PLANT DEMOGRAPHIC STUDIES OF A DESERT ANNUALS
COMMUNITY IN NORTHERN UTAH DOMINATED
BY NONNATIVE WEEDY SPECIES
by
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A thesis submitted in partial fulfillment of the requirements for the degree of
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Field and laboratory investigations were conducted relating to factors controlling distribution and abundance of annual species growing in a disturbed portion of the salt desert shrub zone on fine-textured soils. Dominant species on the site in the two study years were the nonnative, halophytic, late-summer maturing, *Halogeton glomeratus* (Bieb.) C.A. Mey., and *Bassia hyssopifolia* (Pall.) Kuntze. Contrasting amounts of precipitation were received in the two years; in 1974, spring conditions were so dry that two early-maturing, subdominant annuals, *Descurainia pinnata* (Walt.) Britton, and *Lepidium perfoliatum* L. were essentially absent. They successfully reproduced under more favorable 1975 conditions.

Studies on species distribution centered around factors responsible for occurrence of large (20-30m across), adjacent, essentially pure stands of *Bassia* and *Halogeton*. It was determined that few seeds dispersed more than a couple of meters from parent plants; and that seedling establishment success of the species was significantly different in the two vegetation types, commensurate with soil surface physical and chemical
differences. The less drought tolerant Bassia was confined to soils which had higher water potential in summer than the areas occupied by the succulent Halogeton. Bassia responded with more rapid growth when water availability increased, and suppressed Halogeton in both growth chamber competition studies. The adjacent pure communities are believed to be maintained by Bassia's inability to establish on soils dominated by Halogeton, and Bassia's competitive superiority when both species become established together.

Studies on plant abundance involved making quantitative estimates of numbers of seeds or plants per unit area in different life cycle phases during the study period. The objective of these studies was to determine the manner in which each year's seed production was utilized, in terms of dormancy of seeds in soil, germination, mortality, or reproduction. It was determined that residence time of seeds in soil was short, since seeds germinated freely after overwintering. Consequently the vegetation composition was closely related to the previous year's seed production. Tremendous mortality occurs during the seedling establishment phase, as only eight percent of seeds sown into marked quadrats survived until mid May. Mortality during summer was highly density-dependent. Plant plasticity served a homeostatic function on one site which suffered a seed crop failure in 1974. The few plants established there in 1975 became very large so that total seed production was not greatly different from areas which had a substantial amount of seed production in 1974.
INTRODUCTION

An inadvertent but inevitable result of European man's settlement of the western United States was the introduction of several species of weedy, highly competitive, nonnative annual plants. The settler's livestock abused the native vegetation on vast areas of these semiarid rangelands by overgrazing. Intensity of grazing was so high in many areas that the fragile shrub-steppe plant associations were unable to regenerate, often allowing the opportunistic weedy annuals to become dominant on these sites.

Genotypes of these annuals are such that they are highly adapted to colonization and persistence on disturbed ground, thereby preventing regeneration of native perennial plants. Their year to year population instability and relatively low usable production make them unattractive as soil stabilizers or sources of livestock forage. The possible exception to this categorization is cheatgrass (*Bromus tectorum* L.), a late-successional exotic annual which provides some useful livestock forage in the spring season on degraded Great Basin rangelands. The increasing demands for utilization of rangeland resources favor conversion of these undesirable weed communities into more useful perennial bunchgrass stands through herbicide and mechanical techniques followed by seeding (Evans, Young and Eckert, 1969).
Additionally, the increasing tendency of man to modify and manipulate the wildland environment often results in disruption of natural plant communities and accompanying unforeseen population increases by these plastic and persistent weed species. This investigation was undertaken in hopes of discovering some of the major factors controlling plant species distribution and abundance in a community composed mainly of nonnative annual plants in a disturbed area of the sagebrush steppe zone in northern Utah. These studies on population ecology and growth requirements provide fundamental information for range improvement practices since improvements rely on understanding the ecology of the species being manipulated. Additionally, results of this investigation can contribute to an understanding of the basic mechanisms regulating population dynamics and successional trends in these annuals communities.

Desert environments present severe constraints to plant life. Successful species must be able to maintain their populations in spite of little total moisture, irregular occurrence of precipitation events, high temperatures, and wide diurnal temperature fluctuations. Many desert annual species avoid these extreme physical conditions through germination regulation mechanisms or by rapidly completing their life cycles, confining growth to more favorable environmental periods. Other desert annuals are better able to cope with stressful environmental periods, maintaining their populations despite substantial mortality. The success of each species depends mainly on the amount of seed
it is able to produce each year, since it is the sole means of dispersal and regeneration.

As a group, annuals are uniquely suited to plant demographic studies since each year they must develop from seed; whereas perennial plants simply resume growth, as much of their supportive structure is still present from the previous year. Because they do not maintain a fairly permanent biomass structure, continuity of annuals communities is not as great from one year to the next. There are more opportunities for natural selection to act on the genetic variability present in individual seeds of the species present, since each year requirements for germination and seedling establishment must be met before seed production can occur. Consequently, there can often be greater and more rapid changes in vegetation composition through time in communities of annual plants.

The studies for this thesis were conducted in 1974 and 1975 on a community composed almost entirely of annual plants. The dominant species in this community were two late summer flowering nonnative species: *Halogloton glomeratus* (Bieb.) C. A. Mey. and *Bassia hyssopifolia* (Pall.) Kuntze., both in the family Chenopodidaeae. Two subdominant, late spring flowering members of the Cruciferae, Tansy Mustard (*Descurainia pinnata* (Walt.) Britton), the only indigenous species, and Yellowflower Pepperweed (*Lepidium perfoliatum* L.) were present in 1975. Investigations of their ecology primarily attempted to answer two sorts of questions: what were the major factors influencing distributions of the two
species from point to point on the study site, and what were the major factors influencing their abundance from one year to another. The hope was that by studying the population behavior of these species some insights into the ecology of desert annual plants in general might be realized.

Initial interest in the topic of species distribution was fostered by observation of large (20-30 m across), adjacent, essentially pure stands of Bassia and Halogeton on the study site over areas that superficially appeared quite similar. The amount of seed dispersal across the ecotone between the dissimilar stands was investigated as a possible explanation for their occurrence. Other investigations generally compared the response of Bassia and Halogeton to similar sets of conditions in order to discover differences in their ecological tolerances which might provide some explanation for their field distribution. These investigations dealt with seed germinability, seedling establishment success in the two vegetation types, drought tolerance, and competitive interactions between the plants when grown together.

The second set of studies were quantitative in that estimates were made of densities of seeds or plants present in different life cycle stages during the course of the study. Through these estimates I hoped to understand why changes in abundance of the various species occurred within a growing season as well as from one year to the next. Since numbers of seeds per unit area produced each year, or available in the soil for germination, are important determinants of vegetation composition, these
parameters were estimated in both years of the study. The amount of mortality occurring during the seedling establishment phase and throughout the growing season was estimated, as differential mortality at some life cycle stage can account for differences in species abundance. These and several other quantitative estimates enabled construction of several reasonable conjectures explaining observed changes in density, dominance and the successional trend on the study site.

The Study Area

All field studies were conducted on the south Curlew Valley Validation Site of the U.S. International Biological Program, Desert Biome. The Site is located in Box Elder County, northern Utah, approximately 25 kilometers southwest of Snowville, in sections 5-8 of township 13 North, Range 9 West at 1,320 m elevation (Balph, 1973). In the summer of 1973 the Site and some surrounding terrain, several square kilometers in all, was fenced to prevent livestock from disturbing any of the ongoing studies.

Climate in the area is semiarid, with a mean annual precipitation of 25 cm, which is highly variable from year to year. The two years during which this study was conducted, 1974 and 1975, had distinctly different amounts of precipitation. In 1974, precipitation through September was 14.40 cm and in 1975 it was 21.82 cm; the year-long totals were 21.36 and 25.50 cm, respectively. Each year soil moisture is recharged by winter
snowfall and depleted during the dry summer; as much as 60 percent of the precipitation comes in the form of snow (Cook and Stoddart, 1963).

Air temperatures similarly display great variability from day to day as well as diurnally. The annual range is from more than 40°C in summer to less than -20°C in winter, with a 15-20°C difference between day and night temperature quite common. Detailed precipitation and temperature data are available (Gasto, 1969; Balph, 1973).

Soils in the Valley were formed during the Pleistocene epoch under the influence of Lake Bonneville, and are of lacustrine and eolian sediments. Soils on the site have a fairly uniform silt loam texture, minimal profile development, and below about 40 cm, high exchangeable sodium percent and high electrical conductivity (Balph, 1973, p. 282-285). I have classified the soil as a fine silty, mixed, mesic, Xerollic Calciorthid.

In most areas of the Site the soil surface exhibits two features which are of importance in the establishment of annual plants. The high silt and clay fractions cause the soil to shrink and swell, dependent on its water content. This phenomenon has resulted in the development of polygonally-shaped surface peds, roughly 10-20 cm across, which are separated by narrow cracks from 2-5 cm in depth. The other feature has been referred to as a vesicular layer (Blackburn and Skau, 1974; Hugie and Passey, 1964); the peds frequently display a moderate platy structure interlayed with thousands of tiny, gas-containing vesicles which leaven the
soil, giving it a structural appearance similar to a piece of bread. These vesicles increase the porosity of the soil surface, making it effectively drier, due to the gas-containing spaces; and softer, due to the compressibility of the layer. The relationships of these soil properties to annual plant establishment will be discussed later.

Vegetation on the Validation Site was mainly of three different types: a crested wheatgrass seeding, native vegetation dominated by sagebrush (Artemisia tridentata Nutt.), shadscale (Atriplex confertifolia (Torr. and Frem.) S. Wats) and squirreltail (Sitanion hystrix (Nutt.) J. G. Smith), and a disturbed area now dominated by weedy, nonnative annual plants. All field studies for this thesis were conducted in the annuals area. The dominant species in 1974 and 1975 were Bassia hyssopifolia and Halogeton glomeratus. In 1975 significant amounts of Descurainia pinnata, the only native present, and Lepidium perfoliatum were evident. Russian thistle (Salsola kali L.) was found in low numbers in both years.

Scattered clumps of squirreltail and a few patches of sagebrush were almost the only perennials present in this 50 to 70 hectare area. There are numerous remnants of dead sagebrush plants, many with branches still erect, indicating that in the past the area was probably a fairly typical sagebrush-dominated community. Some unknown factor caused the death of these plants; whether a severe outbreak of the sagebrush defoliating moth, Aroga websteri Clarke an extreme drought, a fire or some other cause, the precise history remains unknown.
The Experimental Sites

In May of 1974 four areas in the Validation Site were selected for investigation, each area approximately 25 meters square. All four sites are located on the southwest part of the fenced plot and are contained within an area approximately one-half kilometer long by one-fourth kilometer wide.

The first site (subsequently referred to as hill site), on which the majority of the investigations was done, exhibits an abrupt boundary between nearly pure stands of Bassia and Halogeton as shown in Figure 1. The ecotone occurs over a distance of less than 2.5 m and corresponds with a gentle and scarcely perceptible undulation in the topography. The Halogeton is found on the higher ground, and Bassia is in the depression some 20 to 70 cm lower. A few vigorous clumps of Great Basin wildrye (Elymus cinereus Scribn. and Merr.) are found in the Bassia vegetation along with Tansy Mustard and a sparse population of Russian thistle.

The second site, located near one of the fenced boundaries (and subsequently referred to as fence site) is similar in most respects to the hill site, except that the separation of Bassia and Halogeton communities is not associated with topographic relief.

The third site (subsequently referred to as sage site) was chosen to include an isolated group of sagebrush plants which
Figure 1. View of the ecotone on the hill site in July, 1974. The photograph shows the abrupt boundary between nearly pure stands of Halogoton (foreground) and Bassia (background). Old Descurainia stems (yellow) are also evident in the Bassia vegetation.
occurred in this annuals area. The eastern one-third of the site is a somewhat open stand of mature sage plants, about 30 in all, while the western half is almost exclusively Halogeton. Lepidium occurs scattered between the sage clumps and extends into the open ground away from the sage. This was almost the only place where Lepidium occurred as the dominant annual species.

The fourth site (subsequently referred to as bare site) had the highest density of Sitanion, but seemed to have a lower annual plant density when first observed in the spring of 1974. Bassia and Halogeton were both present here in fairly equal numbers but did not exhibit the negative association so evident on the first two sites.

These four sites served different roles in fulfilling the study objectives. The sage and bare sites were not particularly useful in investigating the causes responsible for adjacent pure stands of Bassia and Halogeton, because they did not display the phenomenon. Rather, the hill and fence sites were the major sources of information on this topic. All four sites contributed to the quantitative seed budget portion of the study.

Study Objectives

The objectives of the study were twofold:

1. To investigate possible factors responsible for occurrence of adjacent, essentially pure stands of Bassia and Halogeton in the field. The assumption here is that since the pure stands were so proximitous, they should have been invaded by the absent species.
This problem was studied in relation to seed germinability and dispersal, seedling establishment, soils differences, plant drought tolerance, and competitive interactions between the species.

2. To gain insights on the relative importance of dormancy, mortality, or reproduction in controlling the dynamics of these annuals communities. By estimating densities of seeds or plants present in different stages of the life cycle, the critical periods controlling plant numbers can be investigated. Since the community is generated anew each year from seed, its trend hinges on the manner in which each year's seed production is dissipated. Whether the seed remains dormant in the soil, germinates and dies, or successfully reproduces—and the amount of seed produced—these are the critical factors determining vegetation composition.
REVIEW OF LITERATURE

This review of literature is divided into three major sections. The first section considers the species studied here, and other alien annuals, in a wide historical, management context. The general attributes of weeds, some of the circumstances surrounding their widespread invasion of western rangelands, factors affecting succession in these annual communities, and the kinds of problems Halogeton creates for stockmen are discussed.

The remaining two sections consider studies more specifically related to the experiments done in this investigation. The second section, Life Cycle Phases, relates pertinent studies which point up some of the important factors determining whether or not a plant will die, survive or grow at a given stage in its life history. The final section, Community Studies, is a detailed examination of several papers on annual plant communities. The salient features of each paper are summarized to provide an idea of various biotic and abiotic factors which influence distribution and abundance of annual plants.

Ecological Role of Annual Weeds

Evolution of weeds

Weeds have unique ecological characteristics which enable them to aggressively occupy habitats where the natural vegetation has
been disturbed or destroyed. Genetically based adaptations for
weediness can be found in all phases of the life history; their
overall effect resulting in species with "general purpose"
genotypes. Baker (1965) has done comparative studies between closely
related taxa, one member being weedy and the other non-weedy. From
these he generalized characteristics of the ideal weed (Baker, 1974),
some of which are: germination requirements met in various
environments, a short period of vegetative growth before flowering,
a lengthy period of seed production, facultative self pollination
or apomixis, high seed output under favorable conditions but plastic
enough to produce some seed under a wide range of conditions, and
having adaptations for short and long distance dispersal.

Breeding systems of most annual weeds involve autogamy or
apomixis, enabling a single individual to colonize an area and to
produce genetically uniform progeny, each one as adapted as the
initial immigrant so that there is no wastage to recombination.
Such breeding systems are ideal for rapid occupation of uniform
habitats and for colonization after long distance dispersal (Baker,
1955).

Alien annuals in the Great Basin

Before 1900 overgrazing was widespread on western rangelands,
creating vast areas in which native vegetation had been seriously
depleted or eradicated (Ellison, 1960). Along with the settlers came
weed seeds, adhering to the fur of their animals or mixed in with
crop seeds. Several introduced annual species were
superbly preadapted to the newly overgrazed lands and rapidly proliferated, preventing regeneration of the native vegetation.

Young, Evans, and Major (1972) review the circumstances surrounding this tremendous invasion by low value, unstable alien annual species and explain its occurrence based on contrasting evolutionary histories of the invading and native species. The aliens are believed to have originated generally in the steppe area of central Asia, which is similarly dominated by *Artemisia* species. The important difference in the history of the two regions is that in Asia nomadic herding of livestock had been practiced for thousands of years, while in the Great Basin there were few large herbivores. Selective pressures had generated the "general purpose" genotypes in these aliens, enabling them to thrive in the disturbed grazing and herding areas. Correspondingly, in the Great Basin there was little development of colonizing ability, and recent overgrazing served to prepare an optimal habitat for the invaders.

These species now occupy millions of acres of western range-lands, and are not nearly as valuable, in terms of forage production, as the native perennial vegetation they have displaced. Millions of dollars have been spent on range improvements and research to convert these lands to valuable, perennial bunchgrasses (Evans, Young, and Eckert, 1969; Young and Evans, 1972, 1975; Evans and Young, 1975; Kay and Owen, 1970; Eckert et al., 1974). Recently, an even more aggressive and less valuable alien grass, Medusahead (*Taeniatherum asperum* (Sim.) Nevski), has been spreading in the
Great Basin (Dahl and Tisdale, 1975; Young and Evans, 1970), indicating that the weed problem is not nearly solved, and although these species are not native, they are definitely a permanent part of the American flora.

Succession in Great Basin annual communities

Studies done in the south-central, sagebrush-grass zone of Idaho—utilizing the same areas—have been published on secondary succession following abandonment of crop land (Piemeisel, 1938, 1945, 1951; Hironaka and Tisdale, 1963). The first year after abandonment (1938) Russian thistle began colonization, followed by increasing dominance by several mustard species (Descurainia sophia (L.) Webb and Sisymbrium altissimum L.) during the second and third years. Cheatgrass began displacing the mustards during the fourth year, and after the fifth year, maintained dominance on the site until the mid-fifties, by which time squirrel-tail (Sitanion hystrix (Nutt.) J. G. Smith) and other native grasses had become dominant.

The causal factors behind the early successional stages can be found in the ecological habits of the species: ability to establish on disturbed sites, tolerance of drought and earliness of maximum growth being the most important. Russian thistle can establish under the extreme microenvironmental conditions present at the soil surface after cropping, while cheatgrass requires development of microrelief and litter deposition (Evans and Young, 1970). Cheatgrass is most drought tolerant, germinates in the fall,
completes its life cycle in June, usurping soil moisture from the other species, which fruit in July and August. Although cheatgrass is initially unable to colonize the disturbed sites, its unique growth habits have enabled it to outcompete most other species wherever disturbance occurs (Klemmedson and Smith, 1964). Figure 2, after Piemeisel's 1951 paper, graphically demonstrates period of growth in relation to soil water content, which favors the early-maturing cheatgrass.

In other weed communities in the Great Basin rates of succession and species involved may be different but the controlling factors, as discovered by Piemeisel, are probably the same. Based on their ecological characteristics Halogeton and Bassia are likely to be found in the colonizing stage of secondary succession, but they are distinctive from other alien annuals in that they are halophytic (Cronin, 1965; Kennedy, 1927).

The Halogeton problem

Halogeton is a widespread poisonous alien annual that has cost stockmen millions of dollars in losses since it was first discovered in Nevada in 1934 (Zappetini, 1953). Plant materials contain an average of 16.5 percent total sodium and potassium oxalates, which cause a lowering of blood serum calcium in animals; if enough Halogeton is eaten within a short time period, death will occur due to asphyxia. Supplemental feeding of calcium salts can diminish the risk of death (Cook and Stoddart, 1953). Several catastrophic poisoning events have occurred in the inter-mountain region in the past, sometimes more than 1000 animals dying
Figure 2. Periods of growth of three successive plant occupants on abandoned cropland in relation to yearly soil moisture trend. Cheatgrass eventually dominates the earlier colonizing species because it grows when soil moisture is more available and usurps moisture from the later maturing species.
in a short period (Bohmont, 1951; Stoddart et al., 1951), but research and management techniques have diminished the likelihood of mass poisonings.

In addition to being poisonous, the high salt content of Halogeton litter may tend to foul the soil, preventing reestablishment of less salt-tolerant species. Laboratory studies (Smith and Rauchfuss, 1958; Kinsinger and Eckert, 1961) have shown that leachate from the plant material adversely affects growth of several rangeland species, and soil physical and chemical properties (Eckert and Kinsinger, 1960). Its succulent habit, drought tolerance, production of two kinds of seed, and affinity for disturbed areas, are characteristics that insure its persistence despite all efforts to eradicate it. Several different publications (Cronin, 1965; Cook, 1965; Frischknecht, 1968; Cronin and Williams, 1966; Tisdale and Zappetini, 1953) and reviews of literature in theses (Jordan, 1973; Johnson, 1957; Zappetini, 1952) give a thorough documentation of the Halogeton problem and attempts to solve it.

**Life Cycle Phases**

**Seed germination**

Seeds serve a role of paramount importance in the maintenance of populations of annual plants, as each year the population must germinate and reestablish itself. Species in different environments have developed an endless variety of germination adaptations enabling them to germinate under conditions that are
likely to allow reproduction. Koller (1972) has presented a comprehensive review of environmental control of seed germination, additional examples of studies on different aspects of seed germination will be presented here.

Halogeton produces black and brown seeds which have different germination requirements. Ninety-five percent of black seeds will germinate after a four week moist-cold (-6°C) treatment. It is believed that the brown seeds germinate discontinuously over a several year period, while nearly all black seeds should germinate in spring after overwintering (Cronin, 1973).

Many weed species are able to germinate at lower osmotic potentials than crop plants, enabling them to commence growth under dryer conditions and gain a competitive advantage (Hoveland and Buchanan, 1973). Similarly, Salsola kali seeds germinate very rapidly; only 14 hours after receiving three-tenths inch of water, the seedlings emerge from soil (Dwyer and Wolde-Yohannis, 1972). Descurainia pinnata, Lepidium perfoliatum, and 17 other species of 233 tested from Nevada and California, developed a layer of mucilage around the seed coat on wetting. This layer influences moisture relations: seeds do not require soil coverage and thus can germinate in a wider variety of microsites (Young and Evans, 1973).

Several studies have shown how variation in germination behavior by a species can help assure its persistence. Palmblad (1969) did germination studies on seed collected from 174
populations representing 105 generally weedy species. Within about one-eighth of these populations, individual plants exhibited germination characteristics that were significantly different from that of a bulk sample of the population. Lindauer and Quinn (1972) studied ecotypic variation in germination of *Danthonia sericea* populations from different habitats along the east coast. Seeds from wet habitats required light for germination while those from dry habitats were inhibited by light. Optimum temperatures for germination were 15-25°C, day-night alternations, similar to field temperatures during spring germination. Baskin and Baskin (1975) found that seeds of *Torilis japonica*, a Eurasian winter annual growing in disturbed habitats in the eastern U.S., are induced into dormancy by winter temperatures. Some of the summer-produced seed germinates in the fall, but most of it does not germinate until the following autumn; the plant thus dividing each year's seed production into two germination periods, insuring its persistence, without immigration, in the event of a seed crop failure.

Several other studies deal with germination of annual plants in a community context (Nott, 1973, 1974; Pemadasa and Lovell, 1975; Young et al., 1970; Young, Evans and Kay, 1975).

**Seedling establishment**

After germination the seedling must establish itself. This phase is generally believed to be critical in the life cycle as there are numerous ways in which mortality may occur.
The task of the seedling plant is to send its radicle into the soil deeply enough and rapidly enough to assure a reliable supply of water, while at the same time the cotyledons must reach the light and begin photosynthesizing before the seed energy reserves are exhausted. It follows that the microtopographic site of seed germination is crucial: if the seed is too exposed, the radicle may dry out; if it is buried too deeply, the shoot may be unable to penetrate the soil surface.

Harper (1961, 1968) and his colleagues and students (Harper and Benton, 1966; Harper, Lovell and Moore, 1970; Ross and Harper, 1972; Sheldon, 1974) have done pioneering work on the relationships between soil surface microtopography and seed morphology and size. They have developed the concept of "safe" germination sites, e.g., positions where a seed's germination and establishment requirements are met. And have hypothesized that species' geographic distributions may be regulated by soil surface properties which control germination.

Here, only a couple of studies can be reviewed. Seed of three Plantago species was sown onto soil that had various discrete microtopographic characters created by placing objects on or in the soil or by making shallow holes in the surface. The species demonstrated distinctly different degrees of establishment success in relation to the surface modifications. Bromus species also showed this response when sown onto soil with differing amounts of surface roughness (Harper, Williams, and Sagar, 1965). Sheldon's work with Asteraceae investigates influences of shape, size and
position of surface lying seeds on germination and seedling establishment. Seeds were placed in specific positions relative to the water-supplying substrates and germination was observed. Different amounts of soil compaction, clay content, and water treatments resulted in variable rates and amounts of germination, establishment and mortality.

Evans and Young (1970, 1972a, b) and their coworkers (Evans et al., 1970) used an applied, field oriented approach to the seedbed ecology of alien annuals in the arid west. These studies have emphasized measurement of physical parameters (air and soil temperature, relative humidity, light intensity, soil moisture potential) of the seedbed and their relationship to weed control and revegetation. Thickness of litter cover, amount of surface roughness, and depth are important factors influencing diurnal and seasonal patterns of the physical microenvironment; they, in turn, control vegetation dynamics.

Recently Evans, Kay and Young (1975) utilized extensive micro-environmental monitoring, seeding of several perennial grass and legume species, and herbicide spraying in the California annual range type. They were able to conclude that available soil moisture permitted germination, seedling emergence and growth, while temperature controlled the general growth rate. Interception of light by the canopy of annual plants is the major factor of competition which prevented establishment of perennial grasses (Phalaris spp.). This shading was virtually restricted to 1-2 cm above the surface but it occurred during critical periods of emergence and growth of the seeded species.
Related studies dealing with seedling establishment have been conducted by Werner (1975c), Friedman and Orshan (1975), Dowling, Clements and McWilliams (1971), and Raynal and Bazzaz (1973).

**Plant competition**

Throughout the vegetative and reproductive phases of the life cycle, plants generally must compete for limited growth resources. Harper (1961, p.1) broadly terms this interference to be "the short and long term hardships that result to organisms from the direct proximity of neighbors." Competition can occur for any resource which can become limited in supply; such as soil water (Hironaka, 1961; Klikoff, 1966; Dahl and Tisdale, 1975; Sharitz and McCormick, 1973), nutrients (Kay and Evans, 1965; Snaydon, 1971; Pemadasa and Lovell, 1974b, Guerrero and Williams, 1975; Hull and Muller, 1976), and light (McCown and Williams, 1968; Werner, 1975b; Grime, 1966). Time of growth initiation (Raynal and Bazzaz, 1975a; Holt, 1972; Ross and Harper, 1972) affects competitive relationships.

The voluminous literature on competition in herbaceous grassland plants and in a wider plant demography context has been thoroughly reviewed by Risser (1969) and Harper and White (1974), respectively. Risser's review states that the direct consequences of density stress on plant populations are normally "(A) Individuals show a plastic response as they adjust to share limiting resources. (B) There is an increase in mortality. (C) Differences become exaggerated within the population, and a hierarchy of exploitation is encouraged" (p.255).
DeWit (1960) did competition studies on crop plants and introduced a delicate experimental design (replacement series) useful in studies of interspecific competition; the total density of plants in a mixed stand is maintained constant, while the proportions of the two species are varied. This design has been used by several authors (Harper, 1964, 1968; Marshall and Jain, 1969).

**Seed production**

Since annual plants can only establish themselves from seed, the amount of seed produced by a plant is a prominent factor in determining plant density the following year. Harper (1966) and Harper and White (1974) indicate that the amount of seed produced per plant is greatly dependent on the growing conditions and the plasticity of the individual involved; a *Papaver rhoeas* plant may produce as few as four seeds when stressed, but under favorable conditions may produce upwards of $3 \times 10^5$ seeds. Salisbury (1942) has surveyed many British species and found that greatest seed production (usually more than $2 \times 10^4$ seeds per plant) was achieved generally by annual species of short-term habitats (wood clearings, exposed mud, etc.).

Wilcott (1973) developed a computer simulation model for desert annuals that, among other things, would predict seed production per square meter from various densities, based on survival, seed production per plant, and rainfall parameters. He also states that the literature on desert annuals is deficient regarding estimates of seed production per plant. Brown (1943)
made estimates of pounds of seed produced per acre for perennial grass and annual weed species in the Kansas short-grass type. Seed production for different species ranged from none to 333 pounds (151 kg) over a three year period. Biswell and Graham (1956) made density counts at the seedling and mature stages in the California annual type and estimated seed production ranged from 400-1,600 pounds per acre (448-1793 kg/ha).

Twenty-five species of annuals in the Mojave Desert have a variable portion of their mature dry weight biomass as fruit, ranging from about 9 to 50 percent (Turner, 1973, p. 86). Hickman (1975) has found that Polygonum cascadense, an annual of non-forested openings in the Cascade Mountains, has a variable reproductive allocation based on a plastic response to environmental unpredictability. He studied populations along a gradient of increasing physical stress (based on several indicators) and found that the portion of total dry biomass allocated to reproduction increased as environmental harshness increased. The mean reproductive allocation (bud, flower, seed) was about 58 percent in the harshest environment. Seed production per plant was highest in the most favorable environment (229 seeds per plant), but on a square meter basis it was highest in the second most stressful habitat ($1.7 \times 10^5/m^2$).

**Seed dispersal**

The dispersal of reproductive propagules is essential for colonization of new habitats by a species. Weedy annuals, in
particular, must have efficient dispersal mechanisms as their habitats are often short-lived. Adaptations for dispersal and the various agents of dispersal are treated in a recent work by van der Pijl (1972). Burrows (1975a, b) has used a mathematical-aerodynamical approach to predict distances and patterns of movement for spores, pollen and dust seeds and for larger seeds having common aerodynamic properties. His studies indicate that flight paths can be calculated precisely, if the pattern of wind movement is known in sufficiently fine detail.

A number of studies indicate that most seeds move only short distances from the parent plant (Pemadasa and Lovell, 1974a; Salisbury, 1964). Werner (1975a) found that deposition of teasel (Dipsacus fullonum L.) seeds followed the negative exponential relationship \[ \log y = 2.74 - 1.69x \] where \( y \) = number of seeds deposited and \( x \) = distance from parent plant in meters. Only about 1 percent of all seed produced was deposited more than 1.5 m from the parent plant. Friedman and Orshan (1975) found that 85 percent of achenes produced fell under the canopy of the parent Artemisia herba-alba plants. Knipe and Springfield (1972) trapped Sporobolus airoides seeds in large barren areas adjacent to vegetated sites. They concluded that although many seeds blew into these areas, due to lack of barriers to movement the seeds generally did not come to rest until they were impeded by existing vegetation, and hence the barren areas persisted.
Seeds in soil

Seeds lying in the soil function as a reserve in case seed crop failure should occur in one or more years; the population can reestablish itself without immigration. Numerous studies, usually done in an agronomic context, indicate that the number of soil seeds is usually vastly greater than the number of growing plants (Brenchley and Warington, 1930, 1933, 1936; Chepil, 1946; Budd, Chepil and Doughty, 1954). Wesson and Wareing (1969a, b) have shown the induction of light sensitivity due to burial in eleven species of weed seeds. Species which had little or no light requirement for germination before a 50 week burial period were completely dependent on exposure to light after recovery. Seeds in subsurface soil showed 62.5 percent more emergence when germinated in light than when kept in continuous darkness. This can account for the flush of weed germination after plowing fields. They further hypothesize that dormancy may be induced in the soil by a seed-produced gas. Stoller and Wax (1974) found that in soil some weed species developed hard seed coats which required acid scarification before germination would occur.

Kropac's (1966) review article considers the merits of different methods of estimating numbers of seeds in soil. There are mainly two techniques in popular use; the first involves taking the soil samples to a greenhouse, spreading them out in a dish, watering them periodically and identifying the seedlings that become established; [the second involves a sieving and washing of
the sample to remove particles of inappropriate size, followed by immersion in a high specific gravity salt solution to cause flotation of organic materials but settling of mineral matter. Seeds are then counted in the organic fraction with aid of a microscope. The germination technique is considerably less time consuming but will give lower estimates as some seeds may remain dormant. The flotation technique can locate more of the seeds but whether or not intact seeds are viable and potentially germinable is another question.

Kropac also studied seed populations from two Czechoslovakian agricultural fields using flotation techniques. He found that more than 93 percent of seeds were of summer or winter annuals, less than 6 percent were from weedy perennials and crop seed was only about 1 percent of the total. He regards 20 percent of the total seeds discovered as "potential weed flora" (e.g. capable of germinating) and on the two sites found \(4 \times 10^4\) and \(1.4 \times 10^5\) "germinable" seeds per square meter to depths of 25 and 30 cm, respectively. Seeds were fairly evenly distributed through the sampled profile. The tremendous numbers of seeds in soil can help account for failures of grass seedings into pastures, as the rate of seeding is usually on the order of 1 percent of the resident seed population, Sumner and Love (1961) and Jalloq (1975) present evidence supporting this.

Major and Pyott (1966) also review the literature on buried viable seeds and conducted a study comparing adjacent grazed and ungrazed bunchgrass sites in California. They used germination to
estimate numbers of seeds in soil. Fourteen seed species were found in the grazed area, but only seven in the ungrazed area. All seed species also occurred as plants in the grazed area, but in the ungrazed area only half the species were present as plants. Total numbers of seeds per square meter to a two inch depth were $8.23 \times 10^3$ and $12.29 \times 10^3$ in the grazed and ungrazed areas, respectively. Of ten perennial species in the area, none had germinable seeds in the soil. They conclude that relative numbers of seeds in soil and plant individuals in the vegetation are poorly correlated.

Roberts and Feast (1972, 1973) studied the periodicity of emergence of 20 weedy species over a six year period in relation to depth of burial and cultivation treatment. Seeds were placed in large pots which were buried to soil level and either remained undisturbed or the soil was thoroughly mixed several times per year. The mixing treatment significantly increased emergence percentage but it also decreased the half-life of viable seeds; in cultivated soil the half-life was less than two years, in uncultivated soil it was six years. Seeds sown at shallow depths emerged in higher percentages but had a lower percentage of ungerminated seeds which were still viable after a five year period.

**Community Studies**

In this section salient features of several studies on annual plant communities will be related. The authors have used different approaches and techniques to understand the factors affecting
species distribution and abundance. After dispersal to a site has occurred, the most successful species completes all of the life cycle phases from seed germination to seed production in order to perpetuate itself. Selection against an individual in any portion of its life cycle will result in diminished seed production; this, in turn, will diminish the abundance of the population. The following studies provide good examples of factors which regulate annual plant populations.

Sharitz and McCormick (1973) have used a life-table approach to study population dynamics of *Sedum smallii* and *Minuartia uniflora* on islands of soil in granite outcrops. Competitive ability, plasticity and tolerance of low soil moisture potential are the major components influencing community patterns. *Sedum* is more tolerant of low soil moisture, but where sufficient moisture is available, *Minuartia* outcompetes it. Thus *Sedum* is the primary invader in succession but is eventually replaced by *Minuartia* as soil accumulates. Mortality in *Sedum* is increased by interspecific competition but greater abiotic stress results in a plastic response and little increase in mortality. Conversely, *Minuartia* experiences mortality due to abiotic stress and interspecific competition, despite plastic responses.

Wilcott (1973) has reviewed much of the literature on desert annuals plant communities. Since then, Mott and McComb (1974) studied patterns of annual plants across undulating topography in an arid region of western Australia. They found more and larger plants associated with slight mounds around shrubs. They felt
this was due to deposition of greater numbers of seeds on mounds by wind and sheet flooding, and differences in soil fertility and water holding capacity. Soils on mounds had a higher organic matter content, which increased available nitrogen, and a greater depth to an impervious hardpan, which provided more water storage capacity than soils in adjacent depressions. Seeds sown on the mound and depression sites showed similar rates of seedling establishment, but more rapid growth was made by plants on mounds. No experimentation was done to substantiate their hypothesis that more seeds were deposited on mounds.

Pemadasa and Lovell (1974a) did similar studies in a sand dune system in Wales. They determined that few annuals grew in the low, wetter portions where perennial plants grew. Annuals were favored in the drier sites by absence of competition from perennial vegetation and the fact that high soil moisture potential was inhibitory to growth. An average of 56 percent of seedlings (of three species) were able to tolerate a 20 day drought in which soil moisture content dropped to 3.3 percent.

Wieland and Bazzaz (1975) have studied the ecophysiology of three codominant, summer annuals in a one-year successional field in Illinois. They found that the species have evolved different, intercompensatory mechanisms for niche separation which allow cohabitation. The species have different rooting depths which correlate with their growth capabilities. *Polygonum pensylvanicum* roots most deeply, assuring a reliable water supply, but it
photosynthesizes most slowly and the rate declines sharply when leaf water potential drops below -6 bars. *Abutilon theophrasti* roots at intermediate depth but photosynthesizes more rapidly, the rate not diminishing until leaf water potential is below -10 bars. *Setaria faberii* exploits the shallowest profile but is able to maintain itself due to greatest rate of photosynthesis, which is still near maximal at -12 bars, a rapid recovery from water stress and a rapid water potential recovery after rain.

In a related study, Raynal and Bazzaz (1975b) investigated two of the same species, and a third, with or without competition from winter annuals. The species exhibited different survivorship and growth capabilities resulting in different degrees of reproductive success. *Ambrosia artemisiifolia* showed no increased mortality under winter annual competition but rather demonstrated phenotypic plasticity involving a reduction in size. Most established individuals were likely to complete their life cycle, although those growing without winter annual competition were larger and produced more seed. *Polygonum pensylvanicum* showed sharp and constant declines in density during both years of the study. Removal of winter annuals enabled production of some seed while competing with other summer annuals. It produced insignificant amounts of seeds in competition with winter annuals and is dependent on open habitats where it can achieve a high reproductive output in the first year, ensuring a large seed pool which will last until a future disturbance.

*Setaria faberii* exhibited a bimodal peak of germination, the early germinants were suppressed by the winter annuals but
those establishing late avoided competition and produced seed since the winter annuals had already completed their life cycle. The early germinating seed population is probably replenished from plants growing in first year successional fields where winter annuals are not present.
MATERIALS AND METHODS

This chapter describes in detail the field and laboratory procedures used to conduct the component experiments of this study. At the start of each subsection, a statement or two describes the intended goal of the experiment, to facilitate understanding its role in achieving the objectives. Taken collectively, the individual experiments provide reasonable evidence pertinent to the twofold objectives of: 1) understanding the factors causing and maintaining adjacent pure stands of Bassia and Halogeton, and 2) quantifying dynamics of seeds and plants through time in hopes of assessing their implications for change in the annuals community.

Bassia-Halogeton Comparative Studies

Density at fixed points

After the four plots were selected their boundaries were defined by driving painted, wooden dowel stakes into the ground at 5 m intervals to form a rectangular grid of stakes. Plots were oriented with their axes in generally north-south and east-west directions. Three of the plots were 25 x 20 m while the hill plot was 30 x 25 m.

These stakes were to be used for general orientation as well as for repeated sampling of plant densities. With the latter in mind, as the stakes were being located, any position which
constituted an irregularity for data collection (such as the base of a sagebrush plant) was moved 50 cm to one side of the grid intersection so that sampling could be confined to vegetation of uniform physiognomy within the area. About 5-8 percent of the stakes were relocated in this fashion.

Density counts of numbers of individuals by species were made at each of these posts on June 24 and September 14, 1974, and in 1975 up to six times between May 26 and August 31. The sampling device was, in all cases, a 10 x 10 cm, rigid, wire frame placed in the northwest quadrant of each stake, with the stake itself serving as the southeast corner of the quadrat. At the first sample period a small wire marker was pushed into the soil at the northwest corner of the quadrat enabling replicated sampling of fixed quadrats by aligning diagonal corners of the frame with the wooden stake and the wire.

Seed dispersal experiment

During the period of seed dissemination in 1974 an experiment was conducted on the hill study area to determine how far Bassia and Halogeton seeds moved from parent plants, and to estimate the proportion of the two kinds of seeds entering the different vegetation types from the 1974 seed crop. On August 28, before seeds had begun to fall, 60 metal plates, each 10 x 15 cm in size, were placed on the plot in three rows, 20 plates per row. One row consisted of plates scattered at more or less equal distances along the boundary between Bassia and Halogeton while
the other two rows were parallel to the first but placed 3 m on either side of it, one in Bassia and the other in Halogeton vegetation. Each plate was fixed to the ground with two pieces of stiff wire.

The upper surface of each plate was coated with a thin layer of Tanglefoot (manufactured by Tanglefoot Company), a very sticky substance designed to catch insects. It served equally well to catch seeds in this experiment and in a similar one conducted by Knipe and Springfield (1972) in New Mexico. As the season progressed and seeds began to fall from plants, they appeared on the sticky plates lying beneath the canopy. At intervals of one or two weeks until November 17, plates which had accumulated many seeds were replaced with clean ones, while plates with few seeds remained in the field. Numbers and kinds of seeds on each plate were recorded in the laboratory.

**Seed germination in relation to water potential**

The ability of seeds to germinate under a range of water potentials was considered to be important to establishment of plants in the field and was tested in the laboratory using sodium chloride (ionic) and polyethylene glycol (non-ionic) solutions. All solutions were mixed from a 0.01 molal calcium chloride stock solution as calcium has been found to have a germination enhancing effect (Chaudhuri and Wiebe, 1968) and is ever-present in Curlew Valley soils. Solutions were CaCl$_2$ stock only (0.5 bar), or were mixed and adjusted to 5, 10, 15, and 20 bars with a thermocouple
psychrometer-microvoltmeter apparatus. Each petri dish contained 50 Bassia or Halogeton seeds and 20 ml of the appropriate solution. There were five replicates for each treatment for each species making a total of 90 dishes. They were randomly arranged in a growth chamber and maintained at 20°C in the dark except for two brief periods to check the progress of germination.

The seed was considered germinated when the radicle was more than 3 mm long. Germinated seeds were tallied and removed from dishes at 63 and 97 hours after being placed in the solutions.

Seedling establishment experiment

Another field experiment was designed to investigate the establishment success of the two species in different vegetation types and on the different study areas. A secondary aspect was to see if treating seeds with Captan powder (a fungicide) would affect their establishment success.

In August, 1974, small cardboard boxes (about 20 x 30 x 5 cm high) were placed at random over patches of soil in the different areas. They served to exclose seeds dispersing from the 1974 seed crop, and, later in the year, the covered plots became receptacles for experimental seeds sown onto the soil. A total of 75 boxes were placed in the field, distributed as follows: on the hill and fence sites, 20 each, with 10 in each of the two vegetation types; sage site, 20, with 10 in the open community away from the sage and 10 at the perimeter of sage canopies; bare site, 15 scattered over the plot.
These boxes remained in place until December 20, at which time the boxes were removed and lots of 200 seeds were sown onto marked 1 dm$^2$ quadrats. Each lot contained 100 Bassia and 100 black Halogeton seeds. Every box received one lot of seeds except for those on the hill site, which received two. The additional treatment on this site was seed which had been coated with Captan. Seeds were scattered evenly within the bounds of the 1 dm$^2$ quadrats and a small amount of water (~25 ml) was poured over it, care being taken to prevent seeds from washing out of the quadrat. At the time seeds were sown, the ground was frozen, so the water soon turned to ice, fixing the seeds on the quadrat. Finally, the quadrat was covered with snow, to further diminish the possibility of seed movement. The following spring on May 16, the quadrats were censused for numbers of established plants.

**Drought tolerance experiment**

An aspect of the ecology of Bassia and Halogeton which was considered important to their distribution on the study site was their relative ability to withstand drought. This investigation, patterned after one done by Pemadasa and Lovell (1974a) was done in the greenhouse during September and October, 1975, using plants grown in pots. It involved growing plants for a short time with an adequate water supply, then letting the pots dry out to a predetermined water content, followed by watering and observing the number of plants surviving the drought treatment.

On August 31, thirty-two styrofoam pots 15 cm in diameter and 12 cm tall were weighed and to each was added, in order, without
mixing, the following: 80 g gravel, 1200 g Thiokol silt loam soil (collected where both species grew), 150 g greenhouse potting soil and 12 g vermiculite, all at oven-dry condition. Before the vermiculite was added, enough Bassia or Halogeton seeds were sown to establish 25 plants per pot. All pots were kept saturated for several days by sitting in large, water-containing pans in the greenhouse. The Bassia plants established well but the Halogeton did not, possible due to the warm (28-32°C) temperatures in the greenhouse. Halogeton seeds were sown again but the plants were kept in the growth chamber at cool temperatures (15°C day, 8°C night) for a week.

The sixteen pots were divided into three treatment groups, differing in severity of drought, and a nondroughted control maintained at 15-20 percent soil water content. Since the weight of the soils and pots were known, it was possible to compute the weight of a pot at a given soil water content. The three treatments were dried to increasingly low levels of soil water content, which took from 10 to 20 days after they dropped below the 20 percent level at which the controls were maintained. After the drought was ended, each pot was returned to the control water content for an additional two weeks, harvested, and dry weight of stems determined.

Soils analyses

Soil sampling and profile descriptions

Samples of soil for several quantitative analyses were collected from two locations in both the Bassia and Halogeton vegetation types of the hill plot in September, 1975. Soil was collected from the
surface three centimeters and at 14-15 and 29-30 centimeters for each point. Analyses were done by the Soil, Plant, and Water Analysis Laboratory at Utah State. Four bulk density measurements to a two-inch depth were taken in each vegetation type of the hill plot using a metal ring. A soil profile was described in both vegetation types.

Psychrometric measurements of soil water potential

In early June, 1975, a total of 24 Wescor (Wescor, Inc., Logan, Utah) thermocouple psychrometers were installed at 4 and 12 cm depths on the hill plot to investigate water availability in the two vegetation types. At the 4 cm depth, pairs of psychrometers were installed with one member under the center of a polygonal soil ped and its companion at the base of one of the cracks adjacent to the ped. The distance between a psychrometer and its mate averaged 5 to 7 cm. Eight of these pairs were installed, four in each vegetation type, and readings were taken on them at bihourly intervals from 6 a.m. to 8 p.m., but starting at 2 p.m. on June 20 and ending at noon on June 24. An S-B Systems microvoltmeter was used for taking the readings. Commencement of sampling coincided with the occurrence of a fairly substantial rainstorm (15 mm) followed by several days of warm weather which dried out the soil.

At the 12 cm depth, eight psychrometers were installed, four in each vegetation type, and readings were taken at irregular intervals until August 5.

After completion of sampling all psychrometers were dug up and calibrated using 0.1, 0.5, 1.0, and 1.5 molal sodium chloride
solutions. Graphs of water potential vs. microvolt output were drawn for each psychrometer. Field microvolt readings, corrected to 25°C, were converted to water potential using these calibration curves (Brown, 1970).

Photographic comparisons of soil peds

In the fall of 1974 ten small areas (approximately 50 x 50 cm) which exhibited particularly evident development of polygonal soil ped structure, were marked and photographed to record the positions of the cracks between soil peds. In fall, 1975, these same areas were again photographed to allow comparisons between the two years to see if the positions of cracks or the shape of surface peds had changed. If cracks closed during the winter wet period, and reopened along different lines on drying, many seeds might become buried at the base of the closed cracks (about 4 cm deep) and would be unlikely to emerge on germination. The slides from the two years were projected side by side to allow visual comparison and sketching of the location of cracks.

Competition experiments

Field watering of plants

On the fence site in June, 1974, 22 points were selected and marked along the Bassia-Halogeton ecotone to conduct an experiment on the effect of watering on plant survival and dry weight biomass. In selecting points for the study, an effort was made to find areas which contained approximately equal numbers of Bassia and
Halogeton. On June 26 density counts were made at each point in two different quadrants, again using the 10 x 10 cm frame. After this initial count half of the plots received one inch of "rain", applied using a large can with holes in the bottom and confined to the experimental area by a circular, metal collar 40 cm in diameter, which was pressed 4 cm into the soil to prevent lateral flow of water. This treatment was repeated weekly through the summer to half the plots, while the others received no water. Some adverse effects occurred to watered plants; soil erosion occurred during water application, causing occasional stems, particularly of Bassia, to bend over and become mud-covered. This disturbance may have been detrimental to plant growth.

Density counts were made at approximately biweekly intervals on the fixed sampling quadrats, accompanied, beginning July 23, by harvests of above and below ground portions of plant material from two of the watered quadrats per sample period. Plants from the control quadrats were not harvested, so that density counts on them could be continued; adjoining areas of unwatered vegetation were harvested to serve as biomass controls for the watered plants.

Harvesting was done using a shovel, first loosening the soil around the selected quadrat to a depth of about 30 cm and then carefully loosening the soil within the plot and removing the plants, maximizing the length of root collected. Roots harvested were seldom more than 15-20 cm in length, since by this depth they had become so fine (<1 mm diameter) that they broke easily. In the laboratory plants were carefully washed to remove all dirt, dried in an oven for approximately 72 hours at 42°C and then
weighed to the nearest milligram. At each sample date 30 plants of each species from the watered and unwatered conditions were randomly selected and weighed.

Growth chamber studies

Two separate competition experiments were done with Bassia and Halogeton based on general experimental designs of Harper (1960, 1961) and deWit (1960) using growth chambers and plants grown in pots. Seed for these experiments was obtained from the Curlew Valley Site by collecting whole plants retaining seed in September, 1974. These were stored outdoors in a dry place for several months and were then gently broken up and put through sieves to separate seeds from other plant material.

Preliminary germination trials showed that a high percentage of Bassia seeds germinated but only about 60 percent of Halogeton black seeds would germinate. Consequently, they were given a stratification treatment, successfully used by Cronin (1973), which amounted to placing the seeds in water for a few hours, allowing imbibition, and then freezing them for a period of four weeks or more. Halogeton black seeds were frozen for 2-1/2 months, whereupon several hundred were thawed and germinated in petri dishes containing water, yielding nearly 95 percent germination within 48 hours.

The next procedure was to establish the seedlings successfully on soil from Curlew Valley. This proved to be a serious problem due to the high silt content of the Thiokol silt loam (Balph, 1973)
and the soil surface structure. This fragile, highly aerated surface crust structure is destroyed when the soil is disturbed. When placed in pots and wetted the soil surface becomes so hard that seeds sown on it cannot send their roots downward, while seeds sown slightly below the surface do not emerge in large numbers.

As a result of this problem several different soil surface amendments were tried in order to obtain a greater percentage emergence of sown seeds. These trials were done using enough seeds and pots to get a rough idea of the emergence percentage for the two species. Seeds were usually soaked in water for about 12 hours before sowing to permit imbibition. Soil in the pots was generally water-saturated and maintained that way for several days after seed sowing. Some of the treatments included sowing seed on the soil surface or about 1/2 cm below the surface, making micro-furrows on the surface before sowing seed, pressing each seed slightly down beneath the surface, or covering the Thiokol soil with a thin layer of peat moss or a potting soil mixture.

The arrangement that worked best involved placing a thin layer of a loamy potting soil mixture over the Thiokol soil, sowing the seeds atop this, and covering them with a 5 mm layer of vermiculite. This regimen gave emergence of 70-80 percent for Bassia and 65-75 percent for Halogeton. Unfortunately this technique was not discovered before the first growth chamber study began, but it made satisfactory establishment of plants possible in subsequent studies.
Timing-proportions study. The first growth chamber study was
designed to test several factors which might be important in the
competitive relations between these two species. Plants were grown
in pots, each pot containing 36 individuals, but the treatments
had different proportions of species, as follows: 0:1, 1/3:2/3, 1/2:
1/2, 2/3:1/3, 1:0. The other experimental factor was the time at
which seeds of the two species were sown into the mixed pots;
both seed species were sown either at the same time or one species
was sown eight days earlier or later than the other. Thus there
were three timing treatments for the mixed pots and five stand
proportions, each treatment replicated four times in a completely
randomized factorial design, making a total of 44 pots.

Each pot was 10 x 10 cm and 15 cm tall. To it were added
the following substances, in order: 15 g vermiculite, 733 g
Thiokol soil, collected at a point where both species were growing,
85 g of a potting soil mix. Soils had been oven dried at 110°C
for several days. Halogeton seeds were thawed and each seed for
every pot was gently pressed slightly into the soil surface; dry
Bassia seeds were scattered evenly on the soil surface. All pots
were placed in a large, water-filled pan overnight to allow the
soil to become saturated. Initially, 24 pots were sown with
only one kind of seed, half receiving Halogeton and half Bassia;
eight days later the other species was sown into the appropriate
mixed pot to implement the timing aspect of the study. When these
seeds were sown the pots were also resaturated to make water
available for imbibition. The soil surface was kept damp during
seedling establishment by wetting it with a spray bottle periodically.

All pots were transferred to a Sherer-Gillette growth chamber after the initial overnight soak. The experimental pots were randomly arranged in a rectangular pattern and were enclosed by a buffering perimeter of non-experimental pots so that all experimentalss were surrounded by four other pots. Every few days the pots were removed from the chamber and replaced in a random order so as to minimize any effects due to differences in temperature or light intensity from point to point within the growth chamber.

At the start of the experiment, 16 new, 40 watt, fluorescent tubes were installed in the chamber along with four 75 watt and four 150 watt incandescent light bulbs. Light intensity in the chamber ranged from 766 to 894 μEinsteins·m⁻²·s⁻¹ (between 400 and 700 nm) at the soil surface on June 6, 1975, as measured by a quantum sensor (Biggs et al., 1971). An outdoor reading taken on a cloudless summer day would be about 2000 μEinsteins. Spectroradiometric readings were also taken in the ultraviolet radiation range from 280-400 nm (see Appendix A).

Photoperiod in the growth chamber was initially set to correspond to a mid-April daylength with incandescent lights coming on about 15 minutes earlier and shutting off about 15 minutes later than the fluorescent tubes. Every few days the daylength was changed, in correspondence with the natural seasonal progression. Temperatures were set using daily averages of bihourly temperature records from the Curlew Valley Site for 1974.
Slight adjustments in growth chamber temperature were sometimes made daily but more often were made every three or four days. The growth chamber was designed such that no temperature fluctuations would occur within the period of a temperature setting. Day and night temperatures were constant over their respective time periods, which is a departure from the continuous temperature variation in nature. The growth chamber was unable to maintain night temperatures below 2°C or day temperatures below 13°C, so that during the initial weeks of the experiment temperatures were sometimes 5 to 7°C warmer than in the field.

Seeds were sown into the pots on May 12, 1975, with the late seeds being added on May 20. The pots were allowed to dry out until they dropped below a soil water content of 20 percent by weight, at which time they were restored to 20 percent water content by adding water. For most pots watering began on about June 1, weights being checked every other day and water replenished as needed.

By the end of June, it was decided to increase the amount of water added to each pot to compensate for weight of plant material that had grown in the pot, so that soil water content would not be underestimated. Plants were collected from the field and their stem length and fresh weight determined. This enabled plotting an approximate relation between height and fresh weight. Average heights of plants in pots were measured and the increase in water requirement computed, varying from 4 to 12 grams for the different treatments. On July 24 this compensation was increased, allowing
for continued plant growth, and varied from 5 to 15 grams. This adjustment amounted to 15 to 20 percent of the water added at each time period.

On July 14 the soil water content was decreased from 20 to 17 percent, reflecting the increasing dryness plants experience in the field. Beginning August 5 water additions were made every day, since plants were large enough to rapidly transpire each day's addition, causing occasional wilting of Bassia.

On September 9 all plants were harvested, stems were clipped at ground level, dried in an oven at 45°C for three days and weighed. Roots were washed from the soil by first removing the soil block from the pot, soaking it in water and then loosening the soil away from the root mass. A series of rinses and sieves were used to remove as much soil as possible from the roots. All roots from each pot were placed in a bag, dried and weighed. It was impossible to distinguish Bassia from Halogeton roots based on any microscopic observation; their separation would have been impossible due to the large number of intertwined roots.

Soils-watering levels study. The second growth chamber study was quite similar to the first but different experimental factors were investigated. Two different soils from the hill plot were used, in which either Bassia or Halogeton grew nearly exclusively. Pots were maintained at different soil water contents of 12, 18 or 24 percent by weight. All pots contained 36 plants in either pure or mixed stand, the mixed pots contained 18 of each species. Thus the different treatments were two soil types, three watering
levels and three stand types, each treatment combination replicated four times making a total of 72 pots in a completely randomized factorial design.

Procedural differences from the first experiment were few. A 5 mm layer of vermiculite was used to cover the loam soil after the seeds had been sown. Seeds were sown October 1 and plants were harvested November 26, as differences between treatments were evident at that time. No additional increment of water was added to compensate for the weight of plants in the pots. Roots were not harvested. In all other respects procedures were the same as in the first study.

Seed Budget-Life Cycle Studies

Field germinability of seeds

On December 20, 1974, twenty-four small packets of seeds were buried at 1 and 3 cm depths in the two different vegetation types on the hill plot. Packets were 5 x 5 cm in size and made of finely woven Saran, with a mesh of about 0.6 mm so that seeds could not fall out. Each packet contained 100 seeds of either Bassia or Halogeton and approximately 20 cc of fine textured seed-free soil. In the field the frozen ground was wetted causing it to soften so that it could be dug and the packets buried. In each vegetation type there were three replicates of each of the species at both depths. In the process of burying the seeds, the soil surface structure was destroyed so that none of the germinated seeds were able to emerge; however, the packets were
dug up the following May and the contents examined for seeds which had failed to germinate.

Soil seed reserves

In July of 1974 and 1975 samples of the soil were collected from the sites and were examined for the numbers of seeds of annual plant species present. Germination had been completed for the current season. The sampling device was a metal frame 1 dm\(^2\) by 3 cm high; it was pressed into the soil to the 3 cm depth, and a shovel was used to remove the sampler and some surrounding soil. A metal plate was forced along the bottom edge of the sampler leaving a soil block of 300 cc which was dumped into a bag.

In 1974, 80 samples were collected, 20 from each site. On the hill and fence sites, two transects of 10 samples each were taken across the ecotone, the sample points spaced 1 m apart with the middle of the transect at the boundary between the vegetation types. On the sage site 10 samples were taken in the open, away from the sagebrush, the other 10 taken within the sagebrush-dominated vegetation. The samples from the bare site were randomly scattered.

In 1975, only 35 samples were taken and the bare site was not sampled. On the hill and fence sites, seven samples were randomly collected within each vegetation type, making a total of 28 samples, while the other seven were from the sagebrush-dominated vegetation on the sage site. The sampling was scaled down because of the labor-intensive and time consuming work in processing and analyzing each sample.
In the laboratory, all samples were processed in the same way. First, any large stems or pieces of plant material were removed from the soil, and it was placed on a large (30 x 30 cm) piece of fine mesh organdy cloth, the corners drawn up and tied, enclosing the soil. Next, the bag was placed in a large pan of water and allowed to soak for several minutes. The bag was then gently squeezed and washed, breaking up the soil aggregates and allowing particles smaller than the bag mesh size (clay and silt particles) to settle out. This washing and rinsing continued through several changes of water until soil no longer sifted out. The remains of the sample were finally washed onto a large piece of filter paper in a Buchner funnel, excess water was removed with suction, the filter paper removed from the funnel and the sample placed in a drying oven at 37°C for several days.

Dried samples were placed on a #40 soil sieve and shaken for a few minutes. The fine fraction passing through the sieve was discarded, as it had been determined that the smallest seeds would not pass through, while that retained on the sieve was divided into two equal portions and one of these examined under low magnification with a dissecting microscope. The different species of seeds were easily recognizable (Figure 3), those that were whole and hard were assumed to be viable (Stoller and Wax, 1974), and were removed with a tweezers and counted. The microscopic examination of the samples was very tedious; ultimately several hundred hours were spent on this phase of the study.
Figure 3. Close-up photograph of seeds of the annual species involved in the study. The two seeds in the lower, central portion of the photograph are of Salsola kali. Above from left to right they are: Halogeton glomeratus, with the winged bract; Lepidium perfoliatum, Bassia hypsopifolia, with the hooks; and Descurainia pinnata on the far right.
Plant establishment from seed in summer

Beginning on July 17, 1974, a number of quadrats 50 x 25 cm in size were watered weekly with a watering can to see if there was a remnant of germinable seed left from the spring pullulation which would respond to summer moisture. Each plot received the equivalent of 25 mm of "rainfall" per week. Water was confined to the plots using metal frames 60 x 35 cm which were pressed into the soil and prevented water from running laterally off the plot. Prior to beginning the watering experiment all live vegetation was removed from each plot, so that newly emergent plants could be noticed. They, in turn, were removed each week.

The hill and fence areas each had a total of 30 pairs of plots, 10 pairs in each vegetation type and 10 along the ecotone. The sage area had 14 pairs of plots, seven in the open and seven in the sagebrush-dominated vegetation. The bare area had 12 pairs scattered randomly over the plot.

During the final two weeks of supplemental watering (September 1-14) the amount added was doubled on 35 plots by supplying 25 mm on a semiweekly basis.

Seed exclosures

The watered plots described above were used along with the previously mentioned covered plots (into which seed was sown), to conduct a study on the effect of exclosure of 1974 fall seed production on the density and composition of 1975 vegetation. One half of the watered plots were covered with cardboard boxes
in mid-September, 1971. These boxes were slightly larger than the plot, were pushed down securely into the soil and rocks placed on top of them so they could not be blown away. They stayed in place until January, 1975—long after fall seed dispersal had ceased—when they were removed; by this time the ground was frozen and snow covered so that no movement of seeds would occur.

The different plots served different purposes in this experiment. The watered, covered plots had no seed input from 1974, so that only seed dating from 1973 or earlier could generate plants for the 1975 community, while the watered, uncovered plots received a natural allotment of the 1974 seed crop. The difference between these treatments would provide an estimate of the contribution to the 1975 vegetation from 1974 seed. Similarly, a difference between covered, unwatered and covered, watered plots would be due to the water applied in 1974. Covered and uncovered watered plots were adjacent to each other and observed in pairs, so as to minimize differences from point to point within the four areas.

On May 26, 1975, density counts were taken of the number of individuals established in the various plots. Each of the watered plots was large enough to accommodate three 1 dm$^2$ subsamples within the plot, while the unwatered plots only had enough space for one 1 dm$^2$ sample. The subsample boundaries were marked and censused at approximately biweekly intervals through the 1975 growing season.
Seed production

In order to make precise estimates of the numbers of seeds produced on the different areas, numerous whole plants were harvested in 1974 and 1975 when seeds were maturing on the plants. In mid-September of both years Bassia and Halogeton plants were sampled while Descurainia and Lepidium, not present in 1974, were sampled only in early July of 1975. The permanent stakes on the areas were used as sampling points, from two to four samples being taken at points 1 m from each stake in the cardinal compass directions. Each sample quadrat was 1 dm²; all plants inside the plot were removed and placed in a bag. The number of points sampled was not the same among the different areas, since some were less densely vegetated than others and required more samples to collect a similar number of reproductive plants. In most cases, enough samples were taken on each area to give 20 or more quadrats containing at least one plant.

The harvested plants were taken to the laboratory where measurements were taken on each one to estimate seed production. For Lepidium, which has large, distinct fruits with two seeds per fruit, the numbers of fruits per plant were counted. For Bassia, Descurainia, and Halogeton the lengths of inflorescences (or fruits in the case of Descurainia) were measured to the nearest millimeter and recorded for all branches of each plant.

To relate these measurements to seed production, similar lengths of inflorescence were measured and all the seeds removed from the flowering stem and counted. A number of stalks were so
measured for each species and the data used to generate a regression of inflorescence length to number of seeds. This was used to estimate seed production per plant, and overall for each plot, based on the inflorescence measurements.
results

bassia-halogeton comparative studies

the objective of studies in this section was to elucidate reasons for the occurrence of adjacent pure stands of bassia and halogeton in several areas of the annuals community on the validation site. the majority of the field studies under this topic were conducted on the hill site, with the fence site also being important. since the sage and bare sites did not exhibit the abrupt ecotone between pure stands, their role in this portion of the investigation was comparatively minor.

density at fixed points

in order to affirm the observation that there were adjacent, substantially pure stands of bassia and halogeton on the fence and hill sites, plants in dm² plots were counted at each of the permanent stakes (spaced in a 5 x 5 m grid) on june 25, 1974. table 1 displays results of these counts as well as repeated counts taken on may 25, 1975; each total represents five or six quadrats for the hill or fence sites, respectively. the totals, except for the fence plot in 1975, indicate abrupt discontinuities in distribution of bassia and halogeton plants and generally a strong negative association between the two species. the very low densities of plants on the fence site in 1975 will be discussed later (see page 124).
Table 1. Totals of Bassia and Halogeton plants established in rows of 1 dm² quadrats, and mean number of plants per quadrat, on June 25, 1974, and May 25, 1975. Totals represent five or six quadrats for hill or fence sites, respectively. Rows, and quadrats within a row were spaced five meters distant.

<table>
<thead>
<tr>
<th></th>
<th>Hill Site</th>
<th>Fence Site</th>
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<tbody>
<tr>
<td></td>
<td>June 25, 1974</td>
<td>May 25, 1975</td>
</tr>
<tr>
<td>West row</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>54</td>
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<tr>
<td></td>
<td>6</td>
<td>77</td>
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<td></td>
<td>0</td>
<td>55</td>
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<tr>
<td></td>
<td>11</td>
<td>123</td>
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<tr>
<td></td>
<td>75</td>
<td>0</td>
</tr>
<tr>
<td>East row</td>
<td>88</td>
<td>0</td>
</tr>
<tr>
<td>Mean number per quadrat ± one standard deviation</td>
<td>7.2 ±12.3</td>
<td>10.6 ±14.6</td>
</tr>
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</table>
Results of similar density counts taken on the sage and bare areas are presented in Table 2. The area of the sage plot in which sagebrush was present is indicated by brackets around the two appropriate rows. The sagebrush undoubtedly influences growth of annual plants, enhancing soil surface physical properties with litter deposition, but also making competition for soil water more keen. On the first sample date in both years mean densities of plants in the sagebrush vegetation were lower than in the surrounding open areas (1974, 1.8 vs 7.2 per dm$^2$; 1975, 6.8 vs 9.8 per dm$^2$) although a two-cell chi-square test showed no significant difference. By the end of the growing season differences in density had diminished between sage and open areas. Observations from the seedling establishment experiment (see page 73) showed that plants grown among sagebrush were markedly smaller— one tenth to one hundredth the size— of plants grown in the open.

The impetus for selecting the bare site as an area to be studied was an impression that it was less densely vegetated than the other areas. The data do not demonstrate this but they do indicate Bassia and Halogetion grew together freely here. This site was the least useful in terms of achieving the experimental objectives, and is mentioned here mainly to indicate mean plant densities relative to the other sites.

The average number of plants per quadrat indicate that drastic differences in density occur from one year to the next as well as from one site to another within a year (Tables 1 and 2). Range managers generally seek conversion of annual ranges into reliably productive perennial grasses due to this
Table 2. Totals of Bassia, Halogeton and Lepidium perfoliatum plants established in rows of 1 dm² quadrats and mean number of plants per quadrat on June 25, 1974, and May 25, 1975. Totals represent five or six quadrats for sage or bare sites, respectively. Rows and quadrats within a row were spaced five meters distant.

<table>
<thead>
<tr>
<th></th>
<th>Sage Site</th>
<th></th>
<th>Bare Site</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Bassia</td>
<td>4</td>
<td>0</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Halogeton</td>
<td>18</td>
<td>18</td>
<td>84</td>
<td>62</td>
</tr>
<tr>
<td>Bassia</td>
<td>0</td>
<td>18</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>Halogeton</td>
<td>21</td>
<td>21</td>
<td>44</td>
<td>4</td>
</tr>
<tr>
<td>Bassia</td>
<td>0</td>
<td>20</td>
<td>44</td>
<td>62</td>
</tr>
<tr>
<td>Halogeton</td>
<td>21</td>
<td>0</td>
<td>21</td>
<td>60</td>
</tr>
<tr>
<td>Bassia</td>
<td>[7]</td>
<td>[0]</td>
<td>[0]</td>
<td>[0]</td>
</tr>
<tr>
<td>Halogeton</td>
<td>[2]</td>
<td>[0]</td>
<td>[148 L 5]</td>
<td>[10]</td>
</tr>
<tr>
<td>Bassia</td>
<td>[7]</td>
<td>[0]</td>
<td>[48 L 5]</td>
<td>[38]</td>
</tr>
<tr>
<td>Halogeton</td>
<td>[2]</td>
<td>[0]</td>
<td>[51]</td>
<td>[51]</td>
</tr>
<tr>
<td>Bassia</td>
<td>[0]</td>
<td>[9]</td>
<td>[70]</td>
<td>[70]</td>
</tr>
<tr>
<td>Halogeton</td>
<td>[9]</td>
<td>[0]</td>
<td>[11]</td>
<td>[11]</td>
</tr>
<tr>
<td>East row</td>
<td>[9]</td>
<td>[72]</td>
<td>[52]</td>
<td>[3]</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>9</td>
<td>20</td>
<td>107</td>
</tr>
</tbody>
</table>

Mean number per quadrat ± one standard deviation

<table>
<thead>
<tr>
<th></th>
<th>Sage Site</th>
<th></th>
<th>Bare Site</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Bassia</td>
<td>0.7</td>
<td>0</td>
<td>4.9</td>
<td>5.1</td>
</tr>
<tr>
<td>Halogeton</td>
<td>4.7</td>
<td>8.1</td>
<td>6.0</td>
<td>8.1</td>
</tr>
<tr>
<td>Bassia</td>
<td>2.0</td>
<td>±2.0</td>
<td>9.1</td>
<td>±9.3</td>
</tr>
<tr>
<td>Halogeton</td>
<td>6.8</td>
<td>±19.8</td>
<td>8.9</td>
<td>±20.2</td>
</tr>
</tbody>
</table>

a L indicates Lepidium perfoliatum.
tremendous year to year variation in annual plant production (Evans, Young and Eckert, 1969). Causative factors generating this instability will be discussed later (see page 154).

**Seeds in soil**

The transect soil seed samples taken across the ecotone on the hill and fence sites in 1974 served not only to estimate the numbers of seeds in soil but also to verify whether or not the abrupt discontinuity in plant distributions extended to distributions of seeds in soil. An accumulation of one species of seed disproportionate to its appearance in the vegetation would indicate a disability of that species to germinate at that point. The data presented in Figure 4 indicate, for the summer of 1974, that seed distributions tend to reflect the vegetation distribution, in that the percent of Bassia seeds in a sample is very much higher in the Bassia vegetation; it drops abruptly across the ecotone and is quite low in the Halogeton vegetation. The samples contained few seeds other than Bassia or Halogeton, so percent Bassia plus percent Halogeton equals 100 in nearly all cases.

**Seed dispersal**

Another possible explanation for the persistence of adjacent pure stands of vegetation on the hill site (Table 1) could be lack of seed dispersal by the absent species. Halogeton and Bassia seeds are quite small (1-2 mm) and light, most likely relying on wind dispersal. An attached, five-winged bract enhances dispersibility of Halogeton black seeds, but the brown seeds are
Figure 4. Percent Bassia seeds found in 50 percent of a 300 cc soil sample, to a 3 cm depth, along transects on the hill and fence sites in July. Samples were spaced 1 m apart and two transects were run on each site. Each point thus represents the mean of two samples. Percent Halogeton seeds equals 100 minus percent Bassia seeds.
enclosed by an appressed bract, making the seed less susceptible
to wind movement. Bassia fruits have five short hooks which
radiate from the central portion of the fruit, allowing them to
be carried long distances in fur of animals or on the trouser
legs of scientific investigators (Figure 3).

Figure 5 and Table 3 summarize results from the experiment
done on the hill site through the fall of 1974 using metal plates
coated with a sticky substance which "trapped" seeds contacting
it. A two tailed T-test on each of the data sets from the three
sampling positions within the hill site showed the numbers of
Bassia and Halogeton seeds caught to be not significantly different
(P>0.05) along the ecotone. However, at positions 3 m east and
west of the ecotone row, differences were highly significant
(P<0.00025 and P<0.0001, respectively). This seems striking
considering the ecotone ranged in width from about 1.5-2.5 m and plants
of the less abundant species were frequently within two meters
of either the east or west row of plates. However, the literature
contains many examples of extremely limited seed dispersal from
parent plants (Friedman and Orshan, 1975; Werner, 1975a).

Table 3. Proportion of Bassia, Halogeton and other seeds "trapped"
on 10 x 15 cm metal plates on the hill site; along the
ecotone between Bassia and Halogeton vegetation and 3 m
on either side of this ecotone row. There were 20 plates
in each row.

<table>
<thead>
<tr>
<th>Seeds</th>
<th>East Row</th>
<th>Ecotone</th>
<th>West Row</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bassia</td>
<td>.915</td>
<td>.255</td>
<td>.033</td>
</tr>
<tr>
<td>Halogeton</td>
<td>.041</td>
<td>.737</td>
<td>.967</td>
</tr>
<tr>
<td>Other species</td>
<td>.044</td>
<td>.008</td>
<td>0</td>
</tr>
</tbody>
</table>

|    | t=4.05 | t=1.78 n.s. | t=5.96 |


The seemingly short dispersal distances can partly be attributed to the presence of a polygonal soil surface structure with cracks up to several centimeters deep separating the peds. Seeds blown along the surface will usually fall into a crack after moving only 20-30 cm, preventing further movement. A high percentage of plants which successfully establish in spring are found emerging from these cracks (Figure 6). The explanation for this seedling distribution may simply be that most of the seeds end up in the cracks; or the cracks may provide a more favorable germination-establishment microenvironment (see page 91 for further discussion).

Seed germination

One possible reason for persistence of the adjacent pure stands of vegetation, allowing for some dispersal into the bordering stand, might be differences in germinability of the two seed species. Heterogeneity in soil surface microenvironmental conditions might favor germination of one species or the other from point to point within the annuals community. One species could be screened from an area by an inability to germinate there. Both a lab and field investigation were done to study germination behavior under different conditions.

Under simulated moisture stress

In the laboratory preliminary tests in petri dishes showed that Bassia seeds germinated freely (90-95 percent) in tap water, as did Halogeton black seeds after a 6 week cold-moist treatment (Cronin, 1973). This experiment investigated germinability through time at different levels of water potential and in sodium chloride (ionic) and
Figure 6. Close-up photograph of soil surface showing pattern of emergence of Halogeton seedlings. Most plants emerge from the cracks between polygonal soil surface peds.
polyethylene glycol (chemically inert) solutions. Figures 7 and 8 and Table 4 summarize results and present statistical analysis for this experiment. From the graphs it is evident that germination takes longer in the low water potential solutions (-15, -20 bars); that sodium chloride permits a higher germination percent than polyethylene glycol, and that the general trend in germinability for both species is about the same.

The factorial analysis of variance, Table 4, supports the latter point, indicating no significant difference in germinability of the two species. Differences in all of the other main effects were highly significant, however, as were several of the interaction terms. Significant differences due to time (53 vs 97 hours) and osmotic pressure (-5 to -20 bars) were to be expected, given the slower imbibition rate at lower water potential, but the difference due to the two chemicals is more interesting.

Several authors (Parmar and Moore, 1966; Wood, Knight and Young, 1976; Young et al., 1968) have germinated seeds in polyethylene glycol and/or sodium chloride solutions. Due to its chemical inertness polyethylene glycol usually gives higher germination percentages than does the sometimes toxic sodium chloride. Contrastingly, these halophytic species germinated significantly better in salt solutions. This salt enhancement of germination may have some physiological basis in seed germination processes.

Several significant interaction terms support and clarify the main effect differences. There are differences in species response to osmotic pressure, time, and chemical effects as three of the interaction
Figure 7. Percent germination after 63 hours of Bassia (0) and Halogeton (X) seeds in sodium chloride (---, ionic) and polyethylene glycol (---, nonionic) solutions of different water potential. n = 5 for each treatment with 50 seeds per dish. Solutions at -0.5 bars contained neither sodium chloride nor polyethylene glycol.
Figure 8. Percent germination after 97 hours of Bassia (0) and Halogeton (X) seeds in sodium chloride (---, ionic) and polyethylene glycol (---, nonionic) solutions of different water potential. $n = 5$ for each treatment with 50 seeds per dish. Solutions at -0.5 bars contained neither sodium chloride nor polyethylene glycol.
Table 4. Analysis of variance for seed germination percentages of Bassia and Halogeton in relation to water potential of solutions of sodium chloride or polyethylene glycol through time; at 63 and 97 hours after immersion in the various solutions. \( n = 3 \) for all treatment combinations.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Mean squares</th>
<th>F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time (T)</td>
<td>1</td>
<td>2873.03</td>
<td>26.69**</td>
</tr>
<tr>
<td>Species (S)</td>
<td>1</td>
<td>265.23</td>
<td>2.47 n.s.</td>
</tr>
<tr>
<td>Chemical (C)</td>
<td>1</td>
<td>3010.23</td>
<td>27.96**</td>
</tr>
<tr>
<td>Osmotic Pressure (OP)</td>
<td>3</td>
<td>46739.09</td>
<td>434.18**</td>
</tr>
<tr>
<td>T x S</td>
<td>1</td>
<td>30.63</td>
<td>0.28 n.s.</td>
</tr>
<tr>
<td>T x C</td>
<td>1</td>
<td>7.23</td>
<td>0.07 n.s.</td>
</tr>
<tr>
<td>T x OP</td>
<td>3</td>
<td>1324.49</td>
<td>12.30**</td>
</tr>
<tr>
<td>S x C</td>
<td>1</td>
<td>235.23</td>
<td>2.19 n.s.</td>
</tr>
<tr>
<td>S x OP</td>
<td>3</td>
<td>1693.36</td>
<td>15.73**</td>
</tr>
<tr>
<td>C x OP</td>
<td>3</td>
<td>1688.49</td>
<td>15.69**</td>
</tr>
<tr>
<td>S x C x OP</td>
<td>3</td>
<td>1122.83</td>
<td>10.43**</td>
</tr>
<tr>
<td>T x C x OP</td>
<td>3</td>
<td>126.69</td>
<td>1.18 n.s.</td>
</tr>
<tr>
<td>T x S x C</td>
<td>1</td>
<td>50.63</td>
<td>0.47 n.s.</td>
</tr>
<tr>
<td>T x S x OP</td>
<td>3</td>
<td>339.96</td>
<td>3.16*</td>
</tr>
<tr>
<td>S x C x T x OP</td>
<td>3</td>
<td>178.09</td>
<td>1.65 n.s.</td>
</tr>
<tr>
<td>Error</td>
<td>128</td>
<td>107.65</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>159</td>
<td>1131.39</td>
<td></td>
</tr>
</tbody>
</table>

n.s. = not significantly different (P>0.05).
* = significant at the 97.5% confidence level.
** = significant at the 99.9% confidence level.
terms incorporating species were significant. Several other interactions involving species were not significant. The other notable significant interaction is chemical x osmotic pressure, indicating that germination response was not the same in the two chemical solutions at different levels of osmotic pressure.

In the field

Corroboration of the above lab experiment on seed germination is provided by results of a field experiment in which Saran mesh packets were buried at one and three centimeter depths. The data in Table 5 evidence a very low and fairly uniform percentage recovery of hard seeds. Mesh size of the packets was too small for seeds to fall out. Considerable care was taken to locate all hard seeds within each seed packet. During this process of microscopic examination numerous seed coats were found, indicating germination had occurred; thus it can be inferred that the few remaining hard seeds were the only ones which had failed to germinate.

The only "trend" in the data, if it can be called that, is that a few more Bassia seeds were recovered from the Halogeton vegetation type. The differences between Bassia and Halogeton are not statistically significant.

Taken together these experiments on seed germination under lab and field conditions provide substantial evidence that there are no important differences in germinability of the two species under the test conditions. Persistence of adjacent pure stands of Bassia and Halogeton cannot be attributed to an inability of one species to germinate in the other vegetation type.
Table 5. Mean number of hard seeds (± one standard deviation) recovered from Saran mesh packets buried in the soil at 1 and 3 cm depths in December, 1974, and recovered in May, 1975. n = 3 for each treatment combination; each packet contained 100 seeds when buried so number recovered equals percent recovered.

<table>
<thead>
<tr>
<th>Vegetation Type</th>
<th>Bassia Seed species</th>
<th>Halogeton Seed species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bassia</td>
<td>Halogeton</td>
<td></td>
</tr>
<tr>
<td>Depth</td>
<td>Seed species</td>
<td>Seed species</td>
</tr>
<tr>
<td></td>
<td>Bassia Halogoton</td>
<td>Bassia Halogoton</td>
</tr>
<tr>
<td>1 centimeter</td>
<td>2.3±2.1 2.7±2.1</td>
<td>4.3±3.5 .7±1.2</td>
</tr>
<tr>
<td>3 centimeters</td>
<td>2.7±1.5 3.0±1.0</td>
<td>7.7±9.9 0</td>
</tr>
</tbody>
</table>

Seedling establishment success

Natural populations of plants growing from seed are most likely to suffer mortality during the establishment phase of the life cycle (Harper, 1967). At this stage the plant must begin photosynthesis as seed energy reserves are nearly exhausted; its root has not yet penetrated deeply enough to insure a reliable water supply, and anatomically it has not hardened sufficiently to be extremely resistant to physical stresses. The microenvironment about the seedling is extremely important in determining whether establishment will occur.

With the above ideas in mind, results of the experiment on seedling establishment are quite informative. On December 20, 1974, seeds were sown onto the soil surface of marked quadrats which had
been covered during the fall seed dispersal period. On May 16, 1975, these quadrats were censused for establishment.

Figure 9 summarizes these data for the four study sites and Table 6 presents $\chi^2$ values for these data. Germination studies in the lab and field, as just related, indicated a uniformly high germinability (92-97 percent) for both species under test conditions. Assuming this occurred the null hypothesis tested here was that establishment success was equal for both species. Only in the Halogeton vegetation type of the fence site was there no significant difference between total numbers of Bassia and Halogeton plants established. This site also had the lowest establishment percent, indicating it was most "severe." In all other study areas either Bassia or Halogeton established significantly better than the other species. In general, establishment success of Halogeton was better than that of Bassia; only on two areas (Bassia vegetation on hill and fence sites) did Bassia establish significantly better than Halogeton.

On the hill site, each vegetation type received an additional group of seeds which had been treated with the fungicide Captan. Greater establishment of Captan treated seeds would have been an indication that fungal decay decremented numbers of viable, untreated seeds. This was not the case though, and after performing a $\chi^2$ test for independence on captan treated vs. non-captan treated seeds, which indicated homogeneous data, the data were combined for other statistical tests.
* means not significantly different, all other Vegetation Type means different at 99.5% confidence level.
Table 6. \( \chi^2 \) values testing establishment and summer survival success for sown Bassia and Halogeton seeds in dm\(^2\) quadrats in different vegetation types at the beginning and end of the growing season in 1975. n = 10 for sage and fence sites, 15 for bare site, and 20 for hill site. Degrees of freedom equals one in all cases.

<table>
<thead>
<tr>
<th>Site</th>
<th>Vegetation Type</th>
<th>May 16 ( \chi^2 )</th>
<th>Interaction ( \chi^2 )</th>
<th>August 31 ( \chi^2 )</th>
<th>Interaction ( \chi^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hill (Captan data pooled)</td>
<td>Bassia</td>
<td>58.1**</td>
<td></td>
<td>115.0**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Halogeton</td>
<td>188.9**</td>
<td></td>
<td>97.7**</td>
<td></td>
</tr>
<tr>
<td>Fence</td>
<td>Bassia</td>
<td>18.8**</td>
<td>6.4*</td>
<td>14.2**</td>
<td>9.2**</td>
</tr>
<tr>
<td></td>
<td>Halogeton</td>
<td>1.1 n.s.</td>
<td></td>
<td>2.3 n.s.</td>
<td></td>
</tr>
<tr>
<td>Sage</td>
<td>Open (Halogeton)</td>
<td>81.6**</td>
<td></td>
<td>34.0**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sage</td>
<td>110.6**</td>
<td></td>
<td>35.0**</td>
<td></td>
</tr>
<tr>
<td>Bare</td>
<td>Mixed</td>
<td>175.6**</td>
<td></td>
<td>82.1**</td>
<td></td>
</tr>
</tbody>
</table>

n.s. = not significantly different (P>0.05).
** = significant at 99.5% confidence level.
* = significant at 97.5% confidence level.
Three more $\chi^2$ tests, for independence or interaction, were done using all the data from the hill, fence, and sage sites to test if establishment behavior of the two species was the same in both vegetation types of each site. For both hill and fence sites the test was significant, indicating that the species established with different degrees of success in the two vegetation types. For the sage site, the test showed no interaction; that is, both species established to the same extent near the sagebrush canopies and in open areas away from sagebrush.

The same $\chi^2$ tests using data from August 31, 1975, of repeated observations of these plots generally had lower values (Table 6). This indicates that differences within the quadrats, in terms of numbers of plants growing there, had diminished through the summer. In nearly all cases these lessened differences were due to a greater mortality of the more abundantly established species in the various vegetation types (Table 7). This is not unexpected as an individual of the dominant species will experience a greater degree of intraspecific competition, having more neighbors of the same species which require essentially the same resources. Contrastingly, the subordinate species survives better, presumably due to less competitive stress, assuming its resource requirements are somewhat different from the dominant species.

Most interesting, though, are the relative amounts of establishment and survival success by the two species shown in Table 7.
Table 7. Total plants established in dm$^2$ quadrats on May 16, 1975 from seed sown in December, 1975; numbers of plants surviving to August 30, 1975; numbers dying and percent dying through the summer. Each quadrat was sown with 100 seeds of each species. n = 10 for all vegetation types except bare, in which n = 15 quadrats.

<table>
<thead>
<tr>
<th>Site</th>
<th>Vegetation Type</th>
<th>Total Plants Present</th>
<th>Number Dying Through Summer</th>
<th>Percent Dying Through Summer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>May 16</td>
<td>August 31</td>
<td>Bassia</td>
</tr>
<tr>
<td>Hill</td>
<td>Bassia</td>
<td>215</td>
<td>125</td>
<td>97</td>
</tr>
<tr>
<td></td>
<td>Bassia (captan)</td>
<td>222</td>
<td>113</td>
<td>91</td>
</tr>
<tr>
<td></td>
<td>Halogeton</td>
<td>12</td>
<td>159</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>Halogeton (captan)</td>
<td>14</td>
<td>100</td>
<td>10</td>
</tr>
<tr>
<td>Fence</td>
<td>Bassia</td>
<td>63</td>
<td>22</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>Halogeton</td>
<td>4</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>Sage</td>
<td>Open (Halogeton)</td>
<td>6</td>
<td>100</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Sage</td>
<td>4</td>
<td>124</td>
<td>2</td>
</tr>
<tr>
<td>Bare</td>
<td>Mixed</td>
<td>36</td>
<td>268</td>
<td>20</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>576*</td>
<td>1019*</td>
<td>274*</td>
</tr>
</tbody>
</table>

*Significant at 99.9% confidence level.
Overall percent mortality for the two species is similar, 52 percent for Bassia versus 56 percent for Halogeton, but the absolute numbers involved are quite different. Only 576 Bassia plants became established but 1019 Halogeton plants did; a two-cell $\chi^2$ test shows these numbers to be significantly different at the 99.9 percent confidence level. The year-end values of 274 Bassia versus 446 Halogeton surviving are also significantly different at the 99.9 percent confidence level. Thus, although equal numbers of seeds of both species were sown into various sites in the field, about 1.8 times more Halogeton plants established and survived to maturity than did Bassia plants.

The mean number of plants established per square decimeter quadrat is also equal to percent establishment as there were 100 seeds of each species in each quadrat (Figure 9). The low establishment, averaging 8 percent over all quadrats and ranging from 0.4 to 22 percent, indicates that a very large portion of seeds in soil never become established as plants. Many of these seedlings emerge from soil only to die within a short time thereafter. On May 16, when first counts of plant establishment were made, nearly all of the quadrats contained evidences of from two to five times as many dead seedlings as live plants. Cronin (1965) documents this high establishment mortality for Halogeton.

Drought tolerance

During the establishment phase and throughout the growth cycle the ability to tolerate drought is particularly important
for survival of plants in arid areas. Distributions of many species are limited by insufficient amounts of water at some critical phase of the growth cycle. Halogeton's succulent habit was a clue to a possible ability to withstand moisture stress.

Table 8 summarizes the results of the comparative study on drought tolerance between Bassia and Halogeton. The data verify Halogeton's presumed drought tolerance, in that its survival percentage was always greater for treatments in which it withstood more days of drought and in which the minimum soil water percent content was lower than for the comparable Bassia treatment.

The data on plant dry weights are more difficult to interpret and are confounded by density effects, as after the water stress period pots had different numbers of survivors. All plants grew about the same length of time from seed (six to seven weeks) and each of the drought treatments received water at the "control" rate for two weeks after the end of its drought. Since dry weights of Bassia and Halogeton "control" plants were not greatly different, one might assume that dry weight of comparably droughted plants should also be similar. This was not the case as dry weights of droughted Halogeton plants were significantly less than those for Bassia.

These differences may simply have been due to the fact that the pots containing Halogeton were more crowded, since fewer had died during the drought period, and therefore each plant grew less. Another explanation might be that the Bassia
Table 8. Duration of drought treatments, minimum water contents (gravimetric), survival percentages and mean plant dry weights at harvest (2 weeks after termination of drought and 6 to 7 weeks after seed sowing) for Bassia and Halogeton grown in pots in the greenhouse during September and October, 1975. n = 4 for all treatments and each pot initially contained 25 plants. Means followed by the same letter are not significantly different at the 95 percent confidence level using Duncan's multiple range test.

<table>
<thead>
<tr>
<th>Duration of drought (days)</th>
<th>Mean minimum soil water percent content (± one standard deviation)</th>
<th>Mean survival percent (± one standard deviation)</th>
<th>Mean dry weight per plant at harvest (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bassia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>15</td>
<td>100</td>
<td>143\textsuperscript{a}</td>
</tr>
<tr>
<td>10</td>
<td>2.9\pm.2</td>
<td>81\pm11.9</td>
<td>116\textsuperscript{a}</td>
</tr>
<tr>
<td>12</td>
<td>2.5\pm.2</td>
<td>72\pm22.4</td>
<td>128\textsuperscript{a}</td>
</tr>
<tr>
<td>14</td>
<td>1.9\pm.3</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Halogeton</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>15</td>
<td>100</td>
<td>125\textsuperscript{a}</td>
</tr>
<tr>
<td>16</td>
<td>2.6\pm.1</td>
<td>97\pm3.8</td>
<td>56\textsuperscript{b}</td>
</tr>
<tr>
<td>18</td>
<td>2.1\pm.2</td>
<td>95\pm3.8</td>
<td>61\textsuperscript{b}</td>
</tr>
<tr>
<td>20</td>
<td>1.7\pm.1</td>
<td>87\pm13.0</td>
<td>41\textsuperscript{b}</td>
</tr>
</tbody>
</table>
plants, despite their susceptibility to mortality, were more resilient and resumed normal growth rates more rapidly than did Halogeton, enabling them to accumulate greater biomass. A third explanation could be that the longer and drier drought treatments Halogeton withstood caused its rate of recovery to be slower, perhaps due to greater physiological dysfunction. A combination of the above hypotheses may explain most of Halogeton's relatively poor recovery from drought.

Soils analyses

Several types of analyses were performed on soils, mainly from the hill site, to compare parameters in the Bassia and Halogeton vegetation types which might correlate with the above differences in seedling establishment success and drought tolerance. An additional aspect was an investigation of the role of cracks between soil surface polygonal peds in relation to seedling germination and seed burial.

Profile descriptions and analytical data

Appendix B contains descriptions of soil profiles in the Bassia and Halogeton vegetation types on the hill site. Generally the two profiles are similar and display little development of distinct horizons. Noticeable dissimilarities are most pronounced at the soil surface where seedling establishment occurs. The Bassia surface is covered with a thin litter layer which is largely absent under Halogeton vegetation.
The surface horizon under Halogeton contained numerous gas-filled vesicles to a depth of 3-6 cm which were not present under Bassia vegetation. Blackburn and Skau (1974) discuss several characteristics of surficial vesicular horizons which adversely affect plant establishment and which will be considered later. A moderate fine platy structure accompanied the vesicular horizon and is likely more of an impediment to root penetration than the subangular blocky-fine granular structure present under Bassia. These comments also apply to the soil surface on the fence site as observations there showed definite similarities to the hill site.

The whole profile for Bassia soil is generally darker than the Halogeton profile, perhaps due to a higher percent organic carbon under Bassia and high exchangeable sodium percent under Halogeton. Both profiles are calcareous throughout, its abundance increasing with depth.

**Analytical data.** Samples of soil were collected from three depths for two different profiles in the two vegetation types of the hill site for analysis regarding several pertinent parameters. Table 9 present results of these analyses, wherein the mean is listed for the two profiles in each vegetation type; values from the two profiles were very close so the means have very low variances.

There are several striking differences in these data considering the profiles are no more than 10 to 12 meters distant. The high exchangeable sodium percent and bulk density and low percent organic carbon for the Halogeton surface soil collectively
Table 9. Results of tests on various soil physical and chemical parameters. Each datum is the mean value from two different profiles in each vegetation type, except for bulk density, in which four samples were taken.

<table>
<thead>
<tr>
<th>Soil type and depth</th>
<th>Bulk density</th>
<th>Percent organic carbon</th>
<th>Exchangeable sodium percent</th>
<th>mmhos/cm $E_{C_e}$</th>
<th>Base saturation percent</th>
<th>CEC</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bassia Soil</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-3 cm (0-5 cm)</td>
<td>0.89±.13*</td>
<td>3.4</td>
<td>1</td>
<td>1.1</td>
<td>60</td>
<td>16.4</td>
<td>7.7</td>
</tr>
<tr>
<td>14-15 cm</td>
<td>1.7</td>
<td>2</td>
<td>0.6</td>
<td>53</td>
<td></td>
<td>17.5</td>
<td>7.8</td>
</tr>
<tr>
<td>29-30 cm</td>
<td>1.4</td>
<td>2</td>
<td>0.6</td>
<td>64</td>
<td></td>
<td>14.3</td>
<td>7.7</td>
</tr>
<tr>
<td>Halogeton Soil</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-3 cm (0-5 cm)</td>
<td>1.16±.11*</td>
<td>1.5</td>
<td>16.5</td>
<td>1.7</td>
<td>44</td>
<td>10.9</td>
<td>8.5</td>
</tr>
<tr>
<td>14-15 cm</td>
<td>0.8</td>
<td>13.5</td>
<td>0.9</td>
<td>38</td>
<td></td>
<td>10.9</td>
<td>8.7</td>
</tr>
<tr>
<td>29-30 cm</td>
<td>0.7</td>
<td>55</td>
<td>14.3</td>
<td>41</td>
<td></td>
<td>11.3</td>
<td>7.8</td>
</tr>
</tbody>
</table>

* Means significantly different at the 99 percent confidence level.
provide evidence for an unfavorable seedling establishment micro-environment. Soils with more than fifteen percent exchangeable sodium are classified as sodic (Hausenbuiller, 1972) and create considerable problems for growth of most plants. The principal effect here is unfavorable surface physical properties created by dispersion of clay and deflocculation of soil colloidal particles. This creates a dense, impenetrable surface crust which is less permeable to air and water and greatly hinders emergence of seedlings.

Although bulk density was significantly greater at the Halogeton soil surface, the measurement probably does not reflect the difference present at the microsite level, since bulk density was averaged over the upper five centimeters of soil. It is generally accepted that Halogeton acts as a "sodium pump" by accumulating high concentrations of sodium in its tissues which are leached to the surface soil upon decomposition of litter (Kinsinger and Eckert, 1961). Thus an exchangeable sodium percentage and concomitant bulk density for the topmost centimeter or half-centimeter of Halogeton soil might produce considerably greater values than those shown in Table 9. These data would more closely represent the microenvironment at a scale relevant to seedling emergence and establishment, and would contrast even more sharply with the data from the Bassia soil. By comparison, the Bassia soil surface parameters of exchangeable sodium percent, bulk density and percent organic carbon characterize a favorable site for seedling establishment.
Dissimilarities are evident in the other parameters but their magnitude is such as to make them unimportant, regarding seedling establishment, relative to the parameters just discussed.

To the 30 cm depth it is evident that the soil profiles have a different chemistry throughout. All measured parameters indicate the Bassia profile should be more favorable to plant growth, with its lower pH and electrical conductivity and higher cation exchange capacity and base saturation percent. By comparison, the Halogeton profile is sodic throughout with ionic salts becoming a definite problem at the 30 cm depth. Nutrient availability here will be lower due to the lower organic carbon percent, base saturation percent and cation exchange capacity.

Field water potential

To see if the previously described differences in drought tolerance of the species might relate to their distribution in the field, a series of measurements of soil water potential was taken in the pure vegetation types of the hill site. Psychrometers buried at a 12 cm depth showed sharply contrasting patterns of soil water potential during the summer of 1975. Figure 10 summarizes the field data and plainly shows the much drier condition of the Halogeton soil from the end of June onward. During the middle part of June (20-26) water potential under Halogeton is rapidly decreasing, but is not as low as in the Bassia vegetation.

These data were separated into two groups, with June 26 being the dividing point, and statistically tested using analysis of
Figure 10. Seasonal trend of soil water potential at 12 cm depth on the hill site in Bassia (o) and Halogeton (x) vegetation. n for each sample point varies from 2 to 4.
covariance techniques, with Julian date being the covariate. This improved the resolution of the analysis by removing variation common to both sites due to the summer-long trend of soil water depletion. The analyses showed at the 99.9 percent confidence level, that the Halogeton soil was significantly wetter than the Bassia soil prior to June 26, but significantly drier after this date.

Recalling the results of the drought tolerance experiment, it would seem that the less drought resistant Bassia would have a more difficult time growing in the drier Halogeton soil. Seed production also might be diminished here since seed is not produced until the end of summer, the driest part of the year.

A fairly reasonable explanation can be advanced for the wetter Halogeton soil in mid-June. There are two factors of importance here: the first is the higher elevation (30-60 cm) of the Halogeton site; the second is the presence on the Bassia site of a luxuriant stand of the early-maturing Descurainia. Relatively abundant soil water early in the growing season would allow capillary movement to the higher Halogeton site, maintaining it relatively wetter. In addition, the rapidly growing Descurainia were likely transpiring significant amounts of water from the Bassia site in order to complete their life cycle in early July.

Soil temperature

Concomitant with the water potential differences in the two sites were soil temperature differences as shown in Figure 11. The
Figure 11. Seasonal trend of soil temperature at 12 cm depth on the hill site in Bassia (O) and Halogeton (X) vegetation. n for each sample point varies from 2 to 4.
graph shows readings taken around midday, for the sake of clarity. But it was evident that Bassia soils were almost always 1 to 2°C cooler than the Halogeton soils, regardless of the time of day the readings were taken. An analysis of covariance similar to the one just described, with Julian dates as the covariate, showed soil temperatures to be significantly different at the 97.5 percent confidence level. The overall adjusted means were 20.2 and 19.0°C for the Halogeton and Bassia soils, respectively. This slight, but significant, difference is another indication of the more advantageous Bassia soil environment in relation to plant growth.

Comparison of crack and ped germination sites

Figure 6 shows a distinctive pattern of seedling establishment, the preponderance of plants emerging from the cracks between soil peds; this investigation attempted to measure differences in soil temperature and water potential between the crack and ped germination sites. The hypothesis here was that cracks served as concentration zones for water from snow melt and, as such, would provide cooler, wetter germination sites with more friable consistence than a position at the same depth but under a soil ped. As stated earlier, bihourly sampling commenced at the end of a two day rainy period followed by a warming trend.

An analysis of variance using a block design to remove parallel variation in readings due to daily and hourly variation in water potential at the measurement sites was not conclusive.
Table 10 shows that through the sampling period some of the psychrometer pairs showed no significant difference in water potential at the crack and ped microsites, while other pairs showed cracks to be significantly wetter or vice versa. Overall within each vegetation type crack and ped microsite means were not significantly different. However, there was a significant difference ($P<0.001$) overall in water potential between the two vegetation types, the Halogetont sites being wetter than the Bassia sites. This supports the 12 cm depth water potential measurements discussed above, for mid-June. There were no detectable patterns of difference in soil temperatures.

The outcome of this investigation does not allow generalization about soil temperature or water potential at crack or ped microsite locations due to heterogeneity in the readings obtained. Considerably more sophisticated sampling instruments and techniques might be able to demonstrate more pronounced differences between crack and ped germination sites, but the magnitude of differences might not be biologically meaningful. Point to point variation in physical parameters at the soil surface is great and undoubtedly affects establishment success of plant species.

Photographic comparisons of polygonal ped structures

It was not possible to make extremely quantitative comparisons of positions of cracks between soil surface ped structures due to shadows on some of the photographs and a slight difference in scale for the two different years. It was evident that there was
Table 10. Mean water potentials in crack and ped sites for four pairs of psychrometers in Bassia and Halogeton vegetation on the hill site. Readings were taken at bihourly intervals from June 20 through 24, 1975.

<table>
<thead>
<tr>
<th></th>
<th>Crack</th>
<th>Ped</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bassia Sites</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>18.3</td>
<td>n.s.</td>
</tr>
<tr>
<td>2</td>
<td>31.8</td>
<td>**</td>
</tr>
<tr>
<td>3</td>
<td>26.3</td>
<td>n.s.</td>
</tr>
<tr>
<td>4</td>
<td>27.5</td>
<td>n.s.</td>
</tr>
<tr>
<td>Average</td>
<td>26.0</td>
<td>n.s.</td>
</tr>
<tr>
<td>Halogeton Sites</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>8.8</td>
<td>*</td>
</tr>
<tr>
<td>2</td>
<td>5.6</td>
<td>*</td>
</tr>
<tr>
<td>3</td>
<td>28.9</td>
<td>n.s.</td>
</tr>
<tr>
<td>4</td>
<td>32.8</td>
<td>n.s.</td>
</tr>
<tr>
<td>Average</td>
<td>19.0</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

* = significantly different at the 95% confidence level.
** = significantly different at the 99.9% confidence level.
n.s. = not significantly different (P>0.05).
little change in the positions of cracks or the shapes of peds from 1974 to 1975. This is to be expected when it is realized that the cracks represent lines of weakness between the more cohesive polygonal surface peds. Once cleaving along a given line, despite swelling of clays in fall and winter, it might be expected that the original cleavage line would be maintained and reinforced along the original lines of weakness between peds.

Hugie and Passey (1964) indicate that on their study sites in the northern Utah-southern Idaho region the cracks between surface peds became less distinct through fall and winter but did not close completely. Their observations and my photographic comparisons seem to indicate that cracks are fairly permanent structures, at least from one year to the next. As such they would not cause many seeds to become buried so deeply in the soil (3-6 cm) that successful emergence would be prevented the following spring.

Competition experiments

Field watering of plants

The ability of plants to respond to supplemental moisture can be an index of their competitive ability, particularly if one species responds with greater growth increases than another. Results of this experiment, conducted along the Bassia-Halogeton ecotone of the fence site, are informative regarding field growth behavior in a dry year (1974).
Figures 12, 13 and 14 present results of this watering experiment with information on plant density, per plant dry weight, and dry weight per square decimeter, respectively. All three figures reveal the striking response of Halogeton to added water. Bassia's response to water is almost undetectable, with only slight differences in its density and biomass in watered and unwatered plots.

Starting from comparable initial densities (Figure 12) on June 26, the watered Halogeton plants show a much slower rate of density decline than any of the other treatments. Table 11 shows results of analysis of variance of this density data, all three of the main effects being significant. Time of harvest caused a significant difference in density as did the watering treatment, and the two plant species. The only significant interaction term was the water x species term, which is understandable due to the dissimilar density responses of watered Bassia and Halogeton plants.

Figure 13 provides more evidence of Halogeton's strong response to water in that individuals were able to accumulate significantly greater dry weight biomass, from essentially similar initial weights. Analysis of variance on these data showed all of the main effects and interaction terms, including the three-way interaction, to be significant. The significant time x water and time x species interactions may be due to the seemingly strange behavior of the watered Bassia plants. The Bassia pattern of weights (Figure 13) is likely an artifact due to the destructive sampling procedure. At each sample period, plants were harvested
Figure 12. Densities of Bassia (0) and Halogeton (X) plants under water supplemented (---) (one inch equivalent per week) or non-water supplemented (------) conditions in the field. Plants grew together and sampled areas were 1 dm². n = 22 in most cases but drops to 18, 14, 10 and 8 for the watered plots over the last four sample dates.
Figure 13. Mean dry weights of Bassia (○) and Halogeton (X) plants under water supplemented (—) or non-water supplemented conditions in the field. Plants grew together in field plots. n = 30 in all cases.
Figure 14. Grams dry weight plant material per dm$^2$ for Bassia (o) and Halogeton (x) under water supplemented (-----) (one inch equivalent per week) or non-water supplemented (----) conditions in the field. n = 30 for individual plant weights; n = 22 to 8 for density.
Table 11. Analysis of variance for plant densities in dm$^2$ quadrats in the field for Bassia and Halogeton, through time and with or without supplemental watering.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Mean squares</th>
<th>F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time (T)</td>
<td>5</td>
<td>605.80</td>
<td>21.87*</td>
</tr>
<tr>
<td>Water (W)</td>
<td>1</td>
<td>433.59</td>
<td>15.65*</td>
</tr>
<tr>
<td>Species (S)</td>
<td>1</td>
<td>1868.81</td>
<td>67.44*</td>
</tr>
<tr>
<td>T x W</td>
<td>5</td>
<td>54.19</td>
<td>1.95 n.s.</td>
</tr>
<tr>
<td>T x S</td>
<td>5</td>
<td>5.72</td>
<td>0.21 n.s.</td>
</tr>
<tr>
<td>W x S</td>
<td>1</td>
<td>318.34</td>
<td>11.49*</td>
</tr>
<tr>
<td>T x W x S</td>
<td>5</td>
<td>19.18</td>
<td>0.69 n.s.</td>
</tr>
<tr>
<td>Error</td>
<td>428</td>
<td>27.70</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>451</td>
<td>41.75</td>
<td></td>
</tr>
</tbody>
</table>

n.s. = not significantly different (P > 0.05).
* = significant at the 99.9% confidence level.
from new plots, and this between plot variability seemed particularly high for the watered Bassia treatment. In contrast, Halogeton's growth response to water is very conspicuous.

Figure 14 was generated from Figures 12 and 13 by multiplying density times per plant dry weight. It shows even more markedly the dominance of the watered Halogeton plants on a grams per square decimeter basis, due to slowest rate of density decline and highest per plant biomass. Again, there are no noticeable trends in the other treatments.

Growth chamber studies

Although the experimental design and the methods used in the two growth chamber competition studies were the same, the experimental factors being investigated were different. In the first study stands of plants were either pure Bassia or Halogeton or of three intermediate proportions. In mixed pots seeds were either sown at the same time or one seed species was sown eight days earlier or later than the other, and plants were grown about 119 days from seed to harvest. All plants were grown in soil which had been collected where both species grew commonly.

In the second study plants were grown on the two different soils from the hill site in pure stands or in a mixed stand with equal numbers of both species. The other experimental factor was three levels of increasing water availability. These plants were only grown 57 days from seed to harvest.
Timing-proportions study. The objectives of this study were to investigate the effect on plant dry weight production of different stand proportions and to see if an 8-day difference in time of growth initiation would influence dry weight while in competition with the other species. These objectives have realistic field implications in that certain areas of vegetation happen to have different ratios of the two species growing proximate to each other; adjacent germination microsites, coupled with dissimilar germination requirements, could easily allow one species to commence growth eight days earlier or later than the other.

Figure 15 summarizes results of this experiment, measured in milligrams dry weight per plant, for Bassia, and Figure 16 presents the same information for Halogeton. In both figures the pure stand pots have been graphed across the timing axis, for clarity, though these pots only contained one species and hence had no timing aspect. Points with the same letter are not significantly different at the 95 percent confidence level by Duncan's multiple range test.

The results show, for Bassia, that the proportion of plants in pots was very important in affecting mean plant dry weight; that is, pots containing few Bassia plants had much larger plants. Over the 119 days that the plants were grown the eight day differential in seed sowing had almost no effect. The most interesting thing, though, is that the pure stand plants were less productive than any of the mixed pot treatments. That is to say, for Bassia, interspecific competition was less intense than
intraspecific competition since individuals were able to accumulate more weight when grown with Halogeton.

The results for Halogeton mixed pots in Figure 16 are not surprising after considering Bassia's behavior. Halogeton shows only slight response to the differing proportions, implying that in all cases it faced stiff competition. This is evident by comparing the milligram scales for the two figures; it immediately becomes apparent that mean Halogeton weights ranged from about one-fifth to one-tenth of those for Bassia. The data provide a clear indication of the competitive superiority of Bassia under the growth chamber conditions.

This strong evidence cannot be explained away with supposition that the growth chamber conditions were inherently unfavorable to Halogeton. By comparing dry weights of plants in pure stands for the species, it is demonstrated that Halogeton was significantly more productive than Bassia ($\bar{X} = 238$ versus $198$ mg per plant). Thus the competitive superiority of Bassia is real and may be due to an advantage in root function. There seemed to be little differential due to competition for light as Halogeton plants in the middle of pots, closely surrounded by other plants, grew as well as those at the frequently more open edges of pots. The evidence seems to point to the ability of Bassia to usurp soil resources to the detriment of Halogeton's growth.

The statistical analysis of Table 12 supports the evidence shown in the two figures. There were highly significant differences ($P<0.001$) due to the species and proportions of plants in pots,
Table 12. Analysis of variance for mean plant dry weight comparing Bassia and Halogeton plants grown in mixed stands of three proportions, with seeds of one species sown at the same time or eight days earlier or later than the other species. There were four replicates per treatment combination and 36 plants per pot.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Mean squares</th>
<th>F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species (S)</td>
<td>1</td>
<td>1.72</td>
<td>5456.06*</td>
</tr>
<tr>
<td>Timing (T)</td>
<td>2</td>
<td>4.24 x 10^{-5}</td>
<td>0.13ns.</td>
</tr>
<tr>
<td>Proportion (P)</td>
<td>2</td>
<td>6.14 x 10^{-2}</td>
<td>194.87*</td>
</tr>
<tr>
<td>S x T</td>
<td>2</td>
<td>4.50 x 10^{-3}</td>
<td>14.28*</td>
</tr>
<tr>
<td>S x P</td>
<td>2</td>
<td>3.67 x 10^{-2}</td>
<td>116.30*</td>
</tr>
<tr>
<td>T x P</td>
<td>4</td>
<td>3.56 x 10^{-4}</td>
<td>1.13ns.</td>
</tr>
<tr>
<td>S x T x P</td>
<td>4</td>
<td>1.85 x 10^{-3}</td>
<td>5.89*</td>
</tr>
<tr>
<td>Error</td>
<td></td>
<td>3.15 x 10^{-4}</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>2.75 x 10^{-2}</td>
<td></td>
</tr>
</tbody>
</table>

n.s. = not significantly different (P>0.05).
* = significantly different at the 99.9% confidence level.
but no significant difference due to the timing of seed sowing. It seems that over a fairly long growth period (119 days), the eight day difference in seed sowing was not very important. However, Halogeton did respond with marginally noticeable growth differences due to the timing effect, as indicated by the significant species x timing interaction. The significant species x proportion interaction was to be expected and the significant three-way interaction is not surprising, due to the complex response surfaces of the species. The pure stand pots were not included in this analysis, as they would have made the design unbalanced since there was no timing factor in their treatment. Their analysis was run separately with mixed pots in which seeds were sown at the same time, so that the design would be balanced. These F-tests indicated the same results as Table 12.

Soils-watering levels study. Additional factors investigated in this experiment were the responses of the two species when grown on the two contrasting soils from the hill site and to increasing water availability, when grown in a growth chamber. There was only one proportion of mixed pots here and plants were grown only 57 days.

Early in the experiment a striking difference became apparent in growth of both species on the two soils. Figures 17 and 18 show pure stand Bassia and Halogeton plants from the contrasting soils after about one month's growth. Both species made greater growth on the Bassia soil. This is not surprising recalling differences in soil chemistry shown in Table 9.
Plants were harvested about three weeks later as it seemed observable differences between treatment combinations were diminishing. Figures 19 and 20 summarize the results of this study for Bassia and Halogeton, respectively. It is apparent that higher soil moisture content enabled Bassia to make significantly greater growth, but there were no differences in production on the two soils. Thus, the condition observed in Figure 17, after one month's growth, disappeared within the next month. The greater growth of Bassia in mixed stand, as found in the previous experiment, is again present.

Figure 20 shows for Halogeton that there was little growth increase at higher soil moisture content, although the pure stand Halogeton grown on Bassia soil showed a slight response. Halogeton's response to the soils was significant inasmuch as pure stand plants grown on Bassia soil grew more than those on Halogeton soil. The mixed pots did not show this and in fact had a uniform, and extremely low, biomass production. The much greater growth of Bassia than Halogeton is again evident here, but in this case the pure stand plants on Halogeton soil did not make any better growth than did those grown with Bassia; however, those in pure stands on Bassia soil were significantly more productive than the mixed stand plants. Thus, the suppression of Halogeton's growth by Bassia is not as evident in this study as in the previous one. This may have been due to the shorter period of growth (57 vs 119 days) here.
o = Bassia Soil
x = Halogeton Soil

Per Plant Mean Dry Weight (mg)
Table 13. Analysis of variance for mean plant dry weight comparing Bassia and Halogeton plants grown on two different soils, at three levels of soil moisture content, and in pure or mixed (1/2:1/2) stands. There were four replicates per treatment combination and 36 plants per pot.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Mean squares</th>
<th>F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species (S)</td>
<td>1</td>
<td>0.20</td>
<td>911.50***</td>
</tr>
<tr>
<td>Proportion (P)</td>
<td>1</td>
<td>$8.44 \times 10^{-3}$</td>
<td>38.01***</td>
</tr>
<tr>
<td>Soils (So)</td>
<td>1</td>
<td>$1.72 \times 10^{-3}$</td>
<td>7.79**</td>
</tr>
<tr>
<td>Water (W)</td>
<td>2</td>
<td>$1.65 \times 10^{-2}$</td>
<td>74.18***</td>
</tr>
<tr>
<td>So x P</td>
<td>1</td>
<td>$5.14 \times 10^{-4}$</td>
<td>2.32 n.s.</td>
</tr>
<tr>
<td>So x S</td>
<td>1</td>
<td>$1.08 \times 10^{-3}$</td>
<td>4.86*</td>
</tr>
<tr>
<td>So x W</td>
<td>2</td>
<td>$1.01 \times 10^{-4}$</td>
<td>0.43 n.s.</td>
</tr>
<tr>
<td>P x S</td>
<td>1</td>
<td>$2.97 \times 10^{-2}$</td>
<td>133.92***</td>
</tr>
<tr>
<td>P x W</td>
<td>2</td>
<td>$3.14 \times 10^{-4}$</td>
<td>1.42 n.s.</td>
</tr>
<tr>
<td>S x W</td>
<td>2</td>
<td>$1.28 \times 10^{-2}$</td>
<td>58.07***</td>
</tr>
<tr>
<td>So x P x S</td>
<td>1</td>
<td>$1.32 \times 10^{-3}$</td>
<td>5.96*</td>
</tr>
<tr>
<td>So x P x W</td>
<td>2</td>
<td>$7.33 \times 10^{-5}$</td>
<td>0.33 n.s.</td>
</tr>
<tr>
<td>P x S x W</td>
<td>2</td>
<td>$1.05 \times 10^{-3}$</td>
<td>4.75*</td>
</tr>
<tr>
<td>So x S x W</td>
<td>2</td>
<td>$4.55 \times 10^{-4}$</td>
<td>2.05 n.s.</td>
</tr>
<tr>
<td>Error</td>
<td>74</td>
<td>$2.22 \times 10^{-4}$</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>95</td>
<td>$3.41 \times 10^{-3}$</td>
<td></td>
</tr>
</tbody>
</table>

* = significant at the 95 percent confidence level.
** = significant at the 99 percent confidence level.
*** = significant at the 99.9 percent confidence level.
n.s. = not significantly different (P>0.05).
Table 13 contains results of the factorial analysis of variance on these data. It supports the major points evident from the figures, and also shows significant differences due to soils and the soils x species interaction; differences which are not as obvious from visual inspection. The significant interactions are pretty much to be expected, based on the main effect differences. The significant three-way interactions require more subtle interpretation and are not as important in a field context as are the other F-tests.

**Seed Budget-Plant Demography Studies**

Studies in this section deal with estimates of densities of seeds or plants at different life cycle stages during the study period. Their objective was to quantify seed-plant dynamics over a two-year period in order to assess the magnitude of vegetation change from one year to the next, and to quantitatively apportion annual seed production into use categories to determine the manner in which each year’s seed production is dissipated. Seeds produced one year will either lie dormant in the soil, germinate, decay, or be consumed the subsequent year. This study does not deal with seed decay or consumption but only considers dormant seeds and the fate of seeds which germinate.

**Soil seed reserves**

A number of studies, usually in an agronomic context, have found very high numbers of viable seeds in soil, on the order of
10^4 to 10^5 per square meter, through the depth of the plowed layer (Brenchley and Warington, 1930; Kropac, 1966). The purpose of this investigation was to estimate numbers of hard (and therefore presumably viable, according to Stoller and Wax, 1974) seeds in soil to a 3 cm depth in late June of 1974 and 1975. This time of year was chosen since it was after essentially all germination had occurred but before any newly-produced seeds had fallen. Total annual seeds in soil are probably near their yearly low at this time and hence represent ungerminated seed reserves.

Figure 21 summarizes these data on soil seed reserves by vegetation type for the different study sites in 1974 and 1975. Neither the bare site nor the open vegetation of the sage site were sampled in 1975 due to the excessive time required to process samples. It is evident that different sites have different densities of seeds in soil; the most pronounced change is that 1975 densities are noticeably lower than those in 1974. Only in the Bassia vegetation of the hill site were there more seeds in soil in 1975 than in 1974. The fence site shows the greatest change between years, 1975 densities are about one-seventh to one-eleventh as great as they were in 1974 for the Bassia and Halogeton vegetation types, respectively.

The only significant differences shown by analysis of variance of these data are the ones just mentioned for the fence site. There were no statistically significant differences between any of the other means, probably due to the high within-treatment
Figure 21. Numbers of hard seeds per square meter to a 3 cm depth on the various study sites in 1974 and 1975. For 1974 estimates n = 10, for 1975 estimates n = 7. Columns with different letters above are significantly different at the 95 percent confidence level using Duncan's multiple range test.
variances. Major and Pyott (1966) in their review on buried viable seeds state that point to point variability in numbers of seeds in soil makes statistically reliable sampling a practical impossibility. Further, they are wary of non-normal data distributions since in the field seeds tend to be aggregated about parent plants. My data were submitted to the W test for normality developed by Shapiro and Wilk (Dunn and Clark, 1974) and were found to be normally distributed, an assumption important in parametric statistics.

Differences between sites within a year are to be expected due to variable amounts of seed production, but the generally lower 1975 densities are a more substantial result.

Figure 22 presents estimates of densities of seeds in soil by species on the study sites in 1974 and 1975. The "other" designation combines both Descurainia and Lepidium seeds. On all of the sites except sage, Descurainia was the major constituent in this category. For the hill, fence and sage sites, which contained two discrete types of vegetation, the seed densities have been computed based on the portion of the plot in which that species occurred. Roughly one-half of the fence site was dominated by Bassia and Descurainia while the other half was dominated by Halogeton. Density of each species was computed based on total number of seeds recovered per unit area divided by the proportion of the plot in which that species occurred. This was considered to be the most realistic way to estimate density.
Figure 22.

Mean numbers of seeds per square meter recovered from soil samples to a 3 cm depth on the different study sites in 1974 and 1975. Numbers atop the columns are densities for that group. Species lumped in the "other" category are Descurainia pinnata and Lepidium perfoliatum. Means are based on 20 samples for 1974 or 14 samples for 1975, except for the 1975 sage site which had 7 samples.
Coefficients of variation for the different species were on the order of 50 to 150 percent; because of this high variability no statistical analyses were attempted. There are, however, several interesting aspects of these data. Nearly all of the species on each site had lower densities of seeds in 1975, with the fence site suffering greatest declines.

The "other" species, Descurainia and Lepidium, did not produce seed in 1974. Their lower 1975 values represent attrition due to germination, decay or consumption without seed reserve replenishment. On the hill site the means indicate 24 percent of the "other" seeds were lost in one year; on the fence and sage sites losses were 81 percent and 70 percent, respectively. Similarly, Halogeton produced no seed on the fence site in 1974 and its attrition rate over one year was 93 percent. Loss rates are likely related to species germination requirements; the drastic drop in numbers of Halogeton seeds seems to indicate that they germinate freely, as has already been related. Nearly all of the Halogeton seeds recovered were of the brown variety, which are nearly impossible to germinate under a variety of laboratory conditions; almost none of the easily germinable black seeds were recovered.

Summer plant establishment

The objective of the watering experiment conducted from mid-July to mid-September in 1974 was to see if there was a significant germinable reserve of seeds in the soil and to estimate its magnitude through counts of emergent seedlings. Very
low numbers of plants emerged during the course of the watering treatment, and only during the first few weeks after its initiation. The average number of plants emerging during the initial weeks was about one to two per each one-eighth square meter quadrat.

These low rates of seedling emergence might be explained by insufficient amounts of water available for seed germination. The weekly addition of one inch equivalent of "rain" might not have raised soil water potential high enough for a long enough time to allow germination. No measurements were taken of soil water content in these plots but the soil surface was evidently damp for one to two days after water addition. In the first two weeks of September the frequency of watering was increased to two one-inch applications per week. There was no emergence in response to the increased water availability.

Another explanation for lack of emergence could be that seeds were dormant and would not germinate even with water abundantly available. The high temperatures of mid-summer might be an environmental cue related to a dormancy-enforcing mechanism preventing germination. Whatever the reason for lack of emergence, data in the previous section indicate there were numerous viable seeds in the soil.

Seed exclosures

An indication of the relative contribution to 1975 vegetation by 1974-produced and pre-1974 produced seed is provided by results of the seed exclosure experiment. Areas of soil which were
covered with cardboard boxes during the seed dispersal period in 1974 received no seed input. Comparable adjacent areas received a natural allotment of seed and differences between the covered and uncovered quadrats are an index to the impact of 1974 seed production, in terms of plants established in 1975. However, seeds under the boxes may have decayed more rapidly during the fall.

Figure 23 summarizes these data from the covered and uncovered quadrats which had been watered during summer, 1974. Data are presented for only three of the sites; densities on the fourth site (fence) were so near zero as to be not worth graphing. Each datum in the figure is the mean of 30 subsamples from 10 different quadrats, each quadrat containing three dm$^2$ subsamples.

The graphs plainly show for the initial sample date of May 26 that plant densities, on all sites, were much lower in the quadrats which had been covered during the seed dispersal period. The hill, sage and bare uncovered quadrats had 12.5, 28.5, and 14.9 times as many total plants established as the adjacent covered quadrats. This indicates that 1974 seed production generated the overwhelming majority of plants which became established in 1975. Correspondingly, 8, 4, and 7 percent of plants growing on the hill, sage, and bare sites can be attributed to seed produced prior to 1974. Seeds of these species seem to have a short residence time in soil. Supporting this idea, the fence area, which had lowest seed production in 1974 also had lowest plant density in 1975.

There are evident differences in initial plant density between the three study sites. Density on May 26 for the covered
Figure 23. Mean numbers of plants (x 100) per square meter growing in 1975 in areas which had either been covered (preventing seed input) or uncovered (allowing seed input) during the seed dispersal period in 1974. Each datum is the mean of 30 dm$^2$ subsamples, 3 subsamples taken from each of 10 quadrats.
quadrats ranged from a low of 10 Halogeton plants per square meter on the sage site to a high of 177 Bassia plants on the hill site. The uncovered quadrats show greater absolute differences in densities, ranging from about 350 Halogeton plants per square meter on the sage site to over 2300 Bassia or Halogeton plants on the hill site. These differences in density are probably related to numbers of seeds in soil available for germination and the favorableness of germination-establishment conditions on each site.

During the summer growing season the covered and uncovered quadrats had significantly different numbers of plant deaths. There was little mortality in the quadrats which had been covered, due, presumably, to their initially low densities. Plants growing in the uncovered quadrats showed substantial density declines; in the early part of the summer the more dense stands (as on the hill site) thinned more rapidly. In July and August the death rate generally diminished indicating that plants surviving to this point had a greater likelihood of maturing.

Results of analysis of variance of these data support the major points just related. For each time period there were significant differences (P<0.01) in density due to the exclosure treatment, and due to the three study sites. The exclosure x site interaction term was also significant (P<0.01), indicating that the density response to the covered and uncovered treatments was not the same on the three sites.
Temporal changes in vegetation

Twice in 1974, in mid-June and mid-September, and six times in 1975 between May 25 and August 31, density counts were made at the permanent plots which had been spaced in a 5 x 5 m grid on the four study sites. These counts provide documentation of changes in vegetation between a dry and wet year (1974, 1975) and, for 1975, the pattern of post-establishment mortality.

Year-to-year differences

Density estimates made near the beginning and end of summer in both years are presented in Table 14 along with F values from analysis of variance done between years for each site on these density estimates. The beginning sampling dates were June 25, 1974, and June 22, 1975; the ending dates were September 4, 1974, and August 31, 1975. Though the dates are not exactly one year apart, they are close.

The four sites exhibit different degrees of change within and between years. The hill site was the most stable, showing no significant differences in density of Bassia or Halogeton at the beginning or end of either year. In contrast, the fence site was quite changeable; it had high densities of both species in June of 1974 and very low densities in June of 1975, hence the significant difference between years. By September of 1974, all the Halogeton had died, and it remained essentially absent through 1975, thus there was a statistically significant difference in density of the two species in September which had not been present in June.
Table 14. Overall mean densities of Bassia and Halogeton plants per square meter at the beginning and end of summer in 1974 and 1975 in permanent plots. Quadrats were 1 dm$^2$. There were 30 quadrats sampled on three of the sites; the hill site had 35 samples.

<table>
<thead>
<tr>
<th>Site</th>
<th>1974</th>
<th>1975</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bassia</td>
<td>Halogeton</td>
<td>Survival</td>
<td>Bassia</td>
<td>Halogeton</td>
<td>Survival</td>
<td>Survival</td>
</tr>
<tr>
<td>Hill</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>717</td>
<td>1063</td>
<td>36 1160</td>
<td>1083</td>
<td>45 0.14</td>
<td>0.42 0.35</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>320</td>
<td>323</td>
<td>0.34 2.01</td>
<td>0.32</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fence</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>1973</td>
<td>1447</td>
<td>5 63</td>
<td>3 85</td>
<td>0.95 31.06**</td>
<td>0.60</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>180</td>
<td>0</td>
<td>0.00 1.80</td>
<td>2.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sage</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>70</td>
<td>473</td>
<td>12 0</td>
<td>780 46</td>
<td>8.38* 0.33</td>
<td>0.85</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>0</td>
<td>63</td>
<td>0.55 3.20</td>
<td>3.20</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bare</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>493</td>
<td>596</td>
<td>14 547</td>
<td>583 47</td>
<td>0.13 0.01</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>77</td>
<td>77</td>
<td>0.68 6.58*</td>
<td>0.68</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* = significantly different at the 97.5 percent confidence level.
** = significantly different at the 99.9 percent confidence level.
The sage site shows no significant difference between years but there is a significant difference in species due to Bassia's near absence. The year and species x year interaction F values approach significance (F at p = .05 is 3.92) for the September date due to the relatively higher Halogeton density in 1975 and Bassia's continued absence. The bare site showed a significant difference in density in September of the two years, the wetter 1975 conditions allowing more plants to survive.

Comparing percent survival in the two years for each site, it was always greater in 1975, probably due to the higher rainfall.

Post-establishment mortality

The patterns of decline in density for Bassia and Halogeton on three of the study sites during the summer of 1975 are shown in Figure 24. It is evident that initial densities are highest on the hill site. Through June and July plants on this site also had the most rapid rate of decline. In August death rate was about the same for all of the sites. The three lower density lines (for bare and sage sites) generally had quite similar mortality through the summer.

These data were submitted to statistical analysis comparing initial and final numbers of plants present between sample dates with the three sites and two plant species as treatments. This analysis showed that there were significant density differences (P<0.001) between sites due, no doubt, to the initially high densities on the hill site. There was no significant difference in density of Bassia or Halogeton on the sites, though.
Figure 24. Mean numbers of Bassia (O) and Halogeton (X) plants per square meter on three different sites during summer 1975. n = 30 for sage and bare sites and 35 for hill site.
The more interesting next step in this analysis was to use covariance techniques to remove effects of initial density differences between treatments for each of the sample dates. After doing this, the significant difference between sites, described above, disappears. This is an indication that changes in density between sample periods are dependent on the number of plants initially present. In fact, a regression analysis containing subsets for the species, the sites, the species x site interaction and the number of plants alive at the previous sample period showed only the final term to be significant ($F = 3,767.65$).

A regression of number of plants alive at one sample period against number of plants present at the previous sample period was highly significant ($F = 4,068.18$, $r^2 = 0.90$). The equation for this relationship was $Y = 0.8350 + 0.7571X$, where $Y$ equals the density of live plants at one of the sample dates and $X$ equals the number that were alive at the previous sample date. This equation does not provide an instantaneous mortality rate, but rather applies to the time periods between sample dates over the summer. The equation represents something of an average death rate, in that covariance removed effects of initial density difference between treatments, and all of the data were used in the analysis.

At the beginning and end of the growing season for these annuals, other factors such as temperature or relative humidity might be more important predictors of mortality. However, during this summer growing period, by which time most plants have
become well established or have already died due to abiotic stress, mortality is closely related to density. This highly density-dependent mortality implies that competition for resources is keen between these plants, in that the number of deaths occurring in the next couple of weeks can be predicted quite well simply by knowing the numbers of plants now present.

Seed production

The final bit of information necessary to produce a fairly complete picture of seed-plant dynamics through time was seed production in 1974 and 1975. These estimates were made using regression and dimensional analysis techniques. For Bassia, Halogeton and Descurainia lengths of flowering stalks, or fruits in Descurainia's case, were measured and the numbers of seeds along that length were counted. These data were then used to generate a regression line for each species using a stepwise multiple regression program which predicted seed number based on inflorescence length, or a transformed variable of inflorescence length.

For each species the equations are as follows:

Bassia: \[ Y = 11.97 + 1.368X, \quad r^2 = 0.98, \quad n = 66 \]

Halogeton: \[ Y = 3.891 + 1.796X, \quad r^2 = 0.53, \quad n = 115 \]

Descurainia: \[ Y = 9.519 + 8.901 \times 10^{-5} X^4, \quad r^2 = 0.59, \quad n = 140 \]

Where number of seeds is \( Y \) and length of fruit-bearing stalk is \( X \) (in millimeters). These regressions are highly significant (\( P<0.01 \)) but the Bassia equation predicts with much narrower confidence limits.
It was evident while measuring the Halogeton and Descurainia stalks that variability was quite high.

By collecting whole plants from the field, measuring lengths of all seed-bearing stalks, and applying the regression equations to the data obtained, it was possible to make estimates of numbers of seeds produced per plant. In the process of collecting plants for measurement a density estimate for each of the fruiting species was obtained. From these two measures several estimates of seed production were generated.

Figure 25 presents data on the total numbers of seeds produced per square meter by all species in 1974 and 1975. It is apparent that all sites had greater seed production in 1975 than in 1974. The bare site showed the least change between the two years, the 1975 amount of $1.88 \times 10^5$ seeds per square meter was about 1.4 times more than the amount produced in 1974. The fence site showed a tremendous difference between the two years, about 52.5 times more seed was produced per square meter here in 1975 than in 1974. Worth recalling here is the fact that most plants on this site died without producing seed in 1974.

With these weedy annuals, size and seed production per plant are indices of vigor. With this in mind, the data on per plant seed production presented in Figure 26 are informative, despite high variability (coefficients of variation ranged from 50 to 250 percent). Descurainia and Lepidium were absent in 1974, but in 1975 generally produced more seeds per plant than the Bassia or Halogeton they grew with, this likely due to their earliness
Figure 25. Total numbers of seeds produced per square meter on the study sites in 1974 and 1975.
Figure 26. Mean number of seeds produced per plant by the different species growing in 1974 and 1975.
of seed production, enabling them to utilize the more abundant
May-June soil water. In turn, the Bassia plants which coexisted
with Descurainia in 1975 on the hill and bare sites were smaller
than in 1974. On these two sites 1975 was a worse year for Bassia
than 1974, even though rainfall was greater. A logical inference
is that Descurainia usurped soil water from Bassia causing it to
be more stressed during summer 1975, and therefore less productive.
Contrastingly, Halogeton shows little variation in seed production
per plant between the two years, except on the fence site.

The story on the fence site is again one of drastic change
between the two years; only small Bassia plants in 1974, but in
1975 the plants are very large. This is due to the very low
densities of plants here, inter-plant distances were great—often
a meter or two—and the high growth potential of individuals was
realized.

Figure 27 converts per plant seed production to a density
basis, computed over the area in which the various species occurred.
The most striking thing is the tremendous density of seed production
by Descurainia on the hill site—nearly 650,000 seeds per square
meter from this dense stand. Bassia again shows lower densities of
seed production on the hill and bare sites while Halogeton shows
higher densities. The increase by Halogeton is not due to differences
in plant size but rather higher plant densities (Table 14). The fence
site, despite its huge plants, did not have tremendously high
densities of seed production due to the low plant densities.
Figure 27. Mean numbers of seeds produced in 1974 and 1975 by species for the four study sites.
DISCUSSION

Dispersal, Establishment, and Competitive Exclusion

Questions of restricted plant species distributions have often been investigated through study of the natural selection process at different life cycle stages. The approach used here and by other authors (Sharitz and McCormick, 1973; Pemadasa and Lovell, 1974a) considers that a species may not be found in an area due to restricted seed dispersal, seed dormancy mechanisms, unfavorable microenvironment for establishment, or inability to withstand competition from other members of the community.

The data from Figures 4, 5, 7, and 8 on numbers of seeds in soil across the Bassia-Halogeton ecotones, seed dispersal, and seed germinability, collectively indicate that reasonable numbers of seeds disperse across the ecotone and germinate in the adjacent monospecific stand. The fairly restricted seed dispersal results in the majority of seeds being deposited near parent plants but the small percentage contaminating the adjacent vegetation should be a nucleus for mutual invasion of the pure stands. Friedman and Orshan (1975) feel that the short dispersal distances of many annuals are adaptive, in that they allow reoccupation of a site which allowed seed production. But colonization of new habitats is also important, particularly with secondary succession in these weed communities, which have short seral stages (Piemeisel, 1951).
The data in Figure 4 on seeds in soil imply that seeds of the absent species have not accumulated in the adjacent vegetation, since the below ground seed population reflects the above ground vegetation composition. The field and lab germination studies corroborate this by demonstrating little difference in the germination behavior of Bassia or Halogeton. This evidence seems fairly strong; that dispersal and germination are not the life cycle stages during which selection restricts the distribution of Bassia or Halogeton on these study sites.

The next group of experiments on success of seedling establishment, drought tolerance of the two species, and differences in soils, provide substantial evidence toward explanation of the adjacent pure stands of Bassia and Halogeton.

Eight percent, the average establishment rate for the seeds sown onto the soil, indicates few seeds become well-established plants. Sharitz and McCormick (1973) also found this for two pioneer annual species which had concave survivorship curves, a great deal of mortality occurred at the seedling stage. Harper (1965) states that environmental tolerance ranges in early stages of plant growth are often very much narrower than what adult plants can withstand. This definitely is the case here as pre-establishment mortality was so much greater than growing season (post-establishment) mortality. Data from Table 7 indicate that of the 8 percent of sown seeds which were established in May, 54 percent died during the growing season. Thus approximately 92 percent of
of seed died by May 16, an additional 46 percent died during summer, leaving about 4 percent of sown seed as reproducing plants.

Seedling establishment success was markedly different in the various vegetation types as 1.8 times more Halogeton plants became established than Bassia (Figure 9). Evans and Young (1970) have documented a similar differential establishment success for cheatgrass, medusahead, and several broadleaf weeds in relation to litter deposition. Friedman and Orshan (1974), however, found that two allopatric varieties of *Medicago laciniata* (L.) Mill. growing in Israel emerged in comparable numbers on their dissimilar, respective sites. Seedling physiological tolerances, weather, and microsite conditions all influence establishment success in the early spring. Cronin (1965) states that sub-freezing temperatures cause little seedling mortality, but that dry periods, particularly when accompanied by wind, are the likely cause of most mortality for Halogeton. The tender seedling tissues can become rapidly dessicated if a wind dries the soil below the penetration depth of the rootlet, and death will ensue. The numerous dead seedlings observed in the sown plots in May support this contention.

Blackburn and Skau (1974) found less favorable soil conditions associated with vesicular soil surface horizons which were evident in interspaces between coppice dunes in Nevada. These vesicularized, interspace areas, as in the Halogeton vegetation, had lower percent carbon, higher pH, bulk density and percent silt. Infiltration rates were lower and sediment production was higher. These areas inimical to plant establishment tend to increase when vegetative cover is removed, and on my sites were best colonized by Halogeton.
Physiological differences between the species coupled with heterogeneous soil surface conditions probably account for much of the differential establishment success. The obvious differences in soil chemistry shown in Table 9 reinforce the inference that Bassia cannot establish as well on more extreme sites while Halogeton can. From results of the drought tolerance experiment (Table 8) it can be inferred that since young Bassia plants (4-5 weeks) are less drought tolerant than those of Halogeton, comparable seedlings in the field might be similarly less tolerant and therefore be restricted to more mesic sites.

There can, however, be year to year differences in degree of establishment success. A very mild spring might allow Bassia to colonize areas generally dominated by Halogeton. The growth chamber study using the two different soils showed that after initial repression of both species on Halogeton soil (establishment phase), that there were not drastic differences in production on the two soils after 57 days growth. Extrapolating this to the field situation, a mild spring might provide an opportunity for Bassia to invade areas which can generally only be colonized by Halogeton. With successful reproduction the successional trend in one or more areas might be shifted.

So, to summarize, it seems the establishment phase is critical in determining vegetation composition from one year to the next, since so much mortality occurs at this stage. Bassia and Halogeton have considerably different requirements for
successful establishment, Bassia is restricted to relatively
mesic microsites but Halogeton can establish under very
severe conditions.

**Competition experiments**

The results of the three experiments on competition seemed
somewhat contradictory as watered Halogeton plants in the
field became much larger (Figure 13) than Bassia plants, but in
the two growth chamber studies Bassia grown in mixed stands far
outstripped Halogeton (Figures 15, 16, 19 and 20).

Differences in density can affect competitive relationships;
for instance, McCown and Williams (1968) found that at low densities
Erodium botrys suppressed Bromus mollis but at very high densities
the situation was reversed, as Bromus proved to be a better
competitor for light. In my experiments, initial field densities
were on the order of 23 to 25 plants per square decimeter, while
all potted plants in growth chambers were at a density of 36
plants per square decimeter pot. This difference, about 1/3 lower
density in the field, probably is not responsible for contrasting
results between field and lab experiments.

Additionally, since no measurements were made of soil water
content in the field, the magnitude of the difference between
field and growth chamber water availability is not known. The
one inch field water applications infiltrated to a depth of about
10 to 15 cm within 24 hours, so roots should have been able to
utilize it. It's fairly reasonable to infer that field conditions
were significantly drier than in either growth chamber study, since
numerous plants died. In the growth chambers there was considerable wilting of Bassia from time to time, but few deaths occurred. Plant roots in the growth chambers were restricted to the 15 cm tall pots but in the field rooting depth was probably considerably greater.

There were also differences in initial growth conditions. The spring of 1974 was quite dry in Curlew Valley, so dry in fact that few Descurainia and Lepidium plants were able to establish, and those that did generally died before June. In contrast, the growth chamber experiments began with saturated soil to insure survival of establishing seedlings. The saturated soil took several weeks to dry to the treatment water content, which was still probably somewhat wetter than the field conditions. Field watering did not begin until the end of June, after plants had been growing around three months; assuming early April germination. Plants in the first growth chamber study were grown only four months, or two months in the second study.

Thus both growth chamber studies can be characterized by wet initial growth conditions and harvest after a shorter period, relative to the field experiment. Under these more mesic conditions Bassia was the aggressor, able to exploit more than its "share" of the factors of the environment.

In the field, however, Bassia did not respond to summer moisture additions but Halogeton did. Though there was no initial difference in weight of plant tops (Figure 13), Halogeton's greater drought tolerance may have allowed it to make more root growth early in the
growing season. This might have enabled it to monopolize the added water and account for Bassia's unresponsiveness.

This unresponsiveness is hard to explain, particularly in light of Bassia's rapid growth in the growth chamber. It may have been that the one inch weekly water additions were not sufficient to allow growth by Bassia; this seems unlikely though. Possibly the dry early season resulted in a stunting which could not be overcome by water applied in July and August. Beatley (1974) states that success of summer-growing populations of Salsola in the Mojave Desert is not necessarily enhanced by summer rains. This may be the case with Bassia, whose ecological characteristics are quite similar to Salsola. If early season moisture is scanty, physiological changes accompanying maturation may prevent rapid vegetative growth later in the season. This hypothesis is supported by the data in Figure 10 on field soil water potential at a 12 cm depth in the Bassia vegetation type. Water potential was about -20 bars and decreased only slightly from June 20 to August 5. It can be assumed that most rooting was below this depth where water potential was higher. Even so, I observed very little growth of these plants during the summer period. This may have been conditioned by the lush growth of the cohabitant Descurainia whose stems averaged 40 to 60 cm tall at maturity in late June. Descurainia definitely usurped moisture from Bassia with its rapid growth rate. Bassia did not grow substantially after Descurainia matured.
The suppression of Halogeton by Bassia in the first (timing-proportion) growth chamber study is evident due to Halogeton's diminished production in mixed stand relative to the pure stand (Figures 15 and 16). Pure stand pots containing Halogeton were significantly more productive in this experiment than Bassia-containing pots. Along the same lines, in the second growth chamber study at low water availability (Figures 19 and 20), and in the control treatment for the drought tolerance experiment (Table 8) there were no significant differences in biomass for the two species grown in pure stands. So it seems growth rates of tops for both species grown in pure stand are comparable over the experimental periods here, up to 119 days. And the suppression of Halogeton by Bassia in mixed stands was real.

In the soils-watering levels study Halogeton was not nearly as responsive to increasing water availability as was Bassia (Figures 19 and 20). This may have been due to the fact that only biomass of plant shoots was measured. The two species may have different root-shoot ratios, Halogeton conceivably putting more energy into root growth, in keeping with its proclivity to occupy harsh sites. If the total plant biomass had been harvested, perhaps Halogeton would have shown a greater response to water. Another explanation might be that under growth chamber conditions, Bassia's growth potential is such that it can rapidly respond to water increases.

In these experiments it is difficult to say what the specific limiting factor for growth is, and why one species grows more rapidly than the other under certain conditions. There seemed
to be no evidences of competition for light, as neither species creates a dense canopy. Determining competitive ability for soil growth resources is difficult to do. Hironaka (1961) investigated relative rate of root development of cheatgrass and medusahead in hopes of explaining the replacement of the former by the latter on many Idaho ranges. He found that vertical root penetration rate was not significantly different for the species in two years. He could not explain medusahead's competitive superiority based on differences in rooting or other ecological habits, particularly since cheatgrass matures two to three weeks earlier than medusahead. Apparently this question is still unanswered as Dahl and Tisdale (1975) characterize sites which favor medusahead invasion but offer no explanation for the mechanism behind its aggressive habits.

Synthesis

The adjacent Bassia and Halogeton pure stands can be explained based on fairly restricted seed dispersal, differential establishment success due to dissimilar soil conditions, drought tolerance and competitive interactions. The fairly restricted seed dispersal results in a low percentage of seeds of the invading species entering the neighboring vegetation. Microsite differences allowed significantly more establishment success of one species than the other on nearly all of the sites (Figure 9). The severe selection at this stage results in the two species being mostly confined to areas where they are likely to reproduce successfully. Halogeton's establishment success was 1.8 times that of Bassia, but growing
season mortality percent was nearly the same (Table 7) for both species, since selection during establishment had already confined the species to sites more favorable for their growth habits.

The drought tolerance and competition experiments demonstrated differential responses of the species to changing degrees of physical and biotic stress factors. Halogeton's succulent tissues enable it to survive drought but it is not as well able to respond rapidly to freely available moisture as Bassia. Contrastingly, Bassia seems to become stunted if moisture is not available early; and despite its narrower ecological tolerance, is the more vigorous competitor if sufficient early season moisture is available.

The abruptness of the ecotone between the communities may be partly attributed to an abrupt change in soils parameters, but more important may be modification of soil surface properties by both species. The species may tend to accentuate the "tension zone" bounding them. Bassia litter enhances soil surface properties pertinent to its establishment by decomposing slowly and becoming incorporated into the surface soil. The sodium-accumulating Halogeton litter decomposes rapidly, causing deterioration of soil surface properties, so that eventually it is about the only species which can become established on these sites.
Seed Budget-Plant Demography Studies

The discussion in the previous section indicated roughly 90 percent of each year's seed production is lost each spring during the seedling establishment period. This is assuming a high percentage of seeds germinate and does not account for losses to decay or seed consumption.

Despite this tremendous mortality dense stands of vegetation were present in May and June of both study years. Tables 1 and 2 indicate that densities ranged from about 70 plants to over 1500 plants per square meter, with the mean at about 800. Densities of seedlings on California annual ranges as reported by Evans, Kay and Young (1975) and Biswell and Graham (1956) are considerably higher than this—on the order of 50,000 per square meter—as a maximum. Franz, Reichman, and Van DeGraff (1973) reported densities of about 55 and 11 plants per square meter for summer and winter annuals, respectively, in the Sonoran Desert near Tucson in 1970-71. Beatley (1967) found only one to three native annual plants per square meter on several different areas of the Nevada Test Site in the Mojave Desert in 1963. Annual plant densities can vary tremendously from year to year and regionally.

On my study sites in 1974, mean summer plant survival, as a percentage of plants established in spring, was 17 percent and in 1975 it was 37 percent based on observations on permanent plots. Evans, Kay and Young (1975) had from 0 to about 30 percent survival success in three different years for all species in California annual grasslands. Beatley (1967), Tevis (1958), and
Juhren, Went and Phillips (1956) all report variable survival of native Mojave annuals ranging from 0 to about 75 percent in different years. It seems that growing season moisture will determine survival success of established plants while germination conditions and numbers of seeds in soil will influence initial stand density. Growing season survival is highly variable dependent on vegetation density and climatic conditions.

Seed production

The critical event influencing composition of these annuals communities, regardless of how many plants establish and survive, is seed production. With annuals the plant can be thought of as the means whereby a seed produces more seeds, the species most successful at this task should eventually gain dominance of a site.Sharitz and McCormick (1973) call per plant seed production reproductive potential. Total seed production per unit area is somewhat independent of plant density, particularly with these weedy annuals; a single individual may produce one seed or upwards of 30,000. In this study it was evident (Figure 26) that per plant seed production was extremely variable, but also quite high.

Sharitz and McCormick (1973) found for their annual, rock outcrop, pioneer species, Sedum smallii produced 114 seeds per plant and Minuartia uniflora produced 305 seeds per plant. Seed production per square meter was $4.69 \times 10^5$ and $2.95 \times 10^5$, respectively for the two species. Hickman (1975) studying
_Polygonum cascadense_ Baker, an annual of the Cascade Mountains, found along a gradient of decreasing physical harshness that reproductive potential increased from 17 to 229 seeds per plant as the environment became more favorable. Seed production per square meter was highest \((1.7 \times 10^5)\) near the harsh end of the gradient as other species cohabitated the more favorable sites and density of _Polygonum_ was lower. Harper (1965) and Salisbury (1964) have indicated that colonizing species in general, and particularly annuals, have high reproductive potential.

There are some trends evident in Figures 26 and 27 on seed production which can be extrapolated to infer the successional trend of the sites. In 1974 seed production per plant and per square meter were generally lower than in 1975. More favorable precipitation in 1975 allowed larger plants and more total seed production. The important thing, though, is that on two of the three sites in which it occurred in 1975, _Descurainia_ produced a higher density of seeds than the other species. It probably also caused _Bassia_ seed production to be diminished over what it might have been by cohabiting the sites favored by _Bassia_ and usurping soil moisture. The expectation would be, confirmed by observations in 1976, that _Descurainia_’s dominance of the site would increase. The principles first hypothesized by Piemeisel (1951), that earlier-maturing species would displace the late maturing initial occupants by usurping soil water definitely apply here. The data on seed production support Piemeisel’s hypothesis.
Soil seed reserves

Seed of these species fall freely from the plant at maturity and come to rest at different locations near the soil surface where they may remain for variable lengths of time dependent on their germination requirements, favorableness of the microsite for germination, likelihood of consumption by rodents, and several other parameters. Numbers of viable seeds lying in soil are an important aspect of ecosystem structure for a couple of reasons. Seeds are an important food source for small mammals and insects, hence influencing the stability of their populations (Reichman, 1975). They also provide a germinable reserve from which plants may reestablish, without additional seed production or immigration, in the event extant vegetation is destroyed in one way or another. For these reasons the magnitude of soil seed populations, in relation to yearly seed production and germination quantities, is of interest.

Residence time of seeds in soil depends on in situ decay and loss rate of seeds, and the amount of germination taking place annually. Ecosystems whose seeds have short residence time in soil are more likely to be unstable, in terms of plant production, as a series of several years with little seed production might result in few available, germinable seeds to generate new plants.

Studies on weed seeds in agricultural soils (Major and Pyott, 1966; Kropac, 1966) often find very high numbers of seeds (on the order of $10^5$ per square meter) in the plowed layer but few of these are germinable because they are deeply buried. There is
strong evidence to indicate that burial induces dormancy in many species and exposure to light is necessary for germination (Wesson and Warzeing, 1969a, b).

Thus the dynamics of seed populations in the top few centimeters of soil may be considerably different from the situation at deeper depths. For instance, Roberts and Feast (1972) mixed several species of weed seeds with soil of 2.5, 7.5 or 15 cm depths and monitored emergence and viability of weed seeds over a five year period. Soil was either cultivated four times a year or left undisturbed. Total seedling emergence from seeds incorporated at 2.5, 7.5 and 15 cm depths was 75, 65 and 54 percent, respectively, for the cultivated treatments and 58, 36 and 21 percent for the undisturbed soil. Their species showed variable rates and total amounts of emergence. Decay rates of seeds which did not emerge were highest with shallow burial and cultivation. Only 6 percent of the ungerminated seeds were recovered from this treatment. Deeper burial and lack of soil mixing prolonged the viability of ungerminated seeds. They conclude that seed burial, even at shallow depths, is sufficient to depress germination and favor survival of viable seeds.

In a subsequent publication (Roberts and Feast, 1973) they found exponential rates of decline in numbers of viable but ungerminated seeds mixed with soil to a 15 cm depth. The mean yearly decrease in numbers of viable seeds was roughly 32 and 12 percent for the cultivated and uncultivated treatments. Thus numbers of viable seeds decreased relatively rapidly.
Contrastingly, Dye (1969) studying seeds in Chihuahuan deserts of southern New Mexico concluded that germination rates were low in relation to numbers of seeds in soil and as a result there were sufficient soil seeds to maintain the population without additions to the seed pool for several years.

Results of this study indicated a very low carryover of soil seeds across more than one growing season. Production of 1975 vegetation was highly dependent on 1974 seed production. The data from seed exclosures, presented in Figure 23, indicated only about 6 percent of plants established in May of 1975 were generated from seed produced prior to 1974. The fence site, which had almost no seed production in 1974, had very low plant densities in 1975 (Table 1). These results indicate a considerable instability in density of vegetation from one year to the next due to the dependence of plant production on seed produced the previous year.

This hypothesis is also supported by soil seed reserve estimates (Figure 21). The 1975 densities were about 25 percent of the 1974 densities. This 75 percent decrease occurred in spite of generally "reasonable" amounts of seed production in 1974. The loss rate of seeds from the top 3 cm of soil here is even more rapid than that observed by Roberts and Feast (1972, 1973). Their comparable, uncultivated treatment indicated about 37 percent emergence and 12 percent viability loss for a total decrease of 49 percent in soil seed numbers over one year.

My results showed a 75 percent mean decrease over one year in spite of 1974 seed production. Losses of seed to rodents may have been considerable, though.
This rapid turnover rate of seeds in the upper 3 cm of soil is likely due to a high percentage germination in the spring. The studies on seed germination (Figures 7 and 8, Table 5) indicated a high germination percent of Bassia and black Halogeton seeds. The Halogeton brown seeds, which were almost the only variety found in the soil seed samples, definitely seem to be the more stable seed reserve, probably due to their more complex germination behavior (Cronin, 1965). Due to lack of disturbance it is unlikely that many seeds would become buried very deeply on this site, and the slow spring snowmelt with gradually warming temperatures seems likely to create very favorable germination conditions. Year to year climatic differences influence the portion of the total seed pool which germinates. Weather conditions in any one year may favor germination of one species more than another.

**Seed budget—plant plasticity**

Combining the estimates of total seed production and total seed reserves for 1974 and 1975, a contrasting picture of seed-plant dynamics becomes evident for the fence and hill sites over the study period. Figures 28 and 29 present these synthesized data for the fence and hill sites, respectively. Seed production and germination and other losses of seeds have been represented as single events across the time scale. The inflowing arrows represent seed production from reproductive plants.

Starting with not greatly different densities of seeds in soil in summer 1974 ($2.73 \times 10^4$ vs $9.16 \times 10^3$ per square meter) the
Yearly seed production

Soil seed reserves

Numbers of Seeds or Plants per Square Meter

Growing season 1974

Winter 1974-75

Growing season 1975

End of 1975 growing season

SEED BUDGET FOR FENCE SITE
SEED BUDGET FOR HILL SITE

- Yearly seed production
- Soil seed reserves

- Growing season 1974: 9.16x10^3
- Winter 1974-75: 1.24x10^5
- Growing season 1975: 5.17x10^3
- End of 1975 growing season: 3.76x10^5

Losses: 1.19x10^5
two sites have tremendously different amounts of seed production
\(5.5 \times 10^3\) vs \(1.15 \times 10^5\) seeds per square meter, fence and hill sites, respectively) at the end of the growing season since most plants on the fence site died. Thus at the end of 1974 there were roughly 3.8 times more seeds available for germination in 1975 on the hill site.

This indicates the importance of each year's seed crop to the level of soil seed reserves, since there is little carryover seed in soil relative to the amount which might be produced each year. Seed production on the hill site in 1974 was 12.5 times greater than the density of seeds in soil, while on the fence site it was only two-tenths of the number of reserve soil seeds. Similar comparisons of this sort can be made from Figures 21 and 25 on seed reserves and seed production. Seed production is roughly 10 to 100 times more than numbers of reserve seeds in soil.

The percentage loss of soil seeds by summer, 1975, was approximately the same for the two sites, a 92 percent loss on the fence site and a 96 percent loss on the hill site. The assumption here is that most of this loss was due to germination. Despite nearly equal percentage losses, the absolute numbers lost per square meter were greatly different on the two sites: \(3.03 \times 10^4\) on the fence site and \(1.19 \times 10^5\) on the hill site. Roughly 3.9 times more seeds were lost from soil on the hill site. As a result many more plants were established on this site in May, 1975 (Table 1).

Since 1975 was a fairly favorable precipitation year the few plants established on the fence site did very well, and due to
their plasticity and tremendous growth potential became very large. Contrastingly, on the hill site plants growing in considerably denser stands suffered under a greater degree of competition, and consequently were much smaller than those on the fence site (Figure 26). Despite these differences in plant size, seed production per unit area in 1975 was not greatly different on the two sites (Figure 25). Figures 28 and 29 indicate that at the end of the 1975 growing season density of soil seeds on the fence site was 76 percent as great as on the hill site whereas at the end of the 1974 season they had been only 26 percent as great.

The near failure of the 1974 seed crop on the fence site affected density of the 1975 vegetation but due to reduced competition and plant plasticity the 1975 seed crop was nearly the same as on the hill site, which had a "normal" amount of seed production in 1974. Thus plant plasticity served a homeostatic function on the fence site resulting in a high amount of 1975 seed production which might not have been expected based on the number of plants growing on the site in spring, 1975.

Plant size does have implications for the successional trend of a site. A single plant established on a low density site can become very large and make a much greater proportionate contribution to the year's seed production than if it had been established on a high density site. Its importance in the subsequent year's vegetation would likely be greater, due to greater representation in the soil seed pool. Rate of vegetation change could be more rapid in low density stands with large plants; the impact of a single invader could be much greater.
Plant size has an additional impact on site development through the manner in which litter is deposited. Small plants undergo decomposition more rapidly due to their smaller stem diameter and the fact that they more easily become pressed against the soil surface by winter snows. They more rapidly provide a positive increment of organic material to the soil surface, while large plants (many plants in 1975 were more than a meter tall and more than 40 cm in diameter) tend to remain erect, withholding their organic material above the soil.

One of the major factors controlling succession in these weedy communities is degree of microsite development, which mainly progresses by deposition of litter (Piemeisel, 1951; Evans and Young, 1970). Dense stands will generate uniform litter deposition while sparse stands with large plants will produce islands of shade and litter. Plants growing in 1976 on the fence site under remnants of the large 1975 plants were observed to be significantly larger and more vigorous than those growing in more exposed locations.

**Pioneering-Colonizing Ability**

As just discussed, the amount of litter deposition on a site plays an important role in determining which of several annual species can establish there. The establishment phase is critical in determining community composition and several authors (Evans and Young, 1970, 1972b; Piemeisel, 1951) have demonstrated that species higher in the successional sequence
of these weed communities require more favorable microsite conditions for establishment. Disturbance and trampling tend to result in a flat, barren soil surface which dries out rapidly and is subject to extreme temperature fluctuations. Only better colonizing species can occupy these extreme sites. Since the Validation Site was fenced in 1973 there has been minimal disturbance and the sere has been progressing.

The earliest colonizers of this site, Bassia, Halogeton, and Russian thistle, in the Chenopodiaceae, produce their seeds in fall after growing through the long summer dry period. Their ability to withstand the drought may be correlated with their ability to establish on extreme sites. That is, a hypothetical species able to establish under extreme conditions, but not able to withstand summer drought, would eventually be restricted to sites where it could establish and reproduce. These species are successful establishing under extreme conditions and can also withstand the dry summer.

In 1975, Halogeton established about 1.8 times more plants from sown seed than did Bassia. Its greater success in establishment indicates its better colonizing ability. It also produces two kinds of seeds which have different germination requirements, enabling it to occupy a wider range of sites. Bassia, on the other hand, was restricted to more mesic microsites and is considerably less drought tolerant than Halogeton. The competition experiments showed, though, that Bassia is capable of making more rapid growth and seems to resume growth faster after being droughted (Table 8).
Regular fall emergence of Bassia was observed but Cronin (personal communication) has observed little Halogeton fall emergence; I observed none. Bassia's fall emergence is somewhat akin to the early growth habits of secondary colonizers described by Piemeisel (Figure 2). Thus it seems Halogeton is the more persistent colonizer on extreme sites; Bassia requires more mesic conditions, but makes more rapid growth when water is available, and outcompetes Halogeton.

Further along this continuum of colonizing ability, Descurainia and Lepidium, in the Cruciferae, appear. Evans et al. (1970) found that germination of both species after about 50 hours at 20°C at -8 bars in polyethylene glycol was only 16 percent. Halogeton and Bassia had well over 75 percent germination under comparable conditions in my study. They also found a very rapid and high percentage emergence of Lepidium from surface soil, when thinly covered, and in loam soil when buried 1 cm deep. Descuriania's requirements for emergence were much more specific. It had poor emergence when sown on the soil surface and when buried 1 cm deep, but had better emergence when covered with a thin layer of soil. Its emergence rate was much slower than Lepidium's. No directly comparable studies have been conducted for Bassia and Halogeton, but observations lead me to believe they would establish more rapidly and under a wider range of conditions than Descurainia.

Young and Evans (1973) also showed these species have mucilaginous seed coats which serve to retain water which has
been imbibed, by providing a shield against moisture vapor loss and which should improve their ability to germinate under dry conditions. Bassia and Halogéton lack such an adaption, but do not need it as they can germinate well under extremely dry conditions.

Despite their narrower tolerance ranges for germination and establishment, *Descurainia* and *Lepidium* eventually will displace Halogéton and Bassia on sites which become sufficiently developed to meet their establishment requirements. This is because they flower in the spring and usurp soil moisture from the later flowering species. They, in turn are often displaced by cheatgrass, if disturbance is withheld for a long enough period.

**Comparisons with Mojave Desert Annuals**

It is also of interest to compare the reproductive strategies of these generally exotic (*Descurainia pinnata* is a native plant), weedy species with communities of annuals from the Mojave Desert, which are composed mainly of native plants. Wilcott (1973) has gleaned the major conclusions from many papers on Mojave annuals, mainly from the work of Juhren, Tevis, Went, Phillips, and Beatley. Several interesting points of comparison will be made.

In both deserts spatial and temporal patterns of annuals distribution are highly variable; in the Mojave they depend on rainfall. In Curlew Valley species distribution and density patterns are mostly dependent on heterogeneity in soil surface conditions pertinent to each species' establishment, and densities of seeds in soil available for germination.
In the Mojave, unless rains of 25 mm or more fall, no germination will occur. This is not important in Curlew Valley as winter snows usually provide plenty of water for germination, but I think these annuals can emerge on less than 25 mm rainfall.

Flowering time of many Mojave species is variable, if moisture is abundant they will grow vegetatively longer; if moisture is scant, they will flower earlier. The Curlew Valley annuals are not this way at all; their phenologic progression is very rigid, varying relatively little regardless of soil moisture status.

Controls on germination were more important in controlling plant numbers than was density-dependent mortality for Mojave species. Only 10-25 percent of total viable soil seeds would germinate after substantial rains. This is definitely not the case with the exotic annuals as germination is almost total (more than 90 percent) for Bassia and Halogeton in the spring. Density-dependent mortality during the summer is the major factor controlling plant numbers during the growing season (Figure 24).

Tevis (1958) was able to induce considerable germination of annuals during the summer and fall by sprinkling less than an inch of water at periodic intervals. The result from my applications of water in summer was almost no germination. Beatley (1974) also intimates the unresponsiveness of Salsola to summer moisture.

It seems that growth and reproductive strategies of annuals in these two deserts are quite different. This is partly due to
the greater aridity of the Mojave Desert but also due to the fact that the annuals there are native and have evolved with the ecosystem. The impression one gets from the above comparisons is that the Mojave annuals are much more finely tuned and responsive to their environment, while the Curlew Valley annuals are programmed, and not closely adapted to their ecosystem. The result is that the exotics suffer a greater degree of mortality, at the seedling stage and probably during the growing season as well. They are able to compensate for this wastage through their weedy habits; plasticity allows a tremendous reproductive potential. The Mojave plants, on the other hand, are more conservative; germination requirements are more precise and growth potential, even under ideal conditions, is probably not as great.

Finally, stability of the two ecosystems depends on different factors. Annuals of the Mojave Desert are an integral part of the ecosystem. They coexist with the perennial vegetation, tapping a stable portion of the environment unused by the perennials. The exotic annuals, however, thrive on disturbance. They grow where the perennials have been trampled, overgrazed or otherwise disturbed and do not compete well in the pristine sagebrush-bunchgrass association. Their niche has been created by man's activities.

Consequently, their high reproductive potential, lack of germination inhibition and rigid phenologic schedule make them successful in the habitats they occupy. They have coevolved with disturbed habitats which are, by definition, changeable.
Their general-purpose genotypes are successful in these open habitats, but rather than competing with the perennials which eventually recolonize, they are displaced to another disturbed location. Disturbance is the only real requirement for insuring their persistence.

Speculation on Year-to-Year and Longer Term Trends

Fencing this site in 1973 changed the course and rate of succession in this annuals community by preventing livestock grazing. The initial disturbance which killed the sagebrush was probably at least 10 years ago as the woody stems are now mostly decomposed. Continued low level grazing disturbance kept this site dominated by the most hardy colonizer, Halogeton, with scattered patches of Bassia, Salsola, Descurainia and Lepidium through 1974. At that time, microsite conditions were still too extreme to allow much of any other species besides Halogeton to become established.

The high amounts of sodium in many areas, both at the soil surface and through the profile, due to the proximity of the Great Salt Lake and Halogeton's presence, adversely affected soil physical properties, diminishing establishment success of the higher successional species. From year to year the establishment success of all species would vary, dependent on the amount of spring soil moisture and the microsite conditions wherever seeds might be. Density of seedling establishment and climatic
favorability would determine the amount of thinning during the summer, plant size, and seed production per plant.

The amount of seed in soil would be an index of maximum seedling density. Following poor seed production years, lower plant densities might be expected; following high seed production years, higher plant densities might be found, other conditions being equal.

It does not necessarily follow that high plant density leads to high seed production. With more intense competition in a high density stand, per plant, and often total, seed production will be lower. Because of this, these communities are subject to wide fluctuations in population numbers. The fence site is an example of this. In 1974 it had highest June plant densities of any of the sites (Table 1), but conditions were so severe and competition for limited resources was so great that nearly all of the plants died. In 1975, densities were much lower and the few large plants produced abundant seed so that in 1976 the plant density observed was considerably higher.

In this fashion the community perpetuated itself prior to fencing the site; Halogeton was generally the dominant, but variable amounts of the other species were present, dependent on seed availability, microsite conditions and grazing (Kennedy, 1927, states Bassia is quite palatable and nutritious).

Fencing the site has discontinued essentially all disturbance and dead plant materials are beginning to accumulate on the site, ameliorating extreme conditions at the soil surface. The
accumulations of litter should, within a few years, allow the higher successional species to increase in dominance. Observations in 1976 gave an impression that Bassia was becoming more abundant relative to Halogeton. Lepidium and Descurainia also seem to have more substantial populations on the site than they did in the two study years. Cheatgrass and the perennial bunchgrass Sitanion hystrix are also on the increase.

These definite changes in community composition may be due to 1976 being a particularly favorable year for the higher successional species. More likely they are due to the continued lack of disturbance, development of the site, and species ecological tolerances.

If the site remains undisturbed, processes of secondary succession should lead to dominance by cheatgrass and Sitanion, with eventual recolonization by perennial shrubs in a similar manner as has been reported by Hironaka and Tisdale (1963). The rate of site development and recolonization, though, may be somewhat slower relative to their site, due to the high sodium content of Curlew Valley soils.
SUMMARY AND CONCLUSIONS

Investigations were conducted in two contrasting precipitation years on a community composed solely of annual plants in a disturbed area of the salt desert shrub zone in northern Utah. 1974 was dry and fairly unfavorable for annual plant growth while 1975 was a more normal precipitation year. The studies centered around factors influencing distribution of the two dominant, nonnative species, *Halogeton glomeratus* and *Bassia hyssopifolia*, which were often found growing in adjacent pure stands. Additional studies involved estimating densities of seeds or plants of all annuals present at several life cycle stages during the study period. Vegetation dynamics of annual communities are controlled by numbers of seeds present for each species through time, since seed is the sole means whereby annuals can regenerate. Changes in densities of seeds or plants were related to changes in community composition.

These studies on basic ecological factors influencing distribution and abundance of annual plant species are of interest since they provide a better understanding of the parameters important in determining community structure. This information can be useful in range improvement practices which convert these relatively undesirable annual communities to reliable, forage producing, perennial bunchgrass stands. Foreknowledge of the possible community response to manipulation can allow more precise prediction of the outcome, which should increase the chances of successful range improvement projects.
The major findings and conclusions are as follows:

1. Vegetation density is extremely changeable from one year to another—due to its dependence on the amount of previous year's seed production and favorableness of spring germination-establishment conditions.

2. Species composition is also changeable, dependent on whether or not seed of all species present can germinate and establish in any year. Community composition can change relatively rapidly over a several year period due to the short residence time of seeds in soil and the rate at which the extreme microenvironmental conditions are being ameliorated on this exclosure site, allowing invasion of higher successional annuals.

3. Reserves of annuals seeds in the top 3cm of soil in mid-summer are on the order of $10^3$ to $10^4$ per square meter and decreased about 10 fold over one year on a site that had scant seed production in 1974. Yearly seed production ($10^4$ to $4\times10^5$ seeds per square meter) can be 10 to 100 times the reserves of seeds in soil.

4. Fall-produced seeds generally don't move very far from parent plants, probably only two to three percent disperse farther than a couple of meters.

5. There were no major differences in germination behavior of Bassia or black Halogeton seeds in field or laboratory situations. Both species germinated better in sodium chloride than polyethylene glycol solutions. After 97 hours about 75 percent of both species seeds had germinated in sodium chloride solutions of $-15$ bars water potential.

6. Only eight percent of 19,000 seeds sown into marked quadrats became established and survived until mid-May. Soil surface micro-environmental conditions and plant physiological tolerances resulted
in significantly greater establishment success of one species than
the other for nearly all sites examined. Overall, 1.8 times more
Halogeton seedlings became established than Bassia seedlings.

7. Young Halogeton plants were substantially more drought
tolerant than Bassia plants, 87 percent survived a longer, more
severe drought than one which resulted in total mortality of Bassia
plants. After being droughted, the surviving Bassia plants seemed
more resilient in their resumption of growth as they were significantly
larger than Halogeton plants by time of harvest.

8. Soil surface physical and chemical properties were strikingly
different in the sites supporting Bassia or Halogeton vegetation.
Halogeton soils were sodic, had a higher bulk density, and lower
percent organic carbon; all of which served to make the surface a
relatively harsh site for establishment of Bassia and other plant species.
Soil water potential during summer was significantly lower and temp­
erature was significantly higher in this soil than in the soil supporting
Bassia vegetation.

9. In growth chamber competition experiments, Bassia suppressed
Halogeton under all conditions. An eight day differential in time of
growth initiation had little effect on per plant biomass of either
species when grown in mixed stands for 119 days. Bassia was more
responsive to increasing water availability. Early on, both species
made better growth on the Bassia soil but differences in per plant
biomass became less pronounced with time on the two different soils.

10. Bassia and Halogeton growing in the field in naturally
mixed stands had comparable biomass and rates of density decline during
the 1974 growing season. With weekly water supplementation beginning
near the end of June, only Halogeton plants responded with biomass increases and lessened rates of density decline. It is hypothesized that Bassia may become stunted if it does not receive sufficient moisture early in the growing season.

11. Attrition rates without seed reservoir replenishment in the top 3cm of soil were 70 to 90 percent over a one year period in which certain species had no seed production. These losses were due to seed germination, decay, and consumption.

12. Only about six percent of plants which became established in 1975 were generated by seed produced prior to 1974. This was due to a lack of germination inhibition, which resulted in a high percentage germination of each year's seed production.

13. Mortality during the 1975 summer was highly density-dependent. The equation $Y = 0.8350 + 0.7571X$ (r-square = 0.90) was a predictor of density of plants alive at sample date $Y$ based on density of live plants at the previous sample date $X$.

14. Total seed production per square meter was higher on all of the sites in 1975 than in 1974. Generally, the early-summer maturing Descurainia produced the highest numbers of seeds per plant in 1975. Bassia plants which cohabited the Descurainia sites were smaller in 1975 than they had been in 1974, possibly because Descurainia caused them to become stunted by preempting available soil water.

15. On one site which had very little seed production in 1974, vegetation density in 1975 was very low. The few plants growing there responded plastically to the low density and became very large, so that 1975 seed production on this site was not much different from areas which had a considerable amount of seed production in 1974.
Plant plasticity served a homeostatic function allowing this site to replenish its seed reserves despite the previous year's seed crop failure.

Overall, these studies contribute to an understanding of major factors influencing distribution of Bassia and Halogeton on this site with regard to seed dispersal, seedling establishment success and drought tolerance commensurate with soil physical and chemical differences, and competitive interactions between the two species. It was found that the establishment phase was critical in determining vegetation composition. Abundance of plants in any year is highly dependent on the previous year's seed production and favorableness of spring germination-establishment conditions. Amount of growing season mortality and number of seeds produced per plant is mainly determined by the availability of soil water and the density of plants which become established. Succession in this ecosystem depends on amelioration of surface microenvironmental extremes, generally brought about by lack of disturbance and litter deposition. Through time, if disturbance is withheld, the rapid growing, early-maturing annuals will displace the present late-maturing dominant occupants.
LITERATURE CITED


APPENDIXES
Appendix A

Spectrum of Radiation Intensity in the Sherer-Gillette Growth Chamber in the Ultraviolet Range from 280-400 Nanometers.
Appendix A. Spectrum of radiation intensity in the Sherer-Gillette growth chamber in the ultraviolet range from 280-400 nanometers.
Appendix B

Descriptions of Soil Profiles Under Bassia and Halogeton Vegetation on the Hill Site.
<table>
<thead>
<tr>
<th>Horizon</th>
<th>Thickness (cm)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>O₁</td>
<td>.5-0 cm</td>
<td>Plant litter, decomposing organic material.</td>
</tr>
<tr>
<td>A₁</td>
<td>0-6 cm</td>
<td>Light brownish gray (2.5 Y6/2) silt loam, dark brown (10YR3/3) moist; moderate fine subangular blocky structure, breaking to moderate, fine granular; soft, very friable, slightly sticky, plastic; abundant fine roots, incorporation of plant debris, moderately calcareous with many small vesicular pores 1-2 mm diameter.</td>
</tr>
<tr>
<td>B₂</td>
<td>6-30 cm</td>
<td>Light brownish gray (2.5Y6/2) silt loam, brown (10YR4/3) moist; weak very fine platy structure breaking to moderate, fine granular; slightly hard, friable, slightly sticky, plastic; frequent fine roots, moderately calcareous occasional fine (1-2 mm) pores.</td>
</tr>
<tr>
<td>C ca</td>
<td>30-60 cm</td>
<td>Light gray (2.5Y7/2) heavy silt loam, grayish brown (2.5Y5/2) moist; moderate medium subangular block structure; hard, firm, sticky, plastic; occasional roots, few pores, extremely calcareous.</td>
</tr>
<tr>
<td>Horizon</td>
<td>Thickness (cm)</td>
<td>Description</td>
</tr>
<tr>
<td>---------</td>
<td>----------------</td>
<td>-------------</td>
</tr>
<tr>
<td>A₁</td>
<td>0-3 cm</td>
<td>Light gray (10YR7/2) silt loam, grayish brown (10YR5/2) moist; moderate to weak fine platy structure; slightly hard, friable, slightly sticky and plastic; abundant coarse and fine roots, moderately calcareous, with abundant vesicular pores (1-3 mm diameter) interlayered between platy structure.</td>
</tr>
<tr>
<td>A₁₂</td>
<td>3-10 cm</td>
<td>Quite similar to above but more compact as the vesicular pores become much less frequent and finally are completely absent.</td>
</tr>
<tr>
<td>B₂</td>
<td>10-36 cm</td>
<td>Light gray (10YR7/2) silt loam, grayish brown (10YR5/2) moist; moderate coarse platy structure; hard, firm, slightly sticky and plastic; moderately calcareous, many roots.</td>
</tr>
<tr>
<td>Cca</td>
<td>36-60 cm</td>
<td>White (10YR8/1) silt loam, yellowish brown (10YR5/4) moist; moderately medium subangular blocky structure; slightly hard, friable, slightly sticky, plastic; moderately calcareous, frequent roots.</td>
</tr>
</tbody>
</table>
VITA

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Master of Science

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Major Field: Range Ecology

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