J. Range Manage.
48:100-107 March 1995

Redberry juniper-herbaceous understory interactions

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Abstract

Basal cover, density, biomass, and species richness of the understory were measured in concentric zones from the stem bases of large redberry juniper (*Juniperus pinchotii* Sudw.) trees to 6 m beyond their canopy edges on a shallow, rocky soil and 2 deep soils in the northern Edwards Plateau of Texas. The juniper-driven successional processes of tree dominance, debilitation of understory dominants, influx of subsidiary species, and the general reduction in diversity, density, and biomass of the herbaceous species were evident on all 3 sites. Juniper interference intensified with increasing proximity to the stem bases. Biomass and basal cover of the herbaceous understory responded to a greater extent than did density and species richness 2 years after large redberry junipers were killed with soil injections of picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid). Herbaceous biomass responses after junipers were killed indicated that the sphere of influence of large junipers was more extensive on the shallow soil than on the deep soils. Herbaceous biomass in the presence of interference by large junipers on the Kimbrough, Angelo clay loam, and Tulia loam soils was 1,300, 1,780, and 1,290 kg ha^{-1}, respectively, compared to 2,140, 2,140, and 1,560 kg ha^{-1} 2 years after the junipers were killed on the 3 sites, respectively. Projected herbaceous biomass when juniper populations on the sites develop into closed-canopy woodlands was 320, 880, and 270 kg ha^{-1} for the Kimbrough, Angelo clay loam, and Tulia loam soils, respectively.

Keywords: *Juniperus pinchotii*, ecology, species richness, succession, competition, picloram

Redberry juniper (*Juniperus pinchotii* Sudw.) is a sprouting evergreen conifer that occurs in Oklahoma, New Mexico, Arizona, and Texas (Correll and Johnston 1979). It is a major woody species on about 4.7 million ha of Texas rangeland (Soil Conservation Service 1985). The increase of redberry juniper in grasslands since the late nineteenth century has been attributed to overgrazing, reduced frequency and intensity of fire, periodic droughts, and climatic conditions more favorable for woody plants (Ellis and Schuster 1968, Smeins 1983). Redberry juniper is considered an invader species on most range sites and it has little economic value. Forage production declines dramatically as redberry juniper canopy cover increases (McPherson and Wright 1990), and dense stands interfere with livestock handling and movement. Many grasslands on the Edwards Plateau of Texas have been converted to juniper-dominated woodlands or to closed-canopy juniper stands.

Grass yield on a redberry juniper-infested site on the Edwards Plateau was 514 kg ha^{-1} compared to 1,942 kg ha^{-1} on an adjacent site where the junipers were controlled with pelleted picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) (Robison and Cross 1970). Grass production decreased linearly on ungrazed areas and logarithmically on grazed areas in the Texas High Plains as redberry juniper canopy cover increased (McPherson and Wright 1990). McPherson et al. (1991) reported a distance-independent interaction between herbaceous vegetation biomass and redberry junipers 1 to 4 m tall on Texas high plains grasslands. They attributed this to the effect of variable tree sizes sampled, understory species composition, overlapping lateral root systems of the junipers, and to an environment sufficiently favorable to overshadow competition for soil water beyond the juniper canopy edges.

Other *Juniperus* species have been reported to have major effects on associated herbaceous vegetation. Basal area of grasses at the stem base of oneseed juniper (*Juniperus monosperma* [Engelm.] Sarge.) in a New Mexico study was only 2 to 5% compared to 31 to 35% at the canopy edge (Schott and Pieper 1985). The relationship between total herbaceous biomass and overstory canopy cover was best expressed by a negative 2nd degree polynomial curve in a pinyon-juniper (*Pinus edulis* [Engelm.]-*J. monosperma*) woodland in south-central New Mexico (Pieper 1990). Herbage production was significantly reduced beneath canopies and at the canopy edges of eastern redcedar (*Juniperus virginiana* L.) in north-central Oklahoma, but the trees did not affect herbage production 1 m or farther beyond the canopy edges (Engle et al. 1987). Herbaceous biomass at the edge of western juniper (*Juniperus occidentalis* Hook.) canopies increased from near 0 to about 1,400 kg ha^{-1} within 4 years after the trees were killed with granular picloram (Evans and Young 1985).

Redberry juniper is an important overstory species in the semi-arid Edwards Plateau of Texas that is rapidly increasing in abundance and dominance, yet its relations with the herbaceous understory have not been studied. Such information is critical to understanding successional mechanisms and the effects of woody species on livestock carrying capacity and wildlife habitat and

Approved by the Director, Texas Agricultural Experiment Station as TA-31483.
Manuscript accepted 1 Sept. 1994.

watershed values of rangeland. The objectives of this study were to quantify the relationship between large redberry junipers and basal cover, density, biomass, and species richness of the herbaceous understory on a shallow, rocky soil and 2 deep soils in the northern Edwards Plateau and to quantify short-term responses of the herbaceous understory to control of large junipers.

Materials and Methods

The study was conducted on the Hugh Stone Ranch, 16 km northwest of San Angelo (Tom Green County), Texas. The area is comprised of approximately 12,800 ha of short- and mid-grass rangeland with a dominant overstory of redberry juniper and honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*). Average annual precipitation is 519 mm, with peaks generally occurring in late spring and early autumn. The average annual temperature is 18°C and the average frost-free period is 232 days (Wiedenfeld and Flores 1976).

Study sites were selected less than 1.6 km apart on soils designated as a Kimbrough association, an Angelo clay loam, and a Tulia loam. The Kimbrough soils (loamy, mixed, thermic, shallow Petrocalcic Calciustolls) are very shallow-to-shallow gravelly loams on undulating topography with 1 to 8% slopes. They have a low available water capacity and loss of rainfall as surface runoff is medium. The surface soil, 10 to 38 cm thick, is underlain by a 3 to 46-cm thick layer of indurated caliche. Major grasses on the site included Wright threeawn (*Aristida wrightii* [Nash] Allred), red grama (*Bouteloua trifida* Thurb.), hairy tridens (*Erioneuron pilosum* [Buckl.] Nash), and Reverchon bristlegrass (*Setaria reverchonii* [Vasey] Pilger). Major forbs were needleleaf bluet (*Hedyotis acerosa* Gray var. *acerosa* Gray ex Benth & Hook), Parks groomwell (*Lithospermum parksii* I.M. Johnst.), mouse ear (*Tiquilia canescens* [DC.] A. Richards.), and longstalk greenthread (*Thelesperma longipes* Gray.). The Kimbrough soil supported 290 redberry junipers >2.0 m tall ha^{-1} along with 250 redberry junipers ha^{-1} 1-2 m tall and 5,981 redberry junipers ha^{-1} <1 m tall (total redberry juniper canopy cover 31%) (Dye 1993).

The Angelo clay loam (fine, mixed, thermic Torrertic Calciustolls) had high available-water capacity, moderately slow permeability, and occurred on <1% slopes. The solum of this soil is 150 to 300 cm thick. Major grasses on the Angelo clay loam were Wright threeawn, common curlymesquite (*Hilaria belangeri* [Steud.] Nash), fall witchgrass (*Leptoloma cognatum* [Schult.] Chase), and Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.). Major forbs included croton (*Croton dioicus* [Cav.] Rosval and *C. potsii* [Klotzch] Muell. Arg.), and gray coldenia. The Angelo clay loam supported 89 redberry junipers >2.0 m tall ha^{-1} along with 70 redberry junipers ha^{-1} 1-2 m tall and 749 redberry junipers ha^{-1} <1 m tall (total redberry juniper canopy cover 7%) (Dye 1993).

The Tulia loam (fine-loamy, carbonatic, thermic Calciorthidic Paleustalfs) had high available-water capacity, moderate permeability, and occurred on 1 to 3% slopes. The solum of this soil is 50 to 100 cm thick over a buried B horizon 50 to 200 cm thick. Dominant grasses were Wright threeawn, Texas grama (*Bouteloua rigidiseta* [Steud.] A.S. Hitch.), fall witchgrass, and buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.). Dominant forbs were croton, gray coldenia, and Parks groomwell. The redberry juniper stand on the Tulia loam included 125 redberry junipers ha^{-1} >2.0 m tall along with 141 redberry junipers ha^{-1} 1-2 m tall and 1,396 redberry junipers ha^{-1} <1 m tall (total redberry juniper canopy cover 12%) (Dye 1993).

Ten of the tallest redberry juniper trees on each site were permanently marked in August 1991. Mean tree heights (±standard deviations) were 3.7 ± 0.3, 3.2 ± 0.3, and 3.3 ± 0.5 m on the Kimbrough, Angelo clay loam, and Tulia loam sites, respectively, and mean canopy diameters were 4.6 ± 0.9, 3.6 ± 0.9, and 3.4 ± 0.7 m on the 3 sites, respectively. Herbaceous vegetation was sampled at 6 locations along a line transect placed in the 4 cardinal directions from each juniper in August 1991. Basal cover, density, standing crop, and species richness were sampled within 6 concentric sampling zones (at stem base, mid-canopy, canopy edge, and at 1, 3, and 6 m beyond canopy edge). Basal cover was estimated by the 10-point frame method (pins 3.8 cm apart) (Brown 1954, Bonham 1989) with one placement of the frame perpendicular to the transect at each sampling location on each transect. Basal cover within each concentric zone on each site was estimated from 400 points in 1991 (10 trees × 4 transects × 10 points) and from 200 points for each zone for both live and dead trees in 1992 and 1993 (5 trees × 4 transects × 10 points). Density was recorded by species within a 60.0 × 33.33-cm quadrat placed at each sampling location on each transect. The herbaceous plants within the quadrat were subsequently harvested at ground level, separated into grasses and forbs, oven dried to a constant weight at 52°C, and weighed. Species richness within each concentric zone was the total number of herbaceous, woody, and succulent species encountered while recording plant densities (Ludwig and Reynolds 1988).

Five of the permanently marked redberry junipers on each site were killed in September 1991 by injecting picloram at 20 ml m^{-1} of tree height 10 to 15 cm into the soil beneath the tree canopies. Other redberry junipers ≥ 0.5 m tall within a 12-m radius of the treated junipers were also killed to eliminate their influence on the herbaceous vegetation. The herbaceous vegetation around live and dead redberry junipers was sampled by the methods given above in late August of 1992 and 1993 to quantify response to the reduction of juniper interference. Sampling locations were shifted 30° from the cardinal directions during sampling in 1992 and 1993. To express whole-tree influence on herbage biomass, total herbage biomass (kg ha^{-1}) within the circular area from stem bases to 6 m beyond the canopy edges of live and dead junipers on each site in 1993 was calculated by summing the product of area (ha) within each concentric sampling zone and the respective biomass estimate (kg ha^{-1}), and dividing this total (kg) by the total area (ha) within this circle.

The experiment was arranged in a completely randomized design with 10 replications (trees) on each site in 1991 and 5 replications each of live and dead trees on each site in 1992 and 1993. Analysis of variance on basal cover, density, biomass, and species richness data revealed significant site × year interactions, so data for each site and year were subjected to separate analyses of variance, and means were separated ($P \leq 0.05$) by LSD where necessary. Since cardinal direction was not significant, data within a sampling zone were pooled over direction. Density data for major understory species were transformed by log (x + 0.5) before analysis of variance, the means were separated ($P \leq 0.05$ or $P \leq 0.10$) by LSD where necessary, and the means were reverse transformed for presentation. Total numbers of species encountered within each sampling zone for each treatment (live or dead trees) during density sampling in 1993 (observed values) were compared to the numbers recorded in 1991 (expected values) by chi-square analyses to evaluate for treatment effects on species richness.

Results

Interaction of Mature Junipers with Understory Species

Monthly precipitation recorded in a rain gauge 10 km from the study area exceeded the long-term average during 9 months of 1991, and total precipitation for the year (798 mm) was 54% above the long-term average. Data collected in 1991 (n= 10 trees/site) generally indicated basal cover of the herbaceous understory was significantly lower adjacent to juniper stems and at mid-canopy compared to canopy edges and beyond on all 3 sites (Fig. 1). A dense mat of dead juniper leaves covered 92 to 97% (ranges of means among 3 sites) of the soil surface at the juniper stem bases, 82 to 90% at mid-canopy, and 55 to 63% at canopy edge (Dye 1993). Basal cover 6 m beyond canopy edges ranged from 4- to >10-fold greater than that at the stem bases. Herbaceous plant basal cover at the edge of juniper canopies on the Kimbrough and Angelo clay loam soils was similar to that 1 to 6 m beyond canopy edges, whereas basal cover at canopy edges on the Tulia loam was significantly lower than that 3 to 6 m beyond juniper canopy edges (Fig. 1).

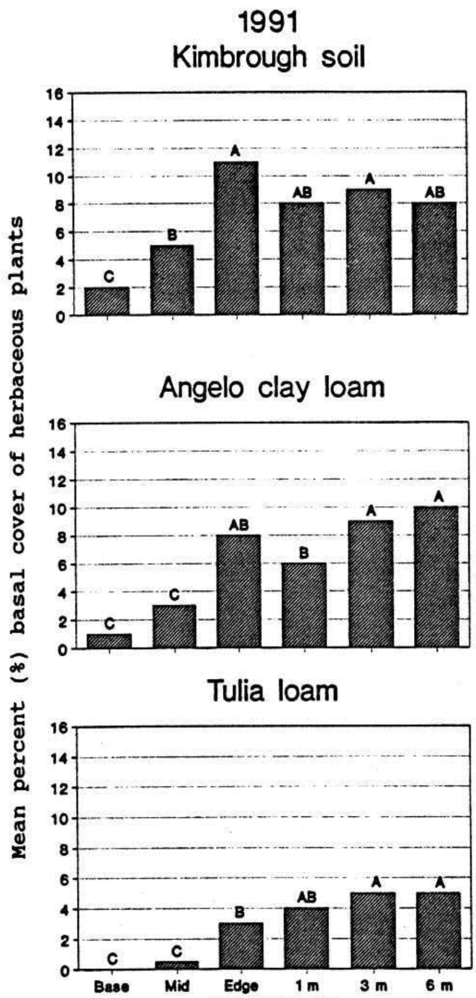

Fig. 1. Mean basal cover (%) of herbaceous plants in 6 sampling locations around redberry junipers on 3 sites (n= 10 trees/site) near San Angelo, Tex. in 1991. Means within a site that subtend different uppercase letters are different (*P*≤0.05).

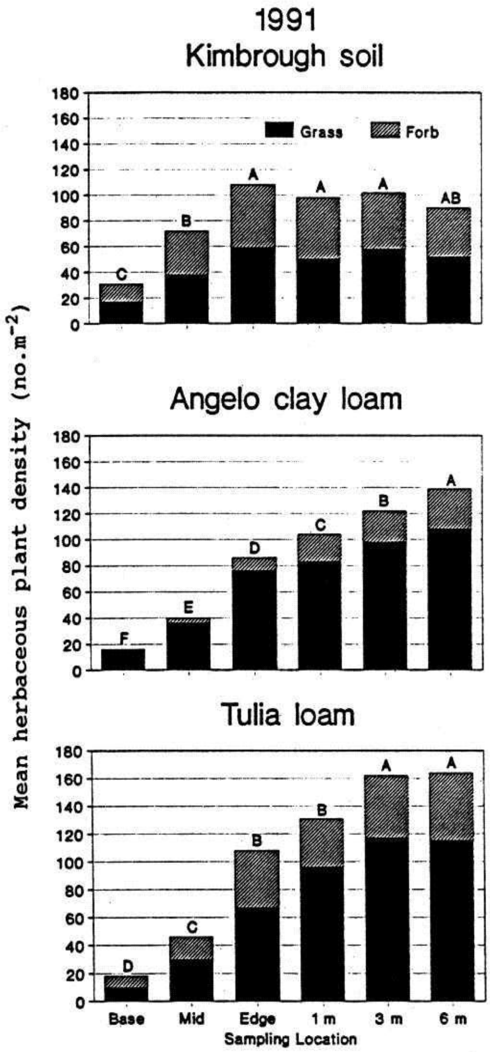

Fig. 2. Mean herbaceous plant densities (no. m^{-2}) in 6 sampling locations around redberry junipers on 3 sites (n= 10 trees/site) near San Angelo, Tex. in 1991. Means within a site that subtend different uppercase letters are different (*P*≤0.05).

Density of grasses and forbs in 1991 was lowest at the base of juniper stems and greatest at the edge of juniper canopies (Kimbrough site) or at 6 m beyond canopy edges (Angelo clay loam and Tulia loam sites) (Fig. 2). Mean densities of herbaceous plants 6 m beyond canopy edges ranged from about 3- to 9-fold greater than at the stem bases.

Total herbaceous biomass increased from stem bases to 6 m beyond canopy edges on the Kimbrough and Angelo clay loam and to 3 m beyond canopy edges on the Tulia loam in 1991 (Fig. 3). Total herbaceous biomass at stem bases on the 3 sites ranged from 120 to 140 kg ha^{-1} compared to a range from 1,160 to 1,990 kg ha^{-1} 6 m beyond juniper canopy edges. Our finding of distance-dependent interactions between large redberry junipers and standing crop of the herbaceous understory is in contrast to the distance-independent interaction found by McPherson et al.

(1991) at 2 sites occupied by the species on the Texas high plains. They reported a reduction in standing crop only midway between the juniper stems and canopy edge, although they did not sample at the stem bases.

Species richness of grasses and forbs was lower ($P \leq 0.05$) in the zone adjacent to juniper stem bases compared to that at the canopy edges and beyond on all 3 sites (Table 1). Furthermore, there were generally fewer herbaceous species in the mid-canopy zone than in other zones outward to 6 m beyond canopy edges. However, species richness of shrubs and succulents was greater ($P \leq 0.05$) in the zones adjacent to juniper stems and at mid-canopy than at canopy edges and in the interspace between large junipers. Total understory species richness was lower ($P \leq 0.05$) in the zone adjacent to juniper stems than in the other zones surrounding large junipers on the Angelo clay loam and Tulia loam sites but not on the Kimbrough association site (Table 1).

Herbaceous species that were most tolerant of redberry juniper interference, i.e. those that were abundant at juniper canopy edges and beyond and also present in lower numbers (≥ 1 m^{-2}) at the stem bases, included threeawns, hairy tridens, buffalograss, needleleaf bluet, and longstalk greenthread (Tables 2-4). Herbs with lesser tolerance, i.e. those that were abundant at canopy edges and beyond but absent or rare (<1 m^{-2}) at stem bases, included red grama, common curlymesquite, Texas grama, Reverchon bristlegrass, leather-weed croton, gray coldenia, and spreading sida (*Sida abutifolia* Mill.). Texas wintergrass, a grass with the C_3 photosynthetic pathway, was the only herbaceous plant more abundant beneath juniper canopies than in the interspaces. Several shrubs and succulents, including redberry juniper, agarito (*Berberis trifoliolata* Moric.) and pricklypear (*Opuntia* spp.) were more abundant beneath large junipers than in the interspaces (Tables 2-4). Littleleaf sumac (*Rhus microphylla* Engelm.), lime pricklyash (*Zanthoxylum hirsutum* Buckl.), and Mormon tea (*Ephedra antisyphylitica* C.A. Meyer) were also present beneath large junipers but absent or rare in the interspaces.

Table 1. Mean species richness in 6 sampling locations around large redberry junipers on a Kimbrough association, Angelo clay loam, and Tulia loam near San Angelo, Tex. in 1991[1].

	Distance from juniper					
	Beneath juniper canopy			Beyond canopy edge		
	Stem base	Mid canopy	Canopy edge	1 m	3 m	6 m
	(number of species)					
Kimbrough Association						
Grasses	1.6 c	2.7 bc	4.5 a	4.1 ab	4.3 a	3.9 ab
Forbs	2.7 b	4.6 a	5.5 a	5.5 a	5.1 a	4.4 a
Shrubs/succulents	2.9 a	2.0 b	1.2 c	0.9 cd	0.3 d	0.3 d
Total	7.2 c	9.3 abc	11.2 a	10.5 ab	9.7 abc	8.6 bc
Angelo clay loam						
Grasses	2.3 c	3.9 b	6.2 a	5.9 a	5.3 a	6.2 a
Forbs	0.5 d	1.6 c	2.3 bc	3.2 ab	2.9 ab	3.8 a
Shrubs/succulents	1.6 a	1.2 a	0.3 b	0.1 b	0.1 b	0.3b
Total	4.4 d	6.7 c	8.8 ab	9.2 ab	8.3 bc	10.3a
Tulia loam						
Grasses	2.3 c	4.8 b	8.0 a	8.0 a	7.7 a	8.1 a
Forbs	1.6 b	2.7 b	4.5 a	5.1 a	5.4 a	4.5 a
Shrubs/succulents	2.5 a	1.8 a	1.0 b	0.3 bc	0.4 bc	0.2 c
Total	6.4 c	9.3 b	13.5 a	13.4 a	13.5 a	12.8 a

[1]Means within a row followed by the same lowercase letter are not different ($P \leq 0.05$).

Table 2. Mean density of major species in 6 sampling locations around large redberry junipers on a Kimbrough soil near San Angelo, Tex. in 1991[1,2].

	Distance from juniper					
	Beneath juniper canopy			Beyond canopy edge		
	Stem base	Mid canopy	Canopy edge	1 m	3 m	6 m
	(plants m^{-2})					
Grasses						
Threeawn	8.8 c	23.0 ab	29.1 a	14.4 bc	11.6 bc	16.2 abc
Sideoats grama	1.6 AB	1.8 A	1.6 AB	0.1 BC	0.0 C	0.2 BC
Hairy tridens	1.6 c	5.0 bc	14.2 a	20.4 a	18.7 a	14.4 ab
Fall witchgrass	0.2	0.4	0.4	0.4	0.5	0.6
Reverchon bristlegrass	0.1	0.6	0.7	1.1	0.8	2.1
Slim tridens	0.2	0.3	0.6	0.7	0.6	0.9
Other grasses	0.4	0.8	1.3	1.4	1.7	0.8
Forbs						
Plains lazydaisy[3]	0.2	0.5	0.9	0.9	1.0	0.8
Needleleaf bluet	1.7 b	6.8 a	11.5 a	13.3 a	10.6 a	6.4 a
Parks groomwell	0.4 b	5.2 a	5.7 a	3.8 ab	2.0 ab	0.5 b
Longstalk greenthread	2.4 B	6.0 AB	10.1 A	8.6 A	6.2 AB	11.3 A
Other forbs	5.2	5.7	6.0	8.0	3.6	3.9
Shrubs/Succulents						
Agarito	1.7 a	0.7 b	0.0 b	0.0 b	0.1 b	0.0 b
Redberry juniper	4.0 ab	6.5 a	6.5 a	1.4 bc	0.2 c	0.0 c
Other shrubs	1.8 a	0.3 b	0.2 b	0.0 b	0.0 b	0.0 b

[1]Means within a row followed by the same lowercase letter are not different ($P \leq 0.05$).
[2]Means within a row followed by the same uppercase letters are not different ($P \leq 0.10$).
[3]*Aphanostephus ramosissimus* DC.

Response to Reducing Juniper Interference

Growing conditions were favorable during 1992 with total precipitation of 749 mm. Precipitation exceeded the long-term average 5 months in 1992. Responses of the herbaceous understory to reduced redberry juniper interference within the first year after herbicide applications reflected the growing conditions and resiliency of the herbaceous species. Responses recorded at the end of the first growing season (August 1992) after mature junipers were killed included: 1) increases ($P \leq 0.05$) in basal cover of herbaceous plants from stem bases out to mid-canopy on the Kimbrough soil; 2) increases ($P \leq 0.05$) in density of herbaceous plants at stem bases and out to mid-canopy on the Kimbrough soil and at the stem bases on the Angelo clay loam; and 3) increases ($P \leq 0.05$) in herbaceous biomass from stem bases out to 3 m beyond canopy edges on the Kimbrough soil and Tulia loam and out to the canopy edges on the Angelo clay loam (Dye 1993).

Growing conditions were less favorable during 1993 than during 1991 and 1992. Rainfall received during January-August 1993 (349 mm) was near the long-term average. However, the preceding autumn was extremely dry. Basal cover of herbaceous plants increased ($P \leq 0.05$) beneath the canopies of dead junipers 2 growing seasons after treatment (Fig. 4). Total basal cover at dead stem bases ranged from 6 to 12 percentage units greater than that at live stem bases, and total basal cover at midcanopy of dead junipers was 10 percentage units greater than that at mid canopy of live trees. Basal cover was similar from the stem bases of dead junipers to 6 m beyond their canopy edges at all 3 sites after 2 growing seasons. In contrast, basal cover around live junipers followed the same pattern observed in 1991, i.e. basal cover generally decreased from 6 m beyond canopy edges to the stem bases on all 3 sites. Basal cover of herbaceous plants at the canopy edges

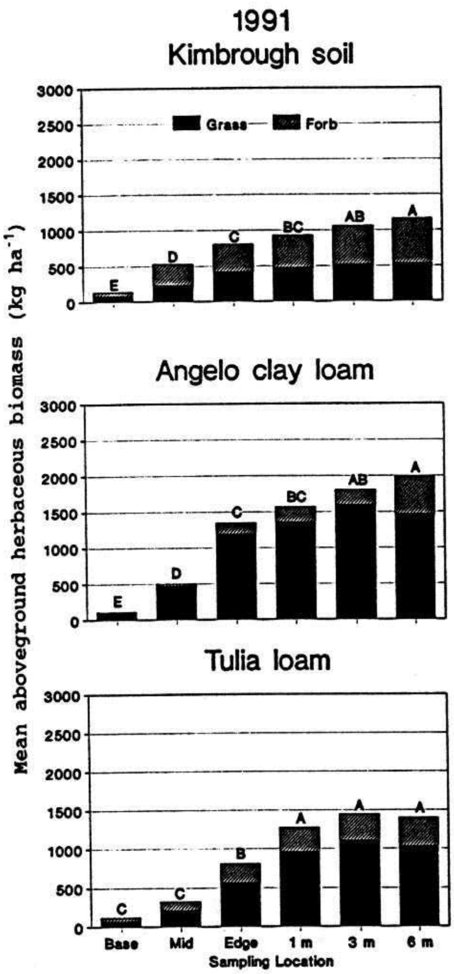

Fig. 3. Mean grass and forb aboveground biomass (kg ha^{-1}) in 6 sampling locations around redberry junipers on 3 sites (n= 10 trees/site) near San Angelo, Tex. in 1991. Means within a site that subtend different uppercase letters are different ($P\leq0.05$).

or beyond was not affected by killing junipers on the 3 sites.

Mean density of herbaceous plants beneath canopies of dead junipers was greater ($P\leq0.05$) than beneath live juniper canopies on the Kimbrough site in 1993, but densities from the canopy edges out to 6 m beyond canopy edges were similar for live and dead trees (Fig. 5). Densities of the herbaceous plants were not affected by killing junipers on the Angelo clay loam site. Herbaceous plant densities were greater at canopy edges and at 1 m beyond canopy edges of dead juniper compared to live juniper on the Tulia loam site in 1993.

Compared to live trees, herbaceous biomass production increased ($P\leq0.05$) in 1993 after junipers were killed on all 3 sites (Fig. 6). Increases ($P\leq0.05$) in biomass occurred from the stem bases out to at least 6 m beyond canopy edges on the Kimbrough soil, from stem bases out to the canopy edges on the Angelo clay loam, and from stem bases to 1 m beyond canopy edges on the Tulia loam. Relative increases in herbaceous biomass were greatest beneath juniper canopies. Total biomass at dead stem bases was 2,520, 2,410, and 1,620 kg ha^{-1} compared to 60, 360, and 110 kg ha^{-1} at live stem bases on the Kimbrough soil, Angelo clay loam, and Tulia loam, respectively. Grass biomass was greater ($P\leq0.05$) beneath dead juniper canopies compared to live juniper canopies on all 3 sites. Reduction of juniper interference resulted in herbage production beneath the canopies similar to that in the interspaces (6-m sampling location) within 2 years, whereas herbage yields around live junipers decreased greatly from the interspaces toward the stem bases as was observed in 1991.

Table 3. Mean density of major species in 6 sampling locations around large redberry junipers on an Angelo clay loam soil near San Angelo, Tex. in 1991[1,2].

	Distance from juniper					
	Beneath juniper canopy			Beyond canopy edge		
	Stem base	Mid canopy	Canopy edge	1 m	3 m	6 m
	(plants m^{-2})					
Grasses						
Threeawn	1.9 B	4.2 AB	5.3 A	5.8 A	6.1 A	8.5 A
Silver bluestem[3]	0.1	0.2	0.6	1.5	1.5	1.2
Red grama	0.0 c	0.4 c	8.0 b	11.6 b	6.4 b	29.8 a
Common curlymesquite	0.3 b	4.9 b	28.2 a	26.9 a	39.2 a	31.9 a
Fall witchgrass	1.9	3.4	4.7	3.0	1.4	1.3
Texas wintergrass	2.1 ab	3.4 a	3.5 a	0.2 b	0.0 b	0.0 b
Other grasses	0.8 c	2.8 bc	4.8 ab	8.8 a	5.2 ab	7.9 a
Forbs						
Croton	0.1 c	0.9 c	1.5 bc	4.8 b	13.2 a	14.5 a
Gray coldenia	0.7 bc	0.1 c	1.1 abc	1.4 abc	1.6 ab	3.1 a
Other forbs	0.3 c	2.0 bc	4.3 ab	7.6 a	6.0 ab	6.4 ab
Shrubs/Succulents	2.3 a	1.8 ab	1.2 abc	0.1 c	0.1 c	0.3 bc

[1]Means within a row followed by the same lowercase letter are not different ($P\leq0.05$).
[2]Means within a row followed by the same uppercase letters are not different ($P\leq0.10$).
[3]*Bothriochloa saccharoides* (Sw.) Rydb.

Calculation of total herbaceous biomass within the entire circular area from stem bases to 6 m beyond canopy edges of live and dead junipers (1993 data) revealed that individual, large junipers reduced herbage standing crops by 18.1, 6.8, and 5.0 kg on the Kimbrough, Angelo clay loam, and Tulia loam soils, respectively. Total biomass within these circular areas around live trees in 1993 was 1,300, 1,780, and 1,290 kg ha^{-1} on the Kimbrough, Angelo clay loam, and Tulia loam soils, respectively, compared to 2,140, 2,140, and 1,560 kg ha^{-1} around dead trees for the 3 soils, respectively.

Chi-square analyses comparing 1991 versus 1993 data on species richness for live and dead junipers revealed no consistent patterns. There were no significant changes within any of the sampling zones in total numbers of understory species on the Tulia loam or within most sampling zones on the Kimbrough soil and Angelo clay loam (data not shown).

Discussion

Redberry Juniper Interference

Interference of large redberry junipers with the herbaceous understory was evident on 2 deep soils with high water-holding capacities and on a shallow, rocky soil with low water-holding capacity. The magnitude of interference, relative to herbaceous plant basal cover, density, herbage biomass, and species richness, intensified with increasing proximity to the juniper stems. Differential responses among the 3 sites in herbage biomass after killing the junipers indicated that the area affected by a juniper was greatest on the more xeric, shallow, rocky Kimbrough soil and least on the deep, nearly level Angelo clay loam. Herbage biomass increased in all zones from juniper stem bases to 6 m beyond juniper canopy edges on the Kimbrough soil, but only out to 1 m beyond canopy edges on the Tulia clay loam and out to

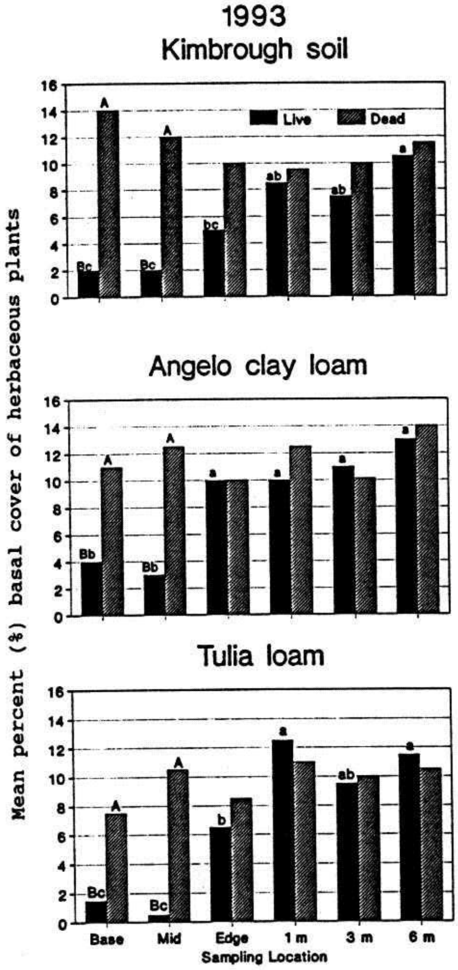

Fig. 4. Mean basal cover (%) of herbaceous plants in 6 sampling locations around live (L) and dead (D) redberry junipers on 3 sites near San Angelo, Tex. in 1993. Means within a site and sampling location that subtend different uppercase letters are different ($P \leq 0.05$). Means within a site and treatment (live or dead) that subtend different lowercase letters are different ($P \leq 0.05$).

the canopy edges on the Angelo clay loam within 2 years after the junipers were killed.

Competition between large junipers and the herbaceous understory for soil water or nutrients was evidently more intense on the Kimbrough soil because it has less soil mass and a lower available-water status compared to the Angelo clay loam and Tulia loam. Junipers growing on shallow soils may have more extensive lateral root systems than those growing on deep soils, and they may rely more heavily upon soil moisture and nutrients within the root zone of the herbaceous plants. The interference of oneseed junipers with the herbaceous understory in northern Arizona was greater on sandy soils than on clay loam soils (Johnsen 1962). The diameter of bare areas beneath oneseed junipers averaged 0.6 m on clay loam soils compared to 1.8 m on sandy soils. The bare areas extended beyond the canopy edges of oneseed junipers $\geq$ 0.6 m tall on sandy soils, but were only evident on trees >1.8 m tall on clay loam soils. Eastern redcedars 2 and 6 m tall on tallgrass prairie in Oklahoma reduced herbage production significantly beneath their canopies, but the reduction at canopy edges was slight and effects beyond canopy edges only occurred in a year of below-normal precipitation (Engle et al. 1987).

Other factors that may contribute to mature redberry juniper interference, in addition to competition for soil water and nutrients, are litter, shade, allelopathy and interception of rainfall by the juniper canopies and litter. Juniper litter cover ranged from 92 to 97% at the juniper stem bases and from 82 to 90% at mid-canopy prior to application of picloram treatments. Picloram defoliated the trees, thus thickening the litter layer and possibly increasing litter cover. The greatest responses to killing junipers in this study were the increases in herbage production and basal cover in the zones with greatest litter cover that had previously been most heavily shaded. This suggests that juniper litter was not allelopathic to grasses and forbs present in these zones, although leachates from the live juniper leaves may have suppressed growth of herbaceous plants beneath the canopies. Our results suggest that juniper interference directly beneath the tree canopies was associated with shading, competition for soil water, nutrients and interception of rainfall. Thurow and Carlson (1994) reported that 62% of the precipitation received in closed-canopy juniper woodlands was lost to interception by the juniper canopies, and about 14.5% of that reaching the soil surface would be intercepted by the juniper litter layer. Juniper interference beyond canopy edges may have been associated with competition for soil water or nutrients, although allelopathic effects from juniper root exudates cannot be ruled out.

Influence of Redberry Junipers on Rangeland Values

The data presented have significant implications relative to the

Table 4. Mean density of major species in 6 sampling locations around large redberry junipers on a Tulia loam soil near San Angelo, Tex. in 1991[1,]

	Distance from juniper					
	Beneath juniper canopy			Beyond canopy edge		
	Stem base	Mid canopy	Canopy edge	1 m	3 m	6 m
	(plants m^{-2})					
Grasses						
Threeawn	3.1 c	4.6 bc	10.4 ab	13.0 a	13.6 a	20.2 a
Texas grama	0.0 b	0.7 b	2.2 ab	5.5 a	5.7 a	6.1 a
Red grama	0.0 c	0.1 c	3.2 b	20.1 a	27.1 a	27.6 a
Buffalograss	1.0	5.6	7.2	5.8	10.0	7.9
Fall witchgrass	0.9	1.9	3.2	3.1	1.9	2.1
Reverchon bristlegrass	0.4 c	3.3 b	5.7 ab	7.2 ab	7.6 ab	11.8 a
Slim tridens[2]	0.2 b	0.2 b	1.6 ab	3.1 a	2.1 a	1.6 ab
Sand dropseed[3]	0.5 d	1.0 cd	4.7 a	3.4 ab	2.1 bc	2.2 bc
Other grasses	0.4 c	3.0 b	7.2 ab	5.9 ab	4.5 ab	8.2 a
Forbs						
Croton	0.0 c	0.5 c	2.3 bc	4.2 ab	8.0 a	5.8 ab
Parks groomwell	2.1	4.7	10.1	3.6	2.4	1.9
Spreading sida	0.3 c	1.2 c	4.7 b	8.2 ab	9.7 ab	12.1 a
Gray coldenia	0.0 d	0.7 cd	2.5 bc	3.2 ab	5.5 ab	6.7 a
Other forbs	1.9	2.1	3.3	4.1	4.5	3.3
Shrubs/Succulents						
Redberry juniper	2.2 a	1.4 ab	1.2 abc	0.3 bcd	0.1 cd	0.0 d
Pricklypear	2.6 a	1.0 b	0.2 bc	0.1 bc	0.2 bc	0.0 c
Other shrubs	0.9 a	1.2 a	0.4 ab	0.0 b	0.0 b	0.1 b

[1]Means within a row followed by the same lowercase letter are not different ($P \leq 0.05$).
[2]Means within a row followed by the same uppercase letters are not different ($P \leq 0.10$).
[3]*Tridens muticus* (Torr.) Nash.
[4]*Sporobolus cryptandrus* (Torr.) Gray.

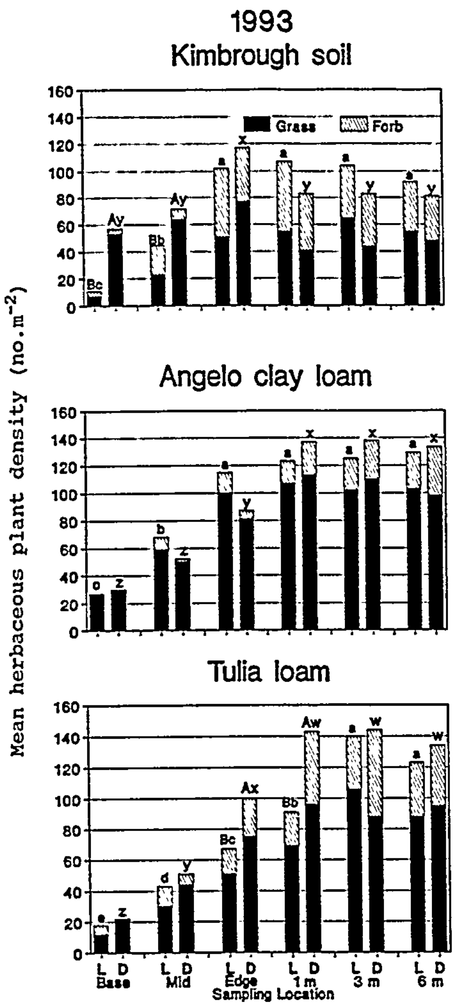

Fig. 5. Mean herbaceous plant density (no. m⁻²) in 6 sampling locations around live (L) and dead (D) redberry junipers on 3 sites near San Angelo, Tex. in 1993. Means within a site and sampling location that subtend different uppercase letters are different ($P \leq 0.05$). Means within a site and treatment (live or dead) that subtend different lowercase letters are different ($P \leq 0.05$).

future values of redberry juniper woodlands for livestock and wildlife production and as watersheds. We project that annual herbage production will decrease to the current weighted average for the stem base and mid-canopy sampling zones for live trees, i.e. 320, 880, and 270 kg ha^{-1} for the Kimbrough, Angelo clay loam, and Tulia loam soils, respectively, as the redberry junipers currently present on these sites mature and create closed-canopy woodlands. These values represent decreases of about 85, 59, and 82% compared to our estimates of potential herbage production for the 3 sites, respectively. The carrying capacity of these sites would be reduced to a greater extent because a substantial proportion of the forage would not be accessible to large herbivores. The dramatic decline in herbaceous species diversity would further degrade the wildlife habitat values of these sites. Vast, dense stands of juniper are not ideal wildlife habitat, nor are they conducive to wildlife management (Rollins and Armstrong 1994). Redberry juniper may contribute >20% of deer diets during winter (Sowell et al. 1985), but it is not considered a "good" forage because its monoterpenes may limit consumption, kill rumen microbes, and be inefficiently detoxified by multifunctional oxidase enzyme systems in the livers of ruminants (Huston et al. 1994). Armstrong (1991) rated juniper as only a "fair" deer forage that was utilized only where more desirable browse was unavailable. In relation to watershed values, dense stands of junipers have negative impacts on deep drainage and recharge of underground aquifers because a high percentage of the rainfall received is lost to interception by juniper canopies and litter and to meet juniper's transpiration requirements (Thurow and Carlson 1994). The negative effects of junipers on herbaceous plant cover in the interspaces decreases the quality of runoff by increasing the sediment load (Thurow and Carlson 1994).

Influence of Redberry Juniper on Succession

The redberry juniper trees observed reflected the successional processes of "tree dominance, debilitation of understory dominants, influx and promotion of subsidiary species, and the overall reduction of understory density" as were reported in single-leaf pinyon (*Pinus monophylla* Torr. and Frem.) stands by Everett et al. (1983). The influx and promotion of other shrub and half-

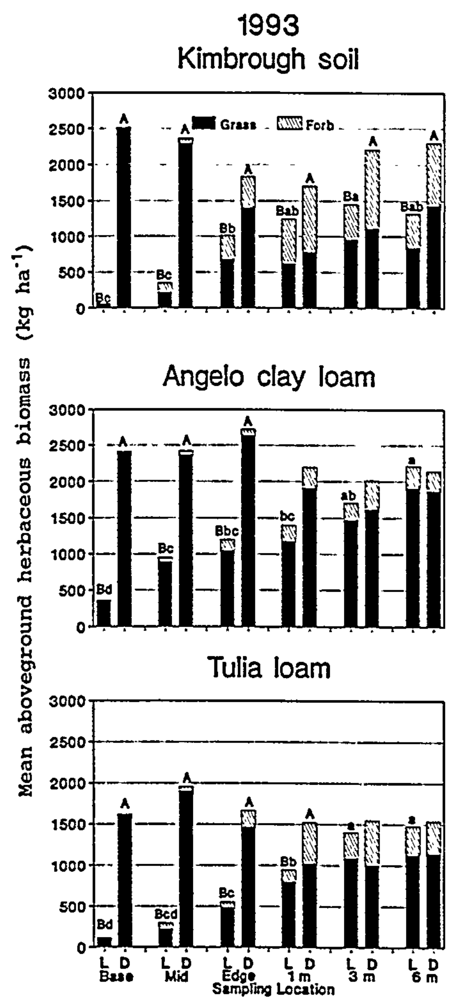

Fig. 6. Mean grass and forb aboveground biomass (kg ha⁻¹) in 6 sampling locations around live (L) and dead (D) redberry junipers on 3 sites near San Angelo, Tex. in 1993. Means within a site and sampling location that subtend different uppercase letters are different ($P \leq 0.05$). Means within a site and treatment (live or dead) that subtend different lowercase letters are different ($P \leq 0.05$).

shrub species beneath junipers has also been reported by Arnold (1964), Armentrout and Pieper (1988) and McPherson et al. (1988). Differences in understory composition in the zones around large redberry junipers suggests the tree influences had created microsites that could facilitate different successional pathways (Cattelino et al. 1979) among the zones surrounding redberry junipers.

The original grasslands that occupied our study sites as well as the current redberry juniper woodland communities represent stable states or seral stages (Archer 1989, Friedel 1991, Laycock 1991). Graminoid-driven succession predominated within the original grassland domain, characterized by low grazing pressure, high fire frequency and intensity, and low probability and rate of woody plant establishment. Heavy, continuous grazing of these areas by cattle, sheep, and goats during the late 1800's and early 1900's weakened the climax grasses, caused major changes in herbaceous species composition, reduced the frequency and intensity of fire, and thus facilitated the establishment of redberry juniper. These communities crossed the threshold from grasslands to juniper-dominated woodlands when sufficient numbers of junipers became established and reached reproductive maturity. Juniper-driven successional processes then began predominating, characterized by debilitation of understory herbaceous plants, a general reduction in understory diversity, density, basal area, and productivity, an influx of subsidiary species, further reduction in fire frequency and intensity, and a high incidence and rate of juniper seedling establishment. These juniper woodlands will not revert to grassland even if grazing is stopped, and furthermore, little or no improvement in range condition would occur if grazing were discontinued. Conversion of these juniper woodlands back to grasslands will require substantial initial intervention (reclamation) by the range manager, e.g., mechanical control methods or herbicides, to substantially reduce the juniper-driven successional processes. Reestablishment of steady state grasslands will require sustained intervention by the range manager, e.g., proper grazing management, periodic application of fire (Rasmussen et al. 1986), and periodic use of mechanical (Wiedemann and Cross 1981) or individual plant treatments (Ueckert and Whisenant 1982, Welch 1991) for maintenance control of redberry juniper.

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