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## Ponderosa Pine and Understory Growth Following Western Juniper Removal

### Abstract

Recent expansions of western juniper are of great concern to land managers throughout the drier regions of the Pacific Northwest. While removal of western juniper has been found to significantly increase understory plant biomass, little information is available on the effect of western juniper removal on the tree species. This research evaluated response of understory plant biomass and cover, and ponderosa pine growth following removal of western juniper. Study sites were established in the ponderosa pine/western juniper ecotone of central Oregon. Total understory plant biomass and cover increased in response to western juniper removal. However, thinning ponderosa pine and leaving western juniper reduced biomass and cover of understory groups below control levels. Ponderosa pine under 5 cm DBH (Diameter at Breast Height) had greater percent growth in the control, where no trees were removed, than trees in treatments where competing trees were removed. Removal of western juniper appears to benefit understory vegetation, but may depress growth of small ponderosa pine trees for the first few years following tree removal.

### Introduction

Encroachment of woody plants into productive shrub-steppe communities with reduction in aboveground net primary production, biological diversity, top soil, and water yields is an important challenge to many land managers throughout the western United States. In central and eastern Oregon, western juniper (*Juniperus occidentalis* Hook.) has doubled its range over the past 80 to 100 years (Caraher 1978). Western juniper's highly competitive nature allows it to invade and dominate plant communities regardless of present site conditions (Burkhardt and Tisdale 1969, 1976, Eddleman 1983, Young and Evans 1981). The increase in western juniper density is usually accompanied by reductions in understory plant biomass (Bedell 1987, Bedell and Bunch 1978, Burkhardt and Tisdale 1976, Caraher 1978, Eddleman 1987, Evans 1984).

Prior to the 1800s western juniper distribution ranged from the edge of the sagebrush steppe to the ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws) forest and occasionally into higher elevation Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands (Fowells 1965). The majority of western juniper trees were limited to rocky ridge tops and areas with shallow rocky soils throughout much of this range (Driscoll 1964). Periodic wildfires and the presence of competitive taxa on more mesic sites limited western juniper to these rocky sites. Recent fire suppression, poor grazing management,

and subtle climatic shifts have been cited as causes for the recent western juniper encroachment (Burkhardt and Tisdale 1976, Driscoll 1964, Eckert 1957, Mehringer and Wigand 1987, Vasek 1966, Young and Evans 1981). These factors may have worked separately or in combination to cause western juniper numbers to increase.

Attention has been focused on the encroachment of western juniper into the drier sagebrush-grassland. Understory plants have generally responded favorably to overstory removal of western juniper (Evans 1984, Vaitkus 1986). No information is available on the effect of western juniper on other trees. It is not known if removal of western juniper in the ponderosa pine-western juniper ecotone will increase growth of ponderosa pine on these marginal sites. The objectives of this study were to: 1) determine the effects of ponderosa pine thinning and western juniper removal on ponderosa pine; and 2) determine the effect of western juniper removal and ponderosa pine thinning on understory vegetation.

### Methods

#### Site Description

Two study sites were located on private land in Crook County, Oregon, near Prineville. The primary site (One) was 26 km southeast of Prineville on a north to northeast facing slope above Comb's Flatt (44° 15' N, 120° 45' W). A second study site (Two) was established 33 km northwest of

Prineville on a south facing slope above Lytle Creek, east of Grizzly Mountain (44° 25' N, 121° 55' W). Sites were selected and established in an ecotone between western juniper woodland and ponderosa pine forest (Franklin and Dyrness 1973). Western juniper dominates these sites. Absence of mature juniper on the sites indicate that a majority of the trees probably established during the last 50 to 60 years when the junipers were actively expanding their range (Eddleman 1987).

Shrub species were similar on both sites. Dominant shrubs were antelope bitterbrush (*Purshia tridentata* (Pursh) OC) (nomenclature follows Hitchcock and Cronquist 1978). Mountain big sagebrush (*Artemisia tridentata* ssp. *vayseyana* (Rydb.) Beetle), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle), and wax currant (*Ribes cereum* Dougl.). Other less abundant shrubs were low sage (*Artemisia arbuscula* Nutt.), grey rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Brit.), green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), snowberry (*Symphoricarpos albus* (L.) Black), and serviceberry (*Amelanchier alnifolia* Nutt.).

Understory vegetation of Site One was dominated by bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), Idaho fescue (*Festuca idahoensis* Elmer), prairie junegrass (*Koeleria cristata* Pers), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. SM), and Sandberg bluegrass (*Poa sandbergii* Vasey). Site Two contained all of the above perennial grasses, but at lower densities. Cheatgrass (*Bromus tectorum* Vasey), six-weeks fescue (*Festuca octiflora* Walt.), and annual agrostis (*Agrostis interrupta* L.) were abundant species on site Two. Site Two also had the annual forbs, autumn willowweed (*Epilobium paniculatum* Nutt. Ex T. & G.), blepharipappus (*Blepharipappus scaber* Hook.), and tarweed (*Madia glomerata* Hook.) at higher densities than Site One.

Soils in the area were formed from weathered volcanic parent material. Soils of Site One were classified as clayey, montmorillonitic, frigid Lithic Argixerolls (Pommerining 1983). Site Two had a mixture of deep and shallow soils. These soils were classified by Pommerining (1983) as sandy, mixed, frigid, Aridic Haploxerolls and could be found mainly on foot slopes. Loamy, skeletal, mixed, frigid Pachic Haploxeroll soil was found on the midslope and slope shoulders.

## Experimental Design

Four 0.4 ha treatments were established in 1984: 1) Control—no treatment; 2) Pine Thinned—pine thinned and western juniper left at pretreatment densities; 3) Juniper Removed—juniper removed and ponderosa pine left at pretreatment densities and; 4) Pine Thinned and Juniper Removed—pine thinned and all juniper removed. The treatments were applied in a randomized block design, with four blocks and four treatments. Three of the four blocks were placed on Site One. The fourth block was placed at Site Two. All ponderosa pine thinning was to an average 5.5 m x 5.5 m spacing (336 trees ha<sup>-1</sup>).

Diameter at breast height (DBH) of all trees were measured prior to treatment and ponderosa pine was measured again in the fall of 1985 and 1986. Diameter was converted to basal area. Basal area growth for each pine was converted to percent growth by dividing current years growth by total tree basal area, including current year's growth. Percent growth values were used in analysis.

In 1985, understory response to western juniper removal and ponderosa pine thinning was determined from herbaceous biomass in each treatment. One hundred 0.2m<sup>2</sup> (50 cm x 40 cm) quadrats were clipped in each treatment. In each quadrat, herbaceous vegetation was clipped to 1 cm height and current years growth was clipped from shrubs. Plots were clipped during the late spring and summer to estimate peak standing crop.

In 1986, cover was used to determine understory response to treatment in addition to biomass. Cover was determined ocularly from 0.2 m<sup>2</sup> quadrats following methods outlined by Anderson (1986). An undetermined number of yearlings steers accidentally grazed blocks two and three on Site One in the spring of 1986. The steers were on the site for approximately three weeks. At the point of discovery the steers were removed, but a significant amount of the current years growth had been removed. Plant biomass was collected on the ungrazed blocks in 1986. Cover of grasses and forbs was collected and aboveground biomass from blocks where no grazing occurred. Plots that had not been grazed were clipped as in 1985 after cover estimation was complete. A simple linear regression was run on biomass and cover to compare understory response (SAS 1986).

Understory biomass and ponderosa pine growth responses were analyzed using analysis of variance.

Because of missing values the ANOVA functions from PROC GLM of SAS were used (SAS 1986). Significantly different means were separated using a Student-Newman-Keuls test at  $P \geq 0.05$  (Steel and Torrie 1980).

## Results

### Understory Plant Response 1985

Understory biomass in all treatments was dominated by grasses and forbs. Total understory biomass in 1985 ranged from 320 to 542 kg ha<sup>-1</sup> (Table 1). Total understory, total grass, and perennial grass biomass in the Juniper Removed treatment was greater than the Pine Thinned treatment, but Pine Thinned, Control and Pine Thinned/Juniper Removed treatments were not different.

Perennial grass biomass significantly exceeded annual grass biomass in all treatments. Perennial grass biomass was dominated by bluebunch wheatgrass, Idaho fescue, bottlebrush squirreltail, and Sandberg bluegrass. Biomass of perennial grasses in the Juniper Removed treatment was greater than the Control or Pine Thinned treatments. Treatment did not affect biomass of bluebunch wheatgrass,

Idaho fescue or forbs. Bottlebrush squirreltail biomass was increased by the Juniper Removal treatment, but not significantly affected by the other treatments. Sandberg bluegrass in the Pine Thinned and Juniper Removed treatments had greater biomass than the Control or Pine Thinned/Juniper Removed treatments. Total annual grass biomass in the Juniper Removed treatment was greater than the biomass of annual grasses in the ponderosa pine thinned treatment. There was no difference in total annual grass biomass between the Control and the treatments where western juniper removal occurred. Total shrub biomass in treatments where western juniper had been removed was greater than treatments with western juniper present.

### Understory Plant Response 1986

Understory herbaceous plant biomass was estimated from regression equations derived from biomass and cover data from blocks 2 and 4. There was a strong relationship between biomass and cover,  $r^2 = 0.88$ ,  $p \geq 0.05$  for total understory production (Table 2). Biomass and cover were also

TABLE 1. Understory plant biomass by treatment one year after treatment.

	Treatments			
	Control	Pine Thinned	Juniper Removed	Pine Thinned/ Juniper Removed
Species	kg ha <sup>-1</sup>	kg ha <sup>-1</sup>	kg ha <sup>-1</sup>	kg ha <sup>-1</sup>
Bluebunch wheatgrass	50.7	47.8	51.7	70.2
Idaho fescue	40.4	32.9	20.5	41.2
Bottlebrush squirreltail	17.7ab*	5.6a	42.0b	19.2ab
Sandberg bluegrass	24.2a	40.6b	47.1b	29.1a
Other perennial grasses	13.3	11.8	18.8	16.6
Total perennial grasses	146.3a	138.6a	209.9b	176.1ab
Total annual grasses	12.9ab	5.6a	28.5b	21.3ab
Total grasses	159.2a	144.2a	238.4b	197.5ab
Perennial forbs	100.2	67.2	91.5	65.7
Annual forbs	112.5	72.8	119.9	87.0
Total	212.8	140.0	211.4	152.7
Big sagebrush	20.0	32.7	51.8	31.5
Total shrubs	35.5ab	36.3a	92.3b	57.3ab
Total	407.5ab	320.5a	542.0b	407.5ab

\*Different letters denote significant differences ( $p \geq 0.05$ ) between treatments, using Student-Newman-Keuls multiple range test.

TABLE 2. Estimates of plant biomass for 1986 using regression equations derived from plant biomass and cover estimates.

Species	Treatments				r <sup>2</sup>
	Control kg ha <sup>-1</sup>	Pine Thinned kg ha <sup>-1</sup>	Juniper Removed kg ha <sup>-1</sup>	Pine Thinned/ Juniper Removed kg ha <sup>-1</sup>	
Bluebunch wheatgrass	97.2	44.4	140.7	125.2	0.89
Idaho fescue	0.0	2.3	4.8	3.5	0.82
Total perennial grasses	178.0	106.8	251.1	245.5	0.78
Total grasses	96.7	54.6	141.0	137.7	0.90
Perennial forb	107.3	97.9	186.8	109.2	0.72
Total	339.4	241.5	462.2	422.6	0.88

TABLE 3. Two year mean percent basal area growth of all ponderosa pine and ponderosa pine in five diameter classes. Percent basal area growth equals current year basal area growth divided by total tree basal area.

All Trees	Control %	Pine Thinned %	Juniper Removed %	Pine Thinned/ Juniper Removed %
1985	1.0	0.8	1.1	1.7
1986	1.6	0.3	1.6	1.1
Total	2.6	1.1	2.7	2.8
Diameter Classes				
Less than 5 cm	45.1a*	21.2bc	19.0c	29.8b
5 cm to 15 cm	5.0	5.6	9.6	8.8
15 cm to 50 cm	3.1	4.3	10.9	4.4
30 cm to 40 cm	4.2	2.0	2.5	2.8
Greater than 40 cm	1.5	0.9	1.6	2.2

\* Different letters denote significant differences ( $p \geq 0.05$ ) between treatments, using Student-Newman-Keuls multiple range test.

significantly correlated from the functional groups, perennial forbs, total grass, and total perennial grass. Estimates of biomass were highest in the Juniper Removed Treatment and lowest in the Pine Thinned treatments. This trend is similar to estimates of understory biomass one year after western juniper removal and ponderosa pine thinning.

### Ponderosa Pine Growth Response

There was no significant differences in percent basal area growth due to treatment when all trees were considered (Table 3). Ponderosa pine under 5 cm DBH were the only group to exhibit a significant response to treatment. Trees in the smallest size class had significantly greater percent basal area growth in the Control than in other treatments (Table 3).

## Discussion

### Understory Biomass and Cover

Western juniper may be the most important competitor of understory plants in juniper/pine ecotone. Total understory biomass was estimated to be higher in the treatments where western juniper was removed. This pattern is similar to basal area response of ponderosa pine, perhaps indicating similar factors influenced both understory and pine response.

Established dominant understory plants on site before treatment were the groups to show the greatest response to western juniper removal. Other studies in central Oregon have found that removal of western juniper increased understory biomass (Bedell and Bunch 1978, Vaitkus 1986, Vaitkus and Eddleman 1991). Perhaps the perennial plants

have the ability to rapidly utilize additional resources made available by tree removal. Established perennial grasses, with fibrous root systems, and their ability to quickly produce leaf area have been found to respond quickly to tree removal. However, this response may be short lived.

Shrub biomass was also highest in treatments where western juniper had been removed. Big sagebrush, a semi-evergreen shrub, is capable of photosynthesis early in spring when most other plants are drawing on reserves to produce leaves (Miller 1988). The deep roots of big sagebrush also permit it to utilize deep water unavailable to many understory plants (Abbott *et al* 1991, Reynolds and Fraley 1989). Sagebrush biomass was lowest in the control, indicating it may have been in competition with ponderosa pine and western juniper. Shrub species appear to have responded to the Pine Thinned treatment indicating release from competition.

### Ponderosa Pine Growth Response

Ponderosa pine trees under 5 cm DBH exhibited a negative response to all treatments. The small trees were most often found under the canopy of another larger woody plant. In a study of western juniper, over 90 percent of the juvenile western trees found were beneath the canopy of larger juniper or mountain big sagebrush (file data, EO-ARC). It is thought that this location provides the juvenile trees with a more moderate microclimate than in the interspace areas where they are exposed to full sunlight. A similar condition may occur with the younger ponderosa pine at this dry end of its range. Removing the overstory trees exposes the smaller trees to greater microclimate fluctuations than experienced under the canopy of a larger tree or shrub. The smaller trees may need time to adjust to the more direct sunlight and greater temperature fluctuations. Shrub and grass biomass also increased following tree removal and may increase competition with smaller ponderosa pine trees.

Other studies of dense stands of larger ponderosa pine have reported a lag in response to thinning (Barrett 1982, Brix and Mitchell 1986, Oliver 1979, Oren *et al.* 1987). The high initial tree densities in this study, 988 trees ha<sup>-1</sup> (western juniper and ponderosa pine), may also have contributed to the thinning response lag. Delayed response has been attributed to many factors. One of the first consequences of thinning is an increase

in root and leaf area of residual trees (Perry 1985). The lag in basal area growth could be caused by the larger trees adding substantial levels of new needles. Roots may need time to grow into areas left vacant by removed trees. Brix and Mitchell (1986) found that root systems of Douglas-fir left after thinning might not be sufficient to absorb the additional moisture.

Oren and others (1987) found that diameter increases of ponderosa pine at lowest stocking densities was over twice that of pine in the highest stocking densities. Growth of ponderosa pine in dense stands after light thinning was found by Oliver (1979) to be below the pre-thinning level in northeastern California. Removing western juniper may be comparable to heavy thinning of ponderosa pine. Far greater numbers of potential competitors were removed (250-300 ha<sup>-1</sup>) from the stand when western juniper was removed, while an average of 53 trees ha<sup>-1</sup> were removed in treatments where ponderosa pine was thinned. Increased exposure of crowns after thinning and insufficient root area may lead to greater transpiration and moisture stress for the tree resulting in little initial growth response after tree removal.

Thinning of ponderosa pine may not be economically practical, especially if western juniper is not treated. Western juniper's aggressive nature may allow it to capitalize on resources made available by thinning, leaving little available for remaining ponderosa pine. Short term thinning response observed in this study indicates that additional growth of residual ponderosa pine would never replace the potential future growth and volume of trees removed during thinning.

Evaluating two years post treatment response may not be enough to determine the effects of ponderosa pine thinning and western juniper removal on residual ponderosa pine growth. However, the understory vegetation did positively respond to western juniper removal and/or ponderosa pine thinning one year after treatment. Less than 11 km away a study conducted in Crook County (Vaitkus 1986, Vaitkus and Eddleman 1991) found that removal of western juniper increased understory biomass markedly the first and second year following western juniper removal. Precipitation is lower on this site and no ponderosa were present. Sandberg bluegrass and perennial forb biomass differed slightly from areas with western juniper present treatments. Release from moisture competition with western juniper seemed to be the

most important factor on these sites (Vaitkus and Eddleman 1991).

Thinned stands are often used as a transitory range until canopy closure occurs and forage biomass falls below usable levels. Thinning for increases in livestock forage alone is often impractical, but when considered as an adjunct to timber improvement, increases in forage yields could become an important part of a farm/forestry program (McConnell and Smith 1970). Conversely, timber values of sparsely forested areas are often overlooked because of their value as spring, fall, and summer range for domestic livestock. Coordination of management objectives could increase the economic value of these areas.

## Literature Cited

- Abbott, M. L., L. Fraley Jr. and T. D. Reynolds. 1991. Root profiles of selected cold desert shrubs and grasses in disturbed and undisturbed soils. *Envir. and Exp. Bot.* 31:165-178.
- Anderson, E. W. 1986. A guide for estimating cover. *Rangelands* 8:236-238.
- Barrett, J. W. 1979. Silviculture of ponderosa pine in the Pacific Northwest: the status of our knowledge. USDA For. Serv. Gen. Tech. Rept. PNW-97. Pacific Northwest Forest and Range Experiment Station 21p.
- Barrett, J. W. 1982. Twenty-year growth of ponderosa pine saplings thinned to five spacings in central Oregon. USDA For. Serv. Res. Pap. PNW-301. Pacific Northwest Forest and Range Experiment Station 17p.
- Bedell, T. E. 1987. Rehabilitation of western juniper rangeland: case history. *In Proc. Pinyon-Juniper Conference.* Everett, R. L. (ed.). 1986. USDA For. Serv. Gen. Tech. Rep. INT-215. Intermountain Forest and Range Experiment. Pp. 313-316.
- Bedell, T. E. and T. R. Bunch. 1978. Effects of western juniper on forage production and livestock grazing management. *In Proc. Western Juniper Ecology and Management Workshop.* Martin, R. E., Dealy, J. E., and Caraher, D. L. (eds.). USDA For. Serv. Gen. Tech. Rep. PNW-74. Pacific Northwest Forest and Range Experiment Station. Pp. 163-169.
- Brix, H. and A. K. Mitchell. 1986. Thinning and nitrogen fertilization effects of soil and tree water stress in a Douglas-fir stand. *Can. J. Res.* 16:1334-1338.
- Burkhardt, J. W. and E. W. Tisdale. 1969. Natural and successional status of western juniper vegetation in Idaho. *J. Range Manage.* 22:264-270.
- Burkhardt, J. W. and E. W. Tisdale. 1976. Causes of juniper invasion in southwestern Idaho. *Ecology* 57:472-484.
- Caraher, D. L. 1978. The spread of western juniper in central Oregon. *In Proc. Western Juniper Ecology and Management Workshop.* Martin, R. E., Dealy, J. E., and Caraher, D. L. (eds.). USDA For. Serv. Gen. Tech. Rep. PNW-74. Pacific Northwest Forest and Range Experiment Station. Pp.3-9.
- Driscoll, R. S. 1964. A relict area in the central Oregon juniper zone. *Ecology* 45:345-353.
- Eckert, R. E. 1957. Vegetation-soil relationships in some (*Artemisia*) types in northern Harney and Lake Counties, Oregon. Ph.D. Thesis. Corvallis, Oregon State University.
- Eddleman, L. E. 1983. Some ecological attributes of western juniper. *In Res. In Rangeland Management.* Agricultural Experiment Station, Oregon State University, Corvallis, Oregon. Spec. Rep. 682.
- Eddleman, L. E. 1987. Establishment and stand development of western juniper in central Oregon. *In Proc. Pinyon-Juniper Conference.* Everett, R. L. (eds.) USDA For. Serv. Gen. Tech. Rep. INT-215. Intermountain Forest and Range Experiment Station. Pp. 255-260
- Evans, R. A. 1984. Plant succession following western juniper control with picloram. *In Proc. Western Juniper Management short Course.* Bedell, T. E. (ed.) Oregon State University Extension Service. Pp. 93-95.
- Fowells, H. A. 1965. Silvics of forest trees of the United States. USDA For. Serv. Agricultural Handbook No. 271.
- Franklin, J. F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Pac. Northwest For. and Range Exp. Sta. Portland, Oregon. Gen. Tech. Rep. PNW-8. 417 p.
- Hitchcock, C. E. and A. Cronquist. 1978. Flora of the Pacific Northwest. University of Washington Press. 730p.
- McConnell, B. R. and J. G. Smith. 1970. Response of understory vegetation to ponderosa pine thinning in eastern Washington. *J. Range Manage.* 23:208-212.
- Mehring, P. J. and P. E. Wigand. 1987. Western juniper in the holocene. *In Proc. Pinyon-Juniper Conference.* Everett, R. L. (ed) USDA For. Serv. Gen. Tech. Rep. INT-215. Intermountain Forest and Range Experiment Station. Pp. 109-120.
- Miller, R. F. 1988. Comparison of water use by (*Artemisia tridentata* ssp. *wyomingensis*) and (*Chrysothamnus viscidiflorus* ssp. *viscidiflorus*). *J. Range Manage.* 41:58-62.
- Miller, R. F. and L. M. Shultz. 1987. Water relations and leaf morphology of (*Juniperus occidentalis*) in the Northern Great Basin. *For. Sci.* 33:690-706.

## Acknowledgements

The authors thank Richard F. Miller, Tony Svejcar, William C. Krueger, Gregg Riegel, and two anonymous reviewers for their comments on earlier drafts of this manuscript. We also thank the Breese family and J.B. Cox for permitting us to conduct the study on their land, and John Jackson of the Oregon Department of Forestry for providing technical assistance during ponderosa pine thinning and western juniper removal. Special thanks to Carol Mc Donald for her help in the final preparation of this manuscript.

- Oliver, W. W. 1979. Growth of planted ponderosa pine thinned to different levels in northern California. USDA For. Serv. Res. Pap. PSW-147. Pacific Southwest Forest and Range Experiment Station.
- Oren, R., R. H. Waring, S. G. Stafford and J. W. Barrett. 1987. Twenty-four years of ponderosa pine growth in relation to canopy leaf area and understory competition. For. Sci. 33:538-547.
- Perry, D. A. 1985. The competition process in forest stands. From: Attributes of Trees as a Crop Plant. Cannell, M. G. R., and Jackson, J. E. (eds.) Institute of Terrestrial Ecology. Abbots Ripton, Hunts, England.
- Pommerining, J. A. 1983. Interim soil survey report of the Brothers Area, Prineville, Oregon District. U.S. Dept. of Interior. BLM. 972 p.
- Reynolds, T. D. and L. Fraley Jr. 1989. Root profiles of some native and exotic plant species in southeastern Idaho. *Envir. Exp. Bot.* 29:241-248.
- SAS. 1986. SAS-STAT User's Guide (Release 6.03). SAS Inst. Inc., Cary, N.C. 1028p.
- Steel, R. G. D. and J. H. Torrie. 1980. Principles and Procedures of Statistics. McGraw-Hill Book Company, Inc., New York.
- Vaitkus, M. R. 1986. Effects of western juniper on understory herbage production in central Oregon. M.S. Thesis, Oregon State University, Corvallis.

*Received 29 April 1993*

*Accepted for publication 3 January 1994*