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The quadrat method of studying vegetation has become an integral part of many of the more important ecological investigations. Although occasionally used throughout the past century for determining the amount of plant material produced or for purposes of enumeration, it was organized into a definite system for the study of the structure and development of vegetation by Pound and Clements (15, 16) and Clements (2, 3, 5) only about eighteen years ago. Since that time it has been used, sometimes in a modified form (12, 21), by numerous investigators both American and European. Indeed, with the rapid increase in the number of successional and other ecological studies the use of the quadrat and its modifications is becoming as universal as it is fundamental (6).

Not a few of the many important problems connected with grazing, land classification, indicator vegetation, afforestation, and reforestation have been solved by the aid of the quadrat method.

By the use of this method Sampson (17) has worked out a system of deferred grazing for the ranges in the national forests whereby the forage crop is utilized in such a way as to maintain the lands at their highest state of productiveness and at the same time give the greatest possible returns to the stock industry. He has also shown in a very concrete and satisfactory manner the application of a knowledge of plant succession to range management (19).

Kearney and his co-workers (10) have employed the quadrat method in the Tooele Valley of Utah, an area typically repre-

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ILLUSTRATIVE EXPERIMENTS IN THE SALT FLATS

A part of the territory adjacent to Lincoln and several square miles in extent is unique in that it is a salt desert, or at least is covered with halophytic vegetation (fig. 1). Although the origin of this salt basin has never been satisfactorily worked out it is believed to be due to the settling of the area to a depth of a few feet. The water of the salt lake originated from an artesian well. Much of this basin is watered by salt springs.

On a portion of these salt flats an area was selected which showed distinct zonation from the bare alkali flat to rather

Fig. 1. A general view of a portion of the salt desert near Lincoln. The chief components of the vegetation are *Dondia depressa* and *Atriplex hastata*.

typical upland prairie. These zones in the order of their sequence are: (1) *Dondia depressa*, (2) *Atriplex hastata* with *A. argentea*, (3) *Distichlis spicata*, and (4) prairie. These may be seen in figure 2. Numerous soil samples were taken which proved conclusively that the zonation was not caused by differences in soil moisture. Indeed, the prairie is only about two feet higher than the bare area. A chemical analysis of the soil in the several zones was then made. Samples were taken to a depth of 8 inches soon after a rain had wet the soil to just that

depth. This gave presumably a rather equal distribution of the salts.[2]

The distribution of the alkali in the various plant communities is shown in the table.

	BARE AREA	DONDIA	ATRIPLEX	DISTICHLIS	PRAIRIE
Na + K	1.502*	1.304	0.878	0.728	0.418
Na₂O	2.024	1.757	1.183	0.981	0.563
Na₂CO₃	3.452	3.004	2.001	1.677	0.963

* In the table, sodium and potassium are given together. There are varying amounts of the two metals though most of the mixture consists of sodium. In the calculations only sodium has been considered and the sodium oxide and sodium carbonate have been calculated from the weight of sodium and potassium as if only sodium was present.

The table at once reveals the salt content as the controlling factor in the distribution of the vegetation. Usually *Salicornia herbacea* accompanies or even precedes *Dondia* in the saltier places but it was not present in the area under consideration. It grows in wet spots on the floor of the basin, in the saltiest of soil, often growing through a crust of salt and is frequently the sole inhabitant. (Cf. figure 3.) *Corispermum hyssopifolium* frequently occurs with *Atriplex* or covers areas exclusively where the situation is subruderal.

The area occupied by these halophytes is alluvial wash where the salt has been deposited by successive overflows year after year. Formerly it was much more extensive. The halophytes are rapidly being replaced by other species and by crop plants as the soil becomes less salty due to better drainage resulting from the straightening of stream courses. The replacement of salt grass by prairie species is often clearly marked. *Agropyrum repens* is often the first invader and is followed by *Sporobolus longifolius, Panicum virgatum, Andropogon furcatus,* and other prairie species. An interesting successional sequence was determined while making a bisect in a rich alluvial flood plain where the water level occurred in gumbo soil at a depth of about

[2] The writer is indebted to Professor C. J. Frankforter of the department of chemistry for these determinations.

Fig. 2.   A small area in the salt basin showing the zonation of *Dondia depressa* (darker border adjoining bare areas), *Atriplex hastata* (upper right portion of the figure especially), *Distichlis spicata* and prairie (just in front of and behind the man in the figure respectively).   The numbers indicate the locations of permanent quadrats.

Fig. 3.   Salt incrustations on *Dondia depressa*, October, 1917.

six feet. Although only an occasional specimen of *Distichlis* was to be seen, the soil contained three distinct strata of its abundant and well-preserved rhizomes at depths of 13, 9, and 6 inches respectively. These indicated successive overflows and deposits. Above these the soil was filled with a dense network of the rhizomes of *Agropyrum repens*. However, only a few of these plants were still alive, the soil being almost completely occupied by alternate areas of *Sporobolus longifolius* and *Bulbilis dactyloides*.

On the ecotones between the several plant zones in the above areas (fig. 2) several quadrats were permanently staked out, photographed and charted in the fall of 1916. Since more striking changes take place yearly among the annuals—*Dondia* and *Atriplex*—than in the more stable grass zones, a few quadrats in areas occupied largely by the former species are chosen for illustration here.

Quadrat 5 was located in such an area that it included bare alkali flat, a narrow zone of *Dondia*, and extended into the *Atriplex* area (fig. 2). Photographs of this quadrat taken in the fall of 1916, 1917, and 1918 respectively are shown in figure 4. The rank growth of *Atriplex* is due to a depression through which surface water drains after rains. The soil on either side is more salty. A study of these figures together with the chart quadrats in figure 5 reveals a number of interesting changes. One of the most striking is the almost total disappearance of *Dondia* in 1917 with the advance of *Atriplex* far out into the former *Dondia* area. A count made on June 1, 1917, showed at that time 63 and 289 Dondias respectively in the first two decimeter rows of the foreground, while the next two consisted of 966 *Dondia* and 169 *Atriplex*, rather evenly distributed. What caused this practically 100% mortality of *Dondia* in this portion of the quadrat and the dominance of *Atriplex* is a question which the student at once appreciates, and can only be solved by visits to the field during the growing season. The drought during July when only 0.56 inch of the 4.01 inches precipitation normal for that month occurred was probably the time of greatest mortality.

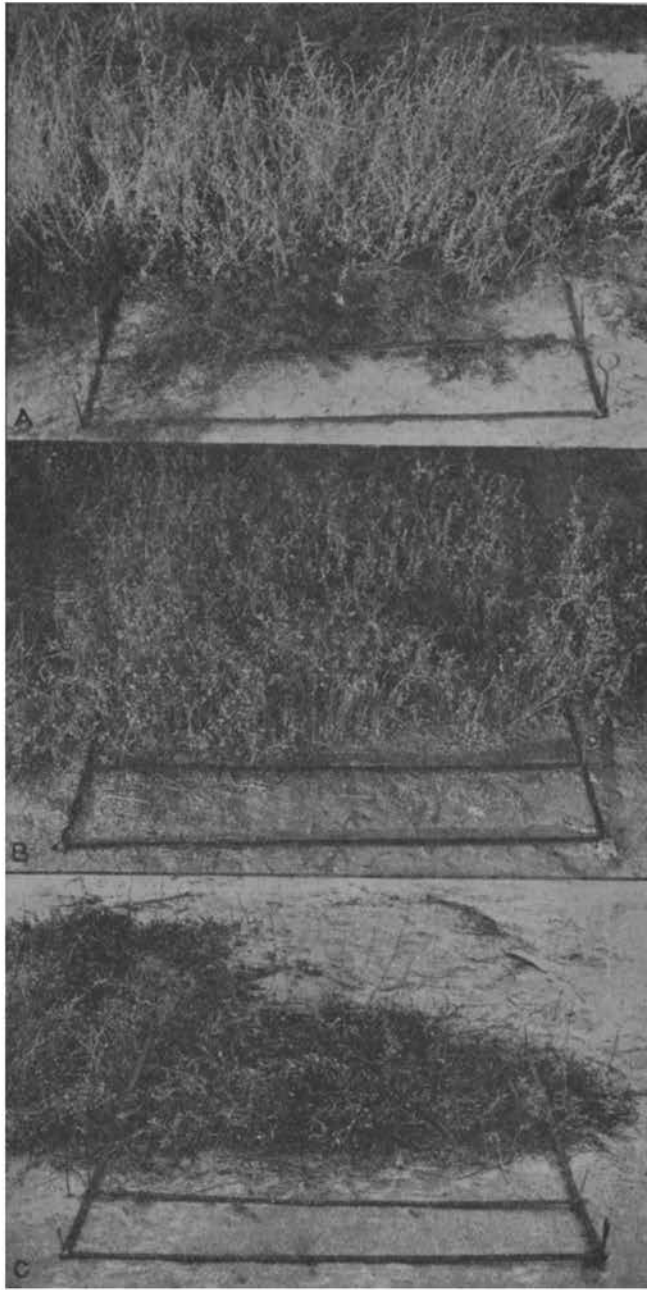The thin stand of *Atriplex*, its small stature, and its presence

Fig. 4. Photographs of quadrat 5 in the salt flats in October, 1916 (A), 1917 (B), and 1918 (C) respectively. The chief species are *Atriplex hastata* and *Dondia depressa*.

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in only the moister portion of the quadrat in 1918 is quite evident. The summer was one of severe drought. From May 1 to September 1 the precipitation was only 52% of the normal. Indeed the area yielded only 26% of its former quota of plants and these were less than half their normal size.

Quadrats 1 and 2, which were adjacent, were located in such a manner that the adjoining portions extended over a small ridge and the other ends into the *Dondia* and *Atriplex* zones.
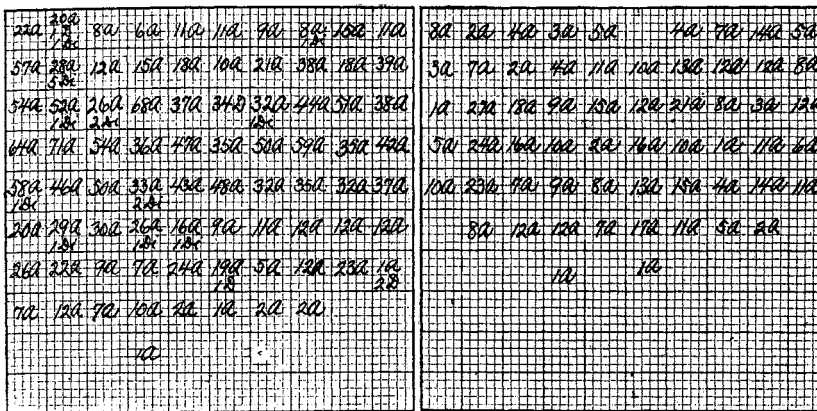

Fig. 5. Quadrat 5 charted in October, 1917 (left) and 1918. A = *Atriplex hastata*, D = *Dondia depressa*, Di = *Distichlis spicata*.

These are shown in figure 6. In 1916 the presence of *Distichlis* on the ridge indicated that it was an old eroding area. In 1917 numerous rhizomes were exposed and by 1918 living plants had entirely disappeared. The invasion of *Dondia* further into both quadrats in 1917 is quite apparent as is also the much greater abundance and extent of *Atriplex*. The small amount of *Dondia*, the reduced number of *Atriplex* and its withdrawal to the more stable portions of the area in 1918 are readily apparent. This agrees with quadrat 5 and is verified by several others.

Such an analysis by students teaches them to think in terms of vegetation and environment. The time employed in charting the quadrats is seldom over half of a day, for two students are

usually assigned to only one or two quadrats. This leaves time
for a general survey of the field. After the quadrating has been
accurately accomplished they are furnished with the records of
preceding years and are required to give a discussion at some
future time of the movements of the vegetation. Not infre-
quently after such class discussion students voluntarily revisit
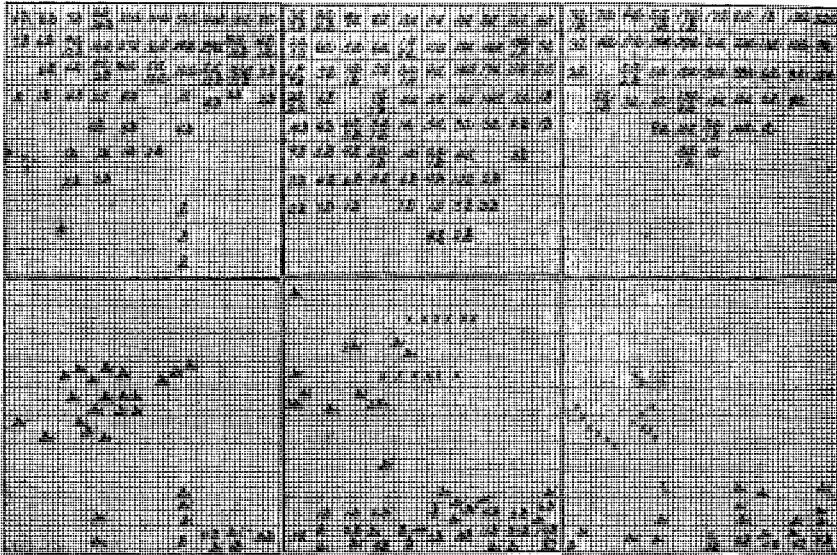the field for further data.   .

Fig. 6. Quadrats 1 and 2 plotted in October, 1916 (left), 1917, and 1918
repectively. A = *Atriplex hastata*, D = *Dondia depressa*, Di = *Distichlis spicata*,
X = rhizomes of *Distichlis*, H = *Hordeum jubatum*, P = *Polygonum aviculare*
R = *Rumex altissimum*.

ILLUSTRATIVE EXPERIMENTS IN THE PRAIRIE

Rather large tracts of native grassland undisturbed except by
mowing are still to be seen in eastern Nebraska. During the
past few years a small area of high prairie has been set aside
for investigational purposes. This is undisturbed except for
denuded quadrats, planted quadrats, bisects, etc. (24). A knoll
in this high prairie is underlaid with a glacial deposit of coarse
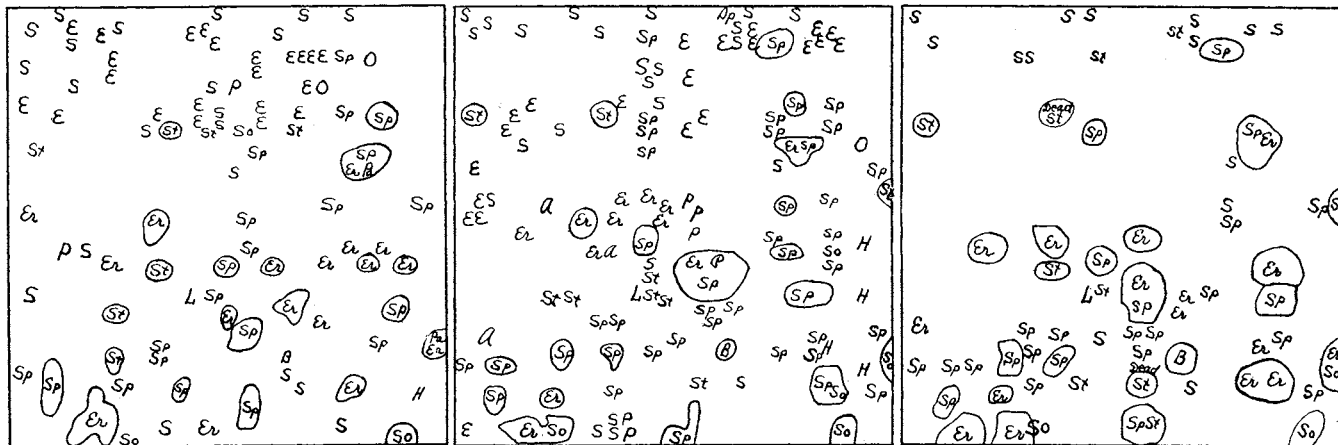
Fig. 7. A quadrat in an unstabilized area in the prairie, charted in October, 1916 (left), 1917, and 1918, respectively. The legend is as follows:

S = *Solidago missouriensis*
E = *Euphorbia serpens*
O = *Onagra biennis*
Sp = *Sporobolus longifolius*
P = *Physalis heterophylla*

St = *Stipa spartea*
So = *Sorghastrum avenaceum*
Er = *Eragrostis pectinacea*
Pa = *Panicum capillare*

L = *Laciniaria punctata*
B = *Bouteloua oligostachya*
H = *Helianthus subrhomboideus*
A = *Ambrosia artemisiaefolia*

next. These data teach greater lessons each year. The fact that all the work has been done by former students adds interest. Such a study makes the method of inference, that is the piecing together the course of development of the associes and consocies found in the region, much clearer and more accurate. Of course such work is further supplemented by permanent quadrats in stabilized areas, denuded quadrats, planted quadrats, ecotone transects extending from shrub to prairie or woodland to shrub, or across the zones of *Spartina*, *Typha*, etc., in ravines, and by bisects. A series of denuded quadrats, each set a year older than the preceding, gives at once the stages leading to stabilization. By means of these permanent studies, coupled of course with factor data and measurements of the plant responses such as transpiration, photosynthesis, and growth in the several habitats, a student is enabled to gain a maximum of results with a minimum expenditure of time.

ILLUSTRATIVE EXPERIMENTS IN RUDERAL VEGETATION

An easy approach to the use of the quadrat method by students whose floristic knowledge is rather limited is by the study of families of large ruderals such as *Ambrosia trifida*, *Helianthus annuus*, *Iva xanthiifolia*, etc. Such work may be used to illustrate certain laws of competition in a very satisfactory manner. Necessarily competition is greatest between individuals or species which make similar or identical demands upon the same supply at the same time.

On April 27, 1916, the plants in three square meters, selected as representative of a waste area, were carefully counted. Then the quadrats were permanently marked. This area consisted of a small level tract of very rich loam soil of alluvial origin. The average number of plants per square meter was 10,500. Practically all were *Ambrosia trifida;* only a few *Polygonum pennsylvanicum* and an occasional *Solanum rostratum* were also present. At this time the plants averaged 9 cm. in height and had roots about 25 cm. long. A count on June 22 gave an average of only 206 plants per square meter, while on July 24 this number had been reduced to 100 per unit area, all of which were rag-

weeds. Of these 30 per cent were dominants with an average height of 2.64 m. while 70 per cent were suppressed and averaged only 1.23 m. in height. The dominants had a diameter of 1.5 cm., the suppressed group were only 0.6 cm. in average diameter.

In October another quadrat where more plants had matured was included and the number, height and diameter of the individuals were recorded. These data are shown in the table.

NUMBER OF PLANTS	AVERAGE HEIGHT	AVERAGE DIAMETER
	m.	cm.
192	2.35	0.7
146	(2.27)	0.9
88	2.50	(1.2)
66	2.66	1.00

Assuming that the quadrat with the 192 survivors had as many plants originally as the average of the other three, i.e., 10,500, then the average mortality in the four areas was 98.8%, that is only 1.2% of the plants reached maturity!

This is certainly a striking lesson in competition. An examination of the table reveals a close relation between the number of individuals and their height and diameter, the plants always being larger (with the exceptions shown in parentheses) where the individuals are fewer. Competition is essentially a decrease of the amount of light, water or solutes available for each individual. By affecting these factors it affects the response of the plant. That water was an important factor was shown by the plants growing in a shallow drainage ditch. They were just as high as those on the adjacent area. Viewed from the tops of the plants one would not suspect a depression was present. On the other hand light was shown to play an important rôle for in quadrats containing an average of 16,000 individuals of *Polygonum aviculare* seedlings on April 27, 2,700 or an average of 17% reached maturity in October. Among these grass-like plants competition for light does not occur in any such degree as with the broadleaved *Ambrosia*.

This experiment was repeated by the class of 1916–17 with similar results. The mortality among *Ambrosia* averaged 95%.

The relation between number and size of plants is shown in the table.

NUMBER OF PLANTS	AVERAGE HEIGHT	AVERAGE DIAMETER
	m.	*cm.*
58	1.58	0.67
40	1.89	0.70
33	2.11	1.01
30	(1.97)	(0.95)

These results are very similar to those preceding.

In the spring of 1918 the struggle among 7,350, 7,100, and 10,350 individuals per square meter respectively was terminated by the area being converted into a garden. However, in the fall an examination was made to see if the same principle applied as regards competition and reduced size to a family of *Iva xanthiifolia*. The results are shown in the following table.

NUMBER OF PLANTS	AVERAGE HEIGHT	AVERAGE DIAMETER
	m.	*mm.*
79	1.67	5.9
59	1.72	7.0
45	1.81	7.2
32	2.11	9.8
29	(2.06)	12.7
25	2.37	13.4

Investigations in other areas will undoubtedly reveal similar relations.

Such studies, so elementary that a class can secure sufficient data for conclusions in a single afternoon, point the way to an investigation and discussion of some of the most fundamental questions of ecology. It involves the problems of aggregation, seed production, size and germinability of seeds, analysis of competition, causes of dominance, reactions, etc. Moreover it throws much light upon many problems in crop ecology (cf. 11). Among these are method and the rate of seeding, *i.e.*, thick or thin stand, uneven germination, and its effect upon yield, competition, effects of weeds upon cultivated crops and upon sum-

mer fallow, and many others. Of course the repeated use of the quadrat method soon reveals its bearing upon problems of grazing, crop estimation, disease survey, and forestry. It furnishes the student with a concrete basis for interpreting work already accomplished along these various economic lines.

In conclusion it may be said that it is the experience of the writer that the use of the quadrat by students teaches accuracy, inculcates habits of close observation and logical reasoning in the field. Too often students in the field are inclined to form superficial generalizations if indeed they are not too puzzled by the complexity of the problems in the general panorama, rather than to lay hold upon this problem or that phenomenon and having reduced it to order gain some definite insight into the behavior of plants in nature.

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