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DISSERTATION

POPULATION DYNAMICS AND ECOLOGICAL CHARACTERISTICS OF *CLEOME MULTICAULIS*, A RARE ANNUAL WETLAND HALOPHYTE OF THE SAN LUIS VALLEY, COLORADO

Submitted by

Carol D. Riley

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2001

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY CAROL D. RILEY ENTITLED: *POPULATION DYNAMICS AND ECOLOGICAL CHARACTERISTICS OF CLEOME MULTICAULIS, A RARE ANNUAL WETLAND HALOPHYTE OF THE SAN LUIS VALLEY, COLORADO* BE ACCEPTED AS FULFILLING IN PART THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee On Graduate Work

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ABSTRACT OF DISSERTATION

POPULATION DYNAMICS AND ECOLOGICAL CHARACTERISTICS OF *CLEOME MULTICAULIS*, A RARE ANNUAL WETLAND HALOPHYTE OF THE SAN LUIS VALLEY, COLORADO

A three-year study characterized the San Luis Valley, Colorado habitat occupied by *Cleome multicaulis*, an annual wetland halophyte. Soils occupied by *C. multicaulis* were moist and saline-sodic, with mean pH of 8.9 (0.58) and mean electrolytic conductivity of 8.5 (8.6) dS/m. Common co-associates were *Distichlis stricta* var. *spicata* and *Juncus balticus*. The response of *Cleome multicaulis* to soil pH is distinct from that of soil conductivity, and increases in pH are associated with enhanced reproductive output of *C. multicaulis*. This study provided no evidence that the germination of *C. multicaulis* seeds coincided with periods of seasonally low soil salinity. A multi-year field experiment (Kalisz 1991) revealed that the conditional probability of seed emergence (std.error = 1.4) declined with seed age from 6% to 1.6%. Seed bank persistence probabilities were influenced by microsite characteristics and did not decline with seed age. Seeds of *C. multicaulis* may float and move laterally during seasonal inundation and were observed to endure multi-year flooding. The population structure of *Cleome multicaulis* is best described as a series of remnant populations persisting temporally as seeds in the soil. Estimates of population growth rates highlight the vulnerability of local populations to above-ground (stem) extinction and the importance of understanding mechanisms of seed bank extinction. Periodic matrix analysis provided the intra-annual detail necessary to distinguish the persistent (1-3 years) and transient (0-1 years) components of seed bank elasticity. Rapidly growing populations of *C. multicaulis* were characterized by large (> 15cm), widely-spaced plants and greater elasticities of growth rate from the transient seed bank, whereas declining populations ($\lambda < 1$) had comparatively greater reliance on the persistent seed bank. Small (< 15cm) reproductive plants appearing late in the growing season contributed little to population growth. Niche dimension in this species is expanded by the presence of a persistence seed bank and management efforts should seek to identify environmental conditions favorable for both above-ground and seed bank growth. Further research is needed to identify pollinator relationships. Management recommendations are made in hopes of increasing the likelihood of *C. multicaulis* population persistence in the San Luis Valley of Colorado and in Wyoming.

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As often happens to a person in the span of seven years, I underwent many personal and professional changes while this study was being conducted. I am incredibly grateful for having been blessed with a wonderful network of support that made the journey possible. Thank you all so very much!

DEDICATION

To Emma, who learned how to pronounce the word "dissertation" before she was 3 years old and who had my early-morning work schedule memorized when she was 3 ½ years old. To Ethan, who (not realizing I was asleep next to him, having finally finished the writing) flew out of bed at 3AM one morning looking for me and cried to his sister, "I can't find Mommy; she's not in her office!" You are my favorite people in the *whole entire* world.

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Chapter 1: General Introduction

The purpose of this study was to investigate the population biology and ecological characteristics of above-ground and below-ground life stages of *Cleome multicaulis*, as well as to identify soil characteristics (soil pH, soil salinity, and soil moisture) that might have important influences on growth and reproduction of this species. The study was undertaken at the request of The Nature Conservancy of Colorado, whose recent land acquisitions in the San Luis Valley have made significant contributions to the preservation of unique San Luis Valley ecosystems. Preliminary studies were conducted in the summer of 1994, with population censuses, a multi-year seed bank field experiment, and laboratory soil analysis carried out between 1995 and 1998. Attempts to germinate seeds and establish seedlings of *C. multicaulis* in the laboratory and greenhouse did not yield sufficient numbers of plants to conduct manipulative experiments in those controlled environments.

My hypothesis was that because *C. multicaulis* inhabits soils that are simultaneously saline and alkaline, the response of above-ground growth (and perhaps of seeds as well) to soil pH and conductivity would be congruent. A second hypothesis was that soil moisture would play a key role in the growth and reproduction of the annual *C. multicaulis* in this ephemeral wetland system. An additional study goal beyond distinguishing plant response to soil characteristics was to investigate the fate of *C. multicaulis* seeds in the soil by conducting a multi-year seed cage experiment following the design of Kalisz (1991). Study efforts also focused on the population dynamics of the species that, although locally abundant in the San Luis Valley, was believed to undergo wide fluctuations in population size from year-to-year. A matrix analysis tool was sought that would allow fine-scale examination of above- and below-ground population dynamics, and which could be used to identify important seasons and life stages that contribute to the population growth of annual species in a variable environment. Lastly, an examination of the nature of rarity in this species was undertaken in the hopes of synthesizing information gathered in order to make informed management recommendations to increase the population persistence of *C. multicaulis* in the San Luis Valley.

Introduction to the Study Organism

The plant on which these studies focused is *Cleome multicaulis* Sesse' & Moçiño ex DC., a member of what historically has been considered the family Capparaceae (but that some now combine into the Brassicaceae) (Judd et al. 1999). Common names used for the plant include Many-stemmed spiderflower, Slender spiderflower, Many-stemmed beeplant, Little beeplant, and Playa spider plant. Although never listed under the 1973 Endangered Species Act, *Cleome multicaulis* was considered a Category 2 candidate for listing under the ESA for the period from 1980 until 1996, when those classifications were abandoned (U.S. Fish and Wildlife 1996).

The species is listed in the state of Colorado as a Species of Concern and as a Sensitive Species under the Bureau of Land Management (BLM) in Colorado (Spackman et al. 1997). In spite of its comparative rarity in Wyoming, the species currently lacks any state conservation status or recognition as a BLM Sensitive Species in Wyoming (Fertig 2000b). Although there has been a recent compilation of historical herbarium collections (Jennings 1998) and several management reports concerning the status and rarity of *C. multicaulis* in Colorado and Wyoming (Graff 1992, Fertig 1993, Spackman et al. 1997, Fertig 2000b), there had been no previous systematic study of the ecological, habitat, and population characteristics of this species prior to the study described here.

Cleome multicaulis was first discovered in central Mexico by Sesse' and Moçiño and subsequently described by DeCandolle in 1824 (deCandolle 1824). *Cleome multicaulis* was apparently first observed in the United States in 1851 in southern New Mexico and Arizona (Jennings 1998), although recently examined accounts may indicate the plant has been present in Wyoming since 1843 (Fertig 2000b).

Described as *Cleome sonorae* Gray (1853) and as *Peritoma sonorae* Rydberg (1906), the species is an annual member of what has historically been considered the family Capparaceae (formerly called Capparidaceae), Sect. *Peritoma* (see discussion of recent taxonomic revision that follows). In the1950s Iltis conducted a focused reassessment of the taxonomic confusion in the genus and recognized the original name (Iltis 1952, 1957, 1958, Fertig 2000b).

Cleome multicaulis is described (Iltis 1958) as a slender, erect, unbranched or sparingly branched glabrous annual, 20-75 cm tall with 3 linear leaflets, each 6-35 mm long and 1-3 mm wide. Sepals are 4 and distinct. The flowers are zygomorphic with 4 distinct petals, described as pink to deep purple and rarely white (Iltis 1958) in a racemose inflorescence subtended by leaf-like 3-foliate bracts and with a bulbous floral disc on each flower. Stamens are 6, distinct and all of one length. The ovary is unilocular with parietal placentation and the style is single and terminal (Cronquist 1988).

The fruit is a capsule (Iltis also refers to it as a silique), obovoid to linear, 9-18mm long and 2-4 mm think, borne on a distinct gynophore 3-10mm long with a 15-22mm long pedicel. Fruits are dehiscent with the valves falling away at maturity and leaving the persistent, frame-like replum (Cronquist 1988). Seeds are described as subglobose, light brown, 1.8-2.5mm long, smooth and lacking any obvious adaptations for dispersal (Iltis 1957).

Fertig notes (2000b) that the original painting of Sesse' and Moçiño that deCandolle apparently used for his species description shows a specimen with multiple basal stems. Iltis (1977) describes the plant as, "unbranched, or with few to many branches from the base of the central stem, or more rarely branched above or with several stems arching outward from the base and lacking a leader." The multi-stemmed habit depicted in Sesse' and Moçiño's painting was almost never encountered in any of the Colorado or Wyoming populations studied recently, and should not be considered typical of the species (Fertig 2000a).

The genus *Cleome* has historically been placed in the family Capparaceae, which includes approximately 800 mostly tropical or subtropical members in 45 genera worldwide. Most researchers have long considered this family to be closely related to the Brassicaceae (Iltis 1957). However, recent molecular (rbCL) evidence has prompted some authors to combine the family with the Brassicaceae (Judd et al. 1999), placing *Capparis* and other genera of the subfamily Capparoideae (Cronquist 1988) in a basal position in the Brassicaceae based on rbCL molecular evidence, woody habit, and the absence of a replum in the fruit (Judd et al. 1999). *Cleome* and other genera in the subfamily Cleomoideae are placed less basally and in closer alliance with existing Brassicaceae based on rbCL molecular data, their herbaceous habit, and the presence of a replum in the fruit (Judd et al. 1999).

Both the Brassicaceae and the Capparaceae are members of the Order Capparales and produce various mustard oils (isothiocyanates derived by hydrolysis of glucosinolates through the intervention of the enzyme myrosin). Cabbage-butterflies and white rusts are among the parasitic groups that apparently have co-evolved to tolerate the presence of these secondary compounds (Cronquist 1988). Chromosome numbers are $X = 8\text{-}17$ in the Capparaceae (Cronquist 1988).

The genus *Cleome* has worldwide distribution and includes among its 200 members numerous species adapted to saline or desert habitats. Only the genus *Capparis* (that includes *Capparis spinosa* L., the pickled flower buds of which are used for seasoning) has a larger number (350) of species in the family. Several members of the genus *Cleome* (e.g., *C. hasslerana, C. spinosa*) are cultivated as garden plants in the United States.

The closest relative to *C. multicaulis* appears to be *Cleome serrulata* Pursh. (Iltis 1958), a taller, more robust plant that also occupies habitat in the San Luis Valley but is typically found in drier, more disturbed habitats than *C. multicaulis*. The leaves of *C. serrulata* were reportedly used as greens by the Navajos although livestock palatability is reportedly poor. The common name "beeplant" apparently arises from the cultivation of this species (at least in the period 1900-1950) as a honey plant (Iltis 1958).

Relatively high concentrations of the compound glucocapparin were detected in *Cleome serrulata* using gas chromatography (Louda et al. 1987). Analysis of *C. multicaulis* secondary compounds has not been done. No evidence has been found for the accumulation of *Cleome* secondary compounds in the soil, nor do the glucosinolates appear to have any allelopathic effect. The effect of any secondary compounds present on herbivore palatability of *C. multicaulis* is unknown.

Corollas of *C. multicaulis* undergo dramatic color change from a light pink to a deep rose color over a period of several days (Steingraeber 1996). Pollinator visitation rates before and after the color change were not measured or observed. When pollinators were excluded using mesh netting in a single study during the growing season of 1995, flowers inside the exclusions still underwent color change.

A white-flowered morph of *C. multicaulis* was located in this study, with approximately 30 white-flowered individuals identified as part of a larger, pink-flowered population in an area of approximately 30m^2 at Russell Lakes. Iltis (1958) mentions in his species description a corolla color of "pink to deep purple, rarely white" (with the latter color reported in the Arizona Flora (1964) by Peebles and Kearney, p. 364). Iltis provides no additional information concerning the white flower morph. White-flowered individuals were not located during the study period at any other locations, nor have they been noted in Wyoming populations (Fertig 2000b). A white form of the closely related *C. serrulata* has been described in the literature (Iltis 1958) but with no ecological explanation given for its presence. The white-flowered *C. multicaulis* plants were located in an area of relatively high soil moisture and (assumedly) low salinity, surrounded by tall vegetation that was primarily *Juncus balticus*.

Distribution and Historical Collections of *Cleome multicaulis*

Collections of *C. multicaulis* have been relatively few and far between since the species was first described in the mid-1800s. Collections were made in Arizona in 1905 and 1944, but Iltis (1958) considers these likely to have come from the same location and represent only a single species occurrence (Iltis 1958). A single sterile plant was collected just on the Arizona side of the Arizona-Mexico border in 1980, along with several individual plants on the Mexico side of the border (Jennings 1998). No collections have been made in Arizona since 1980. Eight or nine collections were apparently made in Mexico between 1851 and 1960 (Iltis 1977, Jennings 1998), although the current status of *C. multicaulis* in Mexico is unknown.

Only a single plant (!) has ever been collected in Texas, just across the border from Mexico (Iltis 1977). Two collections were supposedly made in New Mexico in 1851; Iltis expresses doubt about the accuracy of the second collection, as other collections from the same location were later discovered to have been mislabeled (Iltis 1958). *Cleome multicaulis* has not been located in New Mexico since 1851 and is now presumed to be extinct in the state (Iltis 1958, Jennings 1998).

At least sixteen collections were made in Colorado between 1873 and the mid-1950s (Iltis 1977), although additional historical specimens may exist. Colorado populations have been located in Alamosa, Costilla, Rio Grande, and Saguache Counties, all within the San Luis Valley. No current or historical collections of *C. multicaulis* have been made in Colorado outside the San Luis Valley. In addition to the relatively robust populations of *C. multicaulis* in the San Luis Valley, the only other recently documented occurrence of the species is a population located in 1993 on the edge of Steamboat Lake on the Pathfinder National Wildlife Refuge in southcentral Wyoming.

The presence of *C. multicaulis* was noted in Wyoming for the first time in the 20th century in 1980 from a collection north of Pathfinder Reservoir (Fertig 2000b). Failure to relocate this

1980 population, the lack of suitable habitat in close proximity to the described collection site, and the possibility of a typographic error in reporting the geographic Range on the 1980 specimen label have prompted Fertig (2000b) to suggest that the 1980 population may be coincident with that of Steamboat Lake, exactly six miles to the west. The suggestion was made that dispersing waterfowl carried seeds to a stock pond where the 1980 population was found (O'Kane 1984), but in fact the population found in 1980 was not in close proximity to any stock pond or similar structure (Fertig 2000b).

The intriguing suggestion that *C. multicaulis* may have been collected in Wyoming as early as 1843 (Fertig 2000b) comes from a citation by Iltis (Iltis 1952, 1977) of a "very old collection" of *C. multicaulis* by Gordon at Kew from "Platte River" (with apparently no further information given concerning the collection location on the material available for inspection by Iltis). Fertig feels this collection may have been made by Alexander Gordon, one of four botanists who (in a fascinating coincidence) took an 1843 excursion that passed within 3.5 miles of Steamboat Lake and followed the North Platte and Sweetwater Rivers, whose confluence is currently inundated by Pathfinder Reservoir (Fertig 2000b).

No other Wyoming populations have been found despite recent and repeated (1989, 1992, 1997, 1999, 2000) statewide surveys (Fertig 2000b). The population at Steamboat Lake is currently estimated to include several hundred thousand individuals or more (Fertig 2000b) occupying habitat similar to that of populations in the San Luis Valley and with similar population density.

The population at Steamboat Lake in Wyoming occurs at 5860 ft (1786 m) in a location that receives 9.5 inches (241mm) annual precipitation. Mean maximum and minimum temperatures in January are 31.3 and 11.0 F (-0.4 and -11.7 C) and mean maximum and minimum temperatures in July are 86.2 and 54.4 F (30.1 and 12.4 C) (Fertig 2000b). Soil characteristics at this site have not been determined. Local population density is described as being the greatest on damp (but not flooded) alkali flats with approximately 90% cover of *Spartina gracilis, Distichlis stricta, Juncus balticus, Puccinellia nuttalliana, Scirpus nevadensis,* and *Triglochin maritimum* (Fertig 2000b).

The Association for Biodiversity Information (formerly the Heritage Program of The Nature Conservancy) and the state network of Natural Heritage Programs gives *Cleome multicaulis* a rank of G2G3, indicating that it is intermediate between being "globally imperiled because of rarity" and "rare or local throughout its range" (Fertig 2000b). The species is ranked S2S3 in Colorado, S1 ("critically imperiled") in Arizona and Wyoming, and SH (historical) in New Mexico and Texas (Fertig 2000b). Earlier rankings (as of 1994) gave the species a status of G3S2.

Chapter 2: Introduction to San Luis Valley, Colorado Ecosystems Occupied by *Cleome multicaulis*

Introduction

An introduction is given here to the climate, geologic and hydrologic features of the San Luis Valley ecosystems inhabited by *Cleome multicaulis,* with an overview of soil characteristics common in *C. multicaulis* habitat such as soil salinity and pH. A discussion of physiological plant adaptations to saline and alkaline soils and of species diversity and community composition in saline habitats is necessary to appreciate the unique nature of San Luis Valley wetland ecosystems and to increase recognition of the ecological importance of Valley habitats for *C. multicaulis* and many other species.

Climate, Biotic Resources, and Geologic Features of the San Luis Valley

The San Luis Valley, Colorado habitat occupied by *Cleome multicaulis* comprises high altitude (2750m) cold desert shrubland and saline-alkaline wetland ecosystems extending 160 km from north to south and 100 km from east to west. The valley is bordered by the Sangre de Cristo Mountains on the east, the San Juan mountains on the west, and extends south into New Mexico (Figure 2.1). Extensive valley agriculture and the highest concentration of wetlands in the state of Colorado provide rich nesting and feeding sites for a wide variety of shorebirds, wading birds, raptors, waterfowl, and other animal and plant life. A patchwork complex of state and national wildlife refuges (e.g., Russell Lakes State Wildlife Area, San Luis Lakes State Wildlife Area, Blanca Wetlands, Alamosa and Monte Vista National Wildlife Refuges) provides critical migratory stopovers for Greater Sandhill Cranes, Whooping Cranes, and almost 200 other species of birds (U.S. Fish and Wildlife 1992).

Recognition of the ecological value of San Luis Valley wetlands prompted The Nature Conservancy (TNC) to acquire a total of over 3000 acres at Mishak Lakes Preserve between 1994 and 1999. Acquisition of the 100,000 acre Medano/ Zapata Ranch in 1999 added the largest single

TNC preserve in the state, with San Luis Valley lands now totaling 26% of the acreage currently protected by The Nature Conservancy of Colorado (Nature Conservancy of Colorado 1999).

San Luis Valley wetlands are characterized by low annual precipitation (18 cm 50-yr average), high rates of evapotranspiration (125cm annual average), and low relative humidity (39-78% daily) (Leonard and Wells 1989). Most precipitation in the Valley occurs as July and August thunderstorms that are rarely in excess of 2.5 cm per day (Leonard and Wells 1989, Foutz 1994). Surrounding mountain peaks receiving up to 100cm annual average precipitation drain snowmelt to the valley floor in spring and summer (Leonard and Wells 1989). Climate records used in this study were from Alamosa, Center, Blanca, and Saguache stations. Monthly precipitation totals for each of the four stations are shown for the years 1994-1999 with the exception of months and years for that data were missing (National Climate Data 2001).

Mean daily maximum temperature (average of the past 50 years) is 17.4° C and mean daily minimum temperature (average of the past 50 years) is -4.7° C. When blanketed with winter snows, the expansive and almost treeless floor of the Valley traps cold, sinking nighttime air to produce frequent freezing temperatures (225 days a year with daily minimum temperature below 0° C. When skies are clear, the town of Alamosa routinely records the coldest winter temperatures in the lower 48 states (Foutz 1994). Although geologic features of the valley provide the setting for abundant groundwater, low temperatures limit the San Luis Valley growing season and restrict crop selection to cold tolerant species such as potatoes, quinoa, alfalfa, barley, wheat, and lettuce as well as pasture grasses for cattle, horses, and sheep (Foutz 1994).

The separation and downshifting of tectonic plates has formed a rift valley divided by a series of hinged fault blocks sometimes described as uplifted horsts surrounding by the downshifted graben Valley floor (Leonard and Wells 1989, Foutz 1994). Wind-swept weathering of Tertiary-age San Juan volcanic rocks and Precambrian and Paleozoic Sangre de Cristo metamorphic layers has formed an extensive system of sand dunes at the eastern edge of the Valley, with some dunes rising more than 210m from the Valley floor (Foutz 1994). North of the Rio Grande River, the Valley is a closed basin (an area where rivers and streams flow inward, but not outward) with San Luis Lake in its center.

Hydrology of San Luis Valley Wetlands

Wetlands in the San Luis Valley depend for their continued existence on a local unconfined aquifer (shallow water table) of alluvial deposits laid down above layers of clay and volcanic rock and averaging about 2 m below the soil surface (wetlands) to 4.3m below the surface (drier Valley areas) (Leonard and Wells 1989). Aquifer recharge is difficult to estimate (Leonard and Wells 1989) but consists primarily of excess irrigation water, precipitation in excess of soil field capacity and evapotranspiration demand, upward leakage between the confined and unconfined aquifers, and ground-water underflow into the Valley. Estimates of aquifer recharge from precipitation are about 8% of the total precipitation received (Leonard and Wells 1989). Ground water outflows occur primarily from evapotranspiration of soil, plant, and free-water surfaces (Leonard and Wells 1989). Soil moisture is an important component of evapotranspiration, with the rate of evapotranspiration determined by microsite characteristics (Leonard and Wells 1989). Changes in soil moisture by evapotranspiration will alter the composition of the soil solution through a series of complex interactions between chemical constituents (Stark 1994).

Downward leaching of soluble salts will be minimized when evaporation rates exceed precipitation or in years when irrigation returns decline (Shafroth et al. 1995). The mineral products of weathering (primarily soluble salts of sodium and potassium) are moved by capillary action to the soil surface, where they accumulate and are deposited (Shainberg 1975, Foutz 1994). Rates of capillary action are slowed as depth to the unconfined aquifer increases and by finetextured clay soils (Shainberg 1975, Shafroth et al. 1995). Variation in the spatial distribution of water and solute sources and sinks may create corresponding spatial variability in surface salinity (Shainberg 1975). Fluctuations in water table depth and time lags between precipitation and soil response will create temporal variation in the accumulation of salts in the soil (Shumway and Bertness 1992).

In a model subject to some controversy, the current pumping of groundwater for the Closed Basin water project is assumed to lower evapotranspiration rates (Leonard and Wells 1989). A curve estimating the relationship between depth to the shallow water table and evapotranspiration from greasewood, saltgrass, rabbitbrush, and bare soil was developed. After a 20-year period, gains in the hydrologic budget from decreased evapotranspiration are projected to provide 66% of the total water available for pumping (Leonard and Wells 1989). In the meantime, however, the effects of groundwater pumping in terms of increased soil salinity are unclear and may be considerable.

A lag time of unknown duration likely exists between changes in depth to the unconfined aquifer and adjustments in the rate of capillary action. Ongoing research at Mishak Lakes Preserve seeks to develop comprehensive hydrologic models that address the complexities of San Luis Valley wetlands (Sanderson 1999). Many wetlands found on public lands in the Valley are managed for both game and non-game waterfowl and wildlife species by seasonally adjusting the relative proportions of emergent plant cover versus open water and maintaining saturated soils to promote plant growth (Poiani and Johnson 1993, Haukos and Smith 1996). The degree to which these managed wetlands differ ecologically and hydrologically from the wetland complexes at Mishak Lakes Preserve is still being investigated (Sanderson 1999). Seasonal fluctuations in water levels in the Mishak basins are unpredictable, and although the basins are typically dry by August, they may refill in the winter.

Uniqueness of San Luis Valley Ecosystems

Many wetlands systems studied differ from those in the San Luis Valley in terms of soil characteristics, recharge source, degree of hydrologic isolation among basins, and other ecological factors (Webb and Mendelssohn 1996). Many wetland studies of community and population ecology have focused on coastal salt marshes (Keddy and Ellis 1985, Keddy and Constabel 1986, Bertness and Ellison 1987, Shumway and Bertness 1992), prairie "potholes" of low salinity (Van der Valk and Davis 1978, Poiani and Johnson 1993), and inland salt pans (Ungar 1974, Khan and Weber 1986, Ungar 1987a, Badger and Ungar 1989). Comprehensive summaries of abiotic and biotic components of wetland ecosystems (Leck et al. 1989, Mitsch and Gosselink 1993) fail to address inland saline wetlands (Bolen et al. 1989) characterized by low precipitation and high rates of evaporation (Ungar 1974, Haukos and Smith 1996, Fort and Richards 1998). These ephemeral, dynamic systems are sometimes referred to as playas, although a precise definition appears to be lacking (Haukos and Smith 1996).

The saline wetlands of the San Luis Valley closely resemble playa basins of the Southern High Plains of Texas and in the Owens Valley/Mono Lake ecosystem of central California (Bolen et al. 1989, Haukos and Smith 1996, Brown 1997, Fort and Richards 1998) but with some important differences. Unlike those playas, San Luis Valley wetland basins are not isolated precipitation-fed watersheds with moisture regimes independent of one another (Haukos 1993). Their connection to a subsurface aquifer creates periodic cycles of inundation and drying (Leonard and Wells 1989) that may increase plant cover (Groeneveld and Or 1994) and affect plant community composition, distribution, and abundance.

In the Mono Valley, deep (> 1.2m) water tables favored shrub species similar to those in the San Luis Valley, while shallow (<0.8m) water tables supported herbaceous species (Groeneveld and Or 1994). Soils in the Mono Lake/Owens Valley ecosystems are alkaline (mean pH = 8.79 +- 0.067) but not saline (mean soil conductivity = 0.235 +-0.029 dS/m) (Brown 1997, Dahlgren et al. 1997, Fort and Richards 1998) and therefore differ significantly from the saline-sodic soils of the San Luis Valley as measured in this study (mean pH = 8.87 +- 0.5797; mean Ec = 8.507 +- 8.5816). Species found in the Owens Valley ecosystem include *Distichlis spicata, Sarcobatus vermiculatus, Cleome sparsifolia* (an annual), *Cleomella obtusifolia* (also in what has historically been recognized as the Caper family), *Chrysothamnus nauseosus* and *C. viscidiflorus, Tetradymia tetrameres, Juncus balticus, Carex* sp., *Sporobolus airoides* (alkali sacaton), *Atriplex lentiformis* ssp. torreyi (Torrey saltbush), *A. parryi*, and *A. confertifolia* (Groeneveld and Or 1994, Brown 1997).

The Soil Environment of the San Luis Valley

Soils in habitat occupied by *Cleome multicaulis* in the San Luis Valley may be primarily categorized as saline-sodic (Self 1999) and are often topped with a white layer of soluble salts, particularly in the early spring. Soil salinity in this study was measured as the electrolytic conductivity (Ec) of a saturated paste (Brady and Weil 1999). Soils are generally considered saline if their conductivity (measured in units of deciSiemens/meter (dS/m), millimhos/cm or milliSiemens/cm) is greater than 4.0 (Sposito 1989, Brady and Weil 1999). North America has 16 million ha of salt-affected soils. The salts are primarily chlorides and sulfates of calcium, magnesium, sodium, and potassium (Brady and Weil 1999).

The interaction between soil salinity and alkalinity is complex. Soils of arid and semiarid areas may become alkaline because precipitation is insufficient to leach the base-forming cations (Ca^{2+}, Mg^{2+}, K^+, Na^{+}) that are the product of mineral weathering (Brady and Weil 1999) and that have replaced Al^{3+} and H^+ on the soil exchange complex. Carbonic acid (H_2CO_3) forms when CO_2 from microbial and root respiration reacts with water; in alkaline soils with abundant OH- ions, this dissociates to form bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) ions).

The particular cation(s) that become associated with carbonate anions will influence soil pH. In soils where Ca^{2+} dominates, at least one of the salts that forms ($CaCO_3$) will remain insoluble and not contribute to an increase in pH. Where calcium and magnesium ions dominate the exchange complex of saline soils, pH values are characteristically lower than 8.5 (Sposito 1989, Brady and Weil 1999). The presence of soluble salts such as KCl, $CaCl_2$, NaCl, and $MgCl_2$ will increase soil salinity in arid areas where leaching is insufficient to remove even these soluble compounds. These salts in turn contribute continuous supplies of carbonate and bicarbonate ions, increasing the OH- ions and raising soil pH to values of 10 or more (Sposito 1989, Brady and Weil 1999, Tang and Turner 1999).

The exchangeable sodium present in these sodic soils may have a marked influence on the physical and chemical properties of the soil (Sposito 1989). The presence of large quantities of Na^+ ions (relative to concentrations of Ca^{2+} and Mg^{2+}) will tend to break up soil aggregates because of the comparatively weak attraction of Na^+ ions to the soil colloids. The dispersed colloids clog the soil pores, reducing the downward percolation of water, decreasing hydraulic conductivity, and causing poor aeration (Sposito 1989, Brady and Weil 1999). Very limited air and water movement in some saline-sodic soils also may be a factor in determining which plants can grow on these soils (Sposito 1989). Soils of a sodic nature are unproductive and difficult to manage (Brady and Weil 1999).

Soil pH controls many chemical reactions and availability of essential elements and nutrients (Haukos and Smith 1996). The composition of ions in the soil solution may be important in predicting plant growth characteristics, perhaps even more so than overall soil pH (Falkengren-Grerup 1994). Plants growing in soils with high pH (9-12) can be expected to have reduced stomatal conductance and lowered leaf nutrient concentrations of calcium, iron, manganese, and zinc (Farrell et al. 1996, Tang and Turner 1999). Soils with high pH harm plants in five ways; 1) the caustic influence of the high pH induced by the sodium carbonate and bicarbonate, 2) the toxicity of the HCO_3- and OH^- anions, 3) the adverse effects of active sodium ions on plant metabolism and nutrition, 4) deficiencies in iron, manganese, zinc, and calcium (Ca^{2+}) due to high pH, and 5) oxygen deficiency due to the breakdown of soil structure (Brady and Weil 1999). Because alkalinity usually has such dramatic effects on soil physical and chemical properties, it is likely to be a better integrating and comprehensive index of soil properties than is salinity alone (Daiyuan et al. 1998).

Frequent water-level fluctuations in desert playas may deplete soil nitrogen through an increase in denitrification (Haukos and Smith 1996). Soil flooding, on the other hand, may mix nutrients and increase soil homogeneity (Huenneke and Sharitz 1990), affect oxygen concentration, minimize daily temperature fluctuation, and alter the quantity and wavelength of light (Rabinowitz 1978).

Physiological adaptations of plants to saline and sodic soils

The physiological mechanisms used by *Cleome multicaulis* to increase its salt tolerance were not examined in this study, but would be of great interest for future physiological research. Use of the term "salinity" in discussions of soil characteristics commonly refers to soils high in both total soluble salts and exchangeable sodium, primarily measured through electrolytic conductivity (Ungar 1974, Shainberg 1975). In most studies of saline soils, neither alkalinity nor the sodic nature of the soil are explicitly considered.

Soil effects are felt principally through an alteration of plant osmotic balance, that provokes a reduction in intracellular solute potential via the accumulation of organic acids in order to compensate for high levels of external soluble salts (Ungar 1974, Shainberg 1975). Reduced plant growth, depressed rates of transpiration, reduced water availability, excessive ion accumulation, and reduced uptake of essential mineral nutrients may occur as a result (Shainberg

1975). Plants with high salinity tolerance have lower selectivity against leaf sodium uptake and may isolate sodium from metabolically active leaves by retaining it in roots or stems. Some perennial halophytes accumulate salt in older leaves that are then shed at the end of each year (Ungar 1974, Shainberg 1975).

Increased salinity coincides with an increase in abscissic acid concentration, reduced stomatal aperture, and induction of stomatal closure (Shainberg 1975). High levels of electrolytic conductivty have been shown to affect stomatal conductance and water use, with secondary effects on photosynthetic rate (Farrell et al. 1996). Transpiration, passive uptake of salts, and CO_2 intake are all reduced. There is some evidence for a shift from the C3 to either the C4 or CAM pathways in response to salinity, especially in halophytic plants. The CAM pathway results in lower turnover of water and therefore reduced passive uptake of salts (Shainberg 1975).

Most physiological studies of salt tolerance have focused on yield reductions of crop plants on saline soils. Greenhouse studies have shown that many halophytes (i.e., plants that can grow and reproduce under saline conditions) have the ability to do so under nonsaline conditions as well (Shainberg 1975, Khan and Weber 1986, Badger and Ungar 1989, Foderaro and Ungar 1997). Field experiments with non-crop plants may be complicated by interactions between soil characteristics, competition, and other ecological factors.

Although lab studies have shown that increased etiolation and the inhibition of cell differentiation may occur in the absence of NaCl (Shainberg 1975), a physiological requirement for excess salts does not explain halophyte distributions as accurately as the tolerance by halophytes of low water potentials (Ungar 1974, 1978, Bertness et al. 1992, Khan and Rizvi 1994, Foderaro and Ungar 1997). Changes in plant phenotype in response to changes in soil salinity may include differences in leaf morphology and extent of branching, although the latter effects may be confounded by plant density (Freas and Murphy 1988).

Species Diversity and Community Composition in Saline Habitats

Plant distributions in saline environments are thought to be the result of edaphic conditions (primarily salt tolerance), with soil moisture, climate, topography, and biotic factors of secondary importance (Ungar 1974, West 1989). Upland, less saline soils are often occupied by shrubs in the family Asteraceae (e.g., *Chrysothamnus* sp.). Salt-desert shrublands are dominated by widely distributed members of the Chenopodiaceae, with occasional scattered members of the families Brassicaceae, Fabaceae, and Poaceae (West 1989).

Species found in ephemeral saline wetlands must have the ability to osmotically adjust as water levels and salinity fluctuate from a combination of high evaporation and sporadic rainfall (Ungar 1974). Species diversity declines with even a low incremental increase in soil salinity, with several characteristic plant communities dominating saline landscapes (West 1989).

Communities dominated by saltgrass (*Distichlis stricta* var. *spicata*) may occur in soils of relatively low moisture and a wide range of salinities (as high as 39.8 dS/m) (Ungar 1974, Shumway and Bertness 1992). This dioecious, shallow-rooted perennial rhizomatous grass excretes salts and maintains high osmotic pressure in the cell sap (Ungar 1974) but its growth may be stunted in soils with pH above 9.2 (Ungar 1974, Shumway and Bertness 1992). *Distichlis* responds to short-term disturbance with rapid colonization of bare patches from a persistent seed bank and vegetative spread (Bertness and Ellison 1987) but may later be replaced by slower-growing *Juncus* sp. (Bertness and Ellison 1987). Physiological integration between ramets of clonal perennial grasses such as *Distichlis* may allow those species to share water, nitrate, and potassium that would otherwise be reduced in salt-stressed plants (Bertness et al. 1992, Shumway 1995).

Upland saline shrub communities are often dominated by greasewood (*Sarcobatus vermiculatus*), a species described variously as moderately (West 1989) to highly salt tolerant in its physiology (Donovan et al. 1996). Large taproots extend 3-5m below the soil surface (Ganskopp 1986, Leonard and Wells 1989). *Sarcobatus* also undergoes hydraulic lift, which exploits a vertical gradient in soil moisture to transport water upwards during the night from deep to shallow soils, where it is taken up during the day as stomata open and shoot water potentials drop (Donovan et al. 1999). Unlike many other salt-tolerant chenopods, *Sarcobatus* utilizes the C3 (rather than more water-use efficient C4) photosynthetic pathway (Donovan et al. 1996).

Microsites occupied by *Sarcobatus* exhibit increased salinity as a result of leaf shedding of succulent, sodium-rich leaves (Donovan et al. 1996). Downward leaching of accumulated salts under the shrub canopy is minimized by the lack of periodic flooding in these upland habitats (Ganskopp 1986, Donovan et al. 1996). Seasonal fluctuations in the levels of soil salinity in *Sarcobatus*-occupied microsites are unknown.

Plant communities on soils of high moisture and even standing water are often dominated by vegetatively reproducing species such as *Juncus* sp., *Scirpus* sp., *Salicornia* sp., *Eleocharis* sp. and *Triglochin* sp.(Shumway and Bertness 1992) that may outcompete disturbance-generated annuals (Bertness et al. 1992). The spatial distribution of dominant marsh perennial turf species may be determined by differences in competitive ability and tolerance of the physical environment and may occur primarily as a result of clonal growth (Shumway and Bertness 1992). Although gradients of soil moisture are often invoked to explain wetland plant distributions, responses of soil moisture are not always distinct (Keddy 1982). The recognition of shared responses to soil moisture among wetland species may indicate that other biotic mechanisms need to be invoked to explain the distribution of adult plants (Keddy and Ellis 1985).

Previous studies have found that plant community structure may relate to depth to the water table (Daiyuan et al. 1998) but unquantified biotic and soil physical relationships (e.g., competition, soil texture) may contribute to the distribution of vegetation across a water table gradient and will be unique for each habitat (Webb and Mendelssohn 1996, Donovan et al. 1999). Edaphic factors such as soil moisture may be important in determining community structure on a number of different spatial scales (Daiyuan et al. 1998).

Succession in saline ecosystems such as the San Luis Valley may occur slowly or perhaps not at all (Cooper 1999). Because of a limited species pool in saline environments, short-term community vegetation changes usually consist of autosuccessive species replacement with the same species or those similar in appearance and stature. Primary succession on a longer time scale, to the extent it occurs, is likely to be driven by long-term changes in the water level of saline lakes causing a cyclical pattern of species invasion and retrogression (West 1989). Disturbance by fire is not likely to have been a dominant historical force in this community due to sparse plant cover (West 1989).

Although the mechanism of competitive exclusion is often invoked to explain the elimination of facultative halophytes from moderately saline sites (Ungar 1974, Shainberg 1975), the extent to which this occurs as a result of clonal-growth perennials outcompeting disturbance-generated annuals, and not as a result of salt tolerance, is unknown (Bertness et al. 1992). Both abiotic and biotic factors clearly influence the distribution of plant species in saline habitats (Foderaro and Ungar 1997).

Persistent seed banks may be extensive in size and considered important (Ungar 1987b, Badger and Ungar 1994, Baskin and Baskin 1998) in maintaining populations of halophytes in wetland habitats. In addition to factors affecting the germination and emergence of wetland seeds (Shumway and Bertness 1992, Thompson 1992), seedling and adult survival, tolerance to environmental stress, and interspecific competition (Welling et al. 1988, Bertness 1991) may also be of great importance in determining the distribution of plant species.

The effect of salinity on seed germination has been a subject of interest at least since Darwin investigated the phenomenon (Darwin 1859), and continues to draw the attention of scientists because of its relevance for the global growth of crop plants. Surface soils may have salinities 2-100 times that of the subsoil layers, presenting a much more extreme adaptive environment to seeds than growing plants (Ungar 1978). Life stages of a species may differ strikingly in their salinity tolerance, and some species (e.g., *Hordeum jubatum)* germinate readily at salinities higher than those favorable to growth and reproduction (Badger and Ungar 1989). Many of the field studies undertaken address germination in salt marshes (Ellison 1987, Bertness 1991, Bertness et al. 1992) or inland salt pans (Ungar 1987a, Badger and Ungar 1989, Foderaro and Ungar 1997).

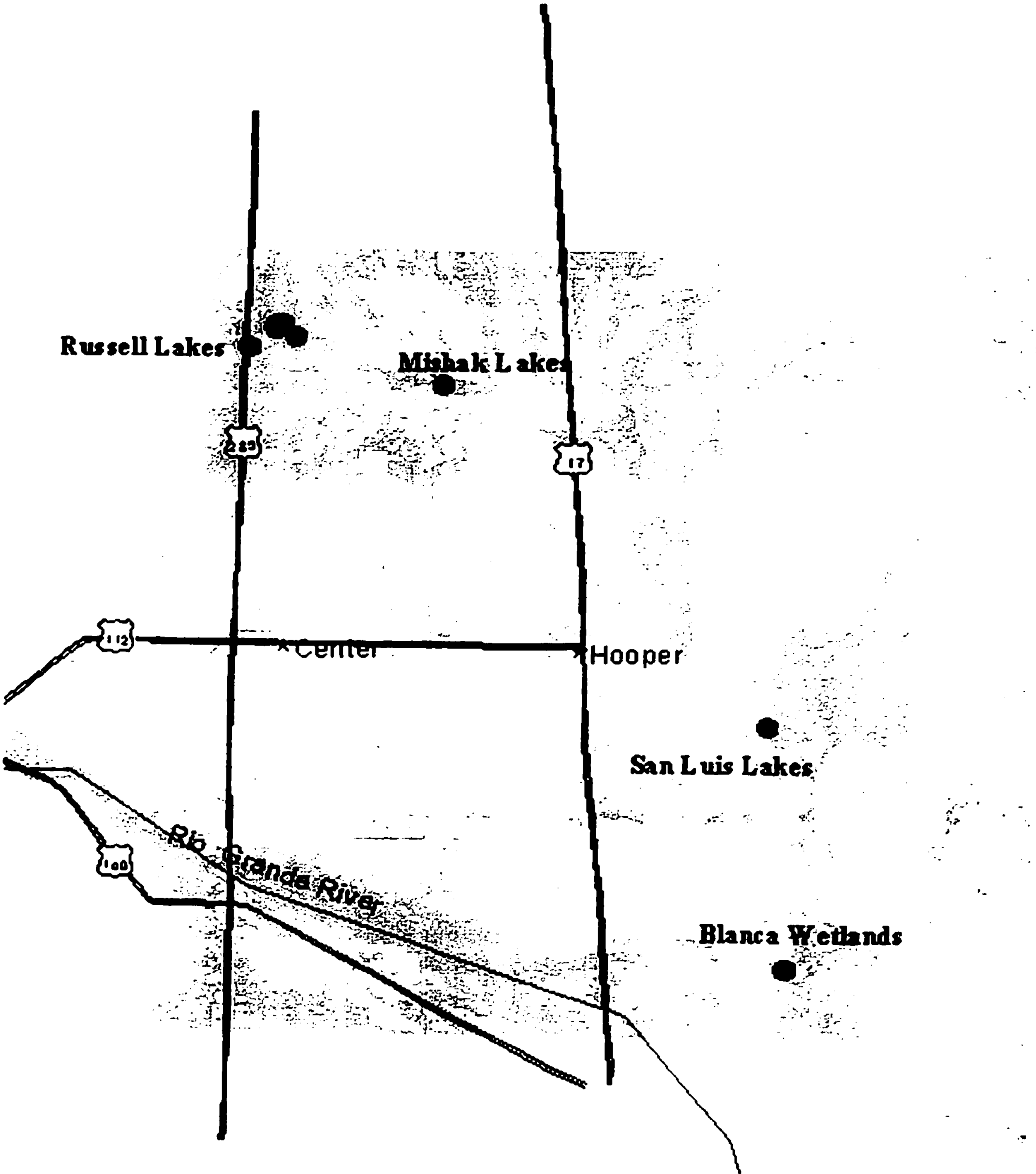

FIGURE 2.1 Map of the San Luis Valley and Study Sites

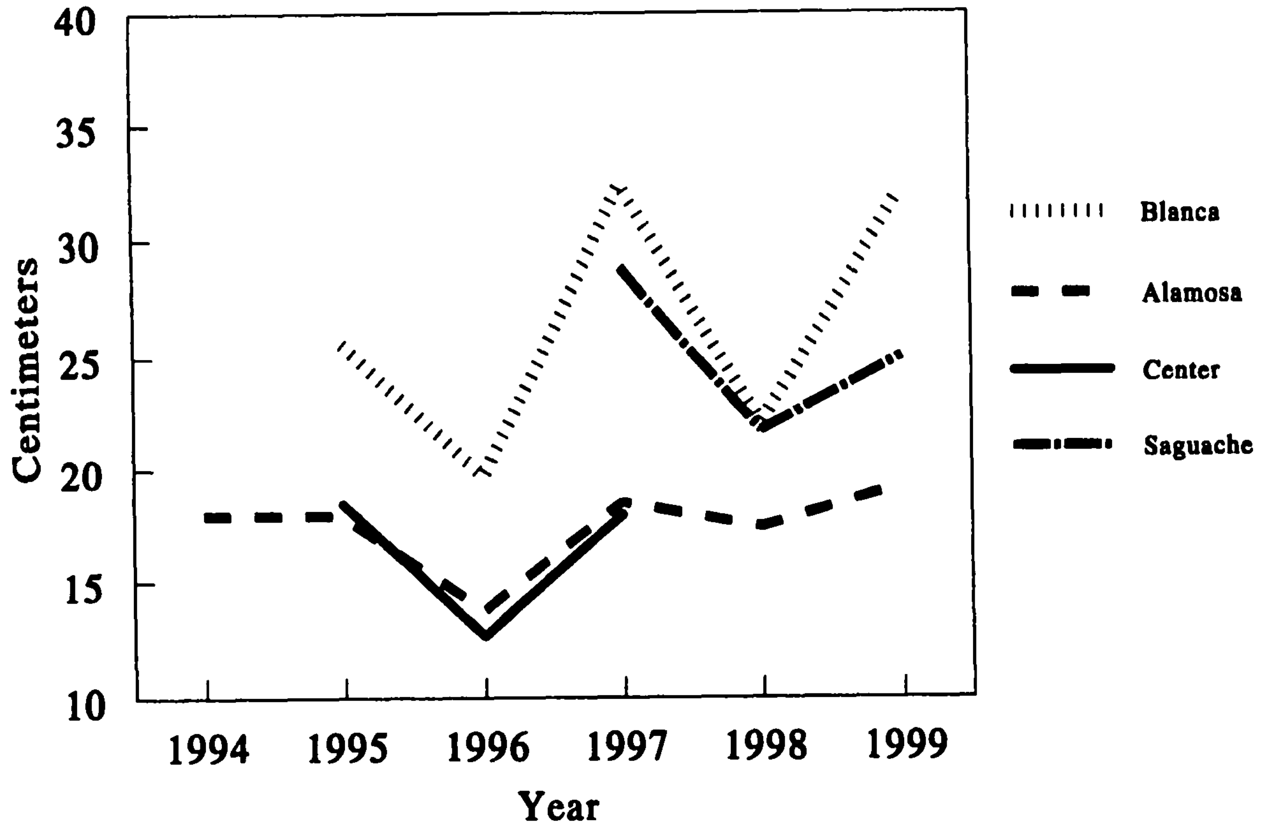

Figure 2.2 Annual Precipitation at Four San Luis Valley Weather Stations, Years 1994-1999

Chapter 3: Soil Characteristics of Habitat Occupied by *Cleome multicaulis* in the San Luis Valley, Colorado and Their Effect on Plant Growth and Reproduction

INTRODUCTION

Ecologists have reached the consensus that heterogeneous environments exist at virtually every spatial and temporal scale (Stanton and Galen 1997) but that realization has not extinguished our intrigue with the complexities of habitat variability and its ecological relevance. Although routine measurements that accurately assess environmental heterogeneity have been described as being "nearly impossible" in principle (Bell and Lechowicz 1994), ecologists nevertheless struggle with the characterization of habitat variability at relevant scales of focus. The distribution of resources in soils is never uniform, and plants experience spatial and temporal variation beyond the scale of the individual through extensions of roots, rhizomes, pollen and seeds (Bell and Lechowicz 1994), with the result that local-scale spatial and temporal variability in environmental conditions can markedly influence plant populations (Huenneke and Sharitz 1990, Kephart and Paladino 1997).

It has been said that organisms, "do not occur where they cannot, but often do not occur where they might" (Kruckeberg and Rabinowitz 1985). An organism's absence from a patch of ground does not distinguish whether the habitat is unsuitable, whether there was a failure of dispersal, or whether the organism reached the patch and was then subject to local or regional forces of extinction (Holsinger and Gottlieb 1991). Not all portions of the climatically suitable range of a plant species may be equally suitable in terms of habitat characteristics (Carey et al. 1995, Haukos and Smith 1996), and not all suitable habitat may be occupied (Pulliam 1996). The ecological processes determining why one particular patch of ground contains many plants while the adjoining square meter contains none has long been a perplexing question for biologists (Kruckeberg and Rabinowitz 1985) and here provides fodder for study and contemplation.

The presence of an organism on a patch of ground likely indicates that suitable habitat exists therein; however, determination of which habitat features are likely to be most important in predicting plant occurrence and success may be as challenging as measuring the dimensions of an "n-dimensional-niche." (Hutchinson 1957). Habitat characteristics measured at a scale that appears to influence the establishment, growth and reproduction of a species may overlook the effect of those characteristics on cryptic life stages such as a persistent seed bank (Mehrhoff 1989b, Falb and Leopold 1993, Sieg and King 1995).

One reason that habitat studies continue is that detailed investigations of the effects of spatial and temporal environmental heterogeneity on the population biology of rare species are considered essential for effective plant conservation, regardless of the cause of rarity (Rabinowitz 1981, Fahrig and Paloheimo 1988, Kephart and Paladino 1997). Studies that reveal the lack of distinguishing habitat characteristics for rare species may challenge us to redefine the relevant scales of study, examine the process behind the pattern, and scrutinize generalizations about causes of rarity.

The study described here examined multiple populations of *Cleome multicaulis* located in the San Luis Valley, Colorado with some populations separated by as much as 100km from one another. (GPS positions of populations used in this study are given in Appendix 3.1). At least one additional population of *C. multicaulis* has been located at Pathfinder National Wildlife Refuge in northcentral Wyoming (Fertig 2000b), although comparisons between the San Luis Valley and Wyoming populations were not made in this study.

A three-year study was undertaken to characterize the distinguishing features of the habitat occupied by *Cleome multicaulis* in the San Luis Valley that may influence the population dynamics of that species, and to determine the extent and nature of the temporal and spatial variation in selected habitat features. Recent and extensive land acquisitions by The Nature Conservancy in the San Luis Valley have provided urgency to the need for management recommendations in order to maintain and increase populations of *C. multicaulis* where it is found.

Comparisons are made in this study among sites of low to high occurrence of the species and among a range of habitats in the San Luis Valley. The design of this study does not allow the detection of properties that might make establishment and growth impossible (Falkengren-Grerup 1994, Wiser 1998).

Habitat attributes that may be important in influencing community composition of wetland habitats similar to those occupied by *C. multicaulis* include soil salinity, pH, soil moisture, organic matter, and the resistence of soil to penetration (Ungar 1987a, Bertness et al. 1992, Haukos and Smith 1996, Daiyuan et al. 1998). Although much attention has been given in the literature to seed germination timing, plant growth, and plant reproductive response in saline soils, little attempt has been made to determine the extent to which plant response to soil salinity and alkalinity may be associated or distinct. The role of soil salinity in determining plant distributions at the population scale of focus has less commonly been examined, and the role of soil pH has hardly ever been questioned as provoking a distinct or associated plant response with conductivity.

Characterization of soil attributes (pH, electrolytic conductivity, and soil moisture) and their patterns of spatial and temporal variation will aid in identifying habitat features of *C. multicaulis* in the San Luis Valley. Examination of the influence of soil characteristics on *C. multicaulis* growth and reproduction will assist in determining whether seed and adult life stages of this species differ in their tolerance and response to soil salinity and alkalinity, and in the determination of whether relevant variation in microhabitat characteristics is prevalent enough to necessitate multiple management approaches.

METHODS

Twelve macroplots (12m x 8m each) were established in the San Luis Valley across a wide range of *C. multicaulis* habitat (Figure 2.1, Appendix 3.1) and according to the prevailing density of *C. multicaulis* populations (Bell and Lechowicz 1994). Seven macroplots were established at Russell Lakes State Wildlife Area (managed by the Colorado Division of Wildlife), one at Mishak Lakes Preserve (owned by The Nature Conservancy), one at San Luis Lakes State Wildlife Area (Colorado Division of Wildlife), and three at Blanca Wetlands (managed by the Bureau of Land Management). The macroplot at Mishak Lakes was censused for the years 1995 and 1996, but not 1997. Within each macroplot, six census quadrats (each 40cm x 40cm) were established in 1995 using a stratified random selection process, with the constraint that three of the six quadrats in each macroplot contained evidence of *C. multicaulis* presence (as evidenced by dead remains from the previous year).

Quadrat size reflected a compromise between choosing quadrats small enough to minimize the probability that small scales of spatial pattern would be missed (Dale 1999) and large enough quadrats to encompass population densities sufficient to detect the effects of density dependence (although densities were not experimentally manipulated in this study). In 1995, 60% of the established census quadrats contained dead growth from at least one previous year plant.

Two additional plots were established along the shoreline of San Luis Lakes in 1995 but were completely flooded in July of that year (prior to seed production in *C. multicaulis*) and remained under water until spring of 1996. Two additional plots were established at Blanca Wetlands in late summer 1995 with the purpose of examining the effect of surface-level fires on subsequent emergence of *C. multicaulis*. One of these sites was burned in January 1996; the second site, that was to serve as the "control" location, became inundated with water in spring 1996 and remained flooded for the remainder of the study. Data from these plots were not included in the analyses.

Macroplots were located in close proximity to wetland basins, which fill and empty at least once and sometimes several times each year. No macroplots were flooded at the time of establishment, but some quadrats did become inundated with standing water during one or more of the census years. Both quadrat-level (1600 cm^2) and macroplot-level ($96m^2$) scales of measurement and analysis were utilized in this study, in order to more accurately characterize soil characteristics at multiple spatial scales (Kephart and Paladino 1997).

Plant associates within each quadrat were identified and ranked as to relative percent cover at the height of the growing season in August 1995. Soil samples were taken using a soil auger of 7cm diameter x 15cm depth. Samples were taken within 15cm of the outside boundary of each 40cm x 40cm census quadrat on June 15 and August 25 1995, and on or within 3 days of May 5, June 15, and August 25 in 1996 and 1997. No soil samples were taken from the Mishak Lakes macroplot in 1997 ($n = 72$ for each sampling date in 1995 and 1996; $n = 66$ for each 1997 sampling date). A second sampling regime removed soils in 1995 and 1996 from the four corners of each macroplot every eight weeks from the end of May through the end of September.

Soils were stored in a cooler with blue ice and transported to the Colorado State University Plant, Soil, and Water Testing Lab within 5 days of collection. Saturated pastes were prepared and allowed to settle overnight; aqueous extracts were then prepared by vacuum extraction and tested for soil pH and electrolytic conductivity using a pH meter and a conductivity meter (Klute and Page 1982, Brady and Weil 1999). Soil moisture was analyzed gravimetrically. Soil samples of approximately equal volume were weighed and then air-dried in an oven at 105 degrees C overnight. Samples were re-weighed when dry and the percentage change in weight was calculated (Klute and Page 1982, Brady and Weil 1999).

Soil texture was assessed once in September 1995 using the tactile method (Klute and Page 1982) from samples taken in late May 1995 and stored in a cool, dry location from May until September. Analysis of anion and cation concentrations in solution was performed on an ion chromatograph using September 1995 samples.

Plant heights were measured once, at the end of the growing season in 1996. The number of seeds per capsule was counted each year using a sample of 10 capsules and was not found to vary either with plant height or from year to year. A single estimate of the number of seeds per fruit (capsule) was subsequently used in all analyses (Klemow and Raynal 1985).

Shallow water wells were constructed in mid-June 1995 using plastic pipe of 10cm diameter with holes drilled at 4cm intervals horizontally and vertically around the pipe. The pipes were sunk 60cm into the middle of each macroplot with 15cm of pipe above the ground level, for a total pipe height of 75cm (Ganskopp 1986). The wells were capped and allowed to reach equilibrium with the surrounding shallow water table. Subsurface fluctuations were measured with a meter stick.

Measurements of shallow water table depth (n = 267) were taken biweekly beginning in early July 1995 and from early May through late August of 1996 and 1997. Pipe heights above the ground level were re-measured at the beginning of 1996 and 1997, respectively, to allow for accurate measurements that incorporated physical settling of the pipe over time. Measurements were taken across 5 dates in 1995 and for 9 dates each in 1996 and 1997. On 62 occasions (23.7% of the total measurements) the depth to the shallow water table exceeded the pipe height and a "detection limit" was reached (22 out of 58 measurements in 1995, 21 out of 108 measurements in 1996, and 21 out of 99 measurements in 1997 reached a detection limit). A greater number of measurements reached the detection limit in 1995 than in subsequent years because no early season (May) samples were taken in that year.

Analysis of Variance Statistical Methods

Analysis of variance using PROC GLM (SAS 1997) was performed in order to determine the effect of estimated percent total plant cover and plant associates on soil pH, conductivity, and soil moisture respectively. Analyses used Type III sums of squares, and Duncan multiple range comparison-wise tests of means were conducted. Values of soil conductivity (Ec) were natural log transformed and values of soil moisture were arcsin-square root transformed in order to meet assumptions of homogeneity of variance.

Repeated Measures Statistical Analyses

In order to assess the temporal and spatial variation in soil characteristics and to determine the effect of soil characteristics on plant growth and reproduction, repeated measures statistical analyses were performed with PROC MIXED of Version 6.12 SAS (SAS 1997), using both date and year as repeated measures. Repeated measures analysis of variance is appropriate for these data because such analyses assume some correlation exists between measurements taken at the same census quadrats over multiple dates and multiple years. Most previously conducted ecological studies using repeated measures analysis have used PROC GLM of SAS (Lesica and Steele 1994, Van der Valk et al. 1994, SAS 1997), that would not have allowed for the complexity of data in this study.

Various repeated measures models carry with them assumptions, particularly regarding the variance-covariance matrix of levels of the within-subject factors. PROC MIXED has fewer assumptions and incorporates a wider range of mixed linear models than do many other repeated measures analyses. Assumptions of the PROC MIXED analyses are:

1. The data are normally distributed
2. The means (expected values) of the data are linear in terms of a certain set of parameters.
3. The variances and covariances of the data are in terms of a different set of parameters, and they exhibit a structure matching one of those available in PROC MIXED.

(SAS 1997).

Because the data are assumed to be normally distributed, they may be modeled entirely in terms of their means and their variances/covariances. Parameters may be either fixed or random in this analysis. An effect is considered fixed if the means of the classes themselves differ; fixed effect parameters may be either qualitative or quantitative. Random effects parameters were utilized for the covariance structure of these data; the variances of the random effects parameters thus became the covariance parameters for this particular structure. Alternative covariance structures (compound symmetry, autoregression, and unstructured covariance matrices) were tested and rejected (Littell et al. 1996). PROC MIXED then uses the method of restricted maximum likelihood to fit the structure selected to the data (SAS 1997). All models calculated Type III sums of squares. Generalized least squares means of fixed effects were then estimated, with almost completely uniform standard errors of each mean (e.g., identical to 3 significant digits). Parameter estimates, differences of the least squares means and confidence limits (chosen at the level alpha =.05) were computed to complete the analysis.

Statistical models employed in this analysis defined both date and year as repeated (i.e., non-randomized) measures, with the exception of any model analyzing reproductive output or survivorship with only a single end-of-season measurement. For those models, year was the sole repeated measure. Models were unbalanced in two ways; no May 1995 measurement was taken, and only eleven (rather than twelve) locations were used in 1997. Because location was a random effect in all the models, this did not adversely affect the model. When the model fits a random effect, only variance components are estimated, rather than a mean being obtained for each possible combination (as with fixed effects) (Chapman 1996).

In order to meet the model assumption that data were normally distributed, plots of residuals versus fits were examined for all dependent variables, and transformation performed where necessary. Values of pH were not transformed. Values of soil conductivity (Ec) were natural log-transformed (Lesch et al. 1998) and for soil moisture (SM), an arcsin transformation was performed on square root values.

In almost all cases of analysis, there was a significant amount of estimated variance between locations (relative to the variance between quadrats, etc.) and therefore quadrats were nested within location rather than being used as independent replicates (Sieg and King 1995). Statistical models are described in Repeated Measures Results and are available from the author upon request. Transformed means were used in all cases to determine tests of significance, whereas untransformed means are presented in tables and charts for comparative purposes.

Multiple Regression Statistical Methods

Multiple regression using PROC REG in SAS (SAS 1997) was used in order to investigate the relationship between the number of fruits (dependent variable) and plant height, total plant density and soil characteristics (independent variables).

RESULTS

Variation in Density across Years

Plant densities of *C. multicaulis* during the census period ranged up to 356 adult plants per 0.4m x 0.4m quadrat (890 plants per m^2) at several sites (Blanca Wetlands sites BW1 and BW2 and Russell Lakes site RL6). Forty-two of 72 quadrats (58.3%) had greater than 200 individuals in each of the census years. The percentage of census quadrats with *C. multicaulis* present ranged from 81.8 - 86.1% during the census period, and both the number of seedlings and the estimated least square mean density of *C. multicaulis* in census quadrats increased between 1995 and 1997 (Table 3.1; Figure 3.1). There was considerable spatial variation in end-of-season plant density between macroplot locations (Table 3.2) and among quadrats within locations (Table 3.3). Of the 72 quadrats censused in 1995 and 1996 (and 66 quadrats censused in 1997), fifteen showed a substantial (e.g., > 100%) increase in density of *C. multicaulis* over the period 1995-1997 and eight showed a substantial (e.g., > 100%) decline.

Repeated Measures Analysis of Plant Density

A model examining the effect of date, year, and the date*year interaction on plant density (square-root) (Table 3.4) revealed that the effect of date was significant, the effect of year was marginally significant ($p = 0.0649$) and the date by year interaction was not significant. The pattern of temporal variation in density of *C. multicaulis* was therefore relatively predictable across each growing season (Figure 3.1). There was considerable spatial variation in above-ground density of *C. multicaulis* both across locations and across quadrats, and quadrats with high plant density one year did not necessarily have high density in subsequent years. The only significant difference comparing estimated least square mean plant density across years was a comparison between date 3 1995 and date 3 1997 ($df = 201$, $p = 0.0340$). Density varied significantly between dates 1, 2, and 3 for each year of the study.

The addition of soil covariates (pH, conductivity, and soil moisture) to the above model (Table 3.5) did not significantly alter the effect of date, year or the date by year interaction. None of the soil covariates themselves had a significant effect on plant density (square root) after adjustment for date, year, and the date by year interaction.

Results of correlation analysis indicate a slightly negative correlation between plant density and both soil pH and soil conductivity, with a non-significant correlation between plant density and soil moisture (Table 3.6). Use of repeated measures analysis is likely to produce a more reliable result because the model with Type III Sums of Squares adjusts for the significant effects of date and the (marginally) significant effect of year before examining any additional effect of soil covariates on the variation in plant density.

Range of Values Encountered in Soil Characteristics

Soil characteristics as measured over the three-year period provide a useful indication of the range of environmental conditions under which *C. multicaulis* individuals exist (Table 3.7). Values of soil pH encountered across the 12 locations and over the three-year sampling period ranged from 7.35 to 10.10 (mean = 8.87, std. dev. = 0.5797). Of the 558 soil measurements taken, 253 (45.3%) had pH values greater than 9.50 (Appendices 3.5, 3.7), and 8 of the 23 measurements taken that had soil pH of 9.80 or greater had *Cleome* present. The quadrat with highest pH and *Cleome* present had a soil pH of 9.95 and density of 72 plants. Quadrats with more than 150 plants had less variability in soil pH than did quadrats with zero plants (Table 3.8). Neither exchangeable sodium percentage (ESP) nor sodium absorption ratios (SAR) were measured. Values of pH measured indicate that the soils are of a saline-sodic nature (Self 1999).

Soil electrolytic conductivity ranged from 0.79 to 67.68 dS/m (mean = 8.507, std. dev. = 8.5816). Of the 25 samples taken that measured soil conductivity (Ec) values greater than 25 dS/m, 3 of those had plant densities < 5 and 4 of them had densities between 11 and 92 (Appendices 3.5, 3.7). The most saline quadrat where *Cleome* was present had a density of 4 plants, and soil conductivity of 41.92 dS/m. Soil conductivity was less variable in quadrats with over 150 plants than it was with lower (or zero) densities of *C. multicaulis* (Table 3.8).

Soil moisture values ranged from 1.23% to 144.24% (mean = 31.66%, std. dev. = 17.303%). Of the 40 measurements taken that had soil moisture levels greater than 60%, 30 of them had *C. multicaulis* present (Appendix 3.6). Soil moisture was not more variable in quadrats with low densities of *C. multicaulis* than it was in high-density quadrats (Table 3.8). Analysis of cations and anions using ion chromatography revealed that major soil cations are Na^+ and K^+ (Ca^+ was not measured), and the predominant anions are Cl^- and SO_4^{-2} Soil textures most commonly present were sandy clay loams (30.2% of samples analyzed), loamy sands (26.3% of samples) and sandy clay and clay soils (both 18.6% of samples). Analysis of soil texture was completed only once (in 1995), using tactile estimation methods.

Repeated Measures Analysis of Soil pH

Repeated measures analysis of the effect of date, year, and the date*year interaction on soil pH (Table 3.9) showed no significant effect of date or year, but the date*year interaction did show a significant effect. The greatest source of variation in soil pH was across locations. Estimation of the least square mean shows that although pH varied across dates within any particular year, there was no consistent pattern of variation (Figure 3.2). Four comparisons across dates within a year showed significant differences and three comparisons across years for a particular date showed significant differences.

Addition of the presence/absence variable to the model of date and year effect on soil pH (Table 3.10) revealed a marginally significant date effect, did not remove the significant date by year interaction, and yielded a significant effect of presence on soil pH. This indicates that after adjusting for the differences in pH due to date, year, and the date*year interaction, there was still some significant estimated variation remaining in pH that could be attributed to the presence or absence of *Cleome* at a particular quadrat. After adjusting for the other model effects, there was now a significant effect of date on pH.

Calculation of the date*yr*presence interaction for purposes of obtaining estimated least square means (Figure 3.2) showed that for six of the eight possible date*yr*presence interactions, values of pH were higher where *Cleome* was present (Table 11). Only two of the date*yr combinations (May 1 and June 15 1997) differed significantly at the level of $p < 0.05$ between sites where the plant was present versus absent. Sites where *C. multicaulis* was absent appeared to fluctuate over the growing season to a greater degree (at least in 1997) than did those where the plant was present (Figure 3.3).

Repeated Measures Analysis of Soil Conductivity

Analysis of soil conductivity (Ec) (Table 3.12) showed no significant effect of date, year, or the date by year interaction. The largest source of estimated variation was between locations. Addition of a presence/absence variable to the model (Table 3.13) revealed that none of the fixed effects were significant. There was a large amount of estimated variation in conductivity across locations. There was no significant difference in soil conductivity between quadrats where *Cleome* was present versus absent (Table 3.14), and when date*year*presence combinations were calculated, soil conductivity was lower where the plant was present in six out of eight of the date*year*presence combinations. Conductivity appeared to fluctuate more across the growing season in quadrats where *C. multicaulis* was absent than in quadrats where the plant was present (Figure 3.5).

Repeated measures analysis to determine whether high densities of *C. multicaulis* contributed to a reduction in soil pH (Table 3.15) or soil conductivity (Table 3.16) through self-shading and reduced evaporation showed that an increase in plant density had no significant effect on either soil pH or soil conductivity after adjustment for the effect of date, year, and the date by year interaction. This suggests a lack of self-shading in quadrats sampled.

Repeated Measures Analysis of Soil Moisture

Repeated measures analysis of soil moisture (Table 3.17) showed that once again the greatest source of variation was across locations. There was a highly significant date effect, but neither the year nor date by year interaction effects were significant. The only comparisons showing significant differences were across dates within a single growing season, and soil moisture declined across the season in each of the years measured (Figure 3.6). Lack of early season measurements in 1995 prevented early versus late season comparisons in that year.

Addition of the presence/absence variable (Table 3.18) did not alter the previously significant date effect, and soil moisture did not differ significantly between quadrats where *Cleome* was present versus absent. Calculation of the date*year*presence interaction revealed that least square mean estimates of soil moisture were higher in four out of eight date*year*presence combinations and lower in the other four combinations (Table 3.19). Soil moisture did not appear to fluctuate more across the growing season in sites where *C. multicaulis* was present as compared to sites where the plant was absent (Figure 3.7).

Seedlings and adult plants of *C. multicaulis* were observed to recover from flooding that was simultaneously shallow (< 20cm depth) and short-term (1-2 weeks) in duration. In one quadrat (RL71), above-ground emergence was delayed several years until water levels receded, and adult mortality was observed in quadrats (e.g., RL44) with prolonged standing water. Multi-year observations from several quadrats (RL21, RL22) indicate that seeds of *C. multicaulis* can withstand submergence early in the season and will subsequently germinate. Seedlings were not observed to emerge while standing water was present, but healthy plants were observed once water levels subsided.

The flooding of two San Luis Lakes macroplots prior to seed set of existing plants in 1995 provided evidence that seeds have the ability to germinate after prolonged inundation. Floodwaters remained at levels above the height of the tallest *C. multicaulis* plants throughout the late summer of 1995 and did not recede until summer 1996, at which time sparsely distributed but robust *C. multicaulis* plants emerged. This population remained and was observed as late as September 2000, with no further encroachment of lakeshore levels.

Repeated Measures Analysis of Reproductive Output

The number of fruits per quadrat was highest in 1996 and then declined in 1997 to a value close to that of 1995 (Table 3.20). Repeated measures analysis of the effect of year on the (square-root) number of fruits (using only year as a repeated measure) (Table 3.21) indicated no significant effect of year. There was low estimated variation between locations and in the location*year interaction (in contrast to other models of soil characteristics and density). The largest amounts of estimated variation were between quadrats (within a location) and from quadrat to quadrat across years.

The addition of soil characteristics as covariates in the above model (Table 3.22) revealed once again a plant response to soil pH that was distinct from that of conductivity. The effect of conductivity on the number of fruits (square-root) was significant and negative (fixed effect estimate = -0.16331273). In contrast, the effect of pH on the number of fruits (square-root) was marginally significant (p = 0.0718) and here positive (fixed effect estimate = 2.75333643). Neither the effect of soil moisture nor the year effect was significant (Table 3.22). This model also had large amounts of unexplained variability.

The number of fruits per reproductive plant was highest in 1995 (Table 3.20). Repeated measures analysis of year and plant density on the number of fruits per reproductive plant (Table 3.23) revealed no significant effect of year or density. Once again, there were low amounts of estimated variation across locations and in the location*year interaction.

The addition of soil characteristics as covariates to the above model (Table 3.24) showed that the effects of both pH and Ec on the number of fruits per reproductive plant (square-root) were significant and once again indicative of a distinct plant response to pH versus conductivity. This was the only model where both soil pH and Ec simultaneously showed significant effects. The effect of soil pH on number of fruits per reproductive plant was a positive one (fixed effect estimate = 0.73074213) whereas the effect of soil Ec on this measure of reproduction was negative (fixed effect estimate = -0.03592944). The effect of year, soil moisture, and density all remained non-significant, and once again there was a large amount of residual (unexplained) variability (Table 3.24).

Multiple Regression Analysis of Reproductive Effort vs. Height

Observational evidence indicated that quadrats with the highest density of *C. multicaulis* plants did not increase in density over the three-year census period, and that plants in high density quadrats were significantly smaller and produced fewer fruits. A multiple regression model was run to investigate the relationship between the number of fruits produced per reproductive plant and mean plant height. The model chosen was:

$$\text{Square-root(Fruits/Reproductive)} = -0.098379 + 0.084681(\text{Height}).$$

Height alone explained 62.56% of the variation in the number of fruits (d.f. = 1; $T = 67.574$; $p = 0.001$). An additional model was run to investigate the relationship between both height and density on fruit production, and only height was significant ($p < 0.0001$). A model that removed the effect of height in order to investigate the relationship between soil pH, Ec, SM and density on fruit production showed no significant model effects.

Correlation Analysis of Plant Height, Soil Characteristics, and Reproductive Effort

Quadrats with lower mean plant height tended to have fewer fruits per reproductive plant, fewer fruits per quadrat overall, and lower soil moisture (Table 3.25). Although there was a negative correlation between soil salinity and the total number of fruits per quadrat, the correlation between soil pH and the number of fruits per reproductive plant was positive.

Repeated Measures Analysis of Survivorship

Survivorship was defined for this study as the number of reproductive plants (censused in early September) divided by the number of seedlings (censused in mid-June), with quadrats having zero density of *C. multicaulis* eliminated from the analysis. In fewer than 7% of the quadrats, additional seedlings appeared subsequent to the "seedling" sampling date of mid-June used in these calculations, and survivorship in these instances was limited to 100%. Survivorship calculated using $\log_{10}$ number of surviving plants from census figures taken every two weeks followed a Type I curve (Figure 3.8).

Repeated measures analysis of the effect of year on survivorship (arcsin) (Table 3.26) indicated no significant effect of year. A large amount of the variance remained unexplained, with the next largest amount of variation coming from the location*year interaction. The addition of soil characteristics as covariates to the above model (Table 3.27) indicated that neither any of the soil characteristics nor year had a significant effect on survivorship, with a large amount of the estimated variation remaining unexplained. Survivorship was lowest at Mishak Lakes (only censused in 1995 and 1996) and location RL6 (Table 3.28).

Repeated Measures Analysis of Depth to the Shallow Water Table

Repeated measures analysis of the date, year, and date*year effect on depth to the shallow water table (Table 3.29) indicated a significant effect of date and the date*year interaction, but no significant effect of year. Depth to the water table showed a large amount of estimated variance across locations, and a location that had a high water table one year might not show the same trend in subsequent years (most likely in response to local temporal microclimate differences in precipitation and evaporation rates).

In 23.7% of the measurements, a detection limit was reached. Because the pattern of water table depth differed from year to year in the later season, no attempt was made to eliminate the later season dates in order to lessen the dampening effect of the detection limit. There were many early-season instances of significant differences in water table depth across date for a particular year. Late-season measurements (that reflected greater water table depths and more frequent instances of the detection limit being reached) did not show significant differences in depth to the water table, perhaps because reaching detection limits produced artificially homogeneous values.

Square-root transformation of the depth variable did not improve the homogeneity of variance and was not performed.

Additional preliminary analyses were conducted to determine the effect of date, year, the date*year interaction, and depth to the shallow water table on each of the three soil characteristics measured (Tables 3.30-3.32). Results indicated that after adjustment for date and year effects, depth to the water table did not have a significant effect either on soil pH (Table 3.30) or soil Ec (Table 3.31). The effect of water table depth on soil moisture was significant after adjustment for the date, year, and date* year effects (Table 3.32).

Plant Associates and Other Ecological Site Characteristics

Fifty-seven out of 72 census quadrats contained *C. multicaulis* at the time plant associates were scored in August of 1995 (Appendix 3.7). Because of potential bias in the visual estimates of slim-stemmed species (such as *C. multicaulis*), this method was not used as an estimate of abundance of any species. Neither interspecific nor intraspecific competition was addressed experimentally in this study. *Cleome multicaulis* was most commonly found with *Juncus balticus* (45.6% of the quadrats containing *Cleome*) and almost as commonly found with *Distichlis stricta* var. *spicata* (36.8% of quadrats with *Cleome).* All three species co-existed in 15.8% of the quadrats containing *C. multicaulis.* In no quadrats were there ever more than three species present, corroborating the low species diversity expected in saline-sodic wetland habitats (Cooper 1999).

Juncus was the dominant species in terms of percent cover in 34 out of the 42 quadrats where it occurred, whereas *Distichlis* dominated in 21 out of 38 quadrats and was second in percent cover in the remaining 17 quadrats. *Distichlis* was never the 3rd ranking species in a quadrat where it was found, and *Juncus* ranked 3rd in only 2 out of 42 quadrats where it was found. Maximum vegetation height in each quadrat (of any plant species present) was not measured, but would have been significantly higher for those quadrats dominated by *Juncus balticus* than for those dominated by *Distichlis stricta* var. *spicata*.

Other species found in the census plots included *Triglochin maritimum*, *Glaux maritima*, *Erigeron philadelphicus*, *Hordeum jubatum*, *Scirpus nevadensis*, *Polygonum aviculare*, *Aster pauciflorus*, and *Eleocharis palustris*. Species in close proximity to census quadrats included *Suaeda depressa*, *Salicornia rubra*, *Typha latifolia*, and *Scirpus americanus*.

Cleome multicaulis rarely dominated the quadrats where it was found. Out of 57 quadrats where it was present, *Cleome* was the dominant species in 8 of those plots (Table 3.33), and 7 of those 8 were found among the three Blanca Wetlands macroplots (BW1, BW2, and BW3). *C. multicaulis* more commonly ranked 2nd (29 out of 57) or 3rd (19 out of 57) in terms of percent cover where it was found.

Cleome multicaulis was often found clustered around the edges of greasewood (*Sarcobatus vermiculatus*), a salt-tolerant shrub that occurred on the drier alkaline flats of the study sites. Placement of the macroplot locations was such that only a single census quadrat contained *Sarcobatus* and *Cleome*. Observations in this study indicate that disturbance may increase the establishment success of *Cleome* and allow seedlings to exploit resources with diminished competition from other species. Numerous robust plants of *Cleome multicaulis* were observed colonizing disturbance-generated bare patches throughout the San Luis Valley, including roadsides and the shores of San Luis Lakes after a flood.

Analysis of Variance - Plant Associates and Total Percent Cover

Analysis of variance using Type III sums of squares was performed in order to investigate the relationship between soil characteristics (pH, Ec, and SM) and descriptive habitat measures (plant associates and total percent cover). Preliminary analysis indicated large effects of both location and quadrat (location), and these were removed from subsequent models in order to examine habitat characteristics in the absence of these variables (Table 3.34). Plant associates were defined as each of the eight most common co-occurring species in the quadrats, and percent cover was the estimated percent total plant cover of all species present (combined).

At the time the soil characteristics and percent cover were assessed, soil pH was the highest of any date and any year measured, and had increased considerably over the growing season. Soil Ec had remained the same across the season but was relatively high, and soil moisture had shown a pattern typical of each of the three years, with a significant decrease as the season progressed.

Quadrats with the highest soil conductivity were often dominated by different plant associates than were those plots with the highest pH (Tables 3.35, 3.36). In this model of analysis of variance both cover and plant associates had significant effects on soil salinity (Table 3.34), with low-salinity quadrats having the greatest total percent plant cover. Quadrats dominated by *Cleome* had soil conductivities ranging from 1.26 dS/m to 31.20 dS/m (Table 3.33).

Total plant cover was found to have a significant negative effect on soil pH (Table 3.34) and the effect of plant associates on soil pH was marginally significant ($p = 0.0554$). Although values of soil pH did not differ significantly across quadrats dominated by various plant associates (Duncan's multiple range test. alpha = 0.05), the eight plots where *C. multicaulis* was the dominant species had higher mean soil pH than plots dominated by any other species besides *Sarcobatus vermiculatus* (Table 3.36). Both cover and plant associates had significant effects on mean soil moisture (Table 3.34). Quadrats dominated by *Cleome* had lower mean soil moisture than those dominated by *Distichlis*, which was somewhat surprising (Table 3.37). Sites where *C. multicaulis* was the second most dominant species in terms of percent cover had significantly higher mean soil moisture (31.85%) than the 8 sites where *C. multicaulis* dominated (15.13%; Table 3.33). Calculation of Pearson's correlation coefficient revealed that quadrats with greater estimated total plant cover (all species combined) tended to be associated with lower soil conductivity ($r = -0.4261$, $p = 0.0002$) and pH ($r = -0.3336$, $p = 0.0039$) but higher soil moisture ($r = 0.3615$, $p = 0.0017$).

DISCUSSION

Plant Density

Plant density in the quadrats measured varied rather predictably by date and with a marginally significant ($p = 0.0649$) effect of year (Table 3.4). Although none of the soil covariates had a significant effect on plant density (Table 3.5), analysis of a limited number of quadrats dominated by *C. multicaulis* revealed that those sites had high pH, fairly dry soils, and relatively low soil salinity (Table 3.33). The variation in plant density of *C. multicaulis* was not explained by soil characteristics measured, and highly saline and alkaline soils were able to support high densities of the plant (Table 3.7). Density had no apparent effect on reproductive output as measured in this study (Tables 3.23). Individual quadrats varied in the above-ground density of plants across years (Table 3.1). Sites with high densities of *C. multicaulis* may not represent optimal habitat (see discussion in Analysis of Plant Associates).

Comparisons in this study of soil characteristics in quadrats where *C. multicaulis* was present versus absent (Tables 3.10, 3.13, 3.18) should not be taken as indicative of features that may explain the larger-scale distribution of this species (Lesica 1992, Menges 1992, Wiser et al. 1998). At the microhabitat scale, however, results of this study were intriguing in terms of revealing an apparent tolerance of *C. multicaulis* to soils with high pH (Table 3.10).

Not all areas of occupied habitat will be equally suitable for a species (Sieg and King 1995), and a species may be occupying a suboptimal site due to dispersal limitations or other constraints. Rare species occupying uncommon habitats may suffer from a lack of study microsites that constitute "typical" species habitat (Wiser et al. 1998). In the examination of species response to habitat differences, presence/absence and density data may reveal different patterns in relation to an environmental factor, particularly if different scales of pattern arise (Dale 1999).

The characterization of rare plant habitat is optimally conducted at several spatial scales and may yield multiple predictive criteria. At the scale of $1m^2$, for example, the best predictors of rare plant occurrence in the Southern Appalachians were available soil cations, potential solar radiation, the proportion of exposed bedrock, and vegetation height, whereas soil depth and percentage shading were found to influence plant density at scales of $100m^2$ (Wiser et al. 1998). No two species were predicted by identical sets of site parameters.

Repeated measures analysis adjusts for temporal correlations between data across dates and years. The possibility of spatial autocorrelation remains unresolved with these analyses, however. One result of spatial autocorrelations is that statistical tests yield more results that appear significant than the data actually justify because there are fewer truly independent observations than the number used in the test (Dale 1999). The extent to which data in this study are likely to be spatially autocorrelated is not known.

Ecological processes responsible for the observed pattern of spatial and temporal variation in density include seed dormancy and the population dynamics of the soil seed bank. Above-ground density of *C. multicaulis* reflects not only patterns of pollen and seed dispersal, but also soil seed bank dynamics such as cycles of seed dormancy, germination cues, spatial patterns of seed movement in the soil, seed predation, and rates of seed decay and physiological death.

Studies that focus on the above-ground growth of rare plant species may find attempts to characterize suitable habitat confounded by the presence of dormant or otherwise cryptic life stages (Mehrhoff 1989a, Falb and Leopold 1993, Sieg and King 1995) that broaden the spatial and temporal dimensions of the species' ecological niche. Measurements of above-ground density for plants with dormant below-ground life stages may provide an unreliable estimation of the influence of environmental factors such as soil pH on plant density (Sieg and King 1995).

Analysis of Plant Associates and Other Ecological Site Characteristics

Studies attempting to predict the occurrence of rare plant species should include analysis of co-occurring species as potential predictive variables (Wiser et al. 1998) in addition to measurement of abiotic conditions. Habitat occupied by *C. multicaulis* in the San Luis Valley, Colorado is most commonly occupied by the co-associates *Distichlis stricta* var.*spicata* and *Juncus balticus* in moist, saline-sodic soils.

Based on the limited sampling and analysis done, it appears that microhabitats occupied by high densities of *C. multicaulis* plants may be characterized as having high pH, fairly dry soils, and relatively low (but variable) salinity in comparison to sites dominated by other co-associated plant species. Quadrats with higher densities of *C. multicaulis* appeared to have plants that were considerably less branched, but the extent to which this is an effect of density versus soil characteristics was not assessed (Ungar 1987a).

Qualitative assessment of habitat characteristics in plots where *Cleome* was ranked as the second most dominant species (indicative of medium levels of plant density) may be more reflective of high-quality habitat than sites occupied at high density. Plots with medium density of *C. multicaulis* were comparatively less alkaline, more mesic, and less saline than plots occupied by higher densities of *C. multicaulis* (Table 3.33). Sites with the greatest density of *C. multicaulis* were not uniformly characterized by high population growth rates in this study (See Periodic Matrix Analysis chapter). Management recommendations should not be focused solely on a goal of increasing plant density as it may not be the best indicator of habitat quality (van Horne 1981).

In the San Luis Valley, it might be expected that periodic flooding on a local scale would (at least temporarily) homogenize soil characteristics, although the extent to which this process occurs is unknown. On the other hand, small-scale patchiness of soil attributes might be maintained by microsite differences in evaporation and percolation rates that result from both abiotic influences and vegetation patterns.

Certain soil characteristics may become limiting at certain times of the year, and certain growth phases may have greater sensitivity to mineral constituents than other phases (Falkengren-Grerup 1994). Concentrations of soil chemical elements during particular months of the year were found to be more important in explaining the variation in shoot length and other plant characteristics than were annual means of element concentrations (Falkengren-Grerup 1994).

Characterization of *C. multicaulis* Response to Soil pH

Cleome multicaulis appears to respond differently to soil pH than it does to soil salinity, in spite of relatively high correlations between measured values of these soil parameters (Table 3.6). *Cleome multicaulis* appears to tolerate soils with higher pH than its close associates *(Distichlis, Juncus)* (Table 3.36), and comparisons of plots where *Cleome* was present versus absent indicated a trend of higher pH where plants were found (Table 3.11). There was no indication (as there was with soil salinity, Figure 3.4) that sites where *C. multicaulis* was present had more uniform soil pH than sites where the plant was absent (Figure 3.3).

The height of *C. multicaulis* plants does not appear to be stunted as a result of alkaline soils. Soil pH varied significantly but in unpredictable and variable patterns across dates and years (Figure 3.2), and patterns of spatial and temporal variability in pH did not match those of either soil conductivity (Figure 3.4) or soil moisture (Figure 3.6). Previous studies have found that the temporal variability of soil pH was dependent upon spatial scale (Kephart and Paladino 1997).

Soil pH and conductivity both had significant effects on some aspect of reproductive output in *C. multicaulis*, but their effect was antagonistic; i.e., increased pH appeared to enhance reproduction while increased conductivity had an inhibitory effect (Tables 3.22, 3.24).

In the San Luis Valley, soils occupied by *C. multicaulis* are both alkaline and highly saline (Table 3.7). Although these soils may be best categorized as saline-sodic, descriptions of such soils (that are simultaneously high in pH and electrolytic conductivity) are not included in several well-known soil references (Sposito 1989, Brady and Weil 1999). The dual role of alkalinity and salinity in terms of plant response (particularly in arid region soils) has received little attention in the literature (Shainberg 1975).

It is apparent in this study that collecting measurements of multiple soil characteristics that are correlated with one another (e.g., soil pH and conductivity, Table 3.6) is not redundant. Measurement of multiple soil characteristics may reveal significant relationships between plant density and selected characteristics but not others (soil moisture and soil pH in that study) (Sieg and King 1995).

Soil conductivity may influence a different suite of life history characteristics than soil pH. Attempts were made in this study to determine whether one life stage (seed, seedling, juvenile, or reproductive stages) had greater sensitivity to a particular soil characteristic than other life stages (Shainberg 1975, Brady and Weil 1999). Initial indications after a single year of study that the seedling stage might be more sensitive to soil pH than later growth stages disappeared when repeated measures analysis was conducted in subsequent years of study.

Some studies of playa wetlands with highly acidic soils have found a negative correlation between conductivity and soil pH, whereas other studies failed to establish any correlative relationship among soil variables (Poiani and Johnson 1993). Even under field conditions where a correlative relationship has been measured between pH and conductivity, management regimes may affect pH but cause no measurable change in conductivity (Poiani and Johnson 1993).

In a study of germination of *Kochia indica* under various conditions of salinity and alkalinity, seeds collected from populations growing under highly saline conditions germinated the most poorly under alkaline conditions in the lab, and seeds collected from alkaline field conditions germinated the most poorly in saline conditions in the lab (Khatri et al. 1991). Studies that measure soil conductivity and not pH (Shafroth et al. 1995) may neglect a habitat component that is potentially important for many species.

Characterization of *C. multicaulis* Response to Soil Salinity

Cleome multicaulis is clearly characterized as a halophyte, growing and reproducing in soils with mean conductivity (Ec) of 8.507 dS/m (std. dev. 8.5816). Soil conductivity values above 8.0 mmhos/cm (= dS/m) have been characterized as being high enough to restrict yield in most crop plants (Allphin and Harper 1997). *C. multicaulis* appears to tolerate soils similar in salinity to those inhabited by *Hordeum jubatum* (Table 3.35), and intermediate in conductivity between soils dominated by *Distichlis* and *Juncus* (Ungar 1974).

Soil conductivity as measured in this study did not vary significantly across dates, years, or in the date*year interaction (Table 3.12). Analysis of above-ground growth appears to indicate that the presence of *C. multicaulis* corresponds with soil patches that are more highly uniform in salinity (Figure 3.5) and usually lower in salinity than surrounding non-occupied patches. Temporal variation in soil salinity has been documented in coastal salt marshes (Bertness et al. 1992), inland salt pans (Ungar 1974) and desert playas (Donovan et al. 1999).

Plants that have prolonged exposure to increased salinity can be expected to experience a greater magnitude and extent of growth effects (Shainberg 1975). Physiological adaptations to high salinity may be costly, and adaptations of a more permanent nature may or may not continue operating in the plant when temporally variable environments experience reduced levels of salinity (Shainberg 1975). Annual species that depend for their establishment on recruitment by seed are directly exposed to the abiotic conditions present in habitat patches they colonize and cannot depend on subsidy from clonal growth (Bertness et al. 1992, Shumway and Bertness 1992).

Repeated measures analysis indicated that after adjustment for year and the other soil characteristics, there was a significant negative effect of soil conductivity on both the number of fruits produced and on the number of fruits per reproductive plant (Tables 3.22, 3.24) Other studies have found that plant senescence occurred more rapidly in high (35dS/m) salinity plots than in low (15 dS/m) salinity plots (Foderaro and Ungar 1997) but few studies have examined the effect of soil salinity on reproductive output.

Where *C. multicaulis* was present on soils that were highly saline in appearance (as evidenced by the white soil crust), plants were stunted in growth and appeared to have few seeds per plant. It did not appear, however, that soil salinity was a significant cause of pre-reproductive plant mortality although experiments to manipulate salinity in the field were not done.

Microsites with increased plant cover may experience reduced evaporation and a corresponding reduction in soil salinity as a result of passive shading (Bertness et al. 1992). Preliminary analysis in this study indicates that an increase in plant density had no significant effect on soil Ec or pH, evidencing no detectable effect of self-shading. Seedlings commonly appeared underneath the previous year's dead growth of *Juncus*, which may have had the effect of reducing evaporation and therefore ameliorating the effects of increased salinity.

Although halophytes found in coastal salt marshes often exploit disturbance- created and highly saline bare patches and are likely restricted to such salt-stressed microsites because they cannot outcompete perennial turf-formers elsewhere (Bertness et al. 1992, Shumway and Bertness 1992), there is no evidence of a similar phenomenon in this study. Visual inspection of the disturbance-generated patches occupied by *C. multicaulis* suggests that salinity (as detected by the degree of salt-encrustment) is not necessarily higher at these microsites, nor did repeated measures analysis provide evidence that census quadrats occupied by *Cleome* in the San Luis Valley had higher salinity than quadrats where *Cleome* was absent. The relative competitive abilities of

Cleome multicaulis and the other species with which it co-occurs were not experimentally assessed in this study.

Effect of Soil Salinity on Seed Germination

Below-ground stages may respond to an array of soil characteristics at broader spatial and longer temporal scales than above-ground life forms (Dale 1999). Detection of a relationship between edaphic characteristics and plant growth must consider soil conditions and the scale of seed or plant response during times of seed maturation, dormancy release, seed germination, and plant growth.

Many single-species studies of halophyte ecology have focused on seed germination under varying conditions of soil salinity, in hopes of determining the range of salinity tolerance for the seed life stage in particular. Previous studies have hypothesized that seasonal fluctuations in soil salinity may be an important factor driving the timing of seed germination for annual halophytes (Khan and Ungar 1984, Woodell 1985, Ungar 1987a, Badger and Ungar 1989, Foderaro and Ungar 1997), in that germination is hypothesized to occur when soil salinities are at a seasonal low.

In the field, high soil salinity, soil moisture, and dark, hypoxic or anoxic soil conditions may interact to delay germination time in salt marsh species (Welling et al. 1988, Shumway and Bertness 1992, Mitsch and Gosselink 1993). Seeds that germinate early in the season may be more resistant to increases in salinity later on because of greater stored reserves (Foderaro and Ungar 1997). Studies that rely exclusively on laboratory germination tests rather than field measurements of germination timing under conditions of naturally occurring variation in soil salinity may miss such interactions and cumulative effects.

The results of this study did not provide evidence that soil salinity was consistently or significantly lower during times of the year when germination of *C. multicaulis* was occurring than during other periods of plant growth (Figure 3.4). Levels of soil salinity in this study increased significantly as the growing season progressed in only one out of three years measured. Seeds may respond to salinity in a way that is distinct from their response to alkalinity (Khatri et al. 1991). Although subsequent analysis of seed cage field experiment data revealed that soil characteristics (pH, Ec, and SM) were not significantly correlated with emergence (number of seedlings), percent viability (as measured by tetrazolium testing), or the number of seeds persisting, further investigations are warranted.

Longer-term repeated measurements of soil salinity and alkalinity are needed to properly characterize the extent of temporal variation in soil characteristics at a scale relevant to below-ground soil seed dynamics. Uniformity in one or both of these soil characteristics may be important in serving as a cue for dormancy release or germination in this species, although evidence in support of this hypothesis is difficult to collect under field conditions. The results of this study do not provide evidence that any predictable pattern exists between levels of soil pH and germination timing in *C. multicaulis* (Figure 3.2). Few studies have examined the effects of soil pH on soil seed bank dynamics (Khatri et al. 1991) and additional dormancy and germination studies of species occupying saline-sodic soils would be extremely valuable in discerning whether a seed response to alkalinity is present in those species and, if present, whether the response to alkalinity and salinity is associated or distinct.

Possibility of Ecotypic Variation or Plasticity of Response in *C. multicaulis*

The lack of a significant effect of above-ground *C. multicaulis* presence on soil conductivity (Table 3.13) indicates that soil salinity does not appear to be one of the factors determining above-ground microsite occupancy by *C. multicaulis* at the scale measured in this study. Attempts to draw simplistic associations between a plant species and soil chemistry may be obfuscated by the presence of species ecotypes (Shainberg 1975, Marrs and Bannister 1978, Shafroth et al. 1995), although the extent to which ecotypes are present in *C. multicaulis* populations was not investigated in this study.

Spatial variation in soil characteristics across the geographic range of a species may result in populations distributed across a gradient of soil characteristics such as pH (Carey et al. 1995). To the extent that physiological adaptations are heritable, there will be selective pressure for ecotypic variation in those traits (Stanton and Galen 1997).

Plant response to soil salinity may vary within a species as a result of differences in climate, soil, or in the genetic makeup of the species (Shainberg 1975, Antlfinger 1982, Allen et al. 1997) and ecotypes may reflect differences in germination ecology as well as above-ground growth. Ecotypes may periodically appear in wild populations in response to increased soil salinity, and may appear sufficiently differentiated as to prompt unique taxonomic treatment (Freas and Murphy 1988).

Year-to-year variability in habitat conditions may be an important selective agent in the evolution of demographic and life-history characteristics of a species (Stearns 1976, Kephart and Paladino 1997). The ability of individual plants to perform well under a wide range of environmental conditions provides evidence of plasticity in phenotypic traits influencing growth (Bell and Lechowicz 1994) which may be a critical life-history attribute allowing persistence in a temporally variable habitat (Klemow and Raynal 1983). The ability to express phenotypic plasticity may itself be a heritable trait (Bell and Lechowicz 1994). The theoretical expectation is that plants exhibiting plasticity at the level of physiology (that allows them to survive and reproduce successfully across a broad range of environments) will express little plasticity in terms of traits more directly related to fitness (Bell and Lechowicz 1994).

Functionally appropriate plasticity that arises from selection pressure will allow plants to increase their survival and reproductive success under a wide variety of environmental conditions and as a consequence may show little correlation with environmental variables (Bell and Lechowicz 1994). If the physiological tolerance of the species is not exceeded in years of unfavorable growth, then phenotypic plasticity in growth may occur and result in little or no net reduction in reproductive capacity (Kephart and Paladino 1997). Field studies are needed to address the prevalence of plasticity in natural populations and to identify the nature and magnitude of plant costs associated with acquiring additional plasticity (Bell and Lechowicz 1994).

Selection may or may not act independently on the responses to different environmental variables (e.g., salinity and alkalinity) rather than simply broadening overall tolerance of the physical environment (Bell and Lechowicz 1994) in terms of above-ground growth or seed bank effects. Previous studies of plasticity in plants occupying saline and alkaline soils have examined plant tolerance for variation in salinity (Roy and Mooney 1982, Bertness et al. 1992, Haukos and Smith 1996) and soil moisture (Quinn 1975) but have neglected consideration of tolerance for variation in soil pH.

The balance between specialization by ecotype (that operates at a genetic scale of the population), and plasticity (that operates at a scale of distance traveled by pollen and seeds) likely shifts among individuals in a population in response to local environmental heterogeneity (Bell and Lechowicz 1994). Empirical evidence to indicate the relative importance of alternative evolutionary strategies such as ecotypic variation in salinity/alkalinity tolerance, plasticity in plant response to salinity and alkalinity, or some combination of these traits has rarely been gathered. The extent to which populations of *C. multicaulis* exhibit ecotypic variation or plasticity in their response to salinity and alkalinity was not measured in this study. Comparative physiological and genetic studies between San Luis Valley and Wyoming populations of *C. multicaulis* would provide valuable insight as to the adaptive strategies of this plant in saline-sodic soils.

Reproductive Output

Reproductive output varied little across years in this study (Tables 3.21, 3.23) and appears to be adversely affected by high soil salinity, unaffected by soil moisture, and positively affected by high soil pH (Tables 3.22, 3.24). Quadrats having large numbers of fruits (or numbers of fruits per reproductive plant) in one year did not necessarily continue that trend of reproductive success in subsequent years. The low variation across locations and in the location*year interaction for both these measures of reproductive output (in contrast to results of repeated measures analysis of soil characteristics) indicates the possibility of compensatory mechanisms of some sort occurring across quadrats so as to stabilize overall reproductive output at the location scale for each location and each year.

Compensatory mechanisms may result in a mixture of high- and low-density quadrats scattered across a location as a result of factors affecting either above-ground growth or seed dormancy release and germination. Compensatory mechanisms operating to stabilize the number of fruits per reproductive plant within a location (when quadrats may vary) might include variation in the number of seeds per capsule, differential rates of pre-maturation seed abortion, variability in pre-dispersal fruit predation, or plasticity in post-fertilization abortion rates. The extent to which these mechanisms may be operating in *C. multicaulis* was not measured in this study.

Characterization of *C. multicaulis* Response to Soil Moisture, Flooding and Drought

Results of this study indicate that, unlike some other halophytes (Ungar 1974), *Cleome multicaulis* appears to have a broad tolerance for the values of soil moisture encountered in its San Luis Valley habitat (Tables 3.18, 3.19). Although qualitative analysis indicates that quadrats dominated by *C. multicaulis* had comparatively dry soils (Table 3.37), field observations indicated that above-ground growth of *C. multicaulis* was enhanced on saturated soils and that plants were vulnerable to both prolonged conditions of flooding and to drought.

Insufficient soil moisture was observed as the most likely cause of complete seed mortality at Mishak Lakes, although increased soil salinity may have been a factor as well. Informal observations indicate that extended drought hastens the senescence of adult *C. multicaulis* plants and dampens reproductive capacity, although formal statistical results do not support this observation. It is possible that extended drought may cause an increase in the relative proportion of small versus large reproductive plants by shifting plant resources to immediate reproduction at the expense of further plant growth. Field experiments would be necessary to investigate the role of soil moisture, intra- and interspecific competition, and other ecological characteristics on the relative proportions of large and small reproductive plants and their respective reproductive output.

Previous studies have found that soil moisture was the dominant factor in determining plant presence in playa communities (Haukos and Smith 1996) although soil strength, pH, and conductivity may also influence playa community composition. Plants may delay the production of inflorescences in response to flooding (Lieffers and Shay 1981). Plants growing at the wet end of soil moisture gradients may be exposed to higher levels of insect predation on fruits and a higher cost of defense through secondary compounds that offsets growth advantages (Louda and Potvin 1995). Even where precipitation is randomly distributed, localized soil properties and differential plant uptake rates will create moisture gradients within a plant community (Robertson and Gross 1994).

The ecological significance of observed relationships between plant density and soil moisture (Table 3.5) may be confounded by dormant, below-ground life stages (Sieg and King 1995). The effect of soil moisture on long-term survival of *C. multicaulis* seeds is not known, although seeds apparently tolerate flooding with greater success than they tolerate excessive soil drying.

Soil moisture in this study showed a clear and consistent decline over the growing season, that may provoke the prediction that for this and other annual species, tolerance to soil moisture may differ between life stages present at different points in the growing season. Previous studies have found seedling emergence and survival to be strongly affected by subsurface moisture (Wood and Morris 1990), although (depending on the moisture gradient present during different life stages) responses to soil moisture in early establishment may be similar or different to those seen in adult distributions (Keddy and Ellis 1985). Populations of a single species may show plasticity of response to soil moisture across several life stages (Quinn 1975).

The range of tolerance of *C. multicaulis* seeds to soil moisture was indicated in this study only via measurement of moisture values once (in July 1996) inside and outside of experimental seed cages (See Seed Chapter for Results). No significant differences in soil moisture were found inside and outside cages, although these measurements were not taken at the time of seed germination. Although it appears that seeds are more tolerant of flooding than extended drought, further field and laboratory experiments are needed to determine the effect of soil moisture on seed germination in this species.

Lowering of water tables in playa communities may adversely affect multiple life stages of a species by increasing adult mortality, reducing seed production, and reducing germination of seeds (Freas and Murphy 1988). Although preliminary analysis of the differential effect of soil characteristics on particular life stages of *C. multicaulis* was inconclusive, further experimental investigation may be warranted to determine if soil moisture has critical effects on a particular life stage of *C. multicaulis* in the San Luis Valley.

Effect of Depth to the Shallow Water Table

In spite of significant correlations between depth to the shallow water table and soil pH, Ec, and moisture (Table 3.6), repeated measures analysis indicated that (after adjustment for a significant date and date*year effect), depth to the water table did not have a significant effect on either soil pH (Table 3.30) or soil Ec (Table 3.31). Repeated measures results did indicate a significant effect of depth to the shallow water table on soil moisture (Table 3.32). Depth to the water table showed a large amount of estimated variance across locations, but there was no significant variation across years, and a location with a high water table one year might not show the same trend in subsequent years (Table 3.29). As with previous conflicting analyses, the repeated measures results here are likely to be more accurate than correlations because they use Type III sums of squares to determine the effect of soil characteristics on water table depth only after adjustment for the date, year, and interaction effect.

The lack of sufficient depth in shallow water wells may have hampered this study's ability to detect significant relationships between shallow water table depth and soil pH or Ec (Tables 3.30, 3.31) and soil moisture may interact with salinity and alkalinity in important ways that have been rarely investigated (Haukos and Smith 1996). Both drought and flooding were likely strong enough environmental influences to cause the above-ground extinction of local populations.

Additional studies are needed to further investigate the time lag likely between changes in shallow water table depth and soil characteristics, and to investigate further any relationship between depth to the shallow water table and soil pH. Hydrologic models being developed and tested at Mishak Lakes should incorporate soil pH in addition to soil salinity as potentially important ecological site characteristics.

Possible Facilitation by *Sarcobatus vermiculatus* Shrubs

In the present study, the density of *C. multicaulis* individuals in drier, upland portions of its habitat was consistently higher under the canopy of *Sarcobatus vermiculatus* shrubs. Arid-zone shrubs have been shown to modify their local microenvironment so as to facilitate growth by increasing local concentrations of soil nutrients (Donovan et al. 1999), reducing soil temperatures (Vasquez-Yanez and A. 1994) lowering light intensity, and increasing the amount of surface organic matter (Cabin et al. 1998). Microsites under the canopy of *S. vermiculatus* may have more consistent (or simply higher) soil moisture due to hydraulic lift occurring in this species (Donovan et al. 1999),

Soil characteristics in the immediate vicinity of greasewood were only measured in one 1600cm^2 area in this study, and the single quadrat dominated by *S. vermiculatus* had higher soil conductivity and pH than sites dominated by *C. multicaulis* (Tables 3.35, 3.36). More extensive analysis by previous authors has found soils immediately under the canopy of *S. vermiculatus* to have higher salinity than soils in surrounding interspaces, although soil pH was not measured (Donovan et al. 1999). The extent and timing of variability in soil salinity under greasewood canopies is unknown, but may have an important influence on *C. multicaulis* above-ground growth. If the variability in soil salinity is lower in canopy microsites than in surrounding areas, then results of soil measurements in this study would suggest that *C. multicaulis* presence might be predicted.

The high pH of the single quadrat dominated by *S. vermiculatus* (Table 3.36) may possibly indicate that this species, like *C. multicaulis*, is found in soils of higher pH than other commonly occurring co-associates. To the extent that this is the case, growth and reproduction of *C. multicaulis* may not be inhibited under the canopy of greasewood, and the tolerance of alkaline soils may allow *C. multicaulis* to colonize these upland sites that might be otherwise unavailable due to competition with other species. Alternatively, microsite conditions under the canopy of *Sarcobatus* might provide a favorable environment for the release of seed dormancy and seed germination while not interfering with the growth of adult plants. Seed bank densities of *Lesquerella fendleri*, a commonly-studied desert annual, were found to be significantly higher under creosote canopies than in the interspaces (Cabin et al. 1998). Additional study of *C. multicaulis* in greasewood-dominated microsites is needed to further investigate this intriguing phenomenon.

Effect of Precipitation on Current Year's Growth

The absence of some significant statistical relationships between soil characteristics and density of above-ground *C. multicaulis* plants may reflect the importance of environmental conditions at the time of seed formation rather than the time of above-ground plant growth (Phillipi 1993b). Other (unmeasured) edaphic characteristics may also be important in predicting the occurrence of *C. multicaulis* at the spatial scales measured in this study.

Although weather station measurements of monthly precipitation were obtained from four Valley locations (Figure 2.1), many data values were missing. Across locations, the most striking time of below-average precipitation was the year 1996. Although additional months showed below-average precipitation at one or all of the measurement sites, insufficient data were available to present deviations from long-term mean values in tabular or graphic form. Spring and summer precipitation does not seem to correspond to any variation seen in this study in terms of reproductive output of *C. multicaulis* during the period 1995-1997. The scale of precipitation reporting is larger than the location scale of *C. multicaulis* populations in the San Luis Valley. Potential effects of precipitation variability and timing on *C. multicaulis* plant growth and development were not detected in this study.

Environmental conditions experienced by maternal plants during seed development may have strong effects on the plants that subsequently grow from seed (Rowe 1968, Schmitt et al. 1992). Precipitation and evaporation patterns of the growing season prior to sampling may be more important than current-season precipitation patterns in predicting above-ground plant density of *C. multicaulis*, although the relationship is likely to be complex and confounded by factors such as plant size (Rowe 1968). Precipitation at the time of seed formation may influence seed dormancy, longevity in the soil, and subsequent emergence (Phillipi 1993a). The lack of a significant relationship in this study between soil moisture and *C. multicaulis* growth and reproductive parameters (e.g., Tables 3.18, 3.22, 3.27) makes it difficult to hypothesize about the effects of precipitation on above-ground *C. multicaulis* growth either in the year of seed maturation or the year of plant growth.

Precipitation and other environmental conditions may have effects on the soil seed bank that are distinct from their effect on above-ground growth, and these effects may become manifest either at the time of seed maturation or at the time of plant growth. High-quality habitat for above-ground growth may not always coincide with similarly high-quality seed bank habitat, and seeds that disperse to habitat patches that appear suitable for above-ground growth may perish before emergence if those patches become or remain hostile to the persistence of soil seeds (Schmitt et al. 1992, Cabin et al. 1998). Environments that might be considered favorable (e.g., increased precipitation at a desert site) during the time of seed formation may paradoxically produce seeds with greater dormancy (Phillipi 1993b). Plants of larger size that produced a greater number of seeds were experimentally determined to produce seeds with greater dormancy as well (Phillipi 1993b).

Conclusion

Plant response to soils that are alkaline or simultaneously saline and alkaline (saline-sodic) often has been ignored in studies of soil salinity, but represents a unique opportunity for the study of spatial and temporal heterogeneity in saline wetland ecosystems. Additional studies are needed to identify the physiological mechanisms that allow seeds and plants of *C. multicaulis* to tolerate soils that are both saline and alkaline. This species provides a unique opportunity to examine the physiological costs of adapting a response to soil pH that is distinct from that of soil salinity, and to determine (with studies that include the Wyoming populations of this species) the extent to which physiological traits show plasticity or ecotypic variation. The presence of a persistent seed

bank in *C. multicaulis* (and its broadened ecological niche) provides the opportunity to extend physiological studies to the below-ground seed dynamics of this unique species in hopes of improving our ability to predict microsite occurrence of this and other rare species.

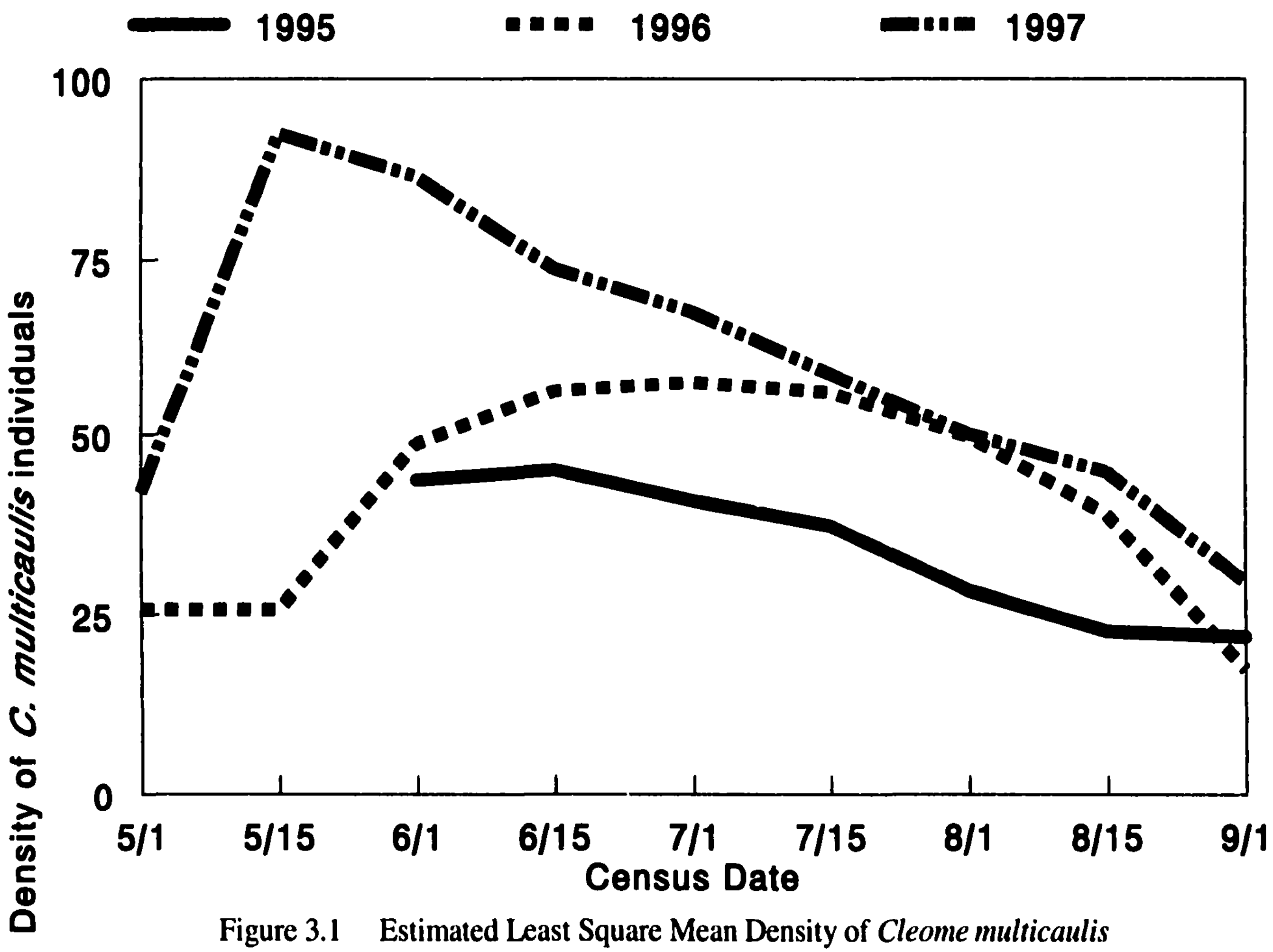

Figure 3.1 Estimated Least Square Mean Density of *Cleome multicaulis* Reproductive Plants Across Quadrats and Locations, Census Years 1995-1997

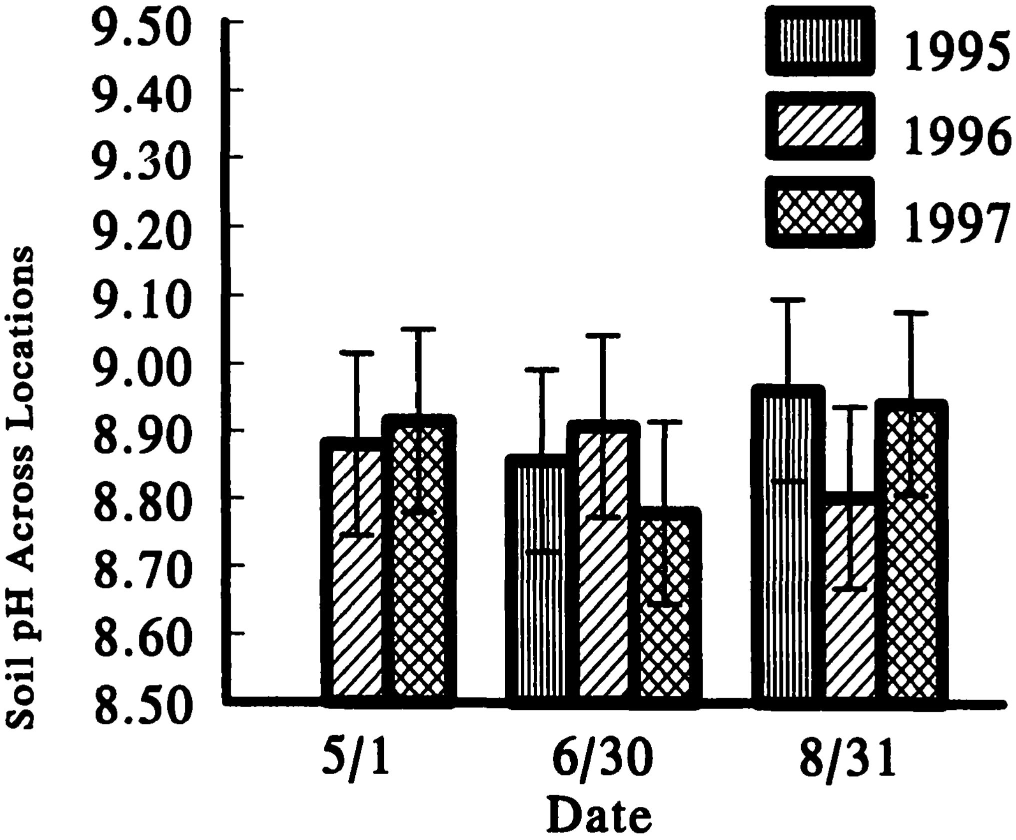

Figure 3.2 Estimated Least Square Means of Soil pH Across Quadrats and Locations for Early, Mid and Late Summer, Census Years 1995-1997

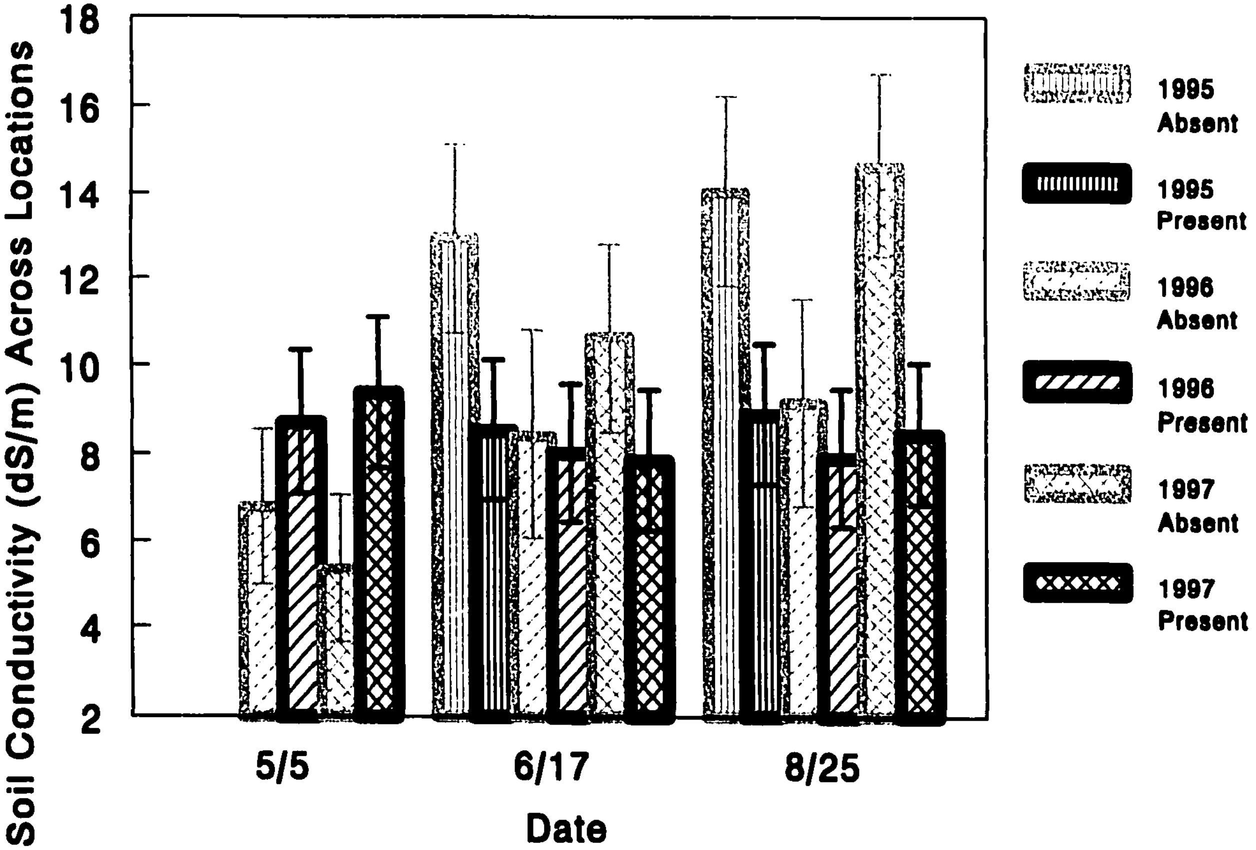

Figure 3.3 Estimated Least Square Means of Soil Conductivity Across the Growing Season in Quadrats (40cm x 40cm) Where *C. multicaulis* is Present as Compared to Quadrats Where *C. multicaulis* is Absent

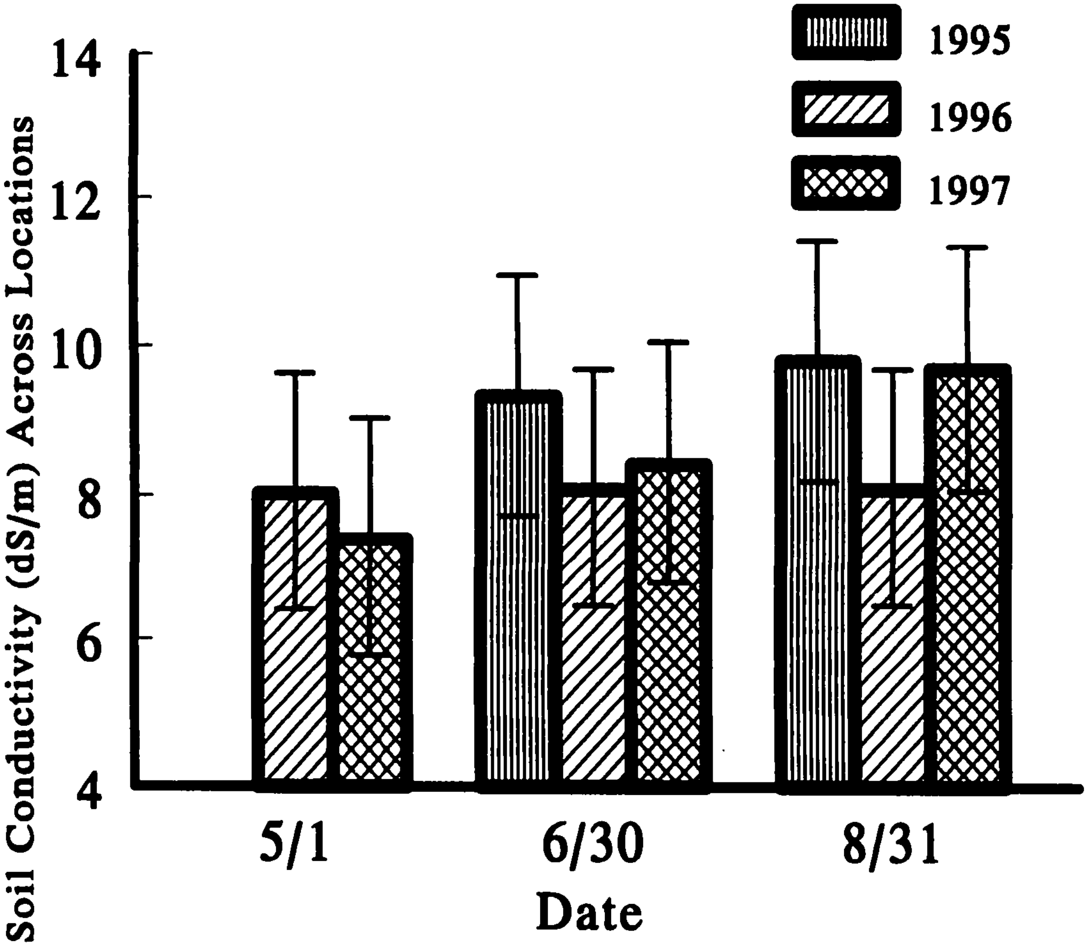

Figure 3.4 Estimated Least Square Means of Soil Conductivity Across Quadrats and Locations for Early, Mid, and Late Summer, Census Years 1995-1997

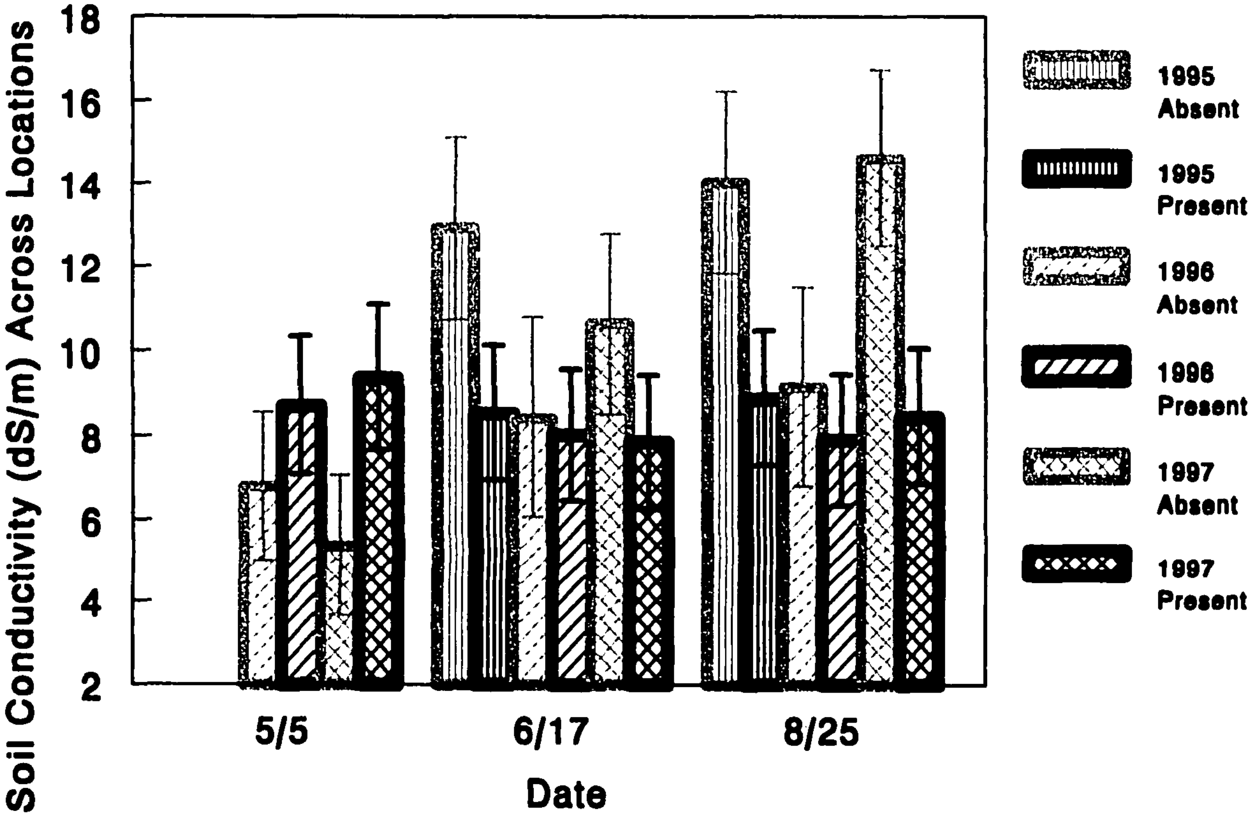

Figure 3.5 Estimated Least Square Means of Soil Conductivity Across the Growing Season in Quadrats (40cm x 40cm) Where *C. multicaulis* is Present as Compared to Quadrats Where *C. multicaulis* is Absent

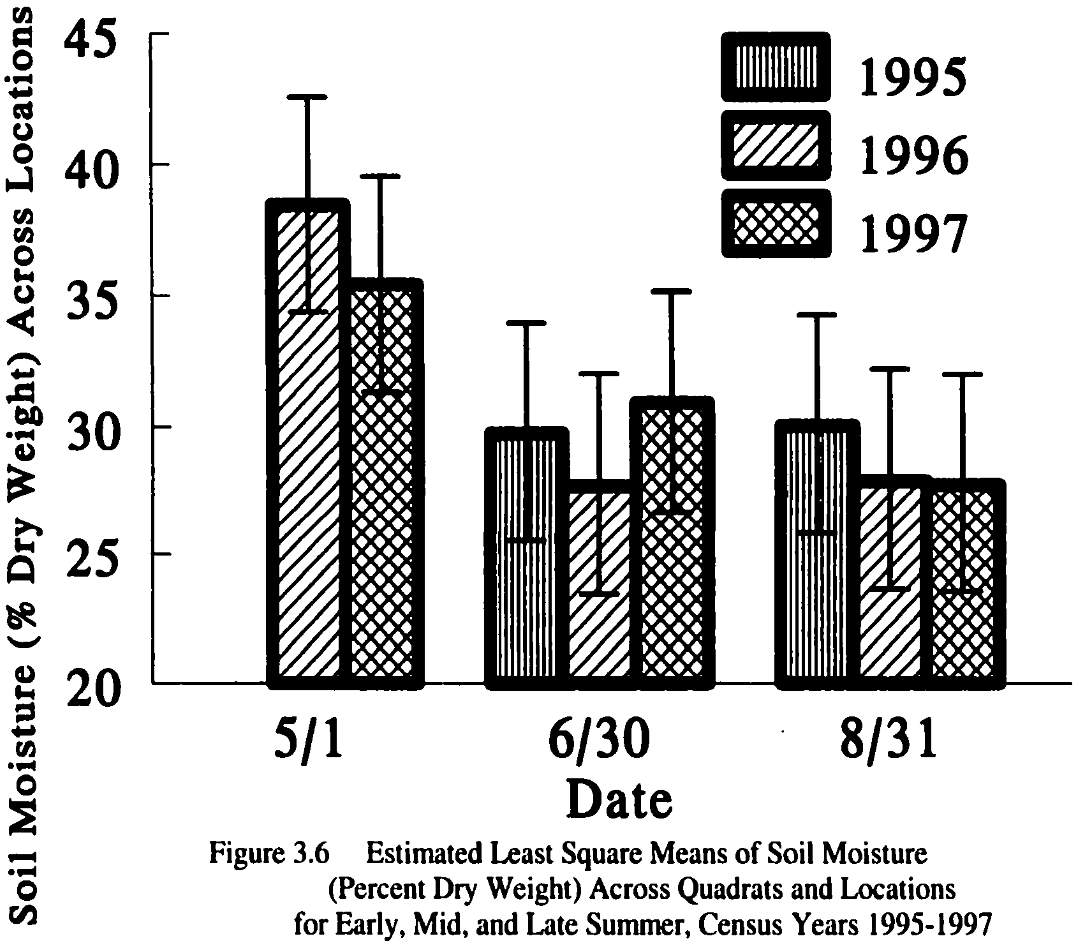

Figure 3.6 Estimated Least Square Means of Soil Moisture (Percent Dry Weight) Across Quadrats and Locations for Early, Mid, and Late Summer, Census Years 1995-1997

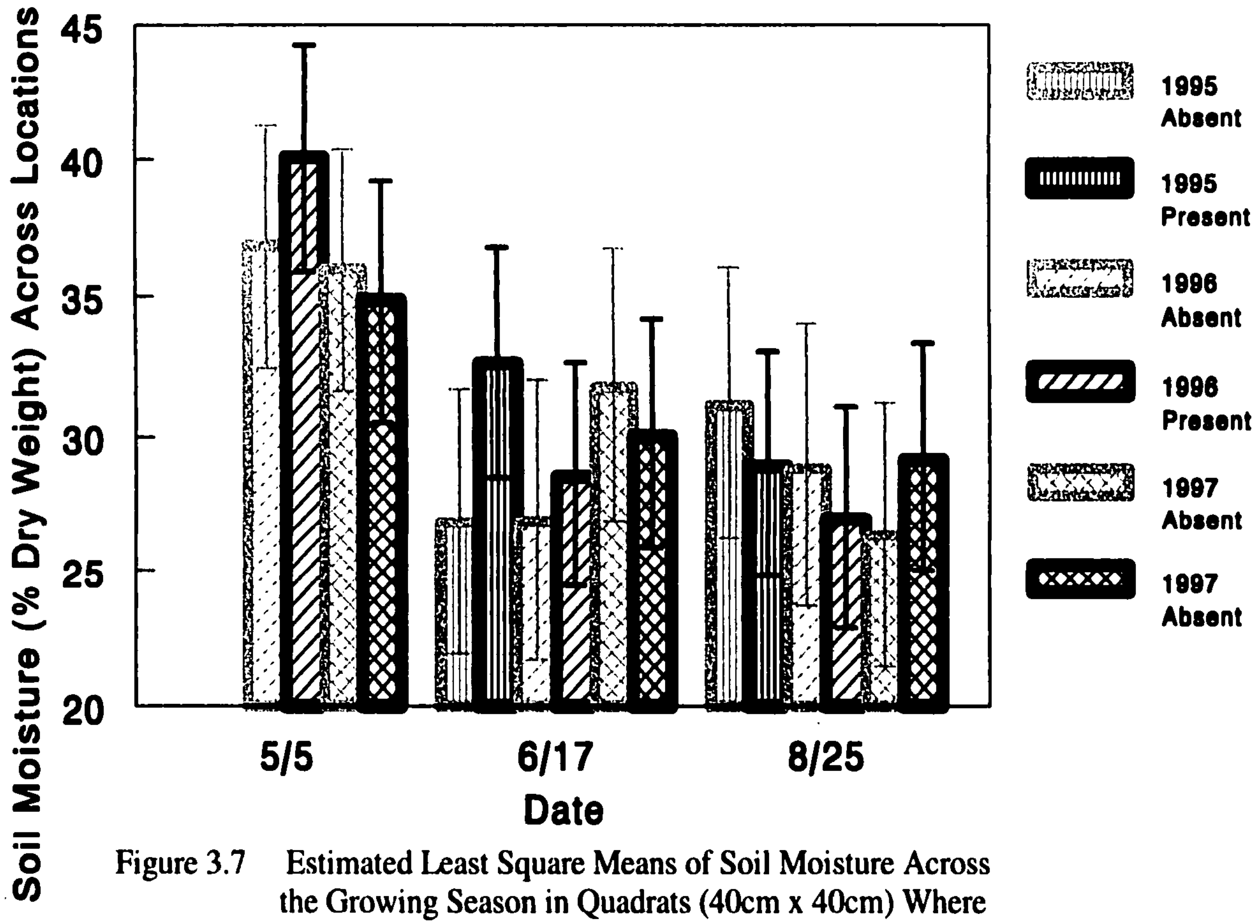

Figure 3.7 Estimated Least Square Means of Soil Moisture Across the Growing Season in Quadrats (40cm x 40cm) Where *C. multicaulis* is Present as Compared to Quadrats Where *C. multicaulis* is Absent

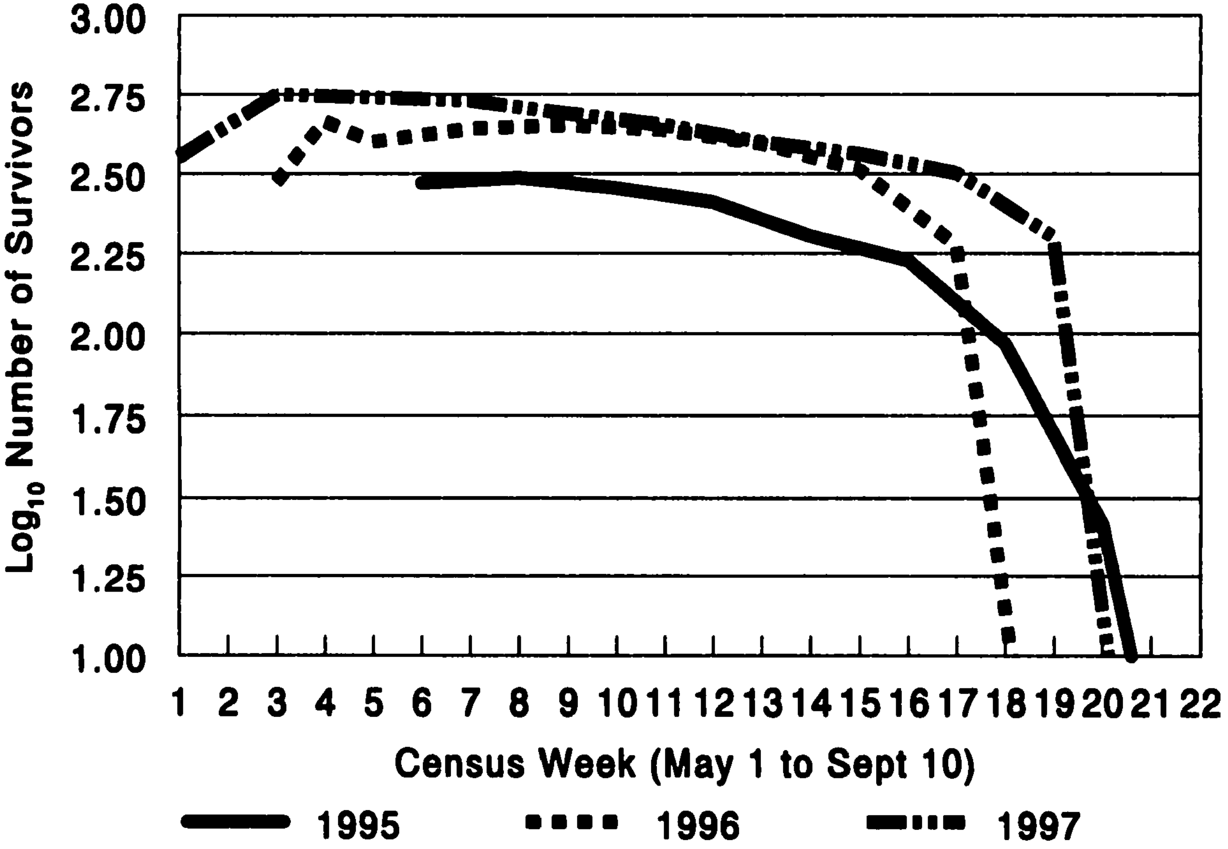

Figure 3.8 Survivorship of *C. multicaulis* to Reproduction

TABLE 3.1 **Summary of *Cleome multicaulis* Occurrence Across Quadrats and Locations for Years 1995-1997**

Year	Total Number of Quadrats with *Cleome multicaulis* Present	Total Density of *Cleome multicaulis* Seedlings Across Quadrats (n = 66) and Locations (n = 11)*	Estimated Least Square Mean Density of *Cleome multicaulis* Reproductive Plants per Quadrat (1600cm^2) (Std. Error)
1995	55 of 66 (83.3%)	3537	37.1 (14.51)
1996	56 of 66 (81.8%)	4664	55.3 (14.27)
1997	54 of 66 (84.8%)	5571	65.9 (14.49)

***Mishak Lakes censuses were taken only in 1995 and 1996 so those data are omitted here for comparative purposes.**

TABLE 3.2 Summary of *Cleome multicaulis* Plant Density by Location (9600 cm^2), Reproductive Life Stage, Census Years 1995-1997

		Year	
Location	**1995**	**1996**	**1997**
BW1	183	171	513
BW2	509	594	686
BW3	107	574	181
RL1	220	74	394
RL2	135	152	316
RL3	98	172	35
RL4	78	44	158
RL5	13	44	87
RL6	307	229	502
RL7	286	565	713
SLL3	18	163	5

Location Key:

BW1	Blanca Wetlands Location 1
BW2	Blanca Wetlands Location 2
BW3	Blanca Wetlands Location 3
RL1	Russell Lakes Location 1
RL2	Russell Lakes Location 2
RL3	Russell Lakes Location 3
RL4	Russell Lakes Location 4
RL5	Russell Lakes Location 5
RL6	Russell Lakes Location 6
RL7	Russell Lakes Location 7
SLL3	San Luis Lakes Location 3

TABLE 3.3 Density of *C. multicaulis* Across Quadrats, Locations, and Years Reproductive Life Stage

Location	Quadrat	1995	1996	1997	Location	Quadrat	1995	1996	1997
BW1	1	71	102	175	RL4	1	0	0	0
	2	0	102	37		2	0	0	0
	3	6	47	214		3	0	0	0
	4	92	18	67		4	37	30	33
	5	0	2	0		5	19	6	48
	6	12	2	20		6	16	8	65
BW2	1	147	136	197	RL5	1	3	8	0
	2	53	104	102		2	0	0	3
	3	49	76	93		3	1	5	24
	4	1	21	74		4	0	0	0
	5	146	0	179		5	7	29	61
	6	87	109	117		6	2	4	22
BW3	1	7	119	0	RL6	1	58	9	8
	2	28	94	12		2	19	10	66
	3	6	148	38		3	40	108	118
	4	19	0	0		4	82	82	101
	5	15	94	26		5	8	12	148
	6	11	2	173		6	78	8	69
RL1	1	96	32	21	RL7	1	0	7	0
	2	27	31	69		2	22	42	113
	3	52	9	172		3	0	0	0
	4	0	0	38		4	10	116	209
	5	0	2	89		5	81	179	145
	6	5	0	5		6	141	251	244
RL2	1	3	15	139	ML1	1	0	0	
	2	6	20	54		2	0	0	
	3	17	10	47		3	10	35	
	4	24	9	32		4	30	25	
	5	50	82	1		5	5	69	
	6	12	17	43		6	43	33	
RL3	1	34	34	3	SLL3	1	1	0	2
	2	7	43	16		2	1	10	0
	3	35	4	1		3	1	0	2
	4	11	85	11		4	3	59	1
	5	3	7	4		5	0	0	0
	6	0	0	0		6	11	0	0

TABLE 3.4 **Summary of Repeated Measures Analysis of Effect of Year, Date and Date*Year Interaction on *C. multicaulis* Density**

Model: Square-Root Plant Density = Date + Year + Date*Year

Random Effects: Location, Quadrat (Location), Location*Year, Quadrat (Location)*Year

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source of Estimated Variation (Random Effects)**
Density of *C. multicaulis*	Date	0.0011**	Location to Location
(Square-Root)	Year	0.0649*	and Quadrat to Quadrat
	Date*Year	0.4523	from Year to Year

** $p < 0.05$
* $p < 0.10$

TABLE 3.5 **Summary of Repeated Measures Analysis of Effect of Soil Characteristics on *C. multicaulis* Density After Adjustment for Year, Date and Date*Year Interaction**

Model: Square-Root Plant Density = Date + Year + Date*Year + Soil pH + Soil Electrolytic Conductivity + Soil Moisture

Random Effects: Location, Quadrat (Location), Location*Year, Quadrat (Location)*Year

Dependent Variable	**Model Fixed Effects**	**p > Type III**	**Largest Source Of Estimated Variation (Random Effects)**
Density of *C. multicaulis*	Date	0.0012**	Location to Location
(Square-Root)	Year	0.0686*	
	Date*Year	0.4793	
	Soil pH	0.3468	
	Soil Conductivity	0.1354	
	Soil Moisture	0.6012	

** $p < 0.05$
* $p < 0.10$

TABLE 3.6 Correlation Analysis of Soil Characteristics Across Quadrats Per Location, Density of *C. multicaulis* Reproductive Plants and Depth to the Shallow Water Table (with Detection Limits)

Soil pH			
	Soil Conductivity (Ec)	r = 0.69810	p = 0.0001**
	Soil Moisture	r = 0.51682	p = 0.0001**
Soil Ec	Soil Moisture	r = 0.29803	p = 0.0001**
Density of *C. multicaulis*			
	Soil pH	r = 0.17777	p = 0.0001**
	Soil Conductivity (Ec)	r = 0.24429	p = 0.0001**
	Soil Moisture	r = 0.04922	p = 0.2457
Depth to the Shallow Water Table			
	Soil pH	r = 0.32351	p = 0.0001**
	Soil Conductivity (Ec)	r = 0.15906	p = 0.0419*
	Soil Moisture	r = 0.39225	p = 0.0001**

** $p < 0.05$
* $p < 0.10$

TABLE 3.7 Estimated Least Square Mean Soil Characteristics and *C. multicaulis* Density by Quadrat (Across Dates) For Census Years 1995-1997

Soil pH	Soil Conductivity	Soil Moisture %	Density of *C. multicaulis*	Loc	Yr	Quadrat
9.50	19.58	15.66%	71	1	95	1
9.05	8.01	29.45%	102	1	96	1
9.15	7.17	22.71%	175	1	97	1
9.30	10.72	21.63%	0	1	95	2
9.05	8.99	58.81%	0	1	96	2
9.15	8.40	12.18%	37	1	97	2
9.10	8.48	14.51%	6	1	95	3
8.95	7.17	7.09%	47	1	96	3
9.00	5.31	13.26%	214	1	97	3
9.70	31.20	13.29%	92	1	95	4
9.55	13.55	15.50%	18	1	96	4
9.05	4.77	17.54%	67	1	97	4
9.75	15.81	10.16%	0	1	95	5
9.75	16.89	17.13%	2	1	96	5
9.85	23.55	9.87%	0	1	97	5
9.65	12.71	12.34%	14	1	95	6
9.20	5.72	13.80%	2	1	96	6
9.25	7.48	7.07%	20	1	97	6
9.75	3.66	1.23%	147	2	95	1
8.75	2.19	14.20%	136	2	96	1
9.30	3.86	12.51%	197	2	97	1
8.70	1.21	29.10%	63	2	95	2
9.10	1.44	21.21%	104	2	96	2
8.65	2.42	19.12%	102	2	97	2
9.05	1.26	6.97%	59	2	95	3
8.75	2.04	14.93%	78	2	96	3
9.85	14.16	14.50%	93	2	97	3
8.45	3.18	18.51%	31	2	95	4
9.55	4.75	34.38%	21	2	96	4
8.30	1.03	20.47%	38	2	97	4
9.35	3.59	2.46%	128	2	95	5
8.80	2.88	16.94%	146	2	96	5
9.25	4.58	13.33%	132	2	97	5
9.60	2.36	6.09%	81	2	95	6
9.30	4.52	11.27%	109	2	96	6
9.20	4.05	14.96%	124	2	97	6
8.65	2.54	24.37%	19	3	95	1
8.10	2.28	26.12%	119	3	96	1
7.90	1.02	23.15%	0	3	97	1
9.05	6.66	24.49%	33	3	95	2
8.15	2.76	22.22%	94	3	96	2

Soil pH	Soil Conductivity	Soil Moisture %	Density of *C. multicaulis*	Loc	Yr	Quadrat
8.35	3.96	25.07%	6	3	97	2
8.20	3.90	25.12%	9	3	95	3
8.30	2.01	22.91%	148	3	96	3
8.80	3.80	24.31%	33	3	97	3
9.00	5.07	17.95%	19	3	95	4
8.45	2.10	30.11%	117	3	96	4
8.30	1.64	24.94%	0	3	97	4
9.10	5.90	23.45%	15	3	95	5
8.75	3.69	23.17%	94	3	96	5
9.10	6.75	22.13%	24	3	97	5
9.90	20.40	11.11%	12	3	95	6
9.35	3.69	14.08%	2	3	96	6
9.75	13.35	8.46%	118	3	97	6
8.35	1.38	62.70%	112	4	95	1
8.15	1.28	35.27%	32	4	96	1
8.20	1.09	8.68%	21	4	97	1
8.25	2.15	54.98%	27	4	95	2
8.30	2.62	91.17%	31	4	96	2
8.65	1.65	73.32%	69	4	97	2
8.70	5.21	30.20%	73	4	95	3
8.6	3.37	22.70%	9	4	96	3
8.05	2.96	25.73%	172	4	97	3
8.05	3.26	83.19%	0	4	95	4
7.8	1.56	31.02%	0	4	96	4
8.45	3.65	26.73%	38	4	97	4
8.75	4.12	26.23%	3	4	95	5
9.1	5.30	28.23%	2	4	96	5
8.7	2.99	24.66%	89	4	97	5
8.65	3.60	26.94%	5	4	95	6
8.6	4.01	25.09%	0	4	96	6
8.55	4.89	26.57%	5	4	97	6
8.95	5.63	28.67%	3	5	95	1
8.55	4.07	36.53%	15	5	96	1
8.45	2.70	28.74%	139	5	97	1
8.70	3.12	23.94%	7	5	95	2
8.1	1.68	48.83%	20	5	96	2
8.65	2.82	34.20%	54	5	97	2
8.80	3.63	44.04%	17	5	95	3
8.75	5.96	31.78%	9	5	96	3
8.65	3.79	28.85%	47	5	97	3
8.65	3.33	44.11%	26	5	95	4
8.25	3.67	29.72%	9	5	96	4
8.35	2.19	52.12%	32	5	97	4
9.10	5.27	28.94%	53	5	95	5
9.05	9.95	31.68%	82	5	96	5
9.35	19.92	43.53%	1	5	97	5
8.95	4.94	30.84%	29	5	95	6
8.85	6.74	29.32%	17	5	96	6
8.65	1.87	28.61%	43	5	97	6

Soil pH	Soil Conductivity	Soil Moisture %	Density of *C. multicaulis*	Loc	Yr	Quadrat
9.15	8.38	41.15%	39	6	95	1
9.2	14.96	34.20%	34	6	96	1
8.9	5.94	39.47%	3	6	97	1
9.25	7.96	31.07%	6	6	95	2
9	10.41	28.69%	42	6	96	2
8.85	6.91	47.49%	16	6	97	2
9.20	8.34	40.54%	40	6	95	3
9.3	21.64	37.37%	4	6	96	3
9.55	23.40	34.66%	1	6	97	3
9.15	6.01	25.48%	11	6	95	4
9.05	10.48	26.44%	85	6	96	4
9.45	16.45	34.34%	11	6	97	4
9.45	12.62	51.96%	2	6	95	5
9.4	17.15	24.20%	7	6	96	5
9.25	10.26	35.49%	4	6	97	5
9.75	58.68	15.15%	0	6	95	6
9.2	13.43	25.94%	0	6	96	6
9.7	28.66	20.21%	0	6	97	6
9.40	2.88	8.71%	0	7	95	1
9.75	25.43	13.38%	0	7	96	1
9.9	44.17	17.92%	0	7	97	1
9.80	24.71	11.50%	0	7	95	2
9.65	21.37	7.88%	0	7	96	2
9.5	23.48	18.48%	0	7	97	2
9.95	62.21	12.18%	0	7	95	3
9.8	34.21	10.46%	0	7	96	3
9.75	41.38	15.62%	0	7	97	3
9.20	7.41	21.78%	39	7	95	4
9.15	13.28	17.66%	30	7	96	4
8.95	11.49	28.43%	48	7	97	4
9.10	5.76	17.85%	20	7	95	5
9.25	12.19	19.65%	6	7	96	5
9.35	12.68	18.31%	65	7	97	5
9.30	13.93	10.30%	19	7	95	6
9.35	14.29	15.40%	8	7	96	6
9.2	13.00	20.66%	12	7	97	6
8.80	4.29	23.18%	3	8	95	1
9.05	13.58	24.94%	6	8	96	1
9.45	17.42	19.33%	2	8	97	1
9.00	4.79	34.33%	0	8	95	2
8.85	10.97	27.90%	0	8	96	2
9.3	16.86	33.44%	20	8	97	2
8.75	5.42	20.04%	1	8	95	3
8.75	9.36	18.78%	5	8	96	3
9.85	31.03	22.96%	0	8	97	3
7.65	1.38	42.69%	0	8	95	4
7.55	1.25	37.31%	0	8	96	4
7.7	1.16	40.15%	35	8	97	4
8.65	3.20	24.71%	7	8	95	5

Soil pH	Soil Conductivity	Soil Moisture %	Density of *C. multicaulis*	Loc	Yr	Quadrat
8.35	4.13	19.79%	29	8	96	5
8.15	2.63	23.96%	22	8	97	5
9.10	3.67	19.83%	2	8	95	6
8.05	2.37	21.78%	4	8	96	6
9	9.97	27.48%	8	8	97	6
7.55	1.67	50.94%	58	9	95	1
8.25	2.45	36.86%	9	9	96	1
8.25	2.92	70.01%	66	9	97	1
7.95	1.10	47.48%	19	9	95	2
8.5	4.05	31.91%	10	9	96	2
8.55	4.21	42.55%	118	9	97	2
8.65	14.71	41.23%	41	9	95	3
8.55	11.78	33.80%	108	9	96	3
8.65	10.55	30.81%	101	9	97	3
7.65	2.51	83.75%	104	9	95	4
8.05	2.90	52.88%	82	9	96	4
7.95	2.74	84.48%	148	9	97	4
7.60	1.09	37.13%	15	9	95	5
8.3	3.66	33.00%	12	9	96	5
7.95	3.89	62.08%	69	9	97	5
8.55	7.60	54.00%	70	9	95	6
7.75	3.29	37.92%	8	9	96	6
8.1	4.96	32.44%	0	9	97	6
7.75	2.29	70.72%	5	10	95	1
8.5	6.74	54.97%	7	10	96	1
8.45	4.75	77.20%	113	10	97	1
8.35	4.76	60.24%	18	10	95	2
8.3	3.50	37.52%	42	10	96	2
8.65	5.16	45.63%	0	10	97	2
7.85	8.28	37.11%	0	10	95	3
7.6	1.67	47.43%	0	10	96	3
8	2.07	37.01%	209	10	97	3
8.95	15.03	47.57%	7	10	95	4
7.95	4.33	39.23%	116	10	96	4
9	8.25	54.83%	145	10	97	4
8.65	5.32	46.48%	107	10	95	5
8.45	3.76	52.31%	179	10	96	5
8.7	5.88	48.24%	244	10	97	5
8.85	8.85	43.93%	149	10	95	6
7.8	2.65	49.84%	221	10	96	6
9.15	7.90	49.87%	2	10	97	6
9.60	16.22	27.18%	0	11	95	1
9.3	13.75	16.27%	3	11	96	1
9.45	20.13	22.43%	0	11	95	2
9.75	25.36	9.24%	25	11	96	2
9.15	9.32	14.95%	12	11	95	3
8.95	9.21	13.98%	35	11	96	3
9.15	10.86	14.38%	31	11	95	4

Soil pH	Soil Conductivity	Soil Moisture %	Density of *C. multicaulis*	Loc	Yr	Quadrat
9.45	15.60	14.61%	25	11	96	4
9.20	9.26	15.23%	6	11	95	5
9.25	11.53	13.54%	69	11	96	5
9.10	6.75	22.17%	58	11	95	6
9.2	7.84	10.36%	34	11	96	6
9.75	19.33	21.03%	2	12	95	1
9.1	7.34	19.09%	3	12	96	1
9.5	12.89	22.21%	2	12	97	1
9.55	21.83	20.13%	1	12	95	2
9.25	12.02	21.02%	8	12	96	2
9.65	21.02	19.08%	0	12	97	2
9.55	30.21	24.93%	1	12	95	3
9.25	10.54	20.86%	15	12	96	3
9.5	9.48	18.43%	2	12	97	3
8.95	7.92	26.68%	3	12	95	4
8.75	5.75	21.88%	58	12	96	4
9.1	6.67	18.77%	1	12	97	4
9.25	11.66	26.51%	0	12	95	5
9.15	10.14	25.39%	32	12	96	5
9.25	4.93	22.00%	0	12	97	5
9.50	6.88	30.45%	16	12	95	6
9.65	34.87	37.48%	11	12	95	6
8.7	6.78	20.82%	47	12	96	6
8.95	17.46	26.36%	0	12	97	6

Location Key:

1	BW1	Blanca Wetlands Location 1
2	BW2	Blanca Wetlands Location 2
3	BW3	Blanca Wetlands Location 3
4	RL1	Russell Lakes Location 1
5	RL2	Russell Lakes Location 2
6	RL3	Russell Lakes Location 3
7	RL4	Russell Lakes Location 4
8	RL5	Russell Lakes Location 5
9	RL6	Russell Lakes Location 6
10	RL7	Russell Lakes Location 7
11	ML1	Mishak Lakes Location 1 (1995 and 1996 only)
12	SLL3	San Luis Lakes Location 3

TABLE 3.8 **Mean Soil Characteristics At Time of Reproduction (Across Locations) for Various Quadrat Densities of *C. multicaulis* Reproductive Plants**

Plant Density per Quadrat ($1600cm^2$)	n	Mean Soil pH	Std. Dev.	Mean Soil Conductivity (dS/m)	Std. Dev.	Mean Soil Moisture % Dry Wt.	Std. Dev.
0	131	8.977	0.723	12.461	13.319	32.370%	18.225
1 - 49	236	8.927	0.512	8.640	6.689	30.773%	15.802
50 - 149	126	8.763	0.547	6.087	5.047	31.802%	19.738
> 150	65	8.654	0.457	4.738	2.915	33.197%	15.706

TABLE 3.9 **Summary of Repeated Measures Analysis of the Effect of Date, Year, and the Date*Year Interaction on Soil pH**

Model: Soil pH = date + year + date*year

Random Effects: Location, Quadrat (Location), Year*Location, Year*Quadrat (Location), Date*Location, Date*Year*Location, Date*Quadrat (Location)

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Soil pH	Date	0.1193	Location to Location
	Year	0.4564	
	Date*Year	0.0069**	

** $p < 0.05$
* $p < 0.10$

TABLE 3.10 **Summary of Repeated Measures Analysis of the Effect of *C. multicaulis* Presence on Soil pH After Adjustment for Date, Year, and the Date*Year Interaction**

Model: Soil pH = Date + Year + Date*Year + Presence

Random Effects: Location, Quadrat (Location), Year*Location, Year*Quadrat (Location), Date*Location, Date*Year*Location, Date*Quadrat (Location)

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Soil pH	Date	0.0591*	Location to Location
	Year	0.4136	
	Date*Year	0.0063**	
	Presence of *C. multicaulis*	0.0466**	

** $p < 0.05$
* $p < 0.10$

TABLE 3.11 **Estimated Least Square Means of Soil pH, Quadrats with *C. multicaulis* Present/Absent In Early, Mid- and Late-Summer, Census Years 1995-1997**

Estimated Least Square Means, Soil pH

	1995		**1996**		**1997**		
Date	Present	Absent	Present	Absent	Present	Absent	Std. Error
May 1	na	na	8.9003	8.8455	9.0130	8.8161	0.1372-0.1406*
June 15	8.8278	8.9875	8.9157	8.8574	8.8155	8.6143	0.1354-0.1618*
Aug 25	8.9688	8.7411	8.8127	8.7411	8.9426	8.9341	0.1354-0.1618*

* Range of standard error estimates given for date x year combinations in that row. Presence or absence indicates census quadrats with at least one *C. multicaulis* individual present at the time of soil sampling.

TABLE 3.12 **Summary of Repeated Measures Analysis of the Effect of Date, Year, and the Date*Year Interaction on Soil Conductivity (Ec)**

Model: ln(Soil Conductivity) = Date + Year + Date*Year

Random Effects: Location, Quadrat (Location), Year*Location, Year*Quadrat (Location), Date*Location, Date*Year*Location, Date*Quadrat (Location)

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Soil Conductivity (ln)	Date	0.1823	Location to Location
	Year	0.5848	
	Date *Year	0.2706	

** $p < 0.05$
* $p < 0.10$

TABLE 3.13 **Summary of Repeated Measures Analysis of the Effect of *C. multicaulis* Presence on Soil Conductivity (Ec) After Adjustment for the Effect of Date, Year, and the Date*Year Interaction**

Model: Soil Conductivity = Date + Year + Date*Year + Presence

Random Effects: Location, Quadrat (Location), Year*Location, Year*Quadrat (Location), Date*Location, Date*Year*Location, Date*Quadrat (Location)

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Soil Conductivity (ln)	Date	0.3358	Location to Location
	Year	0.5600	
	Date*Year	0.2735	
	Presence of *C. multicaulis*	0.1950	

** $p < 0.05$
* $p < 0.10$

TABLE 3.14 Estimated Least Square Means of Soil Conductivity, Quadrats with *Cleome* Present/Absent For Early, Mid- and Late-Summer, Census Years 1995-1997

Estimated Least Square Means, Soil Conductivity (dS/m)

	1995		1996		1997		
Date	Present	Absent	Present	Absent	Present	Absent	Std. Error
May 1	na	na	8.7555	6.7260	9.4715	5.2714	1.6459-1.8101*
June 15	8.5840	12.7183	8.0481	8.2738	8.2406	9.1446	1.5889-2.3687*
Aug 25	8.9293	13.8402	7.9352	9.0049	8.6855	14.1010	1.5889-2.6387*

* Range of standard error estimates given for date x year combinations in that row. Presence or absence indicates census quadrats with at least one *C. multicaulis* individual present at the time of soil sampling.

TABLE 3.15 **Summary of Repeated Measures Analysis of the Effect of Density of *C. multicaulis* on Soil pH**

Model: Soil pH = Date + Year + Date*Year + Density of *C. multicaulis*

Random Effects: Location, Quadrat (Location), Year*Location, Date*Location, Date*Year*Location, Date*Quadrat (Location), Year*Quadrat (Location)

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source Of Estimated Variation (Random Effects)**
Soil pH	Date	0.1872	Location to Location
	Year	0.5194	
	Date*Year	0.0062*	
	Density of *C. multicaulis*	0.3352	

** $p < 0.05$
* $p < 0.10$

TABLE 3.16 **Summary of Repeated Measures Analysis of the Effect of Density of *C. multicaulis* on Soil Conductivity**

Model: Soil Conductivity (ln) = Date + Year + Date*Year + Density of *C. multicaulis*

Random Effects: Location, Quadrat (Location), Year*Location, Date*Location, Date*Year*Location, Date*Quadrat (Location), Year*Quadrat (Location)

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source Of Estimated Variation (Random Effects)**
Soil Conductivity (ln)	Date	0.2021	Location to Location
	Year	0.6852	
	Date*Year	0.2834	
	Density of *C. multicaulis*	0.3250	

** $p < 0.05$
 * $p < 0.10$

TABLE 3.17 **Summary of Repeated Measures Analysis of the Effect of Date, Year, and the Date*Year Interaction on Soil Moisture (Percent Dry Weight)**

Model: Soil Moisture (Arcsin-Square-Root) = Date + Year + Date*Year

Random Effects: Location, Quadrat (Location), Year*Location, Date*Location, Date*Year*Location, Date*Quadrat (Location), Year*Quadrat (Location)

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Soil Moisture	Date	0.0001**	Location to Location
(Arcsin Square-Root)	Year	0.6105	
	Date*Year	0.2295	

** $p < 0.05$
* $p < 0.10$

TABLE 3.18 **Summary of Repeated Measures Analysis of the Effect of *C. multicaulis* Presence on Soil Moisture (Percent Dry Weight) After Adjustment for the Effect of Date, Year, and the Date*Year Interaction**

Model: Soil Moisture (Arcsin-Square-Root) = Date + Year + Date*Year

Random Effects: Location, Quadrat (Location), Year*Location, Date*Location, Date*Year*Location, Date*Quadrat (Location), Year*Quadrat (Location)

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Soil Moisture	Date	0.0001**	Location to Location
(Arcsin Square-Root)	Year	0.6049	
	Date*Year	0.2376	
	Presence of *C. multicaulis*	0.4891	

** $p < 0.05$
* $p < 0.10$

TABLE 3.19 **Estimated Least Square Means, Soil Moisture Percent, Quadrats with *C. mutlicaulis* Present/Absent Early, Mid- and Late-Summer, Census Years 1995-1997**

Estimated LS Means Soil Moisture

	1995		1996		1997		
Date	Present	Absent	Present	Absent	Present	Absent	Std. Error
May 1	na	na	40.081	36.870	34.865	36.004	4.190-4.414*
June 15	32.653	26.840	28.560	26.885	30.029	31.811	4.113-5.182*
Aug 25	28.940	31.141	26.979	28.885	29.178	26.345	4.113-5.182*

* Range of standard error estimates given for date x year combinations in that row. Presence or absence indicates census quadrats with at least one *C. multicaulis* individual present at the time of soil sampling.

TABLE 3.20 **Estimated Least Square Means, Number of Fruits Per Quadrat and Number of Fruits Per Reproductive Plant Across Locations, Census Years 1995-1997**

	1995	1996	1997	Std. Error
Number of Fruits Per Quadrat (1600cm^2)	155.6	160.5	152.1	21.61-23.04
Number of Fruits Per Reproductive Plant	6.87	5.94	6.00	1.17- 1.24

TABLE 3.21 **Summary of Repeated Measures Analysis of the Effect of Year on the Number of Fruits Per Quadrat (1600cm^2)**

Model: Number of Fruits Per Quadrat (Square-Root) = Year

Random Effects: Location, Quadrat (Location), Location*Year

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source Of Estimated Variation (Random Effects)**
Number of Fruits Per	Year	0.8072	Quadrat to Quadrat
Quadrat			within Location
(Square-Root)			

** $p < 0.05$
* $p < 0.10$

TABLE 3.22 **Results of Repeated Measures Analysis of the Effect of Soil Characteristics on Number of Fruits Per Quadrat (1600cm^2) After Adjustment for the Effect of Year**

Model: Number of Fruits (Square-Root) = Year + Soil pH + Soil Conductivity + Soil Moisture

Random Effects: Location, Quadrat (Location), Location*Year

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source Of Estimated Variation (Random Effects)**
Number of Fruits Per	Year	0.7932	Residual
Quadrat (1600 cm^2)	Soil pH	0.0718*	
	Soil Conductivity	0.0394**	
	Soil Moisture	0.6772	

The effect of an increase in Soil pH is to increase the number of fruits per quadrat, whereas the effect of an increase in soil conductivity is to decrease the number of fruits per quadrat.

** $p < 0.05$
* $p < 0.10$

TABLE 3.23 Summary of Repeated Measures Analysis of the Effect of Year and Density of *C. multicaulis* on the Number of Fruits Per Reproductive Plant (Square-Root)

Model: Number of Fruits (Square-Root) = Year + Density of *C. multicaulis*

Random Effects: Location, Quadrat (Location), Location*Year

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Number of Fruits Per Reproductive Plant	Year	0.6650	Residual
Plant (Square-Root)	Density of *C. multicaulis*	0.5138	

** $p < 0.05$
* $p < 0.10$

TABLE 3.24 **Summary of Repeated Measures Analysis of the Effect of Soil Characteristics on the Number of Fruits per Reproductive Plant (Square-Root) After Adjustment for Year and Density of *C. multicaulis***

Model: Number of Fruits (Square-Root) = Year

Random Effects: Location, Quadrat (Location), Location*Year

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source Of Estimated Variation (Random Effects)**
Number of Fruits Per Reproductive Plant	Year	0.6695	Residual
(Square-Root)	Density of *C. multicaulis*	0.6249	
	Soil pH	0.0215**	
	Soil Conductivity	0.0320**	
	Soil Moisture	0.5393	

** $p < 0.05$
* $p < 0.10$

TABLE 3.25 Correlation Analysis of Mean Plant Height per Quadrat (1600cm^2), Mean Soil Characteristics Across Dates, Years, and Locations, and Mean Reproductive Success Across Dates, Years, and Locations

Mean Plant Height Per Quadrat			
	Number of Fruits Per Reproductive Plant	r = 0.66103	p = 0.0001**
	Number of Fruits Per Quadrat (1600cm^2)	r = 0.31512	p = 0.0126**
	Mean Soil pH	r = -0.17221	p = 0.1808
	Mean Soil Conductivity	r = -0.03396	p = 0.7933
	Mean Soil Moisture	r = 0.28832	p = 0.0231**
Number of Fruits Per Quadrat (1600cm^2)			
	Mean Soil pH	r = 0.05245	p = 0.4496
	Mean Soil Conductivity	r = -0.13441	p = 0.0518*
	Mean Soil Moisture	r = -0.08041	p = 0.2460
Number of Fruits Per Reproductive Plant			
	Mean Soil pH	r = 0.15968	p = 0.0206**
	Mean Soil Conductivity	r = 0.07319	p = 0.2911
	Mean Soil Moisture	r = 0-.00998	p = 0.1495

** $p < 0.05$
* $p < 0.10$

TABLE 3.26 **Summary of Repeated Measures Analysis of the Effect of Year on *C. multicaulis* Survivorship to Reproduction**

Model: Survivorship (Arcsin) = Year

Random Effects: Location, Quadrat (Location), Location*Year

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source Of Estimated Variation (Random Effects)**
Survivorship to Reproduction	Year	0.5137	Residual
(Arcsin)			

** $p < 0.05$
* $p < 0.10$

TABLE 3.27 **Summary of Repeated Measures Analysis of the Effect of Soil Characteristics on *C. multicaulis* Survivorship to Reproduction After Adustment for the Effect of Year**

Model: Survivorship (Arcsin) = Year + Soil pH + Soil Conductivity + Soil Moisture

Random Effects: Location, Quadrat (Location), Location*Year

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Survivorship to Reproduction	Year	0.4743	Residual
(Arcsin)	Soil pH	0.5724	
	Soil Conductivity	0.2294	
	Soil Moisture	0.8893	

** $p < 0.05$
* $p < 0.10$

TABLE 3.28 **Soil Characteristics, Plant Density, and Survivorship to Reproduction by Location (Across Quadrats within Location, Across Dates and Across Census Years 1995-1997)**

Location	Soil pH	Soil Conductivity	Soil Moisture Percent	Total Density of *C. multicaulis*	Survivorship
BW1	9.360	12.159	19.65	58.9	66.84
BW2	8.986	4.143	20.19	151.7	58.99
BW3	8.741	5.177	23.08	76.5	63.07
RL1	8.370	2.827	42.67	43.1	59.88
RL2	8.692	5.274	38.07	32.1	62.53
RL3	9.298	13.924	36.88	15.2	85.67
RL4	9.426	18.703	20.06	14.2	51.79
RL5	8.719	7.273	27.37	9.0	75.76
RL6	8.186	4.424	52.29	64.0	42.29
RL7	8.282	4.684	53.99	126.7	60.51
SLL3	9.272	12.514	23.10	13.6	73.35
ML1	9.247	12.451	17.15	53.7	39.07

TABLE 3.29 **Summary of Repeated Measures Analysis of the Effect of Date, Year, and the Date*Year Interaction of Depth to the Shallow Water Table (with Detection Limits)**

Model: Depth to the Shallow Water Table = Date + Year + Date*Year

Random Effects: Location, Date*Location, Year*Location

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source Of Estimated Variation (Random Effects)**
Depth to the Shallow Water Table	Date	0.0001**	Location to Location
	Year	0.4961	
	Date*Year	0.0001**	

** $p < 0.05$
* $p < 0.10$

TABLE 3.30 **Summary of Repeated Measures Analysis of the Effect of Depth to the Shallow Water Table (with Detection Limits) on Soil pH After Adjustment for the Effect of Date, Year, and the Date*Year Interaction**

Model: Depth to the Shallow Water Table = Date + Year + Date*Year

Random Effects: Location, Date*Location, Year*Location

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Soil pH	Date	0.8027	Location to Location
	Year	0.4360	
	Date*Year	0.0536*	
	Depth to the Shallow Water Table	0.1211	

** $p < 0.05$
* $p < 0.10$

TABLE 3.31 Summary of Repeated Measures Analysis of the Effect of Depth to the Shallow Water Table (with Detection Limits) on Soil Conductivity After Adjustment for the Effect of Date, Year, and the Date*Year Interaction

Model: Soil Conductivity (ln) = Date + Year + Date*Year + Depth to the Shallow Water Table

Random Effects: Location, Date*Location, Year*Location

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Soil Conductivity (ln)	Date	0.8995	Location to Location
	Year	0.0312**	
	Date*Year	0.1225	
	Depth to the Shallow Water Table	0.4225	

** $p < 0.05$
* $p < 0.10$

TABLE 3.32 **Summary of Repeated Measures Analysis of the Effect of Depth to the Shallow Water Table (with Detection Limits) on Soil Moisture (Percent Dry Weight) After Adjustment for the**

Model: Soil Moisture (Arcsin Square-Root) = Date + Year + Date*Year + Depth to the Shallow Water Table

Random Effects: Location, Date*Location, Year*Location

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Soil Moisture Percent	Date	0.0010**	Location to Location
(Arcsin Square-Root)	Year	0.0130**	
	Date*Year	0.4638	
	Depth to the Shallow Water Table	0.0485*	

** $p < 0.05$
* $p < 0.10$

TABLE 3.33 Comparative Soil Characteristics Measured in August of 1995 in Quadrats (1600cm^2) with *Cleome* as 1st or 2nd Dominant Species

	Quadrats with *C. multicaulis* as 1st Dominant Species	**Quadrats with *C. multicaulis* as 2nd Dominant Species**
n	8	29
Mean Soil pH (Std. Dev.)	9.28 (0.342)	8.80 (0.650)
Range of Soil pH	8.85 - 9.75	7.55 - 9.90
Mean Soil Conductivity dS/m (Std. Dev.)	9.984 (10.252)	6.402 (5.068)
Range of Soil Conductivity	1.26 - 31.20	1.09 - 20.40
Mean Soil Moisture % Dry Weight (Std. Dev.)	15.75% (13.866)	31.85% (18.65)
Range of Soil Moisture	1.23% - 43.93%	6.09% - 83.75%

TABLE 3.34

Summary of Analysis of Variance of Soil Characteristics (All Plant Species Combined), and Dominant Plant Associate Species Per Quadrat (1600cm^2)

Dependent Variable	Model Effects	d.f.	p > Type III F
Soil pH	Plant Cover	13	0.0355**
	Plant Associate	7	0.0554*
Soil Conductivity	Plant Cover	13	0.0062**
	Plant Associate	7	0.0125**
Soil Moisture	Plant Cover	13	0.0231**
	Plant Associate	7	0.0174**

** $p < 0.05$
* $p < 0.10$

TABLE 3.35 **Soil Conductivity Measured in August 1995 (Sorted High to Low) and Dominant Plant Species per Quadrat (1600cm^2)**

Mean Soil Conductivity (dS/m) (Std. Dev.)	Dominant Plant Species	n
15.03	*Suaeda depressa*	1
13.93	*Sarcobatus vermiculatus*	1
13.008 (12.735)	*Distichlis stricta* var. *spicata*	22
10.02	*Aster pauciflorus*	1
9.984 (10.252)	*Cleome multicaulis*	8
8.036 (11.420)	*Juncus balticus*	37
7.60	*Hordeum jubatum*	1
1.21	*Erigeron philadelphicus*	1

TABLE 3.36 Mean Soil pH Measured in August 1995 (Sorted High to Low) and Dominant Plant Species per Quadrat (1600cm^2)

Mean Soil pH (Std. Dev.)	**Dominant Plant Species**	**n**
9.300	*Sarcobatus vermiculatus*	1
9.281 (0.342)	*Cleome multicaulis*	8
9.210 (0.410)	*Distichlis stricta* var. *spicata*	22
8.950	*Suaeda depressa*	1
8.766 (0.676)	*Juncus balticus*	37
8.650	*Aster pauciflorus*	2
8.550	*Hordeum jubatum*	1
8.532	*Erigeron philadelphicus*	1

TABLE 3.37 **Mean Soil Moisture (Percent Dry Weight) Measured in August 1995 (Sorted High to Low) and Dominant Plant Species per Quadrat (1600cm^2)**

Soil Moisture Percent Dry Weight (Std. Dev.)	**Dominant Plant Species**	**n**
54.00%	*Hordeum jubatum*	1
46.57%	*Suaeda depressa*	1
43.86%	*Aster pauciflorus*	2
36.495% (18.693)	*Juncus balticus*	37
29.10%	*Erigeron philadelphicus*	1
20.222% (6.185)	*Distichlis stricta* var. *spicata*	22
15.748% (13.866)	*Cleome multicaulis*	8
10.30%	*Sarcobatus vermiculatus*	1

Chapter 4: Periodic Matrix Analysis of Seedbank and Above-Ground Life Stages of *Cleome multicaulis*

INTRODUCTION

Many important ecological questions can be addressed by focusing attention on populations of plants. Population studies assist in assessing the biological status of a species, i.e., its population size and stability, identifying the life history stages that have the greatest effect on population growth and species persistence, and determining the biological causes of variation in those life history stages that have a major demographic impact (Schemske et al. 1994). A population may be considered to be a collection of individuals that are sufficiently close to one another geographically that they can find each other and reproduce (Burgman et al. 1993). Studies of rare plants often include some demographic measure of population vital rates (Schemske et al. 1994), and demographic modeling has become a valuable tool for assessing population or metapopulation states, the risk of extinction, and the efficacy of management or experimental strategies (Maschinski et al. 1997).

Plants whose life cycle proceeds from seed to adult and back to seed in a single year are usually described as annuals. Many of these species have a seed bank in the soil that may persist for several years, allowing plants to survive unfavorable conditions for germination by remaining dormant until survival probabilities improve. Because seeds are considered "born" when they mature on the parent plant (Harper 1977), the presence of a persistent seed bank adds age structure to an otherwise annual life cycle for these species, with the result that plants appearing above-ground in any particular year may be comprised of individuals of various ages.

Among plant population biologists, there is a rich history (almost a tradition) of examining the dynamics of plant populations using matrix analyses that recognize differences among individuals with respect to age, size, or developmental stage (Caswell 1997). Early structured population models include Leslie's age-based matrix (Leslie 1945) that was extended by Lefkovitch (Lefkovitch 1965) to represent organisms grouped by stages and has been used extensively to examine details of plant population dynamics (Caswell 1978b, Bierzychudek 1982, Maillette 1982, Huenneke and Marks 1987, Hughes and Connell 1987, Kalisz and McPeek 1992, Horvitz and Schemske 1995).

Plants are considered to be particularly well-suited to stage-based matrix analysis because their rates of growth, survival, and reproduction often depend more on size or developmental stage than age; however, age-based analyses (Werner and Caswell 1977, Law and Edley 1990, Kalisz 1991) or some combination of age-and stage-based analyses (Werner and Caswell 1977, Law and Edley 1990, Lehtila et al. 1994, Ebert 1999) also have been informative.

Structured population (matrix) models consider all individuals at any particular stage as identical while incorporating the different rates at which individuals are born, grow, develop, mature, move, reproduce, and die (Caswell 1997). Recent matrix studies have incorporated increasing complexity to account for the adverse effects of population density on fertility, survival, and growth rates (Caswell 1997, Barbeau and Caswell 1999) as well as the effects of herbivory (Bastrenta et al. 1995) and harvesting (Caswell et al. 1998) on population dynamics.

A discrete-time matrix model is less constraining for annual plants (whose reproduction occurs all at a single time) than for other plant life histories (Ebert 1999). Although many matrix analyses utilize a one-year time step (Silvertown et al. 1993), for an annual plant this would simply estimate the probability of a seed making more seeds (Harper 1977, Schmidt and Lawlor 1983, Lesica 1995). Use of a shorter time step allows closer examination of the correlation between demographic events and environmental conditions (Falkengren-Grerup 1994, Kephart and Paladino 1997) by allowing investigation both of seasonal variation in population dynamics and the population response to inter-annual environmental variability.

For an annual plant with a seed bank, the challenge becomes estimating the probability that seeds of various ages will germinate, grow, reproduce, disperse, or die. The studies described here were conducted on *Cleome multicaulis*, an annual wetland halophyte occupying the San Luis Valley in Colorado. Previous investigations (see Soils Chapter) have characterized the habitat occupied by *C. multicaulis* as multi-dimensional in terms of the scale of temporal and spatial variability of soil pH, soil salinity, and soil moisture.

Populational studies of *Cleome multicaulis* were undertaken in order to determine whether soil characteristics might influence the population dynamics of this annual plant with a persistent (and therefore age-structured) soil seed bank. Periodic matrices in this study allow estimation of the relative importance to population growth of seeds that persist in the soil and seeds that germinate at their next opportunity. Few matrix studies have incorporated seed bank or other cryptic life stages because of the challenges involved in following the fates of seeds.

The studies described here were closely modeled after those of Susan Kalisz (Kalisz 1991, Kalisz and McPeek 1992, 1993) whose work with *Collinsia verna* developed the first empirically-based models of population dynamics incorporating both above- and below-ground life stages of a single species. Evidence gathered in this study of *C. multicaulis* will be used to make management recommendations that focus on life stages that appear to be important for the long-term persistence of this species in the San Luis Valley.

METHODS

Eleven macroplots (12m x 8m each) were established in the San Luis Valley in southcentral Colorado in locations representing a wide range of variability in habitat occupied by *Cleome multicaulis*. A twelfth macroplot located at Mishak Lakes Preserve (owned by The Nature Conservancy) was not included in the analysis of population dynamics due to complete mortality of the experimental seed cages placed at that site. Of the eleven macroplots used here, seven were located at Russell Lakes State Wildlife Area, three at Blanca Wetlands, and one at San Luis Lakes State Wildlife Area. Two additional macroplots were established at San Luis Lakes in 1995 but were completely flooded in July of 1995 and remained under water until spring of 1996. Data from these plots were not included in the analyses

Within each macroplot, six census quadrats (40cm x 40cm) were established in 1995 using a stratified random selection process, with the constraint that three of the six quadrats in each macroplot contained evidence of *C. multicaulis* presence (as evidenced by remains of plants from the previous year. In 1995, 60% of the established census quadrats contained dead stems from at least one previous year plant. Macroplots were located in close proximity to water basins that fill and empty at least once and sometimes several times each year. Macroplots were not located in areas that had standing water at the time of establishment, but some quadrats did flood during one or more of the census years. The most common species co-occurring with *C. multicaulis* was saltgrass (*Distichlis stricta* var. *spicata*), followed by baltic rush (*Juncus balticus*), and greasewood (*Sarcobatus vermiculatus*) (see Results).

Population censuses were conducted every two weeks during the growing seasons of 1995, 1996, and 1997, with the seed cage experiment (see Description below) continuing through the summer of 1998. In 1995, the first census did not occur until early June, but in 1996 and 1997, censuses began in early May and continued until late August/early September. Individual plants were marked with wooden skewers 25cm long x 3mm wide each numbered with a blue masking tape flag. A confounding effect from increased attractiveness of flagged plants to vertebrate grazers was not predicted based on at least one previous study (Ehrlen 1995) but did occur in the one site (Mishak Lakes) where cattle grazing was common.

In several census quadrats where plant densities were greater than 300 (1875 plants per m^2), plants were not marked with individual flags. Seed bank life stages were defined as seeds of age 0-1 years, age 1-2 years, and age 2-3 years. This categorization allowed transition probabilities to differ for seeds of different age (defined as time since seed maturation) (Harper 1977, Hubbell and Werner 1979). Above-ground stages were defined as seedlings (plants under 15cm height), juveniles (plants 15cm or greater in height), small reproductive plants (15cm or less with at least 4 developed flower buds) and large reproductive plants (greater than 15cm height with at least 4 developed flower buds). The magnitude of errors in assigning matrix category sizes (see previous discussion) in this study is not known.

At each census period, the number of seedlings, juveniles, small reproductive plants, and large reproductive plants was tallied, along with the change in the number of individuals in each of those life stages. The number of births and deaths in each life stages was tracked insofar as possible. Causes of mortality were qualitatively assessed by visual inspection.

Matrix Analysis Methods In This Study

Stage-based matrices of size 7 by 7 stages were constructed for each of 11 macroplot locations and each of 3 years of census. Matrix stages were seeds of age 0-1, 1-2, and 2-3 years, seedlings, juveniles (15cm or less with fewer than 5 flower buds), small reproductive plants (15cm or less with flowers or more than 5 buds), and large reproductive plants (over 15cm with flowers or more than 5 buds). Transition probabilities were determined for matrix entries over the growing season using a transition frequency table (Caswell 1989). (See Example, Table 4.1).

Above-ground population census data taken every two weeks were used to track the states and fates of plants as they moved through various life stages. During the two-week time step used to track above-ground growth, transitions were possible from seedling to juvenile, from juvenile to reproductive plant, or directly from seedling to reproductive plant (although the latter was rarely observed) (Figure 4.2). Plants might also remain in the same life stage for more than one two-week time step. Transitions between stages of seed age occurred once yearly, in the fall.

Fecundities were calculated as the number of seeds per reproductive plant. Preliminary analyses indicated that the number of seeds per fruit did not vary significantly across locations and years. The mean estimated number of seeds per fruit for large reproductive plants was calculated from a sample of 112 fruits (Klemow and Raynal 1983) as 7.319 seeds per fruit, and for small reproductive plants as 2.6 seeds per fruit, and those values used to estimate fecundities in each census year.

Neither seed loss nor herbivory were quantified in this study. Very little visual evidence of seed damage was detected, although observational measures of seed damage may underestimate the reduction in seed viability from insect damage (Louda 1994). Seed damage that may have occurred just prior to dispersal had a greater chance of being overlooked because the final census of each growing season did not capture all plants at the same stage of seed maturation. In order to account for any undetected pre-dispersal seed predation and seed abortion, the estimates of fecundity used in the population matrix were reduced by 10%.

Herbivory was observed in these populations only occasionally, and in the form of plant stems grazed from the top. Although some reduction in reproductive output undoubtedly occurred from these grazed plants, this was not a common incident and was not incorporated into estimates of population vital rates in this study.

Because not all quadrats and locations produced seeds at the same time, the decision as to when to conduct a final census (Table 4.2) was made on a quadrat-by-quadrat basis at the point when the vast majority of reproductive plants had produced mature seeds (but prior to fruit dehiscence). In order to standardize the number of two-week time steps per growing season across macroplot locations, macroplots with early plant senescence were augmented with the addition of a single post-seed dispersal transition matrix. This matrix represented stasis in the seed bank, and consisted of transition probabilities with entries of 0.100 for seeds of age 0-1, 1-2, and 2-3 years.

Calculation of Seedbank Transition Probabilities Using a Field Experiment

Transition probabilities for the seed bank stages were calculated using a separate field experiment modeled after Kalisz (Kalisz 1991, Kalisz and McPeek 1992, 1993) that followed the fates of seeds planted in open-topped wire mesh cages (Figure 4.1) in each of the census macroplots. In this experiment, seeds were randomly collected in late summer beginning in 1995 from plants closely surrounding census macroplots. Soil from just outside each macroplot location was exhumed, mixed across locations, and used to fill the double-compartment seed cages with equal volumes of soil on each side. This design allowed one seed cage compartment to serve as a control plot to quantify the number of seeds already present in the soil prior to planting as well as the lateral movement of seeds during the experiment.

Seeds were combined together from several locations after collection, and groups of 200 seeds each were counted with an automated seed counter. Cohorts of 200 seeds were planted in one randomly determined compartment only (which became the "experimental" side) of each of 128 seed cages beginning in fall of 1995. There were a minimum of 9 and a maximum of 17 seed cages in each of the 11 macroplot locations. (No seed cages survived at Mishak Lakes). All cages were located either within the inside boundary of each 12m x 8m macroplot or less than 10m from the outside edge of each macroplot boundary.

Emergent seedlings were censused in both the experimental and control compartments of the seed cages at two-week intervals between May 1 and mid-July of 1996, 1997, and 1998. Once a year, in mid-July, a portion of the seed cages were destructively harvested to provide a quantitative measurement of seed bank persistence. Soil in the seed cages was sieved and the filled seeds extracted, counted, and tested for viability using 1% tetrazolium chloride.

For a seed cage that was three years old, the number of seeds remaining after three years represents the original number of seeds planted, plus the number moving in laterally for each of three years, minus the number gone (dying a physiological death, moving out laterally, or being eaten) for each of three years, minus the number germinating for each of three years. Seeds that died a physiological death would not necessarily remain in the soil and be detected as unfilled during the extraction process in mid-July. Seeds that were noted as absent from the seed cages might have been eaten, might have moved laterally out of that seed cage (e.g., by flooding), or might have died a physiological death. Distinguishment among these seed fates was not attempted for this study, due to the formidable challenge of following populations of seeds under natural conditions.in the field (Kalisz 1991).

Although lateral movement of seeds could be partially accounted for by the presence of seeds in the control side of each seed cage, lateral movement was not quantitatively assessed in this study. The assumption was made that any seeds that moved into and out of seed cages had the same probabilities of emergence and persistence as those seeds that remained stationary. Studies of forest ecosystem seed reintroductions have shown that seed movement by wind, water, or animals may not occur at high enough levels to be detected (Primack 1996). In the San Luis Valley ecosystem of this study, however, lateral seed movement may be important.

Seasonal mortality (e.g., overwinter seed death) was not measured and could not be reliably estimated. Measurement of the actual probability of emergence, survival, and persistence for a single cohort of seeds moving through time was not possible due to the destructive nature of the extraction process. Estimates were therefore obtained for each macroplot location of the conditional probabilities of survival of seeds aged 0-1, 1-2, and 2-3 years, respectively (Kalisz 1991, Kalisz and McPeek 1992, 1993). These transition probabilities were entered into the stage-based matrices, along with the above-ground census data for the corresponding macroplot location, in order to form as complete a picture as possible of the entire life cycle of a *C. multicaulis* population (Table 4.2).

Definitions Used in Construction of the Seedbank Transition Probabilities

The following definitions were used in the model in order to calculate transition probabilities for the seedbank :

Net Seeds Extracted (in mid-July) = Number of Seeds Extracted from Experimental Side of Cage Minus Number of Seeds Extracted from Control Side of Cage

Number of Seeds Persisting in Seed Bank = Net Seeds Extracted Minus Number of Unfilled Seeds

Net Seed Cage Emergence = Number of Seeds Emerging from Experimental Side of Cage Minus Number of Seeds Emerging from Control Side of Cage

Number of Live Seeds Persisting = Number of Seeds Persisting * Percentage Viability for that Seed Cage

Conditional Probability of Survival = Number of Live Seeds Persisting Plus Current Year's Net Seed Cage Emergence/ (200 - Previous Year's Net Seed Cage Emergence).

Note: Current Year's Emergence was not subtracted from the denominator in this calculation, since the calculation was made in mid-April of the current year, prior to seedling emergence for that year.

Conditional probabilities of survival represented the probability of a seed in the seed bank surviving from mid-July of the previous year until mid-April of the current year, based on the age of that seed (i.e., conditioned upon survival to that point) (Kalisz 1991). This formula concentrates mortality into the months between mid-July of one year and mid-April of the subsequent year. Conditional probabilities of seed survival were entered into the matrices as entries in the "stasis" portion of the matrix, early in the calendar year, and for seeds of age 0-1, 1-2, and 2-3 years.

Emergence from the control side of the seed cages was measured and subtracted from the experimental side of each cage in order to account for seeds that might have washed into the seed cage by lateral movement from winter flooding and subsequently germinated. Emergence values were averaged for all seed cages within a location and then used to calculate the probability of seed bank survival in mid-April (see formula, above).

Transition probabilities of seedling emergence at each location were calculated using actual above-ground census figures from each biweekly census of macroplots, and these transition probabilities were entered into a single matrix along with the seed cage estimates of seed bank survival (Table 4.2). Seedling emergence probabilities from the census quadrats (rather than seed cage emergence probabilities) were used to represent matrix transition probabilities for the transitions between seeds and seedlings. This avoided the need to reconcile seed cage emergence probabilities with those from the census quadrats. An additional benefit of using census quadrats to calculate emergence was that the measurement then arose from a naturally-occurring pool of seeds of varying ages, in which selection was operating to choose the most highly-adapted genotypes, rather than the uniformly-aged seed bank that was created in each seed cage (Kalisz 1991).

Transition probabilities were entered into the last matrix of each calendar year to represent both fecundity (number of seeds per reproductive plant) and movement of seeds in the seed bank into the next year (e.g., from age 0-1 years to age 1-2 years and from age 1-2 years to age 2-3 years). Because no stage was defined for seeds of age greater than three years, no transition probabilities were entered for seeds moving past age three.

Transition probabilities on the seed "birthdays" were entered as values of 1.0 into the matrix, which had the effect (mentioned above) of concentrating seed loss between late August of the current year and mid-April of the subsequent year. Although some level of seed loss (due to physiological death, lateral movement out of the seed bank, or seed predation) occurred over the course of the growing season, it was not possible to estimate the proportion of total annual seed loss occurring during these months without destruction of the seed bank.

Seed cages were harvested prior to plants in the cages completing their reproductive cycle.

The design of this experiment did not permit the estimation of probabilities that a seed of age 0-1, 1-2 or 2-3 years would germinate, survive, and itself produce seeds.

Use of Periodic Matrix Products

Originally described in 1966 (Skellam 1966), periodic matrices have been recently adapted to investigate population dynamics in seasonally variable environments (Caswell and Trevisan 1994, Dixon et al. 1997) or in environments that fluctuate among observed states from year to year (Bierzychudek 1982, Huenneke and Marks 1987, Silva et al. 1991). Periodic matrices use an increased number of time steps to provide a deterministic description of temporal variation (within-year or between years) in population dynamics.

Periodic matrix models shorten the matrix time step to correspond more closely to the scale of environmental variation (van Groenendael et al. 1988), incorporating a larger proportion of the information available from demographic observations to more accurately reflect the actual population behavior. Increasing the number of census periods beyond one per year may allow researchers to document the details of cohort emergence and mortality that may otherwise occur on a time scale that escapes detection (Aplet et al. 1994). Seasonal matrices are constructed using a time step shorter than an entire life cycle, then multiplied together to produce an overall description of population dynamics (van Groenendael et al. 1988, Caswell and Trevisan 1994).

Periodic matrices have also been utilized to investigate interannual fluctuation in population dynamics by generating transition probabilities for each year and environmental state (e.g., "good," "bad," "burnt," or "unburnt"). Individual matrices are built and then multiplied together to form a product matrix as an approximation of stochasticity, with a frequency that corresponds to observed natural variation in the population (Silva et al. 1991, Caswell and Trevisan 1994). The extent of positive or negative autocorrelation between individual years or environmental states may have a significant model effect, as will the frequency of different environmental states (Tuljapurkar 1989, Aberg 1992).

Attempts to correlate environmental variables with population characteristics are likely to benefit from detailed, seasonal analysis of population dynamics (Falkengren-Grerup 1994) and finer-scale analysis may be less likely to overlook infrequently observed life stages or demographic events (Charron and Gagnon 1991, Allphin and Harper 1997).

Interpretation of periodic matrix results may be more complicated than other matrix models. Periodic matrices describe such a fine picture in time they may also create delayed responses, in which the demographic effects of an event do not become apparent until several time steps after they occur (Paton 1986, van Groenendael et al. 1988). The interpretation of sensitivities (representing the relative contribution of various life stages to population growth, but not scaled as a proportion) and elasticity values (representing the proportional contribution to population growth rate from various life stages) are more complex for a periodic matrix than for non-periodic matrix analysis.

Calculation of elasticities based on a product matrix (e.g., seasonal matrices multiplied together using matrix multiplication) will be erroneous because individual elasticity values generated in this manner correspond to a combination of matrix entries describing growth, survival, and fecundity, and are therefore difficult to interpret. Elasticity values based on the individual matrices that were themselves combined to form the product will provide a more meaningful analysis of the proportional contributions to overall population growth rate during each seasonal period (Caswell and Trevisan 1994). Some matrix analysis methods (population projections, calculation of damping ratios) have not yet been developed for use with periodic matrix models.

Periodic Matrix Analysis in this Study

In this study, periodic products of population projection matrices were built in order to investigate the variation in population vital rates that might be expected in a heterogeneous environment such as the San Luis Valley (see previous chapter). Using terminology followed by

Caswell (Caswell and Trevisan 1994), the periodic matrices designed in this study may be described as follows.

The complete population cycle was defined as consisting of m "phases", where $m = 11$. The first phase in the cycle was of duration approximately 7 months (overwinter), and the remaining 10 phases were of two-week duration (April to September). Uniformity in the length of periodic matrix phases (projection intervals) is not a model requirement (Caswell and Trevisan 1994). A series of population projection matrices $\mathbf{B}^{(h)}$ (where $h = 1,2,\ldots m$) were built in order to describe within-year variation in vital rates.

The population projection matrices constructed for each phase were $\mathbf{B}^{(1)}\ldots\mathbf{B}^{(11)}$, with $\mathbf{B}^{(1)}$ representing the population projection that is first in the calendar year (i.e., overwinter survival) and $\mathbf{B}^{(11)}$ representing the final end-of-season transition as the seed bank increases in age. In order to describe the population dynamics over the entire cycle (and beginning with the first matrix entry of the year), a matrix product $\mathbf{A}^{(1)}$ was calculated (Caswell and Trevisan 1994) as:

$$\mathbf{A}^{(1)} \quad = [\mathbf{B}^{(m)}\, \mathbf{B}^{(m-1)}\ldots\mathbf{B}^{(1)}] \qquad (1)$$

so that for the first matrix entry of the year, this becomes $\mathbf{A}^1 = \mathbf{B}^{11} * \mathbf{B}^{10} * \mathbf{B}^9 * \ldots \mathbf{B}^1$. In locations where plant senescence occurred earlier than the 11th census period, an extra $\mathbf{B}^{11}$ matrix was added to the series for that location and consisting of transition probabilities of 1.0 for seed bank stasis. Similar matrix products $\mathbf{A}^{(2)}\ldots\ \mathbf{A}^{(11)}$ were calculated by shifting the order of multiplication in the series so that the corresponding $\mathbf{B}^{(2)}\ldots\mathbf{B}^{(11)}$ became the last matrix in the multiplication series (i.e., the matrix on the far right side of the equation). All matrices in this study were primitive and irreducible (See (Caswell 1989, 2001) for definitions and discussion).

The assumption was made in this study that transition probabilities experienced by individual plants did not differ between the beginning and the end of each projection interval. All loss of seeds in the soil was assumed to occur between mid-July and mid-April of the subsequent year. As in all matrix models, transition probabilities are assumed to be uniform for all individual plants in a particular life stage at a particular time and place.

The population growth rate over the entire cycle period is given by the largest (dominant) eigenvalue $\lambda^{(h)}$ of the matrix $\mathbf{A}^{(h)}$. It is a property of periodic matrices that all eigenvalues of the various matrix products $\mathbf{A}^{(h)}$ ($h = 1,2,\ldots m$) for a particular population cycle are identical, and so a superscript on λ becomes unnecessary (Caswell and Trevisan 1994). Eigenvalues were calculated for the periodic matrix products $\mathbf{A}^{(h)}$ of each population cycle using Maple V software. Additional eigenvalues were generated for some $\mathbf{A}^{(h)}$ that consisted of imaginary numbers.

An annual population growth rate was calculated for heuristic purposes using a series of product matrices $\mathbf{B}^{(1)}\ldots\mathbf{B}^{(11)}$ generated using the arithmetical mean value (across locations) of each transition probability as entries in the matrix series.

A second analysis was conducted using the full detail of matrices $\mathbf{B}^{(1)}\ldots\mathbf{B}^{(11)}$ generated for each location and each census year (n = 121 **B** matrices total). Periodic product matrices were calculated using Maple V software for selected periods $\mathbf{A}^1$,$\mathbf{A}^2$, $\mathbf{A}^6$, $\mathbf{A}^{10}$, and $\mathbf{A}^{11}$ for each location and census year (Table 4.2). Product matrices $\mathbf{A}^1$ and $\mathbf{A}^2$ reflected seed bank overwinter survival and seed germination early in the spring, respectively, with $\mathbf{A}^2$ corresponding to the first soil sampling event of the season (Table 4.2). Product matrix $\mathbf{A}^6$ corresponded to the second soil sampling event of the season and represented mid-season growth and stasis. Matrix $\mathbf{A}^{10}$ corresponded to the third soil sampling event of the season, and matrices $\mathbf{A}^{10}$ and $\mathbf{A}^{11}$ represented reproduction and/or seed bank persistence, with some sampling locations completing their seed maturation and dispersal earlier than others. Generation of these selected product matrices $\mathbf{A}^{(h)}$ allowed the subsequent calculation of sensitivity and elasticity values that remained specific to each location and represented critical time periods in the plant's life.

Sensitivity and Elasticity of a Periodic Matrix

Sensitivity analysis of the population growth rates to changes in the (i,j) entries of **A** was performed using the following formula (Caswell 2001). The sensitivity matrix of **A** (known as $\mathbf{S_A}$) was calculated as

$$\mathbf{S_A} = \mathbf{v}\mathbf{w}^{\mathbf{T}} \tag{2}$$

where **T** is the matrix transpose and **v** and **w** are the dominant left and right eigenvectors, respectively, of matrix **A**. An intermediate calculation designated as Matrix **D** (Caswell 2001) was generated as the product of $\mathbf{B}^{11} * \mathbf{B}^{10} * \mathbf{B}^{9} * \ldots \mathbf{B}^{2}$; i.e., as in the definition of product matrix $\mathbf{A}^{1}$, but with the exclusion of the $\mathbf{B}^{1}$ matrix. The sensitivity matrix $\mathbf{S_B}$ was then calculated as

$$\mathbf{S_B} = \mathbf{D}^{\mathbf{T}}\mathbf{S_A} \tag{3}$$

To calculate the elasticity values (and once again using the first seasonal period of the calendar year as an example), each element in the original $\mathbf{B}^{(1)}$ matrix was divided by its corresponding value of λ (calculated for the periodic matrix product $\mathbf{A}^{1}$). The resulting integer was then multiplied by the same (i,j) element of the $\mathbf{S_B}$ sensitivity matrix, and the process repeated for all elements in the original $\mathbf{B}^{(1)}$ matrix. The elasticity values of λ with respect to the entries of $\mathbf{B}^{i}$ sum to 1 for each *i* (de Kroon 1986, Caswell and Trevisan 1994) and represent the proportional contribution of the matrix entries to population growth in each period of the matrix (Caswell and Trevisan 1994).

Use of product matrices $\mathbf{A}^{(h)}$ to calculate elasticities, as was done by McFadden (1991) and described in Caswell and Trevisan (1994), results in confounding of the relative contribution of each life stage as a result of matrix multiplication so that reproductive contribution, for instance, would not be restricted to the top matrix row (Caswell and Trevisan 1994).

Elasticity matrices were calculated in this study using 1) transition probabilities averaged across locations for each of 11 seasonal periods and years (total of 33 matrices) and 2) detailed matrices chosen as representative of five critical seasonal periods in the annual life cycle of *C.*

multicaulis (Table 4.2). Elasticity matrices were generated for those five periods and for each location and year combination, for a total of 165 matrices calculated.

The calculation of confidence intervals for population parameters such as λ requires the use of bootstrapping techniques (McPeek and Kalisz 1993) that were not performed for these data.

Estimated Time to Extinction

The estimated time to (stem) extinction was calculated for those location*year combinations with population growth rate $\lambda < 1.0$ using a formula modified from (Valverde and Silvertown 1997) as $t_e = \ln(0.01)/\ln\lambda$. (See Valverde and Silvertown (1997) for derivation). The assumption was made in this study that a population becomes virtually extinct when it drops to 1% of its initial above-ground population size, whereas the authors used a figure equal to 5% of the initial population size.

RESULTS

Overall Population Dynamics

Quadrats with the highest density of *C. multicaulis (*356 plants*)* were located at Blanca Wetlands (BW1 and BW2) and Russell Lakes (RL6), and 42 of the 72 total quadrats contained more than 200 individuals in each of the census years. In spite of an observed trend of increased *C. multicaulis* density between 1995 and 1997 (Table 3.2), there was only a marginally significant effect of year in a more formal statistical model with square-root transformations of density and including adjustment for the date and date*year interaction effects (Table 3.4. In June of 1995, there were 55 out of 66 quadrats with at least one *C. multicaulis* individual present; in June 1996, 56 out of 66 quadrats had at least one plant, and in June 1997, 54 out of 66 quadrats had at least one *C. multicaulis* individual (Table 3.1).

Analysis of Population Growth Rates

When transition probabilities were combined as arithmetic means across the 11 locations sampled in this study, and a single set of periodic matrices was analyzed for each census year, the annual average population growth rate was 1.92 in 1995, 1.38 in 1996, and 0.90 in 1997. Population growth rates calculated using detailed periodic matrices for each of 11 locations and 3 years ranged from $\lambda = 0.08$ to 10.11 (See Table 4.5), with the seven highest growth rates occurring in 1995 and 1996. Seventeen location x year combinations had λ greater than 1.0 and 16 location x year combinations had λ less than 1.0. Four locations had growth rates $\lambda > 1.0$ for all three census years (BW1, BW3, RL1, and RL7); four locations had growth rates $\lambda < 1.0$ for all three census years (RL3, RL4, RL6, and SLL3), and the remaining three locations (BW2, RL2, RL5) had a combination of expanding and declining population growth rates over the census period. Repeated measures analysis of variance indicated that there was a significant effect of the mean number of fruits per reproductive plant on (ln) population growth rate but only a marginally significant effect of year (Table 4.3). The effect of total plant density on (ln) population growth rate was non-significant. Reproductive plants in this study produced an average of between 1.35 and 23.55 fruits per plant, with an estimated 2.6 - 7.3 seeds per fruit. None of the soil characteristics had a significant effect on ln (population growth rate) after adjustment for the effect of year (Table 3.4).

Survivorship Curves

Survivorship patterns for *C. multicaulis* appear to fit a Type I curve (Figure 3.8) with 3-year mean survivorship to reproductive age ranging from 40.13% to 85.75%, depending on location (Table 4.6). Overall mean survivorship across years and locations was 59.53% and did not differ significantly between years or according to soil characteristics (Tables 3.26, 3.27). Macroplots with the highest growth rates did not necessarily have the highest survivorship, although locations with the two lowest rates of survival (RL6 and RL4) had among the lowest rates of population growth (Table 4.6).

Differences in the mortality rates of large versus small reproductive plants were not easily determined, since the small reproductive life stage only appeared at the very end of the growing season, just prior to senescence of the entire population. In general, mortality of reproductive plants was low except in plots subjected to mid-summer episodes of extreme drought or complete flooding.

Elasticity Matrices

Elasticity matrices were generated for 11 census periods using mean transition probabilities across locations for each year and are available from the author upon request. The variability in timing of both seedling emergence and seed production across locations resulted in the contribution of particular life stages to population growth rate being represented in multiple matrix periods, that increased the difficulty of matrix interpretation.

In order to more clearly track the importance of individual life stages in the population dynamics of *C. multicaulis*, a separate set of detailed elasticity matrices was generated for each of five selected life cycle periods (See Appendix 4.1) for each location and year. Interpretation of population elasticities focused on the contribution to overall population growth of seeds in the seed bank in early spring, and of large and small reproductive plants in late summer. Elasticity values of these life stages are presented here (Tables 4.5, 4.7) in summary form, with the complete detail of the 165 elasticity matrices available from the author upon request.

The proportional contribution of small reproductive plants to population growth in the late summer was minor in comparison to the proportional contribution of large reproductive plants during that time (Table 4.5). The mean elasticity of small reproductive plants was 2.43% (ranging from 0 - 12.41%) and the elasticity of large reproductive plants ranged from 40.94 - 99.99%, with a mean of 85.18% (Table 4.7).

The transient seed bank (ages 0-1) had by far the largest proportional contribution to population growth rate in the early spring of the seed ages measured, with a mean elasticity of 78.32% (Table 4.7). Mean elasticity from the seed bank ages 1-2 was 9.25% and from the seed bank ages 2-3 was 3.43%. The seed bank of ages 2-3 years contributed more than 10% to growth rate in 6 location x year combinations (locations BW2, RL3, RL4, and SLL3), all of which had growth rates under 1.0 (Table 4.5).

Correlations between population growth rate, soil characteristics, plant density, and elasticity measures (Tables 4.9 - 4.12) were calculated. The elasticity of large reproductive plants was positively correlated (with a marginally significant correlation) with elasticities from the transient (aged 0-1 years) seed bank but negatively correlated with elasticities from the persistent (both seeds aged 1-2 and 2-3 years) seed bank (Table 4.9). There was a negative (marginally significant) correlation between the youngest (transient) and oldest (persistent) seed bank elasticity. The elasticity of small reproductive plants was negatively correlated with population growth rate whereas the elasticity of large reproductive plants was positively correlated with growth rate (Table 4.10). In addition, locations with high plant density were associated with increased elasticities from small reproductive plants, although there was no relationship between plant density and elasticity from large reproductive plants (Table 4.11).

Soils of higher pH were associated with populations exhibiting higher elasticities from persistent seeds and lower elasticities from small reproductive plants (Table 4.12). Soils with higher moisture were associated with higher elasticities from small reproductive plants. Elasticities from large reproductive plants showed no significant relationship with any of the soil characteristics.

Locations BW2, RL3, RL4, and SLL3 showed considerable shifts in their seed bank elasticities over the three-year census period, either increasing or decreasing their reliance on the persistent (aged 1-3 years) seed bank for population growth (Table 4.13).

Estimates of Time to Extinction

When estimating the risk of "extinction" for a plant possessing a persistent seed bank, it is extremely useful to clarify whether one is speaking of the extinction of long-lived seeds in the soil (hereafter referred to as *seed bank extinction*) or simply the demise of above-ground plant growth (hereafter referred to as *stem extinction*). Three local populations of *C. multicaulis* were observed to undergo stem extinction during the period 1995-2000. Two populations were flooded at San Luis Lakes in 1995 and one was flooded at Blanca Wetlands sometime between summer 1996 and mid-summer 2000. No subsurface seed bank samples were taken at either site, and neither population contributed data to the analyses in this report. Populations flooded at San Luis Lakes apparently survived as seeds in the soil and became re-established by 1997 along the lake margin. It is not known whether the population flooded at Blanca Wetlands has undergone seed bank extinction as well.

Calculated estimates of the time to extinction (Valverde and Silvertown 1997) here represent the likelihood that the density of above-ground growth will become reduced to 1% of its current value. As λ approaches 1.0 the time to extinction increases exponentially. Fifteen locations are predicted to undergo this drastic reduction in density sometime in the next 1.8 to 33.8 years (Table 4.14), with populations at locations RL3, RL4, RL6, and SLL3 apparently the most vulnerable. Little is known about the likelihood of seed bank extinction at these locations. Density of the soil seed bank was measured just outside location RL6 and appears to be high in comparison to other sites sampled (Table 6.15), but the relationship between seed bank density and the risk of seed bank extinction is unknown for this species.

DISCUSSION

Overall Population Dynamics and Analysis of Population Growth Rates

Macroplots experiencing the highest measured population growth rates λ (Table 4.5) were typically comprised of low-density populations of large plants, often with high fecundity and occupying disturbed or perhaps newly colonized areas. However, not all sites with low plant density grew rapidly, as evidenced by the non-significant correlative relationship between population growth rate and plant density (Table 4.11). Location BW2 had a high population growth rate in 1995 ($\lambda = 4.094$) as well as a high density of *C. multicaulis* (509 plants total). The lowest population growth rate ($\lambda = 0.080$) was measured at a location (RL6) with plant density very similar to the above site (502 plants total).

The highest rates of population growth across all locations occurred in 1995 and 1996, and the lowest population growth rates occurred in 1997. Whether population growth might have been adversely affected by the cumulative effect of researcher presence or the presence of census flags is unknown.

Populations of *C. multicaulis* in this study appeared to vary spatially and temporally in their population growth rate (Table 4.5). Many populations of annual plants show between-year fluctuations in population growth rate, often as a result of changes in successional conditions, shifts to a faster or slower-growing life stage, or in response to changes in environmental conditions (Sarukhan and Gadgil 1974, Werner and Caswell 1977, Caswell 1978b, Bengstsson 1993, Pavlik 1994, Oostermeijer et al. 1996, Kephart and Paladino 1997). Growth rates found among 15 local populations of *Pedicularis furbishae* (Menges 1990) showed considerable temporal variability. Seven of the 15 local populations of *P. furbishae* had $\lambda > 1.0$ for two of the three study years and 4 of 15 populations had $\lambda < 1.0$ for two of the three study years. Growth rates averaged across location were 1.27, 0.77, and 1.02 respectively for each of the three years studied (Menges 1990).

It is not uncommon for populations of annual plants to grow at rates considerably higher than 1.0, with the detailed growth rates reported in this study (ranging from 0.080 to 10.115; see Table 4.5) being fairly typical of those previously reported for other annual species. Growth rates reported for *Ranunculus bulbosus* ranged from 0.09 - 8.17 (Sarukhan and Gadgil 1974) and for *Phlox drummondii*, between 0.43 - 34.06 (with 25% of populations showing λ between 9.0 and 12.0) (Schmidt and Levin 1985). In the only known population study of another *Cleome* species, growth rates of 1.118 were reported for populations of *Cleome droserifolia*, a long-lived perennial native to the mideast with high seedling mortality and possessing a persistent seed bank (Hegazy 1990).

This study of *C. multicaulis* was not designed to allow the comparison of population growth rates with and without the presence of the persistent seed bank because its detailed time steps required accounting for the fates of seeds in the soil. In the only previously conducted study to comprehensively examine the effect of a seed bank on population growth (Kalisz and McPeek 1992), population growth rates using an annual time step and with the seed bank life stage were λ = 1.80 and 0.41 for the two years respectively, whereas population growth rates calculated without the seed bank declined to 1.72 and 0.30, respectively.

Periodic matrices were analyzed in this study at two different levels of detail to yield population growth rates: using mean transition probabilities across locations for each year, and using the full detail of transition probabilities for each of 11 locations and 3 years. While the use of mean or pooled matrices to describe population dynamics over multiple years and locations is fairly common (Law and Edley 1990, Charron and Gagnon 1991, Bengstsson 1993, Bastrenta et al. 1995, Ehrlen 1995), describing a population in terms of its mean transition probabilities may yield misleading results by obscuring details and making the assumption that heterogeneity between locations or years is unimportant (Huenneke and Marks 1987, Horvitz and Schemske 1995, Oostermeijer et al. 1996). Matrices built using mean transition probabilities across locations did not effectively distinguish periods during the life cycle of *C. multicaulis* during which particular life stages might make important contributions to population growth.

Populations with the two highest growth rates (BW196 with $\lambda = 10.115$ and BW395 with $\lambda = 8.985$) were measured in macroplots where the oldest portion of the seed bank contributed nothing to overall population growth rate (Table 4.5). Populations with the three lowest growth rates in this study also had zero elasticities from the oldest portion of the seed bank, although this was likely due to extremely low seed cage emergence at these locations. Macroplots with population growth rates less than 1.0 tended to have higher elasticities from the persistent portion of the seed bank than did locations with high growth rates (Table 4.5).

Silvertown et al.'s compilation of 45 herbaceous perennials (Silvertown et al. 1993) found that species with a persistent seed bank were in almost all cases characterized by high rates of population growth (although repeated measures of population growth were not obtained). Existing matrices in that study were in many cases modified to correct for (eliminate) the presence of the seed pool as a life stage when in fact seeds germinated prior to the first year anniversary of seed production. The effect of this error would have been to underestimate population growth rate λ, to the extent that an artificial seed pool delays recruitment. After making matrix modifications, the authors reported population growth rates ranging from 0.883 to 11.815, with 36 of the 45 perennial species experiencing population growth rates $\lambda > 1.0$. Of the 13 species with a persistent seed bank, the lowest reported population growth rate was 0.996 and the remaining 12 species had $\lambda > 1.0$ (Silvertown et al. 1993).

Analysis of Elasticity Values

Elasticities are calculated as the proportional contribution to population growth rate from various life-history transitions. An interpretation of elasticity values may be illustrated as follows: If the elasticity value of a particular matrix element is 0.5, then a 10% change in that matrix element will result in a (0.5 x 10%) 5% change in the population growth rate λ (Ebert 1999). The elasticity function is not linear, however (Ebert 1999) and so extrapolation is limited to small changes in life-table or matrix values.

Elasticity analysis can be used to reveal the importance of a particular life stage, to suggest transition probabilities of a matrix that may be artificially manipulated, and to analyze the effects of various management strategies. Elasticity does not reveal information regarding the proportional contribution of each stage in explaining variation in the population growth rate, λ (Horvitz et al. 1997); emphasis mine). If a particular matrix entry is zero (i.e., that transition does not occur), then the corresponding measure of elasticity will be zero (Horvitz et al. 1997).

Elasticity values do not indicate the relative sensitivity of life-history transitions to environmental perturbations. Population growth rates may be greatly affected by environmental perturbations to a life stage with only a small elasticity value (Silvertown et al. 1993). Population growth may be limited more by a life stage with great natural variation than by the stage with the highest elasticity value (Schemske et al. 1994).

Seed bank elasticities in this study represented the proportional contribution of the persistent portion of the seed bank to population growth rate in the season of seed germination and allowed identification of the relative importance of newly germinable versus persistent *C. multicaulis* seeds in early spring population growth. Elasticities were considered to be of significant importance if elasticity values are > 10% (Caswell 1989).

Elasticity values (Table 4.5) from the non-persistent portion of the seed bank (seeds ages 0-1 years) appeared to be greater for faster growing populations, whereas elasticities from the persistent portion of the seed bank (seeds aged 1-2 years and 2-3 years) appeared greater for populations experiencing low rates of growth. This suggests that rapidly growing populations may be relying for their growth on the transient portion of the soil seed bank rather than seeds that remain dormant, although the success of persistent seeds in populations with low growth rates may also depend on soil conditions such as pH. Correlation analysis provides preliminary evidence that persistent seeds found in soils of high pH (averaged across quadrats for each location) are not diminished in their ability to contribute to population growth (Table 4.10). Soils of high pH do not therefore appear to present an inhospitable environment for seeds of *C. multicaulis* either of age 2-3 years or 1-3 years combined (Table 4.12).

The association between populations with high growth rates and larger elasticities from large versus small reproductive plants (Table 4.10) reinforces the field observation that rapidly growing populations consisted primarily of low-density plants of large size. Rapidly growing populations showed no correlative relationships with soil characteristics, although sites with higher elasticities from small reproductive plants tended to have higher plant density, lower soil pH and higher soil moisture (Table 4.11). Sites with higher plant density were in turn associated with soils of lower soil salinity (Table 4.11). To the extent that microsite characteristics have the effect of shifting the balance between the relative proportions of large and small reproductive plants in a population, those edaphic features would have the potential to influence the growth rates of *C. multicaulis* populations in this study.

Mean elasticity in this study from seeds of *C. multicaulis* aged 1-2 years was 9.25% and from seeds aged 2-3 years was 3.43% (Table 4.7). One of the few studies to examine seed bank elasticities across species (Silvertown et al. 1993) found an average seed bank elasticity of 6.9% without being able to separate seeds of various ages. Studies of *Collinsia verna* (Kalisz and McPeek 1992, 1993) found that elasticities of seed bank life stages when population growth rate was $\lambda = 1.80$ were 4.3% for seeds persisting 1 year, 0.1% for seeds persisting 2 years, and 0.0008% for seeds persisting 3 years in the soil. When population growth rates dropped to $\lambda = 0.41$ in the second year of study, elasticities rose to 17.5% for seeds persisting 1 year, 2.4% for seeds persisting 2 years, and 1.1% for seeds persisting 3 years (Kalisz and McPeek 1992). Because her study utilized an annual projection interval, transition probabilities for non-persistent seeds were reflected as the probability of a seed germinating and becoming an adult the next year, rather than being included as part of the seed bank life stage.

In this study of *C. multicaulis*, there were several locations (BW2, RL3, RL4, and SLL3) where seed bank elasticities from seeds aged 2-3 years shifted during the three-year census period (Table 4.13) but examination of site characteristics failed to reveal any particular pattern that might explain these shifts. At location BW2, population growth rate λ declined from 4.094 in 1995 to 0.41 in 1996 and 0.37 in 1997, with a corresponding shift in elasticity from the seed bank (seeds aged 2-3 years) from 0.39% in 1995 to 15.65% in 1996 and 13.38% in 1997. Plant density remained high throughout, soil salinity remained the same, soil pH declined and there was a slight increase in soil moisture across the study period.

At location RL3, seed bank elasticity (ages 1-3 years combined) increased dramatically from 11% in 1995 to 59% in 1997. Plant density in this macroplot shifted from 98 in 1995 to 172 in 1996 and then down to 35 total plants in 1997. Soil pH increased with plant density but (somewhat atypically) soil Ec remained essentially unchanged. At location RL4, emergence from the experimental seed cages was extremely low (Table 6.5) and although plant density increased in 1997, seed bank elasticities went to zero. At location SLL3, reliance on the persistent seed bank increased, although the three-year change in plant density was erratic at this site (18, 163, and 5 plants total in years 1995-97 respectively). The 1996 increase in density corresponded here with a decrease in soil salinity (but a slight increase in soil pH) as well as a decrease in the number of fruits per reproductive plant.

Although it was not completed in this study due to the complexities of periodic matrices, one method of gaining further insight into shifts in elasticity and their ecological relevance is to conduct so-called "numerical perturbation analysis" (Horvitz et al. 1997). This technique, that alters transition probabilities and examines the resulting elasticities, has been used to simulate differences in disturbance regimes (Ebert 1999), herbivory (Ehrlen 1995, Lesica 1995) harvesting (Charron and Gagnon 1991), pollinator limitation and the importance of clonal reproduction (Bierzychudek 1982), and reduced mortality due to targeted management practices (Crowder et al. 1994). Perturbation analysis of this sort may also be used to examine a variety of specific, biologically interpretable, simultaneous changes in multiple population vital rates (Horvitz et al. 1997).

As an alternative technique, population growth rates may be set equal to 1.0 via calculation and elasticities examined under the resulting conditions of population stability (Horvitz et al. 1997). Extinction thresholds, the minimum starting number of individuals needed to rebuild a growing population, and estimation of the maximum sustainable rate of harvest are among the approximations that may be determined (Nantel et al. 1996).

For particular species, growth (Silva et al. 1991, Ehrlen 1995) and survival (Kephart and Paladino 1997) may be proportionally more important contributors to population growth than seed production and fecundity (Bengstsson 1993, Bastrenta et al. 1995). Although comparisons in elasticities across taxa are possible, these should consider the sensitivity of elasticity values to the specifics of life stage selection and inconsistencies in the categorization of particular stages (Silvertown et al. 1993, Oostermeijer et al. 1996, Ebert 1999).

Analysis of the spatial and temporal variation in elasticities is seldom undertaken (Oostermeijer et al. 1996) and was not conducted in this study. Some studies have found considerable between-year variation in elasticities (Horvitz and Schemske 1995) whereas others have found that variation in elasticities is of less significance than the temporal and spatial variation in matrix elements (Ehrlen 1995, Oostermeijer et al. 1996). There may be considerable within-species (Silvertown et al. 1993, Ehrlen 1995, Horvitz and Schemske 1995, Oostermeijer et al. 1996) and/or between-habitat variation in elasticities (van Groenendael et al. 1988).

Survivorship Curves

Although survivorship curves generated in this study appear to follow at Type I pattern (Figure 3.8), this should not be considered typical of all annual species under study. Plants that have an annual life cycle (as defined in terms of above-ground growth) may have survivorship curves that follow either a typical Type I, Type II, or Type III pattern (see reviews by (Buchele et al. 1991, Morgan 1995b), with considerable variation across species. In a study of winter annuals, three of ten species showed a Type I survivorship curve, five of ten had a Type II curve, and the remaining two species followed a Type III survivorship pattern (Watkinson 1981). The standardization of survivorship curves should allow for comparisons across species or life habit, although generalizations are difficult to make and the variability in such measurements makes comparisons difficult.

Type I survivorship patterns have been suggested as more common in species with low seed production (e.g., 1.7-3.8 seeds per plant), although seed production in *C. multicaulis* appears to be higher than this (Table 4.6). Type III survivorship curves may be more typical for species producing 300-400 seeds per plant (Watkinson 1981). A single annual species may follow several different survivorship curve patterns during its life cycle (Leverich and Levin 1979). Survivorship curves for cryptic life cycle stages such as a soil seed bank are logistically challenging to develop, and it was not possible to construct a seed survivorship curve in this study.

Survivorship of particular life stages may be correlated with increases in precipitation, and relentless drought often results in complete pre-reproductive mortality of annual species (Klemow and Raynal 1983). Survivorship patterns may vary between types of habitat for a single species as a result of variability in environmental conditions (Kephart and Paladino 1997).

Estimates of Time to Extinction

Several documented stem extinctions occurred in *C. multicaulis* populations during the period of study, but the frequency with which seed bank extinction occurred in this study is unknown. Essentially nothing is known about the relative frequency and timing of stem and seed bank extinction in natural populations. Unanswered questions include: How often does a population of stems go extinct while the seed bank remains? What ecological factors might cause the selective demise of only above-ground growth? Are there extrinsic or intrinsic factors that might result in the simultaneous extinction of both stems and seed banks? How might these phenomena differ across various plant life histories (e.g., woody versus herbaceous, annual versus perennial) and in various habitats?

In this study, populations at locations RL3, RL4, RL6, and SLL3 appeared to have the greatest likelihood of undergoing stem extinction in the next several years (Table 4.14). All populations are potentially vulnerable to stem extinction if water levels increase significantly. Water levels at site RL6 are raised for waterfowl management purposes and populations at that location may be in danger of becoming flooded. Both high soil salinity and rising water levels threaten the population at site RL4. Location SLL3 is not likely to be threatened by rising water levels (the nearby basin hardly ever remained filled for any length of time during the study period) but may be threatened by high soil salinity.

Sites at Mishak Lakes (that experienced complete mortality of seed cages and were not included in the population biology analysis) are vulnerable to trampling by cattle and may be subject to periodic soil dessication. Site BW2 is just on the edge of Mallard Lake at Blanca Wetlands and may be vulnerable to rising water levels that were observed in the fall of 2000. Site RL2 may also be vulnerable to water-level rise from a nearby wetland basin, although this site is more likely to undergo drying during mid- to late-summer than is the basin at BW2.

Growth rate is not always an absolute indicator of a species' fate. Populations may be able to tolerate a single year with $\lambda < 1.0$ if conditions improve early in the subsequent year (Carey et al. 1995). On the other hand, populations showing positive growth rates may still carry some level of extinction risk under conditions of even moderate environmental stochasticity (Menges 1992). If environmental stochasticity is autocorrelated through time then the effects on time to extinction will be difficult to predict (Tuljapurkar 1989). Temporal variability in population dynamics has been argued to increase a population's tendency to become extinct (Pimm et al. 1988) but population variability may in fact contribute little to the probability of extinction if populations unlikely to ever go extinct are assessed differently from those in danger of disappearing (Tracy and George 1992).

Modeling Stochasticity and the use of Product Matrices in Previous Studies of Population Biology

Previous studies using deterministic matrix models such as the one in this study have simulated stochasticity in one of several ways (Burgman et al. 1993). Matrices representing the overall dynamics of a population in "good" or "bad" years were selected either randomly or with particular frequency in order to simulate variation in demographic success as a whole (Bierzychudek 1982, Menges 1990). A favorable year was thus favorable for all life stages (Menges 1990, Burgman et al. 1993). The frequency of different environmental states and the degree of autocorrelation between states (positive or negative) may have significant effects on models such as this (Tuljapurkar 1989, Aberg 1992). As an alternative method, if vital rates are likely to vary independent of one another, then a method that selects elements of the vital rates independently may create a more appropriate stochastic model (Lande and Orzack 1988) but has the drawback of being considerably more computer-intensive, however (Burgman et al. 1993).

Product matrices such as the ones in this study have not been used extensively in the analysis of plant population dynamics. An early study (Huenneke and Marks 1987) calculated annual matrices for each of two locations and each of three years to describe the growth of *Alnus incana* populations, and generated both a matrix using mean transition probabilities across years and a product matrix using matrix multiplication to combine 3 years' worth of annual matrices. The product matrix described population dynamics under the assumption that the variations observed every 3 years would be repeated in a 3-year cycle. To facilitate comparisons between the mean and product matrices, transition probabilities in the mean matrices were raised to the third power to represent three consecutive years of the mean transition rates. The sensitivity matrix was calculated according to Caswell's original formula (Caswell 1978a) rather than the formula subsequently developed to accurately reflect periodic (product) matrices (Caswell and Trevisan 1994).

More recent analyses using periodic product matrices have been developed by Caswell (Caswell and Trevisan 1994, Caswell 2001). Although these discussions extend basic matrix theory to the calculation of sensitivity and elasticity values for periodic matrices, they do not offer advice as to the feasibility of calculating for periodic matrices such commonly used matrix techniques as population projections, the stable (cyclical) stage distribution, log-linear analysis of the variability in vital rates, or the calculation of damping ratios.

In this study, elasticities were used to estimate the proportional contribution of seeds of different ages to reproductive efforts in the early spring, to determine the relative importance of large versus small reproductive plants to overall population growth, and to examine other details of the life stages of *C. multicaulis*. populations. Elasticities of periodic matrix models may be used to indicate at what times of the year growth, survival, and reproduction are most important. The elasticity values of λ with respect to the entries of $\mathbf{B}^i$ sum to 1 for each i (Caswell and Trevisan

1994), with the result that sensitivity of λ to one vital rate at one period in the life cycle may be affected by changes in other rates at other periods in the cycle (Caswell and Trevisan 1994).

Evidence of Density Dependence in Populations of *C. multicaulis*

In this study, there was some evidence of density-dependent reductions in the number of fruits per reproductive plant, although there was no direct and significant correlation between plant density and population growth rates (Table 4.11) Individuals in a population are subject to density-dependence if their average fecundity, reproductive success, or chance of mortality will change as a function of the average population density (Ginzburg et al. 1990). The relative importance of density-dependent factors in population regulation continues to provoke discussion among ecologists (Andrewartha and Birch 1954, Murray 1982, Ginzburg et al. 1990, Rees et al. 1996) and density-dependent factors should not be assumed to have significant importance in all plant populations (Bazzaz 1996).

Most stage-based matrix models do not explicitly account for density-dependence and therefore make the assumption that it does not significantly impact vital rates (Werner and Caswell 1977, Pinero et al. 1984, Crouse et al. 1987, Aplet et al. 1994, Schemske et al. 1994), although density effects may be embedded in existing matrix elements (Nantel et al. 1996). Simulations have shown that population models constructed without adjustments for density-dependence will produce conservative estimates of extinction risk (Ginzburg et al. 1990).

Studies have indicated that there may be advantages to living both at low densities (Menges et al. 1986, Mace and Kershaw 1997) and with closely spaced conspecific neighbors (Kunin 1992, Morgan 1995a, Roll et al. 1997). Any relationship between population density and vital rates may dissipate as densities decline past a certain point (Fischer and Matthies 1998). Plants may have the ability to absorb some of the effects of crowding through plasticity (Bazzaz 1996).

The presence of a persistent seed bank with a low germination fraction each year makes the investigation of density-dependence more complex. The operation of density-dependence in below-ground life stages is difficult to document (Cabin et al. 1997) and was not examined in this study. As seed bank "crowding" increases, emergence from the seed bank might be affected. Density-dependence might have different effects on seeds of different age, and its effects might be of differing magnitude and form between above-ground and seed bank life stages. Further analytical tools such as path analysis might yield additional information regarding the relationship between population growth rate, plant density, and the mean number of fruits per reproductive plant in *C. multicaulis* study populations.

Spatial Structuring in Populations of *C. multicaulis* in the San Luis Valley

The regional structure of local populations of *C. multicaulis* in the San Luis Valley appears to be best described as a remnant population system, at least during the time period of this study. Evidence that local populations can resist extinction in the seed stage comes from the recovery of San Luis Lakes populations from 1995 flooding events. Further examination of subsurface seed populations would be necessary to determine the extent to which local populations that have decreased in above-ground growth may be at risk of seed bank extinction as well.

The spatial extent of *C. multicaulis* local populations was determined exclusively from visual inspection of above-ground growth, and additional seed bank samples will be needed to more accurately determine the spatial distribution of seed bank populations. Measurements of seed bank density, population growth rate, and plant density did not reveal any consistent patterns in this study (Table 4.11, 6.15), although this may be in part because seed bank samples were sometimes taken as much as 10 m from the location of macroplot census quadrats. Populations of *C. multicaulis* may cycle between periods of above-ground abundance and below-ground persistence. Seeds in the soil seed bank have been shown to persist for at least 2 years, and although only a small fraction of the

seed bank germinates each year (Table 6.5) the conditional probability of persistence of the 2-3 year old seeds tested in this study was essentially identical to that of the 1-2 year old seeds.

The study described here was hampered in its ability to detect spatial changes in population density, location, and spatial dimensions because of the use of permanently located census quadrats (Sutter 1996). Detailed mapping of plants on a scale of approximately $1000m^2$ would allow the determination of spatial changes in population structure over a multi-year period.

Remnant population dynamics have been described as a variation of source-sink interactions in which populations contribute migrants by persisting through time rather than dispersing through space. The extent to which populations of *C. multicaulis* might exhibit a combination of (spatial) source-sink dynamics and (temporal) remnant population dynamics is unknown. Long-term observations of locations in close proximity to one another with variability in growth rates (such as sites RL6 and RL7) might shed light on the prevalence of source-sink spatial dynamics in this species.

Spatial patchiness in the plant density of *C. multicaulis* has not been conclusively determined in this study to be the result of soil characteristics measured, since the study did not assess habitat conditions in sites where the plant was absent. Causes of above-ground extinction and sites where high rates of above-ground extinction might occur have not been identified for *C. multicaulis* in the San Luis Valley. Other studies have found that wet habitats may be favorable for plant growth, supporting higher rates of plant establishment, but also may have higher rates of extinction due to catastrophes (Menges 1990). Likely causes of stem extinction of *C. multicaulis* include extremes of soil moisture and prolonged flooding, encroachment by tall perennials, increases in soil salinity of sufficient duration, and possible competition from invasive species. Possible causes of seed bank extinction remain largely unknown.

Plant Metapopulation Dynamics

Recent studies of plant population dynamics (Perry and Gonzalez-Andujar 1993, McEachern et al. 1994, Valverde and Silvertown 1997) have often adopted a metapopulation approach in recognition of the importance of habitat patches and their interaction, but perhaps without the necessary empirical evidence to select metapopulation models as the most compelling of several alternative descriptive paradigms. Examination of the metapopulation approach is necessary in order to identify limitations in its applicability for species with a persistent seed bank and to provide support for the belief that metapopulation structure is of minor importance in *C. multicaulis* population dynamics in the San Luis Valley.

The original metapopulation model (Levins 1969) was developed with the purpose of provoking extinction of crop pests on a regional scale by reducing between-patch migration below a certain threshold. The model has since been adapted for conservation biology (Hess 1996) and expanded in complexity (Hanski and Gilpin 1991), increasing its popularity as a theoretical backdrop against which to place a wide variety of empirical data for both animals and plants (Husband and Barrett 1996). Metapopulations have been described as a set of local populations that interact via dispersing individuals, although not all local populations in a metapopulation neccessarily interact directly with every other local population (Doak and Mills 1994). A key feature of metapopulation structure is that not all suitable habitats are occupied simultaneously and habitat patches will remain vacant for a time (Hanski 1996). Metapopulation persistence is promoted by asynchrony in colonization and extinction dynamics (Doak and Mills 1994). Uncertainty remains for real populations of both plants and animals as to the level of interconnectedness between local populations as well as the actual importance of local population extinction (Harrison 1991, 1994).

Although it seems clear that the population dynamics of some organisms may fit nicely into the metapopulation paradigm (Menges 1990, Hanski 1999), there are conceptual and practical difficulties with adapting metapopulation theory to the study of plants with a persistent seed bank (Husband and Barrett 1996). One argument used to support the description of *Primulus vulgaris* as possessing metapopulation structure was the lack of a persistent seed bank in that species (Valverde and Silvertown 1997). Recognition of subpopulation extinctions of *Mimulus guttatus* (a species described as "occasionally" forming metapopulations) was apparently based on the absence of above-ground growth, although seeds of this species may persist 2-3 years in the soil (Vickery 1990). Plant features other than a seed bank that may complicate the use of animal-oriented metapopulation models (Hanski and Gilpin 1991) include restricted and localized dispersal, the (often very) long life spans of some plants that complicates observations of colonization and extinction, and sporadic seedling recruitment (Eriksson 1996, Husband and Barrett 1996).

Few empirical studies have attempted to untangle the interdependence of within-population and metapopulation processes in order to determine their relative importance (Kadmon and Shmida 1990, Burgman et al. 1993, Schemske et al. 1994), and few descriptions of potential methods to analyze populations using both matrix and metapopulation models have been published in the literature (Nations and Boyce 1997). When cross-disciplinary analysis is attempted, transition matrices may be built to represent population dynamics of each local population. These are then entered as submatrices in a metapopulation matrix that incorporates rates of migration, survival, and reproduction (Horvitz and Schemske 1986, Menges 1990, Akcakaya and Ginsburg 1991, Caswell 1991, Price and Gilpin 1996, Valverde and Silvertown 1997). Menges simulated metapopulation-level stochasticity using matrix selections (Bierzychudek 1982) and added a second level of stochastic effects by modeling the catastrophe-driven extinctions and recolonizations of multiple local populations (Menges 1990).

Source-Sink Population Dynamics

When local populations occupy habitats that vary considerably in environmental conditions and resource distribution, one theoretical prediction is that substantial differences in birth and death rates among populations may be attributed to so-called "source" and "sink" dynamics (Pulliam 1988, Rhodes and Odum 1996). Source populations are described as a "reservoir" or long-term refuge where growth rates are always positive and emigration exceeds immigration (Hanski 1996, Pulliam 1996). Sink populations have negative growth rates, are maintained by dispersal, and will be substantially reduced in size or go extinct without immigration. Once source populations reach a maximum size of breeding individuals, directed dispersal is predicted to occur from the source to the sink (Pulliam 1996).

Direct evidence for source-sink populations in plants is sparse and lacking in experimental evidence, although some anectdotal evidence exists (Keddy 1982, Hubbell and Foster 1987, Kadmon and Shmida 1990, Pulliam 1996). Sink populations may represent habitats where species are present at high densities due to migration from nearby sources, even where the conditions are unfavorable (Pulliam 1996, Hanski 1999). The frequency with which directed dispersal (e.g., from source to sink) is likely to occur in plants is unknown (Eriksson 1996, Hanski 1996) but forms a critical component of source-sink theory.

The source-sink paradigm is sometimes used to predict the suitability of habitat patches by combining measurements of population growth rates λ with population density (Pulliam 1996). Habitat patches where λ substantially exceeds 1.0 for a wide range of densities may be predicted to represent prime conditions, whereas marginal habitat patches are predicted to occur where only very low density populations grow at rates in excess of 1.0 or where environmental stochasticity causes the population growth rate in some years to dip below 1.0. Unsuitable habitat is predicted to occur in patches where population growth rates are less than 1.0 even at very low densities.

There was no clear relationship in this study between population density and growth rates of *C. multicaulis* (Table 10). Locations in this study that might be considered to be prime habitat under the above categorization include BW1, BW3, RL1, and RL7 (Table 3), and unsuitable habitat patches might include SLL3 and RL4. Because this habitat assessment depends on above-ground plant density rather than incorporating some measure of seed bank habitat suitability, however, it is likely to overemphasize the spatial patchiness of habitat suitability and under emphasize the change in habitat conditions over time.

Remnant Population Dynamics in Plants

Remnant populations may be considered a variation of source-sink population dynamics (Pulliam 1988), where sources and sinks are related temporally rather than spatially (Eriksson 1996). Populations "tolerate" times when the high quality habitat becomes low quality and persist in time rather than space, resisting extinction by surviving as only a single life stage under what may be restrictive environmental conditions (Klinkhamer et al. 1987, Venable and Brown 1988, Rees and Long 1993). (Eriksson 1996). There is some evidence that long-lived species with clonal reproduction or a persistent seed bank will tend to form remnant populations, whereas short-lived, highly habitat-specialized plants with good dispersal will tend to form metapopulations (Eriksson 1996).

Although local remnant populations may have growth rates $\lambda < 1$, life cycle characteristics (such as a persistent seed bank) that buffer unfavorable environmental conditions and variability (Kalisz and McPeek 1993, Horvitz and Schemske 1995) are predicted to increase the time to extinction long enough to outlast successional changes until they become favorable for growth once again (Eriksson 1996).

One potential difficulty with the remnant model of population dynamics is that habitat is characterized either as "high-quality" or "low-quality" overall, whereas niche requirements that constitute "high-quality" habitat for above-ground growth may or may not be the same as what comprises favorable habitat for below-ground life stages. Also undefined is the expected response of populations to habitats in transition between high and low quality extremes.

The cause of habitat decline may impact the time period during which patches remain unsuitable for recolonization. If local population extinctions occur because of habitat destruction or the invasion of exotic species, patches that are now unoccupied may not be immediately suitable for recolonization. Temporal habitat changes may be more unpredictable than habitat differences arising from the spatial distribution of habitat patches (Pulliam 1996). For a species with a persistent seed bank it may be particularly difficult to predict when recolonization might occur, since re-establishment may depend more on habitat becoming suitable for dormancy release and seed germination than on the return of habitat suitable for above-ground growth (Hess 1996, Baskin and Baskin 1998).

It seems likely that many species have both local and regional population dynamics (Husband and Barrett 1996) that may be described variously as metapopulation, source-sink, or remnant population structures. Single species, particularly those that are long-lived, may exhibit elements of metapopulation, source-sink, and remnant population dynamics to a varying degree over their lifespan (Eriksson 1996). In order to examine remnant population structure, re-emergence (from dormant seed) and re-establishment (from dispersal) must be distinguished as unique ecological phenomena. Below-ground seed movement and mortality must be quantified and differentiated from extinguishment of above-ground growth. Remnant population structures (or some combination of metapopulation, source-sink, and remnant population dynamics) nevertheless hold the most promise for identifying ecologically relevant population processes for many plant species with the capability to persist over time.

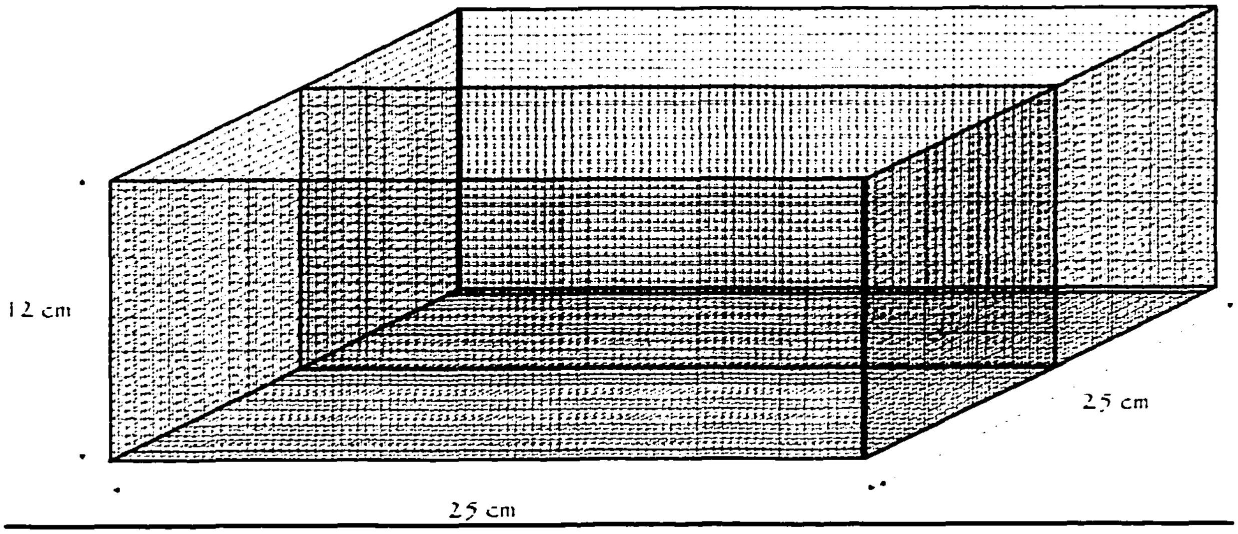

FIGURE 4.1 **Diagram of Seed Cages Used in Multi-Year Field Experiment to Assess the Fates of Seeds in the Soil**

TABLE 4.1 Example Transition Frequency Table Used in This Study (after Caswell 1989), Time Step is Two Weeks (during growing season) Above-ground Growth Only

	6/16/96 to 7/03/96		State (t)		small	large	
		births	seedling	juvenile	reproductive	reproductive	TOTAL
	seed	0	0	0	0	0	0
Fate (t + 1)	seedling	10	841	0	0	0	851
	juvenile	0	63	0	0	0	63
	small reproductive	0	0	0	0	0	0
	large reproductive	0	5	5	0	0	10
	deaths	0	29	0	0	0	29
	TOTAL	10	938	5	0	0	

913 + B - D = 924

Beginning and Ending Plant Census Figures were reconciled as
Beginning Census (913) + B(10) - D(29) = Ending Census (924)

Seed Bank Transition Probabilities were added later as extra columns and rows on the transition frequency table and resulting matrix.

Corresponding Transition Matrix (Above-ground Growth Only)

$$\begin{array}{ccccc} 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.100 & 0.897 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.067 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\ 0.000 & 0.005 & 0.100 & 0.000 & 0.000 \end{array}$$

6/16/96 to 7/03/96

Transition Probabilities were calculated as
0.897 = 841/938
0.067 = 63/938
0.100 = 10/10 and 5/5
0.005 = 5/938

TABLE 4.2 Schedule of Matrix Time Steps, Ecological Events, and Soil Sampling Events

Time Period	Ecological Event(s) and Matrix Entries Made	Time Step Duration	Ending Dates of Time Step (Approx.)
1	Overwinter seed survival Seedbank transition probabilities No above-ground census transitions	Approx. 7 months	mid-April
2	First soil samples taken First above-ground census figures used to estimate seedling emergence	2 weeks	May 3-7
3	Second above-ground census taken	2 weeks	May 17-21
4	Third above-ground census taken	2 weeks	May 31-June 2
5	Fourth above-ground census taken	2 weeks	June 13-16
6	Second soil samples taken Fifth above-ground census taken	2 weeks	June 27-30
7	Sixth above-ground census taken	2 weeks	July 10-14
8	Seventh above-ground census taken	2 weeks	July 24-28
9	Eighth above-ground census taken Earliest seed maturation (1-2 locations)	2 weeks	August 6-10
10	Third soil samples taken Ninth above-ground census Seed maturation (most locations)	2 weeks	August 20-24
11	Final above-ground census Seed maturation (remaining locations) Seed bank "birthdays" (ages increased)	2 weeks	September 3-7

TABLE 4.3 **Summary of Repeated Measures Analysis of the Effect of Year, Number of Fruits Per Reproductive Plant, and Density of *C. multicaulis* per Quadrat ($1600cm^2$) on Population Growth Rate (ln)**

Model: ln (Population Growth Rate) = Year + Mean Number of Fruits per Reproductive Plant + Density of *C. multicaulis*

Random Effects: Location, Year*Location

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source Of Estimated Variation (Random Effects)**
ln (Population Growth Rate)	Year	0.0806*	Location to Location
	Number of Fruits per Reproductive Plant	0.0169**	
	Density of *C. multicaulis* per Quadrat ($1600cm^2$)	0.2490	

** $p < 0.05$
* $p < 0.10$

TABLE 4.4 **Summary of Repeated Measures Analysis of the Effect of Soil Characteristics (Across Dates and Quadrats) on Population Growth Rate (ln) After Adjustment for the Effect of Year**

Model: ln (Population Growth Rate) = Year + Soil pH + Soil Conductivity + Soil Moisture

Random Effects: Location, Year*Location

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Population Growth Rate (ln)	Year	0.1086	Location to Location
	Soil pH	0.4281	
	Soil Conductivity	0.6307	
	Soil Moisture	0.2877	

** $p < 0.05$
* $p < 0.10$

TABLE 4.5 **Population Growth Rates, Mean Density of *C. multicaulis* per Location (Across Quadrats and Dates), Number of Fruits per Reproductive Plant, and Growth Rate Elasticities of Seed Bank Ages 0-1, 1-2, and 2-3 Years and Reproductive Life Stages (Large and Small Reproductive Plants)**

Sorted by Location and Year

Plant Density	Fruit Per Repr. Plant	Loc	Year	Growth Rate λ	Elasticity Seeds 0-1yr	Elasticity Seeds 1-2yr	Elasticity Seeds 2-3yr	Elasticity Small Repr. Plant	Elasticity Large Repr.Plant
183	12.77	1	1995	4.754	99.99	0.01	0	0	99.9
171	12.98	1	1996	10.115	99.85	0.05	0	0	99.8
513	6.13	1	1997	3.041	99.34	0.66	0	0	99.2
509	2.95	2	1995	4.094	96.98	2.63	0.39	1	96.37
594	3.35	2	1996	0.406	59.81	24.54	15.65	1	58.97
686	2.94	2	1997	0.363	66.45	20.17	13.38	9.27	57.19
107	22.28	3	1995	8.985	95.08	4.91	0	0	95.08
574	3.08	3	1996	1.901	86.81	13.19	0	0.17	86.64
181	4.59	3	1997	1.520	82.46	17.54	0	1.75	80.71
220	3.38	4	1995	1.199	89.67	10.33	0	0	89.67
74	7.55	4	1996	3.848	99.42	0.58	0	0	99.42
394	4.16	4	1997	3.076	99.03	0.97	0	1	98.26
135	3.52	5	1995	1.652	95.28	4.7	0.02	0.04	95.24
152	4.86	5	1996	2.354	98.05	1.93	0.02	2.05	95.99
316	2.37	5	1997	0.815	86.97	12.93	0.09	12.41	83.61
98	7.52	6	1995	0.289	88.92	6.49	4.59	0	88.92
172	9.49	6	1996	0.979	95.9	2.88	1.22	2.5	93.4
35	23.55	6	1997	0.296	41.08	34.51	24.52	0.14	40.94
78	5.92	7	1995	0.650	67.19	19.52	13.29	0	67.19
44	3.27	7	1996	0.159	63.51	36.49	0	2.55	60.96
158	1.68	7	1997	0.085	1	0	0	1.26	98.74
13	3.50	8	1995	0.366	92.83	7.17	0	0	92.83
44	10.68	8	1996	3.252	98.75	1.25	0	0	98.74
87	9.60	8	1997	1.246	96.03	3.97	0	0.46	95.56
307	4.10	9	1995	0.873	1	0	0	3.9	96.1
229	1.65	9	1996	0.124	88.18	11.82	0	11.1	77.07
502	1.69	9	1997	0.080	80.46	19.54	0	10.06	70.4
286	2.60	10	1995	3.510	1	0	0	1.26	98.74
565	3.06	10	1996	1.308	96.35	3.63	0.22	3.8	92.55
713	1.75	10	1997	2.140	96.93	3.04	0.03	6.61	90.33
18	6.45	11	1995	0.385	96.81	1.59	1.59	1.57	95.24
163	3.16	11	1996	0.135	77.22	11.39	11.39	5.24	71.99
5	6.17	11	1997	0.242	46.15	26.92	26.92	1.08	45.07

TABLE 4.6 Survivorship, Population Growth Rate, and Reproductive Output by Location (Across Years) With Location Treated Here as a Fixed Model Effect (Results used for Heuristic Purposes Only)

	Survivorship to Reproduction (Std. Error)	**Population Growth Rate (Std. Error)**	**Mean Number of Fruits per Reproductive Plant (Std. Error)**	**Mean Number of Fruits per Quadrat ($1600cm^2$) (Std. Error)**
BW1	66.875% (8.447)	5.919 (1.454)	10.620 (2.33)	331.72 (43.22)
BW2	58.99% (7.446)	1.326	9.078	292.94
BW3	59.37% (7.666)	4.778	9.984	245.33
RL1	56.37% (8.167)	1.952	5.034	141.78
RL2	59.24% (7.446)	1.328	3.583	95.72
RL3	85.71% (8.447)	0.389	13.521	124.72
RL4	51.79% (10.532)	0.154	3.623	78.11
RL5	75.96% (8.447)	1.232	7.926	81.44
RL6	40.13% (7.446)	0.552	2.482	91.78
RL7	56.04% (8.447)	1.809	2.469	245.78
SLL3	61.92% (8.791)	0.144	5.259	41.33

TABLE 4.7 **Descriptive Statistics of Soil Characteristics (Across Quadrats and Dates), Population Growth Rates, Mean Density of *C. multicaulis* Per Location (Across Quadrats and Dates) and Growth Rate Elasticities of Seed Bank and Reproductive Life Stages**

	Mean	**Std. Dev.**	**Range**
Soil pH	8.86	0.449	7.99- 9.50
Soil Conductivity (dS/m)	8.91	6.278	2.54 - 24.37
Soil Moisture (Percent Dry Weight)	29.51%	2.616	10.73 - 53.73%
Density of *C. multicaulis* per Location (Across Quadrats and Dates)	252.3	212.852	5 - 713
Population Growth Rate λ	1.947	2.3778	0.08 - 10.115
Elasticity of Seeds Aged 0-1 years	78.32	29.321	1 - 99.99
Elasticity of Seeds Aged 1-2 years	9.25	10.340	0 - 36.49
Elasticity of Seeds Aged 2-3 years	3.43	7.272	0 - 26.92
Elasticity of Small Reproductive Plants	2.43	3.537	0 - 59.03
Elasticity of Large Reproductive Plants	85.18	16.763	40.94 - 99.99

TABLE 4.8 Soil Characteristics, Density of *C. multicaulis* per Location (Across Quadrats and Dates), Population Growth Rates, and Elasticity of Persistent Seed Bank (Seeds Aged 1-3 yrs Combined)

(Sorted by Population Growth Rate)

Loc	Year	Soil pH	Soil Conductivity	Soil Moisture	Plant Density	Population Growth Rate	Elasticity Seeds 1-3 yrs
1	1996	9.26	10.05	0.2363	171	10.115	0.05
3	1995	8.98	7.41	0.2108	107	8.985	4.91
1	1995	9.50	16.42	0.1460	183	4.754	0.01
2	1995	9.15	2.54	0.1073	509	4.094	3.02
4	1996	8.43	3.02	0.3891	74	3.848	0.58
10	1995	8.40	7.42	0.5101	286	3.510	0
8	1996	8.43	6.94	0.2508	44	3.252	1.25
4	1997	8.43	2.87	0.3095	394	3.076	0.97
1	1997	9.24	9.45	0.1377	513	3.041	0.66
5	1996	8.59	5.34	0.3464	152	2.354	1.95
10	1997	8.66	5.67	0.5213	713	2.140	3.07
3	1996	8.52	2.76	0.2310	574	1.901	13.19
5	1995	8.86	4.32	0.3342	135	1.652	4.72
3	1997	8.70	5.09	0.2134	181	1.520	17.54
10	1996	8.10	3.77	0.4688	565	1.308	3.85
8	1997	8.91	13.18	0.2789	87	1.246	3.97
4	1995	8.46	3.29	0.4737	220	1.199	10.33
6	1996	9.19	14.68	0.2948	172	0.979	4.1
9	1995	7.99	4.78	0.5242	307	0.873	0
5	1997	8.68	5.55	0.3601	316	0.815	13.02
7	1995	9.46	19.48	0.1372	78	0.650	32.81
2	1996	9.04	2.97	0.1882	594	0.406	40.19
11	1995	9.45	20.97	0.2613	18	0.385	3.18
8	1995	8.66	3.79	0.2746	13	0.366	7.17
2	1997	9.09	5.02	0.1581	686	0.363	33.55
6	1997	9.28	15.27	0.3528	35	0.296	59.03
6	1995	9.32	17.00	0.3422	98	0.289	11.08
11	1997	9.32	12.07	0.2114	5	0.242	53.84
7	1996	9.49	20.13	0.1407	44	0.159	36.49
11	1996	9.03	8.76	0.2151	163	0.135	22.78
9	1996	8.23	4.69	0.3773	229	0.124	11.82
7	1997	9.44	24.37	0.1990	158	0.085	0
9	1997	8.24	4.88	0.5373	502	0.080	19.54

TABLE 4.9 Correlations Between Reproductive and Seed Bank Elasticities

	Elasticity of Small Reproductive Plants		Elasticity of Large Reproductive Plants	
	r	p	r	p
Mean Number of Fruits Per Reproductive Plant	-0.42195	0.0144**	-0.06490	0.7197
Elasticity of Seeds 0-1 Years	-0.03258	0.8571	0.30112	0.0886*
Elasticity of Seeds 1-2 Years	0.19673	0.2725	-0.94100	0.0001**
Elasticity of Seeds 2-3 Years	-0.04310	0.8118	-0.84297	0.0001**

	Elasticity of Seeds Aged 1-3 Years Combined	
	r	p
Elasticity of Seeds Aged 0-1 Years	0.30071	0.0890*

** $p < 0.05$
* $p < 0.10$

TABLE 4.10 **Correlations Between Seed Bank and Reproductive Life Stage Elasticities, Soil Characteristics, and Population Growth Rate λ**

	Population Growth Rate λ	
	r	**p**
Elasticity of Seeds Aged 0-1 Years	0.30231	0.0873*
Elasticity of Seeds Aged 1-2 Years	-0.45700	0.0075**
Elasticity of Seeds Aged 2-3 Years	-0.32567	0.0644*
Elasticity of Seeds Aged 1-3 Years (Combined)	-0.43987	0.0104**
Elasticity of Small Reproductive Plants	-0.34548	0.0489**
Elasticity of Large Reproductive Plants	0.48713	0.0040**
Soil pH	0.03967	0.8265
Soil Conductivity	-0.16657	0.3542
Soil Moisture	-0.14761	0.4123

** $p < 0.05$
* $p < 0.10$

TABLE 4.11 **Correlations Between Density of *C. multicaulis*, Soil Characteristics, and Growth and Reproductive Measures**

	Density of *C. multicaulis* (Across Quadrats and Dates)	
	r	**p**
Soil pH	-0.31548	0.0737*
Soil Conductivity	-0.51304	0.0023**
Soil Moisture	0.16258	0.3660
Mean Number of Fruits per Reproductive Plant	-0.43533	0.0113**
Population Growth Rate λ	-0.02340	0.8972
Survivorship of *C. multicaulis* to Reproduction	0.10107	0.1551
Elasticity of Small Reproductive Plants	0.41318	0.0169**
Elasticity of Large Reproductive Plants	-0.00652	0.9713

** $p < 0.05$
* $p < 0.10$

TABLE 4.12 **Correlations Between Soil Characteristics (Across Quadrats and Dates), Growth Rate Elasticities for Seed Bank and Reproductive Life Stages, Population Growth Rate, and Mean Number of Fruits Per Reproductive Plant**

	Soil pH		Soil Conductivity		Soil Moisture	
Elasticities	**r**	**p**	**r**	**p**	**r**	**p**
Seeds Aged 0-1	-0.00937	0.9587	-0.26528	0.1357	-0.15743	0.3816
Seeds Aged 1-2	0.25618	0.1501	0.14107	0.4336	-0.20456	0.2535
Seeds Aged 2-3	0.39578	0.0226*	0.20137	0.2611	-0.24581	0.1679
Seeds Aged 1-3	0.34273	0.0509*	0.18126	0.3127	-0.24200	0.1748
Small Reproductive Plants	-0.33806	0.0543*	-0.24001	0.1785	0.33597	0.0559*
Large Reproductive Plants	-0.26629	0.1341	-0.13460	0.4552	0.17060	0.3425
Growth Rate	0.03967	0.8265	-0.16657	0.3542	-0.14761	0.4123
Number of Fruits Per Reproductive Plant	0.33519	0.0565*	0.27864	0.1164	-0.19074	0.2877

** $p < 0.05$
* $p < 0.10$

TABLE 4.13 Soil pH, Conductivity (Ec) and Soil Moisture, Density of *C. multicaulis* (Across Quadrats and Dates), Number of Fruits Per Reproductive Plant, Population Growth Rate, and Seed Bank Elasticities (Seeds Aged 0-1 Years, 1-2 Years, and 2-3 Years) for Locations With Shifting Seed Bank Elasticities During the Three-Year Census Period

Soil pH	Soil Ec	Soil Moist.	Plant Density	Fruit per Repro	Loc	Year	Popn Growth	Elasticity Seed 0-1yr	Elasticity Seed 1-2yr	Elasticity Seed 2-3yr
9.15	2.54	0.1073	509	2.95	BW2	1995	4.094	96.98	2.63	0.39
8.66	2.97	0.1882	594	3.35	BW2	1996	0.406	59.81	24.54	15.65
7.99	5.02	0.1581	686	2.94	BW2	1997	0.363	66.45	20.17	13.38
8.24	17.00	0.3422	98	7.52	RL3	1995	0.289	88.92	6.49	4.59
9.28	14.68	0.2948	172	9.49	RL3	1996	0.979	95.9	2.88	1.22
8.23	15.27	0.3528	35	23.55	RL3	1997	0.296	41.08	34.51	24.52
9.44	19.48	0.1372	78	5.92	RL4	1995	0.650	67.19	19.52	13.29
8.10	20.13	0.1407	44	3.27	RL4	1996	0.159	63.51	36.49	0
9.03	24.37	0.1990	158	1.68	RL4	1997	0.085	1	0	0
8.43	20.97	0.2613	18	6.45	SLL3	1995	0.385	96.81	1.59	1.59
8.66	8.76	0.2151	163	3.16	SLL3	1996	0.135	77.22	11.39	11.39
8.40	12.07	0.2114	5	6.17	SLL3	1997	0.242	46.15	26.92	26.92

TABLE 4.14 Estimated Time to Extinction, Population Growth Rate and Seed Bank Elasticities

(sorted by Location)

Location	Year	Population Growth	Elasticity Seeds 0-1	Elasticity Seeds 1-2	Elasticity Seeds 2-3	Est.Time to Extinction
BW2	1996	0.406	59.81	24.54	15.65	5.11
BW2	1997	0.363	66.45	20.17	13.38	4.54
RL2	1997	0.815	86.97	12.93	0.09	22.49
RL3	1997	0.296	41.08	34.51	24.52	3.78
RL3	1995	0.289	88.92	6.49	4.59	3.71
RL3	1996	0.979	95.9	2.88	1.22	215.96
RL4	1996	0.159	63.51	36.49	0	2.51
RL4	1995	0.650	67.19	19.52	13.29	10.70
RL4	1997	0.085	1	0	0	1.87
RL5	1995	0.366	92.83	7.17	0	4.58
RL6	1996	0.124	88.18	11.82	0	2.21
RL6	1995	0.873	1	0	0	33.88
RL6	1997	0.080	80.46	19.54	0	1.82
SLL3	1995	0.385	96.81	1.59	1.59	4.82
SLL3	1996	0.135	77.22	11.39	11.39	2.30
SLL3	1997	0.242	46.15	26.92	26.92	3.25

All other location and year combinations had population growth rates > 1.0.

Chapter 5: An Introduction to Seed Ecology - Consideration of Dormancy, Factors Affecting Seed Fates in the Soil, and Demographic, Theoretical, and Genetic Models of Persistent Seed Banks

Introduction

For species with a soil seed bank persisting more than one year, few ecological details have been gathered concerning natural cycles of dormancy release, germination and emergence, seed decay, predation, and lateral movement within the persistent seed bank. Field experiments assessing the sources, timing, variability, and relative importance of ecological influences on seeds in the soil have been difficult to conduct. Because currently used methods of determining the age of seeds require destructive analysis, assessing the influence of seed age on dormancy release, germination, establishment, and subsequent growth has remained a considerable challenge.

Perhaps because studies of seeds have historically been conducted from a variety of agricultural, physiological, and ecological perspectives, the terminology of dormancy and germination remains remarkably inconsistent and conflicting in its usage. Studies of germination in harsh (e.g., saline) environments (Ungar 1987b, Khan and Rizvi 1994) have primarily focused on the hypothesis that germination timing coincides with the amelioration of stressful soil conditions and thereby maximizes plant fitness. Seed dormancy is not uncommon in halophytic species, particularly those occupying salt deserts and salt marshes (Baskin and Baskin 1998)

Theoretical studies of persistent seed banks have concentrated on the role of seeds of differing age conferring an advantage in a "bet-hedging" sense (Cohen 1966, Klinkhamer et al. 1987) as an adaptation for survival in years when environmental conditions are poor for seedling establishment. The evolution of seed dormancy has also been explained as a mechanism to prevent competition between plant siblings or as one of several life cycle traits inherited together that maximize a species' fitness (Baskin and Baskin 1998). Few empirical data have been gathered (Kalisz and McPeek 1993) to support the theories, and little attention has been given to the ecological role of seed banks in less variable environments (Rees et al. 1996, Baskin and Baskin 1998) and in times of plenty (Kalisz and McPeek 1993).

An introduction to several aspects of empirical and theoretical seed ecology is given here as background to the present study of the persistent seed bank of *Cleome multicaulis*, an annual wetland halophyte of the San Luis Valley, Colorado. An overview of the terminology of dormancy is necessary to ensure uniformity in the usage of commonly misapplied terms. A background to the field experiment described in this study to follow the fate of *C. multicaulis* seeds is given through consideration of seed bank sampling regimes, seed recruitment and survivorship, discussion of within- and between-population germination behavior, and an overview of studies examining the population dynamics of seeds in the soil. Lastly, an overview of demographic, theoretical, and genetic studies of persistent seeds is given in order to complete the introduction to the study that follows.

Definitions and Terminologies of Seed Dormancy

A reasonable discussion of seed ecology requires at its outset a discussion of the terminology and definitions of seed dormancy. Attempts to construct a united terminology of dormancy have proven unsuccessful and continue to cause confusion and strife (Vleeshouwers et al. 1995). In the minds of some, seeds that are not germinating are dormant. Harper (Harper 1977) unfortunately contributed to this confusion by categorizing dormancy as a process, respectively, that seeds are born with (innate dormancy), that they achieve after being non-dormant (induced dormancy) or that they have thrust upon them when they fail to germinate due to unfavorable environmental conditions (enforced dormancy).

The phenomena described by Harper occur both as a result of internal seed physiology and external environmental cues (Vleeshouwers et al. 1995), have not been documented in natural populations of seeds (Baskin and Baskin 1998), and serve only to obfuscate the study of seed ecology. The term "dormancy" should properly be reserved to describe physiological blocks within the seed that prevent germination, as opposed to the absence of factors required to evoke germination (Vleeshouwers et al. 1995). Dormancy is therefore a trait of the seed itself, and not a measure of the external conditions to which the seed is currently exposed (e.g., light, temperature) (Vleeshouwers et al. 1995). The degree of dormancy at any particular moment defines the germination requirements of the seed and is influenced by the environmental conditions experienced by the seed during its existence, including conditions present in the maternal environment (Vleeshouwers et al. 1995).

It is not currently possible to measure the dormancy state of a seed directly (Vleeshouwers et al. 1995). An impression of a seed's dormancy can be made by trying to make it germinate, but this does not distinguish between factors that influence dormancy release and those that stimulate germination (Vleeshouwers et al. 1995). Greenhouse studies showing comparative germination success (Thompson and Grime 1979) fail to distinguish species differences in dormancy from those of germination (Vleeshouwers et al. 1995).

In natural populations, seeds survive ungerminated in the soil when unfavorable conditions prevent germination, regardless of the dormancy state of the seeds (Baskin and Baskin 1998). Dormancy prevents germination during times of the year when plants would not survive, and in summer annuals is generally induced by high temperatures and relieved by winter temperatures (Vleeshouwers et al. 1995).

Differentiation between germination and dormancy is important in distinguishing effects of soil nutrients and other soil characteristics. For instance, some studies report that soil moisture and nitrate content influence germination but not dormancy (Vleeshouwers et al. 1995), whereas others maintain that nitrites, nitrates, and soil moisture break physiological dormancy and extend the germination season of some species (Pons 1991, Baskin and Baskin 1998) but not others (Vleeshouwers et al. 1995). Some authors refer to "seed dormancy induced by salt stress" that can be relieved by soaking seeds in gibberellic acid (Khan and Rizvi 1994), and by which they mean failure to germinate.

Baskin and Baskin (Baskin and Baskin 1998) categorize dormancies as endogenous (physiological, morphological, or morphophysiological) and exogenous. Physiological dormancy is caused by a physiological inhibiting mechanism of germination; morphological dormancy is caused by an underdeveloped embryo; and morphophysiological dormancy is caused by a combination of the two factors (Baskin and Baskin 1998). Exogenous dormancies are caused by hard seed coats, germination inhibitors that must leach out of the embryo prior to germination, or woody structures restricting growth of the embryo.

Physiological dormancy occurs when seeds are freshly matured and either do not germinate at all, or germinate at a narrow range of temperatures (Baskin and Baskin 1998). Cold stratification and/or chemical treatments (e.g., gibberellins) are usually necessary to break dormancy. Excised embryos of seeds with physiological dormancy may or may not grow and produce normal seedlings (Baskin and Baskin 1998). Treatment with various giberellic acids (GA_3, for instance) may induce germination but will not isolate differences between seeds categorized as "dormant" or "non-dormant" based on any character other than their germination response (Fox et al. 1995).

Seeds with physiological dormancy exhibit a continuum of changes in their response to temperature and light as they move from dormant to nondormant stages (Baskin and Baskin 1988). Temperature is likely to be the primary factor regulating germination, with light and soil moisture of secondary importance (Baskin et al. 1993). In summer annuals, seeds that germinate in spring and/or summer are either dormant or conditionally dormant at maturity. Seeds that are conditionally dormant germinate at first under a narrow range of environmental conditions (i.e., only at 35/20 or 30/15 degrees C temperatures) and thus avoid fall germination because ambient temperatures are lower than those suitable for germination (Young and Young 1986, Baskin and Baskin 1988, Baskin and Baskin 1998).

As dormancy loss proceeds, seeds become non-dormant and will then germinate over a wide range of environmental conditions, including the same low temperatures at which germination did not occur during the fall (Baskin and Baskin 1998). If seeds fail to germinate in the spring and summer, changes in environmental conditions (especially temperature) result in seeds becoming conditionally dormant once again (Baskin and Baskin 1998). Conditional dormancy may be a more common component of a species' annual dormancy cycle in environmentally unpredictable habitats (Baskin et al. 1993).

Seed Bank Sampling Regimes, Seed Burial Depth, and Emergence Time

Studies of seed bank density utilizing sampling regimes often focus on community-level dynamics (Keddy and Reznicek 1982, Smith and Kadlec 1985, Hassan and West 1986, Cowling et al. 1987, Grillas 1993, Lavorel et al. 1993, Milberg and Hansson 1993, Per and Hanssom 1993, Badger and Ungar 1994, Bekker et al. 1997, Dessaint et al. 1997) rather than population-level processes, in part perhaps because of the enormous number of samples needed to accurately assess seed density on the fine scale required for population studies.

Although it is recognized that the horizontal distribution of seeds is almost never uniform (Thompson and Grime 1979, Baskin and Baskin 1998), little attention has been paid to the vertical arrangement of seeds in the soil. Seed bank samples are commonly extracted from the top 3-4 cm of soil, and seed densities are almost exclusively expressed in two-dimensional terms (e.g., seeds/ m^2). However, samples taken at insufficient depth may result in the erroneous conclusion that persistent seed banks are absent (Zhang and Maun 1994).

The presence of a soil seed bank is sometimes characterized as a species mechanism for temporal rather than spatial dispersal. To the extent this is true, then omitting consideration of the deeply buried seed bank is analogous to ignoring the ecological importance of long-distance dispersal.

Population dynamic processes affecting deeply buried seeds are expected to differ in fundamental ways from the dynamics of shallow seed banks. Deeply buried seeds may be subject to higher mortality (Baskin and Baskin 1998) if they are not moved to a position closer to the soil surface, much as seeds that are dispersed long distances may suffer from increased mortality due to the lack of "safe site" microhabitats (Perry and Gonzalez-Andujar 1993, Schupp 1995). Emergence time may depend more on burial depth than on seed genotype (Bazzaz 1996). Deeply buried seeds may show lower rates of seedling emergence not only from a failure to germinate *in situ* but also from germination and subsequent failure of seedlings to reach the soil surface (Wagner and Spira 1994, Baskin and Baskin 1998).

Soil cultivation will often stimulate the germination of buried seeds and the depth of disturbance is one factor that plays a role in determining what proportion of seeds germinate from the seed bank (Baskin and Baskin 1998). Earthworms may play an important role in bringing buried seeds to the soil surface in their casts and thereby facilitating germination (Baskin and Baskin 1998). The effect of burial depth on seed viability may vary according to species (Baskin and Baskin 1998).

Seedlings that emerge early in the season may have a higher probability of survival to reproduction, higher fruit production, and enjoy a competitive advantage as compared to later-emerging cohorts (Kalisz 1986, Wertis and Ungar 1986, Rees and Long 1992, Stanton and Galen 1997). Where early-season conditions are extreme, however, early emergence may lower rates of survival to reproduction or may have no effect (Kelly 1989).

Seed Age and Seed Recruitment Curves

Measurements of seed bank density neglect to consider the age structure of seeds and fail to reflect the effect of seed age on seed survival, dormancy requirements, seed predation, and decomposition rates. Species differ in the shapes of their seedling recruitment curves as a function of seed age and may not show a constant proportion of seeds germinating each year (Phillipi 1993b, Rees and Long 1993). In Kalisz' comprehensive study of the winter annual *Collinsia verna*, germination percentages were 36%, 3%, and 6% in the first, second, and third autumns after burial (Kalisz 1991).

Rees and Long (Rees and Long 1993) analyzed data from a long-term seed bank experiment to construct curves of seedling recruitment that reflect not only age-specific germination but also age-specific pre-emergence mortality. Their results showed that seed bank decay fit the previously predicted negative exponential pattern in only 23% of the species analyzed, and a wide range of recruitment patterns were detected. Not all species show age-dependent rates of germination, however; a greenhouse study of the rare mustard *Leavenworthia stylosa* found remarkably constant numbers of seeds germinating in the greenhouse each year for a period of 7 years (Baskin and Baskin 1978).

In one of the few series of studies to experimentally examine the effects of seed age, Phillipi (Phillipi 1993a,b) examined whether seeds that failed to germinate (under suitable conditions) in the first year would be as likely to germinate under the same conditions in subsequent years. His results showed that second-year germination did occur, but at lower rates. Even seeds germinating over several years under the same conditions did not have a constant fraction of the remaining seeds germinating each year. Field and greenhouse experiments showed that there was no variation between seeds from first-year plants and seeds from second-year plants in first-year germination (Phillipi 1993a).

Methods of discerning seed age have predominately relied on indirect measurement techniques such as allowing germination of seeds from soil that has been isolated from newly dispersed seed sources for a known number of years (Baskin and Baskin 1998). This technique is labor-intensive and rather impractical for long-lived seed banks.

Radiocarbon dating (using C^{14}/C^{13} ratios) previously required such a large sample of material that it necessitated sacrificing seeds in order to obtain their ages directly. Some seeds could be aged and others planted; however, one could never be certain that the seed ages of each group were the same (Baskin and Baskin 1998). The use of accelerator mass spectrometry has now made it possible to radiocarbon date seeds using samples small enough (5-10mg) to be removed from the seed coat of an emerging seedling (McGraw et al. 1991). Standard deviations of the resulting radiocarbon-derived estimated ages are of such great magnitude from this technique (e.g., +/- 75 years) that its utility is limited in scope, particularly in the case of seed banks of age 5-50 years (McGraw et al. 1991, McGraw 1993).

Given the current limitations in seed aging technology, it is not surprising that long-term (> 10 yr) studies assessing seed age comprised only one-third of the studies examined in a comprehensive review (Baskin and Baskin 1998) even for species whose tendency to form persistent seed banks is well-known (Ungar 1978). The most well-known long-term study of the effect of seed age on germination percentage was begun in 1879 by W.J. Beal. When seeds were exhumed in 1980 after 100 years, three species germinated and more might have done so if their annual cycles of dormancy had been taken into consideration (Baskin and Baskin 1998).

Seed Mortality, Predation, and Survivorship Curves

Causes of seed mortality are often difficult to identify and are therefore often omitted from otherwise comprehensive studies of seed fate (Kalisz 1991), including the study described here. Seed death may occur as a result of aging and physiological damage, pathogens, or seed predators in the soil (Crist and Friese 1993, Jansen and Ison 1995). Seed cages in this study might function as "entrapment microsites" (Fort and Richards 1998) where increased seed densities would attract seed predators. Insect herbivory may affect the production, maturation, or dispersal of seeds (Shumway and Bertness 1992, Louda 1994). Ants often concentrate their efforts on the most abundant small seeds (Roach 1986) and either store viable seeds or destroy the radicle and prevent subsequent germination (Holldobler and Wilson 1990). Ants, slugs, and earthworms may feed even on buried seeds (Baskin and Baskin 1998).

Survivorship curves for seeds buried in the soil have most commonly been shown to follow a Type II survivorship curve (i.e., a constant probability of death or negative exponential curve), although the ecological factors responsible for such a pattern are not always clear (Crist and Friese 1993). A few species showed survivorship patterns that more closely fit a Type I curve (Baskin and Baskin 1998). Seed survivorship may vary within a species (Donald 1993, Purrington and Schmitt 1995) as well as between species (Phillipi 1993b). The design of the study described here did not allow accurate seed survivorship curves to be developed for *C. multicaulis.*

Variation in Germination Behavior Within and Among Populations

Seeds within a single population may differ both in their physiological levels of dormancy and in their response to external germination cues (Young and Young 1986) as a result of heritable genetic variation, influence of the maternal environment, or variation in environmental conditions such as precipitation present at the time of germination (Jain 1982, Hacker 1984, Cabin et al. 1998). Individual plants may produce seeds of different sizes and from different positions along a branch that differ both in terms of viability and/or probability of germination (Cavers and Harper 1966, Wertis and Ungar 1986, Phillipi 1993b, Cheplick 1996). Large plants of *Lepidium lasocarpum* produced seeds in greater number and with greater dormancy, confounding attempts to discern maternal environmental effects (Phillipi 1993a).

Germination polymorphisms among populations may be more common than previously believed (Palmblad 1969, Lindauer and Quinn 1972) although attempts to correlate germination differences with environmental conditions may not always be successful (Meyer and Kitchen 1992). Variation in germination behavior among populations (e.g., *Salicornia europea, Ranunculus repens* and *Plantago lanceolata*) may result in persistent seed banks being formed in some locations but not in others (Sarukhan 1974, Thompson 1979, van Groenendael 1988, Silvertown 1993, Foderaro 1997, Wijte 1996). Inter-populational differences in seed dormancy and germination response may arise from seed size hetermorphism, (Ungar and Riehl 1980, Silvertown 1984, Ellison 1987, Wijte and Gallagher 1996) or from timing differences in the initiation, pace, and duration of seed development (Silvertown 1984, Foderaro and Ungar 1997).

Dormancy and germination polymorphisms may occur as a result of ecotypic variation in response to rainfall (Phillipi 1993b), temperature (Cruden 1974, Hacker 1984) or a temperature-mediated light requirement for germination (Kitchen and Meyers 1992).

Studies of Seed Bank Population Dynamics

Studies of seed bank persistence (the demographic processes acting on the seed bank life stage) should be differentiated from studies of seed persistence (the physiology of dormancy) (Troumbis 1996). Important seed bank demographic processes include seed dispersal; seed predation; seed decay, physiological death, and viability; seed movement in the soil; dormancy release; germination; and emergence. Few studies have examined more than one or two of these processes simultaneously.

Previous studies of seed bank population dynamics include Werner and Caswell's (Werner and Caswell 1977) planting of teasel (*Dipsacus sylvestris*) seeds into various habitats, and Pavone and Reader's (Pavone and Reader 1982) field study of *Medicago lupulina* seeds sown in groups of 200 using 0.8mm mesh fabric cages. In the latter study, germination from the freshly-matured cohort was 78-85%, considerably higher than the typical 30-40% germination seen in the semi-persistent seed bank. By the next summer, 47% of the seed cohort had become mature plants, 22% remained dormant in the soil, and 30% had died (Pavone and Reader 1982).

A seed population model developed using unpublished data for an annual plant of vernal pools (Ebert 1999) indicated that of 490,000 seeds produced, 52% germinated immediately, 43% did not germinate (with unknown sources and rates of mortality), and 5% entered the seed bank. From the seed bank of 25,000 seeds, 1% (250) subsequently germinated, and the fate of the remaining seeds in the soil was unknown. A seed budget for *Atriplex* began with 6849 seedlings in March, from which 140 mature plants survived till October and produced 43,010 seeds. The December seed rain was measured as 32,902 seeds and by January 21,496 seeds survived (Ungar 1987b).

Demographic Seed Bank Models

In spite of the challenges of obtaining empirical data on the fates of seeds in the soil, numerous theoretical models have been developed to predict the dynamics of soil seed banks within an evolutionary perspective. While initial models predicted a 'bet-hedging" strategy that optimized germination, these were later made more complex to incorporate evolutionarily stable strategy theory. Models with an evolutionary perspective have predicted the effect of seed banks on fitness, the relative proportion of various genotypes, and the evolutionary process. Models of seed demographics may incorporate age-dependent seed mortality and germination, plant mortality, and reproduction into plant life cycles so that the adult becomes merely a seed-producing vessel for seeds (Schmidt and Lawlor 1983). This model, unlike others (Harper 1977, Kalisz 1991) and the present study, defines the time of "birth" in plants as the point of seed germination rather than seed maturation.

The demographic model of Klemow and Raynal (Klemow and Raynal 1983) predicts that an annual with Type I survivorship and comparatively low seed production (i.e., fewer than 50 seeds per plant) will have few seeds that survive in the soil longer than 9 months, whereas an annual species with high fecundity and high seedling mortality (Types II and III survivorship curves) is predicted to form long-lived seed banks. *C. multicaulis* in this study would appear to be an exception to the predictions of this model.

Kalisz and McPeek (Kalisz and McPeek 1993) created one of the few empirically-based demographic models that estimated the time to extinction under simulated conditions of temporal demographic stochasticity. By simulating various frequencies of "good" and "bad" demographic years and varying autocorrelation between growth conditions in consecutive years, the authors determined that in years when environmental conditions were most unpredictable, the presence of a persistent seed bank had the effect of slightly increasing population growth rate and time to extinction (Kalisz and McPeek 1993).

In years when the population was increasing, however, the presence of a persistent seed bank had little or no effect on the estimated population growth rate. Under some combinations of autocorrelation and simulated frequency of good years, the effects of the seed bank on population growth rate were negligible or slightly negative and populations with a seed bank actually went extinct sooner than those without (Kalisz and McPeek 1993). Without long-term demographic studies, it is unclear how frequently populations actually experience years that vary in environmental quality. If good years are even moderately common, and/or if the environment is only slightly variable, then studies that describe demographic seed bank effects in times of plenty are clearly needed to provide a comprehensive picture of the ecological role of seed banks.

There is a great need for more sophisticated techniques for estimating seed bank density, spatial and temporal distribution of the seed bank, and seed population dynamics (including seed age) without disturbing the soil. Recent technological innovations such as automated image capture techniques are being refined to allow seed counts in the soil more directly (Buhler and Maxwell 1993). Computer contour mapping may allow visualization of spatial patterns of seed population change during the growing season (Benoit et al. 1992). The need for ecological information concerning the cryptic lives of seeds in the soil is great, and should provoke the initiation of innovations in design and technique as quickly as possible.

Tradeoffs Between Seed Dormancy, Seed Size, and Dispersal

Seed dormancy, dispersal, and seed size may interact as adaptations to reduce the impact of a variable environment (Klinkhamer et al. 1987, Venable and Brown 1988) by allowing plants to average their demographic success temporally (dormancy) or spatially (dispersal). Dispersal may be the best tool because it has no inherent cost other than the cost of mortality, whereas dormancy has a cost of delayed reproduction and changes in seed size have costs in terms of fitness tradeoffs under various environmental conditions (Venable and Brown 1988).

Although some studies have shown a greater tendency for small-seeded species to form persistent seed banks (Phillipi 1993b, Banovetz and Scheiner 1994, Baskin and Baskin 1998) presumably because of the difficulty and expense in defending a large dormant seed in the soil from herbivores and pathogens (Crawley 1997), in other cases the relationship between dormancy and seed size is less clear (Klinkhamer et al. 1987, Thompson et al. 1993, Baskin and Baskin 1998).

Bet-Hedging Models

Populations may respond to environmental variability by evolving life-history variations in order to maximize fitness (Kalisz 1991) or reduce fitness variance (Pake and Venable 1996) For an annual plant, the presence of a persistent seed bank is predicted to reduce variability in fitness by providing a buffer from the consequences of near or complete reproductive failure in unfavorable years. Seed banks are also predicted to dampen success in favorable years by delaying germination that might otherwise improve fitness (Pake and Venable 1996).

Several theoretical models have predicted the adaptive advantages of persistent seed banks for annual species living in temporally variable environments. However, the extent to which the prevalence of persistent seed banks is actually distributed between species occupying habitats that might be considered variable versus those considered predictable is unknown. In addition, little is known about the habitats occupied by populations of species exhibiting interpopulational differences in the degree of seed bank persistence.

Early models by Cohen (Cohen 1966, 1968) theorized that when environmental conditions are variable and years with complete reproductive mortality are common, an annual species would be expected to show high rates of seed production in favorable years and correspondingly high rates of seed dormancy ("bet-hedging") in favorable (but variable) years. Conversely, in predictable habitats when reproduction is assured, the model predicts that high fecundity and seed longevity no longer confer an adaptive advantage. The bet-hedging strategy of seed dormancy maximizes the geometric mean fitness (e.g., growth rate) across years by greatly reducing the variance in fitness across years, at a cost of reducing the expected (arithmetic mean) fitness within each year (Cohen 1968, Phillipi 1993b).

The models of Venable and Lawlor (Venable and Lawlor 1980, Venable 1985, Venable and Brown 1988) address prediction of the optimal germination fraction in populations of annual plants subject to spatial and temporal environmental variability. One of their key model predictions is that if the environment remains uncertain, and depending on the ability of plants to accurately predict the germination environment, then differences in plant dispersal will generate different optimal germination strategies (Venable and Lawlor 1980). Properties of seed dormancy, seed size, and dispersal that allow escape from crowding and competition with siblings may evolve even in environments that lack uncertainty if there is local spatial and/or temporal variation in environmental conditions or spatial structure of the habitat (Venable 1989).

The few empirical studies that have been conducted have revealed multi-year germination patterns that do not always fit an optimizing model of bet-hedging as a response to environmental unpredictability (Phillipi 1993a,b). Extensions of Cohen's original model (Bulmer 1984, Ellner 1985) now include competition and density-dependence in seed yield using an evolutionarily stable strategy approach (Phillipi 1993b), that relaxes the assumption that a constant fraction of the remaining viable seeds will germinate each year.

The model of Rees (Rees 1994) predicts that in a variable environment, selection will mold a trade-off between adult longevity and seed dormancy, the details of which depend on which life-history stage is most variable, whether seeds can detect favorable sites for establishment, and the age/stage structure of the population (Rees 1994). In a constant environment, however, the model prediction is that complete germination is the evolutionarily stable strategy regardless of the longevity of adult plants. The costs of dormancy in a constant environment (in terms of seed mortality prior to germination) are considered to be high, and the evolution of dormancy in such an environment is perceived as a method of reducing competition between siblings (Rees 1994).

Models of MacDonald and Watkinson (MacDonald and Watkinson 1981) showed that the presence of a seed bank can have both a stabilizing effect (speeding up the oscillatory return to a so-called equilibrium population size) and a destabilizing effect (slowing down the exponential return to an equilibrium population size). Their models account for seed age by specifying that the probability of a seed newly arrived into the seed bank producing a seedling is considerably greater than the probability of a seed that has been longer in the seed bank doing so, although additional model modifications to increase the accuracy of accounting for seed age are discussed (MacDonald and Watkinson 1981).

The formation of a persistent seed bank in response to a temporally variable environment requires that the population "tracks" environmental variability with continuous genetic changes (Klemow and Raynal 1983). An alternative life history attribute that releases the population from the difficulty of tracking environmental variability is the development of phenotypic plasticity in growth (Klemow and Raynal 1983). Further empirical evidence is needed to characterize how widespread each strategy is as a response to a temporally variable environment, and to determine the genetic and evolutionary consequences of each strategy (Klemow and Raynal 1983).

Studies are also needed to determine whether a particular strategy may be altered in response to changes in the nature and degree of environmental variability experienced by a species. Klemow and Raynal predict that phenotypic plasticity would allow annuals to reduce growth but maintain high survivorship in years where an unfavorable environment does not exceed the physiological tolerance of the species, whereas in years when environmentally-induced stress exceeds plant tolerance, mortality of above-ground stages would be high and persistence would depend on the maintenance of seeds in the soil (Klemow and Raynal 1983).

Although dormancy is widespread in mesic environments, few studies have examined the role of seed banks in environments where favorable conditions for germination and plant growth are seasonally predictable (Baskin and Baskin 1998). Along an environmental gradient from unpredictable to predictably favorable environments, dormancy may shift from being primarily under genetic control to being a phenotypically plastic trait (Beckstead et al. 1996, Baskin and Baskin 1998)

Studies of Seed Bank Genetic Structure

Templeton and Levin (Templeton and Levin 1979) theorized that the seed pool acts as an evolutionary filter to determine which genotypes can survive in any single year. The quality of the environment in a particular year will determine the selective forces acting on the pool of genotypes present in the soil seed bank. The seed bank becomes dominated by the best genotypes of good years and the genetic impact of seeds produced by the best genotypes in poor years is minimized. Because the seed pool reflects seed production in previous years, it allows information about the absolute quality of various years to influence the evolutionary process (Templeton and Levin 1979). Populations lacking a seed pool, on the other hand, receive evolutionary information only in the form of allele frequencies from the adults of previous generations. Templeton theorized that the evolutionary role of the seed bank was most critical at those loci that interact with variable features of the environment in producing their fitness effects (Templeton and Levin 1979).

Several studies have shown that the presence of a seed bank may actually dampen the genetic response of the population (Hairston and De Stasio 1988) by contributing alleles that "correct" local genetic deviations, narrow the amplitude of fluctuation in allelic frequency, and stabilize the allelic composition and heterozygosity of a population (Epling et al. 1960, Gottlieb 1974, Del Castillo 1994).

The physical structure of seeds adds complexity to their genetic makeup. Seed tissues are composed of a maternally-derived diploid seed coat, a diploid embryo derived equally from maternal and paternal heritage, and endosperm that, if present, may have one of several levels of ploidy. Dormancy may therefore be determined by maternal influence via seed coat manipulations (Cabin et al. 1998) or by embryo influence for species with physiological (non-seed coat) dormancy (Baskin and Baskin 1998).

There is considerable evidence that seed dormancy is under some degree of genetic control (Linder and Schmitt 1995, Cabin et al. 1998). Common garden experiments of numerous *Penstemon* species revealed differences in germination requirements that were strongly genetic in nature (Meyer et al. 1995), and an examination of 124 *Penstemon* species provided evidence of adaptive radiation occurring in the form of habitat-specific strategies of germination timing (Meyer et al. 1995).

Several previous studies of seed bank genetics (Tonsor et al. 1993, Cabin 1996), conducted at the scale of a single seed bank, have both found significant differences between above-ground and seed bank genetic structure. Studies by Tonsor and Kalisz (Tonsor et al. 1993) and McCue and Holtsford (McCue and Holtsford 1998) found higher levels of homozygosity in seeds versus adults. Studies of Cabin (Cabin et al. 1998), on the other hand, found higher levels of heterozygosity in the seed bank than in seedlings, with no comparison to adults. An analysis of the genetic makeup of the seed bank itself using allozymes found differences between seeds that germinate and those that remain dormant (Cabin 1996).

Ecological genetic studies using a buried tundra seed profile with seeds aged 0-200 years (Bennington et al. 1991, McGraw et al. 1991, Vavrek et al. 1991, McGraw 1993) have demonstrated phenotypic and genetic differences between populations derived from seeds of differing age and grown in reciprocal transplants. As improvements in the technology of DNA extraction from seeds and the aging of seeds in the soil continue, further studies are needed to illuminate the genetic and evolutionary role of seeds in the soil and provide evidence that compares with numerous predictions of a theoretical nature.

Chapter 6: Seed Germination Trials and a Multi-Year Field Experiment to Assess the Fates of *C. multicaulis* Seeds in the Soil

INTRODUCTION

If a plant is simply a seed's way of making more seeds (Harper 1977) then ecological studies of plants should surely focus on their below-ground life stages. Although many studies have been carried out to examine the germination of seeds, usually under controlled laboratory and germination chamber conditions, comparatively few have tackled the logistics of following seed fates under more natural circumstances.

The studies described here were conducted on seeds of *Cleome multicaulis*, an annual wetland halophyte that is widespread and fairly common in the San Luis Valley of Colorado and has one documented population in southcentral Wyoming. Although the species may still occur in Mexico, populations have not been found (recently) anywhere else in the world, and *C. multicaulis* is considered globally rare (Nature Conservancy of Colorado 1999).

Initial studies indicated the presence of a persistent seed bank in this species that presented the opportunity to incorporate the seed-bank life stage into studies of the population dynamics of this plant with an otherwise annual cycle of life. In hopes of establishing greenhouse populations of the plant, studies were undertaken to investigate the germination of *Cleome multicaulis* seeds in the laboratory on a limited basis.

A three-year field experiment was designed and conducted following the general model of Kalisz (1991) in order to follow the fates of *C. multicaulis* seeds under natural field conditions. Initial estimates of seed bank density in habitat occupied by *C. multicaulis* were obtained. Age-structured conditional probabilities of seed emergence, survival, and persistence were incorporated into the periodic matrix analysis of *C. multicaulis* population dynamics (See Population Biology Chapter). The seed bank data are here more closely examined in order to better understand the ecological factors promoting persistence of seeds in the soil, and to investigate the role of the seed bank as a temporal and spatial extension of this species' niche.

METHODS

Germination Trials

Germination trials were conducted on freshly matured seeds of *Cleome multicaulis* in the fall and winter of 1994-1995 at the USDA National Seed Storage Laboratory, Fort Collins, CO. Seeds were collected in the field and stored in an unheated garage in a paper bag (Young and Young 1986) for several weeks prior to germination attempts. Seeds were subsequently placed in a petri dish lined with blotter paper and moistened with distilled water before being placed in germination chambers (25 seeds per dish, 30 dishes total) at alternating temperature regimes of 25/15 and 20/10 and constant temperature regimes of 16°, 5°, and 0°C with a 14h daily photoperiod.

Salt solutions consisting of a equal mixture of Na_2SO_4 and NaCl at concentrations of 0%, 0.5%, 1.5%, 3%, and 6% were prepared and used to soak seeds (16 seeds per dish, 25 dishes total) that were then placed in total darkness at 5°C. Cumulative germination was observed after a period of six weeks.

Germination trials were conducted at the University of Kentucky in the fall and winter of 1996-1997 by Dr. Carol Baskin, whose assistance is greatly appreciated. Seeds collected in 1995 had been stored at 5°C in the dark prior to shipping; seeds collected in 1996 had been stored in a paper bag in a cool, dry location prior to being shipped to Kentucky. A total of 75 seeds per treatment (25 seeds per dish, 3 dishes each) were stratified on moistened white quartz sand and placed in growth chambers. Constant temperature regimes consisted of 1°C with constant darkness except when seeds were examined in room light and 5°C with a 14 h daily photoperiod.

Alternating 12/12h daily thermoperiods were set at 15/6, 20/10, 25/15, and 30/15°C, each with a daily photoperiod of 14 hours.

Seed viability was determined in the lab by cutting seeds in half, soaking them in a 1.0% solution of 2,3,5,-triphenyl-2H-tetrazolium chloride for a period of several hours, and examining the embryos for evidence of red stain. This method detects activity for the dehydrogenase enzymes associated with respiratory functions in living plant tissue (Ebener 1996). A solution of 0.1% tetrazolium (commonly used) was determined to be ineffective in distinguishing viable seeds of this species. Embryos were excised from a small number (n = 10) of seeds to determine germinability outside the seed coat.

Analysis of Seed Fates in the Soil

A three-year seed cage field experiment was undertaken in order to follow the fates of seeds in the soil and is described in the Periodic Matrix Analysis Chapter of this report. Conditional probabilities of emergence were calculated as the net seed emergence this year divided by the number of seeds remaining in the soil (of the original 200 planted) after emergence last year (See Population Biology Chapter Methods for written formulas). The conditional probability of persistence was calculated as the number of live seeds persisting in the soil in mid-July divided by the number of seeds remaining in the soil (of the original 200 planted) after emergence both last year and this year.

Conditional probabilities of survival represented the probability of a seed in the seed bank surviving from mid-July of the previous year until mid-April of the current year, based on the age of that seed (i.e., conditioned upon survival to that point) (Kalisz 1991). Current year's emergence was not subtracted from the denominator in the calculation of conditional survival probability, since the calculation was made in mid-April of the current year, prior to seedling emergence. Seed mortality in this formula is concentrated into the months between mid-July of one year and mid-April of the subsequent year. This allows for (but does not distinguish) high microbial activity in the warm summer months, seed predation in the fall and winter, and seed loss due to flooding in the early spring (Baskin 1996). Some studies have found higher rates of fungal and bacterial decomposition when soils are snow-covered than during dry summer conditions (Crist and Friese 1993)

Statistical analysis of the conditional probabilities of emergence, survival, and persistence was conducted using PROC MIXED (SAS 1997). Probabilities were arcsin-square root transformed prior to analysis in order to meet the assumptions of homogeneity of variance. Location here was treated as a fixed effect because the model was balanced by date and location.

Measurements of Seed Bank Density

Soil core samples were taken of the seed bank using a soil core of diameter 5cm and depth 15cm in four locations in 1995 and 1996 and in three locations in 1997 where above-ground density of *C. multicaulis* was high. The purpose of sampling the soil seed bank in this study was to determine the density of persistent seeds in the soil. Samples were therefore taken repeatedly beginning just after germination and until (but not including) the addition of current year's seed rain to the soil. A total of 10 samples were taken at each location on each sampling date, with the exception of the first sampling date in 1995.

Samples were taken on 3 dates in 1995 and 8 dates in 1996 and 1997, respectively, with a total of 120 samples taken in 1995, 320 samples taken in 1996, and 240 samples taken in 1997 (Grand total of 680 samples taken). Samples from a 9th sampling date were determined to contain seeds from the current seed rain, and were omitted from the analysis (Baskin and Baskin 1998). The precision of seed number estimates is improved by taking many small samples rather than a few large ones (Bigwood and Inouye 1988), although even this number of samples is undoubtedly inadequate to accurately characterize the seed bank density. Seeds were extracted using a series of sieves and the number of filled seeds recorded for each sample.

Statistical Methods

Statistical analysis utilized PROC MIXED (SAS 1997) that served both to analyze repeated measures models when necessary (i.e., for emergence and survival data) and as an analysis of variance model when data resulted from destructive (i.e., non-repeated) measures such as the conditional probability of persistence and percent seed viability. While transformed means were used to generate tests of significance, untransformed means are presented in tables and figures for comparative purposes.

RESULTS

Germination Trials

Less than 3% germination of *C. multicaulis* seeds occurred under any of the alternating temperature regimes (25/15 and 20/10°C) or constant temperature regimes (16°C, 5°C, 0°C) with a 14h daily photoperiod. Seeds stratified on moist blotter paper and placed in total darkness at 5°C showed a cumulative total of 17.8% germination after 6 weeks. Less than 2% additional germination occurred when dishes were transferred to growth chambers with various different light/temperature regimes.

After 6 weeks, seeds soaked in salt solutions of NaCl and NaSO4 germinated at least to some extent in salt solutions as high as 3% salt (Table 6.1). Seeds collected in 1996 that were placed at 5°C and wrapped in foil (darkness) showed only 1.8% germination after 12 weeks.

Germination trials conducted by Carol Baskin (Baskin 1997) indicated the greatest germination success at 5°C, with higher cumulative germination percentages from 1995 seeds (Table 6.2) than from those collected in 1996 (Table 6.3). Seeds of *C. multicaulis* most likely possess physiological dormancy (Baskin 1996) as do the vast majority of halophytic species with dormant seeds, and likely undergo annual cycles of dormancy (Baskin et al. 1993, Baskin et al. 1996).

Seed Viability

The viability of *C. multicaulis* seeds did not decline with seed age over the period of the study (Table 6.4). In a model of analysis of variance, both age (d.f. = 2,90; F = 3.63; p = 0.0306) and year (d.f. = 2,20; F = 6.68; p = 0.0060) had a significant effect on seed viability (arcsin). A significant proportion of the seeds harvested in this study were light colored, and tetrazolium tests indicated that both filled, light-colored seeds and dark colored seeds had high (and equal) percentages of viability. When embryos were excised from *C. multicaulis* seeds (from primarily dark-colored morphs), high percentages of germination occurred (Crane 1996).

Analysis of Seed Fates in the Soil

Conditional probabilities of seed emergence (Table 6.5) ranged from 0 - 22.27% (mean = 4.13%, std. dev. 4.92). Conditional probabilities of seed survival ranged from 0.50% - 48.40% survival (mean = 22.44%, std. dev. 10.00), and for seed persistence, the conditional probabilities (Table 6.4) ranged from 0.50 - 45.16% (mean 18.97%, std. dev. 9.82).

Conditional probabilities of emergence and survival were examined using repeated measures analysis (Tables 5.6. 5.8), and the conditional probability of persistence was examined using analysis of variance (PROC MIXED) (SAS 1997) (Table 6.9) There was a significant effect of seed age on the (arcsin square-root) conditional probability of emergence (Table 6.6) but no significant effect of seed age on the conditional probability of either persistence (arcsin square root, Table 6.8) or survival (arcsin square root, Table 6.9). The estimated variation across locations (using a calculated ratio of location to residual covariance parameter estimates, Table 6.8) (Chapman 1996) was highest (in proportion to residual variation) for the conditional probability of persistence, and lowest for the conditional probability of emergence, with intermediate values for the conditional probability of survival. Estimated least square mean conditional probabilities of emergence, survival, and persistence were calculated by seed age (Table 6.11) and by location (the latter for heuristic purposes only, since this required designating location as a fixed effect; Table 6.10).

When data were summarized across years for each location (n = 11), correlations between soil characteristics, population growth rates and elasticities, and conditional probabilities of seed emergence, survival, and persistence were run (Table 6.12). At this level of summary data (Table 6.13), the previously significant correlations between soil Ec and soil moisture and between soil pH and plant density (Table 3.6) were no longer evident. Other previously reported significant correlations (Table 3.6, Table 4.11) remained significant using this level of summary data.

Soil Characteristics in Seed Cages vs. Census Quadrats

Soil characteristics (pH, conductivity, and soil moisture) of the seed cages (Table 6.14) were measured only once using a portion of soil reserved from the experimental seed cages (n = 25) after their destructive harvest in 1996. Although additional soil assessments would have been useful, continued removal of soil from the harvested seed cages for testing would have biased (underestimated) the process of sieving the total quantity of soil harvested to recover the persistent portion of the soil seed bank. Comparisons are made between soil characteristics as measured in the seed cages, soil measurements taken at the same time just outside census quadrats, and the three-year average soil characteristics for all dates and locations. These results indicate that both soil pH and soil salinity were higher in the seed cages than in the nearby census quadrats for the period measured in July of 1996. Levels of soil moisture appeared to be comparable to those in nearby census quadrats at the time of measurement.

Field Observation of Environmental Factors Affecting Germination of *C. multicaulis*

Several populations of *Cleome* were observed to germinate while in standing water, that receded by the time seedlings emerged. Prolonged flooding (e.g., longer than 1-2 weeks) did not allow adult plants to survive. Evidence from the summer 1995 flooding of the San Luis Lakes site indicates that the soil seed bank can tolerate sustained levels of inundation and remain viable and germinable. Laboratory assays to determine the effect of either continuous or periodic inundation on germination success were not conducted in this study.

The absence of a light requirement for germination may account for the observed success of *C. multicaulis* seed germination underneath layers of dead plant litter. Laboratory trials also revealed that seeds of *C. multicaulis* germinated in spite of fungal infection (species unknown), although the extent to which seed-borne fungi affect germination in the field is unknown.

Field observations indicate that *C. multicaulis* germination is facilitated by soil disturbance, as significant numbers of newly emerged seedlings were noted alongside dirt roads and in other disturbed areas. The effect of soil disturbance on germination was not quantitatively assessed in this study.

Analysis of Seed Bank Density of *Cleome multicaulis*

There was a significant effect of year on the density of seeds in the seed bank (square-root) using repeated measures analysis (d.f. = 2,55; F = 15.01; p = 0.0001) but no significant effect of date (d.f. = 7,55; F = 0.60; p = 0.7505). There was a large amount of estimated variation across locations. Insufficient numbers of seeds were extracted at location BW3 and in year 1995 to calculate estimated least square means using the repeated measures model, so simple arithmetic means and standard deviations were calculated for heuristic purposes (Table 6.15).

DISCUSSION

Laboratory Studies of Germination of *Cleome multicaulis*

Limited germination trials at the National Seed Storage Laboratory indicate that seeds of *C. multicaulis* have the ability to germinate (6.3% cumulative germination) in solutions as high as 3% salt (Na_2SO_4 and NaCl), although germination is apparently inhibited in solutions of 6% salt (Table 6.1). These germination trials were conducted in complete darkness because preliminary investigations indicated that germination occurred more readily in the dark than in alternating light/darkness.

Although the germination trials undertaken here were limited in their scope, it appears that seeds of *C. multicaulis* germinate best at temperatures of 1 to 5 °C, germinate in both total darkness and under a 14 hour daily photoperiod (Tables 5.2, 5.3), and have the ability to germinate in solutions as high as 3% Na_2SO_4 and NaCl. Although some halophytes germinate to higher percentages in NaCl concentrations of 0.25 - 0.50% than in distilled water, most halophytes have reduced germination in solutions higher than 1% NaCl (Baskin and Baskin 1998). Seeds of both *Distichlis stricta* var. *spicata* and *Glaux maritima* showed a germination decrease from 75% down to 10% in solutions of 0.5% NaCl (Baskin and Baskin 1998). There is an interaction between temperature and salinity such that salinity tolerance may increase when soil temperatures are low (Badger and Ungar 1989, Foderaro and Ungar 1997). For instance, seeds of *Salicornia pacifica* germinated at 5% NaCl but only when temperatures were at or below 15 °C (Khan and Weber 1986).

Laboratory germination assays were not conducted in this study to determine whether germination is enhanced, inhibited, or unaffected by high pH. Seed responses to pH and soil salinity may be associated or distinct (in the same way as above-ground plant response) and few studies have examined this phenomenon (but see (Khatri et al. 1991)). Soil pH may influence seed germination rates and percentages, but pH has not been shown to change the dormancy state of seeds. Some species will germinate at a wide range of pH values, while others are much more restricted in their germination requirements (Baskin and Baskin 1998).

Low soil temperatures may protect seeds from extremes of pH by inhibiting germination (Lacey and Line 1994). Fewer studies have been conducted on the germination requirements of seeds occupying alkaline habitats than those that are acidic. Seeds allowed to imbibe in salt solutions have been shown to increase the hydrogen ion concentrations around them, thus lowering the pH of their immediate surroundings (Baskin and Baskin 1998). Whether plants of alkaline habitats tolerate (or require) high pH or employ the above strategy to lower the pH of their environment has not been investigated under natural conditions (Baskin and Baskin 1998).

Additional studies in the field and lab are needed to determine whether the seed response of *C. multicaulis* to soil pH and salinity is associated or distinct.

Germination trials done by Carol Baskin (Baskin 1997) at the University of Kentucky indicated that seeds of *Cleome multicaulis* germinate best at a temperature of 5°C in a 14 hour daily photoperiod (Tables 5.2, 5.3). There were striking differences between trials in the percentage of seeds that germinated in darkness at 1°C, with 38.7% cumulative germination from 1995 seeds versus only 6.7% cumulative germination from seeds collected in 1996. In both years, seeds were collected from across several macroplot locations, mixed together, and stored in a paper bag in a cool, dry location until brought inside the lab. Seeds from 1995 were stored over the year in a refrigerator set at 0 °C that remained dark except when other seeds stored inside were examined.

Differences in the relative germinable fraction of 1995 versus 1996 seeds at 1°C may nevertheless reflect handling differences (Baskin 1996). The germination response of seeds from a single species has been found to vary under different storage conditions (Steiner 1968, Cheplick 1996). There may also be year-to-year variation in the annual dormancy cycle of this species (see Discussion which follows).

Seasonal changes in germination response were not assessed in the lab or field due to the difficulties encountered in initial laboratory germination trials (Baskin 1996). Seeds of *C. multicaulis* were likely leaving conditional dormancy and becoming responsive to low temperatures during the time of laboratory germination trials. A study such as this does not distinguish between the factors governing dormancy release and those allowing germination (Vleeshouwers et al. 1995, Baskin and Baskin 1998). Further studies are needed to illuminate the germination requirements and annual dormancy cycle of this species.

To the extent that germination ecotypes occur in *C. multicaulis*, these may not have been adequately randomized when seed collections were made in the field for purposes of germination trials. The extent of germination ecotypes among Colorado and Wyoming populations of *C.*

multicaulis is unknown.

In this study, light-colored seeds of *C. multicaulis* that were filled were shown to have viability equal to that of darker-colored, filled seeds. In contrast, a study of *Cleome serrulata* (the closest relative to *C. multicaulis*) categorized light-colored seed morphs as inviable, apparently without tetrazolium testing (Luce 1983). This reduced reported seed set in her study to levels of approximately 42-47% seed set per fruit. Differences in seed coat color may result from differences in physiological seed maturity (Luce 1983, Young and Young 1986); color morphs (e.g., in several species of *Atriplex)* may also correspond to differences in seed size and result in imbibition differences (Wertis and Ungar 1986).

Seed Viability and Viability Testing Using Tetrazolium Chloride

Viability of *C. multicaulis* seeds is relatively high and does not appear to diminish with seed age (Table 6.4). In contrast to the results of this study, Kalisz' multi-year study of the winter annual *Collinsia verna* seeds in the soil revealed that viability of seeds after one year was 16%; after two years, 12%, and after three years viability dropped to 6% (Kalisz 1991).

Although it is currently the only known technique to determine seed viability and enjoys widespread use, testing with tetrazolium chloride has provoked some measure of controversy, perhaps in part because of the continuing confusion over terminologies of dormancy. Viability testing with tetrazolium simply provides an indication of cellular viability, and does not test the ability of all the cells needed to complete the complex process of germination. As seeds lose viability, nucleic acids, membrane components, and enzymes become damaged, the structural integrity of membranes deteriorates, and organelles may become damaged. The embryo may accumulate chromosome aberrations, most likely due to fragmenting of DNA and often causing genetic damage (Baskin and Baskin 1998). A tetrazolium test does not detect chemical injury to seeds caused by fungicides or insecticides, nor does it detect microorganisms harmful to germinating seedlings (Baskin and Baskin 1998).

Some authors feel that tetrazolium testing effectively distinguishes dormant from non-dormant seeds (Baskin and Baskin 1998), but may not differentiate types of dormancy (e.g., endogenous versus exogenous or seed coat dormancy) (Ebener 1996). Others state that deeply dormant viable seeds sometimes show only minimum staining with tetrazolium chloride (Phillipi 1993b, Pake and Venable 1996). Seeds that are viable and stain red with tetrazolium will not always germinate when factors causing dormancy are overcome (Lindauer and Quinn 1972, Young and Young 1986). Populations of *Danthonia sericea* that differed in their germination response showed no significant interpopulational differences in viability using tetrazolium testing (Lindauer and Quinn 1972)

If indeed tetrazolium testing underestimates the number of viable but dormant seeds (as Phillipi argues), it also is likely to overestimate the number of viable but non-germinable seeds (because germination requires more than simply dormancy release). The magnitude of neither of these effects is easily estimated, but it is possible that their net effect will be minimal and the technique is considered acceptable for purposes of this study.

Analysis of Seed Fates in the Soil

There was little variation in the conditional probability of emergence across locations (Table 6.5) and the highest measure of emergence was location RL1. Younger seeds had a higher conditional probability of emergence (Table 6.5), suggesting that seed age may have a stronger effect on emergence than microsite environmental conditions.

The conditional probability of persistence did appear to vary according to environmental site characteristics between locations (Tables 6.7, 6.9), but did not appear to decline with seed age (Table 6.9). Although the mean conditional probabilities of persistence for seeds aged 1-2 and 2-3 years were essentially identical (Table 6.9) there was higher variability in this measure of persistence for seeds aged 2-3 years (Table 6.13). This may indicate that seeds of *C. multicaulis* have the potential to be long-lived, but the extent to which this potential is realized (i.e., the actual seed bank longevity) may depend on environmental conditions.

Both the conditional probability of survival and persistence were highest at location RL6 (Table 6.10), which is also close to the site with the highest density of the soil seed bank sampled in this study (Table 6.15). The correlations generated for heuristic purposes (sample sizes were limited to 11 data points) between soil moisture (in a range of 15 - 50%) and survival and persistence of seeds aged 2-3 years (Table 6.12) may indicate that moister soils such as those found at location RL6 provide a favorable environment for the persistent seed bank of *C. multicaulis*.

The conditional probability of survival did not decline with seed age in this study (Table 6.8), and any differences in survival across locations as a result of microsite differences were weaker than for the probability of persistence (Table 6.7). Variability in this measure of seed survival was highest for the youngest and oldest seeds and lowest for the seeds aged 1-2 years (Table 6.13).

The presence of soils with high salinity may be associated with reduced conditional probabilities of seed emergence (at least of seeds aged 0-1 and 1-2 years), although these correlations were only marginally significant (Table 6.12). The presence of high pH soils may be associated with reduced emergence of the youngest (age 0-1) seeds as well, although the marginally significant positive correlations between soil pH and measures of persistence and elasticity (Table 6.12) suggest that older seeds may benefit (or at least are not harmed) from being located in high pH soils.

In the only other study to experimentally determine emergence from the seed bank (of *Collinsia verna*, a winter annual), Kalisz (1991) found that the conditional probability of emergence for seeds aged up to one year ranged from 26-40%, in the second year was 3-16%, and in the third year was 8%. The conditional probability of persistence in the seed bank for one year ranged from 22-29%, for two years was 15%, and for three years was 19%. In comparison to

Collinsia verna, *Cleome multicaulis* in this study had considerably lower first-year emergence from the seed bank but comparable conditional probabilities of seed bank persistence, which may indicate that the seed bank of *C. multicaulis* is longer-lived than that of *Collinsia* (Kalisz did not calculate a separate conditional probability of survival (Kalisz 1991)). The seed bank of *Collinsia verna* may show variation in the degree of seed bank persistence in populations from Illinois versus Pennsylvania (Kalisz 1995).

Kalisz found that conditional probabilities of emergence and persistence (for the first year only) varied across her three 75 m transects, as did the probability of plant survival to flowering (but not the probability of survival through the autumn) (Kalisz 1991). The variation in probability of seed bank emergence was attributed to variability in autumn weather conditions, whereas the survival and persistence of dormant seeds was attributed to site conditions such as soil type, aspect, and biotic interactions of the seed with its surroundings (Kalisz 1991). She found that the transect likely subject to the greatest amount of historical flooding (even during her study) had the highest seed bank persistence rate, but stopped short of concluding that selective forces had resulted in the evolution of increased dormancy (sensu Cohen (1967)) at that transect site.

Suggestions for improvement of the experimental protocol used in this study of *C. multicaulis* (that was based heavily on the work of Kalisz) are presented in Appendix 6.1.

Soil Characteristics in Seed Cages versus Census Quadrats

In this study, the effect of containing soil in a mesh cage appears to be to concentrate salts, causing (at least at the time of measurement) apparently increased conductivity and soil pH in the microclimate of the seed cage (Table 6.14). Lack of established (i.e., rooted) vegetation in the seed cages may have increased soil conductivity (Shumway and Bertness 1992) in addition to facilitating lateral movement of seeds. The possible inhibitory effect of high pH and/or Ec on germination was not measured. It is possible that germination inside seed cages may have been enhanced as a result of artificial soil disturbance (soil mixing) and reduced due to higher levels of soil pH and/or salinity, with few net differences observed between germination inside and outside of seed cages. Based on statistical analysis done for other portions of this study (e.g., Table 3.6), the expected effect of increased conductivity in seed cages might be to decrease the reproductive output (and possibly the density) of plants in that seed cage.

Seed cages did not appear to be either wetter or drier than the surrounding environment at the time of measurement in 1996 (Table 6.14). The complete failure of seed cages at Mishak Lakes was likely due to a combination of insufficient soil moisture and high salinity, and seed cages at other locations apparently did not suffer a similar fate. To the extent that soil settling occurred, moisture tended to accumulate in the microsite depressions created inside the cages, but increased moisture in selected seed cages would not necessarily have an adverse effect on soil seed bank dynamics (see discussion above). Topographic depressions may cluster seeds out of the reach of wind, but may also increase density-dependent seedling mortality (Reichman 1984, Bigwood and Inouye 1988). At the density of seeds planted in this study, any effect of density-dependent factors was most likely felt in the first year of germination, since subsequent emergence was so low.

Field Observation of Environmental Factors Affecting Germination of *C. multicaulis*

Seeds of *C. multicaulis* apparently germinate at higher percentages in cold (e.g., 0-5 degrees C) temperatures (Tables 6.2, 6.3), and no evidence exists that they will germinate at high temperatures when freshly mature, as is characteristic of some species with annual cycles of dormancy (Baskin and Baskin 1998). Other studies have shown that temperature appears to be the primary environmental factor regulating germination, with light and soil moisture of secondary importance (Baskin and Baskin 1988), although the factors dictating the success of early life history stages are still poorly understood for most plant species (Shumway and Bertness 1992).

Soil temperatures affect soil water content via evaporation and have a direct effect on microbial activity, which is a key component of organic matter cycling and nutrient availability.

Soil temperatures are determined by the interaction of soil color, texture, and drainage with the input of solar radiation (Wagner and Spira 1994). Germination requirements such as light and tolerance to salinity may vary with soil temperature (Baskin and Baskin 1998).

Soil salinity in areas occupied by *C. multicaulis* in the San Luis Valley is not consistently at its lowest level at the time of year when seeds of this species germinate (Figure 3.4). Preliminary laboratory germination tests indicate that seeds of *C. multicaulis* have some ability to germinate in 3% salt solutions (Table 6.1). Seed sensitivity to salinity may be greater under natural conditions than in the lab, perhaps due to the interaction of plant water stress and soil salt concentrations in the field (Shafroth et al. 1995), and laboratory conditions are likely to represent an oversimplification of most temporally complex germination environments.

Germination studies (both field and lab) have characteristically focused on soil salinity rather than soil pH as the critical ecological factor in seed germination behavior (Ungar 1978, Khan and Ungar 1984, Woodell 1985, Badger and Ungar 1989, Bertness et al. 1992, Allen et al. 1997). Further studies are needed to determine whether the seed life stage of *C. multicaulis* responds distinctly to soil pH in terms of seed density and spatial distribution of the seed bank, emergence, seed viability, persistence, and other seed population dynamic parameters. The variable and unpredictable nature of soil pH documented elsewhere in this study suggests that germination timing in the field may not be cued to this soil parameter.

Although seeds of *Cleome multicaulis* clearly have the capacity to germinate after being flooded in the early spring, the effect of flooding at other times of the year on the viability and/or germinability of *Cleome* seeds is unknown. Frequent changes in water level may have the effect of mixing soil nutrients, smoothing the soil surface, increasing soil homogeneity, and facilitating germination (Huenneke and Sharitz 1990, Smith et al. 1995). The timing of inundation episodes may be important in influencing seed germination to the extent that viability may be reduced in seeds that are subject to flooding at a critical point in their dormancy cycle (Baskin et al. 1996).

Cleome multicaulis seeds apparently have the ability to germinate underneath plant litter, and numerous quadrats contained dense mats of the previous year's vegetative growth, from under which seedlings emerged. The presence of plant litter and/or established plants may inhibit gemination by reducing the variability in temperature, preventing germination of small seeds, or preferentially transmitting wavelengths of light that are inhibitory for germination (van Baalen 1982, Welling et al. 1988, Rees and Long 1993). Seeds persisting in the soil underneath these densely covered patches may be afforded some protection from seed predation. Vegetation may also serve to anchor seeds prior to germination in order to avoid the seeds being washed away in spring floods.

Seeds of *C. multicaulis* germinated in the lab in spite of apparent fungal infection (species unknown). Fungi are ubiquitous in soil and may affect seed survivorship directly by decomposition or by causing disease, or indirectly by altering the seed preference of granivores (Crist and Friese 1993). Few studies have addressed the role of soil fungi and bacteria in seed bank dynamics (Baskin and Baskin 1998). Fungi may produce toxins that interfere with predation by ants or larger animals (Crist and Friese 1993, Baskin and Baskin 1998). Fungal seed pathogens may either inhibit or stimulate germination, the latter through production of ethylene (Baskin and Baskin 1998). Small seeds were found to be more susceptible to decomposition and pathogens than larger seeds (Crist and Friese 1993). In addition to causing seed death, fungi may reduce seedling survivorship. Some studies have found seed-borne fungi to be more common in early-successional annuals than other life-history stages (Bazzaz 1996). The effect of fungi on seed viability and germination in *C. multicaulis* is unknown.

It seems apparent from observations of natural populations of *C. multicaulis* that seed germination is facilitated by soil disturbance. Soil substrate and/or level of soil disturbance may influence germination success in species with and without a persistent seed bank (Pavlik and Manning 1993, Menges 1995). The magnitude of germination enhancement that may have occurred as a result of physically mixing soil prior to the planting of *C. multicaulis* seeds into experimental seed cages is unknown.

The effect of trampling on germination of *C. multicaulis* seeds has not been experimentally determined but remains an important question to address. Co-occurrence of *C. multicaulis* habitat with cattle grazing at Mishak Lakes and bison grazing at the Medano/Zapata Ranch may significantly impact both germination and adult survival of *Cleome*. Harper's classic (but highly simplistic) study of the behavior of seeds in the soil (Harper et al. 1965) was inspired by the observation that increased germination of *Plantago* sp. occurred where the hoof marks of pigs were found. Emergence in all three species studied was increased by simulating trampling through compressions of the soil (Harper et al. 1965).

Other factors that may affect germination include soil particle size, the orientation of the seed in the soil, soil texture, soil strength (resistence to penetration that affects seed burial depth) and small-scale disturbances and variations in microtopography (Keddy and Constabel 1986, Haukos 1993, Stark 1994, Vasquez-Yanez 1994, Bosy and Aarssen 1995, Smith et al. 1995).

Effect of Maternal Environment on Seed Germination

Environmental conditions in the year of seed production may have important influences on the rates of seed germination and dormancy release (Phillipi 1993a,b). In this study, larger plants (with high seed production) occupying areas of low *C. multicaulis* density may provide an importance source of seeds for the soil seed bank, although the relationship between size of the maternal plant and seed bank survival and persistence in this species is not known.

In a study of desert (winter) annuals, sites with greater precipitation in the year of seed maturation produced seeds with more dormancy. Interestingly, increased precipitation at the time of germination correlated with increased seedling emergence, whereas increased precipitation at the time seeds were produced showed a negative correlation with subsequent germination and emergence (Phillipi 1993b). Previous experiments found that summer annuals that experienced more predictable precipitation had significantly higher germination (Freas and Kemp 1983). The ratio of dormant to non-dormant seeds produced may vary depending on the time and season when seed production begins and ends (Silvertown 1984). Late-maturing seeds may have earlier seedling emergence, providing an advantage the subsequent year (Roach 1986).

Seed Bank Densities of *Cleome multicaulis*

The limited sampling of the seed bank conducted in this study (120 samples in 1995, 320 samples in 1996, and 240 samples in 1997) appears to indicate that areas of the highest above-ground density of *C. multicaulis* do not necessarily have the greatest density of soil seeds. The greatest density of plants among the study sites censused was at Blanca Wetlands (locations BW1, BW2, and BW3). Samples of the seed bank taken right outside location BW3 did not show a comparatively large number of soil seeds over the three years censused (Table 6.15) although seeds there had the second-highest conditional probabilities of survival and persistence (Table 6.10).

The sampling site in close proximity to location RL6 had both the highest seed bank densities (Table 6.15) and conditional probabilities of survival and persistence (Table 6.10) measured, yet population growth rates were among the lowest calculated (λ of 0.87, 0.12, and 0.08 over the three years 1995-1997, respectively, Table 4.5). Moist soils at this location may have enhanced seed bank longevity, but not enough to boost population growth.

Methods of estimating seed bank density include either physical extraction (by passing seeds through sieves of consecutively smaller sizes, or by floating seeds in a salt solution) or the emergence method, where soil seed bank samples are placed in a greenhouse to germinate over a period of several months. Comparison of the two techniques indicated that the extraction methods predicted 12,500 seeds of 102 different species, whereas the emergence technique predicted only 3800 seeds of 60 different taxa (Brown 1992). Comparisons of the two methods were not possible in this study because of difficulties encountered in re-creating an optimal greenhouse germination environment for this species.

Seed bank density varies from place to place as a result of irregular clustering and uneven horizontal distributions in a given habitat (Thompson and Grime 1979, Baskin and Baskin 1998). Seed bank densities reported in one comprehensive compilation ranged from 9/m^2 to 24,393/m^2 of soil (Baskin and Baskin 1998).

Several authors have found higher seed bank densities in microclimates underneath shrub canopies (Hassan and West 1986, Cabin et al. 1998). Seed bank densities under canopies of *Sarcobatus vermiculatus* were not measured in this study, although clusters of *C. multicaulis* plants were observed under these shrubs. High seed bank densities of *Lesquerella fendleri* (a desert annual) under creosote canopies were attributed to lower light intensity, lower soil temperature, and greater surface organic matter. Evaporation rates of soil water may also be lower under canopies of creosote, although the presence of shrubs may increase water demand on soils to counteract this effect (Cabin et al. 1998).

Significant ant activity was noted in close vicinity to microsites occupied by *C. multicaulis*; however, the extent of seed predation by ants and other sources of seed mortality were not directly measured in this study. Seeds in the San Luis Valley experience a significant number of days each winter with sub-zero (Fahrenheit) temperatures (Foutz 1994). The physiological response of *C. multicaulis* seeds to extreme cold has not been examined, although the consistently high viability of seeds of age 2-3 years indicates that physiological seed death may not occur for a number of years.

Seeds of *C. multicaulis* appear to germinate more readily in disturbed soils than in those that are undisturbed, but a comparison of seed bank density along a gradient of soil disturbance was not conducted in this study. Higher seed bank densities have been found in disturbed versus undisturbed soils in community-level studies of persistent seed banks (Thompson 1978), but studies have not examined comparative seed bank densities along a disturbance gradient for a single species.

The presence of a persistent seed bank is predicted to increase the uniformity in spatial distribution of adult plants by reducing the large-scale variability in density across the landscape (Bigwood and Inouye 1988), although empirical studies are likely to be confounded by interspecific factors affecting the spatial placement of plants on the landscape. Measurements of seed bank density comparing changes in seed bank density over long (e.g., 10-year) periods of time may obscure high seed turnover occurring between sampling dates (Keeley 1987).

When "birth" of a seed occurs at the time of seed maturation (as is considered in this study), then seeds in the soil may be of uniform age (i.e., a transient seed bank (Thompson 1978)) or diverse ages (i.e., a persistent seed bank). The presence of an age-structured persistent seed bank may ameliorate seed-seed or seed-seedling competitive conflicts by facilitating dispersal through time rather than space (Schupp 1995). Little is known about the relative effects of biotic interactions (competition, predation) on seed banks of even versus uneven-aged seeds.

Seed Dispersal and Lateral Movement

Seed dispersal was indirectly assessed in the seed cage experiment in that seeds dispersing into each cage became part of the resident population, with the assumption that experimental and control sides of the seed cage were evenly impacted by emigration. Dispersal distances of *C. multicaulis* seeds were not directly assessed, in part due to the difficulties of maintaining sticky seed traps close to the soil surface in an environment subject to unpredictable and periodic flooding.

In this study, seeds were observed to float, both in the lab and in the field although seeds of *C. multicaulis* have previously been reported as incapable of waterborne dispersal (Graff 1992). Seeds of *C. multicaulis* lack obvious external morphological structures such as hairs or aerial tissues that might aid in buoyancy (Huiskes et al. 1995). Seed dispersal may be augmented by transport in mud attached to the hooves of cattle (at Mishak Lake Preserve) or bison (at Medano/Zapata Ranch Preserve). Many common (i.e., successful) species associated with disturbed habitats lack any obvious seed structures to aid dispersal (Fenner 1985).

Frequent and periodic flooding of the soil surface in habitat occupied by *C. multicaulis* may facilitate lateral seed movement, although the extent of such movement was not directly assessed in this study. Evidence that at least some small-scale lateral seed movement occurred in this study comes from observed clustering of seedlings despite the uniform sowing of seeds in each cage. Removal of rooted vegetation from the seed cages may have increased lateral movement within and between seed cages (Smith and Kadlec 1985). The ecological importance of lateral seed movement may be minimal in some (e.g., forest) habitats (Primack 1996) and be more extensive in coastal (Grillas 1993) or wetland (Lieffers and Shay 1981) habitats. Seeds of *Triglochin maritima* may float for up to 6 months' time and travel distances of 60km or more, and wetland dispersal may be facilitated by seed attachment to floating vegetation (Ellison 1987).

The lack of connectedness in ephemeral wetlands such as playas may limit opportunities for dispersal and increase dependence on the seed bank for the composition of above-ground vegetation (Haukos 1993). Seeds that are moved via flooding during periods of inundation may become stranded in unsuitable habitat when water levels recede, or may be washed to the soil surface where they are more easily eaten by herbivores (Haukos and Smith 1996).

Habitat patches that are favorable for above-ground growth may or may not be favorable for the long-term existence of soil seeds. Identification of favorable habitat for both seed bank and above-ground life stages may be complex, and seeds may not disperse to areas that are equally favorable for seeds and seedlings. Seeds that extend their temporal occupancy of the soil by forming persistent seed banks will encounter conditions favorable for seed survival in some instances and for seedling survival in other conditions of a variable environment (Schupp 1995). Describing the niche extension of species with persistent seeds in the soil will continue to provide challenges for ecologists wishing to synthesize theoretical predictions with empirical results.

TABLE 6.1

Cumulative Germination of *C. multicaulis* Seeds After 6 Weeks, Complete Darkness, Salt Solutions of Equal Parts NaCl and $NaSO_4$

	0% Salt	0.5% Salt	1.5% Salt	3.0% Salt	6.0% Salt
Cumulative Germination	17.5%	16.3%	7.5%	6.3%	0.0%

TABLE 6.2 **Cumulative Germination Percentages of *C. multicaulis* Seeds Collected in 1995 and Trials Conducted by Carol Baskin**

(Table Courtesy of Carol Baskin)

	1 °	**5°**	**15/16°**	**20/10°**	**25/15°**	**30/15°**
Weeks						
2	0%	0%	1.3%	0%	0%	0%
4	36.0%	22.7%	1.3%	0	0	0
6	36.0%	26.7%	1.3%	0	0	0
8	37.3%	34.7%	1.3%	0	0	0
10	37.3%	40.0%	2.7%	0	0	0
12	38.7%	42.7%	2.7%	0	0	0
14	38.7%	46.7%	2.7%	0	0	0

TABLE 6.3 **Cumulative Germination Percentages of *C. multicaulis* Seeds Collected in 1996 and Trials Conducted by Carol Baskin**
(Table Courtesy of Carol Baskin)

	1 °	**5°**	**15/16°**	**20/10°**	**25/15°**	**30/15°**
Weeks						
2	0%	0%	0%	1.3%	0%	0%
4	0%	1.3%	0%	1.3%	0	0
6	0%	8.0%	1.3%	1.3%	0	0
8	2.7%	16.0%	1.3%	1.3%	0	0
10	2.7%	20.0%	1.3%	1.3%	0	0
12	2.7%	22.7%	1.3%	1.3%	0	0
14	6.7%	29.3%	1.3%	1.3%	0	0

TABLE 6.4 Estimated Least Square Mean Seed Viability by Seed Age and Year of Study

Seed Age	Estimated Least Square Mean Seed Viability (Std. Error)	Year	Estimated Least Square Mean Seed Viability (Std. Error)
0-1 years	82.37% (1.95)	1996	74.98% (3.14)
1-2 years	79.18% (1.98)	1997	80.10% (1.97)
2-3 years	84.74% (3.06)	1998	91.21% (1.92)

TABLE 6.5 Conditional Probabilities of Emergence, Survival, and Persistence by Location and Seed Age

Seed Cage Location	Seed Cage Age	Average Net Emergence	Cond. Probability Emergence	Cond. Probability Survival	Cond. Probability Persistence
1	1	14.1	0.0705	0.2309	0.1725
1	2	3.2	0.0160	0.3043	0.2922
1	3	2.0	0.0105	0.1840	0.1750
2	1	7.1	0.0355	0.3272	0.3025
2	2	21.6	0.1087	0.3045	0.2167
2	3	4.5	0.0272	0.1292	0.1057
3	1	11.8	0.0591	0.4840	0.4516
3	2	15.8	0.0819	0.2244	0.1535
3	3	1.3	0.0072	0.1472	0.1410
4	1	44.6	0.2228	0.3368	0.1467
4	2	26.4	0.1568	0.2304	0.0729
4	3	0.0	0.0000	0.0736	0.0736
5	1	7.3	0.0363	0.1899	0.1594
5	2	1.9	0.0107	0.2072	0.1995
5	3	2.3	0.0116	0.1948	0.1852
6	1	0.9	0.0046	0.1679	0.1641
6	2	3.4	0.0169	0.2542	0.2413
6	3	1.0	0.0051	0.2595	0.2557
7	1	1.9	0.0094	0.2375	0.2303
7	2	0.8	0.0040	0.1769	0.1736
7	3	0.0	0.0000	0.1318	0.1318
8	1	6.8	0.0339	0.0957	0.0640
8	2	12.4	0.0623	0.1108	0.0498
8	3	0.0	0.0000	0.0050	0.0050
9	1	20.6	0.1030	0.2863	0.2043
9	2	0.8	0.0042	0.1717	0.1678
9	3	6.0	0.0333	0.4571	0.4382
10	1	13.3	0.0664	0.2649	0.2126
10	2	7.3	0.0376	0.2192	0.1874
10	3	2.6	0.0141	0.3491	0.3396
11	1	4.0	0.0200	0.2413	0.2259
11	2	6.4	0.0321	0.2325	0.2067
11	3	12.0	0.0623	0.1701	0.1140

TABLE 6.6 **Summary of Repeated Measures Analysis of the Effect of Seed Age on the Conditional Probability of Emergence**

Model: Conditional Probability of Seed Emergence (Arcsin Square-Root) = Seed Age

Random Effects: Location

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Conditional Probability			Residual
of Emergence	Seed Age	0.0196**	

Note: It was not possible to assess the effect of year on the conditional probabilities of emergence, survival, or persistence because the study design did not allow seed cages of each age in each year.

** $p < 0.05$
* $p < 0.10$

TABLE 6.7 Covariance Parameter Estimates for Random Effects in Repeated Measures Models of Conditional Probabilities of Emergence, Survival, and Persistence

Covariance Parameter Estimates	**Conditional Probability of Emergence**	**Conditional Probability of Survival**	**Conditional Probability of Persistence**
Location	0.00121637	0.00398645	0.0066847
Residual	0.00984190	0.01268936	0.01167912
Calculated Ratio of Location to Residual*	0.1236	0.3142	0.5724

* Used to assess the relative variability across locations as compared to residual variance for each conditional probability.

TABLE 6.8 **Summary of Repeated Measures Analysis of the Effect of Seed Age on the Conditional Probability of Survival**

Model: Conditional Probability of Seed Survival (Arcsin Square-Root) = Seed Age

Random Effects: Location

Dependent Variable	**Model Fixed Effects**	**p > Type III F**	**Largest Source Of Estimated Variation (Random Effects)**
Conditional Probability			Location to Location
of Survival	Seed Age	0.1379	

** $p < 0.05$
* $p < 0.10$

TABLE 6.9 **Summary of Analysis of Variance Results of the Effect of Seed Age on the Conditional Probability of Persistence**

Model: Conditional Probability of Seed Persistence (Arcsin Square-Root) = Seed Age

Random Effects: Location

Dependent Variable	Model Fixed Effects	p > Type III F	Largest Source Of Estimated Variation (Random Effects)
Conditional Probability			Location to Location
of Persistence	Seed Age	0.4432	

This model was run as an analysis of variance since seed cages were destructively harvested to determine persistence and no repeated measures were therefore taken.

** $p < 0.05$
* $p < 0.10$

TABLE 6.10 Estimated Least Square Mean Conditional Probabilities of Emergence, Survival, and Persistence by Location, Across Years and Seed Ages

Location	Conditional Probability of Emergence	Conditional Probability of Survival	Conditional Probability of Persistence
BW1	3.23%	23.97%	21.32%
BW2	5.71%	25.36%	20.83%
BW3	4.94%	28.52%	24.87%
RL1	12.65%	21.36%	9.77%
RL2	1.95%	19.73%	18.14%
RL3	0.89%	22.72%	22.04%
RL4	0.45%	18.21%	17.86%
RL5	3.21%	7.05%	3.96%
RL6	4.68%	30.50%	27.01%
RL7	3.94%	27.77%	24.65%
SLL3	3.81%	21.46%	18.22%

TABLE 6.11 **Estimated Least Square Mean Conditional Probabilities of Emergence, Survival, and Persistence by Seed Age, Across Years and Locations**

Seed Age	Conditional Probability of Emergence	Conditional Probability of Survival	Conditional Probability of Persistence
Seeds 0 - 1 years	6.01%	26.02%	21.22%
Seeds 1 - 2 years	4.83%	22.15%	17.83%
Seeds 2-3 years	1.56%	19.10%	17.86%

TABLE 6.12 **Correlations Between Soil Characteristics (Across Dates, Quadrats, Locations, and Years) and Estimated Least Square Mean Conditional Probabilities of Emergence, Survival and Persistence (Across Locations and Years)**

Correlation Variables	**r**	**p**
Soil Moisture vs. Conditional Probability Survival Seeds 2-3 Yr	0.63939	0.0342**
Soil Moisture vs. Conditional Probability Persistence Seeds 2-3 Yr	0.66668	0.0251**
Soil Conductivity vs. Conditional Probability Emergence Seeds 0-1	-0.56621	0.0694*
Soil Conductivity vs. Conditional Probability Emergence Seeds 1-2	-0.57032	0.0669*
Soil pH vs. Conditional Probability Emergence Seeds 0-1 Yr	-0.60501	0.0486**
Soil pH vs. Conditional Probability Persistence Seeds 1-2 Yr	0.55358	0.0773*
Soil pH vs. Soil Moisture^{+}	-0.81329	0.0023**
Soil pH vs. Soil Conductivity^{+}	0.78629	0.0041**
Soil pH vs. Growth Rate Elasticity of Seeds 2-3 Yr	0.55749	0.0748*
Soil Conductivity vs. Density of *C. multicaulis*	-0.60564	0.0483**

** $p < 0.05$
* $p < 0.10$

All other correlations were not significantly different from zero.
$^{+}$Corroborates earlier correlations (Table 3.6 and 4.10)

TABLE 6.13 **Summary Descriptive Statistics for Soil Characteristics (Across Dates, Quadrats, Locations, and Years), Conditional Probabilities of Seed Emergence, Survival, and Persistence (Across Years), and Seed Bank Growth Rate Elasticities By Seed Age**
(Mean Values Used in Correlation Analysis of Table 6.11)
Sample Size = 11

	Mean	Std. Dev.	Minimum	Maximum
Soil pH	8.865	0.4396	8.16	9.46
Soil Conductivity	8.907	5.9658	3.06	21.33
Soil Moisture	29.54%	12.445	15.00%	50.00%
Density of *C. multicaulis* per Location	252.3	181.98	48	596
Number of Fruits Per Reproductive Plant	6.14	3.789	2.47	13.52
Population Growth Rate λ	1.947	1.794	0.25	5.97
Seed Bank Elasticity Ages 0-1 Years	76.17	19.917	43.90	99.73
Seed Bank Elasticity Ages 1-2 Years	10.46	7.205	0.24	23.64
Seed Bank Elasticity Ages 2-3 Years	4.38	7.527	0.0	23.64
Conditional Probability Emergence 0-1 Yr	6.01%	6.130	0.46%	22.28%
Conditional Probability Emergence 1-2 Yr	4.83%	4.947	0.40%	15.68%
Conditional Probability Emergence 2-3 Yr	1.56%	1.893	0%	6.23%
Conditional Probability Survival 0-1 Yr	26.02%	10.169	9.57%	48.40%
Conditional Probability Survival 1-2 Yr	22.15%	5.653	11.08%	30.45%
Conditional Probability Survival 2-3 Yr	19.10%	12.594	0.50%	45.71%
Conditional Probability Persistence 0-1 Yr	21.22%	9.949	6.40%	45.16%
Conditional Probability Persistence 1-2 Yr	17.83%	6.937	4.98%	29.22%
Conditional Probability Persistence 2-3 Yr	17.86%	12.392	0.50%	43.82%

TABLE 6.14 Soil Characteristics in Seed Cages, Measured in July 1996 As Compared to Soil Characteristics in Census Quadrats, Measured in July 1996 and 3-Year Mean Values of Soil Characteristics

Soil Characteristics	Measured in Seed Cages, July 1996	Measured in Census Quadrats, July 1996	Calculated as 3-Year Mean Across Quadrats
Mean Soil pH (Std. Dev.)	9.42 (0.338)	8.85 (0.520)	8.87 (0.580)
Range of Soil pH	8.65-9.85	7.65-9.85	7.35-10.10
Mean Soil Conductivity dS/m (Std. Dev.)	23.91 (21.330)	8.08 (6.090)	8.51 (8.580)
Range of Soil Conductivity	4.12-80.74	1.16-32.86	0.79-67.68
Mean Soil Moisture Percent Dry Weight (Std. Dev.)	28.08% (17.301)	27.78 (11.842)	31.66 (17.298)
Range of Soil Moisture	2.26 %-79.25%	10.84%- 66.57%	1.23%-144.24%

TABLE 6.15 **Mean Seed Bank Density Across Dates by Year and Location (From Measurements of Seed Bank Density)**

Year	Location	Mean Seed Bank Density Across Dates	Std. Dev.
1995	BW3	4	1
	RL2	16	2.65
	RL6	34.75	21.72
1996	BW3	37.88	12.14
	RL2	47.50	23.14
	ML1	84.63	44.69
	RL6	170.50	91.81
1997	BW3	63.38	23.59
	RL2	67.88	46.33
	RL6	197.75	144.15

Chapter 7: The Future of *Cleome multicaulis*: Considerations Regarding Rarity, Potential Habitat Threats, and Recommendations for Management and Future Research

The Management of Rarity in Plants

The first decision to be made concerning management of rare taxa is whether to maintain rare species only in such abundance that they survive (but are still rare), or alternatively to allow species abundance to fluctuate from being rare to being common (Main 1984, Fiedler and Laven 1996). Some ecological phenomena that influence species abundance (e.g., successional changes) may be beyond the capacity of management efforts. If the population is to be allowed to fluctuate, decisions need to be made as to allowable thresholds of abundance.

Strategies for the conservation of rare species should reflect taxon-specific knowledge of the causes and consequences of rarity. Management and modification of land-use practices will likely benefit species that were previously widely distributed and are now in decline as a result of human activities (McIntyre 1992). Protection of habitat may require the reservation of large areas for the successful conservation of sparsely distributed species, whereas species with restricted distributions due to innate rarity or endemism may be adequately protected by the preservation of currently existing populations. Species that are currently widespread but experiencing population decline and that are poorly protected may be at the greatest risk of extinction (McIntyre 1992).

In order for conservation efforts to be successful, there must be an ecological understanding of what constitutes rarity, the dynamic basis of rarity, whether the observed rarity is a natural ecological event or anthropogenic, and depending on the criteria above, what actions may be taken to conserve the species (Main 1984). In addition, there must be a commitment by society to the conservation of rare species (Main 1984). Management efforts should have a legal and enforceable basis, scientifically sound support, and a clear understanding of economically feasible goals for conservation and measures of management success (Main 1984).

Issues surrounding the design of reserves (i.e., the so-called "SLOSS" debate) may be considered in the context of the sessile nature of plants and their potential to form a metapopulation and/or remnant population structure. If small reserves are necessary, these may provide a wider choice of sites for protection for plants than for animals on the basis of demographic considerations such as an indefinite lifespan, persistent seed bank, and vegetative reproduction (Lesica and Allendorf 1995). The extent of connectivity and the facilitation of dispersal should be assessed wherever possible.

Reintroduction efforts should mimic the natural processes of plant dispersal and establishment (Primack 1996). Historic occurrences of a species may not define the best habitats for reintroduction because habitat modifications may have occurred since occupation of those microsites (White 1996). In order to increase chances of reintroduction success, efforts should involve the use of multiple sites and as many plants (or seeds) as possible. The frequency of reintroduction success may be very low and may require several consecutive year attempts (Primack 1996).

Past and Present Distribution and Rarity of *Cleome multicaulis*

Studies conducted here have determined that *Cleome multicaulis* is a species with narrow habitat usage that is locally abundant where found in the San Luis Valley. Although it seems likely that the species also has narrow geographic distribution, the range-wide extent of species occurrence was not assessed in this study and conclusions cannot therefore be drawn concerning this aspect of rarity.

Historical accounts indicate that the species was first collected in Colorado in 1873. The species was collected in 1851 in Arizona and at an unknown date in New Mexico. The Texas collection consists of a single plant collected in one southwestern county right along the Texas-Mexico border. Of eight reported historical occurrences in Mexico (Iltis 1977), at least one occurrence consisted of only a single plant. No other information regarding plant abundance from historical collections is known. Iltis (Iltis 1977) notes that the species is "locally common" in the San Luis Valley but "elsewhere very rare and sporadic", and "probably in danger of extinction."

Populations outside of Colorado and Wyoming are likely to be extinct (Jennings 1998). It seems likely that the plant has never been found at a large number of sites, and has been documented from fewer than 20 major locations in the past two centuries (Fertig 2000b). A series of recent statewide searches in Wyoming failed to reveal additional populations, and it is possible that the extant Wyoming populations have been present, but overlooked, since as long ago as the mid-1840s (Fertig 2000b). Although the species clearly is abundant in the San Luis Valley, no populations have been located in other geographic areas within the state of Colorado.

The recent discovery by Walt Fertig of possible historical accounts of this species in Wyoming in the mid-1800s (Fertig 2000a) has potentially challenged the belief that plants were carried from Colorado's San Luis Valley northwards to southcentral Wyoming on the feet of birds (O'Kane 1984). Determination of the Wyoming population's origin and history (to the extent possible) will be important in categorizing the evolutionary history of *Cleome multicaulis.*

The argument has been made that a taxon possessing a population that is truly historically disjunct is likely paleoendemic in nature, and represents an ancient vestige of a taxon that was previously more widespread and occurred in scattered, isolated populations (Kruckeberg and Rabinowitz 1985). The presence of apparently suitable, but currently unoccupied habitat sites lends credence to the categorization of a taxon as paleoendemic (Kruckeberg and Rabinowitz 1985). Suitable but unoccupied patches of *C. multicaulis* habitat have been noted on a local scale in both the San Luis Valley and Wyoming locations (Fertig 2000b).

Should the presence of Wyoming populations be determined to result from waterfowl migratory dispersal, the species could possibly represent either a paleoendemic or neoendemic taxon (Kruckeberg and Rabinowitz 1985). Genetic analysis is recommended to determine the historical status of the Wyoming populations and to surmise its evolutionary origin.

Assumptions concerning species historical range and abundance should be made with great caution as a result of recognizing a particular taxon as either paleoendemic or neoendemic in nature. Such a designation centers around a time scale that is evolutionary, rather than historical, in scope. Statements (such as those above) describing the previous range of a paleoendemic taxon as 'widespread" should not be construed to mean that the species occupied many portions of a relatively large geographic range as recently as 200-300 years ago, but has now experienced a contraction of that range. Although herbarium collections from several of the states historically occupied by *C. multicaulis* were made from populations of only a single plant, inclusion of those states in a description of rangewide species distribution may allow misleading conclusions to be drawn concerning overall species abundance.

The simple listing of states where the species occurs has given the impression in some state management reports of widespread distribution and sufficient abundance not to warrant conservation concern and should be avoided whenever possible. Statements regarding the percentage decrease in the species range over the recent past may be similarly misleading, and should be made with extreme caution or avoided altogether until more complete rangewide surveys may be conducted for this species.

Determining the Historic Distribution and Abundance of a Species

The assumption is often made that species with what are now disjunct populations previously occupied a much more continuous portion of their geographic range. Degradation of habitat, particularly for wetland and aquatic plants, is often cited as the reason for contraction of the species' range (Fiedler and Laven 1996). Species that are endemic may now be excluded from some portions of their historical range by changes in the quality of previously occupied habitat. Reintroduction efforts for these species should not assume that all parts of a species' historical range are equally suitable (Fiedler and Laven 1996). In addition to a determination of historical range of a species, much useful information may be gleaned from the tracking of a species' abundance over time (Gaston and Kunin 1997). As Harper (Harper 1981) noted, rarity is a property that changes over time, and determination of species' trends in abundance may be critical in order to complete the picture of a species' rarity.

The uncoupling of rarity per se from extinction risk mandates the need for assessment of a species' recent ecological history in order to determine whether populations have recently declined from previously high densities and/or ranges. The time scale that is important in this determination is one that includes human habitation (and is therefore more appropriately anthropological than geological in scale) but that is considerably longer in scope than is possible for an actual population census. Fischer and Stocklin reconstructed the extinction and recolonization history of species for 35 years and found higher rates of local extinction for plants in small populations, those with a short life cycle, and for habitat specialists (Fischer and Stocklin 1997). Examples of studies that have conducted this historical assessment over a longer time frame than 35 years have not been found.

Although the present study of *Cleome multicaulis* provides an excellent example of a species whose ecological history is an unknown but potentially critical component, there are an undetermined number of other rare species for which additional information is needed regarding historical distribution and abundance. Herbarium records may provide preliminary evidence of historical distribution but do not provide an unbiased sampling of the entire distribution of a species. Although specimen labels may provide cursory information regarding local abundance, this information is often completely lacking, or at best is representative of only localized population densities that may not represent typical conditions for the species.

Ecological History as an Interdisciplinary Study

The development of new investigative tools to provide ecological, anthropological, and historical evidence of the distribution and abundance of species represents an exciting new interdisciplinary field of study. Although a single-species approach may be important for the determination of whether a particular species has just recently become rare, additional important information may be gleaned from an examination of community and ecosystem-level characteristics in recent historical time as well. Although reconstructing ecological history requires considerably different investigative and analytic skills than those practiced by most reductionistic ecologists today, the potential rewards are great.

Ecological myths abound, and their perpetuation depends in many instances on assumptions made about the historical distribution and abundance of species. The increased sophistication and rigor of ecology as a scientific discipline has made it unacceptable to rely on ecological "myths" that over-simplify complex ecological processes. Many "myths" arose because of inadequate assumptions, incomplete investigation, or a reluctance to challenge prevailing beliefs. The extinction of the dodo is not likely to have caused the demise of the *Calvaria* tree (Quammen 1998). Ecological stories of the passenger pigeon, the Great Auk, and the American chestnut may be oversimplified as well (Caughley and Gunn 1996). Perhaps the gingko tree was not perpetuated only in the courtyards of Asian royalty for thousands of years.

A more thorough and rigorous examination of ecological circumstances rarely fails to provide an incredibly more interesting and complex explanation for ecological phenomena than the simple relationship originally surmised. Years of study by Peter and Rosemary Grant (Weiner 1994) and their co-workers, for instance, have greatly expanded our knowledge of the Galapagos finches and the process of evolution beyond the simple textbook descriptions of Darwin and his travels.

An appreciation for the details of ecological history will assist in overturning mythical beliefs concerning changes in the distribution and abundance of plants or animals that are exotic species, pests, or pathogens as well as those that are rare. Historical investigations may provide interesting details concerning the starling, the gypsy moth, the potato blight, and other organisms whose history mankind has shared. Examination of ecological history may assist geneticists in their determination of the relative roles of a species' history (e.g., population bottlenecks) in the current population genetic structure.

Development of the tools necessary for determination of ecological history at a variety of ecological scales (from population to landscape) will require creativity and integrative efforts from other scientific and non-scientific disciplines. The time line important for studies of ecological history is, in most cases, shorter than that preserved in the fossil record, but longer than that documentable in ecological field studies today. Knowledge of the ecological history of one taxon (e.g., pathogens or other microbes) might allow information to be gleaned concerning the age of the host (Caughley and Gunn 1996).

Discussions with historians and anthropologists, consultation of historical documents and accounts of travel and exploration, and perhaps even interviews with long-time area residents or others familiar with the flora and fauna of an area may all serve to question previously accepted beliefs and provoke further investigations. Geographic information systems technology might enable landscape attributes to be reconstructed at various points in historical time, in order to extrapolate the distribution and abundance of key species from limited (and perhaps circumstantial) evidence (Margules and Austin 1995). Even examination of packrat middens may provide evidence of the formerly extensive distribution of some tree species (e.g., bristlecone pine, that is now rare) (Kruckeberg and Rabinowitz 1985). In the case of *C. multicaulis*, reconstruction of the hydrological history of the San Luis Valley for the past 500 years might assist in determining whether historical populations of *Cleome* were present in the Valley. Any attempted historical re-construction of habitat requirements should take into consideration that shifts in species ecological tolerances and/or changes in the frequency of species ecotypes might have occurred within the time frame of investigation.

Assessment of Factors Determining the Status of *C. multicaulis*

Based on the recommendations of Kunin (Kunin and Gaston 1993), an assessment may be made of multiple factors in the determination of the status of this rare species, with specific management recommendations to follow (see Recommendations for Management).

The similarity of appearance between *C. multicaulis* and closely related species (*Cleome serrulata*) that may occur in the same area is low. Population vigor (whether stable, increasing, or declining) has considerable spatial and temporal variability, as indicated by periodic matrix analysis. The extent to which variability in numbers of individuals may be due to particular environmental factors that affect long term population trends is considerable. The frequency and density of populations is high in the San Luis Valley and apparently low elsewhere. A single dense population has been confirmed in Wyoming. The species apparently has the ability to self-pollinate, although pollinator identities are unknown. The hypothesized presence of specialized pollinator relationships (e.g with the San Luis Valley sandhills skipper) warrants further investigation before conclusions are drawn as to their importance.

Dispersal of *C. multicaulis* seeds is likely facilitated by wind and possibly water, with assistance from waterfowl probable as well. Reproduction is solely from seed, with a persistent soil seed bank. Seeds have the ability to germinate when inundated with water, although above-ground life stages do not tolerate prolonged flooding. Above-ground competition comes primarily from *Juncus balticus*, perhaps as a result of shading and/or increased soil moisture. The species is not likely to be attractive to collectors and is quite inconspicuous when not in bloom. A disjunct population has been located in Wyoming. The species apparently colonizes disturbed microsites successfully. The soil seed bank is apparently undisturbed by low-intensity surface fires.

Trampling by large herbivores such as cattle or bison is a threat, but little evidence of herbivory was seen. The preferred habitat of the species is intrinsically unpredictable. Potential human-caused threats to habitat stability include drawdown of the shallow aquifer for export out of the San Luis Valley. To the extent that succession occurs in the highly saline/alkaline habitats occupied, the species is threatened by successional invasion of taller wetland perennial species adapted to higher soil moisture than *C. multicaulis*. The species apparently occupies remnant populations that fluctuate greatly in annual above- and below-ground abundance, although the extent of connectivity between local populations is unknown.

Human threats from direct habitat conversion are likely to be less widespread than those from water table drawdown. Trampling by cattle has adversely affected populations in some areas (e.g., ML1, RL1). Although some populations are relatively remote, with restricted access (e.g., Mishak Lakes), others are readily accessible (e.g., RL1) and have experienced negative impacts from human activity in close proximity to plants. In general, populations are readily accessible by humans except when seasonal filling of playa basins isolates populations (e.g., at Mishak Lakes). Some populations are afforded protection at more isolated sites through The Nature Conservancy's now-extensive San Luis Valley land holdings, although these may not represent optimal habitat for the species.

The full extent of *C. multicaulis* populations occurring on private land has not been determined. The species is likely to be of limited horticultural value, and its potential as a source of pharmaceuticals is unlikely based on the characteristics of other close relatives. The potential success of ex-situ conservation efforts is unknown, but may be complicated both by the species occupancy of habitats with unique soil characteristics and by seed dormancy.

Proposed San Luis Valley Water Table Drawdown

Thousands of wells have been completed in the unconfined aquifer of the San Luis Valley and in the upper part of the confined aquifer. Concentrated center-pivot irrigation activity in some areas of the Valley has lowered shallow groundwater wells 6-7 meters between 1969 and 1980 in some areas of the Valley (Leonard and Wells 1989). The Bureau of Reclamation's Closed Basin Project, begun in 1988, has been authorized to withdraw up to 100,000 acre-feet of water per year, mostly from the unconfined aquifer. Model simulations indicate that 168 wells from this project will lower local water tables between 3 - 80 cm (and as much as 8 m) throughout a large part of the Valley (Leonard and Wells 1989). Soil salinity has not been directly addressed in the Closed Basin model simulation, and the effects of the Closed Basin Project on salinity of San Luis Valley soils will probably not be determined for years. When the basins of playa systems are dry, they may generate considerable fine-sized particulate dust (PM_{10} or particles with a diameter less than 10 micrometers) that can cause considerable adverse effects to human health. Overgrazing, vegetation removal, and excessive drawdown of playas for water use have increased dust generation in playas worldwide (Dahlgren et al. 1997).

Groundwater use in the San Luis Valley has been a hotly-contested resource for years, and a planned private development project that would pump 200,000 acre-feet of water per year out of the confined aquifer (deep water table) and export it for use in the greater Denver urban area has been proposed in several different forms and defeated several times in court, only to re-emerge. Although the potential economic impact of halting proposed drawdown of the shallow aquifer in the San Luis Valley would be significant, there are likely to be considerable benefits that occur from retention of local water resources for agricultural needs.

Both above-ground and seedbank populations of *C. multicaulis* throughout the San Luis Valley are likely to experience substantial impact from drawdown of the shallow aquifer, should it occur as a result of current or future water projects. Although recent land acquisitions by The Nature Conservancy will help ensure the survival of plants and animals in the San Luis Valley, the long-term persistence of *C. multicaulis* and other inhabitants of unique San Luis Valley ecosystems depends on the development of balanced and ecologically sound guidelines for the use of San Luis Valley water.

Recommendations for the Management of *C. multicaulis* Populations

Efforts to ensure the long-term persistence of *C. multicaulis* in the San Luis Valley should recognize the global significance of these populations as representative of almost all known occurrences of the plant worldwide. Until further studies of the current rangewide distribution of this species have been conducted, statements regarding the previous extent of habitats occupied by *C. multicaulis* should be made with caution. Restraint should be used with statements implying specialized pollinator relationships as well (e.g., the San Luis Valley skipper) (Nature Conservancy of Colorado 1999), until further studies have investigated the interrelationship of these species.

The practical difficulty in adequately preserving sufficient suitable habitat for a species that may persist as remnant populations for one portion of its life cycle (e.g., the seed bank) is that an additional layer of management complexity is added. Preservation of habitat areas that appear highly suitable for above-ground growth (whether determined by plant density, plant size, or other criteria) may not be sufficient to protect populations in their remnant (seed bank) stage. It is apparent from this study that local populations of *C. multicaulis* in the San Luis Valley vary widely in terms of their population growth rates, and some local populations will possibly face above-ground (stem) extinction in the next 5-10 years if conditions remain the same as they were during the period of this study. In order to improve the probability of long-term persistence of this species in the San Luis Valley (and elsewhere in its range), the following management steps are recommended.

1. Genetic analysis of extant populations is needed to provide valuable information concerning the ecological history of the Wyoming populations and to determine the extent of genetic independence (Gottlieb and Edwards 1992) between the Colorado and Wyoming populations of *C. multicaulis*. The purpose of these studies would be to determine whether the Wyoming population was indeed founded recently as a subpopulation of the plants in the San Luis Valley, or whether, as Walt Fertig has suggested (Fertig 2000b) the species has occupied Wyoming since at least the mid-1800s. A second purpose would be to allow management decisions to be made in order to preserve the genetic diversity of *Cleome multicaulis* throughout its range, since all populations are not currently protected (Hogbin and Peakall 1999) and population selections may have to be made.

2. Special management efforts should be focused on the Wyoming population of *C. multicaulis* because of its disjunct distribution and comparative infrequency. Populations of *C. multicaulis* in Wyoming should be afforded status as a BLM sensitive species. Populations in the San Luis Valley at Blanca Wetlands and Russell Lakes should be recognized as representing optimal habitat for the species, and Colorado populations should retain their BLM sensitive species status as well as retaining recognition as a state species of concern.

3. Soils where *C. multicaulis* is currently present (both in Colorado and Wyoming) should be kept saturated with moisture for the majority of the year. Observations indicate that soils that are too dry may interfere with plant growth and seed bank maintenance, and soils that are too wet will promote the growth of *Juncus balticus* and other tall vegetation that may outcompete *C. multicaulis*. Maintenance of saturated soils is likely to be important in the long-term persistence of this species and does not conflict with current management goals for waterfowl in these habitat areas.

4. Habitat areas that are managed for *C. multicaulis* should include a buffer area of saturated soils surrounding above-ground populations to promote maintenance of the soil seed bank. Conservation measures should preserve suitable habitat for both above-ground and seed bank life stages and protect sufficient numbers of local populations to allow long-term persistence of remnant populations in spite of year-to-year variability in abundance. Surface-level fires conducted during the winter season do not appear to harm the subsequent germination of *C. multicaulis* seeds and may serve to clear out competing vegetation. Flooding of areas of *C. multicaulis* habitat should be restricted to short-term episodes of less than approximately two weeks, with recurrence kept at a minimum. If flooding becomes necessary in currently occupied areas of *C. multicaulis*, growth of nearby populations (as replacements in close proximity) should be encouraged by soil saturation.

5. Although further studies are needed, it appears that *C. multicaulis* does not compete well with invasive species such as *Lepidium latifolium* (whitetop) and efforts should be made to control invasive populations where the species co-exist. Populations on the northern edge of San Luis Lakes appear to be particularly vulnerable to encroachment from existing populations of *L. latifolium*.

6. Populations of *C. multicaulis* at Russell Lakes (site RL1 in particular) are vulnerable to human impact in the form of overnight camping activity, off-road traffic and seasonal waterfowl hunting. Visits to the census sites in fall of 2000 revealed that access to these state-managed lands is being increasingly restricted. However, continued attention should be paid to the impact of human travel and occupancy (including research activities) on populations of *C. multicaulis* at Russell Lakes.

7. Attempts should be made by The Nature Conservancy to acquire habitat for *C. multicaulis* that is similar to that currently occupied by medium and high-density populations of this species at Blanca wetlands and Russell Lakes. These sites should be characterized by the presence of permanent standing water with emergent vegetation surrounded with a vegetation

band of *J. balticus* surrounded by a band of *C. multicaulis*. Consideration should be made of the overall ecological impact of maintaining soils at saturation for existing populations of *C. multicaulis* found on land owned by The Nature Conservancy. A suggested management goal is to maintain soils at saturation wherever that practice does not conflict with goals for the management of other species on TNC lands.

8. Periodic census efforts of this species should continue and should include both measurements of above-ground population dynamics and density estimates of the soil seed bank. Although photo estimation points (Fertig 2000b) may document overall presence or absence of a large, dense population of *C. multicaulis*, such points should not be used as a replacement for long-term studies to identify above- and below-ground population trends. If permanent census plots are desired by The Nature Conservancy at Mishak Lakes and the Zapata Ranch, those areas should be fenced to exclude cattle at Mishak Lakes and (if possible) bison at the Zapata Ranch.

9. Cooperative agreements should be reached between state and Federal agencies, The Nature Conservancy, and private landowners (when possible) so that those responsible for land management in areas where *C. multicaulis* is found may consider habitat requirements for this species when making ecosystem-based management decisions for those lands.

10. Should attempts to reintroduce *C. multicaulis* into suitable habitat become necessary or desirable in order to expand its range or replace local populations lost to flooding, this study has shown that seed collection and sowing are potential (although limited) methods for increasing population sizes. Reintroduction efforts seek to mimic the natural processes of dispersal and establishment, although reintroduction by seed has been shown to be fraught with frequent failure (Primack 1996). Reintroduction efforts should be repeated over a period of several years in order to increase the chances of encountering a "good" year for colonization (Primack 1996).

11. Sown seeds of *C. multicaulis* are unlikely to germinate successfully unless they receive adequate and consistent moisture. Seeds should be sown at least by early fall to allow them to overwinter and experience the range of natural environmental conditions necessary to

break dormancy by spring. An additional unknown factor concerning reintroduction by seed for species with a persistent seed bank is the effect on the soil seed bank of augmenting the existing seed bank with seeds all of a single age (Bowles and McBride 1996).

12. Exclusion of cattle and bison from areas where seeds are beginning to germinate may be necessary in order to avoid damage to the new shoots. The impact of trampling on the *C. multicaulis* soil seed bank during times when above-ground growth is absent is not known, but is not necessarily detrimental. Reintroduction efforts that require site manipulation (especially of soil chemistry) in order to re-create suitable site characteristics for the species are not likely to be successful due to the difficulty of recreating the saline-sodic soil conditions that support *C. multicaulis*. Manipulation of water levels (and the maintenance of saturated soils), on the other hand, is not only possible but will likely continue to be a necessary component of management regimes that benefit this species.

Suggestions for Further Research

Research efforts into the population dynamics and biology of *C. multicaulis* should continue. One key area that warrants further investigation is the mating system and pollination biology of this species, and in particular any relationship that may exist between *C. multicaulis* and the rare San Luis Valley sandhills skipper. Additional field experiments are needed to investigate the fates of seeds in the seed bank over the harsh San Luis Valley winter, to characterize the frequency of lateral seed movement, and to identify the impact of seed bank disturbances resulting from periodic flooding of *C. multicaulis* habitat.

Long-term (5-10 yr) field experiments are needed to determine the seed bank longevity of *C. multicaulis*, to more closely follow seed fates, and to further identify the effect of seed age on seed bank population dynamics. Detailed assessment of seed bank densities and the extent of spatial and temporal variation in seed bank density will help to determine if seed bank stores appear sufficient to allow the successful colonization of new habitat patches in a remnant population structure. The presence of a disjunct Wyoming population of *C. multicaulis* provides a fascinating opportunity to investigate the extent of interpopulational variation in dormancy and germination behavior. Additional germination trials are needed in the lab and field to more clearly categorize the annual dormancy cycle of *C. multicaulis* and to characterize germination requirements so that ex-situ studies of germination, emergence, and growth may be conducted.

Conclusive determination of the original extent of *C. multicaulis* populations across the southwestern U.S. and Mexico may no longer be possible. Collections from Arizona, Texas, and New Mexico have not been recently confirmed, and a decision should be made as to whether the species should be defined as extirpated under the assumption that no sightings have been made in the past 50 years (Reed 1996). To the extent that populations of *C. multicaulis* are persisting in the seed bank life stage, the presence of populations may not be easily detectable (Reed 1996).

A realistic estimate of the original population size of *C. multicaulis* would begin with an informed estimate of the spatial and temporal extent of saline-sodic wetlands prior to human settlement. If the "undisturbed" form of these wetlands more closely resembles the hydrologic regime seen at Mishak Lakes today than it does the more intensely managed wetlands at Blanca and Russell Lakes, it seems likely that whatever populations of *C. multicaulis* existed historically may have been considerably more sparse than those found today in some areas of the San Luis Valley. Until more reliable habitat reconstructions may be drawn, caution should be used in drawing conclusions as to the original extent of *C. multicaulis* populations.

An accurate description of the current U.S. range of this species should be compiled by attempting to locate populations of *C. multicaulis* in Arizona, Texas, and New Mexico. Historical site records may not be of much use in this regard, since extensive land-use changes may have occurred since *C. multicaulis* was collected in those states. However, areas of currently suitable habitat for *C. multicaulis* may be identified in order to concentrate location efforts there. Suitable habitat should also be identified in Wyoming outside Pathfinder Wildlife Refuge and in Colorado outside the San Luis Valley and attempts made to locate additional populations in those states.

The preservation of numerous local populations of *C. multicaulis* will be necessary in order to achieve long-term population stability in the face of fluctuating local population dynamics. Multiple populations of this species in the San Luis Valley are well-established and their habitat requirements appear to be met by current management practices at several publically-managed sites. Like so many other unique species of the San Luis Valley, however, the long-term persistence of *C. multicaulis* is intricately tied to the Valley's remarkable hydrologic systems.

As numerous stakeholders compete for limited water resources in the San Luis Valley, the availability of sufficient groundwater to maintain saturated soils that appear to be optimal for the above-ground and seed bank growth of *C. multicaulis* is in danger of decline. Conservation of habitat for *C. multicaulis* in the San Luis Valley is critical for the global persistence of this species, and the species' remnant population structure requires attention to both above-ground and below-ground habitat needs. Proposed future drawdowns of the shallow San Luis Valley aquifer should be carefully examined for their potential effect on ecological habitat characteristics important for the preservation of *C. multicaulis* and other San Luis Valley species. Efforts to retain adequate water in the San Luis Valley shallow aquifer will be rewarded with the continued preservation of unique San Luis Valley ecosystems that meet the ecological needs of *Cleome multicaulis*, other unique species, and human habitants as well.

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APPENDIX 3.1: GPS Positions of Macroplot Locations (8m x 12m) Used in this Study

Loc	N	Degrees	Minutes	W	Degrees	Minutes	UTM	d	+/- ft.
BW1	N	37	32.581	W	105	43.407	13 436 S 4155	2d	300
BW2	N	37	32.576	W	105	43.292	13 436 S 4155	3d	1000
BW3	N	37	32.574	W	105	43.403	13 436 S 4155	3d	1000
RL1	N	37	57.080	W	106	7.275	13 401 S 4201	3d	300
RL2	N	37	56.989	W	106	7.292	13 401 S 4201	3d	300
RL3	N	37	56.932	W	106	7.192	13 402 S 4201	3d	1000
RL4	N	37	57.097	W	106	6.982	13 402 S 4201	3d	1000
RL5	N	37	56.256	W	106	8.545	13 400 S 4199	3d	1000
RL6/7	N	37	56.602	W	106	6.351	13 403 S 4200	3d	1000
ML1	N	37	54.832	W	105	59.563	13 413 S 4197	3d	1000
SLL3	N	37	41.917	W	105	44.413	13 435 S 4172	3d	1000
SLL1/2*	N	37	41.754	W	105	46.995	13 436 S 4171	2d	1000

* flooded in summer of 1996

Location Key:

BW1	Blanca Wetlands 1
BW2	Blanca Wetlands 2
BW3	Blanca Wetlands 3
RL1	Russell Lakes 1
RL2	Russell Lakes 2
RL3	Russell Lakes 3
RL4	Russell Lakes 4
RL5	Russell Lakes 5
RL6	Russell Lakes 6
RL7	Russell Lakes 7
SLL3	San Luis Lakes 3

APPENDIX 3.2: Plant Density, Soil Salinity (Ec), and Soil Moisture of Quadrats with Soil pH > 9.50, Includes Repeated Measures and Sorted by Soil pH

pH	Ec	SM	Tot Dens	Loc	Quad	Date	Year
10.10	20.04	0.1423	0	7	1	2	95
10.05	48.91	0.2711	0	7	1	2	97
10.00	37.09	0.1422	0	1	5	2	95
10.00	67.68	0.2023	0	6	6	2	95
9.95	21.34	0.2380	0	7	1	1	97
9.95	19.00	0.2357	72	2	3	1	97
9.95	35.07	0.2250	0	7	1	2	96
9.95	62.21	0.1218	0	7	3	3	95
9.9	20.53	0.1725	6	12	3	1	97
9.9	44.17	0.1792	0	7	1	3	97
9.90	20.40	0.1111	12	3	6	3	95
9.85	30.45	0.1474	0	7	3	2	95
9.85	31.03	0.2296	0	8	3	3	97
9.85	21.89	0.1694	4	3	6	2	96
9.85	41.92	0.1997	4	11	1	1	96
9.85	14.16	0.1450	93	2	3	3	97
9.85	23.55	0.0987	0	1	5	3	97
9.85	19.98	0.2740	5	8	6	1	97
9.80	24.71	0.1150	0	7	2	3	95
9.8	12.05	0.1688	0	1	5	1	96
9.8	13.76	0.1369	2	1	5	2	96
9.8	11.60	0.2416	0	2	3	1	96
9.8	34.21	0.1046	0	7	3	3	96
9.75	14.33	0.2322	7	8	3	1	97
9.75	25.36	0.0924	25	11	2	3	96
9.75	16.89	0.1713	2	1	5	3	96
9.75	24.51	0.2426	19	1	2	1	97
9.75	41.38	0.1562	0	7	3	3	97
9.75	32.85	0.2215	0	7	1	1	96
9.75	31.51	0.1917	0	7	3	2	96
9.75	3.66	0.0123	147	2	1	3	95
9.75	58.68	0.1515	0	6	6	3	95
9.75	25.43	0.1338	0	7	1	3	96
9.75	13.35	0.0846	118	3	6	3	97
9.75	15.81	0.1016	0	1	5	3	95
9.75	11.43	0.2423	0	7	2	1	96
9.75	19.33	0.2103	2	12	1	3	95
9.75	29.62	0.2257	0	7	3	1	97
9.75	48.77	0.1781	0	7	3	2	97
9.7	28.66	0.2021	0	6	6	3	97
9.7	25.17	0.4227	43	5	5	1	96
9.7	26.33	0.2791	0	6	6	1	97
9.7	24.75	0.2169	0	12	3	1	96
9.70	24.73	0.2002	3	12	2	2	95

pH	Ec	SM	Tot Dens	Loc	Quad	Date	Year
9.70	31.20	0.1329	92	1	4	3	95
9.70	23.52	0.2181	22	3	5	2	95
9.65	15.88	0.2039	0	12	2	1	97
9.65	21.02	0.1908	0	12	2	3	97
9.65	22.12	0.1954	0	12	2	2	97
9.65	8.88	0.1925	63	2	3	2	97
9.65	10.27	0.1596	0	3	6	1	96
9.65	21.37	0.0788	0	7	2	3	96
9.65	19.70	0.1996	25	7	6	2	95
9.65	34.87	0.3748	11	12	6	3	95
9.65	12.71	0.1234	14	1	6	3	95
9.65	24.28	0.2429	2	8	6	2	95
9.65	20.40	0.2107	0	12	3	2	95
9.60	16.22	0.2718	0	11	1	3	95
9.60	22.91	0.1682	85	1	1	2	95
9.60	2.36	0.0609	81	2	6	3	95
9.60	16.54	0.1719	0	11	1	2	95
9.6	11.53	0.2537	239	3	6	1	97
9.6	22.54	0.2483	11	12	2	2	96
9.6	9.59	0.1817	50	7	4	1	96
9.55	21.83	0.2013	1	12	2	3	95
9.55	30.21	0.2493	1	12	3	3	95
9.55	19.05	0.1651	18	1	6	2	95
9.55	4.75	0.3438	21	2	4	3	96
9.55	23.40	0.3466	1	6	3	3	97
9.55	13.80	0.4400	0	6	5	1	96
9.55	15.71	0.3832	7	6	5	2	96
9.55	8.51	0.5300	29	6	4	1	96
9.55	13.57	0.1387	5	1	6	2	96
9.55	13.55	0.1550	18	1	4	3	96
9.55	10.75	0.2939	0	8	1	1	97
9.55	12.75	0.2335	0	8	3	1	96
9.55	13.79	0.1193	7	11	1	2	96
9.55	16.47	0.2126	24	12	3	2	96

APPENDIX 3.3 Plant Density, Soil pH, and Soil Moisture of Quadrats with Soil Salinity (Ec) > 20.0 dS/m, Includes Repeated Measures and Sorted by Soil Salinity

pH	Ec	SM	Tot Dens	Loc	Quad	Date	Year
10.00	67.68	0.2023	0	6	6	2	95
9.95	62.21	0.1218	0	7	3	3	95
9.75	58.68	0.1515	0	6	6	3	95
10.05	48.91	0.2711	0	7	1	2	97
9.75	48.77	0.1781	0	7	3	2	97
9.9	44.17	0.1792	0	7	1	3	97
9.85	41.92	0.1997	4	11	1	1	96
9.75	41.38	0.1562	0	7	3	3	97
10.00	37.09	0.1422	0	1	5	2	95
9.95	35.07	0.2250	0	7	1	2	96
9.65	34.87	0.3748	11	12	6	3	95
9.8	34.21	0.1046	0	7	3	3	96
9.75	32.85	0.2215	0	7	1	1	96
9.75	31.51	0.1917	0	7	3	2	96
9.70	31.20	0.1329	92	1	4	3	95
9.85	31.03	0.2296	0	8	3	3	97
9.85	30.45	0.1474	0	7	3	2	95
9.55	30.21	0.2493	1	12	3	3	95
9.75	29.62	0.2257	0	7	3	1	97
9.7	28.66	0.2021	0	6	6	3	97
9.7	26.33	0.2791	0	6	6	1	97
9.5	25.57	0.3661	1	6	3	2	97
9.75	25.43	0.1338	0	7	1	3	96
9.75	25.36	0.0924	25	11	2	3	96
9.7	25.17	0.4227	43	5	5	1	96
9.7	24.75	0.2169	0	12	3	1	96
9.70	24.73	0.2002	3	12	2	2	95
9.80	24.71	0.1150	0	7	2	3	95
9.75	24.51	0.2426	19	1	2	1	97
9.65	24.28	0.2429	2	8	6	2	95
9.85	23.55	0.0987	0	1	5	3	97
9.70	23.52	0.2181	22	3	5	2	95
9.5	23.48	0.1848	0	7	2	3	97
9.55	23.40	0.3466	1	6	3	3	97
9.60	22.91	0.1682	85	1	1	2	95
9.6	22.54	0.2483	11	12	2	2	96
9.65	22.12	0.1954	0	12	2	2	97
9.5	22.05	0.2227	2	8	1	2	97
9.85	21.89	0.1694	4	3	6	2	96
9.55	21.83	0.2013	1	12	2	3	95
9.3	21.64	0.3737	4	6	3	3	96
9.65	21.37	0.0788	0	7	2	3	96
9.95	21.34	0.2380	0	7	1	1	97
9.65	21.02	0.1908	0	12	2	3	97

pH	Ec	SM	Tot Dens	Loc	Quad	Date	Year
9.9	20.53	0.1725	6	12	3	1	97
9.90	20.40	0.1111	12	3	6	3	95
9.45	20.13	0.2243	0	11	2	3	95
9.5	20.10	0.2093	84	11	4	1	96
10.10	20.04	0.1423	0	7	1	2	95

APPENDIX 3.4 Soil and Reproductive Characteristics of Sites with Low (< 8.0) and High (> 8.69) Soil pH

pH	Ec	SM	Fr/Quad	Fr/Repro	Tot Dens	Loc	Quad	Year
7.55	1.67	0.5094	281	4.90	58	9	1	1995
7.55	1.25	0.3731	0	0.00	0	8	4	1996
7.60	1.09	0.3713	38	4.80	15	9	5	1995
7.60	1.67	0.4743	0	0.00	0	10	3	1996
7.65	1.38	0.4269	0	0.00	0	8	4	1995
7.65	2.51	0.8375	228	2.80	104	9	4	1995
7.70	1.16	0.4015	0	0.00	35	8	4	1997
7.75	2.29	0.7072	0	0.00	5	10	1	1995
7.75	3.29	0.3792	24	1.71	8	9	6	1996
7.80	2.65	0.4984	358	1.62	221	10	6	1996
7.80	1.56	0.3102	0	0.00	0	4	4	1996
7.85	8.28	0.3711	0	0.00	0	10	3	1995
7.90	1.02	0.2315	0	0.00	0	3	1	1997
7.95	1.10	0.4748	65	3.40	19	9	2	1995
7.95	2.74	0.8448	28	3.11	148	9	4	1997
7.95	4.33	0.3923	547	4.88	116	10	4	1996
7.95	3.89	0.6208	29	1.61	69	9	5	1997
9.70	31.20	0.1329	507	5.50	92	1	4	1995
9.70	28.66	0.2021	0	0.00	0	6	6	1997
9.75	41.38	0.1562	0	0.00	33	7	3	1997
9.75	19.33	0.2103	6	6.00	2	12	1	1995
9.75	25.43	0.1338	0	0.00	0	7	1	1996
9.75	16.89	0.1713	9	4.50	2	1	5	1996
9.75	58.68	0.1515	0	0.00	0	6	6	1995
9.75	13.35	0.0846	563	4.77	118	3	6	1997
9.75	15.81	0.1016	0	0.00	0	1	5	1995
9.75	3.66	0.0123	569	3.90	147	2	1	1995
9.75	25.36	0.0924	110	4.40	25	11	2	1996
9.80	34.21	0.1046	0	0.00	0	7	3	1996
9.80	24.71	0.1150	0	0.00	0	7	2	1995
9.85	23.55	0.0987	0	0.00	0	1	5	1997
9.85	14.16	0.1450	274	3.19	93	2	3	1997
9.85	31.03	0.2296	179	8.95	0	8	3	1997
9.90	44.17	0.1792	0	0.00	0	7	1	1997
9.90	20.40	0.1111	170	15.50	12	3	6	1995
9.95	62.21	0.1218	0	0.00	0	7	3	1995

APPENDIX 3.5 Soil and Reproductive Characteristics of Quadrats With Low (< 2.0) and High (> 20.00) Soil Ec

pH	Ec	SM	Fr/Quad	Fr/Repro	Tot Dens	Loc	Quad	Year
7.90	1.02	0.2315	0	0.00	0	3	1	1997
8.30	1.03	0.2047	104	2.81	38	2	4	1997
7.60	1.09	0.3713	38	4.80	15	9	5	1995
8.20	1.09	0.0868	9	1.50	21	4	1	1997
7.95	1.10	0.4748	65	3.40	19	9	2	1995
7.70	1.16	0.4015	0	0.00	35	8	4	1997
8.70	1.21	0.2910	16	1.50	63	2	2	1995
7.55	1.25	0.3731	0	0.00	0	8	4	1996
9.05	1.26	0.0697	187	3.80	59	2	3	1995
8.15	1.28	0.3527	126	3.94	32	4	1	1996
8.35	1.38	0.6270	276	3.30	112	4	1	1995
7.65	1.38	0.4269	0	0.00	0	8	4	1995
9.10	1.44	0.2121	396	4.08	104	2	2	1996
7.80	1.56	0.3102	0	0.00	0	4	4	1996
8.30	1.64	0.2494	0	0.00	0	3	4	1997
8.65	1.65	0.7332	98	2.58	69	4	2	1997
7.60	1.67	0.4743	0	0.00	0	10	3	1996
7.55	1.67	0.5094	281	4.90	58	9	1	1995
8.10	1.68	0.4883	206	10.30	20	5	2	1996
8.65	1.87	0.2861	120	3.87	43	5	6	1997
9.45	20.13	0.2243	0	0.00	0	11	2	1995
9.90	20.40	0.1111	170	15.50	12	3	6	1995
9.65	21.02	0.1908	0	0.00	0	12	2	1997
9.65	21.37	0.0788	0	0.00	0	7	2	1996
9.30	21.64	0.3737	113	28.25	4	6	3	1996
9.55	21.83	0.2013	6	6.00	1	12	2	1995
9.55	23.40	0.3466	99	99.00	1	6	3	1997
9.50	23.48	0.1848	0	0.00	0	7	2	1997
9.85	23.55	0.0987	0	0.00	0	1	5	1997
9.80	24.71	0.1150	0	0.00	0	7	2	1995
9.75	25.36	0.0924	110	4.40	25	11	2	1996
9.75	25.43	0.1338	0	0.00	0	7	1	1996
9.70	28.66	0.2021	0	0.00	0	6	6	1997
9.55	30.21	0.2493	3	3.00	1	12	3	1995
9.85	31.03	0.2296	179	8.95	0	8	3	1997
9.70	31.20	0.1329	507	5.50	92	1	4	1995
9.80	34.21	0.1046	0	0.00	0	7	3	1996
9.65	34.87	0.3748	209	19.00	11	12	6	1995
9.75	41.38	0.1562	0	0.00	33	7	3	1997
9.90	44.17	0.1792	0	0.00	0	7	1	1997
9.75	58.68	0.1515	0	0.00	0	6	6	1995
9.95	62.21	0.1218	0	0.00	0	7	3	1995

APPENDIX 3.6 Soil and Reproductive Characteristics of Sites With Low (< 10%) and High (> 50%) Soil Moisture

pH	Ec	SM	Fr/Quad	Fr/Repro	Tot Dens	Loc	Quad	Year
9.75	3.66	1.23%	569	3.90	147	2	1	1995
9.35	3.59	2.46%	472	3.50	128	2	5	1995
9.60	2.36	6.09%	435	5.00	81	2	6	1995
9.05	1.26	6.97%	187	3.80	59	2	3	1995
9.25	7.48	7.07%	17	2.43	20	1	6	1997
8.95	7.17	7.09%	934	19.87	47	1	3	1996
9.65	21.37	7.88%	0	0.00	0	7	2	1996
9.75	13.35	8.46%	563	4.77	118	3	6	1997
8.20	1.09	8.68%	9	1.50	21	4	1	1997
9.40	2.88	8.71%	0	0.00	0	7	1	1995
9.75	25.36	9.24%	110	4.40	25	11	2	1996
9.85	23.55	9.87%	0	0.00	0	1	5	1997
7.55	1.67	50.94%	281	4.90	58	9	1	1995
9.45	12.62	51.96%	2	0.10	2	6	5	1995
8.35	2.19	52.12%	36	2.12	32	5	4	1997
8.45	3.76	52.31%	378	2.11	179	10	5	1996
8.05	2.90	52.88%	22	1.22	82	9	4	1996
8.55	7.60	54.00%	363	5.20	70	9	6	1995
9.00	8.25	54.83%	731	3.11	145	10	4	1997
8.50	6.74	54.97%	17	2.43	7	10	1	1996
8.25	2.15	54.98%	164	6.80	27	4	2	1995
9.05	8.99	58.81%	0	0.00	0	1	2	1996
8.35	4.76	60.24%	77	4.10	18	10	2	1995
7.95	3.89	62.08%	29	1.61	69	9	5	1997
8.35	1.38	62.70%	276	3.30	112	4	1	1995
8.25	2.92	70.01%	0	0.00	66	9	1	1997
7.75	2.29	70.72%	0	0.00	5	10	1	1995
8.65	1.65	73.32%	98	2.58	69	4	2	1997
8.45	4.75	77.20%	0	0.00	113	10	1	1997
8.05	3.26	83.19%	0	0.00	0	4	4	1995
7.65	2.51	83.75%	228	2.80	104	9	4	1995
7.95	2.74	84.48%	28	3.11	148	9	4	1997
8.30	2.62	91.17%	344	11.10	31	4	2	1996

Location Key:

BW1	1	RL2	5	RL6	9
BW2	2	RL3	6	RL7	10
BW3	3	RL4	7	SLL3	11
RL1	4	RL5	8		

APPENDIX 3.7 Plant Associates, Percent Cover, Plant Density, and Soil Characteristics, August 1995

pH	Ec	SM	Tot Dens	Loc	Quad	Cover %	Assoc.
9.50	19.58	0.1566	71	BW1	1	100	CM
9.30	10.72	0.2163	0	BW1	2	50	DS
9.10	8.48	0.1451	6	BW1	3	100	DS
9.70	31.20	0.1329	92	BW1	4	80	CM
9.75	15.81	0.1016	0	BW1	5*	30	CM
9.65	12.71	0.1234	14	BW1	6	80	DS
9.75	3.66	0.0123	147	BW2	1	80	CM
8.70	1.21	0.2910	63	BW2	2	100	ER
9.05	1.26	0.0697	59	BW2	3	15	CM
8.45	3.18	0.1851	31	BW2	4	100	JB
9.35	3.59	0.0246	128	BW2	5	80	CM
9.60	2.36	0.0609	81	BW2	6	100	JB
8.65	2.54	0.2437	19	BW3	1	80	DS
9.05	6.66	0.2449	33	BW3	2	80	CM
8.20	3.90	0.2512	9	BW3	3	85	DS
9.00	5.07	0.1795	19	BW3	4	80	CM
9.10	5.90	0.2345	15	BW3	5	95	DS
9.90	20.40	0.1111	12	BW3	6	20	DS
8.35	1.38	0.6270	112	RL1	1	100	JB
8.25	2.15	0.5498	27	RL1	2	100	JB
8.70	5.21	0.3020	73	RL1	3	100	DS
8.05	3.26	0.8319	0	RL1	4	100	JB
8.75	4.12	0.2623	3	RL1	5	100	DS
8.65	3.60	0.2694	5	RL1	6	100	JB
8.95	5.63	0.2867	3	RL2	1	100	DS
8.70	3.12	0.2394	7	RL2	2	100	JB
8.80	3.63	0.4404	17	RL2	3	100	JB
8.65	3.33	0.4411	26	RL2	4	100	JB
9.10	5.27	0.2894	53	RL2	5	100	JB
8.95	4.94	0.3084	29	RL2	6	100	JB
9.15	8.38	0.4115	39	RL3	1	100	JB
9.25	7.96	0.3107	6	RL3	2	100	JB
9.20	8.34	0.4054	40	RL3	3	100	JB
9.15	6.01	0.2548	11	RL3	4	100	JB
9.45	12.62	0.5196	2	RL3	5	100	JB
9.75	58.68	0.1515	0	RL3	6	5	DS
9.40	2.88	0.0871	0	RL4	1	3	DS
9.80	24.71	0.1150	0	RL4	2	5	JB
9.95	62.21	0.1218	0	RL4	3	5	JB
9.20	7.41	0.2178	39	RL4	4	90	DS
9.10	5.76	0.1785	20	RL4	5	100	JB
9.30	13.93	0.1030	19	RL4	6	90	SV
8.80	4.29	0.2318	3	RL5	1	50	JB
9.00	4.79	0.3433	0	RL5	2	30	JB
8.75	5.42	0.2004	1	RL5	3	40	JB

pH	Ec	SM	Tot Dens	Loc	Quad	Cover %	Assoc.
7.65	1.38	0.4269	0	RL5	4	90	JB
8.65	3.20	0.2471	7	RL5	5	80	JB
9.10	3.67	0.1983	2	RL5	6	30	JB
7.55	1.67	0.5094	58	RL6	1	80	JB
7.95	1.10	0.4748	19	RL6	2	80	JB
8.65	14.71	0.4123	41	RL6	3	95	AS
7.65	2.51	0.8375	104	RL6	4	90	JB
7.60	1.09	0.3713	15	RL6	5	100	JB
8.55	7.60	0.5400	70	RL6	6	100	HJ
7.75	2.29	0.7072	5	RL7	1	40	JB
8.35	4.76	0.6024	18	RL7	2	100	JB
7.85	8.28	0.3711	0	RL7	3	70	JB
8.95	15.03	0.4757	7	RL7	4	90	SU
8.65	5.32	0.4648	107	RL7	5	100	AS
8.85	8.85	0.4393	149	RL7	6	100	CM
9.60	16.22	0.2718	0	ML1	1	60	DS
9.45	20.13	0.2243	0	ML1	2	80	DS
9.15	9.32	0.1495	12	ML1	3	80	DS
9.15	10.86	0.1438	31	ML1	4	80	DS
9.20	9.26	0.1523	6	ML1	5	85	DS
9.10	6.75	0.2217	58	ML1	6	95	DS
9.75	19.33	0.2103	2	SLL3	1	30	JB
9.55	21.83	0.2013	1	SLL3	2	80	DS
9.55	30.21	0.2493	1	SLL3	3	80	DS
8.95	7.92	0.2668	3	SLL3	4	80	JB
9.25	11.66	0.2651	0	SLL3	5	100	JB
9.65	34.87	0.3748	11	SLL3	6	100	JB
9.50	6.88	0.3045	16	SLL3	6	100	JB

Key to Plant Associates:

CM	*Cleome multicaulis*
JB	*Juncus balticus*
DS	*Distichlis stricta* var. *spicata*
SV	*Sarcobatus vermiculatus*
ER	*Erigeron philadelphicus*
AS	*Aster pauciflorus*
SU	*Suaeda depressa*

APPENDIX 4.1 Detailed Elasticity Matrices for Each Location and Each Year Six Selected Points During Growing Season (Time Steps 00, 02, 03, 06, 10, 11)

```
Bw195 00
MATRIX([[.9999024478, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0,.9755296147e-4, 0, 0, 0, 0], [0, 0, 0, 0, 0,
0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw195 02
MATRIX([[.1135967041, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [.8864032956, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw195 03
:=MATRIX([[.1135967042, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,.8864032963, 0,
0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw195 06
MATRIX([[.8331327920e-1, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0,.2569631761e-5, 0, 0, 0, 0],
[.2533705252e-1, 0,.2089698177e-4,.1557514487, 0, 0, 0], [0, 0, 0,.4249754342, 0, 0, 0], [0, 0,
0,.1900777580e-4, 0, 0, 0], [0, 0, 0,.8746697976e-1,.1912399988, 0,.3187333314e-1]])
Bw195 10
MATRIX([[0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0,.9755296121e-4, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0,
0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,.9999024464]])
Bw195 11
MATRIX([[0, 0, 0, 0, 0, 0,.9999024466], [0, 0, 0, 0, 0, 0, 0], [0, 0,.9755296125e-4, 0, 0, 0, 0], [0, 0, 0, 0, 0,
0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 4.753703186
```

```
Bw196 00
MATRIX([[.9985031906, 0, 0, 0, 0, 0, 0], [0,.1484532961e-2, 0, 0, 0, 0, 0], [0, 0,.1227809206e-4, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw196 02
MATRIX([[.7949299743e-1, 0, 0, 0, 0, 0, 0], [0,.1227809208e-4, 0, 0, 0, 0, 0], [0, 0,.1117693027e-4, 0, 0,
0, 0], [.9190101924,.1472254870e-2,.1101161839e-5, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0,
0, 0, 0, 0, 0, 0]])
Bw196 06
MATRIX([[.1449223318e-1, 0, 0, 0, 0, 0, 0], [0,.1227809214e-4, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0],
[.1111067963e-1, 0, 0,.3062529323e-1, 0, 0, 0], [0, 0,.2034710183e-5,.2327200966e-1, 0, 0, 0], [0, 0, 0, 0,
0, 0, 0], [0, 0, 0, 0,.4205653541, 0,.4999201184]])
Bw196 10
MATRIX([[0, 0, 0, 0, 0, 0,.9985031894], [.1484532931e-2, 0, 0, 0, 0, 0, 0], [0,.1227809090e-4, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw196 11
MATRIX([[.9985031914, 0, 0, 0, 0, 0, 0], [0,.1484532962e-2, 0, 0, 0, 0, 0], [0, 0,.1227809206e-4, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 10.11467978
```

```
Bw197 00
MATRIX([[.9933741478, 0, 0, 0, 0, 0, 0], [0,.6608600210e-2, 0, 0, 0, 0, 0], [0, 0,.1725224902e-4, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw197 02
MATRIX([[.2418852773e-1, 0, 0, 0, 0, 0, 0], [0,.1725224907e-4, 0, 0, 0, 0, 0], [0, 0,.8535783830e-6, 0, 0,
0, 0], [.9691856190,.6591347964e-2,.1639867071e-4, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0,
```

```
0, 0, 0, 0, 0, 0]])
Bw197 06
MATRIX([[.2418852775e-1, 0, 0, 0, 0, 0, 0], [0,.1725224813e-4, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0,
0,.5550420563, 0, 0, 0], [0, 0, 0,.4065876718, 0, 0, 0], [0, 0, 0,.6550198831e-3, 0, 0, 0], [0, 0,
0,.6562016225e-2,.6947455272e-2, 0, 0]])
Bw197 10
MATRIX([[.1156837736e-2, 0, 0, 0, 0, 0, 0], [0,.8889674746e-6, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,
0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0,.1025597233e-2, 0], [0, 0, 0, 0, 0, 0,.9978166756]])
Bw197 11
MATRIX([[0, 0, 0, 0, 0,.1020084297e-2,.9923540624], [.6608600211e-2, 0, 0, 0, 0, 0, 0],
[0,.1725224747e-4, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0]])
Population Growth Rate = 3.040786198

Bw295 00
MATRIX([[.9698196268, 0, 0, 0, 0, 0, 0], [0,.2627331361e-1, 0, 0, 0, 0, 0], [0, 0,.3907056909e-2, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw295 02
MATRIX([[.4610297794, 0, 0, 0, 0, 0, 0], [0,.5409105838e-2, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0],
[.5087898469,.2086420784e-1,.3907056917e-2, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,
0, 0, 0, 0]])
Bw295 06
MATRIX([[.2627331379e-1, 0, 0, 0, 0, 0, 0], [0,.3907056946e-2, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0,
0,.1562511557, 0, 0, 0], [0, 0, 0,.2622181632,.1245023362e-1, 0, 0], [0, 0, 0,.2178497097e-2, 0, 0, 0], [0, 0,
0, 0,.5336213979, 0,.3100178927e-2]])
Bw295 10
MATRIX([[.9698196269, 0, 0, 0, 0, 0, 0], [0,.2627331362e-1, 0, 0, 0, 0, 0], [0, 0,.3907056909e-2, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw295 11 (same)
MATRIX([[.9698196269, 0, 0, 0, 0, 0, 0], [0,.2627331362e-1, 0, 0, 0, 0, 0], [0, 0,.3907056909e-2, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 4.093585565


Bw296 00
MATRIX([[.5980642525, 0, 0, 0, 0, 0, 0], [0,.2454125758, 0, 0, 0, 0, 0], [0, 0,.1565231719, 0, 0, 0, 0], [0,
0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw296 02
MATRIX([[.4063570344, 0, 0, 0, 0, 0, 0], [0,.1624927110, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0],
[.1917072188,.8291986449e-1,.1565231724, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0,
0, 0]])
Bw296 06
MATRIX([[.2454125760, 0, 0, 0, 0, 0, 0], [0,.1565231725, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0,
0,.5122359517, 0, 0, 0], [0, 0, 0,.2649192062e-1, 0, 0, 0], [0, 0, 0,.2905803815e-2, 0,.3977489676e-3, 0],
[0, 0, 0,.1246678617e-1,.3251668281e-1, 0,.1104935826e-1]])
Bw296 10
MATRIX([[0, 0, 0, 0, 0,.8386628269e-2,.5896776248], [.2454125754, 0, 0, 0, 0, 0, 0], [0,.1565231724, 0,
0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw296 11
MATRIX([[.5980642527, 0, 0, 0, 0, 0, 0], [0,.2454125758, 0, 0, 0, 0, 0], [0, 0,.1565231719, 0, 0, 0, 0], [0,
0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 0.4060987496
```

```
Bw297 00
MATRIX([[.6645553166, 0, 0, 0, 0, 0, 0], [0,.2016574741, 0, 0, 0, 0, 0], [0, 0,.1337872090, 0, 0, 0, 0], [0,
0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
```

```
Bw297 02
MATRIX([[.5116292047, 0, 0, 0, 0, 0, 0], [0,.1383451669, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0],
[.1529261117,.6331230706e-1,.1337872092, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0,
0, 0]])
Bw297 06
MATRIX([[.4219557140, 0, 0, 0, 0, 0, 0], [0,.1337872091, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0,
0,.2115088012, 0, 0, 0], [0, 0, 0,.7333124311e-1, 0, 0, 0], [0, 0, 0,.1703641939e-1, 0,.5468595606e-2, 0],
[0, 0, 0, 0,.9610588041e-1, 0,.4080613735e-1]])
Bw297 10
MATRIX([[.2016574744, 0, 0, 0, 0, 0, 0], [0,.1337872086, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0,.9266147307e-1, 0], [0, 0, 0, 0, 0, 0,.5718938433]])
Bw297 11
MATRIX([[0, 0, 0, 0, 0,.9266147297e-1,.5718938430], [.2016574744, 0, 0, 0, 0, 0, 0], [0,.1337872089, 0,
0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 0.3627648967

Bw395 00
MATRIX([[.9508542162, 0, 0, 0, 0, 0, 0], [0,.4914578405e-1, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0,
0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw395 02
MATRIX([[.4547359767, 0, 0, 0, 0, 0, 0], [0,.1199654125e-1, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0],
[.4961182397,.3714924282e-1, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw395 06
MATRIX([[.1035779299, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0,
0,.2973828821, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [.5486198951e-1, 0, 0, 0,.5441771989, 0, 0]])
Bw395 10
MATRIX([[.9508542161, 0, 0, 0, 0, 0, 0], [0,.4914578406e-1, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0,
0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw395 11
MATRIX([[.9508542161, 0, 0, 0, 0, 0, 0], [0,.4914578406e-1, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0,
0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 8.984857949

Bw396 00
MATRIX([[.8680864323, 0, 0, 0, 0, 0, 0], [0,.1319135674, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw396 02
MATRIX([[.5502376930, 0, 0, 0, 0, 0, 0], [0,.3220025039e-1, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0],
[.3178487395,.9971331708e-1, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw396 06
MATRIX([[.1319135669, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,.6398081414, 0, 0,
0], [0, 0, 0,.1196557820, 0, 0, 0], [0, 0, 0,.1526626522e-3, 0, 0, 0], [0, 0,
0,.7803637957e-2,.9367549955e-1, 0,.6990708926e-2]])
Bw396 10
MATRIX([[0, 0, 0, 0, 0,.1653387408e-2,.8664330443], [.1319135674, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0],
[0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw396 11
MATRIX([[.8680864324, 0, 0, 0, 0, 0, 0], [0,.1319135675, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 1.900898428

Bw397 00
MATRIX([[.8246204365, 0, 0, 0, 0, 0, 0], [0,.1753795637, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw397 02
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MATRIX([[.5065367616, 0, 0, 0, 0, 0, 0], [0,.4281034907e-1, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0],
[.3180836745,.1325692148, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])0, 0,
0]])
Bw397 06
MATRIX([[.2392990997, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [.1803880617e-2, 0,
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0], [0, 0, 0,.4954947360,.6622343590e-1, 0,.9548495386e-1]])
Bw397 10
MATRIX([[0, 0, 0, 0, 0,.1748466778e-1,.8071357685], [.1753795640, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0],
[0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Bw397 11
MATRIX([[.8246204367, 0, 0, 0, 0, 0, 0], [0,.1753795637, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 1.520232637

Rl695 00
MATRIX([[.9999999995, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,
0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Rl695 02
MATRIX([[.9999999996, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,
0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Rl695 06
MATRIX([[0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,.4008351228e-1, 0, 0, 0], [0, 0,
0,.3306694195,.5698763418, 0, 0], [0, 0, 0,.3442498348e-1, 0, 0, 0], [0, 0, 0, 0,.2494574245e-1, 0, 0]])
Rl695 10
MATRIX([[0, 0, 0, 0, 0,.3901039128e-1,.9609896079], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0,
0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Rl695 11
MATRIX([[.9999999996, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,
0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 0.8729121284

Rl696 00
MATRIX([[.8817560324, 0, 0, 0, 0, 0, 0], [0,.1182439674, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Rl696 02
MATRIX([[.8817560331, 0, 0, 0, 0, 0, 0], [0,.1182439674, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Rl696 06
MATRIX([[.1182439672, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,.8817560327, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Rl696 10
MATRIX([[0, 0, 0, 0, 0,.1110427053,.7707133274], [.1182439673, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0,
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Rl696 11
MATRIX([[.8817560326, 0, 0, 0, 0, 0, 0], [0,.1182439674, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 0.1244357181



Rl697 00
MATRIX([[.8046445146, 0, 0, 0, 0, 0, 0], [0,.1953554857, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Rl697 02
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MATRIX([[.8046445148, 0, 0, 0, 0, 0, 0], [0,.1953554858, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Rl697 06
MATRIX([[.1953554859, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,.7734210254, 0, 0,
0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,.3122348952e-1, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Rl697 10
MATRIX([[.1953554859, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0,
0, 0, 0, 0], [0, 0, 0,.2082278659e-2, 0,.9856623965e-1, 0], [0, 0, 0,.3031838274,.4008121697, 0, 0]])
Rl697 11
MATRIX([[0, 0, 0, 0, 0,.1006485182,.7039959975], [.1953554854, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0,
0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0], [0, 0, 0, 0, 0, 0, 0]])
Population Growth Rate = 0.08002858336
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APPENDIX 6.1: Recommendations for Improvement in Field Experiments of Seed Population Dynamics

Thompson (Thompson 1992) recommends that a comprehensive seed bank study obtain multiple estimates of buried seed density, measure seed production and seed rain, and estimate "background" emergence after soil disturbance. Although the study described here clearly meets those recommendations, assumptions of the study are identified here and suggestions for improvement made, with the hope that further studies of seed bank population dynamics will be attempted.

This study was conducted so that seed cages were destructively harvested after 1 year, 2 years, and 3 years in the field. Cages planted for a period of one year might have been in the field from 1995 to 1996 or from 1996 to 1997, and this design introduces the (strong) possibility of an effect from the particular conditions present in any single year. For the cages harvested after a period of two years, it was not possible to assess the number of live seeds in the cage after the first of two years because this would require destructive harvest. The assumption was made, therefore, that the seed behavior of a seed cage harvested after one year was the same as the behavior of seeds after the first of two years in a two-year seed cage. For cages that remained in the field three years, the assumption was made that seed behavior in those cages for the first and second years was the same as the behavior of seed cages harvested after one and two years, respectively.

It is difficult to estimate whether emergence rates from the experimental seed cages were significantly different from emergence rates in the undisturbed soil. As previously discussed, soil disturbance in seed cages was heightened, that may have had the effect of enhancing emergence. Limited soil analysis indicates that seed cages may have had higher soil conductivity and pH, that may have dampened emergence. The effect of soil characteristics on seed germination was not directly measured in this experiment. There were difficulties in obtaining soil samples for the purpose of testing pH, conductivity, and soil moisture while retaining a complete and undisturbed soil sample to accurately assess the number of seeds persisting in the seed cage after harvest.

The use of seed cages with both an "experimental" and "control" compartment had the purpose of determining (by emergence) the background density of seeds in the soil prior to planting. The assumption was made in this study that any effect of physical location on emergence rates (e.g., lateral movement of seeds into a seed cage from elsewhere in the macroplot) would be experienced equally by both the experimental and control portions of each seed cage. Because there was no physical count of seeds present in the seed cage soil prior to planting, any seed cage effects that were not expressed as differential emergence would remain undetected.

Seed cage census data were not used to estimate growth rates of seedlings, juveniles, or adult plants. Plant growth inside seed cages is likely to have been significantly affected by the lack of natural plant cover in the cages. In addition, the confined space of the seed cage made it likely that plant growth inside the cages was disproportionately subject to density-dependent dynamics as compared to the natural habitat. Seed cage emergence data were combined with above-ground census counts (outside the seed cages, on different plants) in order to create an overall picture of plant population dynamics of this species.

In this study, seeds that moved laterally into and out of the seed cages were accounted for by assuming that they impacted the experimental and control portions of each cage equally. Lateral seed movement was not assessed directly in this study, although it may be considerable in this wetland habitat.

Tracking the fate of seeds in the soil requires accounting for the seeds that germinate; seeds that move laterally in the soil or become deeply buried by wind, water, or animals; seeds that become inviable but remain in the soil; seeds that are eaten by predators; seeds that decay and decompose; and seeds that remain viable in the soil. In theory these inputs and outputs of the soil seed bank should be separately measurable, much as the components of above-ground plant population dynamics may be quantified and reconciled into an overall descriptive accounting of population changes over time. In practice, however, the handicap of not being able to count the population of seeds without destroying it becomes a formidable barrier to the effective quantification of seed bank population dynamics.

The assumption was made in this study that seeds that were viable in mid-July (when seed cages were destructively harvested) would have remained viable until the following spring, when germination was scheduled to occur.

Too little is known about how the ecological mechanisms affecting populations of seeds in the soil (e.g., physiological decay, seed predation, deep burial) may vary in magnitude as seeds age. Little is known as well about whether microhabitat differences and year-to-year environmental variation might have greater influences on determining the number of viable seeds in the soil than does seed age. Because seed cages in this experiment consisted of seeds only of a single age, opportunities for selection to act as a filter to select the genotypes from each generation of seeds were constrained. The magnitude of this selection constraint is not known.

Although the design of this study was meant to mimic the natural dispersal and recruitment of *C. multicaulis* seeds, lack of knowledge concerning these processes may have increased the chances of seed cage failure or otherwise altered results in some (unknown) way (Primack 1996).

In order to construct a complete picture of the population dynamics of a seed bank species, it is necessary to determine the probability that seeds of each age will survive to the next reproductive season. Using the current study design, this would require constructing seed cages that provided a microclimate closely comparable to the natural environment in which to sustain plants emerging from planted seeds through the point of seed production. It would also require the use of sufficient numbers of replicate seed cages to control for the variation between years and between locations of seeds of the same age. This is an admirable goal but was not reached in this study.

It is unknown whether seeds of *C. multicaulis* collected from various sites for the purpose of this field experiment differed in their germination response. The random mixing of seeds prior to planting in the field may have overcome some of the interpopulational differences, if they exist, but would not have removed the effect of cage location on germination behavior. Buried bag studies (Crist and Friese 1993, Bazzaz 1996) often make the assumption that intersite germination differences will be minimal and will not obscure differences in germination occurring between seeds buried for varying lengths of time. A buried bag study that attempted to control for the effect of burial site on emergence rate utilized reciprocal transplants (Bazzaz 1996); even so, burial site was determined to be the most important factor influencing emergence rate.

The success of seed cage experiments such as this one may be partially a function of the ability of the microclimate inside each cage to reach equilibrium with the outside soil and vegetation. Kalisz (Kalisz 1995) indicated that although she autoclaved (and then pulverized) soil prior to planting seeds, by the time she harvested seed cages they had experienced multiple episodes of natural precipitation and were well-populated with soil invertebrates and microbes. In this study, the periodic flooding of seed cages that occurred over the study period may have helped to equilibrate

conditions between the seed cages and their external environment. If similar studies are conducted in arid ecosystems, attention should be paid to soil microclimate to ensure adequate equilibration of seed cages with the surrounding soil.