EFFECT OF SIZE AREA OPEN TO COLONIZATION ON SPECIES COMPOSITION IN EARLY OLD FIELD SUCCESSION

> Thesis for the Degree of M. S. MICHIGAN STATE UNIVERSITY ROGER M. DAVIS 1968



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THESIS

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#### ABSTRACT

# EFFECT OF SIZE AREA OPEN TO COLONIZATION ON SPECIES COMPOSITION IN EARLY OLD-FIELD SUCCESSION

by Roger  $\mathbf{M}_{i}^{C_{ij}^{ijk}}$  Davis

This study deals with the effect of size of an area open to colonization in early old-field succession in southwestern Michigan. The prime questions of the study are what effect does opening size (or size of the area available for colonization) have in determining the species present in the openings and how does the existing undisturbed vegetation affect future stages in the succession?

The study was carried out in a newly abandoned field on the Gull Lake Biological Laboratory property in Kalamazoo County, Michigan. The field had been planted to corn in 1964 and abandoned after the fall harvest. In June 1965 openings ranging in size from  $.01m^2-100m^2$  were dug or plowed into the existing undisturbed fallow vegetation. The openings were then sampled in August 1965, June and August 1966, and June 1967. Per cent cover values by species for each

opening were obtained. In addition 0.5m x 2m quadrats of the undisturbed fallow vegetation were sampled in the same manner.

The course of succession was found to be slightly different in the openings as compared with the undisturbed vegetation. Smaller openings were more like the undisturbed vegetation than the larger openings in the first year, but this difference gradually declined in succeeding seasons.

The per cent cover of 14 of the 77 species found appeared to be correlated with the size of the opening. The most striking effect was noted in <u>Amaranthus retroflexus</u> which was significantly positively correlated with increasing opening size. The size of <u>Amaranthus</u> plants also showed an increase with increasing opening size. The majority of the 14 species showing correlations with opening size were positively correlated with increasing opening size though several negative correlations occurred.

These studies suggest that opening sizes smaller than 100 cm<sup>2</sup> would be best for examining various mechanisms operating in producing the organization that develops with the successional process.

For the range of sizes used, evidence indicates that the opening does not affect the later pattern of succession by altering species composition, nor does it seem that the initial dominant annuals have a determining influence on the later pattern of succession, at least for the dominants found here.

# EFFECT OF SIZE AREA OPEN TO COLONIZATION ON SPECIES COMPOSITION IN EARLY OLD-FIELD

# SUCCESSION

Ву

Roger M.<sup>jth.atl</sup> Davis

## A THESIS

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

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# EFFECT OF SIZE AREA OPEN TO COLONIZATION ON SPECIES COMPOSITION IN EARLY OLD-FIELD SUCCESSION

#### I. INTRODUCTION

Succession as described by Margalef (1963) is the process of the community's becoming more precisely adjusted to its environment. Viewed from another perspective, it is the process by which the species of a regional biota colonize and hold their niches against their competitors. Several generation times of the later, long-lived, species populations are necessary to stabilize the system. This process is one of fundamental importance in ecology in particular, and in biology in general. On any particular site if the biological properties of the ecosystem are disturbed (e.g. by clearing, fire, etc.), the process of succession is represented by the sequence of populations that successively occupy the site before the biological array returns to approximately the predisturbance composition. This tendency for complex species arrays to return to a relatively predictable composition is an expression of homeostasis.

Not only does a displaced stable biological array tend to return to its original composition but, large enough subsamples of the array examined at the same time on the same homogenous site tend to follow similar paths at similar rates. The principle of predictable successional sequences is unique to ecology and of fundamental importance to biology. As such it warrants study.

What are the mechanisms involved in the gradual change of terrestrial plant communities from one array of species to another, for example, the change of an abandoned cornfield from its initial array of the crop plus a few weed species to the different arrays found one, two, five, or ten years later? Change comes about as the result of the successful invasion of new species, the inability of species already present to persist, and changes in the proportion of the total universe that each established species population occupies. Does, and if so how does, the species array present at a given time influence or to some measure control the order of future arrays? What effect does the initial vegetation in a succession have on determining the future couse of that succession? Knowledge about the establishment and survival of new species is crucial to answering these questions.

Clements as early as 1916 recognized the importance of bare areas in the process of succession. He states that "Seres originate only in bare areas or in areas in which the original population is destroyed" (Clements, 1916). Milthorpe (1961) more specifically states that "establishment of plants from seed in vegetation occurs only in 'bare areas' arising from the death of previous occupants or from incomplete coverage." Harper et al. (1965) have shown that for many species, germination success is highly sensitive to microsite. Cavers and Harper (1967) have shown that even for species whose seeds germinate freely in almost any situation, seedling survivorship is guite microsite-related. Studies carried out by Caruso (1963) suggested the size of an opening created in an established vegetation had an effect on the survival and reproduction of certain species. He cut holes ranging from 0.5 to 3cm in diameter in oldfield grown bluegrass sod transferred to pots in the greenhouse. Seeds of various plants were then sown in the openings. Caruso found that survival but not germination of Melilotus sp. seeds was significantly positively correlated with the size of the opening. Positive correlations with other species could not be established but indications were

that germination of <u>Solidago canadensis</u>, <u>Aster pilosus</u>, and <u>Monarda fistulosa</u> was affected by the size of the opening. Thus a number of workers have indicated that the existing vegetation influences the probability of establishment of later immigrating species, and Caruso has shown that the opening sizes in an existing vegetation can also influence establishment probabilities of later immigrants.

The present study was made in an attempt to investigate the effect of opening size under field conditions using larger openings than Caruso. The prime question of the study then is what effect does opening size (or the size of the area available for colonization) have on determining the species present in the area and does the existing vegetation affect future stages in the succession?

#### II. LITERATURE REVIEW

#### A. General Trends in Succession

Succession has long been recognized as a fundamental process in the history of ecology. As early as 1916 Clements had written a large volume on the subject in which he reviewed earlier work, some of which was written nearly two hundred years ago (Clements 1916). Though recognized as a process fairly early, detailed population studies of particular successions and succession in general are guite recent. At present our understanding of the successional process is guite limited. Margalef (1963) states a number of axioms which summarize our knowledge of the trends in succession. Some of the axioms are accepted as experimentally confirmed while the validity of others remains untested. In succession there seems to be an increase in species having the ability to accumulate and hold biogenetic elements (biological materials and genetic information) and an increase in total standing stock in productivity terms. In addition it seems

that the ratio of photosynthetic pigment weight (chlorophyl) to total weight drops steadily as succession proceeds. There is an increase then a leveling of biological diversity. There is an increase in order (predictability). Succession seems to progress toward conservation of maximum biomass with minimum relative energy dissipation and toward increased stability. There is an increase of overall information stored chiefly in a level where its preservation is thermodynamically most efficient, and an increase in efficiency of basic processes. Lastly there is an increase in heterogeneity, and a progress from unorganized to organized heterogeneity.

From an evolutionary point of view Woodwell (1965) adds the following nuances to the above trends. Evolution and succession tend to proceed toward the reduction of competition; toward the greater utilization of space and other resources. This is associated with increasing variability and greater diversity in form and function resulting in the filling of more niches. Similar environments tend to support organisms which are similar in form and function if not in species. There is an increase in stability. There is an increase in total photosynthesis and respiration and an increase in total water use.

The trends outlined in the preceeding paragraphs, by no means all experimentally confirmed, are the result of fairly recent investigation. Until recently descriptive work on succession has been the predominant type of study of the process. Limnologists and marine biologists have taken the lead in detailed investigations of succession as seen in the studies cited by Margalef (1963). Within the last decade, ecologists concerned with vascular plant have begun to delve, in a more rigorous manner, into the causes or mechanisms operative in the process of succession.

Succession is seen as a directional change in the dominance hierarchy of species present in a given area through time (Whittaker, 1963, Numata and Yamai, 1955). What causes changes in the hierarchy, or more fundamentally, what factors influence the change in a plant's importance in a given area over a given time?

## B. Factors Involved in Succession

There seems to be three major factors affecting the presence of a plant at any particular point in a succession: the availability of propagules; the availability of an

occupiable microenvironment; and the effect of other organisms. Changes in, and interactions among, these factors produce the particular series of events the aggregate of which we witness as succession.

The available propagules represent the basic information out of which the process of succession molds the changing arrays. These propagules may be visualized as being in two categories: those already present on the site at the initiation of succession (initial inocculum) and those immigrating to the site after succession has begun (Egler, 1954). The available propagule factor has been the subject of a fair amount of study. Its species make-up depends on what plants are within seed dispersal distances, the cultivation practices prior to abandonment of land, the last crop, seed content of the soil at abandonment, and the viability of the seeds in the soil. The soil acts as a seed bank maintaining a supply of seeds available for germination under the proper conditions (the concept of initial floristics of Egler, 1954). The composition of this soil seed bank determines to a great extent the species composition of the initial stages of succession and to a lesser extent affects later stages.

Early studies such as those of Beal (1905, 1911), Darlington (1951), and Goss (1924) investigated the viability of seeds buried for various periods of time. These studies showed that some weed seeds have long viability. Many were still viable after being buried for the twenty years in the Goss study while Darlington found several species buried by Beal germinated after seventy years. Brenchley and Warington (1930, 1936) have studied the weed seed populations of some British soils and discovered that most seeds have a natural period of dormancy which may last up to nine years. There also appeared to be a relation between the type of manuring and the weed flora as a result of the seed content of the manure.

Oosting (1940) studied the viability of seeds in forest and field soils of various ages. The highest number of individual plants germinating from soil samples placed in the greenhouse were in fields abandoned one year while the highest number of species occurred in samples of five year old fields. Some species have poor longevity as shown by lack of germination from soils taken from fields in later successional stages. Germination of seeds of several species in soil from habitats in which parents are

not found indicates the possibility that seeds may lie buried for long periods and retain their viability. Odum (1965) in northern Europe has shown that some seeds apparently can remain viable under proper conditions for 100-600 years. Seeds of <u>Chenopodium album</u> and <u>Spergia arvensis</u> were found viable in archeological sites that appear to be 1700 years old. The soil seed bank extends to a fairly great depth. Robinson and Kust (1962) have shown that witchweed seed may move to a depth of sixty inches in deeply cracking, fine textured tropical soils, indicating that all seed is not stored near the surface. Seeds stored at depth do not germinate until some event brings them to the surface (Odum, 1965).

The soil seed bank, thus, may be a fairly extensive layer composed of the seed accumulation of many years though it would seem that the most recent accumulation would be of more importance in the early stages of succession on fallowed crop land.

One of the selective forces operating on the surface seed pool which is a determining factor in species composition at a given stage of succession is the availability of suitable micro-environments. According to Harper

et al. (1965) the varied micro-environments provided on a soil surface act selectively on mixed seed populations and determine the numbers of effective germination sites. This was shown on artificially created soil surfaces of varied microtopography. Harper and Benton (1966) showed that germination of seeds was sensitive to water tension applied to the soil. The area of contact made between seed and substrate and the degree of exposure of seed to the atmosphere would both affect the seed's moisture relationship, thus seed size and establishment probability of plants from seed may be correlated under natural conditions. Small seeds ought to be less likely to suffer desiccation and in general, seeds of open habitat plants tend to be smaller than those of closed habitats (Salisbury, 1942). Large seeded plants may be at a disadvantage in open habitats.

Thus, the micro-environment acts to screen the propagules allowing selective survivorship which in turn influence the species composition at a given stage. Changes in the variety of available microenvironments either through physical or biological action is a major factor in determining the species present and their position in the hierarchy at any given time. Tied in with the

microenvironment is the overall climatic factor which has a long-term effect on the direction of succession in addition to affecting the course of succession in any particular year through action on germination, survival, and seed production of the species present (Bormann, 1953).

In addition, Rice <u>et al</u>. (1960) have indicated that available nutrients at a site and changes in nutrient availability influence survival and establishment probabilities of certain seedlings. We thus have yet another screening factor acting on the available propagule source and determining the course of succession.

Other variables influencing establishment of oldfield species have also been studied. Clements (1916, 1928) and Keever (1950) both indicate the importance of seed source and dissemination capabilities of plants as factors influencing composition of early successional stages. Keever (1950) and Rice <u>et al</u>. (1960) indicate that some species affect the germination and establishment of others and thus were important in influencing the pattern a given succession takes.

Keever (1950) in investigating mechanisms in early succession on the Piedmont of North Carolina found that both

the timing of the seasonal cycle of individual species and the interactions between species were factors in determining the pattern of succession there. The life cycles of the particular species influences the times at which their propagules are present, when they germinate, and when their peak biomass contribution to the succession occurs.

There are other approaches which have contributed to our understanding of the phenomenon of succession which I will mention only briefly. One is the studies of energy content and flow through communities in various stages of succession, as exemplified by the work of Odum and his colleagues (e.g. Odum 1960, Odum <u>et al</u>. 1962, Golley 1960, Golley 1965). Another approach is the study of pattern in various stages of succession (e.g. Kershaw, 1963). Lastly are the effects of various pesticides such as herbicides and insecticides on the sequences (Woodford and Evans, 1963).

As noted above, much of the work done on succession to date has been of a descriptive nature. Much of this descriptive work has, for various reasons, been done on the Piedmont of the eastern United States (Oosting, 1942, Billings, 1938). One of the more recent is that of Bard (1952) on succession on abandoned farmland in the Piedmont in New

Jersey. She describes a pattern of first year dominance by annuals such as <u>Ambrosia</u> sp. and <u>Oenothera</u> sp. followed in succeeding years by dominance of perennials such as <u>Solidago</u> spp., <u>Aster</u> spp., and <u>Agropyron repens</u> which may remain important for more than 45 years. <u>Juniperus virginiana</u> invades in the first few years and becomes the dominant arborescent layer for the nest sixty years. <u>Quercus</u> spp. and <u>Carya</u> spp. are well established in the understory by the sixtieth year. <u>Rubus</u> spp. and <u>Rhus</u> radicans are the dominant shrubs after 25 years. Within limits the pattern is predictable, indicating the operation of particular processes.

#### C. Michigan Studies

Relatively little work has been done on old-field succession in Michigan. Dice (1931) presented a preliminary classification of the major terrestrial ecologic communities in Michigan and in it included old-field types. Beckwith (1954) described the general pattern of succession on abandoned farm land in Michigan after various cultivation practices, e.g. annual crops, small grains, hay,

etc. He also estimated the rates of invasion of woody plants. In general, the successional sequence he pictured starts with weedy annuals which are of different species depending on time of year the last disturbance occurred and pre-abandonment management practices, followed by a perennial grass stage which is followed in turn by woody plant invasion.

Evans and Cain (1952), Cain and Evans (1952), Clark and Evans (1954), Evans and Dahl (1955), and Wiegert and Evans (1964) have made a detailed study of the perrenial grass stage on the George Reserve in southeast Michigan. They recognized two community types; swales dominated by <u>Poa pratensis</u> and upland vegetation dominated by <u>Poa compressa</u>. The succession appeared to be directed slowly toward deciduous forest climax. The occurrence of micro-successional cycles was also noted.

Cain and Evans (1952) and Clark and Evans (1954) carried out a study of the distribution of three plants in the George Reserve field. Indications of clumping were found in all three species studied. A further investigation was made (Evans and Dahl, 1955) to tie the vegetational structure to environmental factors. Topographic

variability was considered to be the main cause of vegetational variation. Vegetations of depressions occurred on a two layered silt loam while soil of upland was a sand or a sandy loam. Soil texture and depth to plow line also seemed to be factors. The overall pattern in space was visualized as resulting from the interspersion of minor habitats, each with its own selective forces. A considerable degree of equilibrium appeared to have been reached in this grassy stage of succession (Evans and Dahl, 1955).

Wiegert and Evans (1964) have studied primary production and the disappearance of dead vegetation on the same George Reserve field, while Getz (1960) investigated the standing crop biomass of its herbaceous vegetation.

Golley (1960) investigated the energy dynamics of an old-field community near the Michigan State University campus. Caruso (1963) examined patterning in an old-field community in southwestern Michigan.

Other than Dice's (1931) and Beckwith's (1954) studies, however, there has been little major work done on the early stages of old-field succession in Michigan. Curtis (1959) has summarized the work on successional studies in adjacent Wisconsin and these indicate wide areas of agreement with the Michigan picture.

#### III. DESCRIPTION OF AREA

The study area was a 10,000 meter square (50 x 200 m) section of a three hectare field on the Michigan State University Kellogg Gull Lake Biological Station property (See Fig. 1). The field is located in Kalamazoo Co. (Ross Township; T. 1 S, R. 9 W, Section 8) less than onequarter mile from the Kellogg Gull Lake Laboratories on the corner of Gull Drive and B Avenue.

The study area was located on the east end of the field oriented with its long axis running north-south. The area falls in an area of Oshtemo Sandy Loam (Typic Hapludalfs) soil type and is of gently rolling topography.

The field has the following history of croppings:

- 1960 Wheat (fall) 300#<sup>1</sup> 5-20-20 fertilizer, 30# actual nitrogen
- 1961 Wheat seeded to alfalfa (spring)
- 1962 Alfalfa, no fertilizer
- 1963 Planted to corn 250# 6-24-24 fertilizer, 100# actual nitrogen
- 1964 Corn 250# 6-24-24 fertilizer, 100# actual nitrogen

1
# = pounds/acre

Fig. 1. Photograph of study area from the north side in July of 1965.

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Figure 2.--Weed control history. A demonstration experiment of weed control in corn was set up in the fall of 1962 and spring of 1963. The following A through F refers to areas located on Fig. 2. The figure represents a map of the location of plots in the study area.

- A. Amitrol T in fall at 2#/acre Atrazine in spring (May 20) at 2#/acre
- B. Same as A
- C. Control--nothing fall or spring
- C., 2, 4D Ester in spring (May 20) at 1.5#/acre
- D. Atrazine in fall at 4#/acre 2, 4D Ester in spring (May 20) at 1.5#/acre
- E. Atrazine in spring at 2#/acre preplow Atrazine in spring at 2#/acre
- F., Atrazine in fall at 4#/acre
- F. Atrazine in fall at 4#/acre 2, 4D Ester in spring (May 20) at 1.5#/acre

100.00m<sup>2</sup>

1.0m<sup>2</sup> matrix •

The blocks represent:  $.01m^2$   $.10m^2$   $1.00m^2$   $10.00m^2$ 

# an an an A**r**ain an Arainnean an Arainnean an Arainnean Arainne E F F

#### IV. METHODS

The 10,000 square meter study area was divided into four blocks of equal area based on obvious differences in topography in an effort to minimize topographical effects as far as possible. Only two of the blocks (I & III) were used in the study currently reported. Quadrats of the sizes and numbers listed in Table I were plowed or spaded between June 14, and 16, 1965. The quadrats were randomly located allowing for buffer strips between them as listed in Table I. Quadrats of the 100 and 10 square meter classes were tractor plowed while the remainder were hand spaded. Thus there was some variation in the depth and completeness of soil turnover.

In August of 1965, June and August of 1966, and June of 1967, all quadrats were sampled with the exception of the  $0.01m^2$  quadrats which could no longer be accurately delineated after 1965. Visual estimates were made by the author of the per cent area covered (% cover) by each species for each quadrat. Both the  $10m^2$  and  $100m^2$  quadrats into 100  $1m^2$  quadrats. The cover percentages from these two quadrat

Table I.--Size openings created along with the number in each of the two blocks, the total area opened in each block, and the minimum amount of undisturbed space around each opening. The total area of each of the two blocks was 2,500 square meters.

Quad Size	rat m <sup>2</sup>	No./Block	Area/Block m <sup>2</sup>	Buffer Strip m
	0.01	196	1.96	0.20
	0.10	64	6.40	0.84
	1.00	25	25.00	1.00
	10.00	9	90.00	1.00
	100.00	2	200.00	2.00
Matrix	1.00	75	75.00	1.00

sizes are based on analysis of the pooled values for the smaller subdivisions rather than on an overall value obtained for the large quadrat.

In addition, 150 (75 in each block) 0.5 X 2m permanent unplowed quadrats were sampled in the undisturbed (matrix) vegetation each time the plowed quadrats were sampled.

Voucher specimens of species encountered in the quadrats are deposited in the Michigan State University Herbarium, East Lansing, and/or the herbarium of the W. K. Kellogg Gull Lake Laboratory, Hickory Corners, Mich. The nomenclature used follows Fernald (1950).

The basic statistics on the total data were obtained through use of the Bastst Routine of the Michigan State University Computer Laboratory. The five per cent level was used to determine significance throughout. For the  $10m^2$  and  $100m^2$  plots N = the number of subsample plots and all statistics were worked on the subsample data as opposed to any value obtained for the larger block.
#### V. RESULTS

## A. Pattern of Succession

The pattern of succession varies with location and climate. However, in many areas it has been found to be quite predictable within limits. Observation of the fallow field in which the holes were cut (the matrix vegetation) yielded the following pattern: In the fall of 1964 after the corn had been harvested the species found in Table II were found in the field. The species are ranked roughly in order of abundance. In August of 1965, the year following this corn harvest, the undisturbed parts of the fallow field (matrix) had a vegetation with a conspicuous perennial element in its cover. In terms of total per cent cover Lychnis alba and Rhus typhina occupied first and second rank while Potentilla recta was fourth. Annuals and biennials were next with the ranks being: Ambrosia artemisiifolia third, Oxalis stricta fifth, Erigeron annuus sixth, Amaranthus retroflexus seventh, Verbascum thapsus eighth, Medicago lupulina ninth, and Chenopodium album tenth

Table II.--Presence list of species found in study area in November 1964 mostly occupying the rows along with the old corn stalks. The species are arranged in rough order of their importance.

> Amaranthus retroflexus Ambrosia artemisiifolia Chenopodium album Lychnis alba Rhus typhina Panicum capillare Setaria glauca Agropyron repens Bromus inermis Eragrostis sp. Polygonum convolvulus Asclepias syriaca Malva neglecta Solanum nigrum

(see fig. a in Appendix B). The following June these same quadrats showed the species ranked as in fig. g, Appendix B. Again perennials occupy three of the top four ranks. In August of the same year (Fig. 1, Appendix B) <u>Poa</u> pratensis and Erigeron canadensis shared the top dominance rank and the next four most dominant species were perennials (Potentilla recta, Rhus typhina, Lychnis alba, and Agropyron repens in third through sixth total percent cover ranks). In June of 1967 (see fig. q, Appendix B) these same quadrats showed perennials occupying all six of the top dominance ranks, with Poa pratensis now the clear dominant.

Thus in the undisturbed fallow field the general progress of succession following the annual weeds and corn was a mixture of perennial, annual and biennial species followed by perennial - biennial with the biennials declining after 1966 (see Fig. 3,4).

Unlike this fallow vegetation, the openings cut into the field in early June 1965 and left undisturbed thereafter produced an August vegetation dominated by annual species. In large part these were the same species that existed along with the corn crop the preceeding year (see fig. d, e, and f, Appendix B). <u>Amaranthus retroflexus</u>, <u>Lychnis alba</u>, <u>Potentilla recta</u>, <u>Rhus typhina</u>, and <u>Ambrosia artemisiifolia</u> predominated. In the second year there was a loss of some of the first year annuals from the sampled plots (see Table III). These lost species remained absent in the third year







Time (sample date)



Species	Range of Average Percent Cover Among Various Opening Sizes		
Amaranthus retroflexus	3 - 38		
Amaranthus albus	0 - 1.4		
Chenopodium album	0 - 2		
Chenopodium sp.	.1		
Eragrostis reptans	0 - 1.1		
Fragaria sp.	.001		
Mollugo verticillata	0 - 1.4		
Oenothera sp.	.001		
Panicum capillare	0 - 1.9		
Polygonum persicaria	03		
Portulaca sp.	.001		
Solanum nigrum	05		

Table III.--Species appearing in 1965 but not in 1966 or 1967. Values indicate the range in average per cent cover for the various opening sizes.

also. In place of the preceding dominants there occurred an increase in windborne biennials such as <u>Lactuca</u> <u>biennis</u>, <u>Erigeron</u> <u>annuus</u>, and <u>Erigeron</u> <u>canadensis</u>, which showed a **Peak** in June or August of the second year depending on their individual life cycles. These species then declined after their initial peak. Accompanying these changes in annuals and biennials was a gradual increase in several perennials such as <u>Potentilla recta</u>, and especially the grasses <u>Poa pratensis</u>, <u>Poa compressa</u>, and <u>Agropyron repens</u>. By the third season the grasses began to dominate locally in the openings and to displace the annuals and biennials in dominance. Perennials such as <u>Potentilla recta</u> and <u>Rhus typhina</u> continued to increase in abundance and a few woody plant seedlings appeared.

# B. Opening Size

Opening size appears to influence some aspects of the successional patterns. Some species show significantly greater percentage of total cover with increased opening size, others show significantly less. Significance of linear trends was determined using both one way analysis of variance and regression analysis. The five per cent level was used for denoting significance although it should be noted that variance homogeneity did not exist in many cases. Species contributing significantly more cover in

August of 1965 with increasing opening size were: Agropyron repens, Amaranthus retroflexus, Amaranthus albus, Eragrostis reptans, Lychnis alba, and Rhus typhina (Fig. 5). In June 1966 similar significant increases were shown by Agropyron repens, Lactuca biennis, Lychnis alba, Specularia perfoliata, and Erigeron canadensis (Fig. 6,7), in August 1966 by Agropyron repens and Lactuca biennis (Fig. 8), and in June 1967 by Poa pratensis, Erigeron canadensis, and Agropyron repens (Fig. 9). No species showed significantly less cover in August of 1965 as opening size increased, but in June 1966 Arenaria sp., Specularia perfoliata, Trifolium repens and Veronica sp. did (Figs. 6,7). In August 1966 Rumex acetosella and Poa compressa (Fig. 8), and in June 1967 Potentilla recta, Veronica sp., and Poa compressa (Fig. 9) showed trends of decreasing cover with increasing opening size.

<u>Amaranthus retroflexus</u> exhibited the most striking trend of increasing cover with increasing opening size. This tendency to contribute relatively more cover in the larger openings appeared to be related to the size of the plants. Casual estimates showed that individuals ranged from approximately one decimeter in height in the smallest



Fig. 5. Average per cent cover plotted against opening size for species showing trends in August of 1965. Solid lines are significant (5% level) regressions. Specie are: AmR, Amaranthus retroflexus; AmA, Amaranthus albus; AR, Agropyron repens; AA, Ambrosia artemisiifolia; EC, Eragrostis reptans; IA, Lychnis albus; and RT, Rhus typhina.











Fig. 8. Average per cent cover plotted against opening size for species showing trends in August of 1966. Solid lines are significant (5% level) regressions. Species are: AR, Agropyron repens; ErC, Erigeron canadensis; LA, Lychnis alba; LB, Lactuca biennis; PP, Poa pratensis; and PC, Poa compressa.



Opening size (m<sup>2</sup>)

Fig. 9. Average per cent cover plotted against opening size for species showing trends in June of 1967. Solid lines are significant (5% level) regressions. Species are: AR, Agropyron repens; ErC, Erigeron canadensis; PC, Poa compressa; PP, Poa pratensis; PR, Potentilla recta; RA, Rumex acetosella. openings (0.01m<sup>2</sup>) to a meter and a half in the largest (100m<sup>2</sup>). Flowering and seed production occurred throughout the range of sizes but the number of flowers and seeds appeared to be very much larger in the larger openings.

## C. Opening Size and Community Composition

If the existing vegetation has an effect on incoming species, and if size opening affects establishment and survival of species, then the species composition (species hierarchies) of the different sized openings would very likely be different. A comparison of the different sized openings with respect to species composition was made using the coefficient C =  $\frac{2W}{A + B}$  of Bray and Curtis (Austin & Orloci, 1966), where W is the sum of the lesser values of species scores in common in two stands and A + B is the sum of species scores in each stand. Random samples of equal total area  $(13m^2)$  were chosen from the  $1-100m^2$  size classes while all of the 0.1m<sup>2</sup> plots were used, these being the determinant of the 13m<sup>2</sup> total area. The species scores were the average percent cover values. The coefficients obtained are presented in Table IV.

Opening sizes compared	August 1965	June 1966	August 1966	June 1967
0.1 - 1.0	.500	.820	.724	.710
1.0 - 10	.800	.740	.705	.645
10 - 100	.555	.680	.725	.715
0.1 - 100	.361	.640	.805	.770

Table IV.--Coefficients of similarity between vegetation developing in openings of various sizes cut into newly fallowed corn field.

It can be seen that the smallest similarity coefficient (i.e. the greatest vegetation difference) occurs between the  $0.1m^2$  and the  $100m^2$  openings in the first growing season. Since the coefficients do not show a clear trend with increasing opening size, even in the first year, the strong trends with opening size shown in the cover of particular species are probably obscured by the normal high variance in the bulk of the other species which is unrelated to size opening.

## D. Effect of Initial Species

In the light of several earlier studies (e.g. Keever 1950, Rice 1967) it would be useful to know whether the species present at the initial stages of succession have a determining influence on the species composition of later stages. For the 128 0.1m<sup>2</sup> openings plots were made of the per cent cover of Lactuca biennis, Erigeron annuus, Erigeron canadensis, Lychnis alba, Poa pratensis, Poa compressa, Ramex acetosella, and Potentilla recta in August 1966 versus the cover of Amaranthus retroflexus in the preceding August of 1965, the initial dominant that year in the openings and the species most sensitive to size or opening (see Appendix C for graphs). For none of these species was their cover in 1966 directly correlated with the amount of Amaranthus cover in 1965 as determined through observation of the regression graphs, Appendix C.

## VI. DISCUSSION

The complicated process of succession is a guasipredictable (and therefore guasi-orderly) sequence of directional changes in the species makeup and dominance hierarchy among the biota on a site. These directional changes are wrought by the germination or expansion of species already present on the site together with immigration, establishment, reduction and local extinction of these various species populations. There seems little question but that the species already established on a site would exert some influence on the probabilities of success of species appearing subsequently. The species already present might influence germination, seedling survivorship, size of plant, and reproduction and longevity of adults. Modifications of this older vegetation by breaks or openings in the plant cover is one way to study two questions experimentally: over what range of opening size are the effects of such interference by established species detectable? And, do the various species respond similarly to such openings?

In the corn crop annual weeds such as Amaranthus retroflexus, A. alba, Chenopodium album, Ambrosia artemisiifolia, Setaria viridis, etc. occur, but the corn itself is the clear dominant. Weed control and other management operations influence both the amount and kinds of weeds that occur with the crop. In the field studied, fallowing without disturbance after the October 1964 corn harvest gave rise by the subsequent late summer (August 1965) to a vegetation having a major component of nonannual species. These were Lychnis alba, Rhus typhina, Potentilla recta, and Erigeron annuus. Although definitely secondary some annuals were still present such as Ambrosia artemisiifolia, Oxalis stricta, and Amaranthus sp. By the following summer (August 1966) Poa pratensis had achieved first place, and although a biennial (Erigeron canadensis) occupied second place, the characteristic grassy old-field vegetation of southern Michigan was clearly emerging. The June 1967 dominance hierarchy shows the grassy nature even more clearly.

The presence of so much <u>Rhus typhina</u> (staghorn sumac) in this field is a special circumstance owing to its persistence following planting as a cover plant in an abortive

attempt to establish a walnut orchard many years earlier (personal communication from Mr. Harold Webster).

On the openings made in the fallow corn field in June 1965, a pronounced dominance by annual weeds occurred. The vegetation in these openings was developmentally the same age as the corn-weed mixture that preceded the fallow. Amaranthus retroflexus is clearly the species favored when the soil of a fallow corn field is turned over in early June in Michigan. Lychnis alba, though not an annual, is also high but such other annuals as Mollugo verticillata and Ambrosia artemisiifolia tend to be among the top five species in total cover except in the very smallest openings (0.01m<sup>2</sup>). The perennial grasses are well down the dominance hierarchy in the first growing season. By the subsequent late summer (August 1966) biennials, especially Erigeron spp. and Lactuca spp., took over the most prominent role. The perennials Lychnis alba, Agropyron repens, and Rhus typhina were definitely present but secondary. This greater importance of biennials and lower importance of the perennials is a major difference between the undisturbed corn fallow and the openings made in it when they are compared after the same length of development (i.e.

matrix August 1965 compared with openings August 1966). In particular, Erigeron canadensis was much less important in the undisturbed fallow than in the openings. This could largely be a matter of seed source buildup, the weeds in the corn crop providing a very low inocculum of this species. Other differences were the greater importance of Agropyron repens and lower cover of Lychnis alba, Potentilla recta and Oxalis stricta in openings than in the undisturbed fallow. It is not possible to demonstrate whether these particular differences are significant due to the high variance inherent in this vegetation. However, as noted earlier, Agropyron repens does exhibit a positive correlation with increasing opening size which tends to support the notion that something about the undisturbed fallow situation is less favorable for the species. Some, but not all, species that had higher cover in the undisturbed corn fallow than in the openings (e.g. Oxalis stricta, Poa compressa and Potentilla recta) tend to exhibit negative regressions with size of opening in the fallow vegetation. All these species are likely candidates for future studies on mechanisms in old-field succession.

The data presented in Figs. 5 through 9 show that the per cent cover of some species tends to increase significantly with increasing size of opening while other species show a significant decrease. Of the species significantly positively correlated with opening size Amaranthus retroflexus was the most pronounced. It was the dominant in all openings except the smallest (0.01m<sup>2</sup>), in their first growing season. Amaranthus retroflexus has a large capacity for plastic response and its greater per cent cover in the bigger openings appears to be more a reflection of increased size of individuals than increased numbers per unit area. Viewed in reverse this would suggest that increased frequency of establishment of individual plants is inadequate to compensate for the dwarfing effects of the interference by surrounding one year older follow vegetation. The relationship suggests that Amaranthus is very sensitive to interference from established species or from its own decomposition products of the preceding generation. The vegetation surrounding the openings at this time was dominated by Lychnis alba, Rhus typhina, Ambrosia artemisiifolia, Oxalis stricta, and Erigeron annuus. Amaranthus either requires a large area essentially free of effects of these

species or of some other characteristic of the one year older vegetation in order to achieve maximum growth.

While it is tempting to speculate here that herbicides used with the corn crop might also be involved, the presence of vigorous <u>Amaranthus</u> plants with the corn crop itself argue against such an effect.

Unquestionably Amaranthus requires some minimum area free of significant interference for establishment. This minimal area is smaller than  $0.01m^2$  since the species had about 3% average cover in these smallest openings and reached a maximum of 90% on some. Occasional individuals or clusters of individuals were also present in the undisturbed one year old fallow vegetation where this species ranked seventh from the top in total cover contribution. However, the minimal interference-free area probably has a very low frequency after this first full year of fallow, since Amaranthus disappeared from the samples after then. It has been suggested (oral communication Rice, 1967; Gregg and McCormick, 1966) that Amaranthus, like other first year old-field annuals (Keever, 1950), may be inhibited by its own decomposition products as well as those of other oldfield species.

The direct correlation between per cent cover of Amaranthus and area of opening may reflect allelopathic or other kinds of interference by surrounding one year older vegetation. The zone of major interference can hardly extend all the way to the centers of the largest  $100m^2$  opening size. Possibly this is simply a reflection of a decreasing ratio of the area of the inhibited zone to the total area of the opening, i.e., if we were to assume the interference to be restricted to a band one meter inward from the older vegetation, in the  $lm^2$  opening the entire area would be subject to interference, in the 10m<sup>2</sup> opening only about 92% of the area, and in the 100m<sup>2</sup> openings only about 36% would be influenced. A comparison of per cent cover of Amaranthus retroflexus in 36 central versus 36 perimeter  $lm^2$  plots in the  $100m^2$  blocks showed that for the 100m<sup>2</sup> blocks <u>Amaranthus</u> cover was consistently less in the perimeter plots. This difference was significant at the 5% level (t test) in two of the four 100m<sup>2</sup> blocks. This tends to substantiate the idea of interference as a cause for decreased cover of Amaranthus.

No attempt has been made as yet to characterize the nature of the mechanisms responsible for the dwarfing of Amaranthus.

The positive trends of more cover with increasing opening size found for other species, especially in the second and third growing seasons, may be a result of similar interference phenomena. It would seem that there might be a positive correlation between per cent of the area bare of vegetation and opening size since invasion by the older peripheral vegetation, especially the grasses, would reach the whole opening in the smaller ones more rapidly. This in turn would permit species which require bare area for establishment or persistence to remain longer and in greater abundance in larger openings. Thus some of the positive trends found may be due to the varying rapidity with which different sized openings are occupied by perennial vegetation. Or stating it another way, they may be due to the variation in amount of bare or competition-free area in the different sized openings.

Some of the negative trends with increasing opening size may simply reflect the slower rate of invasion from the surrounding one year older undisturbed fallow. <u>Poa pra-</u> <u>tensis</u>, for example, expands vegetatively in addition to new colonizations by seed. However, as noted above, this species increased its per cent cover in the undisturbed

fallow vegetation more rapidly than in the openings cut into this vegetation. This could be an interference phenomenon in the openings from the greater impact of <u>Amaranthus</u> there. Also, it could simply be a more successful retention of fertilizer residues missed by the corn crop by <u>Poa</u> plants established slightly earlier in the succession and subject to less bare ground leaching. <u>Potentilla recta</u> also exhibits higher cover in the original fallow array and less cover in the larger opening sizes.

The possibility exists that some of the species exhibiting significant positive correlations with opening size may simply reflect a greater interference effect from the species noted above which are more important in the smaller openings. <u>Erigeron canadensis</u>, for example, might be adversely affected by higher <u>Poa compressa</u> cover. Correlation studies of the percent cover of these two species in the various individual quadrats did not reveal any such trend. The number of samples available was far too small for identifying any but the most spectacular correlations so the lack of significant correlations can hardly be given great weight.

The positive relationships of cover with opening size for species such as <u>Rhus typhina</u>, <u>Agropyron repens</u>, <u>Lychnis alba</u>, and <u>Poa pratensis</u> may be related to their large vegetative reproductive organs which survive plowing well. This gives these species a distinct advantage in the initial re-vegetation of the large openings where most of the other species must start from the seedling stage. All four species appear to be able to contend with the higher cover of <u>Amaranthus retroflexus</u> that becomes established in these large openings.

The most convincing negative regressions between species cover and size of opening are those of <u>Poa compressa</u> and <u>Potentilla recta</u>. Three other species (<u>Rumex acetosella</u>, <u>Trifolium repens</u>, and <u>Veronica</u> sp.) exhibit significant negative relationships but they are species of small total cover, and it is very possible that underestimations of per cent cover, or the possibility of being overlooked, is much greater for such small or less common individuals on the larger sample units.

Of these, however, it is to be noted that legumes such as <u>Trifolium</u> <u>repens</u> are said to be adversely affected by decomposition products of first year dominant annuals

(Rice <u>et al</u>., 1967). It is possible that the greater masses of decomposing <u>Amaranthus</u> on the larger openings produced a greater suppression of these legumes there as the hierarchies indicate a trend of decreasing legume cover with increasing opening size in June of 1966.

The particular weather sequence that precedes and accompanies the initial establishment of a vegetation on agricultural land is undoubtedly an important variable. No effects are directly relateable in the present study but June and July of 1965 had some droughty periods in the study area. The rhizomatous perennials in the larger openings may have been favored by this more than seed-started species.

The dominance hierarchy was suggested (Whittaker, 1965) as a useful method of portraying both the biomass and the site's resource allocation among the species in an ecosystem. With large representative samples of a vegetation on a homogeneous area these curves tend to approximate the log-normal curve discussed by Preston (1948, 1960) and Clark <u>et al.(1964)</u>. Numata and Yamai (1955) have shown that in annual weed vegetation the hierarchical order changes among the species with the season. Also, their curves were

characterized by flat plateaus which indicated that several species tended to share the same relative dominance position. In the June 1966 hierarchy of total cover for species for this study similar plateaus occur (Appendix B, Figs. i, j, and k). It is suggested that these reflect interim values and as interaction between the species becomes fully developed the log-normal hierarchy tends to be the final outcome. Ogawa and Kira (1953) and more recently Harper (1967) have pointed out the tendency for the log-normal relationship to develop in competition. Interacting plants withdrawing resources from the same pools tend to bring positive feedback into play wherein the individuals getting the slightest advantages in withdrawing resources utilize these resources to build bigger resource trapping machines (roots or tops) which in turn enlarge the advantage. It is possible that under more controlled experimental conditions with more uniform species arrays, careful study of the shifting hierarchical positions among the species may give clues to when and between what species such interactions might be anticipated. In the present study, however, there was far too much variation and the observations too widely spaced in time to draw much from these hierarchical changes.

## VII. SUMMARY AND CONCLUSIONS

- The course of succession is slightly different in openings created in a fallow vegetation as compared to the succession in the undisturbed fallow itself, even when the openings are made the early June following the corn crop.
- 2. The agricultural manipulations made for the corn crop, such as herbicides, high fertilizer, and cultivation, as well as effects from the corn plants themselves are missing in the openings.
- 3. The corn-annual weed first year vegetation of the corn field is represented by the <u>Amaranthus retroflexus</u>dominated vegetation in the openings.
- In the second year the fallow corn field becomes dominated largely by perennials, although the biennial, <u>Erigeron canadensis</u>, is prominent.
- 5. The openings on the other hand are dominated in the second year by biennials. This difference may be due

to several causes: greater biennial seed inocculum in the openings, smaller fertilizer residues, or possibly a greater resistance to decomposition products of <u>Ama-</u> <u>ranthus retroflexus</u>. None of these possible causes was experimentally evaluated.

- 6. By the onset of the third growing season, the differences between the openings and the fallow corn land become less but <u>Poa compressa</u> and <u>Poa pratensis</u> are generally more prominent in the fallow than in the openings.
- 7. Smaller openings are very much more like the fallow corn than are the larger openings, but this difference which is great the first year wanes by the third growing season.
- 8. The per cent cover of 14 of the 77 species appears to be correlated with the size of the opening. Of these 14, the most dramatic effects were observed in <u>Amaran-</u> <u>thus retroflexus</u> which is significantly positively correlated with increasing opening size across the range of 0.01m<sup>2</sup>, 0.1m<sup>2</sup>, 1.0m<sup>2</sup>, and 100m<sup>2</sup> areas.

- 9. This increasing per cent cover of <u>Amaranthus</u> in the larger openings is accompanied by an increase in size of the <u>Amaranthus</u> plants. The mechanisms responsible for the dwarfing in the smaller openings have not been determined in this study.
- 10. Positive correlations between per cent cover and increasing opening size were also observed for other species, several (<u>Agropyron repens</u>, <u>Lychinis alba</u>, <u>Rhus typhina</u>, and <u>Poa pratensis</u>) being populations largely derived from vigorous vegetative propagules which survive plowing in the openings.
- 11. Some species appear to produce greater per cent cover in the smaller openings than in the larger ones. In general these are species that also show greater per cent cover in the undisturbed fallow vegetation. No attempt has been made in this study to investigate the mechanisms that might produce such effects.
- 12. Results from this study suggest that the 10m<sup>2</sup> and the 100m<sup>2</sup> opening sizes are not apt to yield important insights into germination and establishment processes in

old-field vegetation. This study together with that of Caruso (1963) leads to the recommendation that smaller openings, perhaps lcm<sup>2</sup> to 100 m<sup>2</sup>, will be most likely to give clues to processes operating in early old-field succession.

- 13. While some clear vegetation differences are observed in the openings made in first-year fallow vegetation, this study also indicates that older vegetation somewhere between this young age and the 30-year old grassy field of Caruso (1963) may yield the best study medium.
- 14. For the range of sizes used, it seems that the size opening does not affect the pattern of succession by altering species composition, nor does it seem that the initial dominant annuals have a major determining influence on the pattern of succession. This latter is suggested by the lack of correlation of any dominants in the second year with per cent cover of <u>Amaranthus</u> <u>retroflexus</u>, the first year dominant. At least <u>Amaranthus retroflexus</u> does not seem to strongly control future community organization.

- 15. In the long run it might be the initial perennial species composition which may be a greater determinant in early stages of old-field succession. Through their ability to invade and hold space, the early perennials may be the controlling factor in determining the pattern a given succession takes and also the vegetational patterning in space seen in the field at later stages.
- 16. Dominance hierarchies (Whittaker, 1965; Numata, 1955) based on total cover are not a great deal more useful than conventional summaries for visualizing the make-up of old-field vegetation or the changes in it, either within the same growing season or in comparing years. However the hierarchies show up some things worth investigating further, e.g. the close spacing of the top two dominants at times and the plateaus such as occurred in the June 1966 samples. This "close spacing" or plateauing of the tendency for a more log-normal hierarchial arrangement may have merit for identifying potentially interesting species combinations.

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APPENDIX A

LIST OF SPECIES OCCURRING IN SAMPLES

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## LIST OF SPECIES OCCURRING IN SAMPLES

Achillea Millefolium L. Chrysonthemum Leucanthemum L. Agropyron repens (L.) Beauv. Cirsium vulgare (Savi) Amaranthus albus L. Tenore Amaranthus retroflexus L. Digitaria sanguinalis (L.) Scop. Ambrosia artemisiifolia L. Eragrostis reptans (Michx.) Anthemis arvensis L. Nees Erigeron annuus (L.) Pers. Arenaria sp. Erigeron canadensis L. Arabis glabra (L.) Bernh. Aribidopsis Thaliana (L.) Heynh. Fragaria sp. Asclepias syriaca L. Galium Aparine L. Aster sp. Geranium sp. Barbarea vulgaris L. Hypericum sp. Bromus tectorum L. Lactuca biennis (Moench) Fern. Capsella Bursa-pastoris (L.) Medic. Lactuca canadensis var. longifolia (Michx.) Farw. Carex sp. Chenopodium album L. Lepidium canpestre (L.) R. Br. Chenopodium sp.

Lepidium virginicum L. Portulaca sp. Lychnis alba Mill. Potentilla argentea L. Malva neglecta Wallr. Potentilla norvegica L. Medicago lupulina L. Potentilla recta L. Medicago sativa L. Rhus typhina L. Medicago sp. Rumex Acetosella L. Melilotus alba Desv. Rumex crispus L. Melilotus sp. Rumex obtusifolius L. Mollugo verticillata L. Setaria viridis-glauca Nepeta Cataria L. Silene antirrhina L. Oenothera sp. Sisymbrium altissimum L. Oxalis stricta L. Sisymbrium officinale (L.) Scop. Panicum capillare L. Solanum nigrum L. Phleum pratense L. Solidago sp. Physalis pubescens L. Specularia perfoliata Plantago lanceolata L. (L.) A.D.C. Plantago Rugelli Dcne. Stellaria sp. Plantago virginica L. Taraxacum officinale Weber Poa compressa L. Tragopogon major Jacq. Poa pratensis L. Trifolium hybridum L. Polygonum Convolvulus L. Trifolium pratense L. Polygonum Persicaria L. Trifolium repens L.

Trifolium sp.

Ulmus sp.

Verbascum Thapsus L.

Verbena sp.

Veronica sp.

Unknown grass seedlings

Unknown rosette PVL

Unknown rosette

Unknown seedlings

Unknown L

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## APPENDIX B

GRAPHS OF TOTAL PER CENT COVER OF SPECIES VERSUS SPECIES RANK (BASED ON TOTAL COVER) FOR ALL SAMPLING TIMES AND OPENING SIZES



Fig. a. Species abundance hierarchy for undisturbed fallow plots in August 1965. Species ranked by total cover found in 150 plots.







Fig. b. Species abundance hierarchy for .Olm<sup>2</sup> opening plots in August 1965. Species ranked by total per cent cover found in 392 plots.



Fig. c. Species abundance hierarchy for  $0.1m^2$  opening plots in August 1965. Species ranked by total per cent cover found in 128 plots.



Fig. d. Species abundance hierarchy for 1.0m<sup>2</sup> opening plots in August 1965. Species ranked by total per cent cover found in 50 plots.



Fig. e. Species abundance hierarchy for 10m<sup>2</sup> opening plots in August 1965. Species ranked by total per cent coverfound in 18 plots (182 subdivision plots).



Ranked Species

Fig. f. Species abundance hierarchy for 100m<sup>2</sup> plots in August 1965. Species ranked by total per cent cover in 4 (400 subdivision plots) plots.



Fig. g. Species abundance hierarchy for undisturbed fallow plots in June 1966. Species ranked by total per cent cover found in 150 plots.







Ranked Species

Fig. h. Species abundance hierarchy for  $0.1m^2$  opening plots in June 1966. Species ranked by total per cent cover found in 128 plots.



Fig. i. Species abundance hierarchy for 1.0m<sup>2</sup> opening plots in June 1966. Species ranked by total per cent cover found in 50 plots.



Fig. j. Species abundance hierarchy for 10m<sup>2</sup> opening plots in June 1966. Species ranked by total per cent cover found in 18(162 subdivision plots) plots.



Fig. j continued.



Fig. k. Species abundance hicrarchy for 100m<sup>2</sup> opening plots in June 1966. Species ranked by total per cent cover found in 4(400 subdivision plots) plots.



Fig. 1. Species abundance hierarchy for undisturbed fallow plots in August 1966. Species ranked by total per cent cover found in 150 plots.



Fig. m. Species abundance hierarchy for  $0.1m^2$  opening plots in August 1966. Species ranked by total per cent cover found in 128 plots.



Fig. n. Species abundance hierarchy for  $1.0m^2$  opening plots in August 1966. Species ranked by total per cent cover found in 50 plots.



Fig. 0. Species abundance hierarchy for 10m<sup>2</sup> opening plots in August 1966. Species ranked by total per cent cover found in 18(162 subdivision plots) plots.



Fig. p. Species abundance hierarchy for  $100m^2$  opening plots in August 1966. Species ranked by total per cent cover found in 4(400 subdivision plots) plots.



Fig. q. Species abundance hierarchy for undisturbed fallow plots in June 1967. Species ranked by total per cent cover found in 150 plots.

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Fig. r. Species abundance hierarchy for  $0.1m^2$  opening plots in June 1967. Species ranked by total per cent cover found in 128 plots

4 4.1±


Fig. s. Species abundance hierarchy for 1.0m<sup>2</sup> plots in June 1967. Species ranked by total per cent cover found in 50 plots.



Fig. s continued.



Fig. t. Species abundance hierarchy for  $10m^2$  opening plots in June 1967. Species ranked by total per cent cover found in 18(162 subdivision plots) plots.



Fig. t continued.



Fig. u. Species abundance hierarchy for 100m<sup>2</sup> opening plots in June 1967. Species ranked by total per cent cover found in 4(400 subdivision plots) plots.





## APPENDIX C

PLOTS OF REGRESSIONS OF PER CENT COVER OF MAJOR SPECIES OCCURRING IN AUGUST 1966 ON THE PER CENT COVER OF <u>AMARANTHUS RETRO-</u> <u>FLEXUS</u> THAT HAD OCCURRED IN THE SAME

PLOTS IN AUGUST OF 1965



Fig. a. Regression of per cent cover of <u>Poa compressa</u> in Aug. 1965 on per cent cover of <u>Amaranthus retroflexus</u> in Aug. 1965 on 128 O.lm<sup>2</sup> openings cut in a first year fallow field.

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Fig. b. Regression of per cent cover of <u>Rumax acetosella</u> in Aug. 1966 on per cent cover of <u>Amaranthus retroflexus</u> in Aug. 1965 on 128 O.1m<sup>2</sup> openings cut in a first year fallow field.



Fig. c. Regression of per cent cover of Potentilla recta in Aug. 1966 on per cent cover of <u>Amaranthus retroflexus</u> in Aug. 1965 on 123 O.lm<sup>2</sup> openings cut in a first year fallow field.



Fig. d. Regression of per cent cover of Erigeron annuus in Aug. 1966 on per cent cover of <u>Amaranthus retroflexus</u> in Aug. 1965 on 128 O.lm<sup>2</sup> openings cut in a first year fallow field.



Fig. e. Regression of per cent cover of <u>Poa</u> pratensis in Aug. 1966 on per cent cover of <u>Amaranthus retroflexus</u> in Aug. 1965 on 128 O.lm<sup>2</sup> openings cut in a first year fallow field.



Fig. f. Regression of per cent cover of Lactuce biennis in Aug. 1966 on per cent cover of <u>Amaranthus retroflexus</u> in Aug. 1965 on 128 O.lm<sup>2</sup> openings cut in a first year fallow field.



Fig. g. Regression of per cent cover of Lychnis alba in Aug. 1966 on per cent cover of <u>Amaranthus retroflexus</u> in Aug. 1965 on 128 O.lm<sup>2</sup> openings cut in a first year fallow field.

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Fig. h. Regression of per cent cover of <u>Erigeron canadensis</u> in Aug. 1966 on per cent cover of <u>Amarenthus retroflexus</u> in Aug. 1965 on 128 O.lm<sup>2</sup> openings cut in a first year fallow field.

