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POPULATION DYNAMIC CONSEQUENCES AND EVOLUTION OF SEED TRAITS OF *HETEROSPERMA PINNATUM* (ASTERACEAE)¹

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We summarize research on variation in achene morphology of *Heterosperma pinnatum*. Each flowering head has a broad range of achene morphologies. There is no between-year seed bank. There are no ecologically relevant differences in achene size, seedling size, or seedling growth rates of the different morphs. Achenes located centrally in the heads lose dormancy earlier during the period between autumn achene production and the onset (May–July) of the rainy season. This results in relatively more early emergence of central achenes. Awned central achenes also have greater adhesive dispersibility. Emergence, survival, and fecundity were measured for achenes sown into natural populations in central Mexico. When harsh conditions result in few seeds surviving to reproduce, the advantage tends to go to the more “conservative” peripheral achenes. Greenhouse experiments show a strong genetic component to the determination of achene proportions within and among populations and a variety of genetic correlations. Populations with a high proportion of awned achenes tend to be found in vegetation types where they are likely to be ephemeral. A high proportion of central achenes tend to be found in sites with little pre-rainy season precipitation. These patterns are interpreted in terms of selection for dispersal and the within-year timing of germination.

To understand the population dynamic consequences and evolution of seed structure and function it is useful to explore a system with variation in seed biology. Intra-specific variation, especially intrapopulation or intraprogeny variation, provides added control since much of the rest of the biology of the organisms involved is held constant. Thus when we measure the survival, growth, competitive, or reproductive consequences associated with different kinds of seeds we can indeed attribute the differences to the variation in seed structure or function (Venable, 1984). From an evolutionary standpoint, intrapopulation variation permits us to measure the fitness consequences of seed traits as well as the genetic basis of such variation. If populations vary, it is also possible to determine if population differentiation has followed patterns predicted by short-term observations of selective processes.

Seed heteromorphism provides a useful system for exploring the population dynamic consequences and evolution of seed traits. Seed heteromorphism is the production by single individuals of seeds of different morphologies or behaviors (Venable, 1985b). The functions that tend to vary with seed heteromorphism are within- or among-year timing of germination (e.g., *Grindelia squarrosa*, McDonough, 1975; *Hypochoeris glabra*, Baker and O’Dowd, 1982; *Senecio jacobaea*, McEvoy, 1984; *Heterotheca latifolia*, Venable and Levin, 1985b; *Hemizonia increscens*, Tanowitz, Salopek, and Mahall,

1987; and *Hedypnois rhagadioloides*, Kigel, 1992 [all Asteraceae]) dispersal (e.g., *Gymnarrhena micrantha* [Asteraceae], Koller and Roth, 1964; *Abronia* spp. [Nyctaginaceae], Wilson, 1976; *Picris echioides* [Asteraceae], Sorensen, 1978; *Agrostis hiemalis* [Poaceae], Rabinowitz and Rapp, 1979; Baker and O’Dowd, 1982; *Picris* spp. [Asteraceae], Ellner and Shmida, 1984; McEvoy, 1984; Venable and Levin, 1985a; Kigel, 1992; *Spergularia media* [Caryophyllaceae] Telenius, 1992), seed size related phenomena (e.g., competitive ability: *Heterotheca grandiflora* [Asteraceae], Flint and Palmblad, 1978; *Emex spinosa* [Polygonaceae], Weiss, 1980; *Heterotheca latifolia*, Venable, 1985a), survival and fecundity schedules (*Amplicarpum purshii* [Poaceae], Cheplick and Quinn, 1982; Venable and Levin, 1985b), and vulnerability to predation (*Eremocarpus setigerus* [Euphorbiaceae], Cook, Atsatt, and Simon, 1971). While such variation fades into the “normal” within-plant seed variation caused by the time of production and position on the parent plant (reviewed in Gutterman, 1992), there are many cases of dramatic seed heteromorphism with extreme and often discrete forms that demand further functional and evolutionary explanation (e.g., in Asteraceae: Zohary, 1950; Burt, 1977; and Brassicaceae: Voytenko, 1968).

Current explanations of seed heteromorphism are largely adaptationist. Variable seed functions are usually explained in terms of either bet-hedging (adaptive reduction in temporal variation in fitness at the expense of expected or mean fitness; Venable, 1985b), escape from the negative effects of density (Levin, Cohen, and Hastings, 1984; Ellner, 1985), or escape from the negative effects of sib competition (Schoen and Lloyd, 1984; Venable and Brown, 1993). Making more than one type of seed may achieve the reduction in temporal fitness variance characteristic of bet-hedging by ensuring that at least some offspring function appropriately in a variety of environmental cir-

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cumstances. Variable progeny may also result in escape from the negative effects of crowding in variable environments by being spread out in space or time (e.g., dispersive vs. nondispersive or dormant vs. nondormant seed types). Sib competition can be reduced by spreading offspring in space and time in such a fashion that they tend to interact less with relatives and more with non-relatives (regardless of whether any reduction in density is achieved or even whether density varies or not). This is a component of fitness that may favor heteromorphism above and beyond the general crowding effect. Environmental variability in time or space tends to enhance the selective advantage of multiple strategies, at least with regard to the first two factors (Venable and Brown, 1993).

Seed heteromorphisms have been shown to be more common in annuals, plants of arid and semiarid regions, and among weeds, although they are not restricted to such plants (Zohary, 1962; van der Pijl, 1972; Harper, 1977; Ellner and Shmida, 1984). A good example of some of these patterns is the genus *Cryptantha* (Boraginaceae) in western North America. This genus has been separated into two subgenera, one of which (*Oreocarya*) contains 57 species that are all perennial and have homomorphic nutlets. The other subgenus (*Krynitzkia*) consists of all annuals with 15 of the 67 species being heteromorphic and a "tendency" toward heteromorphism in the rest. The majority (73%) of the 15 heteromorphic species are desert plants, while only 23% of the homomorphic annuals are found in the desert (Johnston, 1925; Higgins, 1971, 1979). The predominance among annuals may be partly because seeds are their only venue for persistence. Perennial plants have perennation itself as a mechanism of persistence as well as a variety of options for vegetative spread and multiplication. So, for perennials, monomorphic seeds may represent one component of a multiple perennation/reproduction strategy. The predominance of seed heteromorphism among weeds and plants of arid regions has traditionally been interpreted in terms of the environmental variability inherent in these habitats (Stebbins, 1974; Harper, 1977).

While adaptation plays a prominent role in our explanations of seed heteromorphism, there is an important role for constraint, predisposition, and phylogenetic determinism. Dramatic seed heteromorphisms often occur in taxa where seeds on different parts of the plant have different preexisting constraints on their evolution, for example, ray vs. disk flowers in Compositae (McEvoy, 1984) or chasmogamous vs. cleistogamous flowers in grasses and other groups (Schemske, 1978; Campbell et al., 1983; Cheplick and Clay, 1989). In such groups there is a tendency for seed functions to diverge, each type specializing on some aspect of environmental variation to which it is predisposed while being buffered by the other seed type (Venable, 1985b).

In the present paper we use the variation in achene traits of *Heterosperma pinnatum* Cav., a seed heteromorphic composite, to examine the population dynamic consequences of seed variation and aspects of seed evolution. *Heterosperma pinnatum* is a self-fertilizing summer annual of the central highlands of Mexico extending as far north as southwestern Texas and southeastern Arizona and south to Central America. We will summarize the nature of within- and among-individual and popu-

lation variation, the functional and population dynamic consequences and the genetic basis of the variation, and patterns of population differentiation in seed traits.

VARIATION IN ACHENE MORPHOLOGY

Achene shape varies within fruiting heads with central achenes being long and thin, possessing an awned beak, while peripheral ones have no beak and are short and broad with lateral wings (Fig. 1). For simplicity we have classified achenes into three morphs using the following criteria: central ones are usually five to 15 times as long as wide, possess a beak, and have little or no wing; peripheral achenes are short, wide-winged, concave, and usually at least half as wide as long; intermediate achenes represent a range of intermediate morphologies not conforming to the pure central and peripheral achenes.

The proportion of central, intermediate, and peripheral achenes, and the proportion of achenes with awns, varies among plants within populations and among populations. This can be intuitively grasped by looking at drawings of actual achenes (Fig. 1) or computer-generated achenes drawn as ellipses using achene length and width measurements, and awn presence/absence (Fig. 2).

FUNCTION

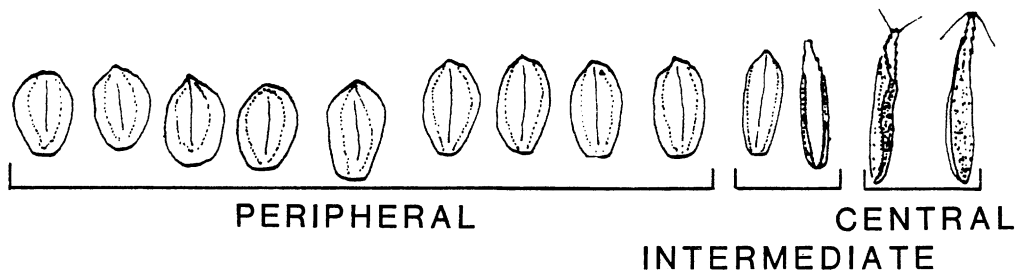
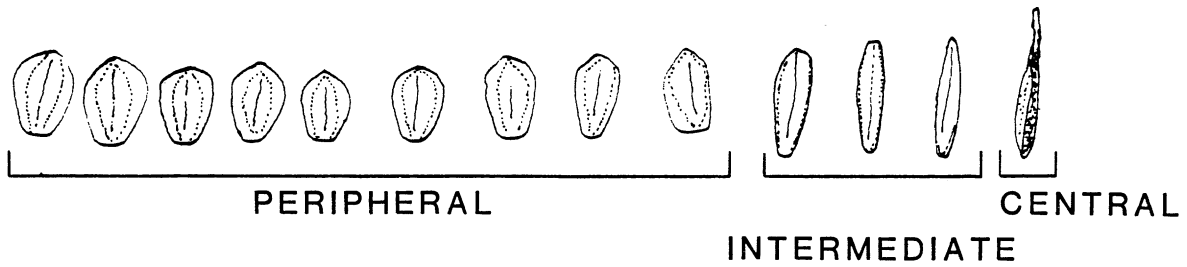
Three important aspects of the ecology of seeds are seed size, germination, and dispersal.

Seed size—Discussions of the ecology of seed size are frequently concerned with the amount of parental provisions available in the seed, normally contained in the endosperm or embryo tissues (Venable, 1992; Westoby, Jurado, and Leishman, 1992). In *Heterosperma*, despite the dramatic differences in seed shape, there are not dramatic differences in either the total biomass of individual achenes or embryo biomass (at maturity, composite achenes have no endosperm; Fig. 3). More importantly, in ecological terms, when achenes of different morphologies have been germinated at the same time, we have not found differences in seedling size, growth rate, or competitive ability (Venable et al., 1987).

Germination—Germination ecology includes two important aspects: the within-year and between-year timing of germination (Venable, 1989). Seed bank experiments carried out in two populations of *Heterosperma* have shown that seed banks diminish to zero during the germination season prior to the deposition of fresh achenes (Fig. 4; Venable et al., 1987). This result has been confirmed by experiments in which nylon mesh bags with achenes and soil have been left in natural populations and censused at various intervals throughout the year. Virtually no achenes survive to the subsequent germination season (Morales, 1986).

There are important differences between central and peripheral achenes in the within-year timing of germination. The life cycle of *Heterosperma* begins with the production of seeds in September–October. In the field they may germinate between March and July, depending on the availability of rains (on one rare occasion, seedlings were observed in February). Plants develop during the

Tula



Mirador

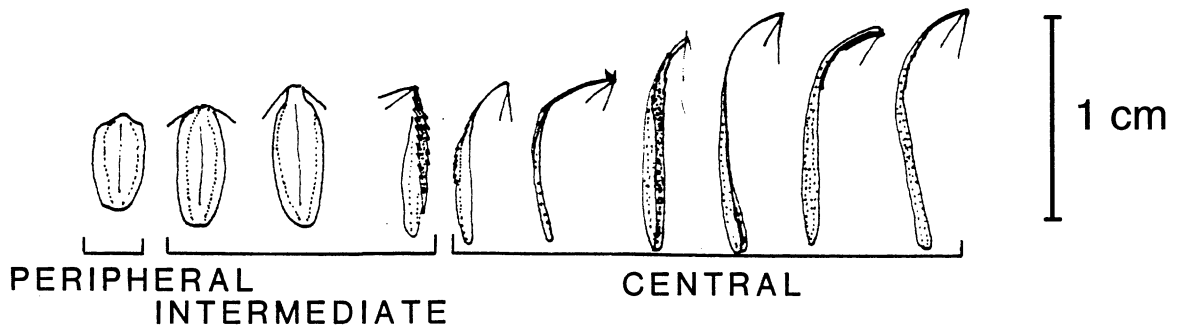
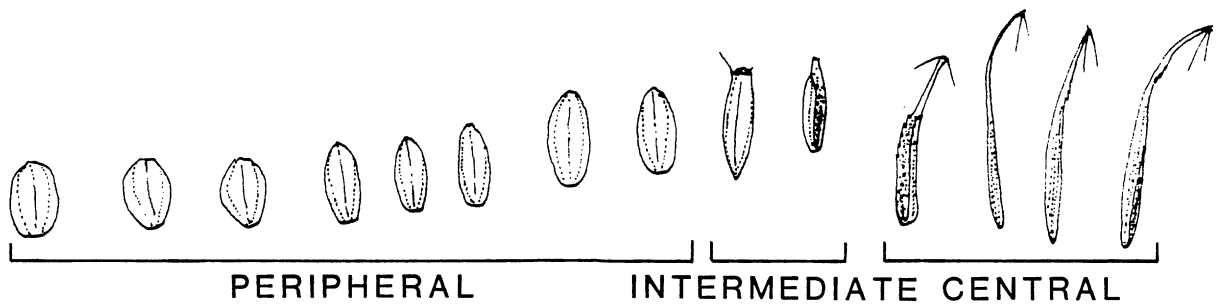


Fig. 1. Achene types from two heads of *Heterosperma pinnatum* from a field site near Tula, Hidalgo and two heads from a site near Guadalajara (Mirador).

summer rainy season and reproduce and die during late summer and fall. The newly produced achenes will not germinate under standard laboratory conditions due to innate dormancy (Venable et al., 1987). In January, cen-

tral achenes recently collected from the seed bank will germinate at a slow rate in agar-filled petri dishes, although they seldom receive sufficient moisture in the field in January and have never been observed to germinate then

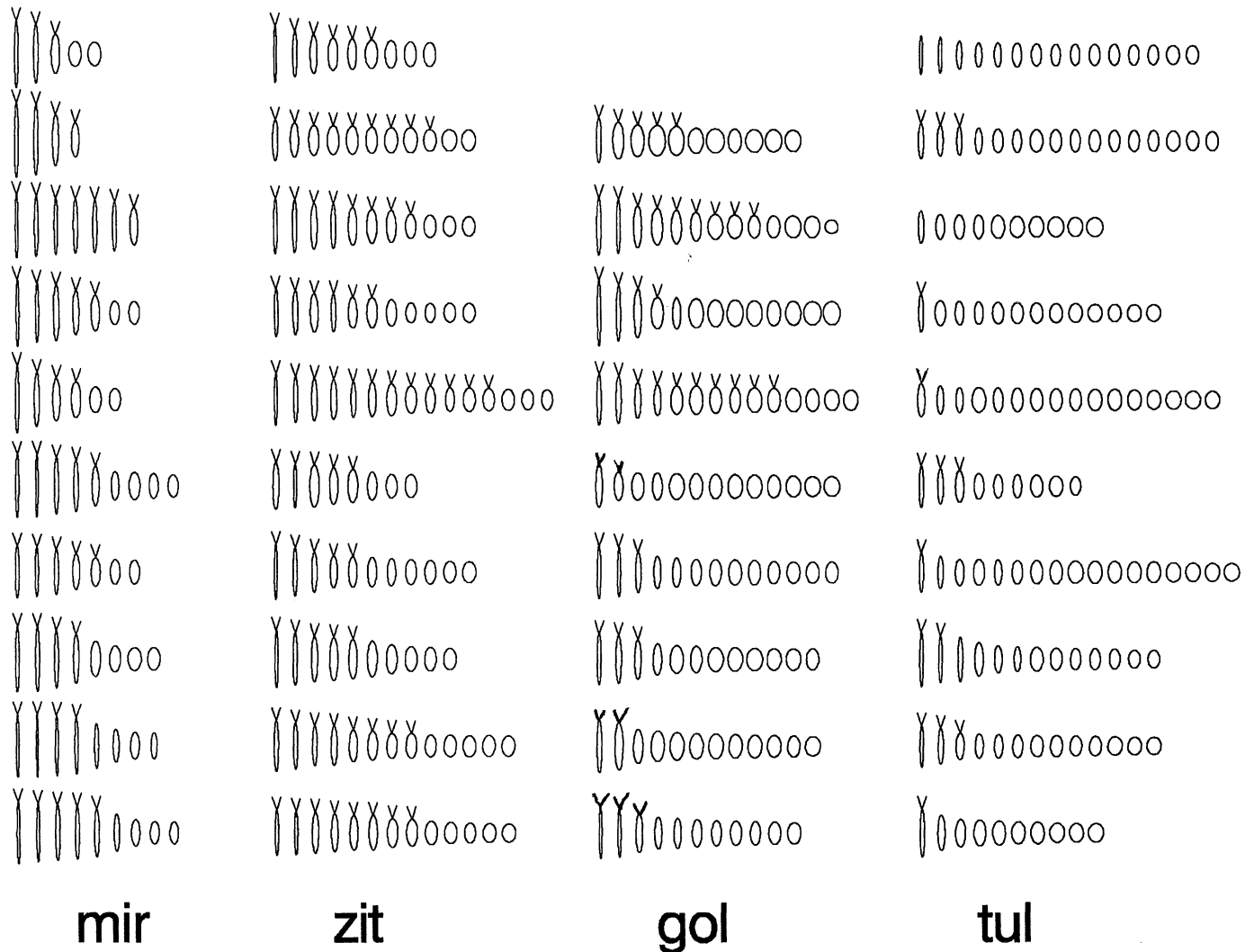


Fig. 2. Achenes represented as ellipses with the lengths and widths of actual achenes of *Heterosperma pinnatum*. Awns have been drawn for achenes that have them. Each line represents a single head from a different individual from the population mentioned. mir = near Guadalajara, Jalisco; zit = Zitácuaro, Michoacán; gol = Golondrinas, Hidalgo; tul = Tula, Hidalgo.

(Fig. 5). Peripheral achenes collected in January are still completely dormant. By March, field-collected central achenes germinate rapidly to high proportions while a few peripheral achenes germinate at a slow rate. By June, both extremes of achene morphology germinate rapidly (intermediate achenes always express intermediate germination biology). Thus while all achenes possess innate dormancy, the central achenes lose theirs earlier in the spring.

Dispersal—Central achenes possess barbed awns and have a greater adhesive dispersibility. Using various artificial dispersal agents (pelts of rabbits, sheep, and cows or balls of string) we have demonstrated that the proportions of mature achenes adhering to dispersal agents in the field is highly correlated with the proportion of the awned central achenes produced in the population (Fig. 6; see Venable et al., 1987).

The functional consequences of the morphological variation can be summarized as follows. Central achenes remain attached to the parent for more time, while the

peripheral ones fall at maturity. Central achenes adhere more readily to animals and lose their innate dormancy earlier in the germination season than peripheral achenes. Other subtle germination differences permit central achenes to germinate under a somewhat broader range of temperature and light (Venable et al., 1987). Intermediate achenes have intermediate behavior. Seed bank carryover between years does not seem to be important for the species, nor is there much ecologically significant variation in seed size.

POPULATION DYNAMIC CONSEQUENCES

To determine the population dynamic consequences of variation in achene morphology and function, we carried out demographic experiments in natural populations of *Heterosperma*. We removed thin strips of soil within the naturally occurring vegetation and replaced it with soil from the same site from which *Heterosperma* achenes had been removed. Into this we sowed known numbers of achenes of each type using randomized block designs (25

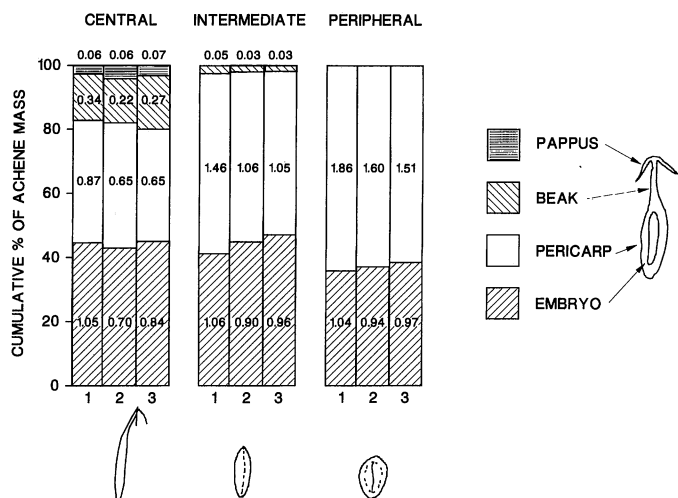


Fig. 3. Cumulative biomass allocation to pappus, beak (minus the beak), and embryo for three populations: near Guadalajara, Jalisco (Mirador) (1), San Bartolo, México (2), and Huichapan, Hidalgo (3). The histograms represent percent of total achene biomass. The numbers represent the weight of achene parts in mg. Eight to 12 achenes of each type were dissected from four plants from each population.

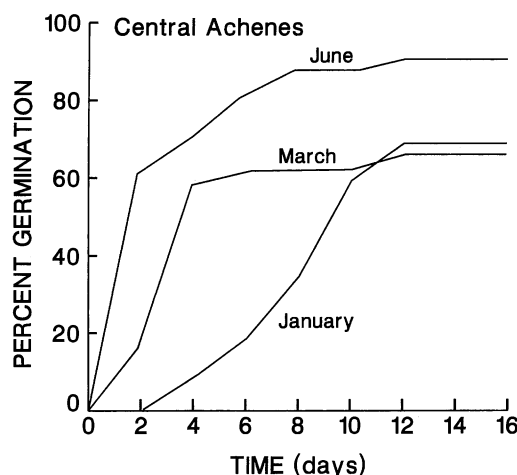
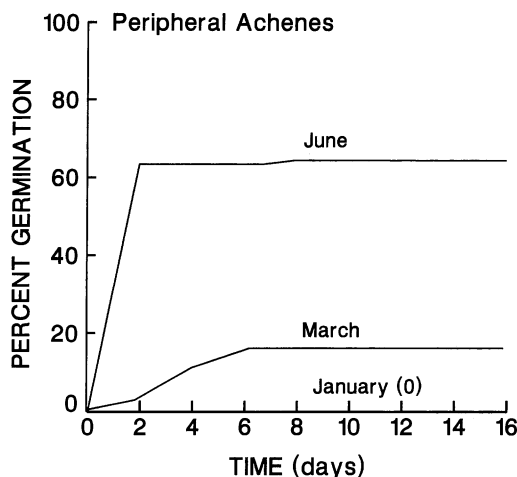


Fig. 5. Results of a germination experiment carried out at several times between the start of the achene production season and the start of the rainy season. Achenes were collected from the natural seed bank within 10 days of each trial.

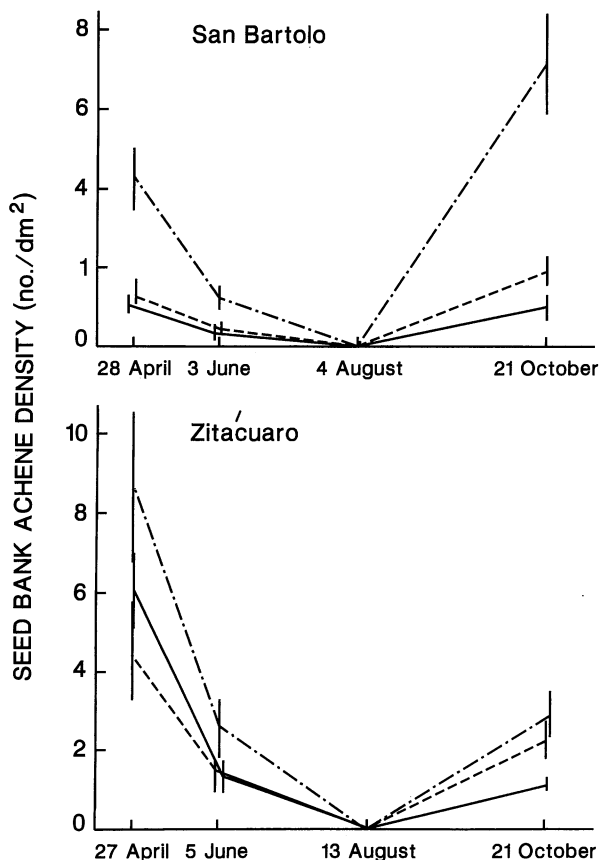


Fig. 4. Seed bank dynamics from the beginning of the germination season until the start of achene production for a population at San Bartolo, México and Zitácuaro, Michoacán. Central (—), intermediate (---), and peripheral achenes (-·-·-). Thirty soil cores, 78 cm² × 5 cm deep, were collected from each population at each date. Vertical bars represent standard errors.

achenes per 50 cm strip, three strips (achene types) per block and nine blocks for the Tlalnepantla population; 50 achenes per 1 m strip, three strips per block and eight blocks for the Tula population). In this way we were able to follow the fates of individual achenes and determine their success at emerging, surviving, and reproducing (Morales, 1986; Venable et al., 1987).

In general, central achenes tend to emerge earlier than peripheral achenes (with intermediate achenes being intermediate in emergence time). Early emergence usually results in lower survival but greater size and reproduction of survivors. However, the magnitude of these differences varies, resulting in shifts in the relative success of achene types.

For example, at the Tlalnepantla, Morelos site there were two cohorts of germination: one in April and one in June. Approximately 40% of the central and intermediate achenes and 30% of the peripheral achenes eventually germinated (Table 1). Of the germinating central achenes, approximately 20% emerged in the first cohort, while less than 10% of the central and peripheral achenes did. The survival of the first cohort was less than half

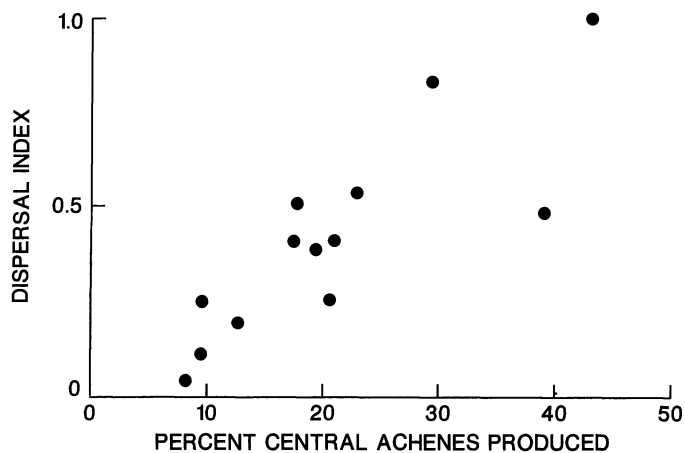


Fig. 6. A dispersal index is plotted against the percent of central achenes produced in each of 13 populations. The dispersal index was defined by first calculating the proportion of mature achenes along a predefined transect that adhered to an artificial dispersal agent, then standardizing these values so that the population with the highest score had a dispersal index of 1.

that of the second. Nevertheless, surviving plants attained larger sizes and reproduced roughly twice as much as the second cohort. The total lifetime success (including emergence, survival, and reproduction) was slightly greater for the intermediate achenes this year in this population. The intermediate germination behavior resulted in greater total germination than the peripheral achenes, but later germination than the central achenes. Since the survival advantage of late germination was greater than the reproductive disadvantage, the intermediate achenes attained a higher fitness through their intermediate germination behavior.

The same qualitative patterns with different quantitative results were observed at the Tula site (Table 1). The size and reproductive advantage of early emergence was small while the survival cost was large. Thus the conservative peripheral achenes were more successful than the less dormant central achenes (Table 1).

By measuring the different components of fitness in demographic experiments, we have been able to determine how variation in achene morphology and function translates into success in natural habitats. When these components of fitness for each achene type are combined into total fitness (germination × survival × fecundity) for a variety of such experiments we can begin to see environmental patterns in the fitness consequences of achene morphology. In Fig. 7, we have plotted the relative success of central achenes (standardized to the average success of all achene types) against an index of environmental harshness (the proportion of all achenes at the particular time and place that were successful at emerging and surviving to reproduction). The graph indicates that in times and places in which achenes on average have a high probability of successfully emerging and surviving to reproductive stage (i.e., low harshness), the more “cavalier” central achenes have higher fitness. Yet where few achenes are successful at producing any offspring, the more “conservative” peripheral germination strategy is more successful.

If such patterns have a consistent relationship to par-

TABLE 1. Demographic consequences of achene morphology. Seeds (225 and 400) of each achene type were sown in randomized block designs at the Tlalnepantla and Tula sites, respectively. Total germination is % of seeds sown; germination of individual cohorts is expressed as % of total germination. Survival is calculated as % of germinated seedlings surviving to the reproductive season. Adult fecundity is the mean number of fruiting heads produced by surviving plants. Relative fitness is the product of germination, survival, and fecundity, standardized such that the most successful achene type had a fitness of 1.

Tlalnepantla, Morelos			
	Central	Intermediate	Peripheral
Germination			
April cohort	20%	9%	8%
June cohort	80%	91%	92%
Total germination	44%	40%	28%
	April cohort		June cohort
Survival (seedling to adult)	15%		40%
Adult size (canopy width, cm)	11.8		5.1
Adult fecundity (fruiting heads)	15.2		6.8
	Central	Intermediate	Peripheral
Relative fitness	0.83	1.0	0.83
Tula, Hidalgo			
	Central	Intermediate	Peripheral
Germination			
May cohort	60%	53%	24%
July cohort	40%	47%	76%
Total germination	37%	40%	37%
	May cohort		July cohort
Survival (seedling to adult)	7%		84%
Adult size (height, cm)	4.7		3.4
	Central	Intermediate	Peripheral
Relative fitness	0.69	0.98	1.0

ticular habitats or geographic locations and if achene type variation is heritable, we might expect there to be adaptive population differentiation with regard to achene traits. Before addressing the question of environmental patterns in population differentiation, we will briefly summarize our understanding of the heritability of variation in achene traits.

GENETIC VARIATION AND COVARIATION

In order to examine the correlation structure of achene traits and the genetic basis of variation and covariation, we grew plants from six populations in the greenhouse. Ten families (roughly ten achenes from each of ten parents) were sown for each population in random positions in the greenhouse. For each resulting adult plant we measured achene and fruiting head traits as well as some life-history and plant size and shape traits. The resulting data were analyzed using quantitative genetic techniques (Venable and Búrquez, 1989, 1990).

For each trait we calculated the broad-sense heritability (the proportion of phenotypic variation that is genetically based) and broad-sense genetic correlations among traits (see Venable and Búrquez, 1989, 1990 for methodological details). These measures give a general sense of the ability of traits to respond to selection and how selection on particular traits may cause indirect selection on others.

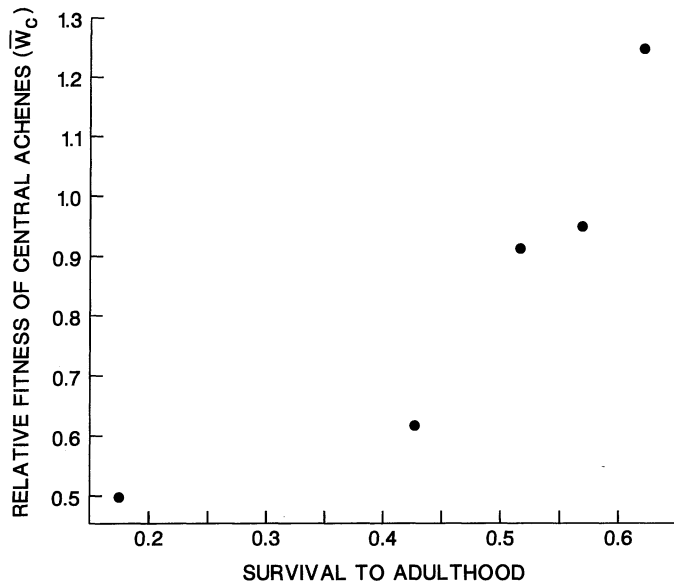


Fig. 7. Graph of relative fitness of central achenes against mean survival of all achenes (from seed to reproductive adult) for five populations. Fitness (germination \times survival \times fecundity) is calculated for each achene type and standardized so that the mean fitness of the three types equals 1. Mean survival of all achene types is considered an indicator of environmental harshness as perceived by *Heterosperma pinnatum*.

The most important results are that traits such as the number of central and peripheral achenes and achenes with awns vary genetically both within and among populations (Table 2). This implies that 1) the selective forces we measured in the field may result in genetic changes in achene and head traits and 2) populations have differentiated in achene and head traits, potentially as a result of natural selection.

Several interesting genetic correlations of achene and head traits were found. For example, the lengths of central and peripheral achenes, the length of awns on central achenes, and the number of achenes per head with awns are all genetically correlated with one another (Table 3a). This indicates that there is some genetic factor that constrains the lengths of achenes and the number and length of awns to vary together. Thus to the extent that these genetic correlations are additive, selection favoring more and longer awns would also result in the production of longer achenes. There is also a genetic correlation between the number of peripheral achenes per head, their width, and the total number of achenes per head (Table 3b). This suggests that selection for more peripheral achenes might result in them being wider and in heads with more achenes. The number of achenes per head is negatively correlated with the number of heads per plant ($r_G = -0.58$), which seems to be an example of a genetically based life-history tradeoff.

Various theoretical arguments (reviewed in Venable, 1989) and some empirical data (Venable and Lawlor, 1980) suggest that natural selection might often favor a negative correlation between achene dispersal and dormancy. This negative correlation is predicted because dispersal and dormancy have partially substitutable effects on bet-hedging, escape from high density, and escape from

TABLE 2. Genetic components of the variation in the number of achenes of various types. The broad-sense heritability is calculated as the ratio of within-population genetic variance to total within-population phenotypic variance under the assumption of inbreeding. The proportion of genetic variance among populations (PGVAP) is represented as the among-population genetic variance divided by the total genetic variance (within and among populations). All reported values are based on significant components of variance ($P < 0.05$) unless otherwise indicated.

Trait	Heritability	PGVAP
Number of central achenes	0.58	0.36
Number of intermediate achenes	0.46	0.10 ns ^a
Number of peripheral achenes	0.46	0.39
Number of awned achenes	0.77	0.30
Total number of achenes	0.39	0.18 ns

^a Not significant.

sib competition: more dormancy results in less selection for dispersal and vice versa. We have found genetic correlations between the number of central achenes (which are less dormant) and the number of achenes with awns and the length of awns (which favor adhesive dispersal; Fig. 3c). Since there seems to be nothing in the development or functioning of these traits that requires dormancy to be negatively correlated with dispersal, these could be examples of genetic correlations molded by natural selection (cf. Cheverud, 1984).

It is noteworthy that, while there is much genetic variation in the number of achenes of each type per head (Table 2), the correlations among achene numbers are relatively low (with the exception of the high correlation

TABLE 3. Broad-sense genetic correlations for traits involving a) achene and awn length, b) number and width of peripheral achenes, c) dispersal and dormancy traits, and d) numbers of the different types of achenes per head.

a)	Length of peripheral achenes	Length of central achenes	Length of awns
Length of central achenes	0.72 ^a		
Length of awns	0.11	0.47	
Number of achenes with awns	0.48 ^b	0.74 ^a	0.82 ^a
b)	Number of peripheral achenes	Width of peripheral achenes	
Width of peripheral achenes	0.44 ^b		
Total number of achenes/head	0.73 ^b	0.48 ^b	
c)	Number of central achenes	Number of achenes with awns	
Number of achenes with awns	0.14		
Length of awns	0.72 ^c	0.82 ^a	
d)	Number of central achenes	Number of peripheral achenes	Number of achenes with awns
Number of peripheral achenes	-0.17		
Number of achenes with awns	0.14	0.21	
Total number of achenes/head	0.32 ^c	0.73 ^b	0.43 ^b

^a $P < 0.01$.

^b $P < 0.001$.

^c $P < 0.02$.

between the total number of achenes and the number of peripheral achenes; Fig. 3d). This high genetic variance together with low genetic covariances may be responsible for the high variation in achene proportions found within and among populations.

POPULATION DIFFERENTIATION

Having established that genetic variation in achene proportions exists both within and among populations we can proceed to address the question of environmental patterns in population differentiation. We will focus on two partially independent traits of clear functional significance. The percent central achenes determines the within-year timing of germination, and the percent of achenes with awns determines dispersibility. While the proportion of central achenes is correlated with the proportion of achenes with awns (the among-population phenotypic correlation is 0.49; $P < 0.05$), there is much independent variation, as can be appreciated by inspecting the seed heads from different populations illustrated in Fig. 2.

Models of the population dynamics of dispersal suggest that we should find a higher proportion of achenes with awns in sites where conditions favorable to *Heterosperma* populations are ephemeral (Venable and Brown, 1993). Fitness in a metapopulation is a compromise between success in the home patch and success in other patches (through dispersal). As patches become more ephemeral, the fitness benefits of staying in the home patch decline while opportunities for colonization increase, thus favoring greater dispersibility (Venable and Brown, 1993). Semiarid sites tend to have fairly open vegetation where *Heterosperma* populations can persist, whereas it is more restricted to areas of disturbance in higher rainfall sites. Vegetation types with closed canopies dominated by large plants are likely to provide more ephemeral sites for annual plants like *Heterosperma* than more open vegetation types.

Our population dynamic results suggest that central achenes should be selected against when early germination is hazardous or when the probability of an achene surviving to reproductive maturity is low. Germination and establishment of *Heterosperma* typically occurs in March–July, with late germination being fairly certain to be followed by more rain (the reliable start of the rainy season). Earlier germination in March–May is riskier with a lower probability of enough follow-up rain to survive to the reliable start of the rainy season, with germination in March (or earlier) being the most risky. Thus we might expect the proportion of central achenes to be associated with weather patterns indicative of high risk in March–May.

To test these predictions with data on population differentiation we measured the proportion of achenes with awns and the proportion of central achenes for 36 populations of *Heterosperma*. We also recorded the general vegetation type as well as the climatic characteristics of each site.

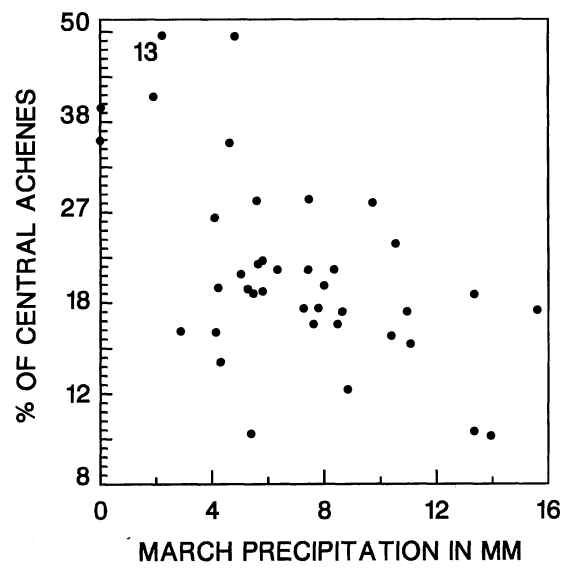
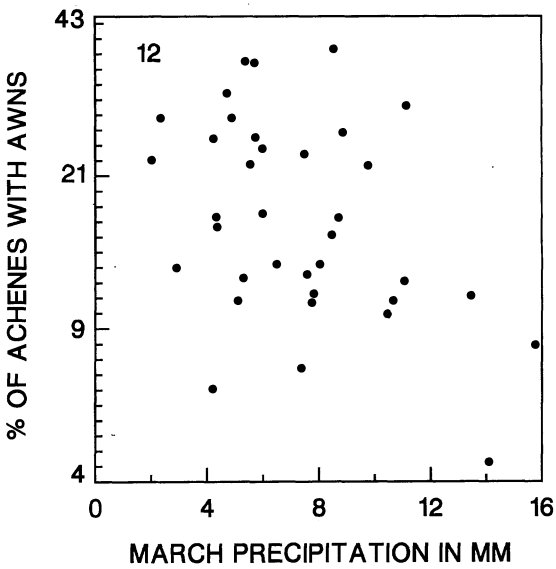
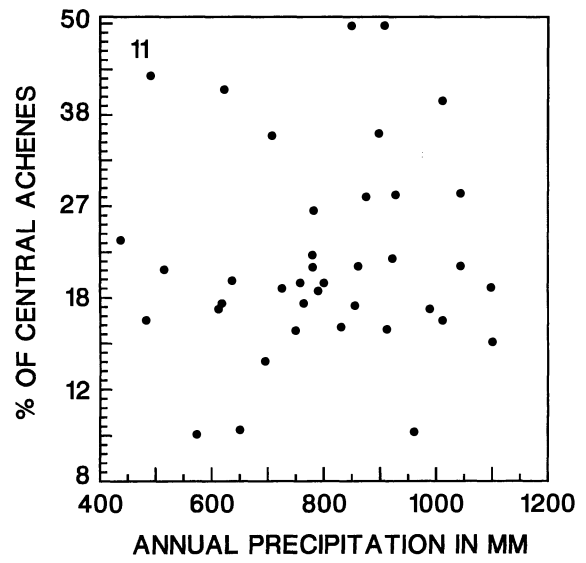
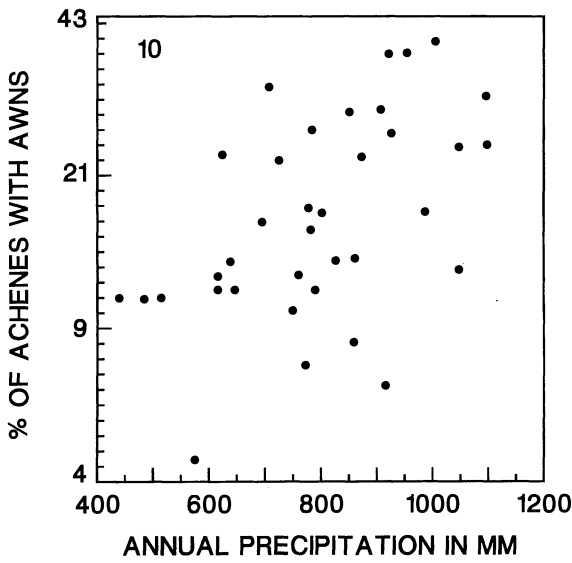
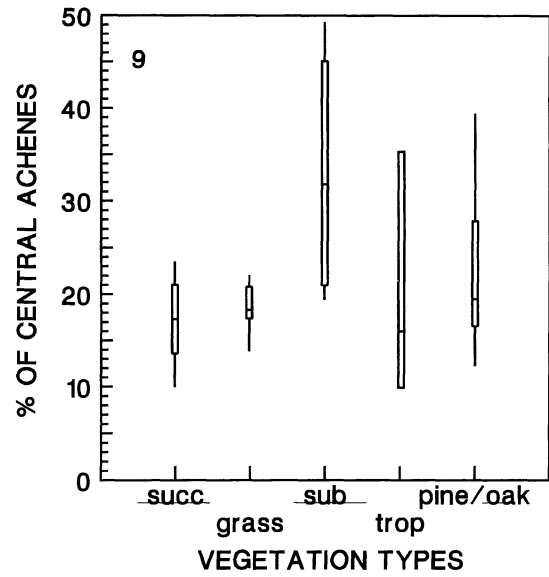
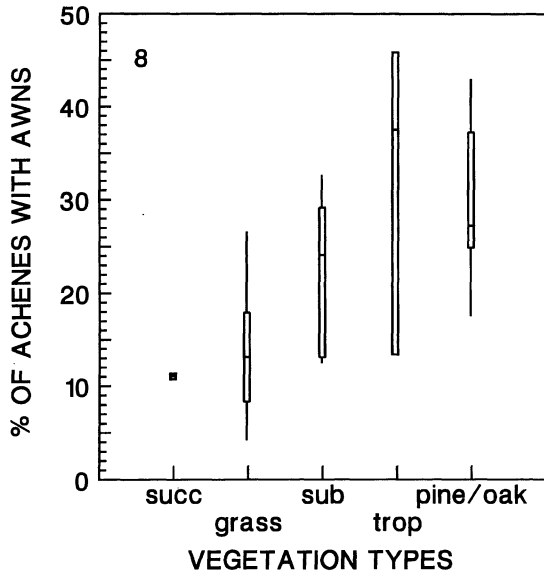
One difficulty in analyzing ecological patterns of population differentiation results from the fact that both plant traits and ecological conditions may be more similar for nearby populations. For example, nearby populations may

be more similar genetically and morphologically due to recent migration or gene flow. Environmental conditions may be similar due to similar topography, climate, and the like. Thus geographic proximity may give rise to spurious correlations between environmental conditions and plant traits. One approach to dealing with such potential problems is to attempt to factor out the effect of geographic proximity. In what follows we will present both the simple correlations between environmental conditions and plant traits and also the partial correlations with geography factored out.

In order to be able to factor out the effects of geographic proximity of sites, we have used a distance matrix approach. Thus for geography, morphology, and ecology, we have constructed matrices of the “distance” between each pair of sites. For geography this consists of the Euclidean distance between two sites, and for morphology and ecology this consists of the difference between sites in the variable of interest, e.g., the difference in mean annual rainfall or the difference in percent of achenes with awns. For vegetation type, the “distances” (actually similarities in this case) consist of a “1” if two sites have the same vegetation type and a “0” if not. Care was taken to use appropriate transformations before calculating our distances (e.g., a logit transformation for achene proportions). We then asked how similar are two distance matrices when we do and do not control for geography. Similarity was assessed using standard matrix correlations, and statistical significance was determined using Mantel-type randomization tests. Where possible we also report ordinary correlations between variables. While the techniques are interesting in themselves, especially with regard to partial matrix correlations, we will refer the reader to Dietz (1983) and Oden and Sokal (1992) for further details and pass directly to the results of our analyses.

There is an increasing proportion of achenes with awns as one moves from more open, arid vegetation types (desert scrub, grassland/savannah) to more closed mesic vegetation types (subtropical scrub, pine/oak forest; Fig. 8; ANOVA, $P < 0.001$). The distance correlation between vegetation type and percent of achenes with awns is significant whether or not the effects of geographic proximity are statistically removed (the Bonferroni-corrected, experiment-wise error rates are $P < 0.006$ and $P < 0.05$ respectively; the interpretation of the sign and magnitude of distance correlations is generally difficult and will not be given here). Also, the percent of achenes with awns tends to increase with mean annual precipitation (Fig. 10; raw correlation = 0.52; Bonferroni $P < 0.01$), although the distance correlation is only marginally significant (Bonferroni $P < 0.07$) and becomes insignificant when the effects of geographic proximity are removed ($P < 0.14$). The percent of achenes with awns is negatively correlated with mean March precipitation (Fig. 12; raw $r = -0.54$; $P < 0.005$), and the distance correlation is significant with and without the effects of geographic proximity removed (both $P < 0.01$).

This pattern is consistent with the prediction that greater dispersibility should be favored in sites with closed vegetation dominated by large plants. In such habitats, favorable conditions for annuals tend to be ephemeral compared to more permanently open sites. While there is a general pattern of greater dispersibility in sites with



greater mean annual precipitation, this pattern is somewhat equivocal since the partial correlations with the effects of geographic proximity of sites removed are not significant. Causal reasons for the relationship between percent of achenes with awns and mean March precipitation remain obscure, although they could be due to the correlation of percent of achenes with awns with the percent of central achenes.

The proportion of central achenes produced in the different vegetation types contrasts with the pattern presented above for the percent achenes with awns: while there is a greater percent of central achenes in the closed canopy subtropical scrub than in the more open savannahs and desert scrub, the percent is also low in the more closed pine/oak forests (Fig. 9; ANOVA, $P < 0.01$ with subtropical scrub being the only significantly different vegetation type Tukey's Studentized Range Test, $P < 0.05$). The distance correlation between the proportion of central achenes produced and vegetation type was insignificant when the effects of the geographic proximity of populations was removed ($P < 0.01$ but $P < 0.15$ with geography removed). Likewise, there is no tendency for percent of central achenes to increase with total annual precipitation using standard correlations or distance correlations (Fig. 11; raw $r = 0.13$; all P s not significant). The strongest pattern is a lower proportion of central achenes in sites that receive greater precipitation in March (Fig. 13; raw $r = -0.55$, $P < 0.005$; distance $P < 0.05$ with or without geographic distance removed).

The latter correlation is interesting in that the principal functional consequence of achene type relates to the loss of dormancy at precisely this time of year (Fig. 5). Thus the population differentiation data suggest that weather events during the early germination season, prior to the reliable onset of the rainy season, are strongly correlated with the proportion of central achenes produced. Fewer of the nondormant central achenes are produced in sites with greater early rain. This suggests that such rainfall events may represent a hazard that can be partially avoided by the production of more conservatively germinating peripheral achenes. Sites with high rainfall in March experience about 14–17 mm precipitation on average with an average of 3 days of appreciable rain that month, but they may receive with as much as 85 mm in record Marches. It is quite likely that rainfall would often be sufficient to trigger germination (25 mm or so) but insufficient to ensure establishment. For example, the demographic data presented above for Tula, Hidalgo (a high early precipitation, low percent central achene site) showed considerable early germination of predominantly central achenes, which had very low survival compared to later germinating achenes.

SUMMARY AND CONCLUSIONS

Seed heteromorphism has indeed proven a useful tool for investigating the population dynamic consequences as well as the evolution of seed traits. *Heterosperma pinatum* produces a range of achene morphologies that vary primarily in dispersibility and within-year timing of germination. Demographic experiments addressed the population dynamic consequences of achene type. Central achenes tend to germinate early in the spring when given the opportunity. This typically results in mortality costs but reproductive benefits to survivors. The quantitative details depend on local conditions in the year in question, especially the timing of rainfall. Genetic variation in achene proportions provides *Heterosperma* with a flexible seed biology that has permitted apparently adaptive population differentiation. A greater proportion of achenes with awns is produced in populations where the natural vegetation is closed resulting in more ephemeral opportunities for populations of an annual plant such as *Heterosperma*. The proportion of central achenes is lowest in sites with considerable pre-rainy season precipitation. It would seem that the early loss of dormancy may frequently result in unsuccessful early germination in such sites, much as we observed in the Tula, Hidalgo population in our demographic experiments. Population differentiation in response to different vegetation types and weather patterns sheds light on the processes by which community patterns in seed biology are generated. By virtue of the large range of variation in seed traits in *Heterosperma*, we can observe intraspecific patterns that mimic to some extent larger interspecific patterns in seed structure and function among communities.

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Figs. 8–13. Patterns of population differentiation in percent of achenes with awns (Figs. 8, 10, 12) and percent of central achenes (Figs. 9, 11, 13). 8. Quantile plots of the mean percent of achenes with awns per population plotted for different vegetation types: desert scrub, grassland, subtropical scrub, tropical deciduous forest, and pine-oak forest. 9. Quantile plots of the mean percent of central achenes per population plotted for different vegetation types. 10. Mean percent of achenes with awns plotted against mean annual precipitation. 11. Mean percent of central achenes plotted against mean annual precipitation. 12. Mean percent of achenes with awns plotted against mean precipitation in March. 13. Mean percent of central achenes plotted against mean precipitation in March.

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