SEEDLING SIZE AND SURVIVAL FOR *CHRYSOTHAMNUS NAUSEOSUS*

Lisa A. Donovan[1], James Mausberg[2], and James R. Ehleringer[2]

ABSTRACT.—Seedling size and survival in relation to summer drought were examined for *Chrysothamnus nauseosus* growing under field and greenhouse conditions. In the field, summer survival rates were less than 2% annually for the three years monitored. The effect of initial seedling height on subsequent survival was examined in both the field and greenhouse by grouping seedlings into live and dead categories on each census date and comparing the initial heights for seedlings in these categories. For a majority of the census dates, the initial height of surviving seedlings was greater than the initial height of those that subsequently died (significant differences ranged from 1 to 8 mm), indicating that seedlings that were taller at the initiation of the drought period had a higher probability of survival. In the greenhouse, taller seedlings had greater shoot and root biomass and rooting depth. Seedlings that are larger (i.e., taller and have greater aboveground biomass) in late spring appear to have a higher probability of surviving the summer drought due to greater rooting depth and hence increased access to moisture in deeper soil layers. Seed availability and safe sites for germination were probably not limiting since large numbers of seedlings successfully germinated in a patchy pattern during the study period. Seedling size and probability of survival were not related to either seedling density or the distance to nearest seedling neighbor. Survival through summer drought appears to be the main limitation to seedling recruitment in this population.

Key words: seedlings, survival, size, distribution, rabbitbrush, Chrysothamnus.

Seedling recruitment is crucial for the maintenance of most plant populations. However, high mortality rates are often associated with the seedling life history stage, and the patterns of reproductively mature individuals in a community may reflect primarily the historical effects of mortality during the seedling stage. Many seedling deaths are attributed to water stress though other abiotic and biotic factors are often involved (Harper 1977, Cook 1979, Fenner 1985). The small size of a newly germinated seedling places it near the soil surface where the largest fluctuations in soil temperature and soil moisture occur (Drew 1979, Caldwell 1985). When soil moisture is lost from shallow layers through evaporation and transpiration, a small root system has limited access to water in deeper soil layers, and the seedling is susceptible to water stress (Harper 1977, Angevine and Chabot 1979, Cook 1979). Even though germination and seedling growth may be timed to minimize the impact of the drought (Beatley 1974, Went 1979), new recruits of perennial species in semiarid environments must be able to persist through a drought during their first year.

The climate of the Great Basin is characterized by cold (below freezing) winters and warm summers where temperatures often exceed 40°C. Soil moisture recharge occurs in late winter and early spring when evaporation is low, and then the lowest monthly precipitation rates co-occur with the high summer temperatures. Summer precipitation events are usually of high intensity and short duration, so that moisture generally does not penetrate deep into the soil. Hence, the Great Basin generally has a hot, dry period from June through August when soil moisture is progressively depleted from surface soil layers (Campbell and Harris 1977, Caldwell 1985). The patterns of precipitation and soil moisture recharge, combined with the tendency to have fine soils, lead to the predominance of grassland and shrub communities in the lower elevations of the Great Basin (West 1988).

Chrysothamnus nauseosus (Pallas) Britt., commonly called rubber rabbitbrush, is a winter-deciduous shrub common throughout the Great Basin. Reproductively mature individuals are deep rooted in comparison to other woody plants in the communities and depend mainly on soil moisture recharged by winter and spring precipitation (Branson et al. 1976, Klepper et al. 1985, Flanagan and Ehleringer 1991, Flanagan et al. 1992, Donovan and Ehleringer in press). Seeds generally germinate in the spring after snowmelt, and both

[1]Department of Land, Air and Water Resources, University of California, Davis, California 95616.
[2]Department of Biology, University of Utah, Salt Lake City, Utah 84112.

seedlings and juveniles of *C. nauseosus* are more water stressed than larger, reproductively mature individuals during drier parts of the growing season (Donovan and Ehleringer 1991, 1992, in press). The pattern of small plants being more water stressed is presumably a function of having shallow roots and is consistent with recent studies in other water-limited habitats (DeLucia and Schlessinger 1990, Knapp and Fahnestock 1990, Cui and Smith 1991). If seedlings are dying as a result of water stress because they have shallow roots, then larger seedlings with deeper roots at the beginning of a drought should have an increased probability of drought survival (Cook 1980).

The objectives of the study were to investigate characteristics related to *C. nauseosus* seedling survival: (1) the timing and extent of seedling mortality in a natural population, (2) the effect of seedling size on subsequent survival during a drought, and (3) the effect of seedling density and distance to mature individuals on both germination and survival.

METHODS

Field Site and Field Studies

The Range Experiment Field Station at Tintic, Utah (39°55' N, 122°03' W, elevation 1775 m), was the site for the field studies as well as the source site for seeds used in the greenhouse studies. *Artemisia tridentata* Nutt. and *Juniperus osteosperma* (Torr.) Little dominated the site until it was cleared and disc-plowed in the early 1950s. Since then the site has recovered, with cattle grazing limited to approximately two weeks each spring except for the study years, during which cattle were excluded. The site, currently occupied by *A. tridentata, C. nauseosus* ssp. *hololeucus*, and perennial bunchgrasses, is most closely associated with the higher elevations of the Sagebrush Steppe vegetation type (West 1988). Soils are sandy loams (Jensen 1983), and the area receives an average of 374 mm of precipitation annually (Owens 1987). Monthly precipitation amounts for the study period were recorded by weather monitoring stations maintained at the Tintic Station by Utah State University personnel. Soil moisture values were determined gravimetrically. Percent soil moisture was converted to soil water potential on the basis of a soil moisture retention curve

developed using soil psychrometers (Wescor PR-55).

Seedling plots were located in a naturally established population of *C. nauseosus*. For 1989–91 seedlings were monitored in square plots 0.3 m to a side and located within 0.5 m of large, reproductively mature shrubs; four plots were established in 1989, and two more were added in 1990. Forty additional seedling plots (designated 1991–40) were established in 1991, each 0.28 × 0.43 m. Within plots, seedling locations were marked with toothpicks, and plots were censused at intervals throughout the growing seasons for number of surviving seedlings. Yearly comparisons of seedling density include only the four plots established in 1989 and monitored consistently throughout the three years.

Of the 1991–40 plots, 20 were randomly located throughout the population, except for avoiding the stems of large shrubs and/or clumps of perennial grasses. The distance was measured from the seedling plots to nearest large shrub of *C. nauseosus* or other woody shrub. The remaining 20 plots were arranged around five mature *C. nauseosus* shrubs, one at each of the four compass directions and 0.5 m distance from the base of the shrub. The 1991–40 plots were characterized visually for percent groundcover of small herbs and annual grasses. Seedlings in each of these plots were initially mapped on a grid, and individual seedlings measured for height (to top of longest leaf) at each census date. Plants were declared dead when they appeared to lack chlorophyll and were brittle.

Greenhouse Studies

Two studies were conducted with *C. nauseosus* plants growing in pots, using the Tintic population as the seed source. For the first study, designated GS1, plants were grown outside the greenhouse during the summer, concurrently with the monitoring of seedlings at the Tintic site during the 1991 season. Seedlings were grown in 1-m-tall pots of 15-cm-diameter PVC (polyvinyl chloride) pipe with bottom caps and drainage holes. The soil mixture consisted of one-third sand, one-third perlite, and one-third mixture of topsoil, organic material, and vermiculite. Plants were started from seed and thinned to two treatment densities after emergence of cotyledons: 13 pots with 5 seedlings per pot (density of

approximately 892 seedlings/m²) and 26 pots with 15 seedlings per pot (density of approximately 2670 seedlings/m²), similar to approximate densities previously observed in field plots. Prior to the appearance of the first true leaves on the seedlings, the soil in the pots was watered to field capacity daily. Subsequently, watering was reduced to simulate field drought, and soils were watered to field capacity every three to five days. Soil moisture content or soil water potential measurements were not made. The watering schedule was based on visual observations that the soil was drying out to at least 8-cm depth between watering and that some seedling mortality was occurring. Seedlings in each pot were mapped on a grid, measured for size, and scored for survival at each census.

The second greenhouse study, designated GS2, was conducted to determine relationships between height, aboveground and belowground biomass, and rooting depth. Plants were grown inside the University of Utah greenhouse, during the winter, using metal halide lamps to simulate summer light regimes. Pots of 15-cm-diameter PVC pipe were 31, 61, or 92 cm in height for rooting depth treatments, with 12, 13, and 28 replicate pots, respectively, for the treatments. The bottom of each pot was capped with clear plexiglas so that root growth at the bottom could be observed. Soil mix was the same as in GS1, and holes at the bottom of each pot provided drainage. Plants were started from seed and were grown one to a pot under well-watered conditions with no added nutrients. Plants were harvested if roots were observed at the bottom of a pot on one of the three harvest dates. At harvest, plant heights were recorded and shoot and roots were dried for determination of biomass.

For the 1991–40 and GS1 studies, initial seedling heights were compared for dead versus live categories at each date. A ratio of variances and an F_{max} test were used to determine whether variances were homogeneous for the field study and greenhouse studies (Sokal and Rohlf 1981). For comparisons of two means, Student's t tests were used when variances were not different, and approximate Student's t tests were used when variances were significantly different (Sokal and Rohlf 1981). For the comparison of seedling height and root biomass as a function of the three

rooting depth classes in GS2, variances were unequal, and a Kruskal-Wallis test was used to determine differences among means (Sokal and Rohlf 1981). Comparisons of numbers of seedlings across years were made with Spearman's rank correlation tests (Sokal and Rohlf 1981).

RESULTS

Field Studies

Monthly precipitation patterns varied between years, and of the years studied, only 1991 approached a pattern similar to the 23-year mean (Fig. 1). However, soil moisture patterns for the study years were more consistent, with a reduction in soil moisture that generally began no later than June. Soil moisture was least available in June–July and then increased in August and September. The shallow soil layer (0–35 cm) had a greater seasonal reduction of soil moisture than the deeper soils (35–70 cm) (Fig. 1).

Survival of *C. nauseosus* seedlings was low for all three years monitored, with 0.3, 1.9, and 1.4% for 1989, 1990, and 1991, respectively, surviving the summer (Fig. 1). Seedling censuses started at different times for each of the three years (March until early June), and survival is presented as a percentage of the maximum number of seedlings marked in a given year. For 1991, seedlings were marked as they germinated in March and April, and seedling numbers were greatest in April when most seedlings still had only cotyledons. Seedling mortality that occurred prior to mid-May appeared to be associated with either damping off, freezing damage, or improper rooting (i.e., seedlings that were not securely anchored in the ground and had ≥ 2 cm of root growth visible aboveground). After mid-May, when most seedlings had formed true leaves, seedling mortality appeared to be predominantly due to drought since seedlings dried in place and became brittle and achlorophyllous, with no evidence of herbivory or nutrient limitation.

In the 1991–40 plots, seedling size was monitored throughout the season, and though many seedlings succumbed to the drought, the surviving seedlings grew larger through the season (Fig. 2). For each sampling date, seedlings were grouped into live and dead categories to compare initial heights for
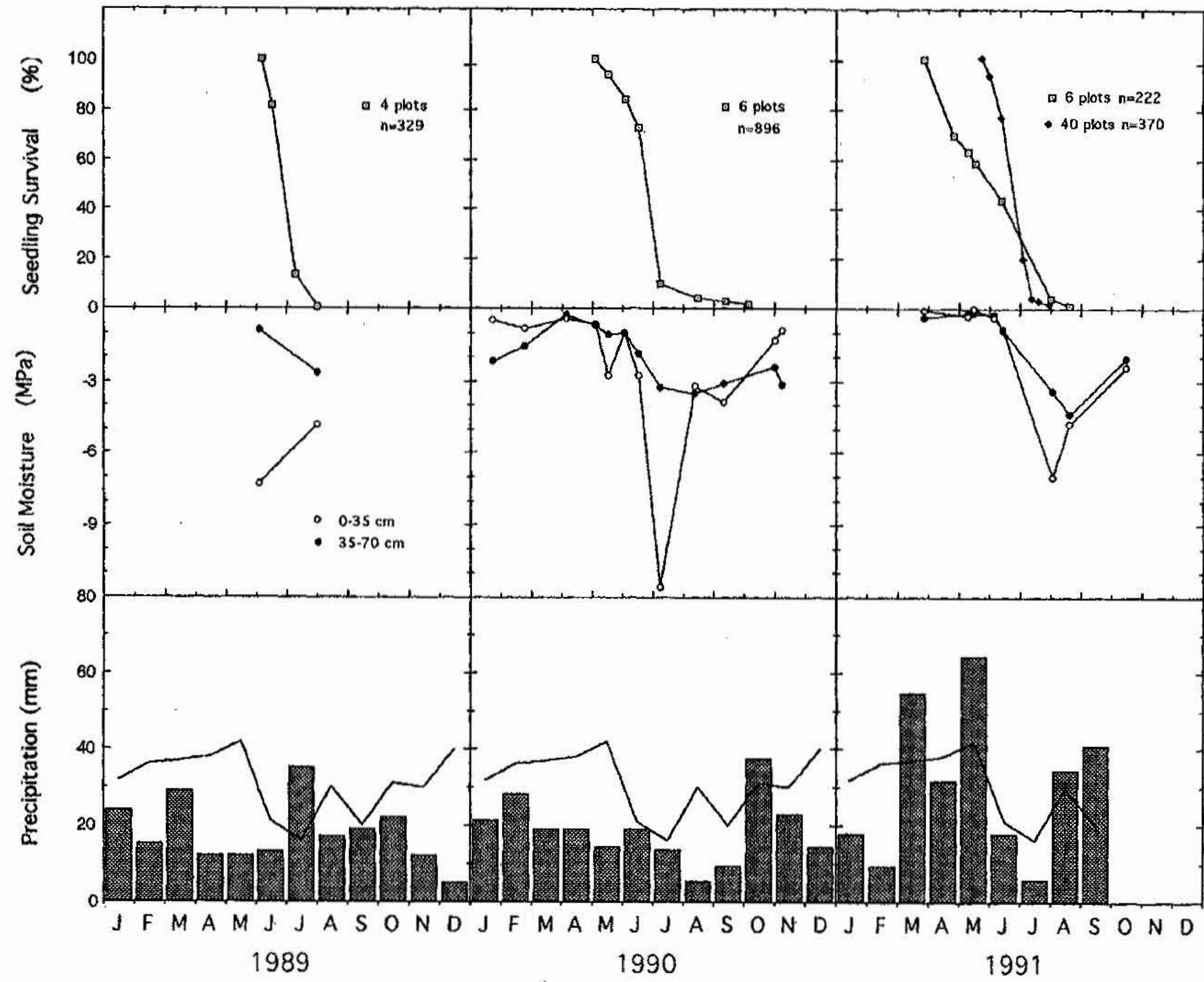
Fig. 1. Seedling survival, soil moisture, and precipitation (bar graph) for *Chrysothamnus nauseosus* at Tintic, Utah, for 1989–91. Solid line in precipitation panel indicates 23-year mean.
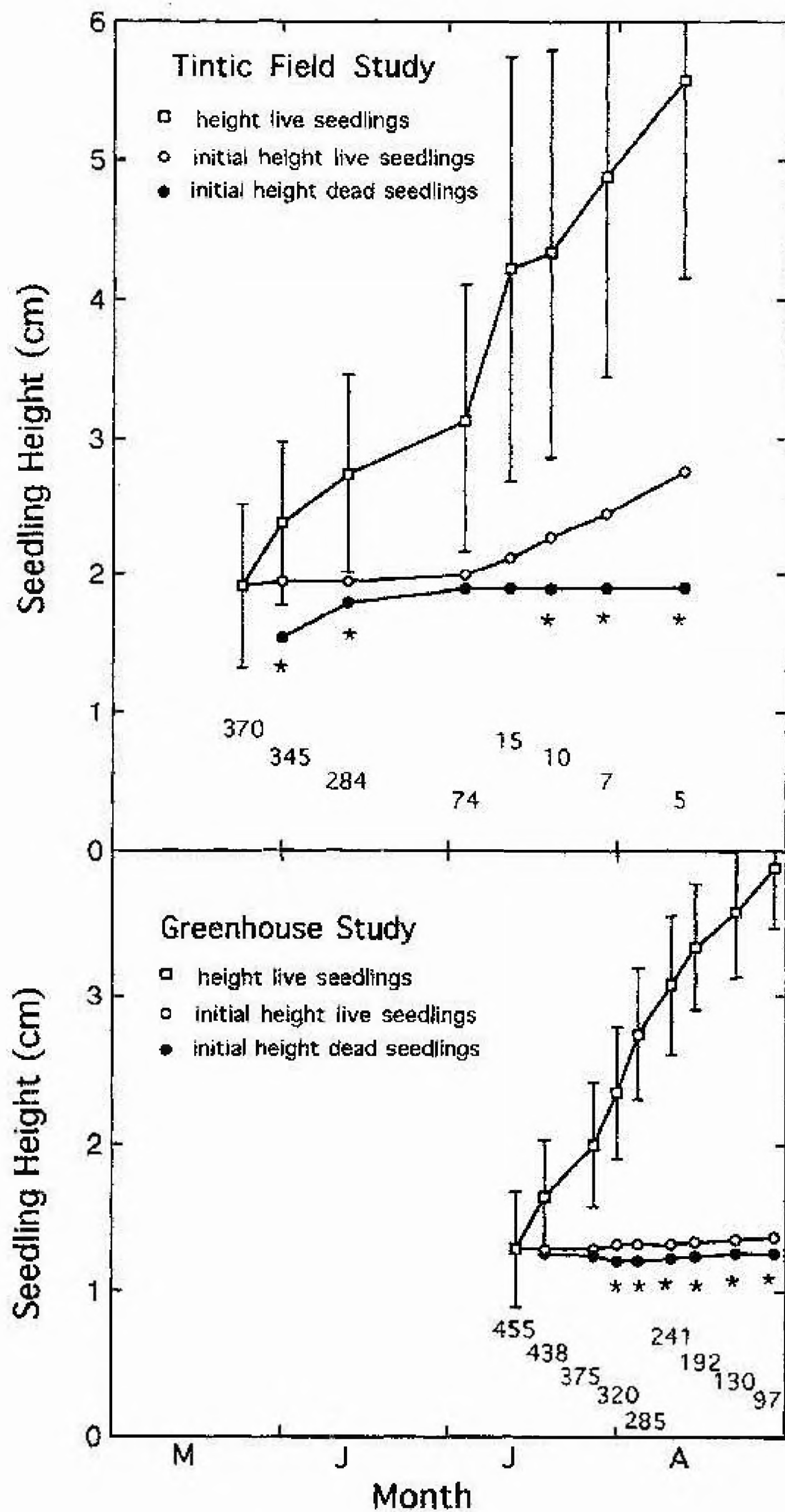
Fig. 2. Height of live seedlings (bars = sd) and initial size of seedlings in alive and dead categories for the Tintic field study and for the greenhouse study. An * along the x axis indicates that initial size for surviving seedlings is significantly greater than the initial size for dead seedlings at that date, $P < .05$. Numbers along x axis indicate number of seedlings alive at each census date.

seedlings in these categories. For most of the sampling dates surviving seedlings had been initially larger (in May) than those that died (Fig. 2). Though the significant differences between the mean initial heights (for subsequent surviving and dead classes) were as small as only 0.1 cm on some dates, the 5 seedlings alive at the end of the study had an initial mean height of 2.7 cm, which was 0.8 cm taller than the mean for the 365 seedlings that had died during the course of the study. To analyze the effect of seedling height

throughout the season, we categorized heights of seedlings alive on each date by whether or not they were alive on the next sampling date. *T* tests (one-tailed) indicate that taller seedlings at any date tended to be more likely to survive until the following census date ($P =$ .07, .001, .04, .18, .11, and .09 for the last six field sampling dates).

Spatial distribution of seedlings was examined for the 1991-40 plots. For the 20 randomly distributed plots, seedling numbers within plots averaged 11.8 ± 17.5, with a range of 0-75 (maximum of 625 seedlings/m^2). The distance of seedling plots to nearest reproductively mature neighbor averaged 1.1 ± 0.25 m, with a range of 0.3-5.0 m. For these randomly distributed plots, the number of seedlings per plot was not significantly correlated with the distance from the plot to nearest mature neighbor ($n = 20$, $r = .173$, $P >$ .05). For the 20 plots systematically oriented within 0.5 m of mature shrubs, numbers of seedlings averaged 7.8 ± 11.4, with a range of 0-41, which was not significantly different from the numbers of seedlings in the random plots ($t = 0.85$, $df = 38$, $P = .4$). However, when the nonrandomly located plots were categorized on the basis of compass orientation, plots located on the north side of the shrub had significantly more seedlings (21.8) than plots located to the east (5.0), west (2.8), and south (1.8) of the large, mature shrubs ($F =$ 6.07, $df = 3$, $P = .006$).

The distance to nearest seedling neighbor averaged 3.6 ± 3.8 cm and ranged from 0.1 to 29.3 cm for 1991-40 plots that contained at least two seedlings. The initial distance to nearest neighbor was not correlated with seedling height at the initiation of the study or at any subsequent census date during the study ($P > .05$ for all correlation coefficients). When seedlings were categorized by live and dead on each date, there were no differences in initial distance to nearest neighbor for these categories ($P > .05$ for all t-test comparisons), indicating that seedlings with closer neighbors were not more likely to die on subsequent dates. Hence, distance to nearest seedling neighbor had no effect on size or survival in the field plots.

The four plots monitored continuously for three years were ranked for total numbers of seedlings and for number of seedlings alive on 6 June (to reduce the effect of having started

the censuses at different times each year). For both total seedling number and number alive in early June, the ranking of the four plots was not consistent across years (Table 1). The total number of seedlings in these four plots ranged from a low of 131 in 1991 to a high of 406 in 1990.

Greenhouse Studies

For GS1 the soil drying resulted in the same type of mortality pattern as observed in the field, though it was displaced by a month since the GS1 drying did not begin until July (Fig. 2). For this study, because seedling size and percentage of seedlings dead on any date did not differ significantly for the density treatments, treatments were combined for all subsequent analyses. The surviving seedlings (n = 97) grew to a mean height of 3.9 ± 0.4 cm by the end of the study. For most of the census dates a comparison of initial sizes for dead versus live seedlings indicated that seedlings surviving to that date were initially larger than those that died (Fig. 2). The distance to nearest seedling neighbor averaged 1.7 ± 1.2 cm, with a range of 0.3–8.2 cm. Similar to the results of the field study, there were no differences in initial distance to nearest neighbor for seedlings categorized as live and dead on each date (P > .05 for all t-test comparisons). The initial distance to nearest seedling neighbor was not correlated with seedling height at the initiation of the study nor with seedling height on any subsequent sampling date (P > .05 for all correlation coefficients).

In GS2 seedlings were grown individually in pots under well-watered conditions. Plant height increased with increased rooting depth (Kruskal-Wallis statistic = 25.6, df = 2, P <.001), though there was variation within each of the rooting-depth classes (Fig. 3). For the 30-, 60-, and 90-cm rooting-depth classes, the average seedling heights were 5.4, 8.2, and 16.7 cm, respectively, but the minimum seedling heights were much more similar, 2.5, 2.0, and 3.5 cm, respectively. The relationship between plant height and rooting depth was mediated through the relationships of rooting depth and root biomass (Fig. 3, Kruskal-Wallis statistic = 20.8, df = 2, P < .001), root biomass and shoot biomass (Fig. 4, r = .89, n = 53, P < .001), and shoot biomass and height (Fig. 4, r = .91, n = 53, P < .001). Due to

TABLE 1. Number of *Chrysothamnus nauseosus* seedlings alive in plots 1–4 for 1989 through 1991 at Tintic, Utah; maximum number marked and (number alive on 6 June).

Plot #	1989 # seedlings	1990 # seedlings	1991 # seedlings
1	96 (96)	387 (235)	43 (37)
2	50 (50)	0 (0)	13 (1)
3	44 (44)	29 (14)	20 (10)
4	139 (139)	48 (6)	55 (29)
total	329 (329)	406 (225)	131 (77)

these significant associations between plant height, biomass, and rooting depth, small differences in plant height and biomass may have indicated large increases in rooting depth.

DISCUSSION

Annual rates of seedling recruitment were low for the *C. nauseosus* population at the Tintic study site. For each year monitored, less than 2% of the marked seedlings survived through the growing season, and the 1989 and 1990 estimates may have erred on the high side since seedlings were not marked until after some mortality had already taken place. In all three years seedling mortality coincided with the progressive declines in soil moisture and appeared to be a result of water stress. These low rates of seedling survival can be compared to estimates of yearly survival for other life history classes of *C. nauseosus* at the same site during the same time period: 83% for 1-year-old juveniles, 98–100% for juveniles greater than 2 years old, and 100% for small and large reproductive plants (Donovan unpublished). The low seedling survival and the timing of mortality for *C. nauseosus* are consistent with those reported for *A. tridentata* at this same field site (Owens 1987).

For both the field and the greenhouse studies, seedlings that survived the drought had initially been taller by only a few millimeters. For the field study there was also a trend for the tallest seedlings on any census date to be more likely to be alive on the following date, though this was not observed in the greenhouse drought study, where the range of heights was much smaller and hence statistically significant differences would be more difficult to obtain. Based on the greenhouse study where seedlings were harvested, the
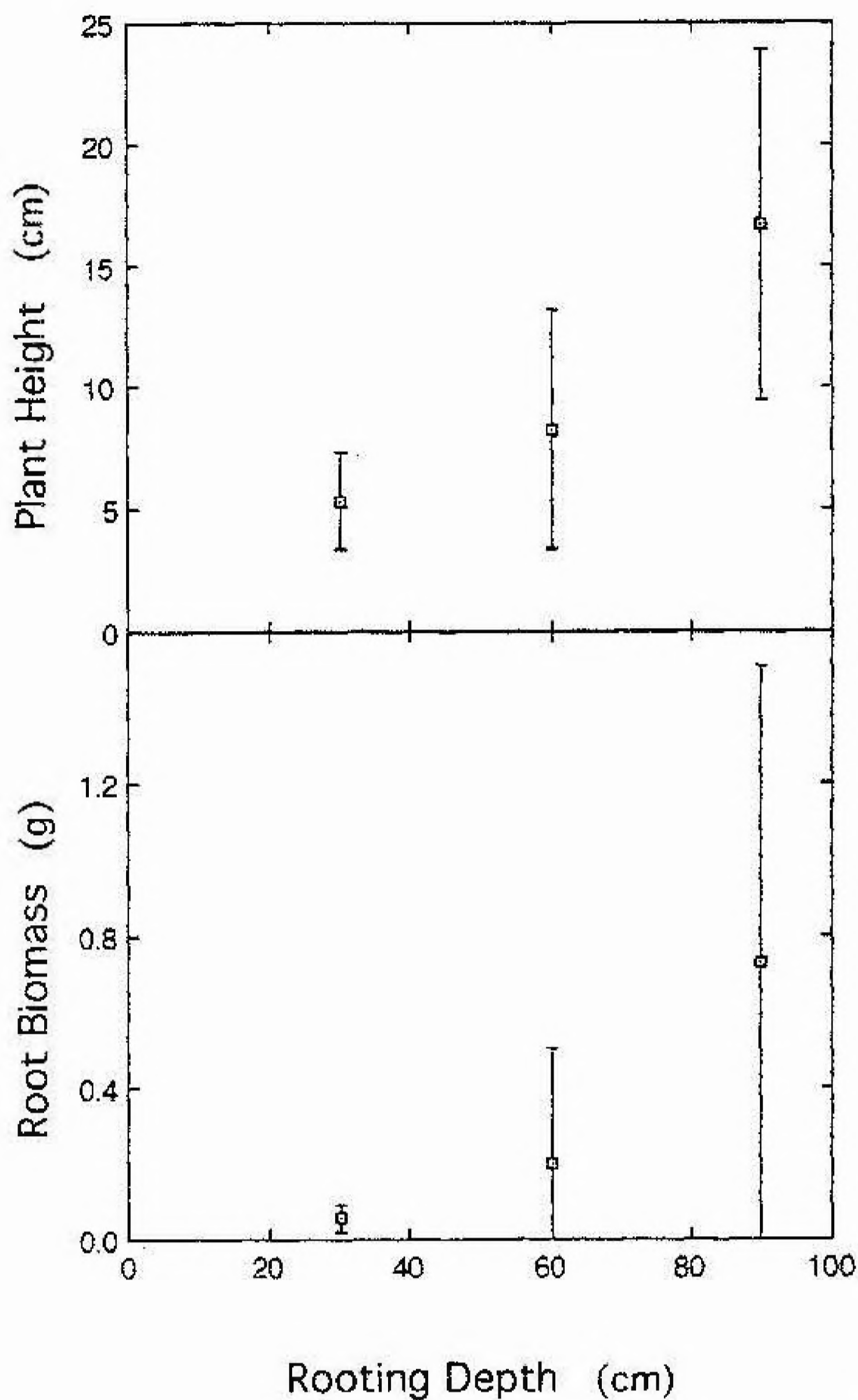
Fig. 3. Plant height and root biomass (mean and sd) as a function of rooting depth for *Chrysothamnus nauseosus* plants grown individually in pots under well watered conditions.

Shoot Biomass (g)

Fig. 4. Relationship of shoot biomass to root biomass (y = 0.07 + 0.51x, r = .89, n = 53, P < .001) and to plant height (y = 18.3 + (9.53*log(x)), r = .91, n = 53, P < .001) for *Chrysothamnus nauseosus* seedlings grown individually in pots under well-watered conditions (same plants as in Fig. 3).

taller seedlings had more root biomass and deeper roots, and hence increased access to deeper soil moisture reserves. While greenhouse seedlings had 43% of their biomass belowground, there are no equivalent estimates for seedlings of other Great Basin shrubs. Mature Great Basin shrubs are known to have 65–90% of their biomass belowground (Caldwell 1985, Dobrowolski et al. 1990). Since the greenhouse biomass study was conducted under well-watered conditions, it may have altered the biomass relationships somewhat because drought can result in greater investment in roots (Kozlowski et al. 1991).

The distance to nearest seedling neighbor was not related to survival in either the field or the greenhouse study. It is perhaps surprising that higher seedling densities and closer seedling neighbors did not result in greater competition-induced water stress and hence
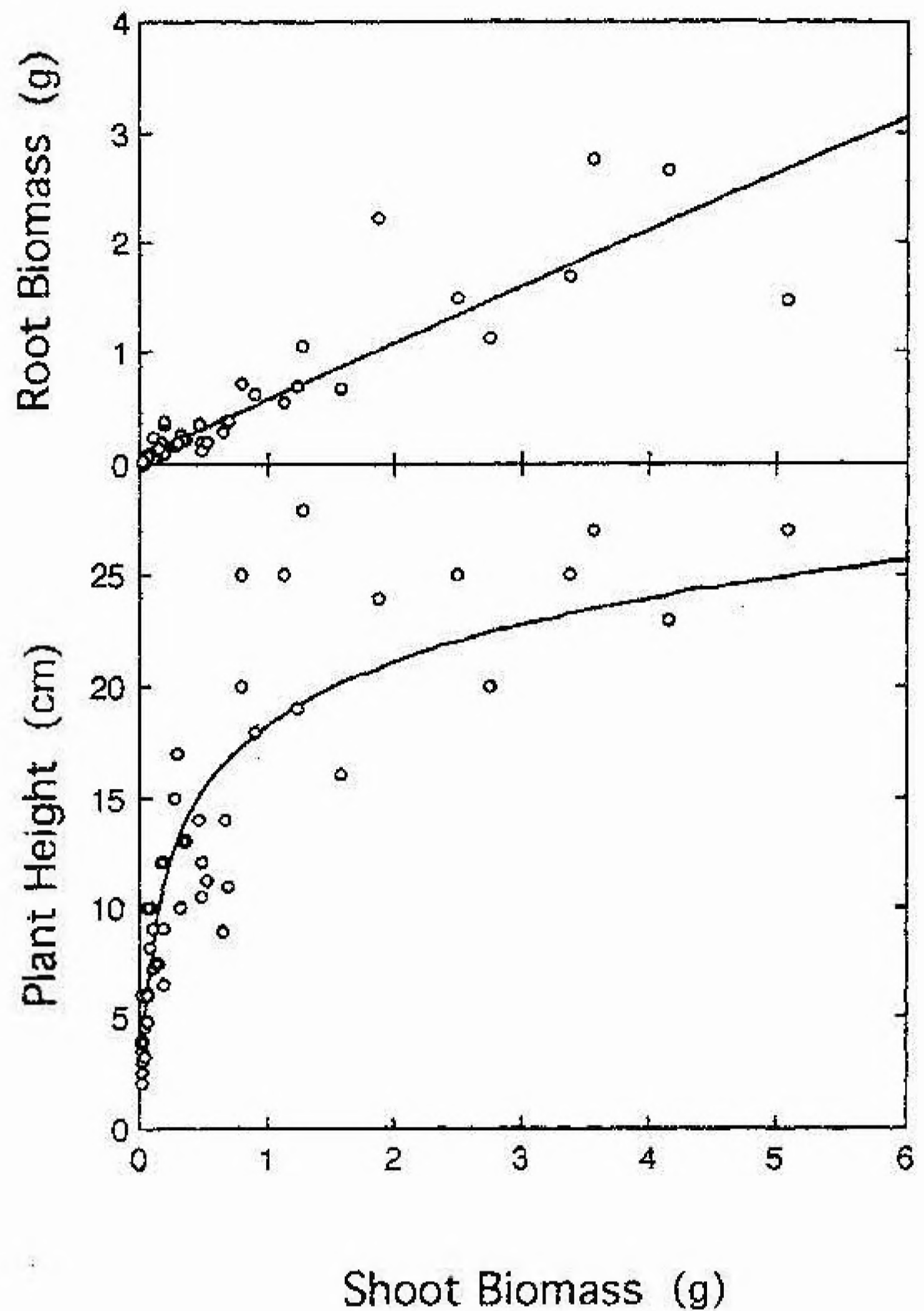
have an impact on survival. For the field, the lack of an effect of distance to neighbor or density, on either seedling size or survival, may have been associated with patchiness or abiotic microsite characteristics, as well as variable biotic interactions with annual and perennial grasses, forbs, and large shrubs (Fowler 1984, 1986, Reichenberger and Pyke 1990). In the greenhouse there were no other competitors and the microenvironment was uniform, but seedling size and survival were still not affected by seedling density or initial distance to nearest seedling neighbor. The greenhouse densities may have been insufficient to cause a detectable effect, or alternatively, the effects may have been from the interaction of many neighbors and not just the closest one (Fowler 1984).

Though the mechanisms leading to the differences in size were not directly assessed in this study, they have important implications

for the patterns resulting from the differential mortality. Seedling size variation may be due to differences in seed size, time of germination, microsite characteristics (abiotic and biotic), and genotypically controlled differences in growth rates (Cook 1980, Fowler 1984, Fenner 1985, Meyer et al. 1989). Since the greenhouse study used seeds collected from mature individuals at the Tintic site, the greenhouse and field studies had similar ranges of seed sizes and seedling genotypes. In the greenhouse studies, seeds were planted at the same time under common conditions and varied relatively little in seedling size at the initiation of the study when most plants had produced the first true leaves. In comparison, the seedlings in the field exhibited greater variation in seedling size, and this may be attributed to greater variation in germination time, abiotic microsite characteristics, and biotic interactions with neighbors (Cook 1980, Fowler 1984, 1986, Owens 1987, Meyer et al. 1989, Reichenberger and Pyke 1990). Regardless of the source of variation in size, it appears that greater seedling size at the beginning of a drought increases access to soil moisture and hence the probability of surviving through the drought. The size-dependent mortality found in our study is consistent with the findings by Cook (1980) that early germinating seedlings of *Viola blanda* were larger and more likely to survive through three successive years, though the cause of mortality in that study was not specified. The high rates of mortality indicate strong potential selection for traits associated with larger seedling size (Cook 1979).

Recruitment of seedlings into the natural population of *C. nauseosus* did not appear to be limited by seed availability or safe sites for germination, since large numbers of seedlings were found even in the dry years of the study. The variation in seedling densities, both spatially and between years, seems to be a common feature of arid and semiarid systems (Mott 1979, Went 1979, West et al. 1979, Owens 1987). The pattern of greater numbers of seedlings germinating on the north side of mature shrubs may be due to greater numbers of seeds or greater availability of safe sites appropriate for germination. Seedling survival may also be enhanced on the north sides of shrubs due to more available soil moisture due to either increased water availability from

later snowmelt or decreased water loss (i.e., decreased solar input and increased litter layer), but too few seedlings survived to test this idea. For seedlings in arid and semiarid habitats, large neighbors have been variously described as affecting the seedling survival as beneficial nurse plants or as disadvantageous competitors (Jordan and Nobel 1979, Owens 1987, Reichenberger and Pyke 1990).

Our studies, conducted during two dry years (1989 and 1990) and an average year (1991), indicate that seedling recruitment can be active in a mature population of *C. nauseosus* during most years. Of course, seedling recruitment would be expected to be greater in wetter years when fewer seedlings are lost to drought stress (Ackerman 1979, West et al. 1979, Owens 1987). Rates of recruitment into mature populations may also differ from those into newly disturbed habitats, such as postfire or chained areas (Young and Evans 1974). However, given that the summer decline in soil moisture is an overriding feature in the Great Basin, larger seedlings with deeper roots may have a greater probability of survival in most years and in most habitats.

ACKNOWLEDGMENTS

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