INTERSPECIFIC PATTERN IN AN OLD-FIELD COMMUNITY IN SOUTHWESTERN MICHIGAN

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ABSTRACT

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by John Louis Caruso

This study deals with the detection of interspecific pattern in an old-field community in Kalamazoo County, Michigan, and is an attempt to ascertain the role of the dominant species in producing part of this pattern. The field was procured by the Federal Government in 1942 and has not been subsequently plowed. The dominant species occupying the community on well-drained Boyer sandy loam is _Poa compressa_, which is distributed in varying abundance and vigor throughout the upland. There are several less abundant species which form conspicuous clumps within the matrix of _P. compressa_.

A plot 40 x 80 meters was marked off in a relatively homogeneous area of vegetation in the summer of 1961. Five hundred of the 3200 possible 1 m^2 quadrats were chosen at random, arranged systematically, and sampled in geographical sequence. Presence of species was

recorded for these quadrats, and the resulting data were examined for positive and negative associations using a 2 X 2 contingency table and a Chi Square (X^2) analysis of significance. Within each of the 1 m^2 quadrats, a nested quadrat measuring 25 X 25 cm was randomly placed. Presence was recorded and cover estimated for each species in the 1/16 m^2 quadrat. The presence data were examined by the analysis of association as above, and the cover data for the 18 more frequent species were subjected to correlation analysis.

Many more negative than positive correlations were found to exist, irrespective of significance, and this is assumed to be due, at least in part, to the spatial limitations of the quadrat itself. The majority of the significantly positive correlations (5% level) are between the less abundant species, while the significantly negative correlations are either between the two most dominant species, *Poa compressa* and *Aster pilosus*, or between one of these and one of the less abundant species. The only exception to this is one significant negative correlation between *Rumex Acetosella* and *Dianthus Armeria*, and both of these are above the mean cover and frequency of the 18 species dealt with.

A hypothesis of spatial exclusion of the less abundant species by the dominant species was made. In an attempt to test this hypothesis, seeds of species significantly correlated with *Poa compressa* at the 5% level, both positively and negatively, and seeds of species too infrequent for tests of significance were sown in successively larger circular openings (0.5 cm, 1 cm, 2 cm and 3 cm) in pots of *P. compressa* sod brought from the study area to the greenhouse. Germination and seedling survival were recorded for each species tested. To date, *Melilotus* spp., which is significantly positively correlated with *P. compressa*, was found to have its seedling survival related to size of opening in sod (1% level, analysis of variance). The larger openings yield a greater number of viable seedlings. Germination of seeds of *Melilotus* spp., however, was not significantly related to size of opening in *P. compressa* sod, although a trend does develop. The experiments with *Aster pilosus* and *Solidago canadensis* var. *scabra* (both negatively correlated with *P. compressa*) and *Monarda fistulosa* and *Verbascum thapsus* (both too infrequent for significance tests) did not produce clear relationships to sod openings. *Solidago*, although giving 70% germination on moist blotter paper, failed to germinate in the openings. *Aster pilosus* and *Monarda fistulosa* germinated slowly in the openings and never gave values approaching those achieved on wet blotter paper. *Verbascum Thapsus*, while giving better germination than the two preceding, did not approach the values for *Melilotus* spp.. There was no significant difference between the opening sizes although more total seeds germinated in large openings.

Because of technique problems, only the *Melilotus* experiments are convincing. They indicate that with adequate moisture seeds shallowly buried in openings as small as 2 cms. in diameter can give germination and survival rates almost as high as laboratory germination percentages. The data for the others, though inconclusive, suggest that further study of their relationships with *P. compressa* is warranted.

The hypothesis that spatial exclusion by the dominants is a factor in the patterns detected, although not confirmed, is still tenable in the light of these experiments.

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By

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INTRODUCTION

A. Scope of Problem

Pattern in vegetation is a manifestation of non-randomness in the plant community. Pattern is, moreover, an external feature of the community by which one may perceive internal ecological organization. According to Hutchinson (1953) pattern is the "structure which results from the distribution of organisms in, or from, their interactions with their environment...."

That individuals in the plant community form patches, and these patches collectively produce the mosaic nature of much vegetation, was eloquently defended by Watt (1947). Ashby (1948) referred to such aggregates as plants in a state of overdispersion, and stated that underdispersion, or the departure from randomness in the direction of uniform spacing, was much less common in nature. Goodall (1952) and Skellam (1952) have also pointed to the general tendency of plants to form aggregates or clumps.

Rather elaborate and precise methods have since been developed to detect the orders of clumping or grouping among plants. The measurements of distance between nearest neighbours in reflexive pairs is a method developed by

Clark and Evans (1954) to determine orders of grouping in one-species populations. Pielou (1961) transformed the approach of Clark and Evans to one in which symmetry between members of two-species populations could be studied.

Groupings of more than one species are seemingly more difficult to elicit from spatial relationships of plants. Grieg-Smith (1957) has reviewed much of the important literature on association and pattern prior to 1956. In addition, Fager (1957), Bray (1956a), McIntosh (1962) and Kershaw (1960, 1963) have made useful contributions to the subject. Byer (1960) studied shifts in interspecific associations along an environmental gradient. McIntosh (1962), in an effort to construct units of vegetation from tests of association, reviewed the methods of Goodall (1952) and Hopkins (1957), but concluded a) that the groups one gets depend upon the significance levels he chooses in selecting associated pairs, and b) there is no non-arbitrary way to decide on probability level.

Kershaw (1960, 1963), although not completely resolving the difficulties associated with interspecific groupings, has nevertheless proposed a method whereby the scale of pattern in association can be defined. His method is one of obtaining the mean square or variance in the joint number of individuals of two species in a given block size. When the variance is plotted against the block (sample unit) size, the peaks of the graph represent the mean area of pattern in the vegetation analyzed. This contribution is of great importance when one considers the many statements concerning pattern, which, in the past, have been based on results obtained from sampling with one fixed size of quadrat.

Regarding the causes of patterning in vegetation, Kershaw (1963) has classified them into pattern types that are encountered in the field. They are: (1) morphological pattern, which in general produces a smaller scale patterning relative to the size of the area sampled, such as that found in plants reproducing by rhizomes, (2) environmental pattern as resulting from the plant's response to its surrounding, which may be on a larger scale than the preceding but not necessarily so, and (3) sociological pattern, which, although traceable to an interaction between organisms, is sometimes impossible to distinguish from environmental pattern. This is a somewhat simplified classification of causes over that proposed by Hutchinson (1953) who used: vectorial (environmental), reproductive, interactive, stochastic and signalling as the categories. Kershaw's substitution of morphological for reproductive is not entirely satisfactory and perhaps both have a place.

If one took a cursory glance at a large number of the papers written on the subject of pattern, he would conclude that distribution patterns of individual species have been of greatest concern (intraspecific pattern), while a much smaller number pertain to interspecific pattern (as inferred from interspecific association). The patterns referred to in this paper are almost exclusively interspecific associations.

The purpose of this study is twofold: (1) to detect spatial pattern among vascular plants in an old-field community, and (2) to determine to what extent the abundant vascular species influence the less abundant species in the manner of spatial exclusion. The bryophytes and lichens, although undoubtedly a part of old-field patterning, were excluded from analysis because of unreliable field identification and cover estimates.

This study can be considered as an initial phase of investigation into patterning in old-field vegetation, and may have particular importance in eliciting questions pertaining to competition and chemo-sociology in such an old-field ecosystem. As Grieg-Smith (1957) points out, the detection and analysis of non-randomness is not an end in itself, rather it is a starting point for further investigation into the factors responsible for the existing spatial characteristics.

The vegetation selected for the study of pattern is in a grass-dominated old-field community. It is relatively simple in composition, and if the conjectures of Grieg-Smith and Kershaw (1958) are correct, the area studied should have a greater intensity and concomitant smaller scale of pattern than the climax type that will eventually arise through succession.

Succession, a dimension of great significance in old-field vegetation, will be given at most a very brief consideration in this paper. Watt (1947) gives a careful analysis of the relation between temporal and spatial patterns in seven communities; Bray (1956b) and Whitford (1949) elucidate temporal and spatial changes in woodlots; Egler (1954) confines himself primarily to temporal pattern in old-field vegetation, preferring the term "development" to "succession" because of the latter term's implication of discontinuity between seres in the progression. Pertinent general references on old-field vegetation include, among others, Clements (1916), Oosting (1942), Keever (1950), Bard (1952) and Odum (1960).

B. Description of the Area

The field chosen for investigation is located in the Ft. Custer Military Reservation in the northeast corner of Kalamazoo County (SW 1/4 of NE 1/4 of Sec. 9, T.2S, R.9W). The longest axis of the field is oriented east and west, with the Ft. Custer Road and the Kalamazoo River forming the main eastern and western boundaries, respectively.

The study area is in the eastern portion of the field. It is somewhat elevated with gently sloping topography, while the unsampled western portion of the field is lower on a terrace nearer the river.

The soil in the study area is mapped on the county soil survey as Oshtemo sandy loam (Perkins and Tyson, 1926). Revision of soil classification since that survey was made requires a separation of Boyer from Oshtemo sandy loam if carbonate material is present less than 42 inches beneath the soil surface. Field determination has shown that the soil is actually Boyer sandy loam under the present soil classification (Frank Austin, Soil Scientist, in voce). The soil on the terrace below is mapped as Oshtemo sandy loam but is believed to be an alluvium of some type.

The floristic differences between the dry study area and the more moist, unsampled river terrace are remarkably similar to the differences for an old-field in southeastern Michigan noted by Evans and Dahl (1955). *Poa compressa* (nomenclature following Gleason and Cronquist, 1963) is the dominant in the dry area, while *Poa pratensis* characterizes the moist area.

P. compressa is virtually everywhere in the upland, and this species forms a more-or-less continuous phase in the community, varying throughout only in number and size of culms. Situated in this varying matrix of bluegrass are several contagiously dispersed lesser abundant species, which collectively produce a pattern of patchiness very much like the complex mosaic encountered by Evans and Cain (1952).

The major patch-forming species are: *Rubus flagellaris* (Fig. 1), *Solidago canadensis* var. *scabra* (Fig. 2), *Solidago juncea*, *Solidago nemoralis*, *Hieracium longipilum*, *Hieracium aurantiacum* and *Saponaria officinalis*. These patches, within which bluegrass is less prominant, belong to a discontinuous phase.

A list of species arranged in order of decreasing frequency is presented for the study area (Appendix-A). Species existing in the area at the time of sampling that did not occur in quadrats are contained in the list, but they are not given a frequency status.

Voucher specimens from the study area are on file in the Beal-Darlington Herbarium at Michigan State University.

C. History of Area

The study area is part of a 41 acre tract procured by the Federal Government 28 September, 1942. The tract was leased 1 March, 1954, to an individual for the purpose of grazing cattle. The lease terminated 31 August, 1958, however, the only grazing recorded was during the period April to October, 1955.

White-tailed deer have been seen on the lower terrace in the field, and there is some evidence of their browsing in the upland. The only other sign of major disturbance in the area is the remnant of an old trail, now existing as a slight depression grown over by vegetation. The trail presumably is an outcome of the maneuvers of the U.S. Army shortly after the land's procurement by the government.

Fig. 1. A 21-year old field showing a patch of Rubus flagellaris in the left foreground. The continuous phase (Poa compressa) on the right and in the background.

Fig. 2. A clone of Solidago canadensis var. scabra in the foreground and another of the same species at mid-distance.

METHODS

A. Sampling

The vegetation in the upland was sampled during the period 20 August to 12 September, 1961. A plot 80 x 40 meters was marked off in a relatively homogeneous area of vegetation. The longest axis of the plot runs north to south (Fig. 3). Five hundred of the 3200 possible 1 x 1 meter quadrats were chosen at random, then they were arranged systematically and sampled in geographical sequence. Presence of species was recorded in each quadrat. Since the degree of association of species depends on the size of quadrat used (Grieg-Smith, 1957), within each 1 m^2 quadrat a nested plot measuring 25 x 25 cm was placed at random. Presence was recorded and cover estimated for each species in the 1/16 m^2 quadrat.

Unfortunately, the cover of Poa compressa was underestimated in the first 269 small quadrats. The author changed techniques in estimating the cover of P. compressa at this point, resulting in 269 uniformly underestimated cover values. The cover error in the first quadrats was rectified by a later calculation of the mean of the underestimated values. This mean was then divided into the mean cover for the remaining 231 more nearly correct values. The resultant quotient was used as a correction factor for each cover value of P. compressa throughout the first 269 quadrats. The possibility of a less reliable cover value for this one species should be kept in mind whenever the greater number of quadrats is used in a cover relationship involving P. compressa.

The presence data obtained from the large and small quadrats were examined for positive and negative associations using a 2 x 2 contingency table and a Chi Square (X^2) analysis of significance. The formula incorporating the correction factor of Yates was used (Walker and Lev, 1953). Species whose expected values of occurrence were less than five were excluded from the Chi Square analysis.

The above analysis for association cannot be used for species having very high frequencies of occurrence (Grieg-Smith, 1957), for example, Poa compressa, which occurs in all 1 m^2 quadrats.

Correlation analysis of per cent cover was selected as a sensitive measure of association for P. compressa. In order to handle the large number of calculations necessary for cover correlations with the many different combinations of species, two programs were established for the Integral Computer at Michigan State University. One program was based on cover data obtained from 484 quadrats. For reasons of missing cover values or obvious errors, 16 of the 500 quadrats were discarded from the cover study. This program incorporates the correction factor for P. compressa cover.

The second program is based on the last 228 quadrats sampled in which the cover values of P. compressa were more accurately estimated in the field (three of the 231 quadrats were discarded for reasons mentioned above).

Because of limitations on card space in the programming, 18 species were used in both correlations. The basis of choice of species for the correlations was frequency of occurrence. The 18 species chosen were those which occurred most frequently and for which there was no problem of field identification. Appendix-B contains a list of species used in both correlations, the species of which are arranged in order of decreasing average per cent cover. The lists are not identical. Poa pratensis is more abundant in the southern portion of the study area and was arbitrarily chosen for the correlation involving the greater number of quadrats. *Leptoloma cognatum* appears to be more abundant in the northern portion of the area, on the other hand, and its relationships were studied only in the correlation involving the northerly 228 quadrats. Similarly, *Ambrosia artemisiifolia* takes the place of *Daucus Carota* in the analysis of data from the fewer quadrats. *Erigeron* is represented in the northerly 228 quadrats as one homogeneous taxon (*E. strigosus*) as opposed to the heterogeneous *Erigeron spp.* referred to in the greater number of quadrats. The later taxon includes a small but unknown amount of *E. annuus*. Finally, because of vegetative and floral senescence, *Melilotus alba* and *M. officinalis* could not always be separated in the field, and henceforth will be referred to collectively as *Melilotus spp*.

B. Experimental

In an attempt to determine whether, and to what extent, the dominant species, *Poa compressa*, limits the numbers of the less abundant species, a model was conceived to study the influence of *P. compressa* on the germination of seeds and survival of seedlings of several of these species. For this purpose, sod from a relatively pure stand of *P. compressa* was collected in the study area in October, 1962 (Fig. 4).

Blocks of bluegrass sod were cut by means of a sharpened hand trowel to a depth of about 5 1/2 inches, including most of the tight, netlike fibrous roots and some mineral soil. These blocks were then trimmed in diameter so they would fit snugly into five-inch pots. The sod samples were transported in the pots to the greenhouse at Michigan State University. A few weeks were allowed for the grass to acclimate itself to the greenhouse environment. Seedlings of any species which appeared were removed during this time. From the date of collection to the termination of the study, the grass was watered regularly and trimmed occasionally to maintain a uniform height of between four and five inches.

Circular openings of four sizes (.5 cm, 1 cm, 2 cm and 3 cm) were cut into the sod by means of cork borers having these respective diameters. The borers were inserted to a depth below the grass rhizosphere so that, upon removal, the plug inside the borer would contain all of the grass roots within a given diameter. The holes were then filled with soil trimmed from the sod blocks and from which all roots were removed. A large fraction of this soil was from below the densest root mat. The soil was tamped lightly and smoothed to correspond with the soil level in the pot.

A wooden disc five inches in diameter placed over the sod in the pot served as a template for locating four openings per pot. Four templates were used, one for each of the four different sized openings. Within each disc, the four holes were of equal size and were uniformly spaced with their centers forming a square measuring 2 1/4 inches on a side. The wooden disc was placed over the pot and the borer was inserted through each of the four holes having a corresponding diameter. Eight pots were used for each of the four different sized openings, thus giving a total of 32 replicates for each size class for each species. The pots were randomly arranged on the greenhouse bench.

Seeds of various species were collected during the summer and fall of 1961, and during the same period in 1962 with the expectation that certain of these would later be used in germination studies. It was desired to use seeds of species that were found to be significantly positively correlated with bluegrass, some that were significantly negatively correlated with bluegrass, and seeds of some species which were relatively infrequent. Only one species was planted in each pot with three seeds in the center of each opening giving a total of 96 seeds sown for each species in each of the different size classes.

Fig. 3. A view diagonally from southwest to northeast across the sampled universe. The stake in the foreground marks the southwest corner; the northeast corner is just to the right of the tall tree in the center.

Fig. 4. A relatively pure stand of Poa compressa from which the sod samples were taken.

RESULTS

A. Pattern

Correlation coefficients obtained from the analysis of cover data from 484 quadrats are presented in matrix form (Table I). For the purpose of comparison, symbols indicating the significance and sign of Chi Square analysis of association in the 499 1/16 m^2 quadrats are found within the complementary portion of the same matrix. The species are arranged along the margin of the matrix from left to right and from top to bottom in order of decreasing average cover values. A similar matrix based on the northerly 228 quadrats only is given in Table II.

It should be noted that there are many more negative than positive correlations in both matrices, irrespective of significance. When the mean number of negative correlations and positive correlations for all species are compared, it is found that the negatives are more numerous (the significance of the difference at the 1% level, T-test).

Looking at only those correlations which are significant at the 5% level the negative cover correlations are almost exclusively found between the two most dominant species _Poa compressa_ and _Aster pilosus_, and between one of these two dominants and less dominant species. The majority of the significant positive correlations, however, are between the less abundant species.

The significance of the tests of association as determined by Chi Square analysis for the 500 m^2 quadrats are presented in Table III. The most frequent species that could be tested was _A. pilosus_ (91.4%) and the least frequent that could be used was _Vitis_ sp. (1.2%) whose expected joint occurrence with _A. pilosus_ reaches five.

Table I. Chi Square levels of significance of association in lower left of table apply to 499 1/16 m^2 quadrats. Cover correlations in upper right of table apply to 484 1/16 m^2 quadrats.

Key: 0+ positive .10 -- negative .01
+ positive .05 * positive .05
++ positive .01 ** positive .01
0- negative .10 * negative .05
- negative .05 ** negative .01

	P. comp.	A. pilos.	R. flagel.	D. Armer.	Melilotus	R. Acet.	P. recta	S. canad.	S. officin.	S. carolin.	S. nemor.	E. coroll.	Erigeron	O. Dillen.	P. praten.	H. longip.	D. Carota	E. laevig.
Poa compressa		** 231	** 240	038	064	042	019	* 096	009	** 112	* 097	042	033	032	047	* 083	006	021
Aster pilosus			** 112	** 116	* 085	066	046	* 076	033	** 111	009	018	008	037	** 110	021	030	050
Rubus flagellaris				* 085	008	011	070	050	040	070	016	050	** 167	002	050	034	021	046
Dianthus Armeria			+		** 152	* 089	* 096	032	030	011	040	056	011	037	** 104	039	008	023
Melilotus spp.		--		+		044	000	049	** 146	028	041	035	032	019	055	031	016	** 133
Rumex Acetosella		++	--	--	--		068	040	022	005	016	043	017	005	040	038	001	017
Potentilla recta			-			-		045	013	047	021	** 147	016	051	012	023	017	026
Solidago canadensis v. scabra									013	015	011	023	015	038	028	021	011	024
Saponaria officinalis		+								006	030	029	027	028	032	024	012	027
Solanum carolinense		--									046	008	024	** 173	** 235	023	012	* 100
Solidago nemoralis				--								063	018	027	023	017	009	013
Euphorbia corollata			0-										055	013	021	** 105	008	018
Erigeron spp.														016	020	032	007	014
Oxalis Dillenii		+				+									019	015	000	014
Poa pratensis		--				--										018	001	021
Hieracium longipilum																	007	015
Daucus Carota																		007
Equisetum laevigatum																		

Table II. Chi Square levels of significance of association in lower left of table apply to 228 1/16 m^2 quadrats. Cover correlations in upper right of table apply to 228 1/16 m^2 quadrats.

Key:
0+ positive .10
+ positive .05
++ positive .01
0- negative .10
- negative .05
-- negative .01
* positive .05
** positive .01
* negative .05
** negative .01

	A. pilos.	P. compr.	D. Armeria	Melilotus	R. Acet.	S. canaden.	P. recta	S. officin.	R. flagell.	S. nemoral.	E. coroll.	S. carolin.	H. longip.	C. Dillenii	E. strigosus	L. cognatum	A. artemis.	E. laevigatum
Aster pilosus		** 360	* 122	083	001	* 129	026	072	* 150	000	075	075	054	079	010	* 132	034	055
Poa compressa			009	* 138	* 127	* 154	093	022	** 182	* 120	008	101	092	093	052	073	016	088
Dianthus Armeria				031	065	053	101	027	033	045	069	058	044	060	015	051	042	036
Melilotus spp.	--		+		081	071	065	** 271	064	042	055	022	036	001	034	041	037	040
Rumex Acetosella				--		035	102	019	** 202	012	069	051	034	009	** 173	016	092	081
Solidago canadensis							066	032	052	003	042	025	027	063	011	017	027	030
Potentilla recta					0-			015	065	038	030	051	052	064	032	039	022	036
Saponaria officinalis									083	034	056	005	031	033	029	034	031	034
Rubus flagellaris										029	045	031	025	024	050	029	025	028
Solidago nemoralis											** 295	** 311	015	035	014	017	015	005
Euphorbia corollata												103	023	040	022	022	002	026
Solanum carolinense	--												023	004	006	023	024	** 448
Hieracium longipilum														030	012	015	013	014
Oxalis Dillenii	0+														032	021	** 174	011
Erigeron strigosus																011	012	013
Leptoloma cognatum			-														015	** 156
Ambrosia artemisiifolia																		015
Equisetum laevigatum																		

Table III. Chi Square levels of significance of association between species in bluegrass old-field vegetation. The 22 missing cells on right hand side of table contain no significant associations, and P. compressa which was ubiquitous could not be tested. N=500 1m2 quadrats except for the * where N=447 due to identification problems in field.

Key:
- 0+ positive .10
- \+ positive .05
- ++ positive .01
- 0- negative .10
- \- negative .05
- -- negative .01

	A. pilosus	D. Armeria	R. Acetosella	P. recta	O. Dillenii	Melilotus spp.	R. flagellaris	E. corollata	L. cognatum	S. nemoralis	S. carolinense	A. artemisiifolia	Erigeron spp.	S. officinalis
Aster pilosus														
Dianthus Armeria														
Rumex Acetosella	+	-												
Potentilla recta		+												
Oxalis Dillenii	++		++											
Melilotus spp.		++	--											
Rubus flagellaris				o-		--								
Euphorbia corollata		+												
Leptoloma cognatum*	+	--	++		o+	--								
Solidago nemoralis	++	--	++	--	++	--	++	++	++					
Solanum carolinense	--					++	--							
Ambrosia artemisiifolia		--						-						
Erigeron spp.	o+				++	-	+		++	++	-			
Saponaria officinalis						+			--	-		o-	o-	
Hieracium longipilum	+	--	++		+	--			++	++				
Daucus Carota					++			o-	-					-
Solidago canadensis v. scabra				--		-				o-		-		
Equisetum laevigatum									++	+	+			
Agropyron repens*	--	+				++		-			++			-
Achillea Millefolium						-	+							
Poa pratensis	--	o+	--			++		o-		--				
Physalis heterophylla								o-			++			
Lactuca canadensis			+			-	o+							
Tragopogan pratensis														
Chrysanthemum leucanthemum			--											
Verbascum thapsis						++								
Panicum sp.			++											
Prunus serotina														
Solidago juncea														
Taraxacum officinale														
Hypericum perforatum			o-											
Plantago lanceolata														
Ulmus americana				-										
Setaria glauca		-												
Trifolium pratense														
Vitis sp.														

B. Germination and Survival Studies

In choosing which of the many possible experiments to make relative to the effect of bluegrass sod on germination and seedling survival, two criteria were considered important. These were a) whether the seeds of a particular species gave dependable and high germination, and b) whether the species was interesting from the standpoint of pattern. Germination trials resulted in the selection of *Melilotus* spp., *Aster pilosus*, *Solidago canadensis* var. *scabra*, *Monarda fistulosa* and *Verbascum Thapsus*. The first is significantly positively associated with *Poa compressa*; the next two are significantly negatively associated with *P. compressa*, and the last two are species present but too infrequent to be used in a significance test.

Mixed seeds of *Melilotus alba* and *M. officinalis* germinated at between 70-80% when moistened on blotter paper in petri dishes in the greenhouse. A mixture of seeds from the same collection sample was planted 18 February, 1963, according to the design described earlier. At each reading, viable seedlings were totalled for each pot. The first reading 13 days after planting discloses a distinctly greater proportion of the seedlings surviving in the larger openings (Table IV). An analysis of variance of the data showed that the survival of *Melilotus* spp. seedlings is related to the size of opening in bluegrass sod, significance at the 1% level. Later readings were taken, and the initial significant difference in seedling survival was found to persist through time.

The above experiment was duplicated by planting seeds in freshly dug openings 23 June, 1963. To study the effect of size opening on germination of seeds in addition to survival of seedlings, the first readings were taken six days after planting (29 June). This was seven days sooner than in the first experiment and only a slight increase in viable seedlings was found in the successively larger openings (Table V). An analysis of variance in data revealed no significant difference in germination between size classes. The readings of 4 July, (11 days after planting) disclosed a greater difference in numbers of viable seedlings, and this difference, through the same analysis, proved to be significant at the 1% level which is very similar to the results of the 13 day readings in the previous experiment.

Seeds of *Aster pilosus* and *Solidago canadensis* var. *scabra*, both negatively correlated with *P. compressa*, and seeds of the two species that are relatively infrequent in the community (*Monarda fistulosa* and *Verbascum Thapsus*) have been sown in the different sized openings in bluegrass sod. At the time of writing, Verbascum Thapsùs is the only other species tested that shows some indication that its seedling survival may depend on the degree of openness in bluegrass sod. It is possible that faulty watering techniques caused the seeds of these very light-seeded species to be displaced into the sod. This may explain the poor germination results which did not give enough data to permit statistical analyses. The results of these plantings, with the exception of S. canadensis var. scabra, are presented in Tables VI and VII. Although S. canadensis var. scabra gave 70% germination on wet blotter paper, no germination was recorded for this species in bluegrass sod.

Table IV. Mean seedling survival out of 12 *Melilotus* seeds per pot for each of four sizes of opening in *P. compressa* sod at 13, 40 and 65 days after sowing. Three seeds were planted 18 February, 1963, in each of four openings of same diameter per pot. Eight pots were used for each size class, giving 96 seeds sown per size class of opening. Germination percentage on wet blotter paper was 75%. A standard error is given with each mean, and the significance of the differences between size classes as determined by analysis of variance is given below for each reading.

Opening in sod	Days after planting		
	13	40	65
0.5 cm	2.500±.598	.750± .278	.875± .295
1.0 cm	3.375±.424	1.375± .420	1.500± .463
2.0 cm	4.500±.628	1.875± .639	1.625± .571
3.0 cm	6.625±.864	4.875±1.141	4.375±1.117
	P=.01	P=.01	P=.01

Table V. Mean seedling survival out of 12 *Melilotus* seeds per pot for each of our sizes of openings in *P. compressa* sod at 6, 11, 17 and 27 days after sowing. Three seeds were planted 23 June, 1963, in each of four openings of same diameter per pot. Eight pots were used for each size class, giving 96 seeds sown per size class of opening. Germination on wet blotter paper was undetermined, but an earlier test in this room gave values approaching 100%. A standard error is given with mean, and the significance of the differences between size classes as determined by analysis of variance is given below for each reading.

Opening in sod	Days after planting			
	6	11	17	27
0.5 cm	6.625±1.068	3.625±.680	3.750±.773	3.875±.789
1.0 cm	7.125± .611	5.500±.824	5.375±.882	5.250±.881
2.0 cm	7.375± .625	6.750±.590	6.875±.667	7.000±.732
3.0 cm	7.625±. 565	7.125±.515	7.250±.559	7.250±.559
	P = not significant	P=.01	P=.01	P=.05

Table VI. Total seedling survival for Aster pilosus and Monarda fistulosa out of 96 seeds planted in each of four sizes of opening in P. compressa sod at 13, 40, 55 and 65 days after sowing. Three seeds were planted 18 February, 1963, in each of four openings of same diameter per pot. Eight pots were used for each size class, giving 96 seeds sown per size class of opening. Germination for A. pilosus and M. fistulosa on wet blotter paper was 40 and 30%, respectively.

Species and opening size	days after planting			
	13	40	55	65
Aster pilosus				
0.5 cm	2	2	5	6
1.0 cm	0	2	2	2
2.0 cm	2	3	3	4
3.0 cm	1	4	6	7
Monarda fistulosa				
0.5 cm	0	3	5	6
1.0 cm	1	2	5	6
2.0 cm	0	3	4	5
3.0 cm	0	1	1	3

Table VII. Total seedling survival for Verbascum Thapsus out of 96 seeds planted in each of four sizes of opening in P. compressa sod at 18, 28, 50 and 55 days after sowing. Three seeds were planted 30 April, 1963, in each of four openings of same diameter per pot. Eight pots were used for each size class, giving 96 seeds sown per size class of opening. Germination on wet blotter paper was 75%.

Opening in sod	days after planting			
	18	28	50	55
0.5 cm	25	28	13	9
1.0 cm	15	18	6	6
2.0 cm	29	35	9	12
3.0 cm	31	34	23	22

DISCUSSION

It is hard to conceive of a vegetation that does not have at least some of its component parts in a non-random spatial arrangement. The pattern or departure from randomness may be subtle, but it is probably extant in all forms of vegetation. It is possible that one stage in the development of vegetation may display more obvious pattern than other stages. According to Scurfield (1956) competition is the main directional force in community pattern and is manifested particularly in succession. Thus, the end state or climax vegetation is seen to be more ordered and to display more pattern. Grieg-Smith and Kershaw (1958) are diametrically opposed to the suggestion made by Scurfield, and moreover, state with some good evidence that spatial arrangement of plants proceeds from randomness in colonizers to non-randomness in the intermediate phases, and finally to a more-or-less random distribution in the end state. Kershaw (1963) refers to earlier work of Grieg-Smith which demonstrates little non-randomness and association in an undisturbed rain forest in Trinidad. Kershaw cites other cases to support the hypothesis. Grieg-Smith and Kershaw do admit that although pattern decreases in intensity in a stable state, the scale of pattern generally increases here. There appears to be a great need for sampling and analysis of various changing communities before one can, with certitude, point to the direction in which pattern increases.

One thing is abundantly clear, the old-field under investigation has obvious morphological pattern (following Kershaw's classification) as exemplified by Solidago canadensis var. scabra; the field has environmental pattern which is somewhat less discernible, for example the change in dominance of Poa compressa to Aster pilosus in the northern portion of the study area (Appendix-B). There is an indication of a sociological pattern in the preponderance of negative correlations of plant cover.

The greater number of negative correlations among the 18 species tested is probably a result of one of the simplest spatial relationships. Within any given quadrat, as one species tends to increase in cover another species will generally tend to decrease in cover. This is due primarily to restriction in area of the quadrat itself (Grieg-Smith, 1957). The negative correlation is magnified when the two species also require slightly different microenvironments or actually prove to be inhibitory to each other.

If a factor is operative which produces an effect that is contrary to the above, then within a given area two species will tend to cancel out the negative tendency. If the factor is strong enough in its action the species will increase together. For example, both species may have similar micro-environmental requirements, or one or both respond favourably to the presence of the other.

It is axiomatic that less abundant species are less capable of occupying ground in the community than the dominant ones. In some cases this may be due to differences in speed of vegetative reproduction, in other cases it may be related to the relative competitive abilities of the dominant and non-dominant species. In either case, in micro-sites in which the dominant does poorly, non-dominant species, provided they can grow well there, are apt to have higher probabilities of occurrence. Many positive associations between non-dominants in the old-field could be due to such breaks in the less-hospitable _Poa_ cover.

The above statements might explain, at least in part, the fact that the significantly positive correlations are more numerous among the less abundant species in both matrices (Tables I and II), while the significant negative correlations are found between _P. compressa_ and _Aster pilosus_, and between either of these species and less abundant species. The only exception is in the case of Rumex Acetosella and Dianthus Armeria which are significantly negatively correlated in cover (P=.05) in the Sample N=484. These two species are also above the mean cover and frequency values of the 18 species studies (Appendix-A, -B).

Spatial exclusion as postulated here is not a new concept. It has been considered as an important element in pattern in vegetation for some time (Ashby, 1948, Cooper, 1961, Pielou, 1960; Kershaw, 1963, among others). Since the dominants occupy more area than the other species, they would be expected to exert a rather major influence on determining the location, abundance and cover of the less dominant and rarer species.

If one does not focus exclusively on spatial exclusion and strong negative correlations, and instead brings into perspective the positive relationships, the concept of groups of plants appears unavoidable in the description of pattern. Fager (1957) has proposed a rather involved method for the determination and analysis of recurrent groups. McIntosh (1962), in his review of methods of group identification, does not mention Fager's proposal, but he does give convincing evidence that no objective method exists at present by which one may group plant species. It seems reasonable to assume that tendencies to occur together rather than strong bonds between individuals form the basis of groups. The levels of these tendencies are functions of many things including the scales of microenvironmental patterns, the sizes and tolerances of the organisms concerned, and not to be forgotten, the size of sampling units for which tendency toward co-occurrences is being tested. These groups are more akin to the patterns presented by the coocurrences of, say, human occupations in a large city than to the organography of a plant. An attempt to portray vegetation in terms of "basic units" such as Hopkins (1947) has described will not be rewarding except possibly in highly patterned vegetation such as occurs in polar or alpine regions.

Nevertheless, it seemed worthwhile in this study to compare groups of positively associated species at the 5% level that were obtained in both correlation and Chi Square analyses. The groups recognized from the samples over the entire field, and from those in the last half only are illustrated in Figures 5 and 6, respectively. The groups are arranged subjectively according to their relative positions with regard to degree of development of bluegrass sod.

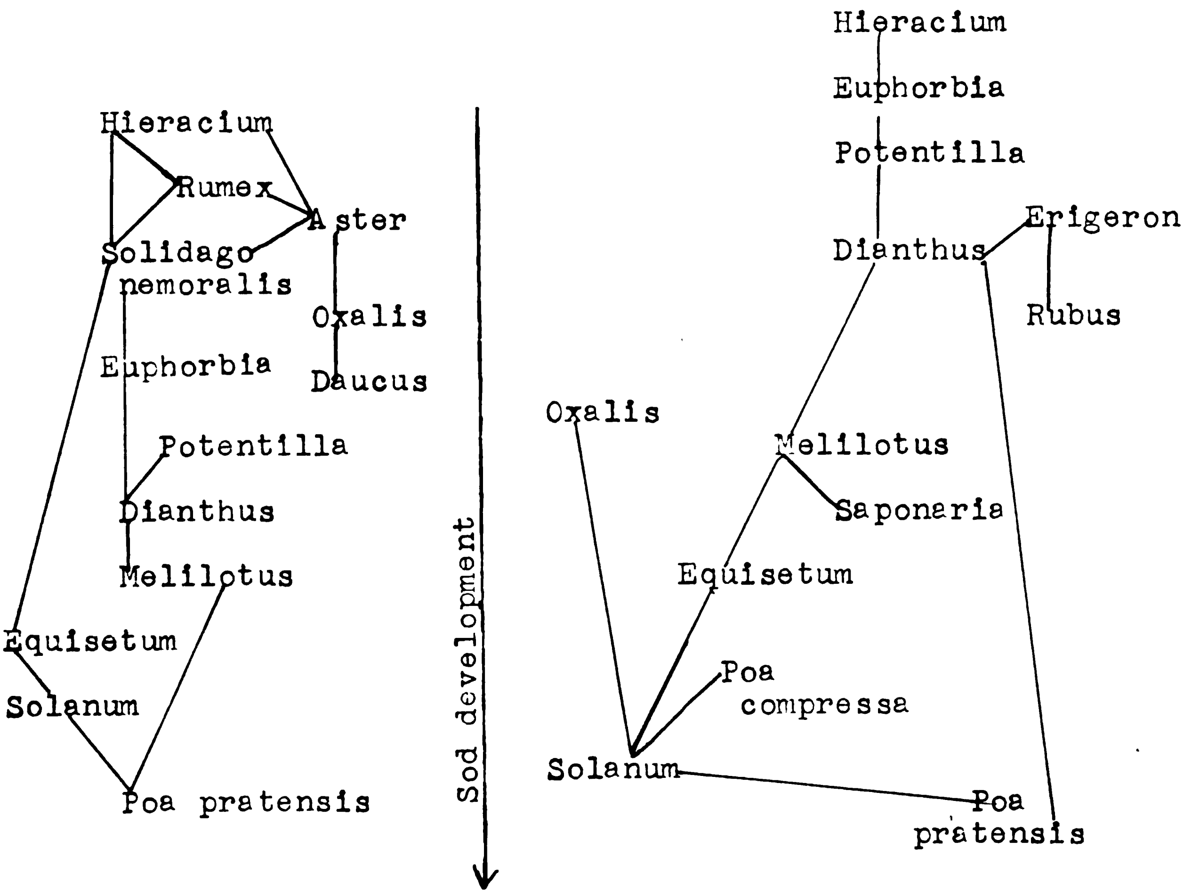

Fig. 5. Constellation diagram showing species grouped according to positive associations (Chi Square significance at 5% level, N=500 1 m^2 quadrats) on left, and correlations of cover significant at 5% level (N=484 1/16 m^2 quadrats) on the right. Between the upper and lower clusters there are some significant negative associations and correlations (see Tables I and III).

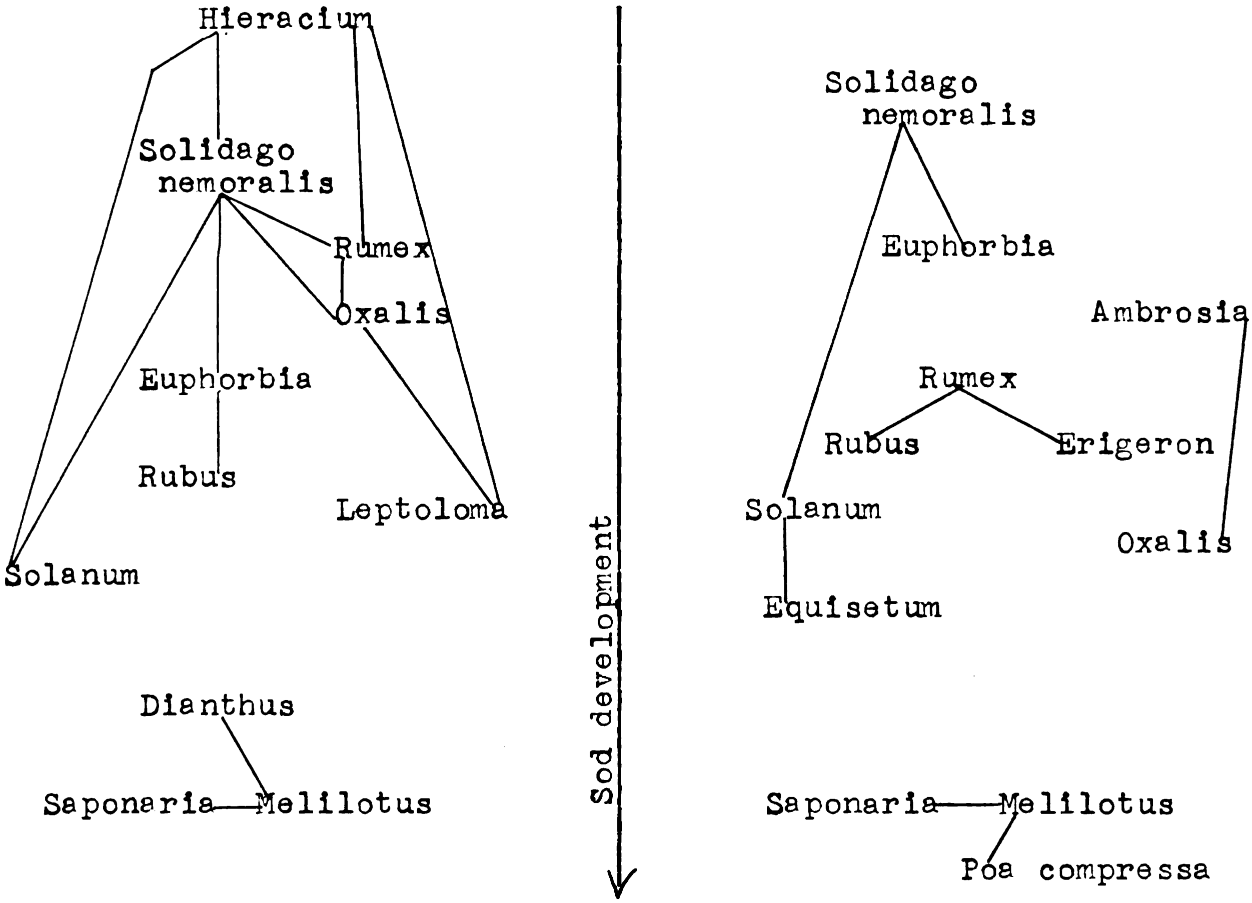

Fig. 6. Constellation diagrams showing species grouped according to positive associations (Chi Square significance at 5% level, N=228 1 m^2 quadrats) on left, and correlations of cover significant at 5% level (N=228 1/16 m^2 quadrats) on the right. Between the upper and lower clusters there are some significant negative correlations (see Table II).

The constellation diagrams, although subjectively constructed, do have a basis in reality. Warner (1945) discovered in Iowa that *P. compressa* in abundance was indicative of low available soil moisture. It was able to withstand drought better than *P. pratensis* but was less of a sod former than the later and could not compete with *P. pratensis* under more favourable moisture conditions. An analagous relationship seems to occur between *P. compressa* and some of the less abundant species in the old-field in this study. *P. compressa* is the primary sod former in the upland phase of the old-field, and just as *P. pratensis* can be considered a later stage of succession in Warner's study, so too *P. compressa* is here considered to be a more advanced and relatively more mesic stage than the *Hieracium*-*Solidago nemoralis* group in Figure 6. Although soil moisture was not studied, the higher organic matter in the soils supporting sod are likely to be more retentive of moisture than the more eroded, less productive bald spots found within the field. These less productive looking sites are occupied by the *Hieracium*-*Solidago* complex which includes *Rumex* and *Oxalis* (Fig. 5) or by the same group with the addition of *Leptoloma* (Fig. 6).

In these same constellation diagrams, *Melilotus* and *Saponaria* tend to occur as a unit. Both species do well on dense sod, and both species are most often conspicuously absent from eroded sites occupied by the complexes referred to previously. On the other hand, the relationships of *Melilotus* spp. and *Saponaria officinalis* with *P. compressa* are quite different.

S. officinalis appears to grow well in areas of *P. compressa* sod, but is not positively correlated with bluegrass. The dense clones, frequently with 10-20 tightly spaced individuals of *S. officinalis*, may spatially exclude *P. compressa* since its cover is clearly less within the clones.

Melilotus spp., on the other hand, is positively correlated with *P. compressa* (10% level, Table I; 5% level, Table II). *Melilotus alba* and *M. officinalis* are leguminous plants containing nitrogen fixing bacteria in their root nodules (Allaway, 1957). Perhaps when these roots decay nitrates are released in sufficient amounts to cause an increase in the number and vigour of bluegrass culms in their proximity. Or it may be that bluegrass sod, having more organic material, retains moisture that is utilized by the legumes. Warner (1945) found that *P. pratensis* sod accumulated greater amounts of organic material in the area he studied.

The results of germination studies on a mixture of seeds of Melilotus alba and M. officinalis show that seed germination in these species is not significantly related to the size of openings in sod, although a trend does exist (Fig. 7). The important point is that germination counts are almost as high as on moist blotters in petri dishes. There appears to be little likelihood of a germination suppressing effect by the sod.

Early seedling survival is correlated with the size of opening in bluegrass, the larger openings yielding the greatest number of viable seedlings (significance at the 1% level, as determined by analysis of variance). After the initial high rate of mortality among seedlings in the small openings, the remaining viable seedlings appear to have a good chance for survival, under conditions of little moisture stress as portrayed by their greenhouse survival curves (Figs. 7, 8). This indicates that self-thinning in Melilotus spp. seedlings is much more pronounced in smaller sized openings in bluegrass. Judging from the slightly etiolated and stringy appearance of many seedlings in these smaller openings, it is possible that this self-thinning is due to competition for light. An underlying principle might be density-dependent mortality which has

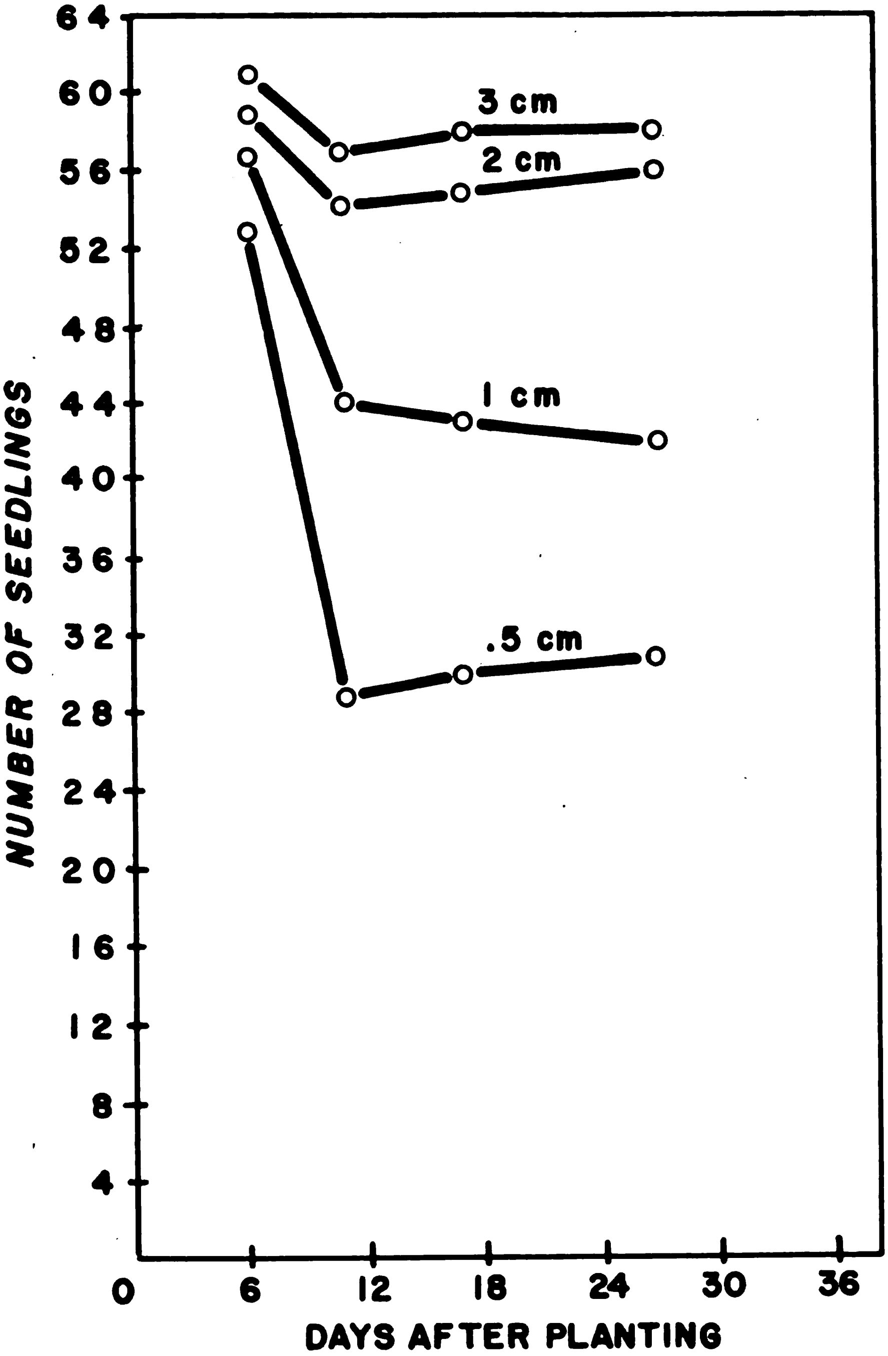

Fig. 7. Survival curves of seedlings of <u>Melilotus</u> spp. in openings in bluegrass sod ranging in diameter size 0.5 to 3 cm. Seeds were sown 23 June, 1963.

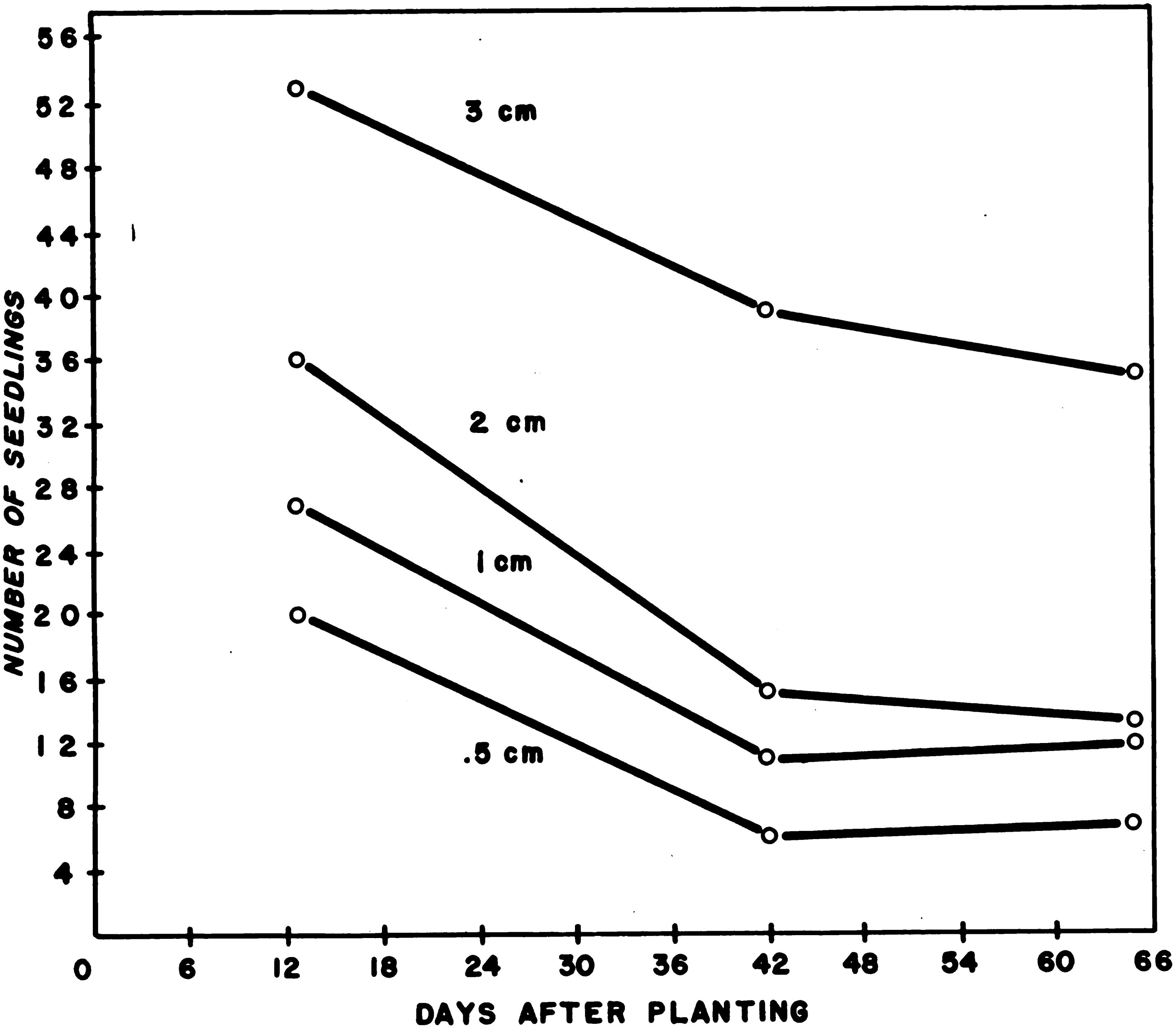

Fig. 8. Survival curves of seedlings of Melilotus spp. in openings in bluegrass sod ranging in diameter size 0.5 to 3 cm. Seeds were sown 18 February, 1963.

been shown to exist for seedlings of other species (Harper, 1961).

The results of the above experiment concur with an unsupported statement made by Milthorpe (1961): "It is reasonably certain that the establishment of plants from seed in vegetation occurs only in 'bare areas' arising from the death of previous occupants or from incomplete coverage". The Melilotus data give some idea of how small the size of opening can be, and also help to distinguish between germination success and seedling survival.

If subsequent experimentation bears out the complete failure of germination of Solidago canadensis var. scabra and the very low and much retarded germination of Aster pilosus and Monarda fistulosa, Milthorpe's suggestion will be further supported, but would indicate that even larger openings are necessary. Further, the negative correlations between the first two of these species and Poa compressa may, in part, reflect this suppression. At this point, however, caution is necessary pending confirmation of these data.

The problems of establishment are not the only basis of pattern. Solidago canadensis var. scabra is a strong clone former (Fig. 2) and once established appears to be able to expand successfully in Poa compressa sod. It appears to preclude many of the other species from growing within its circular boundary. *Poa compressa*, although found within such clumps, is much diminished in cover here. The percentages of cover of the two species are negatively correlated (5% level of significance) in Tables I and II. In the sample N=484, *S. canadensis* var. *scabra* is seen to be the only species having all of its correlations (17) negative in sign; when N=228 only two of the correlations are positive in sign, and these are not significant. The postulate that this *Solidago* tends to preclude other species from growing within its clone could be tested by transplant and seed germination experiments in the field. Specific clumps have been observed for two successive years, and from the size of the clumps and their probable growth rate, they would appear to date back nearly to the time of abandonment.

Cover of other plants may serve as a protective layer for the developing seedlings or basal rosettes in others. *Dianthus Armeria* is a slender, erect plant which overwinters as a green basal rosette. This species appears to do better under the cover of a large number of other species. It is significantly positively correlated with *Poa pratensis*, *Potentilla recta*, *Melilotus* spp. and *Rubus flagellaris* and in the field appeared to be strongly correlated with *Poa compressa* litter.

The interspecific patterns of Solanum carolinense and Equisetum laevigatum are rather puzzling. When the entire study area is considered (N=484) these two species are positively correlated in cover, (significance at the 5% level), and both are identified with the sod forming group (Fig. 5). Once detected from the analysis of the data, this relationship is locally conspicuous in the field, especially in the somewhat lower portion of the study area, which has not suffered erosion. In the slightly elevated section of the study area, where moisture appears to be more limiting and eroded spots more frequent, the Equisetum-Solanum correlation is the strongest of any of the species studied (Table II). However, here the unit is found with the Solidago complex (see Fig. 6). In this drier area the Equisetum-Solanum association appears to reach its peak on the lower portions of convex surfaces in the soil which catch small rivulets of runoff, while the rest of the Solidago nemoralis contingent appears to thrive on the more eroded crests of such convexities. This shift in pattern affiliation needs further study.

Obviously the field is not homogeneous in the strict sense, and the shift in dominance from Poa compressa to Aster pilosus in the northerly section of the study area bears this out. Furthermore, the change in the association of the Equisetum-Solanum complex illustrates that a local change in habitat can exert a profound change in small scale patterning. The analagous work of Hairston and Byer (1954) and Kershaw (1963) lends credence to this statement.

According to Grieg-Smith (1957), sample size has a great effect on the associations that one obtains. Fortunately, data from nested quadrats in this study are available for comparison with results obtained in the larger quadrats (Table III). Moreover, the Chi Square analysis of significance of tests of association for the 1 m^2 quadrats presented in Table III, bring to light a certain amount of interspecific pattern not detectable from the small quadrats.

SUMMARY AND CONCLUSIONS

Interspecific pattern in the vegetation in an old-field was investigated. Correlation of cover of 18 species, whose range in average per cent cover is .01 to .80, disclosed a much higher number of negative than positive correlations, irrespective of significance. This is presumably a simple spatial relationship, due at least in part to the spatial limitations of the quadrat. The 12 significant negative correlations (5% level) occur with one exception, between the two most abundant species Poa compressa and Aster pilosus, and between these two and less abundant species. Ten of the 13 significant positive correlations (5% level) are between the less abundant species. This polarity between dominant and non-dominant species in the distribution of significant positive and negative correlations suggests the possibility that the two dominant species influence the non-dominant species, as well as each other, in the manner of spatial exclusion.

That the action is not all one way is suggested by the reduction in cover of Poa compressa in clones of Rubus flagellaris and Solidago canadensis var. scabra. The later species is negatively

correlated with nearly all other species tested, and field examination suggests it tends to preclude many other species from growing within its circular boundary. The area of these dense clones appears to have been increasing, apparently into areas formerly occupied by Poa compressa.

In order to test whether the results of the correlation and association studies could be interpreted in terms of seedling establishment, a series of experiments was performed. From the analysis of the vegetation, species were grouped into three categories relative to Poa, the primary dominant: negative, positive and infrequent. Germination and seedling survival of representative species in each category were tested in various sized openings (0.5cm, 1 cm, 2 cm and 3 cm) in bluegrass sod. At the time of writing, Melilotus spp. (M. alba and M. officinalis), which are positively related to P. compressa, produced the only convincing results. The germination of seeds of Melilotus spp. proved to be independent of the size of opening in bluegrass sod, although a trend does develop. Further., germination percentages were nearly as high as on wet blotter paper. When tested by analysis of variance, however, early seedling survival is correlated with the size of opening at the 1% level. The two larger openings gave a significantly greater number of seedlings. The survival curves indicate a rapid early drop but then levelled out suggesting the chances for the remaining seedlings to survive will be quite good.

Germination and survival results for the other species were subject to suspicion because of possible displacement by irrigation of the very light seeds, since the seeds were sown at the soil surface. The recorded failure of, or very low and slow rates of germination, if not an artifact, suggest that Poa compressa does exert a rather profound influence on these species even in openings up to 3 cms. in diameter.

Thus the positive cover correlation of bluegrass and sweet clover shown in the sampling for the mature plants occurs in spite of a significant effect on seedlings of sweet clover by bluegrass which appears to be minor at distances between 2 to 3 cms.. It is now desirable to study further germination and seedling performances of the species which are negatively correlated with Poa compressa and those infrequent in fields dominated by its sod.

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APPENDIX-A

Species	% Frequency in 500 1 m^2	% Frequency in 499 1/16 m^2
Poa compressa	100.0	96.4±
Aster pilosus	91.4	66.3
Dianthus Armeria	80.0	46.3
Rumex Acetosella	75.8	48.3
Potentilla recta	60.2	18.0
Oxalis Dillenii	45.8	11.0
Melilotus spp.	45.0	12.0
Rubus flagellaris	37.2	19.4
Euphorbia corollata	31.0	5.0
*Leptoloma cognatum	28.0	8.2
Solidago nemoralis	28.0	5.8
Solanum carolinense	26.8	5.6
Ambrosia artemisiifolia	20.8	1.8
Erigeron spp.	15.4	4.2
Saponaria officinalis	14.8	7.2
Hieracium longipilum	13.4	1.6
Daucus Carota	8.2	1.6
Solidago canadensis v. scabra	7.9	4.8
Equisetum laevigatum	7.6	2.8
*Agropyron repens	6.0	3.4
Achillea Millefolium	5.2	1.2
Poa pratensis	5.0	3.0
Physalis heterophylla	4.2	.8
Lactuca canadensis	3.6	.2
Tragopogan pratensis	3.4	.2
Chrysanthemum leucanthemum	2.6	0
Verbascum Thapsus	2.4	.4
Panicum sp.	2.2	.2
Prunus serotina	2.0	1.0
Solidago juncea	2.0	1.0
Taraxacum officinale	2.0	.2
Hypericum perforatum	1.8	.4
Plantago lanceolata	1.8	.4
Ulmus americana	1.8	.8
Setaria glauca	1.4	.4
Trifolium pratense	1.4	.4
Vitis sp.	1.2	.8
Fraxinus pennsylvanica	1.0	.4
Asclepias syriaca	.8	0

* % frequency for these species is based on 447 quadrats because of their misidentification in the first 53 quadrats.

APPENDIX-A

Species	% Frequency in 500 1 m^2	% Frequency in 499 1/16 m^2
Cornus Amomum	.6	0
Pleum pratense	.6	0
Carya ovata	.4	.2
Hieracium aurantiacum	.4	0
Hieracium Gronovii	.4	0
Monarda fistulosa	.4	0
Quercus Muhlenbergii	.4	.2
Acer saccharum	.2	0
Asclepias tuberosa	.2	0
Cornus stolonifera	.2	0
Dactylis glomerata	.2	0
Parthenocissus quinquefolia	.2	0
Potentilla argentea	.2	0
Prunus Mahaleb	.2	0
Vernonia altissima	.2	0
Cirsium sp.	.2	0

Species occurring in the study area but not sampled:

Anemone virginiana
Anaphalis margaritacea
Apocynum sibiricum
Celtis occidentalis
Desmodium spp.
Oenothera biennis

Species sampled in unknown amounts:

Antennaria sp.
Erigeron annuus
Erigeron strigosus
Melilotus alba
Melilotus officinalis

APPENDIX-B

Species List: program in which N=484.

	Average % cover in 484 1/16 m^2
Poa compressa	10.80
Aster pilosus	9.79
Rubus flagellaris	6.72
Dianthus Armeria	4.21
Melilotus spp.	2.99
Rumex Acetosella	2.65
Potentilla recta	1.66
Solidago canadensis var. scabra	1.48
Saponaria officinalis	1.10
Solanum carolinense	.74
Solidago nemoralis	.59
Euphorbia corollata	.44
Erigeron spp.	.22
Oxalis Dillenii	.15
Poa pratensis	.13
Hieracium longipilum	.12
Daucus Carota	.07
Equisetum laevigatum	.01

Species List: program in which N=228.

	Average % cover in 228 1/16 m^2
Aster pilosus	12.10
Poa compressa	10.83
Dianthus Armeria	4.39
Melilotus spp.	2.80
Rumex Acetosella	2.45
Solidago canadensis var. scabra	2.44
Potentilla recta	1.96
Saponaria officinalis	1.93
Rubus flagellaris	.87
Solidago nemoralis	.49
Euphorbia corollata	.38
Solanum carolinense	.37
Hieracium longipilum	.14
Oxalis Dillenii	.12
Erigeron strigosus	.08
Leptoloma cognatum	.06
Ambrosia artemisiifolia	.03
Equisetum laevigatum	.02