United States
Department of
Agriculture

Forest Service

Pacific Southwest Forest and Range Experiment Station

Research Paper
PSW–198

Stability and Change in Minerotrophic Peatlands, Sierra Nevada of California and Nevada

James W. Bartolome   Don C. Erman   Charles F. Schwarz

Bartolome, James W.; Erman, Don C.; Schwarz, Charles F. 1990. **Stability and change in minerotrophic peatlands, Sierra Nevada of California and Nevada**. Res. Paper PSW-198. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 11 p.

Minerotrophic peatlands or fens in California's Sierra Nevada are small wet meadows surrounded by mixed conifer forest. The dynamics of vegetation change at the meadow edge and the ages and development of fens were investigated, in the Sagehen Creek Basin near Truckee, California, through the use of radiocarbon dating of peat, pollen studies, examination of processes of peat development and accumulation, stand age analysis of trees around peatlands, and evaluation of tree-ring variation. These approaches were used to evaluate both short- and long-term changes. Fens varied in age from more than 8000 years to less than 1000 years old. Results suggest that overall fen development proceeds rapidly, with peat buildup dependent upon adequate moisture supply. During fen development trees repeatedly invade and retreat from the fen edges. The timing of invasions appears unrelated to events such as human disturbance and climatic change. Instead, changes are most likely to result from alterations in groundwater supply in interaction with tree establishment, longevity, and water uptake. Little evidence was found that accepted successional models which emphasize predictable and gradual vegetational development apply to fens in the Sagehen Basin.

Retrieval Terms: wet meadow, fen, plant succession, pine invasion, *Pinus contorta*, lodgepole pine, edge stability, fen persistence, radiocarbon age

The Authors:

JAMES W. BARTOLOME and **DON C. ERMAN** are professors of range ecology and management and fisheries ecology, respectively, in the Department of Forestry and Resource Management at the University of California, Berkeley. At the time of this study, **CHARLES F. SCHWARZ** was a research forester in the Station's Landscape and Urban Forestry Research Unit in Berkeley. He is currently an environmental planner for the Port of Oakland.

Acknowledgments

We thank Bret Olsen and Cathy Bleier for collecting stand age data and preparing tree cores, Paul Sugnet for his ring-counts and cross-dating, Ronald Kelly for statistical treatment of data, and Joe McBride for technical advice. Barbara Brower, Donald Sullivan, and Roger Byrne assisted with pollen analysis. Nancy Erman and Mitchel McClaran provided helpful criticism during and after the study. Harold F. Heady, Ann Dennis, Raymond D. Ratliff, Michael Yoder-Williams, and Bruce Johnson reviewed earlier drafts of the manuscript. This study was funded by Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, under a Cooperative Agreement with the University of California, Berkeley.

Publisher:

Pacific Southwest Forest and Range Experiment Station
P.O. Box 245, Berkeley, California 94701

February 1990

Stability and Change in Minerotrophic Peatlands, Sierra Nevada of California and Nevada

James W. Bartolome   Don C. Erman   Charles F. Schwarz

CONTENTS

IN BRIEF . . .

Bartolome, James W.; Erman, Don C.; Schwarz, Charles F. 1990. **Stability and change in minerotrophic peatlands, Sierra Nevada of California and Nevada.** Res. Paper PSW-198. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 11 p.

Retrieval Terms: wet meadow, fen, plant succession, pine invasion, *Pinus contorta*, lodgepole pine, edge stability, fen persistence, radiocarbon age

Minerotrophic peatlands or fens are small wet meadows surrounded by mixed conifer forests. Sierran meadows are important habitats and recreational resources. Plant succession has a strong impact on the quality of meadows. Concern has been expressed particularly about changes caused by pine invasions. The seral sequences and factors governing plant cover changes and timing are largely unknown for many Sierran meadows. Hence, decisions about management for preservation or restoration are severely hampered. Wet meadows, because of their clear dependence on hydrologic regimes, may provide a simpler system for analysis than other types. Their sensitivity to hydrologic changes makes them particularly sensitive to natural or human perturbations.

The short- and long-term dynamics of vegetation change at the meadow edge and the ages and development of fens were investigated in the Sagehen Creek Basin near Truckee, California, using the following methods and/or procedures:

- Radiocarbon dating of peat deposits
- Examining changes over time of the relative abundance of different types of pollen in peat deposits
- Measuring moss growth rates and changes in peat-deposit surface elevation
- Examining hydrologic conditions controlling peat development and accumulation
- Monitoring seedling establishment and survival
- Analyzing ages of pines in apparently even-aged stands around a fen
- Examining stand ages in relation to annual precipitation variations

The six fens, less than 0.6 mi (1 km) apart, originated at different times between 8700 and 810 years ago. The variation in fen ages indicates that their origin is probably due to recurring natural phenomena affecting the water supply.

Peat age is not consistently related to fen size, location in fen or depth. Several explanations exist for the inconsistent relation between peat depth and age. Within a fen, rates of peat accumulation vary by an order of magnitude; hence, similar depths can have different ages. In some samples modern peat came from as deep as 31 inches (80 cm). These results are supportable by the rapid rates of peat accumulation that have been observed. In addition, reworking of peat by fen dwelling organisms and fluctuations of water levels in peat may transport peat vertically. Past logging activities could have inverted peat layers. The accumulation of layers has been far from a simple aggradation at the surface each year.

In the dry portions of Mason Fen, daily water levels dropped much lower than in wet areas and remained below the surface even at night. Isolation from horizontal flow and lower water levels resulted in a deeper aerobic limit and a more acidic pH in the dry areas—changes favoring tree survival. Seedlings appearing in the dry areas of the fen in 1981 survived, and new seedlings continued to appear despite wet conditions in 1982 and 1983.

The highly variable ages of trees in the bands of even-sized stands paralleling fen borders show they became established over many years rather than during a few drought years. Dead and dying stands and solitary individuals on and around fens indicate that these invaders do not persist. Invasions are most likely to result from alterations of groundwater supply interacting with tree establishment, longevity, and water uptake. Little evidence was found that accepted successional models which emphasize predictable and gradual change from wet meadow to forest apply to Sagehen fens.

The Sagehen data support a succession model for a biologically stable peat-based ecosystem dependent on a reliable supply of water. Where the water supply is marginal for moss growth and maintenance of peat, as near borders and elevated areas, the fen is subject to periodic invasion by lodgepole pines. Pine stands establishing on the peat form a canopy which shades out the mosses, and transpiration by the pines increases water loss from peat layers. The dried peat decomposes, eliminating the peat layer under the stand in a few decades. The stands eventually die, many in their first century, and mosses reoccupy the area and begin building a new peat deposit, continuing the cycle.

Management of pine invasions is not needed for preservation of Sierran fen ecosystems. Fens are persistent features in the landscape. They are not fragile, disappearing vestiges of an ancient glacial event. This type of wet meadow is so persistent that the establishment of pines anywhere on them should be considered a temporary natural fluctuation. Where a normal supply of water continues, fens will persist. Actions which change their water supply will affect the persistence, spatial distribution, and size of fens.

INTRODUCTION

The border between meadows and surrounding forest in California's Sierra Nevada is dynamic. Invasion of trees into meadows, including peatlands, is widely observed. Previous investigations have not adequately explained how long-term factors affect the persistence of and change in the whole landscape unit.

The patterns and causes of change at the fen-forest edge represent a set of ecological and managerial problems. These problems center on the importance of "edge" to visual diversity in the landscape and to wildlife habitat quality. Yet difficulties in defining and describing edges and the differing temporal and spatial scales characteristic of edge changes have restricted the development of even rudimentary models for investigation.

This paper describes a plant succession model of several spatial and temporal scales that can be directly applied to management goals and identification of the causes of change in minerotrophic peatlands, or fens, in the Sierra Nevada of California and Nevada.

The succession model underscores the need for a combination of large- and small-scale as well as short- and long-term information. Long-term changes were described through the use of radiocarbon dating of peat and pollen analysis. Short-term changes were described using dendrochronology, stand age analysis, and monitoring of peat profile changes and the water regime. Collectively, these measurements help to identify important patterns of fen development and to explain variations in developmental history of different fens. The information generated significantly alters the perspective for management and the list of probable causes of natural and anthropogenic change.

PREVIOUS WORK

Peatlands form a distinctive and uncommon meadow type in the Sierra Nevada. Several locations in the Sierra Nevada have been described as "bog" type vegetation. However, the peatlands in the Sagehen Basin lack sphagnum mosses, and their waters are not strongly acidic. Such peatlands are better called minerotrophic peatlands or fens (Erman and Erman 1975). Minerotrophic peatlands are fed by flowing, mineral-rich water with a nearly neutral pH. The peat is generally shallow in the Sagehen Basin, ranging to about 6.6 ft (2 m) deep (Erman 1976), and is derived from partial decomposition of two mosses (*Drepanocladus aduncus* and *Cratoneuron filicinum*) and other herbaceous vegetation.

Work in the Sagehen Basin represents the only detailed scientific study of fens in the Sierra Nevada. Inglenook Fen on the Mendocino Coast was the subject of a detailed, interdisciplinary study (Barry and Schlinger 1977, Erman and Roby 1977). In Sagehen, work has centered on the largest, Mason Fen, beginning with the establishment of permanent transects in 1958 (Erman 1976). Subsequent studies have described the flora (Rae 1970), changes in peat depth (Erman 1976), invertebrates (Erman 1973, 1976; Erman and Erman 1975), and chemical characteristics of fens (Erman and Chouteau 1979). The dynamics of vegetation in and around the fens have not been reported.

Fens are tightly linked to the local hydrological regime. Their nutrient supply, hydrogen ion balance, productivity, and floristics depend on a continuous supply of mineral-rich water (Heinselman 1970, Moore and Bellamy 1973). Episodes of apparent reversal of succession have been found in bog and fen peatlands in the United States and Europe (Godwin and others 1974, Schwintzer and Williams 1974, Walker and Walker 1961). Prehistoric and modern societies have caused change in the development of peatlands, both intentionally (for fuel, grazing, timber, and agriculture), and inadvertently (Bel'skaya 1961, Moore and Beckett 1971, Slater and Agnew 1977). Human impact on Sierra Nevada meadows and fens remains largely speculative except for the recent invasion of Yosemite Valley meadows by pines (Heady and Zinke 1978).

Fens are a type of wet meadow (Ratliff 1982) and hence show some vegetation characteristics associated with other Sierra Nevada meadows. Outside Sagehen, studies of Sierra Nevada fens have been limited to a few on the western slope of the southern Sierra Nevada (Adam 1967, Benedict and Major 1982, Benedict 1982, Wood 1975). Crane (1950) described the condition of wet meadow rangelands on the eastern slope of the Sierra Nevada. These studies suggest that many meadow types in the Sierra Nevada can be related to specific environmental factors.

Meadows have often been described as fragile ecosystems subject to destruction by minor alterations of their environment (VanKat and Major 1978). The most commonly observed vegetation change is the invasion by *Pinus contorta* (Vale 1981, 1982) of meadows in National Parks and National Forests. Considerable effort has been expended to halt invasion of meadows by trees (Heady and Zinke 1978). Wood (1975), however, found that episodes of invasion should be expected. His study of wet meadow stratigraphy showed that periods of meadow establishment and periods of tree invasion alternated over the last several thousand years. Benedict (1982) studied meadow ecology and suggested meadows are stable biological systems and only alteration of their physical environment, particularly water status under the influence of climate, causes changes.

STUDY AREA

The study area is located in the Sagehen Basin, part of the Truckee River watershed on the eastern slope of the Sierra Nevada 7.5 mi (12 km) north of Truckee, California. Thirty-two fens are scattered throughout the 10.8 mi^2 (28 km^2) basin (*fig. 1*).

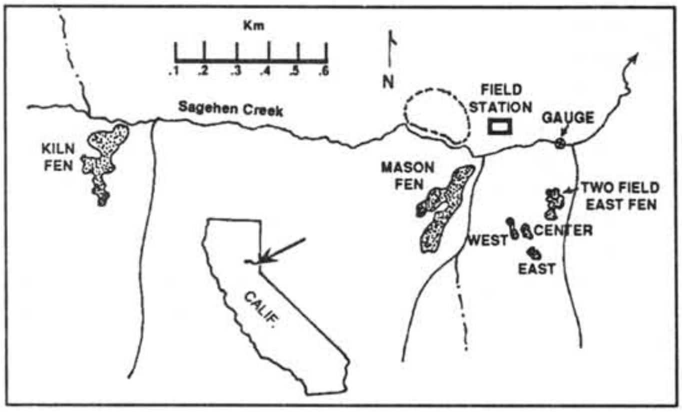

Figure 1—Study fens in the Sagehen Basin, part of the Truckee River watershed, east of the Sierra Nevada crest, in northern California. The dashed line surrounds the area where Jeffrey pines were cored. The United States Geological Survey stream gauge is about 656 feet (200 m) downstream from the Field Station.

The fens in the basin range from less than 0.2 acre (0.1 ha) to 6.7 acres (2.7 ha) in area, and mean peat depths range from 6.8 inches (17.3 cm) to 34.4 inches (87.4 cm) (Erman and Erman 1975). Elevations of the 14 major fens in the basin average 6888 ft (2100 m). Precipitation at the headquarters of the University of California's Sagehen Creek Field Station (elevation 6373 ft [1943 m]), near the largest (Mason) fen, has averaged 35.4 inches (90 cm) annually over the 30 years of record; most precipitation falls as snow (Johnson 1982). Average years are uncommon; the exceptionally dry years of 1976 and 1977 had 36.7 and 20.3 percent of the 30-year average runoff. In contrast, 1982 and 1983 had 221 and 230 percent of the average runoff, respectively.

Vegetation of the Basin consists of a mixture of forests, shrublands, and meadows, with forest dominating (Savage 1973). Forests are dominated by *Abies magnifica* (red fir), *Pinus contorta* (lodgepole pine), and *Pinus jeffreyi* (Jeffrey pine). Where the forest canopy has been removed shrubs are common, particularly *Ceanothus velutinus*. Extensive areas in the basin have been burned in the past. The most recent large fire, the 1960 Donner Burn, burned 7.1 mi^2 (18.4 km^2) above the gaging station in the Sagehen Basin. That area is currently shrubland, with planted *Pinus jeffreyi* just emerging above the brush layer. Older burns have remained in brush; presently over 25 percent of the watershed is shrubland (West 1982).

Meadows are common in the Basin, ranging from very dry upland meadows dominated by forbs and bunchgrasses to wet meadows and riparian areas dominated by several species of Carex (Kosco and Bartolome 1981). The edges of wet meadows in the basin are usually stands of *Pinus contorta*; those of dry meadows are usually *Pinus jeffreyi*.

Fens, the wettest meadows, have a water table near the peat surface. All fens in the basin are associated with perennial springs and seeps (Erman and Erman 1975). Numerous springs in the basin may be a consequence of geological features. Basic andesitic lava, Pleistocene moraines, and alluvium overlay granodiorite bedrock. Groundwater emerges at contacts with the bedrock (Lindgren 1897, Trowbridge 1975).

METHODS

We directed our analyses along five major avenues: (1) radiocarbon (C-14) dating of peat samples from six fens in the basin, (2) analysis of pollen from dated samples taken from various depths in Mason Fen, (3) examination of peat accumulation rates and processes affecting peat development in Mason Fen, (4) stand age analysis of trees around Mason Fen, and (5) evaluation of tree-ring variation and development of a chronology for the Sagehen Basin. Peatlands are a scarce and valuable resource. Those we studied are used for other long-term research studies. Accordingly, we limited our work to observations and analyses of ongoing processes and did not experimentally manipulate the system.

Peat Sampling and Analysis

Peat samples were taken from cores from Mason Fen (*fig. 2*) and two other previously studied large, nearby fens (Two-Fields East Fen, 2.0 acres [8 ha], maximum depth 76.0 inches [193 cm]; Kiln Fen, 5.4 acres [2.2 ha], maximum depth 57.5 inches [146 cm]). Cores were obtained using a Hiller type peat borer, following procedures described in Erman (1976). Additional cores were taken for dating from three previously unstudied fens (West, Center, and East Fens) in the same area. They are small (0.2 acres [0.1 ha]), and are separated by only a few yards (meters) of forest. They may represent different stages of fen formation as indicated by the presence or absence of large, recently fallen trees.

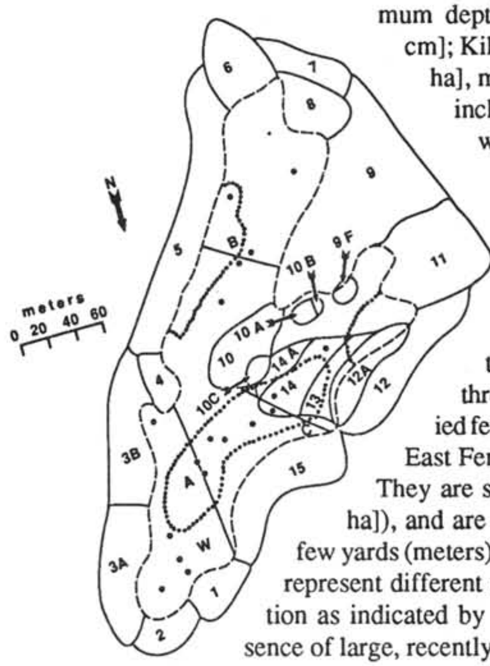

Figure 2—Peat profiles of three transects in Mason Fen. Letters = transects. Numerals = the sampled stands. Dots = peat cores analyzed for carbon-14 age and pollen. Dashed lines = boundary of Mason Fen. Dotted lines = areas dried since the 1976-77 drought. W = water level gauge in wet areas. Transect C was used to measure water levels.

We obtained a total of 38 peat samples from the six fens for dating with C-14 (*fig. 2*). Samples generally measured 0.8 by 3.9 inches (2 by 10 cm) to include sufficient material for carbon dating. To determine maximum ages most samples were taken from the bottom of the peat just above the mineral soil/clay substrate. Several samples were taken from various depths along the same core. The samples were analyzed by Radiocarbon, Ltd., for radiocarbon age in years before the present time (BP) and then dates were corrected to MASCA dates (before the present [BP]).

Peat depths for East, Center, and West Fens were measured along their long axes (197 to 328 ft [60 to 100 m]). Five to seven cores were taken.

Pollen

From five samples taken for C-14 dating from a continuous core in Mason Fen, subsamples were taken for pollen analysis. Standard preparation and mounting produced slides for pollen frequency counts. Pollen identification was based on the reference collection of the pollen laboratory at the Geography Department, University of California, Berkeley.

Changes in the fen surface elevation that reflect peat depth changes were determined by surveying two permanent transects (transects A and B, *fig. 2*). Surface elevations, relative to arbitrary benchmarks on each transect, were obtained at 9.8-ft (3-m) intervals from transit readings of a stadium rod.

Moss Growth and Peat Accumulation

Depth of accumulated (or lost) organic matter at the end of the summer growing season was estimated at the same points on each transect by the "cranked wire" method of Clymo (1970). Beginning in 1975, iron wires with a bend 4.3 inches (11 cm) below their tops were pushed in until the bend was at the fen surface. Changes in the surface elevation were measured from the top of the wire each autumn. After a measurement, each wire was reset so the bend was at the surface.

The transit survey and cranked wire methods give different measures of change in peat deposit depth. The wire method measures annual growth in mosses. However, most of this growth decomposes each year, and in some years or locations, no growth occurs because of low water. The survey over several years reflects cumulative gains and losses and can be compared with the annual increment from the cranked wire measurements.

To determine water levels in areas where recent drying or lodgepole pine establishment occurred we removed a series of small (2.0 inches [5 cm] in diameter) peat cores. Distance of water level from the surface was measured with a hand ruler in early afternoon in summer (the period of lowest water, Erman 1973) and by recording float gauges at two locations. The gauge in the dry area was midway on transect C. In the wet area, it was downslope from transect A (*fig. 2*). In 1981 a permanent 16.4- by 16.4-ft (5- by 5-m) quadrat adjacent to and midway on transect C was set out to count lodgepole pine seedlings.

Extensive areas of Mason Fen dried in the 1976-1977 drought (*fig. 2*). Dry areas were characterized by brown and mostly non-growing mosses and sparse growth of herbaceous vegetation. Wet fen areas contained bright green, growing mosses and a dense growth of herbaceous plants. Measures of pH (Lamotte narrow range color comparator) and aerobic limit (redwood stakes method, Erman 1973) were made at "dry" and remaining "wet" areas. Water level, pH, and aerobic limit have been shown to be critical factors in peatland succession and pine establishment (Boggie 1972, Godwin and others 1974, and Heinselman 1970).

Stand Age Analysis

Initially, 14 visually homogeneous stands around Mason Fen were identified on 1:3000-scale color infrared aerial photographs taken in September 1980. Later these were subdivided on the basis of ground observations into a total of 22 stands. In June 1981 we randomly selected 10 trees from each stand to measure and determine age. Six stands were selected for additional sampling (*fig. 2*). They represented stands characteristic of old and recent invasion of peat (stands 10, 11, 12, 13, and 14) plus an apparent noninvasive old stand (stand 5). The ages of 360 trees were determined: 301 were cored at a height of 24 inches (60 cm) with an increment borer, the remainder were smaller trees which were cut off at ground level and also at 24 inches (60 cm) height.

The east side of the Sierra Nevada was the location of a classical study of tree rings and climate (Hardman and Riel 1936) which showed a close correlation between tree growth and water flow in the Truckee River. To update and extend their data base we cored 25 large *Pinus jeffreyi* on a south-facing slope near Mason Fen (*fig. 1*). Other tree species did not have the ring width variation or sensitivity-to-precipitation variations necessary for dendrochronological determination of climatic variation. Each tree was cored twice on opposite sides at 60 cm height. Cores were mounted, prepared by sanding, cross referenced for date accuracy, and ring width measured in accordance with standard techniques (Fritts 1976). Ring widths were then compared to annual precipitation and stream runoff at the Sagehen Creek Field Station since 1954, Truckee River runoff since 1900, and ring width variation from Hardman and Riel (1936).

RESULTS

Fen Ages

Radiocarbon dates for the six fens revealed ages from modern (less than 200 years BP) to 8000 years BP (*table 1*). Samples from the bottom of the largest fen in the basin, Mason Fen, were of relatively recent origin; the oldest was 1580 BP. No consistent relationship exists between peat depth and age (*table 1*). Although the oldest samples from Mason Fen were from deeper than 25 inches (64 cm) (mean depth of Mason Fen = 23.1 inches [58.8 cm]), much of the deep peat was of relatively recent origin.

Table 1—*Depth and age of peat samples from fens in the lower Sagehen Basin*

	Fens and sample number	Depth	Age (years before present)	95 Pct C.I.[1]
Mason Fen:[2]		*(cm)*		
	1a-81	54	370	+120
	1b-81	35	280	+100
	2-81	80	620	+190
	3-81	85	1330	+110
	4-81	40	500	+140
	5-81	50	370	+100
	6-81	75	1580	+120
	7-81	40	620	+190
	8-81	45	310	+160
	1-82	75	200	+100
	2-82	55	M[3]	-
	3-82	38	M	-
	4-82	66	440	+ 90
	5-82	44	270	+110
	6-82	61	210	+ 90
	7-82	51	M	-
	8-82	82	630	+160
	9-82	71	480	+120
	10-82	55	260	+100
	M-1	71	M	-
	M-2	27	410	+280
	M-3	52	M	-
	M-4	64	1250	+160
	M-5	35	M	-
	M-6	32	430	+160
	1a-83	88	690	+190
	1b-83	70	1190	+200
	2-83	40	560	+180
Center Fen				
	1	30	810	±130
East Fen				
	3	48	780	±110
	4	53	1660	±120
	5a	59	2080	±120
	5b	54	1010	±120
West Fen				
	1	100	8710	±210
	2	121	6870	±170
	3	50	2210	±130
	4	39	630	±140
	5	37	2330	±120
	1b	95	1810	±170
	1c	90	1940	±150
Two Fields East Fen				
	1a	100	1560	±220
	1b	95	1810	±170
	1c	90	1940	±150
Kiln Fen				
	1a	122	2150	±210
	1b	117	1980	±150
	2	92	720	±180

[1]Confidence intervals of 95 percent for age range from 60-270 years. Confidence interval uses t-statistic.

[2]Linear correlation of depth and age for samples yields r^2=0.20.

[3]M = sample age indistinguishable from modern.

One sample from 28 inches (71 cm) was indistinguishable from modern peat.

Samples showed a slight relationship between location and age; younger samples were located in the two upslope southern arms of Mason Fen *(fig. 2)*. Differences due to location are most striking in the samples from the three small fens east of Mason Fen. Maximum peat age in Center Fen (mean depth = 7.6 inches [19.4 cm]) was 810 years BP, but it contained a cut stump of *Pinus contorta* that could not have been more than 150 years old. Much of the fen surface was crossed by large, recently fallen pines—suggesting recent expansion along the margin and downslope. West Fen (mean depth = 24.3 inches [61.7 cm]), of similar size and not 25 yards (23 m) away, had peat ages of up to 8710 years BP at the depth of 39 inches (100 cm). West Fen also had several pine stumps around its margins that had been cut during turn-of-the-century logging. East Fen (mean depth = 24.9 inches [63.3 cm]) peat ages ranged from 789 + 110 years at 18.7 inches (47.5 cm) to 2080 + 120 years at 23.2 inches (59 cm).

Pollen Analyses

Conifer pollen dominates the flora *(table 2)*, with *Pinus* pollen from surrounding forest the most common. The increased amounts of graminoid pollen from the 28-inch (70-cm) sample

Table 2—*Frequency percentages*[1] *for pollen in samples from Mason Fen peat*

	Sample depth *(cm)*				
Pollen type	0	8	38-40	68-70	86-88
Pinus	90	92	79	86	93
Abies	9	7	18	8	4
TCT[2]	T[3]	0	1	2	1
Tsuga	T	0	T	0	0
Acer	0	T	1	T	T
Quercus	0	1	1	1	0
Onagraceae	0	0	T	0	0
Rhamnaceae	0	0	0	1	T
Vitis	0	0	T	T	0
Salix	0	0	T	1	1
Artemisia	1	0	1	1	0
Alnus	0	0	0	1	T
Compositae	0	1	T	2	2
Leguminosae	0	0	0	T	T
Umbelliferae	0	0	0	1	0
Polygonum	1	T	1	0	T
Navarretia	T	0	T	T	0
Gramineae	0	0	2	5	3
Cheno/Am[4]	0	1	0	T	0
Cyperaceae	3	5	11	60	3
Ranunculaceae	T	0	0	0	0
Dryopteris	0	0	T	0	0
Polypodium	0	0	T	T	T
Trilete spore	T	1	0	1	0
Monolete spore	0	0	T	0	0
Arceuthobium	0	0	0	1	0
Pollen conc./cc	52,769	55,100	35,808	78,865	16,232
Age in years BP	M	M	560	1,190	790

[1]Values are calculated as a percentage of the pollen sum per sample.

[2]TCT = Taxaceae/Cupressaceae/Taxodiaceae.

[3]T indicates less than 0.5 percent.

[4]Cheno/Am = Chenopodiaceae/Amaranthaceae.

suggests an increase in those groups at about 1200 years BP. This sample also contained abundant charcoal of both herbaceous and woody plant origin. Interpretation of pollen results is hampered by both the small sample size and the lack of well defined stratigraphy in the peat. Although the samples are from a continuous core, the sample from 35 inches (88 cm) was 500 years younger than the sample from 28 inches (70 cm).

Moss Growth and Peat Accumulation

Annual changes in moss growth measured by the cranked wire method showed initial loss of organic matter on the lower transect (A) in the two years following the drought *(table 3)*. By the end of the 1979 growing season, mean change in height was -0.10 inch (-0.25 cm). The central dry area lost about an inch (several centimeters) of height while the edges, still fed by the spring streams, increased slightly. Some recovery was evident along the entire lower transect by 1980 and by 1982 mean height change was +0.9 inch (+2.4 cm). Drying conditions were less extreme on the upper arm transect (B); changes were positive and greater than 0.4 inch (1.0 cm) per year since 1978 *(table 3)*. The first year of drought (1976) resulted in the lowest mean increase in height on the upper arm transect (0.35 inch [0.89 cm]) and a slowed positive change (0.09 inch [0.24 cm]) on the lower transect as well.

Table 3—*Annual growth of mosses at Mason Fen, Sagehen Basin*[1]

Year		Transect	
		Lower (A)	Upper (B)
1976	$\bar{X}$	0.24 cm	0.89 cm
	n	25	14
	$S_{\bar{x}}$	0.25 cm	0.38 cm
1977		no data	
1978	$\bar{X}$	-0.12 cm	1.40 cm
	n	25	19
	$S_{\bar{x}}$	0.31 cm	0.36 cm
1979	$\bar{X}$	-0.25 cm	1.61 cm
	n	26	18
	$S_{\bar{x}}$	0.34 cm	0.37 cm
1980	$\bar{X}$	0.49 cm	1.73 cm
	n	26	16
	$S_{\bar{x}}$	0.19 cm	0.24 cm
1981	$\bar{X}$	0.61 cm	1.33 cm
	n	27	19
	$S_{\bar{x}}$	0.16 cm	0.32 cm
1982	$\bar{X}$	2.40 cm	2.61 cm
	n	28	18
	$S_{\bar{x}}$	0.30 cm	0.09 cm

[1] $\bar{X}$ = Mean change (cm), sample size (n), and standard errors ($S_{\bar{x}}$) measured on cranked wire from two permanent transects: (A), (B).

Fen elevations, relative to benchmarks on each transect, also showed differences in peat accumulation rates between transects. The lower transect (A) increased in elevation a maximum of about 3.9 inches (9.8 cm) and averaged 2.3 inches (5.9 cm) from 1976 to 1981. Accumulation was predominantly on the upslope wetter half of the transect; little change in elevation occurred on the lower half over five years *(fig. 3)*. On the upper arm, most accumulation was observed at the downslope wetter half of the transect; maximum increase was 1.6 inches (4.0 cm) and averaged 0.6 inch (1.4 cm).

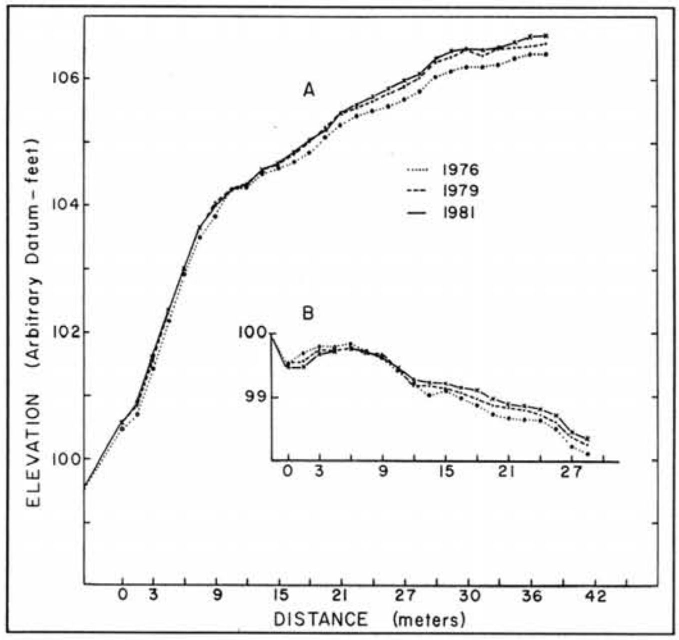

Figure 3—Surface elevations along transects A and B in Mason Fen.

Typically, water levels decline to a low point in mid-afternoon (Erman 1973) because of increased evapotranspiration demand and reduced supply. Recordings of fluctuations from wet and dry areas showed this general pattern still prevailed in 1982. However, water level was consistently lower in the dry than in the wet areas of Mason Fen after 1977 *(fig. 4)*. The maximum change in wet stations was 0.8 inch (2 cm), and water rose to just below the fen surface each night. At the dry stations fluctuations reached 2 inches (5 cm) and highest water levels remained 3.9 inches (10 cm) below the fen surface *(fig. 4)*. Thus in midsummer, water levels in dry areas are substantially lower than in wet.

Additional measures of afternoon water levels, made along a transect (C) across the slope past the dry site recorder, showed levels well below the surface until September, except adjacent to streams *(fig. 5)*.

Aerobic limits and pH conditions further emphasized the differences between wet and dry areas of Mason Fen. Aerobic limits *(table 4)* were consistently deeper in dry (4.6 to 8.6 inches [11.7 to 21.9 cm]) than in wet (3.1 to 3.8 inches [7.8 to 9.7 cm]) areas. The pH of water from core holes was slightly alkaline in wet areas (median of six values, 7.4) and mildly acidic in dry areas (median 6.3). Differences in aerobic limit throughout the

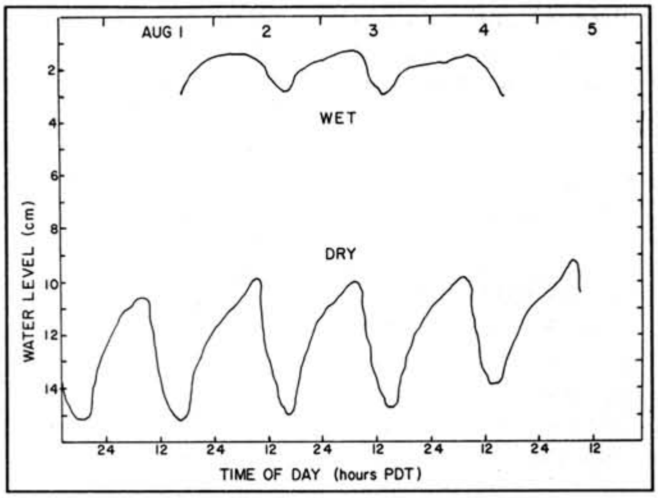

Figure 4—Diel water level changes over a 5-day period in August 1982 in Mason Fen. Vertical axis measures distance below peat surface.

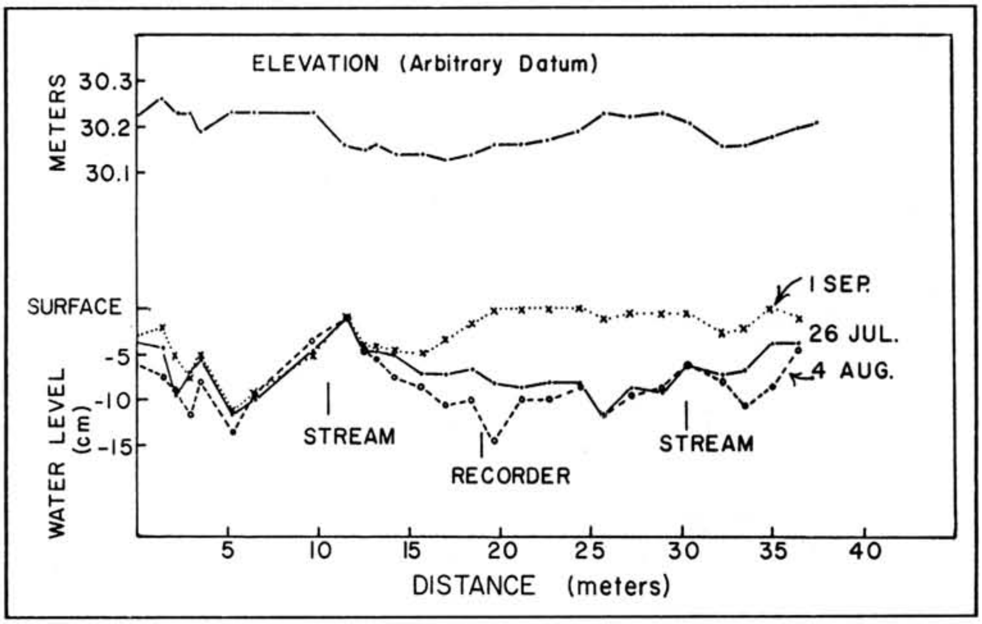

Figure 5—Water levels on transect C across the slope in Mason Fen in summer 1982.

Table 4—*Aerobic limits in Mason Fen at wet and dry sites, 1981*

Site	June 17-19			August 9			August 26-28		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
		(cm)			*(cm)*			*(cm)*	
Wet	11	9.7	3.0	12	9.7	2.5	14	7.8	1.5
Dry	10	11.7	2.5	13	21.9	10.3	12	14.5	7.1

fen were probably greater than observed because wet stations tended to be close to streams. Stations near streams have deeper aerobic limits than stations over a yard (meter) away from streams (Erman 1973).

Stand Ages and Invasion

Tree stands around Mason Fen are nearly pure stands of *Pinus contorta*. A few *Abies magnifica* were found, but none were closer than 33 ft (10 meters) to the fen edge. Five of the 22 stands around Mason Fen had trees greater than 100 years old; older trees were noted along the eastern edge of the fen (stands 3, 4, and 5, *fig. 2*). Stand 5 typifies the older stands found along the two lateral boundaries of the fen and between the two arms (*fig. 6*). Young stands are located at the lower (northeast) end of Mason Fen and at the edges of the upper arms. Of the 22 stands only three did not have seedlings (trees less than 10 years old).

Size proved to be a poor predictor of age, with an overall $r = 0.54$. Although this relationship is statistically significant ($p < 0.01$), the relationship is weak as a predictor; for example, we found two trees of 12 inches (30 cm) diameter at breast height (d.b.h.) in stand 5; at 24 inches (60 cm) height one tree was 215 years old, and the other was 66 years old.

The average time to reach 24-inch (60-cm) height was 11.1 years for the 59-tree sample; thus this value is added to the age data. However, the range of ages from ground level to 24 inches (60 cm) was 3 to 28 years, an unavoidable source of error in the estimates. The sample for ground level age of trees is heavily biased toward small trees, since we could not cut down large trees in the study area. However, when the difference in ages is examined stand by stand and for older versus younger trees, no significant relationship was noted. The oldest cut tree was 62 years, and we assume that the time required to reach 24 inches (60 cm) had not changed for the older trees.

The common belief that invasion occurs as even-aged stands or stands of even-sized *Pinus contorta* is not supported by our data, although many stands showed concentrations of trees in broad age classes. Stands appear to become established as a pulse of rapid recruitment followed by slower continuous additions of trees. Stands 9, 11, and 12 fit this pattern (*fig. 6*). Our data show continued periodic replacement of trees for at least the past 100 years and for 200 years in one stand bordering Mason Fen.

Invasion of trees into peat was evident in the western arm of Mason Fen where numerous small trees have become established. The most recent invasion (stand 14, *fig. 6*) dates from the late 1970's and coincided with drying of peat during the 1976-1977 drought. However, we found trees in this stand which had become established in every year between 1975 and 1978. Counts of lodgepole pines in a 16.4- by 16.4-ft (5- by 5-m) quadrat near transect C revealed 73 seedlings in August 1981. By August 1983, 23 new seedlings were identified.

When current patterns of fen stream branches were compared to those mapped by Erman and Erman (1975), we noted that the channels had changed between 1972 and 1975 to a pattern resulting in a dry area of peat. In stand 13 along the western end of a permanent transect established by Mason and Langenheim in 1958 (*fig. 6*), trees of less than 35 years old were concentrated and the peat had decomposed and disappeared.

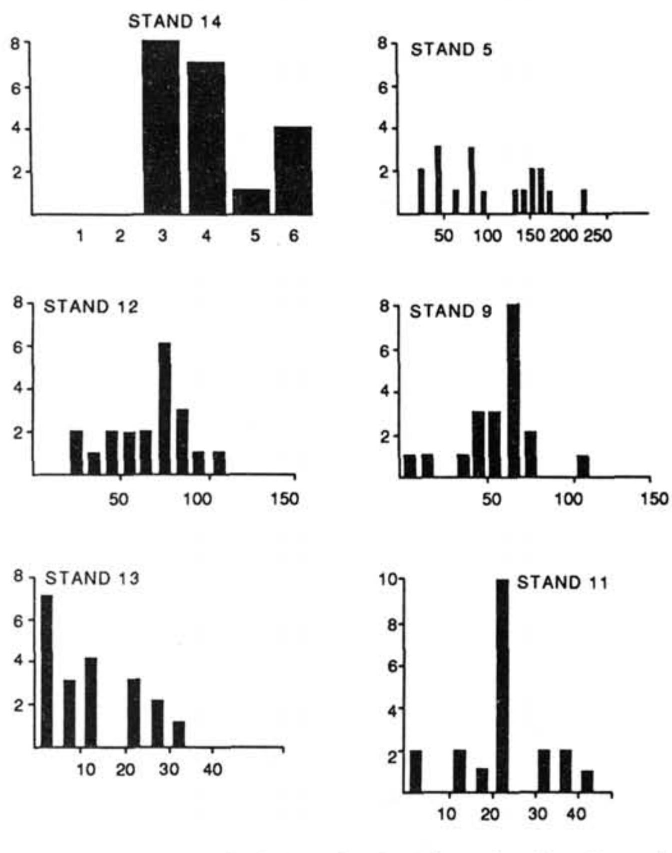

Figure 6—Stand age for lodgepole pines from six selected stands around Mason Fen. Horizontal axis is age at ground level; vertical is number of trees. Y axis is the number of trees.

Tree Growth and Moisture Cycles

When tree ring widths of *Pinus jeffreyi* from the dry slope near Mason Fen are plotted against runoff in Sagehen Creek, the 3-year running averages for the two variables are distinctly out of phase for the past 30 years (*fig. 7*). It appears that the cycles of moisture and tree growth are out of phase. Over the past 80 years several periods of slow tree growth have alternated with periods of rapid tree growth (*fig. 8*). We found no consistent relationship between growth and runoff cycles and stand age.

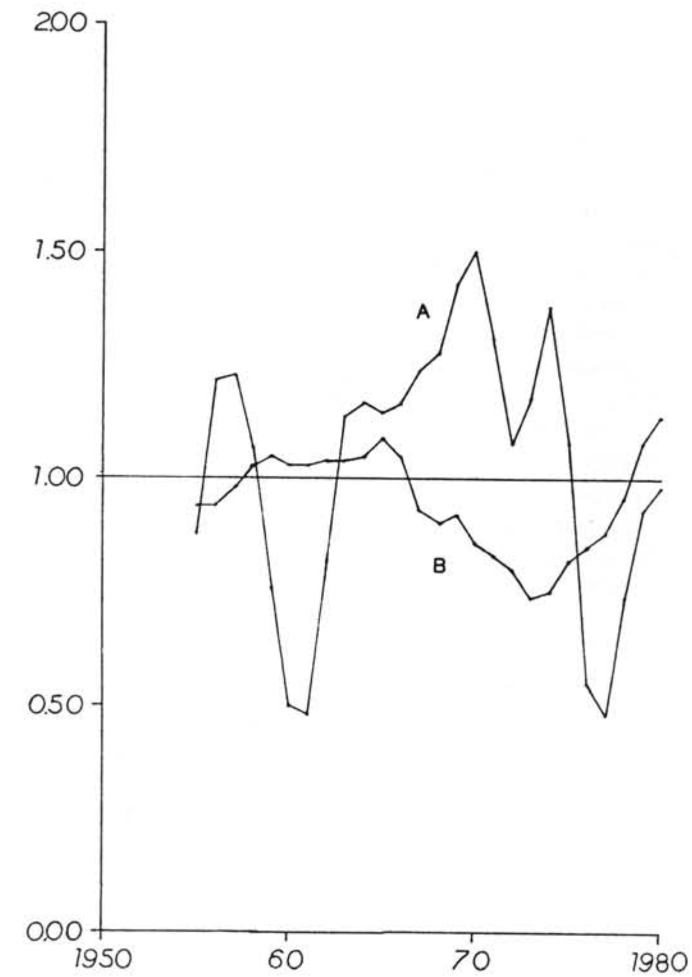

Figure 7—Three-year running averages for stream flow in Sagehen Creek (A) and tree-ring width for Jeffrey pine (B), based on 25 trees and two cores per tree. Values are standardized to the overall mean of 1.0. Tree-ring widths are corrected for age-based changes in tree growth.

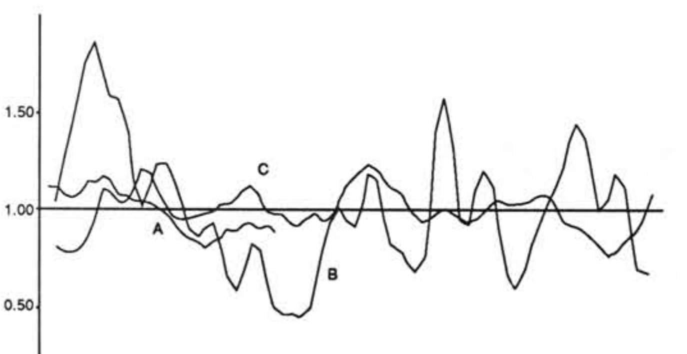

Figure 8—Tree-ring widths and annual stream flow near Sagehen Basin (Northern California). *A* = Tree-ring widths near Truckee River (Hardman and Riel 1936). *B* = Tree-ring widths in the Sagehen Basin. *C* = Truckee River annual flow. Values are 5-year running averages about the overall mean, set at 1.0. Tree-ring widths are corrected for effect of tree age on growth.

DISCUSSION

Fen Age and Stability

Fens in Sagehen Basin are of widely different ages. Peat age is highly variable between fens and not consistently related to fen size, location or depth. Peat from the center of Mason Fen tended to be older than peat from samples closer to the two upper arms of the fen. Mason Fen has been present for at least 1580 years in its current location. The hypothesis proposed by Erman (1976) that the arms were once separate fens that later coalesced is partially supported by the spatial pattern of peat ages. Ages of relatively deep peat near the arm's lower boundary (upper end of transect A) are modern, about 200 years BP. This area is still the fastest growing area measured in the transect by either the cranked wire or surface elevation methods, and is supplied by water draining both arms. Rates of peat buildup (up to 0.8 inch [2.0 cm] per year) suggest that the values for modern peat from as deep as 31 inches (80 cm) are supportable by the rapid rates of peat accumulation that have been observed.

The ages of peat from the three small fens east of Mason Fen differ greatly. One of the small fens has been stable (relatively fixed in location and extent) for at least 8700 years. The evidence for stability is: (1) great age; (2) moderate peat depth/high average depth; and (3) modern (about 100 years old) large stumps at the margin.

Of particular interest in the fen samples is the frequent occurrence of woody plant material, including a cut lodgepole pine stump under the peat. Other evidence of human disturbance was found on Mason fen during the drought. As a dry area lost organic matter, a row of 5.9-ft (1.8-m) long, uniformly cut logs emerged from beneath the peat. These logs were apparently remains of a crude crossing made by loggers in the late 1800's to enable oxen to drag timber across the boggy soils to nearby rail lines.

Pollen

Results from pollen analysis show few differences between samples of differing depths or ages. Although the relative frequencies of some pollen types changed over the past thousand years, pollen-based evidence does not support dramatic change. The high levels of *Cyperaceae* pollen in one sample, associated with abundant charcoal of both tree and herbaceous origin, were puzzling. This sample was from an intermediate depth and age; accordingly it cannot be construed as a clue to the origin of the fen. However, the presence of charcoal indicates at least one major fire at about 1190 years BP either in or around the fen.

Moss Growth and Peat Accumulation

Measurements of average short-term changes in annual growth accumulation and fen elevation show very slow rates of change. Isolation from flowing water caused by two years of drought led to net losses in the drier areas as organic matter decomposed and annual plant production was limited. Previously, the entire fen surface was kept wet by small streams and ground water flowing horizontally downslope near the surface (Erman 1973). Over the period 1976-1981 average surveyed fen elevation increased from 0.1 to 0.5 inch (0.3 to 1.2 cm) per year. A maximum rate of 0.6 inch (1.5 cm) per year occurred at the edges, near continuous water flow, on both transects. Earlier estimates of up to 1.2 inches (3.0 cm) per year had been given for Mason Fen (Rae 1970). Average annual growth measured by the cranked wire method on the two transects never achieved that rate, although it was approached in the wet year of 1982.

Rapid decomposition and slow peat accumulation may be characteristic of fen systems in which annual losses of nearly 50 percent of dry matter production have been measured (Reader and Stewart 1972). By contrast, blanket bogs with *Sphagnum* have grown at rates over 0.4 inch (1 cm) per year (Clymo and Reddaway 1974), and only about 25 percent of annual bog growth decomposes in the first year (Reader and Stewart 1972). However, long-term accumulation rates from Britain and Ireland, computed from radiocarbon dates, showed rates on the order of 7.9 to 31.5 inches (20 to 80 cm) per 1000 years whether from bog or fen (Walker and Walker 1961). Comparable figures for North America range from 39.4 to 78.7 inches (100 to 200 cm) per 1000 years in Pennsylvanian and Canadian bogs (Cameron 1970), and 10.2 to 17.7 inches (26 to 45 cm) per 1000 years for two high elevation Rocky Mountain bogs (Pennak 1963). Based on radiocarbon dates, Mason Fen rates range from 18.5 to 147.6 inches (47 to 375 cm) per 1000 years, compatible with the ranges found by others. Five-year changes in elevation on the two transects indicate higher rates averaging 110.2 to 472.4 inches (280 to 1200 cm) per 1000 years.

Stand Establishment and Survival

Drying of portions of Mason Fen led to changes favoring *Pinus contorta* establishment. Daily water levels dropped much lower and remained inches (several centimeters) below the surface compared to wet areas. In Minnesota bogs, evapotranspiration rates were highest when water levels reached 3.9 inches (10 cm) below the surface (Boelter and Verry 1977). Peat in deeper zones was more decayed and less permeable to water flow than surface peat (Boelter and Verry 1977); thus reflooding from horizontal flow is difficult. Isolation from horizontal flow and lower water levels in Mason Fen have resulted in a deeper aerobic limit and a more acidic pH in the dry areas. Such changes in dry areas favor tree survival (Boggie 1972), and their effects were obvious in Mason Fen. Seedlings appearing in the quadrat near transect C in 1981, after drying of the fen in the 1976-1977 drought, continued to survive and were joined by 1983 by additional individuals despite wetter conditions. Significant tree seedling mortality did not accompany the onset of wet climatic conditions in 1982 and 1983. The process of establishment appears difficult to reverse.

Periods of tree establishment have occurred throughout the past 200 years. One sampled stand originated in the late 1950's and was established on a former area of peat along a permanently marked transect. The array of tree sizes and ages provides evidence for continued filling in of a stand. Except for periodic kills of older trees the stand could persist indefinitely. Stands of *Pinus contorta* throughout its range are susceptible to killing by insects or disease at a relatively young age. Many stands at the borders of fens throughout the basin had dead trees, including a large group adjacent to Stand 4 beside Mason Fen.

We found no consistent relationship between past climate, as inferred from tree rings, and either pollen composition or tree stand age. Tree ring results show periods of rapid and slow tree growth of significant duration several times during the past 760 years (Hardman and Riel 1936). These cycles have been related to stream runoff and precipitation in the long-term (Hardman and Riel 1936), but not in the short-term. The last 30 years in the Sagehen Basin are a good example; tree growth has been out of phase with runoff in Sagehen Creek.

Fen Origins

A major question is how these fens originated. Carbon dating shows the six fens, less than 0.6 mi (1 km) apart, originated at different times between 8700 and 810 years BP. Maximum peat ages of Mason, East, Kiln, and Two-Fields East Fens ranged from about 1600 to 2000 years BP, suggesting a possibly synchronous origin. Yet the adjacent East, Center, and West Fens have greatly different extreme ages. These two groups of fens also appear to have different rates of peat accumulation: faster in Mason, Kiln, and Two-Fields East; slower in East, Center, and West.

The other unusual finding concerns the lack of a consistent relationship between peat depth and age. Several explanations are possible. In part at least, as our results show, rates of peat accumulation vary by an order of magnitude. Hence, within a fen, similar depths can have different ages.

Possible ditching and diversion of water sources to create a dry surface, churning of the fen surface by oxen and logs in transport, and other localized disturbances could lead to inversions of peat layers. Recovery in the past 50 years made the preserved logs the only distinct relic of previous disturbances.

Both water levels and invertebrate detritus feeders fluctuate vertically over 24-hour periods (Erman 1973). These processes can change the vertical distribution of peat and pollen from 0.8 to 3.0 inches (2 to 10 cm) in wet fen areas. In dry areas, the fluctuations are greater; thus deeper zones receive younger organic matter, transported downward by water or biotic activities.

The net result is a complex history of peat accumulation. The accumulation of layers has been far from a simple aggradation at the surface each year. Without such an extensive collection of cores from Mason Fen, this complicated picture would not have shown up.

In Britain, several studies have suggested that development of blanket bogs may be due more to watershed manipulation by early humans than to climate (Godwin and others 1974, Moore and Beckett 1971, and Moore and Bellamy 1973). Land clearing, grazing, and fire have been implicated, primarily through their effects on water supply. In Sierran coniferous forests, fires were naturally common (Wagener 1961). We found evidence of charcoal in peat samples, as did Erman (1976) earlier. Frequent fires may have burned fens during droughts (DeBenedetti and Parsons 1984) and increased long-term water supply by deforestation. Prehistoric use of the Sagehen area by humans is thought to be minor; few archeological sites have been located, and habitation was only for brief periods during hunting migrations.

This Sierran region is also seismically active. Earthquakes may shift the location or volume of springs emerging from contact points between parent rock and overlays of morraine and andesite. Change in spring flow would have an immediate effect on existing fens and could lead to new fen development. As suggested for the similar sub-alpine wet meadows in the Rocky Mountains (Ives 1942), once established, fens appear to be self-perpetuating and stable.

Fen Succession Model

The data from fens in the Sagehen Basin support a model of succession which includes a biologically stable peat-based system dependent on a reliable source of moisture not subject to short-term fluctuations in climate. Where moisture status is marginal for maintenance of peat, as near borders and elevated areas, the peat is subject to periodic invasion by lodgepole pines. Pine stands established in peat may form a closed canopy which shades out the peat and increases transpirational water loss from peat layers. We found one stand where trees had eliminated the peat layer in part of a fen in a few decades. Tree stands eventually die, many of them in their first century, with reestablishment of peat and continuation of the cycle. These are testable (but untested) hypotheses.

CONCLUSIONS

The Sagehen Basin watershed has been thoroughly investigated and its vegetation mapped by the Tahoe National Forest; no locations have been found at which fens were invaded and have not survived. If invasion and disappearance of a small fen, like West Fen, does not occur in over 8000 years, it seems unlikely that pine invasion is a serious threat to the continued existence of these types of wet meadows.

Management of short-term pine invasion is not needed for preservation of the fen ecosystem. The data on peat age provided evidence that fens are persistent features in the landscape. The variation in fen ages indicates that their origin is probably due to recurring changes in the water supply. They are not fragile, disappearing vestiges of an ancient glacial event. The presence of large, old living or dead pines and stumps near their edges indicates that in places fen borders can be stable for hundreds of years. The broad age range of trees in the bands of even-sized stands paralleling fen borders is consistent with the notion that they developed over many years rather than during a few years of drought. In addition to recently established pines, the dead and dying stands and solitary individuals on and around fens indicate that these invaders do not persist. Flowing peat deposits also invade the forest at the toe of the sloping fens, killing the trees. Thus, changes in the vegetation cover on and about fens are temporary fluctuations rather than irreversible events. Where nourishment by water continues normally, peat continues to accumulate in fens. Where it lessens, peat accumulation slows. Where it ceases, peat deposits shrink and disappear, but accumulation begins again if water regimes return to normal.

This type of wet meadow is so persistent that the establishment of pines within the fen ecosystem should be considered a temporary, natural fluctuation, not an indication that managers must act to prevent their loss by plant succession. However, activities which change the water supply will have an effect on the distribution and size of fens.

REFERENCES

Adam, David P. 1967. **Late-pleistocene and recent palynology in the central Sierra Nevada, California**. In: Cushing, E.J.; Wright, H.E., Jr., eds. Quaternary paleoecology—Proceedings, 7th Congress of International Association of Quaternary Research. Proceedings, volume 7; 1965. New Haven: Yale Univ. Press; 275-301.

Barry, W. James; Schlinger, Evert, I., eds. 1977. **Inglenook Fen: a study and plan**. Sacramento: State of California, Department of Parks and Recreation; 212 p.

Bel'skaya, M.A. 1961. **Changes in the physical properties of peat-bog forest soils due to drainage**. Jerusalem: Israel Program for Scientific Translations (From Russian), IPST Cat. 1984. 8 p.

Benedict, Nathan B. 1982. **Mountain meadows: stability and change**. Madrono 29(3):148-153.

Benedict, Nathan B.; Major, Jack. 1982. **A physiographic classification of subalpine meadows of the Sierra Nevada, CA**. Madrono 29(1):1-12.

Boelter, Don H.; Verry, Elon S. 1977. **Peatland and water**. Gen. Tech. Rep. NC-31. St. Paul, MN: North Central Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 22 p.

Boggie, R. 1972. **Effect of water-table height on root development of *Pinus contorta* on deep peat in Scotland**. Oikos 23(3):304-312.

Cameron, Cornelia C. 1970. **Peat deposits of northeastern Pennsylvania**. U.S. Geological Survey Bulletin 1317.A.1. Washington, DC; 90 p.

Clymo, R.S. 1970. **The growth of *Sphagnum*; methods of measurement**. Journal of Ecology 58(1):13-49.

Clymo, R.S.; Reddaway, E.J.F. 1974. **Growth rate of *Sphagnum rubellum* Wils. on pennine blanket bog**. Journal of Ecology 62(1):191-196.

Crane, Basil K. 1950. **Condition and grazing capacity of wet meadows on the east slope of the Sierra Nevada Mountains**. Journal of Range Management 3(4):303-307.

DeBenedetti, Steven H.; Parsons, David J. 1984. **Postfire succession in a Sierran alpine meadow**. American Midland Naturalist 111:118-125.

Erman, Don C. 1973. **Invertebrate movements and some diel seasonal changes in a Sierra Nevada peatland**. Oikos 24(1):85-93.

Erman, Don C. 1976. **Peat depth of Sierra Nevada fens and profile changes from 1958 to 1972 in Mason Fen**. Great Basin Naturalist 36(1):101-107.

Erman, Don C.; Chouteau, Walter C. 1979. **Fine particulate organic carbon output from fens and its effect on benthic macroinvertebrates**. Oikos 32(3):409-415.

Erman, Don C.; Erman, Nancy A. 1975. **Macroinvertebrate composition and production in some Sierra Nevada minerotrophic peatlands**. Ecology 56(3):591-603.

Erman, Don C.; Roby, Kenneth. 1977. **Hydrology**. In: Barry, W. James; Schlinger, Evert I., eds. Inglenook Fen: a study and plan. Sacramento: State of California, Department of Parks and Recreation; 31-51.

Fritts, Harold C. 1976. **Tree-rings and climate**. London: Academic Press; 576 p.

Godwin, H.; Clowes, D.R.; Huntley, B. 1974. **Studies in the ecology of Wicken Fen. V. Development of Fen Carr**. Journal of Ecology 62(1):197-214.

Hardman, George; Riel, Orvis E. 1936. **The relationship between tree growth and stream runoff in the Truckee River Basin, California-Nevada**. Agricultural Experiment Station Bulletin 141. Reno: University of Nevada; 38 p.

Heady, Harold F.; Zinke, Paul J. 1978. **Vegetational changes in Yosemite Valley**. U.S. National Park Service Occasional Paper 5; 25 p.

Heinselman, M.L. 1970. **Landscape evolution, peatland types, and the environment in the Lake Agassiz Region, Minnesota**. Ecological Monographs 40(2):235-261.

Ives, Ronald L. 1942. **Atypical sub-alpine environments**. Ecology 23(1):89-96.

Johnson, Dale E. 1982. **Climate diagram for the University of California Sagehen Creek Field Station**. Madrono 29(2):122-123.

Kosco, Barbara H.; Bartolome, James W. 1981. **The effects of grazing on middle elevation Sierra Nevada meadows**. Proceedings 34th Annual Meeting Society of Range Management. 1981 February 8-13; Tulsa, OK. p. 7.

Lindgren, Waldemar. 1897. **Geological atlas of the United States**. Folio 39 (Truckee Quadrangle). Washington, DC: U.S. Geological Survey; 8 p.

Moore, Peter D.; Beckett, P.J. 1971. **Vegetation and development of Llyn, a Welsh mire**. Nature 231(5302):363-365.

Moore, Peter D.; Bellamy, D.J. 1973. **Peatlands**. New York: Springer-Verlag; 221 p.

Pennak, Robert W. 1963. **Ecological and radiocarbon correlations in some Colorado mountain lake and bog deposits**. Ecology 44(1):1-15.

Rae, Stephen P. 1970. **Studies in the ecology of Mason Bog, Sagehen Creek**. Davis: University of California; 105 p. M.S. Thesis.

Ratliff, Raymond D. 1982. **A meadow site classification system for the Sierra Nevada, California**. Gen. Tech. Rep. PSW-60. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 16 p.

Reader, R.J.; Stewart, J.M. 1972. **The relationship between net primary production and accumulation for a peatland in southeastern Manitoba**. Ecology 53(6):1024-1037.

Savage, Wayne. 1973. **Annotated check list of vascular plants of Sagehen Creek Drainage Basin, Nevada County, California**. Madrono 22(3):115-139.

Schwintzer, Christa R.; Williams, Gary. 1974. **Vegetation changes in a small Michigan bog from 1917 to 1972**. American Midland Naturalist 92(2):447-459.

Slater, F.M.; Agnew, A.D.Q. 1977. **Observations on a peat bog's ability to withstand increasing public pressure**. Biological Conservation 11(1):21-27.

Trowbridge, Barbara A. 1975. **Plants of upper Sagehen Creek Drainage Basin, Nevada County, California**. San Francisco State University; 106 p. M.A. Thesis.

Vale, Thomas R. 1981. **Ages of invasive trees in Dana meadows, Yosemite National Park, California**. Madrono 28(1):45-47.

Vale, Thomas R. 1982. **Plants and people: vegetation change in North America**. Washington, DC: Association of American Geographers; 88 p.

VanKat, John L.; Major, Jack. 1978. **Vegetation changes in Sequoia National Park, California**. Journal of Biogeography 5(4):377-402.

Wagener, Willis W. 1961. **Past fire incidence in Sierra Nevada forests**. Journal of Forestry 59(10):739-748.

Walker, D.; Walker, P.M. 1961. **Stratigraphic evidence of regeneration in some Irish bogs**. Journal of Ecology 49(1):169-185.

West, Christopher I. 1982. **Management options for the Sagehen Creek Basin**. Berkeley: University of California; 110 p. Masters of Forestry Professional Paper.

Wood, Spencer H. 1975. **Holecene stratigraphy and chronology of mountain meadows, Sierra Nevada, California**. Pasadena: California Institute of Technology; 180 p. PhD. dissertation.