The range of western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.) has expanded considerably during the last century, and today these woodlands occupy >1 million ha of the inland Pacific Northwest (Caraher 1978, Miller and Wigand 1994). Studies examining establishment periods of western juniper indicate that expansion began in the late 1800s and, in many locations, has accelerated, including sites in central Oregon (Eddleman 1987), southeastern Oregon (Miller and Rose 1995), and, at least for low sagebrush (*Artemisia arbuscula* Nutt.) sites, in northern California (Young and Evans 1981). Much of this historic expansion differs from prehistoric Holocene expansions since establishment has been primarily confined to the more mesic sagebrush steppe communities rather than downslope into the Wyoming big sagebrush *Artemisia tridentata* spp. *wyomingensis* Nutt. communities (Miller and Wigand 1994:472).

That said, there is evidence that expansion also may be occurring in the most marginal (i.e., xeric) areas (e.g., Knapp and Soulé 1996) in central Oregon despite a trend toward increasing aridity.

Causes of western juniper expansion are complex, likely interactive, and site specific, but generally are linked to some combination of domestic livestock grazing, altered fire regimes, and favorable climatic periods (Burkhardt and Tisdale 1976, Bedell et al. 1993, Miller and Wigand 1994). Additional possibilities include either a biological inertia effect as the seed rain of maturing western juniper increases the number of progeny with time (Miller and Rose 1995), or the effects of elevated atmospheric CO2 preferentially favoring western juniper over herbaceous codominants (Miller and Wigand 1994, Knapp and Soulé 1998). Causes of expansion are difficult to determine, particularly when the role of land-use history complicates interpreting the effects of nonland-use mechanisms. Some sites do exist, however, with a history of minimal human agency. Because of this, the primary purpose of this study is to document the establishment history of western juniper on 2 minimally disturbed research natural areas (RNAs) in central Oregon and to describe how differences in physical characteristics of these sites relate to...
previously documented (Knapp and Soulé 1996, 1998) expansion of western juniper within RNA boundaries.

**STUDY SITES**

Sites chosen for this study are both RNAs managed by the Bureau of Land Management (BLM). As RNAs they are atypical of western juniper woodlands in central Oregon in that their usage is limited, grazing is not allowed, and they are not subject to active fire suppression. Of the 2 sites, Island Research Natural Area (IRNA; Fig. 1) is less disturbed, largely because of its location at the confluence of the Crooked and Deschutes rivers. At 730 m elevation, IRNA is an island mesa surrounded by 60- to 215-m vertical cliffs that limit access. The only historic record of domestic grazing on IRNA was during the 1920s, when sheep grazed on the plateau for 2 consecutive summers (Driscoll 1964, Knapp and Soulé 1996). Surface and subsurface soils are thick loams (25–40 cm) with 1–2% organic matter in the Agency Sandy soil series (USDA-NRCS in press). They support a plant community dominated by *Juniperus occidentalis/Artemisia tridentata/Agropyron spicatum* (western juniper/big sagebrush/bluebunch wheatgrass; Franklin and Dyrness 1988, Knapp and Soulé 1996). The climate is semiarid, with precipitation averaging 25 cm annually, and average temperatures of 18.1°C in July and –0.4°C in January at nearby Prineville (Fig. 1; Karl et al. 1990). As documented by Knapp and Soulé (1996), there have been no recent (since 1960) fires of any significance to western juniper stand dynamics on IRNA. However, there is evidence (e.g., charcoal on snags, areas where tree and shrub associations are not dominant; Driscoll 1964, personal observations 1997) that historical fires may have carried through small sections of IRNA.

**Horse Ridge Research Natural Area** (HRRNA) is approximately 31 km south-southeast of Bend, Oregon (Fig. 1), on rolling terrain of 1250–1430 m. Precipitation at both Prineville and Bend is winter dominated, with Bend recording an annual mean precipitation of 31 cm. Mean temperatures at Bend range from 17.7°C in July to –0.6°C in January (Karl et al. 1990), but the temperatures on HRRNA are likely lower because of elevational cooling. While HRRNA has been a 240-ha fenced exclosure only since 1974, historic impacts of anthropogenic activities have likely been minimal because of a lack of permanent water to support domestic livestock grazing (Hall 1972). The dominant plant community on HRRNA is currently *Juniperus occidentalis/Artemisia tridentata/Festuca idahoensis* (Idaho fescue; Knapp and Soulé 1998). *Carex filifolia* (thread-leaved sedge) is also present and has been classified as the dominant herbaceous species on the site in previous work (Gashwiler 1977, Franklin and Dyrness 1988). Vegetation has developed on the Stookmoor-Westbutte complex soil series, characterized by soils of volcanic ash formed over basaltic and welded tuff colluvium (USDA-NRCS in press). Both Gashwiler (1977) and Knapp and Soulé (1998) suggest that influences of fire on western juniper stand dynamics on HRRNA are minimal. Single or small groups of trees have burned on HRRNA, but fire does not appear to carry well because of insufficient fine fuels.

**METHODS**

**IRNA**

Beginning at a randomly chosen distance between 100 m and 1000 m north-northwest of the southernmost macroplot established by Driscoll (1964), we established 4 macroplot centers at 500-m intervals on a north-northwesterly vector that follows the natural alignment of the plateau. We then established five 0.05-ha plots 30 m from the 4 macroplot centers at azimuths 0, 72, 144, 216, and 288.

To determine the density of mature and juvenile western juniper, we counted all individuals within the 20 plots. All individuals <1 m in height were counted as juveniles, and individuals up to 1.25 m in height were counted as juveniles if they displayed juvenile foliage (i.e., full needle or a mix of needles and awl-like foliage). We also recorded the location of each juvenile using 4 categories: (1) within the canopy of a mature western juniper, (2) within the canopy of a shrub (generally *Artemisia tridentata*, big sagebrush), (3) in grass, or (4) in interspace/rock.

The center point of each 0.05-ha plot was used for dendroecological sampling. Specifically, we sampled 5 western juniper closest to the plot center regardless of age, for a total sample of 100 trees. If the tree was large
enough for us to core without damage (generally basal diameter >5 cm and height >1 m), we obtained 2 core samples using standard techniques (Phipps 1985). Core samples were taken as close to ground level as possible, and the height at which each sample was taken (generally 20–40 cm) was recorded. If the tree was not coreable, its height was recorded and age estimated through regression based on a separate juvenile sample. Seedlings were identified and aged as 0 yr old (i.e., 1997 represents 1st growing season) if the cotyledon was still attached. Collected tree cores were crossdated by the Laboratory of Tree Ring Research (LTRR) in Tucson, Arizona, using standard dendrochronological techniques (Stokes and Smiley 1968). For each tree in the age sample we also recorded height (measuring directly or with a clinometer), basal diameter, sexual development (male—no cones or berries, female—ample cones or berries, mixed—cones or berries present, but scarce), and full or strip bark.

Juvenile sample for regression estimation.—We obtained a separate random sample of $n = 30$ juveniles on land adjacent (<1 km away) to IRNA with similar soils, slope, elevation, aspect, climate, and vegetation association. The use of adjacent land was needed because all work on RNAs must be nondestructive (i.e., no cutting of vegetation allowed). We measured the 30 juveniles, cut them at ground level, and obtained interior dates (dating done by LTRR) using standard techniques (Stokes and Smiley 1968). We then developed linear regression models to estimate age of uncoreable trees based on height, and to adjust for the height at which core samples were taken on mature trees (i.e., how many years did it take the tree to reach the height at which core samples were taken).

Presentation of establishment history.—To examine establishment history, trees were placed into 4 categories and counts made for each decade ending in $1xx7$ (e.g., 1818–1827,
While western juniper has been crossdated successfully in various locations throughout its range (Holmes et al. 1986) and has a high crossdating index (Grissino-Mayer 1993), it was not possible to definitively age each tree in our sample. Because of a combination of heart rot and the asymmetrical nature of western juniper growth, we were unable to reach the pith (or near pith) on all trees dated through core samples. These trees were placed in an “as old as” category, meaning we know only that they are at least as old as the age presented. Trees placed in the “aged” category were samples in which pith was obtained or the ring pattern was tight enough that the innermost ring was within a few rings (±4) of pith. Trees placed in the “regression” category were juveniles aged through regression; seedlings were placed in the “seedling” category.

HRRNA

For HRRNA, methods were identical to IRNA with 2 exceptions. First, on HRRNA we randomly selected 20 sample plots from a 144-station (12 × 12) grid established by Gashwiler (1977). This grid is roughly in the center of the fenced exclosure with plot centers located 40.2 m apart and permanently marked with steel stakes. Second, the juvenile sample for age estimation was collected on land immediately outside the fenced boundaries of the exclosure.

RESULTS

IRNA

Density of western juniper on IRNA was 73 trees ha–1 (81% juvenile, 19% adult). Juveniles were found most frequently under the canopy of mature western juniper (44% of the per hectare count), followed by shrubs (41%), grasses (10%), and interspace or rock (5%).

The separate sample of 100 trees closest to plot centers used to determine establishment history had a slightly different ratio: 64% juvenile and 36% adult. The height of mature (coreable) western juniper ranged from 120 cm to 899 cm (mean = 560 cm, s = 203 cm), with basal diameters of 4–72 cm (mean = 40 cm, s = 21 cm). Most mature trees were females (78%), with 0% male and 22% mixed. All mature trees were full bark.

The age/height relationship developed from the 3rd independent sample was linear and produced the following model:

\[
\text{age} = 8.223 + 0.117(\text{height}); \\
P = 0.0307, R^2 = 0.16.
\]

The model was positively heteroscedastic, with variability in age prediction most pronounced at heights >50 cm. As most trees were cored at 30 cm height, age adjustment for borer height was less influenced by this variability. All trees aged via regression established in the last 3 decades (Fig. 2), and only 15% fall into the “as old as” category. Thus, the time line provides a relatively accurate assessment of establishment history for western juniper on IRNA.

HRRNA

Density of western juniper on HRRNA was 261 trees ha–1 (13% juvenile, 87% adult). Juveniles were found most frequently within grass (49% of the per hectare count), followed by shrubs (29%), within the canopy of a mature western juniper (11%), and in interspace or rock (11%).

Because of an extremely tight ring pattern, 3 mature trees sampled on HRRNA were undatable. Thus, only the 97 trees closest to plot centers were used to determine establishment history. Of these, 15 were juveniles that we dated by regression (no seedlings were found) and 82 were mature. The height of mature (coreable) western juniper ranged from 110 cm to 945 cm (mean = 437 cm, s = 202 cm), with basal diameters of 5–90 cm (mean = 35 cm, s = 21 cm). The majority of trees were of mixed development (66%), followed by male (24%), and female (10%). A small number were strip bark (9%), the remaining full bark (91%).

The age/height relationship was linear and produced a model with the form:

\[
\text{age} = 3.899 + 1.000(\text{height}); \\
P = 0.0001, R^2 = 0.42.
\]

Residuals from this model were randomly distributed. With slower growth rates at HRRNA, trees aged via regression extend back to the 1910s (Fig. 3). While a higher percentage of trees in the HRRNA sample were placed in the “as old as” category (30%), most (70%) were datable through core sampling or regression techniques.
DISCUSSION

The ratio of juveniles to adults at IRNA is high, with >60% of all trees sampled establishing since 1978. Most juveniles have become established within the canopy of either shrubs or western juniper, and there is a high percentage of female trees. IRNA thus exhibits characteristics of an emerging woodland where the importance of nurse-plant sites is paramount to successful establishment, particularly in xeric, low-elevation locations. Burkhardt and Tisdale (1976) have shown that the mortality rate for western juniper seedlings is low, even during drought conditions. Thus, barring a widespread fire that could cause a high rate of mortality, IRNA should exhibit large increases in density and cover in the next several decades as juveniles mature.

The accelerated establishment rate at IRNA in the last 2 decades (Fig. 2) is comparable to establishment data presented by Miller and Rose (1995:40, Fig. 1). Lack of fire, an abundance of nurse plants, and biological inertia manifested through an increased seed rain appear to be synergistically supporting the rapid expansion of western juniper in southeastern Oregon in recent decades (Miller and Rose 1995), and these same factors are a component of the recent history on IRNA. Recent fires are rare (despite the lack of fire suppression) on IRNA, there is a high percentage of female trees (many with copious berry production), and cover and density of trees and shrubs have increased significantly since 1960 (Knapp and Soulé 1996).

Others (Burkhardt and Tisdale 1976:477, Fig. 1; Young and Evans 1981:503, Fig. 4; Eddleman 1987:256, Fig. 1) have documented sharp increases in the rate of expansion of western juniper on disturbed sites during the 20th century, although rates are not as extreme as those found at IRNA during the last 2 decades. Burkhardt and Tisdale (1976) suggest that the
rapid rate of juniper expansion on the Owyhee Plateau in Idaho is related to a cessation of periodic fires caused by fire suppression and a reduction in fine fuels associated with domestic livestock grazing. In addition to fire and grazing, Miller and Rose (1995:43) suggest that “optimal climatic conditions around the turn of the century” may have contributed to the rapid expansion of western juniper on their study sites in southeastern Oregon during the 20th century. While the majority of establishment on IRNA is recent, a minor establishment spike appears to have occurred in the late 1800s, with 6% of sampled trees establishing in the 1880s (Fig. 2).

At HRRNA approximate periods of establishment appear more evenly distributed (Fig. 3). Peaks of establishment occur in the late 1600s and early 1700s, the 1830s, and the 1910s through 1930s, but in no decade are >5 trees (or roughly 5% of the sample) known to have established. Favorable climatic conditions of the late 1800s (Miller and Rose 1995) do not correspond to a peak of establishment on HRRNA.

The presence of nurse-plant sites (i.e., establishment within the canopy of western juniper or big sagebrush) has been suggested as an element of western juniper expansion (e.g., Eddleman 1987, Evans 1988). While the juvenile location data for IRNA support this (i.e., 85% of juveniles growing within the canopy of trees or shrubs), location data on HRRNA do not. Of the more recent establishment dates, these have been contributed by western juniper growing on the more open northeastern slope of HRRNA (nearly half of all juveniles were found in open canopy sites), as opposed to the more densely covered southeastern slope. These results suggest that a cover/density threshold may exist that impedes future establishment of western juniper. Similar conclusions were drawn by Young and Evans (1981:502), who speculated that low western juniper establishment rates in big sagebrush communities of northern California could be the result...
of high juniper cover (40–60%) and interspaces filled with roots that “effectively” excluded their study site stand from much future establishment.

The value of examining establishment periods for western juniper is manifested when coupled with measurements of expansion rates of the corresponding sites. After examining multi-date, large-scale aerial photography during 1961–1994 at IRNA and 1951–1995 at HRRNA, Knapp and Soulé (1996, 1998) determined that cover of western juniper increased by 5.2% and 19.9%, respectively. At HRRNA recent expansion (measured as an increase in cover) has been linked primarily with maturation of adults and with the few juveniles that have established on open canopy sites. Much of the cover change at HRRNA has occurred from significant increases in stems growing from the central trunk of mature trees (Knapp and Soulé 1998). While expansion may continue on HRRNA, especially on the more open northeastern slope, establishment data suggest that the rate of expansion will be much slower than that observed on more open woodlands.

From the standpoint of establishment history, the most important variant for these 2 RNAs, especially IRNA, is the lack of domestic livestock grazing. While grazing is often viewed as an integral driving force behind western juniper expansion, it is nearly absent from the known land-use history of IRNA and has not occurred at HRRNA since the completion of the exclosure fence in 1974. Thus, grazing cannot be identified as a potential driving force behind expansion at IRNA, and its role at HRRNA has likely been minimal.

We recognize that our results are based on 2 sites and thus may not reflect western juniper establishment characteristics on all minimally impacted sites. They do, however, potentially illustrate 3 aspects of western juniper expansion. First, expansion (as manifested as an increase in cover) is not necessarily associated with recent establishment periods but rather may reflect the ongoing effects of canopy and stem development. Second, suitable establishment sites may switch from canopy dependence in emerging woodlands to open sites in maturing woodlands. Third, the role of domestic livestock grazing or active fire suppression is not required for establishment to occur, although extensive fire-free periods, as these 2 sites have experienced (Knapp and Soulé 1996, 1998), certainly must have been conducive for establishment and expansion.

Our knowledge of growth characteristics of western juniper in undisturbed environments is critical in making informed decisions about land management throughout its range. Further research on undisturbed environments, especially comparative analyses of establishment histories of undisturbed sites with adjacent disturbed sites exhibiting the same physical characteristics, should help us understand the driving forces behind juniper expansion on semiarid lands.

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