

THE EFFECTS OF GRASSLAND FRAGMENTATION
ON SPECIES RICHNESS AND COMPOSITION

By

DAI JUN ZHANG

Bachelor of Science
Northeast Forestry University
Harbin, China
1982

Master of Science
University of New Brunswick
Fredericton, Canada
1985

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
December, 1990

Thesis
1990.D
Z 627e

cop. 2

C O P Y R I G H T

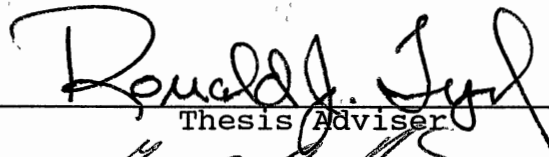
by

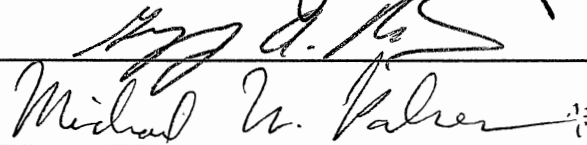
Dai Jun Zhang

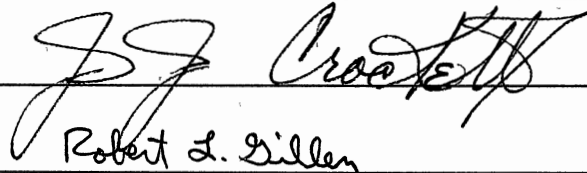
December, 1990

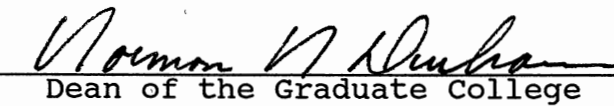
THE EFFECTS OF GRASSLAND FRAGMENTATION
ON SPECIES RICHNESS AND COMPOSITION

Thesis Approved:


Thesis Adviser


Michael W. Palmer


Robert L. Gillen


Dean of the Graduate College

ACKNOWLEDGMENTS

I am very thankful for the constant support, inspiration, and advice of the chairman of my committee, Dr. R.J. Tyrl.

I also thank my thesis adviser, M.W. Palmer, for his insightful opinions, helpful suggestions for parts of the data analysis, and for his generosity in providing me the needed computer software.

My deep appreciation also goes to the members of my committee: Dr. R.L. Gillen, for his valuable comments, suggestions, and introduction to field techniques; Dr. J.J. Crockett for his comments and time in the field; and Dr. G. Plumb, who is my outside committee member from the Department of Geography at the University of Oklahoma, for his willingness to serve on my advisory committee and for his suggestions.

I also thank Dr. D.M. Engle and Dr. W.E. McMurphy in the Department of Agronomy, Oklahoma State University, for their help in identification of species. My appreciation also goes to Larry A. Prather and Joleen Stone for their helping hands in collecting field data. I also thank the staff of USDA Soil Conservation Service in Stillwater for their kindness in providing site information. I am grateful to the friendly landowners of the sites where I conducted this research for their hospitality.

Finally, I thank the community of Oklahoma State

University, especially the faculty and staff of the Department of Botany and Microbiology, for providing me the opportunity to receive academic training at the doctoral level.

TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION	1
II. RESEARCH METHODS	6
Study Area	6
Field Data Collection	11
Data Analysis	12
III. RESULTS	19
Species Richness and Diversity	19
Species Composition in Relation to Area	19
Edge Species Composition and Interior Species Composition	28
Species Composition at Edges Associated with Different Neighbors	46
IV. DISCUSSION	48
Species-Area Relationship	48
Area Effects on Species Composition	54
Edge Effects in Relation to Area Effects	55
Edge Effects on Interior Species Composition	60
Neighbor Effects on Edge Species Composition	62
Conclusions and Recommendations	65
LITERATURE CITED	67
APPENDICES	74
APPENDIX A - EQUATIONS USED IN DATA ANALYSIS	75
APPENDIX B - PRIMARY SAMPLING DATA	77

LIST OF TABLES

Table	Page
1. Locality Information for Ten Grassland Study Sites in Oklahoma	6
2. Species Richness of Each Study Site Estimated by First Order Jackknife	20
3. The Significance Levels, Correlation Coefficients and Parameters Estimated for Linear, Logarithmic, and Exponential Models of Species-Area Relationship	23
4. Species Diversity, Evenness, and Dominance Indices for Each Study Sites Along with Their Means, Standard Deviations and Results of Simple Linear Regression Analysis between the Indices and Area	25
5. Canonical Coefficients and Inter-set Correlations of Environmental Variables (Edgeness and Area) with the First Two Ordination Axes of CCA for the Combined Data of Edge and Interior Species Composition	31
6. Canonical Coefficients and Inter-set Correlations of Environmental Variables (Types of Neighbors) with the First Four Species Axes	47

LIST OF FIGURES

Figure	Page
1. Locations of Study Sites	7
2. Representation of Field Sampling Scheme	13
3. Relationship between Species Richness and Area of Ten Grasslands in north-central Oklahoma	21
4. Relationship between Total Species Composition and Area of Ten Grasslands in North-central Oklahoma as Determined by Detrended Correspondence Analysis	26
5. Relationship between Total Species Composition and Area of Ten Grasslands in North-central Oklahoma as Determined by Canonical Correspondence Analysis	29
6. Effects of Area and Edginess on Species Composition in Ten Grasslands in North-central Oklahoma as Determined by Canonical Correspondence Analysis	32
7. Relationship between Manhattan Distances and Area in Ten Grasslands in North-central Oklahoma	35
8. Residuals of Manhattan Distances versus Area	37
9. Relationship between Edge Species Composition and Area of Ten Grasslands in North-central Oklahoma as Determined by Detrended Correspondence Analysis	39
10. Relationship between Interior Species Composition and Area of Ten Grasslands in North-central Oklahoma as Determined by Detrended Correspondence Analysis	42

Figure	Page
11. Relationship between Interior Species Composition and Area of Ten Grasslands in North-central Oklahoma as Determined by Canonical Correspondence Analysis	44

CHAPTER I

INTRODUCTION

Because of the increase in man's population and economic activities, fragmentation of the natural vegetation in North America has been a significant trend. Vast segments of the continent's natural vegetation are disappearing, while much of the remainder is being fragmented. Such a trend of fragmentation is especially intensive in forest regions. Curtis (1956) reported that the total forest area in Cadiz Township, Green County, Wisconsin was almost 27 times smaller in 1950 than it was in 1831; the average size of forest islands decreased 1,504 times during the same period of time; and the average inter-island distance increased from 153 m in 1882 to 339 m in 1950. Such trends of fragmentation of natural vegetation have also been significant in grassland regions where agricultural activities are predominant (Risser et al. 1981). According to predictions (USDA Forest Service 1981), an additional 25.5 million hectares of grasslands will be lost by 2030 as grasslands are turned into agricultural lands, other vegetation types, or urbanized rights-of-ways, residential areas, and industrial areas.

A number of physical changes are induced by fragmentation: (1) reduced total area of natural vegetation; (2) reduced average sizes of the fragments of natural

vegetation; and (3) increased degree of isolation among the fragments. With respect to the ecological effects caused by these physical changes, Curtis (1956) speculated that, because the small size and increased isolation of the stands tend to prevent easy exchange of individuals or propagules among them, stochastic events in any given stand over a period of years could eliminate one or more species. In addition, as the stands gradually lose species, those remaining may approach unusually low population density.

A positive relationship between species richness and area has been reported for plant communities (Levenson 1981; Weaver and Kellman 1981; Peterken and Game 1984; Currie and Paquin 1987; Nilsson et al. 1989); for fish species richness in relation to drainage areas of stream systems (Eadie et al. 1986; Livingstone et al. 1982; Sheldon 1988); and for game bird and raptor species in rain forest of French Guiana (Thiollay 1989). Exceptions have also been reported (Levenson, 1981; Weaver and Kellman, 1981; Peterken and Game, 1984).

A number of quantitative models have been proposed to simulate the species - area relationship (Fisher et al. 1943; Goodall 1961; Dahl 1960; Arrhenius 1921; Preston 1962). Among them, the logarithmic model (Goodall 1961; Dahl 1960) and the exponential model (Arrhenius 1921, Preston 1962) are more popular.

$$S = p \text{ Log } (A + 1) \quad (\text{Goodall 1961; Dahl 1960})$$

$$S = c A^z \quad (\text{Arrhenius 1921; Preston 1962})$$

Three hypotheses have been proposed to explain the

ecological mechanism behind the positive species - area relationship. May (1975) suggested that increased species richness with increased area was the consequence of increased sample size. The "Habitat Diversity Hypothesis" (Williams 1964) proposed that, as the amount of sampled area increases, new habitats with their associated species are encountered, and thus species number increases with area. The equilibrium theory of island biogeography developed by MacArthur and Wilson (1964) deemphasises the importance of habitat diversity and instead explains the increase in species richness as a function of immigration and extinction rates.

The phenomenon of edge effect and its relationship to fragmentation has also attracted interest (Wales 1972; Ranney et al. 1981; Harris 1984, 1988; Wiens et al. 1985; Lovejoy et al. 1986; Stamps et al. 1987; Quinn and Robinson 1988; Marshall, 1989). Previous research on edge effects have mainly been on edge species composition and its change in relative proportion with area. Edge effect has been proposed to be the main cause of the increase of species richness associated with increased fragmentation.

In addition to edge effect, types of neighbors may also affect a community's structure. Studies have shown that different boundaries lead to differences in both abiotic and biotic exchanges among the neighbors (Evans and Clark 1954; Forman and Godron 1981; Madder 1984; Stamps et al. 1987; Marshall 1989).

Numerous studies (papers in Burgess and Sharpe 1981;

Weaver and Kellman 1981; Peterken and Game 1984; Harris 1984) have been conducted on the effects of forest fragmentation on species richness and community development. In contrast to the intensive studies of the effects of fragmentation in forests, few studies have been undertaken in grasslands. Previous work on the fragmentation of grasslands has focused on California annual grasslands (Quinn and Hastings 1987; Robinson and Quinn 1988; Quinn and Harrison 1988; Murphy and Ehrlich 1989). Little work has been done on the Central Grasslands of North America.

The goal of the research reported here is to examine the effects of fragmentation on the tallgrass prairie. The specific objectives are to determine: (1) whether grassland fragmentation affects the richness and composition of flowering species;

(2) the influence of edge effects on species richness and species composition, specifically

- A. whether edge effects exist,
- B. whether edge species richness changes with area,
- C. how much difference exists between edge and interior,
- D. if there is a difference between edge and interior, whether this difference changes with area, and
- E. if the total species composition changes with area, whether this change is due to the change in edge species composition or due to the change in interior species composition, or due to the

changes in both edge and interior species
composition;

(3) whether differences in neighbor types affect edge
species composition.

CHAPTER II

RESEARCH METHODS

Study Area

Ten grassland sites of different sizes were selected in Payne, Noble, and Pawnee counties of Oklahoma (Figure 1, Table 1). Criteria for selection were four: (1) all study sites had to have similar environmental conditions in terms of climate and soil; (2) all sites had to be in excellent range condition according to the criteria indicated in the Range Condition Class-Guide (USDA Soil Conservation Service 1984); (3) all sites had to be ungrazed; and (4) all had to be remnants of natural grasslands.

The ten study sites are in an area where the average maximum July temperature is 35 °C and the average minimum January temperature is -2.8 °C. The mean annual temperature is 16.1 °C (Cartography Service 1979). The average annual precipitation is 83.8 cm, minimum rainfall occurs in January while maximum monthly rainfall occurs in June, with a secondary maximum in September and a secondary minimum in August. Generally, the largest amounts of precipitation are received in summer with the least amounts received during the winter (Risser et al, 1981).

Potential evapotranspiration is high in this area, with a yearly total of 132 cm of which 94 cm is during the growing season and 38 cm during the nongrowing season. The

Figure 1. Locations of study sites distributed in Noble, Pawnee, and Payne counties of Oklahoma.

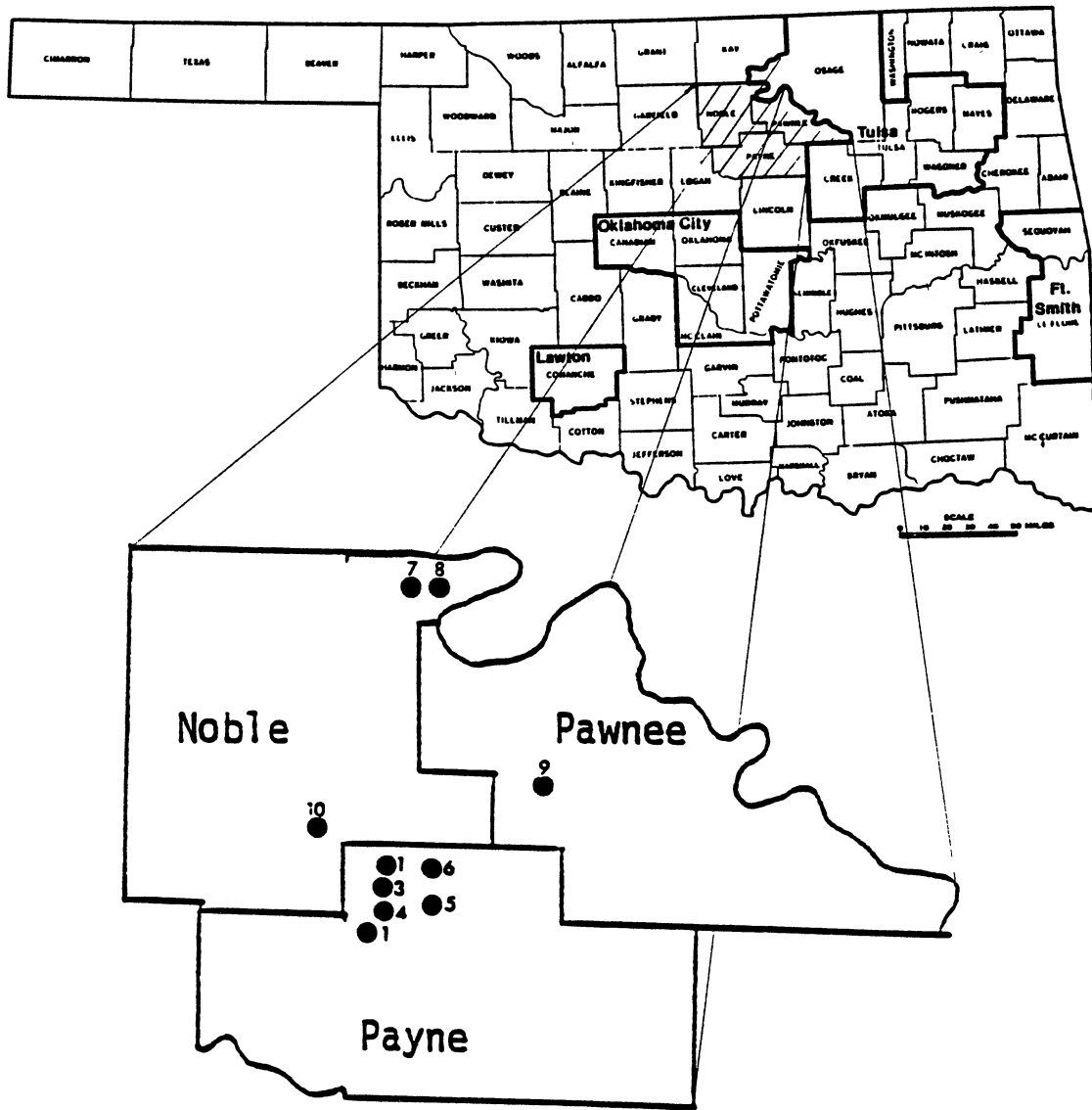


Table 1. Locality information for ten grassland study sites in Oklahoma

Site no.	area (ha)	County	Range, Township, Section
1	10.1	Payne	R2E, T19N, Sec 6, SE1/4
2	32.4	Payne	R2E, T20N, Sec 32, SW1/4
3	16.2	Payne	R2E, T20N, Sec 32, SW1/4
4	42.9	Payne	R2E, T20N, Sec 30, E1/2
5	64.8	Payne	R2E, T20N, Sec 10, NE1/4
6	32.4	Payne	R2E, T20N, Sec 24, SW1/4
7	80.9	Noble	R3E, T24N, Sec 11, W1/2
8	93.1	Noble	R3E, T24N, Sec 12, E1/2
9	64.8	Pawnee	R3E, T23N, Sec 33, E1/2
10	14.2	Noble	R1E, T20N, Sec 34, SW1/4

ratio of precipitation to potential evapotranspiration is 0.63. The growing season averages 216 days, the mean date of last frost day is about 28 March and the mean date of first frost day is about 30 October.

The study sites are situated in two geomorphological provinces, the Central Red Plains and Northern Limestone Cuesta Plains (Curtis and Ham, 1979). The soils are primarily mollisols in the suborder udolls and ustolls which include soils previously called Brunizens, Chernozens, Chestnut and Reddish prairie soils. Leaching is so high that there is no horizon of calcium carbonate, yet base saturation is high. Especially in the upper portions, mollisols are rich in organic matter and slightly acid. The principal textures of these soils are loam and silty clay loam in the A horizon, clay loam to silty clay loam in the B horizon, and loam or silt loam in the C horizon (Risser et al. 1981).

All ten study sites are remnants of the tallgrass prairie. The vegetation is composed of bunchgrasses and sod-forming grasses with a canopy height of less than 1 m. The dominant grasses include Andropogon gerardii (big bluestem), Schizachyrium scoparium (little bluestem), Sorghastrum nutans (indiangrass), and Panicum virgatum (switchgrass). Although grasses produce 80% - 90% of the biomass, forb species exceed grass species by threefold to fourfold (Sims, 1988). Forbs common in the tallgrass prairie are Aster ericoides (heath aster), Liatris punctata (dotted gayfeather), and Solidago missouriensis (Missouri

goldenrod) among others.

All study sites are classified as loamy prairie range sites in excellent range condition. Loamy prairie is a productive range site with deep, loamy upland soils. Big bluestem little bluestem , indiagrass, and switchgrass represent about 70 percent of the vegetation. Principal increaser (species that increase in abundance as a response to grazing) grasses are Bouteloua curtipendula (sideoats grama) and Bouteloua gracilis ex Steud (bluegrama). Amorpha canescens (leadplant), Baptisia Leucophaea (wild-indigo) and Psoralea (scurfpea) are common legumes (Soil Conservation Service 1984).

All study sites are maintained as hay meadows and generally cut about 4 July. Information regarding history of fire and grazing was collected by personal communication with landowners.

Field Data Collection

The modified step - point method of Owensby (1973) was used to sample the vegetation at each site in June, July, and August of 1989. This method was selected to minimize subjectivity in placement of sampling points and selection of species at each point. One thousand thirty-nine points were sampled at each site along 32 transects which divided the grassland uniformly. The transects along the edges were established 0.3 m inside the recognizable boundaries of the grassland. All sampling points nearest the boundary of the study sites were designated edge points and the plant

species present at each point were differentiated from those in the interior (Figure 2). The type of neighbor on each side of the study site was recorded.

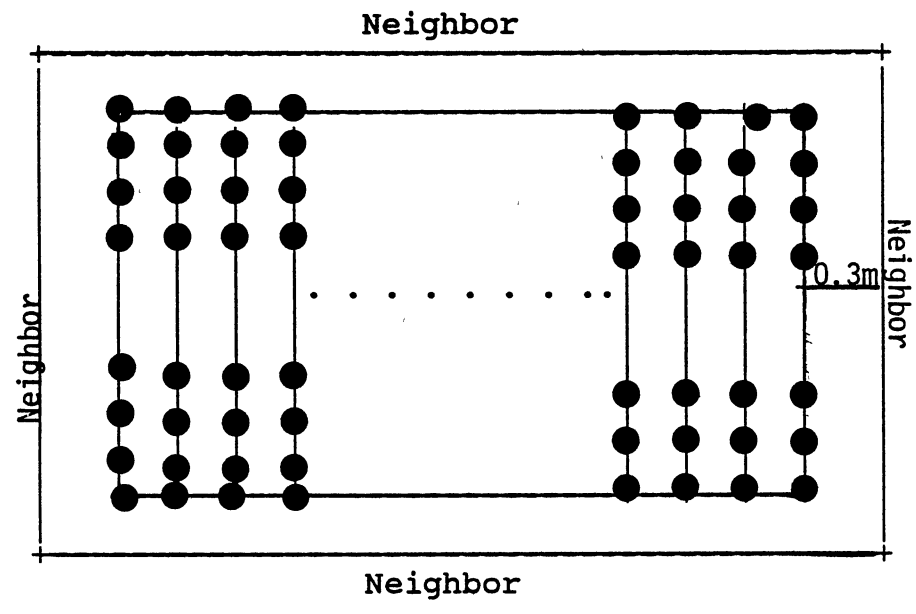
Data Analysis

In order to examine the effects of grassland area on species richness and to have a reasonable estimate of the species richness in the study sites, an extrapolation technique was used. The first-order jackknife method of Heltshe and Forrester (1983) (Appendix A) was selected because it has been shown to give a better estimate of species richness than other techniques (Palmer 1990). Using the values derived by this method the relationship between species richness and area was examined by regression analysis. Three models were fitted to the data: linear, logarithmic (Goodall 1961), and exponential (Preston 1962).

The Shannon - Weaver species diversity index, the Pielou species evenness index, and the Simpson dominance index (Odum 1970) (Appendix A) were calculated for each site to investigate the effect of area on relative abundance of species. Linear regression analyses were performed between areas and these indices.

Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were used to examine the effects of area, edge, and neighbors on species composition of grassland. DCA is an indirect eigenvector ordination technique which is advantageous because positions of samples in the ordination are less distorted by high beta diversity

Figure 2. Representation of field sampling scheme. There are 32 transects and 32 sampling points along each transect; The dots represent sampling points at study sites.



than other techniques (Hill and Gauch 1980; Gauch 1989). DCA reports eigenvalues for the first four ordination axes. The eigenvalue is always a number between 0 and 1; the higher the eigenvalue, the more important the ordination axis. In the weighted averaging methods used in this study, the eigenvalue is a measure of separation of the species distributions along the ordination axis. In DCA, the sample (site) scores along each ordination axis are derived from the species data regardless of any environmental variables. The relationship between environmental variables and species composition has to be derived after the DCA.

CCA is a direct eigenvector ordination technique. It differs from DCA in that the axes are constrained to optimize their relationship with a set of environmental variables whose direction in the ordination can be indicated by arrows with length proportional to their influence. The main utility of CCA is the possibility of showing directly the relation between the environmental variables and the ordination axes (Ter Braak 1986, 1987). The eigenvalues of each ordination axis reported in CCA have the same meaning as that of DCA, yet they are usually smaller than that in DCA because of the restrictions by environmental variables imposed on the sample scores in CCA. Different from DCA, CCA reports two sets of sample scores: sample scores derived from species scores and sample scores which are linear combinations of environmental variables. The former make the species axes while the latter makes the environmental axes (Jongman et al. 1987). CCA also reports canonical

coefficients and inter-set correlation coefficients. Canonical coefficients are computed so as to optimize the fit of the environmental axis to species data and not just to the species axis. Inter-set correlation coefficients are the correlation coefficients between environmental variables and the species axes. The two coefficients provide information on which environmental variable is responsible for the majority of the variation along an ordination axis. In contrast to canonical coefficients, the inter-set correlations do not become unstable when the environmental variables are strongly correlated with each other.

Both DCA and CCA were applied to the total vegetation data to determine whether the overall species composition changes with area. CANOCO software package (Ter Braak 1988) was used to carry out the analysis. The relationship between area and species composition was tested using a Monte Carlo test (Ter Braak 1988) with 99 permutations.

Investigation of the effects of edge on species composition comprised three analyses. First, in order to determine whether the species composition at the edge was significantly different from that in the interior, CCA was performed on a combined file consisting of both edge and interior species composition. Area and Edgeness were used as the environmental variables. Edgeness was considered as a categorical variable, value of the variable was 1 if the sample was from edge and 0 if the sample was at interior. The total number of samples was therefore 20 consisting of 10 samples from the edge and 10 samples from the interior.

A Monte Carlo significance test with 99 permutations was also performed.

Second, Manhattan distances (Faith et al. 1987) (Appendix A) were calculated for each site in order to obtain a quantitative estimate of the difference between edge and interior in terms of species composition. Linear regression was also applied to area and distance values in order to examine whether the difference between edge and interior species composition is related to area.

Third, DCA and CCA were used to analyze the relations between area and interior species composition, and between area and edge species composition. The Monte Carlo significance test with 99 permutations was applied. The analyses were an effort to determine whether the change in total species composition with area was due to a change in interior species composition, or a change in edge species composition, or a change in both.

In order to investigate the effects of the neighbors on edge species composition, the types of neighbors associated with the grasslands were grouped into six categories: (1) wooded area, (2) disturbed land or residence, (3) road (dirt gravel), (4) pasture (slightly or severely grazed), (5) highway (highway or secondary), and (6) cropland (wheatfield). Using the types of neighbors as environmental variables and area as a covariable, a CCA was performed on the edge species composition, followed by a Monte Carlo significance test with 99 permutations. The samples in this analysis were the edges on each of the four aspects of each

site, and the total number of samples was 40.

CHAPTER III

RESULTS

Species Richness and Diversity

In the 1989 growing season, all study sites contained a variety of flowering species (Appendix B). Estimates of species richness of each site as calculated by the first order Jackknife method are presented in Table 2. As can be seen, there was a difference of 31 species between the two extremes in species richness values while the area increased by almost ten times. The smallest site (10.1 ha) had the lowest species richness while the larger sites generally had higher values. The highest estimates of species richness, however, were found at the 32.4 ha and 64.8 ha sites. Site 6 (32.4 ha) had the highest number of species which occurred at only one sampling point. When plotted as a function of area (Figure 3) species richness exhibited an initial rapid increase and then leveled off. When fitted to the species-area models introduced previously, the logarithmic model of Goodall and Dahl (1961) gave the highest significance level and correlation coefficient (Table 3).

Species Composition in Relation to Area

The simple linear regression analysis of the ten areas using the three community indices of diversity, evenness,

Table 2. Species richness of each study site estimated by first order Jackknife.

Site	Area(ha)	Species observed	Species estimated
1	10.1	61	78
10	14.2	82	98
3	16.2	69	84
2	32.4	82	99
6	32.4	77	109
4	42.9	78	95
5	64.8	76	92
9	64.8	92	105
7	80.9	75	95
8	93.1	84	95

Figure 3. Relationship between species richness and area of ten grasslands in north-central Oklahoma.

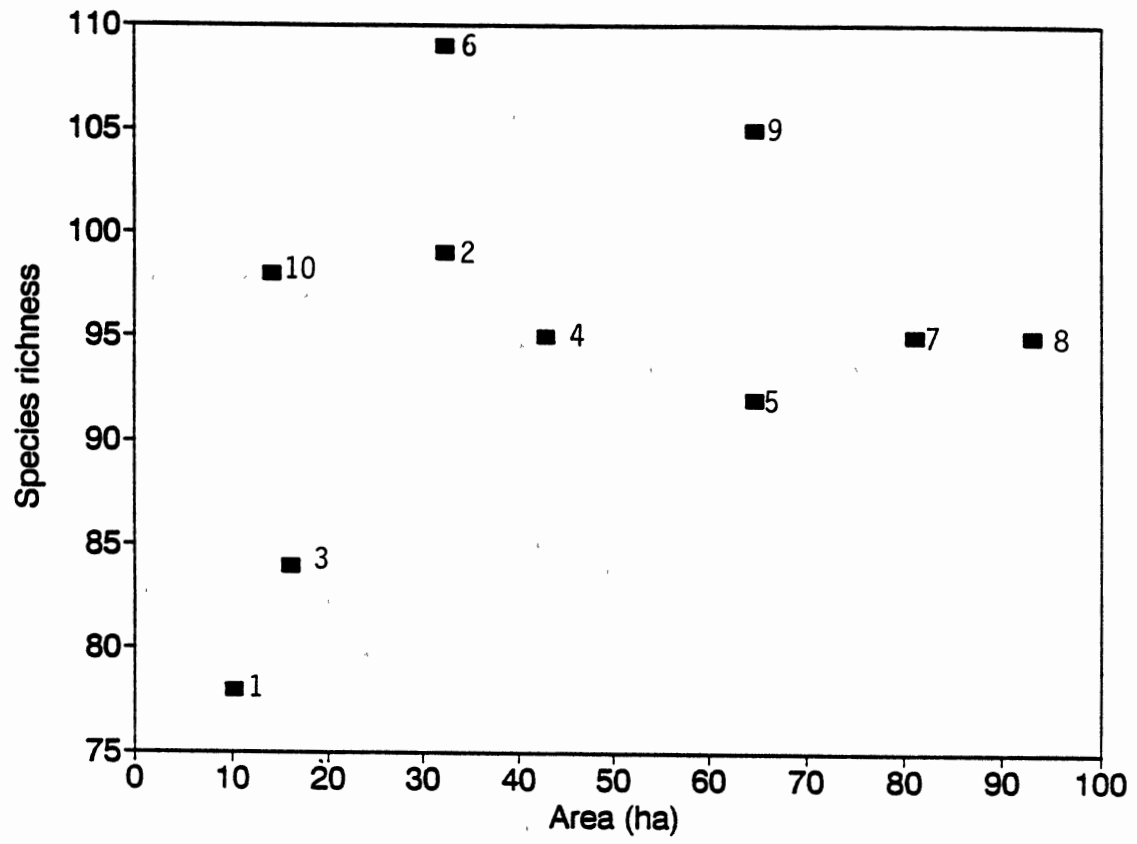


Table 3. The significance levels, correlation coefficients and parameters estimated for linear, logarithmic, and exponential models of species-area relationship

Model	Fitted model	p>F	r
Linear	$s = 90.73 + 0.04 A$	0.39	0.31
Logarithmic	$s = 47.99 + 15.17 \text{Log}(A+1)$	0.07	0.60
Exponential	$s = 70.15 A^{0.067}$	0.13	0.51

and dominance indicated low correlations and relatively low variation in each (Table 4).

In all study sites, Schizachyrium scoparium was the most dominant species with mean relative frequency of 27.3% and a standard deviation of 3.6. Andropogon gerardii also dominated with a mean relative frequency of 13.9 ± 5.3 . Sorghastrum nutans was the third dominant in some sites and exceeded A. gerardii in other sites. Its mean relative frequency was 12.5 ± 4.6 .

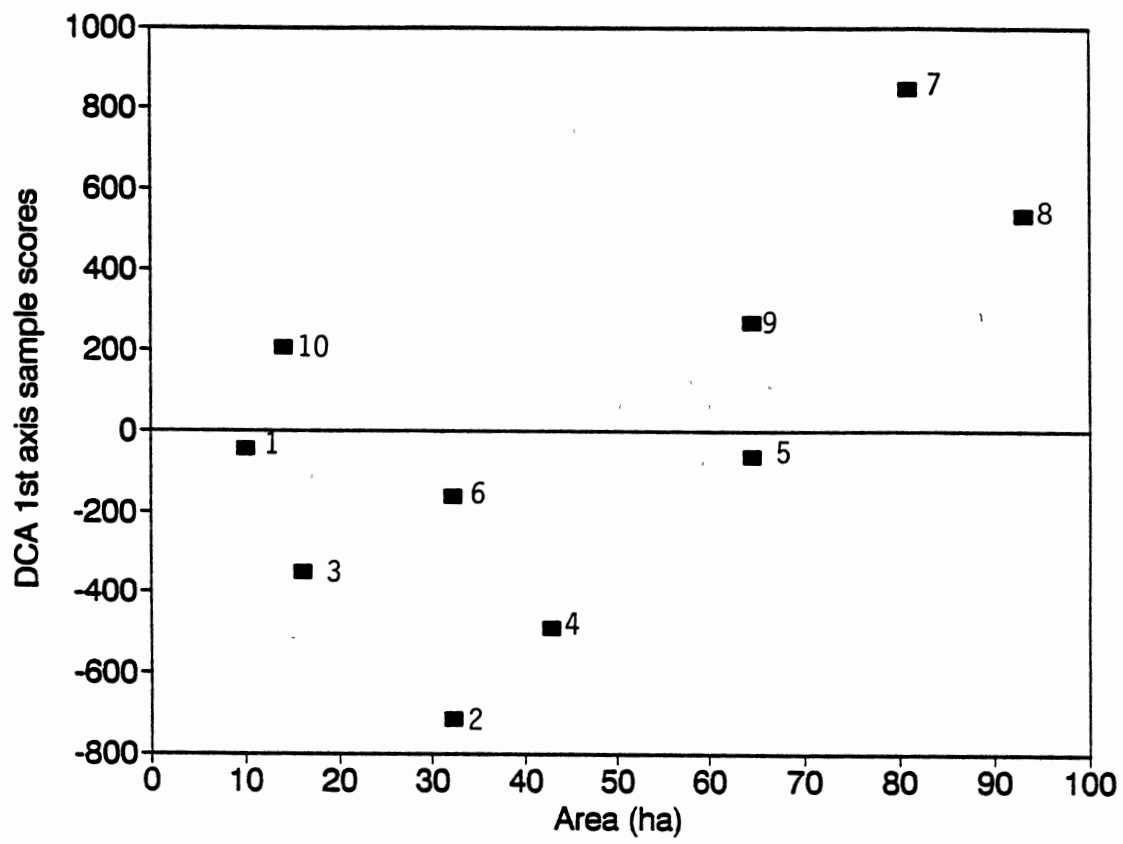
DCA analysis of the total species composition produced eigenvalues of 0.164, 0.115, and 0.069 for the first three species ordination axes. The relatively low eigenvalues indicate the absence of a gradient which would explain the majority of the variation in species composition.

When sample scores along the first species axis were plotted as a function of area (Figure 4), there seemed to be a trend of change in species composition with area. The trend, however, appeared to be less obvious among the sites that were smaller than 64.85 ha. In addition, the trend among the small sites appeared opposite to that exhibited by the large sites. The results from the CCA performed on the same data again produced relatively low eigenvalues (0.100, 0.128, 0.113, and 0.082) for the first four species ordination axes. Compared with the DCA eigenvalue of the first species axis, the eigenvalue of the first CCA species axis which was directly related to area was only 0.064 lower. This may indicate the variation along the first DCA axis can be largely explained by change in area.

Table 4. Species diversity, species evenness, and species dominance indices for each study site, along with their means (\bar{x}), standard deviations (Sd) and results of simple linear regression analysis between the indices and area

site	area (ha)	diversity	evenness	dominance
1	10.1	2.59	0.66	0.13
10	14.2	2.38	0.62	0.16
3	16.2	2.25	0.62	0.15
2	32.4	2.91	0.69	0.09
6	32.4	2.71	0.64	0.13
4	42.9	2.53	0.64	0.12
5	64.8	2.60	0.63	0.14
9	64.8	2.57	0.65	0.13
7	80.9	2.62	0.66	0.13
8	93.1	2.52	0.65	0.16
\bar{x}	-	2.57	0.65	0.13
Sd	-	0.18	0.02	0.02
P(f)	-	0.62	0.60	0.74
r	-	0.17	0.20	0.10

Figure 4. Relationship between total species composition and area of ten grasslands in north-central Oklahoma as determined by Detrended Correspondence Analysis.



When plotting the CCA sample scores against area, the correlation between area and species composition became more distinct (Figure 5). This correlation was also indicated by the relatively high canonical correlation coefficient of 0.88 between sample scores and area. However, it should be pointed out again that the eigenvalue of the first axis was low, indicating a relatively low percentage of the total variation in species data was explained by the first axis. The correlation between sample scores and area was again less clear in the group of relatively small sites in contrast to that in the group of large sites.

The Monte Carlo significance test produced a P-value of 0.12 for the first ordination axis. Although not highly significant, it is strongly suggestive that the correlation between area and the first ordination axis is not due to random chance.

Edge Species Composition and Interior Species Composition

The CCA on the combined data of both interior and edge species composition produced results indicating a significant edge effect (Table 5, Figure 6). The first species axis had a very high eigenvalue (0.802), it therefore accounted for the majority of the total variation in the species data. This axis is highly correlated with edgeness, as indicated by the high canonical coefficient and correlation coefficient. The Monte Carlo significance test on the first axis gave a highly significant level ($P < 0.01$),

Figure 5. Relationship between total species composition and area of ten grasslands in north-central Oklahoma as determined by Canonical Correspondence Analysis.

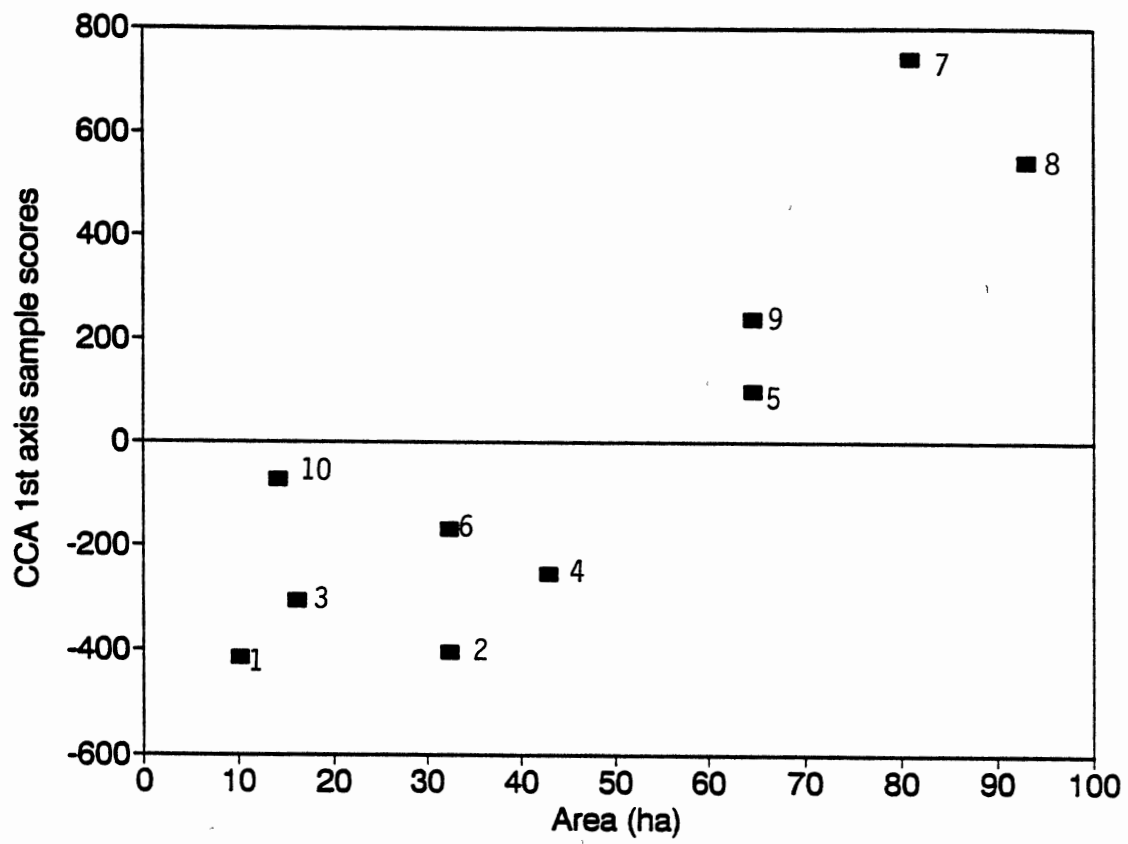
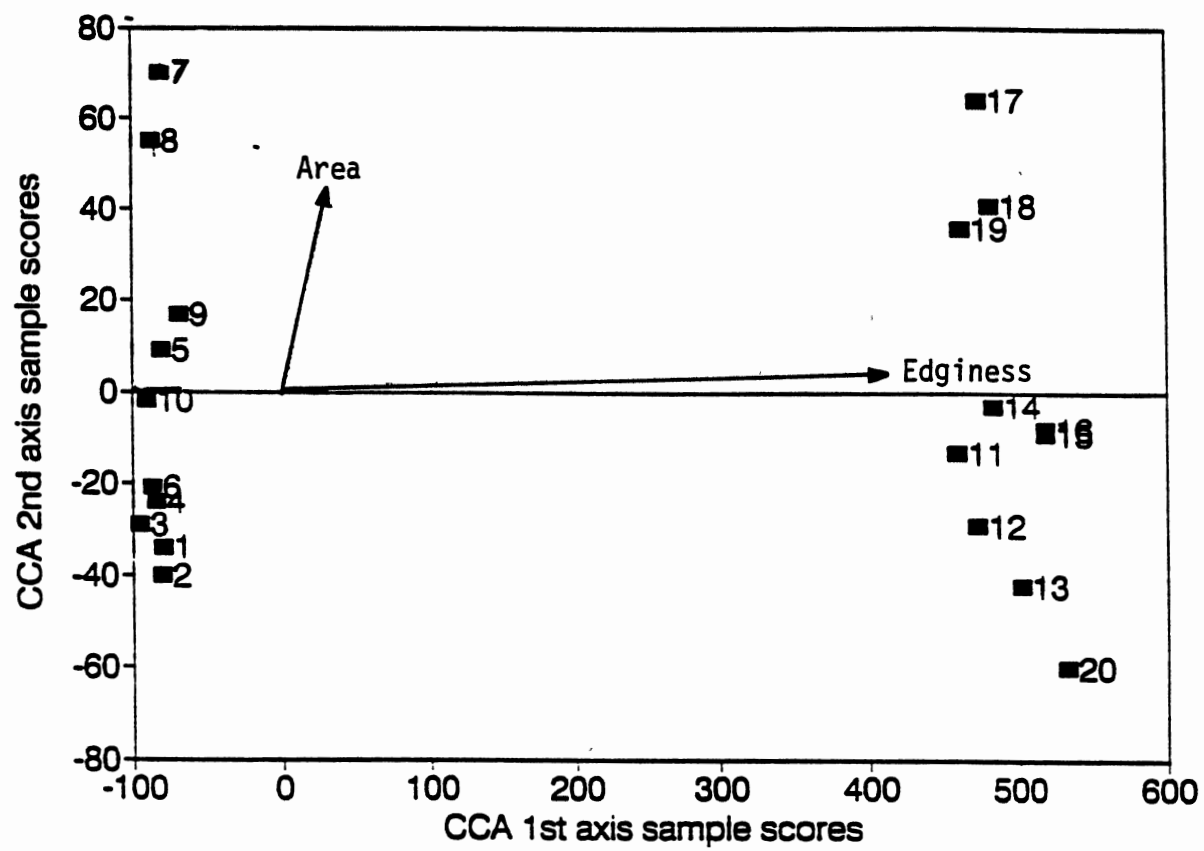


Table 5. Canonical coefficients and inter-set correlations of environmental variables (edgeness and area) with the first two ordination axes of CCA for the combined data of edge and interior species composition.

Environmental Variables	Coefficients		Correlations	
	axis1	axis2	axis1	axis2
Edgeness	-201	1	-998	6
Area	1	31	-23	859

Figure 6. Effects of area and edgeness on species composition in ten grasslands in north-central Oklahoma as determined by Canonical Correspondence Analysis of the combined file of edge and interior species composition.



edgeness was therefore indeed the major factor for explaining the major variation along the first axis.

The second axis had a relatively low eigenvalue (0.087) and was correlated with area (Table 5). According to this information, area accounted for only minor part of total variation.

It was obvious that little correlation existed between edgeness and area, which was indicated by the almost orthogonal ordinate positions of the two environmental variables and was reflected also by the low correlation coefficient between the two.

There was a linear trend of positive correlation between grassland area and the Manhattan Distances (Figure 7), in other words, the difference between edge and interior species composition increased with area. The simple linear regression analysis produced a P-value of 0.10 and a correlation coefficient of 0.54, indicating a fairly close relationship between area and the difference between edge and interior. The plot of the residuals of the regression against area (Figure 8) showed no obvious curvature, indicating the absence of nonlinear factors and, therefore, the confirmation of a linear relationship between area and the distance measures.

The DCA performed on the data set for edge species produced eigenvalues of 0.241, 0.184, and 0.155 for the first three species axes. When the sample scores were plotted against area (Figure 9), no trend of correlation was evident. When CCA was performed on the same data, the

Figure 7. Relationship between Manhattan Distances and area in ten grasslands in north-central Oklahoma.

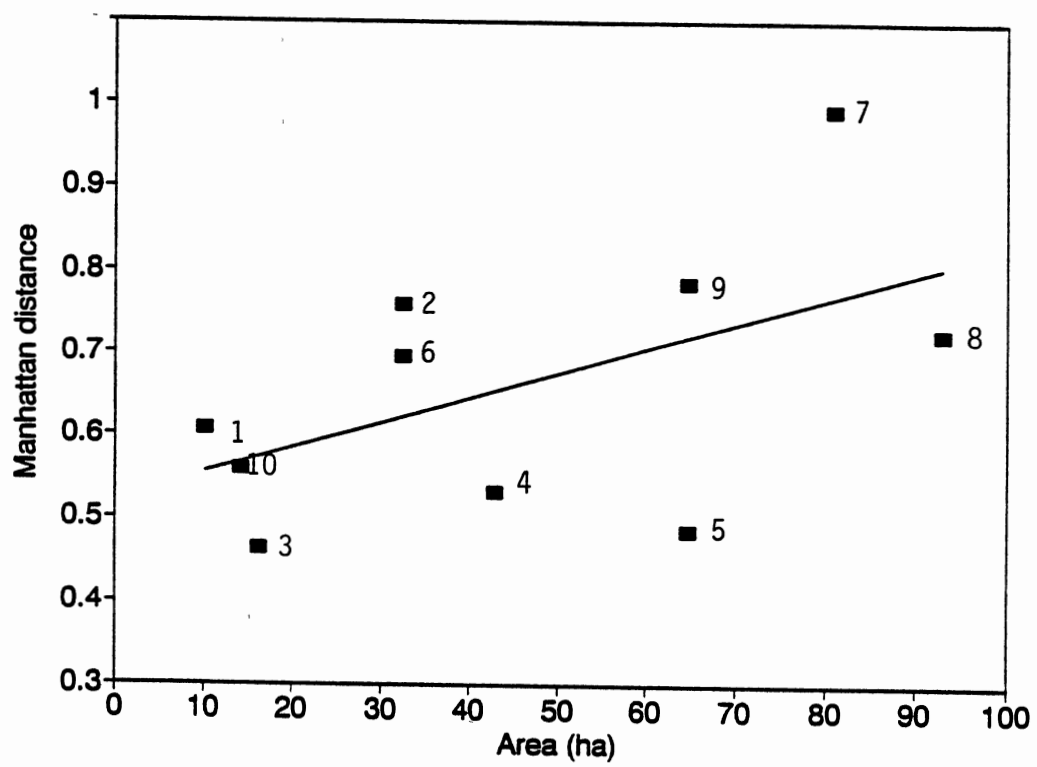


Figure 8. Residuals of the linear regression analysis of Manhattan Distances with area of ten grasslands in north-central Oklahoma.

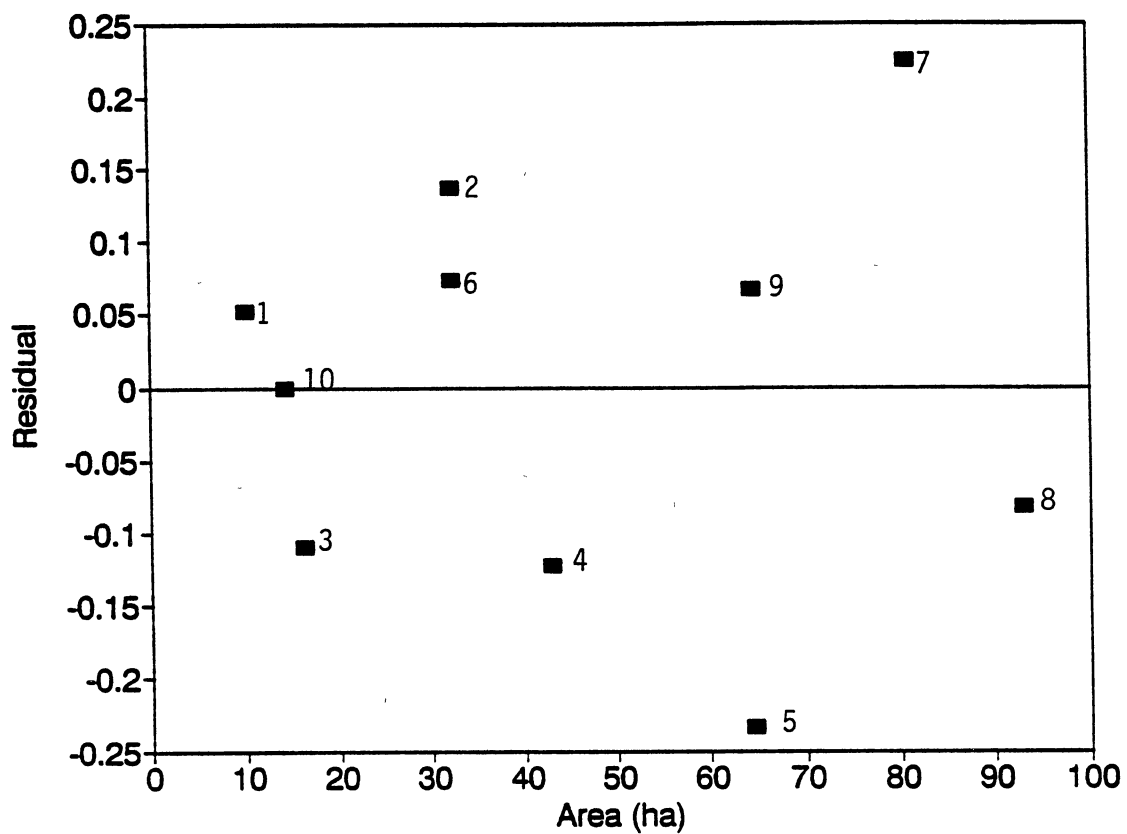
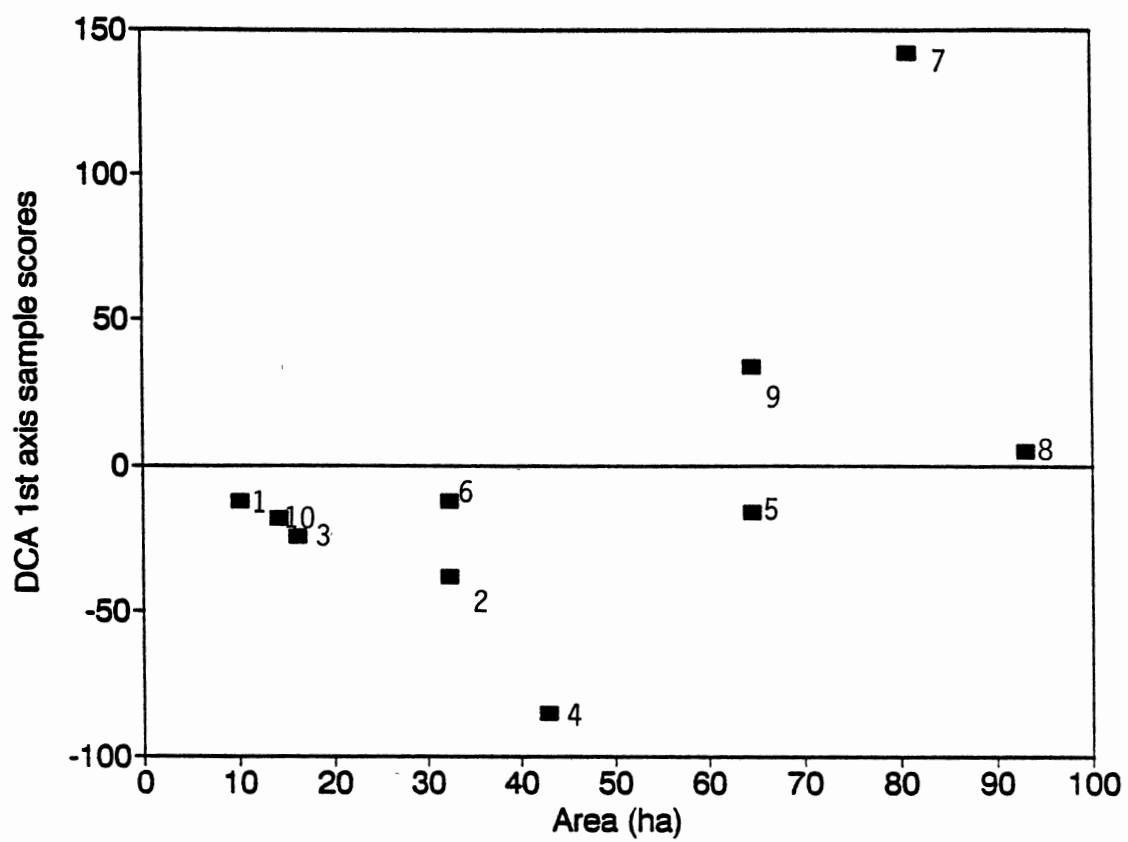


Figure 9. Relationship between edge species composition and area of ten grasslands in north-central Oklahoma as determined by Detrended Correspondence Analysis.



eigenvalues were 0.163, 0.214, and 0.194 for the first three species axis. Compared with the results of DCA, there was a decrease of 0.078 in the eigenvalue for the first species axis. The Monte Carlo significance test on the pattern of sample distribution produced a P-value of 0.26. These results may indicate that the first species axis was responsible for a fair amount of variation in edge species composition. However, area could not explain the majority of the variation, as suggested by the absence of a distinct pattern and the low significance level from the Monte Carlo test.

The DCA performed on the data set for interior species produced eigenvalues of 0.168, 0.113, and 0.070 for the first three species axes. With the exceptions of site 1 (10.1 ha) and site 10 (14.2 ha), the other sites appeared to be arranged along the first species axis according to increasing area (Figure 10). The CCA performed on the same data set produced eigenvalues of 0.100, 0.131, and 0.113 for the first three species axes, and there was a decrease of 0.068 for the eigenvalue of the first species axis. The trend of correlation between area and sample scores became more distinct (Figure 11) with a correlation coefficient of 0.871. The Monte carlo significance test on the sample distribution on the first species axis produced a P-value of 0.10. Area was more closely related to changes in interior species composition than to edge species composition.

Figure 10. Relationship between interior species composition and area of ten grasslands in north-central Oklahoma as determined by Detrended Correspondence Analysis.

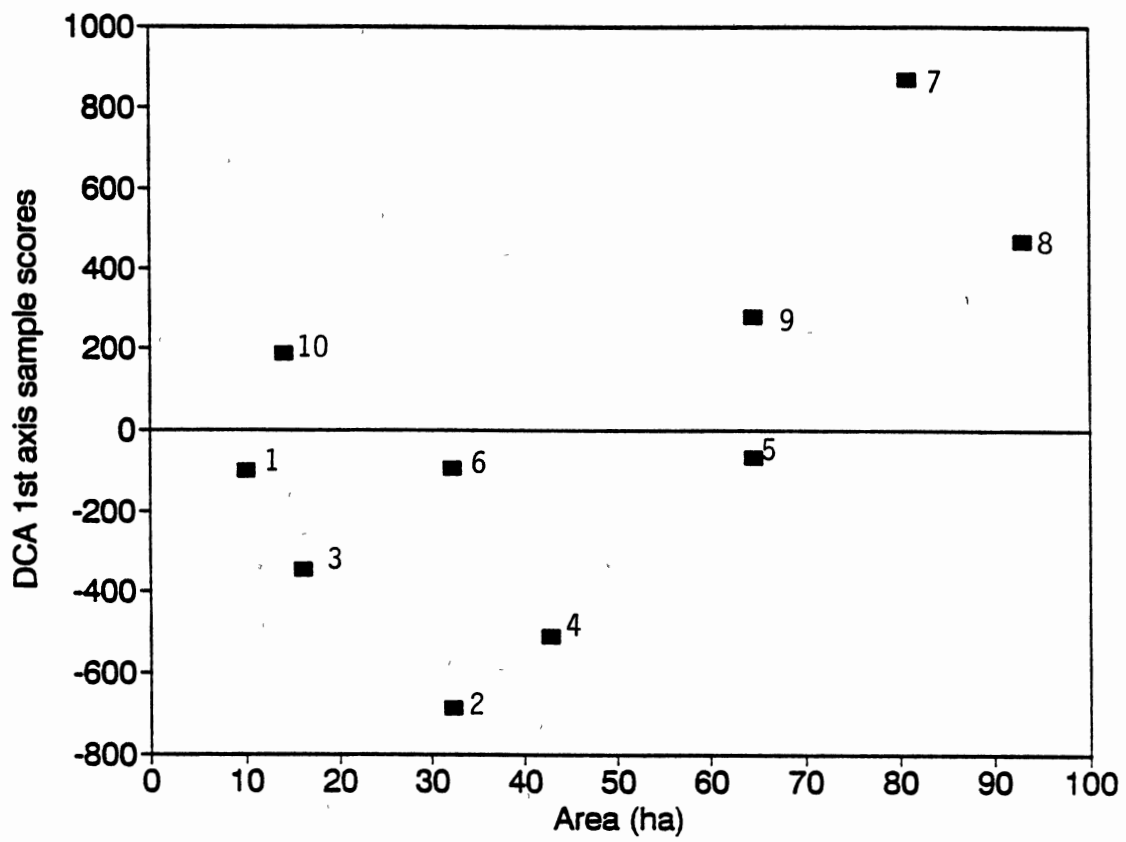
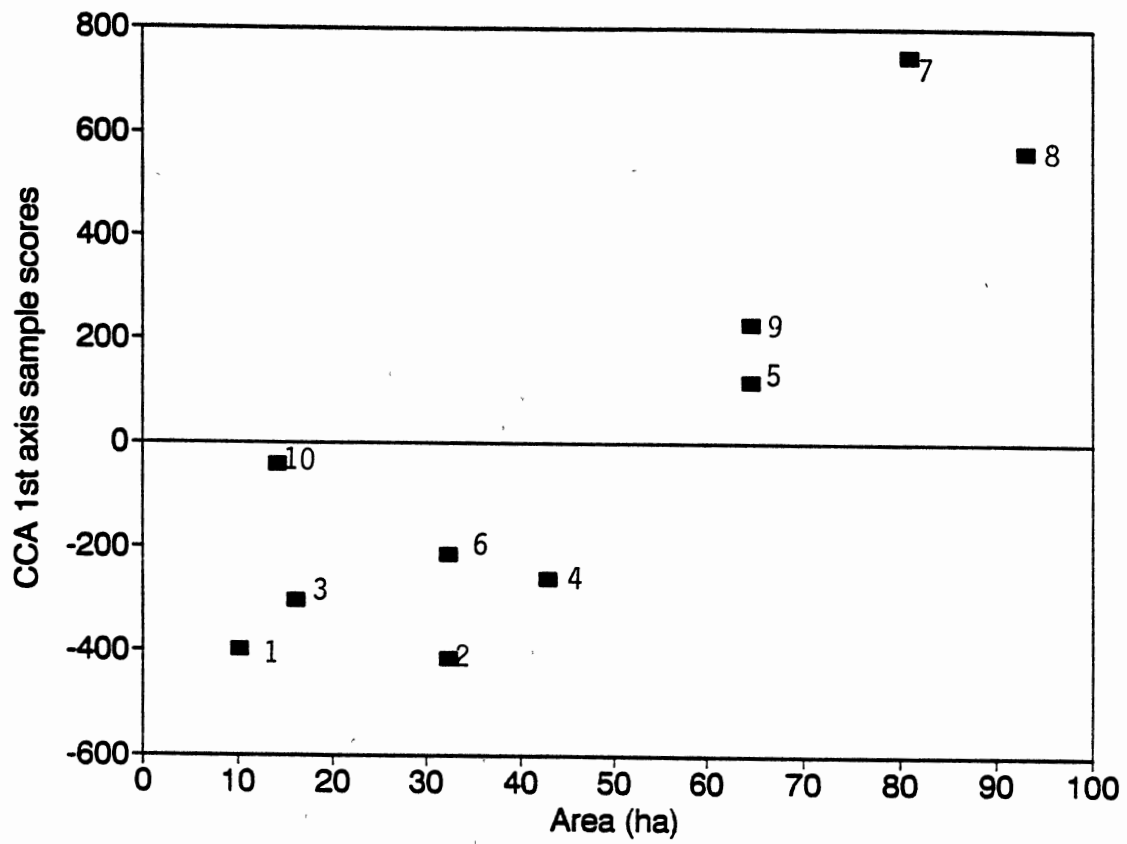


Figure 11. Relationship between interior species composition and area of ten grasslands in north - central Oklahoma as determined by Canonical Correspondance Analysis.



Species Composition at Edges Associated
with Different Neighbors

CCA performed on the edges associated with the six neighbor types produced eigenvalues of 0.152, 0.113, 0.104, and 0.080 for the first four species axes. The small differences among the eigenvalues of the first three axis indicated the absence of a dominant factor in determining the edge species composition. The canonical correlations between the species ordination axes and the neighbor types were relatively low (Table 6), and little separation was found along the first and the second axis among the samples associated with different neighbors. The Monte Carlo significance test on the first species axis produced a P-value of 0.42, indicating absence of significant effect of neighbor types on the edge species composition.

Table 6. Canonical coefficients and inter-set correlations of environmental variables (types of neighbors) with the first four ordination axes.

Environmental Variables	Coefficients				Correlations			
	axis1	axis2	axis3	axis4	axis1	axis2	axis3	axis4
Wood	-252	-484	15	368	-208	165	302	683
Disturbance	134	-510	166	52	525	-365	563	-137
Road	-73	-733	-295	217	456	-140	-704	83
Pasture	-431	-736	-80	74	-672	-185	99	-464
Highway	-91	-370	-23	115	15	14	53	47

CHAPTER IV

DISCUSSION

Species - Area Relationship

According to the results of this study, flowering plant species - area relationship in grasslands agreed with much of the previous research conducted in other communities, i.e. species richness increased with area. However, large variations existed, indicating the presence of other variables affecting species richness. As suggested by Pianka (1983), area itself is probably not the primary factor affecting species richness in most situations, but presumably affects indirectly by increasing the variety of available habitats. Haila (1983) also suggested that the relationship between area and species richness was an indirect one.

Results from a large number of research studies have pointed to the determinant role of habitat heterogeneity in species richness. Nilsson et al. (1989) found that the only factors significantly correlated with total species richness were substrata heterogeneity and substrata fineness. Barkman (1989) also stated that, in addition to area, species richness of habitat islands were also affected by age of the islands and degree of disturbance.

In contrast, Levenson (1981) investigated the species -area relationship in the woodlots in the metropolitan

Milwaukee region. He sampled 43 sites ranging in area from 0.03 ha to 39.96 ha. Even though his largest site was 1,332 times greater in area than his smallest site, Levenson found no correlation between area and species richness ($R=0.01$). It was suggested that, in addition to area, species richness may also be affected by topography, general soil conditions, successional age, degree of disturbance, time since the island development, and interaction with other islands in terms of propagule exchanges with surroundings. In grassland studies, the specific variables may be different, or the order of importance of the variables may be different, but it appears that species richness is likewise affected by more than just area.

It is my view that there are two levels of habitats according to their scales and their relationship to area: microhabitats and macrohabitats. Increase in microhabitats is concomitant with increasing area, i.e., as area increases it is more likely to incorporate new microhabitats due to increased chances in variations in small scale. As a result of such a relation between area and microhabitats, species richness increases with area. This interpretation is essentially the same as the habitat heterogeneity hypothesis (Williams 1964; Shmida and Wilson 1985). On the other hand, the changes in macrohabitats, such as presence of a creek, a steep slope, a trail, or a change in soil type, may not be related to area within a certain range, yet they may play significant role in affecting species richness. If the macrohabitat conditions are equal among samples, a positive

species-area relationship may be observed at a relatively short range of area. If the macrohabitat conditions are not equal, the positive microhabitats-area relationship may be obscured by the macrohabitat changes, so will be the positive species-area relationship. In this case, given the condition that the number of samples is equal, a large range of area is necessary in order to detect a positive species-area relationship.

In the results of species richness from this study, site 6 which was 32.38 ha in area had the highest species richness. According to visual observation, this site had considerable variation in macrohabitats with a wooded ridge, a large depression filled with water, and greater slope than the other sites.

Due to the low number of samples used in this study, the changes in species richness should not be overemphasized. However, detection of a correlated species-area relationship depends on whether an adequate range of area or sample number are used, and this 'adequate range' or 'adequate sample number' depends upon the degree of habitat heterogeneity. Evaluation or estimation of the habitat heterogeneity at different spatial scales should precede the selection of range of area and sample numbers.

This precaution is consistent with findings that the pattern of species richness is scale-dependent. Palmer (1990) found that among-plot standard deviation in magnesium concentration explained more than half of the variation in

species richness of 0.1 ha plots, yet the same variation failed to explain the within-plot variation in species richness. When discussing the almost ubiquitous phenomenon in which species number is stable over several plot sizes, Barkman (1989) wrote: " I therefore believe that every phytocoenosis as a general rule is a compound mosaic, consisting of a coarse pattern, the elements of which consist of a finer pattern, etc." Similarly, it had been proposed that each unit of environment may be composed of a number of subunits, and that this structure may be responsible for the observed patterns of species abundances (Kolasa and Strayer, 1988; Kolasa, 1989). These findings or comments all suggest that different sets of factors may operate at different spatial scales in affecting patterns of species richness and distribution, which should be kept in mind when conducting a research on species - area relationship, or on any phenomena in community ecology and landscape ecology.

Even though abundant evidence is available in proving the determinant role of habitat heterogeneity in species richness, the theory of island biogeography meets a few direct challenges and is still the focus of hot debate (Simberloff and Abele 1982, Soule and Wilcox 1980, Lovejoy and Oren 1981, Wilcox and Murphy 1985). Though I have no direct information from my research with respect to this issue, it is my view that both the habitat-diversity hypothesis and island biogeography theory can partially account for the species-area relationship. In other words,

observed species richness is the combined product of habitat diversity and species immigration and extinction. On oceanic islands, the effects of immigration and extinction may be more obvious than on terrestrial habitat islands, because habitat diversity would not be able to fully display its effect if there are not enough immigrants to occupy them. Terrestrial habitat islands are surrounded by media of different kinds which, in comparison to the ocean, may be a lesser barrier to many species. Also, the source pool of a habitat island is composed of numerous neighbors of its own type which may not be as distant as between an oceanic island and its mainland source pool. Therefore, habitat heterogeneity may play a more significant role in determining species richness.

The species-area curve from this study was better described by the logarithmic model of Dahl (1960) and Goodall (1961) than the exponential model of Arrhenius and Preston. This observation differs from the results of Kilburn (1966) who found the best fit from the exponential model based on his investigation of 6 sites of 3 plant communities in the Midwest. However, Barkman (1989) indicated that highly anthropogenic grass communities showed a better fit to the Dahl-Goodall model. Although the study sites of this research were selected for the absence of major disturbances, they were actually maintained by annual mowing for hay. However, because of the relatively low number of samples, the results should not be considered as strong evidence for, or against, either of the models.

The exponential model of Arrhenius (1921) and Preston (1962) is most popular among north American ecologists. The interpretation of the parameters of c and z spurred numerous investigations. z is of more interest since it is the slope of the $s = c A^z$ function after a logarithmic transformation. The magnitude or changes of z have been cause for considerable debate (Connor and McCoy 1979, Wilcox 1980; Martin 1981; Sugihara 1981, Wright 1988). The z value has been suggested to vary according to degree of isolation (Preston 1962; MacArthur and Wilson 1967; Harris 1984). In cases of non-isolation, it ranges from 0.12 to 0.17 whereas in cases of isolation from 0.19 to 0.37. The divergence of z values for habitat islands (samples) compared to oceanic islands was explained as a failure of habitat islands to represent a complete lognormal ensemble of species (Preston 1962). If z is indeed a measure of degree of isolation, then the low z value of 0.066 from my research would indicate a low degree of isolation among the sample sites. This may reflect the true situation because most of my sites were close in distance to their own type of vegetation, often separated only by fence or narrow dirt road. Moreover, the low z value from this study may also indicate the incompleteness of the samples. In their studies of bird faunas on the Solomon Archipelago, Diamond and Mayr (1976) calculated a z value of 0.025 for the "highly vagile" species and 0.28 for the species with "low vagility" on the same islands. They explained the difference as a result of samples for the "highly vagile" species being less complete

than those of "low vagile" species. On the other hand, disagreement also exists as to the relation between z and degree of isolation. Barkman (1989) analyzed data from several studies and concluded the exponent z was an unsuitable measure for the degree of isolation of habitat islands.

Area Effects on Species Composition

Less direct attention in previous research has been paid to area effects on species composition although qualitative discussions are in existence for edge effects (Levenson 1981; Harris 1984; Wilcove et al. 1986; Lovejoy et al. 1986; Diamond 1988). According to the results of this study, area has no observed effect on species diversity measured by the Shannon-Weaver index, nor on species dominance or evenness measured respectively by Simpson's and Pielou's indices. The homogeneous abundances of the first three dominants throughout the sample sites indicate their insensitivity to changes in area in the absence of other disturbances. However, these three indices are based only on the number of individuals of each species present on the sites, and do not reflect what species are present and what species are absent. In terms of addressing area effects, the presence or absence of certain species are important issues. Large taxonomic collections normally contain a few very abundant species and a long list of less abundant or rare species (Preston 1962; Williams 1964). Area does not seem to affect the most abundant species, rather it changes the

presence or absence of the less abundant species.

According to the results of DCA and CCA performed on total vegetation data, species composition changed with area, with a suggestive p-value (0.12). However, the first DCA axis, which was shown to be related to changes in area by CCA, had a relatively low eigenvalue. When CCA was performed, the eigenvalue became lower, lower than the eigenvalues of the other reported species axis. This suggests the presence of other deterministic environmental factors. Area alone can not account for the major variation in species composition. Yet, within the variation along the first species axis, area seems to be the major factor explaining the changes in species composition. However, it is interesting that such correlation was less clear in the group of smaller sites. At certain spatial scale, environmental heterogeneity may obscure the relation between area and species composition.

Edge Effects in Relation to Area Effects

The classical edge effect is the tendency for increased species richness and density at community boundaries as a result of overlapping communities in addition to organisms which are characteristic of the boundary habitats (Odum 1970). Previous studies indeed found elevated species diversity at edges of different communities (Ranney et al. 1981; Lovejoy et al. 1986; Lukac 1988).

Edge species composition was shown by the CCA results of this study to be significantly different from interior

species composition, and, according to the measure of Manhattan distance and the regression analysis to area, the difference between edge and interior species composition became more distinct as area increased. Therefore, the change in total species composition in response to area could result from (1) lower percentage of edge, and therefore lower percentage of edge species in larger sites; and (2) gradual changes in interior species composition with change in area.

The low correlation between area and edgeness indicates that edge species composition changes little with area. According to the results of DCA and CCA on edge species composition, this indeed is the situation: edge species composition did not show significant change with area. This is easily understandable because habitat conditions on the edges should be similar regardless of the size of the sites. It is therefore clear that edge species composition did not contribute to changes in total species composition.

In contrast with edge species composition, the change in interior species composition in response to increase of area is more distinct than either edge species or total species composition. This may indirectly suggest that the less distinct trend of change in total species composition than that of interior may be partially caused by insensitivity of edge species composition to area. The more noticeable change in interior species composition indicates this change may be the major or at least a very important cause of change in total species composition. This finding

is different from the results of previous research that indicate the change in species composition is the result of change in relative proportion of edge species with area (Harris 1984; Lovejoy et al. 1986).

In relation to the gradual increase in the difference between edge and interior species composition, the statement becomes questionable that there is a size for habitat islands below which interior conditions cannot be found (Levenson 1981). In my point of view, there may not be a physically definable area at which so-called interior conditions are formed. Instead, the interior condition is being formed gradually, no abrupt discontinuity occurs in the edge to interior gradient that would serve to separate edge from interior. In response to change of area, species composition may change from mainly xeric edge species assemblages to mixture of edge and less edge species, and to mixture of edge and less edge and interior species. As area increases, the proportion of each changes. To advance the notion one step further, there may not be a physically definable 'minimum critical area' either. Minimum critical area is defined as a continuous habitat large enough in extent to contain and maintain its characteristic species diversity and species composition (Lovejoy and Oren 1981). However, based on the information from this research, new species appear and species composition changes gradually and continuously as area increases even though the major dominants of the community remain unchanged. How would the so-called 'characteristic species diversity and composition'

be defined? Since discontinuity in species composition is unlikely found, so unlikely would be the nonselective 'minimum critical area', unless an arbitrary definition is used.

Edge effect is different from, yet related to area effect. Lovejoy et al. (1986) presented data which suggested a mixture of area and edge effects. They indicated that edge-related changes were dominant in the smaller isolated reserves, and area effects can only be studied in larger reserves. They were the first to conceptually separate changes in species richness caused by edge from the changes caused by area alone. This necessary distinction was not considered in many previous studies on species-area relationships. In my opinion, area effect is different from pure edge effect yet it must be evaluated in relation to edge effects because the "dominant" role of edge in smaller islands is a reflection of area effect. It would truncate either edge or area effect if studies on edge effect on total species richness or composition are confined to small sites and studies on area effects to large sites.

I consider that edge effect has two components: its buffer effect on interior habitat condition and its different species diversity and composition from the interior. The absolute effects are constant while the relative effects changes with area. In another words, edge effect is confounded with area effect which in turn has two components, one is the change in the ratio of edge to area, and another is changes in habitat heterogeneity and ratio of

extinction to immigration, which is associated with change of area. Such recognition has not been suggested previously.

Physical characteristics of edge may indirectly affect the interior species composition by serving as a 'differential - permeable membrane' to biotic and abiotic influxes to and outflow from a habitat island. This 'membrane' functions differently as a consequence of the physical features of the edge itself, such as its thickness. Such features would determine the degree of the responses of different materials, organisms, or abiotic factors to the edge (Weins et al. 1985). Wales (1972) and Levenson (1981) showed that the edges of small forest islands might play a particularly important role in the development of individual forest islands. Edge vegetation provides propagules of a different species composition than would otherwise be available to interior vegetation replacement process if edge were not present. Ranney et al (1981) believed that because of forest edges, the forest islands they examined had a greater component of shade-intolerant species in the interior than if the same sites were in extensive forest. Our results agree with their notion. With edge being excluded, that is to exclude the factor of relative proportion of edge, the interior species composition of small sites were still different from these of larger sites as shown by the results of distance analysis and by the results of CCA analysis on interior vegetation. This result indicates the presence of larger percentage of edge species

and species with some edge traits in the interior of small sites than in the interior of large sites. However, several aspects of edge effects deserve further investigation, such as (1) whether the change in interior species composition is due to edge effect in serving as a pool of propagules of edge species; (2) whether the change in interior species composition is due to the buffer effect of edge as discussed above; and (3) whether edge affects interior species composition by a combined effects of various aspects including the two mentioned above.

Edge Effects On Interior Species Composition

It is an interesting finding that interior species composition is different among islands of grasslands of different sizes, and this finding can be related to the controversial issue of 'species quantity' versus 'species quality' within the discussion of edge effect and habitat fragmentation.

A number of researchers claim that species diversity could be increased by habitat fragmentation (Higgs and Usher 1980; Gotfryd and Hansell 1986; Simberloff and Gotelli 1984, Quinn and Harrison 1988, Robinson and Quinn 1988), and that subdivision into a number of independent subpopulations may frequently act to decrease the probability of overall extinction in rare species (Quinn and Hastings 1987). The enhanced species diversity was considered to be due to the creation of additional habitat edge within the originally continuous habitat. Therefore, these researchers

deemphasize the detrimental effect of habitat fragmentation on the survival of wild species. However, species are different in their properties, some are specialized in certain types of habitat with relatively narrow ranges of distribution, and are sensitive to disturbances and changes in their habitat. Some species are generalized in having broad ranges of habitat, and being robust to disturbances. Habitat fragmentation increases the edge to interior ratio and results in negative effects on interior species. Species which require extensive and continuous habitat to sustain their population above dangerous level are also negatively affected by habitat fragmentation. Meanwhile the habitat fragmentation may have no effect on, or even may promote, the abundances of edge species and opportunistic r-selected species. This may explain the enhanced species richness in response to the degree of fragmentation as claimed by some ecologists. People should be aware that creation of additional habitat edge within continuous habitat can dramatically increase local species diversity, but it fulfills no conservation objective. The enhanced species richness by additional edge involves enhanced "junk" species at the expense of interior species, edge species, and native species (Murphy 1989, Verner 1986). An example is provided by Murphy's (1989) critique of research done in a winter annual grassland in central California (Robinson and Quinn 1988). Of 42 plant species monitored by Robinson and Quinn, only 11 (26%) were native species. Of these 11, only 3 native plant species (just 7% of the total) were found in

more than 3 sample habitat plots (of a total of 42) per year during the three-year study.'

Neighbor Effects on Edge Species Composition

Abiotic factors such as wind or surface water respond differently to boundary features than do biotic factors such as birds or cattle (Weins et al. 1985; Stamps et al. 1987). Differences also exist within the two categories. For example, a fence can effectively prevent cattle from passing to another patch of grassland while it has little effect on birds' mobility. Consequently, the quantities of immigrant/emigrant propagules disseminated by different vectors would differ at various types of boundaries, and, the types of propagules immigrated to a certain site would be largely dependent on the types of its neighbors. As Ranney et al. (1981) suggested, edge species composition at the early stage of edge development is largely determined by the invasion of propagules from neighboring vegetations. In Dutch limestone grassland, a conspicuous influence of the adjacent communities was observed on the quantitative species composition (Barkman 1989). Similar observations are available from studies in forests. As areas of conserved pristine forest are reduced in size they are increasingly susceptible to significant immigration of species from their neighbors (Janzen 1983).

The neighbor effect is related to the degree to which the two adjacent communities differ; the more distinct difference between two neighbors, the more significantly

they affect each other's species composition. As reasoned by Barkman (1989), with everything else being equal, arable field and active sand dunes will have more influence on a forest edge than meadows, meadows more than heathland, and heathland more than scrub. The least influence will be exerted by adjacent woods of a slightly different type. A field study conducted in West Germany showed that both road construction and agricultural activities contribute to habitat isolation, and highway had much more significant isolation effect on forest-dwelling mice and carabid beetles than cropland (Mader 1984).

Neighbor effect is assumed to be more pronounced in edge species composition of adjacent communities since edge is the first frontier different propagules cross. The lack of significant separations in the CCA ordination among edge species composition bordered by different neighbors was not expected. However, it is still worth mentioning that, along the first species axis, edges bordered by extremely disturbed land, urban development, and road were located at the far higher end, in contrast with edges bordered by wood or pasture which were located at the far lower end of the axis. This pattern fits our expectation based on the information discussed above. Also, according to the ranking of sample scores along the first species axis, the edges facing south and west tend to be at the higher end while the edges facing north and east at the lower end. This trend may suggest confounding effects between neighbor effect and aspect effect. However, these explanations are very

tentative, since none of the trends were shown to be statistically significant.

It should be pointed out that neighbor effect is a complicated issue confounded by many factors which are usually difficult to control under natural settings. This difficulty may partially explain the large amount of research done on species -area relationship while relatively few studies have been carried out on neighbor effects. Arbitrary allocation of the boundary line is one problem involved in the study of neighbor effect (Addicott et al. 1987). One always has to develop criteria for determining the boundaries of a neighborhood. These criteria will be arbitrary, but they should be explicit.

Fences were used in this study as the boundary line, and species 0.3 m inside the fences were sampled as edge vegetation. Although the criteria were specific, they were subjectively chosen for the convenience of field work. Convenience is usually at the expense of closeness to reflecting the true situation and is too often involved in the field data collections of ecological studies. For example, fences may be a good boundary line between two pastures separated only by a fence; yet a fenceline may be far from being the true boundary between a highway construction and the grassland since there is usually a zone of 5 to 8 m wide, or even wider, between the highway and the fenceline. This may be part of the cause for little separation among the edges bordered by different neighbors. True edge effects may be more significant than observed in

this study. Many other factors such as the extent of neighbor, the neighbor's neighbor, aspects, scale of measurement, and smoothness of edge may contribute and complicate the neighbor effect (Forman and Godron 1986, Madder 1984, Addicott et al. 1987, Stamps et al. 1987, Harris 1988, Marshall 1989, Weins 1989).

Such complicated situations can be effectively dealt with by multivariate analysis methods (Gauch 1989). Yet its effectiveness decreases as sample size and number of samples decrease since information or relationship is derived from the redundancy of data. Relatively small sample size may also be one of the causes for the failure in detecting neighbor effect by this study. Large numbers of samples is one of the recommendations for further investigations of neighbor effect.

Conclusions and Recommendations

Species richness of flowering plants in the grassland community is positively related to area, and the relationship is represented better by the logarithmic model proposed by Dahl (1960) and Goodall (1961) than by linear or exponential models.

Total species composition also changes with area. As area increases the interior species composition changes more noticeably than edge species composition. The change in total species composition with area is due to the change in interior species composition and the change in relative proportions of edge and interior. Edge species composition

is significantly different from interior species composition and the difference is positively related to area; however, the increase is gradual and may indicate the lack of practicality of the 'minimum critical area' concept. Neighbor effect is not detected in this study, possibly due to the difficulty in controlling some of the confounding factors. Intensive grassland fragmentation may lead to lower species richness per grassland fragment, and may alter the regional species composition by changing interior species composition, by reducing the proportion of interior species and by increasing the proportion of edge species in each of the grassland fragments.

Due to the limitations of relatively small sample size and short duration of field sampling, the above conclusions are only exploratory and tentative. Long-term studies and large numbers of samples are recommended for further research.

LITERATURE CITED

- Addicott, J.F., J.M. Aho, M.F. Antolin, D.K. Padilla, J.S. Richardson, and D.A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49:340-346.
- Arrhenius, O. 1921. Species and area. *Journal of Ecology* 9:95-99.
- Barkman, J.J. 1989. A critical evaluation of minimum area concepts. *Vegetatio* 85:89-104.
- Burgess, R.L., and D.M. Sharp. eds. 1981. *The Fragmented Forest - Forest Island Dynamics in Man - dominated landscapes*. Springer-Verlag, New York.
- Cartography Service. 1979. *Oklahoma in Maps*. Oklahoma State University, Stillwater, Oklahoma.
- Connor, E.F., E.D. McCoy. 1979. The Statistics and biology of the species-area relationship. *American Naturalist* 113:791-833.
- Currie, D.J., and V. Paquin. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* 329:326-327.
- Curtis, J. T. 1956. The modification of mid-latitude grasslands and forests by man. pp. 721-736 IN W. L. Thomas (ed.) *Man's role in changing the face of earth*. University of Chicago Press, Chicago.
- Curtis, N.M. and W.E. Ham. 1979. Geomorphic provinces of Oklahoma. In K.S. Johnson, C.C. Branson, N.M. Curtis, W.E. Ham, W.E. Harrison, M.V. Marcher, and J.F. Roberts, eds. *Geology and Earth Resources of Oklahoma*. Oklahoma Geological Survey, Education Publication No. 1, Norman, Oklahoma.
- Dahl, E. 1960. Some measures of uniformity in vegetation analysis. *Ecology* 41:805-808.
- Darlington, P.J. 1957. *Zoogeography: the Geographical Distribution of Animals*. John Wiley, New York.
- Diamond, J. 1988. Factors controlling species diversity: overview and synthesis. *Ann. Mo. Bot. Gard.* 75:117-129.
- Eadie, J.M., T.A. Hurley, R.D. Montgomerie, and K.L.

- Teather. 1986. Lakes and rivers as islands: species-area relationships in the fish faunas of Ontario. *Environmental Biology of Fishes* 15:81-89.
- Evans, F.C., and P.J. Clark. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445-453.
- Faith, D.P., P.R. Minchin, L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57-68.
- Fisher, R.A., A.S. Corbert, C.B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* 12:42-58.
- Forman, R.T.T. and M. Godron. 1981. Patches and structural components for a landscape ecology. *BioScience* 31:733-740.
- Forman, R.T.T., M. Godron. 1986. *Landscape Ecology*. John Wiley, New York.
- Gauch, Jr. H.G. 1989. *Multivariate Analysis in Community Ecology*. Cambridge University Press, New York.
- Goodall, D.W. 1961. Objective methods for the classification of vegetation. IV. Pattern and minimal area. *Australian Journal of Botany* 9:162-196.
- Gotfryd, A., and R.I.C. Hansell. 1986. Prediction of bird community metrics in urban woodlots. pages 321-326 in J. Verner, M.L. Morrison, and C.J. Ralph, (eds.) *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison.
- Harris, L.D. 1984. *The Fragmented Forest: Island Biogeographic Theory and the Preservation of Biotic Diversity*. Chicago University Press, Chicago, Illin.
- Harris, L.D. 1988. Edge effects and conservation of biotic diversity. *Conservation Biology* 2(4):330-332.
- Heltsh, J.F., and N.E. Forrester. 1983. Estimating species richness using the Jackknife procedure. *Biometrics* 39:1-12.
- Higgs, A.J., and M.B. Usher. 1980. Should nature reserves be large or small? *Nature* 285:568-569.
- Hill, M.O., and H.G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42:47-58.

- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81-101.
- Janzen, D.H. 1983. No park is an island: increase in interference from outside as park size decreases. *Oikos* 41:402-410.
- Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. van Tongeren 1987. *Data Analysis in Community and Landscape Ecology*. Pudoc, Wageningen, the Netherlands.
- Kilburn, P.D. 1966. Analysis of the species - area relation. *Ecology* 47(5):831-843.
- Kolasa, J., and D. Strayer. 1988. Patterns of the abundance of species: a comparison of two hierarchical models. *Oikos* 53: 235-241.
- Kolasa, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology* 70(1):36-47.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *The American Naturalist* 134(4):624-635.
- Levenson, J.B. 1981. Woodlots as biogeographic islands in Southeastern Wisconsin. In R.L. Burgess and D.M. Sharpe, (eds.) *Forest Island Dynamics in Man-Dominated Landscape*. Springer-Verlag, New York.
- Livingstone, D.A., M. Rowland, and P.E. Bailey. 1982. On the size of African riverine fish faunas. *American Zoologist* 22:361-369.
- Lomolino, M.V., J. H. Brown, and R. Davis. 1989. Island biogeography of montane forest mammals in the American Southwest. *Ecology* 70(1): 180-194.
- Lovejoy, T.E., and D.C. Oren. 1981. The minimum critical size of ecosystems. pages 8-12 in R.L. Burges and D.M. Sharpe, eds. *Forest Island Dynamics in Man - Dominated Landscapes*. Springer - Verlag, New York.
- Lovejoy, T.E., R.O. Bierregaard Jr., A.B. Rylands, J.R. Malcolm. 1986. Edge and other effects of isolation on Amazon forest fragments. page 257-285 in M.E. Soule. (ed.) *Conservation Biology - the Science of Scarcity and Diversity*. Sinauer, Sunderland, Mass.
- Lukac, G. 1988. Some structural characteristics of the stands of the species *Solidago gigantea* Ait. and *Helianthus tuberosus* L. and their ornithocenoses in northwest Croatia (Yugoslavia). *ACTA Botanica Croatica* 47:63-76.

- MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Madder, H.J. 1984. Animal habitat isolation by roads and agricultural fields. *Biological Conservation* 29:81-96.
- Marshall, E.J.P. 1989. Distribution patterns of plants associated with arable field edges. *Journal of Applied Ecology* 26(1):247-257.
- Martin, T.E. 1981. Species - area slopes and coefficients: a caution on their interpretation. *American Naturalist* 118:823-837.
- May, R.M. 1975. Patterns of species abundance and diversity. In M.L. Cody and J.M. Diamond, (eds.) *Ecology and Evolution of Communities*. Belknap, Cambridge, Massachusetts.
- Murphy, D.D., and P.R. Ehrlich. 1989. The conservation biology of California's remnant native grasslands. pages 201-211 in L.F. Huenneke and H.A. Mooney, eds. *Grassland structure and function: California annual grassland*. Kluwer Academic, Dordrecht, Netherlands.
- Murphy, D.D. 1989. Conservation and confusion: wrong species, wrong scale, wrong conclusions. *Conservation Biology* 3(1):82-84.
- Nilsson, C., G. Grelsson, M. Johansson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. *Ecology* 70(1):77-84.
- Odum, E. 1970. *Fundamentals of Ecology*. 3rd edition. W.B. Saunders, Philadelphia.
- Owensby, C.E. 1973. Modified step-point system for botanical composition and basal cover estimates. *Journal of Range Management* 26(4):302-303.
- Palmer, M. 1990. The estimation of species richness by extrapolation. *Ecology* 71(3):1195-1198.
- Palmer, M. 1990. Spatial scale and patterns of species - environment relationships in hardwood forests of the North Carolina Piedmont. *Coenosis*, in press.
- Patil, G.P., and C. Taillie. 1982. Diversity as a concept and its measurement. *Journal of American Statistical Association* 77:548-561.
- Peterken, G.F. and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant

- species in the woodlands of central Lincolnshire. *Journal of Ecology* 72:155-182.
- Pianka, E.R. 1983. *Evolutionary Ecology*. 3rd ed. Harper and Row, New York.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity: part I. *Ecology* 43:185-215.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity: part II. *Ecology* 43:410-432.
- Quinn, J.F., and A. Hastings. 1987. Extinction in subdivided habitats. *Conservation Biology* 1:198-208.
- Quinn, J. F., and S.P. Harrison. 1988. Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* 75:132-140.
- Ranney, J.W., M.C. Bruner, J.B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. *In* R.L. Burgess and D.M. Sharpe, (eds.) *Forest Island Dynamics in Man-Dominated Landscapes*. Springer-Verlag, New York.
- Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton, and J.A. Weins. 1981. *The True Prairie Ecosystem*. Hutchinson Ross, Stroudsburg, Pennsylvania.
- Robinson, E.R. and J.F. Quinn. 1988. Extinction, turnover, and species diversity in an experimentally fragmented California annual grassland. *Oecologia* 76:71-82.
- Sheldon, A.L. 1988. Conservation of stream fishes: patterns of diversity, rarity, and risk. *Conservation Biology* 2(2):149-156.
- Simberloff, D., and L.G. Abele. 1982. Refuge design and island biogeographic theory: effects of fragmentation. *American Naturalist* 120:41-50.
- Simberloff, D. and N. Gotelli. 1984. Effects of insularisation on plant species richness in the prairie-forest ecotone. *Biological Conservation* 29:27-46.
- Sims, P.L. 1988. Grasslands. *In* M.G. Barber and W.D. Billings, eds. *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge, England.
- Shmida, A. and M.V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.
- Soule, M.E., and B.A. Wilcox. (eds.) 1980. *Conservation Biology: an Evolutionary - Ecological Perspective*.

- Sinauer, Sunderland, Mass.
- Stamps, J.A., M. Buechner, V.V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *American Naturalist* 129:533-552.
- Sugihara, G. 1981. $S = cA$, $z = 1/4$: a reply to Connor and McCoy. *American Naturalist* 117:790-793.
- Ter Braak, C. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167-1179.
- Ter Braak, C. 1987. The analysis of vegetation - environment relationships by canonical correspondence analysis. *Vegetatio* 69:79-87.
- Ter Braak, C. 1988. CANOCO - a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). TNO Institute of Applied Computer Science, Statistics Department Wageningen, Wageningen, The Netherlands.
- Thiollay, J.M. 1989. Area requirements for the conservation of rain forest raptors and game birds in French Guiana. *Conservation Biology* 3(2):128-137.
- USDA Forest Service. 1981. An assessment of the forest and rangeland situation in the United States. Forest Resource Report No.22. United States Department of Agricultural, Washington, D.C..
- USDA Soil Conservation Service. 1984. Range Condition Class-Guide. United States Department of Agricultural, Payne County, Oklahoma.
- Verner, J. 1986. Predicting effects of habitat patchiness and fragmentation - researcher's viewpoint. pages 327-329 in J. Verner, M.L. Morrison, and C.J. Ralph, eds. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison.
- Wales, B.A. 1972. Vegetation analysis of north and south edges in a mature oak - hickory forest. *Ecological Monograph* 42:451-471.
- Weaver, M., and M. Kellman. 1981. The effects of forest fragmentation on woodlot tree biotas in Southern Ontario. *Journal of Biogeography* 8:199-210.
- Weins, J.A. 1989. Spatial scaling in ecology. *Functional*

- Ecology 3:385-397.
- Weins, J.A., C.S. Crawford, and J.R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421-427.
- Wilcove, D.S., C.H. Mclellan, and A.P. Dobson, 1986, Habitat fragmentation in the temperate zone. pages 237-256 in M.E. Soule. (ed.) *Conservation Biology - the Science of Scarcity and Diversity*. Sinauer, Sunderland, Mass.
- Wilcox, B.A. 1980. Insular ecology and conservation. In M.E. Soule and B.A. Wilcox (eds.) *Conservation Ecology: An Evolutionary - Ecological Perspective*. Sinauer Associates, Sunderland, Massachussets.
- Wilcox, B.A. and D.D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* 125:879-887.
- Williams, C.B. 1964. *Patterns in the Balance of Nature*. Academic Press, London.
- Wright, S.J. 1988. Patterns of abundance and the form of the species - area relation. *American Naturalist* 131(3):401-411.

APPENDICES

APPENDIX A

EQUATIONS USED IN DATA ANALYSIS

1. First Order Jackknife

$$\text{Jackknife} = S_0 + r_1 (n+1) / n$$

where Jackknife is the estimated species richness, S_0 is the number of species which are present only at one sampling point, and n is the total number of sampling points.

2. Community Indices

(1) Shannon-Weaver species diversity index

$$H = - \sum_{i=1}^s f_i \text{Log}_2 f_i$$

where H is Shannon-Weaver species diversity index, f_i is the relative frequency of species i , and s is the total number of species.

(2) Pielou species evenness index

$$E = H / H_{\max} = H / \text{Log}_2 S$$

Where E is Pielou species evenness index, H is Shannon-Weaver species diversity index, H_{\max} is Shannon-Weaver maximum species diversity index, and S is total number of species.

(3) Simpson species dominance index

$$D = \sum_{i=1}^s (n_i/N)^2$$

where D is Simpson species dominance index, n_i is the number of sampling points of species i , and N is total number of sampling points.

3. Manhattan distance

$$CD_j = \sum_{i=1}^{S_j} |A_{ij} - A'_{ij}|$$

where CD_j is the Manhattan distance value for site j , A_{ij} is the relative frequency of species i at edge of site j , A'_{ij} is the relative frequency of species i at interior of site j . The relative frequency at edge was calculated as the number of sampling points of species i at edge of site j divided by the total sampling points at edge of site j , and the relative frequency at interior was calculated as the number of interior points of species i at site j divided by the total interior points at site j .

APPENDIX B

PRIMARY SAMPLING DATA

SITE	SPECIES	SITE TOTAL	EDGE				
			TOTAL	SOUTH	NORTH	WEST	EAST
1	SCSC	247	26	8	8	4	6
1	ANGE	215	26	4	8	3	11
1	AROL	23	2	0	0	1	1
1	BRJA	26	16	2	3	9	2
1	BUDA	1	0	0	0	0	0
1	CYDA	18	7	0	4	3	0
1	COCY	10	1	0	0	0	1
1	PAOL	50	3	0	2	0	1
1	PAVI	50	8	1	5	0	2
1	SONU	146	12	4	0	1	7
1	SPAS	57	8	1	0	5	2
1	SOHA	3	0	0	0	0	0
1	ASTE	1	0	0	0	0	0
1	ASVI	1	0	0	0	0	0
1	ACMI	11	4	1	1	2	0
1	AMPS	10	6	3	0	2	1
1	ANNE	10	2	0	2	0	0
1	ARLU	6	1	0	0	1	0
1	CARE	9	0	0	0	0	0
1	CYPE	24	5	2	0	2	1
1	ELEO	13	3	0	0	2	1
1	LESP	3	0	0	0	0	0
1	POVE	9	1	0	1	0	0
1	PSTE	2	0	0	0	0	0
1	RUHI	1	0	0	0	0	0
1	SCIR	24	0	0	0	0	0
1	SENE	12	3	0	1	1	1
1	LATH	2	1	1	0	0	0
1	VAOC	2	0	0	0	0	0
1	UMBE	1	0	0	0	0	0
1	PADI	2	0	0	0	0	0
1	SERI	1	0	0	0	0	0
1	UKD1	1	0	0	0	0	0
1	UKD2	3	2	1	0	1	0
1	ERIG	3	1	1	0	0	0
1	PLAN	17	4	4	0	0	0
1	MEAL	1	1	1	0	0	0
1	LIAT	1	0	0	0	0	0

1	DAPU	2	0	0	0	0	0
1	PYHR	2	0	0	0	0	0
1	RUEL	1	0	0	0	0	0
1	LEPI	1	1	0	0	1	0
1	TRAD	1	1	1	0	0	0
1	POPR	9	1	1	0	0	0
1	ERCU	1	0	0	0	0	0
1	UKG3	3	0	0	0	0	0
1	ULAM	1	1	0	1	0	0
1	COTI	1	1	0	1	0	0
1	TOAR	1	0	0	0	0	0
1	TRIF	1	1	0	0	0	1
2	SCSC	236	19	4	6	4	5
2	ANGE	132	26	6	5	5	10
2	AROL	15	1	1	0	0	0
2	BRJA	4	4	1	2	0	1
2	BUDA	6	0	0	0	0	0
2	CYDA	19	6	1	0	3	2
2	COCY	37	3	1	0	2	0
2	PAOL	50	3	0	0	3	0
2	PAVI	62	11	2	5	0	4
2	SONU	91	15	6	2	3	4
2	SPAS	92	9	1	1	5	2
2	ACMI	4	1	0	1	0	0
2	AMPS	6	1	1	0	0	0
2	ANNE	3	0	0	0	0	0
2	ARLU	3	3	1	2	0	0
2	CARE	72	6	1	1	3	1
2	CYPE	26	0	0	0	0	0
2	ELEO	2	0	0	0	0	0
2	LESP	1	0	0	0	0	0
2	POVE	3	1	0	1	0	0
2	PSTE	6	2	0	2	0	0
2	RUHI	3	0	0	0	0	0
2	SCIR	5	1	1	0	0	0
2	SENE	1	0	0	0	0	0
2	BOUT	7	0	0	0	0	0
2	ANVI	5	0	0	0	0	0
2	SPRE	7	1	0	0	0	1
2	UKD2	1	0	0	0	0	0
2	POVE	1	1	0	0	0	0
2	AVFA	11	7	0	4	0	3
2	PASP	5	1	1	0	0	0
2	BOCU	10	6	4	1	1	0
2	SOLI	2	2	1	0	0	1
2	PANI	2	0	0	0	0	0
2	COTI	1	0	0	0	0	0
2	DAPU	2	2	2	0	0	0
2	COMP	18	0	0	0	0	0
2	SYOR	3	3	0	1	1	1
2	RHCO	1	1	0	0	1	0
2	RUDB	25	2	0	1	1	0
2	PSOR	3	0	0	0	0	0
2	ERIG	3	0	0	0	0	0

2	SCUT	1	0	0	0	0	0
2	LITH	2	0	0	0	0	0
2	COCA	2	2	0	0	2	0
2	PEPU	1	0	0	0	0	0
2	OXAL	2	0	0	0	0	0
2	PYRR	3	1	1	0	0	0
2	PLAN	7	0	0	0	0	0
2	CRGL	3	0	0	0	0	0
2	TRIF	1	0	0	0	0	0
2	ASTR	1	0	0	0	0	0
2	LIAT	1	0	0	0	0	0
2	TOAR	1	0	0	0	0	0
2	AMFR	1	0	0	0	0	0
2	CHPI	9	0	0	0	0	0
2	CYPE	1	0	0	0	0	0
2	ASER	2	1	0	0	1	0
2	UKCO	1	0	0	0	0	0
2	LINU	5	0	0	0	0	0
2	PLAN	3	0	0	0	0	0
2	SOGY	2	0	0	0	0	0
2	ASVI	1	0	0	0	0	0
2	NLCO	3	0	0	0	0	0
2	RUEL	1	0	0	0	0	0
3	SCSC	262	29	6	12	5	6
3	ANGE	103	9	3	4	1	1
3	AROL	0	0	0	0	0	0
3	BRJA	2	2	0	1	0	1
3	BUDA	0	0	0	0	0	0
3	CYDA	11	8	0	1	6	1
3	COCY	34	2	0	0	1	1
3	PAOL	36	4	1	2	0	1
3	PAVI	36	5	1	1	3	0
3	SONU	215	34	6	12	7	9
3	SPAS	86	13	9	1	3	0
3	ACMI	1	1	0	0	0	1
3	AMPS	4	4	0	0	3	1
3	ANNE	4	0	0	0	0	0
3	ARLU	1	1	0	0	0	1
3	CARE	159	19	7	4	4	4
3	CYPE	1	1	1	0	0	0
3	ELEO	4	0	0	0	0	0
3	POVE	1	1	1	0	0	0
3	PSTE	4	2	1	0	0	1
3	BOCU	21	6	1	0	4	1
3	BOSA	2	2	0	0	0	2
3	ERIN	1	0	0	0	0	0
3	PASP	28	3	1	1	0	1
3	PETA	1	0	0	0	0	0
3	ASER	1	1	0	0	0	1
3	HEL2	1	1	0	0	1	0
3	UNKF	1	0	0	0	0	0
3	RUEL	2	0	0	0	0	0
3	BAPT	1	1	0	0	0	1
3	SOGY	1	0	0	0	0	0

3	OXAL	1	0	0	0	0	0
3	ERIG	1	1	0	0	0	1
3	CODR	2	1	0	0	1	0
3	PLAN	4	2	0	0	0	2
3	SOLI	2	2	1	0	0	1
3	HEMO	5	0	0	0	0	0
3	HIER	1	0	0	0	0	0
4	SCSC	237	30	11	8	10	1
4	ANGE	97	22	8	3	6	5
4	AROL	1	0	0	0	0	0
4	BRJA	3	2	0	0	2	0
4	BUDA	0	0	0	0	0	0
4	CYDA	13	1	0	1	0	0
4	COCY	24	0	0	0	0	0
4	PAOL	47	1	0	0	0	1
4	PAVI	21	3	0	2	1	0
4	SONU	130	12	7	2	0	3
4	SPAS	166	14	0	3	4	7
4	ACMI	2	0	0	0	0	0
4	AMPS	0	0	0	0	0	0
4	ANNE	5	0	0	0	0	0
4	ARLU	1	1	0	0	1	0
4	CARE	134	19	5	3	1	10
4	CYPE	0	0	0	0	0	0
4	ELEO	17	7	0	4	0	3
4	POVE	3	0	0	0	0	0
4	PSTE	1	0	0	0	0	0
4	RUHI	8	0	0	0	0	0
4	TUKG	2	2	0	1	1	0
4	SILV	2	0	0	0	0	0
4	SETA	1	0	0	0	0	0
4	PASP	13	1	0	0	1	0
4	LECO	1	0	0	0	0	0
4	BOCU	34	6	1	2	0	3
4	BOGR	1	0	0	0	0	0
4	LINU	6	1	0	1	0	0
4	RUEL	3	0	0	0	0	0
4	HEMO	8	1	0	0	0	1
4	BAPT	2	1	1	0	0	0
4	GAIL	5	0	0	0	0	0
4	ECHI	1	0	0	0	0	0
4	SCUT	1	0	0	0	0	0
4	OXAL	1	0	0	0	0	0
4	CHRY	3	0	0	0	0	0
4	CORO	1	0	0	0	0	0
4	HELI	5	5	0	0	5	0
4	ERIG	1	0	0	0	0	0
4	LUKC	21	4	0	2	2	0
4	SABA	2	0	0	0	0	0
4	SOLI	3	1	0	1	0	0
4	SYOR	2	2	0	1	1	0
4	SCHR	1	0	0	0	0	0
4	CORE	3	0	0	0	0	0
4	ASER	2	1	0	0	0	1

4	AMCU	1	0	0	0	0	0
4	EUPA	1	0	0	0	0	0
4	TRFL	1	0	0	0	0	0
4	PLAN	1	0	0	0	0	0
4	ALCS	1	1	0	0	1	0
4	RUBU	1	1	1	0	0	0
5	SCSC	305	37	15	10	10	2
5	ANGE	98	13	1	6	2	4
5	AROL	0	0	0	0	0	0
5	BRJA	18	16	8	2	3	3
5	CYDA	45	4	0	1	3	0
5	COCY	9	0	0	0	0	0
5	PAOL	48	3	0	0	2	1
5	PAVI	54	5	3	1	1	0
5	SONU	168	22	1	1	7	13
5	SPAS	79	5	2	2	1	0
5	ACMI	14	2	0	0	1	1
5	AMPS	3	0	0	0	0	0
5	ANNE	4	0	0	0	0	0
5	ARLU	3	1	0	1	0	0
5	CARE	56	11	0	8	3	0
5	PSTE	4	0	0	0	0	0
5	RUHI	9	1	1	0	0	0
5	SILV	5	3	0	2	0	1
5	BOGR	4	0	0	0	0	0
5	UKSG	1	0	0	0	0	0
5	UKPG	1	0	0	0	0	0
5	BOCU	11	2	0	0	2	0
5	SETA	8	2	0	0	0	2
5	PASP	1	0	0	0	0	0
5	WBHG	1	0	0	0	0	0
5	ABLU	3	1	0	1	0	0
5	LUKG	8	3	0	0	0	3
5	SKLG	1	0	0	0	0	0
5	ELVI	1	0	0	0	0	0
5	DACT	1	0	0	0	0	0
5	CONY	1	1	1	0	0	0
5	OXAL	9	1	1	0	0	0
5	ASER	4	1	1	0	0	0
5	RUEL	1	0	0	0	0	0
5	EUSP	1	0	0	0	0	0
5	LINU	5	1	0	0	0	0
5	SABA	2	0	0	0	0	0
5	RANU	1	0	0	0	0	0
5	LIPU	1	0	0	0	0	0
5	SCHR	1	0	0	0	0	0
5	RATI	1	0	0	0	0	0
5	ASVI	1	0	0	0	0	0
5	SCUT	4	0	0	0	0	0
5	ERIG	3	0	0	0	0	0
5	RUMA	1	0	0	0	0	0
5	JUNC	6	1	0	0	0	1
5	MALL	2	0	0	0	0	0
5	LWEE	1	0	0	0	0	0

5	LUKC	9	2	0	0	1	1
5	DENO	1	0	0	0	0	0
5	SISY	1	0	0	0	0	0
5	SOLI	4	0	0	0	0	0
5	MIMO	1	0	0	0	0	0
5	PLAT	7	0	0	0	0	0
5	POVE	2	0	0	0	0	0
5	MILK	2	2	1	0	0	1
5	SYMP	3	2	0	1	0	1
5	LITH	1	0	0	0	0	0
5	HEDE	1	0	0	0	0	0
6	SCSC	310	33	6	6	7	14
6	ANGE	102	14	5	4	0	5
6	AROL	36	2	0	2	0	0
6	BRJA	27	23	8	10	3	2
6	BUDA	7	0	0	0	0	0
6	CYDA	25	5	2	2	1	0
6	COCY	12	0	0	0	0	0
6	PAOL	41	4	0	1	1	2
6	PAVI	47	4	1	1	2	0
6	SONU	98	16	3	0	10	3
6	SPAS	77	6	3	2	1	2
6	ACMI	1	1	1	0	0	0
6	AMPS	2	2	1	1	0	0
6	ANNE	3	0	0	0	0	0
6	ARLU	1	1	0	0	1	0
6	CARE	74	9	0	1	4	4
6	PSTE	4	0	0	0	0	0
6	RUHI	1	0	0	0	0	0
6	SILV	4	2	1	0	1	0
6	BUKG	9	0	0	0	0	0
6	BOHI	16	0	0	0	0	0
6	SUKG	2	0	0	0	0	0
6	FLBG	1	0	0	0	0	0
6	MUHL	3	3	0	0	1	2
6	BOCU	50	1	1	0	0	0
6	SETA	1	0	0	0	0	0
6	LLBG	3	0	0	0	0	0
6	SAG	1	0	0	0	0	0
6	BOGR	12	0	0	0	0	0
6	PAFL	5	0	0	0	0	0
6	RHIZ	2	0	0	0	0	0
6	BUKG2	2	0	0	0	0	0
6	WHEA	1	1	0	1	0	0
6	ELVI	1	0	0	0	0	0
6	LUKG	1	0	0	0	0	0
6	PASP	4	0	0	0	0	0
6	SHGR	4	0	0	0	0	0
6	ERAG	1	0	0	0	0	0
6	VALE	1	1	1	0	0	0
6	SYMP	1	0	0	0	0	0
6	SCHR	1	0	0	0	0	0
6	TOXI	2	2	0	0	2	0
6	UKSF	1	0	0	0	0	0

6	CONY	2	0	0	0	0	0
6	SOLI	1	1	0	0	1	0
6	SABA	1	0	0	0	0	0
6	EUMA	2	0	0	0	0	0
6	OXAL	2	0	0	0	0	0
6	HELI	1	0	0	0	0	0
6	LVCC	1	0	0	0	0	0
6	TRIF	1	0	0	0	0	0
6	POVE	1	0	0	0	0	0
6	LUKC	8	1	0	1	0	0
6	KRAM	2	0	0	0	0	0
6	PLAN	5	0	0	0	0	0
6	ASCL	1	0	0	0	0	0
6	TRBI	1	0	0	0	0	0
6	SABI	1	1	0	0	0	1
6	UKNF	1	0	0	0	0	0
6	SPIG	1	1	1	0	0	0
6	LMIN	1	1	1	0	0	0
6	UNKA	4	0	0	0	0	0
6	LEPT	1	0	0	0	0	0
6	LINU	1	0	0	0	0	0
6	UKNW	1	1	0	1	0	0
6	LIAT	1	0	0	0	0	0
6	CRAB	1	1	0	1	0	0
6	PLYS	1	1	0	1	0	0
7	SCSC	291	15	10	4	0	1
7	ANGE	176	10	3	4	1	2
7	AROL	8	8	2	0	3	3
7	BRJA	25	14	3	7	2	2
7	BUDA	0	0	0	0	0	0
7	CYDA	72	24	5	1	1	17
7	COCY	0	0	0	0	0	0
7	PAOL	47	4	0	0	2	2
7	PAVI	25	4	0	1	0	3
7	SONU	113	15	1	10	3	1
7	SPAS	15	3	0	2	1	0
7	ACMI	4	0	0	0	0	0
7	AMPS	22	9	0	2	4	3
7	ARLU	1	1	0	1	0	0
7	CARE	17	4	0	1	2	1
7	RUHI	7	1	0	0	1	0
7	BOCU	26	8	1	1	5	1
7	BOHI	1	0	0	0	0	0
7	PASP	18	1	0	0	1	0
7	SMGR	3	0	0	0	0	0
7	LBLO	1	0	0	0	0	0
7	LEPT	28	3	1	0	1	1
7	SOME	1	0	0	0	0	0
7	TEND	1	1	1	0	0	0
7	BARN	7	7	0	0	6	1
7	SCPA	50	2	2	0	0	0
7	SETA	9	4	4	0	0	0
7	ARGR	2	0	0	0	0	0
7	SSWG	3	0	0	0	0	0

7	HAIR	1	0	0	0	0	0
7	OXAL	4	3	1	0	1	1
7	CONY	10	4	1	0	2	1
7	LWED	3	2	0	2	0	0
7	ASER	12	3	2	1	0	0
7	UNKO	1	0	0	0	0	0
7	RUEL	2	0	0	0	0	0
7	VIPO	6	4	2	0	2	0
7	ALTC	1	0	0	0	0	0
7	ASVI	1	0	0	0	0	0
7	SFUP	1	0	0	0	0	0
7	AMOR	1	1	0	1	0	0
7	BUBR	8	0	0	0	0	0
7	LINU	3	0	0	0	0	0
7	PLAN	2	0	0	0	0	0
7	SCUT	1	0	0	0	0	0
7	LESP	2	0	0	0	0	0
7	SABA	1	0	0	0	0	0
7	LUKC	1	0	0	0	0	0
7	EUMA	1	0	0	0	0	0
7	PHYS	1	0	0	0	0	0
7	PETA	1	1	0	1	0	0
7	POKE	1	0	0	0	0	0
7	CALL	1	1	0	0	1	0
7	RUBU	1	0	0	0	0	0
8	SCSC	313	30	5	11	7	7
8	ANGE	250	30	7	6	8	9
8	AROL	10	2	0	0	2	0
8	BRJA	31	18	7	4	5	2
8	BUDA	3	3	1	1	1	0
8	CYDA	60	5	4	0	0	1
8	COCY	0	0	0	0	0	0
8	PAOL	43	5	0	1	1	3
8	PAVI	22	3	0	1	1	1
8	SONU	45	2	1	0	0	1
8	SPAS	36	15	1	10	2	2
8	ACMI	14	2	1	0	0	1
8	AMPS	6	2	0	2	0	0
8	ANNE	2	1	0	0	1	0
8	ARLU	3	2	0	0	1	1
8	CARE	29	7	1	3	2	1
8	RUHI	6	0	0	0	0	0
8	BOCU	21	11	5	1	3	2
8	BOHI	11	3	1	0	2	0
8	SETA	6	0	0	0	0	0
8	BOGR	1	0	0	0	0	0
8	SPAS	12	1	1	0	0	0
8	LEPT	21	4	0	0	1	3
8	TSKG	1	0	0	0	0	0
8	ELCA	1	0	0	0	0	0
8	FUZG	2	2	1	0	0	1
8	HCRA	2	2	2	0	0	0
8	PASP	13	0	0	0	0	0
8	SBLU	5	1	0	0	1	0

8	OXAL	4	1	1	0	0	0
8	ASER	6	3	1	1	0	1
8	VPEA	5	2	1	0	0	1
8	TPEP	6	1	0	0	1	0
8	BUBR	12	2	0	1	0	1
8	CONY	10	0	0	0	0	0
8	RUEL	4	0	0	0	0	0
8	SABA	2	0	0	0	0	0
8	SCHR	1	0	0	0	0	0
8	LUKC	3	0	0	0	0	0
8	LESP	6	1	0	0	1	0
8	LINU	3	0	0	0	0	0
8	POLY	1	1	0	0	0	1
8	PLAN	3	0	0	0	0	0
8	PHYS	1	0	0	0	0	0
8	DIOD	1	0	0	0	0	0
8	LESC	1	0	0	0	0	0
8	EUPA	1	0	0	0	0	0
8	CROT	1	0	0	0	0	0
9	SCSC	283	19	5	2	4	8
9	ANGE	152	22	3	5	8	6
9	AROL	9	4	0	4	0	0
9	BRJA	39	24	3	2	15	4
9	BUDA	0	0	0	0	0	0
9	CYDA	4	2	0	1	1	0
9	COCY	1	0	0	0	0	0
9	PAOL	89	3	1	1	0	1
9	PAVI	12	2	0	1	1	0
9	SONU	157	22	1	10	0	11
9	SPAS	18	4	2	2	0	0
9	ACMI	14	1	0	0	0	0
9	AMPS	36	13	4	2	2	5
9	ANNE	11	1	0	0	0	1
9	CARE	66	15	7	5	3	0
9	PSTE	1	0	0	0	0	0
9	RUHI	6	1	0	1	0	0
9	LEPT	15	3	1	1	1	0
9	BOCU	18	4	0	1	1	2
9	SPAS	2	1	0	0	0	1
9	FBLG	2	1	0	0	1	0
9	ELCA	1	0	0	0	0	0
9	PASP	7	3	0	0	2	1
9	SBLU	2	2	0	0	2	0
9	BOHI	10	3	3	0	0	0
9	SETA	2	0	0	0	0	0
9	MEDI	1	1	1	0	0	0
9	MELA	1	1	0	0	1	0
9	ASER	8	1	1	0	0	0
9	SCHR	1	1	0	0	1	0
9	LINU	2	0	0	0	0	0
9	BROW	8	8	7	0	0	1
9	PLAN	16	4	0	2	2	0
9	LESP	2	1	0	0	0	1
9	CODR	1	1	0	0	1	0

9	DESM	2	2	0	1	1	0
9	AMCA	8	2	1	0	0	1
9	LPLP	3	2	0	1	1	0
9	LUKN	7	1	0	0	0	1
9	JUNC	2	1	1	0	0	0
9	LITH	3	0	0	0	0	0
9	SOLI	2	0	0	0	0	0
9	SABA	5	0	0	0	0	0
9	DAPU	1	1	1	0	0	0
9	SABR	3	0	0	0	0	0
9	HEDE	1	0	0	0	0	0
9	ASCL	1	0	0	0	0	0
9	CONY	1	0	0	0	0	0
9	WPET	2	0	0	0	0	0
9	ERIG	1	0	0	0	0	0
9	DIOD	1	1	0	0	0	1
10	SCSC	350	38	9	10	5	14
10	ANGE	115	14	5	0	5	4
10	AROL	39	1	0	0	0	1
10	BRJA	11	6	1	0	5	0
10	BUDA	4	2	1	0	1	0
10	CYDA	45	2	1	0	1	0
10	PAOL	91	7	2	0	1	4
10	PAVI	29	6	2	1	3	0
10	SONU	150	35	3	8	15	6
10	SPAS	54	5	0	0	2	3
10	ACMI	4	0	0	0	0	0
10	AMPS	5	1	0	1	0	0
10	ANNE	0	0	0	0	0	0
10	ARLU	3	0	0	0	0	0
10	CARE	39	6	3	1	1	1
10	SPAS	8	3	0	1	1	1
10	BOCU	12	2	2	0	0	0
10	PASP	7	0	0	0	0	0
10	BOGR	1	0	0	0	0	0
10	SILV	7	1	0	0	1	0
10	SETA	9	2	0	0	0	2
10	BOHI	2	0	0	0	0	0
10	FSGR	3	3	1	2	0	0
10	LEPT	21	1	0	0	0	1
10	ELCA	2	0	0	0	0	0
10	BRWE	4	2	0	0	1	1
10	SABA	2	1	0	0	0	0
10	LINU	1	0	0	0	0	0
10	CONY	1	1	0	1	0	0
10	DIOD	2	1	0	0	0	1
10	OXAL	1	0	0	0	0	0
10	SRFO	1	1	0	1	0	0
10	TPLP	3	0	0	0	0	0
10	SALM	1	0	0	0	0	0
10	HEMO	1	0	0	0	0	0
10	DESM	1	0	0	0	0	0
10	RUEL	3	0	0	0	0	0
10	LESP	1	0	0	0	0	0

10	PLAN	1	0	0	0	0	0
10	LUKF	1	0	0	0	0	0
10	KRAM	1	0	0	0	0	0
10	SOLI	1	0	0	0	0	0
10	TEUC	1	0	0	0	0	0
10	OESE	1	0	0	0	0	0
10	LECA	1	0	0	0	0	0

* Species names and abbreviations:

Achillea millefolium	-	ACMI
Agropyron sp.	-	AGRO
Ambrosia psilostachya	-	AMPS
Amorpha cenescens	-	AMCE
Amorpha fruticosa	-	AMFR
Andropogon gerardii	-	ANGE
Andropogon virginicus	-	ANVI
Andropogon sp.	-	ANDR
Antennaria neglecta	-	ANNE
Aristida oligantha	-	AROL
Artemisia ludoviciana	-	ARLU
Aster ericoides	-	ASER
Asclepias stenophylla	-	ASST
Asclepias viridis	-	ASVI
Astragalus sp.	-	ASTR
Avena fatua	-	AVFA
Baptisia sp.	-	BAPT
Bothriochloa saccharoides	-	BOSA
Bouteloua curtipendula	-	BOCU
Bouteloua gracilis	-	BOGR
Bouteloua hirsuta	-	BOHI
Bouteloua hispida	-	BOHI
Bromus japonicus	-	BRJA
Buchloe dactyloides	-	BUDA
Callirhoe sp.	-	CALL
Carex sp.	-	CARE
Chrysopsis pilosa	-	CHPI
Chrysopsis sp.	-	CHRY
Coelorachis cylindrica	-	COCY
Conyza canadensis	-	COCA
Conyza sp.	-	CONY
Coreopsis tinctoria	-	COTI
Cornus drummondii	-	CODR
Cotinus sp.	-	COTI
Croton glandulosa	-	CRGL
Croton sp.	-	CROT
Cynodon dactylon	-	CYDA
Dactylis	-	DACT
Daucus pusilis	-	DAPU
Desmanthus sp.	-	DESM
Dianthera sp.	-	DIAN
Digitaria sp.	-	DIGI
Diodia sp.	-	DIOD
Echinacea sp.	-	ECHI

Echinochloa crusgalli	-	ECCR
Eleocharis sp.	-	ELEO
Elymus canadensis	-	ELCA
Elymus virginicus	-	ELVI
Eragrastis curtipedicellata	-	ERCU
Eragrastis intermedia	-	ERIN
Eragrastis sp.	-	ERAG
Erigeron sp.	-	ERIG
Eupatorium sp.	-	EUPA
Euphorbia maculata	-	EUMA
Euphorbia spathulata	-	EUSP
Gaillardia sp.	-	GAIL
Hedeoma sp.	-	HEDE
Hedyotis nigricans	-	HENI
Helianthus mollis	-	HEMO
Helianthus sp.	-	HELI
Hieracium sp.	-	HIER
Juncus sp.	-	JUNC
Koeleria macrantha	-	KOMA
Krameria sp.	-	KRAM
Lathyrus sp.	-	LATH
Lespedeza capitata	-	LECA
Lespedeza sp.	-	LESP
Lepidium sp.	-	LEPI
Leptoloma cognatum	-	LECO
Liatris paniculata	-	LIPA
Liatris sp.	-	LIAT
Linum sp.	-	LINU
Lithospermum sp.	-	LITH
Medicago sp.	-	MEDI
Melilotus alba	-	MEAL
Mimosa sp.	-	MIMO
Muhlenbergia sp.	-	MUHL
Oenothera serrulata	-	OESE
Oxalis sp.	-	OXAL
Panicum hispidum	-	PAHI
Panicum oligosanthos	-	PAOL
Panicum virgatum	-	PAVI
Panicum sp.	-	PANI
Paspalum dilatatum	-	PADI
Paspalum sp.	-	PASP
Petalostemum purpureum	-	PEPU
Physalis sp.	-	PHYS
Plantago sp.	-	PLAN
Poa pratensis	-	POPR
Polygala verticillata	-	POVE
Polygonum sp.	-	POLY
Psoralea tenuifolia	-	PSTE
Pyrrhopappus sp.	-	PYRR
Radicula sp.	-	RADI
Ranunculus sp.	-	RANU
Rhus copallina	-	RHCO
Rubus sp.	-	RUBU
Rudbeckia hirta	-	RUHI

Ruellia humilis	-	RUHU
Ruellia sp.	-	RUEL
Rumex sp.	-	RUME
Sabbatia sp.	-	SABA
Salvia sp.	-	SALV
Schrankia sp.	-	SCHR
Scirpus sp.	-	SCIR
Scutellaria sp.	-	SCUT
Senecio sp.	-	SENE
Serinia sp.	-	SERI
Setaria sp.	-	SETA
Sisyrinchium sp.	-	SISY
Solidago alttissima	-	SOAL
Solidago gymnospermoides	-	SOGY
Solidago sp.	-	SOLI
Sorghastrum nutans	-	SONU
Sorghum halapense	-	SOHA
Sporobolus asper	-	SPAS
Sporobolus repens	-	SPRE
Symphoricarpos orbiculata	-	SYOR
Teucrium sp.	-	TEUC
Torilis arvensis	-	TOAR
Toxicodendron sp.	-	TOXI
Tradescantia sp.	-	TRAD
Tridens flavus	-	TRFL
Trifolium sp.	-	TRIF
Ulmus americana	-	ULAM
Umbelliferae sp.	-	UMBE
Unknown composite	-	UKCO
Unknown dicot1	-	UKD1
Unknown dicot2	-	UKD2
Unknown forb	-	UKNF
Unknown flat-stem grass	-	UKFG
Unknown grass3	-	UKG3
Unknown mint	-	UKMI
Unknown annual	-	UNKA
Unknown little forb	-	UNLF
Unknown soft-round forb	-	SRFO
Unknown weed	-	UKNW
Valerianella sp.	-	VALE
Valpia octoflora	-	VAOC
Vinny pea	-	VPEA

2
VITA

Dai Jun Zhang

Candidate for the Degree of
Doctor of Philosophy

Thesis: THE EFFECTS OF GRASSLAND FRAGMENTATION ON SPECIES
RICHNESS AND SPECIES COMPOSITION

Major Field: Botany

Biographical:

Personal Data: Born in Beijing, People's Republic of
China, October 10, 1957, the daughter of Shao Ming
and Shun Ying Zhang.

Education: Graduated from Jinsha High School,
Heilongjiang, People's Republic of China, in August
1975; received Bachelor of Science Degree in
Forestry from The Northeast Forestry University in
Harbin, People's Republic of China, in January 82;
attended Beijing Language Institute for training
in speaking and writing English from February
1982, to July 1982; received Master of Science in
Forestry from the University of New Brunswick,
Canada, in May 1985; completed requirements for
the Doctor of Philosophy degree in Botany at
Oklahoma State University in December 1990.

Professional Experience: Research Assistant, Department
of Forestry, The Northeast Forestry University,
People's Republic of China, summers, 1980-1981;
Research Assistant, Department of Forest
Resources, The University of New Brunswick, from
February 1983, to May 1985; Teaching Assistant,
Department of Botany, Oklahoma State University,
from September 1985, to May 1990; Research
Assistant, Department of Botany, Oklahoma State
University, Summers, 1988-1989; Teaching Assistant
for Elderhostel program, Oklahoma State
University, May 1990; Teaching Assistant for
Oklahoma Summer Scholars Program, June 1990;
Research Associate, Department of Botany, Oklahoma
State University, July-August 1990.