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Autoecology of the Ruderal Weed Heterotheca grandiflora With Emphasis on Germination Dimorphism

Stephan Dexter Flint
Utah State University

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AUTECOLOGY OF THE RUDERAL WEED HETEROTHECA GRANDIFLORA
WITH EMPHASIS ON GERMINATION DIMORPHISM

by

Stephan Dexter Flint

A thesis submitted in partial fulfillment of the requirements for the degree

of

MASTER OF SCIENCE

in

Biology Ecology

Approved:

Utah State University
Logan, Utah
1977
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Stephan D. Flint
Stephan D. Flint
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ABSTRACT

Autecology of the Ruderal Weed *Heterotheca grandiflora*

With Emphasis on Germination Dimorphism

by

Stephan Dexter Flint, Master of Science

Utah State University 1977

Major Professor: Dr. Ivan G. Palmblad

Department: Biology, and The Ecology Center

Weedy species, as they occupy diverse and unpredictable environments, are expected to possess considerable variability in numerous characteristics, including germination. The visually dimorphic achenes of *Heterotheca grandiflora* Nutt. (Asteraceae) were tested for potentially adaptive differences in their germination, the establishment of the resulting seedlings, and the relative production of the two achene types.

Achenes produced by the disc florets are adapted for dispersal and rapid germination while the ray florets produce smaller achenes lacking a dispersal mechanism, but possessing a more sophisticated physiological system capable of regulating germination. Ray achene germination rates were significantly influenced by different soil surfaces while disc achene germination rates were not. Further, ray achenes (protected by a thicker seed coat) may remain in enforced dormancy until conditions become appropriate for germination.

Under continuously favorable conditions, seedlings from early germinating disc achenes will dominate a mixed stand and suppress
those from later germinating ray achenes. An initially unpredictable environment will eliminate disc seedlings and permit the more dormant ray achenes to germinate in an environment of reduced competition.

Limited tests suggest a greater proportion of the smaller and energetically cheaper ray achenes may be produced when resources are scarce due to drought stress.

These germination characteristics are only one aspect of this taxon's developmental plasticity. The ability to act as an annual or biennial, flower in the rosette stage, and produce seed in great numbers under favorable conditions have all acted together with the germination characteristics to help preadapt this plant for its weedy spread from its original southern California range.

(129 pages)
INTRODUCTION

*Heterotheca grandiflora* Nutt. (Asteraceae) or "telegraphplant" is one of the few native Californian plants to become weedy. Of the 4,875 native species in the California flora [Munz and Keck, 1959, as tabulated by Smith and Holdeke, 1960], Stebbins [1965a] lists only 41 native colonizing species. Thus, the telegraphplant belongs to a category comprising less than 1 percent of the native flora.

Initially, its distribution appears to have been limited to coastal and cismontane southern California [Munz and Keck, 1968]. The probable native range is shown in Figure 1. The telegraphplant may also have been native to Mexico (Sonora and Baja California) and eastern Arizona [Wagenknecht, 1960]. Its distribution in Arizona is particularly confusing; Tidestrom and Kittel [1941] list it from western Arizona, while Kearney and Peebles [1951] and McDougall [1973] report it from central Arizona. The issue is further confounded by the creation of a new species, *Heterotheca psammophila* Wagenknecht, which has representatives in these same central Arizona areas and previously had been erroneously identified as four other *Heterotheca* species [Wagenknecht, 1960].

The telegraphplant underwent a rapid spread northward as the state was settled. By the 1890's-1900's it had reached Contra Costa County near San Francisco Bay [Greene, 1897] and the San Jose area.

---

1 Common name follows *Weed Science Society of America* [1971].
Figure 1. Probable native range of *Heterotheca grandiflora* in California. Sources: Colville [1893]; Harshberger [1911]; Hoover [1970]; Munz and Keck [1968]; Nuttall [1840-41]; Wagenknecht [1960].
It soon occupied an area many times its original range. Currently, as shown in Figure 2, it is found the entire length of the 430 mile long Central Valley, in numerous coastal valleys, the Imperial Valley, and a few locations in the northern Mojave Desert. Its confinement to the roadside in this last location is shown in Figure 3.

Characteristically, floras show it inhabiting sandy sites [Munz and Keck, 1968], disturbed areas [Munz, 1935], roadsides [Higgins, 1949; Hunter, 1960] and dry, frequently rocky slopes within its native range [Nuttall, 1840-41; Thorne, 1967; Lathrope and Thorne, 1968]. Though Jepson [1924] lists it as one of the economically important plants of California, telegraphplant has remained a weed of roadsides and other disturbed areas. It has never become an agricultural pest [Stebbins, 1965a] except when introduced into the pineapple fields of Hawaii [Wagenknecht, 1960].

Each head in the inflorescence of the telegraphplant produces a large number of simple fruits. For brevity these are subsequently referred to as achenes or seeds, or sometimes simply disc and ray. Typically, 30-90 are disc achenes, equipped with a pappus which permits efficient dispersal in wind, and a smaller number (25-40) are somewhat lighter ray achenes, lacking a pappus, which are held by the phyllaries for a brief time before being shed adjacent to the plant. Preliminary germination tests on filter paper demonstrated a pronounced difference in the germination of the two types of achenes; the disc germinated rapidly while the ray did not begin germination until that of the disc was well underway and often nearing completion. A literature search failed to reveal any reports of the germination
Figure 2. Current range of Heterotheea grandiflora in California, Nevada, Utah, and northwestern Arizona. Sources: Beatley [1973], and T. Ackerman, personal communication; Clary #1571, JEPS; Flint #54, UTC; Foreman #102, UC; Howell, et al. [1958]; Hunter [1960]; Munz and Keck [1968]; Raven #17285, UC; R. Knight, Tehama County farm advisor, personal communication; Tracey #16515, UC; Twisselmann [1956]; Welsh #9530, BRY.
Figure 3. *Heterotheca*, 4 km north of Beaver Dam, Arizona. Picture taken 6/21/76 along the abandoned Littlefield - St. George road. Precipitation at Beaver Dam totalled 127.0 mm (5.09 inches) within the 1 year period prior to this picture.
dimorphism in this taxon.

The number and size of individuals in plant populations may be regulated during four progressive life cycle stages which Harper and White [1971] developed into a schematic model. The performance and status of the two morphs were examined within this framework to explore the basic assumption that divergent responses would be adaptive to a weedy life cycle. This would permit plants to become established under diverse conditions.

The model begins with the seed bank, the reserve of seed in the soil as determined by the balance between seed input and loss via germination or death. Which seed are recruited from this reserve depends on their response to the "environmental sieve", which is the interaction between the physiological condition of the seed and the capacity of the seed's position in the substrate to fulfill its germination requirements. Changes in the number of plants due to thinning or changes in size due to plasticity responses follow as the third stage, with seed production and the subsequent seed-rain acting as the final step which periodically replenishes the seed bank.

In the telegraphplant, the possibility exists that the two achene types have differential longevity in the seed bank and respond to different environmental triggers for germination, either by exploiting different safe-sites or by utilizing physiological systems that respond differently to the same safe-site. This delayed germination of part of the population's seed is often interpreted as a means of perpetuating the population when unpredictable biotic and abiotic factors eliminate early germinating seedlings. When these factors are such that these early germinating seedlings survive,
they should be at a competitive advantage and suppress the later germinating seedlings. If one morph could be shown to be more "reliable", an optimal strategy would be to preferentially produce that morph when resources are limiting.
HYPOTHESES

The overall null hypothesis is that there are no differences in the functional characteristics (production, physiology, and germination) between the two morphs. This was examined in specific areas by the following null hypotheses.

1. Germination and growth characteristics of the two morphs have no effect on plant biomass.
   Comment: The two morphs were grown together under potentially competitive conditions. Above ground dry weights of plants from each morph were compared within pots by a two-tailed t-test.

2. Germination timing with respect to droughts does not determine which morph becomes established.
   Comment: Survivorship of the two morphs was compared between well-watered pots and those subjected to a drought after germination had begun.

3. Total disc achene germination in the well-watered pots is not different from disc achene germination prior to the drought in either drought treatment.
   Comment: A completely randomized design (CRD) analysis of variance (ANOVA) compared disc achene germination in the three treatments.

4. Drought-stressed plants produce achenes in the same proportion as do well-watered plants.
   Comment: Production of the two achene types was investigated in greenhouse grown plants. Severely drought stressed plants
were compared with all other available greenhouse grown plants with a two-tailed t-test.

5. Neither germination rate nor percent germination are affected by contrasting soil surfaces.

6. The surface effect is the same for both morphs, i.e., maximum germination occurs on the same surface type for both morphs. Comment: Testing this hypothesis is only possible if hypothesis #5 is rejected. Germination rates and percentages were measured on three soil surfaces for both morphs and were compared with a CRD ANOVA followed by the Duncan's new multiple range test (if the ANOVA indicated significant differences were present) for each morph in the high moisture treatment. Total percent germination [transformed to Arcsin (percent germination)\(^{1/2}\)] was analyzed separately for each moisture regime using the same statistical methods. Comparisons were made between morphs as to the location of maximum and minimum germination rates and percentages. Divergent performance on identical surfaces would be considered adaptive as it suggests the two morphs respond differently to the environmental sieve.

7. The two moisture regimes used have identical effects on germination.
Comment: Percent germination (transformed) for each morph was compared between moisture regimes within each soil surface in the prior experiment by two-tailed t-tests.

8. Ray achene germination is not affected by the location of the achene with respect to the surface, i.e., degree of burial.
Comment: Percent germination (transformed) following rewatering
was compared between disturbed and undisturbed surfaces by two-tailed $t$-tests.

9. Ray achene germination differences between prior moisture regimes are due to differential germination rather than differential mortality.

Comment: Germination following rewatering was compared between flats from different prior moisture regimes but within the same soil surface and disturbance treatment. Comparisons were made by two-tailed $t$-tests. Interactions between surface type, disturbance, and prior moisture regime were examined by a three-way factorial ANOVA with two replicates.

10. The two morphs do not differ in their response to light, rate of imbibition of water, or storage contents.

Comment: These physiological tests are pertinent to understanding the responses of the two morphs to the environmental sieve.

11. Plant leachates have no potential effect on the seed bank via the microflora.

Comment: Species mixes of fungi were grown on treated and untreated agar and the number of colonies used as an indicator of antimicrobial potential. These plant leachates could influence the microflora and thus the seed bank.

Additionally, autecological life history data collected by field observations and greenhouse experiments were compared with the attributes comprising the hypothetical "ideal weed."
LITERATURE REVIEW

Germination Ecology

The significance of various selective pressures upon seed germination and seedling establishment characteristics has been reviewed by Stebbins [1970, 1971] and Lindauer and Quinn [1972]. Stebbins [1970, 1974] further notes that adaptations concerning seedling establishment and reproductive efficiency may be the likely factors responsible for many differences between higher categories (genera, families, and orders) in the angiosperms. The characteristics of the seed of any one species represent a series of adaptive compromises between various selective forces [Harper, et al., 1970; Stebbins, 1971]; thus seedling establishment may be the most critical phase of a plant's life cycle [Harper, 1965a; Stebbins, 1974].

These differing requirements of various species for establishment may partly determine the composition of annual communities due to species' differential responses to yearly environmental variability [Juhren, et al., 1956; Evans, et al., 1975]; these dissimilar requirements may also permit closely related species to coexist in the same area [Harper, et al., 1961; Amen and Bonde, 1964; Koller, 1972].

Though many studies have dealt with various physiological characteristics of seeds, Thompson [1970], Koller [1972] and Linhart [1976] note that most of these give little attention to the adaptive significance of germination characteristics. For example, the effect of light on germination has been extensively studied, with its literature extending back to the late 1800's [Evenari, 1965]. Much
less attention has been given to certain ecological insights concerning seed-light interactions. It is only recently that we see reports similar to King [1975] and Gorski [1975] where light filtering through a canopy changes wavelength and prevents the germination of various species until the habitat is disturbed and establishment becomes possible. As with light, similar large segments of the literature deal with after-ripening [Evenari, 1965], temperature-dormancy interactions [Stokes, 1965], and other physiological processes. Koller [1972] has reviewed methods by which seeds "perceive" these and other factors as environmental triggers.

Some studies have been limited to the adaptations of individual species to their environments. These adaptations sometimes are restricted to a limited number of taxa in an area. For example, the radicle of germinating _Marah_ seed may be carried deep into the soil by the elongating bases of the cotyledons. This may enhance survival in a Mediterranean climate [Schlising, 1969]. Other adaptive strategies may be more widespread. Went [1949] and Juhren, et al. [1956] found germination in numerous desert species was controlled by species specific moisture-temperature combinations which permitted the plants to germinate at a time of year when they could complete their life cycle. Broad generalizations on the performance of seed from various habitat types can sometimes be made. Palmblad [1968a] and Linhart [1976] have shown a tendency for some weedy species to limit their germination with increasing seed density, while plants of closed communities and cultivated species sometimes react in the opposite manner, increasing their germination as density increases [Ballard, 1958; Linhart and Pickett, 1973; Linhart, 1976].
Germination Ecotypes

A number of weedy species will germinate only under fairly specific environmental conditions in the lab [Andersen, 1968]. This must be interpreted cautiously, however, to avoid the notion that all populations of a species have identical germination requirements. In a number of species occupying diverse habitats, selective pressures have caused ecotypic differentiation in germination characteristics. In populations of the grass *Danthonia sericea*, Lindauer and Quinn [1972] found the germination of seed from wet habitats was enhanced by light while that from dry habitats was either not affected or inhibited. The percentage of dormant seed produced varied among the populations, as did the subsequent release of dormancy through after-ripening processes. Similarly, populations of the arctic-alpine grass *Trisetum spicatum* possess germination characteristics with differing responses to light, temperature, and chilling treatment [Clebsch and Billings, 1976].

Temperature requirements for germination seem especially sensitive to selective pressures. Smith [1975a] found lowland populations would not germinate under the temperature regime experienced by alpine populations in five species from the Venezuelan Andes. In a number of experiments, Thompson [1975] has shown germination differences with respect to temperature among 20 European populations of *Silene dioica*, and interpreted these differences as adaptive variations of a common physiological control system.

At times selective pressures may be strong enough to produce morphologically distinct seed types in different populations. Plants of *Spergula arvensis* produce either papillate or nonpapillate seed;
the distribution of the two variants in the British Isles has been correlated with latitude and altitude and they have adaptive differences in their temperature optimums for germination [New, 1958].

Additionally, environmental conditions such as photoperiod [Evenari, et al., 1966; Karssen, 1970; Cook, 1975] and temperature [Austin, 1972; Junttila, 1973] have been shown to influence seed characteristics. In *Taeniatherum asperum* (medusahead), this influence has persisted through some of the early phenological stages [Nelson, et al., 1970]. It often seems uncertain whether this is an adaptive response or a physiological oddity; yet its effects must be considered so that one does not attach geneecological interpretations to behavior influenced by maternal environment [Nelson, et al., 1970].

**Seed Polymorphisms**

Within a population, selective pressures need not favor only one type of germination behavior, especially if the different responses of seeds to environmental triggers may enable some to germinate at a time that will avoid unpredictable frosts, droughts, or other disturbances. These mechanisms are often known as polymorphisms, where the germination behavior of certain members of the population differs dramatically from that of a bulk sample of seed gathered from a large number of plants.

Palmblad [1969] reported this type of germination polymorphism in scattered populations of 15 weedy species; Salisbury [1965] found the same behavior in *Plantago major*. The result of these polymorphisms may be periodic germination flushes as in *Oenothera* [Steiner, 1968], *Isanthus brachiatus* [Baskin and Baskin, 1975], and many other species.
This behavior may be interpreted as the "climatic stimulation of those seeds that have attained the appropriate state" [Salisbury, 1965, p. 514]. Harper [1966] has shown germination polymorphisms in the British poppies since one type of treatment alone will not break the dormancy of all the seed of any one species. Cavers and Harper [1966] found both Rumex crispus and R. obtusifolius had germination polymorphisms and subsequently showed that seed from various plants of R. crispus responded differently to identical environmental storage conditions [Cavers, 1974].

It is often found that seed from different positions on the same plant differ markedly in their germination behavior. In several Aegilops species [Datta, et al., 1970; Wurzburger, et al., 1976], the position of the caryopsis within the spikelet has a controlling influence on the degree of dormancy present. Similarly, position within the inflorescence determines the germination behavior of Polygonum lapathifolium seed [Hammerton, 1967] and Triticum aestivum caryopses [Chaussat and Bouinot, 1975].

Some plants have seeds that are strikingly different in morphology and physiology. This condition is usually associated with weedy behavior and an annual life cycle [Harper, 1965a] or growth in arid and semiarid areas [Zohary, 1962]. It is most common in the Asteraceae (especially, but not exclusively, in the Liguliflorae), Chenopodiaceae, Brassicaceae, and Poaceae and sometimes occurs in the Fabaceae and Apiaceae [Zohary, 1962; Harper, 1965b; Harper, et al., 1970]. This predominance of seed polymorphisms in annuals rather than perennials is further reinforced by an example from Stebbins [1965b]: in Crepis and Hypochoeris (Asteraceae) the annual (and
weedy) species have dimorphic seed but the perennial species of both genera are strictly monomorphic. One of the few exceptions to this generalization is *Alysicarpus monilifer*, a perennial legume from India. The dimorphic behavior of its seed is interpreted as an adaptation to a climate with two distinct growing seasons [Maurya and Ambasht, 1973].

The behavior of dimorphic seed has been investigated in a number of ways, and usually differences in germination behavior are found. In addition, one seed type is often adapted to wind or animal dispersal while the other type lacks these adaptations [Stebbins, 1957, 1971]. Selection may favor differences in either germination, dispersal, or both. For example, dimorphic seed from *Cakile maritima* (Brassicaceae) an annual of the coastal strand, appear to have similar germination requirements but differ greatly in dispersal [Barbour, 1970].

The production of dimorphic seed is achieved by different means in different families [Harper, et al., 1970; Salisbury, 1942]. Disc and ray florets often produce different types of achenes in the Asteraceae, although whether the disc or ray are heavier will vary amongst genera or amongst species. Some Brassicaceae produce larger seed at one end of the fruit than the other and may remain indehiscent at one end. Photoperiod is the trigger for shifting from producing one type of seed to another in many Chenopodiaceae and may, as in *Halogoton* [Williams, 1960], result in the death of the plant soon after the second seed type is produced.

Differences in germination timing between seed morphs of dimorphic species vary greatly among examples available in the
literature. In *Atriplex hortensis*, Nobs and Hagar [1974] found a
difference of nearly 7 days between the mean germination times of
the two morphs and were able to show the delay was caused by a slower
imbibition rate in one morph. Other species, such as *Aegilops ovata*
[Datta, et al., 1970], *Dimorphotheca* spp. [Harper and White, 1974],
and *Halogeton glomeratus* [Robocker, et al., 1969] may have other
mechanisms that maintain a portion of one morph's population dormant
for its first year in the soil. Other differences between seed
types include the presence of chlorophyll in only one morph [Negbi
and Tamari, 1963; Robocker, et al., 1969] and variations in storage
contents [Williams, 1960]. These differences correlate with the
contrasting germination strategies of the two morphs.

Physiologically, different responses between seed types have
been found with respect to temperature optimums and ranges for
germination [Datta, et al., 1970; Williams and Harper, 1965; Baker
and O'Dowd, 1976], cold treatment effects [Howarth and Williams,
1972; Grouzis, et al., 1976], response to nitrates [Williams and
Harper, 1965], sensitivity to osmotic solutions [Datta, et al., 1970;
Grouzis, et al., 1976], the presence or absence of light [Negbi and
Tamari, 1963; Grouzis, et al., 1976], and even the quantitative
response to photoperiod during germination [Koller, 1970]. These
divergent responses of the various seed types are often interpreted
in terms of the species' survival of unforeseeable climatic changes
[Datta, et al., 1970; Nobs and Hagar, 1974], especially in species of
saline habitats where osmotic stress may become especially severe
[Ungar, 1971; Werker and Many, 1974].

Becker [1912] generalized that, among visually polymorphic seed,
the larger germinate more rapidly and often show less dormancy.

Salisbury [1942] reinforced this rule and found very few exceptions. The more recent literature has continued this trend with data for species of Asteraceae [Pandey, 1968], Chenopodiaceae [Beadle, 1952; Williams, 1960; Negbi and Tamari, 1963; Ungar, 1971; Nobs and Hagar, 1974], Poaceae [Datta, et al., 1970], and Fabaceae [Grant-Lipp and Ballard, 1964]. Differences in seed size can result in varying abilities in dispersal, competition, and water relations.

Whether or not the more widely dispersed morph will germinate first varies amongst species. One may assume that, among spherical seeded species, the larger seed are dispersed less [Baker, 1974]. Thus, in Chenopodium album the large, early emerging morph remains near the parent [Williams, 1963]. In species where the larger morph germinates first and also has adaptations for dispersal {e.g., bracts in Atriplex hortensis [Nobs and Hagar, 1974]}, early emerging seedlings would be scattered over a greater area while those near the parent would germinate over a more prolonged period.

Several studies have compared the growth of plants from dimorphic seed sown at the same time. In Atriplex hortensis, grown in separate containers, mean germination times for the two seed morphs were 1.4 and 8.25 days, yet mean time to flowering was only 2 days earlier for plants from the rapidly germinating seed [Nobs and Hagar, 1974]. Baker [1974] compared the growth rates of Atriplex patula var. hastata seedlings germinating at the same time from the two morphs. Even though larger seed produced greater root and shoot growth in their seedlings when compared to those germinating concurrently from the more dormant morph, these growth rate differences disappeared after
the seedlings were 2 months old. *Salisbury* [1942] conducted similar tests with *A. patula* under field conditions and found the larger morph produced seedlings more tolerant of unfavorable climatic conditions.

When competition tests are performed, the results are often of greater ecological significance. In subterranean clover stands, mortality was found to be confined to seedlings derived from smaller seed [Black, 1958] while Schreiber [1967] found the outcome of interspecific competition between *Amaranthus* and *Lotus* (birdsfoot trefoil) changed as different seed weight categories were sown together. Ross and Harper [1972] found that early emerging individuals in a population were able to occupy a disproportionate amount of space and thus were better competitors. Since differences between the seed morphs in embryonic capital, growth rate, and the germination response to climatic factors all interact, the conclusions of competition tests are unique to each species-climate combination.

The contact of a seed with the soil surface is of great importance to its water relations. When placed on a water supplying substrate, smaller seed or those with mucilage had a larger contact to volume ratio and thus germinated better than large or rough seed [Harper and Benton, 1966]. Under natural conditions, the ability of a seed to become oriented properly with respect to the substrate may be crucial for establishment. When seed of two *Bromus* species were sown together in equal proportions, the number of seedlings of each species which became established changed greatly as the soil microtopography went from flat to rough [Harper, *et al*., 1965]. The pappus on achenes of Asteraceae has been shown to orient the seed so that
the scar of attachment is in contact with the substrate. When achenes were sown in "unnatural" positions after the pappus had been removed, germination was greatly reduced [Sheldon, 1974].

The responses of species to "safe-sites" (as defined by Harper, et al. [1961]) varies because of differences in seed morphology and physiology (e.g., the response to burial below light penetration), thus this is another factor permitting a number of species to share the same habitat while also limiting the numbers of individuals that can become established [Harper, et al., 1965; Palmblad, 1968a; Sheldon, 1974]. Further, as mentioned by Harper [1965a] and Palmblad [1969], the divergent performance of different seed morphs can permit them to successfully establish in different "safe-sites", possibly much in the same manner as different species.

In certain species, the production of different seed morphs may vary according to the degree of environmental stress. A number of species in Viola, Stipa, Danthonia, and other genera produce cleistogamous flowers near the base of the plant in addition to cross-fertilizing flowers on the more terminal portion of the plant [Stebbins, 1971]. Koller and Roth [1964] found that Gymnarrhena micrantha (Asteraceae) produced aerial flowers only when environmental conditions were favorable; they were considered a "risky" investment as they needed favorable conditions for successful germination. Subterranean cleistogamous fruits were formed regardless of environmental conditions, established themselves reliably, and were considered a "safe" investment.

While dimorphic achenes may be fairly common in the Asteraceae of some areas (e.g., Palestine [Zohary, 1962]), little information
appears in the literature concerning the mechanisms controlling the proportions of the types of achenes produced. Harper, et al. [1970] briefly mention the proportion of ray to disc florets being genetically controlled such that optimal ratios are produced, and Harper [1965a] cites a communication from Zohary indicating that a geographic cline in the proportion of ray to disc florets exists in *Calendula* in Israel. The proportions of the morphs produced need not remain constant; Baker and O'Dowd [1976] found that density stress altered the ratio in *Hypochoeris glabra* (cat's ear).

In any situation where a sharply defined dimorphism exists with regards to dispersal, we can expect the non-dispersed morph often to be in a more suitable habitat than one dispersed at random. Since leachates from plants have been shown to contain alkaloids, phenolics, vitamins, and numerous other plant constituents [Tukey, 1970] which frequently have effects on adjacent organisms [Rice, 1974], we can expect the non-dispersed seed morph may be influenced by these allelopathic chemicals. Leachates may influence the microflora, as Rice [1964] found they inhibited nitrogen-fixing bacteria, or they may directly retard the germination of seed [Datta and Sinha-Roy, 1975], in some cases by causing anatomical and physiological disruptions in the seedling [Lorber and Muller, 1976].

Harper [1965a] concluded that seed polymorphisms may be a valuable aid to a species behaving as a weed since they provide the potential for the occupation of different microsites while their periodic germination permits a portion of the population to avoid some environmental hazards [Bunting, 1960]. This parallels some characteristics of Baker's [1974] "ideal weed" which would possess
internally controlled intermittent germination and could thus satisfy its germination requirements in many environments. In this way, seed polymorphism aids in achieving some characteristics of the "general purpose genotype" which Baker [1965, 1974] considers conducive to weedy behavior as it increases a plant's tolerance of abiotic conditions by allowing it to become more plastic in its responses to environmental factors.
METHODS AND MATERIALS

Life History

Autecological life history data were collected from field observations and greenhouse photoperiod and breeding system experiments.

Water Relations

The overall availability of water to the telegraph plant and some other roadside species was evaluated with a Scholander pressure chamber [Waring and Cleary, 1967] shortly prior to dawn.

To determine availability of water throughout the day, transpiration ($E_s$) was calculated following Larcher [1975]:

$$E_s = \frac{C_i - C_a}{r}$$

where $C_i$ is leaf water vapor content ($g \text{ cm}^{-3}$), $C_a$ is atmosphere water vapor content, and $r$ is resistance to transpiration ($s \text{ cm}^{-1}$). Leaf resistance was measured as in the greenhouse drought stress tests, with added precaution of shading the leaves before beginning measurements to reduce temperature differences between the sensor and the leaf [Morrow and Slatyer, 1971]. Leaf temperatures (before and after shading) were measured with a Barnes infrared radiation thermometer; air temperature and relative humidity were measured with a Bendix "Psychron" electrically aspirated psychrometer. $C_i$ was obtained using shaded leaf temperatures, assuming saturation of
the leaf with water vapor. $C_a$ was calculated from the psychrometer measurements.

**Temperature Regimes**

Temperature regimes for all experiments conducted in the Percival germination chamber were arbitrarily selected after consulting climatological data for locations throughout the species range (Appendix A). Mean germinator temperatures are given in Table 1.

**Table 1. Mean germinator temperatures. High/low in °C.**

<table>
<thead>
<tr>
<th>Test</th>
<th>Temperatures$^1$</th>
<th>Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Competition</td>
<td>19.0/6.0</td>
<td>74 days</td>
</tr>
<tr>
<td>Soil microtopography</td>
<td>18.5/4.5</td>
<td>through day 38</td>
</tr>
<tr>
<td></td>
<td>11.5/2.0</td>
<td>days 39 - 78</td>
</tr>
<tr>
<td></td>
<td>17.0/6.0</td>
<td>days 79 - 99</td>
</tr>
<tr>
<td>Disturbance of soil</td>
<td>16.0/6.0</td>
<td>19 days</td>
</tr>
<tr>
<td>microtopography</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^1$Temperatures were measured by maximum - minimum recording thermometers.

**Photoperiod**

Cool white fluorescent lights provided a 12 h photoperiod during the warm half of the temperature cycle in all tests conducted in the germinator. This is representative of field conditions during part of the potential germination period, as 12 h photoperiods (sunrise - sunset) occur about September 25 and March 17 throughout this species' range [List, 1968].
Soils

All soil textures used (except the roughest surface in the soil microtopography experiment) were formed by mixing greenhouse soil (clay loam - silt loam - silty clay loam) with sand. This soil mixture approached the range of textural categories (determined by following the hydrometer method of Bouyoucos [1962] as closely as facilities allowed) found where the telegraphplant grows. Textures of soils used in lab tests plus samples from selected field sites are shown in Table 2, and agree with the generalization of Wagenknecht [1960] that taxa in Heterotheca section Heterotheca frequently inhabit sandy areas.

Competition Tests

Achenes were collected from mature plants in Washington County, Utah, during fall of 1974 and were stored at room temperature prior to planting in July 1975. Visibly damaged and shrunken achenes (predominantly either nonviable or lacking an embryo) were removed.

Circular 19 cm diam plastic pots were filled 17 cm deep with a loam soil. Pots were watered prior to the experiment to germinate most contaminating local weed seed. Fifty-four achenes (27 of each morph) were sown per pot at a depth which was only sufficient to prevent movement when they were watered. All achenes were 2.3 cm from their nearest neighbor in a pattern where approximately 65% of the nearest neighbors were of the other morph.

Twelve pots were divided into three treatments; one with an uninterrupted moisture supply and two with droughts initiated after 10 and 12 days of moisture. These droughts persisted until day 41.
Table 2. Laboratory and field soil texture data.

<table>
<thead>
<tr>
<th>Sample&lt;sup&gt;1&lt;/sup&gt;</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
<th>I</th>
<th>J</th>
</tr>
</thead>
<tbody>
<tr>
<td>% sand</td>
<td>43.5</td>
<td>55.0</td>
<td>20.0</td>
<td>80.0</td>
<td>53.0</td>
<td>84.5</td>
<td>89.0</td>
<td>61.0</td>
<td>78.0</td>
<td>87.5</td>
</tr>
<tr>
<td>% silt</td>
<td>32.5</td>
<td>31.5</td>
<td>51.0</td>
<td>15.5</td>
<td>28.0</td>
<td>10.5</td>
<td>6.0</td>
<td>24.0</td>
<td>8.0</td>
<td>9.0</td>
</tr>
<tr>
<td>% clay</td>
<td>24.0</td>
<td>13.5</td>
<td>29.0</td>
<td>4.5</td>
<td>19.0</td>
<td>5.0</td>
<td>5.0</td>
<td>15.0</td>
<td>14.0</td>
<td>3.5</td>
</tr>
<tr>
<td># of replicates</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Soil type</td>
<td>loam</td>
<td>sandy loam</td>
<td>clay loam</td>
<td>loamy loam</td>
<td>loamy sandy loam</td>
<td>loamy sandy loam</td>
<td>sand</td>
<td>sandy loam</td>
<td>sandy loam</td>
<td>sand-loamy sand</td>
</tr>
</tbody>
</table>

Germination was recorded and pots were rerandomized daily for the first 27 days and at irregular intervals thereafter. A template was used to identify emerging seedlings.

The experiment was run in the germinator (see Table 1 for conditions) for 74 days. To achieve more realistic lighting conditions, plants were moved to a warm greenhouse (20 - 25°C, 15.5 h day\(^{-1}\) photoperiod) for the following 29 days. Infestation of the plants with white flies required that the experiment be completed in a growth chamber (Sherer model CEL 37 - 14) set at 23°C day and 10°C night with a photoperiod of 14 h day\(^{-1}\) from a combination of incandescent and fluorescent lights.

While in the germinator, all pots were watered with measured volumes applied as a light spray to prevent disturbing the soil surface. The approximate depths of water applied to the drought treated pots prior to the drought was 2.5 cm; the well watered pots had received 3.0 cm by this time. Except during drought treatments, pots were watered as needed to keep the surface moist. After day 74, pots were either sprinkled or allowed to absorb water from a shallow tray.

Plants from half of the drought treated pots were harvested on day 132, 91 days after the end of the drought. All remaining plants were harvested on day 158, 117 days after the end of the drought (for those so treated). Oven dry weights (37 h at 65°C) were determined for all plants.

Following harvest, pots were placed in a warm greenhouse under various drought-moisture-disturbance combinations for the winter and spring of 1976.
Greenhouse Drought Stress Tests

Seedlings germinated from the fall 1974 Washington County seed crop were planted in the greenhouse during late fall 1974. In spring 1975, while plants were still in the rosette stage, they were transplanted into a loam soil in 17 cm diam, 50 cm deep insulated metal cylinders. A 2.5 cm diam plastic tube discharged water 26 cm below the soil surface to provide more realistic conditions and prevent evaporation.

Plants were watered via the soil surface as needed (usually at 5-6 day intervals) until 7/3/75. Subsequently, measured amounts of water were added via the tubes until after heads had been collected in early October. Plants of similar size (in height and number of stalks) were paired where possible: one was well-watered (usually 400 mL day\(^{-1}\)) while the stressed plant received from 75% to 40% of this amount.

To simulate field conditions, water was added in both the morning and evening. This recharged soil moisture when transpiration was negligible but permitted the plants to deplete their water supply during the day. In stressed plants resistance to gas exchange would increase, much as could happen under heavy transpiration and low soil moisture in the field [Hitchie, 1974].

Diffusive resistances of the bottom surfaces of leaves from the central section of the stalk were measured with a model LI 60 Lambda diffusive resistance meter (horizontal sensor) as described by Kanemasu, et al. [1969]. The meter transit times were read between 30 and 40 μA with a stopwatch and resistance values were obtained from calibration curves. This quantified the relative stomatal apertures
in the different treatments as a means of confirming drought-stress. In addition, the heights of plants were measured at intervals as another potential indicator of drought.

The first head to flower and ripen on each greenhouse plant was from the top of the center stalk. These heads, plus heads in the same position on other stalks, were removed before any achenes were shed and the two morphs were counted.

**Soil Microtopography Tests**

Achenes were collected from approximately 590 ripe heads on 80 plants in Washington County, Utah, and Mojave County, Arizona, on 10/19/75. They were stored at room temperature until germination experiments began in March 1976. All visibly damaged or shrunken (empty) achenes were excluded. Viability of all excluded achenes plus 250 ray and 400 disc achenes from the sorted material was determined by the tetrazolium test (incubation in 0.25% 2,3,5 triphenyl 2H tetrazolium chloride for 23-25 h in the dark; hard ray achenes were punctured prior to incubation). The 200 achenes sown in each experimental unit (flat of soil) were composed of four subsamples selected from different times during the sorting process in order to assure uniformity among the experimental units.

Three contrasting soil surfaces ("flat", "gravelly", and "clods") were prepared with seed free soil (moist soil was autoclaved 15 min at 20 psi) placed approximately 5 cm deep in 17.5 x 12.5 cm cardboard flats. A sandy loam soil without any large soil clods present was used as the flat surface. The gravelly surface was made from soil of identical texture to which angular pea gravel (mostly less than 1 cm
in length) had been added until it comprised 25% of the soil's weight. Additional gravel (125-150 g) was added to the surface of each flat so that very little bare soil was present. A clod surface was assembled using clay loam - silty clay loam soil covered with 2 - 2.5 cm diam chunks of identical texture soil. A few smaller chunks were placed in unfilled spaces.

For the sake of replicability, the roughnesses of the three surfaces were quantified with a "10 pin soil microtopography measuring device" similar to that pictured and described in Harper, et al. [1965, p. 277] and also functionally analogous to one described by Boorman and Woodell [1966]. Ten rods, held by a frame so their upper ends were adjacent to graph paper ruled in mm, were lowered onto the soil surface while the device was kept horizontal by use of a spirit level. Sets of values read off the graph paper were analyzed by methods similar to Harper, et al. [1965]. A completely randomized ANOVA was used with each flat treated as a variable and each set of 10 readings within a flat considered a treatment. The mean square error term of the ANOVA for each variable (flat) is the SM-TV (soil microtopography variance) in mm² for that flat. SM-TV values are presented in Table 3. These SM-TV values will remain unchanged at any height so long as the frame remains horizontal.

This experiment tested the performance of the two achene morphs when sown in pure stands on the three soil surfaces under high and low moisture regimes. Each morph was sown in four replicates on the three soil surface treatments with this design being duplicated for both moisture regimes, producing a total of 48 flats.
Table 3. Soil microtopography variance values.

<table>
<thead>
<tr>
<th>Surface</th>
<th>Number of flats measured</th>
<th>Number of sets of measurements per flat</th>
<th>Mean SM-TV (mm²)</th>
<th>Comparable surfaces in Harper, et al. [1965] (mm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flat</td>
<td>4</td>
<td>5</td>
<td>6.9</td>
<td>6.43 Grade &quot;D&quot;</td>
</tr>
<tr>
<td>Gravelly</td>
<td>4</td>
<td>5</td>
<td>13.6</td>
<td>-</td>
</tr>
<tr>
<td>Clods</td>
<td>8</td>
<td>10</td>
<td>65.8</td>
<td>60.59 Grade &quot;C&quot;</td>
</tr>
</tbody>
</table>

At 200 achenes per flat, a density of nearly one achene per cm² was achieved. Prior microtopography trials have used densities of approximately one seed per 3 cm² [Harper, et al., 1965], one seed per 2 cm² [Evans and Young, 1972] and one seed per cm² [Palmblad, 1968a] in their highest density sowing for both large and small seeded species. Achenes of both morphs were sown from a height of 30 cm following Harper, et al. [1965] and Palmblad [1968a]. A 15.5 x 11 cm template was used to reduce the number of achenes falling close to the edge of the flat.

The experiment was initiated in a warm greenhouse and was moved into the germinator (see Table 1 for conditions) on the third day. All flats were watered by sprinkling from a nozzle moved quickly over a random arrangement of flats. The high moisture flats were sprinkled every second day, while flats under the low moisture regime initially were watered every fourth day. The low moisture treatments reverted to the same two day frequency as the high moisture flats on day 19 for the low moisture disc treatment and on day 38 for the low moisture ray treatment.
Germination was recorded daily for the first 44 days and at 2 to 3 day intervals thereafter. Flats were rerandomized whenever seedlings were counted. Germination rates were calculated for all flats in the moist treatment following the method of Schimpff [1976]. Rates for disc achenes were calculated from data through day 39, with maximum germination being taken at day 41. Data through day 99 was used in calculating rates for ray achene germination, with maximum germination also being taken on day 99. Total percent germination (always expressed as percent of viable seed sown) was recorded for all flats; here disc totals were taken on day 46 and ray totals on day 99.

Following day 99, all flats containing ray achenes were stored dry at warm lab temperatures (20 - 30°C) for 2.5 months. Each treatment of four flats was equally divided, the surfaces of two flats were disturbed, all were watered and returned to the germinator (conditions in Table 1). The device used to disturb the surfaces (a set of nine nails) was thrust into the soil and rotated 90° in four sections of each disturbed flat. Total germination by day 19 was recorded and calculated as the percent of viable seed believed to be remaining in the soil after the initial 99 day germination test.

**Physiological Tests**

*General.* Achenes used in these tests were collected 10/19 and 10/25/75 in Washington County, Utah, and Mohave County, Arizona, and were stored at room temperature until used.

*Light requirements.* Achenes were arranged in monomorphic groups of 50 achenes on filter paper in petri plates. All plates were moistened with 4 ml of tap water, sealed with plastic wrap, and dark
treated plates were wrapped in foil; both morphs were treated identically. Three replicates per treatment per morph were placed in the germinator at 16.0/6.0°C with a 12 h photoperiod. Disc achene germination was recorded after 4 days. Ray achenes failed to germinate until the temperature rose to 25°C on day 21. Percent germination was subsequently recorded after 4 days at room temperature (21°C). Additionally, three foil-wrapped petri plates of 50 disc achenes each were placed in a dark, constant 27°C Sherer growth chamber. Various plates were examined between 4 and 14 days.

**Embryo excision.** One hundred ray achenes were placed on moist filter paper in petri plates, kept at room temperature (20°C), and illuminated by fluorescent light. After 17-50 h of imbibition, 15 embryos were crudely excised and replaced in the petri plates with the undisturbed achenes. Development of excised and unexcised achenes was observed for 5 days following the beginning of imbibition.

**Imbibition rate.** Groups of 50 achenes of each morph were compared in their rates of imbibition when placed between two moist pieces of filter paper. At intervals they were blotted dry twice, weighed in a group on an Ainsworth Type 10 N analytical balance, and then returned to the moist filter paper. Results were calculated as the percentage increase over the dry achene weight. It was necessary to remove the pappus of the disc achenes by singeing it in a gas flame (without damaging the achene itself) since pappus fragments would be shed throughout the experiment.

**Achene storage contents.** Achenes were separated into monomorphic samples of 3 g each, with two replicates for each morph. All shrunken, unfilled achenes and corolla debris were removed. Tetrazolium tests
revealed 98% viability in the disc achenes and 94% viability in the ray achenes; however, both morphs contained embryos in 99% of the sample tested.

Achene weights and weights of different achene components were determined from counted subsamples on an Ainsworth Type 1ON analytical balance. Pappus weight was determined by weighing the disc achenes before and after the pappus was singed off in a gas flame. Achenes of both morphs were germinated on filter paper, the seed coats removed from the cotyledons, dried, weighed, then redried and reweighed.

Storage contents were determined by Dr. James MacMahon's laboratory for percent lipid using a Soxhlet apparatus and an ether extraction technique [AOAC, 1964] and for percent protein (calculated from total nitrogen) using a nitrogen gas analyzer and the Dumas procedure [AOAC, 1970] on 100 mg subsamples of the material from the lipid tests.

Achene components were partitioned into percentages of total weight for the pappus, seed coat, and embryo. Percent lipid and protein data for intact achenes were multiplied by the achene weight to arrive at a value in mg. Percent composition of the embryo was estimated by assuming little or no lipid or protein was present in the seed coat or pappus. (Percent composition of embryo = mg of that compound in achene/embryo weight in mg.) The sum of the lipid and protein percentages was subtracted from 100 to yield the percent carbohydrate in the embryo.

The plant's energy cost for producing each morph was calculated from Penning de Vries [1972, Table 1] with the following assumptions: plant utilizes NO$_3^-$ rather than NH$_4^+$; seed coat and pappus are
cellulose; carbohydrate is stored as sucrose. Morphs were compared in terms of numbers of each morph produced compared to parental investment per head.

**Anti-microbial Tests**

A brief survey test was designed to reveal potential allelopathic chemicals in the telegraph plant. Plant material (the entire aboveground portion of several plants in bud) was collected 9/14/75 in Mojave County, Arizona, transported in an ice chest, and processed within 48 h of harvesting. A leachate was prepared by spraying deionized water over the plant material during a 7 h period. The extract was prepared by homogenizing approximately 200 g of plant material with 500 mL deionized water in a blender. Debris was strained out and rinsed until a final volume of 1800 mL was obtained. The leachate and extract were frozen 1 year, then thawed, stirred, and filtered through sterile Whatman #1 qualitative filter paper on an aspirated Buchner funnel. Rice [1964] found this method sufficient to cleanse his plant extracts.

This material was used in bioassays immediately and eight days later. Sterile 0.05M phosphate buffer (pH 7) was inoculated with species mixes of fungi (two species in the first test, four in the second) and added to all petri plates at 1.0 mL plate⁻¹ for the first test and 0.1 mL plate⁻¹ for the second. Each plate also received 1.0 mL of deionized water (control), leachate, or extract in the first test and 1.9 mL in the second. Partly cooled PDA was poured over this and plates were incubated at room temperature (20 - 21°C). Nine replicates were used for each treatment.
The number of colonies of a species was used as an indicator of anti-microbial potential.
RESULTS

Life History

Field observations on rosettes at the Arizona sites are summarized by Figure 4. Numerous rosettes persisted throughout the summer and did not begin significant growth until the following winter or spring. In more mesic areas, such as some California locations, the plant grows as an annual, as it does in the greenhouse.

From experiments on greenhouse-grown rosettes, the upward growth in the spring was found to be sensitive to photoperiod. Long days (simulated by the night interruption technique) promoted rapid upward growth of only one stalk while short days promoted rosette formation. Naturally lengthening daylengths later promoted the upward growth of several stalks, as often seen in the field (Figure 5). Rosette fate in the first spring may be determined by whether it is large enough to respond to the long day photoperiod cue.

The period of summer rosette growth may be a time of development of a root system capable of supporting rapid growth during the subsequent season. A rosette (6 cm high, 7 cm diam) excavated in the fall at the Beaver Dam site had a taproot greater than 1 mm diam at the final pit depth of 76 cm, while a mature telegraphplant excavated at the sandy Ivins site possessed a taproot still over 1 mm diam when the excavation was abandoned at 135 cm.

Rosettes appear to have a "plastic" response with regards to flowering, as shown in Figure 4. In both Arizona and California during the late fall of 1975, some rosettes produced short flowering stalks
Figure 4. Key points in the life cycle of *Heterotheca grandiflora*. The number of plants responding at different points and surviving (out of 79 plants originally marked) are given in parentheses for the Mojave County, Arizona, populations. The decision points (diamonds) are unknown for field populations; speculation suggests A may be achievement of a sufficient size to respond to long spring photoperiods; B may be a number of factors, possibly extreme drought stress; C may be a requirement for a certain minimum size.
Figure 5. Mean heights of plants under night interruption and natural daylength. Squares = night interruption, circles = natural daylength. Numbers in parentheses represent the mean number of lateral shoots produced.
Flint, #55, UTC]. All surviving plants in this category flowered the following spring also, as did some which remained vegetative in the fall.

Plants flowering in the field during spring continue growing throughout summer and flower again in the fall, together with plants that did not flower at all in the rosette stage. There are indications that fall flowering may be sensitive to photoperiod; artificially shortened days promoted the flowering of large, vegetative plants in the greenhouse.

The plant appears to have some limited self-pollinating ability when pollinators are excluded in the greenhouse, but experiences much improved seed set (especially in the pistillate ray flowers) in the field. Viability of field collected seed (fall 1975) was 89% in disc achenes and 91.5% in ray achenes. Even enclosed heads in the greenhouse had fairly high viability, disc 76% in gelatin capsules, 57% in nylon stockings; ray 24% in the capsules, 28% in the stockings. Undoubtedly the disc florets self-pollinated when the flower grew against the end of the stocking or capsule and additional pollen fell into the pistillate ray florets.

Beeflies (Expoprosopa sp.) are potential pollinators which were frequenting both Heterotheca and Baileya in fall and early summer. Specimens are in the USU insect collection. Though not conclusively identified to species, they closely resemble E. divisa (Coq.).

On all desert sites, a tremendous amount of the fall seed crop was lost to a Lepidopteran larva which entered the heads and consumed part of the immature achenes. No preference between the two types of achenes was noticed. This seed predator was collected in the larval
stages in Washington and Mojave Counties during 10/75 and tentatively identified as Noctuidae. They were brought into the lab where they pupated, three finally emerging 2 - 5 months later. E. W. Rockburne of the Canadian National Collection identified the adults as *Heliothis phloxiphaga* G&R. They are now deposited in the USU insect collection.

**Water Relations**

Xylem balancing pressures (Table 4) are all much less negative than the classic wilting point of -15 bars; thus, the plants have a considerable amount of moisture available to them. The distribution of precipitation (Figure 6) shows the dates of these readings were not during abnormally moist periods. Except for *Larrea*, all species sampled showed xylem balancing pressures less negative than the classic wilting point.

**Table 4. Dawn xylem balancing pressure in *Heterotheca*.** Xylem balancing pressure approximates water potential.

<table>
<thead>
<tr>
<th>date</th>
<th>xylem balancing pressure (bars)</th>
<th>site</th>
<th>number of plants tested</th>
</tr>
</thead>
<tbody>
<tr>
<td>9/12/75</td>
<td>-7.1</td>
<td>B</td>
<td>10</td>
</tr>
<tr>
<td>10/19/75</td>
<td>-9.6</td>
<td>M</td>
<td>6</td>
</tr>
<tr>
<td>10/19/75</td>
<td>-9.8</td>
<td>B</td>
<td>7</td>
</tr>
<tr>
<td>10/20/75</td>
<td>-10.0</td>
<td>I</td>
<td>3</td>
</tr>
<tr>
<td>6/21/76</td>
<td>-7.4</td>
<td>I</td>
<td>6</td>
</tr>
<tr>
<td>6/22/76</td>
<td>-5.8</td>
<td>B</td>
<td>10</td>
</tr>
<tr>
<td>6/23/76</td>
<td>-7.7</td>
<td>M</td>
<td>8</td>
</tr>
</tbody>
</table>

1 Sites: I = Ivins, B = Beaver Dam, M = Mesquite.
Figure 7 represents over 200 individual leaf resistance measurements on a total of 17 plants from the three sites during the 5 day period of June 20 - 24, 1976. Each of the 33 data points used here is the mean of five-six successive readings taken on an individual plant. The vapor pressure deficit (vpd; derived from $C_i - C_a$) curve was compiled from 39 data points.

In order to reasonably represent resistance and transpiration, it was necessary to eliminate six points of Ivins data after 1000 during one especially hot day as resistance rose to 13.5 s cm$^{-1}$. Yet, even at this high resistance, transpiration remained at an average of 1 gH$_2$O dm$^{-2}$ h$^{-1}$ since leaf temperature was at or above air temperature. Several measurements prior to 1000 on this day are responsible for the high transpiration points on the left side of the graph.

Each day, vpd followed time in a regular manner, as one would expect. The lowest vpd point on the graph (0.022 g H$_2$O dm$^{-3}$) could be derived from a situation of leaf temperature = air temperature = 27°C at 15% relative humidity while the highest point (0.034 gH$_2$O dm$^{-3}$) could result from leaf and air temperatures of 34°C with relative humidity at 10%. These values are similar to those measured under field conditions, although more extreme values were obscured by the curve fitting process. Temperatures of 38°C were reached on several afternoons, but accompanying high winds made it impossible to continue making resistance measurements.

Resistance tended to increase slightly in a linear manner throughout the day (regression significant at $P <0.005$). The average value at 0900 would be 6 s cm$^{-1}$, increasing to 8.5 s cm$^{-1}$ at 1600.
Figure 7. Water relations of *Heterotheca* along desert roadsides. Curves summarize 5 days of data, specific relationships between these variables are shown by correlations given in the text.
Product moment correlations (a measure of the degree of inter-dependence) were determined for the three variables using all 39 data points. They indicate a negative correlation between resistance and transpiration (-0.589, \( P < 0.01 \)), a positive correlation between resistance and vpd (+0.673, \( P < 0.01 \)), and no relationship between transpiration and vpd (+0.107, N.S.). As vpd increases through the day, resistance increases and thus partly restricts transpiration. Because of this stomatal control, we see no relationship between transpiration and vpd.

Overall, transpiration remained high (1.4 - 1.5 gH\(_2\)O dm\(^{-2}\) h\(^{-1}\)) throughout the hottest part of the afternoon. Thus, even though it can regulate water loss by stomatal control, this plant loses significant amounts at a time when the natural community is likely under severe drought stress.

Rosette transpiration appeared to be of the same magnitude as that of mature plants. The environment surrounding a rosette may be quite severe; soil surface temperature approached 60°C before air temperature reached 40°C. Thus, the need for a deep root system, even in rosettes, is evident.

Diffusive resistance was also measured in the field on 9/12, 9/13 and 10/19, 1975, although the leaf shading precaution of Morrow and Slatyer [1971] was not followed. Resistance values through all but the hottest portion of the day were comparable to 1976 values.

Site Description

In Utah, the telegraph plant has established itself along the edge of U. S. 91 (the old Littlefield - St. George road) 19 km west
of St. George, near the turnoff to Ivins Reservoir (site "I"). A number of telegraphplants were also found growing adjacent to the reservoir along with Xanthium strumarium\(^1\) and Descurainia sophia. This area, at an altitude of 950 m, is in a shrub community (Artemisia filifolia, Coleogyne ramosissima, Chrysothamnus sp.) a short distance below a juniper woodland. Scattered Yucca angustissima and Prunus fasciculata also occur in the area.

Along U. S. 91 in Arizona (4 and 7 km north of Beaver Dam, site "B"), the telegraphplant was growing along the roadside in a community dominated by Larrea tridentata, Franseria dumosa\(^2\) (which evades the dry period by its drought deciduous habit), and Opuntia (2 species) at an altitude of 650 - 670 m. Occasional representatives of Yucca brevifolia and Hymenoaclea salisola were in the area, with Lycium pallidium in the washes. Bromus rubens, Erodium cicutarium and an Eriogonum were the major annual components in the desert.

Another stand in Arizona was found along Interstate 15, 3 km northeast of the state line at Mesquite, Nevada (site "M") at an altitude of 530 m. The desert community here was composed primarily of Larrea tridentata, Franseria dumosa, Opuntia sp., and Oryzopsis hymenoides.

Table 5 shows the other species growing with Heterotheca and their potential "strategies" for survival in the harsh desert climate.

---

\(^1\) Nomenclature follows both McDougall [1973] and Kearney and Peebles [1951] except where noted.

\(^2\) Current practice is to include Franseria in Ambrosia.
Table 5. Adjacent desert roadside species and their "strategies".

<table>
<thead>
<tr>
<th>Species</th>
<th>Location¹</th>
<th>&quot;Strategy&quot;²,³</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allionia incarnata</td>
<td>I</td>
<td>S, C₄ (W+C)</td>
</tr>
<tr>
<td>Abronia elliptica</td>
<td>I</td>
<td>D</td>
</tr>
<tr>
<td>Aster canescens</td>
<td>B, M, I</td>
<td>P</td>
</tr>
<tr>
<td>Baileya pleniradiata</td>
<td>B, M, I</td>
<td>P</td>
</tr>
<tr>
<td>Bromus rubens</td>
<td>B, I</td>
<td>D</td>
</tr>
<tr>
<td>B. tectorum</td>
<td>B, I</td>
<td>D</td>
</tr>
<tr>
<td>Centaurea melitensis</td>
<td>B</td>
<td>D</td>
</tr>
<tr>
<td>Croton longipes (McDougall only)</td>
<td>B, I</td>
<td>?</td>
</tr>
<tr>
<td>Cynodon daatylon</td>
<td>B</td>
<td>S, C₄ (D+T)</td>
</tr>
<tr>
<td>Datura meteloides</td>
<td>B</td>
<td>S, P</td>
</tr>
<tr>
<td>Descurainia sophia</td>
<td>I</td>
<td>D</td>
</tr>
<tr>
<td>Dithyrea wislizenii</td>
<td>I</td>
<td>D</td>
</tr>
<tr>
<td>Encelia virginensis (McDougall only)</td>
<td>B, I</td>
<td>P</td>
</tr>
<tr>
<td>Erodium cicutarium</td>
<td>B, I</td>
<td>D</td>
</tr>
<tr>
<td>Euphorbia albo-marginata</td>
<td>B, I</td>
<td>S, C₄ (W+C)</td>
</tr>
<tr>
<td>E. parryi</td>
<td>I</td>
<td>C₄ (W+C)</td>
</tr>
<tr>
<td>Hilaria rigid</td>
<td>I</td>
<td>S, P</td>
</tr>
<tr>
<td>Pectis papposa</td>
<td>I</td>
<td>S, C₄ (S+T)</td>
</tr>
<tr>
<td>Rumex hymenosepalus</td>
<td>I</td>
<td>D</td>
</tr>
<tr>
<td>Salsola kali</td>
<td>B, M, I</td>
<td>S, C₄ (W+C)</td>
</tr>
<tr>
<td>Sphaeralcea parvifolia</td>
<td>M, B</td>
<td>P</td>
</tr>
<tr>
<td>Stephanomeria pauciflora</td>
<td>B</td>
<td>P</td>
</tr>
<tr>
<td>Tribulus terrestris</td>
<td>I</td>
<td>S, C₄ (W+C)</td>
</tr>
</tbody>
</table>

¹ I = Ivins, B = Beaver Dam, M = Mesquite. Exact locations and description in text.

² S = vigorous in September, 1975; D = vigorous in May 1976 but dying or dormant in June 1976; P = biennial or perennial

Germination Introduction

Germination in both morphs was of the common epigeous type; the cotyledons are green and presumably photosynthesize. A large proportion of the photosynthate may be allocated to the root system, as seedlings of both morphs sometimes resprouted when the cotyledons and young leaves were removed, even if this was done in the very early stages.

Mature achenes collected in Alameda, Contra Costa, and Los Angeles Counties in California all showed a germination pattern similar to the achenes from Utah and Arizona used in all major tests.

Competition Tests

Disc achenes (subsequently called disc) germinated rapidly in all pots; by day 15, 98.5% of all germinating disc had emerged. Only one disc germinated after the drought in the eight drought treated pots; while in this same set of pots only one ray achene (subsequently called ray) germinated before the drought. An analysis of variance revealed the number of disc germinating in the control was not significantly different from those germinating in either of the other two treatments prior to the drought (Figure 8). Thus, approximately 2.5 cm of moisture applied to these pots before the drought germinated essentially the entire population of viable disc in the soil. The germination progress data and seedling response to drought is illustrated in Figure 8.

A comparison of disc and ray germination in the four control pots, plus the dry weight distributions of plants within pots, is shown in Table 6. Within each pot the mean dry weight of disc plants
Figure 8. Disc and ray germination under well-watered and drought conditions. Disc are represented by closed circles, ray by open squares. Arrows indicate initiation of the droughts. The ray germinating on day 12 was in one of the drought treated pots; all other ray are in the well-watered pots. Maximum disc germination is not significantly different between any of the three treatments (means are 18.5, 17.0, and 16.5; \( F = 0.629 \)).
Table 6. Germination and biomass of plants from disc and ray achenes.

<table>
<thead>
<tr>
<th>Pot #</th>
<th>Achene type</th>
<th>Total</th>
<th>Mortality</th>
<th>Survivors</th>
<th>Days when survivors germinated</th>
<th>Mean dry weight (g)(range)</th>
<th>Difference between morphs (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.2</td>
<td>disc</td>
<td>15</td>
<td>1</td>
<td>14</td>
<td>7 - 13</td>
<td>0.43 (0.23-0.56)</td>
<td>0.22 *</td>
</tr>
<tr>
<td></td>
<td>ray</td>
<td>7</td>
<td>4</td>
<td>3</td>
<td>15 - 19</td>
<td>0.21 (0.11-0.31)</td>
<td></td>
</tr>
<tr>
<td>2.</td>
<td>disc</td>
<td>20</td>
<td>0</td>
<td>20</td>
<td>6 - 15</td>
<td>0.31 (0.18-0.50)</td>
<td>0.29 *</td>
</tr>
<tr>
<td></td>
<td>ray</td>
<td>5</td>
<td>1</td>
<td>4</td>
<td>24 - 91</td>
<td>0.02 (0.01-0.03)</td>
<td></td>
</tr>
<tr>
<td>3.</td>
<td>disc</td>
<td>20</td>
<td>2</td>
<td>18</td>
<td>6 - 15</td>
<td>0.31 (0.16-0.48)</td>
<td>0.26 *</td>
</tr>
<tr>
<td></td>
<td>ray</td>
<td>12</td>
<td>1</td>
<td>11</td>
<td>23 - 97</td>
<td>0.05 (0.01-0.11)</td>
<td></td>
</tr>
<tr>
<td>4.</td>
<td>disc</td>
<td>19</td>
<td>0</td>
<td>19</td>
<td>6 - 13</td>
<td>0.33 (0.11-0.59)</td>
<td>0.24 *</td>
</tr>
<tr>
<td></td>
<td>ray</td>
<td>9</td>
<td>4</td>
<td>5</td>
<td>28 - 67</td>
<td>0.09 (0.07-0.10)</td>
<td></td>
</tr>
</tbody>
</table>

* = significant at P<0.01

1 Plants harvested on day 158.
2 This is the only pot where the ranges overlap.
is significantly greater than those from ray, as shown by the t-test. A comparison of the ranges of dry weights within pots reveals overlap in only one pot. In general, the ray plants were much smaller and heavily shaded by the disc plants.

The progress of germination, disc mortality, and ray biomass at harvest in the drought treated pots is shown in Table 7. Biomass of these ray plants appears comparable to that of disc plants grown under more crowded conditions, although there was at least a 40 day delay in the ray's growing period. Plant development at harvest ranged from seedling to early rosette stages. Ray germination was spread out considerably compared to the disc; 10 - 12 days of moisture germinated essentially the entire disc population (which perished in the subsequent drought) while 91 continuous days of moisture (pots 6, 7, 10, 11) and 117 days (pots 5, 8, 9, 12) germinated only 37.5% and 81%, respectively, of the total number of ray that eventually germinated.

Following harvest, rewatering, and movement into the greenhouse, ray germination resumed within the first two weeks in several pots. Intermittent germination continued, especially after disturbance of the soil surface, until termination of the experiment 11 months after the achenes were sown. Ray which had aged in the soil for 10 months appeared to germinate much sooner after rewatering following drought and disturbance than any freshly sown ray. Data for several pots having prolonged germination are shown in Table 8.

**Greenhouse Drought Stress Tests**

The limited number of severely drought-stressed plants available
<table>
<thead>
<tr>
<th>Pot #</th>
<th>Disc mortality during drought</th>
<th>Ray germination by days</th>
<th>Mean dry weights of ray plants (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>41-132² 132-158³ 158+⁴</td>
<td>Harvest day 132⁵ Harvest day 158⁶</td>
</tr>
<tr>
<td>5</td>
<td>14</td>
<td>9 1 0</td>
<td>- 0.46</td>
</tr>
<tr>
<td>6</td>
<td>16</td>
<td>4 - 3</td>
<td>0.11 -</td>
</tr>
<tr>
<td>7</td>
<td>19</td>
<td>4 - 8</td>
<td>0.14 -</td>
</tr>
<tr>
<td>8</td>
<td>17</td>
<td>5 3 3</td>
<td>- 0.56</td>
</tr>
<tr>
<td>9</td>
<td>17</td>
<td>9 2 2</td>
<td>- 0.28</td>
</tr>
<tr>
<td>10</td>
<td>17</td>
<td>5 - 11</td>
<td>0.08 -</td>
</tr>
<tr>
<td>11</td>
<td>21</td>
<td>5 - 8</td>
<td>0.09 -</td>
</tr>
<tr>
<td>12</td>
<td>13</td>
<td>7 2 4</td>
<td>- 0.39</td>
</tr>
</tbody>
</table>

¹ For pots 5-8, the initial watering ceased on day 10; for pots 9-12 on day 12.
² Drought ended on day 41.
³ Pots 6, 7, 10, and 11 were not watered during this period.
⁴ Period following harvest, pots were kept in greenhouse.
⁵ 91 days since end of drought.
⁶ 117 days since end of drought.
Table 8. Prolonged germination of ray achenes.

<table>
<thead>
<tr>
<th>Pot #</th>
<th>days of moisture</th>
<th># germinating after final drought</th>
<th>days to first emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>230</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>8</td>
<td>250</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>11</td>
<td>230</td>
<td>3</td>
<td>7</td>
</tr>
</tbody>
</table>

1 Approximate total before the final drought, moisture period was not continuous.

2 This drought followed the moisture period in the previous column. The soil surface was disturbed at the end of the drought.

3 Days are taken from the first watering following the drought.

produced a significantly lower ratio of disc to ray than did well-watered plants. Thus, under drought stress, production shifts slightly from a mean of 2.16 disc per ray to a mean of 1.83 disc per ray.

Table 9 shown the ranks, treatments, and disc to ray ratios for all 25 greenhouse plants. The disc:ray values form a continuous distribution with no evident breaks. In plants treated with a late drought (#4) or a moderate drought (#16), these ratios fall among the well-watered plants. The three severely stressed plants (#'s 23, 24, and 25), however, show the lowest ratios. When the means of the first 22 ranking plants (2.16) and the three severely stressed plants (1.83) are compared by a t-test, they are significantly different at $P < 0.001$. Thus, an average head with 119 achenes would have 38 ray and 81 disc. This experiment suggests that, under drought, a head of this size would have 42 ray and 77 disc.
Table 9. Ratio of disc : ray achenes in well-watered and drought-stressed plants. Plants were grown in the greenhouse from Utah and California seed during the 1974-75 and 1975-76 seasons.

<table>
<thead>
<tr>
<th>Rank</th>
<th>Treatment</th>
<th>Mean disc : ray</th>
<th># of heads examined</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>ww(^1) (outside)</td>
<td>2.40</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>ww (short days)</td>
<td>2.38</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>ww</td>
<td>2.35</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>late drought</td>
<td>2.32</td>
<td>3</td>
</tr>
<tr>
<td>5</td>
<td>ww (outside)</td>
<td>2.28</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>ww (long days)</td>
<td>2.26</td>
<td>1</td>
</tr>
<tr>
<td>7</td>
<td>ww (short days)</td>
<td>2.25</td>
<td>1</td>
</tr>
<tr>
<td>8</td>
<td>ww (long days)</td>
<td>2.24</td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td>ww</td>
<td>2.22</td>
<td>2</td>
</tr>
<tr>
<td>10</td>
<td>ww (long days)</td>
<td>2.18</td>
<td>1</td>
</tr>
<tr>
<td>11</td>
<td>ww (short days)</td>
<td>2.17</td>
<td>1</td>
</tr>
<tr>
<td>12</td>
<td>ww</td>
<td>2.17</td>
<td>2</td>
</tr>
<tr>
<td>13</td>
<td>ww (long days)</td>
<td>2.17</td>
<td>1</td>
</tr>
<tr>
<td>14</td>
<td>ww (long days)</td>
<td>2.15</td>
<td>1</td>
</tr>
<tr>
<td>15</td>
<td>ww</td>
<td>2.14</td>
<td>3</td>
</tr>
<tr>
<td>16</td>
<td>moderate drought</td>
<td>2.14</td>
<td>3</td>
</tr>
<tr>
<td>17</td>
<td>ww</td>
<td>2.14</td>
<td>4</td>
</tr>
<tr>
<td>18</td>
<td>ww (outside)</td>
<td>2.11</td>
<td>4</td>
</tr>
<tr>
<td>19</td>
<td>ww (outside)</td>
<td>2.09</td>
<td>3</td>
</tr>
<tr>
<td>20</td>
<td>ww</td>
<td>2.08</td>
<td>3</td>
</tr>
<tr>
<td>21</td>
<td>ww</td>
<td>2.00</td>
<td>3</td>
</tr>
<tr>
<td>22</td>
<td>ww</td>
<td>1.97</td>
<td>2</td>
</tr>
<tr>
<td>23</td>
<td>drought</td>
<td>1.87</td>
<td>3</td>
</tr>
<tr>
<td>24</td>
<td>drought</td>
<td>1.81</td>
<td>4</td>
</tr>
<tr>
<td>25</td>
<td>drought(^2)</td>
<td>1.81</td>
<td>1</td>
</tr>
</tbody>
</table>

\(^1\) well-watered

\(^2\) Head from central stalk lost, only side stalk used.
The degree of stress is illustrated in Figures 9 and 10, which show diffusive resistance values and plant heights for two severely stressed plants, one moderately stressed plant, and two control plants.

**Soil Microtopography Experiments**

**Introduction.** Figure 11 graphically shows germination rates and percentages for all treatments. These data are statistically evaluated in Figures 12, 13, and 14 and in Table 10.

**Rates.** Disc germinated rapidly on all surfaces in the high moisture treatment; there were no significant differences in rates between surfaces. Ray responded differently to these same surfaces; all three surfaces in the high moisture treatment produced significantly different rates (Figure 12). The germination rate was highest on the clod surface and lowest on the gravel surface.

**Total germination.** Under the high moisture regime the germination of disc on the flat and gravel surfaces was significantly greater than on the clod surface. Ray germination on the flat surface was significantly greater than on the other two surfaces (Figure 13). It should be noted that, for ray, the surface with the highest germination rate did not correspond to the surface showing the highest percent germination.

Under the low moisture regime, total disc germination was again greatest on the gravel surface, with significant differences existing between all surfaces. The clod surface again produced the lowest germination percentage. Total ray germination under this regime showed no significant differences between any of the three surfaces (Figure 14).
Figure 9. Plants #15 and 23: growth and diffusive resistance. The value in parentheses is mean diffusive resistance in s cm$^{-1}$. Curves fitted by eye. Plant #15 received 400-500 ml H$_2$O day$^{-1}$, plant #23 received 75-150 ml day$^{-1}$. Both plants had 3 stalks.
Figure 10. Plants #16, 12, and 24: growth and diffusive resistance. The value in parentheses is mean diffusive resistance in s cm⁻¹. Curves fitted by eye. Plant #12 received 400 mL H₂O day⁻¹, plant #16 received 200-300 mL day⁻¹, plant #24 received 150-200 mL day⁻¹.
Figure 11. Germination rates and percentages on the three soil surfaces. Circles represent ray, squares disc; closed figures indicate high moisture regime, open figures low moisture. Dotted lines show rates, solid lines percentages.
Figure 12. Germination rates for different surfaces under the high moisture regime. $F = 41.6$ for ray; 0.63 for disc.

**RAY ACHENES**

- Gravel: 0.074
- Clods: 0.109
- Flat: 0.098

**ANOVA**

- P < 0.01
- P < 0.005
- P < 0.01

Experimental mean = 0.094

**DISC ACHENES**

- Gravel: 0.259
- Clods: 0.260
- Flat: 0.270

**ANOVA**

- N.S.

Experimental mean = 0.263
Figure 13. Percent germination for different surfaces under the high moisture regime. All data transformed to Arcsin (percent germination) $^{1/2}$ $F = 11.0$ for ray, 41.8 for disc.

**RAY ACHENES**

- Gravel: 35.8
  - N.S.
  - ANOVA: $P < 0.01$
  - Clods: 39.5
    - P < 0.05
  - Flat: 47.2

Experimental mean = 40.8

**DISC ACHENES**

- Gravel: 90.0
  - P < 0.01
  - ANOVA: N.S.
  - Clods: 81.1
    - P < 0.005
  - Flat: 89.0

Experimental mean = 86.7
Figure 14. Percent germination for different surfaces under the low moisture regime. All data transformed to Arcsin (percent germination) $^{1/2}$ $F = 1.2$ for ray; 10.3 for disc.

**RAY ACHENES**

![Ray Achenes Diagram]

Experimental mean = 32.6

**DISC ACHENES**

![Disc Achenes Diagram]

Experimental mean = 83.7
Table 10. Comparison of percent germination between high and low moisture regimes on different soil surfaces.

<table>
<thead>
<tr>
<th>Surface</th>
<th>Ray achenes</th>
<th>Disc achenes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>gravel</td>
<td>flat</td>
</tr>
<tr>
<td>High moisture</td>
<td>35.8</td>
<td>47.2</td>
</tr>
<tr>
<td>Low moisture</td>
<td>33.6</td>
<td>29.2</td>
</tr>
<tr>
<td>Difference</td>
<td>2.2</td>
<td>18.0*</td>
</tr>
</tbody>
</table>

1 Percent germination transformed to Arcsin (percent germination)\(^{1/2}\)

2 Only 3 data points available for the low moisture regime in this treatment.

* = P<0.01
On each soil surface the total percent germination under the high moisture regime was numerically greater than under low moisture but the only significant differences for both morphs occurred on the flat surface (Table 10).

Soil surface disturbance following the dry period increased the percentage of ray germinating from the seed bank of the gravel and clod surfaces regardless of the prior moisture regime. Disturbance of the flat surfaces from both prior moisture regimes numerically reduced germination but not significantly so (Table 11).

The prior moisture regime had no effect on ray germination following the dry period except on the disturbed gravel and disturbed clod surfaces (Table 12). In the disturbed gravel treatment, germination was significantly greater in the high moisture regime flats while on the disturbed clod surface significantly greater germination occurred in flats from the low moisture regime.

An analysis of variance (Appendix B) revealed significant differences among surfaces and between disturbance treatments but not between prior moisture regimes. The only significant interaction was between soil surface types and the presence or absence of disturbance.

**Physiological Tests**

Disc germination in complete darkness was comparable to germination in light while ray germination was enhanced by exposure to light (Table 13). Some disc also germinated under a constant 27°C in complete darkness (three plates examined on different days: 4 days - 38%, 7 days - 18%, 14 days - 2%; incomplete germination due to
Table 11. Ray achene germination following the dry period: comparisons between disturbed and undisturbed flats with the \( t \)-test.

<table>
<thead>
<tr>
<th>Surface</th>
<th>Prior moisture regime</th>
<th>Surface treatment</th>
<th>Germination(^1)(^2)</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gravel</td>
<td>low</td>
<td>disturbed</td>
<td>20.2</td>
<td>11.6 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>undisturbed</td>
<td>8.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>high</td>
<td>disturbed</td>
<td>26.9</td>
<td>20.0 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>undisturbed</td>
<td>6.9</td>
<td></td>
</tr>
<tr>
<td>Flat</td>
<td>low</td>
<td>disturbed</td>
<td>9.2</td>
<td>3.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>undisturbed</td>
<td>12.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>high</td>
<td>disturbed</td>
<td>7.3</td>
<td>2.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>undisturbed</td>
<td>10.1</td>
<td></td>
</tr>
<tr>
<td>Clods</td>
<td>low</td>
<td>disturbed</td>
<td>12.0</td>
<td>9.6 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>undisturbed</td>
<td>2.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>high</td>
<td>disturbed</td>
<td>7.7</td>
<td>2.2 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>undisturbed</td>
<td>5.5</td>
<td></td>
</tr>
</tbody>
</table>

* = significant at \( P<0.10 \)

\(^1\) Percent germination transformed to Arcsin (percent germination)\(^{1/2}\)

\(^2\) Calculated from the number of achenes believed remaining in the seed bank after the initial 99 day germination period.
Table 12. Ray achene germination following the dry period: comparisons between different prior moisture regimes with the t-test.

<table>
<thead>
<tr>
<th>Surface</th>
<th>Surface treatment</th>
<th>Prior moisture regime</th>
<th>Germination(^{1,2})</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gravel</td>
<td>disturbed</td>
<td>low</td>
<td>20.2</td>
<td>6.7 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>high</td>
<td>26.9</td>
<td></td>
</tr>
<tr>
<td>Gravel</td>
<td>undisturbed</td>
<td>low</td>
<td>8.6</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>high</td>
<td>6.9</td>
<td></td>
</tr>
<tr>
<td>Flat</td>
<td>disturbed</td>
<td>low</td>
<td>9.2</td>
<td>1.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>high</td>
<td>7.3</td>
<td></td>
</tr>
<tr>
<td>Flat</td>
<td>undisturbed</td>
<td>low</td>
<td>12.5</td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>high</td>
<td>10.1</td>
<td></td>
</tr>
<tr>
<td>Clods</td>
<td>disturbed</td>
<td>low</td>
<td>12.0</td>
<td>4.3 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>high</td>
<td>7.7</td>
<td></td>
</tr>
<tr>
<td>Clods</td>
<td>undisturbed</td>
<td>low</td>
<td>2.4</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>high</td>
<td>5.5</td>
<td></td>
</tr>
</tbody>
</table>

* = significant at P<0.10

\(^1\) Percent germination transformed to Arcsin (percent germination)\(^{1/2}\)

\(^2\) Calculated from the number of achenes believed remaining in the seed bank after the initial 99 day germination period.
Table 13. Germination of ray and disc achenes in light and dark.

<table>
<thead>
<tr>
<th>Achene type</th>
<th>Ray(^1)</th>
<th>Disc(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean percent germination(^3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Light</td>
<td>27.1</td>
<td>70.0</td>
</tr>
<tr>
<td>Dark</td>
<td>5.7</td>
<td>74.0</td>
</tr>
<tr>
<td>Difference</td>
<td>21.4(^*)</td>
<td>4.0</td>
</tr>
</tbody>
</table>

1 Germination measured on day 25.
2 Germination measured on day 4.
3 Transformed to Arcsin (percent germination)\(^1/2\).

\(* = P < 0.05\)

drying of the filter paper).

Disc achenes imbibed water at a faster rate than ray achenes (Figure 15); however, there appear to be other factors also involved in the dormancy of ray achenes. Ray that had imbibed water for a number of days either on filter paper or in the soil became soft but did not germinate.

Thirteen of the 15 excised ray achene embryos developed green cotyledons within 3 days. Four embryos also developed extensive root hairs. At this time no germination was observed among 85 unexcised ray achenes under identical conditions.

The two morphs not only differ in weight, but in the division of this weight between the embryo and the dispersal or protective portions of the achene (Table 14). The seed coat comprised only 25% of the disc weight exclusive of the pappus while it accounted for
Figure 15. Imbibition rates of disc and ray achenes. Disc = ■, ray = ●.
Table 14. Partitioning of weight among achene components.

<table>
<thead>
<tr>
<th>Portion of achene</th>
<th>ray achenes</th>
<th>disc achenes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%</td>
<td>mg</td>
</tr>
<tr>
<td>pappus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>seed coat</td>
<td>63%</td>
<td>0.48</td>
</tr>
<tr>
<td>embryo</td>
<td>37%</td>
<td>0.28</td>
</tr>
<tr>
<td>total</td>
<td>100%</td>
<td>0.76</td>
</tr>
</tbody>
</table>

63% of the ray weight. The embryo of the disc achene, however, weighed more than the entire ray achene. Endosperm was not readily apparent in either morph.

A dramatic difference was found in the amount of protein allocated to each morph (disc = 0.28 mg, ray = 0.09 mg); however, the percent protein of the two embryos was actually quite similar. The total percent lipid in the two morphs was similar; however, the percent of the embryo devoted to lipid differed considerably (41% in the disc, 62% in the ray). Carbohydrate reserves also differed between the embryos, being 24% in the disc and 6% in the ray (Table 15). Differences in the proportion of the achenes occupied by the embryo are responsible for the differences between total allocation to the achene and the composition of the embryo.

The plant expends less energy in producing ray achenes (Table 16), both per individual (total energy: line 1; proportional energy expenditure based on yield in achene weight: line 2) and per head (line 4).
Table 15. Achene storage contents.

<table>
<thead>
<tr>
<th>compound</th>
<th>ray achenes</th>
<th>disc achenes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% of achene</td>
<td>embryo</td>
</tr>
<tr>
<td>protein</td>
<td>12.02 (0.75)</td>
<td>32%</td>
</tr>
<tr>
<td>lipids</td>
<td>23.02 (0.20)</td>
<td>62%</td>
</tr>
<tr>
<td>other(^3)</td>
<td>-</td>
<td>6%</td>
</tr>
<tr>
<td>embryo total</td>
<td>100%</td>
<td>0.28</td>
</tr>
</tbody>
</table>

1 Original data. Percent deviation (differences between the mean and one of the two replicates) is given in parentheses.

2 Based on the assumption little or no protein or lipid is present in the seed coat or pappus.

3 Presumably carbohydrates; obtained by subtraction.

Table 16. Costs of producing ray and disc achenes. Calculated from Penning de Vries [1972, Table 1].

<table>
<thead>
<tr>
<th></th>
<th>RAY</th>
<th>DISC:RAY</th>
<th>DISC</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. equivalent glucose required (mg)(^1)</td>
<td>1.26</td>
<td>1.83</td>
<td>2.30</td>
</tr>
<tr>
<td>2. achene weight / equivalent glucose required</td>
<td>0.60</td>
<td>-</td>
<td>0.55</td>
</tr>
<tr>
<td>3. number of achenes / head</td>
<td>37</td>
<td>2.22</td>
<td>82</td>
</tr>
<tr>
<td>4. equivalent glucose requirement / head; separated by achene type</td>
<td>46.76</td>
<td>4.03</td>
<td>188.30</td>
</tr>
</tbody>
</table>

\(^1\) mg glucose required to produce one achene. Similar calculations are shown for wheat in Bhatia and Rabson [1976].
Antimicrobial Tests

In the first test for antimicrobial potential, no differences were evident between the densities of *Rhizopus* and *Penicillium* in different treatments. After 12 days in the second test, less *Penicillium* colonies were present in the leachate than the control, and an even greater numerical reduction occurred between the leachate and the extract. However, during this second test, bacteria grew in the two treatments; thus, no conclusions can be drawn as either the plant's chemicals or the bacterial populations could have caused the observed effects.
DISCUSSION

Life History

Some generalizations, based on limited field and laboratory data, show that the plasticity in aspects of the telegraphplant's life cycle besides germination may also have helped preadapt this taxon for its weedy success at the time of California's settlement.

Because of the germination dimorphism one would expect that, throughout most of its range, germination would be staggered throughout fall, winter, or spring and occur anytime when there is sufficient moisture over a suitable duration. Seedlings form a rosette, a stage which they retain for variable lengths of time. Plants starting growth in the greenhouse during fall remained as slow growing rosettes until April, when more rapid vertical growth occurred.

Observations of plants in the field suggests there may be a lower size limit below which the rosette will not initiate this vertical growth in its first year. Werner [1975] found that some rosettes of teasel (typically thought of as a biennial) remained vegetative until they achieved sufficient size to flower, the process requiring up to 5 years where competition was severe. In contrast, all telegraphplant rosettes marked in 1975 developed as strict biennials and initiated vertical growth between February and May of 1976. It is not known whether this species possesses the plasticity to retain its rosette stage for several years should conditions be severe. Thus, the telegraphplant is able to behave as either an annual or biennial, as reported in some floras [Muns and Keck, 1968;
Shortening daylengths appear to trigger fall flowering in mature telegraph plants. This would assure that reproduction occurs before late fall rains begin. Regularity in the timing of reproduction is seen in a number of plants even though other aspects of their growth show considerable plasticity [Slade, et al., 1975]. Overall, though, the flowering period is quite flexible; Munz [1974] lists it as January through December. This is undoubtedly due in large part to rosette flowering as shown in Figure 4.

The apparent self-compatibility shown for this taxon contrasts sharply with the self-incompatibility shown for several congeners [Harms, 1965], but the possibility of some type of apomictic mechanism cannot be conclusively eliminated without further tests.

The beeflies frequenting Heterotheca are probably generalized pollinators visiting whatever species are present.

Seed predation by Heliothis philoxiphaga should not have a devastating effect on the population since the mature plants can continue flowering for several months, plus may flower at other times in their life cycle. Thus, numerous achenes may escape predation. Another Heliothis species (H. virescens) has been reported to have Heterotheca subaxillaris as one of its 30 known host plants [Tietz, 1972].

Many aspects of a plant's life cycle can contribute to its weedy behavior. Baker [1962, 1965, 1974] has suggested a number of these attributes which are listed in Table 17 and compared to my data.
Table 17. The ideal (?) weed. Clearly, a plant need not possess all these characteristics to be a successful weed. Combined and modified from Baker [1965, 1974]. Two attributes of perennials (vigorous vegetative reproduction and brittle lower nodes) have been omitted.

<table>
<thead>
<tr>
<th>Weedy characteristic</th>
<th>Expression of characteristic in <em>Heterotheca grandiflora</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1. No overly specialized germination requirements, thus germination can take place in many environments</td>
<td>Even ray are not overly specialized</td>
</tr>
<tr>
<td>2. Internally controlled discontinuous germination, great seed longevity</td>
<td>Yes - in ray</td>
</tr>
<tr>
<td>3. Rapid seedling growth and short time interval between seedling and flowering</td>
<td>No</td>
</tr>
<tr>
<td>4. Continuous seed production as long as conditions permit</td>
<td>Yes - several months plus can flower as rosette</td>
</tr>
<tr>
<td>5. Self-compatible, but not obligatory self-pollinated or apomictic</td>
<td>Most likely</td>
</tr>
<tr>
<td>6. When cross pollinated, unspecialized visitors or wind utilized</td>
<td>Probably - pollinator collected appears to be a generalist</td>
</tr>
<tr>
<td>7. Very high seed output in favorable circumstances</td>
<td>Yes - can easily be many thousand</td>
</tr>
<tr>
<td>8. Produces some seed in a wide range of environmental conditions, tolerant and plastic</td>
<td>Yes - as in rosette flowering</td>
</tr>
<tr>
<td>9. Has adaptations for short- and long-distance dispersal</td>
<td>Yes - the dimorphism</td>
</tr>
<tr>
<td>10. (If a perennial), shows ability to regenerate from severed portions of the rootstalk</td>
<td>Greenhouse evidence suggests damaged rosettes can resprout from roots</td>
</tr>
<tr>
<td>11. Has ability to compete inter-specifically by special means (rosette, choking growth, allelochemics)</td>
<td>No evidence to suggest any special competitive ability</td>
</tr>
</tbody>
</table>
Water Relations

The telegraphplant does not appear to be an especially xerophytic plant; it most likely possesses C$_3$ photosynthesis \cite{Smith and Turner [1975] found no C$_4$ species in the Astereae} and has numerous stomata on both surfaces on its leaves (examined at 128X and 320X in an epi-illumination microscope). The first impression one gets when encountering these plants on desert roadsides is their confinement to the edge of the pavement (Figure 3) where runoff greatly increases their water supply. Their large size may give an illusion of high density (Figure 3), yet, along an 84 m length of road where the more robust (multi-stalked and 60-70 cm tall in June 1976) plants occurred, their approximate density (rosettes excluded) was one telegraphplant m$^{-2}$.

The telegraphplant's roots penetrate deep into the soil. This is unlike the upland hot desert shrubs, typified by Larrea, which have shallow but widely spreading root systems \cite{Chew and Chew, 1965} since rains do not usually penetrate deeply.

Deep roots permit the telegraphplant to tap roadside runoff and thus account for its xylem balancing pressures of less negative than -10 bars (Table 4). Typically, in unmodified areas of these desert communities, water is available during summer only at water potentials more negative than -40 bars \cite{Bamberg et al., 1975; Syvertsen et al., 1975}.

Figure 7 shows that the telegraphplant transpires significant amounts of water throughout the day, yet comparisons with other species are difficult. Due to the small leaf size of many desert plants, transpiration is frequently presented in (g H$_2$O) (g leaf dry weight)$^{-1}$
This is not readily converted to my measurements of $gH_2O \ dm^{-2} h^{-1}$, thus comparisons are limited. The publication of uncalibrated diffusive resistance meter transit times in comparative studies [Mooney and Kummerow, 1971] further frustrates potential comparisons.

Under desert conditions, mesic species with abundant water available {e.g., Phragmites communis (common reed)} have low resistance (2.0 $s \ cm^{-1}$) throughout much of the day and achieve transpiration rates up to 7.8 - 8.4 $g \ dm^{-2} \ h^{-1}$ [Pearcy, et al., 1974]. Species in dry upland sites, as exemplified by Larrea, may follow a daily pattern throughout much of the year of briefly opening their stomata immediately after dawn then maintaining high resistance throughout the rest of the day [Oechel, et al., 1972]. No resistance values appear to have been published for Larrea. Cold desert shrubs (e.g., Artemisia tridentata) typically have resistances of 20 - 40 $s \ cm^{-1}$ as moisture becomes less available in mid-late season [DePuit and Caldwell, 1973]. Chaparral shrubs, with minimum resistances of 2 - 6 $s \ cm^{-1}$ also increase their resistances to high values with the exhaustion of soil moisture [Poole and Miller, 1975].

Site Description

Table 5 shows the other species growing with Heterotheca and their apparent "strategies" for survival in the harsh desert climate. Only Datura meteloides (closely related to Jimson weed) appears to have a strategy (similar to that of the telegraphplant) of continued growth and activity throughout the summer without any special adaptations for conserving water. However, it is a perennial. As its huge leaves represent a significant transpiring surface (at
rates of over 1.0 gH₂O dm⁻²h⁻¹ from the lower leaf surface), it must have a deep root system which taps water available under the roadway. Its distribution, however, is quite scattered, unlike the large stands of the telegraphplant.

A majority of the species collected in September, 1975 possess the C₄ dicarboxylic acid pathway of photosynthesis (e.g., Allionia, Euphorbia, Cynodon) or are perennials which become partly dormant. C₄ species are able to fix more carbon with a smaller stomatal aperture and thus transpire less than a C₃ species for each unit of carbon assimilated [Larcher, 1975]. One of the C₄ species, Pectis papposa, is well known as a summer annual [Went, 1948].

None of those species collected in April 1976 and subsequently dead, dying, or dormant in June 1976 appear to possess the C₄ pathway. They function like spring annuals, germinating either in winter (e.g., Descurainia [Went, 1948]) or late summer (e.g., Erodium cicutarium [Went, 1948]) and complete their life cycle or enter dormancy before soil moisture is depleted.

Of those listed as perennial or biennial, Encelia (perennial) appears to become partly dormant during summer. Others (Aster, Stephanomeria) have very reduced leaves during summer, Stephanomeria (wirelettuce) sometimes appears as nothing more than a tangle of green stems. Developmental plasticity may be present in Baileya (desert marigold) and Sphaeralcea (globe mallow) as their populations have individuals in various stages of dormancy during the summer.

Although I did not encounter it, Eremocarpus setigerus is known to occur along the road several km north of the Beaver Dam site [Noel Holmgren #3841, UTC, "New to Arizona" August 9, 1969]. This
species is functionally very similar to the telegraphplant as it is a C₃ species [Welkie and Caldwell, 1970], a native of California which has become weedy [Stebbins, 1965a] and can produce dimorphic seed [Cook, et al., 1971]. Additionally, it is a summer annual, an infrequent strategy among California species [Baker, 1972].

While it is evident that production should increase along roads due to the increased runoff, it is interesting that an exotic species should be able to take better advantage of this water for summer growth than the native plants. Presumably, the roadway traps moisture under itself in the same manner as Evenari, et al. [1971] found pockets of moisture accumulated under desert stones. As this does not correspond to any habitat available in the unmodified desert community, some of this moisture may be deeper than the roots of native species usually penetrate, or the native species may be "programmed" to different life cycle strategies.

Germination Introduction

The germination dimorphism in the telegraphplant is not a phenomenon restricted to peripheral populations, rather it appears to be a characteristic of the species. Germination of achenes from two widely separated California locations revealed the same general pattern as observed in the southwestern Utah and northwestern Arizona material from the 1974 and 1975 seed crops used in all major experiments. In these populations, disc germinated rapidly while ray germination progressed more slowly, with a smaller proportion of the viable achenes germinating.

Other species in *Heterotheca* section *Heterotheca* may possess
germination dimorphisms; Becker [1912] reported this in *H. lamarckii* (synonymous with *H. subaxillaris* (Lam.) Britt. and Rus. [Wagenknecht, 1960]) while Baskin and Baskin [1976] recently confirmed this in more extensive tests. Plummer and Keever [1963], working with *H. latifolia* Buckley, recognized the two achene types but did not pursue any detailed germination experiments. Previously Keever [1955] had briefly observed germination and found rapid germination in the lab while field germination occurred during both fall and spring.

There are numerous opportunities to attempt comparisons between different experiments and seed crops from different years; however, there are a variety of reasons to avoid this practice. Environmental conditions were seldom identical in different tests and further differences, such as planting seed in some tests and broadcasting it onto the surface in others, had important influences on germination characteristics.

**Competition Tests**

By germinating the two morphs in the same pot it was possible not only to examine competition but also germination where both morphs experienced identical environmental conditions, especially with regards to the drought treatments. The outcome of these competition tests would depend on both the delay in germination of the more dormant morph and any inherent differences in growth rates existing between the two morphs at any stage. The experiment was designed to simulate field conditions rather than to separate the relative contributions of these factors to the observed differences in plant biomass.

Under the environmental conditions of this test (which include
the achenes' locations on or in the substrate), the early emerging
disc were at a competitive advantage when environmental conditions
were constant. They suppressed the later germinating ray as shown
by the biomass values in Table 6. This suppression is likely due to
shading from the larger disc plants and is similar to Black's [1958]
conclusions from subterranean clover. The drought reflected a
fluctuating environment where all disc seedlings perished and later
germinating ray seedlings established successfully, as illustrated
in Figure 8.

Ray plants from monomorphic stands (Table 7) were in the same
weight range as disc plants grown under greater competition (Table 6),
even though these ray germinated much later. While it is difficult
to make comparisons between such greatly different densities, the
data do indicate ray plants can grow well under less competitive
conditions. This is important because smaller seeded morphs sometimes
produce plants which fail to survive even when relatively free from
competition under greenhouse conditions [Pandey, 1968]. Additionally,
the possibility that one morph could be genetically less diverse
due to apomixis has not been disproven although no direct evidence
suggests this.

It is possible ray germination, which generally requires light,
was slowed by burial and disc speeded since the disc's scar of
attachment protruded into deeper, more moist soil. This could
account for the lack of overlap between the germination periods of
the two morphs. Less dramatic differences between disc and ray
germination would probably still have produced mean plant weights
that were significantly different since slight variations in
germination timing may determine success or failure in establishment under competitive conditions [Harper, 1965a]; a 5 day delay in germination reduced biomass by 50% in subterranean clover [Black and Wilkinson, 1963]. Competition between different species may not always be as sensitive to differences in germination timing; Duba [1976] found an eight day difference in planting time of *Halogeton glomeratus* and *Bassia hyssopifolia* to have little overall effect on their final biomass. My within pot biomass ranges only overlapped in one of the four pots. This pot had the least number of surviving seedlings (17) of any of these pots and the overlap was only between one disc and one ray seedling.

Mortality in the control pots (Table 6) resulted from excessive hypocotyl elongation due to the low light intensity in the germinator. Under more normal light levels in the greenhouse, cotyledons remained close to the soil surface. While this low light level in the germinator may be somewhat unrealistic for plant growth, it should be noted that disc were growing longer under this light level and consequently even greater suppression of ray would be expected under high light.

The drought periods used (29 - 31 days without moisture) are not unreasonably long; Heady [1958] reported dry periods of 22, 38, 47, and 48 days between rains spread over three of the five California winters surveyed. Similarly, Evans, et al. [1975] reported soil water potential on a California rangeland reached -8 bars on two occasions after late October and early November rains had initiated seed germination and seedling emergence.
The objection can be raised that disc seedlings are dominating the ray seedlings simply by their numerical superiority. However, there is evidence that the number of ray may not have a great influence. Ross and Harper [1972] found the major factor influencing a seedling's growth rate was the density of seedlings emerging prior to the one being observed; later emerging seedlings had a much smaller effect. Thus, ray plant growth is determined by the number and position of disc plants present. In addition, the difference in mean weights between disc and ray plants where there is the least difference in numbers (18 disc, 11 ray in pot #3 (Table 6)) is the next to the largest weight difference found among the four pots.

These results conform to the conclusions of Harper, et al. [1970] that, when different seed sizes exist within a monospecific population, larger seed produce plants which often dominate the stand and provide the bulk of the biomass of the population. Harper [1965a] emphasizes that, although earlier germination frequently involves increased susceptibility to drought or frost, those individuals surviving will be in a position to pre-empt a greater proportion of the available resources. Ross and Harper [1972] reinforced this with experimental evidence showing early emerging individuals of Dactylis glomerata (cocksfoot) occupied more space than expected just from their longer period of growth.

The establishment of the slower morph after the loss of the more vigorous morph due to adverse biotic or abiotic conditions also fits with the adaptive pattern advanced by many authors [Evenari, et al., 1971; Ungar, 1971; Nobs and Hagar, 1974; Werker and Many, 1974]. Yet, relatively few studies have specifically tested for the
differential mortality of the morphs under realistic conditions as did Salisbury [1942] or Koller and Roth [1964]. Many authors simply infer from their basic laboratory germination data that differential mortality could occur in the field.

When the germination of essentially the entire population of disc achenes by 2.5 cm of moisture over a 10 - 12 d period (Figure 8) is compared to the delayed ray germination {only 37.5% of the eventual maximum in some pots after 91 continuous days of moisture, plus some still germinating after 200 days of moisture (Table 8)}, it emphasizes the different potential ecologies of the two morphs. While this extended germination may not be representative of that in the field since greenhouse temperatures were probably higher than encountered in the field during the moist season, it does show that ray achenes are capable of surviving long periods in moist soil.

Staggered germination in any non-dispersed morph serves to prevent intraspecific competition [Datta, et al., 1970].

A possible after-ripening effect can be seen in the data of Table 8, although a direct comparison with the original planting of that seed may be questionable, since the temperatures differed. Also, there was no true control as fresh achenes were not planted for comparison. In the initial sample of 324 ray, 1 germinated on day 12 before the drought, while in the control pots ray germination did not begin until day 13. After the final drought, soil disturbance, and rewatering, germination in different pots began on days 4, 7, and 8. This more rapid germination would be adaptive since the seed could take immediate advantage of being brought to the surface by a disturbance after a prolonged period of burial. Thomas and Dale [1975]
found a similar decrease in time to germination in *Hieracium flori-bundum* achenes which had aged in the soil.

**Greenhouse Drought Stress Tests**

Since the achene ratio changed with position on the plant, only heads from one position (first head on any stalk) were used. This also prevented the evaluation of field plants as they were in slightly different stages of flowering when achenes were collected.

As shown by the diffusive resistance data for greenhouse plants (included in Figures 9 and 10), their use of water was not unlike the range of values observed in the field. Diffusive resistance was selected as a logical parameter indicating drought stress as both water and CO₂ exchange are reduced (though not to the same extent) by decreased stomatal aperture [Larcher, 1975]. Thus, stressed plants have less photosynthate to allocate to seeds, either to total production or preferentially to one morph. Diffusive resistance reflected drought stress more closely than did the height measurements.

Initially it was thought the determination of viability would be an even more sensitive indicator of which morph was allocated scarce resources in times of stress, as one morph could be aborted more than the other. Sources such as Willis [1973] indicate that, at least for perfect disc florets, one would expect certain self-fertilization if outcrossing was unsuccessful, as occurs in many Asteraceae. *Heterotheca* is in the tribe Astereae where often the style branches of the disc florets undergo pronation (bending toward each other) rather than supinate expansion (spreading apart) as found in the ray florets [Jones, 1976; also personal communication].
Additionally Jones found pollen in the disc florets of Astereae was released before the style became receptive. Together these are believed to help maintain cross-pollination. Selection for outcrossing is strong enough that in one genus of this tribe (Aster) there is a genetic sterility barrier preventing pollination within the same plant or clone [Jones, 1976]. Further, as noted by Harms [1965], members of the Heterotheca subaxillaris complex (H. subaxillaris, H. latifolia, H. psammophila) are not self-fertile. My finding of apparent self-compatibility in H. grandiflora would make this the second known self-compatible taxon in Heterotheca (including Chrysopsis). It is difficult to conclusively exclude the possibility of some form of apomixis, which is common among the Asteraceae, without cytological tests [Stebbins, 1957]; however, variation patterns in H. grandiflora suggest outcrossing [Stebbins, 1965a]. Heterotheca (Chrysopsis) pilosa is the only other known self-compatible taxon in the genus and is further unique as being the only annual plant in Section Chrysopsis [Vernon Harms, personal communication].

The trend toward the production of a greater proportion of ray achenes by the severely stressed plants conforms with expectations that the ray, having more complex germination requirements, is the more "reliable" morph and is produced preferentially when resources are limiting. The same strategy is seen in Gymnarrhena micrantha [Koller and Roth, 1964] which curtails the production of its widely dispersed ("risky") seed morph as soil moisture becomes unfavorable. Perhaps, in the telegraph plant, this is a mechanism to reduce fluctuations in the number of ray produced in an area in different years. Presumably, the number of heads would decrease during drought
due to the plants' indeterminate growth form, thus the change in proportion of the morphs would decrease total disc production in a stand more than ray. Additionally, ray are energetically "cheaper" to produce (see physiology section).

The lack of sufficient replication of the severe drought treatment makes it impossible to draw conclusive results. The low number of replicates was partly due to diverting a number of plants into treatments designed to examine factors influencing flowering since they had become very large but showed no indication of flowering.

It is suspected all disc florets formed seed coats regardless of fertilization while some unfertilized ray florets formed rudimentary seed coats that, although sometimes detected on dried ray ligules, could easily have been lost during counting. If this experiment was repeated, it would be instructive to also count the number of ray florets.

An additional problem was that the moderate (200 - 300 ml d⁻¹ rather than 400 ml d⁻¹) and late (2 weeks subsequent to bud initiation) droughts were ineffective. Most likely the moderate drought was not severe enough; its diffusive resistance (Figure 10) was less than the control for the other pair (Figure 9). The late drought was apparently initiated after achene ratios were determined. Experimental studies indicate the determination of seed number in the apex of Asteraceae may occur early in some species and late in others [Palmblad, 1968b]; thus, results may differ according to the timing of the stress period in relation to apex differentiation.

The inclusion of heads from more than one flowering stalk per plant where possible helps minimize the effect of within-plant variability.
Soil Microtopography Tests

The graphical illustration of the results (Figure 11) uses the log of the soil microtopography variance as its x axis as a means of ranking the surfaces in order of increasing heterogeneity but does not imply this is the only factor operating on germination.

Under the high moisture regime, germination rate for ray but not disc was influenced by the soil surface. The germination rate (mathematically independent of total germination) indicates the speed at which the portion of the seed bank which will germinate that season is exposed to the selective pressures of the environmental sieve. Rate for ray is highest on the clods since most germination occurred early in the test.

Since moisture was not limiting under this regime, differences in percent germination would be due to other aspects of the surface effect. Disc achenes showed no dormancy, thus the reduction of germination on the clod surface is presumably due to mortality as the rigid pappus sometimes failed to orient the achene properly on this surface. Since imbibition in achenes of some Asteraceae is primarily through the site of the scar of attachment [Sheldon, 1974], improper orientation may subject the achene to drought stress even in a moist environment. Disc germination on the clod surface was 97.6% of the viable achenes (before the Arcsin transformation); the other surfaces reached or approached 100%. It is assumed that this mortality was distributed throughout the experiment and was small enough that it did not appreciably alter the rate statistic.

Data from subsequent experiments suggest that the reduction in ray germination observed on gravel and clod surfaces under the high
moisture regime is due to enforced dormancy resulting from burial rather than from mortality. High moisture levels can restrict a seed's gas exchange [Oomes and Elberse, 1976] and could be partly responsible for reduced germination on the gravel surface.

The low moisture regime had the same effect on both morphs in the sense that a significant reduction in germination below that of the high moisture regime only occurred on the flat surface (Table 10). The end result for disc was a progressive decrease in germination from gravel to flat to clods; gravel presumably retained moisture longer than flat and improper achene orientation again caused higher mortality on the clods. Ray germination showed no significant differences among the surfaces; the decrease in germination from that observed on the high moisture flat surfaces is due to enforced dormancy rather than mortality as explained below.

Disturbance increased ray germination by exposing buried achenes to light except on the flat surface where disturbance probably covered as many achenes as it exposed (Table 11). Several factors discussed in the physiology section (p. 90) support the conclusion that ray germination is enhanced by light.

By comparing germination in flats from the two prior moisture regimes following rewatering (Table 12), it was possible to test for ray mortality in the earlier part of the experiment. On the flat surfaces, where one would expect the greatest mortality, the lack of significant differences between prior moisture regimes indicated that none occurred. The disturbed gravel previously under low moisture had less germination than expected, suggesting slight mortality; yet undisturbed gravel did not show this trend. Disturbed clods previously
under low moisture had more germination than expected, suggesting that watering under the higher moisture regime buried a number of achenes which could not be exposed by disturbance. Thus disc undergo mortality in response to drought while ray regulate their germination such that they experience much less mortality even under more severe drought (ray experienced a drought about twice as long as disc).

The conclusions of these t-tests (germination enhancement by disturbance and an overall lack of effect of prior moisture regime) are reinforced by the analysis of variance (Appendix B). The significant influence of the soil surfaces on germination was expected. The interaction between soil surface and disturbance was significant, indicating that disturbance of one soil surface had a different degree of effectiveness than the disturbance of another.

Several approaches could be used to examine the hypothesis that dimorphic seed "perceive" different environmental triggers. One could compare the temperature optima and ranges of the morphs [Datta, et al., 1970; Baker and O'Dowd, 1976; Baskin and Baskin, 1976] or one could examine specific physiological characteristics as done by numerous authors. The approach of using varied soil surfaces has advantages over the second method and could conceivably be combined with the first. It allows the examination of a number of characteristics simultaneously, some which may not be anticipated by the investigator, and suggests which physiological tests are pertinent. The complex microhabitat on the soil surface is best explained by Harper as an environment "... in which to a mustard seed a worm cast is a mountain, a fallen leaf is shade from light (or from the eye of a possible predator), a raindrop is a cataclysm." [John Harper,

Moisture tends to increase with greater soil heterogeneity (in the absence of confounding factors such as gravel) as the surface roughness tends to retain pockets of moisture for those seed that orient themselves properly or land in the correct location [Harper, et al., 1965; Evans and Young, 1972]. Seed size influences water relations [small seed have a larger contact / volume ratio [Harper and Benton, 1966]] as does the degree of burial [Evans and Young, 1972]. Burial also influences temperature [Evans and Young, 1972], light [Thomas and Dale, 1975], and gas exchange [Oomes and Elberse, 1976] at the seed's location on or in the substrate. Gas exchange may be further restricted by excessive soil moisture [Oomes and Elberse, 1976].

Seed requiring light tend to germinate only when close to the surface and thus must be small to avoid an unfavorable water balance [Harper, et al., 1970]. Thus it is not unexpected that the smaller ray achenes of the telegraphplant have a light requirement and the disc do not. The ray have a greater chance of becoming buried before germination due to their greater dormancy and thus derive greater adaptive benefit from this than would disc.

Seed shape and various appendages also influence the seed's performance as a landing device [Harper, et al., 1965; Sheldon, 1974]; in the disc of the telegraphplant the rigid pappus enables it to plant itself on the flat surface (backward facing hairs then anchor it), yet on the clod surface it fails to consistently establish proper contact with the substrate. In contrast, the achenes of Senecio viscosus (stinking groundsel) which also have a pappus, established better on a rough surface than on a smooth surface
The explanation for this seemingly contradictory performance (assuming the achenes of the two species have no great physiological differences) is revealed by Sheldon [1974, Figure 9d]. High humidity collapses the pappus of S. viscousus, permitting it to reorient itself among the crevices but does not push the tip of the achene into a flat surface as it is watered. Different pappus characteristics in the two species may account for the observed differences in establishment.

These data support the position that the two morphs respond to different environmental triggers. Disc achenes may respond primarily to moisture; gravel appeared wettest and flat driest. Since some disc were unable to take advantage of the moisture between the clods, germination on clods fell below that of the drier flat surface. While ray respond to moisture (e.g., the large decrease in germination between the flat surfaces of the two moisture regimes), they also respond to burial as light is one factor influencing their germination. Crusting, a frequent inhibitor of seedling emergence on flat surfaces, probably had little effect here as the subsequent tests indicated no detectable mortality. Different germination rates among ray (but not disc) on various surfaces indicate ray's sensitivity to environmental factors as rate is more responsive to environment than percent germination [Schimpf, 1976].

Physiology

The more rapid ability of the disc to imbibe water (Figure 15) permits it to germinate quickly while the slower rate of imbibition by the ray appears to be only one of a number of factors contributing
to its dormancy. It is doubtful that differential imbibition plays
as important a role here as it does in *Atriplex hortensis* [Nobs and
Hagar, 1974].

Germination in petri plates (Table 13) supports the idea that
ray germination is enhanced by light, as does the embryo excision
data. The rapid development of the excised ray embryos conforms to
the generalization that dormancy is imposed by seed coats in most
light sensitive seed [Wareing, 1969; Wareing and Saunders, 1971]. It
is not uncommon that even morphologically similar seed from a single
plant will differ physiologically in response to light [Kadman-Zahavi,
1960; Smith, 1975b]. Further, Baskin and Baskin [1976] found a much
stronger requirement for light in the ray of *H. subaxillaris* than
in the disc.

Differences between morphs in storage contents and embryo size
were suspected because their physiological performance contrasted
in a number of conditions. Clearly the ray's much heavier seed coat
could provide protection during burial while the disc's lighter coat
need not provide this function as the disc germinated so readily.

Initial examination reveals one perplexing characteristic: the
dispersed disc are heavier than the non-dispersed ray. If the two
morphs do in fact have different breeding systems as suspected, it
would fit with Ali's [1968] conclusions that self-compatability
necessitates heavier seed to overcome the decreased heterozygosity
resulting from self-fertilization. However, I believe other factors
discussed below are more important in this case.

In spite of the importance of different storage contents to
seed ecology [Levin, 1974; Snell, 1976], there appears to be an almost
complete dearth of information available on the composition of
dimorphic seed. *Halogoton glomeratus* [Williams, 1960] seems to be
the only exception. Extensive seed chemistry surveys [Van Etten, et
al., 1961; Earle and Jones, 1962; Van Etten, et al., 1963; Tookey
and Jones, 1965; Jones and Earle, 1966; Van Etten, et al., 1967; Barclay
and Earle, 1974] neglect to acknowledge the existence of dimorphisms
in species possessing them, let alone analyze the two morphs separately.
Since ecological characteristics of seed differing even slightly in
their biochemistry are varied [Schweizer and Ries, 1969; Ching, 1973;
Levin, 1974], this is one aspect that cannot be overlooked. Snell
[1976] even detected changes in seed storage compounds in response
to plant density.

The mature achenes of the telegraph plant lack an evident
endosperm, thus the cotyledons hold the food reserves for the seedling.
This lack of endosperm is typical of the Asteraceae [Esau, 1967].
While the large differences in protein allocated to each morph are
important in terms of demand on the parent plant, this has little
effect on the seed as the percent protein composition of the embryos
differs only slightly. The greater percent lipid in the more dormant
morph contrasts with the higher percent carbohydrate in the rapidly
germinating morph. The roles of these compounds correlate well with
the germination strategies of the two morphs.

Proteins are used by seedlings as sources of nitrogenous com-
pounds in addition to providing carbon skeletons for synthetic
processes. They are not used as energy sources [Levin, 1974] since
the efficiency of storing energy as protein is less than storage as
lipids, starch, or sucrose [Penning de Vries, 1972]. Thus, we would
expect to find little difference in the proportions of protein in the two embryos. It is in the energy storage compounds, lipids and carbohydrates, that we would expect to see differences. Since the breakdown of carbohydrate occurs early in germination [Koller, et al., 1962] and that of lipids somewhat later [Mayer and Shain, 1974], we would expect to see more carbohydrates {probably sugars, as \textit{H. subaxillaris} stores no energy as starch [Earle and Jones, 1962]} in the rapidly germinating morph, as was found. There is an apparent conflict between this strategy and dispersal since carbohydrates contain less energy per gram than lipids [Levin, 1974]. Thus it may be that selective pressures have been more intense for rapid germination of disc than for reducing weight to permit longer dispersal distances. Conversely, it is possible a small weight difference would have a negligible influence on dispersability since this is determined more by pappus geometry than by weight alone. Sheldon and Burrows [1973] found the ratio of pappus diam to achene diam to be a better predictor of the terminal velocity of a falling achene than the ratio of achene weight to pappus weight in a sample of 17 species of Asteraceae.

Less energy is expended in producing ray than disc. (No attempt was made to include corolla material in these calculations.) Though this would be evident by simply comparing weights, line 2 (Table 16) shows that slightly more ray is produced (on a weight basis) for each unit of energy expended. This difference in undoubtedly due to the major weight in ray being energetically "cheap" cellulose while in the disc the embryo (with large amounts of "expensive" lipids and proteins) accounts for more of the weight. Due to the greater number of disc in the average head (line 3) the energy allocated to each
morph on a per head basis is distorted even further (line 4). Thus, the shift to a greater proportion of ray than disc in drought stressed plants would serve to conserve energy in addition to producing a greater proportion of the more "reliable" morph.

The data for *Halogeton* [Williams, 1960] are remarkably similar. The rapidly germinating black seed contained at least twice as much protein on a weight basis as the slower brown seed. Energy storage strategies again paralleled the telegraphplant; black seed stored predominantly sucrose while energy reserves in brown seed were primarily starch.

**Antimicrobial Tests**

Antimicrobial tests were inconclusive due to problems with the test procedures; the probability of expecting ecologically significant allelopathic compounds in this plant is not influenced by these results. Extracts of *H. grandiflora* are toxic to the American cockroach [Heal, et al., 1950] while those of the widespread eastern species *H. sub-axillaris* possess some limited antibacterial and antiviral compounds [Iong, et al., 1972]. Though it is impossible to ascribe any ecological significance to this information, it points out the potential for active compounds in this genus. Thorough tests would involve using leachates of appropriately aged plant material to water achenes planted in a realistic soil system. Since ray achenes may dominate the seed bank in the vicinity of the parent plant, one would expect any system of coevolved adaptive responses to be in the ray rather than disc.
General "Strategies"

Heterogeneity should often be expected in wild seed populations [Koller, 1964], with its development becoming the most pronounced in environments that are variable over time. Modeling predicts extinction in the absence of both dormancy and germination regulating mechanisms in severe desert environments [Wilcox, 1973]. Periodic germination not only provides multiple opportunities for establishment, but it can reduce intraspecific competition [Datta, et al., 1970].

In some visually polymorphic species, the seed which presumably are dispersed less appear to be more specific in their germination requirements [Negbi and Tamar, 1963; Datta, et al., 1970; Baskin and Baskin, 1976]. This follows the theory advanced by MacArthur [1972] that plants with high dispersal powers have a high fraction of their seed germinate during the first moist season while those with low dispersal germinate a much smaller fraction of their seed each year. This idea can be applied to the two morphs of the telegraphplant. Moist disc achenes are capable of germinating rapidly and to a high percentage, in light, dark, constant temperature darkness, and on various soil surfaces. Being the well dispersed morph, these disc encounter an assortment of microsites. Mortality occurs if conditions become unfavorable, yet dispersal assures a greater chance of some seed encountering suitable conditions. Ray achenes are "specialists", as they seldom germinate in the dark, may be more specific in temperature requirements (extrapolating from Baskin and Baskin [1976]), and experience less mortality than disc since they only germinate under more constant moisture conditions. Finally, the soil surface experiments show ray are influenced to a greater extent by the numerous
factors of the environmental sieve and the concomitant after-ripening processes occurring in the seed bank. Since they are poorly dispersed, they cannot rely on the environment to produce heterogeneity, as happens in the disc, but must possess internal mechanisms to prevent mass germination of their entire population.

Preadaptation

Since human disturbance prior to European settlement in California was negligible [Stebbins, 1965a], the weedy abilities of the 41 colonizing species of native Californian plants must be due to either preadaptation {e.g., hexaploid races and selection for vigor in *Claytonia perfoliata* (miner's lettuce) [Stebbins, 1965a]}, hybridization with species only recently introduced {e.g., native *Helianthus bolanderi* with introduced *H. annuus* [Heiser, 1949]} or the creation of new habitats suitable for hybrids {e.g., *Elymus condensatus* × *E. triticoides* [Stebbins and Walters, 1949]}, or the evolution of weedy characteristics within the last 200 years. As *Heterotheca grandiflora* is *n* = 9 [Heiser and Whitaker, 1948], which is generally accepted as the basic chromosome number in the Astereae [Stucky and Jackson, 1975], polyploidy is eliminated as a possible factor. Hybridization with other species in *Heterotheca* section *Heterotheca* is also eliminated as none are reported as introduced into California until 1965 [Munz and Keck, 1968].

Baker [1972] states that some of the weedy tendencies in the California flora are due to preadaptation resulting from a similarity between the original habitats of these taxa and those created by human disturbance. Since other native California colonizers
{Atriplex patula var hastata [Ungar, 1971] and Eremocarpus setigerus (dove weed) [Cook, et al., 1971]} also possess dimorphic seed (putting at least 7% of the native colonizers in this category), I believe this phenomenon, together with the developmental plasticity discussed in the introduction, plays a significant part in the weedy spread of Heterotheca grandiflora.

Recommendations For Future Work

A number of unanswered questions have been raised, most with implications beyond this species. The factors influencing the proportion of the two morphs produced need reexamination with a larger sample size; density should be examined along with drought stress.

The precise breeding systems of the disc and ray florets are unknown. As differences between disc (structurally, and often functionally hermaphroditic) and ray (lacking stamens) are typical for this tribe [Jones, 1976], any information on the breeding system could potentially apply to a number of species. If differences did in fact exist in breeding systems, isoenzyme assays could be used to determine whether the presumably outcrossed morph (ray) was genetically more heterozygous than the presumably self-pollinated one. Field studies could determine whether one type of floret provides more attractive rewards to its pollinators. The impact of the differential longevity, and thus protection from selective forces [Harper, 1966], of genetically different seed of the same species needs to be evaluated in terms of population genetics [Harper and White, 1974]. Additionally, the demographic consequences
of dimorphisms have not been examined, except for work by Lawrence Venable now in progress at the University of Texas.

In a number of genera with dimorphic seed (e.g., *Atriplex*) it is less evident which morph is in reality dispersed more than the other. There may be a general trend in the germination characteristics of the more widely dispersed morphs compared to those retained near the parent. The data on storage contents also suggest a general trend among dimorphic species which remains to be examined.

The growth rates of seedlings could be examined; one would expect differences in light of the types of storage compounds in the two morphs. Perhaps cotyledon size may play a role here as it provides seedlings their initial photosynthetic area. The extent of development of the embryo could be examined anatomically to see if this influences initial growth.

Another broader question is whether or not the predominance of germination dimorphisms among annuals, especially weeds, is real or if it is merely due to their greater economic importance and thus the result of more thorough examination.

The water relations of desert roadside vegetation seems to be an untouched yet important area, since biomass production along desert roadsides is greatly increased over desert production even if the data are averaged over the unproductive road surface itself [Johnson, *et al.*, 1975]. The effect this has on diversity and stability in desert roadside communities (an estimated 22,236 km just in the California desert) is only beginning to be explored [Johnson, *et al.*, 1975].
SUMMARY

The divergent performance of dimorphic achenes from *Heterotheca grandiflora* scatters germination in space and time. Disc achenes, often widely dispersed, readily germinate to a high percentage when moisture is available. If conditions continue being favorable for growth, they are in a position to preempt the available resources; yet an intervening period of unfavorable biotic or abiotic conditions can eliminate the entire cohort. The trade-offs between the two achene types under two contrasting climatic regimes are shown in Figure 16.

The undispersed ray achenes are more responsive to environmental stimuli as their germination rates differed on the three contrasting soil microtopographies, whereas disc achene germination did not. Further, ray differ physiologically from disc since they require light for germination, possess a lower percent of their storage compounds as carbohydrates (a readily available substrate for energy production early in germination), and have a thicker seed coat which might restrict water or gas exchange or resist pathogens. Ray achenes may remain in enforced dormancy for extended periods of time. Thus, as the two morphs respond to different environmental triggers, the species can survive in unpredictable habitats.

Under conditions causing the mortality of germinating disc achenes, the ray population may remain primarily dormant. Scattered ray continue to germinate for a prolonged period. In a mixed stand, however, biomass of ray seedlings is significantly decreased.

Greenhouse tests suggest a greater proportion of ray achenes are
Figure 16. Expected germination and establishment responses of the two morphs to contrasting climatic regimes.
produced by plants under stress. One expects this not only since ray achenes seem to represent more certain future success in the face of variable conditions but also since they require less energy expenditure on the part of the parent plant than do the disc.

A general comparison of disc and ray characteristics is made in Figure 17.

Germination is only one of many factors in a plant's life cycle which determines whether or not it may fulfill a weedy role in the community. Though this germination dimorphism appears adaptive in the unpredictable situations encountered in disturbed habitats, the developmental plasticity and generalist strategies shown by this taxon in the field must also be important in the telegraphplant's spread as a ruderal weed.
<table>
<thead>
<tr>
<th>DISC</th>
<th>GERMINATES FAST AND TO A HIGH PERCENTAGE</th>
<th>FLORETS</th>
<th>1.27mg</th>
<th>POTENTIAL TO BE WELL DISPERSED REQUIREMENTS</th>
<th>SIMPLE GERMINATION REQUIREMENTS</th>
<th>HIGHER CARBOHYDRATES IN EMBRYO</th>
</tr>
</thead>
<tbody>
<tr>
<td>RAY</td>
<td>GERMINATES SLOWLY, SOME ACHENES DORMANT</td>
<td>FLORETS</td>
<td>0.76mg</td>
<td>FALLS TO BASE OF PLANT</td>
<td>MORE COMPLEX GERMINATION REQUIREMENTS</td>
<td>HIGHER LIPIDS IN EMBRYO</td>
</tr>
</tbody>
</table>

Figure 17. Summary of achene characteristics. Scale: 1 cm approximately equals 1 mm.
LITERATURE CITED


Becker, H. 1912. Über die keimung verschiedenartiger früchte und samen bei desselben species. (Concerning the germination of heterogeneous fruits and seeds by the same species). Biehefte Botanisches Centralblatt 29:21-143.


Karssen, C. M. 1970. The light promoted germination of the seeds of Chenopodium album L. III. Effect of the photoperiod during


APPENDICES

<table>
<thead>
<tr>
<th>Month</th>
<th>Location</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
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<td></td>
<td>25/13</td>
<td>25/11</td>
<td>22/15</td>
<td>26/10</td>
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<td>18/06</td>
<td>22/10</td>
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<td>20/04</td>
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<td>11/03</td>
<td>19/08</td>
<td>12/04</td>
<td>14/-1</td>
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<tr>
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<td>18/07</td>
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<td>17/10</td>
<td>16/07</td>
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<td>28/11</td>
<td>32/12</td>
</tr>
</tbody>
</table>

1 Locations: A. Bakersfield, Calif.; B. Antioch, Calif.; C. Los Angeles WSO, Calif.; D. Red Bluff, Calif.; E. Beaver Dam, Arizona.
Table 19. Ray achene germination following the dry period: interactions between surface, prior moisture regime, and disturbance.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
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<tr>
<td>Surface</td>
<td>2</td>
<td>159.29</td>
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<tr>
<td>Prior moisture</td>
<td>1</td>
<td>0.05</td>
<td>0.01</td>
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<tr>
<td>Disturbance</td>
<td>1</td>
<td>232.13</td>
<td>19.36 *</td>
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<tr>
<td>Surface-prior moisture</td>
<td>2</td>
<td>11.39</td>
<td>0.95</td>
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<tr>
<td>Surface-disturbance</td>
<td>2</td>
<td>176.82</td>
<td>14.74 *</td>
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<tr>
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<td>0.39</td>
<td>0.03</td>
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<td>Surface-prior moisture-disturbance</td>
<td>2</td>
<td>31.50</td>
<td>2.63</td>
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<tr>
<td>Total</td>
<td>23</td>
<td>49.33</td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>12</td>
<td>11.99</td>
<td></td>
</tr>
</tbody>
</table>

* = significant at P < 0.005

Tabular $F = 11.75$ at 1 and 12 degrees of freedom, $8.51$ at 2 and 12 degrees of freedom. Both tabular values are for $P < 0.005$. 