

Recent *Juniperus occidentalis* (Western Juniper) expansion on a protected site in central Oregon

PAUL A. KNAPP* and PETER T. SOULÉ†

*Department of Geography, Georgia State University, Atlanta, GA 30303–3083, USA, †Department of Geography and Planning, Appalachian State University, Boone, NC 28608, USA

Abstract

The expansion of *Juniperus occidentalis* (western juniper) has been extensive in the last century, and increases in density and cover have been linked with the indirect effects of domestic livestock grazing (i.e. cessation of periodic fires, increases of nurse-plant sites), and more favourable climatic conditions. In this study, we document changes in vegetation (including *J. occidentalis*) in central Oregon over a 23-year period and relate these changes to their probable causes. In June 1995 we returned to the Horse Ridge Research Natural Area (HRRNA), a site that has a history of minimal anthropogenic impacts, to replicate a 1972 vegetation survey. Using the canopy-intercept method, line intercept method, and aerial photography analysis to measure herbaceous cover, shrub cover and tree cover, respectively, we found significant changes had occurred in the 23-year period between studies. Relative changes of tree, shrub, and perennial herbaceous cover were 59%, 7%, and –38%, respectively. Relative increases in *J. occidentalis* density, as measured by the number of clumps and the number of stems, were 37% and 53%, respectively. Mean maximum height of *J. occidentalis* had increased by 10%. We examined the role of potentially confounding influences (e.g. fire, grazing, pathogens, climatic variability) and found that none of the traditional mechanisms implicated in *J. occidentalis* expansion adequately explained the observed changes. We suggest that the role of biological inertia of both anthropogenic and natural means may have had a profound effect on the *J. occidentalis* ecology of HRRNA.

Keywords: biological inertia, central Oregon, *Juniperus occidentalis* expansion, semirelict site

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Introduction

Juniperus occidentalis (western juniper) expansion in the Pacific North-west during the last century has been well-documented (Burkhardt & Tisdale 1969, 1976; Caraher 1978; Eddleman 1987; Miller & Wigand 1994; Miller & Rose 1995), lending considerable credence to the argument that *J. occidentalis* encroachment may substantially influence ecosystem form and function (Belsky 1996). The best-documented impacts of *J. occidentalis* invasion concern the alterations of shrub and herbaceous cover (Eddleman 1987; Bedell *et al.* 1993), and phytomass production (Vaitkus & Eddleman 1991), while the effects of accelerated soil erosion, increased surface runoff, reduced infiltration, and decreased wildlife habitat,

although often mentioned, are not supported by experimental evidence (Gifford 1987; Belsky 1996).

Historic *J. occidentalis* expansion can be characterized by three major features based on palaeoecological dating methods (tree-ring dating, pollen analysis and plant macrofossils) and historic documents. First, establishment rates for *J. occidentalis* began increasing in the late 1800s and density continued to increase during the 20th century at several locations (e.g. Young & Evans 1981; Eddleman 1987; Miller & Rose 1995). Further, at some locations, establishment rates have increased 'geometrically' since the 1960s (e.g. Miller & Rose 1995). Second, the distribution of *J. occidentalis* is no longer isolated to rocky outcrops (Burkhardt & Tisdale 1976), but has expanded into sagebrush-steppe, riparian, and aspen communities (Miller & Rose 1995), and land area covered has more than doubled in the last century (Miller *et al.* 1987). Third, the rate of

Correspondence: Paul Knapp, fax +1/ 404-651-3235, e-mail gegpak@panther.gsu.edu

historic *J. occidentalis* expansion in the Intermountain Region is unprecedented, and palaeoecological evidence suggests strongly that this period represents the first within the Holocene where *J. occidentalis* has expanded during drier conditions (Miller & Wigand 1994).

Because the onset of *J. occidentalis* invasion was closely linked to EuroAmerican settlement, explanations for *J. occidentalis* establishment have given primacy to direct anthropogenic causes, although climatic changes are also cited often and *J. occidentalis* expansion has occurred in environments that have had minimal anthropogenic disturbances (e.g. Knapp & Soulé 1996). Nearly all studies have cited cessation of fires, or an increase in the fire free interval, as the primary cause (Burkhardt & Tisdale 1976; Young & Evans 1981; Eddleman 1987; Miller & Rose 1995). The main argument is that the introduction of domestic livestock sufficiently reduced the amount of understory herbaceous biomass (fine fuel) that is required to carry fire. Subsequently, fire-induced mortality is reduced for fire-sensitive *J. occidentalis* (Agee 1993). Further, domestic livestock grazing has been shown to favour shrubs (West 1983) that in turn act as nurse plants for *J. occidentalis* seedlings (Eddleman 1987; Evans 1988).

Miller & Wigand (1994) noted that cessation of periodic fires was concurrent with wet and mild conditions (favourable to *J. occidentalis* establishment) during a time of widespread *J. occidentalis* establishment (late 1800s to early 1900s). Studies that have explored expansion and increased dominance of woody species into grass-dominated communities also cite changes in the quantity and/or seasonality of precipitation as a possible cause (Neilson 1986; Ehleringer *et al.* 1991; Archer 1994; Weltzin & McPherson 1995). Neilson & King (1992) noted the amount of winter precipitation recharging deep soil water influences what type of forest/nonforest communities exist, and that intermediate amounts of deep soil water theoretically support open forests like pinyon-juniper woodlands. Thus, changes in winter precipitation may affect distributions of woodlands (Archer 1994).

An additional and controversial mechanism (e.g. Archer *et al.* 1995) linking the expansion of woody species and possible effects of atmospheric CO₂ enrichment is based on several premises: (i) plants growing under elevated atmospheric CO₂ consistently produce greater biomass (Kimball 1983; Kimball & Idso 1983); (ii) increasing atmospheric CO₂ increases water use efficiency (WUE) because of increased photosynthesis and/or reduced transpiration (Idso 1989; Eamus 1991; Polley *et al.* 1993); and (iii) species are better able to cope with environmental stresses (e.g. inadequate water, light and nutrients, high temperatures) under elevated CO₂ levels (Idso & Idso 1994). The effects of elevated atmospheric CO₂ are thought to be expressed best in arid and semiarid climates (Idso

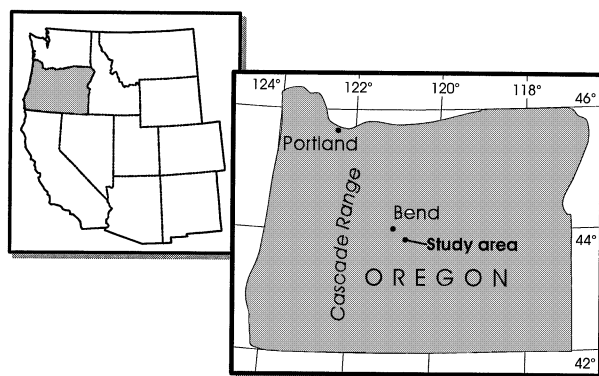


Fig. 1 Location of HRRNA.

1989; Mooney *et al.* 1991; Mayeux *et al.* 1991, 1994), and the benefits may be preferential to woody as opposed to herbaceous species (Idso & Kimball 1993). For example, results from several studies suggest that growth of many high elevation western U.S. conifers exceeded expected growth during the 20th Century possibly because of elevated atmospheric CO₂ (LaMarche *et al.* 1984; Graybill 1987; Graybill & Idso 1993).

Given the ecological and management implications of continued *J. occidentalis* expansion there is an impetus to monitor vegetation change to increase our knowledge of juniper ecology. Longitudinal studies are valuable because they allow for an analysis of the magnitude and direction of change. The value of a longitudinal study is enhanced when confounding factors (e.g. grazing, fire, logging, climate) are either reduced and/or at least known. As such, we assess vegetation changes between 1972 and 1995 on a minimally disturbed Research Natural Area dominated by *J. occidentalis* in central Oregon. Our study objectives were twofold: (i) to characterize the amount and direction of vegetation change for herbs, shrubs, and trees during the 23-year period between studies; and (ii) to examine the most likely mechanisms responsible for the vegetation change.

Methods

Study area

Horse Ridge Research Natural Area (HRRNA) is a minimally disturbed site in central Oregon (Fig. 1). Located ≈ 31 km south-east of Bend, HRRNA is a 240 ha enclosure ranging from 1250 to 1430 m elevation over rolling topography of Columbia Basalts (Hall 1972; BLM 1995). Prior to establishment of a fence in 1974, domestic livestock 'apparently had little impact on the Horse Ridge Research Natural Area' because of a lack of a permanent water source to attract animals (Hall 1972) and the distance from well-traveled public roads (Baldwin 1974).

HRRNA has experienced minimal additional anthropogenic disturbances in the last two decades (Halvorson, pers. comm., 1995).

The climate of HRRNA is semiarid. Annual precipitation at nearby Bend (Fig. 1) is winter-dominated and averages 31 cm. Average temperatures at Bend range from 17.7 °C in July to -0.6 °C in January (Karl *et al.* 1990).

Vegetation on HRRNA is classified as a *Juniperus occidentalis*/*Artemisia tridentata*/*Carex filifolia* (western juniper/big sagebrush/threadleaved sedge) community (Franklin & Dyrness 1988). Foraging pressure is exerted by native herbivores (mule deer and lagomorphs) and granivores (small rodents and ants). Approximately 85% of the HRRNA consists of the Stookmoor–Westbutte complex soil series, including the entire study site. The soil consists of volcanic ash over basaltic and welded tuff colluvium. Basaltic bedrock begins at \approx 61 cm depth (USDA-NRCS, in press).

Vegetation analysis

In 1972, Gashwiler (1977) made vegetation cover measurements on HRRNA based on five components: (i) tree canopy; (ii) tree reproduction; (iii) shrubs; (iv) grasses and sedges; and (v) forbs. Vegetation on HRRNA was sampled from 16 randomly chosen 400 m² circular plots that were part of a 144 station (12 × 12) grid. Each station was spaced 40.2 m apart. The entire grid, located near the centre of HRRNA and with < 25 m vertical relief, represented 19.6 ha. At each circular plot centre, two measuring tapes, each 22.6 m long, crossed at right angles forming 45.2 m of line. Shrub cover and tree cover (< 0.9 m height) were measured by line intercept. Sixteen rectangular microplots (20 × 50 cm) were placed at right angles along one side of the tape at 3 m intervals to estimate canopy cover of each herbaceous species based on methods outlined by Daubenmire (1959). Tree canopy coverage was determined from an oblique photograph taken from the ground over the plot centre. *J. occidentalis* height was measured using a clinometer sighted on the highest tree within each plot.

Three measures of *J. occidentalis* density were taken. First, centred in each of the 400 m² plots was a smaller circular plot (38.5 m²; 3.5 m radius) that was used to measure the cover of all seedlings and saplings less than 5.1 cm d.b.h. (here termed 'tree reproduction rate'). Second, within each of the 400 m² circular plots, *J. occidentalis* tree stems > 5.1 cm (measured at ground level) were measured for diameter. Each 'independently rooted branch was considered a stem' (Gashwiler 1977). Third, the number of 'clumps' (the primary trunk plus stems) per 400 m² plot were counted.

With one exception, we replicated Gashwiler's vegetation survey in June 1995. Replication was made possible

by the permanency of the circular plots, with the centre of each plot marked by a metal stake that included station identification. We were unable to replicate the methodology used to determine tree canopy coverage. Instead, we used large-scale aerial photography (1:7,920–1:31 000) from 1951, 1973, 1979, 1985, 1990, 1994 and 1995 to measure changes in *J. occidentalis* cover. We determined cover by scanning the aerial photographs for the entire 144 grid station area, and then adjusting upwards the photograph size of smaller scale photographs to allow for a comparable scale (and size) to the larger scale photos. We imported the scanned images into a GIS software program, IDRISI, and used the black and white colour contrasts to identify and determine *J. occidentalis* cover.

We compared *J. occidentalis* data with Gashwiler's using difference of means tests to determine if statistically significant changes occurred to vegetation from 1972 to 1995. The specific difference of means tests include: (i) maximum height of *J. occidentalis*, (ii) tree reproduction rate, (iii) tree diameters (based on class size) at ground level, (iv) number of stems greater than 5.1 cm, and (v) number of clumps. Statistical tests with the above groups were possible because the raw data were available.

Since a meteorological monitoring station has never been established on HRRNA, we examined mean monthly temperature and precipitation records from Bend, Oregon, the nearest and most comparable site included in the United States Historical Climatology Network (HCN). The Bend station is \approx 31 km north-west of HRRNA (elevation 1250–1430 m) at an elevation of 1113 m. Our HCN database was complete from January 1902–June 1995.

Prior to statistical analyses we calculated mean temperature and total precipitation for both the seasonal water-year (July to June) and winter (November to February) values. Since HRRNA precipitation is largely concentrated in the winter, and since winter precipitation is largely responsible for recharging the deep soil moisture that woody species in the region need to survive, the use of seasonal water-year (SWY) values of mean temperature and total precipitation is appropriate. Winter patterns also were examined because winter precipitation is the primary constraint on woody vegetation (Neilson & King 1992). We used the November to February period as the winter season because on average over half (52%) of the SWY precipitation falls during these months.

We tested for significant differences in precipitation and temperature values between discrete time periods using the Wilcoxon Rank Sum *W*-test ($P < 0.05$), and we tested for differences between the 23-year period between the two surveys (SWY 1972–94) and the 23-year period prior to Gashwiler 1977) survey (SWY 1949–71). We also tested for differences between the 10-year periods prior

to each vegetation survey (1962–71 compared to 1985–94). The 10-year comparisons are included because Goldberg & Turner (1986) have shown that vegetation in arid regions can exhibit significant responses over time periods as short as 8–10 years. In addition to the difference of means tests, the 10-year periods were compared using a ranking scheme that shows how individual years in these two periods compare to observations over the period of record. Since biennials and annuals can be significantly impacted by even shorter-term climatic conditions, especially precipitation, we also compared the 24- and 12-month periods prior to Gashwiler's (1977) fieldwork in 1972 (July 1970 to June 1972) and our replicate survey (July 1993 to June 1995) using difference of means tests.

The climatic data were examined for linear trends over the two 23-year periods prior to vegetation sampling (1949–71, 1972–94), over the combined 46-year period (1949–94), and over the complete period of record (1902–94). We used temperature and precipitation as the dependent variables and seasonal water-year as the independent variable in a series of bivariate regressions. We examined directional change in the climatic variables using trend slopes from bivariate regression, and tested for significance in the trends using rank correlation (Yin 1993).

Results

Tree, shrub, and herbaceous cover

Total cover of perennial vegetation increased from 45.1% to 51.7% from 1972 to 1995. Vegetation change was characterized by a large increase in *J. occidentalis*, little change in shrubs, and a large decrease in grasses and sedges (Table 1). Changes in all species of forbs were also determined, but the data are not summarily presented as they represent only a small portion of the total vegetation. Total forbs significantly increased. *J. occidentalis* remains the dominant species for HRRNA.

Since Miller & Rose (1995) have reported that *J. occidentalis* expansion has increased geometrically on Steens Mountain in southeastern Oregon since the 1960s, we compared the rate of increase during two 22-year periods 1951–73 and 1973–95, to see if this pattern was also present at HRRNA. It was, with the average annual percentage increase being 0.32 and 0.58 for the earlier and latter periods, respectively (Table 2, Fig. 2). Additionally, *J. occidentalis* cover more than doubled (136% relative increase) on HRRNA from 1951 to 1995 (Table 2, Fig. 2).

Changes in cover of all shrubs were minor with *Artemisia tridentata* remaining the dominant species (Table 1). We observed numerous mature *Artemisia tridentata* indi-

viduals that were either dead or in decreased vigor, but these had been replaced by newly established individuals.

While cover of all grass species declined during the 23-year period, the decline was greatest in *Carex filifolia* and *Agropyron spicatum* (bluebunch wheatgrass) (Table 1). Conversely, cover of *Festuca idahoensis* (Idaho fescue) decreased only slightly. Annual grasses (e.g. *Bromus tectorum* (cheatgrass)) were not present on our study plots, or within the 144 grid station area.

Additional Western Juniper characteristics

By nearly all measures, *J. occidentalis* had increased since 1972 (Fig. 3, Table 3). Mean maximum height of *J. occidentalis*, the density of clumps/400 m², and the density of stems all increased significantly. Of the eight diameter classes measured, six increased, four significantly, with the greatest differences found for the smaller size classes. The only measurement indicative of decreased *J. occidentalis* dominance was tree reproduction, based on individuals < 5.1 cm diameter, but this measure may be somewhat unreliable because it is based on such a small portion of our sample plots.

Possible vegetation change influences at HRRNA

Climate. Trends for all time sequences examined are weakly negative and not significant for both SWY and winter precipitation. SWY temperatures exhibit more persistence, with a significant positive trend for the 1949–94 period. However, SWY temperatures have no significant trends over the 93-year period or the two 23-year periods prior to each vegetation survey. For winter temperatures, no significant trends exist for any of the time periods examined.

Wilcoxon test results for SWY and winter precipitation comparisons show no significant differences between the 23- and 10-year periods prior to the vegetation surveys. Precipitation comparisons over the 24- and 12-month periods also showed no significant differences. For SWY temperature, the 1972–94 period was significantly warmer than the 1949–71 period. All other SWY and winter temperature comparisons showed no significant differences.

Analyses of ranked values of SWY precipitation show that both 10-year periods contain years of extreme aridity, but no top 10 years for wetness (Table 4). The winter rank comparisons show greater differences between the two periods, with the later period clearly drier for both SWY and winter precipitation. For temperature, the rankings reveal that the later period contained more extremes (Table 5). Analyses of the historical climate record for Bend suggest that conditions on HRRNA have not been favourable for an expansion of woody species this century.

Table 1 Cover, composition, and standard error (all in percentage) of plant species within the study area during 1972 and 1995

Life Form/Species	1972 ^a Cover	Composition ^b	SE.	1995 Cover	Composition	SE
Total Perennial Forbs	1.2 ^c	2.7	–	0.96	1.86	0.28
Total Shrubs	5.6	12.4	–	6.02	11.6	0.71
Total Perennial	16.6	36.8	–	10.19	19.7	0.93
Grasses and sedges						
Total Western Juniper	21.7 ^d	48.1	–	34.5	66.7	–
Total Perennial Vegetation	45.1	100.0	–	51.7	100.0	–
Total Annual Vegetation	0.8	–	–	1.92	–	–
Total All Vegetation	45.9	–	–	53.62	–	–
Shrubs						
<i>Artemisia tridentata</i>	5.1	11.3	–	5.33	10.3	0.68
<i>Chrysothamnus vicidiflorus</i>	0.4	0.9	–	0.33	0.6	0.12
<i>Leptodactylon pungens</i>	+	–	–	0.10	0.2	0.06
<i>Tetradymia glabrata</i>	0.1	0.2	–	0.26	0.5	0.11
Grasses and sedges						
<i>Agropyron spicatum</i>	2.8	6.2	–	0.79	1.5	0.23
<i>Bromus tectorum</i> (A)	+	–	–	–	–	–
<i>Carex filifolia</i>	5.9	13.1	–	2.62	5.1	0.46
<i>Carex rossii</i>	+	–	–	–	–	–
<i>Festuca idahoensis</i>	5.7	12.6	–	5.56	10.8	0.65
<i>Koeleria cristata</i>	0.8	1.8	–	0.21	0.4	0.07
<i>Poa secunda</i>	–	–	–	0.12	0.2	0.08
<i>Sitanion hystrix</i>	0.5	1.1	–	0.18	0.3	0.09
<i>Stipa thurberiana</i>	0.8	1.8	–	0.71	1.4	0.25

^a Data from Gashwiler (1977); ^bComposition represents relative amounts of perennial species based on foliar cover; ^c Value determined by subtracting annual species cover from sum as shown in Gashwiler (1977); ^d We used the value determined from a 1973 aerial photograph.

Since the climatic parameters critical to growth of woody species (precipitation/soil moisture, especially winter precipitation) are not significantly different over the time periods prior to both vegetation surveys, the role of climate as a possible confounding influence is diminished.

Fire. Large fires are unlikely to occur on HRRNA since there is insufficient fine fuel (i.e. lack of grasses) necessary to carry fire (Hall 1972; Agee 1993), and the presence of individual fire-scarred trees suggests fires rarely spread. Gashwiler (1977) reported there was 'little evidence that fires [had] burned extensively' on HRRNA, and our observations were likewise; we noted the presence of a few burned trees within the 19.4 ha study area. Prineville BLM fire records for HRRNA report a single fire since 1972 (on 8/27/91) that covered 200 m² and burned eight *J. occidentalis* on the south end of the enclosure well away from the permanent plots (Halvorson 1991). *J. occidentalis* is a 'fire avoider' and highly susceptible to fire in the seedling and sapling stage (Agee 1993). Individuals < 4 m height (Martin 1978) and/or < 50 years old (Burkhardt & Tisdale 1976) suffer high mortality rates during fires (Agee 1993). Many *J. occidentalis* on HRRNA are < 4 m height, and because it may take up to a half century to

reach 4 m, it is unlikely fires have carried through the study site for at least 50 years.

Biotic influences. Neither plant disease nor herbivory appear to have significantly influenced vegetation on HRRNA. *J. occidentalis* is a stress-tolerant, long-lived species (Preston 1968), and is resistant to most pathogens and insects. In the absence of fire, its success rate to maturity is excellent. In some western shrub communities, attacks by pathogenic root rot organisms causing shrub mortality may be linked to periods of increased precipitation that causes waterlogging, thus, increasing soil salinity and decreasing soil oxygen in poorly drained soils (Weber *et al.* 1990). These conditions, however, do not exist at HRRNA.

It is unlikely that herbivores have affected our sampling results significantly. We saw no evidence, based on growth of the herbaceous species, of heavy grazing by mule deer, the primary ungulate grazer. Nor did we see any evidence of mule deer grazing on *J. occidentalis*. Assessing foraging influences by small mammals or insects (i.e. grasshoppers, crickets, caterpillars, and ants) is more difficult (Archer 1994). For example, fluctuating climatic conditions triggering either increases or decreases in animal populations

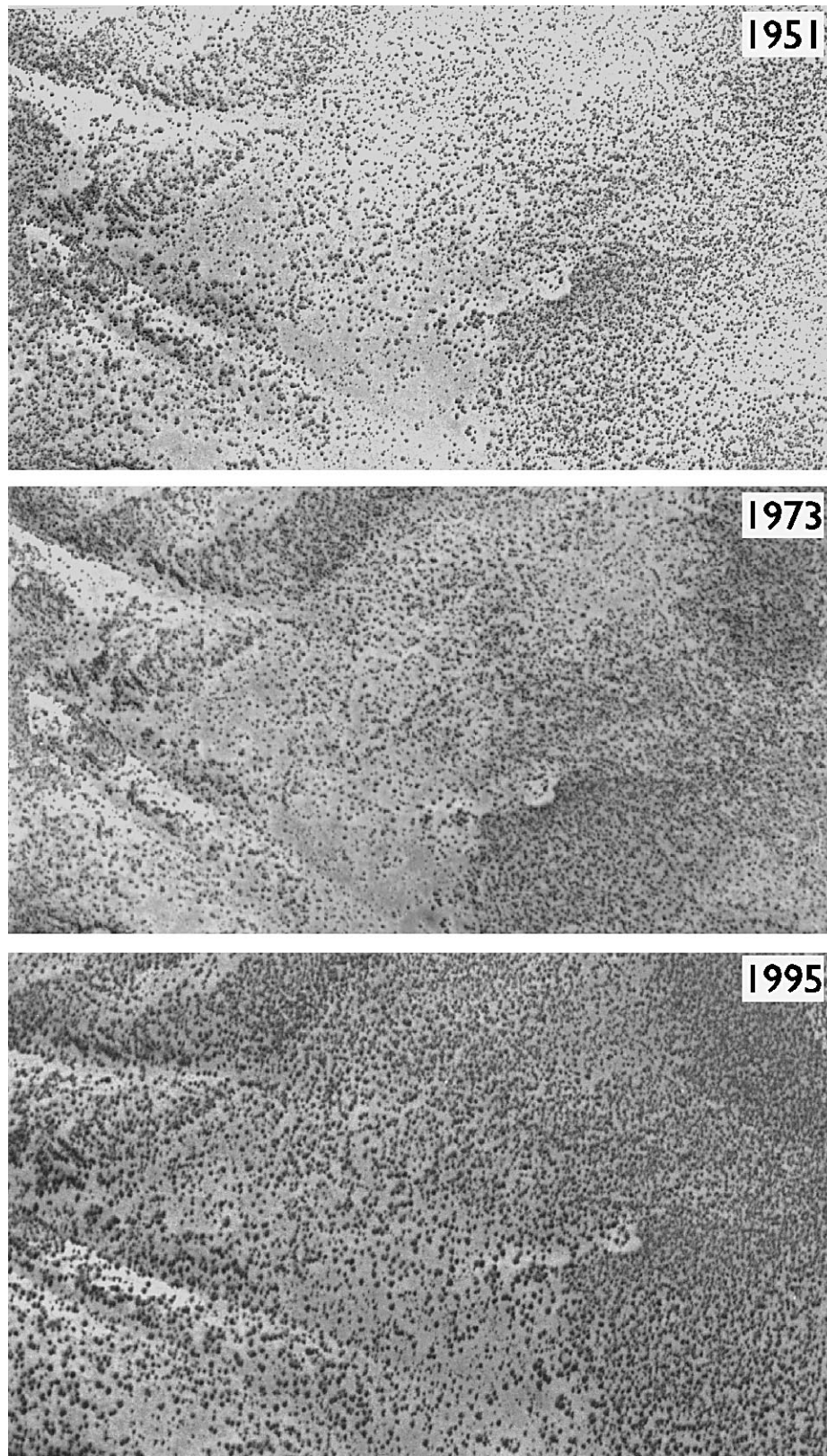


Fig. 2 Aerial photographs of approximate 240 ha HRRNA boundary showing increase of *J. occidentalis* cover and density between 1951 and 1995. Top of each photograph is east. Gashwiler's 19.6 ha study area is approximately centred on the semicircular clear area on the lower right of each photograph. Approximate scale 1:15, 840.

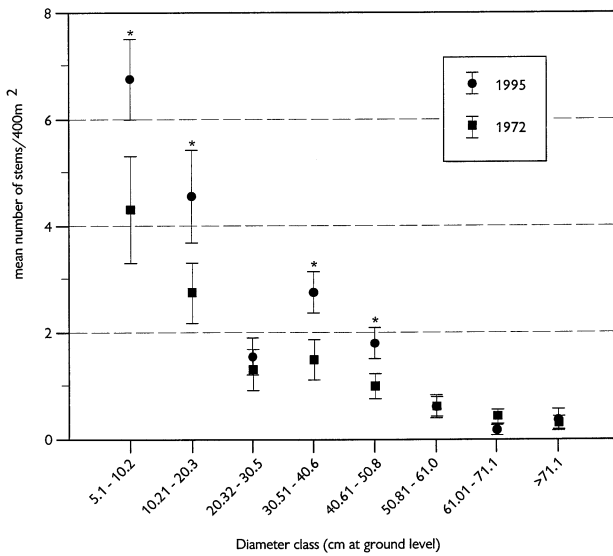


Fig. 3 Mean number of stems/400 m² (± 1 SE) based on diameter class at ground level for 1972 and 1995. * indicates 1995 data significantly different from 1972 data at $P < 0.05$.

Table 2 *Juniperus occidentalis* cover (%) for selected years and characteristics of aerial photographs

Year	Cover	Format	Scale
1995	34.5	B and W	1:9,000
1994	32.3	B and W	1:12,000
1990	31.0	B and W	1:7,920
1985	30.8	B and W	1:28,200
1979	23.6	B and W	1:7,920
1973	21.7	CIR	1:31,000
1951	14.6	B and W	1:15,840

Sources: 1951, 1979, 1990, 1994 (USDA-ASCS Aerial Photography Field Office); 1973 (EROS Data Center); 1985 (WAC); 1995 (Claude Sandell Photography)

Table 3 Mean and SE of selected characteristics of *Juniperus occidentalis* on HRRNA during 1972 and 1995¹.

	1972 Mean ²	SE ²	1995 Mean	SE
Mean maximum tree height (m)	6.57	0.43	7.23*	0.19
Tree reproduction (Mean number of trees < 5.1 cm diameter)/38.5 m ²				
Stems > 91.5 cm height	1.06	0.3	0.93	0.34
Stems < 91.5 cm height	0.31	0.15	0*	0
Number of stems > 5.1 cm/400 m ²	12.18	1.71	18.62*	1.79
Number of clumps/400 m ²	7.53	0.88	10.31*	1.09

¹All comparisons based on 16 replicate samples; ²Values based on raw data supplied by Gashwiler; *Significant from 1972 data at $P < 0.05$

Table 4 Rank comparisons of seasonal water-year (July to June) and winter (November to February) precipitation (cm) at Bend, Oregon for the 10-year period preceding Gashwiler's vegetation survey and the 10-year period preceding the replicate survey.

1962-71 Rank ^a	Year	PPT (cm)	1985-94 Rank	Year	PPT (cm)
<i>SWY precipitation comparison</i>					
62	1962	34.4	50	1985	31.4
8 ^b	1963	19.5	21	1986	24.8
77	1964	39.7	54	1987	31.7
17	1965	23.9	35	1988	26.3
48	1966	31.1	10 ^b	1989	20.6
2 ^b	1967	14.3	27	1990	25.3
63	1968	34.5	7 ^b	1991	18.3
45	1969	30.1	80	1992	40.9
49	1970	31.2	1 ^b	1993	13.9
37	1971	26.8	26	1994	25.3
$\bar{X}_{\text{rank}} = 40.8$		$\bar{X}_{\text{rank}} = 31.1$			
<i>Winter temperature comparison</i>					
46	1962	15.3	78	1985	21.7
31	1963	12.5	29	1986	12.1
89 ^c	1964	32.0	36	1987	13.8
42	1965	14.7	44	1988	14.9
57	1966	17.8	19	1989	10.2
8 ^b	1967	7.9	4 ^b	1990	5.3
47	1968	15.5	11	1991	8.3
67	1969	19.4	65	1992	19.1
64	1970	19.0	5 ^b	1993	5.7
35	1971	13.5	28	1994	12.1
$\bar{X}_{\text{rank}} = 48.6$		$\bar{X}_{\text{rank}} = 31.9$			

^arank is based on 93 years of data (1902-94); ^btop 10 driest years; ^ctop 10 wettest years

may be a source of vegetation change for short (1-2 year) periods (Mueggler 1992). While we are unable to state with certainty that our results are not unduly influenced by fluctuating intensities of herbivore activity, BLM records on the HRRNA compiled during the last 20 years report no intense herbivory and analyses of short-term (1-2 year) climatic conditions showed no significant differences in the years immediately preceding the two vegetation surveys.

Increased seed dispersal by domestic livestock and birds may also confound our analysis. Cattle grazing adjacent to HRRNA may have favoured *J. occidentalis* establishment that in turn led to increases in seed abundance with some seeds subsequently dispersed into HRRNA. Similarly, increased seed dispersion may be attributed to the consumption of *J. occidentalis* berries by birds (e.g. *Turdus migratorius*) and the subsequent deposition of the seeds in HRRNA (Bedell *et al.* 1993; Young & Evans 1981). There is little empirical evidence to implicate domestic grazing as a significant factor of seed dispersal at HRRNA. Grazing pressure in the entire

Table 5 Rank comparisons of seasonal water-year (July to June) and winter (November to February) temperature (°C) at Bend, Oregon for the 10-year period preceding Gashwiler's vegetation survey and the 10-year period preceding the replicate survey.

1962–71 Rank ^a	Year	PPT (cm)	1985–94 Rank	Year	PPT (cm)
<i>SWY precipitation comparison</i>					
38	1962	7.7	51	1985	8.0
29	1963	7.5	87 ^c	1986	9.1
16	1964	7.3	49	1987	7.9
59	1965	8.1	37	1988	7.7
61	1966	8.1	43	1989	7.8
72	1967	8.4	21	1990	7.4
15	1968	7.3	88 ^c	1991	9.3
34	1969	7.7	10 ^b	1992	7.1
12	1970	7.3	57	1993	8.0
44	1971	7.9	58	1994	8.0
$\bar{X}_{\text{rank}} = 38.0$			$\bar{X}_{\text{rank}} = 50.1$		
<i>Winter temperature comparison</i>					
81	1962	2.2	19	1985	0.0
65	1963	1.8	82	1986	2.2
51	1964	1.3	42	1987	1.1
59	1965	1.6	9 ^b	1988	-0.6
89 ^c	1966	2.9	68	1989	1.9
58	1967	1.5	39	1990	1.0
6 ^b	1968	-0.8	83	1991	2.4
78	1969	2.1	1 ^b	1992	-2.4
50	1970	1.3	44	1993	1.1
48	1971	1.2	54	1994	1.3
$\bar{X}_{\text{rank}} = 58.5$			$\bar{X}_{\text{rank}} = 44.1$		

^arank is based on 93 years of data (1902–94); ^btop 10 coldest years ^ctop 10 hottest years

Horse Ridge area by livestock has historically been limited because of the lack of permanent water sources (Halvorson 1995). Additionally, Burkhardt & Tisdale (1976) found that downslope seed dispersal of *J. occidentalis* in southeastern Idaho was limited (2–3 m y⁻¹), and that long range dispersion was insignificant.

Discussion

We found that the two major changes in vegetation characteristics on HRRNA from 1972 to 1995: (i) an increase of *J. occidentalis* cover and density; and, (ii) a decrease in cover of *Carex filifolia* and *Agropyron spicatum*, are in general agreement with other similar *J. occidentalis* studies (e.g. Burkhardt & Tisdale 1976; Eddleman 1987; Miller & Rose 1995). Shrub cover remained virtually unchanged, although we found that much of the *Artemisia tridentata* appeared to be in decreased vigour, but this decline was compensated by the large number of juveniles. Conversely, cover of two of the previous dominant herbaceous species decreased (i.e. *Carex filifolia* and *Agro-*

pyron spicatum) while the third (*Festuca idahoensis*) remained largely unchanged. These changes may reflect the differential ability of species to effectively compete with increasing *J. occidentalis* density and cover based on species-specific characteristics such as root systems (e.g. Eissenstat & Caldwell 1988). Juvenile *J. occidentalis* develop lateral root systems that expand rapidly near the soil surface (Bedell *et al.* 1993), which may place them in direct competition with herbaceous species for soil moisture.

Western juniper cover and density increases: possible Causes

Various factors suggest that the traditional mechanisms of vegetation change are inadequate to explain fully *J. occidentalis* expansion. The rate of historical *J. occidentalis* expansion is unprecedented during the Holocene (Miller & Wigand 1994), and has occurred during a period of warmer/drier conditions. The distribution of pinyon–juniper woodlands in the Great Basin has been linked principally with winter precipitation (Neilson *et al.* 1989, Neilson & King 1992). While the intermediate amount of winter precipitation received in central Oregon is sufficient for the development of an open woodland (Neilson *et al.* 1989), and movement of the juniper woodland/sagebrush steppe ecotone should be particularly sensitive to increases in winter precipitation (*sensu* Neilson 1993), we find that expansion of *J. occidentalis* on HRRNA since 1972 has occurred without significant increases in winter or SWY precipitation.

The most commonly held explanation for *J. occidentalis* expansion, cessation of periodic fires caused by domestic livestock removing fine fuels, may not be necessary for woodland invasion in arid environments. Miller & Wigand (1994) have shown that both the range and density of *J. occidentalis* have undergone substantial fluctuations for several millennia. With the exception of the historic increase, these fluctuations occurred without the influence of either domestic livestock grazing or fire suppression.

Juvenile *J. occidentalis* may be well-suited physiologically for exploiting increases in atmospheric CO₂. Miller *et al.* (1992, 1995) compared CO₂ assimilation rates for juvenile (awl-like foliage present during the first 20+ years growth) and both small and large adult (scale-like foliage) *J. occidentalis*. Juveniles had higher maximum rates of carbon dioxide assimilation that existed 'over a broad range of environmental conditions' than either small adults (170–280% greater) or large adults (160–270% greater). They suggested that high CO₂ assimilation rates may increase intraspecific and interspecific competitiveness, thus facilitating establishment in both *J. occidentalis* and *Artemisia* communities. If increased

atmospheric CO₂ further facilitates establishment and early growth rates it may differentially favour junipers since juniper seedlings have low mortality rates (Burkhardt & Tisdale 1976) and have much greater longevity than any associated shrub or herbaceous species. We note that between 1972 and 1995, *J. occidentalis* establishment, as measured by clump density, increased 37%.

Despite insufficient support for the commonly cited mechanisms, their indirect effects may be linked to the changes observed at HRRNA in at least three ways, illustrating the importance of biological inertia (cf. Neilson 1986). First, *J. occidentalis* expansion may reflect the increase in seed rain (cf. Miller & Rose 1995) from maturing *J. occidentalis* that were established during previous favourable (i.e. wetter) climatic periods such as the late 1800s to early 1900s. As *J. occidentalis* typically do not reach full reproductive maturity until approximately age 75 years (Bedell *et al.* 1993), the rapid expansion corresponds reasonably well with this time period. Similarly, while expansion may not be correlated with recent climatic conditions (e.g. Neilson 1986), it may evince the lagged effects of favourable climatic conditions through the greater longevity and competitive ability of *J. occidentalis* following establishment. Second, *J. occidentalis* expansion that reduces the fine fuel understorey important for ignition and fire spread should continue to decrease the likelihood of fire. Third, if the response to elevated atmospheric CO₂ is preferential to juvenile *J. occidentalis*, this benefit would have been manifested for longer than our study period, perhaps as far back as the late 1800s when atmospheric CO₂ levels began to increase rapidly (Keeling & Whorf 1994; Neftel *et al.* 1994). Thus, the cumulative effects of historic periods of favourable climate, ongoing fire frequency reduction (or extended fire free periods), and continual increases in atmospheric CO₂ may be important features for the expansion of *J. occidentalis* at HRRNA.

Conclusions

We conclude that *J. occidentalis* expansion at HRRNA between 1972 and 1995 cannot be explained adequately by the traditional mechanisms commonly cited. Alternatively, we argue that the expansion could be attributed to the singular or combined effects of: (i) an increase in the seed rain as *J. occidentalis* that established during more climatically favourable periods decades ago become fully reproductive; (ii) the long-term effects of differential longevity and competitiveness of *J. occidentalis* to shrubs and herbaceous species; (iii) an extended fire-free period at HRRNA that allowed fire-susceptible juvenile *J. occidentalis* to mature; and (iv) the possible preferential effects of increasing atmospheric CO₂ on juvenile *J. occidentalis*. Ultimately, it is likely that all of these factors are working

in concert to cause the continued expansion. Although direct anthropogenic disturbances may have largely contributed to the pan-regional increases in *J. occidentalis* cover and density during the last century, comparable increases in *J. occidentalis* density and cover at HRRNA appear to have occurred despite unfavourable climatic conditions, no organized fire management, and the absence of domestic livestock grazing.

This study suggests that the role of biological inertia of both anthropogenic and natural means may have profound impacts on *J. occidentalis* ecology, although these effects are difficult to discern outside of low impact study sites. Future studies on sites such as HRRNA should employ dendrochronological methods that would allow for both the determination of establishment dates and whether tree growth has exceeded growth expected during the 20th Century.

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