Forest Ecology and Management, 50 (1992) 331-350
Elsevier Science Publishers B.V., Amsterdam

Biomass distribution and productivity of *Pinus edulis-Juniperus monosperma* woodlands of north-central Arizona

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(Accepted 18 April 1991)

ABSTRACT

Grier, C.C., Elliott, K.J. and McCullough, D.G., 1992. Biomass distribution and productivity of *Pinus edulis-Juniperus monosperma* woodlands of north-central Arizona. *For. Ecol. Manage., 50:* 331-350.

Above-ground biomass distribution, leaf area, above-ground net primary productivity and foliage characteristics were determined for 90- and 350-year-old *Pinus edulis-Juniperus monosperma ecosystems* on the Colorado Plateau of northern Arizona. These ecosystems have low biomass, leaf area and primary productivity compared with forests in wetter environments. Biomass of the 350-year-old pinyon-juniper stand examined in this study was 54.1 mg ha^{-1}; that of the 90-year-old stand was 23.7 mg ha^{-1}. Above-ground net primary production averaged 2.12 mg ha^{-1} year^{-1} for the young and 2.88 mg ha^{-1} year^{-1} for the mature stand; tree production was about 80% of these values for both stands. Projected ecosystem leaf area (LAI) of the stands was 1.72 m^2 m^{-2} and 1.85 m^2 m^{-2}, respectively. Production efficiency (dry matter production per unit leaf area) was 0.129 kg m^{-2} year^{-1} for the young, and 0.160 kg m^{-2} year^{-1} for the mature stand. Production efficiency of the study sites was below the 0.188 kg m^{-2} year^{-1} reported for xeric, pure juniper stands in the northern Great Basin. Biomass of pinyon-juniper ecosystems of northern Arizona is generally below the 60–121 mg ha^{-1} reported for pinyon-juniper stands of the western Great Basin in Nevada. A climatic gradient with summer precipitation decreasing between southeast Arizona and northwest Nevada occurs in the pinyon-juniper region. Great Basin pinyon-juniper ecosystems lie at the dry-summer end of this gradient while pinyon-juniper ecosystems of the Colorado Plateau lie at about the middle of this gradient. in spite of wetter summers, pinyon-juniper ecosystems of northern Arizona are less productive than those of the Great Basin.

INTRODUCTION

Low woodlands dominated by various pinyon pine and/or juniper species

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are a major feature of the landscape in a large part of the western United States. Approximately 60x 1 0^6 acres in the western states support pinyon-juniper woodland; about half of this total is found in Arizona and New Mexico.

Species composition of this vegetation type varies regionally. In the Great Basin region of Nevada and western Utah, *Pinus monophylla* Torr. (singleleaf pinyon) is the dominant pinyon, *Juniperus osteosperma* (Torr.) Little (Utah juniper) is the dominant juniper, and *Artemesia tridentata* Nutt. (big sagebrush) and several grasses are common associates. In contrast, the dominant pinyon on the Colorado Plateau and along the Mogollon Rim in Arizona and New Mexico is *Pinus edulis* Engelm (pinyon pine), *J. osteosperma*, *J. monosperma* Sarg. (one-seed juniper) and *J. deppeana* Steud. (alligator juniper) are the principal junipers while sagebrush and/or several grass species are common associates. Finally, in the Madrean region (Brown, 1982) centered in the Sierra Madre Mountains of northern Mexico, southwestern New Mexico, and southeastern Arizona, *Pinus cembroides* (Mexican pinyon) and *J. deppeana* are the dominant species.

Climate is an important factor regulating species distribution, phenology, morphology, physiology and productivity of pinyon-juniper ecosystems. Community and ecosystem differences develop along a distinct regional climatic gradient through the southwest. One end of the gradient is centered in the west Texas, southern New Mexico, southeast Arizona region where a true monsoonal climate prevails (National Oceanic and Atmospheric Administration (NOAA), 1974). Here, 50–70% of annual precipitation falls during summer. The other end of the gradient lies in the western Great Basin where virtually no rain falls in summer.

In spite of the area1 extent of pinyon-juniper woodland in the western United States, the literature dealing with ecosystem processes in this cover type is sparse. Earlier research has largely been focused on conversion of pinyon-juniper to grassland (Arnold et al., 1964; Aro, 197 1; Gifford, 1973; Clary et al., 1974; Clary and Jameson, 198 1; Rippel et al., 1983), succession after conversion (Tausch and Tueller, 1977; Kruse et al., 1979; Everett and Sharrow, 1983; Everett and Ward, 1984), pinyon-juniper invasion of grazing lands (Johnsen, 1962; Blackburn and Tueller, 1970; Springfield, 1976; West et al., 1979), fire effects in pinyon-juniper stands (Dwyer and Pieper, 1967; Barney and Frischknect, 1974; McCluskey, 1978; Wright et al., 1979; Gifford, 1982), or estimating amounts of wood present on pinyon-juniper sites (Storey, 1969; Meeuwig and Cooper, 198 1; Miller et al., 198 1).

There has been relatively little research on such ecosystem processes in pinyon-juniper as productivity or nutrient cycling; processes which indicate biological and physical site factors that regulate ecosystem function. Equations have been developed using various tree analysis methods to predict tree volume or biomass and canopy weight from tree characteristics such as diameter, height, and crown diameter (Meeuwig et al., 1978; Budy et al., 1979; Meeuwig and Budy, 1979; Ambrosia et al., 1983; Chojnacky, 1986). Smith and Schuler (1987) and Schuler and Smith (1988) conducted an extensive study of site quality, stand density and leaf area in pinyon-juniper stands of Colorado, New Mexico and Arizona. However, most of this work has been conducted in the Great Basin region of Utah and Nevada in stands composed of singleleaf pinyon (*Pinus monophylla* Torr. and Frem.) and Utah juniper (*J. osteosperma* (Torr) Little).

The work reported in this paper is part of a larger study aimed at determining those factors of the physical and biological environment that regulate productivity in pinyon-juniper woodlands of the western US in general and the Colorado Plateau in particular. The specific objectives of the research described here were to: (1) develop regression equations for estimating component biomass and canopy surface area; (2) describe biomass structure and distribution of these stands; (3) estimate net primary production (NPP) for ecosystems dominated by *Pinus edulis* and *J. monosperma* growing on the Coconino Plateau of northern Arizona.

MATERIALS AND METHODS

Research area

The research site is located in an extensive, mixed pinyon (*Pinus edulis* Engelm.)-one-seed juniper *(J. monosperma* Sarg.) woodland on the Coconino Plateau in north-central Arizona. The Coconino Plateau is a part of the Colorado Plateau geological province. The study site is roughly 12 km southeast of Winona, AZ near the K-V stock tank (Fig. 1) at longitude 111° 22'W and latitude 35° 8'N. The area slopes 5% to the north and lies at an elevation of about 2000 m.

A number of wildfires in the area over the past 400 years have created a coarse-grained (30-90 ha patches) age mosaic. The oldest stands in the study area have an average tree age, based on increment cores, of about 350 years while stands averaging 100 years old are also common in the area. Stands are established slowly in this harsh environment and recruitment of young trees occurs even in the oldest stands. For this reason, stand ages given in this report are intended only as an index of the time elapsed since the last major disturbance. Aside from cattle and sheep grazing, and small patches where fuelwood has been cut, the area has been relatively free of human disturbance.

The research site lies at about the mid-point of the summer precipitation climatic gradient described earlier. The climate is harsh and dry, reflecting its location on a high interior plateau. Annual precipitation ranges between 250 and 410 mm with two pronounced peaks during the year: winter, when Pacific frontal systems move through the area and deposit precipitation mainly as snow, and summer (July and August) when warm, wet air from the Gulf

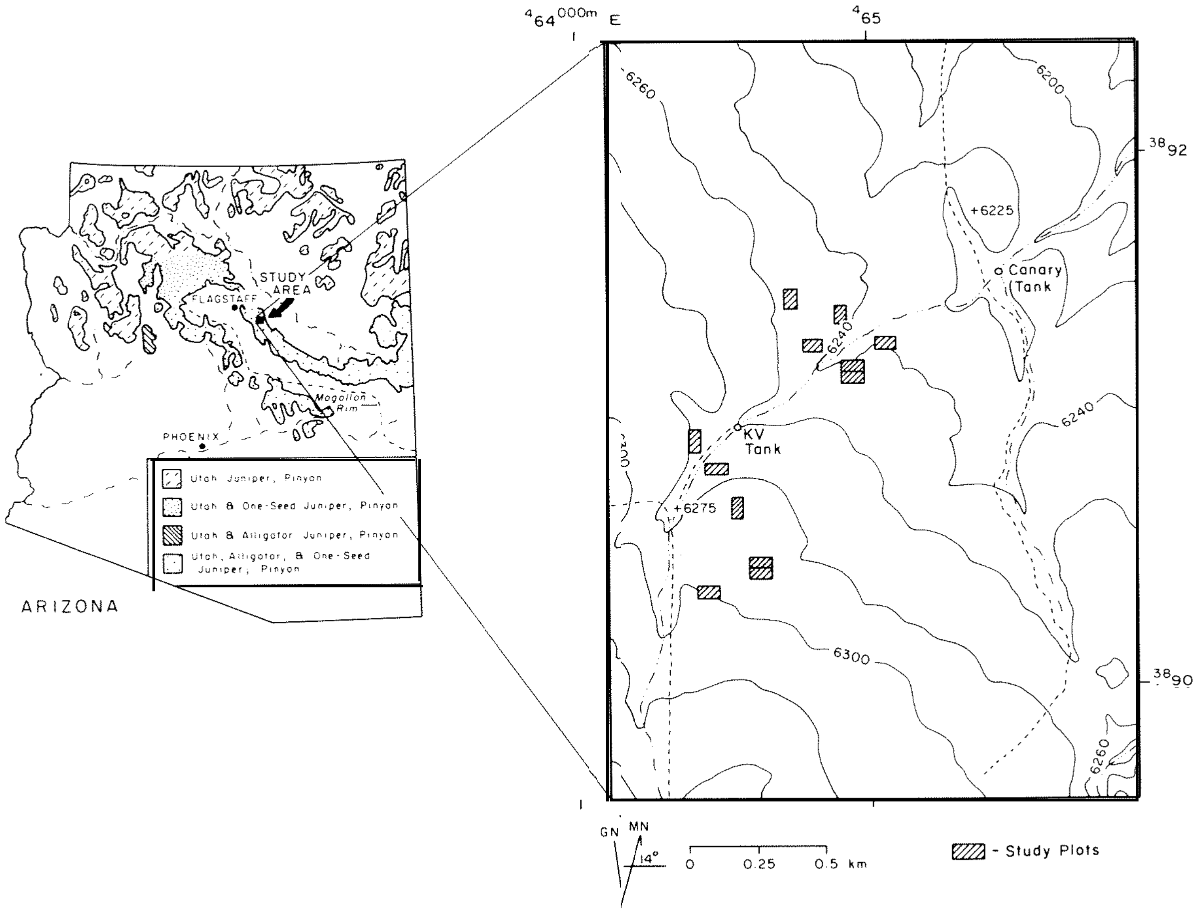

Fig. 1. Plot layout and location of K-V Tank study site for pinyon–juniper study. Plots located south and west of K-V Tank (a mapped stock water tank) in the large-scale diagram are the mature woodand (about 350 years old). Those north and east of K-V Tank are located in the young (about 100 years old) woodland).

of Mexico moves northwest into this region causing frequent thunderstorm activity with brief, heavy rainfall. Precipitation amounts falling in winter and summer are about equal. During spring, the climate is windy and dry with warm days and low relative humidity. These conditions create high evaporative demand.

Mean annual temperature is about 11 °C with mean January and July temperatures of about 2 °C and 22 °C, respectively. The area also has large diurnal temperature changes. On a given winter day, daytime temperatures can reach 10–12 °C while night-time temperatures can go as low as −10° C. The frost-free growing season ranges between 125 and 190 days.

Soils of the study site are mapped by the Soil Conservation Service (Miller and James, 1972; Hendricks, 1985) as the Winona–Boysag association and are classed as mixed Lithic Ustollic Calciorthids and Lithic Ustollic Haplargids. In the study area, these soils are 20-40 cm deep, rocky, and generally have free carbonates in the B-horizon. The soils are formed from the Kaibab Limestone overlaid by l-2 cm of volcanic cinders dating from the most recent eruption in the Sunset Crater volcanic field, about 10 km to the northwest. Soils are of silt loam to clay loam texture and have notable shrinkage on drying. Except for surface layers beneath trees, soils are mildly alkaline (pH 7.3-8.0).

Vegetation on the study area is relatively simple. An overstory of *Pinus edulis* and *J. monosperma* dominates the site. Combined percent ground cover of these two species ranges from 10% to approximately 25% depending on age, surface rock and past disturbance. In openings among the trees (interspaces), the dominant vegetation is blue gramma (*Bouteloua gracilis* (H.B.K.) Lag.) with rabbitbrush (*Chrysothamnus viscidiflorus* (Hook) Nutt.), locoweed (*Astragalus* spp.) and snakeweed (*Guterrezia sarothrae* (Pursh.) Britt) being locally abundant.

Study plots

Study stands were selected from young (roughly 100 years old) and old (over 250 years old) pinyon-juniper stands on the Coconino Plateau based on average percent cover as determined from air photos. Average species composition was determined from on-the-ground transects conducted in stands selected as candidates from air photos.

Six 25 m × 50 m plots were established in April of 1986 in both the young and mature pinyon-juniper stands. Plot corners were permanently marked and the diameter of all trees was measured at the soil surface, the root collar diameter (RCD) . Diameter and species were recorded. All trees were tagged and percent cover of trees and understory vegetation by species, together with tree age, height and several other stand characteristics, were determined using transects along the south plot boundary of each of the six plots in each of the

TABLE 1

Composition and structure of pinyon-juniper stands at the K-V Tank research area near Winona, AZ

Composition and structure	Young stand		Mature stand	
	Pinyon	Juniper	Pinyon	Juniper
Average dbh (cm)	16.2	22.1	25.0	36.6
Average height (m)	4.6	3.4	4.9	5.4
Basal area (m^2 ha^{-1})	5.5	5.3	11.2	18.4
Tree density (stems ha^{-1})	227	117	185	145
Average tree canopy cover (%)	17.8	10.8	20.0	20.1
Average cover *Bouteloua gracilis*		26.2		22.4

two stands. Tree age was determined by counting growth rings on stumps of trees cut for destructive analysis of biomass distributions. Results of tree measurements and transects are summarized in Table 1.

Topography, soils, aspect and geology were virtually identical in the two plot areas.

Biomass and organic matter distribution

Above-ground tree biomass in the two stands was calculated from measured tree diameter and regressions of tree component weight on root collar stem diameter for the two stand age classes and tree species. The regression equations were developed from destructive analysis of 15 *P. edulis* and 2 1 *J. monosperma* trees from areas near but outside the research plots. Trees representing the full diameter range of both species (5-45 cm) were sampled by 2.5 cm diameter classes. Trees were randomly selected from each diameter class for destructive analysis.

Destructive analysis was conducted using minor modifications of procedures outlined by Grier and Logan (1977) and Grier and Milne (198 1). Briefly, the procedure was as follows: tree height and root collar diameter were measured, prior to felling, on each tree selected for analysis. Root collar diameter (RCD) was used as the independent variable in regressions because *J. monosperma* often has several stems originating from a common root system. Where multiple stems originated below the soil, an equivalent diameter (Meeuwig and Budy, 1979) was calculated using the equation:

$$\text{equivalent diameter} = \sqrt{\sum_{i=1}^{n} \mathrm{RCDi}^2}$$

where RCDi is the root collar diameter of each of the individual multiple stems. This calculated equivalent diameter was then used in all further calculations for that tree.

After trees were felled, all branches were removed from the main stem. Branches were segregated into three fuel size classes of < 2.5 cm, 2.5-7.6 cm and > 7.6 cm. Dead branches and dead portions of living branches were sorted into a separate dead branch category. Foliage was clipped and separated from living branches. Pinyon foliage was separated into current and older foliage. Juniper foliage was not separated because current foliage could not be reliably distinguished from older foliage.

Subsamples of live branch, dead branch, stemwood and bark, and current and older foliage were dried at 70°C in the laboratory to determine field moisture content. Fresh weight of all tree components was determined in the field. Fresh weights were converted to dry weights using moisture content determined in the laboratory.

Net primary production

Above-ground net primary production (ANPP) for young and mature stands was computed using the mass balance equation ANPP $= \Delta B + L$, where ΔB is biomass increment (annual biomass accumulation minus branch and stem mortality) and L is litterfall. Basic procedures are outlined by Grier et al. (198 1). Herbivory was ignored in this study.

Average annual biomass increment was estimated for the past 10 years using measured diameter increment and biomass regressions. To provide average annual increment of stem and live branch biomass, the biomass equations were applied to current RCD and to RCD calculated for the trees 10 years ago by subtracting diameter increment over the past 10 years from current diameter. The difference between present biomass and that calculated for plots 10 years ago was ΔB. Because of the constant relation between stem diameter and wood, bark and branch biomass, this was an unbiased way to calculate ΔB. Above-ground detritus production was determined between spring 1986 and spring 1989 by measuring litterfall. Fine litterfall was collected monthly in four randomly located 0.25 m^2 litter traps per plot for a total of 24 traps in the mature stand and 24 traps in the young stand. Litterfall was sorted into foliage and non-foliage fractions, dried at 70° C and weighed.

Foliage production of juniper was estimated to be 25% of the total foliage biomass based on comparisons of annual litterfall and canopy biomass. Pinyon foliage production was estimated using regressions of new foliage biomass on stem diameter.

Interspace vegetation

Above-ground net primary productivity of interspace vegetation was assessed by sequential harvest of small plots every 3 weeks through the 1986 growing season. Production losses to herbivore grazing were not estimated. Cattle had been excluded from the area for the preceding 4 years; however, pronghorn antelope and elk commonly graze in the area. Because *Bouteloua gracilis* comprised 90% and 94% of the total interspace species cover for the mature and young pinyon-juniper stands, respectively, above-ground interspace vegetation biomass estimates for other species are included with *B. gracilis* in the tables. Every 2 weeks from 1 May through 30 September, two 1.0 m^2 subplots randomly located in interspace areas were clipped to ground level in each plot. The clipped samples were separated in the laboratory into three distinct grass foliage age classes: current years dead, older dead, and living tissue. Standing dead material produced the year of sampling (1986) was separated from older dead material. The difference between the two categories was visually obvious: older material was darker, fibrous, and partially decomposed, whereas the current year's standing dead was light colored, erect, and quite commonly green at the base. The minor amounts of other species present were combined in a fourth category. Samples were dried at 70°C to constant weight.

Specific leaf area — leaf urea index

Foliage samples were taken from the middle third of the north, south, east and west side of the canopy on four average-sized pinyon and juniper trees in both young and mature stands to determine specific leaf area. Specific leaf are (SLA) is defined as the projected (shadow) leaf area (cm^2) per unit of foliage weight (g). Both current and older foliage from pinyon were measured. Juniper foliage was pooled into a single age class as new and old foliage could not be reliably distinguished. Projected leaf area was measured using an optical planimeter based on a video camera coupled with a computer having an image analysis program. Samples of foliage from *Pinus monophylla* and *Pinus cembroides* were also taken at a number of locations in Arizona, Utah and Nevada to provide comparative data of specific leaf area of pinyons. These samples were taken from a branch on the east side of the middle third of the crown.

Leaf area index (LAI) of stands was calculated by multiplying leaf biomass of pinyon and juniper in the young and old stand by the appropriate average specific leaf area.

Data analysis

Logarithmic regressions of current and older foliage, new twigs, living and dead branches, stemwood and stem bark, on average stem diameter at root collar were calculated. Regressions were corrected for logarithmic bias according to procedures described by Baskerville (1972).

To test for the effect of stand age on allometric relations, data for trees of each species from young and older stands were pooled. Age was entered in regressions as a dummy variable (0= young, 1 =mature). The regression model:

$$\log Y = a + b \log X1 + c\,X2$$

where Xl is RCD (cm) and X2 is age, was used. The contribution of age to the fit of the regression was interpreted using the F statistic ($P=0.05$) as a test of significance. Except for foliage and twigs, there were no significant differences in tree component biomass between trees from young and mature stands. Tree-age-specific regressions were calculated for new foliage and twigs of pinyon and total foliage of juniper. For all other tree biomass components, data from young and mature stands were pooled by species.

RESULTS

Tree biomass and leaf area characteristics

Logarithmic regression equations calculated from destructive analysis of trees sampled in this study are given in Table 2. In general, there are good correlations between root collar diameter and the biomass of the various components examined during tree analysis. With only a few exceptions, r^2 was greater than 0.79. The exceptions were associated either with foliage or twigs. Mean-square residuals ($S^2y{\cdot}x$) were generally small except those for dead branches on juniper and old twigs, new foliage and new twigs of mature pinyon.

While total foliage of pinyon was not significantly related to stand age, new foliage biomass was significantly different between young and mature pinyon trees. For example, a 20-cm diameter, 80-year-old pinyon in the young stand had about 11 kg of new foliage compared with about 4 kg for a 20-cm diameter, 190-year-old tree in the mature stand. Similarly, total foliage biomass of a 20-cm diameter juniper tree averaged about 11 kg in the young and 9 kg in the mature stand.

Specific leaf area of pinyon varied with foliage age, tree age and canopy position (Table 3). The largest differences were associated with the aspect on the tree. In general, highest specific leaf areas were on the canopy’s north exposure. High values were also associated with new foliage; specific leaf area decreased with foliage age to an average of about 80% of new foliage values.

Specific leaf area of juniper was remarkably constant (Table 3). There was no significant change with either tree age or canopy aspect. There may be

TABLE 2

Regression coefficients, sample size and correlation coefficients for young and mature stands of pinyon and juniper from the K-V Tank study area near Winona, AZ. All regressions are in the form log $Y = a + b \log X$, where X is root collar diameter in cm and Y is component weight in kg and log is the logarithm to the base 10. Equations have been adjusted for logarithmic bias (Baskerville, 1972)

Species Tree components	Regression characteristics'				
	a	b	r^2	$S^2y{\cdot}x$	n
Pinyon					
Pinyon young and mature stand combined					
Stemwood + bark	-2.588	2.955	0.95	0.0316	15
Living branches					
< 2.5 cm	-1.613	2.088	0.95	0.0355	15
2.5–7.6 cm	-2.791	3.007	0.90	0.0522	13
> 7.6 cm	-3.649	3.520	0.85	0.0651	10
Dead branches	-5.400	4.470	0.80	0.0477	14
Total foliage	-0.946	1.565	0.94	0.0392	15
Old foliage	-1.485	1.706	0.74	0.0699	15
Old twigs	-1.873	1.675	0.57	0.1454	15
Total	-1.468	2.582	0.95	0.0087	15
Pinyon young stand					
New foliage	-1.593	2.030	0.90	0.0190	5
New twigs	-2.161	2.149	0.69	0.0904	5
Pinyon mature stand					
New foliage	-1.250	1.417	0.61	0.1229	10
New twigs	-1.674	1.326	0.53	0.1495	10
Juniper					
Juniper: young and mature stands combined					
Stemwood + bark	-2.297	2.431	0.92	0.0436	20
Living branches					
< 2.5 cm	-1.476	1.787	0.86	0.0438	21
2.5-7.6 cm	-1.356	1.782	0.86	0.0349	20
> 7.6 cm	-1.002	1.535	0.62	0.0250	8
Dead branches	-3.543	2.774	0.79	0.1378	20
Foliage twigs	-1.737	1.382	0.79	0.0461	21
Total	-1.157	2.086	0.94	0.0232	21
Juniper young stand					
Total foliage	-1.358	1.841	0.95	0.0156	11
Juniper mature stand					
Total foliage	-0.862	1.399	0.84	0.0347	10

TABLE 3

Specific projected leaf areas for pinyon (*Pinus* ***edulis)*** by needle age and crown position, and juniper ***(Juniperus monosperma)*** by crown position for both the young and mature stands. Values are centimeters squared of projected foliage surface area per gram of foliage dry weight. Samples taken in mid-October 1987 at K-V Tank study site near Winona, AZ

Species	Stand age	Needle age	Crown aspect				
			South	North	West	East	Average
Pinyon	Mature	New	39.4 aw[1]	53.0 bv	35.6 ax	38.8 ax	41.7
		1 -year-old	41.7 ax	43.6 ax	40.0 ax	37.0 ax	40.6
		Older	32.2 ay	38.3 ax	33.4 ax	27.8 ay	32.9
Pinyon	Young	New			32.8 x	–	
Young		1 -year-old	37.5 ax	39.5 ax	44.9 by	47.1 bz	42.4
		Older	31.5 ay	35.7 bx	37.7 bx	37.6 bx	35.6
Juniper	Mature	–	21.0 aw	22.0 aw	19.3 aw	19.4 aw	20.4
Juniper	Young	–	19.2 aw	20.4 abw	22.1 bw	19.6 abw	20.3

‘Values in rows and columns followed by different letters are significantly different ($P < 0.05$) according to SNK multiple-range test (Dixon, 1983); a,b denote row values, w,x,y and z denote column values.

changes with foliage age, but this is difficult to reliably determine in species with an indeterminate growth habit.

Stand biomass distribution

Tree biomass of the mature stand was 2.3 times that of the young stand (Table 4). The mature stand was 3.8 times as old as the young stand so biomass accumulation is clearly not a linear function of age in these ecosystems. Total interspace vegetation biomass was not significantly different between the two different stands.

Foliage was a relatively large proportion of total above-ground tree biomass in these ecosystems. In the young stand, foliage was 20.2% of total living tree biomass compared with 11.5% in the mature stand. Leaf biomass of the mature stand was 1.3 times (significant at $P = 0.05$) that of the young stand while leaf areas were not appreciably different in spite of the age differences. The LAI of the mature stand was not significantly different from that of the young stand ($P = 0.05$), in spite of greater leaf biomass (Table 4).

Branch biomass of both species was large. In the young stand, living branch biomass was 10.7 mg ha-’ or 65% of the total woody biomass. In the mature stand, the proportion of branches was nearly the same amounting to 28.8 mg ha^{-1} or 63% of woody biomass.

The proportion of attached detritus increased with stand age. Dead branches were 4.2% of total tree biomass in the young stand compared with 6.7% in the old stand. Much of the increase was associated with juniper.

TABLE 4

Biomass distribution and leaf area in young and mature pinyon (*Pinus edulis*)–juniper (*Juniperus monosperma*) ecosystems on the K-V Tank study plots near Winona, AZ. Biomass values are in mg ha-’ and are averages for six 25 x 50 m plots in each stand. Between-plot coefficients of variation (CV) were less than 20% except for dead branches where CV= 14% for the young, and 34% for the mature stand

	Young stand			Mature stand		
	Pinyon	Juniper	Total	Pinyon	Juniper	Total
Tree stratum						
Canopy						
Current foliage (pinyon only)	0.70		0.70	0.90		0.90
Older foliage (total for juniper)	1.97	1.72	3.69	1.52	3.28	4.80
Current twigs	0.20		0.20	0.52		0.52
Older foliage-bearing twigs	1.37	0.16	1.53	0.50	0.41	0.91
Total foliage	2.67	1.72	4.39	2.42	3.28	5.70
Total canopy	4.24	1.88	6.12	3.44	3.69	7.13
Living Branches incl. Bark						
< 2.5 cm diameter	2.24	1.09	3.33	3.58	3.49	7.07
2.5-7.6 cm diameter	2.49	1.42	3.91	5.37	8.01	13.38
< 7.6 cm diameter	1.73	1.74	3.47	4.37	3.98	8.35
Total branch	6.46	4.25	IO.71	13.32	15.48	28.80
Dead branches	0.69	0.27	0.96	2.15	1.39	3.54
Stem, wood plus bark	3.38	1.49	4.87	7.17	6.48	13.65
Total tree biomass	14.77	7.89	22.66	26.08	27.04	53.12
Interspace vegetation stratum						
Bouteloua gracilis and assoc.						
Living			0.62			0.52
Standing dead			0.41			0.41
Total			1.03			0.93
Total above-ground biomass			23.69			54.05
Leqfarea index ($m^2\ m^{-2}$)						
Pinyon			1 .oo			0.87
Juniper			0.35			0.67
Total tree			1.35			1.54
Interspace vegetation			0.37			0.31
Ecosystem total			1.72			1.85

In both stands, standing dead material was about 40% of total interspace vegetation biomass during the growing season.

Above-ground net primary productivity (ANPP)

The largest proportion of ANPP in both stands was foliage (Table 5). Tree foliage production alone was 54.2% of ANPP in the young and 59.7% in the

TABLE 5

Above-ground net primary productivity (Mg ha-’ year-’) in young and mature pinyon-juniper stands at the K-V Tank study site near Winona, AZ. Values given are averages for six plots in each stand. Between-plot coefficients of variation are not given but were < 20% except for attached dead material which were 15% and 35% for the young and mature stands respectively

	Young stand			Mature stand		
	Pinyon	Juniper	Total	Pinyon	Juniper	Total
Tree stratum						
Biomass increment						
Living wood	0.20	0.05	0.25	0.32	0.11	0.43
Attached dead	0.02	T	0.02	0.07	0.01	0.08
Bark	0.04	0.01	0.05	0.06	0.02	0.08
Foliage Production’	0.70	0.45	1.15	0.90	0.82	1.72
Total			1.47			2.31
Litterfall			0.03			0.05
Interspace vegetation stratum						
Grass and forbs			0.62			0.52
Above-ground total			2.12			2.88

‘Calculated from regressions of new foliage on stem diameter. Regression for pinyon used for both pinyon and juniper.

mature stand. If production by interspace vegetation, largely *Bouteloua gracilis* foliage, is included, then total ecosystem foliage production was 83.5% and 77.8% of ANPP by the young and mature stands, respectively. Production of woody material is clearly a small percentage of total ANPP in these stands.

Net primary productivity appeared to increase with age in these ecosystems. Above-ground net primary productivity by the mature stand was about 1.3 times that of the young stand. This agrees closely with the difference in leaf biomass, but not with differences in leaf area. The difference in ANPP between the two stands was due largely to the difference in foliage production. The mature stand had ANPP 0.75 mg ha-’ year-’ greater than that of the young stand. Of this amount, 0.57 mg ha-’ year-’ or 76% was foliage production (Table 5).

Interspace dry matter production was 28% of total ANPP in the young, and 18% in the mature stand. These amounts were almost entirely production of *B. gracilis* foliage and inflorescences.

DISCUSSION

Biomass

Tree biomass on the K-V Tank study plots (Table 4) was near the low end of the range reported for pinyon-juniper stands in other parts of the general cover type. Reported above-ground biomass for Great Basin pinyon-juniper ecosystems ranges from 60 to 12 1 mg ha-^{1} for stands in which the oldest trees were generally about 320 years old and 260 years old, respectively (Meeuwig, 1979). These stands were predominantly *Pinus monophylla,* but with a significant proportion of *J. osteosperma* and were growing in the Sweetwater, Monitor and Paradise mountains of Nevada. Leaf biomass of these stands ranged from 9 to 15 mg ha^{-1}, or about 12% of total above-ground tree biomass. These values are about 1 S-2 times tree foliage biomass observed during this study. In the study by Meeuwig, leaf biomass did not correlate well with either woody biomass or basal area, but did correlate ($r^2=0.74$) with percent canopy cover.

In contrast with single-leaf pinyon-dominated Great Basin stands, Gholz (1980) reported total above-ground biomass of a juniper (*J. occidentalis*) big sagebrush (*Artemesia tridentata*) ecosystem in the northwestern Great Basin in Oregon to be 2 1.2 mg ha-^{1}. Leaf biomass of this community was 4.3 mg ha-^{1}, about 20% of total aboveground biomass, or about 60% of tree leaf biomass observed in this study.

Leaf area

The young and mature stands examined during the present study had average projected tree LAI of 1.35 and 1.54, respectively (Table 4). Leaf Area Index (LAI) of the young stand was 88% that of the mature stand. Interspace vegetation in these communities, here largely *Bouteloua gracilis* (blue gramma), added 0.37 and 0.31 $m^2 m^{-2}$ of leaf area to the young and mature stands for ecosystem LAIs of 1.72 and 1.85, respectively. These nearly identical values suggest that leaf area of the young and mature ecosystems are both at, or near, steady state. Considering the age difference for trees in the two stands, leaf area differences are small.

In an extensive study of pinyon-juniper ecosystems on the Colorado Plateau in Arizona, New Mexico, and southwest Colorado, Schuler and Smith (1988) report LAIs for pinyon-dominated stands ranging from near-zero to 2.5 with two exceptional stands having values of 3.0 and 3.5. Leaf Area Index (LAI) of juniper-dominated stands in their study ranged to about 1 .O. Stand leaf area was closely correlated with stand density. Leaf areas and stand densities were relatively uniformly distributed across the range of values given except for the two unusually dense stands previously mentioned.

Leaf areas of the K-V Tank study sites are at about the midpoint of the range reported by Schuler and Smith (1988) for pinyon-juniper ecosystems of the Colorado Plateau. In contrast, LAI for Great Basin *Pinus monophylla-J. osteosperma* stands appears to be greater than for those of the Colorado Plateau. Leaf area index for Great Basin pinyon-juniper was calculated from leaf biomass data reported by Meeuwig (1979) and specific leaf areas for *Pinus monophylla* (32.0 $cm^2 g^{-1}$) and *J. osteosperma* (18.0 $cm^2 g^{-1}$) determined as part of this study. The range of LAI for Great Basin stands was 2..5-4.0; roughly 1.5–2 times values observed on the Colorado Plateau.

Productivity

Net primary productivity

ANPP of the pinyon-juniper sites of this study is low relative to most other forest and woodland sites in North America. Values for the K-V Tank stands were 2.2 mg ha-’ year-’ for the young, and 3.0 mg ha-’ year-’ for the older stand. These are well below the average for North American forests. In a review of the literature of forest and woodland biomass and productivity for North America, Grier et al. (1989) summarize published data on forest productivity. They list an ANPP range from 1.2 mg ha^{-1} $year^{-1}$ for a mixed oak ‘encinal’ woodland in south-eastern Arizona to 37.7 mg ha-’ year-’ for a young *Tsuga heterophylla* stand on a well-watered, fertile soil on the Oregon coast. The average for ANPP was 11.4 mg ha-’ $year^{-1}$ and was calculated as a simple average of reported values, not as an area-weighted mean. Other low-productivity forests are located either in cold or dry or cold-dry regions. For example, in boreal forests, reported ANPP ranged from 0.7 to 7.7 mg ha^{-1} $year^{-1}$ for *Pinus banksiana* in Minnesota and 2.1 mg ha^{-1} year-’ for *Picea mariana* ecosystems in Alaska (Ohman and Grigal, 1979; DeAngelis et al., 198 1). Similarly, in the southwestern United States, ANPP for semi-arid woodlands ranged from 1.5 mg ha^{-1} $year^{-1}$ for an open, mixed oak (largely *Quercus oblongifolia* and Q. *emoryi*) woodland on the lower slopes of the Santa Catalina Mountains of southeastern Arizona to 5.7 mg ha^{-1} year-’ for *Pinus ponderosa* at higher altitudes in the same mountains (Whittaker and Niering, 1975).

In the same study, Whittaker and Niering report ANPP of 1.9 mg ha-’ $year^{-1}$ for a pygmy conifer-oak scrub ecosystem. This community was composed primarily of the conifers *Pinus cembroides* and *J. deppeana,* and sclerophyll broadleaf shrubs such as *Quercus hypoleucoides*, *Garrya wrighti*, *Arctostaphylos pringeli*, and *A. pungens*. This community is clearly not analogous to pinyon-juniper communities of the K-V Tank study site since it contains many species common to interior chaparral associations (Pase and Brown, 1982). Altitude of the Santa Catalina site was about 2050 m; productivity was about the same as the young stand of the K-V Tank site. Ages were also comparable: in the young K-V Tank stand junipers averaged about 90 years old; dominant plants on the Santa Catalina study site averaged about 117 years. In spite of a wide geographic, physiographic and climatic pattern range, productivity of pinyon-juniper ecosystems is low relative to other forest types.

Gholz (1982) determined ANPP for a *J. occidentalis* ecosystem in the northwestern Great Basin to be 1.2 mg ha-’ year-‘. No other data on productivity of pinyon-juniper ecosystems could be located.

Production efficiency

Tree production efficiencies (ANPP/LAI) for the K-V Tank study sites were 0.111 kg m^{-2} year^{-1} and 0.153 kg m^{-2} year^{-1} for the young and mature stands respectively. Whittaker and Niering (1975) reported above-ground ecosystem production efficiency of 0.093 kg m^{-2} year-’ for the pygmy conifer-oak scrub ecosystem they studied in southeast Arizona. In contrast, above-ground ecosystem production efficiencies of the K-V Tank sites (these values include interspace vegetation) were 0.129 kg m^{-2} year-’ and 0.160 kg m^{-2} year-’ for the young and mature stands, respectively. These values are high compared with those for more mesic conifer forests. For example, Whittaker and Niering (1975) list production efficiency values ranging from 0.120 kg m^{-2} year-’ to 0.059 kg m^{-2} year-’ for an altitudinal transect starting in pine–oak forests at 2040 m elevation and continuing through subalpine *Abies lasiocarpa* forest at 2720 m elevation. Production efficiencies in the study by Whittaker and Niering declined with increasing moisture and decreasing temperatures. Similarly, Grier et al. (198 1) reported low production efficiencies for cold, wet, subalpine *Abies amabilis* ecosystems on the west slopes of the Washington Cascade Mountains. Production efficiencies were 0.075 kg m^{-2} year-’ for a rapidly growing 23-year old stand and 0.032 kg m^{-2} year-’ for a 180-year-old stand.

Gholz (1982) determined all-sides leaf area (LA) and ANPP of mature conifer stands (90– 150 years old) along a transect from the coast through the western half of Oregon. We calculated production efficiencies from his data using the conversions to provide projected leaf area: LAI = LA/2.2 for single-needled trees such as *Pseudotsuga menziesii;* LAI=LA/3.1416 for the cylindrical foliage of *Juniperus;* LAI = LA/6.14 16 for three-needled *Pinus ponderosa,* to transform his all-sides leaf areas to projected leaf areas. Most of his study sites were on the cool, damp, west slopes of the Cascades. However, one of his *Pseudotsuga menziesii* stands was located on the dry, eastern rain-shadow slopes of the Coast Range and three study sites were located on the eastern slopes of the Cascade Range. One of the three east-slope Cascade sites was in a mature *Pinus ponderosa* stand, another was located in a *J. occidentalis* stand and the end of the transect was in an *Artemesia tridentata* (big sagebrush) community. Again, production efficiencies were highest in communities adapted to dry conditions. For example, production efficiency of his *J. occidentalis* community was 0.188 kg m^{-2} year-‘, higher than the values for pinyon-juniper sites in Arizona. Similarly, the *Pseudotsuga menziesii* stand on the dry east slopes of the Coast Range had production efficiency of 0.128 kg m^{-2} year^{-1} and the *Pinus ponderosa* stand had a production efficiency of about 0.140 kg m^{-2} year- ‘. Values for the stands growing on the wetter west slopes of the Coast and Cascade Ranges were generally around 0.092 kg m^{-2} $year^{-1}$ with a subalpine *Tsuga mertensiana* stand having a value of 0.069 kg m^{-2} year-‘.

There appears to be a general pattern of production efficiency increasing as the physical environment becomes drier and decreasing as the environment becomes colder. In communities adapted to desert conditions through C4 or CAM photosynthetic pathways, production efficiencies are even higher. For example, Whittaker and Niering (1975) report values between 0.130 and 0.180 kg m^{-2} $year^{-1}$ for ecosystems in the Sonoran Desert of southeastern Arizona. On the other hand, ecosystems adapted to cold environments appear to have low efficiencies. For example, all of the subalpine forests discussed earlier had production efficiencies below 0.070 kg m^{-2} year-‘.

SUMMARY

Biomass distribution, above-ground net primary productivity, production structure and some foliage characteristics were determined for 90- and 350-year-old *Pinus edulis-J. monosperma* stands on the Coconino Plateau of northern Arizona. Pinyon-juniper ecosystems in the southwest occur along a climatic gradient of a decreasing proportion of summer precipitation and increasing summer temperatures from southeastern Arizona toward the Great Basin. Pinyon-juniper ecosystems of northern Arizona are near the middle of this gradient. Above-ground biomass of stands examined in this study was 23.7 mg ha-’ for a 90-year-old stand and 54.1 mg ha-’ for a 350-year-old stand. Projected leaf areas were 1.72 m^2 m^{-2} and 1.85 m^2 m^{-2} respectively. Biomass and leaf area are below values reported for pinyon-juniper stands in the Great Basin in spite of wetter summers. Above-ground net primary productivity of the study stands was 2.12 mg ha-’ $year^{-1}$ for the young and 2.88 mg ha-’ year-’ for the mature stand. These are at the low end of the few comparable values reported in the literature. Production efficiency (PE) of the stands was high compared with forests in more mesic areas. The young stand had an ecosystem PE (including interspace vegetation) of 0.129 kg m^{-2} year-’ that for the mature stand was 0.160 kg m^{-2} year-‘.

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