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ECOLOGY OF ACHENE DIMORPHISM IN *HETEROTHECA LATIFOLIA*

III. CONSEQUENCES OF VARIED WATER AVAILABILITY

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SUMMARY

(1) An experiment was performed to ascertain the relative success of plants derived from the ray and disc achenes of *Heterotheca latifolia* when in competition with one another and potentially short of water. The treatments included pure and mixed sowings with regular watering, and mixed sowings with droughts beginning and ending at various times. The number of living plants was counted at various times during the experiment. Success was measured as total biomass at the end of the experiment, mean biomass per plant, mean height and width of plants, the number of plants alive at the end of the experiment, and the distribution of individual biomasses.

(2) Disc achenes were more successful than ray achenes when a plentiful water supply resulted in a high overall biomass and density at the end of the experiment. The inferior performance of ray achenes is attributed to the combined effects of lower embryo provisioning, lower and later germination, and suppression by the early-germinating disc achenes.

(3) Ray achenes were more successful than disc achenes when water was scarce and overall biomass and density were low at the end of the experiment. Their superior performance resulted from escaping the water shortage by dormancy.

(4) While the disc achene strategy resulted in a higher mean performance across treatments, the ray achene strategy exhibited lower variance in performance. This result is discussed in terms of ideas about fitness in variable environments.

INTRODUCTION

Polymorphic propagules vary in subtle ways that are likely to be reflected in differential demographic success of propagule types (Cheplick & Quinn 1982; Venable & Levin 1985b). The relative success of different propagule types should also depend in important ways on the nature of the environment encountered upon germination. Polymorphic propagules frequently differ in germination and in provisioning or seed size. Seed size may determine the size of seedlings and their success in competitive environments (Black 1956; Cideciyan & Malloch 1982; Weis 1982). Seedlings from large seeds may also survive longer and grow larger when resources are scarce (Grime & Jeffrey 1965; Baker 1972). Germination time is important in the establishment of size hierarchies that determine the outcome of competitive interactions in favourable environments (Ross & Harper 1972; Abul-Fatih & Bazzaz 1979). Yet germination time interacts with environmental 'stress' in complex ways depending on the relative timing of the germination and the stress (Klebesadel 1969; Arthur, Gale & Lawrence 1973; Marks & Prince 1981) so that sometimes late germination is favoured. Furthermore, germination time and provisioning may interact resulting in complex outcomes (e.g. Harper & Clatworthy 1963).

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Germination and provisioning differences are known for the two achene types of the weedy annual composite *Heterotheca latifolia* Buckl. (Venable & Levin 1985a). While ray and disc achene weights do not differ in the population studied, the embryos of disc achenes are heavier than ray embryos. Ray achenes have delayed, staggered germination that increases with achene age and is inhibited by darkness and burial. Disc achenes germinate quickly and completely and are less sensitive to darkness and burial (Venable & Levin 1985a). The present paper explores the fitness consequences of the behavioural diversity of *Heterotheca latifolia* achenes exposed to watering regimes which resulted in differing relative importance of water shortage and competition.

MATERIALS AND METHODS

The distribution, life history, achene structure, germination and dispersal behaviour of *Heterotheca latifolia* are described by Venable & Levin (1985a). Achenes for the present experiment were collected on a single day during autumn 1977 from vigorous plants at the Brackenbridge Field Station of the University of Texas, Austin, Texas, U.S.A. (30° 18′N, 97° 47′W). They were stored at room temperature in the laboratory prior to starting this experiment on 29 January 1978. Unusually small, damaged, or shrunken achenes were discarded. Staining of achene samples with tetrazolium blue indicated high viability (>95%).

Achenes were sown in the University of Texas Botany glasshouse in plastic tubs measuring 28 × 33 × 14 cm deep, filled with sand taken from a natural *H. latifolia* site. This sand was sifted and autoclaved for 3 h to kill any seeds and micro-organisms. *Heterotheca latifolia* achenes were pressed into the soil surface at 1-cm spacing in a rectangular pattern to yield twenty-five rows of twenty achenes (500 per tub). There were five experimental treatments with three replicate tubs each: (i) ray and disc achenes (250 each) were segregated at opposite ends of the tub so that plants interacted only with others of the same achene type. This treatment received enough water (5–20 mm every 1–3 days) to keep the soil moist (abbreviated to RS for *regular* watering and *separate* ray and disc achenes); (ii) regular watering as for (i) but ray and disc achenes alternating along and across rows (abbreviated to RM for *regular* watering and *mixed* ray and disc achenes).

All of the remaining treatments used a 1 : 1 mixture of ray and disc achenes sown in the same pattern as in the RM treatment but droughts beginning and ending at different times interrupted the regular watering: (iii) 2 days of watering (a total of 15 mm of water) followed by 17 days of drought, then resumption of regular watering (abbreviated to SED for *short early drought*); (iv) continuous water for the first 12 days followed by a *short late drought* of 10 days (abbreviated to SLD) followed by resumption of regular watering; (v) regular watering for 12 days followed by a long drought lasting 48 days followed by a resumption of regular watering (LLD for *long late drought*). The number of achenes, rather than the number of seedlings was fixed in order to let normal differences in germination time, germination percentage, and inherent provisioning differences interact with the different watering regimes to determine the relative success of achene types.

The experiment ended after 111 days and each surviving plant was cut at the soil surface, sorted as to ray or disc origin, measured for height and width (maximum horizontal dimension), dried for 48 h at 70 °C and weighed. Total biomass, mean biomass per surviving plant, mean height and width per plant, and number of plants alive at the end of the experiment were each analysed by a two-way analysis of variance. Statistics were calculated on log-transformed data, which resulted in homogeneous variance in all cases.

The main effects were achene type and the five treatments. Orthogonal contrasts were used to test for differences between achene types in each treatment (type-within-treatment contrasts). Duncan's multiple range test was used to group treatment-achene type combinations that did not differ significantly at $P < 0{\cdot}05$. The results of orthogonal contrasts agreed exactly with those of the multiple range test as to which treatments showed no ray-disc differences, and thus are not presented independently.

RESULTS

The relative success of ray and disc achenes depended on sowing and watering treatments for each of the variables measured (two-way analyses of variance, interaction of achene type with treatment, $P \leqslant 0{\cdot}001$ in each case). The two treatments with regular watering (separate and mixed sowings) showed similar germination patterns; ray achenes germinated later and more slowly (Fig. 1; cf. Venable & Levin 1985a). Ray achenes produced 33% as much total biomass as disc achenes when sown in pure stands (Table 1).

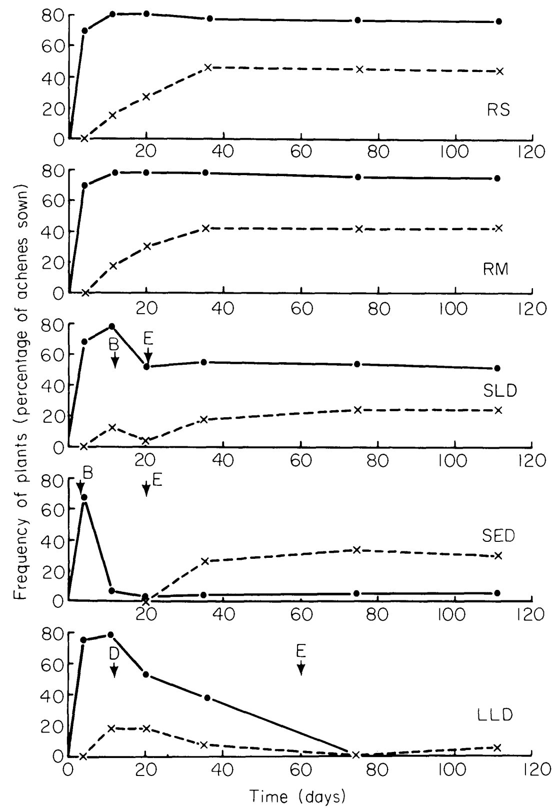

FIG. 1. Changes in numbers (expressed as percentage of the number of achenes sown) over the course of a glass house experiment for *Heterotheca latifolia* plants from ray (x———x) and disc (·———·) achenes in different experimental treatments. The treatments were: RS, regularly-watered pure stands; RM, regularly-watered mixed sowings; SLD, short, late drought; SED, short, early drought; LLD, long, late drought. Symbols: (B), beginning of drought; (E), end of drought (resumption of regular watering).

TABLE 1. Growth and survival of plants from ray and disc achenes of *Heterotheca latifolia* under various treatments in an experiment at Austin, Texas. Treatment results with the same superscript (within each variable, i.e. each pair of rows) were not significantly different ($P > 0{\cdot}05$, Duncan's multiple range test). The treatments were: RS, regularly-watered pure stands; RM, regularly-watered mixed sowings; SLD, short, late drought; SED, short, early drought; LLD, long, late drought.

		Treatment				
		RS	RM	SLD	SED	LLD
Total biomass	disc	$61{\cdot}8^{a}$	$71{\cdot}1^{a}$	$64{\cdot}4^{a}$	$19{\cdot}8^{b}$	0·0
(g)	ray	$20{\cdot}3^{b}$	$7{\cdot}2^{c}$	$4{\cdot}1^{c}$	$23{\cdot}3^{b}$	0·92
Mean weight	disc	$103{\cdot}7^{a,b}$	$132{\cdot}0^{b}$	$182{\cdot}7^{b}$	657·8	0·0
per plant (mg)	ray	$56{\cdot}9^{a,d}$	$22{\cdot}9^{c}$	$24{\cdot}6^{c}$	$99{\cdot}8^{a,b}$	$37{\cdot}6^{c,d}$
Mean height	disc	$21{\cdot}4^{a,d}$	$22{\cdot}1^{2,b}$	$21{\cdot}4^{a,b}$	$29{\cdot}1^{a}$	0·0
per plant (cm)	ray	$14{\cdot}6^{c,d}$	$10{\cdot}6^{c,e}$	$9{\cdot}5^{e}$	$17{\cdot}4^{b,d}$	5·2
Mean width	disc	$2{\cdot}8^{a,b}$	$3{\cdot}0^{a}$	$3{\cdot}7^{a}$	7·3	0·0
of plant (cm)	ray	$2{\cdot}0^{b,d}$	$1{\cdot}6^{c}$	$1{\cdot}8^{c}$	$3{\cdot}5^{a}$	$3{\cdot}7^{a}$
Number of	disc	595^{a}	$552^{a,b}$	$373^{b,c}$	36^{f}	0
plants surviving	ray	$352^{c,d}$	$316^{c,d}$	167^{e}	$226^{d,e}$	23^{f}

Disc achenes produced 15% more total biomass in mixture than in pure stands while ray plants produced 65% less biomass. The mean weight per plant from disc achenes (hereafter called disc plants) was 27% higher in mixture than in pure stands and the mean weight per ray plant was 60% lower. The suppressing effect of mixed sowing on ray plants can be clearly seen in the behaviour of individual plants. The frequency distribution of ray-plant weights in RM not only had a lower mean but was more positively skewed than that of RS (Fig. 2).

The 2 days of watering before the short early drought (SED) was sufficient to trigger almost as much disc achene germination as continuous watering did in the two regular watering treatments (Fig. 1). However, only one out of 750 ray achenes germinated before the drought. Only 4% of the disc seedlings survived the drought and few disc achenes germinated afterwards whereas 32% of the ray achenes germinated afterwards. The drought resulted in low overall densities and the largest ray and disc plants of any treatment. The very few disc plants that survived the drought were virtually free of competition and some of them grew very large (Fig. 2). Despite low numbers, surviving disc plants did achieve nearly the same total biomass as the more numerous but smaller ray plants. The SED was the most favourable treatment for ray plants both individually and as a population (Table 1).

Early-germinating disc seedlings had more time to establish before the short late drought (SLD) occurred and 65% of them survived it. Thirteen per cent of the later-germinating ray achenes germinated before the drought. Of these, only 13% survived, but 24% more germinated after the drought. The ray plants from the SLD achieved a mean biomass similar to those from RM and LLD although their ultimate density was considerably lower than that of the RM and higher than that of the LLD and their size distribution was very positively skewed (Fig. 2). The effect of the SLD on disc plants was one of moderate thinning. The density of disc plants was 32% lower and the final density of ray plants was 47% lower than in the regularly-watered mixture. Reduced density resulted in a total biomass of disc plants similar to that in RM though consisting of fewer heavier plants that were significantly wider.

The long late drought (LLD) caused the most drastic reduction in biomass and numbers and complete extinction of the disc plants. A few ray plants germinated after the drought

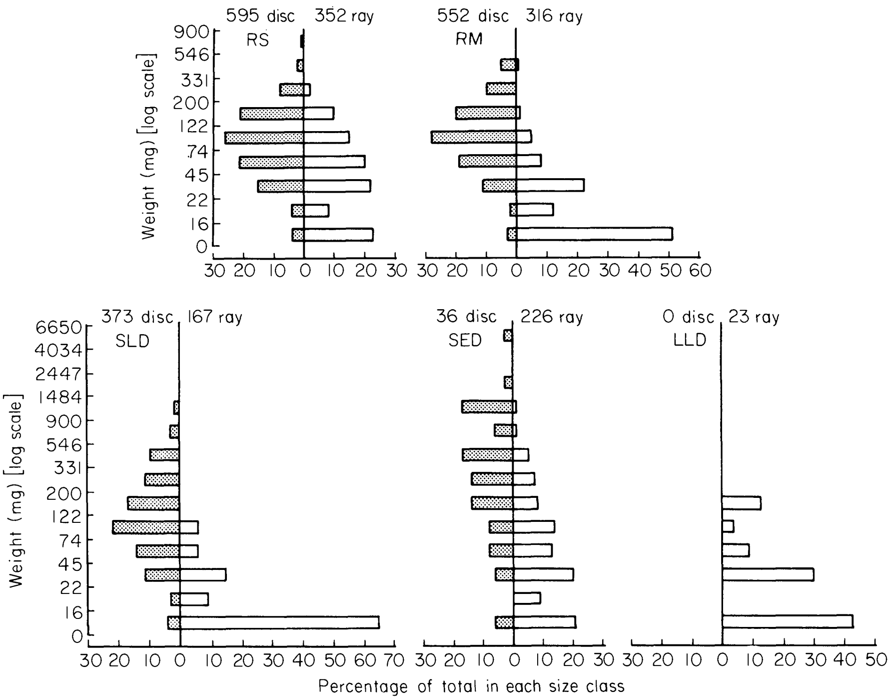

FIG. 2. Frequency distribution of above-ground dry weight of ray and disc plants of *Heterotheca latifolia* alive after 111 days, for each planting and watering treatments, in an experiment carried out at Austin, Texas. The histograms give the percentage of the total number of ray or disc plants found in each size class. The total number of ray and disc plants is specified at the top of each plot. The treatments were: RS, regularly-watered pure stands; RM, regularly-watered mixed sowings; SLD, short, late drought; SED, short, early drought; LLD, long, late drought.

and attained weights similar to those of ray plants from the two regular watering treatments though they were significantly shorter and wider.

DISCUSSION

The experiment demonstrated that when the watering regime is favourable and competition is intense, disc achenes are favoured in both weight and number, while plants from ray achenes are suppressed. Under dry conditions, ray achenes are superior though they never attain the numbers and biomasses that disc plants do in favourable environments.

To what can we attribute the inferior performance of ray achenes under conditions that are favourable for *H. latifolia*? Venable & Levin (1985a) showed that ray embryo weight is 62% that of disc embryos and, under favourable conditions in the laboratory at low densities, the growth rates of seedlings from the two achene types did not differ. Thus, independently of competition, ray plants should be approximately two-thirds as large as disc plants of the same age. In pure stands, mean biomass per surviving ray plant was roughly one half that of disc plants. This was probably due to the inherent provisioning difference, combined with the delayed germination of ray achenes which resulted in a shorter growing period. The total ray plant biomass in pure stands was one-third that of disc plants due to the added effect of lower germination percentage. Finally, the total yield of ray plants in mixture is considerably reduced over the pure stand yield due to suppression by the larger, more successful disc plants. None of the conditions in the current experiment (nor any easily-imagined ones in nature) would give rise to substantial numbers of disc achenes germinating later than ray achenes. This observation, combined with the seed provisioning differences, suggests that high density and competition will usually operate to the detriment of ray plants.

To what can we attribute the superior performance of ray achenes under the two drought regimes which most drastically reduced overall *H. latifolia* biomass and density? The census data (Fig. 1) reveal that the advantage lies in dormancy and germination after droughts, that is escape from as opposed to tolerance of drought. In central Texas, drought is most likely in the early germination season in late summer when a germination-triggering rain is likely to be followed by hot dry weather. As the germination season progresses, the likelihood of follow-up rain increases and lower temperatures result in less rapid desiccation of seedlings. In the present experiment the advantage of dormancy was measured only in the year of achene production. A between-year seed bank would present the possibility of an additional increment in fitness for the escape-in-time strategy of ray achenes. In a field experiment in a natural *H. latifolia* population 25% of ray achenes were still viable in the second germination season following achene production, yet disc achenes did not survive to the second year (Venable & Levin 1985b).

Differential response to competition and extreme conditions has not been studied for many polymorphic-seeded species so it is difficult to make generalizations. The best data have been collected for fruit polymorphisms associated with cleistogamous and chasmogamous flowers and the results contrast sharply with those reported here. *Amphicarpum purshii* (Cheplick & Quinn 1982), *Emex spinosa* (Weiss 1980) and *Gymnarrhena micrantha* (Koller & Roth 1964) all have subterranean and aerial fruits. Seedlings arising from subterranean fruits are larger and more tolerant of water shortage and competition while aerial fruits disperse farther. In contrast, one achene type of *H. latifolia* is the superior competitor, while the other achene type responds more effectively to water shortage by escaping it in time. Better dispersal is accomplished by the superior, not the inferior competitor (Venable & Levin 1985a). Smaller (or more stressed) *A. purshii*, *E. spinosa* and *G. micrantha* individuals produce fewer aerial and relatively more of the large, competitive, subterranean fruits. Smaller plants of *H. latifolia* produce smaller heads which have a greater proportion of the less-competitive, escape-in-time ray achenes (Venable & Levin 1985a).

In *H. latifolia*, ray achene performance was much less variable in the face of different patterns of water availability, though disc performance was superior on the average. A standard approach to investigation of adaptation to environments changing in time assumes that geometric-mean fitness is an appropriate criterion of success (Haldane & Jayakar 1963; Levins 1968). Thus the strategy that maximizes the expectation of $\ln(\lambda)$ where λ is the finite rate of increase, is expected to be the fittest. Either increase of the arithmetic mean or decrease of the variance will result in higher geometric-mean fitness (Gillespie 1977; Real 1980). A mutant *H. latifolia* lineage producing only disc achenes would become extinct the first time an LLD year occurred and no plants survived (there is no between-year seed bank for disc achenes). This happens despite the high mean performance of disc achenes because the variance is large. If a ray strategy or a mixed ray–disc strategy could persist in the face of competition with an all-disc strategy, it would ultimately be more successful, not because of higher mean performance, but because of lower variance in time. For a polymorphic strategy to be more successful than a ray-only strategy, the increase in arithmetic-mean fitness due to the production of disc achenes must raise the geometric-mean fitness more than the increase in variance lowers geometric-mean fitness (Venable 1986). Thus for a polymorphic strategy to persist, it must have a higher geometric-mean fitness than either monomorph. In the case of *H. latifolia* this implies that the polymorphic strategy is fitter than a monomorphic ray strategy because of the high arithmetic mean and fitter than a monomorphic disc strategy because of the high arithmetic mean and fitter than a monomorphic disc strategy because of lower variance.

MacArthur (1972) and Venable & Lawlor (1980) utilize the arithmetic-mean fitness as a criterion of fitness in an independently-varying, patchy environment when seeds can readily disperse among patches. This kind of environmental regime would improve the success of a mutant disc lineage since the patches in which it went extinct could be recolonized. Venable & Levin (1985a) have shown that the disc achenes do indeed have superior dispersal powers which may compensate to some extent for their higher variance in performance and the resulting possibility of local failure.

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