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3 **DEVELOPMENT OF SPECIES DOMINANCE ALONG AN ELEVATIONAL**
4 **GRADIENT: POPULATION DYNAMICS**
5 **OF *Pinus edulis* AND *Juniperus monosperma***
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19 A central theme in plant community ecology is the determination of plant species distributions
20 along gradients of resource availability. We evaluated species-environment relationships within piñon-
21 juniper woodlands in northern New Mexico, USA using canonical correspondence analysis (CCA). The
22 first CCA axis was associated primarily with elevation. Our results showed separation between piñon
23 and juniper along the elevation gradient as expected: piñon is relatively more dominant at higher sites
24 whereas juniper is relatively more dominant at lower sites. To examine how this pattern of dominance
25 might emerge with time, we plotted the position of centroids for three piñon and juniper size-classes along
26 the first CCA axis. We found that small piñons and junipers were distributed relatively uniformly across
27 the gradient, whereas large piñons and junipers were strongly segregated along the gradient, with

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 below-ground resources (Tilman 1988; Coffin and Urban 1988; Smith and Huston 1989; 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).

A major and extensive plant community type of the western US 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; Padien and Lajtha 1992; West 1999). Consequently, the relative density of piñon to juniper increases with increasing elevation (West et al., 1998; Kennedy 1983). The composition of other species within piñon-juniper woodlands also changes with elevation (Barnes 1986; Harner and Harper 1973). Concurrent with changes in elevation in these woodlands are changes in precipitation and temperature, which generally are presumed to increase 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; Betancourt et al. 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

and National Park Service lands (~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 cm to 150 cm 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 a 0.25 ha area. A plot (25 m x 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 approximately 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 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 x 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 (% cover): 0 – 1, 1 – 5, 5 – 25, 25 – 50, 50 – 75, 75 – 95, 95 – 100. Percent cover of total plant basal area, bare soil, litter, rock and cryptogams ("moss") were also recorded for each quadrat.

For canonical correspondence analysis (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

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. *P. edulis* and *J. monosperma* occurred at all sites. The next most frequent species were *Bouteloua gracilis* (98%), *Gutierrezia microcephala* (75%), and *Poa fendleri* (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. *P. edulis* is located on the high elevation side of the elevation arrow, and *J. monosperma* is located towards the lower elevations. The two frequent grass species, *B. gracilis* and *P. fendleri*, occur intermediate to *P. edulis* and *J. monosperma* along the elevation arrow. *Muhlenbergia montana* has the highest elevation location of any species on 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.

P. 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 fig. 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. monosperma* 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, while larger *P. edulis* size classes extend toward higher

1 reduction in fire frequency after about 1880 (Swetnam et al. 1999). However, our ability to assess the
 2 importance of these factors on species differences in seedling establishment is largely precluded given
 3 available data. For example, there are few documented trends in precipitation over this period, and there
 4 is little information on how fire might differentially affect survival of piñon versus juniper. Hence, our
 5 interpretation of the data presented here is based on the assumption that trees of all sizes have
 6 experienced similar conditions for seedling establishment. Harper (1977, p. 604) found these
 7 assumptions to be reasonable for other piñon-juniper woodland sites, and consequently was able to gain
 8 insight into population growth rates within those sites.

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

23 The differences in species dominance that we observed, and attribute to differential mortality,
 24 could result from differences between the species in resource use (i.e., physiology), and resource
 25 acquisition (i.e., rooting patterns relative to plant available water). Piñon and juniper species differ in
 26 resource use in many respects. For example, *J. monosperma* and *P. edulis* differ distinctly in
 27 photosynthesis and water relations—net photosynthesis can proceed at lower water potentials in *J.*
 28 *monosperma* than in *P. edulis* (Lajtha and Barnes 1991; Lajtha and Getz 1993), while sensitivity 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-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. *J. 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 suggest 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, and other observations indicating competitive responses to light (e.g. crown plasticity, Martens et al. 1997), suggest 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 the importance of 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 below-ground 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 below-ground competition for resources along gradients ranging from grassland through forest (Tilman 1988; Coffin and Urban 1988; Smith and Huston;

References

- Allen CD 1989 Changes in the landscape of the Jemez Mountains, New Mexico. Ph.D. Dissertation, University of California, Berkeley, California, USA.
- Allen CD, DD Breshears 1998 Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proc Nat Acad Sci USA* 95:14839-14842.
- Barnes FJ 1986 Carbon gain and water relations in pinyon-juniper habitat types. Ph.D. Dissertation. New Mexico State University, Las Cruces, NM, USA.
- Barnes FJ, GL Cunningham 1987 Water relations and productivity in pinyon-juniper habitat types. Pages 406-417 in R.L. Everett, compiler; *Proceedings—Pinyon-Juniper Conference*, Reno, NV, January 13-16, 1986. USDA Intermountain Research Station Gen. Tech Report INT-215, Ogden, Utah.
- Betancourt JL, TR van Devender, PS Martin 1990 Pack rat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson, Arizona, USA.
- Betancourt JL, EA Pierson, KA Rylander, JA Fairchild-Parks, JS Dean 1993 Influence of history and climate on New Mexico piñon-juniper woodlands. Pages 42-62 in *Managing Piñon-Juniper Ecosystems for Sustainability and Social Needs*, tech. coord., Aldon, A.F. & Shaw D.W.. USDA Forest Service General Technical Report RM-236, Fort Collins, CO.
- Bowen BM 1990 Los Alamos climatology. LA-11735-MS; UC-902. National Technical Information Service, Springfield, VA.
- Breshears DD, FJ Barnes 1999 Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. *Landscape Ecology*, 14: 465-478.
- Breshears DD, OB Myers, SR Johnson, CW Meyer, SN Martens 1997 Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. *Journal of Ecology*, 85: 289-299.
- Caldwell, MM, RW Pearcy, eds. 1994 *Exploitation of environmental heterogeneity by plants : ecophysiological processes above- and belowground*. Academic Press, San Diego, California.

- 1 Flanagan LB, JR Ehleringer, JD Marshall 1992 Differential uptake of summer precipitation among co-
2 occurring trees and shrubs in a pinyon-juniper woodland. *Plant, Cell and Environment*, 15: 831-
3 836.
- 4 Flinn RC, S Archer, TW Boutton, T Harlan 1994 Identification of annual rings in an arid land woody
5 plant, *Prosopis glandulosa*. *Ecology*, 75: 850-853.
- 6 Garcia BJ 1977 Selected characteristics of piñon pine. M.S. Thesis, New Mexico Highlands University,
7 Las Vegas, NM.
- 8 Golluscio RA, OE Sala, WK Lauenroth 1998 Differential use of large summer rainfall events by shrubs
9 and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia*, 115: 17-25.
- 10 Hamer RF, KT Harper 1973 The role of area, heterogeneity, and favorability in plant species diversity of
11 pinyon-juniper ecosystems. *Ecology*, 57: 1254-1263.
- 12 Harper, JL 1977 *Population Biology of Plants*. Academic Press, New York, New York, USA.
- 13 Hoagland BW, SL Collins 1997 Gradient models, gradient analysis, and hierarchical structure in plant
14 communities. *Oikos*, 78: 23-30.
- 15 Holmgren M, M Scheffer, MA Huston 1997 The interplay of facilitation and competition in plant
16 communities. *Ecology*, 78: 1966-1975.
- 17 Jaindl RG, LE Eddleman, PS Doescher 1995 Influence of an environmental gradient on physiology of
18 singleleaf pinyon. *Journal of Range Management*, 48: 224-231.
- 19 Jongman RHG, CJF ter Braak, OFR van Tongeren 1995 *Data analysis in community and landscape*
20 *ecology*. Cambridge University Press, New York.
- 21 Kennedy, KL 1983 A habitat-type classification for the pinyon-juniper woodlands of the Lincoln National
22 Forest. M.S. Thesis, New Mexico State University, Las Cruces, New Mexico, USA.
- 23 Lajtha K, FJ Barnes 1991 Carbon gain and water use in pinyon pine-juniper woodlands of northern New
24 Mexico: field versus phytotron chamber measurements. *Tree Physiology*, 9: 59-67.
- 25 Lajtha K, J Getz 1993 Photosynthesis and water-use efficiency in pinyon-juniper communities along an
26 elevational gradient in northern New Mexico. *Oecologia*, 94: 95-101.
- 27 Lambers H, FS Chapin III, TL Pons 1998 *Plant physiological ecology*. Springer, New York.

- 1 Nyhan JW, LW Hacker, TE Calhoun, DL Young 1978 Soil survey of Los Alamos County, New Mexico.
2 Los Alamos Scientific Laboratory LA-6779-MS, Los Alamos, New Mexico.
- 3 Ogle K, TG Whitham, NS Cobb 2000 Tree-ring variation in pinyon predicts likelihood of death following
4 severe drought. *Ecology*, 81: 3237-3243.
- 5 Ohmann JL, TA Spies 1998 Regional gradient analysis and spatial pattern of woody plant communities
6 of Oregon forests. *Ecological Monographs*, 68: 151-182.
- 7 Padien DJ 1990 Stand structure and nutrient dynamics in a pinyon-juniper community of northern New
8 Mexico. M.S. Thesis, Boston University, Boston, Massachusetts, USA.
- 9 Padien DJ, K Lajtha 1992 Plant spatial pattern and nutrient distribution in pinyon-juniper woodlands
10 along an elevational gradient in northern New Mexico. *International Journal of Plant Sciences*,
11 153: 425-433.
- 12 Phillips FJ 1909 A study of pinon pine. *Botanical Gazette* 48:216-223.
- 13 Pockman WT, JS Sperry, JW O'Leary 1995 Sustained and significant negative water pressure in xylem.
14 *Nature*, 378: 715-716.
- 15 Sala OE, RA Golluscio, WK Lauenroth, A Soriano 1989 Resource partitioning between shrubs and
16 grasses in the Patagonian steppe. *Oecologia*, 81: 501-505.
- 17 Schott MR, RD Pieper 1987 Water relationships of *Quercus undulata*, *Pinus edulis*, and *Juniperus*
18 *monosperma* in seral pinyon-juniper communities of south-central New Mexico. Pages 429-434,
19 in R.L. Everett, compiler; Proceedings—Pinyon-Juniper Conference, Reno, NV, January 13-16,
20 1986. USDA Intermountain Research Station Gen. Tech Report INT-215, Ogden, Utah.
- 21 Smith T, M Huston 1989 A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*,
22 83: 49-70.
- 23 Swetnam TW, CD Allen, JL Betancourt 1999 Applied historical ecology: using the past to manage for the
24 future. *Ecological Applications*, 9: 1189-1206.
- 25 Tausch RJ, NE West, AA Nabi 1981 Tree age and dominance patterns in Great Basin pinyon-juniper
26 woodlands. *Journal of Range Management*, 34: 259-264.
- 27 ter Braak CF 1987 The analysis of vegetation-environment relationships by canonical correspondence
28 analysis. *Vegetation*, 69: 69-77.

Figure Legends

Figure 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; LF1 –ridge, LF2 – upper side slope, LF3 – mid-slope, 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.

Figure 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).

Figure 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 2 standard errors in each of four directions.

Figure 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

Fig. 1

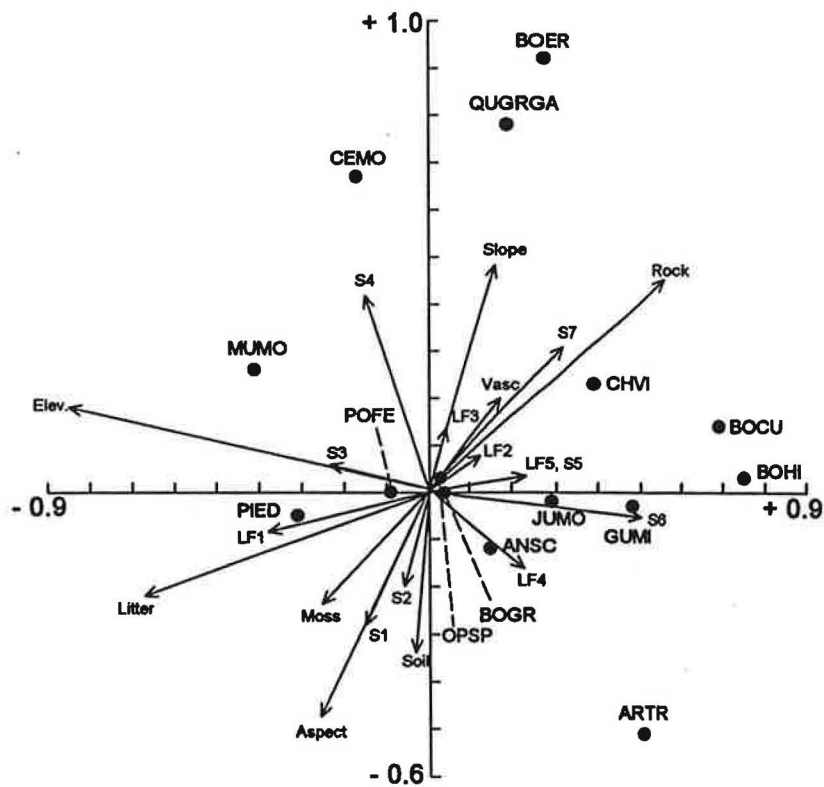


Fig. 5

