

DEVELOPMENT OF SPECIES DOMINANCE ALONG AN ELEVATIONAL GRADIENT: POPULATION DYNAMICS OF *PINUS EDULIS* AND *JUNIPERUS MONOSPERMA*

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We evaluated species-environment relationships within piñon-juniper woodlands in northern New Mexico (United States) using canonical correspondence analysis (CCA). The first CCA axis was associated primarily with elevation. Our results showed separation between piñon and juniper along the elevation gradient, as expected: piñon is relatively more dominant at higher sites, whereas juniper is relatively more dominant at lower sites. To examine how this pattern of dominance might emerge with time, we plotted the position of centroids for three piñon and juniper size classes along the first CCA axis. We found that small piñons and junipers were distributed relatively uniformly across the gradient, whereas large piñons and junipers were strongly segregated along the gradient, with intermediate-sized piñons and junipers intermediate on the CCA axis between small and large. This produced a pattern of increased divergence between the two species that increased with size. We suggest that this pattern emerges as a result of differential mortality between the species rather than as a result of differences in seedling establishment along the gradient. These differences between the species could result from differences in resource use (i.e., physiology) and resource acquisition (i.e., rooting patterns relative to plant available water). We present a conceptual model of how differences between the species in resource acquisition increase with size (age). We suggest that differences in resource acquisition between species, which increase as individuals mature, may play a greater role in determining species dominance along resource gradients than has been previously appreciated.

Keywords: canonical correspondence analysis, piñon-juniper woodland, plant mortality.

Introduction

A central theme in plant community ecology is the determination of plant species distributions along gradients of resource availability (Whittaker 1975; Tilman 1982; Jongman et al. 1995; Hoagland and Collins 1997; Ohmann and Spies 1998). Resource availability is determined by multiple abiotic factors and by plant characteristics that govern resource acquisition and resource use (Tilman 1988; Caldwell and Pearcy 1994; Lambers et al. 1998). Interactions among abiotic factors and plant characteristics are thought to play a major role in determining plant community patterns along resource gradients through competition for above- and belowground resources (Tilman 1988; Smith and Huston 1989; Coffin and Urban 1993; Holmgren et al. 1997). Gradients of resource availability are often associated with gradients of climate, the most apparent of which are related to changes in elevation over short distances. Hence, many studies relating plant species distribution and resource availability have focused on elevational gradients, along which other environmental factors vary concurrently (Conant et al. 1998, 2000; Murphy et al. 1998; Martens et al. 2000).

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A major and extensive plant community type of the western United States that shows striking variation in species composition with elevation is piñon-juniper woodland (West 1988). In these woodlands, the lower elevations are dominated by juniper species, whereas the higher-elevation sites are dominated by piñon species (Phillips 1909; Woodbury 1947; Merkle 1952; Whittaker and Niering 1975; West 1988, 1999; Padien and Lajtha 1992). Consequently, the relative density of piñon to juniper increases with increasing elevation (Kennedy 1983; West et al. 1998). The composition of other species within piñon-juniper woodlands also changes with elevation (Harner and Harper 1973; Barnes 1986). Concurrent with changes in elevation in these woodlands are changes in precipitation and temperature, which generally are presumed to increase the availability of water to plants (Barnes 1986; Padien and Lajtha 1992; Lajtha and Getz 1993). Hence, the elevational segregation of dominance between piñon and juniper species, in addition to associated changes in other species, occurs along gradients of resource availability. The elevational segregation between piñon and juniper species also has been documented in response to temporal variation in climate (Allen 1989; Betancourt et al. 1990, 1993; Miller and Wigand 1994; Allen and Breshears 1998). It appears that piñon-juniper woodland communities may be tightly tied to changes in resource availability associated with elevation. Although plant community composition of piñon-juniper woodlands clearly varies with elevation, studies investigating the more general relationships between species distributions and the multiple factors that determine resource availability are largely lacking.

Species-environment relationships are complex and involve many factors; hence, multivariate analyses are required to detect their interrelationships. A multivariate analysis using detrended correspondence analysis was conducted by Lei (1999) for a large gradient that spanned piñon-juniper communities. Lei found that elevation and several other variables determined plant community composition along that broad gradient. However, the relevance of those results for understanding species distributions within piñon-juniper communities is unclear because the breadth of the gradient was much larger. A multivariate analysis relating piñon-juniper community composition with environmental factors was conducted by Harner and Harper (1973), but that study was limited to analysis of species diversity. A multivariate analysis of species-environment relationships that focuses solely on piñon-juniper communities could provide better insight into the relationships between resource availability and plant species composition.

Our objective was to evaluate species-environment relationships within piñon-juniper woodlands using multivariate analysis (canonical correspondence analysis [CCA]). We studied woodland sites located on the Pajarito Plateau in northern New Mexico (United States), where several recent studies have focused on quantifying and characterizing resource distributions with changes in elevation and increasing density of woody plants (Barnes 1986; Allen 1989; Padien and Lajtha 1992; Martens et al. 2000). Our initial analyses led us to investigate specifically how differences in piñon versus juniper distributions emerge as a function of tree size (and presumably age). Our results highlight the development of species dominance (associated with changes with plant size) along an elevational gradient and suggest that differences in resource acquisition, which increase as individuals age, may play a greater role than has been previously appreciated.

Material and Methods

The study area was located in the Los Alamos National Environmental Research Park, Los Alamos County, New Mexico, with some additional plots on adjacent U.S. Forest Service and National Park Service lands (ca. 35.85°N, 106.27°W). The area is largely on the Pajarito Plateau on the eastern flank of the Jemez Mountains in northern New Mexico. Soils range from 10 to 150 cm in depth, and most soils in the area have developed from Bandelier tuff parent material, which resulted from the consolidation of rhyolite ash and pumice (Nyhan et al. 1978; Davenport et al. 1996). Erosion of the plateau has resulted in a series of mesas and deep canyons joined by steep canyon walls. The canyons dissecting the plateau run mostly east-west, so that slope aspects are predominantly northerly or southerly. Mean annual precipitation increases with elevation on the plateau, from 330 mm at 1945 m elevation to 460 mm at 2249 m elevation (Bowen 1990).

Along the study gradient the piñon species was *Pinus edulis* Engelm. and the juniper species was *Juniperus monosperma* [Engelm.] Sarg. (nomenclature for all species follows Martin and Hutchins 1980–1981). Mature stands were selected for sampling in 1982. These stands were restricted to those showing minimal impact (from logging, grazing, or recreational use) and those with relatively uniform slope and aspect over an 0.25-ha area. A plot (25 m × 15 m) was randomly located in

each of 47 stands. Trees were tallied by species and 5-cm-diameter classes (diameter at base [DAB] measured ca. 15 cm above ground level). Seedlings and juveniles less than 5 cm DAB were recorded by height classes (<1 m and >1 m). Since *J. monosperma* branches extensively from the base, all basal stems of each individual were tallied by 2.5-cm-diameter classes and equivalent DAB estimated using the following formula (Meeuwig and Budy 1981): $DAB = (d_1^2 + d_2^2 + \dots + d_n^2)^{0.5}$, where d_n is the diameter of the n th basal stem. Crown cover of individual trees was estimated from DAB by linear regressions as given by Barnes (1986). Absolute cover for a tree species at a site was determined by summing crown cover for all individuals in a plot.

Shrub and herb cover was estimated in 50 quadrats (20 cm × 50 cm) superimposed on each plot following Daubenmire's technique (Daubenmire 1959). Visual estimates of canopy cover for each species were made using the following cover classes (percent cover): 0%–1%, 1%–5%, 5%–25%, 25%–50%, 50%–75%, 75%–95%, and 95%–100%. Percent cover of total plant basal area, bare soil, litter, rock, and cryptogams ("moss") were also recorded for each quadrat.

For CCA (ter Braak 1987), we used absolute percent cover in the species by site matrix. Log transformation of percent cover did not affect results, so untransformed values were used. Infrequent species (those that occurred in fewer than 5% of the plots) were excluded from the analysis. Percent cover values for *P. edulis* or *J. monosperma* used in CCA analyses were obtained by summing canopy cover for all size class individuals at a site.

We included 10 environmental variables for each site: elevation, aspect, slope angle, percent soil cover, percent rock cover, percent cryptogam cover, percent litter cover, percent vascular plant cover, landform type, and substrate type. Aspect was cosine-transformed to range from 0.0 for southwest (225°) aspects to 2.0 for northeast (45°) aspects. Five landform types (ridge, upper side slope, midslope, lower slope, and bench) and seven substrate types (shallow sandy loam over rhyolite tuff parent material, pumice deposits, tuff outcrop with 5%–30% slopes, tuff outcrop with >30% slopes, stony colluvium at foot of cliffs with 15%–75% slopes, basalt rock outcrop with 3%–15% slopes, basalt rock outcrop with >30% slopes) were included as nominal variables.

Tree DAB size-class data were collapsed into three size classes (1: DAB < 5.0 cm; 2: DAB 5.0–25.0 cm; 3: DAB > 25.0 cm). To relate DAB to age for *P. edulis* we used a relationship we developed from the data of Garcia (1977) for many stands in northern New Mexico: $Age (yr) = 14.82 + 3.65 \times DAB (cm)$ ($n = 210$, $r = 0.83$, $P < 0.0001$). This relationship is similar to that reported by Martens et al. (1997) for one stand of the 47 study sites. From this equation we estimate that a 5-cm-DAB *P. edulis* is ca. 33 yr, and a 25-cm-DAB tree is 106 yr.

To ascertain the environmental relationships of *P. edulis* and *J. monosperma* size classes, centroids for each of the three size classes were calculated. For each size class, the position of the centroid was calculated as the average position of the CCA axis scores of the sites, weighted by the density of individuals in that size class at each site. Centroids were calculated based on site scores for canonical axes 1 and 2 only.

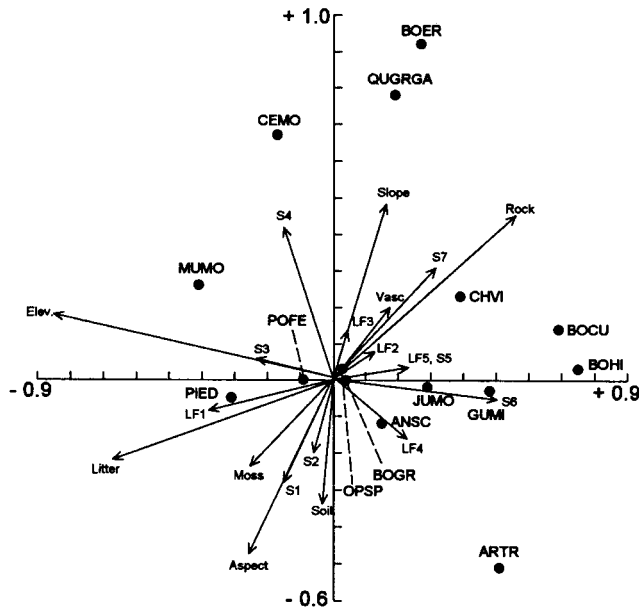


Fig. 1 Biplot for canonical correspondence analysis (CCA) of 47 semiarid woodland study sites. The horizontal axis is the first CCA axis and the vertical axis is the second CCA axis. Species included on the biplot are as follows: ANSC, *Andropogon scoparius*; BOCU, *Bouteloua curtipendula*; BOER, *Bouteloua eriopida*; BOGR, *Bouteloua gracilis*; BOHI, *Bouteloua hirsuta*; CEMO, *Cercocarpus montanus*; CHVI, *Chryopsis villosa*; GUMI, *Gutierrezia microcephala*; JUMO, *Juniperus monosperma*; MUMO, *Muhlenbergia montana*; OPSP, *Opuntia* spp. (prickly pears); PIED, *Pinus edulis*; POFE, *Poa fendleriana*; QUGRGA, *Quercus grisea-gambelii*. Nomenclature follows Martin and Hutchins (1980–1981). Environmental variables are as follows: Aspect, cosine-transformed aspect; Elev, elevation (m); Litter, % cover; Moss, % cryptogam cover; Soil, % cover; Vasc, % cover; Rock, % cover; Slope, degrees; LF1, ridge; LF2, upper side slope; LF3, midslope; LF4, lower slope; LF5, bench; S1, shallow sandy loam over rhyolite tuff parent material; S2, pumice deposits; S3, tuff outcrop with 5%–30% slopes; S4, tuff outcrop with >30% slopes; S5, stony colluvium at foot of cliffs with 15%–75% slopes; S6, basalt rock outcrop with 3%–15% slopes; S7, basalt rock outcrop with >30% slopes.

Results

Sampled sites ranged in elevation from 1670 to 2175 m and in slope from 2% to 58%. Sites occurred most frequently on ridges (36%) or midslopes (30%). Tuff outcrop and rhyolite tuff parent materials together occurred in 55% of the sites. Pumice deposits were encountered in 15% of the sites. Percent rock cover ranged from 0% to 67%, percent soil cover ranged from 6% to 84%, and percent litter cover ranged from 9% to 64%.

Ninety-one species were retained for the CCA analyses. *Pinus edulis* and *Juniperus monosperma* occurred at all sites. The next most frequent species were *Bouteloua gracilis* (98%), *Gutierrezia microcephala* (75%), and *Poa fendleriana* (72%). Species richness ranged from 15 to 35 species per plot. Total absolute cover ranged from 16% to 131%.

A species-environment biplot from the CCA (fig. 1) shows the relationships among species and environmental variables

included in the analysis. *Pinus edulis* is located on the high elevation side of the elevation arrow, and *J. monosperma* is located toward the lower elevations. The two frequent grass species, *B. gracilis* and *P. fendleriana*, occur intermediate to *P. edulis* and *J. monosperma* along the elevation arrow. *Muhlenbergia montana* has the highest elevation location of any species in fig. 1.

CCA eigenvalues for the first four axes were 0.365, 0.136, 0.110, and 0.077, respectively. Together, the four axes accounted for 62.2% of the variance in the species-environment relation, with 33% accounted for by the first axis. A Monte Carlo test of significance for each axis indicated that axis 1 was significant ($F = 5.55$, $P < 0.01$) but that subsequent axes were not significant.

The first canonical axis is dominated by elevation ($r = -0.77$), litter ($r = -0.62$), and percent rock ($r = 0.51$). However, if elevation is included as a covariable in the analysis, the resulting first axis is not significant, as indicated by a Monte Carlo test ($F = 2.55$, $P = 0.19$). Therefore, most of the variation in the first axis is explained by elevation; the other environmental variables do not contribute significantly to the interpretation.

Pinus edulis and *J. monosperma* size classes have frequency distributions that indicate a relatively constant rate of regeneration (fig. 2). There are very few large individuals (>50 cm DAB) for either species. The 5–10-cm size class appears to be somewhat suppressed for both species.

Centroids of the three size classes for *P. edulis* and *J. monosperma* are shown in figure 3. The centroids are generally arrayed along the first canonical axis, indicating that elevation is important. The smallest size classes for *P. edulis* and *J. mono-*

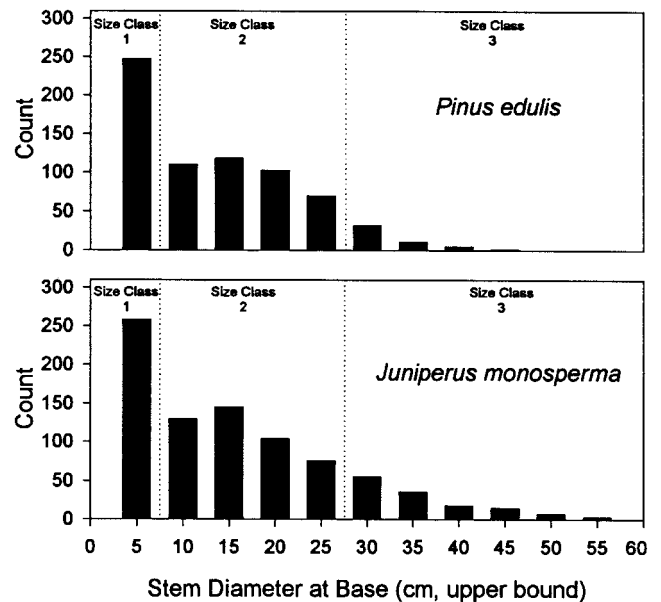


Fig. 2 Size distributions and classes for all study sites for *Pinus edulis* and *Juniperus monosperma*. Trees of each species are subdivided into three size classes on the basis of stem diameter at base (for *J. monosperma*, an effective stem diameter is used). The size classes are denoted with respect to the upper bound of the size class (i.e., size class 1 includes trees <5 cm in diameter).

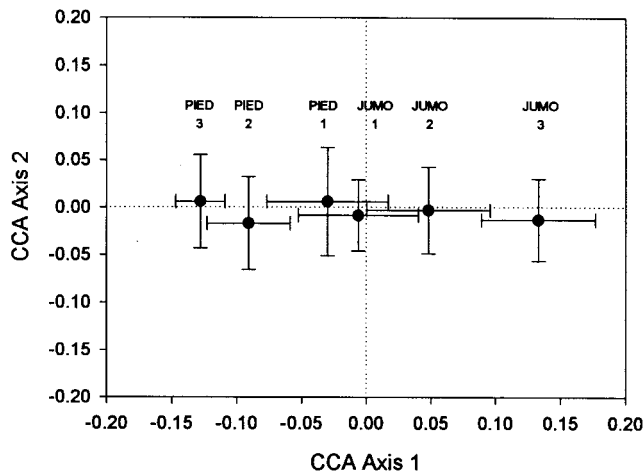


Fig. 3 Centroids for three size classes of *Pinus edulis* (PIED) and *Juniperus monosperma* (JUMO) along canonical correspondence analysis (CCA) axes. Size classes increase from 1 (smallest/youngest) through 3 (largest/oldest), with classes defined as in fig. 2. CCA axis 1 is associated with elevation, as shown in fig. 1. Error bars represent two standard errors in each of four directions.

sperma occur together on the first two axes. Although the smallest size classes for both species occur together, larger size classes of juniper extend along the first axis in the direction of lower elevations, whereas larger *P. edulis* size classes extend toward higher elevations. Note that the underlying CCA axes were based on cover of *P. edulis* and *J. monosperma*, whereas the centroids are based on density of individuals in each size class; therefore, individuals are weighted equally independent of percent cover, precluding spurious correlation that would result if percent cover was used.

Discussion

Our results contribute to an improved understanding of species distributions in piñon-juniper woodland communities along resource gradients. As expected, our results showed separation between piñon and juniper, such that piñon is relatively more dominant at higher sites, whereas juniper is relatively more dominant at lower sites, consistent with many other studies (Phillips 1909; Woodbury 1947; West 1988, 1999; Padien and Lajtha 1992). Although many factors that can influence resource availability were considered in our analysis, elevation emerged as the most significant correlate of piñon-juniper community characteristics (fig. 1) and was the only factor significantly correlated with the first CCA axis. Interestingly, even though large piñons were strongly dominant at the upper end of the gradient and large junipers were dominant at the lower end, we found that small piñons and junipers were distributed relatively uniformly across the gradient (fig. 3). Medium-sized piñons and junipers were intermediate on the CCA axis between small and large trees, producing a pattern of increased divergence between the two species, one that increased with size.

Insights into population dynamics can be obtained from population size–frequency distributions, allowing certain as-

sumptions (Harper 1977, p. 600). An important assumption for this interpretation is that tree size is related to tree age. This relationship has been documented for *Pinus edulis* at our site (Davenport et al. 1996; Martens et al. 1997), and we expect that tree size is related to tree age also for *Juniperus monosperma*, as shown for another semiarid woody species with multiple boles, *Prosopis glandulosa* (Flinn et al. 1994). Another assumption associated with interpreting static patterns in terms of temporal population dynamics is that environmental conditions have been relatively constant through time, such that older and younger trees experienced similar conditions for seedling establishment. Environmental factors that could affect seedling establishment certainly have varied over the period that trees in our study became established, as highlighted by variation in precipitation (Allen and Breshears 1998) and by reduction in fire frequency after ca. 1880 (Swetnam et al. 1999). However, our ability to assess the importance of these factors on species differences in seedling establishment is largely precluded, given the available data. For example, there are few documented trends in precipitation over this period, and there is little information on how fire might differentially affect survival of piñon versus juniper. Hence, our interpretation of the data presented here is based on the assumption that trees of all sizes have experienced similar conditions for seedling establishment. Harper (1977, p. 604) found these assumptions to be reasonable for other piñon-juniper woodland sites and consequently was able to gain insight into population growth rates within those sites.

Using this approach, we suggest that the differences in dominance between different-sized piñon and juniper trees emerge along the gradient as trees age. These spatial distributions could be determined either by differences between the species in seedling establishment along the gradient (Meagher 1943; Chambers et al. 1999) or by differences in tree mortality at later stages along the gradient (Allen 1989; Betancourt et al. 1993; Ogle et al. 2000). Our interpretation of the results (fig. 3) is that the difference is the result of differential mortality between species that increases with size (and presumably age) along the gradient because the observed differences in species dominance were not present in the smallest trees and emerged only as trees moved into larger size classes. This interpretation is further supported by additional site-specific data on seedling distributions. We reanalyzed seedling density data collected by Padien (1990) from six sites along the same gradient and found that the density of seedlings of both species increased with elevation ($r = 0.84$ for piñon, $r = 0.84$ for juniper; $P < 0.05$ for both), as was expected. However, there was no significant correlation between the ratio of piñon to juniper seedlings with elevation ($r = 0.16$; $P = 0.74$), as would be expected if differences in seedling establishment were the cause of the observed segregation between larger individuals of the two species along the gradient.

The differences in species dominance that we observed, and which we attribute to differential mortality, could result from differences between the species in terms of resource use (i.e., physiology) and resource acquisition (i.e., rooting patterns relative to plant available water). Piñon and juniper species differ in resource use in many respects. For example, *J. monosperma* and *P. edulis* differ distinctly in photosynthesis and water relations—net photosynthesis can proceed at lower water po-

tentials in *J. monosperma* than in *P. edulis* (Lajtha and Barnes 1991; Lajtha and Getz 1993), whereas sensitivity of photosynthetic rate to reduction in light is greater for *J. monosperma* than for *P. edulis* (Barnes 1986). Furthermore, water-use efficiency of *J. monosperma* increases with decreasing leaf water potential, but that of *P. edulis* does not. At higher elevations where water is more available, *P. edulis* has a greater maximum net photosynthesis rate than does *J. monosperma*, and this difference apparently results in greater carbon gain (Barnes and Cunningham 1987). These species-specific physiological differences are consistent with the dominance of juniper over piñon at lower elevations, which are typically more water-stressed sites. Similar physiological differences have been documented between *Juniperus osteosperma* and *P. monophylla* (DeLucia et al. 1988, 1989; DeLucia and Schlesinger 1991; Nowak et al. 1999; Williams and Ehleringer 2000). However, along an elevational gradient, resource use among individuals of the same species may not differ, as has been observed for *P. monophylla* (Jaindl et al. 1995). Collectively, these findings indicate that it may be important to consider species differences in resource use.

Piñons and junipers also differ with respect to resource acquisition. A manipulative field study, which was conducted on the Pajarito Plateau as well, demonstrated that *J. monosperma* was able to obtain more shallow soil water from intercanopy locations than was *P. edulis* (Breshears et al. 1997). In addition, other studies have quantified greater temporal variability in the water potential of *J. monosperma* than *P. edulis* (Barnes 1986; Schott and Pieper 1987; Padien and Lajtha 1992), which also indicates that *J. monosperma* uses more shallow soil moisture than does *P. edulis*. The differences in resource acquisition between piñon and juniper may be species specific; that is, some species of juniper may use deeper soil water than some species of piñon. For example, it appears that *J. osteosperma* may use deeper soil water than *P. edulis* (Flanagan et al. 1992, but see Evans and Ehleringer 1994; Williams and Ehleringer 2000). Vertical differences such as these in depth of water acquisition may be important in determining plant community composition in piñon-juniper woodlands (Emerson 1932; Breshears and Barnes 1999; Williams and Ehleringer 2000) and other ecosystems (Sala et al. 1989; Canadell et al. 1996; Casper and Jackson 1997; Golluscio et al. 1998).

We expect that these species-specific differences in depth of water acquisition are minimal for seedlings and increase with age (fig. 4). Consequently, the marginal benefit of deeper soil moisture to the deeper-rooted plant, piñon in this case, increases with increasing age. Under the same model, drought conditions, which preclude the availability of deeper soil moisture, would present a greater risk of mortality to piñon relative to juniper, as has been observed (Allen 1989). The differences between piñon and juniper in both resource use and resource acquisition likely contribute to the segregation that emerges with increasing size along the gradient. In particular, differences in resource acquisition between species may have a disproportionately large effect on the emergence of segregation between the two species because differences in resource acquisition likely increase with increasing plant size (fig. 4), whereas this is not necessarily so with resource use (Lajtha and Barnes 1991).

We propose that differences in both above- and below-

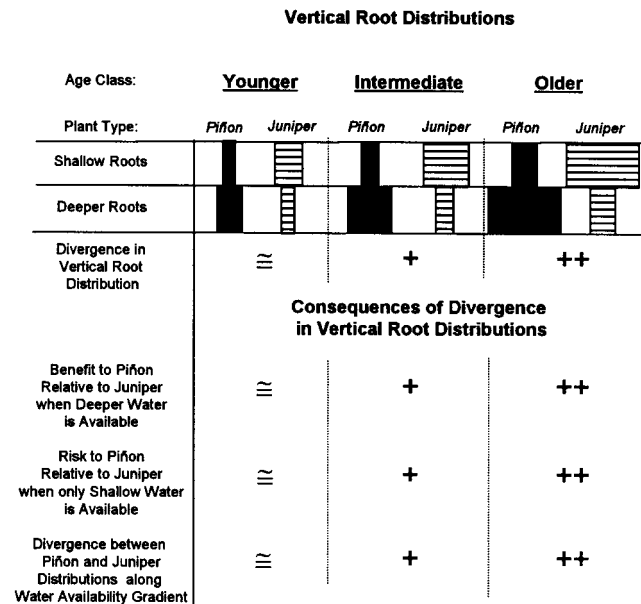


Fig. 4 Conceptual model for species- and size (age)-dependent differences in vertical root distributions between piñon and juniper as a function of increasing age. Consequences of divergence in vertical root distributions are all greatest in the older age classes with respect to benefit to piñon relative to juniper when deeper water is available, risk to piñon relative to juniper when only shallow water is available (e.g., at low elevations, during drought), and divergence between piñon and juniper distributions along a water availability gradient, as shown in fig. 3.

ground resource use and resource acquisition are producing the observed population and community patterns along the gradient. The differences in resource use and resource acquisition between piñon and juniper, we believe, manifest themselves as differential mortality between the species. Linking these factors and mortality are species-specific relationships for xylem cavitation as a function of plant water potential. *Juniperus monosperma* is less sensitive to water-stress-induced cavitation than is *P. edulis* (Pockman et al. 1995; Linton et al. 1998). Furthermore, variability in growth (which results from resource acquisition and use) prior to drought increases the probability of tree mortality in response to drought, as shown for *P. edulis* (Ogle et al. 2000).

These relationships highlight the importance of below-ground competition (for water) along the elevational gradient and are consistent with observed differences in tree spatial patterns that indicate the importance of below-ground competition (Welden et al. 1990; Martens et al. 1997). The documented species-specific differences in resource use with respect to light, as well as other observations indicating competitive responses to light (e.g., crown plasticity; Martens et al. 1997), indicate that above-ground competition for light is also important along this gradient (see also Tausch et al. 1981). As tree density increases, light availability is dramatically reduced (Martens et al. 2000), and light limitation likely becomes more important (Martens et al. 1997). Hence, we believe that our observations of the differences in species dominance along the gradient

and the emergence of that dominance with increasing size are the net result of above- and belowground differences in resource use and resource acquisition along the gradient of resource availability. Our interpretations are consistent with more general perspectives of the relative roles of above- and belowground competition for resources along gradients ranging from grassland through forest (Tilman 1988; Smith and Huston 1989; Coffin and Urban 1993; Holmgren et al. 1997). Our results indicate that differences in resource acquisition between species, which increase as individuals mature, may play a greater role in determining

species dominance along resource gradients than was previously appreciated.

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