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THE ECOLOGY OF SEED HETEROMORPHISM IN *HETEROSPERMA PINNATUM* IN CENTRAL MEXICO[1]

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Abstract. *Heterosperma pinnatum* is an annual composite that produces heteromorphic achenes, with the proportion of achene morphs varying geographically. Field, greenhouse, and laboratory experiments were used to examine the ecological consequences of the heteromorphism. Achenes were classified into three types based on morphology. Central, intermediate, and peripheral morphs, named for the positions occupied within the fruiting head, range in shape from long, thin-beaked achenes with barbed awns (central) to short wide achenes without beaks or awns (peripheral). Considerable within- and between-population phenotypic variation in achene and head characteristics was documented. Field experiments using artificial dispersal agents showed that central achenes are the most likely to adhere to animals and that the proportion of a population's achenes presented for dispersal that adhere depends on the proportion of central achenes produced in the population and on the proportion of achenes with adhesive awns. Once achenes had reached the ground, mean and median secondary dispersal distances were short (<20 cm). Central achenes lose innate dormancy earlier than peripheral achenes during the period between autumn achene production and the onset of the summer rainy season. Germination is inhibited by darkness, though darkness becomes less inhibitive at the onset of the germination season (earlier for central achenes). In the laboratory, peripheral achenes germinated over a slightly narrower range of temperatures than central achenes. Percent germination was greater for central than intermediate achenes, and for intermediate than peripheral achenes, in two natural germination events in the field. Seed bank samples indicated that few if any achenes remain dormant between years. No significant differences in the growth rates of young seedlings were found in the greenhouse. A demographic experiment documented trade-offs resulting from the dormancy differences: central achenes tended to germinate earlier than intermediate and peripheral ones, and early germination resulted in greater mortality, but survivors that had germinated earlier attained greater size and produced more seeds. Intermediate achenes, while intermediate in all components of fitness, had the highest total fitness. This was because they resembled peripheral achenes in germinating late and having high survival, but they resembled central achenes in having higher percent germination. The results of these experiments suggest that achene behavior ranges from "low-risk" (peripheral achenes) to "high-risk" (central achenes) within the progeny of a single individual, while individuals and populations vary in the proportion of offspring exhibiting each type of behavior.

Key words: Compositae; Heterosperma; *Mexico; reproductive biology; seed bank; seed dispersal; seed dormancy; seed heteromorphism.*

INTRODUCTION

When is it adaptive for a single plant simultaneously to produce different kinds of seeds? When environments vary in time, producing any one seed type may result in high year-to-year variance in success at leaving offspring. Population growth, a multiplicative process through time, is lowered when temporal variance in reproductive success is high (Gillespie 1977). The production of two seed types should decrease temporal variation in offspring success. Thus, theory suggests that seed heteromorphism is favored in temporally

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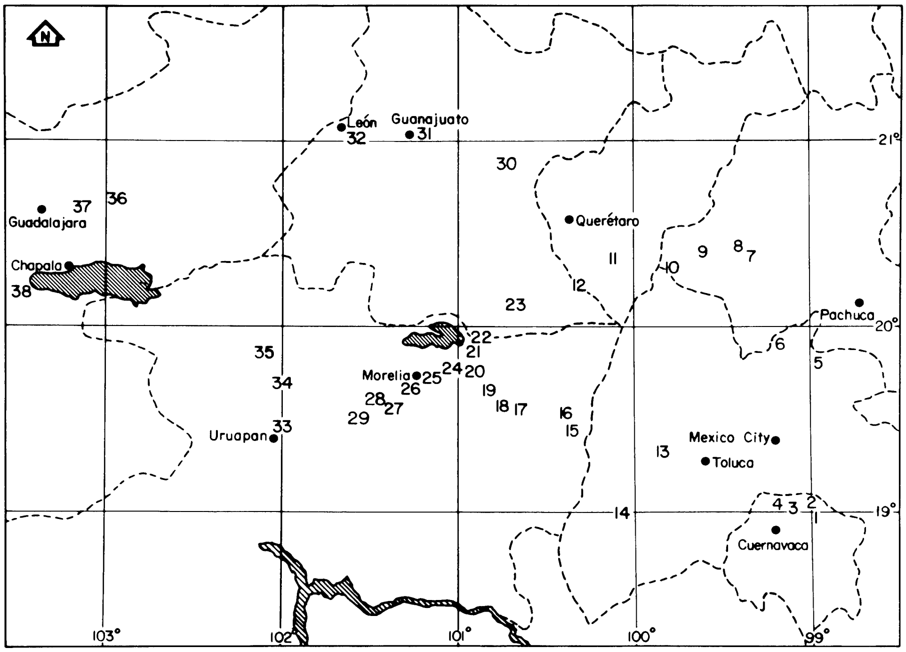

FIG. 1. Map of *Heterosperma pinnatum* population sites used in this study. The region shown is the Mesa Central and Volcanic Axis region of Mexico.

variable environments when variation in reproductive success is high for any single seed morph but lower under heteromorphism because morphs are successful under different conditions (Venable 1985). Lloyd (1984) showed that seed heteromorphism can also be favored by spatial heterogeneity in microsite availability to progeny if seedling success is microhabitat-specific and if greater allocation to either seed type results in diminishing fitness gains from that type because of local density dependence. In both of these scenarios each seed type must yield greater fitness at some time or place and thus types must differ ecologically.

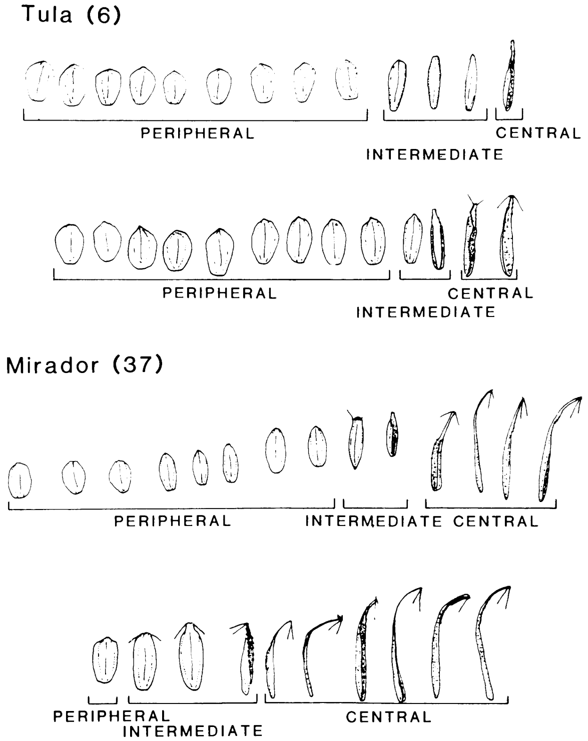

FIG. 2. Achene types for heads of two *Heterosperma pinnatum* individuals from Tula (site 6 on Fig. 1) and two from Mirador (site 37). Note the within- and between-population variation in proportion of achene types.

In light of the theoretical interest in differences among the seed types of heteromorphic species, documentation of such differences and their fitness consequences is desirable. In the present paper the achene heteromorphism in *Heterosperma pinnatum* Cav., an annual composite of Mexico, is described. Differences in dispersal and germination characteristics of achene types are reported, and the demographic consequences of achene differences are examined for one natural population.

MATERIALS AND METHODS

Species

Heterosperma pinnatum is an herbaceous summer annual found from southwest Texas to Arizona and south to Honduras. Achenes are produced in the autumn and remain dormant during the winter dry season. In central Mexico we have seen germination as early as February in response to exceptionally heavy rains, but achenes usually germinate at the beginning of the rainy season in April, May, or June. Plants begin to flower in August and September and most are dead by the end of November. *H. pinnatum* is commonly found in open or disturbed sites, frequently along road-

TABLE 1. Within- and among-population patterns of variation in achene and head traits for 32 populations of *Heterosperma pinnatum* from the Mesa Central and Volcanic Axis region of Mexico (see map, Fig. 1).

	Grand mean	Range of population means	Among-population variance	Within-population variance
Number of achenes per head	10.78	7.27–14.58	3.93	4.86
Central achenes				
Number per head	1.79	0.33–3.85	0.515	0.686
Percent per head*	17.1	3.0–43.9	57.8	62.7
Intermediate achenes				
Number per head	2.99	1.37–5.07	0.655	1.10
Percent per head*	28.3	11.9–46.9	54.2	76.9
Peripheral achenes				
Number per head	6.0	2.74–9.49	3.01	3.01
Percent per head*	54.6	29.8–79.3	84.1	94.2
Awned achenes				
Number per head	4.51	1.37–10.61	5.06	4.19
Percent per head*	43.4	11.5–99.0	493	290
Length of awns on longest achene (cm)	1.70	1.30–1.99	0.033	0.080
Length of longest achene (cm)	8.24	6.14–10.03	0.716	0.804
Awn length/achene length for longest achene	0.212	0.162–0.282	0.00097	0.0015
Mean mass of achenes (mg)				
Central	1.65	1.07–2.14	0.048	0.185
Intermediate	1.82	1.15–2.37	0.0853	0.194
Peripheral	2.17	1.41–3.00	0.194	0.354
Ratio of central : peripheral achene mass	0.80	0.601–1.05	0.0055	0.0252

* Percent of the total number of achenes in a head that are of the indicated type.

sides and occasionally in cultivated fields. In central Mexico it appears to be a permanent part of the natural vegetation in open savannas and in open vegetation on lava flows, but it is also abundant in pine–oak vegetation and other areas where it only occurs in disturbed sites. The populations investigated in this study are from the Eje Volcánico Transversal and Mesa Central (Fig. 1). The following eight sites are referred to by name and number in the text: Tlayacapan (site 1 on Fig. 1), Tlalnepantla (2), San Bartolo (5), Tula (6), Huichapan (9), Temascaltepec (14), Zitácuaro (15), and Mirador (37).

Variation in achene morphology

Achene morphology varies from the periphery to the center of each head and is not determined by floret type as in most Compositae with achene polymorphisms. We have grouped achenes into three "types" for experimental convenience (Fig. 2). Central achenes are long, very narrow, possess a beak, have little or no wing, and are usually 5 to 15 times as long as wide. Peripheral achenes are short, wide winged, concave, and usually at least half as wide as long. Intermediate achenes represent a range of morphologies including anything not conforming to the "pure" central or peripheral types.

Variation among individuals and populations

One complete fruiting head from each of 40 individuals was collected from each of 32 populations. Since achenes fall off readily at maturity, the fruiting heads were collected just prior to maturity, before the phyllaries deflexed. The first eight achene and head characters listed in Table 1 were scored for each individual. For 18 populations we weighed individual achenes from five heads, each from a different individual. Within- and between-population variances in achene and head characters were calculated from nested analyses of variance. A principal components analysis with varimax rotation was performed on the 18 population means. For three populations achenes were dissected and achene parts weighed.

Dispersal

To determine which achene and head characteristics had the greatest influence on adhesive dispersal potential, a dispersal index was calculated for 13 populations. This index was then regressed against achene and head characters. To calculate the index, the number of achenes adhering to an artificial dispersal agent was divided by the estimated density of mature (available for dispersal) achenes. The density of mature fruiting heads and achenes was estimated using the point-centered quarter method (Mueller-Dombois and Ellenberg 1974) in stands of *H. pinnatum.* Distances were measured to 80 mature heads at 20 stations along a 4-m transect in each population. The heads were collected to estimate the number of achenes presented for dispersal. After density was estimated, a ball of cotton string (8.5 × 8.5 cm) was moved along the same transect at inflorescence height (10–30 cm) and the achenes that adhered were counted. The population with the highest index was arbitrarily assigned a value of 1 and the indices for the other populations were corrected accordingly and thus have values between 0 and 1. To check whether the ball of string was saturated with achenes or whether any other nonlinearity was causing the index to vary systematically with transect length or achene density, the cumulative number of adhering achenes was counted every 20 cm in one population with a high index. To determine whether the ball of string differed in any fundamental way from animal fur, balls with the same dimensions were constructed from cow hair, rabbit fur, and sheep wool and three replicate transects were run with each dispersal agent at Tlalnepantla.

In another experiment dispersal on the ground was measured. In open disturbed sites (<10% cover) at Zitácuaro (site 15 on Fig. 1) and Tlalnepantla (2) and in a dense stand of grass (100% cover) at Tlayacapan (1), 100 each of central and peripheral achenes were marked with fluorescent paint and placed around a buried stake. After ≈40 d, achenes were collected from concentric 10 cm wide rings at night using an ultraviolet lamp.

Loss of dormancy

Since achenes are produced in the autumn but do not normally germinate until the following spring and summer, some form of winter dormancy must be in effect. To document this, a germination test was repeated in January, March, and June 1981 on achenes collected from the soil in a natural *H. pinnatum* site. Achenes were collected at Tlalnepantla (2) roughly 10 d prior to initiation of each test. Two replicates each of 50 central and 50 peripheral achenes were sown in agar in Petri dishes on each date (achenes of intermediate morphology exhibit intermediate dormancy properties and were frequently omitted from this and other germination tests to simplify the experimental design). The Petri dishes were placed on a laboratory bench at room temperature (≈20°C) and germination was scored every 2 d for 2 wk. In this experiment and the ones described below, unfilled or damaged achenes were discarded. We have repeatedly found that mature filled achenes of each morph have >95% viability (as indicated by tetrazolium staining and/or visual inspection of embryos). Likewise, >95% of soil-collected achenes that are firm and intact are viable regardless of morph.

Germination in light and dark

This set of experiments documented the responses of achene types to light and dark from the time of achene dispersal to the onset of the rainy season. Achenes from San Bartolo (5) were tested in November 1980, May 1981, March 1982, and December 1982. Achenes were collected from 10 d to 2 mo before testing (thus March and May achenes were collected from the soil). On each date, three agar-filled Petri dishes with 50 central achenes and three dishes of 50 peripheral achenes were wrapped in cellophane. An identical set of petri dishes was wrapped in aluminum foil. The dishes were placed on a laboratory bench at room temperature for 2 wk, then all were opened and scored for germination. These experiments also supplement the previous ones documenting the loss of dormancy during the dry season.

Germination response to temperature

To determine the effect of temperature on germination, achenes were sown in agar in test tubes and placed in a constant temperature germinator at 4°, 12°, 20°, 28°, and 36°. Achenes from San Bartolo (5), collected 21 September 1980, and from Zitácuaro (15), collected 15 November 1980, were sown on 8 May 1981. Four replicates of 25 central and 25 peripheral achenes from each population were incubated at each temperature.

Germination in the field

Natural germination was monitored at the San Bartolo (5) field site. The achene type was determined by the shape of the cotyledons, which conform to the inner dimensions of the pericarp. Thus the long, thin, central achenes have long, thin cotyledons. In a blind test in the greenhouse, D. L. Venable was able to correctly identify 93% of randomly sown seedlings as to type. On 26 April and 23 June (after each of the two major germination flushes in 1981) seedlings were classified as to type. Then the top 5 cm of soil was removed and sifted, and ungerminated achenes were counted (a 236-cm^2 plot was used in April and a 157-cm^2 plot in June). Ungerminated achenes were opened and judged viable if normal fleshy embryos were present. Percent germination of each achene type was determined from the number of seedlings and the number of ungerminated achenes.

Seed bank dynamics

To see if viable seeds survive between years, 30 soil samples (78 cm^2 each, 5 cm deep) were collected from San Bartolo and 30 from Zitácuaro on 27–28 April, 3–5 June, 4–13 August and 21 October 1980. Achenes were removed and scored for viability.

Seedling growth

To compare the growth of seedlings from central and peripheral achenes, 60 each of central and peripheral achenes from San Bartolo (5), Tula (6), Zitácuaro (15), and Temascaltepec (14) were sown in agar. An initial harvest was made when the cotyledons first emerged from the pericarp (after radicle expansion) and four additional harvests were made at 1-d intervals. The seedlings (with radicles intact) were oven-dried at 80° for 24 h and stored in a silica desiccator until weighed.

TABLE 2. Factor loadings for between-population variation in seed and head characters of *Heterosperma pinnatum*. Varimax rotation was performed on principal components.

	Factor 1	Factor 2	Factor 3
Number of achenes per head	0.101	0.915	0.119
Number of central achenes per head	0.283	−0.202	0.891
Number of peripheral achenes per head	−0.033	0.947	−0.130
Number of awned achenes per head	0.682	−0.248	0.342
Length of awn on longest achene	0.675	−0.154	0.446
Length of longest achene	−0.067	0.003	0.875
Mean mass of central achenes	0.951	0.057	−0.005
Mean mass of intermediate achenes	0.923	0.219	−0.150
Ratio of central : peripheral achene mass	0.087	−0.673	0.379

Due to small samples resulting from incomplete germination, the similar, nearby populations of Tula (6) and San Bartolo (5) were combined for analysis, as were those of Zitácuaro (15) and Temascaltepec (14). A linear model explaining the logarithm of seedling dry mass using age, achene type, and population was fitted by least squares to the data.

Demographic behavior

Three hundred each of central, intermediate, and peripheral achenes were sown between 31 March and 2 April 1981 at the Tlalnepantla (2) field site. The achenes were collected from the soil during the previous month and were representative of the natural seed bank. Thirty-six 50-cm rows of 25 achenes each were sown in 12 groups of 3 rows, 1 of each achene morph. Only firm, intact achenes were used. Before sowing, thin strips of soil 5–7 cm wide were removed from each row and replaced with soil from the same site that contained no achenes. A gap of 20 cm of natural vegetation was left between rows, insuring that plants of adjacent rows did not come into contact. Rows were scored at weekly intervals for germination, size changes, reproduction, and death of individual plants. After no more seedlings emerged, plants were censused at intervals of 2 wk or longer until death. Reproduction (number of fruiting heads) was unambiguously scored since receptacles are persistent even after achene dispersal. Size was measured as maximum canopy width. Several blocks were destroyed and the data presented in Results are averages of nine intact blocks (225 achenes of each type).

RESULTS

Variation patterns

There was considerable variation in achene and head characters within and between populations (Table 1). For all traits, the between-population variance was significantly greater than 0 (i.e., population means differed significantly; nested ANOVA, $P < .01$). The large variation among populations in the proportion of central (3–44%) and peripheral (30–79%) achenes and the proportion of achenes with awns (11–99%) are particularly notable. For most characters, variance within populations was slightly greater than the variance of population means.

A principal components analysis demonstrates correlated variation among achene and head traits. Eighty percent of the among-population variation in the achene and head characteristics was explained by three components. Achene mass, length of awns, and number of awned achenes load heavily on one axis (Table 2). The second axis is heavily weighted by the total number of achenes per head and the number of peripheral achenes per head; the ratio of central to peripheral achene mass has a heavy negative loading on this axis as well. The third axis represents the length and number of central achenes. Thus, achene mass and the number and development of awned achenes were correlated among populations, but varied independently of the number of achenes per head and the number of peripheral and central achenes. Populations with more achenes per head tended to have more peripheral achenes and peripheral achenes that weighed more relative to central achenes. The number and size of central achenes varied independently of the other variables.

Achene mass

Among the 18 populations for which whole achenes were weighed, populations that produced a small proportion of central achenes had central achenes that weighed less relative to peripheral achenes (correlation between percent central achenes and the ratio of the mass of central achenes to the mass of peripheral achenes: $r = 0.62$, $P < .01$). The proportional allocation to pericarp, embryo, beak, and pappus was fairly constant among populations for each achene type (Fig. 3). Other achene and head traits differed substantially among the three populations for which achene parts were weighed. Heads from Mirador (37) averaged 8.6 achenes per head, of which 45% were central achenes and 54% were awned. San Bartolo (5) averaged 11.8 achenes per head, 19% of which were central achenes and 54% of which were awned. Huichapan (9) was similar to San Bartolo, with an average of 11.5 achenes per head, 18% of which were central achenes and 64% of which were awned. Central achenes had considerably more mass allocated to dispersal (beak and pappus) than the other achene types.

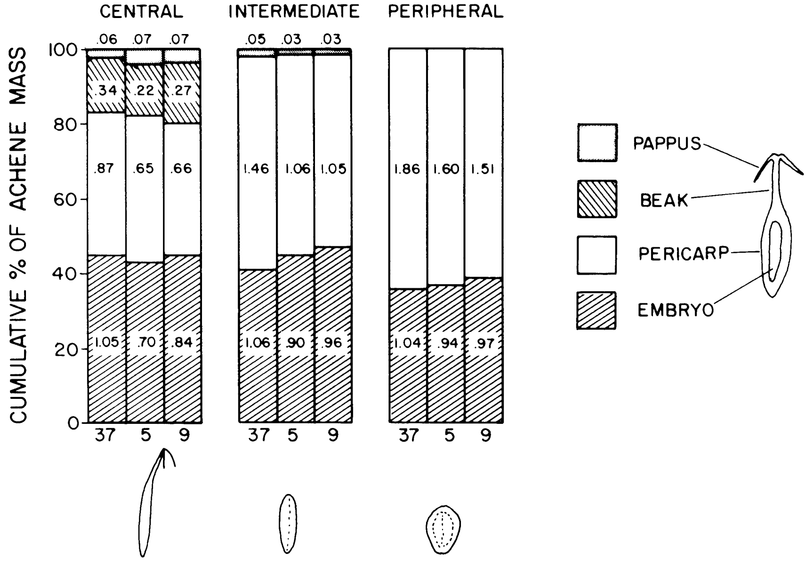

FIG. 3. Cumulative percentage of achene mass allocated to pappus, beak, pericarp (without beak), and embryo. Histograms represent cumulative percent of achene mass and the numbers are actual masses (in milligrams) for achene parts. The three populations illustrated are Mirador (site 37 on Fig. 1), San Bartolo (site 5), and Huichapan (site 9).

Dispersal

The number of achenes adhering to the ball of string was linearly related to distance, with little residual variation ($r^2 = 0.98$). This means that achenes did not saturate the collecting device over the transect length sampled. Thus the results should not vary in any nonlinear way with either achene density or the particular transect length (for lengths less than or equal to the one sampled).

Several lines of evidence other than morphology indicate that central achenes and other awned achenes are more readily dispersed adhesively than awnless peripheral achenes. The adhesive dispersal index was significantly correlated with percent central achenes per head ($r = 0.80$, $P < .01$; Fig. 4), percent peripheral achenes per head ($r = -0.71$, $P < .01$), and percent of achenes with awns ($r = 0.64$, $P < .05$). These variables were highly correlated among themselves, and when any one of them was entered initially into a multiple regression, the addition of any or both of the others did not significantly improve the fit. Because the peripheral achenes tend to fall from the heads shortly after maturing, the percent central achenes among achenes actually presented for dispersal was usually greater than the percent central achenes just prior to maturation (true in 11 out of 13 populations, $P < .025$, two-tailed sign test; means 26.5% vs. 20.7%). Also, the percent of adhering achenes that were central was usually considerably greater than the percent of presented achenes that were central (12 out of 13 populations, $P < .005$, two-tailed sign test; means 52.4% vs. 26.5%), suggesting that central achenes are more dispersible. While central achenes often made up two-thirds or more of the adhering achenes, in some populations they represented only 25% of adhering achenes. These latter populations tended to have few central but many awned achenes (correlation of percent central achenes among dispersed achenes with percent central achenes among awned achenes: $r = 0.66$, $P < .02$).

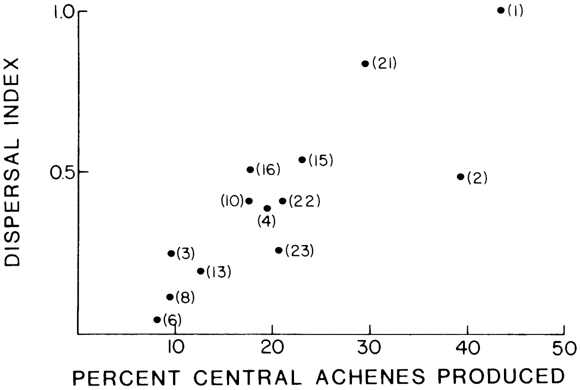

FIG. 4. A dispersal index (based on the percent of mature achenes that adhered to an artificial dispersal agent along a 4-m transect) plotted against the percent of central achenes produced in each of 13 populations (numbers identify the populations on Fig. 1).

There were significant differences in attachment of achenes to different dispersal agents, sheep wool being only 57% as effective as the ball of string at collecting achenes, rabbit fur being 34% as effective, and practically no achenes adhering to the cow hair (0.8% as effective as the ball of string; ANOVA results: achene type, $P < .001$; dispersal agent, $P < .001$). Despite these differences in total number of achenes attaching, there were no differences among dispersal agents in the proportion of different achene types attaching, as judged by the nonsignificant type × agent interaction in log-transformed data.

What happens once achenes reach the ground? At Tlalnepantla the mean dispersal distances were short and similar for the two achene types (central achenes: mean 18.5 cm, median 10–20 cm; peripheral achenes: mean 19.8 cm, median 10–20 cm). A Wilcoxon rank sum test was significant ($P < .02$) indicating that the probability of a peripheral achene going farther than a central achene is $> 1/2$. As can be seen in Fig. 5, most peripheral achenes did go farther than most central achenes. Yet the mean dispersal distances did not differ (randomization test, $P > .5$). The results of these two similar tests are discordant because the dispersal distances for the two achene types have distributions with different shapes (skew: 3.1 for central vs. 1.2 for peripheral; kurtosis: 12.5 for central vs. 5.1 for peripheral). Adhesive central achenes tended to stay close to the point of contact but a few moved out some distance, whereas peripheral achenes moved intermediate distances (Fig. 5). At Zitácuaro, the dispersal distances of central and peripheral achenes were again short, though the peripheral achenes did move significantly farther (central achenes: mean 12.0 cm, median 0–10 cm; peripheral achenes: mean 20.3 cm, median 10–20 cm; randomization test, $P < .02$; Wilcoxon rank sum test, $P < .003$). Again the skew was greater for central achenes (1.45 vs. 0.97) and the distribution of central achenes was slightly more leptokurtic (kurtosis: 4.2 vs. 3.6). Only 47% of central and 36% of peripheral achenes in Zitácuaro and 72% of central and 57% of peripheral achenes in Tlalnepantla were recovered. Since the unrecovered achenes could have been buried, successfully dispersed to greater distances, eaten, or otherwise destroyed, some uncertainty regarding secondary dispersal remains. However, 100% of central and 90% of peripheral achenes were recovered from the dense grassy stand at Tlayacapan, where secondary dispersal was minimal. All achenes were recovered within 20 cm of the source, and dispersal distances did not differ (both central and peripheral achenes: mean 7 cm, median 0–10 cm).

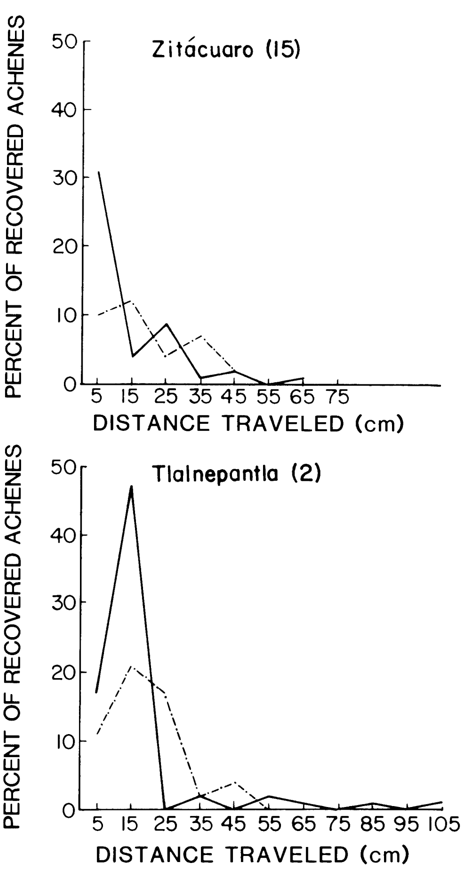

FIG. 5. Dispersal of marked central (——) and peripheral (-·-·-) achenes from a point source on the soil at two low-cover disturbed sites.

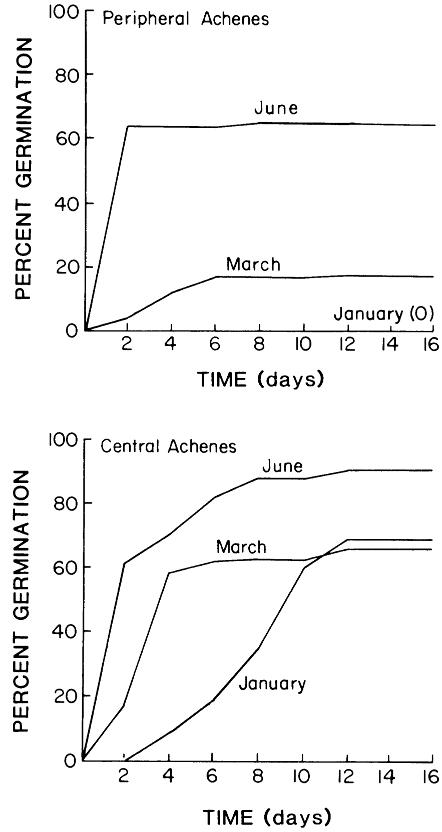

FIG. 6. Results of a germination experiment repeated at different times between the dispersal season and the onset of the rainy season with achenes from Tlalnepantla (site 2 on Fig. 1) collected from the soil 10 d prior to each of the three germination tests. Seeds were germinated in light.

Loss of dormancy

Loss of dormancy between the time of seed set and the onset of the rainy season was more rapid for central than for peripheral achenes (Fig. 6). For central achenes, germination rates differed among sowing dates, as indicated by the significant differences in arcsine proportional germination at day 4 (ANOVA, $P < .04$).

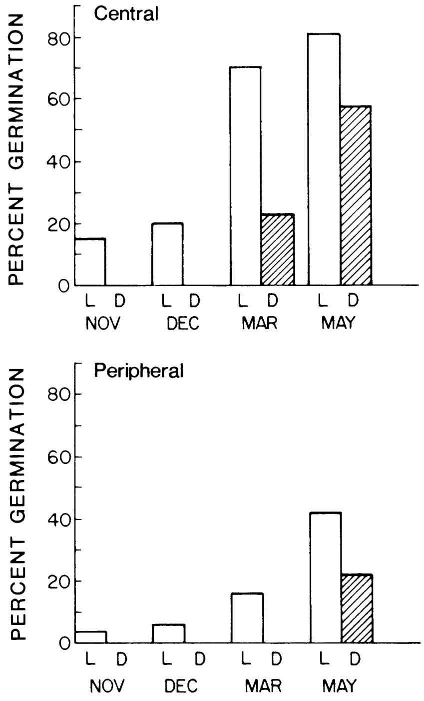

FIG. 7. Germination of achenes from San Bartolo (site 5 on Fig. 1) in light (L) and dark (D) at various times during the period from achene production until the beginning of the rainy season.

Yet total germination (after 2 wk) was not significantly different among dates, indicating that, given enough time, central achenes can germinate on any of these dates. For peripheral achenes, the germination differences among sowing dates were significant after 4 d and after 2 wk ($P < .005$), reflecting the innate dormancy which is in effect until just before the rainy season.

Germination in light and dark

The light/dark germination experiments confirm the earlier loss of dormancy by central achenes (Fig. 7). No peripheral achenes germinated in the dark treatment until May, but 23% of central achenes germinated in the dark treatment in March. Even in May, the proportional difference between germination rates in dark vs. light treatments was greater for peripheral than for central achenes, though this effect was not significant (ANOVA: achene types differ, $P < .001$; light differs from dark $P < .02$; but for the interaction of light and achene type, $P > .05$). The data suggest a tendency for darkness to inhibit the germination of peripheral achenes more than central achenes but this may just be due to the later loss of dormany of peripheral achenes.

Germination response to temperature

For achenes from both San Bartolo (5) and Zitácuaro (15) the variation in germination along the temperature gradient was greater for central than for peripheral achenes (variances of the distribution of germination rate at various temperatures were 74.3 vs. 42.6 for San Bartolo and 40.3 vs. 23.5 for Zitácuaro). The mean germination temperatures for achene types were very similar (16.7°C peripheral vs. 19.4° central for San Bartolo and 17.9° peripheral vs. 15.9° central for Zitácuaro; Fig. 8). An ANOVA of arcsine-transformed percent germination revealed that the effects of temperature, achene type, and population were all significant (in each case, $P < .001$). The significant achene type × temperature interaction ($P < .026$) confirms that central and peripheral achenes respond differently to temperature.

Germination in the field

Germination monitored in 1981 in the San Bartolo (5) field site was consistent with patterns observed in the laboratory (Table 3). In each germination flush, the percent germination of central achenes was higher than that of intermediate achenes, which in turn was higher than that of peripheral achenes. The absolute seed banks of the April and June plots are not directly comparable since the plot sampled in June had considerably higher achene densities than the plot destructively sampled in April. However, the proportions of achene types left

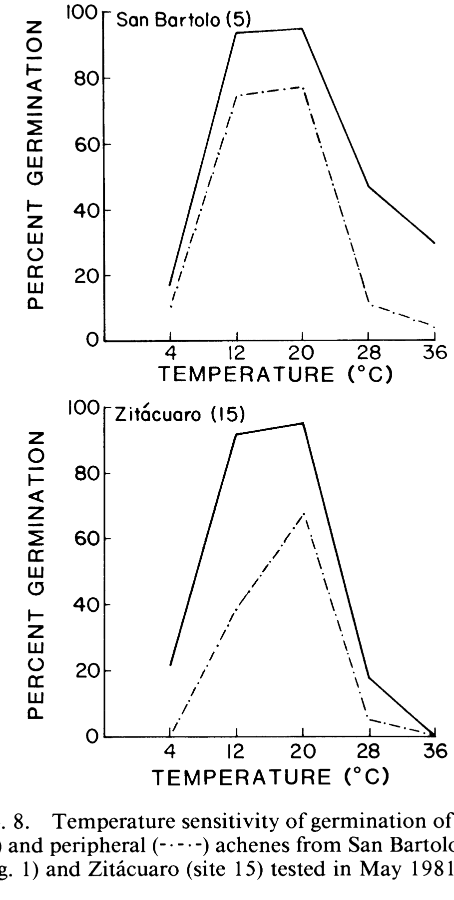

FIG. 8. Temperature sensitivity of germination of central (——) and peripheral (-·-·-) achenes from San Bartolo (site 5 on Fig. 1) and Zitácuaro (site 15) tested in May 1981.

after the April germination flush were very close to the proportions before the June flush: 55% vs. 53% for peripheral, 38% vs. 35% for intermediate, and 17% vs. 12% for central achenes.

Seed bank dynamics

The seed banks at San Bartolo (5) and Zitácuaro (15) showed similar behavior. Achene densities declined precipitously during the germination season and by early August the seed bank was essentially depleted (Fig. 9). In August, 1 viable peripheral achene was found in the 30 samples from Zitácuaro, while 7 were found in 30 samples from San Bartolo. To constitute a between-year seed bank these peripheral achenes would have to remain viable for 8 to 10 more months until the following germination season. The rise in the seed bank after August was due to production and release of new achenes.

Seedling growth

No significant differences or interactions were found for seedling size or growth rates between central and peripheral achene types or between populations. The average growth rate of these seedlings calculated from the regression slope of the logarithm of seedling dry mass on age was 17.7%/d ($P < .001$).

Demographic performance

Earliest germination at Tlalnepantla (2) in 1981 was registered on 24 April. A drought period followed and no further germination was registered until 4 June. Few new seedlings emerged after 11 June. The early germinating cohort involved 8 and 9% of all the peripheral and intermediate achenes that ever germinated, but 19% of the central achenes (Table 4). Only 16% of all seedlings emerging in April survived to reproduce, while 40% of the late germinators did. Although survival was lower for early germinating seedlings, survivors had roughly twice the canopy diameter of late germinating seedlings and produced twice as many fruiting heads. This reproductive difference was not enough, however, to offset the survival difference, so the expected fecundity of early germinating seedlings was slightly lower than that of late germinators.

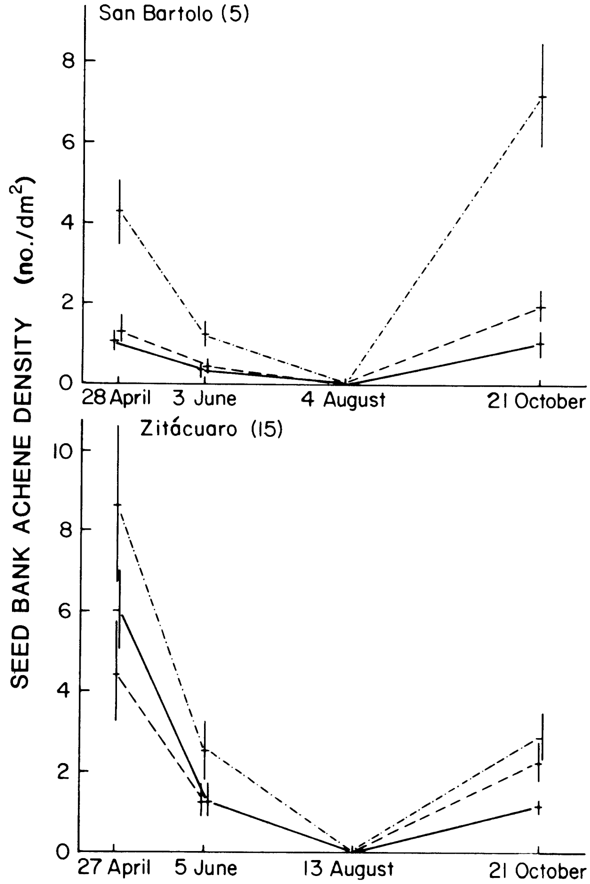

FIG. 9. Seed bank dynamics from the germination season until new fruit production at San Bartolo (site 5 on Fig. 1) and Zitácuaro (site 15) for central (——), intermediate (— — —), and peripheral (-·-·-) achenes in 1980. Vertical bars are ±SE.

The difference in survival between central and peripheral seedlings (28% vs. 47%, respectively) is larger than would be expected based only on time of germination and mean survival differences between early and late germinating seedlings. The conservative germination behavior of peripheral achenes probably improved survival in ways other than the division into early and late cohorts. However, it also resulted in only

TABLE 3. Percent of seed bank germinating in two natural germination flushes of *Heterosperma pinnatum* in 1981 at San Bartolo (site 5 on Fig. 1). After each flush, seedlings were classified as to achene type based on cotyledon shape, then ungerminated achenes were sifted from the underlying soil to determine the proportion of each type.

	Central achenes	Intermediate achenes	Peripheral achenes	χ^2_2
	26 April			
Number of achenes/dm^2 before germination	33.5	67.8	76.3	
Percent germinated	84.8	55.8	42.8	39.3***
	23 June			
Number of achenes/dm^2 before germination	27.4	77.7	117.2	
Percent germinated	95.3	50.0	32.1	57.3***

*** $P < .001$.

TABLE 4. Components of reproductive success for early- and late-germinating central, intermediate, and peripheral achenes of *Heterosperma pinnatum* at Tlanepantla (site 2 on Fig. 1) in 1981.*

	Central achenes	Intermediate achenes	Peripheral achenes	Total
No. achenes sown	225	225	225	675
Percent germination				
Early	8.4 (19.1)	3.6 (8.9)	2.2 (7.8)	4.7 (12.5)
Late	35.6 (80.9)	36.9 (91.1)	26.2 (92.2)	32.9 (87.5)
Total	44.0	40.5	28.4	37.6
Percent survival to reproduction				
Early	10.5	37.5	0	15.6
Late	32.5	39.8	50.8	40.1
Total	28.3	39.5	46.9	37.0
Size of plant at reproduction (cm)				
Early	16.5	8.7	...	11.8
Late	4.0	5.3	5.8	5.1
Total	4.6	5.5	5.8	5.3
No. heads per reproductive adult				
Early	17.5	13.7	...	15.2
Late	6.6	6.7	7.2	6.8
Total	7.4	7.3	7.2	7.3
No. of heads per seedling				
Early	1.8	5.1	0	2.4
Late	2.2	2.7	3.6	2.7
Total	2.1	2.8	3.4	2.7
No. heads per achene sown	0.96	1.16	0.96	

* Germination is reported as percent of achenes of a given type that were sown and (in parentheses) percent of achenes of that type that ever germinated. Survival is presented as percent of achenes of a given achene type that germinated. Size is mean maximum canopy width per plant surviving to reproductive maturity. Also reported are the mean number of heads produced per reproductive adult, per seedling germinated, and per achene sown.

65% as much total germination as for central achenes. Surviving plants from different achene types had roughly the same expected fecundity, so that expected fecundity at germination was highest for peripheral achenes (due to the survival differences). However, expected fecundity per achene sown was highest for intermediate type achenes. This was because they resembled peripheral achenes in having high survival given germination (they also germinate late like peripheral achenes), but approach central achenes in having high total germination. Thus, in this site in this year, intermediate dormancy behavior was favored.

DISCUSSION

Achenes of *Heterosperma pinnatum* produced within a head have a wide range of morphology. The variation in morphology is correlated with the differences in germination and dispersal summarized in Table 5.

The differences in the behavior of achene types can be interpreted in light of the habitat and life history of *H. pinnatum*. The rainy season represents both an opportunity and a challenge to *H. pinnatum*. The opportunity is provided by favorable temperature and moisture conditions for growth and reproduction; the challenge results from the fact that conditions are also favorable to other individuals of the same and different species. Since the exact onset of the rainy season varies from year to year, early spring rains may or may not have adequate follow-up rains to insure survival. Thus, early germination may reduce the probability of successful establishment and survival to adulthood. In the experiment reported here the late germinating achenes had more than a twofold survival advantage. Yet early germinators that successfully established became larger adults with higher rates of reproduction because they had more time to grow and were presumably better competitors (cf. Abul-Fatih and Bazzaz 1979, Venable 1984).

We suggest that the central achenes of *H. pinnatum* represent a high-risk component of the overall fruiting syndrome, since early loss of dormancy entails mortality risks. Yet in years when survival of early germinators is high, central achenes should result in high reproduction. Also, the greater adhesive dispersibility of central achenes results in a higher risk of landing in an unsuitable site but also in a greater possibility of locating superior habitats. Peripheral achenes, which lose dormancy later and have more restricted requirements for germination, represent a low-risk component of the syndrome, with a higher probability of successful establishment even in unfavorable years. Yet they are probably less likely to be dominant individuals in competitive size hierarchies.

How could natural selection favor the production of such a broad range of seed morphologies by single individuals? Fitness is a cumulative, multiplicative

TABLE 5. Summary of the differences in behavior of the two extremes of achene morphology of *Heterosperma pinnatum*. Morph types are shown in Fig. 2.

Central achenes	Peripheral achenes
Remain on the parent until dislodged	Fall rapidly from the head
More likely to adhere to dispersal agents	Less adhesive
Lose innate dormancy earlier	Do not lose innate dormancy until rainy season
Slightly broader temperature range for germination	Slightly narrower temperature range for germination
Germination inhibited by darkness, though less so at the onset of the rainy season	Germination inhibited by darkness, though less so at the onset of the rainy season
No between-year seed bank	No between-year seed bank
Behavior favors earlier germination and greater dispersal with attendant survival risks and opportunities for growth and reproduction	Behavior favors later germination and restricted dispersal with less survival risk but fewer opportunities for growth and reproduction

process through time and as such is sensitive to temporal variation (see Gillespie 1977 on the importance to fitness of temporal mean and variance in offspring number). While the production of more than one kind of seed will not increase the arithmetic average of yearly demographic success, it can increase the geometric average of this multiplicative process by producing a favorable combination of high arithmetic mean over time (e.g., central achenes of *H. pinnatum*) while insuring low temporal variance (e.g., peripheral achenes of *H. pinnatum*). Seed heteromorphisms can result in higher (geometric) average demographic success when expected fecundity varies considerably from year to year and the different seed morphs tend to compensate for each other's reproductive failures (Venable 1985). As an annual plant of open and early successional habitats with a variable onset of the rainy season, *H. pinnatum* must experience considerable year-to-year variation in reproductive success. The differences in morph behavior reported here make it likely that each morph will be more successful under some conditions, thus compensating for reproductive failures of the other morphs and lowering variance in parental reproductive success.

This species represents an example of the high-risk/low-risk (HRLR) seed heteromorphisms discussed by Venable (1985). HRLR heteromorphisms involve the marriage of a high-mean, high-variance morph with a low-mean low-variance morph. While few detailed studies of seed heteromorphism are available, most such investigations reveal HRLR heteromorphisms. When the heteromorphism involves subterranean and aerial fruits (e.g., Koller and Roth 1964, Weiss 1980, Cheplick and Quinn 1982), the subterranean fruits are larger and more tolerant of water shortage and competition. Though these subterranean fruits should provide reliable high reproduction, they are costly to produce. Aerial fruits are small, are produced in greater quantities, and are dispersed farther. Reproductive success per unit investment is likely to be higher, but lesser seed reserves and greater dispersal probably result in more year-to-year variation. In *Amphicarpum purshii*, a proportion of the subterranean fruits remain viable in the soil for a number of years, further reducing their fitness mean and variance. A species with a HRLR polymorphism that does not involve subterranean and aerial fruits is *Heterotheca latifolia* (Venable and Levin 1985). The disk achenes have less dormancy and more dispersal than the seed-bank-forming ray achenes. A cost-benefit analysis for *Heterotheca latifolia* is presented by Venable (1985) along with a list of other species that may have HRLR heteromorphisms.

Substantial differences exist among populations of *H. pinnatum* in the proportions of achene types produced. Populations with a high proportion of central achenes and/or a high proportion of achenes with awns tend to be found in sites where precipitation is higher, and the natural vegetation consist of large mesophytic plants with a closed canopy. In these habitats we would expect selection for dispersal because open sites for annuals are likely to be ephemeral. We would also expect selection for early germination because of the need to establish early to be successful in competition. In contrast, plants with a high proportion of peripheral achenes appear to be more frequent in the more arid sites, where the vegetation tends to be low and open, perhaps permitting more permanent occupancy. Dispersal may be of less importance in such open habitats and aridity makes early germination more risky.

Variation in the proportion of morphs occurs in other species with seed heteromorphisms. In plants with subterranean cleistogamous seeds and aerial chasmogamous seeds, the number of underground seeds is usually fairly constant, while the number of aerial seeds depends upon the size of the plant (e.g., Weiss 1980, Cheplick and Quinn 1982). In other species with cleistogamous/chasmogamous flowers, seed morph proportions vary with the proportion of floral types produced. This variation may correspond to the likelihood of successful outcrossing early or late in the season, or to position on the plant (Schemske 1978, Clay 1983). Variation in morph proportions has been reported in a number of species in which the seed heteromorphism appears to be caused by differences in the development rates of different seed tissues (Silvertown 1984). In these species the morph proportions sometimes vary genetically (Quinlivan 1971), and seasonal variation has been documented as well (e.g., Evenari et al. 1966).

In contrast to the species that show considerable plasticity in proportions of achene types, achene proportions in most heteromorphic composites are less variable since achene type is usually determined by floret type. Ray and disc florets usually have a fairly constant geometric arrangement, so achene proportions tend to follow suit. For example, in *Heterotheca latifolia* achene proportions vary with plant size (and corresponding head size) and change in a regular fashion through the reproductive season (Venable and Levin 1985). However, morph proportions seldom change more than 15%, being constrained by the floral geometry.

The range of variation in morph proportions among individuals and populations of *H. pinnatum* is large for Compositae. The fact that achene type is not determined by floret type frees morph proportions to vary independently of floret proportions. Quantitative genetics experiments have shown that this variation, both within and among populations, is under partial genetic control (D. L. Venable and A. Búrquez, *personal observation*), so selection may shift morph proportions independently of the selective factors impinging on floret proportions. This variation in achene morphology with correlated dormancy and dispersal consequences makes *H. pinnatum* an interesting system for investigating the evolution of seed ecology.

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