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ECOLOGY OF ACHENE DIMORPHISM IN *HETEROOTHECA LATIFOLIA*

II. DEMOGRAPHIC VARIATION WITHIN POPULATIONS

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SUMMARY

(1) Seed bank dynamics, germination, survival, and reproduction were monitored for ray and disc achenes of *Heterotheca latifolia* (Compositae). The achenes were sown into a natural population at different times during the fruiting season according to an experimental design that permitted assessment of spatial variation in demographic behaviour.

(2) The seed bank of disc achenes approached zero in the spring while 24% of the ray seed bank was still viable after one year.

(3) A greater proportion of disc achenes germinated (30%) than of ray achenes (4%). Only the early-produced ray achenes germinated in the year of production, while peak germination of disc achenes resulted from intermediate sowing dates just before the first substantial rains of the season in October.

(4) Survival from germination to reproduction was lower for plants from ray (0.47) than disc achenes (0.75) as a result of their lower probability of seedling establishment. Significant differences in survivorship were found for disc achenes sown at different dates.

(5) The overall superior reproductive performance of adult disc plants was due to plants from late-sown disc achenes which reproduced considerably more than adult plants from the early-sown ray or disc achenes. Late-sown ray achenes germinated little and thus produced few adults.

(6) The capacity for population increase of *H. latifolia* is high with the contribution from disc achenes usually considerably more important than that of ray achenes (the finite rate of increase equalled 17.1–30.7 achenes per year for ray achenes and 232 for disc achenes in the experiment reported here). Plants derived from ray achenes will contribute more, relative to those derived from disc achenes, in declining populations or populations in which disturbance reduces the survival of the growing stage more than the survival of the dormant seed stage.

(7) Significant small-scale spatial variation is reported for germination, survival, and reproduction.

INTRODUCTION

Many species of plants have polymorphic seeds which may differ in morphology, anatomy, germination and dispersal (see Venable & Levin 1985). How do these differences affect population dynamics? Under what natural conditions is each seed type most successful and what demographic advantages accrue to individuals or populations with polymorphic seeds? One approach to answering these questions is to monitor the demographic fates of seed morphs in natural environments.

While the consequences of seed polymorphism can be measured with simple demographic experiments, deeper insights are attained when the experimental design

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permits an assessment of demographic variation in space and time. A population or even a cohort is not demographically uniform but includes a range of germination, survival and reproductive patterns. For example, seeds that mature at different times during the fruiting season may have very different fates. Yet once seeds are in the seed bank their time of entry is usually obscure and variation due to the time seeds mature and enter the seed bank is usually overlooked.

Similarly, an understanding of small-scale spatial variation can deepen our insight into the demographic consequences of seed polymorphism. Is demographic behaviour uniform across a site or does it vary? Small-scale demographic variation is important to our understanding of dispersal and to our understanding of the genetic versus environmental control of life histories.

This paper presents the results of a field experiment conducted with the annual composite, *Heterotheca latifolia*, which produces different achene types from ray and disc florets (Venable & Levin 1985). The two achene types were sown into a natural population at different times during the fruiting season in a design permitting assessment of spatial variation.

MATERIALS AND METHODS

Seed bank experiments

Twenty 1 × 1-m quadrats were chosen at random from a 4 × 20-m area in a *Heterotheca latifolia* Buckl. population in Austin, Texas, U.S.A. (30° 18'N, 97° 47'W). *Heterotheca latifolia* was the dominant plant in this sandy field which is mown once every year or two. One soil sample was taken from each quadrat each month for a year beginning in January 1977. Each sample was drawn from an area of 284 cm² to a depth of 4–8 cm. This depth contained virtually all the viable *H. latifolia* achenes. The achenes were removed by sieving and scored for viability. Fleshy whitish-grey to reddish embryos, with oil droplets visible when the embryo was broken, stained red when treated with tetrazolium blue (indicating that they were viable). All achenes were broken open and considered alive if their embryos were as described.

Samples of fifty achenes (either from ray or disc florets) mixed with soil were placed in non-degradable, fine-mesh polyethylene bags and buried within 2 cm of the soil surface. This experiment utilized the same achene collections as the demographic experiment described below. Ten bags of achenes were buried each month from August to December near the corresponding demographic plots. In this experiment and in the demographic experiment described below, unfilled and damaged achenes were not used. Tests using tetrazolium blue indicated 92–99% viability for the achenes used in the experiments. One bag of each achene type from each of the five burial dates was retrieved on seven separate dates over a 2-year period. Achenes were then placed on moist sand in seed trays at room temperature on a laboratory bench and scored for germination after seven days. Viability was then determined for any ungerminated achenes using the visual criteria described above.

Demographic experiment

Fine-mesh netting was hung around a 13 × 11 m area of a natural *H. latifolia* population in the garden at the University of Texas Brackenridge Field Station in Austin, Texas in the summer of 1977 to inhibit seed movement into the area. Flowering individuals

of *H. latifolia* were removed regularly from the protected area. In each of 5 months during the fruiting season (August–December) freshly produced achenes were planted in four randomly-located replicate plots in the protected area. In addition, seed collected in August and stored in the laboratory was sown in the third and fifth months (to enable a distinction to be made between the effect of sowing date and the time of achene maturation). In each plot, thin layers of soil were removed in strips (to eliminate the existing seed bank) and replaced with sifted sand containing no *H. latifolia* achenes. Each 1 × 1-m plot consisted of five rows, each planted with fifty ray achenes, and five rows, each planted with fifty disc achenes. Each month, four such plots were sown with pairs of ray and disc rows constituting five randomized blocks within each plot.

The germination date was recorded for all plants. From the time of germination, each individual plant was examined at about monthly intervals for size change, reproduction, and death. Heads were counted when they spread open to disperse the mature achenes. The dried receptacle is persistent and the number of fruiting heads is obtained unambiguously by counting and removing dried receptacles and spreading heads. The size of rosettes was calculated as the length times the width of the rosette.

The demographic results were analysed statistically with the program MANOVA of the Statistical Package for the Social Sciences, Version 8.3 (Hull & Nie 1981). In keeping with the experimental design, achene type and sowing date were treated as fixed effects. The replicate plots were treated as random effects nested within sowing dates and the pairs of ray and disc rows were random blocks nested within plots. Analyses with unequal cell frequencies were based on unique sums of squares in order to test only the independent effects of each variable and not effects due to correlations among variables (see Hull & Nie 1981). In order to obtain homogeneous variances, analyses of percentage germination and percentage survival were performed on arcsine-transformed data and analyses of size and reproduction on log-transformed data. Reproduction was found to vary significantly with the number of adults per row and the latter was used as a covariate in the analysis of reproduction. Germination, establishment, survival to reproduction and rosette size did not vary systematically with density. Coefficients of variation were calculated using the grand mean for the demographic variable in question and variance components calculated from the appropriate analysis of variance or covariance.

RESULTS

Seed bank

Both ray- and disc-seed banks declined during the major autumn period of germination in late October (Fig. 1) though the number of disc achenes declined more precipitously (Fig. 2). Carry-over of disc achenes between years was negligible while that of ray achenes was substantial. There was considerable spatial heterogeneity in number of both ray and disc achenes per sample as evidenced by the large 95% c.i. (the coefficient of variation was 81% for ray achenes and 165% for disc achenes).

Complementary data from the achene-burial experiment demonstrate a more rapid decline in the number of live disc achenes than of ray achenes (Table 1). The only disc achenes alive after 1 year came from the December sowing. Seasonal variation in the occurrence of enforced versus innate or induced dormancy is suggested by the fact that the percentage of the retrieved viable achenes which readily germinated in seed trays was highest each autumn during the normal germination season.

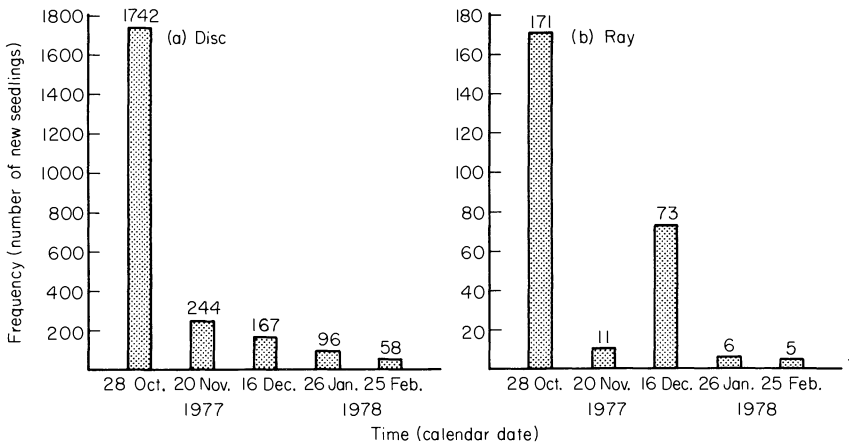


FIG. 1. Number of new seedlings derived from an experimental seed bank of (a) 7000 disc and (b) 7000 ray achenes sown in a natural population of *Heterotheca latifolia* at Austin, Texas.

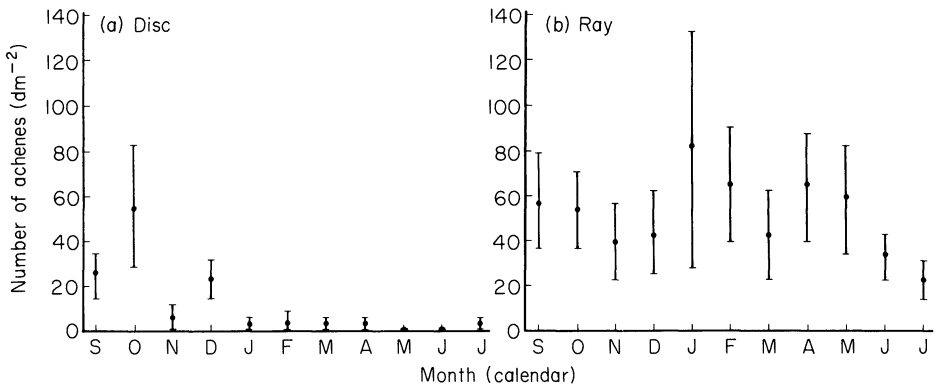


FIG. 2. Changes in mean number (with 95% c.l.) of (a) disc and (b) ray achenes per dm^{-2} in the soil seed bank each month for 1 year in a population of *Heterotheca latifolia* at Austin, Texas.

TABLE 1. Survival (% of viable achenes) of disc and ray achenes of *Heterotheca latifolia* buried in a population at Austin, Texas, and subsequent germination (% of viable achenes) after retrieval on the dates indicated, when watered for a week in seed trays. Each value is the mean or median of five samples of fifty achenes each, each of the samples having been planted on one of five dates between August and December.

| | Date of retrieval | | | | | | |
|---------------------|-------------------|----------|---------|-------------|------------|----------|--------------|
| | 13 December | 16 March | 26 June | 12 November | 9 February | 19 April | 17 September |
| Ray achenes | | | | | | | |
| mean survivorship | 66.0 | 47.8 | 52.4 | 23.6 | 10.4 | 14.0 | 18.5 |
| median survivorship | 64.0 | 46.0 | 58.0 | 24.0 | 10.0 | 16.0 | 16.0 |
| germination | 18.8 | 22.1 | 22.9 | 66.0 | 62.5 | 0.0 | 81.1 |
| Disc achenes | | | | | | | |
| mean survivorship | 54.4 | 32.2 | 37.2 | 8.4 | 4.8 | 5.2 | 0 |
| median survivorship | 54.0 | 28.0 | 34.0 | 0 | 0 | 0 | 0 |
| germination | 73.5 | 44.4 | 25.1 | 90.5 | 100 | 7.7 | — |

Germination

The average germination of 'fresh' achenes (those sown in the month of their production) was 30.5% for disc and 4.1% for ray achenes (Table 2). However, sowing date affected ray and disc achene germination differently ($P < 0.001$ for achene type by sowing date interaction). Among disc achenes, those sown in October had the highest germination. Yet only the early-produced and sown ray achenes (August and September) exceeded 1% germination (Table 2). Considerable variation in germination was found among rows of the same plot and among replicate plots (Table 3).

Achenes produced in August and sown when fresh germinated in October with the first substantial rains of the season. Thus they are similar to achenes from the same harvest that were stored in the laboratory for 2 months and sown in October just before the rains. The ray achenes sown in August had higher germination percentage than those stored in the laboratory for 2 months (Table 2). However, disc achenes sown fresh in August showed lower germination than those stored in the laboratory for 2 months (the achene type by sowing date interaction was significant, $P < 0.01$). While ray achenes apparently lose dormancy faster in the field than in the laboratory, disc achenes either become more dormant or die in the field.

Achenes that were harvested in August and sown in October showed greater

TABLE 2. Percentage germination of ray and disc achenes of *Heterotheca latifolia* from an artificial seed bank, sown on different dates back into a natural field population at Austin, Texas. Values are based on sowings of 1000 achenes in each case. 'Fresh' achenes are those sown in the month of their production.

| Date sown | Germination (%) | |
|----------------|-----------------|------|
| | Disc | Ray |
| Fresh achenes | | |
| August | 30.4 | 12.3 |
| September | 42.2 | 6.2 |
| October | 48.5 | 0.7 |
| November | 25.5 | 1.1 |
| December | 5.8 | 0.1 |
| August achenes | | |
| October | 71.5 | 6.1 |
| December | 7.4 | 0.2 |

TABLE 3. Coefficients of variation (C.V.) for total germination percentage, percentage survival to reproduction, and total reproduction for plants of *Heterotheca latifolia* grown from achenes sown on different dates between August and November into a natural field population at Austin, Texas. Significant differences between plots within dates and between rows within plots for each achene type are shown as: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For survival and reproduction, ray C.V. is based on within-date variation for only two planting dates because very few ray achenes germinated from late plantings. Ray C.V. is thus not directly comparable with disc C.V. which is based on four dates. Significance tests are not possible at the lowest hierarchical level (rows for germination and survival, individuals for reproduction).

| | Individuals | | Rows | | Plots | |
|--------------|-------------|------|------|------|-------|---------|
| | Ray | Disc | Ray | Disc | Ray | Disc |
| Germination | — | — | 65.5 | 29.7 | 42.1* | 19.1* |
| Survival | — | — | 66.8 | 36.0 | N.S. | 24.7*** |
| Reproduction | 34.8 | 32.4 | N.S. | 4.2* | N.S. | 10.2** |

germination than achenes harvested and sown in October ($P < 0.05$). Since these achenes were sown at the same time, the germination differences must be due either to dormancy imposed at time of production or by a loss of dormancy with age. Since laboratory germination experiments have shown that ray achenes lose dormancy with age, but disc achenes do not (Venable & Levin 1985), we conclude that disc achenes produced at different times during the fruiting season possess different dormancy characteristics.

The rates of germination can be compared by considering the proportion of germination that occurred within 10 days after the first rains of the season. For disc achenes this proportion increased from 71% for August-sown achenes to 86% for September-sown achenes and 98% for October-sown achenes ($\chi^2_2 = 120$; $P < 0.001$). The proportion of ray-achene germination that occurred in the first 10 days was 68% for those sown in August, 63% for September and 57% for October ($\chi^2_2 = 0.94$; $P > 0.5$). Thus disc achenes germinated faster than ray achenes, and fresh disc achenes germinated faster than older disc achenes.

Survival

Because few seedlings germinated from late-sown ray achenes (October onward), comparisons of survival of plants from ray and disc achenes (hereafter called ray and disc plants, respectively) deal only with the first two planting dates (August and September). Comparisons over all planting dates only consider disc plants (plants from December-sown disc achenes were also omitted due to low germination). Survival to reproduction did not vary with the density of plants per row for any individual treatment nor when the treatments were combined. The mean survival to reproduction for ray seedlings from the first two planting dates was slightly less than that for disc seedlings ($P = 0.077$, Table 4) and survival was less for ray than disc seedlings in seven out of eight plots ($P < 0.05$, sign test). Differences due to the date of sowing and plot were not significant, nor was the interaction of achene type with sowing date. Sowing date, however, had a significant effect on survival to reproduction when disc seedlings from all four dates were compared ($P < 0.05$); those from October had lower and those from November had higher survival than August- and September-sown achenes. The variation in survival within the 11×13 m study area and within the 1×1 m plots is indicated by the coefficients of variation (Table 3).

Reproduction

Unlike germination, survival and rosette size, reproductive behaviour was influenced by the density of plants per row (Fig. 3). Regressions of the number of flowering heads per

TABLE 4. Percentage of germinated achenes surviving to reproduction, mean number of mature heads per adult, and rosette size on 25 February for plants of *Heterotheca latifolia* grown from achenes sown on different dates between August and November into a natural field population at Austin, Texas. Numbers in parentheses are sample sizes (number of plants). Mean number of heads per plant was adjusted to remove the effect of density (measured as the number of adults per row).

| | Survival (%) | | Heads per adult | | Rosette size (cm ²) | |
|-----------|--------------|------|-----------------|----------|---------------------------------|----------|
| | Disc | Ray | Disc | Ray | Disc | Ray |
| August | 52.7 | 42.2 | 10.7 (164) | 9.6 (52) | 4.0 (199) | 3.0 (59) |
| September | 53.7 | 39.8 | 12.2 (227) | 8.2 (10) | 7.4 (275) | 5.4 (26) |
| October | 32.9 | — | 20.9 (166) | — | 12.0 (203) | — |
| November | 63.7 | — | 31.9 (107) | — | 15.0 (192) | — |

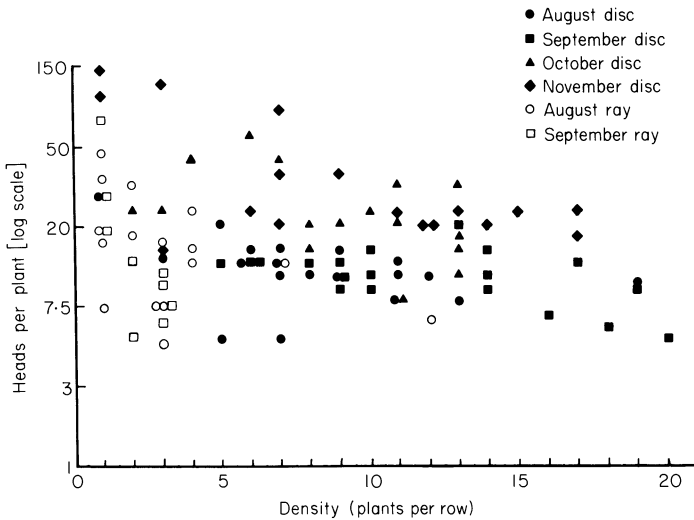


FIG. 3. Relationship between the number of fruiting heads per plant and density (number of adult plants per row) in an experimental population of *Heterotheca latifolia* at Austin, Texas. Row means are plotted for plants from ray achenes from the first two sowing dates and for plants from disc achenes from the first four sowing dates.

plant for plants from disc achenes for the four different planting dates were parallel (none of the possible non-parallel interactions were individually significant and r^2 only increased from 0.60 to 0.62 when all the possible interaction terms were included). To compare the reproduction of ray and disc plants we will assume that the same relationship of reproduction to density applies for ray plants as well. Since the data for ray plants are sparse at high densities, a statistical test of this assumption would be uninformative. However, it is reasonable to expect a similar slope and at worst an approximation to a slightly different negative density relationship for ray plants is produced.

For the first two planting dates, there were no significant differences in adult reproduction attributable to the unique effects of achene type ($P > 0.2$), sowing date ($P > 0.8$), or interaction ($P > 0.3$; Table 4). Disc achene behaviour shows the effect of later sowing dates on fecundity. Adult plants from October and November sowings had higher fecundities ($P \ll 0.001$) than adult plants from the first two sowing dates. Thus, the higher overall reproduction of disc plants was largely due to the success of plants from later sowing dates (few ray plants germinated from these sowing dates). The coefficients of variation for reproduction (with the variance attributable to density removed) are reported in Table 3.

Size

When plant size was assessed for the first two sowing dates, rosettes derived from disc achenes were bigger on 25 February than those derived from ray achenes ($P < 0.05$; unique effects model; Table 4). Rosettes from the second sowing date were bigger than the rosettes from the first sowing date ($P < 0.01$; unique effects model) and the interaction of sowing date with achene type was not significant. Rosettes derived from disc achenes from later sowings were progressively larger ($P < 0.001$).

Cohort analysis

The demographic consequences of being a ray or disc achene in the 1977–78 season can be more fully elaborated by a life-table analysis of cohorts of ray- and disc-derived seedlings. The largest cohort of seedlings, germinating between 15 October and 20 November (Fig. 1), represents 85% of all the disc and 72% of all the ray achenes which germinated. The probability of surviving to any age for this cohort (l_x) was lower for ray- than for disc-derived seedlings (Tables 5 and 6). Lower age-specific survivorship of plants from ray achenes was due to differences in seedling establishment. The probability of surviving any particular age interval, p_x , was almost identical for ray and disc plants at all

TABLE 5. Life table for ray achenes of *Heterotheca latifolia* from the main autumn germination cohort in a population at Austin, Texas.

| Age interval (days) $X-X'$ | Length of interval (days) D_x | Number surviving to end of interval N_x | Age specific survivorship l_x | Single interval survivorship p_x | Life expectancy* (days) E_x | Age specific fecundity (achenes per individual) b_x $l_x b_x$ | |
|-------------------------------|------------------------------------|--|------------------------------------|---------------------------------------|----------------------------------|--|-------|
| 0–48 | 48 | 147 | 1.000 | 1.000 | 140.8 | 0 | 0 |
| 48–90 | 42 | 69 | 0.469 | 0.469 | 226.5 | 0 | 0 |
| 90–120 | 30 | 58 | 0.395 | 0.841 | 223.4 | 0 | 0 |
| 120–162 | 42 | 53 | 0.361 | 0.914 | 213.1 | 0 | 0 |
| 162–208 | 46 | 50 | 0.340 | 0.943 | 182.6 | 0 | 0 |
| 208–242 | 34 | 50 | 0.340 | 1.000 | 136.6 | 15.3 | 5.2 |
| 242–284 | 42 | 50 | 0.340 | 1.000 | 102.6 | 129.5 | 44.1 |
| 284–324 | 42 | 46 | 0.313 | 0.920 | 67.7 | 475.6 | 148.8 |
| 324–359 | 35 | 41 | 0.279 | 0.891 | 31.4 | 318.4 | 88.8 |
| 359–440 | 41 | 15 | 0.102 | 0.366 | 20.5 | 0 | 0 |
| 400–440 | 40 | 0 | 0 | 0 | — | 0 | 0 |

$$*E_x = \frac{\sum_{y=x}^{\infty} D_y \left[\frac{N_y + N_{y'}}{2} \right]}{N_x}$$

TABLE 6. Life table for disc achenes of *Heterotheca latifolia* from the main autumn germination cohort in a population at Austin, Texas.

| Age interval (days) $X-X'$ | Length of interval (days) D_x | Number surviving to end of interval N_x | Age specific survivorship l_x | Single interval survivorship p_x | Life expectancy* (days) E_x | Age specific fecundity (achenes per individual) b_x $l_x b_x$ | |
|-------------------------------|------------------------------------|--|------------------------------------|---------------------------------------|----------------------------------|--|-------|
| 0–48 | 48 | 1238 | 1.000 | 1.000 | 203.3 | 0 | 0 |
| 48–90 | 42 | 924 | 0.746 | 0.746 | 217.4 | 0 | 0 |
| 90–120 | 30 | 770 | 0.622 | 0.833 | 214.6 | 0 | 0 |
| 120–162 | 42 | 703 | 0.568 | 0.913 | 203.7 | 0 | 0 |
| 162–208 | 46 | 635 | 0.513 | 0.903 | 181.2 | 0 | 0 |
| 208–242 | 34 | 628 | 0.507 | 0.989 | 139.0 | 8.9 | 4.5 |
| 242–284 | 42 | 623 | 0.503 | 0.992 | 103.9 | 178.5 | 89.8 |
| 284–324 | 42 | 583 | 0.471 | 0.936 | 67.6 | 620.9 | 292.4 |
| 324–359 | 35 | 501 | 0.405 | 0.859 | 33.3 | 422.6 | 171.0 |
| 359–400 | 41 | 200 | 0.162 | 0.399 | 22.0 | 69.9 | 11.3 |
| 400–440 | 40 | 7 | 0.006 | 0.035 | 22.9 | 7.3 | 0.0 |

* See footnote to table 5.

TABLE 7. Seedling establishment as percentage of germinating achenes and mean number of mature heads per plant for the main autumn germination cohort in a population of *Heterotheca latifolia* at Austin, Texas. Data are reported for plants derived from achenes produced and sown in different months. The number of heads per adult was adjusted to the same common density as in Table 4 (density was measured as the number of adults per row). Values in parentheses are sample sizes (number of plants).

| | Seedling establishment (%) | | Heads per adult | |
|-----------|----------------------------|------|-----------------|-----------|
| | Disc | Ray | Disc | Ray |
| August | 77.6 | 48.3 | 11.0 (111) | 11.2 (28) |
| September | 78.7 | 44.2 | 11.8 (181) | 8.6 (14) |
| October | 49.3 | — | 21.1 (163) | — |
| November | 97.0 | — | 32.4 (159) | — |

but the first census after germination. Though this cohort is defined by a similar germination time, the achenes involved were produced and entered the seed bank at different times. When only plants from this cohort were considered there was no significant difference in seedling establishment between the first two sowing dates (Table 7). Establishment from ray achenes was less than that from disc achenes in all seven plots ($P < 0.01$, sign test). Establishment was lower for October- and higher for November-produced disc achenes than for those produced in the first 2 months ($P < 0.005$).

The number of heads per individual was converted to an estimate of the number of achenes per individual from the mean head size, estimated from ten plants which produced 1038 heads in their reproductive lives. The mean number of achenes per head was 72.3 but only 71% filled to yield 51.2 viable achenes per head at maturity. Age-specific fecundity has roughly the same distribution for plants derived from ray achenes as for those derived from disc achenes except that the values for ray-derived plants are all about three-quarters those for disc-derived plants (Tables 5 and 6). Covariance analyses of reproduction for the plants from this cohort which correct for differences in density (number of adult plants per row), yield parallel results to the analysis presented above for all plants. There was no significant effect of achene type ($P > 0.4$), date ($P > 0.4$), or interaction ($P > 0.2$) for plants from the first two sowing dates, but fecundities were significantly higher for disc plants from later sowing dates ($P < 0.001$; Table 7). Thus, as in the prior analysis of all plants, the higher fecundity of disc plants in this cohort was largely due to the fact that disc achenes produced late the previous autumn became adults which produced many achenes while ray achenes produced late never germinated.

When the sum of values of $l_x b_x$ (Tables 5 and 6) is corrected to overall mean density (using a correction factor based on the difference in mean density for rows of ray and disc plants and the regression of total fecundity on number of plants per row calculated earlier) values of 634 achenes per disc seedling and 217 achenes per ray seedling are obtained. If achene maturation is taken as the beginning (and end) of the life cycle, then the expected contribution of a disc achene to the next year's seed bank is only 232 achenes because about two thirds of the disc achenes did not germinate or survive in the soil. Since 95% of ray achenes did not germinate the expected contribution of a freshly matured ray achene is 11.0 achenes. The survivorship of the ray achenes that never germinated must be added to this giving 11.3 achenes. Thus a freshly produced disc achene contributed approximately twenty times as many achenes to the following year's seed bank as a freshly produced ray achene.

Individual variation

Frequency diagrams of the number of flowering heads per individual are shown in Fig. 4 for ray and disc plants. The majority of seedlings produced no fruiting heads and a small proportion of plants produced a large number of fruiting heads. Disc plants had a

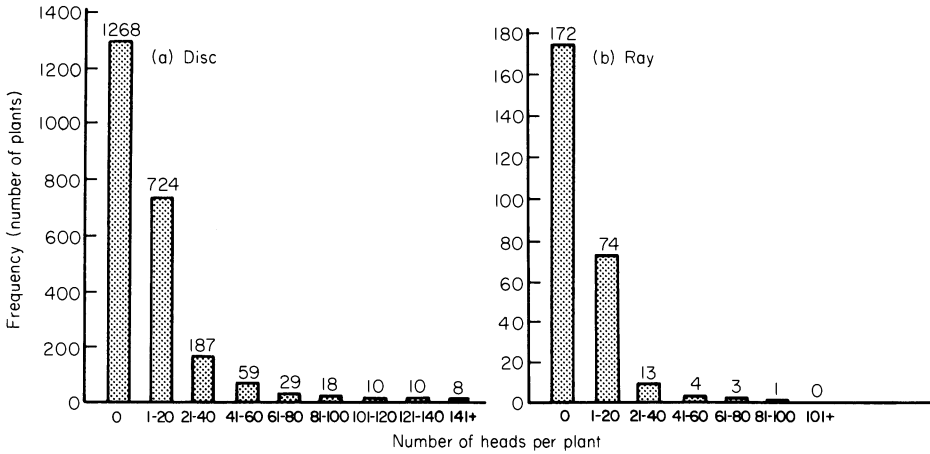


FIG. 4. Frequency distribution of plant fecundities expressed as the number of plants maturing a given number of fruiting heads for (a) plants germinated from disc achenes and (b) plants germinated from ray achenes in an experimental population of *Heterotheca latifolia* at Austin, Texas.

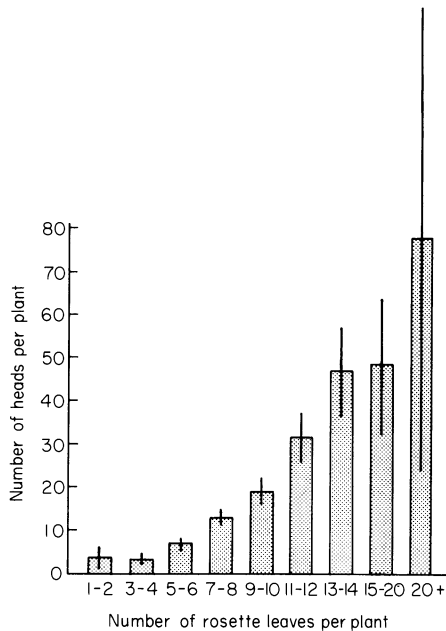


FIG. 5. Mean number of fruiting heads matured per plant (with 95% c.l.) for *Heterotheca latifolia* rosettes of different sizes in late February in a population at Austin, Texas.

relatively greater representation in the higher fecundity classes and a lower proportion of plants in the zero fecundity class than ray plants even though disc plants usually occurred at higher densities ($\chi^2_3 = 11.5$; $P < 0.01$).

Rosette size was significantly correlated to ultimate fecundity (Fig. 5). An analysis of variance revealed no significant differences in fecundity between ray and disc rosettes of the same size class, but the different size classes differed greatly (achene type, $P > 0.30$; number of rosette leaves, $P < 0.001$; interaction, $P > 0.60$). When the number of rosettes per row is used as a covariate, a significant but small proportion of the variation is explained by the covariate and the corrected means do not differ by more than one head per plant from those in Fig. 5.

DISCUSSION

Achene type has many effects on demographic performance in *Heterotheca latifolia* including seed bank dynamics, germination, survival and reproduction. The results reported here demonstrate higher germination, survival and reproduction for disc achenes but greater achene longevity for ray achenes. The following analysis indicates that disc achenes contributed much more to population growth than ray achenes but that achene longevity may play an important role in population growth rates especially if population size varies much from year to year.

The finite rate of increase, λ , may be defined as the number of achenes in next year's seed bank per achene in this year's seed bank. Thus, in addition to freshly produced ray achenes, those remaining from previous years must be considered. Thus population growth via ray (but not disc) achenes depends on whether the population was large or small in previous years. In order to calculate λ we will assume that the size of the previous year's seed bank was the same as that in the year measured and we will assume a 25% between-year carry-over for ray achenes in keeping with the seed bank data. Field and laboratory experiments suggest that older ray achenes have less dormancy than fresh ones (Venable & Levin 1985); indeed 66% of the ray achenes that survived 1 year in the field burial experiment reported here germinated after 1 week on moist sand in seed trays. Thus we might conservatively assume 20–50% germination of the viable old achenes under field conditions. Assuming that survival and reproduction of seedlings germinating from the ray achenes of previous years is the same as that of fresh ray achenes, then λ should equal 17.1–30.7 for ray achenes and 232 for disc achenes. Thus the contribution to growth is roughly seven to thirteen times greater for disc achenes. If the previous year's seed bank were larger than the number of new achenes in the seed bank, a larger proportion of the current year's plants would germinate from the ray achenes of previous years. This would reduce the difference in growth rate between ray and disc achenes. Thus seed bank behaviour and dormancy have important effects on population growth rates (cf. Venable & Lawlor 1980; Schmidt & Lawlor 1983).

The population growth rate in the year of this experiment was very high as might sometimes be expected for an annual plant characteristic of frequently-disturbed environments. *Heterotheca latifolia* is capable of rapid population growth because each individual produces a number of relatively small heads each with numerous small achenes. The planting conditions for this experiment provided an open habitat much like those that occur following disturbance events in the early successional environments in which *H. latifolia* normally grows. The garden site where achenes were collected and the experiment sown is frequently mown or ploughed, yet *H. latifolia* rapidly recovers when the land is

left undisturbed. If the site were to remain undisturbed for several years, *H. latifolia* would undoubtedly have a lower population growth rate in the face of increasing within- and between-species competition. Another factor favouring high population growth was the favourable weather in the year of this experiment. No achenes germinated until late October and there were no subsequent hot dry spells to cause high mortality and low fecundity.

Since disc achenes contributed so much more to population growth, why does *H. latifolia* continue to produce ray achenes? The greater dispersibility of disc achenes (Venable & Levin 1985) makes them more likely to encounter colonizable sites and their higher growth rate makes them better at filling such sites. In contrast, ray achenes buffer population decline and ensure persistence through the disturbances and catastrophic events typical of ruderal environments. The possession of both achene types is a 'high/low-risk strategy' (*sensu* Venable 1986) which protects the population from environmental variability. While production of only disc achenes would result in rapid population growth under favourable conditions, an annual plant without a seed bank is critically vulnerable to what happens under the worst conditions. A polymorphic strategy may actually have the highest geometric average growth rate because of the buffering provided by ray achenes under less favourable conditions (see Gillespie (1977) and Real (1980) on the importance of mean and variance in fitness). The question as to why *H. latifolia* produces both achene types is pursued further in Venable (1985, 1986).

Some of the specific results from this field study warrant further comment. Why was establishment lower for ray seedlings than for disc seedlings? No difference in growth rate of seedlings was found under laboratory conditions but an initial difference in nutrient capital resulted in disc seedlings being larger at any given age (Venable & Levin 1985). Such size advantages often play a role in differential seedling survivorship (e.g. Cook 1979; Grime & Jeffrey 1965). Our data do not exclude the additional possibility that subtle differences over a few days in germination time might also play a role.

Events that happen early in life such as germination, establishment and early growth are critical life history traits which are often important in determining fitness. In the experiment reported here, size hierarchies were well formed by February and fecundity could be accurately predicted by rosette size at that time (cf. Werner 1975).

Changes with time were important in determining the relative success of achene types at leaving offspring. Both ray and disc germination varied with date of seed maturation. Later-produced achenes had higher fecundity, yet hardly any ray seedlings germinated from late-produced achenes. This interaction of variation in germination with variation in fecundity was largely responsible for the superior fitness of disc seedlings. The tendency to consider annual plants as monocarpic obscures the potential demographic differences which may result from within-year variation in time of fruit maturation and release.

Substantial spatial variation in demographic behaviour was demonstrated in the experimental population. The reported levels of variation are large considering that the experimental site was chosen for its apparent uniformity and that the experimental technique should tend to reduce spatial variation. Understanding spatial variation in demographic variables is important to interpreting the significance of local dispersal (Platt 1976). Environmental variation in demographic variables is also important. It results in a slower evolutionary response to natural selection on life histories—spatial (environmental) variation will reduce heritabilities below values estimated under constant controlled conditions (Antonovics & Primack 1982). Significant within-population variation in demographic variables has also been reported in the field studies of Turkington & Harper

(1979); Fowler & Antonovics (1981), Schellner, Newell & Solbrig (1982), and Tremlett, Silvertown, & Tucker (1984).

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