	A
Carya cordiformis	48	20.84	15.84	0.76**	A	2.71**	A
C. ovata	219	9.75	8.29	0.85**	A	1.77**	A
Celtis occidentalis	92	15.05	9.03	0.60**	A	3.83**	A
Crataegus spp.	46	21.49	19.77	0.92	R	1.70**	A
Fagus grandifolia	76	16.56	12.92	0.78**	A	2.24**	A
Fraxinus americana	167	11.17	10.95	0.98	R	1.36**	A
F. nigra	18	34.02	20.41	0.60**	A	2.18**	A
F. quadrangulata	10	46.10	17.52	0.38**	A	17.14**	A
Gleditsia triacanthos	11	43.95	20.66	0.47**	A	14.59**	A
Juglans nigra	68	17.68	16.26	0.92	R	2.11**	A
Ostrya virginiana	42	22.27	19.38	0.87	R	1.72**	A
Prunus serotina	41	22.54	21.42	0.95	R	1.78**	A
Quercus alba	86	15.57	11.52	0.74**	A	2.19**	A
Q. bicolor	43	22.01	20.91	0.95	R	1.60**	A
Q. macrocarpa	69	17.38	16.34	0.94	R	2.57**	A
Q. muehlenbergii	28	27.55	28.10	1.02	R	1.38**	A
Q. palustris	26	28.31	24.06	0.85	R	2.38**	A
Q. rubra	187	10.57	11.51	1.09*	U	1.36**	A
Tilia americana	15	37.64	56.46	1.50**	U	1.30**	A
Ulmus americana	626	5.77	5.31	0.92**	A	1.73**	A
U. rubra	55	19.46	14.40	0.74**	A	3.41**	A

[a]for entire 8.5 ha 1981

[b]expected distance from individual to nearest conspecific, m

[c]mean distance from individual to nearest conspecific, m

[d]A: aggregated, U: uniform, R: random

[e]*: significant at $p \leq 0.05$, **: significant at $p \leq 0.01$

(Amelanchier arborea, Crataegus spp., Fraxinus americana, Juglans nigra, Ostrya virginiana, Prunus serotina, and most Quercus spp.) are randomly distributed within a small patch, but are aggregated at the scale of the forest.

MORISITA'S INDEX.--Plots of Morisita's index at increasing quadrat size are shown in figure 2; species are grouped on the graphs by genus or family except for figure 2h. Of the three Ulmacea, Ulmus americana appears to be least aggregated and, basically is randomly distributed at larger quadrat sizes (fig. 2a). Celtis occidentalis and U. rubra are clumped at most quadrat sizes, with maximal clumping at the 2 m and 4 m quadrats, respectively. Acer saccharum tends to have a uniform pattern at smaller quadrat sizes and a random dispersion at a larger scale (fig. 2b). Uniform dispersion at smaller quadrat sizes is expected as a result of increased intraspecific competition. However, most species do not display such a pattern within smaller areas. Other Acer spp. are clumped, especially A. saccharinum. Carya ovata tends to be more aggregated than C. cordiformis at smaller quadrat sizes, but this trend reverses for larger quadrats (fig. 2c). Juglans nigra is aggregated at all quadrat sizes (fig. 2c). Both Betulaceae members (Carpinus caroliniana and Ostrya virginiana) are aggregated at all scales (fig. 2d). In the Quercus subgenus Erythrobalanus, Q. palustris is highly aggregated, with maximal clumping at 8 m; Quercus rubra is either uniformly or randomly distributed, depending on the quadrat size (fig. 2e). All members of the Quercus subgenus Leucobalanus are noticeably clumped at small and medium quadrat sizes (fig. 2f). The two Fraxinus spp. differ in their degree of aggregation, e.g., aggregation is highest at 2 m for F. americana versus 7 m for F. nigra (fig. 2g). All remaining species (fig. 2h), are aggregated to some degree.

VARIANCE-TO-MEAN RATIO.--Variance-to-mean ratios at various quadrat sizes are shown in table 3. Acer saccharinum has the most aggregated pattern of this genus. Other species which are aggregated at most quadrat sizes include Carpinus caroliniana, Celtis occidentalis, Fraxinus americana, F. nigra, Juglans nigra, Quercus alba, and Q. palustris. Only Quercus rubra has a uniform distribution at most quadrat sizes.

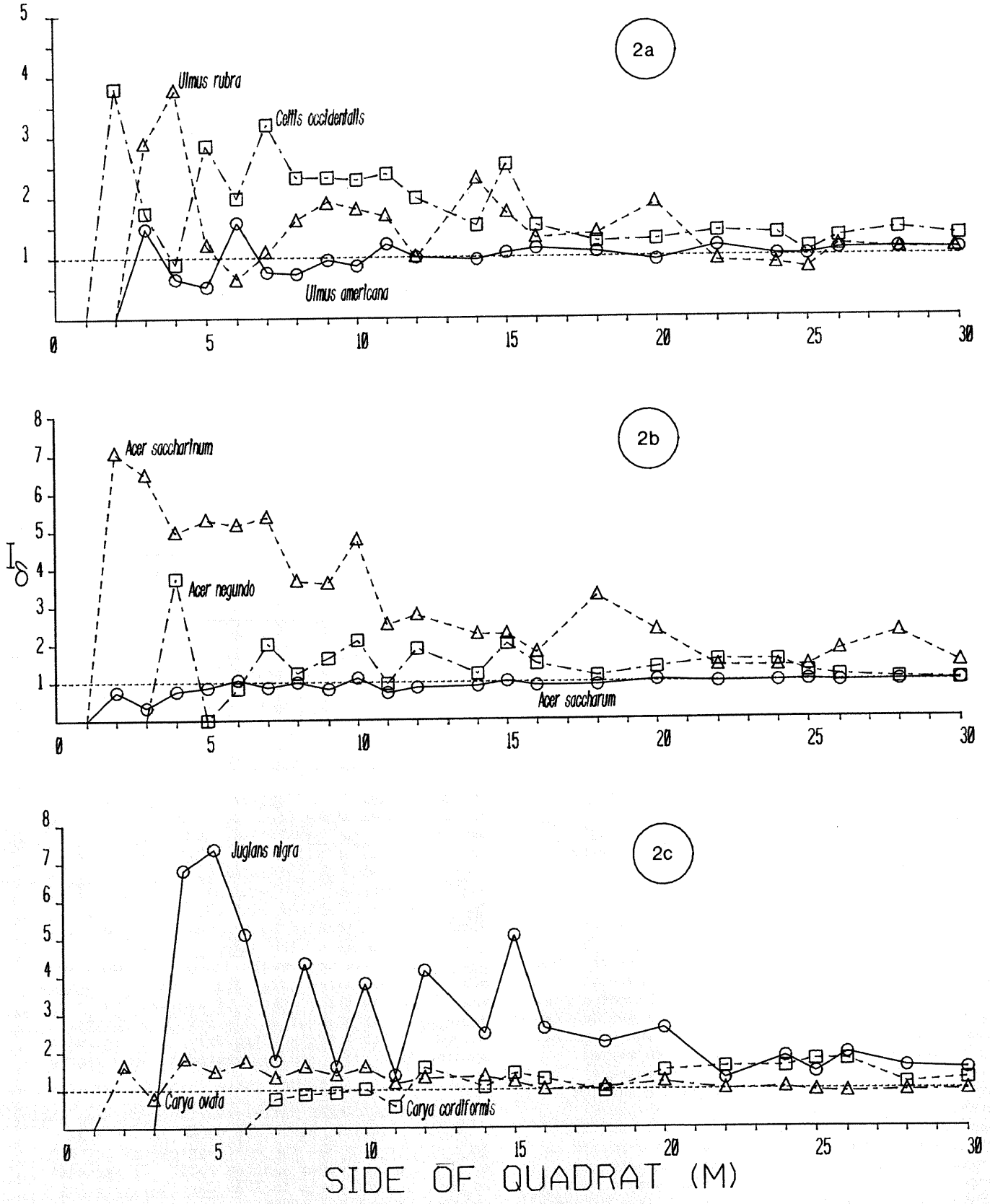


FIGURE 2.--Plots of Morisita's index at various quadrat sizes for each species of Davis-Purdue Research Forest. Values of $I_\delta > 1$ indicate aggregated distribution.

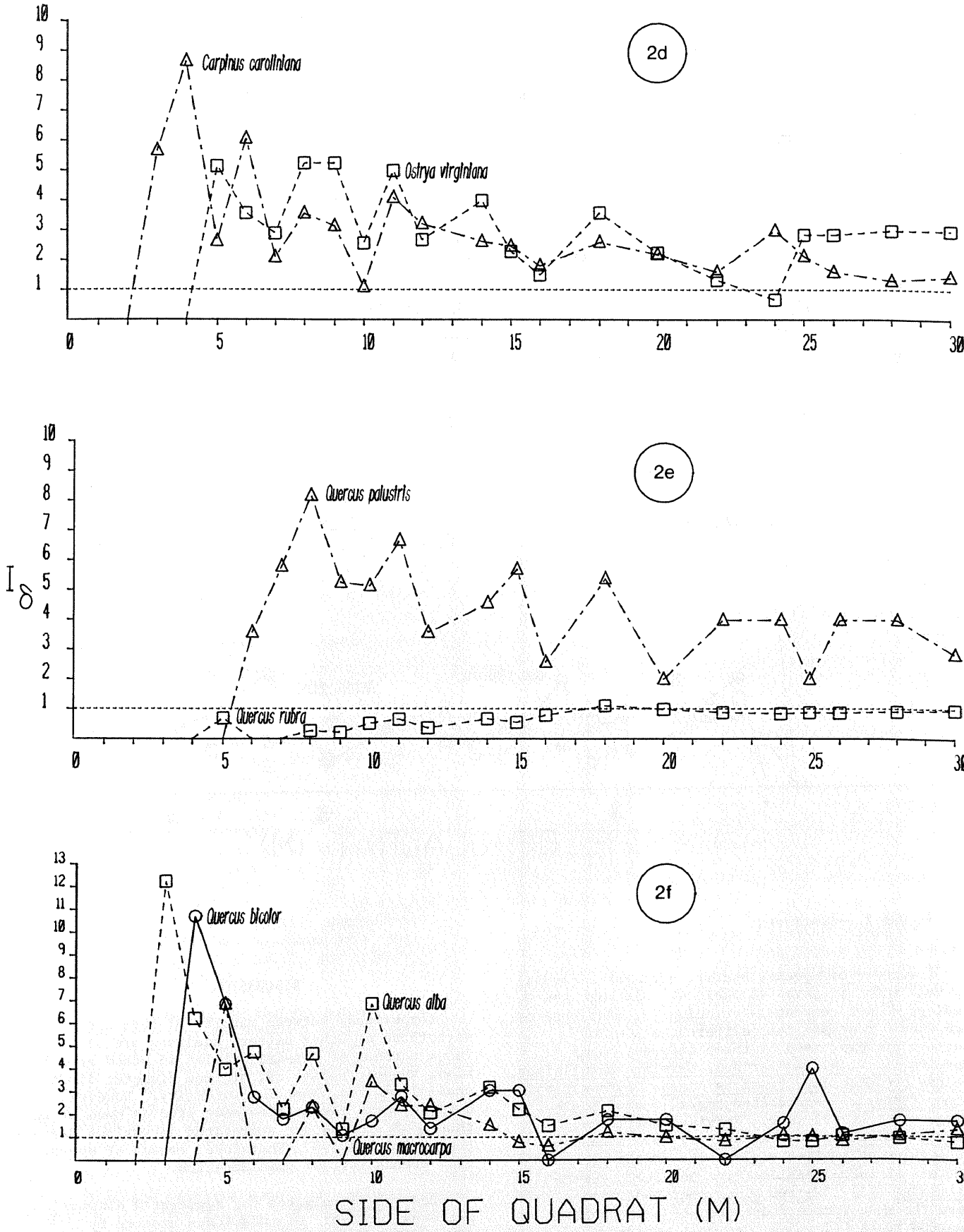
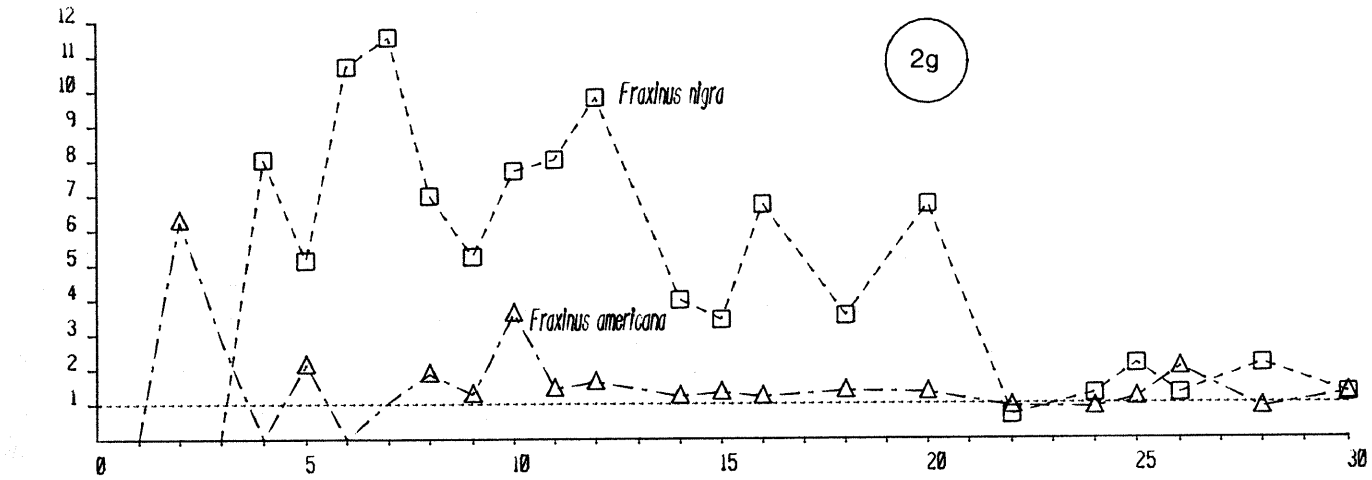


FIGURE 2.--Continued



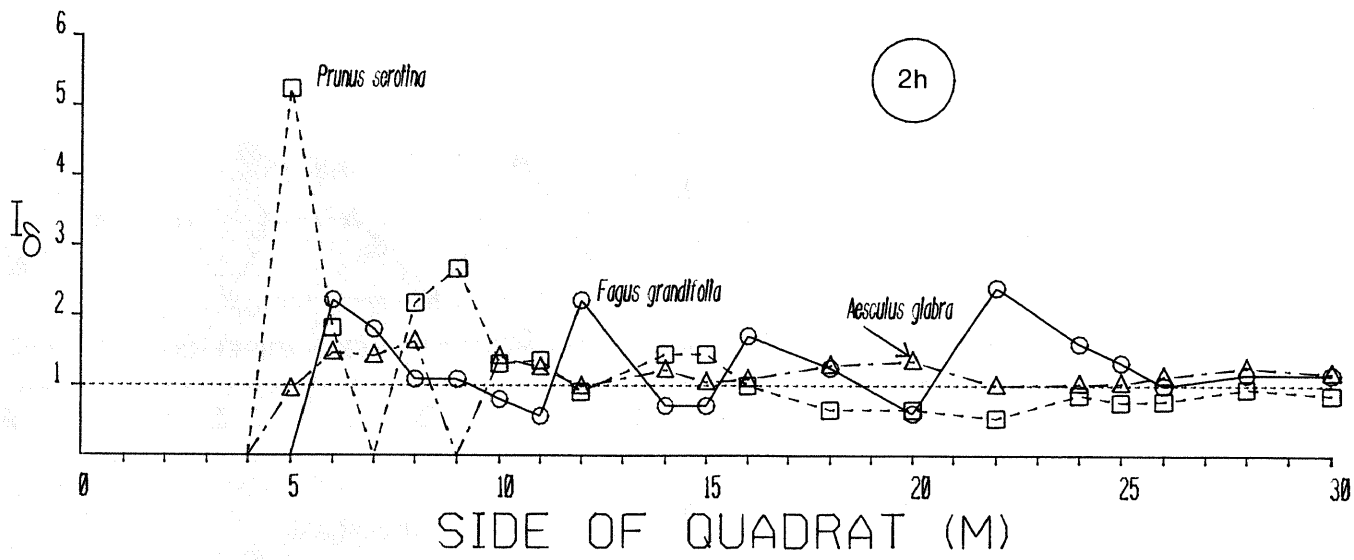


FIGURE 2.--Continued

A summary of species spatial patterns according to each index is given in table 4. Although the 4 indices do not completely coincide for most species, one should remember that different scales of pattern are expressed by these indices. Some species (i.e., A. saccharinum, Carpinus caroliniana, Celtis occidentalis, Fraxinus nigra, Quercus alba, Ulmus rubra) are aggregated regardless of scale (fig. 3a). Others (e.g., Fraxinus americana, Quercus palustris, Q. macrocarpa) have a random dispersion at smaller scales, and an aggregated pattern at larger scales (fig. 3b, 3c). Acer saccharum (fig. 3d) and Ulmus americana appear to have the most random dispersion of all species; Quercus rubra (fig. 3e) the most uniform.

DISCUSSION

Comparisons between results of this study with those of other pattern analyses are of limited value because of dissimilarities in stand properties, edaphic variables, minimum diameter limits, spatial indices, sampling intensity. However, despite these disparities most studies have shown that most species are aggregated to various degrees (Grieg-Smith 1979). Therefore, causes of aggregation demand further consideration.

Reasons promulgated for aggregated dispersion patterns include: microhabitats created by microrelief and/or vegetation present (Beatty 1984,

TABLE 3.--Variance-to-mean ratios for each species at the Davis-Purdue Research Forest at various quadrat sizes. Same plots (0.4 ha) used as for Morisita's index. Ratios not significantly different from 1.0 indicate random distribution, ratios significantly greater than 1.0 indicate aggregated distribution, and ratios significantly less than 1.0 indicate uniform distribution.

Species	Plot Number[a]	Plot Density	Quadrat Size (m)		
			5x5	10x10	15x15
Acer negundo	17	16	1.11	1.14	1.38**
A. saccharinum	31	17	2.49**[b]	1.76**	2.19**
A. saccharum	18	57	0.77	0.88	0.60**
Aesculus glabra	23	19	0.93	1.03	0.92
Carpinus caroliniana	14	14	1.33*	1.58**	1.89**
Carya cordiformis	13	15	0.91	0.94	1.12
C. ovata	13	50	1.28*	1.11	1.19
Celtis occidentalis	19	23	1.14	1.48**	1.66**
Fagus grandifolia	27	10	0.91	0.89	0.90
Fraxinus americana	19	18	1.12	1.42**	1.62**
F. nigra	14	8	1.14	2.11**	2.69**
Juglans nigra	28	14	1.80**	1.72**	2.01**
Ostrya virginiana	18	8	1.26*	1.24	1.09
Prunus serotina	25	11	1.17	0.99	1.00
Quercus alba	36	10	1.38**	1.52**	1.48**
Q. bicolor	19	10	1.36*	1.21	1.18
Q. macrocarpa	26	9	1.13	1.03	1.06
Q. palustris	15	8	0.96	1.48**	2.44**
Q. rubra	16	22	0.87	0.66**	0.68**
Ulmus americana	26	56	0.99	0.97	1.04
Ulmus rubra	19	18	1.11	1.25	1.40**

a = plot numbers correspond to those in figure 1.

b *: significant at $p \leq 0.05$; **: significant at $p \leq 0.01$

Forman and Hahn 1980, Harper et al. 1965. Maguire and Forman 1983, Squiers and Klosterman 1981); soil drainage patterns (Whipple 1980) and nutrient levels (Tilman 1984); seed dispersal patterns and prevalence of vegetative reproduction (Abbott 1984, Hubbell 1979, Veblen et al. 1979); gap colonization (Forman and Hahn 1980, Richards and Williamson 1975, Williamson 1975); past stand disturbances (Smith and Cottam 1967); animal activity (Grieg-Smith 1979); chance (Grieg-Smith 1979); and a combination of these influences. Uniform dispersion is attributed to intraspecific competition (Laessle 1965, Phillips and MacMahon 1981, West 1969); seed predation (Gill 1975); and thinning operations (Payandeh 1974).

Although information on the preceding factors were not collected for the present study, some evidence indicates that many are operative, and interacting in the Davis-Purdue Research Forest. We have observed root sprouting of Aesculus glabra, Fagus grandifolia, and Gleditsia triacanthos in this region, which would partially explain aggregation of these species. Apparently, Celtis occidentalis also reproduces in this manner (Curtis 1959, p. 109).

Soil drainage patterns appear to cause species aggregation at larger scales. For example, Acer saccharinum, Fraxinus nigra, Quercus bicolor, Q. macrocarpa and Q. palustris are restricted to wetter soils. A gradient in soil drainage is probably the most important factor in species distributions, at larger scales.

Gap colonization may be responsible for clumped patterns of several species (e.g., Celtis occidentalis, Carpinus caroliniana, Fraxinus americana, Ostrya virginiana, Prunus serotina, and Ulmus rubra). This aspect will be investigated in the future by analyzing ingrowth within gaps created since 1926.

Populations of smaller size-class trees for other forests are typically aggregated (Christensen 1977, Laessle 1965, Good and Whipple 1982, Whipple 1980). Most Acer saccharum and Ulmus americana are ingrowth since 1926, therefore these species are smaller diameter individuals (Parker et al. 1985). However, both species are somewhat randomly dispersed at all but the largest scales. The near random pattern of these species probably resulted because: (1) these species are shade tolerant (Fowells 1965), therefore do not require a canopy gap to regenerate; (2) their seeds are periodically produced in large quantities, and are wind-dispersed (Schopmeyer 1974); and, (3) much growing space has become available in this stand due to high stem mortality (Parker and Leopold 1983) and possibly grazing in the late 1800s to early 1900s (Parker et al. 1985).

TABLE 4.--Summary of spatial patterns suggested by each index for all species at Davis-Purdue Research Forest.

Species	Spatial Index[a]			
	R	α	I_δ	V:M
Acer negundo	A[b]	A	A/R	R/A[c]
A. saccharinum	A	A	A	A
A. saccharum	A	A	U/R	R/U
Aesculus glabra	A	A	ALL	R
Amelanchier arborea	R	A	-	-
Carpinus caroliniana	A	A	A	A
Carya cordiformis	A	A	ALL	R
C. ovata	A	A	A/R	A/R
Celtis occidentalis	A	A	A	R/A
Crataegus spp.	R	A	-	-
Fagus grandifolia	A	A	ALL	R
Fraxinus americana	R	A	A/R	R/A
F. nigra	A	A	A	R/A
F. quadrangulata	A	A	-	-
Gleditsia triacanthos	A	A	-	-
Juglans nigra	R	A	A	A
Ostrya virginiana	R	A	A	A/R
Prunus serotina	R	A	ALL	R
Quercus alba	A	A	ALL	A
Q. bicolor	R	A	A	A/R
Q. macrocarpa	R	A	ALL	R
Q. muehlenbergii	R	A	-	-
Q. palustris	R	A	A	R/A
Q. rubra	U	A	U/R	R/U
Tilia americana	U	A	-	-
Ulmus americana	A	A	R	R
U. rubra	A	A	A	R/A

[a]R = = Clark-Evans nearest neighbor index, α = Pielou's point-to-plant index

I_δ = Morisita's index of dispersion, V:M = variance-to-mean ratio

[b]A = aggregated, R = random, U = uniform, ALL = all patterns possible depending on quadrat size

[c]R/A = Random in smaller plots, aggregated in larger plots

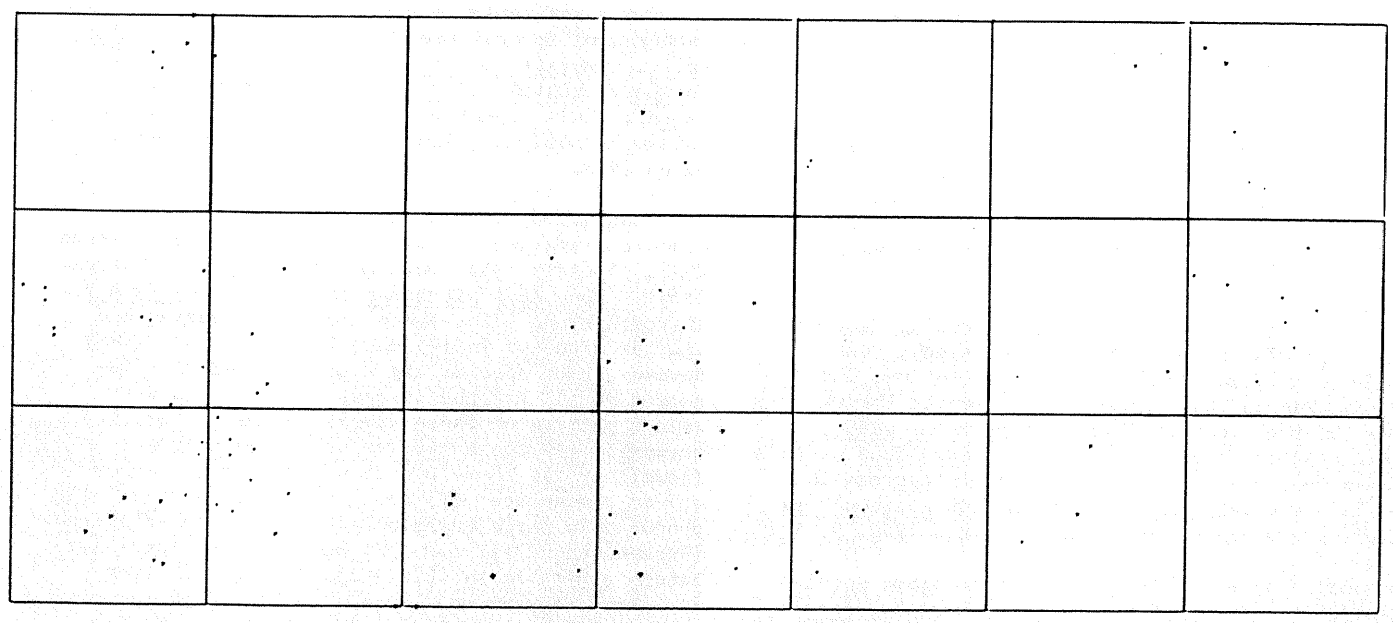


FIGURE 3a.--Map of Quercus alba at Davis-Purdue Research Forest in 1981.

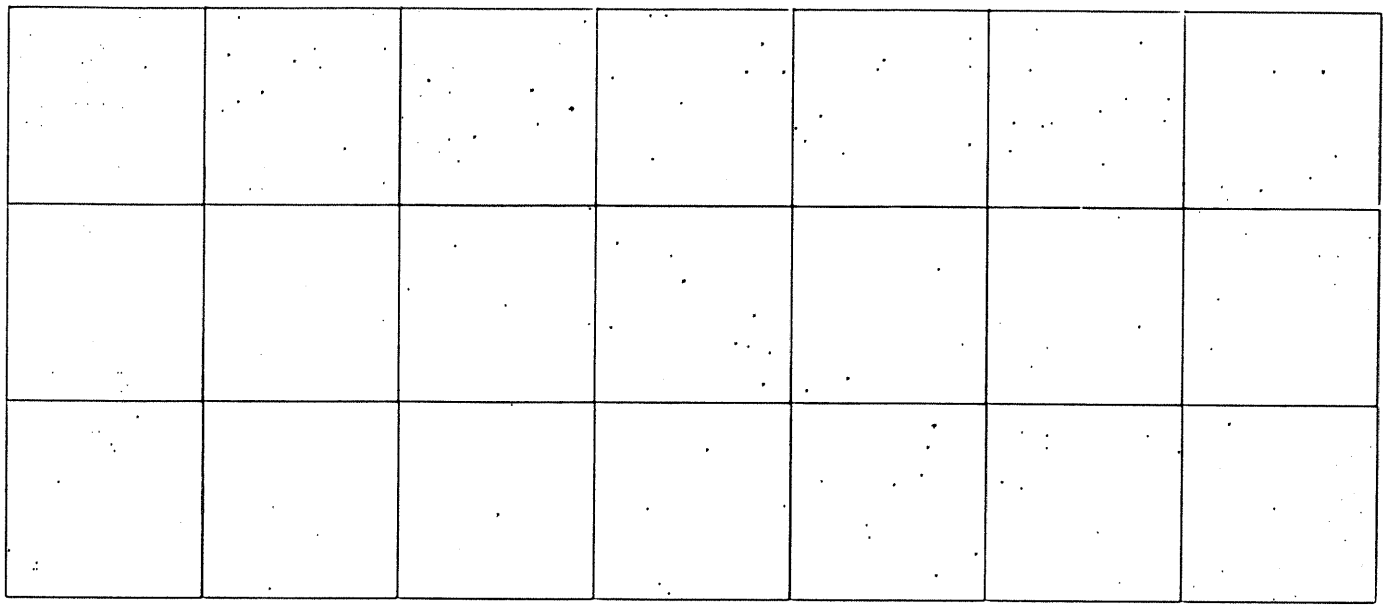


FIGURE 3b.--Map of Fraxinus americana at Davis-Purdue Research Forest in 1981.

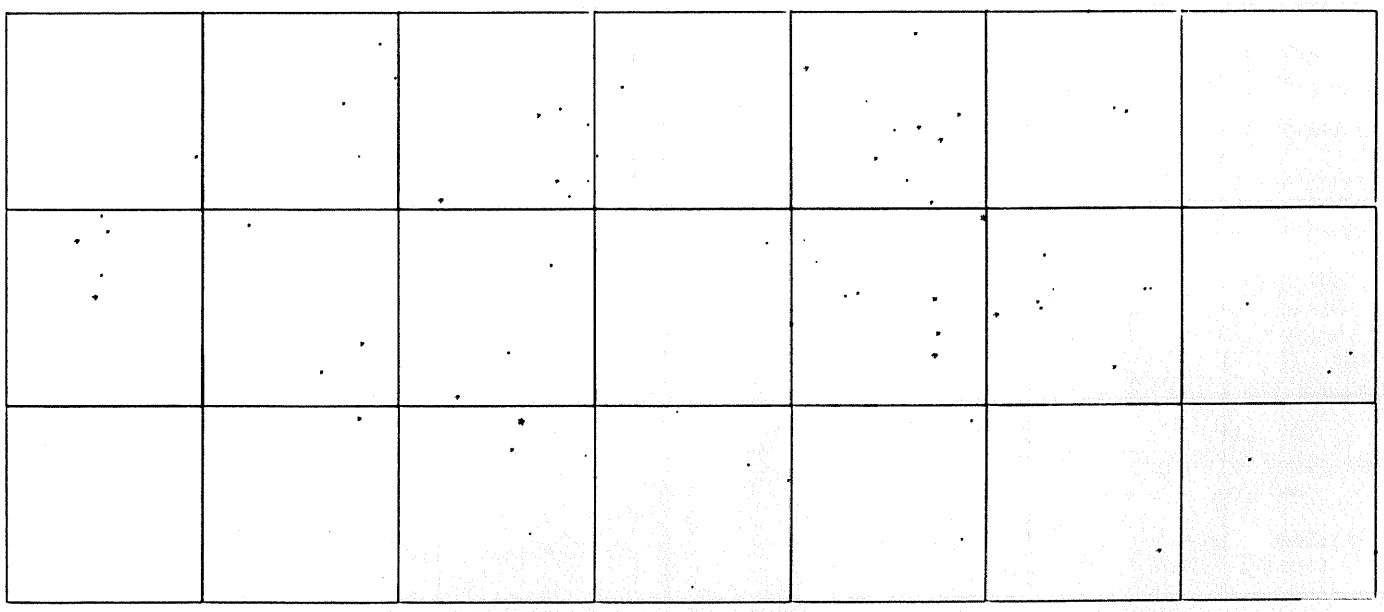


FIGURE 3c.--Map of Quercus macrocarpa at Davis-Purdue Research Forest in 1981.

Research in other stand types indicates that species become more regularly dispersed as succession progresses (Christensen 1977, Cooper 1961, Laessle 1965). Therefore, because of the maturity of this stand, we anticipated regular spacing patterns at the patch scale for species which are primarily restricted to the overstory (i.e., all Quercus spp.). However, uniformity was rare except for Q. rubra. Although intra- and interspecific competition may partially account for the uniformity of Q. rubra, we suspect that limited selection cutting (T. W. Beers, personal communication) and early stand disturbance are primarily responsible.

We question whether a trend towards uniformity over the course of succession actually occurs in mixed hardwood forests of this region, given the large-scale pattern imposed by a "shifting-mosaic steady state" (Bormann and Likens 1979). There may always be local clumping of certain species in mature forests as these species respond to newly formed canopy gaps, and individuals within patches may become less aggregated through competitive

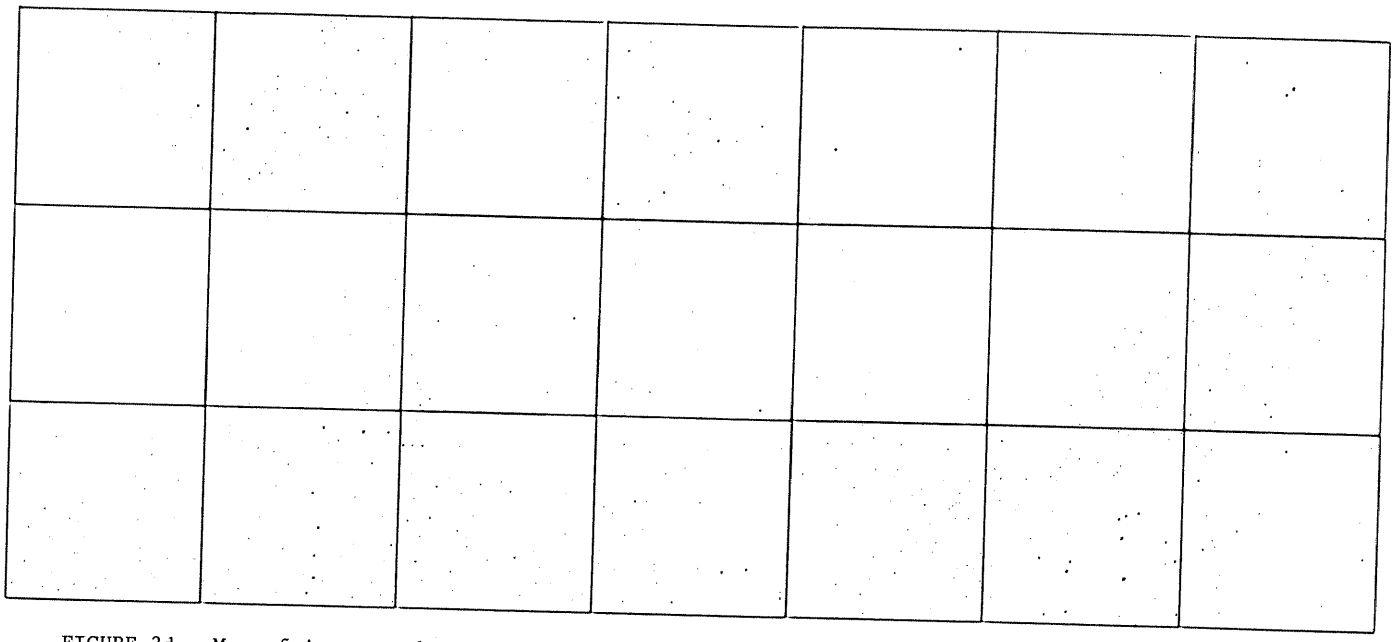


FIGURE 3d.--Map of Acer saccharum at Davis-Purdue Research Forest in 1981.

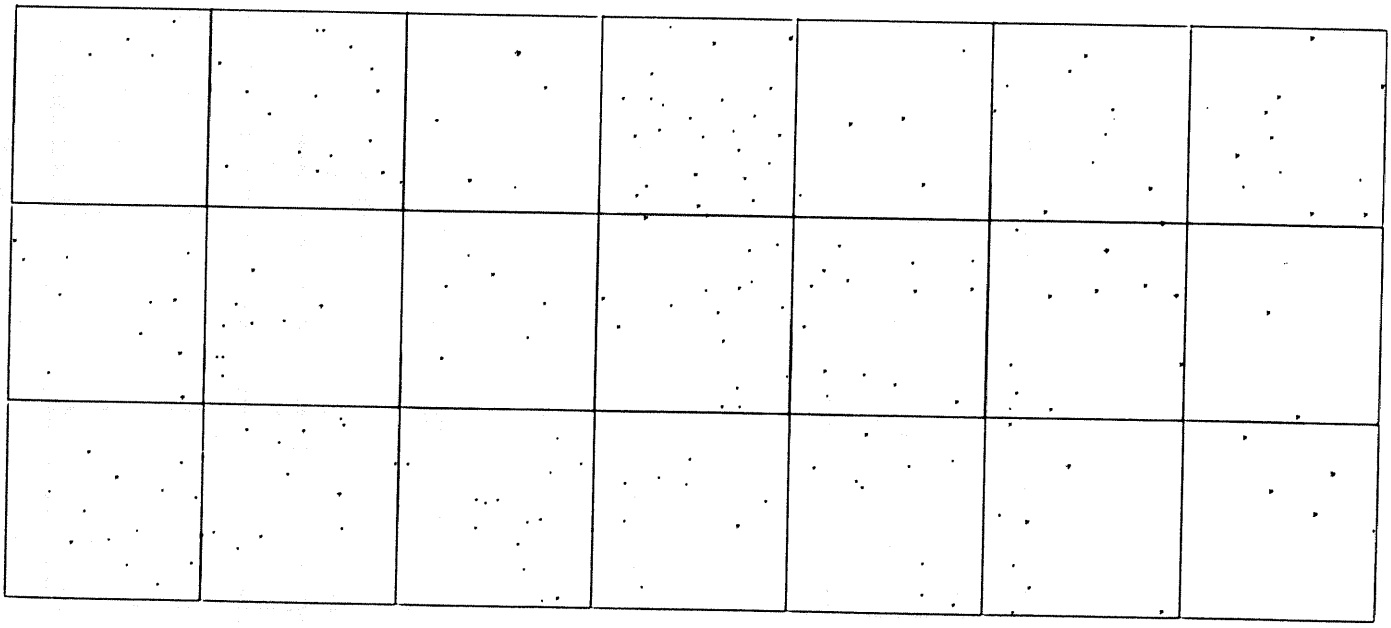


FIGURE 3e.--Map of Quercus rubra at Davis-Purdue Research Forest in 1981.

interactions over time. But we do not know how species spatial patterns are temporally affected by a mosaic of even-aged patches, or whether an isolated woodlot typical of this region is large enough to support a mosaic of species which now dominate the stand. A thorough investigation of how edaphic variables, disturbance (especially gap formation), and existing vegetation influence species spatial patterns is needed. We plan to address some of these questions by comparing current tree spatial patterns with those in 1928.

The major caveat to those contemplating similar research is that stand mapping is quite time consuming, and therefore often limits sampling intensity. For example, a lower diameter limit (e.g., 1.0 cm dbh) in this study would have provided for greater information on species regeneration niches. Some researchers have done spatial analyses without stand mapping (e.g., Clark and Evans 1954, Pielou 1959, Whipple 1980) but problems exist with these methods, especially in the random selection of plants or points and the choice of spatial indices. Once a stand is mapped, the total population can be

sampled. The choice of spatial indices (and there are many others) depends on what information is desired, and the programming and computing facilities available.

Information on tree spatial patterns is valuable to resource managers. For example, forest sampling and stand growth simulation should incorporate spatial data (Payandeh 1974, Payandeh and Ek 1971). However, few such applications are known. Reproduction methods could be chosen based on Morisita's index because this index suggests the size of natural patches (Morisita 1959) and, the size of canopy gaps required to regenerate gap-colonizing species (Williamson 1975). Silvicultural research which utilizes knowledge of natural patch size to regenerate desirable species appears to be lacking.

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