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Source: *Oikos*, Vol. 74, No. 3 (Dec., 1995), pp. 493-502

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

Stable URL: <http://www.jstor.org/stable/3545995>

Accessed: 08/05/2009 13:05

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Landscape and microsite influences on shrub recruitment in a disturbed semi-arid *Quercus-Juniperus* woodland

M. K. Owens, R. B. Wallace and S. R. Archer

Owens, M. K., Wallace, R. B. and Archer, S. R. 1995. Landscape and microsite influences on shrub recruitment in a disturbed semi-arid *Quercus-Juniperus* woodland. – *Oikos* 74: 493–502.

Seedling demography of the leguminous shrubs *Leucaena pulverulenta* and *Acacia berlandieri* was monitored to determine the functional role of microsites in the restoration of disturbed semiarid woodlands. Seeds were sown on replicated landscapes during 1989 and again in 1990 into four microsites after brush clearing: 1) Rocky, with shallow soils (<10 cm) and low vegetative cover (<<50%), 2) Herbaceous, with shallow soils (10 to 20 cm) and nearly 100% cover of perennial short-grasses, 3) Tree, with deep soils (20–30 cm) and 5–10 cm of duff under *Quercus virginiana*/*Juniperus ashei* mottes, and 4) Cleared, resulting from mechanical removal of *Quercus*/*Juniperus* mottes, with deep soils (20–30 cm) and 2–10 cm of duff. Within a landscape, recruitment was greatest on Cleared and Tree (>80%), intermediate on Rocky (65%), and lowest on Herbaceous (36%) microsites. Desiccation appeared to be the primary cause of first-season mortality. Differences between the microsites in seedling height and number of leaves were significant the first planting but not the second. Overwinter mortality of *Leucaena* and *Acacia* seedlings was lowest on Cleared microsites (55 and 7%, respectively) and greatest on microsites dominated by Herbaceous vegetation (100 and 87%, respectively). Survival of established seedlings during the second growing season exceeded 80% for both species on all microsites. *A. berlandieri* had the highest establishment potential and the greatest ecological amplitude, with recruitment after two years being comparable on Cleared, Rocky and Tree microsites (72–78 seedlings). *L. pulverulenta* showed marked preferences for Cleared microsites (47 seedlings established) relative to Rocky (13 seedlings), Tree (12 seedlings) and Herbaceous microsites (0 seedlings).

Spatial variability in emergence between replicated landscapes (range 35 to 78%) was greater than the variability between microsites within a landscape (48 to 62%). Differences in seed disappearance associated with surface runoff from high intensity storms and losses to granivory on Tree microsites were the primary causes of differences in recruitment between landscapes. Inter-landscape variability in granivory and precipitation runoff therefore overshadowed the effects of within-landscape seed placement among first year seedlings. Generalizations of seedling “safe site” characteristics based solely on short-term (one year), pseudoreplicated, within-landscape studies may therefore be misleading. Failure to account for variability in important processes at greater spatial scales may significantly influence the robustness of experimental microsite study results derived from small-scale research.

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Accepted 3 May 1995

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ISSN 0030-1299

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Mechanical clearing of trees and shrubs is widely practiced in dryland ecosystems (Vallentine 1989) to increase forage production of *Quercus/Juniperus* (Skousen et al. 1986), *Eucalyptus* (Scanlan et al. 1991), and *Prosopis* (Heitschmidt et al. 1986, Comejo-Oviedo et al. 1991) savannas and woodlands. The typical outcome of woodland clearing is a landscape mosaic of undisturbed tree clusters or mottes, herbaceous zones, disturbed microsites previously dominated by trees and debris piles of cleared woody vegetation (Everett and Sharrow 1985a). These microsites encompass an array of nutrient (Belsky et al. 1989, Weltzin and Coughenour 1990, Padien and Lajtha 1992), moisture (Gifford and Shaw 1973, Everett and Sharrow 1985b) and light (Liechty et al. 1992, Belsky et al. 1993) combinations which can affect germination, seedling establishment and subsequent patterns of secondary succession.

Seedling establishment may depend largely upon the number or distribution of "safe sites", i.e. microsites suitable for germination and establishment (Harper 1977, Grime 1979), but alteration of landscapes via fire, grazing or anthropogenic activities changes the distribution and characteristics of such microsites (Oswald and Neuenschwander 1993). Removal of evergreen tree canopies may enhance soil moisture (Gifford and Shaw 1973) which may, in turn, enhance seedling emergence and establishment. The soils associated with individual trees and shrubs have higher rates of mineralization (Padien and Lajtha 1992) and are typically enriched in organic matter and nutrients relative to soils in interstitial zones (Belsky et al. 1989, Weltzin and Coughenour 1990). These islands of fertility represent high nutrient/low light microsites which are converted to high nutrient/high light microsites following manipulation. This alteration of resource ratios between microsites should play a crucial role in determining subsequent patterns of plant succession (Tilman 1982), especially in cases where niche differentiation among adult plants is minimal (Davis 1991). It is therefore necessary to understand the relationship between microsite variability and seedling demography of long-lived shrubs in order to successfully revegetate disturbed woodlands.

One strategy for restoring valuable wildlife and livestock forage plants and elevating biodiversity in manipulated woodlands may be to mimic natural processes, whereby N₂-fixing shrubs establish and subsequently facilitate the ingress and establishment of additional species (e.g., McAuliffe 1984, Archer et al. 1988, Vitousek and Walker 1989). Here we examine the feasibility of se-

lectively seeding leguminous shrubs onto the diverse microsites created after clearing semiarid woodlands. We address the specific objective of quantifying seedling emergence, establishment and growth in microsites in disturbed landscapes. The shrubs *Acacia berlandieri* and *Leucaena pulverulenta* were used as a bioassay to determine the effects of microsites on seed and seedling dynamics. We hypothesized that establishment of these leguminous shrubs would be greatest on high light/high nutrient sites resulting from brush clearing, lowest on shaded, high nutrient microsites associated with intact stands of woody vegetation, and intermediate in high light/low nutrient microsites occupied by herbaceous vegetation.

Materials and methods

Study site

The study was conducted on the 24 000-ha Silver Lake ranch on the southwest edge of the Balcones Escarpment of central Texas, ca 60 km northwest of Uvalde, Texas, USA (29°19'N; 100°25'W; maximum elevation 730 m). Temperatures range from a mean daily maximum of 36°C (July) to a mean daily minimum of 4°C (January). Annual rainfall (500 mm) is bimodally distributed with peaks in May-June and September-October.

Two 1.2-ha deer- and rabbit-proof exclosures representing two replicated landscapes (hereafter referred to as L1 and L2) were located 8 km apart. The landscapes were selected such that an observation on one replicate could not have any influence on a similar observation on the second landscape (Hairston 1989) thus avoiding pseudoreplication (Hurlbert 1984). Soils in both landscapes were clayey mollisols with a calcic indurated layer between 15 and 25 cm. Slopes were 1–3 (L1) and 3–5% (L2). Both landscapes were savanna parklands consisting of clusters of woody vegetation separated by herbaceous zones dominated by the short-statured perennial C₄ grasses *Hilaria belangeri* and *Bouteloua trifida*. L1 was originally dominated by a *Quercus virginiana*/*Juniperus ashei* woodland while L2 was dominated by *Q. virginiana*/*J. ashei*/*Pinus cembroides* var. *remota*. The exclosures were mechanically cleared of all but about 15% of arborescent vegetation in March 1989. Undisturbed and mechanically treated landscapes on an adjacent 5000-ha area were visually inspected to ascertain the most abundant microsites. Four common micro-

Table 1. Physical characteristics of the herbaceous (HE), cleared juniper (JU-CL), rocky (RO) and tree (TR) microsites.

Microsite	Soil depth (cm)	Percent disturbance	Soil N (ppm)	Soil P (ppm)	Litter depth (cm)	Dominant vegetation
HE	10–20	<25	6	8.5	0	>90% grass
JU-CL	20–30	>70	15	13	2–10	none
RO	<10	>70	9	10	0	<50% grass
TR	20–30	0	32	13	5–10	oak/juniper

sites (Herbaceous [HE]; Cleared Juniper/Oak mottes [JU-CL]; Rocky [RO] and intact Oak/Juniper mottes [TR]) were selected for study within each landscape (Table 1). Microsites were characterized by measuring soil and litter depth to the closest cm using a metal probe in multiple locations, estimating percent soil disturbance, compositing 3 soil samples from each microsite on each landscape for analysis of soil nitrate and phosphorous (Texas A&M Soils Lab.), and estimating the percent vegetation overstory. The JU-CL and TR microsites varied initially with the relative amount of juniper and oak trees. JU-CL sites were initially dominated by *Juniperus* trees whereas TR sites were a mixture of the 2 species with *Quercus* being the dominant tree. In these landscapes, *Juniperus* is considered an invading species whereas *Quercus* is not. The JU-CL and TR microsites are therefore not equivalent as cleared and not cleared microsites.

Planting and data collection

A total of 480 plots (30 per microsite \times 4 microsites \times 2 landscapes \times 2 species) were selected in 1989 and again in 1990. Plots were selected using a modification of a stratified random sample. Within each landscape, 90 plots of each microsite were arbitrarily selected as being typical of that microsite. Each of these 90 plots were given a unique number and then 60 plots were randomly assigned to one or the other of the 2 species. The remaining 30 plots were abandoned. The selection of experimental plots from a subset of microsite plots rather than from the entire population of microsites may slightly limit the generality of the results. Plots which were used in 1989 were inventoried in 1990 to determine overwinter and second season survival. New plots were selected for the 1990 experiment. Four seeds within each plot were spaced 5 cm apart (1920 total seeds) and were partially buried such that the top portion of seed was visible for censusing. The experiment was initiated when mechanically scarified seed was sown on 7 June, 1989. Seeds and seedlings were inventoried every 7 d during the first month and every 10–21 d during the following 6 weeks in 1989 for a total of 6 observations. The entire experiment was repeated, beginning 22 April, 1990. Inventories of seeds and seedlings were conducted every 7 d in 1990 until 11 October for a total of 19 observations. Germination of scarified *Leucaena* seed in controlled environments was >95% in both years. *Acacia* seed germinability was 82% in 1989 and 94% in 1990.

Seeds with protruding radicles were considered as emerged and marked with color-coded toothpicks. The frequent observation schedule allowed the cause of seed or seedling loss to be identified. Extremely dry conditions before the 1989 experiment required that we add supplemental moisture (1 l) to reach soil field capacity before seeds were planted. The seeds received supplemental water every 1 to 2 d during the 14 d following

planting in 1989 (watered to field capacity) and every 7 d for the following 2 months because of below-average precipitation. During this period, water was added to approximate the normal amount of precipitation for this area. Precipitation in 1990 was above-average during April, May, and July, so supplemental water was applied only at the time of sowing.

Establishment of seedlings at the end of the first growing season (October 1989 or August 1990) was calculated relative to the number of seeds which emerged rather than the number dispersed. Seedlings which survived the 1989 growing season were inventoried in April 1990 and August 1990 for overwinter and second season survival. Shoot length, number of leaves and number of shoots originating at ground level were recorded in August of each year for seedlings emerging in that year.

Environmental characteristics

Precipitation in clearings was measured in each enclosure with a 12.50-cm capacity tubular gauge. Throughfall under tree canopies of the intact mottes (TR) was recorded in 1990. Each throughfall observation was averaged across 3 tree locations, ranging from dense to thin tree canopy. Gauge locations were selected to represent typical microsites. Interstitial and throughfall precipitation were tested for differences based upon 20 precipitation events.

Photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2}\text{s}^{-1}$) at the soil surface was estimated using quantum sensors (Li-Cor, Inc. Lincoln, NE, USA) during three six-d periods (12–17 July, 2–7 August, and 19–24 September, 1990). Each of the six-d periods was a combination of cloudy and cloud-free days. The four microsites sampled for PPFD were Herbaceous, Juniper-Cleared, TR-Canopy edge and TR – Deep canopy. PPFD experienced by seedlings on the RO and JU-CL microsites was assumed to be similar because of the sparse or absent herbaceous cover, so samples were collected only on the JU-CL sites. In the TR microsites, sensors were placed on the edge and at the center of tree mottes. Data were collected using a CR21X data logger (Campbell Scientific, Logan, UT, USA) programmed to record PPFD every 5 min. Data were subsequently reported as hourly means.

Data analysis

The Categorical Data Analysis (CDA) technique for log-linear and logit models was used to analyze emergence and establishment data for each species separately (Fienberg 1985, SAS 1988). Thirty independent plots in each microsite type in each landscape provided probability estimates of either 0, 1, 2, 3, or 4 seedlings emerging or becoming established. In this way, plots were the experimental units rather than plants. CDA models were used with the ordered, ordinal response data of emergence

Table 2. Partitioned likelihood ratio statistic (G^2) of the loglinear models describing emergence of *Acacia* and *Leucaena* seedlings on 4 microsites in a semi-arid woodland. Dashes indicate factors not tested in the model (see text for explanation).

	<i>Acacia</i>			<i>Leucaena</i>					
	1989 and 1990			1989		1990			
	G^2	df		G^2	df	G^2	df		
Year	13.8	1	**	—	—	—	—	—	—
Landscape	3.9	1	*	5.9	1	*	33.7	1	**
Microsite	11.1	3	**	76.6	3	**	3.5	3	NS
Year × Landscape	20.1	1	**	—	—	—	—	—	—
Year × Microsite	5.2	3	NS	—	—	—	—	—	—
Landscape × Microsite	21.9	3	**	2.5	3	NS	18.7	3	**
Year × Landscape × Microsite	2.1	3	NS	—	—	—	—	—	—

NS = nonsignificant, * $P < 0.05$, ** $P < 0.01$.

and establishment. The use of ordered, ordinal data implies that the response variable was multinomially distributed, in this case with five possible outcomes. A small constant (10^{-20}) was added to empty cells for analytical reasons. Data were initially analyzed in a saturated model using the explanatory variables year, landscape, microsite and all interactions. If the 3-way interaction error term was large, data were subsequently analyzed as separate experiments based on year as suggested by Mead (1990). Overwinter survival and survival during the second growing season were also analyzed using CDA. Saturated models for each species included the explanatory variables of landscape, microsite and the 2-way interaction. Log likelihood ratio statistics (G^2) were used in a backward model selection process (Fienberg 1985) to estimate the most parsimonious model. A probability level of $p < 0.05$ was used to determine if a factor should be retained in the final model.

Growth data were analyzed separately for each year with analysis of variance (ANOVA) using species, landscape and microsite as independent variables. Species and microsite variables were considered fixed effects while landscape was a random effect. The ANOVA model included the three main effects and all possible interactions. Expected mean square errors in this mixed effects model were calculated to determine the appropriate error term for all F-tests. Non-significant interactions were dropped from the final model.

PPFD was analyzed using a repeated measures ANOVA with landscape, microsite and month (July, August, September) as independent variables. Hourly observations during the 14 h of daylight were used as the repeated measure because sensors were not moved between hourly samples. The observations collected over the 6-d period within each month served as repetitions of the hourly samples and were averaged before analysis. Expected mean square errors were calculated for this mixed effects model to determine the proper error terms in ANOVA calculations. Differences in precipitation between TR microsites (throughfall) and other microsites (open sites) were compared with a paired t-test using 20 rainfall events as the paired observations.

Results

Microsite environmental characteristics

The type of microsite significantly affected the amount of ground-level PPFD ($F_{3,6} = 6.13$). PPFD was reduced from a daily average of $581 \mu\text{mol m}^{-2}\text{s}^{-1}$ on the JU-CL and RO microsites to $515 \mu\text{mol m}^{-2}\text{s}^{-1}$ on the HE microsites during the relatively cloud-free period in August and July. This 11% reduction was the result of light attenuation by grasses on the HE sites. During the cloudy observation period in September, PPFD was reduced by 70% from $441 \mu\text{mol m}^{-2}\text{s}^{-1}$ on the RO and JU-CL sites to $116 \mu\text{mol m}^{-2}\text{s}^{-1}$ on the HE microsite. At the edge and interior of TR mottes, PPFD was reduced approximately 70% and 85% to an average of 167 and 83 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively in all three months. The interaction between the time of day and microsite type was significant ($F_{39,78} = 4.91$) because PPFD at the edge and interior of the TR mottes did not increase as rapidly within a day as on the other microsites.

Precipitation reaching ground level was reduced about 40% in TR microsites relative to other microsites on both landscapes ($t = 5.55$, $p < 0.0001$). Total precipitation averaged across sample locations in L1 was 5.7 and 3.3 cm in the non-TR and TR sites, respectively. Average precipitation in L2 was 7.5 and 4.5 cm in the non-TR and TR sites, respectively.

Seedling emergence

Shrub seedling emergence varied significantly between the replicate landscapes and seed microsites and between the landscapes and year of observation (Table 2). The residual error term in the *Acacia* emergence model was not significant so a single logit model that included year as an independent term was used for analysis. The residual error in the *Leucaena* emergence model was highly significant ($\chi^2_{3df} = 9.1$), so data were analyzed for each year separately.

The probability of no *Acacia* seedlings emerging in a

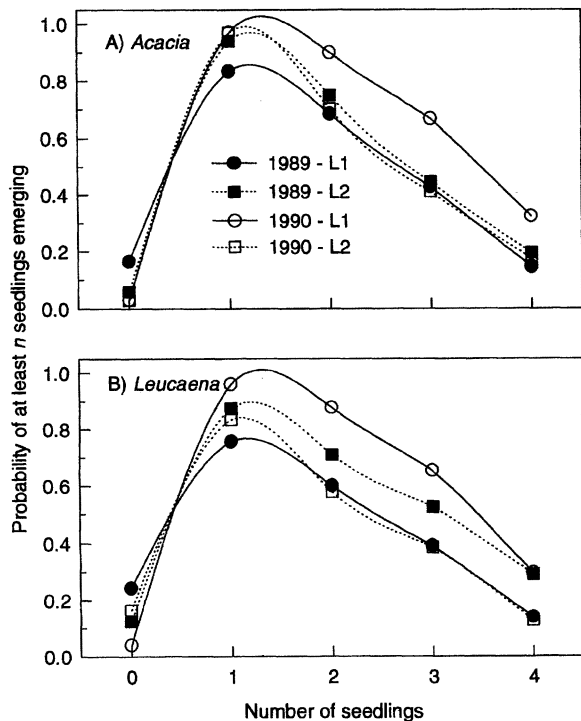


Fig. 1. Probability of A) *Acacia* and B) *Leucaena* seedling emergence in two independent landscapes (L1 and L2) during 1989 and 1990.

microsite plot was generally low in both landscapes (<0.1) except in L1 during 1989 (Fig 1A). The probability of not producing a seedling was twice as high in L1 (1989) than in any other landscape/year combination. Emergence was greatest in L1 during 1990 when more than one-half of the plots produced either 3 or 4 seedlings. In L2, seedling emergence was uniformly distributed over the range of 1 to 4 seedlings with very few plots ($<10\%$) yielding no seedlings. In L1, emergence of individual *Acacia* seeds in TR microsites was substantially lower (overall emergence = 39.5%) than that of seeds in other microsites and 22% of the plots had no seedlings emerge (Fig. 2A). There was no significant difference in the number of plots without *Acacia* seedlings in L2. Averaged over both landscapes, emergence from HE microsites was consistently highest (65%) and emergence on JU-CL and RO microsites (56 and 57%, respectively) were comparable to each other. The greatest variation was observed in the TR microsites which had the lowest emergence in 1989 and the highest emergence in 1990 (Fig. 2A and B).

Leucaena seedling emergence was greater in L2 than L1 during 1989 but greater in L1 than in L2 during 1990 (Table 2, Fig. 1B). Emergence was uniformly distributed in L1 in 1989 and in L2 in 1990 with a probability of approximately 0.2 for a plot to produce any of the possible responses. The number of plots without emerging seedlings was significantly greater for L1 in 1989 than for L1 in 1990 (29 vs 5 plots, respectively). The opposite trend

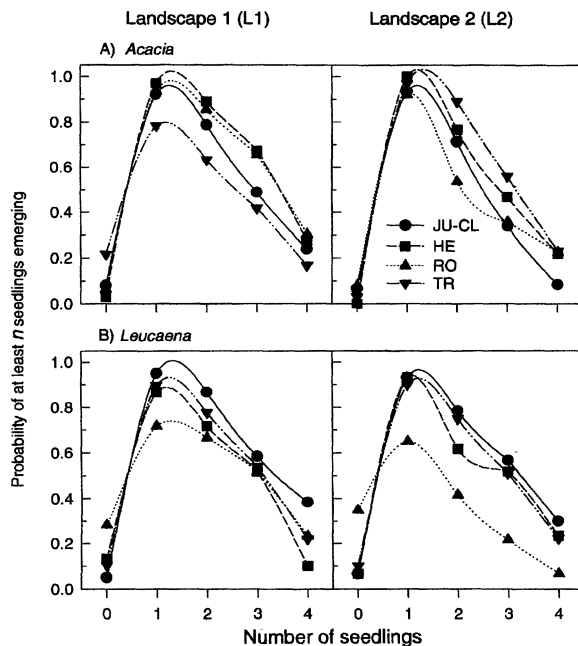


Fig. 2. Probability of A) *Acacia* and B) *Leucaena* seedling emergence with 4 microsites in two independent landscapes (L1 and L2) during 1989 and 1990. Microsite treatments are herbaceous (HE), juniper duff (JU-CL), rock (RO) and tree understory (TR).

was observed in L2, where the number of plots without seedlings was greater in 1990 than in 1989 (20 vs 15, respectively). Emergence was lowest on RO microsites and highest on JU-CL microsites in both landscapes (Fig. 2B). Nearly 30% of the RO microsites in L1 and 40% in L2 produced no seedlings, while only 25 and 5%, respectively, produced 4 seedlings. In contrast, very few plots ($<10\%$) in the JU-CL microsites failed to produce a seedling and most plots (60% in 1989 and 55% in 1990) produced 3 or more seedlings. The observed low emergence in L2-RO microsites was atypical of emergence patterns observed for any other microsite for either *Acacia* or *Leucaena*.

In 1989, granivores removed 23% of the *Acacia* seeds and 10% of the *Leucaena* seeds before emergence in TR microsites in L1. Seed disappearance attributable to granivores (primarily small rodents) was not observed in other microsites of L1 or in L2. Additional losses resulted when seeds were either washed away on the RO microsite or covered by litter on JU-CL and TR microsites following an intense thunderstorm. We estimate *Leucaena* seed disappearance associated with runoff from an 11 cm rainstorm at 57 and 33% in L1 and L2, respectively. In contrast no *Acacia* seeds were lost to runoff.

The patterns of emergence between the microsites and landscapes were different in 1990 than in 1989. The majority of seed disappearance in 1990 was associated with runoff from a rainfall event that delivered 22 cm of pre-

Table 3. Partitioned likelihood ratio statistic (G^2) of the log linear model describing first-year survival of *Acacia* and *Leucaena* seedlings on 4 microsites in a semi-arid woodland.

	<i>Acacia</i>			<i>Leucaena</i>		
	G^2	df		G^2	df	
Year	6.6	1	*	49.7	1	**
Landscape	4.4	1	NS	25.4	1	**
Microsite	99.8	3	**	186.7	3	**
Year \times Landscape	9.9	1	**	22.5	1	**
Year \times Microsite	34.1	3	**	165.6	3	**
Landscape \times Microsite	36.4	3	**	12.3	3	**
Residual	1.0	3	NS	6.5	3	NS

NS = nonsignificant, * $P < 0.05$, ** $P < 0.01$.

precipitation over a 3-day period. Runoff either removed (RO, HE) or buried (JU-CL) 37% of the *Acacia* seeds in L2. Approximately 17% of the *Leucaena* seeds in L2 were either washed away (RO) or buried (JU-CL and TR). Although L1 received a comparable level of rainfall as L2, there were no observed losses in L1 from either runoff or burial for either species. Runoff and burial losses rarely occurred as a loss of all seeds in a plot, but rather individual seeds within a plot were affected (Fig. 2).

Seedling establishment

Establishment at the end of the first growing season was

highly dependent on interactions between year of sowing and landscape, landscape and microsite, and year and microsite for both *Acacia* and *Leucaena* (Table 3). *Acacia* establishment in L1 was very similar in 1989 and 1990 with a probability of approximately 0.2 that a plot would produce any of the possible responses (Fig. 3A). High mortality during 1990 in L2 resulted in no establishment in 40% of the plots and fewer than 10% had either 3 or 4 seedlings. Conversely, during 1989 mortality was low and fewer than 10% of the plots failed to produce a seedling. A majority of the plots (60%) produced either 1 or 2 *Acacia* seedlings. *Leucaena* seedling establishment was much lower than *Acacia* establishment. Most plots (60 to 75%) failed to produce any seedlings, although survival was higher in L2 during 1989. The remaining plots were equally likely to produce from 1 to 4 seedlings (Fig. 3B).

Acacia and *Leucaena* seedling establishment in the four microsites was significantly different in each of the landscapes (Table 3). Seedlings in the HE microsites experienced high mortality in the first growing season, ranging from total mortality of *Leucaena* seedlings in L1 to a 0.4 probability of no *Acacia* seedlings surviving in L2 (Fig. 4A and B). *Acacia* mortality in other microsite types was low in L1, with most plots producing either 2 or 3 seedlings. The distribution of mortality in the RO microsites of L2 was not significantly different than the mortality observed in the HE microsites with most plots producing either 0 or 1 seedlings. Most plots in the JU-CL and TR microsites produced between 1 and 3 seedlings at the end of the first growing season. *Leucaena* mortality was high in all microsites with the exception of the TR microsite in L2; over 50% of all microsite plots did not produce a single established *Leucaena* seedling in either landscape (Fig. 4B). The probability of producing between 1 and 4 seedlings was evenly distributed over the remaining plots. Maximum establishment of 55 seedlings occurred on the low-light TR site (78.5% establishment), and no differences were detected between the high-light JU-CL (5.5 seedlings), RO (3.5 seedlings) and HE (0.5 seedlings) microsites which resulted in 9.3, 2.6 and 0% establishment of emerged seedlings.

Seedling establishment in each of the microsites was

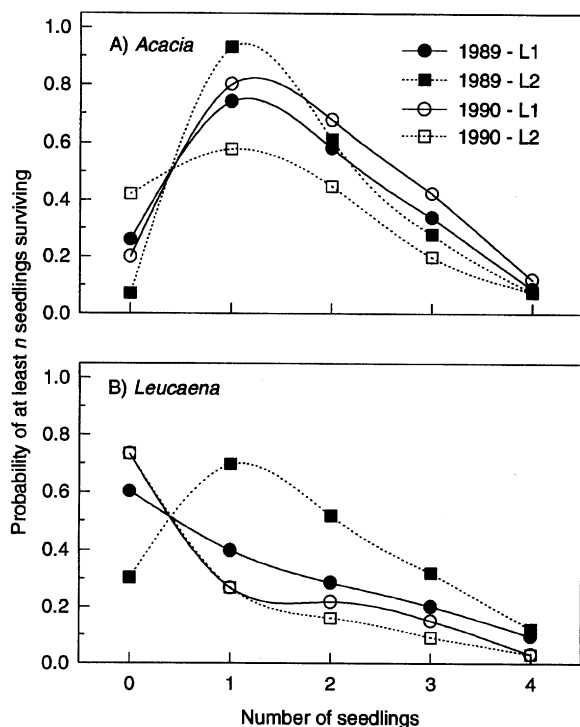


Fig. 3. Probability of A) *Acacia* and B) *Leucaena* seedling establishment in two independent landscapes (L1 and L2) during 1989 and 1990.

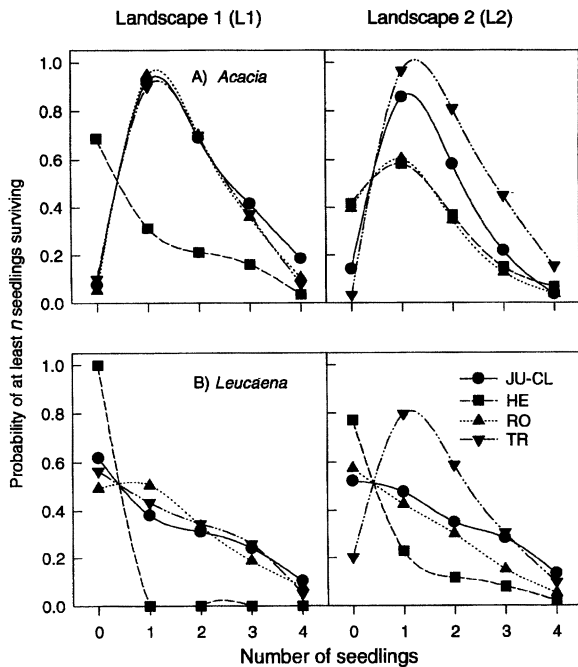


Fig. 4. Probability of A) *Acacia* and B) *Leucaena* seedling establishment within 4 microsites in two independent landscapes (L1 and L2). Microsite treatments are described in Fig. 2.

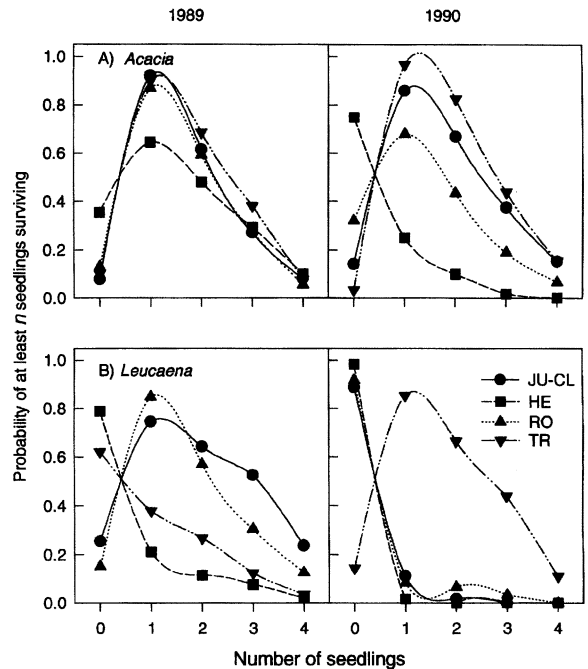


Fig. 5. Probability of A) *Acacia* and B) *Leucaena* seedling establishment within 4 microsites during 1989 and 1990. Microsite treatments are described in Fig. 2.

significantly affected by the year of observation (Table 3, Fig. 5). The probability of 0 establishing *Leucaena* seedlings in any plot of the open microsites (HE, JU-CL, RO, Fig. 5B) ranged from 0.9 to 1.0 during 1990 and from 0.18 to 0.8 during 1989. *Leucaena* seedlings in TR microsites were more likely to survive in 1990 than in any other microsite and year combination. Differences in *Acacia* seedling survival on HE sites between 1989 and 1990 may reflect differences in supplemental watering between years (Fig. 5A). However, differences in 1989 vs 1990 watering regimes had little effect on patterns of survival on shaded TR microsites for either *Leucaena* or *Acacia* and on open sites with low herbaceous cover (JU-CL and RO) for *Acacia*. Low survival (7%) of *Leucaena* in TR microsites of L1 in 1989 appeared associated with rodent herbivory and resulted in only 4 seedlings becoming established. Fifty-one percent of the *Acacia* seedlings in the TR microsites of L1 showed evidence of herbivory in 1989, but survival was relatively high (72%) resulting in 35 seedlings becoming established (Fig. 5A).

Overwinter and second season survival

Overwinter seedling survival (October, 1989 to April, 1990) was affected by microsites, although *Leucaena* survival also varied significantly with an interaction between microsites and the landscapes ($\chi^2_{3df} = 2.39$). Overwinter survival was highest on the JU-CL, intermediate on the TR and RO, and lowest on the HE for both plant

species (Fig. 6). Second-season survival (survival of the seedlings present in April, 1990 through August, 1990) was comparable among landscapes and microsites. Overall, survival for both species was highest in the TR site (97 to 100%), lowest for *Acacia* in the exposed JU-CL site (84%) and for *Leucaena* on the JU-CL and RO sites (81–84%). Seedling recruitment in August, 1990 from the 1989 cohort of seedlings was greatest in the JU-CL microsite for both species. Seventy-eight *Acacia* seedlings from the 240 seeds dispersed in 1989 were alive on the JU-CL microsite in August, 1990. *Leucaena* recruitment was not as high with only 47 seedlings being recruited from the 240 dispersed seeds. *Acacia* recruitment on the RO and TR microsites was similar to the JU-CL microsite with 72 and 74 seedlings, respectively. The HE microsite exhibited the lowest recruitment for both species with only 11 (*Acacia*) and 0 (*Leucaena*) seedlings becoming established.

Seedling growth

Shoot length of seedlings in the 1989 cohort did not differ significantly with plant species ($F_{1,1} = 5.09$), but was affected by the microsite ($F_{3,3} = 17.11$). The high-light, high-fertility microsite (JU-CL) had significantly taller seedlings than on any other microsite, while seedlings on the HE site were significantly shorter than other seedlings (Table 4). Number of leaves on the 1989 cohort of seedlings was also affected by the microsite ($F_{3,3} =$

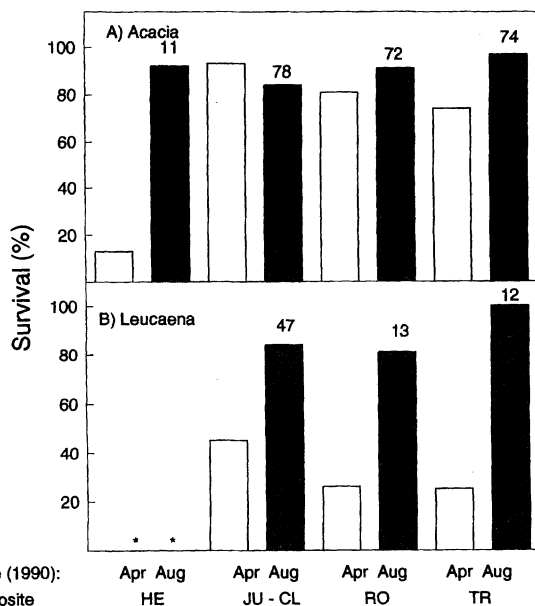


Fig. 6. Overwinter (open bars) and second season (hatched bars) survival (%) of *Acacia* and *Leucaena* seedlings in 4 microsites. Microsite treatments are described in Fig. 2. The * indicates no surviving seedlings. The numbers above the hatched bars represent the actual seedling recruitment at the end of the second growing season.

12.92), but not by the landscape or species. Seedlings on the JU-CL site had more leaves than seedlings on other sites while seedlings on the TR and HE sites had the fewest leaves. Seedlings of both species typically produced a single stem. When seedlings received supplemental water in 1989 shoot development was greatest for both species on the JU-CL site and lowest on the HE site (Table 4). Among the 1990 cohorts, which received minimal supplemental water, there were no significant differences in seedling height or number of leaves between microsites or species.

Discussion

The beneficial role of microsites is to ameliorate the climate or environment immediately around a seed or seedling to enhance plant establishment. In semi-arid environments, seedling emergence and survival are primarily functions of moisture availability (Fowler 1986, Lonsdale and Abrecht 1988, Owens and Norton 1989) and herbaceous competition (Brown and Archer 1989). In our study we expected differences in seedling emergence, survival and growth rates based on potential differences in competition, soil properties and light between microsites. In one year, the highest growth rates for both leguminous shrubs occurred on the microsite which had full sunlight, little vegetative competition and relatively deep soils with high nutrient concentrations (JU-CL); no differences were detectable in the other year. Although low light levels may limit growth and establishment of some leguminous shrubs (Egara and Jones 1977, Bush and Van Auken 1987), we observed significant recruitment and aboveground growth in the shaded TR sites for both species. Survival and growth of both species in the high-light, low-nutrient microsites (HE) were typically lowest, apparently reflecting the shallower soils and the influence of perennial grass competition. *A. belandieri* had the highest establishment and the broadest ecological amplitude with recruitment after two years being comparable on Cleared, Rocky and Tree microsites (72–78 seedlings, Fig. 6). Recruitment of *L. pulverulenta* was lower and primarily concentrated on Cleared microsites (47 seedlings).

Periodic dry conditions during the growing season appeared to be the primary cause of first season mortality of emerged seedlings. Weekly precipitation supplementation in 1989 apparently enhanced *Leucaena* survival on HE, JU-CL, RO and *Acacia* establishment on HE and RO above that of 1990 when natural rainfall was not supplemented (Figs 4, 5). Due to the weekly precipitation supplementation, approximately the same total amount of moisture was received in 1989 as 1990. Thus, regular moisture application separated by short time intervals (ca 4–7 d) appears to have been the criti-

Table 4. Mean (std. error) shoot length and number of leaves of *Acacia* and *Leucaena* seedlings in 4 microsites at the end of the first growing season (see text for details). Microsites are herbaceous (HE), juniper duff (JU-CL), rock (RO) and tree motte (TR).

Microsite	Shoot length (cm)		Number of leaves	
	1989 Cohort	1990 Cohort	1989 Cohort	1990 Cohort
<i>Acacia</i>				
HE	2.9 (0.10)	6.3 (0.69)	4.7 (0.16)	5.6 (0.37)
JU-CL	7.0 (0.35)	5.7 (0.21)	11.6 (0.40)	8.5 (0.28)
RO	5.3 (0.28)	6.5 (0.44)	9.3 (0.33)	9.2 (0.33)
TR	3.8 (0.31)	7.1 (0.29)	5.8 (0.27)	7.3 (0.22)
<i>Leucaena</i>				
HE	2.3 (0.12)	1.5 (1.5)	3.1 (0.22)	2.5 (2.5)
JU-CL	5.1 (0.27)	3.0 (0.89)	8.0 (0.30)	4.6 (0.81)
RO	3.2 (0.20)	2.8 (0.34)	6.5 (0.37)	3.8 (0.41)
TR	3.8 (0.20)	5.9 (0.20)	5.1 (0.31)	4.0 (0.12)

cal factor resulting in elevated establishment in 1989 relative to 1990.

The need for regular, periodic precipitation was ameliorated on the TR microsite. At the center of the TR microsites, light intensity was reduced by 85% compared to open microsites. Thus, soil temperatures, evaporative demand and heat stress would likely have been substantially reduced. The TR site, which also had a substantial duff layer, may be more favorable due to both reduced evaporative demand and higher inherent soil moisture holding capacity. Indeed, TR soils were observed to retain moisture longer than any other soils (pers. obs.). Results for *Leucaena* and *Acacia* substantiate the positive effects of shading and reduction of soil desiccation on survival of semi-arid plants such as *Mimosa pigra* (Lonsdale and Abrecht 1988), Mojave Desert annuals (Smith et al. 1987) and grass seedlings (Fowler 1986).

The influence of seed and seedling microsites on first-year plant recruitment was highly variable between landscapes. Seed predation and runoff following high intensity storms caused emergence to vary by as much as 35% between replications and 20% between years (Fig. 1). These two factors reduced emergence of both species in all microsites with one exception (*Leucaena* HE). The effects of runoff were especially evident on exposed sites with little vegetative cover (RO and JU-CL). Seed movements were not monitored in this study, but disappearance associated with runoff presumably resulted in translocation to other microsites and other portions of the landscape (Reichman 1984).

Seed losses to granivores were small relative to losses from runoff. Seed predation occurred only in the first growing season following vegetation manipulations and only in TR microsites, suggesting that the loss of small mammal habitat may have concentrated granivore activity in the remaining tree islands of one landscape. However, increased predation was not observed in TR microsites of the other landscape, indicating that granivore activities varied significantly from landscape to landscape. Our data would concur with other observations that small mammal use of areas under shrub canopies is greater than use in the interstitial zones in undisturbed semi-arid shrubland (Simonetti 1989).

Spatial variability in herbaceous competition, soil nutrients and light played an important role in establishment of leguminous shrubs within a landscape. However, as noted by Fowler (1988), the rank order of recruitment on microsites varied in a complex fashion between species and between years. In addition, microsite suitability varied between landscapes; the result of differences in granivory, herbivory and seed disappearance associated with rain. Generalizations of seedling "safe site" characteristics based solely on one-year, pseudoreplicated, within-landscape studies may therefore be misleading. Failure to account for variability in important processes at greater spatial scales may significantly reduce the robustness of experimental microsite study generalizations derived from small-scale research.

Acknowledgements – The authors would like to thank J. R. Reynolds and E. de la Garza for assisting in field data collection, to J.S. Murphy for reviewing an earlier draft of the manuscript and to Dr. Jim Calvin for statistical advice. This research was supported by the Moody Foundation of Galveston, Texas and the Texas Agricultural Experiment Station Projects H-6995 and H-6717. This paper is published with the approval of the Director, Texas Agricultural Experiment Station as technical publication TA-30558.

References

- Archer, S., Scifres, C.J., Bassham, C.R. and Maggio, R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. – *Ecol. Monogr.* 58: 111–127.
- Belsky, A.J., Amundson, R.G., Duxberry, J.M., Richa, S.J., Ali, A.R. and Mwonga, S.M. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. – *J. Appl. Ecol.* 26: 1005–1024.
- , Mwonga, S.M., Amundson, R.G., Duxbury, J.M. and Ali, A.R. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. – *J. Appl. Ecol.* 30: 143–155.
- Brown, J. R. and Archer, S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. – *Oecologia* 80: 19–26.
- Bush, J.K. and Van Auken, O.W. 1987. Light requirements for growth of *Prosopis glandulosa* seedlings. – *Southwest. Nat.* 32: 469–473.
- Cornejo-Oviedo, E. H., Meyer, J. M. and Felker, P. 1991. Thinning dense sapling stands of mesquite (*Prosopis glandulosa* var. *glandulosa*) to optimize timber production and pasture improvement. – *For. Ecol. Manage.* 46: 189–200.
- Davis, S. D. 1991. Lack of niche differentiation in adult shrubs implicates the importance of the regeneration niche. – *Trends Ecol. Evol.* 6: 272–274.
- Egara, K. and Jones, R. J. 1977. Effect of shading on the seedling growth of the leguminous shrub *Leucaena leucocephala*. – *Austr. J. Exp. Agric. Anim. Husb.* 17: 976–980.
- Everett, R. L. and Sharrow, S. H. 1985a. Response of grass species to tree harvesting in singleleaf pinyon-Utah juniper stands. – Research Paper INT-334. USDA/Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- and Sharrow, S. H. 1985b. Soil water and temperature in harvested and nonharvested pinyon-juniper stands. – Research Paper INT-342. USDA/Forest Service, Intermountain Forest Range Experiment Station, Ogden, UT.
- Fienberg, S. E. 1985. The analysis of cross-classified categorical data. – MIT Press, Cambridge, MA.
- Fowler, N. L. 1986. Microsite requirements for germination and establishment of three grass species. – *Am. Midl. Nat.* 115: 131–145.
- 1988. What is a safe site?: Neighbor, litter, germination date and patch effects. – *Ecology* 69: 947–961.
- Gifford, G. F. and Shaw, C. B. 1973. Soil moisture patterns on two chained pinyon-juniper sites in Utah. – *J. Range Manage.* 26: 436–440.
- Grime, J.P. 1979. Plant strategies and vegetation processes. – Wiley, New York.
- Hairton, N.G., Sr. 1989. Ecological experiments: Purpose, design and execution. – Cambridge Univ. Press, New York.
- Harper, J.L. 1977. Population biology of plants. – Academic Press, New York.
- Heitschmidt, R.K., Schultz, R.D. and Scifres, C.J. 1986. Herbaceous biomass dynamics and net primary production following chemical control of honey mesquite. – *J. Range Manage.* 39: 67–71.

- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. – *Ecol. Monogr.* 54: 187–211.
- Liechty, H.O., Holmes, M.J., Reed, D.D. and Mroz, G.D. 1992. Changes in microclimate after stand conversion in two northern hardwood stands. – *For. Ecol. Manage.* 50: 253–264.
- Lonsdale, W. M. and Abrecht, D. G. 1988. Seedling mortality in *Mimosa pigra*, an invasive tropical shrub. – *J. Ecol.* 77: 371–385.
- McAuliffe, J.R. 1984. Saguaro-nurse tree associations in the Sonoran desert: competitive effects of saguaros. – *Oecologia* 64: 319–321.
- Mead, R. 1990. The design of experiments. – Cambridge Univ. Press, Cambridge.
- Oswald, B.P. and Neuenschwander, L.F. 1993. Microsite variability and safe site description for western larch germination and establishment. – *Bull. Torrey Bot. Club* 120: 148–156.
- Owens, M. K. and Norton, B. E. 1989. The impact of 'available area' on *Artemisia tridentata* seedling dynamics. – *Vegetatio* 82: 155–162.
- Padien, D.J. and K. Lajtha. 1992. Plant spatial pattern and nutrient distribution in pinyon-juniper woodlands along an elevational gradient in northern New Mexico. – *Int. J. Plant Sci.* 153: 425–433.
- Reichman, O. J. 1984. Spatial and temporal variation of seed distributions in Sonora Desert soils. – *J. Biogeogr.* 11: 1–11.
- S. A. S. 1988. SAS/STAT User's Guide. – SAS Inst., Cary, NC.
- Scanlan, J. C., Wilson, B. J. and Anderson, E. R. 1991. Sustaining productive pastures in the tropics. 2. Managing woody vegetation in grazing lands. – *Trop. Grassl.* 25: 85–90.
- Simonetti, J. A. 1989. Microhabitat use by small mammals in central Chile. – *Oikos* 56: 309–318.
- Skousen, J., Davis, J. N. and Brotherson, J. D. 1986. Comparison of vegetation patterns resulting from bulldozing and two-way chaining on a Utah pinyon-juniper big game range. – *Great Basin Nat.* 46: 508–512.
- Smith, S. D., Patten, D. T. and Monson, R. K. 1987. Effects of artificially imposed shade on a Sonoran desert ecosystem: microclimate and vegetation. – *J. Arid Environ.* 13: 65–82.
- Tilman, D. 1982. Resource competition and community structure. – *Monographs in Population Biology* 17. Princeton Univ. Press, Princeton, NJ.
- Vallentine, J.R. 1989. Range development and improvement. 3rd ed. – Academic Press, New York.
- Vitousek, P.M. and Walker, L.M. 1989. Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation and ecosystem effects. – *Ecol. Monogr.* 59: 247–265.
- Weltzin, J.F. and Coughenour, M.B. 1990. Savanna tree influence on understory vegetation and soil nutrients in north-western Kenya. – *J. Veg. Sc.* 1: 325–334.