

A 4000-YEAR RECORD OF WOODLAND VEGETATION FROM WIND RIVER CANYON, CENTRAL WYOMING

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ABSTRACT.—Plant macrofossil analyses of 16 radiocarbon-dated woodrat middens spanning the past 4000 years from the Wind River Canyon region in central Wyoming provide information concerning late Holocene development of juniper woodlands. The study sites are currently dominated by *Juniperus osteosperma*, with *J. scopulorum* present locally. Woodlands in the region were dominated by *J. scopulorum* from ca 4000 yr BP until at least 2800 yr BP. *Juniperus osteosperma* invaded and expanded before 2000 yr BP. This expansion fits a regional pattern of *J. osteosperma* colonization and expansion in north central Wyoming during a relatively dry period between 2800 and 1000 yr BP. At the time the Wind River Canyon region was colonized by *J. osteosperma*, the species had populations 50–100 km to both the north and south. Long-distance seed dispersal was required for establishment in the study area. Genetic studies are necessary to identify source populations and regions.

Key words: juniper woodlands, vegetation history, woodrat middens, central Wyoming, natural invasions, late Holocene.

Juniper-dominated woodlands are extensive on the flanks of mountain ranges and on coarse-textured bedrock outcrops in basins of the central Rocky Mountain region (Knight 1994, West 1999). In Wyoming, juniper woodlands occupy some 5737 km² (Driese et al. 1997). These woodlands are dominated primarily by *Juniperus scopulorum* (Rocky Mountain juniper), which occurs extensively throughout the Rocky Mountain region, from New Mexico to Canada. However, scattered juniper woodlands in central Wyoming and adjacent Montana are dominated by *J. osteosperma* (Utah juniper; Fig. 1), which occurs primarily in the Great Basin and Colorado Plateau. The Wyoming and Montana populations represent a series of isolated outposts separated from each other by 25–100 km and from the core distribution of the species by 100–500 km. This pattern contrasts with the distribution of *J. osteosperma* in the Colorado Plateau and Great Basin regions, where the species is abundant and widespread, and where populations are typically separated by no more than 10–30 km (Little 1971, West 1999).

Paleoecological records from woodrat middens indicate that *J. osteosperma* populations have occurred in the southwestern Great Basin and southern Colorado Plateau since the last glacial maximum (Cole 1990, Nowak et al.

1994), and that the species colonized southeastern and northeastern Utah during the early Holocene (Betancourt 1990, Sharpe 1991). These observations suggest that the species migrated from the Utah/Wyoming border north and east during the Holocene to occupy its present range. Paleobotanical analyses of an array of fossil woodrat middens throughout the modern range of *J. osteosperma* in Wyoming and adjacent Utah and Montana are revealing the timing, rates, and patterns of its Holocene migration (Lyford et al. 2002a, 2002b).

One of the critical sites in this sampling array is the Wind River Canyon region of central Wyoming because of its central location and the existence of a major north-flowing river running through the canyon, connecting the Wind River Basin with the Bighorn Basin (Fig. 1). The canyon may have served as an important migration corridor for *J. osteosperma* and other north-moving species during the Holocene. Wind River Canyon is the only canyon that bisects the Owl Creek Mountains, which comprise a potential geographic barrier to dispersal between the Bighorn Basin and the Wind River Basin and other basins to the south (Fig. 1). The Wind River/Bighorn River system comprises one of the few north-flowing rivers in western North America, and flood flows may have played an important role in long-distance

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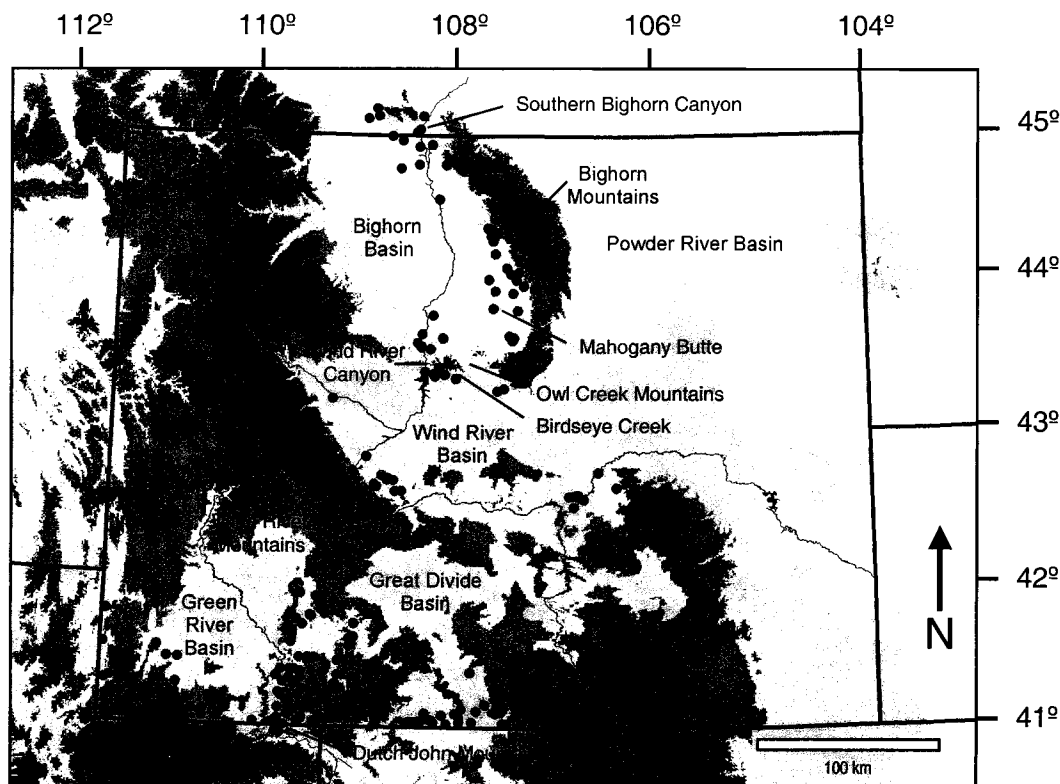


Fig. 1. Map of Wyoming and adjacent states showing elevations (white 900–1500 m, light gray 1500–2100 m, medium gray 2100–2600 m, dark gray ≥ 2600 m), key physiographic features, locations of study sites and other sites mentioned in text, and distribution of *Juniperus osteosperma* (black dots) based on records from the Rocky Mountain Herbarium (<http://www.rmh.uwyo.edu>).

seed dispersal and Holocene migration of southern species.

We conducted a study of woodrat middens collected from the Wind River Canyon region in central Wyoming to better assess the Holocene migration patterns of *Juniperus osteosperma*, to provide information on the history of juniper woodlands at the site, and to determine vegetation composition before and after *J. osteosperma* colonization (Fig. 1). A 13-midden series from lower Wind River Canyon spans the past 4000 years. Three late Holocene middens from Birdseye Creek, 16 km south-southeast of the Wind River Canyon sites, provide additional information and corroboration.

STUDY SITES

Wind River Canyon is a deep, north-trending canyon, 21 km in length, incised into the

Owl Creek Mountains (Figs. 1, 2). The canyon cuts through bedrock ranging from Precambrian metavolcanic rocks at the head of the canyon to limestones of the Permian Phosphoria Formation at the canyon mouth (Maughan 1972, 1987). In between it cuts through a series of Paleozoic limestones and dolomites, particularly those of the Amsden, Madison, Bighorn, Gallatin, and Gros Ventre formations. The primary lithologies exposed in the lowermost 4 km of the canyon, where we conducted our study, are limestones and dolomites of the Park City, Amsden, and Madison formations.

West- and southwest-facing slopes on the east side of lower Wind River Canyon are vegetated by juniper woodlands (Fig. 2). *Juniperus osteosperma* is dominant on these slopes, although *J. scopulorum* occurs locally throughout the canyon, especially in mesic sites (draws, gullies, cliff bases). *Rhus trilobata* occurs locally



Fig. 2. Photo of lower Wind River Canyon near midden-collecting sites. Woodlands in foreground and background are dominated by *Juniperus osteosperma*. View is facing upcanyon, WNW. From a color transparency taken May 1998 by S.T. Jackson.

at cliff bases and in draws. Scattered individuals of *Pinus flexilis* occur throughout the canyon but are not abundant on the lower slopes where we concentrated our collecting efforts. Other plant species on the slopes include shrubs (*Ribes aureus* [at cliff bases], *Artemisia frigida*, *Atriplex canescens*, *Chrysothamnus* spp., *Gutierrezia sarothrae*), grasses (*Oryzopsis hymenoides*, *Bromus tectorum*, *Stipa comata*, *Elymus* sp.), forbs (*Artemisia ludoviciana*, *Cryptantha* spp., *Eriogonum* spp., *Pentstemon* spp.), and succulents (*Opuntia polyacantha*).

Birdseye Creek flows south-southwest, draining uplands of the Owl Creek (Bridger) Mountains immediately east of Wind River Canyon. The creek cuts through a highly faulted series of Paleozoic limestones and dolomites, locally capped by Eocene sediments of the Wind River Formation (Thaden 1980). Middens are in crevices of the Madison Formation. Vegetation in Birdseye Creek Canyon consists of a mosaic of steppe, dominated by *Artemisia tridentata*, and open juniper woodlands, domi-

nated by *Juniperus osteosperma*. Both vegetation types occur within 20 m of our collecting sites. Subdominants include the same species as observed in lower Wind River Canyon.

The climate of central Wyoming is semiarid. Mean annual precipitation at Thermopolis (1948–2000; 1342 m elevation; 8 km N of the Wind River Canyon sites) is 290 mm. Mean annual precipitation at Boysen Dam, at the head of Wind River Canyon (1948–2000; 1416 m elevation; 7.5 km E of the Birdseye Creek sites) is 233 mm. Despite its higher elevation, Boysen Dam receives less precipitation than Thermopolis owing to its isolation at the northern edge of the Wind River Basin, where moisture sources are blocked by the Owl Creek Mountains. Mean July precipitation at Thermopolis and Boysen Dam is respectively 21 and 13 mm; mean January precipitation is respectively 10 and 7 mm. Winters are cold (mean January temperature -5.7°C at Thermopolis and -7.8°C at Boysen Dam) and summers are hot (mean July temperature 22.2°C at Thermopolis and 23.8°C at Boysen Dam).

METHODS

Midden-collecting efforts in Wind River Canyon were concentrated on west-facing slopes in the lower portion of the canyon, where *J. osteosperma* is most abundant. The collecting sites range in elevation from 1365 to 1475 m (Table 1); river elevation in this reach of the canyon is 1340 m and the rim ranges from 1400 to 1650 m. Using standard field techniques (Spaulding et al. 1990), we collected 19 midden samples from crevices and bedrock overhangs. We collected 6 midden samples from Birdseye Creek Canyon, ranging from 1615 to 1700 m in elevation (Table 1). In all cases, weathering rinds were removed in the field, middens were inspected for stratification and contamination, and a sample from the core of the midden was collected. In the laboratory, midden samples were reinspected, dispersed in water, oven-dried, and sieved using 1- and 2-mm mesh screens (Spaulding et al. 1990). We examined the 2-mm sieve fraction thoroughly, separating identifiable plant macrofossils and identifying them using herbarium-documented reference collections. The 1-mm sieve fraction was scanned to identify plant species and morphotypes not represented in the larger fraction. Each plant taxon in each midden was assigned a relative abundance value (1 = single occurrence, 5 = dominant; Spaulding et al. 1990).

Thirteen middens were selected for radiocarbon-dating from Wind River Canyon, and 3 from Birdseye Creek. We obtained conventional ^{14}C dates on samples of *Neotoma* fecal pellets from 8 Wind River Canyon and 2 Birdseye Creek middens. Using accelerator mass spectrometry (AMS), we dated *Juniperus osteosperma* foliage from 6 Wind River Canyon middens and 2 Birdseye Creek middens. We also AMS-dated *J. scopulorum* foliage from another Birdseye Creek midden. AMS dating provides precise dates from small amounts of organic material and hence yielded direct age-estimates for *Juniperus* macrofossils from the middens. We used AMS dating to pinpoint temporal occurrences of *J. osteosperma* at the study sites and in cases where we suspected possible mixing of plant material of different ages.

For the conventional dates, we submitted 3–10 g of *Neotoma* fecal pellets to Geochronology Laboratories (Cambridge, MA) for dating. Targets for AMS dating were prepared at

the USGS Desert Laboratory in Tucson. Samples were pretreated to remove carbonates and acid- and base-soluble organic matter, combusted to CO_2 on a vacuum line, converted to graphite, pressed into targets, and then measured for ^{14}C activity at the University of Arizona–NSF Accelerator Facility.

All ages reported or discussed in this paper are calendar-year ages (years Before Present, with 1950 as the benchmark). Radiocarbon ages were converted to calendar-year ages using the Intcal 98 calibration curve, using Method A (ranges with intercepts) from CALIB 4.3 (Stuiver and Reimer 1993).

RESULTS

The Wind River Canyon middens range in age from 3876 yr BP to modern (Table 1, Fig. 3). Macrofossil assemblages from the 6 middens dating before 2500 BP show relatively little variation; all are dominated by *Juniperus scopulorum*, with *Rhus trilobata* and *Opuntia* also abundant (Fig. 3, Table 2). Most have macrofossils of *J. osteosperma*. The 5 middens post-dating 2000 yr BP contain both *J. osteosperma* and *J. scopulorum*. *Rhus* and *Opuntia* occur as subdominants. *Atriplex* sp. is absent from all of these younger middens, and *Artemisia nova* occurs only in the oldest of these middens (Fig. 3).

One Birdseye Creek midden is dominated by *J. scopulorum* and lacks macrofossils of *J. osteosperma* (Fig. 3, Table 2). It contains macrofossils of *Artemisia nova* and *Atriplex* sp. This midden was dated at 3350 yr BP, and foliage of *J. scopulorum* was AMS-dated at 2923 yr BP. *Juniperus osteosperma* foliage from a 2nd midden, which also contains *J. scopulorum* macrofossils, was AMS-dated at 2137 yr BP. A 3rd midden, dominated by *J. osteosperma*, yielded modern dates (45 yr BP; 42 yr BP AMS). Both of these younger middens lack *Artemisia nova* and *Atriplex* sp.

DISCUSSION

During the last glacial period, *Juniperus osteosperma* populations were restricted to the southern Great Basin and southern Colorado Plateau (Betancourt 1990, Thompson 1990, Nowak et al. 1994, Lyford et al. 2002b). During the late-glacial (13,000–10,000 yr BP), *J. osteosperma* migrated rapidly from northern Arizona to northeastern Utah (Betancourt 1990,

TABLE 1. Radiocarbon age, location, and elevation of middens analyzed from Wind River Canyon (WRC) and Birdseye Creek (BEC). Age estimates in ¹⁴C yr BP include 2 standard errors. Age estimates in calendar-yr BP include median intercept from CALIB 4.2 (Stuiver et al. 1998) and (in parentheses) minimum and maximum ages based on 2 standard errors from minimum and maximum intercepts.

| Midden no. | Lab no. | Material dated | Age (¹⁴ C yr BP) | Age (cal-yr BP) | Latitude | Longitude | Elevation (m) |
|------------|---------|-------------------------------|------------------------------|------------------|--------------|---------------|---------------|
| WRC207B | AA33168 | <i>J. osteosperma</i> foliage | 375 ± 45 | 467 (309–514) | 43°33'28.8"N | 108°12'20.8"W | 1455 |
| WRC240 | AA38266 | <i>J. osteosperma</i> foliage | 430 ± 33 | 505 (341–527) | 43°33'10.1"N | 108°11'42.6"W | 1421 |
| WRC208 | AA38265 | <i>J. osteosperma</i> foliage | 767 ± 43 | 679 (654–760) | 43°33'28.8"N | 108°12'20.8"W | 1455 |
| WRC241B | AA33162 | <i>J. osteosperma</i> foliage | 1680 ± 50 | 1562 (1422–1708) | 43°33'10.1"N | 108°11'42.6"W | 1421 |
| WRC173 | AA38242 | <i>J. osteosperma</i> foliage | 1719 ± 41 | 1675 (1530–1713) | 43°33'52.8"N | 108°12'30.3"W | 1431 |
| WRC212 | AA33156 | <i>J. osteosperma</i> foliage | 1735 ± 50 | 1657 (1529–1815) | 43°33'34.6"N | 108°12'22.1"W | 1482 |
| WRC242 | GX24953 | <i>Neotoma</i> fecal pellets | 1970 ± 75 | 1909 (1723–2118) | 43°33'10.1"N | 108°11'42.6"W | 1421 |
| WRC183 | CX24952 | <i>Neotoma</i> fecal pellets | 2620 ± 130 | 2750 (2351–2992) | 43°33'14.9"N | 108°12'37.6"W | 1416 |
| WRC181C | GX24951 | <i>Neotoma</i> fecal pellets | 2710 ± 80 | 2781 (2736–2965) | 43°33'14.9"N | 108°12'37.6"W | 1416 |
| WRC171A | GX24948 | <i>Neotoma</i> fecal pellets | 2750 ± 75 | 2848 (2747–3058) | 43°33'44.2"N | 108°12'42.5"W | 1367 |
| WRC173 | CX24950 | <i>Neotoma</i> fecal pellets | 3260 ± 80 | 3469 (3274–3687) | 43°33'52.8"N | 108°12'30.3"W | 1431 |
| WRC182 | GX25842 | <i>Neotoma</i> fecal pellets | 3430 ± 80 | 3655 (3471–3889) | 43°33'14.9"N | 108°12'37.6"W | 1416 |
| WRC181A | GX26611 | <i>Neotoma</i> fecal pellets | 3590 ± 60 | 3876 (3698–4086) | 43°33'14.9"N | 108°12'37.6"W | 1416 |
| WRC172 | CX24949 | <i>Neotoma</i> fecal pellets | 3590 ± 80 | 3876 (3644–4144) | 43°33'52.8"N | 108°12'30.3"W | 1431 |
| BEC245A | GX25480 | <i>Neotoma</i> fecal pellets | 80 ± 65 | 45 (0–285) | 43°23'37.1"N | 108°05'17.1"W | 1645 |
| BEC245A | AA33680 | <i>J. osteosperma</i> foliage | 90 ± 45 | 42 (0–277) | 43°23'37.1"N | 108°05'17.1"W | 1645 |
| BEC301 | AA38258 | <i>J. osteosperma</i> foliage | 2155 ± 50 | 2137 (1996–2325) | 43°24'06.7"N | 108°05'16.2"W | 1657 |
| BEC174A | AA33673 | <i>J. osteosperma</i> foliage | 2825 ± 60 | 2923 (2780–3157) | 43°23'34.1"N | 108°05'15.1"W | 1639 |
| BEC174A | GX25479 | <i>Neotoma</i> fecal pellets | 3110 ± 130 | 3350 (2952–3633) | 43°23'34.1"N | 108°05'15.1"W | 1639 |

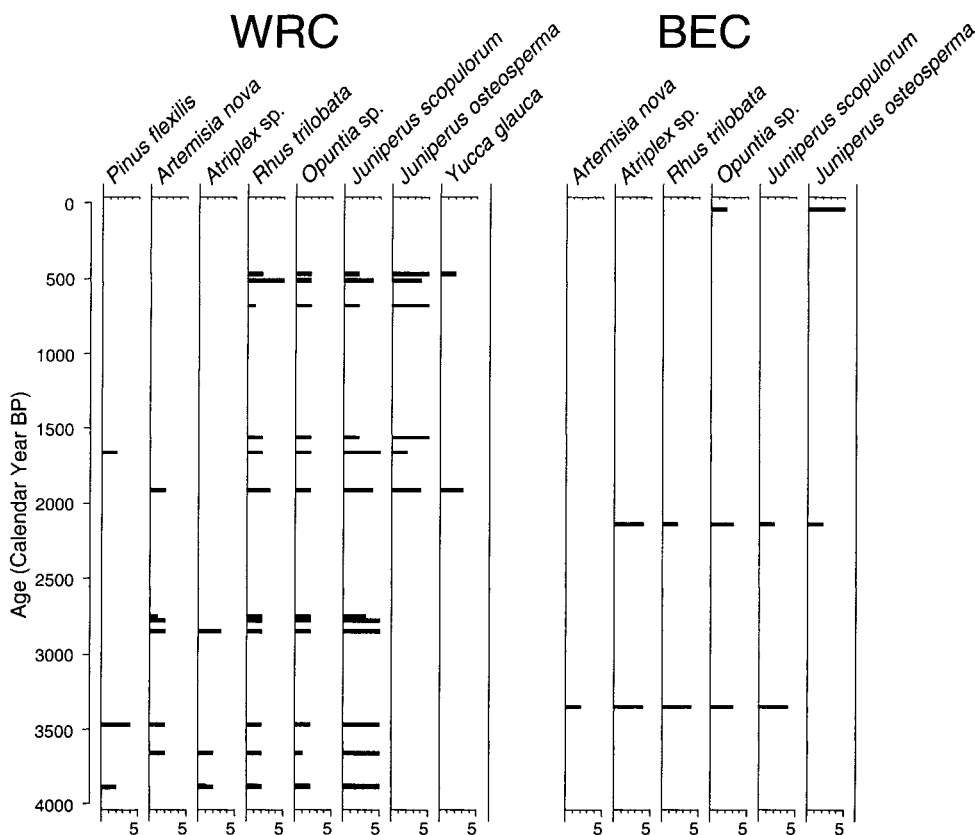


Fig. 3. Relative abundances of macrofossils of selected taxa in woodrat middens from Wind River Canyon (WRC) and Birdseye Creek (BEC).

Sharpe 1991). It was established at Dutch John Mountain, 5 km south of the Utah/Wyoming border, by 9400 yr BP (Jackson, Betancourt, and Lyford, unpublished data). Northeastern Utah was the most likely portal for invasion of *J. osteosperma* and other Great Basin species into Wyoming. The modern distribution of *J. osteosperma* as well as the topographic configuration suggests that migration from the Utah/Wyoming border northward proceeded from southwestern Wyoming to the southeastern foothills of the Wind River Mountains, and then across the Owl Creek/Bridger Mountains into the Bighorn Basin (Fig. 1). As the only drainage cutting across the Owl Creek Mountains, Wind River Canyon would appear to have been an important migration pathway.

Establishment of *J. osteosperma* populations at several sites in the Bighorn Basin predates the 1st occurrences (1900 yr BP at Wind River

Canyon, 2100 at Birdseye Creek) in the Wind River Canyon region. The earliest documented establishments occurred ca 5400 yr BP at Southern Bighorn Canyon, at the northern edge of the Bighorn Basin (Lyford et al. 2002a), and Mahogany Butte, in the southeastern Bighorn Basin (Lyford et al. 2002b; Fig. 1). However, these occurrences predate not only the 1st *J. osteosperma* occurrences in the Wind River Canyon region, but also the oldest middens we have in that region (3900 yr BP).

The migration of *J. osteosperma* in Wyoming occurred by means of rare, long-distance dispersal events spanning 30–100 km or more. Such dispersal events were required to cross geographic barriers (e.g., the Wind River Basin) and are confirmed by the patchy pattern of establishment documented from woodrat midden analyses throughout the region (Lyford et al. 2002b). The Wind River Canyon region may

TABLE 2. Relative abundances of plant macrofossil types in woodrat middens from Wind River Canyon and Birdseye Creek sites. Organ types abbreviated as follows: lf = leaf, n = needle, fl = floret, se = seed, inv = involucre, fr = fruit, st = stem.

| Sample number | | Wind River Canyon | | | | | | | | | | | Birdseye Creek | | | |
|------------------------------------|-----|-------------------|-----|------|------|------|------|------|------|-------------------|------|------|----------------|-----|------|-------------------|
| | | 207B | 240 | 208 | 241B | 212 | 242 | 183 | 181C | 171A | 173 | 182 | 181A | 172 | 245A | 301 |
| Sample age (yr BP) | 467 | 505 | 679 | 1562 | 1657 | 1909 | 2750 | 2781 | 2848 | 3469 ^a | 3566 | 3876 | 3876 | 45 | 2137 | 3350 ^b |
| <i>Artemisia nova</i> (lf) | - | - | - | - | - | 2 | 1 | 2 | 2 | 2 | 2 | - | - | - | - | 2 |
| <i>Artemisia tridentata</i> (lf) | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | - | - |
| <i>Atriplex</i> sp. (fr) | - | - | - | - | - | - | - | - | 3 | - | 2 | 1 | 2 | - | - | 2 |
| <i>Atriplex</i> sp. (lf) | - | - | - | - | - | - | - | - | 2 | - | - | - | 2 | - | 5 | 4 |
| <i>Chrysothamnus</i> sp. (inv) | - | - | - | - | - | - | - | - | - | - | - | - | 2 | - | - | - |
| <i>Cryptantha</i> sp. (lf) | - | - | - | - | - | - | - | - | - | 2 | 2 | - | - | - | - | 2 |
| <i>Elymus</i> sp. (lf) | - | - | - | - | - | - | 2 | - | - | - | - | 1 | - | - | - | 2 |
| <i>Equisetum</i> sp. (st) | - | - | - | - | - | - | - | 2 | - | - | 1 | 2 | - | - | - | - |
| <i>Gutierrezia sarothrae</i> (inv) | - | - | - | - | - | 2 | - | - | 2 | - | - | - | - | - | - | - |
| <i>Hedeoma</i> sp. (se) | - | - | - | - | - | 1 | - | - | 1 | - | - | - | - | - | - | - |
| <i>Juniperus osteosperma</i> (fr) | 2 | - | 2 | 2 | 2 | 2 | - | - | - | - | - | - | - | 1 | - | - |
| <i>Juniperus osteosperma</i> (se) | 3 | 3 | 2 | 3 | 2 | 2 | - | - | - | - | - | - | - | 2 | - | - |
| <i>Juniperus osteosperma</i> (st) | 5 | 4 | 5 | 5 | 2 | 4 | - | - | - | - | - | - | - | 5 | 2 | - |
| <i>Juniperus scopulorum</i> (fr) | - | - | - | - | 2 | 2 | - | 2 | 2 | 2 | 2 | 2 | 3 | - | - | - |
| <i>Juniperus scopulorum</i> (se) | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 4 | 4 | 2 | 2 | 4 | - | 2 | 2 |
| <i>Juniperus scopulorum</i> (st) | 2 | 4 | 2 | 2 | 5 | 4 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | - | 2 | 4 |
| <i>Lappula redowskii</i> (se) | - | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - |
| <i>Lesquerella</i> sp. (lf) | - | - | - | - | - | - | - | 2 | 2 | - | - | - | - | - | - | 2 |
| <i>Lithospermum</i> sp. (se) | - | 1 | - | - | - | 2 | - | - | 1 | 1 | - | - | - | - | - | - |
| <i>Opuntia</i> sp. (se) | - | - | - | 2 | - | - | - | 2 | - | 2 | - | - | - | - | - | 2 |
| <i>Opuntia</i> sp. (st) | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | - | - | 2 | - | 2 | 3 | 2 |
| <i>Oryzopsis hymenoides</i> (se) | - | - | - | 1 | 2 | 2 | - | 1 | - | 2 | - | - | - | - | - | - |
| <i>Pinus flexilis</i> (n) | - | - | - | - | 2 | - | - | - | - | 4 | - | - | 2 | - | - | - |
| <i>Pinus flexilis</i> (se) | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | - |
| <i>Rhus trilobata</i> (se) | 2 | 5 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | - | 2 | 4 |
| <i>Rosa</i> sp. (lf) | - | - | - | - | - | - | - | 3 | - | - | - | 2 | - | - | - | - |
| <i>Rosa</i> sp. (se) | - | - | - | - | - | - | - | 2 | - | - | - | - | - | - | - | - |
| <i>Rosa</i> sp. (st) | - | - | - | - | - | - | 2 | - | - | - | - | - | - | - | - | - |
| <i>Stipa</i> sp. (lf) | - | - | - | - | - | - | - | - | 1 | - | - | - | - | - | - | - |
| <i>Stipa comata</i> (se) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2 |
| <i>Yucca glauca</i> (se) | 1.5 | - | - | - | - | 3 | - | - | - | - | - | - | - | - | - | - |

^aPollage of *Juniperus osteosperma* from this midden was AMS-dated at 1719 radiocarbon yr BP (1675 calendar yr BP). This is regarded as a contaminant; the rest of the midden contents are assigned the age obtained from the *Neotoma* fecal pellets.

^bPollage of *Juniperus scopulorum* from this midden yielded a slightly younger age (see Table 1).

have been skipped in long-distance dispersal events during the mid-Holocene, leading to the initial establishment well north of the region. Under this scenario, the region was first colonized by *J. osteosperma* ~2000 yr BP, either by back-colonization from the Bighorn Basin to the north or by additional dispersal events from populations to the south (SE Wind River Mountains, SW Wyoming).

Alternatively, Wind River Canyon may have been colonized by *J. osteosperma* populations before 5400 yr BP, and did in fact serve as an intermediate site in northward invasion into the Bighorn Basin region. Under this scenario, early populations of *J. osteosperma* underwent local extinction some time before 3900 yr BP, with recolonization ca 2000 yr BP. This hypothesis cannot be excluded given the absence of middens predating 3900 yr BP.

Lyford et al. (2002b) identified a punctuated pattern of *J. osteosperma* migration in northern Wyoming in which establishment occurred during periods of relatively dry climate (ca 5400 yr BP, 2800–1000 yr BP) and colonization of new sites ceased during relatively wet periods (5400–2800 yr BP). Our data are consistent with this pattern; *J. osteosperma* is absent from all middens representing the wet period (3900–2800 yr BP), and the 1st documented occurrences (2100–1900 yr BP) occurred during the dry period.

The populations established 5400 yr BP at southern Bighorn Canyon and Mahogany Butte persisted throughout the subsequent wet period (Lyford et al. 2002a, 2002b). Because the Mahogany Butte site is higher (1800 m) and wetter than Wind River Canyon and Birdseye Creek, Mahogany Butte populations might be expected to be more sensitive to a moisture increase than those in the Wind River Canyon region. *Juniperus osteosperma* populations established in Wind River Canyon at or before 5400 yr BP may have declined but persisted locally after 5400 yr BP, and then expanded in response to the drying trend after 2800 yr BP. The absence of *J. osteosperma* from the 3 middens dating from 2750 to 2850 yr BP as well as the 5 middens dating 3350–3900 yr BP suggests, however, that *J. osteosperma* was absent from the region during the wet period and that the species invaded the canyon by dispersal from distant sources (e.g., in the eastern Bighorn Basin). Woodrats of *Neotoma cinerea*

show a strong preference for collecting *Juniperus* foliage, particularly *J. osteosperma* (Nowak et al. 2000, Lyford 2001), increasing our confidence that absence of *J. osteosperma* from the middens predating 2100 yr BP indicates its absence from the surrounding vegetation.

Our paleological data provide constraints on the history of *J. osteosperma* in the Wind River Canyon region and suggest strongly that current populations were established ca 2000 yr BP from distant sources to the north or south. Those populations may carry a genetic signature of their establishment sources and history. Genetic analyses of the Wind River Canyon populations and potential source populations in the Wind River foothills and the Bighorn Basin might reveal the precise pathway and sequence of invasion of Wind River Canyon.

Juniperus scopulorum populations persisted in Wind River Canyon after the rapid transition to dominance by *J. osteosperma*, in contrast to sites in the Bighorn Basin (e.g., Pryor Mountain and Big Horn Canyon; Lyford et al. 2002a). Wind River Canyon is more mesic than the northern sites, owing to shading by the west canyon wall and to greater surface drainage and groundwater seepage from upper slopes. The locally moist habitats have allowed persistence of *J. scopulorum* over much of the canyon. We cannot determine from the midden records whether *J. scopulorum* was displaced from drier sites when *J. osteosperma* invaded.

Rhus trilobata and *Opuntia* occurred in Wind River Canyon both before and after the establishment of *J. osteosperma*. *Rhus trilobata* is concentrated around locally moist sites (gulches, seeps, cliff bases) and was thus buffered against changes in moisture of the magnitude experienced in the past 4000 years. Similarly, *Opuntia* occurs widely in dry, exposed microsites in the canyon, which have been available regardless of climate regime. The reason for the disappearance of *Artemisia nova* from the canyon between 2500 and 2000 yr BP is unclear. The species did not occur near any of our study sites and is uncommon in the canyon. Its disappearance may have resulted from increasing density of woodlands as *J. osteosperma* populations expanded. The late Holocene appearance of *Yucca glauca* at Wind River Canyon matches a pattern observed in the northern Bighorn Basin by Lyford et al. (2002a).

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LITERATURE CITED

- BETANCOURT, J.L. 1990. Late Quaternary biogeography of the Colorado Plateau. Pages 259–292 in J.L. Betancourt, T.R. Van Devender, and P.S. Martin, editors, *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press, Tucson.
- COLE, K.L. 1990. Late Quaternary vegetation gradients through the Grand Canyon. Pages 240–258 in J.L. Betancourt, T.R. Van Devender, and P.S. Martin, editors, *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press, Tucson.
- DRIESE, K.L., W.A. REINERS, E.H. MERRILL, AND K.G. GEROW. 1997. A digital land cover map of Wyoming, USA: a tool for vegetation analysis. *Journal of Vegetation Science* 8:133–146.
- KNIGHT, D.H. 1994. *Mountains and plains: the ecology of Wyoming landscapes*. Yale University Press, New Haven, CT.
- LITTLE, E.L., JR. 1971. *Atlas of United States trees*. Volume 1. Conifers and important hardwoods. United States Department of Agriculture, Forest Service, Miscellaneous Publication 1146.
- LYFORD, M.E. 2001. The roles of dispersal, climate, and topography in the Holocene migration of Utah juniper into Wyoming and southern Montana. Doctoral dissertation, University of Wyoming, Laramie.
- LYFORD, M.E., J.L. BETANCOURT, AND S.T. JACKSON. 2002a. Holocene vegetation and climate history of the northern Bighorn Basin, southern Montana. *Quaternary Research*: In press.
- LYFORD, M.E., S.T. JACKSON, J.L. BETANCOURT, AND S.T. GRAY. 2002b. Anatomy of a late Holocene plant migration: influence of environmental heterogeneity and climate variability. *Ecology*: In review.
- MAUGHAN, E.K. 1972. Geologic map of the Wedding of the Waters Quadrangle, Hot Springs County, Wyoming. U.S. Geological Survey Geologic Quadrangle Map GQ-1042. Washington, DC.
- . 1987. Wind River Canyon, Wyoming. Pages 191–196 in S.S. Beus, editor, *Geological Society of America Centennial field guide—Rocky Mountain section*. Geological Society of America, Boulder, CO.
- NOWAK, C.L., R.S. NOWAK, R.J. TAUSCH, AND P.E. WIGAND. 1994. A 30,000 year record of vegetation dynamics at a semi-arid locale in the Great Basin. *Journal of Vegetation Science* 5:579–590.
- NOWAK, R.S., C.L. NOWAK, AND R.J. TAUSCH. 2000. Probability that a fossil absent from a sample is also absent from the paleolandscape. *Quaternary Research* 54:144–154.
- SHARPE, S.E. 1991. Late-Pleistocene and Holocene vegetation change in Arches National Park, Grand County, Utah, and Dinosaur National Monument, Moffat County, Colorado. Master's thesis, Northern Arizona University, Flagstaff.
- SPAULDING, W.G., J.L. BETANCOURT, L.K. CROFT, AND K.L. COLE. 1990. Packrat middens: their composition and methods of analysis. Pages 59–84 in J.L. Betancourt, T.R. Van Devender and P.S. Martin, editors, *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press, Tucson.
- STUIVER, M., AND P.J. REIMER. 1993. Extended ^{14}C database and revised CALIB 3.0 ^{14}C age calibration program. *Radiocarbon* 35:215–230.
- THADEN, R.E. 1980. Geologic map of the Birdseye Pass Quadrangle, showing chromolithofacies [*sic*] and coal beds in the Wind River Formation, Fremont and Hot Springs counties, Wyoming. U.S. Geological Survey Geologic Quadrangle Map GQ-1537. Washington, DC.
- THOMPSON, R.S. 1990. Late Quaternary vegetation and climate in the Great Basin. Pages 200–239 in J.L. Betancourt, T.R. Van Devender, and P.S. Martin, editors, *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press, Tucson.
- WEST, N.E. 1999. Juniper-piñon savannas and woodlands of western North America. Pages 288–308 in R.C. Anderson, J.S. Fralish, and J.M. Baskin, editors, *Savannas, barrens, and rock outcrop plant communities of North America*. Cambridge University Press.

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