

Effect of Species Mix on Size/Density and Leaf-Area Relations in Southwest Pinyon/Juniper Woodlands

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ABSTRACT

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The effects of species mix on stand structure and growth are evaluated for 117 pinyon (*Pinus edulis* Engelm.) and juniper (*Juniperus monosperma* (Engelm.) Sarg and *J. osteosperma* (Torr.) Little) woodlands of the southwestern United States. Maximum-size/density relations, leaf area and growth of pure and mixed-species woodlands are compared. Structure of pure and mixed-species woodlands appeared to be restricted by maximum-size/density relations. Maximum Stand Density Index (SDI) for mixed-species woodlands was 30% greater than for pure woodlands. Ceiling leaf areas were 3.6 for mixed-species, 3.5 for pure pinyon and 1.0 for pure juniper woodlands. Ceiling leaf area varied with species mix and soil type. Highest growth of mixed-species woodlands occurred at maximum woodland and pinyon SDI. We suggest that higher size/density, leaf area and growth relations in mixed-species woodlands than in pure woodlands are related to differences in rooting habit and water relations between pinyon and juniper.

INTRODUCTION

The xeric pinyon/juniper woodland of the southwestern United States is a complex and poorly understood mixed-species plant community. Single-species woodlands occur on harsh sites where pinyon is unable to establish or on moist sites where pinyon is a superior competitor to juniper. On the large areas capable of supporting both species, the most evident structural variable which can affect ecological processes and management activity is species mixture. The effect of species mix on ecological processes can be assessed by comparing

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maximum size/density and leaf-area relations for mixed-species and pure woodlands.

Maximum-size/density relations have been widely used to describe the structure of single-species communities undergoing self-thinning (Yoda et al., 1963; Hutchings and Budd, 1981; Long and Smith, 1984; Weller, 1987). While the generality of the self-thinning rule has been questioned (Weller, 1987), Zeide (1987) suggests that maximum-size/density relations based on mean tree diameter may represent a boundary condition of size and density for forest stands. Maximum-size/density relations have been applied to mixed-species communities to describe self-thinning of separate species and the entire community (Bazzaz and Harper, 1976; Malmberg and Smith, 1982).

Leaf-area index of single-species forests has been used as a measure of competition and as an index of productivity (Waring, 1983). Ceiling leaf-area index is related to site factors such as water balance (Grier and Running, 1977) and should be related to environmental variation within the woodland. Leaf area may better reflect site occupancy in mixed-species woodlands than other measures of density.

In this paper, we examine the effects of species mix on size/density relations and leaf area of southwestern pinyon-juniper woodlands. Maximum-size/density relations for dense, mixed and single-species woodlands are compared, estimates of leaf area index are developed, and the effects of species mix and soil type on ceiling leaf area and production of woodlands are examined. In conclusion, we relate species differences in rooting habit and water relations to differences in density, leaf area and productivity between mixed-species and pure woodlands.

METHODS

Study sites

Study sites were located in pinyon-juniper woodlands across the southwestern United States, including New Mexico, Arizona, and southern Colorado. This pinyon-juniper woodland type occupies approximately 12 million ha of semiarid foothills between regional montane forests and adjacent grasslands and shrublands at elevations between 1400 and 2300 m (Springfield, 1976).

Climate and geology are characterized by low precipitation, warm temperatures and poorly developed soils. Mean annual precipitation is between 30 and 50 cm, but can vary with latitude and elevation (Springfield, 1976). Mean annual temperature varies from 4.5 to 16°C, with the frost-free period ranging from 90 to 205 days (Sellers and Hill, 1974). Present vegetation has had a minimal effect on soil characteristics (West et al., 1978), and soil variability results from a diversity of geological substrates (Springfield, 1976). Aridisols, Entisols, and Mollisols, the most common soil orders, have developed from

sandstone, limestone, shale, basalt, or granite (Springfield, 1976; West et al., 1978).

Vegetation classified as pinyon–juniper is diverse, and individual woodlands may be mixtures of three major pine species and five juniper associates. This study is limited to the principal species within the study area, which are pinyon (*Pinus edulis* Engelm.), one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.) and Utah juniper (*J. osteosperma* (Torr.) Little).

Plot technique

A total of 117 variable-sized, fixed-area, temporary plots were established in undisturbed woodlands. Plots were situated to encompass approximately 30–40 live and dead pinyon and juniper trees greater than 25 mm in diameter at stump height (15 cm above the root collar; DSH). Plot size was limited to 0.10 ha in low-density stands. Pure and mixed-species woodlands were sampled across a wide range of site quality, stand density, and species composition.

Soil parent material was determined for each plot, and species, DSH, and total height of each tree were recorded. If a fork occurred below stump height, each stem was measured at stump height, and an equivalent diameter was determined as the square root of the sum of the squared individual stem diameters. Crown and bark characteristics of dead trees were used to estimate whether a tree had died within the last 10 years.

A disk or two cores were removed from each pinyon and juniper tree at stump height, and the heartwood–sapwood transition was marked on all disks and cores. One stem of mean size was sampled for all multiple-stemmed trees. An estimate of sapwood basal area at stump height (A_s) was obtained by measuring sapwood length on each core or along 4 radii of each disk. In the case of multiple-stemmed trees, A_s was determined from the total basal area of the equivalent diameter and the ratio of A_s to the basal area of the sampled stem.

Current and backdated individual tree volume estimates were determined from volume equations based on DSH, height, and for juniper only, the number of stems at stump height (Clendenen, 1979). Ten-year diameter increment was estimated by measuring the last 10 visible annual rings at stump height on each core or along 4 radii on each disk under magnification to $7\times$ with a Banister Incremental Measuring Machine (University Model, Fred C. Henson Co., Mission Viejo, CA). False and missing rings may occur in woodland species, especially juniper, and can result in a biased estimate of increment.

Separate disks or cores were taken at the root collar from the two most vigorous pinyons on each site for determination of total age and site index at base age 200 years (SI_{200} ; Smith and Schuler, 1987). If no vigorous pinyons were located within the plot, two pinyons in the adjacent area were sampled for determination of site index.

Projected tree leaf area (A_1) was sampled on a total of 19 pinyon and 21

juniper trees. Trees were selected to cover the range of tree sizes and physiographic situations represented in the sampled woodlands. Each tree was felled, and the live crown was divided into thirds. Branches from each section of the crown were severed from the main orthotropic stem and weighed to obtain total crown section weight. A representative branch from each crown section was then selected and weighed with the foliage intact. The foliage was then separated from the branch and weighed without any woody material. A subsample from the branch foliage was weighed and measured for projected foliage area using an optical planimeter (LiCor Model No. 3100). Crown section foliage areas were determined from the fresh weights and were summed to obtain total tree projected leaf area. Sapwood cross-sectional area (A_s) was measured on disks taken at stump height and a relation between A_1 and A_s was determined.

Data analysis

We selected a subset of dense woodlands where SDI (Reineke, 1933) was above 600 to examine woodland size/density relations. An SDI of 600 was taken as the lower limit to the 'zone of imminent competition-mortality' (Drew and Flewelling, 1978), since woodland mortality was absent or very low at SDI's below 600 but could be substantial at higher SDI's. We fit the model describing maximum size/density relations proposed by Long and Smith (1984) to data for 45 stands:

$$\ln D_q = \ln K + A \ln N \quad (1)$$

where: N is number of trees ha^{-1} ; D_q , quadratic mean DSH (cm); \ln , natural logarithm; and A and K , constants.

The coefficient A relating $\ln D_q$ to $\ln N$ was tested for significant difference from the expected value of -0.625 . If there was no significant difference, the intercept, $\ln K$, was estimated by fixing a boundary line with a slope of -0.625 along the woodlands of highest SDI's in a manner similar to that of Drew and Flewelling (1977).

To test for differences between pure stands of pinyon, pure stands of juniper, and mixed stands, A and $\ln K$ were estimated for woodlands where pinyon or juniper individually constituted at least 90% of total stand basal area and SDI was greater than 600. *Juniperus monosperma* and *J. osteosperma* were first examined separately and then reexamined collectively. Results were unchanged by combining the data for the two species, so further reference to juniper will designate both juniper species.

RESULTS

Woodlands sampled in this study represented a wide range in density, size and species mixture typical of the southwestern pinyon/juniper type. Stand

Density Index varied from 110 to 1150, number of trees (N) ranged from 200 to 3500 per ha, and quadratic mean DSH (D_q) ranged from 10 to 45 cm. Species mix varied from pure pinyon to pure juniper. The most common soils were derived from volcanic or sandstone parent material.

There was no significant difference between the regression coefficient A (-0.621 for mixed stands, -0.625 for pinyon and -0.631 for juniper) relating $\ln D_q$ to $\ln N$, and the expected value of -0.625 ($P < 0.01$). The intercept ($\ln K$) for mixed-species woodlands was 7.68, equivalent to an SDI of 1150 (Fig. 1). For pure stands of pinyon and pure stands of juniper, the intercept was 7.48, equivalent to an SDI of 870. The highest observed SDI's of pinyon and juniper in mixed-species woodlands, 699 and 844 respectively, did not exceed the observed maximum SDI of pure stands.

Calculated relationships between A_1 and A_s were linear for pinyon and juniper trees (Table 1; Fig. 2). Pinyons sampled for A_1 ranged from 2.5 to 29.3 cm DSH and from 1.5 to 8.5 m in height, junipers from 2.5 to 35.9 cm DSH and 1.5–6.5 m in height. The slope of the relation for pinyon ($0.246 \text{ m}^2 \text{ cm}^{-2}$) was three times greater than the slope of the relation for juniper ($0.084 \text{ m}^2 \text{ cm}^{-2}$).

Woodland and species leaf-area indexes (L) were estimated from the relationship between A_1 and A_s for the same stands used to evaluate size/density relations for pure and mixed-species woodlands. Maximum L was 1.0 for pure juniper woodlands, 3.5 for pure pinyon woodlands, and 3.6 for mixed-species woodlands. These estimates were apparently unaffected by differences in site

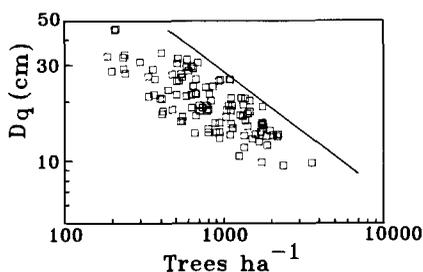


Fig. 1. The maximum-size/density relation for dense, mixed-species, southwestern pinyon/juniper woodlands with the boundary line located at SDI of 1150.

TABLE 1

Equations describing individual-tree projected leaf area (A_1 ; m^2) as a function of sapwood basal area (A_s ; cm^2) at stump height

Species	Equation	r^2	SE
Pinyon	$A_1 = -3.375 + 0.248 (A_s)$	0.86	10.13
Juniper	$A_1 = -0.712 + 0.084 (A_s)$	0.95	2.21

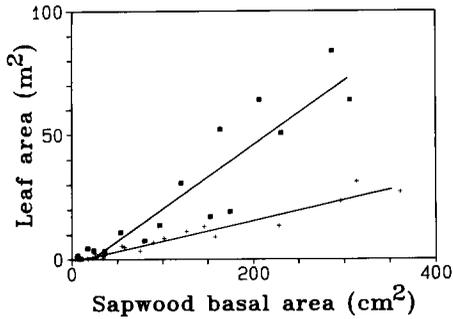


Fig. 2 (left). Individual tree leaf area (A_i ; m^2) as a function of individual tree sapwood area (A_s ; cm^2) at stump height for pinyon (squares) and juniper (crosses) of southwestern woodlands.

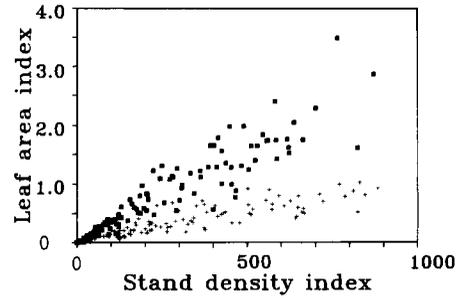


Fig. 3 (right). Leaf area index (L) of pinyon (squares) and juniper (crosses) in relation to species Stand Density Index (SDI) for southwestern woodlands.

TABLE 2

Equations describing Leaf Area Index (L) as a function of Stand Density Index (SDI) by species and soil parent material

Species	Soil parent material	Equation	r^2	L
Pinyon	All	$L=0.0033$ (SDI)	0.85	117
	Sandstone	$L=0.0031$ (SDI)	0.87	49
	Volcanic	$L=0.0038$ (SDI)	0.93	37
Juniper	All	$L=0.0010$ (SDI)	0.69	108
	Sandstone	$L=0.0009$ (SDI)	0.79	46
	Volcanic	$L=0.0015$ (SDI)	0.80	34

quality since there was no apparent linear ($r^2=0.03$) or nonlinear relationship between species mixture and site index.

Consideration of separate species within a woodland resulted in significant, linear correlations between species L and species SDI (Fig. 3). Coefficients of determination were 0.85 for pinyon and 0.76 for juniper. The L :SDI ratio of pinyon (0.0033) was roughly three times greater than the L :SDI ratio of juniper (0.0010). Residual variation in the relation between L and SDI was reduced when woodlands of different soil parent material were considered separately (Table 2). The L :SDI ratio was greater on volcanic soils than on sandstone soils for both species.

Annual volume increment (V_i) of each species was related to L (Table 3). Linear correlations between V_i and L were significant for both pinyon ($P<0.01$) and juniper ($P<0.01$), and the slope of the relation for juniper was about 25%

TABLE 3

Equations describing gross volume increment (V_i) ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$) as a function of leaf area index (L) by species

Species	Equation	r^2	SE ¹
Pinyon	$V_i = 0.0294 + 0.2490 (L)$	0.75	0.0135
Juniper	$V_i = 0.0273 + 0.3040 (L)$	0.78	0.0152

¹Standard error of coefficient

greater than for pinyon. Maximum observed pinyon V_i was $0.9 \text{ m}^3 \text{ha}^{-1} \text{year}^{-1}$, whereas maximum observed juniper V_i was $0.4 \text{ m}^3 \text{ha}^{-1} \text{year}^{-1}$.

DISCUSSION

Structure of dense pinyon/juniper woodlands appears to be restricted by a maximum-size/density relation. The slope of the relation for mixed-species woodlands is similar to the slope reported for mesic forest species (Reineke, 1933; Long, 1985). Interpretation of the slope of size/density relations is subject to caution since the slope may vary between species and sites when size is expressed as biomass or volume (Weller, 1987; Zeide, 1987). However, Zeide (1987) observed less variability in the slope when size is expressed as mean diameter, and suggested that this measure of size more accurately reflects canopy dynamics. Existence of a size/density relation in xeric woodlands, where canopy closure is uncommon, suggests that competition for below-ground resources is critical and that full occupancy may occur in the rooting zone.

Lower maximum SDI for pure than for mixed-species woodlands indicates that woodland structure is also related to species mixture. Woodland SDI is apparently limited by either the maximum woodland SDI of 1150 or the maximum species SDI of 870. For a single-species woodland SDI cannot exceed 870; higher SDI's can occur only in mixed-species woodlands. Maximum density has been related to species mixture in a number of forest types (Gingrich, 1967; Stout and Nyland, 1986). Increased maximum SDI for mixed-species woodlands may reflect differences between inter and intra-specific competition in the woodland environment.

The low ceiling woodland L reflects the xeric nature of the pinyon/juniper woodlands. Observed maximum woodland L (3.6) is about 15% of that reported for coastal forests of the Pacific Northwest and about 25% of that reported for interior coniferous forests (Gholz, 1982; Pearson et al., 1984). Decreased ceiling leaf area was related to lower site water-balance in a transect of community types from moist coastal forests to xeric juniper woodlands (Grier and Running, 1977). The slope of the relation between A_1 and A_s for pinyon ($0.248 \text{ m}^2 \text{cm}^{-1}$) is similar to that reported for *Pinus ponderosa* (Waring et

al., 1982), and the slope for juniper ($0.084 \text{ m}^2 \text{ cm}^{-1}$) is one of the lowest reported for a coniferous species. Low ratios of A_1 to A_s reflect adaptation to xeric climates (Whitehead et al., 1984).

Differences in species mix and soil type also appear to influence ceiling leaf area. A maximum ceiling leaf area of 3.0 for a mixed-species woodland is predicted at SDI of 1150 where pinyon SDI is 870 and juniper SDI is 280 (Table 2). A decrease in the proportion of pinyon for a woodland at maximum SDI results in decreased L since pinyon supports three times more L than juniper at the same SDI. At maximum woodland and pinyon SDI, predicted ceiling L is 3.6 on volcanic soils and 2.6 on sandstone soils. Most soils in semiarid regions have uniformly low nitrogen content (Buol et al., 1980), so fertility may not vary sufficiently to influence the relation between L and SDI. Higher soil water-holding capacity for volcanic soils than for sandstone soils may then be responsible for higher ceiling L .

The linear relations between V_i and L are consistent with the low ceiling L for woodlands. In mesic forests, the relationship between L and V_i is nonlinear, and production is independent of L 's in excess of 6.0 (Waring, 1983). Since ceiling L for mixed-species woodlands is considerably less than 6, a linear relation would be expected. Differences in the relationships between V_i and L for pinyon and juniper must be interpreted with caution because of the possibility of missing or false annual rings in both woodland species. However, the higher slope for juniper is consistent with observations that juniper has a greater seasonal leaf carbon gain per unit of photosynthetic tissue than pinyon over the range of possible leaf water potentials (Barnes and Cunningham, 1987).

We suggest that differences in maximum-size/density relations and leaf-area development between pure and mixed-species woodlands may be a result of species niche specialization. In xeric environments, species variation in root foraging strategies may result in use of separate water resources (Harper, 1977). Depth of potential rooting zones of pinyon and juniper are substantially different. Pinyon roots may reach soil depths of 6 m, whereas juniper roots have been found farther below the soil surface (Foxy and Tierney, 1987). As a result, juniper may be able to avoid water stress by accessing a separate and larger soil-moisture reservoir than pinyon. Hence, competition between pinyon and juniper for the available soil water may be less than the intraspecific competition among individuals of the same species. Also, differences in drought tolerances between the two species have been noted. Photosynthetic activity in pinyon decreases to zero at significantly higher leaf water potentials than in juniper (Barnes and Cunningham, 1987), which allows juniper to actively utilize the site while pinyon photosynthesis is restricted. We believe that these differences in rooting habit and response to drought are responsible for higher size/density relations, greater woodland leaf area, and consequently, higher productivity in mixed-species than in pure woodlands.

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