THE SOUTHWESTERN NATURALIST 34(1):35–45 MARCH 1989

LATE QUATERNARY FOSSILS OF *POA FENDLERIANA* (MUTTONGRASS): HOLOCENE EXPANSIONS OF APOMICTS

ROBERT J. SORENG AND THOMAS R. VAN DEVENDER

ABSTRACT—Modern geographic ranges of sexual and asexual (agamospermous) reproduction in *Poa fendleriana* were determined from the absence of staminate plants in populations and herbaria. Macrofossils in 13 radiocarbon dated packrat (*Neotoma* sp.) middens from four sites in southwestern Arizona and southeastern Utah yielded evidence of the sex, morphological race, and abundance of *P. fendleriana*. Radiocarbon ages on midden materials range from 20,490 to 1,820 years B.P. Sexual reproduction is recorded at 16,000 years B.P. in the Late Wisconsin full-glacial in southern Arizona but not until 3,400 years B.P. in the late Holocene in southeastern Utah. The fossil record suggests that apomicts advanced northward onto the Colorado Plateau in the latest Wisconsin or early Holocene and were followed 5,000 to 7,000 years later by sexual races.

Geographic histories of dominant plant species from late Pleistocene to the present have been pieced together through the use of plant macrofossils from packrat (*Neotoma* sp.) middens, pollen from sedimentary cores, and other paleoclimatic data for many areas in the southwestern United States (Spaulding et al., 1983; Van Devender, 1986). Recently, paleobotanists have become interested in past distributions of cool and warm season grasses because of the strong relationships between their distribution and climate (Teeri and Stowe, 1976; Ehleringer, 1978). Grass remains have been recovered from many packrat middens (L. J. Toolin, pers. comm.), but only a few have been reported. Grasses were reported in chronological midden sequences from southeastern Utah (Betancourt, 1984), the Sacramento Mountains of south-central New Mexico (Van Devender et al., 1984), the Puerto Blanco Mountains of southwestern Arizona (Van Devender, 1987), and the Picacho Peak area of southeastern California (Cole, 1986).

Knowledge of the distribution of apomicts is of particular value because, as pointed out by Stebbins (1950), "the relative constancy of apomicts through hundreds or even thousands of generations makes them valuable indicators of ecological conditions, both in their present habitats and past migration routes." The apomicts of arctic *Poa* must have migrated extensively in the Pleistocene to colonize vast glaciated areas (Nannfeldt, 1940; Muntzing, 1954). Apomicts in general usually have larger geographic ranges and occur at higher elevations and latitudes than their sexual counterparts (Bierzychudek, 1985). In this paper, we examine fossil remains of *Poa fendleriana* (Steud.) Vasey (muttongrass) from packrat middens from Arizona and Utah for evidence of apomixis and evaluate its biogeographical significance for the last 20,490 years in the last glacial (the Wisconsin)/interglacial (the Holocene) cycle.

Muttongrass is a common cool season dioecious grass of western North America. It occurs from upper interior chaparral to subalpine grasslands but is most

TEERI, J. A., AND L. G. STOWE. 1976. Climatic patterns and the distribution of C4 grasses in North America. Oecologia, 23:1–12.

THOMPSON, R. S. 1984. Late Pleistocene and Holocene environments in the Great Basin. Unpubl. Ph.D. dissert., Univ. Arizona, Tucson, 256 pp.

VAN DEVENDER, T. R. 1986. Climatic cadences and composition of Chihuahuan Desert communities: the late Pleistocene packrat midden record. Pp. 285–299, *in* Community ecology (J. Diamond and T. J. Case, eds.). Harper and Row Publ., New York, 665 pp.

———. 1987. Holocene vegetation and climate in the Puerto Blanco Mountains, southwestern Arizona. Quaternary Res., 27:51–72.

VAN DEVENDER, T. R., AND W. G. SPAULDING. 1979. Development of vegetation and climate in the southwestern United States. Science, 204:701–710.

VAN DEVENDER, T. R., J. L. BETANCOURT, AND M. WIMBERLY. 1984. Biogeographic implications of a packrat midden sequence from the Sacramento Mountains, south-central New Mexico. Quaternary Res., 22:344–360.

VAN DEVENDER, T. R., R. S. THOMPSON, AND J. L. BETANCOURT. 1987. Vegetation history in the Southwest: the nature and timing of the Late Wisconsin-Holocene transition. Pp. 323–352, *in* North America and adjacent oceans during the last deglaciation (W. F. Ruddiman and H. E. Wright, Jr., eds.). Geol. Soc. Amer., Boulder, Colorado, 501 pp.

WELLS, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glacio-pluvial. Ecol. Monogr., 53:341–382.

Address of authors: (RJS) *Dept. of Biol., New Mexico State Univ., Las Cruces, NM 88003*; (TRV) *Arizona-Sonora Desert Mus., 2021 N. Kinney Road, Tucson, AZ 85743* (Present address of RJS: *L. H. Bailey Hortorium, Cornell Univ., Ithaca, NY 14853*).

common in openings in lower montane conifer forests with *Pinus ponderosa* (yellow pine), *Pseudotsuga menziesii* (Douglas fir), and *Quercus gambelii* (Gambel oak). Both sexual and asexual populations of this species reproduce by seed. The modern geographical distribution of sexual and apomictic reproduction has been determined for the three subspecies of *P. fendleriana* (Soreng, 1986). The present distribution of apomictic and sexual reproduction in two of the three subspecies of *P. fendleriana* is illustrated in Figs. 1 and 2. Sexual and asexual reproduction are primarily restricted in *P. f.* subsp. *albescens* (Hitchc.) Soreng to the northern Sierra Madre Occidental. In *P. f.* subsp. *fendleriana,* sexual reproduction is primarily restricted to eastern Arizona and the southern Rocky Mountains from southernmost Colorado south to the northern Sierra Madre Oriental in north Coahuila, Mexico. In *P. f.* subsp. *longiligula* (Scribn. and Will.) Soreng, sexual reproduction is primarily restricted to Rocky Mountains in the Wasatch Escarpments and connected mountain chains in Utah and eastern Nevada and the mountains of the southern Colorado Plateau and northwestern Arizona. For the remainder of the paper subspecific names will be used without the "subsp." designation.

The apomicts are distributed in regions with climates similar to those where the corresponding sexual races occur. However, sexually reproducing populations are more likely to be found in relatively mild and mesic environments compared to their apomictic counterparts (Soreng, 1986). The geographic range of asexual reproduction in *P. f. fendleriana* is about three times as broad as that of sexual reproduction, with apomicts concentrated above and below and to the north of sexual populations. In *P. f. longiligula,* the range of asexuals is about 20 times broader, with apomicts distributed above, below, and throughout and extending north, east, and west of the sexual zone. Today, sexual *P. f. longiligula* predominates where winter precipitation is relatively more consistent than where sexual *P. f. fendleriana* predominates.

Materials and Methods—Because the species is dioecious, absence or rarity of staminate plants in herbaria and on-site sampling of sex ratios in populations were used to detect regions of apomictic reproduction. Apomixis was also detected by the formation of seeds in pistillate plants geographically or artificially isolated from pollen. Florets of *P. fendleriana* from fossil packrat middens from Arizona and Utah were examined to determine sex, subspecies, and the presence of seed (Table 1). A few fairly reliable morphological characters on the spikelets distinguish the three subspecies of *P. fendleriana* (Soreng, 1985). Lemmas of *P. f. albescens* are essentially glabrous. Lemmas of the other two subspecies are distinctly villous on the keel and marginal nerves but are somewhat larger and more strongly villous in *P. f. longiligula.* Rachillas are smooth or scabrous or very rarely pilose in *P. f. fendleriana* but are usually hirtellous or less often pilose in *P. f. longiligula.* Apomicts of the latter two subspecies usually have hirtellous rachillas and sometimes moderately scabrous (versus smooth) lemmas. With the exception of some sexually reproducing populations intermediate between *P. f. fendleriana* and *P. f. longiligula,* the majority of plants with intermediate characters are apomictic. Multiple occurrences of fossils of a species within a midden stratum were taken to represent relative abundance of the species near the midden site (Spaulding et al., 1983; Betancourt, 1984; Van Devender, 1986), although grasses may have been less representative than other plants.

Results—Thirteen packrat midden strata contained from 1 to 80 florets of *P. fendleriana* (Table 1).

The Arizona Midden Series—Florets of *P. fendleriana* were found in a midden dated at 20,490 years B.P. (radiocarbon years before 1950) from an elevation

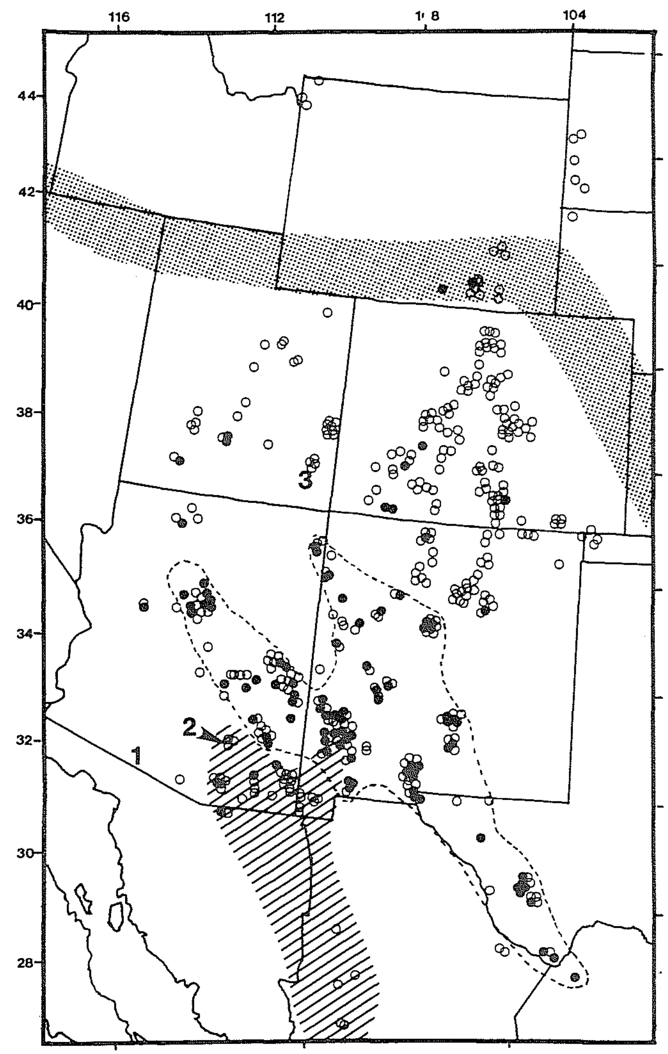

Fig. 1—Distribution of sexes in *P. fendleriana* subsp. *fendleriana* and the present position of Polar Front Gradient in western North America and location of midden samples. Females = open circles, males = solid circles. The primary sexual zone (sex ratio as taken from herbarium samples of 5:1 to 1:1 female to male within counties) is bounded by a dashed line. The polar front gradient (stippled area) marks the modal position of steepest gradient between cool, moist Pacific maritime air to the north and warm, dry subtropical air to the south (after Mitchell, 1976). Range of *P. f.* subsp. *albescens* indicated by diagonal bars. Midden sites at numbers or at arrows: 1 = Ajo Mountains, 2 = Santa Catalina Mountains, 3 = Abajo Mountains.

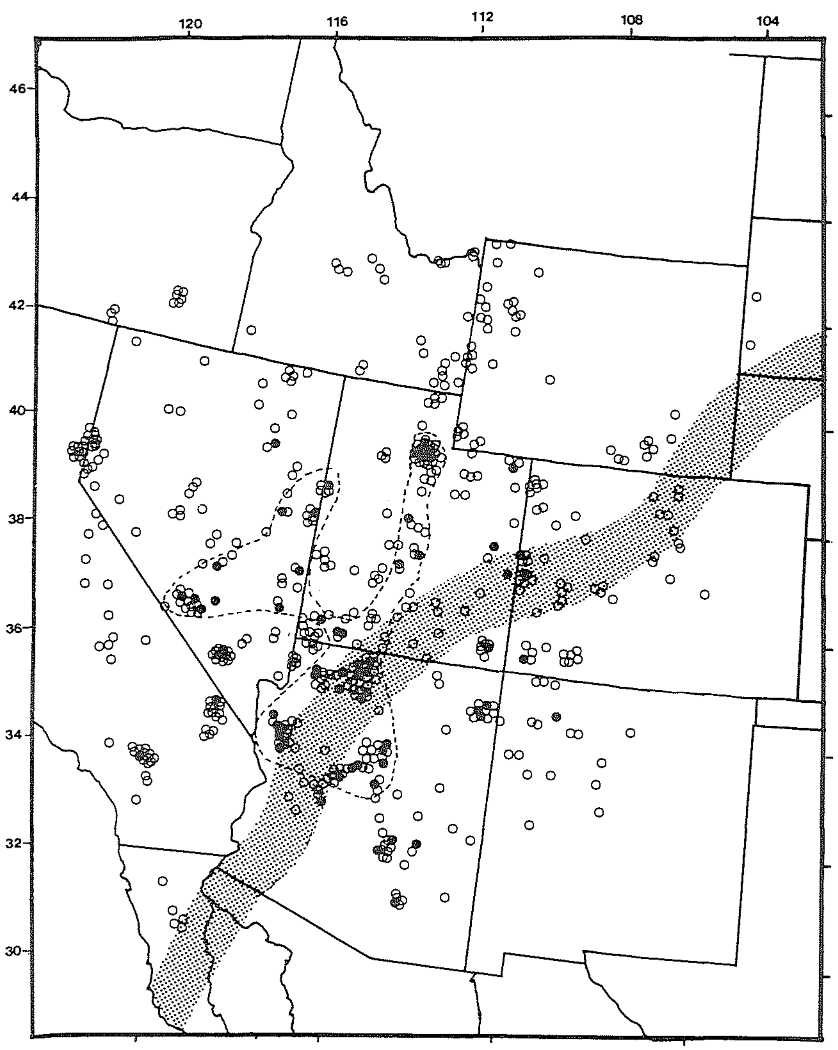

FIG. 2—Distribution of sexes in *P. fendleriana* subsp. *longiligula* and the present position of summer monsoon gradient in western North America. Pistillate plants = open circles, staminate plants = solid circles. The primary sexual zone is bounded by a dashed line. The stippled area marks the modal path of the summer monsoons as they cross the Southwest. Summer convective storms are reduced in frequency to the northwest and are frequent around and to the southeast of the path (after Mitchell, 1976). The position of this gradient is extrapolated south of the United States.

of 975 m in the Ajo Mountains in Organ Pipe Cactus National Monument (32°05′N, 112°21′W; Van Devender, 1987). The midden contained a mesic pinyon-juniper-oak woodland assemblage dominated by *Pinus monophylla* (singleleaf pinyon), *Juniperus scopulorum* (Rocky Mountain juniper), *Artemisia*

TABLE 1—Late Wisconsin and Holocene packrat midden records of *Poa fendleriana* (sex, race, numbers of specimens, and associated midden data and paleovegetation).

Locality—Midden	Elevation (m)	Radiocarbon date (years B.P.)	Laboratory no.	Paleovegetation	*Poa fendleriana* material
Arizona: Pima Co.					
Ajo Mountains					
Montezuma's Head #1A	975	20,490 ± 510	A-1695	Pinyon-juniper-Joshua tree woodland	11 florets, sex indet., no seed = *P. f.* cf. *longiligula*
Santa Catalina Mountains					
Pontatoc Ridge #4B	1,555	17,950 ± 960	A-1851	Arizona cypress forest	Spikelet with 3 pistillate florets = *P. f. longiligula* or *P. f. fendleriana*, or intermediate seed; pistillate floret = *P. f.* cf. *albescens*
Pontatoc Ridge #81-2	1,555	16,400 ± 400	A-2682	Arizona cypress forest	Staminate floret = *P. f. fendleriana*
Utah: San Juan Co.					
Ahajo Mountains					
Allen Canyon #7	2,195	11,310 ± 70	BETA-5756	Mixed-conifer forest	Spikelet with 2 florets with seed, 3 pistillate florets = *P. f. longiligula* or *P. f. fendleriana* or intermediate
Allen Canyon #8	2,195	10,140 ± 190	A-3120	Mixed-conifer forest	Floret, sex indet. = *P. f. longiligula* or *P. f. fendleriana* or intermediate
Allen Canyon #2	2,195	7,200 ± 90	BETA-5586	Pine forest	80 pistillate florets, 50% with seed = *P. f. fendleriana* or intermediate
Allen Canyon #6	2,195	3,400 ± 60	BETA-5583	Pinyon-juniper woodland	Staminate floret, pistillate floret without seed = *P. f. fendleriana*
Allen Canyon #5	2,195	3,000 ± 70	BETA-5585	Pinyon-juniper woodland	5 florets—2 ea. staminate, 2 ea. pistillate, no seed = *P. f. longiligula* or *P. f. fendleriana* or intermediate
Allen Canyon #4	2,195	1,820 ± 50	BETA-5766	Pinyon-juniper woodland	4 florets—3 pistillate, 2 with seed = *P. f. longiligula*
Fishmouth Cave #3	1,585	10,540 ± 180	BETA-5757	Mixed-conifer forest	10 florets—7 pistillate, 2 with seed = *P. f. longiligula* or *P. f. fendleriana* or intermediate
Fishmouth Cave #5	1,585	9,700 ± 110	BETA-5763	Juniper woodland	9 florets—6 pistillate, 2 with seed = *P. f.* ca. *fendleriana* or intermediate
Fishmouth Cave #6	1,585	3,550 ± 60	BETA-5764	Juniper woodland	8 pistillate florets, 3 with seed = *P. f. fendleriana*
Fishmouth Cave #9	1,585	2,260 ± 90	BETA-5765	Juniper woodland	9 pistillate florets, 5 with seed = *P. f. longiligula*

tridentata-type (big sagebrush), and *Yucca brevifolia* (Joshua tree). Mount Ajo, which reaches 1,475 m, could have supported *P. ponderosa* or *P. menziesii* in the Late Wisconsin.

The modern vegetation near the midden site on a steep west-facing slope on Montezuma's Head is a xeric shrub community in the transition between a Sonoran Desert community dominated by *Cercidium microphyllum* (foothills palo verde), *Carnegiea gigantea* (saguaro), and *Stenocereus thurberi* (organ pipe cactus) and desert-grassland. Both *S. thurberi* and a single *Juniperus erythrocarpa* (redberry juniper) are visible from the site. *Poa fendleriana* has not been collected in the Ajo Mountains (Bowers, 1980) and is usually found at elevations over 1,500 m in mountains 200 km to the north and east. This disjunction corresponds to a general 350- to 1,000-m depression of vegetation zones in the southwestern United States during the glacial maximum (Van Devender and Spaulding, 1979). Absence of fossils of *P. fendleriana* in three similar Late Wisconsin middens from the site suggests that this species was not common.

Staminate and pistillate florets of *P. fendleriana* were found in midden samples, dated at 17,950 and 16,400 years B.P., from an elevation of 1,555 m on Pontatoc Ridge in the Santa Catalina Mountains near Tucson (32°21'N, 110°53'W; Van Devender et al., 1987). The midden assemblages record a mesic Arizona cypress forest dominated by *Cupressus arizonica*. Important associates included *P. menziesii, P. ponderosa, Pinus discolor* (border pinyon), *Pinus edulis* × *Pinus monophylla* (Colorado × singleleaf pinyon hybrids), and *Quercus turbinella* (shrub live oak). The modern vegetation at the site is desert-grassland just above palo verde-saguaro desertscrub. *Poa fendleriana* no longer occurs at the site. It presently reaches its lower elevational limit in the Santa Catalina Mountains in an Arizona cypress forest at an elevation of 1,370 m on a north-facing slope in Bear Canyon.

The fossils record *P. fendleriana* at relatively low elevations in mesic forest and woodland communities from 20,490 to 16,400 years B.P. during the Late Wisconsin glacial maximum. However, similar climate and vegetation were probably present in the area during the entire Late Wisconsin until about 11,000 years B.P. (Van Devender, 1987). Paleoclimates with relatively moderate temperatures, especially in summer, and greater annual and winter rainfall prevailed over southern Arizona in the Late Wisconsin (Bryson and Hare, 1974; Van Devender and Spaulding, 1979). Today, *P. fendleriana* is a dominant understory species in yellow pine forest in southern Arizona (Küchler, 1964), although it extends from the interior chaparral to subalpine habitats. Moreover, pine forest was apparently absent from the montane vegetation zonation during the Late Wisconsin when mixed-conifer forest directly contacted pinyon-juniper-oak woodlands (Van Devender et al., 1984). The extensive pine forests of the Mogollon Rim in Arizona are a Holocene development.

The Utah Midden Series—Florets of *P. fendleriana* were found in two adjacent midden series in the Abajo Mountains in southeastern Utah (Betancourt, 1984). Allen Canyon Cave (37°47'N, 109°35'W) middens record subalpine conifers at an elevation of 2,195 m at 11,310 years B.P. in the Late Wisconsin changing to the present mixture of *P. menziesii, P. ponderosa,* and *Juniperus osteosperma* (Utah juniper) in the Holocene. The modern vegetation near the cave is a relatively mesic mixture of pinyon-juniper woodland, mixed-conifer forest, and alcove riparian forest plants. Trees in the area are *Acer glabrum* (Rocky Mountain maple), *Betula occidentalis* (water birch), *Q. gambelii, J. osteosperma, P. edulis, P. ponderosa, Populus tremuloides* (aspen), and *P. menziesii. Poa f. longiligula* probably occurs near the site.

Fishmouth Cave (37°26'N, 109°39'W) middens record mesic mixed-conifer forest dominated by *Pinus flexilis* (limber pine) and *P. menziesii* with *Juniperus communis* (dwarf juniper), *J. scopulorum,* and *Picea pungens* (blue spruce) at 1,585 m in the Late Wisconsin. *Poa fendleriana* was present in four Holocene samples dated between 10,540 and 2,260 years B.P. The modern vegetation near the cave is a juniper woodland/grassland dominated by *J. osteosperma* in association with *A. tridentata, Cercocarpus intricatus* (littleleaf mountain mahogany), and *Fraxinus anomala* (singleleaf ash). *Poa f. longiligula* probably occurs near the site.

Discussion—Packrat midden macrofossil records indicated spatial and temporal changes in subspecies and occurrence of sexual and apomictic reproduction within *P. fendleriana*. A stratum from 3,400 years B.P. had one staminate and one pistillate floret, and the next dated stratum, from 3,000 years B.P., had two staminate and two pistillate florets. Six florets representing at least four different plants provides some support for the assumption that abundance of florets in a stratum reflect relative abundance of the species in the surrounding habitat.

Apomixis is widespread and autonomous (seed develops without pollination) in *P. fendleriana*. Only pistillate plants are present over large portions of the modern range. Several factors suggest apomixis was the most common mode of reproduction throughout the time surveyed. Staminate florets occurred in only three midden strata of 13 with florets. In addition, a high proportion of seed was found in single strata from which staminate florets were not found. Good seed-set in sexual *P. fendleriana* requires such a high density of plants (Soreng, 1986) that male plants would be expected to have been fossilized if these were sexual populations. In contrast, apomictic females usually set abundant seed, averaging four times more seed than sexual females (Soreng, 1986). Morphological intermediacy between *P. f. fendleriana* and *P. f. longiligula* apparent in most florets also suggests the presence of apomicts.

Range Dynamics—The fossil records of *P. fendleriana* and regional paleovegetation records (Spaulding and Peterson, 1980; Wells, 1983; Betancourt, 1984; Cole, 1985) were compared with paleoclimatic models (Antevs, 1948; Bryson and Hare, 1974; Imbrie and Imbrie, 1979) and with present ecological distribution patterns of *P. fendleriana* to suggest the following interpretation of its range dynamics. During the Late Wisconsin full-glacial, the northern limit of *P. fendleriana* was displaced southward into Arizona and New Mexico. Sexually reproducing plants were present in southern areas like the Santa Catalina Mountains where some summer rainfall was still occurring. Even there, the preferred pine forest habitat was not present.

At the end of the Late Wisconsin (about 11,000 years B.P.), the range of *P. fendleriana* probably contracted to higher elevations in the southern mountains as mesic woodland plants disappeared from the desert lowlands. Meanwhile, apomictic *P. fendleriana* expanded northward onto the Colorado Plateau in southeastern Utah by 11,310 years B.P. in the latest Wisconsin (Betancourt, 1984). By the middle Holocene, summer temperatures warmer than today with a summer monsoon precipitation maximum (Van Devender, 1987) eliminated *P. fendleriana* from the lowlands but also led to major northward expansions of other species including *P. ponderosa* (Betancourt, 1984; Van Devender et al., 1984). The midden record of *P. fendleriana* in southeastern Utah reflects a similar pattern. At 7,200 years B.P., it was common (80 florets) at Allen Canyon Cave at an elevation of 2,195 m coincident with peak levels of *P. ponderosa* but absent from Fishmouth Cave at 1,585 m at 6,100 and 3,740 years B.P. (Betancourt, 1984). Sexually reproducing *P. fendleriana* was not recorded at either cave until 3,400 years B.P.

The subspecies of *P. fendleriana* found in the southeastern Utah records also have an interesting historical pattern. The first plants in the area were apomictic *P. f. fendleriana*. Later florets were from *P. f. fendleriana* or *P. f. fendleriana* × *P. f. longiligula* intermediates. By 2,260 years B.P. at Fishmouth Cave and 1,820 years B.P. at Allen Canyon Cave, apomictic *P. f. longiligula* had replaced *P. f. fendleriana*. Today apomictic *P. f. fendleriana* is common above 2,400 m in the adjacent Abajo Mountains and in the nearby Henry and La Sal mountains, where apomictic *P. f. longiligula* is common at lower elevations and occurs near the sites.

Paleoclimates—The geographic spread of apomictic *P. fendleriana* was not directly influenced by the retreat of mountain glaciers or continental ice sheets. The present ranges occupied by *P. f. longiligula* and *P. f. albescens* were never glaciated. About half of the present range occupied by apomictic *P. f. fendleriana* in the Rocky Mountains was covered by ice (Denny, 1970). There are also a few scattered modern records of apomicts of this subspecies in the northern Great Plains as far east as southwestern Manitoba, Canada, in the area covered by the Laurentide Ice Sheet. However, *P. f. fendleriana* occurs primarily below timberline, and it is likely that it entered previously glaciated areas after more cold-adapted vegetation became established.

Study of the present northern distributional limits of *P. f. fendleriana* and *P. f. longiligula* suggests that these taxa would have been isolated much farther south during glacial cycles. As illustrated in Fig. 1, the primary distribution of *P. f. fendleriana* is south of the polar front gradient. That gradient represents the modal position of the steepest transition between cool moist Pacific maritime air and warm dry subtropical air during the winter. The probable migration of *P. fendleriana* northward and to higher elevations as the region warmed in the Holocene is supported by paleovegetation and climatic data (Bryson and Hare, 1974; Wells, 1983). The Late Wisconsin climates of the Great Basin were colder and 15 to 35% wetter than today, mostly in the winter, with much cooler summers (Thompson, 1984).

The southeastern Utah series of middens is from an ecologically sensitive region with respect to post-Pleistocene migration of vegetation (Betancourt, 1984). Today the modal flow of the polar jetstream is across the Columbia Plateau, and this stabilizes the average position of the Polar Front gradient between 40° and 42°N latitude (Fig. 1). During glacial times the modal track

of the polar jetstream appears to have been across the American Southwest between 33° and 37°N (Bryson and Hare, 1974). This and other factors combined to limit northern distributions of many plant species with present northern range limits near the Polar Front to south of 37°N (Van Devender and Spaulding, 1979; Wells, 1983; Betancourt, 1984; Cole, 1985).

The distributions of apomictic and sexual races of *P. fendleriana* can be linked to climate. We know that modern sexually reproducing populations of *P. f. fendleriana* are most likely to be found in mild mesic environments with a dominance of summer precipitation (Soreng, 1986). A few scattered collections of male plants of this subspecies in southern Wyoming and high on the Wasatch Escarpments in Utah from predominantly apomictic populations suggest that sexual reproduction was once more widely distributed. Climatic warming and development of summer monsoonal rains in the middle Holocene might have promoted migration of sexual plants into that region. This interpretation is consistent with interpretations that occurrences of northern disjunct populations and hybrids of *P. monophylla* and *P. edulis* (Lanner and Hutchinson, 1972) and hybrids between *Quercus* species (Muller, 1952; Cottam et al., 1959; Maze, 1968) are relicts of past warmer climates with more summer rains. In contrast to the localized distribution patterns of sexual races, apomicts of *P. fendleriana* and related species appear to be less restricted by climatic conditions and geographic barriers and have consistently broader geographic ranges and climatic tolerances and greater overall abundance (Soreng, 1986). Rather than reaching hotter or drier extremes than their sexual counterparts (they appear to be equally restricted), apomicts are more frequent in colder, and sometimes wetter, regimes with shorter growing seasons.

With Holocene warming, increasing aridity in desert lowlands, and development of the summer monsoon, favorable habitat for *P. fendleriana* was reduced in the south and expanded to higher latitudes and elevations. Climatic shifts since the Pleistocene appear to have restricted "marginal" and rearranged "good" habitat for the sexual races to the south and increased "marginal" habitat to the north favoring expansion of the apomicts but inhibiting the spread of the sexual races. The advantages apomicts have in marginal habitats stem from several sources including density-independent reproduction, greater seed-set, and production of only pistillate offspring (Soreng, 1986). The Holocene development of pine forest in the mountains of Arizona and New Mexico and its spread northward into the Rocky Mountains favored the expansion of sexual and asexual *P. fendleriana*.

The Polar Front gradient seems to define the northern limit of *P. fendleriana* today. Past southward displacement of that gradient and fossil data provide evidence of northward expansion of this species out of the Southwest since the last glacial maximum. Packrat midden fossils of *P. fendleriana* indicate that since the last glacial maximum, apomicts advanced northward first, followed about 5,000 to 7,000 years later by sexual races. Relatively lower colonization capacity and upward constriction of suitable habitat appear to have slowed the migration of sexual races. The abundance of apomicts of this and other *Poa* in colder and previously glaciated areas testifies to their ability to disperse rapidly, as appropriate habitat becomes available with favorable climatic shifts. Climatic changes that appear rapid on a geologic time scale (e.g., 100 to 500 years) are more than adequate for dispersal of apomicts on ecological time scales measured in decades.

L. J. Toolin and J. L. Betancourt kindly provided the fossils studied. Funds were provided by the National Science Foundation in grants DEB 79-2384 to P. S. Martin and BSR 82-14939 to P. S. Martin and T. R. Van Devender. We are indebted to R. Spellenberg and E. Muldavin for their helpful discussion and review of the manuscript.

Literature Cited

ANTEVS, E. 1948. The Great Basin, with emphasis on glacial and postglacial times III. Climatic changes and pre-white man. Bull. Univ. Utah, 38:168–191.

BETANCOURT, J. L. 1984. Late Quaternary plant zonation and climate in southeastern Utah. Great Basin Nat., 44:1–35.

BIERZYCHUDEK, P. 1985. Patterns in plant parthenogenesis. Experientia, 41:1255–1264.

BOWERS, J. E. 1980. Flora of Organ Pipe Cactus National Monument. J. Arizona-Nevada Acad. Sci., 151:1–11, 33–47.

BRYSON, R. A., AND F. K. HARE. 1974. The climates of North America. Pp. 1–47, *in* The climates of North America (R. A. Bryson and F. K. Hare, eds.), Vol. 11 *in* World survey of climatology (H. E. Landsberg, ed.). Elsevier Sci. Publ. Company, Amsterdam, 420 pp.

COLE, K. L. 1985. Past rates of change, species richness, a model of vegetational inertia in the Grand Canyon, Arizona. Amer. Nat., 125:289–303.

———. 1986. The Lower Colorado Valley: a Pleistocene desert. Quaternary Res., 25:392–400.

COTTAM, W. P., J. M. TUCKER, AND R. DROBNICK. 1959. Some clues to Great Basin postpluvial climates provided by oak distribution. Ecology, 40:361–377.

DENNY, C. S. 1970. Glacial geology of conterminous United States. P. 76, *in* The national atlas of the United States of America. U.S. Dept. Interior Geol. Survey, Washington, D.C., 417 pp. (map).

EHLERINGER, J. R. 1978. Implications of quantum yield differences on the distributions of C3 and C4 grasses. Oecologia, 31:255–267.

IMBRIE, J., AND K. P. IMBRIE. 1979. Ice ages: solving the mystery. Enslow Publ., Hillside, New Jersey, 224 pp.

KÜCHLER, A. W. 1964. Potential natural vegetation of the conterminous United States. Spec. Publ., Amer. Geogr. Soc., New York, 36:1–214 (map).

LANNER, R. M., AND E. R. HUTCHINSON. 1972. Relict stands of pinyon hybrids in northern Utah. Great Basin Nat., 32:171–175.

MAZE, J. 1968. Past hybridization between *Quercus macrocarpa* and *Quercus gambelii*. Brittonia, 20:321–333.

MITCHELL, V. L. 1976. The regionalization of climate in the western United States. J. Appl. Meteorology, 15:920–927.

MULLER, C. H. 1952. Ecological control of hybridization in *Quercus*: a factor in the mechanism of evolution. Evolution, 6:147–148.

MUNTZING, A. 1954. The cytological basis of polymorphism in *Poa alpina*. Hereditas, 40:459–516.

NANNFELDT, J. A. 1940. On the polymorphy of *Poa arctica* R. Br., with special reference to its Scandinavian forms. Symb. Bot. Upsala, 4:1–85.

SORENG, R. J. 1985. *Poa* in New Mexico, with a key to middle and southern Rocky Mountain species (Poaceae). Great Basin Nat., 45:395–422.

———. 1986. Distribution and evolutionary significance of apomixis in diclinous *Poa* of western North America. Unpubl. Ph.D. dissert., New Mexico State Univ., Las Cruces, 214 pp.

SPAULDING, W. G., AND K. L. PETERSEN. 1980. Late Pleistocene and early Holocene paleoecology of Cowboy Cave. Univ. Utah Anthropol. Paper, 104:163–177.

SPAULDING, W. G., E. B. LEOPOLD, AND T. R. VAN DEVENDER. 1983. Late Wisconsin paleoecology of the American Southwest. Pp. 259–293, *in* Late-Quaternary environments of the United States (S. C. Porter, ed.). Univ. Minnesota Press, Minneapolis, 407 pp.

STEBBINS, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press., New York, 643 pp.

TEERI, J. A., AND L. G. STOWE. 1976. Climatic patterns and the distribution of C4 grasses in North America. Oecologia, 23:1–12.

THOMPSON, R. S. 1984. Late Pleistocene and Holocene environments in the Great Basin. Unpubl. Ph.D. dissert., Univ. Arizona, Tucson, 256 pp.

VAN DEVENDER, T. R. 1986. Climatic cadences and composition of Chihuahuan Desert communities: the late Pleistocene packrat midden record. Pp. 285–299, *in* Community ecology (J. Diamond and T. J. Case, eds.). Harper and Row Publ., New York, 665 pp.

———. 1987. Holocene vegetation and climate in the Puerto Blanco Mountains, southwestern Arizona. Quaternary Res., 27:51–72.

VAN DEVENDER, T. R., AND W. G. SPAULDING. 1979. Development of vegetation and climate in the southwestern United States. Science, 204:701–710.

VAN DEVENDER, T. R., J. L. BETANCOURT, AND M. WIMBERLY. 1984. Biogeographic implications of a packrat midden sequence from the Sacramento Mountains, south-central New Mexico. Quaternary Res., 22:344–360.

VAN DEVENDER, T. R., R. S. THOMPSON, AND J. L. BETANCOURT. 1987. Vegetation history in the Southwest: the nature and timing of the Late Wisconsin-Holocene transition. Pp. 323–352, *in* North America and adjacent oceans during the last deglaciation (W. F. Ruddiman and H. E. Wright, Jr., eds.). Geol. Soc. Amer., Boulder, Colorado, 501 pp.

WELLS, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecol. Monogr., 53:341–382.

Address of authors: (RJS) *Dept. of Biol., New Mexico State Univ., Las Cruces, NM 88003*; (TRV) *Arizona-Sonora Desert Mus., 2021 N. Kinney Road, Tucson, AZ 85743* (Present address of RJS: *L. H. Bailey Hortorium, Cornell Univ., Ithaca, NY 14853*).