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ECOLOGY OF ACHENE DIMORPHISM IN *HETEROOTHECA LATIFOLIA*

I. ACHENE STRUCTURE, GERMINATION AND DISPERSAL

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SUMMARY

(1) Information is presented on structural differences between achene types of *Heterotheca latifolia* (Compositae), when they are produced, where on the plant they are produced, laboratory germination, seedling growth and dispersal biology.

(2) While weights of ray and disc achenes do not differ significantly (*c.* 730 μg), their structures do. Disc achenes have a wind-dispersed pappus while ray achenes have none. Disc achenes have a thinner and anatomically different pericarp (half as much biomass) compared with ray achenes and disc embryos are 60% heavier than ray embryos.

(3) Plants produce smaller heads with relatively more ray achenes as their reproductive season progresses. Also, larger plants produce larger heads with relatively more disc achenes up to a threshold plant size beyond which head size and the ray to disc quotient is constant.

(4) Fresh disc achenes germinate quickly and completely while ray achenes have delayed and fractional germination which can be enhanced by excision of the embryo. Ray-achene germination increases with achene age and is inhibited by darkness and burial while disc-achene germination is less sensitive to these factors.

(5) While growth rate does not differ between ray and disc seedlings, disc seedlings at a given age are larger due to the initial difference in embryo size.

(6) Dispersal differences are found between ray (lacking a pappus) and disc achenes (with pappus) of the same mass. Wind dispersal is greater for disc than ray achenes. Plant height enhances disc achene dispersal more than ray achene dispersal.

INTRODUCTION

Seed polymorphisms have been described in many species found in variable, unpredictable environments such as frequently disturbed habitats (Harper 1977) and arid and semi-arid environments (Zohary 1937; van der Pijl 1972). Seed polymorphism may increase adaptation to highly variable environments since different seed types may have different properties (e.g. Stebbins 1974), such as different dispersibilities or dispersal agents (Koller & Roth 1964; Wilson 1976; Baker & O'Dowd 1982). Alternative seed morphs usually differ in germination behaviour. Frequently one type has stricter requirements for breaking dormancy (e.g. Becker 1912; Lahiri & Kharabanda 1961; Williams & Harper 1965; Cavers & Harper 1966; Maurya & Ambasth 1973; McDonough 1975; Baskin & Baskin 1976; Evenari, Kadouri & Gutterman 1977; Ungar 1979). Plants from different seed morphs may differ in competitive performance as a result of differences in seed size, time of emergence, or growth rate (Flint & Palmblad 1978; Weiss 1980). Thus seed polymorphisms appear to affect a variety of plant functions.

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Little is known about how seed variation affects the population biology of polymorphic species and how the different seed morphs contribute differentially to fitness. We have studied this in *Heterotheca latifolia* an annual weed with several advantages for such an investigation. First, it has two distinct achene types which facilitates recognition. Secondly because normally plants grow in open and disturbed habitats, any disturbance involved in experimental field sowings is well within the range of natural environmental conditions. Thirdly, the annual life cycle makes demographic analysis relatively simple.

In this paper, we investigate: the basic structural differences between the two achene types; times and positions of production of the achene types; and the consequences of achene dimorphism for germination behaviour, seedling growth, and dispersal.

MATERIALS AND METHODS

The species

Heterotheca latifolia Buckl. (Compositae) belongs to the section *Heterotheca* which contains seven annual species each possessing dimorphic achenes (Wagenknecht 1960). The species occurs from northern Mexico to Kansas and Oklahoma and east to Georgia and New York in the U.S.A. It grows on sandy or rocky ground, on disturbed soils, in open woods, along roadsides, in pastures and in waste ground (Wagenknecht 1960). It has spread north to Illinois and New York in the last 50 years, frequently following railways and roads (Wagenknecht 1960; Plummer & Keever 1963).

Heterotheca latifolia germinates in late summer or autumn. The seedlings develop into overwintering rosettes which bolt in March and April. Reproduction begins in late June and July and continues until the first killing-frost in November or December. Individual heads are open for 2–3 days then close for about 10 days while the fruits fill. Subsequently the heads reopen to present the mature achenes for dispersal. The plants studied in this investigation were from Austin, Texas, U.S.A. (30°18'N, 97°47'W). Voucher specimens are stored in the University of Texas Herbarium (D. Lawrence Venable 79001, 79002, 79003).

Structural differences and achene production

Pappus, pericarp, and embryo weights were determined with a Cahn microbalance for twenty-one each of ray and disc achenes collected from seven plants in September 1979. To observe changes in the quotient of ray to disc achene number with time since reproductive maturity, fruiting heads were collected every 2 weeks from eight plants in nature and daily from five potted plants. The relationship between ray to disc flower quotient and plant size was obtained from a collection of 113 plants of different sizes made in November 1978. A dummy variable regression was used to determine whether the slopes and intercepts varied significantly in the regressions of number of achenes per head and quotient of ray to disc achenes per head against time since reproductive maturity (Draper & Smith 1966).

Dispersal

Four 1-m wide strips were laid for 20 m at right angles to each other from a 1-m square point source of *H. latifolia* plants and were covered with 'Tangle-Trap', a non-drying adhesive substance. The number of achenes landing on 20-cm lengths of strip were counted. Since the linear strips sample a smaller fraction of the possible dispersal sites at greater distances from the source, the data were corrected using the geometric relationship between circumference and radius $N_r = X_r (\pi r/2)$, where N_r equals the corrected number of

achenes at distance r from the centre of the seed source and X_r equals the uncorrected number of achenes at distance r . This correction factor converts the number of achenes landing at a specified distance on the four strips to an estimate of the number of achenes landing at that distance in a continuous ring around the source. One set of strips was constructed for tall plants (average height at which achenes were borne *c.* 80 cm), and one set for short plants (25 cm). The experiments were begun during autumn 1976 and left until the source plants had died or most of the achenes had dispersed.

Germination

Germination experiments were performed on seeds harvested in the autumns of 1976 and 1977. Seeds were stored in the laboratory at room temperature for no more than 2 months. Experiments were done in partitioned seed trays with approximately 3 cm of fine sand like that in which *H. latifolia* commonly grows. Achene type and replicates were randomized within seed trays, placed in a growth chamber with alternating day and night temperatures of 26–28 °C and 14–16 °C, respectively, and a day length of 11.5 h. These conditions correspond with those the species would encounter in mid-October (in Austin, Texas) which is the time of peak germination.

One experiment was performed to determine whether there are changes in dormancy with time, and whether ray and disc achenes change in the same way. Achene type-specific changes in dormancy would have considerable demographic implications. This experiment involved two sowing dates and two achene types with six replicates of twenty-five achenes for each type and sowing date combination. Freshly produced achenes were harvested in August of 1977 and either planted immediately in seed trays or stored in the lab for 2 months before sowing.

The sensitivity of germination to presence or absence of light was determined with two light treatments with three replicates of fifty achenes for each type and treatment combination. Achenes were placed on filter paper in petri dishes with dark replicates carefully wrapped in aluminium foil and light replicates wrapped in cellophane. Germination of dark replicates was determined in a photographic dark room with dim light coming through green filters.

The effect of burial of achenes was determined with five burial treatments with one sample of fifty achenes for each achene type and treatment combination. A more detailed burial experiment was performed for ray achenes with six replicates of thirty achenes each for five burial treatments. For both burial experiments, achenes were sown: (i) on the surface, (ii) barely covered with sand, (iii) 0.5 cm below the soil surface, (iv) 1 cm below the soil surface, and (v) 2 cm below the soil surface.

Seedling growth

Achenes were germinated in seed trays in the laboratory on moist sand receiving a constant water supply. Daily germination records were kept and, after 1 month, all seedlings were washed free of sand and weighed individually. Fresh weight was regressed against age and achene type. Growth rate is calculated as the slope of log fresh weight on age.

RESULTS

Structural differences and achene production

Ray and disc achenes are well differentiated morphologically and anatomically (Fig. 1). The disc achenes have a well-developed pappus of capillary bristles. They are biconvex and

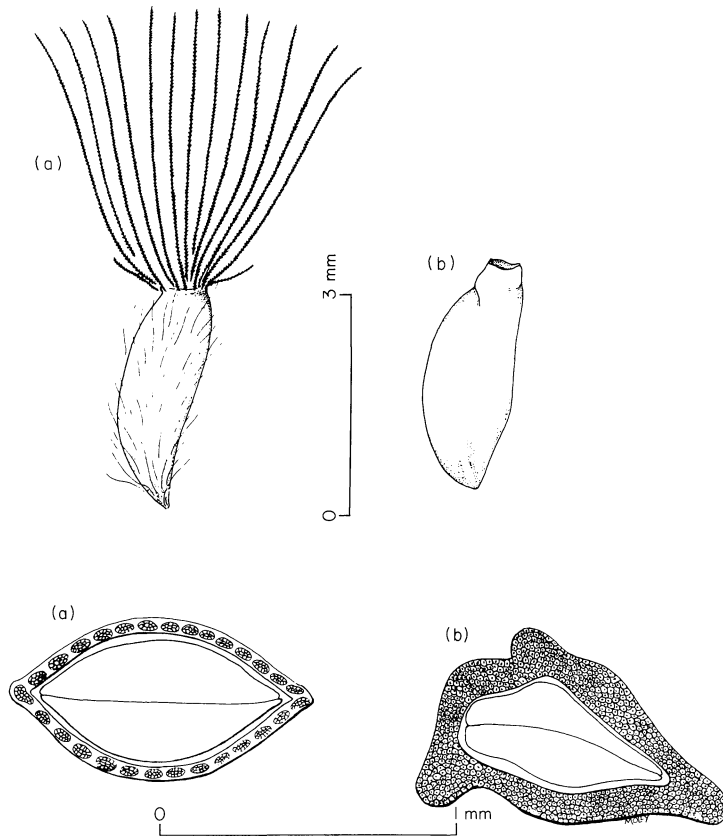


FIG. 1. (a) Disc achene of *Heterotheca latifolia* and cross-section showing bundles of fibres in the pericarp; (b) ray achene and cross-section showing thick layer of fibres in the pericarp.

covered with upward pointing silky hairs. Ray achenes have no pappus, are three-sided, and have smooth waxy coats which are glabrous.

The most prominent anatomical difference between achene types is in the structure of the achene wall or pericarp (Fig. 1). Ray pericarps have a thick, highly lignified layer of fibres as indicated by phloroglucinol-stained sections. Disc pericarps are composed of bundles of lignified fibres separated by areas of suberized or waxy cells, as indicated by phloroglucinol stain for lignin and Sudan IV stain for suberin.

Ray and disc achenes differ in biomass allocation to achene parts (Table 1). Ray achenes have the same weights as disc achenes (t -test, $P > 0.05$). Yet 14% of the weight of disc achenes is pappus though ray achenes have no pappus. The pericarp of the disc achene makes up 28% of the total disc achene weight while the ray pericarp makes up 65% of the total ray achene weight (t -test, $P < 0.001$). Embryos of disc achenes weigh 0.415 mg or about 60% more than those of ray achenes (t -test, $P < 0.001$).

Since ray and disc achenes are produced on each head, both are produced throughout the fruiting season. However, the proportion of achene types can change as the flowering head increases in size. Larger heads (with more achenes) have a greater proportion of disc achenes. The number of achenes per head on a given plant decreases with time in both field

TABLE 1. Fresh weights of achene parts from Texas populations of *Heterotheca latifolia*. Weights are means for twenty-one ray and twenty-one disc achenes, three of each taken from seven plants. Percentages are of total achene weight based on the presented averages. s_w is the within-plant standard deviation. s_b is the standard deviation of plant means (between-plant standard deviation). Weights of all achene parts differ between ray and disc achenes (t -tests, $P < 0.001$) but total achene weight does not differ ($P > 0.05$).

Ray				
Weight				
Achene part	(%)	(mg)	s_w	s_b
Pappus	0	0	—	—
Pericarp	65	0.475	0.062	0.129
Embryo	35	0.256	0.067	0.089
Total	100	0.730	0.081	0.216
Disc				
Weight				
	(%)	(mg)	s_w	s_b
Pappus	14	0.100	0.036	0.010
Pericarp	28	0.196	0.115	—
Embryo	58	0.415	0.169	0.214
Total	100	0.712	0.042	0.250

TABLE 2. Number of achenes per head and quotient of ray to disc achenes regressed against days since reproductive maturity for individual plants of *Heterotheca latifolia* from Texas. Symbols: b , slope; c , intercept; ** $P < 0.001$; *** $P < 0.0001$.

	Plant	Number of achenes per head			Quotient of ray to disc achenes			n
		c	b	r	c	b	r	
Large plants growing in a natural population	1	97.7	-0.304	-0.485***	35.2	0.175	0.492***	98
	2	115.9	-0.431	-0.582***	39.7	0.115	0.392***	108
	3	117.7	-0.434	-0.586***	35.6	0.198	0.575***	114
	4	122.6	-0.634	-0.782***	37.4	0.196	0.697***	110
	5	126.8	-0.465	-0.591***	34.8	0.079	0.356***	108
	6	97.4	-0.251	-0.551***	48.9	0.023	0.086 N.S.	104
	7	107.3	-0.568	-0.586***	44.1	0.157	0.358**	86
	8	103.8	-0.263	-0.449***	48.2	0.172	0.460***	94
	9	105.8	-0.626	-0.657***	42.5	0.137	0.302**	102
	10	98.6	-0.725	-0.762***	44.3	0.408	0.588***	114
Plants grown in watered pots in an experimental garden	1	101.5	-0.638	-0.657***	35.3	0.237	0.540**	37
	2	81.6	-0.346	-0.529**	39.6	0.208	0.496**	39
	3	107.3	-0.445	-0.790***	33.2	0.385	0.719***	30
	4	120.1	-0.688	-0.826***	14.2	0.555	0.719***	36
	5	100.1	-0.416	-0.598***	26.2	0.263	0.537**	34

and garden conditions (Table 2). Since a dummy variable regression indicated that some plants have significantly different slopes and intercepts ($P < 0.001$), regressions are presented for individual plants. The ratio of ray to disc achenes on successive heads of the same plant increases with time since the onset of reproduction despite minor plant to plant variation in slope and intercept (Table 2).

The mean head size also varied with plant size at a given time (in November) during the fruiting season. Head size increases with plant height up to a threshold plant height of about 40 cm (Fig. 2). The quotient of ray to disc achenes decreases rapidly as a function of increasing plant size, down to an asymptote of about 0.6 (Fig. 3). Beyond a threshold plant

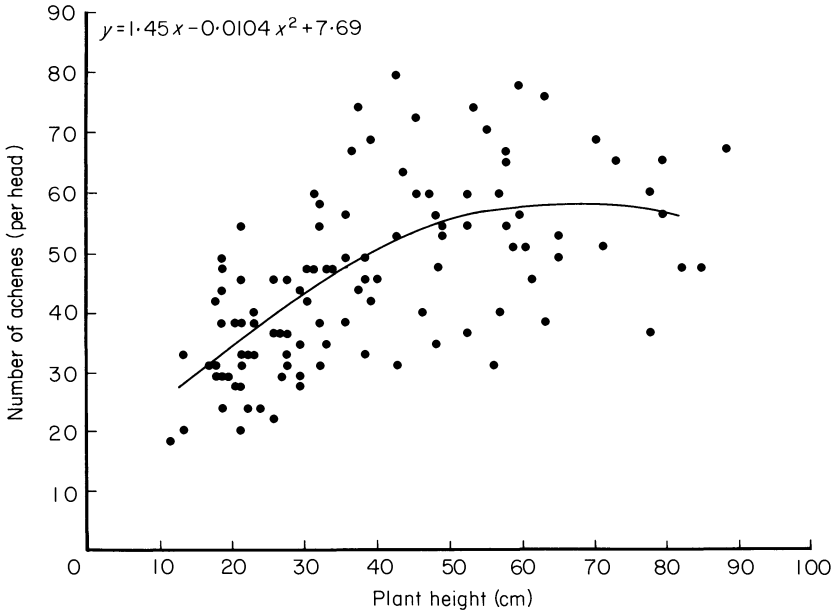


FIG. 2. Number of achenes per head plotted for plants of *Heterotheca latifolia* of different sizes in Texas. Each point represents the mean for one plant. The curve drawn through the points is the best fitting least squares polynomial ($r^2 = 0.422$, F to enter the quadratic term = 14.24, $P < 0.001$).

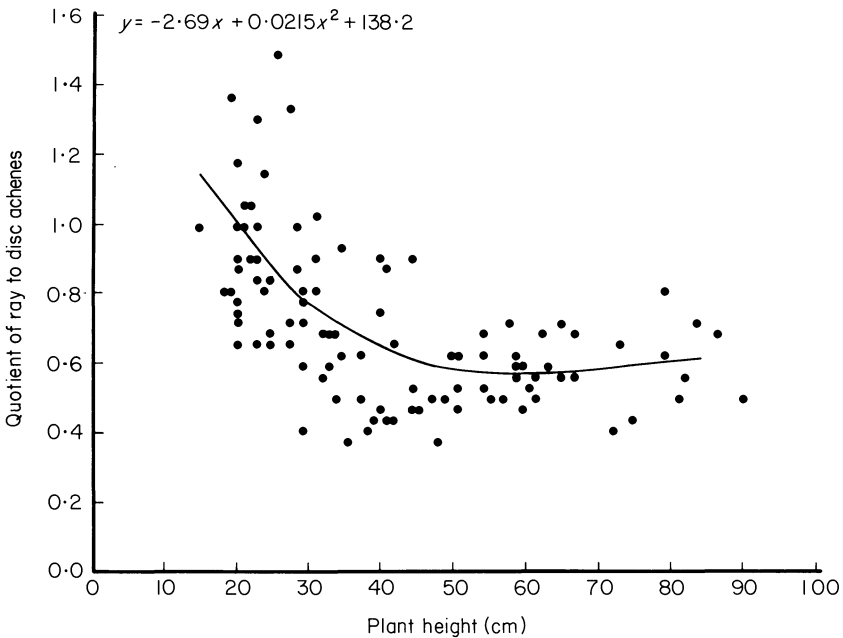


FIG. 3. The quotient of number of ray to disc achenes plotted for plants of different sizes of *Heterotheca latifolia* in a Texas population. Each point represents the average for heads of one plant. The curve drawn through the points is the best fitting least squares polynomial ($r^2 = 0.380$, F to enter the quadratic term = 22.43, $P < 0.001$).

size, achene number is constant and not determined by plant vigour. However, this fixed size decreases regularly through the season.

Dispersal

Over 85% of achenes were dispersed within 5 m of the parent plant (Fig. 4). The mean distance travelled was 0.52 m for ray achenes from short plants, 0.93 m for ray achenes from tall plants, 1.06 m for disc achenes from short plants and 1.65 m for disc achenes from tall plants. Whether achenes come from tall or short plants, disc achenes travel farther on average than ray achenes. The decline in achene deposition with distance from the source can be summarized by the exponential rate of decline of achene numbers with distance. The fitted value for this rate is -0.59 for ray achenes from short and tall plants, -0.47 for disc achenes from short plants and -0.35 for disc achenes from tall plants (Fig. 4). All values were simultaneously fitted with a dummy variable regression, and are significantly different ($P < 0.005$).

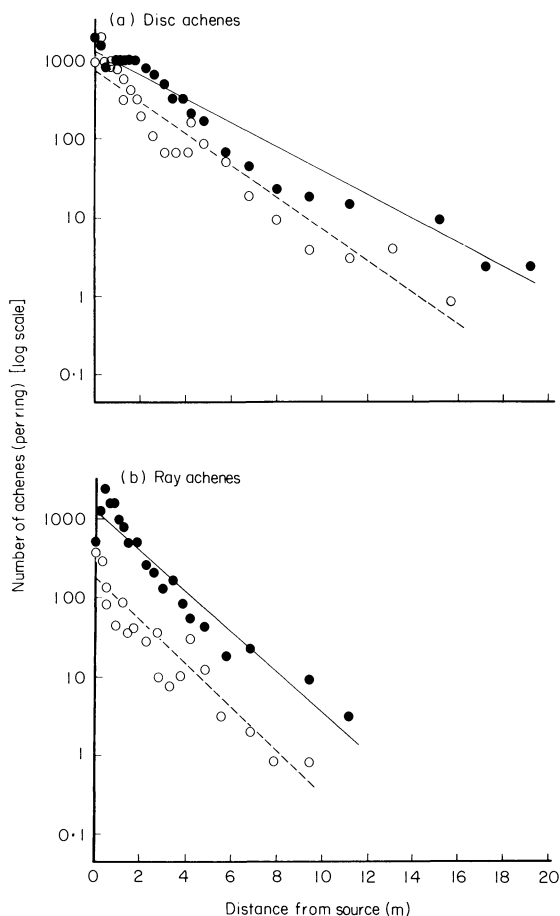


FIG. 4. Number of achenes of *Heterotheca latifolia* dispersed to 20-cm wide rings at various distances from a point source of (a) disc achenes from tall (●—●) (c. 100 cm) and short (○---○) (c. 35 cm) plants; (b) ray achenes from tall (●—●) and short (○---○) plants.

Germination

Disc achenes germinate early (c. 2 days), and rapidly with a high final germination percentage (Fig. 5). Ray achenes germinate later (c. 8–10 days), more slowly and have a low final germination percentage. Achene age influences germination percentages of ray and disc achenes differently (Fig. 5). Ray achenes germinated more rapidly and to higher final percentages when stored for 2 months in the laboratory before testing than when tested fresh (46% v. 21%; $\chi^2_1 = 43.9$, $P < 0.001$). The disc achenes collected in August had about the same final germination percentage after storage for 2 months in the laboratory as when fresh (70% v. 78%; $\chi^2_1 = 6.5$, $P < 0.05$).

The greater dormancy among ray achenes was removed by excising the embryo from the pericarp. When ray embryos were placed in close contact with pericarps in a small moist container they exhibited no dormancy (Table 3). With half the pericarp intact on ray embryos, there was no dormancy either. This suggests that the pericarp does not exert its influence via water soluble inhibitors. Achenes with cracked pericarps germinated more readily than uncracked controls ('germination' in this context means radicle elongation or

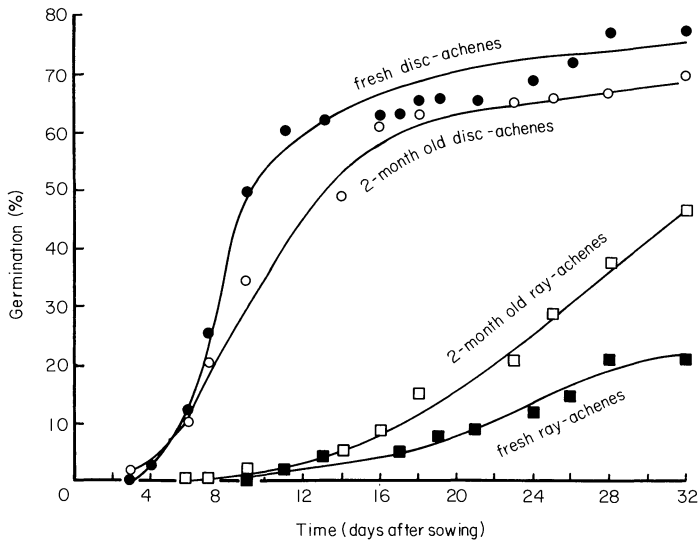


FIG. 5. Effect of age on germination of ray- (□, ■) and disc-achenes (○, ●) of *Heterotheca latifolia* from a Texas population. Filled symbols, fresh achenes; unfilled symbols, 2-month old achenes.

TABLE 3. Percentage germination of ray achenes of *Heterotheca latifolia* from a Texas population with different degrees of pericarp removal. Percentages with the same superscript are not significantly different (χ^2 contingency tests, $P < 0.05$). See text for details.

Time (days)	Excised embryos				
	Without pericarp	With pericarp in contact	Half pericarp removed	Pericarp cracked	Control (untreated)
2	73.3 ^a	73.3 ^a	70.0 ^a	13.3	0.0
6	80.0 ^b	80.0 ^b	93.3 ^b	56.7	3.3
10	—	—	93.3	63.3 ^c	46.7 ^c
Total treated	15	15	30	30	30

cotyledon spreading or greening). However, germination was less than when part or all of the pericarp was removed (Table 3). Since the cracking of achenes ensured access to water and oxygen, the dormancy of ray achenes may be related merely to structural resistance of the thick, lignified ray-achene walls to the swelling of imbibed embryos.

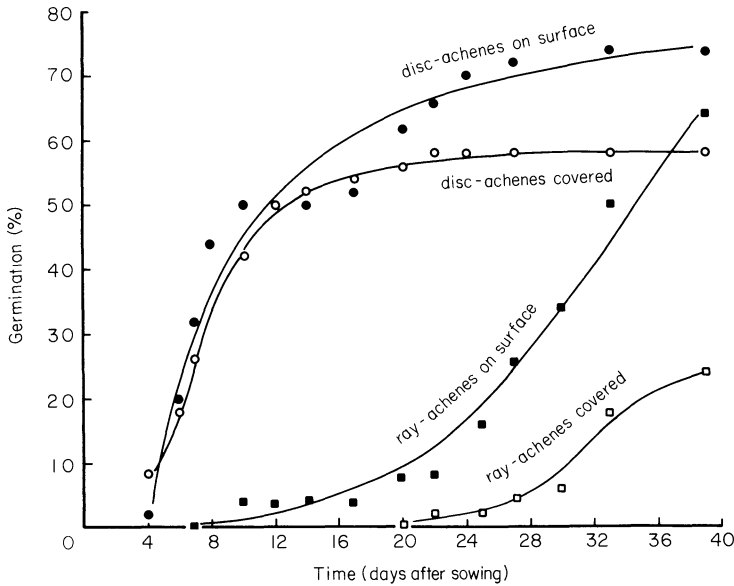


FIG. 6. Effect of slightly covering with soil on germination of ray- (\square , \blacksquare) and disc-achenes (\circ , \bullet) of *Heterotheca latifolia* in Texas. Filled symbols, achenes on surface; unfilled symbols, achenes slightly covered.

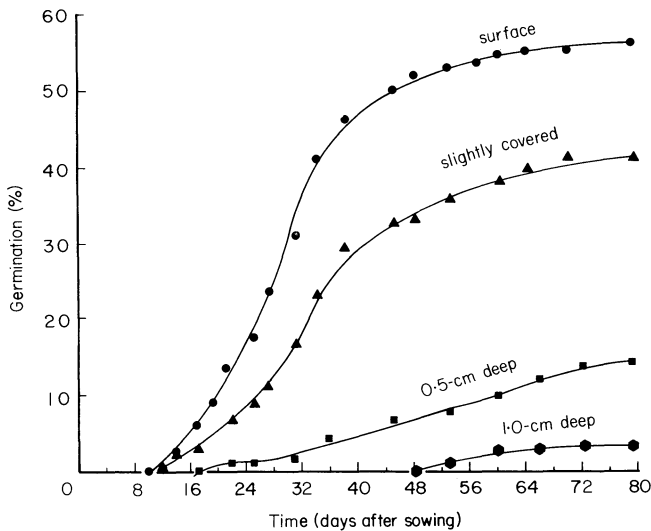


FIG. 7. Effect of burial depth on germination of ray achenes of *Heterotheca latifolia* from a Texas population. Symbols: (\bullet), surface; (\blacktriangle), slightly covered; (\blacksquare) 0.5 cm deep; (\bullet), 1.0 cm deep.

Darkness reduces ray-achene germination more than it does disc-achene germination. Fifty-six per cent of disc achenes germinated in light while 39% germinated in the dark, a germination reduction of about 30% ($\chi^2_1 = 9.04$, $P < 0.005$). Twelve per cent of ray achenes germinated in light while 0.7% germinated in the dark ($\chi^2_1 = 16.24$, $P < 0.001$). This 95% reduction was significantly greater than the 30% reduction of disc germination ($\chi^2_1 = 9.14$, $P < 0.005$).

Disc-achene germination was inhibited little when achenes were slightly covered with sand (58% covered vs 74% uncovered; $\chi^2_1 = 2.85$, N.S.; Fig. 6) but ray germination was substantially reduced (24% covered v. 64% uncovered; $\chi^2_1 = 16.23$, $P < 0.001$). A more detailed burial experiment was performed for ray achenes. Final germination percentages were 68% for achenes at the soil surface, 42% for slightly-covered achenes, 13% for achenes 0.5 cm below the surface, 3% for achenes 1-cm deep, and no germination from 2-cm depth (overall $\chi^2_3 = 212.0$, $P < 0.001$, partial chi-square values for adjacent depths were all greater than 11.8, d.f. = 1, $P < 0.001$; Fig. 7).

Seedling growth

Growth rates did not differ significantly between ray- and disc-derived seedlings (Fig. 8), but the intercepts on the seedling weight axis differed significantly (dummy variable regression, $P < 0.001$). The intercept represents the weight at age zero or a projected difference in embryo weight. The data suggest that for seedlings of the same age, those derived from ray achenes will be smaller due to smaller embryos—not to differences in growth rate. The actual quotient of disc to ray embryo weights is 1.62 which is very close to the predicted value of 1.70 (from the ratio of intercepts). Achenes of Compositae contain no endosperm at maturity and nutrients are stored in the embryo.

DISCUSSION

Achene dimorphism in *Heterotheca latifolia* yields dual germination and dispersal strategies. Ray achenes represent a 'cautious' or 'low-risk' strategy in which germination-controls delay and spread germination over time. Also, ray achenes are dispersed over short distances and tend to remain near the parent. Disc achenes have less control over germination and thus should germinate with the first available rain. This early germination should be advantageous if the environmental conditions following germination are favourable. But, like greater dispersal away from the parent, less control of germination involves risk since achenes will germinate under less certain conditions and over a limited, possibly unfavourable period.

The possession of two achene strategies represents a form of bet-hedging. While higher population growth might frequently result from committing all achenes to the quick-germination disc-achene strategy, this might prove disastrous if early rain was followed by a long, hot drought or severe disturbance. If all achenes were committed to the risk-spreading ray-achene strategy, they might avoid disastrous conditions but would not be capable of high rates of increase under favourable conditions. A dual strategy is a compromise between the exigencies of high growth rate under favourable conditions and perseverance under unfavourable conditions. Successful response to the diverse environmental conditions *H. latifolia* faces might not be as easily accomplished by the production of a single seed type with intermediate properties.

Germination patterns in related species are similar to those in *H. latifolia*, with ray

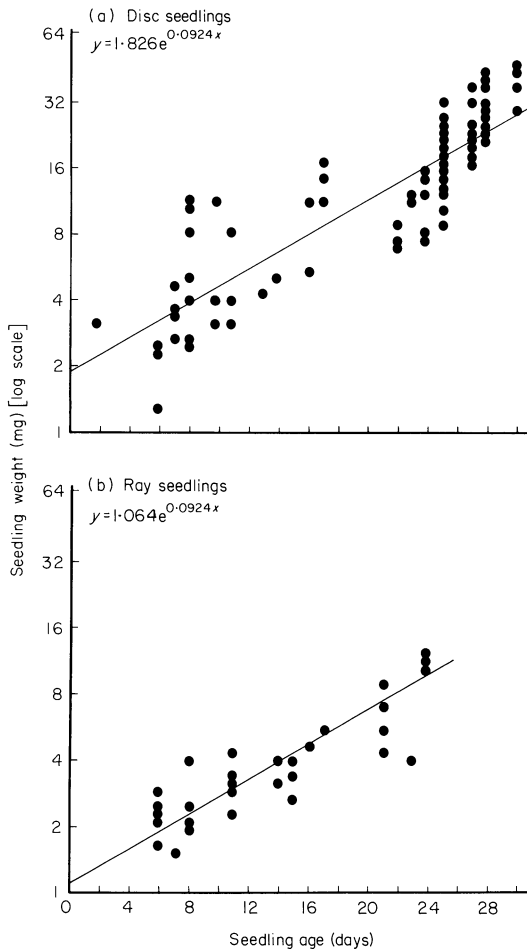


FIG. 8. Fresh weight of (a) disc and (b) ray seedlings of a Texas population of *Heterotheca latifolia* at different ages germinated and grown in uniform conditions in seed trays.

achenes germinating under more restricted conditions than disc achenes. Baskin & Baskin (1976) report that disc achenes of *H. subaxillaris* are not dormant while ray achenes require after-ripening similar to the age-effect reported here for *H. latifolia*. They found that ray dormancy was maintained by low temperature and lost at high temperature. Flint & Palmblad (1978) demonstrated that disc achenes of *H. grandiflora* germinate readily with continuous moisture. In glasshouse experiments, ray achenes of *H. grandiflora* remained dormant with scattered germination over a prolonged period.

To what extent does one seed type germinate under more restricted conditions than another in other polymorphic seeded species? Species exhibiting restricted *v.* less restricted germination behaviour include *Xanthium canadense* (Thornton 1935), *Atriplex dimorphostegia* (Koller 1957), *Halogeton glomeratus* (Williams 1960), *Chenopodium album* (Williams & Harper 1965), *Rumex obtusifolius* and *R. crispus* (Cavers & Harper 1966), *Alysicarpus monilifer* (Maurya & Ambasht 1973) and *Salicornia europea* (Ungar 1979). For example, disc achenes of *Grindelia squarrosa* germinate more rapidly and over

a broader temperature range than ray achenes; they are also less dark-inhibited (McDonough 1975). In other cases it appears that germination of one seed type is more strictly controlled by one environmental factor while germination of the other seed type is controlled by a different factor. For example, beaked achenes of *Hypochoeris glabra* are more light-sensitive whereas unbeaked achenes are more temperature-sensitive (Baker & O'Dowd 1982). In another example of this type, the subterranean propagules of *Emex spinosa* exhibit more dormancy than the aerial propagules, yet the aerial propagules are more light-sensitive (Evenari, Kadouri & Gutterman 1977). A few cases are known with no apparent germination differences between polymorphic achene types (several species in Becker (1912) and *Picris echinoides* (Sorensen 1978)). Thus germination differences in other polymorphic-seeded species are frequently, though not always, consistent with the idea of conservative *v.* high-risk germination strategies.

Although biomass allocation to vegetative versus reproductive function and seed versus vegetative reproduction has been investigated in a range of plant species (e.g. Primack 1979; Abrahamson 1980; Kawano 1981), allocation to different seed functions has not received such attention. Despite equal ray- and disc-achene weight, ray and disc achenes of *Heterotheca latifolia* allocate differently to the pappus, pericarp, and embryo. Ray achenes allocate twice as much biomass to pericarp (protection), 60% as much to embryo (provisioning), and nothing to pappus (dispersal). These allocation differences result in differences in achene function. Disc achenes are dispersed farther by wind than ray achenes. Disc seedlings, coming from larger embryos, are larger at any given age than ray seedlings. The thick pericarp of ray achenes enforces dormancy and ray achenes survive longer in the soil than do disc achenes (Venable & Levin 1985).

The effectiveness of the composite pappus in dispersal is well demonstrated in this study because achenes with and without pappi occur on the same plant and weigh the same. Disc achenes were dispersed farther and had a greater sensitivity of dispersal to plant height. Mean dispersal distances of disc (with pappus) achenes from tall plants are similar to those of pappus-bearing achenes dispersing from tall (90 cm) Compositae such as *Eupatorium cannabinum* or *Senecio jacobea* (c. 1.5–2.0 m distance) (Sheldon & Burrows 1973). Ray achenes from tall plants had mean dispersal distances much less than those of any of the tall pappus-bearing species studied by Sheldon and Burrows (0.9 m). Disc achenes from short plants of *Heterotheca latifolia* are similar in dispersal distance to short (30 cm) pappus-bearing species such as *Erigeron acer*, *Senecio viscosus* and *S. vulgaris* (c. 0.75–1.25 m). Ray achenes (lacking pappus) of short *Heterotheca latifolia* plants had mean dispersal distances similar to the short pappus-bearing Compositae with the highest terminal velocities (least effective parachutes) such as *Carlina vulgaris*, *Leontodon autumnalis*, and *Tragopogon porrifolius* (c. 0.5–0.6 m).

The dependence of seed dispersal on the height of the inflorescence has been reported in other genera with windborne disseminules; e.g. *Senecio jacobea* (Sheldon & Burrows 1973) and *Vulpia fasciculata* (Watkinson 1978). However, differential sensitivity of alternative seed types to plant height has not been reported before. Achenes from tall plants have a greater distance to fall than achenes on short plants. This permits greater lateral displacement before they reach the ground. But height also gives the buoyant pappus of disc achenes greater access to wind. Though ray achenes on tall plants also have greater access to wind this has less effect on their dispersibility in the absence of a buoyant pappus.

In this paper we have made inferences as to how achene behaviour in *Heterotheca latifolia* may translate into differential success in nature. The demographic fates of achene morphs must be monitored in nature in order to test these inferences. The results of such demographic experiments will be reported in a sequel to the present paper.

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