The Effects of Irrigation on Revegetation of Semi-Arid Coastal Sage Scrub in Southern California

Article *in* Environmental Management · November 2000

DOI: 10.1007/s002670010100 · Source: PubMed

Pamela E. Padgett
US Forest Service

DOI: 10.1007/s002670010100

The Effects of Irrigation on Revegetation of Semi-Arid Coastal Sage Scrub in Southern California

PAMELA E. PADGETT[1,*]
SHEILA N. KEE
EDITH B. ALLEN
Department of Botany and Plant Sciences
University of California
Riverside, California 92521-0124, USA

ABSTRACT / To test the appropriateness and applicability of irrigation for restoration of coastal sage scrub, a semi-arid vegetation type native to southern California, a field study comparing four irrigation schedules—no irrigation, spring irrigation only, summer irrigation only, and irrigation year round as needed—was established. A seed mixture of six native shrub species was broadcast, and the effect of irrigation on emergence and establishment was evaluated. Restoration of arid and semi-arid vegetation is challenging because of the severe environmental conditions inherent to these ecosystems. In particular, the low and unpredictable nature of precipitation can limit the chances for successful establishment of perennial species. Under conditions where supplemental irrigation is available, irrigation may make the difference between successful or failed restoration. However, increasing the availability of water through irrigation may result in poor plant adaptation to surviving arid conditions or only temporary success followed by failure once supplemental water is withdrawn. In this study, irrigation stimulated germination in the irrigated plots about a month earlier than the plots dependent on natural rainfall, but this had little lasting effect. Spring and summer irrigation did not improve survival compared to the plots receiving no supplemental water. The largest effect of irrigation was a reduction in survival of several species grown under irrigated conditions as compared to nonirrigated conditions. In plots where water was applied all year long a single species, *Artemisia californica,* represented nearly 100% of the species present at the end of two growing seasons. Irrigation may speed revegetation under some conditions, but was not very effective in establishing natural vegetation structure.

The use of irrigation for the restoration of vegetation native to arid and semi-arid regions is controversial (Perry 1987, Luken 1990, Keator 1994). Though not always feasible or practical, under conditions where extra water can be supplied, it has the advantage of prolonging the growing season and substituting for unpredictable rainfall during drought years. In semi-arid ecosystems, favorable conditions for shrub recruitment are often episodic (Bleak and others 1965, West and others 1979, Jordan and Noble 1981, Silcock 1986, O'Connor 1996). In Mediterranean ecosystems where the majority of precipitation occurs during the winter months, consistent recruitment following severe disturbances is dependent on sufficient winter moisture to allow seedlings to mature quickly enough to withstand the 5–6-month summer dry season (Went 1948, Mooney and Kummerow 1981, Moreno and Oechel 1992). In chaparral ecosystems where precipitation averages 40 to 50 cm, successful recruitment may occur every year (O'Leary 1990, Tyler 1995, Moreno and Oechel 1992).

KEY WORDS: Vegetation restoration; Seedling survival; Species evenness

[1]*Current address:* USDA-Forest Service Fire Research Lab, 4955 Canyon Crest Dr., Riverside, California 92507, USA
*Author to whom correspondence should be addressed.

In desert ecosystems with precipitation generally less that 15 cm, favorable conditions for germination and survival of perennial species may occur as infrequently as once or twice in 15 years (Bleak and others 1965, West and others 1979, Jordan and Noble 1981, Silcock 1986). Where rapid restoration of native arid and semi-arid vegetation is desired, such as following road construction, urban development, or wildfire, irrigation may provide an attractive alternative to dependence on erratic precipitation. Irrigation may also permit the initiation of revegetation programs outside of the normal growing season.

Supplying supplemental water may negatively impact establishment of arid-zone plant species, however (Perry 1987, Luken 1990). Prolonged dry season irrigation of arid-zone plants is known to promote the growth of pathogenic fungi, resulting in shortened life spans (Perry 1987, Keator 1994). During the early stages of seed germination and growth, irrigation may artificially enhance the competitive ability of more mesic species and individuals at the expense of seedlings better adapted to surviving under dry conditions (Lauenroth and Dodd 1978, Gutterman and Evenari 1994). This advantage may not continue unless irrigation is maintained in perpetuity. Particularly when the goal of irrigation is for short-term, rapid establishment—but not for long-term maintenance—establishment of species adapted to irrigated conditions may result in a failure in restoration once irrigation is withdrawn (Elberse and Breman 1990).

Germination of many wildland plants is well regulated to ensure that the timing of emergence is optimal for the survival of the seedling (Went 1948, 1949, Gutterman and Evenari 1990, Bewley and Black 1994). The known mechanisms regulating germination vary widely. Some, such as the phytochrome-red light/far-red light system and temperature stratification are well studied (Bewley and Black 1994). Others, such as nitrate stimulation (Hilhorst and Karssen 1988), smoke responses (Keeley and Frotheringham 1998), or the requirement of some species to pass through a wet/dry/wet cycle prior to germination are less well understood (Bewley and Black 1994). Most mechanisms appear to function in some way to provide environmental cues. In arid and semi-arid environments, the most important environmental condition for seedling survival is the availability of water during early development (Went 1948, 1949, Elberse and Breman 1990). Temperature and light provide secondary cues regarding the time of year, thus the expected duration of the available moisture (Juhren and others 1956, Bewley and Black 1994). Once germinated, the success in establishment is dependent on a successful match of physiological requirements and environmental conditions. In semi-arid regions this usually means an adequate supply of water and nutrients until the seedling is mature enough to withstand a dormant or quiescent period during prolonged dry spells.

Coastal sage scrub (CSS) is a vegetation type that occupies a physiographic position between chaparral and western Mojave shrublands. The distribution of CSS is limited to the populated coastal foothills and inland valleys of southern California, although similar ecosystems occur in Mediterranean regions around the world. Rainfall is limited to the winter months in southern California with a 10-year average for precipitation in CSS of 30 cm. However, total rainfall is quite variable from year to year, ranging between 10 and 45 cm over the same 10-year period. Summer temperatures are intermediate to those of chaparral and the Mojave Desert, typically hot and with low relative humidity. Several plant species common to CSS are also found in chaparral or desert ecosystems (Pavlik and Skinner 1994).

Agricultural and urban development, anthropogenic and natural disturbances, and encroachment by non-native plant species have resulted in CSS ecosystem losses of 70% to 90% of the area originally occupied (Westman 1981, Freudenberger and others 1987, Keeley and Swift 1995, Minnich and Dezzani 1998). This loss of habitat has led to the listing of 10 reptile, 11 mammal, and 26 bird species as threatened or endangered (Keeley and Swift 1995). For this reason, restoration of CSS has become a serious concern in southern California. Yet restoration of Mediterranean ecosystems present significant management challenges because of their proximity to human populations, tendency toward fire and flooding, and in some cases lack of aesthetic appreciation (Mooney 1982). Because CSS shares a number of features of both chaparral and desert ecosystems, information concerning revegetation strategies may be mutually applicable.

In this study we evaluate the use of irrigation in the establishment of six shrub species native to the CSS of southern California. Because significant mortality occurs during the first growing season, particularly in the presence of weedy annuals (Moreno and Oechel 1992, Eliason and Allen 1997), temporary irrigation during the spring or summer months may provide enough additional resources to enhance survival through the first summer drought. Trial plots were seeded with a mixture of the species. The treatments consisted of four different watering regimes: (1) no additional water, (2) irrigation during the spring months only, (3) irrigation during the summer months only, and (4) continual irrigation as needed. Irrigation was provided during the first year and the plots were monitored for 2 years. Monitoring consisted of monthly or bimonthly identification and assessment of numbers and maximum heights of individuals and a final harvest for determination of biomass.

Materials and Methods

Seedbed Preparation

The experiment was conducted at the University of California's Agricultural Research Station in Riverside from November 1995 through June 1997. The site is located at 33°58′ N latitude, 117°17′ W longitude, and at approximately 300 m elevation. Coastal sage scrub was the original vegetation type, but the site has been in agricultural production for more than 50 years. The field was disced and graded smooth in preparation for planting; no furrows were created. The field was divided into 1.5-m-by-1.5-m plots with 1-m walkways between plots. After installation of the irrigation system, the plots were raked to roughen the surface and seeds were hand broadcast on December 5, 1995. Following seeding, the plots were again raked and lightly watered to prevent the seeds from blowing away. A mixture of six species, typical of the CSS community, was used: *Artemisia californica*, *Salvia mellifera*, *Lotus scoparius*, *Eriogonum fasciculatum*, *Encelia californica*, and *Baccharis pilularis*. Species will be referred to by genus in the rest of the text. S&S Seed (Carpinteria, California) donated all of

Table 1. Seeding densities for the individual species (percent live seed and number of seeds per gram was as indicated by the seed vendor)

Species	Seeding rate (g m^{-2})	Pure live seed (%)	Seed/g (# g^{-1})	Live seed (# m^{-2})
Artemisia californica	1.1	10.1	12,277	1364
Encelia californica	0.7	32.3	391	88
Eriogonum fasciculatum	2.65	7.1	1,004	189
Lotus scoparius	0.74	86	1,004	639
Salvia mellifera	1.28	20.5	1,395	366
Baccharis pilularis	0.4	2	11,161	89

the seed. Seeding densities conformed to those used by the California Department of Transportation in standard restoration efforts (Table 1). S&S Seed supplied pure live seed values for each species. No pretreatment of the seed was used to prepare any of the species for planting (Keator 1994). Hand weeding of the plots and walkways was performed as needed.

Irrigation Treatments

Treatments were arranged in a randomized complete block design with six replications. Four irrigation regimes were established within each block: continual watering as required to keep the upper 15 cm moist (December 1995–October 1, 1996), spring watering (March 1–July 1), summer watering (July 1–October 1), and no water. The location of the water regimes within each block was chosen randomly. Watering of all plots was discontinued in October 1996.

An irrigation system was designed with shrub head sprinklers placed in the four corners of all plots (except the no-water plots). The heights of the sprinkler heads were raised from 5 cm at seeding to 45 cm as the plants grew. Water was supplied to the continuous-water plots during the winter when the upper 5 cm of the plots became dry. This evaluation was made by observation. In general, the requirement for supplemental water was low during the cooler seasons when evapotranspiration was low and rainfall adequate. Regular irrigation schedules were begun on March 1, 1996. Both the continuous water and the spring water treatments began with a single application of approximately 2 to 3 cm of water per week. The rate was increased to twice per week (2 to 3 cm per application) in June. On July 1 the spring water treatment was stopped, the summer water treatment initiated, and the continuous water treatment maintained. The irrigation schedule remained two times per week, and the application rate was increased to approximately 5 cm of water per application. On October 1, 1996, all irrigation was stopped.

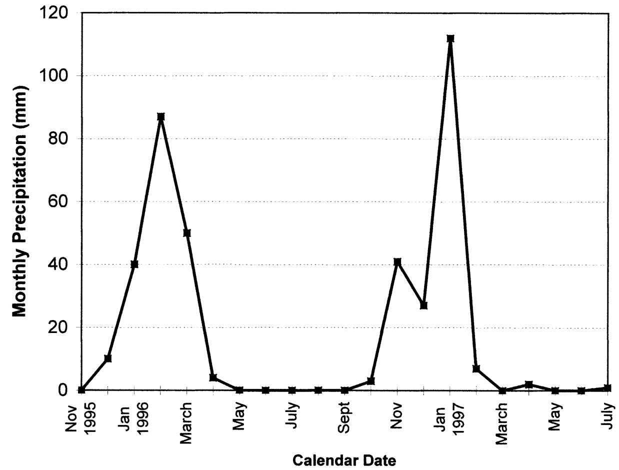

Figure 1. Monthly precipitation November 1995–July 1997. Rain gauges were maintained by the staff of the University of California, Riverside Agricultural Research Station.

Rainfall was measured at the Agricultural Research Station (Figure 1). Rainfall for the first season, November 1995–June 1996, was about 19 cm, lower than the 10-year average of 30 cm for the area. The majority of the precipitation fell in the latter half of the rainy season. Rainfall for July 1996–July 1997 was also lower than average, at about 18 cm for the year. In the second year most of the precipitation occurred in the early part of the rainy season, leading to a dry spring in 1997.

Evaluation Methods

Nondestructive plant measurements were taken on a flexible schedule based on plant phenology: every 2 to 4 weeks during early emergence and during the high mortality time of early summer, and bimonthly during times of slower growth and development. Within each plot a marked 0.125-m^2 quadrat was repeatedly measured using a 50-cm $\times$ 25-cm plot frame. Counts were made of the number of plants by species within the plot, and the height of the tallest individual of each species within the plot frame was noted.

At the end of the second growing season (July 17, 1997), the above-ground, standing biomass of all plants except *Artemisia* was harvested for weight determination. The biomass for *Artemisia* was not determined for two reasons: The estimated biomass was one to two orders of magnitude higher than any of the other species making comparisons to other species irrelevant, and the leaves of *Artemisia* were too dry to harvest quantitatively. The harvest was conducted by removing all plants whose main stem occurred within the center 1 m^2 of the plot. The harvested plants were dried at 60°C until constant weight was reached. The combined weight of flowers, leaves, and stems was recorded.

Statistical Analysis

Data were analyzed using Jandel SigmaStat version 2.0. Seedling emergence data were analyzed by repeated measures ANOVA for the total data set and *t* test for selected dates. The biomass data were analyzed by ANOVA. The data were checked by a normality test function prior to the application of statistical test, and no transformations were needed.

Results

Emergence and Survival

Artemisia seedlings in the continuous water plots emerged earlier than those dependent on natural rainfall (Figure 2A). However, seedling numbers in all of the treatments increased rapidly with precipitation so that maximum densities occurred in all treatments within a week of each other. Seedling numbers in the plots not receiving irrigation (none, spring, summer) were very similar from January until March. Once the spring water treatment was begun in March, germination slowed and densities became significantly lower than in the other treatments. The summer-watered plots contained significantly more seedlings in February than either the spring or no-watered plots, but by June, seedling numbers in all but the continually watered plots were statistically similar. In these plots the densities declined during the first growing season to less than 300 m^{-2}, with a small degree of continued mortality until the conclusion of the experiment. Neither the spring water nor summer water treatment appeared to reverse this trend, nor did the return of natural rainfall in October 1996. The seedling numbers in the continuous water plots remained significantly higher from mid-July 1996 until the seedling count at the conclusion of the experiment. Beginning in February 1997, the average number of seedlings in the continuous water plots dropped from about 750 m^{-2} to about 200 m^{-2}. By June 1997, there was no statistically significant difference among the four irrigation treatments for *Artemisia* seedlings.

Eriogonum seedlings in the continuous water plots emerged rapidly, but the numbers of seedlings declined quickly to 20% of the initial emergence within 3 months (Figure 2B). Emergence of *Eriogonum* in the no-water and summer water plots occurred later and maintained significantly higher seedling numbers than the continuous water treatments until early summer when all of the treatments were statistically similar. Initiation of spring irrigation suppressed germination so that maximum seedling numbers in the spring water plots were never more than 30% of that observed for the no-water and summer water treatments. By April 1997, *Eriogonum* populations were near zero for all of the irrigated treatments, but remained at about 25 m^{-2} in the unirrigated plots.

Salvia demonstrated very poor survival in all treatments (Figure 2C) even though initial emergence was only slightly less than that observed for *Eriogonum*. Similar to *Eriogonum* seedlings, *Salvia* seedlings in spring water plots had significantly lower densities than in the other treatments. The number of surviving seedlings began to decline in early March of the first growing season. Neither spring nor summer irrigation appeared to rescue the declining populations. At the end of the first summer the numbers of seedlings were essentially zero in the sampled subplots and remained that way through the onset of the rainy season until the final harvest.

Encelia, in contrast with the other species, demonstrated very little difference in the emergence and survival under different irrigation regimes (Figure 2D). The observed low densities recorded in late summer of the first year is most likely due to mistaken notation of dormant, leafless seedlings as dead. These dead seedlings releafed with the winter rains. As with *Eriogonum* and *Artemisia*, emergence occurred earliest in the continuous water plots. By early February 1996, the numbers of seedlings growing in the continuous water plots were equivalent to the numbers of seedlings in all the other plots. Other than a slight increase in survival of plants in the continuous water treatment during the first summer, the lack of statistical difference ($P < 0.1$) among treatments continued until the end of the experiment. Once the rainy season began in October 1996, all treatments contained similar numbers of *Encelia* plants.

Lotus seedling emergence occurred at much lower rates relative to the other species, averaging only 10 to 30 seedlings per m^2 (Figure 2E). By summer of the second year, survival of these seedlings was significantly higher in the no-water plots. Irrigation appeared to be deleterious to this species as spring water resulted in suppressed germination. The greatest survival was obtained in the summer water plots prior to initiation of the treatment, but once irrigation began, survival plummeted.

Baccharis was not well suited to this experimental site. No seedlings survived in the sampling subplots after the first summer. Continual irrigation did, however, extend survival nearly a month longer than any of the other treatments.

Survival of Seedlings

The maximum germination rate for *Eriogonum* was poorly correlated with the calculated number of live

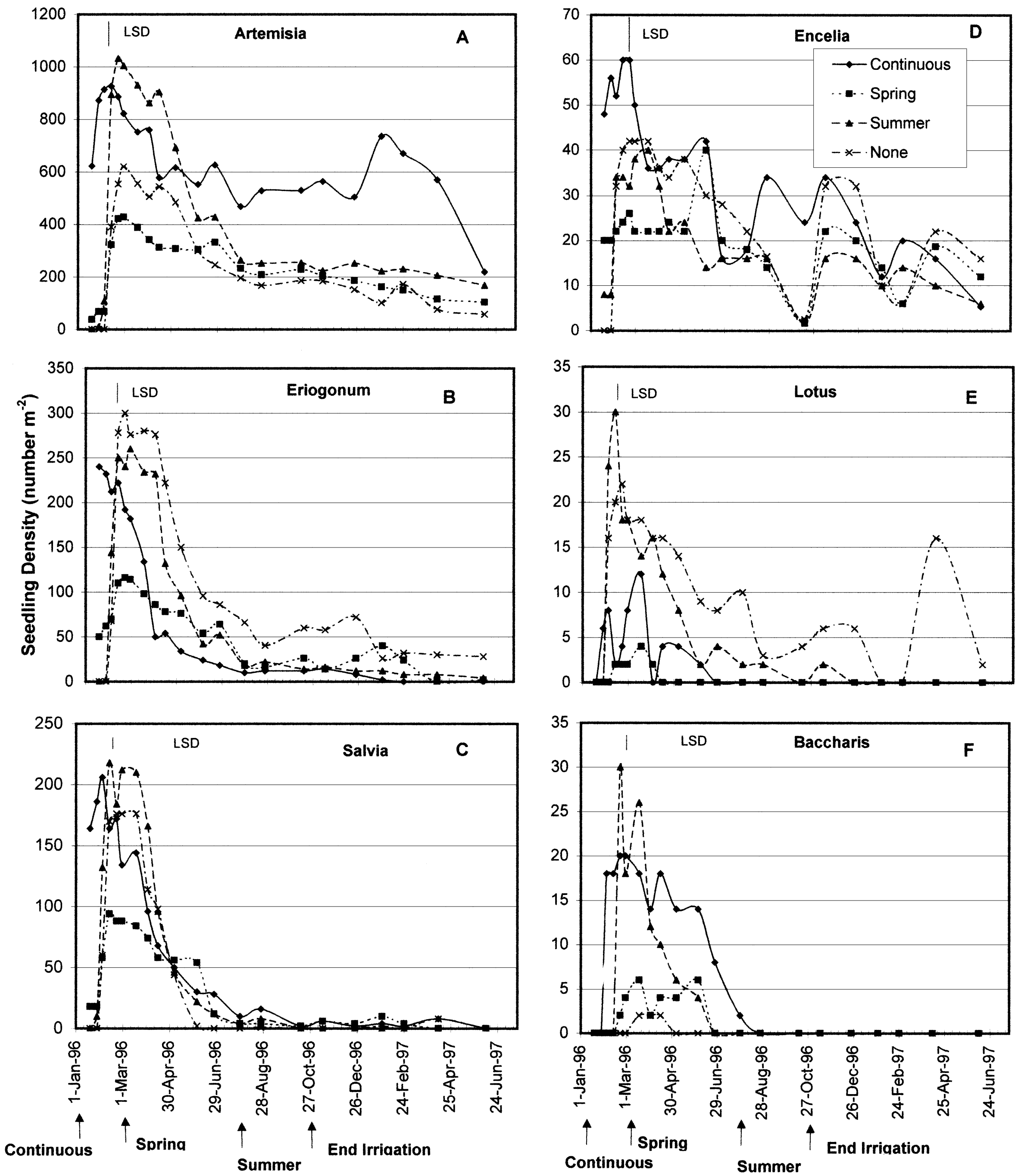

Figure 2. Seedling densities of the six species planted and grown under four irrigation regimes. A 50-cm × 25-cm subplot was established in the center of each plot, and the number of seedlings occurring in the subplot was recorded weekly during the early germination and growth phase and monthly as the seedlings became established. Data shown are the means of six replicate plots with a pooled standard error bar (LSD) shown in the upper left corner of each graph.

seed sown (Table 1, Figure 2). An estimated 50% more seedlings emerged than were theoretically sown. The calculated densities of *Lotus* indicated very poor germination, at less than 3% relative to the theoretical live seed planted. The average germination rates for *Artemisia*, *Encelia*, and *Salvia* were about 50% and for *Baccharis* 17%. Of the total number of seedlings that emerged, nearly 25% of the *Artemisia* in the continuous water and spring water treatments survived the first two growing seasons (Figure 2). The higher survival rate in the spring water treatment appeared to be due primarily to germination being suppressed rather than a rescue by spring irrigation (Figure 2A). Emergence in the summer water plots was equivalent to that in the continuous water plots, but under the summer water regime, survival was 16%. This, however, was significantly higher than the survival of 9% observed in the plots receiving no water.

Nine percent was the highest survival rate for *Eriogonum*, and it occurred in the no-water plots. Survival in the continuous water plots for this species was 0%. In the spring and summer irrigated plots survival was similar at 1.6–1.7%. Survival of *Encelia* under spring water conditions was nearly 50%, but like *Artemisia* this may be due largely to differences in germination rates. *Encelia* exhibited the best survival rates among the six species. In the no-water plots, more than a third of the initial numbers of seedlings were still in place by the summer of 1997, and almost half of the plants growing in the spring water plots were still present at the end of the experiment. Continual watering did not seem to favor establishment of this species, as survival was less than 9%. Survival was 0% for *Baccharis* and less than 1% for *Salvia* and *Lotus* (data not shown).

Biomass Production and Species Composition

Artemisia dominated the species composition in all treatments, with final densities of 100–200 seedling m^{-2} compared to 10–20 m^{-2} for all other species combined (Figure 2). It both outnumbered and was taller than the other species (data not shown). The height of individual *Artemisia* plants was significantly affected by watering regime and responded to the changes in water availability when the irrigation changed from spring water to summer water (Figure 3). From March 1996 until mid-summer, the heights of the *Artemisia* in the continuous-water plot were statistically similar to seedlings growing in the spring water plots, and the summer water seedlings were similar to those in the no-water plot. When the summer water treatment began, seedlings in those plots responded with a significant increase in height, resulting in nonsignificant differences among the irrigation treatments. Seedlings in the no-water treatments remained significantly shorter until the spring of 1997. By the end of the experiment there was no significant difference in *Artemisia* height among the four irrigation treatments. Biomass of this species was not determined because of excessive shattering of the dried leaves and the overwhelming productivity relative to the other species.

For the other five species, the irrigation treatments did not significantly impact seedling heights (data not shown), but it did have a significant impact on the

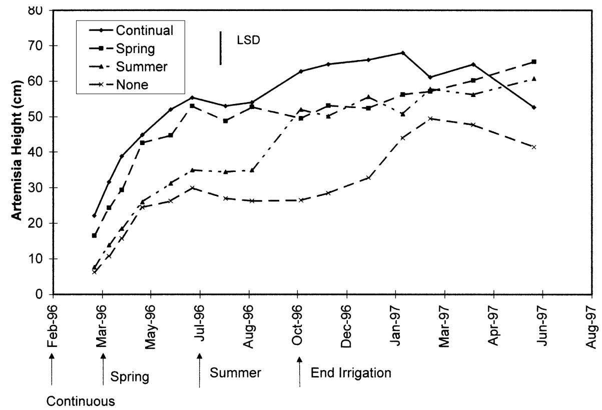

Figure 3. Maximum height of *Artemisia californica* grown under four different irrigation regimes. Data shown are the means of six replicate plots. A pooled standard error (LSD) is indicated next to the legend.

species composition within each of the plots. Overall, the greatest evenness of species as determined by biomass was attained in plots receiving no supplemental water (Figure 4). All plots were dominated by *Artemisia*, but all other species were most prevalent in the no water plots (Figure 4). *Baccharis* was found only in the no-water plots (data not shown). *Encelia* (Figure 4A) survived relatively well in all plots; a trend toward higher biomass accumulation under no water was observed, but the difference was not significant at the $P <$ 0.05 level. *Eriogonum* had better than sixfold biomass accumulation in the no-water plots relative to the other treatments (Figure 4B). Among the irrigation treatments (continuous, spring, summer), there was no significant difference. For *Lotus*, summer water resulted in increased biomass relative to the spring water and continuous water treatments, while the biomass in no water and summer water plots were statistically similar. Spring watering resulted in very low biomass accumulations, and *Lotus* was observed in only one of the continuous water plots (Figure 4C). *Salvia* persisted in all plots, but had significantly more biomass in the no-water and spring water treatments. Summer watering did not appear to rescue this species as the biomass was not significantly different from the biomass of the continuous water plots (Figure 4D).

Discussion

Site Selection and Planting Conditions

The field selected to evaluate the irrigation effects on restoration of native CSS species had a 50-year history of disturbance for agricultural production and is representative of conditions commonly encountered by

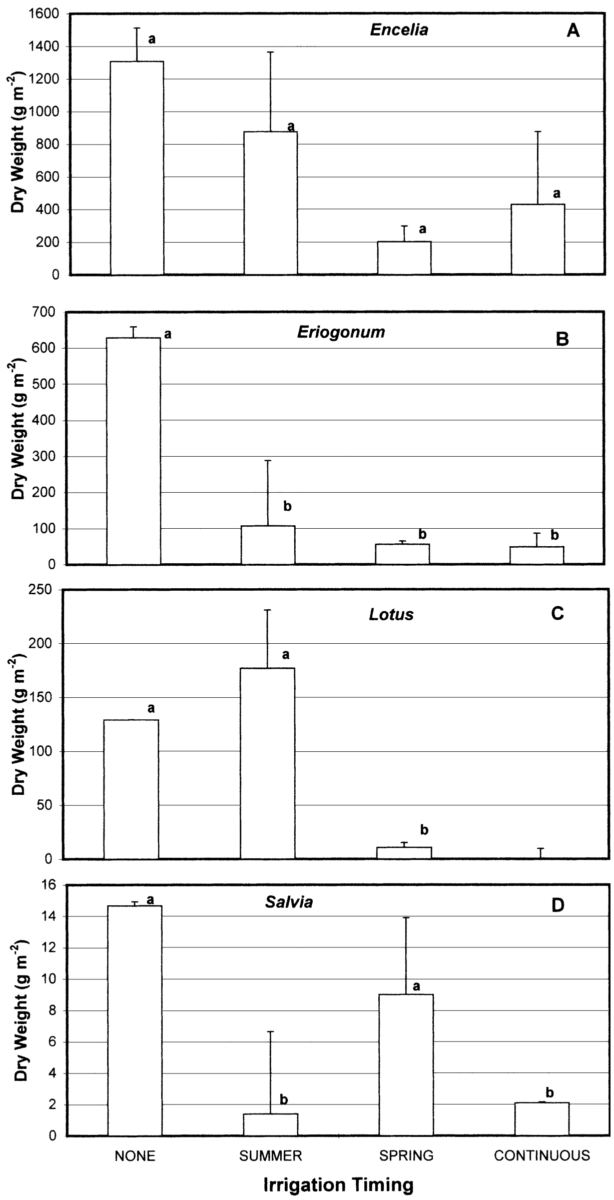

Figure 4. Biomass of four shrub species after two growing seasons. Biomass for *Artemisia californica* is not shown because of difficulty in harvesting and because the estimated biomass was so large compared to the other species. Biomass data for *Baccharis* is also not shown because it only survived in one treatment. Letters next to the data indicate significant differences at the $P < 0.01$ level.

revegetation projects. Based on observations following the initiation of irrigation, the seedbank contained a wide variety of agricultural weed species, but no native perennial species. The plots were homogeneous with respect to soil conditions, as determined by soil nutrient analysis and physical characteristics (data not shown). In these experiments no effort was made to introduce the heterogeneity of natural physical conditions common to CSS. Such modifications might include creating surface unevenness, rock outcrops, or other microsites that would provide a variety of conditions for seedling establishment. Seedbed ecology has an important influence on the development of plant community structure (Call and Roundy 1991), but it can be difficult to create the variety of seedbed conditions common in nature under restoration conditions. The fortuitous match of a seed's morphological characteristics and an abundance of the appropriate microsites can lead to the dominance of single species (Harper and others 1965, Harper 1977). It is possible that the seedbed characteristics may have contributed to the success of *Artemisia* or the failure of *Lotus.*

Where little of the natural features remain, such as after road construction or building projects, the tendency is to overcompensate by increasing the seeding rate and the number of species in the seed mix in an effort to establish a diverse plant community (Vallentine 1989). Clearly, the seed proportions used in this experiment were heavily skewed toward *Artemisia* at 1364 seeds m^{-2} compared to 1371 seed m^{-2} for all other species combined. This, however, is a commonly prescribed seeding rate for CSS restoration projects and may have been developed under slightly different environmental conditions using different seed lots. These results indicate that under these growing conditions the proportion of *Artemisia* seeds in the mixture was excessive, particularly for irrigated conditions. However, it is possible that under the conditions where this seeding rate was developed, establishment of *Artemisia* was more difficult.

Natural rainfall was lower than average for both years of this study, but establishment of native vegetation did not seem to be inhibited by these conditions. Clearly, natural conditions were sufficient for restoration of five out of the six species evaluated.

Irrigation Effects on Emergence and Ground Cover

All six species investigated exhibited high rates of emergence followed by a self-thinning process (Pyke and Archer 1991 and references therein, Moreno and Oechel 1992). The average germination rates of 50% for *Artemisia, Encelia,* and *Salvia* would indicate a successful match between seed and growing conditions. Poor germination for *Baccharis* and *Lotus* suggest either incorrect information regarding the percent pure live seed or a poor match between seedling requirements and the growing conditions. Clearly the reported information was incorrect for *Eriogonum.*

Irrigation resulted in short-lived differences in the timing of germination among the six species. The timing of seed sowing may have been particularly advantageous, however, in that the seeds were sown just a month before significant accumulation of rain, and germination is known to be related to precipitation levels in arid lands (Gutterman and Evenari 1994). It is unknown whether irrigation would have been more advantageous under either earlier or later sowing dates. These data suggest that increasing water availability and concomitant stimulation of earlier germination does not promote a more rapid long-term restoration as compared to nonirrigated conditions.

Although the advantage of earlier germination did not appear to enhance survival, it did increase the growth rate of *Artemisia* and speed closure of the canopy. Closed canopies have an advantage in the reduction of annual and herbaceous weeds. Although the removal of weedy species was not quantified during this study, it can be a significant variable in the successful restoration of native vegetation (Silcock 1986). Furthermore, earlier establishment and rapid growth may aid in slope stabilization and reduce erosion of bare ground. However, the advantage of rapid growth was also relatively short-lived as the canopies of all treatments were closed by the end of the first growing season, eliminating the need for hand weeding in the second year of the experiment.

Irrigation during the spring or summer only was of little benefit to seedling recruitment or to establishment of surviving individuals and even seemed to be deleterious in some cases. The seeding density and emergence rates were sufficiently high to provide enough survivors for stand establishment even in the absence of supplemental water. Poor survival during the first summer is typical for Mediterranean species (Eliason and Allen 1997), but summer irrigation did not affect summer survival. The initiation of spring irrigation suppressed germination in all six species examined, but a greater percentage of the individuals that had emerged prior to the irrigation treatment survived. Summer irrigation had little effect over all; germination and survival were not significantly different from plots receiving no supplemental water.

Irrigation Effects on Survival of Multiple Species

The presence of supplemental water had a significant effect on the species composition as has been suggested by Lauenroth and Dodd (1978) and Elberse and Breman (1990) for arid vegetation. While the difference in numbers of *Artemisia* seedlings was not significant among the no-water, spring water, and summer water treatments, the biomass values for *Encelia, Eriogonum, Lotus,* and *Salvia* were significantly higher in the unwatered plots. *E. fasciculatum* fared particularly poorly under all irrigated conditions and the continuous water treatment appeared to be deleterious to both *Lotus* and *Salvia.*

Coastal sage scrub contains elements of both chaparral and desert vegetation. Like chaparral, the shrubs native to CSS established well with seeding but required no supplemental water, under less than average precipitation. Like desert vegetation, irrigation had a pronounced effect on the species composition and evenness of the vegetation.

Conclusion

Irrigation of a mixture of six species native to CSS resulted in a near monoculture of *A. californica.* This seemed to be due to the very high seeding rate for *Artemisia* and the ability of this species to respond positively to increased water availability under continuous irrigation. Without supplemental water, five of the six species seeded exhibited emergence and survival rates sufficient to close the canopy by the end of the first growing season even in years with lower than normal rainfall. These data suggest that where diversity of plant species is an objective, irrigation was neither necessary nor beneficial. However, there may be advantages of earlier emergence with irrigation where slope stabilization and erosion control are important.

Acknowledgments

Funding for this project was provided in part by the California Department of Transportation. We would like to thank the University of California, Riverside Agricultural Operations personnel, particularly Lisa Warren, for the assistance with the irrigation system and field preparation. The assembly of the irrigation system was made more efficient by the help of Scott Eliason. We are very appreciative of S&S Seed for their generous supply of seed. The field crew consisted of Elise Focht, Stu Hemstreet, Lisa Jones, Nancy Storms, Jane Wahrman, and Tho Vo, without whom this project would have never been completed.

Literature Cited

Bewley, J. D., and M. Black. 1994. Seeds: physiology and germination. Plenum Press, New York, 445 pp.

Bleak, A. T., N. C. Frischknecht, A. P. Plummer, and R. E. Eckert. 1965. Problems in artificial and natural revegetation of the arid shadscale vegetation zone of Utah and Nevada. *Journal of Range Management* 18:49–65.

Call, C. A., and B. A. Roundy. 1991. Perspectives and processes in revegetation of arid and semiarid rangelands. *Journal of Range Management* 44:543–549.

Elberse, W. T., and H. Breman. 1990. Germination and establishment of Sahelian rangeland species. II. Effects of water availability. *Oecologia* 85:32–40.

Eliason, S. A., and E. B. Allen. 1997. Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology* 5:245–255.

Freudenberger, D. O., B. E. Fish, and J. E. Keeley. 1987. Distribution and stability of grasslands in the Los Angeles basin. *Bulletin of Southern California Academic Sciences* 86: 13–26.

Gutterman, Y., and M. Evenari. 1994. The influence of amounts and distribution of irrigation during the hot and dry season on emergence and survival of some desert winter annual plants in the Negev Desert. *Israel Journal of Plant Sciences* 42:1–14.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, 892 pp.

Harper, J. L., J. T. Williams, and G. R. Sagar. 1965. The behavior of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *Journal of Ecology* 52:273–286.

Hilhorst, H. W. M., and C. M. Karssen. 1988. Light, nitrate and gibberellin—effects on germination. *Plant Physiology* 86:591–597.

Jordan, P. W., and P. S. Nobel. 1981. Seedling establishment of *Ferocactus acanthodes* in relation to drought. *Ecology* 62:901–906.

Juhren, M., F. W. Went, and E. Phillips. 1956. Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. *Ecology* 37:318–330.

Keator, G. 1994. Complete garden guide to the native shrubs of California. Chronicle Books, San Francisco, CA, 314 pp.

Keeley, J. E., and C. C. Swift. 1995. Biodiversity and ecosystem functioning in Mediterranean-climate California. Pages 121–183 *in* G. W. Davis and D. M. Richardson (eds.), Mediterranean-type ecosystems: the function of biodiversity. Springer-Verlag, New York.

Keeley, J. E., and C. J. Fotheringham. 1998. Smoke-induced seed germination in California chaparral. *Ecology* 79:2320–2336.

Lauenroth, W. K., and J. L. Dodd. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* 36:211–222.

Luken, J. O. 1990. Directing ecological succession. Chapman and Hall, New York, 251 pp.

Minnich, R. A., and R. J. Dezzani. 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *Western Birds* 29:366–391.

Mooney, H. 1982. Applied and basic research in Mediterranean-climate ecosystems. *In* C. E. Conrad and W. C. Oechel (eds.), Dynamics and management of Mediterranean-type ecosystems. USDA-FS General Technical Report PSW–58.

Mooney, H. A., and J. Kummerow. 1981. Phenological development of plants in Mediterranean-climate regions. Pages 303–307 *in* F. Di Castri, D. W. Goodall, and R. L. Specht (eds.), Ecosystems of the world. 11. Mediterranean-type shrublands. Elsevier Science Publishing Company, New York.

Moreno, J. M., and W. C. Oechel. 1992. Factors controlling postfire seedling establishment in southern California chaparral. *Oecologia* 90:50–60.

O'Connor, T. G. 1996. Hierarchical control over seedling recruitment of the bunch-grass *Themeda triandra* in a semi-arid savanna. *Journal of Applied Ecology* 33:1094–1106.

O'Leary, J. F. 1990. Post-fire diversity patterns in two subassociatiations of Californian coast sage scrub. *Journal of Vegetation Science* 1:173–180.

Pavlik, B. M., and M. W. Skinner. 1994. Ecological characteristics of California's rare plants. Pages 4–7 *in* M. W. Skinner and B. M. Pavlik (eds.), California Native Plant Society's inventory of rare and endangered vascular plants of California. CNPS special publication no. 1.

Perry, B. 1987. Trees and shrubs for dry California landscapes. Plants for Water Conservation Land Design Publishing, San Dimas, CA, 184 pp.

Pyke, D. A., and S. Archer. 1991. Plant-plant interactions affecting plant establishment and persistence on revegetated rangeland. *Journal of Range Management* 44:550–557.

Silcock, R. G. 1986. Strategies for plant introduction and reseeding of semiarid pastoral lands. Pages 268–274 *in* P. J. Ross, P. W. Lynch, and O. B. Williams (eds.), Rangelands: a resource under siege. Australian Academy of Sciences, Canberra, Australia.

Tyler, C. M. 1995. Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology* 83:1009–1020.

Vallentine, J. F. 1989. Range development and improvements, 3d ed. Academic Press, New York, 545 pp.

Went, F. W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. *Ecology* 29:242–535.

Went, F. W. 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. *Ecology* 30:1–13.

West, N. E., K. H. Rea, and R. O. Harniss. 1979. Plant demographic studies in sagebrush-grass communities of southeastern Idaho. *Ecology* 60:376–388.

Westman, W. E. 1981. Diversity relations and succession in Californian coastal sage scrub. *Ecology* 62:170–184.