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Facilitation of Yucca brevifolia recruitment by Mojave Desert shrubs

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FACILITATION OF *Yucca brevifolia* *RECRUITMENT*
BY MOJAVE DESERT SHRUBS

by

Steve Brittingham

A thesis submitted in partial fulfillment
of the requirements for the degree of

Masters of Arts and Science
In
Biological Sciences

Department of Biological Sciences
University of Nevada, Las Vegas
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July 1998

ABSTRACT

Patterns of recruitment for *Yucca brevifolia*_(Joshua tree) were investigated on three elevational transects from 1000 to 2000 m elevation, in the Spring and Sheep Mountain Ranges of southern Nevada. *Yucca brevifolia* is distributed throughout a broad range of plant communities dominated by *Larrea tridentata* and *Ambrosia dumosa* at low elevations, *Coleogyne ramosissima* at mid elevations, and *Artemisia-Pinus-Juniperus* community at upper elevations. The density of *Y. brevifolia* gradually increased from the lowest elevations, peaked at 1600 m, and remained at intermediate levels at high elevations until reaching an abrupt upper elevational limit at 2000 m. Open substrate dominated the study areas, however a large majority of *Y. brevifolia* seedlings were found growing under the canopy of other woody shrubs. This pattern of recruitment did not vary by site or elevation. Thirty-five species of perennial shrubs were identified in the study areas and 16 of these were found in association with at least one *Y. brevifolia* seedling. However, four shrubs were found in a nurse relationship with *Y. brevifolia* above the frequency predicted by either their canopy area or numerical dominance. Seedlings exhibited significant variation in aspect, relative to the center of the nurse shrub. In Lee and Lucky Strike Canyons, recruitment occurred predominately on the east and west sides of nurse shrubs, indicating the importance of specific microhabitats. The local presence of specific perennial shrubs resulted in higher levels of recruitment, causing a distinct pattern of community development, presumably through the amelioration of abiotic stresses.

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ACKNOWLEDGEMENTS

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INTRODUCTION

THE NURSE PLANT RELATIONSHIP

Within the Mojave Desert, as in other severe environments, germination and survival of seedlings are rare events and recruitment of perennial plants most often occurs within the protected microhabitats of established shrub canopies (Smith and Nowak 1990). Since Phillips (1909) reported that seedlings of *Pinus monophylla* (pinyon pine) were found predominately under the canopy of *Artemisia tridentata* (sagebrush) and rarely in the open, strong correlations have been found between the distribution of stress-tolerant species, and less tolerant species unable to regenerate on open substrates. In North American deserts, stress-tolerant perennials such as *Ambrosia* spp. often are the initial colonists of open or disturbed sites (McAuliffe 1988). These colonists then apparently modify microhabitats, allowing the subsequent recruitment and establishment of species that are less stress tolerant. Survival of perennials beneath the canopies of other plants is an important process in structuring arid and semi-arid regions of the world (McAuliffe 1988, Franco and Nobel 1989, Silvertown and Wilson 1994). The greater the abiotic stress within an environment, the greater the potential importance for facilitation (a positive interaction) between plants (Callaway and Walker 1995). Any amelioration of stresses such as cold, heat, salinity, or herbivory is likely to foster survival and growth. Conversely, in environments with low stress and the potential for rapid resource acquisition, competition between plants becomes a dominant interaction. For example, Hillier (1990) observed that in grasslands, facilitation was more important on dry, south-facing slopes while the more mesic north-facing slopes produced a competitive interaction between the same plant species. In the Rocky Mountains of Colorado, Rebertus et al. (1991) found that *Abies lasiocarpa* (subalpine fir) were randomly distributed in low stress sites but were clumped around the stress-resistant *Pinus flexilis* (limber pine) within high stress areas. The importance of facilitation therefore appears to increase with increasing stress.

Plants that ameliorate a stressful environment for seedlings of other plants are termed nurse plants. McAuliffe (1988) found that in the Mojave Desert, 88-95% of the landscape is open substrate. However, 67-85% of *Larrea tridentata* (creosote bush) seedlings were preferentially associated with *Ambrosia* spp. shrubs, which accounted for only 3-6% of the landscape cover. In the northern Sonoran Desert, low-density *Ambrosia* spp. commonly acted as nurse plants for seedlings of *Cercidium microphyllum* (paloverde) (McAuliffe 1986). Suzan et al. (1996) also found that seedlings of various species in the Sonoran Desert were found under the canopy of the nurse plant *Olneya tesota* in much greater proportion than their canopy area would suggest. Such strong nurse preferences have not been consistently documented by all researchers. Callaway (1995) found *Carnegia gigantea* (saguaro) primarily under *C. microphyllum*, but noted that *C. gigantea* seedlings were common under various perennial shrubs. In turn, seedlings of *C. microphyllum* are themselves associated with the canopies of several other shrubs (McAuliffe 1986), further reinforcing the sense that facilitation is a major factor in the community structure of arid regions. Turner (1966) delineated fifteen different shrubs found in association with *C. gigantea* seedlings that were in proportion to their frequencies. The implication from the literature is that there may be no specific biotic characteristics that determine nurse plant selection, but rather a general alteration of the microclimates that produces a more hospitable zone of recruitment.

Nurse plant facilitation mechanisms operate on seedlings directly through amelioration of the high temperatures, high light intensity, low soil moisture, and low soil nitrogen typical of arid lands. Facilitation may also operate indirectly through inhibition of competitors, reduction of herbivore pressure, inoculation of the soil with mycorrhizae, and convergence of dispersal processes (Smith et al. 1983, Miller 1994, Silvertown and Wilson 1994, Callaway 1995).

Shading appears to be the critical attribute of environmental moderation allowing greater recruitment and distribution of desert species. Franco and Nobel (1989) found minimum winter soil surface temperatures in the Sonoran Desert were 1.2°C warmer under the canopy of *Ambrosia deltoidea* and summer maximum temperatures 13.5°C cooler at the center of the bunchgrass *Hilaria rigida* than temperatures measured in open areas. Also in the Sonoran Desert, relative to open substrate temperatures, Suzan et al. (1996) reported a 15°C decrease in summer maximum temperatures and an increase in winter minimum temperatures by 3°C under shrubs. Moderation of high temperature extremes is particularly important for succulent seedlings whose low surface to volume ratio results in poor heat dissipation (Callaway 1995) and subsequent dependence upon modified microhabitats. In addition to the temperature reduction on the plant's surface, shading reduces potential water loss, allowing for continued carbon gain further into periods of vapor pressure deficit than unsheltered plants. When soil water potential increases in mid-summer and stomatal closure occurs, shading also reduces photoinhibition (Callaway 1995). In studies of *C. gigantea* (Nobel 1980) in the Sonoran Desert and of the columnar cactus *Neobuxbaumia tetetzo* in the Viscaino Desert (Valiente-Banuer and Ezcurra 1991), positive water relations were less important than temperature for seedling survival, and for *Quercus douglasii* (blue oak) seedlings (Callaway 1992), protection from predation was less important than temperature moderation. In each experiment noted, improved water relations and exclusion of predators increased longevity, however long-term survival of seedlings was dependent upon protection from temperature extremes.

Callaway (1995) argued that shading is a "cost" in reduced energy for photosynthesis, thereby limiting productivity of the seedling. Holmgren et al (1997) reported that dry conditions reduce a plant's tolerance to shade since aridity results in greater allocation of biomass to underground structures. A higher root to shoot ratio increases the percentage of respiring tissue, thereby increasing the demand for light to maintain a positive carbon balance. However, Smith et al. (1983) found that for *Yucca brevifolia* in the Mojave Desert, light saturation occurred at approximately 25% of midday irradiation and for most species in xeric environments the reduced light within a plant canopy is compensated for by increases in soil moisture (Callaway and Walker 1997). Nurse plants would produce positive benefits only if the soil moisture under the canopy is greater than that required to offset the reduced PAR through increased water vapor conductance (Smith et al. 1983). Nurse plants may also alter soil moisture. Recent studies at Lucky Strike Canyon, in the Spring Mountain Range within the Mojave Desert, have found that open substrates had lower moisture content during wet and dry periods than soil beneath plant canopies, and that different species had different levels of soil moisture under their canopies. The soil under *Coleogyne ramosissima* (blackbrush) had consistently higher moisture content than *Ambrosia dumosa* and *Larrea tridentata*, and it retained greater soil moisture into the dry months, perhaps due to a higher clay content (Walker et al., in review).

Numerous studies have found nutrient enrichment of the soil beneath shrub canopies via litterfall, nitrogen fixation, nutrient pumping by deeply rooted perennials, and organic debris deposition. Franco and Nobel (1989) found significantly higher nitrogen content under the nurse plants *Ambrosia deltoidea* and *Hilaria rigida* that was correlated to increased dry weight of the nursed *Agave deserti* by approximately 60%. In the Mojave Desert, the O and the A horizons are generally absent, while the deposition of silt, sand, and organic material beneath shrubs contributes to increased survival rates of seedlings under perennials.

Across a variety of landscapes (e.g., deserts, wetlands, grasslands, high elevation forests) both facilitation and competition are important factors in the distribution of species and determinants of community structure. Tests of association have consistently found that colonization of stressed environments is not a random process and that seedlings of some species have a high degree of association with mature shrubs. The importance of facilitation varies on a gradient of stress; low intensity stress allows competitive interactions to dominate and to structure community composition. Highly stressful environments increase the importance of facilitation for recruitment and persistence of species requiring amelioration of open substrate conditions.

The objectives of this research were to determine if seedlings of *Yucca brevifolia* display a non-random pattern of recruitment between open substrates and under the canopies of perennial shrubs. If recruitment is found primarily under the canopy of another species, and are some species associated with *Y. brevifolia* more often than predicted by their canopy area or numerical dominance? And does this association change with elevation or site? Does the aspect of the seedling, relative to the nurse plant central stem, influence survivorship?

ECOPHYSIOLOGY OF *YUCCA BREVIFOLIA*

The C_3 monocot *Yucca brevifolia* is the largest non-riparian plant in the Mojave Desert. The boundaries of the Mojave Desert are synonymous with the distribution of *Y. brevifolia* and encompass regions of southern California, southern Nevada, western Arizona, and extreme southwestern Utah. *Yucca brevifolia* is considered a primitive member of the yuccas due to its dichotomous branching pattern and conservative genetic variability (Foster and Gifford 1959). Aging the *Y. brevifolia* tree is problematic, but estimates are made by utilizing an average growth rate of 1.5 cm per year and the plant's average production of three sets of six leaves during each growing season. Rundel and Gibson (1996) estimated large *Y. brevifolia* in Rock Valley (Nevada Test Site), Southern Nevada, to be 200 yr old.

Yucca brevifolia thrives on gravel bajadas (outwash slopes), that descend from the region's mountain ranges. The coarse-grained soils allow higher water infiltration, reducing the volume of surface evaporation, while fine textured soils have higher water-holding capacities (Smith et al. 1997). In areas of limited precipitation and organic matter, the amount of water held within the soil matrix, which is dependent upon soil texture (soil field capacity), becomes a crucial limiting factor in the distribution of *Y. brevifolia*. *Yucca brevifolia* flourishes in soils with a "bimodal" texture (coarse sand mixed with silt and clay particles) and high moisture retention (Hunnings and Peterson 1973). In more mesic areas, any well-sorted soil is sufficient for its survival. Available soil nutrients and soil pH have apparently little effect on the distribution of *Y. brevifolia* (Hunnings and Peterson 1973). The root system of *Y. brevifolia* is shallow but laterally extensive, presumably for water procurement and to withstand the strong winds prevalent in the desert.

Reproduction is both vegetative, from adventitious roots, and sexual. Flowering takes place during April and May, and seeds are shed during summer. Went (1948) reported that the seeds of *Yucca brevifolia* require warm temperatures (20°C-25°C) and moisture for germination. McCleary and Wagner (1973) reported 100% germination of the seeds of *Y. brevifolia* at 20° to 25°C, 24% germination at 15°C and no germination at 10°C. McCleary and Wagner (1973) found that the *Y. brevifolia* is a "short day plant" achieving its maximum growth rate with 10 hr of light and 14 hr of darkness.

The primary climatic factors influencing the distribution of *Y. brevifolia* appear to be precipitation and temperature. Jaegar (1940) reported an annual requirement of 20 to 25 cm of rain. Warm temperatures and rainfall during the summer are necessary for germination to take place (Went 1948, Hunnings and Peterson 1973), while a period of dormancy brought on by winter cold is necessary for survival of *Yucca brevifolia* (Went 1948).

Maximum carbon gain and maximum stomatal opening occur during the moderate temperatures of January to May after which partial stomatal closure begins to occur around mid-day during periods of greatest vapor pressure deficit (Smith et al. 1983). Increasing seasonal desiccation results in almost complete stomatal closure by July when soil water potentials are greatest (-6 MPa) with only a slight early morning opening. *Yucca brevifolia* stomata will respond to episodes of summer rain but remain at almost full closure until the advent of winter precipitation (Smith and Nowak 1990).

Light saturation of the semi-succulent leaves is temperature dependent and occurs at 400 micromoles at low and high temperatures and 600 micromoles at moderate temperatures (Smith et al. 1983). In the Mojave Desert, light intensity is approximately 2,000 micromoles; *Yucca brevifolia* light saturates at approximately 25% of midday irradiance and Larrea tridentata light saturates around 50% of midday irradience (Rendel and Gibson 1996). However, both plants have similar net CO_2 uptake rates, perhaps due to the rosette leaf morphology of *Y. brevifolia* and the angled leaves that are near vertical at the top, to the almost horizontal lower side leaves. This leaf arrangement produces optimal light interception with uniform distribution of PAR (photosynthetically active radiation) throughout the canopy (Smith et al. 1983, Rundel and Gibson 1996).

STUDY SITE

The Mojave Desert, within the Basin and Range geological province, is a region marked by annual weather extremes that supports sparse vegetation cover. The clear dry weather characteristic of the region is a consequence of the stable subtropical high pressure over the northeastern Pacific Ocean (Rundel and Gibson 1996) that produces the dominant westerly and southwesterly winds. Summer thunderstorms that occur in July and August are the result of monsoonal systems of convectional currents drawing moisture northward from the Gulf of California (Rowlands et al. 1977). Regional aridity results from less than 200 mm yr^{-1} precipitation in southern Nevada (at the lowest elevations) with a potential evapotranspiration of more than 2,000 mm yr^{-1} (Smith and Nowak 1990). Most precipitation occurs in the winter, while summer thunderstorms are highly localized and unpredictable. Approximately 42% of the annual precipitation falls during the April-September "growing season" in southern Nevada (Rundel and Gibson 1996).

Edaphic factors often define the vegetative cover that can establish and persist within a region. Lei and Walker (1997) found that Lucky Strike Canyon (Spring Mountain Range, southern Nevada) soils in the open exhibit greater temperature variations than soils beneath shrub canopies, although soils at 15 cm depth showed little temperature variation between open and shaded areas.

The Spring and the Sheep Mountain Ranges, located 65 km north of Las Vegas, Nevada, are major mountain ranges within the Mojave Desert region. They are comprised of limestone-dolomite parent material that produce calcareous soils at lower elevations (Turner 1982). Charleston Peak (3652 m), within the Spring Mountain Range west of Las Vegas, is the highest point within the Mojave Desert, with extreme elevational and ecological variation. There is a well-defined elevational gradient in vegetation with *Larrea tridentata* and *Ambrosia dumosa* dominating lower bajadas, while rockier upper bajadas tend to be dominated by *Coleogyne ramosissima* that, at higher elevations, gives way to *Artemisia tridentata* (Smith and Nowak 1990). In the Sheep and Spring Mountain Ranges of Southern Nevada, *Yucca brevifolia* is found in continuous stands at elevations from 1000 m to 2000 m, ranging from the *Ambrosia-Larrea* zone to the *Artemisia* zone. The elevational and ecological variation, within a localized area, allowed us to test whether the apparent correspondence between *Yucca brevifolia* regeneration and specific plant species could be validated.

METHODS

Three elevational transects were examined, two in the Spring Mountain Range and one in the Sheep Mountain Range in southern Nevada (Fig. 1). The Spring Mountain transects (Lee and Lucky Strike Canyons) had a generally northeast exposure and the Sheep Range transect (Corn Creek) had a southwest exposure. The period of study was from May 1996 to February 1998. Along each transect, a 100 X 50 m study site was established every 200 m in elevation from the lowest (1000 m) to the highest (2000 m) continuous stands of *Yucca brevifolia*. A total of 16 study sites were established, 6 in Lee Canyon, 5 in Lucky Strike, and 5 in Corn Creek. Study sites were located near major access roads (Fig. 1) but at least 20 m away from roadways to eliminate road effects. A *Y. brevifolia* seedling was defined as an unbranched stem, less than 50 cm in height, and at least 50 cm from an adult to avoid seedlings derived vegetatively from mature plant root systems. All but three seedlings were over 1 m from an adult. A nurse plant was classified as any perennial plant that had a *Y. brevifolia* seedling within its vertical canopy area.

Circular plots (11.29 m radius, 400 m^2) and nested sub-plots (3.99 m radius, 50 m^2) were centered at each *Y. brevifolia* seedling within the 100 x 50 m sites. The 400 m^2 plots (n=174) were surveyed for the number of *Y. brevifolia* adults and seedlings. The 50 m^2 sub-plots (n=174) were inventoried for the presence of all woody perennials,

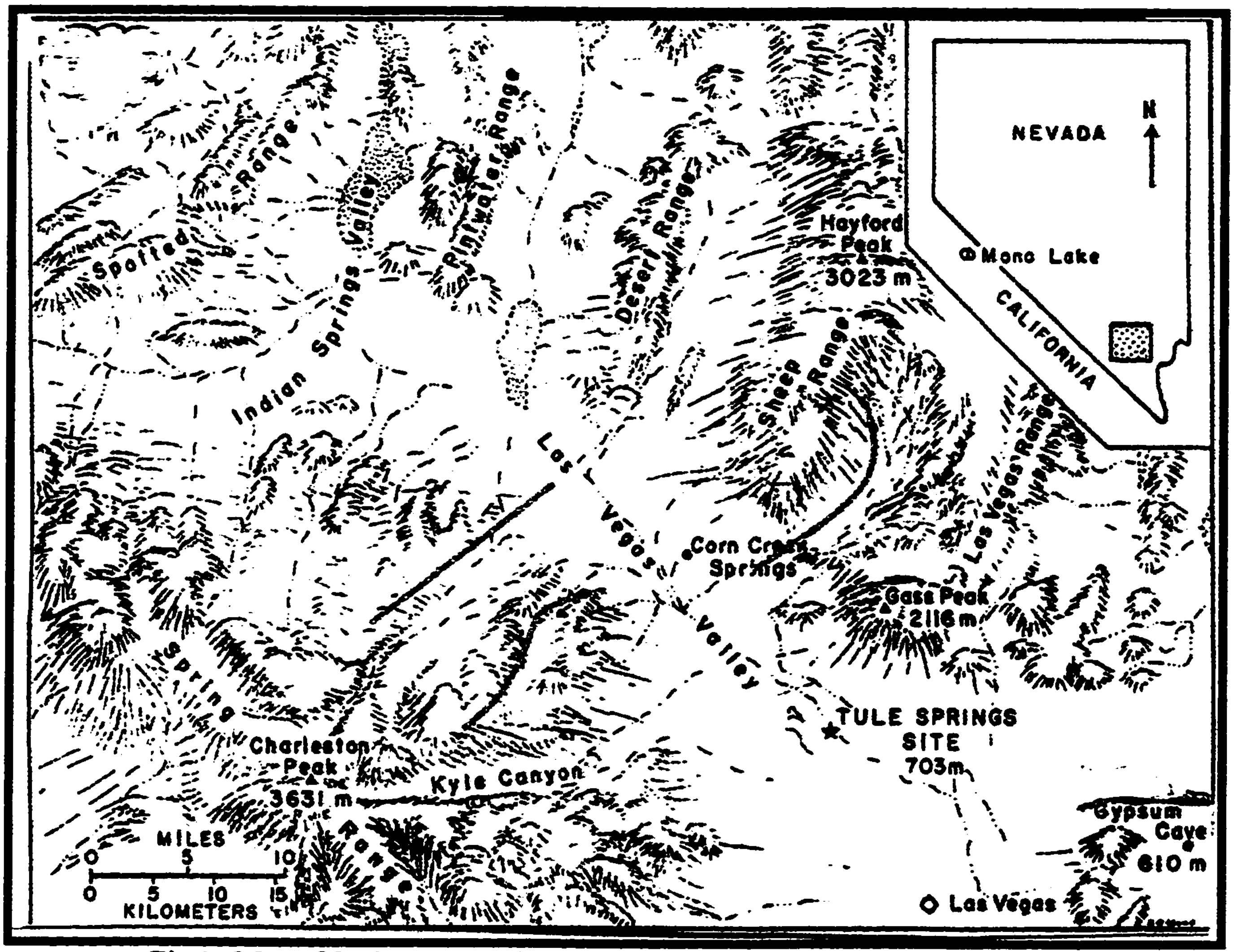

Fig 1. Map of Spring Mountain and Sheep Range transects, southern Nevada. Map by Peter J. Mehringer, Jr from Late Pleistocene Vegetation In the Mohave Desert of Southern Nevada

including secondary *Y. brevifolia* individuals, surrounding each seedling to obtain a species list, canopy coverage of each species, and the number of individuals of each species of perennial plant. Canopy diameters were obtained by multiplying the longest and shortest horizontal dimensions of the plant canopy. The focal seedling around which plots and sub-plots were developed, were seedlings initially encountered, while secondary seedlings were less prominent seedlings found during the intensive inventory, often hidden within the canopy of a shrub.

Seedlings of *Y. brevifolia* were categorized as being located in the open or under the canopy of a shrub. Shrubs containing a *Y. brevifolia* seedling under their canopy were measured for area and height for comparison with conspecifics without seedlings. Seedlings under canopies of shrubs were further categorized by aspect in the four cardinal directions relative to the shrub's central stem. Shrub circumference was divided into four quadrants to categorize seedling aspect relative to shrub center (north aspect: 315°-45°; east aspect: 45°-135°; south aspect: 135°-225°; and west aspect: 225°-315°). The distance from each *Y. brevifolia* seedling to the nearest adult was measured for all seedlings found within the site. Each species was ranked according to percentage of subplot area covered. The area of each nurse plant was measured and recorded separately to compare with the average area of its conspecifics. The abundance of plants and their percentage of total plant numbers were categorized by species within the subplots. The number of each nurse plant species was compared to the canopy area and numerical dominance of all other plant species, to see if nurse plant recruitment was based simply upon canopy area or the number of plants, or if there was a selection process.

Statistical Analysis

One-way analysis of variance (ANOVA) was used to determine if the number of seedlings within 400 m^2 sites differed by elevation. A three-way analysis of variance (ANOVA) was used to detect differences in site, aspect, and elevation in seedling recruitment relative to nurse shrub aspect. The pattern of establishment of seedlings in open substrate or beneath shrub canopies by site and by elevation was tested with Chi square analysis. Significance was tested at the 5% level.

RESULTS

A total of 277 *Yucca brevifolia* seedlings were found in sixteen 100 x 50 m sites along three transects that spanned a gradient from 1000 to 2000 m elevation. Seedlings were found in an elevational range from 1000 m to 2000 m in Lee Canyon, from 1000 m to 1800 m in Lucky Strike Canyon, and from 1200 m to 2000 m at Corn Creek. A large majority of the 277 *Yucca_brevifolia* seedlings (257 or 92.8%) grew within the canopy of other woody shrubs (Fig. 2) even though combined shrub canopy area of all perennial species covered only 20.1% of the area of the sixteen sites. Twenty of the seedlings (7.2%) were found in the open, away from the shade, seed catchment or fertile island effects of any shrub. This pattern of recruitment under shrubs did not vary by site or by elevation gradient (Chi square; P=0.351). Open substrate, consisting of desert pavement, accounted for an average of 79.9% of the 8,700 m^2 area of the intensively surveyed 50 m^2 subplots.

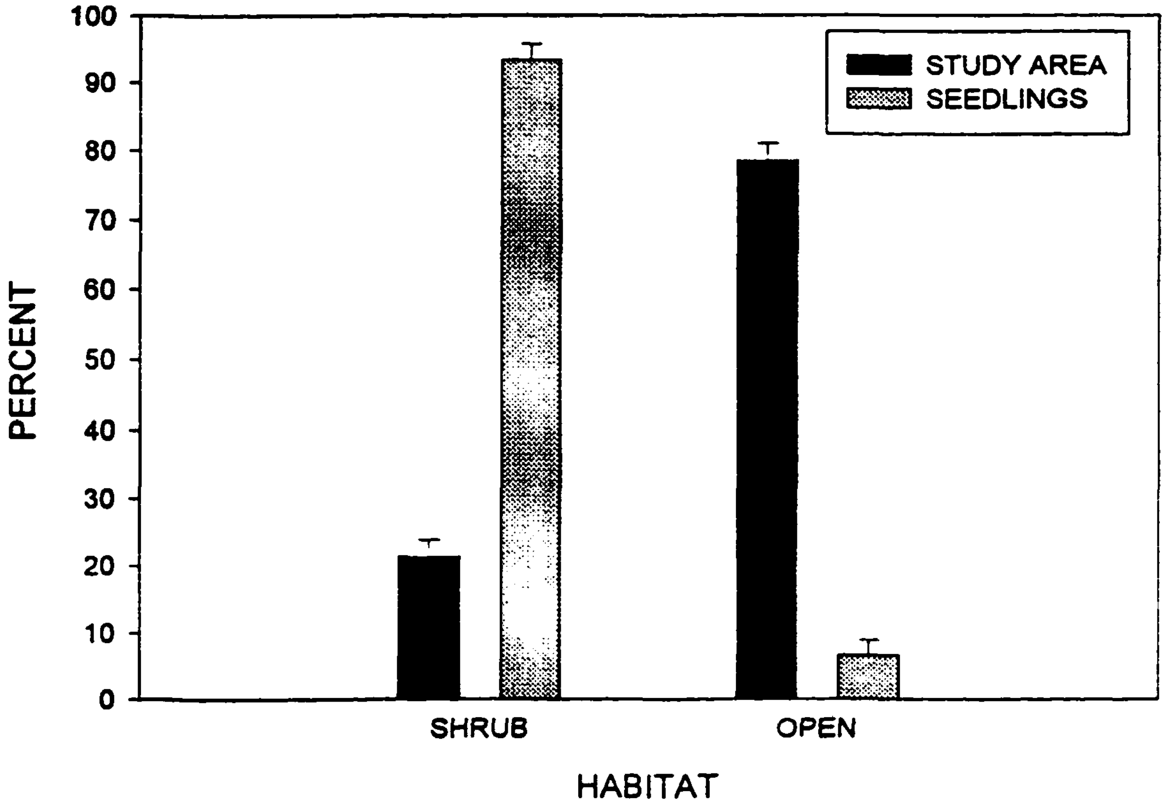

Fig. 2. Percent of open substrate and area under shrubs within all 50 m2 subplots and percent of all seedlings found in both habitats (n= 16 canyon by elevation combinations).

The number of seedlings found within each 400 m^2 plot differed significantly by elevation (one way ANOVA; $P< .01$; Fig 3). The smallest percentage of regeneration was at the lowest elevations: 1000 m (1.4%), 1200 m (7.12%); and the highest percentage of regeneration was found at 1600 m (49.8%), particularly in Lee Canyon (where 34.9% of all *Y. brevifolia* seedlings were found. Intermediate levels of seedlings were found at 1400 m (15.3%), 1800 m (14.2%), and 2000 m (12.1%).

Seedling regeneration in the open also varied significantly by elevation (Fig. 3). Intermediate elevations, presumably those with the least abiotic stress, had highest regeneration of *Y._brevifolia* seedlings in the open. Open space within the 50 m^2 sub-plots ranged from a low of 53.0% at 1800 m in Lucky Strike Canyon, where there was a dense cover of *Fallugia paradoxa* within a wide, dry wash, to 93.9% at Corn Creek at 1800 m. Open ground within the 50 m^2 sub-plots averaged 79.9% of the total area. However, regeneration on open ground accounted for only 7.2% of all *Y. brevifolia* seedlings (20 seedlings). When all three canyons were combined, recruitment on open substrate was highest at the 1600 (29.4%) and 1800 (41.2%) m elevations. However, the density of facilitated seedlings per ha at 1400 and 2000 m was similar to that found at 1800 m, indicating that recruitment in the open was not simply a function of an elevational pattern of establishment also found under shrubs (Fig. 3).

Within the 50 m^2 sub-plots, 10,339 perennial shrubs were identified and measured for canopy area. Thirty-five species were identified and 16 of them were found to be a nurse plant for *Y. brevifolia* seedlings. Nurse plants accounted for 75.8% of the total plant area (Fig. 4) within the sub-plots. *Coleogyne ramosissima* accounted for 43.8% of shrub area for the combined elevations and canyons, with the remaining 15 nurse species accounting

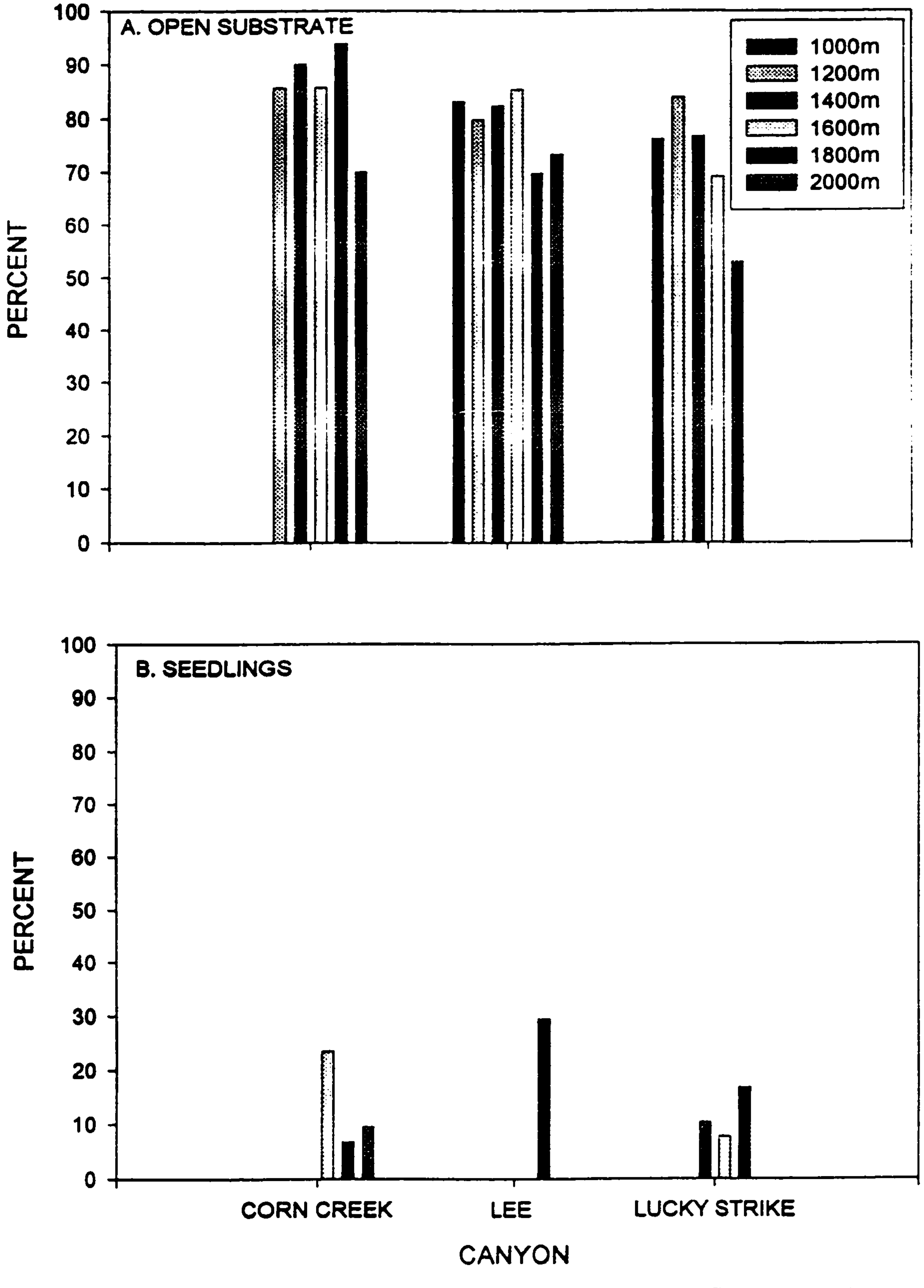

Fig. 3. Percent of area of all 50 m2 subplots (n=172 subplots) that was open substrate and percent of seedlings found in open (n=20 seedlings).

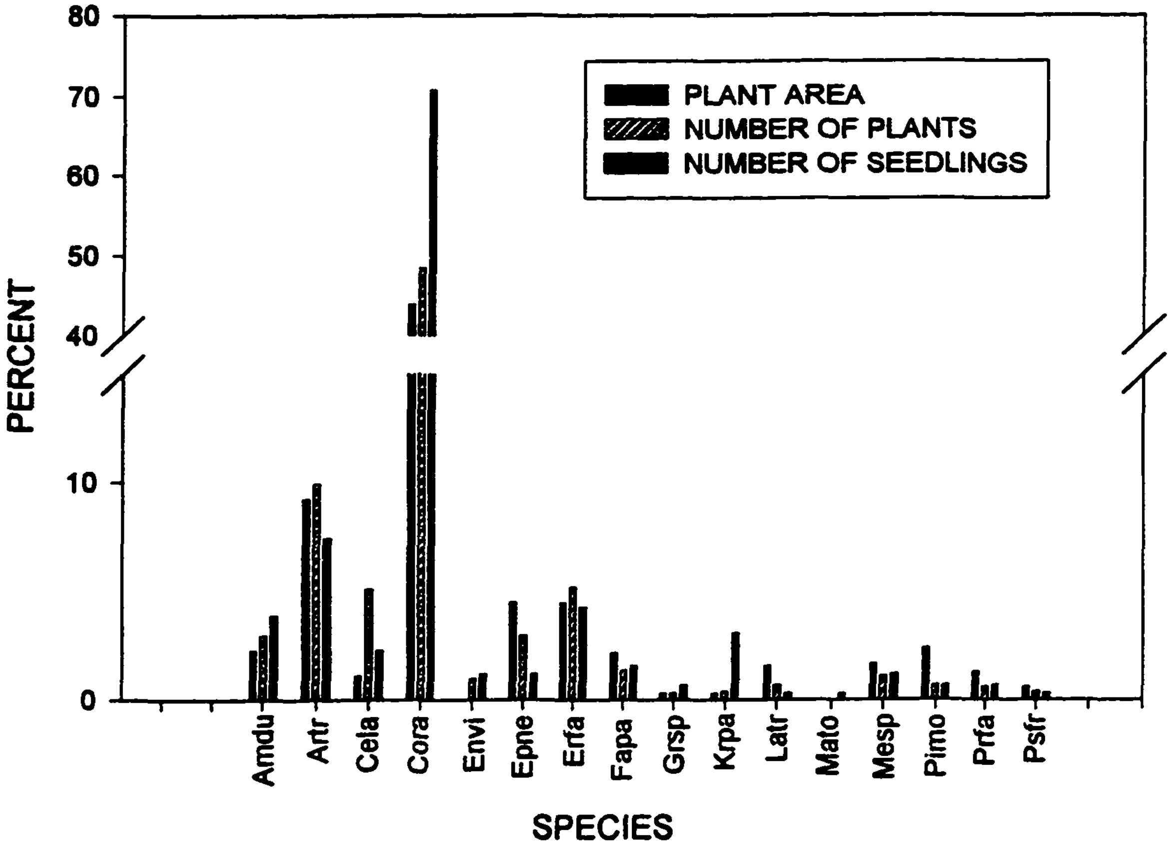

Fig. 4. Percent of plant area of each nurse plant species (total shrub area in all 50 m2 subplots = 1,706 m2), percent of nurse plants (n=7,611 nurse plants), and percent of *Yucca brevifolia* seedlings under nurse plants (n=257 seedlings).

for less than 10 % each (Fig. 4). The numerical breakdown of nurse plant species displayed a similar pattern, with *Coleogyne ramosissima* accounting for 57.4% of all shrubs and remaining shrubs accounted for less than 10% each (Fig. 4). Seedling number per ha was highest at the 1600 m elevation when all canyons were combined. Similarly, 70.8 % of the nursed seedlings (65.5% of all seedlings) were found under the canopy of *Coleogyne* with 7.2% found in the open. The remaining 15 species had less than 7% each of all nursed seedlings. However, *Krameria parvifolia*, *Ambrosia dumosa*, and *Grayia spinosa* had higher percentages of *Y. brevifolia* seedlings than expected (Fig. 4). Most nurse plant species had *Y. brevifolia* seedlings in lower ratios than represented by their canopy and/or numerical dominance would predict. For example, *Artemisia tridentata* accounted for 9.2% of area and 9.9% of all plants, but it harbored only 7.4% of the nursed *Y. brevifolia* seedlings.

The aspect of *Y. brevifolia* seedlings, relative to the center stems of the nurse plants, varied by canyon and elevation (three way ANOVA, P=<0.001). A canyon effect on seedling aspect relative to nurse shrubs was found (P=<0.001), with *Y. brevifolia* seedlings found most often on the east and west sides of nurse plants. The largest variance (P=0.054) in seedling aspect was found between north (15.2% of total nursed seedlings) and east (33.5% of total nursed seedlings). An elevational effect on seedling aspect (P=<0.001) was found for 1600 m, where a predominance of seedlings were found in the eastern quadrant of nurse shrubs compared to all other elevations. Lee Canyon, with a general northeast aspect, had significantly more seedlings to the east (37.0%) and west (29.6%) of nurse plants when all elevations were combined. Corn Creek canyon,

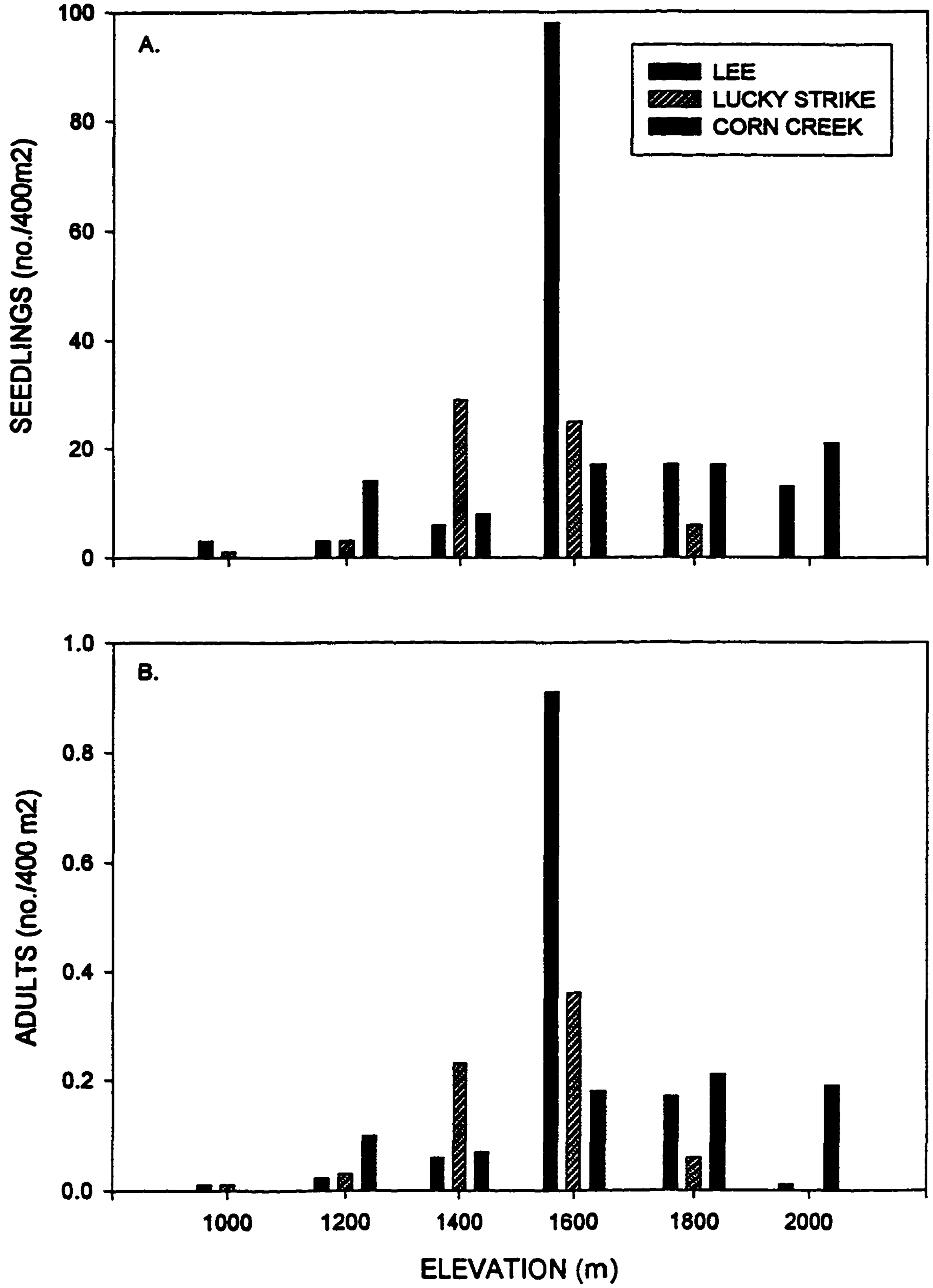

Fig. 5. Comparison of seedling and adult *Yucca brevifolia* densities within 400 m2 plots (n=172 plots).

with a southwest aspect, had a predominance of seedlings growing in the east (33.3%) and the south (34.9%) quadrants of nurse shrubs. The majority (72.7%) of the seedlings within the south quadrant of shrubs in Corn Creek were at 1800-2000 m. More than half (55.6%) of all Corn Creek (southwest aspect) seedlings were found at 1800 m and 2000 m versus 16.9% of all seedlings at those elevations within Lee and Lucky Strike Canyons (northeast aspect). The remainder of seedlings in Corn Creek grew in the north and west quadrants of nurse shrubs (Table 1).

DISCUSSION

The climatic pattern that dominates the Mojave Desert in southern Nevada is responsible for a pattern of vegetation persistence based upon selection to survive a harsh physical environment or ability to take advantage of modified microsites. Perennial shrubs such as *Ambrosia dumosa* at low elevations, *Coleogyne ramosissima* at mid elevations, and *Artemisia tridentata* at higher elevations, are able to successfully colonize open substrates and begin to modify the conditions under their canopies. This process allows less stress-tolerant species such as *Yucca brevifolia* to establish beneath *Coleogyne ramosissima* (personal observation), and *Pinus monophylla* recruitment under *Artemisia tridentata* (Phillips 1909). The phenomenon of facilitation, or nurse plant interaction, allows plants to expand their ranges into otherwise inhospitable environments at the margins of their genetic adaptability.

In the Sheep and Spring Mountain Ranges of Southern Nevada, *Y. brevifolia* is found from 1000 to 2000 m elevation. *Yucca brevifolia* appear to be limited at the lowest elevation by the fine-grained soil characteristics of basin floors (Hunnings and Peterson

Table 1. **Number of *Yucca brevifolia* seedlings found at each of the four cardinal directions from the nurse plant.**

CANYON	NORTH	EAST	SOUTH	WEST	**TOTAL**
Lee	22	50	23	40	**135**
Lucky Strike	8	15	15	21	**59**
Corn Creek	9	21	22	11	**63**
Total	**39**	**86**	**60**	**72**	**257**

1973) and at the highest elevations by low temperature constraints (Smith et al. 1983). Recruitment of *Y. brevifolia* in the open occurred between 1600 and 2000 m elevations in the Corn Creek transect. Corn Creek has an overall southwestern aspect that may have allowed *Y. brevifolia* seedlings to survive without nurse plants at 2000 m. On the northeastern aspect transects (Lucky Strike and Lee Canyons), *Y. brevifolia* seedlings were found in the open only to 1800 m. Franco and Nobel (1989) and Suzan et al. (1996) found that nurse canopies were only 1.2°C to 3.0°C warmer than the surrounding area during seasonal minima. The southwest aspect of Corn Creek may have produced a marginal temperature gain that permitted recruitment at the higher elevation in the open. In Lee Canyon and Lucky Strike Canyon, seedling recruitment on open substrate occurred between 1400 and 1800 m elevations. Soil moisture, soil development, and cooler temperatures increase with altitude, perhaps explaining the lack of open substrate recruitment below 1600 m at Corn Creek and below 1400 m at Lucky Strike Canyon (Fig. 3). Higher elevations may preclude recruitment in the open due to freezing temperatures in the winter.

Although a few physiological studies have been conducted on *Y. brevifolia*, little is known about its requirements for reproductive success, persistence within a highly stressful environment, or interactions with other community members. Recruitment of *Y. brevifolia* is largely dependent upon the existence of microclimates that occur under the canopies of perennial shrubs, most importantly *Coleogyne ramosissima*. The advantages of germination within the canopy of another plant include higher soil moisture, reduced insolation, reduced tissue and soil temperatures, reduced evapotranspirational demand, increased nutrients, reduced herbivory, and reduced wind desiccation. Disadvantages of germination under another plant may include competition for water if the adult plant has a near-surface root system, reduced PAR inhibiting carbon gain, and allelopathy.

Thirty-five species of perennial shrubs were identified within the three transects, and sixteen species were found with *Y. brevifolia* seedlings under them. Regeneration of *Y. brevifolia* occurs almost exclusively (92.8%) under the canopies of densely branched, low-lying perennial shrubs (e.g., *Ambrosia dumosa, Coleogyne ramosissima, Eriogonum fasciculatum, Grayia spinosa, Krameria parvifolia,* and *Thamnosma montana*). Despite similarities in canopy architecture of the nurse plants, there appeared to be a selection process for particular species above that predicted by either canopy area or numerical dominance. If presence of *Y. brevifolia* seedlings beneath a shrub canopy was purely a mechanical process (wind deposition), recruitment would be expected to occur based on total canopy area of each species or by their number within the landscape. *Coleogyne ramosissima* was the most numerous plant (57.4% of total plant density) and had the greatest canopy area (43.8% of total plant area) when all elevations and sites were combined. However *Coleogyne* was nurse plant for 70.8% of all nursed *Y. brevifolia* seedlings. Similarly *Krameria parvifolia* represented 0.3% and 0.4% of the area and number of plants, respectively while being host to 3.1% of *Y. brevifolia* seedlings. Four nurse plant species: *Ambrosia, Coleogyne, Grayia* and *Krameria* had a higher percentage of *Y. brevifolia* seedlings (for *G. spinosa* and *K. parvifolia* more than twice) than expected.

Walker et al. (in review) found species differences in the soil characteristics under shrubs in Lucky Strike Canyon. Soils under *Coleogyne*, perhaps due to the higher clay content, maintained higher soil moisture throughout the year than did *A. dumosa* and *L.*

tridentata. The selection mechanism for *C. ramosissima* over other nurse species may be the more favorable water relations available during the driest period of the year in addition to the canopy effects of reduced temperature, solar radiation, wind desiccation, and lower evapotranspiration. Water availability appears to be the primary limitation, with nitrogen becoming a limiting factor only when water is plentiful (Walker et al., in review). However, mortality of seedlings grown in shade versus seedlings grown in the open and supplied with water, indicates that shading is more important than water relations for the long-term survival of desert seedlings (Valiente-Banuer and Ezcurra 1991).

Eleven nurse species had at least one *Y. brevifolia* seedling under them but in lower ratios than represented by their canopy and/or numerical dominance would predict if facilitation were purely a function of species size or presence. *Artemisia tridentata* accounted for 9.2% of the canopy area and 9.9% of all plants, however it was correlated with only 7.4% of the nursed *Y._brevifolia* seedlings.

Yucca brevifolia seedling recruitment occurred in distinct directional patterns around nurse shrubs based on the overall aspect of the canyon surveyed. In Lee Canyon, east and west quadrants were dominant in seedling recruitment around the nurse plant. The southwest aspect in the Corn Creek area had a predominance of seedlings growing in the east and the south quadrants of nurse shrubs. In Corn Creek, the majority of the seedlings within the south quadrant of the nurse shrub were found at the highest (1800-2000 m) elevations. Perhaps the greater warming, particularly with the low winter sun, in the south quadrant of the shrub was the mechanism that allowed more than half of all Corn

Creek seedlings to establish at 1800 and 2000 m versus 16.9% within Lee and Lucky Strike Canyons.

Little is known about the role of seedling aspect, relative to the nurse shrub, in successful recruitment. However, morning and afternoon sunlight, filtered through more atmosphere (greater reflection, absorption, and scattering) than midday sunlight, has lower flux (amount of light per unit time) than sun shining directly overhead. The quality of shade, especially from 10 AM to 4 PM during the period of highest solar intensity, may explain the high recruitment on west and east sides of shrubs. *Coleogne ramosissima* seedlings had highest mortality on the south side of *C. ramosissima* shrubs in Lucky Strike Canyon (S. Vrooman, pers. comm.). Tang (1997) noted that light varies in quality, quantity, direction, and duration and these factors can control (e.g. stimulate, inhibit) germination. On the east and west sides of shrubs, photosynthesis can occur in the relative coolness of the low, direct morning and late afternoon sun. Morning and late afternoon sunlight produces relatively less heat stress in plant tissues than midday sunlight. Reduced tissue temperature enhances stomatal functioning, maintains protein and membrane integrity and lessens photoinhibition in the summer months (Singla et al. 1997). Light intensity and heating of tissues may explain the selection of the east quadrant (54.5%) of nurse canopies when the 1000 m and 1200 m elevations of all sites were combined.

Holmgren et al. (1997) reported that dry conditions reduce a plant's tolerance to shade because dry conditions require a greater allocation of carbon to the root system in pursuit of water. This increases the percentage of non-photosynthesizing, respiring tissue, thereby increasing the need for light to maintain a positive carbon balance. The reduction of PAR by nurse plant shading would limit productivity of the seedlings. However, *Y. brevifolia* light saturates at 25% of midday irradiance (Smith et al. 1983) and the higher soil moisture levels found under *C. ramosissima* (Walker et al. in review) compensate for the reduced light by allowing greater stomatal opening and extending the period of carbon gain into the dry season. Shading also reduces leaf temperature, thereby reducing the water vapor concentration within the intercellular air spaces. The lower vapor concentration creates a smaller diffusion gradient to the surrounding air, reducing transpiration losses (Rundel and Gibson 1996).

When all canyons were combined for elevation effects on seedling recruitment, the lowest percentages were at 1000 and 1200 m, increasing to a maximum at 1600 m (49.8%), then decreasing at 1800 and 2000 m (12.1%). Smith et al. (1983) concluded that low temperatures act as a constraint upon the range of *Y. brevifolia* at high elevations, while the high temperatures recorded within the Mojave Desert were within its physiological capability. However, the data gathered in the Sheep and Spring Mountain Ranges indicate that low elevations did have sparse levels of seedling recruitment, while the higher elevations had higher recruitment levels until a physiological point (perhaps a critical temperature) where they no longer occurred.

The highest adult and seedling densities of *Y. brevifolia* at the 1600 m elevation suggest optimal conditions for recruitment and persistence exist at this elevation. Maximum seedling growth occurs with a soil temperature of 21°C (Wallace et al. 1970), moderate temperatures produce the highest net photosynthesis rates in *Y. brevifolia* (Smith et al. 1983). On an annual basis the 1600 m elevation, approximately the mid-point of the elevational range of *Y. brevifolia*, would presumably have moderate temperatures between the seasonal minimum and maximum of the local bajadas. It would also have high moisture availability during the primary growth period (January-May) while avoiding the late season cold fronts that often result in high mortality of inflorescences at higher elevations as noted in Lee Canyon in April 1997 (personal observation).

Moderated tissue temperature appears to be the most critical parameter favoring the survival of *Y. brevifolia* seedlings. Previous research has found that higher water availability, critical in xeric environments, will increase the life span of plants regenerating on open substrates, however long term survival of seedlings is dependent on the presence of shade (Nobel 1980, Valiente-Banuer and Ezcurra 1991, Callaway 1992). Shade reduces temperatures by 13.5°C (Franco and Nobel 1989) to15°C (Suzan et al. 1996), creating microhabitat temperature and moisture regimes closer to the optima for photosynthesis and maintenance of leaf cell turgor and membrane function, and shade also lowers the water vapor concentration gradient between intercellular spaces and ambient air. Plant architecture can also help maintain a boundary layer of air near the surface, thereby reducing wind desiccation of the soil and diminishing evapotranspiration. Shaded microenvironments provide seedlings with improved water relations, maintenance of carbon gain longer into the dry season, reduced heat and cold damage to tissues, and avoidance of photoinhibition.

The attributes of shade explain the general mechanisms that permit the recruitment and persistence of *Y. brevifolia* at higher densities under shrubs than in the open. However, our data indicate that there is also a selection process in which *Coleogyne ramosissima, Krameria parvifolia, Grayia spinosa,* and *Ambrosia dumosa* are correlated with *Yucca brevifolia* seedlings in greater numbers than expected based on their canopy area or density. Aspect selection, relative to the nurse plant, also appears to be influential in successful germination. Recruitment of *Y. brevifolia* is based upon microhabitat alterations by specific nurse plants and upon subtle variations in light and shade that have important implications on the physiological requirements for germination and survival of *Y. brevifolia*.

Appendix A. Species Abundance by Canyon: Lee/Lucky Strike/Corn Creek

	1000 M	1200 M	1400 M	1600 M	1800 M	2000 M
Acamptopappus shockleyi (Aca sho)	0 / 0 / *	27/ 0 / 0	29 / 0 / 0	0 / 0 / 0	0 / 0 / 0	0 / * / 0
Ambrosia dumosa (Amb dum)	56 /16 / *	66/ 0 /114	0 / 2 / 0	0 / 0 / 0	0 / 0 / 0	0 / * / 0
Artiplex canescens (Atr can)	21/ 0 / *	0 / 0 / 0	5 / 1 / 0	103/ 2 / 1	7 / 0 / 5	0 / * / 8
Artemisia tridentata (Art tri)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	1 / 36/ 1	344/ * /556
Baileya multiradiata (Bai mul)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 7	0 / 0 / 0	0 / * / 0
Ceritoides lanata (Cer lan)	31/ 12 / *	39/ 1 / 0	247/ 15/ 1	15/ 3 / 0	0 / 0 / 0	0 / * / 0
Chrysothamnus nauseosus (Chr nau)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 1	0 / 0 / 0	0 / * / 5
Coleogyne ramosissima (Col ram)	0 / 0 / *	0 / 47/ 0	23/685/ 0	2570/1165/ 0	419/194/503	0 / * / 330
Echinocactus spp (Ech spp)	0 / 0 / *	0 / 0 / 10	0 / 0 / 0	0 / 0 / 3	0 / 0 / 3	0 / * / 0
Encelia farinosa (Enc far)	0 / 0 / *	0 / 0 / 93	0 / 0 / 0	0 / 0 / 9	0 / 0 / 0	0 / * / 0
Encelia virginensis (Enc vir)	5 / 0 / *	1 / 6 / 122	4 / 14 / 0	0 / 1 / 0	0 / 0 / 0	0 / * / 0
Ephedra nevadensis (Eph nev)	2 / 3 / *	9 / 12 / 1	24/ 70 / 13	109/ 20/ 33	27/ 4 / 1	0 / * / 31
Ephedra viridis (Eph vir)	0 /. 0 / *	0 / 0 / 0	0 / 17 / 0	0 / 62 / 0	0 / 13 / 53	0 / * / 37
Eriogonum fasciculatum (Eri fas)	2 / 0 / *	1 / 2 / 0	2 / 1 / 97	0 / 0 / 380	0 / 0 / 0	0 / * / 0
Fallugia paradoxa (Fal par)	0 / 0 / *	0 / 0 / 0	0 / 0 / 0	0 / 0 / 0	7 /110/ 14	0 / * / 0
Grayia spinosa (Gra spi)	0 / 0 / *	0 / 5 / 0	2 / 0 / 0	47 / 0 / 1	0 / 0 / 0	0 / * / 0

Gutierrezia sarothrae (Gut sar)	0/ 0 / *	0/ 0 /0	0/ 2/ 0	33 / 1 / 0	29/ 0 / 28	127/ * / 4
Hymenoclea salsola (Hym sal)	0/ 0 / *	0/ 0 /0	0 / 42/ 0	0/ 0/ 0	0/ 0/0	0 / * / 0
Juniperus osteosperma (Jun ost)	0/ 0 / *	0/ 0 /0	0/ 0/ 0	0/ 0 /0	0/ 0/ 0	4 / * / 2
Krameria parvifolia (Kra par)	4 / 0 / *	4/ 4 / 10	1 / 0/ 3	0/ 0 / 7	0/ 0/ 0	0/ * / 0
Larrea tridentata (Lar tri)	8 / 6 / *	1 / 0 / 31	1 / 0/ 1	0/ 0 / 0	0/ 0/ 0	0/ * / 0
Lycium andersonii (Lyc and)	0 / 23 / *	2 / 1 / 0	12 / 2 / 0	0/ 0 / 0	0/ 0 /0	0/ * / 0
Machaeranthera tortifolia (Mac tor)	0/ 0 / *	0/ 0 /0	0/ 0 / 5	0/ 0 / 3	0/ 0 /0	0/ * / 0
Menodora spinescens (Men spi)	4 / 0 / *	20/ 2 / 17	33/ 0 / 4	0/ 0 / 0	18/ 0 / 1	0/ * / 0
Opuntia spp. (Opu spp)	4 / 2 / *	7 / 10 / 8	7 / 10/ 1	118/ 8 / 2	16/ 43 / 2	6 / * / 18
Pinus monophylla (Pin mon)	0/ 0 / *	0/ 0 /0	0/ 0/0	0/ 0 / 0	0/ 1 / 0	61/ * / 3
Prunus fasciculata (Pru fas)	7 / 0 / *	0/ 1 / 9	7 / 0 / 21	0/ 7 / 0	0/ 2/ 0	0/ * / 0
Psorothamnus fremontii (Pso fre)	3 / 0 / *	3/ 4 / 13	0/ 0/ 11	0/ 0 / 12	0/ 0 /0	0/ * / 0
Tetradymia axillaris (Tet axi)	0/ 0 / *	0/ 0 /0	0/ 0 / 1	41/ 0 / 8	0/ 0/ 0	0/ * / 0
Thamnosma montana (Tha mon)	0/ 0 / *	0/ 0 / 0	0/ 0 / 0	90/ 143/ 25	0/ 0/ 29	0/ * / 0
Yucca baccata (Yuc bac)	1 / 0 / *	0/ 0 / 3	0 / 11 / 0	132/ 45/ 0	25/ 18 / 49	0/ * / 42
Yucca brevifolia (Yuc bre)	0/ 1 / *	1 / 0 / 0	2 / 3 / 1	38/ 1 / 10	6 / 0 / 15	2 / * / 11
Yucca schidigera (Yuc sch)	2 / 0 / *	3/ 1 / 1	3 / 12 / 12	0/ 1 / 21	0/ 1 / 0	0/ * / 0

Appendix B. Nurse Plant Species: All Canyons and All Elevations

	1000 M	1200 M	1400 M	1600 M	1800 M	2000 M
Lee						
Men spi	1	1		1		
Amb dum	2					
Cer lan		1	4	1		
Kra par		1				
Col ram			1	92	12	
Pru fas			1			
Gra spi				2		
Pin mon						2
Art tri						11
Open				2	5	
Lucky Strike						
Amb dum	1					
Pso fre		1				
Col ram		2	26	23	2	
Eph nev				1		
Fal par					3	
Open			3	2	1	
Corn Creek						
Amb dum		7				
Enc fru		2				
Lar tri		1				
Eri fas		1	3	7		
Kra par			4	3		
Enc vir			1			
Eph nev				2		
Pru fas				1		
Col ralm					13	11
Fal par					1	
Art tri						8
Open				4	1	2
Totals:	**4**	**17**	**43**	**141**	**38**	**34**

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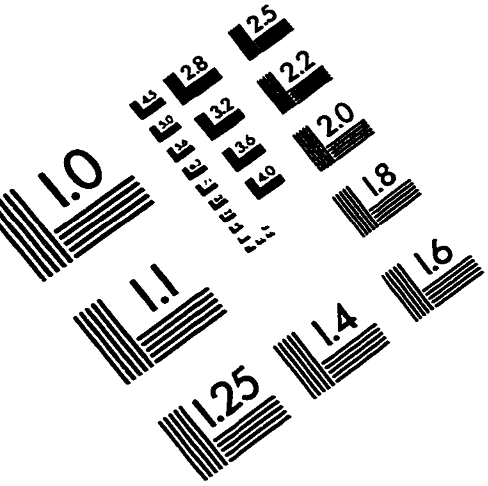
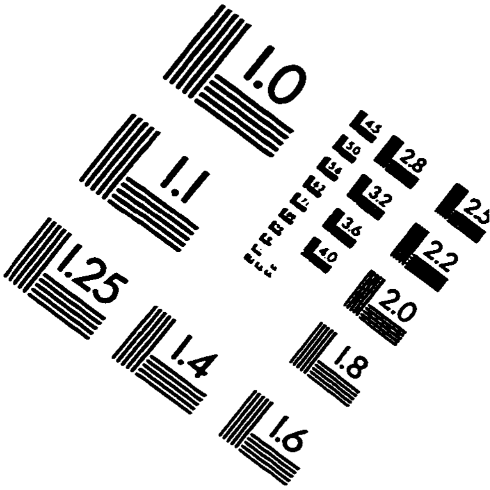
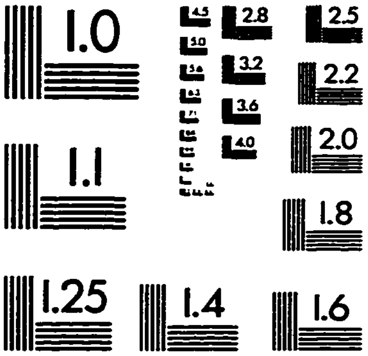
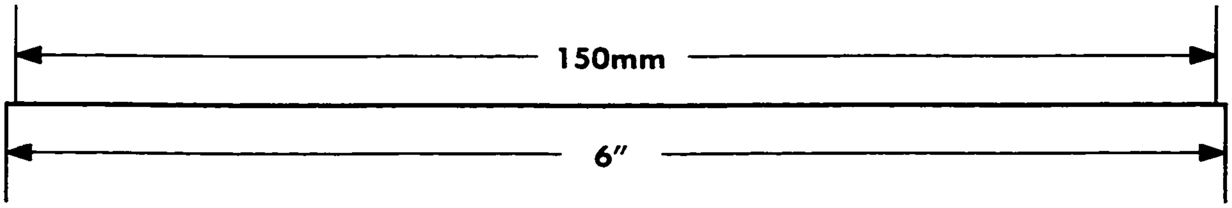
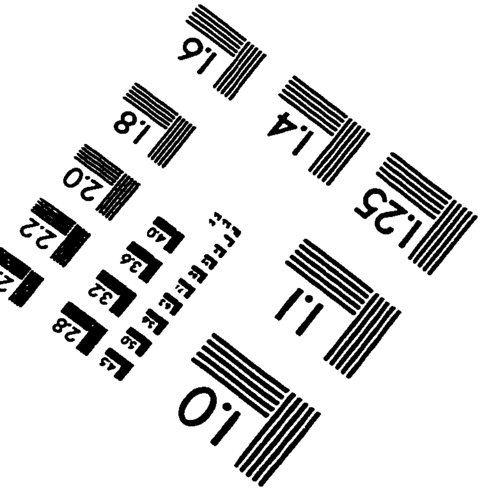
IMAGE EVALUATION TEST TARGET (QA-3)











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