Ecological Effects of the Lawn Lake Flood of 1982, Rocky Mountain National Park

Scientific Monograph NPS/NRROMO/NRSM-93/21
United States Department of the Interior
National Park Service

The National Park Service publishes scientific studies of significant natural resources in units of the National Park System. This research is of scholarly quality and may include any discipline of the biological, physical, or social sciences.

Editorial Staff

Cover Photo: A backdrop of mountains in Rocky Mountain National Park, Colorado, highlights the alluvial fan created by the Lawn Lake flood.

Copies of this report are available from the Publications Coordinator, National Park Service, Natural Resources Publication Office, P.O. Box 25287, Denver, CO 80225-0287.

ISSN 0363-0722

Ecological Effects of the Lawn Lake Flood of 1982, Rocky Mountain National Park

Editors

Henry E. McCutchen

Northern Arizona University
Cooperative Park Studies Unit
Flagstaff, Arizona 86011

Raymond Herrmann

National Park Service
Colorado State University
Water Resources Cooperative Park Studies Unit
Fort Collins, Colorado 80523

David R. Stevens[1]

Rocky Mountain National Park
Estes Park, Colorado 80517

Scientific Monograph NPS/NRROMO/NRSM-93/21
United States Department of the Interior
National Park Service

•1993•

---

[1] Present address: National Park Service Alaska Regional Office, Anchorage, Alaska 99503.

Contents

Page

Foreword ... iv
Hydrology and Geomorphology of the 1982 Lawn Lake Dam Failure, Colorado. *Robert D. Jarrett and John E. Costa* ... 1
Geomorphic Response of the Fall River, Rocky Mountain National Park, Colorado. *John Pitlick* ... 18
Alpine Sediment Movement and Erosion in the Roaring River Watershed, Rocky Mountain National Park. *Rebecca M. Summer* ... 33
Geochemistry of Iron Oxides in the Roaring River Alluvial Fan, Rocky Mountain National Park, Colorado. *M. Iggy Litaor and Richard B. Keigley* ... 55
Micronutrient Status of Tree Species Affected by the Lawn Lake Flood in Rocky Mountain National Park, Colorado. *Kenneth A. Barrick and Mark G. Noble* ... 70
Vegetation Development on the Exposed Shores of Lawn Lake. *Donald H. Mansfield* ... 86
Macroinvertebrate Community Recovery Following Episodic Flooding From an Earthen Dam Failure. *David R. Beeson and Terence P. Boyle* .. 112
Terrestrial Arthropod Fauna of the Alluvial Fan Resulting From the Lawn Lake Flood. *Howard E. Evans* ... 138
Colonization of the Lawn Lake Alluvial Fan by Amphibians: Potential Effects of Biotic and Abiotic Factors. *Linda C. Zimmerman and C. Richard Tracy* ... 148
Changes in Avian Breeding Populations Resulting From the Lawn Lake Flood of 1982. *Ronald A. Ryder and Deborah West Bangs* ... 163
Effects of the Lawn Lake Flood on Local Distribution and Abundance of Mammals. *David M. Armstrong* ... 170
Observations of Plant Ecology on the Lawn Lake Flood Alluvial Fan. *Richard B. Keigley* ... 192

Foreword

Lawn Lake is located at treeline, 3,350 m (10,987 feet) above sea level. It is in one of the most scenic areas of Rocky Mountain National Park, Colorado. In 1903, a privately constructed dam enlarged the lake to store water for irrigation. These activities preceded the designation of Rocky Mountain National Park in 1915; because of the established water rights, the dam continued to be privately managed, maintaining an easement within national park property.

On 15 July 1982, the dam at Lawn Lake failed, probably due to a piping failure. The subsequent flood sent approximately 831,000 m^3 of water cascading down the Roaring River—causing the Cascade Lake Dam to fail—and then continuing through the town of Estes Park. Three people were killed, and nearly $30 million of damage occurred. The president declared Larimer County a disaster area on 22 July 1982.

Failure of the dam released a torrent that scoured the drainage of the Roaring River, inundated adjacent ecosystems, and deposited a large debris fan at the confluence of the Roaring and Fall rivers in the park. The physical and biological effects of the flood were profound, particularly within the park. As perturbations of this type in high-elevation ecosystems are rare, the flood captured the interest of local, national, and international scientists and scholars.

The period following the Lawn Lake Flood was recognized by the National Park Service (NPS) as a rare opportunity to study and better understand ecosystems affected by catastrophic flooding. The present study represents the results of the last 8 years of multidisciplinary research. In 1983, Gustav Swanson, professor emeritus of Colorado State University, focused the NPS effort when he proposed the concept of developing a research consortium for the flood. In May 1983, these thoughts became reality when the park hosted a meeting and field trip for interested investigators. From that first meeting, plans rapidly developed and were put in motion for the organization and funding of a multidisciplinary research effort to investigate the physical and biological effects of the flood as well as the area's subsequent recovery.

The NPS Rocky Mountain Region and the NPS Water Resources Field Support Laboratory initiated the program. Later, additional help was obtained from the National Park Service's Natural Resources Preservation Program.

Contributions of additional value were made by other government and private sources. In addition, many of the contributors to this volume donated their professional skills and talents to these efforts.

The result has been a multidisciplinary scientific study of an unusual event—a study that details many research efforts focused toward understanding the effects of and the response to the catastrophic flood on 15 July 1982. As their titles reflect, the 12 studies presented here have covered many physical and biological science disciplines, including geology, hydrology, chemistry, botany, and zoology. The studies tell the story of the ecological changes that followed the failure of Lawn Lake Dam and the subsequent flood that produced rapid hydrologic changes, including inundation, scouring and deposition (burial), nutrient and mineralogic changes, sediment accommodations, and direct biological effects. Finally, these studies detail the recovery processes that occurred in both aquatic and terrestrial biological communities.

Many important publications on the effects of and the response to the flood were presented before those in this symposium. One of the major ones, published in 1986, is the 78-page U.S. Geological Survey Professional Paper by R. D. Jarrett and J. E. Costa titled *Hydrology, Geomorphology and Dambreak Modeling of the July 15, 1982, Lawn Lake Dam and Cascade Lake Dam Failures, Larimer County, Colorado.* Jarrett and Costa have provided a condensed version of that monograph for this volume. A number of reports and publications have stemmed from the research of Dr. Colin Thorne (Queen Mary College, London, England) and his associates. This series of five reports, printed as technical reports of the NPS Water Resources Field Support Laboratory, are not reprinted in this volume because of space constraints. These reports include *Bedload Transport and Hydraulic Geometry Relations for Fall River, Rocky Mountain National Park, Colorado (1984)*, by John P. Hick; *Bed Material Analysis on the Fall River (1983)*, by David S. Biedenbain; two reports, *Measurements of Bend Flow Hydraulics on the Fall River—at Low Stage (1983)*, and—*at Bank Full Stage (1985)*, by Colin R. Thorne et al.; and *Stream Discharge Rating Curves for the Fall River, Rocky Mountain National Park (1983)*, by Mark Segenthaler. Copies of these reports may be obtained from the U.S. Department of the Interior, National Park Service, Water Resources Division, Fort Collins, Colorado. Another article of interest can be found in the *Journal of Sedimentary Petrology* 57(1):1–18, titled *Sedimentary Processes, Vertical Stratification Sequences, and Geomorphology of the Roaring River Alluvial Fan, Rocky Mountain National Park, Colorado,* by Terence C. Blair.

We again thank the authors and investigators who persisted—with minimal NPS help—to complete their studies. These studies represented a rare opportunity to learn more about a phenomenon of great importance to resources managers within the National Park Service and to land managers everywhere. The results of their work have helped to better understand the nature of riparian changes that occur owning to catastrophic flood events and the recovery process that follows.

James B. Thompson
Superintendent, Rocky Mountain National Park
The Editors

Frontispiece. The alluvial fan that formed on the valley floor after the breaching of the Lawn Lake dam altered the appearance of the landscape and created a new lake (*lower left*). The photo was taken in the summer of 1992.

Hydrology and Geomorphology of the 1982 Lawn Lake Dam Failure, Colorado

Robert D. Jarrett

U.S. Geological Survey
P.O. Box 25046, MS 418
Denver, Colorado 80225

John E. Costa

U.S. Geological Survey
5400 MacArthur Boulevard
Vancouver, Washington 98661

Abstract. Failure of the Lawn Lake Dam released 831,000 m^3 of water with an estimated peak discharge of 510 m^3/s down the Roaring River valley. Floodwaters from Lawn Lake Dam overtopped a second dam with a peak discharge of 204 m^3/s. Cascade Lake Dam, 10.8 km downstream, also failed and increased peak discharge to 453 m^3/s. Cascade Lake Dam, a 5.2-m-high concrete gravity dam with a capacity of 14,900 m^3, failed as 1.28 m of water flowed over its crest. The flood continued down the Fall River into the town of Estes Park, where it caused extensive damage. Peak discharge in the Big Thompson River at Estes Park was 156 m^3/s. We present a summary of the dam failures, hydrologic and dam-break modeling analyses, a discussion of the geomorphic effects of the flood, and an overview of the effects of the flood on the public. The documented 1982 flood indicates the need to improve the understanding of flood processes so that modeling dam-break floods in high-gradient rivers can be improved. These study results provide hydrologic, geomorphic, and flood damage information for the assessment of floods from dam failures and baseline information for scientists conducting related research.

Introduction

> *I started to hear a sound like an airplane. Also, there were loud booms. It got louder and louder. I thought it was breaking the sound barrier. I kept looking for a plane but couldn't see one. I got suspicious and started looking upstream. I saw trees crashing over and a wall of water coming down. I started to run as fast as I could for high ground. There was a deafening roar. I fell and got up and kept running. I stood on high ground and watched it wipe out our campsite. It knocked everything in its path over; Steve [his camping companion] didn't stand a chance.*

With these words, Steven Cashman described his harrowing experience with the flood that swept his camping companion to his death in the Roaring River. Other campers along the Roaring River estimated the wall of water to be 8–10 m high, carrying with it large trees and boulders, so that the water looked like a wet, brown cloud that sounded like extremely loud continuous thunder, or a freight train, or an airplane breaking the sound barrier.

After Cascade Lake Dam failed, two other campers were swept to their deaths a short distance downstream from the dam. The flood caused extensive damage to homes, businesses, and bridges, particularly in the town of Estes Park. Dave Thomas, observing the flood from a point 1.9 km upstream from Estes Park, indicated the floodwave "gradually began to swell—there was no wall of water." In Estes Park, the flood entered the Big Thompson River for a short distance before being contained within Lake Estes by the U.S. Bureau of Reclamation's Olympus Dam, which is about 20 km downstream from Lawn Lake. Peak discharge into Lake Estes—156 m^3/s—occurred about 3 h 40 min after the failure of Lawn Lake Dam. In that brief time, three people were killed and approximately $31 million of total flood damage was incurred. Flood damages included private and public property losses, debris cleanup, and economic losses to businesses in the Estes Park area. As a result of the flood, the president declared Larimer County a disaster area on 22 July 1982.

The Lawn Lake Dam failure provided an opportunity to improve the understanding of hydraulic and geomorphic processes of large floods and their effect on stream channel morphology in mountainous areas. This paper presents the setting, a summary of causes, effects on hydrology and geomorphology, and effects on the public of the dam failures and flood. Dam-break computer modeling was used to provide supplemental hydrologic information and to evaluate various hypothetical scenarios of dam-breach development and probable effects of the failure of Cascade Lake Dam. Documentation and analysis of the flood provide valuable information on the effects of floods from failure of small dams on high-gradient streams. This information can be used for future hazard mitigation related to dam failures and for studying the effects of floods from dam failures. Because the dam-failure flood occurred within National Park System lands, study of this flood enhanced the National Park Service (NPS) dam safety program and its relation to park resources.

Setting

Lawn Lake was an artificially enlarged natural lake occupying a moraine-dammed depression on the southeast side of the Mummy Range in Rocky Mountain National Park, Colorado (Fig. 1). The elevation of the lake is about 3,350 m. Local bedrock consists of Precambrian gneisses and schists that are more than 1.7 billion years old (Peterman et al. 1967). Lawn Lake is fed by the Roaring River, which originates at Crystal Lake, a tarn located about 1.6 km upstream at an elevation of about 3,500 m. Upstream from Lawn Lake, the

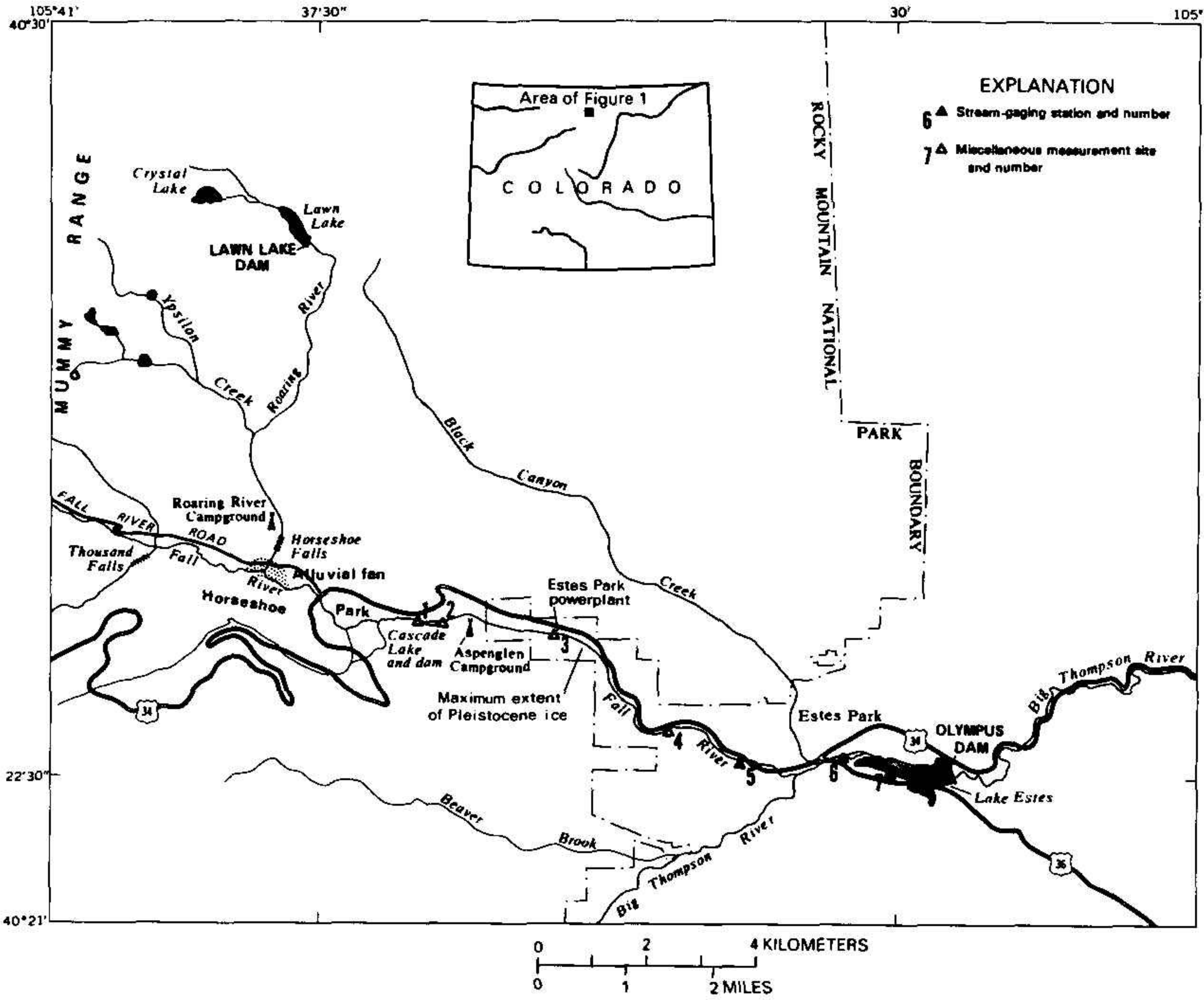


Fig. 1. Area between Lawn Lake Dam and Lake Estes (modified from Jarrett and Costa 1986).

valley is steep and rugged. Downstream from Lawn Lake, the Roaring River descends through an alternating series of steep bedrock falls and gently sloping mountain meadows. Channel slopes range from 5 to 26% and average 10% along the Roaring River (Fig. 2). The Roaring River and Fall River valleys were repeatedly glaciated during the Pleistocene, and an extensive sequence of glacial deposits is located along both valleys. The maximum extent of Pleistocene glaciation is shown in Fig. 1; the most recent glacial advance was during the Pinedale glaciation.

Lawn Lake is at treeline; vegetation along the Roaring River consists of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and aspen (*Populus tremuloides*) forests. The Roaring River joins the Fall River at an elevation of 2,605 m at the west end of Horseshoe Park. Just upstream of Horseshoe Park, the river descends about 150 m over 0.5 km in a series of rapids known collectively as Horseshoe Falls (Fig. 1). Mean annual precipitation in the area varies with elevation, ranging from 508 mm in Estes Park to 1,020 mm or more on the Continental Divide above Lawn Lake.

Horseshoe Park is a flat, moraine-rimmed basin that was occupied by a large glacial lake when terminal moraines dammed the Fall River at the east end of the park. The hills surrounding Horseshoe Park are forested with ponderosa (*Pinus ponderosa*) and lodgepole (*Pinus contorta*) pine and aspen. The

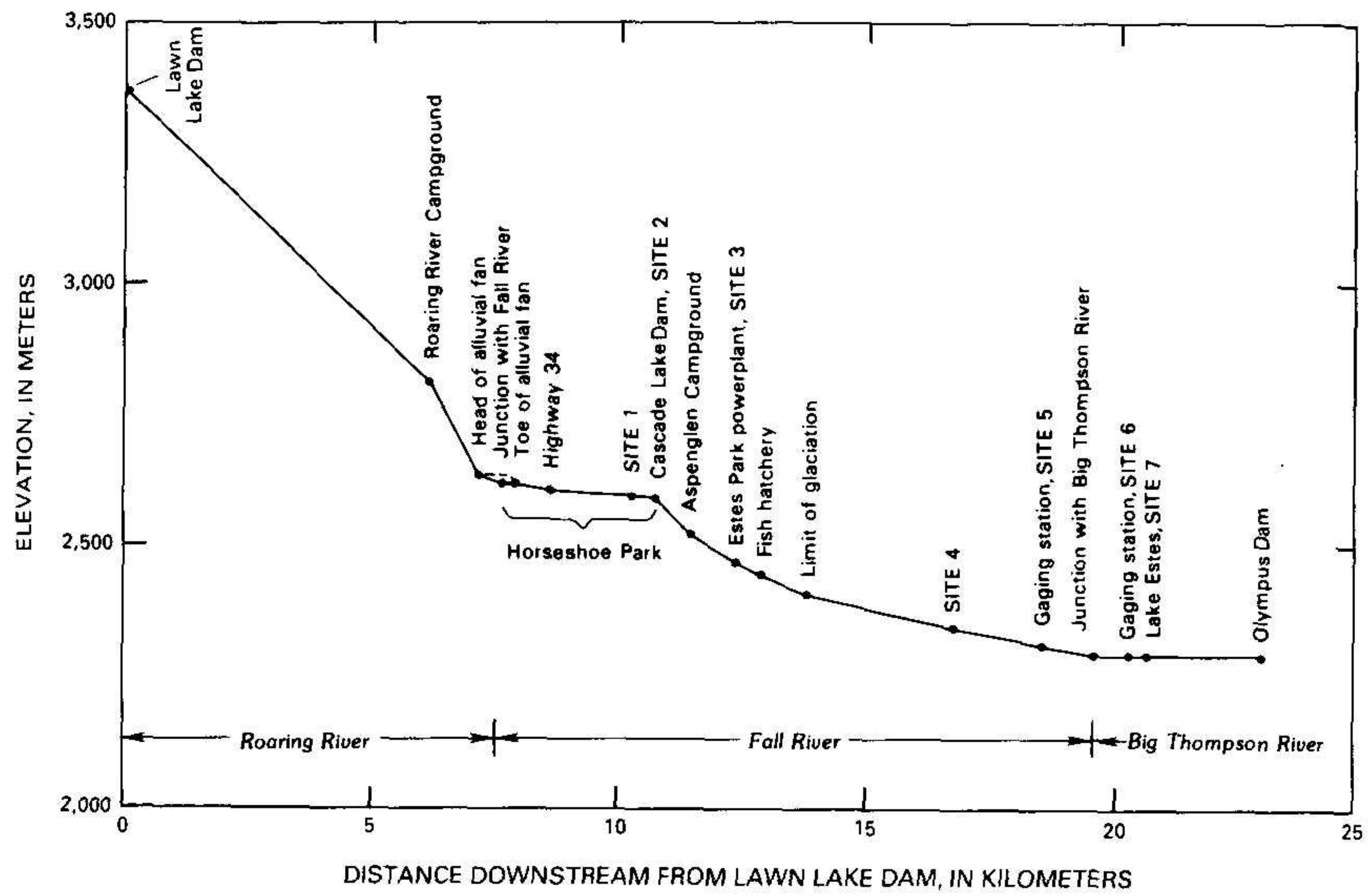


Fig. 2. Longitudinal profile of flood path of the water from Lawn Lake Dam and Cascade Lake Dam failures. Vertical exaggeration 10.5 times (modified from Jarrett and Costa 1986).

floor of Horseshoe Park averages 0.8 km wide and is 4.8 km long, and it is underlain by ground moraine, outwash, and lacustrine sediments. Valley slope is relatively flat, averaging 0.7%. The park is covered by meadow grass; dense willows mark the meandering course (sinuosity is 2.2) of the Fall River. The relatively flat and moderately sinuous Fall River substantially attenuated the floodwave.

The Fall River flows into Cascade Lake at the east end of Horseshoe Park. Cascade Lake, located about 8.5 km west of Estes Park, was an artificial lake privately built in 1908 and obtained by Estes Park for power generation in 1945. Downstream from Cascade Lake, the Fall River gradient steepens to 9% as it flows over a series of Pleistocene terminal moraines and into Aspenglen Campground (Fig. 2).

Downstream from the Estes Park power plant, at an elevation of about 2,440 m and about 1.6 km downstream from Cascade Lake, the Fall River valley narrows noticeably, marking the probable maximum extent of Pleistocene glacial advances (Jones and Quam 1944; Richmond 1960). Downstream from 2,440 m, the Fall River flows down a relatively steep and narrow valley bordered by numerous bedrock outcrops and short, narrow, discontinuous floodplains. In Estes Park, the Fall River joins the Big Thompson River, which flows 1.1 km before entering the west end of Lake Estes. Lake Estes is the large reservoir, created by Olympus Dam, which was completed in 1948 as part of the U.S. Bureau of Reclamation's Colorado–Big Thompson project.

History of the Dams

Lawn Lake Dam was an earthen dam constructed in 1903 by the Farmers Irrigation Ditch and Reservoir Company to impound additional water for irrigation storage in an existing mountain lake. Originally, Lawn Lake was a natural moraine-dammed lake with a surface area of 0.066 km^2. Lawn Lake Dam was constructed of heterogeneous local earthfill—poorly sorted silty sands with varying amounts of fine gravel and considerable amounts of organic material—derived from the surrounding glacial deposits. The maximum thickness of deposits near the dam is 8 m. The underlying Precambrian igneous and metamorphic bedrock is highly fractured and jointed but unweathered. Postflood surveys (Jarrett and Costa 1986) indicated that the dam was 7.9 m high (the water was 7.3 m deep) and 171 m long, and the surface area was 0.17 km^2 at the time of failure (Fig. 3).

Six possible causes of the Lawn Lake Dam failure were investigated by the Office of the State Engineer (1983): (1) overtopping, (2) earthquake shaking, (3) rodent damage, (4) frost penetration, (5) embankment instability, and (6) piping. Data gathered by the Office of the State Engineer (1983) indicated that the most likely cause of the Lawn Lake Dam failure was deterioration of the lead caulking used for the seal between the outlet pipe and the gate valve. The resulting leak eroded a pipe-shaped cavity in the earthfill, creating a void

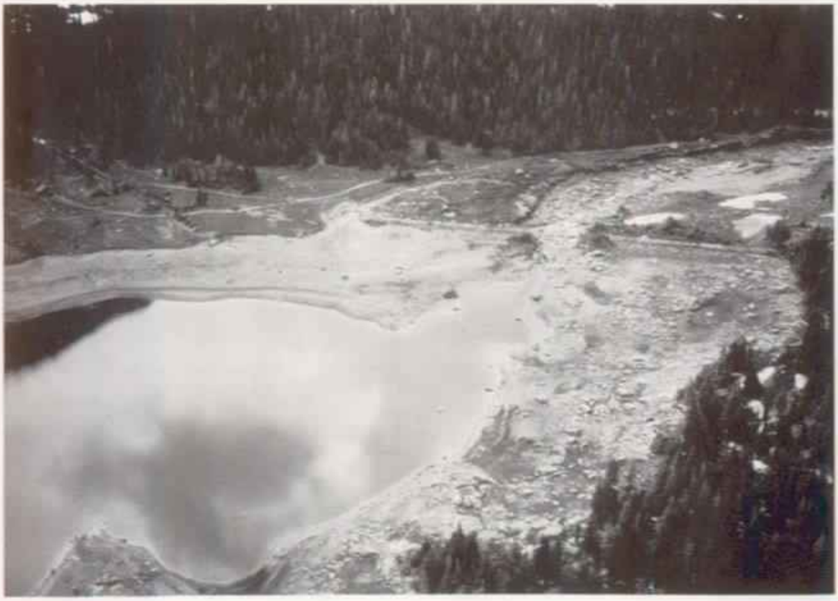


Fig. 3. Aerial view of Lawn Lake about 1 week after the dam failure, showing water still remaining in the natural depression of the original lake (from Jarrett and Costa 1986).

Fig. 4. Empty Cascade Lake before dam failure.

along the outlet pipe. The leak removed easily erodible material until the embankment failed. This process of erosion is called piping.

The following are dimensions of the breach in Lawn Lake Dam: depth of 8.5 m, top width of 29.6 m, and bottom width of 16.8 m (Jarrett and Costa 1986). Following the failure of the dam at about 0530 h, the resulting outflow reached its peak discharge very quickly (estimated to be within 10 min of the breach). The estimated Lawn Lake peak discharge was 510 m^3/s.

Cascade Lake Dam, a 5.2-m-high concrete gravity dam, was on the Fall River in Rocky Mountain National Park, 8.5 km west of Estes Park (Fig. 1). A diversion dam was originally constructed at the site in 1908 for a pipeline to the Estes Park power plant downstream. The power plant supplied electricity to the town of Estes Park. The dam consisted of a concrete wall about 1 m thick, reinforced with a masonry rock buttress on the downstream side (Fig. 4). The foundation and abutments were in glacial terminal-moraine sediments; no bedrock was evident in the foundation. Postflood surveys indicated that before the failure, the maximum depth of water behind Cascade Lake Dam was approximately 4 m deep, the dam was 43.6 m long, and it had a capacity of 14,900 m^3 (Jarrett and Costa 1986). The dam was overtopped by up to 1.28 m of water during the Lawn Lake Flood for nearly 30 min before the dam failed (by tipping over) at 0742 h. Hydrostatic pressure of the water on the dam and erosion of the abutments were probable causes of the dam failure (Fig. 5). At the time of failure, flow into Cascade Lake (site 1; for site locations, see Fig. 1) was approximately 204 m^3/s, and the reservoir capacity, due to the

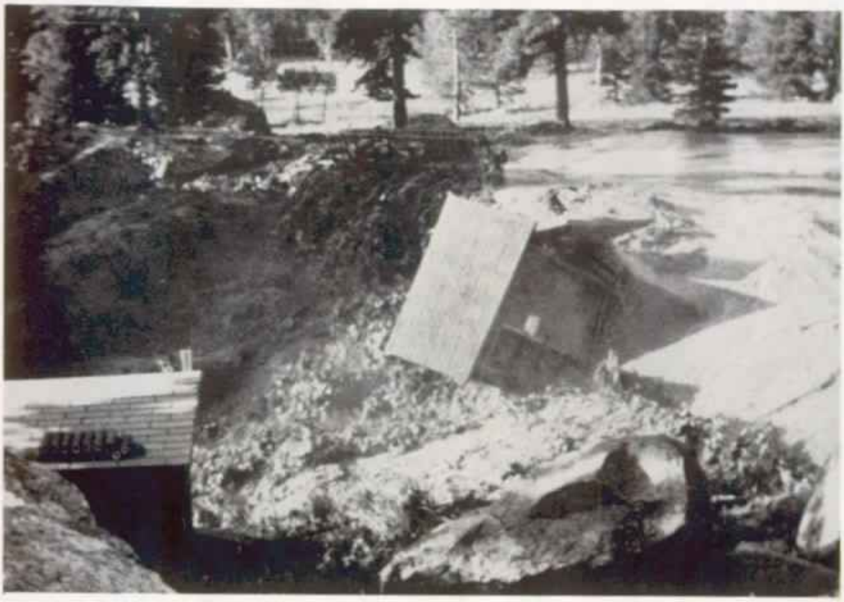


Fig. 5. Cascade Lake Dam in the initial stages of failure.

additional depth of water (1.28 m) above the top of the dam, was about 31,000 m^3 (Jarrett and Costa 1986). The failure of the dam released an estimated peak discharge of 453 m^3/s down the Fall River into Aspenglen Campground, about 0.5 km downstream. Within about 5 min after the dam failure, the flood surge had passed the campground.

Hydrologic Analysis

Dam-break floods should be documented because limited information is available for assessment and hazard mitigation of possible future dam-break floods. Flood data were obtained at two streamflow-gaging stations and at five miscellaneous sites in the flooded area (Fig. 1). These data were used to provide information on peak discharge, velocity, depth, width, area, and travel time. Direct discharge measurements were not made because the flood occurred without warning. Standard U.S. Geological Survey methods were used to indirectly compute peak discharge. These methods included the slope-area method, critical-depth method, and flow-over-weirs method (Jarrett and Costa 1986). These methods all require an assessment of flow resistance; methods of estimating Manning's *n*-values on higher gradient streams (Jarrett 1985) were used. Indirect measurements of peak discharge could not be made upstream from site 1 (Fig. 1); peak discharges were estimated from dam-break modeling. A peak discharge profile from Lawn Lake Dam to Olympus Dam was

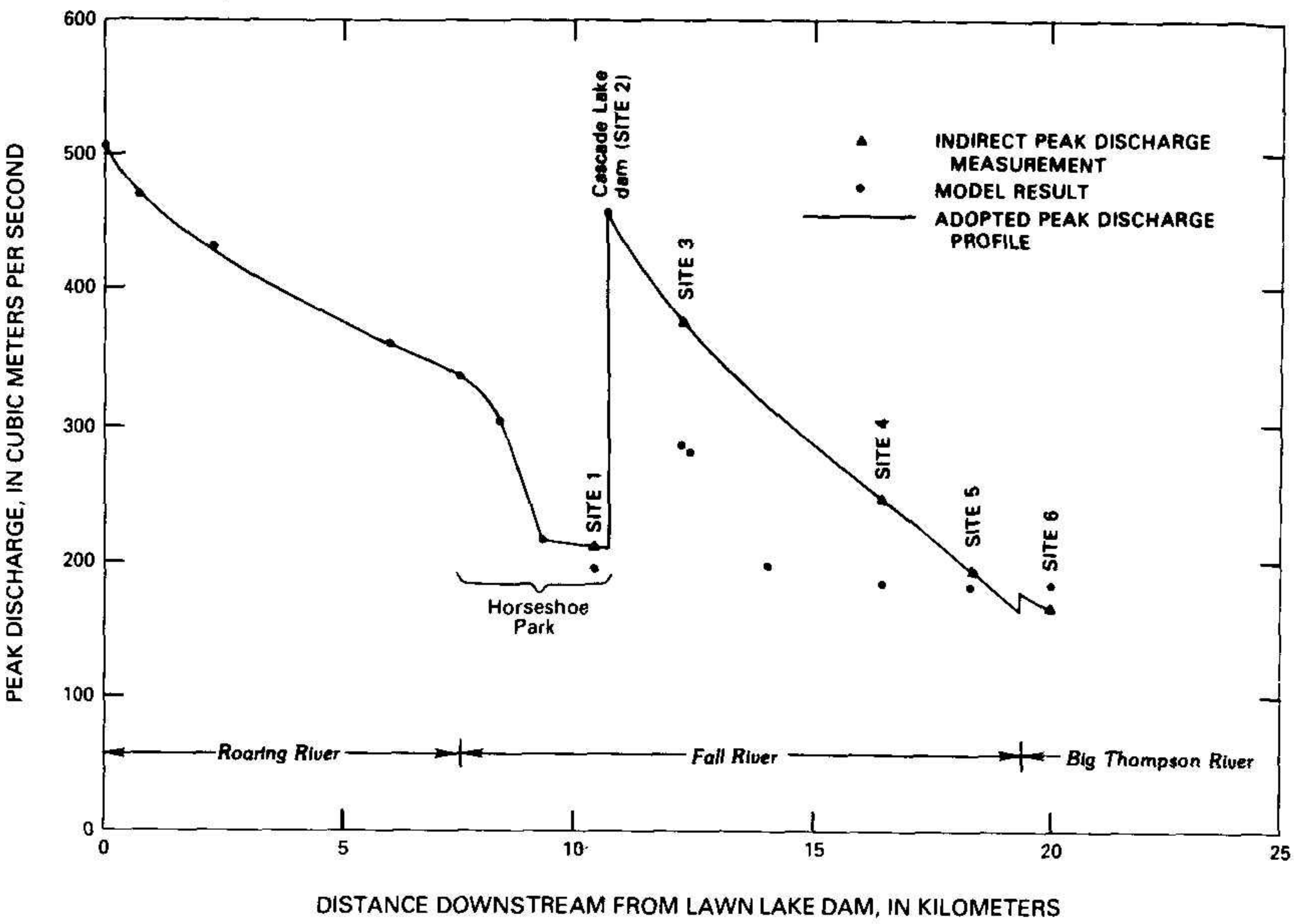


Fig. 6. Peak-discharge profile based on indirect peak-discharge measurements and model results (modified from Jarrett and Costa 1986).

constructed (Fig. 6). The estimated error of peak discharges was about 25%. Indirect peak-discharge estimates were considered more accurate than the dam-break model results; hence, the profile reflects indirect measurements where both results were available. The peak discharge profile indicated the rapid attenuation of peak flows in a downstream direction because of the small volume of the flood. Greatest attenuation occurred in Horseshoe Park, but the peak discharge more than doubled as a result of the near-instantaneous failure (estimated to be about 1 min) of Cascade Lake Dam downstream from Horseshoe Park.

Land surveys were combined with aerial-photography mapping to document pertinent preflood and maximum-flood water-surface levels, to develop topographic maps, and to determine storage capacity data of both lakes (Jarrett and Costa 1986). These surveys indicated that the failure of Lawn Lake Dam released about 831,000 m^3 of water. A substantial amount of water remained in the lake as dead storage. This volume of water probably corresponds to the volume of the original moraine-dammed lake (Fig. 3). Cascade Lake contained about 14,900 m^3 of water before the flood and 31,000 m^3 of water at the time of failure of Cascade Lake Dam. The total volume of water released from the failure of both dams was approximately 845,900 m^3.

The most destructive components of the flood were high shear stresses and high flow velocities, particularly on the Roaring River and on the Fall River immediately downstream from Cascade Lake Dam. The high shear stresses on the channel boundary caused severe channel erosion (Fig. 7). Four-

Fig. 7. Aerial view of the Roaring River valley at river kilometer 1.83; down valley is to the right. From left edge of photo: the channel is scoured to bedrock and is high gradient; a wide depositional reach is at a mountain meadow; a short, high-gradient reach is defined by slope failure on left bank; a flatter depositional reach extends off right edge of photo (from Jarrett and Costa 1986).

teen cross sections were surveyed along the flood path. At each cross section, the water surface elevation, depth, and width corresponding to the peak discharge were measured, the flow area was calculated, and the velocity was computed or estimated (Jarrett and Costa 1986). Average velocities ranged from 1 to 3.8 m/s and generally decreased in a downstream direction; however, local velocities may have been much greater. Maximum depths ranged from 1.95 to 7.25 m; maximum widths ranged from 29.6 to 339 m. Cross-sectional areas ranged from 66 to 277 m^2, generally decreasing downstream, except through Horseshoe Park. Flood profiles and boundaries for Estes Park for the 15 July 1982 flood are presented in a report by the Colorado Water Conservation Board (1983).

Because this flood resulted from dam failures rather than natural causes, conventional flood-frequency analysis is not directly applicable. However, the relative frequency of the 1982 flood can be useful in describing the effects of a flood of this magnitude, its channel-changing processes, and its relation to historic and natural floods. The peak discharge at the mouth of the Roaring River (340 m^3/s) was 30 times greater than the estimated 500-year flood at that site (Jarrett and Costa 1986). In Estes Park, flood depths were 0.76 m above the level of the estimated 500-year flood. At the streamflow-gaging station on the Big Thompson River in Estes Park, peak discharge was 2.1 times greater than the 500-year flood. In 1983, extensive on-site studies were made in Rocky Mountain National Park to investigate whether or not any stratigraphic or geomorphic evidence existed of comparable large postglacial floods in any of the streams that drain into Lake Estes. The sediments and landforms produced by the 1982 flood are distinctive. No evidence of an out-of-bank flood was found in any stream valley that drains into Lake Estes. Geomorphic and sedimentologic evidence suggest this flood was probably the largest in these basins since the retreat of glaciers from the area about 10,000 years ago (Jarrett and Costa 1986, 1988).

Immediately after the flood, U.S. Bureau of Reclamation personnel interviewed residents along the flood path to evaluate the effectiveness of flood warnings (Graham and Brown 1983). This information—with streamflow-gaging station data, Lake Estes inflow data, and stream distance data—provided information to compute the travel time of the floodwave.

Although no one observed the failure of Lawn Lake Dam, interviews with campers near the dam (who heard the flood noise) and with campers downstream from the dam (who saw the flood) put the approximate time of failure at about 0530 h, just before sunrise. According to Stephen Gillette, who was the first person to report the flood at 0623 h, floodwaters reached Horseshoe Falls at about 0615 h and U.S. Highway 34 in Horseshoe Park at 0634 h (Fig. 1). According to L. V. Davis, floodwaters reached Cascade Lake Dam at 0715 h, and the dam failed at 0742 h. Estes Park police reported that floodwaters reached Estes Park a little after 0830 h. Floodwaters reached the Big Thompson River at the Estes Park streamflow-gaging station (site 6) at 0835 h, and U.S. Bureau of Reclamation personnel reported that water levels in Lake Estes started rising at 0847 h.

Travel times for the arrival of the flood were summarized for three channel segments, based on fairly uniform reach hydraulics. The speed of the leading edge of the flood (and probably the peak) averaged 14.6 km/h in the Roaring River, 3.38 km/h in the Fall River through Horseshoe Park, and 6.44 km/h from Cascade Lake Dam to Lake Estes. The speed of the leading edge of the flood averaged 6.11 km/h. Considering the high-gradient channels, these travel times were relatively slow, probably due to the extremely rough channel bottom and large amounts of flood debris, particularly in the Roaring River. The flood's attenuation in Horseshoe Park also reduced the speed of the flood wave. Fortunately for the numerous people in the flood path downstream from Horseshoe Park, the park acted as an efficient flood-retarding basin. By slowing the floodwave, the time available for warning and evacuating was increased.

Geomorphic Effects

Geomorphic effects of the dam failure on the Roaring River were catastrophic. Before the flood, typical dimensions of the Roaring River were 3–5 m wide and 0.3–0.6 m deep, and the channel was filled with numerous large glacial boulders. Following the flood, valley bottoms were severely eroded and rearranged (Fig. 7). Widths varied from 20 to 152 m, and the channel was scoured to ≤15 m locally (Fig. 8). The natural longitudinal profile of the Roaring River is a series of high-gradient reaches separated by low-gradient reaches. Scour occurred along 3,630 m of channel or 56% of the length of the Roaring River; deposition occurred along about 2,835 m in the low-gradient reaches of the valley floor (Fig. 7). The threshold slope separating the scoured reaches from the depositional reaches was about 7–9% (Jarrett and Costa 1986). Layers of sediments deposited in the meadow areas generally were 0.6–2.4 m thick, and local deposit layers were measured to 3 m. Material deposited in each meadow came from the steep, scoured reach immediately upstream. Large boulders or rocks were probably transported no farther than about 300 m, and most probably were moved less than 30 m (Jarrett and Costa 1986).

At the mouth of the Roaring River, a large alluvial fan was deposited on the floor of Horseshoe Park (Figs. 9 and 10). Most sediment was derived just upstream from and in Horseshoe Falls. The fan was mapped from a vertical aerial photograph taken about 4 h after the flood. The area of the fan is 0.175 km^2, and its maximum thickness is 13.4 m in a very small area near the fan apex. Average thickness of the fan is only 1.6 m. The estimated sediment volume of the fan was 278,800 m^3, and the sediment weight was estimated at 753,000 tonnes (Jarrett and Costa 1986).

Fig. 8. Deeply scoured reach in the Roaring River valley downstream from Lawn Lake Dam at river kilometer 0.45. Note that ground moraine was scoured 10.7 m to bedrock. Man (for scale) in *right center* of photo (from Jarrett and Costa 1986).

Fig. 9. The alluvial fan formed at the mouth of the Roaring River. Note the deep scour into the lateral moraine source materials (from Jarrett and Costa 1986).

Characteristics of the surface sediments on the Roaring River alluvial fan changed in a downstream direction. The average diameter of particles changed from 2.3 m (at the fan apex) to 300 mm (midway down the fan) to 0.61 mm (at the toe of the fan overlapping the floodplain of the Fall River; Jarrett and Costa 1986). The single largest boulder known to have been transported onto the surface of the alluvial fan was 4.3 × 5.3 × 6.4 m and weighed an estimated 410 tonnes. The force of the boulder-charged flow battered and destroyed most of the vegetation along the main flow path (Fig. 9). The alluvial fan dammed the Fall River in Horseshoe Park, forming a 0.069 km^2 lake, which is still present (in 1993).

The Fall River reach in Horseshoe Park between the alluvial fan and Cascade Lake is a sinuous meandering stream with a slope of 0.7% (Fig. 2). Lawn Lake floodwaters passed over and across the meanders, but the duration and velocity of the flood were not sufficient to erode or disrupt the channel or floodplain. After the flood passed, much of the floodplain of Horseshoe Park was covered with a thin layer of fine-grained silt and sand.

In the high-gradient reach between Cascade Lake and the Estes Park power plant the average slope is about 8% (Fig. 2). The floodwaters scoured the glacial sediments as much as 10 m. Many trees in the flood path were either broken, undercut and toppled, or severely scarred.

Between the Estes Park power plant and the confluence of the Fall River and the Big Thompson River in Estes Park, the stream slope averages 2.3%. Scour and channel widening were not as pronounced as they were along the steeper parts of the flood path. Scour depths ranged from 0.2 to 0.6 m. Channel

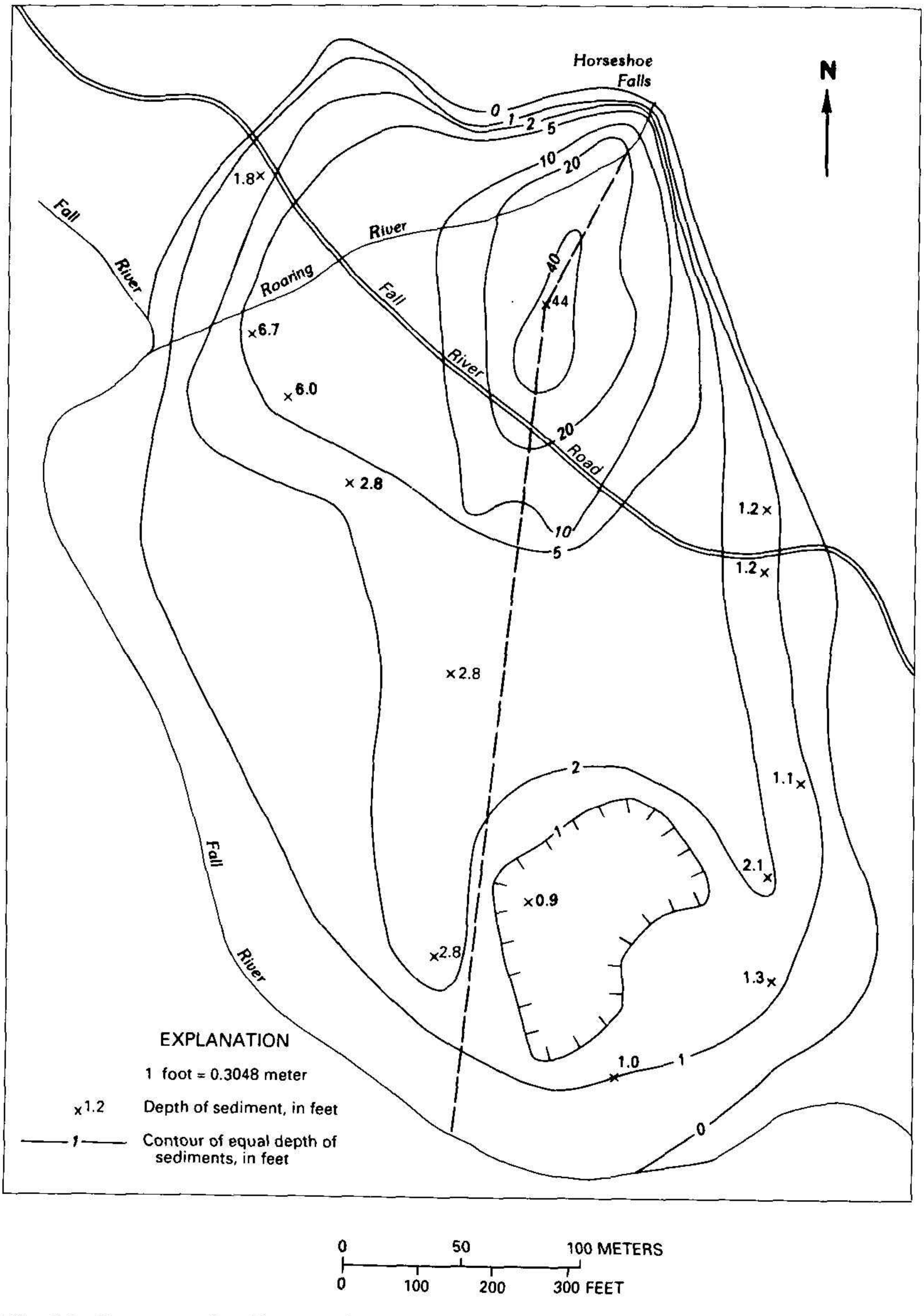


Fig. 10. Contours of sediment thickness in the Roaring River alluvial fan. *Dashed line*: axis of main flow direction (modified from Jarrett and Costa 1986).

deposits were predominantly coarse, bouldery gravel, and sand bars; maximum thickness was about 0.6 m.

No accurate measurements were made of the sediment and debris deposited in Lake Estes by the flood. The U.S. Bureau of Reclamation spent approximately $80,000 for debris and sediment removal following the flood. Before the 1982 flood, sedimentation was not considered a problem in Lake Estes. At least 10 times more sediment was estimated to have been deposited in Lake Estes during the 1983 spring runoff than was deposited by the 1982 flood (Zenas Blevins, U.S. Bureau of Reclamation, 1983, personal communication).

Dam-break Modeling

Hazard mitigation of floods resulting from dam failures requires documenting the processes involved and estimating potential flood discharges, depths, boundaries, and travel times from dam failures. These analyses of dam-break floods are often made using deterministic digital-computer models. Most analyses of dam-break floods have been made on relatively low-gradient rivers. However, because the Lawn Lake Flood occurred on high-gradient rivers (Fig. 2), the flood provided an opportunity to evaluate the applicability of dam-break computer modeling on such rivers. Successfully using such a model enhanced and provided supplemental hydrologic information for evaluating various hypothetical scenarios of dam-breach development and for assessing the effects of the failure of Cascade Lake Dam.

The National Weather Service's dam-break model (Fread 1977), modified by the U.S. Geological Survey (Land 1981), was selected because of its general purpose formulation and its accuracy. The model first computes an outflow breach hydrograph. The floodwave is then routed using hydrologic and hydraulic streamflow routing techniques. The model requires initial boundary conditions, as well as a physical description of the lakes, dams, and the stream-channel reach. For this study, these data were available for calibrating the model to evaluate its applicability to high-gradient rivers. Data for the model included the dam's storage capacity, the water surface elevation for each lake and for each cross section, the channel geometry, and the flow-resistance coefficient estimates for 15 cross sections (Jarrett and Costa 1986).

A trapezoidal breach function (an overtopping failure) was assumed to adequately model the rapidly developed piping failure. The duration of breach development, based on available data, was 10 min for Lawn Lake Dam and 1 min for Cascade Lake Dam (Jarrett and Costa 1986). Model calibration was made to obtain the best fit, based on indirectly measured peak discharges, flood depths, and travel times (Jarrett and Costa 1986). Parameters used for calibration in the model were Manning's roughness coefficient (*n*-values) and flow expansion and contraction coefficients. To calibrate the model, Manning's *n*-values between 0.1 and 0.2, which averaged 78% greater than on-site-selected *n*-values, were required. Subcritical flow predominated based on analysis of observed data; locally short reaches of supercritical flow occurred. These large flow resistance coefficients are supported by Trieste and Jarrett (1987).

Results indicated that the model had the potential to simulate dam-break floods in high-gradient rivers. The range in difference of observed and modeled peak discharges varied from −910 to 17 m^3/s. At worst, the model underpredicted peak discharge by 27% (5.8 km downstream from Cascade Lake Dam, site 3). The range in difference of observed and modeled maximum flood depth was –0.4 to 0.8 m; the average was 0.3 m. The range of difference of observed and modeled travel time was –0.4 to 0.05 h. Considering the complexity of modeling high-gradient rivers, the model reasonably simulated this dam-break flood and could be used to provide supplemental hydrologic information that could not be obtained otherwise. However, we emphasize that model results would have been substantially different without extensive model calibration with observed features of the dam-break flood.

Selected hypothetical scenarios of dam-breach development and probable effects of the failure of Cascade Lake Dam were made. Analyses of possible scenarios were made to estimate the range in possible flood conditions resulting from the failure of Lawn Lake Dam. Greater widths of breach development occurring over short intervals result in larger peak discharges. Comparisons were made for hypothetical breach widths of 7.6 m and 61 m, which were compared with model results of the actual breach width of 16.8 m. For a breach width of 7.6 m, the peak discharge would have been 198 m^3/s less downstream from Lawn Lake Dam to 37 m^3/s less entering Lake Estes. Maximum flood depths averaged 0.3 m lower, and the floodwave would have reached Estes Park at the same time. For this hypothetical case, Cascade Lake Dam still would have failed. For a breach width of 61 m, peak discharge would have been 640 m^3/s greater downstream from Lawn Lake Dam to 153 m^3/s greater entering Lake Estes. Maximum flood depth averaged 0.8 m higher, and the floodwave would have reached Estes Park 0.4 h earlier. The model outflow peak discharge from a worst-case failure of Lawn Lake Dam could have been at least 1,590 m^3/s.

The failure of Cascade Lake Dam probably doubled the peak discharge immediately downstream from the dam and increased the flood stage by an average of 0.2 m. If Cascade Lake Dam had not failed (or had not been present), peak discharge would have been 320 m^3/s less (immediately downstream from the dam) to 14 m^3/s less (entering Lake Estes). Maximum flood depths would have averaged 0.2 m lower, and the flood wave would have reached Lake Estes 0.3 h later.

Flood Aftermath

Since 1890, 130 known dam failures have occurred in Colorado (Colorado Water Conservation Board 1983). Floods from these failures have resulted in low loss of life but high loss of property. Effects from the Lawn Lake and Cascade Lake dam failures were severe, although the flooding only lasted a few hours. Surprisingly few fatalities occurred because of several positive factors related to the flood warning: only 25–30 campers were along the Roaring River, and probably fewer than 20 people were in Horseshoe Park. About 275 people were camping in Aspenglen Campground downstream from Cascade Lake Dam. The Estes Park chief of police estimated that 4,000 to 5,000 residents and tourists were in the floodplain from Cascade Lake to Estes Park.

Three people were killed; all three victims, whose ages ranged from 21 to 36 years, lived outside of Colorado. One victim, while sleeping at a Roaring River campsite, did not survive the "wall of water" and debris. After Cascade Lake Dam failed, two campers who had returned to their campsite in Aspenglen Campground a short distance downstream from the dam were swept to their deaths. The two campers died from flooding, although they had been warned of an approaching flood (but not a dam-failure flood) by fellow campers and park rangers. Apparently these two campers misjudged the magnitude of the flood when they walked back through floodwaters to retrieve camping gear.

Several factors kept the number of fatalities low. The time of day, as well as clear and dry weather, were nearly optimal. Had the dam failed at night, the flood might have gone unnoticed longer and the public would not have had as much time to respond. Once the flood had been detected at Horseshoe Falls, a rapid dissemination of warnings was made within minutes by the National Park Service, the Larimer County sheriff, the Estes Park police, and KSIR radio. The warning also spread rapidly because of the clustering of motels, businesses, and homes. The majority of the public responded quickly to the flood warning. This response was probably due to the public's previous experience with the 1976 Big Thompson River flash flood, which killed 139

Fig. 11. Aerial view of Elkhorn Avenue, Estes Park, looking downstream from river kilometer 19.3. Big Thompson River is in the *top right*-hand corner. Photo courtesy of Zenas Blevins, U.S. Bureau of Reclamation (from Jarrett and Costa 1986).

people, and because of flood warning signs placed along river canyons in Colorado after the 1976 flood (Jarrett and Costa 1986). Also, the floodwave traveled relatively slowly and was attenuated as it passed through Horseshoe Park.

The Colorado Division of Disaster Emergency Services estimated damages to be approximately $31 million. The damage estimate included public and private losses to structures, cleanup of debris, loss of stored irrigation water at Lawn Lake, and consequent agricultural losses and economic losses for businesses in the Estes Park area. The flooding destroyed 18 bridges, damaged road systems, inundated 177 businesses (75% of Estes Park's commercial activity), and damaged 108 private residences (Fig. 11).

Literature Cited

Colorado Water Colorado Conservation Board. 1983. Flood hazard mitigation plan for Colorado. Department of Natural Resources, Denver. 135 pp.

Fread, D. L. 1977. The development and testing of a dam-break flood forecasting model. Pages 164–197 *in* Dam-break flood routing model workshop proceedings. U.S. Water Resources Council, Task Force on Dam-break Flood Routing. Bethesda, Md.

Graham, W. J., and C. A. Brown. 1983. Dam failure warnings evaluated. Page 3 *in* Natural hazards observer. Natural Hazards Research and Applications Information Center Newsletter 7:4. University of Colorado, Boulder.

Jarrett, R. D. 1985. Determination of roughness coefficients for streams in Colorado. U.S. Geological Survey WRIR 85-4004. 54 pp.

Jarrett, R. D., and J. E. Costa. 1986. Hydrology, geomorphology, and dam-break modeling of the July 15, 1982 Lawn Lake Dam and Cascade Lake Dam failures, Larimer County, Colorado. U.S. Geological Survey Professional Paper 1369. 78 pp.

Jarrett, R. D., and J. E. Costa. 1988. Evaluation of the flood hydrology in the Colorado Front Range using precipitation, streamflow, and paleoflood data for the Big Thompson River basin. U.S. Geological Survey WRIR 87-4117. 37 pp.

Jones, W. D., and L. O. Quam. 1944. Glacial landforms in Rocky Mountain National Park. Colorado Journal of Geology 52:217–234.

Land, L. F. 1981. Computer program documentation user's manual—general purpose dam-break flood simulation model (K–634). U.S. Geological Survey WRIR 80-1160. 101 pp.

Office of the State Engineer. 1983. An investigation of the failure of the Lawn Lake Dam, Larimer County, Colorado. 31 pp.

Peterman, Z. E., C. E. Hedge, and W. A. Braddock. 1967. Age of Precambrian events in the northeastern Front Range, Colorado. Journal of Geophysical Research 73(6):2277–2296.

Richmond, G. M. 1960. Glaciation of the east slope of Rocky Mountain National Park, Colorado. Geological Society of America Bulletin 71:1371–1382.

Trieste, D. J., and R. D. Jarrett. 1987. Roughness coefficients of large floods. Pages 32–40 *in* L. G. James and M. J. English, editors. Proceedings of the irrigation systems for the 21st century. Irrigation and Drainage Division Specialty Conference, American Society of Civil Engineers, New York.

Geomorphic Response of the Fall River, Rocky Mountain National Park, Colorado

John Pitlick[1]

Colorado State University
Department of Earth Resources
Fort Collins, Colorado 80523

Abstract. This paper presents the results of an extensive 5-year field study of the geomorphic response of the Fall River following the Lawn Lake Flood in 1982. The flood resulted in changes to the channel geometry, bed material texture, and sediment load of the Fall River. In places, these changes were relatively short-lived, considering the magnitude of the flood. The most significant adjustments of the Roaring River and the Fall River came in the first 2 years following the flood. In this time, the Roaring River and the unconsolidated deposits of the alluvial fan contributed approximately 22,000 metric tons of sediment, increasing the sediment load of the Fall River by a factor of 250 or more. Much of this sediment was transported to the downstream area of Horseshoe Park and deposited as a continuous 2,000-m-long sedimentation zone. Sediment yields of the Roaring River and the alluvial fan decreased dramatically beginning in 1985 and approached background levels when the study ended in 1987. The reduction in sediment yield caused erosion in upstream parts of the sedimentation zone, and the pre-1983 channel was restored by the end of the 1984 runoff. Recovery took longer in distal reaches of the sedimentation zone because transport rates through the downstream portion of Horseshoe Park were lower than in upstream reaches. As of 1987, about 75% of the material initially stored in the sedimentation zone had been eroded. Throughout the study, sediment loads in lower Horseshoe Park were probably several orders of magnitude higher than natural levels and showed little in the way of a declining trend.

Introduction

The Lawn Lake Flood attained peak discharges 2 to 30 times larger than the 500-year flood (Jarrett and Costa 1986), which was far outside the realm of natural events. Therefore, from a hydrologic or geomorphic standpoint, the Lawn Lake Flood is difficult to put into a proper perspective. As an alternative to the conventional socioeconomic and engineering estimates of flood damage

---

[1] Present address: University of Colorado, Department of Geography, Boulder, Colo. 80309.

and return period, the long-term significance of a catastrophe can be assessed by follow-up studies of geomorphic recovery (Wolman and Gerson 1978). Geomorphic recovery provides a context for landscape disturbances—whether caused by floods, landslides, volcanic eruptions, or human activity—in terms of the time required to restore the previous condition. For example, a flood may widen a river by bank erosion; in succeeding years, sediment may be deposited along the banks, gradually reducing its width to the point where the preflood configuration is restored. The recovery process may occur over years, decades, or centuries and, as Wolman and Gerson (1978) suggested, this length of time provides one measure of the importance of the initial perturbation. From a geomorphic standpoint, this view of catastrophes offers more insight into the evolution of landforms than that gained solely from a probabilistic analysis of hydrologic events.

Recovery in fluvial systems has been previously represented by changes in river planform and riparian vegetation (Schumm and Lichty 1963; Burkham 1972; Osterkamp and Costa 1987), hydraulic geometry (Lisle 1982), cross-section form (Costa 1974; Kelsey 1980), sediment storage (Kelsey 1980; Madej 1984; Pitlick 1992), and sediment transport (Newson 1980). Coupling the changes in process rates with the adjustment of landforms is not easily accomplished on a large scale or over a long time, and therefore the studies mentioned have necessarily focused on a single or a few aspects of geomorphic recovery.

The accessibility and scale of the Horseshoe Park setting have made it possible to overcome the drawbacks encountered in previous studies and to reliably document all aspects of the recovery processes. This paper presents results from a 5-year study of changes in channel morphology, bed material composition, and sediment transport on the reach of the Fall River within Horseshoe Park (Fig. 1). The changes observed on this meandering, gravel-bed river were pronounced, and the fact that a wide spectrum of channel pro-

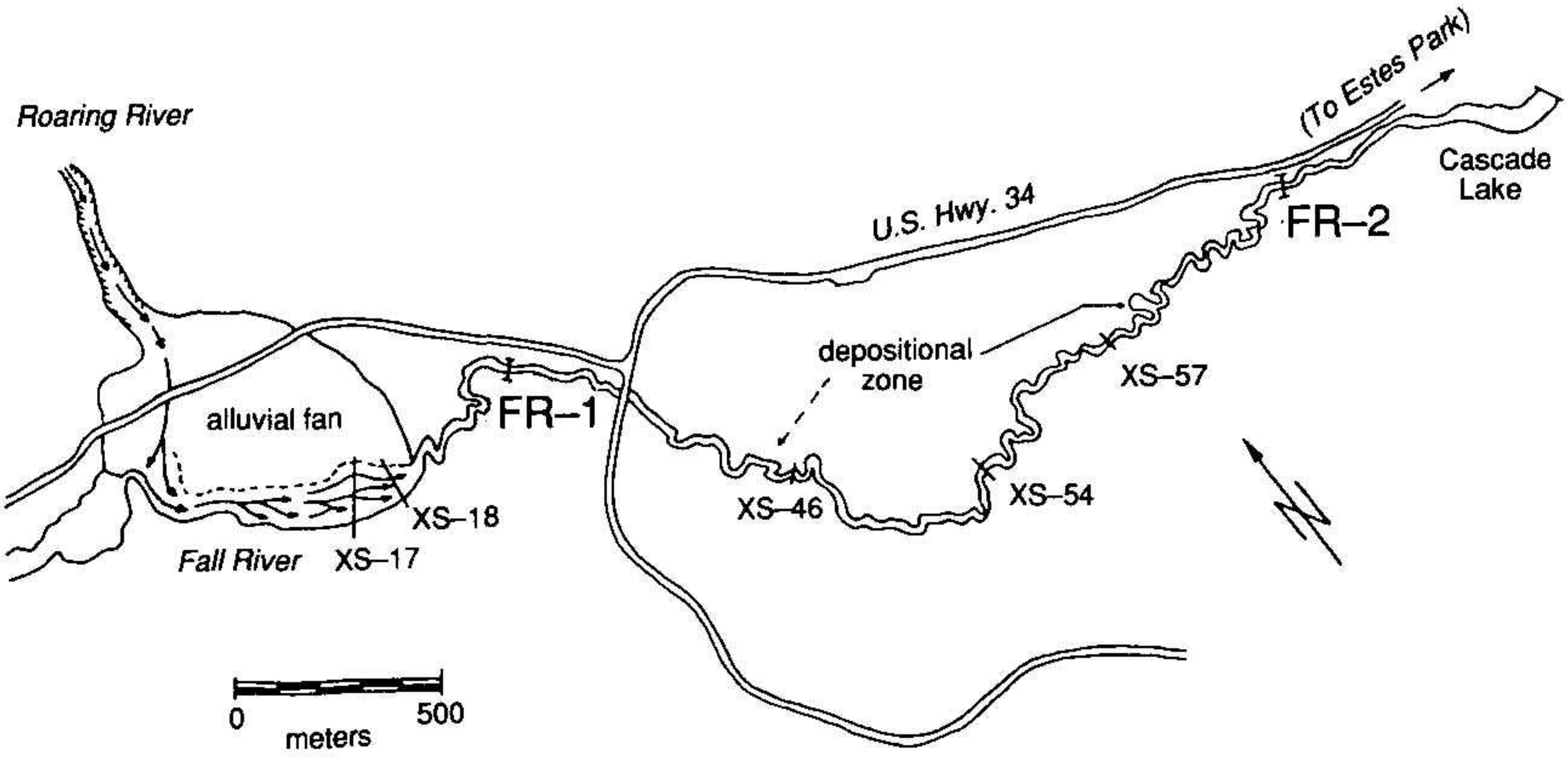


Fig. 1. Horseshoe Park study area and selected sites.

cesses are expressed over less than 5 km makes this study broadly applicable to other disturbed fluvial systems.

Study Area and Methods

The physiographic characteristics of the Roaring River and the Fall River drainages and details of the Lawn Lake Flood are described elsewhere (Summer 1992; Jarrett and Costa 1992) . The important aspects of this setting and the events of the flood as they pertain to the present study can be summarized as follows: Before the Lawn Lake Flood, the Roaring River and the Fall River were typical of alpine–subalpine streams in the Colorado Front Range in that they likely carried little sediment and their channels were stable (Caine 1986). However, the Lawn Lake Flood radically altered this condition by causing extensive erosion and sedimentation along the Roaring River valley. On the steeper reaches of the Roaring River, the flood incised a deep channel into the glacial deposits mantling the valley floor. Sediment was deposited in the lower gradient reaches as a series of discontinuous terraces and fans, the most spectacular of which is located at the mouth of the Roaring River (Fig. 1). These unstable stream banks, terraces, and fans provided a voluminous source of sediment for transport by the Fall River in the years after the Lawn Lake Flood.

As the flood passed through Horseshoe Park, it spread out over the valley floor where its velocity was greatly reduced. The average gradient through Horseshoe Park is about 0.003, and because the floodwaters inundated the valley over a width of several hundred meters (Jarrett and Costa 1986), the flow did not develop sufficient power to erode the coarse bed material and heavily vegetated banks of the Fall River. The sinuous 4-km reach of the Fall River between the Roaring River alluvial fan and Cascade Lake (Fig. 1) was left intact when the floodwaters receded (Jarrett and Costa 1986). Finally, because the Lawn Lake Flood occurred well after the peak snowmelt of 1982, there were few modifications to the Fall River in Horseshoe Park until the next spring, when the 1983 snowmelt runoff season began. Therefore, the changes that have been observed during the past 5 years can be related to a well-defined baseline.

Geomorphic studies in Horseshoe Park were initiated in March 1983 and continued through July 1987. Channel changes on the Fall River were monitored with aerial and ground photographs, surveys of cross sections, and extensive water discharge and sediment load measurements. More than 80 cross sections were established between the mouth of the Roaring River and Cascade Lake (Fig. 1) to monitor changes in channel geometry. Most of these cross sections were established in the first 2 years of the study and were surveyed annually thereafter. Selected cross sections were used to monitor changes in bed material texture. A continuously operating water-stage recorder was installed on the U.S. Highway 34 bridge where it crosses the Fall River (Fig. 1).

The data from this site were used with data from the U.S. Bureau of Reclamation gaging station (10 km downstream) to synthesize a hydrologic record for the Fall River. Instantaneous water and sediment discharge measurements were made throughout the snowmelt at several sites within Horseshoe Park. The most complete data came from a site located 400 m downstream from the alluvial fan terminus (FR-1 in Fig. 1) and another site at the downstream end of Horseshoe Park (FR-2 in Fig. 1). Suspended load was measured with a depth-integrating sampler; bed load was measured with a portable bed load (Helley-Smith) sampler capable of measuring sediment up to 7.6 cm in diameter. In the 5 years of observation, more than 500 bed load samples were collected in the Horseshoe Park study area. These data and the results of related studies were presented elsewhere (Pitlick 1985; Thorne et al. 1985; Pitlick and Harvey 1986, 1987; Pitlick et al. 1987; Pitlick and Thorne 1987; Pitlick 1988a, 1988b).

Hydrology

The Fall River and the Roaring River drainage basins receive between 500 and 1,000 mm of precipitation annually (Jarrett and Costa 1986). Most of this precipitation falls as snow between October and May. The bulk of runoff in these basins is generated from melting winter snowpack, beginning in mid-May and peaking usually in early to mid-June. As is characteristic of most alpine streams in the Colorado Front Range, peak flows on the Fall River are not highly variable and would rarely exceed the mean of the annual flood series by more than a factor of 2 (Pitlick 1988b).

Geomorphic adjustments of the Fall River need to be placed within the context of hydrologic events that have occurred since the Lawn Lake Flood. During the 5-year study, the Fall River experienced a typical range in snowmelt-generated flows: runoff volumes were about equal to the long-term average in 3 of the 5 years—well above average in 1983, and well below average in 1987 (Table). The highest flows recorded within the 5-year study took place in 1983, the year after the Lawn Lake Flood. Many of the geomorphic changes that occurred on the Fall River since the Lawn Lake Flood can be attributed to

Table. *Summary of hydrologic data for the Fall River in Horseshoe Park.*

	1983	1984	1985	1986	1987
Instantaneous peak discharge (m^3/s)	11.9 (8)[a]	10.2 (12)	11.1 (10)	9.7 (16)	7.5 (29)
Highest 1-day mean discharge (m^3/s)	10.7 (6)	8.3 (17)	9.1 (12)	8.5 (13)	6.1 (29)
Highest 30-day mean discharge (m^3/s)	8.3 (1)	5.0 (21)	4.6 (28)	6.7 (8)	3.3 (32)
Days 1.5-year flood (8.2 m^3/s) exceeded	17	1	2	5	0

[a] Numbers in parentheses represent the rank of the flow within the synthetic 40-year record.

the high flows and high sediment transport rates that persisted for nearly a month during the 1983 snowmelt runoff.

Sediment Transport and Changes in Channel Morphology

Horseshoe Park—Upstream of U.S. Highway 34

In Horseshoe Park, the Lawn Lake Flood caused the most dramatic changes where it deposited the alluvial fan at the mouth of the Roaring River (Fig. 1). The former channels of the Fall and Roaring rivers were buried by 280,000 m^3 of poorly sorted sediment more than 14 m deep in places (Jarrett and Costa 1986). The sediment composing the alluvial fan was deposited in a series of avulsive sheetflood events (Blair 1987) that left the fan as an irregular surface drained by a network of poorly integrated distributary channels. Since the Lawn Lake Flood, the Roaring River and the Fall River have begun to reestablish stable channels within this debris.

Initially, the deposits of the Roaring River alluvial fan were poorly sorted, and the distributary channels on the fan were undersized. As the 1983 snowmelt ensued, these channels enlarged by bank erosion and scour. Episodic influxes of sediment from the Roaring River frequently caused the distributary channels to become unstable, shift their positions, and carve new courses across the fan surface. The unconsolidated flood deposits were continually reworked as a result of these avulsions, and the sand-sized fraction of the fan sediment was transported rapidly downstream.

Bed load sediment yields at the gaging station downstream of the alluvial fan (FR-1 in Fig. 1) reached a maximum of 750,000 kg/day during the mid-June peak of the 1983 snowmelt (Fig. 2). The total bed load sediment yield for June and July 1983 was approximately 15.5×10^6 kg and was more than the combined yield of all subsequent years. Surveys of cross sections on the alluvial fan indicated that only about 20% of the sediment transported past FR-1 in 1983 could be accounted for by erosion of the fan itself, so the balance was presumably derived from the upper reaches of the Roaring River (Pitlick 1985).

In the years that followed, failures of the steep banks along the Roaring River were less frequent, and the distal reaches of the alluvial fan became the sole source of sediment for the Fall River. Beginning in 1984, sediment loads at the FR-1 gage dropped sharply and continued to drop through the end of the study (Fig. 2). This decline was in direct response to increased stability on the Roaring River and the alluvial fan and seems to have been independent of hydrologic trends, because in several years—particularly 1986—snowmelt flows were well above average (Table), yet sediment loads continued to decrease. As of late June 1987, when the last bed load measurements were made, the Fall River was carrying only about 3,000 kg of sediment per day at the FR-1 site. On the basis of these data, to say that the Lawn Lake Flood increased the sediment

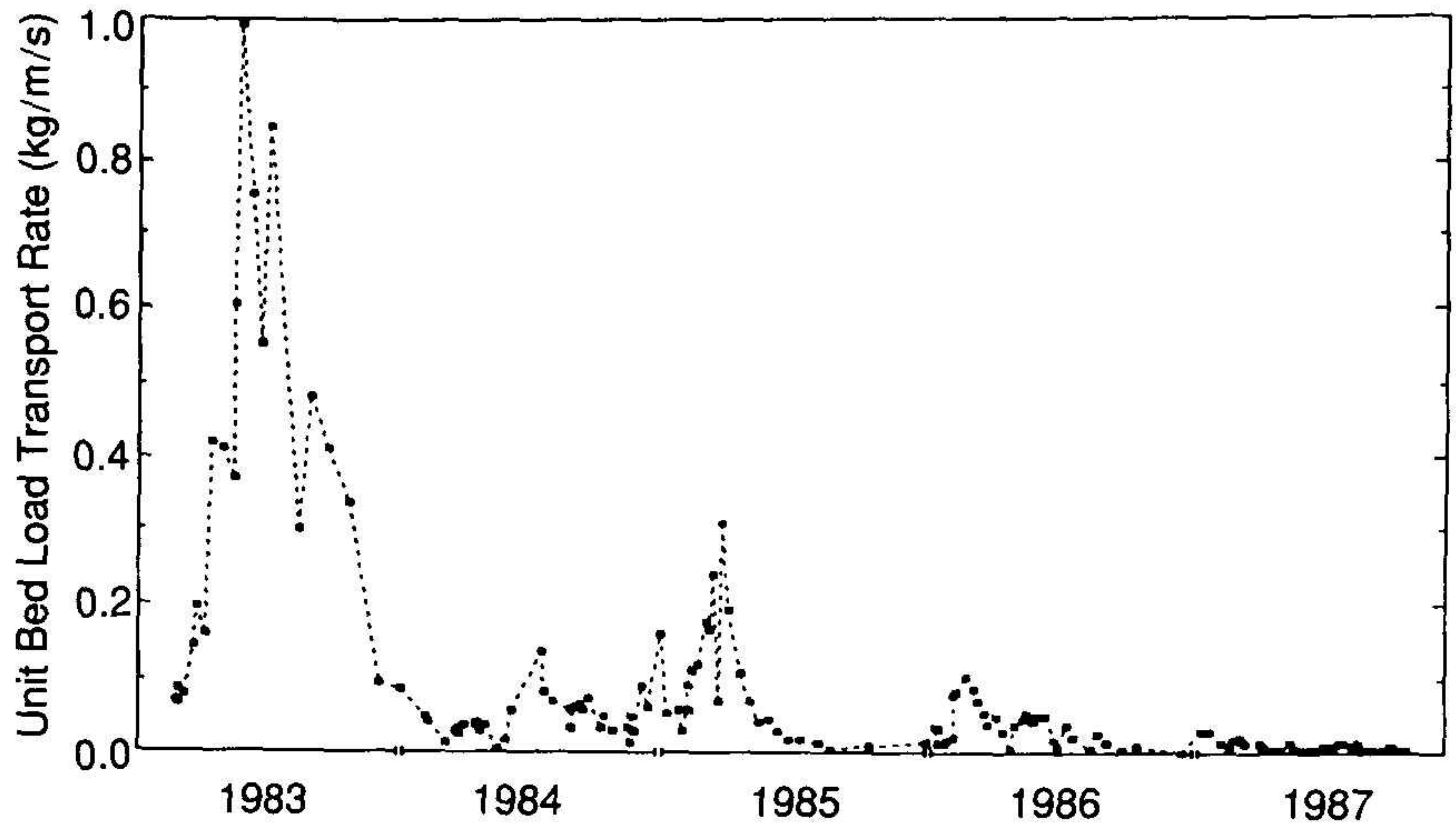


Fig. 2. Trends in bed load transport since the Lawn Lake Flood at the upstream measurement site, FR-1. Note that sediment loads declined rapidly at the FR-1 site as the Roaring River and the alluvial fan stabilized.

load of the Fall River by at least a factor of 250 would be conservative.

The sedimentary texture of the bed load at FR-1 reflected the changes in erosional activity on the Roaring River and the alluvial fan. At the peak of the 1983 snowmelt, the bed load sediment at FR-1 had a sandy texture similar to the deposits composing the distal fan surface and much finer than the gravelly preflood bed material (Fig. 3a). Over time, channels on the alluvial fan developed an armor—a layer of sediment on the channel bed that was coarser than the underlying material. Samples of the bed material at a cross section near the terminus of the alluvial fan (XS-18 in Fig. 1) show the difference in size between the surface and subsurface bed materials (curves 3 and 1 in Fig. 3b). As of 1985, the armor layer had developed a gravelly texture similar to that of the preflood bed material (compare curve 3 in Fig. 3a with curve 3 in Fig. 3b). Also, note the similarity between the texture of the bed load at this time and the texture of the subsurface bed material at XS-18 (curves 1 and 2 in Fig. 3b).

The similarity in these grain size distributions shows that in recent years, the Fall River has derived its sediment load primarily from the material stored beneath the armor layer. Under low and moderate flow conditions, most of the armor layer remains intact, protecting the underlying finer-grained sediment from erosion and transport by the Fall River. But as is typical of many gravel-bed streams, the armor layer in the Fall River becomes active at higher flows, and nearly all sizes of the subsurface bed material can then be found in transport (Parker et al. 1982; Andrews 1983). At high flow the texture of the bed load at FR-1 is nearly the same as the subsurface bed material on the alluvial fan.

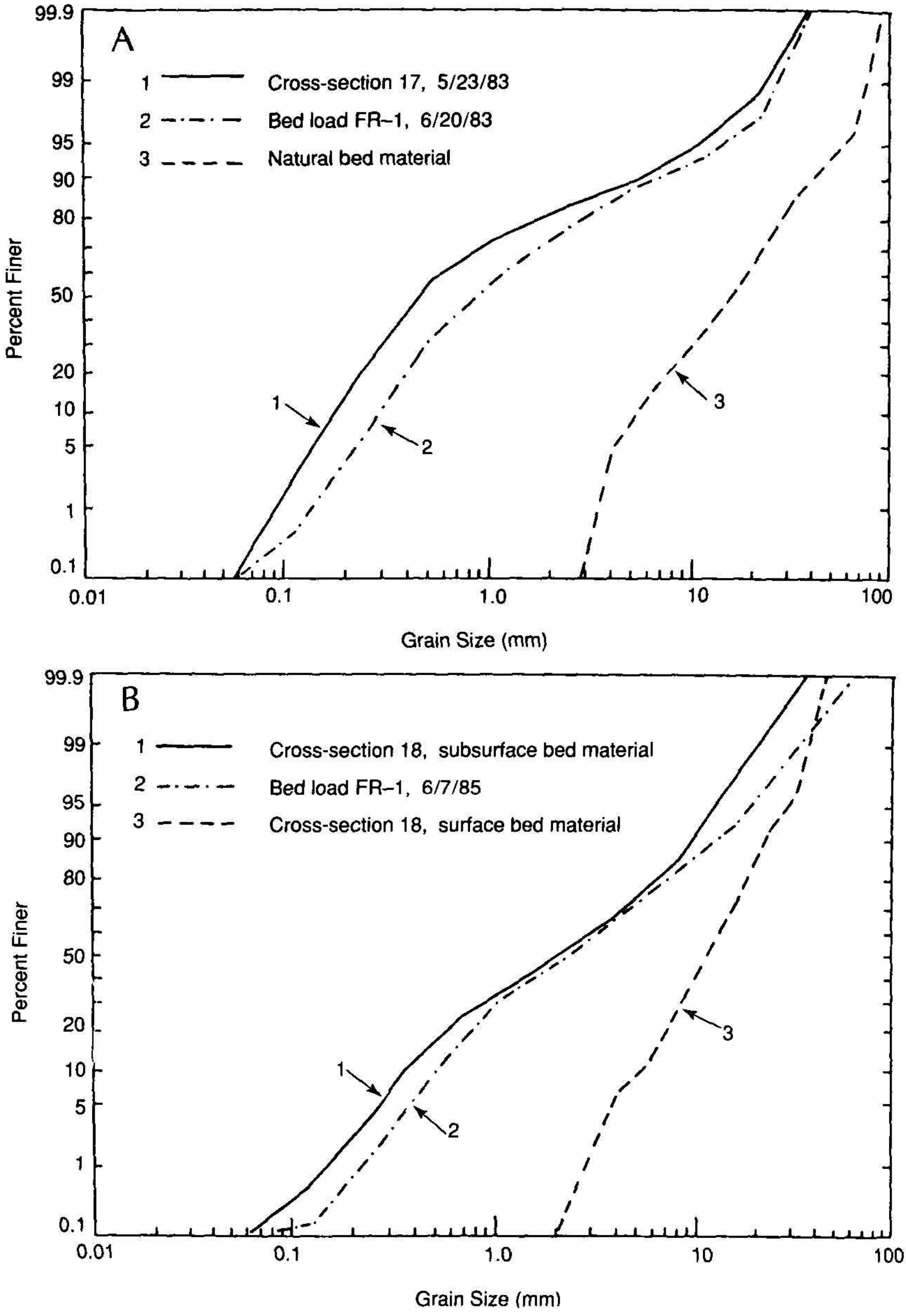


Fig. 3. (A) Grain size distributions for (1) distal alluvial fan sediment, (2) bed load at the FR-1 gaging station at the peak of the 1983 snowmelt, and (3) preflood bed material (data from M. P. Mosely, written communication); (B) grain size distributions for (1) subsurface bed material, (2) bed load at the FR-1 gaging station in June 1985, and (3) armor layer or surface bed material of the Fall River.

Horseshoe Park—Downstream of U.S. Highway 34

The most significant postflood geomorphic changes in Horseshoe Park occurred on the reach of the Fall River between the U.S. Highway 34 bridge and Cascade Lake (Fig. 1). During the 1983 snowmelt, sediment that eroded from the alluvial fan moved rapidly downstream. However, bed load transport could not be maintained through the sinuous reaches of the Fall River, and the channel began to aggrade. By August 1983, the channel had filled to the level of the floodplain, forming a discrete zone of deposition extending from approximately the Highway 34 bridge to a point 2,000 m downstream, where it terminated abruptly (Fig. 1). Aggradation produced a quasi-braided pattern, with much of the flow going overbank in a network of anabranch channels.

Changes in channel geometry at a cross section in the upstream part of the depositional zone illustrate how the Fall River was modified during this period (Fig. 4). This reach of the Fall River was not significantly affected by the Lawn Lake Flood. When this cross section was initially surveyed in June 1983 (survey of 7 June 1983; Fig. 4a), the channel existed in essentially the same condition as before the Lawn Lake Flood. However, as the 1983 snowmelt runoff ensued and sediment loads to this reach increased, the channel began to aggrade. By the end of the 1983 snowmelt, the channel had filled to the level of the floodplain (survey of 20 July 1983; Fig. 4a), burying the former bed of the Fall River under about 1.0 m of sand-sized sediment.

As the Roaring River and the alluvial fan became more stable, the amount of sediment entering this reach fell below what the Fall River could carry. To satisfy this transport capacity, sediment was progressively eroded from the depositional zone, starting first at the upstream end and proceeding at ever-decreasing rates downstream. Upstream parts of the depositional zone degraded rapidly because sediment there ($D_{50} = 2.0$ mm) was mobile about 50% of the time. By the end of the 1984 snowmelt, cross-section 46 had been restored to virtually the same configuration as when it was first surveyed in June 1983 (Fig. 4a).

Cross sections within the downstream part of the depositional zone were not surveyed as part of this study until 1984, when the channel had already aggraded. However, the configuration of the channel before 1983 could be inferred from cross-section surveys conducted soon after the Lawn Lake Flood (Jarrett and Costa 1986). In the vicinity of where the depositional zone formed, these surveys show that the bed of the Fall River was from 1 to 1.5 m below the level of the floodplain (cross-section 54 in Fig. 4b). Degradation at cross-section 54 began in 1985 and continued slowly thereafter (Fig. 4b).

Recovery of the pre-1983 channel configuration in the downstream reaches of the depositional zone has been slower when compared with the upstream reaches because the gradient decreases downstream and therefore so do the sediment transport rates—also, erosion from the upstream reaches has continued to supply sediment, thus satisfying the transport capacity of the lower reaches. Until these reaches become supply-limited, degradation cannot occur.

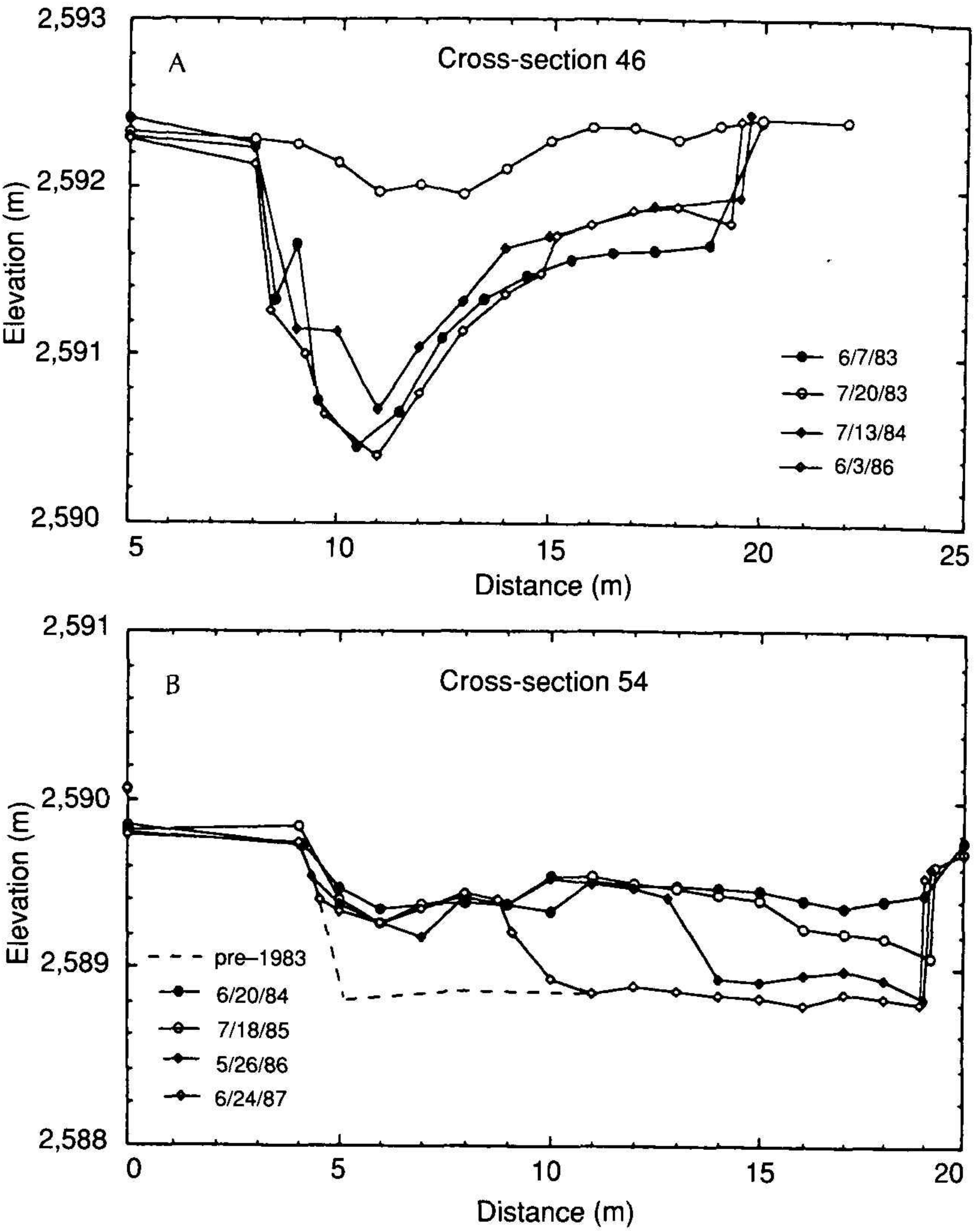


Fig. 4. The Fall River cross sections in (A) the upstream and (B) the middle of the sediment depositional zone. Note that cross-section 46 degraded rapidly while cross-section 54 degraded more slowly.

Sequential changes in bed elevation in the proximal, medial, and distal parts of the depositional zone show how degradation rates have varied (Fig. 5). In the proximal part of the depositional zone, the preaggradation bed elevation was recovered in about 1 year, and little change in bed elevation was observed thereafter (Fig. 5a). In the medial reaches of the depositional zone, recovery has proceeded more slowly, and after 4 years, changes in average bed elevation seem to be approaching an asymptote (Fig. 5b). The recovery of bed elevations is proceeding at yet slower rates in the distal reaches of the deposi-

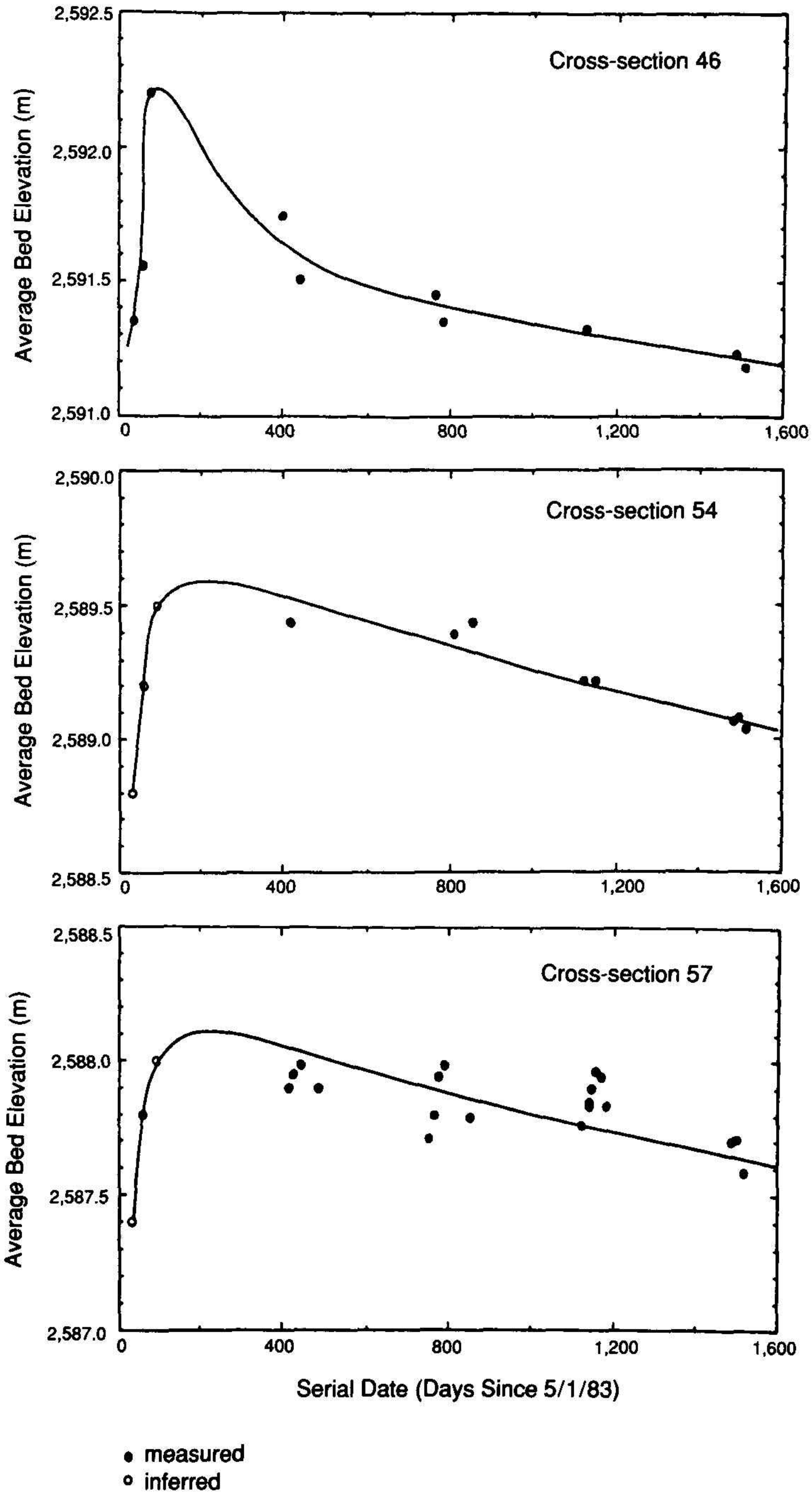


Fig. 5. Changes in bed elevation through time at selected cross sections in the upstream (A), middle (B), and downstream (C) parts of the sediment depositional zone.

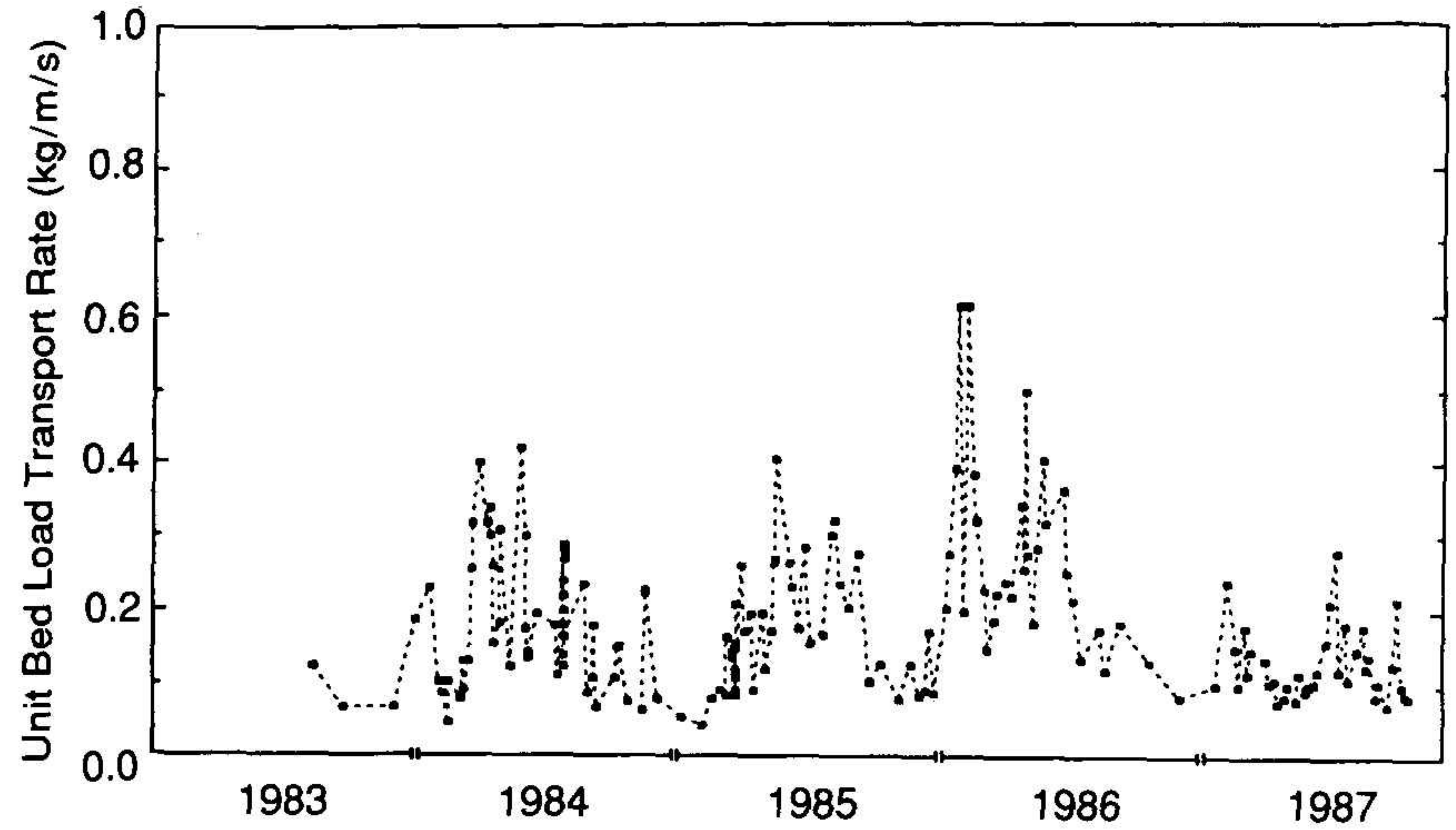


Fig. 6. Trends in bed load transport in the years since the Lawn Lake Flood at the downstream measurement site, FR-2. Note that sediment loads at the FR-2 site have remained high since the Lawn Lake Flood because of continued sediment supply from the depositional zone upstream.

tional zone (Fig. 5c), and full recovery of pre-1983 bed elevations may not occur for a few more years.

Bed load measurements from the downstream sediment sampling station (FR-2 in Fig. 1) follow a trend that is consistent with the channel changes described previously (Fig. 6). Throughout the study, bed load transport rates at FR-2 have only been about half the rates at FR-1 because the channel slope is lower at the downstream gage. The source of the bed load at FR-2 is, of course, the depositional zone, which terminates about 1,000 m upstream of the site. Sediment from the depositional zone is being eroded progressively as described earlier, but as the sediment enters the sinuous reaches in lower Horseshoe Park, its rate of transport decreases. As a result, bed load measurements at the FR-2 gage, although highly variable, indicate little in the way of recovery (Fig. 6). The sediment load of the Fall River, as it leaves Horseshoe Park, will likely remain high for a few more years until the sediment in the depositional zone is exhausted. The contrast between bed load transport at this site and at the site upstream (Fig. 2) is clear, illustrating further how geomorphic processes may be temporally disjointed over relatively short distances.

Summary and Discussion

Since the Lawn Lake Flood of 15 July 1982, the geomorphic response of the Fall River has been manifested by changes in channel geometry, bed material composition, and sediment load. Although the direct effects of the flood were most pronounced in the area of the Roaring River alluvial fan, significant postflood geomorphic changes took place on the undisturbed reaches of the Fall River downstream. On the basis of 5 years of geomorphic study in the Horseshoe Park area, these changes are summarized below.

In the first 2 years after the Lawn Lake Flood, approximately 22,000 metric tons of sediment were delivered to the Fall River from the Roaring River and the alluvial fan. Much of this sediment was deposited in a 2,000-m-long segment of the Fall River downstream of the U.S. Highway 34 bridge. However, by 1985, the erodible banks of the Roaring River had stabilized, and the finer sediment was exhausted from the alluvial fan surface, so sediment loads in the upstream reaches of the Fall River declined dramatically. As of 1987 (when this study ended), the Fall River was carrying very little sediment off the alluvial fan. Barring a catastrophic failure of the steep gully walls of the Roaring River, sediment loads in the upper reaches of the Fall River will likely continue to decline in the future.

The 2,000-m-long depositional zone in lower Horseshoe Park was the primary source of sediment leaving Rocky Mountain National Park from 1984 to 1987. Sediment erosion occurred at diminishing rates from the upstream to the downstream ends of this zone. As of 1987, about 75% of the material had been eroded from the depositional zone. Following the Lawn Lake Flood, sediment loads in lower Horseshoe Park were probably several orders of magnitude higher than natural levels. High sediment loads in this segment of the Fall River will likely persist for a few more years until all the sediment in the depositional zone is exhausted.

The results of this study are broadly applicable to other river systems that have experienced catastrophic floods. The events that followed the Lawn Lake Flood illustrate how secondary effects from a catastrophe may be equally significant to those of the initial perturbation. Although the direct effects of the flood were significant on the Roaring River, the flood gave rise to conditions that led to greater geomorphic change by more commonplace hydrologic events. These changes occurred in the lower reaches of Horseshoe Park where rapid sedimentation in the year following the flood transformed the Fall River from a meandering to a braided stream.

At no time were the Roaring River and the Fall River in the same phase of adjustment, and this study showed how the effects of a single event may be propagated through a river system at variable rates over relatively short distances. The recovery of cross-section shape and channel planform was shown to be proceeding at an ever-decreasing rate from the upstream to the downstream end of this sediment depositional zone. Downstream progressive trends of channel recovery seem to be common in rivers subjected to large and sudden sediment inputs. Similar trends have been reported for rivers in northwestern California (Kelsey 1980; Madej 1984), rivers draining Mount St. Helens (Paine 1984), and large, braided rivers in New Zealand (Griffiths 1979; Beschta 1983) and New Guinea (Pickup et al. 1983).

This study documents the fluvial response to a disturbance in an otherwise stable montane setting. That the sediment loads of the Roaring River and the Fall River are nearing background levels within 5 years of this flood points to the stability of the alpine–subalpine environment. Rapid declines in sediment yield have been reported in other studies of geomorphic recovery in highly disturbed, mountainous terrain (Newson 1980; Collins and Dunne 1986; Pitlick 1992). Also, like the Roaring and Fall rivers, the landscape elements examined in these other studies were located within what might be termed the proximal zone of the fluvial system (Schumm 1977), where the available stream energy was high and the return to stable conditions was enhanced by the fact that sediment was mobile over a wide range of flows. Therefore, although headwater streams may be sensitive to large perturbations (Wolman and Gerson 1978), they may also have the capacity to recover their pre-event condition rapidly if the easily transported sediment can be exhausted.

In formulating their hypothesis of recovery, Wolman and Gerson (1978) also suggested that large rivers would recover from floods faster than small headwater streams. The basis for this suggestion was that as basin scale increases, the frequency of flows that transport sediment and remold the channel also increases. This hypothesis is contradicted by the results presented here. In the Fall River, recovery rates decreased downstream due to the continued influx of sediment from upstream. Wolman and Gerson considered only the changes brought about directly by a flood and not those due to secondary effects as noted previously. To be complete, the recovery concept must consider how large sediment inputs are propagated through the river system. The rate these effects are propagated depends on (1) the magnitude of the initial perturbation, (2) the rate of sediment supply from upstream, and (3) the frequency of flows that are capable of moving sediment in later years. Recovery may be rapid over several years in the proximal reaches of a river inundated with fine-grained sediment that is mobile over a wide range of discharges, but much slower over several decades in the distal reaches of a river continually subjected to high sediment input from upstream.

Acknowledgments

Financial support for this research was provided by the U.S. Department of the Interior, National Park Service, under grants administered by R. Herrmann of the Water Resources Field Support Lab and D. Stevens of Rocky Mountain National Park. Additional funding was provided by S. Mock of the U.S. Army Research Office under grant DAAG29-85-K-0108. I sincerely thank all those who assisted me in the field; in particular, I thank M. D. Harvey for his advice, help, and encouragement through all phases of this project. This manuscript was greatly improved by the reviews of R. D. Jarrett, H. M. Kelsey, M. A. Madej, H. E. McCutchen, and K. van Son.

Literature Cited

Andrews, E. D. 1983. Entrainment of gravel from naturally sorted riverbed material. Bulletin of the Geological Society of America 94:1225–1231.

Beschta, R. L. 1983. Long-term changes in channel widths of the Kowai River, Torlesse Range, New Zealand. Journal of Hydrology (N.Z.) 22:112–122.

Blair, T. C. 1987. Sedimentary processes, vertical stratification sequences and geomorphology of the Roaring River alluvial fan, Rocky Mountain National Park, Colorado. Journal of Sedimentary Petrology 57:1–18.

Burkham, D. E. 1972. Channel changes of the Gila River in Safford Valley, Arizona, 1846–1970. U.S. Geological Survey Professional Paper 655-G. 24 pp.

Caine, T. N. 1986. Sediment movement and storage on alpine slopes in the Colorado Rocky Mountains. Pages 115–137 *in* A. Abrahams, editor. Hillslope processes. Allen & Unwin, Boston.

Collins, B. D., and T. Dunne. 1986. Erosion of tephra from the 1980 eruption of Mount St. Helens. Bulletin of the Geological Society of America 97:896–905.

Costa, J. E. 1974. Response and recovery of a Piedmont watershed from tropical storm Agnes, June 1972. Water Resources Research 10:106–112.

Griffiths, G. A. 1979. Recent sedimentation history of the Waimakariri River, New Zealand. Journal of Hydrology 18:6–28.

Jarrett, R. D., and J. E. Costa. 1986. Hydrology, geomorphology and dam-break modeling of the July 15, 1982 Lawn Lake Dam and Cascade Lake Dam failure, Larimer County, Colorado. U.S. Geological Survey Professional Paper 1369. 78 pp.

Kelsey, H. M. 1980. A sediment budget and an analysis of geomorphic process in the Van Duzen River Basin, northcoastal California 1941–1975. Bulletin of the Geological Society of America 91:1119–1216.

Lisle, T. E. 1982. Effects of aggradation and degradation on pool–riffle morphology in natural gravel channels, northwestern California. Water Resources Research 18:1643–1651.

Madej, M. A. 1984. Recent changes in channel-stored sediment, Redwood Creek, California. Technical Report 11, Redwood National Park, Arcata, Calif. 54 pp.

Newson, M. D. 1980. The geomorphological effectiveness of floods–a contribution stimulated by two recent events in mid-Wales. Earth Surface Processes and Landforms 5:1–16.

Osterkamp, W. R., and J. E. Costa. 1987. Changes accompanying an extraordinary flood on a sand-bed stream. Pages 201–224 *in* L. Mayer and D. Nash, editors. Catastrophic flooding. Allen & Unwin, Boston.

Paine, A. D. M. 1984. Canyon and terrace formation near Mount St. Helens, Washington. M.S. thesis, Colorado State University, Fort Collins. 157 pp.

Parker, G., P. C. Klingemen, and D. McLean. 1982. Bed load and size distributions in paved gravel-bed streams. Journal of Hydraulics Division of the American Society of Civil Engineers 108:544–571.

Pickup, G., R. J. Higgins, and I. Grant. 1983. Modelling sediment transport as a moving wave—the transfer and deposition of mining waste. Journal of Hydrology 60:281–301.

Pitlick, J. 1985. The effect of a major sediment influx on the Fall River, Colorado. M.S. thesis, Colorado State University, Fort Collins. 129 pp.

Pitlick, J. 1988a. Variability of bed load measurement. Water Resources Research 24:173–177.

Pitlick, J. 1988b. The response of coarse-bed rivers to large floods in California and Colorado. Ph.D. thesis, Colorado State University, Fort Collins. 137 pp.

Pitlick, J. 1992. Sediment routing in tributaries of Redwood Creek. *In* K. M. Nolan, H. M. Kelsey, and D. C. Masrron, editors. Geomorphic processes and aquatic habitat in the Redwood Creek basin, northwestern California. U.S. Geological Survey Professional Paper 1454.

Pitlick, J., and M. D. Harvey. 1986. A summary of channel changes and sediment transport in 1985 on the Fall River, Rocky Mountain National Park, Colorado. Unpublished report, Department of Earth Resources, Colorado State University, Fort Collins. 38 pp.

Pitlick, J., T. C. Blair, D. Anthony, and M. D. Harvey. 1987. Sedimentology of Lawn Lake Flood deposits and geomorphic processes in the Fall River, Rocky Mountain National Park, Colorado. Geological Society of America Field Trip Guidebook, Rocky Mountain Section, Boulder. 37 pp.

Pitlick, J., and M. D. Harvey. 1987. Sediment transport and channel changes on the Fall River, Rocky Mountain National Park, Colorado: a progress report. Unpublished report, Department of Earth Resources, Colorado State University, Fort Collins. 33 pp.

Pitlick, J., and C. R. Thorne. 1987. Sediment supply, movement and storage in an unstable gravel-bed river. Pages 151–183 *in* C. R. Thorne, J. C. Bathurst, and R. D. Hey, editors. Sediment transport in gravel-bed rivers. John Wiley & Sons, Chichester.

Schumm, S. A. 1977. The fluvial system. John Wiley & Sons, New York. 338 pp.

Schumm, S. A., and R. W. Lichty. 1963. Channel widening and floodplain construction along Cimarron River in southern Kansas. U.S. Geological Survey Professional Paper 352-D:71–88.

Thorne, C. R., L. W. Zevenbergen, J. Pitlick, S. Rais, J. Bradley, and P. Julien. 1985. Direct measurements of secondary currents in a meandering sand-bed river. Nature 316:746–747.

Wolman, M. G., and R. Gerson. 1978. Relative scales of time and effectiveness of climate in watershed geomorphology. Earth Surface Processes and Landforms 3:189–208.

Alpine Sediment Movement and Erosion in the Roaring River Watershed, Rocky Mountain National Park

Rebecca M. Summer[1]

Rocky Mountain National Park
Estes Park, Colorado 80517

Abstract. Clastic sediment movement was evaluated in the Roaring River watershed in the Mummy Range of the Colorado Front Range. Photogeologic techniques and field work on identifiable landforms were used to develop a terrain classification of sediment transfer. Terrain units formed the bases for assessing contemporary processes of sediment transport and for testing its usefulness in evaluating sediment flux. Contemporary behavior of terrain units suggests relative stability of the present system. The hillslope sediment transfer system seems to act as a closed system and is dominated by internal transfer of sediment moving on slopes and valleys. Current conditions suggest that external transfer by fluvial processes is very low and may increase in response to catastrophic events.

Introduction

With increased use of montane environments, the variety, intensity, and spatial and temporal magnitude of effects on the landscape have also increased. Such uses as water resource development, recreation, grazing, mining, home construction, and transportation conduits invariably result in modified surface water drainage and a temporary increase in soil erosion. In the past, effective erosion control proved to be difficult and sporadic due to combined factors in high alpine ecosystems (e.g., steep slopes, stony and erodible soil, short growing season, cold temperatures, and wind erosion) working against stability.

Mountain slope instability reflected in sediment transfer is receiving recent attention by alpine geomorphologists and glaciologists (Clark 1987). The sediment transfer system encompasses dynamic processes of sediment movement and temporary storage acting on the surface of a watershed. This transfer system forms a basis for assessing physical processes and environmental changes at high altitudes.

---

[1] Present address: 2925 Country Place Circle, Carrollton, Tex. 75006.

One frequent application of sediment transfer studies is the use of estimated sediment output and a sediment budget as a first approximation of either erosion or denudation. Clark (1987) suggested that sediment budgeting has considerable inferential power and should only be utilized with an equally large degree of caution. Temporal variation and short periods of instrumentation make short-term prediction possible, although long-term prediction is unwarranted and impractical.

The sediment system on slopes in the Colorado Rocky Mountains has been studied extensively in the past decade. Many studies conducted in the Front Range have evaluated individual components of sediment transfer (Ives 1980), and Caine (1986) evaluated integrated systems of sediment flux.

The present study of an alpine–subalpine sediment system in the Colorado Front Range develops a method to evaluate short-term (20–50 years) sediment transfer on hillslopes and transport out of a watershed. The empirical problem was to assess clastic sediment movement on the identifiable landforms composing a watershed and to estimate short-term sediment transfer. Two sediment flux systems that are spatially coincident are considered: coarse clastic sediment (>8 mm) and fine clastic sediment (coarse silt to coarse granular sand). Fine and coarse sediment categories correspond with those of Barsch and Caine (1984).

The study was conducted as part of an in-depth assessment of the Roaring River watershed by the National Park Service at Rocky Mountain National Park, Colorado. In 1982, the valley underwent a historically unprecedented flood, with an instantaneous peak discharge of 500 m^3s^{-1} (Jarrett and Costa 1986). Although the flood was a dam failure and not a naturally occurring event, it provided insight into sediment transfer conditions preceding and following a catastrophic event.

Study Area

The Roaring River is the main drainage of the glaciated watershed formed by multiple interfluves and valleys on the southeastern slopes of the Mummy Range (Fig. 1). The drainage area is 30.5 km^2 and underlain by Precambrian Silver Plume and Hagues Peak granites and biotite schist with isolated Tertiary volcanics on the summits (Peterman et al. 1967; Braddock and Cole 1988). Valley glaciers during the Pleistocene eroded deep cirque basins, leaving steep amphitheater walls and serrated ridgelines. Relatively flat to gently rolling erosion surfaces between the valleys form broad interfluves above treeline—more than 3,550 m in elevation. These broad expanses are products of long-continued periglacial mass movement without glacial disruption during the Pleistocene. Permafrost is patchy and occurs beneath many moist alpine willow communities or marshy areas (Ives 1973; Summer 1982).

The Roaring River originates at an elevation of 3,385 m in Crystal Lake. The boulder-bedded stream feeds Lawn Lake and descends across a till-cov-

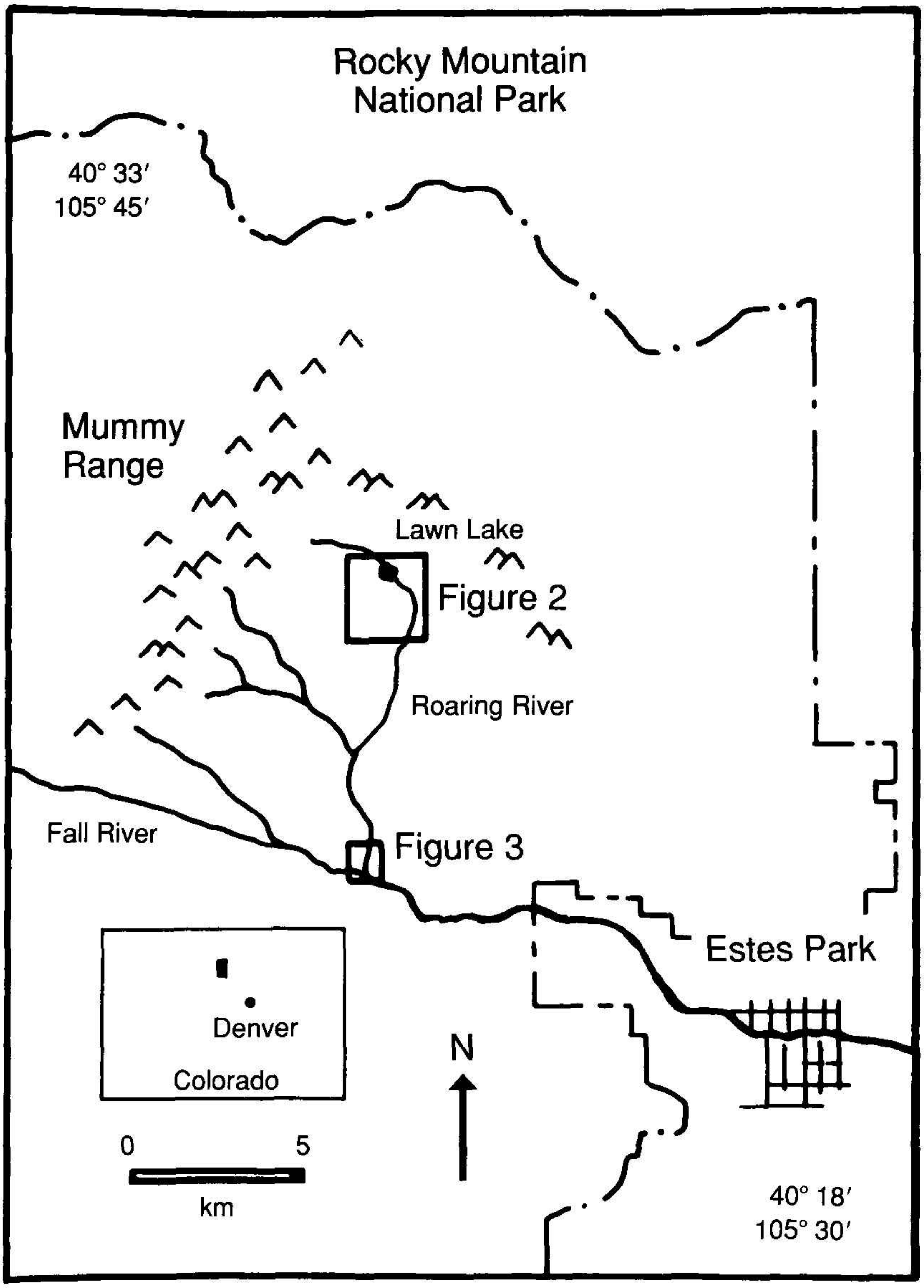


Fig. 1. Location map of Roaring River watershed in the Mummy Range, Rocky Mountain National Park, Colorado.

ered valley, crossing a series of bedrock falls and gently sloping meadows. Stream gradient averages 6°, varying from 3 to 15°, and the steepest section is at Horseshoe Falls near the mouth of the river.

Major topographic features of the watershed were shaped by Pinedale glaciers (Richmond 1960; Miller and Birkeland 1974), and small cirque gla-

Table 1. *Climatic data from the east slope of the Front Range, Colorado.*[a]

Mean	Subalpine	Alpine
Mean daily temperatures (° C)		
January maximum	2.2	−10.1
minimum	−9.2	−16.2
July maximum	24.8	12.5
minimum	10.5	4.4
Mean precipitation (cm)		
Year	57.79	102.08
Maximum month	9.65 (May)	13.77 (January)
Mean wind speed (m/s)		
January	3.6	13.9
July	1.3	5.8

[a] Barry 1973.

ciers continued to erode and modify the landscape during the last 10,000 to 12,000 years. Further discussions of the regional glacial chronology, based on detailed work in the Indian Peaks (20 km south of Rocky Mountain National Park), are given by Benedict (1973, 1981), Birkeland and Shroba (1974), Miller and Birkeland (1974), and Davis (1982, 1987).

The present-day climate of the east slope of the Front Range is cold, windy, and highly variable (Marr 1967; Barry 1973). Summers are short and cool with frequent thunderstorms, while winters are long and cold with snowstorms and wind coming from the west. A summary of climatic characteristics in Table 1 is based on long-term data collection from weather stations on Niwot Ridge, 45 km south of the Mummy Range. Radiocarbon dating and pollen and insect analyses in the Roaring River valley by Elias et al. (1986) indicated that these conditions have prevailed for at least the past 2,400 years in the subalpine zone.

Two broad vegetative zones characterize the Roaring River watershed. The alpine tundra occurs from treeline (averaging 3,350 m in elevation) to 4,121 m and supports alpine grasses and sedges (Nelson 1953; Marr 1967). The subalpine zone lies from treeline to 2,740 m and supports Englemann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and aspen in moist areas. The ecotone between the subalpine and alpine zones occurs from 3,305 to 3,450 m in elevation, where trees in flagged forms and mats occur (Ives and Hanson-Bristow 1983; Hanson-Bristow and Ives 1985). Less than 0.5% of the watershed lies below 2,740 m in the montane zone, characterized by ponderosa pine (*Pinus ponderosa*) and aspen.

Methods

Evaluating sediment movement in the watershed began with gathering geologic, hydrologic, and photographic information. Work by Braddock and

Cole (1988) on bedrock geology, Richmond (1960) on glacial geology, and Pitlick and Thorne (1987) on fluvial sediment transport provided baseline data for assessing the watershed. Seven sets of low-altitude vertical aerial photography, taken from 1946 to 1984, were collected along with oblique aerial photographs.

Information collected from geologic and hydrologic studies was used to evaluate the landscape in the Roaring River watershed using photogeologic techniques and field work. Past field and remote sensing studies conducted by the author in the San Juan Mountains and Front Range of Colorado (Bovis 1976; Knepper 1977; Summer 1980) provided information for defining landscape units. Photography was used extensively to identify characteristics of terrain units expressing surficial sediment movement and mass movement. Field observations in June, August, and January (1987–88) verified the composition and boundaries of the terrain units. Specific criteria for defining terrain units included

1. typical photographic signatures (parallel, wavelike appearance of solifluction lobs, lense-shaped morainal form);
2. boundary conditions (slope break and neighboring terrain unit);
3. vegetative types, spatial distributions, and growth features;
4. surface soil conditions (moisture conditions and erosion features);
5. size and arrangement of surficial materials and presence of lichens;
6. hydrologic features (drainage patterns and springs);
7. bedrock exposure;
8. spatial pattern of landforms or slope complexes; and
9. geometry and size of landform or slope complex.

Finally, the clastic sediment flux was estimated by extrapolating sediment rates measured by Caine (1986) in a similar alpine watershed: the Green Lakes valley, 38 km south of the Mummy Range. Mean mass movement of sediment was monitored seasonally over nearly 20 years. Landforms and landscape composition of the two watersheds were compared and correlated using criteria developed for the Roaring River watershed. Then, mean rates of sediment movement were extrapolated from the Green Lakes valley to the study watershed. Field measurements of channel sediment load in the Roaring River provided a baseline for the sediment budget.

Results

Terrain Classification

The terrain classification of sediment transfer developed for the Roaring River watershed produced mapping units representing surfaces of surficial erosion or mass movement. Terrain units have similar soil, vegetation, and topographic features reflecting physical processes that formed them (Table 2).

Table 2. *Terrain mapping units.*

Unit (map symbol)	Sediment size[a]	Description
Wetland (WL)	f	Poorly drained areas subject to perennial or seasonal saturation
Colluvial slope	f	Soil-mantled slopes subject to downslope movement, soil and frost creep, raindrop splash, sheetwash, and animal burrowing
Accelerated colluvial slope (CSA)	—	Areas of accelerated colluvial activity onslopes of 25–40°
Moderate colluvial slope (CSM)	—	Areas of moderate colluvial activity on slopes of 12–25°
Inactive colluvial slope (CSI)	—	Areas of relatively slight colluvial activity on slopes <12°
Slopewash slope (SWS)	f	Grassy slopes on moderate-to-steep slopes subject to uniform erosion by sheetwash
Talus (TS)	c	Accumulation of rockfall, avalanche, and weathering rock fragments; movement by talus shift
Talus fan (TF)	c	Flattened, cone-shaped deposit formed by accumulation of talus slide and debris flow material
Glacial cirque floor (GCF)	c	Ancient rock glacier debris and unsorted glacial deposits on cirque floor; little movement by talus shift, soil creep
Bedrock outcrop (BO)	c	Surficial exposure of bedrock producing rockfall on steep slopes and runoff
Alluvial fan (AF)	m	Fan-shaped wedge of heterogeneous sediment deposited at confluences of drainage
Recent floodplain (RF)	m	Relatively flat area directly bordering present stream channel; fluvial processes dominate
Debris flow (⟶)	m	Unvegetated debris flow path and steep, ephemeral streams that transport heterogeneous mixtures of debris
Glacial valley floor (GVF)	m	Composite of alluvium, glaciofluvium, and ground moraine in glacial valleys; little movement by overland flow
Landslide (LS)	m	Large-scale failure of surficial unconsolidated material and bedrock blocks by slumping and block slide; little movement by soil creep and talus

Table 2. *Continued.*

Unit (map symbol)	Sediment size[a]	Description
Moraine (mo)	m	Unconsolidated, heterogeneous glacial sediment composed of angular rock fragments in fine matrix forming ridges and mounds

[a]f = fine; c = coarse; m = mixed.

Fine Sediment

A *wetland* is a poorly drained area subject to perennial or seasonal saturation due to a high water table. Hydrogeologic factors govern the occurrence of wetland: flooded areas along streams, lowlands surrounding ponds and lakes, and poorly drained areas where groundwater is forced to the surface by the presence of impermeable substrate (Sloey et al. 1978). Water movement is usually by sheetflow, which induces sediment deposition and results in trapped nutrients and heavy metals attached to sediment (Lance 1983). Wetlands near streams may rapidly contribute fine sediment and organic material to the stream during large flood events. Once vegetation is disrupted, peaty material and high-organic soil that store nutrients and minerals are easily eroded (Windel et al. 1986).

Colluvial slope units are polygenetic, soil-mantled surfaces subject to movement predominantly by soil and frost creep (Benedict 1970; Madole 1976). Creep is a subtle but relatively continuous mass movement of fine sediment downslope under the influence of gravity. Raindrop splash, frost heave, sheetwash, and animal burrowing (Thorn 1978, 1982) contribute to sediment movement, which remains internal to the hillslope. Three subcategories of colluvial slope are defined by slope gradient, vegetation, and the presence of microtopographic features suggesting soil movement.

Accelerated colluvial slope units exhibit active soil and frost creep on sparsely vegetated slopes with inclines from 22 to 35°. A series of surficial ridges and a discontinuous vegetative pattern are common on slopes of the alpine tundra. Frost action during most of the year and raindrop splash locally interact with soil creep on hillslopes (Summer 1982).

Moderate colluvial slope units are moderately vegetated and exhibit less intense soil movement. Slopes range from 12 to 25°, although devegetation by fire, overgrazing, or animal and foot traffic can effectively accelerate soil movement.

Inactive colluvial slope units occur on gentle slopes (<12°) that do not exhibit obvious mass movement features, although a certain low level of soil movement will occur over time. Wide expanses of gently undulating tundra—characterized by thick soils, minimal snow cover, and lush grass cover—are stable components of the alpine landscape (Bovis and Thorn 1981).

Sediment transfer on *slopewash slope* units is characterized by slopewash, the relatively uniform erosion of a slope by overland flow and raindrop impact. This unit occurs on sparsely vegetated, moderate-to-steep slopes below treeline (Moss 1979) where a thin soil mantle overlies bedrock. Slopewash is a diffusive or incisive process depending on soil erodibility, vegetation, slope, and storm intensity and duration (Dunne 1988). Rills (small streamlets of channelized flow) are formed or eradicated, depending on the balance between incision by overland flow and diffusion by raindrop splash. On southeast-facing slopes where snow cover is lost in early spring, slopewash slopes may be heavily grazed, exposing soil to early season erosion-producing precipitation events.

Coarse Sediment

Talus or sheet talus is a highly pervious assemblage of angular rock fragments formed by rockfall, snow avalanches (Caine 1969, 1971; White 1981), and frost weathering of bedrock (Washburn 1979). Talus maintains a characteristic longitudinal gradient across the slope and adjusts this gradient by talus shift. Movement is generally rapid, punctuated, and extremely variable in response to snowmelt and thunderstorms, producing talus and colluvium movement (Wallace 1967; Caine 1976, 1984). *Talus fan* units are accumulations of rock debris in a concentrated zone at the base of talus or at slope breaks. Material is transported to talus fans or alluvial talus (White 1981) by rockfall, talus shift, debris flow, and runoff. Any fine material accumulated is not stored; instead, it is winnowed by wind action or runoff.

Glacial cirque floor is a composite of rock glacial material composed of angular, poorly sorted debris covering a cirque floor. This unit is highly variable, from steep-sided, till-like material forming tongue-shaped protrusions to lobate landforms resembling blockfields and rock glaciers (Outcalt and Benedict 1965; White 1976, 1981). Like talus, active rock glaciers are significant areas of coarse sediment transfer due to sheer volume of material moved downslope. However, present-day subdued topography and lichen-covered debris suggest relative stability with a minimal amount of creep and talus shift.

Bedrock outcrop identifies those units where either the process of rockfall and high runoff occurs on steep slopes (>35°) or high runoff occurs on gentler slopes. Rockfall onto talus and glacial cirque floor units occurs through freezeback, runoff from heavy summer rain, and snowmelt from snow cornices (Caine 1986). On gentler slopes, outcrops act as a stabilizing component on a hillslope. However, relatively impermeable surface or near-surface conditions cause increased runoff and sheetflow, potentially eroding surrounding fine material.

Mixed Sediment

Alluvial fan units are fan-shaped wedges of heterogeneous sediment that accumulate at drainage confluences by deposition from sediment-laden streams.

Fans also form on channel slopes below an abrupt decrease in stream gradient. Fans in the Front Range form primarily from infrequent, high-intensity storms (Costa 1978). More frequent runoff events of lesser magnitude—for example, a 5-year storm event (National Oceanic and Atmospheric Administration 1969–89)—are relatively ineffective in causing change on the fan surface; therefore, sediment movement is low for long periods. Between large erosion events, alluvial material is either reworked by distributary channels or stabilized by vegetation.

Recent floodplain is the relatively flat area directly bordering stream channels and is commonly contained between the first (lowest) set of paired terraces. This unit is the first area to flood during high runoff events. Surface material varies from boulders, cobbles, and fine sediment to grasses, shrubs, willows, and other species that can withstand periodic inundation. Floodplains form temporary sediment storage sites for channel bedload and overland flow material.

Debris flow describes the unvegetated flow path of rapidly moving unconsolidated rock and soil induced by inclusion of water. Ephemeral streams on steep slopes that transport debris are included in this category (Gardner 1986). Debris flows originate from mud and rock slides during heavy thunderstorms (Clark 1974; Sharpe 1974) or from meltwater below glaciers or late-lying snowbanks (personal observation). Numerous debris flows occur on talus and on some accelerated colluvial slopes in cirque basins. Although debris flows do not cover large areas, their numbers make them important in forming talus fans and in modifying or rearranging talus surfaces (White 1981).

Glacial valley floor includes undifferentiated sedimentary deposits composed of alluvial and glaciofluvial sediments and ground moraine. Characteristics of this category include thick stratified and unstratified sediments bordering the floodplain; a gently undulating surface; and a location adjacent to steeper colluvial slopes or talus. Although this unit is inherently stable, unconsolidated sediments can fail by streambank undercutting during high flow events.

The *landslide* unit defines unconsolidated material and bedrock blocks moved by rotational slumping and sliding. Landsliding is a slow to rapid mass failure and, when involving unconsolidated material, is a bulk soil response to soil and water stresses (Caine 1971). Landsliding surpasses other agents of mass movement in volume of sediment moved, but only at individual locales and during the time that these relatively rare catastrophic failures occur (Caine 1983; Young and Saunders 1986). During the normally long recovery between landslide events, soil and frost creep slowly modify the ground surface (Chorley et al. 1985). Although landslides are generally not active now, erosion at the toe of a slide or changes in surface drainage, groundwater movement, or ice formation can reactivate these features (Bovis 1976; Trench 1978).

The *moraine* unit is composed of large glacial boulders and angular to subangular rock fragments within a matrix of fine silt and clay forming mounds,

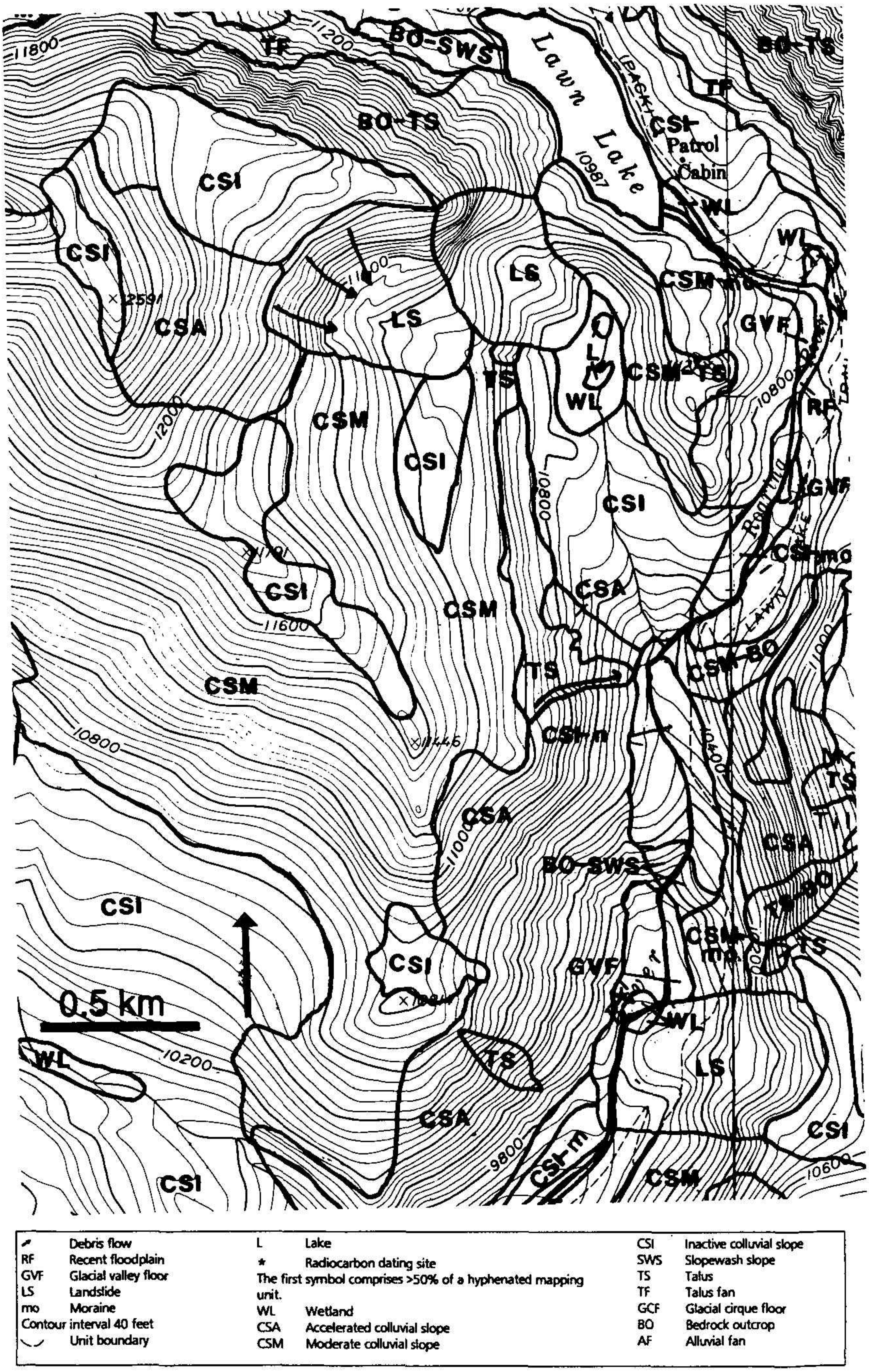


Fig. 2. Geomorphic landscape map of part of the Roaring River watershed, Mummy Range, Colorado Front Range. Based on U.S. Geological Survey, Trail Ridge and Estes Park quadrangles (1957–61).

crescentlike landforms, or ridges. These moraines, mapped with colluvial slope units, indicate the relatively high potential for mass failure of unconsolidated, heterogeneous deposits. In comparison, ground moraine (material in the glacial valley floor unit) does not have as high a susceptibility to mass failure.

Application

Terrain units were mapped over the entire watershed at a scale of 1:24,000; the smallest unit was 1 ha. The river valley before and after the flood was also mapped, at a scale of 1:5,800. Areal distribution and pattern of terrain units are delineated in Fig. 2, and an enlarged map of the river valley is depicted in Fig. 3. Terrain units acting as surfaces of fine sediment transport include 66% of the area, while 28% of the area acts as surfaces of coarse sediment transfer, and 6% of the area acts as surfaces of fine and coarse sediment transfer. Colluvial slope and talus units together compose more than 80% of the watershed (Fig. 4); colluvial slope units (62%) include wide expanses of alpine tundra, and talus units (21%) are associated with bedrock outcrops bordering ridges. Units directly linked to the stream are glacial valley floor (0.5%), recent floodplain (0.2%), alluvial fan (0.3%), and wetlands (1.5%), composing a few percentages of the watershed.

Short-term Sediment Transfer

Field measurements of terrain unit flux over an extended time—that is, 10 to 20 years—were not made in the watershed. Therefore, applying the terrain mapping units to facilitate a sediment budget estimate over time is difficult. However, a methodology for identifying terrain units of sediment transfer is given above, and the following presents an illustrative method of applying terrain units to estimate short-term sediment movement.

Contemporary sediment transfer was estimated by comparative techniques using results of Caine's (1986) synoptic work in a neighboring watershed, Green Lakes valley. Green Lakes valley has similar bedrock type, landforms, soil, vegetation, climate, and aspect to that of the Roaring River watershed. However, the two valleys are dissimilar in size; the Roaring River watershed is about 15 times as large as the Green Lakes valley, which encompasses only alpine and alpine–subalpine ecotone zones. Size of a catchment affects rates of sediment movement; large watersheds in the Front Range have a small percentage of area as talus and varying levels of developed drainage compared to small watersheds. However, for purposes of the study, particularly regarding internal hillslope transfers, the similarity of the two valleys is considered sufficient to warrant extrapolation of rates of sediment movement from one location to the other.

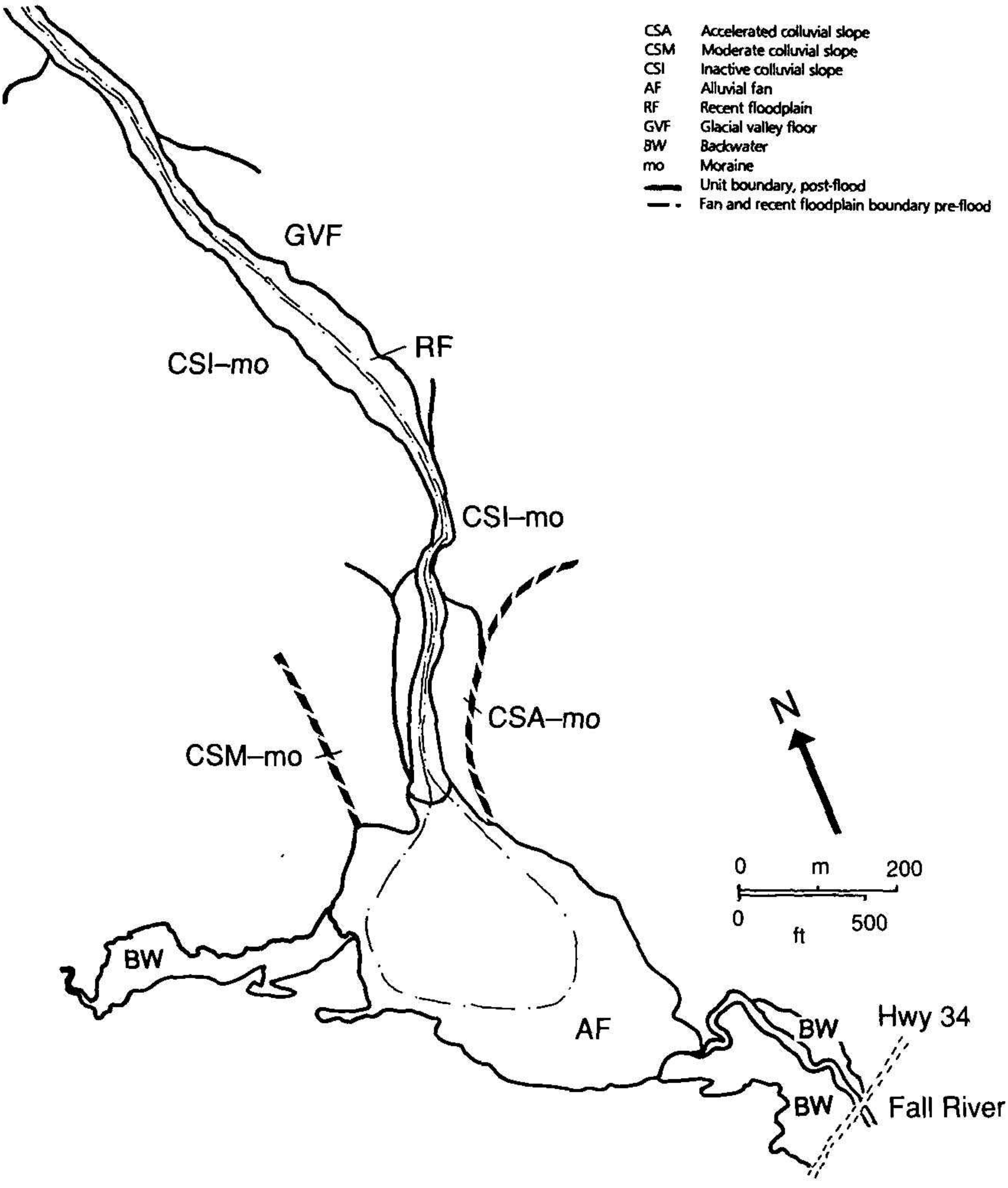


Fig. 3. Postflood geomorphic landscape map of part of the Roaring River valley, Mummy Range, Colorado Front Range. Based on National Park Service aerial photography, 25 August 1965 and 15 July 1982. GVF = glacial valley floor; CSI = inactive colluvial slope; CSM = moderate colluvial slope; CSA = accelerated colluvial slope; mo = moraine; RF = recent floodplain; AF = alluvial fan; BW = backwater.

Rates of sediment movement within the framework of a sediment budget were measured in the Green Lakes valley by a variety of methods (Caine 1986). Rockfall accumulation on snow cover and in traps was measured. Talus shift, debris flows, and glacial flow were measured with stakes and marked material. Fine sediment was monitored by using sediment traps, tracers, snow dust accumulation, and stake movement.

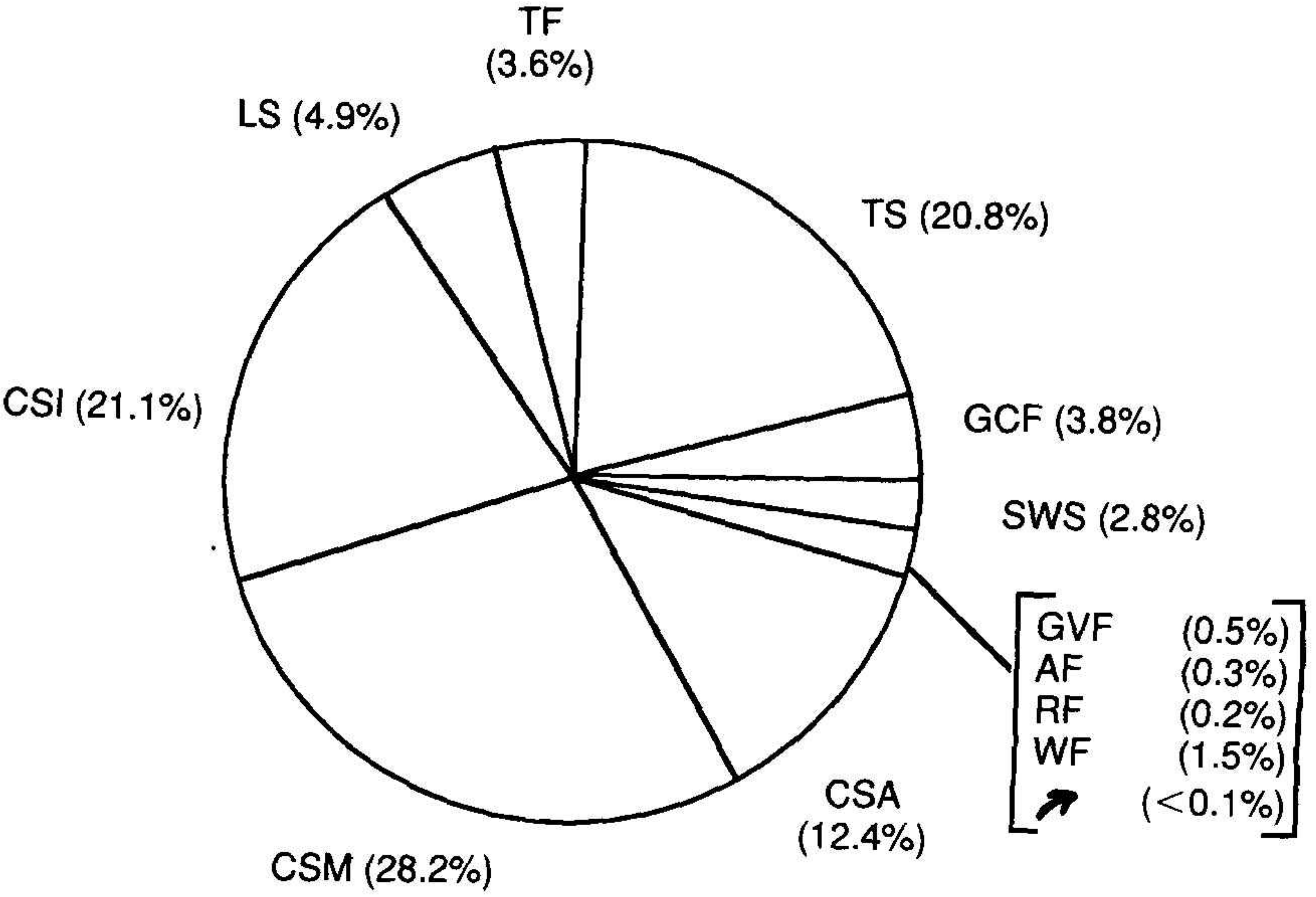


Fig. 4. Percent areal coverage of geomorphic units. Mapping units in parentheses are defined in Table 2.

A sediment budget calculated for the Green Lakes valley was based on fine and coarse sediment groups, as defined in this study. Results (Table 3) indicate that a process group—soil creep and solifluction—dominates fine sediment movement, and the talus shift and rock glacier flow groups dominate coarse sediment movement. Rates of movement by these processes are 5 orders of magnitude greater than all other processes identified.

Table 3. *Sediment budget in Green Lakes valley in the Front Range of the Colorado Rocky Mountains.*[a]

Transport process	m^3/year
Fine sediment	
soil creep and solifluction	95,440
surficial wasting	240
lake sedimentation	13.5
suspended sediment transport	2.47
aeolian transport	20.0
Coarse sediment	
rockfall	10.0
talus accumulation	1.5
talus shift	206,500
debris flow	2.5
rock glacier flow	373,000

[a] Based on 20 years of data collection; Caine 1986.

Rates of sediment movement in the Green Lakes valley were extrapolated to the Roaring River watershed to give an approximation of contemporary movement within the watershed. Coarse sediment movement in the Green Lakes valley was applicable to the entire Roaring River watershed, but fine sediment movement was applied only to the alpine and alpine–subalpine ecotone zones. This areal discretion is based on a review by Benedict (1970) and a study of soil movement 40 km south of the Mummy Range by Bovis (1978), which indicated that subalpine areas exhibit insignificant rates of sediment movement compared with rates in the alpine zone. Therefore, the fine sediment movement in the alpine zone is assumed to reasonably characterize fine sediment movement in the Roaring River watershed over the short term. However, scientists recognize that the assumption of negligible movement in the subalpine zone is crude, and detailed monitoring of the watershed is required for verification.

The resulting extrapolation of sediment rates from the Green Lakes valley to the Roaring River watershed is given in Table 4. Only two process groups are responsible for nearly all sediment transfer in the Green Lakes valley. Coarse sediment movement by talus shift corresponds to the talus units in the Roaring River watershed. The process group—soil creep and solifluction—corresponds to active colluvial slope and slopewash units. Moderate and inactive colluvial slope units exhibit negligible or low levels of sediment movement over the short term and were not included in the sediment budget analysis. These low-relief vegetated areas are similar to stable summits south of the Mummy Range (Burns 1982) and areas surrounding isolated, ice-active alpine features (Benedict 1970).

Rock glacial movement was not included in the analysis because the terrain units in Roaring River watershed associated with rock glaciers (e.g., glacial floor units) appear to be inactive landforms with subdued topography and minimal talus shift and soil creep. This deduction is supported by work of Benedict (1968) and Carroll (1974) on similar tongue-shaped features in the Front Range, indicating that this type of landform has not been an active part of the sediment transport system since the early Holocene.

Table 4. *Extrapolation of data from Green Lakes valley to the Roaring River watershed.*

	Green Lakes (2.12 km^2)[a]		Roaring River (30.45 km^2)	
	Area ha (% of watershed)	Volume m^3/year	Area ha (% of watershed)	Volume m^3/year
Talus shift	41	206,500	375	1,885,700
	(19)	—	(13)	—
Soil creep–solifluction	46	95,440	310	643,200
	(22)	—	(10)	—

[a]Caine 1986.

With regard to external sediment transport, fluvial processes govern sediment transfer and average <1–10 m^3/year in the Roaring River valley (J. C. Pitlick 1987, unpublished data). Pitlick measured bedload with Helley–Smith samplers and suspended load with DH-48 depth-integrated samplers (Pitlick and Thorn 1987). Solute flux was not measured in either the Green Lakes valley or the Roaring River watershed. Based on the review by Barsch and Caine (1984) and work in the Front Range by Thorn (1976), Vitek et al. (1981), and Caine (1984), the geomorphic work done by solute transport is expected to be equivalent to or greater than that of fluvial sediment transport. An expected high rate of work is due to the efficiency of geochemical transport by solution out of the system. Sources of solute include floodplains, lakes, and atmospheric deposits.

Holocene Geomorphic Change

Since deglaciation at the end of Middle Pinedale time, alpine watersheds such as that of the Roaring River have been denuded by slow continuous processes as well as more episodic hillslope and fluvial processes reflecting Holocene glacial advances. These processes include (1) solifluction, (2) talus shift, (3) rock glacier flow, (4) landsliding within unconsolidated glacial material, and (5) fluvial processes. Solifluction was most active as a geomorphic agent in the alpine zone of the Front Range 10,000 to 14,000 years ago but has since ceased to be an effective erosion agent (Benedict 1970). Frost and soil creep replaced solifluction as a dominant sediment transfer agent after Middle Pinedale time, although neither agent is particularly effective today.

Caine (1986) indicated that the cliff–talus system—as seen in catchments like the Roaring River watershed—formed during intervals of more active sediment production and transfer within the last 12,000 years. Even during past times of more rapid sediment transfer, hillslopes remained essentially closed to export of clastic materials to the valley.

Rock glacier flow in the Front Range seems to have occurred over a short time following the retreat of Late Pinedale glaciers (Benedict 1968) and during waxing and waning of smaller Holocene glaciers (White 1971). Examples of these ancient rock glaciers appear within cirque basins in the Roaring River watershed as blocky rubble and lobate and tongue-shaped landforms. Today, these terrain units are relatively stable with partially vegetated surfaces, lichen cover on rock debris, and a subdued debris surface.

Likewise, large slump blocks and debris slumps forming landslide features in the Roaring River watershed are well vegetated and do not appear active. Lake sediment upstream of a landslide located 3.5 km downstream of Lawn Lake (Fig. 2) yielded radiocarbon dates of 9,850 ± 410 years B.P. (GX-11862) and 11,470 ± 420 years B.P. (GX-11863; J. C. Pitlick 1987, unpublished data). These landslides blocked the channel following deglaciation, temporarily caus-

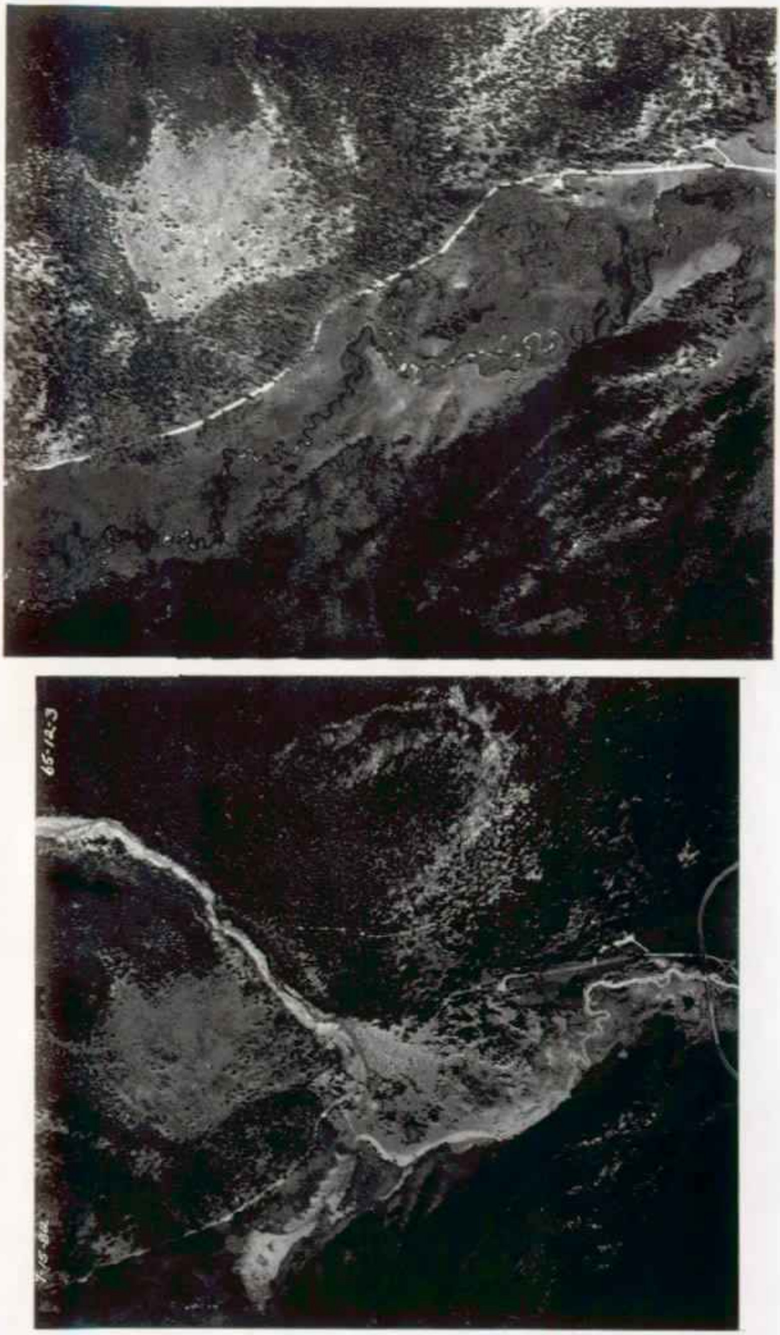


Fig. 5. Low-altitude photographs of alluvial fan: (A) Vegetated fan surface, 29 September 1969; (B) Postflood fan surface, 15 July 1982; from photographic archives of Rocky Mountain National Park.

ing a lake to form. Trench (1978) identified a similar period of active landsliding in post-Middle Pinedale glaciation in the San Juan Mountains of Colorado.

Finally, fluvial landforms in the Roaring River valley, such as well-vegetated terraces, attest to greater sediment transport within and out of the watershed in the past. Increased sediment movement probably occurred in response to waxing and waning of Holocene glaciers. No absolute dating of the terraces has been done to define the timing of the depositional events in the valley.

The most recent fluvial event, the Lawn Lake Flood in 1982, illustrates the types of erosion and sedimentation that may have occurred during Holocene deglaciation (Jarrett and Costa 1986). The flood changed a stream—averaging 3–5 m wide and 0.3–0.6 m deep with no appreciable active fan surface—to an armored channel 20–30+ m wide and 1.6–16 m deep with an associated fan 17.1 ha in area (Jarrett and Costa 1986; Fig. 3). Approximately 278,700 m^3 of material were deposited on an enlarged fan (Fig. 5), and backwater on the Fall River floodplain developed into a 7-ha lake (Blair 1987). Terrain units including recent floodplain, colluvial slope, glacial valley floor, and wetland were eroded during this event. To illustrate the magnitude of the flood, floodwater moved 10% of the previously estimated annual internal sediment budget (Table 4) totally out of the watershed in a matter of hours.

Sediment load was high during the year following the flood, but since then, sediment transport out of the basin has rapidly declined to near preflood transport levels (Pitlick and Thorne 1987). Six years after the flood, erosional processes reflecting flood effects were active only in localized sites along the floodway. Occasional streambank caving and gullying occurred in valley deposits induced by overland flow during rain storms. Winnowing of fine sandy sediment by wind was active on overbank flood deposits, especially during fall and spring. Field observations suggested that (1) contemporary sediment production, transfer, and storage in the study watershed are strikingly similar to preflood conditions; (2) the watershed is surprisingly stable under existing climatic conditions; and (3) the sediment system is essentially closed to export until catastrophic events occur.

Conclusions and Discussion

A classification of contemporary clastic sediment transfer is developed for the Roaring River watershed. Photographic data and comparative studies in the Front Range suggest terrain units act as sediment stores for output during pulsed sediment transfer. Following a catastrophic flood event in the study watershed, behavior of terrain units bordering the channel 6 years later was remarkably similar to preflood conditions, dominated by internal sediment movement and low rates of sediment export.

Extrapolation of sediment flux measured on markedly similar terrain units in the Green Lakes valley provided an estimate of the contemporary sediment budget. Although sediment flux was not measured in the Roaring River watershed, the estimation may be valid in a qualitative sense as evidenced by gullying, slumping, vegetative loss observed in the field, and aerial photography since 1946.

The results and comparisons with adjacent Front Range alpine areas suggested that the slope debris supply may not constitute a major control on mountain streams within a period of several hundred years, as Slaymaker (1974) suggested. Based on these criteria, thousands of years are a more appropriate period under Front Range geomorphic and climatic conditions.

Relative latency of the present-day sediment system is relevant to concepts of erosion control. We need to consider geomorphic thresholds and landscape sensitivity of each terrain unit before identifying appropriate erosion stabilization techniques and their timing. The following highlights those components of the sediment system that are useful in maximizing the effectiveness of erosion control.

1. Nearly all coarse and fine sediment transfer remains on the slope and does not link to stream channels. Colluvial slope units compose the largest portion of the watershed and move fine sediment at slow rates. Coarse sediment movement occurs predominantly as talus shift on talus units.

   Implications: Site disturbance on most of the watershed will greatly increase rates of sediment movement but is not expected to increase sediment yield downstream. Focus erosion control efforts on stabilizing accelerated colluvial action and talus shift. Due to climatic variations and inherently low, continuous rates of movement, disrupted site stabilization may require long periods.
2. Major sources of sediment along stream channels are glacial valley deposit, recent floodplain, and wetland units. Sediment sources are not readily available to streams under the current flow regime. The recent floodplain unit is most active as a sediment supply and temporary storage. Wetlands are highly effective in flood attenuation, sediment and contaminant filtering, and streambank stabilization.

   Implications: Because stream valleys are common sites of homesteads and mountain development, glacial valley, floodplain, and wetland deposits are subject to disturbance. Site disruption may lead to undercutting and mass failure of these sedimentary materials. Increased sediment delivery downstream will be short-lived in response to rainfall and snowmelt runoff events. Avoid disrupting wetland to benefit the integrity of the floodway and downstream water quality.
3. The Lawn Lake Flood represents a catastrophic event unmatched since the Pleistocene, 10,000 years ago. Although striking changes were incurred on the floodplain and alluvial fan, minimal geomorphic change was occurring 6 years later. Landscape components and the drainage network were remarkably similar to preflood conditions with internal clastic sediment movement and low rates of sediment export.

   Implications: If a large runoff-erosion event occurs, erosion of a disturbed site along a stream channel will be initially high, perhaps a sixfold increase in stream sedimentation. Sediment transfer will quickly dissipate with little sediment input into the stream following the flood. Geochemical and solute transport may require large effort to assess effects of disturbances.

Acknowledgments

Funding for this study was provided by Rocky Mountain National Park, Estes Park, Colorado, and the author. Photographic laboratory facilities and numerous insightful discussions were received from D. Stevens of Rocky Mountain National Park. Field discussions with J. Pitlick were of particular value. N. Caine, M. Clark, G. Foster, M. Rieux, O. Slaymaker, R. Smith, and S. White provided advice and useful criticisms of earlier versions of the manuscript. Drafting advice and support were received from U.S. Department of Agriculture, Agricultural Research Service, Morris, Minnesota, and Durant, Oklahoma.

Literature Cited

Barry, R. G. 1973. A climatological transect along the East Slope of the Front Range, Colorado. Arctic and Alpine Research 5:89–110.

Barsch, D., and N. Caine. 1984. The nature of mountain geomorphology. Mountain Research and Development 4:287–298.

Benedict, J. B. 1968. Recent glacial history of an alpine area in the Colorado Front Range, U.S.A. Journal of Glaciology 7:77–87.

Benedict, J. B. 1970. Downslope soil movement in a Colorado alpine region: rates, processes, and climatic significance. Arctic and Alpine Research 2:165–226.

Benedict, J. B. 1973. Chronology of cirque glaciation, Colorado Front Range. Quaternary Research 3:584–599.

Benedict, J. B. 1981. The Fourth of July Valley: glacial geology and archeology of the timberline ecotone. Research Report 3, Center for Mountain Archeology, Ward, Colo. 139 pp.

Birkeland, P. W., and R. R. Shroba. 1974. The status of Quaternary soil-forming intervals in the Western United States. Pages 241–276 *in* W. C. Mahaney, editor. Quaternary environments—proceedings. First York University Research, Geography Monograph 5, York University, Toronto.

Blair, T. C. 1987. Depositional chronology, sedimentary processes, and resulting vertical stratification sequences of Roaring River alluvial fan, Rocky Mountain National Park, Colorado. Journal of Sedimentary Petrology 57:1–18.

Bovis, M. J., editor. 1976. Natural hazards of San Juan County, Colorado. Report to NASA, Institute of Arctic and Alpine Research, University of Colorado, Boulder. 64 pp.

Bovis, M. J. 1978. Soil loss in the Colorado Front Range: sample design and areal verification. Zeitschrift fuer Geomorphologie N.F. 29:10–21.

Bovis, M. J., and C. E. Thorn. 1981. Soil loss variations within a Colorado alpine area. Earth Surface Processes and Landforms 6:151–163.

Braddock, W. A., and J. C. Cole. 1988. Geologic map of Rocky Mountain National Park, Boulder, Grand, Jackson, and Larimer counties, Colorado. U.S. Geological Survey, Lakewood, Colo.

Burns, S. F. 1982. Soil–geomorphic models and the spatial distribution and development of alpine soils. Pages 24–43 *in* C. E. Thorn, editor. Space and time in geomorphology. Allen & Unwin, London.

Caine, N. 1969. A model for alpine talus slope development by slush avalanching. Geology 77:92–100.

Caine, N. 1971. A conceptual model for alpine slope processes. Arctic and Alpine Research 3:319–329.

Caine, T. N. 1976. Summer rainstorms in an alpine environment and their influences on soil erosion, San Juan Mountains, Colorado. Arctic and Alpine Research 8:183–196.

Caine, T. N. 1983. The mountains of northeastern Tasmania: a study of alpine geomorphology. Balkema, Rotterdam. 200 pp.

Caine, T. N. 1984. Elevational contrasts in contemporary geomorphic activity in the Colorado Front Range. Studia Geomorphia Carpatho–Balcanica 16:5–31.

Caine, T. N. 1986. Sediment movement and storage on alpine slopes in the Colorado Rocky Mountains. Pages 115–138 *in* A. D. Abrahams, editor. Hillslope processes. Allen & Unwin, London.

Carroll, T. 1974. Relative age dating techniques and late Quaternary chronology, Arikaree Cirque, Colorado. Geology 2:321–325.

Chorley, R. J., S. A. Schumm, and D. E. Sugden. 1985. Geomorphology. Methuen, New York. 606 pp.

Clark, J. A. 1974. Mudflows in the San Juan Mountains, Colorado: controls and work. M.S. thesis, University of Colorado, Boulder. 102 pp.

Clark, M. J. 1987. The glacio–fluvial sediment system: applications and implications. Pages 499–516 *in* A. M. Gurnell and M. J. Clark, editors. Glacio–fluvial sediment transfer. John Wiley & Sons, New York.

Costa, J. E. 1978. Holocene stratigraphy in flood frequency analysis. Water Resources Research 14:626–632.

Davis, P. T. 1982. Chronology of Holocene glaciation, Arapaho Cirque, Colorado Front Range, U.S.A. Abstracts, XI INQUA Congress, Moscow, U.S.S.R. Page 54.

Davis, P. T. 1987. Late Pleistocene age for type Triple Lakes moraines, Arapaho Cirque, Colorado Front Range. Abstracts, Geological Survey of America 19:270.

Dunne, T. 1988. Sheetwash as a diffusive process stabilizing hillslopes against channel incision. American Geophysical Union, EOS 69:345.

Elias, S. A., S. K. Short, and P. U. Clark. 1986. Paleoenvironmental interpretations of the Late Holocene, Rocky Mountain National Park, Colorado, U.S.A. Revue de Paleobiologie 5:127–142.

Gardner, J. S. 1986. Sediment movement in ephemeral streams on mountain slopes, Canadian Rocky Mountains. Pages 171–192 *in* A. D. Abrahams, editor. Hillslope processes. Allen & Unwin, London.

Hanson–Bristow, K. J., and J. D. Ives. 1985. Composition, form and distribution of the forest–alpine tundra ecotone, Indian Peaks, Colorado, USA. Erdkunde 39:286–295.

Ives, J. D. 1973. Permafrost and its relationship to other environmental parameters in a mid-latitude, high altitude setting, Front Range, Colorado Rocky Mountains. Pages 121–125 *in* Permafrost, the North American contribution to the Second International Conference, National Academy of Sciences, Washington, D.C.

Ives, J. D., editor. 1980. Geoecology of the Colorado Front Range: a study of alpine and subalpine environments. Westview, Boulder, Colo. 484 pp.

Ives, J. D., and K. J. Hanson-Bristow. 1983. Stability and instability of natural and modified upper timberline landscapes in the Colorado Rocky Mountains, USA. Mountain Research and Development 3:149–155.

Jarrett, R. D., and J. E. Costa. 1986. Hydrology, geomorphology, and dam-break modeling of the July 15, 1982, Lawn Lake Dam and Cascade Lake Dam failures, Larimer County, Colorado. U.S. Geological Survey, open-file report 84-612.

Knepper, D., editor. 1977. Natural hazards of northern Hinsdale County, Colorado. Report to NASA, Institute of Arctic and Alpine Research, University of Colorado, Boulder. 162 pp.

Lance, J. C. 1983. Hydrology and nonpoint pollution considerations for a freshwater wetlands model. Proceedings of the National Research Modeling Symposium. U.S. Department of Agriculture, Agricultural Research Service, Washington, D.C. 30:232–236.

Madole, R. F. 1976. Bog stratigraphy, radiocarbon dates, and Pinedale to Holocene glacial history in the Front Range, Colorado. Journal Research, U.S. Geological Survey 4(2):163–169.

Marr, J. W. 1967. Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Series in Biology 81. University of Colorado, Boulder. 134 pp.

Miller, C. D., and P. W. Birkeland. 1974. Probable pre-Neoglacial age of the type Temple Lake moraine, Wyoming. Arctic and Alpine Research 6:301–306.

Moss, A. J. 1979. Thin-flow transportation of solids in arid and non-arid areas: a comparison of processes. IAHS-AISH 128, Canberra, Australia.

National Oceanic and Atmospheric Administration. 1969–1989: Climatological data. National Oceanic Atmospheric Administration, National Climate Center, Asheville, N.C.

Nelson, R. A. 1953. Handbook of Rocky Mountain plants. Dale Stuart King, Tucson. 331 pp.

Outcalt, S. I., and J. B. Benedict. 1965. Photointerpretation of two types of rock glaciers in the Colorado Front Range, U.S.A. Journal of Glaciology 5(42): 849–856.

Peterman, Z. E., C. E. Hedge, and W. A. Braddock. 1967. Age of Precambrian events in the northeastern Front Range, Colorado. Journal of Geophysical Research 73:227–229.

Pitlick, J. C., and C. R. Thorne. 1987. Sediment supply, movement and storage in an unstable gravel-bed river. Pages 151–183 *in* C. R. Thorne, J. C. Bathurst, and R. D. Hey, editors. Sediment transport in gravel-bed rivers. John Wiley & Sons, New York.

Richmond, G. M. 1960. Glaciation of the east slope of Rocky Mountain National Park, Colorado. Geological Society of America Bulletin 77:1371–1381.

Sharpe, D. R. 1974. Mudflows in the San Juan Mountains, Colorado: flow constraints, frequency and erosional effectiveness. M.S. thesis, University of Colorado, Boulder. 131 pp.

Slaymaker, H. O. 1974. Alpine hydrology. Pages 134–155 *in* J. D. Ives and R. G. Barry, editors. Arctic and alpine environments. Methuen, London.

Sloey, W. E., F. L. Sprangler, and C. W. Fetter, Jr. 1978. Management of freshwater wetlands for nutrient assimilation. Pages 291–378 *in* R. E. Good, F. W. Whigham, and R. L. Simpson, editors. Freshwater wetlands: ecological processes and management potential. Academy, New York.

Summer, R. M. 1980. Soil sensitivity and resource management of the alpine tundra, Rocky Mountain National Park, Colorado. Pages 289–298 *in* Proceedings of the Second Conference on Scientific Research in National Parks. National Park Service, Washington, D.C.

Summer, R. M. 1982. Field and laboratory studies on alpine soil erodibility, southern Rocky Mountains, Colorado. Earth Surface Processes and Landforms 7:153–266.

Thorn, C. E. 1976. Quantitative evaluation of nivation in the Colorado Front Range. Geological Society of America Bulletin 87:1169–1178.

Thorn, C. E. 1978. A preliminary assessment of the geomorphic role of pocket gophers in the alpine zone of the Colorado Front Range. Geografiska Annuler 60A:181–187.

Thorn, C. E. 1982. Gopher disturbance: its variability by Braun-Blanquet vegetation units in the Niwot Ridge alpine tundra zone, Colorado Front Range, U.S.A. Arctic and Alpine Research 14:45–51.

Trench, N. 1978. The geomorphology and paleoenvironmental history of the Lake City landslide complex, southwestern Colorado. M.S. thesis, University Colorado, Boulder. 127 pp.

U.S. Geological Survey. 1961. Estes Park. 1957: Trail Ridge. U.S. Geological Survey Quadrangle Maps 1:24,000. Washington, D.C.

Vitek, J. D., A. L. Deutch, and C. G. Parson. 1981. Summer measurements of dissolved ion concentrations in alpine streams. Blanca Peak region, Colorado. Professional Geography 33:436–444.

Wallace, R. G. 1967. Types and rates of alpine mass movement, west edge of Boulder County, Colorado Front Range. M.S. thesis, Ohio State University, Columbus.

Washburn, A. L. 1979. Geocryology: a survey of periglacial processes and environments. Arnold, London. 280 pp.

White, S. E. 1971. Rock glacier studies in the Colorado Front Range, 1961–1968. Arctic and Alpine Research 3:43–76.

White, S. E. 1976. Rock glaciers and block fields: review and new data. Quaternary Research 6:77–97.

White, S. E. 1981. Alpine mass movement forms (noncatastrophic): classification, description and significance. Arctic and Alpine Research 13(2):127–137.

Windel, J. T., B. E. Willard, D. J. Cooper, S. Q. Foster, C. F. Knud-Hansen, L. P. Rink, and G. N. Kiladis. 1986. An ecological characterization of Rocky Mountain montane and subalpine wetlands. U.S. Fish and Wildlife Service, Biological Report 86(11):298.

Young, A., and I. Saunders. 1986. Rates of surface processes and denudation. Pages 3–27 *in* A. D. Abrahams, editor. Hillslope processes. Allen & Unwin, London.

Geochemistry of Iron Oxides in the Roaring River Alluvial Fan, Rocky Mountain National Park, Colorado

M. Iggy Litaor

University of Colorado
Institute of Arctic and Alpine Research
Boulder, Colorado 80309

Richard B. Keigley

National Park Service
P.O. Box 168
Yellowstone National Park, Wyoming 82190

Abstract. The chemistry and mineralogy of iron oxides on the surface of the Roaring River alluvial fan in Rocky Mountain National Park, Colorado, were investigated. Buried soil organic matter and a high water table within the alluvial fan has produced a highly reduced environment that results in elevated dissolved and suspended iron (Fe) concentrations in the interstitial waters. The source of the iron is probably iron oxides within the buried soil and primary iron-bearing minerals such as hornblende, biotite, magnetite, and epidote in the sediments. When the iron-rich solutions reach the surface, the water rapidly oxidizes and amorphous ferric hydroxides precipitate. Between 190 and 370 mmol of iron per kilogram of surficial material were precipitated within 2 months. Noticeable decreases in the total amount of organic carbon (C) and extractable iron (20 and 30%, respectively) in the buried soil were observed during the study (1985–87), which implies a significant reduction in iron dissolution and subsequent deposition across the alluvial fan.

Introduction

The Lawn Lake dam released 10^6 m^3 of water and an estimated peak discharge of 500 m^3/s down the Roaring River valley (Costa and Jarrett 1984). A large alluvial fan was deposited at the mouth of the Roaring River (Fig. 1). The area of the alluvial fan is 171,200 m^2, the average thickness is 1.7 m, and the calculated sediment volume is 191,000 m^3. The texture of the alluvial fan varies from an average size of 2.2 m (boulder) at the head of the fan to sand size at the toe of the fan. Sediment structure, texture, color, and depositional mechanisms were recently described by Blair (1987). The Roaring River allu-

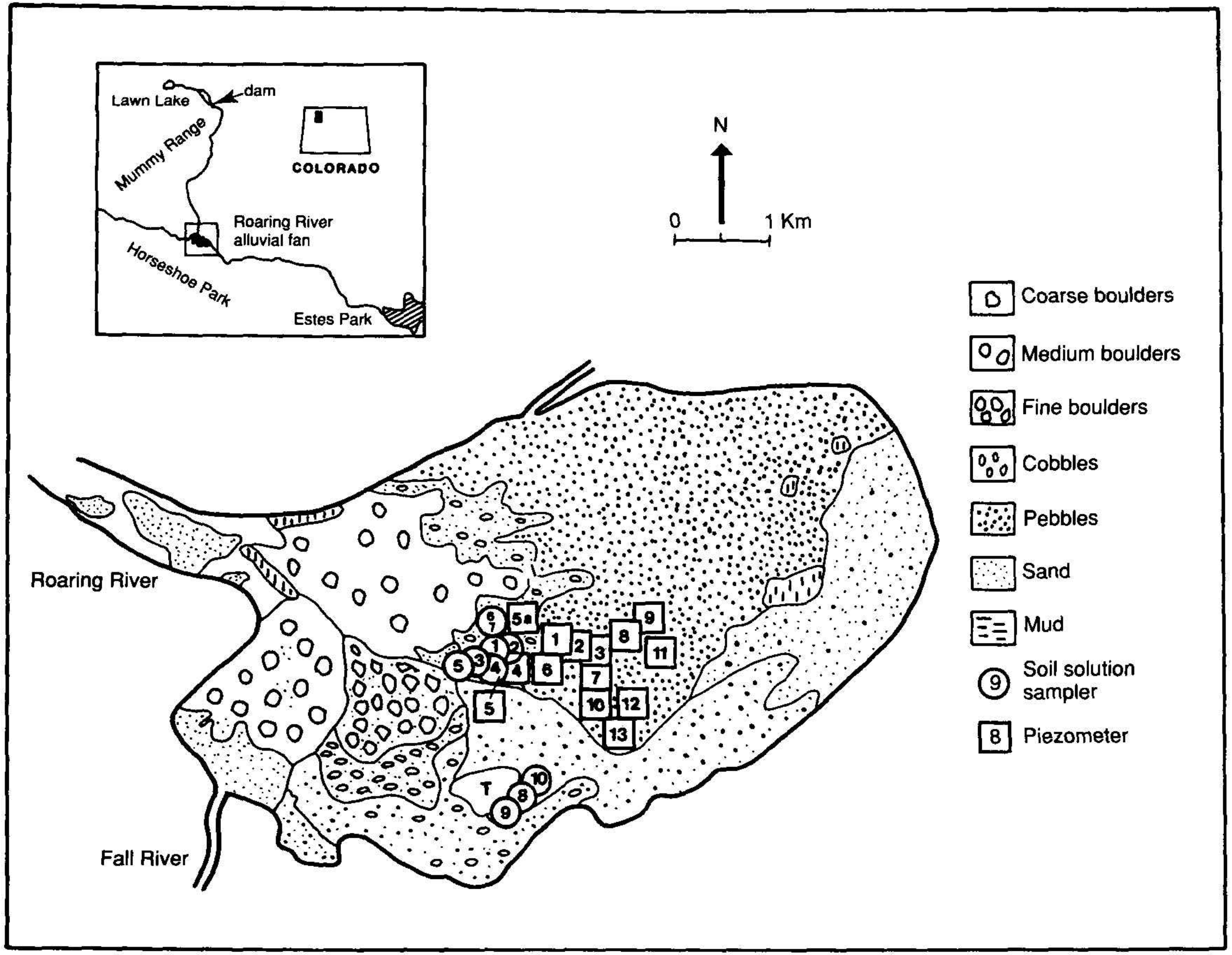


Fig. 1. Roaring River alluvial fan (adapted from Blair 1987). *Numbers* refer to the sites where ceramic porous cup samplers and piezometers are located. The T site is unaffected from the flood.

vial fan dammed the Fall River in Horseshoe Park upstream from the fan, forming a small lake.

While most trees survived the immediate effects of the flood, herbaceous vegetation was covered by sediments. Since the flood, shoots of rhizomatous species such as reedgrass (*Calamagrostis canadensis*) have emerged from buried vegetation to recolonize the site. In 1983, a flush of willow seedlings appeared in moist, sandy sites with densities as high as 20,000 seedlings per square meter; survivorship after 4 years varied greatly (Keigley, unpublished data). Iron oxide precipitate has stained rocks and sands (5YR 4/6 to 2.5YR 4/6-reddish brown, according to revised standard soil color charts) in moist areas of the alluvial fan following the Lawn Lake Flood. Locally, the precipitate has greatly changed the character of the surface of the alluvial fan and will undoubtedly affect the environment of germinating seeds in the future. A substantial uptake of Fe by woody plants was reported by Barrick and Nobel (1985, personal communication), who suggested that Fe toxicity may limit the ability of certain species to become established on the alluvial fan under current conditions. Clearly, Fe geochemistry will be an important factor in controlling vegetation succession.

The newly formed alluvial fan attracted the attention of many scientists and tourists alike. The presence of a well-dated deposit with well-defined hydrological conditions has enabled us to investigate the geochemistry of Fe and to provide geochemical guidelines for present and future geobotanical studies. To achieve this end, sediments and interstitial waters were sampled and various chemical and mineralogical analyses were performed to (1) evaluate the mechanism of Fe weathering and precipitation, (2) determine the source of the iron oxides, and (3) study the spatial and temporal variations of iron oxides in the study area.

Field Techniques

On the basis of examination of aerial photographs and preliminary surveys of sediment and iron oxides, 10 representative sites were selected across the alluvial fan and sampled during the summers of 1985–87. The sites are referred to as alluvial fans 1 through 10 (Fig. 1). Fourteen piezometers were installed along a geobotanical grid to measure the depth and seasonal fluctuation of the water table (Fig. 1). Five pits were excavated, and sediment was sampled for chemical and mineralogical analyses. To determine the rate of Fe precipitation, the surfaces of two sites were scraped after a 2-month accumulation in the summer of 1986, and the Fe content of the uppermost layer was determined. To assess the spatial variability of the freshly precipitated iron oxides across the alluvial fan, 15 sites along the geobotanical grid were scraped in the summer of 1987, and the Fe content of the uppermost layer was determined in each.

Sediment interstitial waters were sampled by ceramic porous cup samplers at each of the 10 sites in the summers of 1985–87. The location and depth of the samplers, pits, and scraped surfaces are summarized in Table 1. The installation, cleaning procedures, and other pertinent information are summarized by Litaor (1988).

When sampling soil interstitial water for iron chemistry, several things should be considered. Severson and Grigal (1976) recommended that an upper tension of 0.01 MPa (megapascal) must be applied to the soil water sampler to monitor solutions that are moving freely in the sediments. If such a low tension is applied, relatively high partial pressure of oxygen ($10^{-3.03}$ to $10^{-3.2}$ MPa) remains in the chamber of the sampler. Sung and Morgan (1980) postulated a general rate law for ferrous oxidation:

$$\frac{-d[\mathrm{Fe(II)}]}{dt} = \frac{\mathrm{KH}[\mathrm{O_2(aq)}]}{[\mathrm{H^+}]}[\mathrm{Fe(II)}]$$

where at 20° C, $\mathrm{KH} = 3 \times 10^{-12}\ \mathrm{min^{-1}\ mol\ liter^{-1}}$.

For practical purposes the equation means that oxidation of ferrous to ferric iron in dilute oxygenated aqueous solutions (ionic strength <0.1) takes place in a matter of seconds. Thus, the following sampling procedure was devised: the chamber of the sampler was thoroughly flushed with inert gas (Ar) before a vacuum was applied. The vacuum was left on for 2–3 h, after which the electrodes apparatus (Eh, pH, and temperature), the filter unit, and the collection vessel were thoroughly flushed with argon and sealed firmly to prevent oxygen from intercepting the extracted solution. The pH, Eh, electrical conductivity, and temperature were recorded, and at least 50 mL of solution were filtered (0.1μm) and immediately preserved with concentrated HCl (hydrochloric acid) for ferrous iron (Fe[II]) determination. The rest of the sample was filtered (0.45μm) and kept cool (4° C) for determination of anions, dissolved organic carbon (DOC), and carbohydrate.

Table 1. *Depth and redox characteristics of the study sites.*

Site[a]	Depth (cm)	Site characteristics
AF 1 (pit)	30	reducing zone
AF 2 (pit)	5	interface reducing–oxidizing zone
AF 3 (scraped surface)	2	oxidizing zone
AF 4 (scraped surface)	35	interface reducing zone
AF 5 (pit)	40	reference site (no iron stains)
AF 6 and 7[b] (pit)	30	reducing zone
AF 8 —	5	oxidizing zone
AF 9 —	2	oxidizing zone
AF 10 —	35	reducing zone

[a] AF = Alluvial fan; 1–10 refers to site (see Fig. 1).
[b] 6 and 7 = two samplers in the same hole.

The Eh measurements were performed potentiometrically using platinum and calomel electrodes. One of the most common problems with Eh measurement is the continuous change (drift) of the electromotive force for long periods. To circumvent this problem, the Eh was measured for a sufficient time to allow temperature equilibration inside the reference electrode (Lindberg 1983). In addition, Muller's (1969) method, which predicts the stable potential at infinite time, was used to estimate the Eh of the samples with drifting potentials. The potential of the reference electrode was checked against a buffer (Zobell solution) as described by Wood (1976).

Laboratory Methods

The Fe(II) concentrations were determined by differential pulse polarography (DPP) using Bioanalytical Systems, BAS-100 electrochemical analyzer interfaced with an EG & G PAR (Model 303A mercury electrode). Five milliliters of acidified sample were purged with argon for 10 min, then 5.0 mL of deoxygenated 0.1M pyrophosphate was added and the differential pulse polarography was performed with the following electrical parameters (relative to saturated Ag/AgCl electrode): initial (mV) = –50, final (mV) = 500, pulse (mV) = –100, scan (mV/s) < 10, peak (mV) = –350, and drop time (s) 0.5. These parameters and other related laboratory practices concerning Fe determination by DPP were empirically established in the geochemical laboratory of the Department of Geological Sciences, University of Colorado at Boulder (John Kempton 1986, personal communication).

Major cations (Ca, Mg, Na, K), total iron, and silica were analyzed by atomic absorption spectrophotometry (Perkin–Elmer Model 2280). Anion concentrations (F, Cl, PO_4, NO_3, SO_4) were analyzed by ion exchange chromatography on a Dionex system 2110i interfaced to a Spectra-Physics SP4270 integrator. The DOC was determined by Beckman carbon analyzer (oxidative, combustion, and infrared detection). Carbohydrates were determined by the phenol–sulfuric acid titration method.

Skogerboe and Wilson (1981) suggested that humic substances play an important role in mineral weathering. Therefore, a column experiment was conducted to assess the importance of humic substances isolated from the soil interstitial waters in weathering reactions of heavy minerals from the sediments of the study area. Fulvic acids (FA) from two interstitial water samples were extracted and characterized by the XAD-8 procedure of Thurman and Malcolm (1981).

Five grams of heavy minerals were separated from the sediment by the bromoform (sp gr 2.89) method. The heavy minerals were thoroughly washed with acetone followed by distilled water to remove any bromoform residue. The heavy minerals were also treated with H_2O_2 (hydrogen peroxide) to remove any organic matter. The iron oxide coating on the heavy minerals was removed by four successive citrate–bicarbonate–dithionite extractions. Then

5 g of heavy minerals were placed in a glass column and distilled water was pumped through the column for 1 week. The distilled water effluent was sampled by the end of the week, and the Fe content was determined.

One hundred milligrams of lyophilized FA (with mean carboxylic content and mean total acidity of 9.5 and 11.8 μeq/mg C, respectively) were placed in 900 mL distilled water and appropriate amounts of CaCl, KCl, and $NaHCO_3$ were added to match the original ionic strength of the interstitial water samples. The pH of the solution was adjusted to the mean pH of the interstitial waters. A subsample of the lyophilized FA was taken to determine the background amount of Fe in the humic substances. The solution was pumped through the column for 1 week, and several subsamples were taken to determine the amount of Fe dissolved from the heavy minerals.

The extractable Fe content on the surface and the sediments of the alluvial fan and in the buried soil were determined by the citrate–bicarbonate–dithionite (crystalline) and oxalate (amorphous) methods (Jackson et al. 1986). Organic carbon content in the sediments and the buried soil was determined by dichromate titration (Allison 1965). The iron oxides, which formed a surface layer (2–5 cm thick), were sampled for mineralogical analyses using a scanning electron microscope. The primary minerals in the sediments were identified by X-ray diffraction and petrographic microscopy.

Iron speciation and Fe^{2+} activity were calculated by the PHREEQE geochemical computer model (Parkhurst et al. 1980) using the thermodynamic values given by Nordstorm et al. (1984). Thermodynamic calculations were corrected for temperature, and ionic strength corrections were made using the extended Debye–Huckel equation.

Results and Discussion

General Characteristics of the Sediment Interstitial Waters

The major element concentrations in the sediment interstitial waters are summarized in Table 2. High correlations ($P < 0.001$) were observed among the concentrations of sodium, calcium, and magnesium, and moderate correlation ($P < 0.001$) with total alkalinity (Table 3). These relations suggest that all the major ions probably originated from the same weathering source, such as primary minerals within the alluvial fan. The organic matter content in the alluvial fan was negligible (<0.9%). However, the soil that was buried by these sediments contains up to 15% organic carbon. This buried soil with the high content of organic carbon and sandy loam texture prevents shallow groundwater from infiltrating downward and supporting a high water table for most of the summer. The water table was observed at a depth of 2 m or more at the head of the alluvial fan, whereas near-surface depths were observed along the geobotanical grid. Little fluctuation in depth of the water table was recorded. The sources of the groundwater are snowmelt and summer thunderstorms. The combination of a high water table (which restricted atmospheric oxygen diffu-

Table 2. *Statistics of the major ions in the sediment interstitial waters in the summers of 1985–1987* (n = *123*).

Ion	Mean	Standard deviation	Range (mg/L^{-1})
Na	3.5	1.3	2.0–7.1
K	5.9	4.5	0.9–1.9
Ca	12.8	6.4	2.8–8.6
Mg	5.2	1.4	2.1–6.8
Fe_T[a]	8.4	6.5	0.0–47.2
Cl	4.4	4.1	0.7–13.6
SO_4^{2-}	0.5	0.9	0.0–4.4
ALK_T[b]	82.1	31.9	35.0–139.0
H_4SiO_4	4.1	1.7	1.7–9.4
SC[c] (μS/cm^{-1})	94.0	40.0	23.0–247.0
pH	6.9	0.4	5.8–7.8

[a]Fe_T = Total dissolved iron.
[b]ALK_T = Total alkalinity.
[c]Specific conductance.

Table 3. *Correlations among major ions in the sediment interstitial waters* (P < *0.001*).

Ion	Na	Ca	Mg	Ct	Fe
Na	—	—	—	—	—
Ca	0.75	—	—	—	—
Mg	0.77	0.92	—	—	—
ALK_T[a]	0.50	0.55	0.50	—	—
Fe	–0.03	–0.16	–0.27	0.45	—

[a]ALK_T = Total alkalinity.

sion) and buried organic matter yielded high partial pressure of carbon dioxide (CO_2; Table 4), probably due to organic matter decomposition. Hence, the elevated CO_2 promotes hydrolysis as one of the major weathering mechanisms within the alluvial fan. The outcome of the hydrolysis process is a large amount of total alkalinity, and subsequently near or above neutral values of pH (Table 2).

The moderate correlation between total dissolved Fe and total alkalinity also suggests that iron hydroxide species (Table 4) are important components in total alkalinity. No correlation was found between Fe and other major cations (Table 3), which suggests that two different mechanisms are operating simultaneously in the study area: hydrolysis reactions that control cations and total alkalinity concentrations, and redox-dependent reactions that affect Fe concentrations in the sediment interstitial waters.

Table 4. *Statistics of iron species (log activity mol/L) in the sediment interstitial waters from five study sites (n = 10).*[a]

	AF1		AF2		AF3		AF4		AF5	
	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD
Fe^{2+}	−3.8	0.4	−4.3	0.3	−6.6	1.3	−3.7	0.5	−5.4	0.7
$FeOH^{+}$	−6.8	0.7	−7.2	0.2	−9.4	0.8	−7.0	0.4	−7.0	0.5
$Fe(OH)_2^{+}$	−5.3	1.2	−4.8	0.7	−5.7	0.2	−5.0	0.3	−4.6	0.1
$Fe(OH)_3^{0}$	−6.6	1.6	−6.1	0.91	−6.81	0.7	−6.6	0.5	−5.7	0.1
$Fe(OH)_4^{-}$	−7.8	2.0	−7.3	1.1	−7.9	1.1	−7.9	0.6	−6.7	0.2
$Fe(OH)^{2+}$	−8.5	0.9	−8.1	0.6	−9.1	0.6	−7.8	0.1	−8.1	0.3
log CO^{2g}	−1.5	0.2	−1.7	0.2	−2.2	0.4	−1.6	0.4	−2.0	0.2

[a] AF = alluvial fan; 1–10 refer to sites (see Fig. 1).

Iron Chemistry of the Sediment Interstitial Waters

The chemical behavior of Fe and its solubility in water depend strongly on the redox potential and pH of the water (Lindsay 1979). A decrease in redox potential and pH increase the solubility of Fe in natural waters. Gotoh and Patrick (1974) found the critical redox potential of Fe reduction and dissolution at pH 6 and 7 was between 300 and 100 mV and was −100 mV at pH 8, but at pH 5, appreciable reduction occurred at 300 mV. The Eh, pH, and Fe(II) concentrations of selected samples are summarized in Table 5. These results suggest that surface waters (sites 3, 8, and 9) have significantly higher Eh values ($P < 0.05$) and lower Fe(II) concentrations ($P < 0.001$) than water collected at greater depths.

Large accumulation of Fe stains on the filters (0.1 μm) indicated that suspended material is an important form of the transported Fe within the alluvial fan. In fact, in all the samples studied, the concentrations of suspended Fe

Table 5. *Statistics of Fe(II), pH, and Eh of the 10 study sites (n = 50).*

	Fe(II) (mg/L^{-1})		pH		Eh(mV)	
Site	Mean	SD[a]	Mean	SD	Mean	SD
AF1	11.2	8.0	6.8	0.3	319	85
AF2	6.4	4.7	7.1	0.2	322	79
AF3	0.5	0.8	7.1	0.3	385	86
AF4	16.4	14.3	6.8	0.3	322	59
AF5	1.2	0.9	7.0	0.3	344	14
AF6 and 7[b]	22.3	16.6	6.8	0.5	305	21
AF8	1.8	1.6	6.9	0.4	357	63
AF9	2.7	1.2	7.3	0.3	361	42
AF10	12.6	6.7	6.8	0.3	297	71

[a] Standard deviation.

[b] Site AF6 and 7 is an experimental site in which two samplers were installed together for variety of comparative studies, such as the effects of filter size, duration of argon flushing, and air versus argon atmosphere.

were much greater than the concentration of dissolved Fe (Table 6). Smith and Hem (1972) showed that in neutral conditions aluminum polymers grew until they became crystalline particles of a few hundredths to a few tenths of a micron in diameter. Hem (1985) suggested that similar polymerization characteristics can be found in Fe chemistry, too. Recently, Fox (1988) showed that the concentration of dissolved Fe in many river waters is in near saturation in respect to colloidal ferric hydroxide $Fe(OH)_{2.35}$. Using the suggested log *K* for this phase (Fox 1988) and plotting it in a solubility–stability diagram (Fig. 2) suggests that most of the Fe concentrations in the sediment interstitial waters are oversaturated in respect to this colloidal phase. However, this oversaturation probably resulted from the contribution of ferrous-organic complexes to the total Fe(II) determination. Similarly, the concentration of dissolved Fe(II) at the surface site 3 (Fig. 2) is oversaturated with respect to amorphous iron hydroxide $Fe(OH)_3$, probably because of the contribution of ferrous-organic complexes to the total Fe(II) determination.

Origin of the Iron Oxides

The combination of a high water table and recently buried organic matter—coupled with sediments containing iron-bearing minerals and newly buried

Table 6. *Iron concentrations of selected sites and dates (suspended forms >0.1 μm).*

		Fe(II) mg/L	
Site	Date	Suspended	Dissolved
AF1	7-2-86	86.9	4.9
	7-22-86	85.0	9.6
	8-8-86	84.8	5.9
	9-16-86	100.1	15.3
AF3	7-2-86	38.0	0.2
	7-22-86	8.8	0.3
	8-8-86	8.4	0.1
	9-16-86	24.4	2.9
AF4	7-2-86	451.0	3.9
	7-22-86	104.0	16.4
	8-8-86	429.0	35.2
	9-16-86	439.0	25.2
AF5	7-2-86	779.0	1.7
	7-22-86	27.9	2.4
	8-8-86	14.2	0.3
	9-16-86	12.9	—
AF6 and 7	7-22-86	17.1	1.1
	8-8-86	36.8	24.0
	9-16-86	140.0	11.3
AF10	6-20-86	1904.0	1.5
	7-2-86	429.0	10.3
	8-8-86	34.2	9.4

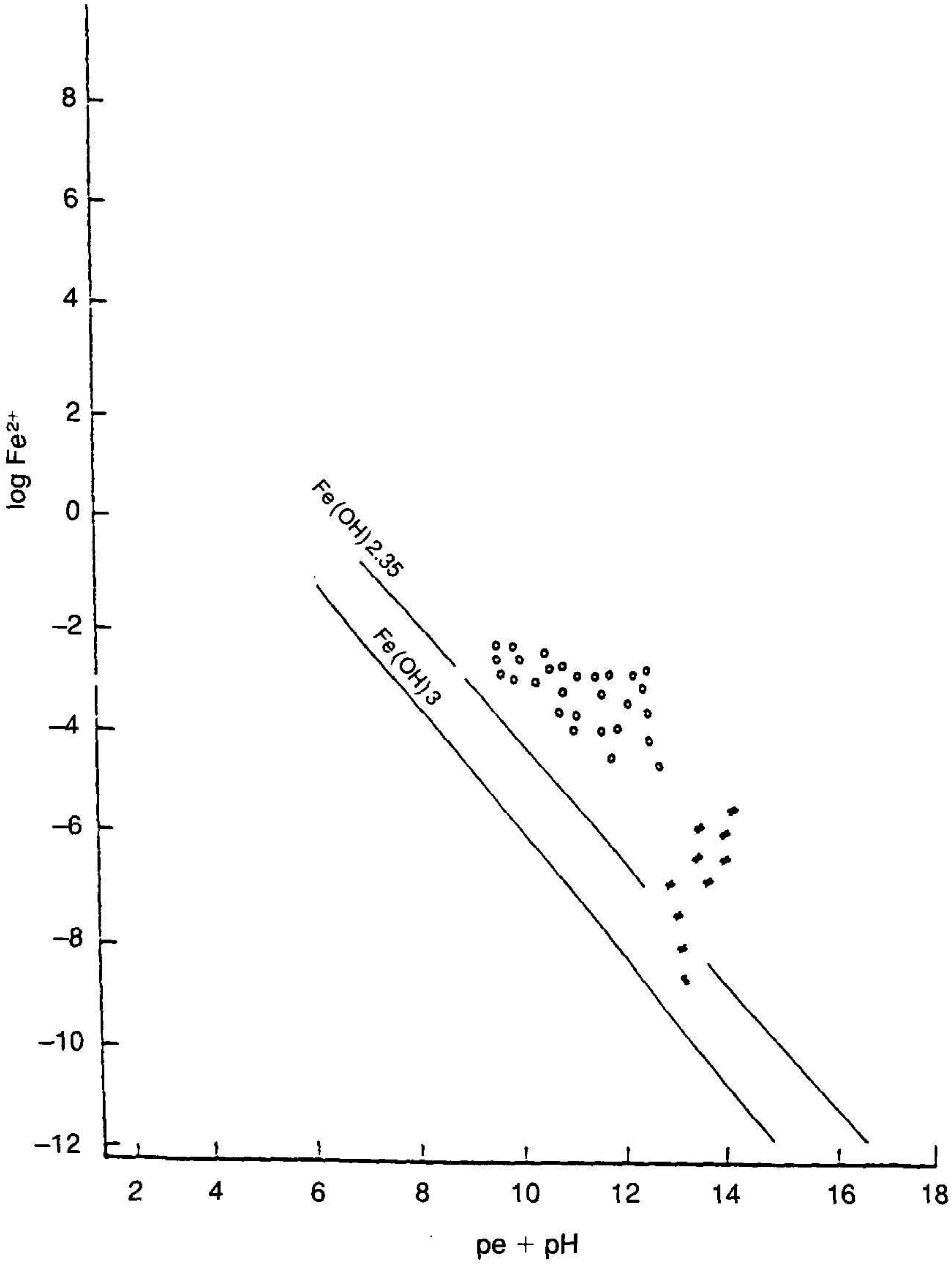


Fig. 2. The effect of redox potential and pH (pe + pH) on Fe solubility and mineral stability in the sediment interstitial waters. # = site 3; o = all other sites.

iron oxides and hydroxides—has generated high concentrations of dissolved and suspended Fe in the sediment interstitial waters. During summer months, a high water table has restricted diffusion of atmospheric oxygen and enhanced a rapid decomposition of organic matter. The organic matter content in the alluvial sediment is negligible (<0.9%), but the buried soil contains up to 15% organic carbon. The sediments of the alluvial fan contain primary minerals with contents of Fe that are relatively high, including amphiboles, biotites, magnetite, and epidote. Moreover, the extractable Fe content from the buried soil consists of 0.5 mol kg^{-1} of amorphous Fe and 0.2 mol kg^{-1} of crystalline and free Fe, which are readily available for reduction processes. The sediment interstitial waters in the study area contain large amounts of dissolved organic carbon ($\bar{x} = 40 \pm 29$ mg/L; $n = 65$). Several highly reduced samples contained up to 90 mg/L in which 15–30% of the carbon was in the form of phenol-titratable carbohydrates. Hence, reduction of iron oxides within the buried soil is probably achieved by oxidation of carbohydrates. Under such conditions, the buried iron oxides are highly unstable and will release large amounts of Fe to solution. Indeed, in laboratory studies, Lovley and Phillips (1986a, 1986b) showed that in anaerobic sediments, a greater potential exists for ferric iron (Fe[III]) reduction with fermentable substrates, fermentation products, and complex organic matter as electron donors. Lovley and Phillips demonstrated that amorphous ferric oxyhydroxide in glucose enrichments was easily reduced to produce high concentrations of Fe(II). Similarly, Couto et al. (1985) found that small amendments of sucrose (1%) increased the amount of Fe(II) by 1,700% in some Brazilian soils.

Wilson and Weber (1979) showed that soil fulvic acids are capable of reducing Fe(III) to Fe(II) under conditions characteristic to natural waters. During the column experiment, approximately 100 μg/L Fe were released from 5 g heavy minerals (chiefly amphiboles, biotites, epidote, and magnetite) by the FA, which implied that the release of Fe from the heavy minerals was extremely slow. Similarly, Skogerboe and Wilson (1981) found that after 15 h, only 60 μg/L of Fe(II) were dissolved from 2 mg of freshly precipitated $Fe(OH)_3$ by FA, suggesting slow reduction of the solid. However, these heavy minerals are an important source of Fe in the formation of the iron oxides due to large volume of sediments (190,000 m^3) in the alluvial fan that contain 10–20% heavy minerals in their sandy fraction.

The sediment interstitial waters that contain large amounts of suspended and dissolved Fe through one of the chemical reactions proposed earlier follow the local hydraulic gradient and occasionally will reach the surface. Subsequently, these waters will rapidly oxidize and the Fe will precipitate out, leaving relatively little dissolved Fe in the surface waters (Table 5). Scanning electron microscope studies showed that an amorphous Fe compound was formed in the surface of the Roaring River alluvial fan (Fig. 3). Kevex X-ray fluorescence analysis of these compounds showed no isomorphic substitution (e.g., aluminum) in the compound structure.

Spatial and Temporal Variations

The rate of precipitation of iron oxide was monitored qualitatively; the surfaces near sites 3 and 4 (Fig. 1) were scraped free of their iron oxides in the beginning of summer 1985. By the end of summer, the iron oxides reprecipitated and the scraped areas became undistinguishable from their undisturbed sur-

Fig. 3. Scanning electron microscope photos (SEM; × 20,000). Amorphous $Fe(OH)_3$ is the only Fe mineral on the surface of alluvial fan.

roundings. During summer 1986, the same areas were scraped again in 2-month intervals and the extractable Fe content (BCD) was determined (Table 7). About 470–540 mmol of Fe kg^{-1} of surface material were precipitated in 1 year (1985–86), while 190–370 mmol Fe kg^{-1} of surface material were precipitated in 2 months in summer 1986. This precipitation pattern suggests that iron oxides have mostly precipitated during the summer months, when a high water table enhanced reduction and transport processes. The difference in iron oxides distribution between the two sites is explained by their local hydrological properties. Site 3 is located in a small stream bed where water flows most of the summer, while site 4 is considerably drier. Moreover,

Table 7. *Iron extracts (CBD) from the surface layer of the Roaring River alluvial fan* (n = *3*).

Site	Date	Fe ($mmol/kg^{-1}$)
AF3	7-22-86 (after 1 year)	540
AF3	9-16-86 (after 2 months)	370
AF4	7-22-86 (after 1 year)	470
AF4	9-16-86 (after 2 months)	190

in higher order streams across the alluvial fan, Fe bacteria have colonized the surface of the sediments, coloring them bright red (10R 6/8 according to the revised standard soil color chart).

The distribution of extractable Fe content across the surface of the alluvial fan and its relation to the depth of the water table is illustrated in Fig. 4. A large variability exists in the amount of extractable Fe within each site. The values depicted in Fig. 4 are the weighted mean of five measurements per site. No iron oxides have been precipitated in the area of piezometers 5 and 5a where the water table fluctuates around 75 cm and deeper. An abrupt increase in iron oxides was observed in areas where the water table was only 40 cm from the surface. This finding suggested an occasional rise in the water table level, especially after intense summer storms. The highest concentrations of iron oxides were found in areas where the water table is almost at the surface (Fig. 4).

The concentration of Fe and the values of pH and specific conductance of the interstitial waters did not change significantly during the study (Table 8).

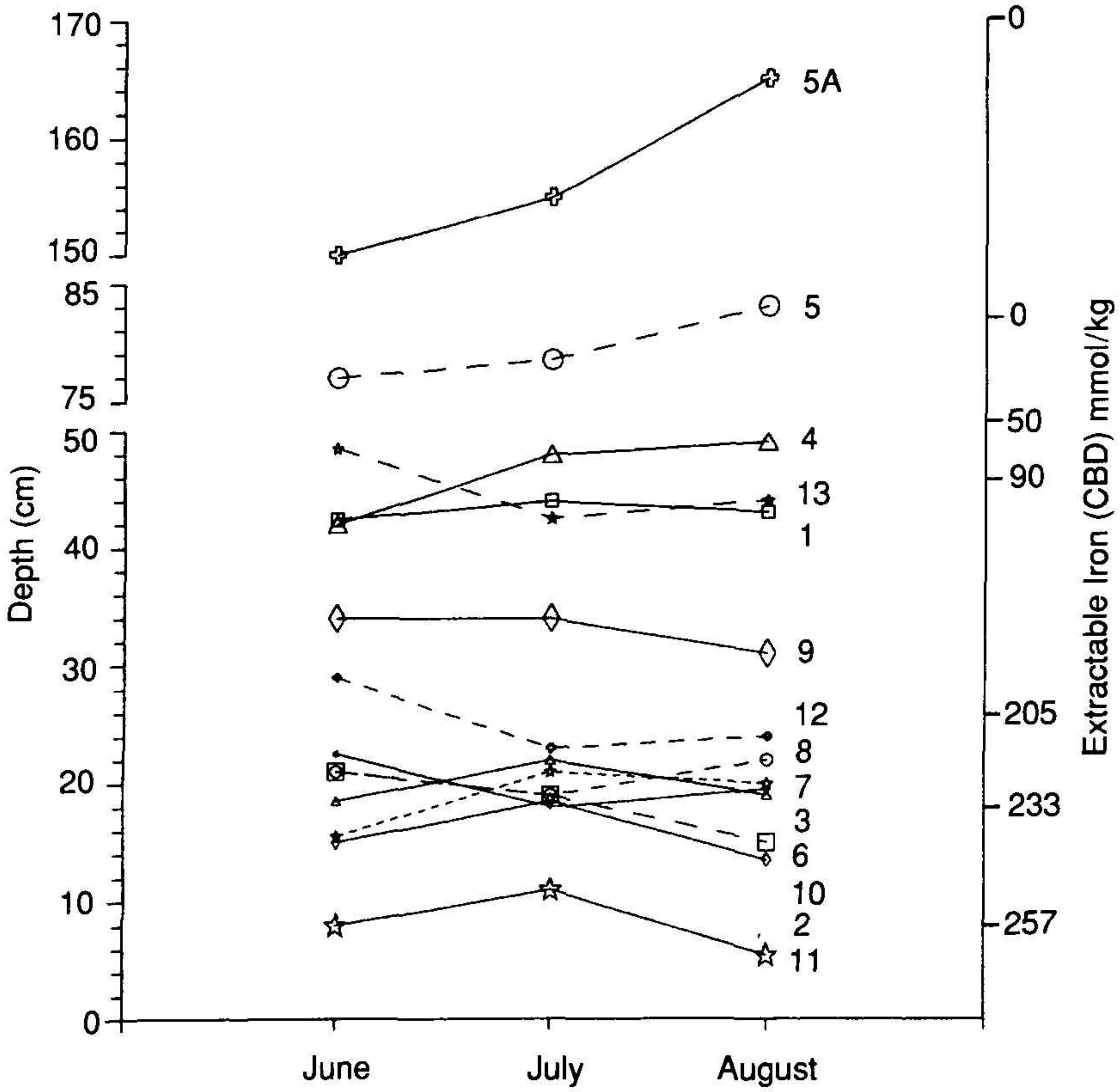


Fig. 4. Depth to water table and iron oxide concentrations across the geobotanical grid (1987 season).

Table 8. *Temporal variations of dissolved and suspended iron, pH, Eh, and specific conductance (SC), 1985–1987.*

		Fe(II) suspended	pH		SC	
Year	*n*	(mg/L)	dissolved	Eh	mV	μS/cm^{-1}
1985	38	154±120	6.6±9.4	6.8±0.3	309±67	103±44
1986	40	357±425	9.9±12	7.0±0.4	357±70	95±36
1987	45	120±100	8.4±11	7.1±0.4	367±81	86±31

However, a noticeable decrease in the total amount of organic carbon and extractable Fe (20 and 30%, respectively) in the buried soil were observed between 1985 and 1987. The decrease in organic carbon content may restrict the source of electrons for future reduction processes and, consequently, may reduce the rate of Fe dissolution and subsequent precipitation across the alluvial fan.

Conclusions

The high concentrations of dissolved, particulate, and suspended Fe in the sediment interstitial waters are the result of oxidation of organic matter and subsequent reduction and dissolution of iron oxides in the buried soil and iron-bearing minerals of the alluvial fan. Most of the Fe in the interstitial waters is transported as suspended iron. About 470–540 mmol of Fe kg^{-1} of surficial material were precipitated during 1986, of which 190–370 mmol Fe kg^{-1} of surficial material were precipitated in summer. The concentration of extractable Fe across the surface of the alluvial fan is highly dependent on the proximity of the water table to the surface.

Acknowledgments

This research was partially supported by Rocky Mountain National Park and the Long Term Ecological Research Project NSF Grants BSR-8012095 and BSR-8514329. We thank J. Kempton, R. D. Lindberg, D. M. McKnight, and D. D. Runnells for their comments and suggestions.

Literature Cited

Allison, L. A. 1965. Organic carbon. *In* C. A. Black et al., editors. Methods of soil analysis, part 2. Agronomy 9:1367–1378.

Blair, T. C. 1987. Sedimentary processes, vertical stratification sequences, and geomorphology of the Roaring River alluvial fan, Rocky Mountain National Park, Colorado. Journal of Sedimentary Petrology 57:1–18.

Costa, J. E., and R. D. Jarrett. 1984. The 1982 Lawn Lake and Cascade Lake dam failures. *In* J. E. Costa. AMQUA 1984. Field trip guidebook 8. University of Colorado, Boulder.

Couto, W., C. Sanzonowicz, and De O. A. Barcellos. 1985. Factors affecting oxidation-reduction processes in an oxisol with seasonal water table. Soil Science Society of America Journal 49:1245–1248.

Gotoh, S., and D. H. Patrick. 1974. Transformation of iron in a waterlogged soil as influenced by redox potential and pH. Soil Science Society of America Proceedings 38:66–71.

Fox, L. E. 1988. The solubility of colloidal ferric hydroxide and its relevance to iron concentrations in river water. Geochimical et Cosmochimica Acta 52:771–777.

Hem, J. D. 1985. Study and interpretation of the chemical characteristics of natural water. 3rd edition. U.S. Geological Survey Water-Supply Paper 2254. 263 pp.

Jackson, M. L., C. H. Lim, and L. W. Zelazny. 1986. Oxides, hydroxides, and aluminosilicates. *In* A. Klute, editor. Methods of soil analysis, part 1. Second edition. Agronomy 9:101–142.

Lindberg, R. D. 1983. A geochemical appraisal of oxidation-reduction potential and interpretation of Eh measurements of ground water. Ph.D. dissertation, University of Colorado, Boulder. 471 pp.

Lindsay, W. L. 1979. Chemical equilibria in soils. John Wiley & Sons, New York. 439 pp.

Litaor, M. I. 1988. Review of soil solution samplers. Water Resources Research 24:727–733.

Lovley, D. R., and E. J. P. Phillips. 1986a. Organic matter mineralization with reduction of ferric iron in anaerobic sediments. Applied Environmental Microbiology 51:683–689.

Lovley, D. R., and E. J. P. Phillips. 1986b. Availability of ferric iron for microbial reduction in bottom sediments of freshwater tidal Potomac River. Applied Environmental Microbiology 52:751–757.

Muller, R. H. 1969. Commentary (on new direction for ion selective electrodes). Analytical Chemistry 41:113A–116A.

Nordstorm, D. K., S. D. Valentime, J. W. Ball, N. L. Plummer, and B. L. Jones. 1984. Partial compilation and revision of basic data in the WATEQ programs. U.S. Geological Survey Water-Resources Investigations Report 84-4186.

Parkhurst, D. L., D. C. Thorstenson, and N. L. Plummer. 1980. PHREEQE—A computer program for geochemical calculations. U.S. Geological Survey, Water Resources Investigations 80-96. 210 pp.

Severson, R. C., and D. F. Grigal. 1976. Soil solution concentrations: effect of extraction time using porous cup under constant tension. Water Resources Bulletin 12:1161–1170.

Skogerboe, R. K., and S. A. Wilson. 1981. Reduction of ionic species by fulvic acid. Analytical Chemistry 53:228–232.

Smith, R. W., and J. D. Hem. 1972. Effect of aging on aluminum hydroxide complexes in dilute aqueous solutions. U.S. Geological Survey Water-Supply Paper 1827-D. 51 pp.

Sung, W., and J. J. Morgan. 1980. Kinetics and product of ferrous iron oxygenation in aqueous systems. Environmental Science Technology 14:561–568.

Thurman, E. M., and R. L. Malcolm. 1981. Preparative isolation of aquatic humic substances. Environmental Science Technology 15:463–466.

Wilson, S. A., and J. H. Weber. 1979. An EPR study of the reduction of vanadium(V) to vanadium (IV) by fulvic acid. Chemical Geology 26:345–354.

Wood, W. W. 1976. Guidelines for collection and field analysis of ground-water samples for selected unstable constituents. Techniques for water-resources investigations of the U.S. Geological Survey, book 1, chapter D2.

Micronutrient Status of Tree Species Affected by the Lawn Lake Flood in Rocky Mountain National Park, Colorado

Kenneth A. Barrick

University of Alaska Fairbanks
Department of Geography
Fairbanks, Alaska 99775

Mark G. Noble

University of Minnesota
Department of Plant Biology
St. Paul, Minnesota 55108

Abstract. The micronutrient status of trees exposed to an iron-enriched root zone was investigated following the Lawn Lake Flood in Rocky Mountain National Park. The species studied represent the upper montane in the Colorado Front Range, including ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), aspen (*Populus tremuloides*), and narrowleaf cottonwood (*Populus angustifolia*). The foliar concentration of Fe, Mn, B, Cu, Zn, and Mo was determined for flood-affected trees (dead, except cottonwood) and normal (healthy) trees. All seven species accumulated Fe, with mean Fe concentration ratios (enriched to normal) ranging from 2.0 to 7.6. A possible threshold of Fe toxicity was observed in five of the populations. A dose–response experiment on lodgepole pine seedlings revealed that a doubling of the Fe to Mn ratio might be a threshold of toxicity for the species. Cottonwood maintained a near normal Fe to Mn ratio despite consuming large amounts of Fe and Mn. The results should be of value in assessing the potential effects of altering the availability of Fe and Mn in forest soils and the effects of Fe and Mn excess in these tree species.

Introduction

The Lawn Lake floodwaters scoured soils from the Roaring River valley and deposited a large alluvial fan in Horseshoe Park. Postflood observations revealed that the flood deposits contained iron-enriched groundwater. The purpose of this research was to investigate the effect of the Fe enrichment on the micronutrient status of the exposed tree species. The Fe enrichment of the root zone provided an excellent opportunity to determine if mature trees were capable of excluding iron, or if high, possibly toxic, concentrations were consumed. The status of the other micronutrients—manganese, boron, copper, zinc, and molybdenum—was also investigated.

The flood-affected species represent the upper montane and subalpine forests of the Colorado Front Range, including ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), aspen (*Populus tremuloides*), and narrowleaf cottonwood (*Populus angustifolia*). Little is known about the threshold of nutrient excess in these forest species, and separating other environmental factors is difficult, so we conducted a dose–response experiment on lodgepole pine to assist in interpreting the results.

Postflood Environment

The unconsolidated sediments of the alluvial fan contained an active groundwater regime for several years following the flood. The water table was within a few centimeters of the surface across much of the flood-affected area and groundwater commonly seeped into shallow surface drainageways. The first evidence of Fe enrichment was highly visible. Yellow-orange ferric hydroxide precipitates stained the seepage points, drainage channels, and other surfaces. The mechanism of enrichment was uncertain, but possible Fe sources included the watershed's silicate rocks being weathered, the soils eroding in the Roaring River valley, or the soils and vegetation being buried by flood deposits. Forest soils commonly contain 0.7–4% Fe (Subcommittee on Iron 1979; for details on the Fe geochemistry of the Lawn Lake Flood deposits see Litaor and Keigley 1993). In addition, we suspected that the groundwater contained increased amounts of Mn, an element closely associated with Fe in soils.

Ferric iron (Fe^{3+}) complexes predominated across the surface of the alluvial fan. However, the groundwater submerged the root zone in an anaerobic environment, where the Fe was chemically reduced to the ferrous state (Fe^{2+}). Therefore, the postflood groundwater contained a large pool of plant-available Fe^{2+}. The Fe enrichment of the root zone led to the hypothesis that the exposed trees were absorbing large amounts of Fe, and that Fe toxicity—or imbalance in the other micronutrients—was involved in the depth of trees across the flood-affected area.

Ferric iron salts and complexes, like those found in normal aerated soils, must be solubilized before Fe can be absorbed by tree roots. Thus, Fe^{3+} must be reduced to Fe^{2+}, or bound by chelators. Trees normally regulate the uptake of Fe by reducing Fe^{3+} through acidifying the medium around the root when Fe is needed (Robb and Pierpoint 1983). Plant self-regulation is defeated when Fe^{2+} floods the root zone, unless the plant can selectively exclude Fe. The consumption of large quantities of micronutrients, including Fe and Mn, is known to be toxic in plants. One or more of the following is assumed to damage critical physiological functions: (1) the metal interferes with enzyme function; (2) the metal serves as an antimetabolite; (3) the metal forms a stable precipitate or chelate with an essential metabolite; (4) the metal catalyzes the decomposition of an essential metabolite; (5) the metal alters the permeability of cell membranes; or (6) the metal replaces important structural or electrochemically important elements in the cell (Bowen 1966).

Trees that suffered no apparent mechanical damage during the flood became chlorotic and succumbed shortly thereafter. By the summer of 1983—1 year after the flood—most of the conifers were dead or dying. Although a few lodgepole pine survived until 1984, most died within the first year. Many conifers located along the shore of Flood Lake, a lake dammed by the flood deposits, began to die in 1983, with the trend continuing into the summer of 1984. The deciduous trees appeared to be healthy until an aspen clone began to die shortly after producing leaves in the spring of 1984. By the summer of 1985, cottonwood was the only flood-affected species represented by healthy trees. Cottonwood remained healthy through the summer of 1990.

Methods

Field Sampling

We collected the foliage samples during the summer of 1984. The flood-affected cottonwood trees were sampled again in 1986 and 1987. All foliage samples were composite samples taken from the circumference of the tree. In conifers, we sampled the mature needle set from the previous growth-year. Most of the trees ranged in age from 20 to 90 years, with a few up to 150 years old.[1] All flood-affected trees were dead when sampled, except cottonwood.

We selected flood-affected trees from the perimeter of the alluvial fan where little or no sediment had accumulated, or in nearby backwater areas where the hydrologic regime was altered. Care was taken to avoid mechanically damaged, insect-damaged, or diseased trees. We selected the healthy, normal trees from nearby areas that best replicated preflood conditions (slope, aspect, soil moisture, and elevation).

---

[1] For detailed information on the age and DBH of the individual trees see Barrick and Noble (1985).

The sample size was as follows (n = flood-affected trees, normal trees): ponderosa pine, $n = 3,3$; lodgepole pine, $n = 5,4$; limber pine, $n = 1,3$; Engelmann spruce, $n = 2,3$; subalpine fir, $n = 6,3$; aspen, $n = 4,3$; and cottonwood, $n = 3,3$. The sample size of flood-affected trees was constrained by the availability of usable individuals.

Dose–Response Experiment

We conducted a dose–response experiment on 2-year-old lodgepole pine seedlings. The seedlings were Colorado nursery stock germinated from seed collected in a local lodgepole forest. Seedlings with similar color, height, circumference, and needle length were placed in four groups by random selection. Each group contained 14 trees ($n = 14$). The trees were potted individually in a sandy loam-growing medium taken from the A_1 horizon of a lodgepole pine forest soil (pH 5.6). We removed coarse fragments from the soil (6.35-mm sieve) and mixed it to a homogeneous consistency before planting the trees. The trees were placed in an environmental chamber for the duration of the experiment.

One group of seedlings received no treatment, while the other three groups received Fe, Mn, and Fe + Mn treatments, respectively. The Fe treatment consisted of an iron chelate, Fe–EDTA, made from a source of ferrous sulfate, with a disodium EDTA chelating agent (Hewitt 1966). The Mn treatment consisted of a solution of manganese sulfate and EDTA. The starting dose for all treatments was 500 mg/L, which was increased to 1,000 mg/L to achieve a lethal dose. The solutions were applied in treatments of 50 mL so as to saturate the root zone, but care was taken to maintain an aerated soil condition between applications. The treatment phase lasted from 10 to 36 weeks.

Laboratory Procedure

Within 8 h of collection, all foliage samples were triple-washed in distilled water to remove dust and other surface contamination. The washed samples were dried in a forced-air oven at 40° C until friable. The dried samples were reduced to a fine powder by grinding. The ground foliage was dry-ashed in a muffle furnace at 485° C. Element concentrations were determined by flame atomic absorption spectroscopy. All concentrations are reported in μg/g dry weight.

Based on a comparison with the National Bureau of Standards pine needle reference material, the accuracy of the 1984 results reported in Fig. 1 was excellent for Mn (98% recovery) and Cu (100% recovery) but should be considered conservative for Fe (58% recovery). Fe recovery improved to 90% in the 1986 and 1987 analyses (Figs. 2 and 3). For comparison, the 1984 data in Fig. 2 was adjusted to be consistent with the 1986 and 1987 recovery rate.

Results

Flood-affected Trees

Figure 1 shows the foliar micronutrient concentration of the seven species investigated. All seven species consumed large amounts of Fe, indicating that these trees were unable to exclude Fe or that exclusion was not advantageous.

The Table provides concentration ratios (enriched plant to normal plant) for the micronutrient elements. The Fe uptake increased 5.6 times in ponderosa pine, 4.6 times in lodgepole pine and cottonwood, and the ratio was at least 2.0 in the other species. The Mn consumption was also above normal levels in four species. The level of Cu, Zn, Mo, and B was stable, except for an increase of Mo in ponderosa pine and a decrease of Zn in cottonwood.[2]

Figure 2 indicates the Fe and Mn content of cottonwood after 2, 4, and 5 years of exposure to the postflood conditions. The Fe contents increased throughout the interval, reaching a mean concentration ratio of 7.6 in the fifth year of exposure. Manganese increased until 1986, then decreased in 1987. The mean Mn concentration ratio was 7.8 by the fifth season of exposure.

Dose–Response Experiment

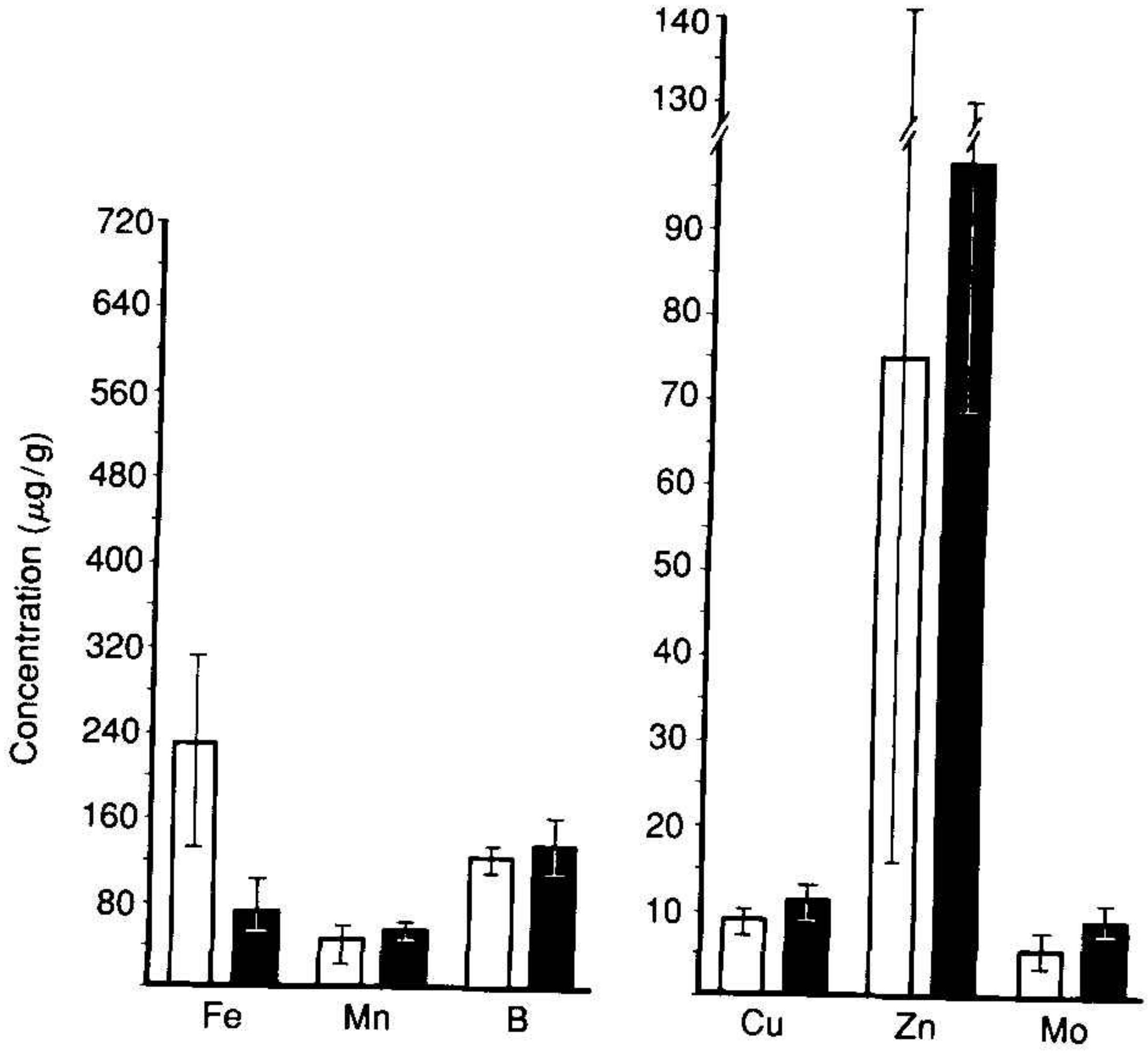
Figure 3 shows the mean Fe and Mn concentration of the treatment and control trees. The Fe treatment values represent the lethal Fe consumption for lodgepole pine seedlings under the experimental conditions. The Fe-treated

Table. *Mean concentration ratios for flood-affected trees (enriched plant to normal plant).*

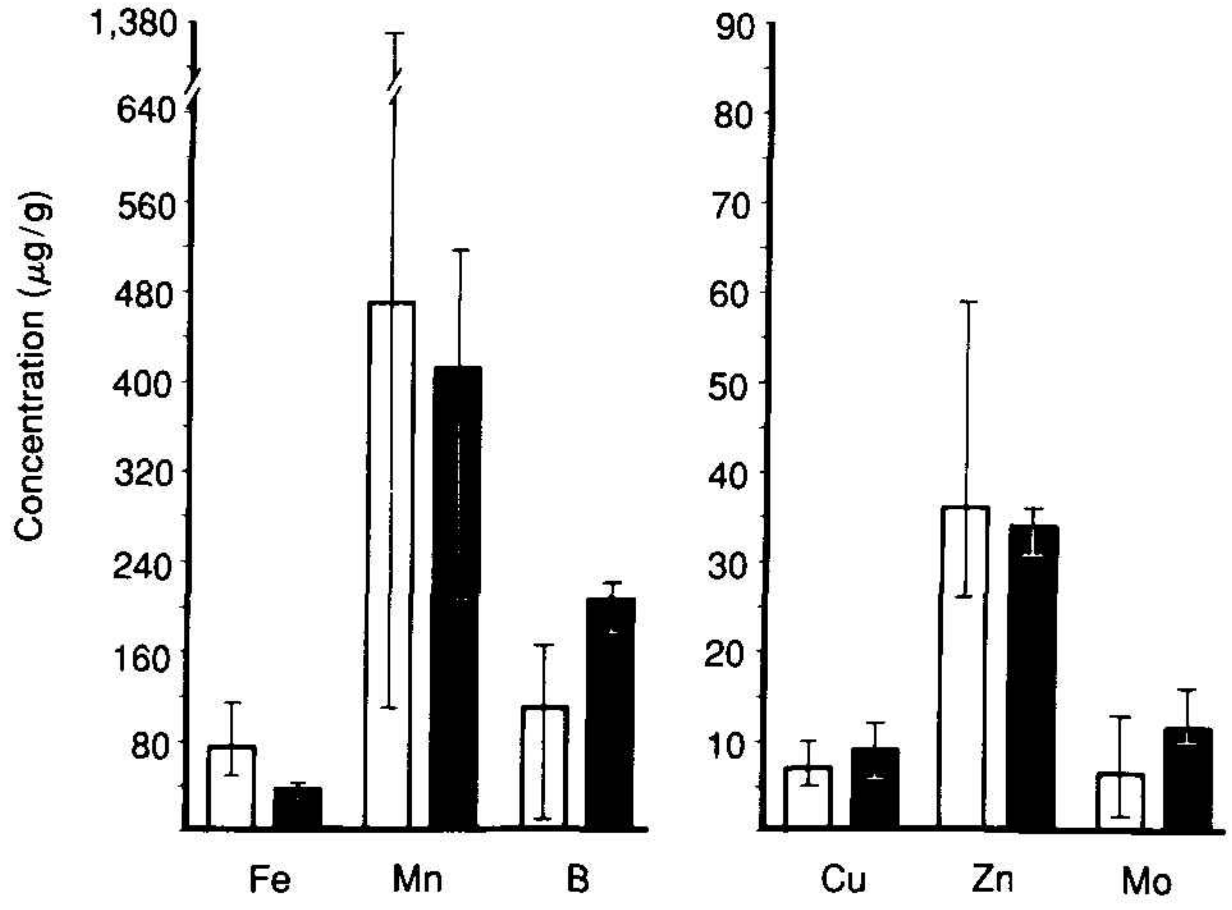
Species	Fe	Mn	B	Cu	Zn	Mo
Ponderosa pine (*Pinus ponderosa*)	5.6	2.5	0.9	1.5	1.7	4.9
Lodgepole pine (*Pinus contorta*)	4.6	2.7	0.8	1.3	0.7	1.1
Limber pine (*Pinus flexilis*)	2.1	0.6	0.9	1.0	0.4	1.3
Engelmann spruce (*Picea engelmannii*)	2.7	1.9	1.0	0.9	0.6	1.3
Subalpine fir (*Abies lasiocarpa*)	2.0	1.1	0.5	0.8	1.1	0.5
Aspen (*Populus tremuloides*)	3.1	0.8	0.9	0.8	0.8	0.6
Narrowleaf cottonwood (*Populus angustifolia*)	4.6	4.5	0.8	0.6	0.2	0.8

---

[2] Much smaller changes in the status of Cu, Zn, or Mo, which normally have relatively low foliar concentrations, might also induce toxicity, deficiency, or important interactive effects.

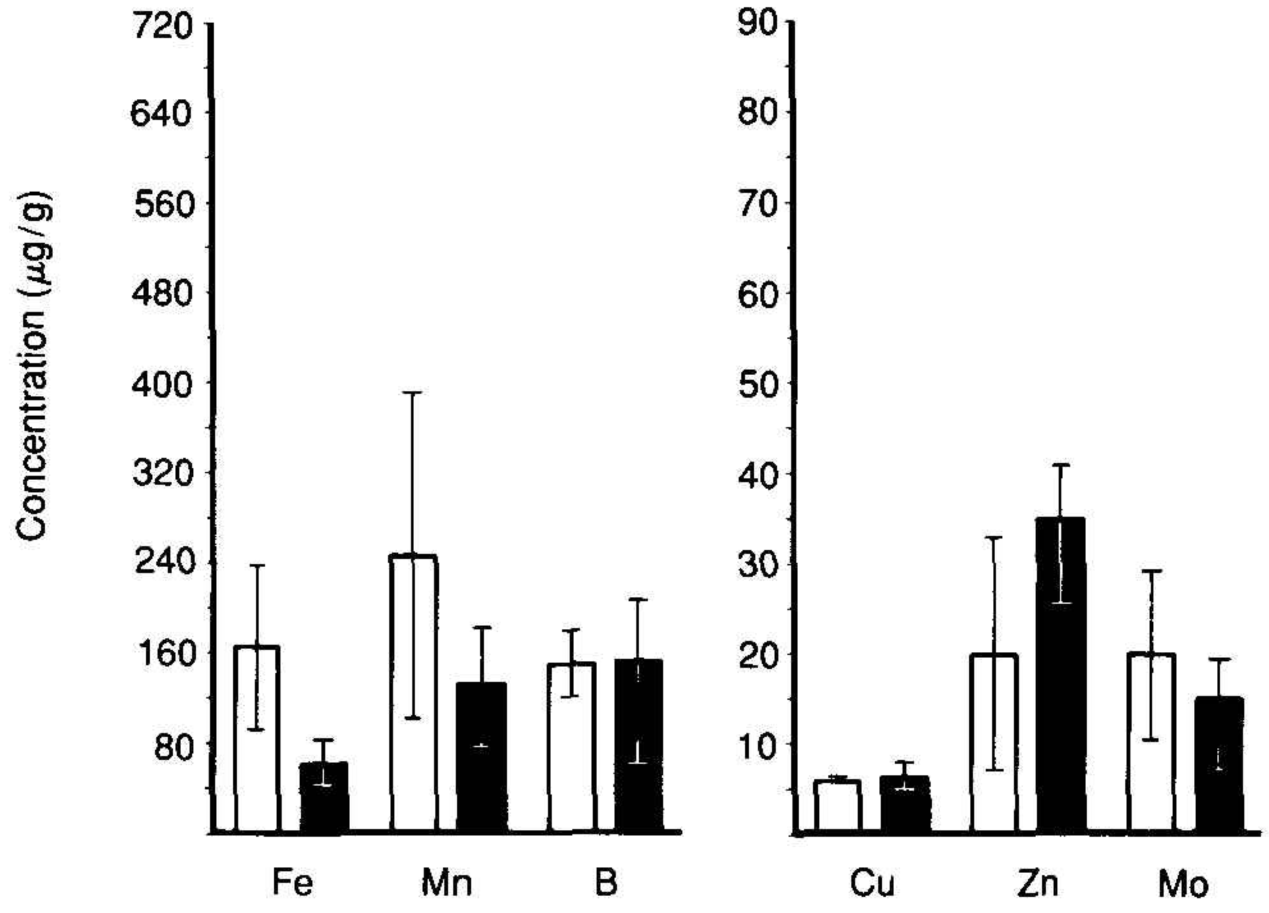


Aspen (*Populus tremuloides*)

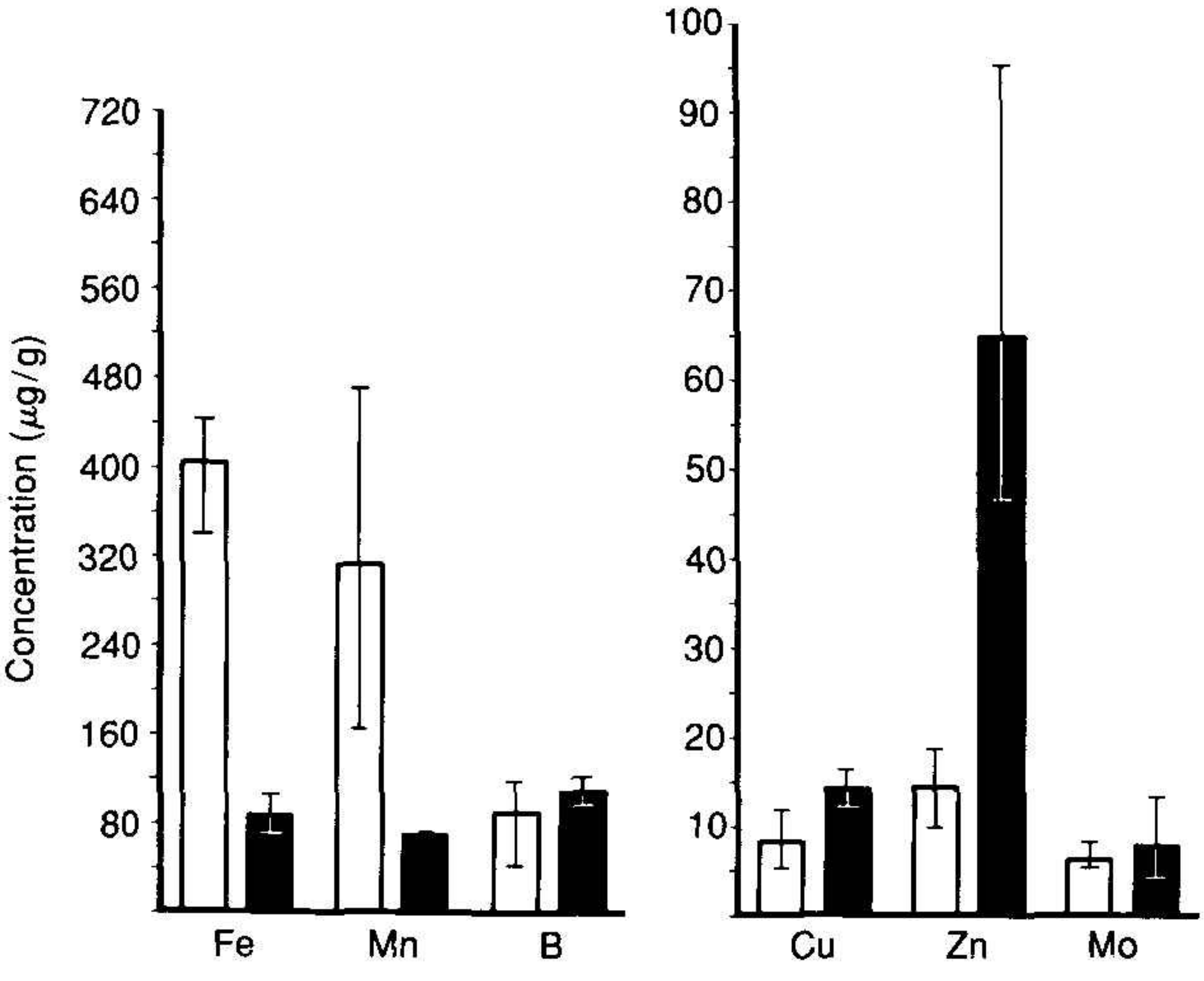


Subalpine fir (*Abies lasiocarpa*)

Fig. 1. Mean (*column*) and range (*bar*) of foliar micronutrient concentrations in flood-affected (*white columns*) and normal (*black columns*) trees.

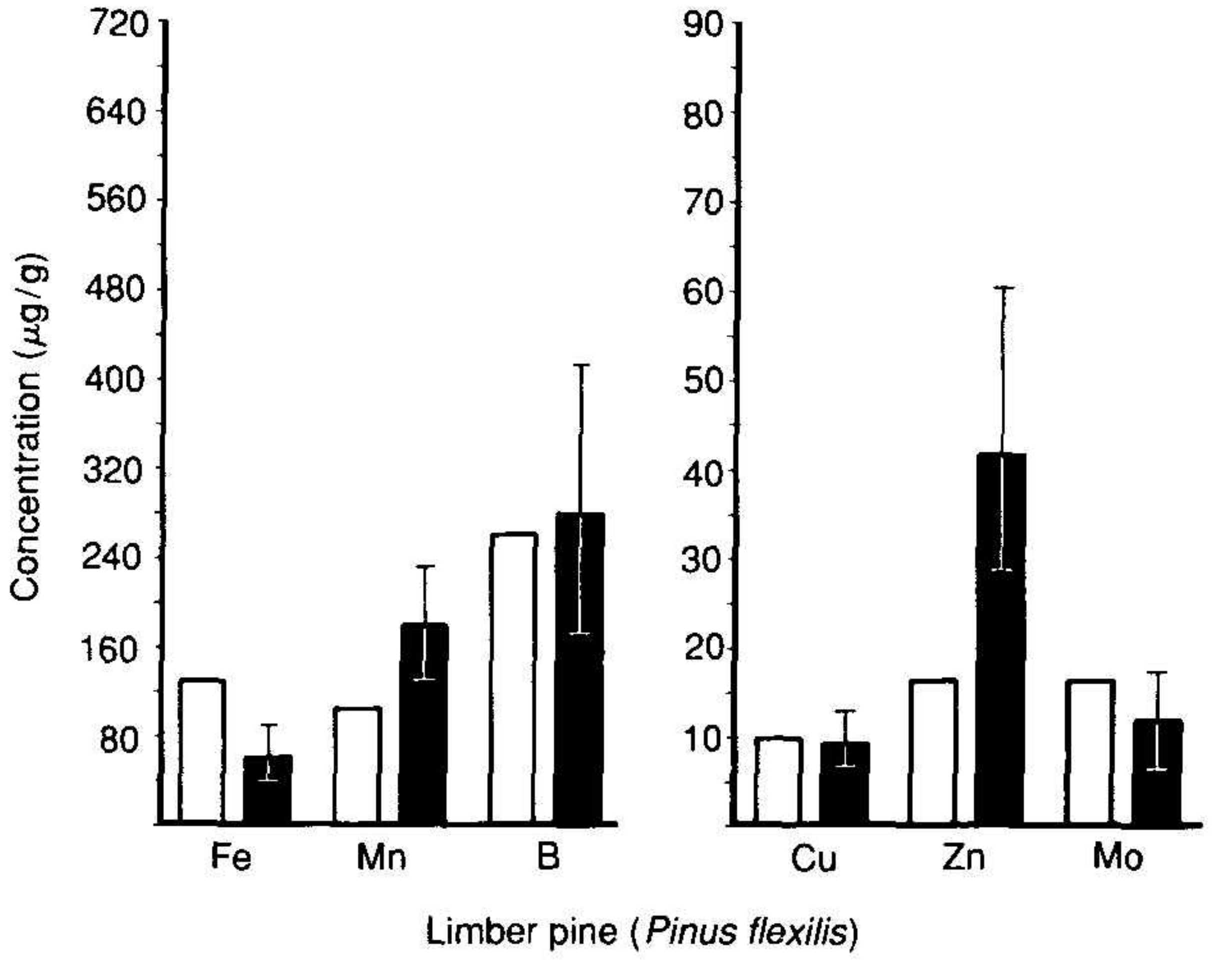


Englemann spruce (*Picea engelmannii*)



Narrowleaf cottonwood (*Populus angustifolia*)

Fig. 1. *Continued.*



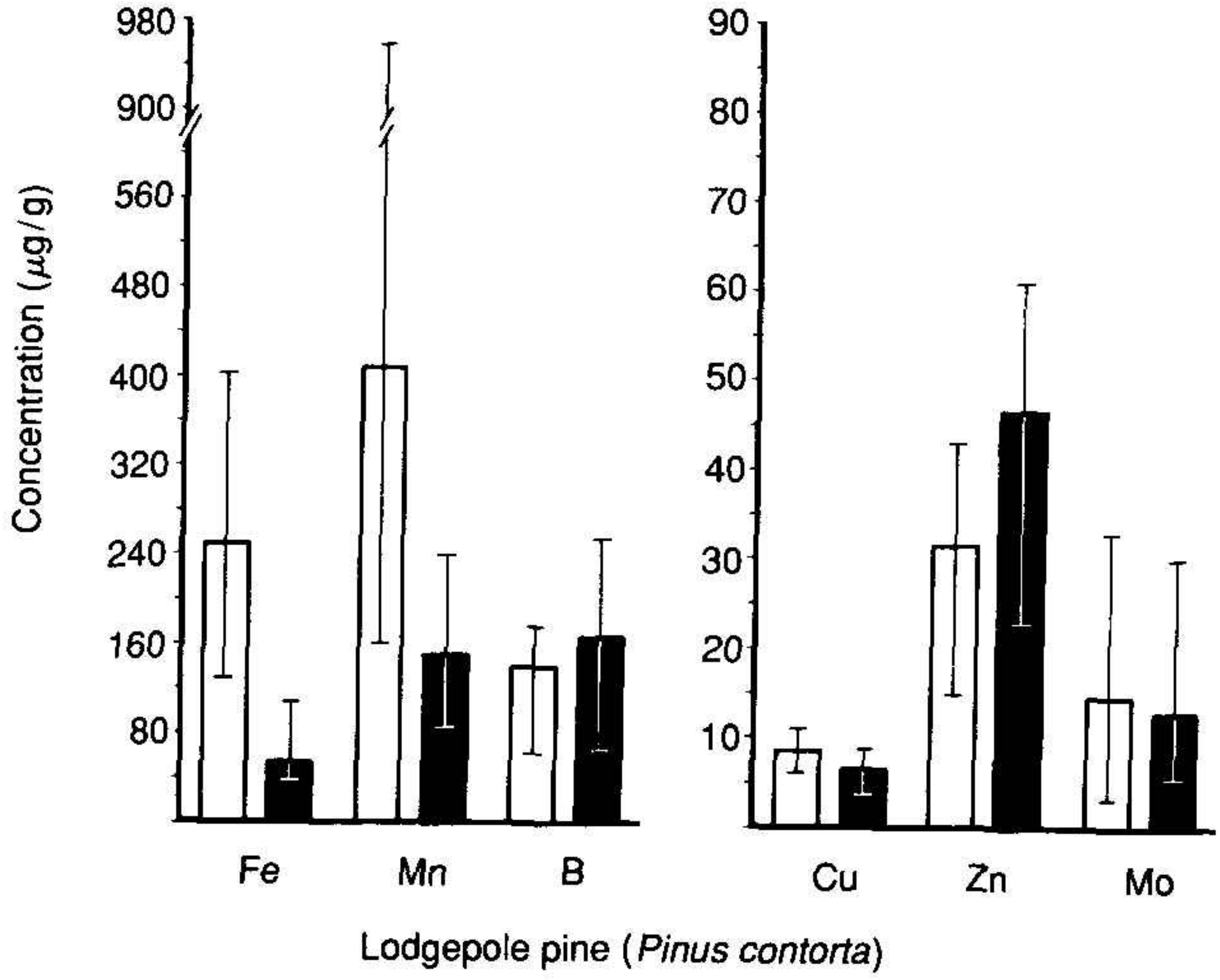


Fig. 1. *Continued.*

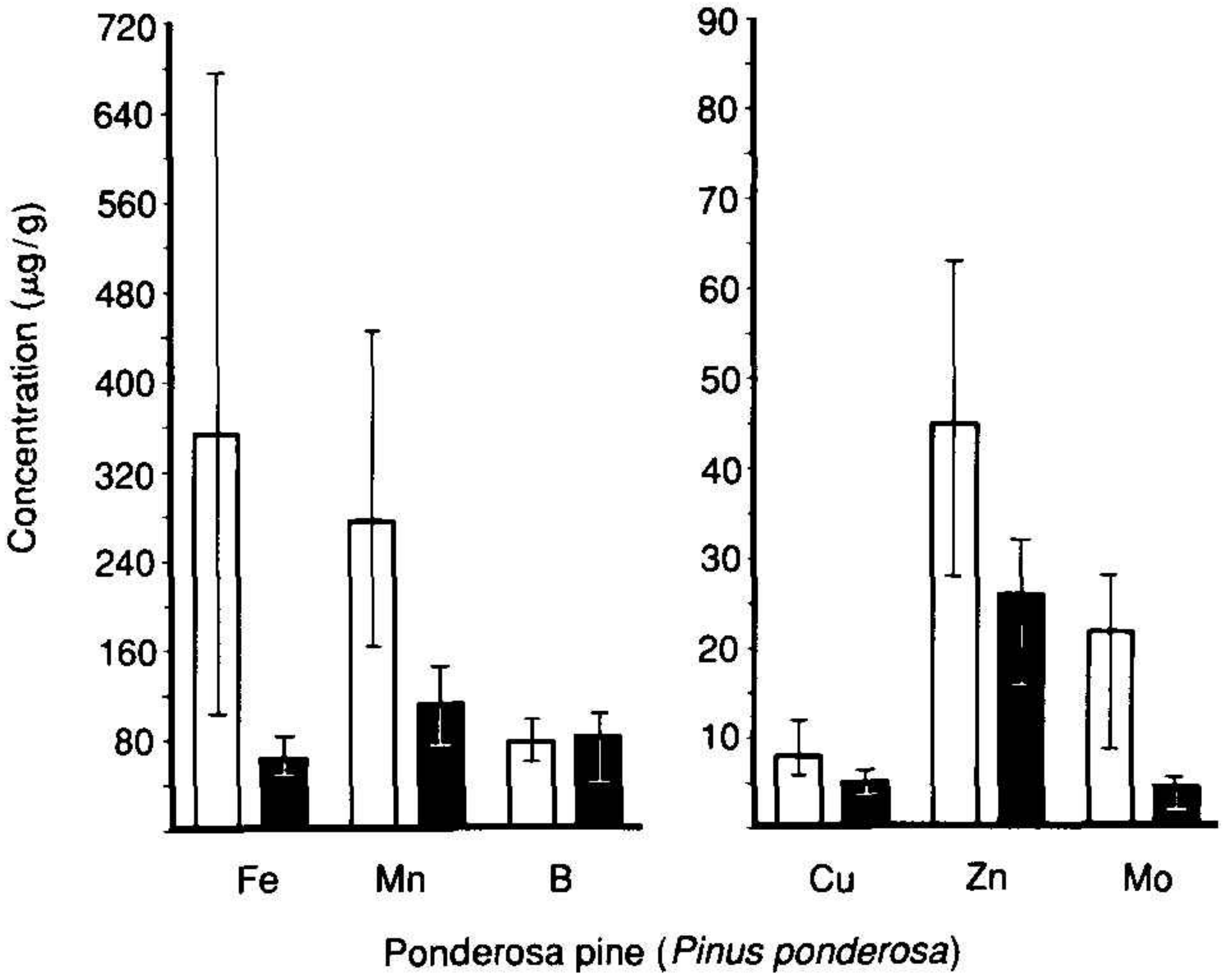


Fig. 1. *Continued.*

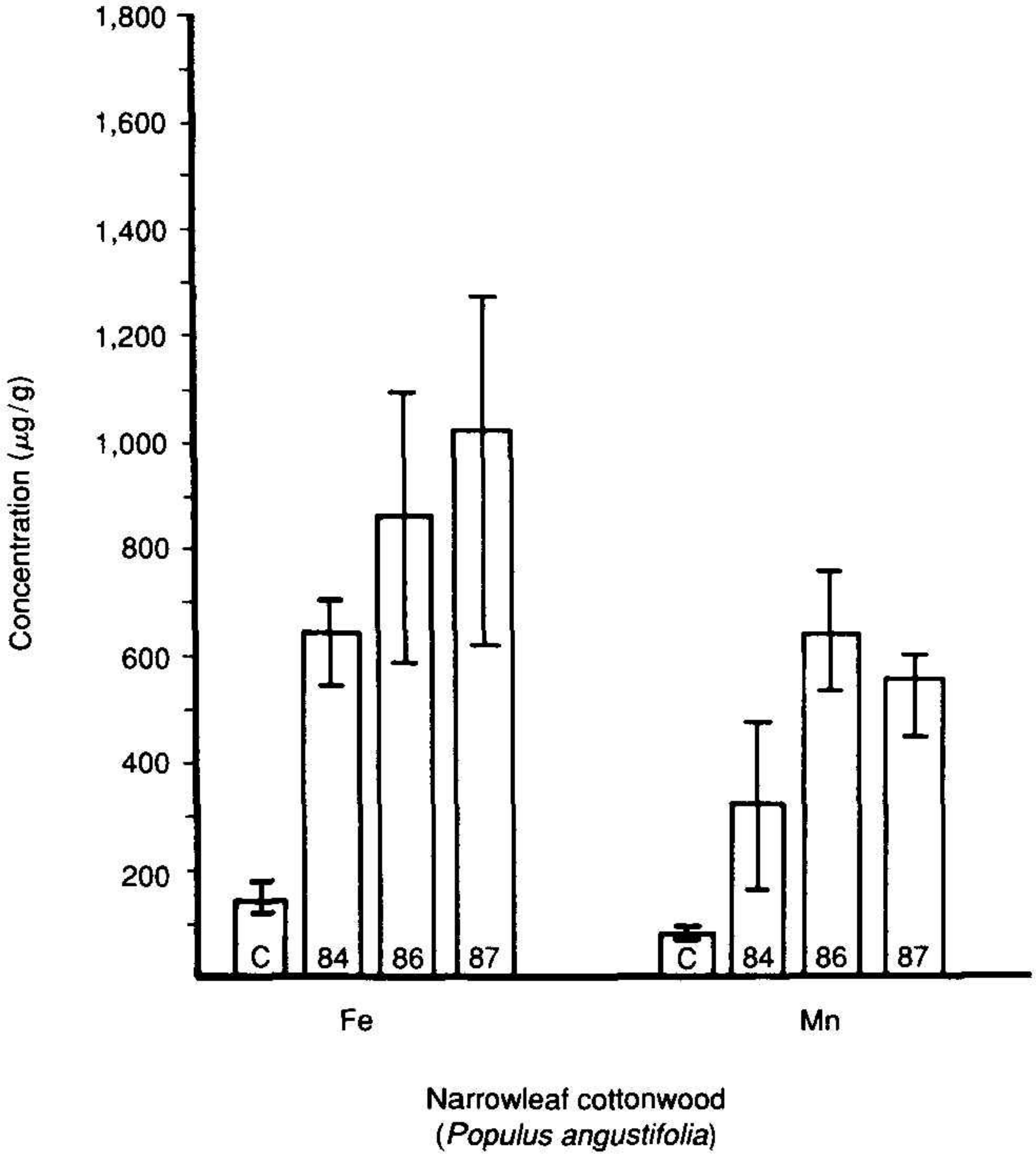


Fig. 2. Mean (*column*) and range (*bar*) of Fe and Mn concentrations in flood-affected narrowleaf cottonwood in 1984, 1986, and 1987; and normal plants (*C*) in 1984.

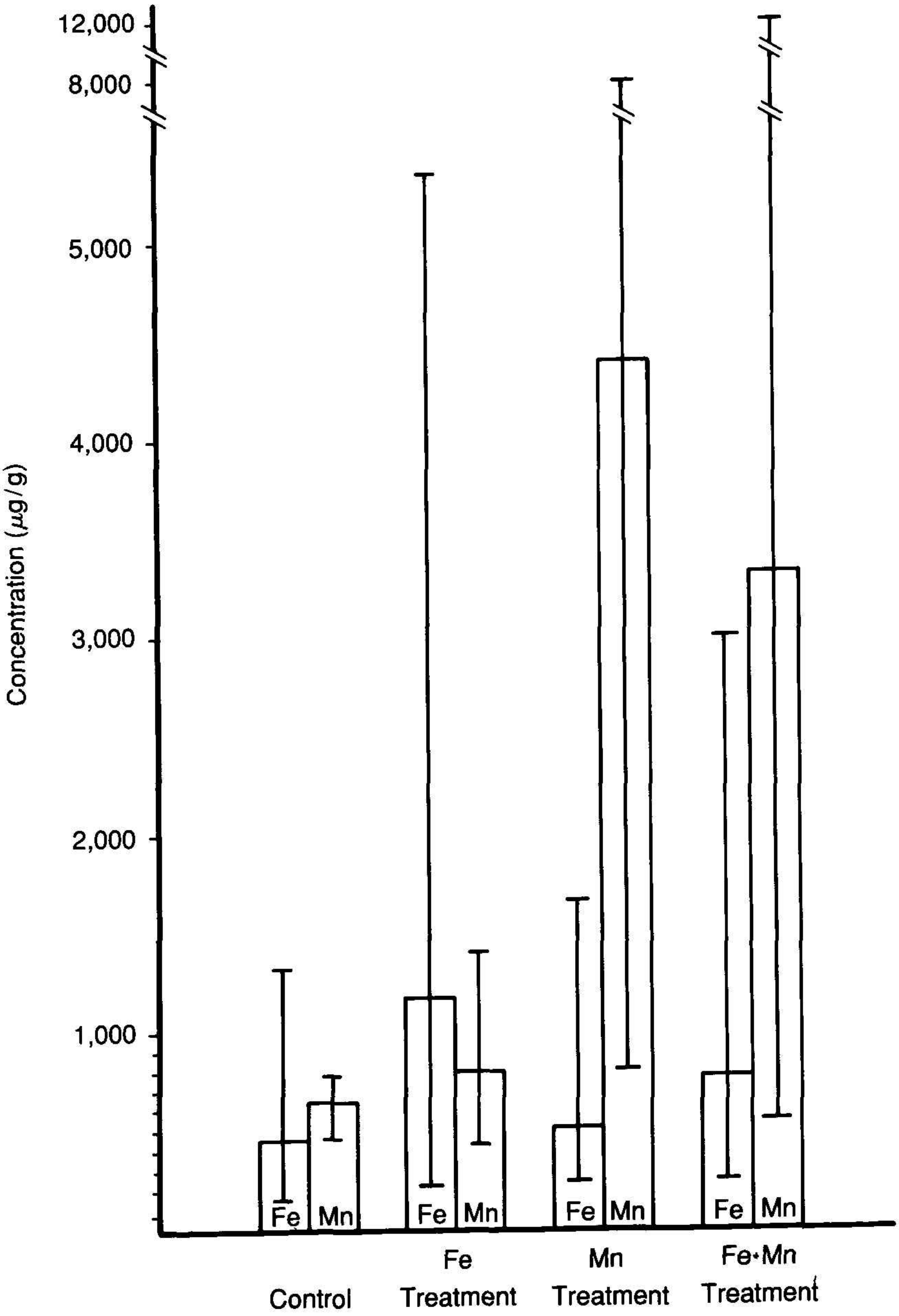


Fig. 3. Mean (*column*) and range (*bar*) of foliar concentrations of Fe and Mn in lodgepole pine seedlings in untreated (*control*) and treated groups of a dose-response experiment.

trees concentrated an average of 2.5 times more Fe than untreated trees. The large range in the Fe values reflects the fact that a few trees had relatively high concentrations in the foliage. All of the treatment combinations resulted in a large range of lethal doses.

Discussion

The trees affected by the Lawn Lake Flood did consume high levels of Fe compared to the normal content of the same species growing nearby. The magnitude of foliar Fe accumulation implies that Fe toxicity might have played a role in tree mortality. Unfortunately, little information is available on the toxicity thresholds for these forest species or for the nutritional ecotypes growing in Rocky Mountain National Park. Most of the dose–response research on mineral toxicity involves agricultural rather than forest plants.

Establishing a toxicity threshold is complicated by variation of the nutrient status within and between individuals and populations, the extent of luxury consumption, and the possibility of numerous multielement interactions. In a natural setting, where mature trees must be observed, other environmental factors introduce the potential for additive, synergistic, or antagonistic effects. Therefore, the discussion of any pattern or threshold observed in these complex systems must be predicated by simplifying assumptions. However, accepting some uncertainty, it is possible to examine the potential role of nutrient excess in the flood-affected trees. We conducted the dose–response experiment to reduce uncertainty, but here the correlation between seedlings and mature trees must be assumed.

Nutrient Variation

The nutrient status of trees is commonly subject to high natural variability. Intraspecific variation exists at the level of the individual plant, between individuals at a site, and between populations exposed to different environments. Therefore, evaluating a change in the nutrient status that might induce toxic effects requires being able to separate the potentially large range of luxury consumption from the toxicity threshold. Also, generalizing toxicity thresholds beyond the ecotype under investigation is difficult. For example, the level of Fe consumed by the flood-affected trees might exceed the toxicity threshold for its species in Horseshoe Park, but even higher levels might be normal at other locations in the species' range.[3]

---

[3] Lodgepole pine is successful with normal Fe concentrations larger than those contained in the flood-affected trees, albeit in other parts of the species' range. Lodgepole pine growing in muskegs in Alaska has a normal Fe content exceeding the levels consumed by the flood-affected lodgepole. Lodgepole pine from sites in Alaska and northwestern Wyoming have higher normal Mn levels than the flooded trees (Barrick and Noble 1987).

Multielement Interaction

Multielement interaction is an important factor when assessing toxic effects in plants. Nutrient imbalance can be a synergistic stress caused by direct toxicity and related deficiencies. An overabundance of a micronutrient can be directly toxic, or it can induce a deficiency in another. For example, excess chromium, cobalt, copper, manganese, nickel, or zinc may induce Fe deficiency in addition to being directly toxic (Treshow 1970). Somers and Shrive (1942) demonstrated that Fe and Mn are interactive in soybeans, with the biological effectiveness of one element depending on the proportionate presence of the other. High amounts of soluble Mn in the plant was invariably associated with low levels of soluble Fe and vice versa. The active Mn oxidized ferrous to ferric ions, resulting in the inactivation and precipitation of Fe in the form of organic complexes, which ultimately created an Fe deficiency. The pathological effects of high levels of precipitated ferric complexes in cells is unknown. Robb and Pierpoint (1983) suggested that free Fe molecules not bound to macromolecules might turn into a kind of redox mill in the cell, with net oxidation of cellular reductants and organic and oxygen radical production. Cell death might result if the amount of superoxide dismutase present is insufficient to keep the oxygen level low. This process might be the main cause of death in plants growing on waterlogged soils where the entrance of Fe^{2+} into the roots cannot be restricted (Robb and Pierpoint 1983).

Thresholds in Flood-affected Trees

The observed range of Fe concentrations in the flood-affected trees does not overlap the Fe contents of normal trees in five species, including ponderosa pine, lodgepole pine, Engelmann spruce, subalpine fir, and aspen (Fig. 1). In fact, an extremely narrow zone (8–40 μg/g) separates the highest Fe concentration in healthy trees and the lowest concentration in the dead trees. This narrow zone between the healthy and dead trees might identify the general position of a critical level of Fe excess in these species. A similar relation exists for Mo in ponderosa pine.

Narrowleaf Cottonwood

Narrowleaf cottonwood remained healthy despite large doses of Fe and Mn. In fact, cottonwood was fertilized by the additional nutrient uptake. Annual wood increments indicated that wood growth increased after the flood.

Cottonwood normally occupies areas subject to anaerobic soils and periodic flooding. Since cottonwood does not exclude Fe, the species might avoid the toxic effect of large doses by maintaining a balance between Fe and Mn. Although the Fe and Mn content of the flood-affected cottonwood increased sevenfold by the fifth year of exposure, the Fe to Mn ratio remained near normal levels. In 1984, 2 years after the flood, the mean Fe to Mn ratio was 2.4, which compares closely with 2.0 for the normal trees. The ratio decreased to 1.4 by 1986 but returned to 1.9 in 1987. In summary, cottonwood exhibited some variation in the mean Fe to Mn ratio when exposed to enriched conditions, but after 5 years the ratio returned to near the normal level of about 2.0. In contrast, the mean Fe to Mn ratio of all the other flood-affected tree species exhibited a much greater change from normal values. The Fe to Mn ratio increased between 1.7 and 3.9 times in the other species, indicating that individuals of these species experienced a shift (imbalance) towards higher Fe before succumbing.

The observed variation in the cottonwood Fe to Mn ratio was relatively small and might be interpreted as the normal seeking response of a system operating in a steady state equilibrium. The changes observed in 1984 and 1986 did return to near normal levels in 1987 when Mn consumption decreased. The decrease in Mn—which brought the ratio back to near normal—possibly represents self-regulation through selective exclusion of Mn. If self-regulation was involved here, other mechanisms besides exclusion might be involved, including interactions with other nutrients or external factors. Nonetheless, the ability to avoid the redox mill through self-regulation of the Fe to Mn ratio might be the mechanism that permits cottonwood to succeed on the outwash of the Lawn Lake Flood and in the riparian zone in general.

Lodgepole Pine: Flood-affected and Dose–Response Trees

The mean Fe concentration ratio in the flood-affected lodgepole pine was 4.6, while the Fe-treated seedlings exhibited a ratio of 2.5. Although the increase in Fe absorbed by the flood-affected lodgepole was nearly twice that of the Fe-treated seedlings, both tree groups had a similar magnitude of change in the Fe to Mn ratio. In the treatment trees, a doubling of Fe with respect to Mn resulted in an increase in the mean Fe to Mn ratio from 0.7 (normal) to 1.4 (Fe-treated). In the flood-affected trees, the fourfold increase in Fe, combined with a doubling of Mn, resulted in an increase in the Fe to Mn ratio from 0.4 (normal) to 1.0 (flooded). Therefore, both the flood-affected and treatment tree groups experienced about a doubling of the Fe to Mn ratio before death. Based on these results, the doubling of the Fe to Mn ratio, representing a change toward higher amounts of Fe relative to Mn, appears to be a more likely critical threshold of toxicity in lodgepole pine than the increase in Fe alone.

Other Effects of Root Zone Flooding

Another potentially important factor in the postflood environment was the prolonged water saturation of the root zone. Although the high water table exposed the trees to a continuous pool of available ions, it might also have induced other negative effects.[4] Root respiration failure may result when water saturates the air spaces in the soil and reduces the oxygen supply to the roots. The effect of root suffocation is progressive; growth is suppressed, leaves become chlorotic, growth ceases, no new roots develop, shoots die back, and death ensues (Treshow 1970). Carbon dioxide accumulation and other toxic metabolic products can also occur with poor gas exchange under anaerobic conditions. However, controversy continues regarding whether plant injury is caused by exclusion of oxygen from the root system, by carbon dioxide accumulation, or from the toxicity of chemically reduced products that predominate in flooded soils (Gill 1970).

The flooding tolerance of trees is determined by the duration of inundation, timing, and the extent of internal oxygen transport. Little information is available on the tolerance of the species tested here, but cases of tree mortality after permanent flooding have been recorded. Coutts and Philipson (1978a, 1978b) and Coutts (1982) investigated the effect of waterlogging on Sitka spruce (*Picea sitchensis*) and lodgepole pine. Root growth of both species stopped within a few days when flooded during the growing season, but little effect was observed during dormant periods. Lodgepole pine roots were more tolerant of waterlogging than spruce, indicating a greater potential for internal oxygen transport. Green (1947) reported that water impoundment had little effect on deciduous trees during the first year, and massive die-off did not occur until the third year. Ahlgren and Hansen (1957) reported that death of northern Minnesota conifers was not evident until 2 years after flooding. In these cases, no attempt was made to determine the relative importance of root suffocation and micronutrient toxicity.

In the case of the flood-affected trees, we were unable to separate the potential effects of micronutrient toxicity from concomitant stresses related to root respiration failure. However, during the dose–response experiment, root respiration failure was not a factor. The similar change in the magnitude of the Fe to Mn ratio under environmental and experimental conditions suggests that the Fe and Mn condition in the flood-affected lodgepole pine was sufficient to cause the observed mortality in this ecotype. Also, most of the flood-affected trees succumbed more rapidly than might be expected from the effect of root zone flooding alone.

Conclusions

Our study demonstrates that seven upper montane tree species accumulate Fe when mobile ions are available at the root zone. Ponderosa pine, lodgepole pine, Engelmann spruce, subalpine fir, and aspen exhibited a narrow range in foliar Fe between the highest concentrations in healthy trees and the lowest content in dead trees. This small difference might represent a toxicity threshold in each of these populations. The results of the dose–response experiment

---

[4] Although the postflood conditions did result in Fe and Mn enrichment of the groundwater, not all flooded soils result in enrichment and subsequent uptake by trees. We investigated Engelmann spruce and subalpine fir in Colorado and lodgepole pine in Wyoming that were subjected to prolonged saturation of the root zone (Barrick and Noble 1987). Although these trees were dead or dying, they did not contain above normal doses of Fe or Mn.

on lodgepole pine suggest that a doubling of the Fe to Mn ratio, reflecting higher Fe with respect to Mn, might be a toxicity threshold for this species.

Unlike the other species, narrowleaf cottonwood remained healthy despite a large increase in Fe and Mn consumption. Cottonwood maintained a relatively stable Fe to Mn ratio through the fifth year of exposure to enriched conditions. This observation suggests that cottonwood might be able to self-regulate the Fe to Mn ratio. The ability to maintain a balanced Fe to Mn ratio might be the mechanism that permits the success of cottonwood in the riparian zone.

Based on these results, most of the tree species representing the upper montane in Colorado will consume large doses of Fe and Mn when these elements are present in available form. Therefore, environmental change that increases the availability of Fe and Mn in forest soils should be assessed, recognizing that the micronutrient status of exposed trees might be modified. Negative effects accompanying micronutrient imbalance in trees will be difficult to trace to gradual changes in soil chemistry, like those that might accompany atmospheric deposition. Weakened populations might be predisposed to other more visible signs of stress, including disease or insect attack. Unfortunately, future studies of long-term change will be difficult or impossible to conduct without baseline research on the nutrient status of normal trees. Also, additional research appears warranted on the mechanism of Fe and Mn toxicity in trees exposed to waterlogged soils.

Acknowledgments

Funding for this research was provided by Rocky Mountain National Park. Laboratory facilities and assistance during analysis was provided by the Mountain Research Station, University of Colorado, and the Institute of Marine Science, University of Alaska Fairbanks. We thank H. McCutchen and D. Stevens for valuable assistance at Rocky Mountain National Park and anonymous reviewers for providing valuable comments on the manuscript.

Literature Cited

Ahlgren, C. E., and H. L. Hansen. 1957. Some effects of temporary flooding on coniferous trees. Journal of Forestry 55:647–650.

Barrick, K. A., and M. G. Noble. 1985. The micronutrient status of tree species affected by the Lawn Lake Flood, Rocky Mountain National Park, Colorado. Unpublished report to Rocky Mountain National Park, National Park Service. 33 pp.

Barrick, K. A., and M. G. Noble. 1987. The micronutrient status of tree species affected by the Lawn Lake Flood, Rocky Mountain National Park, Colorado—final report 1986. Unpublished report to Rocky Mountain National Park, National Park Service. 21 pp.

Bowen, H. J. M. 1966. Trace elements in biochemistry. Academic Press, New York. 241 pp.

Coutts, M. P. 1982. Tolerance of tree roots to waterlogging. V. Growth of woody roots of Sitka spruce and lodgepole pine in waterlogged soil. New Phytologia 90:467–476.

Coutts, M. P., and J. J. Philipson. 1978a. Tolerance of tree roots to waterlogging. I. Survival of Sitka spruce and lodgepole pine. New Phytologia 80:63–69.

Coutts, M. P., and J. J. Philipson. 1978b. Tolerance of tree roots to waterlogging. II. Adaptation of Sitka spruce and lodgepole pine to waterlogged soil. New Phytologia 80:71–77.

Gill, C. J. 1970. The flooding tolerance of woody species—a review. Forestry Abstracts 31:671–688.

Green, W. E. 1947. Effect of water impoundment on tree mortality and growth. Journal of Forestry 45:118–120.

Hewitt, E. J. 1966. *Sand and water culture methods used in the study of plant nutrition.* Commonwealth Agricultural Bureaux, Farnham Royal, England.

Litaor, M. I., and R. Keigley. 1993. Geochemistry of iron oxides in the Roaring River alluvial fan, Rocky Mountain National Park, Colorado. Pages 55–69 *in* H. E. McCutchen, R. Herrmann, and D. R. Stevens, editors. Ecological effects of the Lawn Lake Flood of 1982, Rocky Mountain National Park. National Park Service, Scientific Monograph Series NPS/NRROMO/NRSM–93/21.

Robb, D. A., and W. S. Pierpoint. 1983. Metals and micronutrients: uptake and utilization by plants. Academic Press, New York.

Somers, I. I., and J. W. Shrive. 1942. The iron–manganese relation in plant metabolism. Plant Physiology 17:582–602.

Subcommittee on Iron. 1979. Iron. Committee on medical and biological effects of environmental pollutants. Division of Medical Sciences, National Research Council. University Park Press, Baltimore, Md.

Treshow, M. 1970. Environment and plant response. McGraw-Hill Book Company, New York.

Vegetation Development on the Exposed Shores of Lawn Lake

Donald H. Mansfield

Albertson College of Idaho
Department of Biology
Caldwell, Idaho 83605

Abstract. Permanent plots were established, and the frequency and cover of plant species were monitored from 1985 through 1987 in the disturbed lake margin and meadows surrounding Lawn Lake. Four plant communities were identified in the existing meadows using detrended correspondence analysis and two-way indicator species analysis (TWINSPAN) and were differentiated by indicator species and soil organic matter. Plots in the lake margin formed a continuum along gradients similar to those in the meadows. Three groups of plots that corresponded with lake margin zonation were segregated by TWINSPAN. The east side of the lake had the least cover (7.5% in 1987); the upper zone of the west side of the lake margin, which was vegetated before constructing the Lawn Lake Dam in 1902, had 32% cover by 1987, and the lower margin of the west side of the lake, which was submerged until the dam break in 1982, had 26% cover. During the 3 years of the study, the vegetation became more similar among plots on the west side of the lake, suggesting that where sites were favorable for seedling establishment, the reproduction of plant species already colonizing the lake margin was beginning to define the future direction of the vegetation development. Life history attributes of the species were used to explain the few trends evident in plant succession in the lake margin, lending credibility to individualistic hypotheses, such as the vital attributes model of plant succession.

Introduction

Classical models of vegetation succession predict that vegetation will develop towards a relatively stable, mature form—a climax, in a fairly deterministic fashion (Clements 1916; Diamond 1975). Alternative models invoke the importance of historical accident in vegetation development on a site (Gleason 1926; McCune and Allen 1985). Most current models of vegetation development (succession) accept the role of chance but differ as to the mechanisms of change. Do species initially composing the flora following a disturbance facilitate, tolerate, or inhibit site colonization by subsequent species (Connell and Slatyer 1977)? According to the individualistic hypotheses (sensu Gleason), a plant community that develops following a disturbance will result from responses of individual species—not the collective vegetation—to their environments. In the extreme case of the initial floristics model, vegetation development following disturbance will simply be an expression of the life histories of the plants whose propagules initially colonized the site. This model has been supported in the single-stage primary succession observed on tundra sites (Muller 1952; Webber 1978). Noble and Slatyer (1980) suggested that the vital attributes of species (e.g., such characteristics as seed dispersibility, seed dormancy, and adult longevity) determine their role in vegetation development on a site. The resource ratio model (Tillman 1985) predicts directional and predictable changes in species composition to the same extent that there are directional and predictable changes in the relative availabilities of limiting resources, such as light and nitrogen, to which seral species exhibit differential population responses.

An understanding of the factors controlling vegetation development after a disturbance is essential to guide resource management decisions. Most studies of vegetation development in the central Rocky Mountains have examined tree-dominated communities in response to fire (see those cited in Baker 1983). Perhaps the most comprehensive studies of subalpine or alpine meadow communities in this region are those of Willard (1979) and Komarkova (1980), which relied on the phytosociologic methods of Braun-Blanquet (1932). Lawn Lake in Rocky Mountain National Park offers a unique unforested site for a natural experiment in colonization and revegetation in the subalpine–alpine ecotone.

When Lawn Lake was dammed in 1902, forest, marsh, and meadow communities along the lake margin were inundated. After the dam break on 15 July 1982, the margin of the new lake became exposed for colonization by terrestrial plant species. Two regions of the lake margin became evident during reconnaissance in 1982: a lower zone of gravelly sediment apparently devoid of terrestrial vegetation since the last glaciation and an upper zone that was vegetated before 1902.

The purpose of this study was to (1) describe the plant communities that developed on the disturbed lake margin, (2) learn how communities developing in the upper and lower zones of the lake margin differed, (3) compare developing lake margin communities to existing plant communities in the Lawn Lake basin, and (4) assess how knowledge of existing meadow vegetation can aid in predicting the nature of development on the exposed lake margin. Here, we summarize the results of 3 years of vegetational study in the immediate vicinity of Lawn Lake. The study established a baseline from which long-term observations and experiments can proceed.

Study Area and Methods

Study Area

Lawn Lake is located at 3,355 m, 1 km southwest of Mummy Mountain

(T6N R74W Sections 24 and 25) in Rocky Mountain National Park. Figure 1 illustrates the study site. The site lies at the subalpine–alpine ecotone. The predominant vegetation to the west, south, and east of the lake margin is subalpine forest dominated by *Picea englemannii* and, to a lesser extent, *Abies lasiocarpa.* An extensive unforested area composed mostly of wet meadows lies near the lake outlet to the southeast of the lake. The northeast side of the lake is a mosaic of forest, dry meadow, and wet meadow with meadow openings becoming larger and more frequent to the north and northwest of the lake.

The lower zone of the lake margin (below the pre-1902 water level) is characterized, in general, by coarse gravels. Clay sediment is evident, particularly in the more protected southwest portion of the basin. The most obvious feature of the upper zone of the lake margin is a well-developed organic layer typically overlain by gravelly lake sediments 0.3–3.0 cm deep. At the northwest end of the lake, this organic matter occurs as hummocks up to 1 m deep. On the southwest side of the lake, and to a lesser extent on the east side, remnants of spodosolic forest soils are evident beneath gravelly lake sediment.

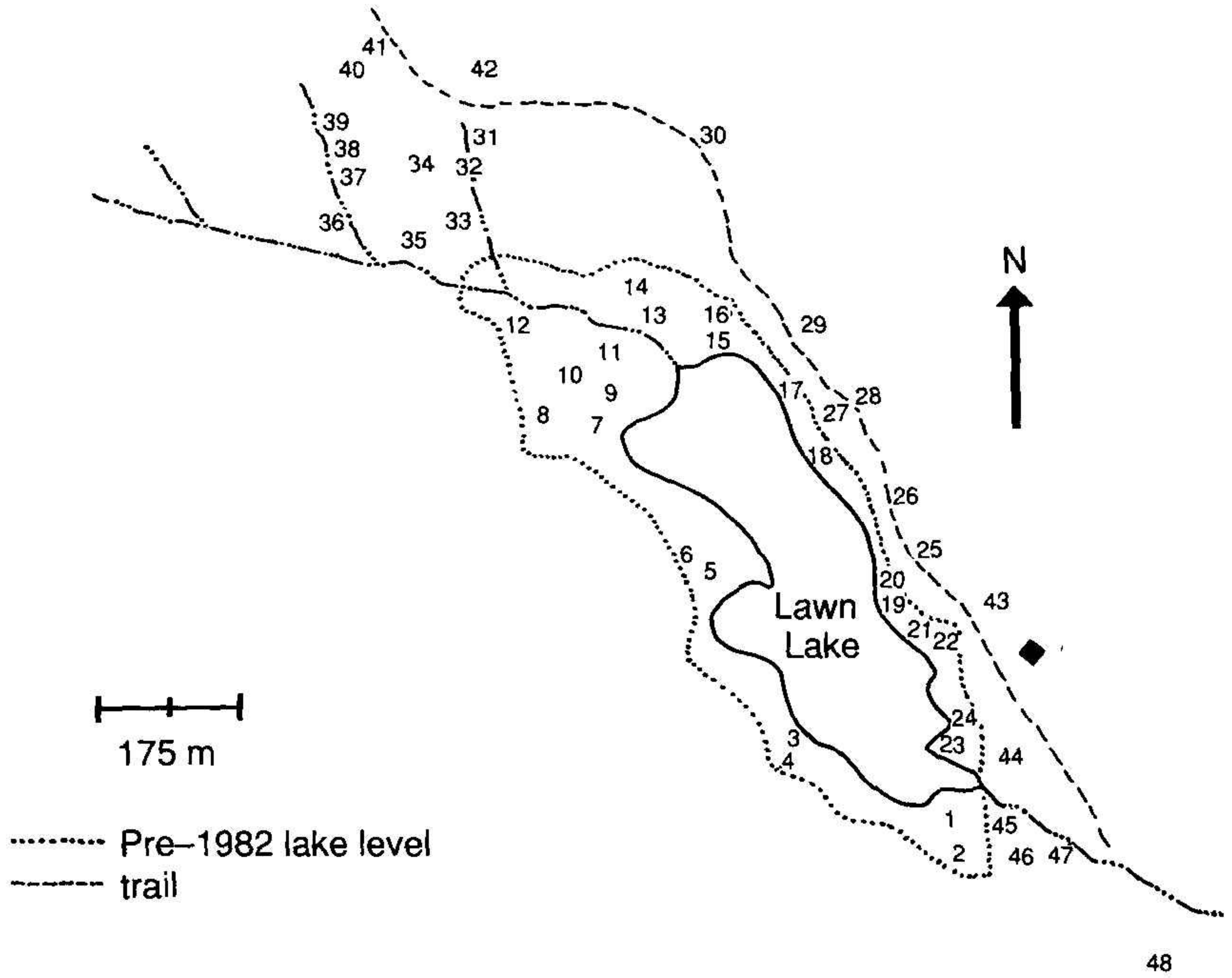


Fig. 1. Location of the 48 study plots in the Lawn Lake vicinity. Plots 1–24 are in the disturbed lake margin, with even-numbered plots in the upper and odd-numbered plots in the lower zone; meadow plots (25–48) are randomly distributed in the mosaic of open areas around the basin.

Human influence in the area is evident along the east side of the lake, where the Lawn Lake trail, a patrol cabin, the backcountry campground, and the remains of the guard station are located. After the 1982 flood, an area of human trampling became evident along the dam and in the lower zone of the east lake margin. By 1987, distinct paths had appeared mainly in the vicinity of the backcountry campgrounds and along the edge of the water.

Sampling Design

Twenty-four 9- × 9-m plots were established in the edaphically disturbed lake margin (lake plots: 1–24), and 24 plots of the same size were placed in open, nonforested vegetated sites in the immediate vicinity of Lawn Lake (meadow plots: 25–48; Fig. 1). Plots ranged in elevation from 3,350 to 3,400 m. All plots were oriented along north–south and east–west axes.

Lake plots were selected in a stratified random procedure from both elevational zones of the pre- and post-1902 emergence level and from three areas in the lake margin (southwest, northwest, and east shores). To randomly sample from both zones, two plots (one upper and one lower) were taken at random intervals (below and above the pre-1902 lake level) along randomly selected transects. Transects were identified until all three areas of noticeably different slope and exposure were represented in the sample—10 plots from the relatively flat, northwest pre-1982 shallow delta, six plots from the low-angle southwest shore, and eight plots from the higher-angle east shore. Two of the east shore plots (17 and 18) were located one per transect because the distance from the lake to the pre-1982 shoreline was less than the width of two plots in the configuration dictated by the design. Because neither plot was entirely located within the lower or upper zone, those plots were not considered in analyses that compared zones.

Meadow plots were selected by locating all possible open sites and randomly assigning plots within possible sites. Plots were located in July 1985 and were marked (for long-term observation) in their northwest and southeast corners by a piece of steel reinforcing bar. Bars generally remained in place; however, one bar was moved, presumably by vandals, and frost heaving caused bars to move in plots 15 and 16.

Vegetation Parameters

Lake plots were sampled in the latter half of July and early August in 1985, 1986, and 1987. Meadow plots were sampled in the latter half of July 1986. Each plot was divided into nine 3- × 3-m quadrats, and frequencies were determined by the presence of species within the quadrats.

A point observation frame (0.5 × 0.5 m) was placed in the northwest corner of each quadrat. The frame contained two layers of crossed threads that allowed for 16 sightings, each 10 cm apart. The frame was leveled before each sampling to ensure a vertical orientation during sighting. Each of the 144 sightings per plot was scored as bare ground, unattached litter, or the one or more species in the vertical line of sight. These point observations were used to compute percent cover for each plot. Litter and standing water never constituted more than 2.5% of the total area sampled, so these areas were included as bare ground in subsequent analyses. Ramet densities were determined for each species in each quadrat in 1987.

Quadrats were relocated using a portable grid and permanent 10-cm spikes embedded in the soil. In this way, we were able to return to each quadrat in subsequent years. Maps and photographs were prepared for each of the nine 1-m^2 sections of the northwest quadrat of selected plots during 1986 and 1987. From these maps, individual ramets were monitored.

Species were identified according to Weber (1976). Changes in nomenclature of some taxa are consistent with Weber (1987). *Poa* species were classified according to Arnow et al. (1980). Voucher specimens were collected and temporarily deposited in The College of Idaho herbarium (CIC).

Species of some genera were pooled due to difficulties in routine field identification. The *Festuca* species evident were predominantly *Festuca brachyphylla*, but some individuals represented in the lake margin grade into those of *F. saximontana*. Both species are included as *Festuca* spp. here. Among the agrostids, *Agrostis variabilis* and *Podagrostis humilis* were indistinguishable without time-consuming observation of the palea; thus, both species were lumped together as *Agrostis* spp. The majority of individuals that were examined microscopically in the field were *Agrostis variabilis*, but both species were well represented. *Agrostis borealis* was also evident to a limited extent (e.g., 2% frequency in 1986). All of these grasses were evident in the lake margin during a preliminary reconnaissance in September 1983. *Draba* species collected included *D. aurea*, *D. albertina*, *D. streptocarpa*, *D. cana*, and other *Draba* species. Here, they are lumped together as *Draba* spp.

Abiotic Parameters

Slope, aspect, and descriptions of soil properties were recorded for each plot, along with the distance from the pre-1982 shoreline. Aspect was ranked as follows: SW = 1, S = 2, W = 3, SE = 4, NW = 5, E = 6, N = 7, and NE = 8. This ranking assumes a gradient from warmest and driest to coolest and wettest (Geiger 1965). Soil core samples of 6 cm diameter and 15 cm depth were collected 20 cm outside each plot's northwest, southwest, and southeast corners on 31 July 1986. Samples were stored on ice until oven-dried at 90° C in the lab. Organic matter content was determined by weight loss following ignition at 700° C for 1 h. Soil pH was determined on a soil:0.1M $CaCl_2$ (1:2 w/w) suspension (Page 1982). Soil particle size estimates were based on the weight fraction of soil that passed through a 1.19-mm sieve. An environmental index for each plot was formed by scaling the abiotic data (slope, aspect, organic content, pH, and particle size) from 0 to 15 and summing equally weighted values for each of the five variables (Sawyer and Kinraide 1980).

Analysis

Data were stored in the VAXVMS computer at Rollins College and retrieved for analysis with SAS (Helwig 1985) and with Cornell Ecology Programs: DECORANA (Hill 1979a) and TWINSPAN (Hill 1979b).

Arcsine square root transformations were performed on cover and frequency data before ordination, classification, correlation, ANOVA, pairwise *t*-tests, or other statistical analyses were conducted (Green 1979). A multivariate detrended correspondence analysis (DCA) was used to define vegetational gradients in all ordinations presented. Groups of plots were classified for description and analysis using the polythetic divisive classification method of two-way indicator species analysis (TWINSPAN; Gauch 1982).

Percent similarity was calculated for each pair of permanent plots in the lake margin using the formulation in Gauch (1982) as used by Frank and del Moral (1986). Statistically significant differences between percent similarity means in 1985 and 1987 were determined for all lake margin plots or groups of plots by using the Wilcoxon signed-rank test.

Results

Abiotic Characteristics of Lake Margin and Meadow Sites

Lake margin and meadow plots had comparable slopes, aspects, and proportions of coarse soil particles (Table 1). The lake margin soils had significantly lower organic content and significantly higher pH than soils in surrounding meadows.

Colonization of the Lake Margin

By 1985, 90 plant species were on the exposed shores adjacent to Lawn Lake. The number of species in the lake margin increased during 1986 and 1987; the majority of new species were perennial forbs and woody plants

Table 1. *Edaphic characteristics of mature meadows and the successional lake margin.*

	Soil pH	Soil organic content (%)	Coarse particles[a]	Slope(°)	Aspect[b]
Lake margin	4.28 ± 0.34	4.88 ± 5.28	0.57 ± 0.23	3.3 ± 2.3	4.2 ± 2.4
Meadow	3.96 ± 0.28	8.10 ± 2.84	0.58 ± 0.20	3.2 ± 2.9	4.5 ± 1.9
Significance[c]	$P < 0.001$	$P < 0.05$	ns[d]	ns	ns

[a] Weight fraction of soil particles >1.19 mm.
[b] Ranked as described in Methods.
[c] Means were compared by a *t*-test.
[d] ns = no significance.

Table 2. *Plant species established in at least 1 of 216 permanent quadrats in the exposed lake margin or established meadows surrounding Lawn Lake.*

Sampled area and date	Brophytes	Grasses	Sedges	Rushes	Forbs Annual	Forbs Perennial	Shrubs–trees	**Total**
Lake 1985	4	8	13	6	5	40	4	90
Lake 1986	5	18	14	6	5	51	4	107
Lake 1987	5	23	16	7	4	60	7	122
Meadow 1986	7	15	16	6	3	68	9	131

(Table 2). The established meadows surrounding the pre-1982 lakeshore had more species than the lake plots did due to the greater number of perennial forb, tree, and shrub species. However, lake plots consistently contained more grass species than meadow plots. Grasses from both nearby tundra (e.g., *Poa lettermanii* and *P. epilis*) and montane (e.g., *Calamagrostis canadensis* and *Festuca saximontana*) sites, appeared in at least some disturbed lakeshore sites, while these species were absent from surrounding meadows.

Of the 3,456 sightings in the lake margin in 1985, 1986, and 1987, 13.5%, 15.5%, and 24.6%, respectively, fell on one or more living plants. Bare ground made up the remainder of the lake margin surface (Table 3). The most frequent lake margin colonizers were *Trisetum spicatum*, *Festuca* spp., *Poa alpina*, *Deschampsia caespitosa*, *Agrostis* spp., *Phleum commutatum*, *Koenigia islandica*, *Juncus drummondii*, and *Draba* spp. Grasses composed the greatest plant cover; of these, *Deschampsia caespitosa* contributed 27% (1986) to 32% (1987). This grass contributed 43% of the relative grass cover in the surrounding meadows.

In 1985, 1986, and 1987, there were 25, 28, and 33 vascular plant species in at least 10% of the 216 lake quadrats. Fifty-five vascular plant species occupied at least 10% of the 216 meadow quadrats. Seven species had achieved densities exceeding one ramet per meter in the lake margin by 1987, most notably *Koenigia islandica* (105 stems per square meter).

Several species well represented in the meadow plots were absent or uncommon in lake plots (Table 3). These species include *Acomastylis rossii*, *Artemisia scopulorum*, *Bistorta bistortoides*, *Caltha leptosepala*, *Erigeron peregrinus*, *Potentilla diversifolia*, *Sibbaldia procumbens*, and *Vaccinium scoparium*. In contrast, some species that were colonizing the lake were found in significantly lower frequencies in the meadow plots ($P < 0.01$). These included *Draba* spp., *Carex praeceptorum*, *Epilobium anagallidifolium*, *Koenigia islandica*, *Minuartia rubella*, *Oxyria digyna*, *Poa glauca*, *Sedum lanceolatum*, and *Stellaria umbellata*.

To determine the flux of species colonizing individual quadrats, the number of false starts was calculated. A false start is defined as a quadrat occupied by at least one individual of a species in 1 year but devoid of any individual of that species the next year (i.e., failed attempts at establishment). Of the species

Table 3. *Plant abundances in lake margin and meadow plots for selected prevalent species. Data are mean percent cover, with frequency (percentage of all quadrats occupied by the species) in parentheses.*[a]

	Lake plots		Meadow plots	
Species	1985	1986	1987	1986
Achillea lanulosa	0.1 (18)	0.1 (25)	0.1 (30)	4.3 (36)
Acomastylis rossii	0 (1)	0 (4)	0 (7)	6.4 (56)
Agrostis spp.[b]	1.1 (63)	1.2 (59)	2.5 (86)	0.3 (13)
Alopecurus aequalis	0.3 (21)	0 (5)	0.5 (48)	0 (0)
Arenaria fendleri	0 (13)	0 (15)	0.1 (24)	0.4 (9)
Artemisia scopulorum	0 (4)	0 (8)	0 (6)	5.6 (59)
Bistorta bistortoides	0 (1)	0 (0)	0 (2)	5.4 (86)
Caltha leptosepala	0 (2)	0 (3)	0 (1)	4.7 (42)
Carex aquatilis	0 (2)	0 (10)	0.4 (13)	5.0 (30)
Carex ebenea	0 (17)	0.1 (27)	0.1 (38)	2.4 (29)
Carex praeceptorum	0.1 (13)	0 (3)	0.1 (13)	0 (0)
Carex scopulorum	0 (1)	0 (6)	0.5 (30)	6.4 (38)
Clementsia rhodantha	0 (13)	0 (18)	0 (15)	0.6 (20)
Deschampsia caespitosa	2.0 (63)	2.3 (72)	4.4 (80)	8.4 (63)
Draba spp.[b]	0 (31)	0.1 (52)	0.1 (57)	0 (17)
Elymus trachycaulus	0 (6)	0 (7)	0 (6)	0.6 (15)
Epilobium anagallidifolium	0.1 (19)	0 (31)	0.1 (31)	0 (4)
Erigeron peregrinus	0 (0)	0 (2)	0 (4)	8.5 (59)
Festuca spp.[b]	0.2 (61)	0.7 (66)	0.8 (86)	1.1 (21)
Juncus drummondii	0.4 (36)	0.7 (51)	1.8 (51)	3.1 (45)
Koenigia islandica	0.6 (40)	1.2 (44)	3.0 (50)	0 (0)
Luzula spicata	0 (22)	0.2 (30)	0.5 (44)	0.6 (35)
Minuartia rubella	0 (6)	0.1 (17)	0.1 (24)	0 (2)
Oxyria digyna	0.1 (15)	0.1 (27)	0.1 (40)	0 (0)
Phleum commutatum	0.1 (30)	0.3 (59)	0.3 (69)	1.5 (44)
Poa alpina	0.3 (58)	0.7 (73)	1.5 (82)	0.3 (19)
Poa fendleriana	0.4 (7)	0 (2)	0 (10)	1.0 (20)
Poa glauca	0.4 (21)	0.3 (33)	0.5 (44)	0.4 (9)
Poa pratensis	0.2 (22)	0.7 (25)	0.7 (38)	0.1 (20)
Poa reflexa	0.2 (37)	0.1 (27)	0.2 (36)	0.2 (26)
Polytrichum poliferum	0 (2)	0.2 (19)	0.3 (21)	3.6 (46)
Potentilla diversifolia	0 (3)	0 (6)	0 (4)	3.1 (61)
Salix phylicifolia	0 (12)	0.1 (21)	0 (28)	0.9 (11)
Sedum lanceolatum	0 (18)	0 (26)	0 (31)	0.1 (6)
Sibbaldia procumbens	0 (0)	0 (0)	0 (1)	6.2 (64)
Stellaria umbellata	0 (21)	0.2 (39)	0.1 (61)	0 (5)
Trisetum spicatum	0.5 (52)	0.5 (67)	0.9 (88)	1.0 (42)
Vaccinium scoparium	0 (0)	0 (0)	0 (0)	4.6 (43)
Veronica wormskjoldii	0 (2)	0 (5)	0 (9)	2.6 (58)
Total grasses	6.0	8.4	13.7	19.5
Total bryophytes	4.5	3.9	1.4	7.7
Bare ground	86.5	84.5	75.4	3.5

[a] Cover values <0.1% not recorded.

[b] In taxonomically difficult groups, congeners were grouped as described in Methods.

with at least one ramet in at least two of the 216 permanent quadrats in 1985 and 1986, all species produced at least one false start during those 2 years. Nineteen species produced false starts in fewer than 10% (a 2-year mean) of the quadrats occupied. This group included the same species that occurred with significantly higher frequencies in the lake margin than in surrounding meadows. Other species exhibiting few false starts were *Achillea lanulosa, Acomastylis rossii, Agrostis* spp., *Deschampsia caespitosa, Festuca* spp., *Juncus drummondii, Poa alpina, Phleum commutatum,* and *Trisetum spicatum.* Eighteen species were much less effective in colonizing the lake margin, having false starts in more than 35% (2-year mean) of the quadrats. This group included local tree species (e.g., *Picea englemannii, Abies lasiocarpa, Pinus contorta*), *Erigeron peregrinus,* and eight species characteristic of the moist meadows in the vicinity of the lake (e.g., *Carex aquatilis, Caltha leptosepala, Calliergon sarmentosum*) and other moist sites (e.g., *Alopecuris aequalis, Rorippa curvipes, Mimulus guttatus,* and *Carex nova*).

Detrended Correspondence Analysis (DCA) and Plot Classification

Frequency data from lake and meadow plots were arrayed together in a two-dimensional ordination using detrended correspondence analysis (DCA) to identify vegetational gradients among plots (Fig. 2). DCA I separated meadow and lake plots completely. When the same data were analyzed by TWINSPAN, the primary plot division occurred between lake margin and meadow plots.

Meadows—Vegetation of the Relatively Stable Surroundings

Meadow plots were analyzed independently of lake plots in subsequent iterations of TWINSPAN. Groups I and II, distinguished by the indicator *Clementsia rhodantha,* were separated by TWINSPAN from III and IV, distinguished by *Trisetum spicatum.* Group I was distinguished from group II by its high frequency of *Aulacomnium palustre.* The best frequency indicator of group III is *Arenaria fendleri,* and the best frequency indicator of group IV is *Carex elynoides.* These communities in the existing meadows around Lawn Lake are illustrated in the dendrogram resulting from TWINSPAN (Fig. 3).

Detrended correspondence analysis of frequency data from meadow plots alone (results not shown), produced the same plot groups (I through IV) as identified in Figs. 2 and 3. The TWINSPAN of meadow plots using frequency or cover data produced the same primary division as shown in the combined DCA of Fig. 2; that is, the six plots of groups I and II were separated from the 18 plots of groups III and IV. *Sibbaldia procumbens, Artemisia scopulorum,* and *Acomastylis rossii* were identified as cover indicators of the 18 plots of groups III and IV, and *Salix phylicifolia* was a cover indicator of the six plots of groups I and II. Thus, DCA II in Fig. 2 separated plots resembling the *Caricetum scopulorum* marsh association (Willard 1979) from those domi-

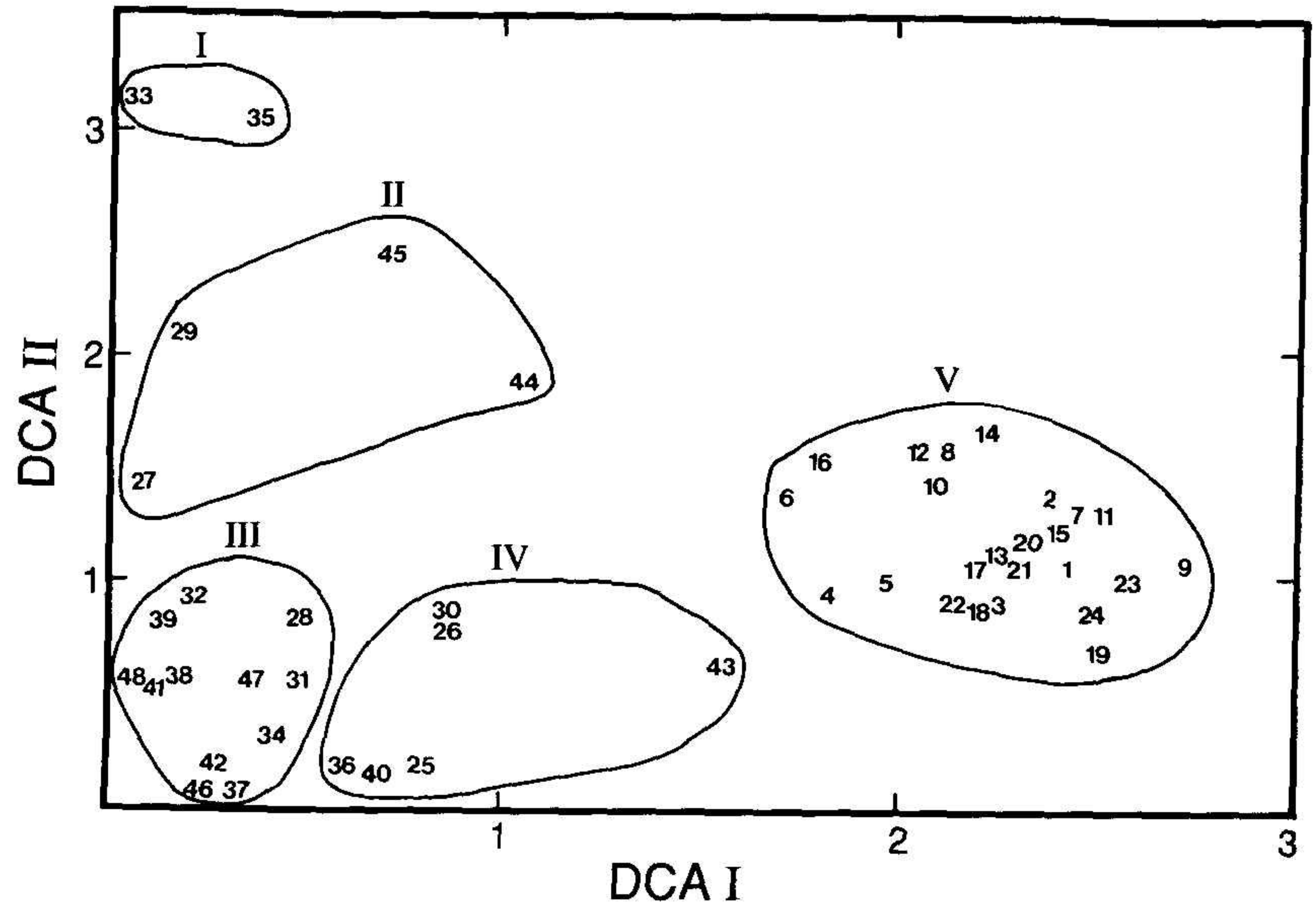


Fig. 2. DCA ordination of study plots in the lake margin and surrounding meadows using plant species frequency data from 1986. Plot groups correspond to classifications identified by TWINSPAN. Plot groups I, II, III, and IV are meadow communities; group V is the successional lake margin.

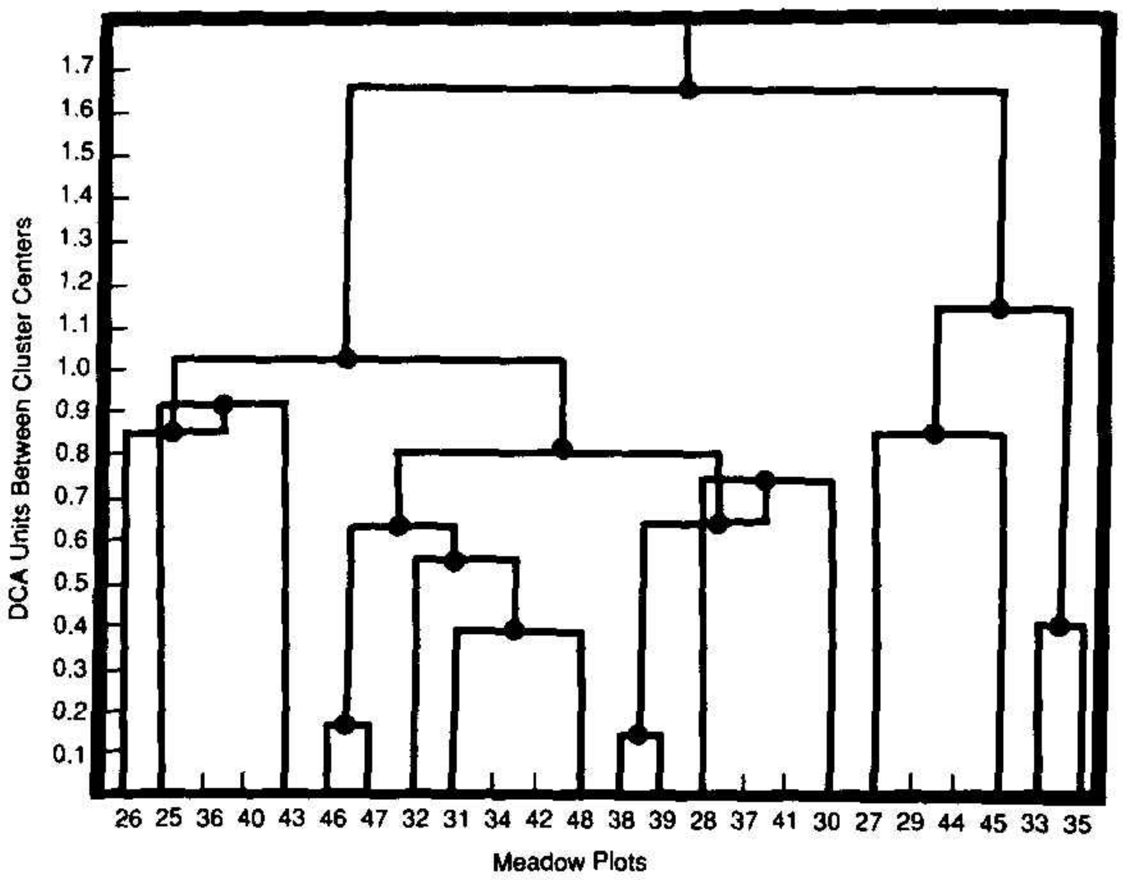


Fig. 3. Dendrogram of meadow plots produced by TWINSPAN. The coordinates for the dichotomies were determined as the euclidean distance in DCA units between the two means of coordinates of plots separated in the DCA ordination.

nated by snowbed or turf association species (*Sibbaldia procumbens, Artemisia scopulorum, Acomastylis rossii,* and *Trisetum spicatum*). *Trisetum spicatum* was an important frequency indicator in the combined ordination (Fig. 2) but not in the ordination of meadow plots. This observation suggests that this species is important in distinguishing the developing lake margin vegetation from the surrounding meadows, but the species is not an important indicator of the structure of the meadow vegetation.

The meadow plot groups identified by DCA and TWINSPAN are further characterized in Table 4. Environmental indices differed significantly among the plot groups ($F = 3.76$; $P < 0.05$).

Plots in group I, with the lowest environmental index, had at least some standing water and were poorly drained, on peaty hummocks, with slopes of <3°. These plots were located in the *Salix*-dominated regions at the northwest end of the study area. Taxa of greatest importance in group I included *Carex aquatilis, Carex scopulorum, Salix phylicifolia, Caltha leptosepala,* and the bryophytes *Drepanocladus exanguiculatus, Sphagnum* sp., and *Aulacomnium palustre.*

Plots of group II were similar to those of group I—low-angle and poorly drained—but group II plots lacked a significant bryoflora. *Carex scopulorum, Caltha leptosepala, Carex aquatilis,* and *Senecio triangularis* dominated this group (Table 4).

Plot group III was dominated by *Bistorta bistortoides, Erigeron peregrinus, Sibbaldia procumbens, Vaccinium scoparium, Artemisia scopulorum, Deschampsia caespitosa, Acomastylis rossii,* and *Veronica wormskjoldii. Polytrichum piliferum, Carex nigricans, Juncus drummondii,* and *Potentilla diversifolia* were also important. This group of plots, the most species-rich in the meadows, was characterized by many species contributing importance. The plots were well drained on sloping soils. Many of these plots were located in areas heavily grazed by ungulates.

Plots of group IV were dominated by *Achillea lanulosa, Deschampsia caespitosa,* and *Carex foena.* Of intermediate importance were *Helictotrichon mortonianum, Artemisia scopulorum, Bistorta bistortoides, Carex elynoides, Solidago multiradiata, Poa glauca, Potentilla diversifolia, Arenaria fendleri, Trisetum spicatum, Acomastylis rossii,* and *Festuca* spp. The plots in this group were located in well-drained soils either on minor ridges or slopes >10°. The plots were also characterized by some disturbance. Plot 43 was in the immediate vicinity of the old patrol cabin site with evidence of the old foundation, stove parts, and eroded soil. Plot 25 was immediately adjacent to one of the backcountry campsites.

Lake Margin—Vegetation Developing Since 1982

To evaluate the structure of the developing lake margin vegetation independently of the surrounding meadows, species frequency data from lake plots in 1986 were analyzed by DCA (Fig. 4). Though these data seemed to form a

Table 4. *Selected vegetational and edaphic characteristics of plot groups (1986) in the mature meadows identified in Fig. 2.*

	Plot groups							
	I		II		III		IV	
Species	Freq.[a]	Cover[a]	Freq.	Cover	Freq.	Cover	Freq.	Cover
Achillea lanulosa	0	0	28	0.0	23	1.1	87	18.0
Acomastylis rossii	11	0	3	0	68	9.2	82	6.5
Arenaria fendleri	0	0	0	0	1	0	40	1.8
Artemisia scopulorum	0	0	14	0	79	7.4	53	7.8
Aulacomnium palustre	50	5.2	0	0	0	0	0	0
Bistorta bistortoides	6	0.3	78	1.8	99	7.3	71	5.7
Caltha leptosepala	78	9.0	86	17.4	30	1.9	4	0.3
Carex aquatilis	100	23.3	50	16.1	14	0.7	4	0.1
Carex ebenea	0	0	3	0	38	2.8	33	4.2
Carex elynoides	0	0	0	0	16	1.8	33	3.5
Carex foena	0	0	0	0	0	0	40	12.9
Carex nigricans	0	0	22	1.7	42	4.8	0	0
Carex scopulorum	50	5.6	86	31.8	21	0.2	22	2.5
Clementsia rhodantha	78	1.0	72	3.1	2	0	0	0
Deschampsia caespitosa	56	1.0	75	1.2	63	9.1	53	15.0
Drepanocladus exanguiculatus	50	32.3	0	0	1	0	0	0
Elymus trachycaulus	0	0	0	0	8	0.1	51	2.6
Erigeron peregrinus	28	1.0	25	3.6	79	13.7	27	1.9
Festuca spp.	0	0	0	0	24	1.6	38	1.1
Helictotrican mortonianum	0	0	0	0	30	1.3	27	9.4
Juncus drummondii	28	4.2	28	2.4	63	4.3	0	0
Luzula spicata	0	0	6	0	50	0.6	26	1.4
Phleum commutatum	0	0	8	1.2	64	1.8	31	1.7
Poa glauca	0	0	3	0	1	0	38	2.0
Polytrichum piliferum	0	0	8	0.2	61	5.9	49	1.9
Potentilla diversifolia	56	2.4	11	0	76	3.5	56	4.7
Salix phylicifolia	100	8.3	8	1.4	1	0	0	0
Senecio triangularis	11	0	50	6.8	11	0	0	0
Sibbaldia procumbens	0	0	22	0	93	11.3	33	0.1
Solidago multiradiata	0	0	0	0	16	0.5	60	3.6
Sphagnum sp.	67	18.0	0	0	0	0	0	0
Trisetum spicatum	0	0	0	0	46	1.2	82	2.0
Vaccinium scoparium	0	0	6	0	74	8.2	2	0.6
Veronica wormskjoldii	0	0	39	1.0	75	4.2	35	0.7
Bare ground	—	6.3	—	5.0	—	2.6	—	1.8
Environmental index	21.6 ± 2 .3		31.2 ± 32		32.3 ± 6.8		38.6 ± 6.5	
Organic matter (%)	10.4 ± 1.2		8.5 ± 2.8		8.2 ± 2.7		6.6 ± 3.5	
pH	4.02 ± 0.10		4.05 ± 0.20		3.87 ± 0.29		4.12 ± 0.30	

---

[a] Percent.

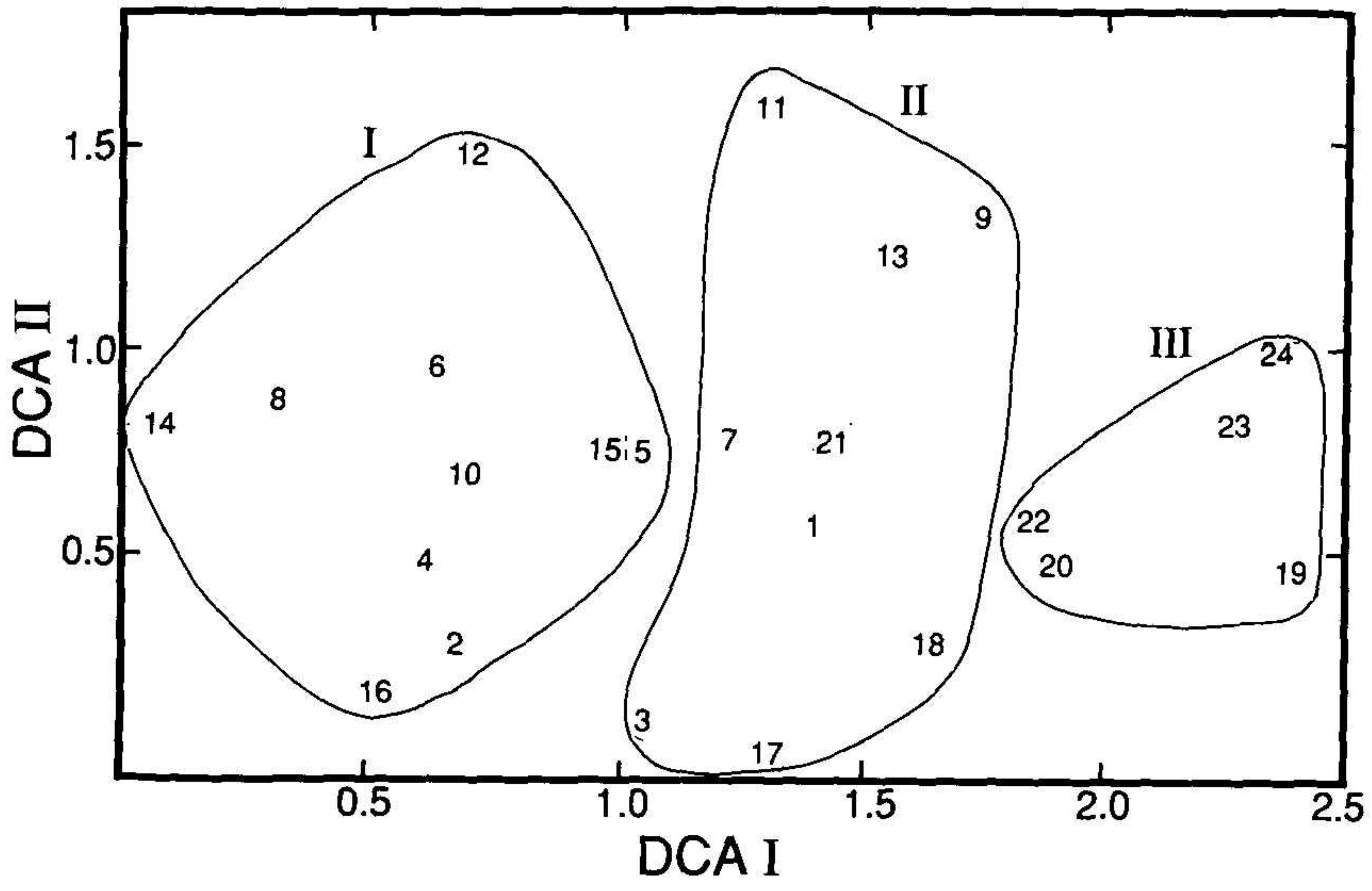


Fig. 4. DCA ordination of lake margin plots using plant species frequency data from 1986. Plot groups I, II, and III were identified by TWINSPAN.

continuum, three groups were distinguished using TWINSPAN. These groups were resolved by DCA I (Fig. 4). *Carex aquatilis* was the indicator of plot group I. *Arenaria fendleri* and *Elymus trachycaulus* were indicators of groups II and III, with group II being best distinguished from group III by a higher frequency of *Koenigia islandica*.

Detrended correspondence analysis of 1985 and 1987 frequency data (ordinations not shown) produced the same nonoverlapping plot groups as shown in Fig. 4. However, TWINSPAN identified slightly different plot groups. In all years, plots of group III were distinguished by *A. fendleri* and *E. trachycaulus*. Plots of group I—except plots 4, 12, and 15—were classified together during all 3 years, with one or more of the following as indicators: *Carex aquatilis, C. scopulorum, C. praeceptorum, Clementsia rhodantha, Epilobium anagallidifolium*, and *Juncus mertensianus*. The remainder of the plots (generally, plot group II in Fig. 4) were classified with plots of group III during the first division of the analysis in 1985 and with plots of group I during the first division of the analysis in 1987. This observation indicates that two components of the lake margin vegetation (groups I and III) have remained fairly distinct throughout the study years, while a third component has changed from having characteristics more similar to group III to having characteristics more similar to group I. Further divisions of plot groups were not consistent among data sets from different years. Consequently, classifying more than three groups could not be reasonably performed now.

The three lake plot groups identified by DCA and TWINSPAN are further characterized in Table 5. Although a clear trend was evident among plot groups,

Table 5. *Selected vegetational and edaphic characteristics of plot groups located in the margin of Lawn Lake as identified in Fig. 4.*

	Plot groups											
	I				II				III			
	Freq.[a]		Cover[a]		Freq.		Cover		Freq.		Cover	
Species	1985	1987	1985	1987	1985	1987	1985	1987	1985	1987	1985	1987
Achillea lanulosa	13	22	0.3	0.1	16	31	0	0.1	31	35	0	0
Agrostis spp.	42	81	1.3	2.7	74	95	1.3	3.7	67	60	0.3	0
Arenaria fendleri	5	8	0.1	0	12	23	0	0.2	29	51	0	0.1
Carex chalciolepis	1	3	0	0	0	1	0	0	2	13	0.1	2.2
Carex ebenea	19	43	0	0.2	19	40	0	0.1	2	11	0	0
Carex scopulorum	1	38	0	0.3	1	28	0	0.8	0	0	0	0
Deschampsia caespitosa	73	95	3.8	8.4	50	75	1.0	1.5	58	42	0.3	1.7
Draba spp.	15	37	0	0.1	38	79	0	0.3	49	51	0.1	0
Elymus trachycaulus	0	0	0	0	4	5	0	0	20	20	0	0
Epilobium anagallidifolium	43	64	0.1	0.3	5	10	0	0.1	0	2	0	0
Festuca spp.	44	66	0.3	0.5	63	95	0.1	1.2	74	89	0.4	0.8
Juncus drummondii	57	77	1.0	3.9	21	40	0.1	0.5	2	4	0	0
Koenigia islandica	51	70	1.3	5.6	50	54	0.3	1.6	0	2	0	0
Luzula spicata	14	39	0	0	27	54	0	1.3	25	36	0	0
Oxyria digyna	13	24	0	0	16	57	0	0.1	15	27	0.4	0.1
Phleum commutatum	44	88	0.2	0.4	21	69	0.1	0.3	7	13	0	0
Poa alpina	39	76	0.2	0.9	73	82	0.2	2.5	60	89	0.4	0.8
Poa fendleriana	0	2	0	0	16	6	0.9	0	2	33	0.3	0
Poa glauca	12	19	0.2	0.3	22	58	0.5	0.5	37	64	0.6	1.1
Poa pratensis	21	48	0	0.4	21	27	0.5	1.4	24	31	0	0
Poa reflexa	43	56	0.2	0.4	35	21	0.4	0.1	13	2	0	0
Salix phylicifolia	18	36	0	0.1	8	27	0	0	7	11	0	0
Sedum lanceolatum	7	9	0	0	30	42	0	0.1	22	51	0	0
Stegonia latifolia	19	39	2.9	1.9	15	6	1.5	0	0	2	0	0
Stellaria umbellata	14	48	0	0.1	30	80	0	0.2	11	38	0	0
Trisetum spicatum	28	71	0.1	0.4	59	96	1.1	2.0	71	89	0.1	0.1
Bare ground	—	—	85.3	68.1	—	—	82.1	74.2	—	—	96.9	92.5
Environmental index	30.8 ± 5.3				30.0 ± 9.5				38.5 ± 4.9			
Organic matter (%)	7.2 ± 6.0				4.6 ± 4.7				0.8 ± 0.4			
pH	4.18 ± 0.27				4.31 ± 0.43				4.42 ± 0.25			

[a] Percent.

differences in the abiotic parameters were not statistically significant by ANOVA. Species whose cover values differed ($P < 0.01$) in 1987 among the three groups (Fig. 4) were *Carex chalciolepis*, *Deschampsia caespitosa*, *Juncus drummondii*, *Stegonia latifolia*, and *Trisetum spicatum*. The portion of bare ground exposed also differed significantly among the three groups.

In addition to the frequency indicators of group I, the following species achieved their highest cover values in this group: *Deschampsia caespitosa, Juncus drummondii, Phleum commutatum, Epilobium anagallidifolium, Salix phylicifolia, Koenigia islandica,* and *Stegonia latifolia.* All plots in the upper zone of the northwest and southwest sides of the lake were in this group. Two other plots in the group were found at breaks in the slope where either soils from the upper zone had crept downslope (plot 15) or groundwater had seeped to the surface (plots 5 and 15).

Plots in group II were located in the lower zone of the lake margin, had intermediate soil organic content, and appeared to have a moderate clay content. *Agrostis* spp., *Trisetum spicatum, Festuca* spp., *Poa alpina,* and *Draba* spp. all achieved their greatest importance in this plot group.

Plots of group III had the highest frequencies of *Poa alpina, Poa glauca, Trisetum spicatum, Festuca* spp., *Sedum lanceolatum, Arenaria fendleri, Achillea lanulosa,* and *Draba* spp. (Table 5). Group III plots were characterized by coarse gravels. However, in one case each, interstitial clays and peat hummocks underlaid the gravels. These plots were well drained. In one case, the peat hummocks (about 0.4 m deep) rested on a substrate of coarse gravels and sands. The absence of *Juncus drummondii* and *Caltha leptosepala* was consistent with the less hydric qualities of these plots.

By 1986, lake plots had already become distinguished along gradients clearly evident among meadow plots (Fig. 2). The lake margin plots with highest DCA II values in Fig. 2 were group I plots in Fig. 4 (e.g., 6, 8, 10, 12, 14, and 16), all lying at the northwest end of the lake in the upper zone having soils of high organic content and low environmental indices. Total cover was significantly greater in the upper zone than in the lower zone of the lake margin in 1986 and 1987. Species cover differed significantly ($t = 2.92$, $P < 0.01$) for only one species—*Trisetum spicatum.*

Two-way analysis of variance was performed to explain the variation observed among abiotic and biotic parameters in lake plots. DCA I positions of plots differed between upper and lower zones and among areas (northwest, southwest, and east) into which the plots were stratified (Table 6). Differences

Table 6. *F-ratios from analysis of variance on DCA I from 1985, 1986, and 1987 DCA's of species frequency data.*

Year	Zone[a]	Area[b]	Zone and area
1985	4.49[c]	6.98[d]	7.05[d]
1986	4.51[c]	22.00[e]	19.33[e]
1987	2.08	29.14[e]	22.07[e]

[a] Compares upper and lower zones of the lake margin.
[b] Refers to the northwest, southwest, and east sides of the lake margin.
[c] $P < 0.05$.
[d] $P < 0.01$.
[e] $P < 0.0001$.

in plot positions in the vegetational gradient between upper and lower zones were significant in 1985 and 1986 but were not significant by 1987. The variation in the data is largely explained by differences among the three areas (southwest, northwest, and east sides). These differences are becoming more pronounced with time; for the vegetation as a whole, the importance of the specific geographic area around the lake is becoming greater than that of elevation above the existing lakeshore. Area differences between southwest and northwest sides were insignificant. Thus, significant differences that were established early during revegetation between the upper and lower zones are most evident along the west shore of the lake. Another DCA was calculated using 3 years of species frequency data from lake margin plots to further clarify trends during the study. Cartesian coordinates of individual plots generally did not fluctuate much from year to year (Fig. 5). Consequently, the three plot groups identified in Fig. 5 contain the same plots as shown in Fig. 4. Some plot positions, however, changed consistently as shown in Fig. 5. In most cases, these plots were the most extreme of their group, and the tendency was to move toward the center of the ordination. Although several factors may be involved in controlling the centralizing tendency of the vegetation, reproduction and subsequent recruitment of seedlings from plant populations established since 1982 in the lake margin offers the most likely explanation. Exceptions to this centralizing tendency were plots 17, 19, 21, and 24, which tended to move from relatively high to still higher DCA I values. All these plots are in

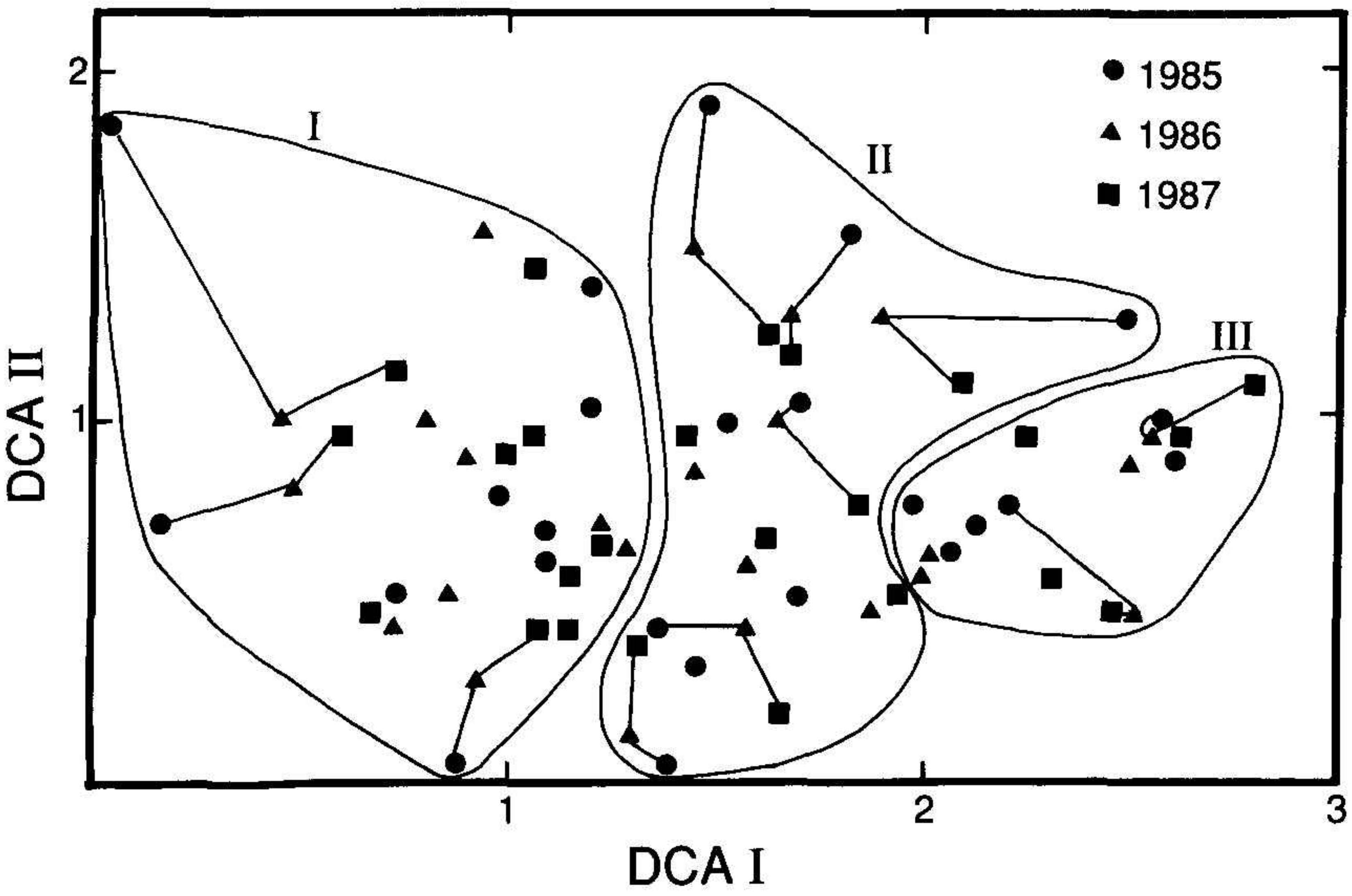


Fig. 5. DCA ordination of lake margin plots including 1985, 1986, and 1987 species frequency data. In all cases, plots from each of the 3 years occurred within the boundaries of the same plot group; therefore, plot groups I, II, and III include the same plots shown in Fig. 4.

areas along the east side of the lake and receive the greatest foot and horse traffic.

Percentage Similarity

The percentage similarity of species cover among all plots in the lake margin increased significantly (by Wilcoxon paired-sample test) between 1985 and 1987. Similarity increased among plots in groups I and II but not in group III. These results indicate that the plots within the northwest and southwest shores of the lake margin started to converge floristically by 1987, as suggested by Fig. 5.

Correlations in the Data Set

To determine correlative relations among species cover, abiotic parameters, and plot positions in the DCA ordinations, Pearson correlation coefficients were calculated (Table 7). The coordinate positions of plots in DCA's

Table 7. *Correlation coefficients among abiotic parameters, ordination coordinates (DCA I and DCA II) and species cover for meadow plots, lake margin plots (cf. Fig. 4), and the combined analysis of lake margin and meadow plots (cf. Fig. 2). The coordinates for the meadow ordination are not shown in other figures.*

	Meadow			Lake			Combined		
Species	Organic[a]	DCA I	DCA II	Organic	DCA I	DCA II	Organic	DCA I	DCA II
Achillea lanulosa	−0.342	−0.579	0.127	0.332	−0.098	0.147	−0.020	-0.369^{c}	0.151
Bistorta bistortoides	0.079	-0.491^{b}	−0.123	—	—	—	0.371^{c}	0.017	0.251
Caltha leptosepala	0.499^{b}	−0.200	−0.236	—	—	—	0.258	0.474^{c}	0.056
Carex aquatilis	0.108	0.428^{b}	0.028	0.278	−0.265	0.001	0.144	0.561^{c}	0.188
Carex ebenea	0.333	0.516^{c}	−0.004	0.301	−0.315	−0.129	0.188	−0.064	0.320^{b}
Carex scopulorum	−0.018	−0.173	0.367	0.064	−0.206	−0.098	0.103	0.373^{c}	0.273
Clementsia rhodantha	0.040	0.401	0.303	—	—	—	0.184	0.465^{c}	0.217
Deschampsia caespitosa	0	0	0	0.465^{b}	-0.520^{c}	0.097	0.269	−0.143	0.269
Juncus drummondii	0	0	0	0.488^{b}	-0.507^{b}	0.005	0.314^{b}	0.185	−0.161
Koenigia islandica	—	—	—	0.411^{b}	0.441^{b}	0.506^{b}	0.224	−0.234	0.195
Poa glauca	0.158	−0.093	0.185	−0.171	-0.431^{b}	−0.280	0.032	−0.022	−0.169
Poa reflexa	0	0	0	0.315	0.346	0.627^{c}	0.246	−0.170	-0.297^{b}
Salix phylicifolia	0.358	−0.043	0.177	0.357	−0.295	−0.102	0.175	0.553^{c}	0.151
Trisetum spicatum	0.131	0.648^{c}	0.155	0.365	0.054	0.260	0.358^{b}	−0.164	0.304^{b}
Environmental index	0.136	-0.616^{c}	0.360	−0.158	0.383	−0.287	−0.043	−0.205	0.330^{b}
Organic matter[a]	0.101	-0.437^{b}	0.282	—	-0.504^{b}	0.541^{c}	—	0.045	0.330^{b}
pH	0.101	−0.064	0.614^{c}	-0.497^{b}	0.362	0.326	-0.423^{c}	−0.058	0.043

[a] Percent.
[b] $P < 0.05$.
[c] $P < 0.01$.

correlated with environmental indices in the meadow analysis but not in either the lake or the combined (meadow and lake margin) analyses. Organic content of the soils correlated with the DCA I in both lake and meadow ordinations and with DCA II in both the lake and the combined ordination, in which the major axis distinguishing among meadow plots was DCA II (Fig. 2). Plot pH was significantly negatively correlated with plot organic content in lake and combined ordinations but not in the meadow ordination. However, in the meadow ordinations, the pH correlated significantly with the second major axis of the vegetational ordination. This correlation suggests that the chemical behavior of the organic matter, or more generally the soils, is not necessarily similar in mature and developing communities, despite the apparent importance of organic matter in both meadow and developing lake margin vegetation and pH in the structure of meadow vegetation.

The cover of several species correlated with the major axis of plot differentiation in all three ordinations, although the individual species showing correlations differed among the ordinations. *Trisetum spicatum* and *Carex ebenea* were the only species that consistently correlated with the corresponding axes of the combined and either the meadow or lake ordinations. The species frequency differences between the meadows and the lake margin are not related to measured abiotic parameters, as indicated by the absence of a significant correlation between any abiotic parameter and DCA I of the combined ordination.

Discussion

Lake Margin Colonization

Within 3 years of the Lawn Lake drainage, a large portion of the plant species from surrounding meadows had appeared in the lake margin. In most cases, species were in extremely low frequencies and cover throughout the lake basin. Between the third and fourth years following the flood, some new species common to at least some of the meadow communities appeared for the first time (e.g., *Senecio triangularis*, *Sibbaldia procumbens*, *Carex elynoides*, *Carex microptera*, and *Castilleja rhexifolia*), while others (e.g., *Deschampsia caespitosa*, *Juncus drummondii*, *Trisetum spicatum*, *Phleum commutatum*, *Poa alpina*, *Salix phylicifolia*, *Festuca* spp., *Koenigia islandica*, and several others) continued to increase in frequency and cover (Table 3).

Of the species that were significantly more frequent in the disturbed lake margin than the surrounding meadows (Table 3), most were annual or short-lived perennial ruderals (Grime 1979) of the higher tundra frost scars or scree slopes (e.g., *Koenigia islandica* and *Minuartia rubella*) or of more xeric montane slopes (e.g., *Sedum lanceolatum* and *Arenaria fendleri*). With the exception of *Koenigia islandica*, these species are a smaller portion of the lake margin flora than the perennial graminoids, which are rapidly colonizing the lake. While some of these grasses (e.g., *Poa alpina*, *Agrostis variabilis*, *Podagrostis humilis, Festuca brachyphylla,* and *Poa glauca*) are in much greater frequency in the disturbed lake margin than in surrounding meadows, others (e.g., *Deschampsia caespitosa, Trisetum spicatum, Phleum commutatum, Poa arctica,* and *Poa reflexa*) are well-established or dominant meadow species. Thus, one should not conclude that the major colonizers on the site are substantively different from the species typifying the mature meadow communities. Interestingly, only one small population of *Koenigia islandica* has been found anywhere in the Lawn Lake drainage upslope from Lawn Lake in 5 years of searching; yet by 1987, this species had achieved the greatest density of any in the lake margin.

A 3-year rate of colonization of the disturbed margin of Lawn Lake by new species was more rapid than the rate of colonization (assessed by either addition of species or increase in cover of individual species) of other sites experiencing primary succession, in which disturbance has left a site devoid of propagules—for example, the volcanic substrates of tropical Krakatoa (Docters van Leeuwen 1929), subarctic Surtsey (Einarsson cf. Miles 1979) or subalpine Mount St. Helens (Wood and del Moral 1987); sand dunes of Ontario (Morrison and Yarranton 1973); or newly exposed glacial till in Glacier Bay (Cooper 1939). Several possible reasons may explain such a high rate of colonization in Lawn Lake. A large number of safe sites (Harper 1977) may exist to which propagules can disperse and become established. A high density of propagules of species with high dispersal capabilities may be moving to the lake margin. High reproductive success may exist among species arriving in the lake margin (high colonizing efficiency of Wood and del Moral 1987). Finally, a combination of these or other factors may be operating.

If the number of safe sites is high, then the number of false starts (failed attempts at establishment) is expected to be fairly low. Two groups of species exhibited few false starts: graminoids that are proliferating in the lake but are also well established in nearby meadows (e.g., *Poa alpina, Trisetum spicatum, Deschampsia caespitosa, Phleum commutatum, Juncus drummondii, Agrostis* spp., and *Festuca* spp.), and annual and relatively short-lived perennial forbs with significantly lower frequencies in nearby meadows (e.g., *Koenigia islandica, Minuartia rubella, Stellaria umbellata, Epilobium anagallidifolium,* and *Draba* spp.). The latter group possesses the ruderal syndrome of attributes (Grime 1979), in which high seed production and high relative growth rates occur. All of these species with few false starts also produced dispersible seeds and numerous seedlings. These attributes were also reported among colonists (including some of these same taxa) of disturbed sites at timberline in the White Mountains (Marchand and Roach 1980).

High false starts at colonization were observed among woody plants, forest understory species (e.g., *Polemonium viscossum*), hydric species, and a few mesic meadow dominants, such as *Erigeron peregrinus*. These species were less likely to sustain reproductive populations, despite initial appearance as seedlings or juveniles, in the absence of site conditions favorable for the adult, established phase (e.g., suitable water relations). Although a low frequency of false starts is evident in those species most effectively colonizing the margin of Lawn Lake, this may be, in part, an artifact of the quadrat size. As the number of ramets per quadrat increases, the ability to detect false starts may decrease.

Attributes of species colonizing other disturbed subalpine sites differ from those observed in this study. For example, species colonizing the barren sites of Mount St. Helens are principally stress tolerators (Wood and del Moral 1987), well adapted to xeric sites on volcanic tuff. At Lawn Lake, the majority of species establishing populations are more ruderal or competitive (e.g., *Deschampsia caespitosa*, *Festuca ovina*, and *Agrostis* spp.) than stress-tolerant (Grime 1979). One would expect more competitive species later in successional development following site preparation by colonizers in classical facilitation models of succession. How can this pattern of colonization in Lawn Lake be explained?

The best sites for colonization of barren surfaces on Mount Fuji were beneath *Polygonum cuspidatum*, where soil organic matter, bulk density, nitrate, and water content were higher than in surrounding sites, contributing to the nurse plant effect (Hirose and Tateno 1984). At Lawn Lake, several soils developed before 1902, with these same properties providing the same facilitation effects for rapid colonization and revegetation following reexposure in 1982. The rapid rate of vegetation development can thus be explained, in part, by the presence of sufficient sites to establish reproductive populations of both ruderal and highly dispersible and more competitive components of the vegetation. The more rapid increase in plant cover on the west side than on the east side of the lake (Table 5) is consistent with this interpretation. On the east side, organic content is minimal, and species with more stress-tolerant attributes (e.g., *Sedum lanceolatum* and *Arenaria fendleri*) are indicator species. Similarly, rapid vegetation development has been observed in the margin of a drained lake in the arctic tundra where nearly complete revegetation occurred in 10–20 years (Carson 1968). Although Willard and Marr (1971) showed that seedlings in the alpine tundra survived better on exposed mineral soils than on remnants of organic-rich A horizons, such species were typically stress-tolerant.

Mesic sites favorable for seedling establishment are well distributed in the margin of Lawn Lake, and species in extremely low frequency or even absent from the Roaring River drainage are developing populations in such sites. Clearly, limitations are preventing establishment of the dominant mesic meadow species that are nearly absent from the lake margin (Table 3), such as *Bistorta bistortoides*, *Sibbaldia procumbens*, *Artemisia scopulorum*, *Potentilla diversifolia*, *Erigeron peregrinus*, and *Acomastylis rossii*. Such attributes as seed viability and seedling survival (e.g., Black and Bliss 1980), dispersal capability (e.g., Wood and del Moral 1987), or biotic interactions may be involved. The dynamics of dispersal between meadow and lake margin and within the lake margin are not examined here.

Community Structure

The structure of the meadow vegetation is evidently controlled to a large extent by abiotic factors, as evident in the differences among plot variables (Table 4) and correlations in the data structure (Table 7). Unlike more complex tundra vegetation (Webber 1978; Willard 1979; Komarkova 1980), the subalpine and ecotonal meadows in the vicinity of Lawn Lake segregated into four major groups, all differentiated along a gradient of organic matter and soil moisture. Meadow group IV, with a significantly higher environmental index and lower organic content than other meadows in the area, had a high frequency of species that are also colonizing the lake margin in high frequency (e.g., *Achillea lanulosa*, *Deschampsia caespitosa*, *Festuca* spp., and *Trisetum spicatum*).

Analysis of the plot ordinations suggests that similar abiotic factors can be used to discriminate among community clusters in the lake margin and the meadows, despite the observation that the dominant species in lake and meadow communities differed. This claim is supported by the fact that more hydric species tend to occupy plots with lower DCA I values in lake margin and meadow ordinations and high DCA II values in the combined ordination (Figs. 2 and 4). Within the lake margin, the major vegetation groups correspond to abiotic conditions—principally the soil organic matter and to a lesser extent the pH (Tables 5 and 7). These three groups corresponded approximately to geographically distinct areas: (1) the upper zone on the northwest and southwest sides of the lake, (2) the lower zone on the northwest and southwest sides of the lake, and (3) the east side of the lake. This distribution further illustrates the importance of abiotic conditions in determining the vegetation structure. Vegetational differences associated with these geographic features were evident within 3 years of the disturbance (Fig. 4; Tables 5 and 6). Such differences may also be related to several other physical or chemical properties that may contribute to the operational environment (Spomer 1973) but have not been rigorously examined here.

The plots with the most hydric conditions in the meadows (group I in Fig. 2) form the least diverse meadow community with the most exposed ground (Table 4), whereas the plots in the lake margin (group I in Fig. 4) on low-angle, peaty sites have the greatest cover and highest diversity in relation to other lake margin plots (Table 5). Not unexpectedly, colonization is most rapid on highly organic hydric to mesic sites in the lake margin. In the meadows, on the other hand, poorly drained sites probably restrict the diversity of mature plants that can tolerate standing water (Webber 1978). Although the upper zone at the northwest end of the lake supports the organic substrate for germination of bog species of meadow group I (e.g., *Caltha leptosepala* and *Clementsia rhodantha*), this community is not clearly developing in the lake margin. The absence of this community in the lake margin is probably due to the occasional decline of soil water potentials below some critical value in the absence of standing water that was present before 1902 when the bog community persisted on the site but is now absent except in small pockets. *Carex scopulorum* and *C. aquatilis* are the only species dominating meadow group I that are beginning to proliferate in the lake margin. Both of these species have wide-spreading rhizomes and are capable of reaching sites where survival of the genet is possible. *Salix* will probably establish on much of this high northwest side of the lake where seedlings have survived and grown, though not reproduced, during the past 3 years. This establishment would be predicted on the basis of its longevity and growth form (Noble and Slatyer 1980). The less hydric sites in this area are likely to remain dominated by the grasses and sedges that are currently becoming established on the site. Lake margin communities may be diverging in the direction of surrounding mesic meadow communities, but such divergence is likely only if meadow species can be recruited at a greater rate in the future than is now occurring.

Little evidence exists that the lake margin is developing toward a climax. However, many of the same species occurring in meadow plots with a recent history of disturbance (plots of meadow group IV) are colonizing edaphically similar disturbed lake margin plots (e.g., those of the east side). These species include *Poa glauca, Arenaria fendleri,* and *Achillea lanulosa.* If these sites are developing deterministically, then one would predict that with time, *Carex foena, Carex elynoides, Artemisia scopulorum,* and other turf species will come to dominate the east margin of the lakeshore as they do in nearby xeric meadows. However, human disturbance on the east side of the lake may prevent such development and may help to maintain a community that is controlled biogenically out of equilibrium.

These results suggest some allogenic (environmental) control of vegetational development (Tansley 1935) in the lake margin, at least in the early stages of development. Unlike the single-stage vegetation development typical of tundra, in which environmental controls of succession are of primary importance (Muller 1952; Webber 1978), a ruderal component is apparent at Lawn Lake. However, in addition to the ruderal species, a set of more competitive species (graminoids) are among the major lake colonizers. Based on numerous successional studies in which a ruderal component exists during early successional stages (Drury and Nisbet 1973; Connell and Slatyer 1977; Bazzaz 1979; Frank and del Moral 1986), we can predict that this component of the vegetation will be replaced at Lawn Lake. The dynamics or mechanisms of replacement are unclear now, although the well-established competitive graminoids will probably proliferate along the northwest and southwest sides of the lake. While a ruderal component may precede a mature meadow's development, the existence of high organic content in the soils on the west side of Lawn Lake probably precludes the role of ruderal species in facilitation there, insofar as facilitation implies edaphic preparation of the site for colonization by late successional species. Indeed, the establishment in the lake margin of many species characteristic of one or more of the mature meadow communities supports the claim that lake margin colonization by these species is more a function of their vital attributes (Noble and Slatyer 1980) than of other species per se. In this regard, vegetation development in the margin of Lawn Lake is wholly consistent with the individualistic hypotheses of succession and is inconsistent with a Clementsian view of development toward a climax.

Trends in Vegetation Development

Long-term successional trends cannot be inferred from a 3-year study. However, during this study, significant trends were observed. First, the vegetation throughout the northwest and southwest portions of the lake margin became more homogeneous. When 3 years of data were analyzed together, plots showing consistent trends in the ordination space either converged toward the center of the ordination or were plots experiencing disturbance that might preclude continued colonization (Fig. 5). Furthermore, the percentage similarity among plots increased significantly between 1985 and 1987. The data suggested that where sites are favorable for seedling establishment, the reproduction by plant species already colonizing the lake margin is beginning to define the future direction of the vegetation. Similar patterns have also been observed in subalpine meadow succession in Mount Rainier National Park over the 35 years following cabin bulldozing (Frank and del Moral 1986).

Second, the convergence in vegetation may be explained in part by a decrease in difference between upper and lower zones of the lake margin. This decrease is evident from (1) the analysis of plot position variance on the major axis of the DCA ordination, and (2) the TWINSPAN classifications showing a shift of group II plots (lower zone plots) from having affinity with group III in 1985 to group I in 1987. The plots of group III are not converging with vegetation from the rest of the lake margin (Fig. 5), which is probably due to the absence, in such coarse soils of low organic content, of sufficient sites for colonization by propagules from lake margin populations.

Summary and Conclusions

1. Permanent plots were established and monitored from 1985 through 1987 in the disturbed lake margin and meadows surrounding Lawn Lake.
2. The margin of Lawn Lake is becoming naturally revegetated after the dam break in 1982. While some lake margin plots have plant cover over 50%, mean cover in the lake margin was 13.5% in 1985, 15.5% in 1986, and 24.6% in 1987. Grasses constituted the species of greatest significance; *Deschampsia caespitosa* was the most important. More grass species were present in the lake margin than in surrounding meadows, but more species of all other plant life forms were present in the meadows.
3. More than 95% of the surrounding meadows was covered by plants. In addition to *Deschampsia caespitosa*, the most frequent species were *Bistorta*

bistortoides, *Erigeron peregrinus*, and *Sibbaldia procumbens*. Four plant communities were identified in the existing meadows using detrended correspondence analysis (DCA) and two-way indicator species analysis (TWINSPAN). Axes of the ordination correlated significantly with organic matter content of soils and an environmental index composed of slope, aspect and soil texture, organic content, and pH.

4. Plots in the lake margin analyzed by DCA and TWINSPAN segregated into three groups. Groups corresponded with lake margin zonation. One group (III) on the east side of the lake had the least cover (7.5% in 1987) and frequency of plant species. Another (I) corresponded approximately to the upper zone of the west side of the lake margin, which was vegetated before the Lawn Lake Dam construction in 1902. This group of plots was colonized most rapidly (32% plant cover in 1987) due to the high frequency of sites available for seedling establishment of both ruderal and graminoid species. A third group (II) corresponded to the lower zone of the west side of the lake margin, which was submerged until the dam break in 1982. This group was intermediate to the other two in several respects.
5. During the 3 years of the study, the vegetation became more similar among plots along the west side of the lake margin, suggesting that where sites were favorable for seedling establishment, the reproduction by plant species already colonizing the lake margin was beginning to define the future direction of the vegetation development.
6. Variations in edaphic features associated with either site history, proximity to seed sources, or both are fundamentally important in controlling initial successional trends. Life history attributes of species were used to explain the few trends evident in the vegetation development of the lake margin, lending credibility to the vital attributes model of succession (Noble and Slatyer 1980).
7. Plant succession at Lawn Lake is similar to secondary succession in benign environments and unlike primary succession in tundra, because ruderal species are active colonizers initially. Although preparation (organic deposition) of some sites currently being colonized occurred nearly 90 years ago when the plant communities were flooded by the Lawn Lake Dam, the evidence is unclear whether the initial colonizers will yield to dominants of one or more of the communities in nearby meadows or whether the dominants will be those species that have been able to colonize the sites early and that are rapidly increasing in cover. Long-term observations will be required to determine the equilibrium species compositions for the lake margin, if indeed an equilibrium is attained.
8. I urge the National Park Service to take advantage of the unique natural experiment offered for ongoing study of revegetation of the subalpine–alpine ecotone of the Lawn Lake area.

Acknowledgments

I thank C. Dott, G. Gianniny, and P. Wiens for invaluable perseverance and fellowship in the field and K. Stark for her careful lab and computer work. All have been dedicated! I am indebted to L. Arnow and J. Flock for identifying species of *Poa* and bryophytes, respectively. J. Anderson, R. del Moral, D. Frank, D. Wiens, and two anonymous reviewers also contributed suggestions. I appreciate the support of D. Primrose, D. Stevens, and other park personnel. The National Park Service supported this work with a grant.

Literature Cited

Arnow, L. A., B. J. Albee, and A. M. Wycoff. 1980. Flora of the central Wasatch front, Utah. University of Utah Printing Service, Salt Lake City.

Baker, W. L. 1983. A bibliography of Colorado vegetation description. Great Basin Naturalist 43:45–64.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics 10:351–372.

Black, A. R., and L. C. Bliss. 1980. Reproductive ecology of *Picea mariana* (Mill.) BSP. at tree line near Inuvik, Northwest Territories. Canadian Ecological Monographs 50:331–354.

Braun-Blanquet, J. 1932. Plant sociology, the study of plant communities (translated from German by G. D. F. Fuller and H. S. Conrad). McGraw Hill, New York.

Carson, C. E. 1968. Radiocarbon dating of lacustrine strands in arctic Alaska. Arctic 21:12–26.

Clements, F. E. 1916. Plant succession. An analysis of the development of vegetation. Carnegie Institute Washington, Washington, D.C.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119–1144.

Cooper, W. S. 1939. A fourth expedition to Glacier Bay, Alaska. Ecology 20:130–159.

Diamond, J. M. 1975. Assembly of species communities. Pages 342–444 *in* M. L. Cody and J. M. Diamond. Ecology and evolution of communities. Belknap, Cambridge, Mass.

Docters van Leeuwen, W. M. 1929. Krakatau's new flora. Proceedings of the Fourth Pacific Science Congress (Batavia) Part 2:56–71g.

Drury, W. H., and I. C. T. Nisbet. 1973. Succession. Journal of the Arnold Arboretum Harvard University 54:331–368.

Frank, D. A., and R. del Moral. 1986. Thirty-five years of secondary succession in a *Festuca viridula–Lupinus latifolius* dominated meadow at Sunrise, Mount Rainier National Park, Washington. Canadian Journal of Botany 64:1232–1236.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, Mass.

Geiger, R. 1965. The climate near the ground. Harvard University Press, Cambridge, Mass.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:7–27.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley & Sons, New York.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, New York.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York.

Helwig, J. T. 1985. SAS introductory guide. SAS Institute, Inc., Carey, N.C.

Hill, M. O. 1979a. DECORANA—a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, N.Y.

Hill, M. O. 1979b. TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, N.Y.

Hirose, T., and M. Tateno. 1984. Soil nitrogen patterns induced by colonization of *Polygonum cuspidatum* on Mt. Fuji. Oecologia (Berlin) 61:218–223.

Komarkova, V. 1980. Classification and ordination in the Indian Peaks area, Colorado Rocky Mountains. Vegetatio 42:149–163.

Marchand, P. J., and D. A. Roach. 1980. Reproduction strategies of pioneering alpine species: seed production, dispersal and germination. Arctic and Alpine Research 12:137–146.

McCune, B., and T. F. H. Allen. 1985. Will similar forest develop on similar sites? Canadian Journal of Botany 63:367–376.

Miles, J. 1979. Vegetation dynamics. Chapman and Hall, New York.

Morrison, R. G., and G. A. Yarranton. 1973. Diversity, richness and evenness during a primary sand dune succession at Grand Bend, Ontario. Canadian Journal of Botany 51:2401–2411.

Muller, C. H. 1952. Plant succession in arctic heath and tundra in northern Scandinavia. Bulletin of the Torrey Botanical Club 79:296–309.

Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5–21.

Page, A. L. 1982. Methods of soil analysis. Part 2: Chemical and microbiological properties. American Society of Agronomy, Inc., Madison, Wis.

Sawyer, D. A., and T. B. Kinraide. 1980. The forest vegetation at higher altitudes in the Chiricahua Mountains, Arizona. American Midland Naturalist 104(2):224–241.

Spomer, G. G. 1973. The concepts of "interaction" and "operational environment" in environmental analyses. Ecology 54:200–204.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284–307.

Tillman, D. 1985. The resource ratio hypothesis of succession. American Naturalist 125:827–852.

Webber, P. J. 1978. Spatial and temporal variation of the vegetation and its production, Barrow, Alaska. Pages 37–112 *in* L. L. Tieszen. Vegetation and production ecology of an Alaskan arctic tundra. Springer-Verlag, New York.

Weber, W. A. 1976. Rocky Mountain flora. Colorado Associated University Press, Boulder.

Weber, W. A. 1987. Colorado flora: Western Slope. Colorado Associated University Press, Boulder.

Willard, B. E. 1979. Plant sociology of alpine tundra Trail Ridge–Rocky Mountain National Park, Colorado. Colorado School of Mines Quarterly 74(4):1–120.

Willard, B. E., and J. W. Marr. 1971. Recovery of alpine tundra under protection after damage by human activities in the Rocky Mountains, Colorado. Biological Conservation 3:181–190.

Wood, D. M., and R. del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. Ecology 68:780–790.

Macroinvertebrate Community Recovery Following Episodic Flooding From an Earthen Dam Failure

David R. Beeson

Advanced Aquatic Technology Associates, Inc.
748 Whalers Way D-200
Fort Collins, Colorado 80523

Terence P. Boyle

National Park Service
Water Resources Division
Colorado State University
Aylesworth NW
Fort Collins, Colorado 80523

Abstract. Benthic macroinvertebrates were sampled in the Fall River and the Roaring River drainages during the summers of 1985 and 1986 to determine macroinvertebrate community recovery from the Lawn Lake Flood. Samples from unaffected sites and flood-affected sites were compared using richness, density, diversity, biotic indices, feeding guild distributions, and measures of similarity. Plecoptera, Ephemeroptera, and Trichoptera were among the 72 taxa observed, indicating that a substantial amount of recovery had occurred. Macroinvertebrate recovery was coincident with substrate development and condition in the flooded region. Differences among flood-affected sites in richness, diversity, and feeding guild distributions due to the flood were reduced in 1986 from 1985 in the upper reaches of the study area and increased between years in the lower reaches. Similarity indices and feeding guild distributions from the farthest-downstream affected site indicated that decreases in diversity and richness during 1986 were due to a shift in taxonomic presence to one that more closely reflects an unaffected site. Based on Percent Similarity Index, the flood-affected sites are estimated to be a minimum of 75% recovered.

Introduction

Benthic macroinvertebrates are being used to assess recovery of stream communities affected by the Lawn Lake Flood in Rocky Mountain National Park. However, few macroinvertebrate data before the flood exist to serve as baseline community data for the affected regions of the Fall River or the Roaring River drainages. Bruinsma (1981) sampled macroinvertebrates at four locations in the Fall River with ornamental bark artificial substrate samplers during late June and early July of 1981 and concluded that the macroinvertebrate community was characteristic of clean water conditions. Two of Bruinsma's sample locations were directly affected by the Lawn Lake floodwaters. One other location—submerged by the formation of a lake immediately upstream from the alluvial debris dam—had formed at the confluence of the Roaring River and the Fall River. Jacobson (1983) sampled macroinvertebrates with kick sampling techniques in the Fall River from May to September of 1982—which includes the flood date—and again during June through August of 1983. Jacobson concluded that the macroinvertebrate assemblage was typical of cold, clean water habitats before the flood in the Fall River and that density and richness were greatly reduced in flood-affected locations after the flood. Direct comparisons from the macroinvertebrate collections from Bruinsma (1981) and Jacobson (1983) for the Fall River before the flood date are difficult due to differences in sampling techniques, data analysis, taxa identification, and sample preservation. Hedin (1980) sampled macroinvertebrates in the Fall River from Chasm Falls to below Cascade Lake but reported only on the Ephemeroptera.

Following the flood, macroinvertebrate samples were collected upstream from the flood-affected regions in the Fall River during 1985 and from the Ypsilon Creek tributary of the Roaring River during 1986 (Beeson et al. 1988). These macroinvertebrate communities provide baseline information and can serve as control sites for comparisons with flooded areas of the Fall River and the Roaring River drainages. The objectives of this study are to document the present condition of the macroinvertebrate community in flood-affected reaches of the Fall River and the Roaring River; and to determine the recovery of the macroinvertebrate communities in the flood-affected reaches of the Fall River and the Roaring River by comparing them to macroinvertebrate communities from unaffected control reaches.

Methods

Structural parameters, functional parameters, and biotic indices were used to describe the macroinvertebrate communities. Three stations for sampling the recovery of macroinvertebrate communities in the Fall River and Roaring River drainages were compared with two unaffected stations. One unaffected station was upstream of the Roaring River confluence and the second was Ypsilon Creek, a tributary of the Roaring River; both were also used as control sites (Fig. 1). Two recovery stations, Fall River Lawn and Fall River East, were in the Fall River downstream from the confluence of the Roaring River and below the alluvial debris fan (Fig. 1). The third recovery site in the Roaring River was situated between Lawn Lake and the Fall River. The control station for the Fall River Lawn and Fall River East was Fall River West, and the control station for the Roaring River was Ypsilon Creek (Beeson et al. 1988). The Fall River Lawn station was located at the western end of Horse-

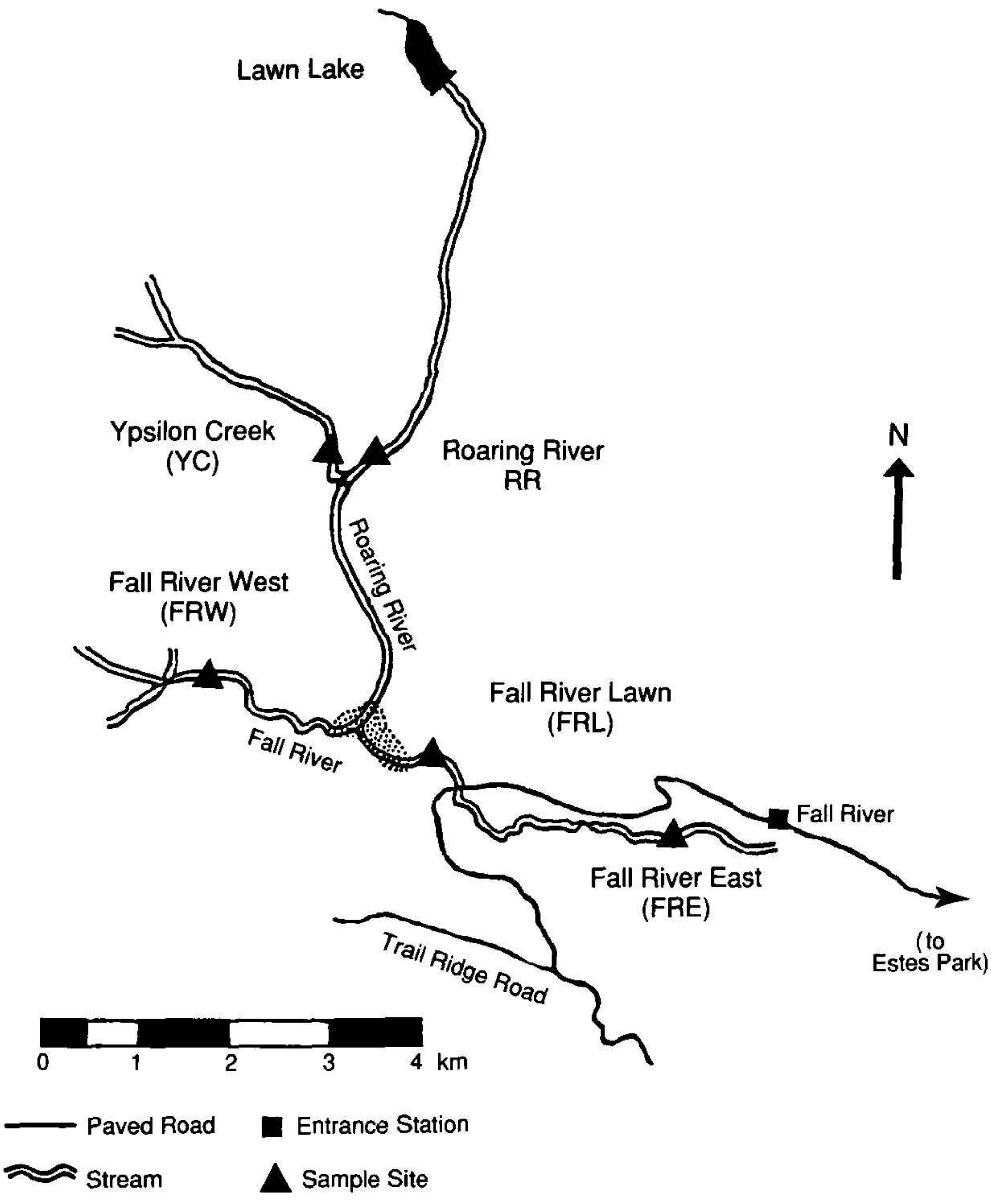


Fig. 1. Location of flood-affected sites Fall River Lawn, Fall River East, and the Roaring River; and the unaffected sites Fall River West and Ypsilon Creek in the Fall River and Roaring River drainages, Rocky Mountain National Park.

shoe Park and Fall River East was located at the eastern end of Horseshoe Park, approximately 0.4 km and 2.7 km, respectively, downstream from the Roaring River alluvial fan. Horseshoe Park is characterized by a typical glacial-formed, flat valley dominated by montane grasses and willows. The Fall River meanders within Horseshoe Park in a single channel with few braids or side channels. The Roaring River station was approximately 4.5 km downstream from Lawn Lake, a location 100 m upstream from the confluence of Ypsilon Creek and the Roaring River. The Roaring River site was characterized by steep side slopes with mixed conifer vegetation of lodgepole pine

(*Pinus contorta*), Englemann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). Floodwaters on the channel caused streambank erosion.

Quantitative macroinvertebrate samples were collected with a 1.0-m^2 aluminum frame secured to the substrate and a standard D-frame kick net of 1.0-mm mesh net positioned immediately downstream. Systematic kicking and brushing within the aluminum frame was done to a depth of 5–10 cm in the substrate material. Samples were taken monthly from Fall River Lawn and at 2-week intervals from Fall River East from early June to late August of 1985. In 1986, all three sites were sampled at 2-week intervals from early June to late August.

To characterize the predominant macroinvertebrate community, three major substrate types occurring in the study streams were sampled at each station: coarse cobble and rubble of approximately 6- to 10-cm diameter in the fast-flowing water in the main stream channel; medium gravels below 5-cm diameter in the slow-flowing water outside the main channel; and fine depositional substrates of sands and silts in pools or backwaters where flow was negligible. Macroinvertebrate samples were kept separate for each substrate and transferred to plastic jars, preserved with a formalin solution, and transported to the laboratory for sorting and identification using keys in Peterson (1960a, 1960b), Allen and Edmunds (1962, 1963, 1965), Jensen (1966), Smith (1968), Hogue (1973), Edmunds et al. (1976), Baumann et al. (1977), Webb (1977), Wiggins (1977), Johnson (1978), Pennak (1978), Morihara and McCafferty (1979), and Merritt and Cummins (1984). A reference collection of sampled macroinvertebrates is maintained at the Applied Research Branch of the Water Resources Division, Colorado State University in Fort Collins.

Richness, density, and community similarity comparisons of the macroinvertebrate communities from each substrate were used to delineate differences between substrate types. The three similarity indices used for macroinvertebrate community comparisons among substrate types were Jaccards Similarity Index (Jaccard 1908), Percent Similarity Index (*PSC*; Whittaker 1952), and the Bray–Curtis Similarity Index (*BCD*; Bray and Curtis 1957).

Richness, density, trophic relations, diversity, and biotic indices were determined on the composite of coarse, medium, and fine substrate samples to establish a complete baseline characterization that includes all habitats for the macroinvertebrate community.

Diversity indices were the Shannon–Weiner Diversity Index (*H'*; Shannon and Weaver 1949):

$$H' = -\sum_{i-1}^{s} \frac{n_i}{n} \, ln \frac{n_i}{n}$$

and Simpson's Diversity Index (*D*; Simpson 1949):

$$D = \sum_{i-1}^{s} \frac{n_i(n_i - 1)}{n(n - 1)}$$

where

s = the number of taxa,

n_i = the number of individuals in taxa (i) in a sample from a population, and

n = the number of individuals in a sample from a population.

The Shannon–Weiner Diversity Index (H') is commonly used in biological literature and has the advantage of being sensitive to rare taxa and not dependent on sample size. Values for the Shannon–Weiner Diversity Index range from zero to a maximum of about five in biological applications, indicating no diversity to maximum diversity, respectively. Simpson's Diversity Index (D) is considered less sensitive to rare taxa and is sample-size dependent (Washington 1984). Simpson's Diversity Index ranges from one for no diversity to zero indicating maximum diversity. Both H' and D were calculated to provide diversity values that are sensitive to rare taxa and sample-size dependent.

Trophic relations for the sampled communities were indicated by functional group breakdown. The functional groups (scraper, shredder, collector–gatherer, collector–filterer, and predator) were assigned to taxa from each sampling location based on designations in Merritt and Cummins (1984).

Two biotic indices that are modified for this study are presented—Chandler's Biotic Index (Chandler 1970) and the Biotic Condition Index (*BCI*) of Winget and Mangum (1979). Chandler's Biotic Index is sensitive to community change induced by organic loading and low dissolved oxygen and is derived by relative values for each collection site based on weighted scores by taxa and taxa abundance, with no upper limit to the index value. The *BCI* is presented as a percent of the ratio between an estimated potential community index (CTQ_p), representative of highest possible water quality and habitat conditions, to an actual index (CTQ_a), derived from the samples. The CTQ_p and CTQ_a are based on tolerance quotients assigned to each taxon present regardless of abundance. The *BCI* was modified for this study by adjusting the CTQ_p value from Winget and Mangum (1979), when many *BCI* values above 100% were obtained. Using the mean CTQ_a from all collections as a replacement CTQ_p value (CTQ_{pr}), values for the *BCI* above 100% were reduced. Using the modified CTQ_{pr} allowed interpretation of the *BCI* without a decrease in index integrity (Dr. F. Mangum, personal communication).

Results

Seventy-two taxa were identified from the three recovery sites (Appendix). Members of the Plecoptera, Ephemeroptera, and Trichoptera orders were present in numbers sufficient to indicate nonpolluted water conditions. The June sample during 1986 for Fall River East was inappropriately sampled and was not included in the analyses.

Density

Density values varied greatly among sites and between years. The lowest and highest densities were recorded during the early June and late August collections at the Fall River Lawn site in 1986. All sites in 1986 showed a general pattern of increasing macroinvertebrate density throughout the sampling period. Annual mean density was not significantly different between the three recovery sites in either sample year (Fig. 2). The 1985 annual mean density at Fall River East (388 organisms per square meter) was higher than at Fall River Lawn, but in 1986, Fall River Lawn showed higher densities (500 organisms per square meter) than Fall River East. Annual mean density in the Roaring River during 1986 (350 organisms per square meter) was significantly less than that from Ypsilon Creek (1,182 organisms per square meter) as shown in Fig. 3a ($n = 12$, least squares difference [*LSD*] = 708.73, $P \leq 0.05$).

Taxon Richness

All sites showed a rich macroinvertebrate community during 1985 and 1986, with all major insect groups present in all samples. The least represented order was Trichoptera with a mean of 11% of total taxon richness, and the most dominant was Ephemeroptera with a mean of 35%. Figure 4 shows Fall River Lawn had the lowest mean richness of 16 genera for the recovery sites, significantly less rich than 24 genera at Fall River West during 1985 ($n = 15$, $LSD = 5.22$, $P \leq 0.05$). In 1986, Fall River East had the lowest mean richness of 17 genera and was significantly less rich than Fall River West ($n = 18$, $LSD = 6.646$, $P \leq 0.05$). The Roaring River site (Fig. 3b) showed the most consistent richness throughout the 1986 sampling period. Annual mean richness of 17 genera at the Roaring River was significantly less than a mean of 29 genera recorded for Ypsilon Creek ($n = 12$, $LSD = 2.2343$, $P \leq 0.05$).

Diversity

Both the Shannon–Weiner Index and Simpson's Index indicated that moderately diverse communities existed at all three recovery sites (Figs. 5–7). The greatest variability in diversity throughout a sampling period occurred in Fall River East during 1985, and the most consistent diversity was in Fall River Lawn during 1986. Figure 5 shows comparisons of annual mean Shannon–Weiner Diversity, and Fig. 6 shows annual mean Simpson's Diversity, indicating Fall River East was signficantly less diverse than Fall River West during both 1985 ($n = 15$, $LSD = 0.418$, $P \leq 0.05$) and 1986 ($n = 18$, $LSD = 0.4717$, $P \leq 0.05$). The Roaring River site was significantly less diverse (Fig. 7) than Ypsilon Creek during 1986 ($n = 12$, $LSD = 0.2727$, $P \leq 0.05$).

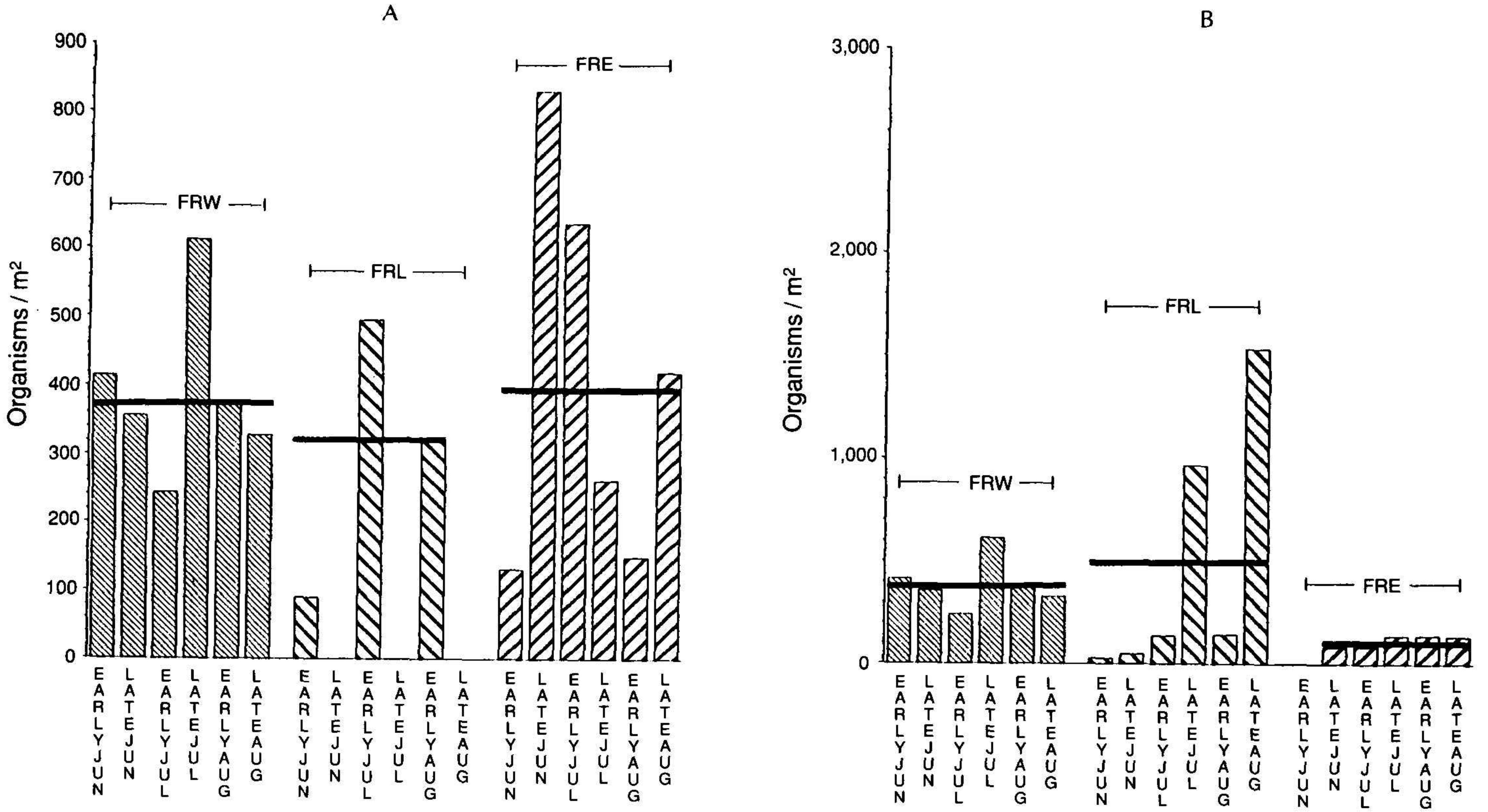


Fig. 2. Density of macroinvertebrates in Fall River East, Fall River Lawn, and Fall River West during 1985 (A) and 1986 (B). Annual mean density values are shown by *horizontal bars*. No significant differences existed between sites.

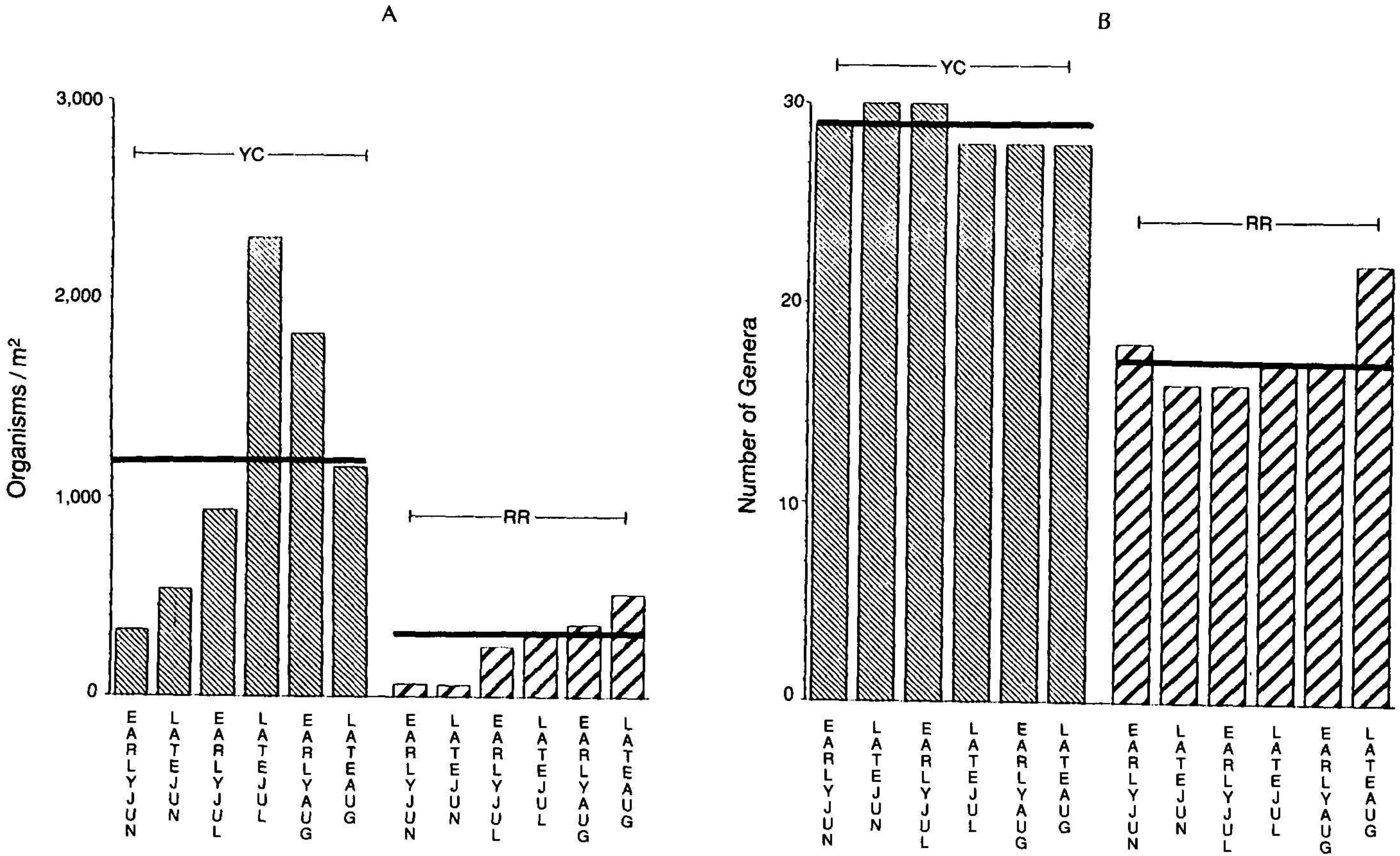


Fig. 3. Density (A) and richness (B) of macroinvertebrates in the Roaring River and Ypsilon Creek during 1986. Annual mean values are shown by *horizontal bars*. The Roaring River was significantly less rich and significantly less dense than Ypsilon Creek.

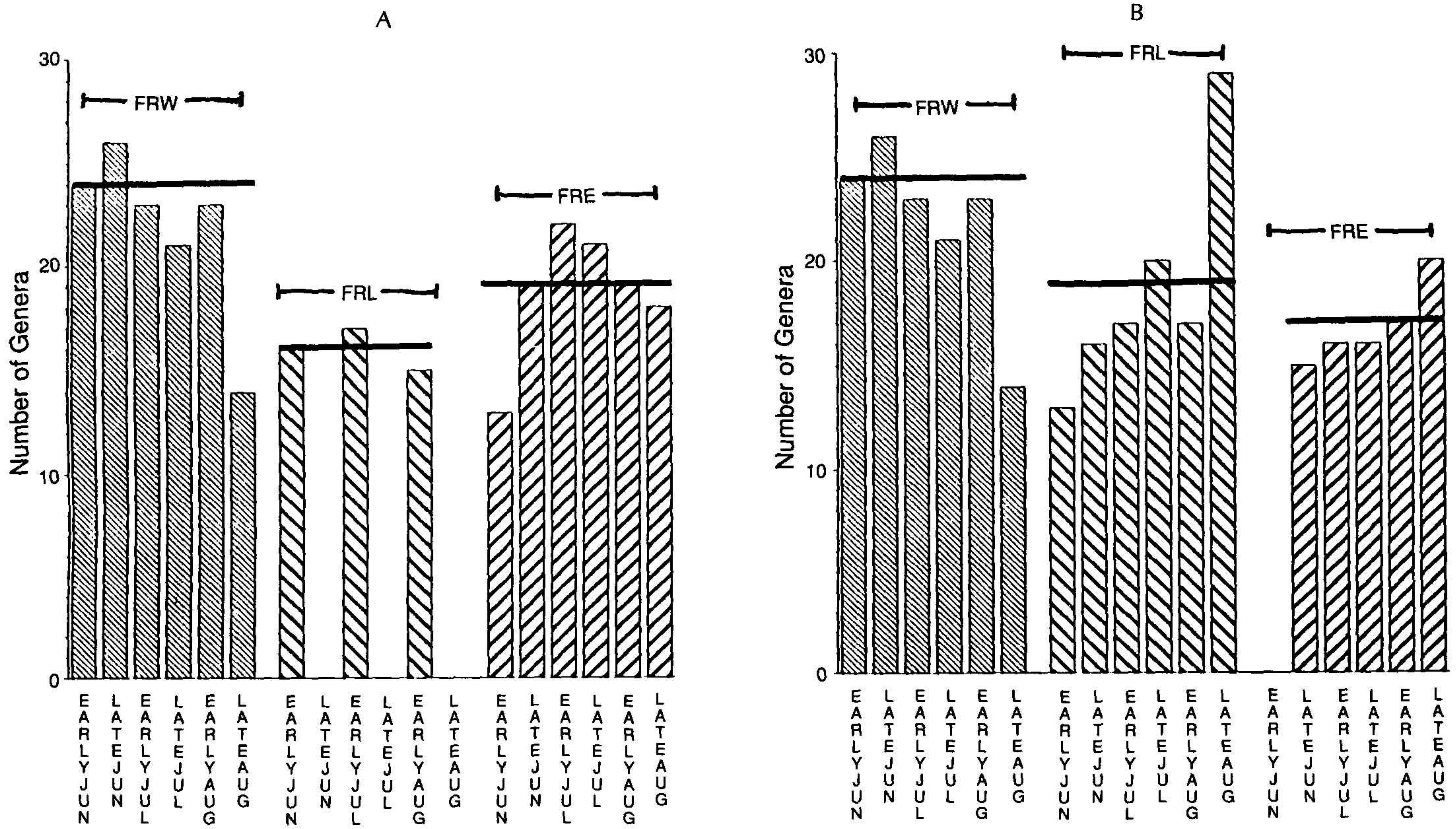


Fig. 4. Richness of macroinvertebrates in Fall River East, Fall River Lawn, and Fall River West during 1985 (A) and 1986 (B). Annual mean richness values are shown by *horizontal bars*. Fall River Lawn was significantly less rich than Fall River West and Fall River East during 1985, and Fall River East was significantly less rich than Fall River West and Fall River Lawn.

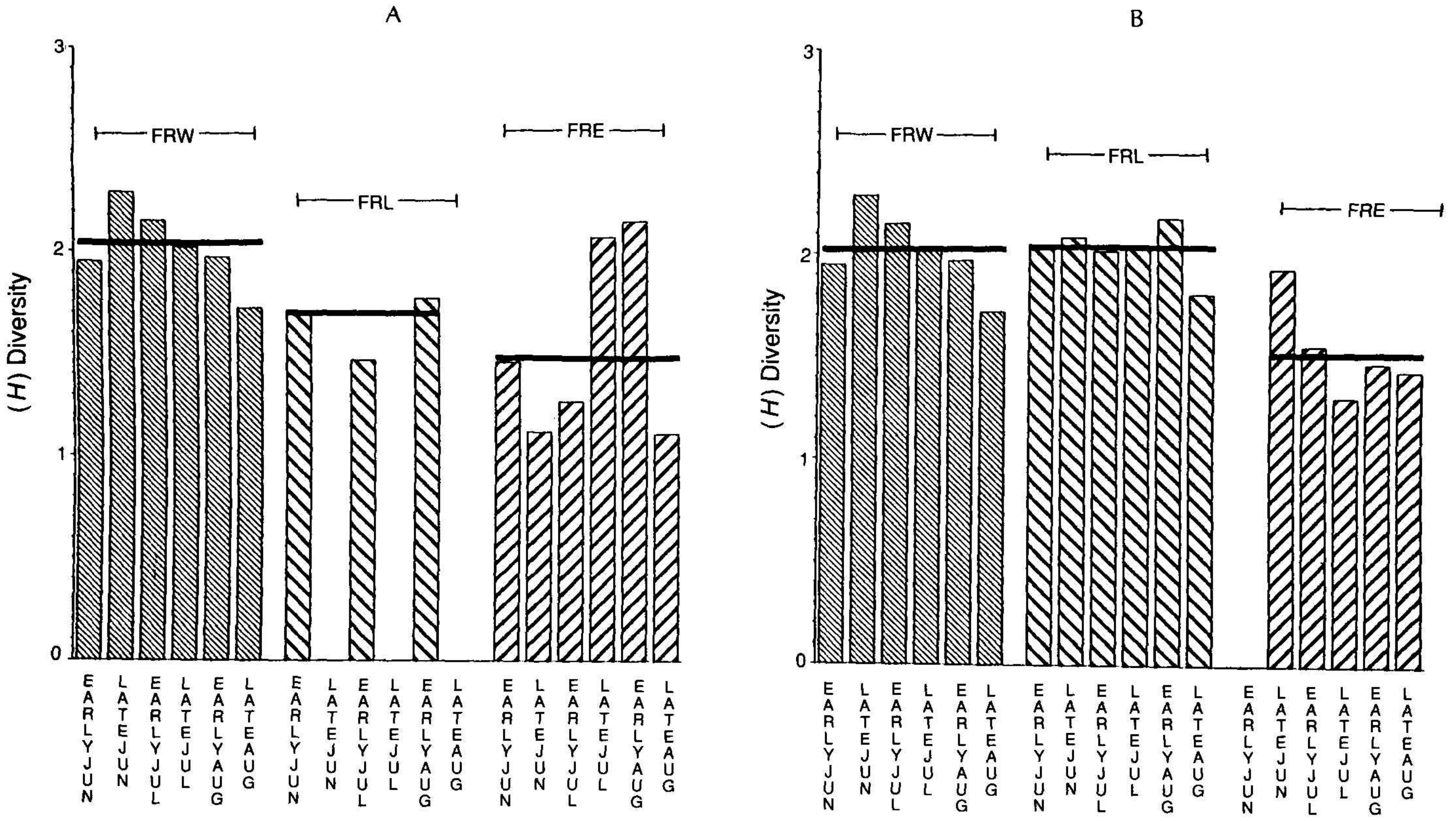


Fig. 5. Shannon–Weiner Diversity for macroinvertebrate communities from Fall River East, Fall River Lawn, and Fall River West during 1985 (A) and 1986 (B). Annual mean diversity values are shown by *horizontal bars*. Fall River East was significantly less diverse than Fall River West and Fall River Lawn.

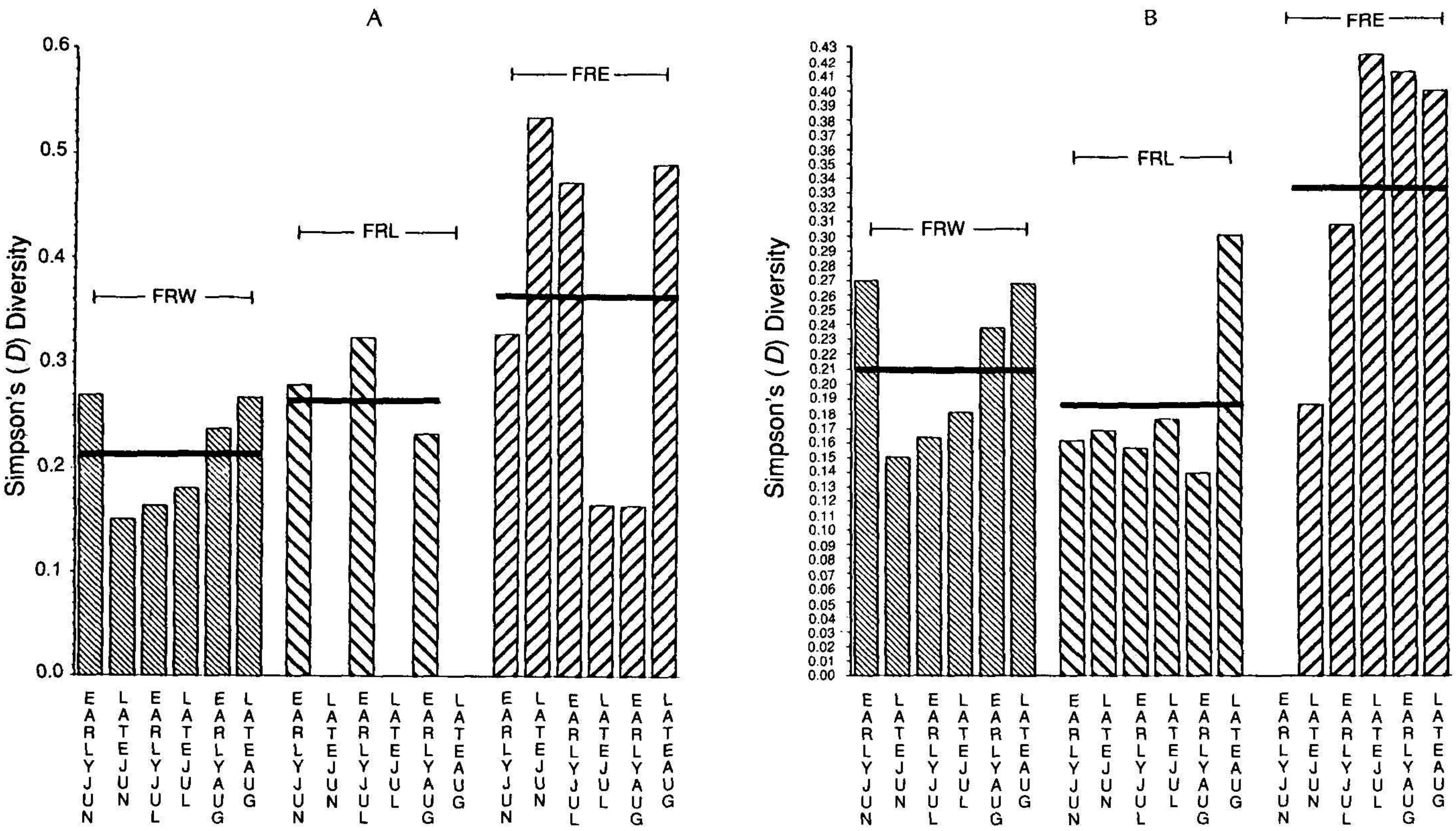


Fig. 6. Simpson's Diversity for macroinvertebrate communities from Fall River East, Fall River Lawn, and Fall River West during 1985 (A) and 1986 (B). Annual mean diversity values are shown by *horizontal bars*. Fall River East was significantly less diverse than Fall River West and Fall River Lawn.

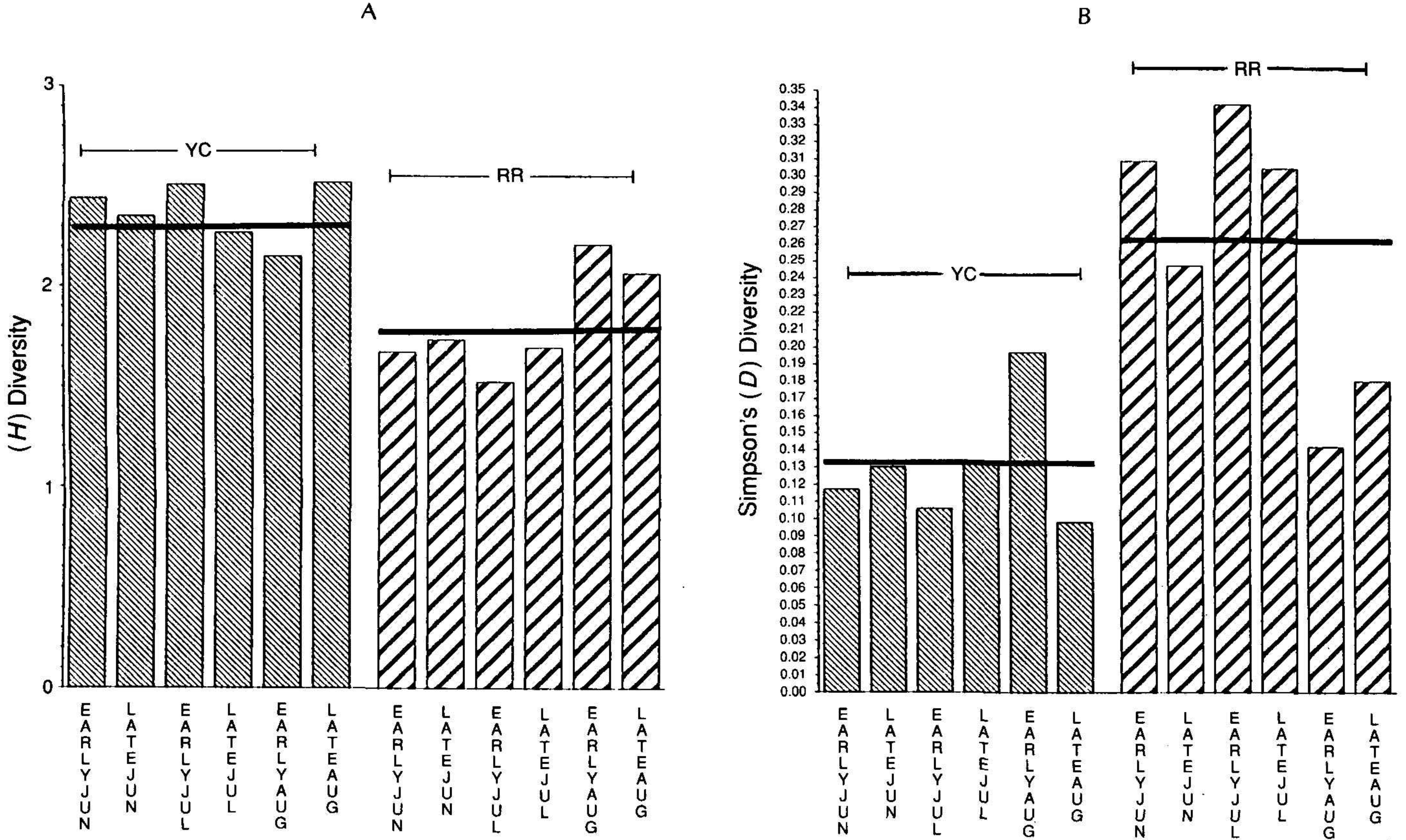


Fig. 7. Shannon–Weiner (A) and Simpson's (B) diversity for macroinvertebrate communities from the Roaring River and Ypsilon Creek during 1986. Annual mean diversity values are shown by *horizontal bars*. Both indices show the Roaring River site was significantly less diverse than Ypsilon Creek.

Trophic Relations

The most predominant trophic group common to all samples was the collector–gatherer feeding guild, while the shredders were the least represented (Figs. 8–10). During 1985 in Fall River Lawn the mean number of predator and scraper organisms were significantly lower than control site Fall River West (n = 15, LSD [predator] = 64.4, $P \leq 0.05$, LSD [scraper] = 104.96, $P \leq 0.05$); however, no significant differences occurred during 1986 (Fig. 8). In Fall River East during 1985, differences in mean numbers of organisms were significantly lower for the scraper (n = 15, LSD = 85.70, $P \leq 0.05$) and collector–gatherer (n = 15, LSD = 280.80, $P \leq 0.05$) guilds, and significantly higher for the collector–filterer guild (n = 15, LSD = 605.7, $P \leq 0.05$) than in Fall River West. In 1986 at Fall River East, only the predator guild was significantly lower (n = 17, LSD = 93.19, $P \leq 0.05$) than at Fall River West (Fig. 9). Figure 10 shows that during 1986 the mean number of predator, scraper, and collector–gatherer organisms were significantly lower in the Roaring River (n = 12, LSD [predator] = 220.19, LSD [scraper] = 619.54, LSD [collector–gatherer] = 1,293.2, $P \leq 0.05$) than at control site Ypsilon Creek.

Biotic Indices

Both Chandler's Biotic Index and the *BCI* indicate all sites were of high-quality habitat and water conditions. All Biotic Index values for the three recovery sites are above the 400 to 500 score level, indicating high water quality (Chandler 1970). Relative to the control site values for Fall River West (Biotic Index = 1,202) and Ypsilon Creek (Biotic Index = 1,393)—the flood-affected sites—Biotic Index scores were not equivalent, indicating that habitat and water quality conditions support full recovery (Table 1).

A *BCI* score of 100 indicates that the collected insect sample (CTQ_a) is 100% of the predicted community (CTQ_p) that would represent the ideal high-quality water and habitat condition (Winget and Mangum 1979). Table 2 shows the lowest individual score (BCI = 64.54) in early June at Fall River Lawn during 1986, indicating the community was not of expected composition for this habitat and water quality. The late June collection 2 weeks later (BCI = 106.17) suggested a rapid change in community structure and reflected an excellent habitat and water quality comparable to a predicted community. The rapid change in community composition at Fall River Lawn may be due to sampling; however, comparisons with the control site values show no significant differences, indicating that Fall River East and Fall River Lawn are reflective of the predicted community. The Roaring River site (BCI = 99.46) reflected the predicted community and was not significantly different from Ypsilon Creek.

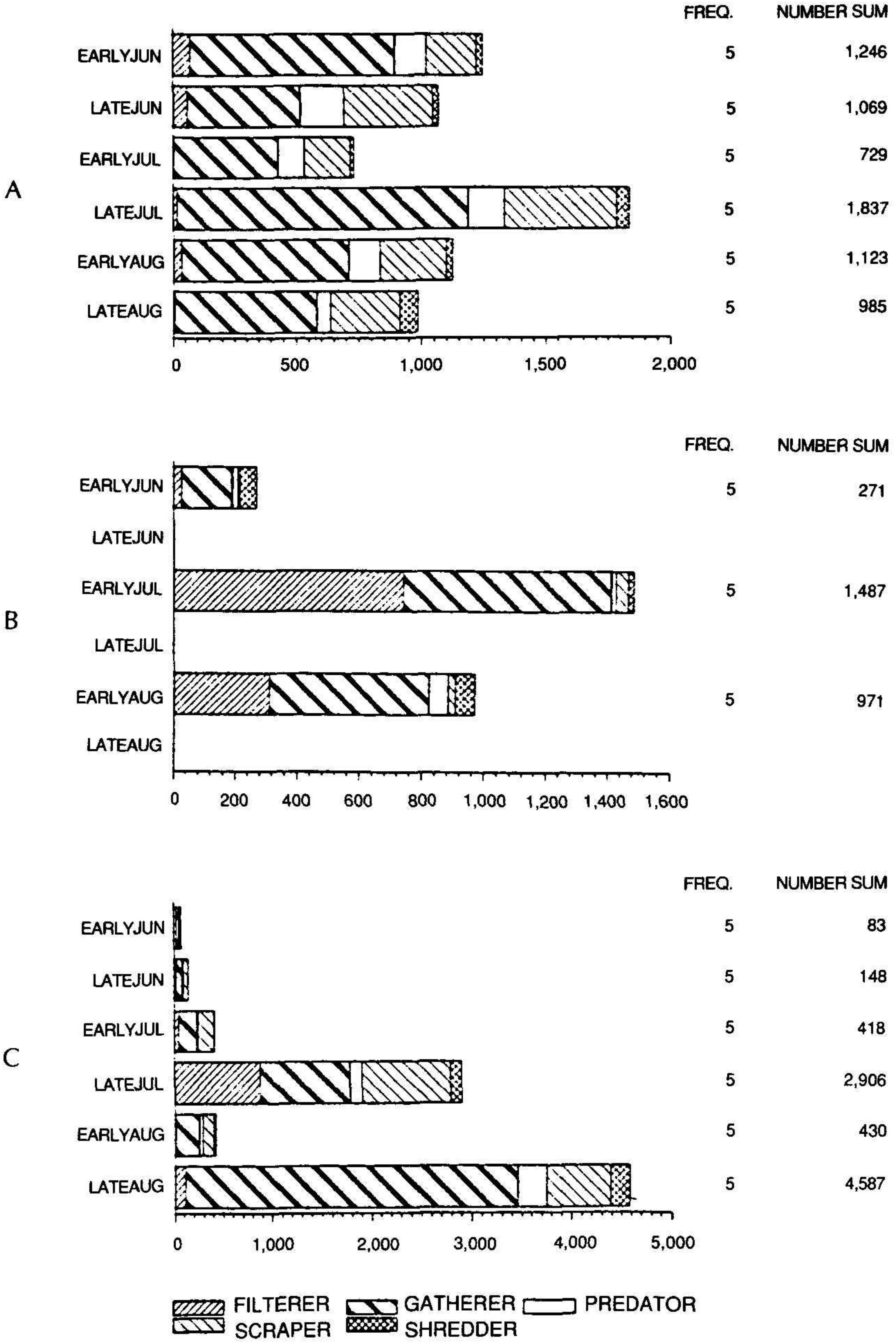


Fig. 8. Macroinvertebrate trophic guild distributions for Fall River West during 1985 (A) and Fall River Lawn during 1985 (B) and 1986 (C). Significant differences were found only during 1985, when the annual mean number of organisms for the predator and scraper trophic guilds in Fall River Lawn was significantly less than in Fall River West.

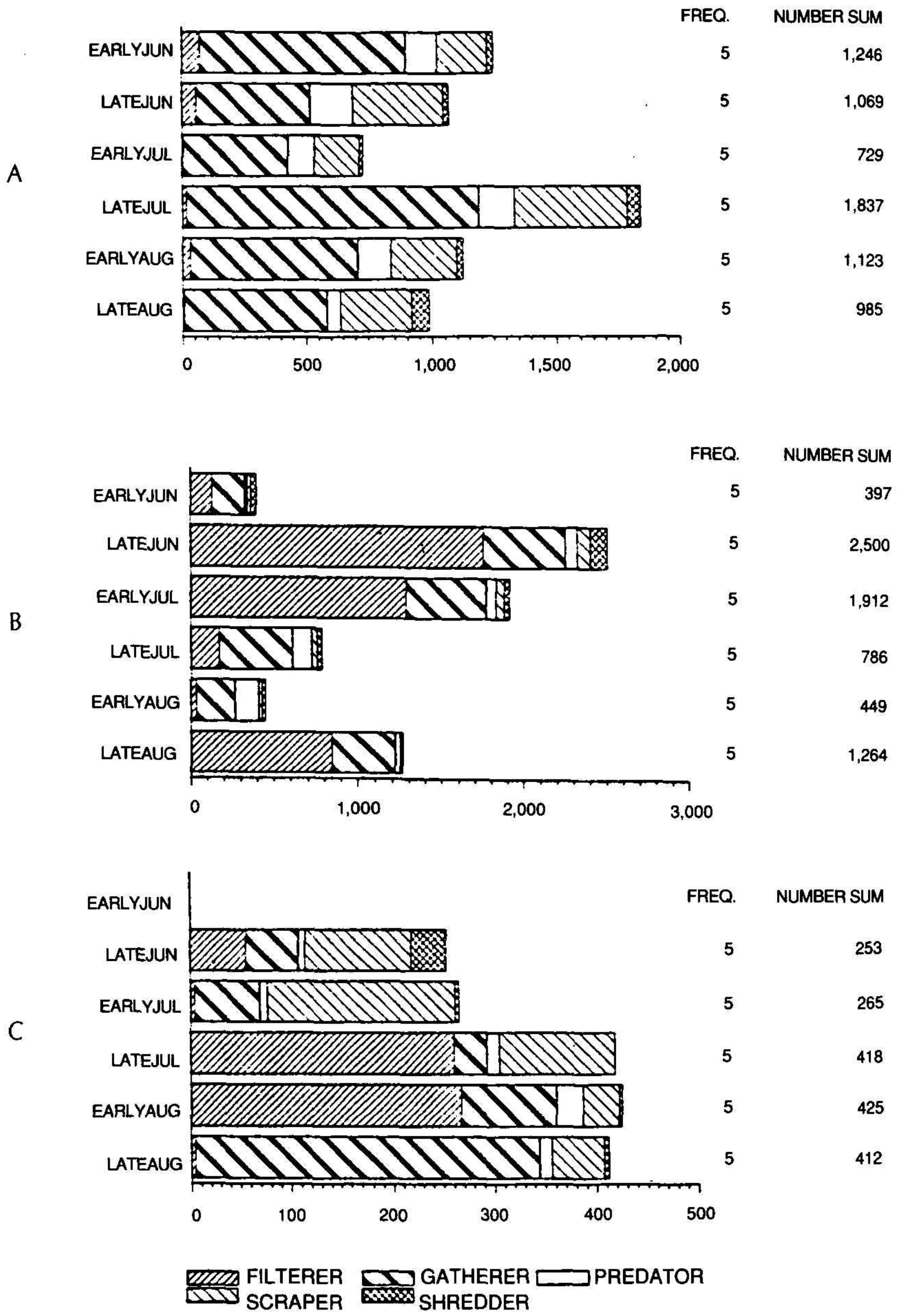


Fig. 9. Macroinvertebrate trophic guild distributions for Fall River West during 1985 (A) and Fall River East during 1985 (B) and 1986 (C). In Fall River East, the annual mean number of organisms was significantly lower in the scraper and collector–gatherer trophic guilds and significantly higher for collector–filterers than in Fall River West during 1985. During 1986, only the predator trophic guild was significantly higher in Fall River East than in Fall River West.

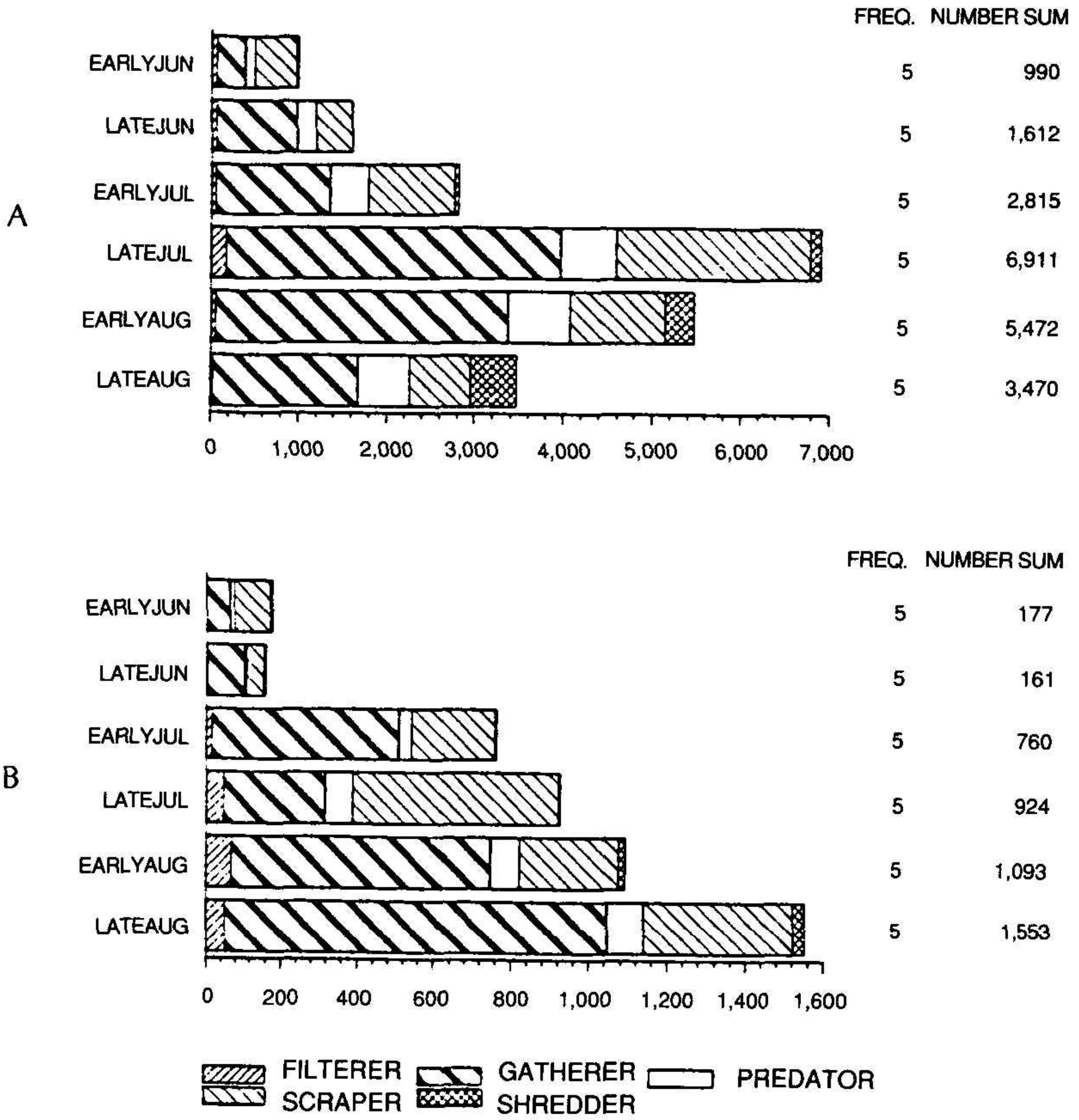


Fig. 10. Macroinvertebrate trophic guild distributions for Ypsilon Creek (A) and the Roaring River (B) during 1986. Annual mean number of organisms was significantly lower in the Roaring River for the scraper, collector–gatherer, and predator trophic guilds.

Table 1. *Chandler's Biotic Index; coarse substrate macroinvertebrate collections.*

		Individual biotic score						
Sample[a]		Early June	Late June	Early July	Late July	Early August	Late August	Biotic index
FRW	1985	1,694	1,441	1,221	1,247	870	740	1,202
FRE	1985	794	988	1,082	777	861	788	882
FRL	1985	1,020	—	762	—	664	—	815
FRE	1986	—	966	908	848	824	675	844
FRL	1986	418	889	968	692	770	1,397	855
YC	1986	1,310	1,078	1,522	1,599	1,420	1,434	1,393
RR	1986	731	791	755	1,048	1,063	1,176	92

[a] FRW = Fall River West; FRE = Fall River East; FRL = Fall River Lawn; YC = Ypsilon Creek; RR = Roaring River.

Table 2. *Biotic Condition Index (*BCI*); coarse substrate macroinvertebrate collections.*

Sample	Early June	Late June	Early July	Late July	Early August	Late August	Mean BCI
Fall River West 1985							
CTQ_{pr}	43	43	43	43	43	43	—
CTQ_a	42.03	39.16	43.48	45.31	48.45	53.73	—
BCI	102.29	109.80	98.89	94.88	88.74	80.02	95.77
Fall River East 1985							
CTQ_{pr}	43	43	43	43	43	43	—
CTQ_a	37.85	41.31	40.71	42.45	38.85	40.29	—
BCI	113.62	104.09	105.64	101.29	106.74	104.37	107.01
Fall River Lawn 1985							
CTQ_{pr}	43	43	43	43	43	43	—
CTQ_a	41.20	—	47.25	—	51.27	—	—
BCI	104.37	—	91.00	—	83.87	—	93.08
Fall River East 1986							
CTQ_{pr}	43	43	43	43	43	43	—
CTQ_a	—	41.07	41.62	43.08	43.08	52.91	—
BCI	—	104.71	103.33	99.81	99.81	81.27	97.78
Fall River Lawn 1986							
CTQ_{pr}	43	43	43	43	43	43	—
CTQ_a	66.63	40.50	39.43	54.36	40.60	47.35	—
BCI	64.54	106.17	109.06	79.10	105.91	90.82	92.60
Ypsilon Creek 1986							
CTQ_{pr}	43	43	43	43	43	43	—
CTQ_a	45.14	43.56	39.42	39.95	44.68	43.12	—
BCI	95.24	98.71	109.07	107.61	96.23	99.71	101.09
Roaring River 1986							
CTQ_{pr}	43	43	43	43	43	43	—
CTQ_a	40.20	42.83	50.18	38.73	45.87	43.44	—
BCI	106.97	100.39	85.69	111.02	93.75	98.98	99.46

Similarity Indices

The similarity indices in Table 3 are based on comparisons of the number and abundances of taxa common at the control sites and the recovery sites. Values indicate that the macroinvertebrate communities from Fall River Lawn and Fall River East were more similar to the control site in 1986 than in 1985. The Roaring River and Ypsilon Creek were the most similar of all comparisons with values of 90.25 for the percent similarity (*PSC*) index, 0.99038 for the similarity (*SIMI*) index, and 0.245 for the *BCD* index.

Chlorophyll a

Chlorophyll *a* values for late July and August 1986 from Fall River Lawn, Fall River East, the Roaring River, and Fall River West are shown in Fig. 11a.

Table 3. *Similarity comparisons between recovery sites and control sites.*

Sample	PSC[a]	SIMI[b]	BCD[c]
	Fall River East to Fall River West		
1985	44.8255	0.49030	0.55175
1986	75.4302	0.88244	0.24570
	Fall River Lawn to Fall River West		
1985	60.9628	0.75740	0.39037
1986	88.6323	0.98309	0.11368
	Roaring River to Ypsilon Creek		
1986	90.2566	0.99038	0.09743

[a] Percent Similarity Index.
[b] Similarity Index.
[c] Bray–Curtis D Index.

No chlorophyll *a* samples were collected from Ypsilon Creek. The magnitude of values indicate little chlorophyll *a* is present in suspended transport at each site. The lowest chlorophyll *a* values were at Fall River West, upstream from the flood-affected region, and the highest chlorophyll *a* value was at Fall River East during early August. The Roaring River site had consistently higher chlorophyll *a* values than all other sites, although differences of mean chlorophyll *a* values from all sites were not significant.

Total Carbon

Suspended organic matter collections indicated that the predominant carbon fraction was the very fine particulate organic matter (VPOM) of less than 63 μm at all sites. Total carbon as the sum of VPOM and the combined coarse particulate organic matter (CPOM) of less than 1.0 mm and fine particulate organic matter (FPOM) of less than 63-μm–1.0-mm fractions are shown for each sample from each site in Fig. 11b. Comparisons of mean total carbon, CPOM, FPOM, and VPOM fractions indicate significant difference in total carbon ($n = 12$, $LSD = 1.674$, $P \leq 0.05$) and VPOM fractions ($n = 12$, $LSD = 1.62$, $P \leq 0.05$) in Fall River Lawn and Fall River East from the control site.

Discussion

Recovery

A review of the Lawn Lake Flood presented by Tunbridge (1983) and macroinvertebrate records of Jacobson (1983) indicated that macroinvertebrate habitats in the path of the floodwaters were disturbed by erosion and sedimentation. Clearly, some degree of recovery has occurred at flood-affected sites

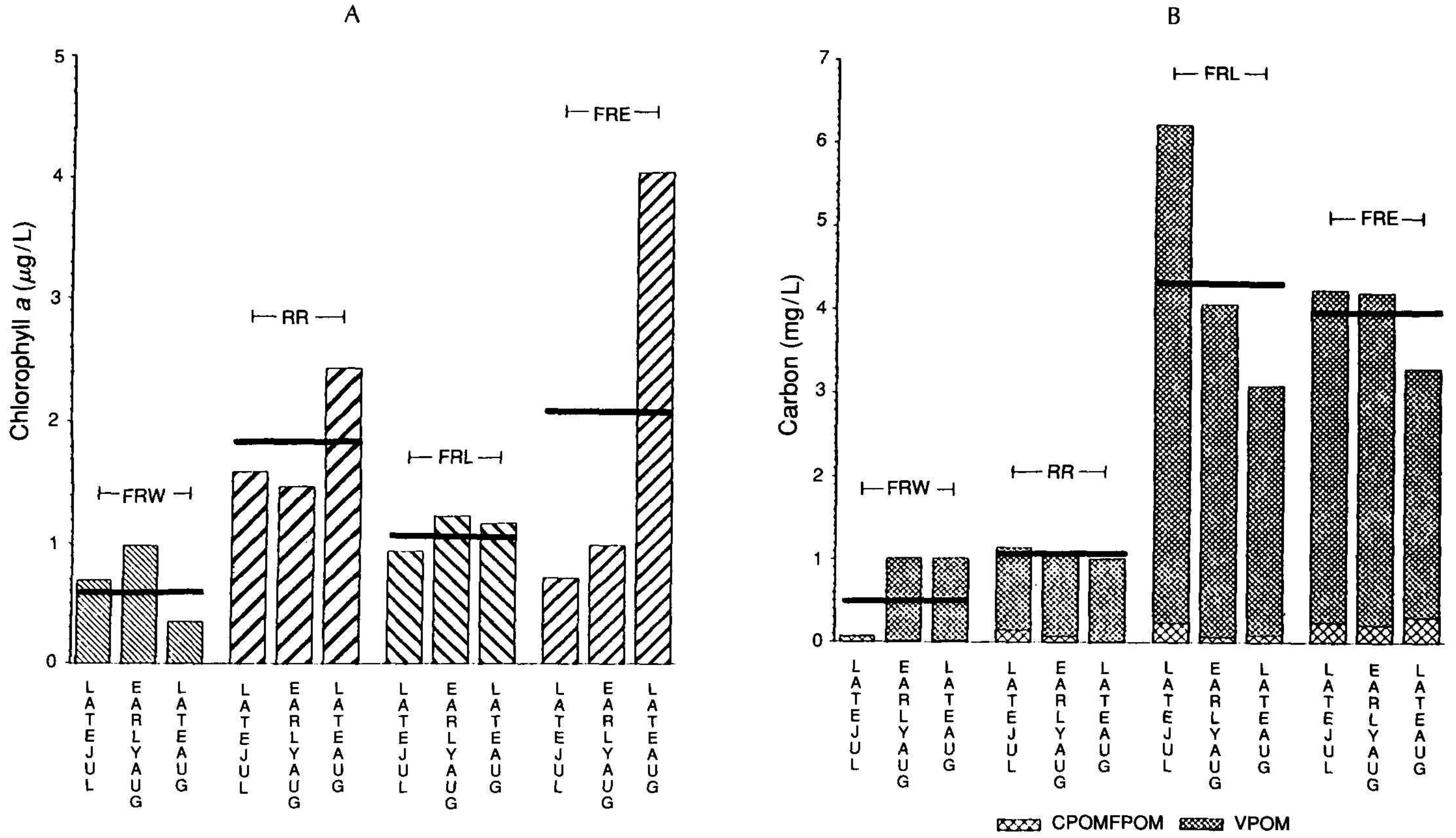


Fig. 11. (A) Chlorophyll *a* for Fall River West, Fall River East, Fall River Lawn, and the Roaring River during 1986. Annual mean chlorophyll *a* values are shown by *horizontal bars*. No significant differences were found between sites. (B) Particulate carbon fractions of VPOM and the combined CPOM and FPOM from Fall River East, Fall River Lawn, Fall River West, and the Roaring River during 1986. Annual mean values of total particulate carbon were significantly higher in Fall River Lawn and Fall River East due to differences in the VPOM fraction.

since the flood event, based on available comparisons to Jacobson (1983) and because macroinvertebrate communities are reflective of a variety of habitats. The erosion and sedimentation resulting from the flood also changed the characteristics of the substrates from preflood conditions. Recent postflood reports on bed material analyses and sediment movement within the flood zone by Biedenharn (1983) indicated presence of fine sands and a highly mobile sediment condition in the reaches upstream from Fall River Lawn. Pitlick and Harvey (1986) documented a reduced bedload transport rate during 1985 at both the Fall River Lawn and Fall River East reaches of Horseshoe Park, as well as a median grain size slightly larger in the Fall River Lawn region than in previous postflood years. During 1986, Pitlick and Harvey (1987) showed a major contrast in sediments between the Fall River Lawn and Fall River East regions. Reduced bedload and sediment transport at Fall River Lawn was attributed to a decreasing sediment supply upstream in the Roaring River. A stationary armor layer also developed as bed material extended downstream to the Fall River Lawn site. The sediment storage zone had provided a median grain size larger than the previous year, but Fall River East lacked sufficient coarse bed material to develop a stationary substrate. This site continued to show disruption and scour from sediment transport (Pitlick and Harvey 1987).

The armored static bed material at Fall River Lawn during 1986 is more consistent with the type of substrate condition in Fall River West. Substrates provide the physical habitat available for macroinvertebrate colonization. Consequently, the substrate condition is an integral part of the recovery process. The development of the stable armor layer in the Fall River Lawn region—but not in the Fall River East region of the flood-affected portion of the river from 1985 to 1986—is reflected in the macroinvertebrate communities.

Recovery at Fall River Lawn

At Fall River Lawn, no significant differences were found in richness and the percent of predator and scraper feeding guilds from Fall River West during 1986. In contrast, significant differences were found during 1985, indicating macroinvertebrate community recovery coincident with the change in substrate condition. In 1985 and 1986, the actual community tolerance value (CTQ_a) of the *BCI* was highly variable (Table 2), indicating an unstable, transitional habitat and macroinvertebrate community. The continued recovery between 1985 and 1986 in Fall River Lawn is supported by a change in similarity values for the *PSC* index, *SIMI* index, and *BCD* index, indicating higher degrees of similarity to the Fall River West macroinvertebrate community during 1986 (Table 3).

Recovery at Fall River East

In Fall River East, the substrates did not reflect a stable armor layer, and significant differences existed between Fall River East and Fall River West, including diversity and the makeup of the filterer, scraper, and collector–gatherer feeding guilds. During 1986, significant differences again included diversity, the predator feeding guild, and richness, suggesting minor changes in the level of recovery between 1985 and 1986. Higher similarity values during 1986 for *PSC* index, *SIMI* index, and *BCD* index, and the reduction of feeding guild differences to only the predators, however, indicated recovery to a community more similar to the control site. The biotic and similarity indices employ taxon identifications to augment the composition of the community unlike richness and diversity, and changes in similarity values and feeding guilds between sample years suggest a change in taxonomic composition in Fall River East.

A review of the taxa indicated that between 1985 and 1986, a reduction in the number of Simuliidae (Diptera) occurred, with concurrent increases in residence time of Trichoptera and Plecoptera and increases in numbers of several Ephemeroptera. These shifts in macroinvertebrate composition agree more with the Fall River West community and account for the greater similarity values in 1986. The substrate condition at Fall River East during 1986 is not reflective of Fall River West, but the larger median grain size in 1986 corresponds to the early stages of an armored substrate condition. Drift-induced immigration of taxa from Fall River West and Fall River Lawn can support continued recovery.

Recovery at the Roaring River

A single year of comparisons between the Roaring River and Ypsilon Creek indicated that the level of recovery is high, although significant differences between these two sites occurred in richness, diversity, density, Chandler's Biotic Index, and the predator, gatherer, and scraper feeding guilds. Taxa that account for the difference in richness between the Roaring River and Ypsilon Creek are considered rare and when combined account for only 1.5% of the total number of organisms collected from Ypsilon Creek during 1985. Rare taxa were equally distributed among the Plecoptera, Ephemeroptera, Diptera, and Trichoptera. Calculation of Chandler's Biotic Index and separation of means for each feeding guild between the Roaring River and Ypsilon Creek were density dependent, and the significant difference in density between the two stations biased these results. Chandler's Biotic Index can be corrected for density by using the Biotic Condition Index, since only the presence or absence of each taxon is considered. The Biotic Condition Index scores indicated the Roaring River was reflective of Ypsilon Creek. A separation of means using *LSD* tests on percentage values of each feeding guild (to correct for differences in density) showed that only the collector–filterer guild was significantly higher in the Roaring River (mean = 7.66%) than in Ypsilon Creek (mean = 3.88%, $n = 12$, $LSD = 3.77$, $P \leq 0.05$). The contribution of only rare taxa to significant differences in richness between the Roaring River and Ypsilon Creek—in combination with the close Biotic Condition Index values and a significant difference in only the collector–filterer feeding guild after correcting for density—indicated a high level of recovery in the Roaring River. High similarity index values for *PSC* index, *SIMI* index, and *BCD* index showed nearly identical community comparisons between the Roaring River and Ypsilon Creek and further indicated a high level of recovery in the Roaring River.

Summary

The results show macroinvertebrate community recovery from the effects of the Lawn Lake Flood in the Fall River and the Roaring River. Variability of significant differences in annual means for richness, diversity, feeding guild distributions, and biotic and similarity indices between Fall River Lawn and Fall River East when compared to a control site during 1985 and 1986 indicated that recovery is progressing toward preflood conditions. Comparisons in the Roaring River drainage between the Roaring River and a control site for structural and functional and biotic community parameters show a significantly lower density of organisms in the Roaring River but indicate a high level of recovery. The recovery process is more advanced in upstream reaches of the flood zone, and the degree of recovery is coincident with stable substrate conditions. Based on community comparisons between flood-affected sites and control sites with the Percent Similarity Index, we estimate that during 1986 the upstream site in the Roaring River was 90% recovered; the midstream site, Fall River Lawn in the upper end of Horseshoe Park, was 88% recovered; and the downstream site, Fall River East in the lower end of Horseshoe Park, was 75% recovered.

This assessment of macroinvertebrate community recovery is based on the assumption of equal habitat conditions in comparisons between affected and unaffected sites. The Fall River West and Ypsilon Creek sites provided a good approximation of habitat conditions and community structure for comparisons, but exact replication of the macroinvertebrate community and habitat was not expected in Fall River East, Fall River Lawn, or the Roaring River. The results of this study demonstrated the importance of using several descriptive tools, including structural, functional, and biotic parameters to analyze and compare macroinvertebrate communities.

Literature Cited

Allen, R. K., and G. F. Edmunds, Jr. 1962. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). V. The subgenus *Drunella* in North America. Miscellaneous Publications of the Entomological Society of America 3:147–179.

Allen, R. K., and G. F. Edmunds, Jr. 1963. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). VI. The subgenus *Serratella* in North America. Annals of the Entomological Society of America 56:583–600.

Allen, R. K., and G. F. Edmunds, Jr. 1965. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). VII. The subgenus *Ephemerella* in North America. Miscellaneous Publications of the Entomological Society of America 4:243–283.

Baumann, R. W., A. R. Gaufin, and R. F. Surdick. 1977. The stoneflies (Plecoptera) of the Rocky Mountains. Memoirs of the American Entomological Society 208–311.

Beeson, D. R., T. P. Boyle, D. Monzingo, and J. S. Rabold. 1988. Macroinvertebrate base line studies of Big Thompson River, Fall River and Ypsilon Creek in Rocky Mountain National Park. Unpublished report, Rocky Mountain National Park, Colo. 65 pp.

Biedenharn, D. S. 1983. Bed material analysis on the Fall River. Water Resources Field Support Laboratory Project Report 83-6P. National Park Service. Colorado State University, Fort Collins. 26 pp.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest of southern Wisconsin. Ecological Monographs 27:325–349.

Bruinsma, L. 1981. Base line data study on the Fall River and Big Thompson River drainage. Unpublished report, Rocky Mountain National Park, Colo. 40 pp.

Chandler, J. R. 1970. A biological approach to water quality management. Water Pollution Control 4:415–422.

Environmental Protection Agency Quality Control Samples. 1978. Instructions for fluorometric analysis of chlorophyll. Environmental Protection Agency Environmental Monitoring and Support Laboratory, Quality Assurance Branch, Cincinnati, Ohio.

Edmunds, G. F., Jr., S. L. Jensen, and L. Berner. 1976. The mayflies of North and Central America. University of Minnesota Press, Minneapolis. 330 pp.

Hedin, L. 1980. The Ephemeroptera community in Fall River, Rocky Mountain National Park. Unpublished report, Rocky Mountain National Park, Colo. 11 pp.

Hogue, C. L. 1973. The net-winged midges or Blephariceridae of California. Bulletin of the California Insect Survey 15:1–83.

Jaccard, P. 1908. Nouvelles recherches sur la distribution florale. Bulletin de la Societe Vaudoise des Sciences Naturelles XLIV(163):223–269.

Jacobson, N. 1983. The effects of the Lawn Lake Flood on macroinvertebrates in the Fall River and the Roaring River. Unpublished report, Rocky Mountain National Park, Colo. 77 pp.

Jensen, S. L. 1966. The mayflies of Idaho (Ephemeroptera). M.S. thesis, University of Utah, Salt Lake City. 366 pp.

Johnson, S. C. 1978. Larvae of *Ephemerella inermis* and *E. infrequens*. Pan-Pacific Entomologist 54:19–25.

May, R. M. 1975. Some notes on estimating the competition matrix a'. Ecology 56:737–741.

Merritt, R. W., and K. W. Cummins, editors. 1984. An introduction to the aquatic insects of North America. Second edition. Kendall/Hunt Publishing Company, Dubuque, Iowa. 722 pp.

Morihara, D. K., and W. P. McCafferty. 1979. The *Baetis* larvae of North America (Ephemeroptera: Baetidae). Transactions of the American Entomological Society 105:139–221.

Pennak, R. W. 1978. Freshwater invertebrates of the United States. Second edition. Wiley–Interscience Publishers. 803 pp.

Peterson, B. V. 1960a. Notes on some natural enemies of Utah blackflies. Canadian Entomologist 92:266–274.

Peterson, B. V. 1960b. The Simuliidae (Diptera) of Utah, part I. Great Basin Naturalist 20:81–104.

Pitlick, J., and M. D. Harvey. 1986. A summary of 1985 channel changes and sediment transport on Fall River, Rocky Mountain National Park, Colorado. Unpublished report, Rocky Mountain National Park, Colo. 38 pp.

Pitlick, J., and M. D. Harvey. 1987. Geomorphic response of Fall River following the Lawn Lake Flood, Rocky Mountain National Park, Colorado. Final report to the Department of Army, U.S. Army Research Office. Contract DAAG29–85–K–0108. 33 pp.

SAS Institute Inc. 1987. SAS/STAT guide for personal computers, version 6 edition. SAS Institute, Inc., Cary, N.C. 378 pp.

Snyder, J. D., and J. A. Trofymow. 1984. A rapid accurate wet oxidation diffusion procedure for determining organic and inorganic carbon in plant and soil samples. Communication in Soil Science and Plant Analysis 15(5):587–597.

Washington, H. G. 1984. Diversity, biotic and similarity indices. A review with special relevance to aquatic ecosystems. Water Resources 18(6):653–694.

Webb, D. W. 1977. The Nearctic Anthericidae (Insecta: Diptera). Journal of the Kansas Entomological Society 50:473–495.

Whittaker, R. H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. Ecological Monographs 22:1.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press. 401 pp.

Winget, R. N., and F. A. Mangum. 1979. Biotic condition index: integrated biological, physical, and chemical stream parameters for management. Aquatic Ecosystem Inventory, Macroinvertebrate Analysis. U.S. Forest Service Intermountain Region publication. 50 pp.

Appendix. List of Taxa Encountered During the Rocky Mountain National Park Macroinvertebrate Sampling, 1985–1986

- **Plecoptera**
  - Nemouridae
    - *Zapada*
    - *Prostoia*
    - *Amphinemura*
    - *Podmosta*
    - *Malenka*
  - Perlodidae
    - *Megarcys*
    - *Isoperla*
    - *Pictetiella*
    - *Kogotus*
    - *Skwala*
    - *Cultus*
  - Chloroperlidae
  - Taeniopterygidae
    - *Taenionema*
  - Perlidae
    - *Hesperoperla*
  - Pteronarcydae
    - *Pteronarcella*
  - Capniidae
    - *Eucapnopsis*
    - *Capnia*
  - Leuctridae
    - *Despaxia*
    - *Paraleuctra*
- **Ephemeroptera**
  - Siphlonuridae
    - *Ameletus*
    - *Siphlonurus*
  - Heptageniidae
    - *Cinygmula*
    - *Rhithrogena*
    - *Epeorus*
    - *Heptagenia*
  - Baetidae
    - *Baetis*
    - *Pseudocloeon*
    - *Cloeon*
  - Ephemerellidae
    - *Drunella*
    - *Ephemerella*
    - *Serratella*
  - Leptophlebiidae
    - *Paraleptophlebia*
- **Trichoptera**
  - Hydroptilidae
    - *Agraylea*
  - Hydropsychidae
    - *Arctopsyche*
  - Glossosomatidae
    - *Glossosoma*
  - Rhyacophilidae
    - *Rhyacophila*
  - Brachycentridae
    - *Brachycentrus*
    - *Amiocentrus*
  - Limnephilidae
    - *Oligophlebodes*
    - *Ecclisomyia*
    - *Limnephilus*
    - *Dicosmoecus*
    - *Onocosmoecus*
    - *Amphicosmoecus*
    - *Psychoglypha*
    - *Pseudostenophylax*
    - *Homophylax*
    - *Psychomyia*
  - Uenoidae
    - *Neothremma*
  - Lepidostomatidae
    - *Lepidostoma*
- **Diptera**
  - Simuliidae
  - Tipulidae
    - *Dicranota*
    - *Antocha*

  - *Hexatoma*
  - *Pedicia*
  - *Rhabdomastix*
  - *Limnophila*
- Empididae
  - *Chelifera*
  - *Oreogeton*
  - *Clinocera*
  - *Hemerodromia*
- Chironomidae
- Blephariceridae
  - *Agathon*
  - *Philorus*
  - *Bibiocephala*
- Athericidae
  - *Atherix*
- Ceratopogonidae
  - *Bezzia*
- Ptychopteridae
  - *Ptychoptera*
- Deuterophlebiidae
  - *Deuterophlebia*
- Psychodidae
  - *Pericoma*
- Dixidae
  - *Dixa*
- Tanyderidae
  - *Protanyderus*

Terrestrial Arthropod Fauna of the Alluvial Fan Resulting From the Lawn Lake Flood

Howard E. Evans

Colorado State University
Departments of Zoology and Entomology
Fort Collins, Colorado 80523

Abstract. Using several sampling methods in a transect across the lower part of the alluvial fan demonstrated that most groups of arthropods were poorly represented 2–3 years after the flood. Most strikingly reduced in numbers were ants, wasps, bees, butterflies, and moths. Although some groups of ground beetles and spiders that were abundant in adjacent forests were also scarce or absent in the alluvium, several small species in both groups appeared to thrive there. Springtails and mites, soil arthropods common in surrounding areas, occurred in the fan in limited numbers but showed occasional abrupt population increases.

Introduction

The Lawn Lake Flood deposited an alluvial fan of about 17 ha at the point where Roaring River enters Horseshoe Park. Most of the vegetation and animal life in this area were destroyed by inundation, scouring, or burial under rocks and sand. Studies in the summers of 1984 and 1985 were designed to determine the effect of this catastrophic event on populations of terrestrial arthropods. Many plant-dependent insects were clearly eliminated with their host plants, though an increase of species attacking dead or decaying plants might have been expected. The extent to which arthropods associated with the soil were affected was not obvious. These studies were primarily, though not exclusively, directed toward the fauna living on or just below the soil surface. Since no broad-scale inventory of arthropods occurring in this area had ever been undertaken, populations in the alluvial fan were compared with those in immediately adjacent areas.

Methods

A transect was established across the alluvial fan and areas adjacent to it. In this part of the fan, the soil was essentially coarse sand, with particle size smaller than 2 mm, overlying the original soil primarily to a depth of 0.3–1.0 m

(Jarrett and Costa 1986). A series of traps or sampling points was established across the transect, varying in number and position depending on the sampling method. For convenience, data were grouped into one of three major areas: areas immediately adjacent on either side, not directly affected by the flood; central part of the alluvial fan, where little living plant life existed; and an area on the east side of the major part of the fan, where living willows (*Salix* spp.) were found with many standing and prostrate dead aspens (*Populus tremuloides*; Figure). Sampling sites were selected away from flowing water or extremely damp soil. The following sampling methods were employed (for fuller descriptions, see Southwood 1978):

1. Soil samples were collected at seven sites 100–150 m apart approximately every 3 weeks from 11 June to 29 August 1984. Each sample was taken from a circle 11 cm in diameter and 6 cm deep. Each was collected in a plastic bag and transferred to a Berlese funnel in the laboratory, where the contents were collected in 80% ethanol and analyzed a week later.
2. In 1984, 11 pitfall traps were placed across the transect 50–75 m apart. In 1985, six traps were used, 100–150 m apart. Traps were 10 cm in diameter and were charged with ethylene glycol. Each was surmounted by a metal plate on which a label was placed explaining the function of the trap (virtually no vandalism or other loss occurred). The contents were collected every 3 weeks, and the arthropods were studied in the laboratory.
3. Two Malaise traps were used for 1 week in each summer month of 1985. These traps were tentlike and designed to collect low-flying insects. Because the traps are conspicuous, they were placed in situations not

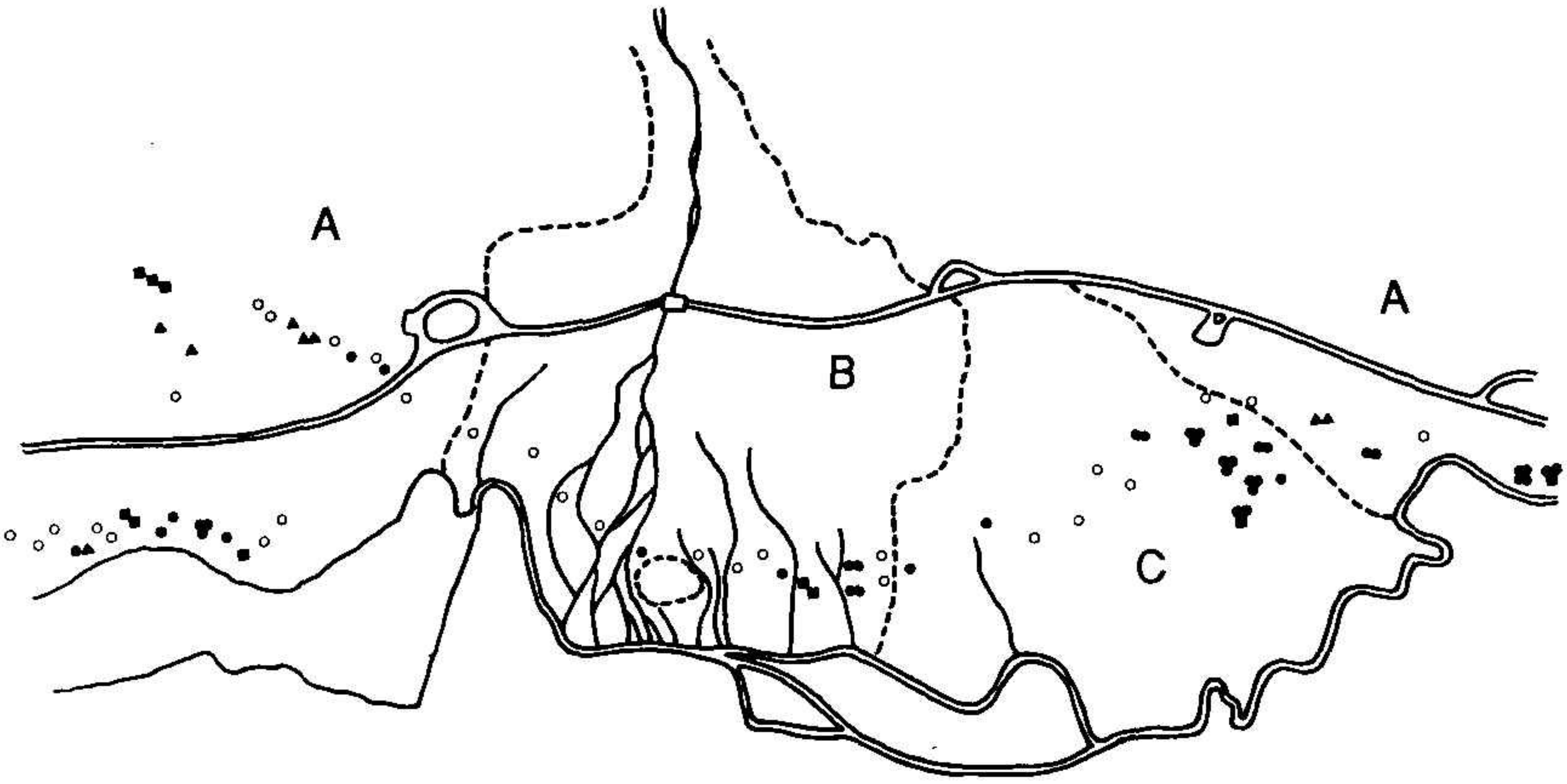


Figure. Map of alluvial fan, drawn from aerial photographs, showing the three study areas: (A) woods and meadows adjacent to fan but undamaged; (B) central part of fan, largely devoid of living vegetation; (C) grove of aspens mostly dead, with patches of living willows, grasses, and mosses. Placement of trap nests: ○ = groups of four traps, unfilled; ● = nests filled by *Ancistrocerus* wasps; ▲ = nests filled by *Passaloecus* wasps; ■ = nests filled by leafcutter bees (Megachilidae).

readily visible from the road, one in area C and one in area A (about 0.5 km up the Fall River valley; none in the central part of the fan, area B). Specimens were collected in 80% ethanol.

4. In 1985, 248 wooden trap nests were placed (in groups of four) in living or dead trees or bushes, from 0.3 to 2.0 m high. These trap nests were designed to induce nesting by bees and wasps that normally nest in hollow twigs or beetle borings in trees (in forested areas many species nest in these situations rather than in the ground). A variety of borings was used, from 3 to 10 mm in diameter. The traps were checked every 2 weeks and fully harvested in late August. Much of the emergence from these traps occurred the following spring. Overall, 60 of the traps (24%) were accepted, which is about average for areas of similar altitude in the Front Range of the Rocky Mountains (H. E. Evans, unpublished data). The location of these traps is shown in the Figure. For a fuller discussion of this technique, see Krombein 1967.

In most cases, specimens collected were sorted only to major groups. However, species-level identifications were made for spiders and ground beetles taken in pitfall traps and for bees and wasps taken in trap nests.

Results

Soil Fauna

As anticipated, the soil fauna consisted mainly of springtails (Collembola) and mites (Acari). The springtails were predominantly of the suborder Arthropleona, while a high percentage of the mites were Orbatida (beetle mites). The few other arthropods taken in soil samples (ants, thrips, beetles, fly larvae) together accounted for only 0.4% of the 2,472 specimens taken. Springtails composed 35% of the season's total, and mites composed 64.6% of the total. Area A (2 sites) contained 56% of the arthropods collected, area C (2 sites) contained 40%, and area B (3 sites in the central part of the alluvial fan) contained only 4%. All groups were most abundant in area A, less so in area C, and scarce in area B (Table 1).

These figures are to a degree misleading, since in fact springtails and mites were scarce in area C through June and July, with a major increase in

Table 1. *Mean numbers of arthropods per soil sample site (cumulative over summer) in each of three areas, 1984.*

Group	A	B	C
Springtails	204	12	116
Mites	389	13	310
Other	31	4	8

numbers of both groups at one site during two collections in August. Three samples taken at this site during June and July totalled only 1 springtail and 43 mites; comparable figures for the 2 August collections were 231 springtails and 540 mites. This increase was likely the result of soil fungi growth at this site. On 29 August, a cluster of fungi was collected near this site and placed in a Berlese funnel; the fungi proved extremely rich in both mites and springtails. In Oregon, numbers of soil arthropods have been found to be correlated with the density of soil fungi (Moldenke et al. 1988).

Clearly, the central part of the alluvial fan provided poor substrate for springtails, mites, and other soil arthropods. In contrast, these organisms were plentiful in areas unaffected by the flood. Generally speaking, soil arthropods were also scarce in the willows and aspen grove (area C), aside from abrupt population increases at localized sites during August.

Surface Fauna

Pitfall traps collected many springtails but few mites. The traps also collected many ants and beetles and smaller numbers of flies, spiders, and other arthropods. The following shows the breakdown of the 5,251 arthropods collected at 11 sites in the course of the summer of 1984: ants, 28%; springtails, 27%; beetles, 16%; flies, 10%; spiders and harvestmen (Phalangida), 7%; and other arthropods, 12%. The last group was diverse, including millipedes, leafhoppers, caterpillars, small parasitoid wasps, and others.

As in the case of soil samples, most groups occurred in diminished numbers in the central part of the alluvial fan (area B). Overall, area A (3 sites) contained 40.7% of the total arthropods (with ants predominating); area C (3 sites), 43.0% (with springtails predominating); and area B (5 sites), 16.3%. Calculation of the mean numbers of each group per sample site provides a more accurate picture of the numbers obtained (Table 2).

Although area B contained only 2% of the ants collected and only 8% of the springtails, different figures were obtained for three other groups: flies, 47%; beetles, 30%; and spiders and harvestmen, 24%. Since these figures contrasted sharply with those of ants and springtails, in 1985 we decided to use the pitfall traps for a species-level study of the beetles (specifically the ground beetles, Carabidae) and the spiders (the flies were exceedingly diverse and

Table 2. *Mean numbers of arthropods per pitfall trap sample site (cumulative over summer) in each of three areas, 1984.*

Group	A	B	C
Ants	356	4	123
Springtails	70	22	367
Flies	58	48	29
Beetles	83	51	119
Spiders and harvestmen	41	16	44

presented too formidable a task in identification). Using data from both seasons, ground beetles were found to constitute a different complex of species in each of the three areas (Table 3). In area A, six species occurred, two of them abundantly. These species are primarily characteristic of moist-to-dry montane forests (G. E. Ball and D. Shpeley, personal communication). With minor exceptions, none of these species occurred in the alluvial fan. Although area B had fewer ground beetles per sample, this area contained several small species of *Bembidion*, one of them (*B. rupicola*) abundantly. These beetles are largely hygrophilous, characteristic of open sand or gravel; however, some occur in drier situations. In a survey of ground beetles at various altitudes in forests and meadows of the Boulder Creek drainage, Mowrer (1975) recorded no species of *Bembidion*.

Area C also contained four species of *Bembidion*, three of them also occurring in area B. Of other species present in area C, *Elaphrus marginicollis* is also characteristic of moist, open places, as is *Agonum sordens*; the latter has often been found with *Salix* species. *Pterostichus adstrictus* occurred in some numbers in both areas B and C. This species is widely distributed, occurring in

Table 3. Ground beetles (Carabidae) taken from pitfall traps in three areas, 1984 and 1985.

Name	A	B	C
Agonum placidum	3	0	0
Agonum sordens	0	0	5
Amara avida	0	0	1
Amara erratica	0	1	0
Amara quenseli	1	0	0
Bembidion (4 other species)[a]	0	5	0
Bembidion bimaculatum	0	6	26
Bembidion grapei	0	1	15
Bembidion nitidum	0	11	0
Bembidion obscurellum	0	10	0
Bembidion rupicola	0	56	7
Bembidion timidum	0	0	2
Calathus ingratus	4	0	1
Carabus taedatus	17	1	0
Elaphrus marginicollis	0	0	5
Loricera pilicornis	0	0	1
Metabletus americanus	5	0	0
Pterostichus adstrictus	0	15	23
Pterostichus protractus	26	0	0
Totals	56	106	86
Stations (*n*)	5	9	4
Mean per station	11.2	11.7	21.5

[a] These were *nitidum*, *gratiosum*, *flebile*, and one unidentified.

a variety of unforested habitats; Mowrer (1975) recorded the species at approximately the same altitude in the Boulder Creek drainage.

Like ground beetles, spiders were also less abundant in area B than in A or C, but certain small species were nevertheless well represented in the central part of the alluvial fan (Table 4). Adjacent parts of the forests and meadows (area A) contained representatives of eight families, compared with three in area B and four in area C. The absence of free-living forms, such as wolf spiders (Lycosidae) and crab spiders (Thomisidae and Philodromidae) in area B is especially noteworthy. The majority of spiders present in the alluvial fan were Linyphiidae (these are sometimes placed in the family Micryphantidae or Erigonidae and are often called dwarf spiders). These spiders spin small webs in moist soil. They occurred in all three areas but were least plentiful in area A. Mowrer (1975) recorded relatively few Linyphiidae in his survey of forests and meadows of the Boulder Creek drainage.

Aerial Fauna

Total catch for the 1985 season in a Malaise trap at the control site (0.5 km up the Fall River valley) was 14,184 specimens, compared with 10,351 in area C (a factor of 1.37). The vast majority (90–94%) of specimens at both areas were flies (Diptera). The number of flies at the control site exceeded that at site C by a factor of 1.35 (12,905:9,584). In two groups of predominantly

Table 4. *Spiders (Araneae) taken in pitfall traps in three areas, 1984 and 1985.*

Name	A	B	C
Linyphiidae[a]	17	40	56
Gnaphosidae			
Orodrassus coloradensis	18	2	2
Drassodes	1	0	0
Clubionidae	2	1	0
Lycosidae			
Schizocosa or *Lycosa*	29	0	20
Tarentula kochii	5	0	0
Thomisidae			
Misumenops	5	0	0
Philodromidae			
Thanatus	11	0	1
Salticidae	1	0	0
Araneidae	1	0	0
Totals	90	43	79
Stations (*n*)	5	9	4
Mean per station	18.0	4.7	19.7

[a] May be *Erigone denticulata.*

nectar-feeding insects, Lepidoptera and Hymenoptera, approximately twice as many specimens were taken at the control site as in area C (Lepidoptera, 99:51; Hymenoptera, 849:422). Bees, which are dependent on flowers for both nectar and pollen, were approximately 5 times as abundant in the control site as in area C (217:42). Only one group of insects (Homoptera) was almost equally represented in both traps (266:289). These insects were primarily leafhoppers, which migrated through the area, mainly in August, and presumably came from sources outside the study areas.

A final study of the aerial fauna involved using trap nests for bees and wasps that commonly nest in hollow twigs and beetle borings in wood. Acceptance of trap nests was highest in area C, possibly because *Ancistrocerus* wasps, which use mud for partitions between cells, found an abundance of mud in this area (Figure; Table 5). These wasps prey on small caterpillars, which they often carry from some distance. Three species were reared from trap nests in the following numbers: *A. catskill*, 111; *A. antilope*, 24; and *A. adiabatus*, 3. The three species were graded by size: female *A. antilope* had a forewing length of about 13 mm, *A. catskill* a forewing length of about 9 mm, and *A. adiabatus* a forewing length of about 7.5 m. The sizes of the borings accepted and the caterpillars used as prey were graded accordingly.

One other species of wasp occupied trap nests, but only in forested parts of area A. This species was *Passaloecus cuspidatus*, a small wasp that uses the pitch of coniferous trees in making cell partitions and provisions the cells with aphids. Lack of readily available pitch in the alluvial fan doubtless explains the absence of these wasps there.

Leafcutter bees (Megachilidae) accepted trap nests in all three areas, most commonly in area A. They line the cells with leaf cuttings and provision them with nectar and pollen. Two species were involved: *Megachile brevis*, 9; and a species of *Osmia*, 2. Several hymenopterous parasites were reared from *Ancistrocerus* nests: *Chrysis coerulans*, 5 (Chrysididae); *Pimpla spatulata*, 5

Table 5. *Number of trap nests accepted by wasps and bees in three areas, 1985.*

Name	A	B	C
Ancistrocerus	17	6	18
Passaloecus	8	0	0
Megachilidae	7	2	2
Total accepted	32	8	20
Total nests	132	56	60
Total accepted[a]	24	14	33
by Ancistrocerus[a]	13	11	30
by *Passaloecus*[a]	6	0	0
by *Megachilidae*[a]	5	3	3

[a] Percent.

(Ichneumonidae); and an undetermined species of Pteromalidae, 6. A parasitic beetle of the genus *Nemognatha* was reared from a *Megachile* nest.

Discussion

Without information on the original arthropod fauna of the area surrounding the junction of the Roaring and Fall rivers (from before the Lawn Lake Flood), the fauna of the alluvial fan produced by the flood was compared with that of surrounding forests and meadows not directly affected by the flood. The eastern side of the fan, where living willows were found with many dead and dying aspens, differed considerably from the central part of the fan, which had been thoroughly scoured and covered with thick alluvium. Therefore, the fauna of this area—area C—was analyzed separately from that of the central part of the fan—area B—and the surrounding meadows and forests—area A (Figure).

The soil fauna was dominated by springtails and mites, as is commonly the case. Both groups were abundant in adjacent meadows and forests but poorly represented in soil samples and in pitfall traps in the alluvial fan. However, occasional samples in area C showed an abrupt increase in numbers of both groups in late summer, possibly as a result of the growth of fungi on detritus in this area.

Surface fauna was dominated by ants. However, ants were almost totally excluded from the alluvial fan in areas B and C, perhaps reflecting both a lack of suitable nesting sites and a lack of adequate prey and homopteran honeydew. Another group of surface–dwelling insects, ground beetles (Carabidae), were well represented in the alluvial fan, although by different species than those occurring in adjacent forests. Evidently, the moist, sandy soil provided a suitable habitat for small beetles of the genus *Bembidion*, most of which are typically found in riparian habitats. Larger ground beetles, such as *Carabus taedatus* and *Pterostichus protractus*, were plentiful in area A but almost totally absent from areas B and C. Similarly, larger, free–living spiders, such as wolf and crab spiders, were mostly absent in the central part of the alluvial fan, although wolf spiders were fairly well represented in pitfall traps in area C. In contrast, dwarf spiders (Linyphiidae) occurred in some numbers in both areas B and C, but were less abundant in area A. The damp, sandy substrate seemed to provide a good habitat for these minute spiders, which spin webs in loose, moist soil.

Collections of flying insects in Malaise traps showed an overall reduced number in area C when compared with an undisturbed area. This reduction was particularly true of groups of insects dependent on nectar as a source of food (Lepidoptera and Hymenoptera). Bees, which are dependent on both nectar and pollen, were 5 times as well represented in the control as in area C. Trap nest use revealed that *Ancistrocerus* wasps and leafcutter bees accepted these artificial cavities in small numbers in the alluvial fan, but *Passaloecus* wasps, which use pitch in nest construction, were excluded.

Arthropod defaunation of the area adjoining the confluence of the Roaring and Fall rivers was clearly extensive. Doubtless, much of the fauna was destroyed or displaced immediately during the flood. Plant life destruction and sand and rock deposition over the original substrate prevented much reoccupation of the area by most arthropods for at least 3 years and probably much longer. In some ways, this defaunation is suggestive of that done experimentally by Simberloff and Wilson (1969) on several islands in the Florida Keys. The reoccupation of the islands was influenced by their size and distance from the mainland, but over time each island acquired an arthropod fauna approximately the same size as it held originally. These islands had a single plant species, red mangrove, which was not destroyed by the methyl bromide used in the defaunation. In the case of the alluvial fan resulting from the Lawn Lake Flood, distance from sources of inoculum was minimal. However, almost total elimination of plant life means that arthropods dependent on plants will not become established until a diverse flora has been developed. Both the flora and fauna will be influenced by the gradual enrichment of the relatively sterile sands and gravels with organic matter. Predaceous arthropods will also remain in small numbers pending herbivore and scavenger establishment.

The most surprising result of these studies is the discovery that several groups of arthropods did appear to thrive in the alluvial fan only 2–3 years after the flood. They are small members of their respective groups—ground beetles and spiders. Also, occasional abrupt increases in the numbers of mites and springtails were noted at sites on the eastern side of the alluvial fan. These groups were all closely associated with the soil and evidently able to flourish in the coarse-grained soil of the fan. This microfauna may be thought of as first in a succession that may, in time, result in a fauna not unlike that which occupied the area before the flood. That a fauna of minute arthropods may be the first to occupy denuded landscapes is a possibility worthy of study in other areas.

Acknowledgments

Special thanks go to M. A. Evans and K. M. O'Neill for assistance in the field work. G. E. Ball and D. Shpeley, of the University of Alberta, kindly identified the ground beetles and provided information on habitats and distribution. W. D. Fronk, of Colorado State University, identified the spiders. C. R. Tracy, also of Colorado State University, made useful comments on an earlier draft of this paper, and voucher specimens have been placed in the collections of Colorado State University.

Literature Cited

Jarrett, R. D., and J. E. Costa. 1986. Hydrology, geomorphology, and dam-break modeling of the July 15, 1982 Lawn Lake Dam and Cascade Lake Dam failures, Larimer County, Colorado. U.S. Geological Survey Professional Paper 1369. 78 pp.

Krombein, K. V. 1967. Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Press, Washington, D.C. 570 pp.

Moldenke, A., G. Parsons, J. McIver, and J. D. Lattin. 1988. Microfauna as sensitive indicators of soil conditions (forest succession, moisture stress). Pages 235–236 *in* Abstracts, 73rd Annual Meeting of the Ecological Society of America, Bulletin of the Ecological Society of America (Suppl.).

Mowrer, K. E. 1975. Altitudinal zonation among selected predaceous arthropods. M.S. thesis, Colorado State University, Fort Collins. 92 pp.

Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology 50:278–296.

Southwood, T. R. E. 1978. Ecological methods with particular reference to the study of insect populations. Second edition. Chapman and Hall, London. 524 pp.

Colonization of the Lawn Lake Alluvial Fan by Amphibians: Potential Effects of Biotic and Abiotic Factors

Linda C. Zimmerman and C. Richard Tracy

Colorado State University
Department of Biology
Fort Collins, Colorado 80523

Abstract. During the first 5 years (1983–87) following the Lawn Lake Flood in Rocky Mountain National Park, we studied amphibian recolonization of the alluvial fan created by the flood. We monitored locations of amphibians, measured levels of iron and other indicators of water quality, and assessed the effect of iron on survivorship and growth of larval amphibians. Three species of amphibians reinvaded the new habitat. Chorus frogs (*Pseudacris triseriata*) began successful breeding activity in 1985, and western toads (*Bufo boreas*) began successful breeding in 1986. Adult tiger salamanders (*Ambystoma tigrinum*) were observed in the new habitat, but they did not reproduce. Following the flood, concentrations of iron in waters of the new habitat increased dramatically, but subsequently they have declined toward ambient levels of unaffected waters. In captivity, chorus frogs grew to greater body dimensions in waters with elevated levels of iron compared with frogs grown in control water. However, western toads and tiger salamanders grew to smaller size in iron-rich water than did salamanders and toads grown in control water.

Introduction

On 15 July 1982, the Lawn Lake Flood in Rocky Mountain National Park, Colorado, deposited an expanse of boulders, rocks, gravel, and sand in the Horseshoe Park area (Fig. 1). This debris formed an alluvial fan, which covered all plants and animals in an area of approximately 1.5 km^2. A pronounced effect of the flood was the leaching of iron from freshly exposed bedrock of Roaring River.

We studied patterns of, and potential constraints on, colonization by amphibians of the new habitat created by the flood. Specifically, we report patterns of recolonization of the disturbed area by all species of amphibians known to inhabit the Endovalley of Rocky Mountain National Park; concentrations of iron and other indicators of water quality in waters on, and surrounding, the alluvial fan formed by the flood; and effects (in the laboratory) of elevated levels of iron on survivorship and size of the three species of amphibians that colonized the new habitat.

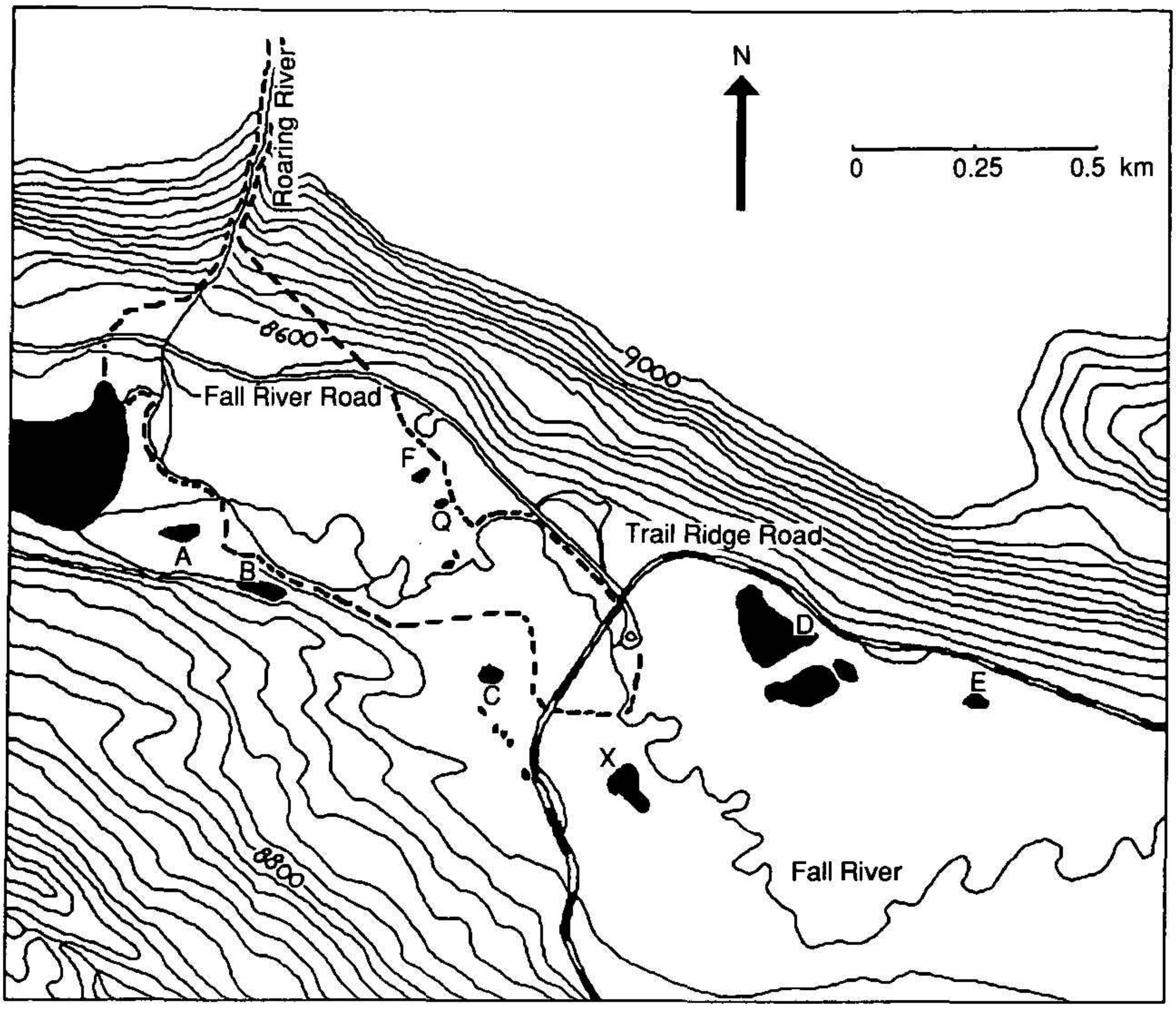


Fig. 1. Map of Horseshoe Park in Rocky Mountain National Park, Colorado. *Dashed lines* indicate the perimeter of the alluvial fan deposited as a result of the Lawn Lake Flood. The new lake, which formed after the flood, is depicted as the large *black area* south of Fall River Road and west of the alluvium. Ponds A–F, Q, X, and other unnamed ponds were areas included in faunal surveys.

Materials and Methods

Our study of amphibian recolonization consisted of three parts: surveying the area affected by the flood—plus adjacent, undisturbed areas—for locations of amphibians; measuring water chemistry on and surrounding the alluvial fan; and conducting bioassays of the effect of iron on survivorship and growth of larval amphibians.

Faunal Surveys

We monitored locations in Horseshoe Park of three species of amphibians, chorus frog (*Pseudacris triseriata*), tiger salamander (*Ambystoma tigrinum*), and western toad (*Bufo boreas*). Faunal surveys were conducted biweekly or bimonthly each year during early May through late July, a period bracketing both reproductive activity of adults and metamorphosis of larvae. Amphibians were detected both visibly and audibly (adult male frogs and toads have species-specific breeding calls) in and around ponds on and adjacent to the alluvial fan. Data consist of qualitative presence–absence information.

Water Chemistry

We measured eight indicators of water quality annually—before (May), during (June), and after (July) runoff—to span the activity season of amphibians in Horseshoe Park. Levels of dissolved O_2, CO_2, pH, NO_3, NH_3, and $CaCO_3$ were measured using field kits for chemical analyses (Hach Chemical, Loveland, Colo.). Water temperature was measured with a mercury thermometer. Iron concentration was determined by flame atomic absorption spectrophotometry from samples collected in the field, preserved with H_2NO_3, transported in Nalgene bottles 37.2 km (60 miles) to Colorado State University, and refrigerated for 1–2 days until analysis.

We established six permanent sites for monitoring seasonal and annual profiles of water chemistry variables. The sites (Fig. 1) were the Fall River west of the alluvial fan; the Fall River at Trail Ridge Road; Pond F; stagnant waters southwest of Pond F; the Roaring River at Fall River Road; and Pond C. Sites 1 and 6 were undisturbed areas outside the alluvial fan (Fig. 1).

Bioassays

Eggs or larvae of chorus frogs, tiger salamanders, and western toads were cultured separately in serial dilutions of iron-containing water to assess the influence of elevated levels of iron on hatching success, survivorship, and growth of amphibians. For the bioassays, iron-rich water was collected from a small pool on the alluvial fan (Site 4) with the highest concentration of iron we measured anywhere on the alluvial fan (and in which no amphibians were observed) and transported to laboratory facilities at Colorado State University. Serial dilutions of iron-rich water were prepared by adding water from South Sheep Lake (Fig. 1). Dilutions and corresponding mean concentrations of iron for the bioassays were

Dilution	Mean Concentration of Iron (mg/L)
0.0	13
0.25	10
0.50	7
0.75	4
1.0	<1

Three liters of each dilution were placed in glass, gallon-sized containers before the addition of amphibian eggs or larvae.

Larvae of chorus frogs were collected from Pond C (Fig. 1) in 1985, eggs of tiger salamanders were collected from South Sheep Lake (Fig. 1) in 1985 and 1986, and eggs of western toads were collected from Pond F (Fig. 1) in

1987. All eggs and larvae were collected in early May of each year, and bioassays began immediately after collection and transport of specimens to the laboratory.

In the laboratory, 15 individuals were selected at random to be assigned to each of two replicates of the dilutions of the iron-rich water. Jars were aligned along a bench near a window that provided ambient photoperiod. Natural lighting from the window was enhanced with fluorescent lighting 24 h/day. Temperature of the water was 22 ± 2° C throughout all bioassay trials.

Food was available daily at ad libitum levels. Chorus frogs and western toads were fed Tetra Min Growth Food (Tetra Werke, West Germany), and tiger salamanders were fed mixed protozoa, *Daphnia*, and tubifex worms. Each morning before feeding, fecal material and uneaten food from the previous day were aspirated from the bottom of each jar, and dead animals were removed and counted. Each week, fresh water was collected from South Sheep Lake (Fig. 1), and new dilutions were prepared into which larvae were transferred with a fine-mesh net. Biweekly, before animals were placed in fresh dilutions, width and length of each individual were measured. Animals were placed on a transparent, plastic petri dish that was positioned on a 1- × 1-mm grid. Width was the distance between the eyes across the dorsal aspect of the head; length was the distance between the anterior tip of the head and the tip of the tail. Measurements were completed within approximately 20 s, and larvae were placed directly into fresh treatment water following measurements. Throughout all bioassays, no mortality was observed that seemed to be related to handling.

Results

Faunal Surveys

1983

Although chorus frogs and tiger salamanders were observed in areas surrounding the alluvial fan, none were detected in the disturbed area. Western toads were neither seen nor heard during surveys in Horseshoe Park.

1984

In areas surrounding the alluvial fan, breeding activity of chorus frogs was observed in late May in all ponds and standing water with a surface area >1 m^2. No breeding activity was observed in Horseshoe Park in June, and very few tadpoles were seen in breeding ponds. No emergence of metamorphosed tadpoles was observed. Eggs and adults of tiger salamanders were seen in ponds surrounding the alluvial fan. Western toads were neither seen nor heard. No amphibians were observed in the new lake formed by the flood, nor in any ponds on the alluvial fan.

1985

Breeding activity of chorus frogs was observed in Ponds A–E, which are adjacent to the alluvial fan, and in Ponds F and Q on the fan (Fig. 1). Breeding of chorus frogs on the fan was the first such observation since the 1982 flood. Adult chorus frogs calling from ponds on the alluvial fan were found only in areas with relatively extensive emergent vegetation. This vegetation was more extensive during 1985 than in earlier years following the flood. Small aggregations of breeding males were observed in early May in waters on and around the alluvial fan. The peak of breeding activity was in late May. Tadpoles were observed in late May and were most abundant by the second week of June. Metamorphosed juveniles emerged from Pond F in early July. Juveniles emerged predominantly on the west bank where vegetation was most dense.

Eggs, juveniles, and adults of tiger salamanders were seen in ponds adjacent to the fan. For the first time since the flood, adults were seen on the fan in Pond F. However, no evidence of reproduction on the fan was observed. No western toads were observed either on or around the fan.

1986

Breeding activity of chorus frogs was observed in ponds adjacent to the fan and, for the second consecutive season, in Ponds F and Q on the fan. Frogs calling from ponds on the fan were found only in areas with extensive emergent vegetation. Newly metamorphosed frogs emerged from Pond F in early July but not from Pond Q, which was dry before tadpoles were seen to emerge from Pond F. Tadpoles and young frogs produced on the fan were subjectively more numerous than in 1985.

Extensive evidence of reproduction of tiger salamanders was seen in ponds surrounding the fan, but no adults or eggs were observed anywhere on the fan.

No adult western toads were seen or heard in Horseshoe Park during the faunal surveys, but we discovered thousands of tadpoles in Pond F on the fan, and they emerged as toadlets in early July.

1987

Breeding activity of chorus frogs was observed in ponds adjacent to and on the fan. Males were heard calling in early May from Ponds F and Q (Fig. 1) and, for the first time, from other small pools on the fan. By late June, breeding activity had stopped, and thousands of tadpoles of both chorus frogs and western toads were seen in Pond F, but none were seen in Pond Q. Emergent vegetation was extensive along the western shores of both Ponds F and Q. By early July, tadpoles were gone, and many juvenile frogs and toads were seen along the northern and western shores of Pond F where emergent vegetation was most dense. Pond Q was dry, and no juveniles were seen near its shores. By late July, Pond F was dry. Chorus frog juveniles were seen clinging predominantly to moist vegetation at a height of 0–3 cm above the ground, and juveniles of western toads were seen predominantly on the ground amidst moist vegetation. Eggs and adults of tiger salamanders were seen in ponds adjacent to the fan, but no tiger salamanders were seen on the fan.

Water Chemistry

Values for concentration of iron are presented in Tables 1, 2, 3, and 4. For pre-, mid-, and postrunoff times during the activity season of amphibians for sites on and surrounding the fan, annual levels of O_2, CO_2, pH, NO_3, NH_3, and $CaCO_3$—plus temperature—are presented in Tables 5, 6, and 7. Since the flood, concentration of iron in waters on the fan has shown a decreasing trend (Fig. 2).

Table 1. *Concentration of iron (mg/L) in water from three sampling sites*[a] *during the activity season of 1983 and 1984.*

Year	Site 1	Site 3	Site 4
1983	n.d.[b]	10	20
1984	n.d.	—	23

[a] Site 1 is on the Fall River approximately 1/4 mile upstream from the new lake formed by the flood; site 3 is Pond F; site 4 is a small stagnant pond southeast of Pond F (see Fig. 1).
[b] Nondetectable levels.

Table 2. *Concentration of iron (mg/L) in water from six sampling sites on three dates during 1985.*

Site[a]	3 May	6 June	9 July
1	n.d.[b]	n.d.	n.d.
2	<1	n.d.	n.d.
3	6	6	7
4	19	8	13
5	1	8	n.d.
6	3	n.d.	5.5

[a] Site 1 is on the Fall River about 1/4 mile upstream from the new lake formed by the flood; site 2 is the Roaring River at Fall River Road; site 3 is Pond F; site 4 is a small stagnant pond southeast of Pond F; site 5 is the Fall River at Trail Ridge Road; site 6 is Pond C (see Fig. 1).
[b] Nondetectable levels.

Table 3. *Concentration of iron (mg/L) in water from six sampling sites on three dates during the 1986 season.*

Site[a]	27 May	17 June	18 July
1	n.d.[b]	n.d.	n.d.
2	n.d.	n.d.	n.d.
3	3.0	3.4	3.8
4	14.0	15.0	10.0
5	n.d.	n.d.	0.3
6	3.0	4.2	4.7

[a] Site 1 is on the Fall River about 1/4 mile upstream from the new lake formed by the flood; site 2 is the Roaring River at Fall River Road; site 3 is Pond F; site 4 is a small stagnant pond southeast of Pond F; site 5 is the Fall River at Trail Ridge Road; site 6 is Pond C (see Fig. 1).
[b] Nondetectable levels.

Table 4. *Concentration of iron (mg/L) in water from six sampling sites on three dates during the 1987 season.*

Site[a]	13 May	23 June	21 July
1	n.d.[b]	n.d.	n.d.
2	0.14	n.d.	n.d.
3	5.4	7.3	7.2
4	5.7	17.8	30.3
5	0.27	0.32	0.29
6	3.0	14.2	—

[a] Site 1 is on the Fall River about 1/4 mile upstream from the new lake formed by the flood; site 2 is the Roaring River at Fall River Road; site 3 is Pond F; site 4 is a small stagnant pond southeast of Pond F; site 5 is the Fall River at Trail Ridge Road; site 6 is Pond C (see Fig. 1).

[b] Nondetectable levels.

Table 5. *Indicators of water quality for six sampling sites on three dates during the 1985 season. Units are mg/L for all values except temperature.*

	Site[a]						
Variable	1	2	3	4	5	6	1985 Date
O_2	7	6	8	6	6	8	3 May
	5	5	5	2	5	2	6 June
	5	5	4	1	4	2	7 July
CO_2	18	19	44	100	20	36	3 May
	40	45	60	90	40	55	6 June
	50	45	70	130	55	65	7 July
pH	7	7	8	6	6.5	7	3 May
	7	6.5	7	6	6.5	6	6 June
	7	6.5	7	6	7	7	7 July
NO3	5	5	n.d.[b]	5	5	4	3 May
	6	3	4.5	5	5	5	6 June
	6	6	3	5	3	7	7 July
NH_3	n.d.	n.d.	0.8	2.7	0.5	1.7	3 May
	0.4	0.6	0.5	0.1	0.4	1.6	6 June
	0.3	0.5	1.6	1.6	0.3	2.5	7 July
$CaCO_3$	12	7	103	137	10	25	3 May
	17	17	102	170	173	4	6 June
	7	5	103	137	6	68	7 July
Temperature (° C)	4	6	19	15	7	—	3 May
	7	9	24	17	10	25	6 June
	10	12	25	18	15	23	7 July

[a] Site 1 is on the Fall River about 1/4 mile upstream from the new lake formed by the flood; site 2 is the Roaring River at Fall River Road; site 3 is Pond F; site 4 is a small stagnant pond southeast of Pond F; site 5 is the Fall River at Trail Ridge Road; site 6 is Pond C (see Fig. 1).

[b] Nondetectable levels.

Table 6. *Indicators of water quality for six sampling sites on three dates during the 1986 season. Units are mg/L for all values except temperature.*

	Site[a]						
Variable	1	2	3	4	5	6	1986 Date
	5	5	3	2	5	2	27 May
O_2	5	6	5	1	5	1	17 June
	5	5	4	1	5	2	18 July
	6	6	7	6	6	7	27 May
pH	6	6	7	6	6	7	17 June
	6	6	7	6	7	6	18 July
	34	28	85	135	28	90	27 May
CO_2	29	29	60	120	32	90	17 June
	29	30	75	125	29	75	18 July
	4	5	2	4	5	5	27 May
NO3	5	5	4	5	5	5	17 June
	5	6	5	4	4	4	18 July
	0.5	0.5	1	2	0.4	1.5	27 May
NH_3	0.8	0.5	0.8	1.8	0.5	2.8	17 June
	0.5	0.4	1	1.1	0.5	1.9	18 July
	12	13	137	188	14	103	27 May
$CaCO_3$	10	8	85	120	8	68	17 June
	13	8	85	103	8	85	18 July
Temperature	7	10	26	22	12	25	27 May
(° C)	2	3	14	16	5	15	17 June
	5	6	21	18	7	13	18 July

[a] Site 1 is on the Fall River about 1/4 mile upstream from the new lake formed by the flood; site 2 is the Roaring River at Fall River Road; site 3 is Pond F; site 4 is a small stagnant pond southeast of Pond F; site 5 is the Fall River at Trail Ridge Road; site 6 is Pond C (see Fig. 1).

[b] Nondetectable levels.

Table 7. *Indicators of water quality for six sampling sites on three dates during the 1987 season. Units are mg/L for all values except temperature.*

	Site[a]						
Variable	1	2	3	4	5	6	1987 Date
	6	5	6	3	5	3.5	13 May
O_2	5	6	2.6	0.3	5	5	23 June
	5	5	—	—	4	—	21 July
	45	75	45	105	35	45	13 May
CO_2	19	11	25	100	25	20	23 June
	12	12	—	—	14	—	21 July

Table 7. *Continued.*

	Site[a]						
Variable	1	2	3	4	5	6	1986 Date
	7	7	7.5	6	6.5	6	13 May
pH	7	7	7	6	7	7	23 June
	7	7	—	—	7.5	—	21 July
	0.3	0.1	0	0.6	0.1	1.4	13 May
NH_3	0.4	0.3	0.7	0.9	0.6	1.4	23 June
	0.2	0.5	—	—	0.5	—	21 July
	9	7	83	85	10	85	13 May
$CaCO_3$	12	13	137	188	13	120	23 June
	10	7	—	—	9	—	21 July
Temperature	6	7	21	18	8	20	13 May
(° C)	7	9	22	14	10	19	23 June
	11	12	—	—	11	—	21 July

[a] Site 1 is on the Fall River about 1/4 mile upstream from the new lake formed by the flood; site 2 is the Roaring River at Fall River Road; site 3 is Pond F; site 4 is a small stagnant pond southeast of Pond F; site 5 is the Fall River at Trail Ridge Road; site 6 is Pond C (see Fig. 1).

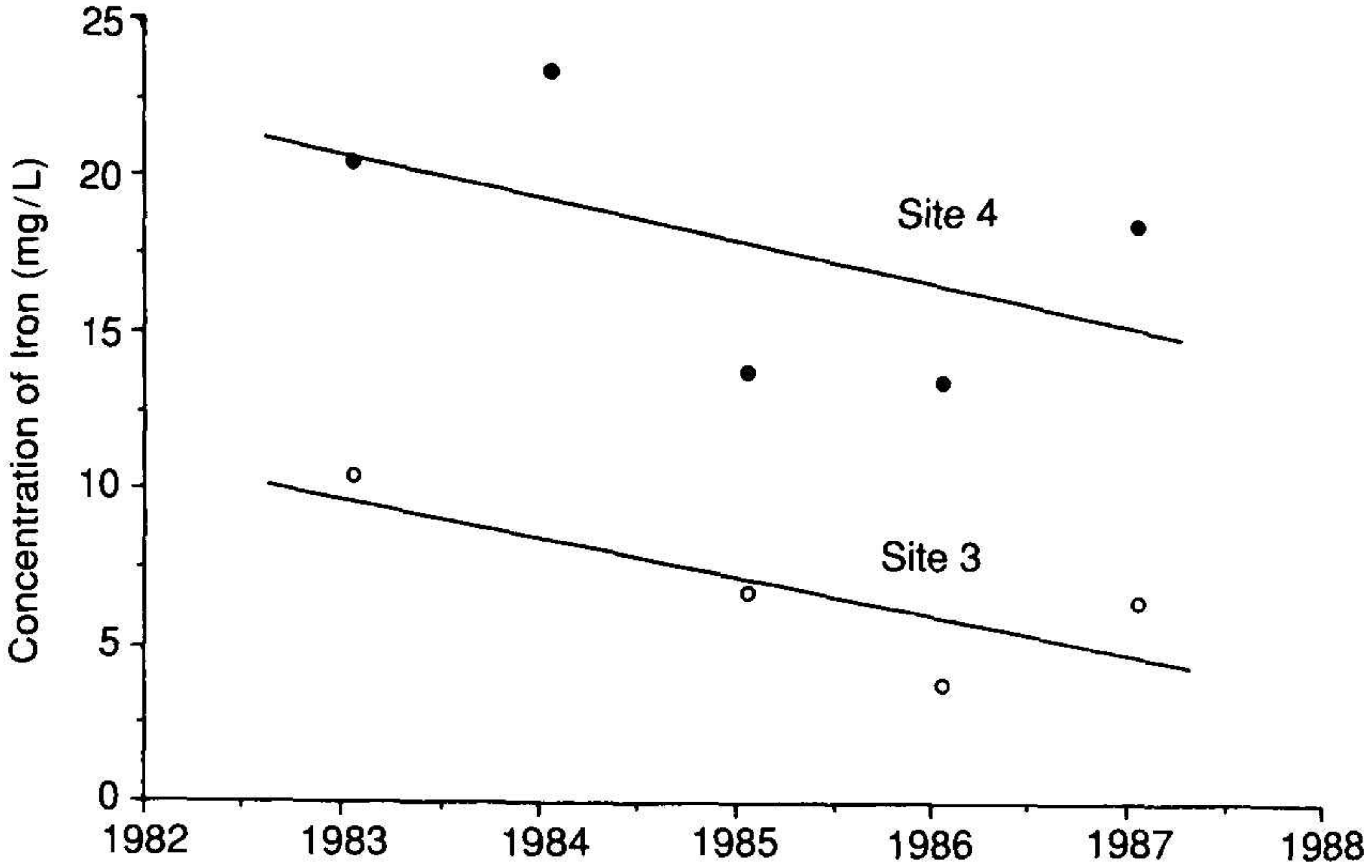


Fig. 2. Mean concentration of iron (mg/L) in waters of two sites on the alluvial fan during the first 5 years following the Lawn Lake Flood. For Site 3, $y = 10.28-1.14\ x$; $F_{1,3} = 2.16$, $P = 0.28$. For Site 4, $y = 21.7 - 1.42\ x$; $F_{1,4} = 1.11$, $P = 0.37$.

Bioassays

Chorus Frog

Mortality in laboratory experiments was statistically indistinguishable ($\chi^2 = 4.09$, $P = 0.46$) for larvae maintained in serial dilutions of iron-containing water. However, lengths of tadpoles were statistically different among treatment groups ($F_{9,95} = 4.65$, $P = 0.05$), and a significant positive correlation between length of tadpoles and concentration of iron was observed ($F_{1,48} = 8.03$, $P = 0.007$; Fig. 3).

Tiger Salamander

No difference was seen in mortality of eggs ($\chi^2 = 0.69$, $P = 0.7$) among treatment groups, but survivorship of larvae decreased with increasing concentration of iron ($\chi^2 = 17.7$, $P = 0.0001$). Moreover, length of larvae was negatively correlated with increasing concentration of iron ($F_{1,126} = 14.5$, $P = 0.0005$; Fig. 4).

Western Toad

Length of larvae was negatively correlated with concentration of iron ($F_{1,6} = 6.78$, $P = 0.04$; Fig. 5).

Discussion

Chorus frogs and western toads seem to have successfully recolonized the altered habitat created by the Lawn Lake Flood in Horseshoe Park. Reinvasion

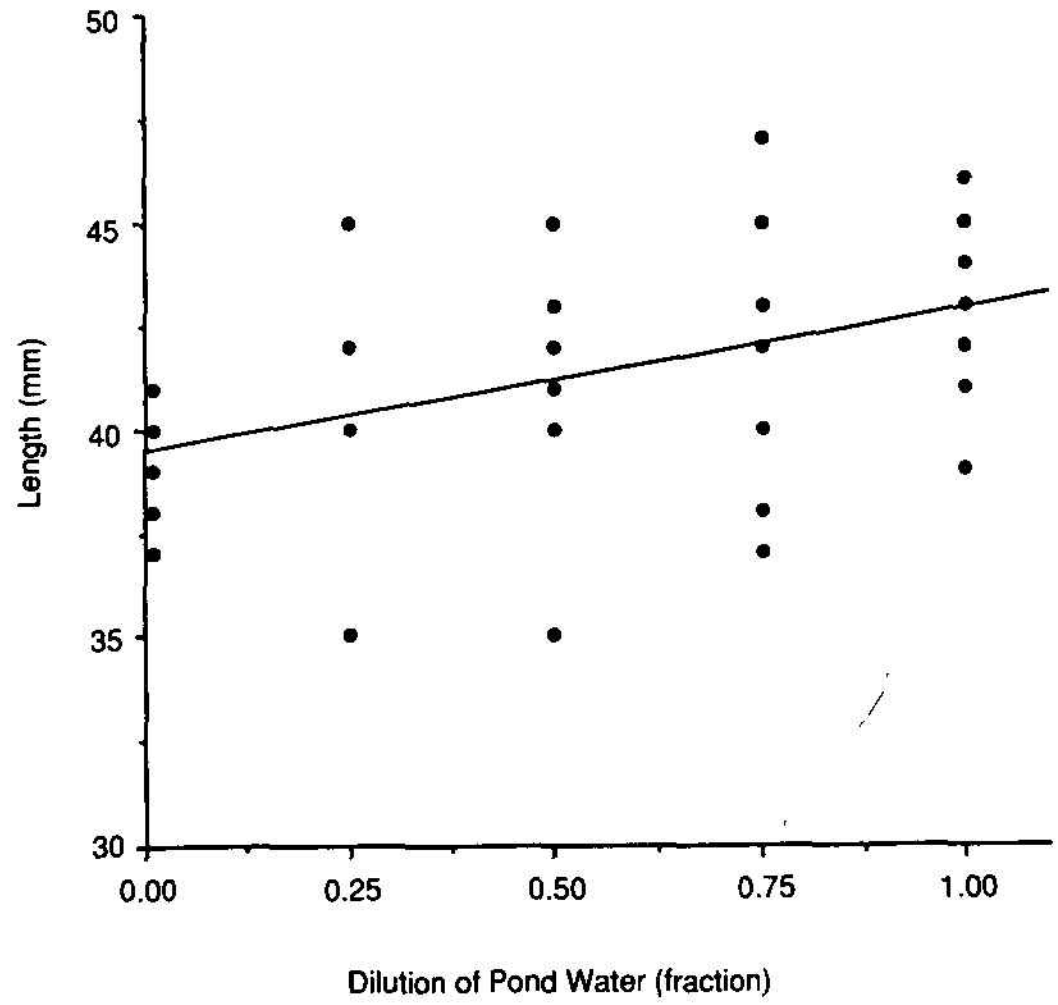


Fig. 3. Total body lengths of larval chorus frogs (*Pseudacris triseriata*) grown in serial dilutions of iron-containing water; $y = 39.47 + 3.44\,x$; $F_{1,48} = 8.03$, $P = 0.0007$.

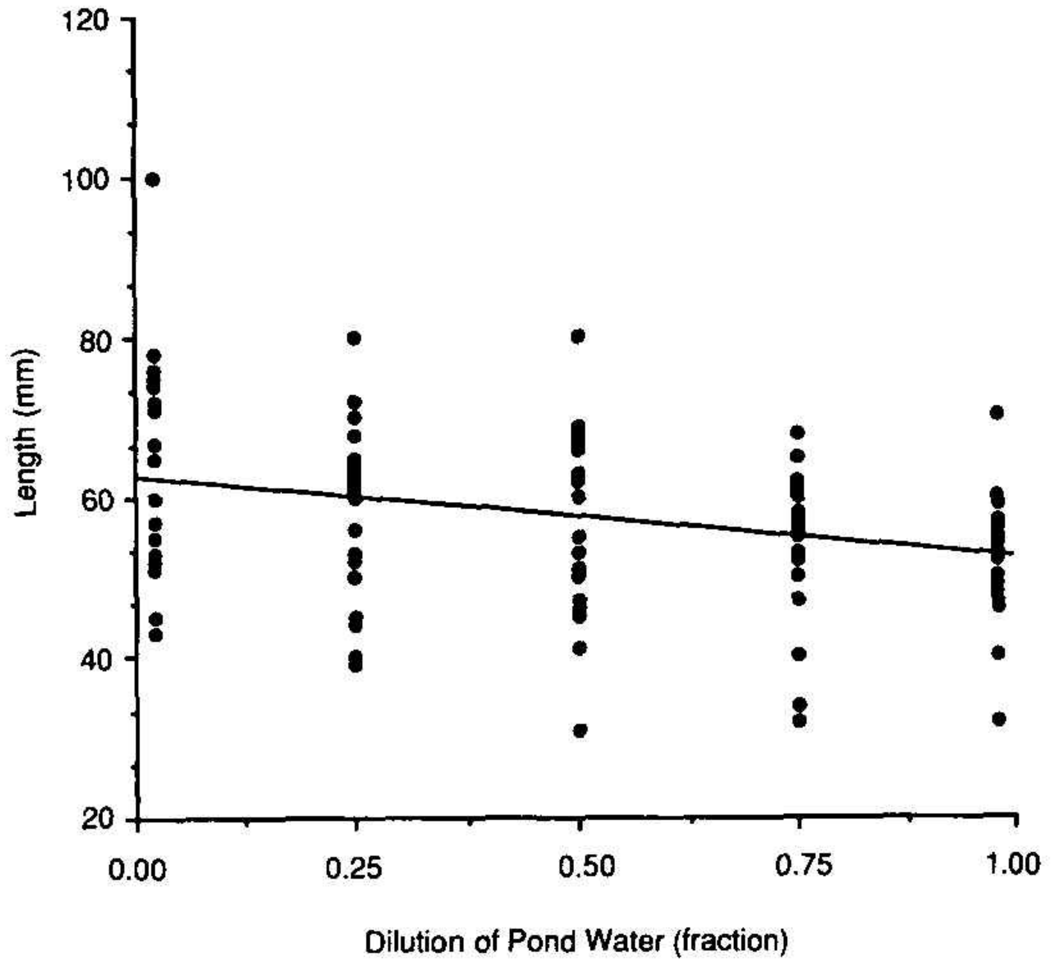


Fig. 4. Total body lengths of larval tiger salamanders (*Ambystoma tigrinum*) grown in serial dilutions of iron–containing water; $y = 62.12 - 10.96\,x$.

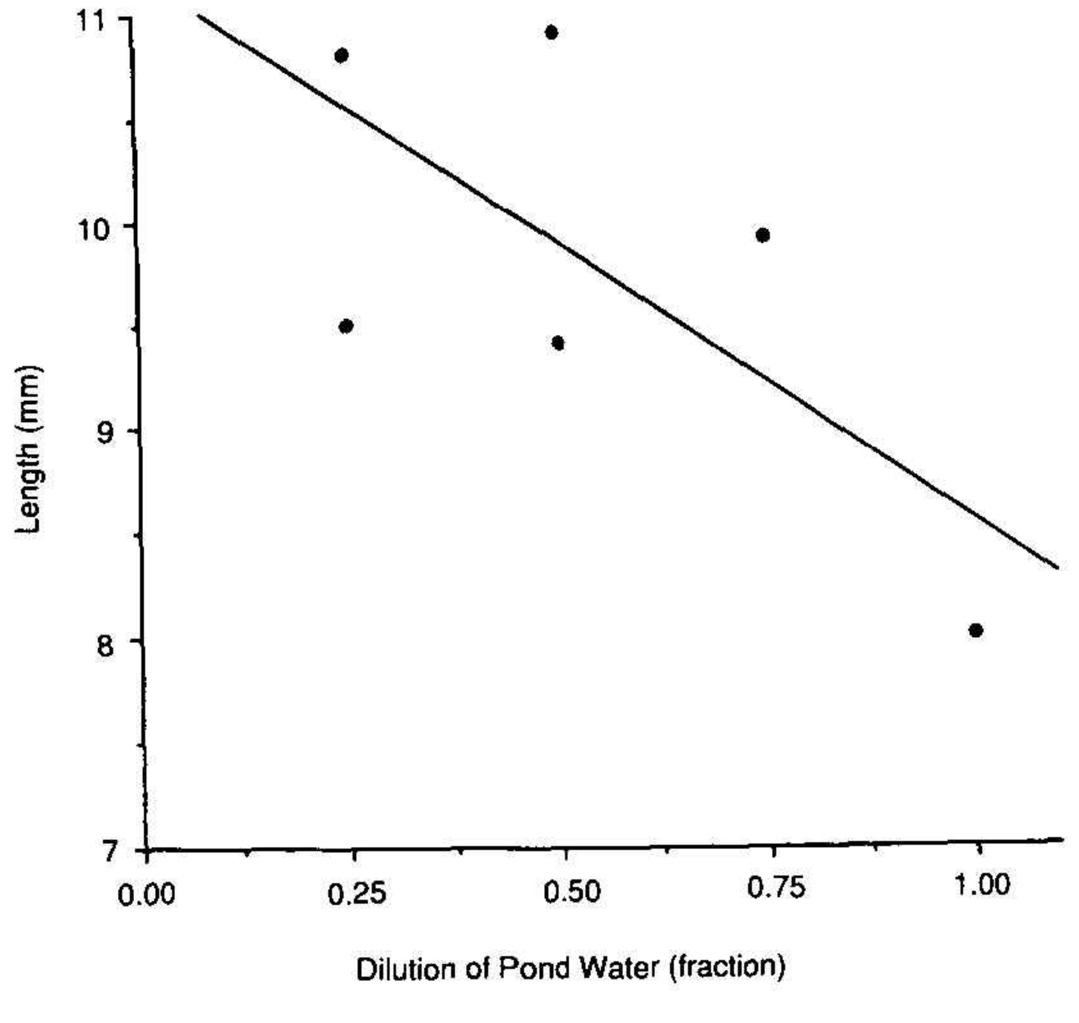


Fig. 5. Total body lengths of larval western toads (*Bufo boreas*) grown in serial dilutions of iron-containing water; $y = 11.22 - 2.68\,x$; $F_{1,6} = 6.78$, $P = 0.04$.

(defined by successful reproduction) of the area began 2 to 3 years after the flood. Several factors may have affected the schedule of recolonization: philopatry (common in anurans); the distance between the alluvial fan and the nearest populations of potential colonizers of the fan; availability of food and cover in the new habitat; and elevated levels of iron in waters of the alluvial fan.

The tendency of frogs and toads to be philopatric (i.e., faithful to particular breeding sites) may have delayed recolonization of the fan. Many species of anuran adults (Tracy and Dole 1969b) and juveniles (Tracy 1971) display a strong tendency to return to breeding or emergence sites. Therefore, colonization by anurans from adjoining areas may have been retarded by a tendency for amphibians to remain where they were. On the other hand, if frogs or toads that were swept away by the flood waters survived, these individuals may have hastened recolonization by being the first to make their way back to the disturbed area. Such homing behavior has been seen in a variety of anuran species (Tracy and Dole 1969a; Goin et al. 1978). However, no data are available to test this hypothesis.

If former residents of the affected area did not recolonize the alluvial fan, then some frogs and toads from surrounding breeding–emergence sites were the colonists. Chorus frogs have moved at least 0.5 km from breeding pools (Spencer 1964), and western toads have moved more than 50 m daily (Campbell 1976). The group of chorus frogs closest to Pond F (the area on the alluvial fan where breeding adults were first observed following the flood; Fig. 1) was that group near Pond C, which was approximately 0.4 km distant when measured between the two nearest shores.

Both chorus frogs and western toads eat a wide variety of invertebrates (Hammerson 1982), and this food began to become available on the fan during the first year following the flood (H. Evans, personal communication). Therefore, availability of food likely did not deter recolonization by anurans.

Chorus frogs breed in marshes, rain pools, bogs, lakes, reservoirs, flooded areas, and other bodies of water lacking a significant current; eggs are typically attached to vegetation in shallow water (Hammerson 1982). Western toads may breed in any body of water lacking a strong current and with gradually descending banks at some point along the margin (Burger and Bragg 1947 *in* Hammerson 1982). Immediately following the flood, many ponds and pools existed on the fan. However, emergent vegetation for cover and attachment of eggs was virtually nonexistent. By 1984, sedges and willows were becoming established on the fan, and by late spring 1985—the first time since the flood that amphibians were observed on the fan—emergent vegetation was well established in Pond F.

Hydroregulation is a process particularly important to amphibians because resistance to cutaneous exchanges of water with the environment is typically low in this group (Spotila and Berman 1976; Tracy 1976, 1982). Therefore, the moist microhabitat provided by low-lying terrestrial vegetation would have been an important microenvironmental characteristic for survival of amphibians in this area (Tracy 1975). Such ground vegetation was lush in 1986 and appeared to be an important microhabitat for juvenile frogs and toads in particular, whose smaller body size accentuates rate of water loss (Tracy 1976).

Tiger salamanders occur in virtually any habitat provided that there is a body of nonflowing water nearby for breeding. They are usually absent from waters inhabited by predatory fishes, bullfrogs, turtles, and crayfish (Hammerson

1982). The stomachs of terrestrial adults are usually empty, but when in water, they eat snails and adult and larval insects; salamander larvae will eat nearly any animal they can catch and swallow, including snails, aquatic insect larvae, tadpoles of the western toad, and amphibian eggs (Hammerson 1982). Because Ponds F and Q on the alluvial fan were nonflowing, harbored no predators, and contained food (especially amphibian eggs and larvae and larval dragonflies), these ponds seemed well suited as a habitat for tiger salamanders. However, we observed no evidence of reproduction by tiger salamanders on the fan during the first 5 years following the flood, despite successful reproduction on the fan by other amphibian species.

One possible explanation for the failure of breeding tiger salamanders to recolonize the disturbed habitat during the first 5 years after the flood is the presence of elevated concentrations of iron in waters of the alluvial fan (Tables 1, 2, 3, and 4; Fig. 2). In our bioassays, survivorship and length of larvae decreased with increasing concentration of iron. Deleterious effects of iron and other heavy metals have been reported for eggs, larvae, and adults of a variety of aquatic vertebrates. For example, all larval western toads in water with concentrations of $FeSO_4$ ranging from 30 to 288 mg/L died within 24 h to 20 days, but all larvae metamorphosed in water with concentrations of $FeSO_4$ ranging from 3 to 20 mg/L (Porter and Hakanson 1976). This nonlethal range of concentrations of iron is similar to the range of concentrations of iron in our bioassays (see Materials and Methods) and in the field (Tables 1, 2, 3, and 4; Fig. 2).

In another study, LC50 values at 96 h for nickel and chromium (heavy metals bracketing iron in the Periodic Table) were 25.3 and 49.3 mg/L, respectively, in larvae of *Bufo melanostictus* (Khangarot and Ray 1987). These values may bracket similar values for iron by anuran larvae of Rocky Mountain National Park. The highest concentration of iron we measured was 30.3 mg/L (Table 4) in an area where no amphibians were observed during our studies.

All eggs of rainbow trout (*Oncorhynchus mykiss*) died in 3 weeks when raised in water with 3.4 mg/L $FeCl_3$ and in 6 weeks at a concentration of 2.2 mg/L; however, fingerlings exposed to 3.4 mg/L showed no adverse effects (Goettl and Davies 1977). Additionally, pH of water decreased with increasing concentration of $FeCl_3$, due to the hydrolysis of this compound to $Fe(OH)_3$ with the release of hydrogen ions. $Fe(OH)_3$ is a yellow-brown precipitate that likely settled on top of eggs and smothered them, while fingerlings were able to swim clear of the precipitate (Goettl and Davies 1977). We observed a yellow-brown precipitate in iron-containing waters of the alluvial fan as well as in iron-containing waters of bioassays conducted in the laboratory. In our studies, the amount of precipitate formed seemed to increase with increasing concentration of iron. Nonetheless, egg mortality of chorus frogs and tiger salamanders did not increase with increasing concentration of iron. Moreover, length of chorus frog larvae increased with increasing concentration of iron in our bioassays (Fig. 3). However, lengths of larvae of tiger salamanders and western toads decreased with increasing concentration of iron (Figs. 4 and 5).

Low pH could be detrimental to amphibians. However, all of our values for pH of waters on and off the fan (Tables 5, 6, and 7) range between 6 and 7. This may be because pH is buffered by $CaCO_3$. The concentration of this compound is consistently highest in iron-containing waters on the fan (Tables 5, 6, and 7).

Reduced glucose levels and sluggishness have been observed in common shiners (*Luxilus cornutus*) exposed to 3 mg/L $Fe(OH)_3$ suspension (Brenner et al. 1976). However, physiological mechanisms causing mortality or changed growth patterns in amphibians reared in waters containing iron (or other heavy metals) remain unknown. Furthermore, our results indicate that species-specific differences will influence responses of amphibians to similar sets of environmental variables.

Differences in species-specific response to high concentrations of iron in water is intriguing. Neither the physiological mechanisms nor the selective advantages (or disadvantages) of these responses are well understood. An ability to predict the outcomes of major abiotic changes—like those represented in the Lawn Lake Flood—requires an increase in our understanding of the physiological responses of amphibian eggs and larvae to unusually high concentrations of minerals that are potentially part of the aquatic environments of these animals. Thus, we suggest that further research into the remarkable differences in species-specific responses of amphibians to water chemistry is an important area of both pure and applied research.

Summary

Three species of amphibians reinvaded the alluvial fan created by the Lawn Lake Flood of 15 July 1982. Of the three, chorus frogs began successful breeding activity in ponds on the fan in 1985, and western toads began successful breeding in 1986. Adult tiger salamanders were occasionally seen on the fan and were known to breed successfully in ponds surrounding the fan, but they did not reproduce in ponds on the fan during the study (1983 to 1987).

Growth of larval chorus frogs was enhanced by iron-rich water common in ponds in the years following the flood. However, larval western toads grown in high concentrations of iron-rich water were shorter than those grown in control water. Tiger salamander larvae were stunted, and mortality was higher, in iron-rich water. Thus, the presence of iron in ponds on the alluvial fan may have prevented reinvasion of tiger salamanders, slowed reinvasion of western toads, and was unrelated to reinvasion of the alluvial fan by chorus frogs.

The most dramatic difference in water chemistry between waters on the alluvial fan and those from nearby rivers was the high concentration of iron. Nevertheless, iron concentrations in ponds on the fan have been declining and should approach ambient levels by the mid-1990's. Thus, we expect that, within the next 5 years, salamander reproduction on the fan may commence.

Acknowledgments

We thank J. Rauscher for helpful discussion and for analysis of water samples; D. Pettus for helpful discussion, assistance in the field, and for providing eggs of *Pseudacris triseriata* for preliminary bioassays; W. Barnes, D. Newman, and J. Zegers for help with bioassays and for assistance in the field; and L. Draski, H. Evans, K. Hammond, K. O'Neill, H. Snell, J. Swift, and C. Tracy for assistance in the field.

Literature Cited

Brenner, F. J., S. Corbett, and R. Shertzer. 1976. Effect of $Fe(OH)_3$ suspension on blood chemistry of the common shiner *Notropus cornutus*. Transactions of the American Fisheries Society 1976 (3):450–455.

Campbell, J. B. 1976. Environmental controls on boreal toad populations in the San Juan Mountains. Pages 289–295 *in* H. W. Steinhoff and J. D. Ives. Ecological impacts of snowpack augmentation in the San Juan Mountains, Colorado. Final Report, San Juan Ecology Project, Colorado State University Publications, Fort Collins.

Goettl, J. P., Jr., and P. H. Davies. 1977. Water pollution studies. Job Progress Report, Federal Aid Project F–33–R–12. Colorado Division of Wildlife. 68 pp.

Goin, C. J., O. B. Goin, and G. R. Zug. 1978. Introduction to herpetology. W. H. Freeman and Company, San Francisco, Calif.

Hammerson, G. A. 1982. Amphibians and reptiles in Colorado. Colorado Division of Wildlife, Denver.

Khangarot, B. S., and P. K. Ray. 1987. Sensitivity of toad tadpoles, *Bufo melanostictus* (Schneider), to heavy metals. Bulletin of Environmental Contamination and Toxicology 38:523–527.

Porter, K. R., and D. E. Hakanson. 1976. Toxicity of mine drainage to embryonic and larval boreal toads. Copeia 1976 (2):327–331.

Spencer, A. W. 1964. The relationship of dispersal and migration to gene flow in the boreal chorus frog. Ph.D. dissertation, Colorado State University, Fort Collins.

Spotila, J. R., and E. Berman. 1976. The role of the skin in the evaporative water loss from amphibians and reptiles. Comparative Biochemistry and Physiology 55A:407–411.

Tracy, C. R. 1971. Evidence for the use of celestial cues by dispersing immature California toads (*Bufo boreas*). Copeia 1971(1): 145–147.

Tracy, C. R. 1975. Water and energy relations of terrestrial amphibians: insights from mechanistic models. Pages 325–346 *in* D. M. Gates and R. Schmerl, editors. Perspectives of biophysical ecology. Springer-Verlag, New York.

Tracy, C. R. 1976. A model of the dynamic exchanges of water and energy between a terrestrial amphibian and its environment. Ecological Monographs 46(3):293–326.

Tracy, C. R. 1982. Biophysical modelling in reptilian physiology and ecology. Pages 275–321 *in* C. Gans and F. H. Pough, editors. Biology of the reptilia, vol. 12. Academic Press, London.

Tracy, C. R., and J. W. Dole. 1969a. Orientation of displaced California toads, *Bufo boreas*, to their breeding sites. Copeia 1969(4):693–700.

Tracy, C. R., and J. W. Dole. 1969b. Evidence of celestial orientation by California toads (*Bufo boreas*) during breeding migration. Bulletin Southern California Academy of Sciences 68(1):10–18.

Changes in Avian Breeding Populations Resulting From the Lawn Lake Flood of 1982

Ronald A. Ryder

Colorado State University
Department of Fishery and Wildlife Biology
Fort Collins, Colorado 80523

Deborah West Bangs

Estes Park Public Schools
Estes Park, Colorado 80517

Abstract. Breeding populations of birds were censused for 5 years (1983–87) on a 12-ha area severely altered by alluvial deposits left by the Lawn Lake Flood of 1982. Birds were censused for 4 years (1984–87) on an upstream 12-ha plot not affected by the flood to serve as a control. After a 1-year decline in the treated (flooded) area, birds increased in total breeding pairs and in total species for 3 years but showed a slight decline during the fifth breeding season. The recovery in numbers was mainly in native sparrows (especially Lincoln sparrows [*Melospiza lincolnii*] and white-crowned sparrows [*Zonotrichia leucophrys*]) nesting in the willows, which showed remarkable recovery and release after the flood. Wilson's warblers (*Wilsonia pusilla*) also showed a good recovery (×2 increase). Avian populations on the control area contained more species and fluctuated mildly year to year, but for the last 3 years had fewer total territorial males than did the treated area.

Introduction

The objectives of this 5-year study were to (1) document breeding populations of birds in an aspen (*Populus tremuloides*)–coniferous forest stand severely altered by alluvial deposits and (2) compare and contrast species and individual numbers of birds nesting in the above stand with an area nearby relatively unaffected by the flood.

Aspen groves are among the richest and most productive of breeding habitats for birds in Colorado, as has been shown by Beidleman (1954), Bottroff (1974), Flack (1976), Hansley (1977, 1978, 1979, 1981), and Winternitz (1980). We hope our findings will provide a better understanding of breeding bird responses to habitat alteration. Results should be applicable to similar disturbances related to road construction, surface mining, and water developments, which might destroy aspen–conifer habitats.

Methods

Two study sites, each 200 × 600 m (12 ha), were established in 1983. Both were mainly on the northern side of the Fall River. One site immediately east of the Roaring River (the treated area) was severely disturbed by the flood. Many trees, both aspen and conifer, were washed away or killed by the flood debris or were killed eventually by the deposits of alluvium (Keigley 1992). Also, eating of aspen by elk has been more severe on the treated area. The untreated or control area upstream from the Roaring River lies on either side of the paved Fall River Road (Figure).

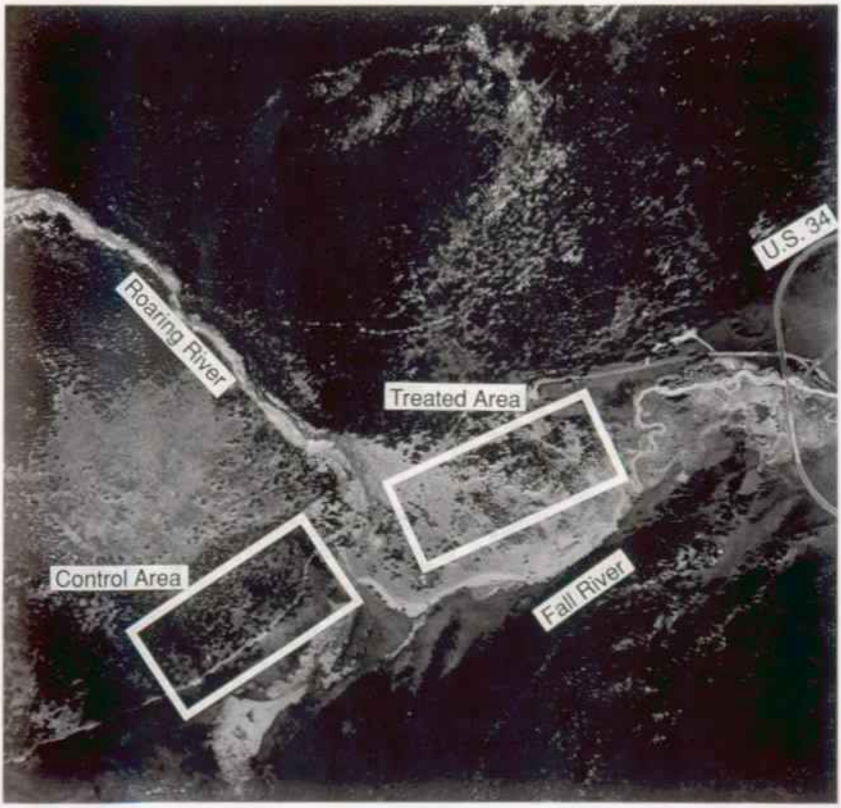


Figure. Aerial photo after the Lawn Lake Flood (1982) showing the bird census areas.

Territorial pairs of nesting birds were noted using the spot-mapping method described by Hall (1946), Williamson (1964), Robbins (1970), Van Velzen (1972), and Ryder (1986).

Results

Bangs conducted 11 counts in 1983, 10 each in 1984 and 1985, and 8 each in 1986 and 1987 on the treated area, while Ryder made 11 counts on the control area in 1984, 10 in 1985, and 8 each in 1986 and 1987 (Table 1). In 1986, Ryder was assisted by J. Ligon. All counts were made in the early morning. In 1984, more species and territorial males were noted in the control area than in the treated area. In 1985, a decline was noted in the control area, whereas both territorial pairs and species increased in the treated area (Table 2).

In 1986, both areas showed increases in species and territorial pairs, but a slight decline occurred in 1987 in the treated area and an increase occurred in the control area. Lincoln sparrows (*Melospiza lincolnii*) continued to increase in the treated area, probably benefitting by the more open conditions resulting from the flood damage as well as an increase in grasses, forbs, and willows. House wrens (*Troglodytes aedon*) were much more abundant in the control plot, no doubt reflecting their preference for more shrub understory. American robins (*Turdus migratorius*), European starlings (*Sturnus vulgaris*), and yellow-rumped warblers (*Dendroica coronata*) continued to be more abundant in the control area. Spotted sandpipers (*Actitis macularia*) increased in the treated area in 1986 but declined slightly in 1987. Common snipe (*Gallinago gallinago*) nested for the first time in the control area in 1986 but just south of the area in 1987. Warbling vireos (*Vireo gilvus*) increased in the control area in 1987 after a 3-year decline. They showed a delayed decrease on the treated area. The parasitic brown-headed cowbird (*Molothrus ater*) increased on both areas in 1986 but showed a slight decline on the treated area in 1987 (Table 2).

Table 1. *Comparisons of avian study plots, 1983–1987, Lawn Lake Flood area, Rocky Mountain National Park, Colorado.*

	Treated area[a]					Control area[b]			
Statistics	1983	1984	1985	1986	1987	1984	1985	1986	1987
Days counted	11	10	10	8	8	11	10	8	8
Total hours	33	31	30	25	25	32	25	23.5	24.5
Total species	19	20	21	24	22	25	22	26	25
Visitors (not included in totals)	10	14	11	9	11	15	20	21	18
Territorial males	71	80	90.5	106	102	96	76.5	79	84

[a] Observer: Bangs.
[b] Observer: 1984,1985 and 1987 = Ryder; 1986 = Ryder–Ligon.

Table 2. *Territorial pairs of birds recorded (V = visitor only).*

	Treated area					Control area			
Species	1983	1984	1985	1986	1987	1984	1985	1986	1987
1. Northern pygmy-owl (*Glaucidium gnoma*)	—	—	—	—	V	—	1.0	—	—
2. Spotted sandpiper (*Actitis macularia*)	2.0	2.0	4.0	5.5	4.5	V	V	V	V
3. Common snipe (*Gallinago gallinago*)	—	—	—	—	—	V	V	1.0	V
4. Broad-tailed hummingbird (*Selasphorus platycercus*)	4.0	6.5	8.0	6.0	4.0	V	V	1.0	1.0
5. Red-naped sapsucker (*Sphyrapicus nuchalis*)	3.0	3.0	4.0	3.0	3.0	3.0	3.0	4.0	2.0
6. Williamson's sapsucker (*Sphyrapicus thyroideus*)	—	—	—	—	—	1.0	V	V	1.0
7. Three-toed woodpecker (*Picoides tridactylus*)	—	—	—	—	—	—	1.0	V	V
8. Northern flicker (*Colaptes auratus*)	1.0	V	1.0	1.0	2.0	1.0	3.5	3.0	2.0
9. Downy woodpecker (*Picoides pubescens*)	—	—	1.0	—	—	—	1.0	V	—
10. Hairy woodpecker (*Picoides villosus*)	—	—	—	V	—	V	V	1.0	V
11. Western wood-pewee (*Contopus sordidulus*)	1.5	3.0	2.0	2.5	4.0	4.0	2.0	1.0	1.0
12. Hammond's flycatcher (*Empidonax hammondii*)	—	—	—	—	—	3.0	2.0	2.0	2.0
13. Cordilleran flycatcher (*Empidonax occidentalis*)	—	—	—	—	1.0	—	—	—	—
14. Dusky flycatcher (*Empidonax oberholseri*)	—	—	—	1.0	2.0	—	—	V	—
15. Tree swallow (*Tachycineta bicolor*)	8.0	12.5	14.0	13.0	12.0	8.5	8.0	13.0	15.0
16. Violet-green swallow (*Tachycineta thalassina*)	—	1.0	3.0	2.0	2.5	V	V	V	V
17. Steller's jay (*Cyanocitta stelleri*)	V	V	—	V	V	V	V	2.0	1.0
18. Black-billed magpie (*Pica pica*)	1.0	0.5	V	V	V	2.0	2.0	1.0	1.0
19. American crow (*Corvus brachyrhynchos*)	—	—	—	—	V	V	V	2.0	1.0
20. Common raven (*Corvus corax*)	—	—	—	—	V	—	—	—	V
21. Mountain chickadee (*Parus gambeli*)	1.0	V	—	—	—	2.0	1.0	1.0	1.0
22. Red-breasted nuthatch (*Sitta canadensis*)	V	—	—	—	—	1.5	2.0	V	1.0

Table 2. *Continued.*

	Treated area					Control area			
Species	1983	1984	1985	1986	1987	1984	1985	1986	1987
23. White-breasted nuthatch (*Sitta carolinensis*)	—	0.5	—	1.0	—	3.0	2.0	1.0	V
24. Pygmy nuthatch (*Sitta pygmaea*)	—	—	—	—	—	V	V	1.0	1.0
25. House wren (*Troglodytes aedon*)	6.5	5.0	4.5	5.0	8.0	14.0	14.0	14.0	13.0
26. Ruby-crowned kinglet (*Regulus calendula*)	2.0	—	V	—	—	3.0	2.0	3.0	3.0
27. Mountain bluebird (*Sialia currucoides*)	1.0	2.5	2.0	2.0	2.0	V	V	—	V
28. American robin (*Turdus migratorius*)	9.0	6.5	5.0	6.0	6.0	12.0	13.0	12.0	16.0
29. European starling (*Sturnus vulgaris*)	—	V	—	V	—	3.0	2.0	3.0	3.0
30. Warbling vireo (*Vireo gilvus*)	6.0	4.0	5.0	6.0	3.0	14.5	6.0	2.0	5.0
31. Yellow warbler (*Dendroica petechia*)	—	V	V	2.0	3.0	—	—	—	V
32. Yellow-rumped warbler (*Dendroica coronata*)	V	1.0	1.0	1.5	1.0	3.5	3.0	3.0	3.0
33. MacGillivray's warbler (*Oporornis tolmiei*)	—	—	—	—	—	1.0	_	V	—
34. Wilson's warbler (*Wilsonia pusilla*)	5.0	9.0	8.0	10.0	10.0	0.5	V	1.0	V
35. Western tanager (*Piranga ludoviciana*)	—	—	—	—	—	1.0	V	V	V
36. Black-headed grosbeak (*Pheucticus melanocephalus*)	—	—	—	—	V	—	—	V	1.0
37. Chipping sparrow (*Spizella passerina*)	V	V	—	—	—	3.0	1.0	1.0	2.0
38. Fox sparrow (*Passerella iliaca*)	—	—	—	1.0	1.0	—	—	—	—
39. Song sparrow (*Melospiza melodia*)	2.0	1.0	3.0	4.0	3.0	V	—	V	V
40. Lincoln's sparrow (*Melospiza lincolnii*)	9.0	8.0	10.5	14.5	15.5	3.0	3.0	4.0	5.0
41. White-crowned sparrow (*Zonotrichia leucophrys*)	4.0	4.0	8.5	11.0	11.0	V	V	V	V
42. Dark-eyed junco (*Junco hyemalis*)	V	V	V	—	—	1.0	2.0	1.5	1.0
43. Red-winged blackbird (*Agelaius phoeniceus*)	V	V	V	V	1.0	V	V	V	V
44. Brown-headed cowbird (*Molothrus ater*)	2.0	3.0	2.0	3.0	2.5	V	V	1.0	1.0

Table 2. *Continued.*

	Treated area					Control area			
Species	1983	1984	1985	1986	1987	1984	1985	1986	1987
45. Cassin's finch (*Carpodacus cassinii*)	V	1.0	—	—	—	1.0	V	V	V
46. Pine siskin (*Carduelis pinus*)	3.0	6.0	3.0	3.0	V	2.0	V	V	1.0
47. Evening grosbeak (*Coccothraustes vespertinus*)	V	V	1.0	1.0	—	4.5	3.0	V	V
48. Green-tailed towhee (*Pipilo chlorurus*)	V	V	V	1.0	—	—	—	0.5	—
Total pairs	71.0	80.0	90.5	106.0	102.0	96.0	76.5	79.0	84.0
Total species	19	20	21	24	22	25	22	26	25

Discussion

For 4 years after the treated area was severely altered by the flood and resulting alluvial deposits, the breeding bird populations showed a steady increase in number of species (19 to 24) and in number of territorial males (71 to 106), but there was a slight decline in both categories (to 22 species and 102 territorial males) in the fifth year. The increases (and leveling off) occurred mostly with the native sparrows, particularly the Lincoln sparrow. In contrast, the control area showed erratic fluctuations in avian populations, probably not related to the flood. Total species observed were greater in the control area (Table 1), but the treated area had higher densities after a low immediately following the flood. The erratic fluctuations in the control area were believed to be related to a severe outbreak of spruce budworm, which defoliated many conifers in 1985 and 1986. By 1987, many Douglas-fir (*Pseudotsuga menziesii*) in the control area were dead but not yet soft snags, which eventually may provide more homes for cavity-nesters.

In brief, ground- and shrub-nesting passerines seemed to recover rapidly following the flood, especially in the new growth of forbs and willows released by the removal of larger aspen and conifers.

Literature Cited

Beidleman, R. G. 1954. The cottonwood river-bottom community as a vertebrate habitat. Ph.D. thesis, University of Colorado, Boulder.

Bottroff, R. L. 1974. Cottonwood habitat for birds in Colorado. American Birds 28:975–979.

Flack, J. A. D. 1976. Bird populations of aspen forest in western North America. Ornithology Monograph 19. 97 pp.

Hall, G. A. 1946. Breeding-bird censuses—why and how. Audubon Field Notes 18:413–416.

Hansley, P. L. 1977. Breeding bird census: open aspen grove-scattered conifers. American Birds 31:72–73.

Hansley, P. L. 1978. Breeding bird census: open aspen grove-scattered conifers. American Birds 32:87.

Hansley, P. L. 1979. Breeding bird census: open aspen grove-scattered conifers. American Birds 33:74.

Hansley, P. L. 1981. Breeding bird census: open aspen grove-scattered conifers. American Birds 35:88.

Robbins, C. S. 1970. Recommendations for an international standard for a mapping method in bird census work. Audubon Field Notes 24:723–726.

Ryder, R. A. 1986. Songbirds. Pages 291–312 *in* A. Y. Cooperrider, R. J. Boyd, and H. R. Stuart, editors. Inventory and monitoring of wildlife habitat. U.S. Bureau of Land Management. 858 pp.

Van Velzen, W. T. 1972. Breeding-bird census instructions. American Birds 26:927–931.

Williamson, K. 1964. Bird census work in woodland. Bird Study 11:1–22.

Winternitz, B. L. 1980. Birds in aspen. Pages 247–257 *in* R. M. DeGraaf, technical coordinator. Workshop Proceedings: Management of Forests and Grasslands for Nongame Birds, U.S. Forest Service, General Technical Report INT-86. 535 pp.

Effects of the Lawn Lake Flood on Local Distribution and Abundance of Mammals

David M. Armstrong

University of Colorado
University Museum and Natural Science Program
Campus Box 218
Boulder, Colorado 80309

Abstract. The Lawn Lake Flood in Rocky Mountain National Park provided a unique opportunity for longitudinal and comparative research on ecological change in mammalian assemblages following disturbance. During four seasons (1984–87), six transects were studied on or near the disturbed area, with an undisturbed (control) and a disturbed (treatment) condition for each of three habitat types—willow flats, montane woodlands, and subalpine forest. Predictions were that disturbed sites (compared to adjacent, undisturbed communities) would show (1) lower richness and evenness of species; (2) an age structure of small mammals biased toward younger classes; (3) smaller populations or biomass of small mammals; (4) a bias toward euryoecious species; and (5) less use by larger mammals. Variation in use of transects by mammals from year to year made trends obscure or nonexistent. However, extrinsic factors, either biotic or abiotic, probably are important influences on numbers of small mammals, and longer-term studies—on a scale of decades rather than merely months or years—are essential to understanding secondary succession following such a profound disturbance.

Introduction

Jarrett and Costa (1986) detailed and modeled the hydrology of the flood event, probably the largest flood—therefore one of the most profound ecological disturbances—in the affected drainages since glacial times. Reviewing relevant literature and emphasizing the importance of long-term studies to document ecological succession, Armstrong (1984, 1985a, 1985b, 1986b, 1988) reported interim results of the first years of a 4-year investigation of the local distribution of mammals in the area of Rocky Mountain National Park most strongly influenced by the flood.

Studies of mammals within Rocky Mountain National Park have been surprisingly few (see Armstrong 1975 and 1987 [for bibliographies]; Telleen 1978; Carey et al. 1980; Bowen et al. 1981; McLean et al. 1981). However, the ecological distribution of mammals of the southern Rocky Mountains is well known. Data for situations comparable to that in Rocky Mountain National

Park are available from Grand County (Vaughan 1969; Armstrong 1977), Larimer County (Spencer and Pettus 1966), Boulder County (Quick 1964; Merritt and Merritt 1978a, 1978b, 1980; Stinson 1978), Gilpin County (Williams 1955), Clear Creek County (Trippe *in* Coues 1874), and Park County (Brewer 1871; Allen 1874; Blake and Blake 1969), all in Colorado. Cary (1911) studied the ecological distribution of mammals statewide in terms of Merriam's classical concept of life zones, and Warren (1910, 1942, and elsewhere—see Armstrong 1986a for complete bibliography) provided a wealth of anecdotal information. Lechleitner (1969) provided a thorough, nontechnical account of the biology of Colorado mammals, and Armstrong (1972) documented and analyzed patterns of ecological and geographic distribution. Armstrong (1975, 1987) provided semitechnical accounts of mammals of Rocky Mountain National Park.

Despite a wealth of descriptive information on ecological distribution of mammals in the region, studies to date have been done over short periods. Except for long-term studies of beaver (*Castor canadensis*) colonies (Neff 1959), virtually no direct knowledge exists of mammals during ecological succession.

Ecological succession is changes in biotic communities over time. Odum (1969) provided a summary of the classical concept in modern terms and characterized the process as orderly and reasonably directional (and therefore predictable), resulting from change in the physical environment by the biotic community and culminating in a stabilized ecosystem.

For the animal component of the biotic community, Odum (1969) proposed the following features as descriptive of early successional stages (such as those represented by areas inundated by the Lawn Lake Flood): food chains, linear; species richness, low; species evenness, low; niche specialization, broad; size of organisms, small; life cycles, short; growth rates, rapid ("*r*-selected" species); selection pressure for higher production (quantity rather than quality); stability, poor; entropy, high; and information content, low. Although not all of these descriptions were evaluated formally, they generally did characterize the mammalian assemblage of the Lawn Lake Flood site.

Emlen (1973) provided a succinct evolutionary synopsis of succession. Horn (1976) argued in a brief, critical, and mostly cogent review that succession is a replacement of individuals of species and not a transcendent, emergent property of communities. This observation is a truism that is recalled too seldom. Obviously, homeostatic cells and individuals have the genetic information—the "know-how"—for survival and reproduction on a particular site. Causal processes and mechanisms at the level of individual organisms do seem, however, to predict broad patterns at the level of biotic communities and ecosystems. Typically, animal succession tracks plant succession, because the vegetation integrates the physical environment into resources (food, cover) exploitable by animals.

Succession can be understood either by pursuing longitudinal studies of a single site over ecological time (usually years to decades) or by comparatively studying several sites presumed or known to be at different stages of recovery from disturbance. The Lawn Lake Flood created an opportunity for both kinds of studies. This paper provides a baseline for longitudinal studies and reports results of a brief comparative study of response of mammals to disturbance. Comparisons involve disturbed biotic communities (treated) and adjacent, relatively undisturbed systems (control) presumably representing preflood conditions.

The general purpose of the studies was to test several predictions derived from ecological theory (or conventional wisdom) relevant to successional change following profound disruption of ecosystems. Those predictions are as follows: compared to adjacent, undisturbed communities, profoundly disturbed sites should show (1) lower species diversity (both species richness and species evenness); (2) age structure in small mammals biased toward younger age classes; (3) lower biomass of small mammals and probably lower populations of species other than the most euryoecious; (4) a bias toward euryoecious species, such as deer mice (*Peromyscus maniculatus*); and (5) less use by large mammals (because productivity is negligible or low, usable cover is minimal, and transit is made difficult by flood-deposited obstacles—such as downed timber and boulders).

Study Area and Methods

A dam failure at Lawn Lake—an irrigation reservoir in Rocky Mountain National Park, Larimer County, Colorado—released a torrent that deposited a 17.1-ha debris fan at the confluence of the Roaring and Fall rivers (McCutchen and Stevens 1984; Jarrett and Costa 1986). The debris fan and immediately adjacent areas (S 1/2 sec. 12, T. 5 N, R. 74 W, ca. 2,620 m) were the primary study sites.

Small mammals were studied on a series of six pairs of double transects, each single transect consisting of 25 stations, set at 5-m intervals. Paired transects were situated 10 m apart, and their ends were marked temporarily with wooden stakes. Each station was set with a large (75 x 75 x 245 mm) or small (45 x 60 x 170 mm) Sherman live trap. Each pair of parallel transects totalled 240 m long. Assuming that each trap samples a roughly circular area with a radius of 5 m, such an array of trapping stations samples an area of roughly 0.25 ha. Traps were run continuously for four days without prebaiting.

Traps were checked at least four times daily (early and late morning, mid-afternoon, and early evening). Under sunny conditions (when trap deaths can occur within minutes), or when heavy tourist traffic and vandalism disturbed grids, traps were checked almost continually. Transects were monitored from 30 July to 4 August 1984, 17 to 21 August 1985, 12 to 16 August 1986, and 17 to 21 August 1987—a total of 3,700 trapnights. (In 1984, two transects each were run for 5 nights because vandalism influenced the rate of capture on one of the previous days.) For greater detail on field methods by year, see Armstrong (1984, 1985b, 1986b).

All mammals captured were identified to species; sexed; weighed to the nearest 0.1 g on a Pesola spring scale; assigned a relative age (juvenile, subadult, adult) on the basis of body size and texture and color of pelage; marked (by toe-clipping); and released. Note was made of a simple descriptor of microhabitat at the site of each capture.

The presence and relative abundance of larger mammals—and those, such as the northern pocket gopher (*Thomomys talpoides*), that are not susceptible to capture in standard live traps—were assessed by counts of individual animals, and their certain sign (pellet groups, tracks, gopher mounds) was sampled on cruises of the same transects for small mammals. Such field work was conducted approximately bimonthly, as weather conditions permitted tracking, on 21 separate trips during the 42-month study. All statistical routines were performed with an IBM-PC using "STAT1" nonparametric statistical programs from H & H Software (Emporia, Kansas). Rohlf and Sokal (1969) provided the statistical tables.

Here, I use *treatment* to refer to sites disturbed by the Lawn Lake Flood and *control* to indicate sites undisturbed by the flood. Such "undisturbed" sites have, of course, been disturbed by influences biotic and physical, anthropogenic and otherwise, over the past several millenia.

Six transects were run each year, a control and a treatment transect for each of three habitat types: willow (*Salix* sp.) stand over meadow (C-1) and willow stand over flood-scoured mud flat (T-1); mixed coniferous forest on steep slope (C-2) and boulder field (T-2); and mixed conifer–aspen (*Populus tremuloides*) forest (C-3) and alluvial gravel fan (T-3). Table 1 describes vegetation of the transects in terms of the following coverage classes: 1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–100%. A brief qualitative description of each transect (as of 1986) follows:

Transect C-1—Willow stand over meadow. Mosaic of habitat types including willow, aspen, and meadow situations on fairly flat terrain; area inter-

Table 1. *Mean coverage of transects on the Lawn Lake Flood study area, August 1986.*

	Cover[a]				
Transect	Grass	Herbs	Solid rock	Shrub canopy	Tree canopy
T-1 (Scoured willows)	3.0	0.2	2.3	2.3	0.0
C-1 (Willows)	2.9	1.5	1.2	1.4	0.8
T-2 (Boulder field)	0.2	0.1	5.0	0.0	0.3
C-2 (Mixed conifers)	1.7	1.4	3.9	0.6	1.3
T-3 (Gravel fan)	1.1	0.2	4.7	0.7	0.1
C-3 (Conifer–aspen)	3.0	2.6	2.1	0.3	1.4

[a] Recorded by coverage class: 1 = 0–5%; 2 = 5–25%; 3 = 25–50%; 4 = 50–75%; 5 = 75–100%.

sected by inactive, revegetated beaver canals; cover of grasses and open woodland or willow stands nearly complete; soils mostly sandy loams.

Transect T-1—Willow stand over flood-scoured mud flat. Terrain virtually the same as C-1, but ground cover of herbs and grasses less; shrub synusia, however, intact, composed exclusively of willows; area dissected by beaver canals, apparently inactive; soils not present, substrate unaltered sand or silt, virtually devoid of organic matter or pedologic structure.

Transect C-2—Mixed coniferous forest on steep slope. Mesic, mixed coniferous forest of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and Engelmann spruce (*Picea engelmannii*) on steep, south-facing slope; canopy cover of trees sporadic, less dense lower on slope than higher; slope broken by numerous rock outcrops, seeps, and springs; ground cover extensive, mostly of herbs, except beneath trees where coverage was near zero; shrub synusia predominated by *Ribes*, well developed around rocks; Rocky Mountain maple (*Acer glabrum*) present in moist areas; soils rocky loams.

Transect T-2—Boulder field. Gently sloping area covered before flood with mixed coniferous forest; trees mostly removed by flood, except for occasional dead stems, now essentially no vegetation on site; cover of boulders (to several cubic meters) through cobbles; substrate between boulders mostly coarse sand and some gravel, devoid of organic matter; (250-cc samples of substrate were taken at each of 50 trap stations and covered with 500 mL water; other than copious pollen, flotation yielded one bark beetle, one Douglas-fir seed, and a modest number of conifer needles and fragments); additional cover provided by occasional fallen timber.

Transect C-3—Mixed conifer–aspen forest. Open stand of ponderosa pine, aspen, and Douglas-fir on generally flat site; tree canopy coverage about 20% (mean cover class, 1.4); understory of forbs and grasses nearly complete except on active pocket gopher mounds; some fallen timber and a few exposed rocks; low shrubs (kinnikinnic [*Arctostaphylos uva-ursi*]; common juniper [*Juniperus communis*]) overtop herb layer in places.

Transect T-3—Alluvial gravel fan. Gentle slope below boulder field in area occupied by mixed forest of aspen and conifers before flood; site marked by widely scattered boulders, to 1 m across, on generally sandy to gravelly substrate; occasional standing dead aspens and ponderosa pines, numerous projecting logs, and piles of flotsam including logs to 40 cm in diameter; other than seedling willows, living vegetation negligible except along bottom of transect where some mature willows and grasses remain.

Results and Discussion

During the study, 22 species of mammals were seen—about 37% of the nonvolant species to be expected in the habitats represented in the study area and about 33% of the nonvolant mammals present today in Rocky Mountain National Park (Armstrong 1987). Table 2 is a qualitative summary of mam-

Table 2. *Mammals observed (as individuals or certain sign) on transects on the Lawn Lake Flood study area, 1984–1987.*

	Transect					
Species	C-1	T-1	C-2	T-2	C-3	T-3
Montane shrew (*Sorex monticolus*)	X	X	X	—	X	—
Nuttall's cottontail (*Sylvilagus nuttallii*)	–	X	X	X	X	X
Snowshoe hare (*Lepus americanus*)	–	X	—	—	—	—
Least chipmunk (*Tamias minimus*)	X	X	X	—	—	—
Uinta chipmunk (*Tamias umbrinus*)	X	—	X	—	X	—
Wyoming ground squirrel (*Spermophilus elegans*)	X	—	—	—	—	—
Golden-mantled ground squirrel (*Spermophilus lateralis*)	—	X	X	X	X	—
Abert's squirrel (*Sciurus aberti*)	—	—	X	—	X	—
Chickaree or red squirrel (*Tamiasciurus hudsonicus*)	—	—	X	—	X	—
Northern pocket gopher (*Thomomys talpoides*)	X	—	X	—	X	—
Beaver (*Castor canadensis*)	X	X	—	—	—	—
Deer mouse (*Peromyscus maniculatus*)	X	X	X	X	X	X
Montane vole (*Microtus montanus*)	X	X	—	—	—	—
Long-tailed vole (*Microtus longicaudus*)	X	—	—	—	X	X
Western jumping mouse (*Zapus princeps*)	X	X	—	—	—	—
Porcupine (*Erethizon dorsatum*)	—	—	—	—	X	—
Coyote (*Canis latrans*)	X	X	—	X	X	X
Marten (*Martes americana*)	—	—	X	—	X	—
Long-tailed weasel (*Mustela frenata*)	X	X	—	X	—	X
Wapiti or elk (*Cervus elaphus*)	X	X	X	X	X	X
Mule deer (*Odocoileus hemionus*)	—	X	X	X	—	X
Bighorn sheep (*Ovis canadensis*)	—	—	X	—	—	—
Totals (species richness)	13	13	13	9	14	7

mals observed (as individuals or as their certain, fresh sign) on the six transects, and Tables 3 and 4 present detailed quantitative data and summary data by transect by year.

Table 4 compares data year by year with the nonparametric Kruskal–Wallis statistic, *H*. *H* is indicated for each comparison; none is statistically significant. Treatment and control transects were compared year by year on each of the variables in Table 4 using the nonparametric Mann–Whitney *U* test; none of the values was statistically significant. Finally, all disturbed transects were pooled and compared with all control transects pooled by the Mann–Whitney *U* test; none of the values was statistically significant. Nonetheless, patterns of interest were found in the data.

Table 3. *Number of individuals of species of small mammals captured on each transect on Lawn Lake Flood study area.*

		Transect						
Species	Year	T-1	C-1	T-2	C-2	T-3	C-3	**Total**
Montane shrew	1984	2.0	3.0	—	1.0	—	3.0	9.0
(*Sorex monticolus*)	1985	—	—	—	—	—	—	—
	1986	2.0	—	—	—	—	—	2.0
	1987	7.0	1.0	1.0	—	—	—	9.0
	Average	2.7	1.0	0.2	0.2	—	0.7	5.0
Least chipmunk	1984	1.0	—	—	1.0	—	1.0	3.0
(*Tamias minimus*)	1985	—	—	—	—	—	—	—
	1986	—	1.0	—	1.0	—	1.0	3.0
	1987	—	5.0	3.0	10.0	—	—	18.0
	Average	0.2	1.5	0.7	3.0	—	0.5	6.0
Uinta chipmunk	1984	—	—	—	1.0	—	—	1.0
(*Tamias umbrinus*)	1985	—	—	—	—	—	—	—
	1986	—	—	—	2.0	—	—	2.0
	1987	—	—	—	—	—	—	—
	Average	—	—	—	0.7	—	—	0.7
Wyoming ground squirrel	1984	—	4.0	—	—	—	—	4.0
(*Spermophilus elegans*)	1985	—	—	—	—	—	—	—
	1986	—	—	—	—	—	—	—
	1987	—	—	—	—	—	—	—
	Average	—	—	1.0	—	—	—	1.0
Golden-mantled ground	1984	—	—	—	—	—	—	—
squirrel	1985	—	—	3.0	1.0	—	—	4.0
(*Spermophilus lateralis*)	1986	—	—	2.0	6.0	—	2.0	10.0
	1987	—	—	9.0	4.0	—	—	13.0
	Average	—	—	3.5	2.7	—	0.5	6.7

Table 3. *Continued.*

Species	Year	T-1	C-1	T-2	C-2	T-3	C-3	**Total**
Deer mouse (*Peromyscus maniculatus*)	1984	15.0	16.0	24.0	25.0	18.0	23.0	121.0
	1985	7.0	7.0	14.0	7.0	5.0	3.0	44.0
	1986	11.0	8.0	18.0	14.0	14.0	17.0	82.0
	1987	4.0	13.0	50.0	18.0	11.0	11.0	107.0
	Average	8.5	11.0	26.5	16.0	12.0	13.5	88.5
Montane vole (*Microtus montanus*)	1984	2.0	1.0	—	—	—	—	3.0
	1985	—	—	—	—	—	—	—
	1986	—	—	—	—	—	—	—
	1987	—	1.0	—	—	—	1.0	2.0
	Average	0.5	0.5	—	—	—	0.2	1.2
Long-tailed vole (*Microtus longicaudus*)	1984	1.0	4.0	—	—	4.0	11.0	20.0
	1985	2.0	—	—	—	—	—	2.0
	1986	—	—	—	—	—	1.0	1.0
	1987	—	1.0	—	—	—	1.0	2.0
	Average	0.7	1.2	—	—	1.0	3.2	6.2
Western jumping mouse (*Zapus princeps*)	1984	3.0	—	—	—	—	—	3.0
	1985	4.0	—	—	—	—	—	4.0
	1986	—	1.0	—	—	—	—	1.0
	1987	1.0	—	—	—	—	—	1.0
	Average	2.0	0.2	—	—	—	—	2.2
Total	1984	24.0	28.0	24.0	28.0	22.0	37.0	163.0
	1985	13.0	7.0	17.0	8.0	5.0	3.0	53.0
	1986	13.0	10.0	20.0	23.0	18.0	21.0	110.0
	1987	12.0	21.0	63.0	32.0	11.0	13.0	152.0
	Average	15.5	16.5	31.0	22.8	14.0	18.5	119.5

Table 4. *Comparative summary of trapping results on the Lawn Lake Flood study area, 1984–1987, with 4-year averages.*[a]

		Transect						
Variable	Year	T-1	C-1	T-2	C-2	T-3	C-3	Average
		Species captured						
	1984	6.0	5.0	1.0	4.0	2.0	4.0	3.7
	1985	3.0	1.0	2.0	2.0	1.0	1.0	1.8
	1986	2.0	2.0	2.0	4.0	1.0	4.0	2.5
	1987	3.0	5.0	4.0	3.0	1.0	3.0	3.2
	Average	3.4	3.2	2.3	3.2	1.2	3.0	2.8

H = 7.4104 n. s.

Table 4. *Continued.*

		Transect						
Variable	Year	T-1	C-1	T-2	C-2	T-3	C-3	Average
Different individuals captured								
	1984	24.0	28.0	24.0	28.0	22.0	37.0	27.2
	1985	13.0	7.0	17.0	6.0	5.0	3.0	9.0
	1986	13.0	10.0	20.0	23.0	14.0	21.0	16.8
	1987	12.0	21.0	63.0	32.0	11.0	13.0	25.3
	Average	15.5	16.5	31.0	22.2	13.0	18.5	19.58
H = 3.8718 n. s.								
Recaptures								
	1984	15.0	20.0	23.0	23.0	22.0	21.0	21.0
	1985	1.0	1.0	18.0	8.0	7.0	1.0	5.7
	1986	2.0	6.0	18.0	21.0	10.0	9.0	11.0
	1987	1.0	9.0	29.0	17.0	5.0	10.0	11.8
	Average	4.8	9.0	22.0	17.2	11.0	10.2	12.38
H = 9.9524 n. s.								
Total captures								
	1984	39.0	48.0	48.0	52.0	44.0	58.0	48.2
	1985	14.0	8.0	35.0	14.0	12.0	4.0	14.7
	1986	15.0	16.0	38.0	44.0	24.0	30.0	27.8
	1987	13.0	30.0	92.0	49.0	16.0	23.0	37.2
	Average	20.2	25.5	53.2	39.8	24.0	28.8	31.98
H = 6.1985 n. s.								
***H'* Diversity**								
	1984	0.535	0.536	0.000	0.199	0.206	0.410	0.420
	1985	1.420	0.000	0.673	0.544	0.000	0.000	0.879
	1986	0.619	0.922	0.469	1.455	0.000	0.988	0.742
	1987	1.281	1.549	0.969	1.366	0.000	0.773	0.990
	Average	0.964	0.677	0.813	0.891	0.052	0.543	0.758
H = 7.8088 n. s.								
Simpson's *D*								
	1984	0.591	0.643	0.000	0.206	0.312	0.536	0.432
	1985	0.704	0.000	0.309	0.250	0.000	0.000	0.421
	1986	0.272	0.200	0.189	0.575	0.000	0.348	0.264
	1987	0.591	0.581	0.353	0.589	0.000	0.295	0.402
	Average	0.540	0.356	0.213	0.405	0.078	0.295	0.380
H = 8.1882 n. s.								
Total biomass (grams)[b]								
	1984	251.0	377.0	315.0	397.0	286.0	585.0	368.5
	1985	141.0	120.0	176.0	106.0	67.0	57.0	127.8
	1986	144.0	173.0	233.0	362.0	186.0	284.0	230.3
	1987	126.0	178.0	889.0	673.0	178.0	214.0	376.3
	Average	190.5	212.0	403.0	384.5	179.3	285.0	275.72
H = 3.6341 n.s.								

Table 4. *Continued.*

		Transect						
Variable	Year	T-1	C-1	T-2	C-2	T-3	C-3	Average
	Total biomass accounted for by *Peromyscus maniculatus*							
	1984	68.5	67.6	100.0	85.9	76.2	57.5	75.9
	1985	44.2	100.0	100.0	100.0	100.0	100.0	90.7
	1986	91.7	68.2	100.0	51.9	100.0	73.6	80.9
	1987	57.1	100.0	77.7	26.6	100.0	66.8	71.4
	Average	65.48	83.95	94.42	66.10	94.05	74.48	79.72
H = 8.2412 n.s.								
	Individuals due to *Peromyscus maniculatus*							
	1984	62.5	57.1	100.0	89.3	81.8	62.2	74.2
	1985	53.8	100.0	82.4	87.5	100.0	100.0	83.0
	1986	84.6	80.0	90.0	60.9	77.8	81.0	74.5
	1987	33.3	61.9	78.1	56.2	100.0	91.6	70.0
	Average	58.55	74.75	87.62	73.48	89.90	83.70	75.48
H = 6.3452 n.s.								

[a] Critical value of H (Kruskal–Wallis statistic) is 11.070; df = 5.

[b] Figure does not include biomass of *Spermophilus elegans* or *Spermophilus lateralis*, neither of which is sampled consistently with Sherman live traps of sizes used.

Species Diversity

Species are not distributed randomly in environments. Populations have resource needs, limits of tolerance, and symbiotic interactions. Thus, various parameters of populations and communities vary over space and time. One prediction was that species diversity would be greater on undisturbed sites than on disturbed sites. Species diversity within an assemblage or community has two distinctive components: species richness and species evenness. Species richness (Table 2) on the transects ranged from 7 to 14. Probably due to small sample sizes, a Kruskal–Wallis test showed no significant difference among transects in species richness ($H = 5.0000$). However, mean species evenness on the control transects was 12.6; on disturbed transects it was 9.7. One disturbed transect (T-1—scoured willows) had species richness as high as the corresponding control, whereas the other two disturbed transects showed lower species richness than their undisturbed controls. In fact, the shrub synusia of the flood-scoured willow stand was mostly intact, and even ground cover (grasses and forbs) was present in patches. The effect of the flood on this transect was less profound than elsewhere in the study area.

In Table 4, note entries for H' diversity (the Shannon–Weiner index, calculated after the method of Lloyd et al. 1968, using logarithms base 2, the resulting unit of diversity therefore being expressed in bits per individual) and for Simpson's Diversity (D; calculated after Poole 1974). Both indices measure species evenness. Spearman's rank correlation coefficient (r_s) between the two indices was 0.713, a highly significant correlation, as would be expected. Correlation (r_s) between number of individuals captured and percentage of individuals captured that were deer mice was –0.4273, also significant ($P < 0.05$). In other words, the fewer individuals caught, the greater the likelihood that those individuals would be the ubiquitous deer mouse.

Evenness diversity varies strongly from year to year within transects as well as between transects. No orderly change was found in diversity with time (and probably none should have been expected in only a 4-year study). The overall pattern of H' follows: T-1 > C-2 > T-2 > average > C-1 > C-3 >> T-3. The pattern of D was similar, as follows: T-1 > C-2 > average > C-1 > C-3 > T-2 >> T-3. By the Kruskal–Wallis test, the H statistic was 7.8088 for H' diversity and 8.1881 for Simpson's D; neither was statistically significant. No particular pattern was found in the diversity indices. Average H' on disturbed transects was 0.609 and on controls was 0.703; average D on disturbed transects was 0.277 and on controls was 0.352. Highest evenness diversity was seen on C-1 (1987), C-2 (1986), and T-1 (1985); lowest values (no diversity) were calculated for several transects on which *Peromyscus maniculatus* was the only species captured.

Relative Abundance

All animals captured were marked and released, but frequent vandalism of traplines precluded using even regression-based removal estimates of populations. Nonetheless, trapping success provides a rough index of relative abundance.

One probably would expect higher populations on undisturbed transects than on disturbed transects, if only because habitats are more diverse and primary production is greater. However, strong variation from year to year obscured any pattern of variation among transects in total number of different individuals captured (Table 4). As a 4-year average, numbers vary minimally (Kruskal–Wallis $H = 3.8718$, not significant). Also, no significant difference was found among transects in the number of recaptures ($H = 9.9524$) or the total number of captures ($H = 6.1985$).

Peromyscus maniculatus is a notoriously euryoecious species (Baker 1968), especially in the absence of competitors (Armstrong 1979). Disturbed transects did yield more captures of deer mice than did undisturbed transects (average: 47/year versus 40/year), but the difference was not statistically significant.

Overall trapping success (4-year grand mean) was 9.9%. Percentage trapping success (i.e., numbers per 100 trapnights) varied among species as follows: *Sorex monticolus*, 0.4%; *Tamias minimus*, 0.5%; *Tamias umbrinus*, 0.05%; *Spermophilus elegans*, 0.06%; *Spermophilus lateralis*, 0.5%; *Peromyscus maniculatus*, 7.3%; *Microtus montanus*, 0.1%; and *Microtus longicaudus*, 0.5%. Percentage success also varied from year to year: 1984, 13.5%; 1985, 4.2%; 1986, 8.4%; and 1987, 12.7%.

The most extensive studies to date of small mammals in Rocky Mountain National Park were conducted in the mid-1970's to investigate the ecology of sylvatic Colorado tick fever. Bowen et al. (1981) and McLean et al. (1981)

reported on studies (involving 13,672 trapnights) conducted over a wide range of conditions in the park, at elevations ranging from 2,440 m (Moraine Park) to 3,500 m (tundra on Trail Ridge). Carey et al. (1980) reported on related studies at Moraine Park and Beaver Meadows, involving 46,000 trapnights. None of those studies reported captures by habitat type. However, the following shows capture success of selected species (the first number was calculated from data from Bowen et al. [1981], and the second number was calculated from data from Carey et al. [1980]): *Tamias minimus*, 1.2%, 1.5%; *Tamias umbrinus*, 1.0%, 0.1%; *Spermophilus elegans*, 2.0%, 2.5%; *Spermophilus lateralis*, 2.2%, 3.0%; and *Peromyscus maniculatus*, about 6.3%, 8.4% (assuming that only Sherman live traps captured deer mice). These findings are roughly comparable to this study.

Age Distribution

Another prediction was that small mammals on disturbed sites would show populations biased toward younger age classes. Disturbed sites could provide a dispersal sink for young animals. This phenomenon was suggested strongly by data from 1984, when young deer mice were so numerous on the boulder field (T-2) that they were captured both day and night (Armstrong 1984). During the study, only one species (*P. maniculatus*) was taken with sufficient frequency to evaluate this prediction. Table 5 indicates age and sex distribu-

Table 5. *Age and sex distribution of* Peromyscus maniculatus *on each of six transects on the Lawn Lake Flood study area in 1984, 1985, and 1986.*

		Transect						
Gender and age	Year	T-1	C-1	T-2	C-2	T-3	C-3	**Totals**(%)
Male—adult	1984	2.0	4.0	3.0	3.0	3.0	5.0	18.2
	1985	2.0	2.0	2.0	1.0	1.0	2.0	26.3
	1986	1.0	5.0	5.0	2.0	1.0	5.0	27.1
	3-year mean	1.7	3.7	3.3	2.0	1.7	4.0	23.9
Male—subadult	1984	3.0	0.0	2.0	6.0	4.0	3.0	16.4
	1985	1.0	0.0	2.0	1.0	1.0	0.0	13.2
	1986	1.0	0.0	3.0	0.0	0.0	2.0	8.6
	3-year mean	1.7	0.0	2.3	2.3	1.7	1.7	12.3
Male—juvenile	1984	3.0	0.0	1.0	3.0	3.0	2.0	10.9
	1985	0.0	0.0	5.0	0.0	1.0	0.0	15.8
	1986	1.0	0.0	2.0	2.0	3.0	0.0	11.4
	3-year mean	1.3	0.0	2.0	1.7	2.3	0.7	12.7
Female—adult	1984	2.0	2.0	6.0	2.0	3.0	4.0	17.3
	1985	3.0	3.0	2.0	2.0	0.0	1.0	28.9
	1986	0.0	1.0	0.0	4.0	4.0	4.0	18.6
	3-year mean	1.7	2.0	2.7	2.7	2.3	3.0	21.6

Table 5. *Continued.*

		Transect						
Gender and age	Year	T-1	C-1	T-2	C-2	T-3	C-3	**Totals(%)**
Female— subadult	1984	1.0	9.0	5.0	3.0	1.0	4.0	20.9
	1985	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	1986	3.0	1.0	4.0	0.0	1.0	0.0	12.9
	3-year mean	1.4	3.4	3.1	1.1	0.8	1.4	11.3
Female— juvenile	1984	2.0	0.0	3.0	6.0	2.0	5.0	16.4
	1985	1.0	0.0	2.0	1.0	2.0	0.0	15.8
	1986	1.0	1.0	2.0	4.0	2.0	5.0	21.4
	3-year mean	1.3	0.3	2.3	3.7	2.0	3.3	17.9
				Summary				
Total	1984	13.0	15.0	20.0	23.0	16.0	23.0	—
	1985	7.0	5.0	13.0	5.0	5.0	3.0	—
	1986	7.0	8.0	16.0	12.0	11.0	16.0	—
	3-year mean	9.0	9.3	16.3	13.3	10.7	14.0	—
Male (%)	1984	61.5	26.7	30.0	52.2	62.5	47.8	45.5
	1985	42.9	40.0	69.2	40.0	60.0	66.7	55.3
	1986	42.9	62.5	62.5	33.3	36.3	43.8	47.1
	3-year mean	49.1	43.0	53.9	41.8	52.9	52.8	49.3
Female (%)	1984	38.5	73.3	70.0	47.8	37.5	52.2	54.5
	1985	57.1	60.0	30.8	60.0	40.0	33.3	44.7
	1986	57.1	37.5	37.5	66.7	63.7	56.2	52.9
	3-year mean	50.9	56.9	46.1	58.2	47.0	47.2	50.7
Adult (%)	1984	30.8	40.0	45.0	21.7	37.5	39.1	35.7
	1985	71.4	100.0	30.7	60.0	20.0	100.0	55.2
	1986	14.3	75.0	31.2	50.0	45.5	50.2	44.4
	3-year mean	38.8	71.7	35.6	43.9	34.3	63.1	45.1
Subadult (%)	1984	30.8	60.0	35.0	39.1	31.3	30.4	37.8
	1985	14.3	0.0	15.4	20.0	20.0	0.0	13.1
	1986	57.1	12.5	43.8	0.0	9.1	12.5	22.5
	3-year mean	34.1	24.2	31.4	19.7	20.1	14.3	24.5
Juvenile (%)	1984	38.5	0.0	20.0	39.1	31.3	30.4	26.6
	1985	14.3	0.0	53.8	20.0	60.0	0.0	31.6
	1986	28.6	12.5	25.0	50.0	45.4	31.2	32.1
	3-year mean	27.1	4.2	32.9	36.4	45.6	20.5	30.1
Immature male (%)	1984	38.5	26.7	20.0	39.1	43.8	21.7	34.6
	1985	14.3	0.0	53.8	20.0	40.0	0.0	21.4
	1986	28.6	0.0	31.2	16.7	27.3	12.5	19.4
	3-year mean	27.1	8.9	35.0	25.3	37.0	11.4	24.1

tion of deer mice on six transects over 3 years. (Data for 1987 are not included because of possible differences in aging criteria between observers; attempts to re-age 1987 captives on the basis of weight were unsuccessful.) The percentage of adults was significantly higher ($\chi^2 = 22.627$, 2 df) on undisturbed transects, confirming the prediction. No consistent change was found with time in the percentage of adults taken on any transect.

Sex Ratio

Table 5 also indicates sex ratio of deer mice. One might expect more males on the disturbed transects because males are known to have larger home ranges than females (see Merritt and Merritt 1978a). However, a comparison of disturbed and undisturbed transects with the Mann–Whitney test indicated no significant difference ($U = 32$). Average percentage of males by year varied from 45.5% to 55.3%, an insignificant deviation from the 50% expected ($\chi^2 =$ 5.652, 2 df).

Biomass

Biomass of small mammals was predicted to be lower on disturbed transects. The pattern observed was T-2 > C-2 > C-3 > average > C-1 > T-1 > T-3. However, the Kruskal–Wallis test suggested no significant difference among transects ($H = 1.094$). Four-year mean biomass by transect varied from about 180 g on T-3 to more than 400 g on T-2. Variation from year to year was significant (Kruskal–Wallis $H = 11.28$, 3 df, $P < 0.05$); biomass was lowest in 1985 and was especially low that year on transect pair 3 (outwash gravel–mixed forest). Any differences among all transects or between treatments and controls was obscured by variation between years. Also, elimination from consideration of species (e.g., northern pocket gophers, Wyoming ground squirrels, and golden-mantled ground squirrels) not sampled consistently by live traps of the sizes and kinds used presumably minimized differences between transects. In fact, actual biomass of small mammals surely was higher on some undisturbed controls than on corresponding disturbed transects. Pocket gophers were abundant only on undisturbed transects, Wyoming ground squirrels were found only on C-1, and golden-mantled ground squirrels and chipmunks (*Tamias* spp.) were common only on transects C-2 and C-3 (until 1987, when golden-mantled ground squirrels became abundant on the boulder field, T-2).

Euryoecious Species

Another prediction was that disturbed transects would show a bias toward euryoecious species, such as deer mice, because such mammalian "weeds" are the first species to occupy disturbed sites. Table 4 indicates by transect by year the percentage of total individuals taken that were deer mice. A Kruskal–

Table 6. *Spearman rank correlation coefficients for habitat variables and 4-year average values for a number of variables of the small mammal assemblage on the Lawn Lake Flood study area.*

Habitat variable (coverage)	Individuals	Species	Shannon-Weiner	Simpson's *D*	Total biomass	Individual *Peromyscus maniculatus* (% of total)
Graminoids	–0.3189	0.6765[a]	0.2029	0.6377[a]	–0.3189	–0.6377[a]
Herbs	–0.0580	0.2647	–0.2899	0.6087[a]	–0.0580	–0.2319
Bare soil, rock	–0.6000[a]	–0.5798[a]	0.2857	–0.4857[a]	0.2571	0.4857[a]
Shrubs	–0.7714[a]	0.4857	0.2571	0.5429[a]	–0.7720[a]	–0.5428[a]
Trees	0.5429[a]	–0.0580	–0.2571	–0.0286	0.5428[a]	0.0286

[a]Statistical significance: critical value of r_s (22 df) = 0.359, $P = 0.05$.

Wallis test was not significant ($H = 6.3452$, 5 df). Table 4 also indicates the percentage of total biomass accounted for by deer mice. Overall comparison was not significant ($H = 8.9792$, 5 df).

Table 6 indicates the Spearman rank correlation coefficient (r_s) between a number of habitat variables (Table 1) and 4-year average values for several variables describing the assemblage of small mammals. Species richness was positively correlated with the extent of coverage by graminoids and the extent of shrub coverage, and richness correlated negatively with the amount of bare rock or soil. Evenness diversity, as measured by Simpson's *D*, correlated positively with all habitat variables except tree coverage. Diversity, as measured by the Shannon–Weiner (*H'*) index, showed no significant correlation with any habitat variable. Biomass correlated negatively with shrub (mostly willow) coverage and positively with tree coverage. In the latter instance, this correlation probably represented a broader correlation with increased structural complexity of the habitat. Willows would not be expected to support great biomass; the habitat is highly productive of just one plant genus and life form and soil–water relations probably militate against most semifossorial species. The percentage contribution of the deer mouse to the total capture was correlated negatively with the coverage of graminoids (and therefore with the presence of *Microtus*) and with shrubs, which on the study area mostly are willows, habitat for voles and jumping mice. The percentage capture of deer mice was, however, positively correlated with the coverage of rock and bare soil. *Peromyscus maniculatus* is the most saxicoline of abundant small mammals in the study area and the only species present on the boulder field (T-2) for the first 3 years of the study.

Ecological Distribution

As part of the ecological baseline function of this study, a single-word descriptor of the habitat was noted at the site of each capture or recapture. The

Table 7. *Percentage of captures of five species of small mammals on the Lawn Lake Flood study area (1984–1987) with respect to simple descriptors of habitat.*

	Sorex monticolus	*Tamias minimus*	*Spermophilus lateralis*	*Peromyscus maniculatus*	*Microtus longicaudus*
Physical descriptors					
Boulder	4	33	62	34	—
Cobble	—	—	—	2	—
Gravel	—	—	—	3	—
Sand	9	4	—	8	3
Soil	—	—	—	1	—
Biotic descriptors					
Log	—	—	6	2	1
Trees	9				3
Ponderosa pine	—	33	19	13	
Douglas-fir	—	—	—	1	3
Aspen		—	—	1	—
Shrubs	22				—
Willow	—	4	—	7	
Juniper	—	—	—	1	17
Other	9	—	—	4	17
Forbs		—	—	3	—
Graminoids	44				7
Grass	—	25	12	20	
Sedges	—	—	—	—	25

percentage distribution of captures with respect to particular descriptors for the five species most commonly captured is shown in Table 7. The actual number of descriptors per species ranged from 4 (for *Spermophilus lateralis*) to 26 (for *Peromyscus maniculatus*); however, most shrubs and all herbs were pooled in Table 7 to minimize rounding error. Species less commonly captured tended to be even more narrowly distributed than the species tabulated; specifically, all captures of *Zapus princeps* were beneath willows, all of *Spermophilus elegans* were with grasses, 2 of 3 captures of *Tamias umbrinus* were associated with boulders, and points of captures of 5 of 6 *Microtus montanus* were described by grass. The percentage distribution of captures by descriptor provide a qualitative indication of habitat use. *Sorex monticolus* and *Microtus longicaudus* were associated strongly with grasses and willows; *Tamias minimus* inhabits rocky areas in open ponderosa pine woodland with an understory of grasses, a habitat similar to that of *Spermophilus lateralis*. *Peromyscus maniculatus* shows a great range of habitat descriptors; only boulders described the site of more than one-third of captures. These results are consistent with those of previous studies (e.g., Armstrong 1977; Stinson 1978).

A diversity index (Simpson's *D*) based on percentage association (to scale observations across species and thereby minimize influence of greatly different sample sizes) provides a crude measure of habitat niche breadth. The measure for the five species captured most frequently was *Sorex monticolus*, 0.7380; *Tamias minimus*, 0.7236; *Spermophilus lateralis*, 0.5198; *Microtus longicaudus*, 0.7384; and *Peromyscus maniculatus*, 0.8215.

Mid-sized and Large Mammals

Table 8 indicates average numbers of observations of several kinds of mammalian sign on belts 2 m wide along each of the six 250-m transects (pairs of parallel 125-m transects) on 21 bimonthly field trips. Several classes of sign—for example, pellet groups of mule deer (*Odocoileus hemionus*); pellet groups of cottontail rabbits (*Sylvilagus nuttallii*); tracks of weasels (*Mustela* sp.); feces of coyotes (*Canis latrans*)—were too scarce on the transects to provide interesting comparisons. Other sorts of sign (e.g., pocket gopher mounds) occurred (and would be expected) only on particular transects with suitable vegetation; specifically, use of C-3 and C-1 was extensive and use of other transects was negligible, although a pocket gopher mound was observed on the barren sand of the scoured willow transect (T-1) in 1987.

Table 9 indicates Spearman rank correlation coefficients for habitat variables (Table 1) and 4-year average numbers of observations for several kinds of mammalian sign (from Table 8). The critical value for Spearman's r_s for 30 df, < 0.306 ($P < 0.05$). There was a significant and strong negative correlation between bare soil–sand–rock and all categories of sign. Elk (*Cervus elaphus*) pellet groups correlated strongly and positively with all classes of vegetational cover. A similar relation existed for pocket gopher mounds, which also showed strong avoidance of areas with open soil and bare rock and a bias toward all

Table 8. *Average number of observations of several kinds of mammalian sign on 2-m belts along each of six 250-m transects during each of 21 bimonthly field trips on Lawn Lake Flood study area in 1984–1987.*[a]

	Transect					
Sign	T-1	C-1	T-2	C-2	T-3	C-3
Elk pellet groups	8.1	10.9	0.3	2.1	5.2	14.1
Elk tracks	8.7	7.6	0.1	0.9	6.1	3.1
Deer pellet groups	0.1	0.0	0.3	0.6	0.0	0.2
Deer tracks	0.1	0.0	0.1	0.1	0.0	0.0
Rabbit pellet groups	0.2	0.0	0.1	0.2	0.0	0.0
Rabbit tracks	0.3	0.1	0.1	1.2	0.0	0.4
Pocket gopher mounds	0.1	7.9	0.0	0.4	0.0	6.2
Coyote feces	0.3	0.2	0.0	0.1	0.1	0.3
Coyote tracks	0.6	3.4	0.1	0.0	0.3	0.5
Weasel tracks	0.3	0.1	0.1	0.0	0.1	0.0

[a] Nonzero values of less than 0.1 have been rounded up to 0.1.

Table 9. *Spearman rank correlation coefficients for habitat variables and 4-year average numbers of observations of several kinds of mammalian sign on the Lawn Lake Flood study area.*

Coverage	Elk pellet groups	Deer pellet groups	Pocket gopher mounds	Rabbit tracks	Coyote tracks
Rock, soil	–0.8857[a]	0.3531	–0.9276[a]	–0.5161[a]	–0.7714[a]
Grasses	0.8407[a]	–0.0746	0.6471[a]	0.8008[a]	0.6378[a]
Forbs	0.8117[a]	–0.209	0.8971[a]	0.4620[a]	0.3768[a]
Shrubs	0.3714[a]	–0.7356[a]	0.2319	–0.0359	0.6571[a]
Trees	0.3143[a]	–0.2609	0.6378[a]	–0.3339[a]	0.002

[a] Statistical significance, $P < 0.05$.

vegetated areas except willow thickets. The scarcity of rabbit tracks precluded assessing any pattern of habitat use. Coyote tracks were most abundant on transect C-1, correlating positively with coverage of grasses, forbs, and shrubs, but not trees. Presuming that small mammals are an attractive resource, one might reasonably suppose that coyote use would correlate with abundance of small mammals. However, R between density of coyote tracks and both small mammal biomass and numbers of individual small mammals (Table 4) was –0.5429, which is statistically significant ($P < 0.05$). However, this negative relation does not necessarily indicate that coyotes are depressing numbers of small mammals on the study site. Coyote sign never was common in the area, and the few fecal droppings recovered indicated diets mostly of elk carrion.

As predicted, elk use of undisturbed transects was higher than on disturbed transects 1 and 3. Elk use was low on both T-2 and C-2. In winter, elk bedded on transect C-3, the mixed forest, and they moved commonly across T-3 and T-1 to water. Large mammals were not observed to use the boulder field (T-2). Elk, deer, and occasional groups of bighorn sheep (*Ovis canadensis*) moved on a game trail across the upper end of the coniferous forest (C-2). Correlation between counts of elk pellet groups (Table 8) and coverage of bare soil, rock, or both (Table 1) was significant (–0.8857, $P < 0.05$).

This research was designed to provide baseline data on mammals of the area influenced by the Lawn Lake Flood and to evaluate effects of the flood and recovery from those effects by generating comparative data on disturbed and undisturbed sites. Variation from year to year was wide. Initial data from 1984 substantiated most predictions. In comparison with disturbed sites, control transects showed higher species richness and evenness, greater biomass, a greater predominance of adult animals, and less domination of samples by the classic mammalian "weed," *Peromyscus maniculatus*. In addition, use of undisturbed control transects by large mammals was substantially higher than was the use of areas disturbed by the flood.

In 1985, trends changed dramatically. Numbers of small mammals captured dropped precipitously. Furthermore, undisturbed control transects did not differ from disturbed treatment transects as predicted. On the contrary, disturbed transects showed somewhat greater species diversity, a bias toward older animals, and less bias toward deer mice. Large mammals continued to be more frequent on control transects than on disturbed transects, however. Data from 1986 and 1987 generally shifted back toward the pattern observed in 1984, although trends were less pronounced. Because of year-to-year variation, predictions—while substantiated on average and in general—mostly were not statistically demonstrable.

A priori predictions were based on a general expectation that succession following disturbance would be strongly driven by biotic factors, especially by factors intrinsic to species populations (recruitment, competition, and dispersal). Because most predictions were not strongly confirmed, either extrinsic factors (biotic or abiotic) were operating to distort the intrinsic dynamic of the populations or the time-scale of the study was inappropriate to the time-scale on which succession is operating—or both.

Mammalian ecological distribution and density are influenced directly or indirectly by vegetation. For small, herbivorous mammals, in particular, vegetational structure is a strong predictor of species occurrence (Armstrong 1977). Although plant ecologists would record changes in detail during the study, in broadest terms, plant succession on disturbed transects—other than the reestablishment of willows and some grasses at the lower end of the gravel outwash fan (T-3)—was minimal over the 4-year study. Changes in mammalian distribution corresponding with subtle changes in vegetation probably would have been imperceptible.

Weather is a strong abiotic influence on populations of small mammals. In particular, Merritt and Merritt (1978b, 1980) demonstrated the importance of an insulating blanket of snow to overwinter survival of deer mice in a subalpine forest in northern Boulder County (immediately south of Rocky Mountain National Park). Strong change in populations from one year to the next (as was seen from 1984 to 1985) leads one to wonder about possible abiotic influence. However, weather records (from the power station at the west end of Lake Estes, 11 km east–southeast of the Lawn Lake study area and about 280 m lower in elevation) revealed no episodes of the kind known to suppress populations (e.g., early season cold without snow). In those data, no appreciable difference was found between the winters of 1983–84 and 1984–85.

Another possible set of influences on populations of small mammals is extrinsic biotic factors, such as disease and predation. This study provided no data on disease (although it may be noteworthy that no Wyoming ground squirrels were captured or seen in the summer of 1986 or 1987, and this species apparently is particularly susceptible to sylvatic plague [Lechleitner 1969]). Data on predation are sketchy. Sign of coyotes—the carnivore most often observed on the study area—was never common, but in the field data on which Table 8 was based, no appreciable change was found in distribution or abundance of coyotes from one year to the next.

Ryder (1985) reported northern pygmy owls (*Glaucidium gnoma*) nesting in the study area in the summer of 1985. The owls surely could have had an effect on mammalian populations. Pellets from those owls obtained by Ryder yielded mandibles of *Sorex* cf. *monticolus*, *Microtus* cf. *longicaudus*, and *Peromyscus* cf. *maniculatus* in addition to feathers and hair. The meager remains obviously allow no quantitative assessment of predation, but they do document its occurrence.

Conclusions

A 4-year study of the mammals at the Lawn Lake Flood site has provided strong indication that disturbed areas receive less use by large mammals than do undisturbed controls. Results on small mammals were less clear. Variation from year to year meant that a number of predictions were not substantiated consistently. Variables of weather did not account for the patterns observed, and data on extrinsic biotic factors, such as predation and disease, were inadequate. Clearly, however, the time-scale of the present study was too brief to see pronounced trends in succession within mammalian assemblages. One should not expect succession in consumers to be more rapid than that in producers, and plant succession on the site has been slow.

This study has established a baseline of data on disturbed and undisturbed conditions near the time of the Lawn Lake Flood. These data will provide a basis of comparison in long-term studies. Such studies are to be encouraged. Halvorson (1984) reviewed strategies and functions of research on small vertebrates in research natural areas, providing suggestions germane to the Lawn Lake Flood site. Long-term monitoring, on a scale of decades rather than months to years, is needed to sort through short-term deviations and hence to reveal long-term trends. Simple, economical techniques should be designed to generate data that are biologically meaningful and suitable for electronic processing. Finally, pilot studies should be used to explore suitability of methods and feasibility of goals. The studies reported here are in some ways inconclusive, because they were simply too brief relative to the phenomena under investigation. However, one can hope that the studies will provide a demonstration of the potential value of recurrent study over many years and thus provide a useful foundation for longer-term, definitive studies.

Acknowledgments

For assistance in the field, I thank J. D. Armstrong of Olympia, Washington, R. A. Adams of Boulder, Colorado, and S. L. Jessup of Loveland, Colorado. Students in Mammalogy (EPOB 476/576) visited the area with me in the fall semesters of 1985, 1986, and 1987; students in Honors 348 (The Natural History of America) surveyed the site in 1987; and students from the BioEnviron

Field Trip of Fairview High School (Boulder; J. R. Sorensen, teacher) visited the site with me in May of 1986 and 1987. Each of these student groups added to the fund of observations of the study area. D. R. Stevens arranged for research and entry permits and camping space, and he and H. E. McCutchen arranged financial support. N. Doesken of the Colorado Climate Center, Department of Atmospheric Science, Colorado State University, provided weather data. L. C. Armstrong helped with clerical chores.

Literature Cited

Allen, J. A. 1874. Notes on the mammals of portions of Kansas, Colorado, Wyoming and Utah. Bulletin of the Essex Institute 6:43–66.

Armstrong, D. M. 1972. Distribution of mammals in Colorado. University of Kansas Museum of Natural History Monograph 3:1–415.

Armstrong, D. M. 1975. Rocky Mountain mammals: a handbook of mammals of Rocky Mountain National Park and Shadow Mountain National Recreation Area, Colorado. Rocky Mountain Nature Association, Estes Park, Colo. 174 pp.

Armstrong, D. M. 1977. Ecological distribution of small mammals in the Upper Williams Fork Basin, Grand County, Colorado. Southwestern Naturalist 22:289–304.

Armstrong, D. M. 1979. Ecological distribution of rodents in Canyonlands National Park, Utah. Great Basin Naturalist Memoirs 39:199–205.

Armstrong, D. M. 1984. Effects of the Lawn Lake Flood on the local distribution of mammals: preliminary report. Processed report. 25 pp.

Armstrong, D. M. 1985a. Effects of the Lawn Lake Flood on mammals. Journal of the Colorado–Wyoming Academy of Science 17(1):20. (Abstract)

Armstrong, D. M. 1985b. Effects of the Lawn Lake Flood on the local distribution of mammals: second annual report. Processed report. 25 pp.

Armstrong, D. M. 1986a. Edward Royal Warren (1860–1942) and the development of Coloradan mammalogy. American Zoologist 26:363–370.

Armstrong, D. M. 1986b. A three-year study of the effects of the Lawn Lake Flood on the local distribution of mammals. Processed report. 34 pp.

Armstrong, D. M. 1987. Rocky Mountain mammals: a handbook of mammals of Rocky Mountain National Park and vicinity. Colorado Associated Universities Press, Boulder. 223 pp.

Armstrong, D. M. 1988. The effects of the Lawn Lake Flood on the local distribution and abundance of mammals. Processed report. 52 pp.

Baker, R. H. 1968. Habitats and distribution. Pages 75–97 *in* J. A. King, editor. Biology of *Peromyscus* (Rodentia). American Society of Mammalogy, Special Publication 2.

Blake, I. H., and A. Blake. 1969. An ecological study of timberline and alpine areas, Mount Lincoln, Park County, Colorado. University of Nebraska Studies (New Series) 40:1–59.

Bowen, G. S., R. G. McLean, R. B. Shriner, D. B. Francy, K. S. Pokorny, J. M. Trimble, R. A. Bolin, A. M. Barnes, C. H. Calisher, and D. J. Muth. 1981. The ecology of Colorado tick fever in Rocky Mountain National Park in 1974. II. Infection in small mammals. American Journal of Tropical Medicine and Hygiene 30:490–496.

Brewer, W. H. 1871. Animal life in the Rocky Mountains of Colorado. American Naturalist 5:220–223.

Carey, A. B., R. G. McLean, and G. O. Maupin. 1980. The structure of a Colorado tick fever ecosystem. Ecological Monographs 50:131–151.

Cary, M. 1911. A biological survey of Colorado. North American Fauna 33:1–256.

Coues, E. 1874. Birds of the Northwest.... U.S. Geological and Geographical Survey of the Territories, Miscellaneous Publication 3:1–791.

Emlen, J. M. 1973. Ecology: an evolutionary approach. Addison–Wesley Publishing Company, Reading, Mass. 493 pp.

Halvorson, C. H. 1984. Long-term monitoring of small vertebrates: a review with suggestions. Pages 11–21 *in* J. L. Johnson, J. F. Franklin, and R. G. Krebill, editors. Research natural areas: baseline monitoring and management. Intermountain Forest and Range Experiment Station, U.S. Forest Service General Technical Report INT-173.

Horn, H. S. 1976. Succession. Pages 187–204 *in* R. M. May, editor. Theoretical ecology, principles and applications. W. B. Saunders Company, Philadelphia, Pa.

Jarrett, R. D., and J. E. Costa. 1986. Hydrology, geomorphology, and dam-break modeling of the July 15, 1982 Lawn Lake Dam and Cascade Lake Dam failures, Larimer County, Colorado. U.S. Geological Survey, Professional Papers 1369:1–78.

Lechleitner, R. R. 1969. Wild mammals of Colorado.... Pruett Publishing Company, Boulder, Colo. 254 pp.

Lloyd, M., J. H. Zar, and J. R. Karr. 1968. On the calculation of information—theoretical measures of diversity. American Midland Naturalist 79:257–272.

McCutchen, H. E., and D. R. Stevens. 1984. Consortium turns flood disaster into scientific learning experience. Park Science 4(4):4–7.

McLean, R. G., D. B. Francy, G. S. Bowen, R. E. Bailey, C. H. Calisher, and A. M. Barnes. 1981. The ecology of Colorado tick fever in Rocky Mountain National Park in 1974. I. Objectives, study design, and summary of principal findings. American Journal of Tropical Medicine and Hygiene 30:483–489.

Merritt, J. F., and J. M. Merritt. 1978a. Seasonal home ranges and activity of small mammals of a Colorado subalpine forest. Acta Theriologica 23:195–202.

Merritt, J. F., and J. M. Merritt. 1978b. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. Journal of Mammalogy 59:576–598.

Merritt, J. F., and J. M. Merritt. 1980. Population ecology of the deer mouse (*Peromyscus maniculatus*) in the Front Range of Colorado. Annals of the Carnegie Museum 49:113–130.

Neff, D. J. 1959. A seventy-year history of a Colorado beaver colony. Journal of Mammalogy 40:381–387.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Poole, R. W. 1974. An introduction to quantitative ecology. McGraw-Hill, New York. 532 pp.

Quick, H. F. 1964. Survey of the mammals. Pages 81–89 *in* H. G. Rodeck, editor. The natural history of the Boulder area. University of Colorado Museum Leaflet 13.

Rohlf, F. J., and R. R. Sokal. 1969. Statistical tables. W. H. Freeman, San Francisco. 253 pp.

Ryder, R. A. 1985. Changes in avian breeding populations resulting from the Lawn Lake Flood of 1982. Processed report. 6 pp.

Spencer, A. W., and D. Pettus. 1966. Habitat preferences of five sympatric species of long-tailed shrews. Ecology 47:77–683.

Stinson, N., Jr. 1978. Habitat structure and rodent species diversity on north and south-facing slopes in the Colorado lower montane zone. Southwestern Naturalist 23:77–84.

Telleen, S. L. 1978. Structural niches of *Eutamias minimus* and *E. umbrinus* in Rocky Mountain National Park. Ph.D. dissertation, University of Colorado, Boulder. 141 pp.

Vaughan, T. A. 1969. Reproduction and population densities in a montane small mammal fauna. University of Kansas Museum of Natural History Miscellaneous Publication 51:51–74.

Warren, E. R. 1910. The mammals of Colorado.... Putnam, New York. 300 pp.

Warren, E. R. 1942. The mammals of Colorado.... 2nd (revised) edition. University of Oklahoma Press, Norman. 300 pp.

Williams, O. 1955. Distribution of mice and shrews in a Colorado montane forest. Journal of Mammalogy 36:221–231.

Observations of Plant Ecology on the Lawn Lake Flood Alluvial Fan

Richard B. Keigley

National Park Service
P.O. Box 168
Yellowstone National Park, Wyoming 82190

Abstract. Sediment from the Lawn Lake Flood covered a willow carr community in Horseshoe Park. In 1983 and 1984, revegetation was strongly influenced by the environmental conditions established immediately following the flood, including topographic gradient, sediment grain size, and the presence of surviving vegetation. One important aspect of early revegetation was the establishment of a dense stand of willow seedlings. In subsequent years, revegetation was also affected by changes in initial conditions, such as the alteration of the original surface texture by wind erosion and by the precipitation of ferric hydroxides. Those subsequent changes are believed to have caused a great reduction in the continued establishment of willow from seed.

Factors Immediately Following the Flood

General Topography

The Lawn Lake Flood released 1,234 m^3 of water (Jarret and Costa 1986). Some 278,750 m^3 of material was eroded, some of which was deposited as an alluvial fan in Horseshoe Park (Fig. 1). The fan can be divided into two areas based on sediment texture and topographic gradient. On the northwest end of the fan, the sediments are coarse and are deposited on a steep topographic gradient. In this area of the alluvial fan, boulders are common. On the southern and eastern ends of the fan, the sediment is finer and forms a relatively gentle topographic gradient. Here the coarsest sediment is cobble-sized or smaller. Because we felt that plant succession would occur much more rapidly in the more gentle and finer alluvial fan segment, this study concentrated on the southern and eastern areas of the fan where sediments are predominantly sand-sized.

Grain Size of the Original Sediment

In the study area of the alluvial fan, grain size varies primarily along a landscape-level topographic gradient formed by the floor of Horseshoe Park. Superimposed on this gradient, local factors also affected the size of the sedi-

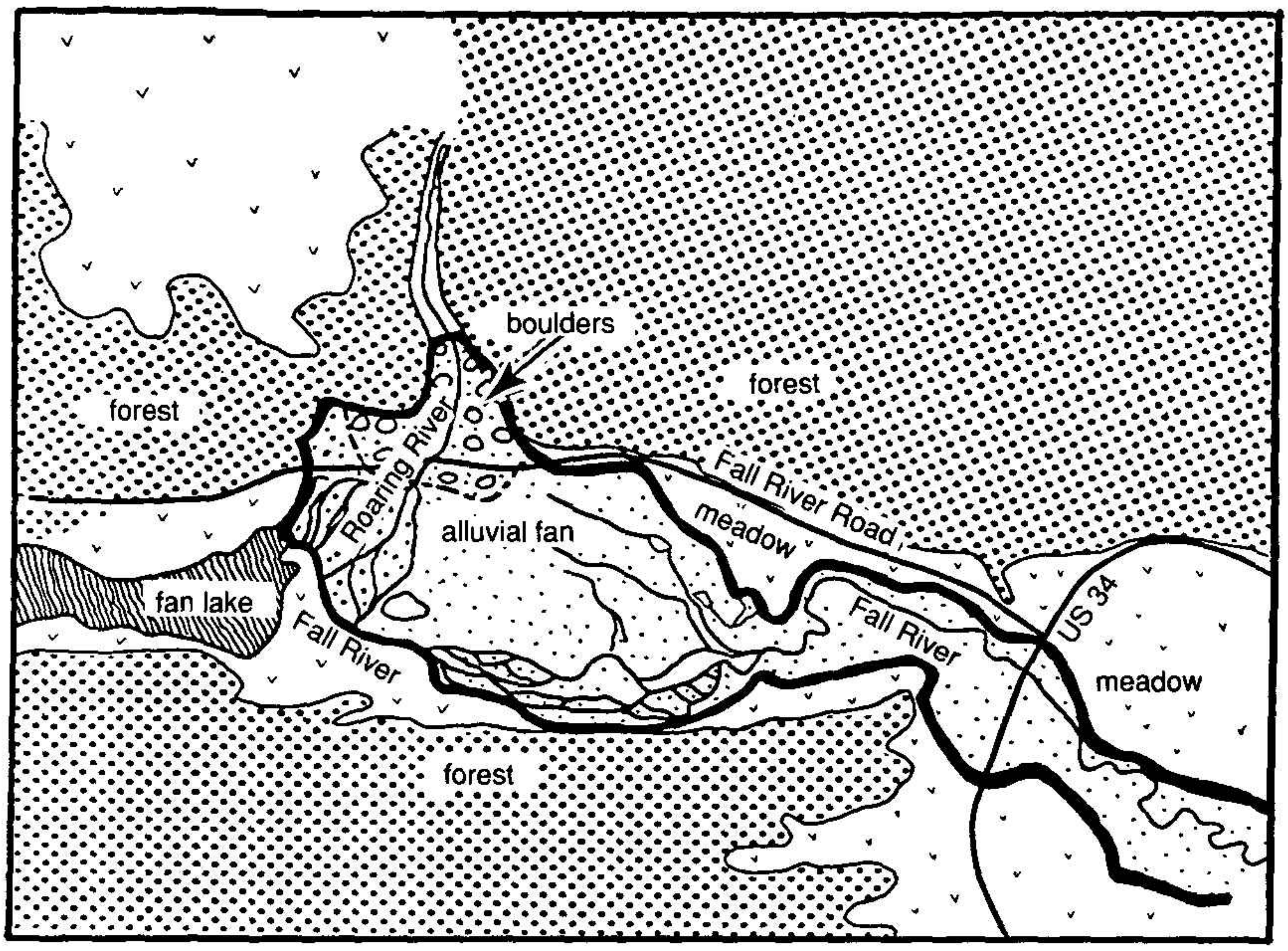


Fig. 1. Map showing the location of the alluvial fan relative to the roads in Horseshoe Park. The border of the alluvial fan is indicated by the *heavy outline*. The study concentrated on the sandy part of the alluvial fan.

ment particles deposited by the flood. To measure sediment grain size, samples were taken in 1984 from 27 locations on the alluvial fan. In the 2 years since the flood, the sediment at some sites was observed to have been altered by subsequent erosion or deposition. To minimize the effects of postflood processes, samples used to interpret the qualities of the original sediment were taken from 10 cm deep. Samples weighing approximately 100 g were air-dried and mechanically sieved for 15 min. Grain size was described using phi values midway between the screen on which the fraction was caught and the screen above (Folk 1968). A weighted average phi size was calculated and used to describe the size distribution of sediment over the sample area (Fig. 2).

Based on the data presented in Fig. 2, the landscape-level topographic gradient caused sediment sizes to become finer along a gradient from northwest to southeast. Two local features also appear to have been factors in determining grain size. Fine-grained sediments are associated with stands of vegetation. Within those stands, it was inferred that friction reduced the flow velocity of the floodwater, which enabled comparatively finer-grained particles to settle.

A second local feature appears to have been the confinement in flow that occurred when water flowed over open areas that were bound by adjacent stands of vegetation. Because the flow of water through the stands was impeded, water was diverted through the open area separating the stands. Once

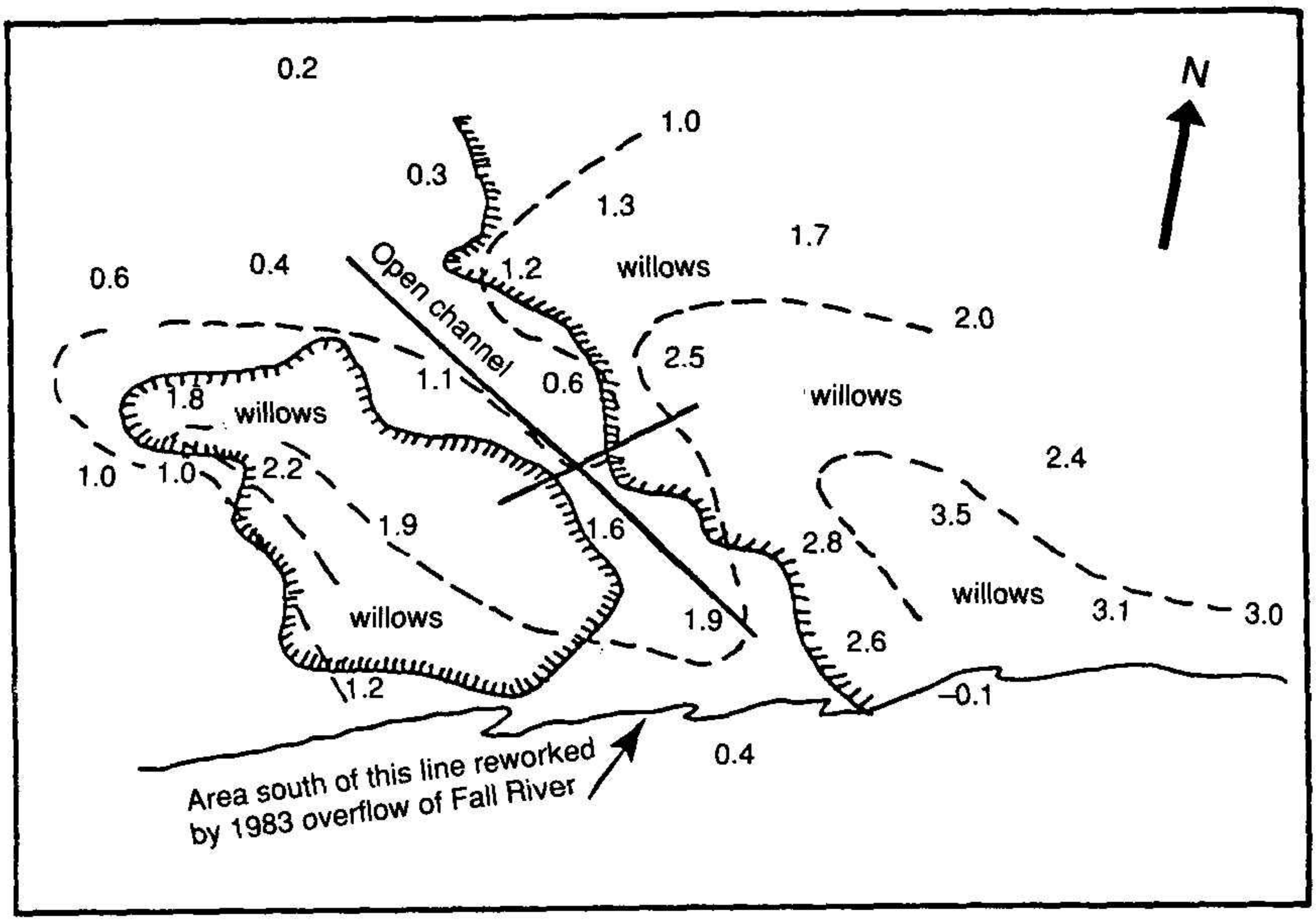


Fig. 2. Grain sizes of the sediment deposited by the 1982 flood, estimated by sampling (in 1984) from a depth of 10 cm. Samples were sieved to a 1-phi size class interval. Topographic gradient of Horseshoe Park was the principle factor controlling the sorting of the sediment. Stands of vegetation caused finer sediment to be locally deposited.

confined flow was established between the stands, the water had a greater ability to transport a coarse sediment load. One such channel is identified in Fig. 2 by the transect A-A'.

To document in more detail the effect of flow confined by vegetation, additional samples were collected in 1986 from 10 cm deep along transect B-B' (Fig. 2). In Fig. 3, samples A, B, and C demonstrated a coarsening of the sediment, from the shelter of vegetation to the center of the channel. On the western end of the transect (point A), flow was impeded by mature willows. On the remainder of the transect (points B, C, and D), flow was not impeded by vegetation. The sample taken from within the current channel (point D) was undoubtedly composed of sediment deposited under more recent, low-energy regimes compared with the environment at the time of the flood.

Hydrology

Drainage channels within the study area radiate away from the zone where the Roaring River flows through the morainal boulders. Based on this pattern of flow, most groundwater seems to enter the study area at this point rather than from the Fall River (from the south) or from the more gentle, lower reaches of the Roaring River (from the west). Within the study area, a general change in soil moisture occurs near the surface that varies between dry in the

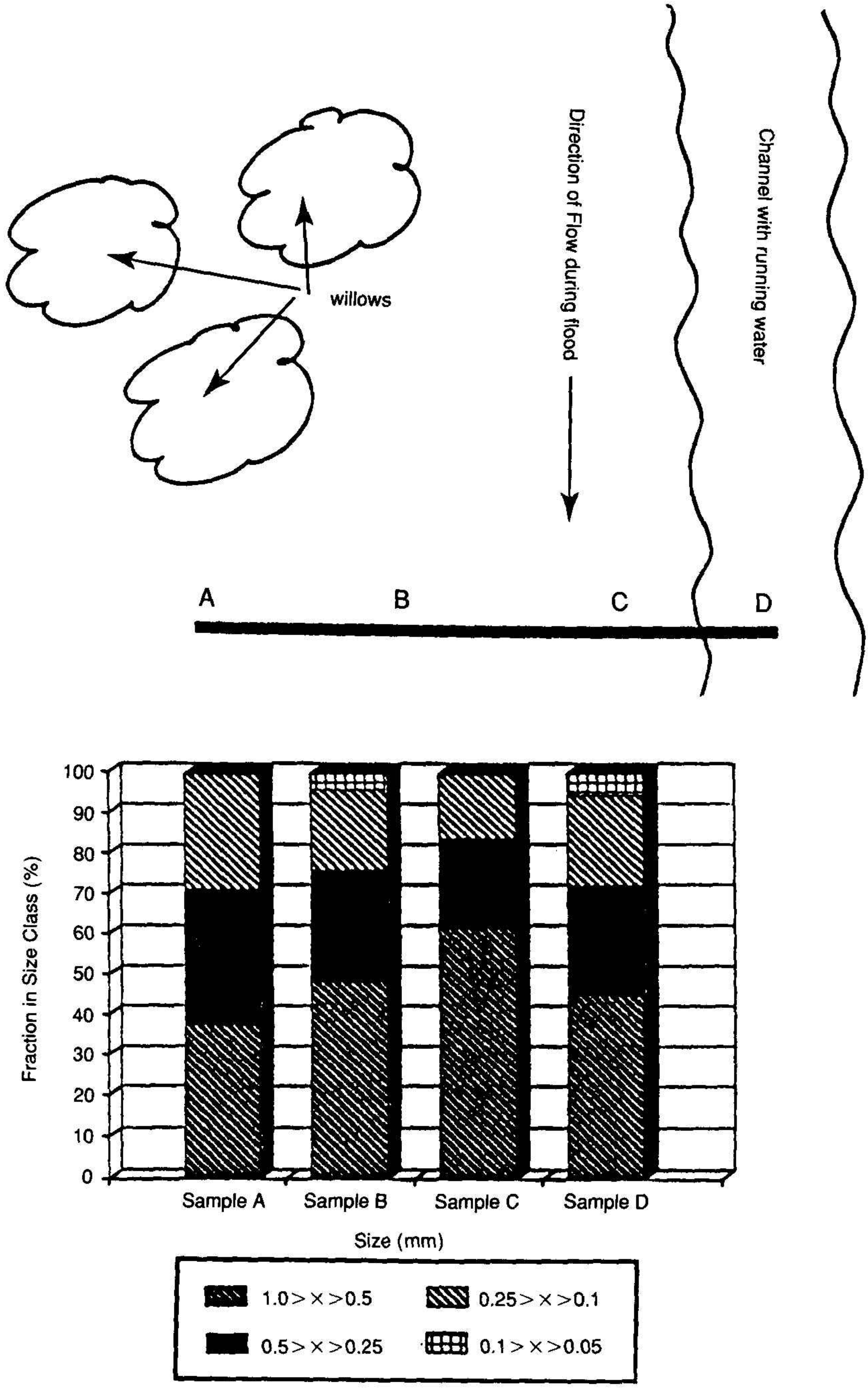


Fig. 3. As shown by samples A, B, and C, mean sediment size increased along a transect running from the shelter of a dense strand of willow to an exposed position in the center of the channel. The original flood sediment of sample D has been reworked by subsequent flow through the channel.

northwest, wet in center, and dry in the southeast. These moisture differences were attributed to three factors: flow velocity, sediment depth, and the dispersal of water onto the valley of Horseshoe Park. The dry surface within the northwest portion of the study area was primarily attributed to a high groundwater flow velocity. This high velocity results partly from the hydraulic head imparted by a steep topographic gradient and partly from the porosity of the coarse sediment making up this portion of the alluvial fan. Because of the high groundwater flow velocity, all water entering the system can be transported through this segment within the sediment body.

The moist surface in the central study area is attributed in part to reduced flow velocity (compared with that described above) and in part to decreased sediment depth. A gentle topographic gradient and a fine-grained sediment combine to reduce flow velocity to the point that subsurface flow is incapable of removing all the water input into the groundwater system; excess water must exit as surface flow. Another factor contributing to increased moisture at the surface is the decreasing thickness of flood sediment along a northwest–southeast gradient. Because groundwater can flow more rapidly through the sand-sized flood sediment than through the silt and clay-sized soil buried by the flood, most subsurface flow takes place within the flood sediment. As the sediment thickness decreases to the southeast, excess water must exit as surface flow.

The dry surface in the southeast part of the study area is attributed in part to water flowing over the surface and in part to water dispersing over a larger area of sediment. The surface water draining the central part of the study area removes water from the system much more rapidly than groundwater could flow alone. This rapid transport decreases the volume of water available to move through the sediment body. Also, throughout the southeast part of the area, water is dispersed onto the broader area of the alluvial fan.

Once groundwater emerges to the surface, the flow is concentrated in channels. Some channels run through open areas between dense stands of vegetation—the high-energy transport condition described in the previous section. These channel positions are interpreted to be relics of the flows existing at the time of the flood. Other channels arise at the base of debris jams where trees, shrubs, or local topographic relief caused logs and other debris to accumulate during the flood. The rapid change in topographic gradient has caused seeps to form at the base of the rubble. The channels formed by these relatively small flows are enlarged by the runoff from summer thunderstorms.

Differences exist in soil moisture perpendicular to drainage channels, with the wettest sediment naturally being closest to the channel. While the areas between channels are commonly moist in the upper reaches, interfluves in the lower reaches sometimes become quite dry. In these lower reaches, the radiating channels diverge onto the broader end of the alluvial fan and cause the interfluve distances to be greater than those of the upper reaches.

Small-scale differences in soil moisture may be produced by subtle differences in surface relief and surface texture. Elk hoofprints are one common source of microrelief. The differences in grain size at the surface can also have a significant effect on soil moisture. Successful seed germination and subsequently mature vegetation establishment are strongly controlled by the environment near the surface. The long-term development of vegetation will not only be determined by early conditions of the surface environment, but also by the changes resulting from physical and chemical alteration of the original sediment. Some of these changes are described in the following section.

Changes in Early Environmental Conditions

Water Chemistry

Samples were taken in the summer of 1984 to determine the chemical nature of four areas: the Roaring River, the alluvial fan, the Fall River (above and below the study area), and a willow carr 2 km upstream from the alluvial fan. The Roaring River was sampled because it is the likely source of groundwater flowing through the alluvial fan. Any differences between water from the Roaring River and water from the alluvial fan is attributed to processes taking place within the alluvial fan. The Fall River was sampled from both above and below the fan; differences between those samples could be attributed to chemical input from the alluvial fan. The willow carr upstream provided an estimate of the preflood condition.

The water was drawn using an Antilla pump through a 0.47-μm filter. Nitric acid (to a volume of 1%) was added to the sample as a preservative. The results of atomic absorption spectrophotometric analysis are presented in Table 1. Iron was present in considerable concentration in both groundwater and surface water of the alluvial fan. The concentration in the Fall River and in the willow carr upstream was lower by a factor of about 50. Compared with normal groundwater, as measured beneath the upstream willow carr, the groundwater of the alluvial fan was highly chemically enriched. Iron and manganese may have been present in toxic concentrations (Barrick and Noble 1993).

Precipitation of Iron on the Surface of the Sand

Within a few weeks of the flood, a red stain appeared alongside the Roaring River channel near the base of the boulders (D. Stevens, Rocky Mountain National Park, personal communication). Such stains are common in local wetlands and are attributed to the precipitation of ferric hydroxides. As the summer of 1983 progressed, the light beige color of the sand typical of the fresh sediment was altered in some places to a rust red. Below the surface, the sand was dark grey to blue. The grey-blue color is indicative of an anaerobic, reducing chemical environment, and the red is indicative of an aerobic, oxidizing environment. By the end of the summer of 1983, areas in which the surface

Table 1. *Comparison of water chemistry between sites on the alluvial fan, equivalent sites in an undisturbed willow carr community, and surface water from the Fall River and the Roaring River, 1984.*[a]

	Mean (SE)					
Sample	K	Na	Fe	Mn	Ca	Mg
Surface water from	0.3	3.3	0.2	n. d.[b]	1.5	0.4
Roaring River	(0.1)	(0.0)	(0.0)	n. d.	(0.1)	(0.0)
Groundwater from	0.2	4.6	0.2	n. d.	1.7	0.6
undisturbed willow carr	(0.0)	(0.0)	(0.0)	n. d.	(0.4)	(0.3)
Surface water from	0.4	0.7	0.1	n. d.	1.7	0.6
undisturbed willow carr	(0.1)	(0.1)	(0.1)	n. d.	(0.1)	(0.0)
Groundwater from	2.2	21.8	24.0	0.6	21.8	7.8
alluvial fan	(0.2)	(0.3)	(2.2)	(0.2)	(1.7)	(0.4)
Surface water from	2.4	2.4	21.8	1.6	19.8	6.5
alluvial fan	(0.2)	(0.1)	(2.2)	(0.1)	(0.4)	(0.3)
Surface water from	0.4	1.8	0.5	n.d.	2.2	0.7
Fall River below alluvial fan	(0.0)	(0.1)	(0.1)	n.d.	(0.1)	(0.0)

[a] Water draining off the alluvial fan was considerably chemically enriched compared to water from other areas; $N = 3$; data in meq/L.

[b] No data.

was chronically moist had the following profile: a deep rust zone about 2 to 3 mm thick at the surface that changed over a distance of 1 or 2 mm to a deep blue or grey. An Orion ion-selective electrode was used to measure redox potential in the reduced zones below the surface. Values ranging from +100 mV to +200 mV were typical; a redox potential below +250 mV is considered to be anaerobic (Etherington 1982).

Iron occurs in two valence states: +2 (ferrous iron), and +3 (ferric iron). Ferrous iron ionizes readily in water, is highly soluble, and imparts a grey or blue color to the soil. Ferric iron usually forms an insoluble precipitate as an oxide or hydroxide and colors a soil red. In 1984, a hypothesis was developed to explain the observed pattern of ferric hydroxide precipitation. The iron was assumed to originate from the buried willow carr soil or from the alluvial sand now covering that soil. The willow carr soil would naturally contain a high percentage of organic matter, the remains of roots, and other decomposing plant material. As the organic matter decomposed, oxygen would be drawn from the soil–water solution to supply aerobic decomposers. Because the solubility of oxygen in water is limited, demand would soon exceed supply and the system would become anaerobic. Once the system was anaerobic, ferric iron (the normal state in an oxidized soil) would be reduced to ferrous iron and, being soluble, would be transported by groundwater. But once ferrous iron was exposed to oxygen at the surface of the soil column, that iron would be oxidized back to a ferric state. In places, this precipitate formed solid crust covering the sandy sediment.

From 1985 through 1987, Litaor and Keigley (1993) studied iron chemistry on the alluvial fan. Based on a decrease in soil carbon (the fuel for reduction) over the years of the study, the researchers concluded that the intensity of crust formation would be reduced within the next few decades. Indeed, many areas of the alluvial fan that once had sharply contrasting red and grey zones now (1988) have a dull reddish section at the top that grades over a few centimeters to a light grey zone.

Some plants growing in the anaerobic sand during the early years dramatically illustrated one adaptation to wetland life. Living roots require oxygen for metabolism and many plants depend on the diffusion of oxygen from air spaces in the soil to supply this need. Wetland plants, however, may grow where soil oxygen is not present. The plants have a specialized tissue (aerenchyma) that enables oxygen to enter the plant aboveground and diffuse, through the tissue, to belowground parts. In a process termed "radial oxygen loss," surplus oxygen may diffuse away from the root to where it can oxidize ferrous iron. The effect is to produce radial zones (around roots), 1 to 2 mm thick, of a red precipitate in an otherwise grey medium. In summer 1988, the results of this process were still observed associated with willows and Canadian reedgrass (*Calamagrostis canadensis*) on many parts of the fan.

Changes in Surface Texture

Since the flood, the surface texture of the alluvial fan has changed in response to erosion, deposition, and chemical precipitation. In summer 1983, the Fall River overflowed its banks and reworked much of the sediment lying adjacent to the channel. One effect of the reworking was to increase mean grain size as shown in Fig. 2.

Wind erosion was also significant during the early history of the alluvial fan. Aeolian ripple marks and dunes southwest of the junction of Highway 34 and the Fall River were observed by spring 1983. By the summer of 1984, erosion by wind was armoring the surface of the alluvial fan by selectively removing the finer fraction of the sediment. Sediment samples were taken on the surface of the alluvial fan at the same locations described in Fig. 2. By comparing samples taken at the surface with samples taken at 10 cm (a depth assumed to be unaffected by subsequent erosion or deposition), we saw the change in the distribution of grain-size classes. As in Fig. 2, mean grain size was used to compare the textures. The samples described in Fig. 4 were taken at a site exposed to the prevailing westerly wind and clearly showed how the texture at the surface became coarser than that of the original sediment.

I believe that the degree of armoring depends on a number of factors, one being the extent to which the site is sheltered from prevailing winds. Soil moisture is another important factor—wet sediment is not as easily entrained by wind as dry sediment. Finally, wetter portions of the alluvial fan are covered by a layer of ice in winter and during that time are not subject to wind erosion. The moisture may be due to ground- and surface water or may result

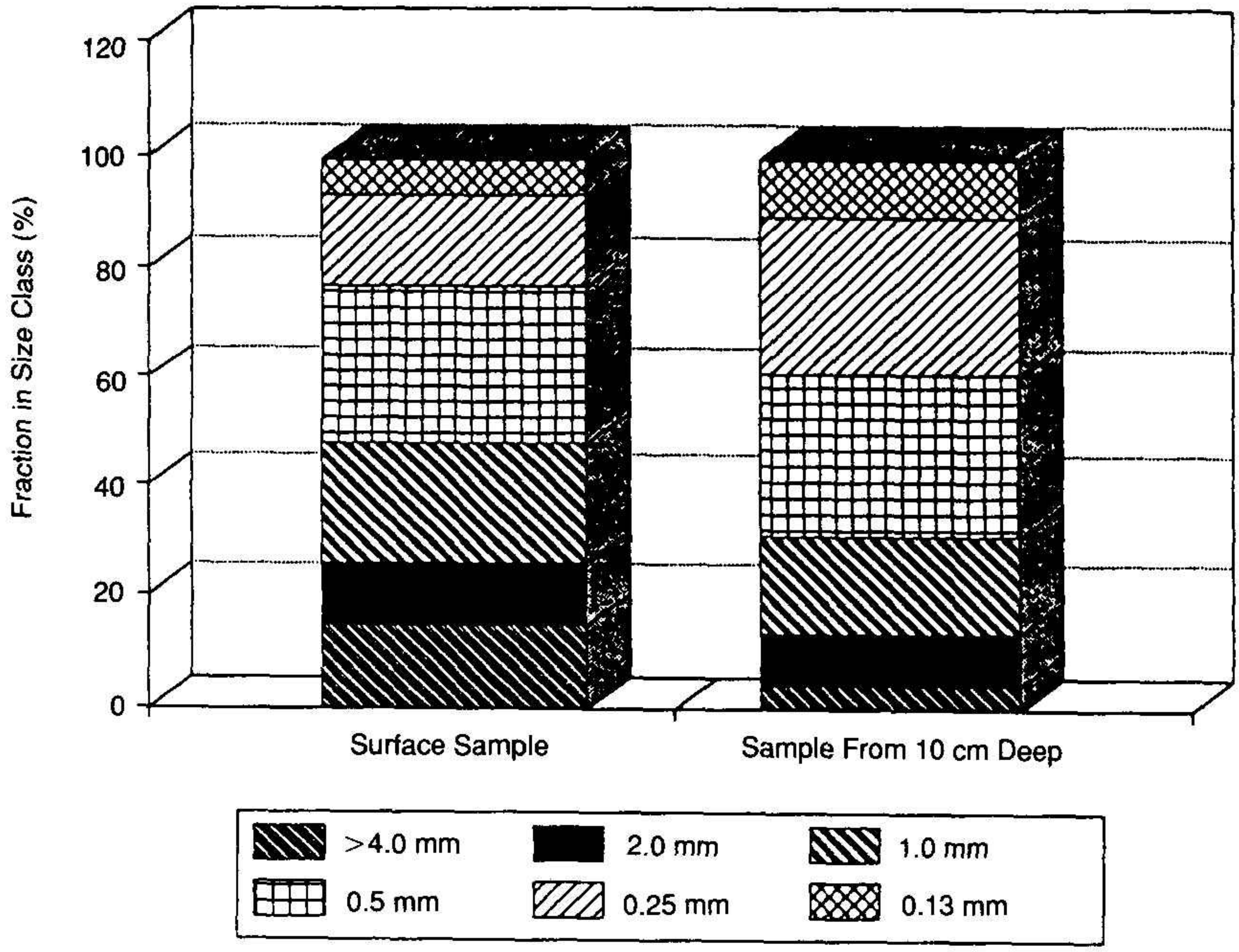


Fig. 4. In exposed locations,wind has eroded the fine particles from the surface. The particle-size distributions described were taken from an exposed site that is intermittently moist. The sample taken from 10-cm deep is assumed to be representative of the sediment deposited by the flood.

from snow accumulation. These factors can be highly variable over a short distance, so no simple map of armoring can be prepared.

Another phenomenon altering the surface texture was the precipitation of ferric hydroxides, as described earlier. Locally, the precipitate forms a fine-grained crust that is substantially different from the surface of the original alluvial sediment. Moist areas adjacent to drainage channels were most affected. Groundwater infrequently affects drier sites, so ferric hydroxide precipitation is limited there. Crust development within the stream channels was also limited. In summer, thunderstorms caused large volumes of water to flow through the channels, and during those periods, sediment transport was obvious. Even though iron probably precipitated within the channel, water movement was sufficient to remove the precipitate about as rapidly as it was formed.

In the eastern portion of the study area, dunes have formed in the lee of willows, creating a distinctive change in the local soil. The material making up the dunes probably originated from the finer fraction removed during the armoring of areas situated to the west. Where shrubs are isolated from one another, the character of the dune is obvious. Adjacent and east of the shrub, the dune typically rises 20 cm above nearby ground level. The dune tapers to the original postflood ground level within 1 m east of the shrub. Where shrubs grow in close proximity, the individual dunes are not clearly distinguishable from one another.

Samples were taken from a well-defined dune and an adjacent bare area so that the two soil types could be compared. The samples were sieved and pippeted by Colorado State University's Soils Laboratory. The difference between the two soils is shown graphically in Fig. 5, which shows that the soil of the dune is composed of considerably finer material than that of the adjacent soil.

Chemical analyses were also run by the Colorado State University Soils Laboratory (Table 2). The soil of the dune had a significantly higher percentage of organic matter, much of which was believed to be the remains of an undetermined diminutive moss. With the exception of NO3 and P, the concentration of all nutrients was significantly greater in the dune soil than in the soil adjacent. However, total nitrogen of the dune soil was greater by a factor of 10. I believe that the NO3 released from organic matter was rapidly consumed by vegetation.

Due to the increased moisture retention associated with fine-textured soils (in combination with higher nutrient concentrations), this soil is more fertile than adjacent soils developing on the alluvial sediment. Soil fertility not sheltered by the willows may even decrease as fine-grained sediments are lost to erosion.

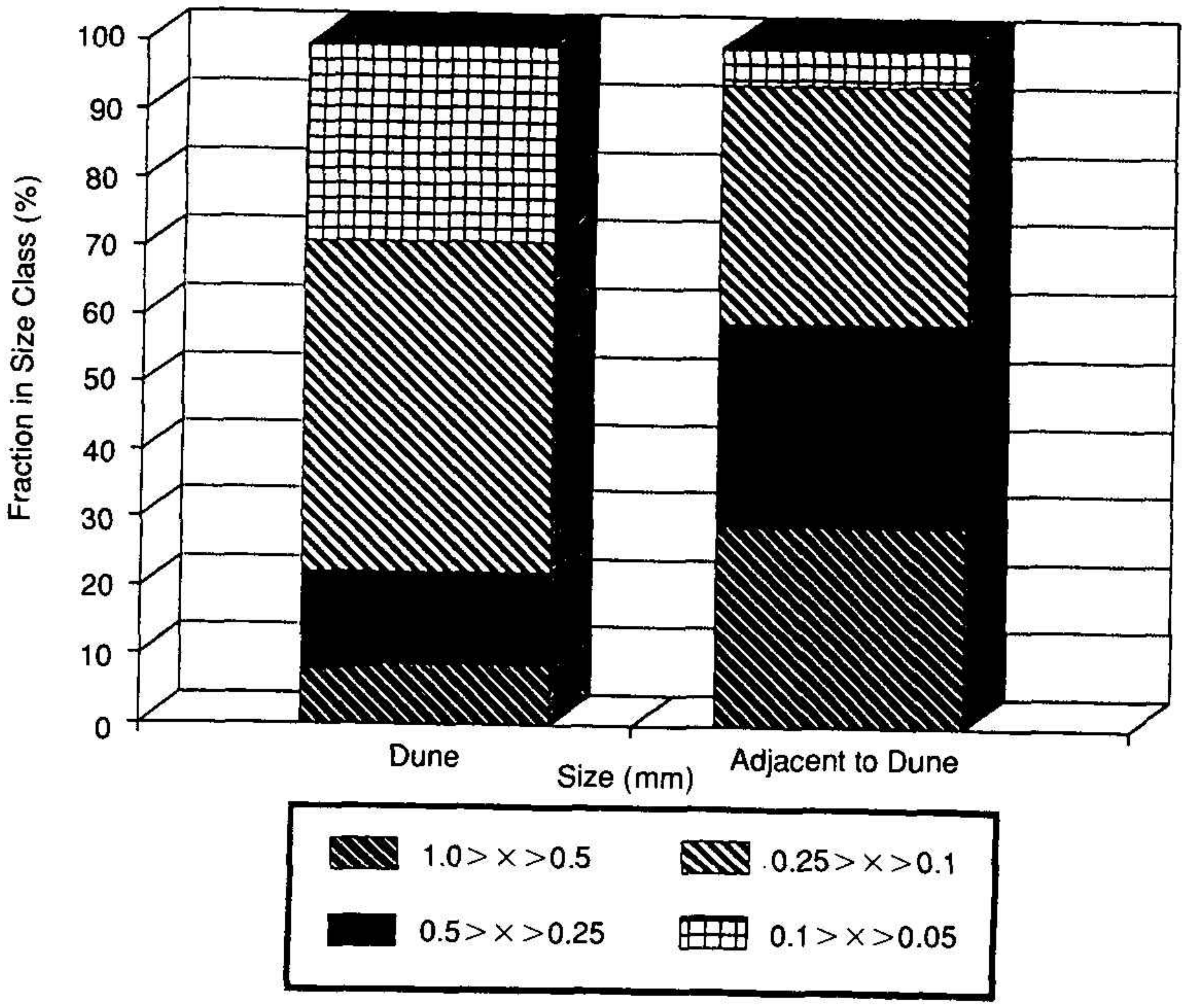


Fig. 5. Dunes are forming in the lee of some willows. At these sites, deposition has produced finer-grained soils compared to adjacent locations that do not experience deposition. The chemical characteristics of these sites are also different as a result of the addition of fine-grained particles as well as differences in vegetation.

Table 2. *Comparison of soil chemistry between that of aeolian dune formed in lee of willow and soil formed by original flood sediment. See Fig. 5 for description of grain sizes of the two soil types.*

	Mean (SE)										
Sample	pH	OM[a]	NO3	P	K	Zn	Fe	Mn	Cu	Total *N* (%)	CEC[b]
Dune soil	7.2	1.3	1.0	1.0	55.7	0.9	62.6	8.5	2.4	0.4	4.7
	(0.2)	(0.1)	(0.0)	(0.3)	(1.7)	(0.0)	(14.1)	(0.8)	(0.1)	(0.0)	(0.7)
Soil adjacent	7.1	0.1	1.0	0.9	11.3	0.2	25.4	1.9	0.4	0.0	1.3
to dune	(0.1)	(0.0)	(0.0)	(0.3)	(2.7)	(0.0)	(1.9)	(0.2)	(0.0)	(0.0)	(1.13)

[a] Organic matter.
[b] Cation exchange capacity in meq/100 g.

In 1983, the physical and chemical environment of the sandy areas of the alluvial fan appeared relatively uniform and one would have predicted that, at most, a few different kinds of plant communities would have existed. But the kinds of change described in this section superimposed a highly variable mosaic over what was initially a relatively simple landscape. These changes produced a diverse group of plant communities.

Influence of Physical, Chemical, and Biotic Factors on Plant Survival and Establishment

Distribution of Vegetation Over the Alluvial Fan

Successional studies offer the opportunity to observe a variety of interactions. These interactions could be generally classified as occuring between (1) different environmental components, (2) plants and the environment, and (3) plants. The two previous sections have focused on interactions between environmental components. One effect of that kind of interaction was to determine the complexity of successional pathways. We will examine interactions between plants and the environment, mostly from the perspective of the environment as the controlling factor. The situation in which plants control environmental change (such as the increased organic matter in the dune soil described earlier) is important but was not investigated in detail. The study of interactions between plants (for example, competition for resources) is also important if one is to most fully determine successional factors, but this kind of study would require experimental manipulation and was beyond the scope of this study.

Here, I examine how environmental factors shaped changes in vegetation. Those changes can be classified as changes that resulted from mortality of plants present before the flood; changes in vegetation that survived the effects of the flood; and changes that resulted from the immigration of new individuals onto the alluvial fan.

Mortality

Much of the preflood vegetation that was low in stature was buried and killed by the flood sediment. Larger trees and shrubs surviving the immediate trauma faced other risks. By the summer of 1983, some individual aspens (*Populus tremuloides*) were seriously girdled by elk. Elk browse both twigs and bark—the bark of the aspen is tender. If an aspen survives the immediate effect of browsing, scar tissue develops over the bite mark on the trunk; years of accumulated scar tissue commonly form a blackened area that extends from ground level to as high as an elk can reach. The scar tissue is unpalatable to elk, and often, enough phloem is preserved to permit a young aspen to grow to a large tree in spite of the near-girdling. On the alluvial fan, up to 1 m of sediment was deposited around the base of many mature aspens. In winter 1982–83, elk walking on the alluvial fan were presented with previously unreachable aspen bark, bark that had no scar tissue. Within the first winter, many of the aspen had been completely girdled by elk and died. Others were partially girdled and perhaps made more susceptible to mortality from other causes. Mature aspen that were not heavily girdled survived on the alluvial fan for up to 3 years, but by fall 1986, almost all aspen were dead, possibly as a result of waterlogged soil conditions after the flood. Toxic levels of iron and manganese may also have been a contributing factor (Barrick and Noble 1993).

By summer 1985, lodgepole pine (*Pinus contorta*) and Englemann spruce (*Picea engelmannii*) were largely eliminated. The anaerobic environment may have caused the mortality; again, increased levels of soluble iron and manganese may have been a factor. Near the base of the boulders of the alluvial fan, in the drier zone of the sediment, mature individuals of narrowleaf cottonwood (*Populus angustifolia*) survive. The bark of mature narrowleaf cottonwood is not palatable to elk, and the soil in this area is not as saturated as that found elsewhere on the alluvial fan.

Survivors

In 1983, the summer following the flood, I found that most willows (*Salix* spp.) could survive partial burial by sediment. In many cases, the original form (or habit) of the shrub was altered by the emergence of new shoots from buried branches. I also found that *Calamagrostis canadensis* and field horsetail (*Equisetum arvense*) would survive the flood to become important components of the postflood flora. The shoots of those species emerged from the rhizomes of buried plants.

In its natural setting, *Calamagrostis* typically grows in slightly elevated portions of the willow carr. After the flood, these were the kinds of areas in which *Calamagrostis* subsequently reappeared. *Calamagrostis* frequently emerged to the side of aspen trunks downstream from the flow of floodwater. Apparently, rhizomes were scoured away from around the upstream side of the trunk during the flood. Another postflood emergence situation was from around the base of surviving willow shrubs; in undisturbed willow carrs, *Calamagrostis* frequently is associated with mature willow. Also, *Calamagrostis* frequently grows on top of old beaver dams in undisturbed willow carrs. After the flood, emerging *Calamagrostis* formed linear patterns that marked the location of dams, even though the structure itself was completely buried by sediment. In 1983 and 1984, when little other vegetation existed, the patterns were especially striking; however, subsequent growth of other kinds of vegetation somewhat obscured them.

Equisetum arvense typically grows in undisturbed willow carrs at densities of a few stems per square meter; occasionally one finds much denser stands, and these are usually associated with especially wet areas. In 1983, a few stems of *Equisetum* emerged from beneath the sediment. Like *Calamagrostis*, the *Equisetum* was associated with the base of trees and shrubs, and the shoots did not emerge great distances from patches of surviving vegetation.

By fall 1984, *Equisetum* was an important cover over many parts of the fan. The rhizomes of *Equisetum* grow vertically from their preburial depth to the top of permanently moist sand, where they again spread horizontally. Shoots develop from the rhizomes that may in turn produce additional shoots from their leaf axils. With additional shoots (as many as five) produced at a few whorls along the plant, the potential for reproduction was explosive. In many places, the *Equisetum* assumes an almost turflike quality. Because most areas of the alluvial fan have moist sand near or at the surface, the rhizomes of *Equisetum* may eventually underlay most of the fan.

Immigration

The process of immigration is controlled by several factors: (1) the nature of the plant propagule, (2) the source of propagules, (3) the transport medium, (4) the depositional environment encountered by the propagule, and (5) the specific physiological requirements of the individual species. We can classify the source of propagules according to the distance they must travel. Some propagules originate from plants growing on the fan, some from adjacent plant communities, and others from remote locations, most notably the alpine tundra. *Koenigia islandica*, *Minuartia rubella*, and *Silene acaulis*, found growing on the fan, most probably originated from the alpine tundra above Lawn Lake. Other species, such as *Deschampsia cespitosa*, are found from upper montane to alpine; therefore, the origin of these propagules is uncertain.

Monkey flower (*Mimulus gemmiparus*), previously known from only three other locations in the park, also grows on the alluvial fan (Yeatts 1987). This annual plant propagates itself vegetatively by a specialized petiole and is listed as a Category 2 species by the U.S. Department of the Interior, Fish and Wildlife Service. (Category 2 species are candidates under review for formal listing as threatened or endangered.) The location of monkey flower found on the alluvial fan indicates origin from a fourth, unidentified source within the park. The plant has been found at only one location outside Rocky Mountain National Park.

Transport medium has played an important role in determining the kinds of immigrating species and the locations in which they may grow. Seeds having plumed appendages, such as those of willow, are adapted for dispersal by wind and may be deposited over a wide area. In contrast, propagules dispersed primarily by water may be limited to locations over which water has flowed. The seeds of some species may be moved by both wind and water.

The transport medium controls the path traveled by the propagules. Prevailing wind direction on the alluvial fan is primarily from west to east. The flow of water on the western end of the alluvial fan is primarily north to south; on the central portion of the fan, water flows northwest to southeast. Depending on the structure of the propagule, the path traveled may be highly directional.

Koenigia, *Minuartia*, and *Silene*, described earlier, are found on the fan almost exclusively in the braided channels of the Roaring River flowing through the western portion of the alluvial fan. These immigrants were almost certainly transported from the tundra by way of the Roaring River drainage. These plants have small, naked seeds that are borne close to the ground and are probably not easily entrained by wind; transport may be limited to water.

Other species, such as those of greater stature (and so releasing seeds from a greater height) or species producing seeds more easily entrained by wind, may be transported by both wind and water. For example, *Juncus arcticus* has small, spherically shaped seeds that would seem to be poorly suited to be transported by wind, yet some individuals of this species occupy locations between water courses where transport by stream is unlikely. The seeds of *J. arcticus* are dispersed from 40 to 50 cm above ground level, a height possibly great enough to allow aerial transport by wind. *Juncus arcticus* also grows profusely along drainage courses where seeds are likely transported by water. Other species, such as *J. ensifolius*, exhibit a similar pattern. But distribution is not conclusive evidence explaining the role of seed transport, since the ultimate appearance of a plant depends not only on the arrival of the seed, but also on the suitability of the environment for germination and the establishment of that particular plant. Experimental manipulation would be required to separate the two effects.

The fourth of the five factors listed earlier that affect immigration is depositional environment. Depositional environment can affect the fate of a plant in three ways. First, the site may be more or less conducive to deposition. For example, small seeds may not be deposited in high-velocity reaches of a stream channel. Second, site conditions affect germination. The term *safe site* has been used to describe the condition favorable for seed germination and seedling establishment of a given species (Harper 1977). And third, site conditions determine the vegetative growth and reproductive capacity of the mature plant. As described earlier, depositional environments on the alluvial fan changed significantly in the first few years in response to physical and chemical forces.

As a result, conditions that were optimum for a given species at one time might later change to an unfavorable environment.

Changes in the rate of establishment may reflect parallel changes in two or more of the factors described above. For example, in 1983 *Juncus buffonius* individuals were rare; in 1984, they were occasional. By 1985, *J. buffonius* was widespread throughout the alluvial fan. *Juncus buffonius* is an annual rush reproducing from seed. The increased distribution could have been caused by increased numbers of safe sites (due to chemical or physical changes) or by increased numbers of seeds caused by a shift from a remote source of propagules to a local source. I believe that the increased importance of *J. buffonius* is primarily due to the increasingly greater volume of local seeds.

In the case of *Silene acaulis*, the depositional environment of the alluvial fan resulted in a growth rate that far exceeded that expected of a plant of the same species growing on alpine tundra. *Silene* typically grows on dry, windswept sites in the alpine and forms cushions that are said to require many years to achieve diameters of 10–20 cm. On the alluvial fan, specimens were found in 1987 with diameters of about 20 cm. An individual with a diameter of 10 cm was observed on the newly exposed surface of Lawn Lake (elevation 3,349 m) in 1985. These individuals could only have maximum ages of 4 and 2 years, respectively. Under normal circumstances in the alpine, the deep taproot of *Silene* may be restricted to fissures in the rock in which nutrient supplies are more limited than the nutrients available in the mantle of lakebed and alluvial sediments.

Willows

In May of 1983, the sand of the alluvial fan appeared so sterile that most observers believed a long time would pass before vegetation could colonize the fresh sediment. Within 2 months, the sand was dotted with tiny leaves that were soon identified as being seedlings of *Salix*. Some patches had seedling densities as high as 20,000/m^2, but densities of 1,500/m^2 were most typical throughout the alluvial fan. In an undisturbed willow carr, willow seedlings appear only occasionally and are usually limited to sites having a well-drained mineral soil, such as on the alluvial fan formed where streams enter the calm water of beaver ponds or on meander bars of dry stream channels.

Willow seeds are roundish, small (about 0.7 mm), and have a collar at about the middle from which extend several hairs that range to about 5 mm long. When the capsules open and the seeds are exposed to air, the hairs spread to a cottony form that is easily caught by light breezes. Mechanical disturbance can separate the seed from the collar and plume. On the fan, seeds are probably transported to their site of deposition primarily by wind; seeds falling in channels of running water are probably carried out of the area. Willow seeds are viable for only a few days (Schopmeyer 1974).

The source of willow seeds falling on the alluvial fan could have been either from local, surviving shrubs or from plants to the west up the Fall River drainage. Because willow seeds are easily carried by wind, we can't be certain of the source of the new seedlings. However, once fully entrained in high wind, seeds are probably carried a long distance. Around the base of mature shrubs there was often a dense accumulation of seedlings produced by seeds that apparently dispersed in still air and fell directly to the ground.

Seeds dispersed under light wind conditions are probably spread rather evenly, each point on the alluvial fan having a fairly equal probability of receiving some. But the final distribution of willow shrubs is determined not only by seed rain, but also by depositional environment and the individual's physiological requirements. One critical aspect of depositional environment is the likelihood of the seed being transported again from its initial resting place. Observations were made in 1986 to determine how differences in topography might affect the number of seeds available for germination. Willow seeds were counted along a topographic transect within quadrats measuring 10 × 25 cm. The seeds were identified primarily by observing the attached plume. Because the plumes soon separate from the seeds, making the seeds difficult to see, the number of seeds counted in each quadrat do not represent annual seed rain, but instead represent the seed rain occurring in the recent past, before the plumes separated from the seed.

In Fig. 6, the number of seeds per quadrat is plotted above a line defining the topography of the transect. No seeds were found in the elevated topography in the central portion of the transect. Sand on high topography dries rapidly; the plumes probably remain erect and the seeds are apt to be moved again by wind. Most seeds were found on the moist slope in the eastern part of the transect. As seeds become moist, the plumes collapse and cling to the soil. The moist seeds are not likely to be moved again by wind. Seeds deposited in channel bottoms are apt to be washed away. Even though they may be evenly dispersed by light wind, most seem to remain in zones that are neither very dry nor very wet (i.e., they do not contain running water). Because a willow seed is viable for a short time, the first few days following dispersal are important in determining its future fate.

Once a viable seed has come to rest, its next crucial test is that of germination and seedling establishment. Data were collected in 1983 from permanently marked 10- × 25-cm quadrats to determine germination rates within different environments across the alluvial fan. Sample sites were selected to include as much variety as existed; they ranged from locations that were dry and exposed to moist locations sheltered by nearby shrubs. In 1984, the plan was to count the number of surviving 1-year-old seedlings in those permanent quadrats to determine the number of seedlings that survived 1 year. Unfortunately, elk trampled most of the permanent plots, leaving only a few intact.

In Table 3, sites are characterized by their degree of shelter and by soil moisture. In some areas, no seedlings could be found, so the complete mortality of seedlings was obvious even though the exact quadrat location could not be determined. The seed germination that dispersed in still air onto moist ground under shrubs was remarkable (almost 20,000/m^2); about 50% of the

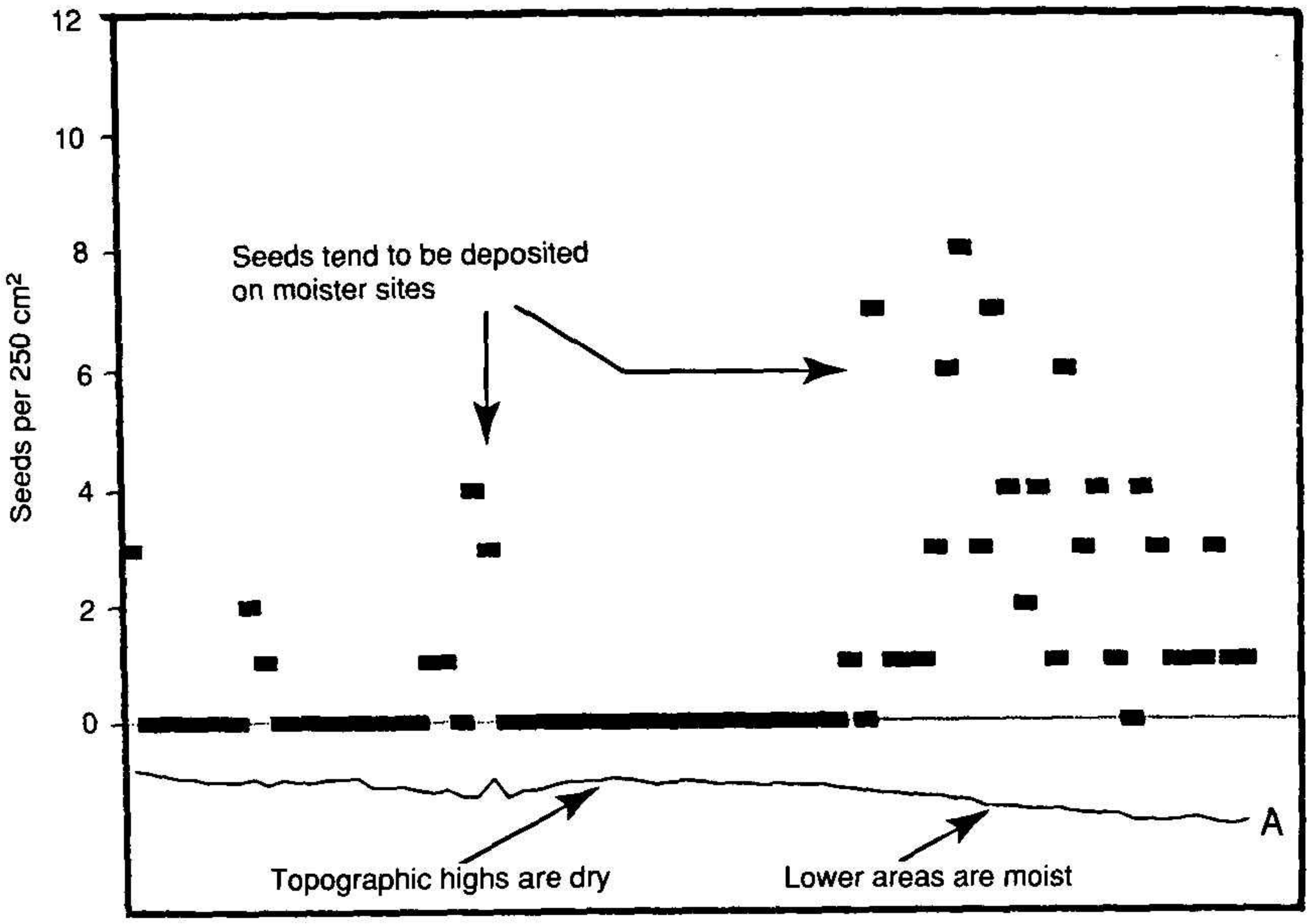


Fig. 6. The number of seeds deposited during a period was measured across a topographic transect. The bottom line (A) describes the profile of that transect. Most seeds were found on moist terrain, intermediate between the very dry and very wet portions of the transect. Seeds that landed on the dry areas were probably blown off by wind; seeds landing in the lowest sites were probably removed by running water.

ground was covered by tiny seedling leaves. At the end of summer, these plants were significantly smaller than seedlings growing elsewhere. Although some seedlings of that dense cohort survived to the 1984 census, all were dead by the end of the 1984 field season. Fewer seeds germinated under sheltered,

Table 3. *A comparison of germination and 1-year survival of willow (*Salix *spp.) related to different types of environment on the alluvial fan.*

Sample site[a]	1983		1984		Survival(%)
Sheltered, wet[b]	6,560[c]	(1,280)	few[d]	—	small
Sheltered, moist	19,840	(1,680)	(40)	(100)	2
Sheltered, dry	520	(160)	0	—	0
Exposed,[e] moist	2,520	(400)	1,480	(240)	68
Exposed, dry	480	(40)	0	—	0

[a] Samples consisted of three 10- × 25-cm quadrats.

[b] Sheltered sites were situated within dense stands of willow; wet sites had substrates that were saturated at the surface over the entire growing season.

[c] Numbers per square meter.

[d] The permanent quadrats were trampled by elk in winter 1983–84. The assessment that few would have survived is based on observation of seedlings growing outside the permanent quadrats.

[e] Exposed sites had no vegetation nearby.

wet conditions (6,560/m^2) Because the permanent plots were destroyed by trampling, exact survival is unknown, but a few seedlings were in the general area. A few juveniles persisted through the date of the last observation in 1988. Few seeds germinated under dry, sheltered conditions and, within the plots, none survived. However, this type of site is one in which aeolian dunes are being formed (as described earlier), and some seedlings have become established elsewhere on this fine-textured substrate. Under exposed, moist conditions, modest germination (2,250/m^2) was followed by high survival (68%). These conditions have the most successful establishment. Under exposed, dry conditions, few seeds germinated and all (within the permanent plots) were killed by sand erosion.

One of the most interesting aspects of willow immigration was the short time over which soil conditions were appropriate for establishment. A few seedlings of the 1984 cohort were observed to survive to 1985. While seeds germinated on sandy, moist areas from 1985 through 1988, no 1-year-old seedlings were observed to result from those cohorts. Most of the juvenile willows on the alluvial fan are of the 1983 cohort. We believe that germination conditions were altered by the chemical and physical changes described earlier in this chapter.

Seeds were germinated in flats containing coarse sand (collected from the surface of the alluvial fan), medium-grained sand (collected from 10 cm deep), ferric hydroxide crust, and leaf mulch (like that present at the base of willow shrubs from 1984 onward). The only seeds to show substantial germination were those grown on the medium sand. The ferric hydroxide crust seemed to be either too wet or too dry. The precipitate forms under conditions that may be too wet, and therefore too anaerobic, for germination. Once formed, the precipitate often dries to a hard crust that may either be too dry for water uptake by the seed or perhaps so slick that seeds are blown away by wind. The coarse sand and leaf mulch both seem too dry to sustain germination.

In 1986, the topographic transect used to measure seed deposition was also used as another measure of seedling survival. The number of juveniles was counted in 0.25- × 0.25-m quadrats. The length of the longest shoot was also measured for each plant. The density data are plotted in Fig. 7, where juveniles are seen to be present at about the same locations as those in which the seeds were found (compare with Fig. 6). Because this location is not one of the permanent 1983 plots, no specific comparison can be made with the initial number of seedlings that were present. But as a rough estimate (using 2,520/m^2 as initial seedling density in 1983), only about 2% survived from germination through 3 years.

The distribution of seeds or seedlings may not be a good predictor of which individual plants will ultimately come to dominate the willow population, either in stature or by producing additional progeny. An average shoot length was calculated for each quadrat by dividing the sum of the shoot lengths by the number of individuals present in the plot and used as a measure of vigor (Fig. 8). The drier portions of the transect produced some of the largest shrubs.

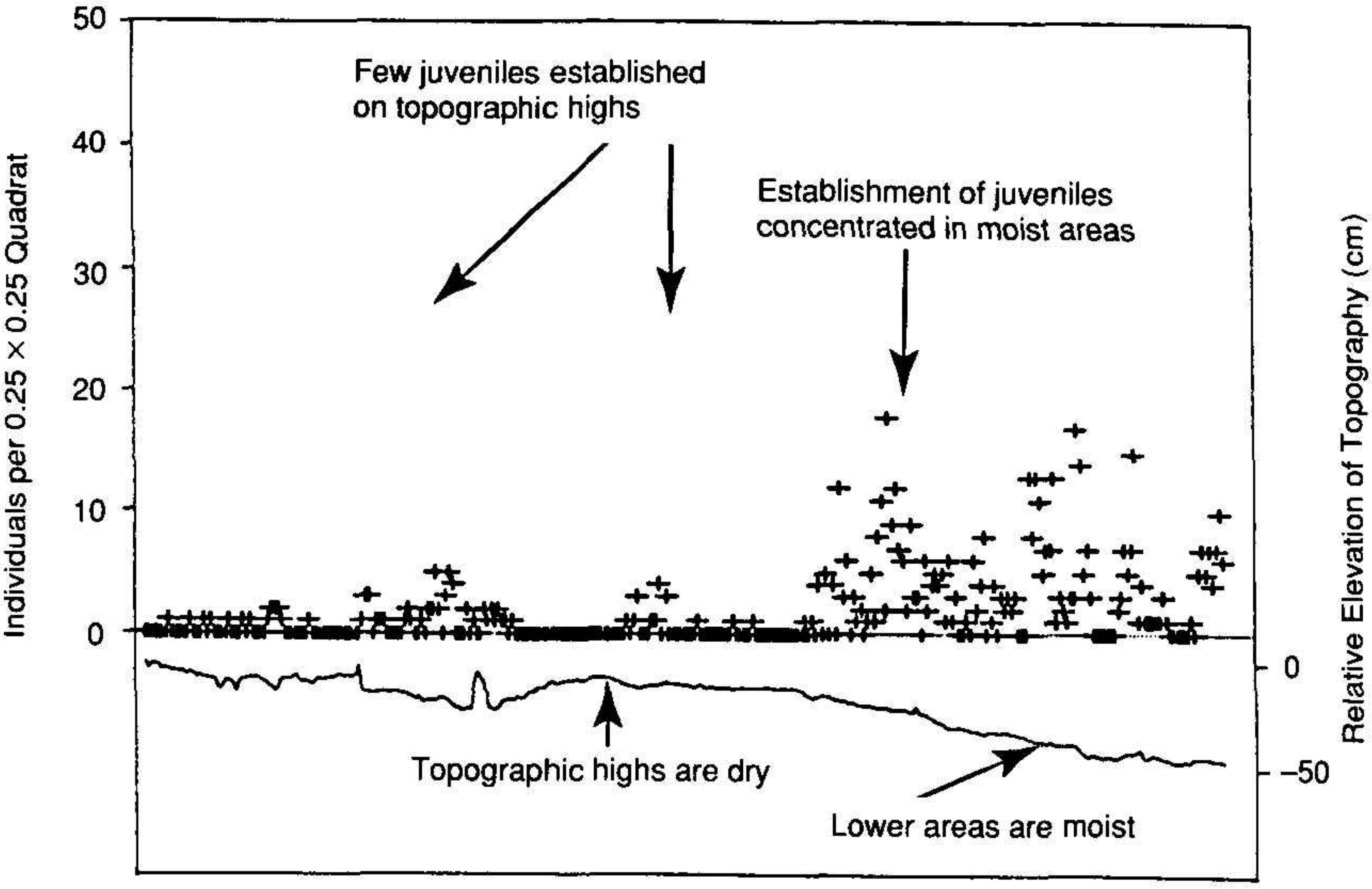


Fig. 7. Numbers of juvenile willow were observed along a topographic transect similar to that described in Fig. 6. The relation between numbers of juveniles and topographic location was found to be similar to that between the density of seed deposition and topography as described in Fig. 6.

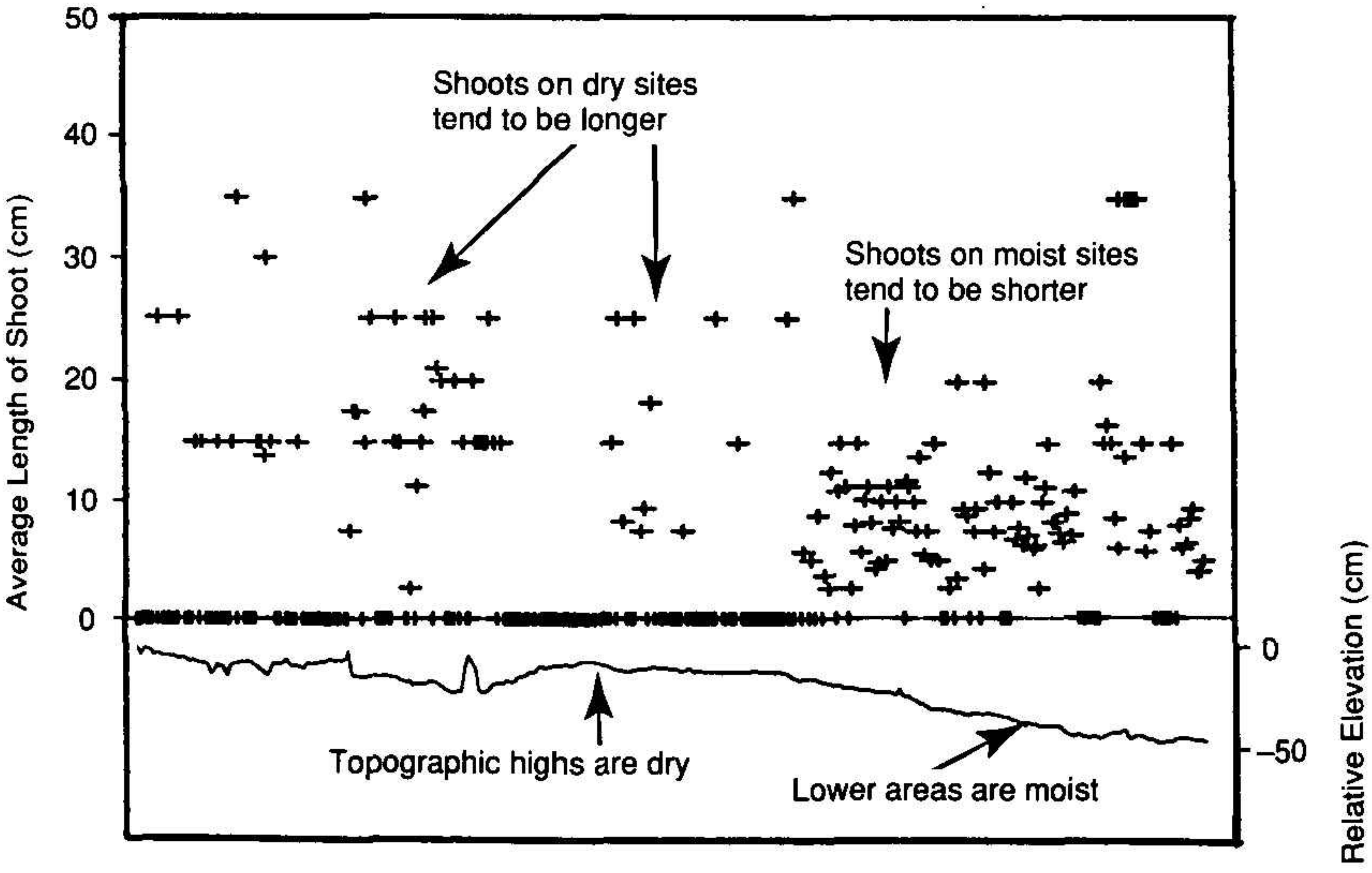


Fig. 8. Drier sites with a low density of juveniles had a greater mean shoot length compared with that of plants on moister sites; differences could be due to either the effects of competition or to the fact that conditions favorable for seed germination and seeding establishment are different from conditions favorable for plant development.

Therefore, even though those sites are not the most favorable in terms of either seed deposition or seedling establishment, they may ultimately be the source of the dominant individuals within the population.

Distribution of Plants With Respect to Environmental Gradients

Three factors seem most important in determining the character of existing plant communities: soil moisture, initial texture of the sediment, and proximity to surviving vegetation. Of the three, perhaps initial texture is the most fundamentally important. The texture can be roughly classified into two groups: coarse sediment consisting primarily of boulders, cobbles, and gravel; and finer sediment consisting primarily of sand.

The coarse sediment is found in the boulder rubble along the Roaring River drainage and in the western portion of the alluvial fan. The boulder rubble could be characterized as being dry and having virtually no surviving vegetation; among the boulders, new vegetation is sparse. In the area southwest of the boulders where the sediment is composed mostly of cobbles, a small stand of *Populus angustifolia* is the principle surviving vegetation. The Roaring River braids across this portion of the alluvial fan, meandering from one side to the other. Sites not close to a stream channel may be quite dry and soil moisture may vary greatly depending on the position of the channel at any given time. Weedy plants, such as sheep sorrel (*Acetosella vulgaris*), are found as isolated individuals. Lodgepole pine (*Pinus contorta*) seedlings now grow on sites where mature *P. contorta* died.

As described in an earlier section, moist, braided-stream bottoms are also sites on which alpine plants are found. The remainder of the alluvial fan, which consists of sand-sized sediment, can be classified according to whether or not surviving vegetation is present and the degree of soil moisture. Stands of surviving *Salix* spp. are found in both wet and dry areas of the fan. *Salix monticola*, *S. geyeriana*, *S. phylicifolia*, *S. drummondiana*, and *S. exigua* have been collected on the fan, with the first two species by far the most common.

Surviving *Salix*, growing in what are now moist-to-wet conditions, are found in the central portion of the fan and along the northern perimeter. Under these conditions, *Calamagrostis canadensis* and *Equisetum arvense* are important associates. Locally, *E. arvense* forms dense stands that virtually cover the ground. *Calamagrostis canadensis* is restricted mostly to the vicinity of shrubs and dead aspen. Many of the species growing under moist conditions where no survivors exist also grow among the willows, but their relative importance is significantly reduced by the dense growth of *E. arvense*.

Surviving *Salix* growing under dry conditions are found primarily in the eastern and southern portion of the alluvial fan. Here, *E. arvense* is locally present but not at the density found with *Salix* in moist sites. On the dry areas, *C. canadensis* has expanded from the base of willow shrubs to become an important component of the flora. These sites also have fine material deposited by wind, which created conditions suitable for willow seedling immigration.

Under dry soil moisture conditions where no surviving shrubs or trees exist, few plants have become established. While these areas may be moist for short periods, for much of the summer the sand is hot and dry. The grasses redtop (*Agrostis alba*) and timothy (*Phleum pratense*) are among the few species found in the drier areas and may establish themselves by rapid root growth into the moist zone lying beneath the surface before the upper soil zones become excessively dry. In places, rhizomes of *E. arvense* originating from as far away as 10 m have been excavated from beneath dry sand. In time, shoots of *E. arvense* may form dense stands and ameliorate the dry conditions that exist now.

The immigration of individuals onto the alluvial fan is most visible on moist sites where no surviving vegetation exists. As described earlier, willows were the first to make a significant appearance, with a surge in population numbers in 1983 followed by a dramatic decline; we estimated that under the best of conditions, only roughly 2% survived from 1983 through 1988. In contrast, *J. buffonius* started out more slowly with only a few, isolated individuals and progressed to populations that have locally come to dominate some areas.

Three kinds of plants dominate the moist, open areas: *Salix* sp., *J. buffonius*, and mosses. The willow is probably *Salix monticola*, but identification with certainty is impossible. The most frequently occurring mosses are *Leptobryum pyriforme*, *Bryum creberrimum*, and *Funaria hygrometrica* (Flock 1987). In 1988, cover percent was estimated using quadrats 1.0 × 0.5 m for willow and *Juncus* and 10 × 25 cm for mosses. The quadrats were ranked by a subjective estimate of soil moisture obtained largely by noting where the quadrats were located with respect to topographic relief. Figure 9 shows how soil moisture affects the cover percent of the plants.

While moss and willow clearly decline at both the wet and dry end of the spectrum, *J. buffonius* increases in biomass up to a shallow depth of standing or running water. Presumably, problems relating to seed deposition, not excessive moisture, limit the ability of the plant to extend its range into very wet sites.

Mosses may be more important along the drier end of the spectrum than is evident from Fig. 9. Areas where 50% cover was measured may have resulted from previous stands being trampled by elk. Patches of sand, roughly a hoofprint in outline, overlay buried moss. In fall, considerable evidence existed of disturbance by elk throughout the alluvial fan.

In the wet areas of the channel basins, a variety of wetland plants are found. Among the most common are *Carex utriculata*, *Carex aquatilis*, *Agrostis scabra*, *Deschampsia cespitosa*, *Glyceria maxima*, *Epilobium* sp., *Juncus buffonius* (along the edge), *Juncus ensifolius*, and *Callitriche palustris*.

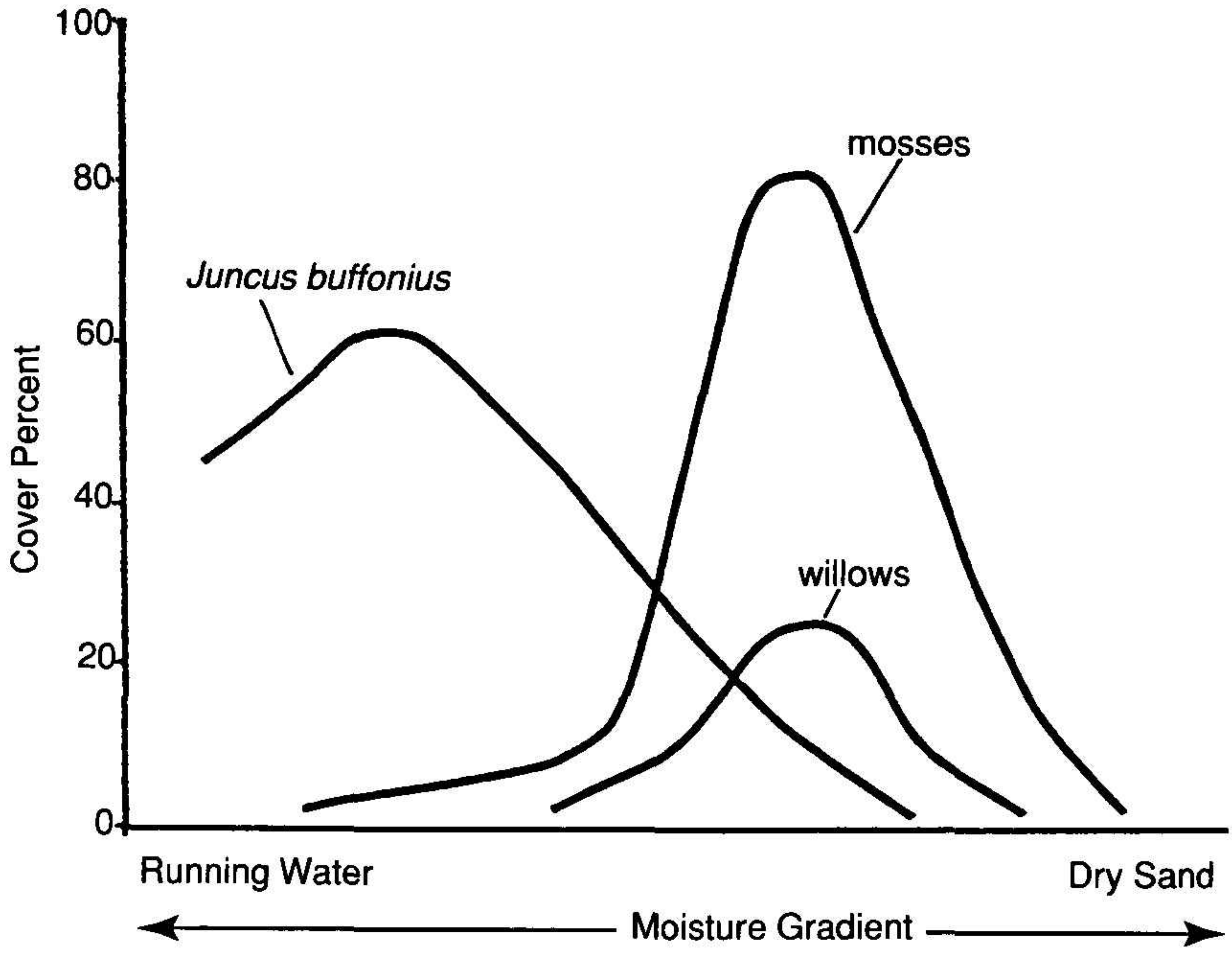


Fig. 9. Willows, mosses, and *Juncus buffonius* dominate much of the alluvial fan in which mature willows are not established. The distribution of the plants is largely determined by soil moisture. The cover percent curves of willow and moss are symmetrical—the plants are probably limited at either end of the gradient by moisture. The asymmetric curve shown for *J. buffonius* probably results from limitation by moisture (at the dry end of the scale) and by failure of seedings to become established in flowing water.

In general, the greatest diversity of species on the alluvial fan is found closest to areas not covered by flood sediment; this area provides a source of propagules. The northern perimeter of the alluvial fan is probably most exposed to a variety of propagules. Along this perimeter, the variety of species available for immigration is determined, in part, by the presence of plants introduced during the operation of a homestead in the area.

Because of the shallow depth of sediment along the edge of the alluvial fan, it is often difficult to determine whether a given plant originated as an immigrant (from seed) or whether the plant emerged as a survivor of the flood. Wild raspberry (*Rubus idaeus*), for example, was found soon after the flood growing among the base of willows along the northern part of the alluvial fan; these individuals possibly are survivors.

Other species have clearly become established as immigrants originating from the northern margin; *Phleum pratense* and *Agrostis alba* are notable examples. Both species are exotic and were probably introduced as pasture grasses before the land on which they were cultivated was acquired by the National Park Service. Both species rapidly became established throughout the alluvial fan, but their patterns of distribution differ. While *Phleum* grows in a relatively dispersed distribution, *Agrostis* has locally formed dense stands, and the density of both species on the alluvial fan decreases from north to south. Canada thistle (*Cirsium arvense*) is another exotic making inroads onto the alluvial fan. Other exotics, such as yellow sweet clover (*Melilotus officinalis*) and great mullein (*Verbascum thapsus*), are mostly limited to the margin of the road running along the northern perimeter of the fan.

Literature Cited

Barrick, K., and M. Noble. 1993. The micronutrient status of tree species affected by the Lawn Lake Flood, Rocky Mountain National Park, Colorado. Pages 70–85 *in* H. E. McCutchen, R. Herrmann, and D. R. Stevens, editors. Ecological effects of the Lawn Lake Flood of 1982, Rocky Mountain National Park. National Park Service, Scientific Monograph NPS/NRROMO/NRSM-93/21.

Etherington, J. R. 1982. Environment and plant ecology. John Wiley & Sons, New York.

Flock, J. W. 1987. Baseline inventory and mapping of mosses of Lawn Lake alluvial fan, Rocky Mountain National Park. Unpublished final report, Rocky Mountain National Park, Colo.

Folk, R. L. 1968. Petrology of sedimentary rocks. Hemphill's, Austin, Tex.

Harper, J. R. 1977. Population biology of plants. Academic Press, London.

Jarrett, R. D., and J. E. Costa. 1986. Hydrology, geomorphology, and dam-break modeling of the July 15, 1982 Lawn Lake Dam and Cascade Lake Dam failures, Larimer County, Colorado. U.S. Geological Survey Professional Paper 1369. 78 pp.

Litaor, M. I., and R. B. Keigley. 1993. Geochemistry of iron oxides in the Roaring River alluvial fan, Rocky Mountain National Park, Colorado. Pages 55–69 *in* H. E. McCutchen, R. Herrmann, and D. R. Stevens, editors. Ecological effects of the Lawn Lake Flood of 1982, Rocky Mountain National Park. National Park Service, Scientific Monograph NPS/NRROMO/NRSM-93/21.

Schopmeyer, C. S., technical coordinator. 1974. Seeds of woody plants in the United States. U.S. Forest Service, Agricultural Handbook 450.

Yeatts, L. 1987. Survey of Rocky Mountain National Park to document special interest plants and the general flora. Report prepared for the National Park Service by the Denver Botanic Gardens, Colo.

☆ U.S. GOVERNMENT PRINTING OFFICE: 1993 — 776-201

March 3, 1849

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural and cultural resources. This includes fostering wise use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people. The department also promotes the goals of the Take Pride in America campaign by encouraging stewardship and citizen responsibility for the public lands and promoting citizen participation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

NPS D-172 •March 1993•