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Tree dispersion in oak-dominated forests along an environmental gradient

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Summary. Spatial pattern was analyzed in seventeen stands of oak-dominated forest to address the hypothesis that species tended to be aggregated under favorable conditions and widely spaced in xeric, nutrient poor conditions. Trees were sampled at 80–100 points in each stand with the distance-to-nearest neighbor method. Soil samples were collected in each stand for analysis of total nitrogen, total phosphorus, total potassium, soil pH, soil texture, and soil organic matter. Growing season precipitation was also recorded from climate stations near each stand. *Quercus stellata* (Wang.) dominated 10 stands, *Q. marilandica* (Muenchh.) dominated three stands and these species were codominant in four stands. Principal components analysis identified a soil texture/fertility gradient across the study area. *Quercus stellata* and all species combined were aggregated in most stands, whereas *Q. marilandica* was mostly randomly distributed within a stand. Small trees of all species combined tended to be aggregated and large trees were randomly dispersed in all but two stands, suggesting competition. Mean distance between large-large pairs was always greater than mean distance between small-small pairs in all stands, but this difference was only significant in one stand. Correlations between nearest neighbor distance and combined size of nearest neighbors were significant and positive in 12 of 17 stands. In all cases, however, slopes were shallow suggesting that competition is weak in these communities and has a limited effect on spacing of neighboring trees. Contrary to our hypothesis, trees were more aggregated on coarse-textured soils with low organic matter content. For all species combined, degree of aggregation was unrelated to growing season precipitation. Aggregation appears to be common in these forests because environmental stress in many stands reduces growth rates. Trees have not yet reached a size at which competition or other interactions can greatly increase interplant distances and reduce the degree of aggregation. A simple graphical model is developed to describe the relationship between patterns, stress and competition in plant communities.

Key words: Aggregation – Competition – Forest – Oklahoma – Pattern analysis

It is well known that spatial pattern in plant communities varies at different spatial scales in response to biotic and abiotic constraints (Greig-Smith 1979). At a small spatial scale, non-random patterns among members of a plant community may result from underlying patterns in the physical environment or interactions between the plants and other organisms in the community (Pielou 1962; Greig-Smith 1979). For example, aggregation may occur in a heterogeneous habitat where seeds germinate at favorable microsites or where vegetative reproduction or seeds with a small radius of dispersal are abundant (Pielou 1960). Regular patterns and wide spacing among individuals may result from competition, allelopathy, herbivory, or harsh environmental conditions (Janzen 1970; Gill 1975; Stowe and Wade 1979; Waller 1981; Conner and Bowers 1987). Random patterns may occur when interactions are inoperative, or when positive and negative forces operate simultaneously.

In plant communities, the interplay between environmental favorability and competition has often been suggested as a primary determinant of small-scale spatial pattern. Competition theory implies that interspecific interactions ultimately lead to increased distances between plants from mortality of one of a pair of neighbors, resulting in a more regular distribution of individuals (Conner and Bowers 1987). For example, many studies of desert vegetation have indicated that competition for moisture resulted in a regular distribution of shrubs (Beals 1968; Yeaton et al. 1977; Phillips and MacMahon 1981; Ismail and Babikir 1986). Young plants were found to be aggregated in deserts, whereas larger, older plants were regularly spaced. Thus, competition may be an important factor creating random to regular patterns in arid environments. Under more favorable conditions, such as temperate and tropical forests, dominant species are often aggregated (Armesto et al. 1986). The results of such studies, however, depend on the scale over which

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vegetation and environment are sampled, and the sensitivity of indices used to detect departures from randomness. Indeed, most indices are biased toward detecting aggregated rather than regular distributions (Beals 1968).

With few exceptions (e.g., Woodell et al. 1969; Barbour and Diaz 1973; Phillips and MacMahon 1981), most studies of pattern are limited to one stand. In lieu of the experimental removal of plants, between stand comparisons can provide insight into environmental determinants of competition and pattern in plant communities. For example, Sherwood and Risser (1979) measured spatial pattern in four forests across a moisture gradient in Oklahoma, USA. They hypothesized that pattern would change from regular to aggregated from west to east across the moisture gradient. Instead, they found pattern to be either random or aggregated in each stand. The four stands they sampled, however, included three different forest communities, a pinyon-juniper stand, two oak forests, and a pine-hardwood stand. The different dominants may be well adapted to the environmental conditions of each stand. Therefore, in this study we sampled small-scale spatial patterns of trees in "Crosstimbers" oak forests across a complex environmental gradient in Oklahoma.

Methods

Study area

The Crosstimbers, a forest region ranging from southeastern Kansas through Oklahoma into north-central Texas, are a southwestern extension of the eastern deciduous forest in North America (Dyksterhuis 1948; Rice and Penfound 1959; Risser and Rice 1971). Annual rainfall varies from 65 cm in the northwest to 120 cm in the southeast. Soils are generally sandy and low in fertility (Johnson and Risser 1972). These factors restrict the southwest distribution of many eastern deciduous forest species, which reduces forest diversity in this region (Risser and Rice 1971). *Quercus stellata* (Wang.) and *Q. marilandica* (Muenchh.) are the dominant tree species in the Crosstimbers (Dyksterhuis 1948; Rice and Penfound 1959) and these two oaks occur together throughout most of central and eastern Oklahoma (Fig. 1).

Field methods

Seventeen stands in relatively flat to gently rolling topography were selected throughout the Crosstimbers based on three criteria: (1) each stand had to have an area of at least 15 ha, (2) the stands had to be relatively undisturbed by cutting or grazing, and (3) canopy composition was restricted to or strongly dominated by *Q. stellata* and *Q. marilandica*. Samples were not located in the extreme south-central and eastern portions of the Crosstimbers (Fig. 1) because we could not locate stands that met our stand selection criteria.

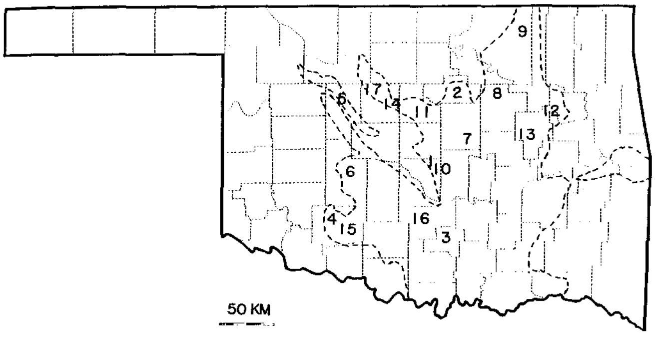

Fig. 1. Distribution of seventeen sample sites in the oak-dominated Crosstimbers region (outlined area) of Oklahoma

Vegetation was sampled in each stand using the distance-to-nearest-neighbor method (Cottam and Curtis 1956; Pielou 1959). Depending on the size of the stand, 80 to 100 random points located along 3 to 4 parallel transects were sampled in each stand. At each point, the distances from the point to the nearest tree and from this tree to its nearest neighbor were measured. The species and diameter at breast height (dbh) were recorded for each tree. If the tree closest to each random point and its nearest neighbor were the same species, then only those two trees were sampled. If the two nearest neighbors were different species, then the distance to the nearest tree of the same species was also measured for the determination of intraspecific patterns. Thus, three trees were included at some sample points. Only trees greater than 10 cm dbh were sampled.

Ten soil samples were collected from random locations within each stand. For each soil sample, the litter layer was removed and soil was collected to a depth of 10 cm. Long-term average growing season precipitation (April to September) was determined from the climate recording station closest to each stand.

Soil analyses

All soil samples from one stand were mixed and divided into three subsamples for analysis. Organic matter content was determined by loss-on-ignition (Allen et al 1986). Soil texture was analyzed with the Bouyoucos hydrometer method. Soil pH, total N, P, and K were measured by the Oklahoma State University Soils Testing Laboratory. Although total N is less informative than available N, it does provide a comparative index of soil fertility in conjunction with information on the other environmental parameters in each stand.

Data analyses

The T-square index of spatial pattern (Diggle et al. 1976, Diggle 1983) was used to determine pattern for individuals of *Q. stellata, Q. marilandica*, and all species combined in each stand. This index (C) is a ratio of the squared point-to-plant distances (x_i), and squared plant-to-nearest-neighbor distances (y_i):

$$C = \frac{\sum_{i}^{N} [x_i^2/(x_i^2 + 1/2y_i^2)]}{N} \qquad (1)$$

where N is the total number of points sampled. The index is based on the assumption that in a random population of individuals, the distance from a random point to an individual will be, on average, half the distance from one individual to another. Thus, a value of $C = 0.5$ indicates randomness, $C < 0.5$ indicates regularity, and $C > 0.5$ indicates aggregation (C ranges from 0 to 1). The significance of departure from randomness was determined as:

$$Z = \frac{C - 0.5}{\sqrt{1/(12N)}} \qquad (2)$$

where $Z > 1.96$ indicates a significant departure from randomness (Ludwig and Reynolds 1988).

Trees were divided into small (10–20 cm dbh) and large (> 20 cm dbh) size classes. Spatial pattern was calculated for small trees in all but one stand and for large trees in twelve stands in which sample size of large-large pairs was adequate (> 10 points). Regressions of distances between nearest neighbors (m) and sum of their sizes (dbh) were used to infer competition within stands. (Yeaton and Cody 1976, Waller 1981, Wright and Howe 1987, Welden et al. 1988). A significant positive relationship between nearest neighbor distances and sum of their sizes indicates that larger individuals are spaced farther apart than smaller individuals, a pattern that often is interpreted to result from competition (Conner and Bowers 1987). Sum of sizes was used as the independent variable and distance between neighbors as the dependent variable. Essentially, each variable may be regarded as a cause and an effect of the other (Welden et al. 1988). This form of regression is useful, however, because it provides a separate measure of the intensity and importance of competition. The slope of the regression is a direct measure of the intensity of competition, while the coefficient of determination (r^2) is a measure of the importance of competition as reflected by the distance between nearest neighbors (Welden et al. 1988).

Principal components analysis (PCA) of a correlation matrix (standardized data) of seven environmental variables (growing season precipitation, soil pH, organic matter, total N, P, K, and percent sand) was used to relate the distribution of stands along a regional environmental gradient. Although PCA is not a popular technique for vegetation ordinations (Gauch 1982), it is an appropriate method for analyzing matrices of environmental variables. Essentially, PCA reduces the complexity in a multivariate data set by combining the original variables into a few orthogonal principal components. The analysis derives correlation coefficients indicating the relationship of each environmental variable to each principal component producing complex environmental gradients along each component axis. The position of each sample is then projected onto each component (c.f., Collins and Good 1987; Collins 1990). Regional changes in spatial pattern associated with each environmental parameter were determined with univariate and stepwise (forward) multiple regression.

Results

Environmental and compositional gradients

The first axis of the principal components analysis accounted for 42.6% of the variance in the correlation matrix (Fig. 2). This axis produced a soil texture/fertility gradient separating stands with more soil organic matter and phosphorus from stands with more coarse textured soils, greater precipitation, and more nitrogen. The nitrogen gradient was strongly influenced by stand 11, which may have received some fertilizer drift from adjacent agricultural fields. The second PCA axis accounted for 29.6% of the remaining variance and reflected a percent sand/potassium gradient.

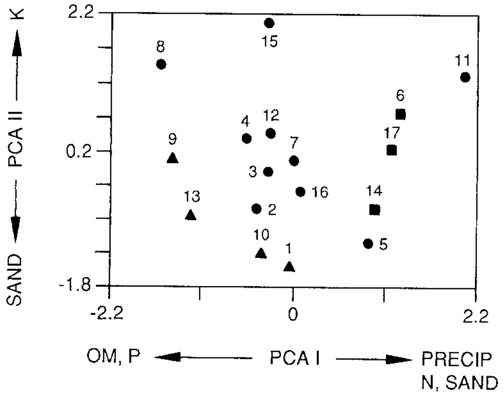

Fig. 2. Principal components analysis of environmental variables for seventeen stands of Crosstimbers forest in Oklahoma. Axes I and II account for 72.2% of the variance in the correlation matrix of environmental variables. Circles represent stands dominated by *Quercus stellata,* squares represent stands dominated by *Quercus marilandica,* and triangles are mixed stands

Quercus stellata was dominant (accounted for >65% of the trees sampled) in 10 stands, *Q. marilandica* dominated three stands, and these species were codominant in four stands. Other tree species in these forests included *Carya texana, Bumelia lanuginosa, Celtis occidentalis, Celtis laevigata,* and *Ulmus americana.* These taxa together accounted for 1–2% of the individuals in each stand, except in stands 3 and 10 where they accounted for 5% of the individuals sampled. The stands in which *Q. marilandica* dominated occurred on low fertility sandy soils (Fig. 2). Stands in which these species shared dominance were in areas with less sand and higher soil phosphorus and organic matter content. Thus, codominance occurs on the most fertile soils, *Q. stellata* dominates on less fertile areas, and *Q. marilandica* forms nearly pure stands on very coarse textured soils.

Spatial pattern within stands

Trees were aggregated in 14 of 17 stands and randomly distributed in the remaining three stands (Table 1). Individuals of *Q. stellata* were aggregated in 10 of 15 stands, whereas individuals of *Q. marilandica* were aggregated in three stands, regularly distributed in two stands, and randomly dispersed in ten stands. In general, the aggregation noted for all species combined was a result of aggregation by the dominant species in a stand. The degree of aggregation of *Q. stellata* was not correlated with aggregation of *Q. marilandica. Quercus marilandica* was uncommon in one stand where it was regularly dispersed (stand 16); however, it was a codominant in the other stand, one of the few in which *Q. stellata* and all species combined were randomly dispersed.

Small-small (10–20 cm dbh) and large-large (>20 cm dbh) size class comparisons could only be performed for all species combined because of the small number of samples of appropriately paired occurrences. Small trees were aggregated in 12 of 16 stands (Table 1). Although sample sizes were often small (11–27 points), large trees tended to be randomly dispersed with two exceptions. Large trees were aggregated in stands 2 and 6, and nearly so in stand 12 ($0.05<P<0.10$). The index of spatial pattern, however, was significantly smaller for large-large versus small-small pairs ($\bar{X}=0.58$ and 0.65, respectively, $F=6.52$, $P=0.02$) indicating that large trees were less aggregated than small trees. In addition, the mean distance between large-large pairs of trees was always greater than the mean distance between small-small pairs, but this relationship was significant in only one of eleven possible comparisons (Table 2). The decrease in aggregation and increase in distance between pairs of large trees may result from interference between individuals as tree size increases.

Regressions of distances between nearest neighbors and the sum of their sizes were significant and positive in 12 of 17 stands (Table 2). The slopes were fairly consistent ranging from 0.005 to 0.06. These regressions rarely accounted for more than 10% of the variance in

Table 1. T-square index of spatial pattern (C) and significance test (|Z|) for *Quercus stellata, Q. marilandica,* all species combined in each stand, small-small pairs (10–20 cm dbh), and large pairs (> 20 cm dbh)

Stand	Dominant species	All species combined		*Quercus stellata*		*Quercus marilandica*		Small-small		Large-large	
		C	Z	C	Z	C	Z	C	Z	C	Z
1.	Both	0.59	3.06* A	0.47	0.67	0.55	1.38	0.56	1.42	0.64	1.79
2.	*Q. stellata*	0.66	5.55* A	0.64	4.28* A	0.46	0.64	0.69	5.03* A	0.70	2.26* A
3.	*Q. stellata*	0.58	2.80* A	0.58	2.60* A	–	–	0.56	1.77	–	–
4.	*Q. stellata*	0.54	1.45	0.54	1.16	0.43	1.21	0.57	1.10	0.57	1.54
5.	*Q. stellata*	0.67	5.74* A	0.67	4.74* A	0.52	0.41	0.70	5.81* A	–	–
6.	*Q. marilandica*	0.69	6.01* A	0.68	3.15* A	0.66	4.11* A	0.70	4.87* A	0.68	2.65* A
7.	*Q. stellata*	0.62	3.61* A	0.60	3.01* A	–	–	0.65	3.15* A	0.54	0.51
8.	*Q. stellata*	0.57	2.52* A	0.55	1.41	0.44	1.02	0.63	3.28* A	0.56	0.66
9.	Both	0.53	0.84	0.53	0.65	0.32	3.54* R	0.58	1.87	0.43	0.93
10.	Both	0.64	5.00* A	0.62	3.18* A	0.49	0.12	0.66	4.44* A	–	–
11.	*Q. stellata*	0.69	6.03* A	0.69	5.04* A	0.61	1.90	0.69	4.88* A	–	–
12.	*Q. stellata*	0.62	4.09* A	0.58	2.31* A	0.45	0.80	0.65	4.29* A	0.66	1.94
13.	Both	0.62	4.16* A	0.59	2.55* A	0.50	0.07	0.66	4.44* A	0.47	0.33
14.	*Q. marilandica*	0.65	5.23* A	–	–	0.65	5.23* A	0.65	4.29* A	–	–
15.	*Q. stellata*	0.52	0.55	0.49	0.28	0.46	0.65	–	–	0.49	0.19
16.	*Q. stellata*	0.62	4.07* A	0.64	4.22* A	0.28	2.66* R	0.67	4.36* A	0.62	1.29
17.	*Q. marilandica*	0.58	2.73* A	–	–	0.58	2.73* A	0.63	2.82* A	0.54	0.68

* = departure from randonness ($P < 0.05$), R = regular, A = aggregated

Table 2. Number of points sampled per stand (N), mean distance (m) between nearest neighbors, small-small and large-large nearest neighbors (n = number of pairs), and statistics for regression of distance between nearest neighbors and the sum of their sizes in each stand

Stand	N	Mean Distance	Small-small	Large-large(n)	Slope	r^2	F	p
1.	100	2.09	1.86	2.53(11)	0.005	0.001	0.1	0.71
2.	100	2.00	1.35	2.35(11)	0.05	0.21	26.6	0.0001
3.	100	1.89	–	–	0.007	0.003	0.3	0.58
4.	100	2.83	2.27	3.23(18)	0.02	0.09	9.6	0.003
5.	100	1.64	–	–	0.02	0.014	1.4	0.23
6.	83	1.72	1.77	2.22(18)	0.04	0.13	11.6	0.001
7.	80	1.96	1.34	2.31(11)	0.03	0.06	4.5	0.02
8.	100	2.32	2.00	2.39(11)	0.04	0.09	9.1	0.003
9.	95	2.36	2.05	4.06(16)	0.02	0.05	4.3	0.04
10.	100	1.66	–	–	0.03	0.06	6.1	0.02
11.	84	1.32	–	–	0.02	0.03	2.6	0.11
12.	100	1.91	1.58	2.11(13)	0.03	0.07	7.1	0.009
13.	100	1.78	1.98	2.69(11)	0.06	0.18	21.2	0.0001
14.	100	1.25	–	–	0.02	0.02	2.4	0.13
15.	100	2.55	–	–	0.02	0.10	10.8	0.001
16.	90	1.79	1.76	2.12(10)	0.03	0.08	7.9	0.006
17.	100	1.98	1.42	2.32*(27)	0.05	0.09	9.6	0.003

* indicates significantly different mean distance between small-small and large-large pairs within a stand based on analysis of variance

the data. These distance-summed sizes regressions imply reciprocity in competitive ability between neighbors, yet such an assumption is probably invalid for drastically unequally sized individuals. If asymmetric competitive interactions exist, they would reduce the slope and significance of the regressions. To remove this bias, the distance versus summed sizes regressions were recalculated after removing large-small pairs with > 10 cm difference in size between members of the pairs. In all cases, the regression slopes either decreased or remained the same. In stands 7 and 8, the significant regression using all pairs became insignificant when removing drastically unequally sized pairs. Thus, the results are not seriously biased by unusually close pairs of trees in which one member of the pair dramatically suppresses the growth of the other tree. There were no significant correlations between the intensity (slope) and importance (coefficient of determination) of competition and any environmental parameter.

Spatial pattern among stands

The index of spatial pattern for all species combined was positively correlated with percent sand ($r = 0.69$, $P = 0.002$, Fig. 3), and negatively correlated with organic matter content ($r = -0.57$, $P = 0.02$). These two soil variables were negatively correlated, however ($r = -0.82$,

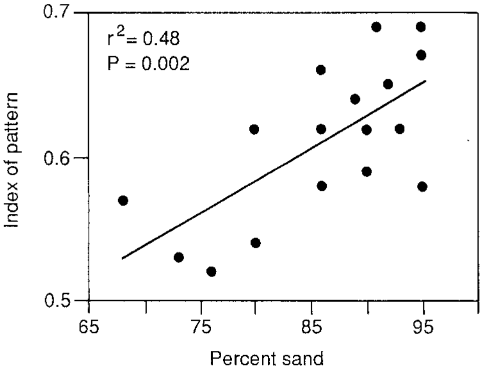

Fig. 3. Correlation of percent sand versus degree of spatial pattern for all species combined in seventeen forest stands. Higher values of the index of pattern indicate greater degree of aggregation

$P = 0.001$). Only percent sand entered into a stepwise multiple regression with the index of spatial pattern as the dependent variable, no other environmental variable accounted for a significant amount of the remaining variation. Correlations between percent sand and pattern of large trees or pattern of small trees were not significant ($r = 0.37$ and 0.45, $P = 0.27$ and 0.08 for large and small trees, respectively). Thus, it is the combined pattern of all trees in a stand that is responding to environmental constraints across the soil texture gradient.

The relationships between environmental factors and pattern of *Q. stellata* were the same as for all species combined ($r = 0.64$, $P = 0.04$ and $r = -0.52$, $P = 0.05$ for percent sand and organic matter, respectively). Pattern of *Q. marilandica* was positively correlated with percent sand ($r = 0.53$, $P = 0.04$) and growing season precipitation ($r = 0.61$, $P = 0.02$). Therefore, in opposition to our original hypothesis, individuals are more aggregated under environmental conditions that are less favorable for plant growth. There was no relationship between index of spatial pattern and either latitude or longitude.

Discussion

Pattern within stands

In general, spatial patterns of both all species and all size classes combined, and those for small size classes alone were aggregated. Larger trees tended to be randomly dispersed, however. The small sample sizes in most of these stands may limit our ability to detect non-random patterns for large trees. These results are congruent with numerous other studies of pattern in shrub and forest communities; that is, most species in plant communities are aggregated to some degree (e.g., Risser and Zedler 1968; Hubbell 1980; Forman and Hahn 1980; Armesto et al. 1986; Cody 1986; Ward and Parker 1989). Other studies have indicated that spatial pattern changes from aggregated to random as plant size and competition increase during succession (Christensen 1977; Phillips and MacMahon 1981). Such a trajectory could eventually result in regular patterns which have been used to infer competition (Conner and Bowers 1987).

Although species dispersions may remain clumped, the distance between nearest neighbors nevertheless increases as a product of competitive interactions. Regressions of distance between nearest neighbors and the sum of their sizes can be used as an index of competition within a stand (Yeaton and Cody 1976; Waller 1981; Welden et al. 1988), although few studies have verified experimentally the relationship between competition and spacing in plant communities (Fonteyn and Mahall 1981; Welden et al. 1988). In our study, nearest neighbor summed-sizes regressions were positive and significant in 12 of 17 stands. The slopes were equivalent in most stands suggesting that the intensity of competition is relatively constant in these communities. It is difficult to interpret and compare slopes among studies because of the different measures for plant size (canopy size of shrubs versus tree dbh) and distance (m, cm) used. The slopes of the regressions in this study are all shallow, however, suggesting that competition is relatively weak in most of these stands.

The importance of competition within a stand is measured by the coefficient of determination of the regression. Values of the coefficient of determination in our study ranged from 0.001 to 0.21 ($\overline{X} = 0.08$). These values are generally smaller than those reported for trees (range 0.00–0.48, $\overline{X} = 0.19$) and shrubs (range 0.02–0.88, $\overline{X} = 0.25$) in Colorado (Welden et al. 1988), and for desert shrubs in the southwestern US (range 0.04–0.53, $\overline{X} = 0.12$ [Phillips and MacMahon 1981]; range 0.05–0.83, $\overline{X} = 0.30$ [Yeaton and Cody 1976]; range 0.04–0.42, $\overline{X} = 0.14$ [Cody 1986]). This would suggest that competition was not one of the primary factors affecting distance relationships in the forests we studied. The degree of aggregation in these stands would provide further support for the idea that the importance and intensity of competition, relative to other factors, is low in these stands. The fact that large trees are less aggregated and farther apart than small trees provides some evidence that interspecific interactions have some effect on species distributions in these forests. In fact, the $-3/2$ power law would predict that larger trees must be spaced farther apart than smaller trees as basal area increases and density decreases (Weller 1987).

Conceivably, the weak relationship in the distance-summed sizes regressions could result, in part, from within-stand environmental heterogeneity. Because of the large-scale scope of this study we were unable to focus on detailed within-stand neighbor-neighbor analyses in relation to environmental pattern. The large number of points sampled per stand, however, should allow us to detect general patterns in species distribution and distance relationships within a stand. It is necessary to recognize that we are, in fact, addressing the importance of competition relative to other factors as noted by Welden and Slauson (1986). Thus, the low r^2's in our study may be interpreted to mean that competition is occurring, but it is a less important factor affecting spatial pattern in this stand than other factors such as environmental stress.

Quercus stellata usually occurred in small clusters of 2–6 individuals. Because this species may reproduce vegetatively, especially under moisture stress (Fowells 1965), some clusters probably represent a single individual, resulting in small-scale aggregation. This can not explain aggregation throughout every stand, however. Oak acorns are dispersed by vertebrates and thus aggregation may also commonly arise from seed dispersal by squirrels and birds (Smith and Folmer 1972, Howe 1989). Gill (1975) and Sherwood and Risser (1979) found *Q. stellata* to be aggregated in New Jersey and Oklahoma, respectively, in accord with the results of our study.

Quercus marilandica was aggregated in three stands where it was dominant and randomly dispersed in most other stands. This species is a dominant on dry, nutrient poor soils (Johnson and Risser 1972, Hall and McPherson 1980). This species is short-lived, slow growing (Miller and Lamb 1985), and susceptible to periodic droughts and disturbances (Rice and Penfound 1959). Its occurrence as a dominant on very sandy soils is maintained by higher levels of precipitation (Fig. 2). Numerous dead individuals of *Q. marilandica* of varied sizes, often with broken stems, were found in these forests but only a few large, dead individuals of *Q. stellata* were observed. The latter species is longer lived and more drought resistant than most other oaks (Fowells 1965) which may account for the smaller number of dead stems observed compared to *Q. marilandica*. Random dispersion of *Q. marilandica* was also reported by Gill (1975) and Sherwood and Risser (1979).

Spatial pattern among stands

Although there is a clear environmental gradient within the oak dominated forests of Oklahoma, the soils supporting the Crosstimbers are generally sandy and low in fertility (Rice and Penfound 1959; Johnson and Risser 1972). In contrast to our hypothesis, trees in these stands tended to be more aggregated as soil fertility decreased. In fact, density is positively correlated with percent sand ($r = 0.69$, $P = 0.002$). Other studies have reported that density and degree of aggregation increase with precipitation and increasingly coarse-textured soils (Woodell et al. 1969, Barbour and Diaz 1973, Phillips and MacMahon 1981). We argue, however, that soil texture is the key variable influencing the degree of spatial pattern rather than precipitation. In our study, only percent sand entered into a stepwise multiple regression of degree of aggregation of all species combined versus environmental variables. Neither aggregation nor density were correlated with precipitation. Many forests in the region of the Crosstimbers of Oklahoma have originated from savanna as a result of fire suppression during the last 100 years (Rice and Penfound 1959; Dooley and Collins 1984).

Current competitive interactions appear to be too weak in these communities to lead to random or widely spaced patterns. Low soil organic matter content, hot and dry summers, and periodic drought probably reduce the importance of competition in these forests. Reader (1990) recently demonstrated that low nutrient conditions may constrain competitive interactions among plants.

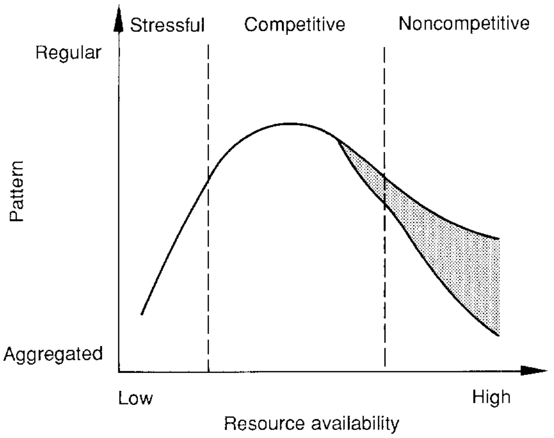

Fig. 4. Model showing the hypothetical relationship between pattern in plant populations in response to environmental stress and resource availability

Menge and Sutherland (1987) suggested that community structure is controlled by a gradient of factors ranging from stress to competition and then predation. As stress decreases, competition increases up to a point where resources are no longer limiting. At this point other factors, such as predation, control community structure. We propose a simple graphical model, based on the model of Menge and Sutherland (1987), relating spatial pattern to competition and resource availability (Fig. 4). As noted by Grime (1979, 1989), environmental stress reduces growth rates to such an extent that competitive interactions among individuals are reduced. Reduced growth rates may decrease the rate of competitive displacement of individuals in a population (Huston 1979). Thus, under stressful conditions populations may be aggregated (Fig. 4). Although regular patterns among shrubs have been detected in stressful habitats such as deserts, random and aggregated patterns still appear to be the norm (Phillips and MacMahon 1981). Indeed, individuals of the cactus *Copiapoa* sp. were aggregated in the Atacama Desert of northern Chile, one of the most arid deserts in the world (Gulmon et al. 1979). As resource abundance increases, competitive interactions increase which may lead to wider spacing and random or possibly regular patterns among individuals. Under conditions of resource abundance, interspecific interactions become less important determinants of spatial pattern. Instead, within community pattern will be a function of factors such as environmental grain, dispersal, vegetative reproduction, herbivory, and disturbance (Greig-Smith 1979). Thus, degree of aggregation may not always be interpreted to imply favorable environments and reduced competitive interactions among species within some plant communities.

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