EFFECT OF IMMIGRATION TIME ON THE ESTABLISHMENT OF WILD CARROT POPULATIONS IN EARLY OLD-FIELD SUCCESSION

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BUFORD R. HOLT
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This is to certify that the

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EFFECT OF INITIATION TIME ON THE ESTABLISHMENT OF
WILD CARROT POPULATIONS IN EARLY OLD-FIELD SUCCESSION

presented by

Buford R. Holt

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Major professor

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ABSTRACT

EFFECT OF IMMIGRATION TIME ON THE ESTABLISHMENT OF WILD CARROT POPULATIONS IN EARLY OLD-FIELD SUCCESSION

By

Buford R. Holt

The effect of a small difference in immigration time on the life table characteristics and consequent establishment success of Daucus carota L. (Umbelliferae) was examined in early old-field succession in southern Michigan. Seedling emergence, survival to flowering, and seed production were monitored and correlations between these phenomena and the percent cover of the more abundant associated species were examined.

The study area was a 100 x 100 meter section of a former corn field which had been divided into 25 16 x 16 meter plots separated by four meter buffer strips. Seeds were sown at three seed rates in December 1966 in replicated plots at the end of their first or third fallow year. Seeds were sown in 260 $0.24 m^2$ quadrats in each fallow. Of these 260 quadrats, 10 were sown with 188 seeds each (low rate), 10 with 814 seeds (high rate), and 240 with 412 seeds (intermediate rate). To insure the presence of bare plots during the spring

germination pulse, non-carrot vegetation on 30 of 240 quadrats sown at the intermediate rate was clipped prior to seeding and at intervals during the first growing season. The vegetation composition was assessed in all quadrats by visual estimation of the percent cover of each species. In December 1967 seed were sown in 30 quadrats in each of three sod types: Agropyron repens, Poa compressa, and bare ground. Individual emerging seedlings in these quadrats were marked and their survival monitored during their first growing season.

Establishment of reproductive populations was most affected by events preceding seedling emergence, and was negatively correlated with the abundance of other plant species. In unclipped quadrats sown with 412 seeds (1740 seed/m^2) mean seedling densities in the first growing season represented 38% of the seed sown in the younger fallow and 18% in the older fallow. Early post-emergence mortality was not determined in 1967, but in 1968 was equivalent to only 3 to 14% of the total seedling emergence in quadrats sown the preceding fall. In the quadrats sown in 1966, percent post-emergence mortality during the first two years of growth was relatively independent of both intraspecific density and the percent cover of other species. Juvenile mortality was highest during the winter and during summer droughts. No Daucus reproduction occurred in the older fallow in the first growing season, but in the younger fallow, reproductive plants represented 0.7% of the seed sown, and 3.5% of the live plants. Second year reproductives represented 0.2% and 3% of the seed sown in the young and old fallows respectively, i.e., 7 and 37% of the individuals surviving to the second summer. The first year seed crop was largely destroyed by unknown herbivores, but second year seed production was equal to 89% of the seed sown in the older fallow, and 1300% of the seed sown in the younger fallow. Both the number of flowers and the air dry weight of seed produced per quadrat were linearly related to the number of reproductive plants. The number of reproductives was proportional to carrot density irrespective of age of fallow. The probability of reproduction in the second growing season was negatively correlated with the more common grass species and Melilotus alba, the most abundant forb.

Small delays in the arrival time of Daucus seed may significantly alter both its ecesis success and the rate of subsequent population buildup. The magnitude of the effect varies with the composition of the previously established vegetation. Since Daucus can persist for several decades in Michigan old-fields it may be representative of non-vegetatively propagated old-field species. If so, seedling establishment and age of initial reproduction are the life history phenomena most sensitive to the time of immigration and mechanisms responsible for these effects warrant further study.

EFFECT OF IMMIGRATION TIME ON THE ESTABLISHMENT OF WILD CARROT POPULATIONS IN EARLY OLD-FIELD SUCCESSION

By

Buford Reid Holt

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INTRODUCTION

Plant species characteristic of the initial stages of old-field succession undergo rapid and quasi-predictable changes in population size. These changes, which are frequently associated with the appearance or disappearance of other species, have been extensively described in cross-sectional studies (e.g., Oosting, 1942; Bard, 1952; Beckwith, 1954), but experimental examination is essentially lacking. The effects of fertilization (Davidson, 1962, 1967), size of area of denudation (Davis, 1968), and faunal impoverishment (Malone, 1969) on vegetation composition have been investigated in the field, and possible causes of dominance shifts have been examined in the laboratory (Keever, 1950; Rice, 1964, 1967). The role of changing life table characteristics of constituent species is, however, unknown.

The objective of this study was to evaluate, in an old-field succession, the effect of a small difference in immigration time on the life table characteristics and consequent establishment success of a plant population. Specifically, the objectives were to determine the effect of arrival time on seedling emergence, survival to flowering, and seed production; and to determine whether these effects are correlated with the amounts of the more abundant species of the previously established vegetation.

MATERIALS AND SITE

Daucus carota L. (Umbelliferae), the wild carrot or Anne's Lace, was selected for its ease of manipulation, and virtual absence from the study area, a site on which it would normally occur. This near absence apparently was due to the limited immediate seed source. Individual plants are easily recognized, short-lived, and easily censused. Flowers and seeds are large enough to be counted easily. In southern Michigan, naturally dispersed Daucus seed germinate primarily in the early spring, although very slight additional germination occurs throughout the remaining growing season. Surviving seedlings form rosettes which either bolt and flower during the plant's first growing season, or overwinter and flower in subsequent years. The plants die as the seeds mature and the seeds are shed in the fall and winter.

The study area was a 100 x 100 meter section of a former corn field set aside for studies on early old-field succession. The field is located on Gull Lake Biological Station property at the intersection of Gull Lake Drive and B Avenue, Ross Township (T. 1 S, R. 9 W.), Kalamazoo County, Michigan. The soil is well drained Fox Sandy Loam (Typic

Hapludalf) on flat to gently rolling glacial drift of Cary Age. The site had been farmed for approximately a century, and in the recent past has had a varied crop history. It was planted with hybrid walnut trees about 1938 (Harold Webster, personal communication; USDA photo BDB-3-50), but returned to general farming between 1950 and 1955 (USDA photo BDB-1G-95 and BDW-1P-47). Between 1960 and 1964 the site was planted with wheat, alfalfa, and corn (Zea mays). Fertilizer (250 pounds/acre 6-24-24; 100 pounds actual nitrogen) was last applied in 1964 with the final corn crop. Herbicides were last applied in November, 1962 and May, 1963 for a demonstration of quackgrass (Agropyron repens) control (Figure 1).

Cantlon et al. (unpublished) initiated basic studies of old-field succession in the study area in the fall of 1964. They divided the area into 25 16 x 16 meter plots separated by four meter buffer strips, and grouped the plots in five blocks. Blocks III, IV, and V were established primarily with respect to the uneven topography, but blocks I and II, both on level ground, were partitioned to minimize the anticipated number of missing plots per block. Although these plots (I-68, II-68) were subsequently retained, blocks I and II were irregularly partitioned. Each year since 1964 one plot from each block has been selected at random, plowed and left fallow (Figure 2). Davis (1968) and Cantlon et al. (unpublished data) have documented

FIGURE 1

Approximate Distribution of Herbicide Treatments Applied in the Fall-1962 and Spring-1963 as Part of Management Prior to Initiation of Old-Field Studies. The borders of the 25 20 x 20 meter plots of Cantlon et al. (unpublished) are represented by the background grid. The remaining walnut trees are indicated by circles. The location of strips of contiguous carrot quadrats are indicated by checkered bars for plots plowed in 1966 and by solid bars for plots plowed in 1964. The widths of the checkered and solid bars are not to scale.

Br = Burned during the last half of May 1963.

L = Lorox (Linuron) [3-(3,4-dichlorophenyl)-1-methoxy-1-methylurea] was applied at 1 1/2 pounds/acre.

AT$_1$ = Atrazine (2-chloro-4-ethylamino-6-isopropylamino-1,3,5-triazine) was applied at the rate of 4 pounds/acre; 2 pounds/acre on May 6 and 2 pounds/acre on May 20, 1963.

AM = Amitrol-T (3-amino-1,2,4-triazole plus ammonium thiocynate) was applied at 2 pounds/acre on May 6, 1963.

AT$_2$ = Atrazine was applied at 2 pounds/acre in the spring of 1963.

DAL 2,4-D = Dalapon (2,2-dicholopropionic acid) was applied at 12 pounds/acre on November 7, 1962. 2,4-D (2,4-dichlorophenoxyacetic acid) was applied at 1 1/2 pounds/acre on May 20, 1963.

AT$_2$ 2,4-D = Atrazine was applied at 2 pounds/acre in the spring of 1963. 2,4-D was applied at 1 1/2 pounds/acre on May 20, 1963.

AT$_3$ 2,4-D = Atrazine was applied at 4 pounds/acre on November 7, 1962. 2,4-D was applied at 1 1/2 pounds/acre on May 20, 1963.

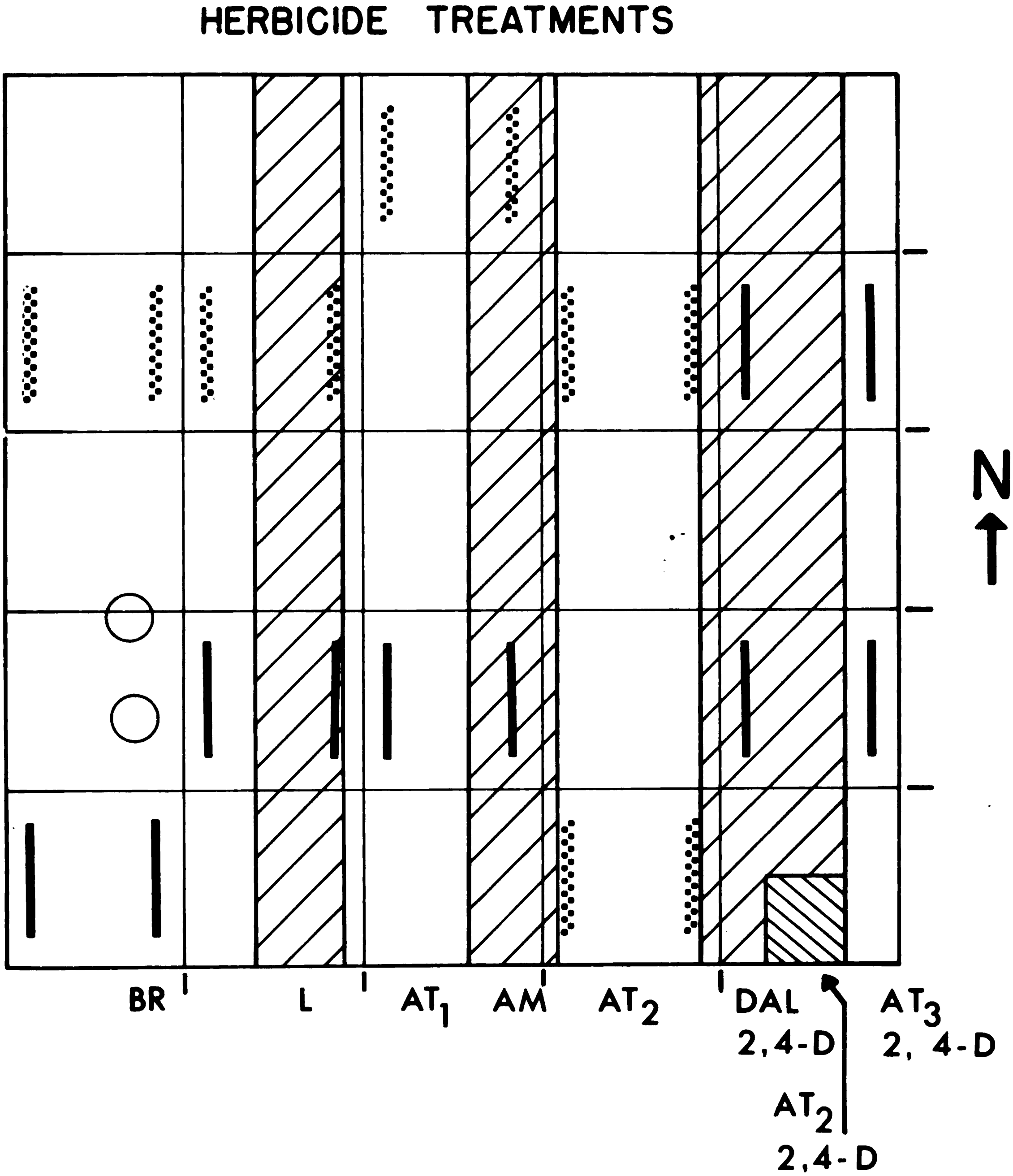


FIGURE 1

FIGURE 2

Distribution of Blocks, Strips of *Daucus* Quadrats, and the Small Indigenous *Daucus* Population. The background grid is the same as in Figure 1. The numbered squares represent the portions of the plots committed to the previously initiated study by Cantlon et al. Widths of the strips representing quadrats are exaggerated (X 2). The Roman numerals indicate the block number, and arabic numerals indicate the year of fallowing. The topography characteristic of each block is:

Block I	Flat upland.
Block II	Flat to very gently sloping upland.
Block III	Flat to gently sloping.
Block IV	Gently sloping upland.
Block V	Flat to gently sloping lowland.

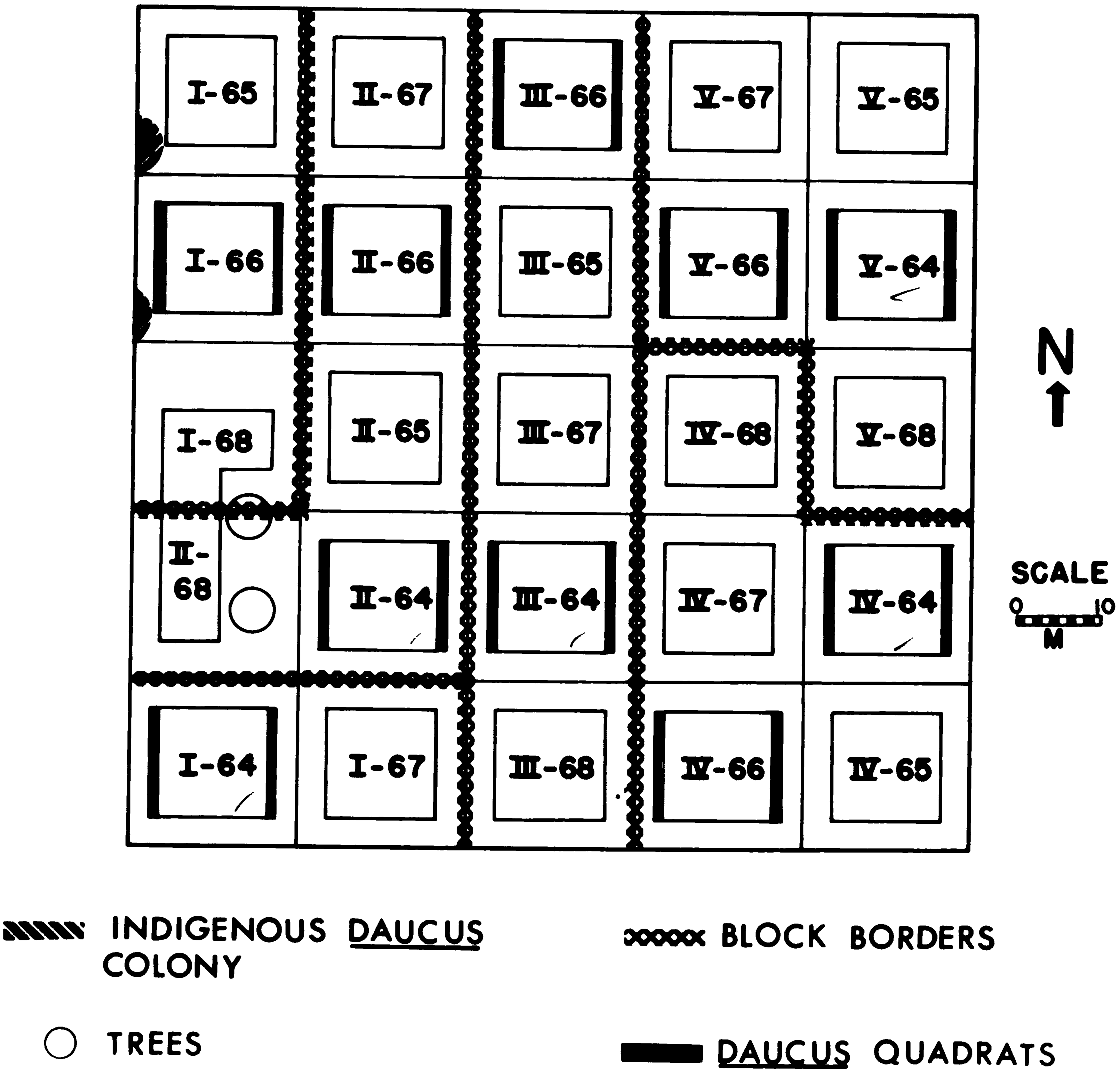

I-65
II-67
III-66
V-67
V-65
I-66
II-66
III-65
V-66
V-64
I-68
II-65
III-67
IV-68
V-68
II-68
II-64
III-64
IV-67
IV-64
I-64
I-67
III-68
IV-66
IV-65
N
SCALE
0
10
M
INDIGENOUS DAUCUS COLONY
BLOCK BORDERS
TREES
DAUCUS QUADRATS

FIGURE 2

vegetational change since 1964 in the 100 x 100 meter study area and adjacent parts of the former corn field. *Daucus* was absent from the field except for a small colony at the edge of the study area (Figure 2).

Vascular plant nonmenclature follows Gleason and Cronquist (1963). Voucher specimens, collected in cooperation with Mr. Roger Davis (1968), have been deposited in the Beal-Darlington Herbarium, Michigan State University.

METHODS

Effect of Immigration Time

Seeds were collected October 8, 1966 from a naturally occurring population 3.3 km from the study area. Seeds were taken from first and second order umbels (nomenclature of Borthwick, 1931), and stored in ventilated containers at room temperature (23-28°C).

Immigration time was controlled by sowing seeds in fields of different ages. Seeds were sown at three rates in a replicated randomized block design on December 16 and 26, 1966 in plots last plowed or cultivated June 27, 1966 and early summer 1964. The 260 0.24 square meter (47.5 x 50 cm) quadrats used in each age of fallow were located in strips of 26, placed along the two more homogeneous borders of each plot, i.e., parallel to the plow furrows (Figure 2). Within each strip, 24 quadrats were sown with approximately 412 seeds, one with approximately 816 seeds, and one with approximately 188 seeds, i.e., the rates were approximately 1740, 3440, and 790 seeds per square meter (Tables 1 and 2). Seeds were broadcast by hand within each quadrat to simulate natural dispersal. Seed numbers were estimated by weight.

TABLE 1

Verification of the Mean Number of Seeds Weighed and Placed in Seed Packets

Planting Rate	Number of Seed Packets Counted	Mean Number of Seeds per Packet (± S.E.)
High	6	818 ± 6.0
Intermediate	5	414 ± 7.8
Low	7	191 ± 3.3

TABLE 2

Number of Seeds Lodged in Seed Packets After Sowing

Planting Rate	Number of Seed Packets Counted	Mean Number of Seeds per Packet (± S.E.)
High	19	1.8 ± 0.5
Intermediate	118	2.0 ± 0.5
Low	35	2.5 ± 0.5

Foliage and litter were removed from three quadrats per strip prior to sowing, to insure the presence of coverless quadrats during the initial germination pulse. Continued removal of all cover was not feasible, but the non-carrot vegetation in these quadrats was partially removed by clipping on May 2, June 13-17, and August 10-11, 1967.

Vegetation composition was assessed in each quadrat by visual estimation of the percent cover of each species. Initial cover readings and carrot censuses were taken concurrently between April 11 and May 18, 1967. Subsequent cover readings were taken July 10 to August 10, 1967, and July 6 to July 21, 1968.

Minimal estimates of seed emigration, after sowing, were based on rosette counts outside the sown quadrats in the second growing season (July 5-6, 1968). Counts were made in 0.24 m^2 quadrats, laid end to end to form transects. These transects were perpendicular to, and extended one meter upslope and two meters downslope from, three randomly selected quadrats in each strip. Transects were approximately parallel to the direction of the gentle slope of the field. Conversion of rosette counts to seed emigration estimates assumed: 1) 100% germination; 2) survival probability equal to that observed for the same date in the permanent quadrats (P=0.36 in both fallows); 3) independence of germination percentages and seed densities; 4) absence of further seed immigration into the field. Data of Cantlon et al. (unpublished) for changes in *Daucus* cover values in 150 meter square quadrats per age of fallow justify the latter assumption.

Estimates of potential field germination in the first and second growing seasons were based on laboratory germination tests. In December 1966 fifteen lots of 100 seeds each were placed on moist blotters in petri dishes, then placed in -5°C (six dishes) or in 4°C (nine dishes) for 30-38 days. They were then removed to room temperature (23-28°C) and germination was monitored for 20 days. In March 1968 two 200-seed lots of these same seed were placed on moist blotters at room temperature for 28 days. Cold treatment was not applied since previous germination tests had shown that seeds were unaffected by cold treatment following prolonged storage.

Field estimates of seedling emergence and rosette survival were based on inventories during the first two growing seasons. Carrots were censused in all quadrats April 11 to May 18, 1967; September 3 to 11, 1967; March 27 to April 13, 1968; June 26 to July 3, 1968; and September 25 to 28, 1968. Multiple counts were made during March and April 1968 since new leaf production during the first two weeks of April caused apparent increases in the number of overwintering rosettes. Counts were continued until a constant estimate was obtained. A randomly selected subsample of 41 quadrats in each age of fallow was also inventoried May 25 to 27, 1967; July 23, 1967; October 24, 1967; April 10, 1968; August 21 and 22, 1968; and April 26, 1969. On April 28 and May 23, 1968 new seedlings in the subsample quadrats were marked with plastic toothpicks, permitting estimation of minimal second year germination percentages.

Estimates of potential seed production in 1967 were based on empirically derived relationships between the number of flowers per inflorescence and the diameters of the discoid inflorescences. Estimates for inflorescences greater than 5 cm in diameter were based on a regression of flower numbers on $\log_{10}$ inflorescence diameter ($N=19$, $r= 0.95$). Estimates for smaller inflorescences were based on the assumption that the flowers and inflorescences are circular and that the number of flowers/umbel can be approximated by the number of circles of arbitrary size which can be packed in a larger circle of given diameter. The diameter of the small circles (3.5 cm) in this model was chosen to fit both the observed values for small inflorescences and the regression value for inflorescences 5 cm in diameter (Figure 3). Due to the frequent occurrence of ellipsoidal umbels, two measurements were made per inflorescence (major and minor axes), and their mean was used as the estimate of umbel diameter. Each umbel was measured when the central flowers were in anthesis.

Diameters of severely damaged (chewed) umbels were estimated by the distance between tips of umbellet peduncles, or if totally destroyed, were assumed to equal the mean size of measurable umbels in the same quadrat. Each umbel measured was labeled with a paper tag. Conversion of flower numbers to potential seed numbers assumed that all flowers possessed two viable ovules. Since most flowers in the first growing season were borne in primary umbels, this assumption probably caused minor overestimation of potential seed production (cf. Quagliotti, 1967). All umbels were measured in 1967; none in 1968.

Actual seed production per quadrat was estimated by air dry weight of cleaned seed. The seed were hand threshed, sieved, and cleaned in a South Dakota model A seed blower. In 1968, data for seed yield/quadrat were inadvertantly lost for 45 quadrats. These losses were replaced by estimates constructed from the sums of yield estimates for individual plants. These estimates of seed yield per individual were based on a regression ($r=0.89$, $F_{1,37} = 5.16$) of $\log_{10}$ seed weight on $\log_{10}$ stem base diameter (Figure 4). Since the slope of this log-log regression line was greater than one, overestimates of seed yield tended to greatly exceed the underestimates. To correct this bias, estimates of seed yield per quadrat were adjusted by use of the regression $\log_{10}$ corrected seed weight = $-0.164 + 0.801 \log_{10}$ estimated seed weight ($F_{1,60} = 105.6$). The correction was quite large

FIGURE 3

Number of Flowers/Inflorescence as a Function of Inflorescence Size. The solid line is based on a regression of flower numbers on $\log_{10}$ inflorescence diameter ($y = -2700 + 4740X$). The broken line is based on a model of tightly packed circles (see text).

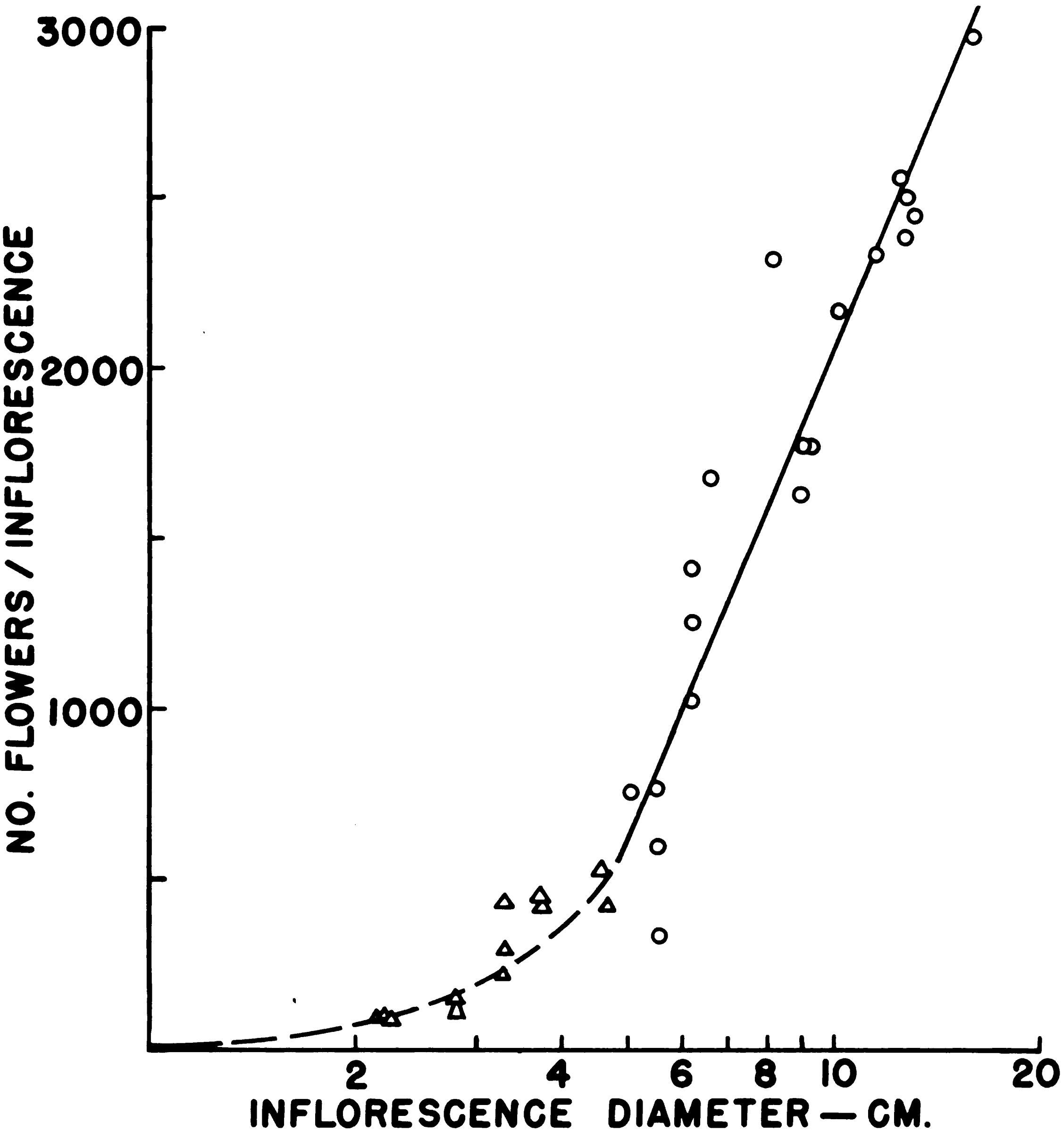

3000
2000
1000
NO. FLOWERS / INFLORESCENCE
2
4
6
8
10
20
INFLORESCENCE DIAMETER — CM.

FIGURE 3

FIGURE 4

Regression of Log_{10} Air Dry Seed Yield per Plant on Log_{10} Stem Base Diameter. The mean air dry seed weight was approximately 0.79 ± 0.09 mg/seed.

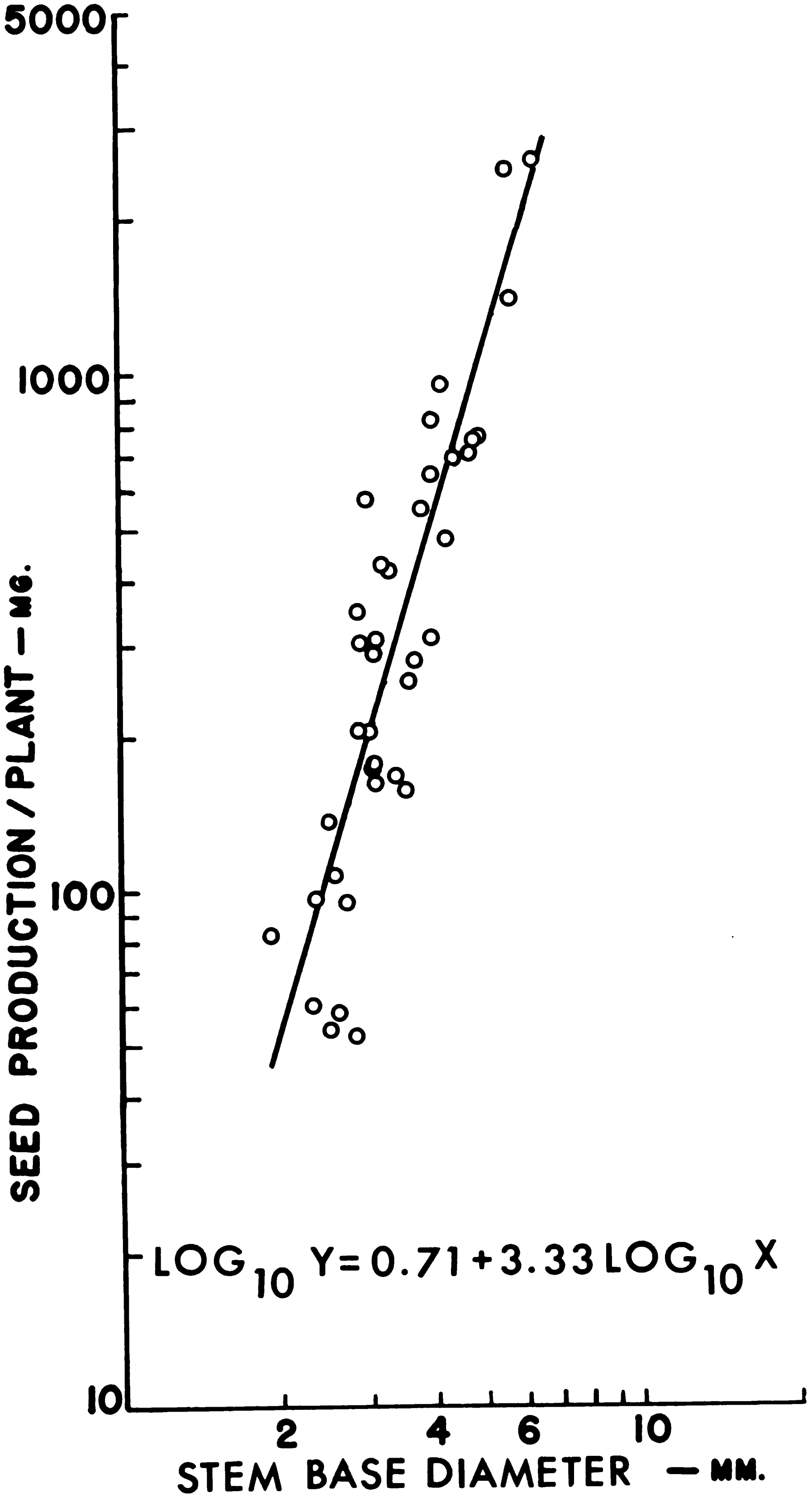

5000
1000
100
10
SEED PRODUCTION / PLANT — MG.
LOG10 Y = 0.71 + 3.33 LOG10 X
2
4
6
10
STEM BASE DIAMETER — MM.

FIGURE 4

(i.e., mean actual seed weight equaled 22 and 75% of the mean estimated weight in the old and young fallows respectively) but it was needed in less than 10% of the quadrats. The term stem base, as used in the estimation of individual seed yield, refers to the easily identified ring of leaf scars at the root-stem junction. In exceptional cases where this area was grossly enlarged relative to the adjacent portions of the stem-root axis, measurements were taken just below the leaf scar zone.

All seed were harvested in 1967 and 1968. In 1967 seed bearing umbels were harvested individually over a period of eight weeks, as their outermost seeds turned brown. In 1968, the umbels within each quadrat were harvested simultaneously. All quadrats were harvested between September 19 and 22, 1968. This harvest was timed to permit as many seed as possible to be harvested at the same maturation stage as seed harvested in 1967, without permitting appreciable seed loss from early maturing umbels. In both years seed produced by plants outside the quadrats were harvested and discarded.

Establishment success of the second generation was assessed by sowing part of the 1967 seed crop in quadrats near the parent plant, i.e., in areas where seed presumably would have fallen. Eighteen 0.06 m^2 (25 x 25 cm) quadrats were placed in vegetation subjectively assessed as resembling that in which the parents had grown. To determine whether marked differences existed in the emergence of seedlings from the seeds of annuals and biennials, six of these quadrats were sown with seeds from putative biennials. Seeds were harvested October 12, 1967 from known annuals in the study area, and from putative biennials in the population used as the 1966 seed source. All seeds were sown December 13, 1967 at the rate of 50 seeds per quadrat (800 seeds/m^2). Emerging seedlings were marked with plastic toothpicks until May 16, 1968, the end of the initial germination pulse. Subsequent findings, however, suggest that very small numbers of new seedlings continued to appear throughout the summer.

Partitioning of Seedling Establishment Failure

The role of post-emergence mortality as a source of differential seedling establishment was assessed in the field by labeling individual seedlings and monitoring their survival. Seeds collected October 12, 1967, from putative biennials, were sown in 90 0.06 square meter quadrats, 30 of which were placed in each of three vegetation types: bare ground, *Agropyron repens* sod, and *Poa compressa* sod. These quadrats were placed in areas of homogeneous sod near the quadrat strips used in the main experiment. Emerging seedlings were marked with plastic toothpicks and censused at least weekly during the spring germination pulse. Censuses were infrequent during the summer.

Estimates of potential germination were based on laboratory tests conducted immediately after seed harvest (October 12, 1967). Ten lots of 25 seeds each were placed on moist blotters in the cold (-1 to 1.5°C) for 16 days. Observation stopped two weeks after seeds were returned to room temperature.

In the greenhouse, the assessment of post-emergence mortality was combined with an attempt to separate the effects of live grass and litter on seedling establishment. Seven sod and litter combinations were used: 1) bare soil; 2) Agropyron repens sod plus its litter; 3) A. repens sod alone; 4) A. repens litter alone; 5) Poa compressa sod plus its litter; 6) P. compressa sod alone; 7) P. compressa litter alone. Sod, soil, and fresh litter (i.e., standing dead) were collected October 31, 1967 within the 4 hectare (10 acre) field containing the study area. Litter was air dried and stored at room temperature. Sod and soil were stored in an unheated greenhouse prior to potting on November 26 and 27, 1967. Twenty-four five-inch (13 cm) porous clay pots were prepared of each of the seven sod-litter combinations. Old litter was removed from all sod pots and was replaced where appropriate with sufficient fresh litter to cover the soil surface (1 to 4.8 gm). The grass was clipped to a height of 5 cm, then half of the pots were placed in a cold frame on December 6 to simulate field conditions, while the other half were retained at 17°C. Pots were randomized in the cold frame and their bases were packed in peat moss. Seeds collected October 16, 1967 were sown at the rate of 20 seeds per pot. Pots were then covered with 1/4 inch mesh hardware cloth.

Emergence, age specific mortality, and early development of <u>Daucus</u> seedlings were monitored in the pots retained in the greenhouse. To insure high potential germination in the absence of cold treatment, these pots were sown with thoroughly after-ripened seed gathered in 1966. Twenty seeds were sown per pot (approximately 1500 seeds/m^2) on December 8, 1967, and pot positions were randomized. Emerging seedlings were labeled with colored toothpicks, a different color being used at each census to permit evaluation of age specific survival and development rates. Estimates of potential germination were based on two lots of 25 seeds in petri dishes placed in the greenhouse December 19. Estimates of development rates were based on the rate of appearance of new leaves during the first 18 days following initiation of seedling emergence. At the end of the experiment, the sod, litter, and carrots in each pot were harvested. Sod and litter were air dried, then weighed on an O'Haus triple beam balance to ± 0.1 gm. Carrots were oven dried at $80^{\circ}C$ for a minimum of one day and then weighed to ± 1 mg.

Seedling emergence and post-emergence survival were monitored in the cold-treated pots after they were returned to the greenhouse. Pots were moved into the 17°C greenhouse February 18, 1968. The bench was partitioned into two blocks, a central and a peripheral block, and pots were randomized within the blocks. A buffer strip of bare, soil-filled pots was placed around the peripheral block. Pots were watered at least weekly with 200-300 ml of distilled water during the period of maximum emergence and with tap water thereafter. Emerging seedlings were marked with toothpicks.

Temperature control was faulty throughout the period of study, but the variations were not serious until the latter part of the study (late March) when the temperature ranged from 11 to 30°C.

Statistics

Except for cover data, all percentages were transformed to angles (Snedecor, 1956). Cover data were not transformed since cover values, given an adequate sample, tend to approach a normal distribution (Holscher et al., 1958; Ursic and McClurkin, 1958).

To meet the assumption of linearity, correlations of carrot performance with the cover of other species were based only on quadrats in which the sum of cover values of dominant species, other than the one being examined, was less than 20%. This value was arbitrarily chosen as a compromise between avoidance of small sample sizes and the presence of significant quantities of species other than the two being correlated. Graphical analysis of selected sets of data indicate that this procedure restored linearity. Only quadrats sown with 412 seeds/quadrat were included. Correlations of cover values and seedling emergence in 1967 were based on quadrats sampled between April 28 and May 14, a period in which net changes in *Daucus* abundance were absent. Correlations of litter, bare ground, and total cover were based on all of the 177 quadrats sampled during this period.

Tests of significance were based on standard procedures (t-test, ANOVA, Duncan's Multiple Range) given by Snedecor (1956) and Kirk (1968). Means cited in the text are accompanied by their standard errors.

RESULTS

Effect of Immigration Time

In the first growing season seedling densities at the end of the spring germination pulse (Figure 5) were greater in the younger than in the older fallow ($t_{148} = 9.46$, $P < .001$), despite greater seed emigration in the younger fallow (Figure 6). Potential (laboratory) germination was 65%, but seedling densities in the two ages of fallow, after correction for emigration, represented only 42 and 18% of the seed sown in the young and old fallows respectively. Seedling densities were positively correlated with percent bare ground ($F_{1,175} = 128.4$, $P < .001$), and negatively correlated with each of the dominant perennial herbs (Table 3). Correlations with _Rhus typhina_ and _Melilotus alba_ were not calculated since their April-May cover values were negligible.

Estimated seed emigration (Figure 6) was significantly greater in the younger than in the older fallow ($t_{47} = 6.28$, $P < .01$). Log_{10} estimated seed loss was negatively correlated with litter ($r = 0.81$, $F_{1,50} = 98.15$, $P < .01$), and live cover ($r = 0.49$, $F_{1,50} = 15.94$, $P < .01$), implying that seed losses declined exponentially with increased cover.

FIGURE 5

Time Courses of Net Seedling Emergence in Old and Young Fallows. Points represent mean (± 2 S.E.) carrot densities in fields fallowed in 1964 (O) and 1966 (●). Seeds were sown in December 1966 at the rate of 412 seeds/$0.24m^2$.

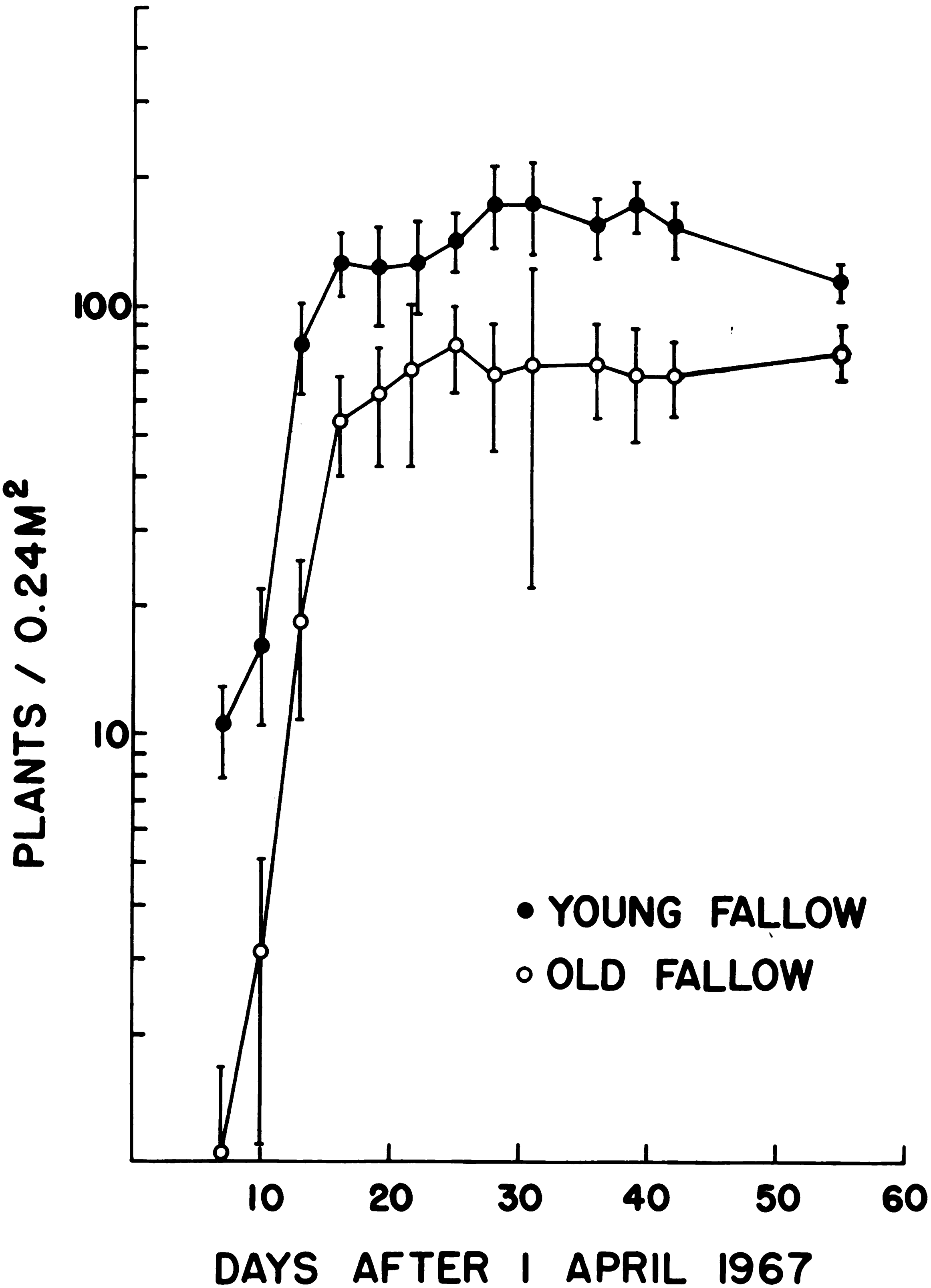

PLANTS / 0.24M²
100
10
10
20
30
40
50
60
DAYS AFTER 1 APRIL 1967
● YOUNG FALLOW
○ OLD FALLOW

FIGURE 5

FIGURE 6

Mean Number of Rosettes Resulting from Emigrant Seeds. Data are based on rosettes occurring outside sown plots during the second growing season. Data for the older fallow (O) are means of 22 quadrats and data for the younger fallow (●) are means of 27 quadrats (——) or 25 quadrats (----). Two quadrats in the vicinity of the highly localized indigenous carrot population are excluded from the means connected by the broken line (----). Only unclipped quadrats sown at the rate of 412 seeds/0.24m^2 are included.

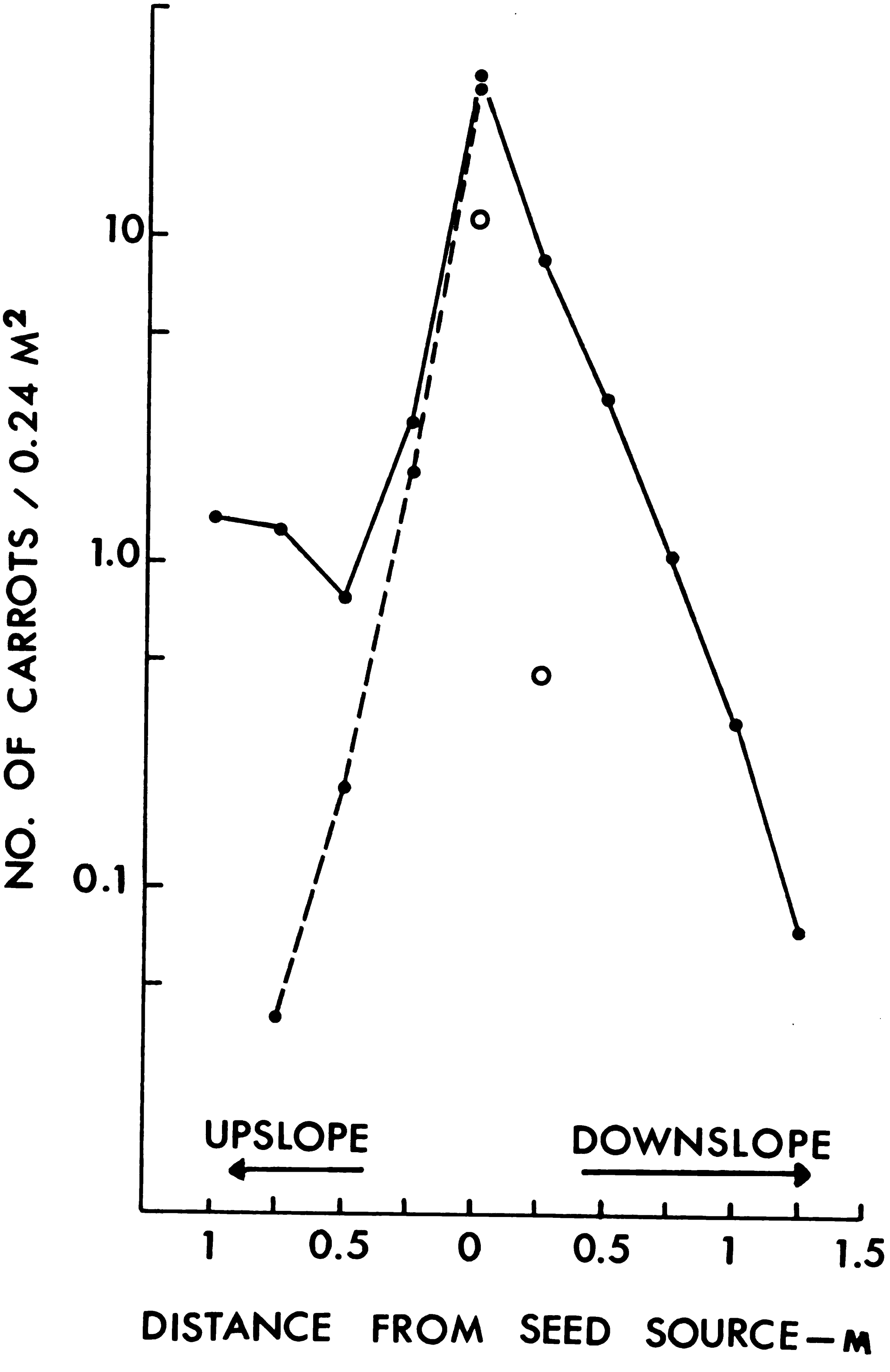

NO. OF CARROTS / 0.24 M²
10
1.0
0.1
UPSLOPE
DOWNSLOPE
1
0.5
0
0.5
1
1.5
DISTANCE FROM SEED SOURCE—M

FIGURE 6

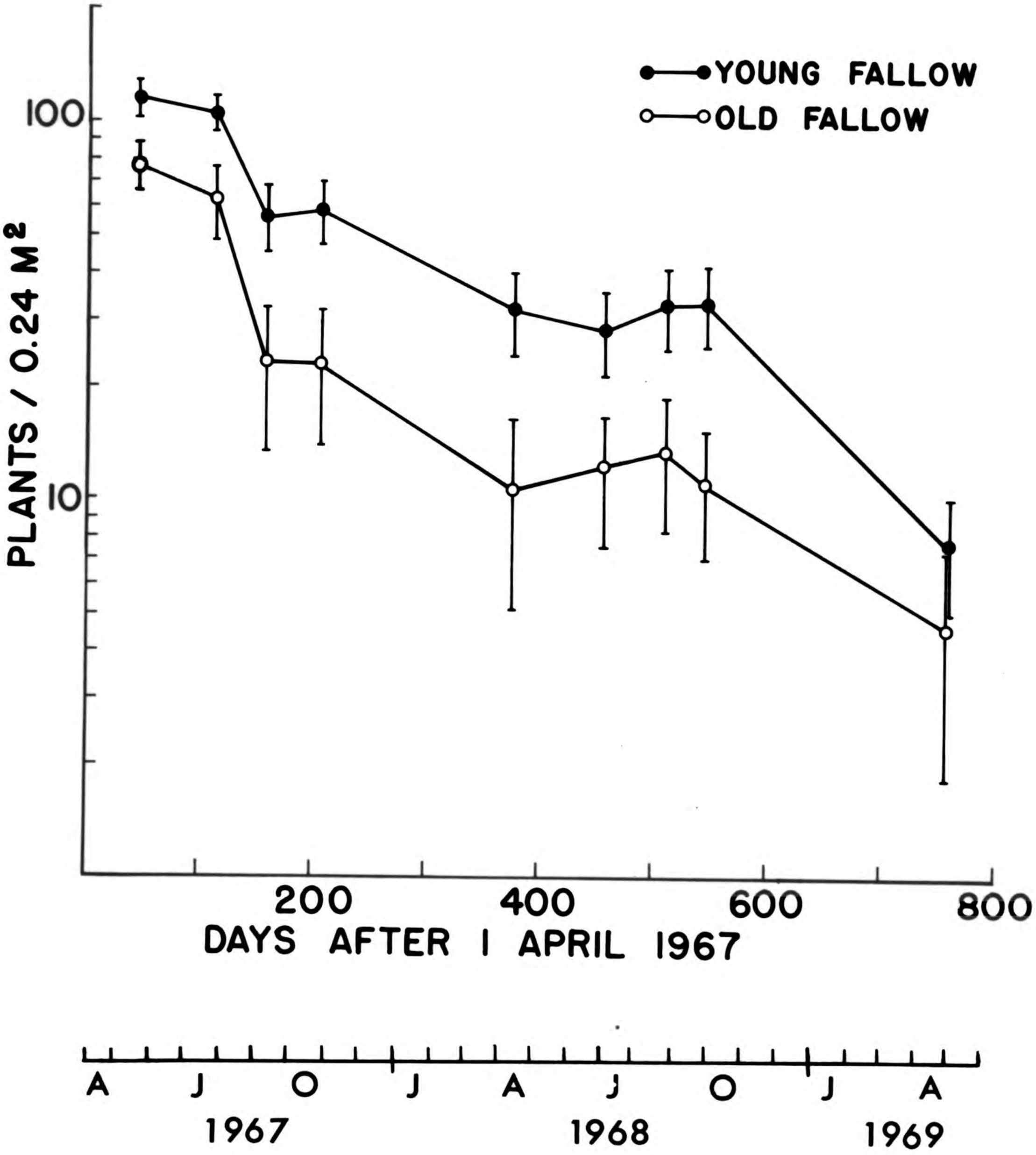
Seedling emergence in the second growing season was negligible in both ages of fallow. Estimated percent emergence accounted for less than 1% of the seed sown in 1966, even though seed not accounted for by prior germination or emigration represented 42 and 80% of the original seed input in the young and old fallows respectively, if one makes the unwarranted assumption that no mortality occurred prior to seedling emergence. Potential (laboratory) second season germination of the same seed was 81%.

Seedlings were observed but not counted in the third growing season. The seedling densities appeared to be low, although considerably higher than in the previous year.

Mortality rates during the first two growing seasons were quite variable, but percent mortality was relatively independent of the age of fallow (Figure 7), the cover of the dominant herbaceous species (Figure 8), and intraspecific density (Figure 9). The correlations between <u>Daucus</u> density and the cover of particular dominant species tended to increase during the first two years (Table 3). Partial removal of the other species, by clipping, had little effect on the survival of <u>Daucus</u> rosettes, but did enhance seedling establishment in the older fallow (Figure 10). Intraspecific density accounted for very little variance although graphs of percent survival as a function of initial density suggested that the maximum survival probabilities were proportional to the reciprocal of intraspecific density.

FIGURE 7

Time Courses of Rosette Survival in Old and Young Fallows. Points represent means of 41 quadrats (± 2 S.E.) in each age of fallow (O = Old, ● = Young). The same 41 quadrats per age of fallow were used for each inventory.



YOUNG FALLOW
OLD FALLOW
PLANTS / 0.24 M²
100
10
200
400
600
800
DAYS AFTER 1 APRIL 1967
A
J
O
J
A
J
O
J
A
1967
1968
1969

FIGURE 7

FIGURE 8

Relation Between Total Grass Cover and Rosette Survival. Data for the two ages of fallow are pooled. Quadrats are the same as in Figure 7.

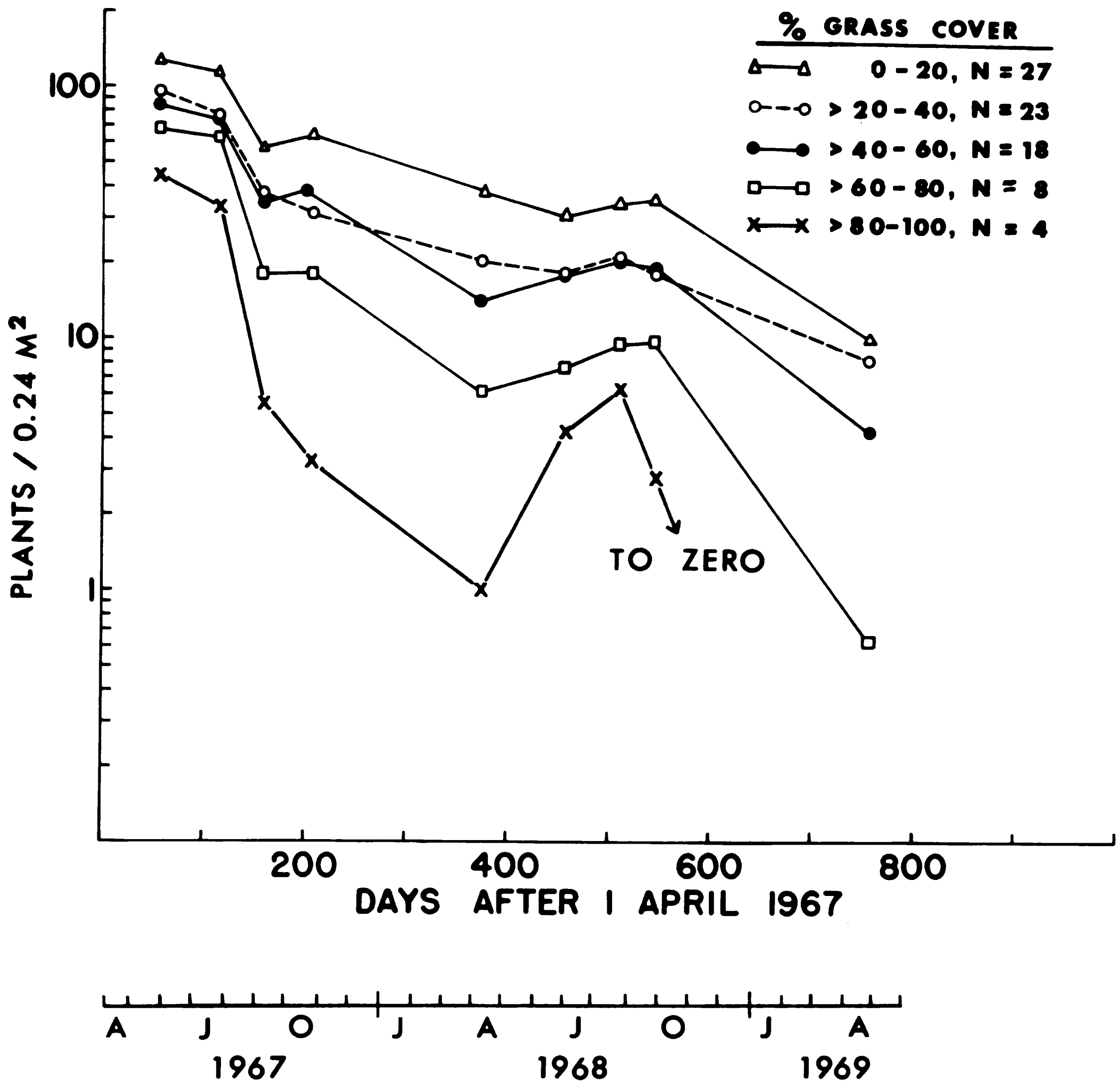

% GRASS COVER
0 - 20, N = 27
> 20 - 40, N = 23
> 40 - 60, N = 18
> 60 - 80, N = 8
> 80-100, N = 4
PLANTS / 0.24 M²
100
10
1
TO ZERO
200
400
600
800
DAYS AFTER 1 APRIL 1967
A
J
O
J
A
J
O
J
A
1967
1968
1969

FIGURE 8

FIGURE 9

Effect of Sowing Rate on Rosette Survival. Seed rates were 188 (low), 412 (intermediate), and 816 (high) seeds/0.24m^2 quadrats. Data for the intermediate seed rates are from Figure 7. N=10 for high and low seed rates in the young fallow and N=9* for high and low seed rates in the old fallow. Solid symbols (●, ▲, ■) represent values for the young fallow and hollow symbols (○, △, □) represent values for the older fallow.

---

* The discrepancy in sample sizes in the two ages of fallow is a result of sowing two of the clipped quadrats at the wrong rates.

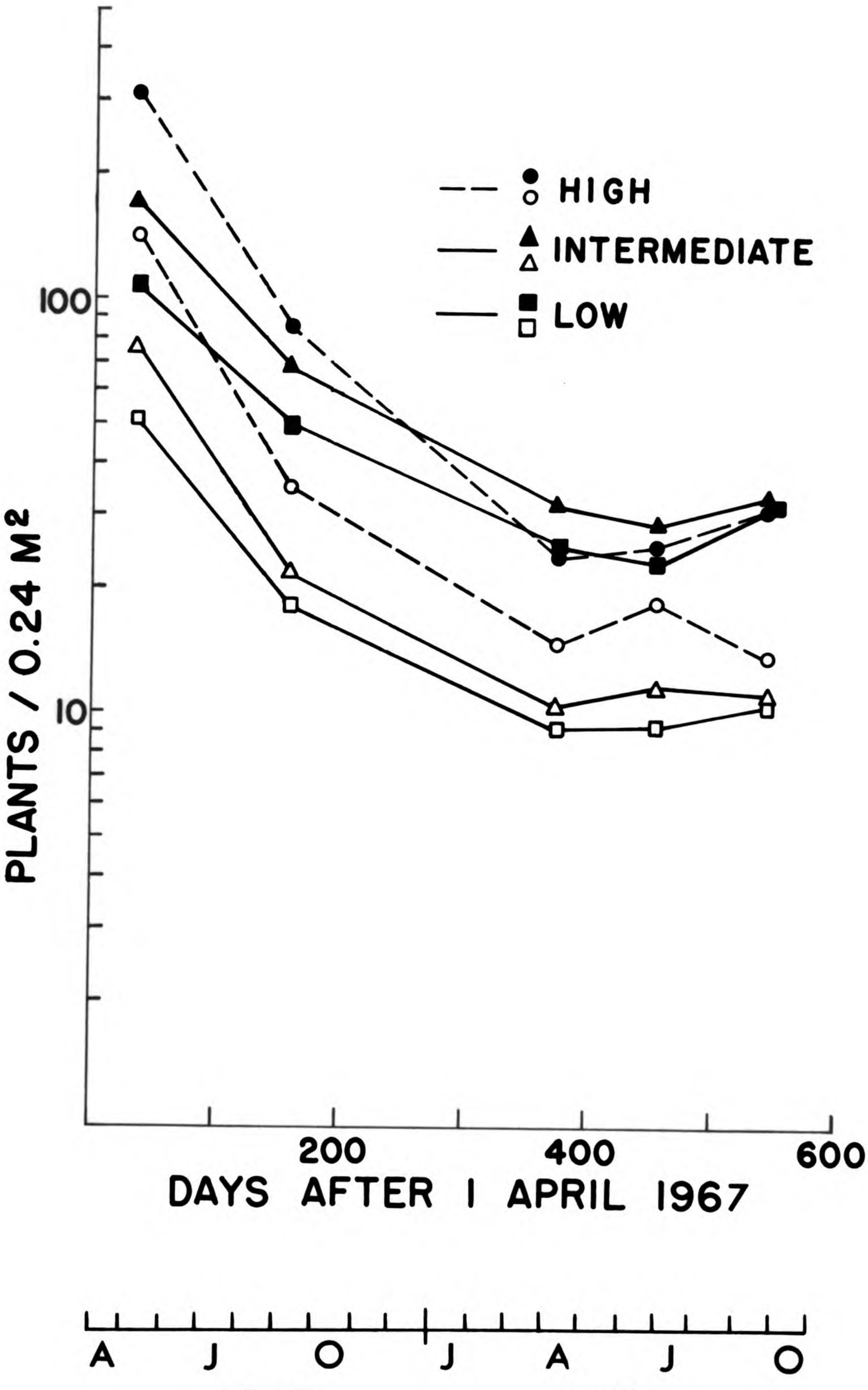

HIGH
INTERMEDIATE
LOW
100
10
PLANTS / 0.24 M²
200
400
600
DAYS AFTER 1 APRIL 1967
A
J
O
J
A
J
O
1967
1968

FIGURE 9

TABLE 3

CORRELATIONS OF DAUCUS DENSITY WITH THE MORE PROMINANT VASCULAR PLANT SPECIES OCCURRING IN THE QUADRATS

	SPRING 1967			FALL 1967			FALL 1968		
	N	r	F	N	r	F	N	r	F
Rhus typhina	-	-	-	34	-0.154	0.78	48	-0.124	6.53
Melilotus alba	-	-	-	30	-0.561	12.84**	69	-0.768	96.21***
Poa pratensis	35	-0.711	33.80***	41	-0.625	24.96***	51	-0.744	60.89***
Poa compressa	35	-0.330	4.02	22	-0.379	3.35	44	-0.496	13.71***
Agropyron repens	87	-0.396	15.83***	165	-0.204	7.09**	120	-0.812	228.01***

N = Number of quadrats
r = Correlation coefficient (Pearson's r)
F = F ratio
** = Probability < .01
*** = Probability < .001

FIGURE 10

Effect of Clipping the Associated Vegetation on Daucus Survival. Unclipped data (----) are from Figure 7. Clipped data (———) represent means of 28* and 30 quadrats in the old (O) and young (●) fallows, respectively. Seeds were sown at the rate of 412 seeds/$0.24m^2$.

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* Discrepancy in sample size is a result of a sowing error.

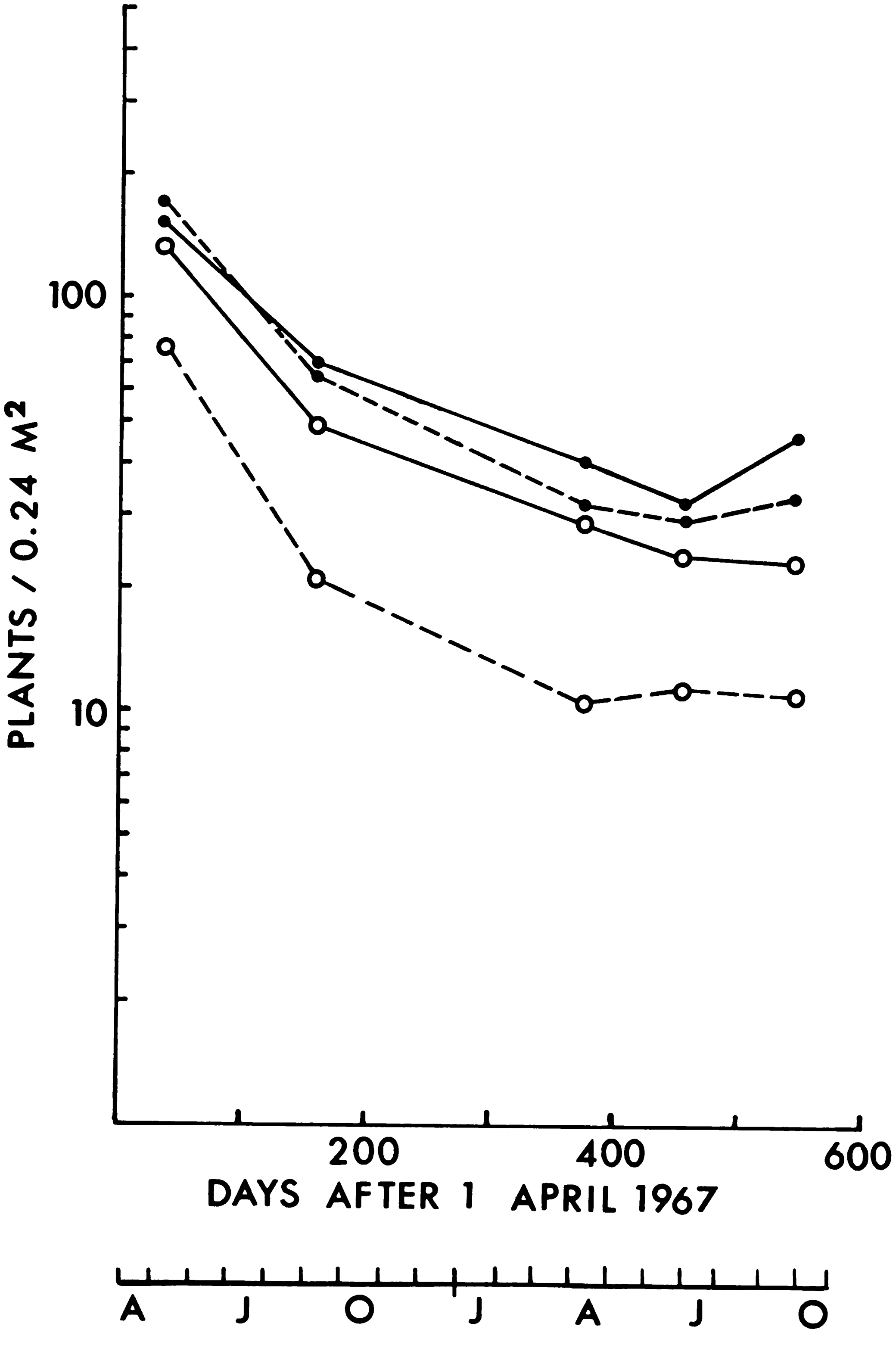
PLANTS / 0.24 M²
100
10
200
400
600
DAYS AFTER 1 APRIL 1967
A
J
O
J
A
J
O
1967
1968

FIGURE 10

Highest mortality rates occurred during the winter and during summer droughts. Percent winter-kill was remarkably constant when corrected for normal post-fruiting mortality in the preceding fall. Drought was concurrent with exceedingly heavy grazing pressure in the summer of 1967 which resulted in complete defoliation of most of the rosettes. Grazers were not identified, but the defoliation coincided with the immigration of large numbers of mature and late instar Acridid grasshoppers following the harvesting of an adjacent hay field.

Reproduction occurred in both the first and second growing seasons in the younger fallow, but was delayed in the older fallow until the second growing season. One individual in a clipped quadrat in the older fallow flowered in the first year, but failed to set seed. In the younger fallow, 3.5% of the plants alive at the end of the first growing season were reproductive. In the second year, 37% of the individuals in the younger fallow, and 7% in the older fallow were reproductive. Potential seed production based on estimates of numbers of flowers for the first growing season was 4900 ± 3000 seeds per quadrat (0.24 m^2) in the younger, and essentially none in the older fallow. Most of this potential seed crop was destroyed by herbivores prior to seed maturation. Actual seed production based on air-dry weight of seeds produced in the second growing season was 5300 ± 1100 seeds per quadrat in the younger fallow and 370 ± 190 seeds per quadrat in the older fallow.

Reproduction probability of Daucus in the second growing season was negatively correlated with the cover of the more abundant species (Table 4). Reproduction probability declined non-linearly with increases in aggregate grass cover, i.e., the cover of the dominant herbaceous life form (Figure 11). The number of reproductives per quadrat was proportional to population density ($r = 0.89$, $F_{1,518} = 1667$). Since reproductive plants in the first year occurred in relatively few quadrats, correlations were not run between first year carrot reproduction and the percent cover of other species.

Clipping the grasses and non-carrot vegetation during the first growing season markedly enhanced second year carrot reproduction. A mean of 28.0 ± 3.1 individuals per clipped quadrat flowered in the younger, and 5.1 ± 1.2 individuals flowered in the older fallow. These values represent two- and seven-fold increases relative to the unclipped quadrats, whereas densities in the clipped quadrats at flowering were only 1.4 and 1.3 times the densities in the unclipped quadrats.

Flower and seed production were proportional to the number of reproductive individuals (Figures 12 and 13), implying that mean flower and seed yields per reproductive individual were nearly constant over the observed density range. The partitioning of seed production among the

TABLE 4

CORRELATION BETWEEN THE PERCENT COVER OF THE PROMINENT VASCULAR PLANTS AND THE PROBABILITY OF FLOWERING IN THE 2nd GROWING SEASON

SPECIES	N	r	F	P
Rhus typhina	48	-0.492	14.68	< .001
Melilotus alba	69	-0.401	12.80	< .001
Poa pratensis	48	-0.841	110.83	< .001
Poa compressa	44	-0.388	7.44	< .01
Agropyron repens	115	-0.726	127.97	< .001

Arcsin transformation (Snedecor, 1956) was used for reproduction probabilities.

FIGURE 11

Relation between Total Grass Cover and Reproduction Probability. Points represent means (± 2 S.E.) of untransformed data. Seed were sown December 1966 in plots fallowed since either summer 1964 or 1966 at the rate of 412 seeds/0.24m^2. Data for the two ages of fallow were pooled.

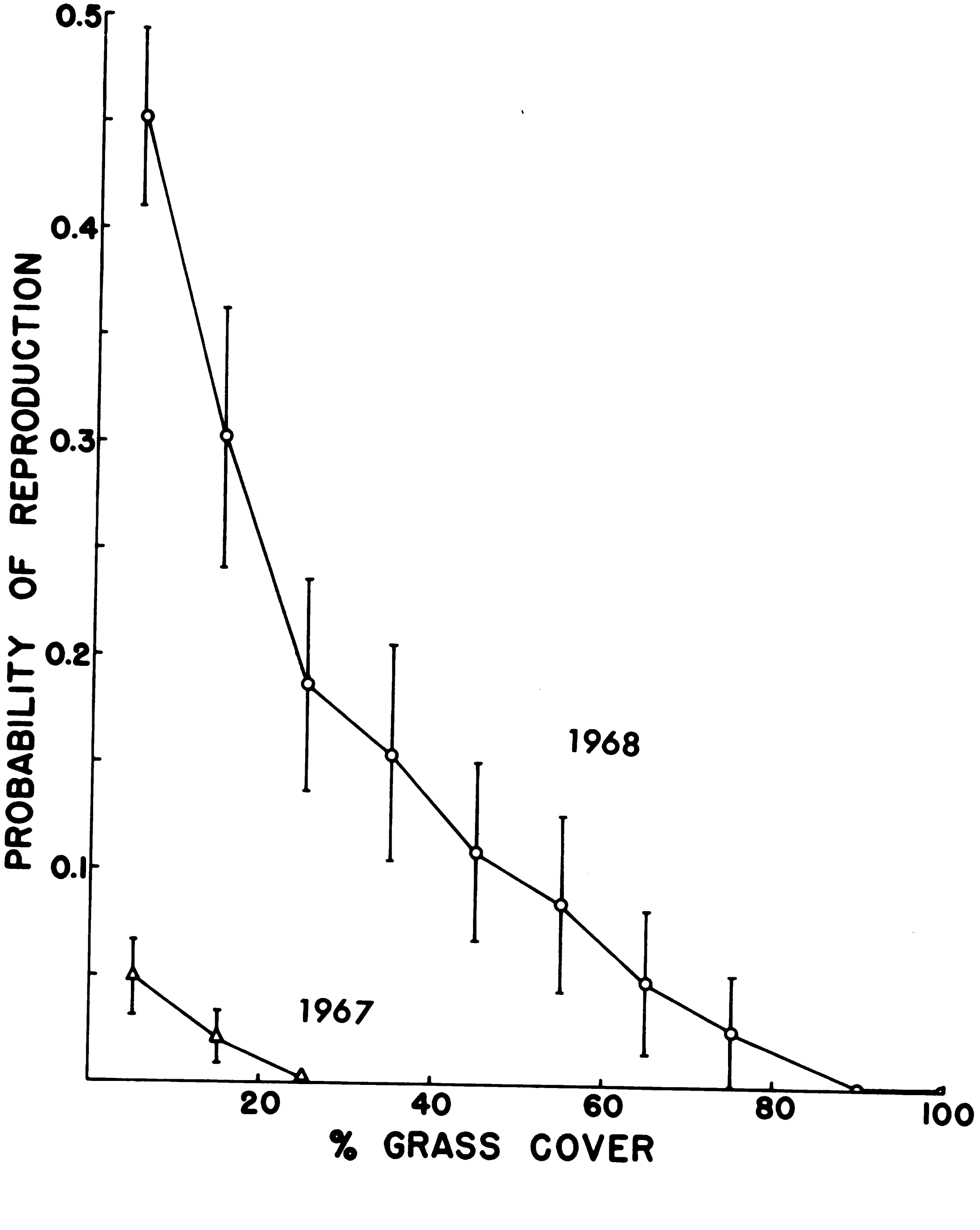
0.5
0.4
0.3
0.2
0.1
PROBABILITY OF REPRODUCTION
1968
1967
20
40
60
80
100
% GRASS COVER

FIGURE 11

FIGURE 12

Regression of Estimated Flower Production on the Number of Reproductives/0.24m^2. Flower number estimates are based on two diameter measurements of each inflorescence. Data for the two fallows are pooled. The regression ($r = 0.84$, $N = 94$) is accompanied by confidence intervals.

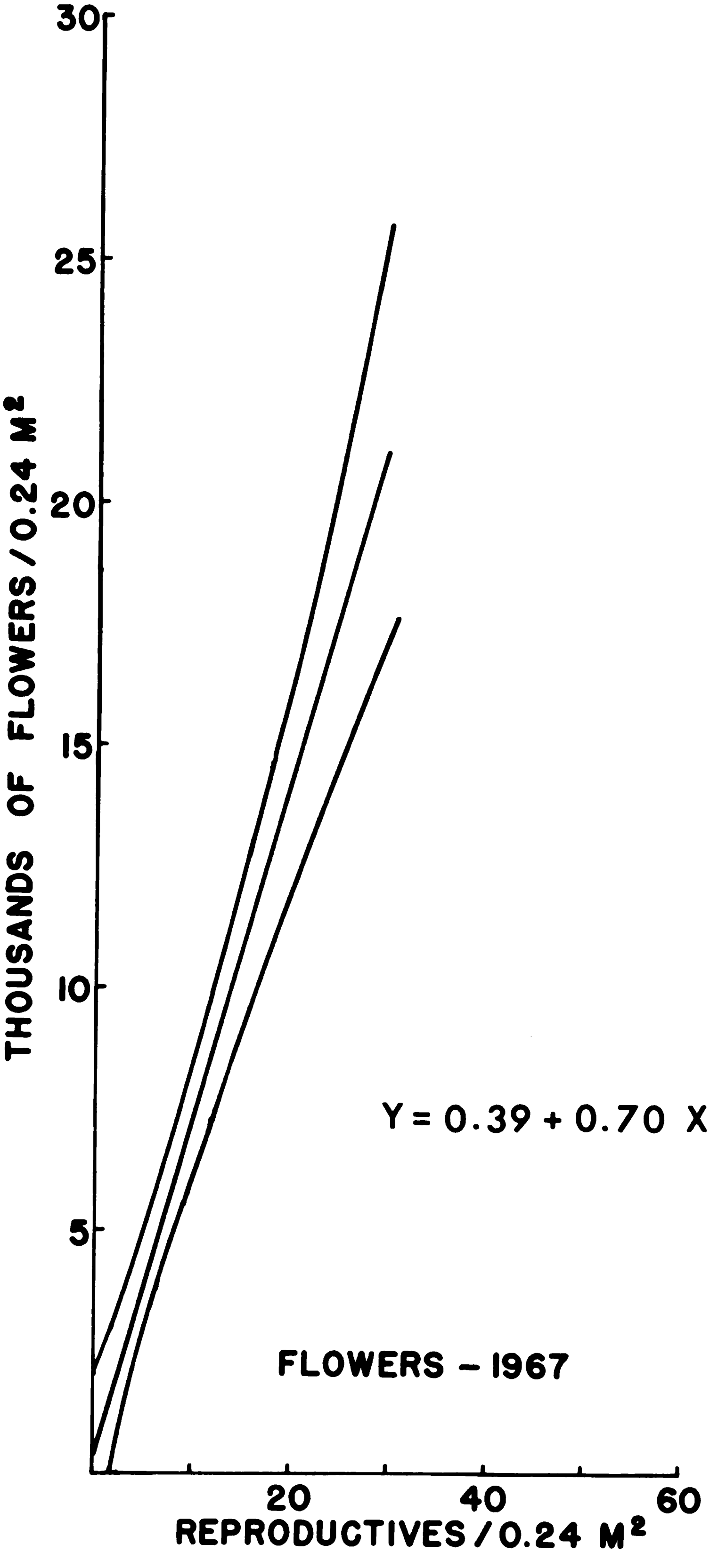
30
25
20
15
10
5
THOUSANDS OF FLOWERS/0.24 M²
Y = 0.39 + 0.70 X
FLOWERS – 1967
20
40
60
REPRODUCTIVES/0.24 M²

FIGURE 12

FIGURE 13

Regression of Seed Production in Grams Air Dry Weight on the Number of Reproductives. The regression (r = 0.86, N = 296) is accompanied by 95% confidence intervals. Data for the two fallows are pooled and quadrats without reproductives are excluded.

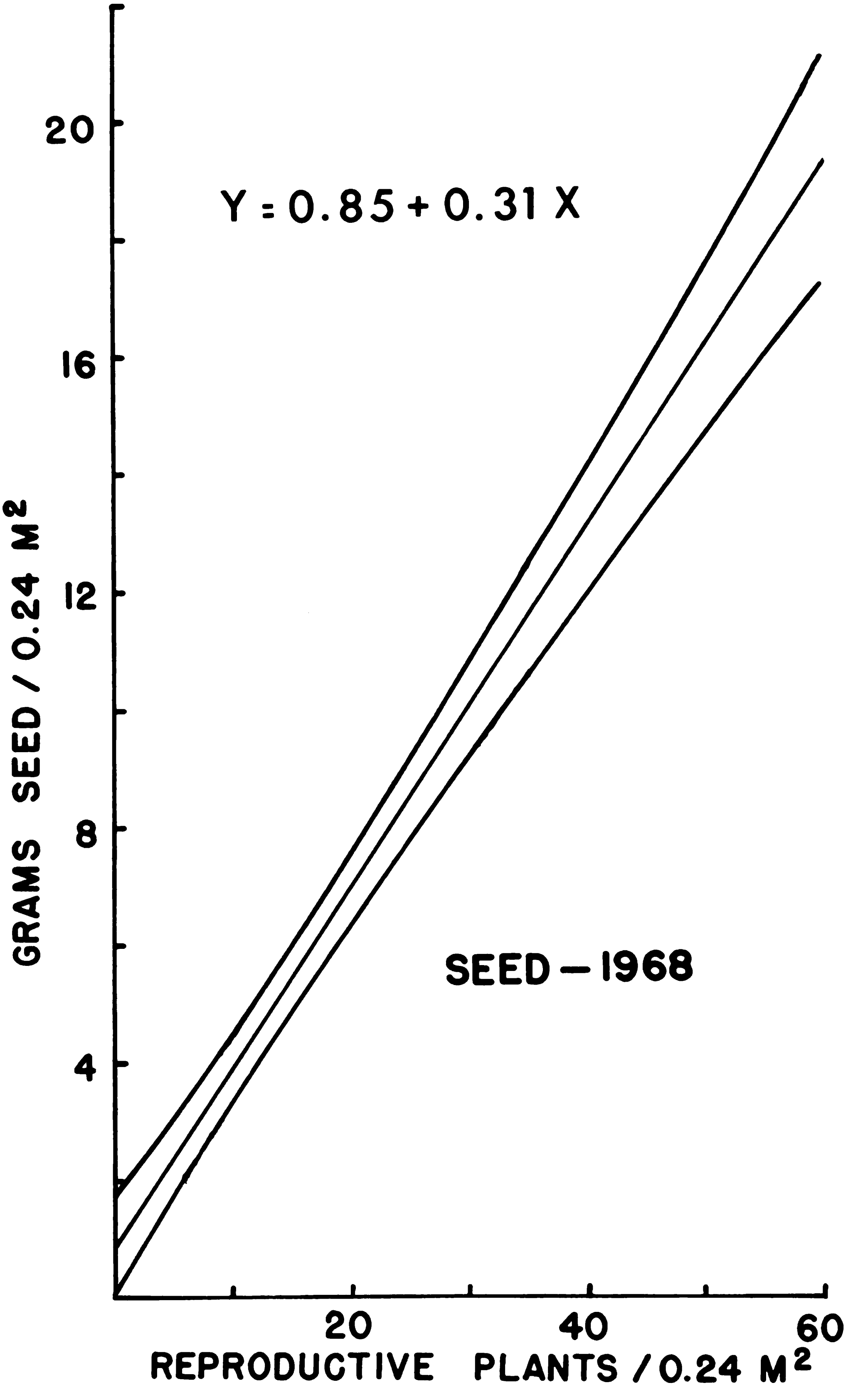
Y = 0.85 + 0.31 X
SEED – 1968
GRAMS SEED / 0.24 M²
20
16
12
8
4
20
40
60
REPRODUCTIVE PLANTS / 0.24 M²

FIGURE 13

reproductive individuals in a random sample of the population is shown in Figure 14.

Approximately 50% of the seed sown in the vicinity of the parent plants in 1967 resulted in established seedlings in 1968, but annual reproduction by these individuals was absent. Very few new individuals (easily identified by their conspicuous cotyledons) were observed coming from this sowing in the second growing season (1969). The number of emerged seedlings resulting from seed of annuals and putative biennials was the same. These data were consequently lumped as "sparse _Agropyron_ sod" (Figures 15 and 16) for comparison with concurrent germination in the second field experiment.

Failure of Seedling Establishment

Post-emergence seedling mortality had little effect on seedling establishment in 1968. Mortality during the spring germination pulse was equivalent to only 3 to 14% of the total emergence (Figure 15). The highest percent mortality as well as the greatest emergence occurred in the presence of Agropyron sod. The lowest seedling densities were associated with _Poa compressa_ sod.

Peak emergence rates occurred in late April but emergence continued at low levels throughout the summer, despite the frequent occurrence of heavy rain that might be expected to give subsequent pulses of germination (Dale

FIGURE 14

Frequency Distribution of Seed Production/Biennial Plant. Data are from the 82 quadrat sample of Figure 7. Seed yield is expressed as gms of air-dry seed per plant.

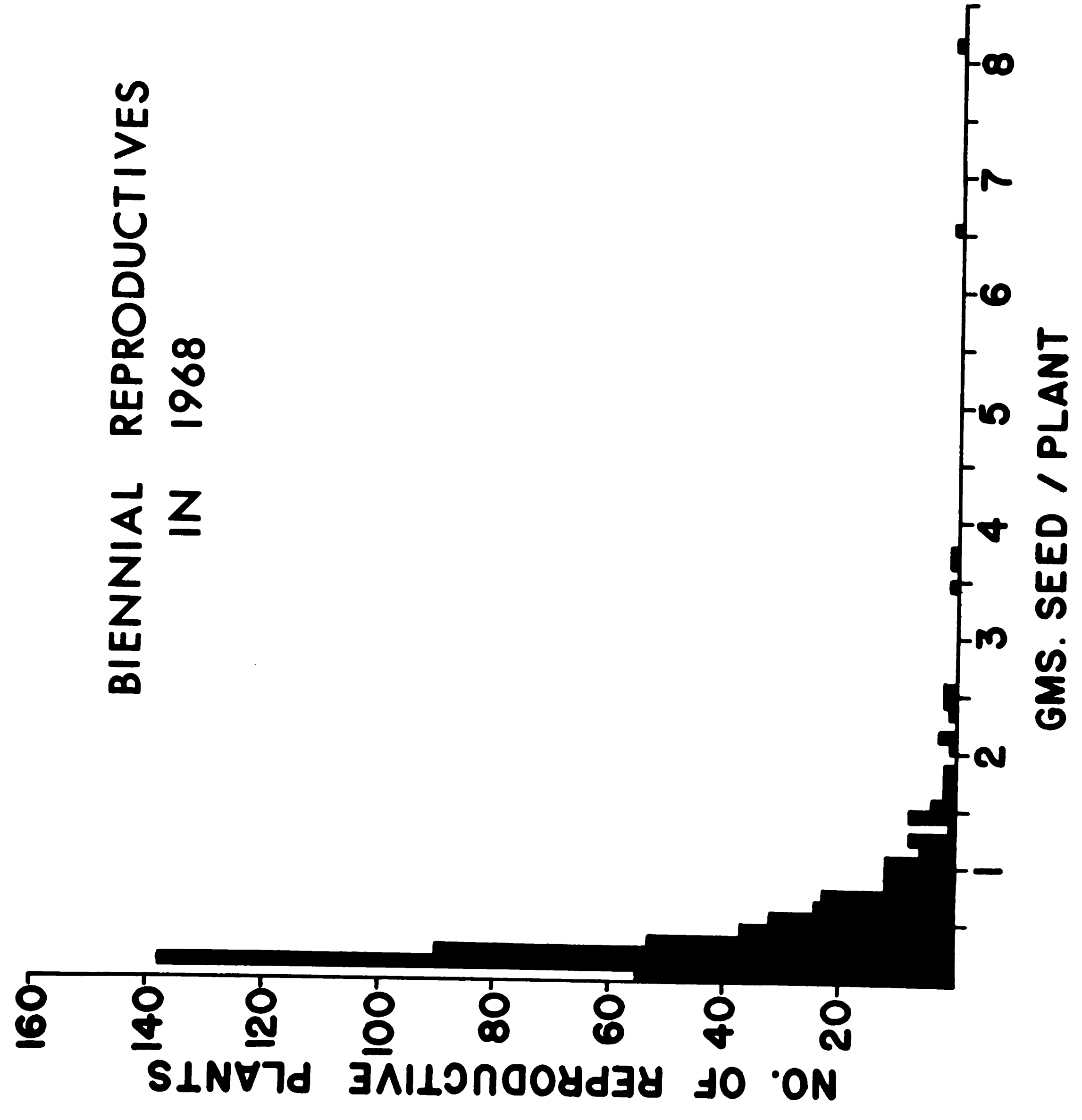
BIENNIAL REPRODUCTIVES
IN 1968
NO. OF REPRODUCTIVE PLANTS
160
140
120
100
80
60
40
20
GMS. SEED / PLANT
1
2
3
4
5
6
7
8

FIGURE 14

FIGURE 15

Histograms of Mean Seedling Emergence and Concurrent Mortality. Means (± 2 S.E.) are given for total emergence (clear) and total mortality (cross-hatched) during the spring of 1968 for seedlings resulting from seeds sown in December 1967. Seeds were sown on bare ground (B), in dense *Agropyron repens* sod (DA), in sparse *Agropyron* sod (SA), and in *Poa compressa* sod (P). N = 30 for each treatment except sparse *Agropyron* (N = 18). The B quadrats were in plots fallowed in 1967, the SA quadrats were in plots fallowed in 1966, and the P and DA quadrats were in plots fallowed in 1964.

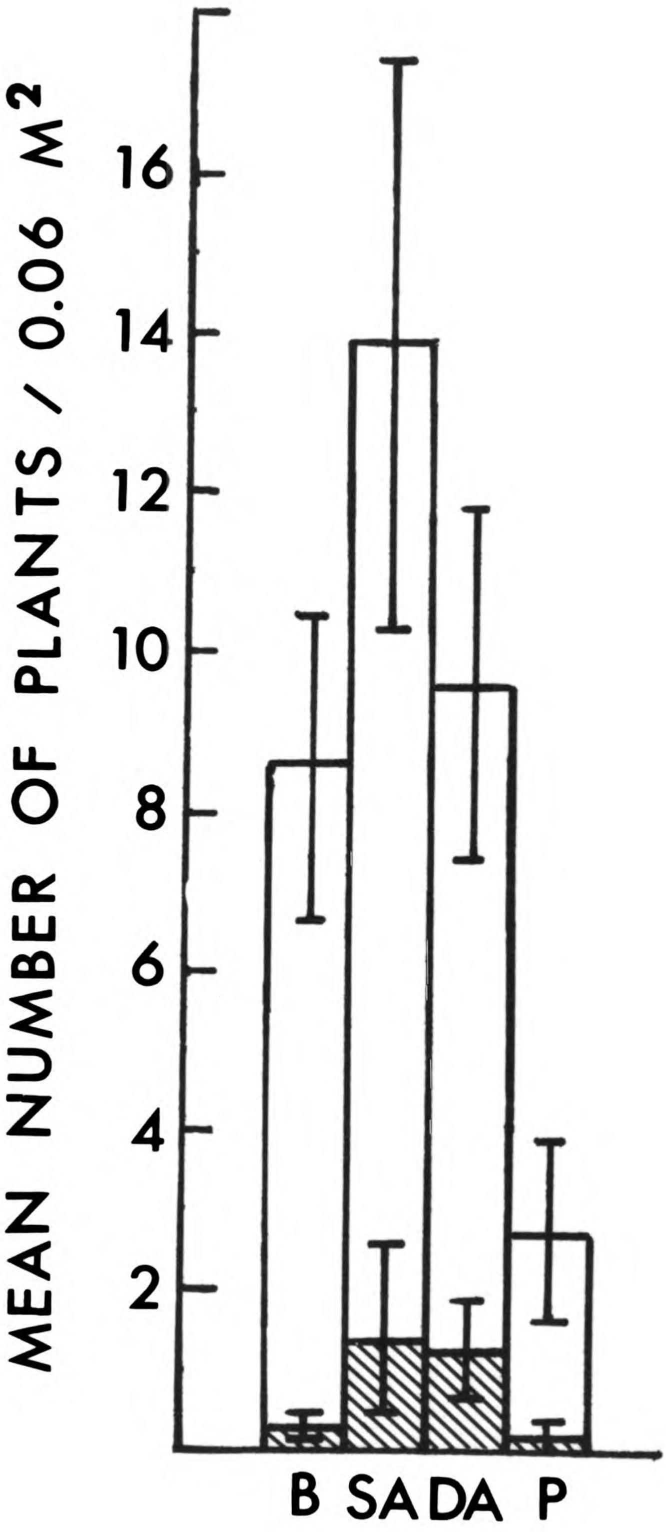

FIGURE 15

FIGURE 16

Mean Number of Live _Daucus_ Plants Resulting from Seed Sown in December 1967 in Four Sod Types. The 1968 counts (clear) are all seedlings and the 1969 counts (checkered) are largely one-year-old rosettes. Counts were made May 8, 1968 and April 26, 1969. Rosettes resulting from emigrant seeds are included. Sample sizes and confidence intervals are as given in Figure 15.

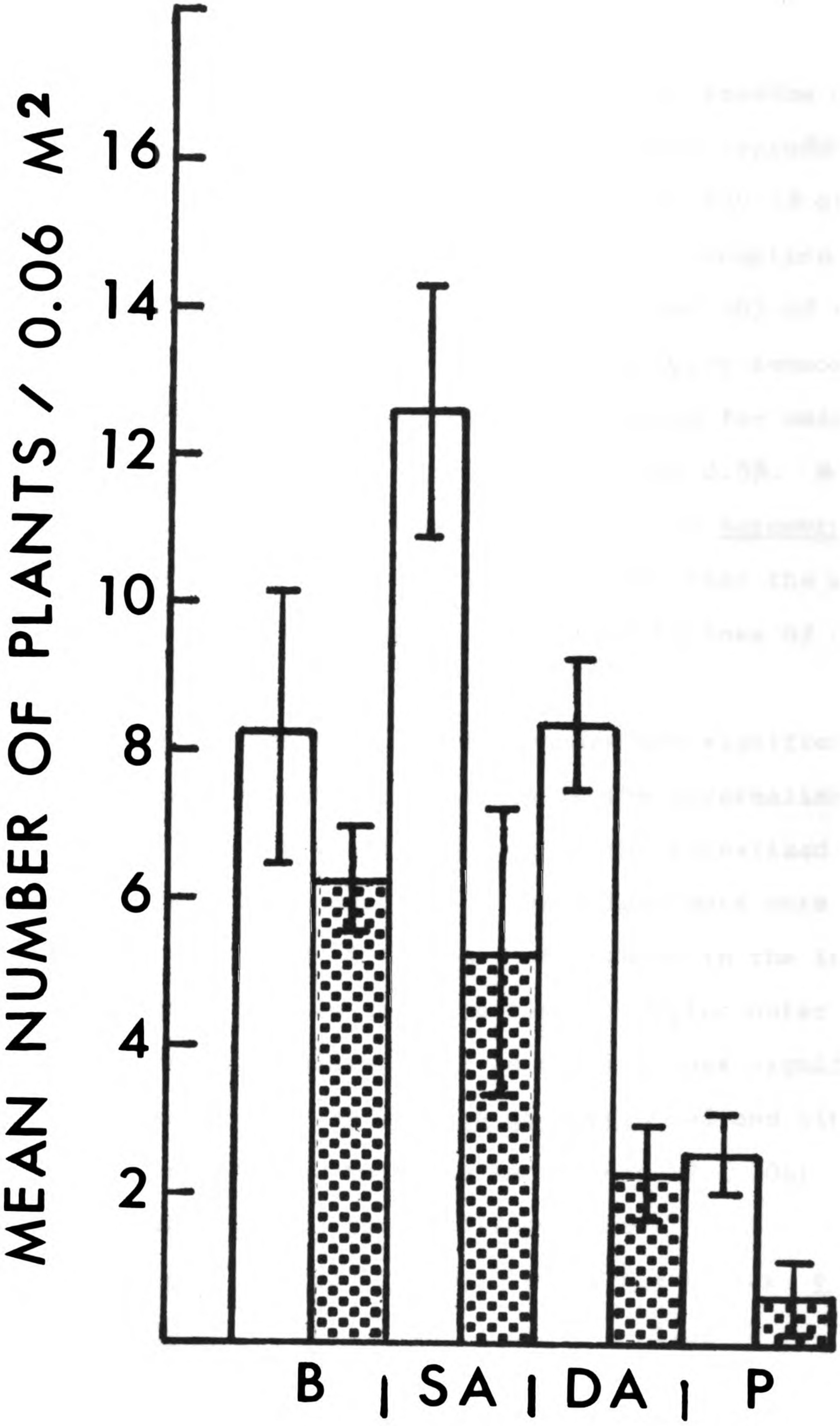

FIGURE 16

and Harrison, 1966).

Subsequent development was comparable to results obtained in the previous growing season. Annual reproduction occurred only on bare ground, where approximately 1% of the individuals flowered and set seed. With the exception of quadrats on bare ground (Figure 16), less than 50% of the individuals survived to begin the second growing season. Estimated second year germination (uncorrected for emigration) of seed sown on bare ground in 1967 was 0.5%. No additional emergence was observed in quadrats in *Agropyron* or *Poa* sod, even though observations were made after the spring germination pulse was completed, and prior to loss of conspicuous cotyledons.

Seedling emergence in the greenhouse was significantly altered by the sod-litter treatments in the unvernalized pots ($F_{6,77} = 5.09$, $P < .01$) but not in the vernalized pots although block differences in the vernalized pots were significant ($F_{1,70} = 9.23$, $P < .005$). Emergence in the inner block was higher than in the more rapidly drying outer block. In the unvernalized pots germination was significantly suppressed only by the *Poa compressa* sod and litter treatment (Duncan's New Multiple Range Test, $P < .05$). The mean[1] number of emerged seedlings were:

Agropyron	Bare	*A.* Litter	*Poa*	*P.* Litter	*A.*+ Litter	*P.*+ Litter
10.00	9.33	8.92	7.42	7.26	7.08	4.08

---

[1] A break in the underlining indicates a significant difference.

The presence of sod (9.7 ± 0.6 gm dry weight/pot) significantly ($t_{82} = 6.42$, $P < .001$) altered the growth rates of carrot seedlings, had little effect on survival, and had no effect on early development as indicated by the number of new leaves produced. Mean carrot dry weight per pot was 2.56 mg ± 0.2 in the presence of grass, but was 16.8 mg ± 2.6 in bare or litter covered pots. Mortality was negligible with the exception of the bare pots and a few sod pots in which slugs were initially present.

DISCUSSION

Plant species characteristic of the initial stages of old-field succession undergo rapid and quasi-predictable changes in population size. These changes have been extensively described in cross-sectional studies, but experimental examination is essentially lacking. Keever (1950) and Rice (1964, 1967) have investigated possible causal mechanisms in the laboratory but have not demonstrated their occurrence in the field. Demographic analysis of successional changes is lacking, and is uncommon for plant populations in general (cf. Harper, 1967). Agronomic studies indicate that germination and seedling survival are generally the most critical phases of population establishment for plant species (Harper, 1965; Cavers and Harper, 1967), but the regulatory processes operative after population establishment are complex and insufficiently studied to warrant generalization at this time.

In the present study, ecesis[1] of <u>Daucus</u> <u>carota</u> L. was most sensitive to events preceding seedling emergence, and was negatively correlated with the abundance of other plant

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[1] Ecesis, as defined by Clements (1916), is the establishment of a reproductive population.

species. Populations established from seed sown in first year fallow vegetation were significantly larger, began reproduction one year sooner, and produced more seed per unit area than populations established from seed in a third year fallow. Juvenile survival was relatively insensitive to the age of fallow.

The timing of germination in the field appears to have been primarily determined by temperature. The duration of the initial germination pulses in both the laboratory and the field were in fair agreement with the experimental data of Kotowski (1926), and their initiation occurred, in both 1967 (Figure 5) and 1968, within two weeks of the permanent soil thaw at the 4 inch depth at the Michigan State University Horticultural Farm (the best available index of soil thaw). The rain-induced midsummer germination pulses reported for latitudinally similar southern Ontario (Dale and Harrison, 1966; Harrison and Dale, 1966) were not observed, but this may reflect the late date at which the seeds were sown in the Ontario study (at least two weeks after the completion of the spring germination pulse in southern Michigan).

Seedling densities in the field were negatively correlated with the cover of each of the sod-forming grasses in 1967. Correlations with *Agropyron repens* and *Poa pratensis* were significant, and the correlation with *P. compressa* was nearly so (Table 3). The reason for the lack of a significant correlation with *P. compressa* is not apparent, although the small sample size may be partially responsible. In plots established one year later seedling densities were lower in the presence of *P. compressa* sod than in either *Agropyron* sod or bare ground (Figure 15). The differential emergence in sparse and dense *Agropyron* sods agreed with correlations obtained in 1967, but the differential between bare ground and sparse sod did not. The low emergence on bare soil in 1968 may have been caused by a more rapid drying of the surface layers of soil in the absence of litter cover. Very dry soils delay (Doneen and MacGillivray, 1943) or suppress carrot germination (Heydecker, 1962, 1963). Harper (1955) noted that the greatest mortality of maize seedlings occurred with those combinations of soil moisture and temperature that just prevented, or restricted, growth. He interpreted these results as an enhanced susceptibility to pathogens. Similar interactions of moisture, temperature, and disease might account for much of the differential emergence observed in the present study, but cannot be distinguished from germination suppression or seed predation, since censuses were based on counts of emerged seedlings.

Attempted separation of the effects of litter and live grass in the greenhouse was equivocal, probably because of unrealistically low litter applications. Litter applications, about 3 gm per pot, were approximately one-tenth the amount reported for *Poa compressa* sod in southeastern Michigan

(Weigert and Evans, 1964). The significant reduction in the number of emerged seedlings in the presence of _Poa_ sod plus litter, but not in any of the other sod-litter combinations, may have reflected small scale differences in litter cover. The numerous live tillers of _Poa_ prevented dispersion of the litter during watering, whereas litter movements in sparsely tillered (_Agropyron_) and sodless pots tended to create small openings. The reason for the absence of similar results in pots of _Poa_ sod and litter that had been placed in the cold frame is not apparent.

Early post-emergence seedling mortality apparently accounted for very little of the observed differential germination associated with the presence of other species. The magnitude of this mortality in 1967 is not known, but only 3 to 14% of the seedlings emerging in the field in 1968 died during the spring germination pulse, i.e., net germination closely approximated gross germination (Figure 15). Post-emergence mortality in the greenhouse was negligible in all treatments.

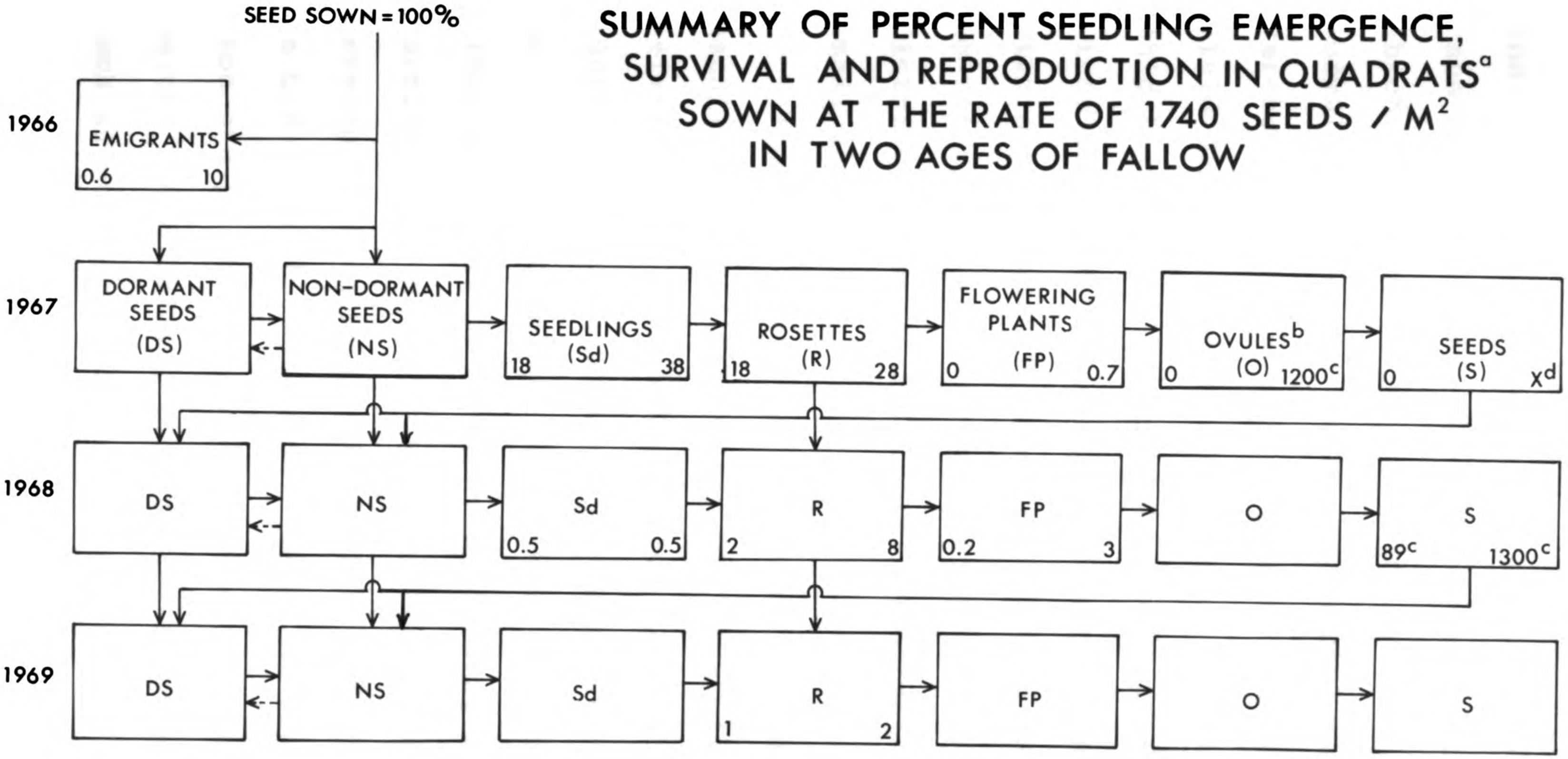
Mortality rates exhibited considerable seasonal variation, but were proportionately similar in the two ages of fallow during the first two growing seasons (Figure 7). The high mortality rates occurring during summer drought and during the long winters seem to be superimposed on a more subtle but constant mortality associated with either total sod development (Figure 8) or the abundance of individual species (Table 3). The clearest such relationship was with Melilotus alba (Table 3), a species which germinated simultaneously with Daucus, but grew both taller and more rapidly, forming a dense canopy. Differential mortality rates during the second winter (Figure 7) resulted from the larger number of post-fruiting deaths in the more reproductive younger fallow population (Figure 17).

Projection of the survivorship rates of the two populations suggests that, in the absence of establishment of new age classes, the sizes of the two populations will converge as a result of mortality associated with differential reproduction. Assuming constant mortality rates, the densities of the two populations will be approximately 4 plants/m^2 at the start of the fourth growing season and less than 0.4 plants/m^2 by the sixth growing season. The establishment of new plants from seed sown in the two fallows at the end of the first growing season (Figure 15) suggests, however, that convergence would be retarded if the seeds were not harvested. The marked difference in seed yield per unit area in the two fallows (Figure 17) suggests that the population in the young fallow would initially increase while the population in the older fallow would probably decline fairly rapidly.

The frequency distribution of seed yield (air-dry weight) per reproductive plant was not normal (Figure 14). Approximately 40% of the individuals produced between 0.1

FIGURE 17

Summary of Percent Seedling Emergence, Survival and Reproduction in Quadrats Sown at the Rate of 1740 Seeds/m^2 in Two Ages of Fallow. Rosette numbers represent counts made at the beginning of the respective growing seasons.



SUMMARY OF PERCENT SEEDLING EMERGENCE, SURVIVAL AND REPRODUCTION IN QUADRATS[a] SOWN AT THE RATE OF 1740 SEEDS / M^2 IN TWO AGES OF FALLOW

[a] 41 QUADRATS / AGE OF FALLOW

[b] OVULES = FLOWERS X 2

[c] OVULE AND SEED PRODUCTION EXPRESSED AS PERCENT OF THE SEED SOWN

[d] SEED CROP DESTROYED

KEY

OLD FALLOW YOUNG FALLOW

FIGURE 17

and 0.3 gm of seed, 40% produced between 0.3 and 1.0 gm, and 10% produced more than 1 gm. Koyama and Kira (1956) have shown that size distributions in plant populations which are relatively free of interference are approximately normal, and tend to become log-normal with increasing interference. This tendency is possibly accentuated in the seed yield distribution as a result of the allometric relationship between seed yield and plant size (Figure 4). Further, since the reproduction probability of Daucus is correlated with plant size (cf. Hawthorn, 1951), the smallest plants do not appear in the reproductive class, resulting in a distribution approximating a log-normal truncated on the small size end.

The seed yield per unit area, in contrast to the usually observed asymptotic or "parabolic" yield-density relationships (cf. DeWit, 1960; Bleasdale, 1967; Palmblad, 1968) observed in obligate annuals was directly proportional to density. Density, at the time of flowering, was determined primarily by the initial density and the age at reproduction, both of which were negatively associated with sod development (Table 3, Figure 11). The frequent correlation, in biennials (cf. Dickson, 1958), of the onset of reproduction and plant size suggests that the reproductive delays in the field reflect sod-induced suppression of growth rates, such as were observed in the greenhouse. Similar reproductive delays have been observed in grassland perennials in the field (Linkola, 1935) and are implicit in the greenhouse data of Palmblad (1968). This suggests that reductions in reproductive rates associated with interference may, for perennials and facultative annuals, be expressed as delayed reproduction rather than the reduced fecundity exhibited by obligate annuals.

Delayed reproduction for a species like Daucus carota which lacks efficient mechanisms for both mass dispersal and vegetative multiplication, could cause a several fold difference in the size of the colonized area and possibly alter the persistence of the population. Short generation times would have little effect on population persistence if the site were to rapidly become seed saturated, i.e., if the effect of augmentation of the seed supply were negligible. If, however, seed saturation were absent or delayed, the shorter generation times observed in the early arriving populations might lead to rapid increases in density (cf. Cole, 1954; Lewontin, 1965). Since subsequent mortality appears to be independent of population density, higher initial densities would be expected to prolong the persistence of the population if conditions subsequently became unfavorable for further seedling establishment.

If continued establishment remains possible, but restricted, the probability that a seed will land on a site suitable for germination would be approximated by the product of the number of "safe areas" (minimal areas of substrate suitable for germination) and the number of potentially effective seeds (viable, nondormant seeds). If the total safe area is negatively correlated with sod development, as the seedling emergence data suggest (Table 3), the number of safe areas would be expected to decline rapidly in young fallows. In older fallows, however, the smaller number of safe areas would probably decrease more slowly to a minimal level. As both the number of safe areas (safe sites of Harper et al., 1965) and the number of potentially effective seeds decline, their product, the probability that an effective seed will encounter a safe site, would be expected to decrease very rapidly. Thus, an earlier arriving *Daucus* population which succeeds in establishing a high initial population density with consequent early and large seed production, would tend to have a higher probability of persistence than a later arriving one.

Generalizing the findings of the present study suggests that the large density variations observed in naturally occurring populations in southern lower Michigan largely reflect various combinations of immigration time and continuing disturbance. In particular, the sharp disparity between the population densities in roadsides and adjacent, seemingly similar, old-field vegetations probably reflects enhanced seedling establishment in the periodically mowed roadside vegetation, coupled with occasional successful reproduction.

CONCLUSIONS

Conclusions Concerning *Daucus*

1. Arrival in the third rather than the first year of a succession results in significant reduction in the density and potential growth rate of wild carrot populations.

2. For the years studied, post-emergence seedling mortality was less important than emergence success in determining the size of a *Daucus* population.

3. Seedling establishment is negatively correlated with both total cover and the major component species of the established plant cover.

4. The number of emerged seedlings is affected by the age of fallow, but the relative rate of emergence (numbers emerging per day as percent of total emergence) apparently is not.

5. Intra-seasonal emergence rates decline rapidly following the spring emergence pulse.

6. Germination of seed surviving to the second growing season is modest and probably has little effect on population size of Daucus.

7. Mortality rates of wild carrot populations are relatively independent of intraspecific density and the intensity of sod development.

8. Mortality rates are highest during the winter and during summer drought.

9. Reproduction is delayed in the presence of well-developed sods.

10. Reproduction probability in the second growing season is negatively correlated with the percent cover of the more abundant species, and is markedly enhanced by partial removal of the shoots of associated plant species.

11. Flower and seed yields per unit area of wild carrot are directly proportional to intraspecific density in the ranges encountered in this study.

12. The partitioning of seed production among the members of the population is not normal, but rather appears to approximate a truncated log normal.

13. The projected population duration, ignoring second and later generations, would approximate six to ten years.

Conclusions General to Succession

1. Small delays in arrival time may significantly alter both ecesis success and the rate of subsequent population buildup.

2. The magnitude of the effect varies with the composition as well as the age of the previously established vegetation.

3. If Daucus is representative, the most sensitive life history determinants of population growth rate are seedling establishment and the age of reproduction.

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LITERATURE CITED

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