EXPERIMENTAL MANIPULATIONS OF FERTILE ISLANDS AND NURSE PLANT EFFECTS IN THE MOJAVE DESERT, USA

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ABSTRACT.—In a mixed desert shrub community we removed and added shrub canopies to examine above- and belowground influences of 3 species of shrubs on islands of soil fertility and the survival of transplanted *Ambrosia dumosa* seedlings. Soils sampled under shrubs in the wet season had higher pH, water content, organic matter, and both total and mineralizable nitrogen than soils in adjacent open areas, confirming a widely established pattern in arid lands. However, we also found species differences in soil parameters. Soils under *Coleogyne ramosissima* had highest pH, soils under *A. dumosa* had highest water content and nitrogen mineralization rates, and soils under *Larrea tridentata* had lowest water content. Soils sampled under shrubs in the dry season, 7 months after experimental shrub removal, maintained higher organic matter and total and mineralizable nitrogen content than adjacent open soils, but pH and water were altered by shrub manipulations. Species differences persisted only in soil water levels (*A. dumosa* soils were driest). Over a 1-year period, transplanted *A. dumosa* seedlings had highest survivorship in shrub removal and open treatments and died most rapidly under control shrubs of all 3 species, suggesting that shrubs had a strong negative effect on seedling survival, even in the presence of higher organic matter, nutrients, and (initially) higher water content of fertile islands. Our results suggest that nurse plants and islands of soil fertility have the potential to facilitate growth of other species by nutrient additions, but that the net effect of nurse plants can be negative due to shading and/or root competition.

Key words: competition, facilitation, aridland soils, Ambrosia dumosa, Coleogyne ramosissima, Larrea tridentata.

The pattern of higher soil fertility under desert shrubs than in adjacent open areas is well documented for arid lands (Charley and West 1975, Virginia 1986, Franco and Nobel 1989, Garner and Steinberger 1989, Schlesinger et al. 1996). Colonization of open areas (e.g., by species in the genus *Ambrosia*; McAuliffe 1988) apparently begins a cycle of habitat amelioration in deserts in which organic matter is built up from plant litter and entrapment of wind-blown debris, and further enhanced by secondary colonization of other shrubs and annuals. Animals presumably contribute to soil nutrients, and their burrowing under shrubs increases soil aeration and water infiltration to deeper soil layers (Garner and Steinberger 1989). These "fertile islands" under desert shrubs are therefore distinguished from adjacent open areas between shrub canopies by higher levels of organic matter and soil nutrients, higher rates of nutrient turnover, higher soil water content, higher productivity of annual plants, and increased soil microbe and vertebrate animal activity. Although these properties of fertile islands may enhance recruitment of new seedlings under shrubs,

shrub roots may also compete with seedlings for available nutrients and water, and canopies of established shrubs may reduce light levels enough to limit primary productivity of understory seedlings (Charley and West 1975, Franco and Nobel 1989, Hunter 1989, Callaway et al. 1996). The net effect of these potentially positive and negative attributes of desert shrubs on recruitment of new seedlings can best be examined with experimental manipulations of fertile islands and associated shrubs.

Fertile islands have important effects on the dynamics of desert ecosystems. Experimental studies of desert ecology have demonstrated that establishment and growth of dominant shrub species are limited by nitrogen and water (Fonteyn and Mahall 1981, Lajtha 1987, Smith et al. 1987, Fisher et al. 1988, Lajtha and Whitford 1989). Thus, it is not surprising that there is strong evidence from arid lands of nurse plants that facilitate establishment of other species (McAuliffe 1984, 1988, Franco and Nobel 1989). As the facilitated plant grows, it may eventually out-compete the nurse plant. The fertile island can thus become the center of a centuries-long process of colonization and

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succession where nutrient cycling, plant productivity, and animal activities are all higher than in intershrub spaces.

In this study we experimentally examined similarities and differences between above- and belowground influences of 3 species of desert shrubs on properties of fertile islands and transplanted seedlings by removing and adding shrub canopies. Species differences in fertile island characteristics were recognized by Charley and West (1975) but rarely have been examined experimentally. We examined the effect of shrub canopy removal treatments on survival of transplanted seedlings of *Ambrosia dumosa,* a species that may be critical for establishing new fertile islands in the Mojave Desert (cf. McAuliffe 1988). Our manipulations (Fig. 1) compared 5 treatments with various combinations of aboveground shade effects, belowground nutrient effects, and belowground root competition effects of desert shrubs.

METHODS

Study Area

This study was conducted on a bajada (slope) in Lucky Strike Canyon (36°23′N, 115°28′W; 1127 m elevation) on the east side of the Spring Mountain Range, 50 km northwest of Las Vegas, Nevada, in the Mojave Desert of the southwestern United States. The study area includes vegetation typical of regional desert bajadas and is located at the lower elevational boundary of the *Coleogyne ramosissima* Torr. (blackbrush) plant community (found between 1100 and 2000 m elevation in the Mojave Desert) and the upper boundary of a plant community dominated by *Ambrosia dumosa* (Gray) Payne (white bursage; Lei and Walker 1997a, 1997b). *Larrea tridentata* Cov. (creosote bush) is a co-dominant in the *A. dumosa* community. Shrub diversity is higher at this ecotone than at any other elevation on the bajada. Other common species include *Krascheninnikovia lanata, Krameria erecta, Ephedra nevadensis, E. viridis,* and *Acamptopappus shockleyi.* For further descriptions of regional vegetation see Beatley (1975) or Rundel and Gibson (1996). Nomenclature follows Hickman (1993).

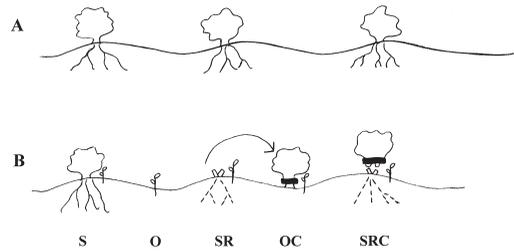Experiments described here are part of a larger study of shrub dynamics on permanent

Fig. 1. Diagram of natural pattern of islands of high soil fertility under shrubs and less fertile spaces between shrubs (top) and 5 treatments into which *Ambrosia dumosa* seedlings were transplanted (bottom): S = control shrub, O = control open area, SR = removal of aboveground shrub, OC = addition of cut shrub from SR to an open area, SRC = removal followed by replacement of cut shrub in situ.

plots distributed along an elevational gradient from 1030 m to 1850 m in Lucky Strike Canyon. The study site is located on a 13-km-long by 2-km-wide bajada with an average vertical slope of <5°. The slope lacks a central drainage channel but has multiple ephemeral channels scattered across the entire bajada that average 1–2 m deep; our study sites were only on the broad, raised benches between washes. Soils of the canyon are limestone-derived with cemented petrocalcic horizons (caliche) beginning at depths of 15–80 cm. Desert pavement and cryptobiotic crusts (cf. Evans and Belnap 1999) are moderately well developed at the site. Lucky Strike Canyon is characterized by hot summers above 35°C and cold winters below –10°C. Summer rainfall usually occurs during thunderstorms in July and August, but most precipitation comes as winter rains that are widespread and may last several days. Snow is occasional and not long lasting, and mean annual precipitation at the site is <200 mm. Precipitation increases with elevation and temperature decreases with elevation (Rowlands et al. 1982). During the study period (March 1995–May 1996) total precipitation and maximum and minimum temperatures were 780 mm, 32°C, and –20°C at Kyle Canyon (2135 m elevation) above Lucky Strike Canyon and 69 mm, 40°C, and –7°C at Corn Creek (880 m elevation) at the base of Lucky Strike Canyon (National Climatic Data Center 1995, 1996). Relative humidity was typically low (<20%) and evaporation high during summer months.

Plot Designs, Treatments, and Measurements

We examined responses of soil parameters and of transplanted *A. dumosa* seedlings to experimental removals and additions of *A. dumosa*, *L. tridentata*, and *C. ramosissima* shrub canopies. In March 1995 we randomly selected 24 locations (8 sets of shrubs for each of 3 species) at approximately 15-m intervals along a 360-m transect perpendicular to the slope of the bajada. At each location we selected (within a 10-m radius of the chosen point on the transect) a set of 3 shrubs of the same species and 2 open spaces and initiated the following treatments: unaltered shrub (S); removal of all aboveground portions of a shrub (SR) by clipping stems at ground level; removal as in SR, followed immediately by replacement of the cut shrub in situ with wire tiedowns (shrub removal plus shrub canopy addition; SRC); open surface at least 50 cm from any shrub (O); and addition of SR shrub canopy to an open site with tie-downs (OC; Fig. 1). Stump sprouts from the SR and SRC treatments were removed as needed during the experiment. Less than 15% of cut stumps sprouted.

Immediately preceding the treatments (March 1995) and 7 months following treatment initiation (October 1995), surface soils (0–8 cm deep; A_o and A_1 horizons) were sampled in each treatment following removal of any loose organic debris (O horizons). Transplanted seedlings were located on the east-northeast side of each shrub to minimize solar radiation; soils were collected first (March) to the south and subsequently (October) to the north of focal shrubs in order not to disrupt transplants. Soils were immediately passed through a 2-mm sieve, then placed in air-tight soil canisters and refrigerated at 5°C prior to analysis within 72 hours of collection.

After removal of 20 g of soil for analysis of nitrogen mineralization, soils were weighed, dried at 105°C to a constant mass, and re-weighed to determine soil moisture content and dry mass of sieved fines per volume (an approximation of bulk density). Soil pH was determined with a glass electrode on a 2-g sample of dry soil saturated with 5 mL deionized water (McLean 1982). We used the Bouyoucos hydrometer method (Day 1982) to determine particle size. Organic matter content of soils was determined by mass loss after ignition

at 550°C (Black 1965). We took care to avoid higher temperatures that would cause loss of carbonates. After oven-drying, a 0.4-g sample of each soil was digested in sulfuric acid with a mercuric oxide catalyst and then analyzed colorimetrically for total Kjeldahl nitrogen using an automated salicylate procedure (Environmental Protection Agency 1984). We measured dry mass per volume and particle size only in October.

In situ methods for assessing available nitrogen are not suitable for desert soils because water potentials fluctuate greatly between rainstorms and long dry periods (Lajtha and Schlesinger 1986). Laboratory incubations allowed us to compare potential mineralization among treatments, but our values do not represent field conditions. The available nitrogen pool was determined on 10 g of fresh soil after extraction in 100 mL 2M KCl for 4 hours on a shaker. After the soil had settled, we analyzed the supernatant for available N (Keeney and Nelson 1982) using an automated Cd reduction procedure (NO_2 and NO_3) and an automated phenol procedure (NH_4; Alpkem 1991). An additional 10 g of fresh soil was placed in a 40-mL tube that was then filled with distilled water and placed in a 40°C oven for 1 week, after which NH_4 levels were again determined. Water was added as needed to ensure an anaerobic environment. Nitrogen mineralization was then reported as the difference between post-incubation and pre-incubation $NH_4 + NO_2 + NO_3$ concentrations (Keeney 1982, Lober and Reeder 1993).

Ambrosia dumosa seedlings were grown from locally collected seeds in 20-cm-deep cone-shaped containers (77.2 cm^3) in a greenhouse from December 1994 to March 1995. Each potted plant was watered weekly as needed to keep the soil moist until the final month when watering was reduced. Nutrients were applied twice (12 mL Miracle Gro dissolved in 20 L of tap water) during the 4-month period. In March 1995 the largest 252 seedlings (10–18 cm tall) were chosen. Twelve seedlings were removed for initial biomass determination. To ensure survival of at least 1 transplant per replicate, 2 seedlings were planted at each of the 8 replicates of 5 treatments for the 3 species of shrubs (total = 240 seedlings). Where both seedlings per replicate survived transplanting, the smaller one was removed within 6 weeks of planting to ensure

survival of 1 seedling per replicate during the 60 weeks of the experiment. Seedlings at each replicate were caged within a cylinder of 0.25-inch (0.63-cm) mesh hardware cloth, 15 cm in diameter and 15 cm (under shrubs) to 30 cm (open sites) tall. Lower edges of the cages were buried and secured with nails to prevent rodent herbivory. Tops of the cages were left open. Only 2 incidents of herbivory were detected. Seedlings were watered (1 L plant^{-1} week^{-1}) for 3 weeks after planting. Seedling heights were measured 12 and 24 weeks after planting. We compared treatment effects on survivorship of seedlings (low survival after 60 weeks precluded destructive harvests).

Statistical Analyses

Soils sampled in March (preceding shrub manipulations) from the shrub and open environments were compared with a MANOVA (SAS 1988), and significant differences between treatments (shrub versus open) or species (*A. dumosa, L. tridentata, C. ramosissima*) were further examined with 2-way ANOVA followed by Student-Newman-Keuls and Tukey tests for multiple comparisons. Soils from October (28 weeks after treatment initiation) were also analyzed with MANOVA followed by 2-way ANOVA to compare treatments (S, SR, SRC, O, and OC) and species. October values for dry mass per volume and particle size were compared with 2-way ANOVA. Transplant heights were analyzed with 2-way ANOVAs. Transplant survivorship was analyzed with a 2-way ANOVA (treatment and species), followed by Kruskall-Wallis 1-way ANOVAs on ranks (treatment, species) using the number of weeks each seedling survived (Sigma Stat 1995). Transplant survivorship was also analyzed by logistic regression of the number of seedlings alive or dead on the last sample date (Sigma Stat 1995). Significance was determined at $P = 0.05$.

RESULTS

Soils

Soils sampled in March (prior to our shrub manipulations) differed by both treatment and species (Table 1). Soil pH, water, organic matter, Kjeldahl nitrogen, and nitrogen mineralization were all higher under shrubs than in adjacent open areas (Tables 1, 2, Fig. 2). Species differences also emerged: soils under *C. ramosissima* had higher pH and lower mineralizable nitrogen than soils under *A. dumosa* shrubs (Table 1, Fig. 2). Soils under *L. tridentata* had pH levels similar to *A. dumosa* and mineralizable nitrogen similar to *C. ramosissima.* There were no species differences in soil water and no significant treatment-by-species interactions in March. Dry mass per volume and particle size (measured only in October) both varied between S and O treatments. Dry mass per volume was higher in open habitats (adjacent to *L. tridentata:* 1.22 ± 0.02 g cm^{-3}; *C. ramosissima*: 1.28 ± 0.03; *A. dumosa*: 1.29 ± 0.03; $P < 0.001$) than in soils under shrubs (*L. tridentata*: 0.98 ± 0.04; *C. ramosissima:* 1.02 ± 0.04; *A. dumosa*: 0.96 ± 0.03). This difference was due to lower sand and silt and higher clay content (less air spaces) in open soils than in soils beneath shrubs (data not shown; $P < 0.01$). Species differences were not found in dry mass per volume, or percent sand or silt, but *C. ramosissima* soils had higher clay content than the other 2 species (data not shown; $P < 0.001$). These soil results not only confirm the presence of islands of fertility under shrubs at the site but suggest that there are species differences in soil characteristics of fertile islands.

In October 1995 both treatment and species effects were again significant in the overall MANOVA (Table 1). Soil organic matter, Kjeldahl nitrogen, and nitrogen mineralization were still higher in shrub-related treatments (S, SR, SRC) than the open (O, OC), but earlier treatment differences in pH and water content were no longer found (Table 1). Species differences were found only in soil water where soils associated with *C. ramosissima* and *L. tridentata* were wetter than *A. dumosa* soils (Tables 1, 2).

Transplants

Mean heights of transplanted *A. dumosa* seedlings did not differ significantly by treatment ($P = 0.37$) or shrub species ($P = 0.86$) 3 or 6 months after planting**.** Transplant survivorship (Fig. 3) did not differ among species ($P = 0.67$) but did differ among treatments ($P < 0.001$) with the 2-way (parametric) ANOVA. There was no significant interaction between treatment and species ($P = 0.77$). However, assumptions of normality and equality of variances both failed on the 2-way ANOVA.

TABLE 1. Summary table of MANOVA of soil variables for March and October 1995 soil samples. In March, 2 treatments (TRT; open and shrub) were compared. In October, 5 treatments were compared (open, shrub, shrub removal, shrub removal plus shrub canopy addition, and canopy addition). For both dates 3 species (SPP; *Ambrosia dumosa, Larrea tridentata, Coleogyne ramosissima*) were compared. There were no significant treatment-by-species interactions in March ($P = 0.56$; df = 8) or October ($P = 0.15$; df = 8).

Source	MANOVA	df	pH		Water		Organic matter		Kjeldahl nitrogen		Mineralizable nitrogen	
			F	P	F	P	F	P	F	P	F	P
MARCH												
TRT	0.0001	1	3.05	0.0200	12.2	0.0007	31.75	0.0001	29.62	0.0001	3.55	0.0093
SPP	0.0001	2	6.68	0.0019	1.46	0.2373	1.09	0.3407	0.57	0.5662	17.95	0.0001
OCTOBER												
TRT	0.0001	4	1.19	0.3181	1.07	0.3776	15.39	0.0001	20.87	0.0001	6.35	0.0001
SPP	0.0001	2	1.43	0.2438	20.25	0.0001	2.93	0.0578	2.80	0.0655	1.02	0.3644

TABLE 2. Gravimetric soil water content (percent) for March and October soil samples (mean $\pm s_{\bar{x}}$, $N = 8$; treatments are: O = open, S = shrub, SR = shrub removal, SRC = shrub removal and canopy replacement, OC = shrub canopy addition). Statistical comparisons are indicated in Table 1.

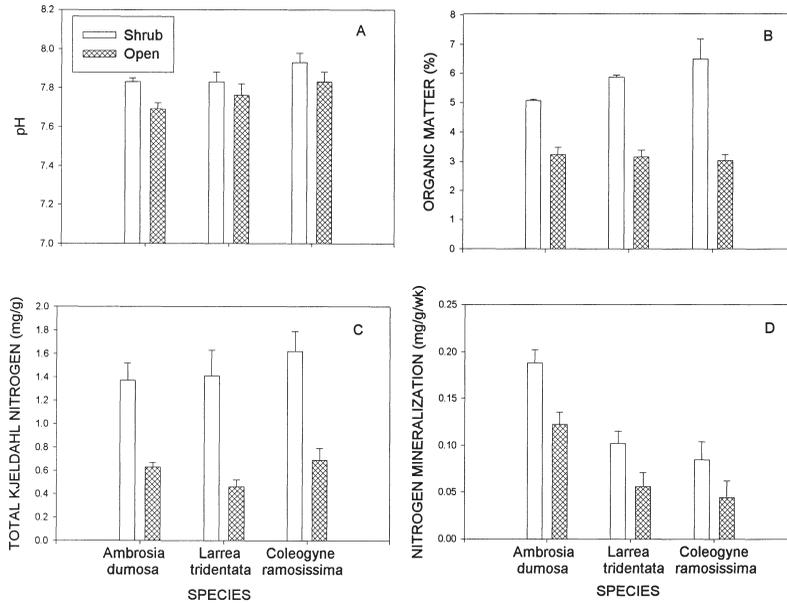| Treatment	*Ambrosia dumosa*	*Larrea tridentata*	*Coleogyne ramosissima*
MARCH			
O	13.27 ± 0.25	11.83 ± 0.35	12.88 ± 0.39
S	14.25 ± 0.32	13.36 ± 0.38	13.39 ± 0.32
OCTOBER			
O	0.02 ± 0.01	0.16 ± 0.04	0.17 ± 0.04
S	0.06 ± 0.03	0.19 ± 0.04	0.27 ± 0.08
SR	0.01 ± 0.01	0.16 ± 0.04	0.19 ± 0.05
SRC	0.06 ± 0.03	0.21 ± 0.06	0.21 ± 0.04
OC	0.06 ± 0.04	0.15 ± 0.04	0.27 ± 0.06

Fig. 2. Values of 4 soil parameters (A: pH; B: organic matter; C: total Kjeldahl nitrogen; D: nitrogen mineralization) for shrub (S) and open (O) treatments associated with 3 shrub species (*Ambrosia dumosa, Larrea tridentata, Coleogyne ramosissima*) from March 1995 samples (prior to treatment initiation; mean ± $s_{\bar{x}}$, N = 8). All shrub-versus-open comparisons were significantly different. See text for species differences.

Therefore, we performed subsequent 1-way (nonparametric) ANOVAs on ranks that yielded similar results (species: $P = 0.56$; treatments: $P < 0.001$). Survival was always highest ($P < 0.05$; Tukey and Student-Newman-Keuls multiple comparisons following 2-way ANOVA) in the SR treatment (fertile island but no canopy) followed by the O treatment (neither fertile island nor canopy). Survival was also relatively high in the SRC treatment (fertile island and canopy but no root competition) for *A. dumosa* and *C. ramosissima*. Survival was lowest ($P < 0.05$) in the S treatment for *A. dumosa* and *C. ramosissima* and relatively low for *L. tridentata*. Shrub canopy therefore had the most negative effect (O > OC, SR > SRC), even overriding apparent positive effects of fertile islands (O > SRC). The logistic regression model was rejected, indicating that species and treatment were not good predictors of transplant survivorship.

The influence of soil characteristics on individual seedlings was tested by regressing total weeks of survival against all soil variables and against principal components constructed from combined soil variables. None of these multiple regressions was significant either within or across treatments ($P > 0.20$).

DISCUSSION

The establishment of desert plants is often facilitated by nurse plants that provide shade, fertile soils, and perhaps protection from herbivores for new seedlings (McAuliffe 1984, Franco and Nobel 1989, Callaway and Walker 1997). *Ambrosia dumosa* is able to become established in open desert soils without the aid of a nurse plant canopy (McAuliffe 1988) and may be a critical species for the establishment of other common desert plants such as *L. tridentata*. Understanding what limits establishment and growth of *A. dumosa* seedlings can provide insights into why and how *A. dumosa* can begin a new cycle of fertile island development. Canopy removal experiments in this study not only confirmed the common pattern of fertile islands under desert shrubs, but also detected differences in soil characteristics beneath different species of shrubs. Transplant responses to treatments indicated the positive influence of increased soil nutrients under shrubs but the overall net negative impact of shrubs on *A. dumosa* seedlings through competition (for nutrients, light, and water). These negative impacts may partly
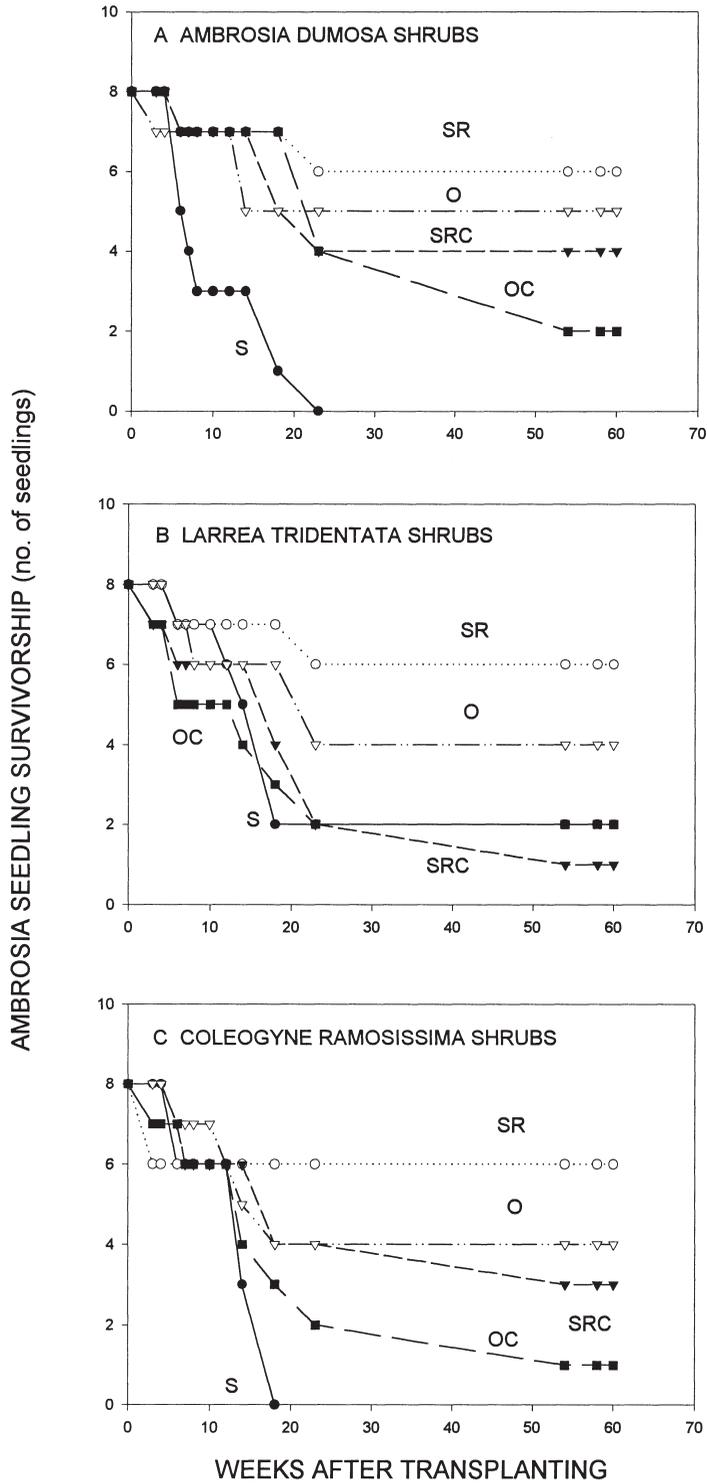
Fig. 3. Survival of transplanted *Ambrosia dumosa* seedlings associated with *Ambrosia dumosa* shrubs (A), *Larrea tridentata* shrubs (B), and *Coleogyne ramosissima* shrubs (C) in the S, O, SR, SRC, and OC treatments described in Figure 1.

explain why *A. dumosa* establishment occurs primarily in open spaces between shrub canopies.

All 7 measured soil variables (pH, water, organic matter, dry mass per volume, particle size, total and mineralizable nitrogen) were more favorable for plant growth under existing shrubs than in adjacent open spaces. These results support conclusions from other studies of fertile islands (e.g., Garcia-Moya and McKell 1970, Charley and West 1975, Klemmedson and Barth 1975, Virginia 1986, Halvorson et al. 1994, Schlesinger et al. 1996) that have found abundant evidence of spatial heterogeneity in soil properties of arid lands. Our values for soil organic matter under shrubs are comparable to another study from Lucky Strike Canyon (2–6%, Lei and Walker 1997b) but higher than other Mojave Desert studies (2–3%, Bolling and Walker 2000; 1.5–4.1%, Rundel and Gibson 1996) where surface organic soils (A$_o$ horizon) were removed. Our values from the open spaces are also higher than generally reported, perhaps due to the high cover (25%, D. Thompson personal observation) of cryptobiotic crusts in our open sites.

Species differences in soil characteristics were detected among soils collected underneath 3 shrub species. These differences may cause differential survival of *A. dumosa* seedlings, although such differences were not seen in this experiment (see below). In March, soils under *A. dumosa* shrubs had higher rates of nitrogen mineralization than soils under *C. ramosissima* or *L. tridentata*. Considering the additional allelopathic effect that has been demonstrated for *L. tridentata* roots (Mahall and Callaway 1992), *L. tridentata* shrubs may provide the least favorable environment for seedlings. During the drier period in October, soils under *C. ramosissima* were wettest, perhaps reflecting moisture retention of higher clay values under *C. ramosissima.* Organic matter and Kjeldahl nitrogen tended (nonsignificantly) to be different among species in October. Analyses of a larger data set including other elevations (Thompson et al. unpublished data) indicate that soils under *A. dumosa* shrubs have lower organic matter levels than soils beneath *L. tridentata* and *C. ramosissima* shrubs.

Survivorship of *A. dumosa* transplants did not differ among nurse plant species, despite differences in soil characteristics. These results suggest that survival is affected by variables or combinations of variables more important than individual soil variables. Highest survivorship was in the SR treatment for all shrub species, suggesting benefits of the fertile island soil environment (higher nutrients, water, and organic matter) and a high light environment. The fact that *A. dumosa* survivorship was better in SR and SRC than under intact shrubs (S) further suggests a lack of root competition may be important to seedling survivorship (Fig. 4). The next highest survivorship was in the O treatment for all species, suggesting that any of the remaining treatments (S, OC, SRC), each of which includes a shrub canopy, was worse for *A. dumosa* seedlings than the high light but low nutrient environment in the open. The S treatment had lowest *A. dumosa* survivorship, probably due to combined negative effects of shrub canopy and root competition.

Only 39.2% of all transplanted seedlings survived the 60-week period. However, differences in timing of mortality among treatments are likely to have important consequences for seedling establishment. The Mojave Desert is characterized by infrequent and spatially patchy rainfall (Smith et al. 1997). Nearly dry seedlings are able to recover and sprout leaves within days following rainfall (F. Landau personal observation). On average, the longer a seedling can survive through a dry period, the more likely that it will experience rains and survive to become a mature shrub.

Interactions between the effects of light (or presence of shrub canopy) and fertile island soil conditions, and the relative importance of light, nutrients, and root competition, can be inferred from survivorship patterns of the *A. dumosa* transplants. Light appeared to be a limiting factor whether nutrients were low (O > OC) or high (SR > SRC, S). In contrast, nutrients were not limiting at low light (OC > S, no pattern for OC and SRC) but were limiting at high light (SR > O). These patterns suggest the most important factor is the negative effect of shrub canopy presence (Miriti et al. 1998), followed by the positive effect of fertile island nutrients. Root competition (or the presence of live roots) appears to be a 3rd variable that also had a negative effect (SRC > S). Competition for water by nearby adult plants can reduce seedling growth (Fonteyn and Mahall 1981, Fowler, 1986, Nobel and Franco 1986).
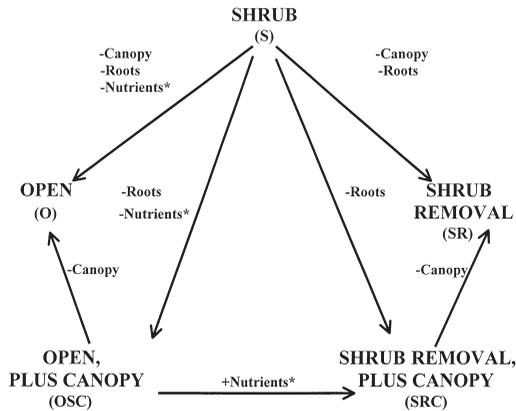
Fig. 4. Summary of how the 5 treatments (S, SR, SRC, OC, O) altered above- (shade and other canopy effects) and belowground (nutrients, roots) environments for transplanted *Ambrosia dumosa* seedlings. Asterisk implies addition or subtraction of not only nutrients but other soil properties of fertile islands.

Shade is normally considered advantageous to seedling establishment in deserts because it reduces temperature extremes and water loss.

Although we took no light measurements in this study, we did measure photosynthetic photon flux density (using a Licor 1000) 5 months after initiation of identical treatments with *A. dumosa* in a later experiment at the same site (May 1998). Despite leaf loss, the SRC (mean ± $s_{\bar{x}}$: 398 ± 43 micromoles m^{-2} sec^{-1}; $N = 30$) and OC (414 ± 42) treatments remained as shaded as the intact shrubs (S treatment: 492 ± 42) and all 3 "shrub" treatments were significantly more shaded than open treatments (O: 1009 ± 42; SR: 1004 ± 42). Branches of *A. dumosa* (and equally dense branches of *C. ramosissima*) apparently provided nearly as much shade as leaves and branches combined. In contrast, *L. tridentata* has a very low leaf area index (Chew and Chew 1965, Smith et al. 1997), so leaf loss presumably does not markedly increase light transmission to the ground.

Soil moisture is considered to be a critical environmental variable affecting establishment and growth of desert plants and may affect nutrient availability (e.g., nitrogen is limiting only when water is plentiful; Fisher et al. 1988, Sharifi et al. 1988, Lajtha and Whitford 1989). This experiment was initiated during a wet spring, and the March soil samples were collected 2 days after a rainstorm. Following rains

in late May (10 weeks after transplanting), there was a 28-week drought. During this drought most *A. dumosa* transplant mortality occurred. There was no significant correlation between October gravimetric soil moisture at each transplant and individual transplant survivorship (P-values ranged between 0.30 and 0.70). More detailed measurements might have helped explain survivorship in terms of soil moisture because gravimetric soil content may not closely reflect water available for plant growth. Nevertheless, driest habitats (SR, O) had highest survivorship and the wettest habitat (S) had lowest survivorship, suggesting that in a drought water is not as limiting as light (or absence of shade). Therefore, our results during a drought may be typical of the dynamics of seedling establishment in more mesic periods as well. Alternatively, shrub roots may have been so efficient at removing available water (Fonteyn and Mahall 1981, Hunter 1989) that the below-shrub environment was actually too dry for seedlings during our study. In wetter years root competition from the shrub may be less detrimental to seedling establishment.

Species differences in soil water were present only in the dry (October) sampling period (*C. ramosissima* = *L. tridentata* > *A. dumosa*). Canopy architecture might help explain why *L. tridentata* soils were wetter than *A. dumosa* soils in the dry season. The canopy of *L. tridentata* is shaped like an inverted cone (Ludwig et al. 1975), and this shape may maximize condensation of water vapor and stem flow from its relatively tall, spreading branches. However, this shape also allows soil surface evaporation because of the openness of the surface beneath it; *A. dumosa* and *C. ramosissima* are hemispherical in shape with foliage almost to the ground, reducing loss from surface evaporation. Therefore, other explanations such as more efficient water extraction by *A. dumosa* roots (D. Neuman personal communication) must also be considered.

Ambrosia dumosa seedlings survived better in the open (O) than under shrubs (S), supporting McAuliffe's (1988) assertion that *Ambrosia* is a colonizer of open habitats. When it does colonize under shrubs (or in exposed fertile islands caused by shrub mortality), it has a different set of environmental characteristics to cope with under each shrub species. For example, Smith et al. (1987) found that artificial

shade in the Sonoran Desert increased soil nutrients in both shrub canopies and open desert, but patterns of increase differed between *A. deltoidea* and *L. tridentata* shrubs. Differential responses to these variations in microsite ultimately impact distribution and zonation of desert shrub species. Our study site, at the ecotone between *A. dumosa*– and *C. ramosissima*–dominated communities, is the type of environment where shrub species replacements are most likely to lead to shifts in community composition along the elevational gradient. For example, the lower boundary of *C. ramosissima* in the Mojave Desert has shifted at least 100 m several times in the last 1000 years (Cole and Webb 1985, Hunter and McAuliffe 1994). Current studies are addressing how responses to shrub removals vary at different elevations in Lucky Strike Canyon and how episodic recruitment of *L. tridentata* and *C. ramossisima* seedlings is affected by shrub species and shrub-induced microsites.

McAuliffe (1988) proposed that the establishment of seedlings of *A. dumosa* in open areas may initiate fertile island development where this species occurs in arid regions of southwestern United States. We have demonstrated that 3 interacting variables (shade, nutrients, roots; Fig. 4) affect the initial survival of *A. dumosa* seedlings. However, shrubs differ in their soil chemistry and may provide unique habitats for seedling establishment. Removal of a shrub with retention of the fertile island beneath it provided the best environment for *A. dumosa* seedling establishment (light and nutrient addition), followed by open habitats (light addition). Shaded habitats with or without nutrients were poorer habitats for establishment, and the intact shrub environment (minus light, nutrient addition, root competition) was the worst environment. These results provide a mechanistic explanation for McAuliffe's hypothesis and suggest *A. dumosa* establishment will be most likely to occur in open habitats that have some nutrient enrichment.

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