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ECOLOGICAL STUDIES IN THE COLORADO ALPINE

A FESTSCHRIFT FOR JOHN W. MARR

Edited by
James C. Halfpenny

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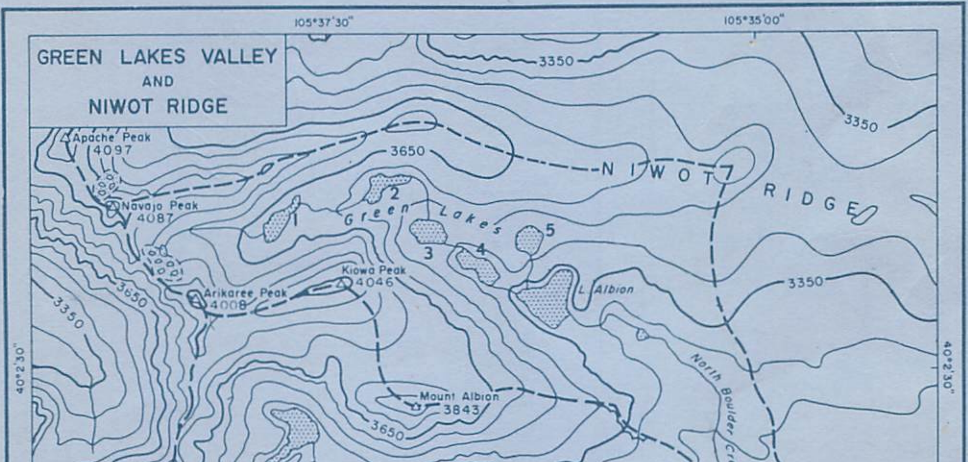

A Contribution to
University of Colorado
Long-Term Ecological Research

Occasional Paper No. 37
1982

INSTITUTE OF ARCTIC AND ALPINE RESEARCH • UNIVERSITY OF COLORADO • BOULDER

ECOLOGICAL STUDIES

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University of Colorado
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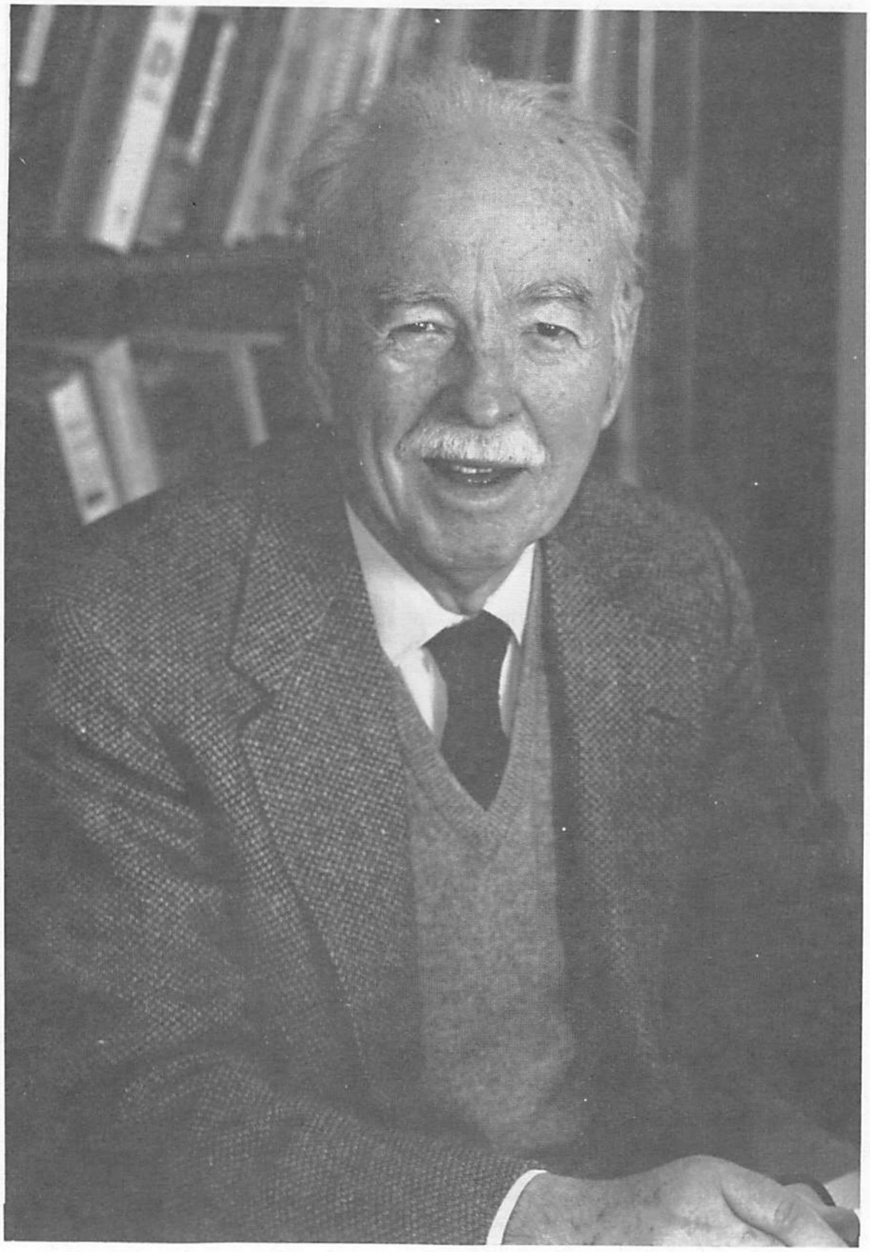
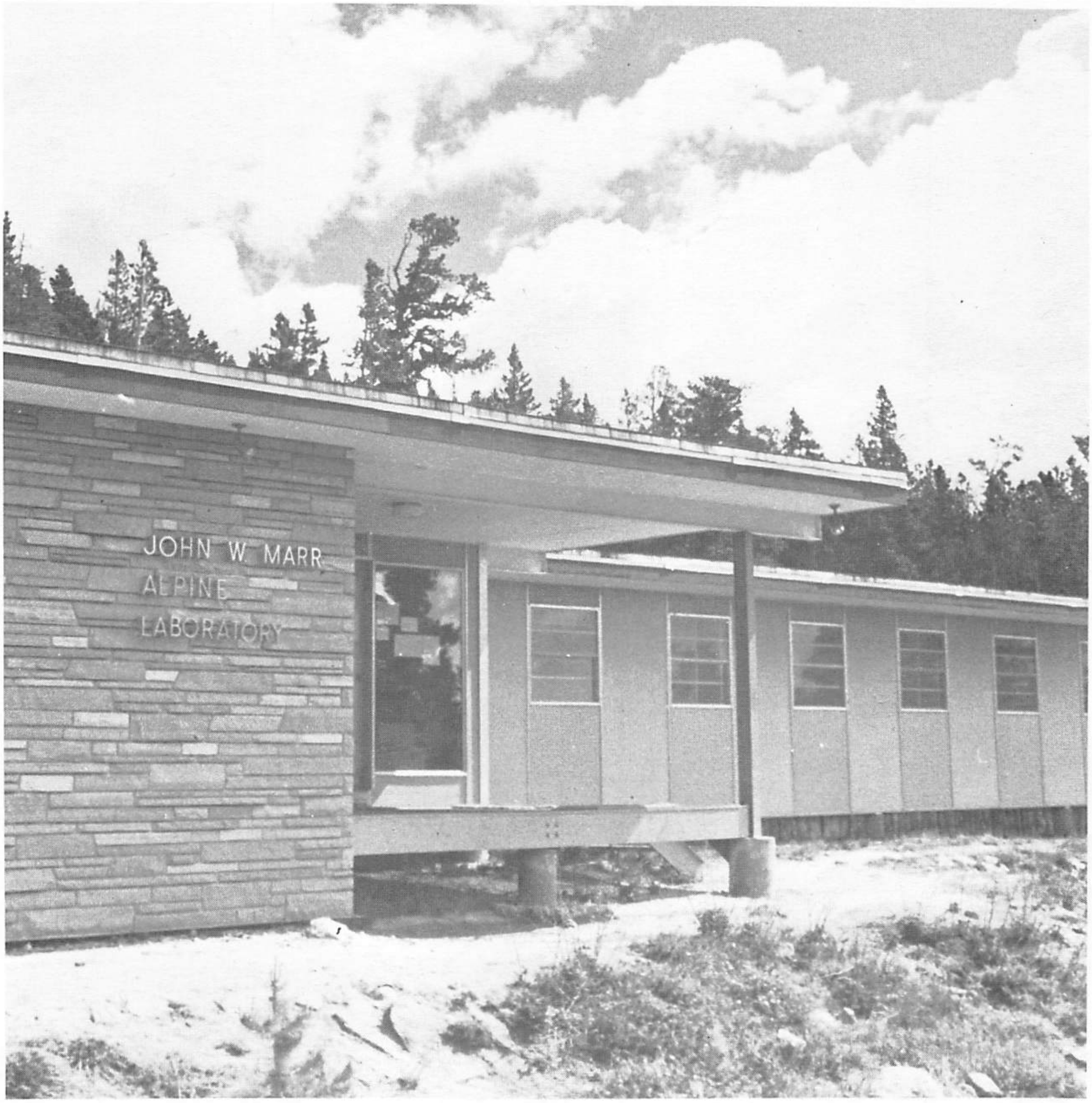


John W. Marr, founder of the Institute of Arctic and Alpine Research



John W. Marr Alpine Laboratory, Mountain Research Station

PREFACE

A Festschrift for John W. Marr

This collection of papers has been assembled with love and respect for Professor John Winton Marr. Its publication honors Professor Marr, at the time of his retirement from the University of Colorado, for his contributions to long-term ecological research in the Colorado alpine.

Professor Marr is one of our finest faculty members, his long and distinguished career at the University of Colorado began in 1944. Professor Marr is an outstanding teacher and was the 1982 recipient of the Stearns teaching award. He has made major contributions to the understanding of Colorado plant ecology. Professor Marr's experience as a U.S. Air Force Arctic Specialist during World War II and his doctoral research in the Canadian Arctic led him to realize the value of the University field station as a teaching and research tool. In 1946 following its brief use as a rest and recreational center for returning World War II veterans, he began his famous Winter Ecology classes which opened the way for the facility to become a year-round operation. This led to the founding by Professor Marr of the Institute of Arctic and Alpine Ecology in 1951. Soon afterwards it became the Institute of Arctic and Alpine Research. Professor Marr was appointed director of the new institute by University President Robert L. Stearns in 1951 and he remained as director for 16 years until 1967.

The present acronym for the institute, INSTAAR, came after Professor Marr's term as Director. Today, thanks to the strong foundations which Professor Marr laid, INSTAAR enjoys a role as the foremost institute in the nation dealing with mountain and polar problems; INSTAAR also has an excellent international reputation.

This volume will be presented to Professor Marr during the rededication and naming of the John W. Marr Alpine Laboratory at the University of Colorado Mountain Research Station on July 16, 1982. The Alpine Laboratory was built in 1962 by funds secured by Professor Marr. Twenty years later the building is still the center of research at the Mountain Research Station and we are proud that he has allowed us to name it in his honor.

This book, Occasional Paper number 37 of the Institute of Arctic and Alpine Research represents the first formal report of the University of Colorado, Long-Term Ecological Research project (CULTER). This report reviews the understanding of the alpine ecosystems as a first step in the CULTER which is monitoring and studying the alpine ecosystem as exemplified on Niwot Ridge and in Green Lakes Valley above the Mountain Research Station. Five University of Colorado departments and 23 senior scientists are involved in CULTER which is coordinated by INSTAAR. CULTER is part of a formal national Long-Term Ecological Research Program (LTER) sponsored by the National Science Foundation (NSF), Division of Environmental Biology. CULTER is one of eleven projects which are funded in this program. Each represents a North American major biome or ecological situation. CULTER is now in its second year of a five-year funding cycle; the NSF grant award for the first five years totals $1,300,000. None of this would have been possible without the heritage of research begun by Professor Marr.

This collection of papers has been edited by Dr. James C. Halfpenny who is Field Director of the Mountain Research Station and Coordinator of the CULTER program. I thank Dr. Halfpenny and the staff of INSTAAR who have worked with great devotion and effort for our cause.

Dr. Patrick J. Webber
Director, Institute of Arctic and Alpine Research
Professor, Environmental, Population and
Organismic Biology

ACKNOWLEDGMENTS

I should like to thank my predecessor as Field Director of the Mountain Research Station, Misha Plam, who was instrumental in urging our colleagues and to apply for the Long-Term Ecological Research grant. Dr. James T. Callahan of the National Science Foundation kindly provided advice and reviewed the draft manuscript of this volume. Dr. Linda Brown and Mr. Oren Pollak reviewed several of the papers. Mr. Gregory Jones supplied the photo of John Marr.

I should like to thank a special individual who is not acknowledged elsewhere in this volume. He is Mr. Thomas Platt, manager of the City of Boulder Watershed. For decades Tom has provided access to, and knowledge of a large part of our study area. He has helped and encouraged many workers along the way.

My appreciation goes to each and every author for their fine contributions. A special thanksare due Fatima Al-Rahim and Kathleen Salzberg.Ms. Al-Rahim joined the CULTER team after we started the final manuscript preparation and did an outstanding job putting the manuscript together on the word processor. Mrs. Salzberg's expertise in editing and layout made possible a polished, finished product.

I would like to thank Dr. Patrick J. Webber, present Director of INSTAAR and Principal Investigator of CULTER, for his advice, help, and determination in preparing this volume.

The preparation of the camera ready copy of this publication was funded from a grant from the National Science Foundation (DEB-8012095) and the printing costs were provided by the University of Colorado Committee on University Scholarly Publications.

James C. Halfpenny, Editor
Field Director
Mountain Research Station
Institute of Arctic and Alpine Research

INTRODUCTION

Continuous long-term ecological research dealing with Colorado tundra dates from 1951, when Professor John W. Marr initiated the Front Range climatological network and his studies of the alpine treeline. The uppermost weather stations were located on tundra areas of Niwot Ridge. Since then, many students and scientists have worked on Niwot Ridge. Their projects have produced theses, dissertations, and papers under the auspices of several projects. Four projects of note are the East Slope Ecology Project (Atomic Energy Commission) (1956-1964), the International Biological Programme Tundra Biome (National Science Foundation) (1971-1974), San Juan Ecology Project (Bureau of Reclamation) (1970-1976), and Remote Sensing in Mountainous Areas (National Aeronautic and Space Administration) (1971-1980).

The first major report from Niwot Ridge research was Professor John Marr's Ecosystems of the East Slope of the Front Range in Colorado (1961). It is "required" reading for scientists working on Niwot Ridge. A second important reference isa synthesis collection, Geoecology of the Colorado Front Range (Ives, 1980) which contains many previously published papers collected under overviews in each discipline. It is to be hoped that the present volume, which builds on the initial work of Professor Marr and that in the Ives' collection, also will become required reading. It is designed as a state-of-science review of mountain ecology, especially for Colorado and the Niwot Ridge area. Occasional Paper Number 37 was produced as part of the prelude to the National Science Foundation's (NSF) Long-Term Ecological Research Program (LTER). The University of Colorado's program has become known as CULTER.

Long-Term Ecological Research (LTER)

The Division of Environmental Biology of NSF developed a new program which would emphasize long-term ecological research in 1979 (NSF, 1979). This new program allowed the study of environmental phenomena which do not fit into the usual two- or three-year grant period; it was designed for programs which might extend past the lifetime of a given researcher. LTER projects involve groups of investigators working at large, secure, and biologically diverse sites.

The goals of LTER are to augment the progress of ecosystem science through (1) collection of comparative data at a given network of sites representing major biotic regions of the U.S. and (2) cooperative evaluation of the scientific, technical, and managerial problems associated with long-term comparative research.

Core research topics include (1) pattern and control of primary production; 2) spatial and temporal distribution of populations selected to represent trophic structure; (3) pattern and control of organic matter accumulation in surface layers and sediments; (4) patterns of inorganic inputs and movements of nutrients through soils. groundwater. and surface waters. and (5) patterns and frequency of disturbances to the research site.

Baseline characterization of macroclimate. geology. soils and sediments. flora and fauna. and disturbance history will be undertaken in support of five core research areas.

In open competition eleven sites have been picked by NSF to form the LTER Network (Figure 1). These sites range in elevation from sea level to 4087 m on our CULTER site. The diversity of sites is enormous including, but not limited to: coastal estuaries, prairie grasslands. river systems, coastal forests. and alpine tundra.

University of Colorado Long-Term Ecological Research Program (CULTER)

The Niwot Ridge/Green Lakes Valley drainage system is the base area for CULTER's research efforts (Figure 2). This drainage system includes high peaks, glaciers, periglacial features, permafrost, alpine lakes. and tundra flora and fauna. The topography is rugged and varies from 3268 to 4087 m within 6 km. Weather conditions are harsh with a 60-d growing season. temperatures down to -37°C, and wind gusts greater than 160 km/h occur 9 mon/yr. Precipitation averages 40 cm and wind speed 42 km/h.

The CULTER study area is part of the City of Boulder Watershed and the Niwot Ridge Biosphere Reserve (designated by UNESCO and the U.S. Congress in 1979). The general public has been excluded from the Watershed since the early 1920s. Therefore. the Watershed offers a pristine area for comparison to other areas more heavily impacted by people. The whole area is of critical interest due to its location between the Denver-Boulder megalopolis on the east and coal and oil-shale development on the west. Niwot Ridge also is designated as an Experimental Ecological Reserve by the National Science Foundation.

Several subprojects comprise the CULTER study. Pathways of major information and data flow between the major study units are shown in Figure 3. At the start of the project CULTER scientists have emphasized studies of the historical and Holocene record because of the need to define the natural variability of past environments thereby providing a perspective on the present and a chance to predict the future. We have collated much of the available data in all subprojects. Later work will be concerned primarily with the real time period of LTER funding and extrapolations will be made forward and backward in time (Figure 4). Synthesis of knowledge and experience gained early in the project will provide information for management decisions in the future.

A unifying site-level hypothesis was

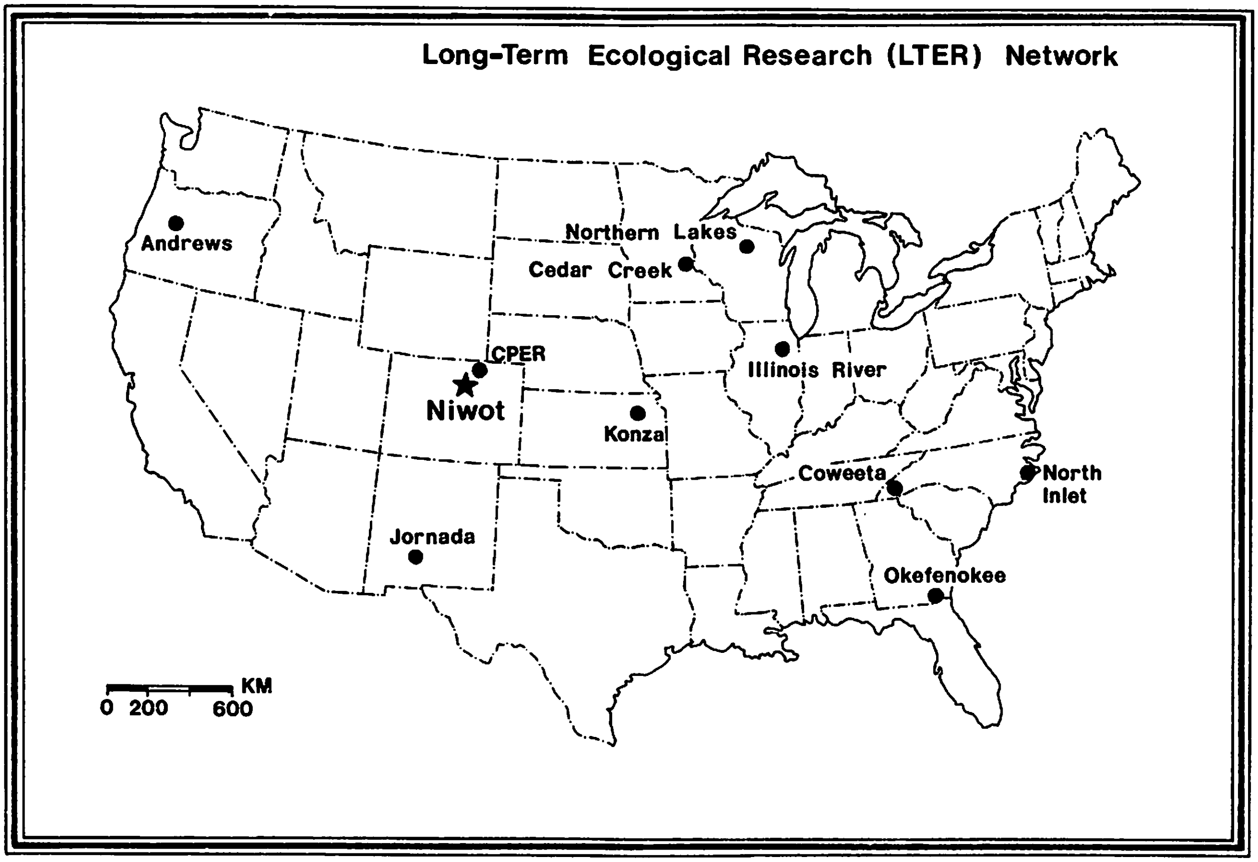


Figure 1. The current LTER sites comprising the national network are Niwot (Alpine tundra, University of Colorado); Andrews (Coniferous forest, Oregon State University and U.S. Forest Service): Cedar Creek (Oak savanna, University of Minnesota): Coweeta (Deciduous forest University of Georgia) and U.S. Forest Service); Colorado Prairie Ecological Reserve (CPER) (Shortgrass steppe, Colorado State University); Illinois River (Large river ecosystems, Illinois Natural History Survey); Jornada (Desert grassland and scrub, New Mexico State University): Konza (Tallgrass prairie, Kansas State Univeristy); North Inlet (Coastal marine ecosystems, University of South Carolina); Northern Lakes (Freshwater lakes, University of Wisconsin); Okefenokee (Freshwater swamp, University of Georgia and U.S. Fish and Wildlife Service).

developed based on the premise that the alpine ecosystem is a reflection of past, rather than present, climatic conditions. Our hypothesis is that, given such a relict status, the effect of (moderate) perturbations will be to accelerate the adjustment of the system to a state commensurate with present climate. Other (catastrophic) disturbances, for example those leading to irreversible soil loss are not included directly in tests of this hypothesis. However, the effects of catastrophic disturbances may be detected by experiments involving moderate perturbations. Subprojects, where possible, are developing hypotheses tied to the central hypothesis.

Just prior to and during the initiation of CULTER studies, investigators were asked to prepare a state-of-the-science review pertaining to their field. Emphasis was to be placed first on the Niwot Ridge area and secondarily on Colorado alpine tundra. Some unpublished original studies also were available to round out the knowledge of the Niwot study area. When the decision was made to put these reports into book form to honor Professor Marr, non-CULTER scientists were encouraged to join this effort. As a result, there is a wide range of topics and types of coverage. The resulting volume is far from complete but we hope it will serve as another milestone and synthesis for scientists working in the alpine, especially the Colorado Front Range.

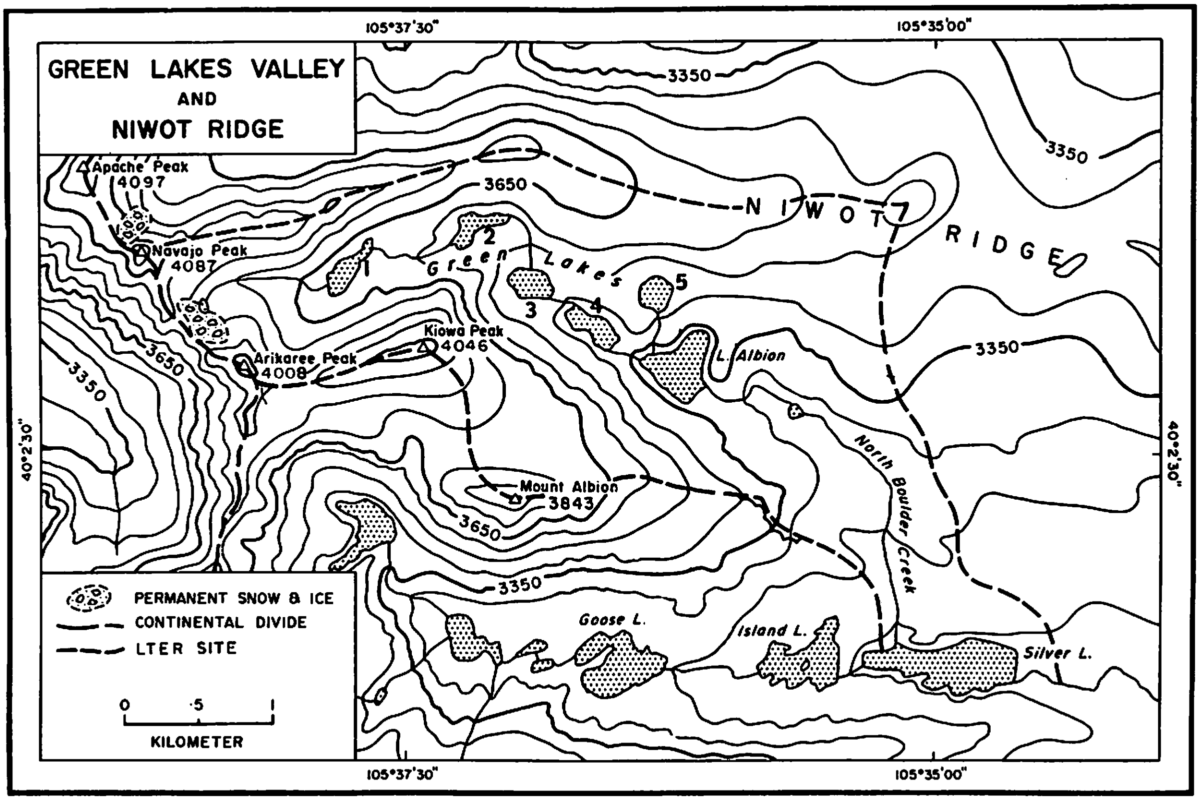


Figure 2. Green Lakes Valley and Niwot Ridge.

Ecological Studies in the Colorado Alpine reviews several abiotic and biotic components of mountain ecosystems. The availability of personnel with expertise determined which components would be included. Later studies will be designed to add the important missing components. One such obvious omission is insect herbivores.

S.E. White's paper lays the framework for all natural science studies by examining the structure and physiography of the Colorado Front Range. He provides a picture of the bedrock geology upon which today's ecosystems occur. White also summarizes the current knowledge of Front Range glaciations. This provides the background for H. Nichol's review of Quaternary history of the vegetation, especially the treelines, and climate.

N. Caine and D.E. Greenland papers cover abiotic processes at work today. Caine examines the partial contributing area concept as it relates to the influence of wind on water and sediment flows in Green Lakes valley. Greenland reviews the atmospheric research of several groups and briefly explores the question of increased acid precipitation in the Niwot Ridge area. He also defines a method for making energy budget measurements under advective conditions.

D.E. May and P.J. Webber provide a basis for plant community studies in the Alpine. Their vegetation map and productivity estimates for the Saddle will be invaluable for other scientists considering energy flow. Two other plant community papers are co-authored by P.J. Webber. J.C. Emerick and P.J. Webber report on the effects of increased snowpack on plant production. D.E. May, P.J. Webber and T.A. May report on experiments to examine the success of transplanting of whole plants with a view to possible application for ecosystem restoration.

Dramatic weather conditions and low diversity ecosystems in the high mountains make evolutionary studies appealing. C.L. Jolls considers reproductive "stategy" and resultant plant success in the alpine while M.L. Grant. J.B. Mitton, and Y.B. Linhart review the ecology and genetics of

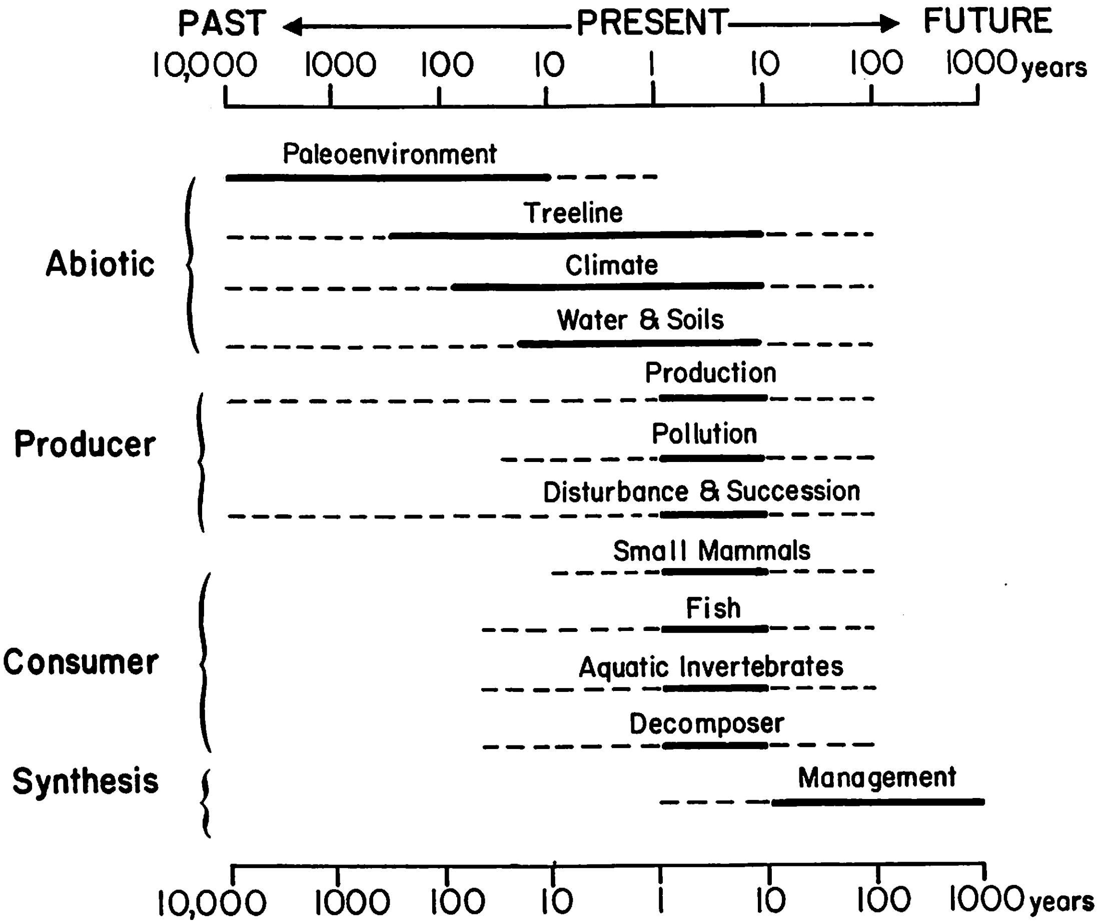


Figure 3. Possible time spans of CULTER alpine subprojects.

forest trees. These reports contribute to an increased knowledge of plant population biology which is needed for sound management practices. E.K. Bonde, J.W. Flock, and S. Shushan review the effects of air pollution on plants and consider the use of sensitive tundra species for monitoring and predicting the effect of increased air pollution on primary productivity.

In the past, Front Range tundra animal studies have not received much attention. J.C. Halfpenny and C.H. Southwick summarize past mammal projects and review the state of knowledge about mammal community and population ecology. They make a detailed comparison with the larger Arctic literature. J.T.Windell and S.Q. Foster summarize pre-LTER information on unexploited alpine fish populations including the threatened greenback cutthroat trout. This study is only possible because of the protected status of the Green Lakes valley. J.T. Bushnell and P.R. Pennak and N.M. Butler summarize the scant record of alpine invertebrates, make a preliminary comparison of the Green Lakes and their associated streams with other alpine regions, and outline much needed research for above treeline regions.

Finally, W.A. Shulls surveys the roles of bacteria in decomposition. He compares the taxonomic structure of arctic and alpine tundra communities and discusses the implications of differing species compositions.

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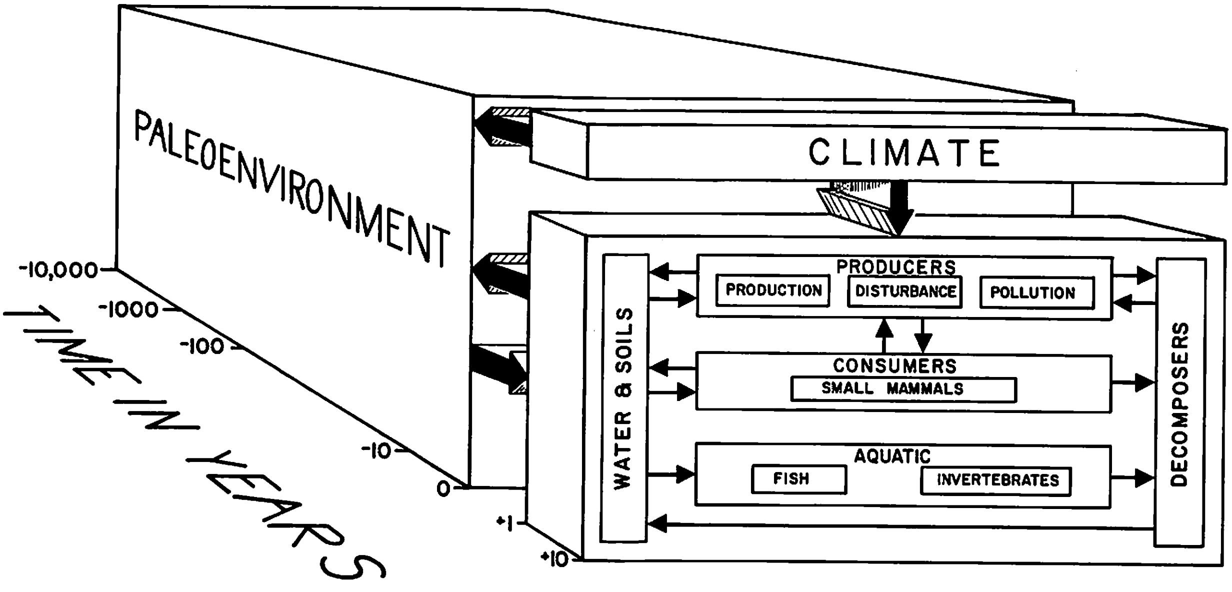

Figure 4. Major information and data flow between the CULTER subprojects.

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PHYSICAL AND GEOLOGICAL NATURE OF THE INDIAN PEAKS, COLORADO FRONT RANGE

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ABSTRACT

The 14 Indian Peaks of Colorado Front Range average > 4000 m along the Continental Divide. The area is drained eastward by six stream valleys, westward by three, traversed by four mountain passes on the south, one on the north, but by only one across the high center. Rolling hills, incised by great valleys, rise gradually from the eastern plains in giant steps to abundant glaciated valleys, many big cirques, remnants of old upland surfaces above 3500 m, and a few tiny glaciers. West of the Divide, excavation by vigorous streams and massive glaciers formed an impressive range of west-facing peaks.

The oldest of three Precambrian-aged rocks, a series of dark gneisses, were melted into most in the south by granodiorite, the Boulder Creek pluton, and, in turn, all rocks engulfed primarily in the north by quartz monzonite, the Silver Plume pluton. Small Cenozoic stocks of distinctive rock invaded the central area introducing valuable mineral deposits. The Arapaho Pass Fault, across the south edge, elevated Indian Peaks 100 m north of it and allowed streams to erode along it far to the west.

Four principal groups of glacial deposits similar to those in other Rocky Mountain ranges, occur. Evidence of Pre-Bull Lake glaciation is scarce and scattered. Bull Lake glaciation produced extensive valley glacier systems on both sides of the Divide, excavating deep cirques and forming broad now-subdued moraines. Pinedale glaciation resulted in as many but slightly shorter glacier systems, reoccupying almost all Bull Lake cirques and depositing bulky huge lateral moraines. Neoglaciation of three episodes left small cirque moraines or large rock glaciers in most cirques and three kinds of talus along valley walls.

INTRODUCTION

The Indian Peaks section of the Colorado Front Range is a small mountain world of outstanding scenery where 10 of the 14 peaks along the Continental Divide have Indian tribe names. All 14 of these peaks but one are above 3900 m, with a mean altitude of over 4000 m. From the physiographic viewpoint, the Indian Peaks occur within the Boulder District of the Northern Colorado Front Range (Fenneman, 1931) 33 km west and northwest of Boulder, a short distance from Colorado's large metropolitan areas. In addition, an Indian Peaks Wilderness Area was established in 1978, which completely surrounded and includes the Indian Peaks (see Figure 1). It adjoins the south edge of Rocky Mountain National Park, and extends south almost to Rollins Pass. Its west edge, east of Granby Reservoir, extends south around Monarch Lake and includes all of Arapaho Creek valley (Figure 2). Its east edge is quite irregular since it excludes certain lands to allow for the creation of an International Biosphere Reserve on Niwot Ridge, site of Professor John W. Marr's original research area and Mountain Ecology courses, and for continuation of the City of Boulder public water supply, and for future alpine skiing areas.

The purpose of this paper in part is to call attention to the physical and geological nature of the Indian Peaks, give insight into the bedrock and glacial character of the mountain region, and to mention how its past geologic history controls its appearance as we know it today. This is the high alpine country that inspired John Marr to initiate ecological and environmental projects and to involve scores of students and scholars for more than 30 yr from all over the world.

PHYSICAL NATURE

The impressive snow-covered Indian Peaks, easily visible from well-populated parts of Colorado, form the loftiest continuous line of summits in the Front Range. The tallest peaks from south to north are South Arapaho, 4086 m; an unnamed peak east of South Arapaho, 3976 m; North Arapaho, 4118 m; Mount Albion, 3845 m; Kiowa, 4050 m; Arikaree, 4010 m; Navaho, 4090 m; Apache, 4100 m; Shoshoni, 3955 m; South Pawnee, 3928 m; Pawnee, 3947 m; Mount Toll, 3958 m; Paiute, 3922 m; and Mount Audubon, 4033 m (Figures 2 and 3). Four well-used mountain passes in the southern part of the Indian Peaks (Arapaho Pass, Devils Thumb Pass, Rollins Pass, Rogers Pass) allow easy foot travel from east or west, as does Buchanan Pass 5 km south of Rocky Mountain National Park. Pawnee Pass, more than 200 m higher than any of the other passes, is the only pass through the highest central part of the Indian Peaks (Figures 1 and 2). This part of Colorado Front Range is drained eastward by South, Middle, and North Boulder creeks, and by South, Middle, and North St. Vrain creeks. Arapaho Creek, Cascade Creek, and Buchanan Creek flow westward from the Indian Peaks into Granby Reservoir and thence into the Colorado River.

The east side of the Front Range ascends to the Indian Peaks by several giant steps from the City of Boulder at 1630 m to a series of ridges with rolling surfaces at 2500 to 2600 m which are dissected by valleys 250 m deep. Along these ridges and beyond the limit of most glaciation, tors and rock knobs of various sizes and shapes project 10 to 30 m above a sparse forest (Figure

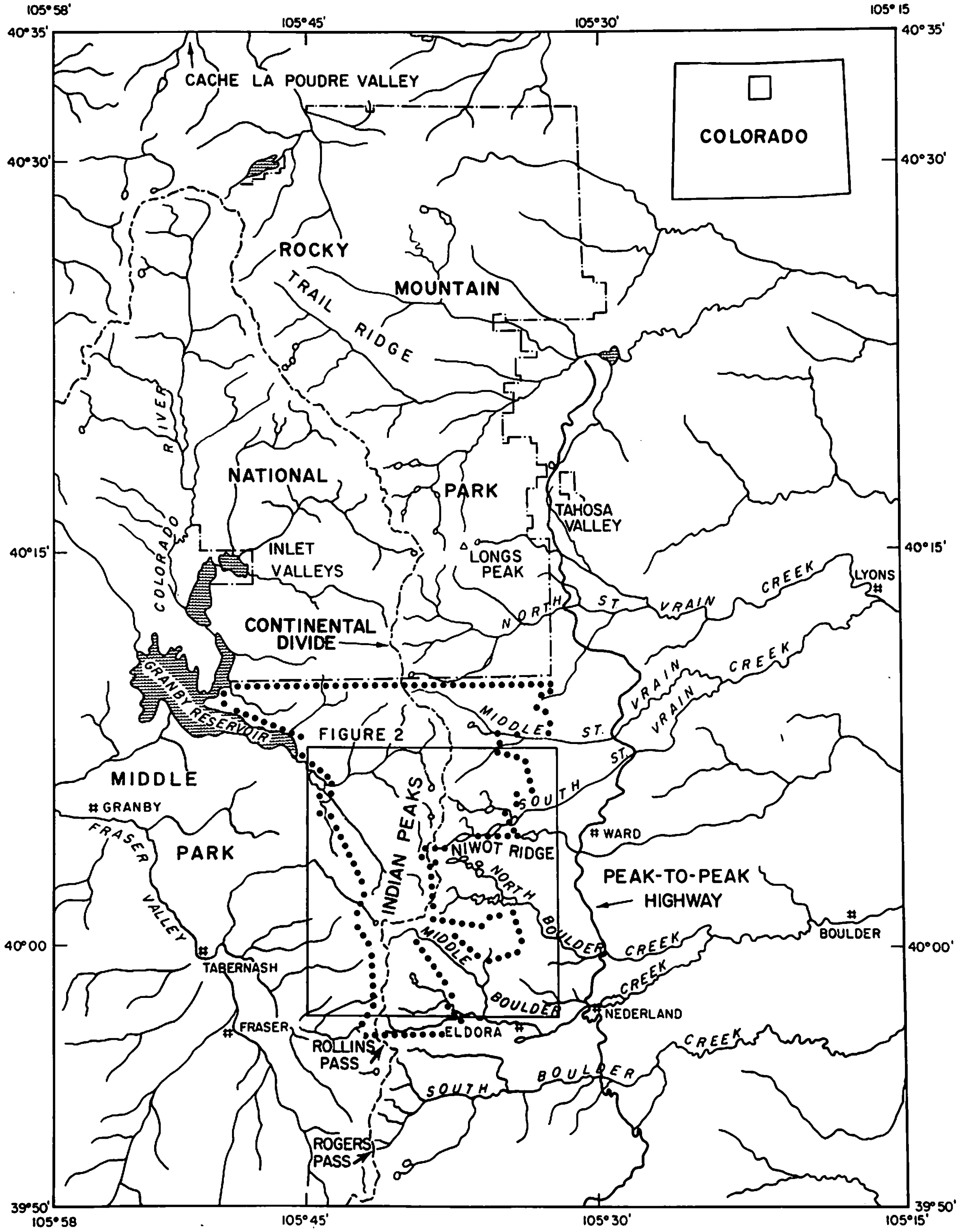

Figure 1. Location map of Indian Peaks area, Colorado Front Range. Approximate boundary of Indian Peaks area, Colorado Front Range. Approximate boundary of Indian Peaks Wilderness Area shown by crosses. Rocky Mountain National Park and area of Map 2 (figure 2 on map) are indicated. Based on U.S.G.S. Denver Mountain Area map.

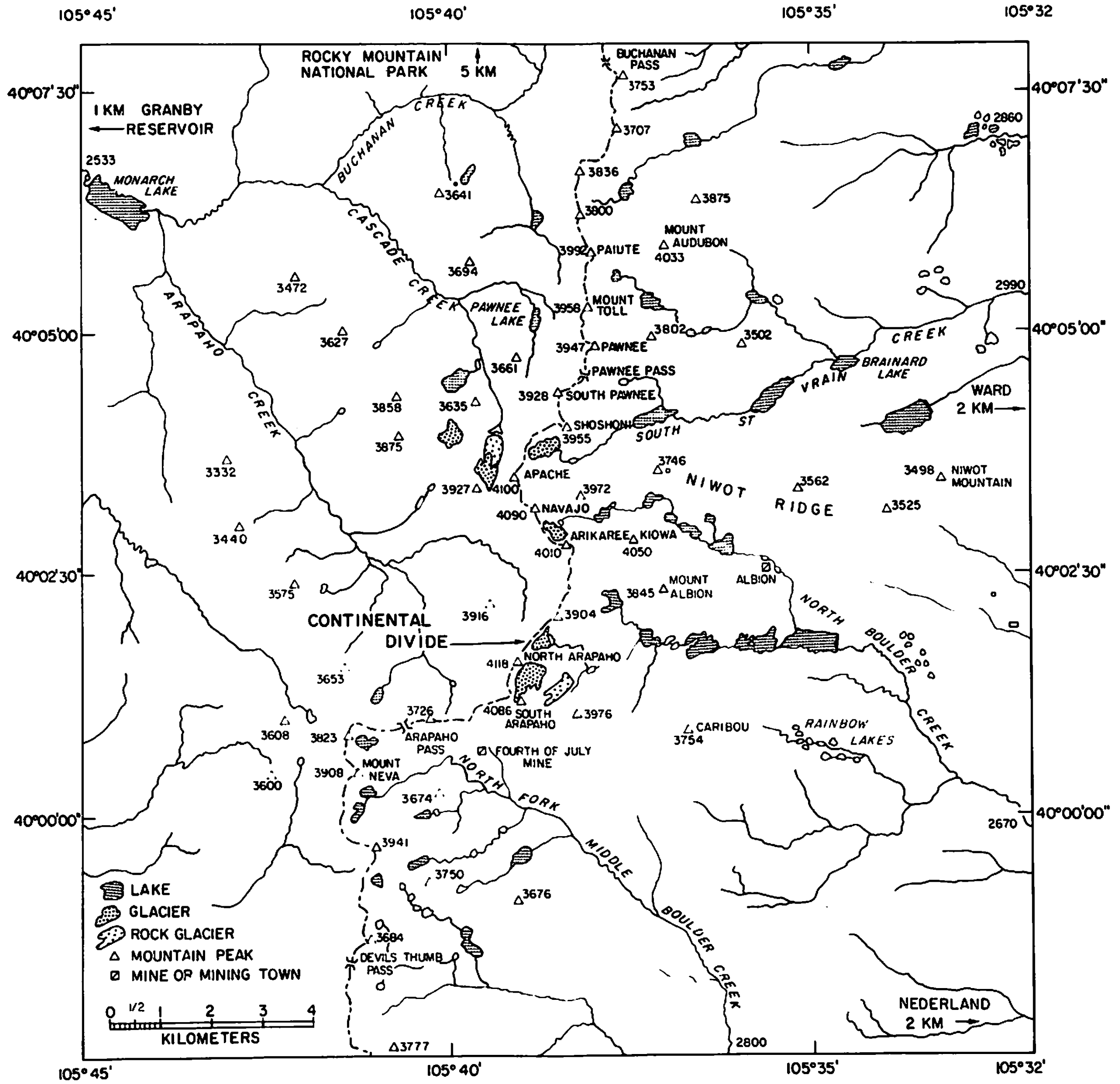

Figure 2. Indian Peaks, Colorado Range, showing peaks, passes, ridges by altitudes, creeks and lakes. Altitudes in meters. Based on U.S.G.S. Ward and Monarch Lake quadrangles.

Figure 3. View west toward the Indian Peaks along the Continental Divide, from South Arapaho Peak (far left) to Mount Toll (T far right). Niwot Ridge, an extensive erosional remnant of a former upland surface, is marked N. Photo by Roland Baumgartner.

Figure 4. View north toward intermediate level erosion surfaces at altitudes of 2500 to 2600 m, east of limit of glaciation, with tors and rock knobs rising above the forest.

4). The tors also were studied recently by Street (1973) but mainly in reference to their value as indicators of nonglaciation. Farther west the ridges mount more steeply to meet at 3400 to 3500 m the remnants of a broad upland surface. These upland remnants rise gradually and continuously westward above treelimit (at about 3475 m) for 1 - 6 km to 3700-3900 m, eventually reaching the actual Continental Divide. Some of the remnants terminate as narrow aretes (e.g., Niwot Ridge) due to the deep incision of cirques on both sides (Figure 3).

Valleys open out to the east and are narrow and deep beyond the limit of glaciation. Steeper gradients are marked by rapids and waterfalls in the gorges, but, within the border of glaciation the valley floors are broader with gentle gradients. Valleys become dissected again still farther west with U-shaped cross profiles and sharp rock steps along their floors. Many lakes in glacier-scoured excavations on the valley floors are deepened by rock and concrete dams for late-summer water storage. Most valleys widen in their uppermost reaches and end in single or double cirques (Figures 5 and 6). Glaciated hanging tributary valleys enter the main valleys mainly from the north. The larger cirques are scooped out more than 500 m below the remnant upland surfaces and high peaks, producing a relief of more than 640 m. Today four small glaciers (Arapaho, Henderson, Arikaree, and Isabelle) inherit four of the 11 cirques (Figure 2), with thin firn fields in a few of the others. Cirque and valley floors provide plenty of room where alpine mass-movement deposits collect. One complex tongue-shaped rock glacier is in the double cirque east of South Arapaho Peak. High cliffs broken by faults, joints, and fractures allow numerous couloirs to form, and rockfall talus and alluvial talus, and lobate rock glaciers, accumulate below these couloirs (Wallace, 1967). This region is the type locality of Caine's (1974) hypothetical alpine slope profile, with its interfluve, free face, talus foot and storage area, and valley floor.

Figure 5. View north along Continental Divide from Rollins Pass (at bottom of photo) to Arapaho Pass, of cirques eroded into east side of broad upland surface along the Divide crest. Photo by J. E. Damuth.

The Indian Peaks area is readily accessible by road from the east by Middle Boulder Creek or Middle St. Vrain Creek, or from the south or north by a paved mountain road skirting just east of the peaks, known locally as Peak-to-Peak Highway (State Highway 160). A few roads lead westward into the upper valleys from this highway, one from Nederland to Eldora and the North Fork of Middle Boulder Creek and then by trail 4 km to Arapaho Pass at 3630 m, one from 10 km north of Nederland to Rainbow Lakes in North Boulder Creek and then by trail to Caribou Peak, and one west of Ward to Brainard Lake in South St. Vrain Creek and by trail 6.5 km to Pawnee Pass at 3825 m. This east side once was served by the Colorado and Northwestern Railroad (later the Denver, Boulder, and Western) from Boulder up Four Mile Canyon to Ward, and then south to Eldora. In the 1870s, east slope officials planned to connect their side of the Range with Middle Park by wagon road across Arapaho Pass. The road was constructed above the North Fork of Middle Boulder Creek and all the way past the Fourth of July Mine, over Arapaho Pass, and then across the Divide on the near-vertical north face of Mount Neva as per agreement, but the west slope road never materialized. Part of this old road now is the hiking trail east of Arapahoe Pass. Nine kilometers to the south, a similar wagon road was cleverly engineered along ridges and over Rollins Pass. David H. Moffat completed his Denver, Northwestern & Pacific Railroad in 1904 by a different route around the heads of cirques, along the edges of cliffs, and over the same pass, building a glorified station at the summit called Corona. In the northern part of the Indian Peaks, an old logging road still allows access 8 km up Middle St. Vrain Creek from Peak-to-Peak Highway to the hiking trail and then 3.5 km over Buchanan Pass at 3610 m.

The west side of the Indian Peaks rises in a gradual ascent of 1500 m from the town of Granby in Middle Park (Figure 1) to the peaks over a distance of 20 to 15 km across thickly forested ridges and valleys. The valleys are V-shaped, 200-300 m deep, and have gentle gradients to the northwest. Relief, however, increases to 550-570 m inside the glacial limit. Treelimit there is about 3500 m. Valleys open out to the northwest, but next to the high peaks they bend south (Figure 2), an orientation providing maximum protection from insolation and enhancing deep cirque excavation, as has recently been verified by Haefner (1976). As a result, large cirque amphitheaters produce an imposing vertical scarp of battlements towering 650-725 m above the cirque floors (Figure 7). Due to this profound dissection, upland surface remnants west of the Divide occur only southwest of Arapaho Pass and northwest of Mount Audubon. Two tiny glaciers (Fair and Peck) are heir to two of the seven cirques on this side, with a fast-moving tongue-shaped rock glacier at the front of the Fair Glacier (Figure 2). Voluminous mass movement deposits, especially rockfall talus, cover the lower cliffs of the high battlements below actively enlarging couloirs.

Access from west side to east may be made by Arapaho Creek to Arapaho Pass 14 km from the trailhead at Monarch Lake, or by Cascade Creek to Pawnee Lake 12 km from Monarch Lake and an abrupt 655 m climb over Pawnee Pass. Old logging roads from Tabernash and Fraser, and also the "Moffat Road" right-of-way make Rollins Pass accessible.

BEDROCK GEOLOGY

This large mountainous area is underlain by three domains of Precambrian rocks: (1) gneisses of several kinds, (2) Boulder Creek granodiorite, and (3) Silver Plume quartz monzonite. The northern half is mainly gneisses invaded by a large quartz monzonite pluton (batholith), whereas the southern half is primarily gneisses and a huge granodiorite pluton (Figure 8 P€). East of the Divide several early Cenozoic stocks also underlie a part of the area. Short faults disrupt the region, some are mineralized by varying amounts, and one fault influences the topography.

The earliest Precambrian metamorphic rocks (Figure 8) include a series of hornblende gneisses, several varieties of biotite gneisses, and a foliated quartz monzonite (Gable, 1969; Pearson and Speltz, 1975; Gable and Madole, 1976; Pearson and U.S. Bureau Mines, 1980). Earlier workers gave all these rocks formational names, but the names are no longer used. They were sediments more than 1800 million years (m.y.) ago, but now are intensively folded and metamorphosed. Dark gray foliated rocks stand out clearly on some vertical cliffs (upper South St. Vrain Creek valley). Some of these older Precambrian rocks are not jointed and thus offer so much resistance to erosion they stand as high peaks, especially in the northern part of the area.

Although most of the Indian Peaks consisted once only of the older Precambrian rocks, several plutons have melted into the area. The first of these was the Boulder Creek granodiorite (Figure 8, Xbc), a gray coarse-grained, locally porphyritic, intrusive rock ranging from a quartz diorite to quartz monzonite (Gable and Madole, 1976). Large aligned phenocrysts 1-4 cm long create an attractive rock to acquire. This granodiorite invaded the older gneisses about 1710 m.y. ago, and underlies much of the south-central part as well as extending from Rollins Pass northward to the old mining town of Albion (Figure 8). It also comprises the broad, west-sloping upland surface northwest of Rollins Pass.

In time, the southern part was broken by scores of small dikes of black hornblendite, and the northern part engulfed by the Silver Plume quartz monzonite (Figure 8, Ysp) about 1440 m.y. ago (Gable 1969; Gable and Madole, 1976). The Silver Plume is a light to dark gray, coarse-grained, equigranular to porphyritic rock. Eye-catching twinned white orthoclase phenocrysts, 1 x 3 cm and etched into high relief on weathered rock surfaces, make it an exciting collector's item. Large plutons of Silver Plume occupy much of the northeast part of the area, and some of the highest peaks north of North Arapaho Peak to north of Mount Aububon are of this rock (Figure 8). In Rocky Mountain National Park, a very similar rock is recognized as one climbs Longs Peak and some of the nearby lower peaks.

Continuing with a very brief geologic history of the whole Front Range, after a period of erosion, marine sediments accumulated and about 300 m.y. ago regional uplift produced the Ancestral Rockies. These along with older rocks were severely eroded. More sediments collected on the land and in the sea around the Ancestral Rockies for another 230 m.y. Their remnants now make the colorful foothill rocks of the Front Range. About 70 m.y. ago, the Rockies began to rise again in the first of a long series of repeated uplifts, periods of volcanism, and long episodes of erosion (Richmond, 1974).

About 68 m.y. ago, Cenozoic stocks (Figure 8, Ci) melted into the region east of the Divide. One stock is in the southeast, another large one extends from the old town of Albion to Mount Audubon, and several small bodies are farther north. Their complex nature is revealed in Wahlstrom's (1940) study of the Audubon-Albion stock. These rocks are mineralogically distinctive and are important as easily-identified indicator rocks in any glacial geology study here. Valuable minerals are associated with them, and they once were mined extensively, e.g., at Albion and around the town of Ward. About 64 m.y. ago, dikes and sills intruded the dipping foothill rocks along the east edge of the Front Range (Larson and Hoblitt, 1973).

After uplift with accompanying volcanic

Figure 6. View west toward Continental Divide, including Navajo Peak (isolated square-top peak on left skyline), lower Apache Peak in center, and Shoshoni Peak (highest peak on skyline), at head of upper South St. Vrain Creek valley. Isabelle Lake in foreground is one of many lakes dammed for late-summer water storage.

Figure 7. View north from Mount Neva summit of west side of Indian Peaks (right edge of photo) and deeply glaciated Arapaho Creek valley (left edge of photo). Peaks on distant skyline are in Rocky Mountain National Park.

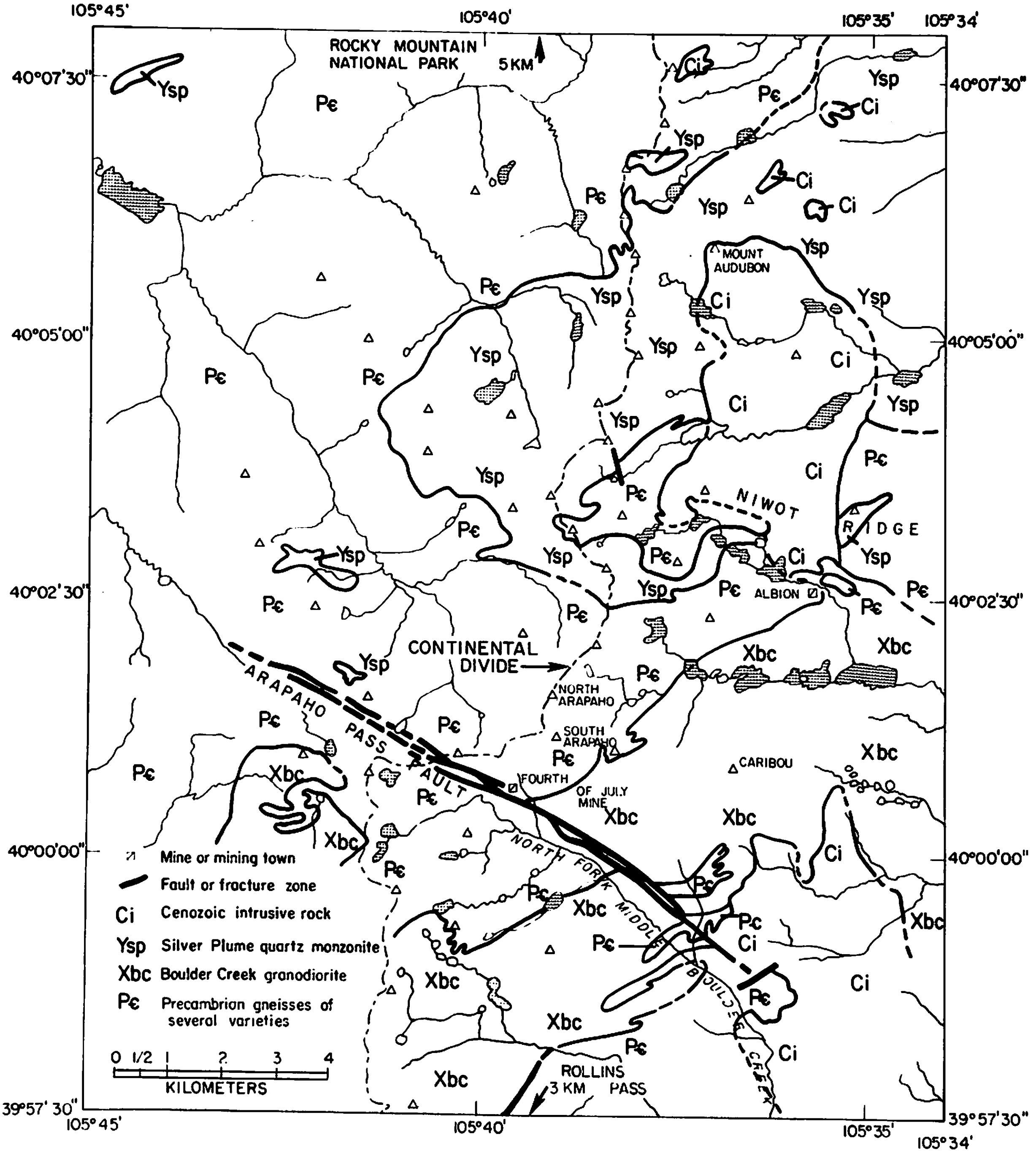

Figure 8. Geologic map of Indian Peaks, Colorado Front Range, modified from field map by Pearson and Speltz, 1975.

activity after 54 m.y. ago, the region was eroded to a widespread erosion surface 40 m.y. ago. Additional uplift took place with the hilltops at 1500-1800 mand canyons eroded below them. Vulcanism from 37 to 34 m.y. ago created thick ashfalls, burying mountain flanks and filling the canyons; lavaflows 150 m thick filled some canyons 28 m.y. ago. Renewed uplift 18 m.y. ago allowed streams then to excavate the canyons. Summit areas were eroded to round hills and gentle slopes at 2400 m right across the 28-m.y.-old lavaflows, with remnants of this broad upland surface still remaining near the Divide, e.g., Niwot Ridge and the other upland surfaces, and even Trail Ridge in the Rocky Mountain National Park. A final broad uplift 7 to 5 m.y. ago, with renewed movement along old faults and uplift with the high peaks area, brought some summits well above 3900 m, e.g., all the Indian Peaks, and especially Longs Peak, elevated to 4346 m (Richmond, 1974).

One of the faults that influences the scenery in the Indian Peaks is the Arapaho Pass Fault (Figure 8). It cuts across the south edge of the Peaks where the North Fork of Middle Boulder Creek parallels it for more than 6 km (Figure 9). The weakly mineralized Fourth of July mining area is located along it. The Indian Peaks all are in the upfaulted massif north of the fault (Figure 10). South of the fault, the mean altitude of 29 highest peaks along the Divide is only 3830 m. North of Mount Audubon and in the National Park, the mean altitude of 29 highest peaks along the Divide is 3895 m. Thus, the Indian Peaks are faulted more than 100 m above the Front Range to the northand to the south. The precipitous rise of 670 m from the fault at Fourth of July Mine to South Arapaho Peak (Figure 10) is noted by Pearson and Speltz (1975), who suggest the possibility of late Cenozoic movement along this fault. Erosion of the fault zone and the consequent westward-eroding head of the main stream here has pushed the Divide 3 km westward toward Mount Nevada (Figure 2).

After the last uplift, tributary streams heading in the uplands removed most of the fluvial gravels from the ridges between streams, except those on the crests of some upland remnants nearest the Divide. Five large, easily recognizable-remnants of the post-18-m.y.-old erosion surface in the Indian Peaks are (1) east of South Arapaho Peak and including Caribou Peak at 3755 m (Figure 10); (2) between Mount Albion and Kiowa Peak at 3720 m; (3) east of Navajo Peak, i.e., Niwot Ridge, extending 6 km east to Niwot Mountain at 3498 m; (4) at the east end of the ridge east of Pawnee Peak at 3500 m; and (5) encircling the east slopes of Mount Audubon at 3840 m (Figure 3). Four other small but even higher upland remnants occur also along the Divide. All now have periglacial block slopes and block fields on them (White, 1976; Figures 8, 9). The large remnants listed here and several others, mapped by Madole, more than 10 km still farther north have rubbly rock detritus on them, closely resembling till in the valleys below them and is derived of rock fragments from the Divide west of them. This rock detritus (also known as a diamicton) formerly was believed to be of glacial origin (Wahlstrom, 1947; Madole, 1963; Bonnett, 1970a). It more likely is of alluvial origin (Madole, pers. comm., 1978; Madole and Shroba, 1979) despite its close resemblance to till, the presence of many subangular boulders up to 4 m in size, and the chipped surface texture of quartz grains in the fine-grained matrix. Similar upland gravel deposits in the Southern Rocky Mountains also are postulated to be alluvial in origin (Scott, 1975). The importance of the origin of these deposits (the diamictons) and their significance to the recent history of the region is emphasized by Madole (1976a).

GLACIAL GEOLOGY

Complete syntheses of mountain glaciation pertinent to the Indian Peaks by Madole (1976a) and Meierding and Birkeland (1980) are now available. An account of the multiple glaciations in nearby Rocky Mountain National Park by Richmond (1974) is very useful. The best descriptions of glacial events that occurred in the Indian Peaks west of the Divide is by Meierding (1977).

Four main stratigraphic units of glacial origin identified are deposits of pre-Bull Lake glaciation, Bull Lake glaciation, Pinedale glaciation, and Neoglaciation. Since the ages of these Indian Peaks glaciations are inferred equivalent to the ages of glaciations at the type localities in the Wind River Mountains of Wyoming, based on moraine morphology, degree of soil-profile development, and relative-age dating criteria comparisons, Wind River Mountain names are extended south and applied to glaciations in Colorado Front Range by all workers in this field.

Evidence of the oldest valley glaciation of inferred pre-Bull Lake age is sketchy and widely scattered. Till presumably of this age is in Tahosa Valley east of Longs Peak, at 2780 m, mapped in the mid-1950s, and extends in altitude down to 2560 m. Richmond (1974) also reported on this till, as did Madole (1963, 1969) in North St. Vrain Creek valley. Farther south, till possibly of this age is in North Boulder Creek valley at 2485 m and in Middle Boulder Creek valley at 2455 m (Bonnett, 1970a).

The next stages of valley glaciation are well recognized and mapped in detail on both sides of the Divide (Bonnett, 1970a; Madole, 1960, 1963, 1969; Meierding, 1977). Three glacier systems of inferred Bull Lake age were in the drainage basin of Boulder Creek: a two-tributary system in South Boulder Creek valley flowed eastward 12 km to 2655 m east of Tolland; a three-tributary system in Middle Boulder Creek valley moved 19 km downvalley to Nederland at 2500 m, the northern-most tributary glacier of which originated in and covered the Arapaho Pass area; and a large system in North Boulder Creek valley extended 13 km to near Peak-to-Peak Highway at 2530 m. This glacier system excavated five

Figure 9. View to northwest of low peaks along Continental Divide, in foreground, south of Mount Neva, and glaciated upper Colorado River valley beyond. Arapaho Pass Fault extends from lower right corner northwest to Arapaho Pass in center of photo. The forested Arapaho Creek valley beyond reaches northwest to Granby Reservoir. Photo by J. E. Damuth.

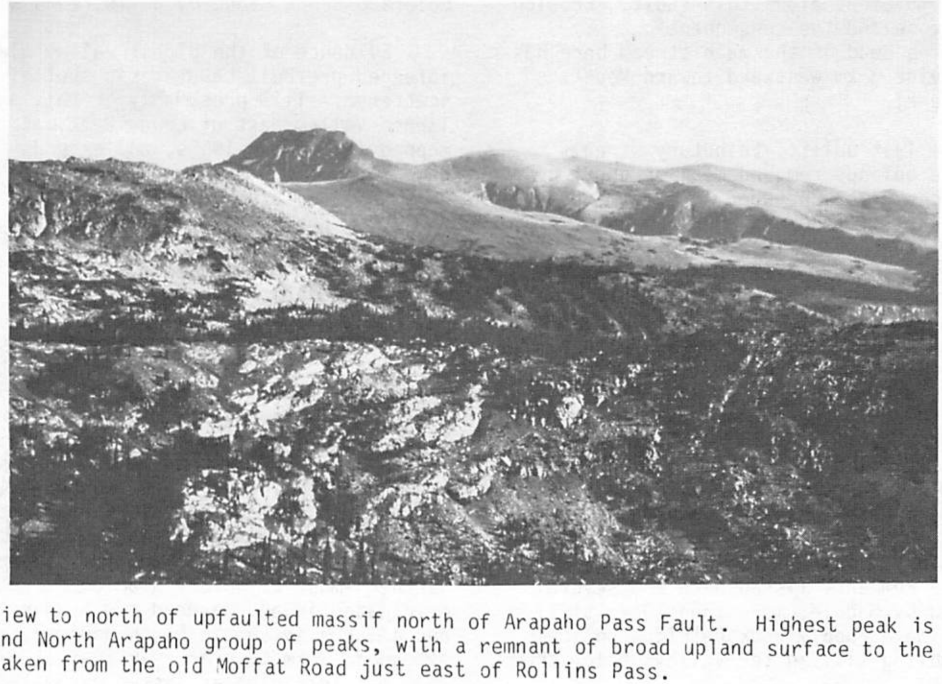

Figure 10. View to north of upfaulted massif north of Arapaho Pass Fault. Highest peak is the South and North Arapaho group of peaks, with a remnant of broad upland surface to the east. Photo taken from the old Moffat Road just east of Rollins Pass.

cirques from South Arapaho Peak north to Navaho Peak. North of Niwot Ridge, three glacier systems formed in the St. Vrain Creek drainage basin: a two-tributary system in South St. Vrain Creek valley 13 km long moved along thenorth edge of Niwot Ridge to several positions at 2700 m and 2745 m, past Peak-to-Peak Highway, leaving large moraines there, and scooping out six cirques from Navajo Peak north to Mount Audubon (Figure 3); a two-tributary system in Middle St. Vrain Creek valley flowed 15 km to Peak-to-Peak Highway at 2580 m; and a three-tributary system in North St. Vrain Creek valley in Rocky Mountain National Park traveled 14 km to beyond Peak-to-Peak Highway at 2400 m, the lowest altitude reached on the east side. Acurate dating of these equivalents of Bull Lake glaciations in the Front Range has not yet been accomplished, but on the basis of dating of other similar deposits, such as Bull Lake tills in Yellowstone National Park which in turn are related to K/Ar-dated lavaflows, these glaciations may have begun about 125,000 yr ago and may have ended about 87,000 yr ago, but certainly ended before about 70,000 yr ago (Richmond, 1974; Madole, 1976a: Figure 3).

Glacier systems of inferred Pinedale age developed later in these same valleys almost to the same lengths and altitudes so that the previous descriptions made here of Bull Lake glaciers should satisfy any need for Pinedale glacier descriptions. Pinedale glaciers left huge moraines easily seen along Peak-to-Peak Highway 1-3 km north of Ward where the road cuts through them. In South St. Vrain and Middle St. Vrain Creek valleys, Pinedale moraines truncated and overrode older Bull Lake moraines. In the high peaks area, some Bull Lake cirques were not used by Pinedale ice and remain hanging above Pinedale ice-deepened valley floors; these older Bull Lake cirques now are choked with Pinedale periglacial debris. Early Pinedale glaciation may have begun about 29,000 yr ago (Madole, 1976a: Figure 3), most of Pinedale till was deposited between about 14,600 yr and 8000 yr ago (Madole, 1976b), a glacial stade shortly before 9915 yr ago is identified in the cirques east of the Arapaho Peaks (Benedict, 1973), and deglaciation was complete or nearly so in North Boulder Creek valley south of Niwot Ridge 7900 to 6240 yr ago (Bonnett, 1970b).

Neoglaciation in the Indian Peaks is resented by three distinct episodes (Madole, 1972), now named and dated by Benedict (1973): Triple Lakes, 5000 to 3000 yr BP; Audubon 1850 to 950 yr BP; and Arapaho Peak, 300 to 100 yr BP. These latest events of refrigeration produced block fields and other periglacial deposits on adjacent ridgetops and upland surfaces, tongue-shaped and lobate rock glaciers (White, 1976), and much rockfall talus and alluvial talus in the valleys below Wallace, 1967). Permafrost still remains inside the rock glaciers and talus on the south sides of the valley floors, beneath thick peat and palsas in the centers of several of the upper valley floors, and in bedrock along the north sides of ridgetops, e.g., in the old mine shafts east of Arapaho Pass.

In the Upper Colorado River basin west of the Indian Peaks and also west of the National Park, Meierding (1977) recognized the same four major units of glaciation as occurs east of the Divide. One huge south-flowing glacier system moved from Cache la Poudre Valley (Figure 1) 32 km down the Colorado River Valley, terminating at Granby Reservoir at 2530 m. More than ten tributary glaciers joined this main glacier from the Inlet Valleys and other valleys from the east, and seven tributary glaciers entered it from the west. Another large glacier system 24 km long flowed west and northwest from Arapaho Creek (Figure 8), Cascade Creek, and Buchanan Creek valleys to Granby Reservoir at 2470 m (Ives, 1938; Madole et al., 1972; Meierding, 1977). This one glacier system and its many tributaries eroded 20 cirques from the alpine area west of the Divide. Farther south a glacier system in the Fraser Valley and its small tributary valleys flowed northward 11 to 16 km, stopping at 2680 m to 2800 m (Madole et al., 1972). On this west side of the Front Range, widespread outwash deposits of two inferred pre-Bull Lake age glaciations rest on a large mesa northeast of Granby. The multiple glaciations of both Bull Lake and Pinedale ages advanced and retreated in similar manner to those east of the Divide (Meierding, 1977; Nelson et al., 1979). Neoglaciation is easily recognized in the upper-most valleys and cirques by small moraines, tongue-shaped and lobate rock glaciers, and much talus.

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WATER AND SEDIMENT FLOWS IN THE GREEN LAKES VALLEY, COLORADO FRONT RANGE

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ABSTRACT

This paper reviews work on the water and sediment fluxes in the Green Lakes Valley in light of the partial contributing area concept. As in other alpine areas, wind drifting off the winter snow into accumulation sites gives the partial areas where streamflow is generated. Many of these contributing areas are closely integrated into the channel network which allows quick hydrologic responses and a high hydrologic efficieny . Quick responses are also evident in rain generated flows. On the other hand, sediment fluxes in the Green Lakes Valley suggest only low levels of activity (ca. an order of magnitude lower than in other alpine areas). However, sediment fluxes are spatially variable: snowdrift sites and windblown areas having sediment yields 1 or 2 orders of magnitude greater than talus or vegetation-covered slopes. Geochemical losses from the basin also appear to be low and to be derived largely from snow drift situations. Despite strong coupling of the sediment and water flux systems, the partial areas responsible for sediment and water yields are not entirely identical: windswept areas seem to contribute proportionately more to sediment fluxes than to water flows.

INTRODUCTION

Partial area concepts have been basic to recent advances in our understanding of forest hydrology and streamflow generation in mid-latitude areas (e.g., Hewlett and Hibbert, 1967; Dunne and Black, 1970; Dunne et al., 1975; Gregory and Walling, 1973; Anderson and Burt, 1978). In alpine areas, models of streamflow generation from snowmelt have implicitly involved a simple partial area concept for a long time: the flow is produced from only those areas of the catchment with a snow cover, and these are clearly variable in time as they contract during the summer. Equivalent models suggest that the sediment yields from a stream basin derive from only the small fraction of it which is unstable and capable of delivering sediment to the main drainage channel (Caine, 1974: Trimble, 1981). In alpine areas, these partial contributing areas (of sediment yield) are often, though not exclusively, the same as the source areas of streamflow from snowmelt. This correspondence arises from (1) the lack of a vegetation cover in areas of greatest snow accumulation: (2) the concentration of wind-blown dust into such drift sites: and (3) the acceleration of weathering rates in such zones of excess moisture.

Present work in the Green Lakes Valley is aimed at defining the source areas (and times) of water and sediment movement through that alpine system and so at an understanding of the water and

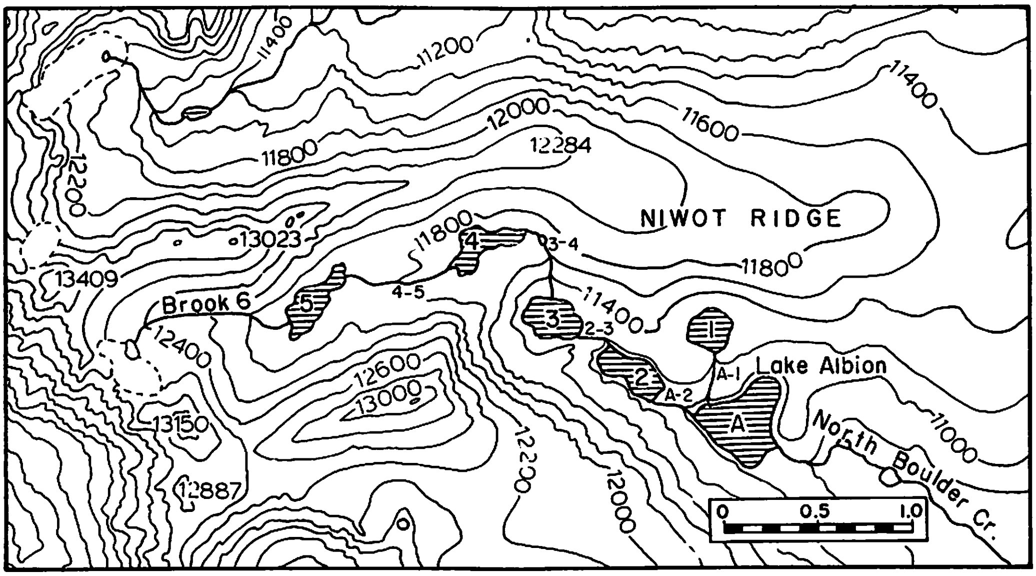

Figure 1. Map shows study area. Elevations are in feet.

sediment budgets of the basin. By defining these partial areas and the manner in which they vary with time, we should be defining also those parts of the abiotic system most susceptible to change and those most capable of impacting other components of the entire alpine system. Further, expansion and contraction of these partial areas in a long time scale should be related to the evidence of varying sediment and water yields gained from lake sedimentation rates.

This report is intended to be a review of previous work on hydrologic processes and soil and sediment movement in the Green Lakes Valley and on Niwot Ridge. It is meant to indicate the most active components of the system, thus the ones most responsible for its response in terms of water and sediment yield. The field area has been the setting of much basic research, especially on periglacial mass wasting, which has been reviewed and reprinted in Ives (1980). Therefore, there is little need for a comprehensive review of all published work on the geomorphology and hydrology of the area. Only that pertaining to the system dynamics is considered here. This should allow the definition of the areas of most interest in terms of streamflow generation and sediment movement.

The paper proceeds from a brief description of the field area to a consideration of its hydrology and then to the nature of erosion and sedimentation within it. This leads to a final evaluation of the important source areas and travel paths of water and sediment within the catchment. These are the areas on which further research as part of LTER is being developed.

THE FIELD AREA

University of Colorado, Long-Term Ecological Research (CULTER) work is concentrated in the catchment of North Boulder Creek above lake Albion at 3345 m elevation (Figure 1). This alpine stream basin appears typical of the high-elevation environment of the east slope of the Colorado Front Range and includes Niwot Ridge, the northern drainage divide, where work on the alpine system has been conducted through INSTAAR for more than 30 yr.

The basin has an area of 5.46 km^2, of which 0.40 km^2 is in six permanent lakes. It comprises two contrasting sectors: the upper basin (2.10 km^2 area) includes all the area draining into and through Green Lake 4; and the lower basin (3.36 km^2, area) between Green Lake 4 and Lake Albion. The Upper Green Lakes Valley consists of a high alpine environment with steep rock walls and talus slopes, a valley floor of glaciated bedrock and a large number of permanents snowbanks (including Arikaree Glacier below the Continental Divide). The Lower Green Lakes Valley contains fewer cliff-talus slopes and has generally debris-mantled valley sides with lower gradients, rounded interfluves and a more extensive soil and vegetation cover on the valley floor. A steep, bedrock valley-step of about 75 m height between Green Lakes 3 and 4 separates the two sectors of the valley.

Hydrographically, the catchment is a relatively simple linear cascade of five lakes, with only Green Lake 1 on the north valley wall subsidiary to this sequence. The contrast between the upper and lower sections of the valley is maintained in the lake sequence. The upper lakes are natural ones whose level has been lowered by excavation oftheir outlet channels by approximately 1 m. The lower lakes, including Green Lake 1, have had their maximum water level raised by dam construction and are periodically drawn down. The characteristics of the lakes are summarized in Table 1.

The stream channels in the basin are almost invariably steep and rocky, with the shallow flow diverging and converging around large boulders. The channels are generally floored with cobbles and gravel and appear to be sufficiently well armored to prevent much sediment movement even in times of peak flow. During the spring snowmelt, the flows are occasionally forced out of the channels by ice blockages and superimposed from the snow cover onto the valley floor. It is likely that stream erosion only has a direct impact at these times. At other times, sand and silt may be observed in motion through channels and rills draining from snowbanks, but this sediment flux does not continue in an obvious manner through the main channels of the catchment.

The Green Lakes Valley has not previously been examined as a single system, although partial fluxes of sediment have been estimated for small segments of it. Most of this work has been aimed at evaluating only mass transport of the sediment on the debris-covered sections of the hillslopes and so cannot be readily integrated into a sediment budget for the entire catchment.

HYDROLOGY

The hydrology of the alpine zone of the southern Rocky mountains has been reviewed in general terms by Martinelli (1975) who emphasizes the importance of wind-distributed snow in the system. This theme is evident also in the work done locally on Niwot Ridge and in the Green Lakes Valley which is summarized in Ives (1980). Within this field area, previous work on hydrologic processes and water fluxes has been sporadic and poorly coordinated, though there is much more information available than that in published records. At different times and sites within the Green Lakes catchment, a variety of hydrologic elements have been measured or estimated as part of earlier research work, although the only estimation of a water budget for the entire catchment is that of Carroll (1976). This was estimated for only one flow season (1973). This study defines some of the hydrologic characteristics of the upper basin that merit further research. They include the highly

Table 1. The Green Lakes physical data

	Elev. (m)	Area (ha)	Max. depth (m)	Mean depth (m)	Volume (m^3x10^3)
Lake Albion	3345	12.8	?	?	?
Green Lake 1	3425	4.1	7.6	3.7	150
Green Lake 2	3410	6.8	16.2	7.8	523
Green Lake 3	3440	7.5	15.8	8.7	647
Green Lake 4	3515	5.3	13.1	4.0	215
Green Lake 5	3625	3.0	7.6	4.0	121

Source: Unpublished surveys made by R. McNeely (1969).

Table 2. Water Budget: Upper Green Lakes Valley[a]

Weeks	Q_{gen} 1	Snow-melt 2	P 3	E (wet) 4	E (medium) 5	E (unveg.) 6	Error	Efficiency (%)
1-5	63.50	59.46	8.54	.45	.13	1.04	-2.88	93.4
1-9	79.65	66.54	13.12	.78	.23	1.68	2.68	99.9
(May 18 - Oct 31) Year	94.53	67.63	32.48	1.54	.45	4.33	.73	94.4

Explanation:

[a] Values (cm) are estimated for 1973 from Carroll (1976).

O_{gen}: generated discharge

P: precipitation during the period

E: evapotranspiration

Error: 1 - (2 + 3 - 4 - 5 - 6)

variable nature of the early season hydrography (which occurs when the flow most probably has most effect in terms of sediment and nutrient fluxes (Colbeck, 1981) and the high efficiency of the catchment in terms of water yield (Table 2). Both of these characteristics are typical of alpine systems (e.g., Leaf, 1971) and are suggestive of quick responses from small contributing source areas that change rapidly in both time and space.

Empirical studies derived from field observations and records are reviewed here. These will provide the basis for calibrating simulation models to the Green Lakes basin but this model-fitting has not yet been performed.

Field Studies

A descriptive catchment model which summarizes the main components of the basin system gives a convenient basis for a review of hydrologic work done in any stream basin (Figure 2). In its simplest form, such a model distinguishes the elements of water input to the system; internal transfers within the system, and eventual consumptive use or outflow from it. Any of these three can be and must be expanded to to take into account temporal and spatial variations in the state of ground surface, the soil, the channel network, and the various storage elements within the basin.

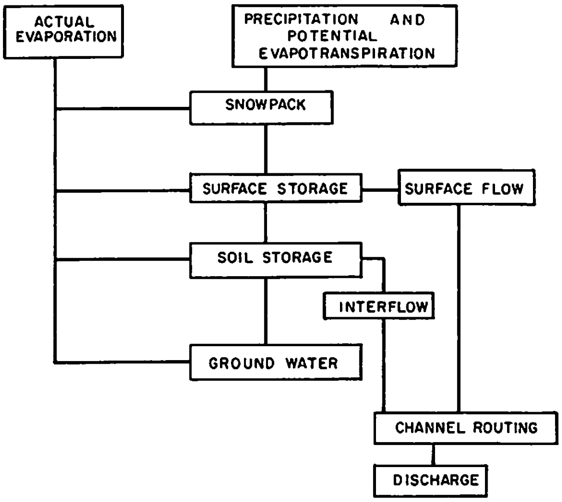

Figure 2. Water fluxes in the alpine system.

Input. A relatively long record of precipitation on Niwot Ridge has been summarized and described by Barry (1972), and this will be maintained through the period of work in LTER. Other records of shorter duration are available for stations within the Green Lakes Valley. These serve to define some of the contrasts between the ridge-crest situation and that of the valley floor (where more precipitation is recorded). Short periods (unpublished) also serve to define the spatial variability of summer precipitation from convective storms in the valley (Barry, 1972).

Since winter precipitation and snow accumulation are especially susceptible to wind drifting, work on the process of snow transport is especially important to many aspects of alpine ecology. Early observations of wind drifting in the field area were made by Martinelli and these have been extended by the modeling of Berg (1976) and by Thorn (1974) in connection with the geomorphic processes related to snow accumulation. This empirical work and photographic records of the field area show the predictability of snow accumulation sites (and even the amounts of snow in them), which is common to almost all alpine areas (Martinelli, 1975). This predictability in the pattern of snow distribution within the alpine, even in years of very different snowfall patterns, was the basis on which Carroll (1974) designed a stratified sampling scheme for measuring snow water content in the Green Lakes Valley. It also provides the repetitive pattern needed for the identification of the source areas of streamflow generated by snowmelt.

The generation of water by snowmelt within this field area has been measured in a number of studies by repeated observations on ablation stakes. This includes the work done by Carroll in estimating a water budget for the upper basin, by Johnson (1979) and Alford (1973) in evaluating the mass budgets of Arikaree Glacier, and by Thorn (1974) and Caine (unpublished) in estimating water production from snow banks. Rates of water production by snowmelt vary up to about 5 cm w.e./d during the ablation season (which may start as early as May 1 in the Upper Green Lakes Valley). As yet, there has been no comprehensive attempt to map the distribution of these areas of water production, nor to relate them to the channel network which they obviously feed.

Internal Transfers. There has been little work done in the Green Lakes Valley on the rates and controls of water movement through the slope and channel systems. These are likely to be quite complex, reflecting the variable substrate of the alpine system, and their evaluation requires the modelling of transfers through or over snow, vegetation, soil, and rock, any of which may be frozen or thawed. Past measurements have been restricted to the observation of soil moisture and its changes on debris-mantled slopes where the water content is related to vegetation growth, solifluction and freeze-thaw processes within the soil. Similarly, the few observations made of stream discharge through the tributary channels of the catchment have not been made at equivalent periods and so cannot be integrated to give even crude estimates of transmission rates through different sections of the stream system. Transfers to and from ground water also have not been estimated in the past and are unlikely to be evaluated well during LTER work, because of the difficulty of defining volumes of ground water storage and the great local variability of storage capacity in glaciated terrain of this type.

Available records of flow discharges from the upper valley suggest that internal transfers of water are rapid (e.g. Figure 3). Flow responses to the diurnal cycle of water production by snow melt show a lag of about 10 h at the outlet from Green Lake 4. Approximately the same delay is evident in the response to rainfall (Figure 3), although this flow must derive from different source areas. This similarity suggests that the two lakes in the upper basin are important controls of the flow response, controls that may be absent during the early part of the runoff season when the lake surfaces still have a continuous cover of ice.

Output. Past records of channel flows within the main drainage system of the Green Lakes Valley are available for a small number of stations during the flow seasons, 1969-1974 and 1981. In most of these years, a partial record (or better) is available for the discharge from Green Lake 4, while records from stations at the outlet from Green Lake 5 and at the main stream inlet to Lake Albion are available for shorter periods. In mid-season 1981, an LTER recording site was established on the main drainage near the old town of Albion. In general, these records do not include the early season flows as a continuous record because of the problems of access to the channels at that time. They do suggest the maximum dischargesdue to snowmelt within the different sectors of the valley flows of up to 0.26 m^3/s (22,000 m^3/d) have been recorded at Green Lake 5, of up to 0.45 m^3/s (39,000 m^3/d) at Green Lake 4, 0.71 m^3/s (61,000 m^3/d) at the inlet to Lake Albion, and more than 0.75 m^3/s (65,000 m^3/d) through North Boulder Creek near the townsite of Albion. The period of most complete record is that for 1973 which was used by Carroll (1976) in estimating a water budget for the upper basin. The storage and recession characteristics of that part of the catchment have been estimated from that record. In 1973 the upper basin yielded approximately 2 x 10^6 m^3 of water as streamflow.

The output of water through evaporation and transpiration remains almost unknown for the alpine system. Carroll's (1976) estimate of the runoff efficiency of the upper basin (94%) suggests that evapotranspiration is relatively slight, but this is a reflection of the small proportion of this part of the catchment covered by vegetation (13%) and standing water and wet vegetation (13%). Estimates of the actual evaporation amounts from different surfaces within the upper basin are summarized (with other components of the water budget) in Table 2 which is based on the 1973 flow season.

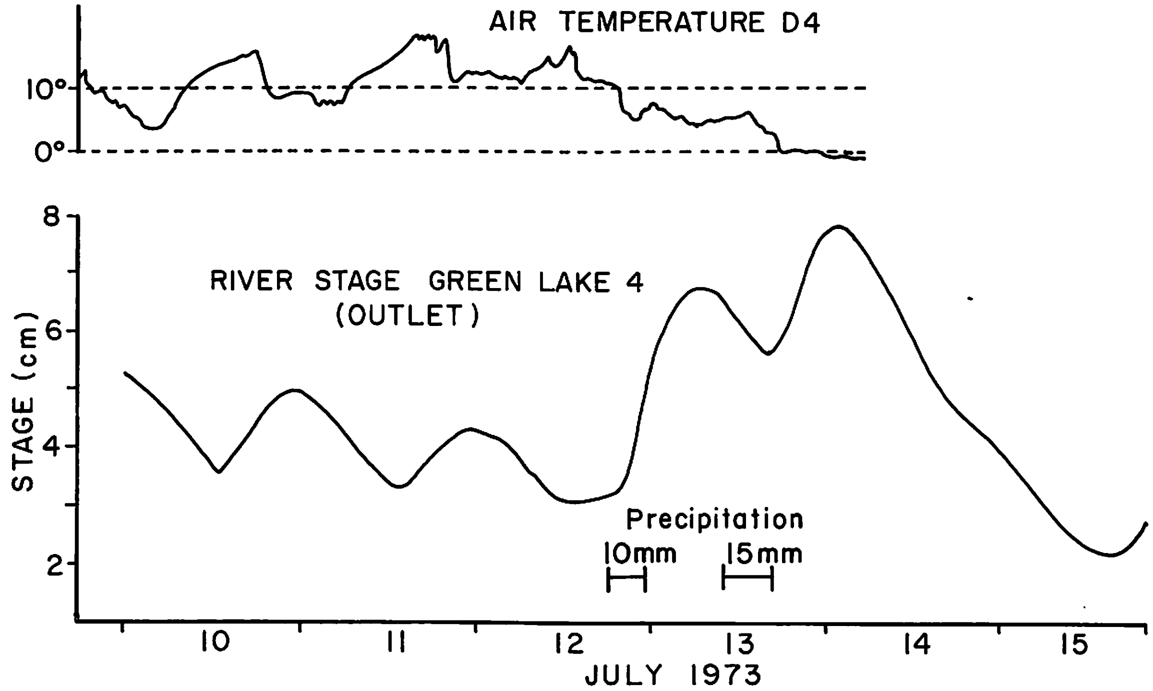

Figure 3. Stream discharge: upper Green Lakes, July 1973. From Caine, unpublished records.

Further Work

Modeling of the hydrologic system of the Green Lakes Valley has not yet been attempted, although a number of deterministic models are now available which could be adapted to the catchment (e.g. Leaf and Brink, 1973). Problems of parameterizing basin characteristics (Johnson and Pilgrim, 1973) may be encountered in such an application but are not likely to be great, considering the amount of knowledge about the basin that is available. More serious problems are likely to arise from areas of ignorance, in particular those pertaining to flows and conditions in the basin prior to the seasonal peak flow. (The late season flows are now well known and readily described by classical recession models with a rainfall component.

Problems with the early season flows arise from a number of sources, all of which deserve further empirical work. First, there is the fact that we still have few continuous records of flow stages and volumes during the period before the highest flows of the season. Second, and corresponding to the first, is the lack of a straight-forward way of defining the areas contributing to streamflow at a time when not all of the snowpack in the basin has become isothermal. At this time, only part of the snow cover is contributing melt-water and that part is not easily identified. Third, the partial area of isothermal snow which is contributing to streamflow seems to be especially dynamic in nature, shrinking and expanding by an order of magnitude or more in any 24-h period. This is suggested by the marked fluctuations in streamflow that occur early in the season, though it needs to be defined by detailed mapping of snow conditions and water movement. Finally, a condition which exacerbates these problems is the uncertainty of the timing of flows at this season: the start of streamflow varies by as much as a month from year-to-year. For these reasons, and for purposes of modeling, the hydrologic responses of the basin during May and June will remain the focus of further study in this enquiry.

EROSION AND SEDIMENT FLUX

Caine (1974) presents a simple model for the mass fluxes of sediment through alpine systems which was based upon studies in the alpine zone of the Colorado Front Range. The movement of sediment into, through, and out of the alpine system may be considered in three components whose dynamics and nature differ with the effective mass of the sediment they include. First, there is a coarse sediment subsystem comprising cliffs, talus, and rock glacier forms. This component involves little material exchange with the environment outside the alpine and so may be modeled as a closed system with respect to mass (Figure 4). It also tends to be a weathering-

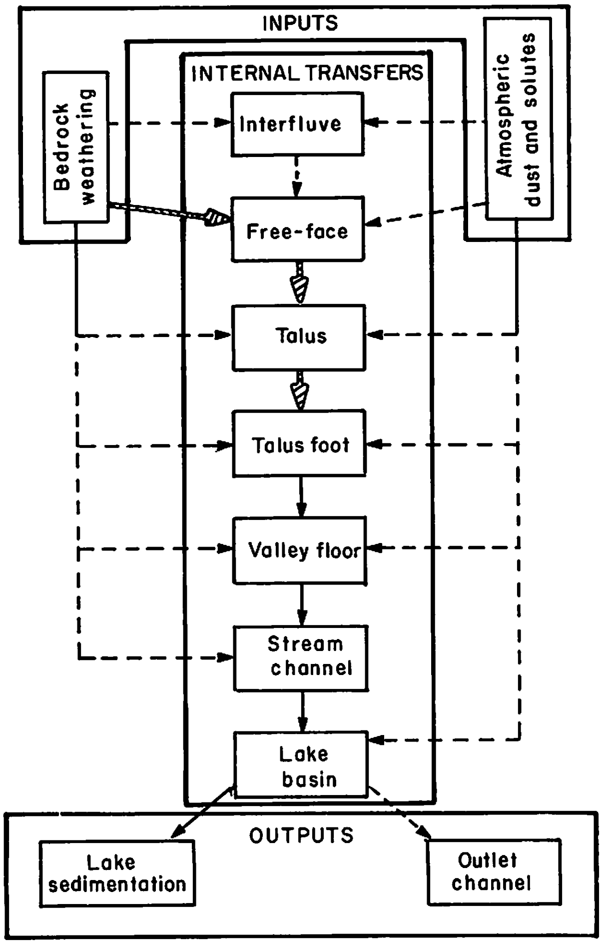

Figure 4. A sediment transfer model (from Caine, 1974).

limited system with respect to waste production on the cliff and this influences its dynamics. Second, there is the cascade of fine clastic sediment (less than about 8 mm in size) which is the main input of sediment to the alpine lakes today. This subsystem takes part in mass exchanges with the area outside for study basin and soil and sediment studies suggest that these exchanges are of particular importance in the alpine of the Colorado Front Range. In the fine-sediment subsystem, wind-transported sediment is brought into (and removed from) the basin; fluvially transported sediment is transferred through the slope and channel components of the system and discharged as either lake sedimentation or sediment yield through the stream channel (Figure 4). Third there is a geochemical cascade of materials transported with liquid water in solution. This involves important exchanges with the environment outside the study basin and closely interacts with the dynamics of vegetation productivity/decomposition. It has, however, received much less attention in past studies of the Colorado alpine than the dynamics of clastic sediment movement.

The Coarse Debris Cascade

S.E. White has been responsible, both directly and indirectly, for most of the work performed to date on the dynamics of the talus and rock glacier systems of the Green Lakes Valley and neighboring areas. He and his students (e.g., Wallace, 1968) have conducted studies of surface mass wasting rates (by shift, creep, and settling) on a number of the taluses of the study area. In addition, they have documented the static properties of many of the characteristics of the talus, including textural studies (McSaveney, 1971) and a classification of talus form which is now widely used (White, 1968). Other records of talus acccumulation, rock fall, and avalanche transport processes in the Green Lakes Valley were made during the 1968-1973 period.

All of these records suggest rates of cliff retreat of up to 0.7 mm/yr, with talus movement rates up to 5 cm/yr in a thin surface layer (Caine, 1974). These rates tend to be lower than those estimated in other mountain areas (e.g., Rapp, 1960; Caine, 1976; Söderman, 1980). This suggests that the coarse debris cascade in the Colorado Front Range is relatively inactive and its dynamics may not warrant a great amount of further work. In the Canadian Rockies and elsewhere in Colorado, rates of transfer to and through the talus are as much as an order of magnitude greater than those recorded in the Green Lakes Valley (e.g., Caine, 1976; Luckman, 1971; Gardner, 1979). Rates of rock glacier movement, at the lower end of the cascade, also appear to be lower in the Front Range than elsewhere. White (1971) record rates of 5 cm/yr to 10 cm/yr which are almost an order of magnitude lower than those reported by Wahrhaftig and Cox (1959) and Barsch (1969). Despite this lower level of activity, the controls and form of the coarse debris cascade are similar to those elsewhere. They include a high level of variability in both space and time in all parts of the cascade which necessitates large samples and long periods of empirical study.

The Fine Sediment Cascade

In the Green Lakes catchment, some parts of the fine sediment cascade have been studied extensively, though other parts remain almost unknown. Soil development and distributions have recently been described in both valley floor and ridge crest situations by Burns (1980), who includes an interpretation of the source and local movement of fine sediment during soil development. On the debris-mantled interfluve of Niwot Ridge, rates of mass flux by solifluction and frost creep have been monitored over a long period by Benedict (1970). Rates of movement in the upper 50 cm of the mantle vary up to 43 mm/yr, but are usually less than 1mm/yr over most of the (dry) ridge surface. Surface erosion processes have been measured for shorter periods in a variety of situations, including zones of meltwater transport around snow banks (Thorn, 1976), as well as in areas of dry tundra (Bovis, 1978). Soil erosion and transport by the wind, following exposure by fossorial mammals, has also been estimated by Thorn (1978) and Burns (1980). These studies of surface erosion show losses of up to 80 g/m^2/yr on the dry tundra and very much more activity in nivation hollows where meltwater is available (up to 2800 g/m^2/yr; Thorn, 1976). In contrast, only slight sediment transport occurs from vegetated, wet alpine meadows, though these may contribute much to the dissolved organic content of drainage waters (Thurman, pers. comm., 1982).

These observations, which have been made almost exclusively on Niwot Ridge, are concordant with those from other alpine areas. They show clear dependence of much mass wasting and erosion on the hydrologic system. Thus, mass wasting and frost effects are maximized in areas with a high water table in the fall, while surficial erosionis concentrated into areas of snow accumulation where there is little vegetation to impede melt-water transport. Surface transport, probablyreflecting rainsplash, is also effective in dry tundra situations where the soil is exposed by disturbance. Thus, the source areas for water flow and sediment flux are not entirely the same and the two need to be treated separately; wet meadow areas, for example, probably contribute much water to streamflow but disproportionately less sediment flux.

The mechanisms and rates of soil movement under these conditions appear to be similar to those found in other alpine areas (e.g., Rapp, 1960; Caine, 1976; Söderman, 1980). In the past, mass-wasting rates on Niwot Ridge have been greater than those of today, by a factor of about 10, and this has been interpreted (by analogy with contemporary controls) as a response to greater precipitation or wetter conditions at the end of the melt season (Benedict, 1970).

Apart from Thorn's (1974, 1976) work on nivation processes which are directly related to important source areas for streamflow, little of this effort has pointed to the rates and mechanisms of sediment transport to alpine stream channels. Further, there has been no work on fluvial transport along the stream system of the Green Lakes Valley. Initial estimates of sedimentation in Green Lake 4 (where the sediment must derive from the immediately adjacent slopes and channels) suggest an accumulation rate between 0.15 and 0.20 mm/yr for the last 6000 yr (Caine, 1974). This is approximately the same as the rate estimated for the last 4000 yr in Long Lake, north of Niwot Ridge (0.22 mm/yr; Andrews, pers. comm., 1981). Such rates of sedimentationclosely reflect sediment transport by the streams of the Front Range for empirical estimates of the sediment-trapping efficiency of the Green Lakes suggests that less than 15% of the sediment transported to any one of them will move through it (Heinemann, 1981). Sediment flow into the lakes has only been noted by field workers at times of high water discharge. If this occurs from snowmelt at a time when much of the basin is still snow covered, it is very difficult to observ the dynamics of sediment entrainment and delivery in snowdrift sites (where there may be more than 10 m of snow). Yet, these seem likely to be sourc areas for sediment transported to the lakes at these times for intermediate storage of the sediment in the stream channels is not obvious. Finally, the interaction of rain-generated runoff with that derived from snowmelt has not yet been evaluated with respect to sediment delivery to the lakes.

The Geochemical Cascade

Apart from studies on nutrient cycling and soil chemistry conducted during ecological work and soil surveys, there has been little work on the contemporary geochemical system of the Green Lakes area. On the other hand, the results of rock weathering have been used frequently in relative-age dating of clastic deposits in this part of the Rockies (Thorn, 1976; Carroll, 1974). This indicates that chemical activity is significant, although it does little to define its present dynamics. The evidence of postglacial soil development on the valley floors has the same kind of indirect significance to chemical cycling in the alpine, though it too fails to clearly define rates and volumes of solute transport and translocation.

Unpublished observations in the Upper Green Lakes Valley are summarized in Figure 5, which suggests a low rate of solute loss from the system as in other alpine areas (McPherson, 1971; Caine, 1976). This is corroborated by estimates of the total dissolved solid (TDS) content of snow and meltwater (Thorn, 1976; Caine, unpublished). Temporal variations in TDS suggest a flushing of

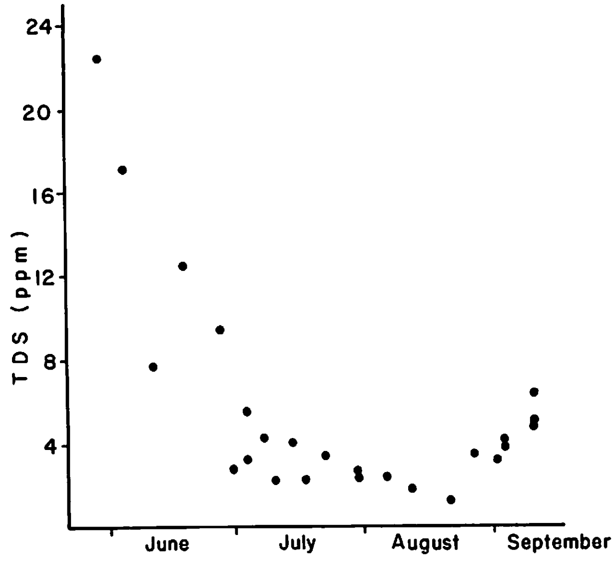

Figure 5. Total dissolved solids: Green Lake 4 outlet.

solutes from the system at the time of maximum snowmelt and this event has also been reported from adjacent catchments (Thurman, personal communication, 1981), as well as those in the San Juan Mountains (Caine, 1976). The late-season (September) increase in TDS occurs at a time of very low flow volumes and is likely to reflect the dominance of ground water sources to streamflow at that time. Again, the equivalent pattern was found in other mountain areas (Caine, 1976).

DISCUSSION

This review shows that some important parts of the sediment and water flux systems have not been considered in past work in the Green Lakes Valley. These omissions clearly arise from the fact that previous studies have not had a basin-wide evaluation as their objective; instead, they have sought to estimate the influence of single factors, sites, or components. Despite lack of coordination, these studies provide a basis for further work by defining the magnitude of many exchanges, and the areas in which further observation is needed. The most obvious lacunae are those which involve the transport of water and fine sediment through the fluvial system of the catchment and the operation of the geochemical system in the alpine. The following are three topics on which future work will be concentrated, and which derive from the gaps in our present knowledge of the alpine system of the Colorado Front Range.

Partial Area Contributions

The concept of partial contributing areas is obviously an important one in understanding the generation of streamflow in alpine areas. In this environment, the concept requires some modification to take into account differences with respect to runoff generated from snowmelt and rainfall. Both of these contributions vary spatially and temporally, though their changes may follow a consistent pattern during any summer, and one that is repeated each year. Prior to peak flow, the area contribution to snowmelt runoff is probably expanding, as more of the snowpack becomes ripe, even as some areas are losing snow cover by complete ablation. Following peak flow and after the basin snow cover is isothermal, the snowmelt contributing area is reduced asymtotically along a recession curve that should be related to the streamflow recession. Together, these changes lead to the flow hydrograph and the sigmoid curve of change in snow covered area which approximates the inverse of the integrated seasonal flows (e.g., Leaf, 1971).

Areas contributing to a flow response to rainfall also change through time and in a way that may be associated with the snow cover if the latter is responsible for areas of a high water table. These are likely to be areas of bare bedrock, open talus, or meadows with high water table, as well as the channels and lakes into which a direct input from precipitation occurs. Contributing areas for fine sediment flux to the fluvial system are not entirely the same as those for water, though snowbank situations are clearly of great importance in supplying both water and sediment. Other areas that supply streamflow, on the other hand, appear to contribute little to the sediment transfers in the system. These include the areas of wet meadow and willow vegetation. At present, areas of bedrock and talus cannot be evaluated, in even a preliminary way, for their influence on the fine sediment budget of the basin. Intuitively, they seem likely to contribute relatively little from bedrock weathering, though they may be important as areas from which acumulated dustfall is readily removed by runoff and flushed into the stream and lake system.

Catchment Efficiency

Carroll's conclusion that the Upper Green Lakes basin is remarkably efficient in terms of water production (Carroll, 1976) was based on only a single season of observation. Therefore, it deserves further testing, as flow records in future seasons will allow. This test is linked to the evaluation of partial areas, since it is the very high efficiency of contributing zones and the concentration of water into them that accounts for the basin response. In that respect, the importance to the alpine hydrologic system in terms of snow drifting and distribution is of clear importance. In these terms, it may be important to define the catchment responses on a shorter time scale than that of the entire melt season, and that is obviously necessary in any work intended to calibrate watershed models for parts of the system. The apparent correspondence between recession coefficients for the snow-covered area within the basin and the streamflow recession during rain-free periods, which has been reported elsewhere (Caine, 1976), is a further characteristic worth testing in this environment. It could prove useful in modeling and in predicting streamflow from the alpine.

In terms of general hydrologic responses, one great lack in previous records from the Green Lakes Valley involves the period during late-spring, following the start of streamflow and before the seasonal peak. It is important that this be evaluated with a continuous record, although it may prove a difficult logistic problem (because of access to suitable channel sections at that time). These problems will receive immediate attention in future work.

The concept of catchment efficiency may also be applicable to the study of particulate transport through the system, particularly since much of the fine sediment seems to derive from the atmosphere. In this case, a budget of the inputs of atmpospheric dustfall, and its disposition within the system (including transport to lake basins and the outlet channel), could allow estimation of the dynamics of fine sediment through the terrestrial and fluvial system.

Magnitude-Frequency Analysis

Much of the work that has already been completed on the geomorphic processes of the alpine area of Niwot Ridge allow an initial estimate of relative magnitudes of different event and their spatial distribution. Further observations, by extending the record, will enhance this as will observations of other processes. However, it should be recognized that the recurrence interval of many geomorphic events that are important in alpine areas is so long that there may be little opportunity of defining them by direct observation. For this, the record preserved in the landforms and the sediments in the alpine will probably be more important than contemporary records.

CONCLUSION

The heritage of research on Niwot Ridge and in the Green Lakes Valley is a strong one in many areas of earth science and one on which this part of the LTER program can build. However, it includes some serious gaps in knowledge and it is to these that attention should first be focussed so as to derive first approximations of their significance. In addition, there continues to be a need to evaluate more fully the past records that area available to us.

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AIR QUALITY
AND SURFACE ENERGY BUDGET

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ABSTRACT

Previous and current work on the air quality of the Niwot Ridge area is reviewed. Most studies focus on the possibility of polluted air arriving from the urban Front Range corridor to the east. Surprisingly low values of pH (high acidity) have been noted in wet deposition. Future LTER studies will seek to determine whether the polluted air travels above the 3000-m level onto the ridge, and also will monitor air at about 3485 m arriving from the west. Previous work on surface energy budgets on the Niwot Ridge tundra surface are also reviewed. A methodology for making energy budget measurements under advective conditions is outlined. This involves making horizontal as well as vertical measurements. Later studies will attempt to develop models for temporal and spatial extrapolation of the energy budget values.

A happy coincidence of circumstances has led to the examination of aspects of the air quality on and near Niwot Ridge by several groups of investigators. These include teams of scientists from the University of Colorado, the National Oceanographic and Atmospheric Administration (NOAA), the Ford Motor Company, and the National Center for Atmospheric Research (NCAR), as well as groups from elsewhere. The study site for most of these investigators is the Mountain Research Station C-1 climatic station (3030 m) located in a lodgepole pine forest clearing. One of the most persistent and productive studies has been made by Drs. William Lewis and and Michael Grant from the University of Colorado, Department of Environmental, Population, and Organismic Biology in their investigation of the nutrient cycling of the Como watershed at 2910 m. The majority of federal government sponsored programs tend to be long-term projects which have not yet yielded publications. Peripheral sources of air quality data relating to the Niwot site are the monitoring network of the State of Colorado and the National Atmospheric Deposition program. There are probably few montane sites whose air is so well investigated. At the same time the need for such investigations is acute. Emissions of many pollutants are likely to increase both on the eastern side of the Continental Divide due to increased expansion of the Colorado Front Range urban corridor, and on the western side associated with potentially enormous energy-related development.

The studies by Lewis and Grant (1978. 1979a. 1980a, 1980b: Grant and Lewis. 1981) have attracted most attention for their discovery of unexpectedly low pH values for bulk precipitation and a significant downward trend in this value since 1975. They attribute increasing acidity to increasing amounts of nitric acid in the precipitation. While being decidedly acidic. the precipitation shows comparatively low levels of sulfates ($SO_4{}^{2-}$). However. rather large amounts of calcium (Ca^{2+}) and sodium (Na^{2+}) in both wet and dry fallout suggest to the investigators that terrestrial sources are a major source of the deposition. Wet and dry deposition of twenty substances is being monitored by Lewis and Grant on a weekly basis.

A summary of the major federal government studies on air quality performed out of the Mountain Research Station near Niwot Ridge has been made by Professor Misha Plam, the former Mountain Research Station Director. These are either long-term projects or the analysis is not complete or both. Consequently. with certain exceptions noted below, the major results from these studies are not yet available. The major projects are :

(1) NOAA in cooperation with The University of Colorado Chemistry Department: Fred Fehsenfeld (Aeronomy Laboratory. NOAA) and R. Sievers (Chemistry. C.U.) This is a long-term project started in July 1978. The NOAA installation at C-1 is undertaking to measure nonurban air. Background levels of "clean air" (NO. NO_2. O_3. CO_1) are being measured in order to understand the nonurban chemistry of odd nitrogen. Diurnal and seasonal variations have been marked. Weather data from C-1 provided by the Mountain Research Station.

(2) NOAA (Aeronomy Laboratory)· Dr. Philip A. Wilksch. This project involves spectrometric determination of the concentration of tropospheric trace species. A white light source has been located on the roof of the Alpine Laboratory, Mountain Research Station. beaming toward Fritz Peak observatory. about 12 km south of Niwot Ridge, where a spectrometer is used to detect and measure the absorption due to the gas of interest. Presently observations are being made on nitrogen dioxide.

(3) NOAA. Geophysical Monitoring for Climate: Dr. Water Komhyr and Dr. Kirby Hansen. This is a long-term project started in 1975. Measurements of carbon dioxide and freon. Sampling done by Mr. John Clark, former research meteorologist of the Mountain Research Station and now continued by Mr. Mark Losleben.

(4) NCAR. Dr. Leroy Heidt. This project started in June 1978 and was terminated in June 1979. Rare gas and fluorocarbon were sampled on Niwot Ridge. Sampling was done by Mr. John Clark.

(5) Colorado College, Colorado Springs: Dr. Barry J. Heubert. This is a three-year program started in January 1979. In conjunction with NOAA Aeronomy Lab and in addition to their studies NO_3, vapor and many aerosol constituents have been measured at C-1.

(6) Ford Motor Company (Physics Department): Dr. C.C. Wang, Mr. L.G. Davis, Mr. E. Hamilton. This on-going project started in August 1979. Hydroxyl radical (OH) concentrations in clean air are being measured using a laser-induced fluoroscence technique. New collaborating research is being undertaken with NOAA and the Mountain Research Station.

(7) University of Michigan, Chemistry Department: Thomas Kelly (graduate student). This was a six-month program, October 1978 - May 1979. Atmospheric pollutants were measured for study of atmospheric chemistry.

Results from these studies which have been published or are near publication include those from the Ford Motor Company and NOAA Aeronomy Laboratory (Davis et al., 1982), who are working together, and those of Heubert, who is also sponsored by the same laboratory. The first set of results are based on limited data but clearly suggest a significant increase in the hydroxyl radical (OH) in the air when winds are from the urban pollution source east of the measurement site, but low levels of OH when winds are from the west. The work of Heubert suggests that the vast majority of the nitric acid vapor (HNO_3) also comes from the urban Front Range corridor. Heuber also indicates that the ratio of HNO_3/NO_x is not usually greater than unity, which modelers predict it should be and attempt to explain this discrepancy by suggesting that HNO_3 is removed faster, by dry deposition, than modelers had predicted. Although Lewis and Grant have not felt they have enough information to point to the location of the probable anthropogenic source of the acid precipitation which they record, these other preliminary results suggest the Front Range urban corridor as the probable culprit. Whether this is or is not true, or only partially true, studies of air flow around the Long-Term Ecologica Research site, as proposed in our program, became particularly relevant to the LTER program as a whole.

An important feature of the meteorology of the Front Range is that air from the east often does not gain access to altitudes above 3000 m. Thus, it may be that the results from most of the studies outlined above are not altogether typical of the alpine tundra. Consequently, when the standard NADP monitoring station is established at 3485 m and well above treeline, it will give in formation directly relating to the tundra and of considerable interest is comparison with the data described above.

SURFACE ENERGY BUDGET

The inflow and outflow of heat energy to and from the earth's surface is of major concern to atmospheric scientists and biologists alike. Usually, several minor methods of heat flux are neglected and the energy budget equation, based on the law of conservation of energy is expressed as

$$Q^* + LE + H + G = 0$$

where Q^* is net radiation, LE is heat used in evapotranspiration (latent heat), H is sensible heat (enthalpy), and G is ground heat flow. This approach has two major advantages for ecological applications where vegetated surfaces are involved. First, Q^* represents the radiant energy available to the plant surface, and calculation of the value of this parameter can yield data pertinent to plant photosynthetic activity. Second, calculation of LE is directly related to ambient and internal water conditions of the plant, specifically water availability or stress due to lack of water.

There are very few actual measurements of energy budgets of an alpine terrain surface and fewer of alpine tundra surface, owing to the physical difficulties of operating delicate instrumentation in such environments. Greenland (1973) estimated an energy budget for a valley in the New Zealand Southern Alps but this was not on a tundra surface. Terjung et al. (1969) took 11 h of observations over tundra on White Mountain Peak, California, and Greenland (1978) recorded some radiation budget values at times of solstice for Niwot Ridge. However, the major pioneering work to collect complete energy budget values for the North American alpine tundra remains that of LeDrew (1975) and LeDrew and Weller (1978).

LeDrew determined the surface energy budget for the summer season of 1973. The average partitioning of energy was as follows: Net Radiation (Q^*) 298 ly/d (100%), sensible heat flux 113 ly/d (39%), Soil Heat Flux 37 ly/d (12%). The major problems encountered by LeDrew were the advection of cool dry air across the measuring site and the heterogene of the surface which also leads to potential problems of advection. LeDrew solved these problems by using small weighing lysimeters to give values of LE independent of those resulting from standard one dimensional (vertical) equations for the turbulent fluxes of sensible and latent heat.

The atmospheric part of the Long-Term Environmental Research program proposes to obtain more measurements of the energy budget over the alpine tundra in order to test the hypothesis that anomalous conditions of plant stress are mainly determined by soil moisture imbalances which are, in turn, weather related. The present approach towards the estimation of energy budgets for the Niwot Ridge LTER program will consider these aspects that could be termed observational techniques modeling under advective conditions, and extrapolative modeling.

Observationally, standard instruments will be used for measuring the radiative and soil heat fluxes. The turbulent fluxes, however, will be measured by a reversing wet and dry bulb thermometer system that uses only temperature differences measured by themocouples (Oke, 1978: 309). A novel approach to this application will be the use of two sites for measurements and use of diodes to measure temperature differences at the same heights above the surface between the two sites. This experimental design should give the necessary observational data to address the two-dimensional heat flux problems caused by advection.

The theoretical background to the two dimensional energy budget problem has been outlined by Rao et al. (1974) and several others. Essentially the problem involves having about twice as many unknowns as there are differential and other equations that describe the situation. Rao, for example, lists the equations governing the advection problem as including

(1) Three steady-state equations for the mean field of momentum, heat and moisture;
(2) The continuity equation;
(3) Three transport equations for the turbulent fluxes of momentum heat and moisture;
(4) Two equations for temperature and humidity variances;
(5) An equation for the covariance of moisture and heat.

The problem is solved using higher order closure techniques and finite difference numerical solutions. The higher order closure techniques approximate the unknowns in terms of other basic variables for which equations can be expressed. The finite difference numerical solutions compose a variety of computer related applied mathematical techniques for splitting a continuously changing variable up into changes at discrete time intervals. The solution of the differential equations also requires a knowledge of appropriate boundary conditions. Part of this knowledge is based on observational data. This, or a somewhat similar, theoretical approach will be applied to the data generated by the LTER field studies and should give considerable insight into the physical reality of atmospheric-earth surface processes above the tundra surface.

Since the observational measurements are difficult to achieve, a modeling approach is clearly warranted for extrapolation of data obtained at one site out to other sites. The only serious attempt to do this for alpine terrain has been that of Dozier and Outcalt (1979). These writers used the Outcalt/Myrup equilibrium surface temperature aproach applied to points on a two dimensional grid in complex terrain. To the extent that the method could be tested with observational data, it seems an encouraging start. It would be more realistic, however, if some kind of horizontal mass continuity and wind field modeling could be incorporated into the technique. A goal of the LTER Niwot Ridge atmospheric program is to develop an effective extrapolative model along these lines.

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REVIEW OF LATE QUATERNARY HISTORY OF VEGETATION AND CLIMATE IN THE MOUNTAINS OF COLORADO

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ABSTRACT

Data on Colorado's vegetational climatic history is surveyed, emphasizing the potential usefulness of such studies in, e.g. forest management. Three major palynological studies of Holocene upper treeline movements from the Front Range and the San Juans are reviewed, and the disagreements between them are shown to be more apparent than real. The pollen diagrams in these studies demonstrated higher alpine treelines during the Holocene, up to 300 m above present forest limits. The revised climatic scheme deduced from palynology shows that in recent millennia alpine treelines have been falling due to colder climate, with further elevational reductions in the past few centuries. This implies that damage to the upper subalpine forest may be irreversible, since the climatic limits for seedling regeneration may be below the present treeline.

A palynological study of the lower timberline-grassland ecotone near Crested Butte reflected several elevational changes during the last 15,000 yr. At Winter Park, a five-part till and organic sequence recorded late Pinedale glacier activity, back to 30,500 BP. At Devlins Park a detailed palynological study from 22,000 to 12,000 BP recorded a lower tree line and a climate 4 to 8°C colder than now.

INTRODUCTION

The study of plant ecology of the late Quaternary period and climatic inferences drawn from that data are of considerable intrinsic interest, but they gain immeasurably in significance where such knowledge can be applied to modern environmental managment problems. In the following review, which updates the survey of nearly two decades ago (Martin and Mehringer, 1965), we can see that the debate over the geologically recent history of the Colorado subalpine treeline is of more than academic interest. If the recent movement of the forest limit has been upslope, then continuation of that process will help to heal damage done to the upper subalpine forest, as tree regeneration aided by ameliorating alpine climates fills in the gaps caused by fire, windthrow, or beetle damage. By contrast, if the upper limit of tree-growth is being forced downslope by recent (and continued) climatic cooling in the alpine, then we can expect that fire-scars in the uppermost subalpine forest will not heal, and the ecotone will be increasingly vulnerable to human and natural damage. The answer to this and related questions (e.g., the role of bark beetle infestations prior to human management of the forests) can only be answered by paleoecological data, which predate our brief scientific observations.

THE HOLOCENE

The remarkable dearth of geologically recent paleoenvironmental data for the Colorado Rocky-Mountain region is well illustrated in the thorough survey by Martin and Mehringer (1965: 433-452). Prior to that, the work of Pennak (1963) was the only representative of published Holocene palynology for the Front Range, with the Ph.D. thesis studies of Maher (1961, 1963) representing the southern Colorado mountains. Dr. Robert Pennak was largely self-taught in the field of palynology, and he employed the technique (with ^{14}C dating) to establish minimum deglaciation ages for lakes he studied as a limnologist. He also analyzed organic content, phosphates, and additional microfossils (sponge spicules, cladocera). Pennak reported few pollen taxa (total five) in his study of two lakes and two bogs, which ranged from 2600 to 3200 m elevation. His pollen diagrams suggest that in the mid-Holocene period there was a grass episode with reduced tree pollen at higher elevations, during a Hypisthermal episode 6000 to 3000 yr BP. Then followed the return of climax vegetation with possibly cooler, moister climate.

Maher (1972) drew on Pennak's field experience at Redrock Lake (3100 m) in Boulder County to extend the Holocene sediment record to deeper and older materials than those found by Pennak at the same lake basin (Figure 1). This study reported the first "absolute" pollen analyses for the western United States and the first use of confidence intervals for the pollen data. Maher drew upon his long experience in sampling modern surface pollen deposition to form analogs for contemporary pollen and vegetational assemblages in the Holocene sediments, particularly employing ratios of spruce and pine pollen to estimate the apparent elevational distance of the sediment site from the alpine treeline.

The interpretation of Holocene events that Maher (1972) offers is fundamentally different from the climatic histories of the eastern and central United States, and indeed can be described as being in antiphase (but with similar timing) to much of the rest of the North American climatic reconstructions. From 10,000 to 7600 yr BP the climate was said to be cooler and wetter than present; from 7600 to 6700 BP the treeline elevation was similar to now and so by implication was the summer climate at 3100 m. Summer climate from 6700 to 3000 BP was interpreted as cooler

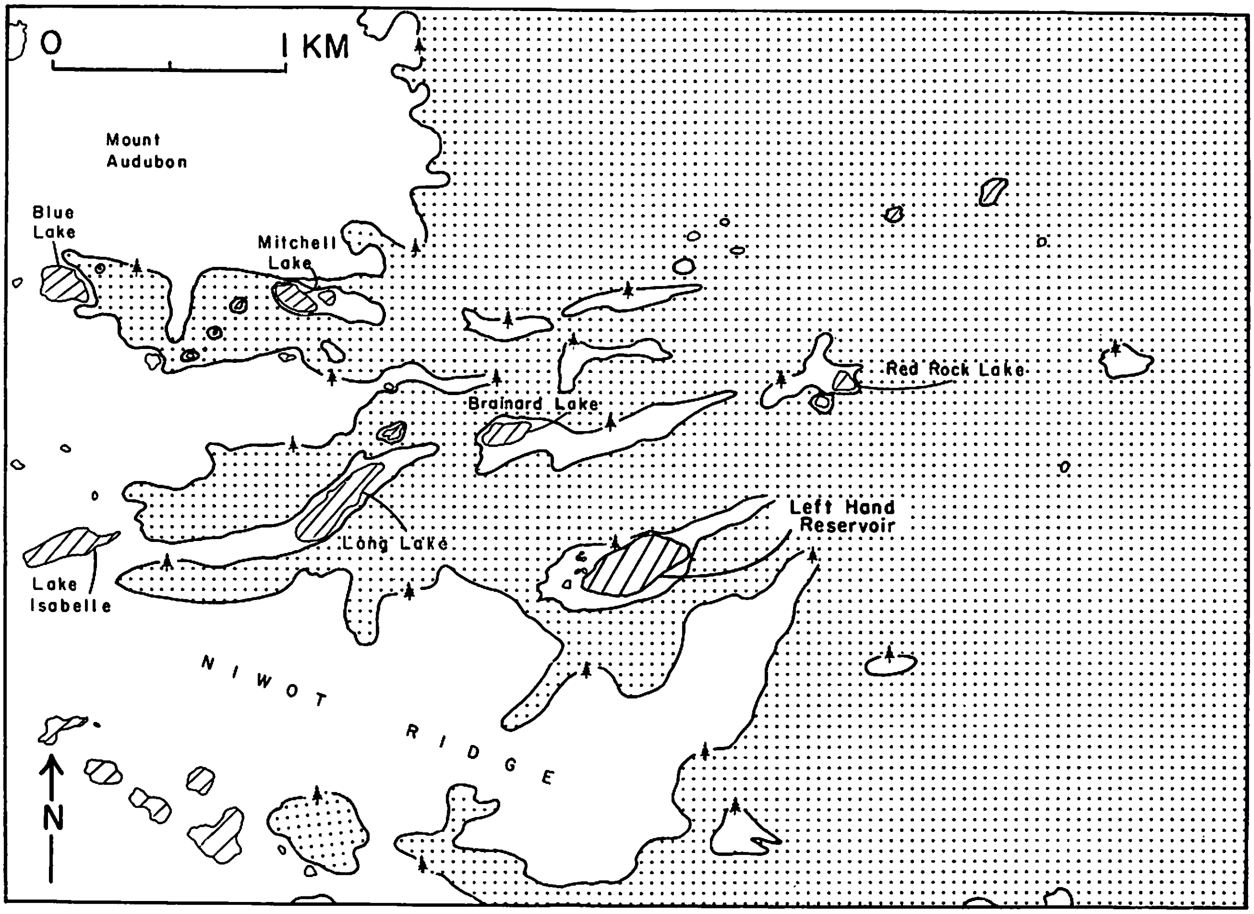

Figure 1. Indians Peak area pollen study sites; (forest area hatched).

than present, and from 3000 BP until today was said to have experienced higher treelines due to warmer summer climates. It is notable that a mid-Holocene, warm, dry period was not recognized (cf. Pennak [1963] above, and see below for discussion.)

While the Front Range is thinly represented in the field of Holocene ecological studies, there are two recent studies of the Holocene environmental record from the alpine of southern Colorado. The first, by Andrews, Carrara, King, and Stuckenrath (1975), is an examination of palynology and bog stratigraphy at Hurricane Basin, San Juan Mountains (Figure 2), which demonstrates changes in elevation of upper treeline. The study also includes data on deglaciation, Neoglaciation, and the influx of clastic minerogenic sediments into these cirque basins as additional indices of environmental change. However, in this study modern pollen samples were not employed as analogs for the past pollen counts, and the fossil pollen data were presented only as relative percentage diagrams. The study was aided by ^{14}C dating of subfossil timbers indicative of past tree cover of these high-elevation (ca. 3500 m) sites. The interpretation of the climatic history from the single pollen diagram at Hurricane Basin suggests that from 9620 ± 75 BP to 8400 BP the climate was cooler and/or wetter than at present; from about 8400 to 3500 or 3000 BP summer climate was warmer, with higher treeline; from ca. 3500 or 3000 BP the cirque basin was cooler and/or wetter than now; and suggests that post-280 BP warming has elevated the treeline.

The implications for glacial history include the radiocarbon assays from the earliest organic sediments in these northeast-facing cirques, establishing ice-free conditions at 9000 BP, with the suggestion that south-facing cirques might have lost their ice by 11,000 BP. Andrews et al. (1975: 182) make the point that the studies of peat stratigraphy, mineral content of organic sediment, plus the pollen and plant macrofossil record exceed in climatic sensitivity the glacial record of ice advance and retreat.

The record of treeline displacement in this San Juan Mountains study, and the inferred climatic history, is in complete contrast to

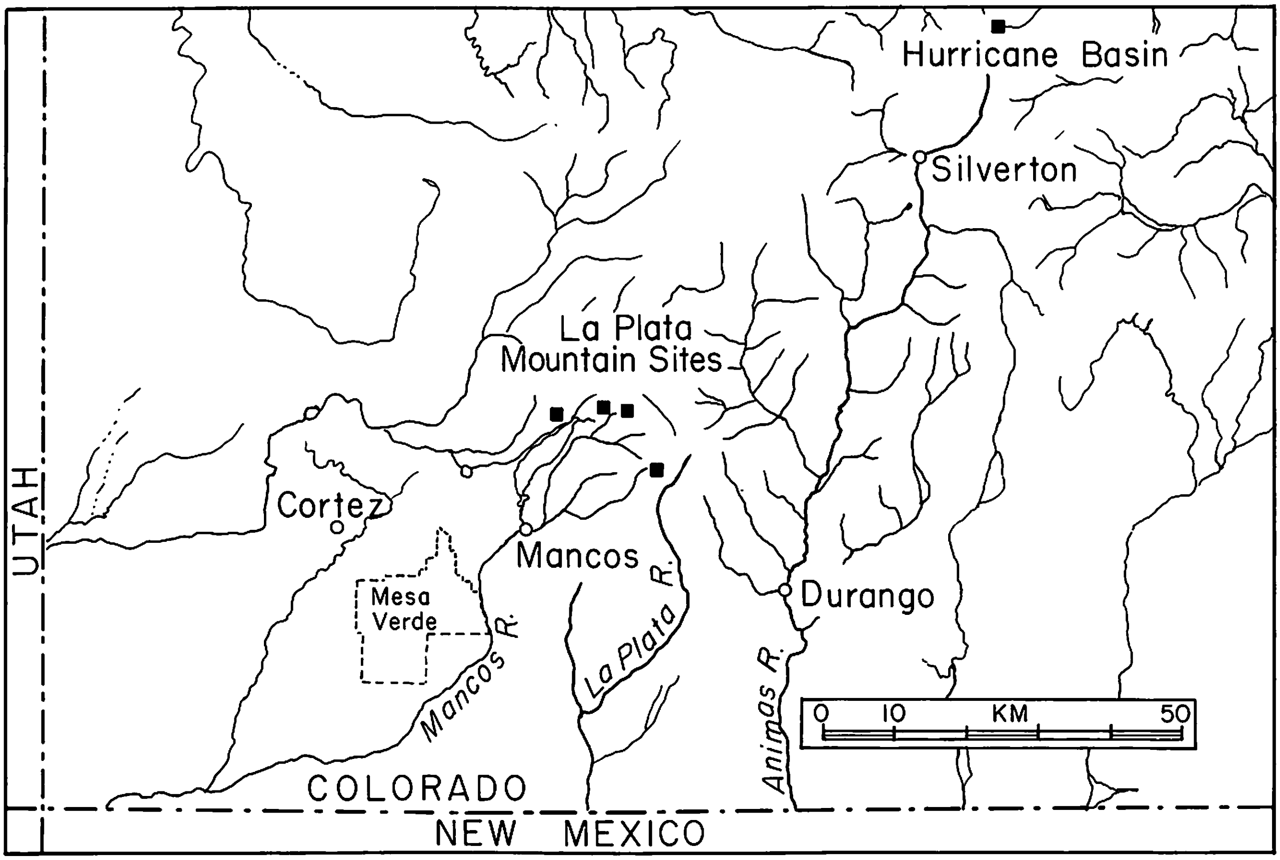

Figure 2. Southern Colorado Mountain pollen study sites.

Maher's (1972) Front Range interpretation. These San Juan paleoclimatic findings are broadly synchronous and parallel to similar studies elsewhere (e.g., Denton and Karlen, 1973; LaMarche, 1974). Some possible support for the concept of wetter and cooler climate in the last few millenia may be reflected in several examples of downslope movement of minerogenic materials burying ^{14}C-dated organic sediments between 3000 and 2000 BP, for example, at 2580 ± 90 BP (GaK-2827) in Andrews et al. (1975: 195); at 2520 ± 90 BP (WIS - 69) at Engineer Mountain Bog, San Juan Mountains, collected by Maher and dated by Bender et al. (1966); and at 2505 ± 105 BP (SI-4762) on the west slope of the Front Range (collected by Andrews and Nichols).

In the second recent study from southern Colorado, Petersen and Mehringer (1976) employed high standards of palynological analysis in their work on postglacial timberline fluctuations, in the La Plata Mountains, southwestern Colorado (Figure 2.) A subalpine meadow at 3290 m in the headwaters of the San Juan River provided a well-dated record of treeline elevation changes over the past 9800^{14}C yr. Modern pollen samples were collected and usedas analogs in this study to aid interpretation of past events, and spruce to pine ratios were also employed to deduce treeline movements. A fundamental strength of this record is that the toal area above timberline would be greatly altered by elevation changes in the forest-tundra ecotone (Petersen and Mehringer, 1976: 285); a depression of this ecotone by only 110 m would double the tundra area above treeline at this locality. There were major upward movements of treeline about 8500 BP, and again at about 6700 BP resulting from both warmer climatic episodes. A major downslope retreat of treeline ocurred at 2500 BP as climate cooled. The last 2500 yr of the sedimentary deposit is greatly compressed, and so that part of the record is less clear, but there was some evidence of downslope retreat of treeline under colder conditions since 300 BP.

In a recent study in the Front Range, Davis et al. (1979) sampled the sediments of Butterfly Lake in the Arapaho Cirque, which contained sediments greater than 4.6 m in depth and greater than 5400 ± 240 yr old. They used x-radiographic, paleomagnetic, grain size, and organic matter measurements to elucidate the sedimentation history; palynological studies are anticipated. Wood fragments from about 6300 to 5600 BP (estimated dates) raise the prospect of identifying a Hypsithermal treeline extension upslope, though wind transport may also conceivably be a factor. Davis et al. recognized the effects of the Little Ice Age in their core ca. 300 to 100 BP.

Discussion of the Upper Treeline Record

The three major palynological studies (Maher, 1972; Andrews et al., 1975; Petersen and Mehringer, 1976) have produced three somewhat different interpretations of Holocene climatic history. Those from southern Colorado contrast with Maher's (1972) Front Range scheme. One immediately apparent deficiency in all three studies is that none of them has companion studies by the same author in the same area which would serve to clarify some of these differences, which in the southern Colorado area may be more apparent than real. The two southern sites are only 85 km apart, and it is clear that in early Holocene time they shared the warmer summer climate which at both sites led to major upward movements of treeline by about 8500 BP. Petersen and Mehringer's (1976) evidence for higher treeline about 6700 BP was not a feature of the Andrews et al. (1975) report, but the latter study had no ^{14}C control on the pollen diagram between 8300 and 3500 BP. During that time there was evidence from the spruce:pine ratios (Andrews et al., 1975, Figure 8) of relatively warm climate from perhaps 7000 to 5000 BP, thus broadly resembling the La Plata findings (Petersen and Mehringer, 1976). The southern Colorado sites are in broad agreement too in the cooling following 4000 (at ca. 3500 BP) and through 3000 BP. The brief episode of warming in La Plata Mountains at 2500 BP and the immediate cooling afterwards was not identified in the San Juans, possibly because at the latter site very few pollen samples represent this episode. There were only four samples between 3500 and 1300 BP, or about one sample per 600 yr. A final possible discrepancy arises from the topmost pollen sample in Andrews et al. (1975) diagram, said to show recent (post-280 BP) warming, in contrast to La Plata cooling. However, in Andrews et al. (1975) the temperature increase is deduced from only one sample, and factors such as differential concentration of tree pollen in slow-growing surface sediments may be a contributory factor in this case. Relict timbers above the San Juan site, dating from ca. 300 BP, imply a recent cooling and seem more reliable as evidence. Thus, reexamination of the evidence for apparently conflicting climatic interpretations even in most recent times can yield alternative and parallel climatic histories.

The contrast with Maher's (1972) record is so sharp that it is essentially in complete antiphase relationship to the above schemes. One potential error is that the spruce:pine ratios may give a dichotamous indication of treeline position, as Maher (1972: 549) notes, with each ratio of spruce:pine percentages representing pollen fallout values identical at places both below and above treeline. (Note that some method of making absolute counts for modern pollen deposition on moss polsters would solve this problem.) This leaves the possibility that the ratios preferred by Maher (1972) in his Figure 7 are misleading. We may note that his "absolute" pollen diagram shows spruce pollen numbers peaking at 8500 BP, the same time as the warm episode (with high spruce values) at the two southern Colorado sites described above, and that spruce pollen values at Redrock Lake then fluctuated until there was a marked decline in spruce between 4000 and 3000 BP, as pine pollen numbers increased. Maher has assumed that in the upper part of the diagram, the increased number of pine pollen relative to spruce pollen was the result of higher vegetation zones, as pine forest approached the site. However, his modern pollen samples (Maher, 1963, 1972) and those of Petersen and Mehringer (1976) show that increased pine pollen numbers also are characteristic of alpine tundra areas, with the added criterion of reduced spruce values and higher sagebrush (Artemisia) numbers. Maher's (1972) late Holocene data from Redrock Lake show increased sagebrish (Artemisia) numbers with higher pine and lower spruce values, with more grasses and other herbaceous pollen taxa, consistent with a decrease of treeline elevation and a downslope spread of tundra.

The higher pine numbers in the last 3000 to 4000 years at Redrock Lake demand an explanation consistent with a lower treeline if this alternative explanation to Maher's (1972) is to be acceptable. One possibility is illustrated by the work of Tauber (1967, 1977), who finds that much pollen release is contained within and below the forest canopy, and that filtration of windblown pollen on tree trunks and branches is a significant loss of airborne pollen; thus forest thinning could actually increase local pollen deposition. A possible application to Redrock Lake would be as follows: as the upper treeline retreated downslope or the uppermost woodlands thinned out due to climatic cooling, spruce pollen production would be reduced while the relatively unaffected pine pollen influx from lower elevations passed through the degenerating spruce forest in greater quantities due to reduced filtration losses on fewer and thinner trees.

In a study of the paleo-ecology of Chaco Canyon, New Mexico, Hall (1977) has compared the history of the San Juans (Andrews et al., 1975; Petersen and Medringer, 1976) to his study area, and noted the similarities. Hall argued against the interpretation of increased pine pollen as an index of higher tree line in late Holocene times, as proposed by Maher (1972). Hall (1977) suggested that a downslope shift in vegetational zones due to cooling climate would have the affect of enlarging the area extent of pine forest and therefore increasing the pine pollen influx at alpine elevations. In a brief discussion Hall (1977, p. 1615) did not provide additional evidence for the topographic situation downslope from Redrock Lake which would allow pine to increase its cover at the expense of other ecosystems. This seems to be one of several mechanisms (in addition to my comments above) which provide alternatives to Maher's (1972) explanation of increased pine pollen numbers arising from warmer climate. Even in the late Pleistocene tundra environment of the Colorado Front Range at Devlins Park, Legg and Baker (1980) note that pine and sagebrush pollen (Artemisia) dominated the pollen diagram. It is notable that these two pollen taxa increased in the late Holocene at Redrock (Maher, 1972), when I suggest (above that alpine tundra expansion occurred.

Within the mid-Holocene period, "absolute" spruce values at Redrock Lake had a secondary peak between 7000 and 6000 BP, broadly synochronous with spruce peaks in the southern Colorado sites, there interpreted as a warm episode. The low spruce numbers from 3000 BP to present are in very clear contrast in Maher's (1972) Figure 2 to the earlier high spruce values, and could be interpreted as agreeing with the two southern Colorado sites as being generally cool. Thus there is the clear possibility that all three of these Colorado climatic histories can be interpreted uniformly.

On the other hand, if Maher's (1972) interpretation of aniphase Holocene climatic behavior is correct, then this area is important for the comprehension of the climatic history of the Northern Hemisphere. Maher's (1972) study would have been clarified had he located ancient timbers at or near his site, as Andrews et al. (1975) and Petersen and Mehringer (1976) were fortunate enough to do; but in the Niwot Ridge - Redrock Lake area of the Front Range such relict timbers are essentially unknown at present, for reasons unclear to us now. Currently S.K. Short, J.T. Andrews and I are recovering, dating, and analyzing pollen from lake-sediment cores from an altitudinal sequence of lake basins close to Redrock Lake (Long Lake, Mitchell Lake, Blue Lake, Lake Isabelle, Figure 1). These range in elevation through the subalpine forest up to the forest-tundra ecotone and above, and we hope to clarify the status of Front Range paleoclimatic history from these sediments. A ^{14}C date 11,800 ± 450 (GX -7723) has been given to the basal sediments of Long Lake (sampled by Nichols), which is about 200 m above Redrock Lake, and is over 2000 yr older.

Paleoecology of the Lower Timberline

The Holocene history of the lower timber-line-prairie ecotone has received little attention from palynologists, so the study by Markgraf and Scott (1981) is most welcome. A single site near Crested Butte was analyzed, where erosion had exposed a 5.8-m section of former lake sediments, representing the last 15,000 yr. The section lay at 2800 m elevation, about 200 m below modern timberline. Markgraf and Scott interpret the palynological sequence as showing two major climatic changes, from cool-moist to warm-moist conditionsat 10,000 yr BP, and a shift to warm-dry climate at 4000 BP. They relate these findings to possible changes in the southern boundary of Pacific winter storms, and the summer monsoon limit which now only reaches central Colorado.

PLEISTOCENE SEDIMENTS

Because of the prolonged failure to find any Pleistocene peats or lake sediments in the Front Range, some authorities have assumed that such materials do not exist. The accidental discovery of organic sediments below till in a large pit dug for a ski-lift tower at Winter Park (Andrews et al., 1976) suggests that more such deposits may await discovery in this area. The following summary of this data is derived from thesis material (Millington, 1976).

The excavation reached down 13 m below present ground surface, to within a few meters of bedrock according to seismic data, and revealed a sequence of five cyclothems, with organic lake sediments and peats intercalated in the minerogenic deposits (glacial tills). The lowest organic waterlain sediments were dated 30,480 ± 2800 BP (DIC - 482). This date is sufficiently near the assay limits of the dating equipment used that the possibility of an infinite ^{14}C date cannot be excluded, though the pit excavation made possible the collection of large samples. This date of about 30,500 BP is the oldest known to us for late Pleistocene materials for the Front Range.

The oldest episode represented one of several retreats of the former Fraser Glacier, when ponding occurred behind ice or moraines which dammed the valley of the Mary Jane Creek. Palynology (including "absolute" dry weight counts and modern polster studies) suggests that summer temperatures at 30,500 BP were similar to modern temperatures at that elevation (2940 m a.s.l.), and conditions were somewhat wetter. After a subsequent mid-Pinedale advance, peat accumulated from 13,740 + 160 BP (DIC - 671) to 12,380 ± 180 BP (DIC - 516). That episode registered a summer climate apparently warmer than modern, as upper montane parkland covered the site. The last part of the interstadial (ending at 12,380 ± 180 BP) saw cooling affect the vegetation, and ice of the Winter Park Advance ended the organic sequence. Subsequent early or mid-Holocene sediments were not seen in the sides of this large excavation, extending over 20 by 15 m. It was not until 4260 ± 130 BP (DIC - 130) that peat growth began again here, and continued until recent times.

This gap in sedimentation representing the warmest part of the Holocene is not yet explained satisfactorily. Without other contemporary data from the western slope of the Front Range, we cannot know whether there were climatic conditions (such as warm dry summers) which prevented continuous accumulation and preservation of sediments. A possible explanation offered by Millington (1976) was that flooding removed the sediments.

When sedimentation began again after 4260 ± 130 BP, the subalpine forest occupied the site, but until about 4000 BP sedimentation was repeatedly interrrupted by fires, with much charcoal being included in the peat. From 4000 BP onwards the charcoal from this burning was greatly reduced, as climate became cooler and moister. Perhaps there is a clue in this brief episode (4200 to 4000 BP) as to why peats were not preserved from earlier Holocene times: perhaps the peat was destroyed by fires, possibly fostered by dry climatic conditions. After 4000 BP the subalpine forest was able to regenerate without much fire disturbance, but by about 1400 BP the productivity of the forest (as measured by "absolute" pollen counts) was markedly reduced, with little recovery from that condition to the present day.

More recent work on late Pleistocene lake sediments at Devlins Park in the Front Range is reported by Legg and Baker (1980), using sediments ponded by the last major advance of Pinedale ice, from 22,400 to 12,180 BP. The pollen diagram is dominated by sagebrush (*Artemisia*) and pine, and the site was above treeline throughout this time. Spruce:pine pollen ratios suggest that treeline averaged 500 m lower than modern limits, indicating mean July temperatures were about 5°C lower than today.

Note

The following comment by Professor Louis J. Maher, Jr. dated 19 January 1978 is reproduced in full, consequent upon correspondence between him and Professor Nichols.

> I have read with a good deal of interest Dr. Nichol's excellent review of the palynology of the Colorado Rockies. He is exactly right that the same pollen data may be subject to different interpretations. This seems especially true for my own work in the Front Range and in the San Juan Mountains as I seem to have arrived at a view of the local Holocene vegetation and climate history different from everyone else! I try to keep a sense of humor about this, and I welcome others to interpret my data as they wish. Dr. Nichols offers good advice when he suggests the need for additional studies of pollen and macrofossils near the localities already studied but at sites with different elevations and surrounding vegetation. Careful work with well-dated stratigraphic sequences may force me to change my current views. I look forward to finding out whether this will be necessary.

ACKNOWLEDGMENTS

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SPATIAL AND TEMPORAL VARIATION OF THE VEGETATION AND ITS PRODUCTIVITY, NIWOT RIDGE, COLORADO

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ABSTRACT

A description of the vegetation, its environmental controls, and its seasonal production and phenologic patterns is provided as a background for further studies in the same ecosystem during the Long-Term Ecological Research program of the National Science Foundation.

The vegetation and flora of Niwot Ridge is representative of the alpine region of the southern Rocky Mountains and physiognomically representative of dry alpine tundra vegetation in general. A clustering method was used to classify stands into the principal vegetation noda within the Saddle area of Niwot Ridge: Dry *Kobresia* meadow, Dry *Silene* fellfield, Moist *Salix* shrub tundra, Moist *Deschampsia* meadow, *Sibbaldia* snowbed, and Wet *Caltha* meadow. Indirect ordination methods identified the major controlling complex environmental gradients; soil moisture, snow cover and duration, and substrate disturbance. Species growth forms, noda, standing crop, and productivity are described within the framework provided by the ordination. Net annual aboveground productivity ranged from 103 to 205 g/m^2 with an average value of 170 g/m^2 for the Saddle. Belowground standing crops of biomass ranged from 2000 to 4500 g/m^2 and above to belowground biomass ratios ranged from 1:3 to 1:25. In a typical year, the onset of growth is controlled by disappearance of snow cover. A 10-d period of rapid growth follows snow melt in late May and early June. Most production ceases after 60 to 70 d or in the first days of August, and ripe seeds are available by September.

INTRODUCTION

Alpine plant ecology in the Colorado Front Range began with Cooper (1908, Long's Peak) and Cox (1933, James Peak). The foresight and pioneering work of Professor John W. Marr, his colleagues, and his students led the way to the present data base and understanding of the Colorado alpine vegetation. Observations come primarily from Niwot Ridge and from Trail Ridge (Griggs, 1956; Holway and Ward, 1963, 1965; Willard, 1963, 1979; Marr and Willard, 1970; Edleman et al., 1964; Zwinger and Willard, 1972). There is a 30-yr history of observations of Niwot Ridge (Marr, 1961), but only a few of these have been documented in the literature. Many of the Niwot Ridge studies have been theses or dissertations (Osburn, 1958; Caldwell, 1968; Ehleringer, 1973; Johnson, 1973; May, 1973, 1976; Fareed, 1973; Emerick, 1976; Flock, 1976; Komárková, 1976). Several of these studies have been partially reported in the literature and represent the activities of the International Biological Programme (IBP) Tundra Biome (Caldwell et al., 1974; Johnson and Caldwell, 1974; LeDrew and Emerick, 1974; Webber, 1974; Fareed and Caldwell, 1975; Webber et al., 1976; Flock, 1978; Komárková and Webber, 1978; Komárková, 1979). The principal phytosociological studies from the above are Willard, (1963, 1979) May (1973) and Komárková (1976). Ives and Webber (1980) have reviewed the main Front Range literature in plant ecology. There exists only one principal study of spatial distribution of primary production (May, 1976).

This paper examines the factors which control the structure, composition, and productivity of tundra vegetation, and the variation in seasonal patterns of growth of alpine tundra on Niwot Ridge. It provides a framework against which other studies of plant physiology, plant ecology, and ecosystem modeling on Niwot Ridge can be viewed (Johnson and Caldwell, 1974; Fareed and Caldwell, 1975; Ehleringer and Miller, 1975; Flock, 1976; Webber et al., 1976). In addition, this work is useful for comparing Niwot Ridge to circumpolar arctic and alpine regions in conjunction with IBP and the alpine project of the current Long-Term Ecological Research program of the National Science Foundation. Although the main effort of the U.S. Tundra Biome program of IBP was primarily concerned with arctic tundra as exemplified by Barrow, Alaska (Brown et al., 1980), this alpine study was established for comparative purposes, since the alpine areas of lower latitudes also require analysis for a full understanding of cold-dominated environments. Webber (1978) provides a companion paper dealing with the Barrow vegetation.

SITE OVERVIEW

Niwot Ridge is a wind-swept, tundra upland in the Colorado Front Range due west of Boulder. The Ridge begins on the Continental Divide at the summit of Navajo Peak (4085 m) and extends eastward as a narrow arete for about 2 km before it widens into round knolls and shallow saddles (Benedict, 1970; Figure 1). The bedrock of Niwot Ridge is igneous and metamorphic mainly of Precambrian origin. During the Wisconsin stage of the Pleistocene, the Bull Lake and Pinedale glaciations (Madole, 1969) occurred in the valleys to the north and south of Niwot Ridge, but the ridge itself was not covered. The main site is located on a saddle of Niwot Ridge and is 3650 m.a.s.l. at latitude 40°3'N and longitude 105°36'W. It is approximately 25 ha in area.

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Figure 1. Aerial view along Niwot Ridge toward the Continental Divide. The Saddle area is indicated by arrows (3600 m). Photo by J.D. Ives.

The Saddle of Niwot Ridge is 225 m below and 3.4 km east of the long-term climatic station (D-1) from which the following climatic statement was derived. Partial records were kept for the Saddle during the tenure of IBP. They suggest small differences between sites D-1 and the Saddle (LeDrew et al., unpublished manuscript); for example, the sheltered saddle site is warmer by 1.1 to 2.9°C and the standard deviation of temperature maxima and minima are less than for more exposed sites. The climate and energy receipt of D-1 are presented in Figure 2. The data were derived from Barry (1973). The average length of the growing season is 90 d (Webber, 1974) and is characterized by a warmer and drier climate than the arctic tundra at Barrow (Webber, 1978). The July mean temperature is 8.5°C with a mean total precipitation of 1021 mm. In spite of the much higher rainfall, the drier climate of Niwot Ridge results from lower relative humidities and greater insolation than Barrow. The steep, well-drained, coarsely textured substrate and frequent high winds also contribute to the dryness of the climate. The winters are cold; January has a mean temperature of -13.2°C and mean precipitation of 131.3 mm. The snow drifts extensively, and while sheltered places may accumulate large amounts, other areas are kept virtually snow free and exposed throughout the winter. Winds are stronger in January (49.9 km/h^{-1}) than in July (20.9 km/h^{-1}). Gusts occur all year but are stronger and more frequent in

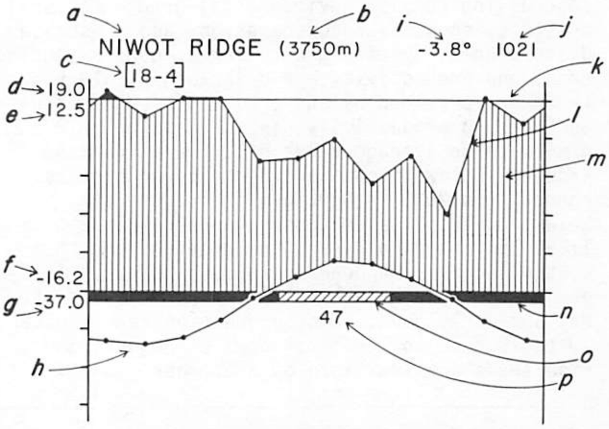

Figure 2. Climatic diagram for Niwot Ridge. After Walter and Leith (1967) on the basis of data from Barry (1972), 1973) (Komárková, 1976). Abscissa: months (January-December), ordinate: one division + 10°C or 20 mm precipitation, a--station name, b--elevation in meters c--duration of observation in years (the first firgure indicates temperature, the second precipitation), d--highest recorded temperature in °C, e--mean daily maximum temperature of the warmest month, f--mean daily minimum temperature of the coldest month, g--lowest recorded temperature, h--curve of mean monthly temperature, i--

mean annual temperature, j--mean annual temperature, j--mean annual precipitation in mm, k--line of 100 mm precipitation, 1--curve of mean monthly precipitation, m--the relative humid season, n--months with mean daily minimum temperature below 0°C, o--months with absolute minimum below 0°C, p--mean duration of frost-free period in days (after Walter, 1973).

winter. Mean high gusts for January are 112.9 km/ h^{-1} and July 65.8 km/h^{-1}.

There is a greater variety of soil types on Niwot Ridge than at Point Barrow. Most soils are coarse textured well drained, with thin surface horizons, and often with a characteristic loess fraction in the upper horizons (Komárková, 1976). The loess may be an important source of nutrients. Soils are predominantly acid (pH 4.5 to 5.5), but occasionally slightly basic. Base saturation values are higher than at Barrow (Webber, 1978). Permafrost is only sporadic on the ridge (Ives, 1973) and is too deep to influence vegetation.

The Ridge is bounded to the north, south, and east by a *Picea engelmannii*-*Abies lasiocarpa* forest. The Forest-Tundra transition is marked by krummholz forms at elevations from 3350 to 3500 m. a.s.l. The vegetation of the ridge above the transition corresponds to the middle and upper alpine zone of Walter (1973); it is characterized by closed herbaceous meadow on level ground which gives way to disintegrating mats where solifluction is prevalent. The flora and vegetation are representative of the entire alpine region of the southern Rocky Mountains (Webber et al., 1976). Diversity both in terms of numbers of species and community types is more than twice that of the arctic tundra at Barrow. Approximately 40% of the ridge is covered with fellfield communities characterized by *Trifolium dasyphyllum* and *Selaginella densa* and 20% is covered with meadows dominated by *Kobresia myosuroides*. The latter has been regarded as climax (Cox, 1933; Marr, 1961). Both fellfield and *Kobresia* meadows are dry and have little winter snow cover. The remainder of the vegetation consists of wet meadows, moist meadows with *Caltha leptosepala*, shrub stands with *Salix planifolia*, and snowbeds with *Sibbaldia procumbens* and *Carex pyrenaica*. The most ubiquitous plant of this alpine tundra is *Acomastylis rossii* which occurs in every community. Mosses and lichens are never abundant in any community type. However, mosses are most abundant in moist sites where *Aulacomnium palustre* and *Drepanocladus uncinatus* are characteristic. Lichens are most abundant in dry sites where *Peltigera canina* and *Leconora polytropa* are characteristics species.

There is perhaps no single striking feature of the Saddle. In spring a large snowpack in the lee of a hill to the west draws attention, while in autumn the dryness and stony nature of the terrain leaves a lasting impression. In winter the extensive snow-free areas appear remarkable. The predominance of dry sites, which is the result primarily of the well-drained surfaces and strong winds are responsible for the dominance of fellfields and dry meadows.

Niwot Ridge is relatively undisturbed. The Albion Trail crossed the ridge until the 1920s. Sheep grazing was terminated in 1948 and was never extensive. Cows, goats, and horses occasionally crossed the ridge. Vehicle traffic is restricted to an unpaved road. Scientists and a few hikers probably make the largest impact on the ridge, but it is insufficient to effect the majority of biological investigations. During 1976 and occasionally thereafter cattle grazed over the entire ridge in spite of U.S. Forest Service regulations prohibiting grazing. Grazing and trampling by these animals affected the vegetation cover and disturbed the substrate. Some vegetation experiments were destroyed, however, it appears now that Niwot Ridge is once again free of domestic grazers.

Disturbance and instability of substrates play a large role in the dynamics of this alpine tundra. The natural triggering agent of this disturbance is the pocket gopher (*Thomomys talpoides*) which lives beneath the vegetation while feeding and nesting (Osburn, 1958). It is active year-round and brings to the surface large quantities of soil. Rain, meltwater, and wind cause the soil to erode from the site of excavation. The site may be further eroded by needle-ice activity on the bare ground and subsequent strong winds (Osburn, 1958). Erosion triggered by the gopher causes the meadows to erode and this increases the extent of the fellfield communities. Osburn (1958), Marr (1961), and Willard (1963) have described the recovery of these deflated gopher workings and thus describe a successional cycle; but the rate of recovery through soil build-up can only be extremely slow taking hundreds of years.

METHODS

Sampling for this report began at the Saddle site during 1971 and continued for four growing seasons. However, some observations were made both prior to 1971 and since 1974. Both the field and laboratory techniques used here have their origins in our previous work (Webber, 1971; May, 1973; Webber et al., 1976; Webber, 1978) and also in IBP Tundra Biome workshops (Heal, 1971).

Vegetation may be viewed either as a continuum or as a series of distinct plant communities (Major, 1961; Whittaker, 1962; Webber, 1971; Shimwell, 1972). Each view demands a separate family of techniques; the continuum is studied through gradient analysis (Whittaker, 1967) and vegetation units through *classification*. Each set of techniques gives *different and* useful information about vegetation and they are used to complement one another in this study. Classification, in which plant communities are recognized and named, permits easier communication, mapping, and plot replication and experimentation. Whereas gradient analysis permits a more powerful identification of environmental controls and provides an environmental framework for the description of species distribution and productivity.

The basic sampling design called for the establishment of many permanent plots which spanned the gamut of vegetation in the Saddle. These plots were sampled for seasonal variations of biotic and abiotic measurements. No plots were located on any apparent disturbed surfaces. Thirty plots were established in the Saddle. Each plot measures 1 x 10 m in length. This size approximates the minimal area of most tundra vegetation and the shape is compatible with most tundra patterns; for example, along contours on mountain sides or wet depressions (Webber, 1971). Species composition, cover, and frequency were established for each square meter of each plot and an importance value called Species Index (the sum of relative frequency and relative cover) was derived for each species within the plot (Webber, 1971; May, 1973). Both vascular plants and cryptogams were sampled. Simple abiotic descriptions such as aspect, slope, drainage characteristics, and stability were recorded for each plot at the time of sampling. Soil samples were collected from just below the vegetation mat to an average depth of 10 cm. Chemical and physical analysis of soils was performed in the laboratory using standard techniques (May, 1973). Percentages of sands, silts and clays, organic content, water holding capacity, pH, ammonium, nitrate, and phosphate were determined for each soil sample. At intervals of 10 d through two growing seasons gravimetric moisture was measured at a depth of 10 cm on each plot. Snow depth, snow cover, and date of snowmelt surveys were conducted for 4 yr. In the Saddle, soil and plant canopy temperature measurements were made for each plot every 2 h over an 18-mon period (May and Webber, 1975).

Classification was achieved by clustering plots or stands on the basis of their species composition using the average linkage method of Sokal and Sneath (1963). The resulting clusters of stands with similar composition correspond to specific habits. These units represent broad vegetation types somewhat above the level of the association (sensu Braun-Blanquet, 1932). Each cluster is called a stand nodum and is named on the basis of its species composition and habitat characteristics (Lambert and Dale, 1964; Webber, 1971). The vegetation at any location within the study area can be assigned to its nodum. A vegetation map showing the extent and distribution of noda was made at a scale of 1:10,000.

Gradient analysis was achieved using the indirect stand ordination method of Bray and Curtis (1957). The ordinations were based on stand species composition and subsequent correlation of the resulting ordination axes with measured stand environmental variables. Highly correlating variables are hypothesized to be controlling. However, a cause and effect relationship is not established. A further point of explanation with regard to ordination is required. The axes of the ordinations are best described as complex environmental gradients (sensu Whittaker, 1967). A complex gradient is a complex of interrelated and interdependent factors some of which may be identified because they correlate with the axis while others may remain unknown because they have not been measured. To recapitulate, no cause and effect is established by the term major controlling complex gradient. An ordination is an expression of the variation within the sampled universe, here the vegetation of the Niwot Ridge Saddle, and thus indicates the contributing controls on the vegetation within the study sites.

Since the early work of Raunkiaer (1934), the importance of plant growth-forms as strategic adaptations to the tundra environment has always been emphasized (Bliss, 1962a; Tikhomirov, 1963; Chabot and Billings, 1972). Certainly the most obvious common denominator between alpine and arctic tundras is their growth-form composition. The growth-form categories used here are similar to those used for the Barrow tundra (Webber, 1978). They are based primarily on the nature of the shoot habit, some categories, however, tend to be more systematic or phylogenetic in character; for example, bryophytes and lichens. However, bryophytes and lichens seem to be valid growth-forms in the tundra.

The spatial and temporal variation of standing crop and net primary productivity was established by harvesting two 0.1 m^2 (20 x 50 cm) quadrats from each plot during the period of peak aboveground vascular biomass. Peak aboveground biomass usually occurs in mid-July on Niwot Ridge (May, 1973). The quadrats were clipped at soil level, the contents of each quadrat kept separate and frozen for later processing. Two soil and root cores (7.6 cm in diameter) were taken to the maximum possible depth in each quadrat. Usually a depth of 25 cm was achieved before stones prevented deeper sampling. The soil cores were also frozen until they could be washed and seived in order to retrieve the roots and other belowground organs. The thawed vascular plants were partioned into ten functional fractions. Current year's growth and previous standing material were isolated and these were each separated into dead woody, live woody, live herbaceous and dead herbaceous fractions. Stem bases, and litter and prostrate dead comprised the remaining two fractions. Belowground material was separated into stem bases, live roots, and dead roots; the separation of roots into live and dead was made only on the basis of color and texture (Webber and May, 1977). All sorted material was over-dried at 105°C for 24 h and then cooled and weighed.

Estimates of net primary productivity were made only for the aboveground vascular plant portion of the vegetation. These estimates were based on the weight of the harvested growth of the current season and no allowance was made for grazing or for increments to previous years aboveground woody structures.

The temporal variation of standing crop and net primary production was assessed only for two vegetation types in the Saddle. The seasonal course of production was estimated in a dry *Kobresia* meadow and moist *Deschampsia* meadow. The temporal variation of standing crop and primary production was obtained by following their courses within the 1971 growing season and by comparing the peak seasonal harvests of several years. These data were collected by clipping 5, 0.1-m^2 (20 x 50 cm) quadrats every 10 d.

Phenological studies of nine selected flowering plants were made during 1972, 1973, and 1974 for Niwot Ridge. The observations were made once a week from the period of snowmelt to late summer. The following phenophases were recorded and used to construct phenophase diagrams similar to those of Lieth (1970): (1) vegetative growth; (2) closed blossoms; (3) open blossoms; (4) developing fruits; and (5) ripe fruits. A complete report of the Niwot Ridge phenological study is available (May, 1976). At Niwot Ridge *Kobresia myosuroides*, *Deschampsia caespitosa*, *Acomastylis rossii*, and *Caltha leptosepala* were followed on the dry *Kobresia* meadow and the moist *Deschampsia* meadow.

RESULTS

Gradient Analysis

An indirect ordination was constructed using the 30 vegetation plots. The axes of the ordination were correlated with 19 measured abiotic variables. Only those variables which had significant correlations are discussed. Figure 3 shows the distribution of four significant abiotic variables within the three-dimensional space of the ordination. This ordination framework provided by the phytosociological axes is the basis for describing the distribution of the vegetation noda, species, growth-forms, and various productivity and standing crop fractions in terms of the controlling environmental variables. The first axis of the ordination correlated with soil moisture, the second with the amount of snow cover and duration, and the third with the presence of ammonium in the substrate. In addition, it was apparent from field observation that substrate disturbance caused by pocket gophers also correlated with the third axis. The factors which correlated with the ordination axes are intercorrelated and their relationships are complex. The nature of these complex gradients can be seen when the abiotic variables are clustered according to their intercorrelation with one another and with the ordination axes (Table 1). Three clusters were identified and each axis is a member of one cluster. Even though certain variables such as snow cover and moisture are highly correlated, they are distinguishable on two separate axes within the ordination (Figure 4). However, each axis is a complex of interrelated environmental variables.

Vegetation Units and Their Distribution

Six noda were established (Figure 5) from 30 plots in the Saddle. Each nodum was identified and given a Roman numeral and name based on its characteristic species and its position within the complex moisture, snow, and substrate gradients of the ordination (Table 2). Nodum III was separated into shrub tundra and moist meadow noda because of the differences in growth-forms of species. Nodum IIIA included taller deciduous shrubs (10 to 30 cm in height), while Nodum IIIB included dwarf deciduous shrubs (0 to 3 cm in height) (Table 3). Figure 6 illustrates representative plots from each nodum which indicates the distinct differences in physiognomy of the noda. The vegetation map of the Saddle and its environs is given in Figure 7. Komárková and Webber (1978) mapped the entire area of Niwot Ridge above treeline. The Saddle can thus be compared with the entire ridge. The area occupied by each nodum is given in Table 2. These estimates were derived by planimetry of the maps. The greatest percentage of surface area on Niwot Ridge is classified as fellfield (43%) whereas the greatest aerial extent in the Saddle is occupied by the dry meadow (27%) and moist meadow (28%). The aerial extent of shurb tundra, snowbed, and wet meadow noda is relatively consistent over the entire ridge. A further picture of spatial distribution of the noda across the Saddle region is given by an idealized profile of the major landforms of the study area (Figure 8). The mean nodal values of Species Index for each species, the total number of species in each of the major taxonomic entities for each nodum, the mean relative cover of each growth-form for each nodum, and some mean values of selected abiotic variables for each nodum are given in Tables 3, 4, 5, and 6, respectively.

Although the noda seem fairly distinct in the dendrogram and habitat descriptions, it is difficult to single out characteristic species for each nodum. Few species are unique to a nodum and most occur in several noda. The following descriptions point out the principal characteristics of each nodum.

Nodum I, the Dry *Kobresia myosuroides* meadow, is the second most extensive vegetation type in the Saddle (27%) and usually occurs immediately downslope from fellfields (Figures 6 and 8). The moisture regime is similar to that of the fellfields but snow accumulation in dry meadows is higher (Table 6). *Kobresia myosuroides* is the dominant species and forms dense tufts which block the wind resulting in snow accumulation on the lee side of the clumps. *Selaginella densa* and *Acomastylis rossii* are other characteristic

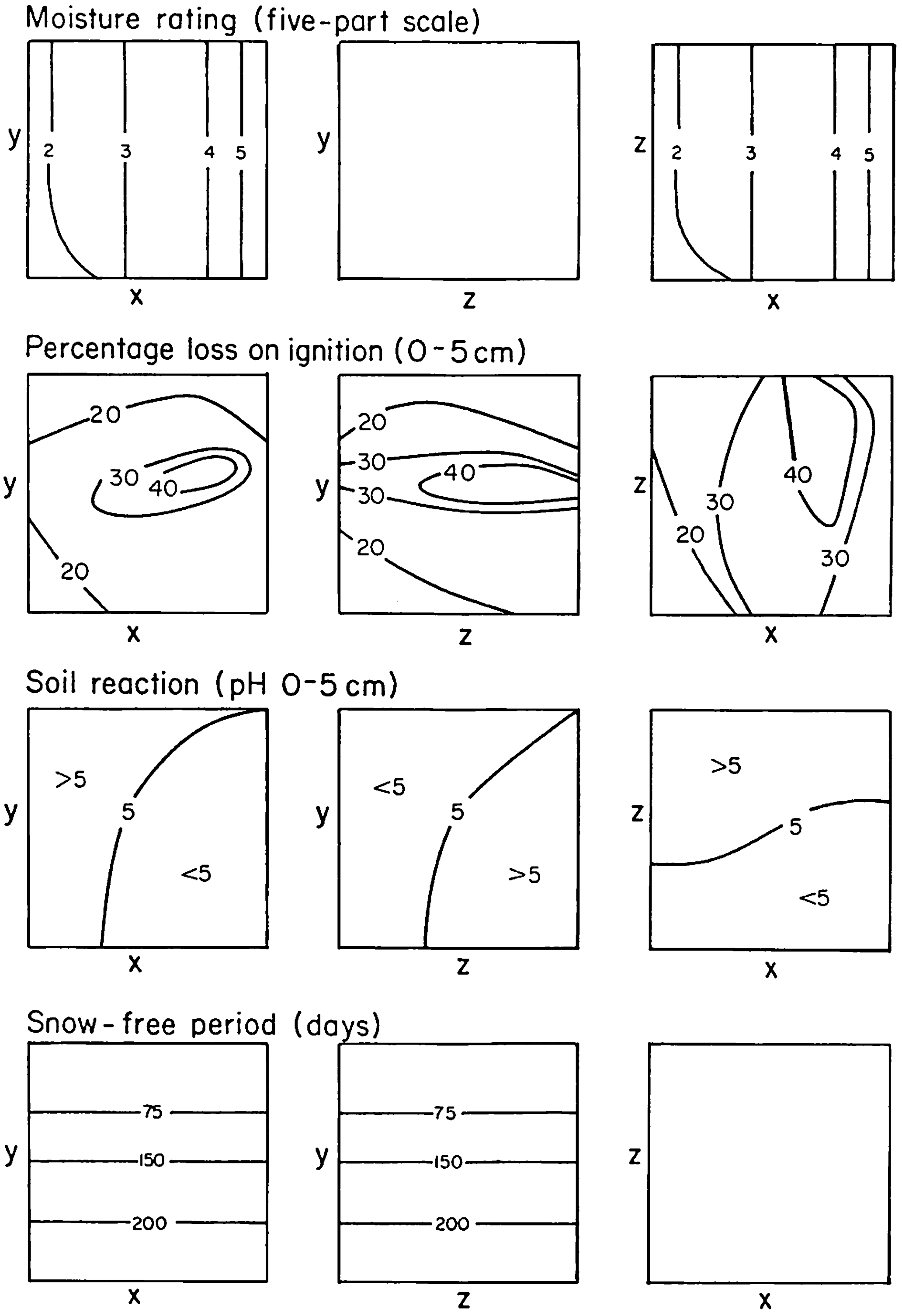

Figure 3. Distribution of four abiotic variables within the three principal elevations of the ordintion. The substrate trends indicated are used to interpret the environmental distribution of various components of the vegetation. All measurements were made in 1971.

Table 1. List of significant correlations between stand ordination axis values and some plot abiotic variables. Measurements from 30 plots were used. Correlation was established with the Pearson's product moment correlation coefficient (r) and significance was arbitrarily defined as any r value with P less than 0.01. Negative correlations are underlined. Correlation variables in each row are listed in sequence of decreasing correlation.

CLUSTER 1	
First Ordination Axis (BCX)	MOI, *SNO*, *BCY*, BS. *PEH*, AL3
Stand moisture regime (MOI)	BCX, *SNO*, *BCY*, *FE3*
Soil reaction (PEH)	BS, *AL3*, H
Aluminum in soil solution (AL3)	H, *BS*, CEC, *PEH*, BCX
Base saturation (BS)	PEH, CA2, *BCX*
CLUSTER 2	
Second Ordination Axis (BCY)	*SNO*, BCX, MOI
Snow free days (SNO)	*BCY*, MOI, *BCX*
CLUSTER 3	
Third Ordination Axis (BCZ)	NH4
Ammonium in soil solution (NH4)	WHC. CEC. PL1

CEC - Cation exchange capacity
CA2 - Calcium in soil solution
H - Exchangeable Hydrogen
WHC - Water holding capacity
PLI - Percentage weight loss on ignition

Table 2. Nodal names, their characteristic species and their areal extent over the whole tundra area Niwot Ridge and in the Saddle proper.

NODUM		CHARACTERISTIC SPECIES	WHOLE RIDGE MAP*	SADDLE MAP (figure 7)
I	DRY MEADOW	*Kobresia myosuroides*, *Selaginella densa*, *Acomastylis rossii*, *Tortula ruralis*, *Dactylina madreporiformis*	22	27
II	FELLFIELD	*Trifolium dasyphyllum*, *Silene acaulis*, *Carex rupestris*, *Polytrichum piliferum*, *Alectoria minuscula*	43	17
IIIA	SHRUB TUNDRA	*Salix planifolia*, *Lophozia hatcheri*. *Peltgigera aphthosa*	4	2
IIIB	MOIST MEADOW	*Acomastylis rossii*, *Deschampsia caespitosa*, *Desmatodon latifolia*	22	28
IV	SNOWBED	*Sibbaldia procumbens*, *Carex pyrenaica*, *Anthelia juratzkana*, *Toninia cumulata*	3	5
V	WET MEADOW	*Caltha leptosepala*, *Carex scopulorum*, *Aulacomnium palustre*	3	8
Stones and Scree			3	13

*Komarkova and Webber, 1978

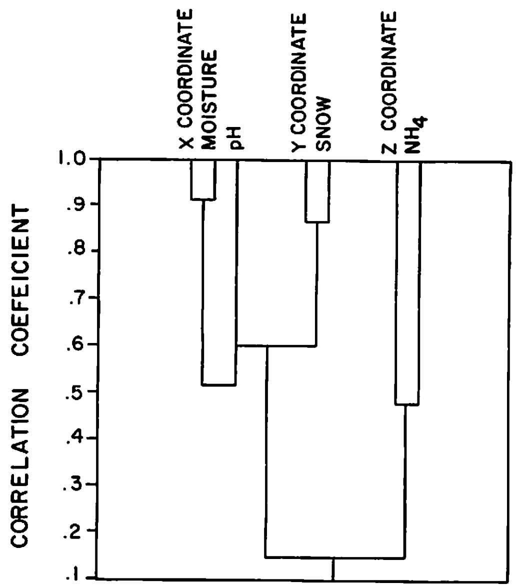

Figure 4. Correlation dendogram of the relationship of the four major substrate variables with themselves and the three principal coordinates of the ordination.

species in the dry meadow. This nodum also has the highest number of herbaceous dicotyledons (39) and the highest total number of species (110) of any of the noda in the study site.

Nodum II, the Dry Silene acaulis fellfield, occupies only 17% of the Saddle study site but is the most extensive vegetation type on the whole tundra area of Niwot Ridge (Table 2). Fellfields develop on dry, wind-swept ridges that are relatively snow-free throughout the winter. Low cushion and mat-forming dicotyledons are the characteristic growth-form on the rocky substrate. Silene acaulis and Trifolium dasyphyllum are the common cushion plants and lichens compose the greatest number of species (39). The growing season is longest in the fellfields and seasonal temperature fluctuation is high in these sites. Winter temperatures are low because of lack of protective snow cover and summer temperatures are high because plant cover is sparse and the ground surface is exposed to intense radiation.

Nodum III moist Salix planifolia shrub tundra comprises the smallest surface area on Niwot Ridge and in the study site (Table 2). It is characteristic of moist depressions or small polygons and is the only nodum with deciduous shrubs greater than 3 cm in height. Salix planifolia is the common shrub species in polygon troughs or depressions and erect dicotyledons are the dominant growth-form in the understory. Acomastylis rossii and Trifolium parryi are the most important herbaceous plants. The moist substrate and shade provide the best conditions for the largest number of bryophytes (30) in the Saddle (Table 4).

The vegetation in Nodum IIIB. the moist Acomastylis rossii meadow. is similar to that of Nodum IIIA with the absense of Salix planifolia. An abundance of dicotyledons and the largest number of monocotyledons (22) distinguish it from other noda. Deschampsia caespitosa and Acomastylis rossii are the dominant species. Moist meadows cover the greatest area in the Saddle (28%) although they are second in extent over the entire Ridge. Both Nodum IIIA and Nodum IIIB have moist substrates due to the high water table in the center of the Saddle and the abundance of meltwater released from the snowbank on the west slope (Figure 8).

Nodum IV, the Sibbaldia procumbens snowbed. is located in the lee of the stone terraces on the west side of the Saddle (Figure 8) and occupies a small area (5%) of the study site. Deep spring snow accumulation recedes late resulting in the shortest growing season of all noda (Table 6). Percentages of soil moisture are high while meltwater is available. then moisture decreased in sandy and well-drained substrate later in the growing season. Only 50 different plant species are present in the snowbed and the majority of them are caespitose graminoids or mat-forming dicotyledons (Table 5). Sibbaldia procumbens and Carex pyrenaica are the characteristic species.

Nodum V, wet Caltha leptosepala meadow, occupies a small depression in the Saddle (8%) area). It occupies poorly drained, wet sites dominated by Pedicularis groenlandica and Carex scopulorum. Caltha leptosepala is a characteristic species. This nodum is distinguished from all others by soils that are highly organic (Table 5). Spring snow is deep and soils remain saturated throughout most of the growing season. Hence there are twice as many bryophytes (24) than lichens (12) present in this nodum (Table 4).

Standing Crop and Productivity

The standing crop fractions at peak season illustrate the differences in production for the vegetation types in the Saddle. In general, net aboveground productivity for vascular plants was highest in the mesic noda which have little or no substrate disturbance and lower in dry, snow-free sites, snowbeds, and very wet sites. More specifically, aboveground productivity varies from about 164 g/m^2 yr in moist sites to 130 g/m^2 yr in wet sites (Table 7). Above ground standing crop, which includes litter, reaches a maximum and may exceed 2000 g/m^2 in moist, moderately snow-covered, stable sites which support willow shrub. Wet sites have the lowest standing crops which may be as low as 500 g/m^2 (Table 7).

Maximum belowground biomass coincides with

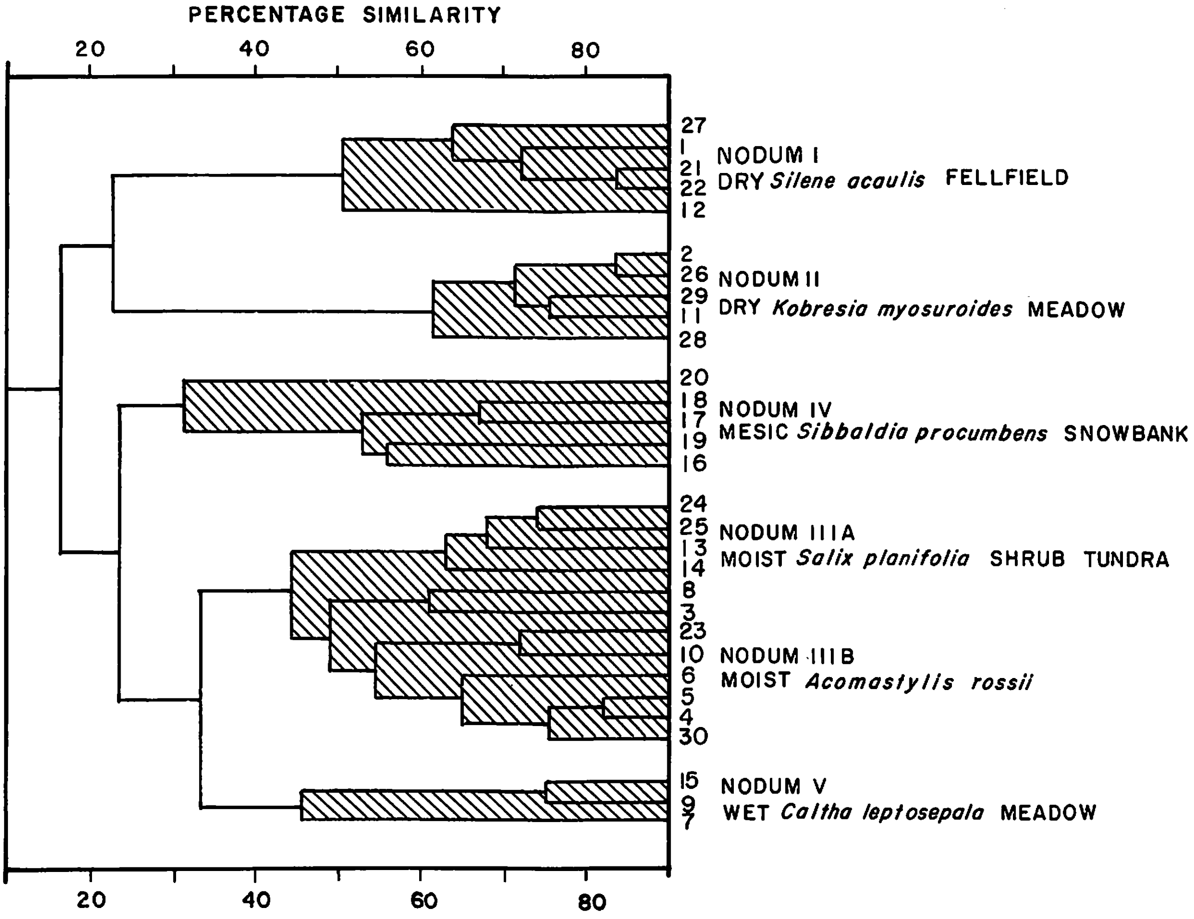

Figure 5. Dendorgram showing the similarity relationships between the 30 sample vegetation stands. Six clusters of noda are identified and have been named on the basis of habitat and characteristic species.

Figure 6A. Nodum II. Dry fellfield dominated by Trifolium dasyphyllum and Silene acaulis. Plot is situated on an exposed, rocky knoll on the east side of the Saddle.

Figure 6B. Nodum I. Dry Kobresia meadow. Over one quarter of the study area is covered with this nodum.

Figure 6C. Nodum IIIA. Salix planifolia shrub tundra. This nodum is restricted to the moist polygon area in the center of the Saddle.

Figure 6E. Nodum IV. Snowbed. This habitat is as rocky as the fellfield nodum but is dominated by Sibbaldia procumbens and Juncus drummondii.

Figure 6D. Nodum IIIB. Moist Deschampsia meadow. Acomastylis rossii commonly occurs between the grassy clumps.

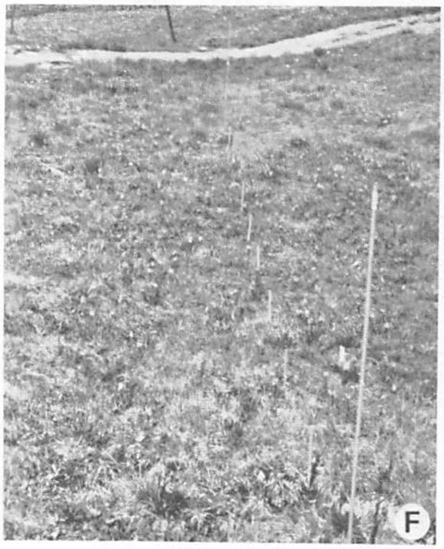

Figure 6F. Nodum V. Wet Caltha leptosepala meadow. Carex scopulorum is codominant with Caltha leptosepala in this stand.

Table 3. A representative list of the species occurring in 30 vegetation stands in the Saddle and their nodal occurrence. The mean nodal values of Species Index are given. The number of stands per nodum is given in parentheses after the nodal number. Species are listed within the major growth-form groups and alphabetically arranged within these groups. A complete species list for the Saddle is presented in May (1973). Growth form codes are P - pteriodophytes, MD - mat dicotyledon, ED - erect dicotyledon, RD - rosette dicotyledon, CD - cushion dicotyledon, CG - caespitose monotyledon, SG - single shooted monocotyledon, BR - bryophyte, LI - lichen.

SPECIES	GROWTH-FORM	VEGETATIVE NODA					
		I(5)	II(5)	IIIA(4)	IIIB(8)	IV(5)	V(3)
PTERIDOPHYTES							
Botrychium lunaria	P	-	-	-	0.3	-	-
Selaginella densa	P	9.4	10.6	-	-	-	-
SHRUBS							
Picea engelmannii	ES	-	-	0.1	-	-	-
Salix arctica	DS	-	-	0.6	0.4	0.2	7.0
Salix nivalis	DS	0.3	-	0.6	-	-	-
Salix planifolia	DS	-	-	31.3	-	-	-
HERBACEOUS DICOTYLEDONS							
Antennaria alpina	MD	0.5	-	0.2	-	0.9	3.6
Arenaria fendleri	ED	1.4	3.7	-	-	-	-
Artemisia pattersonii	ED	0.6	4.9	-	-	-	-
Artemisia scopulorum	ED	3.2	5.7	11.5	20.0	4.3	4.6
Bistorta bistortoides	ED	4.6	4.4	6.9	12.6	2.8	2.8
Bistorta vivipara	ED	5.3	0.1	5.9	2.1	-	4.9
Caltha leptosepala	ED	-	-	15.5	9.2	1.7	37.8
Castilleja occidentalis	ED	-	3.1	1.4	4.2	-	-
Cerastium arvense	MD	3.3	0.9	0.9	0.8	-	-
Chionophila jamesii	ED	-	-	1.0	7.8	0.2	-
Draba aurea	RD	1.8	3.4	-	-	-	-
Draba crassifolia	CD	-	-	0.1	0.6	3.1	-
Eritrichum aretioides	CD	2.5	3.8	-	-	-	-
Erigeron melanocephalus	ED	-	-	-	-	9.2	-
Erigeron pinnatisectus	ED	-	3.7	-	-	-	-
Erigeron simplex	ED	3.1	0.2	5.4	10.9	0.2	5.3
Gentiana algida	RD	0.1	0.2	5.1	3.9	-	5.1
Gentianella amarella	ED	-	-	3.5	-	-	2.8
Acomastylis rossii	ED	11.4	12.3	13.2	26.2	6.2	2.9
Haplopappus pygmaeus	CD	0.4	7.9	-	-	-	-
Hymenoxys acaulis	RD	-	3.0	-	-	-	-
Lewisia pygmaea	RD	0.5	-	0.4	4.7	7.3	-
Minuartia biflora	MD	5.0	0.7	-	6.3	11.0	-
Minuartia obtusiloba	CD	2.3	16.3	1.5	-	-	-
Oreoxis alpina	ED	5.8	5.4	-	-	-	-
Parenychia pulvinata	CD	-	8.9	-	-	-	-
Pedicularis groenlandica	ED	-	-	0.5	1.3	-	11.4
Phlox sibirica	CD	1.6	4.5	-	-	-	-
Potentilla diversifolia	ED	0.6	-	5.2	2.8	-	6.9
Primula parryi	RD	-	-	-	-	6.3	0.2
Ranunculus adoneus	ED	-	-	-	0.1	4.8	-
Saxifraga rhomboidea	RD	3.5	0.4	0.4	1.3	-	-
Sedum lanceolatum	MD	1.8	3.3	0.1	0.4	-	-
Sedum rhodanthum	ED	-	-	1.1	0.9	-	3.2
Senecio crocatus	ED	-	-	-	0.1	-	6.5
Sibbaldia procumbens	MD	-	-	0.7	2.4	36.9	3.5
Silene acaulis	CD	2.6	14.7	0.6	0.8	-	-
Stellaria laeta	MD	1.4	-	4.8	3.1	-	-
Thlaspi montanum	RD	2.8	0.9	-	0.1	-	-
Trifolium dasyphyllum	MD	0.8	17.7	-	-	-	-
Trifolium nanum	MD	-	3.8	-	-	-	-
Trifolium parryi	MD	3.2	-	20.8	5.5	14.7	4.2
MONOCOYTLEDONS							
Agrostis borealis	CG	0.4	-	2.8	3.4	-	9.0
Carex brevipes	CG	-	3.2	-	-	-	-
Carex nigricans	SG	-	-	0.2	-	3.6	4.4
Carex phaeocephala	CG	-	-	-	2.5	5.9	1.0
Carex pyrenaica	CG	-	-	-	-	32.5	4.5
Carex rupestris	SG	7.5	12.5	0.1	1.4	0.2	-
Carex scopulorum	SG	0.2	-	16.6	4.0	3.1	31.4
Deschampsia caespitosa	CG	4.2	-	10.3	34.2	10.5	17.5
Festuca brachyphylla	CG	5.8	9.2	5.4	6.6	8.3	0.6
Helictotrichon mortonianum	CG	-	2.1	-	-	-	-
Juncus biglumis	CG	-	-	-	0.1	-	2.5
Juncus drummondii	CG	-	-	-	-	14.5	4.5
Kobresia myosuroides	CG	69.3	0.5	1.4	-	-	-
Lloydia serotina	SG	5.1	4.3	2.6	3.6	-	0.4
Luzula spicata	CG	0.6	5.4	2.9	2.7	0.3	-
Poa alpina	CG	0.5	-	1.0	0.8	2.0	1.2
Poa arctica	SG	-	-	2.8	0.3	5.8	1.0
Poa glauca	CG	3.9	4.1	1.2	0.1	-	-
Trisetum spicatum	CG	3.6	-	2.7	2.8	0.9	-
BRYOPHYTES							
Anthelia juratzkana	BR	-	-	-	-	+	-
Aulacomnium palustre	BR	-	-	+	+	-	+
Bryum stenotrichum	BR	+	+	+	+	+	+
Desmatodon latifolius	BR	+	-	-	+	-	-
Drepanocladus unicatus	BR	-	-	+	+	-	+
Lophozia hatcheri	BR	-	-	+	-	-	+
Pohlia nutans	BR	+	-	+	+	-	+
Polytrichum piliferum	BR	-	+	+	+	+	-
Tortula ruralis	BR	+	-	-	-	-	-
LICHENS							
Alectora minuscula	LI	+	+	-	-	-	-
Caloplaca tiroliensis	LI	+	+	-	+	-	-
Candelariella aurella	LI	+	+	-	-	-	-
Cetraria islandica	LI	+	+	+	-	-	-
Cladonia pyxidata	LI	+	+	+	+	+	+
Coelocaulon aculeatum	LI	+	+	-	-	-	-
Dactylina madreporiformis	LI	+	+	-	+	-	-
Drepanocladus uncinatus	LI	-	-	+	+	-	+
Lecanora polytropa	LI	+	+	-	+	+	+
Pachyospora verrucosa	LI	+	+	-	-	-	-
Peltigera apthosa	LI	-	-	+	-	-	-
Rhizocarpon geographicum	LI	+	+	+	+	+	+
Thamnolia vermicularis	LI	+	+	-	-	-	-
Toninia cumulata	LI	-	-	-	-	+	-

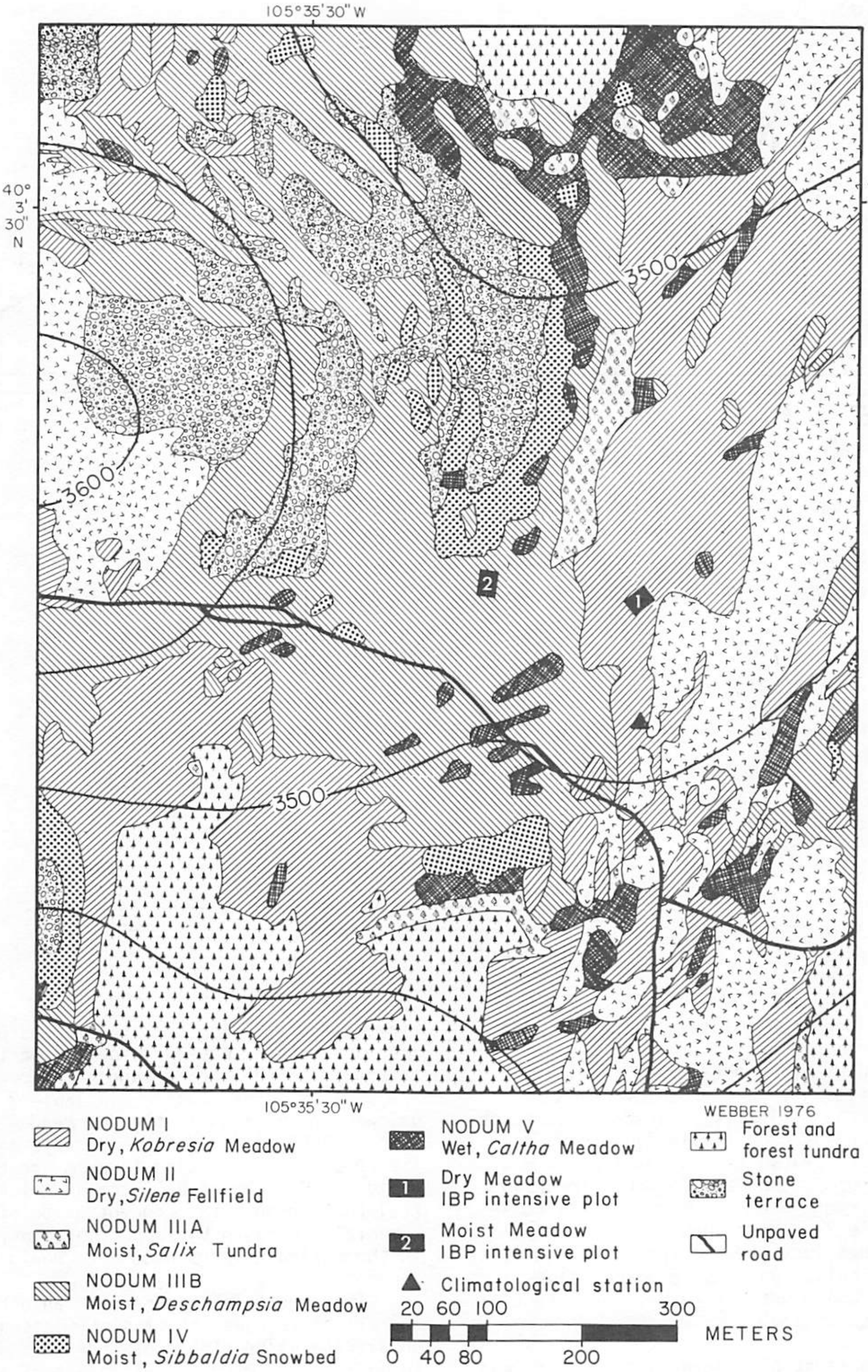

Figure 7. Nodal vegetation map of the Saddle area of Niwot Ridge.

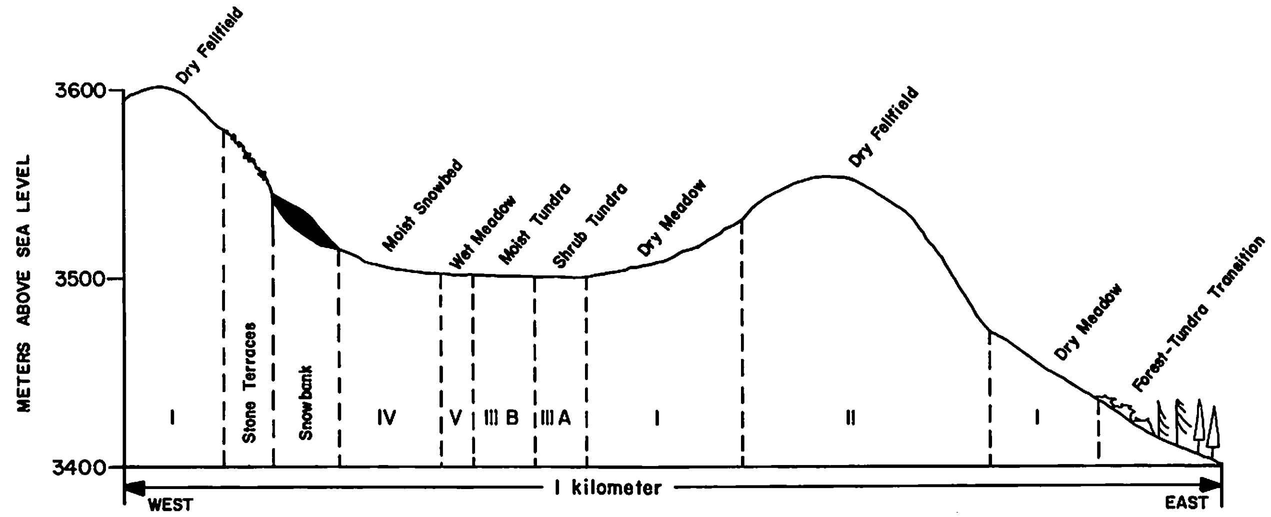

Figure 8. Idealized profile showing distribution of noda across the Saddle area of Niwot Ridge.

Table 4. The total number of species per vegetation nodum in the Saddle. Niwot Ridge.

TAXON	VEGETATION NODA					
	I	II	IIIA	IIIB	IV	V
Woody Dicotyledon	1	0	4	1	1	1
Herbaceous Dicotyledon	39	34	28	32	17	23
Monocotyledon	17	12	17	22	13	14
Bryophyte	7	3	30	21	10	24
Lichen	46	39	16	18	9	12
TOTAL	110	88	95	94	50	74

Maximum belowground biomass coincides with maximum aboveground standing crop and may exceed 4400 g/m^2 in the shrub tundra sites (Table). However, wet sites have higher belowground biomass values than drier sties in contrast to the aboveground standing crop (Table 7). Snowbeds have the smallest belowground biomass which may be less than 1200 g/m^2. Aboveground to belowground biomass ratios range from greater than 1:3 to less than 1:25 (Table 7). Most snowbed and fellfield sites have values just greater than 1:10 and most dry meadow and moist tundra sites have values just less than 1:10 while wet tundra has consistently low ratios close to 1:20.

A larger harvest of belowground material was completed within each nodum using a pit sampling method to depths of over one meter (Webber and May, 1977). The pit sampling provided belowground biomass and standing crop values which generally are larger than those provided by coring at peak season; also the aboveground to belowground ratios are smaller. For example, in Table 7, the belowground biomass in the dry meadow changes from 1534 to 3556 g/m^2 and the A:B ratio decreases from 1:9 to 1:17. Harvesting to even greater depths would further change belowground values but we feel that because the concentration of belowground material occurs in the upper horizons, any changes in the estimates presented here would be small.

The vegetation map permits an estimate of the overall aboveground biomass of the study area if an average value of biomass for each nodum is used in conjunction with the estimates of areal extent (Table 8). This exercise provides an average value of aboveground vascular biomass of 169 g/m^2 for the whole map area for the 1971 growing

Table 5. The distribution of the major plant growth-form types (Webber. 1978) in the Niwot Ridge Vegetation Noda. Values are Species Index. A specific example of each growth form is given for each nodum and the values for characteristic growth-form(s) are underlined.

GROWTH FORM	NODA						EXAMPLE OF GROWTH FORM
	DRY MEADOW (I)	FELLFIELD (II)	SHRUB TUNDRA (IIIA)	MOIST MEADOW (IIIB)	SNOWBED (IV)	WET MEADOW (V)	
Caespitose monocotyledon	96.2	27.3	32.2	56.3	75.3	49.6	*Deschampsia caespitosa*
Single-shooted monocotyledon	13.2	17.6	23.1	10.4	12.7	32.7	*Carex scopulorum*
Cushion dicot	10.7	53.0	0.3	0.6	3.1	0	*Silene acaulis*
Mat-forming dicot	16.8	30.5	29.6	19.2	64.4	11.7	*Trifolium dasyphyllum*
Rosetted dicot	12.7	8.8	5.9	10.3	13.6	5.2	*Saxifraga rhomboidea*
Erect dicot	43.2	49.5	76.5	100.4	31.7	93.6	*Acomastylis rossii*
Deciduous shrub 3 cm	0.3	0	1.1	0.4	0.2	7.0	*Salix nivalis*
Deciduous shrub 10 cm	0	0	31.5	0	0	0	*Salix planifolia*
Pteriodophyte	9.3	10.6	0	0.2	0	0	*Selaginella densa*
Lichen	15.2	40.9	5.2	6.4	10.3	6.6	*Cladonia pyxidata*
Bryophyte	4.6	5.6	10.8	9.7	37.2	37.4	*Polytrichum piliferum*

season.

Each vegetation nodum has a unique distribution within the ordination (Figure 9). This figure provides a visual nodum to soil moisture, snow cover, and substrate stability. Also, the interpretation of the enviornment for each nodum is compatible with the average value for environmental factors for each nodum (Table 6). Along the moisture gradient the noda are arranged from dry (I) to wet (V) with mesic noda (IIIA, IIIB) in between. Along the gradient of disturbance the moist meadow (IIIB) is the most disturbed site and substrate stability increases in the shrub tundra (IIIA) and wet meadows (V).

Distribution of Species and Growth-forms

The distribution of 10 common species within the ordination is given in Figure 10. Statements concerning the environmental tolerances or controls of each species can be suggested from the plot of each species within the ordination framework. For example, *Acomastylis rossii* is a ubiquitous or wide-ranging species in the Saddle and occurs in both wet and dry sites with greatest abundance in moist sites (top right, Figure 10). *Acomastylis* is also a characteristic species in disturbed areas. In contrast, *Silene acaulis* is a narrow ranging species and has a distribution restricted to dry. snow-free areas as indicated by its abundance at the dry end of the moisture and snow gradient (top left. Figure 20). *Carex rupestris*. *Kobresia myosuroides*. *Bistorta vivipara*, *Sibbaldia procumbens*. and *Caltha leptosepala* are narrow-ranging species while *Artemisia scopulorum*, *Deschampsia caespitosa*, and *Bistorta bistortoides* are wide-ranging. Some species may have similar distributions along one or two axes, but each is unique when all three axes are considered. For example, *Carex rupestris* and *Kobresia myosuroides* have similar moisture and snow tolerances but differ in their response to substrate disturbance (Figure 10).

Each growth-form has a distinct distribution within the ordination (Figure 11). Deciduous shrubs and erect dicotyledons are abundant on the moist sites while cushion dicotyledons. pteridophytes. and lichens are more abundant on dry, snow-free sites. Mat-forming dicotyledons occur in areas of high snow accumulation. The snow cover of single-shooted graminoids increases in moist sites as does the abundance of bryophytes. The dominant growth-form in the Saddle is the caespitose graminoid: this growth-form is bimodal and has high values in both

Table 6. Some selected abiotic variables for the six vegetation noda on Niwot Ridge. Values are means with standard errors from the plots within each nodum.

VARIABLES	I(5)	II(5)	IIIA(4)	IIIB(8)	IV(5)	V(3)
Snow depth (cm)*	9	<10	20	35	100	73
Soil moisture (%)**	42.2 + 12.3	31.9 ± 5.8	187.5 ± 29.7	60.2 + 4.8	26.5 + 4.2	180.7 ± 38.8
Length of growing season (days)***	105 ± 5	109 ± 4	96 + 5	88 ± 4	88 ± 5	52 ± 6
Temperature (°C)****						
Aboveground	7.4	9.2	6.9	7.1	2.4	6.1
Belowground	6.6	7.8	5.4	6.8	2.8	5.1
Organic matter (%)	27 + 1	19 ± 3	29 ± 9	32 ± 2	14 + 3	41 ± 6
pH	5.4 ± 0.1	5.2 ± 0.2	5.1 + 0.1	4.7 ± 0.1	4.9 ± 0.1	4.8 + 0.1
Ammonium (mg g^{-1})	1.5 ± 0.3	1.1 + 0.2	7.6 ± 3.9	2.5 ± 0.7	1.3 + 0.3	5/1 + 1.1

* Mean of mean annual snow depth from 1971-1975.
** Percentage by weight at peak growing season, 1974.
*** Mean of 1972-1974, based on length of snowfree period with air temperatures above freezing.
**** Mean daily mean for day period from July 13-19, 1974.

dry and moist meadows. These patterns of growth-form in the Saddle can be used to compare the vegetation of Niwot Ridge with other tundra sites.

Seasonal Variation.

Figure 12 illustrates the seasonal progression of the various fractions of the standing crop for the dry *Kobresia* meadow (Nodum I) and the moist *Deschampsia meadow* (Nodum IIIB) for 1971. Yearly variation in the length of the growing season influenced the biomass production and phenological development of vascular plants in the Saddle. The peak of current year's growth was reached approximately 7 d earlier in the *Kobresia* meadow compared with the *Deschampsia* meadow. This appears to be related to the differences in length of growing season for the two sites. Vegetative growth began 7 to 14 d earlier in the *Kobresia* site whereas longer snow duration delayed onset of growth in the *Deschampsia* meadow.

Figure 12 also illustrates the proportionate seasonal contributions of vascular plant fractions to the total standing crop of the vegetation sites. The alive reproductive structures comprise a small dry weight fraction of the standing crop. In the *Kobresia* meadow the biomass of reproductive structures, such as in florescences and flowers, peaks well before the peak of aboveground biomass. In the *Deschampsia* meadow the reproductive and current year's biomass peak together around 1 August. Most senescence of current year's growth ocurs after peak season. The standing dead fraction does not change significantly during the growing season. The litter and prostrate dead fraction increases in dry weight during the growing season.

Another description of plant response to yearly variation can be obtained by examining phenological development of various plant species in the Saddle (Figure 13). In 1974 the onset of vegetative growth for most species occurred towards the end of the first week of June. Blossoms began to appear towards the end of June and peak blooming for most species occurs in mid to late July. Fruits begin developing in mid-July, but few ripe fruits with well-formed seeds appear before mid-August. The phenological response of most species, however, is influenced by seasonal variation in environmental variables such as snow cover and soil moisture. For example, in 1973, a late spring snowfall and mean daily temperatures below freezing during the first week in June (May and Webber, 1975) delayed the onset of the growing season by 2 to 4 wk (Figure 13). Growth of species in the moist meadow nodum was delayed longer than growth by species in the dry meadow because the latter sites are usually snow-free in the spring. Delays in the onset of vegetative growth in 1973 caused subsequent delays in the flower and developing fruit phenophases for most species. However, although each species may begin growth and flower at different times, there is less variation in the timing of the appearance of ripe fruits. This event usually occurs from mid to late August.

The noda in the Saddle may be are arranged according to phenological sequence (Figure 13).

Table 7. Vascular vegetation fractions at peak aboveground living biomass for thirty plots from the six principal noda of the Saddle on Niwot Ridge for 1971. Above to belowground ratios are based on live vascular plant material. All average nodal values are oven-dry weights in g m^{-2}. Standard errors of the mean are included.

PLANT FRACTIONS	VEGETATION NODA (Number of Plots)					
	I (5) DRY MEADOW	II (5) FELLFIELD	IIIA (4) SHRUB TUNDRA	IIIB (8) MOIST MEADOW	IV (5) SNOWBED	V (3) WET MEADOW
ABOVEGROUND						
Herbaceous biomass	164.3 ± 13.2	171.0 + 15.7	205.6 ± 69.8	196.1 + 12.9	124.3 ± 9.5	133.8 ± 28.3
Herbaceous standing dead	164.5 + 8.2	247.8 ± 44.7	125.6 + 27.9	260.2 ± 66.1	76.6 ± 20.0	122.2 + 29.7
Stem bases	288.5 ± 43.8	92.2 + 17.6	77.2 ± 26.6	171.1 ± 27.6	54.8 + 9.3	81.2 ± 14.9
Litter and prostrate dead	306.7 ± 31.1	220.6 + 48.0	497.5 ± 133.7	347.9 ± 28.4	253.2 + 73.0	299.8 ± 32.2
Woody current years production			149.2 + 104.2			2.2 + 2.7
Woody previous years production			480.5 + 821.5			
Woody standing dead			65.6 ± 44.8			
Standing crop	924.0 ± 82.7	731.6 + 54.2	1601.0 ± 451.8	975.2 + 117.9	508.9 ± 131.0	639.2 ± 99.8
BELOWGROUND						
BELOWGROUND BIOMASS:						
Peak season core-1971	1739	1534	4398	2090	1208	2927
Pit cores -1973	2267	3556	4300	4079	3245	4485
Belowground Standing Crop:						
Peak season core-1971	2929	1858	5008	2563	1502	3583
Pit cores -1973	2627	4536	5150	5396	3792	4485
ABOVE:BELOWGROUND BIOMASS RATIOS						
Peak season core-1971	1:11	1:9	1:6	1:11	1:10	1:21
Pit core -1973	1:14	1:17	1:3	1:25	1:24	1:20

The sequence corresponds to the snow gradient with vegetative growth and fruit maturation occurring first in the noda that are snow-free earliest in the spring (fellfield and dry meadow) and last in the noda that melt out later in the season (snowbed and wet meadow)

DISCUSSION

Environmental Controls

The primary physical factor controlling vegetative growth-form and productivity patterns on Niwot Ridge is climate. The cold-dominated climate is constant for other alpine tundra sites in North America. This study is concerned, however with more proximal factors which control plant distribution and performance on Niwot Ridge.

The ordination indicates that the principal controlling factors of the species compostion of the vegetation of the Niwot Ridge Saddle are soil moisture, snow cover and duration and substrate stability (Webber, 1974). The substrate variables are highly interrelated. Figure 14 is a summary of the major controls on the vegetation of Niwot Ridge. It is based on field observation, inference, and many statistical correlations in an earlier study (May, 1973). The arrows indicate the direction of control. The complete matrix of arrows is not given and only the strongly substantiated or inferred controls are indicated. The thickness of the arrows indicates their relative importance. Thus the strong control of

Table 8. The percentage of the total area covered by each nodal unit in the Saddle map (figure 7) and the corresponding peak season aboveground vascular biomass value in 1971 for each nodum.

NODA		% TOTAL AREA OF MAP	PEAK SEASON ABOVEGROUND VASCULAR BIOMASS g m^{-2}	% BIOMASS CONTRIBUTION
I	DRY MEADOW	27	164.3	26
II	FELLFIELD	17	171.0	18
IIIA	SHRUB TUNDRA	2	835.3	13
IIIB	MOIST MEADOW	28	196.1	33
IV	SNOWBED	5	124.3	3
V	WET MEADOW	8	133.8	6
	STORES AND SCREE	13	0.10	1
	MEAN		233.54	

The mean aboveground vascular biomass of the entire map area 166 (g m^{-2})

* Number of plots

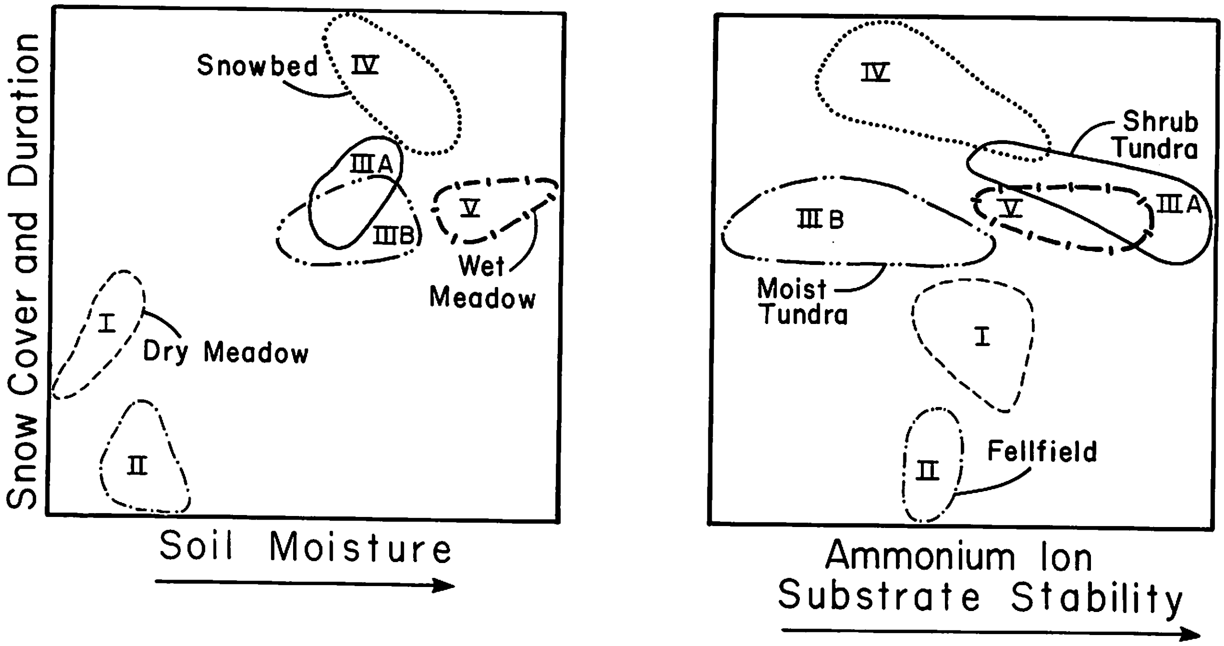

Figure 9. The distribution of the six noda within the ordination. The nodal numbers are given in Table 2.

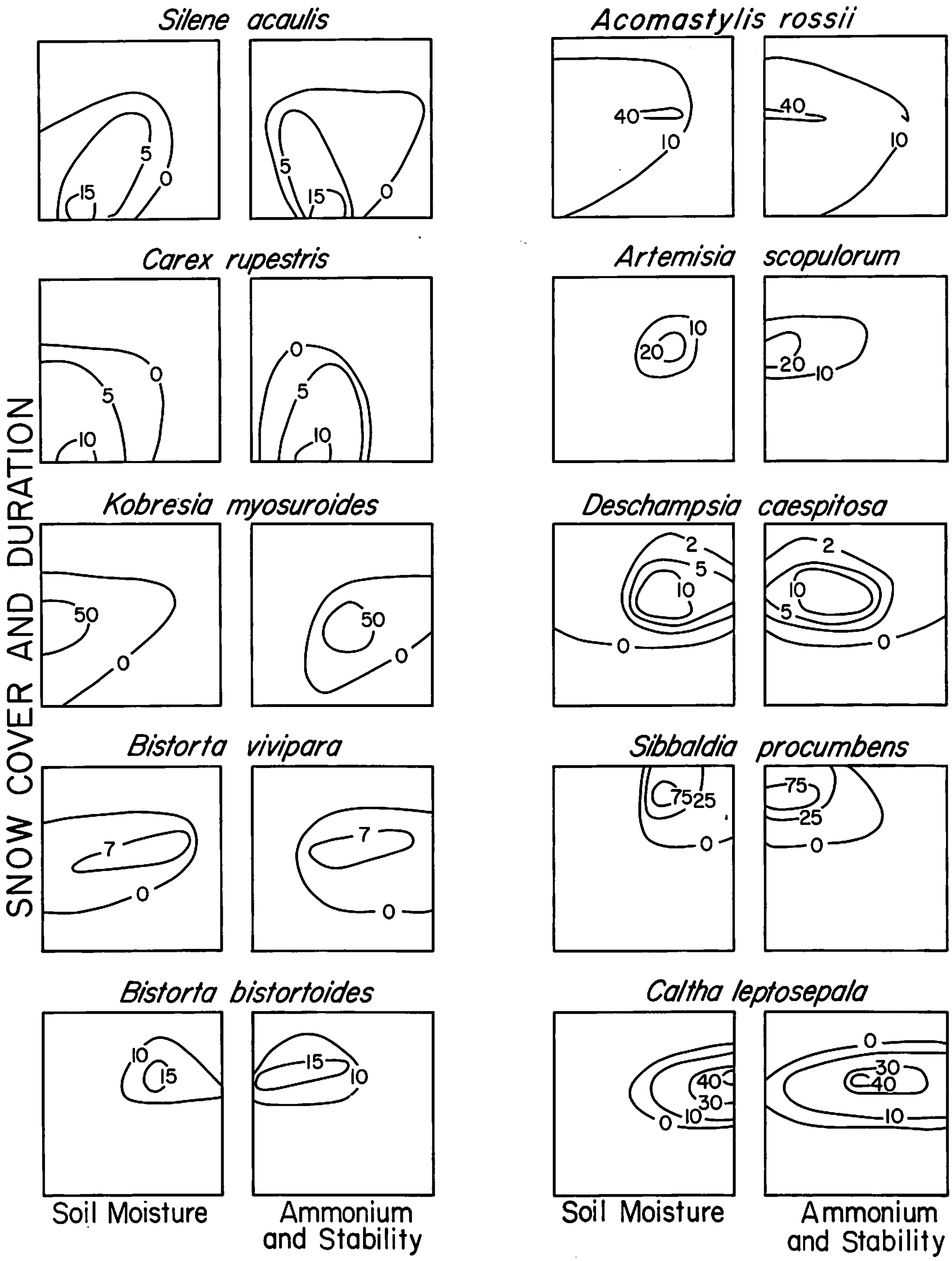

Figure 10. The distribution of ten species within the three principal axes of the ordination. The axis positions correspond to those in the first two frames of Figure 9. Isoline values are Species Index.

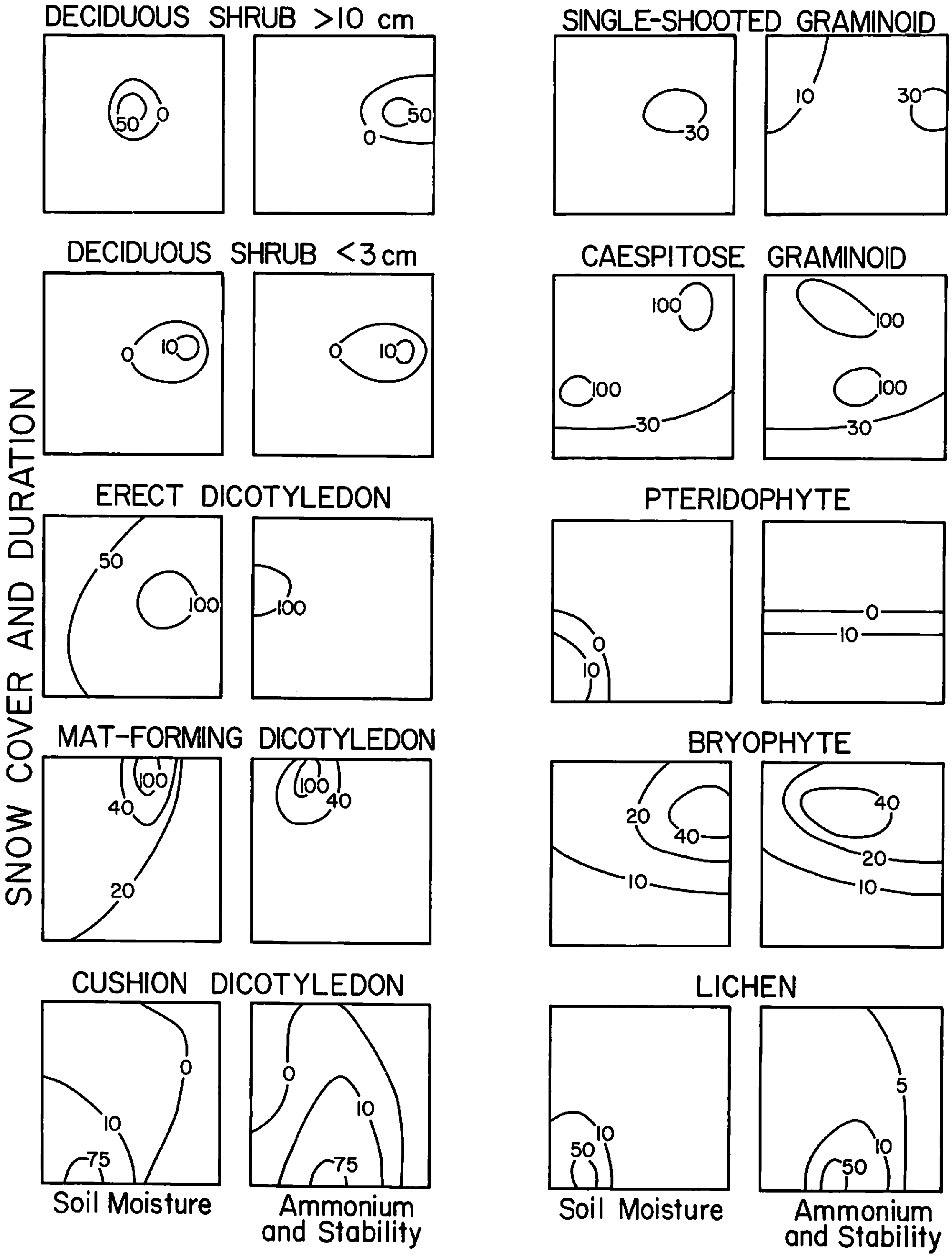

Figure 11. The distribution of ten growth forms within the two principal elevations of the ordination. Isolines of Species Index have been drawn for each growth form.

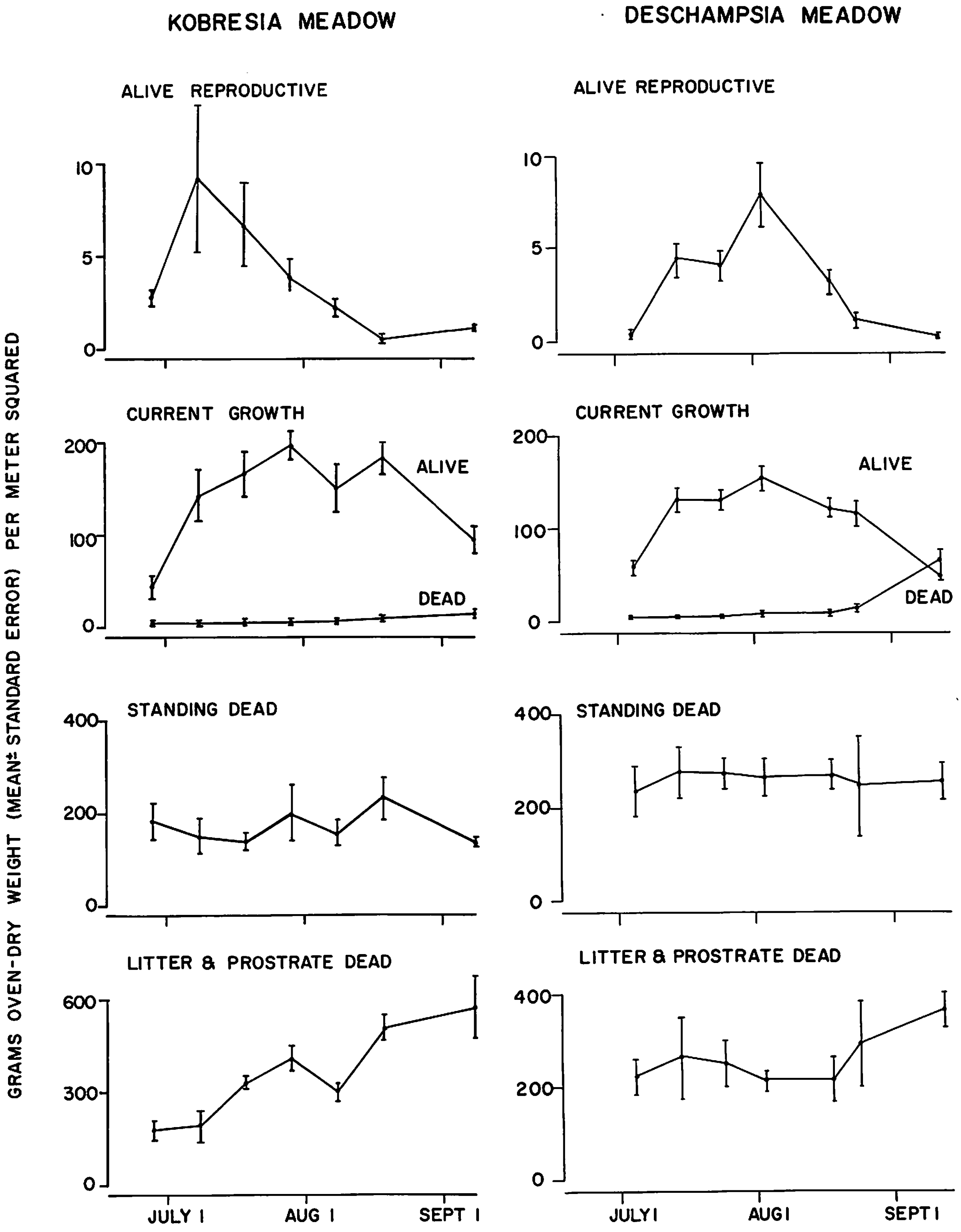

Figure 12. The seasonal progression of some aboveground seasonal crop fractions for the dry Kobresia nodum and the moist Deschampsia nodum. Production estimates were made in 1971.

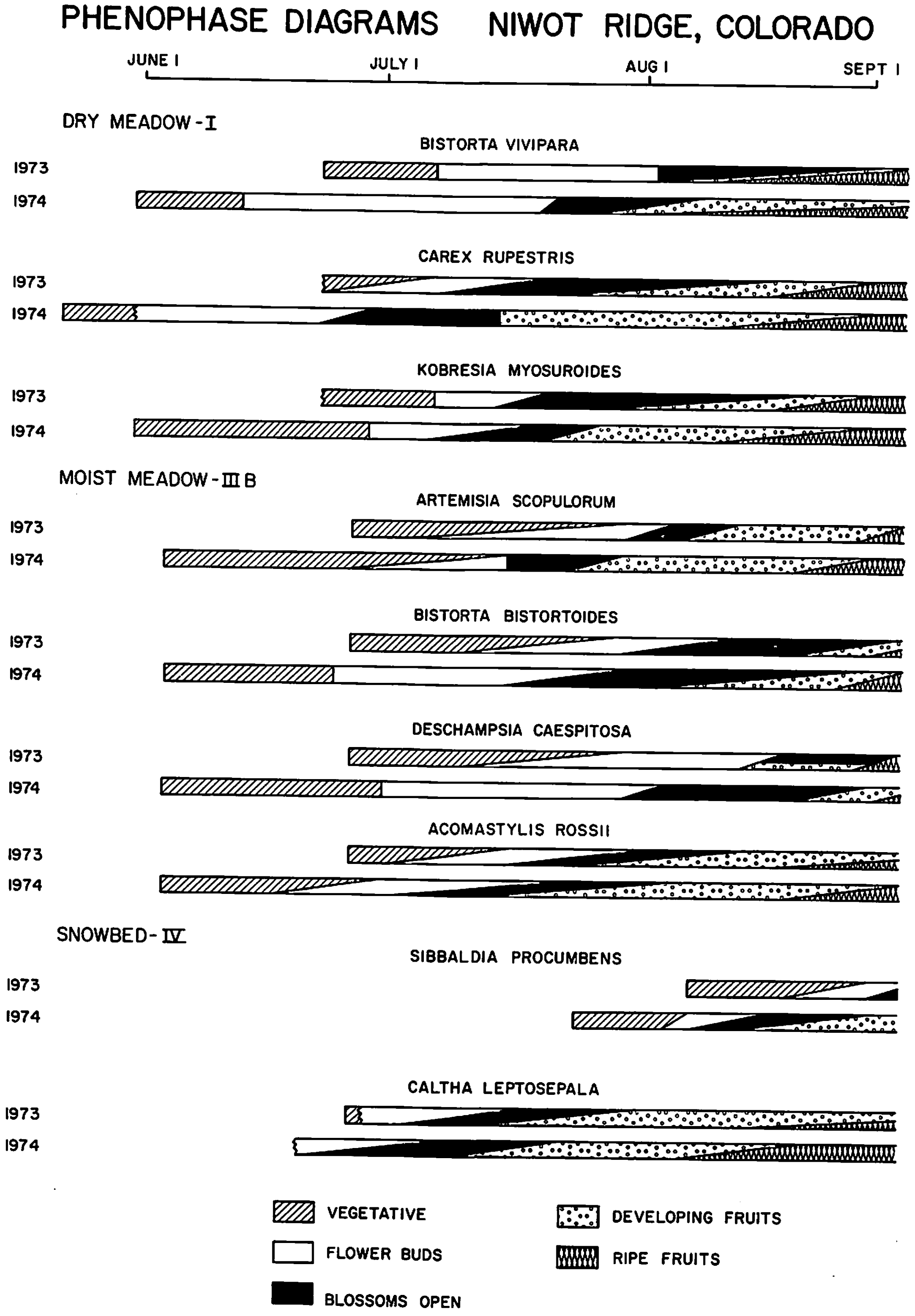

Figure 13. Phenophase diagrams of nine common vascular plant species at Niwot Ridge. The species are arranged according to nodum where measured, and phenological development for each species is shown for two years.

relief over the water complex and its subsequent control over vegetation is shown by heavy arrows Wind, snow and relief together control the water complex which subsequently controls distribution of vegetation.

Other abiotic variables that have previously been determined as sufficiently important to plant distribution in alpine tundras include soil temperature, soil nutrients, and soil stability (Scott and Billings, 1964). In May et al. (1982, this volume) soil temperatures for these sites are reported. Soil temperature is closely tied to snow cover which is dependent on topography. Unlike arctic tundra the presence of permafrost is not significant in alpine tundra in Colorado. In winter, snow-free sites have the lowest above and belowground temperatures whereas snow covered sites are the warmest due to the insulating effects of the snow.

May (1973) measured the soil nutrients in the various sites on Niwot Ridge. Ammonium showed moderately distinct patterns with the various other abiotic factors. Figure 14 suggests that nutrient supply is under some control of soil temperature and water. Soil thaw enables soil nutrients to be withdrawn by plants whereas water and drainage affect the rate of nutrient return to the soil from litter.

Overall, the substrates of Niwot Ridge are relatively stable. Geomorphological processes that disturb the surface are restricted to special sites. Solifluction, and cryoturbation do not appear to be major factors in the dynamics of present vegetation. However, disturbance from gopher activity creates the most distinct patterns with microrelief and vegetation. The effect of this activity on different vegetation types has been documented by Osburn (1958). Thorn (1982) has made an analysis of the distribution of gopher disturbance across Niwot Ridge.

It is important to note that feedback effects from the vegetation exist for all factors. For example, soil stability is affected by the absence or presence of soil binding vegetation roots. Similarly, gopher activity is dependent upon snowcover and forage availability. However, these influences are secondary when minor compared to the more proximal effect of wind, snow and water on the vegetation.

Distribution of Species, Growth-forms and Noda

The distribution of species, growth-forms, and noda recorded here conform well with those reported by earlier workers (species--Marr, 1961; Willard, 1963; Komarkova, 1976, 1979: growth-forms--Daubenmire, 1941; Holch et al., 1941; Billings, 1979: noda--Marr, 1961; Willard, 1963; Komarkova, 1963, 1976, 1979). The noda described here were compared by Komarkova and Webber (1978) with the more rigorous classification units of the Braun-Blanquet vegetations hierarchy. Some noda comprise several Associations, for example dry meadow and moist meadow, while others comprise only a few, for example fellfield and snowbed. The broader noda also contain more wide-ranging and ubiquitous species and also have a more varied environment.

Productivity

There have been several measurements of primary production for arctic tundra (for example, Bliss, 1962b; Alexandrova, 1970; Webber, 1974; 1978; Wielgolaski, 1975) but only a few for alpine tundra (Billings and Bliss, 1959; Scott and Billings, 1964; and Webber, 1974). Of the latter there is a need for better estimates of total productivity of large areas of tundra.

The patterns of primary productivity on Niwot Ridge are similar to those of other alpine areas in the Rocky Mountains (Mooney and Billing, 1960; Páulson, 1960; and Scott and Billings, 1964) and other North American alpine sites (Bliss, 1966, 1970). The range of values for aboveground vascular production within the site indicate that production is related to the microenvironmental complexes. Production is highest in sites which are moist, have complete winter snow cover at moderate depths, and have little or no substrate disturbance. Production is lowest in sites at the extremes of the moisture/snow gradient such as dry, snow-free sites, late snowbeds, and wet areas. The values for the amount of belowground standing crop found on Niwot Ridge are higher than those for some tundra sites (Mooney and Billings, 1960; Scott and Billings, 1964: and Dennis and Johnson, 1970) but similar to others. For example, Bliss (1966) reports values of 3634 g/m^2 for the New England alpine and Alexandrova (1970) reports a value of 6226 g/m^2 for typical arctic tundra in the USSR (Webber and May, 1977).

The patterns of aboveground standing crop, belowground biomass, and above:belowground ratios in the Saddle demonstrate that the principal controlling site factors are water availability, length of growing season (determined by snow cover), exposure (lack of winter snow protection), and soil stability. However, correlations between vegetation productivity and standing crops and environmental variables are low. May (1973) was able to predict primary productivity from environmental variables for a few vegetation types but confidence levels were low.

Errors of sampling and large natural variation combine to weaken correlations (Bliss, 1966). Scott and Billings (1964) emphasized that since plant mass is a combination of individual species, each with specific physiological response to environmental conditions, future work would have to define and measure quantitative variables more precisely. Yet we believe that these estimates of primary productivity exemplify the trends in alpine tundras since tundra production is primarily the sum of only a few species and many of the factors controlling production affect all species similarly (Webber and May, 1977). It

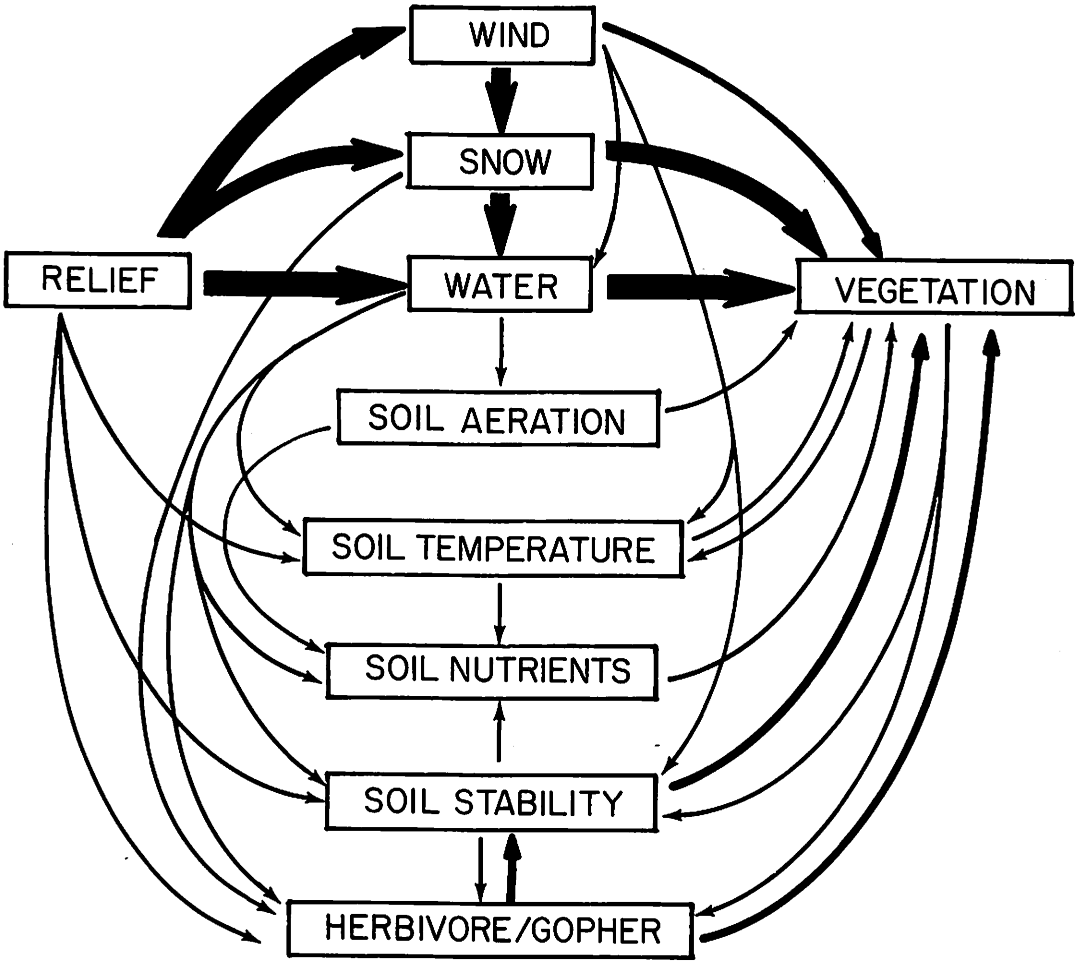

Figure 14. The principal components of the environmental complex as it controls the vegetation at Niwot Ridge. The major controls are indicated by heavy arrows. The complete matrix of feedback arrows is not given; only substantiated or strongly inferred interactions are shown.

is to be hoped that better sampling methods in the future will provide more reliable insights into the controls of production and standing crop at the vegetation level.

Seasonal Variation

It has been observed and carefully documented that growth of tundra species responds closely to soil thaw and disappearance of snow. Sorensen (1941) noted the soil thaw did not start until the snow had disappeared and he emphasized the great control of snow cover over plant life and development in the Greenland tundra. Holway and Ward (1965) and May (1977) have also noted the control of snow cover over plant productivity development.

The first rapid aboveground productivity within an individual nodum corresponds to the onset of vegetative growth which is controlled by snow duration for that particular site. Clearly, biomass production is positively correlated with phenological development of plant species. Within a single growing season, phenological development of plant species is influenced by the moisture regime of the microenvironment. The growing season is longest in dry, snow-free fellfields and shortest in snowbeds. The onset of vegetative growth and subsequent phenological development of plants may differ from 2 to 4 wk between noda or between different growing seasons. Most species compensate for initial delays in growth and complete their development to the ripe fruit phenophase. However, it is possible that seed production and seed viability may be reduced during shortened growing seasons. Controlled germination experiments are required to test this hypothesis (Webber et al. 1976; May, 1976).

SUMMARY AND CONCLUSIONS

1. The principal objective of this study was to provide a description of the vegetation on Niwot Ridge, Colorado. This description is intended as a framework within which other studies from Niwot Ridge on plant and animal physiology, plant and animal ecology, and ecosystem modeling can be viewed and based. In addition, the study can be used for comparing the vegetation of Niwot Ridge with that of other alpine and tundra regions.

2. The vegetation and flora of Niwot Ridge are representative of the alpine region of the Front Range of the Rocky Mountains. The predominant species, growth-forms and plant communities of the Ridge are those associated with cool, dry, windswept surfaces. Two-thirds of the surface of the Saddle and more of the entire Ridge is occupied by dry meadows and fellfields.

3. A strong data base has been gathered from 30 1 X 10 m permanently marked vegetation plots. These plots were established in 1971. Each plot was sampled for cover and frequency of each species. The physical and chemical properties of the soil were measured for each plot. Other abiotic characteristics such as duration of snow cover and soil moisture content were measured at intervals of 10-14 days over four growing seasons. Soil temperature was measured at 2-h intervals, over an 18 mon period. Clip-harvesting within each plot at the peak of the growing season provided aboveground standing crop estimates. Also during a single growing season clip-harvest samples were collected every 10 d in order to estimate the seasonal pattern of standing crop and primary production. The belowground material was sampled by coring and standing crop estimates were determined.

4. The 30 plots were classified by clustering on the basis of species compostion. The resulting clusters were called vegetation noda and named according to their general moisture, species and physiognomic characteristics. Six noda were identified for the study area. They are named as follows: Nodum I - Dry *Kobresia* meadow; Nodum II -Dry, *Silene* fellfield; Nodum IIIA - Moist *Salix* shrub tundra; Nodum IIIB - Moist *Deschampsia* meadow; Nodum IV - *Sibbaldia* snowbed; and Nodum V - Wet *Caltha* meadow. These Noda permit the classification of the plots and the interpretation of the environment for each nodum.

5. An indirect ordination was constructed of the 30 plots. The axes of the ordination were correlated with 19 measured abiotic variables. The three variables that correlate highest with axes of ordination are considered to be major controls of the complex gradients. These complexes are, in order of importance, soil moisture, snow cover and duration, and substrate stability. The framework provided by the axes of the ordination was used to describe the distribution of species, growth-forms, noda, various standing crop fractions and ratios, productivity, and other environmental controls.

6. The vegetation types in the Saddle of Niwot Ridge is dominated by herbaceous dicotyledons and lichens. Many of the species within these general taxa have broad ecological amplitudes and occur in nearly all noda. Other species are narrow-ranging and occur in specific habitats. The distribution of these species makes some vegetation units broad and more heterogeneous than others. However, each species has a unique distribution as shown by a characteristic location within the ordination. Ten plant growth-forms were recognized and each of these also has a characteristic distribution. The patterns of species and growth-form distribution on Niwot Ridge are similar for alpine tundra in North America.

7. Nodal means of aboveground net productivity of vascular plants ranged from 130 to 205 $g/m^2/yr$. Aboveground standing crop estimates ranged from 500 g/m^2 to over 2000 g/m^2. Aboveground vascular productivity generally increased along the moisture gradient from dry sites to moist sites then decreases in wet sites. The mean nodal belowground biomass ranges from 2000 g/m^2 to 4500 g/m^2 with estimates increasing from dry to wet sites. Shrub tundra and wet meadows have the highest belowground biomass. Above to belowground (A·B) ratios of biomass ranged from 1:3 to 1:25. Ratios were highest in shrub tundra and lowest in moist meadows. A nodal map drawn on the basis of landform boundaries and the predominant nodum contained therein permitted an areal estimate to be made of the extent of each nodum. A mean value for the Saddle area of net aboveground vascular biomass is estimated at 166 g/m^2.

8. Annual productivity correlates with the onset of vegetative growth which is controlled by snow duration in the Saddle. Fellfields and dry *Kobresia* meadows are snow-free earliest in the growing season and reach peak aboveground productivity 10 to 14 d before moist *Deschampsia* meadow or wet meadow noda. Biomass production also is dependent on phenological development of plant species. Vegetative growth occurs soon after snow melt. Plants complete most of their production by early August (60 to 70 d) and usually produce ripe seeds by September (90 to 100 days). Seed production and seed viability may be reduced during shortened growing seasons. This emphasizes the importance of vegetative propagation and the perennial habit in tundra

plants.

9. This study has provided the quantification of species distribution and productivity along principal gradients in the Saddle area of Niwot Ridge. The analysis includes an ordination, classification scheme, and vegetation map of the representative vegetation types on Niwot Ridge. This information should provide the necessary data base from which further study of the structure and function of the primary producer component of this ecosystem can be made.

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THE EFFECTS OF AUGMENTED WINTER SNOW COVER ON THE CANOPY STRUCTURE OF ALPINE VEGETATION

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ABSTRACT

Snow fences were used to augment winter snowpack on intensive study sites in three alpine areas in Colorado. These areas were in the Williams Lake and Eldorado Lake basins in the San Juan Mountain Range, and on Niwot Ridge in the Front Range. The effects of increased snow cover on foliage structure were studied at each area on a dry meadow, dominated by Kobresia myosuroides, and a mesic meadow, dominated by Geum (Acomastylis) rossii. The seasonal development of foliage area index on control plots was compared to that on nearby experimental plots situated in the lee of fences erected at each intensive study site. Soil moisture and temperature was also monitored on each plot. Differences in foliage area between experimental and control plots was generally related to the delay in growth onset, brought about by the fence-generated snowdrifts. Local effects of the drifts on soil temperature and moisture were small and apparent for two weeks or less following snow melt. Early season differences in total foliage area between plots were frequently significant (95 percent confidence level); in most cases, later observations revealed that these differences diminished to below-significant levels as the season progressed.

INTRODUCTION

The practice of cloud seeding is becoming recognized and used as a method for augmenting winter snowpack in mountain areas during periods of climatic drought. While this form of weather modification may be effective as a tool for water resource management, its environmental implications are still poorly understood. In an attempt to assess the effect of augmented snowpack on alpine tundra canopy structure and microclimate, a study was conducted during the period of 1971-1976 in the San Juan Mountains and the Front Range of Colorado.

Snow fences were used in the study to increase snow depth on selected plots; data on plant growth and selected microclimatic parameters from these plots allows a preliminary assessment of the influence of increased snowpack on tundra canopy development. Similar studies have been conducted elsewhere in the Colorado alpine (Bell and Bliss, 1979) and in Montana (Weaver and Super, 1972). While snow fences will not duplicate the temporal pattern of snowpack augmentation produced by cloud seeding, their use does provide an inexpensive method of locally increasing snow cover. If the fences are properly designed, this increase can be within the limits of natural site variability. The snow cover is characterized by a more temporally continuous snow mat during the wintertime, and a delay of spring snow-free conditions from a few days up to a month may be produced.

Increased winter snow cover can be expected to affect tundra vegetation in several ways. Ensuing delays in spring melt will decrease the length of the growing season; the timing of snow release has an important influence on the reproductive processes and annual production (Billings and Bliss, 1959; Holway and Ward, 1963; Canaday and Fonda, 1974; Fareed and Caldwell, 1975). However, plant response to a shortened growing season may not be shown as a decrease in aboveground production. Belowground reserves of carbohydrates or nutrients may be reduced; such reserves are very important in the ability of tundra vegetation to successfully reproduce or withstand poor growing conditions on a long-term basis (Mooney and Billings, 1960; Fonda and Bliss, 1966). Also, prolonged occurrence of cold meltwater from augmented snow accumulation may be expected to affect soil temperature and moisture and thus be a factor in early plant growth and development (Holway and Ward, 1963).

Plant canopy structure is strongly related to primary production. The spatial arrangement of leaves greatly affects light interception, gas exchange, leaf temperature, plant water relations, and other factors important to the photosynthetic process (Monteith, 1965; Hunt and Cooper, 1967; Miller and Tieszen, 1972). Delayed or reduced canopy development stemming from augmentation of local snowpacks may significantly reduce the amount of photosynthate available for storage, growth, and maintenance in tundra plants. Because of these considerations, assessment of the effects of increased snow cover on canopy architecture was judged to be a fundamental step toward the analysis of weather modification impacts on the long-term stability of alpine tundra ecosystems.

Field sites selected for intensive study were located at Williams Lake basin (37° 37' N; 107° 09' W) and Eldorado Lake basin (37° 43' N; 107° 33' W) in the San Juan Mountains of southern Colorado and on Niwot Ridge (40° 03' N; 105° 36' W) in the Colorado Front Range. All three areas are above treeline and have a range of vegetation types that are representative of the southern Rocky Mountain alpine. These areas represent a series from high alpine tundra in the Eldoraado Lake basin (3900 m) through middle elevation tundra in the Williams Lake basin to low alpine tundra on Niwot Ridge (3500 m). Eldorado Lake basin and Niwot Ridge are located on acidic rocks

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whereas William Lake basin is underlain by basic volcanic rocks. This difference in rock types is reflected in the soil types, the floras, and the vegetation.

Intensive Study Sites

Snow fences were installed at two intensive study sites in each basin in the San Juan Mountains and on Niwot Ridge. The fences in Williams Lake basin were installed first in August 1970, those in Eldorado Lake basin during September 1971, and those on Niwot Ridge during September 1973. The sites included a *Geum* (*Acomastylis*) (see end note) slope and a *Kobresia* meadow at each area. This choice facilitated between-area comparisons since the respective plant communities are similar. These two community types also are characteristic of a large part, perhaps 50%, of the tundra vegetation in the San Juan Mountains and the Front Range.

The *Kobresia* sites are dominated by short sedges and grasses, mainly *Kobresia myosuroides* (Vill.) Fiori & Paol. and *Festuca brachyphylla* Schult. and short herbs such as *Bistorta vivipara* (L.) S. Gray, *Geum rossii* (R. Br.) Ser., and *Oreoxis bakeri* Coult. & Rose. The *Geum* sites are characterized by a predominance of low herbs mainly *Geum rossii*, *Caltha leptosepala* D. C., *Trifolium* spp., and *Artemisia scopulorum* Gray; some tall grasses (e.g., *Deschampsia caespitosa* (L.) Beauv.) and sedges also occur.

An experimental and a control plot were located on each site in an area of relatively homogeneous vegetation. Each plot was 1 by 10 m and was permanently delineated by steel stakes. Similar plot dimensions were used by Webber (1971) in a study of arctic tundra vegetation, and were based on the size and shape of vegetation and substrate patterns. The long axis of each plot was oriented approximately perpendicular to the prevailing wind direction. In most cases, the snow fences were located 5 m to windward of, and parallel to, the experimental plot. The fences were removed each spring and reinstalled in the fall to prevent summer wind-shielding effects on the experimental plots (Figure 1.).

A Canadian snow fence pattern was used in the study. Fences were constructed of standard wooden snow fence mats supported by six vertical steel fence posts. The fences were approximately 1.2 m high and 15 m long, and were erected with no gap at the base. The snow fence mat consisted of 3.5-cm-wide vertical laths separated by spaces of the same width, which produced a fence density of 50%. Experience has shown that under optimum conditions, a fence having these specifications can be expected to produce a drift with its windward edge against the fence and maximum depths of approximately 1 m located 3 to 5 m behind the fence.

The snow fences which have been used in this study produce drifts with depths of approximately the same magnitude as would be expected during years of high winter and spring snowfall (such as that observed during the 1972/73 winter in San Juans) on the control intensive study sites. Therefore, the fences were useful in estimating snow-related effects on plant canopy growth and development, but probably did not greatly perturb the natural system beyond conditions attainable by cloud seeding.

SAMPLING METHODS

Changes in canopy structure may be more easily measured as a plant response to increased snow cover than by standing crop and clip harvest measurements alone. Foliage area index (FAI: ratio of foliage surface area to ground surface

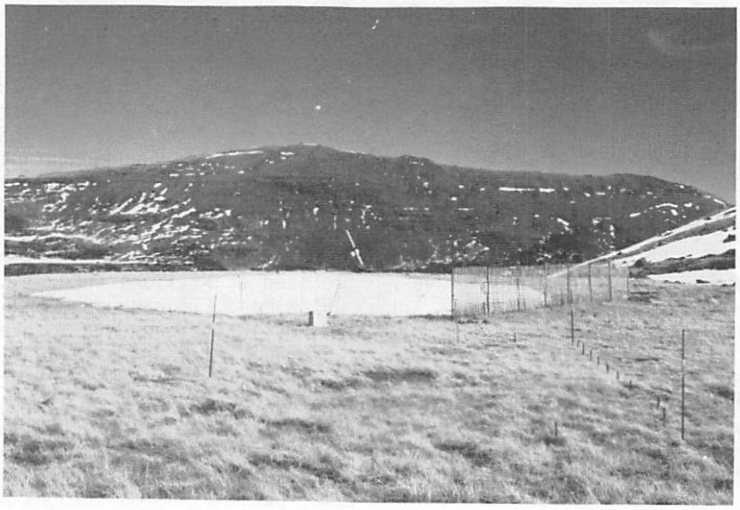

Figure 1. The snowdrift behind the snowfence on a *Kobresia* meadow at Williams Lake basin. The control plot which is free of snow may be seen in the foreground.

area) profiles and leaf angle (LA) profiles are two important descriptors of canopy structure. These were estimated using an inclined point quadrat technique modified from Warren Wilson (1959) (Emerick, 1976). Because it is nondestructive, the same plot may be sampled repeatedly through the growing season.

In 1972, beginning and peak season (period of greatest aboveground vascular biomass during the growing season) estimates of the FAI profile were obtained for the San Juan plots. During the 1973 season in the San Juans, vegetation was sampled by point quadrating every 2 wk and once a month in Eldorado Lake basin in 1974. No estimates of FAI were made during 1974 in Williams Lake basin. Foliage Area Index profiles were estimated biweekly during the 1974 growing season on Niwot Ridge.

Soil moisture and temperature were measured in 1973 in the San Juans and on Niwot Ridge in 1974. Two soil samples of the upper 5 cm of soil were collected weekly from each plot and analyzed for gravimetric moisture content (ratio of weight of water to the total weight of the oven-dried soil sample). The samples were collected with a 7.6 cm-diameter soil corer or with a trowel (depending on soil rockiness); field weight of the samples was approximately 300 g per sample. Stones larger than 1 cm in diameter were removed from the sample during collection.

Soil temperatures were measured on each plot with a multichannel temperature recorder using thermistors as sensing elements (Emerick, 1971). One canopy probe (variable height and shielded only by the plant canopy) and three soil probes (1, 10, and 30 cm depths) were implanted on each plot and were automatically read every two hours by the recorder. A hygrothermograph in a standard meteorological screen was located at both San Juan basins and at Niwot Ridge.

RESULTS AND DISCUSSION

Between-plot differences in most measurements were closely related to snow fence effectiveness, that is, the ability of the fence to generate more snow cover than would normally occur. The most effective fences were on *Kobresia* meadows. These are the sites where the greatest contrasts in snow release dates, soil moisture and temperature, and canopy development generally were recorded in reference to control plots. Striking plant responses in these locations are not unexpected, since *Kobresia* communities normally occupy drier sites, while mesic areas favor *Geum* communities. Therefore, the presence of a snowdrift and shortening of the growing season represents a much greater disruption of natural environmental conditions on the *Kobresia* meadow than on the moister sites.

Depending on the overall spring snow, wind, and radiation conditions, drifts behind the fences produced delays in snow release (when 50% of the 1 x 10 m plot became snow free) ranging from a few days to three weeks. Release dates of the experimental plots lagged those recorded for the control plots by at least 10 d on the *Kobresia* sites. The lags were generally shorter on the *Geum* sites. Between-plot differences in snow cover also were less. Prior to 1973, snow release had already occurred on all sites before the first field observers reached the basins in early June. The alpine areas in the San Juan Mountains received more snowfall and less wind during 1973 (data from Red Mountain Pass, Ives et al., 1972, 1973) than was recorded in 1972 and snow melt occurred much later. Relatively deep snow (20 to 100 cm) was measured on the control plots at these sites during early spring of 1973 and was attributed to low winds and little snow redistribution. Observed depths during comparable times in other years were generally less than 20 cm. Snow depths on the experimental plots usually ranged from 50 to 100 cm.

Local effects of snowdrifts on soil temperature and moisture were limited. Meltwater apparently drained through the coarse-textured soils as rapidly as it was released, except for areas having poor drainage or those occurring below large melting snowbanks. As soon as snow release occurred, the soil temperatures at a depth of 10 cm rose steadily and stabilized near surrounding ground temperatures within 2 wk. Initial between-plot differences ranged from 5 to 11°C and usually declined to less than 1°C. A typical seasonal course of soil temperatures is shown in Figure 2. A similar trend was observed by Thorn (1979) on Niwot Ridge. He also measured soil temperatures and infrared emittance from the ground near melting snowbanks and observed that the banks did not influence materially surface soil temperature more than 5 m away, even in wet areas.

Soil moisture data show little difference between experimental and control plots in the Eldorado Lake and Niwot Ridge sites, and only small between-plot differences (10 to 20%) at the Williams Lake sites. Soil moisture was typically slightly higher on the experimental plots during the first week following snow release as shown by a representative seasonal course in Figure 3, from the Niwot Ridge *Kobresia* site in 1974.

Foliage Area Index data from the 1972, 1973, and 1974 field seasons show, in general, increased differences between experimental and control plots in total live FAI and vertical FAI distributions with increased delays in the onset of growth. Table 1 shows differences between experimental and control plots in total live FAI at selected sampling dates. Statistically significant differences (95% confidence level) in total live FAI estimates between control and experimental plots occurred on all San Juan sites in 1973, following the winter and spring of heavy snowfall, and large drifts had accumulated behind many of the fences. Significant differences were observed in other years but were more infrequent.

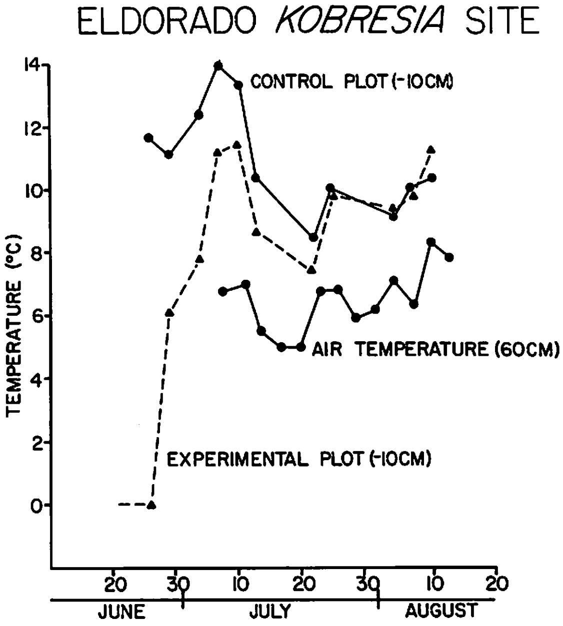

Figure 2. Soil temperature during the summer of 1973 at a depth of 10 cm on the experimental and control plots of the Eldorado Lake Kobresia site. Air temperature at the Eldorado Lake meteorlogical station is also shown. Points represent 5-d means.

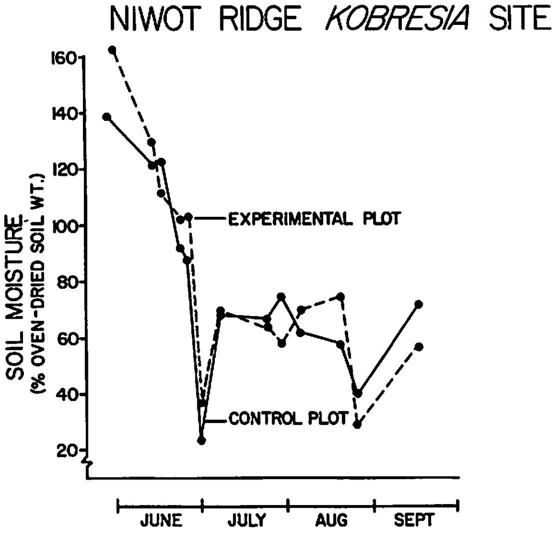

Figure 3. Gravimetric soil moisture on the Niwot Ridge Kobresia site during 1974.

Significant between-plot differences on Niwot Ridge were not observed except on the Geum site, following a long delay in snow release. This delay, in part, was caused by a late spring snowstorm which augmented the drift behind the Geum snow fence. The storm had little effect on the Kobresia site since the fence there had been removed a few days before.

In spite of significant between-plot differences early in the growing season on some sites, later differences were commonly insignificant. Occasionally, FAI became greater on plots where onset of growth was delayed, thus "catching up" and partially compensating for the delay, at least in terms of seasonal foliage development. Delays of 2 wk or more generally retarded canopy development for much of the growing season, particularily on the Kobresia sites. In these instances, most of the foliage area was restricted to the lower levels in the canopy.

A notable phenomenon was the loss of much of the standing and attached dead canopy components on the experimental plots. This was attributed to greater decomposition rates under the snowdrifts and was visually obvious on the Williams Lake and Niwot Ridge Kobresia sites (Figure 4), where the normally blonde-appearing meadow of early spring exhibited a conspicuous dark area where the fence-generated snowdrifts had been. On close inspection, this was found to result from a reduction in standing and attached dead, and a matting down of the remaining dead plant material. This reduction was observed throughout the duration of the study on all Kobresia sites. However, differences were not significant at the 95% confidence level except in Eldorado Lake basin where, in 1972, the loss was estimated to be approximately 80%.

The accelerated loss in weight of plant litter under winter snow cover has been examined by Webber et al. (1976). Snowdrifts were shown to have a pronounced effect on the decomposition rates of plant litter which had been set out in nylon mesh envelopes. Decomposition processes, in this case, include bacterial and fungal decay, comminution by soil invertebrates, and leaching processes. However, knowledge of the effect of these losses on nutrient cycling and primary production is incomplete. Increased nutrient release might enhance production, although released nutrients can be leached from the root zone or be removed from the site by meltwater before they are utilized.

The loss of these standing and attached dead components in the canopy could have a significant effect on photosynthesis to the extent that canopy microclimate is altered. Kobresia communities, which characteristically retain large portions of dead foliage in the canopy, could absorb substantially more radiation. On the other hand, increased radiation and wind speeds during dry periods might be expected to produce greater

Table 1. The effect of snow fences on the foliage area index of live vegetation for selected dates on the Geum and Kobresia sites at all three study locations.

Location	Date	Foliage Area Index Control	Foliage Area Index Experimental	Difference between plot means[1]	Approximate Delay[2] (days)
WILLIAMS LAKE BASIN					
Geum Site	6-05-72	0.1892	0.4765	-0.2873*	5
	7-28-72	1.7108	1.7608	-0.0500	
	6-19-73	1.4300	.7216	0.7084*	13
	7-16-73	1.3332	1.1440	0.1892	
Kobresia Site	6-05-72	0.4674	0.3427	0.1247	14
	7-28-72	1.2124	1.2584	-0.0460	
	6-19-73	0.5894	0.3256	0.2638*	11
	7-16-73	1.1704	0.5892	0.5812*	
ELDORADO LAKE BASIN					
Geum Site	7-05-72	1.4298	1.9426	-0.5128	3
	8-16-72	1.4667	1.4750	-0.0083	
	6-29-73	0.1584	0.3432	-0.1848*	7
	7-18-73	0.8090	0.8756	-0.0666	
	6-10-74	0.5170	0.2200	0.2970*	10
	6-28-74	0.9130	0.8910	0.0220	
	8-13-74	1.4640	1.4544	0.0096	
Kobresia Site	7-05-72	0.7591	0.4976	0.2615*	7
	8-16-72	0.9108	0.7810	0.1298	
	6-29-73	0.4444	0.0616	0.3828*	22
	7-18-73	0.7610	0.3802	0.3808	
	6-10-74	0.2600	0.1760	0.0840	9
	6-28-74	0.5060	0.4950	0.0110	
	8-13-74	0.4955	0.6820	-0.1865	
NIWOT RIDGE					
Geum Site	7-01-74	1.5019	0.4080	1.0939*	21
	7-31-74	1.4432	1.9756	-0.5324	
Kobresia Site	6-28-74	1.8013	1.5927	-0.2086	10
	7-23-74	1.3860	1.5224	-0.1364	

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[1] Each foliage area index value represents the mean of FAI estimates from each of the 10 square-meter quadrats on the plot. Differences are control - experimental FAI Values.

[2] The number of days that snow release on the experimental plot followed that on the control plot.

*Indicates a statistically significant difference at the 95% confidence level between FAI estimates on the control and experimental plots.

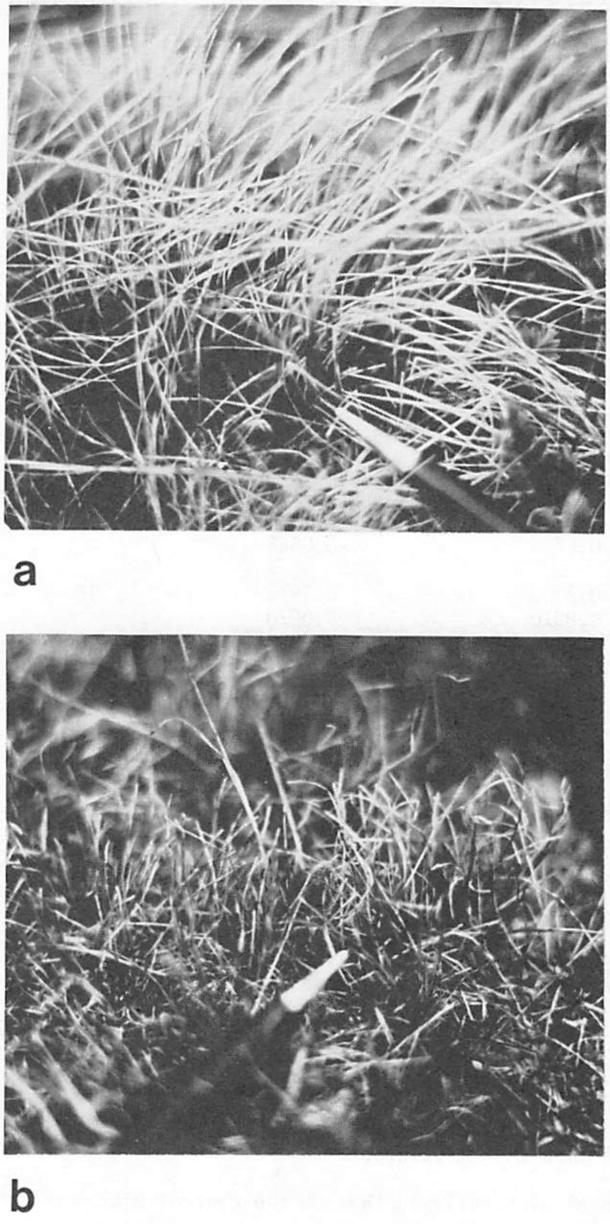

Figure 4. Close view of the Kobresia myosuroides canopy on the control (a) and experimental (b) plots of Williams Lake basin Kobresia site in early June, 1972, showing the loss and matting down of the standing and attached dead canopy component on the experimental plot. For scale, the white pencil tip is approximately 1.3 cm long.

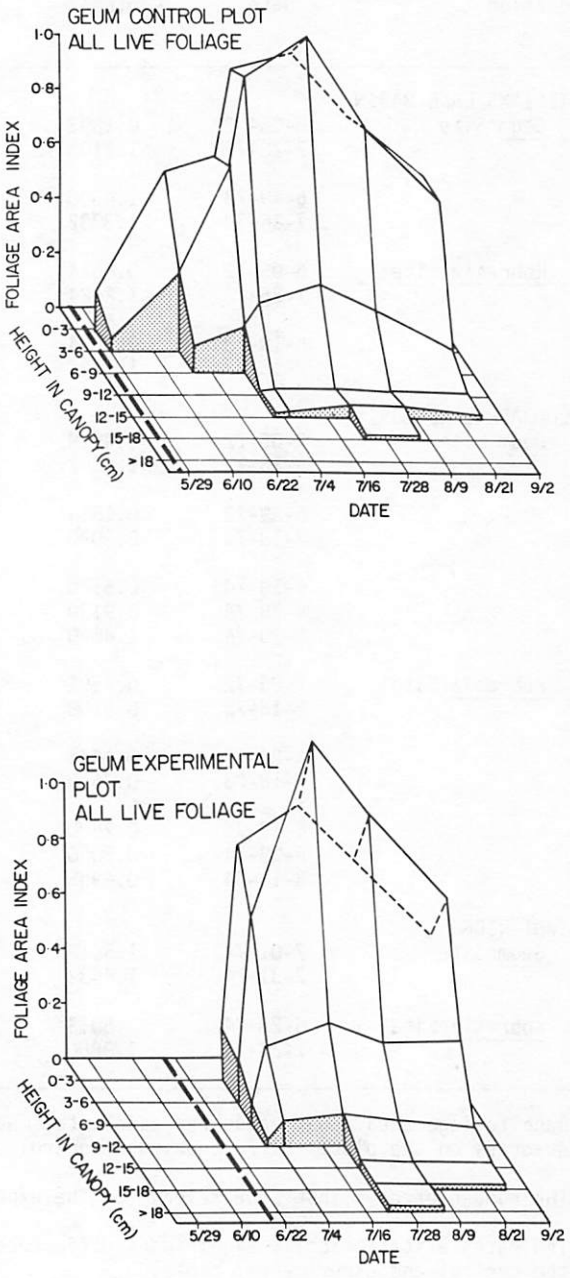

Figure 5. Seasonal development of total live foliage on the Niwot Ridge Geum site, 1974. Dates of snow release are May 23 and June 19 for the control and experimental plots, respectively, shown by the dashed line.

transpirational losses, resulting in increased moisture stresses and decreased production. Loss of scenescent foliage probably would have a lesser effect on the Geum communities, in which this material constitutes a smaller proportion of the canopy, particularily in the upper levels.

Seasonal development of the plant canopy on Niwot Ridge during 1974 was characterized by a rapid, progressive increase of foliage area into the upper levels of the canopy following onset of growth (Figures 5 and 6). This trend can be seen also in the seasonal progressions of the individual dominant species, Geum rossii, Kobresia myosuroides, and Deschampsia caespitosa (Figures 7, 8, and 9). The truncated appearance of the foliage on the Geum experimental plot when compared to that of the control plot resulted from the relatively long delay (approximately 3 wk) in the onset of growth on the experimental plot.

Total mean live FAI values and their standard errors for the dominant species on the Niwot Ridge sites are shown in Tables 2 and 3. Foliage Area Index values for most of these species on the experimental plot exceeded control plot values later in the 1974 season, particularily on the Geum site.

Foliage inclinations generally increased on both sites from late June to late August 1974. There were no substantial between-plot differences in foliage inclination, although the vegetation on the Kobresia site was generally more erect than that on the Geum site, with the mean inclinations for all levels occurring in the 70 - 85° and 65 - 75° ranges, respectively. Most of the canopy on the Niwot Ridge sites was below the 10 cm height, although some reproductive structures approached 20 cm in height. These isolated structures commonly had foliage inclinations of 80 - 90°.

CONCLUSIONS

Snow can affect plant processes in several ways, for example, by mechanical loading, shortening the growing season, and by changing the soil moisture and temperature regimes. The greatest effect of increased snow cover is to delay plant development which reduces the time and radiation available for photosynthesis. Except for poorly drained sites, soil temperature and moisture are not substantially different from normal conditions after a few days following snow melt. The small differences at the beginning of the season are probably not significant factors in annual production.

The effects on plant canopy development of delayed growth are generally greater with increased delay. However, the belowground carbohydrate reserves may serve to offset the effects of the delay, and the canopy might, at least for delays of up to 3 wk, eventually achieve normal or near-normal development. However, over an extended time the cost to these reserves in terms of depletion of the carbon or energy budget may be substantial (Billings et al., 1977). Estimates made during peak aseason of FAI show few significant differences between experimental and control plots. Similarly, there seemed to be no snow effect on leaf inclination. While effects of increased snow cover on possible depletion of belowground carbohydrate reserves were not assessed, such information would be useful in determining the long-term effects of augmented snowback on tundra vegetation.

ACKNOWLEDGEMENTS

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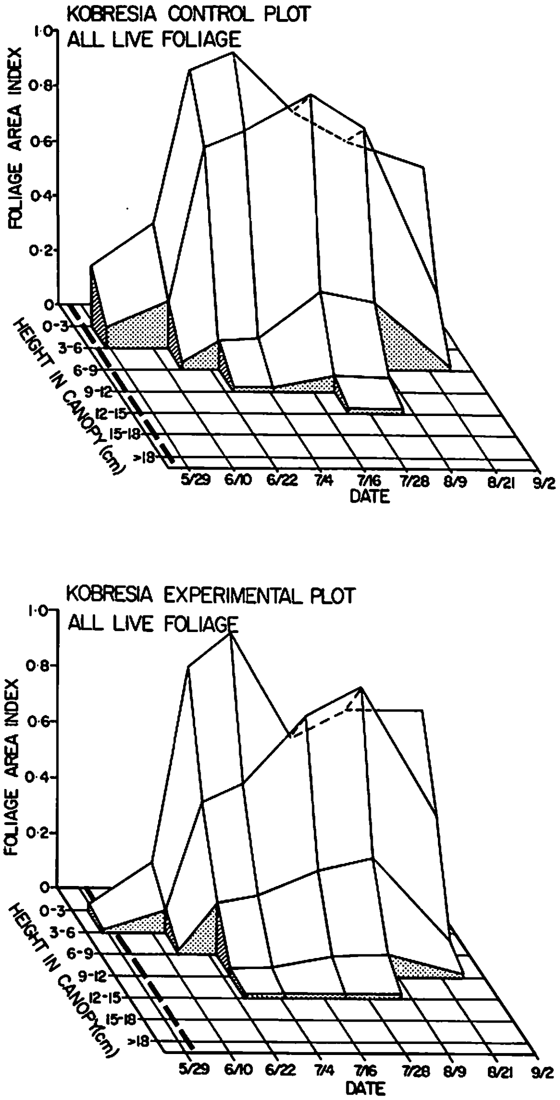

Figure 6. Seasonal development of total live foliage on the Niwot Ridge Kobresia site, 1974. Snow release dates are May 21 and 31 for the control and experimental plots, respectively, shown by the dashed line.

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EDITOR'S NOTE

The authors have used the older generic epithet, *Geum rossii* in both the text and figures. Dr. William Weber has renamed this species *Acomastylis rossii* (*Rocky Mountain Flora*, 1976 Colorado Associated University Press, Boulder).

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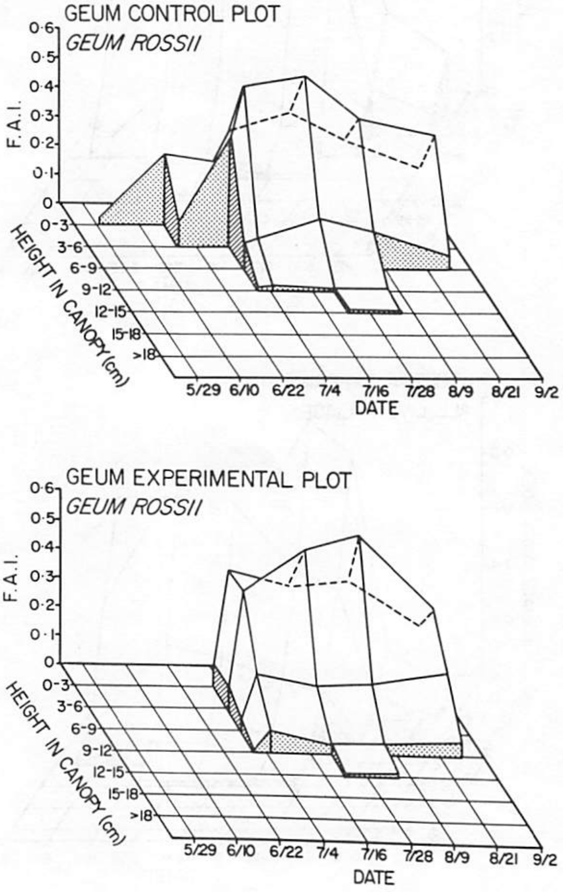

Figure 7. Seasonal development of *Geum rossii* in the canopy of the Niwot Ridge *Geum* site, 1974, shown by the dashed line.

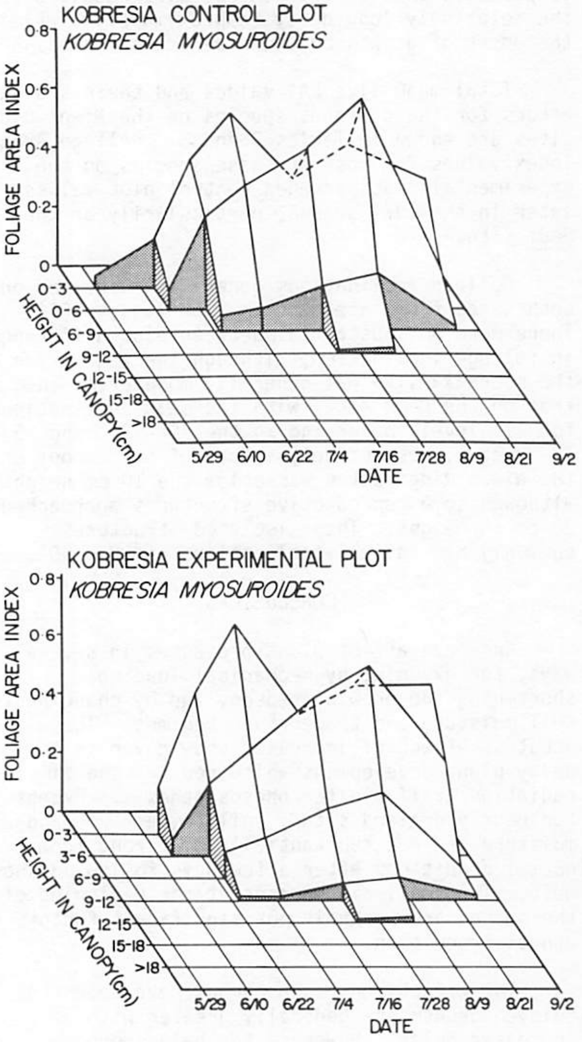

Figure 8. Seasonal development of *Kobresia myosuroides* in the canopy of the Niwot Ridge *Kobresia* site, 1974, shown by the dashed line.

Table 2. Total mean live foliage area index (FAI) values and their standard errors (SE) for the dominant plant species on the Niwot Ridge *Geum* plots on three dates during 1974.

	1 July				31 July				21 August			
	Control		Experimental		Control		Experimental		Control		Experimental	
Species	FAI	SE	FAI	SE	FAI	SE	FAI	SE	FAI	SE	FAI	SE
Geum rossii	.687*	.110	.197*	.038	.697	.073	.801	.101	.499*	.076	.818*	.139
Deschampsia caespitosa	.082*	.040	.018*	.007	.132	.032	.180	.050	.086	.019	.158	.049
Bistorta bistortoides	.057	.016	.031	.009	.123	.021	.110	.034	.026	.011	.194	.150
Caltha leptosepala	.210*	.056	.070*	.023	.171	.044	.242	.059	.127	.028	.185	.038
All Live Foliage	1.502*	.203	.408*	.086	1.443	.138	1.976	.163	1.044*	.067	1.538*	.134

*Indicates statistically significant difference between corresponding mean values at the 95% confidence level.

Table 3. Total mean live foliage area index (FAI) values and their standard errors (SE) for the dominant plant species on the Niwot Ridge *Kobresia* plots on three dates during 1974.

	28 June				23 July				20 August			
	Control		Experimental		Control		Experimental		Control		Experimental	
Species	FAI	SE	FAI	SE	FAI	SE	FAI	SE	FAI	SE	FAI	SE
Kobresia myosuroides	.780	.117	.820	.106	.708	.083	.920	.122	.546	.100	.559	.108
Geum rossii	.649*	.134	.340*	.091	.458	.098	.303	.063	.276	.062	.185	.037
Bistorta vivipara	.156*	.030	.095*	.025	.101	.023	.145	.024	.026*	.012	.352*	.011
All Live Foliage	1.801	.164	1.593	.173	1.386	.121	1.522	.179	.928	.107	.889	.118

*Indicates statistically significant difference between corresponding mean values at the 95% confidence level.

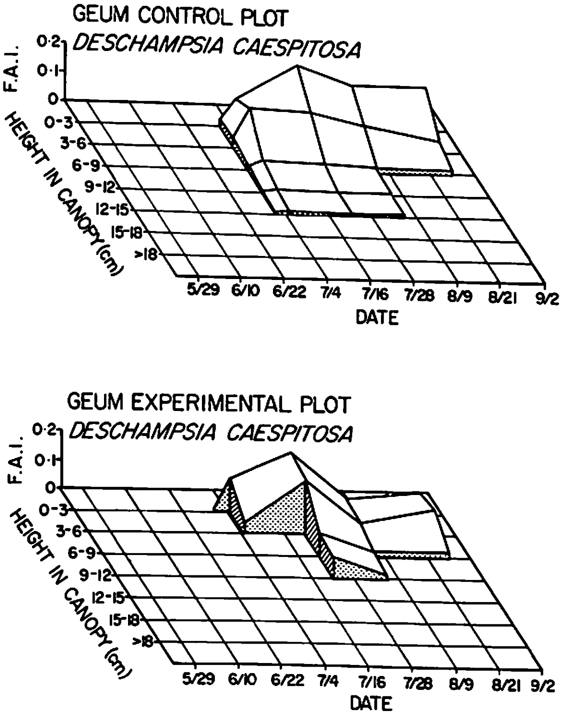

Figure 9. Seasonal development of Deschampsia caespitosa in the canopy of the Niwot Ridge Geum site, 1974, shown by the dashed line.

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SUCCESS OF TRANSPLANTED ALPINE PLANTS ON NIWOT RIDGE, COLORADO

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ABSTRACT

The success of vegetative transplanting of mature alpine plants as an expedient alternative to planting with native seeds or seedlings is assessed. Mature individuals of six native alpine tundra plant species (two dicotyledons and four monocotyledons) were transplanted within and between six alpine microenvironments. Overall success in the experimental plots ranged from 98% (n= 280) for *Descampsia caespitosa* (L.) Beauv. to 17% (n = 140) for *Carex rupestris* Bell. The most important determinant for transplant success was root form with species having deep tap roots, fleshy roots, well-developed secondary roots, and/or dense, fibrous roots without rhizomes being most resilient to transplantings. The fellfield microenvironment was the only one to clearly inhibit transplant success. This was due to rocky, dry and windy conditions, and extreme variability in aboveground and belowground temperatures. Success of transplanting, particularly into extreme microenvironments, was greatest when plants were taken from the species.

INTRODUCTION

Brown and Johnston (1978a) estimated that 11.8% of alpine tundra in the western United States of America (excluding Alaska) requires rehabilitation due to physical disturbances (Harrington, 1946; Willard and Marr, 1970; Bell and Bliss, 1973; Etter, 1973; Greller, 1974; Marr, 1974; Thilenius, 1975; Gregg, 1976; Brown, Johnston, and Johnson, 1978; Brown, Johnston, and Van Cleve, 1978). These disturbed sites require the reestablishment of plant cover to the predisturbance state as quickly as possible (Brown and Johnston, 1978a; Webber and Ives, 1978). Unfortunately, recovery and revegetation is a naturally slow process (e.g. Willard and Marr, 1971; Bell and Bliss, 1973; Greller, 1974; Webber and Ives, 1978). As a result, transplanting of mature plants has been suggested (Brown and Johnston, 1978a; Brown, Johnston, and Johnson, 1978) as a mechanism to speed the rate of revegetation of disturbed alpine tundra. Webber and Ives (1978) agreed that transplanting is a sound approach to tundra reclamation, because it is the most realistic solution to reclamation firmly based on phytocoenological principles.

Cook (1976) was not enthusiastic about transplanting as a tool for surface rehabilitation because of high costs and questionable suitability for large areas. It has been estimated (National Academy of Sciences. 1974: Cook. 1976) that direct on-site costs for other surface rehabilitation procedures in the American west vary between U.S. $1100 and $6800 for each hectare depending upon the specific rehabilitation problems (Johnson. Brown, and Cravens. 1975: Brown. Johnston and Van Cleve. 1978). These figures do not account for inflated costs, the application of supplemental water, protection during the establishment phase, and nonuse of the disturbed site which would all increase total rehabilitation costs markedly. Webber and Ives (1978) stressed that the long-term success of seeding efforts is uncertain. In light of this uncertainty and the long time required to establish sustaining plant communities by seeding, transplanting may be more cost competitive than Cook (1976) believed. Unfortunately, biological data are not available to begin an accurate comparison of feasibility.

We know of three projects which have measured or are measuring transplant success of mature plants onto alpine tundra. Brown and Johnston (1976) transplanted 76 dormant individuals of *Antennaria lanata* (Hook.) Greene. *Carex paysonis* Clokey, *Carex nigricans* C. A. Meyers. *Deschampsia caespitosa*. and *Poa alpina* L. onto an alpine mine disturbance in Montana. Brown and Johnston (1978b) also documented survival the year following transplanting of 3909 grass plugs of native *Agropyron scribneri* Vasey. *A. trachycaulum* (Link) Malte. *Deschampsia caespitosa*. *Phleum alpinum* L.. *Poa alpina*. and *Trisetum spicatum* (L.) Richt. in the same area. In the White Mountains of New Hampshire. 1407 individuals of *Juncus trifidus* L.. *Arenaria groenlandica* (Retz.) Spreng, *Carex bigelowii* Torr.. and *Diapensia lapponica* L. were transplanted in 1977 onto stabilized sites (D.A. Roach and P.J. Marchand. personal communication). Graber (1980) transplanted *Potentilla robbinsiana* Oakes seedlings grown in the greenhouse onto 18 sites on Mt. Washington, New Hampshire. This paper reports on success of six native alpine tundra species (two dicotyledons and four monocotyledons) 2 yr following transplanting within and among six alpine microenvironments in 1973 on Niwot Ridge, Colorado.

Niwot Ridge (40°3'N. 105°36'W) was a suitable site to evaluate the success of transplanting, because it includes a variety of microenvironments due to direct and indirect enviornmental gradients in close proximity to one another so that climate is the same throughout. The vegetation and physical enviornment of this area have been well documented (Marr. 1961; Marr et al.. 1968a, 1968b; Barry, 1973; 1976: Komárková 1976: Webber and May, 1977; Komárková and Webber. 1978).

Thirty sampled strands from the six vegetatation units or noda identified by Webber

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(1972) May (1973), and May and Webber (1973) form the basis of the environmental measurements of this study. Snow depth and cover were estimted for each sampled stand every 10 to 14 d from December to June by averaging five probes to the nearest 1 cm and by subjective evaluation to the nearest 5%, respectively. Length of growing season was defined as the number of days from spring snowmelt (<50% snow cover) when mean daily temperatures also remained above 0°C to 15 September when most species had senesced. Gravimetric soil moisture was measured every 7 d by drying (14 h at 105°C) samples taken at 10 cm belowground. Soil and shaded plant-canopy temperatures were measured at 10 cm belowground and 5 cm aboveground at 2-h intervals using a system developed by Emerick (1976).

Experimental plots were delineated in sites with plant species composition visually similar to the sampled stands comprising each nodum. Two experimental plots were established in the snowbed, one near an early-melting snowbed and one below a late-melting snowbed. Average-sized individuals of six plant species varying in natural history and ecological tolerance were transplanted from noda where they were common to experimental plots of their own and different habitats. Transplanting was done in June and July of 1973 by carefully excavating the root system and removing soil from the roots prior to replanting. Transplants were watered for several weeks to minimize early mortality. Transplants were considered to be successfully established if aboveground vegetative growth occurred in growing seasons after that of transplanting.

Descriptions of plant species are according to Harrington (1954) and Weber (1972).

DESCRIPTION OF NODA

Frequency of occurrence and mean percent relative cover of the most common plant species are presented by noda in Table 1. Seasonal changes in gravimetric soil moisture, mean annual snow depth, length of growing season, and aboveground and belowground soil temperature for the six noda are shown in Figures 1 to 3, respectively.

The fellfield was mostly snow-free during winter causing aboveground and belowground temperatures to be coldest, except for the dry meadow nodum aboveground. The snow-free conditions also resulted in an early, rapid increase in aboveground and belowground temperatures during spring. The fellfield had the longest growing season and was driest by the end of the growing season. This nodum included the second largest number of herbaceous dicotyledon species (Table 2). It also had the largest and smallest relative cover of herbaceous dicotyledons and monocotyledons, respectively (Table 2). The fellfield was dominated by Trifolium dasyphyllum, Minuartia obtusiloba, and Silene acaulis.

The snowbed had the greatest snow depth and the shortest growing season (about 14 d difference between early and late snowbeds). The extensive snow cover minimized the drop in aboveground and belowground winter temperatures and moderated the summer temperature maxima belowground. Even with the extensive snow cover. soil moisture was similar to that in the fellfield throughout the shortened growing season. Relative cover was evenly divided between monocotyledons and herbaceous dicotyledons (Table 2). This nodum included the smallest number of herbaceous dicotyledons (Table 2). The snowbed was dominated by Sibbaldia procumbens and Carex pyrenaica.

The dry meadow had slightly greater snow depth than the fellfield but had comparably low aboveground and belowground winter temperatures. Soil moisture was similar to that in the fellfield and snowbed as all are well-drained. This nodum included the largest number of herbaceous dicotyledons but was dominated by monocotyledons (Table 2). Relative cover of monocotyledons was larger than for any other noda (Table 2). The dry meadow was dominated by Kobresia myosuroides.

The moist meadow and shrub tundra were intermediate in most conditions. However, the shrub tundra had a higher water table resulting in a higher soil moisture, comparable even to the wet meadow. The shrub tundra had slightly less snow cover and a slightly longer growing season in comparison to the moist meadow. Numbers of species of plant groups are similar, but relative cover of woody dicotyledons and monocotyledons was greater and smaller in the shrub tundra, respectively (Table 2). Deschampsia caespitosa were considered to be successfully established if and Acomastylis rossii dominated in the moist meadow while Salix planifolia and Trifolium parryi dominated the shrub tundra.

The wet meadow was consistently wet due to a high water table and had relatively long-lasting snow cover. Aboveground and belowground temperatures approximated those in the snowbed. Relative cover was nearly evenly split between the herbaceous dicotyledons and the monocotyledons (Table 2). The wet meadow was dominated by Caltha leptosepala and Carex scopulorum.

RESULTS AND DISCUSSION

A total of 1190 individuals were transplanted to the seven nodal experimental plots. Success of all transplants was greatest for Deschampsia caespitosa (98%, n = 280) followed by Kobresia myosuroides (83%, n = 70). Acomastylis rossii (79%, n = 490), Carex pyrenaica (70%, n = 70), Sibbaldia procumbens (44%, n = 140), and Carex rupestris (17%, n = 140).

Deschampsia caespitosa is a perennial grass with fibrous roots and no rhizomes. It was the dominant grass species in the sampled stands and occurred in all noda but the fellfield (Table 1). Kobresia myosuroides is a perennial sedge also with a fibrous root system and no rhizomes. It occurred in all but the wet meadow and snowbed noda; however, it was most abundant by far in the

Table 1. Frequency of occurrence (F) and mean percent relative cover (RC) of plant species with greater than 5% RC in at least one nodum of the 30 sampled stands. Noda are listed according to length of growing season from the longest (fellfield) to the shortest (snowbed). Plant species are ranked according to frequency of ocurrence in all sampled stands.

Plant Species	Fellfield (n = 5)		Dry Meadow (n = 5)		Shrub Tundra (n = 4)		Moist Meadow (n = 8)		Wet Meadow (n = 3)		Snowbed (n = 5)		All stands (n = 30)
	(F)	RC	(F)	RC	(F)	RC	(F)	RC	(F)	RC	(F)	RC	(F)
Acomastylis rossii (R. Br.) Greene	(5)	7.9	(5)	6.9	(4)	8.4	(8)	19.9	(2)	0.7	(5)	1.7	(29)
Artemisia scopulorum Gray	(5)	2.9	(5)	0.5	(4)	6.7	(8)	13.7	(2)	1.3	(4)	0.2	(28)
Bistorta bistortoides (Pursh) Small	(5)	1.9	(5)	1.2	(4)	2.8	(8)	6.3	(2)	0.3	(3)	0.5	(27)
Deschampsia caespitosa (L.) Beauv.[1]/	(0)	-	(4)	2.4	(4)	5.5	(8)	27.9	(3)	10.5	(4)	3.7	(23)
Erigeron simplex Green	(1)	0.0[2]/	(4)	0.3	(4)	1.0	(8)	6.1	(3)	1.6	(1)	0.0[2]/	(21)
Trifolium parryi Gray	(0)	-	(3)	1.6	(4)	17.1	(8)	1.9	(2)	2.0	(3)	11.7	(20)
Carex scopulorum Holm	(0)	-	(2)	0.0[2]/	(4)	11.7	(6)	1.8	(3)	25.9	(4)	0.1	(19)
Carex rupestris Bell. ex All.[1]/	(5)	8.1	(5)	3.1	(1)	0.0[2]/	(4)	0.2	(0)	-	(1)	0.0[2]/	(16)
Caltha leptosepala D.C.	(0)	-	(0)	-	(4)	10.7	(7)	4.5	(3)	30.7	(1)	0.2	(15)
Silene acaulis L.	(5)	10.5	(5)	0.4	(2)	0.0[2]/	(2)	0.4	(0)	-	(0)	-	(14)
Sibbaldia procumbens L.[1]/	(0)	-	(0)	-	(2)	0.0[2]/	(4)	1.1	(1)	0.3	(5)	28.0	(12)
Minuartia obtusiloba (Rydb.) House	(5)	11.4	(3)	0.6	(3)	0.01	(0)	-	(0)	-	(0)	-	(11)
Kobresia myosuroides (Vill.) Fiori & Paol.[1]/	(2)	0.2	(5)	64.7	(3)	0.2	(1)	0.0[2]/	(0)	-	(0)	-	(11)
Selaginella densa Rydb.	(5)	6.0	(5)	5.0	(0)	-	(0)	-	(0)	-	(0)	-	(10)
Carex pyrenaica Wahl.[1]/	(0)	-	(0)	-	(0)	-	(0)	-	(2)	3.6	(5)	23.6	(7)
Juncus drummondii Mey.	(0)	-	(0)	-	(0)	-	(0)	-	(2)	0.8	(4)	9.8	(6)
Trifolium dasphyllum T. & G.	(5)	13.6	(1)	0.1	(0)	-	(0)	-	(0)	-	(0)	-	(6)
Parenychia pulvinata Gray	(5)	8.9	(1)	0.1	(0)	-	(0)	-	(0)	-	(0)	-	(6)
Salix planifolia Pursh	(0)	-	(0)	-	(4)	28.1	(0)	-	(0)	-	(0)	-	(4)

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[1]/Transplanted plant species.

[2]/Present but less than 0.5% RC.

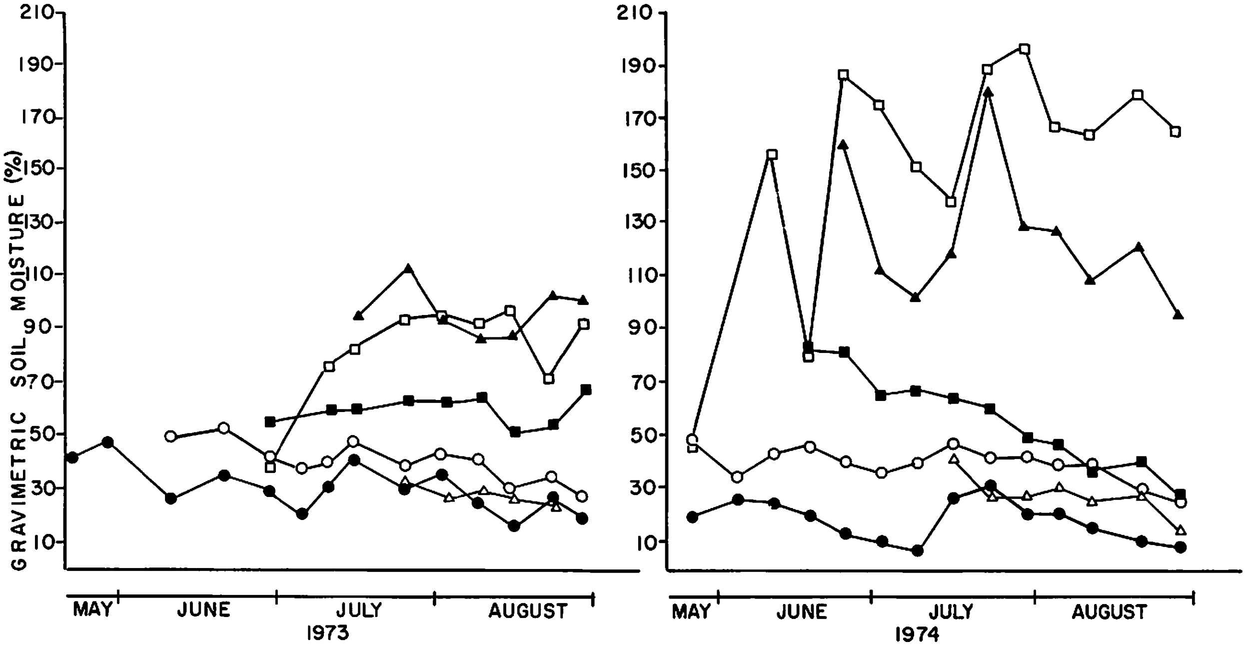

Figure 1. Percent gravimetric soil moisture at 10 cm belowground for the 1973 and 1974 growing seasons on Niwot Ridge, Colorado in the fellfield (●), dry meadow (○), shrub tundra (□), moist meadow (■), wet meadow (▲), and snowbed (△) noda.

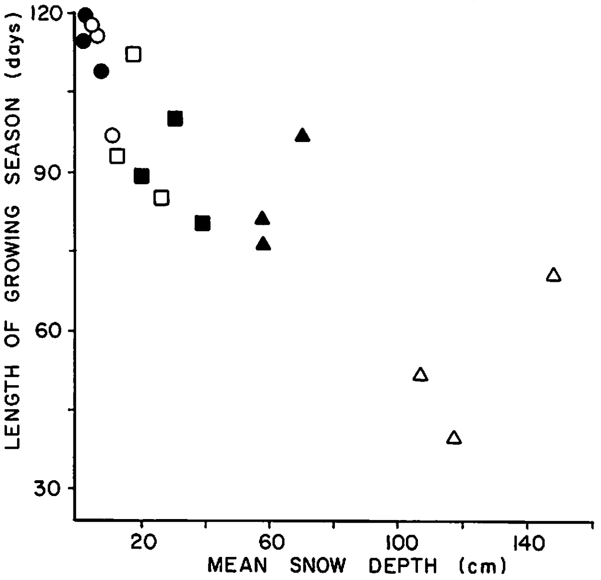

Figure 2. The relationship of mean snow depth to the length of the subsequent growing seasons of 1972-1974 on Niwot Ridge, Colorado in the fellfield (●), dry meadow (○), shrub tundra (□), moist meadow (■), wet meadow (▲), and snowbed (△) noda. In every case, the growing season was longest in 1972 and shortest in 1973.

dry meadow (Table 1). Carex pyrenaica is a perennial sedge with fibrous roots that grows in dense clumps. It was important in the snowbed but also occurred in only the wet meadow (Table 1). In contrast, Acomastylis rossii is a perennial, herbaceous dicotyledon that has abundant secondary roots and a long tap root. It was the most ubiquitous species in the sampled stands and substantially contributed to relative cover in all but the wet meadow and snowbed noda (Table 1).

also occurred in only the wet meadow (Table 1). In contrast, Acomastylis rossii is a perennial, herbaceous dicotyledon that has abundant secondary

In contrast to the species with 70% or greater overall success, Carex rupestris is a perennial sedge with shallow, fibrous roots and scaly rootstocks. Even though it occurred in all but the wet meadow, it was most abundant in the fellfield and dry meadow noda (Table 1). Sibbaldia procumbens is a perennial, herbaceous dicotyledon with shallow, fibrous roots and aboveground, creeping rootstocks. It is a dwarf, caespitose plant that occurs in all but the fellfield and dry meadow noda; however, its relative cover was substantial only in the snowbed (Table 1).

Success was not uniform among all noda and varied for all transplants between 83% (wet meadow) and 44% (fellfield) (Table 3). Success in other noda was nearer to that in the wet meadow than that in the fellfield (Table 3). Success among noda by individual species was more variable that what was suggested by success of all transplants. For example, Deschampsia caespitosa was transplanted successfully to all noda, and Carex rupestris was transplanted with moderate success to only the dry meadow (Table 3). Carex pyrenaica had poor transplant success in noda with the longest (fellfield) and shortest (late snowbed) growing seasons (Table 3).

Precise determinants of transplant success are unknown, but the data presented here suggest

Table 2. Mean percent relative cover (RC) and number of species (NS) of plant species groups according to noda from the longest (fellfield) to the shortest (snowbed) growing season.

	Fellfield (NS) RC	Dry Meadow (NS) RC	Shrub Tundra (NS) RC	Moist Meadow (NS) RC	Wet Meadow (NS) RC	Snowbed (NS) RC
Plant species groups	(n = 5)	(n = 5)	(n = 4)	(n = 8)	(n = 3)	(n = 5)
Pteridophyta	(1.0) 6.0	(1.0) 5.0	(0.0) -	(0.1) 0.0[1]/	(0.0) -	(0.0) -
Spermatophyta						
Woody Dicotyledonae	(0.0) -	(0.2) 0.0[1]/	(2.3) 28.1	(0.3) 0.0[1]/	(0.7) 3.6	(0.2) 0.0[1]/
Herbaceous Dicotyledonae	(22.8) 75.5	(24.6) 19.6	(18.5) 52.2	(16.5) 65.0	(14.7) 51.3	(9.8) 54.3
Monocotyledoneae	(7.8) 18.1	(10.6) 75.4	(11.8) 19.4	(9.3) 34.9	(8.7) 45.4	(7.6) 45.7

[1]/Present but less than 0.5% RC.

relationships which we believe are reasonable. The nature of plant species root systems seems to strongly influence transplant success. Monocotyledons and herbaceous dicotyledons with low success have shallow, fibrous roots and rootstocks. In contrast, monocotyledons with high success also have fibrous roots but have no rhizomes or other rootstocks which can be broken during transplanting. Acomastylis rossii has a long tap root which has always broken during transplanting, but it also has an extensive system of secondary roots which apparently permitted high transplant success.

The ecological tolerance of species was apparently not a major determinant of transplant success. Both ubiquitous and ecologically restricted species were transplanted successfully to nearly all noda. Therefore, the low success of Carex rupestris was likely not due solely to its restricted ecological distribution in only the fellfield and dry meadow noda.

The nature of the microenviornment seems to be important in determining transplant success. Except for Deschampsia caespitosa, all species had lower success in the fellfield which is rocky, dry, windy, and has extreme fluctuations in temperature. This is illustrated best by Acomastylis rossii which had an overall success of 46% in the fellfield, while success in the other noda varied between 80% (late snowbed) and 93% (wet meadow). There was no clear reduction in overall success attributable to other microenvironments.

Graber (1980) reported high mortality of Potentilla robbinsiana transplants after 3 yr in all sites but fellfields (65% average success) where this species occurs naturally. On our study site, ecologically restricted species tended to occur in the microenvironmental extremes (fellfield and dry meadow noda versus wet meadow and snowbed noda) (Table 1). Carex rupestris and Kobresia myosuroides were most abundant in the fellfield and dry meadow noda, respectively, while Sibbaldia procumbens and Carex pyrenaica were most abundant in the snowbed. Of these species, only Carex rupestris was more successful where it occurred naturally in the dry meadow. Therefore, it seems that greater success cannot be assured by transplanting species that are naturally adapted to a particular microenvironment.

Of the species transplanted, Deschampsia caespitosa clearly had the highest success. It was even greater than the 72% survival in Montana of transplanted plugs (n = 993) grown from seeds collected the previous year (Brown and Johnson, 1978b). Deschampsia caespitosa was also found (Marr et al.. 1974) to tolerate the ecological modification of Colorado alpine tundra by pipeline construction. Brown and Johnston (1978b) reported that overall, first-year survival of transplanted native grasses was 75%.

In contrast to species with high transplant success, Marr et al., (1974) reported that Acomastylis rossii and Sibbaldia procumbens were much reduced in cover by pipeline construction. Our data supports the limited stress tolerance of Sibbaldia procumbens, but they do not support limited stress tolerance of Acomastylis rossii. This discrepancy may be due to enhanced survival by watering in our study, but we do not know the magnitude of this effect.

Our data support those (Brown and Johnston, 1978a; Brown, Johnston. Johnson. 1978; Webber and Ives, 1978) who believe rehabilitation of disturbed alpine tundra can be aided by transplanting mature individuals. The most difficult microenvironment to rehabilitate by transplanting is the fellfield. Fellfields are naturally dominated by herbaceous dicots of special growth form to stabilize the site. Monocots seem to be most promising for use in transplanting but occur in low abundance in the fellfield. Therefore, special effort should be made to avoid disturbing the vegetation of

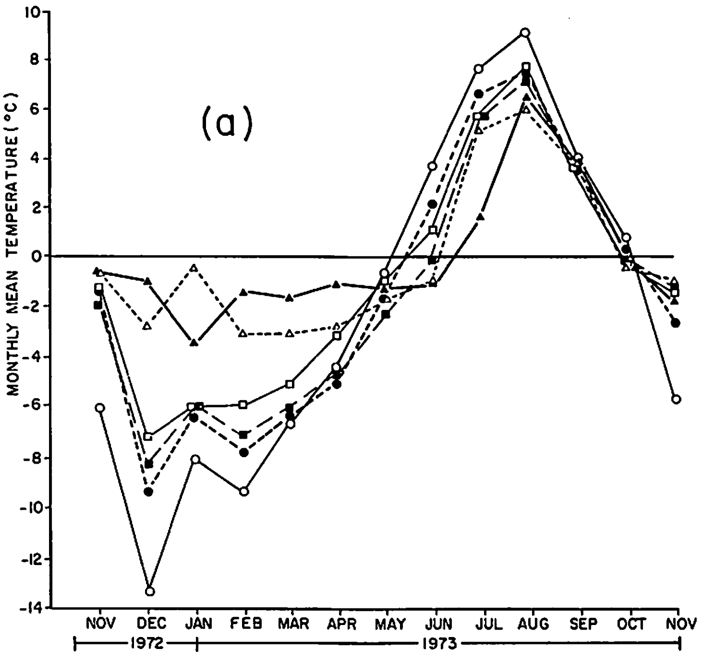

Figure 3a. Monthly mean temperatures at 10 cm belowground from November 1972 to November, 1973 on Niwot Ridge, Colorado in the fellfield (●), dry meadow (○), shrub tundra (□), moist meadow (■), wet meadow (▲), and snowbed (△) noda.

fellfields.

The source of plants for transplanting remains an uncertainty. Use of naturally occurring sod clumps to establish vegetation cover would most likely be successful, because Brown and Johnston (1976) measured complete success of one-year transplants of native species from road cuts. However, the procurement of sod clumps would cause disturbances that might require rehabilitation. The best prospects for use of sod clumps would be from homogeneous stands of either *Kobresia myosuroides* in the dry meadow or *Deschampsia caespitosa* in the wet meadow. These sites are protected by winter snow cover and would revegetate by surrounding vegetation. Since we have shown that alpine tundra plants will be successful outside their natural enviornment, it may be possible to grow native species in controlled seedbeds as a source of sod clumps.

It is unlikely that disturbed alpine tundra can be returned to predisturbance species composition in a short time. However, patterns are emerging from this and related research which will permit the selection of native alpine tundra species with the best prospects for transplanting either as individual plants or as sod clumps to stabilize exposed sites. In contrast, little research has been done to evaluate how to enhance revegetation efforts by changing the microenvironment. Since we have shown that duration of snowcover using snow fences.

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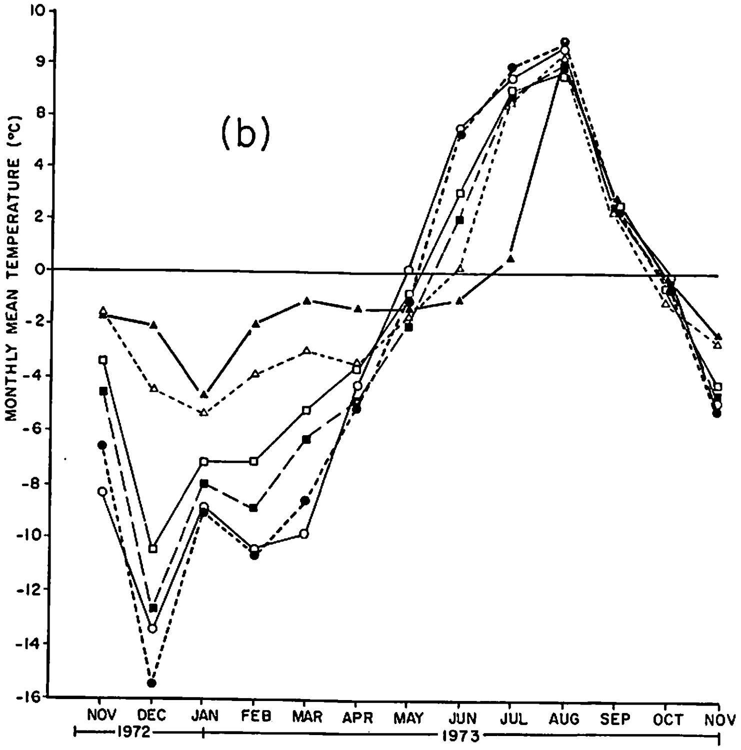

Figure 3b. Monthly mean temperature at 5 cm aboveground from November, 1973 to November, 1973 on Niwot Ridge, Colorado in the fellfield (●), dry meadow (○), shrub tundra (□), moist meadow (■), wet meadow (▲), and snowbed (△) noda.

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Table 3. Percent success of transplants according to relocation from the longest (fellfield) to the shortest (snowbed) growing season. Plant species are in order of frequency of occurrence in the 30 sampled stands from greatest (*Acomastylis rossii*) to least (*Carex pyrenaica*).

Transplanted plant species		Fellfield	Dry Meadow	Shrub Tundra	Moist Meadow	Wet Meadow	Early snowbed	Late snowbed
Acomastylis rossii (R. Br.) Greene	(n = 70)	46[1]	81[1]	87[1]	81[1]	93[1]	83[1]	80
Deschampsia caespitosa (L.) Beauv.	(n = 40)	90	95	100[1]	100[1]	100[1]	100	100[1]
Carex rupestris Bell. ex. All.	(n = 20)	15[1]	60[1]	0	20	15	0	10
Sibbaldia procumbens L.	(n = 20)	5	0	65	80	65	55[1]	40[1]
Kobresia myosuroides (Vill.) Fiori & Paol.	(n = 10)	30	90[1]	100	90	100	90	80
Carex pyrenaica (Wahl.)	(n = 10)	0	80	90	100	100	80[1]	40
Total	(n = 170)	44	73	78	80	83	74	69

[1] Ten individuals were transplanted within this noda and from this noda to all other noda.

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PLANT POPULATION BIOLOGY ABOVE TIMBERLINE: BIOTIC SELECTIVE PRESSURES AND PLANT REPRODUCTIVE SUCCESS

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ABSTRACT

A greater knowledge of alpine plant population biology is needed for sound management practices and our general understanding of ecology and evolution. In terms of their life-history traits, much of the distinctive character of alpine taxa also is observed in perennials at lower elevations. There is, as yet, a lack of extensive, long-term information with which to make generalizations about alpine life-history characters and their evolution. Increasing evidence suggests that many different reproductive strategies exist above timberline. Sexual reproduction can represent a considerable investment and be highly successful, particularly when interpreted for the entire life span of the individual. Even though physical aspects of the environment have been emphasized in the past, biotic aspects, such as allelopathy, competition, herbivory, levels of genetic variability, parasitism, phenotypic plasticity, and pollination syndromes, are important components of the selective milieu and merit further study above timberline.

INTRODUCTION

Population biology is a synthetic discipline whose concerns are patterns, origins, and adaptive values of genetic and phenotypic variation in time and space. Utilizing aspects of genetics, ecology, physiology, and systematics, population biology seeks to understand how individuals, populations, and communities function, and to develop predictive theories modeling this function (Solbrig, 1976).

A major precept of plant population biology deals with variation along environmental gradients. Wide-ranging species show variation, correlated with habitat differences, due to the action of natural selection molding locally adapted populations from the pool of genetic variability of the species (Heslop-Harrison, 1964). The study of species in relation to elevational gradients has greatly aided our understanding of plant growth and reproduction. Stebbins (1979), in his survey of the past 50 yr in the study of evolution, lists several major contributions in plant population biology, many of which have been made using high-elevation species. These studies include an assessment of how much plant variation is genetic, compared to environmental modifications of the phenotype (Turesson, 1922, 1925, 1931; Clausen et al., 1940, 1948) and how much of the intra- and interpopulation differences are due to single genes having large effects on phenotypes versus multilocus inheritance of quantitative characters (Clausen et al., 1948; Clausen and Hiesey, 1958). The role of polyploidy in plant evolution also has been elucidated using high-elevation species (Johnston et al., 1965; Löve and Löve, 1967).

Solbrig (1976) argues that by integrating knowledge of life span, herbivory, competition, and reproduction, general predictions of plant response to environmental perturbations are possible. These predictions are particularly important in the alpine. Increasing human impact has necessitated restoration practices which require an understanding of population dynamics, succession, reproduction, and interaction among alpine taxa. The problem of alpine restoration is evident from the voluminous increase in management and applied literature (Harrington, 1946; Marr and Willard, 1970; Willard and Marr, 1971; Bell and Bliss, 1973; Berg et al., 1974; Greller, 1974; Belsky, 1975; Thilenius, 1975; Brown and Johnston, 1976; Zuck and Brown, 1976; Brown et al., 1978a, 1978b; Kenny, 1978, Webber and Ives, 1978; Johnson, 1979).

Because an organism's resources are limited, fitness represents trade-offs among aspects of growth, maintenance, and reproduction. If we could predict the trade-offs among these components of plant success, we could increase our awareness of the general ecological and evolutionary aspects of successful ecosystem management. In Solbrig's (1976) view, these predictions are possible through the knowledge of processes (physiological and biochemical) underlying plant adaptations to the abiotic environment, competition, and defense, in addition to knowledge of the environoment. The colonizing potential of species and their suitability for revegetation practices needs to be assessed (May, 1976; May et al., 1982, this volume).

Since the earliest study of alpine zones in the 18th century (Tranquillini, 1964), the major focus has been floristic investigations of elevational zones and the climatic causes of this zonation. Only recently, has the focus drifted away from community-level floristics or autecological studies of adaptation to microclimatic variation. Our understanding of the macro- and microclimatic regime of the alpine is extensive, particularly for Niwot Ridge and the Front Range (Marr, 1961; Gates and Janke, 1966; Caldwell, 1968; Salisbury et al., 1968; Barry, 1973; Caldwell et al., 1980; Ives, 1980). Also, the physiology of alpine plants has been the subject of much research (Mooney and Billings, 1960, 1961, 1965; Spomer, 1961, 1962, 1964; Bliss, 1962a; Hadley and Bliss, 1964; Salisbury and Spomer, 1964; Tranquillini, 1964; Billings et al., 1966, 1971; Fonda and Bliss, 1966; Chabot and

and Billings, 1972; Johnson and Caldwell, 1974; Ehleringer and Miller, 1975a, 1975b; Wallace and Harrison, 1978; Chapin, 1981; Oberbauer and Billings, 1981; Robberecht et al., 1981; Vetter-Sauchyn, 1981; to name only a few).A major gap in our knowledge of alpine ecosystems lies in our understanding of plant population biology, particularly the diversity of plant reproductive strategies and biotic selective pressures which help shape these strategies. Alpine plant ecology has been reviewed admirably elsewhere (Bliss, 1962b, 1971; Billings and Mooney, 1968; Billings, 1974a, 1974b). Furthermore, many aspects of population biology, notably the extensive literature on physiological ecology as well as a few on population genetics, floristics, and pollination, will be overlooked in this paper for the sake of brevity, although they would be appropriate inclusions. This paper will emphasize alpine plant reproductive strategies, with emphasis on sexual modes, as illuminated by recent developments in the literature, and will speculate on several biotic as well as abiotic forces which may help shape these tactics.

DETERRENTS TO POPULATION STUDIES ABOVE TIMBERLINE

A number of traits of alpine species like other plant taxa, and their tundra habitats, have been a source of unceasing frustration to population biologists. The perenniality of most tundra species (Daubenmire, 1943; Bliss, 1971; Billings, 1974a) necessitates long-term observation over the course of many growing seasons. Herbaceous tundra plants are difficult, if not impossible to age. In plants, however, size rather than age seems to be more closely related to survivorship and reproduction (Werner, 1975). Unpredictable phenology, slow growth rates, short growing seasons, and harsh climate have made alpine regions unattractive to some. The small sizes of alpine plants, their organs, and populations have deterred some researchers. However, given that the unit of adaptation and evolution is the local population with an effective population size which may be only a few meters across for some plant species (Bradshaw, 1972; Levin and Kerster, 1974, 1975) problems of small populations do not seem that imposing.

POPULATION DYNAMICS

Precious little of the population dynamics of alpine plant taxa has been confronted, with the exception of natality (seed production, germination, and seedling establishment). The work of Callaghan and Marchand and their students is a promising exception. Callaghan (1976) called for the determination of life-histories of clones and populations to aid our understanding of interspecific competition and seral changes in community structure. Callaghan and Collins (1976) presented the population dynamics of four important tundra growth forms (moss, herbaceous perennial, graminoid, and dwarf shrub). After laborious excavations and enumeration of growth rates, their data supported long-term inferences that turnover of individuals is slow. Short-term, adverse environmental conditions affected only the younger individuals. Callaghan (1976) developed a transition probability matrix for Carex bigelowii from excavation of the rhizome system. This matrix included age-specific reproductive, mortality, and survival factors. Mortality was high in young juveniles, but survival increased to a maximum value of 92.1% for tillers with 16 to 20 leaves, and later decreased due to senescence. Callaghan suggested that documentation of tundra plant life cycles will help us interpret differences in the stability of population growth rates in a long-term context, as was done by Sarukhan and Gadgil (1974). Other efforts to model aspects of alpine population dynamics are promising (Callaghan, 1976; Callaghan and Collins, 1976, 1981; Marchand and Sproul, 1981).

For many alpine plants, the study of population dynamics is hindered by problems with the identification of an individual genet or ramet. Callaghan and Collins (1981) have advocated the study of the dynamics of shoot apicies. Growing shoots represent natality and those ceasing to grow, mortality. This technique would be appropriate for species whose shoots can become vegetative propagules through fragmentation, e.g. Sedum lanceolatum. For review of this approach, see White (1979).

The demography of alpine plant parts has revealed a division of labor among organs of different ages. The first tillers of the growing season in Rostkovia magellanica assume a pioneering function, producing a long rhizome and many leaves. Subsequently, a tiller with a short rhizome and quickly expanding leaves is produced, which aids assimilation and colonization (Callaghan, 1976). Among generations of tillers of alpine Carex bigelowii, the younger tillers are largely photosynthetic and the older ones are active in the uptake of water and other nutrients.

LONGEVITY

Few annuals are represented above timberline (Bliss, 1962a, 1971). In Colorado, of 250 species (Rydberg, 1914 cited in Bliss, 1962a), Koenigia islandica is one of the few tundra annuals. However, Griggs (1956: 19) spoke of Draba crassifolia (albertina Greene) as "an annual or perhaps biennial ephermeral." Similarly, he stated that Hymenoxys grandiflora was monocarpic; it flowered once and died, just like a "biennial."

The longevity of many tundra species is unknown. Although counting annual rings in the stems of evergreen shrubs or the underground organs of herbaceous perennials is possible, caution is advised (see Werner, 1978). The development of false rings is particularly a problem in tundra environments (Barrow et al., 1968). While it is possible to calculate age based on average growth rates, e.g. 10 leaves per year for tundra graminoids (Callaghan and Collins, 1981), year-to-year variability in growth rates necessitates that these estimates be based on several years of observation.

Given the most conservative estimates, most tundra species show relatively long life spans: 6 yr for the moss, Polytrichum alpestre, at least 5 to 7 yr in graminoids (Callaghan and Collins, 1981), at least 5 yr for the herbaceous perennial, Sedum lanceolatum (Jolls, Vetter-Sauchyn, pers. obs.), 26 yr for Polygonum viviparum, and 109 yr for Vaccinium vitis-idaea (Callaghan and Collins, 1981). Griggs (1956) estimated that a Silene cushion 50 cm in diameter observed by Schroter (1926) in the Tatra Mountains was a century old. Sørensen (1941) suggested that a greater life span in the arctic could compensate for decreased growth rates, and may be one explanation for the paucity of tundra annuals. Indeed, Callaghan and Collins (1981) have observed that dwarf shrubs in more severe environments have greater maximum life spans in spite of decreased growth rates. These authors note that life spans of tundra plants are not totally plastic and may have a genetic component. I have suggested (Jolls, 1980b) that longevity may vary along an elevantional transect and serve to delineate ecotypes. Thus, despite less freqent sexual events, the reproductive capacity of a longer-lived alpine plant may equal that of a shorter-lived conspecific at lower elevations which flowers more frequently. Williams (1970) used the presence of the previous year's scape to determine perenniality and found that Androsace septentrionalis was annual at lower elevations, yet lived more than one growing season in the alpine. He hypothesized that perenniality would afford the genotype survival of at least one of the poor growing seasons likely to occur above timberline.

SEEDLING ABUNDANCE AND SURVIVAL

Seedlings of certain species can be rare above timberline (Osburn, 1958; Klikoff, 1965; Callaghan, 1976; Lindeberg-Johnson, 1981; Jolls and Bock, submitted) in so far as their occurence may be limited to "favorable" years. Successful reproduction requires the accumulation of reserves, the appropirate thermal and photoperiodic regime (Billings, 1974a), and sufficient soil moisture (Klikoff, 1965), and rates of snow melt which do not retard development (Billings and Bliss, 1959; Holway and Ward, 1963). Fruit and seed have to escape excessive predation (Klikoff, 1965; Lindeberg-Johnson, 1981). Seeds must be dispersed to suitable microsites, attain sufficient biomass to survive the winter, escape drought, needle-ice activity, predation, and competition. It is not surprising that estimates of the time required for recovery of tundra range from 25 (Thoraug, 1979) to hundreds or thousands of years (Willard and Marr, 1971; Brown et al., 1978b). Some seeds, however, do escape all these perils for seedlings of certain species have been reported to be abundant in certain years, in certain microsites (Griggs, 1956; Osburn, 1961; Jolls, 1980b; Callaghan and Collins, 1981).

As noted by Jolls and Bock (submitted) for Sedum lanceolatum and by Lindeberg-Johnson (1981) for Caltha leptosepala, high seedling densities often occur in areas of high adult densities. Thus, to some degree, adults and juveniles may respond to the same environmental conditions. Alternatively, these microsites of high seedling as well as high adult densities may have been favorable for population recruitment in the past. The co-occurrence of high seedling and adult densities may simply be a consequence of more adults producing more seeds, but Jolls and Bock (submitted) showed that seedling densities of Sedum lanceolatum are reduced significantly above timberline even when corrections are made for elevational differences in adult population densities.

Mortality during the first winter may most limit seedling success. Marchand and Sproul, (1981) have developed a model predicting alpine recovery. Increasing winter survival from 3% to their highest observed value of 13% cut time to partial recovery almost in half. However, a 15-fold increase in the density of broadcast seed biomass reduced recovery time by 50 to 70% in their model.

Physical stresses have been emphasized, but it is unclear which factors or combination of factors limit seedling success. Soil drought during the first growing season (Bliss, 1958; Osburn, 1958, 1961; Klikoff, 1965; Billings and Mooney, 1968; Bonde, 1968; Bell and Bliss, 1980) and spring and early summer needle-ice activity inhibit establishment (Osburn, 1958; Brink, 1964; Klikoff, 1965; ; Billings and Mooney, 1968; Bonde, 1968). Although Osburn (1958) is frequently cited as evidence that soil churning and needle ice formation are major contributors to seedling demise, he reported these processes for only one of the three stands he investigated on Niwot Ridge. Jolls and Bock (submitted) found similar mortality of Sedum lanceolatum seedlings during the growing season along an elevational gradient in the Front Range. Roach and Marchand (pers. comm.) have executed a critical set of experiments to determine which factors influence alpine seedling success. Over 7000 seeds of Arenaria groenlandica, Juncus trifidus,and Potentilla tridentata were sown between 1978 and 1980 on Franconia Ridge, White Mountains, New Hampshire. Field-based recruitment and mortality were monitored at 3-7 d intervals, paralleled by a similar study under controlled conditions. It was concluded that seedling populations above timberline were subject to random factors; their dynamics can be adequately described by purely stochastic processes (Marchand, pers. comm., 1981). However, it may be that seedling success is more predictable in other tundra areas.

ABIOTIC SELECTIVE PRESSURES

Most studies stress the role of the physical environment in shaping vegetation patterns above timberline. Studies conclude that the extension of lowland taxa into the alpine is limited by tundra low temperatures (Daubenmire, 1943; Mooney, 1966), high winds (Warren Wilson, 1959; Johnson and Billings, 1962), and low reproductive capacity (Osburn, 1958; Mooney and Billings, 1961; Sayers and Ward, 1966). The downward distribution of alpine species to lower elevations is reportedly limited by high temperatures as they affect vernalization requirements (Godfrey, 1969), water availability, and successful seedling establishment (Daubenmire, 1943; Dahl, 1951; Mooney, 1966; Godfrey, 1969). Water availability is a major environmental constraint on tundra plant growth (Osburn, 1958, Callaghan and Collins, 1981; May et al., 1982, this volume).

BIOTIC SELECTIVE PRESSURES

Discussing the new ecological genetics, Antonovics (1976) argued that the abundance and distribution of a species is basically a genetic problem. He suggested that species patterns are limited by the lack of genetic variability for tolerances, the swamping effects of gene flow, trade-offs among fitness components, or coevolutionary limits imposed by competitors and predators, rather than physiological tolerances. I also believe that biotic selective pressures may play an important role in shaping plant adaptations above timberline. With our current knowledge of tundra plant dynamics, we can begin to investigate alpine plant-plant and plant-animal interactions, and to consider their evolutionary consequences.

Other authors (Billings, 1974a) have noted biotic selective pressures in the alpine. Jaccard (1912) referred to two types of selection influencing alpine plants: eliminative, dealing with, in his words, "ecological" (climate, soil) and "biological" (the degree of relative adaption) factors and distributive, involving sociological factors such as competition. Although Jaccard concluded that the "ecological factors" resulted in the presence or absence of a species, "sociological factors" (competition) were responsible for determining the local distribution of those species not eliminated by the physical environment.

PLANT-PLANT INTERACTIONS

Competition from taller, more vigorous, drought tolerant lowland species has been hypothesized to limit the downward distribution of alpine plants (Dahl, 1951; Rochow, 1970; Walter, 1973). Lindeberg-Johnson (1981) stressed that biotic as well as "physiological" factors may affect the ranges of high elevation species. Her work with Caltha letopsepala, using experimental manipulation of plant density, photoperiod, and thermal regime, suggests that the greater leaf production typical of plants at high elevations is due to inter- and intraspecific competition for light. In excavated subalpine and alpine plots of Caltha and other species, Caltha proved to be a weak competitor and was soon crowded out by the more vigorous dicotyledons and graminoids. She found that an increase in total plant density produced a decrease in the number of leaves per individual of Caltha, average leaf area, the length of the primary root, and the number of lateral roots in plants raised from seed.

Competition has been prominent in Griggs' (1940, 1956) discussions of alpine environments. He suggested that the distinctive character of arctic and alpine vegetation was, in his view, the "absence of closed associations produced by competition" (1940: 579). Griggs argued that no evidence existed to support the notion that alpine species preferred severe climates, rather they had evolved the ability to tolerate such environments. Griggs observed alpine taxa at low elevations along rivers, in rocky places, on shores, barrens, and refuges in bogs. This alsowas noted by Walter (1973). Griggs concluded that alpine habitats were similar in plant microclimate to pioneer stages of succession. Only in regions where life was too hazardous for forest species to invade could alpine plants persist.

Competition, even early in the life cycle, may shape patterns of abundance and distribution above tree limit as well as the elevational range of plants. Griggs (1956) noted 93 host-invader pairs of vascular plants on a fellfield community atop Trail Ridge, Rocky Mountain National Park. Invasion by runners of Haplopappus pygmaeus, Mertensia viridis, Phlox caespitosa, Sedum lanceolatum, S. rosea, and Trifolium parryi, as well as seedling encroachment, were hypothesized to reduce growth rates and displace the host by "direct competition by roots or otherwise." Griggs observed that invasion by a runner was backed by the photosynthetic capacity of a well-established plant, but seedlings carried no reserves beyond those in the seed, and as a result, must be competitively superior to the host.

Competitive mechanisms shaping succession above timberline also were noted by Klikoff (1965) in the Sierra Nevada and by Billings and Mooney (1959) in Wyoming, although competition per se was not discussed. Klikoff did evoke competition, however, in discussing the limited distribution of species confined to rock communities: "the few plants limited to these communities may be so restricted because of an inability to compete in the meadows" (1965: 206).

Biotic selective pressures may also determine seedling success. Griggs (1956), Osburn (1961), Bliss (1971), and Callaghan and Collins (1981) are a few who report high seedling abundance in tundra microsites which may result in high competition among a cohort in limited safe-sites. Although seedling survival of Trifolium nanum was comparable between cushion plant communities and more exposed habitats, mortality may have been due to competition for water, nutrients, and light (Bonde, 1968). This hypothesis also has been suggested for clumped juveniles of Sedum lancelolatum (Jolls, 1980b) and individuals invading mature cushion plants (Griggs, 1956). Lindeberg-Johnson (1981) found high seedling densities in microsites created by adults of *Caltha leptosepala*. This may be another example of intraspecific competition. She also noted that this "parental care" may afford seedlings protection from drought or predation.

Competition has been inferred to be one factor responsible for phenotypic differences among populations and individuals, and plant parts. In Colorado, Wyoming, and Montana, Lindeberg-Johnson (1981) observed that within a site, areas with greatest total vegetation cover had the lowest percent cover by *Caltha leptosepala*. A similar pattern of decreasing density of *Sedum lanceolatum* with increasing total vegetation cover along an elevational transect was reported by Jolls (1980b). The circumpolar arctic-alpine *Carex bigelowii* may exhibit competition for parental resources among tillers of different ages (Callaghan, 1976). The tillers produced at maturity, when most tillers are produced, showed reduced growth rates compared to younger tillers having fewer siblings. Callaghan also observed a segregation between parent and asexually produced progeny. This tactic may prevent competition among tillers of the same clone during colonization of nutrient-poor areas.

Intraspecific competition affects resource allocation patterns of lowland taxa (Abrahamson and Gadgil, 1973; Gaines et al., 1974; Hickman, 1975) and also may shape alpine growth habits. Lindeberg-Johnson (1981) found a positive relationship between rhizome branching in *Caltha leptosepala* and density of individuals.

A striking affect of competition on sexual versus asexual modes of reproduction in an alpine species was reported by Lee and Harmer (1980). In an experimental array set up in the greenhouse, viviparously produced plantlets of *Dechampsia alpina* showed a reduced total dry weight and tiller production compared to plants raised from seeds. Plantlets may have an advantage over seedlings if propagules establish close together.

PLANT-ANIMAL INTERACTIONS

Animal activity, in addition to pollination, also may shape the vegetation character above timberline. Osburn (1958), Willard (1963, 1979) and Stoecker (1976) have noted a number of effects due to pocket gopher (*Thomomys talpoides*) burrowing and foraging. These include growth inhibition, injury, or death caused directly by shredding or tunnelling and indirect impact through soil removal. Osburn (1958) also noted that pocket gopher activity could promote plant establishment and growth in winter snow accumulation sites where mounds and castings served as reasonably good seed beds. Klikoff (1965) noted effects on community composition in the alpine of the Sierra Nevada due to burrowing and seed consumption by pocket gophers.

The influence of predation on plant reproduction, seedling establishment, and growth has been noted by others (Bliss, 1971; Mosquin, 1971). A significantly greater percentage of *Caltha* reproductive structures showed signs of predation from the yellow-bellied marmot (*Marmota flaviventris*) and deer mice (*Peromyscus* sp.) in the lower subalpine than the alpine populations, suggesting that predation may limit the downward distribution of species (Lindeberg-Johnson, 1981). She stresses that predation losses must be considered in the estimation of reproductive potential, particularily in comparative studies. The effects of domestic grazing and management needs on the alpine tundra have been discussed (Griggs, 1956; Paulsen, 1960; Marr, 1964; Thilenius, 1975). However, little work has been done on the impact of native tundra herbivores as a force affecting plant evolution (Osburn, 1958; Paddock, 1961; Stoecker and Bock, 1971; May and Braun, 1972). Thilenius (1975) noted that the potentially important role of invertebrate herbivory has been virtually ignored except by a few authors (Gregg, 1947; Alexander, 1951; Taussig, 1962).

LIFE HISTORY CHARACTERS

Genetic and Phenotypic Variability

Genetic polymorphisms play a role in determining fitness (Schaffer, 1974). The study of levels of genetic variability, phenotypic plasticity, and trade-offs among growth and reproduction can greatly aid our understanding of plant distribution patterns (Antonovics, 1976). Although experimental studies have provided some understanding of alpine plant ecological genetics (Kerner von Marilaun, 1891; Clausen et al., 1940, 1948; Clausen and Hiesey, 1958; Mooney, 1963; Robertson and Ward, 1970; Rochow, 1970; May et al., 1982, this volume), little work dealing with population genetic differentiation has been done.

Given the difficulty of cultivating many tundra species, this lack of study of alpine plant population genetics is not surprising. All too often, we are unable to determine the genetic component of phenotypic variation we see in the field. However, there is evidence suggesting pronounced intraspecific genetic differentiation among alpine populations, as has been observed in lowland taxa (Hamrick and Allard, 1972; Linhart, 1974). May et al. (1982, this volume) observed the greatest transplant success for those individuals from the species' optimal habitat, suggesting interpopulation differences which may have a genetic basis. Similarly, in *Polygonum viviparum*, as environmental severity increased, interpopulation differences exceeded geographic ones, although at the more favorable locations, interpopulation variation became more pronounced (Callaghan and Collins, 1981). On Niwot Ridge, a number of species assayed have heterozygous loci (M. Grant and B. Hawkes, pers. comm., and electrophoretically detectable enzymatic variation may exist among sites along a moisture gradient.

Phenotypic plasticity is an important adaptation in plants (Bradshaw, 1965; Harper, 1966; Hickman, 1975) and is one component of reproductive strategy (Giesel, 1974). Considerable plasticity exists in morphology and growth form of alpine Achillea and Potentilla (Clausen et al., 1940, 1948), Androsace septentrionalis (Williams, 1970), Caltha leptosepala (Lindeberg-Johnson, 1981), Epilobium augustifolium (Flint, 1980), Polygonum cascadense (Hickman, 1975), and Phleum sp. and Sedum sp. (Woodward, 1975, 1979a, 1979b; Woodward and Pigott, 1975; Clausen, 1975; Jolls, 1980a, 1980b; Vetter-Sauchyn, 1981). Environmental modification of physiological characters, particularly development, have been reported for Achillea and Potentilla at high elevations (Clausen et al., 1940, 1948), Acomastylis rossii (Billings and Bliss, 1959; Spomer and Salisbury, 1968; May, 1976), Saxifraga caespitosa (Mulroy, 1979), Caltha leptosepala (Lindeberg-Johnson, 1981), and other Colorado alpine species (Holway and Ward, 1963). The plasticity of tundra genotypes may be an important adaptation to the heterogeneous alpine environments, as shown for Polygonum cascadense (Hickman, 1975).

Some alpine species have breeding systems which may result in considerable genetic variability, however, little is known of compatibility, pollination syndromes, or pollinator fidelity (the work of Macior, Kevan, Pleasants, and students is a notable exception). Many species are presumed to be self-fertile (Bliss, 1962b) yet some are allogamous. Self-compatibility is rare but possible in Caltha leptosepala (Lindeberg-Johnson, 1981) and low in Sedum lanceolatum (Clausen, pers. comm.). Substantial heterozygosity may exist even in self-fertile alpine species (Jain, 1976). Masters (1978) found that congers of Saxifraga species were self-fertile in the arctic, but required cross-fertilization in the alpine. Pollinators, particularly bumblebees, can be prevalent in arctic-alpine ecosystems (Swan, 1961; Kevan, 1972) and several highly co-evolved systems exist, e.g. Pedicularis groenlandica-Bombus sp. (Macior, 1968). The levels of population differentiation in allogamous taxa will differ depending upon pollinator fidelity.

Genetic turnover may be slow on the tundra due to slow growth rates, perenniality, and the infrequency of successful sexual reproduction. However, there is insufficient evidence to refute high levels of genetic variability in alpine taxa.

Sexual vs. Asexual Reproduction

The reproductive strategies of alpine plants, particularly sexual versus asexual reproduction, has received considerable attention. However, the significance of sexual reproduction in the tundra should not be inferred from studies which deal with asexual frequency or success of sexual efforts in a few taxa or over a portion of the individual's life span. The "relative importance" or "role" of sexual versus asexual reproduction above timberline is probably the same as that at lower elevations, for genotypes must be able to cope with environmental heterogeneity. Empirical and theoretical studies of life-history evolution suggest that sexual modes are more important in heterogeneous environments but the degree of temporal heterogeneity in the tundra is unclear. Pleasants (1977) and Byron (1980) found that environmental fluctuations were more predictable in the alpine than subalpine areas of Colorado. Byron also cited Michael C. Grant (pers. comm.) who found that for certain parameters, the alpine is more predictable than lowland sites even though it is characterized by large fluctuations. We need to know how sensitive plant growth and reproduction are to these macrometerological variables before the role of sexual reproduction and environmental heterogeneity above timberline can be assessed.

It has been concluded, based on observations of low seed or spore production (Holch et al., 1941 cited by Marr, 1961; Holway and Ward, 1963, Callaghan and Collins, 1981) and low rates of seedling establishment in the tundra (Billings and Mooney, 1968) that sexual reproduction is highly variable and less successful above timberline. Success, however, does not necessarily imply "role" or "importance"; we must not extend patterns in a few species and microsites to generalizations for the ecosystem. Sexual reproduction may predominate in drier alpine sites while vegetative modes dominate in more mesic habitats (Billings and Mooney, 1968). Seed and spore production decrease with increasing severity of microclimate (Bliss, 1958; Billings and Mooney, 1968; Callaghan and Collins, 1976; Billings, 1974b).

Levels of sexual reproduction in the alpine may not be as low as previously supposed, given the life histories of these perennial species. Callaghan and Collins (1976) observed that seed and spore production under more favorable conditions exceeded ramet production and balanced the greater mortality of progeny produced by sexual modes. However, they also found that although seedlings of dwarf shrubs were common, vegetative reproduction was more frequent. This pattern of greater asexual reproduction and low seedling success punctuated with highly successful sexual episodes is typical of longer-lived perennials (Tamm, 1956; Harper, 1977). In long-lived species, sexual modes need to produce new combinations only in favorable years and proliferate these genotypes by vegetative means (Billings and Mooney, 1968; Billings, 1974a; Lee and Harmer, 1980). "Low" levels of sexuality in Carex bigelowii in the alpine (Callaghan, 1976) also can be found in lowland graminoids. Baker (1974) concluded that low seed production in temperate perennial grasslands was selected for by sustained grazing pressure, which enhanced selection for rhizomatous or stoloniferous perennials. It is possible that the "low" levels of sexual reproduction observed in alpine taxa may have been shaped by these types of biotic as well as abiotic factors.

The assessment of sexual modes relative to vegetative propagation depends on how reproductive effort or success is determined (Douglas, 1981; Thompson and Stewart, 1981; Jolls, in preparation). Jolls (1980b) and Vetter-Sauchyn (1981) working with *Sedum lanceolatum* along the same elevational transect in the Front Range of Colorado came to different conclusions concerning the importance of sexual efforts. The proportion of total plant biomass as inflorescences (Jolls, 1980b) and the frequency of plants with inflorescences (Vetter-Sauchyn, 1981) decreased at higher elevations, indicating that sexual reproduction is less prevalent in the alpine. However, based on total caloric investment patterns, seedling survival during the growing season and seedling:adult ratios, Jolls (1980b) and Jolls and Bock (submitted) concluded that sexual modes can be just as successful and represent even a greater investment in the alpine as at lower elevations.

For certain species, sexual reproduction represents a considerable investment and can be quite successful above timberline in certain growing seasons. Diploids of *Epilobium angustifolium* occur at higher elevations and produce seed which germinates more readily than the tetraploids, which occur at lower elevations. The tetrapoloids, however, did produce more seed (Flint, 1980). In phytotron studies of these same races, Flint did observe a shift from vegetative to sexual reproduction in response to warmer temperatures. It would appear that when given the chance, sexual reproduction is manifest above timberline. The smaller alpine individuals of *Mimulus primuloides* produce fewer flowers and fewer seeds because flower production is correlated with plant size and genetically determined (Douglas, 1981). However, alpine forms allocated the highest proportion of resources to sexual reproduction. Williams (1970) found more seeds produced by *Androsace septentrionalis* at the highest elevations. It is noteworthy that although Douglas (1981) suggested that reproduction in *Mimulus* is sensitive to biotic stresses at low elevations and physical factors at higher ones, she does consider interspecific competition as a factor shaping the highest elevational populations. Again, the expression and success of sexual reproduction also may be subject to biotic selective pressures as well as the physical factors above timberline. Thisalso has been suggested for *Sedum lanceolatum* (Jolls, 1980b).

Not only does the success of sexual reproduction vary among populations of the same species across time and habitats, but different species in the alpine exhibit different life-history tactics. Early investigators noted the colonizing tendencies of *Silene acaulis* (Griggs, 1956), *Acomastylis rossii*, and *Trifolium* spp. (Osburn, 1958). More recently, many alpine species have been labeled "opportunistic" in their reproductive behavior (Billings and Mooney, 1968; Callaghan, 1976). Based on cover, frequency of occurrence, flower and seed production, and germination characteristics, Marchand and Roach (1980) concluded that *Arenaria groenlandica* and *Juncus trifidus* combined perennial longevity with high reproductive output more typical of annuals. With such information, we can develop predictive models of life-history evolution and the empirical tests dealing with the apportionment of plant energy between sexual and vegetative reproduction (Schaffer, 1977) and reproduction in a varying environment (Cohen, 1966).

The comparative roles of sexual versus asexual reproduction have been dealt with using viviparous taxa. Lee and Harmer (1980) contended that the apparent prominence of this reproductive mode in arctic-alpine taxa was due to the success of a few viviparous species. They noted that the success of a viviparous species could be related to the greater size of the plantlet compared to a seed and its ability to photosynthesize. Funk (1979) found that vegetatively produced plantlets of *Saxifraga cernua* became established twice as fast as seeds. Despite these advantages of viviparous progeny, *Festuca vivipara* did not achieve a growth advantage over seeds of the comparable sexual *F. ovina* under controlled conditions (Lee and Harmer, 1980). Lee and Harmer stressed that vivipary and other asexual modes can only proliferate successful genotypes. Survival of the progeny depends on parental resources and the same environmental conditions experienced by the parent. Sexually produced progeny, on the other hand, may gamble on environmental heterogeneity, their success dependent on a long sequence of environmentally determined steps which cannot be tracked by the parent (Callaghan and Collins, 1976).

Studies of taxa having apomictic and seminiferous populations (*Saxifraga cernua*: Wehrmeister and Bonde, 1977; Funk, 1979) or even taxa in which individuals are viviparous and then produce seed sexually (*Festuca vivipara*: Lee and Harmer, 1980) can elucidate the consequences of asexual and sexual modes. However, the existing body of work suggests that the success of sexual reproduction is no more predictable nor may its importance or role be more readily generalized for species above timberline than below.

SUMMARY

A number of significant contributions to our understanding of ecology and evolution have been made using alpine species. Our increasing need for sound management practices make a greater knowledge of plant population dynamics above timberline paramount. This should occur through a synthesis of empirical and theoretical aspects of ecology, genetics, physiology, and systematics.

Population turnover is slow among these long-lived individuals, with high mortality confined to seedling and juvenile stages, a pattern characteristic of many lowland herbaceous perennials. A division of labor may exist among plant parts in some alpine taxa. Seedlings can be rare or abundant, depending upon species, microsite, and year. Although many physical factors are responsible for the high seedling mortality often observed, survival in certain tundras seems subject to stochastic processes, some of which are biological.

Historically, most studies have stressed abiotic features as the major selective pressures in the alpine. Increasing evidence, however, suggests that biotic factors, such as competition, pollination syndromes, breeding systems, and herbivory, play important roles in shaping alpine plant population dynamics. Intra- and interspecific plant competition as well as interactions among different plant parts may serve to limit the abundance of species which are physiologically adapted to the alpine environment. Allelochemic interactions among alpine plants have been virtually ignored.

Animals are also an important selective pressure in the alpine, shaping plant growth and reproduction through their foraging, home-building, and other activities. Highly coevolved relationships exist among plants and their pollinators. These relationships mold plant response at the level of the individual (flower morphology, pollen and nectar composition, seed set) and the population (synchrony of flowering, levels of heterozygosity). The possibility of allelochemic, mechanical, and phenological deterrents to herbivory above timberline merits further investigation.

The number of life-history tactics observable above timberline preclude generalizations about alpine reproductive strategies, particularly the significance of sexual modes. The investment in and success of sexual reproduction should be judiciously assessed using numerical and phsyiological techniques over the long- and short-term. The conservative investment by alpine perennials in sexual reproduction is typical of similar growth habits at lower elevations. Some of these species, however, may exhibit investment patterns and germination syndromes characteristic of annuals or weedy colonists. It is possible that although highly variable, the tundra is a predictable environment, especially for a long-lived species. Over the long-term, sexual success may be high for a perennial, even though sexual modes fail during some years. Patterns of success in many taxa suggest that the alpine tundra may not be as stressful as many have assumed, at least not for the plants which persist there. This same point was emphasized by Harper and White (1974: 449): "However, on the whole, the presence of a species that is persistent in an area implies that it is (or has become) tolerant of the major recurrent hazards that characterize that environment; ...". The need for long-term study such as that pioneered by John Marr on Niwot Ridge is essential to our understanding of alpine plant dynamics and evolutionary ecology.

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ECOLOGICAL AND EVOLUTIONARY STUDIES
OF
FOREST TREES IN COLORADO

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ABSTRACT

Forest tree components of the Colorado Front Range ecosystems have recently been studied from several ecological and genetical perspectives. Among the chief results of this work are (1) microgeographic differentiation, even among these long-lived, wind-pollinated perennials, is common; (2) levels of genetic variability are high compared to herbaceous vegetation; (3) temporal genetic differentiation; is weak compared to spatial differentiation, (4) overall levels of protein heterozygosity are often correlated with radial growth rates and/or radial growth rate variability; (5) age and size structures of ponderosa, limber, and lodgepole pine and Engelmann spruce show significantly different distributions which, in turn, appear to correlate with the successional status of each species; (6) aspen clones show strong patterns of differentiation in adult sex ratios along an elevational gradient; (7) Englemann spruce and Colorado blue spruce show no signs of hydridization as assessed by protein phenotype patterns; and (8) significant differences in morphology and protein genotypes were detected among mountain pine beetles which emerged from their different host tree species.

DEDICATION

"The ecological theater
and the evolutionary play"

With that apt and trenchant title, G. Evelyn Hutchinson (1965) identified the crucial relationship between evolutionists and ecologists. Evolutionary biologists invest their energies in projects aimed at understanding the dynamic processes which produce organic change across generations. Ecologists invest their energies in projects aimed at understanding the biotic and abiotic contexts within which evolution occurs. Progress in evolutionary biology is dependent upon, and perhaps limited by, our understanding of ecological processes. John W. Marr established much of the ecological context of regional evolutionary research with his "Ecosystems of the east slope of the Front Range in Colorado" (1961). This publication has been used as the foundation for many of the ecological and evolutionary studies conducted during the subsequent two decades. This centerpiece of Marr's research remains a valuable, viable contribution to biolgical science. In addition, many biologists and the authors of this chapter in particular, have benefited from the facilities available at the Mountain Research Station, formerly Science Lodge, snuggled in the lee of Niwot Ridge. The founding and persistence of this major research facility are primarily attributable to the vision and determination of John Marr.

John, we salute you.

INTRODUCTION

Following the example set by Professor Marr, forest biologists at Boulder have focused much effort on the study of local communities. These studies have taken advantage of the environmental diversity found between the campus in Boulder and the nearby Continental Divide. Studies of the evolutionary play in the theater of Colorado forests have combined with the perspectives and tools of ecologists, geneticists, and population biologists. These studies do not represent a single effort focused upon one phenomenon, species, or community, but are the product of an abiding interest in ecology and evolution within a group of biologists who enjoy the natural history of forest trees. In some cases, one aspect of the natural history of a tree suggests a study, but in others, questions residing in the literature are explored utilizing the most appropriate species locally available. The following is a precis of these studies, loosely arranged under the headings Patterns of Genetic Variation, Demography and Dynamics, and Additional Evolutionary Studies.

PATTERNS OF GENETIC VARIATION

Population structure, the pattern of distribution of genotypes in space, is influenced by natural selection reflecting biotic and abiotic heterogeneity, mating system and dispersal of the species. Numerous studies, primarily of annual plants, have revealed genetic heterogeneity within and among populations, often associated with environmental heterogeneity. We have extended these observations to several species of forest trees.

Variation in Space

Our studies of population structures of forest trees have relied heavily upon protein polymorphisms detected from homogenates of seeds, seedlings, or the foliage of mature trees (Mitton et al., 1977, 1979; Linhart et al., 1981a). Tissue homogenates are absorbed onto paper wicks, subjected to electrophoresis in a starch gel, and enzymes are detected with the aid of specific histochemical stains. The genotypes of individual trees are interpreted from the patterns of proteins on the gels.

Forest biologists have long recognized

geographic variation within species, and that awareness is reflected in practices of revegetation and the designation of seed collection zones. Briefly stated, trees are adapted to the environments in which they are found, and their viability, growth, and fertility decreases as they are tested or planted in increasingly alien environments. Despite this well-founded generalization, the expectation for patterns of geographic variation of forest trees contrasts strongly with the growing corpus of empirical data on herbaceous plants. Herbaceous plants may be genetically differentiated on a truly microgeographic scale; substantial differences can be detected over distances of a few meters. Forest trees, however, evoke visions of vast stands, composed of millions of individuals, bathed in pollen borne on the wind and have been pointed to as exceptions to the local differentiation pattern (Endler, 1977). These views did not deny the possibility of geographic variation within a species, but neither did they lead us to expect genetic differentiation over small distances.

Empirical data on geographic variation in Engelmann spruce, subalpine fir, and ponderosa pine are inconsistent with the preconceived expectations mentioned above. Grant and Mitton (1977) sampled three major growth forms of trees -- spire, flag, and krummholz -- in both Englemann spruce and subalpine fir. Despite the fact that the sample localities were all within 2 km of one another, statistically significant differentiation was noted in peroxidase proteins of both species. Ponderosa pine exhibits consistent patterns of differentiation for a peroxidase polymorphism between relatively warm and dry south-facing slopes and relatively wetter and cooler north-facing slopes in steep and narrow canyons (Mitton et al., 1977); in addition, the differentiation seen on a microgeographic scale (within canyons) is consistent with differentiation seen on a larger scale, associated with elevation and temperature. Heterozygotes for the peroxidase protein are more common on south-facing slopes than they are on north-facing slopes and this same genotype is also more common at lower, warmer, and drier sites than at higher, cooler, wetter sites (Mitton et al., 1977, 1980b). These studies suggest that forest trees are similar to species of herbaceous plants in that they exhibit patterns of differentiation which seem to reflect adaptation to fine-scale environmental heterogeneity. Indeed, intensive studies of two stands of trees near Boulder reveal fine-scale heterogeneity of allelic frequencies which may reflect family groups in these stands of ponderosapine (Linhart et al., 1980, 1981a). One stand of 217 trees may be partitioned into six loose clusters which have different patterns of reproductive effort, different age and size distributions, different levels of parasitism by wooly aphids and cone beetles, different browse pressure by deer, and different frequencies of protein polymorphisms. Similar patterns were found in the other stand. We suggest that these groups are not unrelated trees differentiated according to undetected environmental heterogeneity, but are different groups of related individuals.

Variation in Time

Genetic differentiation may occur among populations in space, or, viewed in another way, a single population may experience genetic differentiation through time.

Four studies have made quantitative estimates of the relative importance of genetic differentiation over time versus local spatial differentiation in Colorado forest trees. The results are in agreement: spatial differences, even over very short distances, are greater than temporal differences.

A sample of 217 ponderosa pine at the mouth of Boulder Canyon exhibit patterns of microgeographic variation within the site, but there is no evidence of differentiation over time in this population (Linhart et al., 1980, 1981a). A study of colonization of new sites by ponderosa pine (Beckman, 1977) revealed differentiation over time at a peroxidase polymorphism; heterozygotes (adapted to warmer, drier environments) were highly successful in initially colonizing the site, but once the canopy closed, most of the successful establishment was accomplished by a homozygote apparently adapted to cooler, wetter environments. A study of succession of sites occupied primarily by Douglas-fir revealed only a subtle pattern of differentiation over time (Davis, 1981). A study of microgeographic variation and differentiation over time in lodgepole pine (Knowles, 1980) revealed significant differentiation in space, but no differentiation in time.

The Level of Outcrossing in Ponderosa Pine

Repeated patterns of genetic microgeographic differentiation in forest trees forced us to reexamine the asumptions that led us to expect a pattern of spatial homogeneity. Either gene flow is highly restricted, perhaps due to selfing or limited movement of pollen and seed, or natural selection is stronger than we anticipated. Estimates of the level of outcrossing in ponderosa pine using both alpine seedlings and protein polymorphisms (Mitton et al., 1977, 1981b) were consistent with prior expectations--approximately 95% of seeds are produced by outcrossing. The patterns of microgeographic differentiation are not attributable to an unexpectedly low level of outcrossing, but are probably produced by limited gene flow via seeds, or strong natural selection, or a combination of the two.

Protein Heterozygosity and Its Association with Growth Rate and Cone Production

Studies of protein polymorphisms in many different species allow us to compare the levels of genetic variation among different groups of species. These comparative studies reveal that forest trees have more genetic variation than any other groups of species examined to date (Hamrick et al., 1979). Several mechanisms may be postulated to explain high levels of genetic variation in forest trees, but we first explored the possibility that protein polymorphisms may influence growth rates and fertility. Levels of protein heterozygosity were found to be related to growth variability in aspen (Mitton and Grant, 1980), ponderosa pine (Knowles and Grant, 1981; Mitton et al. 1981b), and lodgepole pine (Knowles and Mitton, 1980). In both aspen and ponderosa pine, protein heterozygosity was positively related to growth variability, but in lodgepole pine, the correlation was negative. These patterns are of both theoretical and practical interest and certainly warrant further study.

Production of female cones is related to protein heterozygosity in ponderosa pine (Linhart et al., 1979; Linhart and Mitton, unpublished). The number of female cones produced by each of 199 trees was counted for four consecutive years at a site at the lower edge of Boulder Canyon. Cone production is a function of both age and diameter at breast height in this population, but protein genotype is also related to the number of cones produced per tree. Highly heterozygous trees produced approximately the number of cones predicted by the age and diameter of the tree, but predominantly homozygous trees produced either many more or many fewer than the number of cones predicted by the age and diameter of the tree.

DEMOGRAPHY AND DYNAMICS

The age distribution of stands of forest trees may differ between species. Such differences provide insight into the ecology of each species and seem to be related to the most common successional role played by each species.

Knowles and Grant (1982) report comparative age and size structures for several stands of Englemann spruce, ponderosa, limber and lodgepole pine in the Front Range. Lodgepole pine showed age structure patterns consistent with its pioneering habit but stands were not even-aged as is commonly assumed. They showed a near-normal distribution of ages despite being even-sized (Knowles and Grant, 1982). The coefficient of determination from regression of diameter on age was 0.03, illustrating the very weak link between size and age in these stands.

Spruce and ponderosa pine showed very broad age structures consistent with a "climax" (Whipple and Dix, 1979) successional character; spruce also formed much older stands. Size structure patterns for these two taxa were remarkably similar despite the fact each is found in extremely different environments. This size coincidence argues for the existence of general forces operating similarly in each species. The size-age relationship is much stronger in spruce and ponderosa pine; the coefficients of determination were, respectively, 0.34 and 0.26 (Knowles and Grant, 1982). Limber pine showed an age structure intermediate between lodgepole on the one hand and spruce and ponderosa on the other, indicative of its fugitive ecological character.

ADDITIONAL EVOLUTIONARY STUDIES

Reproductive biology, a critical aspect of the conifer evolutionary play, is just beginning to receive the attention that it deserves. The next few years should produce a substantial increase in our understanding of patterns of reproduction and the reasons why they vary among species.

Alexander (1974) summarized the status of our knowledge of forest tree reproduction from a silvicultural perspective while Schubert (1974) did so for ponderosa pine. Hamrick et al. (1979) reviewed published data on life histories of plant species and the amounts of protein variation found in those species. Differences were found in the relative levels of genetic variation in comparisons of widespread versus narrowly distributed species and between weedy and climax species, but the majority of variation was explained by the length of the life cycle and the maximum fecundity of the species. Species which lived longer and which produced greater numbers of seeds exhibited the highest levels of genetic variation.

Sturgeon (1979) provided evidence that ponderosa pine populations in California which have a history of heavy infestation of western pine beetles are differentiated from stands with no history of beetle infestations. In Colorado, no differences in monoterpene profiles were detected in comparisons of ponderosa pine resistant or susceptible to attack by the mountain pine beetle (Sturgeon, 1980), but beetles emerging from the three host tree species (ponderosa, lodgepole, and limber pine) differed in size, shape, and protein genotype. This work suggests that forest trees and forest insects produce reciprocal evolutionary challenges.

The spruce budworm is a well known significant pest in Colorado conifers (Alexander, 1974) causing substantial economic losses. Less well known is the spruce seed worm, Laspereysia youngana, which destroys seeds within the cones but generates no outward symptoms of tree destruction. One of us (MCG) measured cone infestation rate near 100% with seed crop destruction above 40% in one season on Niwot Ridge. Similarly, the cone beetle (Conopthorus ponderosae) is an important destroyer of cones in ponderosa pine and can reduce cone crops of stands by 50% or more in any one year. The other major cone predator of ponderosa pine is the tassel-eared squirrel (Sciurus aberti). Each of these animals is particularly damaging in years when the cone crop is scanty; furthermore, they damage a significantly greater proportion of cones on trees with few cones as compared to trees with many cones (Larson and Schubert, 1970; Linhart and Mitton, unpublished).

Sturgeon and Mitton (1980) have suggested that cone color variants in white fir play a thermoregulatory role, with purple cones having a higher energy absorptive capacity. The purple cone morph is decidedly more common at the upper elevations of the species distribution.

Patterns of variation along elevational gradients have also been observed in aspen. Grant and Mitton (1979) reported strong gradients of sex ratios with a moderate predominance of females at low elevations and a striking predominance of males at high elevations. The growth of females exceeded that of males at all elevations, but the decrease in growth rate with elevation was more pronounced in females.

Electrophoretic techniques also have been brought to bear on the rather old question of the relative taxonomic status of Colorado blue spruce (Picea pungens) vis-a-vis Englemann spruce (Picea engelmannii). Several investigators have reported extensive hybridization between these species, but attempts to experimentally cross these species have not been successful. Mitton and Andalora (1981) could find no genetic evidence of introgression between the taxa even in zones of morphological intermediacy.

FUTURE DIRECTIONS

Current and future studies of Colorado forest systems have already, and will increasingly provide baseline patterns from which sound management practices can be developed. As human population density increases in Colorado, this type of information will increase in practical significance. We see the following areas of evolution and ecology to be most in need of attention:

(1) Studies which relate the physiological ecology of each tree species to population ecology characteristics and these, inturn, to community and ecosystem attributes.

(2) Studies which test the generality of patterns established in the Front Range, especially those relating heterozygosity to growth rate variation and reproductive output, age structures, and forest dynamics, as well as those which test predictive patterns of spatial genetic differentiation.

(3) Studies which relate patterns of genetic variation directly to adaptive responses. We suggest that peroxidase variation and fungal infection susceptibility may provide a potentially fruitful system. Genetic propensity for vegetative propagation among treeline forms may be another.

(4) Studies which quantify parameters of the mating system for species other than ponderosa pine.

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AIR POLLUTION AND THE ECOLOGY OF PLANTS

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ABSTRACT

The pollution of air by gases and particulates is having an increasingly harmful effect on organisms throughout the world, particularly in the vicinity of industrialized and urbanized aras. Natural ecosystems are being subjected to pollution stress, and the effects of acid rain and higher carbon dioxide levels associated with air pollution may be of global significance in reducing productivity and modifying ecosystems.

Some of the major air pollutants are sulfur dioxide, ozone, peroxyacetyl nitrate, oxides of nitrogen, fluoride, and particulates. Carbon dioxide may also be considered a pollutant because of the potential effects of increasing atmospheric concentrations on climate. Various patterns of visible damage to plants may result from acute toxicity at high levels of pollutants, whereas chronic symptoms produced by low concentrations over long periods may involve reduced metabolic activity and growth.

Specific symptoms of individual pollutants have been identified in various plants, and lichens and mosses have been found to be particularly sensitive. Sensitive species can be utilized as indicators of pollution to establish whether and where harmful levels are reaching alpine regions of Colorado, and what the effects are likely to be on the productivity and species composition of alpine plant communities.

INTRODUCTION

"Air pollution" generally refers to the atmospheric accumulation of gases or particulate matter above natural levels to the extent that they harm living things and damage materials utilized by man (Nash, 1973a). In this present discussion the reference will be to substances that are detrimental to the growth and development of plants (bacteria, fungi, lichens, algae, bryophytes, and vascular plants) and thus ultimately affect their survival and general ecological relations. Although the effects of pollutants will be considered in general terms, the potential relations of these substances to the alpine plants of Colorado will be emphasized.

It is highly probable that urbanization in the Front Range Corridor of Colorado extending along the base of the Rocky Mountains, roughly from Fort Collins to Pueblo, and its concomitant effects on air pollution will increase in the immediate future. No doubt the pollution will be significant to alpine regions, since some of the alpine areas lie about 30 km from this corridor in which the population is expected to double within a few years. The air pollution associated with local population growth has been observed to extend toward the Continental Divide on occasion for a number of years, and undoubtedly pollution has been increasing in frequency of occurrence and will continue to increase.

Acid precipitation in Colorado was first reported by Lewis and Grant (1980) at the Mountain Research Station of the University of Colorado, about 600 m below timberline. Their study, which began in 1975 on nutrient cycling in a mountain watershed, produced data showing a downward trend in the pH of precipitation from an average of 5.43 to 4.63 over a 3-yr period. This was the first indication that the Front Range of the Colorado Rocky Mountains was being subjected to acid precipitation. Since June 1978 a number of studies directly concerned with air quality on Niwot Ridge and in the vicinity of the Mountain Research Station have been initiated by researchers from the Aeronomy Laboratory of the National Oceanic and Atmospheric Administration, Boulder; Colorado College, Colorado Springs; the Cooperative Institute for Research in Environmental Sciences, Boulder; the Ford Motor Company; Metropolitan State College, Denver; the National Center for Atmospheric Research, Boulder; the University of Colorado Chemistry Department; and the University of Michigan Chemistry Department (see article on "Air Quality and Surface Energy Budget" by D.E. Greenland in this volume. These studies show large fluctuations in concentrations of pollutants. Nitrogen oxides range from below 100 parts per trillion to 20 parts per billion, ozone levels range from 10 parts per billion to 120 parts per billion, and carbon monoxide from 150 parts per billion to 500 parts per billion. Average pH measurements of 4.7 for snow and 4.3 for rain have been determined (Fehsenfeld, 1981), with the normal pH considered to be around 5.7.

There are not enough data to show with certainty what the sources of alpine pollution are, but it is assumed that upslope winds bring pollutants from the Front Range Corridor (Kelly and Stedman, 1980). Vimont and Grant (1981) have studied acid precipitation at various mountain sites in Colorado. They have found, at a location slightly to the north of Niwot Ridge, that there is a precipitation maximum during air flow from the east, which would carry pollutants from urbanized areas. It is possible that pollution might also come from areas farther to the west (Lewis and Grant, 1980). The prevailing winds of the region are from the northwest, especially during the winter months, and rapidly increasing population on the Western Slope of the Rockies and increasing industrialization of the area will certainly provide new sources of air pollution. Development of the oil-shale industry in western Colorado in Garfield, Rio Blanco, and Mesa counties and the increased use of coal-fired power plants upwind from alpine areas, coupled with proposed reductions in air quality standards, will inevitably lead to increased concentrations of pollutants in alpine regions of the state. The establishment of a standard monitoring station by the National Atmospheric Deposition Program in the Niwot Ridge area will provide information directly relating to the alpine tundra (D.E. Greenland, "Air Quality and Surface Energy Budget" in this volume).

AIR POLLUTION AS A REGIONAL AND WORLD-WIDE PHENOMENON

A voluminous literature on the effects of air pollutants on plants has accumulated since the beginning of the century and particularly in the last decade (Ferry et al., 1973; Naegele, 1973; Mudd and Kozlowski, 1975; Mansfield, 1976; Hutchinson and Havas, 1980), as the association of urbanization and industrialization with injury to plants has become evident. The earlier reports were concerned with "smoke" (for example, Haselhoff and Lindau, 1903) and industrial effluents (Stoklasa, 1923; Hill and Thomas, 1933). More recent concern developed in good part from the widespread effects of so-called "smog" in the Los Angeles Basin after World War II (Middleton et al., 1950) and the resulting attention to the nature and origin of the phytotoxic constituents of air pollution. Concern also has developed in Europe over the long-distance migration of air pollutants from heavily industrialized areas such as the Ruhr Valley of Germany to Scandinavia and elsewhere (Bolin, 1971) and from the eastern United States into Canada. A world-wide trend toward building taller smoke stacks to reduce local levels of air pollution has contributed to changing the pollution problem from a local to a regional one, or perhaps even to a global one.

The relation of air pollution to acid rain and its effects on land and water ecosystems has received increasing attention in recent years (Likens and Bormann, 1974; Likens et al., 1979; Hutchinson and Havas, 1980; Patrick et al., 1981). Cowling and Linthurst (1981) have presented a review concerning present knowledge about acid precipitation and its ecological effects. Deposition of acid in rain and snow in Europe, in general, reflects long-distance transport of air pollutants from the sources of emission. Regions which have been recently glaciated, have highly siliceous bedrock, or have thin soils low in buffering and cation-exchange capacity are especially sensitive to acid precipitation (Cowling and Linthurst, 1981). The Rocky Mountains are included in these regions (Likens et al., 1979).

THE NATURE OF AIR POLLUTANTS

Air-borne pollutants have increased both in amount and complexity in the last few decades. Improved analytic techniques and the determination of dose-response relationships between various substances and plants has shown the most important phytotoxic ones to be sulfur dioxide, hydrogen fluoride, ozone, nitrogen oxides, and peroxyacetyl nitrate (Treshow, 1970). Lesser pollutants are ethylene, ammonia, chlorine, and particulates. Particulates may be "dusts" containing arsenic, cadmium, copper, fluorides, iron, lead, nickel, and zinc compounds (Vandergrift et al., 1971).

Acid sols derived from sulfur dioxide, nitrogen oxides, and chlorine may result in acidification of soils (Likens and Bormann, 1974). Carbon dioxide also should be included in the definition given at the beginning of this review in that it apparently is accumulating above natural levels in the atmosphere because of increasing combustion of fuels and has the potential for drastically influencing living organisms (Dixon and Lodge, 1965).

THE EFFECTS OF SOME OF THE MAJOR AIR POLLUTANTS ON PLANTS

Acute and Chronic Symptoms of Injury

Injury to plants by air pollutants may become acute when concentrations are high, leading to various patterns of visible damage such as the death (necrosis) of areas of leaf tissue, yellowing of green tissue (chlorosis), premature leafdrop, and excessive blossom or fruit-drop among vascular plants. Necrotic lesions result from disruption of cell membrane permeability and leakage of cell contents into intercellular spaces, followed by collapse of affected tissue (Taylor, 1973).

Chronic symptoms caused by low concentrations of pollutants over long periods of time may not lead to readily recognizable physical symptoms but rather to reduction of metabolic activities such as photosynthesis and respiration. Changes in growth rate, reduction in leaf area and stem length, faster aging of foliage, and a reduction in total dry weight may also result. There may be a delay in floral initiation and in flower production, as well as an inability to fruit and set seed (Feder, 1973). Altered growth rates, reduced size, and changes in reproductive capacity usually can be detected only by comparison with plants growing under nonpolluted conditions. The lack of readily visible effects of low pollutant concentration has led to the use of the expression "hidden injury" (Stoklasa, 1923). McCune et al. (1967), after considering the history of the concept of hidden injury, conclude that the expression is inadequate and should be abandoned.

Sulfur Dioxide

Sulfur dioxide in small amounts is a natural component of the atmosphere, since biological oxidation of sulfides is a universal phenomenon. Toxic concentrations of this substance, however, have appeared with the growth of large cities, increasing industrial development, and increasing combustion of sulfur-containing coal and petroleum products by vehicles, industries, power plants, and home heating units. Sulfur dioxide dissolves in water of the air and water of various surfaces (Terraglio and Mangenelli, 1967), or it may be oxidized to sulfur trioxide and finally to sulfuric acid (Treshow, 1970). The acid may be washed from the atmosphere by precipitation, may be neutralized by reacting with various compounds in the air, or may be removed by gravity. Its persistence in the air depends upon the amount of precipitation and the reactivity of other atmospheric components.

In vascular plants, gas enters through stomata, and cell injury becomes apparent when concentrations rise sufficiently high to initiate shrinking and collapse of mesophyll cells, as in experimentally treated alfalfa (Katz et al., 1939; Katz, 1952). In treated bean plants the mesophyll cells near the lower epidermis are damaged first. Chloroplasts disintegrate, cells become plasomolyzed, and the protoplasts collapse (Solberg and Adams, 1956). Acute macroscopic injury is characterized by rapid disappearance of chlorophyll, breakdown of cells, and development of necrosis, followed by general growth suppression (Treshow, 1970). Conditions which favor open stomata predispose the plant to injury from sulfur dioxide. Under conditions of water stress, stomata close and thereby protect the plant (Mudd, 1975). Guderian and Schönbeck (1971) found a distinct diurnal pattern of sulfur dioxide accumulation in plants, the concentration being highest in the late morning. Their studies indicated the degree of injury is dependent on the stage of development of the plant.

Gases also can enter the plant through the cuticle, and, while stomatal uptake is important, cuticular uptake has been found to account for more than half the sulfur dioxide absorbed by cereal plants (Fowler, 1980). Since cuticular surfaces can be eroded by acid rain (Jacobson, 1980), uptake of sulfur dioxide may be increased.

Lichens have been recognized as being particularly sensitive to air pollution since 1859 (James, 1973a), and especially to sulfur dioxide, but it was not until 1941 that lichen distribution was correlated with sulfur dioxide levels (Hawksworth, 1973). Lichens may be especially sensitive to pollution because they are symbiotic organisms, and only if the delicate balance between the fungal and algal components is maintained will the relationship be successful (Nieboer et al., 1976). Laboratory studies in which a variety of lichen species was exposed to sulfur dioxide fumigation have generally shown a reduction in rates of photosynthesis and/or respiration (Showman, 1972; Richardson and Puckett,1973; Baddeley et al., 1973; Nieboer et al., 1976; Beekley and Hoffman, 1981). Studies of sulfur dioxide fumigation effects on chlorophyll destruction in lichens have given conflicting results. Nash (1973b) reported breakdown of chlorophyll by conversion to phaeophytins, while Beekley and Hoffman (1981) reported no phaeophytinization. Beekley and Hoffman (1981) suggest that different lichen species and sulfur dioxide concentrations used in the two studies may explain the contrast in results. While sulfur dioxide is generally considered to have an inhibitory effect on lichens, it has been shown to have a stimulatory effect at very low concentrations (Sheridan et al., 1976). The possibility of stimulation must be considered for all groups of plants and for all types of pollutants.

The lichen *Parmelia caperata* showed significant reduction in chlorophyll on exposure to 50 parts per hundred million of sulfur dioxide and complete destruction at 200 to 400 parts per hundred million during short-term fumigation experiments (Nash, 1973b). The highest hourly concentration of sulfur dioxide in New York City recorded from 1957 to 1968 was 230 parts per hundred million, and the highest 24-h average was 90 parts per hundred million, indicating that *Parmelia caperata* would not survive in New York City (Nash, 1973b). Gilbert, in his study in Newcastle-upon-Tyne (Great Britain), noted that most bryophytes did not survive when average winter concentrations of sulfur dioxide exceeded 1.7 parts per hundred million (LeBlanc and Rao, 1975).

Bryophytes are apparently as sensitive to air pollution as lichens, and both are typically absent from urban and industrial centers (LeBlanc, 1961; Rao and LeBlanc, 1967; Skye, 1968; Gilbert, 1970; Nash and Nash, 1974). Limited attention has been given to the effects of air pollution on fungi, bacteria, and viruses. However, since sulfurdioxide has been used for a long time as a fumigant to control pathogenic fungi and bacteria, its effects on these organisms are fairly well recognized. What is not well understood is the interaction between pathogens and plants damaged by air pollution. Pathogens are important in the ecology of plant communities, and factors influencing pathogens will influence the communities (Treshow, 1975). An increase in the deposition of sulfur compounds leads to an increase in acidification of soils. The number of beneficial soil bacteria may be reduced, and a relative increase in the abundance of fungi, attributed to reduced competition, may take place (Alexander, 1980).

Ozone

Beginning with Richards et al. in 1958, ozone damage has been described for many ornamental and agronomic crops (Treshow, 1970). Combustion processes, particularly those of automobile engines, result in the emission of various oxides of nitrogen, mostly nitrogen dioxide. The action of light on nitrogen dioxide results in a splitting of the molecule into nitrogen monoxide and atomic oxygen; the latter combines with molecular oxygen of the atmosphere to form ozone (Shuck, 1973). A normal ozone level exists in the "unpolluted" atmosphere, but phytotoxic concentrations develop in the atmosphere of large urban centers, such as that along the Colorado Front Range.

Ozone probably causes more damage to vegetation than any other pollutant in the United States, and two or more hours of exposure to 10 parts per hundred million may cause acute injury to very sensitive plants (Taylor, 1973). Ozone, as well as sulfur dioxide, enters higher plants though the stomata, although guard cells quickly close upon exposure. The structure and permeability of cell membranes in leaves are immediately disrupted, and metabolic activities are affected by this strong oxidant. Even low concentrations result in drastic reductions in photosynthesis and transpiration (Hill and Littlefield, 1969), with an increase in the rate of respiration. Cessation of growth, senescence, and leaf abscission follow. Necrotic flecking appears on the upper leaf surfaces of sensitive plants, and histological examination shows damage similar to that caused by sulfur dioxide.

Ozone is not as toxic to fungi as is sulfur dioxide. Furthermore, only certain stages of the fungal life cycle are sensitive, and since various stages occur at the same time within a population, only a small portion may be susceptible during an acute exposure period, leaving a major portion of the population unaffected (Treshow, 1975). In legumes, root nodules containing the bacterium *Rhizobium* decrease in number, size, and weight when treated with ozone (Treshow, 1975).

Exposure of a cultivar of tobacco to 15 parts per hundred million of ozone for 1 h resulted in flecking in leaves (Heath, 1975). Growth of tomato plants for 45 d in ozone levels of 8 to 10 parts per hundred million resulted in decreased plant height, internode length, and dry weight (Manning and Feder, 1976). In the Los Angeles Basin, ozone levels on a slightly smoggy day average 10 to 20 parts per hundred million, with levels reaching 50 to 80 parts per hundred million on very smoggy days (Heath, 1975).

Peroxyacetyl Nitrate (PAN)

Another photochemical oxidant, PAN, a constituent of "smog," is a reaction product of ozone and unsaturated hydrocarbons in the presence of sunlight (Haagen-Smit et al., 1952). Mixtures of ozone, olefin (hydrocarbon), and nitrogen oxides result in the formation of a group of related compounds, of which PAN is a principal constituent (Darley et al., 1959, 1966), and fumigation studies have established the importance of these compounds as phytotoxic photochemical oxidants. In higher plants, PAN injury is characterized by glazing or bronzing of the lower epidermis of leaves, a chlorotic stippling, or (in monocots) the occurrence of transverse banding (Taylor, 1969; Taylor and MacLean, 1970). Chloroplasts are injured by PAN, and so photosynthesis and growth are quickly inhibited by this pollutant (Thomson et al., 1965).

Nitrogen Oxides

Nitrogen oxides (NO, NO_2, N_2O_4) are the products of combustion at high temperatures in the presence of nitrogen, so the motor vehicles and all types of heating apparatuses associated with urban development are prominent sources of these pollutants. Nitrogen oxides have been found to cause two main symptoms of injury in vascular plants: collapsed, light-colored lesions between the veins; and a glossy sheen on leaf surfaces (Benedict and Breen, 1955). Necrotic lesions coupled with growth suppression have been noted at lower concentrations (Taylor and Eaton, 1966). Extremely high doses of nitrogen dioxide for a few minutes may stimulate leaf drop without any sign of necrosis or chlorosis (Taylor, 1973). Nitrogen dioxide in fumigation experiments causes a truction of chlorophyll in lichens, with resulting effects on photosynthesis (Nash, 1976), and there may be synergistic effects with sulfur dioxide (Taylor et al., 1975; Nash, 1976). Nitrogen oxides converted to acid in precipitation can have positive effects on plants as well as negative ones, since nitrogen is required for the synthesis of proteins and nucleic acids (Cowling and Linthurst, 1981). Nitric acid from automobile pollution is the major component of acid precipitation along the west coast of the United States (Cowling and Linthurst, 1981) and along the Front Range in Colorado (Lewis and Grant, 1980). On the other hand, sulfuric acid is the major component of acidity along the east coast, where industrial and power plant emissions are the main contributors.

Two fumigations with nitrogen oxide at concentrations of 400 parts per hundred million for 6 h were sufficient to cause acute injury (chlorosis) in the lichens *Lecanora chrysoleuca* and *Usnea cavernosa* (Nash, 1976). Navel oranges showed increased leaf drop and reduced yield after being exposed to concentrations of 25 parts per hundred million or less of nitrogen dioxide continuously for 8 mon (Taylor et al., 1975). Concentrations of nitrogen oxides as high as 300 parts per hundred million have been measured in air in the Los Angeles Basin, but levels seldom exceed 100 parts per million; thus acute injuries from nitrogen dioxide may not be of great concern. However, it has been found in fumigation experiments that when nitrogen dioxide and sulfur dioxide are used in combination, injuries result which are absent if either pollutant is used alone (Nash, 1976).

Fluoride

Fluoride is abundant in the earth's crust in aluminum ores, and heating these in refining processes leads to at least localized pollution (Treshow, 1970). Fluoride entering by way of stomata in vascular plants accumulates at the tips and margins of leaves, and chlorosis and necrosis develop in these areas (Zimmerman and Hitchcock, 1956; Adams et al., 1963; McCune et al., 1964; Treshow and Pack, 1970). Lichens and mosses, as well as higher plants, are injured by fluoride. Mild chlorosis to severe browning of leaves, as well as a decrease in sporophyte production, was observed in the moss *Polytrichum commune* (Roberts et al., 1979). Bleaching or chlorosis followed by necrosis have been reported by Gilbert (1973) in the lichens *Parmelia saxatilis*, *Parmelia sulcata*, and *Xanthoria parietina*.

Particulates

Particulate pollutants may be transported at least 5000 km to contribute to the formation of haze in the arctic atmosphere (Kerr, 1981), so transport to alpine regions of the United States is clearly likely. Fly ash and other substances apparently derived from coal-burning power plants of industrial areas of the worlds are constituents of such haze. Trace elements, including arsenic, manganese, lead, zinc, selenium, and others potentially toxic to plants are associated with fly-ash particles (Linton et al., 1976; Gutenmann et al., 1976; Nash and Sommerfeld, 1981).

Particulate matter may be directly injurious to plants by screening light on plant surfaces, by plugging stomatal openings, or by direct chemical reaction with plant tissue. Indirectly, particulates may affect plants by changing soil pH and by increasing susceptibility to infection by pathogens or to insect predation (Lerman and Darley, 1975).

Lichens and bryophytes are considered to be better indicators of particulate fallout than deciduous plants for several reasons: (1) they have perennially exposed plant bodies, (2) absorb water and nutrients effectively from the air, (3) have large surface-area-to-weight ratios, (4) and have an unusual capacity to concentrate air-borne and water-soluble material in their bodies (Rao et al., 1977). Epiphytic lichens and bryophytes, which have no access to the soil, are useful for monitoring particulate fallout, since the levels of particulates accumulated in them reflect aerial particulate concentrations (Clough, 1975).

Carbon Dioxide

Retorting of carbonate minerals and organic matter in oil shales of Colorado, Utah, and Wyoming and burning of the oil produced may have particularly important climatic consequences. These processes could release one-and-one-half to five times more carbon dioxide than the burning of presently available oil for the same amount of usable energy (Sundquist and Miller, 1980). Precipitation patterns in North America may change as a result of increasing atmospheric carbon dioxide (Hansen et al., 1981). A decrease in antarctic summer pack-ice between 1973 and 1980, although agreeing with predicted impacts of increase of carbon dioxide on global temperatures, may possibly be explained by natural climatic variation due to other causes (Kukla and Gavin, 1981).

Injury, whether the result of acute, high levels of pollution or low levels over long periods of time, can result in alterations in composition of a plant community through changes in patterns of distribution and abundance of sensitive species (Will-Wolf, 1980a, 1980b) or or through death of sensitive species (Heck, 1973). Even if high levels of pollutants are reduced through source-control methods, it appears that low levels over long periods of time will have a significant impact on plant communities.

SPECIES SENSITIVITY AND INDICATORS OF POLLUTION

Plant species vary widely in sensitivity to air pollution. Lichens have been considered to be particularly sensitive, and their distribution in relation to pollution sources and their reactions to pollutants in laboratory studies have been emphasized (Skye, 1965, 1968, 1979; Ferry et al., 1973; Nash 1973b, 1976). Some lichens are highly sensitive, whereas others are quite insensitive and have replaced the sensitive species in areas of high pollution (Hawksworth and Rose, 1970; Hawksworth et al., 1973, 1974).

Bryophytes are recognized as reliable indicators of air pollution. LeBlanc and Rao (1975: 239) state, "It is now recognized that despite wide differences in their botanical affinity, lichens and bryophytes are outstandingly similar in their response to air pollution and that certain species, especially the epiphytic ones, can be reliable pollution indicators. In fact, they could provide the simplest and most economical tool for assessing an air pollution problem in time and space."

In higher plants, variation in sensitivity to air pollutants has received a good deal of attention on the intraspecific level among plants of economic importance such as tobacco (Heath, 1975; Rich, 1975), white pine (Karnosky, 1981), and tomato and bean (Manning and Feder, 1976). Intraspecific variation in pollution tolerance under natural conditions must be considered, since some of the discrepancies encountered in determining threshold levels of pollution injury or degree of species sensitivity may be related to such variation (Bell and Mudd, 1976).

A great number of species has been tested in the laboratory or studied in the field. Since the primary purpose of this review is to provide a framework for a study of the effects of air pollution on alpine plants in the Colorado Rocky Mountains, the following list of plants is restricted to those which are present or likely to be present in the Niwot Ridge study area. No vascular plants are included, since the major emphasis of pollution studies on higher plants has been with cultivated or ornamental species. Studies on noncultivated species have been done primarily on plants from low altitudes, forested regions, and more humid climates. General results of specific studies are given for each species.

Bryophytes

Amblystegium serpens (Hedw.) B.S.G. var. *juratzkanum* (Schimp.) Rau et Herv.: tolerant to air pollution in urban and suburban sites (Stringer and Stringer, 1974).

Ceratodon purpureus (Hedw.) Brid.: not a good indicator of heavy metal pollution, probably because it has small leaf surfaces and thick-walled cells (Rejment-Grochowska, 1976).

Hylocomnium splendens (Hedw.) B.S.G.: great capacity to absorb heavy metals (Tyler, 1971).

Hypnum cupressiforme (Hedw.): used in industrial areas of Wales to measure airborne heavy metals, but results only semiquantitative (Rao et al., 1977).

Marchantia polymorpha L.: lead-tolerant strains found in Glasgow, Scotland. (Bradshaw, 1976).

Pohlia nutans (Hedw.) Lindb.: tolerant to nickel (Nash, 1973a).

Polytrichum juniperinum Willd. ex Hedw.: good indicator of heavy metals (Rejment-Grochowska, 1976).

Polytrichum piliferum Hedw.: good indicator of heavy metals (Rejment-Grochowska, 1976).

Tortula ruralis (Hedw.) Gaertn., Meyer et Scherb.: reduced photosynthesis resulted largely from acid hydrolysis of chlorophyll *a* as a result of subjection to simulated acid rain (Sheridan and Rosenstreter, 1973).

Lichens

Buellia punctata (Hoffm.) Mass.: semitolerant to sulfur dioxide levels of 3.2 to 3.9 parts per hundred million (Johnsen and Søchting, 1973).

Cetraria cucullata (Bell.) Ach.: exposure to in situ sulfur dioxide fumigation for a little over one month resulted in a reduction in photosynthesis and chlorophyll content (Moser et al., 1980).

Cetraria nivalis (L.) Ach.: injured when exposed to aqueous sulfur dioxide at 225 parts per million for ten minutes (Nieboer et al., 1976).

Lecanora chrysoleuca (Sm.) Ach.: total chlorophyll destruction after fumigation with 400 parts per hundred million nitrogen dioxide for six hours (Nash, 1976).

Peltigera aphthosa (L.) Willd.: not very sensitive to aqueous sulfur dioxide at 225 parts per million for ten minutes (Nieboer et al., 1976).

FACTORS AFFECTING RESPONSE TO POLLUTION

The degree of sensitivity of plant species can be affected by either environmental or biological (genetic) factors:

Environmental factors

(1) Particulate deposition has been found to double with a doubling of wind speed (Puckett and Finegan, 1980), and the degree of exposure to wind thus may determine whether a plant will be able to survive. Plants growing in rock crevices or depressions, protected by other vegetation, or located leeward of large objects will be less exposed to pollutant-carrying winds, enabling sensitive species to survive in sheltered niches within polluted areas. LeBlanc and Rao (1975) refer to these species as pollution evaders rather than pollution tolerаters.

(2) Snow cover, which protects plants from cold and drought, also protects them from pollutants. However, this wintertime protection may be offset by exposure to sudden, high levels of pollutants when snow melts (Havas and Huttunen, 1980). Laboratory and field experiments have shown that 50 to 80% of the pollutants is released when the first 30% of the snow melts, and concentrations may be five to ten times higher than the concentrations in bulk snow (Gjessing, 1977; Seip, 1980).

(3) The presence of moisture (snow, rain, dew, or mist), and thus whether pollutants are deposited in dry or wet form, may determine how rapidly pollutants are absorbed by a plant. Wind-tunnel experiments have shown that wet deposition of sulfur dioxide results in more rapid absorption by leaves than dry deposition (Horntvedt et al., 1981). Some lichens are insensitive to sulfur dioxide when they are dry (Nash, 1973b; LeBlanc and Rao, 1975; Nieboer et al., 1976), which may explain why lichens in drier, more continental climates appear to be relatively unaffected by sulfur dioxide (Marsh and Nash, 1979).

(4) The buffering capacity of the substrate is important. Species found on naturally acidic substrates are usually more sensitive to sulfur dioxide pollution than those found on basic substrates because of buffering by the latter (LeBlanc and Rao, 1975). Some plant species have narrow pH tolerances, and slight changes in pH may be deleterious.

(5) Nutrients which stimulate growth nitrogen and sulfur, for example) may be added to the substrate by air pollution (Cowling and Linthurst, 1981).

(6) Acidification of the substrate increases weathering rates of minerals and also increases

leaching of exchangeable plant nutrients and toxic metal cations (Cowling and Linthurst, 1981).

Biological Factors

(1) The symbiotic relationship between algae and fungi in lichens appears to make lichens especially responsive to pollution (Nieboer et al., 1976), but this does not necessarily mean that all lichens are equally responsive or are more sensitive than other species of plants.

(2) Evergreen plants may be better indicators of pollution than deciduous ones, since evergreens may be chronically exposed to pollution throughout the year.

(3) Plants with highly divided surfaces have greater exposure to air pollutants than compact plants (LeBlanc and Rao, 1975; Rao et al., 1977).

(4) Species with cuticle or protective coatings are less vulnerable to pollutants than those without such features (Rao et al., 1977).

(5) Epiphytic plants may be more exposed to the air and so are subjected to greater amounts of pollutants than are plants growing on soil.

(6) Plant hairs, lichen cilia, pits, and rough or sticky surfaces trap pollutants more effectively than is the case in plants with smooth surfaces, and thus plants with these characteristics appear to be more sensitive (LeBlanc and Rao, 1975; Jacobson, 1980; Rao et al., 1977).

(7) Relatively high internal pH in a plant helps to reduce the toxic effects of acids (LeBlanc and Rao, 1975) because of neutralization of acids derived from pollutants.

(8) The stage of development of plants at the time of exposure to pollutants may affect the degree of sensitivity. Ascospore germination of some lichen species in inhibited by metal salts (Pyatt, 1976), and pollution by copper and zinc reduces spore germination in the moss *Funaria* and gemmaling growth in the liverwort *Marchantia* (Coombes and Lepp, 1974). Leaves exposed to acid rain are most susceptible to lesion formation just before or during enlargement (Jacobson, 1980).

(9) A high degree of tolerance to large accumulations of metallic ions in certain lichens enables them to occupy areas with high levels of metal pollution (James, 1973b; Nash and Sommerfeld, 1980). It is thought the ions are bound in the cell walls, where they have little or no effect on cell metabolism (Farrar, 1973).

ECOLOGICAL IMPLICATIONS OF AIR POLLUTION

Effects on Primary Productivity

It is quite clear that inasmuch as high pollutant concentrations produce rapid, acute effects on leaves, primary production is drastically affected. Pollutants penetrate the intercellular spaces through the stomata in higher plants and then move with the apoplastic water towards the epidermal region. Changes in osmotic potential induced by pollutants create water imbalances and cause closure of stomata, resulting in the inhibition of photosynthesis (Heath, 1980). Increased levels of visible injury are correlated with the degree of opening of stomata (Runeckles, 1974; Runeckles and Rosen, 1974, 1977). The "hidden injury" caused by low but chronic pollutant concentrations (discussed in "Acute and Chronic Symptoms of Injury," this article) is basically a destruction of chlorophyll and loss of productivity (Dugger and Ting, 1970).

Examples of reduced productivity caused by air pollution are numerous among crop plants. A decrease in yield accompanied by a reduction in chlorophyll content of almost 50% was noted in grapes exposed to naturally occurring smog for 14 wk (Feder, 1973). Avocado seedlings exposed to synthetic smog for 8 wk showed 35% reduction in leaf area, 56% reduction in stem weight, 65% reduction in root volume, and also root-weight reduction. Stunting and death of large numbers of trees have been documented in highly polluted areas throughout the world. Studies in northern Finland show that a narrowing of annual growth rings occurs for up to 10 yr preceding the death of trees near industrial areas (Havas and Huttunen, 1980). Reductions in growth rates of lichens exposed to air pollution are difficult to measure, since they grow very slowly (Farrar, 1973; Hale, 1973) and do not grow uniformly throughout life (Beschel, 1973; Hale, 1973; Armstrong, 1974).

Effects on Species Composition of Communities and Ecosystems

Reduced productivity or vigor in a pollution-sensitive species can lead to its elimination because of inability to tolerate pollution, or it can result in its elimination because of the inability to compete with resistant species. In either event, death of a species or of many species leads to a change in community structure (Heck, 1973).

Pollutant-induced community change has been documented in southern California in ponderosa pine/sugar pine/white fir forest exposed to chronic air pollution (Miller, 1973). The pollutants apparently eliminate ponderosa pines from the forest and cause reduction of photosynthetic activity and suppression of growth in the other tree species, and there may be an increased incidence of attack by bark beetles on affected ponderosa pines. The successional trends as ponderosa pines decline in numbers will probably favor the development of shrubs and other more tolerant species (Miller, 1973).

Prolonged exposure to high concentrations of sulfur dioxide in the Copper Basin area of

Tennessee led to the destruction of thousands of acres of native deciduous forest and its replacement by grassland vegetation (Hursh, 1948). Soils were eroded, and ultimately the climate of the area was altered. Gordon and Gorham (1963) reported a marked reduction in the number of species within 15 km of a sulfur dioxide source, with trees replaced by shrubs and low-growing vegetation. Guderian (1967) has shown that population changes occur under conditions of controlled fumigation, with sensitive species being replaced.

Rose and Wallace (1974) list the epiphytic bryophytes that have diminished in Britain, probably as a result of air pollution. The moss Bryum argenteum appears to have adapted well to urbanization and to be almost immune to sulfur dioxide pollution, however, and various bryophytes are invading polluted areas.

Studies of changes in lichen communities in Britain (Hawksworth et al., 1974) showed that in regions with high sulfur dioxide levels in winter about 90 species of corticolous (bark) lichens had disappeared or become rare, while only two species (Parmeliopsis ambigua and Lecanora conizaeoides) had increased. A reduction in luxuriance and fertility was noted in areas of high pollution levels. Species growing on siliceous rocks with low buffering capacity showed the same trends as the corticolous communities, while species growing on calcareous rocks were affected to a lesser degree.

As discussed previously, an important aspect of air pollution is its relation to acid precipitation (Likens and Bormann, 1974; Lewis and Grant, 1980). Strong acids are derived from sulfur dioxide (sulfuric acid), from nitrogen oxides (nitric acid), and from chloride (hydrochloric acid), and pH values as low as 2.1 have been observed in rain and snow in the northeastern United States. The addition of acid to soil causes increased leaching of minerals. Acid rain on foliage can also lead to an increased loss of minerals and other substances directly from plants, since plants are leaky systems (Barbour, 1973).

There is concern about global increase in the atmospheric concentration of carbon dioxide from the burning of fossil fuels, as discussed in "The Effects of Some of the Major Air Pollutants on Plants" in this article. Carbon dioxide may be considered a "pollutant" in that the possibility of gradually increasing concentrations having harmful affects on vegetation exists. One potential influence derives from the so-called "greenhouse effect" resulting in increasing temperatures on the surface of the earth. Temperature change may alter the physiological activities of various species and ultimately result in changes in community structure.

Increased carbon dioxide concentration also may affect plant growth and community structure through increased rates of photosynthesis, increased branching, greater stem elongation, increased leaf area in seedlings, and changes in time of flowering (Kramer, 1981). Stomatal conductivity of some plants is reduced by increased carbon dioxide concentration, and photosynthesis per unit of leaf area may decrease in some species. Increase in carbon dioxide "will probably have least effect on growth of plants in closed stands where light, water, and mineral nutrition, separately or collectively, already are limiting the rate of photosynthesis" (Kramer, 1981: 32). Differences in responses of C_3 and C_4 plants, and of determinate and indeterminate plants, may affect species composition in some ecosystems (Patterson and Flint, 1980).

NEEDED RESEARCH AND CONCLUSIONS

Virtually no research has been done on the influence of air pollutants on alpine plants, probably because the alpine areas of the world have been fairly isolated from sources of pollution until relatively recent times. With the increasing extent of areas affected, however, and with the increasing amount of pollutants entering the atmosphere close to alpine regions, such as those of the mountain ranges of Colorado, alpine plants will be likely to suffer injury. "Hidden" effects on primary productivity will presumably appear first, with visible damage, particularly to sensitive species that may serve as indicators, becoming evident as concentrations increase. Many lichens and bryophytes have been shown to be particularly sensitive to various pollutants, and since these plants are prominent in the alpine ecosystem, some of them may serve as "indicator species" in the Indian Peaks area of Colorado.

The choice of species to be studied for their potential use as pollution indicators should be based on their biological characteristics as well as the habitat they occupy. Biological characteristics that need to be considered include the number and location of stomata on leaves of vascular plants; the presence or absence of cuticle, protective waxy coatings, or nonwetting body surfaces; the texture of body surfaces; and whether the plant body is compact or finely divided. Species from areas exposed to wind and from sheltered areas, from wet and dry areas, and from snow-covered and snow-free areas should be represented.

Laboratory research on the effects of various concentrations of pollutants on germination, establishment of young plants, primary production, and reproduction in alpine plants is needed. Studies should be undertaken to determine the relationships of pollution to the composition of the soil flora and fauna and also to the physical properties of the soil. Analysis of soil pH and buffering capacity should be conducted in relation to a study of the pH of precipitation and meltwater.

Species determined to be sensitive indicators of pollution and species which are tolerant to pollution should be monitored in the field for vigor, reproduction, and survival. Finally, change in community composition which may be attributed to pollution needs thorough investigation.

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SMALL MAMMAL HERBIVORES
OF THE COLORADO ALPINE TUNDRA

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ABSTRACT

This paper reviews published and current studies on the small mammal herbivores of alpine tundra, as background for long-term ecological research at the Mountain Research Station of The University of Colorado. Many detailed studies of the arctic tundra mammalian community exist, but the ecologically more diverse alpine tundra has received scant attention. The origin and history, since the beginning of the present interglacial, of Colorado alpine mammals is reviewed. The history of mammal research on Niwot Ridge is summarized. Papers by Williams, Paddock, Quick, Krear, Osburn, Enger, Horn, Pattie, Thorn, and Burns, and Halfpenny are included. A picture of the community and population ecology of alpine tundra small mammalian herbivores is developed. Topics covered include community composition, habitat preference, biomass and secondary productivity, species density, home range and territoriality, and life-history traits.

INTRODUCTION

Alpine tundra has ecosystem properties which afford outstanding opportunities for the study of herbivore populations. These properties include: (1) a relatively simple trophic structure with short, direct food chains, (2) closely coupled relationships between primary production and herbivore consumption, (3) a high degree of dependence on a limited resource base, resulting in herbivore populations of maximum efficiency, (4) direct linkages between weather, snowpack, primary production, and herbivore ecology, (5) relatively observable interspecific relationships within the herbivore community, and (6) rather close and precise niche separation of herbivore species.

Because of these and related ecological properties, the tundra environment affords unique opportunities to study the population and community ecology of herbivores, and also long-term ecological impacts of environmental perturbation.

Alpine tundra has a surprising abundance and diversity of mammals. Of the 32 species of mammals observed on Niwot Ridge, approximately 20 are herbivores, and of these 12 are small herbivores, ranging in size from mice and voles to marmots. The small mammal herbivore community at Niwot Ridge includes two species of mice (Peromyscus maniculatus and Zapus princeps), bushy-tailed woodrat (Neotoma cinerea), four voles (Microtus montanus, M. longicaudus, Phenacomys intermedius, and Clethronomys gapperi), least chipmunk (Eutamias mimus), golden-mantled ground squirrel (Spermophilus lateralis), northern pocket gopher (Thomomys talpoides), pika (Ochotona princeps), yellow-bellied marmot (Marmota flaviventris), snowshoe hare (Lepus americana), and porcupine (Erithizon dorsatum). At any one site, usually seven or eight of these species may be present. The hares, and porcupines are transients.

Niwot Ridge has a substantially greater diversity of mammalian herbivores than a comparable area of arctic tundra, where usually only two to five species of small mammal herbivores may be present -- typically two species of lemmings, the brown lemming (Lemmus sibericus) and the collared lemming (Dicrostonyx torquatus); arctic ground squirrels (Spermophilus parryii); arctic hare (Lepus arcticus); and the tundra vole (Microtus oeconomus). The mammalian community in arctic tundra tends to be strongly dominated by one or two species, usually lemmings or arctic ground squirrels. Both arctic and alpine tundra have large ungulate herbivores such as caribou in the arctic and mule deer, sheep, or elk in the alpine, but these large ungulates are very mobile and only transient in any one locality.

The greater diversity of the mammalian community in alpine tundra may contribute to two important ecological attributes: namely, greater niche differentiation among the mammalian community of alpine tundra and greater stability of the mammalian biomass. Both of these points require further study, however; at this time they cannot be accepted as established facts.

Although mammal communities in the arctic tundra have been studied in detail (Fuller et al., 1977; Batzli et al., 1980), there is a paucity of published papers dealing with the mammals of the alpine tundra. Certain species have been studied in detail, such as the pika, Ochotona princeps and the marmot, Marmota flaviventris (Miller and Zwickel, 1972; Armitage, 1974; Smith, 1974a, 1974b; Johns and Armitage, 1979). Comparable information on other species is lacking. Hoffmann (1974) reviewed the status of knowledge on tundra mammals, both arctic and alpine, and focused on trophic structure within the tundra ecosystem. Brown, L.N. (1971) considered mountains in the southwestern United States as islands and looked at the historical biogeography of the mammalian species found in the alpine of the desert mountains. Findley and Anderson (1956) reviewed the zoogeography of Colorado mountains (see below). Swan (1952) studied Microtus mexicanus at approximately 4600 m in Mexico. These voles represent the highest documented population of mammals in North America. Williams and Finney (1964) briefly analyzed the stomach contents of alpine mice for the presence of Endozone, a phycomycete fungus. Halfpenny (1980) studied population ecology, life histories and reproductive strategies of Peromyscus maniculatus in the Colorado alpine.

HISTORICAL ASPECTS OF THE COLORADO TUNDRA MAMMALS

Findley and Anderson (1956) considered the mammals of the Colorado Mountains to be of recent geologic origin. Most mammals were able to repopulate the Colorado mountains during the late Pleistocene. Later two isolating barriers developed, the Green River and Wyoming Basin. Due to these barriers the fauna of the Colorado mountains is distinct from the rest of the western United States mountains at the subspecies and species levels.

Little is known about the distribution of mammals in the alpine tundra since the close of the Pleistocene. Conditions in the tundra are not favorable for the preservation of fossils. However, Benedict and Olson (1978) have found hunting camps and drive fences in the Colorado tundra near Niwot Ridge. These archaeological sites date from 6000 BP, a time when a substantial drying of the climate may have forced archaic hunters into high mountain areas, where they hunted buffalo and sheep.

There have been major changes in the composition of the tundra fauna since the arrival of the first settlers. Bison (Bison bison) still roamed the tundra when the white settlers arrived although they were exterminated in the late 1800's (Fryxell, 1926, 1928; Warren, 1927; Beidleman, 1955). Beidleman (1955) reported skeletal specimens of bison from the tundra in the Snowy Range in Wyoming and Niwot Ridge in Colorado. Additional unreported bison horns found on Niwot Ridge are housed at the Mountain Research Station Museum.

Both elk (Cervus canadensis) and mountain sheep (Ovis canadensis) were found in the tundra, but with the coming of the gold rush many of these animals were extirpated over large portions of their range. Elks were thought to have been exterminated by the 1920s from the Front Range (Armstrong, 1972). Elks were reintroduced during the early 20th century. Although mountain sheep were present on Niwot Ridge, they now have been extirpated from the area.

Undoubtedly, the extirpation of two large herbivores, the bison and the mountain sheep, has had a dramatic impact on the tundra vegetation. Experiments measuring primary productivity under a grazing regime including bison and sheep are needed in order to fully understand the alpine ecosystem. In recent years domestic sheep have been pastured on Colorado tundra. Although sheep grazing once was common on Niwot Ridge, the grazing allotment was not stocked after 1949 (U.S. Forest Service, Boulder District Office).

HISTORY OF MAMMAL STUDIES OF NIWOT RIDGE

Although the Colorado Front Range tundra provides an attractive region for research in mammalian ecology, few studies have been undertaken in this high-elevation region. May (1980) in his review of the animal ecology of the Rocky Mountain tundra did not list any publications on mammals from the Front Range. Armstrong (1972) listed several studies on individual species, but most were cursory. Several studies have been conducted in the Niwot Ridge region but few have been published. Overall there is a definite lack of research on mammalian ecology in alpine habitats.

The earliest tundra mammal studies on Niwot Ridge were initiated by Mark Paddock in 1960. Paddock established four permanent snap-trap grids on the west end of Niwot Ridge. Lines were trapped three days each August until 1964 but the data were not compiled until 1967 (see Horn below).

Krear (1965) studied pikas on the north side of Niwot Ridge just below timberline. He found that 15 pikas harvested 55% of the available forage (2360 kg/acre) or 76 kg per animal. Predation was considered an insignificant influence on pika although juvenile pika remains were found in coyote scat. Four mammals and eight birds were considered as potential predators. Vocalizations, and daily and seasonal behavior patterns were studied.

The first major mammal ecology study on Niwot Ridge was undertaken by Horace Quick (1966). Quick's project, "The Small Mammal Populations and Ecological Variations in an Alpine Watershed," was part of a large study under William Osburn, (1966). Quick sampled 202 plots in 20 plant communities. Eight of the communities were in the alpine tundra (krummholz, "gopher garden," fellfield, moist meadow, Kobresia dry meadow, solifluction terrace, frost boil ground, and patterned ground).

During the period from 1 June to 15 September 1964, 826 small mammals were trapped in 30,434 trap-nights. Various population and reproductive characteristics were analyzed for the six species caught (P. maniculatus, C. gapperi, M. montanus, P. intermedius, Z. princeps, and S. merriami). The identification of S. merriami is doubtful and the shrews trapped were probably one of the other shrew species which have been recorded in the region. The characteristics analyzed include population density, sex ratio, age class, reproductive status, and weight. The optimum habitat and frequency of occurrence in each habitat were determined. Finally, the yearly turnover in biomass was estimated for P. maniculatus.

Osburn (1966) studied the radioecology of subalpine mammals. His analyses found radioactive contamination in body parts and distribution through several food chains. While predators such as the weasel (*Mustela erminea*) and the bobcat (*Felis rufus*) had radioactivity concentrations of 7.5 and 6.5 picocuries of flesh, respectively grazing animals such as pikas, *Ochotona princeps*, and *Microtus* had concentrations of 78 and 28 picocuries per gram of flesh, respectively. Small mammals were suggested as one of the most radiosensitive groups, because of the direct contact of their fur with contaminated vegetation which they also eat.

The summer of 1967 was very active on Niwot Ridge with the NSF College Teacher Research Participants under Dr. John Marr conducting three mammal studies (Enger, 1967; Horn, 1967; Pattie, 1967). Donald Pattie established a permanent live-trap grid in the Saddle and four snap-trap grids. The live-trap grid was trapped from 22 June to 21 August, 1967. Densities were estimated for *P. maniculatus*, *M. montanus*, *P. intermedius*, and *O. princeps*. Home ranges were calculated and sex ratios recorded.

Horn (1967) re-established Paddock's permanent lines and obtained one more year of data. The data from the 6 years (including that of Paddock) were summarized for four habitats: dry meadow (*Kobresia*), moist meadow (solifluction terrace), mixed community, and willow-sedge. A general decrease in the numbers of *Peromyscus* was noted during the study and it was hypothesized that this was due to increased moisture in the habitats during the study.

A second live-trap grid, which crossed the ecotone east of the Trough, was established by Enger (1967). He mapped the general vegetation pattern on the grid and conducted trapping from 30 June to 19 August, 1967. Enger also established three additional snap-trap lines. Habitat preferences and population densities for *P. maniculatus* and *C. gapperi* were estimated. Population densities of mice and voles ranged from 0.3 to 1.0 per ha.

Thorn (1978) made a preliminary assessment of the geomorphic role of pocket gophers at the Saddle, Niwot Ridge. The general relationship between gopher territories and snow depth was estimated. Gophers were found to occupy 22-25% of the snow covered areas. Average territory size and population estimates were made. Gophers were estimated to lower the tundra surface 0.03 to 0.04 cm/yr.

Burns (1980) measured the impact of the northern pocket gopher (*T. talpoides*) on soil erosion in the tundra. He found 91% of pocket gopher activity to be restricted to early-melting snow-cover sites, those sites where the snow had melted by early June. Pocket gophers averaged 10.6 gophers/ha at these sites (Burns, 1979). The average gopher was estimated to bring 100,940 cm^3 of dirt to the surface each year and the resultant erosion of the mounds was estimated to lower the tundra surface about 0.0037 cm/yr.

Halfpenny (1980) studied the life-history traits, growth and reproductive strategies of *P. maniculatus* from Mt. Evans (4300 m) and the Mountain Research Station (3000 m). The Mt. Evans site is the highest site from which *Peromyscus* have been documented. At 4300 m their life expectancy was 127 days, while at 3000 m, just below timberline, life expectancy was 102 days. This study was part of an analysis of reproductive strategies over an elevational gradient of 2700 m.

Halfpenny and Ingraham (unpublished) have documented the phenology of reproduction in *Phenacomys intermedius* on Niwot Ridge. They also made initial estimates of habitat preferences.

During August 1980 a live-trap grid was established in the *Kobresia* meadow west of D-1 (Halfpenny, unpublished). This grid was trapped through 15 October, 1980. Mice and voles have been marked, and densities and home range estimates are being made.

Meaney (1981) has been studying the cheek scent marking behavior of pika on the West Knoll of Niwot Ridge. Cheek marking is a specific behavior during which olfactory deposits from the cheekglands are deposited on the rocks. Her research attempts to determine the function of this behavior. She has marked 30 animals and made initial determinations of territory size and population densities. Pika densities have been calculated at 12 to 15/ha.

Several comparative studies are available for the subalpine zone of Niwot Ridge. Merritt, (1976) and Merritt and Merritt (1978, 1980) have analyzed the population ecology and energy relations of *P. maniculatus* and *C. gapperi*. Stinson (1977, 1978a, 1978b) looked at species diversity, resource partitioning, microhabitat selection, and demography of various small mammals. Halfpenny (1980) analyzed life-history traits, growth, and reproductive strategies in *Peromyscus*. Several comparative studies of note exist for other subalpine zones in Colorado. Williams (1955a, 1955b, 1955c, 1959) and Williams and Finney have studied diet, food habitats, home range and distribution. Vaughan (1969, 1974) studied reproduction and population densities of montane small mammals in central Colorado.

Conner (unpublished) is expanding the work of Krear (1965). He is trying to determine the number of distinct vocalizations of pikas and the situations under which they are used. Further work on the role of vocalizations in the establishment and maintainence of territories is planned.

COMMUNITY ECOLOGY

Habitat Preference

Hoffmann (1974) analyzed the habitat preferences of mammals of the Beartooth Plateau. Predicted habitat preferences (based on Hoffmann) for the herbivorous small mammals of Niwot Ridge are shown in Table 1. These predicted preferences should serve as initial estimates for small mammals on Niwot Ridge until more detailed studies are available. Studies designed to define habitat preferences, as "viewed" by the small mammals, not as vegetational associations recognized a priori, would be best (Armstrong 1977, 1979).

Quick (1966) determined habitat preferences for alpine mammals on Niwot Ridge. His studies were divided into three time periods: 7 June to 28 July, 3 August to 20 September, and 17 September to 9 October, 1964. *Microtus montanus* were found to prefer solifluction terraces (wet meadows) and krummholz while *Peromyscus* preferred fellfields during the first period. *Microtus* preferred "gopher gardens" and *Phenacomys* preferred alpine meadows (moist meadows) during the second time period. *Peromyscus* preferred patterned ground and *Phenacomys* preferred solifluction terraces (wet meadows) during the third time period (fall). *Microtus* seemed to be associated with wet but not saturated areas. *Phenacomys* " find their most favored habitat in mosaics with solifluctions terraces that provide elevated areas to which the animal can retreat during wet periods when the basins are flooded" (Quick, 1966). Other than the few papers cited above, detailed studies of habitat preferences of alpine small mammal herbivores are lacking. Most alpine tundra studies have served mainly to provide checklists of species present and make preliminary determinations of habitat preferences (Brown, 1967; Pattie and Verbeek, 1967). Considerably more work on habitat preference needs to be done. No papers exist relating habitat preference to diet. Williams and Finney (1964) did find *Endozone*, a phycomycete fungus in the stomachs of alpine mice and voles.

Community Composition

Several studies from Niwot Ridge provide an indication of the species composition in the various habitats (Table 2). Most of the studies were not designed to sample the diurnal mammals and data are lacking on pika. Therefore only the nocturnal and crepuscular small mammal herbivores are compared.

Two species, *Peromyscus* and *Phenacomys* were found in most habitats. *Phenacomys* were the most ubiquitous species having been captured in all habitats studied. However, only in the moist meadows was it a major component of the community. Halfpenny and Ingraham (unpublished) and Quick (1966) found *Phenacomys* to be the only other species of the dry meadow and polygon areas. *Peromyscus* were found in all but the willow-sedge habitat. They are the most important species in drier habitats, particularly in patterned ground and dry meadow areas, and to a lesser extent in the krummholz. Quick (1966) found *Peromyscus* to be the most ubiquitous animal in his studies.

Other species are more restricted in habitat. *Microtus* spp. are most important in the willow-sedge community (91%), a wet habitat with a lot of overhead cover. They also represent a major species of moist meadows (36%). Both *Clethrionomys* and *Eutamias* were found only in the krummholz where *Clethrionomys* represented about 26% of the small mammal community and *Eutamias* about 14%. Shrews were taken only in moist meadows (*S. nanus*) and willow-sedge areas (*S. vagranus*) (Horn, 1967).

The habitats studied represent a moisture gradient as follows: patterned ground-dry meadows (least moisture), krummholz, moist meadows, willow-sedge (most moisture). Over this gradient the percentage composition of *Peromyscus* in each habitat decreased with a increase in moisture. The occurrence of *Microtus* sp. increased with increased moisture, reaching a peak in the willow-sedge community. *Phenacomys* were most significant in habitats intermediate in moisture. Quick (1966) suggested *Microtus* and *Phenacomys* "trade-off" habitats. *Microtus* occupied wetter habitats of a given area during wetter years. *Phenacomys* occupied drier habitats of a given area during drier seasons. If this is true, it would be interesting to know the effect of increased snowfall on these populations. One would expect *Microtus* populations to be favored in years of heavy snowfall and *Phenacomys* in years of light snowfall.

Biomass and Production

No estimates of mammalian herbivore biomass or secondary productivity have been published for the alpine tundra. Quick (1966) calculated the weight of "*Peromyscus* bodies returned to the soil" by two different methods. The estimates were 118.6 g/ha/yr and 131.7 g/ha/yr for the year 1964. Due to the inability to sample young before recruitment these estimates might be off by a factor of two. Assuming a stable population, these figures would be an estimate of the annual net production of *Peromyscus*. Quick's figures, however, include both subalpine and tundra populations.

The small mammal biomass of the subalpine has been estimated in two studies (Table 3). Anderson et al. (1980) estimated biomass at 1287 to 3538 g/ha while Vaughan (1978) estimated the biomass at 3173 to 3538 g/ha. The two mammals contributing the most to total biomass were *Thomomys talpoides* (83%) and *Lepus americana* (54%) (Anderson et al., 1980).

Table 1. Herbivorous small mammals of Niwot Ridge arranged according to their suspected habitat preferences. Based on Hoffmann (1974).

Mammal	Krummholz	Cliff Talus	Rock Polygons	Fellfield	Dry Meadow	Moist Meadow	Sedge Tussock	Willow-Sedge
O. princeps		1	2					
L. townsendii*				2	1	2		
S. lateralis		1	2					
M. flaviventris		1	2		3			
E. minimus*	1	2	3					
T. talpoides	3				1	2		
P. maniculatus	1	1	1	2	2	3	4	
P. intermedius	1	3	3	3	3	2		
C. gapperi	1	2	3					
M. montanus					4	1	3	2
M. longicaudus						1	2	3

*These species are rare on Niwot Ridge.

Table 2. Mammalian species composition for various tundra habitats. Each study was assigned to a habitat type (after Hoffmann, 1974) based on the author's description of the habitat. Sample size are in parenthesis.

SOURCE	Quick[a] (1966)	Horn (1967)	Halfpenny (1980)	Quick[a] (1966)	Horn (1967)	Horn (1967)	Pattie (1967)	Enger (1967)	Quick[a] (1966)
HABITAT	Patterned Ground	Dry Meadow	Dry Meadow	Dry to Moist	Moist Meadow	Willow Sage	Krummholz	Krummholz	Gopher Garden
SAMPLE DATE	Aug.	Aug.[b]	Aug.-Oct.	Aug.	Aug.[b]	Aug.[b]	Jun.,Aug.	Jun.-Aug.	Aug.
SPECIES									
P. maniculatus	90%	88% (29)[a]	88%[d] (46)	54%	29%[c] (4)		45% (5)	52% (32)	90%
M. montanus		6%(2)	10%[4] (5)	3%	36% (5)	91% (10)			5%
M. longicaudus								5% (3)	
P. intermedius	10%	6 (2)	29%[d] (1)	43%	36% (5)	9% (1)	9% (1)	5% (3)	2%
C. gapperi							27% (3)	26% (16)	2%
E. minimus							18% (2)	11% (7)	
	100%	100% (33)	100% (52)	100%	101% (14)	100% (11)	99% (11)	99% (61)	
OTHERS									
O. princeps		(4)			(1)	(1)			
S. vagrans						(3)			
S. nanus					(3)				

[a] Percent composition was derived from density figures.
[b] Summation of 5 yr of data from Paddock and Horn (1961, 1962, 1963, 1964, and 1967).
[c] Peromyscus were captured in 1 yr only.
[d] The voles appeared to be transients as no vole was ever recaptured.

POPULATION ECOLOGY

Species Density

Population densities vary substantially between species, seasons, and years. Estimated densities vary from 46.0 /ha for *Thomomys talpoides* to 0.2 /ha *Phenacomys intermedius* (Tables 4 and 5). Seasonal population densities may vary from 0.9 per ha in July to 19.1/ha in October for *P. Maniculatus* (Table 5). Between years, but during the same season, population densities of small mammals in alpine tundra may vary. *Ochotona* varied from 3.4 to 8.0 animals/ha during a five year study at Loveland Pass, Colorado (Table 6) (Whitworth and Southwick, 1980). Yearly variation is indicated by the change in numbers of small mammal herbivores trapped over several years at permanent sites on Niwot Ridge (Table 7).

Overwintering population densities are extremely low (Table 5). At the Niwot Ridge Saddle, Pattie (1967) found 0.9 *Peromyscus* per hectare and no other species in July. At the Niwot Ecotone grid Enger (1967) found 0.3 *Peromyscus* and 0.6 *Clethrionomys* per hectare (30 June to 12 July) for an overall density of 0.9 animals per hectare. By August densities have increased with total animal density for four species in "gopher gardens" as high as 16 animals per hectare (Quick, 1966). Densities may continue to increase until October when 19.1 *Peromyscus* per hectare were recorded in the mild fall of 1980 (Halfpenny, unpublished). Under the right conditions, densities of *Peromyscus* may be even higher than the 19.1/ha. The highest density recorded on the tundra is 20.3 mice per hectare at Niwot Ridge in October 1980 (Halfpenny, unpublished), but Halfpenny (1980) captured 33.3 animals per 100 trap-nights on Mt. Evans, which is four times the number of mice per 100 trap-nights taken on Niwot Ridge in October 1980.

Densities of voles on Niwot Ridge are apparently lower than those of the deer mice. *Microtus* and *Phenacomys* are absent from the early July surveys at the Niwot Saddle. In August *Microtus* varied from 0.4/ha (dry to moist meadow) to 2.4 (dry meadow), while *Phenacomys* varied from 0.2/ha (mixed habitat in the Saddle) to 4.9/ha (dry to moist meadow). The highest densities of *Clethrionomys*, 0.6/ha, were found in July in the krummholz. Brown (1967) sampled several alpine tundra habitats in Wyoming during a full summer. He found *M. montanus* to be present in greater densities than *Peromyscus*. His total numbers of mice per 100 trap-nights were *M. montanus*, 3.5: *M. longicaudus*, 0.3, *C. gapperi*, 0.0; *P. intermedius*, 0.3; and *P. maniculatus*, 2.8 for a total of 6.9 mice and voles/100 trap-nights.

Ochotona population densities in the tundra vary considerably, both between years and between sites (Tables 6 and 8). The lowest densities, 1.3/ha were observed by Kawamichi (1976) while the highest densities, 12 to 15/ha, were found by Meany (1981) on Niwot Ridge. These data do not reflect seasonal variation.

No population density estimates for *Marmota* are available for Niwot Ridge. Jones and Armitage (1979) found densities of 3.5 to 8.5 marmots/ha at North Pole Basin, central Colorado (Table 8).

Both Thorn (1978) and Burns (1979, 1980) have estimated pocket gopher, *T. talpoides*, densities on Niwot Ridge (Table 8). Their estimates differ considerably: 10.6 gophers/ha by Burns (1979, 1980) and 40 to 46.0/ha by Thorn (1978). However, neither author indicated the time of year when their estimates were made and hence the differences may be due to sampling at different points in the population cycle.

Home Range and Territory

Few data are available for small mammal home ranges in the tundra. Pattie (1967) used the average distance between captures to estimate home range (Table 5). He found the home range of *Peromyscus* to vary by both sex and age class. Adult males averaged 72 m between successive captures, adult females averaged 59 m, and subadults averaged 63 m. The average distance between captures for all animals was 69 m.

The territories of adult *Ochotona* vary from 1141 m^2 (Meaney, 1981) to 1228 m^2 (Kawamichi, 1976) (Table 8). Meaney has shown both age and sex differences on Niwot Ridge. Males had a home range of 1231 m^2, females had a home range of 1051 m^2, and juveniles had a range of 527 m^2.

Johns and Armitage (1979) found *Marmota* in central Colorado to have a home range of about 5500 m^2. Thorn (1978) estimated the home range of *T. talpoides* on Niwot Ridge to be 54 m^2. He felt that the presence of snow cover restricted home range size and cited examples for areas lacking snow where the home ranges are large.

Life-History Traits

Few data are available on the life-history traits of the small mammals from the alpine tundra. Quick (1966) collected life-history data but reported summaries which include both alpine and tundra animals. Quick indicated that breeding started earlier in the subalpine, a fact which would add variation when the two zones were lumped. Enger (1967), Horn (1967), and Pattie (1967) collected some life-history data but it is of limited extent.

Halfpenny (1980) reported life-history data for *Peromyscus maniculatus* from Mt. Evans and the subalpine zone at the Mountain Research Station (Table 9). Mt. Evans is at 4300 m and the growing season is short. For comparison there are only 43 frost-free days at D-1 station on Niwot Ridge, 3730 m. The breeding season was between 90 to 120 d. Estimated dates of first conception based on the growth of juveniles captured in June varied

Table 3. Biomass estimates for the subalpine.

Habitat	Area	Species	Biomass (g/ha)	Source
Subalpine Meadow	N.E. Logan, Utah	*C. gapperi* *E. minimus* *E. umbrinus* *Glaucomys sabrinus* *P. maniculatus* *Tamiasciurus hudsonicus* *Erethizon dorsatum* *Lepus americanus*	1287-3770	Anderson, et al. (1980)
Subalpine Meadow	Rabbit Ears Pass, Colorado	5 Species	3173-3538	Vaughan (1974)

Table 4. Maximum population density for tundra small herbivore species.

Species	Source	Date of estimate	Habitat	Density (#/ha)
P. maniculatus	Halfpenny (unpublished)	Oct.	*Kobresia*	19.1
M. montanus *M. longicaudus*	Halfpenny (unpublished)	Aug.	*Kobresia*	2.4
P. intermedius	Quick (1966)	Aug.	Moist-Dry Meadow	4.9
C. gapperi	Enger (1967)	Jul.	Krummholz	0.6
O. princeps	Meaney (unpublished)	Aug.	Boulder Field	12-15
T. talpoides	Thorn (1978)	No date	Mixed Meadow	46.0
M. flaviventris	Johns and Armitage (1979)	No date	------------	8.5

Table 5. Density and home range size for small mammal herbivores on Niwot Ridge. The source and location is given first. Density is given in hectares.

Source	Peromyscus Maniculatus	Microtus Montanus	Phenacomys Intermedius	Ochotona Princeps	Clethrionomys Gapperi	Total Density
Pattie (1967)						
Location Saddle						
Habitat Mixed						
Density (15 July)	.9	1.3	.2	1.1		.9
Density (7 Aug.)	1.6					4.2
Home Range	X̄ = 69m					
(Mean Distances Adult	= 72					
between captures) Adult	= 59					
Subad.	= 63					
Quick (1966)						
Habitat "Gopher Garden" (Aug.)	14.4	.8	.4		.4	16.0
Moist-Dry Meadow (Aug.)	6.2	.4	4.9			11.5
Patterned Ground (Aug.)	7.4		.8			8.2
Enger (1967)						
Location Ecotone						
Density (30 Jun.-12 July)	.3(.5)[a]				.6(.5)[1]	.9
Density (4-17 Aug.)	.6				.4	1.0
Halfpenny (Unpublished)						
Location D-1						
Habitat Dry Meadow						
Density (13-15 Aug.)	3.6(3)[a]	1.2				4.8
Density (27-29 Aug.)	4.8(4)	2.4				7.2
Density (13-15 Sept.)	14.3(5)		1.2			15.5
Density (11-13 Oct.)	13.1(4)	1.2				14.3
	19.1(8)	1.2				20.3
Halfpenny (1980)						
Location Mt. Evans Rock						
Habitat Dry Meadow						
Density (June)	(3.9)[a]					
Density (Aug.)	(9.5)					
Density (Sept.)	(33.3)					

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[a] The number in parentheses is the number of animals captured per 100 trap-nights.

Table 6. Estimated pika populations in August at Loveland Pass (Whitworth and Southwick, 1980).

Study Areas		1976	1977	1978	1979	1980
Loveland Pass	(.48)	3.5 (.19)	4.4 (.36)	3.4 (.49)	5.4	8.0
Arapahoe Basin		6.2	9.7 (.54)	3.9 (.28)	4.5 (.43)	5.6 (.39)

[a]Pika/hectare; study areas 4.05 to 5.3 ha. ($\bar{X}$ = 4.6 ha). Percent young in parenthesis.

Table 7. Number of small mammal herbivores taken in August of different years from four snap-trap lines on Niwot Ridge. Data are from Horn (1967).

Species	1960	1961	1962	1963	1964	1967
P. maniculatus	23	12	0	10	10	5
M. montanus	2	2	2	2	2	11
P. intermedius	0	2	1	4	3	0
O. princeps	0	0	1	3	0	2

Table 8. Population densities and home ranges (territories) for Colorado alpine populations for *O. princeps*, *M. flaviventris*, and *T. talpoides*.

Species	Source	Area	Numbers/Ha	Home Range (territory) (m^2)
O. princeps	Kamamichi (1976)	Loveland Pass	1.3 - 6.4	1228
O. princeps	Southwick (1980)	Loveland Pass	3.4 - 8.0	-----
O. princeps	and Whitworth	Arapahoe Basin	3.9 - 9.7	
	Meaney (1981)	Saddle, Niwot Ridge	12 - 15	1141 all 1231 males 1051 females 527 juveniles
M. flaviventris	Johns and Armitage (1979)	North Pole Basin,	3.5 - 8.5	5484
T. talpoides	Thorn (1978)	Saddle, Niwot Ridge	40 - 46.0	54
T. *taloides*	Burns (1980)	Niwot Ridge	10.6	-----

Table 9. Summary of key ecological traits for P. maniculatus from Mt. Evans (4,300 m) and Mountain Research Station (2,730 m). Data from Halfpenny (1980).

	Mountain Research Station	Mt. Evans
Physical		
Elevation (m)	2730	4300
Frost-free days	59	<47
Animals per 100 trap-nights (June 1978)	3.7	3.9
Breeding season (days)	141	90-120
Reproduction		
Litter size (laboratory)		
$\bar{x}$ (mode) range	5.1 (5) 2-9	6.4 (7) 4-8
Litter size (field)		
$\bar{x}$ (mode) range	5.7 (6) 4-7	6.4 (7) 5-7
Litters per year	3.5	1.1
Reproductive efficiency (%)	38.6	46.1
Growth		
Weight of neonates (g)	1.71	1.65
Weight of female at parturition (g)	23.52	26.88
20 day growth rate	.093	.089
Age at weaning (days)	18.56	18.93
Survivorship and Mortality		
Median Ecological Longevity	51	121
Mean life expectancy	102	127
Juvenile survivorship (%)	13.2	5.6
Adult mortality (%)	8.0	9.1
Juvenile adult ratio	1.65	.62

from 31 May to 11 June. Litter size averaged 6.4 (mode 7); females averaged about one litter per year. Several different estimates of the number of litters per year averaged 0.78, with a figure of 1.1 from the best estimation method. Females averaged 26.9 g at parturition, the young 1.65 g for a reproductive efficiency of 46%. The median ecological longevity was 121 d, and the juvenile to adult mortality ratio was 0.62. Merritt (1976) and Stinson (1977, 1978a) provide comparative data for the subalpine.

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INVERTEBRATE COMMUNITIES AND DYNAMICS OF ALPINE FLOWAGES

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ABSTRACT

This review is a prelude to current invertebrate investigations of the Green Lakes drainage system in the Rocky Mountain Front Range. Descending in elevation, late summer temperatures range from 1°C to over 10°C between the six lakes. Previous Colorado alpine studies reveal total dissolved solids (TDS) range from less than 9.1 to 49 mg/l (largely inorganic). Alpine lakes, generally have low plankton diversity, with oligochaetes, chironomids, and sometimes nematodes, dominating the benthic fauna. In high elevation streams, insects are dominant with chironomids most abundant at higher elevations, and other Diptera, Trichoptera, Ephemeroptera, and Plecoptera becoming better represented at lower elevation alpine zones. The Green Lakes drainage is generally consistent with these observations, but among other taxa found in abundance are the mollusk Pisidium sp., the platyhelminth, Polycelis coronata, Hydra sp., and, in lesser abundance, Coleoptera, acarines, tardigrades, and the leech, Glossiphonia complanta.

A few collections of the Green Lakes stream insects in 1960 by Elgmork and Saether (1970) are the only studies germane to this flowage system. They found chironomids and simuliids together comprised 85% of the community.

Published information on alpine lakes and streams of North America and elsewhere are generally consistent in many respects, but may vary in faunal diversity and abiotic characteristics. Selected papers of comparative interest are reviewed.

INTRODUCTION

This review is a prelude to the study of various aspects of invertebrate communities and changes in invertebrate diversity within six lakes and connecting streams of the Green Lakes drainage system of the Front Range of the Rocky Mountains. This drainage system is the alpine portion of the Boulder City Watershed located wholly within Boulder County. Many papers have been published as alpine studies, but a majority consider lakes and streams within agricultural zones or areas surrounded by forests. It must be emphasized that the study of the Green Lakes drainage is unique for two fundamental reasons. First, this study is truly alpine in the sense that only the lowest station is at treeline or within the krummholz. All other stations are surrounded by barren rocks and open tundra slopes. The elevation ranges from 3200 to 3800 m, covering a flowage of about 5 km. Second, this is a study of a flowage system including a chain of six lakes and intervening streams. There appear to be no studies of such a total system for this elevation and few for lower elevations. The flowage system is fed by snowmelt from snow-covered slopes and glaciers. The lakes are cold, oligotrophic, nonstratified drainage lakes with summer temperatures ranging from <1°C to perhaps 10°C for the lowest lakes. Maximum depth of the lakes ranges from 7 to 16-m, with maximum depth increasing down the flowage. Substrate composition is similar for all the lakes, with a rocky substrate along the shore changing to predominantly silt/clay at the mid-lake bottom.

LITERATURE REVIEW

Colorado

The only studies directly germane to the Green Lakes drainage system are those of Elgmork and Saether (1970) and Saether (1970). These studies resulted from collections of invertebrates, principally insect larvae and nymphs, from the intervening streams of the Green Lakes flowage. Little information is given for the lakes, and collections were made only on 7 and 11 June, and 8 to 13 July 1960. Descriptive information about the drainage region and stream organisms given makes these publications valuable for a long-term study.

Elgmork and Saether (1970) describe the intervening streams of the Green Lakes drainage system as "typical high mountain brooks" with a swift current, a bottom of variable size stones, often covered by mosses (at least six species), occasional blue-green algae, and at the lowest elevation colonies of Nostoc. The borders of the brook were snow covered in certain locations even in July. At the lowest station (3300 m.a.s.l.) the water temperature was 10°C in mid-July and the upper station was <1°C. No published information on water chemistry is available, but R.W. Pennak (1941) sampled Lake Albion, the lowest of the lakes, and found 18.8 mg/L. Total Dissolved Solids (T.D.S.) of which 13.6 mg/L were inorganic. The geology of the region suggests an exceptionally low level of electrolytes.

Elgmork and Saether (1970) found two dipterans, Eukiefferiella sp. G. and Prosimulium esselbaughi, to be the most abundant and ubiquitous throughout the intervening streams, and the great majority of identified species were chironomids (total 34 species), more than 99% being Orthocladinae (a group typical of rapid streams at high altitudes). The Simuliidae were the second most abundant group and together with the chironomids composed 85% of all organisms collected. Of far lesser abundance were the "Vermes," presumably Oligochaeta and Nematoda (the former including Chaetogaster diastrophus, Nais variabilis, and Mesenchytraeus sp.). Next in order of abundance were the Ephemeroptera, Plecoptera, Trichoptera, other insects and other invertebrates. Other invertebrates include Hydra sp., the cold-water turbellarian Polycelis coronata (known from the Black Hills of South Dakota westward in mountainous regions to the Pacific Coastal area (Hyman and Jones, 1959), the tardigrade Macrobiotus and the Acarines Sperchon glandulosus, Lebertia atelodon, and Aturus fontinalis. Elgmork and Saether divided the stream flowage into four distinct zones defined by relative changes in community structure associated with a temperature gradient. Such zonations result from gradients of environmental factors in addition to temperature and may be amplified by competitive exclusion (see Hutchinson, 1953). Macan (1962) stresses the importance of biotic factors promoting zonation in streams. Elgmork and Saether (1970) report a "relative increase in the number of chironomids" within zones in the upstream direction and a relative increase in the number of Annelids and Ephemeroptera in the downstream direction. Plecoptera and Trichoptera are absent from the coldest waters, only appearing in the lower half of the flowage where the water temperature ranged from 5° to 10°C. With the exception of the lowest portion of the flowage, the zonation described by Elgmork and Saether agrees very well with the mountain brook divisions suggested by Thienemann (1954) based on genera of chironomids.

The second paper on the invertebrates of intervening streams of the Green Lakes system (Saether, 1970) is entirely taxonomic and essentially on the Insecta. In this paper he discusses one new species of Trichoptera and a new genus and species of Ephydridae.

Pennak (1963) has characterized the typical alpine lake as a "cold tarn with a rock, rubble and gravel basin, with nearby snowfields and glacierets, even in midsummer. Inflow and outflow are high so that there is little opportunity for biological or chemical "aging' of the water." Thus these lakes can be considered indefinitely "juvenile" through time, remaining extremely oligotrophic. The total plankton is consistently low and Pennak states that for Colorado alpine lakes they average annually fewer than 100,000 phytoplankton cells, 60 rotifers, and 15 immature and adult entomostracans per liter. In markedly unproductive alpine lakes these numbers may be as low as 10,000, 10, and 2 per liter, respectively. He further states that physical and chemical conditions during prolonged seasons of ice cover are little known. The phytoplankton are dominated by diatoms, notably Asterionella, Melosira, and Synedra. Myxophyceae (largely chroococcales) are generally second in abundance. Certain copepod species are generally restricted to cold alpine lakes, i.e., Diaptomus shoshone, D. coloradensis, and D. arapahoensis. Endemic cladoceran species are not known from high lakes.

Pennak (1955) states that Summit Lake (Mt. Evans, Boulder Co., elevation 3384 m.a.s.l.) has a summer maximum temperature of 10°C and a mean for June to September of 5.5°C. The mean depth is 7.0-m with nearly 100% oxygen saturation at the lake bottom. It is presumed that oxygen exhaustion does not occur in midwinter despite the persistent thick ice and snow cover. The hydrogen concentration was near neutrality, as might be expected. Total residue was 17.38 mg/L. The annual mean for seston (particulate organic matter) was 1.49 mg/L. The mean annual cells/liter of phytoplankton were as follows: small green flagellates (mostly Dinobryon), 47,100; chlorophyceae, 9,000; Myxophyceae (mostly Chroococcus), 23,200; Diatoms (mostly Asterionella, Melosira, and Fragilaria), 154,700. The greatest population count, dominated by Asterionella, was on 19 July (303,000 cells/liter). The mean annual standing crop of zooplankton in organisms/liter was as follows: Rotatoria, 24 (five species dominated by Conochiloides dossuarius, Polyarthra vulgaris, and Synchaeta pectinata with a lower abundance for Fininia terminalis and Keratella cochlearis); Copepods, 8, (only Cyclops bicuspidatus with a maximum concentration of 13/L); Cladocera, 15/L (only Bosmina longirostris with a maximum of 83/L on 30 August). Three years later Daphnia longispina was abundant. Pennak concluded that there was no momentary correlation between phytoplankton populations and zooplankton grazers; and there are seldom notable relationships between pulses of zooplankton and pulses of algae.

Among the other lakes studied by Pennak (1955) was Brainard Lake (elevation 3140 m.a.s.l.). Unlike the higher Summit Lake with only a narrow outlet, Brainard Lake, somewhat below treeline, has a rapid inflow and outflow stream. It is ice covered 7 months while Summit Lake is ice covered 9 to 9.5 months of the year. Oxygen is close to saturation during the open season. Information was provided on seston and bound and free CO_2.

Mean values for phytoplankton abundance were given, and in some cases were less than for Summit Lake. Ceratium hirundinela was the most common protozoan, as it was in Summit Lake. Similarly to Summit Lake, Polyarthra vulgaris was the most important rotifer and Cyclops bicuspidatus the copepod representative (with a maximum of 10 organisms/l). Likewise Bosmina longirostris was present along with Chydorus spaericus and Daphnia pulex.

Papers by Olive (1953), Reed and Olive (1958), and Reed (1970) all provide information on the chemical, physical, and biological characteristics of Colorado lakes. Olive (1953) found T.D.S. to be approximately 26 ppm in lakes at elevations of 3300-3600 m.a.s.l. The phytoplankton species agree with those previously mentioned. In the higher lakes *Diaptomus shoshone* and *D. coloradensis* were predominant copepods and *Keratella cochlearis*, *Conochilus unicornis*, and *Filinia longiseta* were predominant rotifers. Four other rotifers were found occasionally. The cladocerans *Chydorus sphaericus*, *Daphnia longispina*, and *Ceriodaphnia reticula* were found in low abundance and only *Holopedium gibberum* was occasionally abundant in a high lake. Among entomostracans, Reed and Olive (1958) found only *Diaptomus connexus* restricted to alpine lakes and *Diaptomus shoshone* and *Holopedium gibberum* in both alpine and subalpine lakes of Colorado. *Diaptomus coloradensis* and *Polyphemus pediculus* were found in alpine, subalpine, and montane lakes, and *Daphnia longispina* and *Daphnia pulex* are eurytopic from plains to alpine lakes. *D. longispina* was the most common and evenly distributed of the *Daphnia* species. Reed's (1970) paper includes information on three Colorado lakes (Green Lake, Blue Lake, and Mills Lake) all at elevations greater than 3000 m.a.s.l. The two lower lakes, one a rapid flowage lake, had maximum depths of just over 8-m and maximum temperature of nearly 12°C. Both had four genera of entomostracans, several phytoplankters, a single rotifer, (*Keratella*). The highest lake, (3520 m.a.s.l.) had a maximum depth of seven meters and a maximum temperature of 7.2. This lake was fed by snowmelt and glacial runoff (rapid flushing) and had the poorest plankton populations in terms of diversity and numbers i.e., two genera of phytoplankton, the rotifier *Keratella* and two entomostracans, *Daphnia* and *Diaptomus*.

Nelson (1976) investigated three Colorado Lakes (East Ute, Abyss, and Summit) above 3600 m.a.s.l. with mean temperatures of 7.6 to 8°C. *Daphnia pulex* was found in all three, *Daphnia rosea* was common in one only,and *Holopedium gibberum* in another. The copepods *Diaptomus shoshone* and *D. coloradensis* were abundant in one lake each, again consistent with other alpine reports of these species. One notable exception to the expected fauna was observed by Brinley (1950), when only cyclopoid copepods were found in the lakes of Rocky Mountain National Park.

Patalas (1964) reports that alpine lakes in northern Colorado at elevations greater than 3200 m.a.s.l. had T.D.S. ranging from 9.7 to 49 mg/L. The number of crustacea per liter in these lakes varied from 0.003 to 28. The characteristic cladocerans (four) were species most frequently reported in earlier cited references. The dominant cladocerans are likewise consistent with these earlier reports. Patalas discusses the interaction of factors associated with high altitude, and the concentration of dissolved solids, in dictating species diversity and abundance. Similar results were cited by Hermann (1978) in his investigations of the chemical, physical, and biological characteristics of Long Lake.

Durrell and Norton (1960) and Quinn (1962) provide physical, chemical, and biological information for lakes in the Grand Mesa area and the Rainbow Lakes, respectively, but these lakes are all at montane altitudes. Early papers by Juday (1906, 1907) discuss the physical characteristics, plankton, and vegetation of lakes not higher than 2800 m.a.s.l. Most notable for lakes at this subalpine level are the greater diverstiy of crustacea, particularly Cladocera, and the presence of rooted aquatic vegetation including three species of *Potamogeton*. Shantz (1907), for lakes located at above 3100 m, found rooted vegetation only in adjacent marshes, with mosses and algae abundant in small pools. Some lakes had a sparse plankton, but *Diaptomus shoshone* was abundant in Dead Lake. Physical data, including substrate composition, was given. The early papers by Dodds (1915, 1917, 1920, 1924) include plankton keys, and discussions of organisms associated with life zones in Colorado. Many of the common forms for the alpine have been referred to in previous citations. Dodds (1917) stresses that differences between alpine lakes are determined more by the size and position of lakeside snowbanks than by elevational differences. Dodds (1924) found 18 species of entomostracans above 3100 m.a.s.l. of which 8 species were limited to such elevations.

Pennak's (1968) paper on winter limnology is the one important regional study of this nature for Colorado lakes higher than 3200 m.a.s.l. (Tea Lake, Black Lake, and Pass Lake). Pennak found that summer populations of copepods were ten times more abundant than winter populations. Cladoceran populations were similarly low, but winter rotifer populations were "remarkable for their high densities." The discussions of biological, chemical, and physical characteristics will serve as valuable comparative information for future winter studies of the Green Lakes. Other papers by Pennak (1950, 1966), providing chemical, physical, and biological data for lakes generally below 3000 m, are important in that they provide discussions of relative species dominance and diversity among planktonic organisms. Pennak (1966) found that open water contained 96% more copepod individuals, 80% more cladocerans, and 112% more rotifers than the adjacent macrophyte zone. Additional references include Pennak (1941, 1957, and 1976).

An aid to the identification of alpine desmids is provided by Prescott (1935).

High-altitude stream studies are far more limited in number than lake studies for Colorado. Among the most important stream studies for elevations above 3000-m are those of Elgmork and Saether (1970) and Saether (1970) discussed in detail earlier. Another important high-altitude stream study (altitude 3045 m.a.s.l.) is that of Short and Ward (1980) on the Joe Wright Creek. They found aquatic insects comprised 95% of the total macroinvertebrates, and ephemeropterans were decidedly the most abundant for both years of the study. Plecoptera, Coleoptera, and Diptera were relatively much less abundant, and Trichoptera were less abundant. With lesser snowpack in 1976, the second year of study, the density of macroinvertebrates was reduced by nearly 50% (1467 organisms/m^2). Other groups quantified were Hydracarina and Oligochaeta. The mean water temperature for both years was 1.2 and 1.5°C during the study period, the pH nearly neutral, and there was little algal growth on the coarse gravel and cobble bottom. The stream characteristics were similar to those of the Green Lakes streams, but there were variations in the relative importance of different taxa. Ward (1975) examined bottom-fauna/substrate relationships at 1677-m for a stream whose headwaters originated at 3350 to 3650 m.a.s.l. The stream environment was described as "a clear, unpolluted trout stream with soft water, neutral pH, and a mosaic of substrate types. Rooted aquatics were absent and epilithic algae poorly developed." (Ward, 1975). The following relationships were revealed: in sand Oligochaeta and Diptera dominated; on gravel Oligochaeta, Diptera, and Ephemeroptera dominated; amongst rubble Ephemeroptera and Trichoptera were most numerous; and on bedrock Trichoptera and Diptera were found most commonly.

Other stream studies of background interest for Colorado are those of Dodds and Hisaw (1925), Ward and Short (1978), and Pennak and LaVelle (1979). Some biological information for a montane level stream is given by Quinn (1980). A final reference concerning the yeild of dissolved substances from a mountain watershed at 2900-m is that of Lewis and Grant (1980a). Among their findings was a tripling in the export of nitrates from rocks in a year of minimum snowpack and maximum soil frost. Acid precipitation in high Colorado lakes is also discussed by Lewis and Gran (1980b).

Certain observations are apparent from a the a review of the alpine literature for Colorado. Most of the biological literature for lakes concerns the plankton with little on the Aufwuchs or benthos; there are stenotopic and eurytopic species and intermediate forms. While there is much similarity regarding chemical and physical factors unique to alpine lakes and streams, it is evident that these simple ecosystems may be subject to imbalance by subtle changes in their climate, whether induced by natural causes or man.

Temperate and Subarctic North America (Excluding Colorado)

In addition to displaying low temperatures, long periods under ice, and high O_2 concentration characteristics of the Colorado alpine lakes, lakes in similar environments throughout North America share numerous other characteristics typical of high-altitude systems. Probably the most uniform characteristic is that of hydrogen ion concentration, which generally centers around the neutral value of 7.0 (Rawson, 1953; Robertson, 1947; and Reimers et al., 1968).

The biotic component of these high-altitude lakes is equally sparse, with all trophic levels having low species diversity (Rabe, 1968). A similar lack of species diversity has been observed by Bushnell and Byron (1979) on the Cumberland Peninsula of Baffin Island, which compared in number to the two or three microcrustacean species characterizing Colorado alpine lakes (Pennak, 1957; Patalas, 1964). In certain alpine lakes of Wyoming and the Sierras, rotifers are the most conspicuous members of the zooplankton, with *Keratella*, *Kellicottia*, *Polyarthra*, and *Filinnia* species being the principal representatives (Robertson, 1947; Eriksen et al., 1962). Gravimetrically, however, it is the copepods and cladocerans that dominate the zooplankton. The calanoid *Diaptomus* has been observed in lakes ranging from the Cumberland Peninsula (Bushnell and Byron, 1979) to western Canadian alpine (Rawson, 1953; Anderson, (1971) to the high Sierras (Reimers, 1958). *Daphnia* is the most common cladoceran and there is often a very specific and restricted *Dapnia/Diaptomus* relationship. In the western Canadian alpine, Anderson (1971) observed that the co-occurrence of *Diaptomus arcticus* and *Daphnia* middendorffaina appeared to be restricted to the alpine lakes, while the co-occurrence of *Diaptomus shoshone* and *Daphnia pulex* was limited more to subalpine lakes. He also noted that *Cyclops biscuspidatus* was found in alpine and subalpine lakes, but only in the absence of *D. arcticus* and *D. shoshone*.

The benthic fauna of alpine systems tends to be fairly consistent throughout western North America. Nearly every investigator has reported the presence of chironomids as the dominant benthic organisms, reflecting the findings of Elgmork and Saether (1970) in their study of the Green Lakes flowage. In addition to the chironomids, the community also might have oligochaetes as second in abundance (Robertson, 1947) or *Pisidium* as the second dominant (Eriksen et al., 1962) or all three groups together forming the dominant benthic representatives (Taylor and Erman, 1980). In concluding their Kings Canyon study, it is rather interesting that Taylor and Erman found no direct correlation between invertebrate density and physical and chemical factors (e.g., organic carbon, nitrate nitrogen, substrate type flushing rate), while Robertson (1947) noted that, in his study of two connected Wyoming lakes, the lake with the greatest flushing rate also had the smallest populations of oligochaetes and chironomids.

In general, alpine ponds have characteristics very similar to those of high-altitude lakes, both in biotic and abiotic features. The zooplankton tends to consist mainly of only a few species of crustaceans, with cladocerans and/or copepods the dominant representatives. As in the alpine lakes, diaptomids are common. In some ponds in Alberta, diaptomids were ten times more abundant than the other zooplankton (Anderson, 1967), with nauplii reaching peak abundance in late April and adults reaching peak numbers just prior to complete freezing of the water column. Schmitz's (1959) studies of two Colorado alpine ponds also noted cladocerans and copepods as the dominant groups, but *Daphnia pulex* (so common in the high-altitude lakes) was the dominant species. In the same study, the dominant benthic invertebrate groups were observed to be Diptera (Chironomidae), Pelecypoda (Sphaeriddae) and Oligochaeta (Tubificidae), once again reflecting the dominant groups of alpine lakes.

The benthic fauna of alpine streams differs from that observed in the lakes. Here it is the insect component that dominates, especially Ephemeroptera, Trichoptera, and Plecoptera. In the Medicine Bow Mountains (Blake, 1945), ephemeropteran nymphs were most abundant, both in total number and in number of species. Of the two streams studied, dipterans were abundant only in the smaller, colder (9°C) stream, where *Polycelis coronata* (common in Colorado high mountains) was also found. Waters (1969) also observed that insects dominated the invertebrate fauna and that *Rhyacophila* and *Acroneuria* were the main invertebrate predators, with no mention of the predaceous *Chaetogaster* found in the Green Lakes stream system (Elgmork and Saether, 1970).

Regions outside North America

Throughout the remainder of the world, alpine lakes and streams are characterized by the same environmental conditions typical of the North American mountain lakes. Once again, temperatures remain low and pH values are generally in the neutral range. As elevation increases, such factors as temperature, total dissolved solids, total nutrients, and pH tend to be decreased (Hutchinson, 1937; Oleksynowa and Komornicki, 1965). Phosphorous levels decrease with increasing elevation until it becomes the crucial limiting factor for primary production by phytoplankton (Pechlaner, 1966; Pechlaner et al., 1970). As might be expected, due to the adverse conditions associated with high elevation these lakes are also quite low in productivity, possessing very simple community structure and tending to range from oligotrophic to ultraoligotrophic (Synowiec, 1965; Zutshi et al., 1972; Pechlaner, 1979).

As stated previously, the high-elevation lakes are of very simple community structure and low productivity. Accordingly, the zooplankton tends to consist of two or three principal representatives of rotifers, cladocerans, and copepods, although the very deep lakes usually have greater variety (Sowa, 1965). The combination of copepods (especially *Cyclops* or *Boeckella* spp.) and rotifers (*Keratella* spp. or *Polyarthra* spp.) were most commonly mentioned as the principal components of the plankton. In Tyrol, *P. dolichoptera*, *K. hiemalis*, and *C. abyssorum tatricus* make up 99% of the total zooplankton community (Pechlaner et al., 1970). A similar combination of *P. dolichoptera*, *K. hiemalis*, and *C. abyssorum tatricus* also has been reported in alpine lakes of the Tatra Mountains (Gliwicz, 1967), while in Lake Titicaca two species of *Boeckella* and *K. quadrata* are most abundant zooplankton (Ueno, 1967). Apparently the cladoceran/copepod associations so frequently reported in North America are not as common in other alpine areas, for much less mention is made of the cladocerans as a major plankton component. In the high alpine lakes near Mt. Everest, the principal plankton consists of *Diaptomus jurisovitchi* and either *Daphnia Tiber tana* (in the shallow, clear water lakes) or longispina-type Daphnia (in the deep/or turbid lakes). Within this system there are also no fish or other major carnivores (Löffler, 1969). All three groups (calanoids, cladocerans, and rotifers) are most abundant in the older Andean lakes, while the tropical alpine lakes of East Africa are extremely poor in all types of zooplankton, especially rotifers (Löffler, 1964). The dry tropical high-elevation lakes tend to have extreme diurnal fluctuations in temperature, especially in the shallow lakes, and the daily temperature maxima might exceed the tolerance range for the majority of the plankton.

The low level of productivity becomes evident when investigating the phytoplankton component. Once again the desmids are typically the dominant group, but the total population of the phytoplankton is low, often far exceeded by that of the zooplankton (Thomasson, 1952).

Tropical alpine lakes also differ from those of North America in the composition of the benthic fauna. Nematodes are frequently predominant, with chironomids and oligochaetes occurring in smaller numbers (Pechlaner et al., 1970, and 1972). In the lakes of the Mt. Everest region, chironomids are of great importance in terms of biomass, while oligochaetes are of only slight importance, being present in only a few lakes. Of interest is the importance of tardigrades in the Mt. Everest lakes, where they are second in number only to the nematodes (Löffler, 1969). The ability of the benthic organisms to survive the often adverse environment of the alpine lakes is reflected in the fauna of the Hindu Kush, where the highest lake has only benthic organisms. Here, trichopterans form the top of the food web, acting as efficient and highly successful predators (James and Hubbick, 1969).

The high-elevation streams are similar to the lakes in possessing a very simple community structure. As in North American streams, chironomids tend to be major benthic organisms, representing 40 to 90% of the total population. There have been observed downstream trends in faunal change, with chironomids being the only faunal component at the stream origin and species diversity increasing downstream (Kownacki and Kownacka, 1971). Similar faunal transitions have been observed in the high-elevation streams of Peru (Illies, 1964), where the insect fauna tends to vary according to the temperature and rate of flow at each station, and those observed at the highest stations are specifically adpted to the low temperatures and high O_2 at those sites.

NEEDED RESEARCH

After baseline samples have been collected and analyzed, there are a number of hypotheses that should be tested concerning community structure and environmental influences of the alpine flowage. With sufficient time and manpower, it is hoped that the majority of these questions might be investigated and answered.

(1) Are there differences in size, growth rate, reproductive rate, etc. of organisms between different stations?
(2) Do grazers in alpine limnetic plankton communities rely heavily on fine particulate detritus and bacteria for food, rather than relying on intact algal cells?
(3) How lethal is the effect of frazil and anchor ice on the benthic and Aufwuchs communities in alpine streams?
(4) Do "deadwater" or "backwater" zones of little or no water flow serve as recruitment zones for deposition of detritus and subsequent nutrient dispersal for replenshing populations?
(5) Are there changes in trophic structure associated with change in elevation, or as compared between lake and stream systems (e.g. predators vs. nonpredators or scrapers v.s. shredders vs. collectors as observed by Cummins [1974]?
(6) How sensitive are alpine species to pollutants and similar environmental alterations (e.g., increased acid rain recently reported in the Indian Peaks [Lewis and Grant, 1980]?
(7) Of what importance is the lithophyton as a nutrient source and as a community microhabitat?
(8) What is the energy flow through the biotic community? How much is contributed by allochthonous material vs. in situ primary production?
(9) What are the winter conditions in the lakes? Is there depletion of the oxygen while under prolonged ice cover?
(10) What is the effect of scouring during peak snowmelt on community structure and allochthonous input? During drought years, would the resultant decrease in organism loss be countered by a decrease in allochthonous nutrients, due to decreased scouring action?

Additional research is needed most obviously in analyzing the phytoplankton community including nanoplankton studies) and in determining the importance of the microbial community (e.g., bacteria). These groups are extremely important in the aquatic food chain both as a food source and in the recycling and availability of nutrients.

DISCUSSION

The productivity of alpine lakes is usually far less than that observed in similar lakes at lower levels, directly reflecting the the interactions between edaphic factors, climate, and lake basin morphology. When conditions are best suited for high productivity, the soluble mineral content of the surrounding soil/rocks is high, the climate warm, and the lake basin is shallow. In the typical high-altitude lake, however, the surrounding soil/rocks are extremely poor in soluble substances, and the climatic conditions tend to be very severe. These two factors occur at such extremes that, when combined, their negative influences far outweigh the favorable aspects of a shallow basin. This effect was observed in the Canadian high-elevation Bow Lake (Rawson, 1941). Compounding the edaphic and climatic problems is the decrease in drainage area associated with increased elevation. Not only are there lower nutrient levels in the soils, but there is also greater physiological difficulty in acquiring what little is available due to the low temperatures. The nutrient problem is not quite so severe for those lakes receiving glacial runoff, for the glacial clays carried in the meltwater tend to be rich in phosphorous (Thomasson, 1956). In addition to those conditions resulting from the high-elevation, there is also an appreciable effect due to latitudinal position. The year-round cold temperatures associated with the alpine lakes and streams are common without regard to latitude; however, the duration of snow and ice cover is directly correlated with latitude. Hence, the alpine lakes and streams of the higher latitudes also are faced with a short growing season. Also associated with the higher latitudes is an increase in the lethal effects of frazil and anchor ice on the benthos and Aufwuchs of the alpine stream community.

Another characteristic associated with alpine lakes is the high oxygen content, often found to exceed 100% saturation. Given these oxygen-rich conditions, the fate of nutrients that do enter the lake is rapid extinction, as they are irretrievably lost due to binding with the oxidized clay sediments. Such a phenomenon was observed by Hall et al. (1970) when testing the effect of different nutrient levels on zooplankton densities. Under high oxygen conditions, there was not a marked difference in zooplankton response between low and moderate levels of nutrient application. When high levels of nutrients were added, the highest zooplankton biomass was obtained, suggesting that the binding mechanism was saturated and nutrients could accumulate in the water column, available for uptake by the plankton.

The low productivity of high alpine lakes is very obviously reflected in the biotic component, where the communities tend to be rather simple and dominated by only a few species. A look at the rotifer populations in these lakes offers a good example of the simplicity of community structure. Usually abundant in numbers and species at lower elevations, the rotifer population of a high-elevation community might consist of only one species (Anderson, 1977), but generally two or more species are found. The fauna usually consist not only of cold stenthermic species restricted to that environment, but also eurythermal species which are often worldwide in their distribution (Thomasson, 1956). The degree of biotic interaction, coupled with the environmental limitations of certain species, result in an associated change in species composition along the elevational gradient. Faunal replacement is most readily seen in lotic systems where, as one follows the course of a stream, the change in elevation is associated with a change in species composition. In alpine streams, the rate of change is rather low compared to lower elevation streams, with a 50% change in species composition in the alpine, requiring as much as 1000 m change in elevation (Allan, 1975). This low rate of community change most likely reflects the low density communities (therefore, low biotic interactions) associated with alpine regions.

The concept of a "recruitment" zone in the relatively calm backwaters of flowage systems has been suggested in the findings of Robertson (1947). His study centered on two stream-connected lakes located 30 m above timber line in the Wind River Range of Wyoming. In the uppermost lake, the source stream entered and then exited from a small side arm of the lake without flowing through the main body, to then enter the second lake. When comparing the benthic fauna of the three lake zones (upper lake, east arm and lower lake), the upper lake far exceeded the other two (high flushing) aras in terms of faunal density. The zooplankton were also slightly more numerous (in average number per liter) in the slow flushing upper lake.

In summary, there are a number of papers that deal with alpine aquatic systems. The majority of these papers have concentrated on the plankton of the lakes, while little information concerns lake benthos, Aufwuchs, or alpine stream communities. One of the major features of the lake plankton is the aspect of a stentopic component of organisms confined to alpine lakes, while other organisms are more eurytopic and found in lower elevation life zones. With the exception of a few studies of small flowages (e.g., Robertson, 1947; and Quinn, 1962), there is little information available on such an extended stream/lake flowage system.

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THE STATUS OF UNEXPLOITED FISH POPULATIONS IN THE GREEN LAKES VALLEY, AN ALPINE WATERSHED, COLORADO FRONT RANGE

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ABSTRACT

This review attempts to summarize available information related to the unexploited alpine fish populations in the Green Lakes valley, located within the Front Range of the Colorado Rocky Mountains in the Roosevelt National Forest. This review is a prelude to a five-year study which is part of the Colorado University Long-Term Ecological Research Program. Study of the alpine fish populations is unique for several reasons. No published literature exists on unexploited alpine fish populations and those in the Valley have not been exploited since 1927 (over 55 yr). The study area is part of the much larger drainage system which forms a municipal water supply, owned, operated, and managed by the City of Boulder in Boulder County. The Green Lakes drainage is wholly alpine, contains the Arikaree Glacier, Green Lakes 1 through 5, Albion Lake, and the north branch of North Boulder Creek. The watershed is mostly fenced above the 2800-m elevation, patrolled and no public access is permitted. Albion Lake and Green Lakes 1-5 were sampled by gill netting in 1973. Results indicated populations of brook trout *Salvelinus fontinalis*, in Albion Lake and Green Lakes 2 and 3. No fish were caught in Green Lakes, 1, 4, and 5. Length and weight data for the populations indicate small fish that undergo slow growth with some individuals 15 yr and older. Study of the Green Lakes valley and North Boulder Creek assumes additional significance considering that the greenback cutthroat trout, *Salmo clarki stomias*, is found in lakes and streams to the north and south of the valley and that the species is on the federal and state list of threatened species. Brook trout dominate North Boulder Creek and appear to have replaced the greenback trout within the last several years.

INTRODUCTION

This review was prepared in advance of the initiation of a long-term ecological research study of the unexploited fish populations in an alpine watershed, the Green Lakes valley. The valley is located within the Front Range of the Colorado Rocky Mountains in the Roosevelt National Forest (Figure 1). It is part of the much larger drainage system which forms a municipal water supply, owned,operated, and managed by the City of Boulder in Boulder County, Colorado.

The watershed includes two major drainage systems that lie south of Niwot Ridge and the Arapaho Moraine. The smaller and more northern Green Lakes valley drainage is wholly alpine, contains the Arikaree Glacier, six alpine lakes, and the north branch of North Boulder Creek. The larger Silver Lakes valley drainage lies south of the Green Lakes valley, begins at the Arapaho Glacier, and contains 11 alpine and subalpine lakes and the south branch of North Boulder Creek. The watershed is mostly fenced above the 2800-m elevation; it is patrolled and no public access has been permitted to the area for over 55 years.

Pennak (1976) used the term "alpine lakes" to include only those bodies of water situated in the zone extending down to 300 m below the normal climatic timberline. Depending on latitude and other land features, the alpine zone begins at about 2400 to 3700 m. The lakes in the Green Lakes valley range in elevation from 3200 m (Lake Albion) to 3800 m (Green Lakes 5) which is at the upper end ofthe alpine lake zone. The upper Green Lakes, 4 and 5, are unmodified whereas Lake Albion and Green Lakes 1, 2, and 3 have been slightly enlarged by raising their outlets.

Brook trout can spawn successfully in many alpine lakes, although their resulting high densities may inhibit growth (Nelson, 1970). Lake populations of rainbow and cutthroat trout require streams for spawning. The inlet and outlet tributaries of many alpine lakes are unsuitable as spawning habitats.

The study of the alpine fish populations in the Green Lakes valley is valuable for several reasons. No published literature exists on unexploited alpine fish populations and those populations in the Valley have not been exploited since 1927 (Dieffenback, 1966). Therefore, the lakes in the Green Lakes Valley may be the only ones out of more than 2000 Colorado natural lakes that can serve as "experimental controls." Many Colorado lakes support trout populations and essentially all of them are located in the mountains at elevations between 2400 and 4080 m. Most are small, for example 90% are less than 8 ha, and usually less than 15 m deep (Nelson, 1976). Consequently, the overall resource comprises only about 6500 surface ha.

Surveys of the Green Lakes and fishes in the Valley have been limited to the Colorado Trout Lake Studies by Nelson (1968, 1972, 1974, 1976). Survey data are limited to the presence or absence of fish in the lakes, length-weight frequency analysis, and stomach analysis. No other published data have been reported for the vital statistics of the fish populations in the Green Lakes valley.

GREEN LAKES VALLEY FISHES

The first fisheries data for the Green Lakes Valley were reported by Nelson (1968). The lowermost lake (Albion) in the Green Lakes valley was surveyed in 1967 by catching fish with a flyrod. The 24 fish caught were all brook trout (Salvelinus fontinalis) that averaged 276 mm in length (range 211-305) and 205 g in weight (range 140-275). Stomach analysis from ten of the trout indicated a predominance of terrestrial insects (48%), followed in importance by miscellaneous aquatic insects (37%), zooplankton (11%), and debris (4%).

Lake Albion and Green Lakes 1-5 were sampled by gill netting in 1973 (Nelson, 1976) and in 1981 (Nelson, unpublished). Results indicated populations of brook trout in Lake Albion and Green Lakes 2 and 3, but no fish were caught in Green Lakes, 1, 4, and 5.

NORTH BOULDER CREEK (NORTH BRANCH) FISHES

The Green Lakes valley includes the north Branch of North Boulder Creek. The creek arises as an alpine first-order stream at its source, the Arikaree Glacier, close to the Continental Divide at an altitude of about 3800 m. The creek drops precipitously while passing through five of the six lakes in the drainage (Lake Albion and Green Lakes 2 through 5). A very small and very precipitious intermittent stream from Green Lake 1 causes the mainstem of North Boulder Creek to become a second-order segment. Below Lake Albion (3300-m) the creek passes through an alpine-subalpine transition zone into a wet meadow followed by a heavily canopied subalpine zone of very steep gradient. The lower reach immediately above Silver Lake is steep with numerous small waterfalls, which form a partial barrier that is insurmountable by fish except during the spring runoff.

Cope (1959) collected fish from the North Branch of North Boulder Creek in 1955 which were later examined by Miller (unpublished), Curator of Fishes, University of Michigan. The specimens differed from other races of Salmo clarki and it was proposed that they might represent the endemic greenback cutthroat trout Salmo clarki stomias. By 1978 it was learned that the pure populations inhabiting North Boulder Creek almost were completely displaced by a population of brook trout and only ten native greenback trout remained. The remaining ten were,transplanted in hope of saving the population, to rehabilitated Black Hollow Creek, a tributary to the Cache La Poudre River in Larimer County, Colorado. Subsequent investigation of Black Hollow Creek revealed reinvasion of brook trout and no evidence of greenback trout existence (Diffenback, 1966; Behnke and Zarn, 1976). No other published information is available on thefish population of North Boulder Creek.

Diffenback (1966) concluded that brook trout dominate North Boulder Creek and appear to have replaced the greenback cutthroat. Brook trout have access to reaches downstream of Lake Albion but can no longer migrate upstream from Silver Lake because the inlet passes through a raised culvert.

Study of the Green Lakes valley and North Boulder Creek assumes additional significance considering that greenback trout are found in the lakes and streams to the north and south of the valley and that the species is on the federal and state list of threatened species.

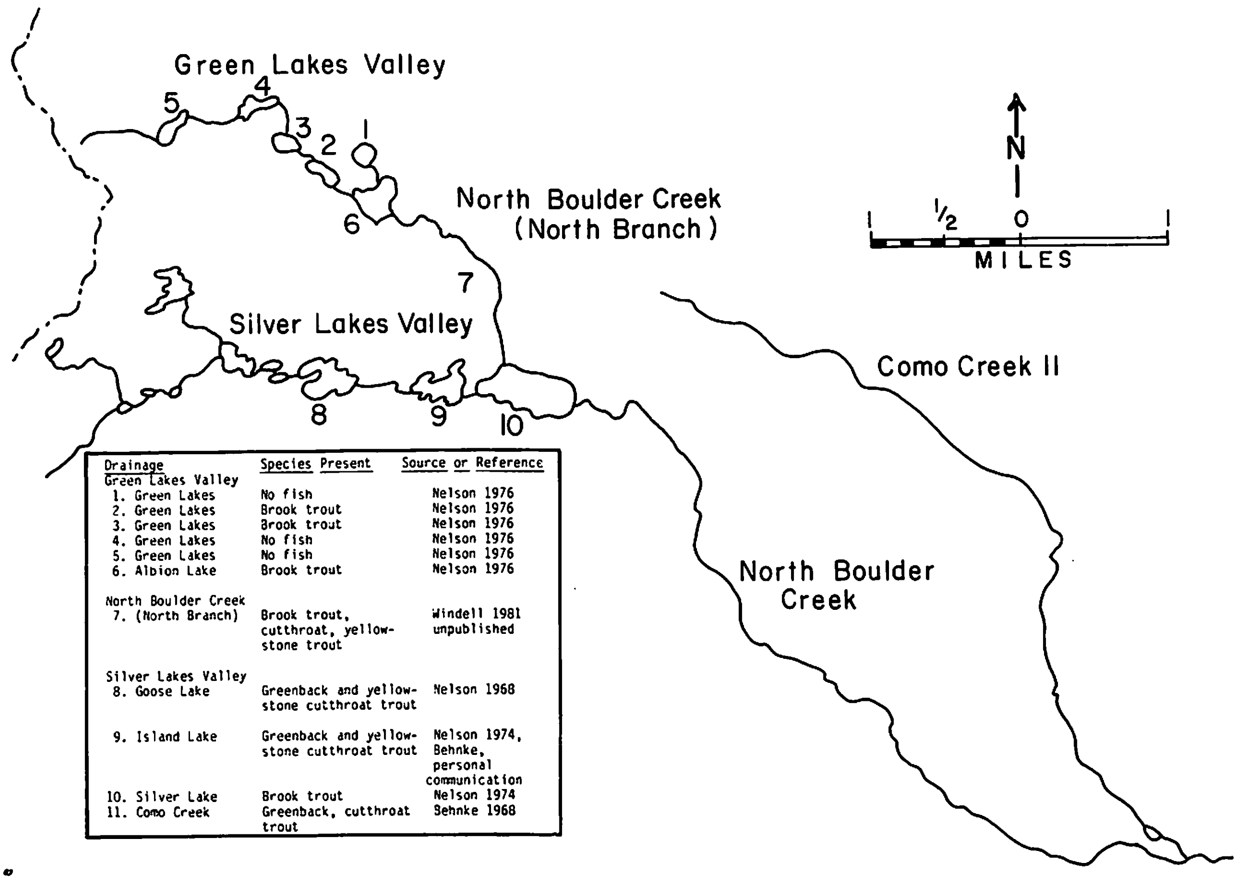
A genetically pure self-reproducing population of greenback trout currently survives in Como Creek, a tributary to North Boulder Creek (Behnke, 1968). Como Creek is a small subalpine second-order stream located in an adjacent drainage basin immediately to the north of the Green Lakes valley (Figure 1). A series of cascades and falls in the creeks lower reaches forms a natural barrier and prevents immigration of competitive exotic species such as the brook trout.

Island Lake contains a genetically pure, self-reproducing population of greenback cutthroat trout in spite of being mixed with the Yellowstone cutthroat trout (Behnke, pers. comm.). Goose Lake contains both subspecies but is dominated by Yellowstone cutthroat trout, Salmo clarki lewisi. Nelson (1974) and Behnke and Zarn (1976) reported a mixed population of brook trout and cutthroat trout in Silver Lake. The population in Island Lake is relatively dense and the fish are small. The population in Goose Lake is much less dense and fish reach a good size (Nelson, 1968). These differences are probably related to the presence of relatively good spawning habitat in the inlet to Island Lake but poor spawning sites in the inlet of Goose Lake.

HISTORICAL SIGNIFICANCE OF THE GREENBACK TROUT

Early history reports indicated that the cutthroat trout of the South Platte River was collected from the Platte River near Fort Riley, Kansas, and described by Cope (1856) as Salmo stomias. Later Cope (1871) reported the original stated area of collection to be in error and that the cutthroat trout in fact inhabited the Kansas River. However, confusion about the type location increased when Jordan (1891) reported that the Kansas River contained no trout and adopted the name stomias for the trout of the Platte River. With the identification of several subspecies, the name Salmo mykiss clarki was adopted to refer to cutthroat trout on both sides of the Cascade Range. Some of these subspecies were native to Colorado, but the greenback cutthroat was the only native salmonid existing in the mountain waters of the Arkansas River and the South Platte River systems (Behnke and Zarn, 1976).

Miller (1950) interpreted the cutthroat trout (Salmo clarki Richardson) series to include 11 subspecies. Taxonomy at the subspecific level is difficult because of inadequate early description and mixing of populations by man (Dieffenback, 1966). Present day taxonomic descriptions of the greenback trout have been derived from aggregates



Drainage	Species Present	Source or Reference
Green Lakes Valley		
1. Green Lakes	No fish	Nelson 1976
2. Green Lakes	Brook trout	Nelson 1976
3. Green Lakes	Brook trout	Nelson 1976
4. Green Lakes	No fish	Nelson 1976
5. Green Lakes	No fish	Nelson 1976
6. Albion Lake	Brook trout	Nelson 1976
North Boulder Creek		
7. (North Branch)	Brook trout, cutthroat, yellowstone trout	Windell 1981 unpublished
Silver Lakes Valley		
8. Goose Lake	Greenback and yellowstone cutthroat trout	Nelson 1968
9. Island Lake	Greenback and yellowstone cutthroat trout	Nelson 1974, Behnke, personal communication
10. Silver Lake	Brook trout	Nelson 1974
11. Como Creek	Greenback, cutthroat trout	Behnke 1968

Figure 1. Distribution of Fish species in upper Boulder Creek Drainage.

of information ranging from original descriptions and old museum specimens to actual examinations of suspected pure populations (Behnke and Zarn, 1976). The greenback cutthroat trout subsequently became known as Salmo clarki stomias.

Origin of the Greenback Trout

Behnke and Zarn (1976) reported that the greenback trout shows many taxonomic similarities with the Colorado River cutthroat trout, Salmo clarki pleuriticus, and hypothesized that the greenback trout was derived from an ancient headwater transfer from the Colorado River to the South Platte River drainage. Although similar, the greeenback trout is characterized by the largest spots and most numerous scales of all the subspecies of S. clarki. The striking spotting pattern and intense coloration of mature fish is the most diagnostic field character. The subspecies not only has the largest (round to oblong) spots of any cutthroat trout, but they appear concentrated posteriorly on the caudal peduncle area.

Original Range

The original range of the greenback cutthroat trout included Colorado and a small portion of southeastern Wyoming (Figure 2). Specifically, the range included headwater foothill streams and lakes and extended slightly past the foothills onto the plains before the warmer waters at lower elevations produced unsuitable habitat (Jordan, 1891; Juday, 1907).

Habitat Requirements

The habitat requirements of the greenback trout appears similar to other native cutthroat trout (Bulkley, 1963; Nelson, 1972). Circumstantial evidence indicates that all of the factors relating to habitat alteration and introduction of nonnative trouts, which have been proven responsible for declines in native populations within the interior United States, have had a particularly severe impact on the greenback trout. Therefore, two prime causes appear to be responsible for the decline and disappearance of the greenback from its historical range including the Green Lakes valley: (1) historical land-use practices such as irrigation, timbering, mining, pollution, etc. and (2) introduction of competing (nonnative or exotic) species, notably the eastern brook trout and the Yellowstone cutthroat. However, the introduction of exotic species is thought to be the major reason for the displacement. Displacement may be directly related to a later spawning period than other resident species which thereby confers a size advantage over the greenback or that predation of eggs by exotic species may be responsible for displacement and/or extinction.

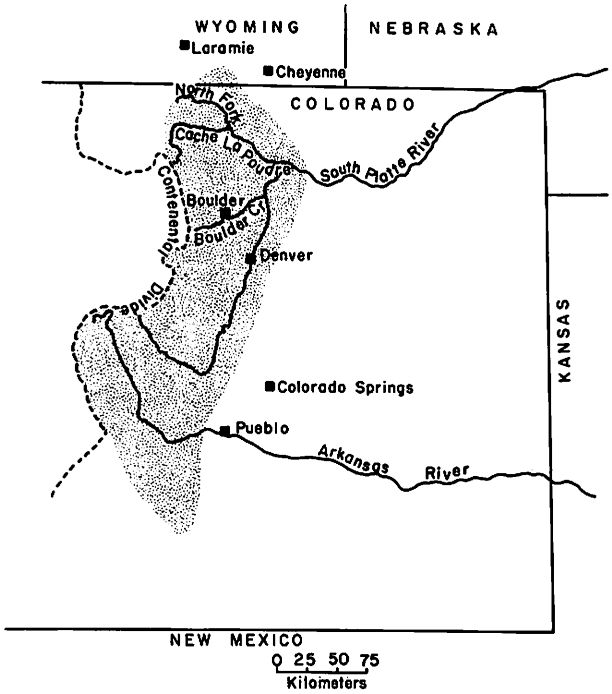


Figure 2. Original Range of Greenback Cutthroat Trout. Salmo clarkii stomias.

Current Status of Greenback Trout

Conservation efforts that first began in the late 1950s were formalized into a "greenback recovery team" in 1975 administered by the Colorado Division of Wildlife. The "team" included members from the U.S. Forest Service, National Park Service, U.S. Fish and Wildlife Service, and the Leadville National Fish Hatchery. The primary objective of the team and the recovery plan was to restore by the year 2000 S.c. stomias to a nonendangered and nonthreatened status in suitable habitat, such as headwater streams and lakes throughout its historic range.

Salmo clarki stomias was placed on the Federal Endangered Species List in 1968. However, this classification prohibited active management programs and restoration projects. On-going conservation efforts and an improved status caused the "Greenback Recovery Team" to recommend a change in the federal classification from "endangered" to "threatened." This request was granted by the State of Colorado and later by the Federal Government on 18 May 1978.

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A REVIEW OF SOME ASPECTS OF BACTERIOLOGICAL DECOMPOSITION OF PLANT LITTER IN THE COLORADO ALPINE

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ABSTRACT

A review of the role of bacteria in decay of alpine plant material and nutrient release is presented. These roles are discussed in relation to the high alpine area (3750 m). Because there are very few alpine studies published, a comparison is made by inference with the Arctic and Fennoscandian ecosystems.

The type of microorganisms found in soil and litter are discussed along with the factors involved in bacterial growth, such as soil temperature, pH, moisture, and climate.

This discussion is followed by an indirect comparison of Arctic tundra ecosystem with the alpine. This comparison includes a taxonomic structure of the microflora in the Arctic with with a discussion of the implications of such a taxonomic structure. Because of the complex nature of the bacterial ecosystem there are several models for the prediction of what may be occurring in the arctic tundra. These are GRESP, DECOMP and ABISKO. A short discussion is given of the Fennoscandian arctic tundra as a model for the alpine.

The paper closes with a discussion of what is known about the Colorado alpine.

INTRODUCTION

This literature review will determine the role of bacteria in the decay of alpine plant material and nutrient release and discuss these topics with respect to the Niwot Ridge high alpine station (D-1) at 3750 m and to some sites in the Saddle of the Niwot Ridge at 3353 m.

None of the studies involving alpine soil bacteria published since 1950 (Breuillaud and Grizon, 1951; Faust and Nimios, 1968; Shulls, 1976) reports on the degradation of alpine plant litter. However, the number of studies on decay of plant matter outside the alpine is extremely large, as illustrated by the two-volume work edited by Dickinson and Pugh (1974). Soil bacteria play a great role in the decay of plant matter (Alexander, 1961; Boyd et al., 1966; ; Parkinson et al., 1972). However, only selected papers dealing specifically with plant litter decomposition and nutrient flow will be cited. This review will not attempt to discuss material written before 1950.

Traditionally, energy flow and material cycling have been discussed from the perspective of the plant-herbivore-carnivore sequence, with only minor emphasis on the role of bacterial decomposition. Decomposition, however, is an important process. Approximately 52% of primary production products are utilized by bacteria in their own respiration, while about 3% of the total litter is utilized by herbivores and their predators (Teal, 1962). Most biomass ultimately becomes litter and is utilized by decomposing organisms. In a cold-dominated northern ecosystem, decomposition is slow, and the nutrients stored in the litter may exceed that of the biomass. In more temperate ecosystems, the speed of decomposition depends on moisture. Decomposition is fastest in tropical ecosystems (Swift et al., 1979).

Litter decomposition research started with observations in 1879 by P.E. Muller on the woodland and heathland soils of Denmark. Muller described beechwood litter as a deposit of forest detritus intimately mixed with the mineral soil, and in the upper horizons he observed earthworm action. He distinguished beech mor as a peaty deposit, rich in mycelium, sharply differing from the upper litter layer. The description of these two different types of humus became the foundation of the concept of humus types as a biological system in which vegetable, organic matter, microflora, and soil fauna interact to produce plant nutrients (Satchell, 1974). Rodin and Bazilevich (1967) described the production and mineral cycling of terrestrial vegetation in relation to litter-layer biomass as a function of leaf fall.

MICROFLORA IN DECOMPOSITION

Type of Biomass Utilized by Bacteria

Plant litter is composed of six main chemical substances: (1) cellulose, (2) hemicellulose, (3) lignin, (4) carbohydrates, (5) amino acids and aliphatic ethers (ether and/or alcohol soluble compounds, such as fats, oils, waxes, resins, and pigments), and (6) proteins. The degradation of the plant constituents follows a specific sequence controlled by the enzymes produced by microorganisms. Since 1970, attempts have been made to discover which enzymes are produced by the population of bacteria present in a given soil sample. Bacteria isolated from soil also have been examined in pure culture to determine their ability to produce certain enzymes and to investigate any regulatory mechanisms that may be involved. Many species of bacteria have similar enzymes, or enzymes that function similarly. The bacteria involved in decomposing litter are best classified in physiological groups such as cellulolytic bacteria which reproduce enzymes that decompose cellulose (Frankland, 1974).

Numerous studies have been performed on colonization of living and dead materials by microorganisms (Hudson, 1968). Those studies led Hudson to develop a model which suggests that senescent and dead tissue are sequentially colonized. Briefly, the model states that the primary colonizers are saprophytic organisms that degrade simple carbohydrates, whereas secondary and tertiary colonizers degrade increasingly more complex carbohydrates such as cellulose and hemicellulose. Lignin is the last substrate to be degraded. Summer and autumn were periods of maximum microbial colonization. Different groups of bacteria showed seasonal preferences.

Generally, bacteria are the first invaders of the young leaves, and their numbers increase during the growing season (Bray and Gorham, 1964). After litter fall there is an initial increase in bacterial numbers, probably due to more moisture, but species composition does not change. Bacteria already on the leaf start to multiply profusely, but the rate decreases with time. Litter may be invaded during the later stages of decomposition by soil bacteria not commonly found in the phyllophane. Soil bacteria include, for example, actinomycetes and Bacillus species. The pattern of litter fall varies in different climatic zones. In the Northern Hemisphere, leaf fall is normally concentrated in a rather short autumnal period, often with a peak in October or November. In the alpine, litter fall occurs in August and September.

Decay Processes in Litter

The first chemical change that occurs in litter is decomposition of carbohydrates, including starches, followed by pectins and soluble nitrogenous compounds. Inorganic ions are lost from the system through leaching. The second wave of microbial activity generally follows mechanical disintegration of the litter and consists of action by cellulolytic bacteria. The remaining lignin and hemicellulose products in the litter are decomposed slowly by leaf-dwelling Basidiomycetes (Herling, 1967). Soil samples also contain lignin decomposing organisms.

Webber (1976) studied the effect of decomposition of leaves of Geum rossii and Salix planifolia, both on the soil and at depth, by enclosing them in fine nylon mesh envelopes. Weight loss was measured at 1, 2, and 4 yr. The largest loss occurred during the first year due to breakdown of carbohydrates and minerals. Buried envelopes in a more complex ecosystem than those on the surface of the soil showed greater variation in decay rates. Greater losses in weight occurred in the soil than on the surface. The data showed clear-cut evidence that moisture played a major role in decomposition by microorganisms. The type of leaf surface and the presence of materials such as gums, which were cold-water soluble, also influenced first-year decomposition.

Recently, Odier et al. (1981) demonstrated that gram negative aerobic bacteria (Pseudomonadacecae and Neisseriaceae) have the ability to assimilate lignin without any cosubstrates. Tests were done incubating the organisms in three ways with dioxane lignin, milled wood preparations, and poplar wood labeled with $^{14}CO_2$. Release of $^{14}CO_2$ by Pseudomonas sp. from the labeled poplar wood demonstrated that complete mineralization of the lignin had occurred.

Decomposition in different ecosystems is characterized by flexibility of the system, accumulation of huge masses of organisms, and synthesis and resynthesis of organic compounds. There is a stepwise decomposition process leading into the nutrient cycle for plants. In general, the organic matter compounds utilized first by the bacteria are the water soluble compounds. Utilization of sugar compounds and the various organic acids follow (Eklund and Gyllenberg, 1974). Rainfall and acidic soil moisture will extract organic soluble compounds and aid in transporting them from the surface to deeper litter layers as cited by Eklund and Gyllenberg (1974). Soil bacteria follow this leaching process through the soil column. Eklund and Gyllenberg (1974) found that in most environments fungi are the primary decomposers, while bacteria are only secondary.

Types of Microorganisms Found in Litter

Controversy exists as to the type of microorganisms that occur in litter. Dickinson and Pugh (1965) have shown that root surfaces of Halimione portulacoides, in a salt-marsh system, are colonized by fungal communities. Dickinson (1966), who did a systematic study on the phylloplane, also showed that fungi (Cladosporium, Stemphylium, and Alternaria) would colonize the leaves of Pisum. Alternaria appeared to have saprophytic activity on Pisum and Cladosporium sporulated soon after death of the leaves. He stated that leaf physiology influenced fungi growth, which in turn was influenced by climatic factors.

Herling (1967) showed that ten species of fungi could be isolated from oak leaf litter decomposing in an acid soil. He had difficulty in isolating these fungi from the leaves because of a poor growth response to the media. Pugh (1958) studied, by isolation from surface-sterilized leaf tissue, the distribution of fungi growing on Carex paniculata leaves which were collected at intervals during a 2-yr study. Changes in fungi species were recorded as decomposition proceeded. The commonest species isolated from these leaves were Cephalosporium acremonium, Cladosporium herbacum, Fusarium velmorum, Trichodema viride, and species of Mucor and Penicillium. The most frequently occurring species were Metasphaeria cumana and Stysanus stermonites. These isolations correlated with higher temperature and lower water content of the leaf tissues during the summer months.

Evidence presented by Rosenzweig and Stotsky (1980) indicates that environmental factors such as pH and glucose concentrations produce antagonism between fungi and bacteria in the soil. Inhibition of *Aspergillus niger* by *Serratia marcescens* could be eliminated if the ratio of carbon to nitrogen was adjusted from 23:1 to 10:1 with ammonium nitrate. Andrews et al. (1980) demonstrated that Douglas-fir terpene, α-pinene, was able to inhibit the growth of a variety of bacteria and yeast.

Holm and Jensen (1972) studied the bacterial population in different parts of a Danish beech forest and concluded that there were more bacteria in the soil than in the litter. The dominant bacteria in the rhizosphere were nonspore forming, nonpigmented, gram-negative rods. They found that in the phyllosphere, yellow-pigmented rods were the dominant organisms. The dominant bacteria in the soil were spore formers, *Arthobacteria*-like rods and actinomycetes, the latter dominating the subsoils. The biomass calculation was about 1 g dry weight of bacteria per square meter distributed as follows: 40.44% in the mull layer, 45.38% in the mineral subsoil, 10.78% in the litter, 2.26% in the rhizosphere, and 1.2% in the phyllosphere.

Traditional studies of soil bacteria have been concerned with taxonomic identification. The degradation of the plant constituents follow a specific sequence controlled by the enzymes produced by microorganisms. A procedure that will relate bacterial soil numbers to their ability to produce certain enzymes, such as proteases, pectinases, amylases, lipases and cellulase in the soil is needed. Such information will add to our knowledge of how numbers of bacteria and distribution of biochemical activities are related to the characteristics of individual soils.

Hankin et al. (1974) examined the bacterial population of soils of cultivated land, pasture, orchard, forest litter, tidal marsh, and swamp in Connecticut. They also developed a mineral salts medium and, by the use of enrichment culture technique, were able to detect the biochemical activities of the bacteria present in these soils in order of increasing frequency: Cellulolytic > pectinolytic > amylolytic > lipolytic > proteolytic. Protein and starch degradation was related to soil type, while the degradation of pectin, cellulose, and lipid by bacteria was not influenced by soil type.

Physical Factors Affecting Bacterial Growth in Litter

Sorensen (1974), in some rather interesting experiments, found that the rate of decomposition was increased by wetting and decomposition was slowed in a dry sample or in one that was drying.

Witkamp (1966) showed that microbial respiration was controlled in decreasing order of importance by temperature, bacterial density, moisture, and length of time elapsed since leaf drop. Production of CO_2 was higher for rapid decomposition and was influenced by the species of leaves which were, in turn, dominated by certain types of bacteria. If fungi were involved, CO_2 release and rate of decomposition was slower. The rate of weight loss of plant parts was positively correlated with bacterial population size.

Howard and Howard (1979) attempted to relate decomposition of litter to temperature and moisture by measuring bacterial respiration in a constant volume respirometer. Tests were run on leaf litter from four species of trees and shrubs. Complex mathematical models were needed to explain the interrelationship between temperature, moisture, litter weight loss, and decomposition rate. Results were complicated further by the physiology of microorganism populations specific to plant species.

Howard and Howard (1980) showed that the leaves of different species in a forest, the soil on which the trees grew, and the climate influenced bacterial decomposition. Main effects shown were that weight loss of the leaf and respiration of the bacteria were directly proportional to the moisture content and pH. The number of bacteria isolated in Hudson's (1968) studies were affected by humidity, temperature, and sunlight.

The microbial population becomes more heterogeneous as decomposition occurs, increasing the probability of direct synergistic and antagonistic interreactions between the different organisms involved. Ljungholme et al. (1979), using microcalorimetric observations of microbial activity in soil, showed that pH has little or no effect on community composition, even if the pH has been lowered by two units.

TUNDRA ECOSYSTEMS

One can attempt to extrapolate from the literature on decomposition and nutrient cycling in the temperate zone to the tundra; very little microbiological data are available from the alpine tundra. The International Biological Programme Tundra Biome studies, although they are from the Arctic, Canadian, and Fennoscandian tundra sites, can be used for indirect examples of what may occur in the drier alpine tundra. Microorganism biomass is the smallest of the trophic levels in most ecosystems, but it is fundamental to regulation of ecosystem function. Bacterial biomass estimates made during the 1973 studies at Barrow were 2.12×10^{-1} gdw m^{-2} (meadows), 0.137×10^{-1} gdw m^{-2} (basins), 0.821×10^{-1} gdw m^{-2} (troughs), and 0.372×10^{-1} gdw m^{-2} (rims) (Bunnell et al., 1980).

There are fewer species of bacteria in the tundra soils than in soils of the temperate zone (Widden, 1977). Actinomycetes are reduced or may be absent due to the acidic, organic nature of the soil, while they do appear in the drier, less acid areas (Widden, 1977). The dominate species isolated in the tundra at Barrow were gram-negative, short rods; in wet meadows the most frequent genera were Pseudomonas, Achromobacter, and Flavobacterium, and in the drier areas, three species of Achromobacter and Cytophaga hutchinsonii were the most frequent (Dunican and Rosswall, 1974).

The numbers and species of gram-positive bacteria including spore-forming bacteria found by Dunican and Rosswall (1974) were the same as those found by Boyd et al. (1966) in the Arctic and Shulls (1976) in the alpine tundra. These were Arthobacter, Bacillus, and Corynebacterium.

Living plants are quite resistant to attack by bacteria and fungi, although plant surfaces are normally inhabited by epiphytic bacteria and fungi. These grow slowly and do little harm other than perhaps hastening normal senescence and death of the plant which then will be decomposed by bacteria and fungi (Goksøgr, 1975). Population change in bacteria is more rapid than that in fungi. Thus, in the tundra, because of lower temperature and higher moisture, the bacteria can quickly become dominant (Bunnell et al., 1980). It is a fallacy to assume that the fungi have a set of enzymes which give them an advantage in a given substrate and that bacteria have another set of enzymes. Both groups of organisms compete for any or all substrates available to them. There are some situations in which fungi will begin the process of decomposition and bacteria will finish it. However, this successional pattern may be the exception rather than the rule.

Taxonomic Structure of the Microflora in the Arctic

An extensive investigation of bacterial populations in the soil was carried out in the coastal tundra at Barrow, Alaska, by Bunnell et al. (1980). They found that the microflora had the same low species diversity evident among the plants and the herbivores. The microflora was characterized by rapidly changing bacteria populations which degraded smaller molecular compounds, and slowly changing fungal populations which were capable of degrading larger molecules. Organic matter accumulation in the tundra system reflects the historical imbalance between production and decomposition in the Arctic.

Bunnell et al. (1980) state that caution should be observed in regard to isolation techniques, as they, in general, select only a portion of the total viable flora. Bacteria and fungi that grow easily on artificial media do not necessarily reflect the dominant flora in the soil. This problem was addressed by examining bacterial groups as they contributed to the transformation of carbon, nitrogen, and sulfur. Tundra soils had fewer species than those found in the temperate zone.

Nelson (1977) has suggested some reasons for the high frequency of Pseudomonas, Arthobacter, and Bacillus. The Pseudomonas spp. were very resistant to starvation stress, which is a possible adaptation to the low amounts of soil nutrients found in arctic soils. Arthobacter spp. were tolerant to freezing and thawing effects when inoculated into sterile soil. The Bacillus spp., which were not encountered in great numbers, were more sensitive to the above stresses.

Anaerobic bacteria have been reported in tundra soils by Dunican and Rosswall (1974) and Clarholm et al. (1975). The Barrow study by Bunnell et al. (1980) inferred the presence of anaerobic bacteria, because significant quantities of adenosine triphosphate (ATP) were found in soils at depths where there was low oxygen content. When wet soils were heated, significant amounts of methane evolved. One of these investigators (Benoit, unpublished data cited by Bunnell et al., 1980) isolated methane bacteria from such soil.

Free-living, aerobic, nitrogen-fixing bacteria (i.e. Azobacter spp.) have been identified in both arctic and antarctic soils. The numbers were low and fixation of nitrogen by the acetylene reduction test has not been demonstrated (Boyd and Boyd, 1962; Boyd et al., 1966; Stutz, 1977). Waughman and Bellamy (1980) have demonstrated the presence of nitrogenase in peats from Canada and Norway. They found that the rate of nitrogenase activity was affected by temperature. The concentration of soluble nitrogen was high and the rate of nitrogenase activity was lower in peat from the northern latitudes as compared with peat from lower latitudes.

The soils in the Arctic tend to be too wet and too acidic for maximum bacteriological growth. At the Barrow site, meadow soils are rich in ammonia and low in nitrates. This would indicate the presence of nitrifying bacteria. Dunican and Rosswall (1974) reported that denitrifying bacteria were in abundance. Five percent of the total aerobic population were Pseudomonas, and 65% of those isolated were closely related to Pseudomonas denitrificans.

In contrast to the denitrifying bacteria in the arctic tundra, the chemoautotrophic bacteria are scarce or nonexistent. Sulfur is important for plants, but the concentration of inorganic sulfur is very low, less than 1 ppm, in the arctic tundra, while 50 to 100 ppm have been reported from temperate regions (Walker, 1957; Bunnell et al., 1980). The wet organic environment may favor accumulation of hydrogen sulfide, the terminal product in anaerobic mineralization of proteins. Hydrogen sulfide is toxic to many aerobic bacteria and could influence the nutrition of plants. Boyd

(1967) reported that autotropic sulfur-oxidizing bacteria are absent in the Arctic. Bunnell et al. (1980), by the use of enrichment cultures at pH 2 and 7, found that sulfur-oxidizing bacteria are very rare or absent at Barrow. Rosswall and Svensson (1974) were unable to demonstrate photosynthetic sulfur-reducing bacteria in Arctic soils at Barrow. Dunican and Rosswall (1974) have demonstrated sulfur-reducing bacteria from both Arctic and Antarctic soils. Ponds and soils at Barrow have high concentrations of iron, but no chemoautotrophs capable of oxidizing ferrous iron were detected (Bunnell et al., 1980).

Microbial Biomass in the Arctic

The measurement of microbial biomass is useful in establishing the relationships between the microflora and its environment. Seasonal averages of bacterial density and biomass are calculated by estimating the volume from density and percentage dry weight measurements. Bunnell et al. (1980) found the highest density of bacteria in troughs (10.5×10^6 gdw^{-1}) and the lowest in basins (0.574×10^6 gdw^{-1}). Rims were next (1.31×10^6 gdw^{-1}), and meadows had the median bacterial density (7.73×10^6 gdw^{-1}). The pattern of bacterial biomass changes with depth, the highest occurs at 0-2 cm while the lowest occurs at 7-12 cm. Bunnel et al. (1980) found that one season (1971) of collection the biomass was at 16 g cm^2 of which 75% was bacterial. Clark and Paul (1970) found the biomass was 77 gm m^2 at 10 cm depth (in grasslands soil) of which 31% was bacteria. This data indicates that the biomass in the Arctic is at the 2 cm depth during the summer months with the activities concentrated in the surface layer of the soil.

Bacterial Activity and Decomposition in the Arctic

The physical and chemical changes that occur around a substrate that is being decomposed cannot be separated easily from the activities of bacteria and other microbial activities. The degradation of plants is generally measured by weight loss and specific chemical changes that occur during disintegration and mineralization of the organic residue present (Flanagan and Bunnell, 1980). These interactions may occur by induced senescence and autolysis in moribund tissue. The weight loss from organic tissues may occur independently of bacterial activity by leaching of snowmelt. The decomposition by bacteria may be indirectly modified by the activities of soil invertebrates, protozoa, and soil algae. These alter the environment by physical structure change, modification of pH, and supply rates of oxygen.

Organic matter is decomposed, resulting in synthesis and resynthesis of bacterial tissues which can themselves decompose and contribute to further bacterial production of biomass. The Arctic has few substrates; although the protein reserve is present but is locked in the permafrost. Bacteria become highly efficient in dissolving, assimilating, and incorporating these available organic remains. These processes are influenced by climatic and substrate variables (Gray and Williams, 1971).

Aerobic conditions allow bacteria to decompose the substrate complex of organic molecules to end products, i.e. CO_2, H_2O, and minerals. Anaerobiosis produces end products that are a variety of organic and inorganic substrates.

This breakdown of plant remains results in loss of weight and change in physical structure and energy content. Therefore, all the above changes could be used to measure decomposition. One must also recognize the different enzymatic reactions that utilize and exploit the substrate. Enzymes respond differently to temperature, moisture, oxygen, and pH in the environment.

Measurement of microbial biomass during decomposition will allow one to relate the abundance of the major decomposing agents to substrate availability and quality. With data from the laboratory on bacterial growth and yield, one can approximate bacterial production in the field (Flanagan and Bunnell, 1980). These patterns of decomposition can be defined by the above data and equated to the mineralization process under both aerobic and anerobic conditions. Most soil microbial populations are heterotrophic, and the organisms compete for the various substrates. In addition, not all these microorganisms utilize and compete for the same substrate.

Flanagan and Bunnell (1980) divide the decomposer organisms at Barrow into two main categories based on chemical composition, pattern of dissolution, and utilization by microorganisms: (1) Low molecular weight, water and/or 80% ethanol-soluble fractions that are readily leachable. This group contains approximately 25% of aboveground plant products, the bulk of plant leaf nitrogen, phosporus, and potassium. (2) More recalcitrant compounds like lignin, cellulose, hemicellulose, pectin, and starch. These represent the bulk of available organic substrate, but are relatively poor in nitrogen, phosphorus, and potassium (Flanagan and Veum, 1974).

Cellulose in the Arctic is decomposed by *Cytophaga* which varied from 10^5 (gdw soil)$^{-1}$ to 10^6 (gdw soil)$^{-1}$. After thaw, most bacteria present will act on the partially degraded substrates. Benoit (unpublished data cited by Flanagan and Bunnell, 1980) used 200 randomly selected aerobic types of bacteria isolated from 0 to 2 cm soil depth from wet meadows and studied these bacteria utilizing specific carbon sources. Ninety-two percent of the bacteria used succinic acid, and 84% used citric acid. Carbohydrates, such as glucose, maltose, and starch, were utilized by 78, 66, and 42% of the bacteria tested. 28% of these bacteria used pectin, 25% used lactic acid, and 5% used cellulose. Humic substrates use oxygen for enzymes to cleave the aromatic ring. When these materials move from the surface they enter less aerobic conditions and probably have a marked reduction in their decomposition. Bacteria and fungi exhibit different capacities to act on humus because of their differential abilities to survive low oxygen tensions and may be instrumental in accumulation of organic matter in the soil horizon.

Little, if anything is known about the physiological activity in the soil of the anaerobic bacteria present. As stated previously, enrichment techniques can indicate the presence of cellulose, decomposers, and methane-producers. No evidence was obtained that humic materials can be acted upon by anaerobic bacteria, and, as a result, their activity is limited to a pool of rapidly decomposable material from moribund belowground plant parts (Flanagan and Bunnell, 1980).

Therefore, continued decomposition becomes a stepwise action of both aerobic and anaerobic bacteria. All of these actions are influenced by abiotic conditions such as temperature and soil oxygen, which are associated with moisture. In an attempt to correlate these actions Bunnell et al. (1977a) produced three simulation models (GRESP, DECOMP, ABISKO) which relate "microbial activities quantitatively and unambiguously to the environment phenomena." GRESP (Bunnell et al., 1977a) relates respiratory response of bacterial populations to the changing temperature and moisture. DECOMP (Bunnell et al.,1977b) looks at substrate chemistry and respiration. ABISKO (Bunnell and Scoullar, 1975) attempts to integrate the effects of changing weather and substrate chemistry within an ecosystem framework.

The first model (GRESP) treats aerobic respiration as a function of the supply rates of water, oxygen, and organic nutrients. The assumption is made that microbial respiration is related to the moisture potential of the substrate via salination processes. Temperature and substrate characteristics are treated as a substrate-specific Q_{10}. GRESP deals with a complex hypothesis and the model does have problems, but ecological results can be predicted from it. GRESP predicts carbon dioxide evolution more accurately from above ground substrates than from tundra soils. Actual measurements show that the model is only 78 to 84% accurate in predicting variability in respiration rates in aerobic soils (Flanagan and Bunnell, 1980).

Howard and Howard (1979) also attempted to model respiration in decomposing litter by relating it to temperature and moisture. They used three models: (1) respiration against temperature, (2) Q_{10} model and (3) Arrhenius model (logarithm of respiration against 1/T°K). They found it difficult to model respiration and CO_2 evolution. Part of the problem is the complex effect of moisture, differences on the physiology of populations of decomposer microorganisms and different plant materials. The GRESP model attempts to solve the moisture problem by assuming two moisture processes.

The DECOMP model provides a framework that will allow laboratory measurements to be extrapolated to predict total loss of substrate weight and change in composition of substrate. This model does give reasonably close agreement between simulated and measured values of standing dead material (Bunnell et al. 1977b).

Bunnell and Scoullar (1975) have evaluated the ABISKO model for the tundra biome research area at Barrow. This involved in situ measurements of CO_2 evolution with the cumulated totals of a simulated respiration. It is a complex model but it is not as specific as GRESP and DECOMP are for bacteria.

Fennoscandian Tundra Ecosystems and Decomposition

Tundra ecosystems of northern Finland, Norway, and Sweden can be used in developing a base line for comparison to the alpine tundra.

The smallest component of an ecosystem is the biomass of bacteria, but it is of fundamental importance in regulating the ecosystem. Here the greater proportion of primary production passes directly through the decomposer system. Odum (1968) has shown that the ratio of energy flow (kcal m^{-2} d^{-1}) to biomass (g m^{-2} d^{-1}) is 1000 for soil bacteria. The relatively high activity of bacteria, as the decomposing organisms, is shown by the index of energy flow (kcal m^{-2} d^{-1}) divided by biomass (g m^{-2}), which has been calculated to be 1000 (Odum, 1968; Teal, 1962). Clarholm et al. (1975) indirectly studied energy flow for bacteria by measuring decomposition of plant litter. The tundra site investigated had a low pH and low oxygen concentration (microaerophilic to anaerobic). These conditions are common to waterlogged milieu, like peat. The plant production exceeds the rate of decomposition and removal, and organic material accumulates in the form of peat. Thus peat is an indication of low activity of soil bacteria. Clarholm et al. (1975) concluded that direct bacterial counts provided the best estimate of "locked up" energy.

The bacterial counts in the subalpine heath were 225 x 10^{-4} gdw for the A horizon, 9.1 x 10^{-4} gdw for the B horizon. The counts agree with those of Boyd's (1958) site at Barrow and Shulls (1976) in the Colorado alpine tundra. Bacterial numbers and biomass fluctuated greatly with season and depth of soil sample. Adaptation to temperature was found with 84% growing of the tested species at 2°C and only 5% growing at 37°C. There was a tolerance to pH, i.e. at pH 5.5, 44% grew while at the meadow site only 4% (Benoit, unpublished data in Flanagan et al. 1981).

The species of bacteria found by Clarholm et al. (1975) were limited: Nitrosomonas, Nitrobacter, Pseudomonas, and Bacillus. The predominate group were the Bacillus.

Berg et al. (1975) used cellulose as a model substance in studying decomposition rates in the Fennoscandian tundra. They felt it was useful for comparative studies because it was free of leaching associated with litter, samples were simple to prepare and analyze for weight loss, it was not difficult to compare the different rates associated with litter, and practically all plant material contains cellulose in amounts ranging from a few percent in grasses to as high as 40% in wood. Degradation of cellulose is also restricted to few groups of microorganisms, bacteria, fungi, and actinomycetes.

The material used was dried sheet cellulose, containing 100% glucan and 0.04% ash (Rosswall and Veum, 1971), and a very porous cellulose preparation containing 85% glucan, 10% xylan, 5% mannan, and 0.2% ash (Berg and Rosswall, 1972). These samples were buried at 2, 10, and 20 cm, and weight loss was observed. The rate of decomposition by weight loss was 3% in both mire and wet meadow. If birch and pine were present, varying rates were observed (Berg et al., 1975). In general, 6 to 14% decomposition was observed in the tundra. The higher rate was in open heath but under *Calamagrostis*; the higher rate was probably due to conservation of moisture by the plant cover. The average weight losses after 2 years were 57% at 2 cm, 45% at 10 cm, and 11% at 20 cm. Fertilization of cellulose samples with nitrogen sources speeded up the weight loss, which suggests that normally there is a lack of available nitrogen. Addition of phosphorus did not effect the rate of weight loss.

The majority of microorganisms in the Fennoscandian ecological systems seem to be fungi; 80% were composed of the following genera: *Penicillium*, *Chrysosporium*, and *Humicola*. However, a large percentage of the *mycelia* were sterile. The reason seems to be inherent in the soils, mainly wet peat with pH 5.0, anaerobic or microaerophilic, i.e. conditions that favor bacteria and not fungi.

Colorado Alpine Tundra

Elements of both the arctic and Fennoscandian sites are reflected in the alpine tundra. The alpine tundra is a harsh ecosystem, with a well-defined vegetation, but bacteriologically it seems to resemble grasslands, forest, or arctic tundra. The soil pH is at 6.5 rather than 5.5 commonly found in arctic sites. The abiotic parameters fit very few areas. This is a unique ecosystem.

Shulls (1976) found that four genera of fungi occurred in the alpine tundra. They were *Mucor*, *Penicillium*, *Oidium*, and *Aspergillus*. No *thermophilic or anaerobic bacteria* were found. The predominant bacteria are chemautotrophs and heterotrophs. Many are facultatively anaerobic; some are aerobic. They are species of *Bacillus*, *Pseudomonas*, *Micrococcus*, *Erwina*, *Arthobacter*, *and actinomycetes. These bacteria seem to grow* best in the mesophilic temperature range (5 to 25°C). The bacterial data are similar to that of Ivarson's (1956) from the permafrost tundra soil of the MacKenzie River Valley.

The seasonal differences between the Arctic and the Colorado alpine are probably due to moisture conditions. During the winter at high elevations, soils are dried out by high winds. Moisture may be partially restored by snowfall, but frequently the high winds also remove the snow cover as it thaws, exposing the soil again. Similar conditions also occur in the Arctic during winter. In the alpine during the summer, sudden daily rain storms maintain the moisture (Shulls, 1976). Numbers of bacteria flora of alpine soils from the Niwot Ridge are in agreement with those found in the Montana alpine (Faust and Nimios, 1968). These bacteria are heterotrophic, aerobic, or microaerophilic (Cameron, 1971) and, as noted by Boyd (1967), arctic polar soil populations are primarily mesophilic bacteria. These same observations were substantiated with the Colorado alpine bacteria (Shulls, 1976). Arctic and alpine populations grow best at 15 to 22°C, which is within the minimum mesophilic range.

Shulls and Mancinelli (1982) have investigated the complex problem of characterizing the various bacterial nutritional types that are present in the alpine environment. Samples collected from the plains, grasslands, lower montane, upper montane, and subalpine forest were used as a control or standard for comparison with the bacteria found in the alpine tundra. The harsh alpine environment found above 3300 m must be compared with some other area, such as lower elevations, to determine the effect of such a harsh environment on the microbial population. The contrast between the lower areas and the alpine becomes startling when the bacterial digestion of starch, cellulose, pectin, and protein is examined. At 3300 m, only cellulose, pectin, and starch digestion exist, whereas from 1680 to 3200 m proteolytic activity also occurred. Some bacteria that are involved in the nitrogen cycle were found to be present. Soil changes with elevation; forest soils tend to be acidic and as elevation increases, the pH tends to increase to near neutral. The normal pH range is in alpine soils is 5.0 to 6.8 but most soil bacteria tolerate these differences quite well.

The alpine tundra shows acceleration of growth, blooming, and seed setting for many plants. This is due, in part, to climate and to plant nutrition. Nitrogen is one of the most important elements needed by a plant for these growth processes and is probably the limiting nutrient in the alpine environment. We have found on Niwot Ridge free-living nitrogen-fixing bacteria but no symbiotic nitrogen fixers. Nitrogen must come from somewhere in the system. *Trifolium* spp. and *Lupine* spp. are symbiotic *nitrogen-fixing alpine plants*, but are not present ubiquitously. We suggest that the primary source of nitrogen, is that fixed abiotically by lightning and air ionization. The secondary source may be from the recycling of plant protein through leaching and microbial degradation.

It is evident that there is a large biomass accumulation which supports a huge mass of organisms that synthesize and resynthesize organic compounds. It appears to begin with the degradation of litter and is probably aided by the rainfall, although little occurs.

We have shown that as elevation increases, the number of amylolytic, cellulolytic, and pectinolytic bacteria also increases. In addition, it seems that in the alpine, fungal decomposition of litter is secondary to that of bacteria. This is probably due to the higher pH of the soil and the drier conditions. The proteolytic group of bacteria seem to dominate in the soil of lower elevations.

CONCLUDING REMARKS

The alpine is a unique place. It is a harsh ecosystem, but the resemblance to the Arctic tundra ceases with the weather system. Its vegetation is well defined, but with a variety of species. The soils resemble those of temperate forest and meadows with a diversity of bacterial species. There are two general differences that set the alpine tundra apart and these are very fundamental to the total ecosystem. They are the way nitrogen is supplied to the soil, and the altitude influence on the type of enzymes produced by the heterotrophic bacteria present.

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