TEMPORAL ASSOCIATIONS AMONG WOODLAND PLANTS IN SOUTHERN MICHIGAN

Thesis for the Degree of M. S.
MICHIGAN STATE UNIVERSITY
RICHARD ANDERSON FLANDERS, JR.
1971

ABSTRACT

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By

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This study was an investigation into the presence of temporal associations among woodland species in five maple-beech-mixed hardwood stands in southern Michigan. Such information concerning species interactions on a time basis provides insight into the development of species patterns.

Sampling was done between May and September in 1970 and in May and June in 1971 using three sampling techniques and three quadrat sizes. Presence-absence data were recorded. Chi-square and/or Cole's Index of Interspecific Association were used to detect presence and/or degree of association. While all significant associations were recorded, emphasis was placed on the interpretation of the temporal associations between spring ephemerals and summer species. Results were interpreted in relation to quadrat size ($\frac{1}{2}$m x $\frac{1}{2}$m, 1m x 1m, and 5m x 5m), difference in species frequencies, and limitations of the selected, contiguous, and random quadrat techniques utilized.

Interspecific association was common in most stands. Certain temporal associations appear to prevail among several stands while others exist in single stands. Positive temporal associations may result from similarities in habitat requirements combined with niche differentiation while allelopathic influences are suggested to explain certain negative associations.

Certain species assemblages detected by association analysis and emphasized by constellation diagrams appeared to be stand specific. This is probably due to stand individuality resulting from variations in past history, topography and soils.

Random quadrat data indicated that many species are highly clumped. Such contagiousness among woodland plants results mainly from extensive vegetative reproduction.

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Richard Anderson Flanders, Jr.

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Botany and Plant Pathology

1971

DEDICATION

To my loving wife Donna without whose encouragement and dedication this study would not have been possible.

ACKNOWLEDGEMENTS

I would like to gratefully acknowledge the assistance and guidance of Dr. Stephen N. Stephenson, my major professor, under whose direction the problem was carried out. I am indebted to Dr. Peter G. Murphy who offered helpful suggestions during the course of this study and who volunteered his time to participate in the thesis defense. I also wish to thank Dr. Gerhardt Schneider for permitting research in Toumey Woodlot and who graciously offered his time for consultations concerning the study.

Special thanks are due to Frank Reed for offering useful suggestions during several phases of this study and for time spent in reviewing the manuscript. I would also like to acknowledge the aid provided by Robert Moskowitz in preparing the computer programs necessary for the data analysis. Use of the Michigan State University Computing facilities was made possible through support, in part, from the National Science Foundation.

Finally, I wish to thank Dr. William B. Drew for securing monetary support for the research and for advice as a member of my committee.

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INTRODUCTION

Studies concerning the interaction among species in forest or woodland communities usually emphasize associations that exist at a particular point in time, ordinarily during the aestival period (Gleason, 1924; McIntosh, 1951; and Bray, 1956). These studies have often ignored the presence of a well developed herbaceous vernal element such as is typical of the mesic sugar maple-American beech (*Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh.) woodlands though this element may comprise a significant portion of the total annual biomass of the understory herbaceous vegetation. Perennials such as trout-lily (*Erythronium americanum* Ker.), toothwort (*Dentaria laciniata* Muhl.), spring beauty (*Claytonia virginica* L.), dutchman's breeches (*Dicentra cucullaria* (L.) Bernh.) and squirrel corn (*Dicentra canadensis* (Goldie) Walp.) are commonly observed spring ephemerals which occur in aggregations of different sizes and densities. Individuals within these aggregations may be found in close proximity to one another apparently competing for available nutrients, sunlight and soil moisture (Salisbury, 1929). Smith and Cottam (1967) suggested that spring ephemerals may affect the subsequent development of other woodland herbs. Consequently, the mutual occurrence or non-occurrence between an ephemeral and a "summer" species within a defined area may result in these species being associated on a time basis—thus a "temporal" association.

This study was formulated to determine whether temporal associations exist between herbaceous species, and, if so, to suggest possible interplant influences and environmental factors which might account for these associations.

LITERATURE REVIEW

The fact that the vegetation of most plant communities is distributed in a non-random fashion has been shown by many authors (e.g. Ashby, 1935; Clapham, 1936; Cole, 1946; Cain & Evans, 1952; Clark & Evans, 1954; Kershaw, 1963, 1964; Greig-Smith, 1964; Pielou, 1969). Several explanations of the causes of non-randomness have been offered, among which are vegetative reproduction, heavy seed, antibiotic effects, competition, preconditioning of an area by a species previously occupying a site, drainage patterns, moisture, humidity, light, soil texture, soil depth, soil chemistry, species phenology, microrelief, windfall depressions and mounds, burning and solifluction terraces (Smith and Cottom, 1967). In mature woodland situations, vegetative reproduction is probably the main factor involved in clumping. This has been pointed out by Whitford (1949) in a study of 26 uneven-aged stands in southern Wisconsin and northern Illinois. Whitford was interested in the relationship of clonal growth to the distribution pattern of understory species. He found that vegetatively produced individuals usually lie in close proximity to the parent plant resulting in contagious groupings.

Several studies have been made relating to an analysis of the degree of aggregation in herbaceous woodland vegetation. McIntosh (1957) used the degree of contagiousness in vegetation as a measure of the heterogeneity of an area. Byer (1960) and McIntosh (1962) felt that sampling a heterogeneous area served to indicate interspecific relationships which otherwise would become apparent only by analyzing many samples collected from separate homogeneous stands. Thus they infer that determining interspecific vegetational patterns in limited yet heterogeneous areas is valid since existing patterns are the result of non-randomly distributed populations. Struik and Curtis (1962) have applied a Chi-square test to determine the apparent homogeneity of a site before they proceeded to apply a measure of interspecific association between component species. This procedure of testing for homogeneity apparently is the result of supposed problems inherent in using interspecific association indexes when the presence or lack of association is strongly affected by the size of the area being sampled. For example, suppose a two species population is very common in a small area. Sampling the small area may not provide evidence for association between the species, but if we include in the above sample a large surrounding area which contains neither of the species, we may find that they are strongly associated. This is due to the fact that in a 2 x 2 contingency table (Appendix A) the proportion of the number of (d) quadrats (neither species present) will be greater in the larger area sampled than the proportion sampled in the small area. Bray (1956), Cottom et al. (1957) and Greig-Smith (1964) have stated that the procedure of inflating the number of (d) quadrats invalidates the test for association. Pielou (1969, p. 170) disagrees. She states that:

> It seems often to be believed that to include in a sample a great many quadrats that for unknown reasons may be incapable of containing either of the species invalidates an association test in some way. The notion seems to be that the evidence for positive association has been obtained by cheating. This is not so. If large areas of ground contain neither of the species, it is reasonable to conclude that the two species resemble each other in the conditions they will not tolerate. This in itself shows that they are associated in the sense that there is considerable overlap in their tolerance ranges. The search for association of this type should obviously not be restricted to small homogeneous areas. If we wish to know whether two species will react similarly to environmental conditions, it is absurd to insist that sampling be confined to a homogeneous area throughout

which the conditions are constant. To do so would rule out the possibility of finding different responses to different conditions.

Thus the existence of association is strongly dependant upon sample size and the range of suitable habitat types sampled (Cole, 1946). The final analysis must take these points into consideration since associations present in one sample (or woodlot) may not be present in another.

Various interrelationships among species of the herbaceous stratum of several forest types have been investigated. Smith and Cottom (1967) studied ten southern Wisconsin maple-basswood (Acer saccharum-Tilia americana) stands using a belt transect containing 500 contiguous square foot quadrats to show aggregation and association among species of the herb layer. Presence-absence data rather than densities were collected due to the problem of recognizing true "individuals" because of vegetative reproduction. D/d values (actual density/expected density, where D is the number of occupied quadrats within a five foot segment and d is the number of occupied quadrats expected if the population were random), and, run-gap values (average frequency within the grouped runs/average frequency within the grouped gaps) were determined. Smith and Cottom found that individual species aggregation patterns differed widely between stands. In some stands a species was completely absent while in another it existed in large aggregations. They attributed this phenomenon to historical events which presumable resulted in great diversity between these stands. Cole's Index (Cole, 1949) was used to relate the spatial pattern of one species to that of another. There were 125 significant associations which were related to similarities and differences in habitat requirements or alternations of photosynthetic season.

Several studies have attempted to correlate temperature, solar radiation and microclimate with phenological events of spring ephemerals (Vezina, 1965; Jackson, 1966; Risser, 1967). Autecological studies of several of these common species have been done as well (Blodgett, 1900; Dandeno, 1907; Holm, 1925). However, few studies have been made relating to the detection of association between spring ephemerals and longer lived "summer" species. Struik and Curtis (1962) analyzed a rectangular 1.7 hectare area within a mesic woodlot in southern Wisconsin. Using 10m x 10m meter contiguous quadrats and presence-absence data, interspecific association values were calculated by Cole's Index. Of primary interest are the significant associations they found between spring and summer species. For example, Dentaria was found to be negatively associated with Viola pubescens Ait. and Erythronium albidum Nutt. was negatively associated with V. pubescens, Uvularia grandiflora Sm. and Actaea pachypoda Ell. They suggested that large quadrat size probably eliminated association effects caused by allelopathic reactions or other direct interplant influences between species and theorized that any correlations were probably the result of similarities or differences in habitat requirements. They found that 56% of the species studied were significantly associated with topography.

Byer (1960) analyzed the associations among plant species found along a soil moisture and vegetation gradient from a jack pine (Pinus banksiana Lamb.) stand to a leatherleaf (Chamaedaphne calyculata (L.) Moench) bog in Crawford County, Michigan. He collected presence and cover data within 400, 1m x 1m random quadrats. The analysis, utilizing Cole's method and product-moment correlation coefficients, indicated that the positive and negative associations were due in large part to past or present environmental conditions. He also noted that the overall vegetational pattern was one of strongly aggregated populations.

DESCRIPTION OF STUDY AREA

The woodlots included in this study are located in Ingham County, East Lansing, Michigan on the Michigan State University campus (T3-T4N, R1-R2W). These areas were set aside as managed timber stands or as natural areas when the land was originally acquired by Michigan State University.

Climatological data indicates even distribution of precipitation throughout the year with a 31-year average of 77 cm/year. The mean annual temperature for the same period was 8.6°C. Prevailing winds are from the southwest, averaging 49 cm/sec. There are about 160 frost free days from May to October. Average relative humidity measured at 1:00 P.M. for the last seven years was 62%. (Data from United States Weather Bureau with stations in Lansing and on the Michigan State University campus in East Lansing). Mean annual temperature and precipitation readings for 1970 are normal compared with the 31 year average, although during the first six months of 1971, the precipitation was 21.3 cm below normal.

The general physiography of the area is typified by Pennsylvanian-aged bedrock overlain most recently by glacial deposits of the Cary substage of the Wisconsin ice sheet (Martin, 1955). Several undulating moraines, level till and outwash plains, and remnants of glacial drainageways comprise the local relief. Soils in the woodlots belong to Gray-Brown Podzolic and Humic Gley Great Soil Groups, now termed alfisols (Soil Survey Staff, U.S. Dept. Agric., 1967). The dominant soil type is Hillsdale sandy loam with Conover loam of secondary importance (Veatch, 1941). These are well drained and somewhat poorly drained soils respectively, developed from calcareous till. The natural vegetation of these soils is sugar maple, beech, oak (Quercus spp.), hickory (Carya spp.), ash (Fraxinus spp.) and elm (Ulmus americana L.) (Veatch, 1953).

Baker Woodlot

Baker Woodlot is a 73.7 acre tract located in the $E\frac{1}{2}$ of the $SW\frac{1}{4}$ of Sec. 19, T4N, R1W of the Michigan Meridian. This woodlot was included in the original land grant to the University in 1855 having been originally a part of the Burr farm. Gillis (1969) states that the woodlot is probably a remnant of the forest that was cut over about 100 years ago. He considered it predominantly a beech-maple woods with pockets of other tree assemblages which he related to soil type and drainage characteristics. The canopy is presently dominated by sugar maple and beech with oaks (Quercus rubra var. borealis (Michx. f.) Farw. especially), white ash (Fraxinus americana L.), black cherry (Prunus serotina Ehrh.) and basswood (Tilia americana L.) of secondary importance. The shrub layer consists mainly of red-berried elder (Sambucus pubens Michx.), dogwood (Cornus spp.), spice bush (Lindera benzoin (L.) Blume.) and sassafras (Sassafras albidum (Nutt.) Nees). The ground flora is well developed, although the dense summer canopy restricts some species to occasional openings. The topography is gently rolling, having an average elevation of about 262 meters above sea level with a range of 5.5 meters from the ponded areas to the upland sites.

Baker Woodlot has been a multiple use area for many years. Walking paths existing before 1920 were widened for horse trails. Several of the earlier walking paths have grown up and new paths established. The south side of the woods adjacent to a railroad right-of-way was clear cut at the beginning of the century and planted in pine, black locust and balsam fir[1]. Mr. Herbert remembers a giant black gum (Nyssa sylvatica Marsh.) tree being removed in the early 1920's, this being the only known individual of the species being recorded in the woodlot. Perhaps other uncommon relicts of a warmer southern climate have met a similar fate. Records indicate that timber cutting had been done prior to 1894 and also in 1938 and 1948 throughout the woods for fuel wood and for valuable hardwoods. The northeast section is presently undergoing a light group selection cutting by the Department of Forestry. Their records indicate that grazing has not been permitted within the woodlot, and no fires have occurred since 1894.

The soils in Baker Woodlot are diverse. Hillsdale and Spinks soils are the most common well-drained soils found on the upland sites. Lower areas are somewhat poorly to very poorly drained, with Wauseon, Conover and Carlisle muck the prevailing soils.

Hudson Woodlot

Hudson Woodlot is a 17.7 acre tract located in the SE$\frac{1}{4}$ of the SW$\frac{1}{4}$ of Sec. 30, T4N, R1W of the Michigan Meridian. The woodlot and surrounding fields were purchased from the Ralph Hudson family in 1941. This family raised cattle, pigs and other animals on a farm adjacent to the present woodlot and allowed these animals free access to the area. Extensive grazing and rooting by pigs probably destroyed much of the understory vegetation, giving an open park-like appearance (Herbert,

[1] Personal communication from Paul A. Herbert, retired Professor of Forestry at Michigan State University.

personal communication). Periodic selective cuttings (especially on the southern half of the woodlot) and removal of downed timber for fuel greatly disturbed the natural canopy. Following university purchase, the property was fenced off thus allowing the understory to recover. The canopy is now composed of second growth hardwoods, especially sugar maple and beech. Sugar maple reproduction has been extensive and has resulted in dense areas of young saplings throughout most of the woodlot. The spring and summer flora is very limited in extent.

The topography of Hudson Woodlot is generally gently to moderately sloping. Most of the soils are well drained Hillsdale sandy loams or Spinks loamy fine sands.

Toumey Woodlot

Toumey Woodlot, located in the NE$\frac{1}{4}$ of the SE$\frac{1}{4}$ of Sec. 30, T4N, R1W of the Michigan Meridian, is a relatively undisturbed 15 acre preserve purchased from the Frank Bennett estate in 1939. This tract has been maintained as a natural area since at least 1852 with no known fires or grazing (Schneider, 1966).

The dominant vegetation is old growth sugar maple and beech with basswood, black cherry, white ash and northern red oak of secondary importance. Red-berried elder is the most common shrub in openings. Maple seedlings and saplings are very common even though seedling mortality is high in such "virgin" stands (Schneider, 1966). The vernal ground cover is well developed as in Baker Woodlot but the summer flora is less diverse than in Baker probably due to more disturbed conditions and greater topographical heterogeneity prevalent in Baker Woodlot.

The topography of the woodlot varies from 259 meters above sea level in the eastern ponded area to 271 meters on the central upland. Hillsdale sandy loam is the common soil type of the western upland area, while Spinks, Conover and Carlisle series are found in the eastern lowland.

Sandhill Woodlot

Sandhill Woodlot is approximately 44 acres in area located in the NW$\frac{1}{4}$ of the SE$\frac{1}{4}$ of Sec. 6, T3N, R1W of the Michigan Meridian. The property was purchased by Michigan State University from the Lott and Wieland families in the early 1960's. It is bordered on the east by a drainage ditch and on the west by abandoned agricultural fields. The north and south borders lie adjacent to Interstate 96 and Sandhill Road, respectively.

Sugar maple and beech are dominant in the overstory of the woodlot with several other hardwoods of secondary importance. The shrub layer is well developed in old openings and on the border areas. Sumac (*Rhus* spp.) is common on the southern border near the pine plantation. The herb layer is diverse throughout the year, varying in abundance according to soil moisture.

The relief is moderately sloping with an elevation range of 259 to 271 meters above sea level. Well drained upland soils (Spinks loamy sand and Miami loam) and imperfectly drained Conover soils are common.

Bear Lake Natural Area

Bear Lake Natural Area is located in the SW$\frac{1}{4}$ of the NE$\frac{1}{4}$ of Sec. 35, T4N, R2W of the Michigan Meridian. The bog and lowland forest comprises about 75 acres while the site studied, the upland hardwood stand to the south, consists of about 25 acres.

Sugar maple is the dominant canopy species on this site while basswood, northern red oak, black cherry and eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch.) are of secondary abundance. Aspens (*Populus* spp.) become very common north of this upland site where the conditions are more moist. Common shrubby species of the upland include alternate-leaved dogwood (*Cornus alternifolia* L.f.); viburnum (*Viburnum* spp.) and witch hazel (*Hamamelis virginiana* L.). Grape (*Vitis* sp.) is very common in openings. The ground cover is well developed both in the spring and summer. At the southern border of the woods, parallel with the cleared power line right-of-way, a dense ground cover exists, composed of weedy elements mixed with the typical woodland species. Such infiltration by these gap-phase species will probably continue as long as the power line opening is maintained.

The upland woods is generally level and gently slopes to the north toward the bog. The soil type in the upland woods is the well drained Miami sandy loam. This grades into the poorly drained Carlisle muck surrounding the bog.

METHODS

Whitford's (1949) selected quadrat technique was employed to emphasize certain associations and to avoid sites where the selected species were absent. Selected plots were obtained by starting at the edge of a woodlot and walking until a site was encountered that contained at least one species of interest. A meter square quadrat was placed around the clump of individuals if the aggregation was small. If the aggregation was larger than a meter in diameter several quadrats were placed within or including a segment of the grouping. Thus, both species and quadrat placement were non-random. This design was used to establish four areas of 100 quadrats each, two in Baker Woodlot, and two in Toumey Woodlot.

Since the above technique has statistical limitations due to non-randomness, two other methods were also employed.

In the second technique, a grid 100m x 100m (1 hectare or approximately 2.5 acres), which contained 400 contiguous 5m x 5m quadrats, was established in an area of relatively homogeneous soil in Baker Woodlot. The entire grid was partitioned with string and stakes to distinguish each quadrat. Sampling was carried out in August (1970) for the summer flora and in May (1971) for the spring ephemerals.

The third technique involved quadrats one-half meter on a side situated along north-south and east-west 100 m transects selected in areas of even topography and homogeneous soil type (Hillsdale sandy loam) in Baker, Toumey, Sandhill and Hudson Woodlots and Bear Lake Natural Area. Using both sides of the transect line, one hundred quadrats were randomly selected out of a total of 400, or a total of 200 random quadrats per woodlot. These were established in April (1971) and data on presence of vernal species was collected at this time. Sampling for the summer flora was done the last week of May (1971).

Both woody and herbaceous species were sampled using the second technique while only non-woody species were considered with the first and third. Presence or absence of selected species was the criterion used in these analyses. Seventy-five of the most common species plus a lumped category for Carex spp. were listed alphabetically on computer data sheets. The data were later transfered to IBM cards and analyzed on the CDC 6500 computer at the Michigan State University Computer Center. Constancy of species pairs and Chi-square were the measures used to detect the presence (not degree) of association in the first method (Greig-Smith, 1964). For the other sampling techniques, significance of association was tested by Chi-square and a relative measure of interspecific association was determined by Cole's Index (Cole, 1949) (see Appendix A). For all analyses, a species that occurred in less than twenty quadrats was deleted from the comparisons.

While the above methods are important in understanding present relationships that exist among herbaceous species at a given site, they give little information concerning how certain associations may originate. After collecting preliminary data it appeared that certain ephemeral species were negatively associated with certain "summer" species. I originally planned to carry out greenhouse experiments to determine whether litter, root exudates or foliage cover provided by an ephemeral (or "summer" species) could affect the seed germination of later (or earlier) developing species. This was based on the premise that initially interspecific interference existed between an established plant of one species and the seed or seedling of another present in the same area. A literature survey to determine the germination requirements of some of these woodland species indicated that many of these species require prolonged periods of alternating cold and warm temperatures to break epicotyl and/or hypocotyl dormancy (Barton, 1942, 1944, 1948). Reference to Table 1 indicates that there is a minimum of six to twelve months between the collection and initial conditioning treatments and the final development of cotyledons. Temperature treatments were tried using this information but low seed viability and other factors produced poor results after more than a year. Thus this aspect of the study was abandoned and I decided to limit myself to attempt to test the occurrence of temporal associations and not to attempt a demonstration of causality.

In this paper "spring ephemeral" refers to those species which emerge rapidly in the spring, produce vegetative and reproductive structures, and then return to a dormant state about the time the canopy closes. Thus such plants differ from the spring wildflowers and summer species in that they do not retain foliage during the summer months. Plants here classified as ephemerals are indicated by an asterisk in Table 2.

Specimens of the herbaceous flora were collected and are on file in the Beal-Darlington Herbarium of Michigan State University. Nomenclature follows Fernald (1950).

Table 1. Pretreatment requirements of some woodland herbs[2]

Species	Pretreatment For Root Production		Requirement For Germination of Root and Growth of Seedling Before Pretreatment For Epicotyl Dormancy		Pretreatment For Epicotyl Dormancy	
	Temp. (°F.)	Time (Mos.)	Temp. (°F.)	Time	Temp. (°F.)	Time (Mos.)
Sanquinaria canadensis	41	3	70	6	41	3
Smilacina racemosa	41	6	70	3	41-50	3
Polygonatum commutatum	33-50	4	70	3-5	33-50	3
Trillium grandiflorum	41-50	3	70	3	41-50	3-5
Asarum canadense			68	3	41	3

[2] Data from Barton and Crocker (1948)

RESULTS

To facilitate analysis results are separated into sections according to sampling technique. Constellation diagrams were constructed showing associations between species as determined by Chi-square following the technique of DeVries (1952, 1954). However, no attempt was made to indicate degrees of associations by length or width of lines.

Species connected by unbroken lines are positively associated; those connected by dashed lines are negatively associated. Species lists indicating per cent frequency (number of occurrences of a species divided by the total number of quadrats) for each species are shown in Tables 2 and 3. These tables show that the abundance of spring ephemerals varies from very common (Claytonia and Erythronium) to rare (Erigenia bulbosa (Michx.) Nutt.) in the five woodlots studied. One species (Isopyrum biternatum (Raf.) T. & G.) occurred only in Sandhill Woodlot. The two Dicentras (D. canadensis and D. cucullaria) and Erigenia were found only in Bear Lake Natural Area and Sandhill Woodlot. The remaining ephemerals (Claytonia, Erythronium and Dentaria) occurred in all five stands.

Selected Quadrat Technique

The presence or absence of significant[3] interspecific association within selected quadrats in Baker and Toumey Woodlots is depicted in matrix form in Tables 4 and 5. Constellation diagrams (Figures 1 and 2) were constructed following the procedure of McIntosh (1962). These

[3] "Significant" indicates statistical significance at the 5% level.

Table 2. List of selected species for random ($\frac{1}{2}$m x $\frac{1}{2}$m) and selected (1m x 1m) quadrats with percent frequency indicated for each woodlot.

Species	Frequency (%) Hudson n=200 $\frac{1}{2}$x$\frac{1}{2}$m	Toumey n=200 $\frac{1}{2}$x$\frac{1}{2}$m/	Toumey 1x1m	Bear Lake n=200 $\frac{1}{2}$ x $\frac{1}{2}$m	Baker n=196 & 190 $\frac{1}{2}$x$\frac{1}{2}$m	Baker 1x1m	Sandhill n=200 $\frac{1}{2}$ x $\frac{1}{2}$m
Actaea pachypoda				6.5	.5		.5
Allium tricoccum				69.5			1.5
Amphicarpa bracteata				8.0	4.6		3.0
Arisaema triphyllum	6.5	1.0	33.0	0.5		14.7	.5
Aster macrophyllus				3.0	5.1		
Brachyelytrum erectum				11.0	10.2		1.5
Carex spp.		1.5		31.5	1.0		5.0
Caulophyllum thalictroides				23.5	.5	25.8	1.5
Circaea quadrisulcata	2.0	3.5	34.5	1.5	16.8	35.3	4.5
*Claytonia virginica	46.5	94.5	44.5	72.5	95.9	64.2	91.5
Collinsonia canadensis					16.3		
Cryptotaenia canadensis				5.5	8.2	12.6	11.0
*Dentaria laciniata	22.0	13.0	38.0	31.5	6.1	34.7	19.0
Desmodium glutinosum				3.0	1.5		
*Dicentra canadensis				4.5			72.0
*D. cucullaria				26.5			17.5
*Erigenia bulbosa				5.5			2.5
*Erythronium americanum	72.5	83.5	74.5	92.5	96.4	60.5	60.0
Eupatorium purpureum				4.0	.5		
Galium aparine				5.5	17.9	41.1	39.0
G. triflorum		3.0		.5			
Geranium maculatum				3.0	69.4	41.6	
Geum canadense							3.0
Hydrophyllum apendiculatum				8.5			
Hystrix patula							6.0
*Isopyrum biternatum							39.0
Laportea canadensis							1.0
Mianthemum canadense				2.5	.5		
Osmorhiza claytoni				30.0	38.3	54.7	10.0
Phlox divaricata		.5		.5			1.5
Phryma leptostacha				2.5			2.0
Podophyllum peltatum	1.5		10.0			21.1	2.0
Polygonatum pubescens		2.0	22.0	27.5	16.8	25.3	.5
Polygonum virginianum					6.1		3.5
Prenanthes altissima				32.0	30.6		
Sanicula gregaria				34.5	25.5	26.3	2.0
Sanquinaria canadensis	.5		33.0		4.6		6.0
Smilacina racemosa				42.5	5.6	21.1	.5
Solidago caesia				23.0	12.8	21.1	
Trillium grandiflorum					16.8	31.1	.5
Uvularia grandiflora				4.0			
Viola canadensis	.5	3.5	18.0	8.5			33.5
V. pubescens		18.5	21.5	57.5	41.8	46.3	38.5
V. sororia		4.0		18.0	12.8	30.5	23.0

* Spring ephemerals

Table 3. Species list and frequency (%) for contiguous 5m x 5m quadrats in Baker Woodlot

Species	Frequency (%)
Acer nigrum	5.3
A. rubrum	18.0
A. saccharum	99.8
Actaea pachypoda	36.8
Adiantum pedatum	1.3
Aesculus octandra	.3
Allium tricoccum	1.0
Amphicarpa bracteata	15.0
Arisaema triphyllum	6.0
Asarum canadense	3.8
Aster macrophyllus	5.8
Athyrium filix-femina	.3
Berberis thunbergii	3.5
Boehmeria cylindrica	1.8
Botrychium dissectum	.3
B. virginianum	26.5
Campanula americana	.8
Carex spp.	31.3
Carya cordiformis	45.5
Caulophyllum thalictroides	39.3
Circaea quadrisulcata	42.8
Claytonia virginica	99.8
Collinsonia canadensis	20.8
Cornus alternifolia	18.8
Corylus americana	.5
Cryptotaenia canadensis	39.5
Cypripedium calceolus	1.5
Dentaria laciniata	92.8
Desmodium glutinosum	4.0
D. nudiflorum	.5
Dryopteris spinulosa	2.0
Equisetum hyemale	1.8
Erigeron philadelphicus	.3
Erythronium americanum	83.3
Euonymus alatus	.3
E. obovatus	45.0
Eupatorium purpureum	4.5
Fagus grandifolia	27.0
Fraxinus americana	70.8
Galium aparine	98.8
G. circaezans	3.5
G. triflorum	11.3
Geranium maculatum	23.3
Geum canadense	14.8
Hamamelis virginiana	6.8
Helianthus decapetalus	5.5
Hepatica acutiloba	.3
Hydrastis canadensis	2.3

Table 3. (continued)

Species	Frequency (%)
Hystrix patula	1.8
Impatiens capensis	.3
Laportea canadensis	2.3
Lindera benzoin	73.5
Lonicera spp.	3.5
Mianthemum canadense	.5
Onoclea sensibilus	.5
Osmorhiza claytoni	96.5
O. longistylis	.3
Ostrya virginiana	12.3
Panax quinquefolia	5.5
Parthocissus quinquefolia	59.5
Phlox divaricata	.3
Phryma leptostachya	31.0
Phytolacca americana	.3
Pilea pumila	1.3
Podophyllum peltatum	2.0
Polygonatum pubescens	54.0
Polygonum virginianum	54.3
Polymnia canadensis	.3
Populus deltoides	.5
Prenanthes altissima	8.3
Prunus serotina	36.5
P. virginiana	20.8
Quercus rubra var. borealis	48.5
Ranunculus abortivus	1.3
Ribes spp.	44.3
Rubus spp.	2.3
Sambucus pubens	56.8
Sanicula gregaria	91.0
S. trifoliata	17.5
Sanquinaria canadensis	1.3
Sassafras albidum	2.0
Smilacina racemosa	12.8
Smilax herbacea	3.3
S. hispida	20.8
Solidago caesia	43.8
Thalictrum dioicum	2.0
Tilia americana	34.0
Toxicodendron radicans	20.3
Trillium grandiflorum	32.0
Ulmus rubra	84.5
Urtica gracilis	.3
Uvularia grandiflora	5.2
Viburnum acerifolium	6.0
V. lentago	.5
Viola canadensis	.5
V. pubescens	79.5
V. rostrata	5.5

Species	Frequency (%)
V. sororia	52.8
Vitis palmata	.3
V. riparia	1.3
Zanthoxylum americanum	4.3

Table 4. Significant positive and negative (-) associations as determined by Chi-square for Baker Woodlot selected quadrat data * (p=.05) ** (p=.01) *** (p<.005) 0=no significant correlation

	Caulophyllum	Circaea	Claytonia	Cryptotaenia	Dentaria	G. aparine	Geranium	O. claytoni	Podophyllum	Polygonatum	S. gregaria	Smilacina	Solidago	Trillium	V. pubescens	V. sororia	Frequency (%)
Arisaema	***	**	-***	0	-*	-**	0	-***	0	0	0	-***	0	0	0	***	14.7
Caulophyllum		0	-***	0	-**	0	0	-*	0	0	-***	0	-*	0	0	0	25.8
Circaea			-***	0	-***	-***	0	-*	0	0	0	0	0	0	0	0	35.3
Claytonia				***	***	***	0	***	0	***	***	0	0	***	**	0	64.2
Cryptotaenia				0	**	0	*	0	0	0	***	0	*	0	0	***	12.6
Dentaria					0	***	0	***	0	*	***	-*	0	*	0	0	34.7
Erythronium						*	***	0	-***	0	0	0	*	0	0	*	60.5
Galium aparine							-***	***	0	0	0	0	0	***	0	0	41.4
Geranium								-***	-*	0	*	**	0	0	0	***	41.6
Osmorhiza claytoni									0	***	0	-***	0	***	0	0	52.1
Podophyllum										0	0	0	-*	0	-***	0	21.1
Sanicula gregaria											0	0	***	0	***	***	26.3
Smilacina												0	***	0	0	0	21.1
Solidago													0	0	0	*	21.1
Viola pubescens															0	***	46.3
Frequency (%)														31.1		30.5	

Table 5. Significant positive and negative (-) associations as determined by Chi-square from Toumey Woodlot selected quadrat data *(p=.05) **(p=.01) ***(p<.005) 0=no significant correlation

Species	Claytonia	Erythronium	Podophyllum	Polygonatum	Sanquinaria	V. canadensis	Viola pubescens	Frequency (%)
Arisaema	-***	-***	-***	-***	0	0	-***	33.0
Circaea	0	0	0	0	***	0	0	34.5
Claytonia	0	***	0	0	0	0	***	44.5
Dentaria		0	-***	0	***	***	0	38.0
Erythronium		0	0	0	*	**	***	74.5
Podophyllum			0	0	-***	-*	0	10.0
Polygonatum				0	-***	-*	0	22.0
Sanquinaria					0	***	*	33.0
Viola canadensis						0	*	18.5
Frequency (%)							21.5	

Figure 1. Constellation diagram showing significant Chi-square associations from Baker Woodlot selected quadrat data ($p < .005$). Positive association ——; negative association - - -. Group 1. (*Claytonia*, *Dentaria*, *Polygonatum*, *Cryptotaenia*, *Trillium*, *Viola pubescens*, *Galium aparine*, *Viola sororia*, *Osmorhiza*, *Sanicula gregaria*. Group 2. The remainder.

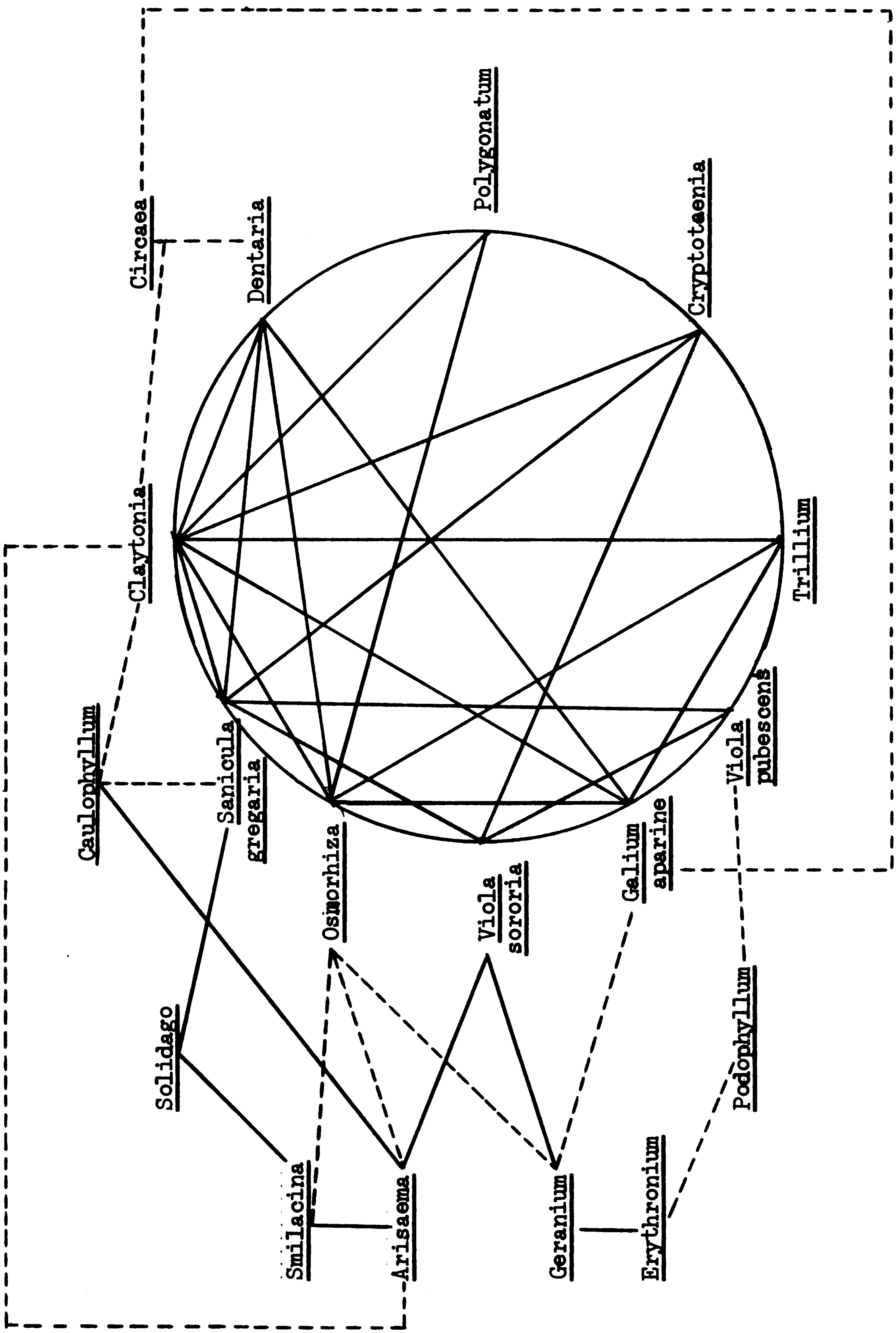
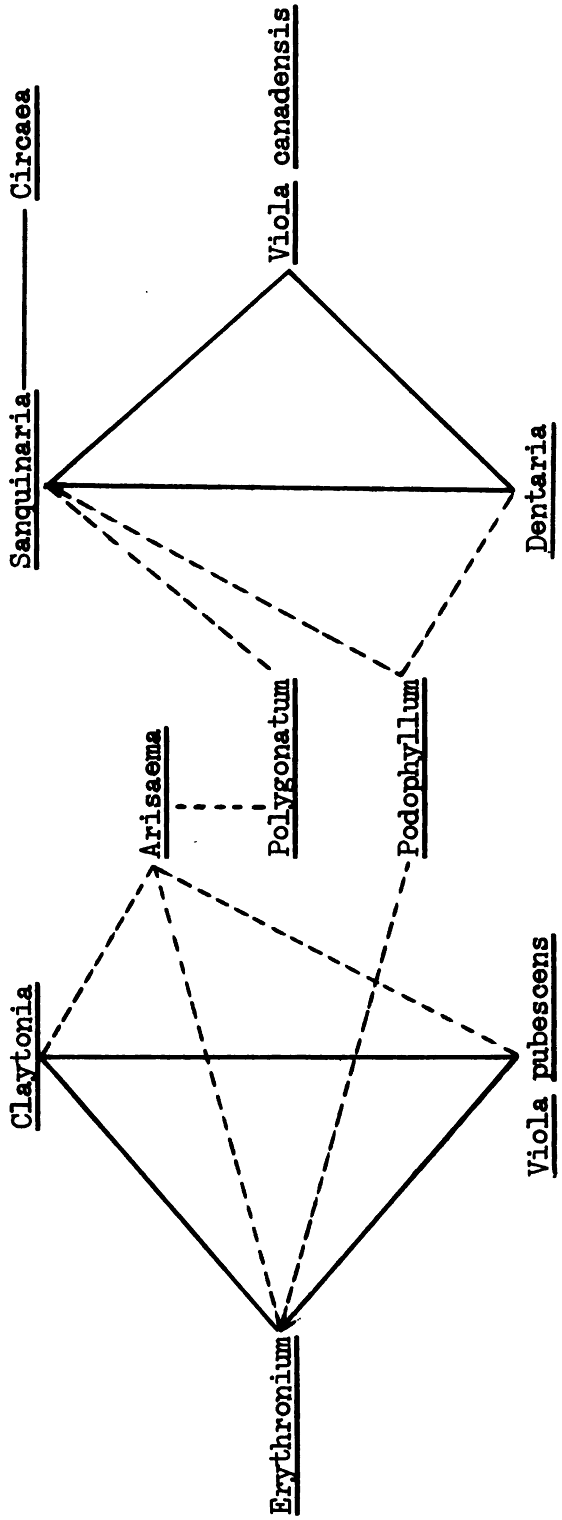

Polygonatum
Cryptotaenia
Dentaria
Circaea
Claytonia
Trillium
Caulophyllum
Sanicula gregaria
Osmorhiza
Viola sororia
Galium aparine
Viola pubescens
Podophyllum
Solidago
Smilacina
Arisaema
Geranium
Erythronium

Figure 2. Constellation diagram showing significant Chi-square associations from Toumey Woodlot selected quadrat data ($p < .005$). Positive association ——; Negative association - - -. Group 1. (*Claytonia*, *Erythronium*, *Viola pubescens*); Group 2. (*Sanquinaria*, *Viola canadensis*, *Dentaria*). Group 3. The remainder.


Circaea
Viola canadensis
Sanguinaria
Dentaria
Polygonatum
Podophyllum
Arisaema
Claytonia
Viola pubescens
Erythronium

emphasize very highly significant[4] associations among species pairs. The following generalizations can be made based upon these data.

Chi-square analysis for association resulted in twenty-one significant values out of forty-five 2 x 2 contingency tables (46.7%) computed from Toumey Woodlot data and sixty significant values out of 153 tables (39.2%) computed from Baker Woodlot data. Of these values 65.4% were very highly significant. This is indicative of the extensive nature of interplant associations in the sampled area.

A temporal relationship appears to exist between Claytonia and Arisaema triphyllum (L.) Schott (very highly significant negative association) and between Claytonia and Viola pubescens (highly significant[5] positive association) in both woodlots at the $1m^2$ quadrat size.

Temporal relationships also appear to exist on an individual stand basis. Dentaria is significantly positively associated with Osmorhiza, Claytonia (Michx.) C. B. Clarke, Polygonatum pubescens (Willd.) Pursh., Sanicula gregaria Bickn., Trillium grandiflorum (Michx.) Salisb. and Cryptotaenia canadensis (L.) DC. in Baker Woodlot and with Sanquinaria canadensis L. and Viola canadensis L. in Toumey. In Baker Woodlot, Dentaria is negatively correlated with Smilacina racemosa (L.) Desf., Arisaema, Caulophyllum thalictroides (L.) Michx., and Circaea quadrisulcata (Maxim.) Franch. and Sav. while in Toumey, it is negatively associated with Podophyllum peltatum L. The per cent frequency of Dentaria is very similar between the two woodlots. Also, Claytonia is positively associated with Cryptotaenia, Osmorhiza,

4 "Very highly" significant indicates significance at the .5% level.

5 "Highly significant" refers to significance at the 1% level.

Polygonatum, Sanicula gregaria and Trillium and negatively correlated with Caulophyllum, and Circaea in Baker. Erythronium is positively associated with Geranium maculatum L., Solidago caesia L. and Viola sororia Willd. in Baker and with Sanquinaria, Viola canadensis and Viola pubescens in Toumey.

The presence of significant negative associations between Podophyllum and several other species (Erythronium, Dentaria, Geranium, Viola pubescens, Solidago, Sanquinaria and Arisaema) and the lack of significant positive associations implies exclusion of certain species from sites occupied by Podophyllum.

The constellation diagram showing very highly significant associations between species in Toumey Woodlot suggests that there are two distinct groupings of species connected to each other by common negative associations of a third group. Thus Erythronium, Claytonia and Viola pubescens (Group 1) are usually found positively associated as are those species within Group 2 (Dentaria, Viola canadensis, Sanquinaria, Circaea quadrisulcata (Maxim.) Franch. and Sav.). These two groups are negatively associated with Arisaema, Polygonatum and Podophyllum. It should be noted that Group 1 contains two spring ephemerals (Erythronium and Claytonia) and Group 2 contains one (Dentaria).

The constellation diagram for Baker Woodlot selected quadrats suggests two barely distinct groups interconnected by very highly significant negative associations. Group 1 contains Claytonia, Dentaria, Polygonatum, Cryptotaenia, Trillium, Viola pubescens, Galium aparine L., Viola sororia, Osmorhiza and Sanicula gregaria while Group 2 consists of the remaining positively and negatively associated species.

Certain significant associations shown by this technique and at this quadrat size (1m x 1m) also are significant with other sampling techniques and at other quadrat sizes. (See Table 6). For example, the temporal association between Claytonia virginica and Viola pubescens is significant not only in Baker and Toumey Woodlots with the 1m x 1m quadrat size, but also in the 5m x 5m Baker Woodlot quadrats and in the Bear Lake Natural Area and Sandhill Woodlot $\frac{1}{2}$m x $\frac{1}{2}$m quadrats. (For further discussion see page 39).

Contiguous Quadrat Technique

Significant Cole's Index of Interspecific Association values from Baker Woodlot contiguous quadrat data are shown in matrix form in Table 7. A constellation diagram (Figure 3) indicates very highly significant association values. A list showing per cent frequency of each species is shown in Table 3. Figure 4 indicates the species frequency per quadrat and is a measure of quadrat diversity. The following generalizations are based on these data.

Association analysis by Cole's Index resulted in 321 (or 27.3%) significant values out of a total of 1176, 2 x 2 contingency tables computed. Of these values 50.8% were very highly significant.

Positive temporal associations between spring and summer species appear to exist between Claytonia and Viola pubescens; Dentaria and Galium triflorum; Dentaria and Viola sororia; Erythronium and Galium triflorum Michx.; Erythronium and Uvularia; Erythronium and Viola sororia; Erythronium and Lindera; Erythronium and Botrychium virginianum (L.) Sw. and Erythronium and Circaea. Negative temporal relationships appear to exist between Claytonia and Arisaema; Dentaria and Prunus

Table 6. Significant positive and negative (-) associations between spring ephemerals and other species at various quadrat sizes as determined by Chi-square *(p=.05) **(p=.01) ***(p<.005) 0=no significant correlation

Species Comparisons	Sample Size: 196	190	400	200	200	200	200	200
Quadrat Size	½x½m	1x1m	5x5m	½x½m	1x1m	½x½m	½x½m	½x½m
	Baker			Toumey		Bear Lake	Sandhill	Hudson
Claytonia vs. *Arisaema*		-***	-***		-***			
Claytonia vs. *Dentaria*		***				***		
Claytonia vs. *Erythronium*	***			***	***		***	***
Claytonia vs. *Viola pubescens*		**	*		***	***	*	
Dentaria vs. *Erythronium*			***	*		*		**
Dentaria vs. *Smilacina*		-*				***		
Erythronium vs. *Galium aparine*		*	**				*	
Erythronium vs. *Geranium*	*	***						
Erythronium vs. *Solidago*		*				-*		
Erythronium vs. *Viola pubescens*					***		***	
Erythronium vs. *Viola sororia*		*	***					

Table 7. Frequency and positive and negative (-) Cole's Index coefficients from Baker Woodlot contiguous quadrat data. Significance determined by Chi-square. *(p=.05). **(p=.01). ***(p < .005). O=no significant correlation.

	Aster	Botrychium v.	Carex spp.	Caulophyllum	Circaea	Claytonia	Collinsonia	Cryptotaenia	Erythronium	Galium a.	Galium t.	Geranium	Helianthus	Phryma	Polygonatum	Polygonum	Prenanthes	Sanicula g.	Sanicula t.	Smilacina
Actaea									-.174						.157				.471	
Amphicarpa	.233	.289	.268		.368		.368	.587			.399	.197	.251			.563	.456	.815	.232	
Arisaema				.383		-1.00			-.249						.728					
Aster			.368		.392			.425			.218			.307		.815	.147		.368	
Botrychium v.			.136	-.255	.160		.213		.437		.333			.125			.258	.581	.145	
Carex spp.				-.266				.246		-.709	.237	.327				.213	.339		.231	.173
Caulophyllum									-.312		-.377				.155		-.184			.258
Circaea							.243	.248	.276		.573					.374	.735			
Claytonia																				
Collinsonia								.343			.383		.312	.179		.368	.428		.117	.134
Cryptotaenia									-.235		.522	.253		.134		.433	.399	.648	.292	
Dentaria									.234		1.000									
Erythronium										.320	.735									
Galium a.																			-.358	
Galium t.												.160	.334	.195		.759	.428			
Geranium																.329			.162	.182
Geum																				
Helianthus																.603	.158			.166
Osmorhiza c.																				
Phryma																.189			.255	
Polygonatum																				.403
Polygonum																	.735			
Prenanthes																				
Sanicula g.																				
Sanicula t.																				
Smilacina																				
Solidago																				
Trillium																				
Uvularia																				
Viola p.																				
Viola s.																				
Acer r.																				
Carya																				
Cornus																				
Euonymus																				
Fagus																				
Fraxinus																				
Lindera																				
Parthenocissus																				
Prunus s.																				
Prunus v.																				
Quercus																				
Sambucus																				
Tilia																				

	Solidago	Trillium	Uvularia	Viola p.	Viola s.	Acer r.	Carya	Cornus	Euonymus	Fagus	Fraxinus	Lindera	Parthenocissus	Prunus s.	Prunus v.	Quercus	Sambucus	Tilia	Toxicodendron	Ulmus	Freq.
Actaea													.160								3[illegible]
Amphicarpa	.556		.272	.837	.577			.303			.373	.362			.138	.288		.495	.268-	.11[illegible]	[illegible]
Arisaema				-.214							-.352			.344				-.355			6.0
Aster	.459			1.000							.703	.669		-.324				.339			5.8
Botrychium v.	.396			.546	.261						.548	.353		-.225			-.233	.242	.160-	.139	26.5
Carex spp.	.374		.448		.357								.249						.174		31.3
Caulophyllum	-.185				-.203														.167	.353	39.3
Circaea	.127				.367		-.142	.231	-.147			.309						.286			42.8
Claytonia				1.000																	99.8
Collinsonia	.367			.586	-.439	.124		.176				.341	.256		.103	.235		.302	.135-	.159	20.8
Cryptotaenia	.224	-.209	.449	.413	.277			.381	-.147			.277			.184	.177	.151	.234	.327		39.5
Dentaria					.346										-.288						92.8
Erythronium			1.000		.434		-.213		-.237			.190	-.300		-.171	-.218				-.326	89.3
Galium a.														-.685						-1.000	98.9
Galium t.	.502			.783	.938			.282	-.411		.820	1.[illegible]		-.513			-.375	.588		-.130	11.3
Geranium	.179		.255		.383							.427	.318		.199					-.193	23.3
Geum			.334-	.126					-.363											-.115	14.8
Helianthus	.515				.711			.217	-.598			.827	.551					.518			5.5
Osmorhiza c.																.355					96.5
Phryma	.197	-.219		.292	.181						.228	.293			.144	.136		.194			31.0
Polygonatum		.232											.388				-.133			-.413	54.0
Polygonum	.538		.480	.213	.273			.339	-.124			.770			.343			.341	.296		54.3
Prenanthes	.385		.273	.852	.343	.224		.366	-.598		.586	.769		-.502	.197			.423		-.173	8.3
Sanicula g.				.161								.209						.573			91.0
Sanicula t.	.144			.443				.309				.510			.223	.279		.384	.140		17.5
Smilacina						.139							.384	-.409	.332			.2[illegible]			12.8
Solidago			.407	.415	.372	.284		.383			.318	.260	.224	-.431	.186		-.188	.288	.384-	.323	43.8
Trillium											-.108				-.360		-.146				32.0
Uvularia					.597			.297	-.474											-.285	5.2
Viola p.							-.202			-.131				-.193	.412			.318			79.5
Viola s.												.332		-.130				.348	.321-	.429	52.8
Acer r.											.626					.218		.343			16.0
Carya								-.259												.436	45.0
Cornus														-.269	.125			.192			19.9
Euonymus												-.269		-.183	.186				-.291		45.3
Fagus																	-.233			-.152	27.0
Fraxinus												.165		-.179			-.289	.432	.451-	.368	70.8
Lindera														-.145				.446	.349		73.8
Parthenocissus																				-.334	59.5
Prunus s.															-.637		.303	-.214		.322	36.5
Prunus v.																.305		.160			20.8
Quercus																		.172			46.5
Sambucus																				.439	56.[illegible]
Tilia																			.194		34.[illegible]

Figure 3. Constellation diagram showing significant Chi-square associations in Baker Woodlot contiguous quadrats ($p=.005$). Positive association ——; Negative association - - -. Group 1. (*Prunus serotina*, *Ulmus*, *Sambucus*); Group 2. (*Prunus virginiana*, *Smilacina*, *Polygonatum*, *Trillium*, *Parthenocissus*, *Arisaema*); Group 3. The remainder.

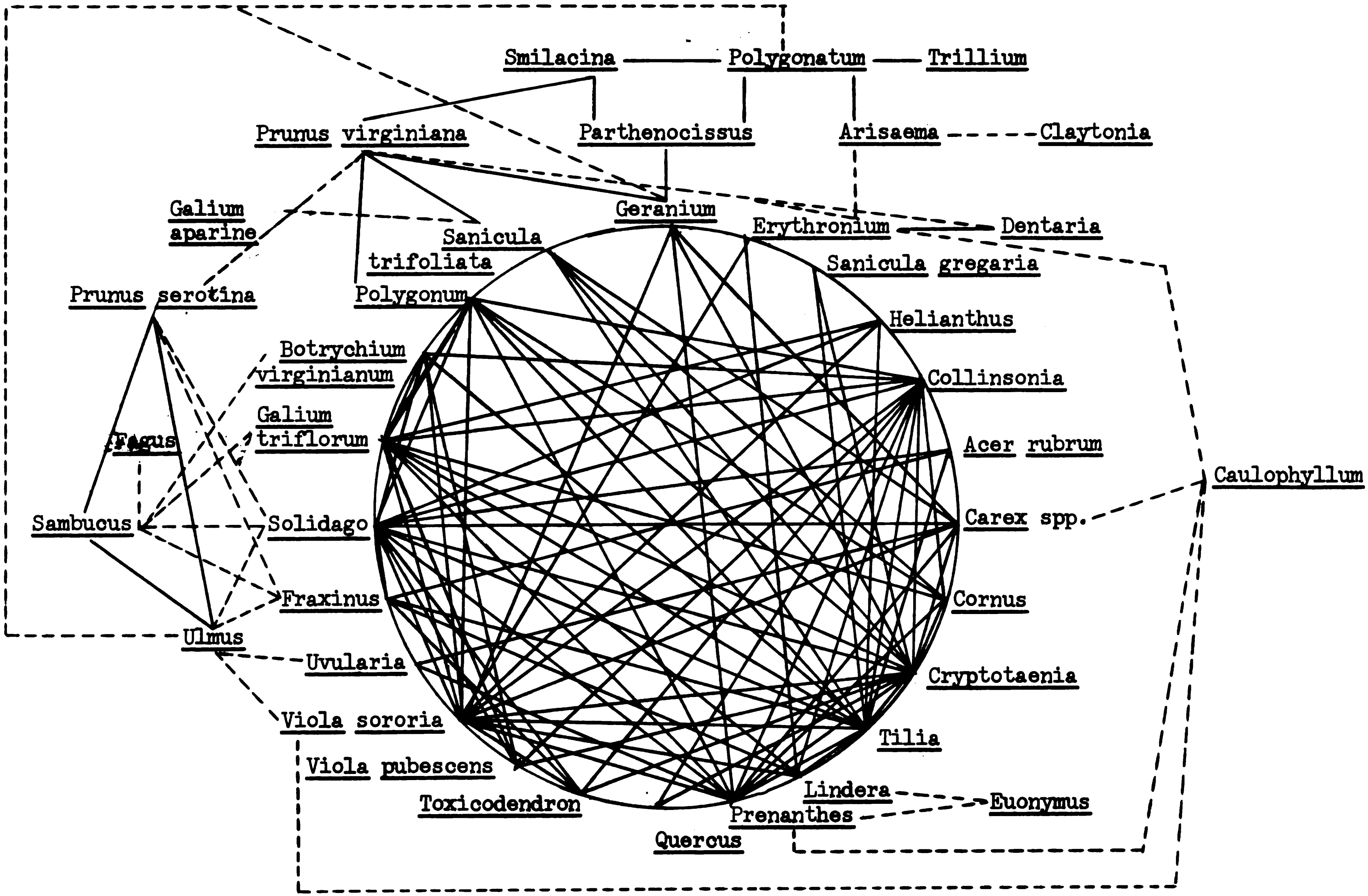
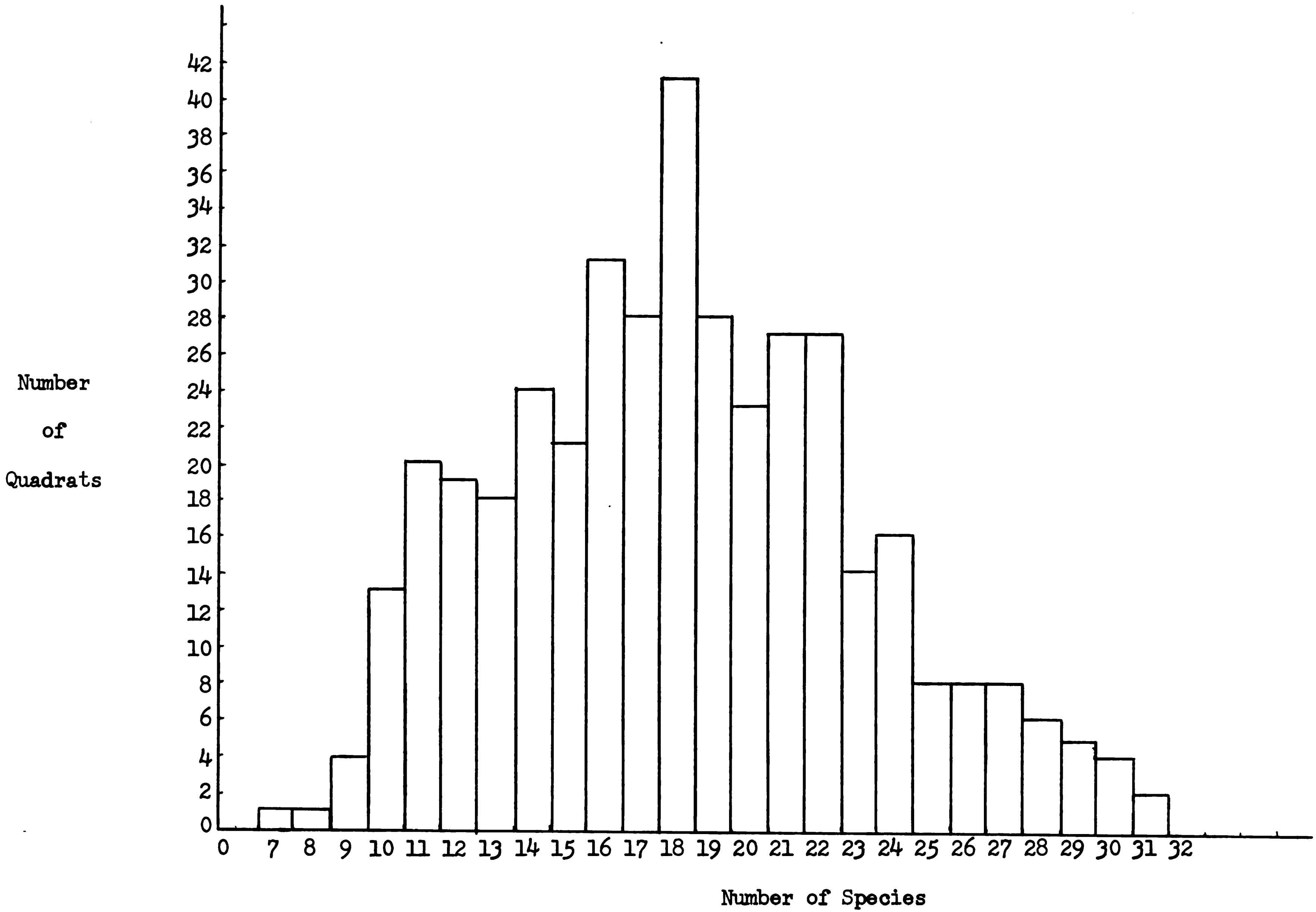

Smilacina
Polygonatum
Trillium
Prunus virginiana
Parthenocissus
Arisaema
Claytonia
Galium aparine
Geranium
Erythronium
Dentaria
Sanicula trifoliata
Sanicula gregaria
Prunus serotina
Polygonum
Helianthus
Botrychium virginianum
Collinsonia
Galium triflorum
Acer rubrum
Fagus
Caulophyllum
Sambucus
Solidago
Carex spp.
Fraxinus
Cornus
Ulmus
Uvularia
Cryptotaenia
Viola sororia
Tilia
Viola pubescens
Lindera
Euonymus
Toxicodendron
Prenanthes
Quercus

Figure 4. Frequency distribution of species as an indication of quadrat diversity in Baker Woodlot contiguous 5m x 5m quadrats.


Number
of
Quadrats
42
40
38
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
0
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
Number of Species

virginiana L., Erythronium and Carya cordiformis (Wang.) K. Koch, Erythronium and Actaea, Erythronium and Euonymus obovatus Nutt, Erythronium and Arisaema, Erythronium and Parthenocissus quinquefolia (L.) Planch., Erythronium and Caulophyllum, Erythronium and P. virginiana, Erythronium and Quercus, Erythronium and Ulmus rubra Muhl., Galium aparine and Sanicula trifoliata Bichn., G. aparine and P. serotina, G. aparine and Ulmus, and G. aparine and Carex spp.

The constellation diagram in Figure 3 indicates that there are three main groups of species interconnected by positive and negative associations. Group 1 is comprised of three positively associated woody species (Prunus serotina, Ulmus rubra, and Sambucus) which are negatively associated with species of Groups 2 and 3. Group 2 contains two woody species (Parthenocissus and Prunus serotina) plus four herbs, none of which are ephemerals (Smilacina racemosa (L.) Desf., Polygonatum, Trillium, and Arisaema). Group 2 is connected to Group 3 by positive associations with Geranium, Sanicula trifoliata and Polygonum virginianum L. and is separated by a negative association with Erythronium.

The existence of high species diversity in the area sampled (1 hectare) is evident in Table 3 as well as on an individual quadrat basis as shown in Figure 4.

Varying degrees of aggregation exemplified by different species is apparent. Such pattern is likely due to vegetative reproduction tempered by past history (such as initial availability of reproductive stock).

Random Quadrat Technique

The results of statistical analysis of the random quadrat data by means of Cole's Index are shown in Tables 8 through 11. An overall comparison of these results for all woodlots studied is provided by Table 12. Constellation diagrams were constructed from this data for Bear Lake Natural Area and Sandhill and Baker Woodlots (Figures 5 through 7) to emphasize the very highly significant associations; however, no diagrams were constructed for Toumey and Hudson Woodlots due to limited data. Table 13 provides coefficients of similarity calculated from per cent frequency data from all random quadrats to provide a measure of stand similarity. The following generalizations are based on these results.

Of the seven spring ephemerals analyzed in the five woodlots, there appears to be several significant temporal associations with later species. *Claytonia* and *Viola pubescens* are positively associated in Bear Lake Natural Area and Sandhill Woodlots, being present together in four of the five stands studied. Of the twenty-seven other significant association values existing between species in single stands, six associations are negative. The high number of significant single-stand correlations between spring ephemerals and summer species is probably partly a function of sampling technique and stand individuality.

Observation of variation in the structure of the ground flora among the five woodlots is supported by these analyses. Variations in species composition and degree of aggregation of species may result in different mosaics of pattern in adjacent stands. A simple single axis ordination (Figure 8) of these coefficients of similarity shows a wide floristic difference on a per cent frequency basis between Hudson and Bear Lake

Table 8. Frequency and positive and negative (-) Cole's Index coefficients from Bear Lake Natural Area random quadrat data. Significance determined by Chi-square *(p=.05) **(p=.01) ***(p<.005) 0=no significant correlation

	Carex spp.	Caulophyllum	Claytonia	Dentaria	Erythronium	Osmorhiza	Polygonatum	P. altissima	S. gregaria	Smilacina	Solidago	V. pubescens	V. sororia	Dicentra cucullaria	Frequency (%)
Allium tricoccum	-.186 *	.581 ***	.451 ***	0	0	.344 *	0	0	.335 *	.344 ***	0	.287 ***	0	0	69.5
Brachy-elytrum erectum	0	0	0	.270 *	0	0	0	.398 ***	.375 *	0	0	0	0	0	11.0
Carex spp.		0	-.283 ***	0	0	0	0	.230 ***	0	0	0	-.337 ***	0	0	31.5
Caulophyllum			.613 ***	0	0	0	0	0	0	.260 *	0	0	0	0	23.5
Claytonia				.596 ***	0	0	0	0	0	.529 ***	-.220 **	.368 ***	0	.588 ***	72.5
Dentaria					.788 *	0	0	0	0	.255 ***	0	0	0	0	31.5
Erythronium						-.429 **	1.000 *	0	0	.686 *	-.307 *	0	0	0	92.5
Polygonatum							0	0	0	0	-.605 ***	0	0	0	27.5
Prenanthes altissima								0	0	0	0	-.212 *	0	0	32.0
Sanicula gregaria									0	0	0	0	0	.251 ***	34.5
Smilacina											-.335 *	.197 *	0	0	42.5
Viola pubescens												0	-.420 ***	0	57.5
Frequency (%)						30.0					23.0		18.0	26.5	

Table 9. Frequency and positive and negative (-) Cole's Index coefficients from Baker Woodlot random quadrat data Significance determined by Chi-square *(p=.05) **(p=.01) ***(p<.005) 0=no significant correlation

Species	Circaea	Erythronium	G. aparine	Geranium	Prenanthes	S. gregaria	Solidago	Trillium	V. sororia	Frequency (%)
Brachyelytrum	.218 *	0	.209 *	0	0	.262 *	.312 ***	0	0	10.2
Circaea	0	0	.152 *	0	0	.186 *	0	0	.423 ***	16.8
Claytonia	0	.702 ***	0	.820 ***	0	0	0	0	- .284 *	95.9
Collinsonia	0	0	0	0	0	0	0	.173 *	0	16.3
Erythronium		0	0	.588 *	0	0	0	0	0	96.4
Galium aparine			0	0	.259 *	0	0	.152 *	0	17.9
Geranium				0	0	.543 ***	0	0	0	69.4
Polygonatum					.258 *	0	0	0	0	16.8
Sanicula gregaria						0	0	0	.248 *	25.5
Solidago							0	0	.266 ***	12.8
Trillium								0	-1.000 *	16.8
Frequency (%)					30.6				12.8	

Table 10. Frequency and positive and negative (-) Cole's Index coefficients from Sandhill Woodlot random quadrat data Significance determined by Chi-square *(p=.05) **(p=.01) ***(p<.005) 0=no significant correlation

	Erythronium	G. aparine	Isopyrum	Osmorhiza	V. canadensis	V. pubescens	V. sororia	D. canadensis	D. cucullaria	Frequency (%)
Claytonia	.608 ***	0	0	0	0	.694 *	0	0	0	91.5
Cryptotaenia	0	0	-.767 ***	.157 *	0	0	0	0	.229 *	11.0
Erythronium	0	.231 *	0	0	0	.318 ***	0	0	0	60.0
Galium aparine		0	.180 *	0	0	.212 ***	0	-.180 *	0	39.0
Isopyrum			0	0	0	0	.323 ***	-.356 ***	0	39.0
Osmorhiza				0	-.851 ***	0	0	0	.333 ***	10.0
Viola canadensis					0	0	-.611 ***	.414 **	0	33.5
Dicentra cucullaria						0	0	-.246 *	0	17.5
Frequency (%)						38.5	23.0		47.0	

Table 11. Frequency and positive Cole's Index coefficients from Toumey Woodlot and Hudson Woodlot random quadrat data Significance determined by Chi-square *(p=.05) **(p=.01) ***(p<.05) 0=no significant correlation

Toumey Woodlot

Species	Erythronium	Viola pubescens	Frequency (%)
Claytonia	.673***	0	94.5
Dentaria	1.000*	.245***	13.0
Frequency (%)	83.5	18.5	

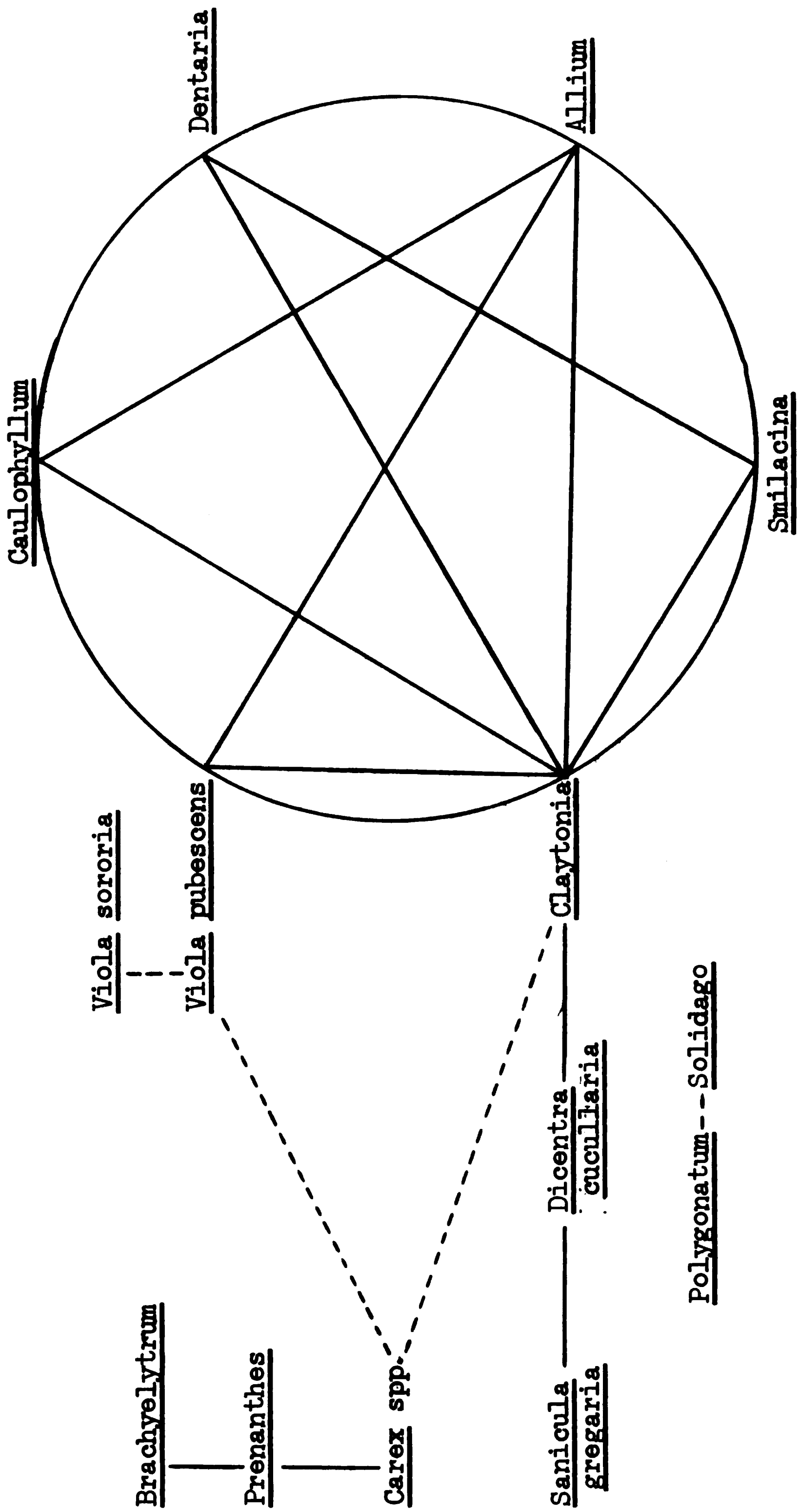
Hudson Woodlot

Species	Erythronium	Frequency (%)
Claytonia	.413***	46.5
Dentaria	.587**	22.0
Frequency (%)	72.5	

Table 12. Positive (upper left) and negative (upper right) significant association values (p <.05) from random quadrat data as related to the number of stands in which both species of the pair being tested are found (lower value).

Species	Brachyelytrum	Carex spp.	Caulophyllum	Circaea	Claytonia	Collinsonia	Cryptotaenia	Dentaria	Erythronium	G. aparine	Geranium	Isopyrum	O. claytoni	Prenanthes	Polygonatum	S. gregaria	Smilacina	Solidago	Trillium	V. canadensis	V. pubescens	V. sororia	D. cucullaria	D. canadensis
Allium tricoccum	0-0/3	0-1/2	1-0/2	0-0/3	1-0/2	0-0/0	0-0/3	0-0/2	0-0/2	0-0/2	0-0/1	0-0/1	1-0/2	0-0/1	0-0/2	1-0/2	1-0/2	0-0/1	0-0/1	0-0/2	1-0/2	0-0/2	0-0/2	0-0/2
Brachyelytrum erectum		0-0/3	0-0/3	1-0/3	0-0/3	0-0/1	0-0/3	1-0/3	0-0/3	1-0/3	0-0/2	0-0/1	0-0/3	1-0/2	0-0/3	2-0/3	0-0/3	1-0/2	0-0/2	0-0/2	0-0/3	0-0/3	0-0/2	0-0/2
Carex spp.			0-0/3	0-0/4	0-1/3	0-0/1	0-0/3	0-0/3	0-0/3	0-0/3	0-0/2	0-0/1	0-0/3	1-0/2	0-0/3	0-0/3	0-0/3	0-0/2	0-0/2	0-0/2	0-1/3	0-0/3	0-0/2	0-0/2
Caulophyllum thalictroides				0-0/3	1-0/2	0-0/1	0-0/3	0-0/2	0-0/3	0-0/3	0-0/2	0-0/1	0-0/3	0-0/2	0-0/3	0-0/3	1-0/3	0-0/2	0-0/2	0-0/3	0-0/3	0-0/3	0-0/2	0-0/2
Circaea quadrisulcata					0-0/5	0-0/1	0-0/3	0-0/5	0-0/5	1-0/4	0-0/2	0-0/5	0-0/3	0-0/2	0-0/3	1-0/3	0-0/3	0-0/2	0-0/2	0-0/4	0-0/4	1-0/4	0-0/2	0-0/2
Claytonia virginica						0-0/1	0-0/3	1-0/5	4-0/5	0-0/4	1-0/2	0-0/1	0-0/3	0-0/2	0-0/4	0-0/3	1-0/3	0-1/2	0-0/2	0-0/4	2-0/4	0-1/4	1-0/2	0-0/2
Collinsonia canadensis							0-0/1	0-0/1	0-0/1	0-0/1	0-0/1	0-0/0	0-0/1	0-0/1	0-0/1	0-0/1	0-0/1	0-0/1	1-0/1	0-0/0	0-0/1	0-0/1	0-0/0	0-0/0
Cryptotaenia canadensis								0-0/3	0-0/3	0-0/3	0-0/2	0-1/1	1-0/3	0-0/2	0-0/3	0-0/3	0-0/2	0-0/3	0-0/2	0-0/2	0-0/3	0-0/3	1-0/2	0-0/2
Dentaria laciniata									2-0/5	0-0/4	0-0/2	0-0/1	0-0/3	0-0/2	0-0/4	0-0/3	1-0/3	0-0/2	0-0/2	0-0/4	1-0/4	0-0/4	0-0/2	0-0/2
Erythronium americanum										1-0/4	1-0/2	0-0/1	0-1/3	0-0/2	1-0/4	0-0/3	1-0/3	0-1/2	0-0/2	0-0/4	1-0/4	0-0/4	0-0/2	0-0/2
Galium aparine											0-0/2	1-0/1	0-0/3	1-0/2	0-0/4	0-0/3	0-0/3	0-0/2	1-0/2	0-0/3	1-0/4	0-0/4	0-0/2	0-1/2
Geranium maculatum												0-0/0	0-0/2	0-0/2	0-0/2	1-0/2	0-0/2	0-0/2	0-0/1	0-0/1	0-0/2	0-0/2	0-0/1	0-0/1
Isopyrum biternatum													0-0/1	0-0/0	0-0/1	0-0/1	0-0/1	0-0/0	0-0/1	0-0/1	0-0/1	1-0/1	0-0/1	0-1/1
Osmorhiza claytoni														0-0/2	0-0/3	0-0/3	0-0/3	0-0/2	0-0/2	0-0/2	0-0/3	0-0/3	1-0/2	0-0/2
Prenanthes altissima															1-0/2	0-0/2	0-0/2	0-0/2	0-0/1	0-0/1	0-1/2	0-0/2	0-0/1	0-0/1
Polygonatum pubescens																0-0/3	0-0/3	0-1/2	0-0/2	0-0/3	0-0/4	0-0/4	0-0/2	0-0/2
Sanicula gregaria																	0-0/3	0-0/2	0-0/2	0-0/2	0-0/3	1-0/3	1-0/2	0-0/2
Smilacina racemosa																		0-1/2	0-0/2	0-0/2	1-0/3	0-0/3	0-0/2	0-0/2
Solidago caesia																			0-0/1	0-0/1	0-0/2	1-0/2	0-0/1	0-0/1
Trillium grandiflorum																				0-0/1	0-0/2	0-1/2	0-0/1	0-0/1
Viola canadensis																					0-0/3	0-1/2	0-0/2	1-0/2
Viola pubescens																						0-1/4	0-0/2	0-0/2
Viola sororia																							0-0/2	0-0/2
Dicentra cucullaria																								0-1/2

Figure 5. Constellation diagram showing significant Chi-square associations in Bear Lake Natural Area random quadrats ($p < .005$). Positive association ——; negative association - - -. Group 1. (Brachyelytrum, Prenanthes, Carex spp.); Group 2. (Polygonatum, Solidago); Group 3. The remainder.


Dentaria
Allium
Caulophyllum
Smilacina
Viola pubescens
Claytonia
Viola sororia
Viola pubescens
Claytonia
Dicentra cucullaria
Polygonatum--Solidago
Brachyelytrum
Prenanthes
Carex spp.
Sanicula gregaria

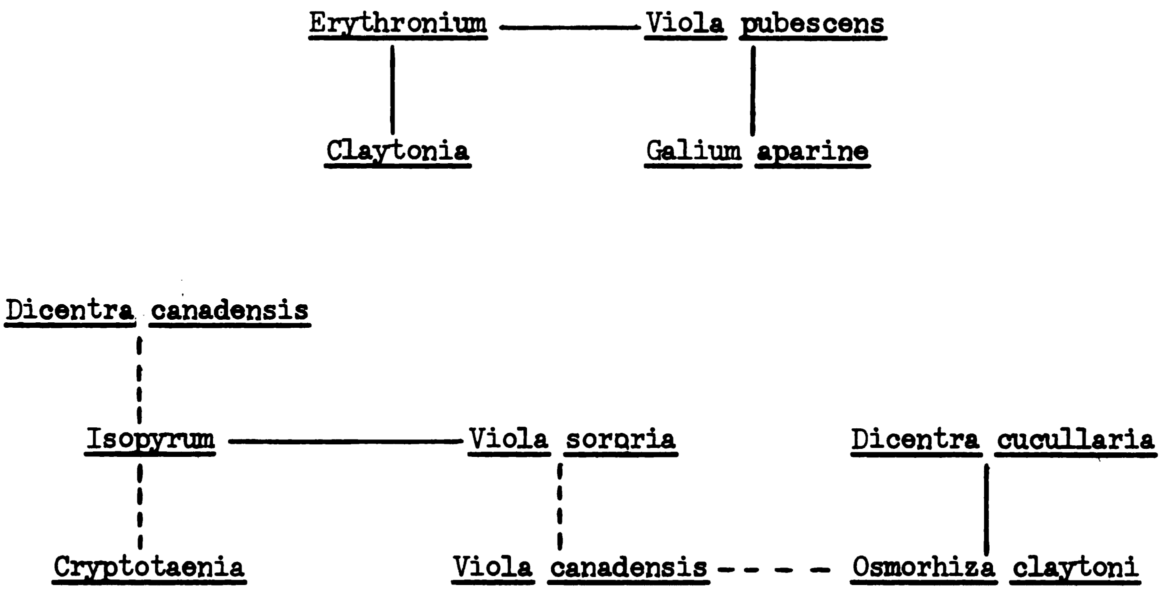


Figure 6. Diagram showing significant Chi-square associations in Sandhill Woodlot random quadrats ($p < .005$). Positive association ——; negative association - - -. Group 1. (Erythronium, Claytonia, Viola pubescens, Galium aparine); Group 2. The remainder.

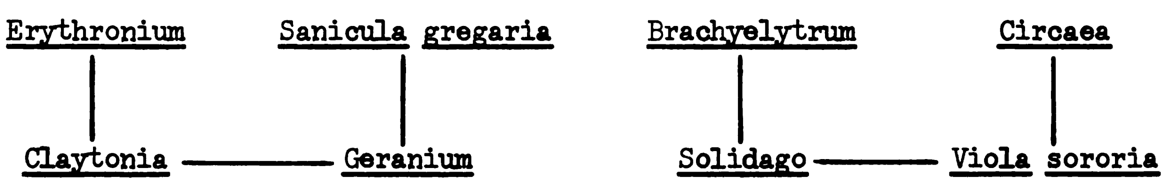


Figure 7. Diagram showing significant Chi-square associations in Baker Woodlot random quadrats ($p < .005$). Positive association ——. Group 1. (Claytonia, Erythronium, Geranium, Sanicula gregaria; Group 2. The remainder.

Table 13. Matrix of coefficients of similarity calculated from per cent frequency data from all random quadrats.[6]

Woodlot	Hudson	Bear Lake	Baker	Sandhill	Toumey
Hudson	0	.336	.357	.398	.712
Bear Lake		0	.609	.469	.434
Baker			0	.502	.538
Sandhill				0	.538
Toumey					0

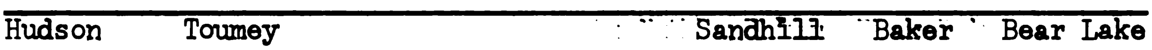


Figure 8. Single axis ordination of coefficients of similarity.

[6] See Appendix B for calculation of coefficient of similarity.

Natural Area while the other stands show progressively greater or lesser correlation with these end points or "reference stands" depending on their relative positions along the axis.

Association analysis by Cole's Index provided thirty-five very highly significant values out of 300, 2 x 2 contingency tables computed from random quadrat data for all five woodlots.

The constellation diagram constructed from Bear Lake Natural Area data (Figure 5) indicates the presence of three groupings of species. Group 1 consists of Brachyelytrum erectum (Schreb.) Beauv., Prenanthes altissima L. and Carex spp. interconnected to Group 3 by negative associations between Carex spp. and Claytonia and between Carex spp. and Viola pubescens. Group 2 is an outlyer consisting of Polygonatum and Solidago and has no significant positive associations with species of either of the other two groups. Species groupings are also suggested in diagrams from Sandhill Woodlot and Baker Woodlot data.

The number of positive associations among ephemeral species was greater than the number of negative associations (nine positive vs. two negative). This trend is also found among summer species (twenty-six positive vs. nine negative associations).

DISCUSSION

Association and Pattern Effects

No clear distinction has been made in the preceeding paragraphs between association and pattern effects. The idea that these two effects are distinctly separable is not entirely valid, being largely dependent on the scale of the pattern being discussed (see page 51). Kershaw (1964) listed four major causes of association among plants, namely:

1. similarities and differences in environmental requirements,
2. modification of the environment by one species allowing the establishment of other species,
3. production of toxic substances by plants,
4. competition.

Yet these causes of association are in many ways similar to Kershaw's (1964) list of causes of pattern, which are:

1. vegetative spread,
2. heavy seeds,
3. cyclical regeneration in patches,
4. major and minor discontinuities caused by changes in environmental variables (soil moisture, soil depth, etc.),
5. species to species interaction.

Kershaw (1964, p. 122) specifically relates this last category (referred to as "sociological pattern") to causes of association when he states:

> The causal factors of sociological pattern are not only dependent on the competitive ability of an individual (which may also be, in part, dependent on the micro-environment), but also on the possible presence of toxins exuded by an individual, and its age.

In many communities aggregated species will necessarily show positive or negative associations with other species due to the nature of overlapping similarities and differences in habitat requirements alone (Hurlbert, 1969). That such overlapping ecological requirements are important in determining the structure of the herbaceous ground flora is shown by the results of analysis of the contiguous quadrat data from Baker Woodlot. Too large to show competitive or allelopathic interactions between component species, the 5m x 5m quadrat size used apparently provides a good measure of similarities and differences in micro-habitat requirements among associated species (this was also pointed out by Struik and Curtis, 1962).

Variations in the degree of aggregation among species often results in differing scales of pattern. Bray (1956) recognized three levels of vegetational pattern: 1. geographic, 2. communal and 3. interspecific. The first is a function of the geographic distribution of species and their mutual occurrence within the same geographic area. The second refers to species interaction within the community as a whole when such a community exists in a homogeneous geographic area. The third category refers to pattern which is the result of direct reaction of species with each other within defined communities. The pattern we are concerned with here falls in the latter two categories.

The most probable causes of such medium and small scale pattern in woodland situations include vegetative reproduction, heavy seeds, past history (such as initial availability of reproductive stock and disturbance effects), and interaction of species on species and individuals on individuals (or "sociological pattern"). In relation to sociological pattern Kershaw (1964, p. 122) states:

> These small-scale sociological effects often take the form of a mosaic of patches of different density levels dynamically related to each other in time and space.

This is particularly appropriate in the present study. One mosaic of aggregated species populations exists in the early spring and overlaps with a second mosaic of summer species populations. That these phenophasic species groups are related to one another was shown by association analysis by Cole's Index of Interspecific Association.

Temporal Associations and The Temporal Niche

The existence of patterns and associations among plant species is largely a function of time. Successional stages composed of different species arrays have progressed in undisturbed habitats to a "mature" steady state--the "climax community"--where niche differentiation is most pronounced. Whittaker (1970, p. 35) states that:

> ... species have evolved in relation to one another,...they influence one another's populations,...some are competing, and...these will have evolved in such ways that competition is reduced by niche differentiation.

If we accept this premise of reduction of interspecific competition in mature systems by niche divergence, we can perhaps apply these ideas to association and pattern effects (both temporal and spatial) among woodland species. For instance, temporal associations indicated in this study may in large part be due to the development of temporal niches. This would allow two or more positively associated species to draw upon the resources of a given area at different times during the growing season and thus limit interplant interference effects. For example, Claytonia virginica (a spring ephemeral) and Viola pubescens (a "summer" species) were shown to be significantly positively associated at three quadrat sizes by association analysis. It therefore appears that temporal niche differentiation allows both species to have similar environmental requirements yet allows them to exist in close proximity without strong competition for limiting resources.

Spatial niche divergence also allows positive association among species with similar phenophases. For example, it was noted that some species (Trillium grandiflorum for example) possess underground storage organs (corms, bulbs, tubers, rhizomes) that normally exist at depths in excess of 10 cm while other species (Polygonatum pubescens for example) possess structures which lie at shallower depths (0 - 10 cm). Thus it is conceivable that such summer species could exist together in the same general area and yet avoid competition by drawing upon resources at different soil depths. Although such spatial relations were computed by association analysis in this study and are listed in the foregoing tables, their interpretation has been a limited part of this study.

Negative Associations and Allelopathic Influences

The existence of negative associations (temporal and spatial) probably involves a more detailed explanation, since such associations may be a function of different habitat requirements, competition effects, or production of allelopathic exudates which might tend through time to exclude species from sites already preempted by another species. Two species having similar habitat requirements and phenophases and growing in the same area would be expected to compete with each other for the available resources. If one species gained a slight advantage over the other in securing these requirements, eventually we would expect this species to eliminate its competitor, possibly leading to a negative association between these species (Smith and Cottam, 1967). This probably explains some of the negative associations existing between species within the same phenophasic grouping as indicated in the analysis of random quadrat data (two negative associations among spring ephemerals and nine among summer species). The reason that more species are not negatively associated within groups is probably due to spatial niche differentiation which tends to reduce competition. It is suggested that certain significant negative temporal associations may arise from allelopathic inhibitions of certain species by another, especially with densely aggregated species. For example, Claytonia and Arisaema triphyllum were found to be negatively associated at the 5m x 5m and the 1m x 1m quadrat sizes in Baker and Toumey Woodlots. An explanation of such a phenomenon might include the possible production of some toxic substance by Arisaema which somehow eliminates or inhibits the tubers of Claytonia when they grow too close to an established individual. Or perhaps the seedlings of Arisaema do not survive in a dense Claytonia aggregation due to the presence of some allelopathic substance produced by Claytonia. An alternate explanation of the latter relationship is that Arisaema seedlings cannot proliferate in densely packed Claytonia aggregations because of the finite space available. A third possibility is that the two species have dissimilar environmental requirements. However, in regard to the last suggestion, cursory observations make it difficult to imagine that sites containing Arisaema differ appreciably from sites containing Claytonia.

The importance of allelopathy in affecting associations between species is also suggested in the case of Podophyllum peltatum, although dense foliage present from the early spring through the middle of the summer may in itself strongly influence the ability of other species to occur within a clone. Significant negative, temporal associations were found between Podophyllum vs. Erythronium, and Podophyllum vs. Dentaria while significant negative spatial associations were noted with Podophyllum vs. Geranium, Viola pubescens, Solidago, Sanquinaria and Arisaema at the 1m x 1m quadrat size in Baker and Toumey Woodlots. No significant positive associations were found between Podophyllum and other species. Thus the production of rhizome or root exudate coupled with dense foliage effects is probably the best explanation for negative associations since dissimilarities in habitat requirements are highly unlikely.

Interstand Floristic Similarity

Variation in floristic composition between stands present in the same geographical area such as found in this study is not uncommon (Braun, 1950; Smith and Cottam, 1967). Differences may be attributable in part to variations in past history, soil type, soil moisture, topography, natural and man-made disturbances (grazing, fires, logging), distance from seed source and selective predation. A coefficient of similarity applied to the random quadrat data shows a wide floristic difference on a percent frequency basis between Hudson Woodlot and Bear Lake Natural Area and a high floristic similarity between Hudson and Toumey Woodlots. The Sandhill and Baker Woodlots and Bear Lake Natural Area were clumped together on one end of the single axis ordination thus showing floristic similarity. The lack of similarity between Hudson Woodlot and the other three areas was traced to differences in the past history of these areas. It seems that Hudson has suffered from grazing and rooting by pigs, which likely resulted in partial destruction of the ground flora. This flora is only now beginning to redevelop. The other woodlots, on the other hand, have never been grazed and thus possess long-standing populations. The reason for the similarity between populations in Toumey and Hudson Woodlots is probably related to topography. The Toumey transects were located in relatively dry upland soils which tends to reduce diversity. Thus the two areas, while differing in degrees of disturbance, may appear to be floristically similar for different reasons.

Differences in degrees of aggregation among species in the five woodlots studied were also noted. Some areas contained widespread populations of a particular species (Erythronium, for example) while in other areas these species exist in discrete patches separated by sparsely vegetated sites. Generally, more species appeared to exist in clumped or contagious groupings than as randomly distributed arrays.

That some spring ephemerals can be very common in one woodlot and completely lacking in surrounding woodlots is often difficult to explain. Mechanisms of long distance dispersal for the spring ephemerals studied are particularly puzzling since most reproduction is currently vegetative. This can result in only a limited areal spread per growing season (Whitford, 1951). However, vegetative reproduction was probably not always the predominant means of population expansion since such a mechanism could not possibly account for present distribution patterns in glaciated areas even if we allow a full 12,000 years with maximum yearly rhizome growth.

Perhaps there are less obvious seed dispersal mechanisms that are important. For example, the presence of insect attracting tissues (caruncle) produced on the surface of seeds and special modifications of the plants themselves which aid in "presenting" the seeds to insects (such as the bending down of mature capsules in Sanquinaria) may help to explain some dispersal patterns (van der Pijl, 1969). Among those species studied, dutchman's breeches, trout-lily, bloodroot and trillium possess this caruncle adaptation. The prevalence of herbaceous summer species is more easily understood in light of their seed and fruit adaptations for animal and wind dispersal (the latter mainly in gap-phase species) combined with asexual reproduction.

While stand composition may vary in the same general locality, a comparison of average percent frequency values of the species noted in this study with results of other ground flora investigations indicates that the woodlots sampled are fairly typical of maple-beech-mixed hardwood stands in the mid-west (Cain, 1935; Williams, 1936; Potzger, 1940; Curtis, 1959). However, an interesting by-product of the analysis of the Baker Woodlot contiguous quadrat data was the high species richness in the area sampled (101 species in the 1 hectare area) as well as on an individual quadrat basis (range of 7-32 species per 5m x 5m quadrat). Such diversity does not appear to be typical for a mature maple-beech-mixed hardwoods stand and probably reflects the influence of human disturbance combined with topographical heterogeneity (such as large numbers of tip-up mounds).

Quadrat Size

The importance of interpreting results of any sampling technique as a function of quadrat size has been stressed by many researchers (for example, Curtis and McIntosh, 1950; Goodall, 1952; Kershaw, 1964; Pielou, 1969). It is obvious that the larger the quadrat size the greater the chance that positive associations will be found. Also, as quadrat size decreases it will approach individual plant size and result in negative associations since no two plants would be able to utilize the same finite space (Williams and Lambert, 1959; Dawson, 1951). Ideally for association analysis, quadrat size should be larger than the smallest individuals present but no larger than the scale of interaction of the species with one another or with habitat variables (Greig-Smith, 1964). But since it is impossible to vary quadrat size to fit each size class of plant and since the scale of pattern is not easily detected it is usually best to use several quadrat sizes and interpret results of association analysis with this in mind. Results of this study seem to indicate that the 1m x 1m and the 5m x 5m quadrats were too large to reflect interplant interference effects and thus most associations were related to similarities and differences in habitat requirements. The presence of associations (temporal and spatial) as indicated thru the use of the random quadrats is of interest considering the ($\frac{1}{2}$m x $\frac{1}{2}$m) quadrat size and the large sample size (total of 996 quadrats). At this quadrat size, interplant influences should be important and competition for limiting resources sharp resulting in biologically meaningful associations. Twenty-eight significant temporal associations were found at this quadrat size, six of which were negative associations. Such relationships can be related to niche differentiation, competition and allelopathic influences as mentioned above.

Constellation Diagrams

The technique of showing very highly significant associations between species by means of constellation diagrams provides insight concerning species assemblages. Often species that occur together in groups have similar habitat requirements and are negatively associated with members of other groups having different requirements. Agnew (1961) constructed similar diagrams to show species interrelationships based on interspecific correlation and found that the resulting groups were well aligned with such habitat features as pH.

The constellation diagram from the Toumey Woodlot selected quadrats suggests two groupings of species, both groups containing spring ephemerals. The most likely explanation of the distinctiveness of the groupings is that the species of Group 1 (Claytonia, Erythronium and Viola pubescens) were mainly limited to upland well-drained sites in the western half of the woodlot while those of Group 2 (Sanguinaria, Dentaria and Viola canadensis) occured mainly in the less well-drained lowland areas in the eastern half. The constellation diagram based on the Baker Woodlot selected quadrats does not suggest any sharp differences between species grouping even though two groups were arbitrarily designated. General uniformity of habitat and quadrat size is probably responsible for the large number of significant positive associations.

The constellation diagram from the Baker Woodlot contiguous quadrat data indicates the presence of three distinct species groups. Group 1 is made up entirely of woody species (Prunus serotina, Ulmus rubra and Sambucus pubens). Group 2 contains six species, one of which is a tree (Prunus virginiana), another a woody vine (Parthenocissus quinquefolia) and the rest aestival herbs (Smilacina, Polygonatum, Trillium and Arisaema). This group is interconnected to Group 3 by three positive associations, but is negatively associated with Group 1. The reasons for associations between herbs and woody plants are not clear. Associations among woody species can be related to similarities and differences in microhabitat requirements, as can associations between most of the herbaceous species.

Finally, constellation diagrams from Bear Lake Natural Area and Sandhill and Baker Woodlot random quadrat data indicate several groupings of species on the basis of association analysis. Negative temporal associations (Claytonia vs. Carex spp. and Isopyrum biternatum vs. Cryptotaenia canadensis) may be due to the influence of allelopathic effects coupled with space limitations or competition, while positive temporal associations are probably the result of aforementioned niche differentiation coupled with similar site requirements.

Limitations of Sampling Techniques and Measures of Association

Any sampling procedure that involves a subjective designation of sampling units runs the risk of producing results that are difficult to interpret. This was found to be somewhat of a problem with the selected quadrat technique since quadrat selection was non-random and quadrats were not independent of each other. Nevertheless such a technique provides a measure of association between those species of special interest while excluding sites which may provide little useful information pertaining to temporal associations.

The contiguous quadrat technique is usually used for the detection of various scales of pattern although it has been utilized in detection of association (Struik and Curtis, 1962; Kershaw, 1964). However, Piélou (1969, p. 178) stated that such a technique might affect the interpretation of association due to the confounding effects of quadrat spacing and quadrat size. While this may be true, in this study the technique was used more as a measure of detecting the presence of certain associations on a large scale without being overly concerned with the detection of various scales of pattern or with the interpretation of the biological significance of the results. As it turned out, this technique seems to be a poor means of detecting association resulting from interplant influences, at least at the quadrat size used (5m x 5m).

The random quadrat technique coupled with rather small quadrat size probably provides the best basis for a measure of association, at least statistically speaking. Nevertheless this must be balanced with the fact that much of the data collected may not add to the detection of temporal association since this method often results in the collection of data from plots having no spring and/or summer species present. Such information concerning mutual non-occurrence of two species expresses itself in a 2 x 2 contingency table in the form of "inflated" or over-represented "d" categories which some researchers say produces significant associations when there is no biological basis for such an association (see discussion page 4).

There has been some controversy as to whether the Chi-square test is suitable as a measure of interspecific association (Hurlbert, 1969) although it has been used as such by Williams and Lambert (1959). One of the problems appears to be that the test is sensitive to the total number of quadrats sampled. In the present study the number of quadrats was sufficiently large and uniform in both woodlots (approximately 200, 1m x 1m quadrats in each) so that this was not considered a problem. Also, the Chi-square test was applied to the selected quadrats only to test whether species pairs were independent of each other, this being the null hypothesis for the comparisons being made. Another criticism of Chi-square is that it is sometimes influenced by the species frequencies (Hurlbert, 1969).

It appears that the above-mentioned problems are offset by the fact that the test can be used as a measure of association when the quadrats are non-random (Grieg-Smith, 1964). Even more importantly, the commonly used measure to detect the relative degree of association between species (Cole's Index) utilizes the Chi-square test anyway, to test the significance of the Cole coefficients.

Cole's Index is based on the assumption that each change in the number of joint occurrences between two species represents a constant increment in the amount of observed associations between the species. Its value provides the realized proportion of the possible association which might have been obtained (Cole, 1949). This index has been used widely to detect the relative degree of association among plants, even though it was originally applied as a measure of association between parasites on rats. The main disadvantage of using this index is that it is based on presence-absence data alone which precludes a measure of the relative abundance of interacting individuals. Thus density-dependent interactions affecting the presence of interspecific association may go undetected. It must also be stressed that such a measure of association gives no information concerning the causes of association. Further experimental work is necessary before general statements concerning cause-affect relations are biologically meaningful.

SUMMARY AND CONCLUSIONS

This study describes the presence of interspecific associations among species in five woodlots on the campus of Michigan State University, East Lansing, Ingham County, Michigan.

Sampling of the flora was done during portions of the 1970 and 1971 growing seasons. Three sampling techniques and three quadrat sizes were used. Presence or absence of selected species was the criterion used in the sampling. Chi-square and/or Cole's Index of Interspecific Association were used to detect presence and/or degree of association. While all significant associations which were detected by these statistical tests were recorded, emphasis was placed on the interpretation of temporal associations, that is, associations existing between spring ephemerals and summer species.

Results were interpreted in relation to quadrat size used, differences in species frequencies, and special limitations of the selected, contiguous and random quadrat techniques. For example, the 1m x 1m and 5m x 5m quadrat sizes used probably were too large to detect direct interplant influences and thus associations were interpreted as a function of similarities and differences in habitat requirements between the involved species. Wide differences in per cent frequency between two species may inflate the significance level of Cole's Index values due to the nature of the Chi-square test. The limitations of non-random sampling were discussed in relation to the selected quadrat technique employed. The major conclusions drawn from this study are listed below.

1. The large number (475 out of 1674, 2 x 2 tables or 28%) of significant Chi-square and Cole's Index values indicate that inter-

specific association is common in most of the stands studied at the quadrat sizes used.

2. Temporal associations exist between species both on a single and multiple stand basis. Positive associations probably result from similar habitat requirements combined with temporal niche differentiation while allelopathic influences are suggested as explanations for certain negative associations.

3. Certain species assemblages detected by association analysis and emphasized by constellation diagrams appear to exist only within particular woodlots. This is probably indicative of stand individuality due to variations in past history (including disturbance effects), topography and soils.

4. Random quadrat data indicate that many species are highly clumped, densely aggregated patches being separated by rather sparsely vegetated areas. The most probable cause of such clumped vegetational patterns in mature woodland situations is the tendency for vegetative reproduction to produce dense aggregations.

5. Further research is suggested in an attempt to ascertain actual biological causes of temporal associations between selected species. Smaller quadrat dimensions based on average plant size are suggested to accentuate interplant influences. Quantitative data such as biomass determinations or other abundance estimates perhaps would provide more meaningful results when coupled with the techniques utilized in this study.

LITERATURE CITED

Agnew, A. D. Q. 1961. The ecology of Juncus effusus L. in North Wales. Jour. Ecology. 49:83-102.

Ashby, E. 1935. The quantitative analysis of vegetation. Ann. Bot. 49:779-802.

Barton, L. V. and E. M. Schroeder. 1942. Dormancy in seeds of Convollaria majalis L. and Smilacina racemosa (L.) Desf. Cont. Boyce Thompson Inst. 12:277-300.

Barton, L. V. 1944. Some seeds showing special dormancy. Boyce Thompson Inst. 13:259-271.

Barton, L. V. and W. Crocker. 1948. Twenty years of seed research. Faber & Faber, Ltd., London. 148 pp.

Blodgett, F. H. 1900. Vegetative reproduction and multiplication in Erythronium. Torrey Bot. Club. 27:305-315.

Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner Pub. Co., Darien, Conn. 596 pp.

Bray, J. R. 1956. A study of the mutual occurrence of plant species. Ecology. 37:21-28.

Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325-349.

Byer, M. D. 1960. An analysis of pattern and interspecific association along a soil moisture gradient on the jack pine plains of northern lower Michigan. M.S. Thesis, Michigan State University. 257 pp.

Cain, S. A. 1935. Studies on virgin hardwood forest: III. Warren's Woods, a beech-maple climax forest in Berrien Co., Michigan. Ecology. 16:500-513.

Cain, S. A. and F. C. Evans. 1952. The distribution patterns of three plant species in an old-field community in southeastern Michigan. Cont. Lab. Vert. Biol., U. of Mich. Press, Ann Arbor. No. 52.

Clapham, A. R. 1936. Over-dispersion in grassland communities and the use of statistical methods of plant ecology. Jour. Ecology. 24:232-251.

Clark, Philip J. and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology. 35:445-453.

Cole, L. C. 1946. A theory for analyzing contagiously distributed populations. Ecology. 27:329-341.

Cole, L. C. 1949. The measurement of interspecific association. Ecology. 30:411-424.

Cottam, G. C., J. T. Curtis and A. J. Catana, Jr. 1957. Some sampling characteristics of a series of aggregated populations. Ecology. 38:610-622.

Curtis, J. T. and R. P. McIntosh. 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology. 31:434-455.

Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continum in the prairie-forest border region of Wisconsin. Ecology. 32:476-496.

Curtis, J. T. 1959. The vegetation of Wisconsin--an ordination of plant communities. Univ. of Wisc. Press, Madison. 657 pp.

Dandeno, J. B. 1907. Vegetative reproduction in Erythronium americanum. Mich. Acad. Sci. 9th Report. 64-67.

Dawson, G. W. P. 1951. A method for investigating the relationship between the distribution of individuals of different species in a plant community. Ecology. 32:332-334.

DeVries, D. M. 1952. Objective combinations of species. Acta. Bot. Neerl. 1:497-499.

DeVries, D. M., J. P. Baretta and G. Hamning. 1954. Constellations of frequent herbage plants based upon their correlation in occurrence. Vegetatio. 5:105-111.

Fernald, M. L. 1950. Gray's Manual of Botany. 8th ed. American Book Co., Boston. 1932 pp.

Gillis, W. T. 1969. The systematics and ecology of poison-ivy and the poison-oaks (Toxicodendron, Anacardiaceae). Ph.D. Thesis, Michigan State Univ. 491 pp.

Gleason, H. A. 1924. The structure of the beech-maple association in northern Michigan. Mich. Acad. Sci. Arts and Letters. 4:285-296.

Goodall, D. W. 1952. Quantitative aspects of plant distribution. Biol. Rev. 27:194-245.

Greig-Smith, P. 1964. Quantitative plant ecology. Butterworth's Scientific Pub., London. 256 pp.

Holm, T. 1925. Hibernation and rejuvenation exemplified by North American herbs. Am. Mid. Nat. IX:439-512.

Hurlbert, S. H. 1969. A coefficient of interspecific association. Ecology. 50:1-9.

Jackson, M. T. 1966. Effects of microclimate on spring flowering phenology. Ecology. 47:407-415.

Kershaw, K. A. 1963. Pattern in vegetation and its causality. Ecology. 44:377-388.

Kershaw, K. A. 1964. Quantitative and dynamic ecology. American Elsevier Pub. Co., Inc., New York. 183 pp.

Lieth, H. 1970. Phenology in productivity studies. p. 29-46. In: Analysis of temperate forest ecosystems. (D. E. Reichle, ed.) Springer-Verlag, New York.

Martin, H. M. 1955. Map of the surface formations of the southern peninsula of Michigan. Michigan Dept. Conserv. Geol. Survey Div. Publ. 49.

McIntosh, R. P. 1957. The York Woods, a case history of forest succession in southern Wisconsin. Ecology. 38:29-37.

McIntosh, R. P. 1962. Pattern in a forest community. Ecology. 43:25-33.

Pielou, E. C. 1969. An introduction to mathematical ecology. John Wiley & Sons, New York. 286 pp.

Potzger, J. E. and R. C. Friesner. 1940. A phytosociological study of the herbaceous plants in two types of forests in central Indiana. Butler. Univ. Bot. Stud. 4:163-180.

Risser, P. and G. Cottam. 1967. Influence of temperature on the dormancy of some spring ephemerals. Ecology. 48:500-502.

Salisbury, E. J. 1929. The biological equipment of species in relation to competition. Jour. Ecology. 17:198-222.

Schneider, G. 1966. A twenty year investigation in a sugar maple-beech stand in southern Michigan. Ag. Exp. Sta. Research Bull. 15. Michigan State Univ. 61 pp.

Soil Survey Staff. 1967. Supplement to soil classification system, 7th approximation. Soil Conservation Service, U.S. Dept. of Agriculture, Washington, D.C.

Smith, B. E. and G. Cottam. 1967. Spatial relationships of mesic forest herbs in southern Wisconsin. Ecology. 48:546-558.

Struik, G. J. and J. T. Curtis. 1962. Herb distribution in an _Acer saccharum_ forest. Amer. Midland Nat. 68:285-296.

van der Pijl, L. 1969. Principles of dispersal in higher plants. Springer-Verlag, New York. 153 pp.

Veatch, J. O. 1941. Soil survey of Ingham County, Michigan. U.S. Dept. Agr. Bur. Plant Industry, Series 1933. No. 36, 43 pp. Map.

Veatch, J. O. 1953. Soils and land of Michigan. Mich. State Coll. Press., E. Lansing, Mich. 241 pp.

Vezina, P. E. and M. M. Grandtner. 1965. Phenological observations of spring geophytes in Quebec. Ecology. 46:869-872.

Whitford, P. B. 1949. Distribution of woodland plants in relation to succession and clonal growth. Ecology. 30:199-208.

Whitford, P. B. 1951. Estimation of the ages of forest stands in the prairie-forest border region. Ecology. 32:143-147.

Whittaker, R. H. 1970. Communities and ecosystems. Macmillan Co., Toronto, Ontario. 162 pp.

Williams, A. B. 1936. Composition and dynamics of a beech-maple climax community. Ecol. Monogr. 6:318-408.

Williams, W. T. and J. M. Lambert. 1959. Multivariate methods in plant ecology. I. Association analysis in plant communities. Jour. Ecol. 47:83-101.

APPENDICES

APPENDIX A

Arrangement of a 2 x 2 contingency table and statistical tests used in analyzing association between species.

Species A[7]

	Species B: Present	Species B: Absent	
Number of times present	a	b	a+b
Number of times absent	c	d	c+d
	a+c	b+d	n=a+b+c+d

Computation of Chi-square using the above table.

$$x^2 = \frac{(ad-bc)^2 n}{(a+b)(a+c)(c+d)(b+d)}$$

Computation of Cole's Index of Interspecific Association (C_7)[8]

When $ad \geq bc$:

$$C_7 = \frac{ad-bc}{(a+b)(b+d)}$$

When $bc > ad$ and $d \geq a$:

$$C_7 = \frac{ad-bc}{(a+b)(a+c)}$$

When $bc > ad$ and $a > d$:

$$C_7 = \frac{ad-bc}{(b+d)(c+d)}$$

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7 The convention was adopted that species A was the species that was least frequent, i.e. $a+b \leq (a+c)$.

8 Significance of this sample statistic was ascertained by the above Chi-square test.

APPENDIX B

Computational formula for an index of floristic similarity[9]

Coefficient of similarity

$$C = \frac{2w}{a+b}$$

where a is the sum of the per cent frequencies of all species in one stand, b is the similar sum for a second stand, and w is the sum of the lower of the two per cent frequency values for those species which are common to both stands. Perfect similarity theoretically produces a value of +1.0 and perfect dissimilarity a value of 0.0. Due to sampling error, the maximum value expected for high similarity is around 0.8 instead of 1.0.

[9] Bray and Curtis (1957).