Factors Affecting Seeds in a Sagebrush-Steppe Ecosystem and Implications for the Dispersion of an Annual Plant Species, Cheatgrass (Bromus Tectorum L.)

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FACTORS AFFECTING SEEDS IN A SAGEBRUSH-STEPPE ECOSYSTEM

AND IMPLICATIONS FOR THE DISPERSION OF

AN ANNUAL PLANT SPECIES, CHEATGRASS

(Bromus tectorum L.)

by

Michael Ira Kelrick

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

of

DOCTOR OF PHILOSOPHY

in

Biology Ecology
ACKNOWLEDGMENTS

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Missouri Department of Conservation.

Michael Ira Kelrick
"...one simply woke up one fine spring to find the range dominated by a new weed."

"All field workers in cheat country wear high boots."

-- Aldo Leopold

From 'Oregon and Utah, Cheat takes over',

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ABSTRACT

Factors Affecting Seeds in a Sagebrush-Steppe Ecosystem and Implications for the Dispersion of an Annual Plant Species, Cheatgrass

(Bromus tectorum L.)

by

Michael Ira Kelrick, Doctor of Philosophy

Utah State University, 1991

I investigated how shrub-induced spatial heterogeneity influenced and was manifested by a representative ground-story plant species at a sagebrush-steppe site in southwestern Wyoming. The dispersion of cheatgrass (Bromus tectorum) reflected differences between undershrub (higher plant densities) and interspace (between shrubs, supporting lower densities) microenvironments, hence the population ecology of this annual species served as a biological probe of shrub-associated patch structure in this community. Since cheatgrass is an annual, factors affecting the seed portion of its life cycle were of special interest. First, attributes of the above- and below-ground seed pool were characterized. The environment-wide seed depositional pattern was assessed using seed traps of several designs, and the legacy of seed incorporation into the soil was examined by separating seeds from soil samples. For both components of the seed pool, annuals' seeds predominated. Seeds at the surface were subject to substantial redistribution, moving readily
through interspace, and their deposition was related to both the interaction of wind and shrub canopies and the presence of litter. More annuals' seeds were encountered in undershrub than in interspace soils; seeds of cheatgrass were restricted to the soil surface. Second, a manipulative experiment tested effects of granivory/herbivory and presence/absence of a replicate shrub's canopy upon success of cheatgrass plants arising from known numbers of seeds introduced into undershrub versus interspace microenvironments. While biomass of plants in treatments accessible to herbivores was less than that of protected plants, consumers did not affect plant densities, and herbivore effects were not microenvironment-specific. Shrub canopy removal had no effect on plant success, and, contrary to expectations based on the dispersion of indigenous plants, interspace plants fared better than undershrub counterparts. Finally, demographic fates of individually marked seeds were observed, to disentangle effects of microenvironment from effects of microenvironment-specific surface types on determining safe sites. Littered microsites were strongly associated with undershrub microenvironments, and on these surfaces, cheatgrass seeds were less likely to move and to suffer depredation, and more likely to become favorably positioned for subsequent germination and establishment, than on bare ground surfaces typifying interspace.
CHAPTER I
INTRODUCTION

General background: aridland ecosystems

In many aridland ecosystems, shrubs not only form the dominant physiognomic element of the community, but also serve as foci of various structural and functional attributes of the system (Crawford and Gosz 1982, Noy-Meir 1985, Whitford 1986). This description applies to the three North American warm deserts (MacMahon and Wagner 1985) as well as to the temperate deserts and semi-deserts (West 1983b) of this continent. The combined physical and ecological prominence of shrubs means that their dispersion imposes a template of spatial heterogeneity in these aridland communities (Price and Reichman 1987). Such shrub-induced heterogeneity, at a local scale, inspires a rudimentary conceptualization of aridland communities as mosaics of as few as two types of patches (Pickett and White 1985): one associated with a shrub’s canopy (henceforth, undershrub or U), the other associated with the space separating shrubs (interspace or I). Organisms inhabiting aridlands can be expected to both reflect and respond to this patch structure (e.g., Allen and MacMahon 1985, Wiens 1985). In aridlands, such relatively simple patch structure can afford a particularly unobstructed view of the dynamic, reciprocal interplay of community pattern and process (in the spirit of Watt 1947).

Ground-story herbaceous plant species in aridlands often manifest strongly differentiated dispersions with respect to the shrub-induced mosaic of microenvironments (e.g., Shmida and Whittaker 1981). Shreve
(1931) alluded to this phenomenon, and Went (1942) provided a ground-breaking ecological treatment of shrub-associated herbs. Since then, extensive documentation of positive and negative associations between ground-story and shrub species in North American warm deserts and shrublands has accumulated steadily. Causal mechanisms responsible for these associations are of interest as examples of both antagonistic and mutualistic species-species interactions among plants (Hunter and Aarssen 1988), and many mechanisms have been suggested and/or directly investigated. Elucidating the determinants of the dispersion of a ground-story species population with respect to shrubs in its community is a complex problem, given the nature and number of potential influents (Table 1.1). Further, many of the mechanisms are neither independent nor mutually exclusive. Some individual mechanisms can produce multiple and potentially contradictory effects, due to interactions dependent on the species and/or the particular conditions involved. Additional complexity is injected when shrub-mediated indirect effects (i.e., those including species other than the shrub and ground-story species of interest) are important. This multiplicity of mechanisms is well illustrated by the controversy which arose from attempts to ascribe characteristic bare zones, observed where California chaparral and coastal sage shrub species contact annual grasslands, to specific causes: allelopathy (e.g., Muller 1966), herbivory by small mammals and birds (e.g., Bartolomew 1970), some combination of allelopathy and herbivory (e.g., Muller and del Moral 1971) or a more elaborate consideration also incorporating patchy soil moisture conditions in shrub stands (e.g., Halligan 1973) and suppression of ground-story species by shrub uptake of water and nutrients (Swank and Oechel 1991).
Among ground-story plant species in aridlands, annuals are often abundant and functionally significant components, being "particularly important in coupling primary production to the infrequent, unpredictable precipitation that limits the productivity of most arid systems" (Brown et al. 1979, p. 202). Several characteristics of annuals indicate that they are likely to be sensitive to a shrub-induced microenvironmental mosaic. First, the vegetative portion of an annual's life cycle is short relative to that of the shrubs; therefore, a pattern of U and I microenvironments is temporally stable, from the annual's perspective. Second, a substantial portion of the annual's life cycle is spent in a relatively mobile form, as a seed or fruit, susceptible to spatially non-random biotic and abiotic dispersal and deposition. Third, for annuals, germination and establishment (as opposed to clonal growth for many perennial plants) are critical for population persistence and are potentially hazardous processes, especially in the relatively harsh abiotic conditions of arid ecosystems (e.g., Tevis 1958, Beatley 1967, Mott and McComb 1974, MacMahon and Schimpf 1981, Mack and Pyke 1983, Fenner 1985). It is clear that, for some aridland annual species, coarse attributes of the "environmental sieve" determining germination safe sites (Harper 1977) coincide with differences between U and I microenvironments (Table 1.1). Fourth, annuals may provide both the primary food resource for a diverse guild of aridland granivores (Brown et al. 1979), as well as vegetative matter for herbivorous consumers (e.g., Beatley 1969). These animals may exercise foraging preferences between U and I microenvironments (Table 1.1). In short, annuals are excellent model organisms for probing the implications of shrub-induced environmental patchiness; indeed, the majority of examples cited in
Table 1.1 involve aridland annuals. A final general advantage of studying annuals is that all aspects of their life cycle can be observed in a single year. Thus, with annuals, achieving a comprehensive understanding of relationships between a species' biology and its demography is feasible (Hickman 1979).

**Specific background: shrub-steppe ecosystems**

Most of the evidence for shrub/annual associations presented in Table 1.1 derives from warm desert and chaparral ecosystems, but the research described herein was conducted in a sagebrush-steppe ecosystem (as classified by West 1983b). A distinguishing characteristic of the sagebrush-steppe is that annuals were apparently but a minor component of this vegetation in its "pristine" state (Tisdale et al. 1965, Young et al. 1972, West 1983a). However, two consequences of the encroachment of European settlers into the Great Basin and Intermountain regions -- the advent of disturbance wrought by domesticated herbivores (Mack and Thompson 1982) and the contemporaneous, auspicious introduction of several alien plant species (Young et al. 1972, Mack 1981) -- have resulted in the successful "intrusion" of a number of Eurasian annuals into the plant communities of the sagebrush-steppe. Among these, the most ubiquitous and best known is cheatgrass (*Bromus tectorum*) (Stewart and Hull 1949, Klemmedson and Smith 1964, Young and Evans 1973, Mack 1981, Upadhyaya et al. 1986).

Numerous attributes of *Bromus tectorum* recommend it as a model species for studying shrub-associated effects on the autecology of a sagebrush-steppe annual. First, despite its alien provenance, the species is firmly ensconced in the sagebrush-steppe of North America
(Mack 1981); it "characterizes the landscape on millions of acres in the Great Basin" (Young and Evans 1973, p. 410). B. tectorum is probably the most common annual species in the shrub-steppe vegetation of western North America. Second, although the rapidity and geographical scope of the integration of B. tectorum into these communities were clearly facilitated by human disturbance (Stewart and Hull 1949, Piemeisel 1951, Hulbert 1955, Beatley 1966, Young et al. 1972, Mack 1981), rare observations from extraordinary localities where grazing and other human-initiated effects were minimal or absent indicate that B. tectorum entered and has maintained a presence in relatively intact communities as well (Daubenmire 1942, Klemmedson and Smith 1964, Tisdale et al. 1965, Harris 1967). Mack (1981) speculated that B. tectorum now "occupies the niches" of the indigenous colonizing annual grasses Festuca microstachys, F. octoflora and Bromus carinatus, which it has apparently displaced, an argument consistent with the observations of B. tectorum in undisturbed shrub-steppe communities. Features of the biology of B. tectorum obviously predisposed the species for its success on this continent; thus, this species can accommodate, and therefore should reflect, the shrub-induced microenvironmental heterogeneity typical of the sagebrush-steppe ecosystem.

Third, an extensive literature exists (for a recent review, see Upadhyaya et al. 1986) describing aspects of both the biology of the species, including germination (e.g., Steinbauer and Grigsby 1957, Palmblad 1969, Evans and Young 1970, Young et al. 1971, Evans and Young 1972, Hull and Hansen 1974, Young and Evans 1975, Thill et al. 1979, Milby and Johnson 1987, Buman and Abernethy 1988) and growth and development (e.g., Hulbert 1955, Klemmedson and Smith 1964, Thill et al.
1984) and its ecology, including energy and nutrient balance (Hinds 1975), population dynamics (e.g., Young et al. 1969, Mack and Pyke 1983, 1984, Young and Evans 1985, Pyke 1986), interactions with other plant species (e.g., Holmgren 1956, Harris 1967, Harris and Wilson 1970, Bookman and Mack 1982, 1983, Bookman 1983, Buman et al. 1988), interactions with consumers (e.g., La Tourrette et al. 1971, Kelrick et al. 1986, Pyke 1986) and community roles (e.g., Piemeisel 1951, Allen and Knight 1984, Evans and Young 1985, Hassan and West 1986). Finally, seeds of *B. tectorum* are relatively large and readily harvestable, and seedlings are easily recognized, enabling development of the research protocols to be described later.

This study investigated factors determining the dispersion of *Bromus tectorum* with respect to shrubs in a sagebrush-steppe ecosystem, examining several of the potential causal mechanisms listed in Table 1.1. Efforts were concentrated on the seed portion of the species' life cycle. This emphasis is appropriate, on at least two counts. Unpredictability of the shrub-steppe environment causes great year-to-year (and even cohort-to-cohort within a season) variation in success of the ephemeral vegetative/reproductive portion of this species' life cycle (Mack and Pyke 1983); this elevates the significance of the persistent seed portion of the life cycle in controlling population dynamics (e.g., Young and Evans 1985). Also, current attributes of a population's structure (e.g., its local dispersion) and their future expression in the plant community are linked via the processes impinging on its requirements for regeneration (Bullock 1976, Grubb 1977). For an annual species to continue occurring at a particular site, these requirements are ineluctable. To understand the ecology of annual plants, a quanti-
tative, demographic approach to the seed portion of the life cycle is needed (Cavers 1983).

Research objectives and hypotheses

Consideration of the determinants of *B. tectorum* dispersion yields several potential (not mutually exclusive) processes acting at various times during the annual's life cycle. Initially, the seed dispersion achieved by dispersal and seed survival could largely determine plant dispersion, if germination, establishment and survivorship of vegetative individuals were all relatively uniform for all microenvironments. Alternatively, even perfectly regular seed depositional patterns could be substantially modified by non-uniform success in germination and establishment. Finally, regardless of the pattern manifested by emerging seedlings, differences in microenvironment-specific survivorship of vegetative plants could further edit the dispersion and affect the pattern of future seed inputs. This study attempted to distinguish among these three processes and/or to assess their relative importance, and it proceeded along three analogous fronts: 1) a primarily mensurative documentation of the spatial pattern of seed deposition and composition of the soil seed bank; 2) a manipulative experiment to observe the effects of shrub presence vs. absence, U vs. I microenvironments and granivory/herbivory on plant success; and 3) manipulative experiments to observe the fates of seeds (in terms of producing plants) on surfaces characteristic of U and I microenvironments. Concepts and hypotheses addressed in these three efforts are presented in the following corresponding sections.
Spatial pattern of seeds

Most seeds are thought to come to rest at short distances from the parent plant (e.g., Salisbury 1942, Janzen 1970, Levin and Kerster 1974, Werner 1975, Harper 1977, Watkinson 1978b, Ellner and Shmida 1981, Rabinowitz and Rapp 1981, Fenner 1985, Morse and Schmitt 1985). In fact, such descriptions apply strictly to seed movement between the parent plant and ground and thus de-emphasize potentially significant, subsequent transport ("interphase [c]" of Sagar and Mortimer 1976, "Phase II dispersal" of Watkinson 1978b). In many aridlands, where obstructing vegetation is relatively sparse, winds are often strong and surface run-off can accompany sudden downpours, surface-lying seeds are especially susceptible to abiotically mediated redistribution (Reichman 1984, Price and Reichman 1987). To establish the role of seed dispersion in determining plant dispersion in an aridland ecosystem, an environment-wide seed depositional pattern (i.e., the result of dynamics affecting dehisced seeds) must be characterized.

Surface-lying seeds which neither produce plants nor succumb to depredation may become a part of the soil seed bank (Cook 1980, Roberts 1981). Here, seeds may lie dormant, "dispersing in time" until favorable conditions stimulate germination, or until mortality occurs. Species composition and respective densities of seeds in the soil reflect the history of a microsite in two senses related to microenvironmentally differentiated dispersion. The seed bank may exhibit small-scale heterogeneity: 1) due to a consistent pattern of abiotically or biotically mediated (e.g., caching) deposition and subsequent incorporation into the soil in excess of germination or other losses; and 2) due to the locally restricted accumulation and burial of seeds (again, in excess of
losses) at sites persistently favorable for germination, establishment and maturation to reproduction of pertinent species, resulting from short seed dispersal distances from parents in those sites (see references above). Even in communities with a relatively homogeneous vegetation and continuous cover, highly non-random dispersions of soil seeds at small spatial scales have been observed (e.g., Thompson 1986).

To relate seed depositional patterns to plant dispersion, knowledge of seed densities in and on the soil must be detailed by plant species, since species composition of the seed bank may deviate substantially from (e.g., Major and Pyott 1966, Thompson and Grime 1979, Rabinowitz 1981, Thompson 1986, Osman et al. 1987) or resemble (e.g., Schenkeveld and Verkaar 1984, Hassan and West 1986, Henderson et al. 1988) extant vegetation. The degree of similarity between species compositions of the seed bank and the plant community at a site reflects the relative abilities of each species' seeds, once deposited, to persist in the soil, as well as the extent of plant species turnover through time resulting from disturbance and/or successional change there. Since the pool of species involved in aridland succession is relatively limited (MacMahon and Wagner 1985, Webb et al. 1987), substantial species correspondence between seed bank and vegetative individuals at a site is to be expected in these communities (viz., Henderson et al. 1988).

Whatever their species composition, it is clear that seed banks of several North American aridlands are spatially heterogeneous (Young and Evans 1975, Nelson and Chew 1977, Parmenter and MacMahon 1983, Reichman 1984, Hassan and West 1986, Osman et al. 1987, Price and Reichman 1987, Henderson et al. 1988), as might be expected of "open habitats" (Thompson 1986). For annuals with relatively short-lived seeds, the horizon
tal dispersion of seeds in the soil at a single point in time may be a strong indicator of subsequent near-term plant dispersion. *B. tectorum* may exhibit such a transient soil seed reserve (Mack and Pyke 1983, but cf. Young and Evans 1985).

The following null hypotheses concerning the spatial pattern of seeds on and in the soil were addressed.

1) Surface seed densities in U microenvironments do not differ from those in I microenvironments.

2) Surface seed densities are not correlated with contemporaneous depth of microtopographic relief.

3) Surface seed densities around individual shrubs are not correlated with prevailing wind direction.

4) Surface seed densities of annual species' seeds are not correlated with contemporaneous densities of mature annual plants.

5) The presence of litter has no effect on numbers of seeds deposited in U or I microenvironments.

6) Soil seed densities in U microenvironments do not differ from those in I microenvironments.

7) Soil seed densities of annual species' seeds are not correlated with contemporaneous densities of mature annual plants.

**Success of plants in U and I microenvironments**

Various factors, potentially conflicting and of unequal magnitudes in space and time, might effect differential success of annual plants in U versus I microenvironments (Table 1.1). U and I microenvironments are the extremes of a complex-gradient (Shmida and Whittaker 1981) along which many attributes of the environment change simultaneously. Among
those which are direct effects of shrubs (Table 1.1), some can be attributed to the presence of a living shrub (e.g., soilwater extraction and the influence on near- and undershrub microclimate), but others are consequences of shrub presence in the past, and may persist with or without continued presence of a living shrub (e.g., enhanced nutrient and organic matter content, and greater water-holding capacity of U soils) (see references in Table 1.1). Distinguishing between the effects of these two classes of factors is amenable to experimentation by removing the above-ground portion of live shrubs and comparing the success of annuals in pre-removal U and I microenvironments with that of U and I annuals associated with intact shrubs.

In the sagebrush-steppe ecosystem, all of the shrub effects mentioned above have been documented for the dominant shrub, big sagebrush, *Artemisia tridentata*. Several authors have described the water extracting capability of *A. tridentata* and implications for deleterious effects on ground-story species (Robertson 1947, Campbell and Harris 1977, Sturges 1977; but cf. Richards and Caldwell 1987). By contrast, Young and Evans (1975) wrote of the extremely favorable conditions under, but not between, *A. tridentata* canopies for germination and establishment of *B. tectorum*. Microenvironmental evolution leading to the development of "islands of fertility" around individual *A. tridentata* shrubs, with assumed positive effects for subsidiary herbaceous species, has been described for sagebrush-dominated communities growing on soils derived from several differing substrate types (e.g., Hazlett and Hoffman 1975, Charley and West 1975, Mack 1977, Hassan and West 1986).

Among indirect effects (Table 1.1), the activity of rodents as granivores and herbivores is likely to be of consequence, since these
may be the most abundant vertebrate consumers in the sagebrush-steppe ecosystem (McAdoo and Klebenow 1979, West 1983a). Both seeds and plants of several annual species, including *B. tectorum*, contribute to the diets of common sagebrush-steppe rodents (Johnson 1961, La Tourrette et al. 1971, Kritzman 1974, Pyke 1986), but the spatial editing of annual species' seed/plant dispersions resulting from such consumption seems to be unexplored in the sagebrush-steppe ecosystem (but see Price and Jenkins 1986 for a review of the effects of granivorous rodents on seed fates; Bartholomew 1970, Halligan 1973, Nelson and Chew 1977, Reichman 1979, Jaksic and Fuentes 1980, Hay and Fuller 1981, for examples from other arid ecosystems; and Casper 1987 for an investigation of a perennial herb in a sagebrush-juniper community). If sagebrush-steppe rodents cache seeds (La Tourrette et al. 1971, Kritzman 1974, Broome 1988) preferentially in either U or I microenvironments, then germination from abandoned caches (e.g., Reichman 1979) could contribute to non-random plant dispersion with respect to shrubs. Shallow burial from caching (to \( \approx 2 \text{ cm} \)) would likely enhance germination and establishment with respect to that of surface-lying seeds, though emergence from greater depths would likely be diminished (Hull 1964, personal observation).

Harvester ants (*Pogonomyrmex* spp.) may also be influential consumers, or simply agents of mortality, affecting annuals' seeds (Willard and Crowell 1965, Whitford 1978) and plants (via disk-clearing, Willard and Crowell 1965, Clark and Comanor 1975). Yet these ants may indirectly stimulate local proliferations of some annual species, which germinate in colony refuse piles (Rissing 1986, personal observation) or on abandoned mounds (Coffin and Lauenroth 1990). Thus, harvester ants certainly play a role in molding the spatial structure of sagebrush-
steppe annuals' populations, but whether and how their foraging is sensitive to U/I heterogeneity is only recently being explored (Fewell 1988, Crist and MacMahon 1991).

The following null hypotheses concerning the establishment and success of plants of an annual species (B. tectorum) with respect to the U/I microenvironmental gradient were addressed.

1) There is no difference in either numbers established or success of annual plants recruited from seeds introduced into U vs. I microenvironments.

2) There is no difference in either numbers established or success of annual plants recruited from seeds introduced around shrubs whose canopies were later removed vs. around shrubs with intact canopies.

3) Rodent foraging and consumption have no effect on the numbers of annual seeds available for germination and establishment, nor on the success of annual plants.

4) There is no relationship between the intensity of rodent foraging and consumption of annual seeds and plants, and U/I microenvironmental patch structure.

**Seed/microsite interactions**

The transition from seed to plant occurs in a "safe site" (Harper et al. 1961), a microsite at the scale of a single seed, where conditions for germination, emergence and establishment are successively satisfied (Harper et al. 1965, Sheldon 1974) and where hazards (e.g., competitors, predators, pathogens or toxic agents) are absent or inoperative (Harper 1977). While the subtle but significant differences among species in their germination requirements, coupled with the substantial
spatial heterogeneity of habitats when viewed at the scale of a single seed, have been invoked to help explain species composition and coexistence in plant communities (e.g., Grubb 1977, Blom 1978, Silvertown 1981, Grubb 1986, Peart and Clifford 1987), much less attention has been directed at investigating how the spatial distribution of safe sites might determine the dispersion of plants (but see Pemadasa and Lovell 1974, Platt 1975, Young and Evans 1975, Platt 1976, Watkinson 1978a, Friedman and Stein 1980, Thompson 1980, Augspurger 1984, Clark and Clark 1984, Mittelbach and Gross 1984, Crawley and Nachapong 1985, Goldberg 1985, Hobbs and Mooney 1985, Webb and Willson 1985, Grubb 1986, Fowler 1988 and Schupp 1988a,b for studies bearing on this problem). One reason for this relative neglect is that discerning a microsite capable of "nurturing" a seed to planthood may seem an intractable problem. Fenner (1985, p. 87) reasoned that "a site is only safe in retrospect," implying that recognizing safe sites before they are indicated subsequently by plant occupancy is, at worst, a methodological paradox. However, another attitude is promoted by the work of Peart (1979, 1981, 1984), in which a highly detailed examination of seed/microsite interactions for several grass species culminated in an understanding of the local distribution of these species on the basis of availability of suitable microsites for seedling recruitment (Peart and Clifford 1987). Even having acknowledged that it is conceptually feasible for an observer to recognize a safe site, still, an intimate knowledge of seed "behavior" under natural conditions, at a fine scale of resolution, is required. Acquisition of such knowledge is difficult, yet it is necessary to make sense of plant population structure (Hickman 1979, Hutchings 1986), population dynamics (Primack and Levy 1988) and the ecologi-
Past research on the recruitment of B. tectorum populations in sagebrush-steppe communities has associated presence of litter with physical microsite conditions favorable for germination and establishment (Evans and Young 1970, Evans and Young 1972, Young and Evans 1975). This simple scenario seems to allow straightforward prediction of B. tectorum dispersion, but it obscures several interrelated mechanisms that could be contributing determinants. First, since the distribution of litter in arid shrublands is typically strongly concentrated around shrubs (Muller 1953, Daubenmire 1970, Garcia-Moya and McKell 1970, Young and Evans 1975, West 1979), it may be shrub canopy effects (e.g., moderation of U surface temperature fluctuations via shading and reduction of nocturnal long-wave heat loss to a cold sky) that are most important in creating conditions conducive to germination and establishment, rather than litter per se. Second, seeds may accumulate around shrubs along with other litter components, and thus, germination and establishment may appear concentrated in littered areas, despite an equivalent abundance of unexploited potential safe sites in unlittered areas. Third, the hazards experienced by seeds may differ in littered versus unlittered microenvironments, which could in turn influence litter-associated recruitment. Given that littered surfaces are associated with shrubs, making most U microenvironments littered and most I microenvironments unlittered, it remains to disentangle effects of a particular microenvironment on germination and establishment from those of the surface type (littered or unlittered) predictably encountered in that microenvironment.
The following null hypotheses concerning seed/microsite interactions -- including seed mobility, germination and plant establishment -- of an annual species (B. tectorum) were addressed.

1) There is no difference in mobility between seeds in U and those in I microenvironments.

2) Seed mobility is unrelated to surface texture (i.e., littered or unlittered), regardless of microenvironment.

3) There is no difference in germination and establishment between U and I microenvironments.

4) Germination and establishment are unrelated to surface texture, regardless of microenvironment.

5) There is no interaction between surface texture and microenvironment affecting the success of germination and establishment.
Table 1.1. A compilation of proposed mechanisms causing positive and negative associations between the dominant life form and ground-story species in aridland plant communities. Direct effects are those which involve only the physiognomic dominant and ground-story species of the association, while indirect effects involve other species as well. Shrubs are the dominant life forms of the interactions except as noted.

POSITIVE ASSOCIATIONS

Direct effects


2) Shrubs act as windbreaks, and thereby as local sites concentrating the deposition of windblown soil and litter, resulting in "improved local soil conditions" (Muller 1953, Daubenmire 1970, Garcia-Moya and McKell 1970, Young and Evans 1975, West 1979).

Table 1.1. (continued)

4) Shrubs ameliorate the undershrub microclimate: by daytime shading
(Shreve 1931 [tree], Garcia-Moya and McKell 1970, Lowe and Hinds
1971 [tree], Halvorson and Patten 1975); by reducing nighttime
long-wave heat loss (Lowe and Hinds 1971 [tree]); by breaking
desiccating winds (Soriano and Sala 1986); by moderating undercan-
opy temperature fluctuations such that undershrub conditions are
more optimal for seed germination (Shreve 1931 [tree]) or are less
likely to induce secondary dormancy in undershrub seeds (Young and
Evans 1975).

5) The localized input of organic material beneath shrub canopies im-
proves the water-holding capacity of undershrub soils (Muller and

6) Shrubs induce local soil-chemical changes resulting in shrub-centered
"islands of fertility" (Garcia-Moya and McKell 1970, Charley and
West 1975, Charley and West 1977, Mack 1977, Nelson and Chew 1977,
Tiedemann and Klemmedson 1986 [tree]).

7) Shrubs catch and funnel rainfall (Halligan 1973).

8) Shrubs deliver water from deep in the soil column to nearer-surface
layers (via hydraulic lift), where ground-story plants are rooted
(Richards and Caldwell 1987, Caldwell and Richards 1989).

Indirect effects

1) Shrubs shelter ground-story plants and/or their seeds from herbivores
and/or granivores (Keeley and Johnson 1977, Nelson and Chew 1977,
Jaksic and Fuentes 1980).
Table 1.1. (continued)

2) Shrubs ameliorate the undershrub microenvironment, thereby providing abiotic conditions conducive to maintaining microbial activity, leading to increased mineralization of organic material (Charley and West 1977).

3) Both saprophytic and mutualistic (mycorrhizal) fungi are more abundant in undershrub microenvironments, conceivably enhancing both availability of and access to nutrient products of decomposition (Allen and MacMahon 1985).

4) Undershrub microenvironments may be preferred for seed caching by rodents, which may result in recruitment of plants from abandoned caches (La Tourrette et al. 1971, Reichman 1979).

NEGATIVE ASSOCIATIONS

Direct effects


2) Shrubs contribute to the production of water-repellent soils beneath their canopies (Adams et al. 1970).

3) Shrubs intercept rainfall and shed it and/or facilitate its evaporation back into the atmosphere, decreasing undershrub moisture reception (Halligan 1973, Tromble 1988).

4) The density of shrub canopies prevents germination and establishment from occurring beneath them (Muller 1953, Halvorson and Patten 1975).
Table 1.1. (continued)


6) Nutrient uptake by shrubs limits resources available for growth of ground-story herbs (Swank and Oechel 1991).

Indirect effects


3) Shrubs provide cover for mammalian granivores and herbivores, protecting these consumers from their predators, thereby leading to increased rates of primary consumption in undershrub microenvironments (Kotler 1984).

4) By having provided favorable sites for establishment of shrub-associated perennial plants in the past, current recruitment in undershrub and near-canopy microenvironments is limited by insufficient water (Soriano and Sala 1986).
STUDY SITE, CONVENTIONS AND PREMISES

Study site

Research was conducted on an unmined portion of the Kemmerer Coal Mine, Pittsburgh & Midway Coal Mining Co., approximately 8 km SW of Kemmerer, Lincoln County, Wyoming (41°43'0" N, 110°37'0" W, elevation ~2100 m). Mean annual precipitation is ~22.6 cm, with snow the predominant input, though mean monthly precipitation peaks in May and June (~2.5 cm/mo each). Mean monthly temperatures range between -8°C (January) and 17°C (July). (All estimates summarize 40 years' data; see Parmenter and MacMahon 1983 for a climate diagram for Kemmerer, Wyoming.) Study plots were established in a shallow E-W-trending wash, extending perpendicularly from a ridge of calcareous silt- and sandstone. The soil is classified as a coarse, loamy mixed calcareous frigid typic Ustifluvent (D. Lewis, U. S. Soil Conservation Service, in Parmenter and MacMahon 1983).

The study site falls within the region classified by West (1983a) as Western Intermountain Sagebrush Steppe. Big sagebrush (Artemisia tridentata) dominated the landscape, although diminutive rabbitbrush (Chrysothamnus viscidiflorus) individuals were equally numerous (Table 2.1). Several other shrub or woody species were present, though relatively rare. These included shadscale species (Atriplex confertifolia, A. gardneri), black sagebrush (Artemisia arbuscula), spineless horsebrush (Tetradymia canescens), winterfat (Ceratoides lanata), snowberry (Symphoricarpos oreophilus), bitterbrush (Purshia tridentata), prickly
gilia (Leptodactylon pungens) and a buckwheat (Eriogonum microthecum).

The majority of conspicuous ground-story herbaceous species were perennial grasses including bluegrasses (Poa spp.), Indian ricegrass (Oryzopsis [Stipa] hymenoides), needle-and-thread (Stipa comata), squirrel-tail (Sitanion hystrix), foxtail barley (Hordeum jubatum), and western wheatgrass (Pascopyrum smithii). Cheatgrass (Bromus tectorum), an annual grass, was very common. A great variety of forb species were present; whether perennial or annual, these were generally inconspicuous, rare or both. Combined cover of shrubs (Table 2.1) and ground-story vegetation was substantially less than 100% for the site as a whole.

Descriptions of other aspects of the site can be found in Parmenter and MacMahon (1983), Parmenter et al. (1985), Kelrick et al. (1986) and Broome (1988).

Conventions

For the purposes of this research, I regarded the sagebrush-steppe ecosystem represented at the study site as composed of two ecologically distinct microenvironments -- undershrub and interspace. Since Artemisia tridentata was the dominant shrub at the site, all sampling and experimentation focused on individuals of this species as sampling units, to which "undershrub" and "interspace" applied. Field protocols required the identification of U and I locations; therefore, operational definitions of U and I were adopted to lend consistency to the research (see Fig. 2.1). These definitions provided the flexibility required to accommodate the highly irregular canopy configurations of Artemisia tridentata individuals, while assigning ecologically meaningful U and I
locations. Care was exercised in applying these conventions to avoid the possibility that an I location with respect to the sampled shrub would be too near the canopy of an adjacent shrub.

Six 20- X 30-m plots were established in 1980, and one 30- X 30-m plot in 1986. These did not correspond to particular treatments or replicates in any experimental or sampling design. Rather, they served the dual purposes of providing coordinate systems for locating randomly selected sample shrubs within them and of minimizing investigator-related disturbances (e.g., the considerable soil surface disruption from trampling) by delimiting plot boundaries which were crossed as infrequently as possible. Site vegetation appeared relatively homogeneous, and no attempt was made to assess differences among the plots.

Premises

Microenvironment-sensitive plant dispersion

Research described herein was prompted by the field observation that densities of Bromus tectorum individuals appeared greater in U than in I microenvironments at the study site. This impression -- a premise upon which the research was developed -- was quantified in both 1981 and 1986.

In early June of 1981, just prior to the full maturation of caryopses, numbers of B. tectorum individuals in 25 pairs (U and I) of 1-dm² quadrats were counted. The study site was crossed repeatedly with transects, each at a 30° angle to the preceding one. At each randomly selected sample point along a transect, the nearest Artemisia tridentata individual became the sampled shrub. All counts were collected in the NE quadrant extending from the base of the sampled shrub. Height and
cover components were measured for the sampled shrub and its nearest neighbor in the NE quadrant; the distance between the two was also recorded. The U quadrat was placed with its E edge aligned N-S and its SE corner at the U location. The I quadrat was centered on the I location.

In 1986, this effort was expanded and refined. One hundred paired 1-dm² quadrats were used in a June count, 25 in each of the four cardinal directions (rotated systematically with each successive shrub) with respect to the sampled shrubs. Sampled shrubs were constrained to be within 1 m of the transect point; if no shrub was encountered, sampling continued at the next randomly determined transect point. If a selected shrub did not present appropriate U and I microenvironments (e.g., overlapping canopies with adjacent shrub individuals in the cardinal direction of interest), it was not sampled, and sampling proceeded at the next transect point. (This eliminated only 22 of 122 transect points [≈18%].) Both U and I locations served as centers of quadrats. Corners of the quadrats were marked with toothpicks to facilitate their relocation; the following mid-November, densities of fall-germinated seedlings were counted for the first 15 pairs of quadrats still unobscured by snow (no N-facing quadrats were accessible). Measurements of sampled shrubs and nearest neighbors were collected as in 1981.

Immediately subsequent to the November, 1986 census, soil samples (cylindrical, 1 dm² in area, to a depth of 2 cm) centered on the U or I location (the quadrat center) were collected to ascertain the numbers of germinable seeds present. For 12 shrubs (i.e., 12 pairs of U and I soil samples), 150 cm³ subsamples of this material were spread thinly (over ≈500 cm²) on potting medium and maintained under greenhouse conditions
until germination ceased (18 days total; terminated after five consecutive days with no further germination and a careful, unsuccessful visual search for more potentially germinable seeds).

Results of these mensurations supported the premise that the dispersion of *B. tectorum* reflected differences in U versus I microenvironments (Table 2.2); U densities were consistently significantly greater when paired U and I quadrat densities at each sampled shrub were compared with randomized t-tests (Bradley 1968). Although an ANOVA (analysis of variance) of June, 1986 data revealed a significant interaction between microenvironment and compass direction with respect to the sampled shrub \( (F = 4.07; \text{df} = 3.96; P = 0.009) \), when these data, with U and I densities paired by shrub and grouped by direction, were subjected to randomized t-tests, all but E-facing U and I quadrat pairs were significantly different (U densities > I densities), and these just failed significance \( (P = 0.06) \). The temporal stability of this dispersion pattern at the study site, at least for the duration of my research effort (six yr), is indicated by the consistency of the results in Table 2.2, as well as strong positive correlations among densities of plants and germinable seeds from the "permanent" U and I quadrats sampled in June and November of 1986 (Table 2.3).

The potential influences of sampled shrub canopy cover, distance of quadrats from the canopy edge and proximity of nearest neighbor on densities of *B. tectorum* were evaluated with parametric correlations (using June densities from both 1981 and 1986). No significant correlations were obtained (Table 2.4), indicating that differences among canopy configurations and neighborhoods of individual shrubs are apparently less important determinants of associated U and I densities of *B.*
tectorum than are other physical and biotic factors distinguishing the two microenvironments.

Microenvironment-sensitive soil attributes

Samples of mineral soil from U and I microenvironments (cylindrical, 200 cm$^3$ in volume, to a depth of 2 cm) were analyzed by the Soil Testing Laboratory of Utah State University for: 1) % water (dry weight basis) at 1/3 atmosphere, using a pressure plate apparatus (Richards 1948); 2) % organic matter (dry weight basis), using a colorimetric indicator of amount of organic C present (Sims and Haby 1971); 3) % total N (dry weight basis), using the standard Kjeldahl technique; and 4) %'s sand, silt and clay (i.e., a standard textural analysis). These samples were collected from paired U and I locations in all four cardinal directions, at each of eight randomly selected shrubs (64 samples total), between September 24 and November 5, 1981. Seeds in the soil seed bank were removed from the samples (see Chapter III) prior to their analysis for soil attributes.

Results of an ANOVA of soil attribute data (% N, % organic matter and % water at 1/3 atmosphere) are presented in Table 2.5. There were no significant differences among direction means for any of the three dependent variables (Tables 2.5 and 2.6). Significant differences were found between U and I means for % N and % organic material (U means greater), but not for % water. Such elevated levels of nutrients and organic matter in near- and undershrub microenvironments accord with the "island of fertility" concept documented by numerous studies in aridland plant communities (citations in Table 1.1). Although the non-significant result for water-holding capacity was counterintuitive (on the
basis of the significant difference in % organic matter), it was corrob­
orated by a non-significant paired t-value of -1.008 (n = 32, \( P = 0.165 \))
in a randomized t-test of U and I % water variates paired by direction
within each shrub. Apparently, the uniformly coarse texture of the soil
at the study site (59 of 64 samples classified as sand or loamy sand;
mean ± SE % sand content of all samples was 85.44 ± 0.51) may determine
water-holding capacity of soil at the study site to a greater degree
than even marked differences in the distribution of organic material can
influence it. Clearly, there were measurable differences between U and
I soil attributes at the study site, even based on the crude assessments
described; the relevance of these differences to the dispersion of B. tectorum will be discussed in the appropriate subsequent chapters.
Table 2.1. Estimates of density and percent cover of shrub species at the study site, based on point-centered quarter data (Mueller-Dombois and Ellenberg 1974)\(^a\).

<table>
<thead>
<tr>
<th>Species</th>
<th>Density(^b) (No./ha)</th>
<th>% cover(^c)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Artemisia tridentata</em></td>
<td>11086</td>
<td>21.23</td>
</tr>
<tr>
<td><em>Chrysothamnus viscidiflorus</em></td>
<td>10666</td>
<td>3.61</td>
</tr>
<tr>
<td><em>Tetradymia canescens</em></td>
<td>1176</td>
<td>0.59</td>
</tr>
<tr>
<td><em>Atriplex gardneri</em></td>
<td>1008</td>
<td>TR</td>
</tr>
<tr>
<td><em>Ceratoides lanata</em></td>
<td>840</td>
<td>TR</td>
</tr>
<tr>
<td><em>Eriogonum microthecum</em></td>
<td>R</td>
<td>TR</td>
</tr>
<tr>
<td><em>Artemisia arbuscula</em></td>
<td>R</td>
<td>TR</td>
</tr>
<tr>
<td><em>Leptodactylon pungens</em></td>
<td>R</td>
<td>TR</td>
</tr>
<tr>
<td><em>Symphoricarpos oreophilus</em></td>
<td>R</td>
<td>TR</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>25195</strong></td>
<td><strong>26.00</strong></td>
</tr>
</tbody>
</table>

\(^a\)n = 75 points sampled, or 300 shrubs.

\(^b\)R = rare; i.e., ≤ 2 individuals among 300 shrubs measured.

\(^c\)TR = trace; i.e., ≤ 0.50 %. 
Table 2.2. Estimates of mean densities of *Bromus tectorum* in paired 1-dm$^2$ U and I quadrats (one pair per sampled shrub), and results of randomized t-tests comparing U and I densities.

<table>
<thead>
<tr>
<th>Year</th>
<th>Undershrub Mean ± SE</th>
<th>Interspace Mean ± SE</th>
<th>Per shrub difference, U minus I Mean ± SE</th>
<th>Paired t-value</th>
<th>One-tailed significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1981$^a$</td>
<td>14.48 ± 4.15</td>
<td>7.68 ± 1.53</td>
<td>6.80 ± 3.41</td>
<td>1.994</td>
<td>P = 0.012</td>
</tr>
<tr>
<td>1986$^b$</td>
<td>6.87 ± 0.69</td>
<td>3.27 ± 0.43</td>
<td>3.60 ± 0.71</td>
<td>5.051</td>
<td>P &lt; 0.0001</td>
</tr>
<tr>
<td>1986$^c$</td>
<td>7.53 ± 1.55</td>
<td>3.07 ± 1.21</td>
<td>4.47 ± 1.42</td>
<td>3.144</td>
<td>P = 0.002</td>
</tr>
</tbody>
</table>

*a* Sampled in June, $n = 25$ pairs.

*b* Sampled in June, $n = 100$ pairs.

*c* Sampled in November, $n = 15$ pairs.
Table 2.3. Parametric correlation coefficients\(^a\) (probability values below in parentheses) among numbers of plants and germinable seeds of *Bromus tectorum* from permanent, paired 1-dm\(^2\) U and I quadrats, 1986. Values above the diagonal are for U quadrats, below the diagonal for I quadrats.

<table>
<thead>
<tr>
<th></th>
<th>June density</th>
<th>November density</th>
<th>No. germinable seeds(^b)</th>
<th>Total no. individuals(^c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>June density</td>
<td>0.564</td>
<td>0.866 (&lt; 0.001)</td>
<td>0.619 (0.032)</td>
<td>0.627 (0.029)</td>
</tr>
<tr>
<td>November density</td>
<td>0.811 (0.001)</td>
<td>0.916 (&lt; 0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. germinable seeds</td>
<td>0.799 (0.002)</td>
<td>0.977 (&lt; 0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total no. individuals</td>
<td>0.880 (0.001)</td>
<td>0.920 (&lt; 0.001)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)\(df = 10\).

\(^b\)Per 150 cm\(^3\) soil and/or litter, sampled to a depth of 2 cm.

\(^c\)Plants plus germinable seeds in November.
Table 2.4. Parametric correlation coefficients (probability values below in parentheses) between quadrat densities of *Bromus tectorum* and selected attributes of sampled shrubs, from June, 1981 and 1986.

<table>
<thead>
<tr>
<th>Variables used</th>
<th>1981 (^a)</th>
<th>1986 (^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Undershrub density and shrub canopy area ((cm^2))</td>
<td>-0.163</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>(0.437)</td>
<td>(0.907)</td>
</tr>
<tr>
<td>Undershrub density and distance to canopy edge ((cm))</td>
<td>-0.011</td>
<td>0.053</td>
</tr>
<tr>
<td></td>
<td>(0.958)</td>
<td>(0.603)</td>
</tr>
<tr>
<td>Interspace density and distance to canopy edge ((cm))</td>
<td>-0.067</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>(0.750)</td>
<td>(0.861)</td>
</tr>
<tr>
<td>Interspace density and distance to nearest neighbor ((cm))</td>
<td>-0.140</td>
<td>0.031</td>
</tr>
<tr>
<td></td>
<td>(0.524)</td>
<td>(0.761)</td>
</tr>
</tbody>
</table>

\(^a\)All df = 23, except for correlation with nearest neighbor distance, for which df = 21.

\(^b\)All df = 98, except for correlation with nearest neighbor distance, for which df = 95.
Table 2.5. Results of an analysis of variance of three attributes of undershrub and interspace soil samples.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom(^a)</th>
<th>Attribute(^b)</th>
<th>F-value</th>
<th>Significance(^c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Direction</td>
<td>3,21</td>
<td>% N</td>
<td>2.03</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% OM</td>
<td>1.39</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% water</td>
<td>2.08</td>
<td>NS</td>
</tr>
<tr>
<td>Microenvironment</td>
<td>1,7</td>
<td>% N</td>
<td>17.23</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% OM</td>
<td>20.43</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% water</td>
<td>0.67</td>
<td>NS</td>
</tr>
<tr>
<td>Direction X Micro-environment</td>
<td>3,21</td>
<td>% N</td>
<td>2.75</td>
<td>0.10&gt;P&gt;0.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% OM</td>
<td>1.03</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>% water</td>
<td>1.37</td>
<td>NS</td>
</tr>
</tbody>
</table>

\(^a\)Degrees of freedom listed are: those for the source of variation, those for the appropriate error against which it was tested.

\(^b\)% N = percent total nitrogen; % OM = percent organic matter; % water = percent water at 1/3 atmosphere (all dry weight basis).

\(^c\)Statistical significance. NS = not significant; i.e., P > 0.05.
Table 2.6. Means ± SE of soil attributes from undershrub and interspace soil samples, presented according to the two main factors in the sampling design.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Factor</th>
<th>Level&lt;sup&gt;a&lt;/sup&gt;</th>
<th>% N</th>
<th>% organic matter</th>
<th>% water at 1/3 atmosphere</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Direction</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>N</td>
<td>0.083 ± 0.0079</td>
<td>2.15 ± 0.28</td>
<td>6.76 ± 0.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>W</td>
<td>0.063 ± 0.0049</td>
<td>1.60 ± 0.12</td>
<td>6.08 ± 0.26</td>
</tr>
<tr>
<td></td>
<td></td>
<td>S</td>
<td>0.074 ± 0.0054</td>
<td>2.01 ± 0.32</td>
<td>7.01 ± 0.31</td>
</tr>
<tr>
<td></td>
<td></td>
<td>E</td>
<td>0.078 ± 0.0056</td>
<td>2.01 ± 0.17</td>
<td>6.99 ± 0.27</td>
</tr>
<tr>
<td></td>
<td>Micro-environment&lt;sup&gt;b&lt;/sup&gt;</td>
<td>U</td>
<td>0.081 ± 0.0043*</td>
<td>2.16 ± 0.17*</td>
<td>6.54 ± 0.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>I</td>
<td>0.068 ± 0.0042</td>
<td>1.73 ± 0.15</td>
<td>6.88 ± 0.23</td>
</tr>
</tbody>
</table>

<sup>a</sup>For Direction, letters denote the four cardinal directions; for Microenvironment, U = undershrub, I = interspace.

<sup>b</sup>For a particular attribute, means with asterisks are statistically greater, determined by significant F-values in ANOVA.
CONVENTION FOR DEFINITION OF UNDERSHRUB AND INTERSPACE LOCATIONS
CHAPTER III
SEED DYNAMICS IN A PATCHY ENVIRONMENT

Introduction

To understand the dispersion of a plant species' population, the dispersal of its propagules must be acknowledged as "part of the process by which an established and stabilized population maintains itself within the ever-shifting 'islands' that constitute the pattern within established vegetation" (Harper 1977, p. 34). In a sagebrush-steppe ecosystem, where relatively small-scale spatial heterogeneity is great (Wiens 1985), seed movements and depositional patterns may reflect processes affecting them which are microenvironment-specific. Flux rates of seeds across "patch boundaries" defining U and I microenvironments are likely to be asymmetric (Reichman 1984, Wiens et al. 1985), maintaining or even sharpening the distinction between patch types over time. For annuals especially, patch-determined mobility of seeds alone could largely delimit the dispersion of vegetative individuals.

However, the source of newly recruited individuals need not be restricted to contemporary, surface-lying seeds. Many plant species have seeds which persist over long periods of time in the soil (Cook 1980), and, should new vegetative individuals be drawn from this pool, they superimpose on the dispersion of plants recruiting from currently deposited seeds a "memory" of spatial heterogeneity governing past dispersal (Templeton and Levin 1979). The dispersion of annuals, perhaps those of arid, unpredictable environments in particular, are likely to be influenced by periodic contributions of plants from their often
extensive seed banks (Venable and Lawlor 1980).

Here, I describe an effort to document the environment-wide depositional pattern of seeds in a sagebrush-steppe system, and the legacy of past depositional patterns preserved in the soil seed bank. The primary focus of this effort was to elucidate the degree of shrub-imposed spatial heterogeneity on the processes determining how seeds move and where they ultimately reside. Some attention was also devoted to understanding the effects of microtopography and substrate texture on seed mobility. This documentary study was aimed at understanding how the dispersion of seeds related to the dispersion of an annual plant species of interest, *Bromus tectorum*, in this system.

**Methods**

**Surface seed sampling**

Seed traps were installed around 15 randomly selected shrubs on June 24 and 25, 1981, just prior to initial maturation of annuals' seeds. Eight "standard" traps (four U, four I) surrounded each shrub; these were 9-cm (~66 cm² surface area) plastic petri dishes, whose internal surfaces had been coated with soil from the site to provide a roughness similar to that of bare ground in the field. Traps were imbedded such that their lips were flush with the ground surface. No effort was made to restrict access to traps by foraging animals. Standard traps were placed on shrub-centered radii, parallel and perpendicular to the direction of the prevailing wind, in U and I locations (Fig. 3.1). Mean wind direction (hourly means of 30 measurements/h) at 38 cm above ground level (mean shrub height determined by vegetation sampling) between May 15 and 20, 1981 was 15°N of magnetic W; this corroborated,
for the study site, more extensive observations elsewhere on the Kemmer­
er Mine indicating a pronounced and consistent prevailing westerly wind. Therefore, seed traps were oriented on magnetic N-S and E-W axes and are identified here as EU (eastern undershrub), NI (northern interspace) and so forth.

It was suspected that seeds (note that throughout, I use "seed" to indicate the natural diaspore, whether it is botanically a seed or not) moved extensively along the ground once they were shed from parent plants; therefore, they would move into and out of seed traps. This presented a sampling problem, since the research intention -- to de­scribe the environment-wide seed depositional pattern -- necessarily implied that seeds should not cease their movements "unnaturally" due to the traps themselves. To characterize the sampling peculiarities of the standard trap, three additional trap types were installed adjacent to the EI trap at each shrub. These were: 1) a pitfall trap (a buried can covered with a funnel) with the same circumference as the standard trap; 2) a filled trap (a 9-cm petri dish installed as the standard trap was, filled with sifted soil from the field); and 3) a crack trap, which had the same depth and perimeter as, but a surface area (~5.1 cm²) only ~7% of, the standard trap.

In addition to this shrub-centered sampling, some subjectively chosen microsites were also sampled. Two sets of five standard traps each were installed in N-S transects (perpendicular to the prevailing wind direction) crossing the rise bounding the study site wash on the south. Five other standard traps were placed in natural depressions (probably abandoned ground squirrel excavations) of varying depths along this rise.
Shrub traps were sampled five times during the 1981 field season: June 29-30; July 21-22; August 6-7; September 2-3; and September 23-24. Rise transect traps were sampled on the last three dates, rise depression traps on the last two dates. A car vacuum cleaner powered by a small 12V battery was used to empty the traps. Each trap's contents were then transferred to a paper bag. Seeds were removed from samples by hand under a dissecting microscope at 7X. Initially, a library of "type specimens" was assembled and seeds were categorized according to these types. Later, having become familiar with the range of variability in morphology and condition of particular types, they were identified using herbarium specimens, a seed collection from the Kemmerer Mine (Johnson 1984) and the literature (Martin and Barkley 1961).

Potentially countable items (probable seeds) were individually examined, dissected and judged "sound" or not. Only sound seeds -- those with firm, intact tissues showing no sign of discoloration or other degradation -- were included in counts. Alternatives to this method of developing numbers of seeds exist. In fact, the most common method is to subject samples to greenhouse conditions and count and identify plants which arise (e.g., Bigwood and Inouye 1988). However, if germination conditions are not met (an unknown at the outset), inaccurate counts and/or incomplete characterization of species composition result (Gross 1990). Rarely, investigators have utilized 2,3,5-triphenyltetrazolium chloride (Grabe 1970) to test for viable seeds once having separated putative candidates from the sample (e.g., Johnson 1984, Hassan and West 1986). On the basis of extensive experience with both simple dissection and dissection combined with use of tetrazolium, I have found that dissection alone is at least as reliable a method as
is tetrazolium testing, and that, with dissection, interpretation is often less ambiguous. Either of these is much more likely to be more accurate than simply placing samples in supposedly appropriate conditions for germination, although other workers processing samples from comparable environments would disagree (cf. Young and Evans 1975).

In 1986, prompted by insights gained from 1981 data, effects of charging standard traps with known quantities of litter on numbers and kinds of seeds captured was investigated. Pairs of standard traps -- one of each pair initially containing 2 g of seed-free litter from the site -- were installed around 10 randomly selected shrubs (litter-charged = L+, without litter = L-). At each replicate shrub, two pairs of traps were installed, one in each microenvironment (U and I), and, for each microenvironment, in the cardinal direction where the most seeds had been trapped in 1981 (east for U, north for I; Fig. 3.2). At each microenvironment location, the pair of traps was placed with their centers on a N-S axis through the location point and with walls of the traps within 1 cm of the location point. For half the replicate shrubs, the northern trap of each pair initially contained litter; for the remaining shrubs, the southern trap was charged. Traps were installed at seven replicate shrubs on August 19 and at the remaining three on August 22. Traps at shrubs 1-7 were harvested after 9 d on August 28; the remaining traps were recovered after 13 d on September 4.

Soil seed sampling

Soil samples were collected around eight randomly selected shrubs between September 24 and November 5, 1981. Eight samples were removed around each shrub, in the pattern used for installing standard seed
traps (Fig. 3.1). At each sample location, a 1-dm² quadrat centered on the sample location was vacuumed free of litter. A cylindrical steel pipe (100 cm² cross-sectional area) with a sharpened wall was pushed into the mineral soil to a depth of 2 cm, and the enclosed 200 cm³ of soil composed the sample. Air-dried samples were shaken on stacked 2-mm and 0.351-mm sieves. The coarsest fraction (>2 mm; litter and pebbles) was set aside for examination; the finest (<0.351 mm) contained no seeds, and the soil was reserved for analysis (Chapter II). The intermediate fraction was washed in water (while contained in a 0.495-mm sieve, a mesh sufficiently fine to contain seeds of all species encountered in the seed trap sampling described above) to remove the few remaining sand-size particles, then air-dried. Seeds were picked from this material as well as the 2-mm fraction of the original sieving and identified, using procedures described for the seed trap samples.

Analysis

Two sets of type specimens could not be reliably identified beyond the generic level (Eriogonum, Poa), because at least two species of both genera occurred at the study site and morphologies of the congeneric seeds were very similar. For the purposes of statistical analyses, counts for each of these genera were treated as representing a single taxon; for convenience, these are referred to as "species" herein.

From the basic counts of numbers of seeds of all species per trap or soil sample (henceforth, SEEDS) collected as described above, three other variables were also derived: 1) number of species represented per sample (SPP), 2) number of seeds of annuals per sample (ANNUALS) and 3) number of seeds of B. tectorum per sample (BROTEC). All analyses
were conducted on all four dependent variables, though results typically indicated that there were few or no differences among the four.

For 1981 seed trap samples, data from standard traps were examined with one ANOVA, while data from the three experimental traps, with the EI trap serving as the "control," were analyzed separately. These data were severely skewed right (e.g., 262 of 600 samples from standard traps contained two seeds or less, and individual SEEDS values range from 0 to 107) and concurrently, variances increased with means. Both these conditions violate assumptions of ANOVA; conservative F-tests result and subsequent mean comparisons are less than trustworthy. Despite these aberrations, many highly significant F-tests were obtained (Tables 3.1 and 3.2). ANOVA results with original SEEDS data from standard traps were confirmed by virtually identical results from a second ANOVA using data transformed by a power function derived by the iterative Box-Cox procedure (Sokal and Rohlf 1981), which estimates simultaneously the best transformation to normality and homoscedasticity. A moderate approach to mean comparisons was adopted by using Tukey's method (test criterion = studentized range, Q), which displays excellent control of experimentwise error rate (SAS 1987, Day and Quinn 1989), rather than either standard LSD tests (found to be excessively liberal) or the Games and Howell method for heterogeneous variances (excessively conservative). Randomized paired t-tests (see Chapter II) allowed shrub-by-shrub comparisons of SEEDS for experimental traps.

Categorical data analysis (Fienberg 1985) was used to construct loglinear models of treatment effects on observed frequencies of experimental seed traps which did and did not contain seeds when sampled. Once the most parsimonious model was chosen, differences among levels of
treatments still included in the model could be tested (CATMOD procedure of PC SAS; SAS 1987). A log likelihood ratio test was used similarly to test for differences among directions in frequencies of shrub-centered standard traps which did and did not contain seeds; the test allowed identification of subgroups of treatment levels which did not differ among themselves, akin to parametric simultaneous test procedures (Rohlf 1987).

Parametric correlations were used to test for associations between physical attributes of replicate shrubs (canopy diameter and height, and distance between sample locations and canopy edge [DIST]) and the four dependent variables.

For 1986 seed trap samples, differences in mass between initial litter contents of the traps and that upon collection (LITTERWT), as well as variables derived from seed counts, were analyzed. Contingency table analysis allowed comparison of traps which did and did not contain seeds.

When processing soil samples, most *B. tectorum* seeds were found in the >2-cm fraction, which corresponded to compressed, tangled material (predominantly *B. tectorum* stems) at the mineral soil surface, not removed by initial vacuuming of litter. Since very few seeds of other species were found in this fraction, two ANOVA's were conducted with these data -- one with (BROMUS+) and a second without (BROMUS-) counts of *B. tectorum* seeds included. BROMUS- data probably more accurately reflected the real seed content of the mineral soil seed reserve; the presence of most, if not all, of the *B. tectorum* seeds in the "soil samples" can be viewed as an artifact of sampling and processing techniques, since the seeds were observed primarily on, not within, the
soil.

Results

Surface seed sampling, 1981

Seeds of at least 23 species from 10 families were collected from seed traps (Appendix A.1). Classified by life history, nine were annual species and 14 biennials/perennials; by life form, 12 were forbs, seven grasses and four shrubs. Of the 5886 "sound" seeds separated from samples, only one eluded identification to at least genus level. Seeds of annuals contributed ≈78.3% of the total; ≈51.2% were seeds of *B. tectorum*.

The four dependent variables (SEEDS, SPP, BROTEC and ANNUALS) displayed generally similar responses, according to factors included in the ANOVA’s (Tables 3.1 and 3.2). This was corroborated by highly significant positive correlations between SEEDS and the other three variables for data from the standard traps (SPP -- \( r = 0.590 \); BROTEC -- \( r = 0.894 \); ANNUALS -- \( r = 0.973 \); for all \( r \)'s, df = 598, \( P < 0.01 \)). Therefore, in many cases, only results for SEEDS are presented in detail.

**Standard traps, shrub-centered** -- Means for all four variables differed significantly among sample periods (Tables 3.1 and 3.3). Mean values were highest for sample period two (July 21/22), although SEEDS data converted to a per day basis (dividing by number of days elapsed between sampling periods) indicated a monotonic decline throughout the entire season (Fig. 3.3). The latter result is consistent with the large majority of SEEDS contributed by annuals, in that the initial flush of
seed deposition by several annual species whose seeds were most commonly found in seed traps (including \textit{B. tectorum}, \textit{Lappula redowskii}, \textit{Cryptantha watsonii}, \textit{Collinsia parviflora} and \textit{Gilia tweedyi}) just preceded the first sampling period. Neither the mean values of SEEDS per day (Fig. 3.3) nor differences in those values between successive sampling dates were correlated with the number of days between sampling dates.

Means for all variables also differed significantly among directions (Table 3.1), although Tukey’s test did not distinguish among means for BROTEC (Table 3.3). When data for all variables were pooled over microenvironments and sampling dates, mean values of samples from N traps were greatest, followed in decreasing order by those for E, W and S (Table 3.3). This ranking of directions was not consistent in all sampling periods (for SEEDS, Fig. 3.4; also indicated by significant \(F\)-tests for Sampling period X Direction interactions [Table 3.1]). In sampling periods one and four, mean values of SEEDS from E traps were greatest, and in sampling period one, mean SEEDS from S traps exceeded that from N traps as well. In general, N and E traps together accounted for the majority of seeds collected (\(\approx\)65.7% across all sampling periods); this generalization was contradicted only in sampling period one, when \(\approx\)55.7% of seeds were found in S and E traps (Fig. 3.4).

Means for all variables did not differ significantly between microenvironments (Table 3.1), although means for I traps were consistently greater than those for U traps (Table 3.3). This relationship held in all sampling periods for SEEDS (Fig. 3.5, and non-significant \(F\)-test for the Sampling period X Microenvironment interaction [Table 3.1]). When means of SEEDS were pooled over sampling periods and portrayed according to both direction and microenvironment, the relationship
between U and I traps just described no longer applied (Fig. 3.6, and significant F-test for the Direction X Microenvironment interaction [Table 3.1]). For N and S traps, significantly more seeds were found in the I microenvironment (randomized t-tests using paired U and I variates; for N -- $t = -4.27$, for S -- $t = -3.47$; $n = 75$ and $P < 0.001$ for both tests). For E traps, the opposite was true (i.e., more seeds in U traps; $t = 2.15$, $n = 75$, $P = 0.01$), while for W traps, there was no significant difference between SEEDS from U and I microenvironments ($t = -0.41$, $n = 75$, $P = 0.351$). These direction/microenvironment relationships were, at least qualitatively, consistent in all five sampling periods (non-significant F-tests for Direction X Microenvironment X Sampling period interactions [Table 3.1]).

Influences of individual shrubs on seed depositional patterns around them were concealed in the ANOVA because shrubs were replicates. Correlations of shrub attributes and SEEDS data (variously subdivided) indicated that such influences were likely (Table 3.4). SEEDS values for NU, EU and EI traps (pooled across all sampling periods) were significantly positively correlated with shrub height, and, for EI traps, a positive correlation with DIST was also obtained. Individual shrub canopy areas (mean ± SE = 4718 ± 1052 cm$^2$) were not significantly correlated with shrub heights (mean ± SE = 56.7 ± 4.8 cm). However, shrub heights were significantly positively correlated with DIST in the E direction ($r = 0.542$, df = 13, $P < 0.05$), implying that the taller the shrub, the more exaggerated the canopy towards the east.

Loglinear analysis of the frequencies of traps that did or did not contain seeds when sampled, revealed a weak interaction between direction and microenvironment (data pooled over all sampling periods).
Subsequent log likelihood tests of these data split by U and I categories demonstrated: 1) a significant lack of independence for the U data, with EU traps being the most likely to have contained seeds, and 2) non-significance for the I data (Table 3.5). When data were considered by directions, no U vs. I comparison was significant.

Experimental traps.--Significant differences among means were found for both main sources of variation -- Sampling period and Trap type -- for all four dependent variables (Table 3.2). The general pattern over the five sampling periods for any one trap type (Fig. 3.7) was similar to that already described for standard traps (cf. Fig. 3.3). Among the four trap types, in all sampling periods, SEEDS in pitfall traps > SEEDS in standard traps > SEEDS in filled and crack traps (Fig. 3.7). Although this relationship was qualitatively consistent, statistically significant differences among means were limited to SEEDS in pitfall traps exceeding SEEDS in the other three trap types, and this, only in the first four sampling periods (for Trap type X Sampling period interaction means, Tukey's \( MSD_{0.05} = 10.85, n = 15 \)). As was true of data from standard traps, data from experimental traps were characterized by large and heterogeneous variances which hindered discrimination among treatment means (note error bars in Fig. 3.7). However, randomized t-tests of SEEDS variates (paired sets from two trap types) pooled across all sampling periods (Table 3.6) substantiated the qualitative relationship among trap types described above, which mean comparisons based on a pooled error term had obscured.

Data for BROTEC and ANNUALS displayed patterns identical to that of SEEDS already described. However, according to Tukey's mean comparison criterion (\( MSD_{0.05} = 0.54, n = 75 \)), the significance of differences
among means for SPP was altered. SPP in pitfall traps (mean ± SE = 2.88 ± 0.18) > SPP in standard traps (1.73 ± 0.16) > SPP in crack traps (1.16 ± 0.13) and in filled traps (1.09 ± 0.11). These results were corroborated by individual t-tests assuming heterogeneous variances between SPP in pitfall vs. standard traps (t = 4.86, df = 74, P < 0.001) and SPP in standard vs. crack traps (t = 2.80, df = 74, P < 0.005). Thus, considering all four dependent variables tested, the disparity among SPP means for different trap types was especially great (note particularly large F-value for SPP, Table 3.2), despite large variances. These differences among SPP values seemed larger than might be expected solely on the basis of a significant positive correlation between SEEDS and SPP (r = 0.591, df = 298, P < 0.01).

Loglinear analysis of frequencies of traps which did or did not contain seeds (Table 3.7) yielded results with patterns mirroring those from the ANOVA of discrete seed counts data. Significantly more pitfall traps were found containing seeds than standard traps; significantly more standard traps contained seeds than either filled or crack traps, and these last two did not differ significantly.

Data from experimental traps provided bases for extrapolations characterizing seed dynamics. For example, given two assumptions -- 1) the probability of a seed passing over (and thus falling into) a pitfall trap was representative of that for any other I area (i.e., pitfall traps were not seed magnets), and 2) seed losses while in pitfall traps were negligible -- SEEDS data from pitfall traps allowed the calculation of a conservative estimate of a mean ± SE daily seed influx per m² of interspace of 35.61 ± 5.41. Given a similar assumption about the representative nature of the probability of a seed occurring on the
surface of a filled trap, SEEDS data from this trap type allowed an estimate of the mean ± SE instantaneous surface seed pool per m² of unli-tered, unvegetated interspace of 507.12 ± 142.27. (Both estimates were based on means over all sampling periods.) The comparison of standard trap SEEDS vs. those encountered in adjacent pitfall traps provided a naive estimate of the proportion of the daily influx of seeds which may ultimately remain at a given site, assuming that the attributes responsible for "stopping" a seed at that site were approximated by conditions produced in a standard trap. Resultant mean ± SE estimates ranged between 0.244 ± 0.090 for the fifth and final sampling period to 0.622 ± 0.210 for sampling period four, with a mean ± SE pooled over all sampling periods of 0.455 ± 0.071.

**Standard traps, rise transects and depressions**.--Seed traps located in depressions contained significantly more seeds than those in rise transects (SEEDS means ± SE were 8.70 ± 3.33 and 0.53 ± 0.16, respectively; \( t = 2.452 \), calculated critical \( t_{0.05} = 2.228 \) [variances assumed unequal and unequal sample sizes]). Despite the extremely small sample size, SEEDS was highly positively correlated with the depth of depression traps below the adjacent land surface \( (r = 0.822, df = 8, P < 0.01) \).

**Soil seed sampling**

Seeds of at least 16 species from nine families were found in soil samples (Appendix A.2). Classified by life history, eight were annual species and eight biennials/perennials; by life form, nine were forbs, four grasses and three shrubs. Of the 1984 "sound" seeds separated from samples, only two could not be identified to at least genus level. Seeds of annuals contributed ≈88.1% of the total; of these annuals'
seeds, a majority was composed of those of two species -- *B. tectorum* (≈39.8%) and *Collinsia parviflora* (≈29.4%). Despite the large proportion of SEEDS contributed to soil samples by *B. tectorum*, annuals' seeds still represented ≈81.6% of the total seeds in the "bromeless" (BROMUS-) data set.

All four dependent variables displayed similar patterns in the analyses, except that SPP alone showed a significant difference between U and I microenvironments when the complete data set (BROMUS+) was used. (The resolution of this discrepancy is described later.) For BROMUS+ data, SEEDS was significantly positively correlated with the other three dependent variables (SPP -- \( r = 0.455 \), BROTEC -- \( r = 0.770 \), ANNUALS -- \( r = 0.993 \); all df = 62, all \( P < 0.01 \)); for BROMUS- data, SEEDS was likewise correlated with the remaining two variables (SPP -- \( r = 0.631 \), ANNUALS -- \( r = 0.985 \); all df = 62, all \( P < 0.01 \)). Thus, as was true for seed trap data, most detailed results presented describe only SEEDS.

For both BROMUS+ and BROMUS- data, no significant F-tests for the Direction factor were observed (Tables 3.8 and 3.9). The Direction X Microenvironment interaction was likewise not a significant source of variation in either version of the analyses. However, the U mean was significantly greater than the I mean for SPP using BROMUS+ data, and, using BROMUS- data, all three variables had significantly larger U means.

Although the U mean for SEEDS was greater than that for I using BROMUS+ data (mean ± SE were, respectively, 35.38 ± 4.69 and 26.63 ± 4.62), the difference was masked by large variances. In addition, this relationship between the two microenvironments was not consistent in all directions (Fig. 3.8). Both the large variances and the reversal of the
pooled pattern for E samples were attributable to a few samples containing extremely large numbers of *B. tectorum* seeds. When U and I BROMUS+ variates were paired by direction within each shrub, yielding 32 sets of paired variates, a randomized *t*-test (insensitive to variances) indicated significantly more SEEDS in the U microenvironment (mean difference = 8.75, paired *t* = 1.796, *n* = 32, one-tailed *P* = 0.04). This result was corroborated by significant *F*-tests for the Microenvironment factor using BROMUS- data (Table 3.9) and a consistent pattern of U vs. I SEEDS means (with smaller variances) for these data (Fig. 3.8).

Attributes of individual shrubs were generally not significantly correlated with SEEDS (parametric correlations using BROMUS- data; Table 3.10). Exceptions were significant negative correlations between DIST in the N direction and SEEDS, for both U and I samples. Neither shrub canopy area nor shrub height were significantly correlated with their associated DIST measurements in parametric correlations.

*Surface seed sampling, 1986*

Seeds of at least 10 species from seven families were recovered from seed traps in 1986 (Appendix A.1). Classified by life history, six were annual species and four biennials/perennials; by life form, six were forbs, two grasses and two shrubs. Only 66 "sound" seeds were encountered in samples. Of these, two could not be identified to at least genus level, and these appeared to be conspecific with the single unknown from the 1981 seed trap samples. Seeds of annuals contributed ≈87.9% of the total, mostly composed of those of two species — *B. tectorum* (50.0% of all seeds) and *Lappula redowskii* (≈21.2%).

Though the duration of this mensuration was relatively short, seed
trap contents indicated substantial net fluxes of litter both into and out of individual traps. The magnitudes of either gains or losses were strongly affected by microenvironment and initial state (i.e., litter-charged or not; Table 3.11). L+ traps tended to lose litter, and to a much greater extent in I microenvironments, while L- traps accumulated more litter in U microenvironments (significant Microenvironment X Litter interaction, Table 3.11; Table 3.12). Although variability among traps was great (Table 3.12), randomized paired t-tests of U vs. I litter-charged traps, as well as U and I uncharged traps, demonstrated that these differences in litter loss and gain rates, respectively, were statistically significant (for L+ traps -- t = 6.69, one-tailed P < 0.0001; for L- traps, t = 4.12, one-tailed P = 0.001).

Numbers of seeds of all species recovered from seed traps were extremely variable and the sample size was relatively small, so that despite a particularly large mean value for U L+ traps (Table 3.12), there was no significant effect of microenvironment in the ANOVA (Table 3.11). However, a 2 X 2 contingency table assessing the independence of microenvironment and initial litter status yielded a significant likelihood ratio statistic (G = 8.342, df = 1, P = 0.004); U L+ traps harbored a disproportionately large share of all seeds (38), and U L- traps, an unexpectedly small share (5). This last result was counterintuitive and may reflect animals foraging preferentially in the unlittered seed traps. SEEDS for I traps did not differ on the basis of initial litter content. L+ traps contained more than 75% of all seeds encountered, significantly more than L- traps (Table 3.11). Fisher's exact test of a two-way contingency table of frequencies of the four trap types (i.e., U L+, U L-, I L+ and I L-) that did and did not contain seeds when
harvested was highly significant (two-tailed $P = 0.0033$). Of the four trap types, only $U L+$ traps had seeds in all 10 replicates.

For numbers of seeds of *B. tectorum* per trap, only the interaction of microenvironment and initial litter status was a significant source of variation (Table 3.11). $U L+$ traps had the greatest BROTEC (11 total; Table 3.12), but $I L-$ traps had nearly as many (9 total). Most of the *B. tectorum* seeds in $I L-$ traps derived from two entire flowering culms which lodged, one apiece, in two separate traps. By contrast, all other seeds (of all species) in traps were free of their maternal plants. A consequence of limited sample size in this effort was that chance local events, like the transport of entire plants into $I$ traps, could have large impact on the outcomes of statistical tests.

**Discussion**

*Species composition of seed pools*

Apart from the abundant and apparent *B. tectorum*, plants of annual species were inconspicuous components of the vegetation at the study site, by virtue of both their diminutive size and brief tenure in the vegetative state. Yet, seeds of annuals contributed the predominant fractions of the above- as well as the below-ground seed pools at the site. In this sense, seed pools at the study site resembled those examined from warm deserts (e.g., Price and Reichman 1987, Henderson et al. 1988, Kemp 1989). There were no species represented in the soil or seed trap samples which were not also observed readily in the contemporary vegetation (similar concordance was observed by Henderson et al. [1988] at a semi-arid shortgrass site in New Mexico).

Species encountered in soil samples comprised a subset of those
removed from seed traps. Not surprisingly, those species whose proportional contributions were greater in soil than seed trap samples produce small, grossly globular seeds, with smooth seed coats and no appendages (e.g., Collinsia parviflora and Polygonum douglassii). These tend to penetrate the substrate rapidly and effectively (Harper et al. 1970).

By contrast, seeds like those of B. tectorum and Lappula redowskii, with awns and hooks, respectively, were more often observed associated with litter, and may have been inhibited by their anatomy from being incorporated into the mineral soil.

For seed trap data, statistical results for numbers of species paralleled those for number of seeds per trap, with one interesting exception. Among experimental traps, SPP diverged to a greater degree among trap types than did SEEDS. Pitfall traps had significantly more SPP than did standard traps, which in turn exhibited significantly more than crack traps. These three trap types represented increasingly selective depositional conditions for prospective trapbound seeds. Pitfall traps "accepted" anything, while standard traps may have favored small dense seeds which would not escape and continue movement and/or seeds with appendages which might have become entangled in material already in the traps. Crack traps presented the most restrictive conditions; some seeds would not fit into the traps, or would bridge their narrow openings and move beyond them if not oriented parallel to their long axis (e.g., B. tectorum).

The prevalence of B. tectorum seeds, both in litter associated with soil samples and in seed traps, was striking. Density at the soil surface extrapolated from the maximum number found in a single standard seed trap was equivalent to nearly 12,000 B. tectorum seeds per m², with
a mean ± SE for all 1981 standard trap samples indicating almost 493 ± 47.59 seeds per m². Estimates of plant densities during the growing season just prior to installing the seed traps, appropriately scaled to a m², were even higher (e.g., relatively low I density was 768 ± 153; Chapter II; Table 2). Deficits between estimates of U and I surface seed pools (which were "snapshots" in time) and U and I plant densities for B. tectorum demonstrated that, on average, persistent deposition and accumulation at a particular microenvironmental site would be required to yield the number of plants observed.

Temporal dynamics

Despite a monotonic decline throughout the field season in SEEDS recovered on a per trap-day basis (Fig. 3.3), the ongoing collection of fresh-looking seeds for many weeks after parental annual plants had vanished made it clear that substantial redistribution of surface-lying seeds was occurring. The estimate of seed flux rate in I microenvironments derived from differences between standard and pitfall traps supported this conclusion. According to these data, slightly more than half of all seeds arriving at EI standard traps did not stay to be harvested. Observations of marked B. tectorum seeds (Chapter V) and mapping of marked seeds of B. tectorum and Stipa viridula (Kelrick, unpublished data) have also substantiated extensive seed movements, on the order of 10's of cm, during particular 3- to 4-d intervals at the study site. Finally, the considerable emigration of litter from I L+ traps in 1986 (Table 3.12) and concurrent accumulation in U L- traps was further validation of patch-to-patch-scale mobility of organic materials at the study site.
The significance of this mode of dispersal (Watkinson's [1978b]
"phase II dispersal") for the eventual dispersion of seeds and plants
cannot be overemphasized, because it is only occasionally explicitly
acknowledged, and rarely measured, in studies of plant population dynam­
ics. In communities where bare ground is a predictable feature, redis­
tribution of seeds on the surface by wind and/or runoff (e.g., Friedman
and Stein 1980) is likely to be an important process determining spatial
relationships of plants (Reichman 1984). The careful and elegant work
of Keddy (1982), investigating an annual grass of sand dunes, and of
Kadmon and Shmida (1990), documenting the population dynamics of an
annual grass of Middle Eastern and North African deserts, has illustrat­
ed how the observed broad-scale dispersion of plants has been maintained
by extensive horizontal movement of surface-lying seeds from high-fecun­
dity patches acting as net seed exporters, to lower-productivity patch­
es, where plants can establish but not thrive.

A premise of the design of the 1981 seed trap configuration (Fig.
3.1) was that wind-driven dispersal was the major mode of seed movement
at the site. Hence, temporal variation in the cardinal direction (with
respect to a replicate shrub's canopy) receiving the most seed deposi­
tion was to be expected, as winds shifted. Isolated sagebrush shrubs
influence local air turbulence in such a way that deposition of en­
trained particles may be most likely on the lee side (Hipps and Allen
1987). Presence of persistent prevailing westerly winds at the study
site led to the expectation that E traps would contain the most seeds.
While E traps consistently captured more seeds than W or S traps, con­
tents of N traps exceeded those of E traps in some sampling periods
(Fig. 3.4). It is plausible that the strong, convective, summer thunder
storms which often blew in from the SSW (down-valley) at the study site were responsible for intermittent, but extensive, seed movement, favoring deposition on the N side of shrubs. Alternatively, I microenvironments may function as "seed highways," with the bulk of seed movement trending E-W. If this were the case, then placing seed traps "in the way" would have favored deposition in NI and SI traps. This latter view was supported by the Direction X Microenvironment interaction for results pooled across all sampling periods (Fig. 3.6).

Spatial patterns

Based on the dispersion of ground-story herbaceous plants at the study site, an expectation was that more seeds would collect in U than in I microenvironments. The I is substantially bare ground, and, if conventional wisdom about spatially restricted seed shadows is correct (e.g., Werner 1975), then U microenvironments, with greater plant abundance, should also have exhibited more seeds. This was not the case for 1981 seed trap data (Fig. 3.5); I traps pooled across directions had greater (but not significantly greater) SEEDS in all sampling periods. Results in 1986 were similarly equivocal. Though the U L+ traps did capture the majority of seeds, differences between trap contents from the two microenvironments were non-significant.

A statistically significant and distinctive microenvironmental pattern did emerge when 1981 data were partitioned according to direction with respect to shrub canopy. SEEDS in U traps did exceed those in I traps, but only for E traps (Fig. 3.6), while NI and SI traps had consistently more SEEDS than their U counterparts. WU and WI traps did not differ significantly and, like S traps, contributed only a small
proportion of the total number of seeds from all eight standard traps at any replicate shrub. These results reinforce the conjecture above regarding zones of wind-driven seed movement vs. deposition around individual shrubs. Westerly and, less commonly, southerly winds would favor E and N deposition. Positive correlations between shrub height and SEEDS for three of the four N and E traps (Table 3.4) lend further support for the role of wind and its interaction with individual shrub canopies in moving seeds and in depositing them in a spatially non-random manner. Also, of all standard trap locations, EU traps were the most likely to have contained any seeds when harvested (Table 3.5).

For soil samples, distinctions between microenvironments were clouded when counts of seeds of *B. tectorum* were included in analyses. Many researchers have mentioned in passing that *B. tectorum* seeds are concentrated in the litter, based on substrate characteristics where germination is typically observed in the field (e.g., Hinds 1975). Evans and Young (1970) suggested that the awn and light weight of *B. tectorum* seeds facilitated dispersal but hampered burial. Young and Evans (1975) reported that from 60 to nearly 90% of germinable *B. tectorum* seeds in soil samples to a depth of 5 cm were located in the surface-lying litter fraction, and stated explicitly (p. 360) that "many of the germinable caryopses recovered from 0 to 2.5 cm in the soil, under shrub canopies, probably were dropped there inadvertently from the litter when the samples were collected." These comments agreed with my observation that few seeds of *B. tectorum* were part of the mineral soil component of my samples, and bolstered the decision to exclude counts of *B. tectorum* seeds for a more meaningful analysis of the true soil seed pool. Apart from the work of Young and Evans (1975) mentioned above, I
have encountered no other study which, for ecologically pertinent reasons, sought to separate explicitly the surface-lying seed pool from the soil pool, as was accomplished in this study.

With BROMUS- data, significantly larger SEEDS values obtained for U samples. (Even with BROMUS+ data, U values were larger when analyzed as paired samples rather than with ANOVA.) Values for U and I means from BROMUS+ data were very similar to those presented by Parmenter and MacMahon (1983), based on samples collected immediately N of the study site. (Mean ± SE for U and I: Parmenter and MacMahon -- 40.95 ± 4.32 and 23.22 ± 3.57; this study -- 35.38 ± 4.69 and 26.23 ± 4.62.) However, mean SEEDS in the true soil seed pool (i.e., BROMUS-) were much lower for both microenvironments (for U -- 27.13 ± 3.52; for I -- 13.13 ± 1.63). These values (roughly 4000 and 2000 seeds per m² for U and I, respectively) are much lower than estimates of shrub-associated soil seed bank size, sometimes including the surface litter component, from other aridland sites (e.g., Nelson and Chew 1977, Reichman 1984, Price and Reichman 1987, Kemp 1989).

Effects of microtopography and litter

Surface-lying seeds may come to their final residence by becoming lodged against an obstruction, falling into a depression from which extrication is unlikely or simply being shielded from the motive forces (wind, water or animals) driving phase II dispersal. The microtopographical heterogeneity of surfaces encountered by seeds enhances patchy seed dispersions in arid environments (Reichman 1984, Kemp 1989).

In this study, more SEEDS accumulated in traps installed in subjectively chosen depressions than in nearby standard traps traversing a
broad rise. If mean values of SEEDS for crack traps are scaled on a per cm² basis to compare with values from the EI standard trap, then cracks were roughly 7X as effective at capturing seeds as standard traps. This was probably attributable to seeds being less likely to reinitiate movement once falling into a crack. On the other hand, cracks were significantly less likely to contain any seeds (Table 3.7), despite a perimeter length equivalent to that of a standard trap. Thus, although seed retention was apparently better for crack traps, the smaller target they presented to the environment rendered their SEEDS values significantly lower than the adjacent standard traps.

On the microtopographic scale, surface texture strongly influenced seed deposition patterns. The small numbers of seeds observed on the surface of filled traps, contrasted with the large numbers discovered in pitfall traps (Fig. 3.7), demonstrated how vagile seeds were at the study site. Litter decreased emigratory seed movements, and, once encountered, served as a depository for previously mobile seeds. The significant effect of litter-charging seed traps in 1986 illustrated litter functioning in these manners. Further, SEEDS from individual standard traps in 1981 was positively correlated with litter mass in those traps (r = 0.583, df = 598, P < 0.001).

A recent review of the influence of litter on plant community structure emphasized data from forests, old fields and grasslands, and depicted litter conventionally as "dead plant material of small size lying loose on the ground" (Facelli and Pickett 1991, p. 4). Despite a thorough discussion of litter dynamics and the intimate interactions of litter with the processes of germination and establishment, these authors maintained an implicit distinction between litter movement/depos-
tion and that of seeds. In aridland ecosystems and other sparsely vegetated landscapes, it is may be more meaningful to characterize seeds of many species as a living component of the litter. The results of this study demonstrated that seeds must have experienced extensive horizontal displacements, which paralleled, or perhaps sometimes coincided with, litter accumulations. In these systems, I suggest that depositional patterns of litter indicate and in many instances may control depositional patterns of seeds. Thus, the two are both conceptually and functionally linked.

*Regarding the dispersion of Bromus tectorum*

Large numbers of *B. tectorum* seeds were observed among surface-lying seeds. They were clearly capable of considerable mobility and were recovered in abundance from I as well as U traps. If occurrence in I traps were interpreted as indicating the location of their ultimate stopping points, then this would lead to the argument that depositional patterns of *B. tectorum* seeds did not accord with the strong disparity in plant densities in U vs. I microenvironments (Chapter II). However, I do not endorse this view, and suggest that seeds of *B. tectorum* were essentially part of the flux of materials continually moving through the I matrix. These materials tend to accumulate beneath shrub canopies (Chapter I; Table 1.1), where they can contribute to the characteristically more plentiful U plant recruitment in the subsequent growing seasons.
Table 3.1. Results of analyses of variance of four dependent variables from shrub-centered standard seed trap sampling, 1981.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
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<td>SPP</td>
<td>20.25</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>4.79</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>3.97</td>
<td>P&lt;0.01</td>
</tr>
</tbody>
</table>
Table 3.1. (continued)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Variable&lt;sup&gt;b&lt;/sup&gt;</th>
<th>F-value</th>
<th>Significance&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Direction X Sampling period</td>
<td>12,392</td>
<td>SEEDS</td>
<td>2.40</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>1.32</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>1.98</td>
<td>P&lt;0.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>3.52</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Microenvironment X Sampling period</td>
<td>4,392</td>
<td>SEEDS</td>
<td>1.98</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>0.92</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>2.22</td>
<td>0.10&gt;P&gt;0.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>0.71</td>
<td>NS</td>
</tr>
<tr>
<td>Direction X Microenvironment X Sampling period</td>
<td>12,392</td>
<td>SEEDS</td>
<td>1.68</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>1.07</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>1.50</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>1.66</td>
<td>NS</td>
</tr>
</tbody>
</table>

<sup>a</sup>Degrees of freedom listed are: those for the source of variation, those for the appropriate error against which it was tested.

<sup>b</sup>SEEDS = number of seeds of all species per trap; SPP = number of species per trap; ANNUALS = number of seeds of annual plants per trap; BROTEC = number of seeds of Bromus tectorum per trap.

<sup>c</sup>Statistical significance. NS = not significant; i.e., P > 0.05.
Table 3.2. Results of analyses of variance of four dependent variables from seed trap sampling of three experimental traps and the adjacent standard trap, 1981.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Variable&lt;sup&gt;b&lt;/sup&gt;</th>
<th>F-value</th>
<th>Significance&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trap type</td>
<td>3,42</td>
<td>SEEDS</td>
<td>2.40</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>1.32</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>1.98</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>3.52</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Sampling period</td>
<td>4,56</td>
<td>SEEDS</td>
<td>1.98</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>0.92</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>2.22</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>0.71</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td>Trap type X Sampling period</td>
<td>12,168</td>
<td>SEEDS</td>
<td>1.68</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>1.07</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>1.50</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>1.66</td>
<td>P&lt;0.001</td>
</tr>
</tbody>
</table>

<sup>a</sup>Degrees of freedom listed are: those for the source of variation, those for the appropriate error against which it was tested.

<sup>b</sup>SEEDS = number of seeds of all species per trap; SPP = number of species per trap; ANNUALS = number of seeds of annual plants per trap; BROTEC = number of seeds of *Bromus tectorum* per trap.

<sup>c</sup>Statistical significance. NS = not significant; i.e., P > 0.05.
Table 3.3. Means$^a \pm$SE per trap of data from shrub-centered standard seed traps, 1981, presented according to the three main factors of the sampling design.

<table>
<thead>
<tr>
<th>Variable$^b$</th>
<th>Factor</th>
<th>Level$^c$</th>
<th>SEEDS</th>
<th>SPP</th>
<th>ANNUALS</th>
<th>BROTEC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sampling</td>
<td>Level$^c$</td>
<td>SEEDS</td>
<td>SPP</td>
<td>ANNUALS</td>
<td>BROTEC</td>
</tr>
<tr>
<td></td>
<td>period</td>
<td>(n=120)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>4.12 ± 0.41$^e$</td>
<td>1.55 ± 0.09$^e$</td>
<td>3.05 ± 0.41$^{de}$</td>
<td>1.74 ± 0.29$^e$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>10.68 ± 1.29$^d$</td>
<td>2.31 ± 0.11$^d$</td>
<td>8.37 ± 1.26$^d$</td>
<td>6.28 ± 1.13$^d$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>6.16 ± 1.05$^e$</td>
<td>1.91 ± 0.13$^{de}$</td>
<td>4.71 ± 0.85$^{de}$</td>
<td>2.81 ± 0.48$^{de}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>7.12 ± 1.01$^{de}$</td>
<td>1.90 ± 0.12$^{de}$</td>
<td>5.89 ± 0.99$^{de}$</td>
<td>3.99 ± 0.78$^{de}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>2.64 ± 0.43$^e$</td>
<td>1.08 ± 0.11$^f$</td>
<td>2.26 ± 0.40$^e$</td>
<td>1.44 ± 0.31$^e$</td>
</tr>
<tr>
<td></td>
<td>Direction</td>
<td>(n=150)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>N</td>
<td>8.69 ±1.15$^d$</td>
<td>2.09 ± 0.13$^d$</td>
<td>7.11 ± 1.01$^d$</td>
<td>4.73 ± 0.81$^d$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>W</td>
<td>4.29 ± 0.55$^e$</td>
<td>1.50 ± 0.09$^e$</td>
<td>3.38 ± 0.52$^e$</td>
<td>2.27 ± 0.41$^d$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>S</td>
<td>4.13 ± 0.44$^e$</td>
<td>1.45 ± 0.09$^e$</td>
<td>2.93 ± 0.39$^e$</td>
<td>1.88 ± 0.28$^d$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>E</td>
<td>7.46 ± 0.97$^{de}$</td>
<td>1.95 ± 0.11$^{de}$</td>
<td>6.00 ± 0.96$^{de}$</td>
<td>4.13 ± 0.81$^d$</td>
</tr>
<tr>
<td></td>
<td>Micro-</td>
<td>(n=300)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>environment</td>
<td>I</td>
<td>5.24 ± 0.53</td>
<td>1.68 ± 0.07</td>
<td>4.00 ± 0.52</td>
<td>2.83 ± 0.44</td>
</tr>
</tbody>
</table>

$^a$Within a factor, means for a particular variable with similar superscripted letters are not significantly different (Tukey's test). No significant F-tests were obtained for Microenvironment.

$^b$SEEDS = number of seeds of all species per planter; SPP = number of species per planter; ANNUALS = number of seeds of annual plants per planter; BROTEC = number of seeds of Bromus tectorum per planter.

$^c$For Direction, letters denote the four cardinal directions; for Microenvironment, U = undershrub, I = interspace.
Table 3.4. Correlation coefficients for parametric correlations\textsuperscript{a} of shrub attributes and various subsets of data\textsuperscript{b} from shrub-centered standard seed traps, 1981.

<table>
<thead>
<tr>
<th>Shrub attribute</th>
<th>Canopy area</th>
<th>Height</th>
<th>Distance\textsuperscript{d}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean of 8 traps per shrub</td>
<td>-0.001</td>
<td>0.492</td>
<td>------</td>
</tr>
<tr>
<td>NU</td>
<td>0.231</td>
<td>0.640*</td>
<td>0.407</td>
</tr>
<tr>
<td>NI</td>
<td>-0.121</td>
<td>0.085</td>
<td>-0.015</td>
</tr>
<tr>
<td>WU</td>
<td>0.075</td>
<td>0.409</td>
<td>-0.055</td>
</tr>
<tr>
<td>WI</td>
<td>-0.155</td>
<td>0.405</td>
<td>-0.309</td>
</tr>
<tr>
<td>SU</td>
<td>-0.128</td>
<td>0.151</td>
<td>0.388</td>
</tr>
<tr>
<td>SI</td>
<td>-0.224</td>
<td>0.065</td>
<td>-0.340</td>
</tr>
<tr>
<td>EU</td>
<td>0.162</td>
<td>0.571*</td>
<td>0.407</td>
</tr>
<tr>
<td>EI</td>
<td>0.011</td>
<td>0.735**</td>
<td>0.675**</td>
</tr>
</tbody>
</table>

\textsuperscript{a}DF = 13.

\textsuperscript{b}Number of seeds of all species per planter (SEEDS), pooled over all sampling periods.

\textsuperscript{c}N, W, S and E denote cardinal directions; U = undershrub, I = interspace.

\textsuperscript{d}Distance = distance between the canopy edge and a trap location.

\*P < 0.05; \**P < 0.01.
Table 3.5. Frequencies of shrub-centered standard traps, 1981, which did and did not contain seeds when sampled (pooled over all sampling periods), with results of log likelihood ratio tests.

<table>
<thead>
<tr>
<th>Direction</th>
<th>Presence of seeds</th>
<th>Presence of seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>EAST</td>
<td>70</td>
<td>a</td>
</tr>
<tr>
<td>NORTH</td>
<td>65</td>
<td>a,b</td>
</tr>
<tr>
<td>WEST</td>
<td>64</td>
<td>a,b</td>
</tr>
<tr>
<td>SOUTH</td>
<td>57</td>
<td>b</td>
</tr>
</tbody>
</table>

$G_{adj} = 9.118, \ P<0.05$  
$G_{adj} = 6.048, \ 0.5>P>0.1$

Data with similar letters comprise non-significant subgroups.
Table 3.6. Results\textsuperscript{a} of randomized t-tests\textsuperscript{b} comparing numbers of seeds of all species (SEEDS) found in the three experimental seed traps and the adjacent standard trap, 1981.

<table>
<thead>
<tr>
<th>Data compared</th>
<th>Mean difference</th>
<th>Paired t-value</th>
<th>Significance\textsuperscript{c}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pitfall vs. standard</td>
<td>15.45</td>
<td>5.28</td>
<td>( P&lt;0.001 )</td>
</tr>
<tr>
<td>Standard vs. crack</td>
<td>2.71</td>
<td>2.93</td>
<td>( P&lt;0.001 )</td>
</tr>
<tr>
<td>Standard vs. filled</td>
<td>2.59</td>
<td>4.37</td>
<td>( P&lt;0.001 )</td>
</tr>
<tr>
<td>Filled vs. crack</td>
<td>0.12</td>
<td>0.14</td>
<td>( P=0.462 )</td>
</tr>
</tbody>
</table>

\textsuperscript{a}In summary: Pitfall > standard > filled and crack.

\textsuperscript{b}n = 75 for all tests.

\textsuperscript{c}Statistical significance (one-tailed).
Table 3.7. Results$^a$ of non-orthogonal contrasts of data from three experimental seed traps and the adjacent standard trap, 1981, produced in a loglinear analysis$^b$ of frequencies of traps which did or did not contain seeds when sampled.

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Z-value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pitfall vs. all others</td>
<td>3.597</td>
<td>$P&lt;0.001$</td>
</tr>
<tr>
<td>Standard vs. filled and crack</td>
<td>2.948</td>
<td>$P&lt;0.005$</td>
</tr>
<tr>
<td>Pitfall vs. standard</td>
<td>2.395</td>
<td>$P&lt;0.05$</td>
</tr>
<tr>
<td>Standard vs. filled</td>
<td>2.746</td>
<td>$P&lt;0.01$</td>
</tr>
<tr>
<td>Standard vs. crack</td>
<td>2.580</td>
<td>$P&lt;0.01$</td>
</tr>
<tr>
<td>Filled vs. crack</td>
<td>-0.185</td>
<td>NS</td>
</tr>
</tbody>
</table>

$^a$In summary: Pitfall > standard > crack and filled.

$^b$The most parsimonious model included the simple effects of Sampling period and Trap type ($X^2 = 7.821$, df = 12, $P = 0.799$).

$^c$Contrasts used data pooled over all sampling periods.

$^d$A significant Z-value indicated a statistical difference in frequencies of traps containing seeds when sampled, between elements in the associated contrast.

$^e$Statistical significance. NS = not significant; i.e., $P > 0.05$. 
Table 3.8. Results of analyses of variance of four dependent variables from soil seed sampling, using the entire data set (BROMUS+).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Variable&lt;sup&gt;b&lt;/sup&gt;</th>
<th>F-value</th>
<th>Significance&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Direction</td>
<td>3,21</td>
<td>SEEDS</td>
<td>0.80</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>1.54</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>0.82</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>0.44</td>
<td>NS</td>
</tr>
<tr>
<td>Microenvironment</td>
<td>1,7</td>
<td>SEEDS</td>
<td>3.24</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>8.70</td>
<td>P&lt;0.025</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>3.05</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>2.31</td>
<td>NS</td>
</tr>
<tr>
<td>Direction X Micro-</td>
<td>3,21</td>
<td>SEEDS</td>
<td>1.25</td>
<td>NS</td>
</tr>
<tr>
<td>environment</td>
<td></td>
<td>SPP</td>
<td>0.69</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>1.15</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>1.34</td>
<td>NS</td>
</tr>
</tbody>
</table>

<sup>a</sup>Degrees of freedom listed are: those for the source of variation, those for the appropriate error against which it was tested.

<sup>b</sup>SEEDS = number of seeds of all species per trap; SPP = number of species per trap; ANNUALS = number of seeds of annual plants per trap; BROTEC = number of seeds of Bromus tectorum per trap.

<sup>c</sup>Statistical significance. NS = not significant; i.e., P > 0.05.
Table 3.9. Results of analyses of variance of three dependent variables from soil seed sampling, using data excluding counts of *Bromus tectorum* seeds (BROMUS-).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Variable&lt;sup&gt;b&lt;/sup&gt;</th>
<th>F-value</th>
<th>Significance&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Direction</td>
<td>3,21</td>
<td>SEEDS</td>
<td>1.68</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>1.54</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>1.98</td>
<td>NS</td>
</tr>
<tr>
<td>Microenvironment</td>
<td>1,7</td>
<td>SEEDS</td>
<td>18.47</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>8.70</td>
<td>P&lt;0.025</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>18.98</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td>Direction X Micro-environment</td>
<td>3,21</td>
<td>SEEDS</td>
<td>0.80</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPP</td>
<td>0.69</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ANNUALS</td>
<td>1.09</td>
<td>NS</td>
</tr>
</tbody>
</table>

<sup>a</sup>Degrees of freedom listed are: those for the source of variation, those for the appropriate error against which it was tested.

<sup>b</sup>SEEDS = number of seeds of all species per trap; SPP = number of species per trap; ANNUALS = number of seeds of annual plants per trap.

<sup>c</sup>Statistical significance. NS = not significant; i.e., P > 0.05.
Table 3.10. Correlation coefficients for parametric correlations\(^a\) of shrub attributes and various subsets of data\(^b\) from soil seed sampling.

<table>
<thead>
<tr>
<th>Data category(^c)</th>
<th>Canopy area</th>
<th>Height</th>
<th>Distance(^d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean of 8 traps per shrub</td>
<td>-0.161</td>
<td>0.013</td>
<td>-</td>
</tr>
<tr>
<td>NU</td>
<td>-0.039</td>
<td>-0.456</td>
<td>-0.890**</td>
</tr>
<tr>
<td>NI</td>
<td>-0.284</td>
<td>-0.218</td>
<td>-0.858**</td>
</tr>
<tr>
<td>WU</td>
<td>-0.314</td>
<td>0.237</td>
<td>0.181</td>
</tr>
<tr>
<td>WI</td>
<td>0.196</td>
<td>0.222</td>
<td>-0.202</td>
</tr>
<tr>
<td>SU</td>
<td>0.036</td>
<td>0.402</td>
<td>-0.022</td>
</tr>
<tr>
<td>SI</td>
<td>0.269</td>
<td>0.333</td>
<td>-0.205</td>
</tr>
<tr>
<td>EU</td>
<td>-0.510</td>
<td>-0.225</td>
<td>0.342</td>
</tr>
<tr>
<td>EI</td>
<td>0.451</td>
<td>0.320</td>
<td>0.107</td>
</tr>
</tbody>
</table>

\(^a\)DF = 6.

\(^b\)Number of seeds of all species per planter (SEEDS), using data with Bromus tectorum counts excluded (BROMUS-), pooled over all sampling periods.

\(^c\)Abbreviations as in Table 3.4.

\(^d\)Distance = distance between the canopy edge and a trap location.

\(^{**}P < 0.01\).
Table 3.11. Results of analyses of variance of three dependent variables from seed trap sampling of standard traps with and without an initial charge of litter, 1986.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Variable&lt;sup&gt;b&lt;/sup&gt;</th>
<th>F-value</th>
<th>Significance&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microenvironment</td>
<td>1,18</td>
<td>LITTERWT</td>
<td>61.37</td>
<td>P&lt;0.0005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SEEDS</td>
<td>2.57</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>0.02</td>
<td>NS</td>
</tr>
<tr>
<td>Litter presence/absence</td>
<td>1,18</td>
<td>LITTERWT</td>
<td>93.91</td>
<td>P&lt;0.0005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SEEDS</td>
<td>12.12</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>0.30</td>
<td>NS</td>
</tr>
<tr>
<td>Microenvironment X Litter</td>
<td>1,18</td>
<td>LITTERWT</td>
<td>19.32</td>
<td>P&lt;0.0005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SEEDS</td>
<td>8.42</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BROTEC</td>
<td>7.42</td>
<td>P&lt;0.05</td>
</tr>
</tbody>
</table>

<sup>a</sup>Degrees of freedom listed are: those for the source of variation, those for the appropriate error against which it was tested.

<sup>b</sup>LITTERWT = final litter mass (at trap collection) minus original litter mass (at installation); SEEDS = number of seeds of all species per trap; BROTEC = number of seeds of *Bromus tectorum* per trap.

<sup>c</sup>Statistical significance. NS = not significant; i.e., P > 0.05.
Table 3.12. Means ± SE per trap of data from standard seed traps with and without an initial charge of litter, 1986.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Litter charge</th>
<th>Variable&lt;sup&gt;a&lt;/sup&gt;</th>
<th>LITTERWT</th>
<th>SEEDS</th>
<th>BROTEC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.469 ± 0.086</td>
<td>0.500 ± 0.269</td>
<td>0.200 ± 0.200</td>
</tr>
<tr>
<td>Undershrub</td>
<td>No</td>
<td></td>
<td>-0.106 ± 0.148</td>
<td>3.800 ± 0.998</td>
<td>1.100 ± 0.348</td>
</tr>
<tr>
<td></td>
<td>Yes</td>
<td></td>
<td></td>
<td>1.300 ± 0.300</td>
<td>0.300 ± 0.153</td>
</tr>
<tr>
<td>Interspace</td>
<td>No</td>
<td></td>
<td>0.115 ± 0.023</td>
<td>1.000 ± 0.394</td>
<td>0.900 ± 0.407</td>
</tr>
<tr>
<td></td>
<td>Yes</td>
<td></td>
<td>-1.412 ± 0.128</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>LITTERWT = final litter mass (at trap collection) minus original litter mass (at installation); SEEDS = number of seeds of all species per trap; BROTEC = number of seeds of *Bromus tectorum* per trap.
SEED TRAP SAMPLING 1981
15 SHRUBS
5 SAMPLING PERIODS
SEED TRAP SAMPLING 1986
10 SHRUBS
1 SAMPLING PERIOD

← NORTH

SEED TRAP INITIALLY CONTAINING LITTER

SEED TRAP INITIALLY WITHOUT LITTER
SAMPLING DATES

MEAN # SEEDS PER TRAP

JUN 29/30
JUL 22/23
AUG 6/7
SEP 2/3
SEP 23/24

MEAN # SEEDS PER DAY

0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1

0
2
4
6
8
10
12
14

MEAN # SEEDS PER TRAP PER DAY
MICROENVIRONMENT X SAMPLING PERIOD

![Bar chart showing mean number of seeds per trap by microenvironment and sampling period.](chart)

- **JUN 29/30**: Undershrub 4, Interspace 5
- **JUL 22/23**: Undershrub 8, Interspace 12
- **AUG 6/7**: Undershrub 6, Interspace 8
- **SEP 2/3**: Undershrub 6, Interspace 7
- **SEP 23/24**: Undershrub 2, Interspace 3
EXPERIMENTAL TRAP TYPE X SAMPLING PERIOD

MEAN # SEEDS PER TRAP

JUN 29/30  JUL 22/23  AUG 6/7  SEP 2/3  SEP 23/24

SAMPLING DATES
CHAPTER IV

THE DISPERSION OF BROMUS TECTORUM: FACTORS AFFECTING PLANTS

Introduction

Distinctive associations between herbaceous species and shrubs, both positive and negative, are well-documented features of many arid and semiarid plant communities (e.g., Went 1942, Muller 1953, Halligan 1973, Hazlett and Hoffman 1975, Friedman et al. 1977, Jaksic and Fuentes 1980, Shmida and Whittaker 1981). In most instances, though, causes of these patterns are not thoroughly understood. The multitude of presumed and/or observed factors potentially influencing the dispersion of ground-story plants in these shrub-dominated systems (Chapter I; Table 1.1) provides a rich framework for manipulative experiments aimed at identifying the determinants of their shrub-associated patterns.

From the perspective of a ground-story plant, many abiotic conditions and resources can be substantially modified by shrub presence in its immediate locale. For example, shrubs can cast shade, break wind, funnel (Halligan 1973) or intercept (Tromble 1988) rainfall and influence radiative heat exchange (Lowe and Hinds 1971). Further, once occupied by a shrub, a site is likely to become locally enriched in nutrients with respect to the adjacent shrubless matrix (Charley and West 1975, 1977). Such shrub-associated "islands of fertility" can develop because both deposition and decomposition of litter are favored beneath and in close proximity to shrubs (Garcia-Moya and McKell 1970, Mack 1977, Allen and MacMahon 1985).

Another class of factors are consequences of more direct biotic interactions between shrubs and ground-story plants. Shrubs can extract
water from the soil, potentially reducing its availability to ground-
story herbaceous plants (Sturges 1977, Caldwell 1979, Swank and Oechel
1991), but they may also leak water obtained from deep in the soil
column to nearer-surface horizons, which more shallowly rooted ground-
story components can utilize (Richards and Caldwell 1987, Caldwell and
Richards 1989). Allelopathic interactions have been described (Muller
1969, Friedman et al. 1977). Shrubs may also deplete shallow soil
horizons of nutrients required by ground-story herbaceous species (Swank
and Oechel 1991).

Besides such direct effects, shrubs mediate a host of indirect
biotic phenomena which might impinge upon ground-story plants. Many
primary consumers (e.g., Parker and Root 1981), especially rodents
(Thompson 1982, Kotler 1984), may center their activities near and under
shrubs. The spatially non-random resource use of these important arid-
land consumers, involving seed foraging and/or caching (La Tourrette et
al. 1971, Reichman 1979, Price and Waser 1985), granivory and herbivory
(Bartholomew 1970, Nelson and Chew 1977), could be a potent influence on
ground-story plant dispersion with respect to shrubs.

I attempted to elucidate the determinants of the strong, consist-
ent and persistent positive association between B. tectorum plants and
Artemisia tridentata shrubs at the study site with a manipulative exper-
iment, involving the introduction of known numbers of B. tectorum seeds
and the assessment of plants arising from those seeds. The experimental
design incorporated the potential effects of 1) shrub presence/absence,
2) microenvironment (U versus I) and 3) rodent activity (granivory
and/or herbivory), acting in concert to influence the dispersion of B.
tectorum plants at this site.
Methods

Experimental design

This experiment was conducted in two successive growing seasons, using two different cohorts of seeds, in 1980 and 1981. Each year, recently matured seeds were collected from a *B. tectorum* stand directly adjacent to the study site (within 100 m). "Planters" (9-cm plastic petri dishes whose bottoms had been cut out and replaced with nylon mesh window screening) were inserted into appropriate locations in the field such that they were flush with the ground surface. Seeds were then sown at a depth of 5 mm into pre-sifted and steamed (to eliminate any unintroduced propagules), field-collected soil contained in the planters. Three exclosure treatments were imposed at each replicate sagebrush shrub to assess the potential effects of granivory/herbivory on the success of experimentally introduced *B. tectorum*: 1) an intact exclosure (EX treatment); 2) a similar exclosure with doors, to allow rodent access while testing for the effect of the structure itself (RC [rodent control] treatment); and 3) no exclosure (EC [exclosure control] treatment).

In 1980, three radiating 1.5-m transects extending from U to I microenvironments were installed around each of 10 shrubs. Along each transect, three planters were placed at 0.5-m intervals (undershrub [U], middle [M], interspace[I]) and each of these three transects received one of the three exclosure treatments (Fig. 4.1). Exclosures were constructed of lightweight lumber frames and 0.6-cm hardware cloth. They enclosed an area 0.5 m X 1.5 m with walls 60 cm high, with an additional 15 cm of wall buried. Aluminum flashing affixed to the tops of walls
prevented entry by climbing rodents. Two hundred seeds were planted per planter. To address the influence of shrub presence, five of the 10 shrubs were sawn off at the base after emplacement of the planters and exclosures. The experiment was installed between September 5 and 16 and was harvested the following June 9-12 (1981).

In 1981, several refinements were incorporated to improve the experiment. The large exclosures used in 1980 could only be accommodated by shrubs with particularly high canopies and thus shrubs had been subjectively chosen. A further defect was that the exclosures themselves had dictated planter placement, so that "undershrub" and "interspace" had no consistent operational (or ecological) interpretation. To allow the use of both randomly selected shrubs and the U and I definitions presented earlier (Chapter II; Fig. 2.1), small exclosures surrounding individual planters were used. These were 0.6-cm hardware cloth boxes measuring 15 cm on a side which were buried to a depth of 5 cm upon installation. Other changes implemented were (Fig. 4.2): 1) two planters per transect (1 U, 1 I) rather than three; 2) 50 seeds per planter rather than 200, to facilitate counting of germinants during fall and spring; 3) 15 replicate shrubs rather than than 10; and 4) elimination of shrub removal as a treatment (no significant effect in 1980). The experiment was installed between August 16 and 19 and was harvested the following June 16-18 (1982).

Viability of the seed lot collected in 1981 was tested using 2,3,5-triphenyltetrazolium chloride (Grabe 1970). Ten replicates of 25 seeds each were imbibed in distilled water for 24 h at room temperature, then incubated in a 1% tetrazolium solution for 30 h at 30°C in darkness. Mean ± SE % viability was 98.4 ± 0.55) thus there was no need to
adjust field results accordingly.

In both years, four variables were measured as indicators of "plant success": 1) total number of plants per planter (PLANTS); 2) shoot length of 10 randomly selected plants (or of all plants in the planter if <10), converted to mean shoot length per plant (SHTLEN); 3) number of spikelets on those plants whose shoot lengths were measured, converted to mean number of spikelets per plant (SPKLT); and 4) dry weight of biomass per planter (WT; roots were clipped off at the mesh screening, and remaining material was dried for four days at 50°C). For the 1981 cohort, the number of emerged seedlings was counted once during fall (November 5) and once the following spring (May 9).

Analysis

Separate analyses of variance (ANOVA's) were employed for each year's four measures of plant success. When warranted, subsequent comparisons among treatment levels were accomplished with Tukey's studentized range procedure (Sokal and Rohlf 1981, SAS 1987). In both years, variances associated with certain treatment level means for some of the variables measured were heterogeneous. Such violations of the assumptions of ANOVA tend to obscure real differences among sample means (Sokal and Rohlf 1981). In 1981, strong treatment effects overwhelmed this tendency. For 1980 data, if F-tests of treatment effects based on pooled errors yielded marginally significant results and variances of those treatment levels were heterogeneous, then individual t-tests assuming unequal variances served to compare treatment level means. The degree to which measures of plant success were associated with particular shrubs was tested via parametric correlations with shrub attributes.
Effects on per plant measures of success associated with the density of plants within individual planters were also tested with parametric correlations.

Results

Design differences between the 1980 and 1981 versions of this experiment precluded analyzing their data in a single ANOVA; however, grand means of the variables (i.e., pooled over all treatments) were compared (Table 4.1). Significantly more PLANTS and greater WT in 1980 were likely attributable to the larger number of seeds planted in 1980 (200, vs. 50 in 1981). The significantly reduced SHTLEN in 1981 was probably not caused primarily by a restriction of shoot elongation within the "lidded" exclosures used (note that this affected only about two thirds of plants measured); 1981 plants inside exclosures had significantly greater mean SHTLEN than that of unexclosed controls (Fig. 4.3). Remarkably, no differences between SPKLT nor mean weights per plant (WT/PLNT) were observed. In 1981, a significantly greater proportion of seeds planted produced plants encountered at harvest (37.7%, vs. 30.2% in 1980; PLANTS normalized to 50 seeds per planter).

No treatment interaction was a significant source of variation in either year of this experiment (Tables 4.3 and 4.4). Also, Shrub presence/absence (1980 only) produced no significant effects (Tables 4.2 and 4.3). Therefore, all statistically pertinent results could be portrayed by segregating data according to the two main sources of variation common to both years -- Microenvironment and Exclosure treatment (Figs. 4.3, 4.4 and 4.5). For exclosure treatments, data of both years could be meaningfully considered together, since treatments and total
number of planters per treatment were the same (Fig. 4.3). This was not the case for microenvironment (Figs. 4.4 and 4.5).

Exclosure treatments had qualitatively consistent effects in both years of the study (Fig. 4.3). Across the three exclosure types, PLANTS was not significantly different in either year, although it was least in the exclosures with doors (RC treatment) in both years. For the other three variables, in both years, mean values were highest for the intact exclosures (EX treatment) and decreased uniformly through the RC to the unexclosed (EC) treatment. The degree of statistical significance varied among variables and between years, but values for the EX treatment were always significantly greater than those for the EC treatment. This was true even for SHTLEN in 1981, despite both the use of lidded exclosures and that values of SHTLEN in the EC treatment were not significantly different between years ($t = 1.56, df = 58, 0.20 > P > 0.10$).

Effects of planting microenvironment were less directly comparable across the two years than those of exclosure treatments, at least in part because of the changes in design described earlier. In 1980, only mean values of PLANTS differed significantly among microenvironments; M planters had the greatest PLANTS (Fig. 4.4). For the other three variables, any real treatment effects were masked by large variances (coefficients of variation ranged from 26.7% to 77.0%). In 1981, although variances were also large (coefficients of variation from 19.6% to 103.5%), treatment effects were unequivocal. For all four variables, mean values for the I treatment were significantly greater (Fig. 4.5).

Mean counts of PLANTS obtained for the 1981 cohort consistently indicated more individuals present at harvest than during the previous
fall or spring (Fig. 4.6). Mean PLANTS in U vs. I treatments were significantly different on all three census dates (November 5 -- $F_{1,14} = 26.15$, $P < 0.001$; May 9 -- $F_{1,14} = 12.10$, $P < 0.005$; June 16-18 [harvest] -- $F_{1,14} = 12.89$, $P < 0.005$), while those for the three exclosure treatments were not for any date. Means of the three census dates for any single treatment did not differ statistically for any of the treatments.

Since individual plants were not marked, it was impossible to ascertain the exact quantitative extent of winter death and subsequent spring germination "replacing" dead fall-germinated individuals. However, this must have occurred in at least 24 of the 90 planters, indicated by declines in PLANTS between the first two censuses followed by increases between the last two. Planters for which a decrease in PLANTS between fall and spring censuses was recorded (34 of 90 possible) were not contagiously associated with particular shrubs -- that is, their distribution did not depart from the expected probabilities of a binomial distribution ($X^2 = 7.675$, df = 5, $0.5 < P > 0.1$). Neither were they distributed unevenly among the three exclosure types. However, significantly more of these planters were in the I microenvironment (log likelihood ratio test; $G_{adj} = 4.70$, df = 1, $0.05 > P > 0.025$), especially those accessible by rodents (RC and EC treatments; 16 of 22 possible).

Although variability among shrubs (replicates) was substantial in both years of the study (coefficients of variation of the mean of shrub means for the four variables ranged from 13.7% to 28.5% in 1980, 16.9% to 37.8% in 1981), responses of the group of four measures of plant success did not vary in concert consistently from shrub to shrub. In 1980, this was indirectly indicated by the non-significant $F$-test for
the Shrub presence/absence treatment (Table 4.3). Using 1981 data, further substantiation derived from correlations between individual shrub attributes -- height (cm), canopy area (cm²) and distance between the canopy edge and a planter location (cm) -- and each of the four dependent variables, both when separated into U and I subsets and when pooled across treatments. No significant correlation coefficients were obtained (3 shrub attributes X 3 data "groupings" X 4 dependent variables = 36 possible coefficients), though at least one would be expected by chance alone among this number of tests.

Plant density and components of yield, variously measured, have been shown repeatedly to be functionally related (Harper 1977). Since all plants in this experiment were confined to the ≈66 cm² of each planter (i.e., PLANTS is an index of density), such density-yield relationships could be examined (Table 4.5). In general, PLANTS was significantly positively correlated with WT; this relationship was especially strong in 1981, when densities were significantly lower. The influence of density on yield was illustrated most clearly by correlations of data from the EX treatment, which presumably eliminated the confounding impact of herbivory on yield. In 1980 (mean density ≈0.94 plants/cm²), density was negatively correlated with all three yield variables expressed on a per plant basis (SPKLT, SHTLEN and WT/PLNT). By contrast, in 1981 (mean density ≈0.38 plants/cm²), positive correlations obtained.
Discussion

Effects of microenvironment

The most striking outcome of these experiments was that plant success in U and I microenvironments did not accord with the marked disparity between U and I densities consistently observed for indigenous plants at the study site (Chapter II). A naive expectation, supported by the literature (e.g., Evans and Young 1972), was that experimental plants would fare better in U microenvironments, but this was not the case. In 1980, the one significant result among microenvironments was more PLANTS in M planters. For this singular result, I can offer no plausible explanation. Both M and I planters in 1980 were located beyond the canopies of replicate shrubs, making these locations "I-like" by the conventions defining I locations in the 1981 version of the experiment. The large exclosure structures of the 1980 experiment necessitated the purposeful choice of replicate shrubs with unusually high canopies. As a result, U microenvironmental conditions associated with such shrubs may not have been as distinct from I conditions, as is arguably the case for more "typical" shrubs (Chapter I; Table 1.1). Mostly equivocal results therefore ensued (Fig. 4.4).

For 1981 data, though, this argument cannot be invoked. The smaller exclosures used in 1981 allowed the implementation of rigorous, more ecologically pertinent criteria defining U and I locations (Chapter II; Fig. 2.1), utilized for all aspects of the study except the 1980 planting experiment. Further, replicate shrubs were selected at random. In 1981, I plants were significantly more successful by all measures, including density (Fig. 4.5). This last difference was consistent
throughout the winter and spring, during which germination leading to recruitment apparently continued, even after May 9 (Fig. 4.6). How can these results be reconciled with the dispersion exhibited by indigenous *B. tectorum* plants?

Several results indicated that a number of plausible, expected differences between U and I microenvironments were not operational during either planting experiment. First, it should be noted that many of the putative advantages of the U microenvironment engendering positive associations between ground-story species and shrubs involve more favorable moisture conditions for plants growing beneath shrub canopies (Chapter I; Table 1.1). In both 1980 and 1981, the growing seasons for *B. tectorum* were unusually wet (Table 4.6); total precipitation over the 10-month period was roughly 132% and 137% of the 1951-1980 mean, for 1980 and 1981 respectively. Both years, precipitation was particularly abundant during October through December, when the bulk of germination and establishment was likely occurring (for 1981, Fig. 4.5). If in most years, I plants are more likely than U plants to suffer drought-induced detriments to growth or even fatal desiccation (e.g., see Chapter V for demographic data for indigenous plants in 1986; Fig. 5.9), then this difference between U and I microenvironments may have been diminished or eliminated during the relatively wet years when these experiments were conducted.

Second, burial of introduced seeds was intended to fix their location and to facilitate distinguishing experimental plants in each planter from those arising from immigrant indigenous seeds. However, this practice unintentionally provided premium microsite conditions for successful germination and establishment (Evans and Young 1970, 1972,
Young and Evans 1985). If U microenvironments naturally harbor more safe sites than I ones, then the protocol of the experiment prevented this difference from affecting the results much, especially given the unusually moist conditions already mentioned.

Third, lack of a significant effect of shrub removal in 1980 (Tables 4.2 and 4.3) and similar lack of significance for the interaction of this factor with microenvironment meant that direct biotic effects of shrubs (e.g., by depleting limited soil moisture) were not important in differentiating U and I microenvironments under the conditions of this experiment. Although this result was surprising, it was reinforced by the consistent lack of correlation of any dependent variable measured in 1981 with several physical attributes of the replicate shrubs, even when data were analyzed separately by microenvironment.

Reports from past research have disagreed about the degree to which sagebrush and *B. tectorum* plants might interact in partitioning a potentially scarce soilwater resource. While Sturges (1977), Caldwell (1979) and others have labeled sagebrush a superior competitor for water, even in near-surface soil horizons, evidence marshalled in thorough reviews of cheatgrass biology by Klemmedson and Smith (1964) and Thill et al. (1984) supported the view that *B. tectorum* is little influenced by native sagebrush-steppe species, primarily because its phenology and capacity to elaborate roots at low temperatures allow it to utilize soil moisture at a time of year when it is relatively abundant. If any resource partitioning were occurring, its intensity would be influenced strongly by the amount and timing of precipitation. Relatively wet years in 1980 and 1981 reduced the likelihood that experimental *B. tectorum* plants and replicate shrubs were partitioning a scarce
soilwater resource.

The statistical results described above which opposed inferring biotic effects regarding soil moisture, likewise did not support negative allelopathic effects of replicate shrubs on U plants. Although *Artemisia tridentata* has been described as being a producer of allelochemicals responsible for a number of detriments suffered by neighboring plants (West 1983a and citations therein), its litter is a preferred germination microsite for *B. tectorum* seeds (Young and Evans 1975), rather than an inhibitor. Further, any putative antibiotic effects of volatiles or leachates from sagebrush leaves may have been diluted during the unusually moist years when the planting experiments were conducted.

The sole result clearly indicating an effect related to proximity to a shrub canopy was the apparent greater probability of I plants to experience overwintering mortality in 1981. This was probably not attributable to a direct negative biotic effect of the sagebrush on *B. tectorum* plants. Frost-heaving can be a significant source of mortality for *B. tectorum* seedlings (Mack and Pyke 1984). At the study site, the sandy soil is perched atop a fairly shallow calcium carbonate hardpan (at 20-30 cm; M. Kelrick, personal observation), promoting prolonged periods of persistently moist soil when precipitation is sufficient and timely. These conditions were likely to have occurred during late autumn of both experimental years, when temperatures also fluctuate around 0°C. Under these conditions, I often observed frost-heaving being more common in I microenvironments, presumably because the insulative effects of U litter and the environment of radiative exchange beneath shrub canopies both acted to maintain higher U soil temperatures
at night.

Finally, despite significant differences in soil attributes which might indicate more favorable nutrient status in U than in I microenvironments (Chapter II; Table 2.6), growth measures of U and I plants did not reflect such differences in either year of the study. Although Kline (1973) demonstrated that B. tectorum plants beneath sagebrush canopies were more efficient at converting the more abundant U nitrogen into plant biomass, Klemmedson and Smith (1964, p. 229) cited unpublished work of Pearse which reported that B. tectorum "does well on soils low in nitrogen," and neither work clarified what level of N might be potentially limiting for B. tectorum plant growth. A further impediment to interpreting measurements of soil nutrients in my study is that soil samples were only collected once, in early to mid-autumn, 1981; such data cannot be considered indicative of soil nutrient status throughout the duration of the experiments. Thus, although shrubs apparently did represent "islands of fertility" at the study site, it is not clear that elevated levels of nutrients in U microenvironments exerted any differential effects on growth of B. tectorum under these experimental conditions.

The simplest explanation of the superior performance of I plants (i.e., WT, SHTLEN and SPKLT) in 1981 (Fig. 4.5) is that these plants should have had access to greater irradiance of photosynthetically active wavelengths than U plants, ceteris paribus. Based on a series of greenhouse experiments involving plant-canopy-shaded control individuals and similar plants exposed to supplemental irradiance, Bookman and Mack (1983) suggested that B. tectorum plants are relatively sensitive to the effects of shading on potential rates of carbon gain. These authors
speculated (p. 407) that, for *B. tectorum* individuals beneath other vegetation, canopy-shading "is the initial cause for decreased productivity and fitness in shaded environments, but the inability of roots to grow towards available resources may be the ultimate cause of mortality for these plants." A larger flux of photosynthetically active radiation affords plants greater potential carbon gain, but typically at the expense of an increased heat load for leaves as well as increased transpirational demand. Thus, if water is limiting, being subjected to greater irradiance may be a disadvantage. Under unusually wet conditions, though, *I* plants may be able to capitalize on the greater irradiance they likely experience. The speculation of Bookman and Mack (1983), then, is not only a viable explanation for the significantly greater vigor of *I* plants in 1981 (when moisture was apparently sufficient), but also provides a tentative mechanism leading to the significantly lower densities of *U* plants observed, a result more difficult to explain.

*Effects of exclosures*

Foraging activities of several potential granivorous and/or herbivorous rodent species were targeted with the exclosure treatments. A substantial body of work describes these consumers at this site (Parmenter and MacMahon 1983, Parmenter et al. 1984, Kelrick et al. 1986, Broome 1988, Maguire 1990) and has indicated that the deermouse (*Peromyscus maniculatus*) was by far the most abundant rodent species at the site.

A preconception during the design of this experiment was that differences in PLANTS resulting from rodent activity were most likely to
be due to granivory rather than herbivory. Several previous exclosure studies investigated granivores' influence on annual plant recruitment from both introduced and indigenous seeds in shrub-dominated and annual grassland systems, and had demonstrated significantly greater densities of plants in exclosure-protected microenvironments (e.g., Bartholomew 1970, Halligan 1973, Borchert and Jain 1978, Inouye et al. 1980). By contrast, no differences in PLANTS were observed among exclosure types in either year of this study. Although small excavations were observed on several occasions in RC exclosures or in the vicinity of EC planters, no sign of digging was ever observed in a planter.

Burial of experimental seeds may have deterred granivory, given the identities of potential granivores at the site. The most likely candidates were Peromyscus maniculatus and the pocket mouse, Perognathus parvus (Kelrick et al. 1986). Although P. maniculatus is credited with detecting and consuming buried seeds in the field and under laboratory conditions (Howard and Cole 1967 and citations therein), these mice were notably poor at locating seeds of Oryzopsis hymenoides (a preferred food item [Kelrick et al. 1986]) buried beneath sand at a variety of moisture levels (Johnson and Jorgensen 1981). The pocket mouse, a heteromyid likely to be more strictly granivorous than Peromyscus (Reichman 1975), is also probably more adept at finding buried seeds (Johnson and Jorgensen 1981); however, only a handful of Perognathus individuals were encountered during three years of extensive live-trapping at the site. Thus, buried seeds may have been relatively safe from rodent granivores at this site. Also, seeds of B. tectorum appear to be a relatively low-ranked food item for shrub-steppe granivores, when other choices are available (Kelrick et al. 1986 and citations therein), further reducing
the chance that seed predation played a role in determining PLANTS in this study.

Values for the remaining three dependent variables (WT, SHTLEN and SPKLT) were all significantly smaller for unexclosed planters than those measured for protected planters, in both years of the study (Fig. 4.3). Means of variables from RC exclosures were consistently intermediate between those for protected and unprotected planters, supporting the notion that effects of the exclosure structures themselves were unlikely to have been responsible for the differences observed. Rather, it was probably grazing that reduced the mean size and reproductive output of unexclosed plants. I noted direct consequences of grazing among unexclosed plants, a number of which exhibited clipped shoot bases along with regrown flowering culms. This observation was particularly striking, since, during four growing seasons, I had never encountered an indigenous B. tectorum plant at the study site with more than a single flowering culm.

Although Uinta ground squirrels (Spermophilus armatus) were observed on occasion clipping B. tectorum plants at the study site, the most likely grazer was Peromyscus maniculatus. Vegetation may be a substantial portion of the diet of P. maniculatus during certain parts of the year (Kritzman 1974, Parmenter and MacMahon 1983), and the species is known to consume B. tectorum plants (Pyke 1986). On the basis of demographic mapping of individual plants inside and outside of an exclosure, Pyke (1986) was able to conclude that grazing had little effect on mortality of B. tectorum plants, but did cause decreases in biomass and seed production whose magnitudes correlated with severity of grazing. Pyke’s results parallel the effects ascribed to grazing in
this study. It is possible that grazing in this experiment could have caused mortality as well, but that it went unrecognized because it was compensated by recruitment.

Non-significant interactions between microenvironment and exclosure treatments in both years of the study (Tables 4.3 and 4.4) indicated that there was not strong, shrub-centered spatial patterning to the grazing damage observed in the experiment.

Exclosures may have exerted unintended effects that must not be overlooked. For example, altered air circulation around exclosed plants may have affected convective exchanges (especially heat) between plants and the atmosphere. Radiative exchange (particularly for plants in lidded exclosures) may also have been modified. Since such effects were not measured, it is unclear how they may have been manifested in the results. However, given the major differences in exclosure designs between the two years of the study and the consistency of both years' results (Fig. 4.3), it seems unlikely that an artifactual effect due to exclosures was an important factor in these experiments.

Effects of density

Plants respond to a broad range of densities plastically, accommodating by regulating the number of modules comprising their bodies, or less importantly, by regulating modular sizes (White and Harper 1970). Palmblad (1968) grew *B. tectorum* plants at densities ranging from one to 200 plants per 24 cm², and found that both mean weight per plant and mean number of seeds produced per plant (both calculated from pot means presented in the paper) decreased monotonically with density. When data were pooled across all treatments for each year of my study, there was
no significant difference between 1980 and 1981 values of either WT/PLNT or SPKLT, despite a more than three-fold larger mean PLANTS value in 1980 (Table 4.1). However, when data were grouped by exclosure treatment, 1980 data for these two variables from the EX treatment were significantly negatively correlated with PLANTS (Table 4.5). WT/PLNT for the RC treatment in 1980 was also significantly negatively correlated with PLANTS. Thus, densities averaging roughly one plant per cm² were sufficient to stimulate plastic reductions in the same two attributes measured in Palmblad's study, but these reductions could only be perceived when grazing was prevented. Removal of tissue by herbivores in the EC treatment may have diminished the intensity of intraspecific interference enough in these planters to alleviate density-sensitive plastic growth reductions.

Mean SHTLEN (pooled over all treatments) of 1980 plants significantly exceeded that of plants in 1981 (Table 4.1). Restriction of shoot elongation in 1981 by the lidded exclosures used cannot be the sole explanation for this result, since not all plants grew in exclosures, and since fully exclosed plants had significantly longer shoots in 1981 than unexclosed controls (Fig.4.3). Rather, photomorphogenetic effects (Schopfer 1984) may have influenced shoot length, another plastic response to the difference in densities in the two years. Density-dependent interference for light interception can induce stem elongation. With grand means of individual shoot biomasses similar in both years of the study (Table 4.1), greater SHTLEN for 1980 plants may reflect differential biomass allocation leading to greater stem elongation stimulated by their higher densities.

Mean plant densities, pooled over all treatments, from both years
of the planting experiment (Table 4.1; PLANTS per 66 cm²) exceeded mean densities of indigenous B. tectorum plants in either microenvironment in both 1981 and 1986 (cf. Chapter II; Table 2.2). However, there was substantial overlap among individual sample values recorded in all four instances, indicating that results of the planting experiment were not artifacts of unrealistically high experimental densities. 1981 was probably a particularly favorable year for recruitment of indigenous plants (cf. densities for 1981 and 1986, Chapter II; Table 2.2). Thus, in view of the relatively high densities obtained in the 1981 planting experiment, positive correlations between PLANTS and other variables measured (Table 4.5) support the contention that density-dependent mortality (a more dire effect of elevated density) was unlikely to be an important factor determining local plant numbers at the study site.

Conclusions

The results of this experiment demonstrated clearly that, given appropriate conditions for germination and establishment, I plants can be as successful, or more so, than U counterparts. Effects of granivores and herbivores, foraging in a spatially non-random manner, also could not account for differences in numbers of indigenous plants in U vs. I microenvironments. While there were density effects on mean plant size and reproductive potential in protected planters during 1980, the experimental densities associated with such effects were several times larger than those observed when indigenous plants were sampled (cf. Tables 2.2 and 4.1). Further, density and mean plant attributes were positively correlated in 1981, despite experimental densities well above those of indigenous plants. Apparently, intrinsic density-dependent
responses cannot be invoked to explain differences in numbers of B. tectorum plants in U and I microenvironments. The discrepancy between these outcomes and the naturally occurring dispersion identified the critical role of seed fates and safe sites in determining the spatial structure of the B. tectorum population at this sagebrush-steppe site.
Table 4.1. Grand means of several variables from both years of the Bromus tectorum planting experiment, with results of t-tests\textsuperscript{a} comparing the two years' data.

<table>
<thead>
<tr>
<th>Variable\textsuperscript{c}</th>
<th>1980</th>
<th>1981</th>
<th>t-value</th>
<th>Significance\textsuperscript{d}</th>
</tr>
</thead>
<tbody>
<tr>
<td>PLANTS</td>
<td>60.33 ± 3.00</td>
<td>18.87 ± 1.36</td>
<td>12.58</td>
<td>( P &lt; 0.001 )</td>
</tr>
<tr>
<td>WT</td>
<td>0.91 ± 0.058</td>
<td>0.37 ± 0.032</td>
<td>8.16</td>
<td>( P &lt; 0.001 )</td>
</tr>
<tr>
<td>SPKLT</td>
<td>2.85 ± 0.18</td>
<td>3.12 ± 0.16</td>
<td>-1.12</td>
<td>NS</td>
</tr>
<tr>
<td>SHTLEN</td>
<td>17.37 ± 0.51</td>
<td>13.48 ± 0.49</td>
<td>5.46</td>
<td>( P &lt; 0.001 )</td>
</tr>
<tr>
<td>WT/PLNT</td>
<td>0.018 ± 0.0013</td>
<td>0.018 ± 0.0012</td>
<td>0.55</td>
<td>NS</td>
</tr>
<tr>
<td>PLANTS/50 seeds</td>
<td>15.08 ± 0.75</td>
<td>18.87 ± 1.36</td>
<td>-8.02</td>
<td>( P &lt; 0.001 )</td>
</tr>
</tbody>
</table>

\textsuperscript{a}Assuming heterogeneous variances; for all tests, \( df = 89 \).

\textsuperscript{b}n = 90.

\textsuperscript{c}PLANTS = number of plants per planter; WT = total dry weight (g) of all plants per planter; SPKLT = mean number of spikelets per plant from a particular planter; SHTLEN = mean shoot length (cm) per plant from a particular planter; WT/PLNT = mean weight per plant from a particular planter (WT divided by PLANTS); PLANTS/50 seeds = for 1980, PLANTS divided by 4, and for 1981, PLANTS.

\textsuperscript{d}Statistical significance. NS = not significant; i.e., \( P > 0.05 \).
Table 4.2. Means\(^a\) ± SE of four dependent variables from the *Bromus tectorum* planting experiment, 1980, presented according to presence or absence of the above-ground portion of the replicate shrub.

\begin{table}[h]
\centering
\begin{tabular}{llll}
\hline
\textbf{Shrub treatment} & \\
\hline
\textbf{Variable} & \textbf{Present} & \textbf{Removed} & \\
\hline
PLANTS & 59.60 ± 3.92 & 61.07 ± 4.59 & \\
WT & 0.85 ± 0.054 & 0.97 ± 0.102 & \\
SPKLT & 26.58 ± 1.89 & 30.33 ± 3.00 & \\
SHTLEN & 17.75 ± 0.59 & 16.98 ± 0.85 & \\
\hline
\end{tabular}
\end{table}

\(^a\)\(n = 45\).

\(^b\)Variable names as in Table 4.1.
Table 4.3. Results of analyses of variance of four dependent variables from the *Bromus tectorum* planting experiment, 1980.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom&lt;br&gt;&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Variable&lt;br&gt;&lt;sup&gt;b&lt;/sup&gt;</th>
<th>F-value</th>
<th>Significance&lt;br&gt;&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub presence/absence</td>
<td>1,8</td>
<td>PLANTS</td>
<td>0.41</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WT</td>
<td>1.05</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>0.51</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>0.24</td>
<td>NS</td>
</tr>
<tr>
<td>Exclosure treatment</td>
<td>2,16</td>
<td>PLANTS</td>
<td>0.32</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WT</td>
<td>3.04</td>
<td>0.10&gt;P&gt;0.05*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>2.66</td>
<td>NS*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>11.30</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td>Shrub presence X Exclosure treatment</td>
<td>2,16</td>
<td>PLANTS</td>
<td>0.80</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WT</td>
<td>0.71</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>0.37</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>1.16</td>
<td>NS</td>
</tr>
<tr>
<td>Microenvironment</td>
<td>2,8</td>
<td>PLANTS</td>
<td>6.15</td>
<td>P&lt;0.025</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WT</td>
<td>2.28</td>
<td>NS*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>2.89</td>
<td>NS*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>3.63</td>
<td>0.10&gt;P&gt;0.05</td>
</tr>
</tbody>
</table>
Table 4.3. (continued)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Variable</th>
<th>F-value</th>
<th>Significance&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub presence X Micro-environment</td>
<td>2,40</td>
<td>PLANTS</td>
<td>1.58</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WT</td>
<td>0.26</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>0.27</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>0.22</td>
<td>NS</td>
</tr>
<tr>
<td>Exclosure treatment X Microenvironment</td>
<td>4,40</td>
<td>PLANTS</td>
<td>0.59</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WT</td>
<td>0.65</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>0.13</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>0.25</td>
<td>NS</td>
</tr>
<tr>
<td>Shrub presence X Exclosure treatment X Microenvironment</td>
<td>4,40</td>
<td>PLANTS</td>
<td>1.38</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WT</td>
<td>1.32</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>0.31</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>0.29</td>
<td>NS</td>
</tr>
</tbody>
</table>

<sup>a</sup> Degrees of freedom listed are: those for the source of variation, those for the appropriate error against which it was tested.

<sup>b</sup> Variable names as in Table 4.1.

<sup>c</sup> Statistical significance. NS = not significant; i.e., \( P > 0.05 \).

*Variances of means for these variables were heterogeneous.*
Table 4.4. Results of analyses of variance of four dependent variables from the *Bromus tectorum* planting experiment, 1981.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Variable&lt;sup&gt;b&lt;/sup&gt;</th>
<th>F-value</th>
<th>Significance&lt;sup&gt;c&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microenvironment</td>
<td>1,14</td>
<td>PLANTS</td>
<td>12.89</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WT</td>
<td>26.78</td>
<td>P&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>13.97</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>7.18</td>
<td>P&lt;0.05*</td>
</tr>
<tr>
<td>Exclosure treatment</td>
<td>2,28</td>
<td>PLANTS</td>
<td>1.54</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WT</td>
<td>8.74</td>
<td>P&lt;0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>6.23</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>4.27</td>
<td>P&lt;0.05</td>
</tr>
<tr>
<td>Microenvironment X</td>
<td>2,28</td>
<td>PLANTS</td>
<td>1.42</td>
<td>NS</td>
</tr>
<tr>
<td>Exclosure treatment</td>
<td></td>
<td>WT</td>
<td>0.21</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SPKLT</td>
<td>0.65</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SHTLEN</td>
<td>0.69</td>
<td>NS</td>
</tr>
</tbody>
</table>

<sup>a</sup>Degrees of freedom listed are: those for the source of variation, those for the appropriate error against which it was tested.

<sup>b</sup>Variable names as in Table 4.1.

<sup>c</sup>Statistical significance. NS = not significant; i.e., P > 0.05.

*Variances of means for this variable were heterogeneous.
Table 4.5. Correlation coefficients for parametric correlations\(^a\) of number of plants per planter (PLANTS) with other dependent variables from the *Bromus tectorum* planting experiment.

<table>
<thead>
<tr>
<th>Treatment(^c)</th>
<th>Year</th>
<th>WT</th>
<th>SPKLT</th>
<th>SHTLEN</th>
<th>WT/PLNT</th>
</tr>
</thead>
<tbody>
<tr>
<td>EX</td>
<td>1980</td>
<td>0.402*</td>
<td>-0.545**</td>
<td>-0.343</td>
<td>-0.625**</td>
</tr>
<tr>
<td></td>
<td>1981</td>
<td>0.785**</td>
<td>0.409*</td>
<td>0.579**</td>
<td>0.345</td>
</tr>
<tr>
<td>RC</td>
<td>1980</td>
<td>0.306</td>
<td>-0.311</td>
<td>-0.253</td>
<td>-0.471**</td>
</tr>
<tr>
<td></td>
<td>1981</td>
<td>0.896**</td>
<td>0.340</td>
<td>0.328</td>
<td>0.394*</td>
</tr>
<tr>
<td>EC</td>
<td>1980</td>
<td>0.754**</td>
<td>-0.120</td>
<td>0.309</td>
<td>-0.248</td>
</tr>
<tr>
<td></td>
<td>1981</td>
<td>0.760**</td>
<td>-0.135</td>
<td>0.119</td>
<td>-0.200</td>
</tr>
<tr>
<td>All combined</td>
<td>1980</td>
<td>0.388*</td>
<td>-0.308</td>
<td>-0.072</td>
<td>-0.423*</td>
</tr>
<tr>
<td>combined</td>
<td>1981</td>
<td>0.780**</td>
<td>0.197</td>
<td>0.347</td>
<td>0.148</td>
</tr>
</tbody>
</table>

\(^a\)DF = 88.

\(^b\)Variable names as in Table 4.1.

\(^c\)EX = intact exclosure; RC = exclosure with doors; EC = unexclosed.

\(* P < 0.05; \,** P < 0.01\).
Table 4.6. Monthly total precipitation from the Kemmerer, Wyoming NOAA station during the 1980 and 1981 *Bromus tectorum* planting experiments and its relationship to 1951-1980 mean values from the same station.

<table>
<thead>
<tr>
<th>Month</th>
<th>Total (mm)</th>
<th>% of 30-yr mean</th>
<th>Total (mm)</th>
<th>% of 30-yr mean</th>
<th>Total (mm)</th>
<th>% of 30-yr mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>7.4</td>
<td>42</td>
<td>22.5</td>
<td>129</td>
<td></td>
<td></td>
</tr>
<tr>
<td>February</td>
<td>7.9</td>
<td>54</td>
<td>14.0</td>
<td>97</td>
<td></td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>33.3</td>
<td>256</td>
<td>36.8</td>
<td>283</td>
<td></td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>14.2</td>
<td>78</td>
<td>37.8</td>
<td>212</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>72.4</td>
<td>232</td>
<td>50.0</td>
<td>160</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>14.2</td>
<td>47</td>
<td>3.8</td>
<td>13</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>18.8</td>
<td>119</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>3.3</td>
<td>21</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>37.1</td>
<td>180</td>
<td>9.4</td>
<td>46</td>
<td></td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>22.9</td>
<td>129</td>
<td>45.2</td>
<td>254</td>
<td></td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>42.0</td>
<td>268</td>
<td>30.0</td>
<td>191</td>
<td></td>
<td></td>
</tr>
<tr>
<td>December</td>
<td>38.5</td>
<td>236</td>
<td>40.1</td>
<td>246</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
1980 PLANTING EXPERIMENT
10 SHRUBS
200 SEEDS PER PLANTER

EC TREATMENT

RC TREATMENT

EX TREATMENT
1981 PLANTING EXPERIMENT
15 SHRUBS
50 SEEDS PER PLANTER

EC TREATMENT

RC TREATMENT

EX TREATMENT

15cm
1980 PLANTING EXPERIMENT

**NUMBER OF PLANTS**

- U: 11
- M: 57
- I: 54

**SPIKELETS/PLANT**

- U: 3.5
- M: 3.0
- I: 2.5

**DRY WEIGHT (g)**

- U: 1.0
- M: 1.2
- I: 1.4

**SHOOT LENGTH (cm)**

- U: 15
- M: 18
- I: 21

**Microenvironment**

- U: Upper
- M: Middle
- I: Lower
1981 PLANTING EXPERIMENT

MICROENVIRONMENT

<table>
<thead>
<tr>
<th>NUMBER OF PLANTS</th>
<th>SPIKELETS/PLANT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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CHAPTER V

THE DISPERSION OF BROMUS TECTORUM: FACTORS AFFECTING SEEDS

Introduction

The dispersion pattern exhibited by any plant species population at a particular site and time is fundamentally determined by two prior events: 1) the arrival of its viable propagules at the site, and 2) the growth of individual plants from among those propagules. Many other influences (e.g., seed predation, herbivory or density-dependent mortality) may modify, but are not likely to efface, the spatial template established by these two basic processes. For annual plants, whose life history precludes vegetative propagation, these two processes affect the seed portion of the life cycle. The first is seed dispersal, the second involves both germination and establishment. Careful field observation of the fates of annuals' seeds during the time interval separating successive yearly cohorts of growing plants may elucidate important determinants of the dispersion of those plants (Watkinson 1978a,b; Keddy 1982; Smith 1983; Westelaken and Maun 1985).

The prevailing conceptual framework highlighting the importance of processes affecting the seed portion of the life cycle in plant population ecology is embodied in the term "safe site" (Harper et al. 1961). Harper (1977, p. 112) defined a safe site as a zone in which a seed may find itself which provides (a) the stimuli required for breakage of seed dormancy, (b) the conditions required for the germination processes to proceed and (c) the resources (water and oxygen) which are consumed in the course of germination. In addition a 'safe site' is one from which specific hazards are absent -- such as predators, competitors, toxic soil constituents and pre-emergence pathogens.
While the notion of the safe site is both conceptually cogent and broadly acknowledged (e.g., Harper et al. 1965, Silvertown 1981, Fowler 1986, Andersen 1989, Silvertown and Smith 1989, Watkinson 1990), the term describes a phenomenon which is operationally elusive. Among many imaginable difficulties that might prevent learning what safe sites are like in the field and how they influence plant population structure and dynamics, two are most apparent. First, to be truly pertinent, observations and measurements aimed at characterizing a microsite that may be a safe site must be gathered at the appropriate scale--that of a single seed and newly germinating seedling. Second, in many instances, the location of a safe site is only indicated by the existence of a newly established plant, as a fait accompli, since the germinating seed was previously buried or otherwise not readily observable. When demographic analyses are to be undertaken, both these impediments are amplified by the requirement to link safe site characterizations with fates of unambiguously identifiable individual seeds.

Results of previous work (Chapters III, IV) attempting to ascertain mechanisms determining the distinctive dispersion of Bromus tectorum at a sagebrush-steppe site in SW Wyoming (Chapter II) did not account satisfactorily for the observed pattern of plants; by elimination, factors affecting the seed portion of the life cycle seemed to be critical determinants of the natural dispersion of B. tectorum at this site. Several lines of reasoning converged to indicate that the relationship between seed fates and plant dispersion was itself connected to the functional role of litter. 1) The distribution of litter at the research site was strongly associated with shrubs (see Garcia-Moya and McKell 1970, Halvorson and Patten 1975, Nelson and Chew 1977, West 1979)
and therefore generally parallelled the dispersion of *Bromus* plants.

2) Litter can modify microclimatic conditions at the soil surface in favor of *Bromus* germination and establishment in artificially seeded and littered treatments (Evans and Young 1970). An important *caveat* is that measurements such as those described by Evans and Young may or may not aptly reflect conditions affecting a germinating plant embryo, since the scale at which measurements were collected was not that of a safe site.

3) In contrast with the comparatively smooth soil surface where litter is absent (microenvironments), the convoluted structure of litter and associated interstices may provide the most likely ultimate lodging for shed *Bromus* seeds being transported along the ground by wind or water (Phase II dispersal of Watkinson [1978b]).

4) The structure of litter and associated interstices may provide a high density of safe sites (Harper 1977). Within this structure, seeds may be particularly likely to become buried and/or to assume an embryo-down attitude, either of which is likely to improve imbibition contributing to successful germination (see Sheldon 1974; Peart 1979). Litter around a germinating seed may also provide a restrictive framework against which the force of radicle growth can be exerted, facilitating radicle penetration of mineral soil (Peart 1981).

The aim of this phase of my research was to assess the demography of seeds as a function of their interactions with surfaces in the field, and, in turn, how these interactions might be reflected in the dispersion of *Bromus tectorum* plants at the study site. In accord with the premises presented above, two objectives were pursued: 1) investigating the functioning of litter as seed depository and 2) examining the fates of individual *Bromus* seeds on littered versus bare mineral soil sur-
faces. A crucial working assumption for linking litter effects to the observed dispersion pattern was that a predictable, strong correspondence existed between microenvironment and surface texture: that U microenvironments were littered and I microenvironments were bare ground. It remained to experimentally disentangle the potential confounding of effects of a particular microenvironment and those of the surface type assumed to be predictably encountered in that microenvironment.

Methods

Two approaches were used to observe fates of *B. tectorum* seeds in U and I microenvironments (or their associated surface textures); both involved repeated observations of introduced seeds marked with nail polish. In the first approach, marked seeds were released in naturally occurring U and I microenvironments (henceforth, free seeds experiment). In the second, marked seeds were confined to artificial, constructed surfaces and adjacent natural controls (henceforth, tethered seeds experiment).

In both experiments, an individual sagebrush shrub constituted a replicate. Replicate shrubs were chosen using a random numbers table to generate coordinates within a 30- X 30-m plot. Determination of U and I locations at each shrub was according to the established conventions (Chapter II; Fig. 2.1); any necessary modifications are detailed below.

Marking seeds

Among the handful of studies (Naylor 1972, Mortimer 1974, Watkinson 1978a,b, Blom and Van Heeswijk 1984, Westelaken and Maun 1985) in which paints of various types have been used to mark seeds, only Blom
and Van Heeswijk (1984) documented effects of the marking method on germination. In their study, total germination percentage of *Plantago lanceolata* seeds was unaffected by marking with latex paint, although marked seeds required slightly longer to germinate.

I conducted several preliminary investigations to ascertain potential effects of my marking method on germination. A greenhouse germination trial involved a three-way factorial, completely randomized design with two levels of moisture supplied, seeds marked with nail polish or left unmarked and seeds deposited on the surface of either mineral soil or soil covered with litter. Two replicates of each of the eight treatment combinations were initiated with 25 seeds apiece. Seeds, soil and litter all derived from the field site. Ninety-nine of 100 seeds had tested viable using 2,3,5-triphenyl tetrazolium chloride (Grabe 1970) prior to the trial. Seeds were marked by coating the distal third of the lemma and the awn extending from the lemma with polish (the method eventually used in field experiments); thus, polish was as far as possible from the embryo-end of the caryopsis. Each group of 25 seeds was dropped down a PVC pipe (45 cm X 6.5 cm I.D.) onto its surface treatment so that seeds could assume their natural attitude.

In further growth chamber trials, seeds were marked with both nail polish and fly-tying cement (essentially clear nail polish, used in the tethered seeds experiment; see below). To enhance the likelihood of observing detrimental effects, these trials included applying both substances directly to embryos protected only by the seed coat (i.e., embryos from which the natural investing tissue of the dispersal unit -- the lemma of the caryopsis -- had been removed).
Free seeds experiment

The design of this experiment was conceived around suspicions that 1) prevailing westerly winds were the main agent of Phase II seed dispersal, 2) the bulk of seed movement across the surface was therefore eastward and 3) seeds were more likely to move from I into U microenvironments than vice versa.

At each of five shrubs, 200 marked seeds were released on April 18, 1986, prior to observations of spring germination of indigenous seeds (Fig. 5.1). Four groups of 25 seeds, each group marked a different color, were released in U microenvironments in the four cardinal compass directions. Ten groups of 10 seeds were released in I microenvironments along two lines on the prevailing windward (i.e., west) side of a shrub, five groups along each line. Each line's seeds were of one color; both of these colors were distinct from those used for U seeds, making six colors in all. Interspace lines were oriented N-S and located at 1/3 and 2/3 of the distance between the replicate shrub's western canopy edge and that of the nearest neighbor shrub to the west. The five groups of seeds (per I line) were placed at equal intervals along each line, the total length of which exceeded by 10 cm at each end the extent of the N-S axis through the center of the replicate shrub's canopy. A piece of galvanized steel flashing 1.5 times the length of the same N-S canopy axis and parallel to it, and 15 cm in height, was installed on the lee (east) side of the replicate shrub to serve as a catchment for marked seeds dispersing downwind of the replicate shrub. This barrier was placed as far from the replicate shrub as possible to minimize any effects it may have exerted on small scale air turbulence influencing seed movements.
Seed release points were marked with small steel pins. Seeds were dropped down a PVC pipe (45 cm X 6.5 cm I.D.) centered over the release point. Use of the pipe satisfied several objectives: 1) during free fall, seeds could assume a natural attitude with respect to the surface prior to landing; 2) seeds were less likely to pile atop one another than if they were simply dumped out of a small envelope; 3) seeds could be released in a repeatable manner without regard to microenvironment (the pipe was used to penetrate the shrub canopy so that seeds could be dropped vertically onto U release points); and 4) seeds were not blown away by wind during the act of releasing them.

The correspondence between microenvironments and surface textures (i.e., U, littered; I, predominantly bare ground) was a premise in the conception of this experiment, but was addressed directly by characterizing the surface texture of 1-dm² quadrats centered on every seed release point (n = 20 for U microenvironments; n = 50 for I microenvironments). U quadrats were classified into one of four litter cover categories (0 - 25%, 26 - 50%, 51 - 75% or 76 - 100% covered). I quadrats were assigned to one of six subjectively derived classes: quadrats were labelled bare ground (B), vegetated (V) or littered (L) if one of these three surfaces was the large majority of the quadrat area. Otherwise, quadrats were described as combinations of two of the above three classes, because the surface was covered roughly equally by both (B/V, V/L or L/B).

Seeds used in this experiment had been collected from plants at the study site in June, 1982. Viability of these seeds, which had been stored at room temperature in a paper bag, was essentially 100% (only one non-viable seed in four replicates of 25 seeds each tested with
tetrazolium). Any seeds with obvious damage were excluded during the marking procedure.

The experiment was monitored on nine dates: April 22, May 2, 6, 13, 20, 23, 27, 30 and June 3. On each sampling date, an attempt was made to account for every seed initially released in I quadrats and to observe whether it had germinated and in what kind of microsite germination had occurred. ("Germination," for all sampling dates except the last, meant observation of emergence of the coleoptile from the caryopsis.) Plants arising from I marked seeds were identified in the field with colored plastic cocktail toothpicks, and their fates were subsequently recorded. Numbers of seeds still observable within the 1-dm² quadrat areas around each I release point were recorded, and distances dispersed by seeds outside these areas were measured.

Observations of U seeds could only be conducted at a distance, to avoid disturbing the ground surface around the replicate shrubs, so that numbers of U marked seeds which had germinated were approximate until the experiment was harvested. On June 3, when indigenous B. tectorum plants were filling fruits, all marked seeds/plants which could be located were harvested. Since emerging hypocotyls pierced the lemma and thereby threaded the paint-marked tissue onto the developing root, numbers of "germinated" marked seeds used in the data analyses included those whose germination had only proceeded as far as hypocotyl emergence. These were recognized only by virtue of harvesting the experiment.

**Tethered seeds experiment**

The experiment was installed on September 16 and 17, 1986. At
each replicate shrub, six groups of seeds were placed, three per microenvironment (i.e., U and I; Fig. 5.2). In each microenvironment, three surface treatments (one group of seeds per treatment) were present: a natural (control) surface (N), a constructed surface similar to the surface of that microenvironment (i.e., littered [L] for U and bare ground [B] for I) and a constructed "complementary" surface (i.e., similar to the surface of the other microenvironment: bare ground for U, littered for I). Thus, this experiment represented a split-plot design, with microenvironment as the "whole-plot" factor and surface type as the "subplot" factor (Petersen 1985).

N surface treatment locations were classified according to extent of litter present (1 = 0-25% litter covered; 2 = 26-50%; 3 = 51-75%; and 4 = 76-100%). All but a single NU sites were 100% litter covered; this exception was >50% litter covered (i.e., 3). Nine of the 12 NI sites were scored as 1, two sites as 2 and one site as 3.

 Constructed surfaces were made by imbedding galvanized steel rings (2 cm tall X 12 cm in diameter) in the ground until flush with the ground surface, and removing the contained soil and/or litter to a depth of ≈1.5 cm. Resulting holes were filled with the appropriate material (all gathered just outside of the 30- X 30-m plot) -- litter, or mineral soil from either U or I microenvironments. Each natural surface treatment was centered on the appropriate (U or I) location (i.e., at the appropriate radial distance from a shrub trunk), and was allowed a diameter of 12 cm. The two constructed surface treatments per microenvironment were placed along arcs determined by the the U and I radial distances, with rings placed directly adjacent to and on either side of the natural treatments (≈1 cm between treatments). Each group
of seeds, then, occupied a 12-cm diameter circle of surface (henceforth, an arena).

Each treatment received a group of 16 painted seeds, each of which was individually attached to its own black, silk, fly-tying thread (5 cm in length). Each thread was positioned perpendicular to the long axis of the seed and secured to the central portion of the lemma with a small drop of fly-tying cement (similar to clear nail polish). Threads from four seeds (all marked the same color) were individually tied to a #2 steel split ring (5 mm in diameter). In all, four different colors of seeds were used; each treatment received four "ring's worth" of seeds (= 16 seeds total), one "ring's worth" of each of the four colors. A steel pin in the center of each arena anchored the rings. Seeds were placed in the treatments such that: 1) each color was consistently associated with a particular compass quadrant so that relative position of origin was known for all 16 seeds; 2) seeds were near, but not at, the full extent of their tethers, to maximize space between individual seeds without eliminating the possibility of movement in any direction; 3) seeds were initially horizontal, with the lemma up (a "natural" attitude on bare ground in the field); and 4) the degree to which vegetation and litter influenced the initial position of the tether was minimized (e.g., by carefully threading the seed under a potential obstruction rather than laying the thread over it). This last convention was a concern only in the NU treatment. The six treatments, with 16 seeds per treatment (= 96 seeds per shrub), were installed at each of 12 sagebrush shrubs such that there were three replicate installations for each of the four cardinal compass directions. The compass quadrant within which treatments were installed was determined systematically by
advancing 90° at each successive replicate shrub.

Seeds used in this experiment were collected in mid-June, 1986 from *B. tectorum* plants which had grown within the 30- X 30-m quadrat containing replicate shrubs for the tethered seeds experiment. They were 100% viable (tetrazolium tests of four replicates of 25 seeds each) and nearly 100% germinable at room temperature (≈23°C) by mid-September (mean ± SE of four replicates of eight painted seeds each was 7.5 ± 0.5).

This experiment was intended to indicate the effects of surface texture on the germination and establishment of *B. tectorum* as well as to isolate these effects from other potentially important microenvironment-specific influences. I hoped that tethering seeds would allow the implementation of a manipulative design with some assurance that sufficient observations could be made of the fates of seeds on particular surface textures in the field. Some anticipated disadvantages of this technique, potentially limiting its utility, were 1) the degree to which tethering would prevent a seed from "behaving" as it would untethered, 2) the importance of such artifactual "behavior" on the subsequent fate of the seed, and 3) the degree to which animals, especially granivores, would treat experimental, introduced seeds differently from indigenous ones and novel, experimental arenas differently from control surfaces. None of these concerns could be adequately addressed without conducting the experiment, since I have encountered no studies documenting the relatively long-term fates of individual seeds in a manipulative field experiment, and only one (Schupp 1988b) describing the use of tethers to secure seeds. 

The experiment was monitored on 14 dates over a 9-month period, the
final date coinciding with fruit maturation of indigenous 1986-87 co-
HORTS OF B. TECTORUM: September 22, 30, October 7, 16, 21, 28, November
13, 21, 28, December 19 (1986), March 6, April 21, June 3, and June 23
(1987). Some treatments were partially obscured by thin, fine snow
cover on November 13 (23 of 72), November 21 (54 of 72) and December 19
(one of 72); on these dates, observations of certain seeds within a
treatment may have been hindered, but newly emerged plants could be
recorded. On each sampling date, each of the 1152 seeds in the experi-
ment was recorded as being in one of five "states" (Table 5.1). Seed-
lings arising from marked seeds were identified with colored plastic
cocktail toothpicks and monitored individually thereafter. On December
19, the last observation date until the subsequent spring snowmelt,
seeds classified as "in good microsites" were also marked with tooth-
picks, and this method was continued for the March 6 and April 21 obser-
vation dates. On June 23, just prior to when indigenous B. TECTORUM
plants began shedding caryopses, surviving experimental plants were
harvested. For the purposes of seed survivorship analyses, June 23
marked the terminus of the cohort of experimental seeds (only 53 intro-
duced, marked seeds were observed on June 3).

Survivorship of indigenous fall-germinating plants

To provide a basis for comparison of survivorship patterns of
plants arising from experimentally introduced seeds in the tethered
seeds experiment, contemporaneous fates of indigenous B. TECTORUM
plants were observed. Once having noticed germination of indigenous B.
tectorum seeds on August 28, 1986, three 25- X 50-cm quadrats, their
long dimensions oriented radially from the trunks of three sagebrush
shrubs, were established on September 4 and 5 to collect survival data of naturally occurring U and I seedlings during the first several weeks of the tethered seeds experiment. Quadrats were chosen to contain interspace in which I plants were particularly plentiful, since, generally, I plants were much rarer than U plants. No effort was made to measure relative amounts of U and I microenvironments composing the quadrats. For the purposes of analysis, plants trunkward of the shrub canopy edge were deemed U plants, and all remaining were I plants. A total of 40 U and 85 I seedlings were identified with toothpicks and their survival was monitored four times during the fall: September 22, October 7, 21 and November 21.

Analysis

Free seeds experiment.--By June 3, all germinants and seedlings derived from marked seeds had desiccated, eliminating the possibility of examining differences in plant survivorship between microenvironments. Analyses of germination frequencies in the various quadrat types were pursued using a variety of log likelihood ratio tests of goodness-of-fit, as well as contingency table tests of independence. The difference between numbers of marked seeds germinating in U versus I microenvironments was assessed with Student's t-test.

Tethered seeds experiment.--Only 27 seeds ever germinated and produced observable plants, precluding most of the originally planned analyses based on numbers of plants or their patterns of survivorship. Nonetheless, observations of seed "states" allowed numerous analyses of seed fates. Treating seeds and plants jointly as "living individuals" enabled examination of whole-cohort survivorship from seed to plant death.
Numerous statistical approaches serve to evaluate demographic/survivorship data. These can be conceptually organized according to two fundamental questions that can be addressed with such data, clearly defined by Pyke and Thompson (1986, p. 240): "(1) Does a higher proportion of individuals in population 1 reach age x than in population 2?" and "(2) Is the life-span of a typical individual in population 1 longer than that of a typical individual in population 2?". The first question requires an approach aimed at analyzing differences among treatments at a single point in time, and might involve one to many separate such temporal snapshots of the populations of interest. Pyke and Thompson (1986) suggested that contingency table tests with $X^2$-like distributions are appropriate in these circumstances, but they did not mention that such tests cannot provide the resolution among treatment effects in a partially nested design (like that used in this study) analogous to that possible with ANOVA/mean comparison procedures. Neither did these authors mention that if variation among replicates is known or suspected (i.e., replicates should be treated as blocks, as is the case for shrubs in this experiment), then pooling frequency data across replicates into a single contingency table is not only a loss of information, but a source of weakened inference.

The Cochran-Mantel-Haenszel (CMH) statistics extend $X^2$-like tests of single two-dimensional contingency tables to accommodate greater dimensionality (strata) for replicates and/or multiple classification factors (SAS 1987). The general association statistic is particularly well-suited for data of the tethered seeds experiment. It assumes fixed margin totals for each two-way table (satisfied by my data, with 16 seeds per treatment) and does not require large counts (e.g., $>$ five)
per table cell, only large overall sample size (also satisfied, with 1152 seeds in all) (Landis et al. 1978, SAS 1987). CMH statistics provide stratum-adjusted tests of the two-way table of interest, thus affording within-factor distinctions among levels of a factor (e.g., among the three surface treatments in the tethered seeds experiment), when adjusted for effects represented in other dimensions (to extend the above analogy, adjusting for replicate shrubs and microenvironment). (I used the general association CMH statistic to test for differences in overall shape of survivorship curves by constructing two-way tables with interval number between sample dates as one dimension and levels of a main effect [Microenvironment or Surface type] as the second. Numbers of seeds unambiguously depredated and/or unequivocally lost provided the cell counts.) A shortcoming of the CMH statistics is that they have low power for rejecting the hypothesis of no association when patterns of association for some strata are balanced by opposite patterns in other strata. In the case of a statistically significant result, however, this potential ambiguity is of no consequence.

A second method of addressing the need for within-factor mean comparisons with demographic snapshot data is to transform the original variates of interest collected on a single sample date to ranks, then to perform an ANOVA and subsequent mean comparison tests on the ranks (Conover and Iman 1981). This is essentially an extension of the methodology of the Kruskal-Wallis and Friedman's tests (i.e., non-parametric ANOVA's) to more complex experimental designs. I used this approach to test for differences among treatments in numbers of living individuals present (seeds plus plants) for several sample dates. Tukey's test or the Tukey-Kramer procedure for unequal sample sizes were used for mean
comparisons, when appropriate after significant ANOVA F-tests (SAS 1987, Day and Quinn 1989). Non-orthogonal contrasts testing a priori hypotheses (i.e., planned comparisons) involving Microenvironment X Surface interaction means (to assess whether results on constructed surfaces differed from those on natural controls due to artifactual effects) were accomplished by estimating appropriate sums of squares using the GLM procedure of PC SAS (SAS 1987). These contrast F-tests were verified using estimates of minimum significant differences (MSD's) between means, derived with the Tukey-Kramer procedure, and were evaluated for significance against probabilities adjusted for an experimentwise error rate of $P = 0.05$ by the Dunn-Sidak method (Sokal and Rohlf 1981, Day and Quinn 1989).

The same statistical approach served to test whether seeds occurred in "good microsites" differentially among the experimental arenas. Data were expressed first as proportions of all seeds present observed in such microsites, to alleviate the problem caused by ever-decreasing total numbers of observable seeds as the experiment progressed. Then, for each sampling date, fractions were ranked. Several of the earliest sampling dates (those prior to October 28) were not included in this analysis because few seeds had been incorporated into the surface material, aside from some which had been buried by rodent activity. Also, by late October, a majority of the seeds had become detached from their tethers, and thus any test of the likelihood of their acquiring a "good microsite" was more validly applied to later observations. Data from November 21 and 26 were ignored due to many missing observations (snow covered arenas), and data from after March 6 were also not included because, after 6 to 7 months in the field, many arenas had no observable
seeds remaining.

The unavoidably equivocal nature of observations of seed fates in this experiment made the second question posed by Pyke and Thompson -- that of comparing lifespans -- a challenge. Note that the "lost" state (Table 5.1) was a catchall for seeds whose fates were unknown at a particular observation time. Some obvious causes included depredation with no recognizable traces present when observed, burial (in which case the seed was present, but invisible), investigator error (seed was present and visible, but escaped detection) and dispersal substantially beyond the treatment arenas; none of these or any other possible causes of loss could be ascertained at census time. Indeed, some seeds in the "lost" category at one sample date would reappear in subsequent observations. Such uncertainty made any inferences based on analyses of lifespans derived strictly from survivorship curves less than trustworthy, even though original observations were back-corrected to account for seeds not seen on a particular day, but actually present, based on subsequent observations. Furthermore, the capacity for within-treatment comparisons in more complex experimental designs, as mentioned above, was not a feature of any of the techniques described by Pyke and Thompson or other appropriate sources (Hollander and Wolfe 1973, Lee 1980, Lawless 1982).

Yet, data characterizing numbers of unambiguously depredated seeds contained important information. First, a contingency analysis allowed distinctions in frequencies of depredated seeds among surface types. Second, these data provided a conservative basis for constructing survivorship curves, with predation the sole source of seed loss. In this analysis, seeds which were lost to unknown fates were treated as right-
censored data; that is, these seeds were known to have survived to a certain time without having been depredated (and therefore should contribute to any estimate of mean lifespan), prior to being lost to the experiment. Survivorship functions were estimated for each treatment's 16 seeds using the Kaplan-Meier (also known as the product-limit) method (Lee 1980, SAS 1985), which has the important advantage of presupposing nothing about the distribution of failure times (for a brief discussion of this issue, see Pyke and Thompson 1986). Based on these survivorship function estimates, the LIFETEST procedure of SAS (SAS 1985) provided estimates of the mean lifespans and accompanying standard errors for each of the 72 treatments (12 replicate shrubs X 2 microenvironments X 3 surface types). These could then be treated as the dependent variable in an ANOVA. Only treatments with two or more unambiguously depredated seeds were included in this ANOVA (eliminating 14 treatments). Since the dependent variates were actually means, with variance estimates available, sums of squares were weighted by the inverse of the squared standard errors (Freund and Littell 1981). Contrasts of Microenvironment X Surface means were conducted as described earlier.

Survivorship of indigenous fall-germinating plants.--The difference in survivorship between U and I seedlings was tested using the general association CMH statistic. The two-way table of interest was Microenvironment X observation interval number, with replicate quadrats as an additional dimension. Cell counts were numbers of plants dying during that interval. An additional interval of unspecified length accommodated counts of plants still surviving at the last observation date.
Results

Marking seeds

Among the three main factors in the greenhouse germination trial (i.e., marking treatment, surface type and moisture), only amount of water supplied significantly affected total number of seeds which germinated \( (F_{1,8} = 44.80, P = 0.0002) \). More seeds germinated in the more thoroughly watered treatment (Fig. 5.3). No interaction was a significant factor in the ANOVA. Although there were differences between seeds with and without polish, both in ultimate number germinated and in the time trajectory of the process (Fig. 5.3), variability among replicates was rather large and mean differences were not consistent in all interactions. By contrast with results from well watered replicates, when less thoroughly watered, more seeds marked with polish germinated, and these somewhat faster, than unmarked counterparts (Fig. 5.3). This probably had most to do with how seeds landed and whether or not their embryos were favorably positioned to contact the water-supplying substrate. (Water was supplied from below the planters used, so that seeds did not move from their original landing attitudes unless nudged by other germinating embryos.) Apparently because they were heavier, painted seeds more often landed advantageously, especially in the litter-covered replicates. This made little difference if ample water was available, but was more apparent in the drier treatment.

Thus, polish did not appear to have a detrimental effect on germination in the greenhouse trial. This conclusion was substantiated by successful germination of bare embryos (i.e., no palea and lemma), even when polish or fly-tying cement was applied directly to the embryo-end.
of the seed.

Free seeds experiment

Of the 1000 seeds originally released on April 18, 887 were recovered on June 3. Nearly all U seeds were found (482, or 96.4% of the total released), while substantially fewer I seeds were encountered (405, or 81%). Recovery rates corresponded with observed seed movements. U seeds had experienced small, if any, apparent lateral displacements; the presence of litter apparently impeded such movement (19 of 20 U release point surfaces were 100% litter-covered). However, many I seeds had migrated significantly from their release points. The most conservative estimate of the longest seed movement observed was > 35 cm (an I seed); dozens of I seeds had moved in excess of 10 cm, and several were found in or near littered microenvironments below their replicate shrub's canopy edge on June 3. No seeds were ever encountered along the leeward flashing barriers. On May 30, when counts of I seeds derived from visual inspection of a 1-dm² quadrat around each release point, only 257 seeds were recorded, attesting not only to the extensive movements of I seeds, but also to their incorporation into the substrate. Many I seeds were eventually recovered, having been buried beneath litter or largely covered by the sandy mineral soil. Such results of wind- and water-driven rearrangement of surficial materials and microtopography, especially of I microenvironments, were readily observed during this experiment.

Spring germination of indigenous seeds was first observed on May 6, and of introduced marked seeds in both U and I microenvironments, on May 20. Prior to the June 3 harvest, only I germinants (based on coleoptile
emergence) could be counted with certainty; these numbered 18, all occurring within the 1-dm² quadrats centered on the release points. Estimates of number of U germinants (based on coleoptile emergence) were 30 on May 27, and 25 on May 30. By June 3, cool, moist spring conditions had been succeeded suddenly by much drier, warmer ones, leading to the death, apparently by desiccation, of new seedlings which had arisen from indigenous and marked seeds alike. (Surface temperatures, measured with an infrared thermometer on the afternoon of May 30, reached 52.6°C for bare ground, and 44.8°C for littered U sites on the south of shrubs.) No spring-germinated seedling succeeded in producing more than one true leaf before dying.

Numbers of germinants recorded at harvest on June 3 included not only those with shoot growth, but also embryos whose hypocotyls alone had emerged from the caryopses (typically, the first tissue to do so). In nearly all cases, the emergent root tissues of these latter individuals were entirely desiccated. Significantly more marked seeds germinated in U than in I microenvironments (mean per shrub ± SE for U, 11.8 ± 1.28; for I, 7.4 ± 1.33; \( t = 2.495, \text{ df } = 8, P < 0.05 \)). U germinants were observed in significantly greater numbers on south and west exposures than expected, and this was consistent for all five replicate shrubs (Table 5.2).

The 18 germinants observed within I quadrats prior to June 3 were also distributed non-randomly with respect to the surface types present among the 50 quadrats (Fig. 5.4). The frequency distribution of these germinants among quadrats of the six surface types was compared in goodness-of-fit tests against each of two expectations: 1) that all surface types should have equal numbers of germinants (i.e., three apiece) and
2) that each quadrat should have an equal probability of supporting germination conditions. In both cases, the test statistic \( G \), adjusted by the Williams' correction [Sokal and Rohlf 1981]) indicated significant deviations from the expected distributions (for test 1,
\[
G_{adj} = 11.40, \ df = 5, \ P < 0.05; \ \text{for test 2, } G_{adj} = 13.71, \ df = 5, \ P < 0.025.
\]
Furthermore, a contingency analysis (Table 5.3) demonstrated that the abundant bare ground quadrats supported less germination than expected, while germination was strongly associated with quadrats containing litter and vegetation. Thus, germination of marked \( B. \ tectorum \) seeds in U microenvironments was most likely to occur on surface types like those predictably encountered in U microenvironments.

**Tethered seeds experiment**

Of the 1152 seeds introduced, 27 germinated (≈2.2%), and nine of these plants were still alive on June 3 (Fig. 5.5). By June 23, when the experiment was terminated and plants were harvested, three of those alive on June 3 were missing. Three of the six plants harvested produced caryopses; in all, eight fruits were collected, the products of a total of seven spikelets. Assuming that the five spikelets recorded on June 3 for the plants missing on June 23 contributed roughly one caryopsis apiece, the reproductive output of this cohort of 1152 introduced seeds was approximately 13 caryopses.

So few seeds germinated, that no valid statistical assessment of a pattern linking likelihood of germination to a particular microenvironment or surface type was possible. Nonetheless, detailed observations of seed/microsite interactions provided some important insights about the nature of a safe site for \( B. \ tectorum \). Of the 20 seeds which germi-
nated by December 19, 12 were in arenas in which unequivocal signs of rodent activity had been repeatedly noted. Apparently, rodents (most likely the deermouse, *Peromyscus maniculatus*; see Parmenter and MacMahon 1983, Kelrick et al. 1986 and Broome 1988) were attracted to the constructed arenas, predominately to BU treatments. Analyses of contingency tables of arena types with and without signs of rodent digging for the first six sample dates (up to and including October 28) all indicated significant lack of independence (all Fisher's exact test *P*-values < 0.01), primarily due to the unusually high frequencies of activity observed at BU arenas. Ten of the 20 fall germinants arose in BU arenas, and these seeds encountered safe sites incidentally, via their complete or partial burial in mineral soil by an excavating rodent.

From field observation of many hundreds of newly germinating, indigenous seeds, a practical, working "image" of a "good microsite" was developed (i.e., a seed situated in such a microsite was particularly likely to germinate; see operational definition in Table 5.1). Of the seven seeds which germinated in the spring of 1987, four had been previously identified and marked with toothpicks as being in "good microsites" for at least one prior sampling date. Of the eight fall germinants not in arenas in which rodent activity was unequivocally indicated, four had been described as in good microsites on earlier sampling dates. (Note that these latter observations may be somewhat less certain, because the seeds were not marked with toothpicks, so that the possibility of mistaken identification of individual seeds is greater.) Despite the small sample sizes, it is clear that some physical aspects of what constitutes a safe site for *B. tectorum* -- in this case, the
attitude of the seed in relation to material at the surface -- were recognizable and were ascertained, lending credence to the operational definition used in the field (Table 5.1).

Once seeds began interacting with the surface textures to which they had been introduced, constructed littered arenas consistently harbored the greatest proportion of seeds in good microsites (Table 5.4 and Fig. 5.6). Results of contrasts supported the notion that seeds behaved similarly on constructed surfaces and the natural ones they mimicked. In U microenvironments, results on L and N arenas generally agreed and were jointly often different from BU arenas, while in I microenvironments, results from B and N arenas were not significantly different, but these jointly displayed a smaller proportion of seeds in good microsites than did LI arenas. Aside from the December 19 sampling date, when more seeds in good microsites were observed in U arenas, there were no significant differences between U and I arenas, for data pooled over all surface types (Table 5.4). However, insight derived from the December 19 observations is significant because ecological factors affecting seed fates were apparently especially "active" during the three weeks prior to this date. This sampling date followed a period of substantial seed movement and some disappearance, consequences of processes which combined to favor the acquisition of good microsites by U seeds. The former process enhanced favorable seed dispositions, particularly on littered surfaces. Influence of the latter process was greatest on bare ground surfaces, where seed predation was a contributing factor (predation was also responsible for seed losses from a few NU arenas during this interval, leading to a significant LU vs. NU contrast [Table 5.4]).
Many more U seeds suffered depredation than I seeds, yet separate log likelihood tests for each microenvironment showed that there were consistent, significant differences in numbers of depredated seeds among surface types in both microenvironments (Table 5.5). The most frequent observations of seed depredation were from B arenas. Results of the ANOVA of Kaplan-Meier estimates of mean seed lifespans likewise showed that seeds in U microenvironments were significantly more likely to experience depredation than I counterparts (Table 5.6). Seed lifespans also varied according to surface type. When the variance associated with each lifespan estimate was used as a weighting factor in the ANOVA, estimates of mean lifespans ("least squares means" estimates for unbalanced designs by the GLM procedure of PC-SAS [SAS 1987]) for each of the three surfaces differed significantly from one another (mean ± SE for L arenas -- 168.32 ± 12.95; for N arenas -- 158.85 ± 11.01; for B arenas -- 89.80 ± 8.47). Although mean lifespans differed between microenvironments, the relationships among lifespans observed for the three surface types within each microenvironment were consistent (Fig. 5.7; non-significant Microenvironment X Surface interaction [Table 5.6]). Seeds on B surfaces were most likely to suffer predation, regardless of microenvironment.

Non-orthogonal contrasts of surface type means within each microenvironment were intended to test whether or not differential depredation was due to surface type, or rather to the predilection of the likely granivores (rodents) for the novelty of investigator-constructed surfaces (Table 5.6). For U surfaces, L and N mean lifespans were indistinguishable, indicating that a constructed littered surface was treated much like the natural one it was meant to simulate. However,
the contrast of means of the two constructed surfaces (B and L) against the N control was significant; this was due to the very short lifespans of seeds on BU surfaces. For I surfaces, the analogous contrast of constructed versus control surfaces was non-significant, but seeds on BI surfaces experienced significantly shorter mean lifespans than those on NI surfaces, the model for BI constructed arenas. In both microenvironments, it was the large impact of seed predation on bare ground surfaces which determined these results.

The analysis of seed lifespans presented above documented significant differences among treatments in verifiable seed losses due to predation, but did not acknowledge the influence of "lost" seeds (i.e., those unaccounted for, Table 5.1) on the numbers of propagules potentially capable of yielding plants in the various treatments. An analysis of numbers of living individuals (seeds plus plants) present at several observation dates provided a complementary perspective. Results of these ANOVA's (Table 5.7) corroborated surface- and microenvironment-specific patterns of seed persistence expected on the basis of lifespan data described above. During the first five to six weeks of the study, extending into early November, there were significantly more living individuals present in I than in U microenvironments. Later, this difference disappeared as the number of observable seeds and plants dwindled. Throughout the duration of the study, numbers of individuals present in B arenas were consistently significantly lower than in either L or N arenas, in both microenvironments. The Microenvironment X Surface interaction was a significant factor only on the first sampling date, five days after the experiment was installed, because many seeds disappeared from BU arenas within the first few days after seeds were
deposited in the field. Meanwhile, seeds in remaining arenas went essentially undisturbed during this interval. As was the case for the lifespan data, nearly all of the significant contrasts were attributable to what happened on B surfaces of both microenvironments. Very few living individuals were present in these arenas for most of the experiment, and this caused joint means for constructed arenas to differ from natural controls, despite the general equivalence of N and L arena means, when considered separately, in each microenvironment.

The strong parallels between results of the seed lifespan analysis based on unambiguous depredation and those derived strictly from presence data indicated that seeds which were unaccounted for did not obviously bias observations of important processes affecting seed survival differentially by microenvironment and/or surface. A third analysis provided further support. Tests of survivorship curves of all living individuals (seeds and plants combined; Figs. 5.8 and 5.9), accomplished via multidimensional contingency table analysis (CMH statistic) of numbers of "seeds gone" (comprising seeds unambiguously depredated and/or unequivocally lost) during each interval, revealed significant differences between microenvironments and among surfaces. Survival rates of I seeds were greater than those of U seeds (CMH general association statistic = 122.191, df = 14, P < 0.001). Among surface types, seed survival was poorest in B arenas (Fig. 5.9; CMH general association statistic = 246.213, df = 28, P < 0.001); this is reflected in the marked abundance of B seeds with very short lifespans in both microenvironments.
Survivorship of indigenous fall-germinating plants

Of the original 125 plants marked, eight (three U, five I) were eliminated from consideration because identifying toothpicks were disrupted by pronghorn antelope (*Antilocarpa americana*) treads. By November 21, nearly 12 weeks after having been marked originally, 42.5% of I plants (34 of 80) were dead, while only four of 37 U plants had died (10.8%). Most mortality occurred during the first 4-5 weeks after germination (Fig. 5.10), and was concentrated among I seedlings arising from seeds buried in microtopographic "basins," with little or no litter cover. The majority of I plants surviving to November 21 were located in pockets of litter which had accumulated in small irregularities in the microtopography. Survival rate of U seedlings was significantly greater than that of I seedlings (CMH general association statistic = 14.435, df = 4, P = 0.006).

Discussion

Seeds which do and do not become plants

"From among the vast numbers of seeds present in the soil and arriving on the surface through dispersal, only a tiny fraction germinates to give seedlings" (Harper 1977, p. 112). Harper’s statement illuminates the very important role that mortality during the seed stage of the plant life cycle might play. Since the population dynamics of annual plant species (in the vegetative phase) are so closely linked to seed fates, this perspective has special pertinence for these plants. The intuitive appeal of the suite of life history attributes classically associated with the annual habit (e.g., Begon and Mortimer 1986) --
profligate production of progeny, massive juvenile mortality, rapid
growth and substantial reproductive success for surviving individuals --
has resulted in a focus on the vegetative portion of the life cycle, and
has diverted plant ecologists' attention away from processes influencing
what is perhaps the most critical portion of the life cycle of annual
plants: when the embryonic plant is within the seed (Cavers 1983). In
the discussion which follows, I use "seedling" or "plant" in reference
to the vegetative/reproductive phase of the annual plant life cycle and
"seed" to denote that portion of the plant's embryonic life prior to
germination.

Contrary to conventional intuition, not all annual plants exhibit
high rates of juvenile mortality, whether assessed at the seed or seed-
ling stage (Symonides 1988). Although the data are scant, it is clear
that some annual species produce rather few seeds per individual, and
both seeds and resultant plants apparently enjoy high survival rates
(e.g., Vulpia fasciculata; Watkinson 1978a, 1990). Thus, standard
assumptions about demographic attributes of annuals must be questioned
and examined critically.

A major weakness of virtually all studies to date which have
attempted to infer population attributes from demographic data is that
any quantification of seed fates has been by indirect derivation rather
than direct observation. For annuals, this approach is particularly
treacherous because: 1) as already mentioned, the seed portion of the
life cycle is so pivotal; 2) many important environmental factors may
operate primarily on the seed portion of the life cycle, and these will
go unrecognized; and 3) there is no way to assess the goodness of such
population-level inferences, if fates of individual seeds remain shroud-
ed in mystery. The results of my efforts to learn the demographic fates of seeds under field conditions provided insights which helped explain the dispersion of *B. tectorum* plants at the study site more satisfactorily than the results presented heretofore (Chapters III, IV).

Of the 2152 marked seeds introduced for the free and tethered seeds experiments, only 123 (≈5.7%) were observed to germinate, and only nine survived to reproductive maturity (≈0.42%). Under these experimental conditions, tracking the fates of perhaps 10 times as many seeds might have yielded sufficiently large numbers of plants to allow a temporally continuous and unequivocal linkage between seed fates and plant dispersion/success. Nonetheless, consistent distinctions emerged differentiating seeds which did germinate and those which did not. Surveying the ground surface from standing height, these distinctions appeared subtle, if perceptible at all; upon intimate examination at the scale of the seed, they were unmistakably clear.

In the free seeds experiment, germination was more common in U than in I microenvironments. Germination that did occur was predominately and disproportionately within quadrats whose surfaces were not bare ground (Fig. 5.4). Littered and/or vegetated surfaces were obviously critical determinants or indicators of favorable germination conditions in this experiment. By contrast, in the tethered seeds experiment, 17 of 27 germinants were in B or NI arenas, which were, for the most part, bare ground. Ten of the germinants and five of the plants harvested at maturity were in BU arenas. Thus, *B. tectorum* does not require litter for successful germination and establishment, despite its frequently cited association with it (Evans and Young 1972, Young and Evans 1975, 1985).
Burial in either microenvironment, followed by appropriate sustained moisture conditions, can yield established plants, as the planting experiments (Chapter IV) made clear. It appears to be the likelihood of burial, multiplied by the likelihood of sustained favorable moisture conditions occurring subsequently, which makes natural germination and establishment rather uncommon. Many germinants emerging from complete burial were observed among indigenous seedlings monitored in 1986 (Fig. 5.10), but most of these died, apparently by desiccation. Seeds are perhaps more likely to encounter favorable conditions for both germination and establishment on littered surfaces, and may be more likely to come ultimately to rest in litter as well (see below). Unergminated seeds recovered when harvesting the free seeds experiment were tested for viability with tetrazolium (three replicates of 10 randomly chosen seeds), and were >90% viable, indicating that absence of appropriate germination conditions, rather than seed death, controlled the amount of germination observed.

Seed mobility

The larger percentage of seeds recovered from U than from I microenvironments in the free seeds experiment, as well as direct measurement of movements of marked seeds, all of which originated from I release points, demonstrated that I seeds were more mobile than U seeds. Seeds categorized as "lost" during the early and middle phases of the tethered seeds experiment were also concentrated among the B arenas, although some seeds were certainly "lost" to either burial by rodents or undetected depredation rather than by emigration from the arenas. Numbers of seeds "lost" from U vs. I natural surfaces also differed
markedly in the tethered seeds experiment. After 70 d in the field, 45.3% of all NI seeds were lost, and by 170 d, 59.4%; for NU seeds, comparable figures were only 26.7% and 32.8%, respectively. These observations accord with the inference drawn from seed trap data (Chapter III), that I microenvironments (primarily bare ground surfaces) are seed throughways and U microenvironments, seed depositories.

Microenvironment-specific seed survivorship

Three different approaches to characterizing seed survivorship (or mortality) were undertaken, in an attempt to deal rigorously with potential ambiguities in the data engendered by the "lost" seeds observations. I examined patterns: 1) of seed lifespans (considering seeds unambiguously depredated as the sole source of mortality; Table 5.6, Fig. 5.7); 2) in numbers of living individuals (seeds plus plants; Table 5.7) and 3) of survivorship curves, assessed as numbers of seeds "gone" (the complement of pattern 2; Figs. 5.8 and 5.9). Concordance of these three analytic perspectives allowed the following summarizations of seed survivorship during the tethered seeds experiment. Seeds were at greater risk of perishing by predation in U than in I microenvironments, but this result was determined chiefly by the rapid depletion of a substantial proportion of seeds on BU surfaces. In I microenvironments, where natural arena-sized expanses of unvegetated, unlittered surfaces were common but not ubiquitous, seeds on B surfaces were at greater risk than those on natural control surfaces. Finally, in both microenvironments, seeds on littered surfaces were most likely to persist longest. Given that B. tectorum exhibits a "flexible life history" (Young and Evans 1985, p. 489) and is capable of continuous germination throughout the
fall, winter and spring (Mack and Pyke 1983; also Fig. 5.5, tethered seeds experiment), longer persistence of seeds on littered surfaces enhances the probability of their experiencing the intermittent and unpredictable conditions allowing germination and establishment. Littered surfaces were strongly associated with U microenvironments at the study site.

The substantial impact of granivory on marked seeds in the tethered seeds experiment opposed observations of granivores’ avoidance of *B. tectorum* seeds in past research at this site (Kelrick et al. 1986, Broome 1988). The likely consumer was *Peromyscus maniculatus*, which does eat seeds of *B. tectorum* (Johnson 1961, Kritzman 1974), but apparently does not prefer them when other food items are available (Everett et al. 1978). Consumption of *B. tectorum* seeds in this study exemplifies the important influences of resource background and season on foraging preferences of shrub-steppe granivores (Kelrick et al. 1986).

**Seed/microsite interactions**

At a spatial scale smaller than microenvironment (10’s of cm at the study site), the fates of seeds can be determined by phenomena whose scope is no larger than the seed itself — the microsite. A microsite is a safe site if germination and establishment can proceed there. Many workers have invoked the term "safe site" to describe their investigations (e.g., Silvertown 1981, Fowler 1986, Andersen 1989, Silvertown and Smith 1989, Watkinson 1990), but none of these has actually measured or observed phenomena operating at the pertinent spatial and temporal scales — that of a single seed during the time prior to and just after germination, while the seedling "catches on." For example, in a paper
entitled "What is a safe site?" (Fowler 1988), no variables bearing on the fates of experimentally introduced seeds were measured, and the location and spatial scale of "safe sites" were defined by the appearance of already germinated and establishing seedlings. Admittedly, identifying the point at which a seedling is "established" is problematic (Fenner 1987), but I maintain that, in most investigations, the processes operating to render the microsite a safe site have already acted! To my knowledge, no previous study has reported on the dynamic interactions of individually marked seeds with the substrate surface under field conditions, interactions that essentially define the scale of the microsite and its attributes.

Classic work of Harper et al. (1965) and Sheldon (1974), more recently extended by Peart (1979, 1981, 1984), has illustrated the critical, interacting effects of surface texture and diaspore morphology on germination success. In the tethered seeds experiment, I observed that individual seeds of *B. tectorum* were being frequently reoriented with respect to the ground surface and its microtopography. When a seed adopted the most common attitude observed on bare ground, it resembled a boat, concave up, with both the awn and embryo-end in the air, out of contact with the substrate. By contrast, on a littered surface, the embryo-end was often directed downward, into a crevice in the litter. The somewhat heavier embryo-end appeared to reinforce the propensity for the seed to penetrate the litter material and the lightweight awn was often observed rustling in the wind, further enhancing penetration. The flattened crosssection of *B. tectorum* seed must also contribute to its ability to lodge, embryo-end down, in litter. If the embryo's proximity to a water-providing substrate is important for germination and estab-
lishment (Peart 1979, 1981), then *B. tectorum* seeds in litter, or partially buried, embryo-end down, will fare better than seeds lying on bare ground as described above. Moreover, litter can provide a restricting framework, to counter the force of the radicle penetrating the substrate (Peart 1981). In the field and greenhouse, I observed *B. tectorum* seeds germinating on bare ground whose embryo-ends were elevated from the ground surface by their elongating radicles, which were failing to enter the soil. Under these circumstances, newly germinated seeds often perished. Upon these observations, I based the definition of the "good microsite" category in the tethered seeds experiment (Table 5.1). My ability to identify good microsites and sometimes predict future germination indicated that it was possible to recognize a safe site before a plant indicated its presence.

In the tethered seeds experiment, proportions of seeds present in good microsites were greatest on littered surfaces, whether natural or constructed (Table 5.4, Fig. 5.6). Seventeen of 18 germinants with emergent coleoptiles observed in I microenvironments in the free seeds experiment were also oriented embryo-end down. To the degree that the seed/microsite interactions determine germination and establishment success, it seems clear that littered microsites are more likely to become safe sites than are bare ground microsites.

**Artifactual effects**

It is reasonable to evaluate the degree to which a manipulation such as the tethered seeds experiment introduces effects which may modify, obscure or reverse the natural phenomena of interest. For example, how marking seeds with nail polish would affect germination was
unknown, though concern about detrimental effects were diminished by the greenhouse and growth chamber trials previously detailed. Also, tethering seeds may have hampered their ability to interact naturally with the substrate and adopt their typical attitude with respect to the surface, thus preventing the subtle differences in seed position described above to play a role in determining which seeds successfully germinated and established. Fortunately, most seeds were detached from their tethers within three to four weeks of being placed in the field, after which seeds were free to "behave" unencumbered.

Another concern was the extraordinary attraction that the experiment may have provided for rodents, probably Peromyscus maniculatus. I wondered if the novelty of the constructed arenas was contributing to the high rate of seed predation on B surfaces. The significant disparity between mean seed survival times (seed predation the sole source of mortality) for NI (control bare ground model) vs. BI (constructed bare ground mimic) arenas seemed to indicate an artifactual effect of the constructed surface (Fig. 5.7). However, it must be noted that nearly all of the NI arenas had some litter or vegetation, so that they cannot be considered entirely analogous to BI surfaces. Furthermore, L surfaces were the most conspicuously novel among the I arenas and therefore perhaps most liable to artifactual effects, yet seeds on these surfaces experienced the least predation (Fig. 5.7). Results for NU (the control) and LU (the mimic) arenas were indistinguishable. It should also be noted that, in a particular microenvironment, adjacent arenas were separated by only 1-2 cm, so that a mouse could have been standing in one arena and consuming seeds from the treatment next door. A parsimonious explanation is that the responsible consumer perceived B. tectorum
seeds more readily on B surfaces than on littered surfaces.

A final consideration is why so few plants were produced from tethered seeds. Despite that I observed marked seeds under natural conditions for nearly nine months, I noticed that experimentally introduced seeds rarely became entirely buried in the littered treatments (NU, LU, LI). Yet, indigenous seedlings arising within NU arenas were nearly always completely beneath litter. The tethered seeds experiment was installed in mid-September, but fruits of *B. tectorum* plants at the study site typically began disarticulating during mid-June. During early summer, indigenous seeds were experiencing phase II dispersal, while at the same time, *Artemisia tridentata* shrubs were shedding their ephemeral leaves (Caldwell 1979). A summer’s worth of redistribution and deposition/accumulation of these two litter components may situate indigenous *B. tectorum* seeds in premium microsites for germination. Seeds introduced for the tethered seeds experiment, on the other hand, may have had too little time to acquire such choice microsites before conditions suitable for the typical fall pulse of germination had passed.

**Survivorship of plants**

Significantly higher mortality among individually marked indigenous I plants was observed (Fig. 5.10). Mack and Pyke (1983) documented extensive demographic variation among sites, cohorts in a single growing season and individuals within a cohort for *B. tectorum* populations growing in eastern Washington. Although the sample size from the tethered seeds experiment is very small, the same kind of variability in length of lifespans among cohorts as well as for individuals within
cohorts can be noted. Germination was continuous and extended until as late as June, while mortality was strongly focussed on two intervals (in April and June), each characterized by drought conditions of differing duration (Fig. 5.5).

Conclusions

For the vast majority of plant species, the fates of seeds are virtually unknown. In this instance, the patchy horizontal structure of the sagebrush-steppe plant community and the biology of *Bromus tectorum* together afforded a novel opportunity to explore the implications of seed fates for the population ecology of this annual species.

Factors affecting the seeds of *B. tectorum* were related to its distinctive dispersion at the study site. Seeds in U microenvironments, typically littered surfaces, were likely to reside there, while seeds in I microenvironments were likely to be moved across the ground surface, probably to come to rest in litter. Although seeds in U microenvironments were at greater risk of depredation by (rodent) granivores, seeds on littered surfaces (associated strongly with U microenvironments) were less likely to be consumed than those on bare ground. Seeds were more likely to adopt an attitude favorable for germination when on littered surfaces than when on bare ground. Germination was greater in U than in I microenvironments (free seeds experiment) and was strongly influenced by microsite conditions (e.g., burial) in the tethered seeds experiment. Survival rates of seeds and plants were both higher in U than in I microenvironments. Finally, indigenous I seedlings plants exhibited greater mortality than U plants.

Factors affecting the seeds of *B. tectorum* at this sagebrush-
steppe site clearly favored those in U microenvironments, and the nature of seed dispersal was such that seeds were predisposed to accumulate in U microenvironments. All else being equal, one would predict, based on the fates of seeds in this system, that U microenvironments would support greater densities of plants than I microenvironments.
Table 5.1. Categories of "states" to which observations of marked seeds were assigned in the tethered seeds experiment, along with operational definitions of the states used to distinguish them.

<table>
<thead>
<tr>
<th>State</th>
<th>Operational definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Present, in good microsite</td>
<td>Seed visible, callus-end (i.e., embryo-end) down at a substantial angle from horizontal, callus-end of caryopsis at least half buried</td>
</tr>
<tr>
<td>Present, not in good microsite</td>
<td>Seed visible, but not callus-end down and/or not at least half buried</td>
</tr>
<tr>
<td>Unambiguously depredated</td>
<td>Trace of paint-marked caryopsis encountered which, on basis of past observations, could only have derived from newly destroyed seed</td>
</tr>
<tr>
<td>Germinated</td>
<td>Emergent coleoptile visible</td>
</tr>
<tr>
<td>Lost</td>
<td>All seeds not accounted for in other states</td>
</tr>
</tbody>
</table>
Table 5.2. Total number of U germinants in free seeds experiment, by compass direction, along with results of a replicated goodness-of-fit test (Sokal and Rohlf 1981) comparing observed results against equal numbers of germinants in all compass directions.

<table>
<thead>
<tr>
<th>Replicate shrub</th>
<th>N</th>
<th>E</th>
<th>S</th>
<th>W</th>
<th>Row totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>0</td>
<td>4</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>3</td>
<td>10</td>
<td>2</td>
<td>16</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>2</td>
<td>6</td>
<td>4</td>
<td>12</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>3</td>
<td>5</td>
<td>4</td>
<td>12</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>0</td>
<td>5</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Column totals</td>
<td>4</td>
<td>8</td>
<td>30</td>
<td>17</td>
<td>59</td>
</tr>
</tbody>
</table>

Test for homogeneity of replicates
\[ G_h = 15.74, \text{df} = 12, 0.5 > P > 0.1. \]

Test for goodness-of-fit to equal number of germinants in all compass directions
\[ G_p = 27.196, \text{df} = 3, P < 0.001. \]
Table 5.3. Contingency table of frequency of quadrats (followed by cell Chi-square value in parentheses), categorized by surface type, in which germination (based on emergent coleoptile) was and was not observed in the free seeds experiment, along with probabilities of observing such a configuration.

<table>
<thead>
<tr>
<th>Quadrat surface type</th>
<th>Germination observed</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Yes</td>
<td>No</td>
<td></td>
<td>Row totals</td>
</tr>
<tr>
<td>Bare</td>
<td>2 (2.56)</td>
<td>19 (1.00)</td>
<td></td>
<td>21</td>
</tr>
<tr>
<td>Bare/vegetated</td>
<td>3 (0.55)</td>
<td>4 (0.21)</td>
<td></td>
<td>7</td>
</tr>
<tr>
<td>Vegetated</td>
<td>2 (0.06)</td>
<td>4 (0.02)</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>Vegetated/littered</td>
<td>5 (3.40)</td>
<td>3 (1.32)</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>Littered</td>
<td>1 (0.03)</td>
<td>2 (0.01)</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Littered/bare</td>
<td>1 (0.11)</td>
<td>4 (0.04)</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td><strong>Column totals</strong></td>
<td><strong>14</strong></td>
<td><strong>36</strong></td>
<td></td>
<td><strong>50</strong></td>
</tr>
</tbody>
</table>

Fisher’s exact test (2-tailed)

\[ P = 0.0523 \]

Exact multinomial probability of this distribution of 14 instances of germination being observed among six quadrat types

\[ P = 0.003678 \]
Table 5.4. Results\textsuperscript{a} of analyses of variance of ranks of proportions of seeds present which were in "good microsites" on various sampling dates during the tethered seeds experiment.

<table>
<thead>
<tr>
<th>Sampling date\textsuperscript{c}</th>
<th>Micro</th>
<th>Surf</th>
<th>Micro X Surf</th>
<th>L vs. N</th>
<th>N+L vs. B</th>
<th>B vs. N</th>
<th>B+N vs. L</th>
<th>Contrasts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct 28</td>
<td>0.03</td>
<td>0.62</td>
<td>0.04</td>
<td>0.27</td>
<td>0.24</td>
<td>0.03</td>
<td>0.78</td>
<td>NS</td>
</tr>
<tr>
<td>Nov 13</td>
<td>0.09</td>
<td>9.03</td>
<td>3.09</td>
<td>0.06</td>
<td>8.42</td>
<td>0.06</td>
<td>15.51</td>
<td>NS</td>
</tr>
<tr>
<td>Nov 26</td>
<td>2.18</td>
<td>13.40</td>
<td>1.82</td>
<td>0.50</td>
<td>9.15</td>
<td>0.85</td>
<td>19.95</td>
<td>L &gt; N, B</td>
</tr>
<tr>
<td>Dec 19</td>
<td>12.33</td>
<td>15.75</td>
<td>0.77</td>
<td>7.53</td>
<td>3.46</td>
<td>2.69</td>
<td>19.85</td>
<td>0.005</td>
</tr>
</tbody>
</table>

\textsuperscript{a} Results of analyses of variance of ranks of proportions of seeds present which were in "good microsites" on various sampling dates during the tethered seeds experiment.

\textsuperscript{b} Factors.

\textsuperscript{c} Sampling date.

\textsuperscript{d} Significant at the 0.001 level.
Table 5.4. (continued)

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Factors</th>
<th>Undershrub</th>
<th>Interspace</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mar 6</td>
<td>2.66</td>
<td>5.50</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>NS</td>
<td>0.009</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>--</td>
<td>L &gt; N,B</td>
<td>--</td>
</tr>
</tbody>
</table>

*a* Data presented in each table cell are: top -- value of F-test; middle -- value of P, if < 0.10, otherwise "NS"; bottom -- statistical relationship of levels from within-factor comparisons or contrasts, if F-test was significant. Letters representing means are arranged such that largest values are leftmost or at top, smallest values are rightmost or at bottom of each group. U = undershrub, I = interspace, B = bare, N = natural (control), L = littered. Means of levels connected by accompanying vertical lines are not significantly different.

*b* Main effects and their interaction in a split-plot design, with Microenvironment (Micro) the main plot treatment, and Surface (Surf) the sub-plot treatment.

*c* Sample sizes (n = 72, if no missing data) were: Oct 28, n = 72; Nov 13, n = 49; Nov 26, n = 71; Dec 19, n = 67; Mar 6, n = 61.

*d* In these cases, P < 0.0005.
Table 5.5. Frequencies of seeds which were and were not identified as unambiguously depredated (pooled over all replicates), categorized by surface treatment and microenvironment, tethered seeds experiment, with results of log likelihood ratio tests.

<table>
<thead>
<tr>
<th>Surface treatment</th>
<th>UNDERSHRUB</th>
<th>INTERSPACE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Seeds depredated</td>
<td>Seeds depredated</td>
</tr>
<tr>
<td></td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Bare</td>
<td>89</td>
<td>103</td>
</tr>
<tr>
<td>Natural</td>
<td>70</td>
<td>122</td>
</tr>
<tr>
<td>Littered</td>
<td>64</td>
<td>128</td>
</tr>
</tbody>
</table>

\[ G_{adj} = 7.41, \ P < 0.025 \]

\[ G_{adj} = 6.54, \ P < 0.05 \]
Table 5.6. Results of an analysis of variance of estimated mean seed lifespans\textsuperscript{a} in the tethered seeds experiment.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom\textsuperscript{b}</th>
<th>F-value</th>
<th>Significance\textsuperscript{c}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microenvironment</td>
<td>1,10</td>
<td>6.10</td>
<td>$P &lt; 0.05$</td>
</tr>
<tr>
<td>Surface</td>
<td>2,31</td>
<td>12.86</td>
<td>$P &lt; 0.0001$</td>
</tr>
<tr>
<td>Microenvironment X Surface</td>
<td>2,31</td>
<td>0.33</td>
<td>NS</td>
</tr>
<tr>
<td>CONTRASTS\textsuperscript{d}</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Undershrub</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Littered vs. natural</td>
<td>1,31</td>
<td>0.06</td>
<td>NS</td>
</tr>
<tr>
<td>Both constructed vs. natural</td>
<td>1,31</td>
<td>4.59</td>
<td>$P &lt; 0.05$</td>
</tr>
<tr>
<td>Interspace</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bare vs. natural</td>
<td>1,31</td>
<td>7.99</td>
<td>$P &lt; 0.01$</td>
</tr>
<tr>
<td>Both constructed vs. natural</td>
<td>1,31</td>
<td>1.26</td>
<td>NS</td>
</tr>
</tbody>
</table>

\textsuperscript{a}Lifespans estimated via the Kaplan-Meier method from right-censored data, with seed predation the sole source of mortality.

\textsuperscript{b}Degrees of freedom listed are: those for the source of variation, those for the appropriate error against which it was tested. In some cases, values of degrees of freedom were estimated as a result of unbalanced data.

\textsuperscript{c}Statistical significance. NS = not significant; i.e., $P > 0.05$.

\textsuperscript{d}Non-orthogonal. Note that the appropriate $\alpha$-level for each test (corresponding to the nominal 0.05, but that accounts for experimentwise error) is 0.0127, according to the Dunn-Sidák method (Sokal and Rohlf 1981).
Table 5.7.  Results of analyses of variance of ranks of numbers of living individuals (seeds plus plants) present on various sampling dates during the tethered seeds experiment.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sep 22</td>
<td>5.65</td>
<td>6.27</td>
<td>8.07</td>
<td>0.56</td>
<td>10.62</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>0.03</td>
<td>0.0044</td>
<td>0.001</td>
<td>NS</td>
<td>0.002</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>I &gt; U N</td>
<td>B=NI=LI,</td>
<td>--</td>
<td>N &gt; B+L</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>but</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>NU,LU &gt; BU</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sep 30</td>
<td>5.40</td>
<td>13.27</td>
<td>1.68</td>
<td>1.77</td>
<td>12.30</td>
<td>4.63</td>
</tr>
<tr>
<td></td>
<td>0.03</td>
<td>0.0001</td>
<td>NS</td>
<td>NS</td>
<td>0.001</td>
<td>0.037</td>
</tr>
<tr>
<td></td>
<td>I &gt; U L,N &gt; B</td>
<td>--</td>
<td>--</td>
<td>N &gt; B+L</td>
<td>N &gt; B</td>
<td>--</td>
</tr>
<tr>
<td>Oct 7</td>
<td>5.89</td>
<td>20.01</td>
<td>2.91</td>
<td>4.30</td>
<td>22.15</td>
<td>7.34</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.0001</td>
<td>0.07</td>
<td>0.044</td>
<td>0.0001</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td>I &gt; U L,N &gt; B</td>
<td>--</td>
<td>--</td>
<td>N &gt; L</td>
<td>N &gt; B+L</td>
<td>N &gt; B</td>
</tr>
<tr>
<td>Oct 16</td>
<td>8.93</td>
<td>29.75</td>
<td>2.18</td>
<td>3.94</td>
<td>25.19</td>
<td>14.09</td>
</tr>
<tr>
<td></td>
<td>0.007</td>
<td>0.0001</td>
<td>0.05</td>
<td>0.0001</td>
<td>0.0005</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>I &gt; U L,N &gt; B</td>
<td>--</td>
<td>--</td>
<td>N &gt; L</td>
<td>N &gt; B+L</td>
<td>N &gt; B</td>
</tr>
<tr>
<td>Oct 21</td>
<td>7.34</td>
<td>30.54</td>
<td>1.30</td>
<td>2.63</td>
<td>21.50</td>
<td>17.39</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>0.0001</td>
<td>NS</td>
<td>NS</td>
<td>0.0001</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>I &gt; U L,N &gt; B</td>
<td>--</td>
<td>--</td>
<td>N &gt; B+L</td>
<td>N &gt; B</td>
<td>N &gt; B+L</td>
</tr>
</tbody>
</table>
Table 5.7. (continued)

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Micro</th>
<th>Surf</th>
<th>Micro X Surf</th>
<th>Undershrub</th>
<th>Interspace</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L vs. N</td>
<td>B+L vs. N</td>
<td>B vs. N</td>
<td>B+L vs. N</td>
<td></td>
</tr>
<tr>
<td>Oct 28</td>
<td>6.66</td>
<td>26.06</td>
<td>2.27</td>
<td>5.14</td>
<td>24.24</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.0001</td>
<td>NS</td>
<td>0.028</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>I &gt; U</td>
<td>L,N &gt; B</td>
<td>--</td>
<td>N &gt; L</td>
<td>N &gt; B+L</td>
</tr>
<tr>
<td>Nov 13</td>
<td>4.04</td>
<td>16.65</td>
<td>0.03</td>
<td>3.32</td>
<td>14.70</td>
</tr>
<tr>
<td></td>
<td>0.06</td>
<td>0.0001</td>
<td>NS</td>
<td>0.09</td>
<td>0.0008</td>
</tr>
<tr>
<td></td>
<td>--</td>
<td>L,N &gt; B</td>
<td>--</td>
<td>--</td>
<td>N &gt; B+L</td>
</tr>
<tr>
<td>Nov 26</td>
<td>4.18</td>
<td>15.06</td>
<td>0.66</td>
<td>1.76</td>
<td>11.33</td>
</tr>
<tr>
<td></td>
<td>0.053</td>
<td>0.0001</td>
<td>NS</td>
<td>NS</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>--</td>
<td>L,N &gt; B</td>
<td>--</td>
<td>--</td>
<td>N &gt; B+L</td>
</tr>
<tr>
<td>Dec 19</td>
<td>1.22</td>
<td>16.42</td>
<td>0.72</td>
<td>0.74</td>
<td>9.80</td>
</tr>
<tr>
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<td>NS</td>
<td>0.0001</td>
<td>NS</td>
<td>NS</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>--</td>
<td>L,N &gt; B</td>
<td>--</td>
<td>--</td>
<td>N &gt; B+L</td>
</tr>
<tr>
<td>Mar 6</td>
<td>0.65</td>
<td>12.07</td>
<td>0.67</td>
<td>0.95</td>
<td>7.86</td>
</tr>
<tr>
<td></td>
<td>NS</td>
<td>0.0001</td>
<td>NS</td>
<td>NS</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>--</td>
<td>L,N &gt; B</td>
<td>--</td>
<td>--</td>
<td>N &gt; B+L</td>
</tr>
<tr>
<td>Sampling date</td>
<td>Micro</td>
<td>Surf</td>
<td>Micro X Surf</td>
<td>Undershrub</td>
<td>Interspace</td>
</tr>
<tr>
<td>---------------</td>
<td>-------</td>
<td>------</td>
<td>--------------</td>
<td>------------</td>
<td>------------</td>
</tr>
<tr>
<td>Apr 21</td>
<td>0.23</td>
<td>6.12</td>
<td>0.49</td>
<td>0.00 0.91</td>
<td>5.01 0.73</td>
</tr>
<tr>
<td>NS</td>
<td>0.005</td>
<td>NS</td>
<td>NS</td>
<td>NS NS</td>
<td>0.030 NS</td>
</tr>
<tr>
<td>--</td>
<td>L,N &gt; B</td>
<td>--</td>
<td>--</td>
<td>N &gt; B</td>
<td>--</td>
</tr>
</tbody>
</table>

aData presented in each table cell are: top -- value of F-test; middle -- value of P, if < 0.10, otherwise "NS"; bottom -- statistical relationship of means of levels from within-factor comparisons or contrasts, if F-test was significant, or P < 0.05. Letters representing means are arranged such that largest values are leftmost or at top, smallest values are rightmost or at bottom of each group. U = undershrub, I = interspace, B = bare, N = natural (control), L = littered. Means of levels connected by accompanying vertical lines are not significantly different.

bNon-orthogonal. Note that the appropriate α-level for each test (corresponding to the nominal 0.05, but that accounts for experimentwise error) is 0.0127, according to the Dunn-Sidak method (Sokal and Rohlf 1981).

cMain effects and their interaction in a split-plot design, with Microenvironment (Micro) the main plot treatment, and Surface (Surf) the sub-plot treatment.

dSample sizes were n = 72 for all dates except: Nov 13, n = 49; and Dec 19, n = 71.
FREE SEEDS EXPERIMENT
5 SHRUBS
200 SEEDS TOTAL PER SHRUB

FLASING BARRIER

10 cm

UNDERSHRUB
25 SEEDS AT EACH RELEASE POINT

INTERSPACE
10 SEEDS AT EACH RELEASE POINT

SAGEBRUSH CANOPY

SAGEBRUSH CANOPY

SAGEBRUSH CANOPY

DIRECTION OF PREVAILING WIND (WESTERLY)
TETHERED SEEDS EXPERIMENT
12 SHRUBS
96 SEEDS TOTAL PER SHRUB

- CONSTRUCTED BARE GROUND SURFACE TREATMENT
- NATURAL (CONTROL) SURFACE TREATMENT
- CONSTRUCTED LITTERED SURFACE TREATMENT
LIFESPANS OF PLANTS

DATE

PRECIPITATION (mm)

SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL
SURVIVAL AS A FUNCTION OF SEED PREDATION

![Graph showing survival times in different microenvironments]
UNDERSHRUB SURVIVORSHIP

NUMBER OF INDIVIDUALS (log scale)

MONTH

LIFESPAN

NUMBER OF INDIVIDUALS

LIFESPAN (days)

- Bare
- Natural
- Littered
SURVIVORSHIP OF INDIGENOUS PLANTS

NUMBER OF INDIVIDUALS (log scale)

MONTH

- Undershrub
- Interspace
CHAPTER VI
SYNTHESIS

Generality of results

Certainly, many of the detailed phenomena involving microsite-level interactions of *B. tectorum* seeds observed in this study were inherently idiosyncratic. For example, even within plant communities recognized as sagebrush-steppe, differences in available moisture and successional status result in herbaceous cover values ranging from $<50\%$ to nearly $200\%$ (West 1988). Thus, not all sagebrush-dominated communities have interspaces whose abiotic features are as distinct from those of the undershrub as was true in this study. Consequently, safe site acquisition may be much less tightly associated with undershrub microenvironments at other sagebrush-steppe sites. In a similar vein, a different soil type, even if the plant community structure were identical to that at the study site, would likely change the interplay between seeds and substrate governing germination and establishment. In contrast to the sandy soils of the study site, swelling/shrinking cycles manifested in response to wetting/drying of more clayey soils, as well as the susceptibility of these soils to cryoturbation, could promote burial of *B. tectorum* seeds. In soils allowing such vertical movements by seeds, successful germination and establishment might again be more disconnected from both littered surfaces and undershrub microenvironments.

On the other hand, several aspects of the study do stand as examples complementing work with other species and/or in other ecosystems. For example, Chambers et al. (1991) examined the propensities of dia-
spores of various morphologies to move horizontally across and vertically into experimental substrates of known particle sizes, installed under field conditions in alpine tundra. These authors concluded that:
1) when substrate particle size is small relative to the diaspore, horizontal movement of diaspores predominates over vertical incorporation into the substrate column; and 2) diaspore morphological attributes such as high eccentricity (large length:width ratio) and presence of appendages can impede deep penetration into a substrate of relatively small particle size. These observations of seed/substrate interactions "on exposed soils in windy environments" (words of Chambers et al.) aptly describe the "behavior" of *B. tectorum* seeds in the interspace in this study, and reinforce the importance ascribed to phase II dispersal (Watkinson 1978b) in relatively unobstructed landscapes, like many aridlands and alpine tundras present. On the basis of collections from seed traps placed at a Sonoran Desert site, Reichman (1981) also concluded that interspaces were seed highways, and, in a graphic comment (p. 9), suggested that "seeds may move across the soil surface . . . like pebbles in a stream." Thus, in plant communities exhibiting sparse cover, seeds of species that are unlikely to enter the mineral soil promptly can be considered as living components of the litter, subject to similar processes of redistribution and accumulation. This conceptual approach should expedite identification of factors influencing the seed portion of their life cycles.

The mechanistic descriptions of seed/litter interactions developed in this study help clarify the frequently observed association between litter and *B. tectorum* plants (Evans and Young 1972, Young and Evans 1975, 1985). Results of this study indicated that litter had demograph-
ic effects on *B. tectorum* in at least three ways. First, seeds on littered surfaces were safer from predators. Second, seeds on littered surfaces were observed more frequently in positions facilitating imbibition of the embryo. Finally, partial or complete burial by litter enhanced successful penetration of the water-supplying substrate by the radicle prior to embryonic desiccation; litter apparently afforded some restraint against the force of radicle elongation into a resistant substrate surface (Peart 1981). These demographic advantages conferred by litter can translate into population features, such as the distinctive dispersion observed at the study site. If generally applicable, they may also contribute to the remarkable ability of *B. tectorum* to invade and dominate sites throughout its recently acquired range in North America (Mack 1981). *B. tectorum* itself produces a relatively abundant and persistent fine litter which may function to promote its demographic success, via positive effects on its own germination and establishment, and perhaps at the expense of recruitment by other species. Such site pre-emption by dead remains of a previous generation's plants and their negative effects on seedling survival of other co-occurring species (by *Poa annua*; Bergelson 1990) illustrate a realm of interactions between litter and seeds/seedlings whose rich implications for population and community dynamics are largely unexplored (Facelli and Pickett 1991).

**Particular contributions of this study**

There is a sense in which the research described herein might be viewed as simply a reaffirmation of extant work on the biology and ecology of *Bromus tectorum*. The species is extremely well-studied (see
Chapter I), and my research, in many respects, paralleled authoritative, comprehensive descriptions of the population ecology of the species provided by Mack and Pyke (1983, 1984), Young and Evans (1985) and Pyke (1986). Such a view, though, neglects several valuable, alternative perspectives deriving from my study which warrant explicit mention.

First, rather than just an exposition of the autecology and demography of *Bromus tectorum*, this research can be more broadly construed as an investigation of the spatially heterogeneous structure and functioning of the sagebrush-steppe ecosystem, for which *Bromus tectorum* served as an effective biological probe. Among those facets of the *B. tectorum* life cycle studied, all manifested and/or contributed to ecologically significant distinctions between U and I microenvironments (Table 6.1). This emphasizes how remarkably steep the complex-gradient (Shmida and Whittaker 1981) between the two microenvironments might be for some species; life could be very different for two *B. tectorum* individuals (seeds or plants) within 10 cm of another, if a shrub canopy overhung one but not the other.

Second, this research clearly illustrated the expression of linkages across various levels of biological organization. Shmida and Whittaker (1981), in concluding a community-level analysis of patterns in species diversity of two shrub-dominated aridlands, proposed (p. 248) that a further objective of such pattern research was the "investigation of species autecology and population dynamics in relation to the microsite mosaic and flow of populations through microsites . . . ." Thus, the linkage between population level phenomena and community pattern could be demonstrated. The population ecology of *Bromus tectorum* portrayed herein fulfilled this objective, and data collected on the seed
and distributions of other annual species hinted at other microenvironment-specific factors influencing attributes of their populations as well.

In addition to recognition of a population-community linkage, there is increasing interest among theoretical ecologists in incorporating variability among individuals into models describing population- and/or community-level phenomena (e.g., Huston et al. 1988, Koehl 1989). Again, this research revealed a system in which knowledge of microenvironment-specific fates of individual B. tectorum seeds seemed to translate well into the observed spatial structure of the vegetative plant population. Microenvironment-specific growth and reproductive success of individual plants, which appeared at odds with the observed dispersion of the population, was apparently overshadowed by subsequent seed depositional patterns imposed by the spatial structure of the physiognomic dominant of the community (see also Kadmon and Shmida 1990). Thus, my work demonstrated an interplay involving differences in fates of individuals, population structure and functional attributes of the community.

Finally, the research described herein represents the only instance I have encountered in which individual seeds were monitored under ecologically pertinent field conditions from germination through to the successful production of the subsequent generation of seeds. Though the approach adopted in this kind of research is only applicable under certain conditions and to particular species, it nonetheless demonstrated that the study of seed demography is not a wholly intractable problem. Additional detailed investigations of the fates of seeds under natural conditions are sure to be forthcoming, since the kinds of eco-
logical and evolutionary questions which such investigations might address (e.g., Kalisz 1991) are essentially unapproachable without data characterizing this critical portion of a plant's life (Primack and Levy 1988, Winn 1989). This study, then, responded to the injunction of Hickman (1979, p. 263), later echoed by Cavers (1983) and Price and Jenkins (1986), regarding the seed stage, during which the vast majority of plant mortality occurs: that is, "... knowledge of seed fates is miniscule. Much work is needed here to understand plant responses to spatial and temporal heterogeneity..." In elucidating the fates of B. tectorum seeds at the study site, substantial progress was made towards describing the causal factors determining the dispersion of this annual plant species in a patchy environment.
Table 6.1. A synopsis of how various aspects of the population ecology of *Bromus tectorum* reflect the small-scale, shrub-associated patch structure (i.e., microenvironments) at the study site. For each process/attribute, microenvironments are scored relative to one another: + denotes higher or better, - denotes lower or worse.

<table>
<thead>
<tr>
<th>Process/attribute</th>
<th>Microenvironment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Undershrub</td>
</tr>
<tr>
<td>Seed mobility</td>
<td>-</td>
</tr>
<tr>
<td>Risk of depredation:</td>
<td></td>
</tr>
<tr>
<td>as a function of location</td>
<td>+</td>
</tr>
<tr>
<td>as a function of surface type</td>
<td>-</td>
</tr>
<tr>
<td>Probability of seed occupying safe site</td>
<td>+</td>
</tr>
<tr>
<td>Germination</td>
<td>+</td>
</tr>
<tr>
<td>Seedling survival</td>
<td>+</td>
</tr>
<tr>
<td>Vigor of established plants</td>
<td>-</td>
</tr>
<tr>
<td>Density of plants</td>
<td>+</td>
</tr>
</tbody>
</table>


Harris, G. A. 1967. Some competitive relationships between *Agropyron scapatum* and *Bromus tectorum*. Ecological Monographs 37:89-111.


Maguire, K. A. 1990. Relative seed preferences of the deer mouse (Peromyscus maniculatus): field and laboratory observations. M. S. thesis, Utah State University, Logan, Utah, USA.


______. 1988b. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51:71-78.


APPENDIX
Table A.1. A list of plant species whose seeds were found in seed traps in 1981. Asterisks denote species whose seeds were also found in seed traps in 1986.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Life form</th>
<th>Life history</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amaranthus albus</em></td>
<td>Amaranthaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td><em>Arabis holboellii</em></td>
<td>Brassicaceae</td>
<td>forb</td>
<td>bi-/perennial</td>
</tr>
<tr>
<td><em>Artemisia tridentata</em></td>
<td>Asteraceae</td>
<td>shrub</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Atriplex gardneri</em></td>
<td>Chenopodiaceae</td>
<td>shrub</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Bromus tectorum</em></td>
<td>Poaceae</td>
<td>grass</td>
<td>annual</td>
</tr>
<tr>
<td><em>Chrysothamnus viscidiflorus</em></td>
<td>Chenopodiaceae</td>
<td>shrub</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Collinsia parviflora</em></td>
<td>Scrophulariaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td><em>Cryptantha flavoculata</em></td>
<td>Boraginaceae</td>
<td>forb</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Cryptantha watsonii</em></td>
<td>Boraginaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td><em>Descurainia sophia</em></td>
<td>Brassicaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td><em>Elymus cinereus</em></td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Eriogonum spp.</em></td>
<td>Polygonaceae</td>
<td>forb/shrub</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Gilia tweedyi</em></td>
<td>Polemoniaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td><em>Hordeum jubatum</em></td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Lappula redowskii</em></td>
<td>Boraginaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td><em>Opuntia polyacantha</em></td>
<td>Cactaceae</td>
<td>forb</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Oryzopsis hymenoides</em></td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Phlox longifolia</em></td>
<td>Polemoniaceae</td>
<td>forb</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Poa spp.</em></td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
<tr>
<td><em>Polygonum douglasii</em></td>
<td>Polygonaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td><em>Salsola kali</em></td>
<td>Chenopodiaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td>Species</td>
<td>Family</td>
<td>Life form</td>
<td>Life history</td>
</tr>
<tr>
<td>-----------------</td>
<td>----------</td>
<td>-----------</td>
<td>--------------</td>
</tr>
<tr>
<td>Sitanion hystrix</td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
<tr>
<td>Stipa comata</td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
</tbody>
</table>
Table A.2. A list of plant species whose seeds were found in soil seed samples.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Life form</th>
<th>Life history</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amaranthus albus</td>
<td>Amaranthaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td>Arabis holboellii</td>
<td>Brassicaceae</td>
<td>forb</td>
<td>bi-/perennial</td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>Asteraceae</td>
<td>shrub</td>
<td>perennial</td>
</tr>
<tr>
<td>Bromus tectorum</td>
<td>Poaceae</td>
<td>grass</td>
<td>annual</td>
</tr>
<tr>
<td>Chenopodium album</td>
<td>Chenopodiaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td>Chrysothamnus viscidiflorus</td>
<td>Chenopodiaceae</td>
<td>shrub</td>
<td>perennial</td>
</tr>
<tr>
<td>Collinsia parviflora</td>
<td>Scrophulariaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td>Cryptantha watsonii</td>
<td>Boraginaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td>Descurainia sophia</td>
<td>Brassicaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td>Eriogonum spp.</td>
<td>Polygonaceae</td>
<td>forb/shrub</td>
<td>perennial</td>
</tr>
<tr>
<td>Gilia tweedyi</td>
<td>Polemoniaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td>Lappula redowskii</td>
<td>Boraginaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td>Oryzopsis hymenoides</td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
<tr>
<td>Poa spp.</td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
<tr>
<td>Polygonum douglasii</td>
<td>Polygonaceae</td>
<td>forb</td>
<td>annual</td>
</tr>
<tr>
<td>Sitanion hystrix</td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
<tr>
<td>Stipa comata</td>
<td>Poaceae</td>
<td>grass</td>
<td>perennial</td>
</tr>
</tbody>
</table>
CURRICULUM VITAE

Michael Ira Kelrick

PRESENT POSITION

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PERSONAL INFORMATION

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EDUCATION


American Field Service scholarship, 1972. Americans Abroad high school exchange program, Instituto de Educacao "Dr. Getulio Vargas", Sorocaba, Sao Paulo, Brasil. (Senior year of high school)

AWARDS

Vice President’s Fellowship, Utah State University, Logan, Utah (1986/87).

Summer Research Fellowship, Utah State University, Logan, Utah (1982).

University Research Fellowship, Utah State University, Logan, Utah (1981/82).

University Research Fellowship, Utah State University, Logan, Utah (1979/80).
EXTERNAL GRANTS

The seed ecology of Missouri bladder-pod (Lesquerella filiformis). Submitted to the U.S. Fish and Wildlife Service via the Missouri Department of Conservation. 2 years; $16,000. Funded March, 1990.


The effects of several management practices on the demography of Missouri bladder-pod (Lesquerella filiformis). Submitted to the U.S. Fish and Wildlife Service via the Missouri Department of Conservation. 2 years; $7,900. Pending.

PUBLICATIONS


PRESENTATIONS


PROFESSIONAL AFFILIATIONS

American Institute of Biological Sciences
Ecological Society of America
Missouri Academy of Sciences
Missouri Native Plants Society, Kirksville chapter
Sigma Xi

MANUSCRIPT REVIEWS

Agriculture, Ecosystems and Environment
American Midland Naturalist
Ecology
Great Basin Naturalist