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Holocene Vegetation and Climate History of the Northern Bighorn Basin, Southern Montana

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Records of Holocene vegetation and climate change at low elevations (<2000 m) are rare in the central Rocky Mountain region. We developed a record of Holocene vegetation and climate change from 55 ^{14}C-dated woodrat middens at two low-elevation sites (1275 to 1590 m), currently vegetated by *Juniperus osteosperma* woodlands, in the northern Bighorn Basin. Macrofossil and pollen analyses show that the early Holocene was cooler than today, with warming and drying in the middle Holocene. During the Holocene, boreal (*Juniperus communis, J. horizontalis*) and montane species (*J. scopulorum*) were replaced by a Great Basin species (*J. osteosperma*). *J. osteosperma* colonized the east side of the Pryor Mountains 4700 ^{14}C yr B.P. Downward movement of lower treeline indicates wetter conditions between 4400 and 2700 ^{14}C yr B.P. Increased aridity after 2700 ^{14}C yr B.P. initiated expansion of *J. osteosperma* from the east to west side of the Pryor Mountains.

Key Words: **Rocky Mountains; woodrat middens; paleoecology; paleoclimate; Holocene; plant migration.**

INTRODUCTION

Late Quaternary vegetational and climatic changes in the foothills and basins of the central Rocky Mountains are poorly documented. Natural lakes are rare below 2000 m. Although pollen sequences from subalpine and alpine lakes indicate late Quaternary shifts in climate and vegetational patterns (Burkart, 1976; Whitlock, 1993; Whitlock *et al*., 1995; Fall *et al*., 1995), extrapolation to the extensive areas at lower elevations is problematic. Studies of dune activity within the Rocky Mountain basins and adjacent Great Plains also indicate Holocene changes in effective moisture (Forman *et al*., 2001), but these records do not provide direct information about vegetation composition and need to be corroborated by other paleoclimate proxies.

Woodrat middens are among the few archives that preserve evidence of vegetational change in arid and semiarid regions at temporal scales of 10^2 to 10^4 yr. More than 2000 middens have been dated and analyzed from western North America (Webb and Betancourt, 1990), but the midden record remains largely unexploited north of 40°N, despite suitable terrain and climate. The northern Bighorn Basin of north-central Wyoming and south-central Montana (Fig. 1) is one such northerly setting where woodrat middens preserve a record of low-elevation vegetation change.

Rocky Mountain, Great Plains, and Great Basin floras converge in the northern Bighorn Basin (Knight *et al*., 1987; DeVelice and Lesica, 1993; McCarthy, 1996). Fifty-three Great Basin species, including two locally dominant woody species, *Cercocarpus ledifolius* and *Juniperus osteosperma*, reach their northeasternmost limits at the northern edge of the Bighorn Basin (McCarthy, 1996). During the late Quaternary, the relatively low (2300-m) Continental Divide across southwestern Wyoming may have served as a weak filter for northeastward dispersal and migration of elements of the Great Basin flora to the edge of the northern Great Plains. Great Basin species in Wyoming and southern Montana are confined to narrow elevational and latitudinal wedges that correspond to discrete climatic envelopes.

We present plant macrofossil and pollen analyses of 55 ^{14}C-dated woodrat middens from two low-elevation areas at the northern edge of the Bighorn Basin in southern Montana (Fig. 1). Although separated by only 30 km, the areas differ in elevation by 200 m, which allows us to refine Holocene paleoclimate estimates for the northern Bighorn Basin and the central Rocky Mountains.

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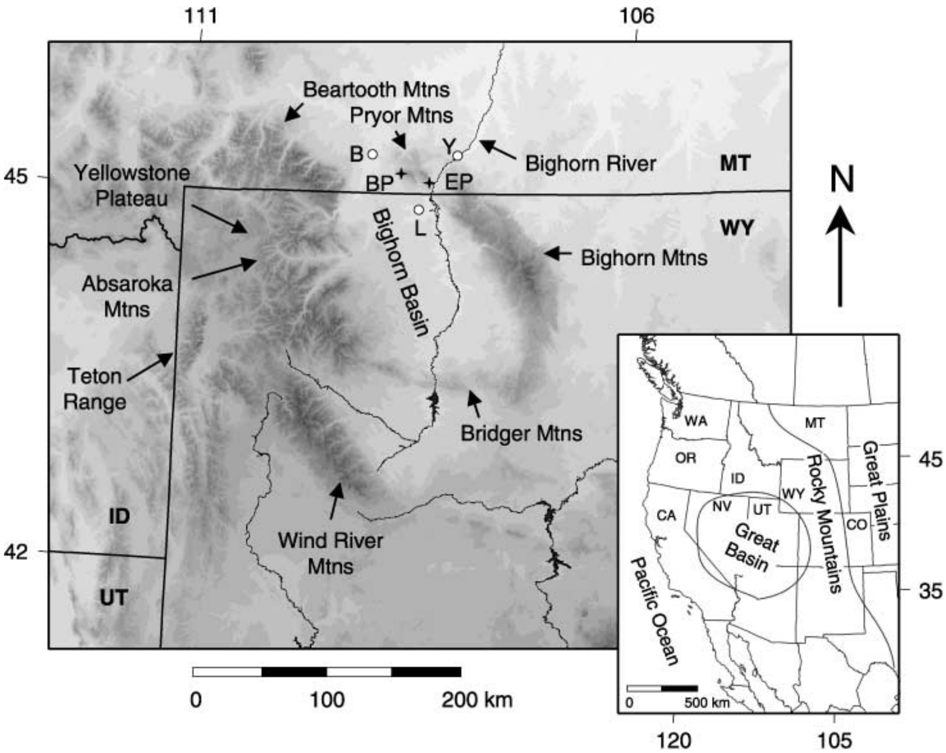

FIG. 1. Pryor Mountain region showing the location of Big Pryor (BP) and East Pryor (EP) midden collection sites. Climate stations include Bridger (B), Lovell (L), Yellowtail Dam (Y). CA = California; CO = Colorado; ID = Idaho; MT = Montana; Mtns = Mountains; NV = Nevada; OR = Oregon; UT = Utah; WA = Washington.

STUDY AREA

Woodrat middens were collected from the west slope of Big Pryor Mountain (Big Pryor) and the east slope of East Pryor Mountain and southern Bighorn Canyon (East Pryor) (Figs. 1 and 2). The Big Pryor study area is 7 km northeast of Warren, Montana, with collection sites ranging from 1490 to 1560 m elevation (Table 1). The East Pryor study area is approximately 30 km east of Big Pryor and 30 km northeast of Lovell, Wyoming (Fig. 1); midden sites range from 1275 to 1590 m elevation (Table 1).

Climate

The Pryor Mountains straddle a climatic boundary between the semiarid Bighorn Basin to the south and the subhumid Great Plains to the north. The Bighorn Basin lies in the winter rainshadow of the Absaroka Mountains and Yellowstone Plateau to the west and the summer rainshadow of the Bighorn Mountains to the east and southeast and the Pryor Mountains to the north. Mean annual precipitation ranges from 177 mm at Lovell (1169 m) to 295 mm at Bridger (1127 m) and 478 mm at Yellowtail Dam (1007 m).

About half of the annual precipitation in the northern Great Plains and Bighorn Basin falls between April and July. Much of this moisture is delivered from the Gulf of Mexico to the central and western Plains by a nocturnal low-level jet (Helfand and Schubert, 1995; Higgins *et al*., 1997). Although early summer (May–June) moisture primarily affects the Great Plains, it extends into Montana as far west as the northern Yellowstone region (Whitlock and Bartlein, 1993). However, the Bighorn Basin receives relatively little precipitation associated with the low-level jet owing to the eastern and northern rainshadow. Average minimum temperatures are lower in the Bighorn Basin than in the Great Plains owing to thermal inversions, but average maximum temperatures are comparable (−15.5 to 31.5°C at Lovell; −11.5 to 31.0°C at Bridger; −8.6 to 32.6°C at Yellowtail Dam).

Vegetation

Lower slopes of Big Pryor Mountain (1500–1800 m) are dominated by *Juniperus osteosperma*, with *Juniperus scopulorum* and *Pinus flexilis* scattered along the north-facing slopes (Fig. 3). *Juniperus osteosperma* yields to *J. scopulorum* and *Pinus flexilis* between 1800 and 2000 m. *Pseudotsuga menziesii, Pinus ponderosa*, and *Juniperus horizontalis* occur along north-facing slopes and in mesic canyon bottoms. Above 2000 m, coniferous forest (*Pinus flexilis, Pseudotsuga menziesii, Abies lasiocarpa, Picea engelmannii*) is interspersed with open meadows.

Southern Bighorn Canyon and lower slopes of East Pryor Mountain (<1650 m) are vegetated by *Juniperus osteosperma* and mixed *J. osteosperma/Cercocarpus ledifolius* woodlands and by *C. ledifolius* shrublands (Knight *et al*., 1987) (Fig. 3).

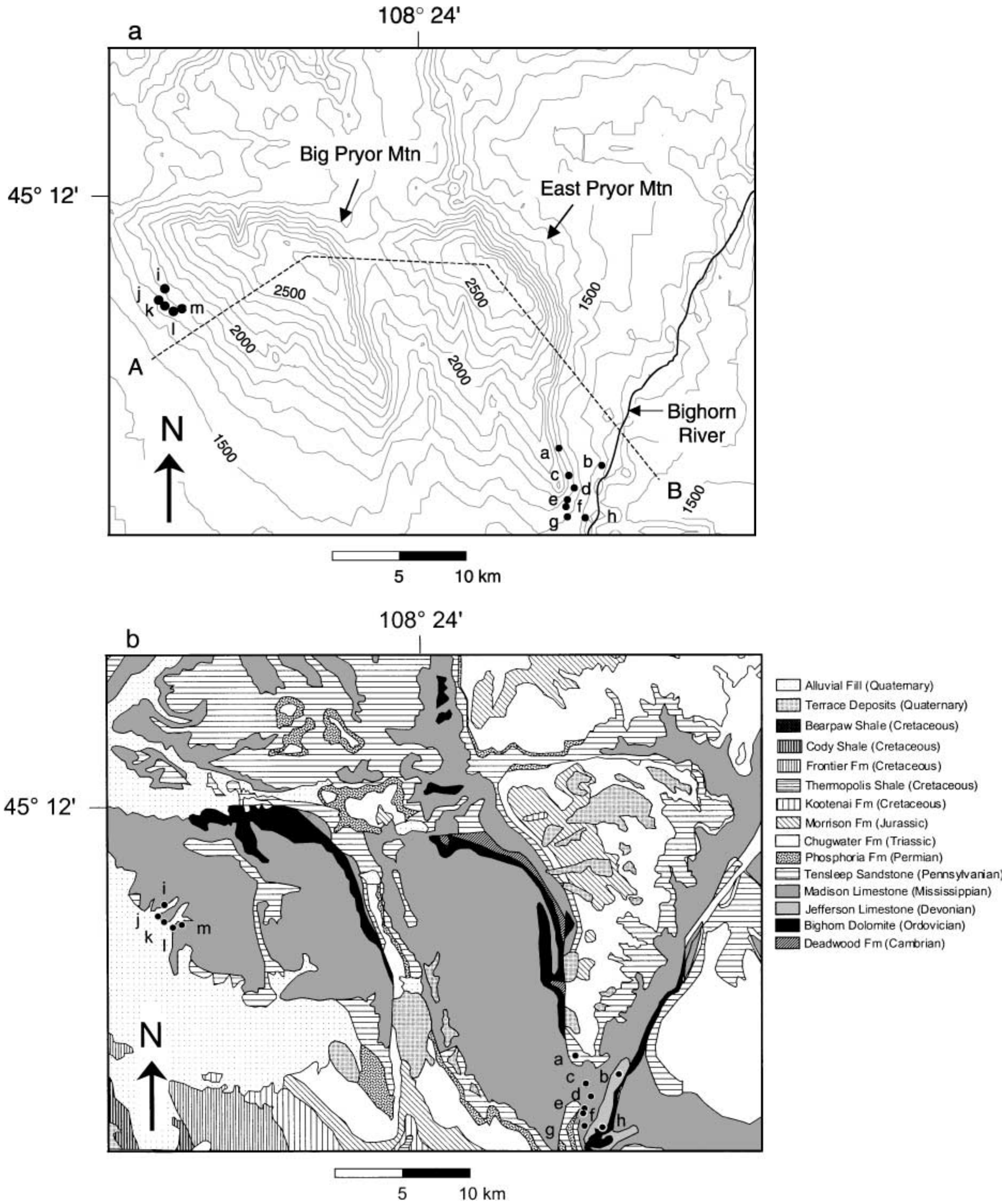

FIG. 2. a) Elevation map and b) geologic map of the Pryor Mountain region depicting the location of midden collection sites at Big Pryor and East Pryor Mountains. Dotted line in (a) represents the transect (point A to B) used to create the latitudinal profile in Fig. 3. Middens collected at each location are as follows: a) 146; b) 111a, 111b, 112, 113, 114d, 115b1, 129, 148, 176b, 176c, 176d, 177; c) 184, 185, 186, 188; d) 189b, 189d, 189f; e) 190a1, 190a2, 190d, 191; f) 149a, 149b, 149c, 150; g) 151, 152a, 153, 205; h) 187b; i) 127, 128; j) 142a, 142c1, 142c2; k) 101b, 102b, 102c, 103a, 105, 108a2, 141, 154a; l) 143b, 143c, 144a2, 144a3, 145; m) 158a, 158c, 158d1. Mtn = Mountain.

TABLE 1
Radiocarbon Age, Location, and Elevation of Collected and Analyzed Middens from Big Pryor and East Pryor

Midden	Lab no.	Material dated	Species dated	Age (^{14}C yr B.P.)	Age range at 2 SD (cal yr B.P.)[a]	Latitude	Longitude	Elevation (m)
				Big Pryor Sites				
145	GX-24361	pellets		490 ± 70	330–650	N45°07.907′	W108°38.490′	1500
154A	GX-24362	pellets		1160 ± 70	930–1260	N45°08.437′	W108°38.703′	1524
105	GX-24430	pellets		1580 ± 70	1310–1690	N45°08.353′	W108°38.883′	1518
103A	GX-24356	pellets		1620 ± 70	1350–1690	N45°08.353′	W108°38.883′	1518
103A	AA-31692	twigs	*J. osteosperma*	1660 ± 50	1420–1690	N45°08.353′	W108°38.883′	1518
142C1	GX-24414	pellets		1785 ± 80	1530–1890	N45°08.517′	W108°39.045′	1490
158A	GX-24363	pellets		2310 ± 75	2130–2710	N45°08.048′	W108°38.175′	1564
158A	AA-33157	twigs	*J. osteosperma*	2415 ± 50	2340–2710	N45°08.048′	W108°38.175′	1564
128	GX-24358	pellets		2370 ± 75	2160–2710	N45°09.167′	W108°39.167′	1554
127	GX-24357	pellets		2840 ± 85	2770–3240	N45°09.167′	W108°39.167′	1554
127	AA-31685	twigs	*J. osteosperma*	1620 ± 45	1410–1690	N45°09.167′	W108°39.167′	1554
142C2	GX-24360	pellets		3190 ± 80	3210–3630	N45°08.517′	W108°39.045′	1490
158C	GX-24364	pellets		3240 ± 80	3270–3680	N45°08.048′	W108°38.175′	1564
158C	AA-31684	twigs	*J. osteosperma*	1220 ± 50	990–1270	N45°08.048′	W108°38.175′	1564
101B	GX-24354	pellets		3285 ± 75	3360–3690	N45°08.353′	W108°38.883′	1518
142A	GX-24342	pellets		5490 ± 190	5910–6720	N45°08.517′	W108°39.045′	1490
141	GX-24359	pellets		5880 ± 170	6310–7180	N45°08.265′	W108°38.561′	1524
141	AA-33165	needles	*J. communis*	8320 ± 80	9030–9520	N45°08.265′	W108°38.561′	1524
143C	GX-24343	pellets		6510 ± 230	6810–7790	N45°07.907′	W108°38.490′	1500
143C	AA-33159	needles	*J. communis*	8590 ± 70	9470–9700	N45°07.907′	W108°38.490′	1500
143B	GX-24344	pellets		8190 ± 420	8170–10,210	N45°07.907′	W108°38.490′	1500
158D1	GX-24340	pellets		9100 ± 280	9530–11,160	N45°08.048′	W108°38.175′	1564
102C	GX-24355	pellets		9980 ± 140	11,170–12,270	N45°08.353′	W108°38.883′	1548
102B	AA-31687	twigs	*J. scopulorum*	7295 ± 60	7970–8190	N45°08.353′	W108°38.883′	1548
144A2	AA-31682	twigs	*J. scopulorum*	7615 ± 60	8340–8540	N45°07.907′	W108°38.490′	1500
144A3	AA-33158	needles	*J. communis*	9080 ± 110	9920–10,500	N45°07.907′	W108°38.490′	1500
108A2	AA-33163	needles	*J. communis*	9100 ± 70	10,160–10,470	N45°08.436′	W108°38.704′	1518
				East Pryor Sites				
176D	GX-24420	pellets		460 ± 65	320–620	N45°02.739′	W108°15.074′	1274
176C	GX-24560	pellets		915 ± 65	690–950	N45°02.739′	W108°15.074′	1274
152A	GX-24419	pellets		1160 ± 65	930–1260	N45°00.883′	W108°16.802′	1402
184	GX-24434	pellets		1415 ± 65	1190–1410	N45°01.775′	W108°16.400′	1524
151	GX-24418	pellets		1515 ± 70	1290–1540	N45°00.960′	W108°16.738′	1372
205	GX-24423	pellets		1570 ± 70	1310–1690	N45°00.893′	W108°16.072′	1402
112	GX-24415	pellets		1595 ± 70	1330–1690	N45°02.250′	W108°15.033′	1311
114D	GX-24501	pellets		1795 ± 70	1540–1880	N45°02.300′	W108°15.017′	1311
176B	GX-24559	pellets		1880 ± 70	1630–1990	N45°02.739′	W108°15.074′	1274
148	GX-24417	pellets		1950 ± 120	1570–2300	N45°02.518′	W108°15.010′	1274
185	GX-24428	pellets		2175 ± 195	1710–2740	N45°01.775′	W108°16.400′	1530
185	AA-31694	twigs	*J. scopulorum*	1555 ± 50	1330–1540	N45°01.775′	W108°16.400′	1530
188	GX-24422	pellets		2665 ± 75	2620–2920	N45°01.775′	W108°16.400′	1591
177	GX-24433	pellets		2860 ± 75	2780–3240	N45°02.633′	W108°15.000′	1274
189D	GX-24502	pellets		3210 ± 80	3270–3630	N45°01.500′	W108°16.650′	1582
129	GX-24432	pellets		3285 ± 90	3280–3720	N45°02.717′	W108°15.000′	1274
187B	GX-24435	pellets		3340 ± 75	3390–3820	N45°00.900′	W108°15.600′	1311
186	GX-24429	pellets		3880 ± 250	3620–4960	N45°01.775′	W108°16.400′	1530
186	AA-31688	twigs	*J. osteosperma*	3065 ± 55	3080–3380	N45°01.775′	W108°16.400′	1530
190A1	GX-24503	pellets		4440 ± 90	4830–5320	N45°01.290′	W108°16.720′	1402
111A	GX-24425	pellets		4630 ± 160	4860–5660	N45°02.250′	W108°15.033′	1311
111A	AA-31683	twigs	*J. osteosperma*	4090 ± 45	4420–4820	N45°02.250′	W108°15.033′	1311
111B	GX-24426	pellets		5170 ± 180	5590–6310	N45°02.250′	W108°15.033′	1311
111B	AA-33154	twigs	*J. osteosperma*	4670 ± 60	5300–5590	N45°02.250′	W108°15.033′	1311
115C	GX-24431	pellets		5575 ± 95	6200–6620	N45°02.555′	W108°15.045′	1280
146	GX-24416	pellets		5660 ± 95	6290–6720	N45°03.205′	W108°16.120′	1548
153	AA-33164	twigs	*J. osteosperma*	450 ± 50	330–550	N45°00.883′	W108°16.802′	1402
113	AA-31681	twigs	*J. osteosperma*	1460 ± 45	1290–1420	N45°02.300′	W108°15.017′	1311
191	AA-33169	twigs	*J. osteosperma*	1800 ± 55	1570–1870	N45°01.500′	W108°16.650′	1493

TABLE 1—*Continued*

Midden	Lab no.	Material dated	Species dated	Age (^{14}C yr B.P.)	Age range at 2 SD (cal yr B.P.)[a]	Latitude	Longitude	Elevation (m)
189B	AA-33161	needles	*P. flexilis*	2950 ± 50	2950–3320	N45°01.500′	W108°16.650′	1582
190D	AA-31691	twigs	*J. osteosperma*	3080 ± 100	2970–3470	N45°01.290′	W108°16.720′	1402
189F	AA-33166	needles	*P. flexilis*	3180 ± 60	3270–3550	N45°01.500′	W108°16.650′	1582
115B-1	AA-33167	twigs	*J. osteosperma*	4315 ± 60	4740–5040	N45°02.555′	W108°15.045′	1280
150	AA-31679	twigs	*J. osteosperma*	4425 ± 50	4860–5290	N45°01.037′	W108°16.693′	1432
190A2	AA-33678	twigs	*J. osteosperma*	4635 ± 45	5300–5570	N45°01.290′	W108°16.720′	1402
149C	AA-31680	twigs	*J. scopulorum*	9470 ± 90	10,430–11,160	N45°01.128′	W108°16.698′	1372
149C	AA-31686	needles	*J. communis*	9725 ± 65	10,790–11,230	N45°01.128′	W108°16.698′	1372
149B	AA-31693	needles	*J. communis*	9810 ± 80	11,120–11,340	N45°01.128′	W108°16.698′	1372
149A	AA-31689	twigs	*J. scopulorum*	9875 ± 75	11,170–11,550	N45°01.128′	W108°16.698′	1372
149A	AA-31690	needles	*J. communis*	10105 ± 75	11,260–12,290	N45°01.128′	W108°16.698′	1372

[a] Calibrated according to Stuiver and Reimer (1993) and Stuiver *et al*. (1998), B.P. = A.D. 1950.

The absence of *J. scopulorum* and *P. flexilis* and the high abundance of *Atriplex* at the East Pryor sites indicates drier climate than at the Big Pryor sites. *J. osteosperma* is replaced in northern Bighorn Canyon by *J. scopulorum, Pinus ponderosa*, and *Pseudotsuga menziesii*, corresponding to wetter conditions north of the Bighorn Mountains rainshadow (Knight *et al*., 1987). In southern Bighorn Canyon, *J. osteosperma* is replaced by low-density stands of *J. scopulorum* and *Pinus flexilis* above 1650 m. Forests above 1900 m are dominated by *P. flexilis, P. menziesii, Abies lasiocarpa*, and *P. engelmannii*.

METHODS

Midden Collection and Processing

We collected 119 woodrat middens (66 from Big Pryor and 53 from East Pryor) from crevices and rock shelters in Mississippian Madison Limestone and Pennsylvanian Tensleep Sandstone (Fig. 2), mostly on south-facing slopes where *Juniperus osteosperma* is dominant. Midden collection and reduction techniques followed Spaulding *et al*. (1990).

Dried midden samples were weighed and separated into three size classes (<1 mm, 1–2 mm, and >2 mm) using 1-mm and 2-mm mesh screens. Plant remains in the largest size class were sorted and identified to the highest taxonomic resolution possible based on comparisons with reference specimens collected in the field and obtained from the Rocky Mountain Herbarium (University of Wyoming). Plant remains were identified in a portion of the middle size class. Each taxon was tallied and plotted using a relative abundance scale from 1 to 5 (1 = single occurrence, 5 = dominant) (Spaulding *et al*., 1990).

A subsample (10–20 g) of each midden was removed for pollen analysis. Pollen samples were soaked in water until completely dispersed and then wet-screened through a 180-μm mesh to remove large particles. The screened solution was stirred vigorously and allowed to sit for 30 seconds, permitting large particles to settle to the bottom. We pipetted 100 ml of liquid spanning the entire vertical profile of the fluid, centrifuged it

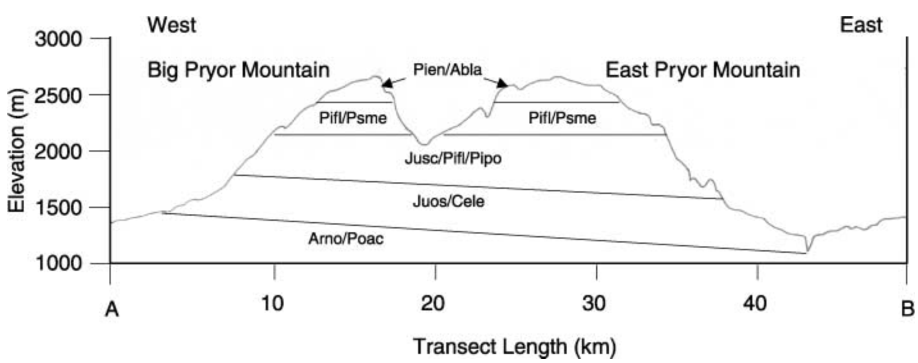

FIG. 3. Latitudinal profile of the Pryor Mountain region (3× vertical exaggeration). The transect line used to create this profile appears as the dotted line (point A to B) in Fig. 2a. Vegetation zones are as follows: Arno/Poac, *Artemisia nova* and grass; Juos/Cele, *Juniperus osteosperma* and *Cercocarpus ledifolius*; Jusc/Pifl/Pipo, *J. scopulorum, Pinus flexilis*, and *Pinus ponderosa*; Pifl/Psme, *Pinus flexilis* and *Pseudotsuga menzeisii*; Pien/Abla, *Picea engelmannii* and *Abies lasiocarpa*.

to concentrate the pollen sample, and processed according to standard procedures (Jackson, 1999). Pollen was counted until at least 200 arboreal pollen grains were recorded (arboreal taxa included Cupressaceae). Total number of grains identified per sample ranged from 318 to 561 (mean = 393).

Radiocarbon Dating

We dated 55 middens. Fecal pellets of 17 Big Pryor and 22 East Pryor middens were dated by conventional ^{14}C methods (Table 1). Accelerator mass spectrometry (AMS) dating was used when samples had insufficient material for conventional dating, mixing of midden assemblages was suspected, or the age of a particular fossil was critical. Plant remains were AMS-dated from 4 Big Pryor and 12 East Pryor undated middens, and AMS dates of plant remains were obtained from 6 Big Pryor and 4 East Pryor middens already dated by conventional means (Table 1).

Comparisons of conventional and AMS dates indicate concordance for two middens (Big Pryor 103A, 158A), but different ages for eight middens (Big Pryor 127, 141, 143C, 158C; East Pryor 111A, 111B, 185, 186) (Fig. 4). Big Pryor 127 and 158C are dominated by *J. scopulorum* and contain one and two *J. osteosperma* seeds, respectively. These seeds are younger contaminants (Table 1) and, in view of their scarcity, we accept the conventional dates as representative of the remaining midden assemblage. AMS dates of *J. communis* scales that occur sparsely in Big Pryor 141 and 143C are significantly older than the corresponding pellet dates (Table 1). We treat these samples as unmixed, except for the *J. communis* material. An AMS date of *J. scopulorum* stems in East Pryor 185 is younger than conventionally dated fecal pellets indicating potential mixing, but the remaining assemblage is indistinguishable from contemporary middens.

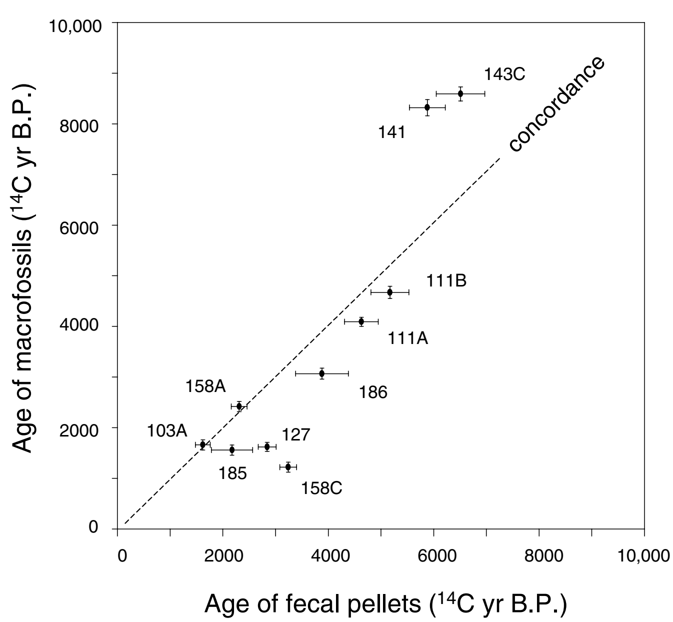

FIG. 4. Comparison of conventional dates of fecal pellets and accelerator mass spectometry dates of macrofossils.

In contrast, East Pryor 111A, 111B, and 186 appear to be mixed assemblages. In each case, the AMS date of *J. osteosperma* is younger than the conventional date. However, because macrofossil assemblages of these middens are similar to middens of comparable age from these sites and dissimilar to older and younger middens, we retain these middens provisionally in our data set (midden ages defined by conventional dates).

FOSSIL ASSEMBLAGES

Big Pryor Mountain

The five early Holocene (10,000–8200 ^{14}C yr B.P.) middens are dominated by *Juniperus communis, J. scopulorum*, and *Pinus flexilis* macrofossils (Fig. 5, Table 1). *J. communis* is dominant in the oldest midden, which also contains fern (*Adiantum* type) spores and abundant Asteraceae pollen. Younger middens of early Holocene age have more *J. scopulorum* and *P. flexilis* macrofossils, and higher percentages of *P. flexilis* and Chenopodiaceae pollen. *Atriplex* sp., *Cryptantha* sp., and *Krascheninnikovia lanata* only occur in the youngest midden (8200 ^{14}C yr B.P.).

Five middle Holocene (7600–5500 ^{14}C yr B.P.) middens are characterized by absence of *J. communis*, dominance of *J. scopulorum* and *P. flexilis*, and consistent occurrence of *J. horizontalis* (Fig. 5). *Atriplex* sp. is also abundant in the mid-Holocene middens, which also have high percentages of Chenopodiaceae pollen.

Late Holocene middens, dating 3500 to 2500 ^{14}C yr B.P., are dominated by *J. scopulorum* and *P. flexilis*, but they lack *Atriplex* sp., as do all younger middens. *J. scopulorum* decreases in abundance with the first appearance of *J. osteosperma* 2400 ^{14}C yr B.P., after which *J. osteosperma* becomes dominant in the middens. *Artemisia nova* and *Cercocarpus ledifolius* initially appear at 3200 and 2300 ^{14}C yr B.P., respectively, and both are sporadically present in the younger middens. Middens dating $\geq$2800 ^{14}C yr B.P. and younger contain abundant *Yucca glauca* macrofossils.

Mead (1982) reported a midden from Bear Canyon, at 1585 m elevation 12 km SE of our Big Pryor study area, dated at 10,260 ± 100 ^{14}C yr B.P., with an apparently mixed assemblage of *Juniperus communis, J. scopulorum*, and *J. osteosperma.* We found similar middens at some of our sites, but in each case determined that a late Holocene midden containing *J. osteosperma* had been pasted onto or mixed with an eroded early Holocene midden dominated by *J. communis.* This was confirmed when we obtained an AMS date of 2162 ± 44 ^{14}C yr B.P. (AA-41986) on *J. osteosperma* foliage from the original midden collected by Mead.

East Pryor Mountain/Southern Bighorn Canyon

The 34 middens from East Pryor are mostly middle to late Holocene (<5700 ^{14}C yr B.P.) in age (Table 1; Fig. 6). Three middens dating between 10,100 and 9500 ^{14}C yr B.P. are small and contain few plant macrofossils (all *J. communis* and

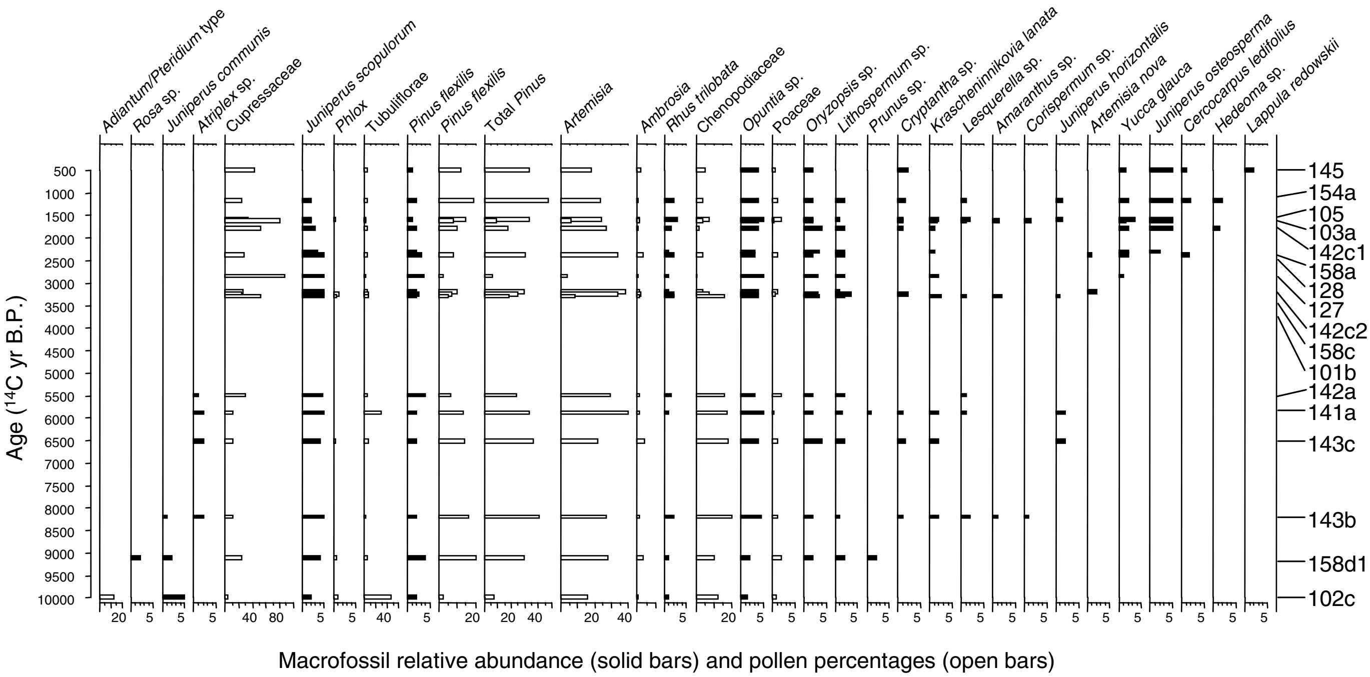

FIG. 5. Macrofossil and pollen data for Big Pryor Mountain middens.

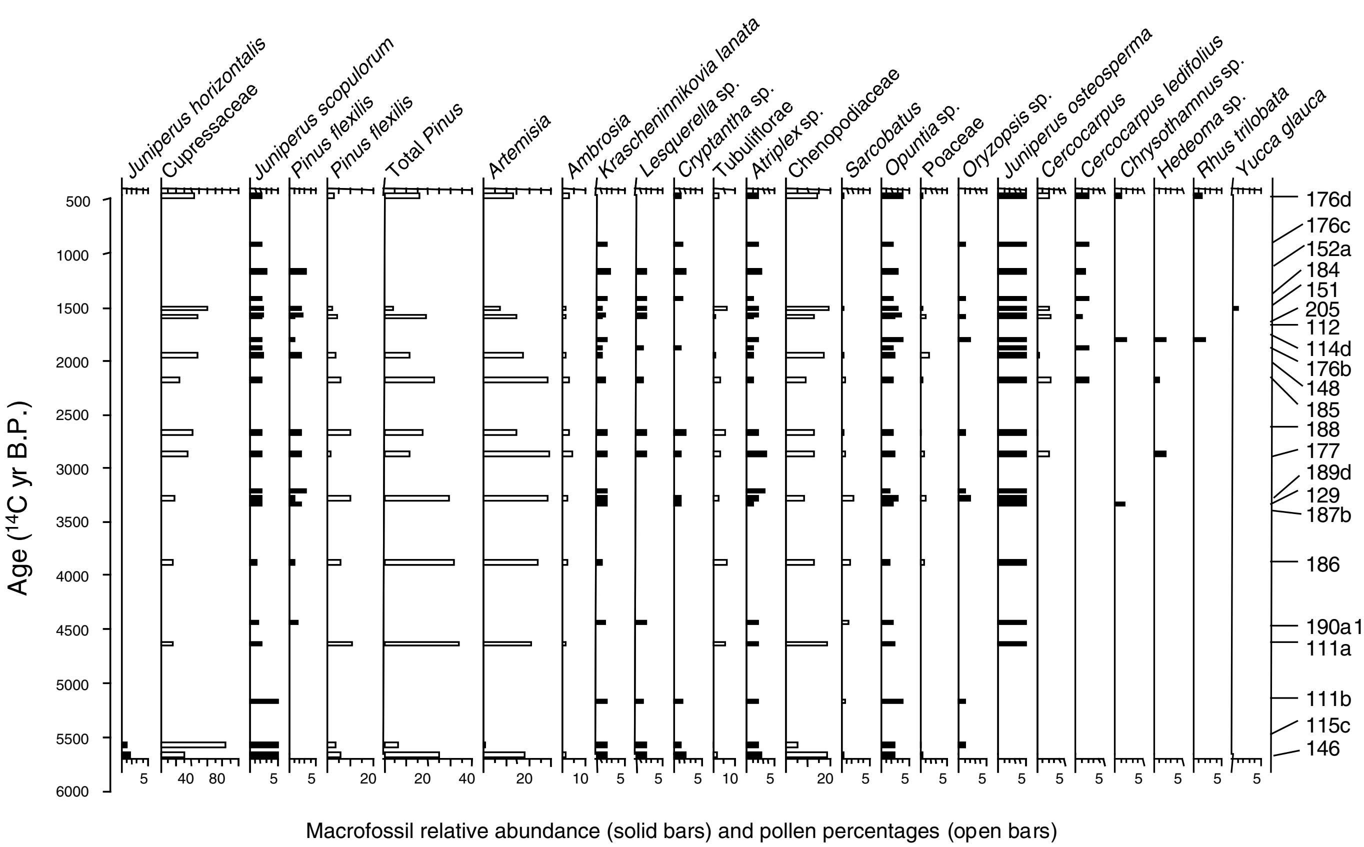

FIG. 6. Macrofossil and pollen data for East Pryor Mountain/Southern Bighorn Canyon middens.

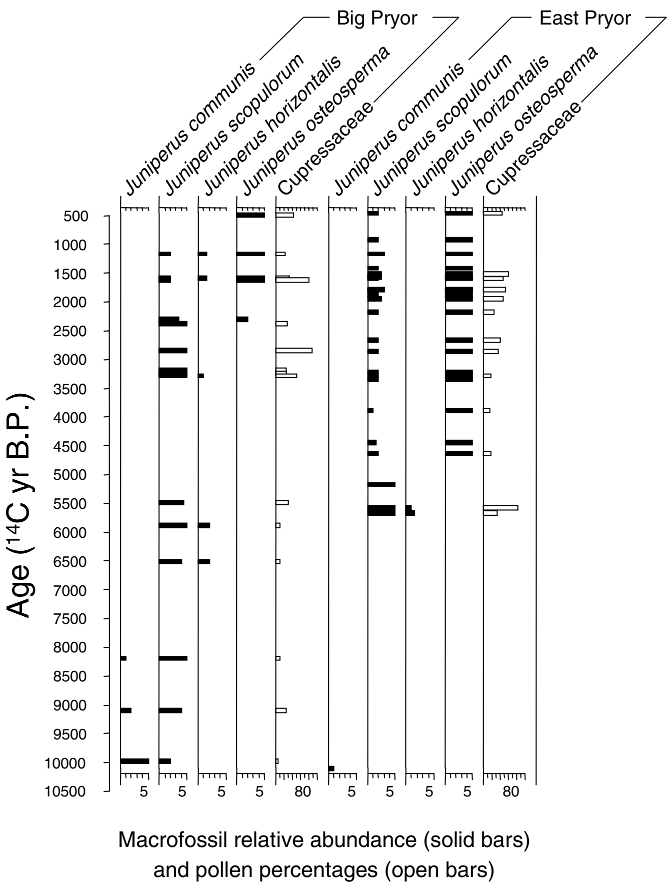

FIG. 7. Summary diagram comparing macrofossil and pollen data for juniper species at Big Pryor and East Pryor study areas.

J. scopulorum). *J. communis* is absent from all the younger middens (<5700 ^{14}C yr B.P.).

Middens dated from 5700 to 5200 ^{14}C yr B.P. are dominated by *J. scopulorum*, but *J. osteosperma* is the most abundant juniper species after its first appearance 4700 ^{14}C yr B.P. (Fig. 6). Abundance of *J. scopulorum* macrofossils decreases following the first occurrence of *J. osteosperma. J. horizontalis* occurs in middens dated 5600 and 5700 ^{14}C yr B.P. *P. flexilis* first appears in a midden dated 4400 ^{14}C yr B.P. All of the mid- and late Holocene (5700–500 ^{14}C yr B.P.) middens contain abundant *Atriplex* sp. and *Kraschenninikovia lanata* macrofossils and high percentages of Chenopodiaceae pollen.

J. osteosperma macrofossils are abundant in all late Holocene (3900–500 ^{14}C yr B.P.) middens. All middens dating from 4400 to 2700 ^{14}C yr B.P. contain *P. flexilis* macrofossils, and *P. flexilis* pollen percentages are highest between 3300 and 1200 ^{14}C yr B.P. *Cercocarpus* pollen first occurs at 3300 ^{14}C yr B.P., and *C. ledifolius* macrofossils first occur at 2200 ^{14}C yr B.P. and are well-represented in the younger middens. *Chrysothamnus* sp. and *Yucca glauca* are first documented at 3300 and 1500 ^{14}C yr B.P., respectively, but neither occur consistently in the younger middens.

Comparison between Big Pryor and East Pryor

Juniperus communis and *J. scopulorum* occurred at both study areas in the early Holocene. *J. communis* disappeared and *J. horizontalis* first appeared during the middle Holocene. *J. scopulorum* remained the dominant juniper at both areas until the arrival of *J. osteosperma* (Fig. 7). *J. osteosperma* appeared earlier at East Pryor (4700 ^{14}C yr B.P.) than Big Pryor (2400 ^{14}C yr B.P.), a difference of ∼3000 cal yr. *P. flexilis* fossils occur in all middens at Big Pryor, but only between 4400 and 1200 ^{14}C yr B.P. at East Pryor. *Atriplex* sp. is also abundant in both middle Holocene records, but disappears at Big Pryor in the late Holocene. Late Holocene *Yucca glauca* and *Artemisia nova* are more common at Big Pryor than at East Pryor. *Cercocarpus ledifolius* was first recorded in late Holocene Big Pryor and East Pryor middens of comparable age (2300 ^{14}C yr B.P.).

HOLOCENE VEGETATION AND CLIMATE HISTORY OF THE NORTHERN BIGHORN BASIN

Early and Middle Holocene

The presence of *Juniperus communis* in East Pryor and Big Pryor assemblages indicates a relatively cool and moist climate from 10,000 to at least 8200 ^{14}C yr B.P. *J. communis* presently inhabits areas 300 m above the collection sites, primarily on north-facing slopes. Based on current temperature and precipitation gradients with elevation from the western Bighorn Mountains, a 300 m displacement of *J. communis* would require an increase in January and July precipitation of at least 9.3 ± 4.9 mm (mean ±1 standard deviation) and 5.2 ± 2.8 mm, respectively, and a lowering of July temperatures by at least 2.4 ± 0.6°C. Cool, wet conditions are also suggested by the occurrence of *Rosa* sp. and *Prunus* sp. macrofossils and high percentages of *Adiantum* spores ca. 10,000 ^{14}C yr B.P. at Big Pryor (Fig. 5).

A modest warming and drying trend between 9100 and 8200 ^{14}C yr B.P. is marked by decreasing abundance of *J. communis* and the appearance and increase of xerophytic taxa (*Opuntia* sp., *Lithospermum* sp., *Atriplex* sp., *Cryptantha* sp., *Krascheninnikovia lanata*, *Lesquerella* sp., *Amaranthus* sp., *Corispermum* sp.) at Big Pryor. Increased percentages of Chenopodiaceae pollen during this transition probably represent local increases of *Krascheninnikovia* and *Atriplex*. These species may have occupied deep, finer textured soils of the valley fill, while *J. communis, J. scopulorum*, and *Pinus flexilis* persisted in the adjacent box canyons.

Increased aridity during the middle Holocene is indicated by a shift in juniper species, from boreal (*Juniperus communis, J. horizontalis*) and and montane species (*J. scopulorum*), to a Great Basin species (*J. osteosperma*) at East Pryor. The shift from *J. communis* to *J. horizontalis*, another prostrate juniper, indicates drier conditions; *J. horizontalis* currently extends to lower elevations than *J. communis* in the region. The arrival of *J. osteosperma* at East Pryor 4700 ^{14}C yr B.P. coincides with a decrease in *J. scopulorum*, also suggesting increasingly

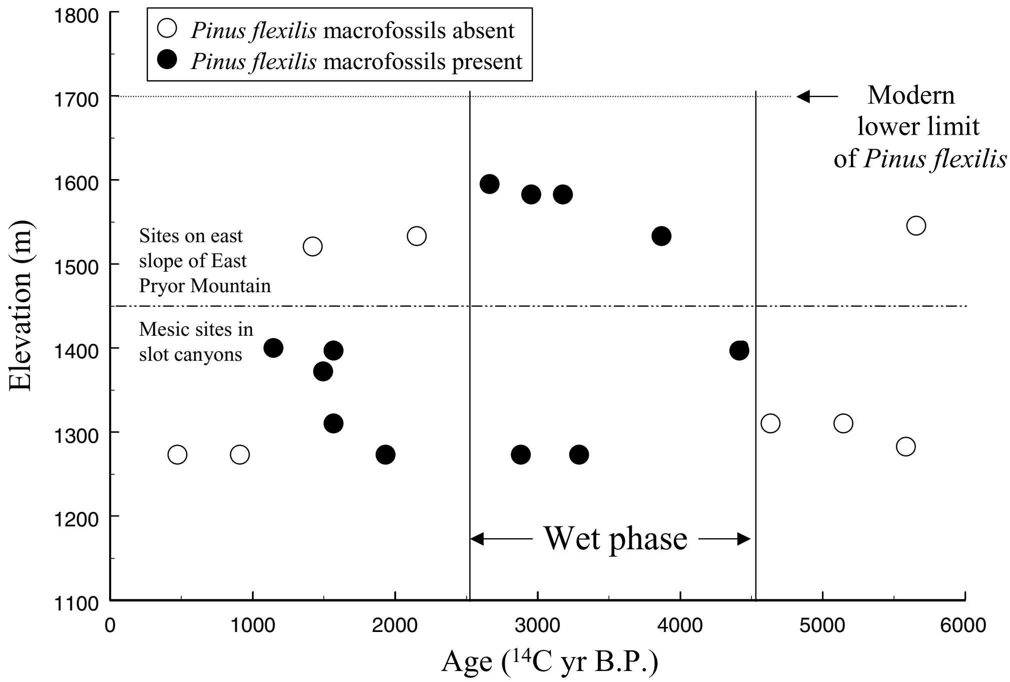

FIG. 8. Presence and absence of *Pinus flexilis* macrofossils for East Pryor middens as a function of age and elevation.

arid conditions. Moreover, the abundance of *Atriplex* sp. in both records, accompanied by high Chenopodiaceae pollen percentages and the presence of *Cryptantha* sp., *Lithospermum* sp., *Krascheninnikovia lanata*, and *Lesquerella* sp. suggests warm, dry conditions.

The early Holocene transition from cool and moist to warm and dry at Big Pryor is also recorded at other sites in the Central Rocky Mountain region. Rapid warming is recorded after 10,600 ^{14}C yr B.P. in the Wind River Mountains, Wyoming (Fall *et al.*, 1995), between 10,500 and 9,500 ^{14}C yr B.P. in the southern Yellowstone and Grand Teton region (Whitlock, 1993) and between 10,800 and 10,000 ^{14}C yr B.P. at Swan Lake (Bright, 1966) and Grays Lake (Beiswenger, 1991) in Southeastern Idaho. Other sites in the Yellowstone region show a more gradual shift from cool and moist conditions to warm and dry conditions between 11,800 and 9000 ^{14}C yr B.P. (Waddington and Wright, 1974; Baker, 1976; Gennett and Baker, 1986). A similar transition to greater aridity occurs between 11,000 and 10,000 ^{14}C yr B.P. on the Northern Great Plains as recorded at Moon Lake, Southeastern North Dakota, and Cottonwood Lake, Central South Dakota (Laird *et al.*, 1998), and the Black Hills, Southwestern South Dakota (Fredlund and Tieszen, 1997).

Late Holocene

A wet phase between 4400 and 2700 ^{14}C yr B.P. is indicated by shifts of several species in the East Pryor and Big Pryor macrofossil and pollen records. *Atriplex*, although abundant in middle Holocene middens at Big Pryor, is absent after 5500 ^{14}C yr B.P., and Chenopodiaceae pollen percentages drop concurrently (Fig. 5). *Atriplex* persisted throughout this wet phase at the drier East Pryor sites (Fig. 6).

The late Holocene wet phase permitted downward expansion of *Pinus flexilis* at East Pryor. *P. flexilis* is absent from all middens >4400 ^{14}C yr B.P. but occurs in all samples between 4400 and 2700 ^{14}C yr B.P. (Fig. 8). The disappearance of *P. flexilis* from the more drought-sensitive slopes of East Pryor Mountain at 2700 ^{14}C yr B.P. indicates onset of drier conditions. In contrast, *P. flexilis* persisted until 1200 ^{14}C yr B.P. in the relatively mesic box canyons below 1450 m elevation (Fig. 8). Increased moisture is also recorded between ca. 4400 and 2700 ^{14}C yr B.P. at sites in eastern and western Washington (Mack *et al.*, 1978a, 1978b; Barnosky, 1981, 1985a, 1985b), eastern Oregon (Wigand, 1987; Mehringer and Wigand, 1990), northern Idaho (Mack *et al.*, 1978c), western Montana (Mehringer *et al.*, 1977; Mack *et al.*, 1983), and western Wyoming (Whitlock, 1993; Fall *et al.*, 1995).

Increased aridity after 2700 ^{14}C yr B.P. is documented by the establishment of several Great Basin species, including *Juniperus osteosperma* at Big Pryor and *Cercocarpus ledifolius* at Big and East Pryor. Migration lag is unlikely to account for the delay of ∼3000 cal yr between East Pryor and Big Pryor in arrival of *J. osteosperma*, given their proximity to each other (30 km). *J. osteosperma* migrated from southeast Utah (Betancourt, 1990) to northeast Utah (Sharpe, 1991), a distance of 400 km, in less than 1000 yr, and from northeast Utah to East Pryor (550 km) in less than 4000 yr. Each of these migrations probably involved multiple dispersal events of greater than 30 km. Because *J. osteosperma* appeared at Big Pryor as *P. flexilis* disappeared from East Pryor, a climatic threshold was apparently crossed between 3000 and 2500 ^{14}C yr B.P. that allowed *J. osteosperma* to colonize at Big Pryor.

Magnitude of Late Holocene Wet Phase

The migration pattern of *Juniperus osteosperma* in the Pryor Mountain region provides a means to estimate the magnitude of climate change experienced during the wet phase between ca. 4400 and 2700 ^{14}C yr B.P. Because *J. osteosperma* was absent at Big Pryor between 4400 and 2700 ^{14}C yr B.P., conditions at its current upper elevational limits at Big Pryor aid in estimating the minimum climate change required. Wetting and cooling corresponding to a 200 m increase in elevation would exclude *J. osteosperma* from Big Pryor. A decrease in minimum temperature of 0.6 $\pm$ 0.3°C in January and 1.6 $\pm$ 0.4°C in July, and an increase in minimum precipitation of 6.2 $\pm$ 3.3 mm in January and 3.5 $\pm$ 1.9 mm in July relative to modern, would be necessary to prohibit *J. osteosperma* from growing on the west slope of Big Pryor Mountain. These calculations are based on elevational gradients in climate determined from mean January and July precipitation and temperature from 16 climate stations in the Bighorn Mountain region (Wyoming stations include Arminto, Beartrap Meadow, Buffalo, Burgess Junction, Dome Lake, Hansen Sawmill, Lovell, Parkman, Powder River Pass, Shell, Shell Creek, Sheridan, Tensleep; Montana stations include Cook City, Gardiner, Red Lodge).

The persistence of *J. osteosperma* at East Pryor during the late Holocene wet phase also provides a basis for estimating the maximum change in temperature and precipitation. Wetting and cooling by an equivalent of 400 m elevation would drive *J. osteosperma* from Bighorn Canyon. Thus, maximum estimates of cooling and wetting during the late Holocene wet phase are 1.2 $\pm$ 0.7°C and 12.4 $\pm$ 6.5 mm for January and 3.2 $\pm$ 0.8°C and 6.9 $\pm$ 3.7 mm for July.

CONCLUSIONS

Climate warming throughout the early and middle Holocene in the northern Bighorn Basin is indicated by a shift in juniper species from *Juniperus communis* ultimately to *J. osteosperma*. Climatic cooling and wetting between 4400 and 2700 ^{14}C yr B.P. is documented by an elevational depression of *Pinus flexilis*. Based on the colonization pattern of *J. osteosperma*, the temperature decrease during the wet phase is estimated to be 0.6–1.2°C cooler than today in January and 1.6–3.2°C cooler in July, and January and July precipitation is estimated to be 6.2–12.4 mm and 3.5–6.9 mm greater than today, respectively.

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