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Plants are seldom distributed uniformly, if an area of much size is considered, since even the smallest environmental differences may affect the success of some species. This study is an attempt to correlate the non-random distribution of plants in one prairie area with one measurable environmental factor, namely water-holding capacity. The well known phenomenon of zonation concerns a marked change in environment and therefore in species, and, as seems quite obvious, therefore also a change in plant communities. What might seem more obvious than real, however, is the boundary between any two of these so-called communities. It is possible that one cause of "contagious" distribution might be related to local differences in microhabitat, or in other words, a sort of patchwork of the zonation concept. Cain and Evans (1952) list differences in reproduction as one possible cause of species distribution within a stand. Evans and Dahl (1955) concluded that topographic variability was primarily responsible for the major distribution pattern of vegetation in a 50-year-old abandoned field. The effect of these minor topographic differences on soil moisture was inferred but not determined.

Preliminary Studies of the Area: The problem of attempting to explain the distribution patterns of plants in a relatively small area was encountered on the Faville Grove Prairie. This area is a part of the University of Wisconsin Arboretum System and is located in Jefferson County, Wisconsin, about five miles north of Lake Mills. Hawkins (1940) reveals that the original land survey in 1838 mapped this exact location as prairie. Apparently the native vegetation has never been plowed or grazed although parts of the area have been mowed in the past and fires have been historically of frequent occurrence.

Whitson, *et al*, (1916) mapped two soil types in the area, both in the Clyde series. The greater portion of the area is Clyde silt loam, of lacustrine origin, and is fairly level. One slight ridge of Clyde loam is of alluvial origin, has a slightly sandy texture, and doubtless represents the remains of an ancient levee. East of the ridge, and largely parallel to it, is a depression which possibly represents an old river bed. The Crawfish River is at present only a few hundred feet farther east and occasionally floods this depression so that, even now, soil formation through deposition is still taking place.

Several locations in the Faville Prairie were used in a study of seasonal variations in soil moisture in relation to the distribution of prairie and forest communities. (Partch 1949) The data obtained for the Faville Prairie locations are reproduced in Table 1.

Table 1. Average monthly soil moisture percentages for five stations on the Faville Prairie.

Station	Depth of Samples	Months								
		M	A	M	J	J	A	S	O	N
A	6″	142	95	86	74	50	41	49	45	55
	12″	wt*	51	49	43	33	26	27	28	37
	24″	wt	36	33	30	25	21	23	24	29
	36″		wt	33	32	24	23	23	25	30
B	6″	134	134	103	71	46	46	46	47	59
	12″	wt	48	42	39	31	24	27	27	34
	24″		wt	32	32	29	22	23	24	32
	36″			wt	33	27	22	26	26	37
C	6″	55	44	40	31	22	15	27	26	24
	12″	38	31	26	22	20	12	15	17	19
	24″	31	30	29	24	22	15	15	18	21
	36″		28	27	25	24	20	22	23	30
D	6″	wt	wt	wt	100	105	61	92	75	87
	12″			wt	51	53	41	48	49	49
	24″				wt	55	41	42	wt	
	36″				wt	38	37	39	wt	
E	6″	wt	wt	wt	141	82	73	42	77	52
	12″				58	40	46	32	41	50

*wt means no sample because of water table

Stations A, B, C and D were sampled for three years and Station E for one year. In plotting these data it becomes apparent that the seasonal variations are quite different even within this limited area. These data show both trend and level. It was shown that the general trend of these percentages, and those of many other plant communities in the same region, were all surprisingly similar and actually seemed to be correlated with the local seasonal precipitation and temperature curves. Thus the trend of the seasonal soil moisture curves cannot explain the differences found in types of prairie or forest communities. The level or actual percentage, however, does seem quite distinct, especially of the six-inch layer. In other words, a seasonal curve of the soil moisture at the six-inch level for a high prairie, also called mesic prairie by Curtis (1959), always looks distinct from a low or wet-mesic prairie or from a prairie slough. The general percentage level is probably a characteristic of the soil and not the climate, except to some extent micro-climate. It is believed that the water-holding capacity of the soil furnishes an easily obtained index to this level.

The water-holding capacities of the soils at the stations on the Faville Prairie were plotted with other prairie soils to show the ranges of water-holding capacities in the various types of prairie (Figure 1). The type of community was determined by subjective judgment on much the same basis as that used by Curtis and Greene (1949), and it is probably significant that the types show overlap. This again raises the perennial question: where does one community end and another begin, both vegetationally and environmentally?

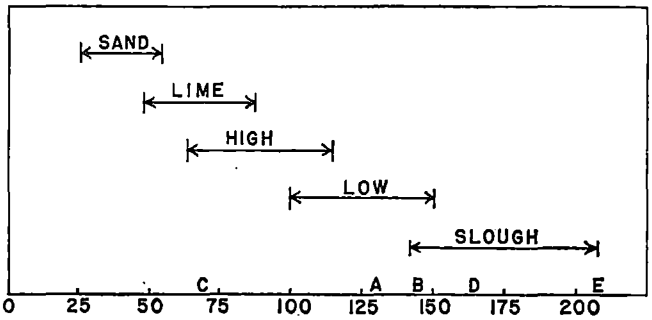

FIGURE 1: The location and amplitude of several prairie types on a water-holding capacity scale.

METHODS: To determine the relation between the water-holding capacity and the distribution of species, a grid was made on a part of the Faville Prairie using twelve rows of fifteen quadrats each, with all rows 100 feet apart as indicated in Figure 2. Thus an area 1200 feet by 1500 feet, or a little over 40 acres, was sampled. It is believed that both this size and the history of the area have allowed any species to long since occupy any or all of the area that provided favorable conditions.

Species lists were made for each of the four square meter quadrats. These were checked in the spring, summer, and early fall so that practically all of the species have been found. Some grasses may have been insufficiently represented since they were checked only if in the fruiting condition.

A soil sample from the surface three inches was obtained from each quadrat and its water-holding capacity determined (Hilgard, 1906). These water-holding capacities were grouped into classes. To insure that all classes contained at least five quadrats, the upper poorly represented portion of the scale was divided into two parts of greater magnitude than the usual class size of 20 scalar divisions (Table 2). Each of the classes contained a certain number of quadrats and therefore also a certain percentage of the total quadrats. These numbers and percentages are also given at the beginning of Table 2.

The number of quadrats in each class in which a given species occurred was likewise determined. From the number of quadrats in each class and the number of these quadrats in which a given species occurred, the percentage of occurrence could be calculated for each species in each class. Thus class number 2 (from 80 to 100 percent) contains 16 quadrats. *Blephilia ciliata* occurs at 8 of these 16 quadrats. Thus *Blephilia ciliata* has a 50

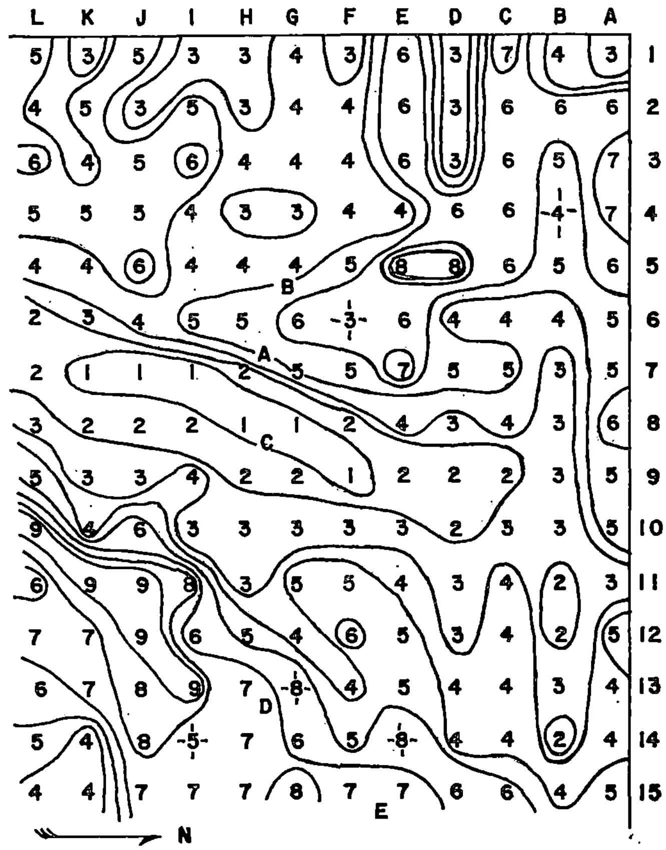

FIGURE 2: Map of Faville Prairie showing the areal distribution of water-holding capacity classes.

TABLE 2. Frequency distribution in water-holding capacity classes of species found in five or more quadrats on the Faville Prairie.

Class Number	1	2	3	4	5	6	7	8	9	Freq. in 180 Quads
Class Size	60-80	80-100	100-120	120-140	140-160	160-180	180-200	200-250	250-320	
Total Quadrats	6	16	33	41	32	26	13	8	5	
% of total Quadrats	3	9	18	23	18	14	7	4	3	
Achillea Millefolium	(83)*	38	18	7	9	8				13.8
Andropogon Gerardi		19	24	15	(31)	12				16.6
Andropogon scoparius	(83)	56	39	22	22	12	15			26.6
Anemone canadensis		38	24	24	(47)	19	15		20	26.1
Antennaria sp.	17	6	(15)	5						5.0
Apocynum cannabinum			3	17	(22)	12	8	12		11.1
Arenaria lateriflora		6	(9	5	9)	8				6.1
Asclepias Sullivantii		6		5		(12)				3.3
Asclepias syriaca	17	19	24	(27)	22	12				18.3
Aster azureus	(100)	81	58	32	31	23	23			38.8
Aster novae-angliae			9	2	6	8	15		(40)	6.6
Blephilia ciliata	17	(50)	12	5						8.3

TABLE 2. (Continued)

Class Number	1	2	3	4	5	6	7	8	9	Freq. in 180 Quads
Class Size	60-80	80-100	100-120	120-140	140-160	160-180	180-200	200-250	250-320	
Calamagrostis canadensis			6	7	12	4	15	25	(40)	8.8
Carex Bicknellii	(100)	50	24	5	3					13.8
Carex sp.					6	12	15	(25)	20	5.5
Comandra umbellata	(67)	6	9							4.4
Convolvulus sepium	17	(19)	15	15	3					8.8
Dodecatheon Meadia	33	6	(27	27)	19	23	8			20.0
Epilobium glandulosum				5	9	12	23	38	(80)	10.0
Erigeron philadelphicus			3	(10)	6	4				5.0
Erigeron strigosus	(50)	13	15	5	6					8.3
Eupatorium maculatum						4	15	12	(60)	5.0
Eupatorium perfoliatum				2	3	4	15	25	(100)	8.8
Euphorbia corollata	(100)	63	6	2						10.5
Fragaria virginiana		6	9	7	(16)	8				7.7
Galium tinctorium			12	2	3	(15)	8	12		7.2
Gentiana clausa			(9)	5	6					3.8
Helenium autumnale				2	9	19	46	50	(80)	16.6
Helianthus grosseserratus		31	(48)	39	28	23	8	12		30.0
Heuchera Richardsonii	(100)	19	6	2	3	4				7.7
Hypoxis hirsuta	(100)	88	67	51	44	27	15	12		48.3
Iris virginica			21	31	(38)	27		(50)	20	24.4
Lespedeza capitata	(50)	6	3							2.7
Liatris pycnostachya	67	38	(67)	51	31	31	23			41.1
Lithospermum canescens			6	2	6					2.7
Lobelia spicata			3	2	3					2.7
Lycopus spp.	17	31	18	31	22	31	31	50	(100)	29.4
Lysimachia quadrifolia			30	(39)	28	31	31			26.1
Lythrum alatum			12	15	(22)	15		25		13.8
Mentha arvensis				5	9	8	23	50	(100)	10.5
Panicum sp.	(67)	25	6	10						7.7
Petalostemum purpureum		(13)	6	5	3	4				4.4
Phalaris arundinacea					3	15	31	(38)	20	7.2
Phlox pilosa	(33)	6	18	12	12	4	8			11.1
Physostegia sp.							8	12	(40)	3.3
Polygonum natans					3	4	8	12	(20)	5.0
Potentilla arguta	(50)	6	12			4				5.0
Potentilla simplex	(67)	13	6	5		4	8			6.6
Pycnanthemum virginianum			33	37	(38)	23	15	12		28.3
Ratibida pinnata	67	(81)	64	39	41	15	8			40.0
Rosa sp.	(50)	25	15	7	19	8		12		13.3
Rudbeckia hirta	(67)	19	36	34	16	15	23			25.0
Rumex verticillatus				5	6	8	31	50	(80)	10.0
Salix sp.		12	30	34	34	31	23	(38)		28.3
Scutellaria epilobiifolia						4	8	25	(40)	3.3
Senecio aureus			9	12	12	(19)	8			10.0
Silphium laciniatum		19	33	54	53	(58)	23	25		47.8
Silphium terebinth.	33	56	(61)	54	47	31	15			43.3
Sisyrinchium sp.	33	(81)	30	10	3	4				16.6
Sium suave				10	(12)	4				8.3
Smilacina stellata	(67)	6	3							3.3
Solidago altissima and S. gigantea	17	19	24	47	34	58	62	25	80	39.4
Solidago nemoralis	(83)	56	45	20		4	8			22.2
Solidago Riddellii	33	31	39	(41	41)	19	8			31.1
Solidago rigida	(100)	56	54	10	9	8				23.3
Sorghastrum nutans			12	5	6	(15	15)			7.7
Spartina pectinata		12	27	24	(47)	19	8	12		23.8
Spiraea alba		6	24	22	41	(46)	8	12		25.5
Stachys palustris			6	12	19	12	54	(75)	40	17.1
Thalictrum dasycarpum	17	12	21	12	(22)	12				13.8
Valeriana edulis			9	5	3	12	(23)			6.6
Verbena hastata		12	6	12	12	12	38	38	(80)	15.5
Vernonia fasciculata					16	19	8	(25)	20	14.4
Veronicastrum virginicum			6	24	22	(27)				14.4
Viola cucullata		19	9	24	(25)	8	8			15.0
Total number of species	32	45	61	64	60	61	44	29	20	
Number to reach optimum	19	5	6	4	11	7	2	6	13	

*Parentheses mean optimum reached in that class percent rate of occurrence or frequency in this class. The frequencies thus obtained are given in Table 2. Only those species are included which occurred in at least 5 of the 180 quadrats.

RESULTS: The range in water-holding capacity, from 66% to 314%, is considerable. The areal distribution of the classes is mapped in Figure 2. The number of quadrats within each of the classes is not the same. Figure 2 reveals that the classes are distributed in gradient patterns on the land. There is one small area which contains all the lowest water-holding capacities and another which contains most of the highest. Between these extremes the gradient changes with surprisingly few irregularities. Each gradient does not occupy the same space along any two transects. One transect 300 feet long (from quadrat 7-K to quadrat 10-L, Figure 2) includes all nine classes, whereas many transects 500 feet long are within one class.

Vegetation likewise has exhibited a considerable lack of homogeneity. Slightly more than half of all the species found on the area occurred in less than five of the quadrats or did not occur in any. Even those 75 species occurring in five or more quadrats and thus included in Table 2 show definite areas of presence or absence (Figure 3).

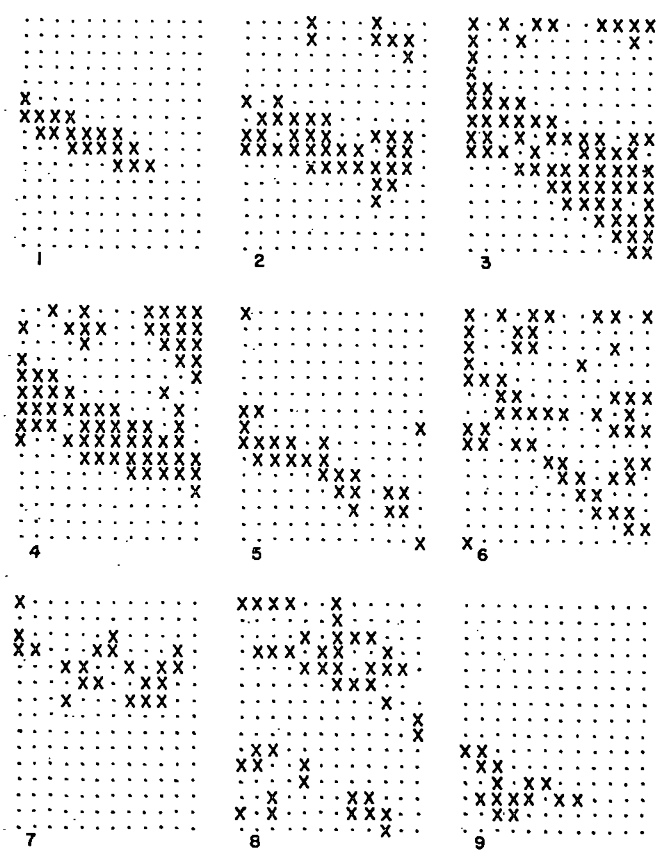

FIGURE 3: Areal distribution of some species on the Faville Prairie.

1. *Euphorbia corollata*
2. *Solidago rigida*
3. *Ratibida pinnata*
4. *Aster azureus*
5. *Thalictrum dasycarpum*
6. *Solidago Riddellii*
7. *Apocynum cannabinum*
8. *Iris virginica*
9. *Eupatorium perfoliatum*

The species show distribution not only in space but also within the water-holding capacity classes. From the data presented in Table 2 several aspects of occurrence may be differentiated. Immediately noticeable is the fact that a species may be either present or absent in any one class. This leads to different numbers of species in each class. Four classes near the center of the scale are seen to contain sixty or more species each (still considering only those in Table 2), which is possible because the species found there have several centers of occurrence. There is one group, called Group 1, in which the 25 species do not reach either of the extreme classes. Another group, Group 2, of 31 species extends to the dry end but not to the wet end, whereas Group 3 of 18 species reaches to the wettest class but not the driest. All species in Table 2 except one – *Physostegia sp.* – extend into the central 100–180 per cent range, thus accounting for the sixty or more species in each of the included classes.

If sampling were completely accurate, Group 1 would represent a number of species which, here in this restricted area, find both the upper and lower limits of their ecological range for this one soil moisture characteristic. Here is found the second aspect of occurrence illustrated – a species is present within a certain range or amplitude, the limits of which would no doubt be extended with more extensive sampling in other areas. Only *Lycopus* ranges into all classes. It is not known whether this represents more than one species. One pair of species, *Solidago gigantea* and *Solidago altissima*, was erroneously checked as one species. One or the other of these was found in all classes. No positively identified species did range into all classes. *Hypoxis hirsuta* and *Phlox pilosa*, checked during a dry spring, ranged into all classes except the wettest. Some species, such as *Euphorbia corollata*, *Lespedeza capitata*, and *Smilacina stellata*, seem definitely restricted to the drier water-holding capacities. Some such as *Eupatorium maculatum*, *Physostegia sp.* and *Scutellaria epilobiifolia*, seem equally restricted to the wetter water-holding capacities. This restricted distribution is even more pronounced with some species that were not found in at least five quadrats: *Typha latifolia*, *Sagittaria sp.*, and *Acorus calamus* at the wet end and *Gnaphalium sp.*, *Linum sulcatum*, and *Viola pedata* at the dry end.

TABLE 3. The number of species to reach their amplitude limits in each of the water-holding capacity classes.

	1	2	3	4	5	6	7	8	9
Group 1 (Number reaching dry limit in each class)		11	13	1					
(Number reaching wet limit in each class)					3	8	5	9	
Group 2 (Number reaching dry limit in area only)		2	4	5	4	2	1		
Group 3 (Number reaching wet limit in area only)			5	4	3	6	10	2	
Total reaching dry limit in area		13	17	6	4	2	1		
Total reaching wet limit in area			5	4	6	14	15	11	

The fact that all amplitudes reach an upper and a lower limit somewhere may be designated as the third aspect of occurrence. The occurrence of species as shown in Table 2 is seldom interrupted to give a false limit of amplitude. Considering the possibility of a complete and accurate sample, most every species of the Faville Prairie reaches at least one amplitude limit here. The number of species to reach their amplitude limit in each class is presented in Table 3.

The fact that large numbers reach their limits in the third and seventh classes suggests that these are two transition zones. On the other hand, the quadrats in classes 4 and 5 should represent a fairly homogeneous area, since relatively few species reach their limits here. To test this homogeneity the frequencies of species in all 180 quadrats may be compared with the frequencies of those occurring in classes 4 and 5.

CONCLUSIONS AND SUMMARY: The Faville Prairie has a great range in water-holding capacities and considerable variation in local plant distribution. The water-holding capacities, placed in classes, is not equal in amount of area included in each class nor are these classes distributed at random over the area. On the contrary, definite patterns or zonations seem to exist.

Maps of species distribution reveal non-random patterns. Each part of the area is seen to be transitional to some adjacent part because no two species have the same micro-geographic ranges. The occurrence of a species may be determined for each of the classes, thus arriving at a better idea of the ecological range of that species even if for only one environmental factor.

Several aspects of occurrence have been recognized: 1. Every species has an ecological range or amplitude when plotted along a scale of water-holding capacity classes. Each amplitude has a beginning and an end; therefore, depending on the class, a species may be present or absent.

Data for Raunkiaer frequency distribution diagrams are as follows:

Frequency for	Number of Quadrats	Number of Species	Raunkiaer Frequency Classes 1	2	3	4	5
All water-holding capacity classes	180	75	72.5%	21.5%	6.0%	0	0
Water-holding capacity classes 4 and 5......	73	69	67.0%	24.0%	8.5%	0	0

These data are quite similar. They indicate that most of the species are not highly ubiquitous in either portion of the area.

The behavior of any species is not the same in all classes within its amplitude. This fourth aspect of occurrence is reflected in almost normal distributions within each amplitude. The mode of such a distribution may be thought of as the optimum water-holding capacity for each species. This is shown in Table 2 as the class in which any species reaches its highest per cent frequency. Several such distribution curves are shown in Figure 4. For most species the mode occurs in one definite class with decreases evident on both sides. When the high frequency occurs in either the first or the last class only one slope of frequency decrease is seen. The two end classes appear to contain the greatest number of modal species merely because the true modes of many would be beyond the limits of the study area (see the totals at the end of Table 2). The other high point in the center class between water-holding capacities of 140 and 160 per cent corresponds to the transition between low prairie and prairie slough as shown in Figure 1. Here such species as *Anemone canadensis*, *Apocynum cannabinum*, *Iris virginica*, *Pycnanthemum virginianum*, *Spartina pectinata* and *Thalictrum dasycarpum* find their optima. These may be considered as species which find the most favorable conditions in the lower parts of low prairies and do not range into either of the extreme classes as found in this area.

The affinities of species in the same genus for different moisture conditions often shows marked contrast. *Aster azureus* and *Aster novae-angliae* are seen to be at, or near, their optima at the two extremes of this area. *Solidago* and *Silphium spp.* are also modal in different portions of the scale.

2. The amplitudes differ in extent. Of those species which occur in at least 5 of the 180 quadrats, most of them have amplitudes covering 5, 6, or 7 classes or over 100 per cent water-holding capacity. There are other species with greater or with less amplitude size. Obviously water-holding capacity is not the only limiting factor. Many amplitude limits are not reached in this area. Where an upper or lower limit does occur in the area, exhibited by all but doubtful species, it is usually at some definite class. The occurrence of a species seldom skips classes to re-appear at some distant class. Even in those few cases studied of a species amplitude changing from one year to the next, classes were added or evacuated in blocks.

3. The amplitudes differ in position or location on the scale. The greater number of species occur in the centrally located classes, which would probably be the case in any study area since added to the species which occur throughout most of the classes, and therefore most of the area, there are those with amplitudes nearer the extremes. In any class of the scale there are always some species which have reached their limit.

4. A species responds differently in various parts of the amplitude. Although measured only by frequency of occurrence, it is evident that each class differs in its importance to the species. The frequencies for any one species result essentially in a normal distribution which thus has an optimum with two decreasing segments on either side. It is quite significant that species do not continue with equal importance up to a certain point on the scale and then disappear completely. It is believed that all

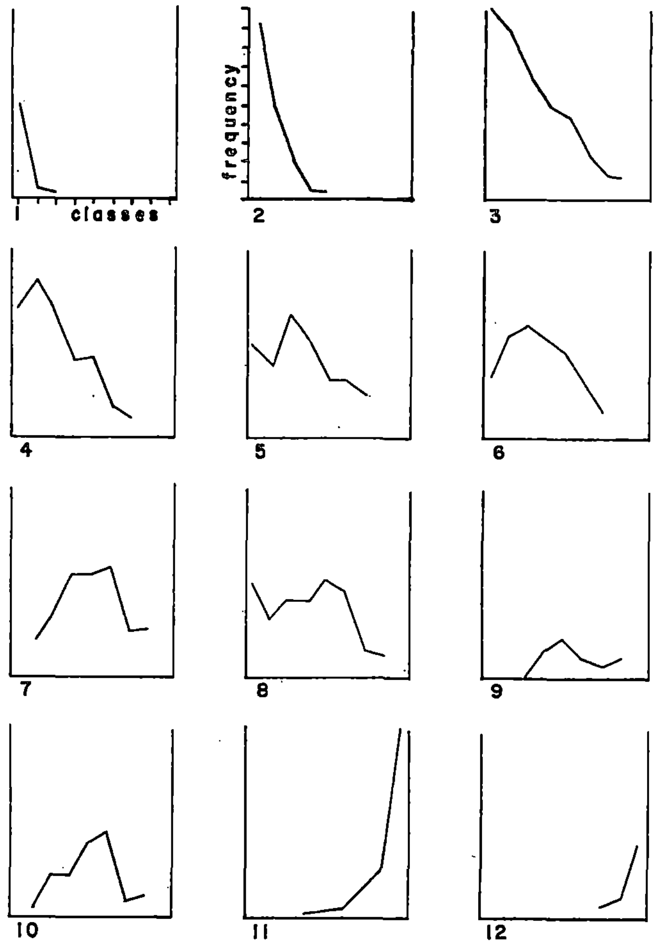

FIGURE 4: Frequency distribution in water-holding capacity classes.

1. *Lespedeza capitata*	7. *Silphium laciniatum*
2. *Carex Bicknellii*	8. *Phlox pilosa*
3. *Hypoxis hirsuta*	9. *Apocynum cannabinum*
4. *Ratibida pinnata*	10. *Spiraea alba*
5. *Liatris pycnostachya*	11. *Eupatorium perfoliatum*
6. *Silphium terebinthinaceum*	12. *Physostegia sp.*

species on any environmental scale would show similar relationships. Many of the species do not reach their optima in this area and so their distribution is marked solely by some limited part of one of the decreasing segments. This latter fact is responsible for the false accumulation of optima in either of the extreme classes. It is believed that the largest number of optima fall naturally into a centrally located class because the species which can find favorable conditions there will never be affected by great changes that are normal in the two extreme classes. Not all optima in any class are equal. The position has been determined for one soil moisture characteristic; the height of the mode is just as dependent on other environmental characteristics.

These data indicate that geographic boundaries cannot be relied upon to give ecological boundaries to any plant community. The species in any stand are present because they find conditions favorable for a part or all of their amplitudes. There is a range of conditions found in any area. If an area has environmental variations there will always be some species which are adversely affected by the extremes. When two species, each occurring only at opposite extremes, are examined as to degree of association, it is no wonder that they show great independence. The amplitudes of the two may not overlap, and if not, the two species could never really be a part of the same community even though occurring in the same stand or study area. For example, *Blephilia ciliata* was never found in the same quadrat with *Eupatorium maculatum*, or *Heuchera* with *Physostegia*, or *Lespedeza* with *Vernonia*.

It is seen in Table 2 that any one water-holding capacity class has a certain group of species. An adjacent class has some of the same species, usually in different proportions, has lost some of these species, and has added some new species. This process continues in either direction on the scale. Only the rapid change, in space, in another factor can change the pace of this process, which must then be placed on a scale of this new factor. Any one species is seen to reach the limits of its own amplitude and its own optimum within this amplitude independent of the limits and optima of most other species. Thus the group of species found in any one arbitrary water-holding capacity class may be considered as an arbitrary community, but, as such, is not totally distinct from communities adjacent to it on an environmental scale. Each one is, ecologically, merely transitional between its two adjacent communities.

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