SEED DISPERSAL, SEED GERMINATION AND SEEDLING ESTABLISHMENT OF HIERACIUM AURANTIACUM IN AN OLDFIELD COMMUNITY

Thesis for the Degree of M. S.
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1970

Z ~~[illegible]~~ 186

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Oct. 10, 1990

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K209

Plate 1. *Hieracium aurantiacum* L.
Louden Oldfield. June, 1969.

ABSTRACT

SEED DISPERSAL, SEED GERMINATION AND SEEDLING ESTABLISHMENT OF *HIERACIUM AURANTIACUM* IN AN OLDFIELD COMMUNITY

By

Basil G. Stergios

Seed dispersal, seed germination and seedling establishment in *Hieracium aurantiacum* were studied in an 18-year-old oldfield community in southwestern Michigan. Most of the seed produced was deposited within 2 meters of the source. Seeds deposited nearest the source were found to be significantly larger and more viable than those deposited at a distance. Seedling survival appeared to be enhanced by establishment within the parent population rather than establishment in adjacent vegetation. Germination of seeds produced early in the year was significantly greater than that of seeds produced later in the year; cold treatment greatly enhanced germination in the late seed, but not in seed produced early in the season. Exclosure experiments indicated that insect predation and seedling mortality increases through the summer. These results suggest that although seed production in this species is

high, successful reproduction by seed seems confined primarily to areas already occupied by the parent population and appears relatively unimportant in the colonization of adjacent vegetated areas.

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By

Basil G. Stergios

A THESIS

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I wish to express my appreciation to Dr. William B. Drew for his continued support and encouragement throughout the development of this study.

I wish to thank Dr. George Lauff, Director of the Kellogg Biological Field Station for the use of facilities for this investigation.

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INTRODUCTION

Many of the plant species of advanced successional communities possess, in addition to well developed and significant means of seed production and dispersal, some means of vegetative reproduction. Despite abundant seed production by these species there is rarely evidence of extensive propagation by seedling establishment. On the other hand, vegetative reproduction is obvious in oldfields and other successional habitats, being largely responsible for the highly patterned nature of these communities.

The purpose of this investigation was to determine the importance of achene (and thus seed) reproduction in the population dynamics of a typical oldfield plant species, orange hawkweed (*Hieracium aurantiacum* L.). Three aspects of achene biology were considered: 1. seed production and dispersal from selected populations (aggregations); 2. seed size and germination behavior relative to dispersal gradients; and 3. seedling establishment and survival in the field.

Putwain, et al. (1968) found essentially no seed reproduction by *Rumex acetosella* in English pasture-lands, the population having been maintained primarily by vegetative reproduction. Harper (1967) points out that reproduction by seed and by vegetative means each represent differing components of a population's "r" value (intrinsic rate of increase) or biotic (reproductive) potential. The greater biotic potential inherent in seed reproduction is largely offset by high seedling mortality in the field (Salisbury, 1942; Harper, 1967). However, the biotic potential inherent in vegetative reproduction is smaller, but involves a lower mortality risk than in seedlings (Harper, 1967). Thus, the investments made by the plant for vegetative reproduction are more secure (Harper, 1967). Salisbury (1942) points out that seed plants reproducing vegetatively have a decided advantage over non-vegetatively reproduced plants, especially under adverse environmental and competitive conditions, and are assured successful propagation even when seeds are ineffectively or sparsely produced.

METHODS AND MATERIALS

Description of the Study Area

The study area is located at the W. K. Kellogg Biological Station in the northwest corner of Ross township in northern Kalamazoo County (T1S, R9W, Section 5) on the former William Louden farm (now part of the W. K. Kellogg Biological Station). The Louden oldfield is approximately 332 meters by 201 meters, with the long axis orientated north and south (Appendix D, plates 3 & 4). The study area is well isolated from other oldfield weed seed sources by cultivated areas on three sides and woodland on the other. It is bounded on the north by the Zeal Langshaw farm, on the west by the former Bailey farm (now part of the W. K. Kellogg Biological Station), and on the south by the continuation of the Louden farm.

The area where the field is located is part of the Gull Lake out-wash plain, consisting primarily of sand with very little gravel (Leverett & Taylor, 1915). The local relief of the area is dominated by ice-melt pit depressions, some of which are now lakes.

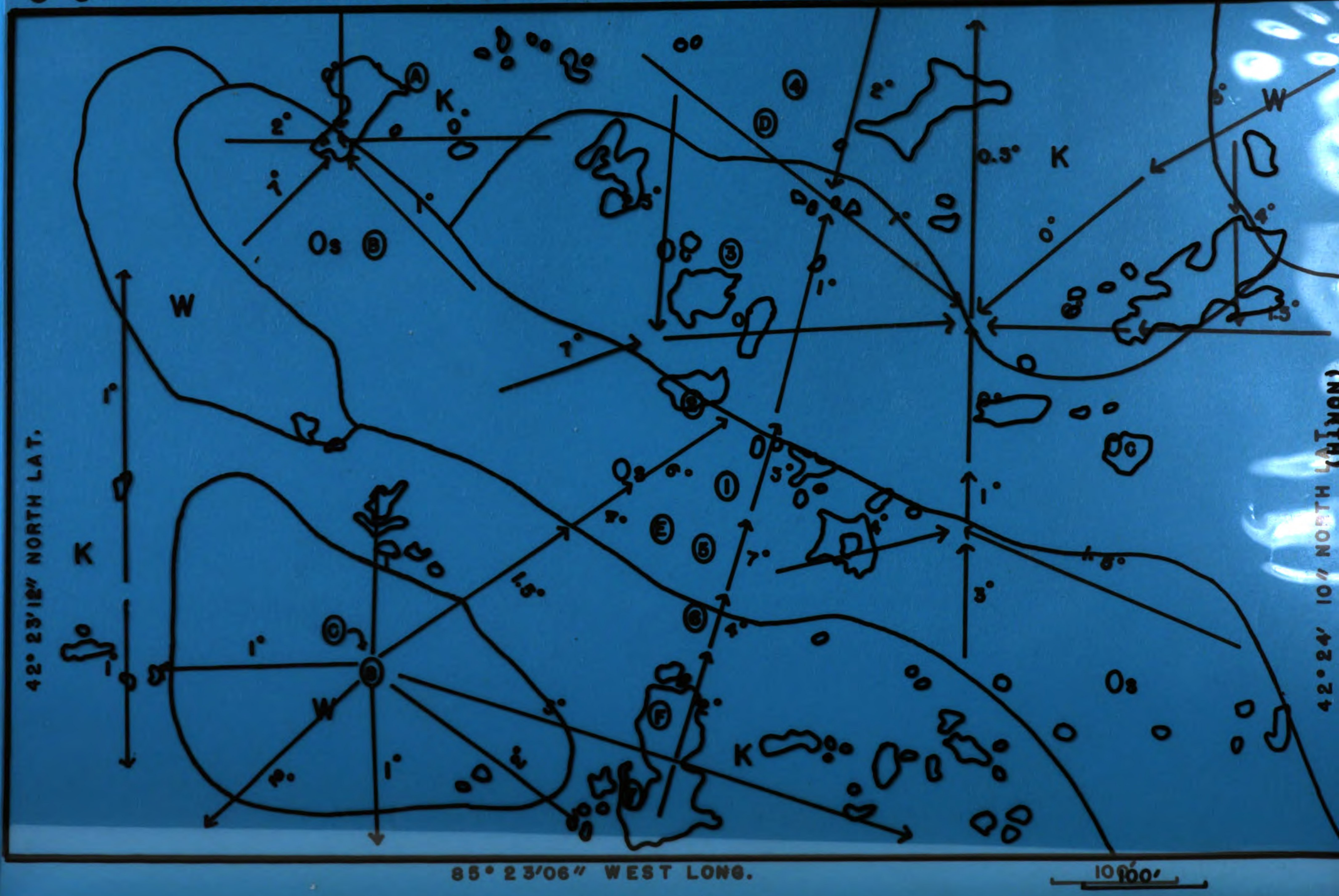
The topography of the area is varied (Fig. 1 and overlays). It consists of an upper, generally level area

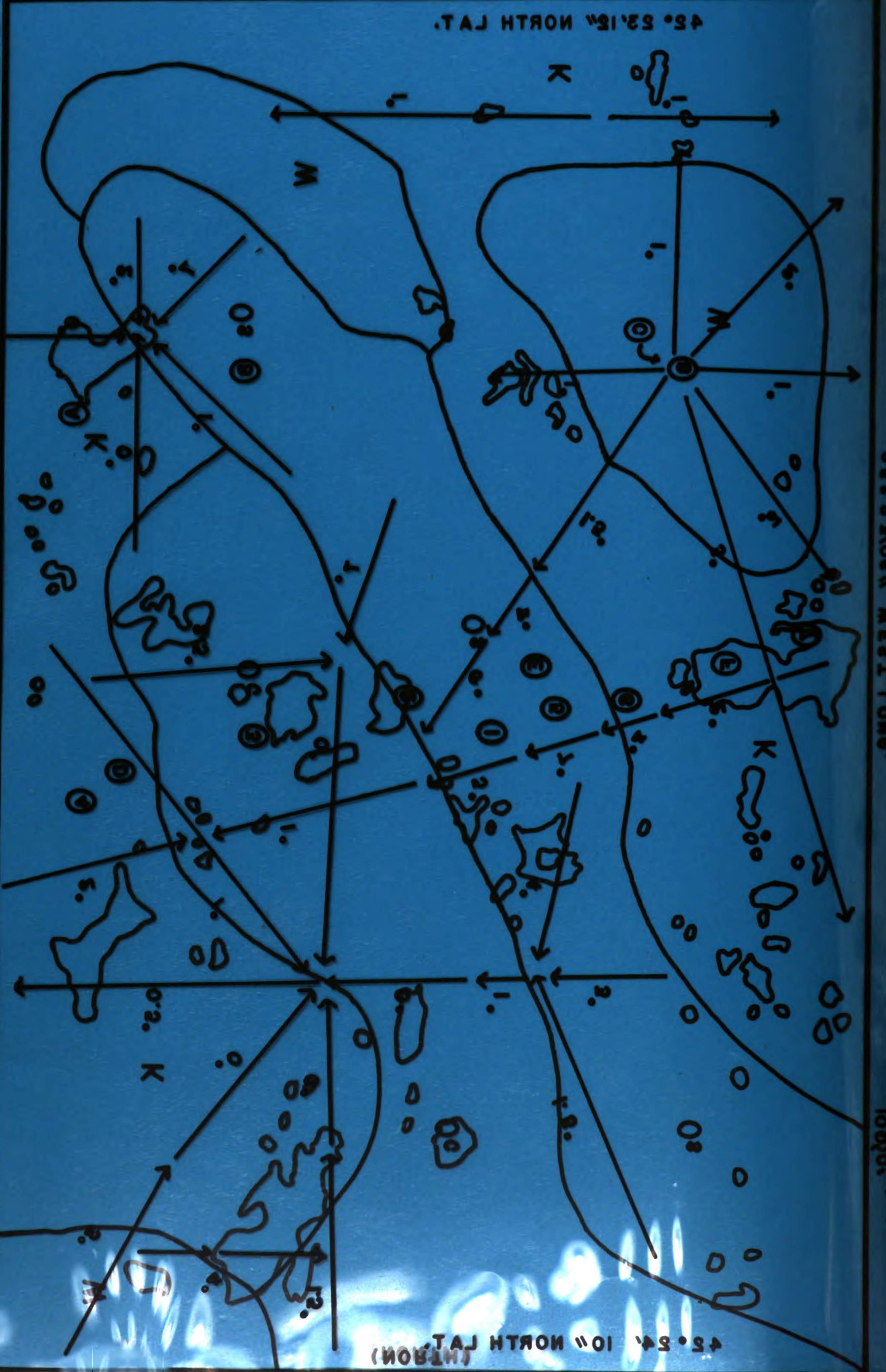
Fig. 1. Aerial photograph of the Louden oldfield (one inch = 100 ft.) with accompanying overlays:

A. Distribution of *H. aurantiacum* aggregations in the study area.

B. Distribution of soil types in the study area determined from soil profiles.

C. Slope description of the study area; soil sample sites and soil profile sites.


(A)...(F) = SAMPLED SITES
DISTRIBUTION OF SOIL TYPES IN THE LOUDEN OLD FIELD DETERMINED FROM SOIL PROFILES
→ INDICATES SLOPE DIRECTION (UPWARDS, WITH DEGREES GIVEN)
(1)...(8) = SOIL PROFILE SITES
K = KALAMAZOO SANDY LOAM; Os = OSHTEMO SANDY LOAM; O = [illegible] SANDY LOAM; W = WASHTENAW LOAM
DISTRIBUTION OF AGGREGATIONS OF HIERACIUM AURANTIACUM
85° 24' 17" WEST LONG.
42° 23'12" NORTH LAT.
42° 24' 10" NORTH LAT.
(NORTH)
85° 23'06" WEST LONG.
100'
K
W
Os
A
B
C
D
E
F
1
2
3
4
5
6
7
8
0.5°
1°
1.5°
2°
3°
4°
5°
7°


42° 23'12" NORTH LAT.
42° 24' 10" NORTH LAT.
(HURON)
85° 52'06" WEST LONG.
1000'
K
W
.1
.2
.3
.4
.5
.6
.7
.8
0.2
1.6

ABRAMS AERIAL SURVEY CORPORATION
LANSING 3, MICHIGAN

to the west-north-west that drops off abruptly to a depression in the northwest corner, and a more extensive lower area to the east and southeast. The field is cut diagonally from the northeast to the southwest corner by a 4° to 7° slope that has been subject in places to rather severe erosion. There are areas of definite truncation of the soil profile (Appendix B) as well as areas of marked slopewash accumulation. The latter condition is most pronounced in the southeast corner of the field (Profile site C, Fig. 1).

Soil analyses of the study area (see Fig. 1 for locations) were made on six samples. All analyses were done by the soil testing laboratory at Michigan State University. The results of these analyses are given in Appendix A.

From eight soil profiles taken in the field (Appendix B), four possible soil types were identified: Oshtemo sandy loam, Kalamazoo sandy loam, Ockley sandy loam, and Washtenaw loam--an alluvial soil (personal communication with Ivan F. Schneider, Department of Soil Science, Michigan State University). Based on relationships of these soil types to topographical features in the field, the soils were mapped as shown in Fig. 1.

The floristic composition between the upper and lower areas of the Louden oldfield is similar to that encountered by Caruso (1963) in the Ft. Custer Military

Reservation. *Poa compressa* appears to be of greater importance in the upper area while in the lower area *Agropyron repens* is more commonly encountered.

Interspaced among the matrix of *Poa* and *Agropyron* are aggregations of other species, which form a pattern of patchiness similar to that described by Caruso (1963), and Evans and Cain (1952). Also, numerous shrubs and small trees are invading the field.

Some of the most important species which occur in the study area are *Antennaria plantaginifolia*, *Chrysanthemum leucanthemum*, *Hieracium aurantiacum*, *Hieracium florentinum*, *Hieracium pratense*, *Rubus flagellaris*, *Agrostis hymalis* var. *hymalis*, *Solidago canadensis*, *Solidago juncea*, *Solidago nemoralis*, *Solidago graminifolia*, and *Solidago missouriensis*. A list of the 118 species found in the Louden oldfield between May and September, 1969, is given in Appendix C. Botanical nomenclature follows Gleason (1963), Gleason and Cronquist (1965), and Gould (1968). Voucher specimens from the study area have been placed in the Beal-Darlington Herbarium, Michigan State University.

History of the Study Area

The study area had been utilized for crop farming before 1911 but lay fallow until 1915. Due to unfavorable topography, which was subject to frequent erosion, the field was not cropped but was fenced off and used for pasturing sheep intermittently from 1915 until about 1942. During the seasons when no sheep were present, the field lay idle. Cropping began in 1942 and continued until 1948. During this period, corn and other grain crops were planted, giving very poor yields (personal communication with Margaret Louden, Hickory Corners, Michigan). The crops were generally rotated; oats were planted in the spring and wheat in the autumn of one year followed by corn the next. The field is believed never to have been marled or manured to any extent. Apparently herbicides were never applied to the field. Hay and alfalfa were also grown, but only in the very southern most portion of the field (from examination of the series of actual photographs made since 1938 it appears that this portion was periodically under cultivation as part of an adjacent field to the south). The field lay fallow until 1951, at which time it was planted with wheat.

Description of the Plant Studied

Orange hawkweed is native to Europe but is now widely distributed from Newfoundland to New Jersey, west to Minnesota and northern Indiana (Fernald, 1950). It has been found as far south as West Virginia to the tip of the northern panhandle, and further south in the Allegheny Mountains to the East (Myers, 1950). In the Tyrol and Austria it has been cultivated for some time as an ornamental (Pugsely, 1921). Orange hawkweed has been reported from an elevation of 5500 feet on Mt. Washington (Harris, 1930), and from higher elevations in Europe (Zahn, 1923).

The time when orange hawkweed enters the successional sequence of an oldfield has not been recorded. This entry undoubtedly varies considerably with particular combinations of soil types, other plant competitors, and surrounding environmental conditions. Adjacent to the study area, individuals of *H. aurantiacum* were found in the third year stage in three independent oldfield study plots (unpublished data, Dr. John Cantlon, Department of Botany & Plant Pathology, Michigan State University).

Seed Dispersal and Seed Size (Volume)

Seed dispersal of *Hieracium aurantiacum* was determined from six aggregations in 1968 (five in 1969) selected for their similar size and their isolation from other aggregations. Three line transects (extending radially 25 dm in 1968; 35 dm in 1969, from the center of each aggregation) were randomly selected. Three observations were made at each half-meter along these dispersal gradients by trapping seeds on plastic container lids coated with 'Tanglefoot' brand bird repellant (distributed by John Dill, Inc., Kalamazoo, Michigan). The lids were supported 10 cm above the ground by plastic stakes. The traps were installed just prior to the initial seed production period of mid-June. They were collected about 20 days later after most of the seed crop had been dispersed.

Seed deposition (field seed pool) at varying distances between aggregations of *H. aurantiacum* in the study area was examined (June and July, 1969). Six pairs of aggregations were selected with distances between each of them of 2, 6, 8, 14, 16, and 20 meters respectively. Three seed traps were placed at each meter interval along each transect. The traps were collected and the seeds counted at the end of the initial seed production period.

Seed volume was calculated (to hundredths of a mm^3) by measuring the lengths and diameters of seventy seeds trapped from each half-meter increment along the dispersal gradient. The equation

$$V = \pi r^2 0.8L + 1/3 \pi r^2 0.2L$$

represents total volume of each seed; four-fifths of the total seed volume taken as the volume of a cylinder and one-fifth as a cone (where r is the radius and L is the length).

Germination Studies in the Laboratory

In order to examine the relationship between germination and distance of dispersal, seeds were trapped for the germination studies along transects from six aggregations. Seventy-five seeds were sown in similar trays on moist soil from the study area. Two germination replicates were employed for each increment along the gradient. The trays were covered with cheese cloth and maintained at room temperature. All the seeds had previously been cold treated for 90 days at 0°C. The number of germinated seeds was recorded every two days until all germination had ceased (16 days). Volume rather than weight was used as an indication of seed size to avoid possible error in weight caused by the "tanglefoot" compound.

In order to determine the relationship between germination and time of seed production in *H. aurantiacum*, seeds were collected from the Louden oldfield at monthly intervals from June through September, 1969. The seeds were germinated on moist soil in petri plates. Some of the plates were stored at 0°C for 30 days before germination tests were begun. The remainder of the seeds were germinated immediately upon collection from the field. Percentage germination was recorded every two days.

Seedling Establishment and Survival Studies

To determine the effect of predation on seedling mortality, 19 sets of insect exclosures were erected. The exclosures were constructed of plastic screening and placed over 4-dm^2 plots at the edge of *H. aurantiacum* aggregations in the study area (Plate 2). The experiment was begun in March, 1969. All 38 plots were inoculated with 1000 seeds collected from the same aggregations during June, 1968. The control screens were elevated 15 cm above the ground and the sides were slit to allow the entry of flying insects. The tops of the control exclosures were permanently sealed at the bottom and kept temporarily closed at the top by clothespins. The experimental plots were sprayed with insecticide twice weekly and surviving seedlings were counted once per week from May through September.

Seedling establishment and survival was measured in 1968 from seeds deposited inside aggregations. Eighty-eight 4-dm^2 plots all of similar size were selected at random from six aggregations. Surviving seedlings, having been marked with plastic toothpicks, were those that had remained since the previous sampling. The following April (1969) the plots were again sampled to determine the number of over-wintered seedlings. Establishment and survival was measured in vegetated areas adjacent to the aggregations in 1969. Two hundred and forty 4-dm^2 plots were selected along 3-meter transects radiating from the aggregations. Seedlings in these plots were sampled every seven days as previously described.

RESULTS

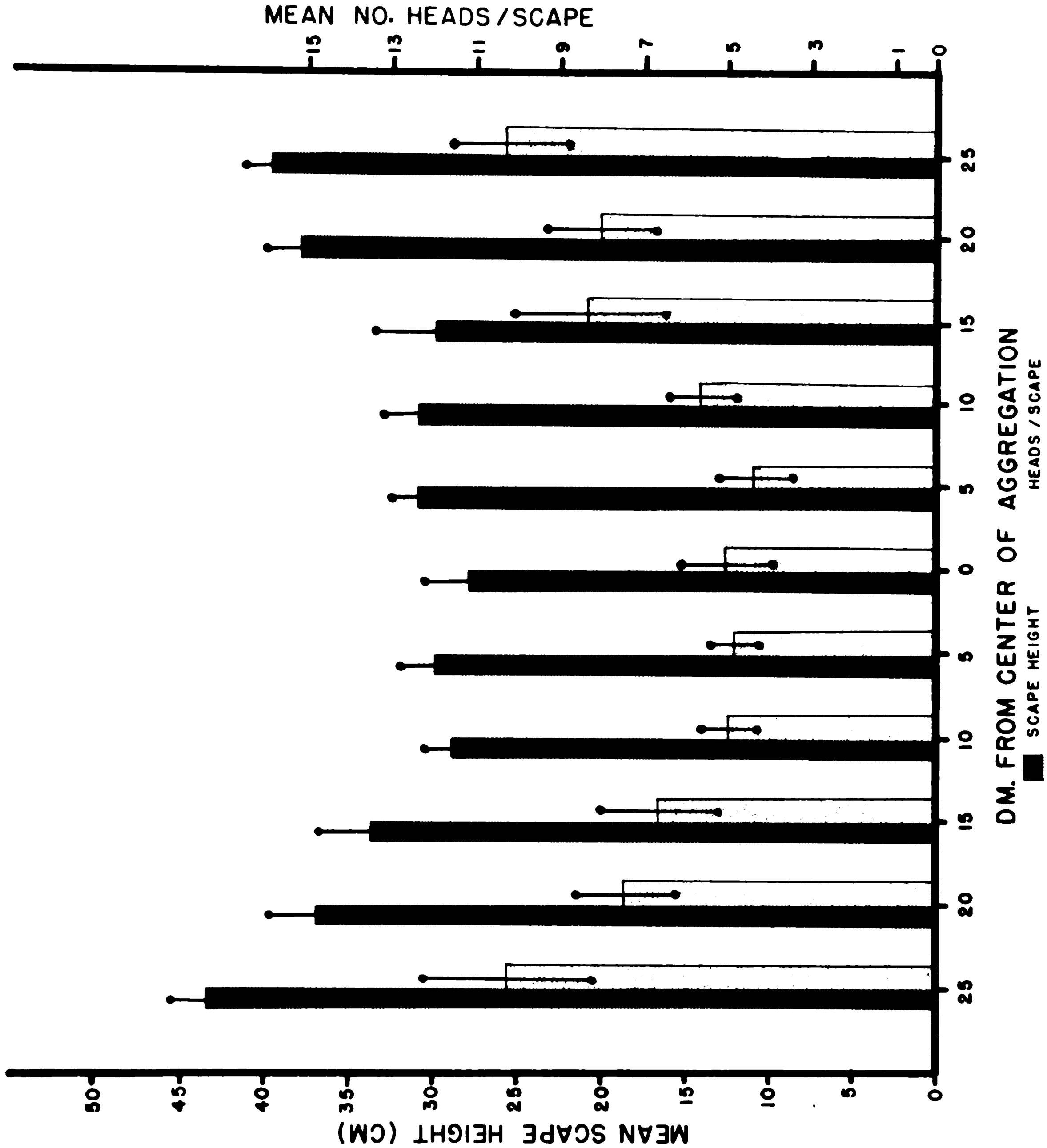
General Population Behavior and Phenology

Most of the stoloniferous growth in *Hieracium aurantiacum* occurs early in the season (mid-May to the end of June). The young rosettes become established during the remainder of the season. In the spring of the following year bolting occurs. In 1969 anthesis occurred between May 21 and June 7. By late June the initial flowering had ceased, and seeds had matured in about one-fourth of the Louden oldfield population. Seedlings which became established did not mature during the same season. After an initial phase of vigorous growth the seedlings became dormant for the rest of the season.

Scapes produced at the outer limits of *H. aurantiacum* aggregations were significantly taller than those at the center, and the number of flowering heads per scape was significantly greater at the periphery than toward the center (Fig. 2). Differences in rosette density across an aggregation were not measured.

Since the aggregations sampled were probably 10 or more years old, one might expect some differences in the various parts of the population. Koyama and Kira (1956)

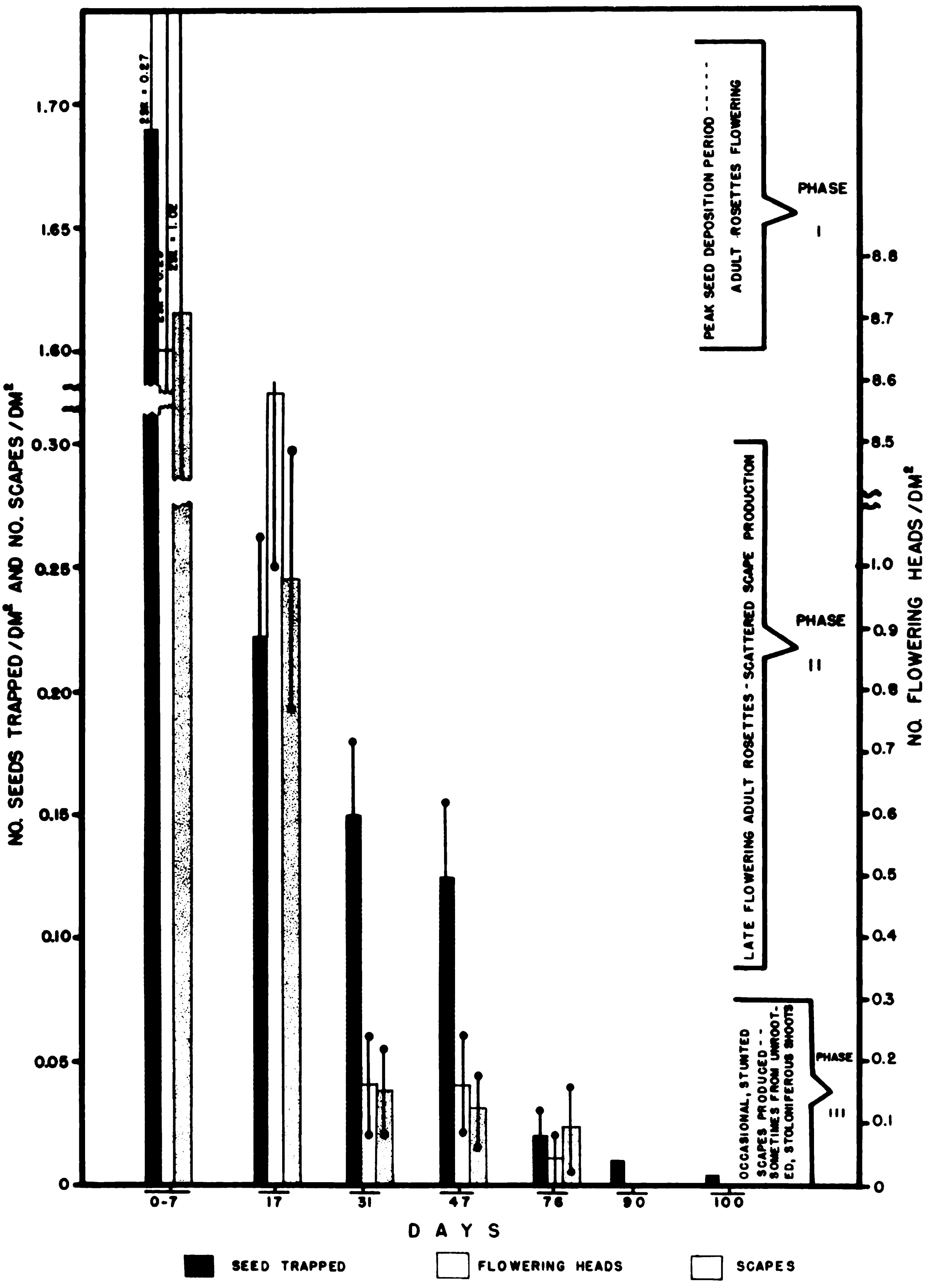
Fig. 2. Mean length of individual scapes across four aggregations of *H. aurantiacum*. Mean number of flowering heads per scape across the same aggregations. The points represent ±2S$\bar{X}$.


MEAN NO. HEADS/SCAPE
15
13
11
9
7
5
3
1
0
MEAN SCAPE HEIGHT (CM)
50
45
40
35
30
25
20
15
10
5
0
25
20
15
10
5
0
5
10
15
20
25
DM. FROM CENTER OF AGGREGATION
SCAPE HEIGHT
HEADS / SCAPE

and Stern (1965) showed that in time an increase in density within older portions of a plant population forces a sharing of limited resources with a compensating reduction in development of individuals. Less vigorous plants may be competing for sites long occupied by *H. aurantiacum* in the center of the aggregation, while more vigorous colonizers occupy the outer edge.

Reproduction within populations of *H. aurantiacum* declined rapidly after the initial bolting early in the season. Seed production (as represented by seed deposition) was closely correlated with flowering head and scape production (Fig. 3). The continued appearance of seeds after most scape production had stopped apparently resulted from the presence of plants in adjacent areas not sampled and previously dispersed seeds that had fallen or been blown onto the traps. A decrease in the number of seeds per head further indicated a decline in reproductive vigor as the season progressed. Seeds from the flowering heads of individuals in eight aggregations were counted in June, 1969 and again in September. The mean number of seeds per head produced was 74 in June and 58 in September. The difference in the number of seeds per head between the two periods was significant ($t = 7.8$; $p = <0.05$; $N = 14$).

Fig. 3. Seed, scape and flowering head production in *H. aurantiacum* aggregations from July 15 to Nov. 1, 1968. Variance estimates are $2S\bar{X}$.

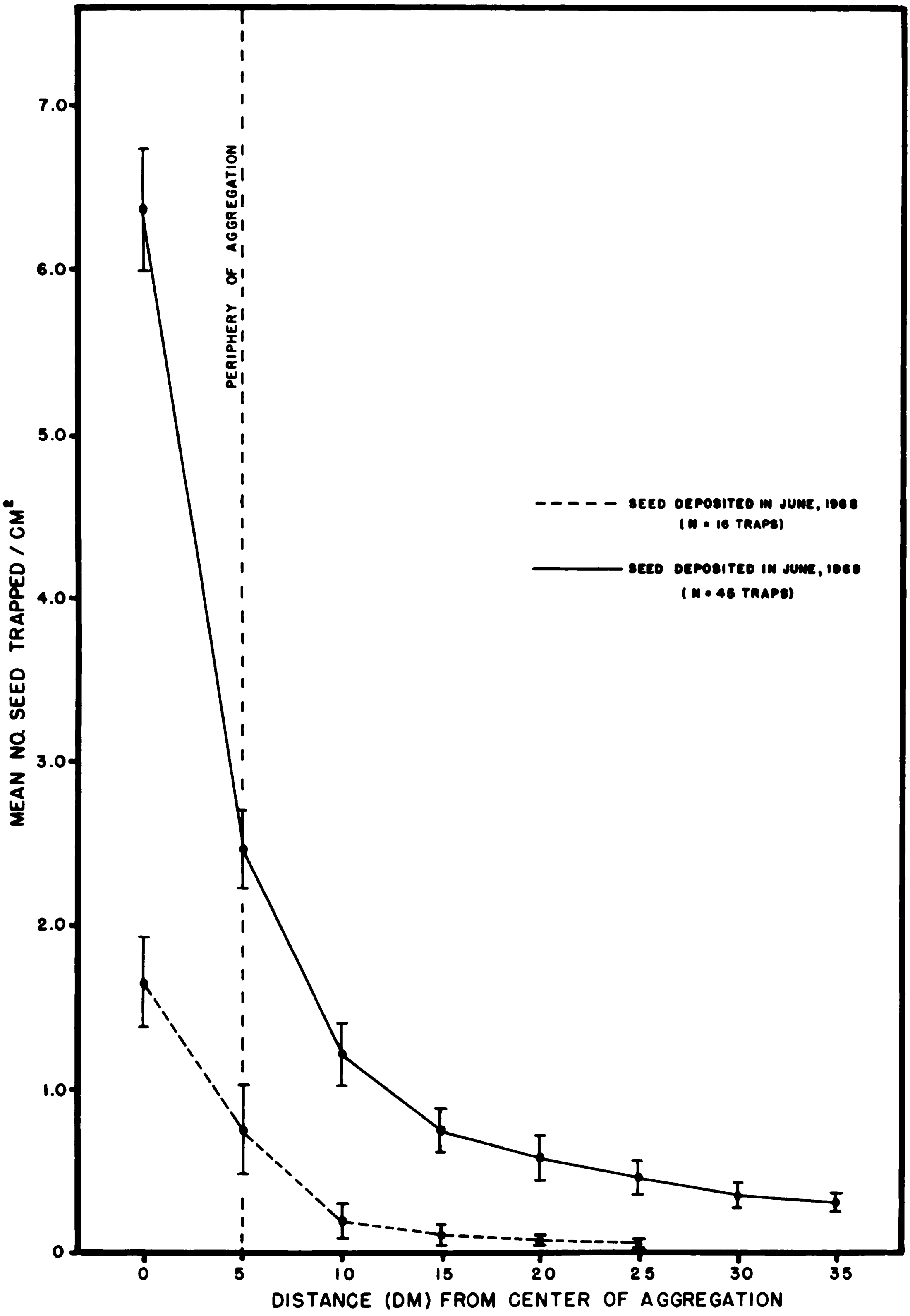
NO. SEEDS TRAPPED / DM² AND NO. SCAPES / DM²
1.70
1.65
1.60
0.30
0.25
0.20
0.15
0.10
0.05
0
2SE = 0.27
2SE = 1.02
NO. FLOWERING HEADS / DM²
8.8
8.7
8.6
8.5
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0-7
17
31
47
76
90
100
DAYS
SEED TRAPPED
FLOWERING HEADS
SCAPES
PEAK SEED DEPOSITION PERIOD - - - - -
ADULT ROSETTES FLOWERING
PHASE I
LATE FLOWERING ADULT ROSETTES - SCATTERED SCAPE PRODUCTION
PHASE II
OCCASIONAL, STUNTED SCAPES PRODUCED - - SOMETIMES FROM UNROOTED, STOLONIFEROUS SHOOTS
PHASE III

Seed Dispersal and Deposition

Seed trap results showed that deposition was restricted primarily to within 25 dm of the source aggregations (Fig. 4). An analysis of variance of the data from the 1969 transects revealed no significant differences between total seed output of the aggregations sampled ($F_{14, 345} = 0.84$; $p = >0.05$). This also indicates that wind had very little influence on the direction of dispersal since sample transects were randomly orientated. Data from both 1968 and 1969 indicated that the pattern of dispersal of seeds with respect to distance from the aggregation resembled a negatively sloped exponential curve similar to that discussed by Wolfenbarger (1946) and Faulwetter (1917) for dispersal of propagules from a source. In keeping with this pattern, the majority of *H. aurantiacum* seeds dispersed were deposited before they had left the aggregation (Fig. 4). Similar seed dispersal patterns have been reported by Isaac (1930) for douglas-fir, and also for black spruce (Lake States Exper. Sta., 1939; (cited by Wolfenbarger, 1946)). Hafmann (1911) suggested that the exponential reduction in numbers of gymnosperm seedlings from a seed source reflected the seed dispersal pattern.

The dispersal pattern of seeds of *H. aurantiacum* suggested that deposition never reaches zero, but stabilizes at about 0.5 seeds per cm^2 in the area 2 to 2.5 meters

Fig. 4. Seed trap results. Points indicate mean seed numbers per cm^2. Estimates of dispersion are $2S\bar{X}$.


MEAN NO. SEED TRAPPED / CM²
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
PERIPHERY OF AGGREGATION
SEED DEPOSITED IN JUNE, 1968
(N = 16 TRAPS)
SEED DEPOSITED IN JUNE, 1969
(N = 45 TRAPS)
0
5
10
15
20
25
30
35
DISTANCE (DM) FROM CENTER OF AGGREGATION

beyond the seed source (Fig. 5). This is to be expected (Wolfenbarger, 1946) in dispersal distributions like those already described.

Seed Size

In the vicinity of *H. aurantiacum* aggregations in the Louden oldfield, seed volume and distance dispersed were closely related (Fig. 6). The seeds from any given point on the gradients did not differ significantly in their volumes. The smaller seeds were dispersed farther and, over the distance sampled, the relationship was nearly linear. Variability in seed size has been shown to play an important role in the propagative potential of certain plants (Black, 1956 & 1957; Cavers & Harper, 1966; Janzen, 1969; Salisbury, 1942). Salisbury (1942) points out that smaller seeds are more widely and efficiently dispersed. He indicates that wider dispersal enables a more probable dissemination to all suitable habitats.

The relationship between seed germination of *H. aurantiacum* and distance of dispersal is shown in Fig. 7. The daily percentage germination for each increment of the gradient is also given. The germinability (to 16 days) declined significantly as the distance of dispersal increased. Smaller seeds that were dispersed greater distances showed lower germinability and a tendency for increased germination after an initial delay (Fig. 7).

Fig. 5. Mean seed deposition (field seed pool) along transects of varying lengths. Variance estimates are ±2$S_{\bar{x}}$.

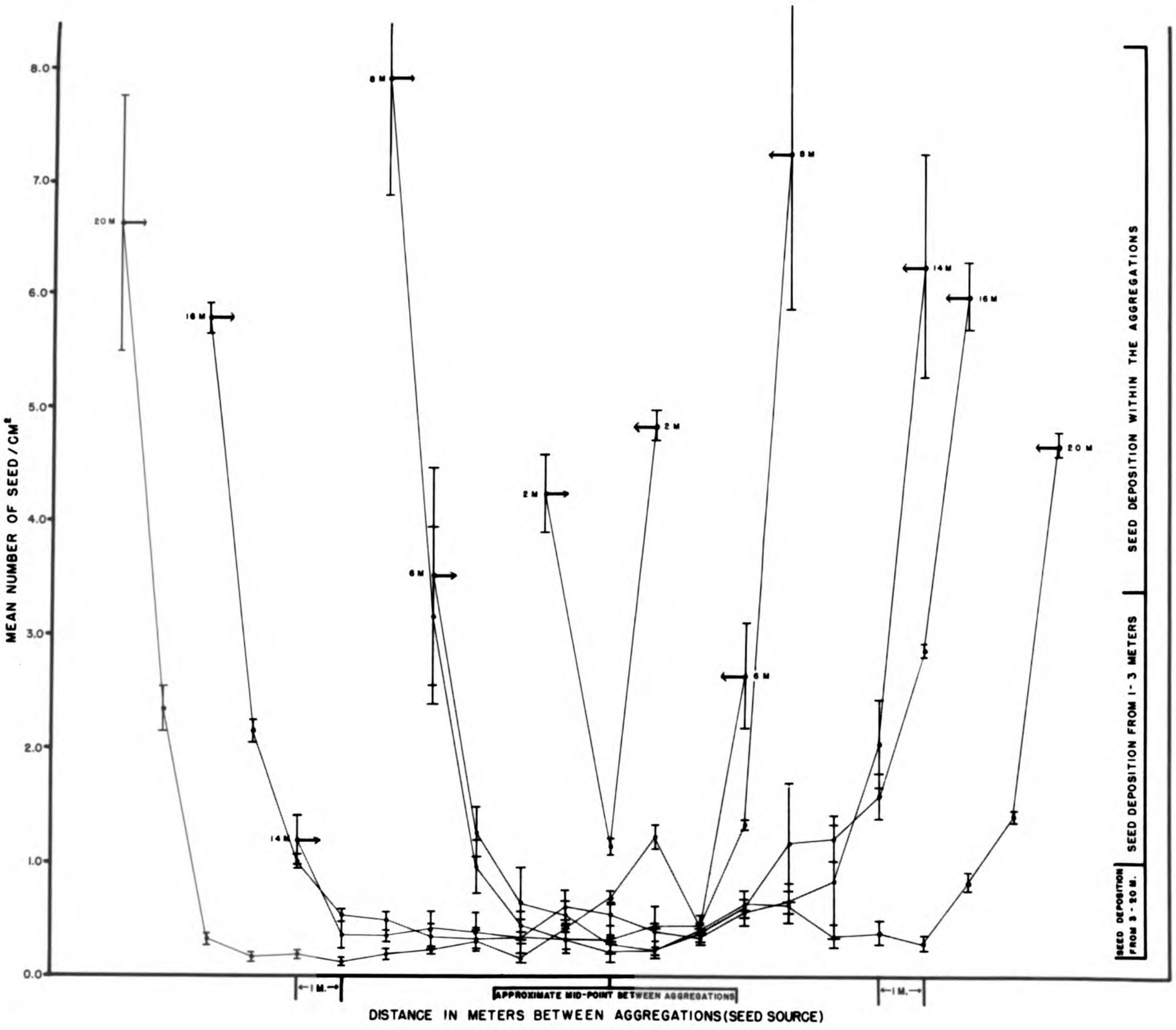

MEAN NUMBER OF SEED / CM²
0.0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
20 M
16 M
14 M
8 M
6 M
2 M
2 M
6 M
8 M
14 M
16 M
20 M
←1 M.→
APPROXIMATE MID-POINT BETWEEN AGGREGATIONS
←1 M.→
DISTANCE IN METERS BETWEEN AGGREGATIONS (SEED SOURCE)
SEED DEPOSITION FROM 3 - 20 M.
SEED DEPOSITION FROM 1 - 3 METERS
SEED DEPOSITION WITHIN THE AGGREGATIONS

Fig. 6. Relationship betweed seed size and distance dispersed. 95% confidence limits are indicated.

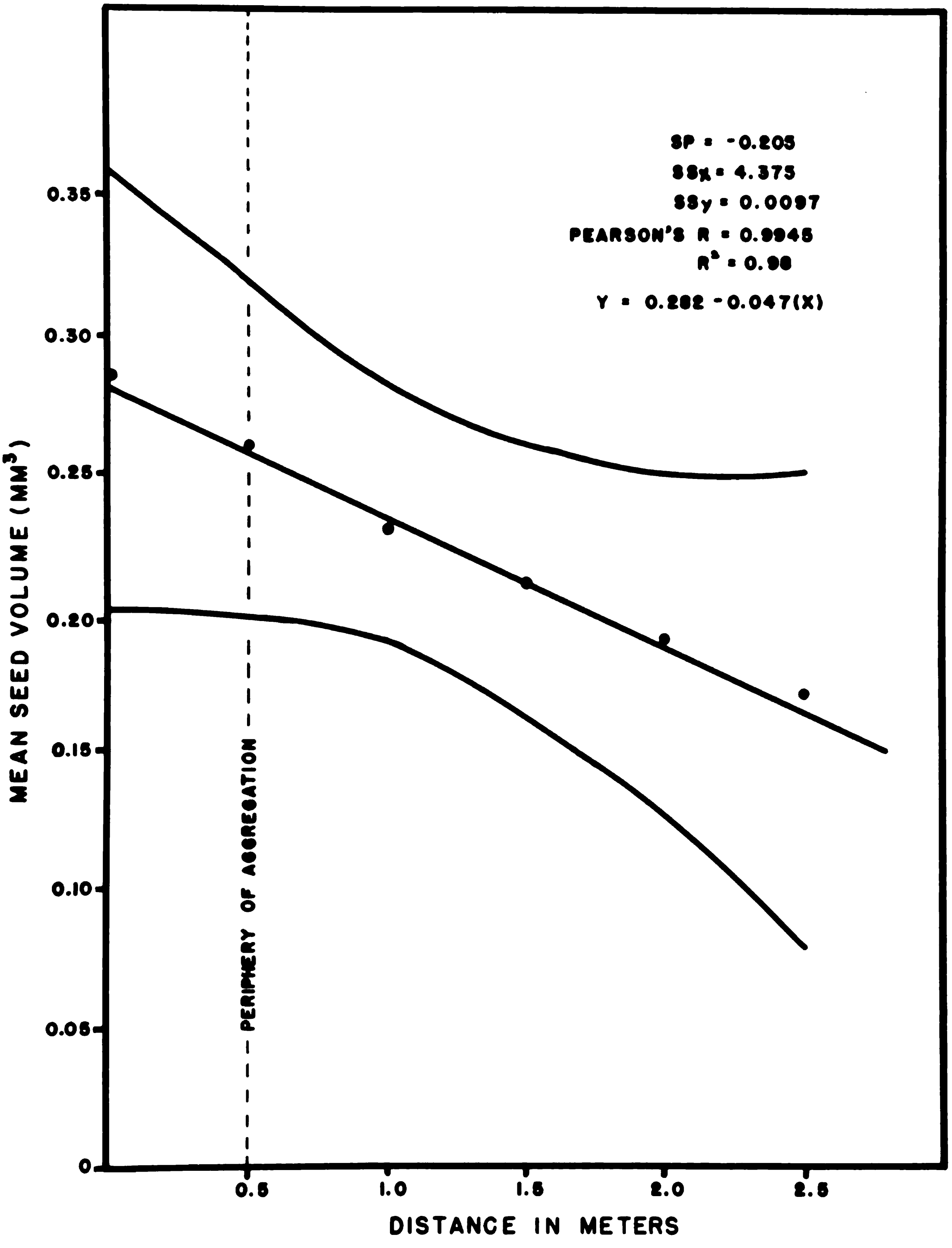
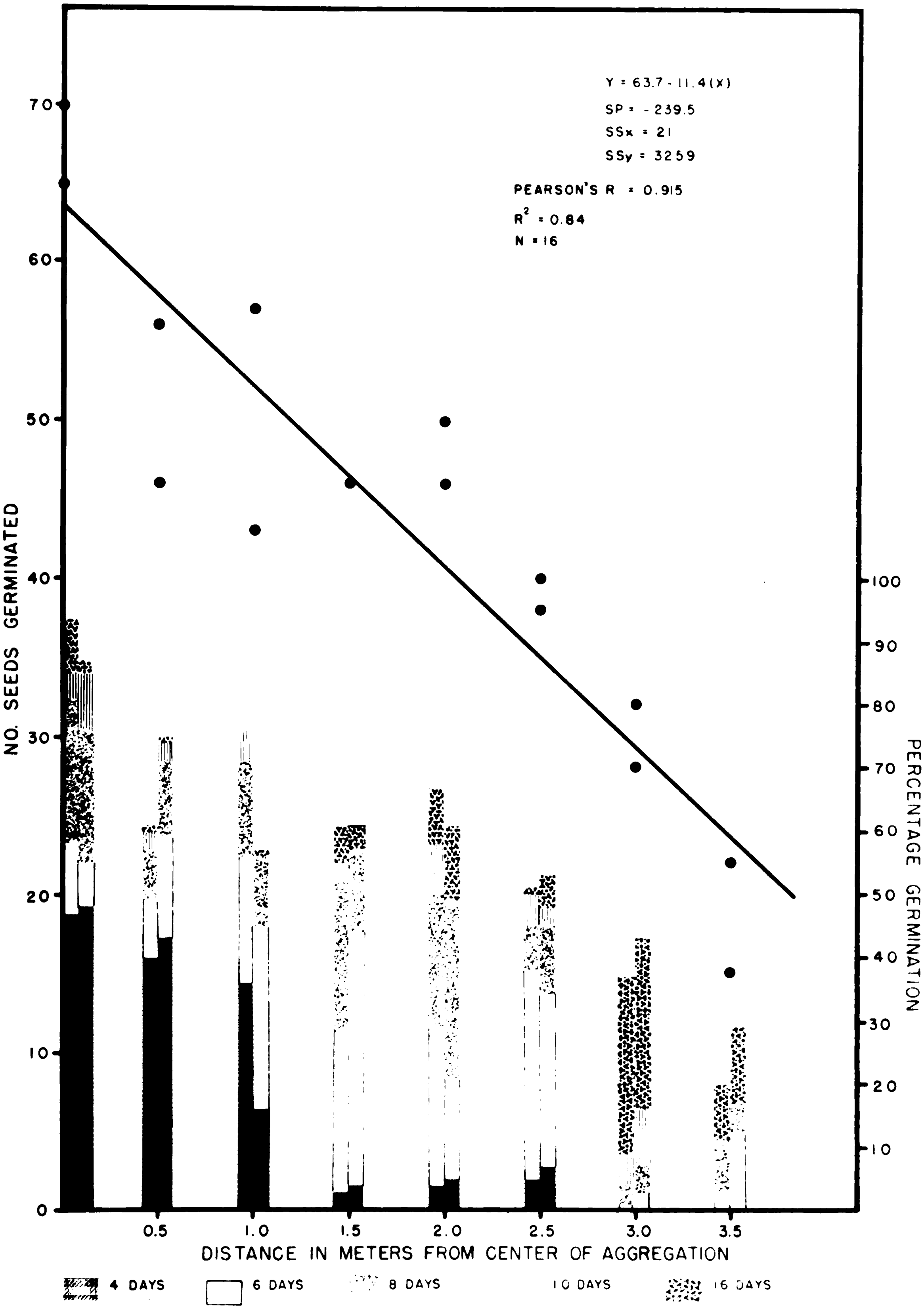

SP = -0.205
SSx = 4.375
SSy = 0.0097
PEARSON'S R = 0.9945
R² = 0.98
Y = 0.282 - 0.047(X)
PERIPHERY OF AGGREGATION
MEAN SEED VOLUME (MM³)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0
0.5
1.0
1.5
2.0
2.5
DISTANCE IN METERS

Fig. 7. Relationship between total seed germination and distance of dispersal. Bars indicate per diem percentage germination.


Y = 63.7 - 11.4(X)
SP = - 239.5
SSx = 21
SSy = 3259
PEARSON'S R = 0.915
R^2 = 0.84
N = 16
NO. SEEDS GERMINATED
0
10
20
30
40
50
60
70
PERCENTAGE GERMINATION
10
20
30
40
50
60
70
80
90
100
0.5
1.0
1.5
2.0
2.5
3.0
3.5
DISTANCE IN METERS FROM CENTER OF AGGREGATION
4 DAYS
6 DAYS
8 DAYS
10 DAYS
16 DAYS

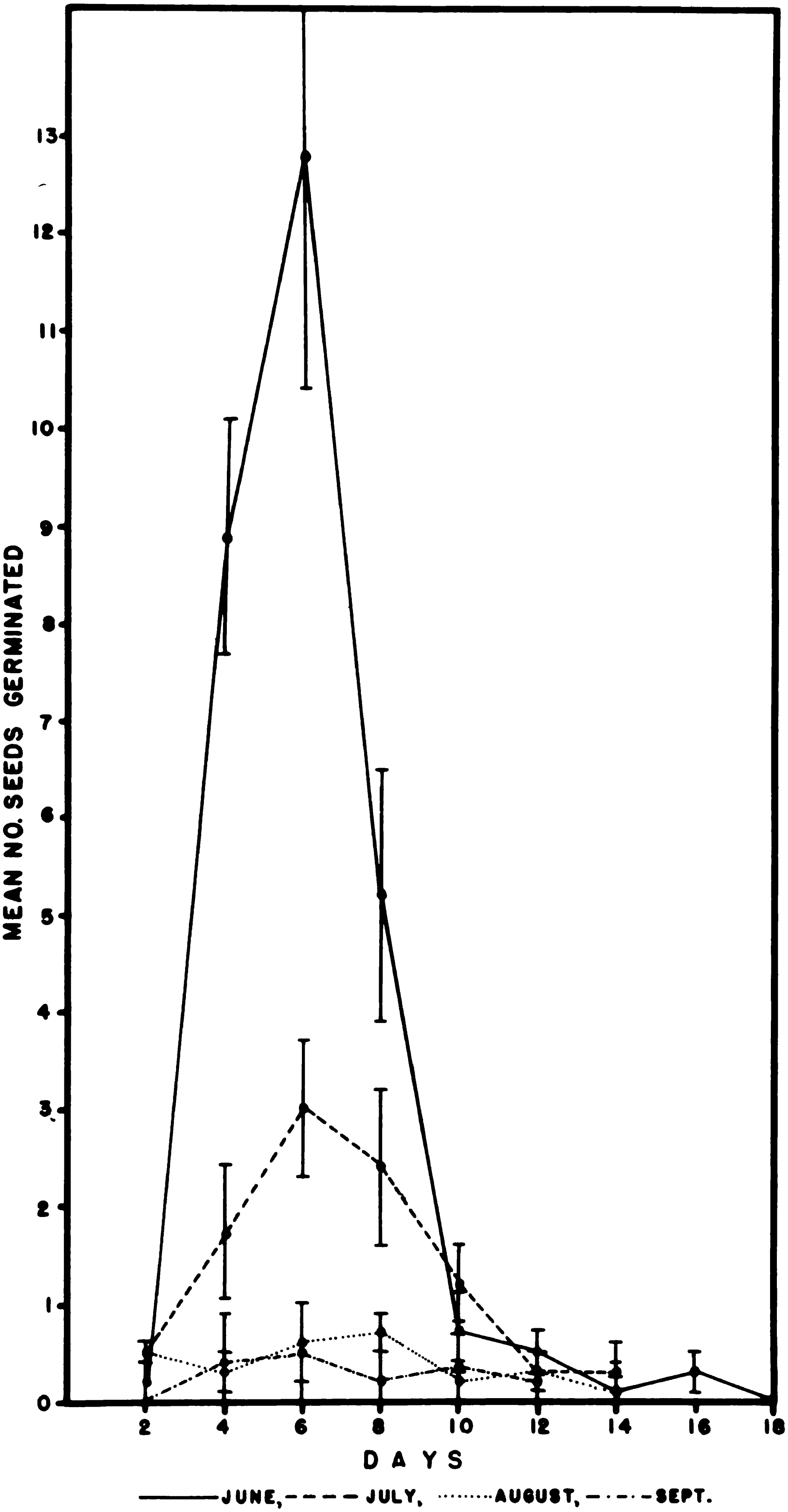
Seeds trapped with "tanglefoot" showed no significant differences in germinability from seeds not so contaminated ($t = 2.4$; $p = >0.05$; $N = 6$).

A number of investigators have pointed out the apparent relationship between germinability and seed polymorphism. Johnson (1935) observed that the percentage germination in *Avena* was closely correlated with the average seed weight. Becker (1912, cited by Salisbury, 1942) showed that seeds of two different sizes of *Rapistrum* and *Cakile* differed in their germinability. Cavers and Harper (1966) found that germination of *Rumex* was significantly higher in seed from the upper part of the panicle than from the lower. They also found that, in general, the upper seeds were heavier than the lower.

Germination Studies in the Laboratory

Seeds of *Hieracium aurantiacum* produced at different times during the season showed a significant difference in germinability for the first 10 days when germinated without cold treatment (Fig. 8). The germinability of seeds produced in June was far greater than that of seeds produced during the latter part of the season. There was no significant difference in the germinability of seeds collected from different aggregations.

Fig. 8. Mean number of seeds germinated without a cold period at monthly intervals from June through September, 1969. Variance is given by ±2$S\bar{x}$.


MEAN NO. SEEDS GERMINATED
0
1
2
3
4
5
6
7
8
9
10
11
12
13
2
4
6
8
10
12
14
16
18
DAYS
JUNE,
JULY,
AUGUST,
SEPT.

Cold treatment greatly enhanced germination of *H. aurantiacum* seeds produced during the latter part of the season (Figs. 9 & 10). The cumulative percentage germination of the June seeds was not appreciably affected by cold treatment (Fig. 10), but the proportion that germinated during the first two days was greater for the cold treated seeds (Figs. 9 & 10).

The effects of cold treatment on seed germination are well documented. Storage of *Avena fatua* at freezing temperatures resulted in increased germination (Johnson, 1935). Steinbauer and Grigsby (1956) indicate that *Saponaria officinalis* requires previous exposure to one week at 5°C for induction of germination. Percentage germination of *Daucus* and *Oenothera* was increased by exposure to cold (0° - 12°C) in light (Gardner, 1921).

Failure of late season *H. aurantiacum* seeds to germinate readily may be due to dormancy. These late season seeds were still viable, as evidenced by an increased germination following cold treatment (Fig. 10). Although any prolonged dormancy in seeds of *H. aurantiacum* has not been investigated, there are probably mechanisms for delaying germination of seeds produced at the end of the season until the following spring. Seedlings resulting from late season germination would be exposed to prolonged drought, insect predation, and frost damage. Although mature plants in general are capable of withstanding severe

Fig. 9. Mean number of seeds germinated after cold treatment. Seed from monthly intervals (June through September, 1969). Variance is given by $\pm 2S\bar{x}$.

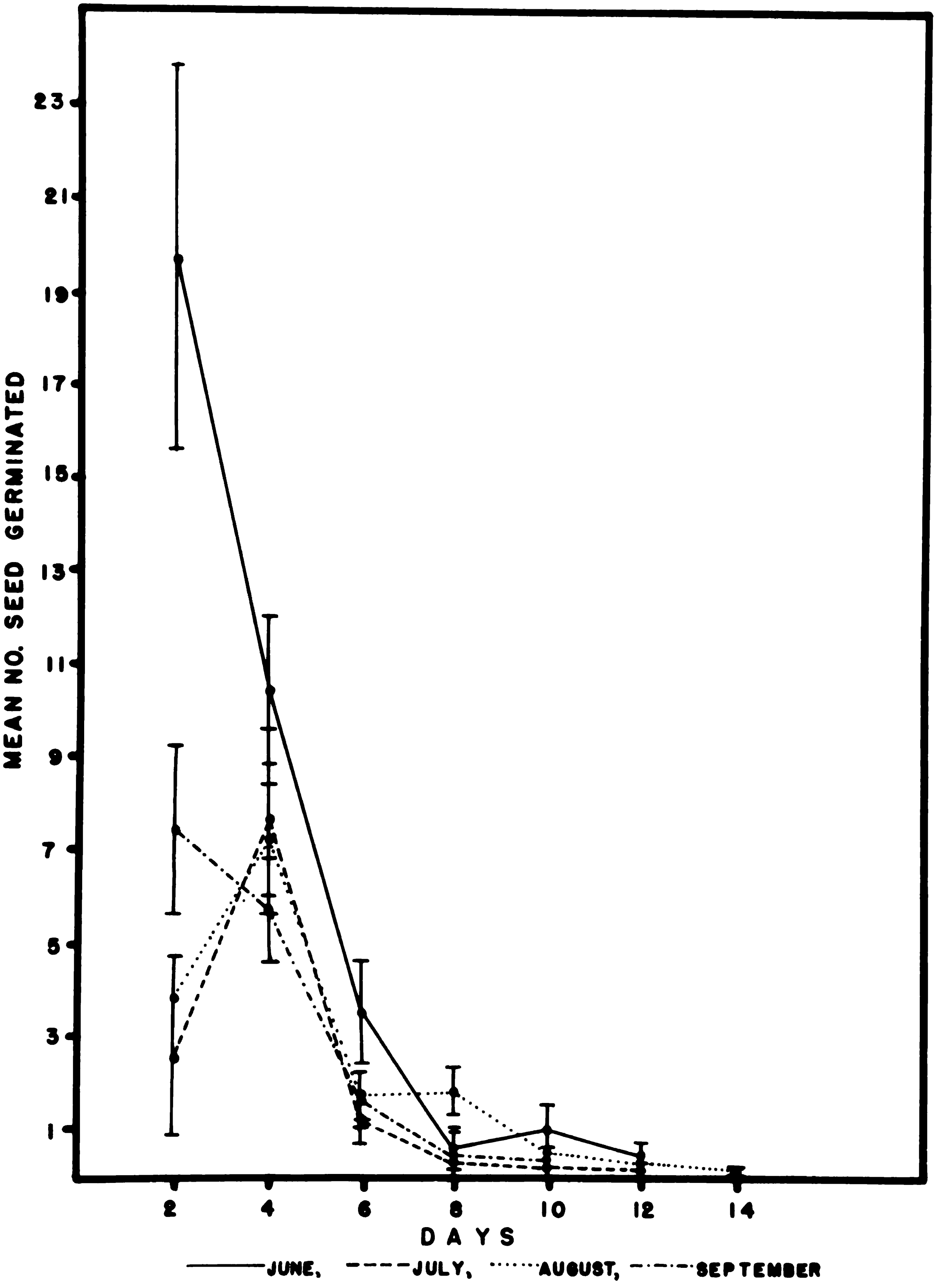
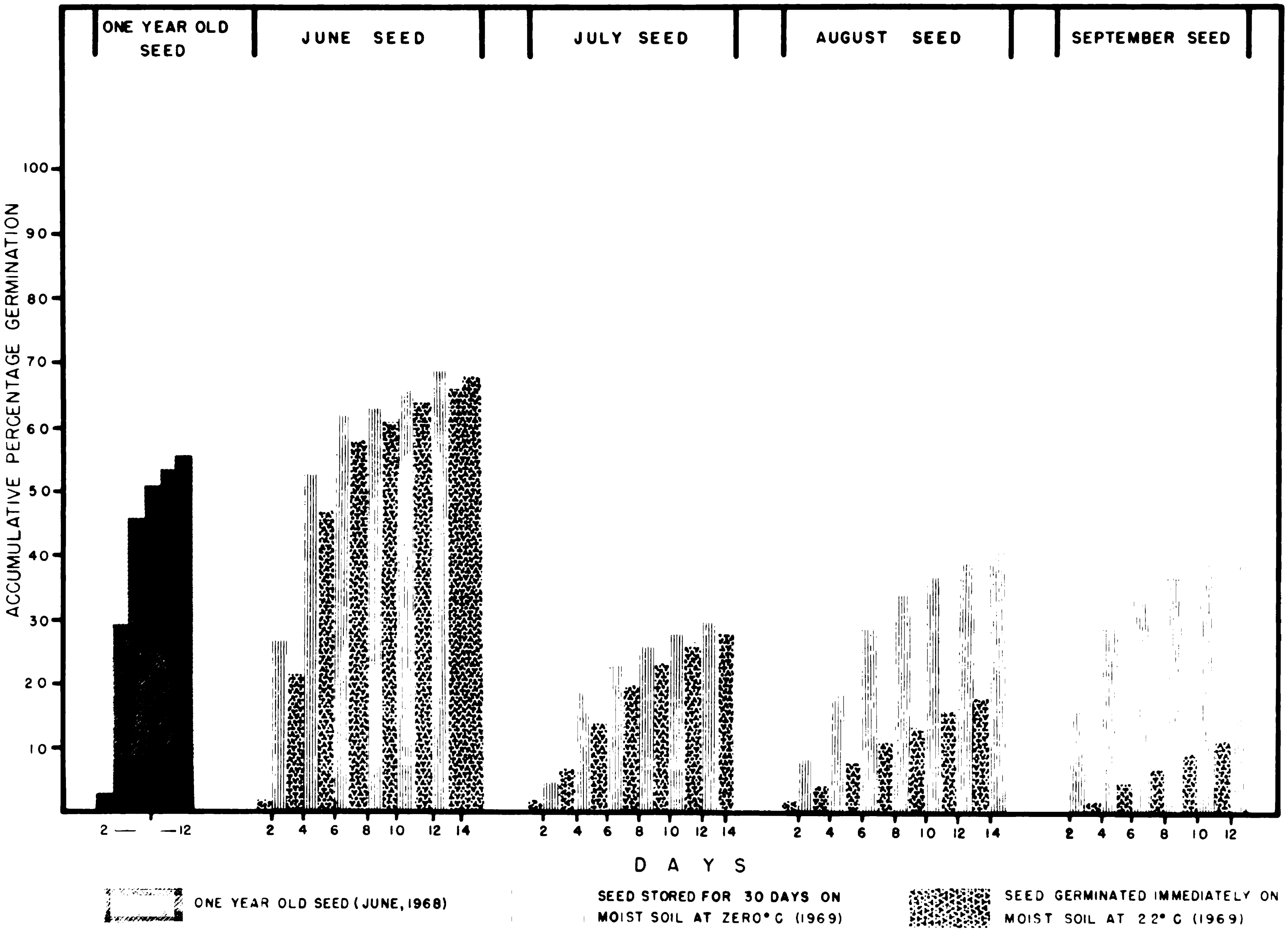

MEAN NO. SEED GERMINATED
23
21
19
17
15
13
11
9
7
5
3
1
2
4
6
8
10
12
14
DAYS
JUNE,
JULY,
AUGUST,
SEPTEMBER

Fig. 10. Cumulative percentage germination with and without a cold period of seed produced at four monthly intervals during summer, 1969, and of seeds stored for one year.


ONE YEAR OLD SEED
JUNE SEED
JULY SEED
AUGUST SEED
SEPTEMBER SEED
ACCUMULATIVE PERCENTAGE GERMINATION
100
90
80
70
60
50
40
30
20
10
2 — —12
2 4 6 8 10 12 14
2 4 6 8 10 12 14
2 4 6 8 10 12 14
2 4 6 8 10 12
D A Y S
ONE YEAR OLD SEED (JUNE, 1968)
SEED STORED FOR 30 DAYS ON MOIST SOIL AT ZERO° C (1969)
SEED GERMINATED IMMEDIATELY ON MOIST SOIL AT 22° C (1969)

cold and dry spells, their seedlings are readily killed (Cavers & Harper, 1964).

Delayed and intermittent germination caused by seed dormancy is probably genetic in nature (Cavers & Harper, 1966). Gustafsson (1935) looked at germination behavior in the genus *Hieracium*, in which embryos of apomictic species developed independently of the development of the achene. This resulted in the dispersal of mature achenes whose embryos were at different stages of development. He postulates that some seed embryos may continue nuclear division and eventually mature, resulting in delayed germination. Other embryos may never develop to maturity after dispersal, and the seeds become inviable. Since apomixis has been demonstrated in *H. aurantiacum* (Gustafsson, 1946 & 1947; Stebbins, 1941 & 1950), it is possible that delayed germination in the smaller (less developed) seeds in the Gull Lake area populations resulted from a similar mechanism.

The percentage germination of *H. aurantiacum* seeds collected in June, 1968 and aged for one year in a dry container was slightly below that of seeds germinated fresh in 1969 from the same aggregations. No fresh seeds were germinated in 1968. Experiments have indicated that storage of seeds tends to decrease germinability (Gustafsson, 1935; Gardner, 1921). However, Steinbauer and Grigsby (1960) obtained no germinability differences with *Rumex*.

Seedling Establishment and Survival

Results from experiments in the field indicated that many seedlings of *Hieracium aurantiacum* died largely from predation by grasshoppers. From early spring until late July, 1969, the number of seedlings and resulting survival was not significantly different among the plots (Fig. 11). From the first week in August the survival of seedlings in the unprotected plots continued to be significantly lower than in the protected plots. A general downward trend in over-all seedling survival toward the latter part of the season may have been due in part to a severe dry spell. Desiccated seedlings not touched by predators were observed in dried-out surface soil in both the protected and unprotected plots. Cavers and Harper (1967) pointed out the difficulty of determining the causes of sudden mid or late season mortality. In their studies with *Rumex* (1967), disappearances coincided with mid-summer drought and heavy rains. The precise causes of seedling death remained an unsolved problem.

Seedling survival inside aggregations in 1968 was significantly greater than that occurring in adjacent vegetated areas in 1969 (Fig. 12). The possible error introduced by comparing data from two different seasons was not determined. However, differences in weather and also in *H. aurantiacum* seed production between the two years (Fig. 4)

Fig. 11. Mean log (T+1) number of surviving seedlings protected and unprotected from predators during summer, 1969. Variance is given by ±2S$\bar{x}$.

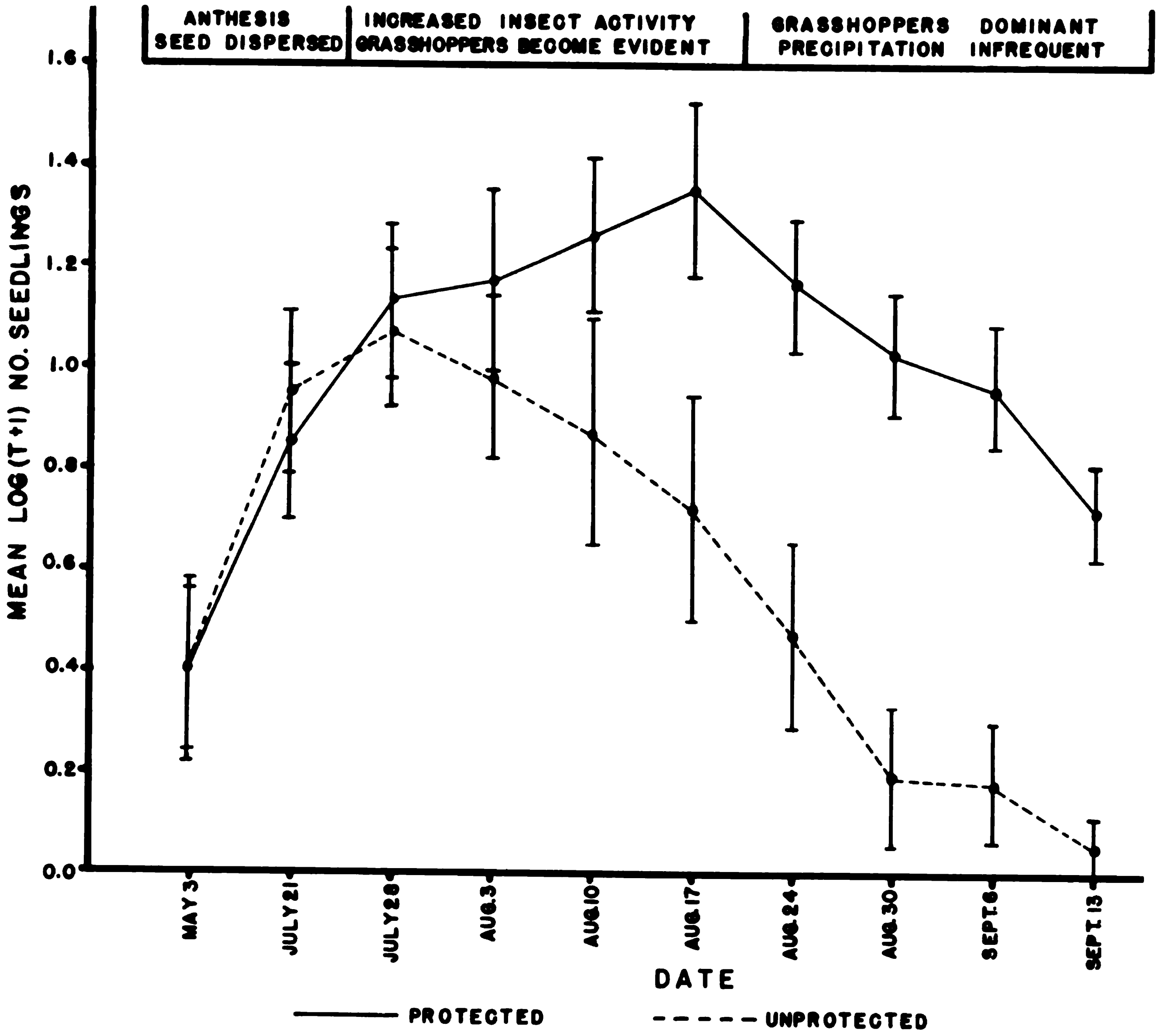
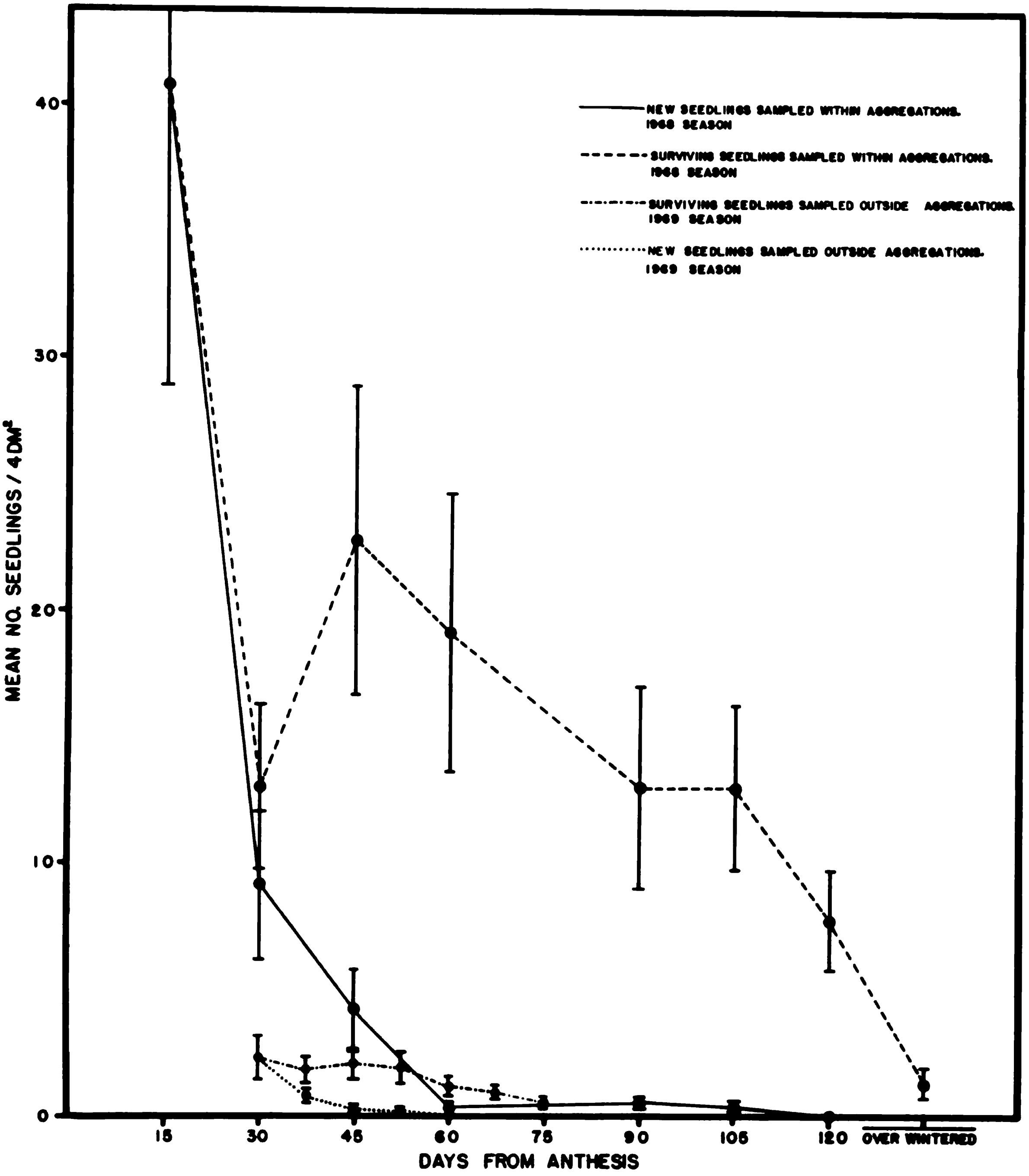

ANTHESIS
SEED DISPERSED
INCREASED INSECT ACTIVITY
GRASSHOPPERS BECOME EVIDENT
GRASSHOPPERS DOMINANT
PRECIPITATION INFREQUENT
MEAN LOG(T+1) NO. SEEDLINGS
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
MAY 3
JULY 21
JULY 28
AUG. 3
AUG. 10
AUG. 17
AUG. 24
AUG. 30
SEPT. 6
SEPT. 13
DATE
PROTECTED
UNPROTECTED

Fig. 12. Mean number of new seedlings inside and outside aggregations of *H. aurantiacum*. Variance estimates are ±2$S\bar{x}$.


NEW SEEDLINGS SAMPLED WITHIN AGGREGATIONS. 1968 SEASON
SURVIVING SEEDLINGS SAMPLED WITHIN AGGREGATIONS. 1968 SEASON
SURVIVING SEEDLINGS SAMPLED OUTSIDE AGGREGATIONS. 1969 SEASON
NEW SEEDLINGS SAMPLED OUTSIDE AGGREGATIONS. 1969 SEASON
MEAN NO. SEEDLINGS / 4DM²
40
30
20
10
0
15
30
45
60
75
90
105
120
OVER WINTERED
DAYS FROM ANTHESIS

suggests that it may be significant. Cavers and Harper (1967) found that many seedlings of *Rumex* established during the summer died. Few *H. aurantiacum* seedlings survived the winter in the Louden oldfield aggregations (Fig. 12). Most seedlings that disappeared did so during the cotyledon stage. Vegetated areas immediately surrounding aggregations of *H. aurantiacum* in the Louden oldfield resemble the 'closed communities' referred to by Cavers and Harper (1967). Seeds of *Rumex* readily germinated in these closed habitats, but resulting seedlings failed to survive.

DISCUSSION

The Louden oldfield is typical of an advanced successional community, where diversity of and competition among plant species is high (Hanson & Churchill, 1961; Bard, 1952; Clements, 1916; Keever, 1950). Both vegetative reproduction and reproduction by seed occur among plants in the Louden oldfield community. The highly patterned nature of this community is indicative of relatively successful vegetative reproduction and fairly limited seed dispersal.

Aggregations of *Hieracium aurantiacum* in the Louden oldfield community appear to become stabilized by vegetative reproduction, then tend to resist further colonization by seedlings. Vegetated areas adjacent to these populations are also 'closed' to colonization by invading seeds of *H. aurantiacum*, and establishment is even more strongly resisted in these areas.

My results suggest that successful propagation of *H. aurantiacum* in a local area is achieved primarily by vegetative means. The majority of orange hawkweed seeds produced appear to be deposited within rather than beyond the source aggregation. Reduction of seed size and germinability appear to occur as a function of distance of dispersal. Seedlings that do manage to become established, either

within the parent population or in an adjacent 'closed community,' soon succumb to excessive dry spells, predation, and winter kill. Harper, in 1967, issued the challenge: "What is the relative energy expended in producing a vegetative propagule and a seed? Can this expenditure be related to the relative risks of establishment by the two means of the relative ecological importance of local and long distance spread?" Salisbury (1942), and Harper et al. (1966; 1967), have suggested that the main function of seeds is to locate suitable habitats for colonization via long distance dispersal, to locate receptive sites for immediate germination at any distance from the seed source, and to saturate so-called closed communities and remain dormant until successional changes or other disturbances occur which create sites favorable for germination and survival. A relatively large amount of seed would be needed to fulfill all of these roles simultaneously.

SUMMARY

1. Scape height and number of flowering heads per plant are significantly greater at the periphery than toward the center of an aggregation of *Hieracium aurantiacum*.
2. Most of the seed is produced during a short period in early summer. Seed production drops off sharply as the season continues.
3. The number of seeds per flowering head produced in June is significantly greater than the number produced in September.
4. Seed dispersal and deposition is restricted primarily to an area 20 to 25 dm beyond the source population. Beyond 25 dm, seed deposition stabilizes at about 0.5 seeds per cm^2.
5. There is a close negative correlation between seed volume and the distance of its dispersal to 25 dm beyond the source aggregation.
6. The germinability of seeds is negatively correlated with distance of dispersal to 35 dm beyond the aggregation.

7. Seeds collected during August and September do not germinate readily without a cold treatment, whereas seeds collected in June show a high proportion of germination with or without a cold treatment.
8. The germination of seeds produced early in the season is significantly greater than that of seeds produced later in the season.
9. Established seedlings protected by exclosures survive significantly better than those exposed to predation by insects.
10. Survival of seedlings established within parent aggregations appears to be significantly greater than that of those established in adjacent vegetated areas. Mortality among over-wintered seedlings is high.

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LITERATURE CITED

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APPENDIX A

Soil analyses at six sites from two east - west transects (aerial photograph, Fig. 1 in the text)

APPENDIX A

Soil analyses at six sites taken from two east - west transects in the Louden oldfield (Fig. 1 in the text). Data prepared by the soil testing laboratory at Michigan State University from methods developed by personnel in the Department of Soil Science, Michigan State University.

Test	Sites					
	A	B	C	D	E	F
Soil pH	5.1	5.3	4.9	5.1	5.1	5.2
Buffer pH	6.6	6.4	6.2	6.4	6.7	6.6
*P (Kg. per hectare)	17.8	22.2	146.7	12.2	25.6	85.6
K (Kg. per hectare)	30	90	614.4	97.8	97.8	67.8
Calcium (Kg. per hectare)	355.6	1141	1141	355.6	717.8	355.6
Mg (Kg. per hectare)	55.6	202	202	97.8	217.8	55.6
Carbon (%)	0.89	0.42	2.47	0.90	0.62	0.83
Organic matter (%)	1.53	0.72	4.26	1.55	1.07	1.43
*P (% total exchangeable)	3.3	3.1	17.6	8.9	4.4	7.2
Calcium (% total exchangeable)	76.8	74.9	63.7	62.5	64.5	73.7
Mg (% total exchangeable)	20.0	22.2	18.8	28.8	31.3	19.2

*(method of anlaysis was the Bray T - 1, as appears in Pro. Soil Sci. of Amer. Vol. 29: 677-678. 1965.)

APPENDIX B

Soil profiles taken from eight sites in the Louden oldfield (aerial photograph, Fig. 1 in the text)

APPENDIX B

Soil profiles taken from eight sites in the Louden oldfield. July, 1969. Classification based on U.S.D.A. (August, 1960).

<u>SITE ONE</u>: Oshtemo loamy sand

Ap: 0" - 9" Loamy sand

Bt: 9" - 15" Sandy clay loam

IIC: 15" - 48" Sand

<u>SITE TWO</u>: Ockley loamy sand

Ap: 0" - 5" Loamy sand (truncated)

AB: 5" - 9" Sandy clay loam

B21t: 9" - 27" Sandy clay loam - clay loam

B22t: 27" - 48" Clay - clay loam (till)

IIC: to 54" Sand

<u>SITE THREE</u>: Ockley sandy loam

Ap: 0" - 9" Sandy loam

B21t: 9" - 18" Sandy clay loam - clay loam

B22t: 18" - 48" Clay - clay loam (till)

IIC: to 58" Sand

SITE FOUR: Kalamazoo loam

Ap: 0" - 9" Loam

AB: 9" - 14" Sandy loam

Bt: 14" - 28" Sandy clay loam

IIC: 28" - 48" Sand

SITE FIVE: Oshtemo sandy loam

Ap: 0" - 9" Sandy loam

AB: 9" - 14" Sandy loam

Bt: 14" - 20" Sandy clay loam - clay loam

IIC: 20" - 48" Sand

SITE SIX: Kalamazoo sandy loam

Ap: 0" - 9" Sandy loam

A2: 4" - 12" Loamy sand

AB: 18" - 22" Sandy loam

Bt: 22" - 38" Sandy clay loam

IIC: 38" - 48" Sand

SITE SEVEN: Kalamazoo sandy loam

Ap: 0" - 4" Sandy loam (truncated)

A2: 4" - 12" Loamy sand

Bt: 12" - 24" Sandy clay loam

IIC: 24" - 48" Sand

SITE EIGHT: Washtenaw loam (alluvial soil)

Ap: 0" - 9" Loam

9" - 48" Loam

(no mottles, no horizons)

APPENDIX C

List of species occurring in the Louden oldfield. May - October, 1969.

APPENDIX C

List of species occurring in the Louden oldfield from May through October, 1969.

Herbs

Achillea millefolium L.

Agrostis hymalis (Walt) BSP. var. hymalis

Agropyron repens (L.) Beauv.

Allium vineale L.

Ambrosia artemisiifolia L.

*Andropogon scoparius Michx.

Antennaria plantaginifolia (L.) Richards

Anthemis arvensis L.

Apocynum sibiricum Jacq.

Asclepias syriaca L.

Asclepias tuberosa L.

Aster ericoides L.

Barbarea vulgaris R. Br.

Berteroa incana (L.) DC.

Bromus inermis Leyes

Capsella bursa-pastoris (L.) Medic.

Carex normalis Mackenzie

Carex pensylvanica Lam.

Centaurea maculosa Lam.

Cerastium nutans Raf.

Cerastium vulgatum L.

Chondrilla juncea L.

Chrysanthemum leucanthemum L.

Cirsium vulgare (Savi) Tenore

Convolvulus spithamaeus L.

Dactylis glomerata L.

Danthonia spicata (L.) Beauv.

Daucus carota L.

Desmodium rotundifolium DC.

Dianthus armeria L.

Eragrostis spectabilis (Pursh) Steud.

Erigeron annuus (L.) Pers.

Erigeron strigosus Muhl.

*Schizachyrium scoparium (Mich.) Nash. (Gould, 1968).

Euphorbia corollata L.

Euphorbia esula L.

Gnaphalium obtusifolium L.

Hieracium aurantiacum L.

Hieracium aurantiacum X florentinum

Hieracium florentinum All.

Hieracium floribundum Wimmer & Grab.

Hieracium gronovii L.

Hieracium longipilum Torr.

Hieracium pratense Tausch.

Hieracium pratense X florentinum

Hypericum perforatum L.

Juncus tenuis Wild.

Lactuca canadensis L. (Yellow fls.)

Lactuca canadensis L. (White fls.)

Lepidium campestre (L.) R. Br.

Lepidum virginicum L.

Leptoloma cognatum (Schult) Chase

Lychnis alba Mill

Medicago lupulina L.

Medicago sativa L.

Melilotus alba Desr.

Melilotus officinalis (L.) Desr.

Monarda fistulosa L.

Nothoscordum bivalve (L.) Britt.

Oenothera biennis L.

Oxalis dillenii Jacq.

Oxalis stricta L.

Panicum sp.

Panicum depauperatum Muhl

Phleum pratense L.

Physalis heterophylla Noes.

Plantago aristata Michx.

Plantago lanceolata L.

Plantago major L.

Poa compressa L.

Poa pratensis L.

Potentilla argentea L.

Potentilla canadensis L.

Potentilla recta L.

Prunella vulgaris L.

Rudbeckia hirta L.

Rumex acetosella L.

Rumex crispus L.

Solidago canadensis L.

Solidago graminifolia (L.) Salisb.

Solidago juncea Ait.

Solidago missouriensis Nutt.

Solidago nemoralis Ait.

Solidago speciosa Nutt.

Spiranthes tuberosa Raf.

Taraxacum officinale Weber

Tragopogon dubius Scop.

Trifolium hybridum L.

Trifolium pratense L.

Trifolium repens L.

Verbascum blattaria L.

Verbascum thapsus L.

Vernonia missurica Raf.

Veronica arvensis L.

Vines

Celastrus scandens L.

Parthenocissus quinquefolia (L.) Planch.

Toxicodendron radicans L.

Vitis riparia Michx.

Shrubs

Apocynum androsaemifolium L.

Cornus alternifolia L.f.

Cornus racemosa Lam.

Crataegus sp.

Lonicera tatarica L.

Rhus typhina L.

Rosa multiflora Thumb.

Rubus flagellaris L.

Trees & Saplings

Acer negundo L.

Acer saccharinum L.

Acer saccharum Marsh.

Carya glabra (Mill) Sweet

Carya ovata (Mill) K. Koch

Malus sp.

Pinus sylvestris L.

Prunus serotina Ehrh.

Quercus velutina Lam.

Rhamnus frangula L.

Sassafras albidum (Nutt.) Nees.

Ulmus rubra Muhl.

Non-Vascular

Cladonia cristatella

Cladonia rangiferina

Caldonia chlorophaea

APPENDIX D

Colored Plates

Plate 2. A view of two aggregations of *Hieracium aurantiacum* L. in the Louden oldfield, also showing the exclosure design.

Plate 3. An over-all view of the Louden oldfield looking from north to south. June, 1969.

Fig. a. View toward the Southwest

Fig. b. View toward the Southeast


A


B

Plate 4. A panoramic view of the Louden oldfield. June, 1969.

Fig. a. View to the Southeast from the West end.

Fig. b. View to the Northeast from the West end.

Fig. c. View to the West from the West end.

Fig. d. View to the North from the Southwest end.

Fig. e. View to the Northeast from the Southwest end.

Fig. f. View to the West from the Southwest end.


A


B


C


D


E


F

Plate 5. Demonstrating the use of a portable auto vacuum cleaner adapted for seed collection in the field.

Plate 6. A comparison of two species of Hieracium and a putative hybrid, showing differences in the color of the rays and size of the inflorescence.

A - *Hieracium aurantiacum*

B - *Hieracium florentinum*

C - *H. aurantiacum* X *H. florentinum* (putative)


B
C
A

Plate 7. A comparison of two species of *Hieracium* and a putative hybrid, showing a close-up of the rays and their color differences.

A - *Hieracium aurantiacum*

B - *Hieracium florentinum*

C - *H. aurantiacum* X *H. florentinum* (putative)


A
C
B

Plate 8. A comparison of two species of *Hieracium* and a putative hybrid, showing differences in pubescence and texture of the basal leaves.

A - *Hieracium aurantiacum*

B - *Hieracium florentinum*

C - *H. aurantiacum* X *H. florentinum* (putative)


A
C
B

APPENDIX E

Additional remarks concerning *H. aurantiacum* and the putative hybrid *H. aurantiacum* X *H. florentinum* from the Louden old-field. Summer, 1969.

APPENDIX E

Most of the literature available on *Hieracium aurantiacum* concerns genetic studies related to apomictic behavior. *Hieracium aurantiacum* is part of an agamic complex in which there exists an intimate association between apomixis, hybridization, and polyploidy (Babcock & Stebbins, 1938; Stebbins, 1950). *Hieracium* subg. *Pilosella* and subg. *Archieracium* represent two such groups. Gustafsson (1935) and Stebbins (1941) have distinguished these groups in that the latter reproduces apomictically by diplospory or generative apospory, while the former reproduces by somatic apospory followed by parthenogenesis. The same investigators suggest that in the diplosporous groups, obligately apomictic species are dominant. In those complexes where somatic apospory is present (e.g. *H.* subg. *Pilosella)*, the dominants are facultative apomicts which regularly produce some sexual offspring. The gradual rather than sudden evolution of the apomictic process seems most likely to occur in those complexes where somatic apospory is present (Stebbins, 1941). It is further suggested (Babcock & Stebbins, 1938; Stebbins, 1941) that in most or all agamic complexes, facultative apomicts precede obligate ones in the development of the complex. The presence of only obligate apomicts in a complex may indicate that the group is relatively old and considerably removed from its sexual ancestors (e.g. *H.* subg. *Archieracium,* and *Crepis).*

Hieracium aurantiacum is a facultative, tetraploid apomict, reproducing seed by somatic apospory followed by parthenogenesis (Gustafsson, 1947; Stebbins, 1941). In the anthers, fairly regular meiosis occurs and pollen formation is normal (Darlington, 1932; Stebbins, 1941). In pollen which I examined, no aborted grains were observed.

The basic chromosome number of *Hieracium aurantiacum* is nine (Darlington & Wylie, 1955), and the 2n number is 36.

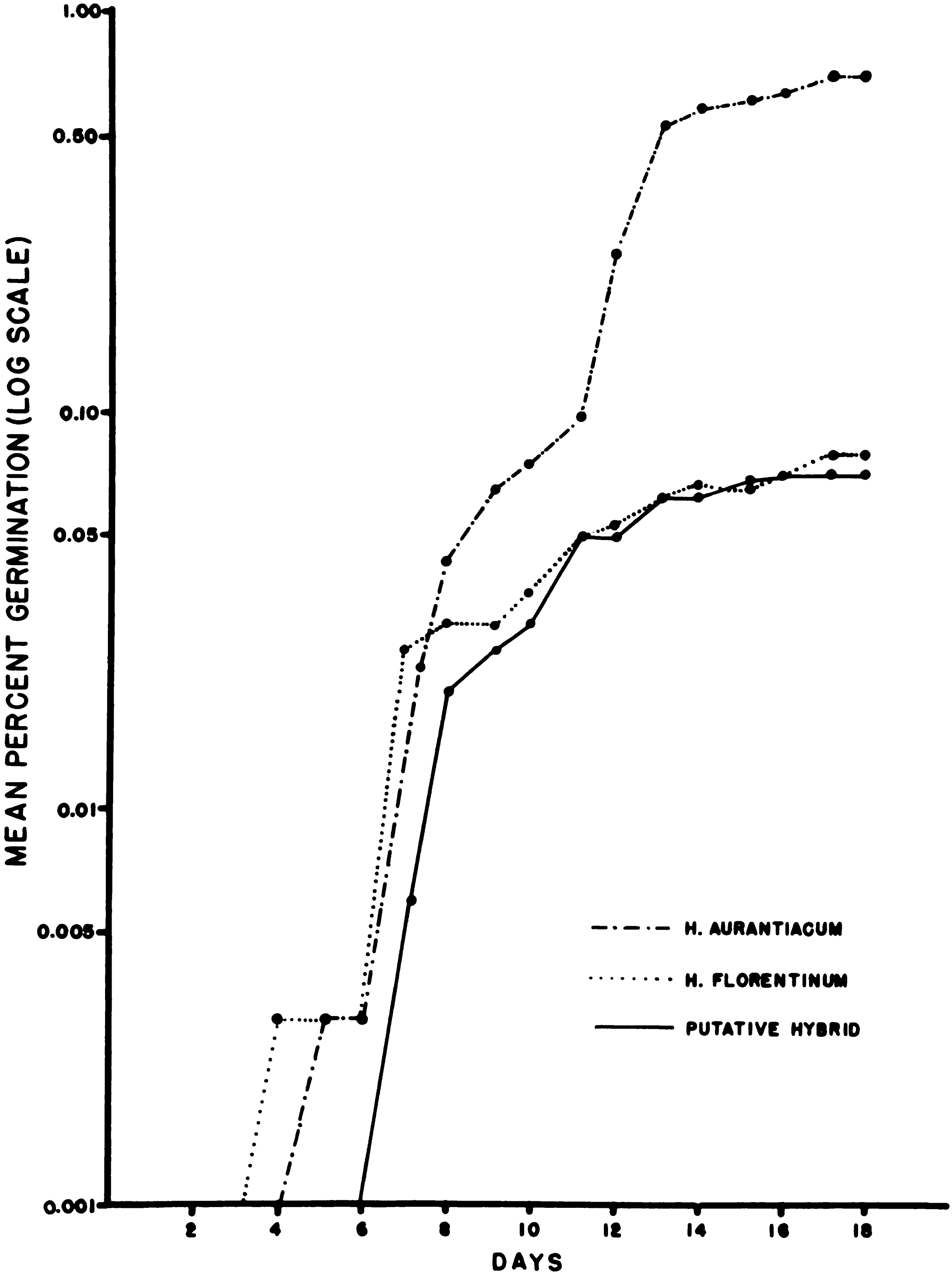
Hybridization and out-crossing have been observed to occur frequently in *Hieracium aurantiacum* (Ostenfeld, 1910; 1912). In the Louden oldfield (summer, 1969) I collected a putative hybrid of *H. aurantiacum* X *H. florentinum.* The plant occurred only occasionally and was found exclusively among individuals of the more widely distributed, non-vegetatively reproducing *H. florentinum.* No individuals were discovered in or near aggregations of *Hieracium aurantiacum,* and only one was found in an area completely free from all species of *Hieracium.* The putative hybrid grew either as scattered individuals or in small patches.

The hybrid plants are about equal in height with the taller *H. florentinum.* The basal leaves, stems, and inflorescences possess features characteristic of both parents (Appendix D, Plates 6 & 8). The outer corollas are orange along the margins with red bands down their centers, while in *H. florentinum* they are bright yellow and in *H. aurantiacum* deep red (Plates 6 & 7). The putative hybrid does not appear to reproduce vegetatively.

Pollen grains from the suspected hybrid were examined and all appeared to have nuclei, indicating probable viability. Existing small patches of the putative hybrid in the Louden oldfield indicated that not only did the plant have viable pollen, but that at least some of the seeds produced were also viable. Seed heads were collected from both solitary individuals and those in patches. Examination of the seeds revealed that only about 20% of all those collected appeared "normal" or in a viable condition, whereas about 98% of the parents' seeds appeared normal. The sterile seed is readily distinguished by its soft, light-brown coat and lack of an embryo. Normal seed appears black, firm and plump. Embryos can be observed. Similar criteria for distinguishing between sterile and potentially viable seed were described by Gustafsson (1935) for several species of *Hieracium*.

Seeds from the suspected hybrid *H. aurantiacum* X *H. florentinum* were germinated at room temperature on moist blotting paper in petri plates. Seeds from the parent plants were also germinated under similar conditions (Fig. 13). All seeds which could immediately be determined as

Fig. 13. Cumulative mean percentage germination of *Hieracium aurantiacum*, *H. florentinum*, and putative *H. aurantiacum* X *H. florentinum* seeds sown on moist blotting paper in petri plates. June, 1969.


MEAN PERCENT GERMINATION (LOG SCALE)
1.00
0.50
0.10
0.05
0.01
0.005
0.001
2
4
6
8
10
12
14
16
18
DAYS
H. AURANTIACUM
H. FLORENTINUM
PUTATIVE HYBRID

sterile were excluded from the experiment. *Hieracium aurantiacum* showed a higher percentage germination than did the suspected hybrid, and was significantly different in total germinability from both the hybrid and *H. florentinum* ($t = 3.01$; $p = <0.05$; $N = 12$). No explanation can be given for the relatively low germination of *H. florentinum*. The low percentage of over-all germinability in the three plants can be accounted for in part by fungal attack in the petri plates.