

PLANT SPATIAL PATTERN AND NUTRIENT DISTRIBUTION IN PINYON-JUNIPER WOODLANDS ALONG AN ELEVATIONAL GRADIENT IN NORTHERN NEW MEXICO

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Plant and soil resource spatial patterns were measured in pinyon-juniper communities in northern New Mexico over an elevational gradient that also served as a water-availability gradient to examine the role of resource competition and resource availability in determining plant spatial patterns. Total canopy coverage increased with increasing elevation. Percent coverage of juniper declined with elevation and, with the exception of one site, that of pinyon increased. Water appeared to be a strong factor in the maintenance of stand structure and plant distribution in this pinyon-juniper ecosystem. Plant water stress was greater during the dry season at the low-elevation, low-density sites than at the upper-elevation, higher-density sites. At the upper-elevation sites, plant distributions were significantly more clumped than at the drier sites; only at these low-elevation sites was there a significantly negative relationship between plant size and distance to nearest neighbor and a trend toward regular spacing. Juveniles were significantly clumped with respect to adults at all sites, with this trend most significant in seedlings, but seedlings did not show an affinity for the canopy of conspecific adults. Nitrogen availability was greater in canopy soils than in intercanopy soils, although a significant water-availability gradient was not seen across a canopy-intercanopy transect. Thus seedling establishment patterns could result from nutrient-availability differences, shade protection, or seed-dispersal and germination patterns, but probably not from microsite water differences.

Introduction

The importance of spatial distributions in plant communities has been debated for many years (Ford 1975; Hamill and Wright 1986). The debate has centered on whether distribution patterns in plant populations can indicate competition within these populations. The three spatial patterns that are most commonly statistically defined are random, regular, and clumped (Pielou 1960). In a random pattern the position of an individual is statistically independent of the location of its neighbors. A clumped, or aggregated, distribution is underdistributed when compared with a random distribution and may arise for several reasons. Juveniles in tree stands are often clumped near parent trees, due to either seed-dispersal mechanisms (Christensen 1977) or a heterogeneous distribution of soil resources. In a regular, or overdistributed, pattern individuals are evenly located at discrete distances; this has often been taken to indicate competition for soil resources (Barbour and Diaz 1973). In addition, nonrandom mortality of individuals during stand development can result in regular distributions in previously clumped stands (Leps and Kindlmann 1987). Similarly, the distributions of nutrients as well as water have been demonstrated to be important influences of stand structure, especially in desert ecosystems (Lauenroth et al.

1978; Fisher et al. 1988; Lajtha and Whitford 1989; Lajtha and Barnes 1991).

A distinct shift in the spatial patterns of tree-dominated ecosystems can be observed as stands age. Christensen (1977) observed broad changes in stand structure and spatial pattern as an oak-hickory forest approached climax. In a 23-yr study he observed a shift in the overall pattern of individuals from random to regular and a decrease in the number of juveniles within the population. An examination of the population by size class showed smaller individuals clumped and adults to be either random or regularly distributed throughout the study.

Similar trends have been reported in desert ecosystems. In the absence of competition between species, some annuals have been shown to germinate almost exclusively beneath the canopies of desert shrubs such as *Larrea tridentata* and *Ambrosia dumosa* (Muller 1953). A tendency for germination to occur preferentially near canopy in desert communities has been shown in the desert shrubs *A. dumosa*, *Erigonium fasciculatum*, *Sphaeralcea ambigua*, and *Mirabilis bigelovii* (Wright and Howe 1987). This has been attributed to a combination of resource availability and decreased light level underneath canopies.

Researchers have also documented spatially heterogeneous distributions of nutrients in arid ecosystems. Schlesinger et al. (1990) postulated that the spatial heterogeneity of nutrients and litter would increase with increasing aridity or with desertification. With desertification and increased shrub dominance, nutrients would accumulate in areas under plant canopies at the expense of open soils. The dispersion of nutrients

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would shift from a semiarid grassland, where nutrients are uniformly distributed, to a semiarid shrubland that produces a heterogeneous distribution of nutrients. Such heterogeneity in soil resources could certainly be expected to influence seedling germination and plant success.

Although there has been much attention given to soil and plant heterogeneity in arid ecosystems, only a limited amount of work has been done in less xeric areas dominated by semiarid tree species. The pinyon-juniper woodland ecosystem covers in excess of 30 million hectares across the western United States primarily at elevations of 1,200–1,500 m in Nevada, Utah, New Mexico, Colorado, and California. Pinyon-juniper is found commonly on mesas, plateaus, and mountain slopes in areas with highly eroded and erodible soils. The woodland generally consists of one of three pinyon species with one of six juniper species. Juniper mixes with desert grasslands at low elevations and ponderosa pine at higher elevations. Species of pinyon pine have been found to be more water limited at low elevations than juniper and exhibit a more limited elevational distribution (Barnes 1986).

The purpose of this study was to observe changes in spatial patterns of dominant tree species along an environmental gradient in a pinyon (*Pinus edulis* Engelm.) juniper (*Juniperus monosperma* [Engelm.] Sarg.) community of northern New Mexico. We hypothesized that:

1. Seedlings would be located preferentially underneath the canopy of conspecific adults at all sites.
2. Juveniles would be clustered around adults at all sites. This should be most evident at the drier sites where location of seedling establishment is more important to survival.
3. Water and nutrient availability would be greatest under tree canopies, and these canopy effects would be greatest at the driest sites.
4. A positive linear relationship between size and distance to nearest neighbor would be observed at all sites. This effect would be most significant at the driest sites where competition for water would be the most important factor maintaining stand structure.

Material and methods

STUDY SITE

The study area was located on the Pajarito Plateau at the eastern edge of the Jemez Mountains in Los Alamos County, New Mexico. Five sites were within the Los Alamos National Environmental Research Park, and a sixth site was on U.S. Forest Service land in the adjacent Bandelier National Monument. The entire area is underlain by a single parent material of Bandelier Tuff consisting of welded and nonwelded rhyolite of Pleistocene origin. The land surrounding Los Alamos

has been protected from disruptive land-management techniques for over 40 yr. Pinyon and juniper represent the only dominant tree and shrub species at these sites; although small tuft grasses, cacti, and forbs are present in intercanopy spaces, they do not contribute significantly to total stand biomass.

The climate at Los Alamos is semiarid mountain temperate. Annual precipitation averages 45 cm with 75% of this between May and October as rainfall. Winter precipitation is usually in the form of snow (130 cm annually), accounting for only 25% of water inputs. Monthly temperatures range from a low of -9°C to a high of 35°C (Los Alamos National Laboratory 1987).

Sites were selected along the elevational gradient that makes up the Pajarito Plateau. Six plots were established during 1988 and 1989. Plots were randomly selected within the constraint of being as undisturbed as possible. Flat, level areas with a minimal number of runoff channels and a lack of evidence of fuel-wood cutting were selected.

SITE MAPPING

All plots were mapped during one of two consecutive field seasons. Each plant was located using X-Y coordinates to within 0.1 m. Plants were classified into five height classes. Species, height class, number of boles at ground level, and basal diameter were recorded for individuals greater than 1.0 m in height. Except where noted, plants were considered to be adults if greater than 1.0 m in height, corresponding to the top three height classes. In junipers with multiple boles, all boles were summed for each plant. Basal diameter was measured to the nearest 0.25 cm as close to ground level as possible.

Seedlings under the canopy of each tree were recorded by species. Under adults with overlapping canopies seedlings were counted as belonging partially to both canopies. Percentage canopy cover in each plot was estimated by determining the cover at a minimum of 100 stratified random points within the plot by recording presence of pinyon and juniper at 10–15 random points along each of 10 parallel lines.

SPATIAL ANALYSIS

We used both distance-based and quadrat-based methods of spatial analysis using a C program to reproduce plant distributions on a Sun Microsystems computer. For each site, 100 circular, randomly centered quadrats were generated in a computer simulation and individuals within each counted. Quadrats were generated around each adult plant in the population and numbers of each species within these tabulated.

Quadrat data were analyzed for departure from randomness using several techniques. The variance-to-mean ratio test compares the numbers of

individuals per quadrat to a random model; in a random population, the ratio of variance to mean approaches 1.0 (Chapman 1936; Fonteyn and Mahall 1981). Morisita's Index of Dispersion similarly measures the variability of plant densities within generated quadrats; variability is lowest in regularly distributed populations and greatest in clumped populations (Morisita 1959). The relationship between plant size and distance to nearest neighbor was also calculated as an index of competition (Pielou 1960; Yeaton et al. 1985), using basal diameter as an index of plant size.

An analysis of the distribution of juveniles with respect to adults was performed using techniques of Wright (1982). Both intra- and interspecific juvenile vs. adult comparisons were made. Plants 2.0 m or greater in height were defined as adults. Expected distributions were generated by assuming a large, uniformly distributed number of juveniles (at 0.25-m intervals; Wright and Howe 1987) within the plot and calculating the probability of finding an adult within the test distance. Observed distributions were generated by using the plotted locations of actual juveniles and adults. Observed and expected values were compared at quadrat radii from 0.5 to 10.0 m in 0.5-m increments.

The Wright analysis was repeated comparing pinyon and juniper adult distributions to test for significant species interactions at each site. Significant differences between observed and expected values in the Wright analysis were detected using a Kolmogorov-Smirnov test.

WATER RELATIONS

Predawn xylem pressure potentials (XPPs) were measured with a Scholander pressure chamber for juniper at 2-wk intervals during the dry season in June and July and once after the first rain of the wet season. Two samples from each of 10 adult junipers per site were collected before dawn, kept in airtight bags, and stored in a cold dark container prior to measurement. All sites were sampled on the same day. Soil moisture content was measured in August within 48 h of rainfall to test for differences in soil water availability by canopy type and coverage. Percent water was measured in soils using time domain reflectometry (TDR) for the 0–15-cm depth of mineral soil (IRAM's Soil Moisture Probe). Changes in water content were recorded at 1-m intervals beginning at the center of a canopy and extending into an intercanopy space.

SOIL ANALYSIS

Soil samples were taken at each site for soil biogeochemical analysis. Sampling was done in a single day after a period of 1 wk without measurable precipitation. Ten samples were taken

from each of the three canopy types classified as pinyon, juniper, or open. Sample locations were chosen randomly within each plot. Intact fresh plant litter was cleared from the surface prior to sampling to a 5-cm depth with a bulk density corer. Soils were passed through a #10 standard sieve (#9 mesh, 2.00 mm) and air-dried.

Aerobic laboratory incubations were used to estimate mineralization and nitrification rates in all soils (Powers 1980; Lajtha 1988). A second index of nitrogen availability was made by use of an in situ resin bag technique (DiStephano and Gholz 1986; Lajtha 1988). Equal proportions of Dowex 1-X8 anion exchange resin and Dowex 50W-X8 cation exchange resin (both 20–50 mesh) were mixed after initialization treatment rinses with 0.5 M NaHCO_3 and dilute HCl, respectively. A volume of the resin mixture corresponding to 24 g moist resin was placed in 50 cm² undyed nylon stocking material (Kayser-Roth, Burlington, N.C.). Resin bags were secured to the bottom of a 13-cm-deep soil core taken using a section of thin-walled 5-cm-diameter PVC pipe. The top layer of loose plant litter was cleared away prior to coring. The pipe remained in situ with the bag attached to retain any ions transported vertically through the soil. Plant litter was replaced around and on top of the core to maintain natural conditions. Initial samples were taken within 30 cm of the replaced soil cores at that time. Resins were buried during the July dry season and remained until early October. Total mineral nitrogen was desorbed from the resin mixture using 1.0 M KCl for 3 h. Standard solutions were prepared by allowing new resin bags to absorb ions in mixed standard solutions for 3 h. These standards were then desorbed as for the field-collected samples.

STATISTICAL ANALYSIS

The GLM procedure of SAS (SAS Institute 1985) was used to perform all ANOVAs on nutrient data. When the GLM indicated statistical significance, Tukey's HSD studentized range test was used to separate differences among categories.

Results

Canopy coverage increased with elevation (fig. 1). Percent coverage by juniper declined with elevation, and, with the exception of one site, both canopy coverage and plant density of pinyon increased. The relative density of juniper increased from a low at TA-33, peaked at the middle-elevation sites (Lower Slobovia and White Rock), and decreased at TA-51 and Bandelier as pinyon became dominant. Total plant density ranged from 184 plants·ha⁻¹ at TA-33, the lowest-elevation and most open site, to 612 plants·ha⁻¹ at the most densely covered site.

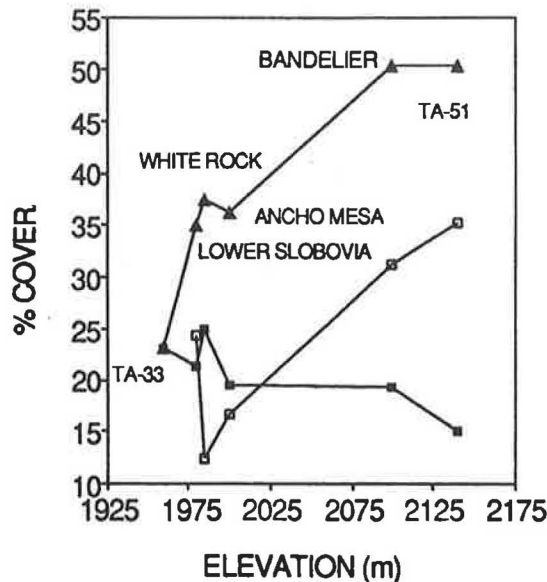


Fig. 1 Percent canopy cover by species in a *Pinus edulis*-*Juniperus monosperma* ecosystem along an elevational gradient in northern New Mexico.

WATER RELATIONS

Predawn XPPs for juniper decreased at all sites during the dry season (fig. 2). The greatest difference among sites was during seasons of lowest XPP. During peak drought, juniper at the three lowest-elevation sites had significantly lower XPPs than the three higher-elevation sites. After the wet season began, pressure potentials rose quickly and apparent site differences decreased. Soil moisture analysis by TDR showed that although there was a trend toward greater water availability at canopy edges compared to directly underneath the canopy at all sites measured, this

trend was variable and not statistically significant (fig. 3).

SPATIAL ANALYSIS

The comparison of adult and juvenile distributions by the method of Hamill and Wright (1986) showed a significantly positive relationship between the two distributions at each site when both species were combined for the analysis (fig. 4). At each site juveniles were closer than expected to adults in test quadrat radii ranging from 0.5 to 4.0 m, although this trend was not always significant at each quadrat size. Results were less uniform when species were analyzed separately. Juniper juveniles were positively associated with adult junipers at only three of the six sites. Pinyon juveniles showed a trend of being further from adult pinyon than expected at the three lowest elevations where pinyon occurred and showed no pattern at the upper-elevation sites.

Seedlings (under 2 yr) of pinyon and juniper were found to be located preferentially under canopy at all sites ($P < .001$) but did not show a significant affinity for the canopy of either species.

The Wright analysis comparing the adult distributions of pinyon and juniper showed significantly nonrandom patterns (fig. 5). Adult pinyon were significantly further than expected from adult juniper at each site for at least one quadrat size, although this trend was not necessarily significant over a broad range of quadrat radii. At three of the five sites containing both pinyon and juniper (Bandelier, White Rock, and Ancho Mesa), adult junipers were negatively associated with adult pinyon yet did not differ from a random association at the other sites.

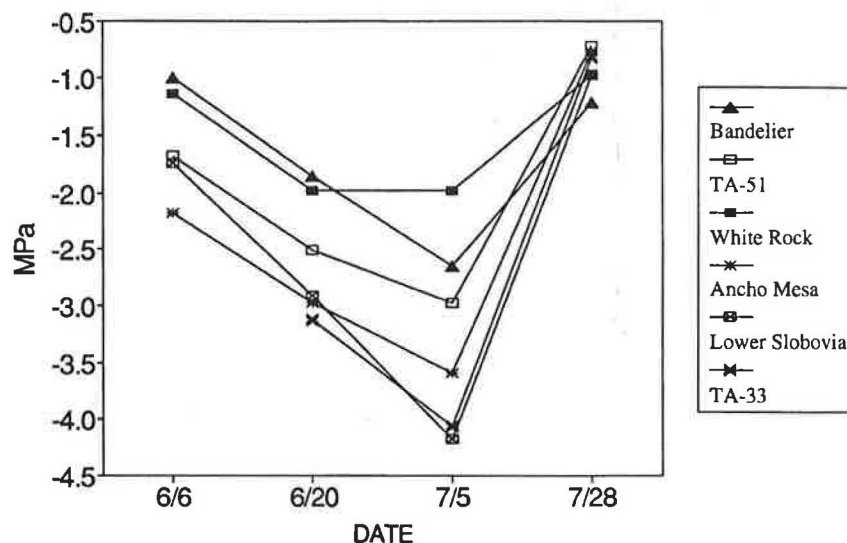


Fig. 2 Predawn xylem water potentials of *Juniperus monosperma* taken at six sites along an elevational gradient in northern New Mexico.

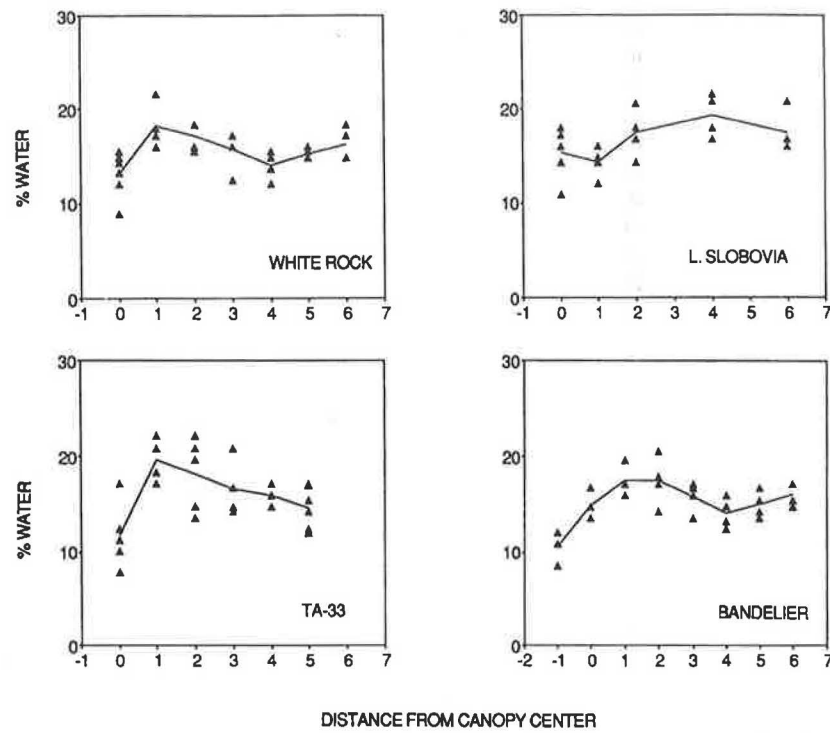


Fig. 3 Percent water as measured by TDR in surface soils from representative transects extending from canopy centers to intercanopy spaces.

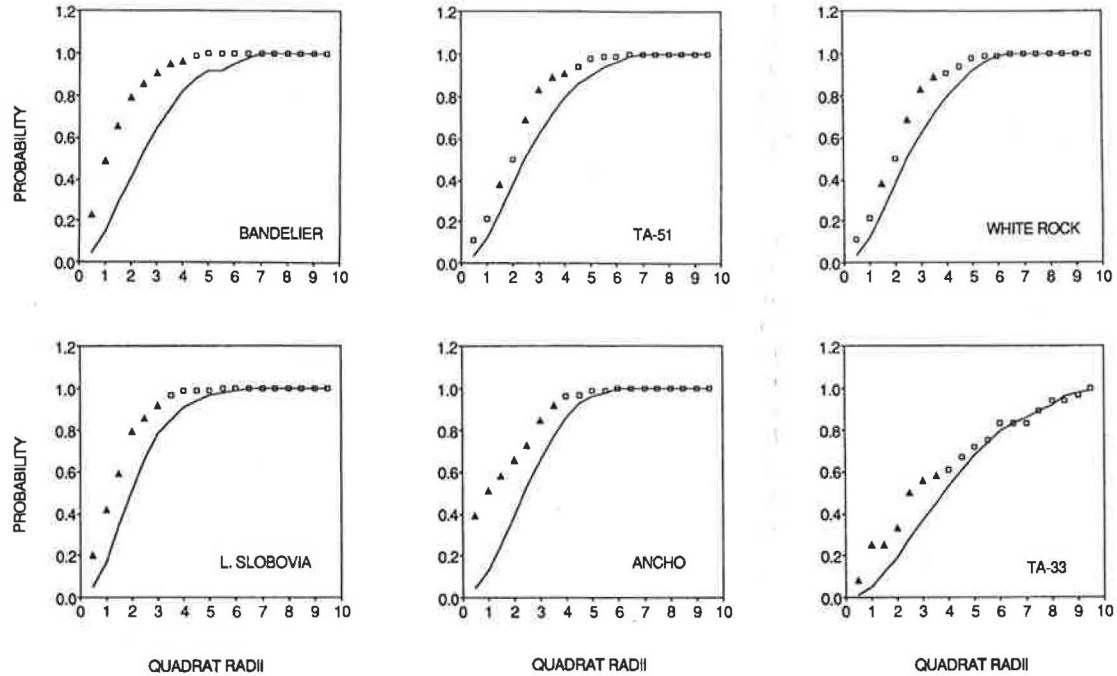


Fig. 4 The Wright statistics describing the relatedness of the juvenile and adult distributions of *Juniperus monosperma* (juniper) and *Pinus edulis* (pinyon), both species analyzed together. Solid line indicates the probability of locating an adult plant within the given quadrat radius for regularly spaced points that were computer generated at 0.25-m intervals; open squares indicate the probability of locating an adult within the given quadrat radius centered on each observed juvenile in the plot; filled triangles indicate an observed value that is significantly different ($P < .05$) from the even-distribution value.

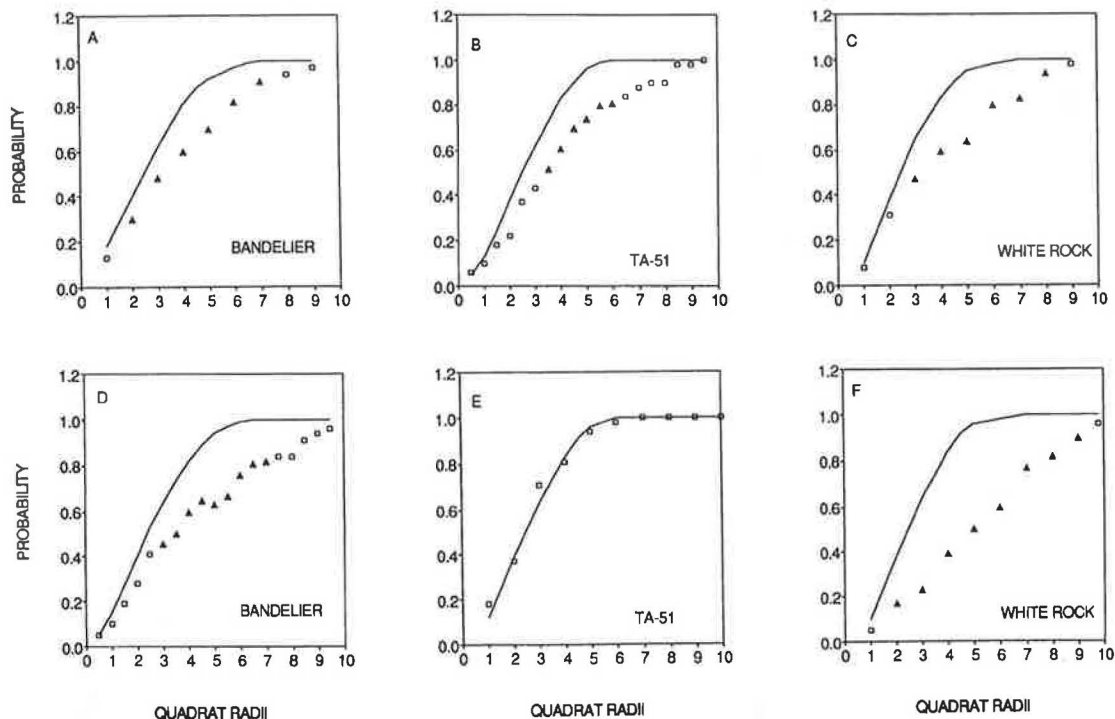


Fig. 5 Wright statistics describing the relatedness of the distributions of adult *Pinus edulis* (pinyon) and *Juniperus monosperma* (juniper). A–C, The distribution of pinyon with respect to juniper. Solid line indicates the probability of locating an adult juniper within the given quadrat radius for regularly spaced points that were computer generated at 0.25-m intervals; open squares indicate the probability of locating an adult juniper within the given quadrat radius centered on each observed pinyon in the plot; filled triangles indicate an observed value that is significantly different ($P < .05$) from the even-distribution value. D–F, the distribution of juniper with respect to pinyon. Solid line indicates the probability of locating an adult pinyon within the given quadrat radius for regularly spaced points that were computer generated at 0.25-m intervals; open squares indicate the probability of locating an adult pinyon within the given quadrat radius centered on each observed juniper in the plot; filled triangles indicate an observed value that is significantly different ($P < .05$) from the even-distribution value.

Nearest-neighbor analysis showed that there was a significant negative relationship between plant size and distance to nearest neighbor at TA-33 and Ancho Mesa, the two lowest-elevation sites, when all adults of both species were analyzed together ($P < .05$, $r^2 = .22$). Adult junipers, when analyzed separately, showed the same negative relationship between size and distance to the nearest conspecific adult at these sites ($P < .05$, $r^2 = .20$). Adult pinyon did not show a significant nearest-neighbor relationship at any site.

Morisita's Index of Dispersion indicated clumping at some scale at each site, with this effect most pronounced at the four upper-elevation sites (table 1). When the same quadrat data were analyzed by the variance-to-mean ratio, the four highest-elevation sites similarly had significantly clumped adult populations. TA-33 and Ancho Mesa did not differ from a random distribution, although Ancho Mesa demonstrated a tendency toward regularity.

NITROGEN AVAILABILITY

An ANOVA comparing laboratory rates of mineralization and nitrification showed signifi-

cantly greater N turnover in soils under canopies than in the intercanopy spaces when all sites were combined (table 2). Lab indices of N mineralization were always greater in canopy than in intercanopy soils, although this trend was significant only in the two lowest-elevation sites. Lab indices of nitrification were significantly greater in canopy than in intercanopy soils at the four lowest-elevation sites. However, at the two highest-elevation sites, this pattern was reversed. In situ measurements of mineralization and nitrification also showed significantly greater rates of N turnover in soils under canopies than in intercanopy spaces, with the exception of Ancho Mesa. There were no significant differences in rates of mineralization or nitrification in juniper vs. pinyon canopy soils.

Discussion

Stand structure changed significantly along the elevational gradient, consistent with reported trends in species cover and dominance along elevational gradients in pinyon-juniper as reported by West et al. (1978). The most obvious change is the increasing dominance of pinyon at the high-

Table 1
MORISITA'S INDEX OF DISPERSION MEASURED IN A PINUS
EDULIS-JUNIPERUS MONOSPERMA COMMUNITY

Site and quadrat radius	Pinyon	Juniper	Combined
White Rock:			
1	30.00*	2.78	4.39*
2	3.85	1.29	1.01
3	2.06*	.79	.89
4	1.15	1.18	1.00
5	1.57*	1.27*	1.12*
6	1.65*	1.14*	1.06
7	1.52*	1.07	1.01
8	1.41*	1.07*	.99
9	1.34*	1.08*	.99
10	1.23*	1.05	.96
TA-51:			
1	1.28	6.66	4.09*
2	1.22	.74	1.51
3	.92	1.92*	1.28*
4	.98	1.95*	1.32*
5	.98	1.55*	1.26*
6	.92	1.34*	1.74*
7	.96	1.26*	1.15*
8	.95	1.20*	1.09*
9	.94	1.15*	1.07*
10	.96	1.17*	1.08*
Lower Slobovia:			
1	2.50	.00	1.85
2	2.24*	1.33	1.04
3	1.03	1.13	1.13*
4	1.12*	1.07	1.11*
5	1.08*	1.08	1.06*
6	1.12*	1.04	1.09*
7	1.21*	1.65*	1.12*
8	1.13*	.01	1.09*
9	1.09*	.01	1.43*
10	1.07*	.95	1.05*
Bandelier:			
1	.00*	8.88*	4.17
2	2.12*	2.92*	2.09*
3	1.63*	3.22*	1.77*
4	1.48*	3.23*	1.59*
5	1.33*	2.90*	1.43*
6	1.22*	2.20*	1.22*
7	1.21*	1.65*	1.11*
8	1.22*	1.59*	1.08*
9	1.17*	1.54*	1.05*
10	1.19*	1.51*	1.03*
Ancho Mesa:			
1	10.00*	3.29*	2.34*
2	2.77	2.16*	1.50
3	2.85*	1.16	1.07
4	1.14*	1.16	1.05
5	1.49*	.97	.98
6	.87	.98	.95
7	.85	.97	.94
8	.99	1.01	.94
9	.99	1.04	.97
10	1.01	1.02	.97
TA-33:			
1		.00	
2		1.47*	
3		1.19	
4		1.39*	
5		.94	
6		1.04	
7		.99	
8		1.04	
9		1.02	
10		.95	

er-elevation sites. Studies have suggested that juniper is not environmentally limited but rather is outcompeted by pinyon at higher elevations (Barnes 1986).

As the dry season progressed, XPPs decreased at all sites. At the driest point in the season plants at the lowest-elevation sites had the lowest xylem water potentials, in agreement with our initial hypothesis. However, these results do not agree with some other recent studies. Schlesinger et al. (1989) found in a *Larrea tridentata* population in the Mojave Desert that areas receiving less overland flow of water had higher XPPs, i.e., less water stress, than control plants. They theorized that the low-density population was under less competitive stress for available water than the control group. Barnes (1986) also found higher pressure potentials in low-density populations of pinyon-juniper when compared with denser stands at higher elevations, where, presumably, precipitation was greater and evaporation lower. Perhaps in her higher-elevation sites the large number of individuals drawing on the available soil water resulted in strong competition within the stand. It is the balances among the abiotic water inputs and losses and biotic demand that determine the resulting water stress in any given site, and this can, presumably, change from year to year with a natural variation in precipitation input. For example, during a drier-than-average year, competition for available water might be greatest in the densest stands.

Spatial analyses showed that adults at TA-33 and Ancho Mesa were randomly distributed, rather than clumped as at the upper-elevation sites. These two sites also showed a significant positive correlation between basal diameter and distance to nearest neighbor. Although these results do not prove the existence of competition either past or present (see, e.g., Fonteyn and Mahall 1981), they do suggest that the spatial relationships of individuals at these more xeric sites are controlled by competition for resources, presumably water.

Yeaton et al. (1985) demonstrated correlations between size and distance to nearest neighbor in three species of *Yucca*, namely, *Yucca brevifolia*, *Y. schidigera*, and *Y. baccata*. Similar results have been reported for *Pinus ponderosa* (Pielou 1960), *L. tridentata* and *Ambrosia dumosa* (Cox 1987), and *Erigonum inflatum* (Wright 1982). Nearest-neighbor analyses in the current study produced a significant regression of size and distance at the two lowest-elevation sites. However, the regres-

Note. Species were tested independently and together using 100 random quadrats.

* $P < .05$.

Table 2
RATES OF MINERALIZATION AND NITRIFICATION (± 1 SE) FOR
LABORATORY AND FIELD CORE INCUBATIONS IN SOIL BENEATH
CANOPY (pinyon and juniper combined)
AND INTERCANOPY SOILS

Site and canopy	Laboratory incubation ($\mu\text{g}\cdot\text{g}\cdot\text{soil}\cdot\text{d}$)		In situ incubation ($\mu\text{g}\cdot\text{g}\cdot 90\text{ d}$)	
	Nitrifi- cation	Mineral- ization	Nitrifi- cation	Mineral- ization
Bandelier:				
I	2.7 ^a	1.0 ^a	1.8 ^a	2.9 ^a
C	1.8 ^b	1.6 ^a	2.7 ^b	3.9 ^a
TA-51:				
I	1.7 ^a	.3 ^a	.5 ^a	.6 ^a
C	.5 ^b	.5 ^a	1.7 ^b	1.8 ^b
White rock:				
I	.6 ^a	.8 ^a	.6 ^a	2.9 ^a
C	1.6 ^b	1.2 ^a	1.6 ^b	2.7 ^a
Lower Slobovia:				
I	.5 ^a	.0 ^a	.5 ^a	.1 ^a
C	.9 ^a	.1 ^a	.9 ^a	1.0 ^b
Ancho Mesa:				
I	.9 ^a	.6 ^a	1.9 ^a	3.2 ^a
C	1.9 ^b	1.2 ^b	.9 ^b	1.3 ^b
TA-33:				
I	.5 ^a	.3 ^a	.5 ^a	.7 ^a
C	1.5 ^b	1.1 ^b	1.5 ^b	2.4 ^b

Note. Pairs with different letter designations indicate significant differences. I = intercanopy; C = canopy.

sion explained less than 22% of the variation in these populations, suggesting that other factors are equally important in controlling the distribution of adults. Such factors may include random mortality of individuals, heterogeneous distribution of resources, and seed-dispersal mechanisms.

The Wright analysis examining adult distributions of pinyon and juniper showed that the distributions of the two species are related. At four of the six sites a negative association was observed between species; adult plants were more likely to have conspecific neighbors than neighbors of the codominant species. This analysis suggests that there is a long-term interaction causing a nonrandom distribution of adults. One possibility is that limited seed-dispersal mechanisms result in a clumped pattern within a species distribution. In the absence of a mechanism that would cause association between species or a very high degree of competition, contagious distributions would be expected within a species provided there was no overriding environmental limitation. This could be an important determinant of stand structure if intraspecific competition for resources is stronger than interspecific competition.

Individuals of different species might associate because of different rooting depths and experience a lesser degree of competition than in con-

specific pairs. Yeaton and Cody (1976) found that, while competition occurred between both interspecific and intraspecific pairs of the desert shrubs *Y. schidigera*, *Opuntia acanthocarpa*, and *Y. ramosissima*, individuals of different species occur significantly closer together than individuals of the same species. In contrast to these results, Fonteyn and Mahall (1981), using plant removal experiments, found that interference between species was greater than interference within species in a *Larrea-Ambrosia* population.

The Wright statistic analyzing the relatedness of adult and juvenile populations showed that in all cases juveniles were closer than expected to adults. Analysis of conspecific adults and juveniles showed more mixed results. Juniper juveniles either were positively associated with conspecific adults or were not different from a random pattern. Pinyon juveniles showed a moderate trend toward a more positive association with juniper canopies than with pinyon canopies, perhaps suggesting either that the juniper canopy is a more favorable environment for seedling germination or that there might be slight allelopathic effects under the pinyon canopy. We were not able to gain support for our hypothesis that juveniles would be more associated with adults at the driest sites; the need for the moderating effects of a canopy seemed to prevail across the entire gradient.

Nitrification rates estimated in both laboratory and in situ analyses showed that soils under canopy generally had greater rates of nitrogen turnover than intercanopy soils, but that there were no differences between juniper and pinyon canopy soils. These findings agree with previous work in pinyon-juniper woodlands and other semiarid ecosystems (Klopatek and Klopatek 1986; Lajtha and Schlesinger 1986; Tiedemann 1986), where the presence or absence of a canopy is generally more significant than differences among species that form the canopy. These results also support the observation that seedlings were associated with the presence of a canopy in general, but not necessarily with a conspecific canopy, particularly in the case of pinyon juveniles.

Seedling establishment and survival across sites occurred with the greatest frequency under canopy, without affinity for the canopy of a particular species. This was attributed to the moderating effects of a plant canopy. Greater available nitrogen was found in soils under canopies, although a significant water-availability gradient was not seen across a canopy-intercanopy transect.

The survival of a seedling to adult is dependent on a variety of factors that change throughout the life history of an individual. Seedling establishment and survival past the first few years is more likely under canopy due to the increased nitrogen in the upper soil horizon and shade from direct

light. As an individual ages, it is forced to compete for greater resources with a nearby adult that has a preestablished root system. This results in increased stress on juveniles located in proximity to other individuals. It is during times of greatest environmental stress that this competition will be strongest and have the greatest influence on stand structure.

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