traces were similar to curve a with mixed layers about 400 m deep. The temperatures of these mixed layers varied from 18.0° to 18.7°C. The coldest layers were found to the east, and the warmest layers were found near 31.5°N, 75°W. Salinities ranged from 36.47 to 36.51° per mil, and oxygen values were between 4.9 and 5.4 ml/liter. These are close to saturation values and indicate that most of these layers formed this winter.

These observations indicate that the atmosphere can, in the course of one winter, significantly change the topography of the main thermocline in the northwestern Sargasso Sea. This implies that the baroclinic volume transports in and near the Gulf Stream are also strongly affected. Worthington (*6*) has postulated that the Gulf Stream system, at least in part, is maintained by the thermodynamic processes that produce 18°C water. He suggested that outbreaks of polar continental air in winter cause deep vertical mixing of 18°C water south of the Gulf Stream and somehow deepen the main thermocline in this region. At present, the process that creates the deep mixed layers and deepens the main thermocline is unknown. Whether it is a convergence somehow caused by the cooling of the upper part of the water column, a convergence due to the winter wind stress distribution, or a result of some other factor needs to be clarified.

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3 June 1977; revised 22 August 1977

Holocene Woodlands in the Southwestern Deserts

Abstract. *Twenty-nine radiocarbon-dated pack rat middens document woodland communities in the deserts of the southwestern United States less than 10,000 years ago. A synchronous change from woodland to desert or grassland occurred about 8000 years ago in the Chihuahuan, Sonoran, and Mohave deserts. A shift of the Aleutian low and the winter storm track to the north, which resulted in drastically reduced winter precipitation in these areas, is inferred. The shift to nonpluvial climates in the Southwest lagged behind the beginning of nonglacial climates in the North because the melting continental glaciers contined to affect general circulation patterns.*

The southwestern United States is presently arid or semiarid and includes four deserts that differ in climate and biota. Aridity in the Southwest is presumably a late Tertiary development that favored the evolution and immigration of desert-adapted plants and animals and the formation of desert biotic communities (*1*). However, late Pleistocene pollen and plant macrofossils from the Southwest have consistently recorded woodland or forest. The formation of the present desert communities occurred during the Holocene or postglacial period that followed the last glaciopluvial period. The Holocene-Pleistocene boundary for the Southwest was placed at 12,000 years ago based on pollen records in Arizona and Nevada (*2*). However, the existence of woodland plant communities for thousands of years later than 12,000 years ago is documented by well-preserved fossils in ancient pack rat (*Neotoma*) middens in the deserts themselves. In this report I reexamine the early Holocene vegetational and inferred climatic transitions for the southwestern deserts.

Pack rat middens with radiocarbon dates from 11,000 to more than 40,000 radiocarbon years before present (B.P.) contain records of late Wisconsin vegetation in many areas of the southwestern United States. Most of these records are of woodland plants in areas that are now desert. In these areas, the environmental gradients are elevational gradients, where temperature decreases and precipitation increases with elevation. Desert communities are in the lowest, hottest, driest areas, with juniper and piñon-juniper woodlands in the higher, more mesic areas.

In the northern Chihuahuan Desert of Trans-Pecos Texas, piñon-juniper woodland extended from an elevation of 1495 m in the Guadalupe Mountains to 600 m near the Rio Grande in the Big Bend (*3*). In the Sonoran Desert of Arizona and adjacent California, single-needle piñon (*Pinus monophylla*) grew as low as 510 m, while more xeric juniper woodland grew as low as 260 m (*4, 10*). In the Mohave Desert of Nevada, a xeric juniper woodland with scant piñon occurred at 1100 to 1830 m (*5*). In southern Nevada and northeastern California, single-needle piñon was recorded as low as 730 m (*5, 6*). There are additional records of juniper woodland and piñon-juniper woodland from the western Mohave Desert (*7*).

Many desert species are associated with the woodland plants in the fossil midden assemblages. Extralocal taxa that no longer grow near the midden sites usually comprise 25 to 35 percent of the macrofossils. Many plants in the assemblages still grow at the site (*4, 8*). Many of the desert taxa in middens collected in the Sonoran Desert are dominants in the present Mohave Desert communities 150 to 395 km to the north. Joshua tree (*Yucca brevifolia*) and big sagebrush (*Artemisia tridentata*) were recently found in midden samples from Montezuma's Head in the Ajo Mountains of Organ Pipe Cactus National Monument, Arizona. The site is about 395 km south of the nearest big sagebrush locality in Arizona, and only about 35 km north of the Mexican border. These samples also contained single-needle piñon, juniper, and shrub live oak (*Quercus turbinella ajoensis*). The assemblages have been radiocarbon dated at 13,500 ± 390 B.P. (laboratory number A-1698, *Juniperus*), 17,830 ± 870 B.P. (A-1697, *Pinus monophylla–Juniperus* mix), 20,490 ± 510 B.P. (A-1695, *Juniperus*), and 21,840 ± 650 B.P. (A-1696, *Pinus monophylla*). The midden records of Mohave Desert species farther south than their present range suggest that the Mohave Desert occupied a relatively greater area in the late Pleistocene.

The only midden record of a late Pleistocene desert community without woodland associates is that of Wellton Hills No. 1 at an elevation of 160 m in Yuma County, Arizona, dated at 10,580 ± 550 B.P. (A-1407, *Larrea divaricata*). It contained creosote bush (*Larrea divaricata*) and white bur-sage (*Ambrosia dumosa*), which still grow in the area today (*4*). Creosote bush and white bur-sage are widespread codominants in both Sonoran and Mohave Desert low-elevation communities. Late Wisconsin macrofossils of characteristic Sonoran Desert species, such as paloverde (*Cercidium microphyllum* and *C. floridum*) and saguaro (*Cereus giganteus*), have not been found, and presumably these species were in Mexican refugia.

The Pleistocene is unique as the only geological epoch that is defined by climatic change rather than by evolutionary changes in faunas. Evidence of climatic change can be found in many biological and geological phenomena and, as a result, the beginning and ending boundaries of the Pleistocene have been difficult to define. Important changes in various records suggesting the beginning of postglacial climates and the beginning of the Holocene have been set at various times ranging from 14,500 to 10,150 years ago. The glacial record in the western United States suggests that postglacial climates began about 14,000 years ago (*9*). However, the vegetational records of ancient pack rat middens in the desert areas farther south still have "full-glacial" vegetation until about 13,000 years ago. As mentioned earlier (*2*), the pollen record from the Southwest placed the beginning of the Holocene at 12,000 to 11,200 years ago. Recently a claim was made that the postglacial origin of the Chihuahuan Desert took place less than 11,500 years ago, based on the fossil midden record of the Big Bend of Texas (*10*). New middens from the northern Chihuahuan Desert provide a more complete sequence of bioclimatic changes. About 11,000 years ago, piñon (*Pinus edulis* and *P. cembroides*) dropped out of the piñon-juniper woodland that previously covered the northern Chihuahuan Desert and a more xeric juniper-oak woodland remained. The youngest radiocarbon date for a midden containing piñon from the northern Chihuahuan Desert (Quitman Mountains No. 1, Hudspeth County, Texas) is 10,910 ± 170 B.P. (A-1612, *Juniperus*) (*11*).

However, a surprising number of ancient middens containing woodland assemblages have been dated at less than 10,000 years ago. A total of 29 such dates is available from woodland middens from the southwestern deserts (Table 1). The youngest woodland midden from the northern Chihuahuan Desert (Hueco Mountains No. 1B, Hudspeth County, Texas) is dated at 8150 ± 170 B.P. (A-1614, *Juniperus*) (*11*). This midden contained juniper (*Juniperus* sp.), a shrub oak (*Quercus pungens*), mountain mahogany (*Cercocarpus montanus* var. *paucidentatus*), and approximately 25 other species, but did not contain such important species in the present Chihuahuan Desert communities as creosote bush (*Larrea divaricata*), lechuguilla (*Agave lecheguilla*), ocotillo (*Fouquieria splendens*), and sotol (*Dasylirion* sp.). The youngest woodland midden from the Sonoran Desert (New Water Mountains No. 2, Yuma County, Arizona) is dated at 7870 ± 750 B.P. (A-1284, *Juniperus*) (*4*). Again, the fossil assemblage contained juniper, a shrub oak (*Quercus turbinella*), and mountain mahogany, but in association with desert species such as brittlebush (*Encelia farinosa*), turpentine-broom (*Thamnosma montana*), and California barrel cactus (*Ferocactus acanthodes*). However, saguaro, paloverde, ocotillo, and creosote bush were

Table 1. Radiocarbon dates less than 10,000 B.P. from pack rat middens containing woodland assemblages in the Chihuahuan, Sonoran, and Mohave deserts. Abbreviations: Ag, *Agave utahensis*; F, *Fraxinus anomala*; J, *Juniperus* spp.; Nb, *Nolina bigelovii*; Nm, *Nolina microcarpa*; Op, *Opuntia phaeacantha/violacea*; Q, *Quercus pungens*; T, miscellaneous twigs; U, uriniferous material; and Yt, *Yucca torreyi*.

State and county	Midden	Elevation (m)	Carbon-14 date (B.P.)	Laboratory number and material dated	Community	Reference
Texas						
Hudspeth	Hueco Mountains No. 1B	1280	8150 ± 170	A-1614 J	Juniper, oak, mountain mahogany	(*11*)
El Paso	Navar Ranch No. 4C	1370	8920 ± 370	A-1649 Q	Juniper, oak, cane cholla	(*11*)
Hudspeth	Hueco Mountains No. 1A	1280	9380 ± 130	A-1613 Yt	Juniper, oak, mountain mahogany	(*11*)
El Paso	Hueco Tanks No. 2	1420	9380 ± 270	A-1647 Op	Juniper, oak, wild cherry	TR*
Arizona						
Yuma	New Water Mountains No.2	615	7870 ± 750	A-1284 J	Juniper, oak, shad-scale, cactus	(*4*)
Mohave	Vulture Canyon No. 12	600	8540 ± 180	A-1568 F	Juniper, single-leaf ash, Utah agave	(*8*)
Mohave	Desert Almond No. 7A†	550	8560 ± 260	A-1469 J	Juniper, single-leaf ash, desert almond	(*8*)
Mohave	Desert Almond No. 8†	575	8850 ± 150	A-1547 Nm	Juniper, bear-grass, desert almond	(*8*)
Mohave	Desert Almond No. 7B†	550	9650 ± 360	A-1428 J	Juniper, single-leaf ash, desert almond	(*8*)
Mohave	Rampart Cave Stake 50	530	9520 ± 400	A-1451 F	Juniper, single-leaf ash, Utah agave	(*8*)
Mohave	Rampart Cave Stake 50	530	9520 ± 330	A-1452 Ag	Juniper, single-leaf ash, Utah agave	(*8*)
Mohave	Rampart Cave Stake 50	530	9770 ± 160	A-1450 J	Juniper, single-leaf ash, Utah agave	(*8*)
Mohave	Needle-eye Canyon No. 1	550	9770 ± 250	A-1618 J	Juniper, single-leaf ash	(*8*)
California						
San Bernardino	Lucerne Valley No. 14	1005	7800 ± 300	UCR-249 J	Juniper, cliff rose	(*7*)
San Bernardino	Lucerne Valley No. 12	1005	7820 ± 600	UCR-185 T	Juniper, Joshua tree	(*7*)
San Bernardino	Lucerne Valley No. 11	1005	8300 ± 700	UCR-186 J	Juniper, Joshua tree	(*7*)
San Bernardino	Redtail Peaks No. 1	520	8910 ± 380	A-1580 J	Juniper, Joshua tree, bear-grass	(*4*)
San Bernardino	Negro Butte	1070	9140 ± 140	U	Juniper, Joshua tree, cliff rose	(*5*)
San Bernardino	Redtail Peaks No. 1	520	9160 ± 170	A-1668 J	Juniper, Joshua tree, bear-grass	TR
San Bernardino	Redtail Peaks No. 5	510	9600 ± 160	A-1663 Nb	Juniper, bear-grass	TR
San Bernardino	Redtail Peaks No. 6	495	9600 ± 170	A-1655 J	Juniper, bear-grass, banana yucca	TR
Inyo	Titus Canyon	1130	9680 ± 300	UCR-347 J	Juniper, Joshua tree	(*17*)
San Bernardino	Whipple Mountains No. 3	520	9920 ± 130	A-1551 Nb	Juniper, bear-grass, banana yucca	TR
San Bernardino	Whipple Mountains No. 2	520	9980 ± 180	A-1538 J	Juniper, bear-grass, banana yucca	TR
Nevada						
Clark	Mercury Ridge No. 2	1280	7800 ± 150	UCLA-560 U	Juniper, blackbrush, desert almond	(*5*)
Clark	Spotted Range No. 1	1830	8420 ± 100	U	Juniper, shad-scale, desert almond	(*5*)
Clark	Mercury Ridge No. 1	1390	9000 ± 250	UCLA-559 U	Juniper, mountain mahogany	(*5*)
Clark	Aysees Peak	1525	9320 ± 300	UCLA-644 U	Juniper, blackbrush, mountain mahogany	(*5*)
Clark	Spotted Range No. 2	1550	9450 ± 90	U	Piñon, juniper, blackbrush	(*5*)

*TR, this report. †Formerly called Emery Falls (*8*).

not in the midden and are common today. The youngest woodland date for the northern Mohave Desert (Mercury Ridge No. 2, Clark County, Nevada) is 7800 ± 150 B.P. (UCLA-560, uriniferous material) (*5*). Important plants in this midden were juniper, big sagebrush (*Artemisia tridentata* ssp. *nova*), blackbrush (*Coleogyne ramosissima*), and desert almond (*Prunus fasciculata*). In the Mohave Desert of the Grand Canyon (Vulture Canyon No. 12, Mohave County, Arizona), the youngest date is 8540 ± 180 B.P. (A-1568, *Fraxinus anomala*) (*8*). Important species in this midden are juniper, single-leaf ash (*Fraxinus anomala*), and sandpaper bush (*Mortonia scabrella*), which do not grow at the site today. In the westernmost Mohave Desert (Lucerne Valley No. 14, San Bernardino County, California), the youngest date is 7800 ± 300 B.P. (UCR-249, *Juniperus*) (*7*). Important species in this midden are juniper and cliff rose (*Purshia glandulosa*), while the present desert community contains creosote bush, white bur-sage, and Mohave yucca (*Yucca schidigera*). Considering the standard deviations and differences in laboratory techniques, the clustering of these dates for the last record of woodland in the deserts around 8000 years ago in areas from 106° to 117°W and 32° to 38°N at elevations of 520 to 1830 m is remarkable.

The changes seen in the pollen records from 12,000 to 11,000 years ago are not necessarily in conflict with the existence of woodland species in the deserts until 8000 years ago. The middens document range extensions on the southern and lower elevational limits of woodland species, where they are probably limited by available moisture. Pollen records, which census communities from regional areas, are not limited to these southern and lower elevational margins. The changes between 12,000 and 11,000 years ago are probably temperature changes that are reflected in mesic piñon-juniper or Mexican pine-oak woodland and pine forests. As these communities moved up the mountains and were reduced in area, the amount of pine pollen reaching the deposition sites decreased.

By, or soon after, 8000 years ago, the woodland trees and shrubs disappeared from fossil pack rat middens. In the Sonoran and Mohave deserts in the United States, desertscrub communities formed, or entered from the south, soon after 8000 years ago. Radiocarbon dates for middens containing only desert species from the Mohave Desert (Lucerne Peak No. 1 and Sunset Cove No. 1, Newberry Cave, San Bernardino County, California) are 5800 ± 250 B.P. (UCR-135, *Larrea divaricata*), 5880 ± 250 B.P. (UCR-134, miscellaneous twigs) (*7*), and 7400 ± 100 B.P. (*5*), respectively. In the northern Chihuahuan Desert, the final formation of desertscrub communities probably occurred later. In the Hueco Mountains (El Paso and Hudspeth counties, Texas), old middens record a grassland community in the period between the xeric juniper woodland and the modern desertscrub communities.

I suggest that the vegetational changes recorded 8000 years ago in early Holocene pack rat middens can be explained by changes in the general circulation of the atmosphere related to the melting of the continental ice sheets. During the full-glacial (before 13,000 years ago), the northern part of the North American continent was covered by the Laurentide and Cordilleran continental glaciers. The temperature gradient between the equator and the glaciers was steeper, causing the southward displacement of the subtropical Pacific high anticyclone. The Cordilleran ice sheet probably amplified the upper-level trough, which resulted in a southward displacement of the polar jet stream and the winter storm track. The Arctic air mass was trapped north of the glaciers in the Arctic Ocean, which was frozen over at that time (*12*). The extremely cold, dense air probably flowed across the exposed Bering land bridge into the warmer northern Pacific Ocean. As the warmer ocean water warmed the Arctic air, it was able to hold more moisture and was probably modified into a wet air mass. The combination of these conditions resulted in the intensification of the Aleutian low cyclone at a more southerly latitude. As the position and intensity of the Aleutian low regulate the frequency and intensity of winter frontal storms that move onto the continent, the late Wisconsin climate of much of the Southwest was probably characterized by heavy winter precipitation.

Middens in the Sonoran and southern Mohave deserts record a dramatic expansion of northern and higher-elevation Mohave and Great Basin desert species to southerly and low-elevation areas during the late Wisconsin and early Holocene (*4*). Present populations of many of these species, including Joshua tree, blackbrush, shad-scale, and single-needle piñon are in areas with winter precipitation maxima. Similar expansions by woodland or desert species presently living in summer rainfall areas have not been found.

The Cordilleran ice sheet began to wane about 14,000 years ago and, by about 9000 years ago, had shrunk into montane glaciers in higher areas (*13*). The retreating Laurentide ice sheet was well into central Canada by 8500 years ago. Soon after 8000 years ago, it frag-

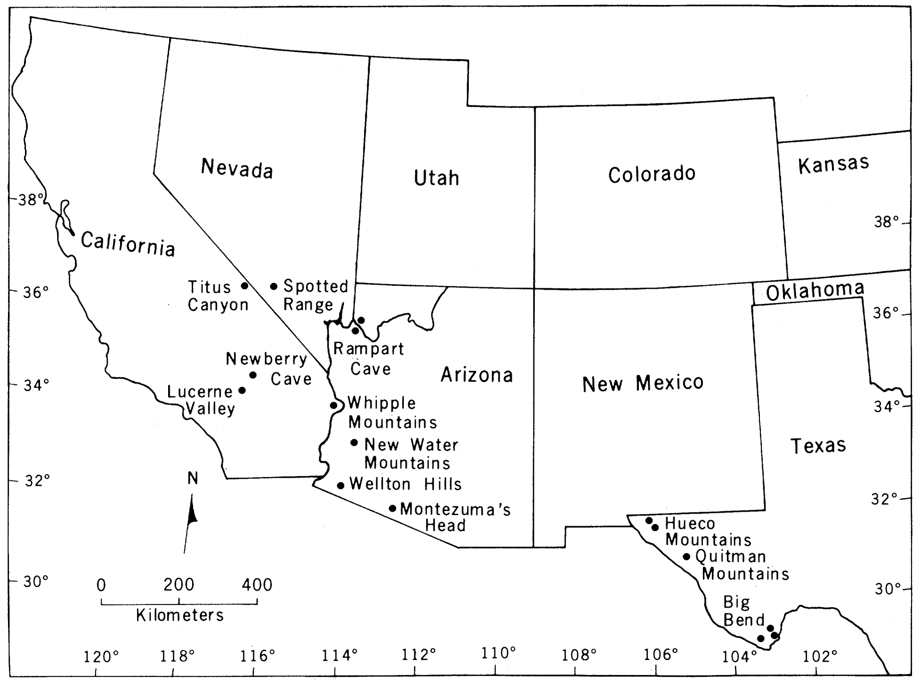

Fig. 1. Locality map for pack rat midden sites mentioned in the text and Table 1. The series of middens are from Big Bend [Burro Mesa, Dagger Mountain, and Maravillas Canyon (*3*)], the Hueco Mountains (Hueco Mountains and Navar Ranch), Lucerne Valley [Lucerne Valley and Negro Butte (*5, 7*)], Rampart Cave (Desert Almond Canyon, Needle-eye Canyon, Rampart Cave, and Vulture Canyon), Spotted Range [Aysees Peak, Mercury Ridge, and Spotted Range (*5*)], and the Whipple Mountains (Redtail Peaks and Whipple Mountains).

mented into several areas with the incursion of ocean water into Hudson Bay (*14*). Changes in the proportions of land, water, and ice, with related changes in albedo and energy balance, resulted in the development of the present circulation patterns and storm frequencies. The development of the prairie communities in the Great Plains by 9000 to 8000 years ago was apparently related to dry Pacific air reaching the Great Plains for the first time (*15*). The transition from woodland to desert or grassland throughout the southwestern deserts 8000 years ago was probably the result of the shift of the Aleutian low and the winter storm track into their present northerly position, resulting in less winter precipitation.

Late Pleistocene pluvial climates in the southwestern United States were generally contemporaneous with glacial climates in the northern part of the continent. The dry playa lakes in the Southwest contained water when the glaciers were well developed. The existence of continental glaciers modified general circulation patterns and caused pluvial southwestern climates. With a shift from glacial to nonglacial climates, continental glaciers took thousands of years to recede because of the large amounts of energy required to melt the ice. Changes in pluvial climates would lag behind changes in glacial climates as long as the glaciers existed. The relatively xeric woodland between 11,000 and 8000 years ago in the Southwest may have occurred in such a lag period. Postpluvial conditions finally dried the playa lakes and allowed the formation of desert and grassland communities after 8000 years ago, when heavy winter precipitation diminished in the Southwest.

An important inference from this interpretation is that winter precipitation was probably the most important climatic parameter affecting late Wisconsin and early Holocene plant distributions in the Southwest. This is not to say that temperature regimes, such as mild winters and cool summers, were not important. Another implication is that the effect of late Pleistocene winter pluvial climates had a southerly limit, and desert refugia should have been in Mexico. Fossil middens from the northern Mexican deserts could be used to test this inference. Related cultural inferences would be that the Paleo-Indians of the southwestern United States lived in mesic woodlands and grasslands and that cultural transitions from Clovis to Folsom to Desert Archaic cultures may have been related to transitions in climate and vegetation. Finally, since the last transition to desert climates and vegetation was about 3000 years later than the extinction of large mammals such as mastodon, mammoth, horse, and camel 11,000 years ago (*16*), changes in climate or vegetation are unlikely to have caused extinction.

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18. Special thanks are due to the following for discussion of many of the ideas presented in this report: K. L. Petersen, Washington State University; A. H. Harris, University of Texas, El Paso; T. J. King, Jr., University of California, Los Angeles; W. B. Woolfenden, K. K. Hirschboeck, A. V. Douglas, G. R. Brackenridge, R. S. Thompson, W. G. Spaulding, T. J. Blasing, K. L. Cole, A. V. McCord, and J. Zauderer, University of Arizona; and A. M. Phillips, III, Museum of Northern Arizona, Flagstaff. A. Long, Radiocarbon Laboratory, University of Arizona, provided radiocarbon dates. Financial support was provided by NSF grants DEB 75-13944 and DEB 76-19784 to P. S. Martin and T. R. Van Devender, University of Arizona. B. M. Fink, P. S. Martin, W. G. Spaulding, and K. K. Hirschboeck edited the manuscript. Contribution No. 735, Department of Geosciences, University of Arizona.

21 October 1976; revised 18 May 1977

Conservation of Potassium in the *Pinus resinosa* Ecosystem

Abstract. *Rubidium-potassium ratios were determined on foliage, litter, and surface soils of plots in two plantations of* Pinus resinosa *41 to 46 years old previously fertilized once with potassium. Calculations based on indigenous soil rubidium as the "tagging" ion demonstrate that after 9 years some 60 percent of the foliage potassium is still derived from the fertilizer, and after 23 years about 40 percent of the foliage potassium is derived from the fertilizer. Additional fertilizer potassium is present in soil and litter, indicating the high retention of this mobile element in the pine ecosystem.*

The soil compartments and fluxes of forest nutrient cycles are poorly quantified but only in part because of the long times and large variabilities involved. Nutrient sources and sinks throughout the tree rooting volume are not readily measured, and thus attempted mass balances for the entire system do not reliably describe circulation within the soil. Few tracers are suitable for long-term studies. Use of radioactive Cs has illuminated several aspects of the short-term circulation of cations, but the minute quantities are tightly sorbed by clay minerals and cannot duplicate the behavior of its congener K (*1*).

We have used the "reverse tracer" technique of Hafez and Stout (*2*) to follow the fate of added K in simple ecosystems of *Pinus resinosa* Ait., red or Norway pine. Plantations of this species on formerly cultivated sandy outwash soils in northern New York State commonly display symptoms of acute K deficiency. Deficient stands respond to single applications of K fertilizers by marked increases in canopy density and by height and diameter growth (*3*). Surprisingly, growth responses to single applications of K (112 kg/ha) have continued for more than 25 years (*4*).

Such prolonged response can plausibly be attributed to efficient recycling of the added K. An alternative hypothesis is "pump-priming" by the initial fertilization; that is, recovery from acute deficiency might result in intensive exploitation of subsoil layers, which often contain "reserve" K (80 to 300 mg per kilogram of soil) extractable by treat-