Ecological Investigations of the Tundra Biome in the Prudhoe Bay Region, Alaska

Edited by Jerry Brown

Biological Papers of the University of Alaska
Special Report Number 2 October, 1975

Ecological Investigations of the Tundra Biome in the Prudhoe Bay Region, Alaska

Edited by

Jerry Brown, Director
U.S. Tundra Biome
U.S. Army Cold Regions Research
and Engineering Laboratory
Hanover, New Hampshire 03755

Biological Papers of the University of Alaska
Special Report Number 2 October, 1975

BIOLOGICAL PAPERS OF THE UNIVERSITY OF ALASKA

Library of Congress Catalog Card Number: 75-620095

Abstract

During the period 1970-1974, the U.S. Tundra Biome Program, which was stationed primarily out of Barrow, performed a series of environmental and terrestrial ecological studies at Prudhoe Bay.

This volume reports specifically on the Prudhoe results and is divided into three major subdivisions: (1) abiotic and soil investigations; (2) plant investigations, and (3) animal investigations. The abiotic section contains papers on the air and soil temperature regimes; the snow cover, particularly its properties adjacent to the roadnet; major soil and landform associations, and the chemical composition of soils, runoff, lakes, and rivers. The plant section contains reports on a general vegetation survey; a follow-up vegetation mapping project, and a study of the growth of arctic, boreal, and alpine biotypes in an experimental transplant garden. The animal section contains reports on the tundra invertebrates; the bird, lemming, and fox populations, and the behavioral and physiological investigations of caribou and several experimental reindeer. Appendices contain a checklist of the vascular, bryophyte, and lichen flora of the Prudhoe Bay area and selected data on vegetation. Several of the papers draw comparisons with the Barrow tundra.

The volume includes a considerable number of tables in its attempt to document for the first time the abiotic, flora, and fauna of this relatively unknown arctic tundra landscape.

In Memoriam

This volume is dedicated to the memory of Scott Parrish, who died in a plane crash on 26 August 1974. During the period 1971-1974, Scott was involved directly in many aspects of the Biome's Prudhoe Bay research. This included arranging and expediting the program's logistic requirements, design of experiments, data reduction for several projects, and overall guidance to Biome personnel on research activities and opportunities at Prudhoe. We considered Scott both a friend and scientific colleague. His thoughts on and concerns for the environment were highly respected. The loss of his experience and personal knowledge of the Prudhoe area is irretrievable. We hope that this volume will record for the future both Scott's memory and his interests in the tundra.

Table of Contents

Appendix A

Appendix B

Plate I

Preface

This volume contains project reports on research sponsored and coordinated under the U. S. Tundra Biome Program of the International Biological Program (IBP) at Prudhoe Bay, Alaska.

Comprehensive Biome research was initiated at Barrow in 1970. The Prudhoe Bay area was selected as a second arctic coastal plain site in order to gather comparative and validation data for the more comprehensive Barrow investigations. In addition, the Prudhoe area was essentially unknown ecologically, and the program's presence in northern Alaska, with its large ecological research team, afforded an excellent opportunity to gather data of a basic bioenvironmental nature at Prudhoe. To this end, a series of studies ranging from one to three summers' duration and reconnaissance observations were conducted in areas easily accessible from the road network.

Funding of these Prudhoe research efforts has been largely shared amongst industry sources, the State of Alaska, and the National Science Foundation. Without exception, the logistical costs at Prudhoe were paid from funds provided by the Prudhoe Bay Environmental Subcommittee which, since 1970, have amounted to $282,000. Portions of these funds have been used to support direct research, and individual reports in this volume acknowledge their use. However, the magnitude of the Biome's program at Prudhoe would not have been possible without the core-funded, National Science Foundation support of the 5-year Tundra Biome Program, a program jointly supported at NSF by the Office of Polar Programs (OPP) and the International Biological Program (Ecosystems Analysis Section). This NSF program was largely funded for the Barrow intensive site which, in turn, provided personnel for the Prudhoe research. The Barrow and, subsequently, the Prudhoe projects were supported in the field by and provided with laboratory equipment from the Naval Arctic Research Laboratory at Barrow. Partial funding for the Prudhoe research has been derived from the State of Alaska and from nonrestrictive grants from individual oil companies to the University of Alaska's Tundra Biome Center (Dr. George C. West, Director). The following is a list of contributing companies through 1974:

Atlantic Richfield Company
Alyeska Pipeline Service Company
BP Alaska, Inc.
Cities Service Company
Exxon Company, USA (Humble Oil & Refining Company)
Gulf Oil Corporation
Marathon Oil Company
Mobil Oil Corporation
Prudhoe Bay Environmental Subcommittee
Shell Oil Company
Standard Oil Company of California
Standard Oil (Indiana) Foundation, Inc.
Sun Oil Company

We wish to acknowledge the many individuals and companies involved at Prudhoe who made the conduct of this program possible. The operators, BP Alaska, Inc. (Western Section) and Atlantic Richfield Company (Eastern Section), and their staff did everything possible to facilitate the accomplishment of our projects. BP, and particularly Charlie Wark, lent considerable support in making lab and field space available and solving operational questions. Angus Gavin of Atlantic Richfield Company provided a considerable amount of background information on the birds and wildlife of the area as well as logistical assistance. The staff and facilities of Mukluk Freight Lines provided excellent working and living conditions. Nabors Alaska Drilling Inc. provided additional field lab facilities. Both helicopter and fixed wing flights were provided by the operating companies, Alyeska, and others, and this assistance is gratefully acknowledged by all projects.

The initial volume preparation was performed at the U. S. Army Cold Regions Research and Engineering Laboratory under an interagency agreement with NSF for Tundra Biome management and publications. The CRREL editorial staff, Mr. Stephen Bowen, editor, and Mr. Harold Larsen, illustrator, is acknowledged for its early assistance in volume preparation. The final copy preparation, editing, and drafting was performed under the editorship of Ms. Laurie McNicholas and the graphics supervision of Ms. Mary Aho of the University of Alaska's Arctic Environmental Information and Data Center (Mr. David Hickok, Director).

Dr. Stephen F. MacLean, Jr. prepared the introduction and, along with Dr. West, provided considerable assistance in critical review and development of the volume. Barbara and David Murray provided verification of the usage of all plant names in the volume.

Jerry Brown, Editor

Geographical setting of the U.S. IBP Tundra Biome study area at Prudhoe Bay.


70°
148°50'
148°40'


ARCTIC
OCEA
160°
150°
140°
70°
70°
68°
CHUKCHI SEA
BEAUFORT SEA
COLVILLE RIVER
NOATAK RIVER

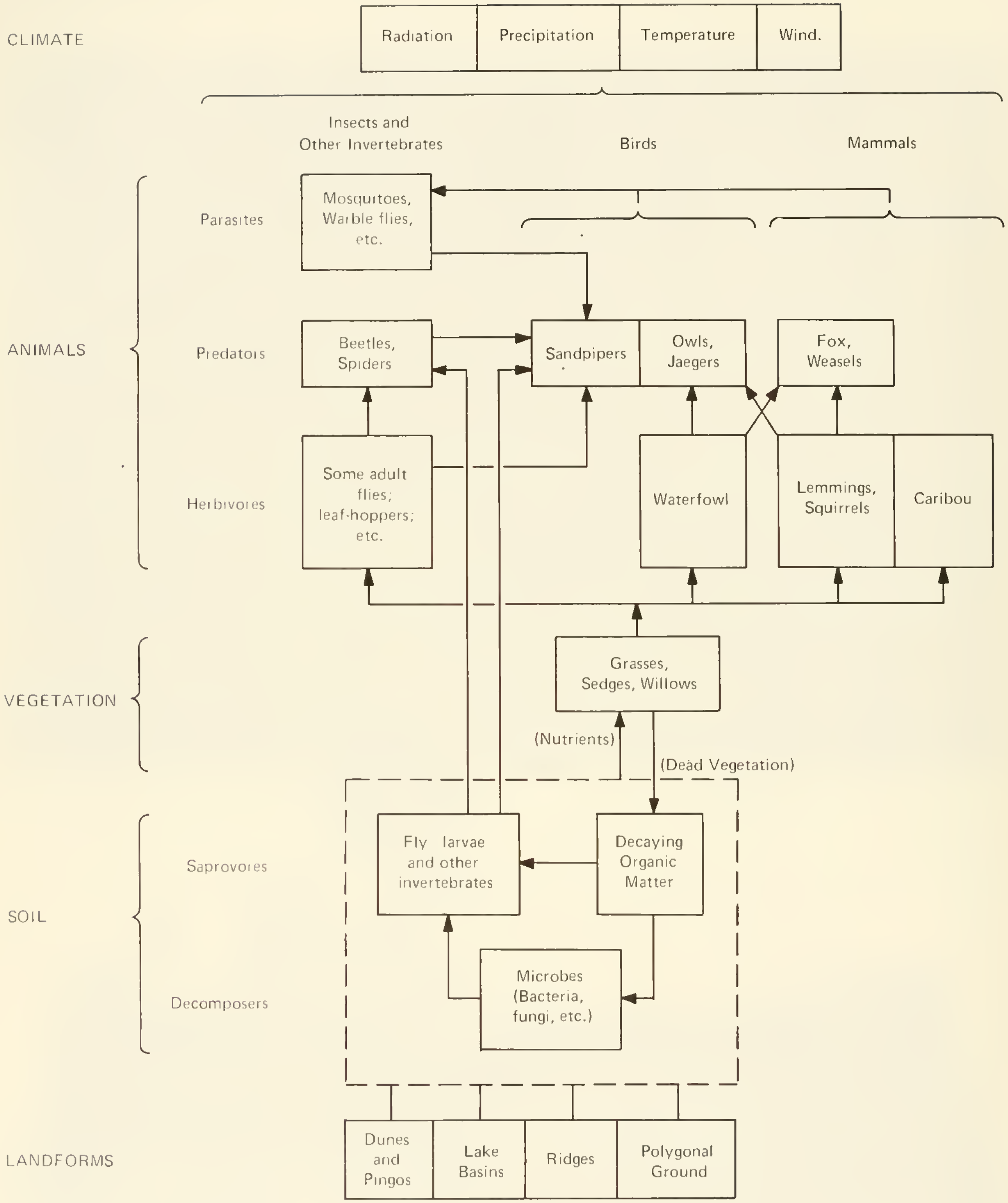


Fig. 1. *Flow diagram of major components of the Prudhoe terrestrial tundra and their interrelationships.*

Introduction

The approach of the Biome studies of the International Biological Program centers around the ecosystem concept. We view the soil, the vegetation, the microorganisms, and the various animal species as parts of an integrated natural system. Their interactions, as influenced by climate, landforms, and other "abiotic" factors, produce the natural ecosystems that we know (grassland, forest, desert, etc.). The tundra ecosystem is dominated by the low winter temperature; short, cool growing season, and (at least on the coastal plain of northern Alaska) flat topography and presence of permafrost (perennially frozen ground) close to the surface.

The vegetation that grows under these conditions is characteristically low in stature and dominated by grasses and grass-like sedges. The variety or diversity of both plant and animal species is low. Marked seasonality of ecosystem function is an obvious and important feature of tundra. A simplified view of ecosystem organization at Prudhoe Bay is shown in Fig. 1.

Our approach to the study of the tundra ecosystem involves:

1. Identification of the plant, animal, and soil organisms that make up the system, and their distribution in space (e.g., across major landforms) and time.
2. Measurement of the climatic and other abiotic variables that influence the system.
3. Description of the functioning of the plant, animal, and soil elements of the system (e.g., plant production, caribou grazing, lemming reproduction).
4. Study of the interactions between the major ecosystem processes of primary production, consumption by animals, and decomposition and mineral nutrient cycling.

An important tool of ecosystem research is the ecological model. The model is a formalization of our biological understanding of the system. Specific biological processes or interactions are described by one or a set of logical and mathematical expressions; the entire system may be regarded as a set of simultaneous interactions. The ability of these expressions to mimic the real system offers a test of our biological understanding of the systems and identifies gaps and weaknesses. Completed ecological models may provide some degree of predictive power in answering "What would happen if . . ." questions.

The scope and intensity of research at Prudhoe Bay has not been sufficient for the construction of a "whole system" ecological model; however, models have been constructed for particular biological processes (e.g., caribou grazing), and data collected at Prudhoe Bay will be used to test models developed through more intensive research at Barrow. Thus, Prudhoe Bay data are being used to test the generality of results obtained at Barrow and other international tundra sites. Another purpose of this volume is to present observations and data gathered by Tundra Biome scientists so that the region can be better known to future investigators, the industry, and others involved in activities at Prudhoe Bay.

Abiotic and Soil Investigations

Automatic, year-round weather station installed on a pingo at Prudhoe Bay. Data collected on strips charts included radiation, wind speed and direction, air and soil surface temperatures, and precipitation. The station was operated by the University of Alaska's Geophysical Institute.

David Atwood, USACRREL

Selected Climatic and Soil Thermal Characteristics of the Prudhoe Bay Region

JERRY BROWN and RICHARD K. HAUGEN
U. S. Army Cold Regions Research and
Engineering Laboratory
Hanover, New Hampshire 03755

and

SCOTT PARRISH*
Tundra Biome Center
University of Alaska
Fairbanks, Alaska 99701

Introduction

Biological, ecological, and environmental phenomena are dependent to a significant degree upon the air and soil thermal regimes. The climate of the Prudhoe Bay region was virtually unknown prior to 1969. The National Weather Service stations at Barrow and Barter Island provide the short- and long-term records from which to compare Prudhoe's climatic position in the coastal plain. Based on previous analyses of North Slope air temperatures (Watson 1959; Searby and Hunter 1971), Prudhoe Bay should lie within the following temperature ranges:

Mean maximum January between -20° and -23° C

Mean minimum January between -27° and -30° C

Mean maximum July less than +8° C

Mean minimum July between 1° and 2° C

Although a variety of standard climatic data have been obtained for the immediate Prudhoe Bay area over the past 4 to 5 years, air temperature is emphasized in this report as this is the only parameter for which there are reasonably continuous and reliable records. Selected precipitation, soil temperature, and thaw data are also presented to provide initial data for this relatively unknown region of the North Slope.

The objectives of this report are: (1) To compare the limited air temperature and precipitation records for Prudhoe Bay with a comparable period for Barrow and Barter Island, (2) to examine annual and seasonal temperature variations at Prudhoe Bay, (3) to characterize differences in the temperature regimes of coastal and inland sites, and (4) to present limited soil temperature and thaw data.

Methods

Reasonably consistent climatic data are available from four principal sites (Fig. 1):

(1) BP Alaska, Inc. radio station in the vicinity of the Mukluk Camp: This includes wind speed and direction and air temperature on a mast, recorded continuously. For the present report, daily minimum and maximum air temperatures were obtained from the original records. These records were made available by BP Alaska, Inc. and appear to offer the most consistent and continuous set of temperatures for the Prudhoe Bay area. The data from this site

---

*Deceased.

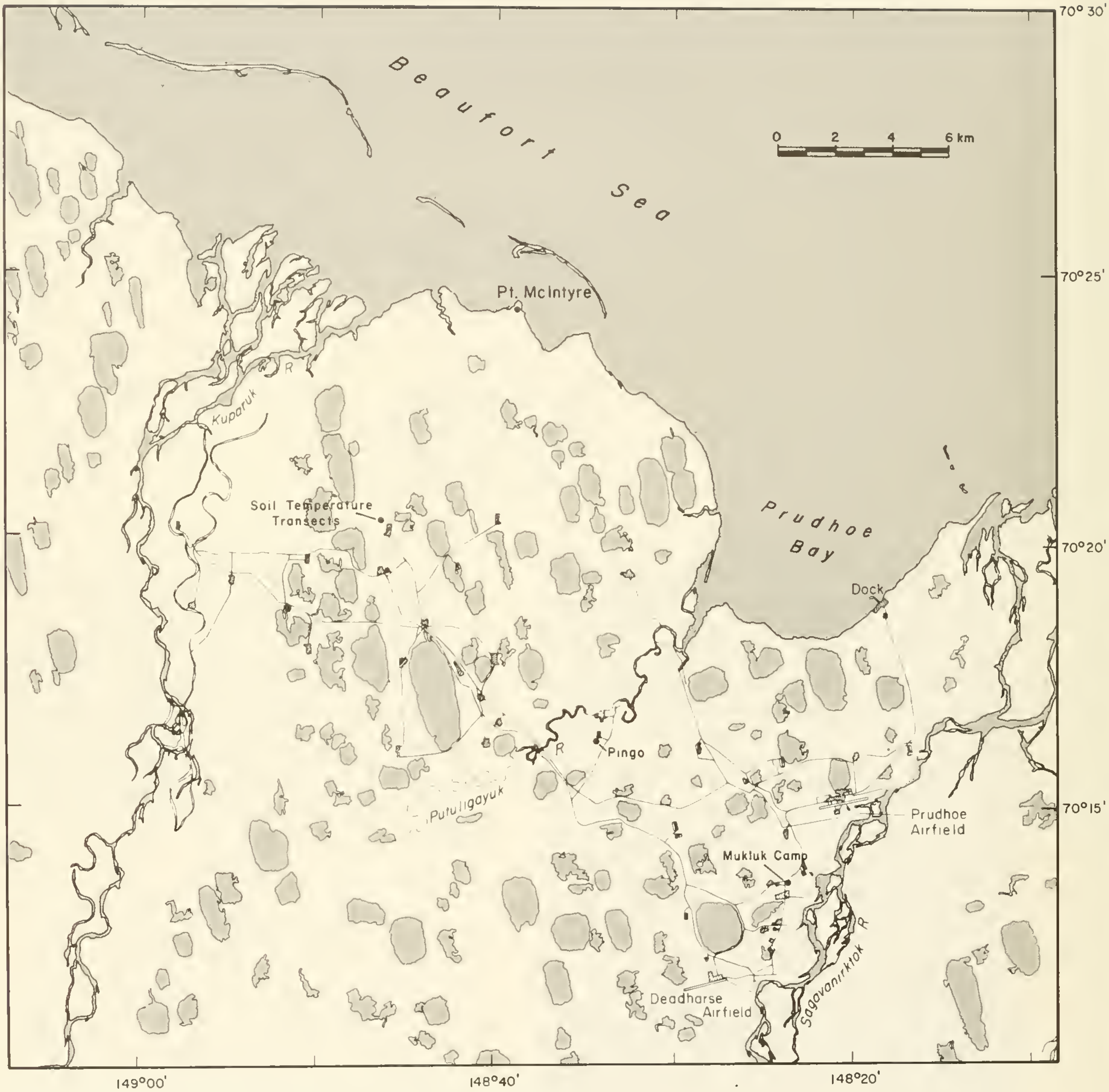


Fig. 1. *Location of climatic and soil temperature stations.*

are referred to as Prudhoe (Mukluk) in this report; the location is about 8 km inland from Prudhoe Bay itself.

(2) Prudhoe Airfield Tower: These data have been acquired by the Atlantic Richfield Company since 1967, and observations have been essentially continuous since 1968. These data are not reported in the National Weather Service's Alaska Climatic Data Summaries, although they are available from the National Climatic Center. In general, these data appear to be adequate for most purposes and probably compose the best record available by virtue of its length. A comparison of Prudhoe Tower data with data from Mukluk Camp is presented in Table 1 for 1970-1973. Averaged over this 4-year period, there is a difference of only 0.8° C in mean annual temperature for the two stations with Mukluk Camp being slightly colder. This difference could be actual.

(3) Deadhorse Airfield: Data are hourly during the period of airfield operation, but are usually missing early morning observations.

(4) Happy Valley Camp: This station is operated by Alyeska and has been reported to the National Climatic Center since 1970. It is also now listed in the Alaska Climatic Summary (National Weather Service), but data are often missing. This has been the only station recently in regular operation that is representative of the interior portion of the North Slope.

Table 1

Comparison of Prudhoe Bay air temperatures (°C).

	Mukluk Camp			Prudhoe Tower			Mukluk Camp			Prudhoe Tower		
	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
	1970						1971					
Jan				-24.7	-30.5	-27.6	-28.5	-37.3	-32.9	-27.4	-36.8	-32.1
Feb	-25.8	-32.2	-29.0	-24.7	-31.9	-28.3	-33.8	-40.3	-37.1	-33.5	-40.1	-36.8
Mar	-25.9	-32.5	-29.2	-25.5	-32.4	-29.0	-25.7	-33.7	-29.7	-24.9	-32.6	-28.7
Apr	-15.1	-22.1	-18.6	-15.2	-21.9	-18.6	-16.6	-26.8	-21.7	-17.3	-26.8	-21.7
May	-4.7	-9.8	-7.2	-3.2	-9.6	-6.4	-3.9	-9.8	-6.8	-3.7	-9.6	-6.7
June	5.0	-0.9	2.1	5.2	-0.4	2.3	7.4	0.7	4.1	7.4	1.4	4.4
July	9.2	1.6	5.4	8.4	2.0	5.2	11.3	3.1	7.2	11.5	3.9	7.7
Aug	7.9	1.8	4.8	7.8	2.3	5.1	5.8	-0.5	2.7	6.1	0.6	3.3
Sept	0.4	-5.4	-2.5	-0.1	-4.9	-2.5	1.7	-2.7	-0.5	2.3	-1.6	0.5
Oct	-13.9	-20.5	-17.2	-14.7	-20.2	-17.4	-9.4	-17.9	-13.6	-8.0	-15.9	-11.9
Nov	-15.4	-23.6	-19.5	-15.2	-23.7	-19.4	-17.2	-24.2	-20.7	-16.7	-23.2	-19.9
Dec	-23.6	-31.5	-27.6	-22.7	-30.5	-26.6	-25.6	-31.4	-28.4	-25.7	-29.4	-27.6
Annual means				-10.4	-16.8	-13.6	-11.2	-18.4	-14.8	-10.8	-17.5	-14.2
	1972						1973					
Jan	-26.3	-32.6	-29.4	-26.4	-31.2	-28.8	-22.6	-31.3	-26.9	-24.4	-29.1	-26.7
Feb	-29.2	-32.6	-32.2	-29.1	-34.8	-31.9	-25.1	-32.3	-28.7	-25.3	-30.3	-27.8
Mar	-28.3	-34.7	-31.5	-28.2	-34.1	-31.1	-29.9	-37.4	-33.7	-29.5	-35.9	-32.7
Apr	-16.7	-26.3	-21.5	-15.7	-24.3	-20.1	-13.7	-24.4	-19.1	-13.8	-22.3	-18.0
May	-3.9	-10.7	-7.3	-2.9	-8.6	-5.8	-2.5	-8.4	-5.4	-2.2	-7.1	-4.7
June	4.7	-0.3	2.2	4.6	0.9	2.7	4.5	-0.1	2.2	4.3	0.9	2.6
July	10.6	2.1	6.3	10.1	4.0	7.1	11.1	2.4	6.8	11.2	4.8	8.0
Aug	9.2	2.3	5.7	9.4	3.6	6.5	9.8	3.1	6.4	9.7	4.6	7.2
Sept	0.4	-3.9	-1.8	0.9	-1.2	-0.7	4.5	-1.2	1.7	4.8	0.4	2.6
Oct	-4.6	-12.6	-8.6	-4.8	-9.8	-7.3	-7.2	-13.7	-10.4	-7.1	-11.1	-9.1
Nov	-15.9	-20.9	-18.4	-15.7	-19.3	-17.6	-14.3	-20.6	-17.4	-15.3	-18.8	-17.1
Dec	-19.0	-26.4	-22.7	-19.8	-24.6	-22.0	-19.3	-25.9	-22.6	-19.9	-23.8	-21.9
Annual means	-9.9	-16.7	-13.3	-9.8	-15.1	-12.4	-8.7	-15.8	-12.3	-8.9	-14.0	-11.4

In addition to these sites, the Tundra Biome established several locations of various duration. In order to establish the magnitude of the spring and summer temperature gradient from the coast inland, recording thermographs in standard shelters were deployed in 1972 and 1973 at Point McIntyre and on a terrace along the Sagavanirktok River approximately 16 km south of the Deadhorse Airfield. An automatic, battery operated weather station was installed in the Biome study area on the pingo east of the Putuliagayuk River and operated intermittently between 1971 and 1973. The 1971 precipitation data are from a lake adjacent to the Biome study area (Kane and Carlson 1973). Other projects have collected climatic data in the Prudhoe Bay area, notably the Gas Arctic project located across from the Mukluk Camp. Casual comparisons of these data have been made but are not discussed in the report.

Table 2

Mean monthly and annual temperatures (°C) for Barrow, Prudhoe, and Barter Island (1970-1973)*

	1973			1972			1971		
	Barrow	Prudhoe	Barter Island	Barrow	Prudhoe	Barter Island	Barrow	Prudhoe	Barter Island
Jan	-25.3	-26.9	-24.6	-26.8	-29.4	-26.9	-28.6	-32.9	-30.4
Feb	-25.1	-28.7	-26.9	-28.4	-32.4	-28.8	-32.3	-37.1	-34.6
Mar	-29.3	-33.7	-31.6	-28.7	-31.5	-28.5	-27.9	-29.7	-28.4
Apr	-19.3	-19.1	-18.8	-20.2	-21.5	-20.3	-20.3	-21.7	-21.3
May	-7.2	-5.4	-5.4	-7.7	-7.3	-7.3	-8.1	-6.8	-6.5
June	0.7	2.2	1.2	0.3	2.2	1.2	1.7	4.1	2.7
July	4.3	6.8	4.9	6.1	6.3	4.1	4.7	7.2	6.1
Aug	4.3	6.4	4.3	4.8	5.7	5.2	0.8	2.7	2.0
Sept	1.1	1.7	1.7	-0.4	-1.8	-0.9	-0.2	-0.5	-0.8
Oct	-7.0	-10.4	-9.0	-6.1	-8.6	-6.3	-9.9	-13.6	-11.4
Nov	-13.4	-17.4	-16.4	-17.0	-18.4	-17.3	-18.1	-20.7	-17.4
Dec.	-20.8	-22.6	-21.2	-19.3	-22.7	-20.4	-24.1	-28.4	-24.6
Annual	-11.4	-12.3	-11.8	-11.9	-13.3	-12.2	-13.5	-14.8	-13.7

	1970			1970-1973 Mean			(1941-1970) 30-Year Normals	
	Barrow	Prudhoe	Barter Island	Barrow	Prudhoe	Barter Island	Barrow	Barter Island
Jan	-24.7	-27.6	-26.5	-26.3	-29.2	-27.1	-25.9	-26.2
Feb	-27.2	-29.0	-27.3	-28.2	-31.8	-29.4	-28.1	-28.6
Mar	-28.0	-29.2	-28.5	-28.5	-31.0	-29.2	-26.2	-25.9
Apr	-19.4	-18.6	-18.1	-19.8	-20.2	-19.6	-18.3	-17.7
May	-7.2	-7.2	-6.7	-7.6	-6.7	-6.5	-7.2	-6.1
June	0.5	2.1	0.8	0.8	2.6	1.4	0.6	1.2
July	3.2	5.4	3.8	4.6	6.4	4.7	3.7	4.4
Aug	1.7	-4.8	4.7	2.9	4.8	4.1	3.1	3.8
Sept	-3.5	-2.5	-2.8	-0.8	-0.8	-0.7	-0.9	-0.2
Oct	-17.5	-17.2	-16.2	-10.1	-12.5	-10.7	-9.3	-8.7
Nov	-20.1	-19.5	-18.2	-17.2	-19.0	-17.3	-18.1	-17.7
Dec	-23.4	-27.6	-26.0	-21.8	-25.3	-23.1	-24.6	-24.7
Annual	-13.8	-13.9	-13.4	-12.7	-13.6	-12.8	-12.6	-12.2

*Source: Barrow and Barter Island: National Weather Service. Prudhoe Bay: BP Alaska, Inc. Mukluk site with several intervals of missing data filled in with Prudhoe tower data.

Freeze-thaw degree-day indices were computed by the standard technique of summing the daily departure from 0° C. Progression of seasonal soil thaw was determined by Bilgin (1975) for the summer of 1972 using a probing technique. Soil temperatures were also recorded in 1972 on Grant recorders for a polygon area north of Pad F, and the data reduced at 3-hour intervals.

Results

Table 2 presents the mean monthly and annual temperature data for Barrow, Prudhoe, and Barter Island. Prudhoe clearly has warmer summers and colder winters than either Barrow or Barter Island. The effect of continentality only a few kilometers inland from the ocean is exemplified by the Prudhoe data and, as will be shown, the effect becomes rapidly more pronounced further inland.

As shown in Table 2, the annual temperature regimes at Prudhoe paralleled those of Barrow and Barter Island in terms of individual warm and cold seasons as well as annual averages. Annual averages for both 1970 and 1971 were cooler than 1972 and 1973 across the entire coastal plain. The variations from year to year of Prudhoe temperatures are further demonstrated in Table 3, based on January and July mean monthly maximum and minimum values.

Table 3

Maximum and minimum monthly temperatures (°C) for January and July at Prudhoe (1970-1973)

	January		July	
Year	Max.	Min.	Max.	Min.
1973	-22.6	-31.3	11.1	2.4
1972	-26.3	-32.6	10.6	2.1
1971	-28.5	-37.3	11.3	3.1
1970	-24.7	-30.5	9.2	1.6

It is observed in Table 4 that the most notable differences between the coastal stations, Barrow and Barter Island, and the inland stations, Prudhoe and Happy Valley, are in the summer warmth. Even comparing the coolest summers at the inland stations with the warmest summers of the coastal stations, the summer degree-day accumulations for the interior stations are consistently greater. The coldest winters at Barrow, on the other hand, can be as cold as or even colder than the inland stations. This is undoubtedly due to the presence of the ice cover which, in effect, creates a more continental climatic situation for the coastal stations during the winter.

Table 4

Comparison of mean monthly temperatures and thawing degree-days (°C) at coastal and inland stations.

	Mean Monthly Temperatures and Thaw Degree-Days			
	June	July	Aug	Total Thaw Degree-Days
		1972		
Barrow	0.3 (9)	6.1 (189)	4.8 (148)	346
Point McIntyre	0.3 (9)	3.9 (120)	4.6 (142)	271
Barter Island	1.2 (36)	4.1 (127)	5.2 (161)	324
Prudhoe	2.7 (81)	6.3 (195)	5.7 (176)	452
16 km south	2.5 (75)	7.3 (226)	6.5 (201)	502
Happy Valley	8.1 (243)	12.6 (390)	9.8 (303)	936
		1973		
Barrow	0.7 (21)	4.3 (133)	4.3 (133)	286
Point McIntyre	0.7 (21*)	4.5 (139)	4.6 (133*)	254
Barter Island	1.2 (36)	4.9 (151)	4.3 (133)	320
Prudhoe	2.2 (66)	6.8 (210)	6.4 (198)	474
Happy Valley	8.7 (261)	12.2 (378)	7.5 (232)	871

*Partial months (12-30 June; 1-24 August)

At Prudhoe, the mean maximum values for July in excess of 10°C are significantly greater than would have been estimated using only data from the immediate coastal stations at Barrow and Barter Island.

The steepness of the summer temperature gradient from the Arctic coastline inland is illustrated in Table 5. Summer data from two stations, Point McIntyre on the coast and a location approximately 16 km south of Deadhorse, are incorporated to provide continuity. Considering a total distance of approximately 144 km from Point McIntyre south to Happy Valley, the increase of total thaw season degree-days is 5 degree (°C) days per kilometer proceeding inland. The temperature gradient may also be characterized by July temperature differences. Based on the data given in Table 4, an average increase of July mean temperature away from the coast is 5.9°C $(100\ \mathrm{km})^{-1}$. Some comparable data are available inland of Barrow. Temperature data obtained in 1966 by Johnson and Kelley at Meade River, 120 km south of Barrow, showed a 6.5°C difference from Barrow (North Meadow Lake) temperatures for the month of July. This gives an inland temperature increase of 5.4°C $(100\ \mathrm{km})^{-1}$, almost identical to the rate determined for the Point McIntyre-Happy Valley gradient. Also based on the Meade River data, a total thaw season degree-day gradient of 3.9°C km^{-1} was calculated, about one degree C less than indicated for the Point McIntyre-Happy Valley gradient. Climatic gradients have also been observed from Barrow southward by Clebsch and Shanks (1968). Increases for rainfall, evaporation, and evapotranspiration were observed between Barrow and their study site 55 km inland. Temperature observations were limited to weekly maximum and minimum values in that study, and are not directly comparable to the above analysis. All of the other parameters measured, however, clearly indicated increased warmth and moisture gradients toward the inland study site. These are important gradients for many types of environmental phenomena and should be considered in any study utilizing coastal temperature data to represent conditions some distance from the coast.

Table 5

Annual thaw/freeze degree-day (°C) accumulations 1970-1973

	Summer 1970/ Winter 1970-71	Summer 1971/ Winter 1971-72	Summer 1972/ Winter 1972-73
Barrow	273/5417	295/4891	320/4496
Barter Island	372/5520	352/5063	402/4585
Prudhoe	529/5739	564/5469	617/4835
Happy Valley	890/5331	1020/5081	956/5372

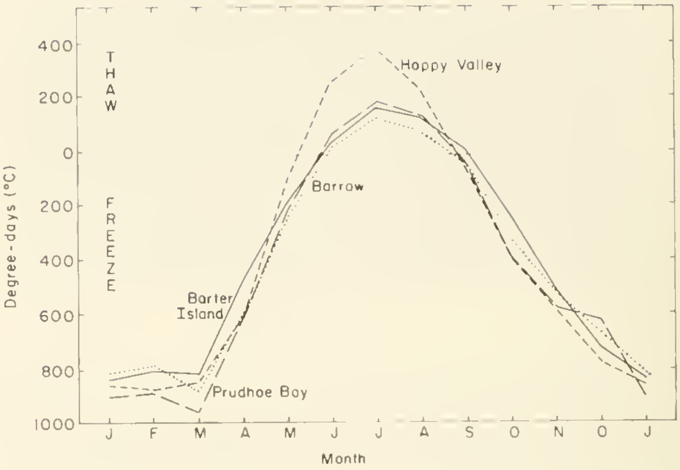


Fig. 2. *Freeze-thaw regimes for principal North Slope stations.*

Fig. 2 illustrates the annual freeze-thaw regimes for the principal North Slope stations for the period of similar record. The similarity of the freeze season, the increased warmth, and greater temperature amplitude of inland locations discussed above can be observed.

Precipitation

It is difficult to assess the variation of precipitation regimes as was done with air temperatures because precipitation values show greater fluctuations and were not obtained at all stations. The only long-term records, Barrow and Barter Island, indicate that Barter Island receives considerably more summer precipitation than Barrow (Table 6). The only available summer precipitation data for Prudhoe Bay are from 1971 (Kane and Carlson) since Biome observations were considered anomolous. The monthly totals are low compared to other stations on the North Slope. Summer precipitation amounts appear to increase inland as evidenced by partial records for Happy Valley, and as previously indicated by Clebsch and Shanks (1968) for the Barrow area.

Soil thaw

In 1972 Bilgin (1975) measured the progression of soil thaw at 14 different sites. Soils varied in texture, organic content, moisture, slope and resulting vegetative cover. The range in maximum soil thaw by late August was between 25 cm in wet organic soil and 90 cm in the dry sandy upland soils. Fig. 3 contains plots of thaw progression in four distinct soil conditions. This range in soil thaw over relatively small distances is common for northern Alaska and has been reported for a detailed transect in the Barrow area (Brown 1969).

Soil Temperature

Soil temperatures as influenced by polygon microrelief were recorded at six locations at 3-hr intervals during summer 1972. The sites were located within a 15-m radius with duplicate sites selected in a polygon trough, on a polygon rim, and in a polygon center. Fig. 4 is an idealized cross-section and plan view of the site.

Fig. 5 contains the daily mean values for each of the three microrelief positions at 1, 5, and 10 cm depths and the Prudhoe air temperature record.

The July and August 1972 mean daily temperatures in the upper 1 to 10 cm soil were within the range of 2° to 12.5° C. The maximum daily mean temperatures at 10 cm were below 8° C. The extremes in mean daily temperatures were encountered in the polygon trough with core 3 being the coolest (2° to 6.5° C) and core 6 the warmest (3.5° to 12.5° C). These differences are undoubtedly due to local microrelief and soil properties. Temperatures at these shallow soil depths closely reflected daily air temperatures.

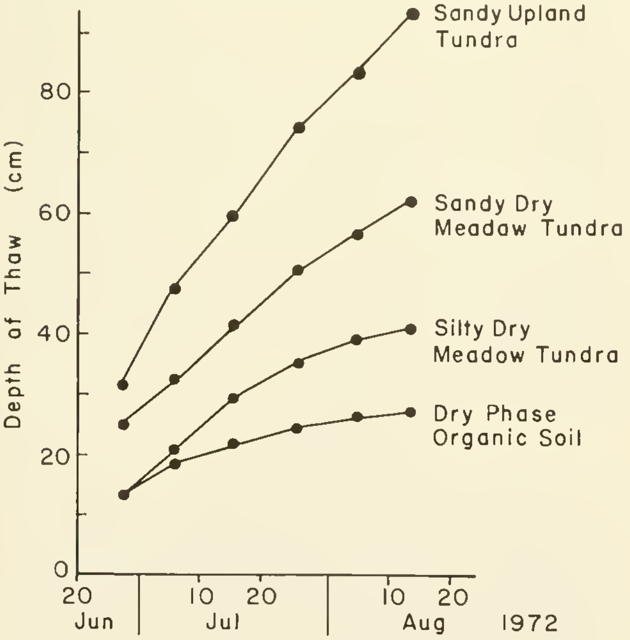


Fig. 3. *Seasonal progression of thaw for four Prudhoe Bay soils (Bilgin 1975).*

Table 6

Comparison of 1971 precipitation data (mm)

	June (13-30 June)	July	August	September
Barrow	trace	24.9	8.9	4.3
Barter Island	2.0	76.5	10.7	23.1
Prudhoe Bay (near Pingo Site)	2.5	20.3	16.5	6.9
Happy Valley	5.1*	50.8	20.1	–

*Value wholly or partially estimated.

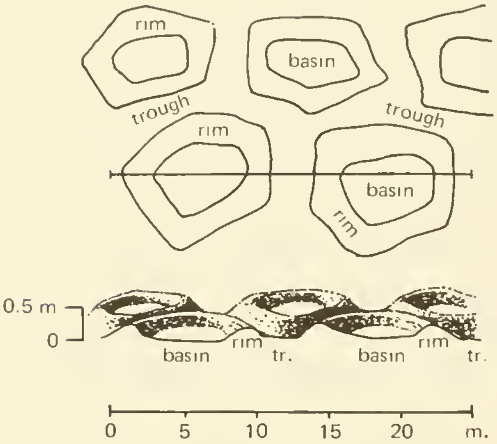


Fig. 4. *Idealized cross-section and plan view of polygon microrelief for soil temperature measurements.*

Since gravel pads and roads cover a significant portion of the Prudhoe landscape, it is important to know how they influence near-surface temperature and thaw regimes. Temperatures of gravel surfaces as compared to air

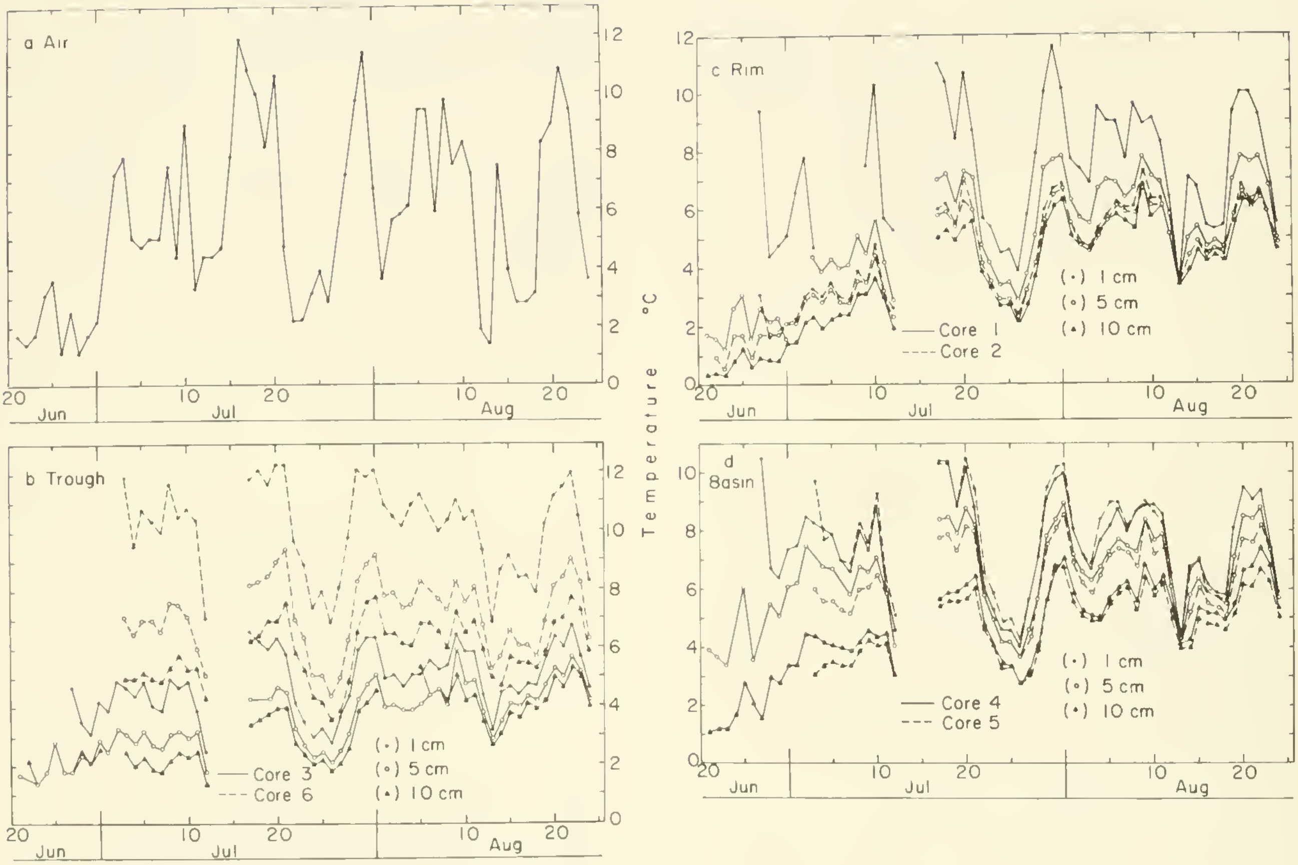


Fig. 5. *Daily mean temperature values for air and microrelief positions at 1, 5, and 10 cm depths.*

temperatures in a standard shelter were obtained by the authors in 1974. Gravel temperatures within a centimeter of the bare surface were recorded between 19 July and 3 September 1974 on pad F. During this period the mean air temperature was 7.0°C, and the mean surface temperature of gravel was 9.2° C. Regression of daily average surface and air temperatures yielded the equation $Y = 3.60 + 0.785X$ where Y is the average daily surface temperature and X is the average daily air temperature. The correlation coefficient (r) for this relationship is 0.90. Based on this analysis, an air-gravel surface temperature relationship is defined. The regression equation can be applied to Prudhoe summer air temperature data as input to thawing and freezing computations and modeling.

Conclusions

It is apparent that the area adjacent to the road net at Prudhoe can be characterized as an inland coastal climate and is significantly different than the immediate coastal climate as characterized by Barrow, Barter Island, and the summer temperature record at Point McIntyre. The shift to a true continental temperature regime occurs only a few kilometers inland of the coastline during the summer, although the winter ice cover off the coast reduces temperature differences during the freezing season and provides a near-continental temperature pattern even to the coastal stations.

Acknowledgments

A large number of people have assisted in the acquisition and processing of these data. Helicopter time was provided by both Alyeska and Atlantic Richfield in servicing the remote stations at Prudhoe Bay. Robert Timmer assisted in servicing these stations in 1972. Funds from the Prudhoe Bay Environmental Subcommittee and BP Alaska, Inc. to the University of Alaska were utilized by Scott Parrish and others involved in the field work. National Science Foundation and Corps of Engineers funding to USA CRREL were employed by the senior authors. Martha Greer and Carolyn Merry of CRREL assisted in processing the air temperature data. Soil temperature data were acquired and reduced by Dr. Stephen MacLean, University of Alaska, and computer processed by Cecil Goodwin, University of Michigan.

References

Bilgin, A. (1975). Nutrient status of surface waters as related to soils and other environmental factors in a tundra ecosystem. Ph.D. dissertation. Rutgers University, New Brunswick, N. J., 201 pp.

Brown, J. (1969). Soil properties developed in the complex tundra relief of northern Alaska, *Biul. Peryglacjalny* 18:153-167.

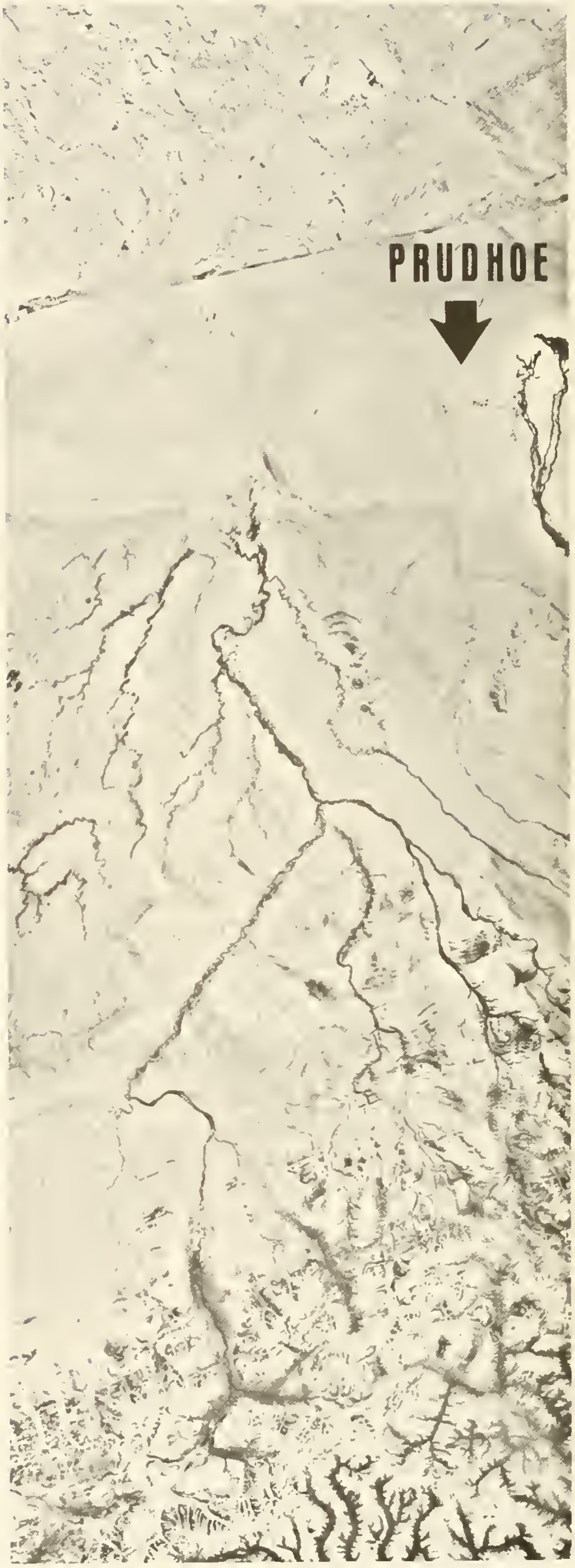
Clebsch, E. E. C. and R. E. Shanks (1968). Summer climatic gradients and vegetation near Barrow, Alaska, *Arctic* 21:161-171.

Kane, D. L. and R. F. Carlson (1973). Hydrology of the Central Arctic river basins of Alaska. Institute of Water Resources, University of Alaska, Report No. IWR-41, 51 pp.

Johnson, P. L. and J. J. Kelley, Jr. (1966). Results and reprints of ecological investigations, Meade River, Alaska (summer 1966). USA CRREL Internal Report 467.

Searby, H. W. and M. Hunter (1971). Climate of the North Slope, Alaska. NOAA Technical Memorandum AR-4, Anchorage, Alaska.

Watson, C. E. (1959). Climates of the State, Alaska. Climatography of the United States No. 60-49. U. S. Department of Commerce, 24 pp.



NASA Contract NAS5-21833, Task 4

Mosaic of three ERTS images of the Colville River area obtained on 27 May 1973. The Prudhoe Bay road system can be clearly seen to the west of the open Sagavanirktok River at the upper right corner.

Observations on the Seasonal Snow Cover and Radiation Climate at Prudhoe Bay, Alaska during 1972

CARL BENSON, BJORN HOLMGREN*, ROBERT TIMMER**, and GUNTER WELLER
Geophysical Institute
University of Alaska
Fairbanks, Alaska 99701

SCOTT PARRISH***
Tundra Biome Center
University of Alaska
Fairbanks, Alaska 99701

Introduction

The snow structure on the Arctic Slope in general consists of a hard, high density, fine-grained, wind packed layer, overlying a coarse, low density, depth hoar layer; it resembles the top annual stratigraphic unit of the perennial dry snow facies of the Greenland or Antarctic ice sheets. It differs markedly from the snow of interior Alaska between the Brooks Range and Alaska Range. The latter is characterized by low density, steep temperature gradients, and a thick basal depth hoar layer which sometimes makes up two-thirds or more of the snow pack.

Measurements on the 1971-1972 seasonal snow cover at Prudhoe Bay were made during September 1971 and, most extensively, in the spring of 1972. Some supplementary measurements were also made at Prudhoe Bay during the spring of 1973. The Prudhoe Bay observations were made in the context of long-term observations on physical properties of Alaskan snow cover which began in 1961. However, they focused on specific problems in the Prudhoe Bay area which result from industrial activities. Fig. 1 shows the location of traverses and sample sites in the Prudhoe Bay area.

An attempt was made to determine the amount of snow on the ground and to define the nature of the drift patterns caused by wind. The water equivalent of the snow was determined from measurements of its depth and density. Snow temperature and density profiles were measured together with characteristics such as hardness and grain size, a general stratigraphic description of the snowpack and the type of base (i.e., grass, ice, gravel, etc.) The amount of dust and coarser sediment contained in the snow was determined by melting and filtering snow samples. The electrical conductance of the melt water from these samples was also measured. The sources of the sediments were bare ground areas in and adjacent to the Sagavanirktok River channels and the road network. An attempt was made to determine the effect of dust on snow melt rate.

The distribution of snow by wind drifting is an impressive feature about the Arctic Slope in general. The winds which cause the drifting are

---

*Current address: Meteorologiska Institutionen, Observatone Parken, Uppsala, Sweden.

**Current address: University of New Mexico, Albuquerque, New Mexico 87131.

***Deceased.

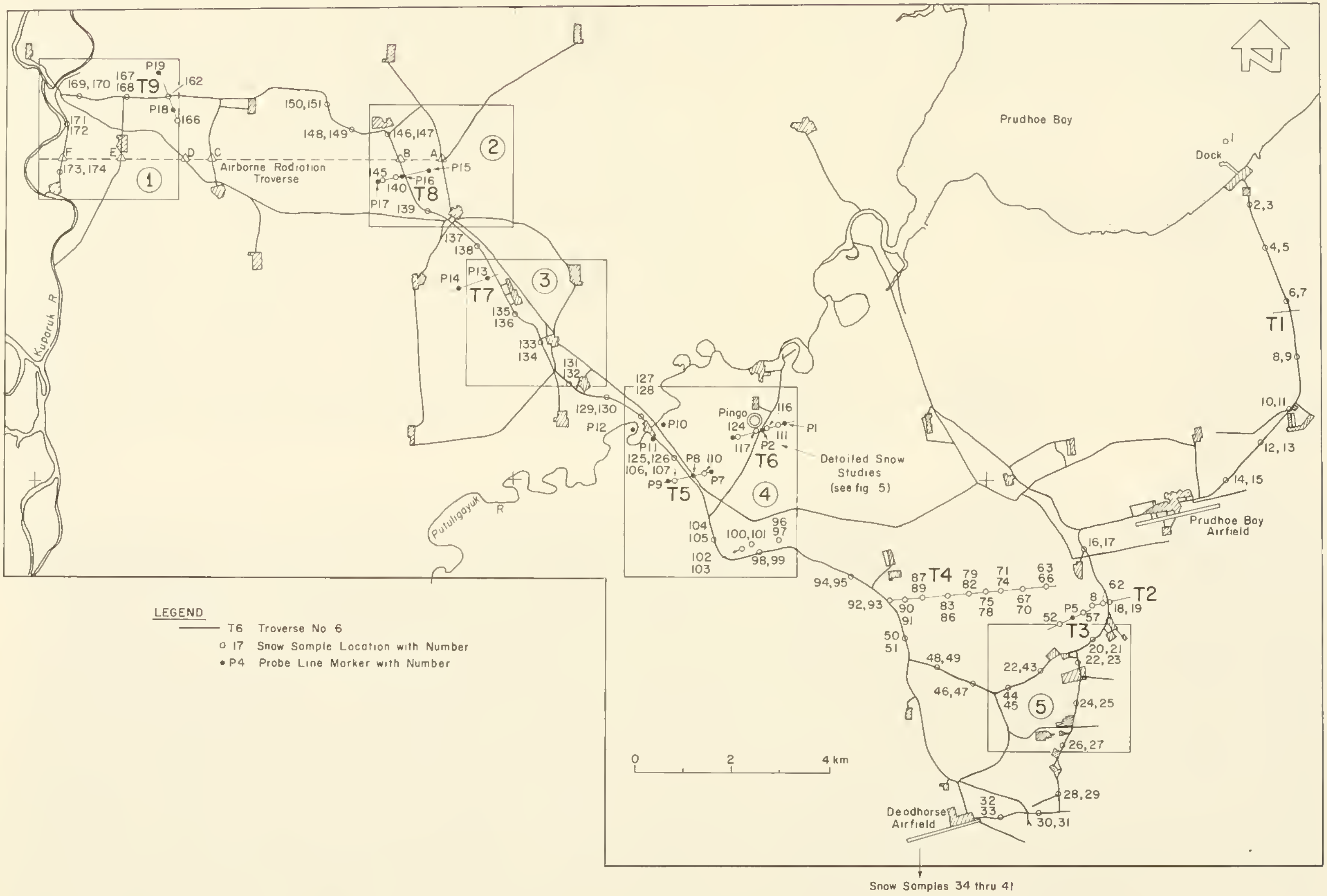


Fig. 1. *Map of Prudhoe Bay area with traverse and sample sites. The sequential photos in Figures 17-21, which show the progress of snowmelt, were taken in rectangular areas 1-5, respectively.*

remarkably constant in direction. Two directions are important: (a) storm winds, which bring new snow, are generally from the west and (b) prevailing winds, which primarily serve to redistribute snow on the ground, are from the east. The two aircraft runways in the Prudhoe Bay area are aligned with the prevailing winds. Also, the lakes in this region have a pronounced tendency to become elongated in a direction perpendicular to the prevailing winds; an explanation of this was provided by Carson and Hussey (1962). West winds are slightly more important for snow drifting in the Prudhoe Bay area, while the east winds are more important for moving dust. Because of drifting, the snow thickness varies from almost nothing up to 2 m in this region. Before discussing such variations, it will be useful for us to discuss the techniques of measurement and, in the next section, to consider the physical characteristics of the snow and some of the processes involved in its melting.

Three methods of measurement were used to observe the snow itself:

1. **Pit studies:** Standard snow stratigraphy studies as used in Greenland and parts of Arctic Alaska (Benson 1962, 1967, and 1969) were used to make detailed studies of the snowpack (Figs. 7 and 9). Thermometers and density sample tubes (500 cm^3 volume) were inserted horizontally into the exposed pit wall (Fig. 7). The samples were taken in such a way that density values could be calculated for each layer. The layers were plotted with sharp boundaries to indicate the stratified nature of the snow.

2. **Vertical cores:** A large number of vertical cores were made by driving an aluminum tube, sharpened on one end, through the entire snowpack. Snow was removed from around the tube, a metal plate was inserted at the base, and the contents were placed into a plastic bag for measurements of average snow density, dust content, and electrical conductance of the derived meltwater. Before emptying the contents into the bag, the base of the sample was examined and any loose soil or grass was removed; if this material could not be removed another sample was taken. This sampling technique was used on all of the traverses and dust collection sites. It has the advantage of sampling

Fig. 2. *Photo of snow, 6 September 1971.*

Fig. 3. *Photo of snow, 13 April 1972.*

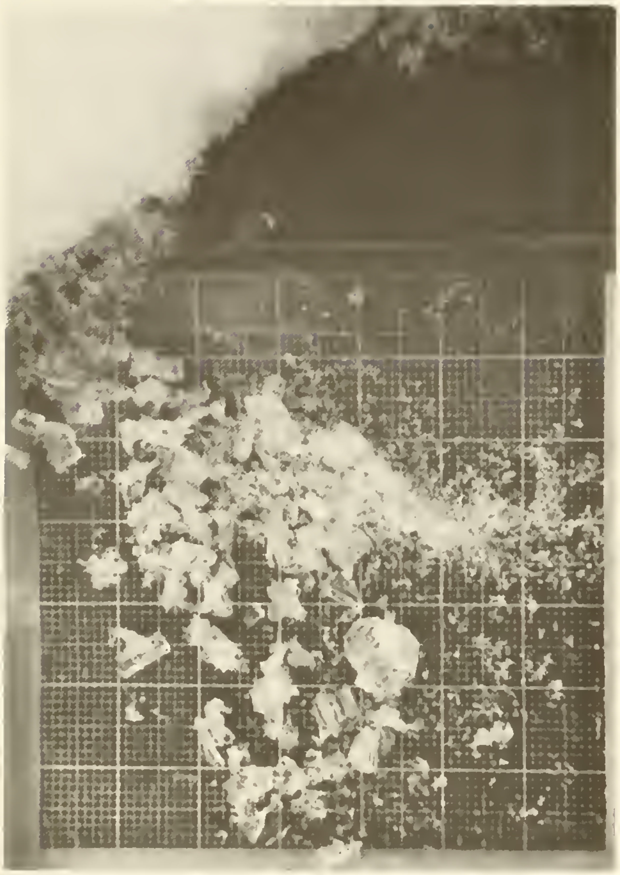


Fig. 4. *Contrast between depth hoar crystals and overlying fine-grained snow.*

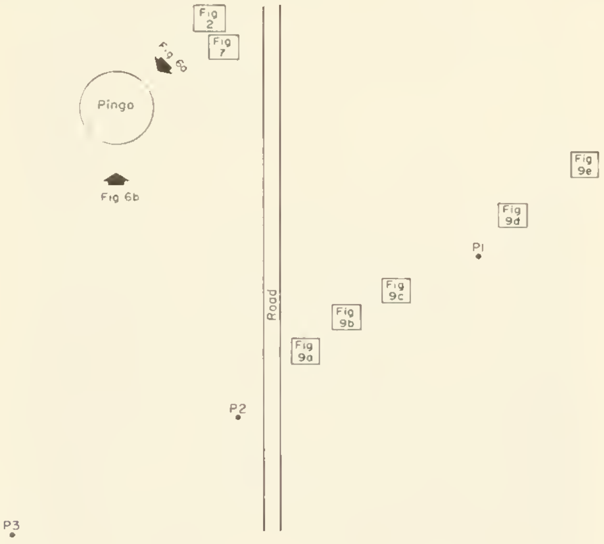


Fig. 5. *Sketch map of test area near pingo and P2.*

the entire snowpack including any ice lenses that may be in it, as referred to below.

3. **Snow probing:** In addition to the above measurements, which yield information on physical characteristics of the snow, a snow probing method was used extensively to determine snow depth along nine selected traverses (Fig. 1). The probing was done with a steel rod, graduated in centimeters, which was poked through the snow at 2 m intervals several times during May and early June. This technique provides a rapid means of measuring snowdrift distributions.

Physical Characteristics of the Snow

General features

The snow cover formed at Prudhoe Bay before the first of September in 1971. An example of its appearance, exposed in a shallow pit on 6 September, is shown in Fig. 2. In this place the snow was only 13 cm deep, coarse and wet at the bottom, with an icy crust 2-3 cm above the base. Some complexity already was apparent, especially in contact with clumps of vegetation.

In some places the snow depth did not increase much during the entire winter, as shown in the photograph (Fig. 3) taken near Barrow on 13 April 1972. In this example the snow depth varied from 10 to 17 cm, the bottom temperature was -13° C, and the coarse crystalline depth hoar layer at the base of the snow varied in thickness from 1 to 5 cm. In places where the snow is more than 40 cm deep, the basal depth hoar layer may be 20 cm thick. (In interior Alaska the entire snowpack may be predominantly depth hoar.) The contrast between depth hoar crystals from the base of the snowpack and the finer grained material from the top is illustrated in Fig. 4. Depth hoar crystals with dimensions of 1 cm are common, but grains in the fine-grained snow are generally less than 1 mm diameter. Between these extremes is a medium-grained (1-2 mm) snow which is generally intermediate in grain size, hardness and density. The fine-grained snow is often wind packed and hard—frequently called a wind slab. Another extreme case, the most unstable of all, is fresh new snow which is usually transformed rather quickly into one of the other types.

In summary, the stratigraphy of snow on the Arctic Slope can generally be described by referring to only four major varieties of snow. In approximate order from top to bottom in the snow pack these are:

Snow type	Range of Grain size (mm)	Range of density (g cm^{-3})*
1. Fresh new snow, variable crystal forms	0.5 to 1.0 sometimes <0.5	0.15 to 0.20
2. Wind slab, hard, fine-grained	0.5 to 1.0	0.35 to 0.45
3. Medium-grained snow	1 to 2	0.23 to 0.35
4. Depth hoar, coarse loosely-bonded crystals	5 to 10	0.20 to 0.30

Fig. 6a. *Pingo, 6 September 1971.*

Fig. 6b. *Pingo, 14 April 1972.*

Spring thaw

Some case examples of the snow structure measured during the spring near the Tundra Biome pingo site at Prudhoe Bay (Figs. 1 and 5) will be discussed. Figs. 6a and 6b shows the pingo, with the automatic recording weather station on top of it, during fall and spring. The photograph of early fall snow structure shown in Fig. 2 was taken at the time and place when the photograph in Fig. 6a was taken (6 September 1971).

A typical example of the snow structure on the tundra during spring, prior to melting (Table 1), is shown in Fig. 7; this profile was measured 350 m NE of P-2 (Fig. 5) on 14 April 1972 (Fig. 7). Three layers were easily distinguished by brushing the side of the pit to reveal differences in resistance to abrasion. They show up clearly in the photograph and in the density and stratigraphy data which are plotted below it; they may be briefly summarized as follows:

1. Top—fine-grained (0.5-1.0 mm), wind packed, density = 0.36 g cm^{-3}.
2. Middle—medium-grained (1-2 mm), density = 0.26 g cm^{-3}.
3. Bottom—coarse-grained, depth hoar crystals (5-10 mm), density = 0.19 g cm^{-3}.

The total water equivalent of the snowpack in this example was 12.5 cm H_2O as determined by integrating the depth-density profile; the amount of heat required to raise its temperature

---

*The density ranges are only approximate and indicate the differences one may expect between these snow types.

to the melting point was 102 cal cm^{-2} (Table 2). After raising its temperature to 0° C, another 1,000 cal cm^{-2} would be required to melt it. However, the actual melt process is complicated by localized percolation and refreezing of meltwater in the snow after slight melting occurs on the snow surface. This percolating water refreezes to form a complex network of ice glands (nearly vertical, pipelike structures) and ice lenses throughout the snow and at the tundra-snow interface. The process is analogous to the formation of superimposed ice on glaciers (Trabant, Fahl, and Benson 1975). These masses of ice within the tundra snow may remain for several weeks and may significantly modify the snowpack as a habitat for small animals such as lemmings, which live under the snow, or large animals such as caribou, which feed by breaking through it. The 1972 spring provided an excellent example of the process involved in forming these ice masses in the snow. The snow was subjected to slight surface melting on 6-7 May when the maximum air temperature was above freezing. After 7 May the maximum air temperature remained below freezing until 27 May, as summarized in Table I and Fig. 8.

Figs. 9a, 9b, and 9c show snow profiles* measured along a traverse line east from P-2 (Fig. 5) on 14 May. The pit study plotted in Fig. 9a, made only 8 m east of the road, is in the drifted snow alongside the roadbank. The pit studies in Figs. 9b and 9c are far enough from the road to be essentially unaffected by it; the same is true of the profiles in Figs. 9d and 9e, which were measured on 16 May. A deposit of fresh new snow appears at the top of each of these profiles. It was deposited between 11-13 May and overlies the surface melt crust produced on 6-7 May. In addition to the melt crust which formed on the snow surface of 6-7 May, there were ice glands, lenses, and layers in the snow. These are shown in black in the stratigraphic columns of Figs. 7 and 9. The location of these ice lenses at the base of a fine-grained layer is common. They also form in such stratigraphic locations in the deep snow of glaciers. In the examples shown here, they are most commonly at the top of the depth hoar layer. Later in the melt season ice layers form at the base of the depth hoar layer; at Prudhoe Bay in 1972 this did not occur until the end of May and during the first week of June. Similar timing for the formation of ice masses at the base of the snow was observed at Barrow and Prudhoe Bay during the spring of 1973.

Fig. 7. *Combined photo and data plot, 200 m east of pingo, 14 April 1972.*

---

*Unfortunately, a Rammsonde penetrometer was not available during these measurements. Typical Rammsonde profiles in tundra snow are available (Benson 1969), and a detailed study of the snow at Barrow using Ram hardness profiles was carried out during the 1972-1973 winter by Melchior and Benson.

Table 1

Prudhoe Bay, Alaska, maximum and minimum temperatures °C May 1972 (See Fig. 8)

Date	Maximum	Minimum
1	-6.1	-16.1
2	1.1	-14.4
3	-10.0	-17.8
4	-7.8	-16.7
5	-0.6	-14.4
6	1.7	-6.1
7	2.2	-1.7
8	-0.6	-5.6
9	-1.1	-12.2
10	-5.6	-16.7
11	-5.0	-15.6
12	-3.3	-12.2
13	-3.9	-7.2
14	-5.7	-13.3
15	-10.6	-15.6
16	-10.6	-20.0
17	-11.1	-16.1
18	-9.7	-18.9
19	-10.6	-15.6
20	-8.9	-14.4
21	-7.2	-12.8
22	-3.9	-15.6
23	-3.9	-11.7
24	-2.8	-10.0
25	-1.7	-9.4
26	-2.2	-7.8
27	1.1	-6.7
28	5.6	-3.3
29	1.1	-1.7
30	0	-2.2
31	0.6	-1.7

The snow temperature profiles in Fig. 9 contain information on processes operating in the snow. In Figs. 9b and 9c the temperature decreases from -3±1°C at the snow surface to about -10°C at the bottom. However, we know that the surface temperature was at 0°C during 6-7 May because of the melt crust and the evidence of percolation and refreezing of meltwater in the snow. These profiles also have anomalously high temperatures adjacent to the ice lenses in the snow. These temperature anomalies, caused by the release of latent heat as percolating meltwater refroze to form the ice lenses, have already been smoothed considerably. Initially, they can be quite pronounced, as has been seen in polar glaciers (Benson 1962, pp. 22-23 and Fig. 25). The amount of percolating meltwater in these examples may be estimated from the thickness of the ice lenses and the increase in density involved in forming them. The total amount of ice in the stratigraphic columns was about 1 cm, varying from 0.5 to 2 cm. Most of the ice lenses occurred at the base of or within the fine-grained hard layer. The increase in density was in the range of 0.5 to 0.6 g cm^{-3}. Thus, in these cases the amount of latent heat added at the surface but released at depth within the snow was about 40 to 50 cal cm^{-2}. This is a significant part of the total amount of heat which was required on 14 April to bring the snow to the melting point.

During the time when the percolation process operates, the tundra snow cover may undergo significant daily temperature variations in addition to the longer sort of variations summarized in Table 1 and Fig. 8. Indeed, the tundra snow is so shallow that temperature variations imposed at the surface are transmitted rapidly to the bottom even without the action of percolating meltwater. This is especially clear when one compares the temperature profiles of Figs. 9b and 9c with those of Figs. 9d and 9e, which were measured only 2 days later. The system remained below the melting point during this time, so there was no latent heat transfer by percolation and refreezing. To facilitate the comparison, we have plotted five of the temperature profiles* from Figs. 7 and 9 on a single diagram (Fig. 10). The mid-May cooling trend is clearly apparent. Indeed, the amount of heat required to raise the snow to its melting point (the "cold content"), was only 34 cal cm^{-2} in both Figs. 9b and 9c. Two days later, on 16 May, it had increased to 63 cal cm^{-2} (Fig. 9d). It was 87 cal cm^{-2} in Fig. 9e, but that profile has a slightly larger mass. The water equivalent of the snow, profiled in Figs. 7 and 9, and its cold content are summarized in Table 2.

---

*The profile in Fig. 9a was omitted because the depth was anomalous.

It is instructive to attempt to calculate temperature variations and heat exchange in the snow which result from the daily energy fluxes at the surface. Difficulties lie in the uncertain values for the thermal diffusivity of tundra snow and the fact that air convection may play a significant role in the snow (Trabant and Benson 1972). Published thermal diffusivity values for snow vary widely. This is mainly because of the variability in snow itself; it is reasonable to expect variations in diffusivity values by a factor of 2 or more in a typical tundra snowpack. A useful summary of thermal data for snow was provided by Hansen (1951), and from it we find diffusivity values suitable for tundra snow ranging between 0.0030 and 0.0050 $cm^2\ sec^{-1}$. However, Sorge (1935) found a higher range of value for the packed snow of the Greenland Ice Sheet. His values would be especially appropriate for the wind packed layers on the tundra. Thus, it is reasonable for us to use the range from 0.0030 to 0.0060 $cm^2\ sec^{-1}$.

Table 2

Water equivalent and "cold content" summary of data plotted in Figs. 7 and 9.

The water equivalent is calculated by integrating the depth-density profile. The "cold content" is a measure of the amount of heat required to raise the snow to the melting point.

A general summary of the data is as follows:

Reference	Total depth	Average Density $g\ cm^{-3}$	Total Water Equivalent cm H_2O	Total Cold Content $cal\ cm^{-2}$
Fig. 7	47	0.266	12.51	102
Fig. 9a	117	0.345	40.45	161
Fig. 9b	36.5	0.329	12.03	34
Fig. 9c	35	0.307	10.75	34
Fig. 9d	42	0.285	11.97	63
Fig. 9e	46	0.324	14.92	87

The detailed summary of each profile is tabulated below with the columns labeled as follows:

h = height above soil surface	(cm)
Δ h = height interval	(cm)
ρ = snow density	($g\ cm^{-3}$)
ΔWE = water equivalent of height interval, Δh	($g\ cm^{-2}$)
ΣWE = cumulative water equivalent of snow from bottom to height Δh	($g\ cm^{-2}$)

(Note the units of ΔWE and ΣWE can also be thought of as the height of a column of water, i.e., (cm H_2O)

c = Specific heat of ice	($cal\ g^{-1} C^{-1}$)
ΔT = Difference between measured snow temperature and 0°C	(°C)
ΔQ = Heat required to raise the temperature of the given increment of snow to 0°C. $\Delta Q = (\Delta WE) \times c \times \Delta T$	($cal\ cm^{-2}$)
ΣQ = Sum of ΔQ values	($cal\ cm^{-2}$)

Table 2 continued

h	Δh	ρ	ΔWE	ΣWE	c	ΔT	ΔQ	ΣQ
14 April 1972	350 m NE of P2, near Pingo (Fig. 7)							
0-17	17	0.19	3.23	3.23	.5	17	27.4	27.4
17-33	16	0.265	4.24	7.47	.5	16.2	34.4	61.8
33-47	14	0.36	5.04	12.51	.5	16	40.3	102.1
14 May 1972	28 m E of P-2 (Fig. 9a)							
00-9	9	0.275	2.48	2.48	.5	12	14.85	14.85
9-19	10	0.340	3.40	5.88	.5	11.5	19.55	34.40
19-30	11	0.365	4.02	9.90	.5	10.5	21.08	55.48
30-38	8	0.322	2.58	12.48	.5	9.5	12.24	67.72
38-51	13	0.449	5.84	18.32	.5	9	26.27	93.99
51-67	16	0.310	4.96	23.28	.5	8	19.84	113.83
67-68	1	0.900	0.90	24.18	.5	7.5	3.38	117.20
68-83	15	0.440	6.60	30.78	.5	6	19.80	137.00
83-84	1	0.90*	0.90	31.68	.5	6	2.70	139.70
84-95	11	0.340	3.74	35.42	.5	5.5	10.28	149.98
95-101	6	0.500	3.00	38.42	.5	5.5	8.25	158.23
101-117	16	0.127	2.03	40.45	.5	3	3.05	161.28
14 May 1972	40 m E of P2 (Fig. 9b)							
0-10	10	0.215	2.15	2.15	.5	9.5	10.2	10.2
10-21	11	0.310	3.41	5.56	.5	7	11.9	22.1
21-24	3	0.90*	2.7	8.26	.5	4	5.4	27.5
24-31	7	0.421	2.95	11.21	.5	4	5.9	33.4
31-36.5	5.5	0.15*	0.825	12.03	.5	2	0.82	34.2
14 May 1972	90 m E of P-2 (Fig. 9c)							
0-12	12	.205	2.46	2.46	.5	9	11.07	11.07
12-14	2	.90*	4.26	4.26	.5	7.5	6.75	17.82
14-25	11	.282	7.36	7.36	.5	6	9.31	27.13
25-33	8	.386	10.45	10.45	.5	5	7.72	34.85
33-35	2	.15*	10.75	10.75	.5	4	0.60	35.45
16 May 1972	200 m E of P-2 (Fig. 9d)							
0-16	16	0.210	3.36	3.36	.5	10.7	17.98	17.98
16-16.5	0.5	0.90*	.45	3.81	.5	10	2.25	20.23
16.5-32	15.5	0.407	6.31	10.12	.5	10	31.54	51.77
32-42	10	0.185	1.85	11.97	.5	12	11.1	62.87
16 May 1972	300 m E of P-2 (Fig. 9e)							
0-14	14	0.206	2.88	2.88	.5	10.5	15.41	15.41
14-15	1	0.90*	0.90	3.78	.5	11	4.95	20.36
15-17	2	0.350	0.7	4.48	.5	11	3.85	24.21
17-18.5	1.5	0.90*	1.35	5.83	.5	11	7.42	31.64
18.5-37	18.5	0.360	6.66	12.49	.5	12	39.96	71.6
37-40	3	0.510	1.53	14.02	.5	12.5	9.56	81.16
40-46	6	0.15*	0.90	14.92	.5	13	5.85	87.01

*This density value was estimated. The error in other density values is about ±0.003 g cm^{-3}.

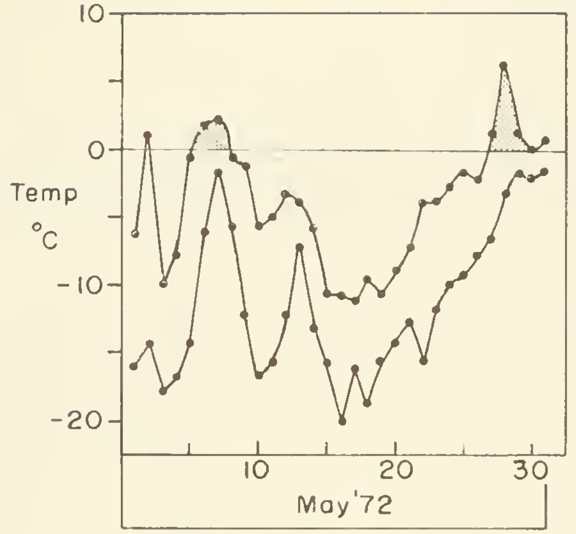
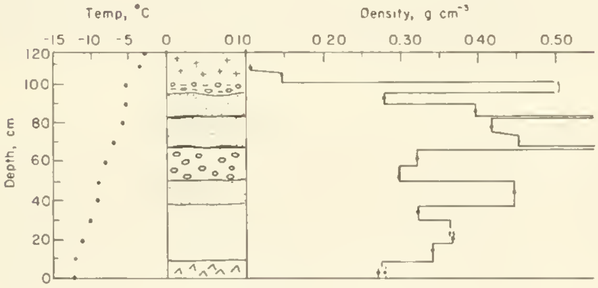
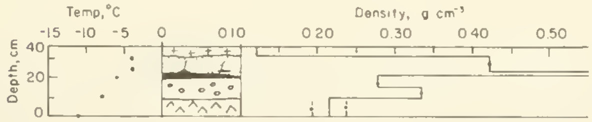


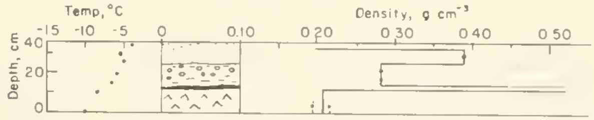
Fig. 8. *Air temperature plot for May 1972.*



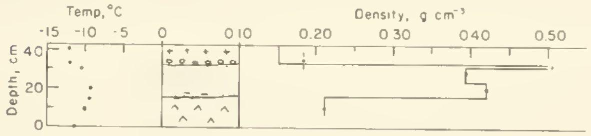
a 28 meters east of P2
(8 meters east of road)



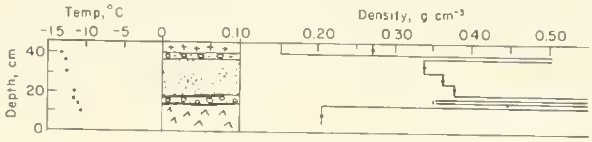
b 40 meters east of P2



c 90 meters east of P2



d 200 meters east of P2



e 300 meters east of P2

Fig. 9. *Pit data from Prudhoe Bay.*

Based on the data from mid-May (Table 1 and Fig. 8), when daily range of air temperature was 10 to 20° C, let us consider a daily temperature variation of 12° C (from -1° C to -13° C) and calculate the range of temperatures at 10 cm depth intervals in a snowpack 40 cm thick. The range at a selected depth Z is given by

$$T_R = 2T_o e^{-Z\sqrt{\frac{\Pi}{\alpha P}}}$$

where T_o is the temperature amplitude at the surface

Z is depth below snow surface (cm)

α is thermal diffusivity (cm^2 sec^{-1})

and P is the period, i.e., 1 day (86,400 sec)

The calculated results are summarized in Table 3 and Fig. 11. These values are consistent with the magnitudes of temperature change observed in the snowpack during the cooling trend between 14-16 May (Fig. 10). We can now estimate the daily heat exchange in the snowpack during May by a simple calculation. To do this, we shall use the bottom 40 cm of density data from Fig. 9e (i.e., neglect the top 6 cm of fresh snow) together with the temperature ranges obtained in Table 3 with diffusivity = 0.0050 cm^2 sec^{-1}. The calculations are summarized in Table 4.

In mid-April 1972 the cold content of the snow cover at Prudhoe Bay was about 100 cal cm^{-2}, and the daily heat exchange in the snow was about one-quarter of this. When melting occurs at the snow surface, it is accompanied by localized percolation of meltwater which refreezes to form a complex net of ice glands, lenses, and layers within the snow. The amount of heat transported downward into the snow by the percolation process is about 45 cal cm^{-2} for each cm of ice thickness formed. Some of this heat is lost in the daily cooling cycle, but a significant amount goes into warming the lower parts of the snowpack. When melting begins to wet a thick part of the snowpack, the temperature profiles take the shape of the dashed line in Fig. 10. A gradient exists in the lower part, but it varies laterally in the snow because of the inhomogeneous distribution of ice masses. During the spring only a small amount of heat must be added to raise the temperature of the entire snowpack to the melting point, yet it takes a long time for this to happen. Throughout this time the snow structure can undergo significant changes from only a few days of abnormally warm weather. The warm spell in early May 1972 reduced the amount of heat required to only one-third of the amount required in mid-April. However, a few cool days in mid-May doubled the amount required. Furthermore, ice lenses produced by the warm spell in early May remained in the snow for a month.

Distribution of Snow and Windblown Dust

The locations of traverses and of snow sample sites are indicated in Fig. 1. Some data on snow characteristics were presented above. A summary of the data obtained mainly from vertical core samples at 176 sample sites is presented in Table 5. To facilitate digestion of these data, they will be discussed according to: (a) water equivalent, (b) snow drifting and, (c) dust drifting.

Water equivalent of the snow

It is not easy to simply cite a single value for the amount of snow on the tundra. This is because of the variability in snow depth and density produced by wind drifting and the complexity of small-scale topographic features. We have attempted to determine average values for snow depth and density which can be used to calculate the water equivalent of snow on the tundra apart from drift traps such as banks of lakes and rivers.

The average depth of undisturbed snow on the tundra at Prudhoe Bay in May 1972 was 32 cm. This value is based on 871 probe depth values that were all made more than 150 m from any road or other disturbance that may cause drifting.

The average density, based on the detailed studies shown in Figs. 7 and 9, was 0.309 g cm^{-3}. The water equivalent from these studies averaged 12.4 cm H_2O (Table 2, excluding the drift case of Fig. 9a). If we use the average density value from these studies together with the average depth of 32 cm, we obtain an average value of 9.9 cm water equivalent.

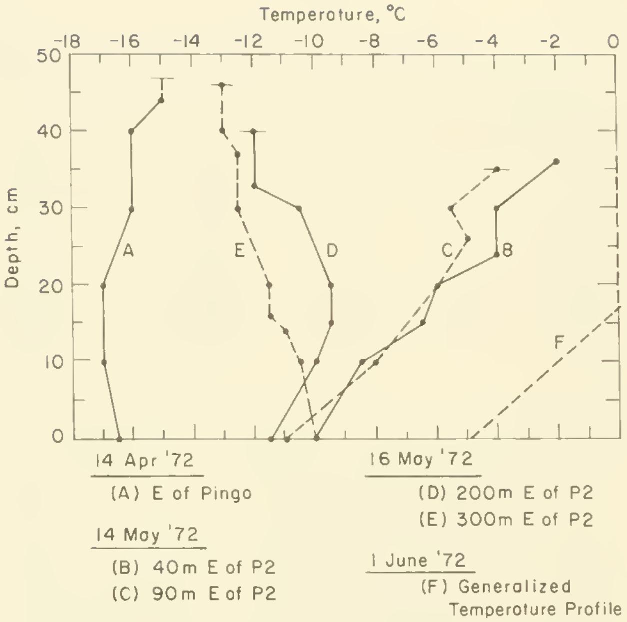


Fig. 10. *Summary of temperature profiles from Figs. 7 and 9.*

Table 3

Calculated range of temperature in the snow, using three values for diffusivity, α, in units of cm^{2}sec^{-1}

Depth below snow surface (cm)	Temperature range °C		
	(α = 0.0030)	(α = 0.0050)	(α = 0.0060)
0	12.0	12.0	12.0
10	3.0	5.1	5.5
20	1.3	2.2	2.5
30	.44	.93	1.2
40	.15	.40	.53

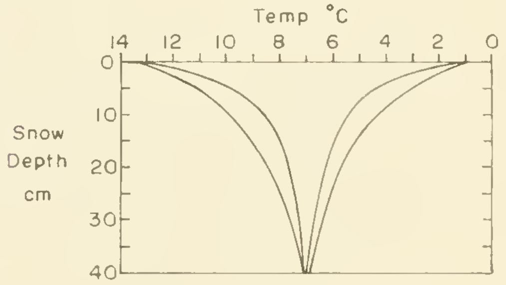


Fig. 11. *Calculated daily temperature ranges.*

Table 4

Daily heat exchange in the snowpack during May (when melting does not occur).

Depth below snow surface (cm)	ΔZ* (cm)	ρ g cm^{-3}	ΔWE g cm^{-2}	ΣWE g cm^{-2}	ΔT °C	ΔQ cal cm^{-2}	ΣQ cal cm^{-2}
0-3	3.0	0.51	1.53	1.53	10.0	7.6	7.6
3-21.5	18.5	0.360	6.66	8.19	4.0	13.3	20.9
21.5-23.0	1.5	0.900	1.35	9.54	1.6	1.1	22.0
23.0-25	2.0	0.350	0.70	10.24	1.4	0.5	22.5
25-26	1.0	0.900	0.90	11.14	1.4	0.6	23.1
26-40	14.0	0.206	2.88	14.02	1.0	1.4	24.5

*The symbols used at the top of the table are explained in Table 2.

A higher average density value of 0.338 g cm^{-3} was obtained by using the vertical core sampling method along traverse T-4* on 20 May; using this value together with the average depth of 32 cm, we obtained an average value of 10.8 cm water equivalent.

A density of 0.324 g cm^{-3} is obtained by averaging the values from the detailed studies with those from traverse 4. If we use this value together with the average depth of 32 cm, we obtain an average water equivalent of 10.4 cm. The latter value is consistent with Fig. 12, which summarizes all of the 150 values of water equivalent data from Table 5, and we will use it.

In summary, we shall use the following values for the tundra snow at Prudhoe Bay during May 1972:

Average depth = 32 cm;

Average density = 0.324 g cm^{-3};

Average water equivalent = 10.4 cm H_2O.

Snow drifting

Snow depth profiles along three selected traverses are plotted in Fig. 13. These traverses were either parallel (T-5 and T-6) or perpendicular (T-9) to the winds (Fig. 1). The road in T-5 is nearly perpendicular to the winds, and large drifts form adjacent to it. The road in T-6 makes an oblique angle with the winds, and the road in T-9 is nearly parallel with the winds. In the latter case no drifting is caused by the road. The probe depth data are plotted as if the base of the snowpack were a horizontal plane. This is not true, of course, and most of the irregularities in thickness result from the irregular bottom topography; the upper surface is smoother (Fig. 6b).

A convenient way to summarize the quantity of snow in the drifts is to measure their cross-sectional areas and to compare them with an "average cross-sectional area," obtained by

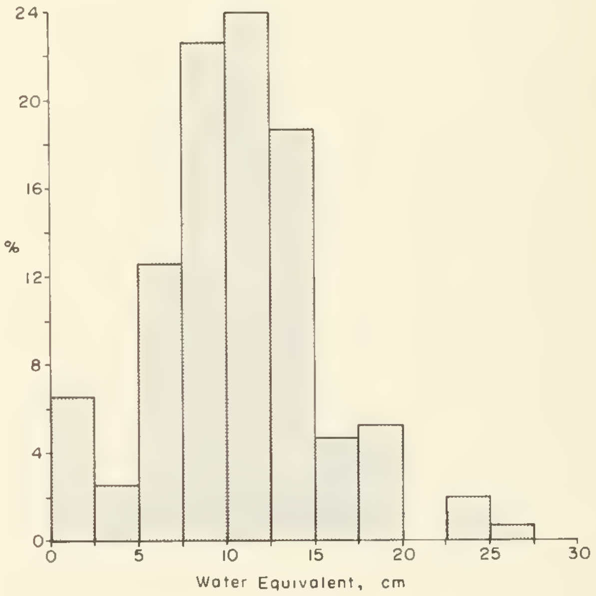


Fig. 12. *Histogram of water equivalents.*

---

*This is the only traverse in which sufficient density samples (15) were taken away from the influence of roads, prior to melting. (See Table 5 and Fig. 1).

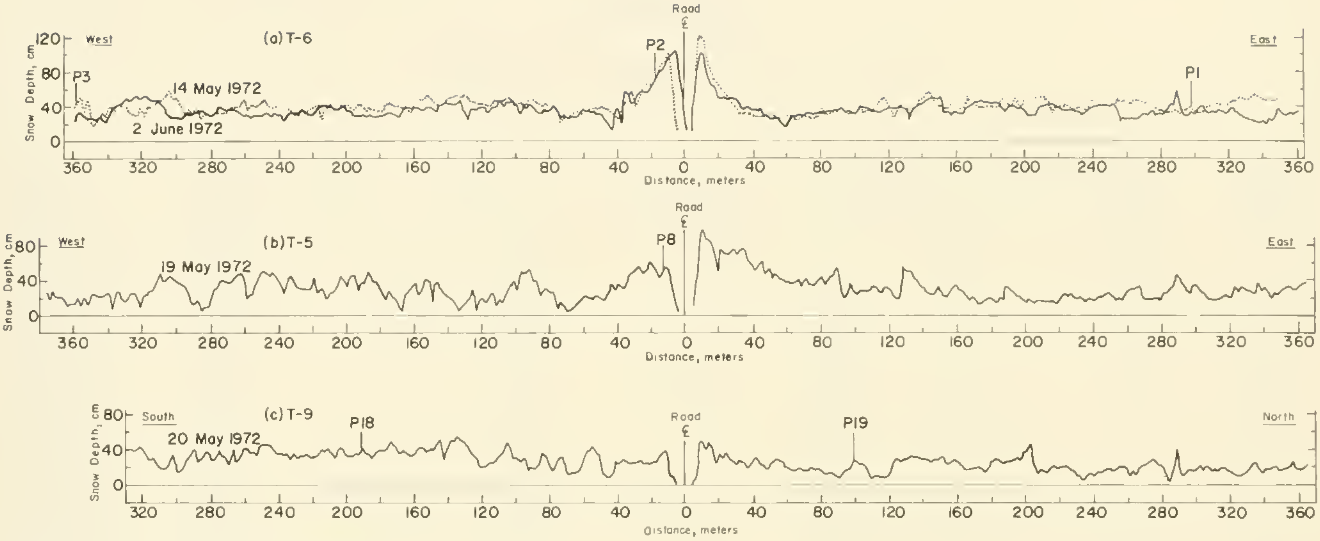


Fig. 13. *Snow depth profiles.*

using the average depth of 32 cm. This has been done from the edge of the road out to a distance of 150 m where the drift effect of the road is negligible. The results, summarized in Table 6, show that the drifted snow adjacent to roads generally has a greater than average cross-sectional area. However, there are exceptions, the most notable of which is in traverse T-9 where the cross-section area is 75 to 85% of the average value. This may be because traverse T-9 was made on the relatively high ground between two lakes and perpendicular to the winds. The road produced no significant drifting here because it was parallel to the winds; thus, there is no significant difference between the cross-sectional areas measured on different sides of the road. Other exceptions are traverses T-1 and T-3, which lie close to the Sagavanirktok River; the cross-sectional areas of their drifts are about average or slightly less than average. Traverse T-1 is located on relatively high ground and near the sand dune area that extends westward from the river toward the dock road. This apparently is an area of higher wind erosion, as evidenced by the fact that some of the sand dunes remain bare of snow all winter. The road may serve as a partial barrier to the erosional effect of the wind and may explain why the drift on the west side is larger in this case. Similar arguments may apply to traverse T-3; although it is not near sand dunes, it is on the highest ground of all traverses.

Traverses T-6 and T-7 are complex cases. Their snow drifts have greater than average cross-sectional areas, but they are nearly symmetrical on either side of the road. This would imply that the east and west winds were equally effective in moving snow. However, T-6 crosses obliquely to the road, and the amount of snow available to make drifts at this site may be affected by the larger road system and associated drifts lying to the west of it (see traverse T-5). Traverse T-7 may be complex because it lies adjacent to two parallel roads and its west end is on a large lake (Fig. 1).

Traverses T-5 and T-8 show the greatest departure from average and the greatest difference between cross-sectional areas on the east and west sides of the road. The cross-sectional area on the east side is twice that of the west side out to a distance of 80 m from the road. This indicates more effective transport of snow from the west winds. It is consistent with the observation that winter storm winds, which bring new snow and have higher speeds, blow from the west (Conover 1960). The prevailing winds blow from the northeast. This appears to be a general relationship on the Arctic Slope. In large drifts on river and lake banks, the drifts formed by west winds vary in size considerably from year to year, but those formed by east winds remain essentially the same size from year to year (Benson 1969).

Table 5

General summary of vertical core sample data.

Sample number	1972 Date	Snow depth (cm)	Average density (g cm^{-3})	Water equivalent (cm)	Sediments Dust, sand, etc. mg·cm^{-2}	mg·cm^{-3}	Electric cond. μmho·cm^{-1}	Bottom type
1	May 21	16.5	0.351	5.8	0.474	0.082	750	Sea Ice
2	21	34	0.334	11.3	1.555	0.137	63	Tundra
3	21	32.5	0.321	10.4	0.950	0.091	102	Grass
4	21	19	0.529	10.1	8.198	0.815	94	–
5	21	33	0.380	12.5	9.369	0.747	63	Ice
6	21	42	0.377	15.9	7.768	0.490	120	Grass
7	21	32	0.270	8.7	1.414	0.162	64	Grass
8	21	41	0.254	10.4	10.003	0.959	62	Grass
9	21	36	0.255	9.2	0.996	0.109	36	Grass
10	21	19	0.397	7.5	13.322	1.766	180	Dune
11	21	33	0.337	11.1	5.406	0.487	124	Grass
12	21	33	0.311	10.3	8.016	0.781	111	Ice & Grass
13	21	15	0.355	5.3	7.328	1.377	114	Grass
14	21	15	0.353	5.3	0.812	0.153	63	Ice
15	21	17	0.392	6.7	4.366	0.660	80	Ice & Grass
16	23	47	0.379	17.8	7.554	0.424	60	Grass
17	23	22	0.431	9.5	22.703	2.391	78	Ice
18	23	39	0.353	13.8	14.860	1.079	103	Grass
19	23	36	0.465	16.7	24.453	1.462	141	Ice
20	23	17	0.367	6.2	1.215	0.195	82	Ice
21	23	20	0.360	7.2	0.775	0.108	81	Grass
22	23	21	0.419	8.8	2.104	0.239	79	Ice
23	23	30	0.317	9.5	1.438	0.151	55	Ice
24	23	24	0.362	8.7	0.860	0.099	69	Grass
25	23	24	0.374	9.0	0.637	0.071	53	Grass
26	23	35	0.271	9.5	2.060	0.217	75	Grass
27	23	27	0.278	7.5	4.957	0.660	94	Grass & Ice
28	23	40	0.369	14.8	2.981	0.202	73	Ice
29	23	34	0.323	11.0	1.353	0.123	61	Grass
30	23	20	0.372	7.4	1.849	0.249	96	Grass
31	23	29	0.443	12.9	1.378	0.107	75	Grass
32	23	23	0.365	8.4	1.356	0.162	71	Grass
33	23	30	0.420	12.6	4.546	0.361	1003	Ice & Grass
34	22	41	0.389	16.0	16.865	1.057	76	Grass
35	22	41	0.326	13.4	1.878	0.141	47	Grass
36	22	30	0.336	10.1	15.514	1.539	84	Grass
37	22	30	0.286	8.6	10.574	1.234	81	Grass
38	22	35	0.329	11.5	0.197	0.017	14	Grass
39	22	35	0.317	11.1	0.267	0.024	20	Grass
40	22	23	0.239	5.5	0.153	0.028	20	Grass
41	22	23	0.290	6.7	0.131	0.020	11	Grass
42	26	28	0.432	12.1	2.126	0.176	89	Ice & Grass
43	26	35	0.415	14.5	6.016	0.415	84	Dirt
44	26	26	0.407	10.6	3.477	0.329	98	Grass & Ice
45	26	33	0.408	13.5	2.845	0.211	85	Grass
46	26	59	0.400	23.6	2.921	0.124	51	–
47	26	32	0.465	14.9	2.862	0.192	82	Ice
48	26	38	0.380	14.5	0.833	0.058	42	Ice
49	26	28	0.447	12.5	24.127	1.927	66	Ice
50	26	30	0.371	11.1	1.849	0.166	127	Ice
51	26	21	0.485	10.2	7.355	0.721	74	Ice
52	19	–	0.381	–	0.445	0.131	41	–
53	19	–	0.354	–	0.274	0.052	33	–
54	19	–	0.358	–	0.756	0.236	43	–
55	19	–	0.420	–	0.988	0.157	57	–
56	19	–	0.359	–	0.960	0.281	5	–
57	19	–	0.391	–	2.085	0.360	11	–
58	19	–	0.302	–	1.279	0.027	25	–

Table 5 continued

Sample number	Date	Snow depth (cm)	Average density (g cm^{-3})	Water equivalent (cm)	Sediments Dust, sand, etc.		Electric cond.	Bottom type
					mg·cm^{-2}	mg·cm^{-3}	μmho·cm^{-1}	
59	May 19	–	0.378	–	2.126	0.626	55	–
60	19	–	0.346	–	1.789	0.086	55	–
61	19	–	0.387	–	11.980	2.151	56	–
62	19	–	0.330	–	7.355	1.872	57	–
63	20	–	0.410	–	1.587	0.319	75	–
64	20	–	0.418	–	1.796	0.353	63	–
65	20	31	0.325	10.1	0.233	0.023	23	Grass
66	20	31	0.290	9.0	0.447	0.050	26	Grass
67	20	–	0.247	–	1.295	0.432	77	–
68	20	–	0.268	–	0.129	0.040	19	–
69	20	16	0.371	6.0	0.165	0.028	61	Ice
70	20	16	0.387	6.2	0.350	0.056	37	Ice
71	20	–	0.384	–	0.683	0.146	54	–
72	20	–	0.356	–	0.841	0.195	58	–
73	20	35	0.336	11.8	0.724	0.062	42	Grass
74	20	35	0.329	11.5	0.673	0.059	31	Grass
75	20	–	0.256	–	0.053	0.017	10	–
76	20	–	0.254	–	0.078	0.025	12	–
77	20	39	0.351	13.7	0.683	0.050	44	Grass
78	20	39	0.332	13.0	0.724	0.056	31	Grass
79	20	–	0.379	–	0.469	0.102	50	–
80	20	–	0.373	–	0.449	0.100	29	–
81	20	41	0.221	9.1	0.447	0.049	23	Grass
82	20	41	0.336	13.8	0.880	0.064	21	Grass
83	20	–	0.265	–	0.051	0.016	10	–
84	20	–	0.267	–	0.185	0.057	9	–
85	20	31	0.334	10.4	0.313	0.030	30	Ice
86	20	31	0.343	10.6	0.367	0.035	30	Ice
87	20	–	0.366	–	0.301	0.068	36	–
88	20	40	0.371	14.8	0.761	0.051	35	Ice
89	20	40	0.368	14.7	0.741	0.050	30	Ice
90	20	–	0.407	–	0.398	0.081	44	–
91	20	30	0.410	12.3	1.995	0.162	56	Grass
92	20	–	0.384	–	0.367	0.079	40	Grass
93	20	29	0.318	9.2	0.717	0.078	79	Grass
94	26	24	0.460	11.0	7.729	0.700	78	Ice
95	26	53	0.435	23.0	2.826	0.123	39	–
96	22	25	0.314	7.9	0.377	0.048	16	Tundra
97	22	25	0.345	8.6	1.662	0.193	25	Tundra
98	26	28	0.417	11.7	12.025	1.031	146	Ice
99	26	52	0.348	18.1	3.365	0.186	57	Grass
100	22	24	0.275	6.6	0.700	0.106	24	Grass
101	22	24	0.355	8.5	0.688	0.081	18	Grass
102	22	26	0.289	7.5	0.379	0.051	30	Grass
103	22	26	0.310	8.1	0.685	0.085	40	Grass
104	26	39	0.298	11.6	3.601	0.310	66	Grass
105	26	40	0.312	12.5	1.538	0.123	36	Grass
106	26	34	0.367	12.5	8.222	0.658	129	Grass
107	26	61	0.406	24.8	0.950	0.038	77	–
108	26	26	0.318	8.3	0.841	0.102	37	Grass
109	26	26	0.453	11.8	0.311	0.026	19	Ice
110	26	36	0.328	11.8	0.248	0.021	16	Ice
111	26	22	0.299	6.6	0.515	0.078	16	Grass
112	26	29	0.277	8.0	0.296	0.037	32	Grass
113	26	32	0.248	7.9	0.073	0.009	34	Grass
114	26	41	0.354	14.5	0.658	0.045	65	Grass
115	June 8	24	0.177	4.3	0.075	0.018	12	Ice
116	8	24	0.201	4.8	0.034	0.007	6	Ice
117	May 26	20	0.365	7.3	0.083	0.011	14	Ice

Table 5 continued

Sample number	Date	Snow depth (cm)	Average density (g cm^{-3})	Water equivalent (cm)	Sediments Dust, sand, etc.		Electric cond. μmho·cm^{-1}	Bottom type
					mg·cm^{-2}	mg·cm^{-3}		
118	May 26	43	0.345	14.8	2.005	0.135	54	Grass
119	26	33	0.262	8.6	0.790	0.092	48	Grass
120	26	41	0.355	14.6	0.350	0.024	24	Grass
121	26	42	0.334	14.0	0.260	0.019	16	Grass & Ice
122	26	36	0.292	10.5	0.996	0.095	49	Ice & Grass
123	26	41	0.353	14.5	0.649	0.045	40	Ice & Grass
124	26	38	0.367	14.0	0.224	0.016	18	Grass
125	26	34	0.367	12.5	8.203	0.658	81	Dirt
126	26	39	0.337	13.2	1.434	0.109	64	Grass
127	24	33	0.378	12.5	14.724	1.181	116	Grass
128	24	40	0.438	17.5	2.911	0.166	55	Ice & Grass
129	24	30	0.396	11.9	5.005	0.422	72	Ice
130	24	29	0.365	10.6	2.877	0.272	92	Ice
131	24	47	0.381	17.9	2.935	0.164	78	Ice
132	24	31	0.431	13.4	2.029	0.152	969	Grass
133	24	23	0.325	7.5	5.732	0.768	969	Dirt
134	24	21	0.362	7.6	2.141	0.282	92	Grass
135	25	51	0.353	18.0	7.809	0.434	87	Grass
136	25	42	0.394	16.5	0.778	0.047	39	Ice
137	25	66	0.408	27.0	1.084	0.040	25	–
138	25	34	0.236	8.0	8.589	1.069	105	Grass
139	25	16	0.317	5.1	2.576	0.508	133	Grass
140	25	52	0.358	18.6	218.495	11.724	98	Ice
141	25	20	0.216	4.3	9.806	2.274	98	Ice & Grass
142	25	20	0.227	4.5	6.755	1.487	74	Grass
143	25	36	0.378	13.6	1.295	0.095	76	Ice
144	25	19	0.293	5.6	3.037	0.546	64	Grass & Ice
145	25	40	0.274	11.0	5.462	0.499	62	Ice
146	25	46	0.369	17.0	22.319	1.315	87	Ice
147	25	34	0.232	7.9	4.028	0.510	81	Grass
148	25	38	0.309	11.7	3.023	0.258	72	Grass
149	25	41	0.341	14.0	7.075	0.506	74	Ice
150	25	36	0.432	15.6	13.312	0.855	78	Ice
151	25	53	0.344	18.2	4.852	0.266	70	–
152	15	3	0.344	1.2	24.500	24.050	–	–
153	15	3	0.258	0.8	5.830	7.730	–	–
154	15	3	0.243	0.7	2.395	3.315	–	–
155	15	4	0.263	1.3	10.800	13.800	–	–
156	15	2	0.175	0.4	9.300	17.910	–	–
157	15	4	0.290	1.2	9.720	11.300	–	–
158	15	3	0.191	0.6	6.205	10.980	–	–
159	15	4	0.394	1.6	4.300	3.315	–	–
160	15	3	0.129	0.4	2.395	4.725	–	–
161	15	3	0.123	0.4	0.678	1.382	–	–
162	25	40	0.452	18.1	18.794	1.050	98	Ice
163	25	31	0.295	9.1	11.621	1.272	43	Grass
164	25	28	0.229	6.4	–	–	–	Grass
165	25	30	0.276	8.3	0.432	0.052	25	Grass
166	25	43	0.254	10.9	0.396	0.036	14	Grass
167	25	28	0.300	8.4	8.161	0.971	30	Ice
168	25	38	0.398	15.1	2.435	0.161	35	Grass
169	25	28	0.353	9.9	12.569	1.275	34	Ice
170	25	41	0.285	11.7	1.064	0.091	30	Grass
171	24	21	0.362	7.6	2.141	0.282	92	Grass
172	24	21	0.239	5.0	0.510	0.102	21	Grass
173	24	30	0.281	8.4	2.658	0.316	39	Grass
174	24	38	0.257	9.8	0.950	0.097	19	Grass
175	June 5	40	0.328	13.1	1.557	0.119	219	Grass
176	5	40	0.268	10.7	2.099	0.196	564	Grass

Table 6

Cross-sectional area of snowdrifts.

Traverse	Total 80 m from road East	 West	E/W	Total 150 m from road E 150	 W 150	E/W
T-1						
Area (m^2)	25.0	26.9	0.93	29.2	36.9	0.79
Ratio	0.98	1.05		0.61	0.77	
T-3						
Area (m^2)	22.0	28.2	0.78	35.8	45.4	0.79
Ratio	0.86	1.10		0.74	0.94	
T-5						
Area (m^2)	43.7	22.2	1.97	65.5	38.9	1.68
Ratio	1.71	0.87		1.36	0.81	
T-6						
Area (m^2)	30.7	35.4	0.87	41.0	60.3	0.68
Ratio	1.20	1.38		0.85	1.26	
T-7						
Area (m^2)	37.6	38.2	0.98	–	–	
Ratio	1.47	1.49				
T-8						
Area (m^2)	51.2	22.1	2.32	70.4	41.9	1.68
Ratio	2.0	0.86		1.47	0.87	

Traverse	Total 80 m from road North	 South	N/S	Total 150 m from road North	 South	N/S
T-9						
Area (m^2)	19.9	21.7	0.92	35.5	36.0	0.99
Ratio	0.78	0.85		0.74	0.75	

For each traverse, the top row indicates the cross sectional area of the drift from the road to 80 m and to 150 m. The second row, labeled "Ratio" compares the cross sectional area of the drift with the cross section area that would be made by a similar cut through snow with the constant average depth of 32 cm. At a distance of 80 m this area would be 25.6 m^2, at a distance of 150 m it would be 150 m^2.

The cross-sectional areas summarized in Table 6 indicate the general distribution of drifted snow. However, they do not directly yield information on the water equivalent in these drifts because the hard-packed drifted snow generally has higher density than the average tundra snowpack. A trend to higher average density has been observed with increased snow depth. This can be seen in Fig. 9a, compared with the shallower pit studies. Based on data from drift traps along the Arctic Slope, the following general relationship has been established (Benson 1969).

Depth range (cm)	Average density ($g\ cm^{-3}$)
0-50	0.34
50-100	0.35
100-150	0.37
150-200	0.39
200-250	0.41
250-300	0.42

If we use these values we can calculate the water equivalent of slices of the drifts summarized in Table 6. The water equivalent of such a slice

Table 7

Water equivalent of a thin slice of the drift extending in both directions from road compared with average snow cover.

Traverse	E 80 m	W 80 m	E/W	E 150 m	W 150 m	E/W
T-1						
Mass (kg)	86.300	91.700	0.94	100.650	125.750	0.80
Relative mass	(1.04)	(1.10)		(0.64)	(0.81)	
T-3						
Mass (kg)	74.900	96.400	0.78	121.800	154.850	0.79
Relative mass	(0.90)	(1.16)		(0.78)	(0.99)	
T-5						
Mass (kg)	151.800	76.250	1.99	226.350	133.350	1.70
Relative mass	(1.82)	(0.92)		(1.45)	(0.85)	
T-6						
Mass (kg)	105.950	121.700	0.87	173.950	206.400	0.84
Relative mass	(1.27)	(1.46)		(1.12)	(1.32)	
T-7						
Mass (kg)	129.950	133.000	0.98			
Relative mass	(1.56)	(1.60)				
T-8						
Mass (kg)	179.100	75.200	2.38	244.450	142.550	1.71
Relative mass	(2.15)	(0.90)		(1.57)	(0.913)	

Traverse	N 80 m	S 80 m	N/S	N 150 m	S 150 m	N/S
T-9						
Mass (kg)	67.600	74.250	0.91	155.350	122.950	1.26
Relative mass	(0.81)	(0.89)		(1.0)	(0.79)	

For each traverse, the top row indicates the mass (kg) of 1 cm thick vertical slice of the snowdrift extending in each direction from a road. The second row, labeled "Relative mass," compares the mass of a slice through the drift with a slice of "average" snow, i.e., with constant water equivalent of 10.4 cm H_2O (10.4 g cm^{-2}) throughout its length. The mass of this average slice would be 83.2 kg if it is 80 m long, and 156.0 kg if it is 150 m long.

through the measured drift can then be compared with a slice throughout "average snowpack" as determined earlier. This is done in Table 7. The results are similar to those in Table 6, but they give the water equivalent of the drifts directly in comparison with the average tundra snow.

Windblown dust

The movement of dust and coarser sediments by the wind is related to snow drifting, but there is an interesting difference. The most effective winds in moving these sediments are clearly from the east. The east winds move several times more dust than do the west winds. There are two main reasons for this:

(a) There is a noticeable change in the direction of the strongest winds with the seasons. This was well summarized by Conover (1960, p. 10) from Barter Island wind roses. The strongest and most frequent winds of winter are from the west. They yield progressively from April through July to winds that are predominantly from the northeast.

(b) During the time when the strong west winds are most active there is little exposed sediment, so they move snow. When the northeast winds become more active the spring thaw exposes sediments in the dune area (east of T-1) and along the river channels. Also, the roads become sources of dust when they become snow-free during spring in direct proportion to the amount of traffic on them (see sequential photographs).

Some comparisons of the amounts of dust on the east and west sides of major roads are presented in Table 8, which is based on the data of Table 5. The electrical conductance of the meltwater obtained from the samples is also tabulated in Table 8. The conductance values were either measured at 25° C, or corrected to 25° C by the following relationship:

$$C_{25} = M_c \times 0.01\ [1 + 0.025(25 - T)]$$

where C_{25} is the conductance at 25° C, M_c is the measured conductance at temperature T, and the conductivity cell constant is 0.01.

It was not possible to determine the variation of the temperature coefficient for the water, and precision of 10% was considered adequate, so the single temperature coefficient of 0.025 was used. This should ". . . be satisfactory for all natural waters" (Smith 1962).

In the center part of the Prudhoe Bay area, especially along the main NW trending road, there is generally a significantly higher dust content on the west side of the road than on the east side. These are the simplest cases to interpret because the roads are clearly the dominant sources of dust. The dust distribution indicates that the east winds move the most dust. As we move to the eastern part of the area, especially along the road between the Prudhoe Bay airfield and the dock, we note that the west/east ratio becomes less than unity. It does not mean that the west winds are more effective dust movers in this region. Instead, it indicates that the dune area to the east of the road contributes more dust than does the road. Indeed, the road must act as a partial barrier to westward movement of sediments from the dunes. This seems to be verified by the fact that the road itself acts as a source of sediments; yet, the dust moving west from it does not add enough material to equal that from the dunes on the east. In places where the roads trend east-west, the difference in dust content between the two sides decreases. In these cases the distance south or north of the road is indicated together with a parenthetical indication of east and west components where they exist.

The data on electrical conductance of meltwater follow the same general trend as do the dust content data. Occasionally, we find an abnormally high conductance value such as in sample 33 by the airport, which is the highest value of all. Another high value was obtained for sample 1 (not in Table 8), which is on the sea ice and most likely is contaminated by brine.

Snow Melting

In the dune area east of traverse T-1, we have observed beautiful marblelike mixtures of snow and sand in drifts during winter. Prior to melting these look like mixtures of different colored sand grains. By late April and the beginning of May, such features are rare because the snow begins to evaporate and to melt as solar radiation is absorbed by the darker sand grains. This process continues until patches of bare soil and vegetation are exposed. Water vapor is lost

Fig. 14. *Photo of hoarfrost crystals on snow.*

Table 8

Sample No.	Distance East or West of road (m)	Dust Content (g cm^{-2}) x 10^{-4}	Ratio W/E	Electrical Conductance μmho cm^{-1}	Ratio W/E
146	25 W	223	5.57	87	1.07
147	25 E	40		81	
138	25 W	86	7.81	105	4.23
137	30 E	11		25	
135	25 W	78	9.75	87	2.24
136	25 E	8		39	
133	25 W	57	2.71	969	10.56
134	25 E	21		92	
131	25 W	29	1.45	78	0.08
132	25 E	20		969	
129	25 S(W)	50	1.72	72	0.78
130	25 N(E)	29		92	
127	25 SW	147	5.06	116	2.11
128	25 NE	29		55	
125	25 W	82	5.85	81	1.27
126	25 E	14		64	
106	25 S(W)	82	8.20	129	1.69
107	25 N(E)	10		77	
104	25 W	36	2.40	66	1.83
105	25 E	15		36	
99	25 S	34	0.28	57	0.38
98	25 N	120		146	
94	25 W	77	2.75	78	2.00
95	25 E	28		39	
51	25 W	74	4.11	74	0.58
50	25 E	18		127	
49	25 S(W)	241	30.12	66	1.51
48	25 N(E)	8		44	
47	25 S(W)	29	1.00	82	1.61
46	25 N(E)	29		51	
44	25 S(W)	35	1.25	98	1.14
45	25 N(E)	28		85	
43	25 N(W)	60	3.14	84	0.95
42	25 S(E)	21		89	
32	25 S	14	0.31	71	0.07
33	25 N	45		1003	
30	25 S	18	1.28	96	1.27
31	25 N	14		75	
29	25 W	14	0.46	61	0.83
28	25 E	30		73	
27	25 W	50	2.50	94	1.25
26	25 E	20		75	

Table 8 continued.

Sample No.	Distance East or West of road (m)	Dust Content $(\mathrm{g\,cm^{-2}}) \times 10^{-4}$	Ratio W/E	Electrical Conductance $\mu\mathrm{mho\,cm^{-1}}$	Ratio W/E
25	25 W	6	0.66	53	0.75
24	25 E	9		69	
23	25 W	14	0.66	55	0.70
22	25 E	21		79	
21	25 S	8	0.66	81	0.98
20	25 N	12		82	
19	25 W	245	0.64	141	1.36
18	25 E	149		103	
17	25 W	227	2.98	78	1.29
16	25 E	76		60	
15	25 W	44	5.50	80	1.26
14	25 E	8		63	
13	25 W	73	0.91	114	1.02
12	25 E	80		111	
11	W	54	0.40	124	0.68
10	E	133		180	
9	25 W	10	0.10	36	0.58
8	25 E	100		62	
7	25 W	14	0.17	64	0.53
6	25 E	78		120	
5	25 W	94	1.14	63	0.67
4	25 E	82		94	
3	40 W	10	0.62	102	1.61
2	50 E	16		63	

by evaporation (sublimation) from the exposed soil and vegetation. The bare patches appear first on the south slopes of the dunes. Some of these were examined in detail during the afternoon of 19 April 1973. The south faces of exposed dirt had 5-8 cm of dry powdery soil on top of hard frozen ground. The north sides of these same patches had less than 0.5 cm of dry powdery soil on top of the hard frozen soil. This indicates a significant difference in the amount of drying action produced by the sun and wind. The temperature 2 cm below the soil surface on the south side was -5.8 to -7.5°C; it was -11°C at the soil surface on the north side. The snow temperature was -16 to -17°C throughout its 20 cm depth at nearby places; the time of day was 1610 and 1700.

A typical example of a small sand hill is shown in Fig. 14. The view is toward the north. Note the hoarfrost crystals growing on the adjacent snow surface; these are formed downwind of the exposed bare patches. The crystals grow partly because water vapor, which enters the air over the bare patch, condenses as it moves downwind in air that cools as it passes over the snow surface. The crystals were generally on the south sides of dunes and they began immediately downwind of exposed bare patches of ground. A good example of this is shown in Fig. 15, which looks west from the dune area toward the road near traverse T-1. The frost crystals appear on the south side but not on the north side of the dune, and a bare patch of soil was immediately upwind of the frost crystal area. The snow

Fig. 15. *Photo of hoarfrost crystals on snow from dirt patch.*

Fig. 16. *Snow with sastrugi and blades of vegetation.*

in this area was shallower than the average thickness in 1973, just as it was in 1972 (see traverse 1 data in Tables 6 and 7). It was also wind sculptured and had bits of vegetation protruding through it (Figs. 15 and 16). When melting begins it spreads outward from the bits of protruding vegetation, which act as centers for ablation, as do the bare soil patches.

The progress of snowmelt can be seen by looking at sequential aerial photographs that were taken between 24 May and 30 June 1972. No melt had occurred by 24 May except along heavily traveled roads. There are five sequences of photographs, and their locations are indicated by the rectangular areas blocked out in Fig. 1. The sequences are as follows:

Sequential Photographs: Set Number 1.
BP pad "N" area during breakup 1972

a. 24 May
b. 5 June
c. 9 June
d. 12 June
e. 15 June
f. 30 June

Arrow located on west side of Pad N and pointing east.

Sequential Photographs: Set No. 2.
BP Gathering Center No. 1 during breakup 1972

a. 24 May
b. 5 June
c. 11 June
d. 13 June

Arrow located on east side of G.C. No. 1 and pointing west.

Sequential Photographs: Set No. 3.
BP Gathering Center No. 3 during breakup 1972

a. 24 May
b. 5 June
c. 9 June
d. 15 June

Arrow located on east side of GC No. 3 and pointing west.

Sequential Photographs: Set No. 4.
IBP Tundra Biome intensive study site
during breakup 1972

a. 24 May
b. 5 June
c. 11 June
d. 13 June
e. 15 June
f. 30 June

Arrow located at intersection of BP Spine Road and Put River No. 1 Road and pointing south.

Sequential Photographs: Set No. 5.
BP Storage Yard area during breakup 1972

a.	24 May	Arrow located at west end of storage pad and pointing east.
b.	5 June	
c.	9 June	
d.	11 June	

Some brief comments on these sets of photographs are in order:

Set Number 1:

1a. The gravel haul road on the left and the main road which runs east-west had heavy traffic, so they were dusty, and dust spread over the adjacent snow. The north-south trending road by the arrow had no traffic and, consequently, no dust.

1c and 1d. The effect of road orientation relative to wind is especially clear. The N-S road has the largest drifts, and they are larger on the east than on the west sides, as is consistent with the data from traverses T-5 and T-8 (see Tables 6 and 7).

Set Number 2:

2a. The effect of a heavily traveled road on producing early snowmelt is very clear in this photograph.

2b. The snow is nearly gone from around the heavily traveled road, but large drifts remain adjacent to the N-S road to left of center.

2c and 2d. Ponds of water are visible on the east side of the main road to right of center. This ponding is produced by the road and will contribute to its destruction. It results from the buildup of large drifts adjacent to the road, and the rapid melting of these drifts because of the dust deposited on them by heavy traffic.

Set Number 3:

3a. The dust from heavily traveled roads is producing melt adjacent to the roads before the clean snow on the tundra has begun to melt. This contributes to the formation of ice masses in and at the base of the snow near the roads (see text).

3c. The larger amount of snow drifting is clearly on the east side of the roads. This indicates more effective transport of snow by the west winds. The location is midway between traverses 5 and 8, both of which showed this asymmetrical distribution of drifted snow (see Tables 6 and 7 and Fig. 13).

Set Number 4:

4a and 4b. The larger snow drifting on the east side combined with the larger dust drifting on the west side of the roads is apparent, especially in 4b.

4c. A minimum of snow quantity about 100 m from the roads appears to exist in some places. This phenomenon is well displayed along the roads by the arrow, especially to the left of the arrow.

4d, e, and f. Note the dry lake near the arrowhead in 4d on 13 June; it was full of water on 15 June (photo 4e), but dry again on 30 June (photo 4f).

Set Number 5:

This set of photographs shows the overwhelming effect of dust from the Sagavanirktok River channel in ablating snow. In 5b and 5c the most effective snow drifting is on the east sides of the roads—from west winds. On the other hand, the dust is moving west—from east winds.

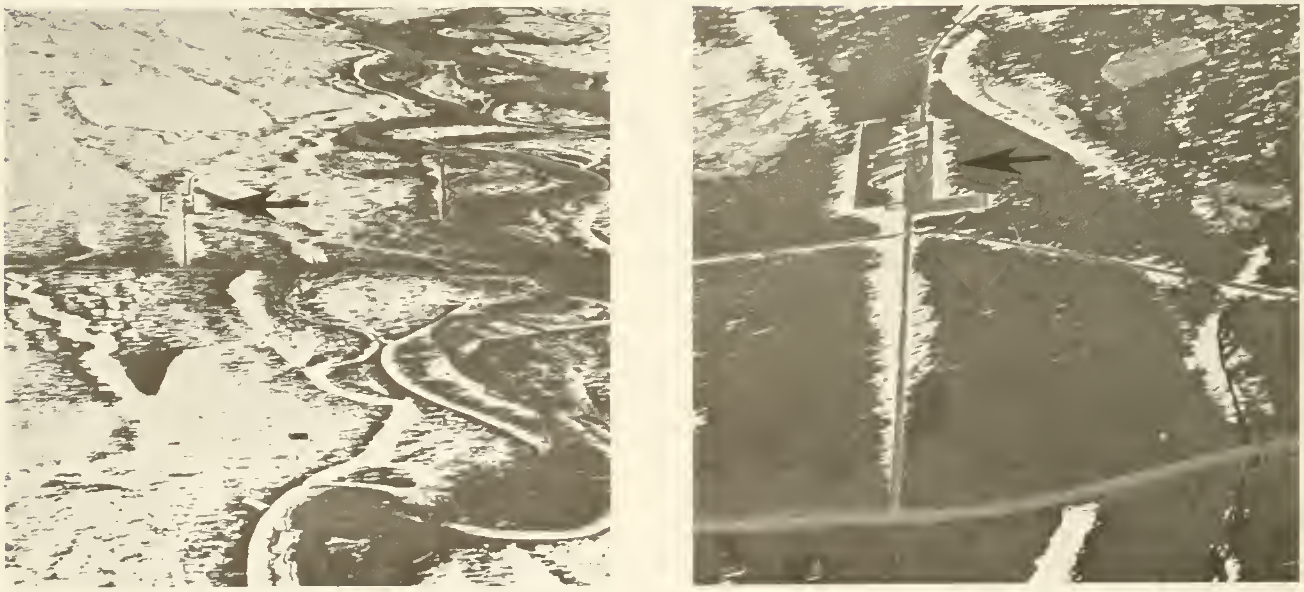
Radiation Climate and Snow Breakup

The main objective of this section is to present radiation measurements made at Prudhoe Bay from early spring throughout the summer seasons of 1972 and 1973 and relate these data to the melting of snow cover in these areas. The observations are relatively simple compared with the complex, full energy budget measurements reported elsewhere (Weller et al. 1974). The intention is to demonstrate to what extent such data can be used to explain physical processes at the tundra surface. The melting of the snow cover is of particular interest in this context since it probably represents the single most dynamic microclimatic event on the tundra.

The outgoing and incoming long-wave and short-wave radiations were measured by Eppley precision pyrgeometers and pyranometers, respectively—two of each at Prudhoe Bay in 1972. The radiation equipment used at Prudhoe Bay in 1973 was the same as in 1972, except that the reflected short-wave radiation was

a. 24 May 1972 (N view).

c. 9 June 1972 (S view).



b. 5 June 1972 (S view).

d. 12 June 1972 (S view).

Fig. 17. *Sequential photographs (above and on opposite page) of the BP Pad "N" area during breakup 1972. (Arrow located on west side of pad and pointing due east).*

e. 15 June 1972 (S view).

f. 30 June 1972 (S view).

measured by a Moll-Gorczynski pyranometer. In principle, the determination of the net radiation by measurements of its four basic components is superior to the integrated measurements using a single all-wave net radiometer. This is particularly so if the aim is to describe the radiation fluxes in terms of cloud, surface type, temperature, or other meteorological parameters.

Unfortunately, the Eppley precision long-wave pyrgeometers, which had become available only relatively recently, proved to be subject to large errors. In spite of extensive calibrations, both in the field by comparison with a Barnes thermal radiometer and in the laboratory with a black body device, we could not obtain consistent results. The errors are partly due to long-wave emission by the KRS-5 dome, supposedly semitransparent to long-wave radiation and having a low emissivity (Eppley Laboratory, 1972). After some time in use, it appears that the domes acquire an emissivity that is far from negligible. Furthermore, probably because of convection effects induced by considerable solar heating of the dark colored domes, the calibration factors are not the same when the instruments point upward and downward. Although it is reported that the Eppley pyrgeometers may be used with some success if, among other things, the temperature of the KRS-5 dome is monitored, our experience with them shows that they are unsuitable as field instruments in their present design. We are not using the results of the pyrgeometer measurements in the present discussion.

The Eppley short-wave pyranometers used in the present investigation were compared a few times in the field for internal consistency. Before and after the field season in 1972 and 1973, two of the pyranometers used were calibrated against a Linke-Feussner actinometer. The results of these calibrations gave factors within 1-2% of those recommended by the manufacturer.

For the summer temperature and humidity measurements, we used recording thermohygrographs in standard, white-painted instrument shelters. Calibrations were carried out with an Assmann psychrometer in connection with changes of the paper record.

The observations were made at sites adjacent to the Gas Arctic Research Station in 1972 and to the Bechtel Garage in 1973. The albedo data at Prudhoe Bay do not represent the undisturbed tundra since the snow in that area is generally contaminated by dust from industrial activities, mainly road dust, and by natural dust from sand dunes in the Sagavanirktok River delta area.

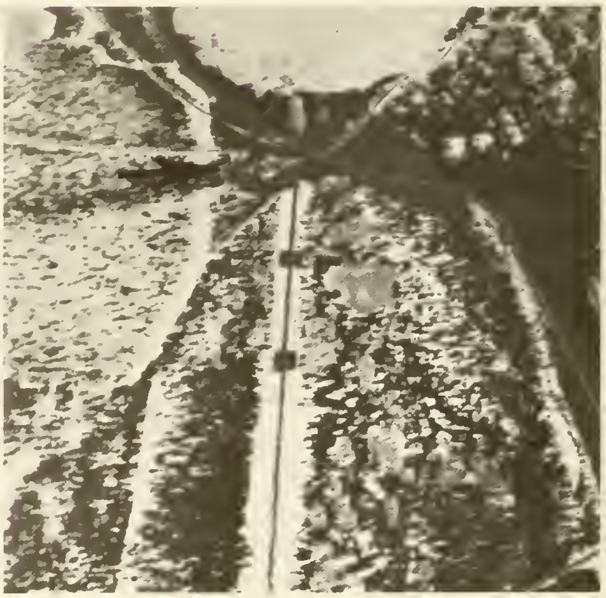
The actual measuring locations were selected to represent approximately average snow conditions. Albedo measurements over a shallow snowpack in situations with high incoming solar radiation are extremely sensitive to any man-made or natural disturbances. Although care was taken to disturb the snowpack as little as possible in connection with installation of the equipment and daily maintenance and inspection, some disturbances of the snowpack could not be avoided. These disturbances had a noticeable effect on the breakup patterns around the radiometer stands.

The variations of the incoming short-wave radiation and the albedo at Prudhoe Bay for the summers of 1972 and 1973 are given in Fig. 22. The general features of the radiation regime for coastal tundra are well-known since the radiation climate at Barrow has been investigated for many years (Ray 1885; Thornthwaite and Mather 1956, 1958; Kelley et al. 1964, 1969; Lieske and Stroschein 1968; Lieske and Bailey 1969; Weaver 1969, 1970; Weller et al. 1972, 1974; Maykut and Church 1973). During breakup, there is generally a sharp drop of the albedo from values above 80% to values of about 15-20%. The lowest values are obtained when the tundra is wet (Weller et al. 1972). At Prudhoe Bay the albedo generally varied between 10 and 15% after breakup in 1973.

One of the most striking features in Fig. 22 is the high variability of the incoming radiation. The cloud conditions along the coastal zone of the Arctic Ocean are similar throughout the summer with persistent decks of low stratus. On the average the National Weather Service stations at Barrow and Barter Island have cloudiness at or above 8 tenths from May to October with a main maximum in August-September and a secondary maximum in May. The decrease in cloudiness in the middle of the summer has been ascribed by Sverdrup (1933) to a weaker inversion during that period.

The transmissivity of the stratus for solar radiation is highly variable. Although the stratus

a. 24 May 1972 (NE view).



b. 5 June 1972 (S view).

Fig. 18. *Sequential photographs (above and opposite page) of BP Gathering Center No. 1 during breakup 1972. (Arrow located on east side of GC- No. 1 and pointing due west).*

c. *11 June 1972 (S view).*

d. *13 June 1972 (S view).*

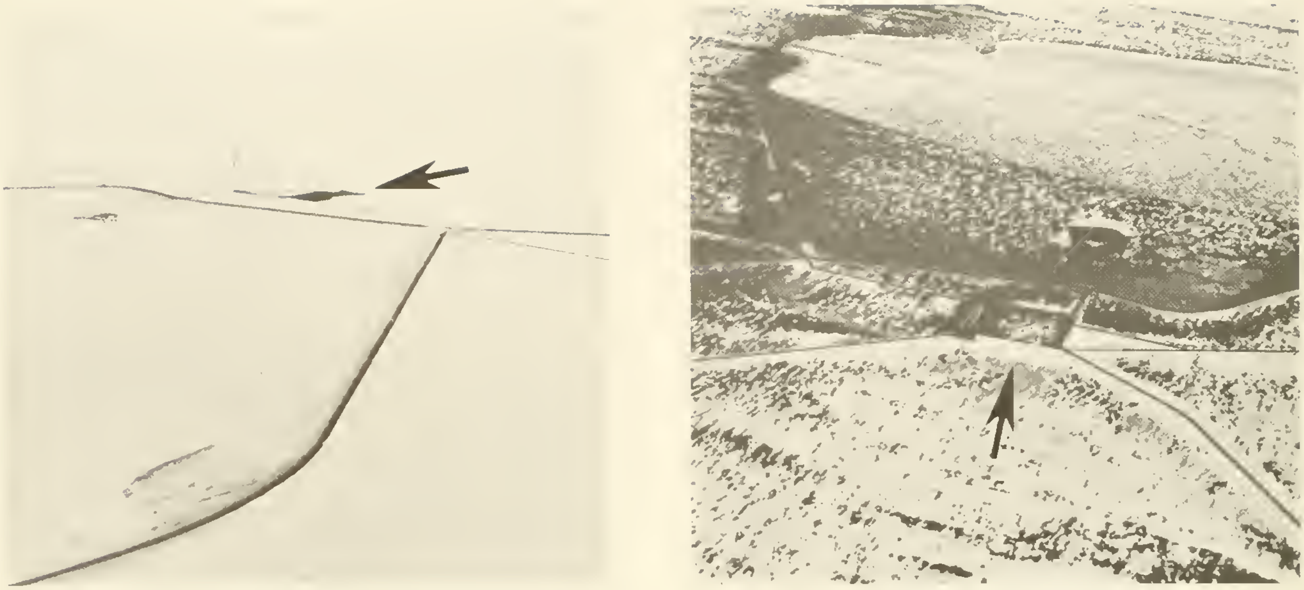
are layer clouds, their optical properties are not very homogeneous. The cloud forms are often a transitional form between stratus and stratocumulus. Frequently, the sun becomes visible through the cloud layers. The variations of the incoming solar radiation often suggested waves within the cloud layers inducing regular variations of the radiation intensity. Also the emissivity of the thin stratus clouds appeared to be highly variable.

The albedo and the surface and weather conditions

The changes of the albedo in connection with snowmelt and onset of the snow cover cause a startling increase of the net radiation and of the turbulent, sensible, and latent heat transfers at the surface (Weller et al. 1972). The most obvious climatic parameter affecting the snow melting is the air temperature. Daily values of the albedo and air temperature at screen height are shown in Fig. 23 (see also Fig. 8 and Table 1). As the air temperature increases and melting starts, the albedo decreases. At low air temperatures, the positive net radiation during the daytime is either used for heat conduction into the snowpack, or for transport of sensible or latent heat into the atmosphere. As the air temperature increases toward or above 0°C, the positive net radiation also increases, and this excess energy is used to melt and evaporate snow and to heat the air and soil in the relative proportions shown by the energy balance (Weller et al. 1974).

The daily Prudhoe Bay temperature data are from the unpublished BP radio station data obtained in the vicinity of the Mukluk Camp (Brown et al., this volume) about 8 km from the coast.

One may note that in the Prudhoe Bay area, the albedo in 1972 appears to decrease in connection with relatively low daily air temperatures. This is probably due to dust contamination of the snow. In May 1973 the albedo values are for a short time above 80%, even with air temperatures above freezing, but then they drop suddenly. The observation site in 1973 was not the same as in 1972, and the influence from dust may have been slightly less in 1973. Furthermore, on 24 May 1973 a thin layer of new snow



a. 24 May 1972 (NE view).

c. 9 June 1972 (SW view).

b. 5 June 1972 (SW view).

d. 15 June 1972 (SE view).

Fig. 19. *Sequential photographs of BP gathering center location No. 3 during break-up 1972. (Arrow located on east side of GC- No. 3 pad and pointing due west).*

was observed on top of the old snowpack, which temporarily increased the albedo.

The albedo variations shown in Fig. 23 are only typical values that vary from one spot to another, particularly during melting. During breakup the snow cover disintegrates into patches, with bare ground appearing at an early stage where the snow is shallow. The albedo of the remaining snow patches should generally be much higher than the values representing the latter part of the melting period shown in Fig. 23. One might guess that for clean snow the albedo remains around 70% or so, except during the last stages, when the snow generally was coarse-grained and perhaps often consisted of superimposed ice. The albedo of the snow patches might then have been considerably lower. On 5 June 1973 the total snow area in the vicinity of the measuring site at Prudhoe Bay was estimated to be approximately 15% of the tundra surface. Away from the road system and the camps, etc., the snow area was estimated to be approximately 50% on the same day.

It is obvious that point albedo measurements cannot be used for interpretations of the average conditions over larger areas during snowmelt. An illustration of this is shown in Table 9, where values are given of the incoming solar radiation, the albedo, and the absorbed radiation at two measuring places 8 m apart, but with a 10-20 cm deep trench causing slightly increased snow accumulation under one of the sensors. The difference in absorbed radiation between these two adjacent places during this 10-day melting period is almost 700 cal cm^{-2}, corresponding to the energy required to melt about 9 g of ice per sq cm, or almost the entire snowpack, as far as the average conditions go.

The influence of various climatic parameters and microtopography on the breakup is obviously very complex. As long as the albedo is high, the net radiation is generally higher with overcast skies than with clear skies (Liljequist 1956; Holmgren 1971; Ambach 1974). Later, when the albedo is lowered by melting, the net radiation will be higher with clear than with cloudy skies.

Table 9

Daily insolation, albedo, and difference in absorbed radiation at two adjacent observation sites at Prudhoe Bay.

Day	Insolation cal day^{-1}	A_1 %	A_2 %	ΔA %	Difference in absorbed radiation cal day^{-1}
05.26	720	68	68	0	0
05.27	675	65	67	2	14
05.28	575	57	66	9	52
05.29	361	55	65	10	36
05.30	449	48	63	15	67
05.31	321	50	67	17	55
06.01	273	40	61	21	57
06.02	317	34	56	22	70
06.03	310	31	53	22	68
06.04	382	27	46	19	73
06.05	434	29	51	22	95
06.06	453	24	40	16	72
06.07	511	15	20	5	26
06.08	590	15	15	0	0
Sum	6371				685

Satellite observations show that the breakup on the Arctic Slope generally proceeds from the upper foothills into the coastal plains (Holmgren et al. 1975). Furthermore, the melt season advances faster along the major rivers when meltwater, flowing down the rivers, floods the snow cover, reduces the albedo, and causes increased absorption of radiation. On the regional scale there exists a north-to-south temperature gradient from the coast and inland toward the valleys in the Brooks Range in spite of an increase in elevations from sea level to about 600 m over that distance (Conover 1960). At Prudhoe Bay temperature gradients from the shore to about 25 km inland were measured to investigate possible effects on the breakup by the proximity to the Arctic Ocean (Brown et al., this volume). Fig. 24 shows some maximum and minimum daily temperatures from Point McIntyre, 75 m from the shore, and from a point on the Sagavanirktok River, approximately 20 km south of the Deadhorse Airfield. The greatest differences are observed in the maximum temperatures during the main summer period. In spring, before and during the first part of the snowmelt, the temperature differences are hardly significant for either the maximum or minimum temperatures. The same applies for the period around freezeup. The minimum temperatures are on the average only a few degrees above 0° C in midsummer. The surface temperature contrast between land and sea is apparently small at night.

Table 10

Observations of radiation temperatures of various surfaces at Prudhoe Bay, 1972 and 1973.

Day	Time A.D.T.	Surface Temp.	Surface Type	Cloud Temp.	Cloud Type
1972					
08.22	21.35	6.4	Grass	-35.0	Ci 10/10
	21.35	8.9	Puddle	-35.0	Ci 10/10
08.23	15.30	10.0	Grass	No meas.	AsCi 10/10
09.20	14.22	0.2	Melting snow	- 5.6	FsSt 10/10
	14.22	0.9	Mud, dark brown	- 5.6	FsSt 10/10
	14.22	1.6	Gravel	- 5.6	FsSt 10/10
	15.30	- 0.3	Sea ice	- 3.3	FsSt 10/10
	15.30	0.4	Sand	- 3.3	FsSt 10/10
	15.30	- 0.6	Snow	- 3.3	FsSt 10/10
	15.30	- 0.9	Sea water	- 3.3	FsSt 10/10
	20.25	- 2.1	Snow grass	- 7.4	FsSt 10/10
09.21	15.45	- 4.6	Snow on top of pingo	–	Cs 2/10
	15.45	1.2	Soil on top of pingo	–	Cs 2/10
	15.45	- 2.6	Snow on slope facing sun	–	Cs 2/10
	15.45	7.9	Soil on slope facing sun	–	Cs 2/10
	15.45	- 6.6	Snow on shaded slope	–	Cs 2/10
	15.45	- 6.1	Soil on shaded slope	–	Cs 2/10
	21.00	-10.6	Snow grass	–	Cs 2/10
1973					
06.06	13.45	2.4	Water logged tundra	2.6	St 10/10
	13.45	4.9	Small puddles	2.6	St 10/10
07.15	15.03	7.9	Wet tundra	0.9	St 10/10
09.06	22.00	3.5	Lake	No meas.	St 10/10 Drizzle
	22.00	1.4	Gravel	No meas.	St 10/10 Drizzle
09.07	09.50	3.5	Lake	- 3.6	St 10/10
	09.50	2.6	Gravel	- 3.6	St 10/10
10.11	14.02	3.6	Snow	- 5.6	St 10/10
	14.02	0.0	Slush at the bottom of the snow cover		

Visual observations in connection with occasional helicopter flights on 4 and 5 June 1973 did not indicate that the breakup on the coast was later than it was a few tens of kilometers inland. In the Prudhoe Bay area a slight advancement of the breakup could be observed, however. Earth Resources Technology Satellite (ERTS) images of Prudhoe Bay on 27 May 1973 also indicated that the breakup in the coastal zone was not much influenced by distance to the shore. On the other hand, the influence of natural and man-made dust was quite obvious in the satellite data (Holmgren et al. 1975).

Another feature of the surface characteristics during breakup is the large spatial and temporal variability of the surface temperatures. Table 10 gives radiation temperatures of various surfaces as measured by a Barnes thermal radiometer with a field of view of about 2° and sensitive to radiation within the 8-14 μm band. The values in Table 10 represent averages of a few readings for each surface type. In the individual case, the local temperature variations might be much higher. As soon as the ground becomes bare of snow in early spring, the surface temperature increases rapidly at daytime because of the increase of the absorbed solar radiation. At night the temperature differences between various surface types are generally small. With high surface temperature and increased turbulent fluxes of sensible and latent heat from the bare ground, one may generally expect increased rates of melting as warm and moist air is advected over the remaining snow. On the microscale, stable internal boundary layers will prevail over the bare ground.

We also observed rapid increases of the water temperature of the puddles due to high values of the solar radiation, allowing high rates of evaporation. Several times during the breakup period we observed fog-smoke over ice-free ponds and over the waterlogged tundra in relatively cold weather, indicating high rates of evaporation. During a 4-day period after snowmelt in June 1971, Weller et al. (1972) found evaporation rates of 4.5 mm per day at Barrow.

Melting of a snowpack with high albedo generally starts when the air temperature increases toward 0°C. The importance of the vertical turbulent fluxes of sensible and latent heat in the melting process and, indirectly, the air temperature, is especially apparent during brief spells of warm weather in early spring. For instance, the rise of air temperatures above 0°C in connection with warm air advection on 5-6 May 1972 at Prudhoe Bay induced melting and the formation of ice lenses within the snowpack (see **Physical Characteristics of the Snow**, above). After the air temperature decreased, the percolating meltwater in the snowpack refroze again.

During the main breakup period on the tundra, the influence of the air temperatures is not as evident as during the early spring period. On the other hand, there are reasons to always consider the melting above an extensive snowfield as the combined effect of the net radiation at the surface and the warm air advection since the total radiation budget of the surface-atmosphere system is always negative over a snow surface. In other words, the energy input from the snow surface into the atmosphere is too small to compensate for the radiation energy losses of the atmosphere. This is why melting at the surface is closely related to advectional effects above the surface.

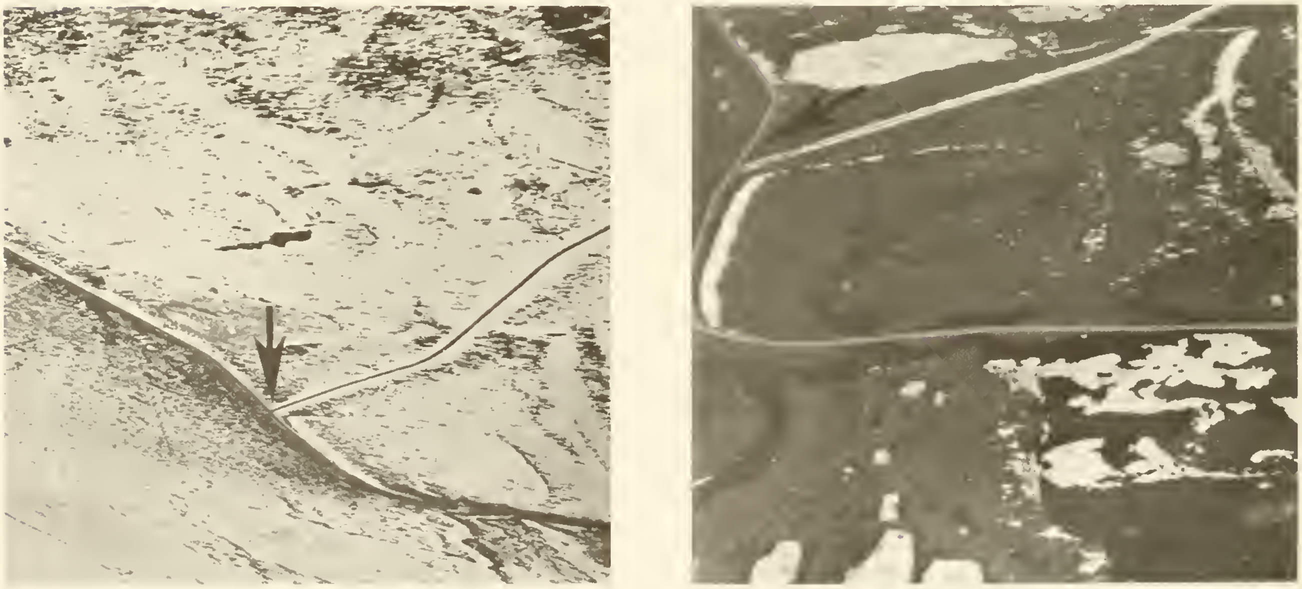
Since the air temperatures at the end of May and at the beginning of June appear to vary around 0°C in the coastal zone of the Arctic Ocean, with relatively small variations in different weather situations, the advection effects on the melting process may become less apparent than during the brief early melting periods. Also, as bare patches of the ground appear, a rapid warming of the surface takes place, changing the microclimate around and over the remaining snow patches. At this stage, the large-scale advection effects should become less important in relation to the advection on the microscale.

Exactly when the snow starts to melt and exactly when it is gone is a matter of subjective judgment. Roughly, the melting takes place in 2-4 weeks. During part of that period the snow surface is at the melting point. However, especially when light melting occurs intermittently, it is difficult to judge whether or not the surface is melting. Any single meteorological parameter is then a rather poor indicator of the snow surface temperature. Part of the problem is related to the fact that snow is semitransparent to short-wave radiation. The short-wave incoming radiation that penetrates the surface is absorbed at depth, most of it within the first few centimeters. At the surface the emitted long-wave radiation is generally greater than the incoming long-wave radiation, and the net radiation budget of the uppermost surface layer may be negative. In situations with air temperatures slightly above or below 0°C, the surface is often frozen, while internal melting occurs in the snowpack. The penetration of solar radiation into the snowpack and the physics of the melting have been discussed in detail by Liljequist (1956).

Toward the end of the breakup the flat tundra may be regarded as an extensive shallow lake, as far as the surface conditions go. The highest amounts of snow accumulation are found in shallow depressions and in the sastrugi. Ground observations and also observations during helicopter flights in the Prudhoe Bay area on 4 and 5 June 1973 indicated that a considerable damming of the meltwater may be caused by the snow and possibly by the superimposed ice in the natural shallow drainage channels. As the

a. *24 May 1972 (N view).*

c. *11 June 1972 (S view).*



b. *5 June 1972 (N view).*

d. *13 June 1972 (S view).*

Fig. 20. *Sequential photographs (above and opposite page) of the IBP Tundra Biome intensive site during breakup 1972. (Arrow located at intersection of BP Spine Road and Put River No. 1 road and pointing due south).*

e. 15 June 1972 (N view).

f. 30 June 1972 (S view).

general conditions for snowmelt on the tundra become more favorable toward the end of the melting period with increasing air and water temperatures, the remaining snow may suddenly disappear, allowing a rapid drainage of the meltwater. This may contribute to the sharp peaks in the hydrograph curves of the rivers that originate on the coastal plains (Carlson et al. 1974; Dingman 1973). A few days after peaking, the runoff from melting subsides greatly. Since much of the subdued tundra terrain was observed to be waterlogged during a considerable time after the snowmelt in 1972 and 1973, but with decreasing depths of the standing water, it seems likely that a substantial amount of the meltwater evaporates from the tundra surface each year, although part of the meltwater may infiltrate the active layer. Observations on the Meade River and in the Noluck Lake region indicate that much of the snow may disappear before runoff occurs (Benson 1969; Johnson and Kistner, 1967).

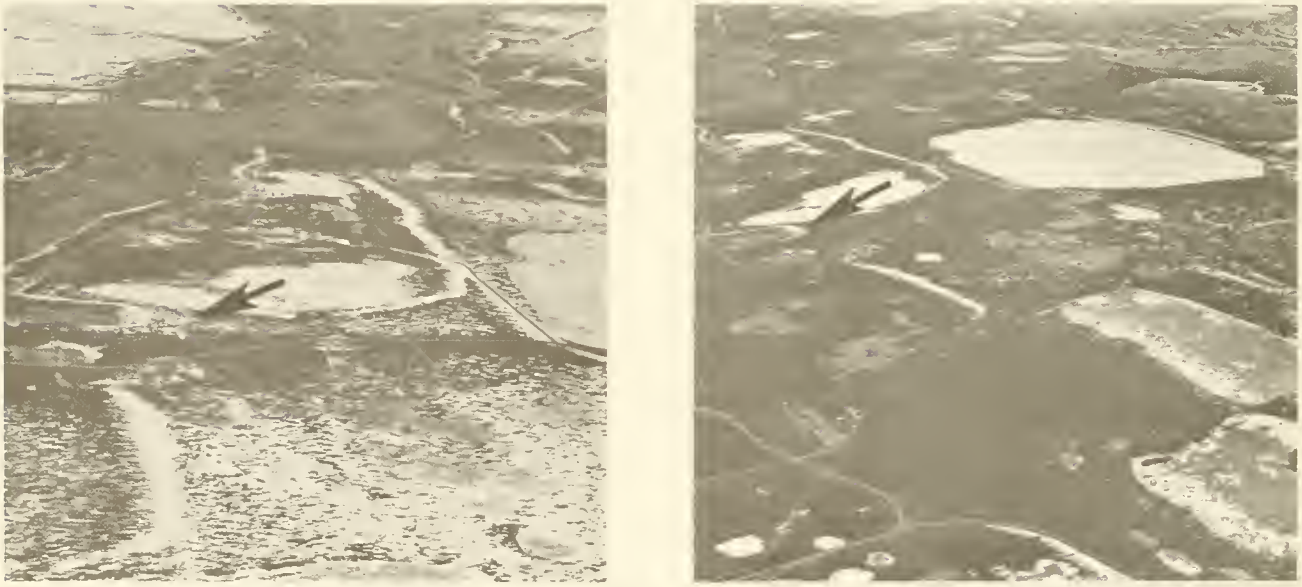
Concluding Remarks

The seasonal snow cover on the Arctic Slope near Prudhoe Bay contains about 10 cm water equivalent. The snow in the Brooks Range is about three times this amount. The snow is subject to drifting from east and west winds; the west winds are more effective than the east winds as snow drifters. Dust is blown onto the snow from the channels of the Sagavanirktok River and, after April, from roads which have traffic. The dust from roads is proportional to the amount of traffic (see sequential photographs). The riverbed and adjacent dune areas produce much more dust than do the roads. The east winds are more effective than the west winds as dust movers.

The first melt action produces ice lenses, layers, and glands in the snow. These are impervious to airflow and produce structural and thermal effects that may be significant to animals such as lemmings, which live under the snow. The melt that produces these ice masses may come a month before the temperature of the entire snowpack is raised to the melting point. The thaw period proceeds by rapid melting of the snow from centers of ablation such as

a. 24 May 1972 (NE view).

c. 9 June 1972 (S view).



b. 5 June 1972 (S view).

d. 11 June 1972 (SW view).

Fig. 21. *Sequential photographs of BP storage yard during breakup 1972. (Arrow located at west end of storage pad and pointing due east).*

dune areas, roads, and, near the end of the season, from protruding bits of vegetation. Once the temperature of the entire snowpack reaches the melting point and melt action is continuous, the snow will disappear in about 2 weeks. In 1972 the snow did not reach 0°C throughout until after 28 May. By 8 June 25% to 50% of the ground was snow free; by 9 June it was 50% snow free.

A strong gradient exists in the tundra climate. The coastal influence maintains the snow cover at Prudhoe Bay and Barrow for several weeks longer than at sites only 50 to 100 km inland. On 7 June 1972 there was no snow on the tundra south of Franklin Bluffs, yet the snow was still present in the Prudhoe Bay region. The images from ERTS may be especially useful in observing this phenomenon.

Acknowledgments

This project was funded primarily from NSF funds provided to the Tundra Biome Program at the University of Alaska. Supplemental assistance was provided by the State of Alaska and industry funds.

References

Ambach, W. (1974). The influence of cloudiness on the net radiation balance of a snow surface with high albedo. *J. Glaciol.*, 13(67):73-84.

Benson, C. S. (1962). Stratigraphic studies in the snow and firn of the Greenland Ice Sheet. SIPRE(CRREL) Research Report 70, 93 pp.

______. (1967). A reconnaissance snow survey of Interior Alaska. Geophysical Institute, University of Alaska, Report UAGR-190, December 1967, 71 pp.

______. (1969). The seasonal snow cover of Arctic Alaska. Arctic Institute of North America (AINA) Research Paper No. 51, 80 pp.

Brown, J., R. K. Haugen, and S. Parrish (This volume). Selected climatic and soil thermal characteristics of the Prudhoe Bay region.

Carlson, R. F., W. R. Norton, and J. McDougal (1974). Modeling snowmelt runoff in an arctic coastal plain. Institute of Water Resources, University of Alaska, Report No. IWR-43, 72 pp.

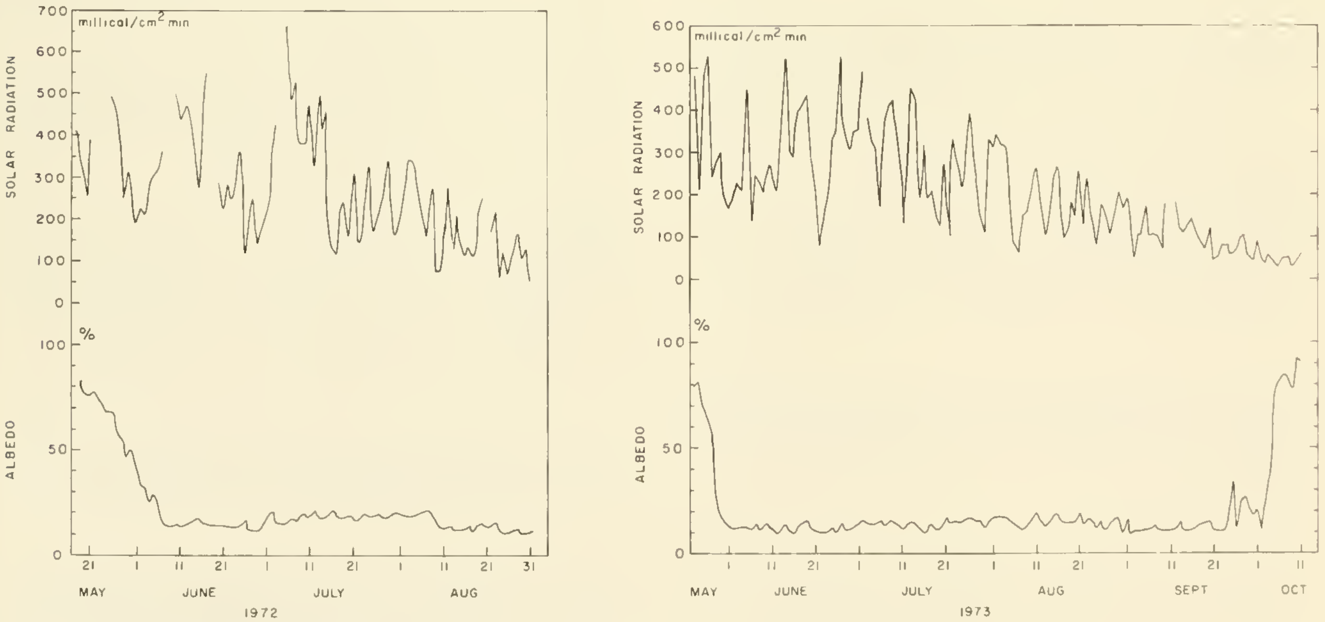


Fig. 22. *Incoming short-wave radiation and albedo at Prudhoe Bay during the summers of 1972 and 1973.*

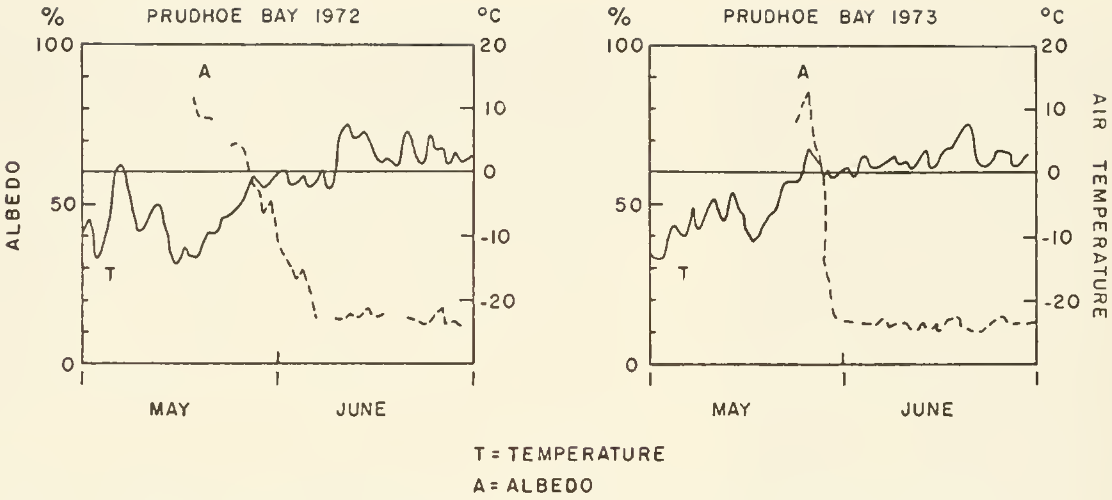


Fig. 23. *Albedo and air temperature during the melting of the snow cover at Prudhoe Bay.*

Carson, C. E. and K. M. Hussey (1962). The oriented lakes of Arctic Alaska. *J. Geol.,* 70(4):417-439.

Conover, J. H. (1960). Macro- and microclimatology of the Arctic Slope of Alaska. Quartermaster Research and Engineering Center, Environmental Protection Research Division, U. S. Army. Technical Report EP-139, Natick, Mass., 65 pp.

Dingman, S. L. (1973). The water balance in Arctic and subarctic regions. Annotated bibliography and preliminary assessment. CRREL Special Report 187, Hanover, N. H., 131 pp.

Eppley Laboratory, Inc. (1972). Instruments for the measurement of the components of solar and terrestrial radiation. Instruction Manual, Newport, R. I., 34 pp.

Hansen, B. L. (1951). Thermal properties. Chapter V of Review of the Properties of Snow and Ice. SIPRE(CRREL) Report 4, pp. 52-59.

Holmgren, B. (1971). Climate and energy on a subpolar ice cap in summer, Part B, wind and temperature field in the low layer on the top plateau of the ice cap. Uppsala, Universitet Meteorologiska, Institutionen, Meddelande, No. 108, 43 pp. (Arctic Institute of North America Devon Island Expedition, 1961-1963).

Holmgren, B., C. Benson, and G. Weller (1975). A study of the breakup of the Arctic Slope of Alaska by ground, air and satellite observations. *In* "Climate of the Arctic" (G. Weller and S. A. Bowling, eds.) Proc. AAAS-AMS Symp., Fairbanks, Alaska, August 1973, Geophysical Institute, University of Alaska, pp. 358-366.

Johnson, P. L. and F. B. Kistner (1967). Breakup of ice, Meade River, Alaska, USA CRREL Special Report No. 118, 12 pp.

Kelley, J. J., D. T. Bailey, and B. J. Lieske (1964). Radiative energy exchange over Arctic land and sea: Data 1962. Scientific Report, Dept. Atmos. Sci., University of Washington, Seattle, 205 pp.

Kelley, J. J. and D. F. Weaver (1969). Physical processes at the surface of the Arctic tundra. *Arctic,* 22(4):425-437.

Lieske, B. J. and L. A. Stroschein (1968). Radiation regime over Arctic tundra. Scientific Report, Dept. Atmos. Sci., University of Washington, Seattle, 23 pp.

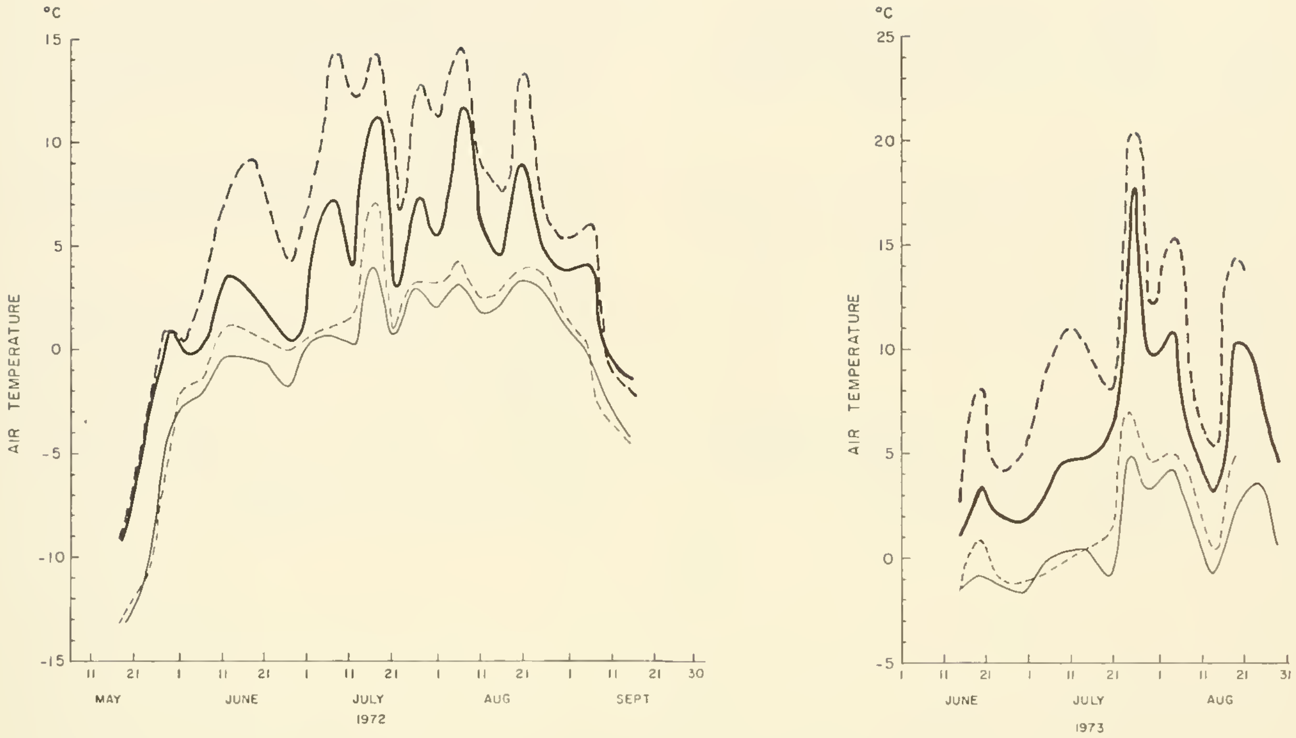


Fig. 24. *Maximum (dashed lines) and minimum (solid lines) daily air temperatures at Point McIntyre on the coast (thin lines) and 25 km inland (thick lines) during 1972 and 1973 in the vicinity of Prudhoe Bay.*

Lieske, B. J. and D. T. Bailey (1969). Radiative energy exchange over Arctic land and sea. Scientific Report, Dept. Atmos. Sci., University of Washington, Seattle, 27 pp.

Liljequist, G. H. (1956). Part 1: Energy exchange of an Antarctic snow field. Shortwave radiation. Norwegian-British-Swedish Antarctic Expedition, 1949-52. Scientific Results, Vol. II, Norsk Polar-institutt, Oslo, Norway.

Maykut, G. A. and P. E. Church (1973). Radiation climate of Barrow, Alaska, 1962-66. *J. Appl. Meteorol.*, 12(4):620-628.

Ray, P. (1885). Report of the international polar expedition to Point Barrow, Alaska. U. S. Government Printing Office, Washington, D. C., 686 pp.

Smith, S. H. (1962). Temperature correction in conductivity measurements. *Limnol. Oceanogr.*, 7:330-334.

Sorge, E. (1935). Glaziologische Untersuchungen in Eismitte, in Wissenschaftliche Ergebnisse der Deutschen Gronland—Expedition Alfred Wegener 1929 and 1930/1931. Band III Glaziologie, pp. 62-263.

Sverdrup, H. U. (1933). Meteorology, Part 1: Discussion. The Norwegian north polar expedition with the "Maud," 1918-1925. Scientific Results, Vol. II, Bergen, Norway.

Thornthwaite, C. and J. Mather (1956). Microclimatic investigations at Point Barrow, Alaska, 1956. Drexel Inst. Tech. Publ. Climatology, 9, No. 1, 51 pp.

______. (1958). Microclimatic investigations at Point Barrow, Alaska, 1957-1958. Drexel Inst. Tech. Publ. Climatology, 11, No. 2, 237 pp.

Trabant, D. C. and C. S. Benson (1972). Field experiments on the development of depth hoar. Geological Society of America, Memoir 135; Studies in Mineralogy and Pre-Cambrian Geology (B. R. Doe and D. K. Smith, eds.), pp. 309-322.

Trabant, D. C., C. B. Fahl, and C. S. Benson (In press). Mass balance of McCall Glacier, Brooks Range, Alaska during the 1971 and 1972 hydrologic years. *J. Glaciol.*

Weaver, D. F. (1969). Radiation regime over Arctic tundra, 1965. Scientific Rept. Dept. Atmos. Sci., University of Washington, Seattle, 260 pp.

______. (1970). Radiation regime over Arctic tundra and lakes, Scientific Rept. Dept. Atmos. Sci., University of Washington, Seattle, 112 pp.

Weller, G., S. Cubley, S. Parker, D. Trabant, and C. Benson (1972). The tundra climate during snowmelt at Barrow, Alaska. *Arctic,* 25(4):291-300.

Weller, G., C. Benson, and B. Holmgren (1974). The microclimates of the arctic tundra. *J. Appl. Meteorol.,* 13:854-862.

A species of Eriophorum *surrounds a pingo.*

EXXON Company, U.S.A.

Soil and Landform Associations at Prudhoe Bay, Alaska: A Soils Map of the Tundra Biome Area

KAYE R. EVERETT
Department of Agronomy and Institute of Polar Studies
The Ohio State University
Columbus, Ohio 43210

Introduction

The relationship between soils and topography has been recognized for a long time and forms one of the tenets of pedology.* Ideally, soils are arranged along a topographic (moisture) gradient. Soils representing the modal points of the principal elements of the gradient possess unique morphological, physical, and chemical characteristics. Thus, within a not too broadly defined region, the definition of landscape units provides reasonable predictability as to their soils. A similar relationship exists for vegetation.

In an area such as Prudhoe Bay, which generally lacks significant large-scale topographic contrasts, the morphologic identification and landscape association of soils is complex. Here microtopographic contrasts associated with patterned ground must be used to understand the character of the soils.

Although microrelief contrasts are commonly less than 0.5 m on much of the patterned ground, soils possessing unique characteristics occur in a predictable fashion on the different elements of the pattern. Thus, on landscapes which lack pronounced topographic contrast but possess areally extensive ground patterns, such as polygonal cells, soil associations can be delineated with reasonable accuracy.

Objectives

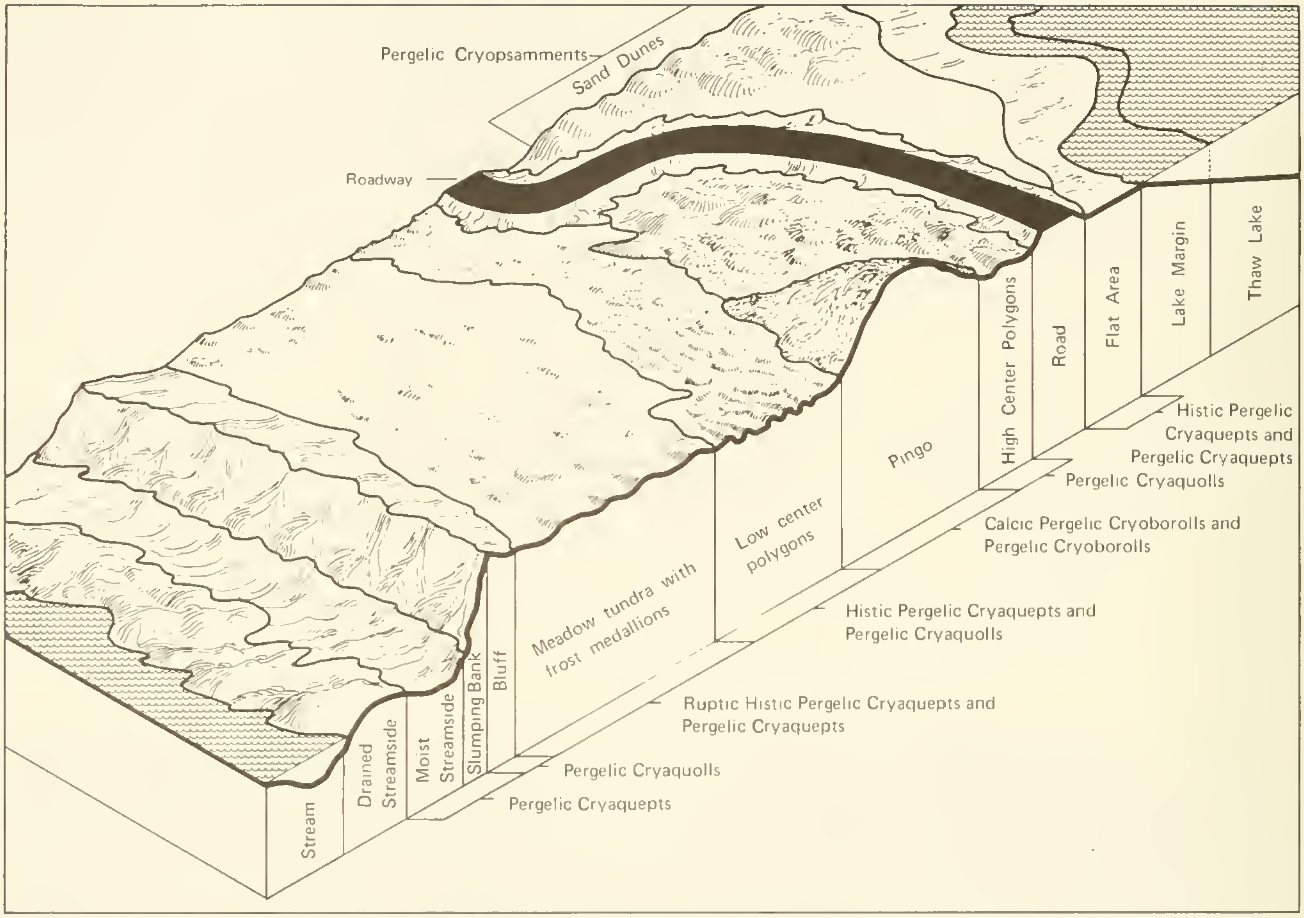
The primary objectives of the 1973 Prudhoe Bay soils program were: (1) to characterize and delineate the principal soil-topographic or microtopographic associations which occur in the main Tundra Biome study area; and (2) to construct a practical numerical key through which a maximum amount of soils and landform data could be represented on a large-scale map.

Principal topographic (macro and micro) elements recognized on Plate I

The area selected for soils-landform and vegetation mapping is representative of the Prudhoe Bay Unit as a whole. It includes several moderately large tundra ponds and a number of small ones; a pingo and an associated, ridge-like element, and portions of two active drainage channels which provide varied topography and drainage along the margin of the area. The remainder of the area consists of gently sloping

---

*Pedology is the branch of soil science which deals with the investigation of the natural laws governing the origin, formation, and distribution of soils.



Dennis Kuklok, Arctic Environmental Information and Data Center, University of Alaska

Fig. 1. *Schematic representation of the Prudhoe Bay terrain showing the spatial relationships among soils and terrain types. See Webber and Walker (this volume) for relationships with vegetation types. As a consequence of the thaw lakes, which continue to modify the land surface, both landforms and their soils range widely in age (Brown 1965). Radiocarbon dates of 9330 ± 150 Y.B.P. and 8690 ± 145 Y.B.P. were obtained from reworked organic materials beneath lake bottom deposits in a large active thaw lake in the vicinity of the Tundra Biome study area. These organic materials are believed to have been derived from a land surface(s) into which the thaw lake has expanded.*

interfluves with wide expanses of patterned tundra and relatively featureless, very wet, drained, or intermittent lake basins (Fig. 1).

Because of the large mapping scale and the intimate association between ground pattern and soil type, most of the 10 relief elements recognized on the soils map (Plate I) are ground pattern forms. The characteristics of the forms generally follow a microrelief classification system developed for the Barrow tundra (Carey 1972). Certain modifications and additions to this classification were required by the Prudhoe Bay terrain.

The terrain-relief classes used in Plate I are based on the character of the ground surface (its pattern or lack of pattern) and the amount of vertical relief found in the field and recognizable in aerial photographs. These are outlined as follows:

Soils Map Unit No.	Terrain-Relief Type
1.	High-center polygons covering two-thirds or more of the ground surface; center-trough contrast, 0.5-1 m.
2.	High-center polygons covering two-thirds or more of the ground surface; center-trough contrast, 0.5 m or less.
3.	Low-center polygons covering two-thirds or more of the ground surface; center-rim contrast, 0.5-1 m.
4.	Low-center polygons covering two-thirds or more of the ground surface; center-rim contrast, 0.5 m or less.
5.	Transitional features; mixed high- and low-center polygons with neither exceeding three-quarters of the area, *or* low-center polygons in which the trough depth greatly exceeds the rim-center contrast.
6.	Steep, eroding (collapsing) stream or pond margin banks.
7.	Polygonal ground surface pattern. Polygons are neither high- nor low-center; relief contrast, 15 cm.
8.	Hummocky ground, either in the form of rounded hummocks 30 cm or more in height, *or* flat-topped polygonal hummocks 30 to 50 cm in diameter and 30 cm or less in height.
9.	Aligned, discontinuous hummock ridges.
10.	No apparent ground surface pattern.

In an effort to place the terrain-relief classes in a regional context, they are combined with slope classes on Plate I; 0 to 2%; > 2 to 6%, and > 6%.

Principal soil types recognized on Plate I

Five distinct soil types have been recognized within the area covered by Plate I, and at least two others occur beyond its limits.

As a general rule, the region's soils are shallow; the mean August thaw depth is approximately 43 cm, with a range between 25 and 60 cm. The soils are mostly at or near saturation throughout much of the thaw period. Moisture contents range from less than 100% (on a weight basis) for those soils on the more elevated and/or better drained topographic positions to as much as 400% on the lower and/or more poorly drained sites. An August mean value of 225% is probably reasonable for the map area.

With the exception of active frost medallions and some other mineral soil areas, the majority of soils have a surface horizon composed of a variable thickness of fibrous, peaty organic materials. The surface horizon may be underlain by one or more mineral horizons which commonly contain wide-ranging amounts of organic materials. Although the great majority of the soils have a peaty (organic) surface horizon, few qualify as organic soils (Histosols) under present definitions of the National Soil Taxonomy (Soil Survey Staff, in press). Most fall within the definitions of a mineral soil order composed of soils showing, in this area, relatively weak horizon development. Names at the suborder level are indicative of soil wetness. They are prefaced at still lower orders of classification by the letters (Cry), reflecting the cold soil temperatures. Finally, one or more qualifying terms may precede the soil name which indicate the presence of a significant organic horizon at the surface (histic), or the fact the soils contain permafrost and may be subjected to some form of frost disturbance (pergelic). A soil classification scheme proposed by Tedrow et al. (1958) and commonly employed by arctic tundra ecologists is presented for correlation.

Each of the distinct soil types encountered in the map area is given a numerical designation. On the soils map, the soil-type number designations, in a combination of one to three digits, precede the terrain-relief number designation. The map symbol is completed by the addition of a number designation indicative of the regional slope angle. The last digit indicates the textural class of the mineral soil. All digits or digit groups are offset by commas.

The most extensive soil type found within the map area, and probably regionally as well, is a meadow tundra soil termed Histic Pergelic Cryaquept (map unit No. 3). These soils ordinarily occur in association with one or more of the other major soil types by virtue of their widespread occurrence in the depressed centers of polygons fitting the definitions of terrain-relief map units 3 or 4. The following profile is representative of this soil.

Soil type: Histic Pergelic Cryaquept*

Terrain-relief: Low-center polygons (No. 3), discontinuous rims.

Portion of element: Center; low, < 10 cm hummocks cover 10% of surface.

Vegetation: *Scorpidium scorpioides* and other mosses; *Carex* spp. *Eriophorum sp.* and *Salix* sp.

Slope: 0%

Depth in cm:	
0-8	Greyish brown (10 YR 5/2**); organic; fiber content 20% composed of *Carex* spp. and *S. scorpioides;* considerable included carbonate; roots abundant; boundary abrupt, smooth. Very dark greyish brown (10 YR 3/2) to dark greyish brown (10 YR 4/2); organic loamy fine sand; fiber content 30%; fibers break down with difficulty; roots common; carbonate reaction; boundary abrupt, smooth.
8-20	Very dark greyish brown (10 YR 3/2) loamy fine sand; medium and coarse fiber; fiber content 50%; fibers break down easily; carbonate reaction; roots common; boundary abrupt, smooth.
20-25	Very dark greyish brown (10 YR 3/2) and very dark brown (10 YR 2/2) organic fine sand; medium and coarse fibers; fiber content 50%; fibers break down easily and nearly completely; carbonate reaction; weak platy structure; roots few; boundary abrupt, smooth.
25-26.5	Very dark greyish brown (10 YR 3/2) very fine sandy loam; very weak carbonate reaction; weak platy structure; frost.

These soils are normally alkaline throughout the profile, ranging between pH 7.0 and 8.0. Soils of this group occasionally may have very high sodium levels. August field moisture is near 200% (oven dried basis—odb). The means of the few fluid transmission rates available for these soils indicate $K = 10.2 \text{ cm hr}^{-1}$ in the upper 10 cm, decreasing to $K = 8.4 \text{ cm hr}^{-1}$ between 10 and 20 cm.

A soil very closely associated with the one just described is designated on Plate I as map unit 4. However, it is restricted in its distribution to polygon center areas with standing water or to nonpatterned areas with standing water near ponds. There is not sufficient morphological reason within the confines of the National Soil Taxonomy to classify it differently from soil unit No. 3. The soils do differ, however, primarily in that those designated No. 4 may have organic horizons which are somewhat thicker and less decomposed than those of soil unit No. 3. August water tables seldom drop below the ground surface. Saturated hydraulic conductivities are usually somewhat higher in the No. 4 soils, due probably to increased porosity of the less decomposed and thicker organic horizon.

Soils designated as unit No. 2 on Plate I occupy the raised polygon rims and are associated especially with terrain-relief unit 3. These soils with slight morphologic variations can also be associated with any of the first 6 terrain-relief units. Because they occupy the drier (better-drained) sites, they are commonly associated with raised center polygons along eroding stream

---

* All classification assignments are tentative.

** Refers to Munsell color charts.

or pond banks. Soils of this group have been designated as Pergelic Cryaquolls. This classification recognizes the distribution of finely divided organic materials and dark coloration throughout much of these shallow profiles as well as their wetness. Like most other soil types of the area, they are alkaline with pH's generally greater than 7.0. They have relatively low moisture contents—the August mean is near 150% (odb). Much of this moisture is retained in capillary pores (as opposed to free-draining voids in the fibrous organic horizons of the soils just described). Hydraulic conductivity values are close to K = 7.0 cm hr^{-1} in the upper 10 cm of the profile and reflect the somewhat looser, occasionally granular, texture of this horizon. Below 10 cm, values drop to K = 1.2 cm hr^{-1}.

As will be noted in the profile below, these soils often display a thin (1 cm or less), oxidized band immediately above an equally thin zone of nodular carbonates somewhere in the near surface horizons. Such features indicate aerobic conditions during the summer months with precipitation of carbonates and oxidation of iron.

The following profile is representative of soil unit No. 2.

Soil type:	Pergelic Cryaquoll
Terrain-relief element:	Units 1 through 6, especially low-center polygons (No. 3) and steep eroding stream or pond banks (No. 6).
Portion of element:	Rims and high-center polygons.
Vegetation:	*Dryas integrifolia; Salix* spp.; *Papaver* sp., and acrocarpous mosses.
Slope:	0-10%

Depth in cm:

0-5	Dark brown (7.5 YR 3/2) to very dark greyish brown (10 YR 3/2) organic loamy fine sand and silt; many uncoated quartz grains; organic matter medium to coarse fibrous; roots abundant; boundary abrupt, smooth.
5-8	Yellowish red (5 YR 5/6) organic silt loam; quartz grains heavily coated with iron; massive; roots common; free nodular carbonates near lower boundary; boundary abrupt, irregular.
8-20	Very dark brown (10 YR 2/2) to very dark greyish brown (10 YR 3/2) organic loam or loamy fine sand; fiber content 40-50%; breaks down easily; massive to coarse, weak platy structure; boundary abrupt, smooth.
20-38	Very dark brown (10 YR 2/2) to very dark greyish brown (10 YR 3/2) loamy fine sand; finely divided organic matter < 5%. Massive to weak, coarse platy structure; fine gravel skeleton (1-2 cm) and > 2% of volume; stem fragments; boundary clear, smooth.
38-50	Very dark brown (10 YR 2/2) to dark yellowish brown (10 YR 4/4) loam or silt loam; may have an organic component; massive, or strong, coarse platy structure; numerous pebbles; frost.

The soils designated unit 1 on Plate I are among the more interesting, from the standpoint of soil genesis, but least extensive soils in the map area. Deeply thawed and well-drained, they are developed in sands and gravels on the top and flanks of pingos and sand and gravel ridges which may be associated with pingos. The ground surface frequently has a lag gravel and/or a hummocky microrelief (where slope angles approach 10% or more). The lag fragments display carbonate encrustations on their lower surface.

These soils have many characteristics common to the Pergelic Cryaquolls just described. They probably represent the fullest expression of the regional climate in the well-drained environment. The following, somewhat abbreviated profile is representative of this soil.

Soil type:	Calcic Pergelic Cryoboroll
Terrain-relief element:	Pingos and related sand and gravel ridges.

Portion of element:	Crest and upper flanks of the slope.
Vegetation:	*Dryas integrifolia, Cassiope tetragona,* lichens and mosses.
Slope:	10-13%

Depth in cm:

0-15	Very dark brown (10 YR 2/2) organic loam; massive to weakly granular in the upper few centimeters; gravel skeleton ~ 5%; free carbonates throughout; carbonate accumulation on most skeletal fragments to a depth of 7.5 cm; roots common; boundary abrupt, wavy.
15-25	Dark brown to brown (10 YR 4/3) medium sand; massive; pebbles few; roots common; boundary abrupt, irregular.
25-30+	Yellowish brown (10 YR 5/6) fine and medium gravelly coarse sand; massive to somewhat loose; larger skeletal fragments have carbonate crusts on their underside and silt coats on top; roots few.

The carbonate accumulations beneath the surface lag as well as on the underside of the skeletal fragments within the profile are indicative of the xeric environmental conditions in which they formed. The deposition of silt coats on gravel fragments at depth suggests seasonal downward movement of fines, probably due to infrequent, heavy summer rains. The exposed position of the soils precludes a snow cover sufficient to provide meltwater. The net water movement is upward, however, as in soils of map unit 2.

The final soil type recognized on Plate I occurs in frost medallions (non-sorted circles); it is designated as soils unit 7 and classified as a Pergelic Cryaquept. These soils have a textural range from loam through loamy sand to sand. They occur as circular areas ranging from unvegetated mineral soil to those completely covered with a vegetation assemblage distinct from the surrounding meadow tundra (soil map unit 3). Those lacking vegetation undergo intense seasonal frost heaving and desiccation. Most frost medallions have some vegetation cover, and those which have been stable for an extended period have an organic horizon up to several centimeters thick. Beneath the organic horizon (if present), is a horizon which is normally above the water table and in which oxidation is the dominant process. Below this horizon, seasonal fluctuations in the water table produce alternating oxidizing and reducing conditions which impart a mottled appearance to the soil. Below this zone, reducing conditions dominate.

Thaw depth beneath the frost medallions is commonly double that of the surrounding meadow tundra, in part, because the medallions lack the insulation of the thicker organic horizons of soil unit 3. The occurrence of frost medallions is restricted to areas of meadow tundra. This association may be further restricted to meadow tundra areas underlain by sandy textured, mineral materials. Their aerial extent ranges widely from a few percent of the surface to near 50%.

The following profile is representative of soil unit 7.

Soil type:	Pergelic Cryaquept.
Terrain-relief element:	Polygonal surface with neither high- nor low-center polygons.
Portion of element:	Not applicable.
Vegetation:	*Saxifraga oppositifolia; Carex* spp.; moss; lichens (*Thamnolia* sp. and *Dactylina* sp.).
Slope:	4%

Depth in cm:

0-5	Very dark greyish brown (10 YR 3/2) organic loam; soft, weak, fine aggregate structure; roots common; boundary abrupt, irregular or broken.
5-9	Yellowish brown (10 YR 5/6) to yellowish red (5 YR 4/6) silty fine sand; intermixed with dark greyish brown (10 YR 4/2) silty medium sand; massive; fine nodular carbonates near 5 cm; occasional pea gravel; roots common; boundary abrupt, irregular.
9-14	Dark greenish grey (5 GY 4/1) silty medium sand; massive; strong,

	coarse yellowish brown (10 YR 5/4-5/6) mottles; occasional fine gravel skeleton; roots few; boundary abrupt, smooth.
14-23	Dark grey (5 Y 4/1) medium and coarse sand; massive; occasional fine gravel skeleton; boundary abrupt, smooth.
23-45	Dark grey (5 Y 4/1) fine and medium sand; massive; moderate, coarse, light olive brown (2.5 Y 5/4) mottles; few roots and fine gravel; frost.

These soils have an alkaline pH and display a strong carbonate reaction to HCl throughout their profiles.

In 1974 the mapping was extended to the entire roadnet area, and by late 1975 a compiled soils map will be prepared.

Acknowledgments

This project was funded as a subcontract from the Tundra Biome Center to the Institute of Polar Studies, Ohio State University, and utilized the Prudhoe Bay Environmental Subcommittee funds. Initial drafting of the soils map was accomplished at the Institute of Arctic and Alpine Research, University of Colorado, in conjunction with the vegetation map. Both maps appear on Plate 1.

References

Brown, J. (1965). Radiocarbon dating, Barrow, Alaska. *Arctic*, 18:36-48.

Carey, K. L. (1972). Classification, mapping and measurement of the distribution of microrelief from airphotos: Barrow, Alaska. Pages 17-27 *in* Terrain and coastal conditions on the Arctic Alaskan Coastal Plain; Arctic environmental data package supplement 1. P.V. Sellmann, K.L. Carey, C. Keeler, and A. D. Hartwell. USA CRREL Special Report 165.

Soil Survey Staff (In press). Soil taxonomy, a basic system of soil classification for making and interpreting soil surveys. Soil Conservation Service, U. S. Dept. of Agri. Handbook No. 436.

Tedrow, J. C. F., J. V. Drew, D. E. Hill, and L. A. Douglas (1958). Major genetic soils of the Arctic Slope of Alaska. *J. Soil Sci.*, 9:33-45.

Scott Parrish

Aerial oblique of U.S. Tundra Biome study area. (See Plate 1.) Fertilizer runoff plots appear in upper portion of photograph between stream and snowdrift.

Nutrient Regimes of Soils, Landscapes, Lakes, and Streams, Prudhoe Bay, Alaska

LOWELL A. DOUGLAS and AYTEKIN BILGIN*
Department of Soils and Crops
Rutgers University
New Brunswick, New Jersey 08903

Introduction

The concentration of many nutrients in a hydrological system may be defined as functions of the rate of solubilization and dilution effects. The former includes sources of nutrients derived from mineral and organic soil and sediments and precipitation, and the latter includes climatic and geomorphic factors. In this study we have investigated streams and lakes near Prudhoe Bay to define climatic, geomorphic, and soil factors which affect the amount of dissolved nutrients found in these tundra drainage systems.

Durum and Haffty (1961) concluded that the major sources of nutrients in streams and lakes were weathering and soil formation. Cleaves et al. (1970) concluded that in some watersheds "chemical weathering presently is the dominant agent of erosion." Several investigators have reported differences in the quantities of dissolved nutrients in streams and lakes (Brown et al. 1962; Kalff 1968; Toth and Ott 1969). These investigators have sampled water bodies associated with geologic formations of contrasting composition. In this study we investigated the effect of soil types, all of which had been developed from the same parent material (geologic formation), on the nutrient level of several arctic streams and lakes. Included in this study was an evaluation of the proportion of fertilizer that will be lost to surface runoff after application on tundra soils. The results presented are part of a doctoral dissertation that was completed as this volume went to press (Bilgin 1975).

Methods

Water sampling was initiated in late June 1971 approximately 40 days after spring thaw and continued through August. The 1972 sampling was initiated in early June at the time of spring thaw and continued through mid-August.

During 1971 investigations, one 1-liter sample was passed through a column of mixed-bed ion exchange resin; the rest was used for the determination of carbonate, bicarbonate, and chloride titrimetrically (Brown et al. 1962). The column was returned to Rutgers University, eluted with 100 ml of 2.5 N HCl, and calcium, magnesium, potassium, and sodium were determined by atomic absorption. Phenyl mercuric acetate was added to the second set of samples and stored. At 3-week intervals these samples were taken to the Naval Arctic Research Laboratory at Barrow and ammonia-nitrogen, phosphate, and ferrous and ferric iron were determined colorimetrically using Hach methods.

---

*Deceased.

Table 1

Chemical characteristics of soils in the vicinity of the Prudhoe Bay region.

Depth (cm)	Organic Matter %	Carbonates %	pH	CEC		E.C.	Soluble cations ppm			
				Na	NH_4	µmho	Ca	Mg	Na	K
				meq (100 g)$^{-1}$						
				Meadow Tundra Soil						
75-01(120)*										
3.8-17	27.1	1.51	7.2	N.D.	53.0	477	55.0	5.3	7.2	2.6
17-29	9.4	5.5	6.4	N.D.	23.3	73	13.0	1.0	2.0	.2
29-53	18.6	.76	7.1	N.D.	45.1	240	35.7	2.4	3.1	.2
72-302										
0-14	31.1	1.48	7.6	58.0	55.5	379	50.7	4.1	5.2	2.4
14-26	10.1	1.17	7.8	26.4	26.5	197	23.3	1.3	9.2	1.1
16-31	7.7	1.42	7.9	23.2	21.7	157	22.9	1.2	2.7	.2
				Wet Meadow Tundra Soil						
76-02(30)										
0-21	17.8	2.26	7.5	42.8	33.2	360	45.3	1.3	7.2	1.5
21-46	4.6	3.37	7.7	13.0	7.5	193	25.7	1.7	4.3	1.3
46-53	5.5	1.97	7.6	10.9	7.4	197	29.0	.9	3.3	.5
				Wet Meadow Tundra Soil						
78-111(b)										
0-7.5	32.0	.74	7.1	N.D.	42.4	520	54.7	6.9	10.5	13.8
7.5-28	23.6	.99	6.8	N.D.	40.1	441	55.0	4.8	5.5	1.5
				Bog Soil						
72-Tr-2										
0-7.5	36.0	.53	6.7	95.7	89.3	405	50.7	9.5	7.8	2.8
7.5-17	41.3	.38	6.6	96.7	100.4	308	23.0	6.3	5.1	1.5
17-35	34.8	.47	6.8	81.2	66.3	237	36.0	4.3	3.5	.9
35-66	31.7	1.13	7.0	65.2	62.8	502	60.0	4.4	2.5	.3
66 +	34.0	.62	7.0	79.7	69.1	551	61.3	7.2	14.4	1.8
				Half Bog Soil						
72-312										
0-9.0	67.5	.84	6.0	93.0	90.7	800	61.3	10.6	43.3	10.9
9.0-22	58.6	.50	5.6	94.2	71.6	430	37.3	5.5	27.9	4.0
22-32	65.7	.59	5.9	84.8	67.7	600	36.7	5.7	48.3	5.7
32-41+	4.6	3.10	7.6	10.9	11.1	167	25.0	1.0	3.4	1.3
78-108										
0-18	33.4	.65	6.7	49.3	40.1	561	60.0	12.2	10.4	8.9
18-38	32.4	.70	6.7	40.6	31.4	451	48.7	9.2	7.5	3.6

*See Bilgin (1975) for details of site description and locations.

In 1972 all the determinations, except Ca, Mg, Na, and K, were made in Prudhoe Bay using the same methods. For the aforementioned cations, separate 125 ml samples were taken at the same sampling dates and returned to Rutgers University for determination by atomic absorption.

On the soils, organic matter was estimated by loss of weight between 110°C and 450°C. Particle size distribution was determined by the hydrometer method (Day 1965). Conductivity and soluble cations were determined on the solution phase of a 1:7 soil to water mixture. Sodium exchange capacity was determined at pH 8.2 (Richards 1954), and ammonia exchange capacity was determined at pH 7.0 (Busenberg and Clemency 1973).

Two 0.4-hectare plots on opposite sides of a small stream on the Tundra Biome intensive site were selected for fertilizer-runoff studies (site 76-02). On 14 July 1971 and also in 1972, 113.4 kg of 10-10-10 fertilizer were placed on each of these plots, nitrogen being in the form of nitrate. A 3 m border on which no fertilizers were applied was maintained on both sides of the stream. Water samples were collected from different locations upstream and downstream from this site for comparison.

Results and Discussion

Soils

The Prudhoe Bay area, part of the Arctic Coastal Plain of Alaska, is an unglaciated area of marine and nonmarine sediments (Brown 1969; Tedrow and Brown 1967; O'Sullivan 1961). It is dominated by oriented lakes, some of which are connected to one another with small drainage channels. These lakes migrate across the frozen land surface, eroding the old basins and creating new ones (Carson and Hussey 1959, 1960).

In recent studies, the poorly drained soils of the Arctic Coastal Plain have been classified as Tundra soils and Bog soils (Brown 1969; Douglas and Tedrow 1953, 1960; Tedrow and Brown 1967; Tedrow et al. 1958). Depending on the drainage and wetness, Tundra soils have been classified as Upland Tundra, which defines the well-drained conditions, and Meadow Tundra, where wetter conditions exist.

The sediments of the area are calcareous (Douglas and Tedrow 1960) and are often capped with a calcareous loess less than 30 cm thick. The area is characterized by long slopes of 2-4% and Upland Tundra soils. Although the soils show uniformity in some general characteristics, they vary significantly in the depth of the active layer, organic matter content, degree of wetness, texture, structure, and chemical and geomorphic characteristics. Well-drained, deep, sandy soils are dominant on the banks and terraces along the Kuparuk, Putuligayuk and Sagavanirktok Rivers, on beach ridges, and along the coast, while shallowly thawed, organic-rich, silty soils dominate the poorly drained lowlands. The depth of thaw varies considerably within short distances, depending on topography, texture, degree of wetness, and amount of organic matter.

The presence of permafrost under a shallow active layer influences soil formation in the arctic region (Hill and Tedrow 1961). The glei process dominates the lowlands where the soils are in a saturated condition during the summer, while maximum profile development exists in the relatively deeper, well-drained upland soils.

Generally, bogs are mildly to strongly acid, but due to the carbonate-bearing sediments, some bogs in the Prudhoe Bay area tend to be alkaline in reaction. Depending on moisture and amount of organic matter, these soils are classified as Bogs and Half-Bogs.

Within these general soil types, patterned ground is widespread in the area (Brown 1967; Drew and Tedrow 1962; Tedrow 1962; Tedrow and Harries 1960; Webber and Walker, this volume; Everett, this volume). The distribution and type depend on geomorphic setting, age, and soil texture. Ice-wedge polygons are common in wetter soils and along the old shorelines of drained lakes, while nonsorted polygons and frost scars are dominant in the drier Upland Tundra soils (Brown 1967, 1969; Tedrow 1965).

In this study soils were classified according to the system of Tedrow et al. (1958). Everett's report (this volume) contains the National Soil Taxonomy equivalents. Since the study area is relatively small, data presented in Table 1 may be considered representative of most of the soils of the interfluve between the Sagavanirktok and Kuparuk Rivers within 12 to 20 km of the Arctic Ocean. These soils have many characteristics that have been previously reported for soils

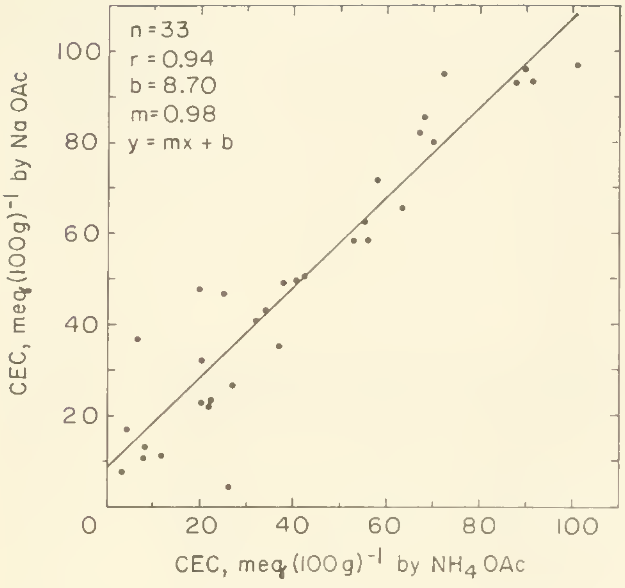


Fig. 1. *Relationship of Na exchange capacity to NH_4 exchange capacity.*

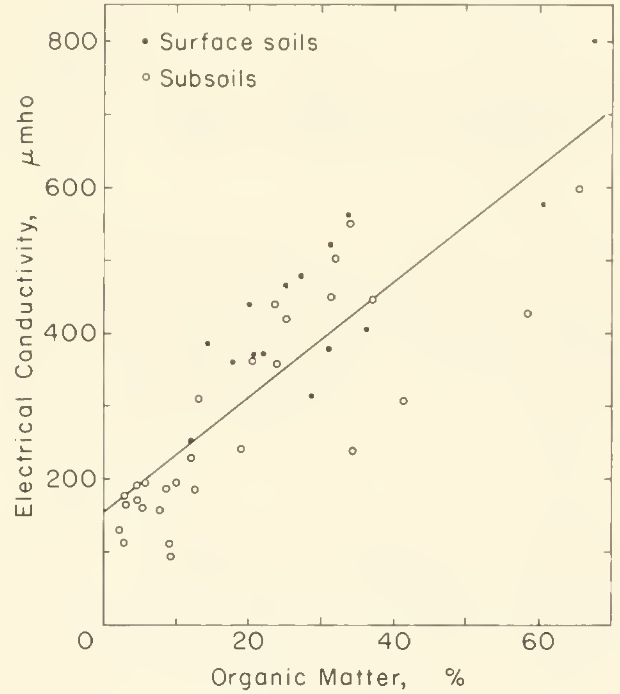


Fig. 2. *Relationship of electrical conductivity of (1:7 soil:water) soil extracts to percent soil organic matter.*

of the area—shallow active layer, much organic matter, calcareous, pH proportional to carbonates, appreciable soluble salts, etc. It was not possible to accurately determine exchangeable cations because of the solubility of carbonates, which gave a sum of exchangeable cations several times as large as cation exchange capacity, analytically correct but obviously impossible. Cation exchange capacity was proportional to the amount of organic matter in the soil.

Sodium exchange capacity was, in nearly every instance, a little larger than ammonia exchange capacity; in other words, all soils have an ammonia fixing capacity (Fig. 1). It should be noted that sodium exchange capacity determinations were made at pH 8.2, and ammonia exchange capacities were made at pH 7. The pH dependent exchange capacity (pH 8.2 - 7) was found to be 1.2 to 2 meq (100 g)$^{-1}$. Subtracting this value from the calculated ammonia fixing capacity showed that the typical soil of the area has an ammonia fixing capacity of about 7 meq (100 g)$^{-1}$, and that this value was independent of soil organic matter content.

The relationship of electrical conductivity of soil solutions to organic matter content of the same soils is shown in Fig. 2. Electrical conductivity is a measure of the amount of readily soluble salts present in a soil. In the Prudhoe Bay area, this value is dependent on the organic matter contents of the soil. Soils high in organic matter are usually found on the lower relief positions in the relatively low, undulating Prudhoe Bay landscape. Often these soils have water standing on their surface during much of the summer. There are two possible explanations for the accumulation of soluble salts in the low-lying organic soils.

1. The water standing on these soils forms a good evaporation surface, and soluble salts are concentrated by evaporation.

2. Much of the water found at lower elevations represents runoff (either surface or subsurface) from upland surfaces. This runoff water has been in actual physical contact with the soil for a longer period of time than the upland waters. One seldom finds equilibrium conditions in a soil since, with the comparatively short times involved, concentration of ions in the soil seldom reaches equilibrium solubilities. However, water

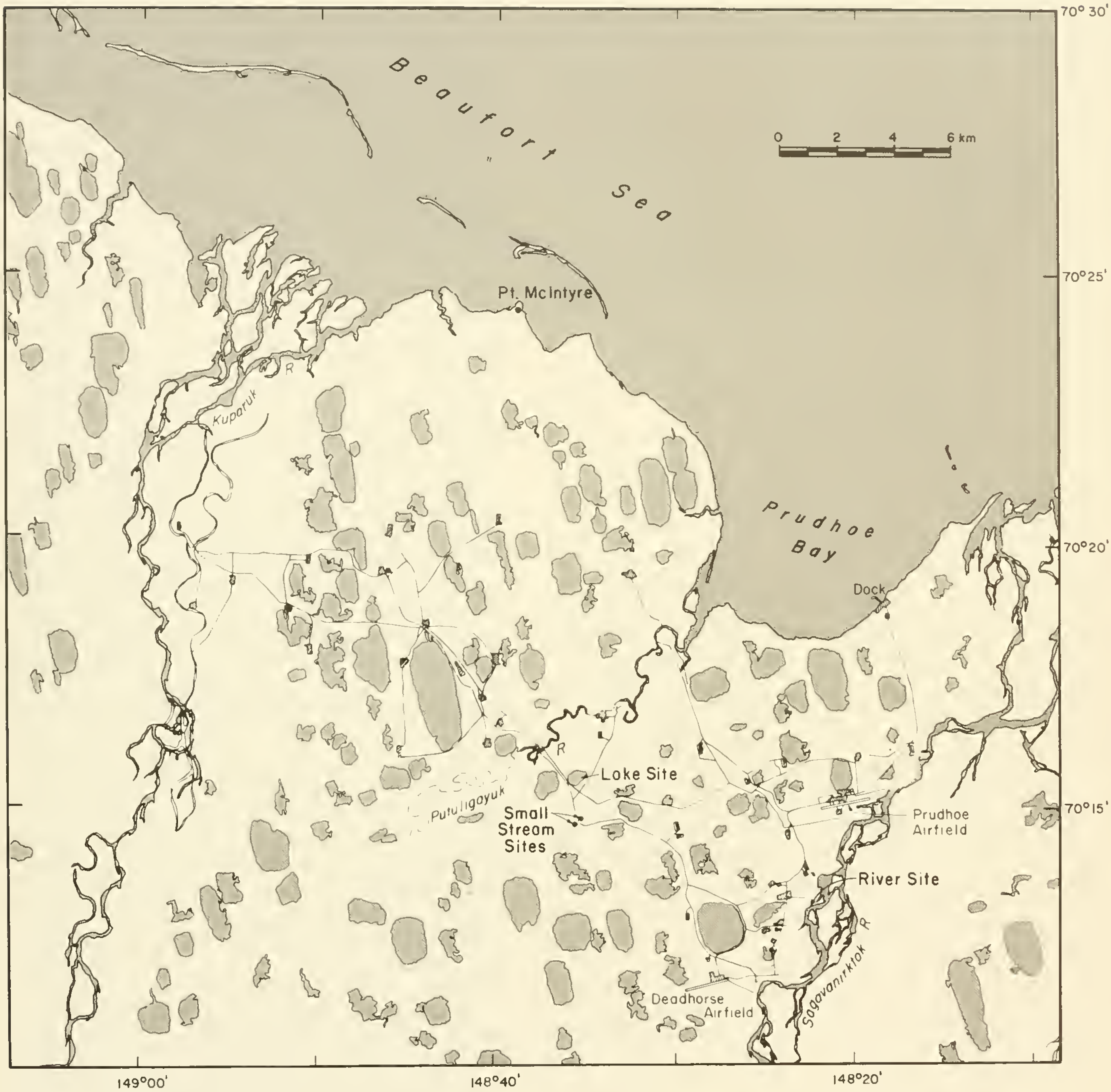


Fig. 3. *Water sampling sites.*

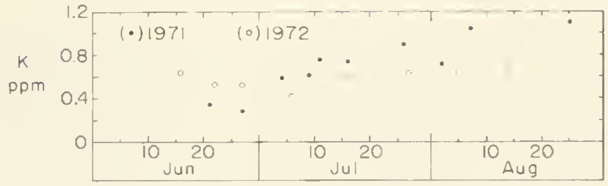


Fig. 4. *Potassium content of a small lake, 1971 and 1972.*

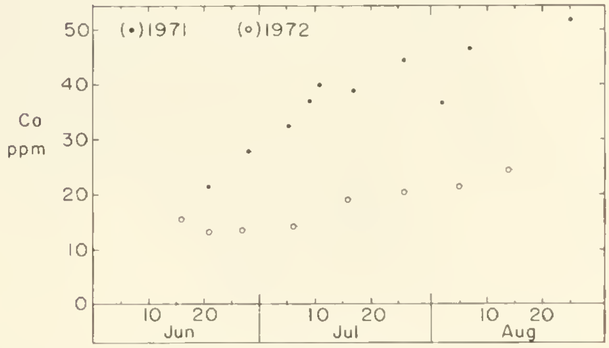


Fig. 5. *Calcium content of a small lake.*

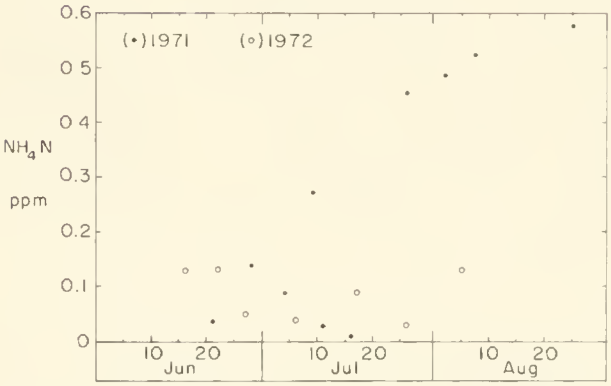


Fig. 6. *Ammonia-N content of a small lake, 1971 and 1972.*

that is in contact with the soil for long periods of time should come closer to reaching equilibrium solubilities.

Actually, both of the above conditions are probably responsible for causing higher soluble salt contents in low-lying organic soils.

Lakes and rivers

Of the numerous water sampling locations studied, several sampling sites are shown in Fig. 3. The data from these sites are discussed in this report because they represent trends to be expected in small lakes, small streams and larger rivers in the area.

Small lakes: Fig. 4, 5, and 6 show the concentrations of potassium, calcium and ammonia in a small lake for 1971 and 1972. The amount of potassium and calcium in this lake in 1971 was approximately 20-100% greater than comparable data for 1972. The ammonia concentration in 1971 was up to 500% greater than comparable concentrations found in 1972. With each of the ions, potassium, calcium and ammonia, early season values in 1971 were essentially the same as seasonally comparable values in 1972. During July and August in 1971, the concentration of these ions increased much more than the increase in concentration of the same ions during the 1972 summer. It should be noted that rainfall data are available for 1971, but comparable data are not available for 1972, which was a much wetter year than 1971. Many low areas that lost all standing water in 1971 had standing water throughout the 1972 field season. It is our opinion that the differences in slope between 1971 and 1972 are, in part, caused by these rainfall differences. In both 1971 and 1972, observations on water level in this lake were made. The depth of water decreased as the season advanced. If one assumes that all of this loss was caused by evaporation, the concentration caused by evaporation does not account for the increased amounts of calcium or ammonia found in August of 1971. Since lakes occupy low-lying positions, the same explanations used to describe the soil-organic matter, soluble salt relationships apply here.

Small streams: The small stream discussed here drained the Tundra Biome intensive site and was sampled at two locations, one above and one downstream from the areas where fertilizers were applied (Figs. 7-12). At no time was fertilizer runoff detected in the stream.

Early season runoff at breakup was observed in 1972. Potassium contents were very high in this melting snow-runoff. This study area was adjacent to the roadnet, and considerable dust from the road was found in the snow (Benson et al. this volume). It is generally agreed that dust particles in water are a major source of potassium in water, and are probably the source of this early season potassium.

The contrasts between upstream and downstream stations in 1971 and 1972 are revealing. In 1971 flow in this stream was low in late season. Between these stations the water spread out and was shallow, warmed up, and biological activity was high. In 1972, the increased rainfall caused increased runoff, deeper water, cooler water, and less biological activity. The biological uptake of ammonia caused a decrease in soluble ammonia between the upstream and downstream sites in 1971. Increased temperatures and biological activity caused calcium to precipitate between these stations in 1971 (Hynes 1970, p. 43). In 1972, with increased flow, calcium followed its usual trend of increased concentration as the season advanced, and there was little difference between upstream and downstream sites.

Large rivers: The calcium, potassium, and ammonia concentrations in the Sagavanirktok River are shown in Figs. 13, 14, and 15. The calcium and potassium levels of this large river may be contrasted with the trends observed in lakes and small streams in that the levels of these ions do not increase during the summer in the Sagavanirktok. The lowest ammonia concentrations we observed were found in the Sagavanirktok during the summer of 1972.

Nitrate, phosphate, iron: The minimum detection limit for nitrate was 0.01 ppm nitrate nitrogen. In all waters in 1971 nitrate was usually 0.01 ppm or less. Slightly higher nitrate concentrations were observed at most sampling sites in 1972. The minimum detection limit for phosphate was 0.01 ppm. Most samples had less than 0.03 ppm phosphate, with no observable seasonal trends.

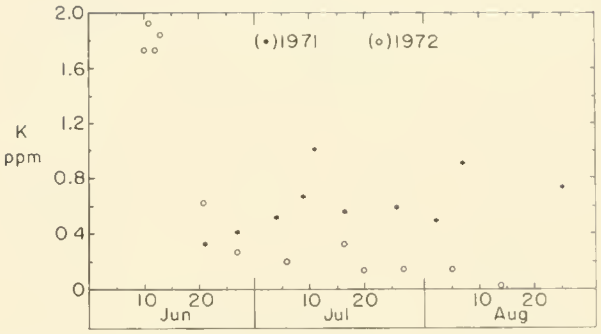


Fig. 7. *Potassium content of a small stream, 1971 and 1972 (upstream).*

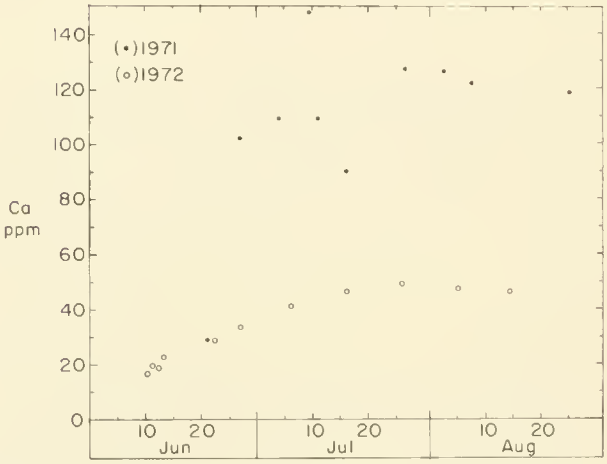


Fig. 8. *Calcium content of a small stream, 1971 and 1972 (upstream).*

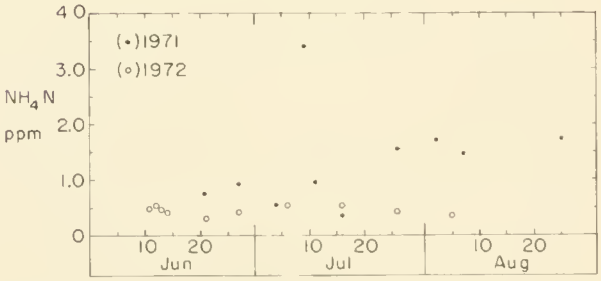


Fig. 9. *Ammonia-N content of a small stream, 1971 and 1972 (upstream).*

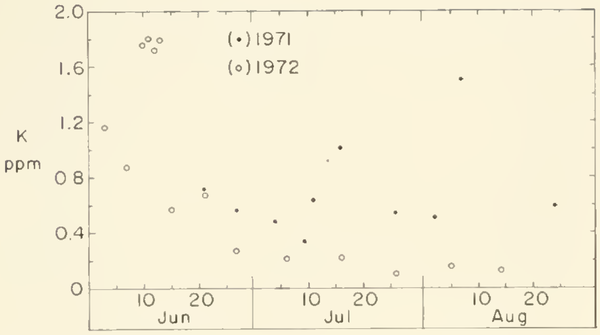


Fig. 10. *Potassium content of a small stream, 1971 and 1972 (downstream).*

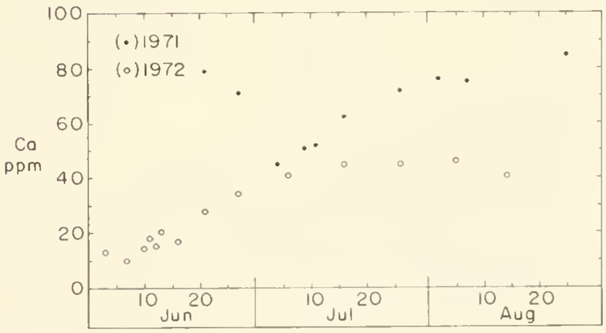


Fig. 11. *Calcium content of a small stream, 1971 and 1972 (downstream).*

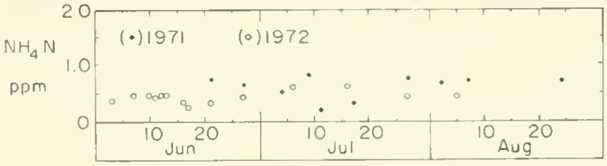


Fig. 12. *Ammonia-N content of a small stream, 1971 and 1972 (downstream).*

Considerable particulate iron was found, 0.01 to 0.5 ppm being the usual range. Particulate iron was proportional to water aeration, being higher where water flowed rapidly with much splash or where water was very shallow and slow flowing. Conditions which are conducive to high particulate (ferric) iron result in low soluble (ferrous) iron. One small stream had a very high soluble iron load (0.2 to 2.0 ppm); the concentration was low in June and increased through July and August.

Conclusions

In small streams and lakes a dramatic change in concentration of soluble nutrients occurs during the spring melt. The meltwater effectively flushes out the stream or lake. As the season progresses, runoff water (both surface and subsurface) increases the concentration of nutrients in these lakes and small streams. In some local cases the concentration of nutrients may be controlled by oxidation or biological reactions.

In small watersheds the concentration of nutrients in streams and lakes is proportional to the size of the watershed and the proportion of the watershed occupied by organic soils.

In large rivers nutrient concentrations are relatively stable. The large amount of water in these rivers acts as a buffer, so that a complete flushing action is not carried out by the spring melt.

In both small and large watersheds the nutrient levels are inversely proportional to rainfall.

Acknowledgments

Funds for this project were provided by the Prudhoe Bay Environmental Subcommittee; laboratory space at Prudhoe was provided by BP Alaska, Inc. and laboratory equipment by NARL from Barrow.

References

Bilgin, A. (1975). Nutrient status of surface waters as related to soils and other environmental factors in a tundra ecosystem. Ph.D. dissertation. Rutgers University, New Brunswick, N. J., 201 pp.

Brown, J. (1967). Tundra soils formed over ice-wedges, northern Alaska. *Soil Sci. Soc. Amer. Proc.*, 31:686-691.

______. (1969). Soil properties developed on the complex tundra relief of northern Alaska. *Biul. Peryglacjalny,* 18:153-166.

Brown, J., C. L. Grant, F. C. Ugolini, and J. C. F. Tedrow (1962). Mineral composition of some drainage waters from arctic Alaska. *J. Geophys. Res.,* 67:2447-2453.

Busenberg, E. and C. V. Clemency (1973). Determination of cation exchange capacity of clays and soils using an ammonium electrode. *Clays and Clay Min.*, 21:213-218.

Carson, C. E. and K. M. Hussey (1959). The multiple-working hypothesis as applied to Alaska's oriented lakes, *Iowa Aca. Sci. Proc.,* 66:334-349.

______. (1960). Hydrodynamics in three arctic lakes. *J. Geol.,* 68:585-600.

Cleaves, E. T., A. E. Godfrey, and O. P. Bricker (1970). Geochemical balance of a small watershed and its geomorphic implications. *Geol. Soc. Amer. Bull.*, 81:3015-3032.

Day, P. R. (1965). Particle fractionation and particle-size analysis. *In* "Methods of Analysis," Part 1 (C. A. Black, ed.). Amer. Soc. Agron. Madison, Wis., 770 pp.

Douglas, L. A. and J. C. F. Tedrow (1960). Tundra soils of arctic Alaska. 7th Int. Cong. of Soil Sci., Madison, Wis., Vol. 4, pp. 2447-2453.

Drew, J. V. and J. C. F. Tedrow (1962). Arctic soil classification and patterned ground. *Arctic,* 15:109-116.

Durum, W. H. and J. Haffty (1961). Occurrences of minor elements in water. U. S. Geological Survey, Circ. 445, 11 pp.

Everett, K. R. (This volume). Soil and landform associations at Prudhoe Bay, Alaska: A soils map of the Tundra Biome area.

Hill, D. E. and J. C. F. Tedrow (1961). Weathering and soil formation in the arctic environment. *Amer. J. Sci.*, 259:84-101.

Hynes, H. B. N. (1970). "The ecology of running waters." University of Toronto Press, Toronto, 555 pp.

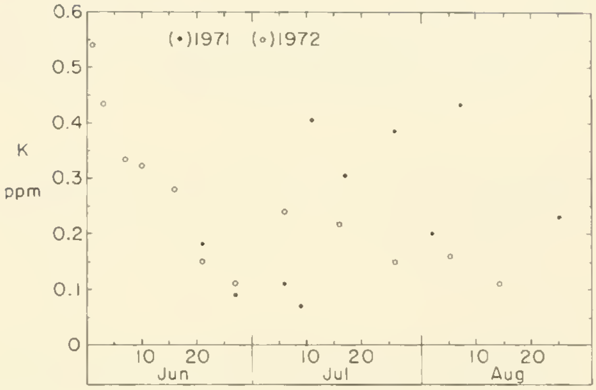


Fig. 13. *Potassium content of the Sagavanirktok River, 1971 and 1972.*

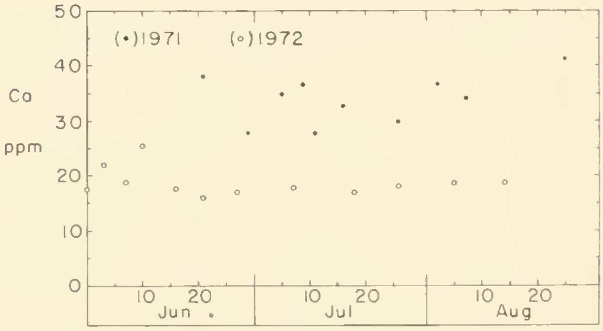


Fig. 14. *Calcium content of the Sagavanirktok River, 1971 and 1972.*

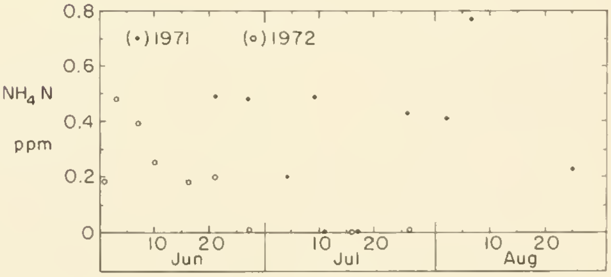


Fig. 15. *Ammonia-N content of the Sagavanirktok River, 1971 and 1972.*

Kalff, J. (1968). Some physical and chemical characteristics of arctic fresh waters in Alaska and northwestern Canada. *J. Fish Res. Bd. Canada,* 25:2575-2587.

O'Sullivan, J. B. (1961). Quaternary geology of the Arctic Coastal Plain, northern Alaska. Ph.D. thesis. Iowa State University, 191 pp.

Richards, L. A., ed. (1954). Diagnosis and improvement of saline and alkali soils. U.S.D.A. Handbook Co. U. S. Gov. Print. Off., Washington, D. C., 160 pp.

Tedrow, J. C. F. (1962). Morphological evidence of frost action in arctic soils. *Biuletyn Peryglacjalny*, 11:343-352.

______. (1965). Concerning genesis of the buried organic matter in tundra soil. *Soil Sci. Soc. Amer. Proc.,* 29:89-90.

Tedrow, J. C. F. and J. Brown (1967). Soils of arctic Alaska. Pages 283-293 *in* Arctic and alpine environments (H. E. Wright, Jr. and W. H. Osborn, eds.). Indiana University Press.

Tedrow, J. C. F. and H. Harries (1960). Tundra soil in relation to vegetation, permafrost and glaciation. *Oikos*, 11:237-249.

Tedrow, J. C. F., J. V. Drew, D. E. Hill, and L. A. Douglas (1958). Major genetic soils of the Arctic Slope of Alaska. *J. Soil Sci.*, 9:33-45.

Toth, S. J. and A. N. Ott (1969). Composition of surface waters of New Jersey in relation to soil series. Waters of the Big Flat Brook and the Paulins Kill, Pequest and Musconetcong Rivers. *Bull. N. J. Acad. Sci.*, 14:29-36.

Webber, P. J. and D. A. Walker (This volume). Vegetation and landscape analysis at Prudhoe Bay, Alaska: A vegetation map of the Tundra Biome study area.

Plant Investigations

Wet coastal tundra in vicinity of Pt. McIntyre.

C.D. Evans, Arctic Environmental Information and Data Center, University of Alaska, 16 June 1971

Vegetation Survey
of the
Prudhoe Bay Region

BONITA J. NEILAND
Department of Land Resources
University of Alaska
Fairbanks, Alaska 99701

and

JEROME R. HOK
Alaska Department of Environmental Conservation
Juneau, Alaska 99801

Introduction

In July 1971 a survey was made of the tundra in the vicinity of Prudhoe Bay to obtain information on distributional patterns of species, plant communities, and major environmental features. The survey was limited to areas of ready access from the road system. The general area was grossly subdivided into "landscape units" based on macro- and microtopography, surface material, apparent moisture, and vegetational physiognomy and continuity. Three such units were recognized: (1) dunes complex; (2) pingos and steep banks; and (3) plains. Only the gently undulating plains were dealt with at more than reconnaissance levels, and it is that unit which is discussed here.

Methods

The extensive plains landscape unit was subjectively subdivided into subunits — areas of one-half to several hectares in size, each relatively homogeneous and different in general appearance from all other subunits. A subunit might be fairly uniform throughout (e.g., "smooth dry plain," an area of relatively high relief and a coarse, springy matted vegetation), or it might be a complex (e.g., the low-center polygon subunit, composed of polygon centers with vegetation similar to that of the wet smooth plain, but separated by ridges having vegetation more similar to a smooth dry plain).

Twenty-three stands were surveyed, and presence lists of species were compiled. Quadrat frequency sampling was carried out in 14 stands (i.e., specific communities). Nine of the presence-only stands included sites sampled for frequency; a total of 28 different stands were sampled for presence. "Stand" selection was based on vegetational appearance within the complex subunits (i.e., in a low-center polygon subunit, one set of quadrats was placed in the centers, another set on the ridges). Quadrat placement was systematic, and quadrat number and size were largely determined by species diversity and uniformity of distribution; an attempt was made to keep the most frequent species in the 70-80% range. Ten to 30 quadrats, 1/4 m^2 or 1/8 m^2 in size, were employed per stand.

A one-dimensional ordination of species and stands, based on presence, was constructed by visual means, with floristically similar stands placed as close together as possible, and species ranked with other species of similar distribution on the stand array (Table 1). Stands sampled for frequency were then arrayed in the same order as those sampled for presence, and species' percentage frequency was indicated (Table 2).

Table 1

Array of species and stands

Species	Ordination rank*																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Melandrium sp.		●											●			●												
Salix ovalifolia																●	●											
Viviparous grass									●								●											
Cardamine pratensis																	●	●										
Carex marina					●						●																	
Alopecurus alpinus		●							●				●				●											
Carex saxatilis		●	●		●		●				●				●	●				●								
alga		●	●	●	●	●		●							●	●												
Scorpidium scorpioides	●	●	●	●	●	●	●	●			●		●		●	●												
Eriophorum scheuchzeri			●		●																							
Saxifraga cernua									●					●														
Carex rariflora		●		●		●		●									●											
Pedicularis sudetica		●	●		●	●	●	●	●		●	●	●		●	●	●		●									
Melandrium apetalum														●		●		●	●	●					●			
Dupontia fisheri								●	●	●		●					●	●										
Saxifraga hirculus		●			●				●	●		●	●	●	●		●	●	●		●	●					●	
Eriophorum angustifolium		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●		●	●	●	●	●			
Carex aquatilis	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●									
Carex atrofusca					●	●					●	●	●		●	●			●	●								
Poa arctica										●				●			●	●		●	●	●	●					●
Polygonum viviparum					●	●		●	●	●	●	●	●	●	●	●	●		●	●	●	●		●	●	●	●	
Salix reticulata							●	●		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Salix arctica				●			●	●		●		●	●	●	●	●	●			●	●	●	●	●				●
Equisetum variegatum			●	●		●	●			●	●	●	●	●			●	●	●		●			●	●			
Carex membranacea					●					●	●		●		●	●		●		●	●	●	●	●	●	●		
Dryas integrifolia						●				●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●			●
Carex misandra											●		●	●	●	●		●	●	●	●	●			●	●	●	●
Thamnolia subuliformis													●		●	●		●	●	●	●	●			●	●		
Pedicularis lanata/arctica										●	●	●	●	●	●	●	●		●	●	●	●	●	●				
Salix lanata								●			●	●	●	●			●	●						●				
Stellaria laeta								●						●			●				●	●	●		●			
Eriophorum vaginatum											●	●	●		●	●		●	●	●	●	●	●					
Senecio atropurpureus											●		●	●				●	●		●	●	●			●	●	
Carex bigelowii										●	●	●	●		●	●	●	●	●		●	●	●					●
Eutrema edwardsii														●						●	●		●					
Arctagrostis latifolia														●	●	●	●			●	●	●	●	●		●		
Saxifraga hieracifolia																		●			●	●			●			
Draba sp.									●			●	●	●			●	●	●	●			●	●				
Papaver macounii										●			●	●	●	●		●	●	●	●	●			●			
Dactylina arctica															●	●			●	●		●	●			●	●	
Carex scirpoidea											●				●	●					●			●	●	●		
Silene acaulis																			●			●	●		●	●		
Draba alpina																		●	●	●	●	●	●			●		
Chrysanthemum integrifolium															●	●			●	●	●		●	●	●	●		

Table 1 (continued)

Ordination rank*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Saxifraga oppositifolia													●		●	●		●	●	●	●	●	●	●	●	●		
Astragalus umbellatus																					●	●	●		●	●		
Pedicularis capitata														●					●					●	●	●		
Parrya nudicaulis																							●	●		●		
Cassiope tetragona													●							●	●	●	●		●			
Salix rotundifolia																				●		●	●	●		●		
Saussurea angustifolia															●	●					●	●	●		●	●		
Luzula arctica																						●	●		●	●		
Artemisia borealis																								●				
Juncus biglumis																					●		●	●				
Cardamine sp.																				●		●	●					
Trisetum spicatum																				●								
Minuartia arctica																				●	●	●	●	●	●			
Oxyria digyna																						●						
Cerastium beeringianum																				●		●						
Hierchloe pauciflora																						●						
Braya pilosa																								●				
Carex rupestris																						●						
Kobresia myosuroides																								●				
Oxytropis nigrescens																								●				
Oxytropis deflexa																								●				

*See text for stand description

Stands sampled for presence-only were larger than those sampled for frequency, and in some of the latter stands, which were not sampled for presence, some rare species were undoubtedly missed in the quadrats. The result is that the presence lists for the frequency stands are shorter than those for the presence stands. The error introduced is probably not great since only rare species would be involved, but the lists are not entirely comparable.

Species and Community Patterns

Subunits recognized in the plains landscape are outlined below:

Simple subunits: of more or less uniform appearance overall.

1. Old lake beds: no longer with permanent standing water, although small ponds might be found in some portions.
2. Smooth plain, dry, wet or intermediate: very uniform in appearance with respect to both vegetation and microtopography.
3. Indistinct old polygons: pattern still discernible, but little present microtopographic variation.
4. Patterned plain: vegetational variation apparent, but little microtopographic variation, and not divisible into one or two distinct components.

Complex subunits: composed of one or two fairly discrete communities.

1. Low-center polygons: depressed wet centers with water standing on or very close to the surface all season, separated by raised ridges covered by dry, springy mats of low vegetation.
2. High-center polygons, with either sand-silt or organic surface materials: raised centers covered by springy mats of low vegetation, separated by troughs 30-60 cm deep covered by wet sods.

Table 2

Species frequency in sampled stands. Stands ranked as in Table 1

Ordination rank*	1	2	4	6	7	13	16	17	20	20	21	23	24	25
Species														
Melandrium sp.							5							
Salix ovalifolia							10						70	
Viviparous grass													3	
Cardamine pratensis														
Carex marina					10									
Alopecurus alpinus							t	3						
Carex saxatilis		3			15		5							
alga		13	70	36			5							
Scorpidium scorpioides	100	83	100	66	75									
Eriophorum scheuchzeri							5							
Carex rariflora				10										
Pedicularis sudetica		16	90	43	65		15	20						
Melandrium apetalum							5	10	5					3
Dupontia fisheri							5							
Saxifraga hirculus				3				46			7			
Eriophorum angustifolium		73	100	66	90			80			3			t
Carex aquatilis	100	93	100	63	10		95	93						
Poa arctica								73						
Polygonum viviparum				3		5	25	93	55	30	27	20	3	10
Salix reticulata					5	65	10	60	75	45	3	40	27	47
Salix arctica					20			56			63		90	
Equisetum variegatum			20	23	10	5	70	30	15		26		20	33
Carex membranacea						95			25	95	90			80
Dryas integrifolia				3		95	10	3	100	95	80	96	96	80
Carex misandra							5		30		10			33
Thamnolia subuliformis									95	95	36	100		10
Pedicularis lanata/arctica						5		16		30	7	10	27	30
Salix lanata						10	15		10				13	
Stellaria laeta												37	7	7
Eriophorum vaginatum											23	17		
Senecio atropurpureus											3			
Carex bigelowii						90		3			53			
Eutrema edwardsii							20				50			
Arctagrostis latifolia									5		53	3		
Draba sp.							5							
Papaver macounii							5		30	25	23			
Dactylina arctica									55	60	27	40		
Carex scirpoidea							5			5		20	33	3
Silene acaulis														
Draba alpina									15	10	3	23		3
Chrysanthemum integrifolium									25	30	27		93	30
Saxifraga oppositifolia							40		100	90	23	3	23	40
Astragalus umbellatus												67		43
Pedicularis capitata									40	15			13	7

Table 2 (continued)

Ordination rank*	1	2	4	6	7	13	16	17	20	20	21	23	24	25
Parrya nudicaulis													17	
Cassiope tetragona										35				40
Salix rotundifolia									5		3	13	10	93
Saussurea angustifolia												33		7
Luzula arctica												7		17
Artemisia borealis													10	
Juncus biglumis							5				7	3		
Minuartia arctica									5	35		23	7	10
Oxyria digyna														
Hierchloe pauciflora												7		
Braya pilosa													7	
Carex rupestris												10		
Kobresia myosuroides													57	
Oxytropis nigrescens													3	
Oxytropis deflexa													43	

*See text for stand description

3. Ridged plain, wet or dry: similar to either wet or dry smooth plain, but with the surface interrupted by irregular ridges and hummocks of 10-15 cm in height.

"Wet" or "dry" designations refer to apparent surface moisture during the period of the study. Each subdivision includes only stands that are relatively extreme in appearance. Many areas did not fit into this classification and did not appear to be simple intergrades between the recognized subunits.

The array of species and stands on the basis of presence is shown in Table 1. Species frequency values, with species and stands in the order developed and displayed in Table 1, are shown in Table 2. Neither species nor stands would be expected to show an entirely compact arrangement on a one-dimensional array, but the fact that these are as compact as they were found to be suggests that one major environmental gradient exerts strong influence on these patterns. In both tables, the rank numbers represent the following site types: (1) the centers of low-center polygons; (2) flat areas of ridged wet plain; (3) flat areas of ridged wet plain; (4) seasonal high water area surrounding a lake; (5) flat areas of ridged wet plain; (6) seasonal high water area around a lake; (7) smooth wet plain; (8) centers of low-center polygons; (9) seasonal high water area around a lake; (10) seasonal high water area around a lake; (11) ridges of low-center polygons; (12) intermediate smooth plain; (13) intermediate smooth plain; (14) ridges of low-center polygons; (15) dry smooth plain; (16) indistinct old polygons; (17) smooth dry plain; (18) smooth dry plain; (19) ridges of low-center polygons, now flooded by waters backed up by a gravel road; (20) centers of high-center polygons with organic surface; (21) dry smooth plain; (22) dry smooth plain; (23) dry smooth plain; (24) centers of high-center polygons with sand-silt surface; (25) centers of high-center polygons with sand-silt surface; (26) dry patterned plain; (27) ridges of ridged wet plain; (28) ridges of ridged wet plain.

The basic array shown in Table 1 clearly corresponds with general gradients of apparent microtopographic relief and surface moisture (from low to high and wet to dry, respectively, as the array is numbered). Since both are complex environmental features, the specific "causal" factors may well vary along these gradients. The extreme community types are conspicuous in the field: (1) a low wet type that was consistently greener in color than any of the more raised areas and was characterized by an open stand of rhizomatous sedges, chiefly *Carex* *aquatilis*, and a dense ground cover of the moss, *Scorpidium scorpioides;* and (2) a dry type, characterized by much standing dead plant material, which gives the type a grey-brown coloration, and having a somewhat rubbly, hummocky surface of mixed sedges, small shrubs and various herbs. In between these two extremes is an array of species occurrence as shown in both tables that makes classification into separate community types extremely difficult. Stands that fit the more or less wet category are somewhat easier to lump together than are stands that fit the more or less dry category, which shows high variation, and, at present, it seems that the vegetational and floristic shifts are far too subtle in this area of low variation in relief, plant size and life form to develop a rational and useful classification scheme. Sufficient departures from smooth normal curves can be seen in the frequency arrays of Table 2 to suggest that at least one more major environmental gradient may be operative in these patterns. The one-dimensional ordination does reveal some informative patterns of species and community distributions.

In Table 1 the general species'order is that of a gradual shift from those of wet stands to those of dry stands, moving from the top of the column toward the bottom. Characteristic species toward the wet (top) are an unidentified alga, *Scorpidium scorpioides, Pedicularis sudetica, Eriophorum angustifolium,* and *Carex aquatilis.* To this group, as the alga and *Scorpidium* decreased, were added *Polygonum viviparum, Salix reticulata, Salix arctica, Equisetum variegatum,* and *Carex membranacea.* Largely confined to the center of the array were *Cardamine pratensis, Carex marina, Melandrium apetalum, Dupontia fisheri, Carex atrofusca, Pedicularis lanata/arctica* (not distinguished consistently in the field), *Eriophorum vaginatum, Carex bigelowii,* and *Eutrema edwardsii.* Toward the dry end of the species list, stands were characterized by *Dryas integrifolia, Carex misandra, C. bigelowii, Arctagrostis latifolia, Draba* spp., *Papaver macounii, Chrysanthemum integrifolium, Saxifraga hirculus* and *S. oppositifolia.* Additional species of the sand-silt surfaced high-center polygons and the dry patterned plain are those lowest in the list. When species presence is plotted against the stand ordination (Table 1), although gaps are expected and do occur in a one-dimensional array, a fairly gradual change is seen progressing from left to right. The progression of vegetational groups is from one group of species that dominate and characterize the wet centers of low-center polygons, the flat areas of ridged wet plains, the smooth wet plains, and the areas of seasonally high water immediately around lakes; through various intermediate mixtures of species that characterize the smooth plains, the ridges of low-center polygons, and the dry smooth plain; to the groups that dominate and characterize the centers of high-center polygons, the patterned plains, and ridges in wet ridged plains. Stands 1 and 28 had no species in common; no one species was found in all stands, and only *Eriophorum angustifolium, Polygonum viviparum,* and *Salix reticulata* had presence values above 75%.

When the frequency values for the species of the 14 sampled stands are arrayed on the same basic ordination (Table 2), although smooth normal curves are rare, most species show fairly consistent patterns, with stands having high values being close together and the stands of low value arrayed in one or both directions away from these. Only *Carex aquatilis* and *Scorpidium scorpioides* show similar patterns of frequency distribution. Twenty-two of the total 59 species are found with percent frequency at or above 50% in one stand or another, yielding a fairly high number of important species, as compared with species that are rare within or between stands. Diversity, both in numbers of species and in number of individuals (to the extent that frequency here reflects density), is highest in the stands toward the dry end of the array. There are sufficient departures from normal curves to suggest strongly the need for additional frequency sampling and development of a two-dimensional array.

Acknowledgment

We thank David F. Murray and Barbara M. Murray for assistance with the site selections and plant identifications. The Prudhoe Bay Environmental Subcommittee and the State of Alaska assisted in funding these studies through the Tundra Biome Center, University of Alaska.

Jerry Brown, USACRREL,
18 June 1975

Low angle oblique of polygonal ground. Water filled troughs are underlain by ice wedges. The background shows flat coastal topography characteristic of the Prudhoe tundra, and the foreground is late snowdrift associated with the pingo relief.

Vegetation and Landscape Analysis at Prudhoe Bay, Alaska: A Vegetation Map of the Tundra Biome Study Area

PATRICK J. WEBBER and DONALD A. WALKER
Institute of Arctic and Alpine Research and
Department of Environmental, Population and Organismic Biology
University of Colorado, Boulder, Colorado 80302

Introduction

The goal of this project is to produce a series of vegetation maps at a scale of 1:6,000 of the immediate operating areas of the Prudhoe Bay region. These maps will provide a baseline inventory for the area, and analysis of them can direct the future development and management of this and similar areas. In this report we will present the first map of the series which is confined to the region bordering 6 km of road in the vicinity of the Tundra Biome study area (Plate I). The map is based on a simple classification which can be constructed and interpreted by non-botanists with only a few days of training. Concomitant with the construction of the vegetation map, a soils map of the same area was made (Everett, this volume) to contribute to the same objectives as those of the present study. The soils map is also presented on Plate I.

Vegetation types

The vegetation of the Tundra Biome area is fairly representative of the Prudhoe Bay roadnet system. Sand dune and seashore habitats and their plant communities are, however, absent. We have recognized 13 vegetation types within the mapped area. A list of these, with brief descriptions of their characteristic species content and microsite preference, is presented in Table 1. Some of these types, for example types 10 (pingos) and 11 (river bluffs), are rather broad or mixed and may need to be subdivided at a later date. The vegetation types can be described in simple terms so that they can be readily identified by non-botanists using only a few characteristics. For example, the six most common vegetation types can be identified with the knowledge of a few simple plant life forms (herb, shrub, moss, crust lichen, and fruticose lichen) and a few plant genera *(Dryas, Salix, Drepanocladus,* and *Scorpidium).* The species composition and cover of all 13 types are given in Table 2, and all 13 types are illustrated in Fig. 1. Murray and Murray (this volume) report the plant species for the Prudhoe area as of Fall 1974. Rastorfer et al. (1973) report a partial bryophyte composition of select Prudhoe areas.

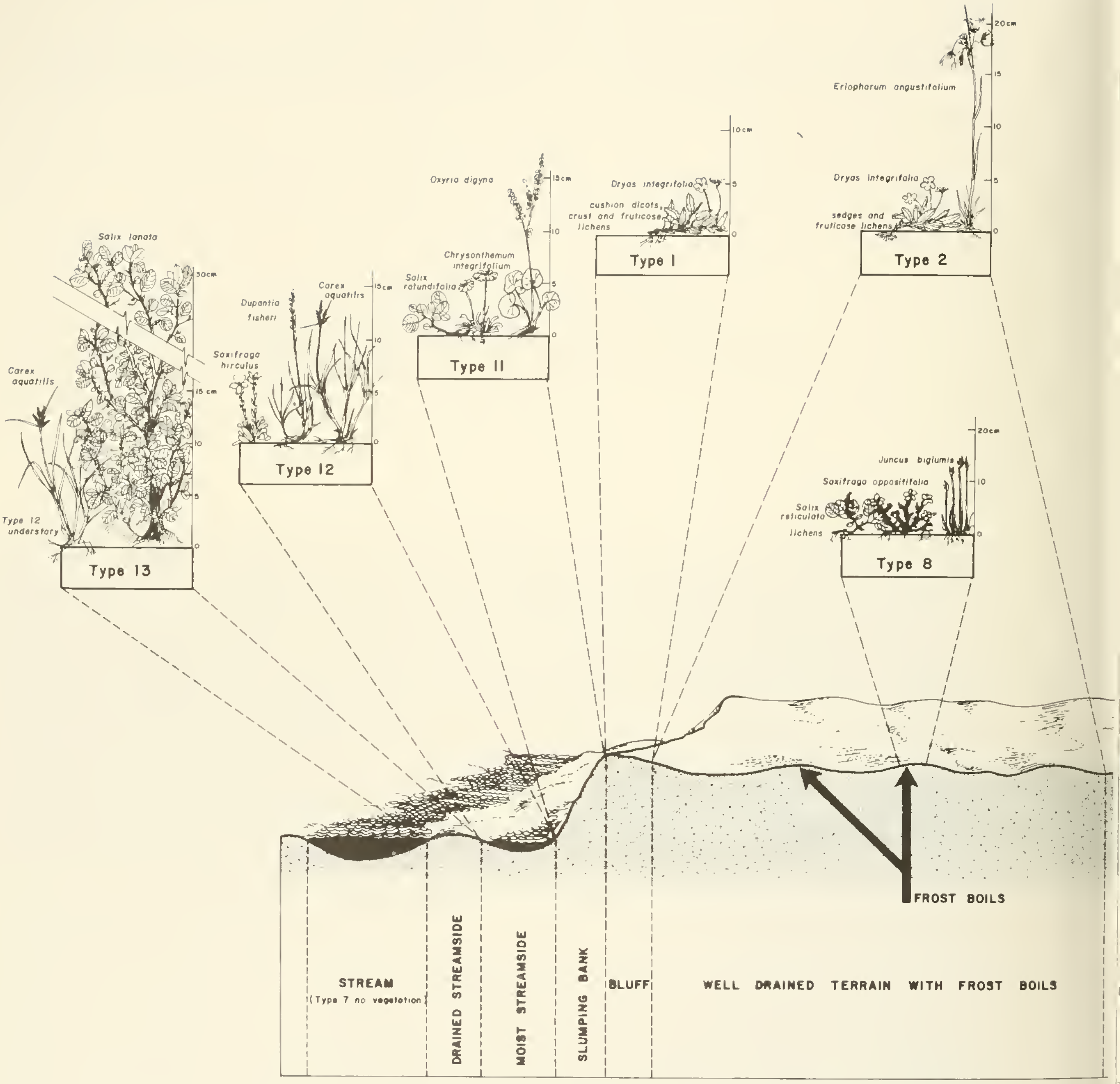
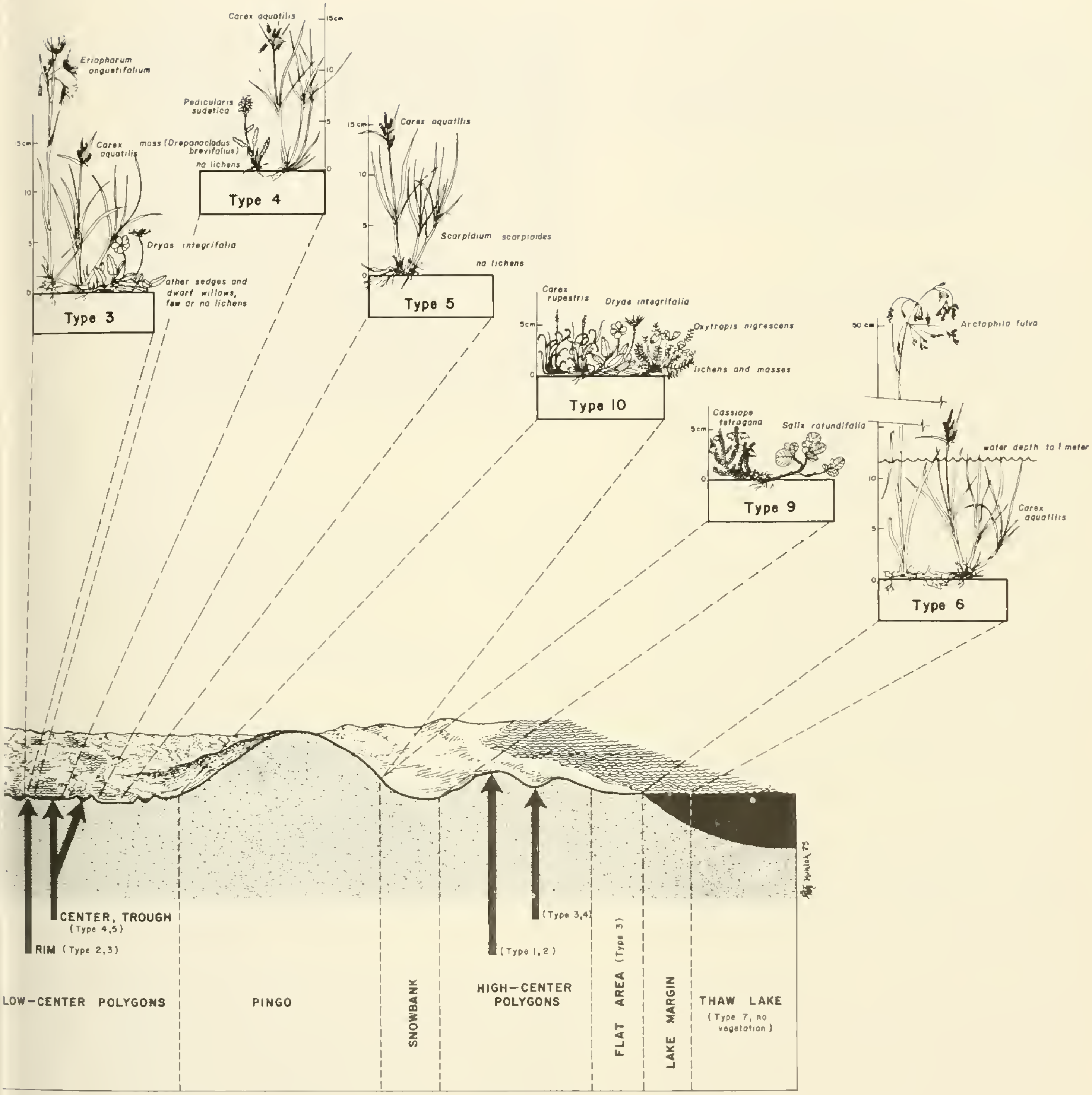


Fig. 1. *Schematic representation of the Prudhoe Bay terrain showing the topographic and spatial interrelations of the 13 vegetation types.*



Dennis Kuklok, Arctic Environmental Information and Data Center, University of Alaska

Table 1

The vegetation types mapped within the Tundra Biome study area, Prudhoe Bay, Alaska. For each type the characteristic species and microsites are given.

Characteristic Species	Characteristic Microsite
Most Common Types:	
1. *Dryas integrifolia* and crust lichens. Several other cushion dicotyledons and fruticose lichens.	Tops of high-centered polygons, small ridges and high creek bluffs.
2. *Dryas integrifolia* and *Cetraria* spp. Several other fruticose lichens and sedges. Few or no crustose lichens.	Dry polygon rims, and well drained areas.
3. *Carex aquatilis* and/or *Eriophorum angustifolium* and *Dryas integrifolia*. Several other sedges and dwarf willows. Very few or no lichens.	Polygon rims and flat areas that are not continually wet.
4. *Carex aquatilis* and/or *Eriophorum angustifolium* and *Drepanocladus* spp., usually with *Pedicularis sudetica*. No lichens.	Centers of many low-centered polygons, troughs and poorly drained areas, such as pond margins.
5. *Carex aquatilis* and *Scorpidium scorpioides*. No lichens.	Very wet areas where there is shallow standing water throughout the summer. Wet polygon troughs and pond margins.
6. *Carex aquatilis* and/or *Arctophila fulva*. No mosses or lichens.	Standing water of moderate depth (30-100 cm). Lake margins and thermokarst pits.
7. No vegetation.	Deep water (> 100 cm).
8. *Saxifraga oppositifolia* and *Salix reticulata* often with *Juncus biglumis* and several lichens.	Frost boils.
Snowbanks and Pingos:	
9. *Cassiope tetragona* and *Salix rotundifolia*.	Snowbanks.
10. Diverse vegetation with *Dryas integrifolia*, *Oxytropis nigrescens* and *Carex rupestris*. Several lichens and mosses.	Pingos.
Stream, River, and Lake Margins:	
11. Diverse vegetation with *Salix rotundifolia*, *Chrysanthemum integrifolium* and *Oxyria digyna*.	Slumping river bluffs, areas of erosion and/or solifluction.
12. *Carex aquatilis* and *Dupontia fisheri* with *Saxifraga hirculus* and other dicotyledons.	Stream banks.
13. *Salix lanata* and *Carex aquatilis*. Shrubby willows with a Type 12 understory.	Stream and lake banks.

Type 3 vegetation of Carex aquatilis, Eriophorum angustifolium, Dryas integrifolia *and several* Salix *species.*

The following dichotomous key, which is based on plant rather than geomorphic or habitat parameters, illustrates the simplicity of the identification process:

Key to the most common vegetation types of the Prudhoe Bay area

1. Lichens abundant 2.
   Lichens rare 3.
2. Many fruticose and crust lichens . . Type 1
   Mostly fruticose lichens . . . . Type 2
3. *Dryas* and/or *Salix* spp. abundant . . Type 3
   Dryas and/or *Salix* spp. rare 4.
4. Mosses rare . . . . Type 6
   Mosses abundant 5.
5. *Drepanocladus* species dominant . . Type 4
   Scorpidium dominant . . . . Type 5

We plan to develop a key to all vegetation types. Other functional keys using a variety of parameters could be made, but we want to avoid mixing descriptors to reduce the problem of circular reasoning when maps are subsequently analyzed and used. Nevertheless, vegetation, habitat, and geomorphology are intimately interrelated, and it is difficult to map them separately at this scale (1:3,000) because of the fine mosaic and patterning of this tundra. But we believe our method will allow a separate analysis.

We have set up and sampled a number of permanent vegetation plots in both disturbed and undisturbed areas. These plots will serve as baselines for any subsequent changes. We have also set up specimen plots of each vegetation type which can serve as training and reference samples for other potential vegetation users or mappers; these will also serve as permanent baseline plots.

Mapping Method

The maps were initially constructed in the laboratory using July 1972 CRREL, 1:3,000, black-and-white, air photographs on which major landscape units were then outlined. These units were identified on the basis of uniform tone, texture, and pattern. Each of these units was visited in the field, their boundaries checked and changed as necessary, and their vegetation and geomorphologic features described. The intimate interrelatedness of geomorphic and plant patterns makes it difficult to produce separate vegetation and geomorphic maps. Our map (Plate I), however, shows the prevalent or most abundant vegetation type for each landscape unit and also records the geomorphic features and other frequent vegetation types which occur within a unit. The vegetation and geomorphic record is given by a formula of letters and numbers. The numbers in the formula indicate the vegetation types. On polygonal ground the vegetation types are listed in 2 or 3 groups of microsites separated by semicolons (;). The first group is the vegetation on the polygon centers; the second, vegetation on the rims, and the third, vegetation in the polygon troughs. A dash indicates the absence of a group or microsite category. The letter for the most abundant vegetation type is underlined. The letters preceding the numbers in the formula indicate the geomorphic features of each map unit: P — polygonal ground; F — flat or gently sloping terrain where ice-wedges are masked or ill-defined; R — small ridges and hills; S — streams and stream margins; W — dunes; L — lakes and ponds, and H — pingos. Often a subscript is used to further define the geomorphic feature: F — flat polygons; L — low centered polygons; H — high centered polygons; M — mixed polygons; B — river bluffs; f — frost boils; s — sandy soil; t — thermokarst pits; and r — reticulate-ridged flats.

Table 2

Plant composition of the vegetation types recognized within the Tundra Biome study area at Prudhoe Bay, Alaska. Values are means of percentage cover estimates from a variable number of 1m^2 quadrats. These data are still preliminary and not all species encountered have been included. No attempt has been made to arrange the rows and columns in any ecological sequence.

	Vegetation type (number quadrats per type)											
Life-form and species	1(10)	2(10)	3(10)	4(10)	5(10)	6(10)	8(10)	9(3)	10(3)	11(4)	12(8)	13(6)
Erect Shrubs:												
Cassiope tetragona		0.4						16.0	5.8			
Salix lanata	0.1	0.1	0.5	0.1							0.1	42.6
Total	0.1	0.5	0.5	0.1				16.0	5.8		0.1	42.6
Prostrate shrubs:												
Dryas integrifolia	48.7	59.8	20.0				16.5	23.3	18.3	1.2	0.1	0.1
Salix arctica	0.1	6.1	8.0	0.2			1.2	0.2		0.1	2.5	6.4
Salix ovalifolia	0.1	0.2	2.6								2.8	0.8
Salix reticulata	2.9	2.1	2.5				0.2	1.7		4.5	0.6	18.3
Salix rotundifolia	0.6	0.1					0.1	35.8		23.1		0.8
Total	52.4	68.3	33.1	0.2			18.0	61.0	18.3	28.9	6.0	26.4
Cushion and mat dicots:												
Astragalus umbellatus	0.1	0.6						0.1	0.2			
Cerastium beeringianum									1.7			
Minuartia arctica	0.1	0.1					0.2	1.3		1.0		
Minuartia rossii							0.1					
Oxytropis nigrescens	0.1								5.0	0.1		
Saxifraga oppositifolia	9.4	1.8	0.6	0.5			6.1	8.3		7.5	0.6	
Silene acaulis										4.4		
Total	9.7	2.5	0.6	0.5			6.4	9.7	6.9	13.0	0.6	
Single dicots:												
Androsace chamaejasme									0.2			
Braya spp.		0.1		0.5			0.1		1.9	1.2		
Cardamine digitata	0.1	0.5					0.1	0.2				0.3
Cardamine pratensis											0.1	1.2
Caltha palustris						0.8				0.2		
Chrysanthemum integrifolium	0.8	0.1					0.1	0.3		1.5		
Draba alpina	0.3	0.1					0.2					
Hippuris vulgaris						1.5						
Lesquerella arctica									0.3			
Lloydia serotina									1.8			
Melandrium apetalum							0.2	0.2			0.1	
Oxyria digyna										8.8		
Papaver macounii	0.2	0.3					0.1	0.2				
Parrya nudicaulis	0.1	0.1						1.0		0.1		0.1
Pedicularis capitata	1.0	0.2	0.1							0.1		
Pedicularis lanata	0.1	0.3					0.2					0.1
Pedicularis sudetica			0.2	2.0								0.9
Polygonum viviparum	0.4	0.2	1.3		0.1		0.2	1.0		1.6	0.1	0.1
Potentilla hookeriana									0.2	1.4		
Ranunculus pedatifidus									1.7			
Saussurea angustifolia	0.1											
Saxifraga cernua		0.1										0.7
Saxifraga hirculus			0.2				0.1				1.4	0.7
Senecio atropurpureus		0.1						0.2				0.1
Stellaria laeta							0.1				0.1	1.6
Valeriana capitata											0.6	
Total	3.2	2.6	1.8	2.5	0.1	2.3	1.5	3.3	6.1	15.0	3.1	7.6

Table 2 (continued)

Vegetation Type	1	2	3	4	5	6	8	9	10	11	12	13
Monocots, sedges:												
Carex aquatilis		4.0	11.2	17.5	19.0	16.5	2.2	5.8			31.6	22.9
Carex atrofusca				0.1								
Carex bigelowii	0.1	3.2			0.1			0.2		0.1	0.6	0.1
Carex misandra	0.6	0.1		0.2						0.1		
Carex rotundata		0.1										
Carex rupestris	2.8						3.3		7.5			
Carex scirpoidea		0.2	0.1									
Eriophorum angustifolium	2.4	11.0	11.6	23.2	7.5		7.4	6.7		0.1	5.3	10.1
Eriophorum vaginatum		0.4						0.1				
Total	5.9	21.2	24.1	41.2	26.6	16.5	12.9	12.8	7.5	0.3	37.7	33.0
Monocots, grasses:												
Alapecurus alpinus	0.1	0.5										
Arctagrostis latifolia	0.2	0.2					2.0	2.0		2.5	0.6	
Arctophila fulva						12.5						
Dupontia fisheri	0.4		0.1	0.9		0.5	0.1				19.8	13.7
Festuca baffinensis							1.7	5.8	1.2			
Poa arctica										0.1		
Total	0.7	0.7	0.1	0.9		13.0	3.8	7.8	1.2	2.6	20.4	13.7
Rushes and horsetails:												
Equisetum variegatum	0.5	0.4	2.6	0.2	0.1		0.2	2.0		2.5	0.1	0.2
Juncus biglumis	0.1	0.4					3.4					
Total	0.6	0.8	2.6	0.2	0.1		3.6	2.0		2.5	0.1	0.2
Mosses:												
Bryum sp.		0.1	14.2	3.1							15.3	12.5
Calliergon richardsonii		0.1	3.9	3.1	1.5		1.6				3.9	1.0
Campylium stellatum		2.9	3.1	1.1							13.6	9.0
Distichium capillaceum	2.2	0.9	11.2	0.1			9.5	20.0		10.0	1.4	9.5
Drepanocladus lycopodioides				23.1	1.5							
Drepanocladus uncinatus	8.9	14.1	56.5	5.6			10.8				22.5	55.6
Hypnum sp.	12.2	15.8	5.8				7.5	5.0	12.5	1.2		
Tomenthypnum nitens	2.0	65.5	40.1				11.5	18.8	12.5	0.1	5.4	19.5
Tortula ruralis	0.1	0.1	0.6						5.8			
Scorpidium scorpioides				4.6	30.2	0.5						
Total	25.4	105.5	136.0	43.0	33.2	0.5	40.9	43.8	30.8	11.3	62.1	107.1
Lichens:												
Black crusts	11.7						6.8					
Grey crusts	2.0											
White crusts	23.9	0.1					1.6		1.7	0.1		
Alectoria nigricans		0.1										
Cetraria cucullata	0.4	1.1					0.2		1.8			
Cetraria islandica	0.4	0.6					0.2	0.2				
Cetraria nivalis	0.1	0.1							0.3			
Cetraria richardsonii	0.1	0.2										
Cladonia spp.	0.1	0.2					1.0					
Dactylina arctica	1.8	1.0					0.6		1.8			
Peltigera aphthosa							0.1					
Peltigera canina	0.1	0.1										
Solonina sp.	0.1	0.3	0.1				0.6	1.7				
Stereocaulon sp.	0.5	0.2					4.6	1.7				
Thamnolia subuliformis	5.4	7.8	0.1				6.5	0.8	1.8	1.2		0.1
Total	46.9	11.9	0.2				22.2	4.4	7.4	1.3		0.1
Total cover	145.5	223.3	210.2	122.0	60.0	32.3	107.7	156.7	88.6	78.9	143.9	239.7
Total number of species	49	59	30	22	8	6	41	29	22	27	27	30

D or d indicates either heavy or light disturbance respectively, the nature of which may be further defined by a subscript: l — organic or inorganic litter from road construction; g — gravel, equipment tracks, dust from road; and i — areas of impounded water. The disturbance symbols may stand alone or follow the vegetation numbers.

The following examples illustrate the nature and interpretation of the formulae:

$F_f2,\underline{8}$ Flat terrain with frost boils supporting type 2 vegetation of *Dryas* and fruticose lichens and type 8 vegetation of *Saxifraga oppositifolia* and *Salix reticulata*; the latter vegetation type predominating. Familiarity with the vegetation and the region permits further interpretation that type 2 vegetation occurs on stable surfaces while type 8 is restricted to the frost boils.

$P_H\underline{1};\text{-};3d$ A region of lightly disturbed, high center polygons with type 1 vegetation of *Dryas* and crust lichens on the raised centers, with no distinct rims, and with type 3 vegetation of *Carex aquatilis*, and/or *Eriophorum angustifolium*, and dwarf shrubs in the troughs.

Discussion

Vegetation. Neiland and Hok (this volume) and White et al. (this volume) have provided useful descriptions of the Prudhoe Bay vegetation. The units presented here, although slightly different in content and concept, can be cross-matched with these studies. A detailed comparison is beyond the scope of this report. Table 3, however, attempts a brief comparison of the units recognized by T. Skogland in White et al. (this volume).

The 6 most common vegetation types occur along a complex site moisture gradient. This sequence from dry (Type 1) to wet (Type 6) can be seen in Table 3. A moisture ranking for all 13 types reported here from dry to wet would be: Types 1 and 10, Type 8, Type 2, Type 9, Type 3, Type 11, Type 13, Type 4, Type 12, Type 5, Type 6, and Type 7. This sequence is not linear. Fig. 1 shows the topographic and spatial interrelations of each vegetation type. It shows that the principal environmental control on the vegetation is site moisture as controlled by topography.

There is a strong correspondence between the vegetation map and the soil map (Plate I) of the same area (Table 4). Admittedly, there is some circularity involved in the latter statement because the same photographic base and a landscape unit approach was used for both maps, but the soil-vegetation and site moisture correspondence is inescapable.

The vegetation at Prudhoe Bay can be related to that of the whole Coastal Plain (Wiggins 1951; Britton 1957) and even with vegetation of other arctic regions; for example, the Eastern

Table 3

Approximate equivalents between the vegetation units used by White et al. (this volume) and those in this report.

White et al. (this volume)	Webber and Walker (this report)	Notes
Dryas integrifolia heath	Type 1	very dry
	Type 2	dry
	Type 3	moist
Eriophorum angustifolium polygon marsh	Types 3 and 4	extensive
Carex aquatilis marsh	Type 4	wet
	Type 5	very wet
	Type 6	emergent
Salix rotundifolia snowbed	Type 9 and/or 11	
Dupontia fisheri brook/meadow	Type 12	not extensive
Salix ovalifolia sand dunes	Types 15, 16, and 17	provisional numbers; not elaborated here

Canadian Arctic (Polunin 1948) and the Western Taimyr, USSR (Matveyeva et al. 1973). While the Prudhoe Bay vegetation is sufficiently distant from these other localities within the tundra continuum that the present units will not be wholly applicable elsewhere, it is our opinion that the method would be applicable.

The Prudhoe Bay vegetation is more diverse and contains a richer flora than vegetation at Point Barrow. This is the result of a slightly warmer growing season (Brown et al., this volume), combined with a more varied terrain and habitat spectrum.

Mapping. Mapping landscape units and describing their content with a series of symbols is a commonly accepted procedure (Kuchler 1967, pp. 190-194). It is a very appropriate method in these patterned landscapes, and pedologists and a geomorphologist (Brown 1969; Carey 1972; Everett, this volume), have used it effectively. The mapping method is relatively rapid and with experience, it is possible to map at this scale a square kilometer of moderately varied terrain in one man-day. The map appears to represent the vegetation of an area quite well, and potential users have found the map effective and easy to read.

The tonal shading of a prevalent vegetation type on the map is potentially misleading because a prevalent or most abundant type may occupy only a very small part of a landscape unit. This has not been a serious problem so far, but we are considering adding to the formula some quantitative assessment of each vegetation type within the landscape unit.

Type 6 vegetation of Carex aquatilis *and* Arctophila fulva *as emergent aquatic plants.*

Table 4

Correspondence of the soil types recognized in the IBP study area (Everett, this volume) and the present vegetation types at Prudhoe Bay. The most frequent vegetation corresponding to a soil type is underlined.

Soil Type (Everett, this volume) Number and Name	Vegetation Type (Webber and Walker, this report) Number
1. *Pergelic Cryoboroll*	1 and 10
2. *Pergelic Cryaquoll*	1, 2, 3, and 9
3. *Pergelic cryaquept*	2, 3, and 4
4. *Histic Pergelic Cryaquoll* (standing water)	4, 5
7. *Pergelic Cryaquept*	8

Map Utilization. We have not yet made any detailed analyses of the maps. It is our intention to complete the series of maps for the entire operating area. We will continue to monitor our permanent quadrats and analyze any observed changes. We also plan to make a phytosociological analysis which will elucidate, in detail, the environmental factors controlling the distribution of plants and vegetation at Prudhoe Bay.

With a reasonably complete understanding of the controls and dynamics of the Prudhoe ecosystem, we will be able to produce a series of derived or secondary maps. These maps may be viewed as management tools in the development of arctic oil fields. The derived maps will depict subjects such as vegetation productivity; distribution of ground ice and drainage patterns, and vegetation susceptibility to such potential hazards as future road construction, water impoundment, oil spills, and impact of air pollution. After additional areas have been mapped for soils, and as the soil/vegetation correspondences are more firmly established, soils maps might be obtained indirectly from vegetation maps. This would certainly be faster than directly mapping soils, which at the moment requires considerable field labor. Maps could be made to show wildlife distribution and range utilization; such maps could be used to suggest which areas could be set aside for wildlife feeding, denning, or nesting and which areas have lesser ecological benefits or costs. Although the speed of the present mapping method is acceptable for our current objectives we, as well as others, are exploring the possibility of using more rapid remote sensing methods such as computer classification and plotting and color enhancement. In these endeavors, our present maps provide excellent and essential "ground truth." At the moment, however, it is our experience that automatic techniques cannot successfully produce maps of large areas at scales of 1:3,000 or smaller because of the mosaic and patterning which makes each tundra landscape unit unique.

Conclusions

We have presented a vegetation map of a small portion of the Prudhoe Bay oil field. We believe the method of mapping we have developed is simple, easily taught, reasonably rapid, and effective. From these maps, with the addition of simple field observations and measurements and with subsequent analysis, it will be possible to develop recommendations for the effective management and husbandry of the tundra ecosystem at Prudhoe Bay. The permanent plots which we have established will serve as an important baseline against which the effects of the development of the oil field on the tundra ecosystem can be gauged.

Acknowledgments

We wish to acknowledge the many fruitful discussions we had with Dr. Kaye R. Everett, who produced the soils map which serves as a companion to our vegetation map. We thank John Batty, who acted as field assistant and gave unflaggingly of his expertise in tundra plant identification and vegetation mapping. Ms. Vicki Dow provided us with valuable drafting help in the production of the maps and figures. We would also like to thank Dr. Jerry Brown, Director of the Tundra Biome, who encouraged us to do this work; the Naval Arctic Research Laboratory at Point Barrow and Mukluk Freight Line at Prudhoe Bay, which provided field support. The late Scott Parrish provided us with coordination background information on Prudhoe Bay. The mapping project was primarily financed from Prudhoe Bay Environmental Subcommittee funds through a subcontract from the Tundra Biome Center, University of Alaska, to the University of Colorado. However, considerable degree of effort from the NSF Tundra Biome grant (GV-29350) to the University of Colorado was provided as similar efforts were under way on the Barrow site.

References

Britton, M. E. (1967). Vegetation of the Arctic tundra. Pages 67-130 *in* Arctic Biology (H. P. Hanson, ed.). Oregon State University Press.

Brown, J. (1969). Soils of the Okpilak River region, Alaska. Pages 93-128 *in* The periglacial environment, past and present (T. L. Péwé, ed.). McGill-Queen's University Press.

Brown, J., R. K. Haugen, and S. Parrish (This volume). Selected climatic and soil thermal characteristics of the Prudhoe Bay region.

Type 8 vegetation of active frost boils with little vegetation as a result of disturbance by road construction equipment.

Carey, K. L. (1972). Classification, mapping and measurement of the distribution of microrelief from airphotos: Barrow, Alaska. Pages 17-27 *in* Terrain and coastal conditions of the Arctic Alaskan Coastal Plain; Arctic environmental data package supplement 1. P. V. Sellman, K. L. Carey, C. Keeler, A. D. Hartwell. USA CRREL Special Report 165, Hanover, New Hampshire.

Everett, K. R. (This volume). Soil and landform associations at Prudhoe Bay, Alaska: A soils map of the Tundra Biome area.

Kuchler, A. W. (1967). Vegetation Mapping. Ronald Press, New York, 422 pp.

Matveyeva, N. V., T. G. Polozova, L. S. Blagodatskyh, and E. V. Dorogostaiskaya (1973). A brief sketch of the vegetation in the region of the Taimyr Biogeocoenological Station. Pages 7-49 *in* Biogeocoenoses of Taimyr tundra and their productivity (B. A. Tikhomirov and N. V. Matveyeva, eds.). Nauka, Leningrad, vol. 2. (Available as Tundra Biome translation.)

Murray, B. M. and D. F. Murray (This volume). Provisional checklist of the vascular, bryophyte, and lichen flora of Prudhoe Bay, Alaska.

Neiland, B. J. and J. R. Hok (This volume). Vegetation survey of the Prudhoe Bay region.

Polunin, N. (1948). Botany of the Canadian Eastern Arctic, Part III; Vegetation and ecology. National Museum of Canada Bull. 104, 304 pp.

Rastorfer, J. R., H. J. Webster, and D. K. Smith (1973). Floristic and ecological studies of bryophytes of selected habitats at Prudhoe Bay, Alaska. The Ohio State University Institute of Polar Studies, Report No. 49, 20 pp.

White, R. G., B. R. Thomson, T. Skogland, S. J. Person, D. E. Russell, D. F. Holleman, and J. R. Luick (This volume). Ecology of caribou at Prudhoe Bay, Alaska.

Wiggins, I. L. (1951). "The distribution of vascular plants on polygonal ground near Point Barrow, Alaska." Contr. Dudley Herbarium, Stanford University Press, 318 pp.

Manuscript submitted January 1974.

Transplant garden with pingo in background at Prudhoe Bay.

Institute of Agricultural Sciences,
University of Alaska

Responses of Arctic, Boreal, and Alpine Biotypes in Reciprocal Transplants

WILLIAM W. MITCHELL and JAY D. McKENDRICK
Institute of Agricultural Sciences
University of Alaska
Palmer, Alaska 99645

Introduction

Transplant gardens were established in 1972 at Prudhoe Bay (arctic site, Fig. 1) and Palmer (boreal site, Fig. 2) in Alaska. Responses of perennial plants obtained from arctic, boreal, and temperate locations were compared when grown under relatively uniform conditions at these two northern sites. Forty different biotypes in six grass species from locations in Alaska and Colorado were entered in the study. An additional study was conducted in 1972 and 1973 at both sites comparing 1 year's growth of seeded materials in phytometers. This report sums the results obtained in the transplant study through the 1974 growing season.

Transplant Study

Procedures

Each biotype included in the transplant study was subdivided for pre-establishment in the greenhouse prior to transplanting in the field. Round pots, 33 cm across and 20 cm deep, were filled with a mica peat mix and placed in holes dug about 25 cm deep in the two gardens. The plants were transplanted into these pots in the Palmer garden on June 13, 1972 and into the Prudhoe garden (Fig. 3) on June 18, 1972. Each pot was fertilized with a mix supplying N, P, and K at the rate of 45, 79, and 74 kg ha^{-1} respectively, at the time of transplant and again at the start of the 1974 growing season. The plants were watered in the Palmer garden as needed. No watering was necessary in the Prudhoe garden.

Measurements were conducted in mid-August in the Palmer garden and late August in the Prudhoe garden. The earlier measurements were necessary in the Palmer garden because of earlier maturing dates at the boreal site. Two plants of each accession were measured for the following characteristics:

1. median height to nearest cm of taller growing leaves when extended;
2. median height to nearest cm of taller growing culms;
3. median width to nearest mm of most typical leaves;
4. number of flowering culms;
5. extent of basal spread in cm;
6. density of shoot growth judged according to 5 classes (1-5; sparse to dense);
7. weight of shoots clipped off at ground level and oven-dried at 60° C., and
8. oven-dry weight of roots (attempted but abandoned for reason given below).

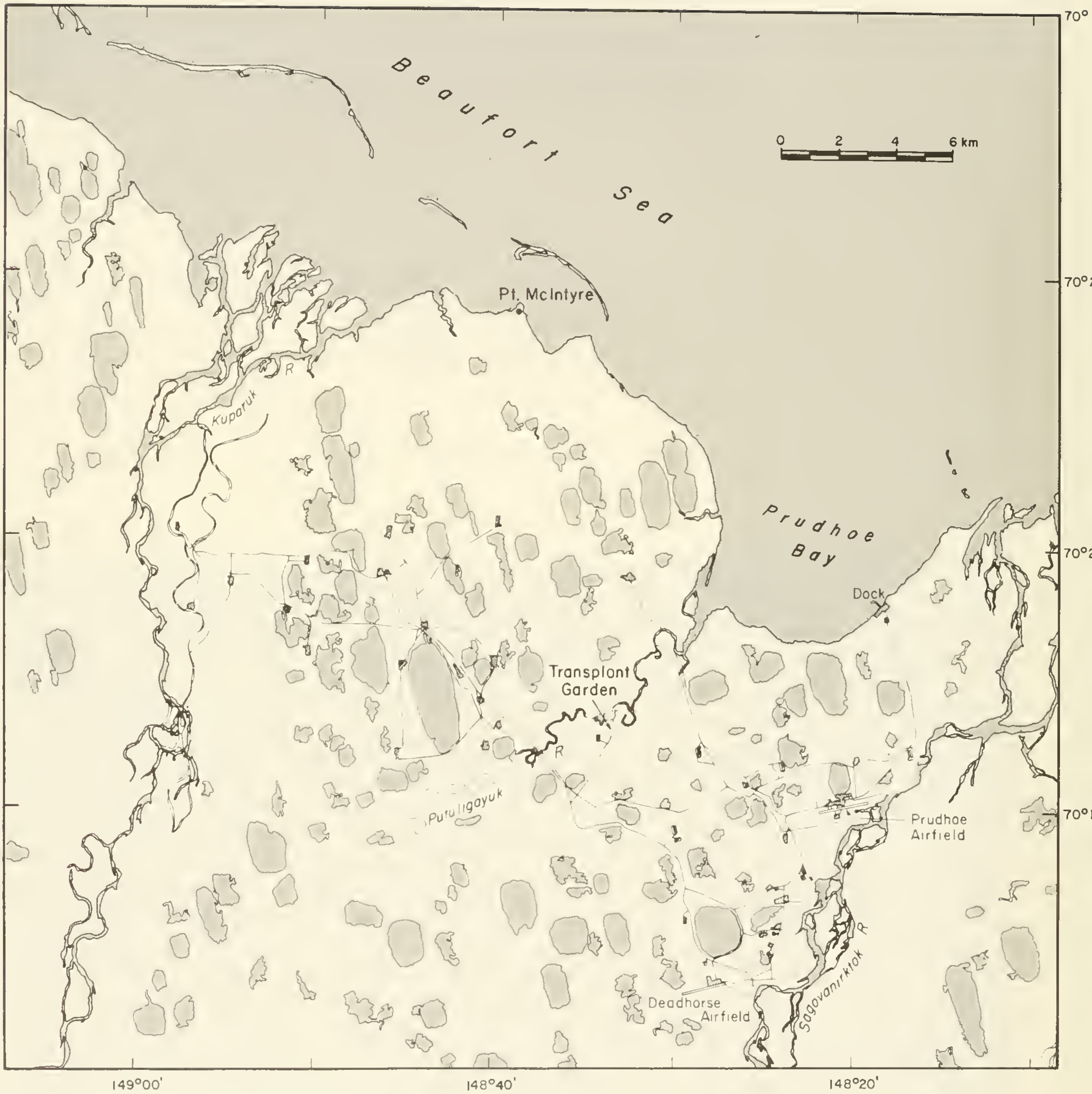


Fig. 1. *Prudhoe Bay area with location of transplant garden.*

Measurements of two plants of each accession were averaged for each character.

Periodic observations were made of flowering times (anthesis) in the Palmer garden. Flowering material was examined at the end of the season for the production of seed, but no quantitative measure was obtained of seed production.

An effort to obtain root weights was prevented by the nature of the mica peat growing medium. It was impossible to separate the mica peat from the mass of root material developed in the second season by the perennial plants without losing an unknown but significant quantity of root material in the washing process.

Following are the origins, elevations, and habitat information for the transplant entries. Locations of the collection sites for the Alaskan entries are denoted in Fig. 2.

Alopecurus alpinus

Alaska:
Accession No. 126– Barrow; 15 m; arctic tundra
No. 134 & 135– Prudhoe Bay; 15 m; arctic tundra
No. 136– Atigun Canyon; 910 m; arctic tundra
No. 129– Fort Yukon; 140 m; boreal, riverbank
No. 137– Anchor R., Kenai Peninsula; 245 m; coastal forest, meadow

Colorado:
No. 130 & 131– Summit Lake; 3910 m; alpine meadow

Deschampsia caespitosa (sensu lato)

Alaska:
Accession No. 138– Meade River; 15 m; arctic tundra
No. 142– Prudhoe Bay; 15 m; arctic tundra
No. 147– Franklin Bluffs; 90 m; arctic, river bluff
No. 143 & 144– Caribou Mt.; 670 m; alpine tundra
No. 145 & 146– Copper Center; 350 m; boreal, riverbank
No. 148– Turnagain Pass; 300 m; subalpine meadow

Colorado:
No. 140– Niwot Ridge; 3600 m; alpine meadow
No. 141– Summit Lake; 3910 m; alpine meadow
No. 139– Rollins Pass; 3555 m; alpine meadow

Arctagrostis latifolia

Alaska:
Accession
No. 155 & 156– Prudhoe Bay; 15 m; arctic tundra
No. 154– Eagle Summit; 1130 m; alpine tundra
No. 149, 150 & 151– Tok Junction; 490 m; boreal forest, bog
No. 153– Eureka; 1110 m; low alpine shrub community
No. 154– Hatcher Pass; 855 m; alpine tundra

Calamagrostis inexpansa

Alaska:
Accession
No. 158, 159 & 162– Sagwon; 200 m; arctic, riverbank
No. 164– Galbraith Lake; 855 m; arctic, riverbank
No. 160– Dietrich Valley; 425 m; subarctic riverbank
No. 161 & 165– Glennallen; 610 m; boreal, bog
No. 163– Palmer, near sea level; boreal, tidal flats

Festuca rubra

Alaska:
Accession No. 166– Franklin Bluffs; 90 m; arctic, river bottom
No. 168– Sagwon; 200 m; arctic, river bottom
No. 167– McKinley Park; 1070 m; alpine tundra
No. 169– Anchor R., Kenai Peninsula; 245 m; coastal forest, meadow

Poa alpina

Colorado:
Accession No. 157– Niwot Ridge; 3600 m; alpine meadow

Results

Flowering culm production was highly variable among both the arctic and boreal entries within species. Most of the arctic entries increased in flowering culm production at both gardens in the second and third growing seasons. Many of the boreal entries declined in number of flowering culms at Palmer in the third season, particularly if they had produced a large number in the preceding season. Most of the boreal entries succeeded in flowering at Prudhoe, but many produced very few culms. A few were

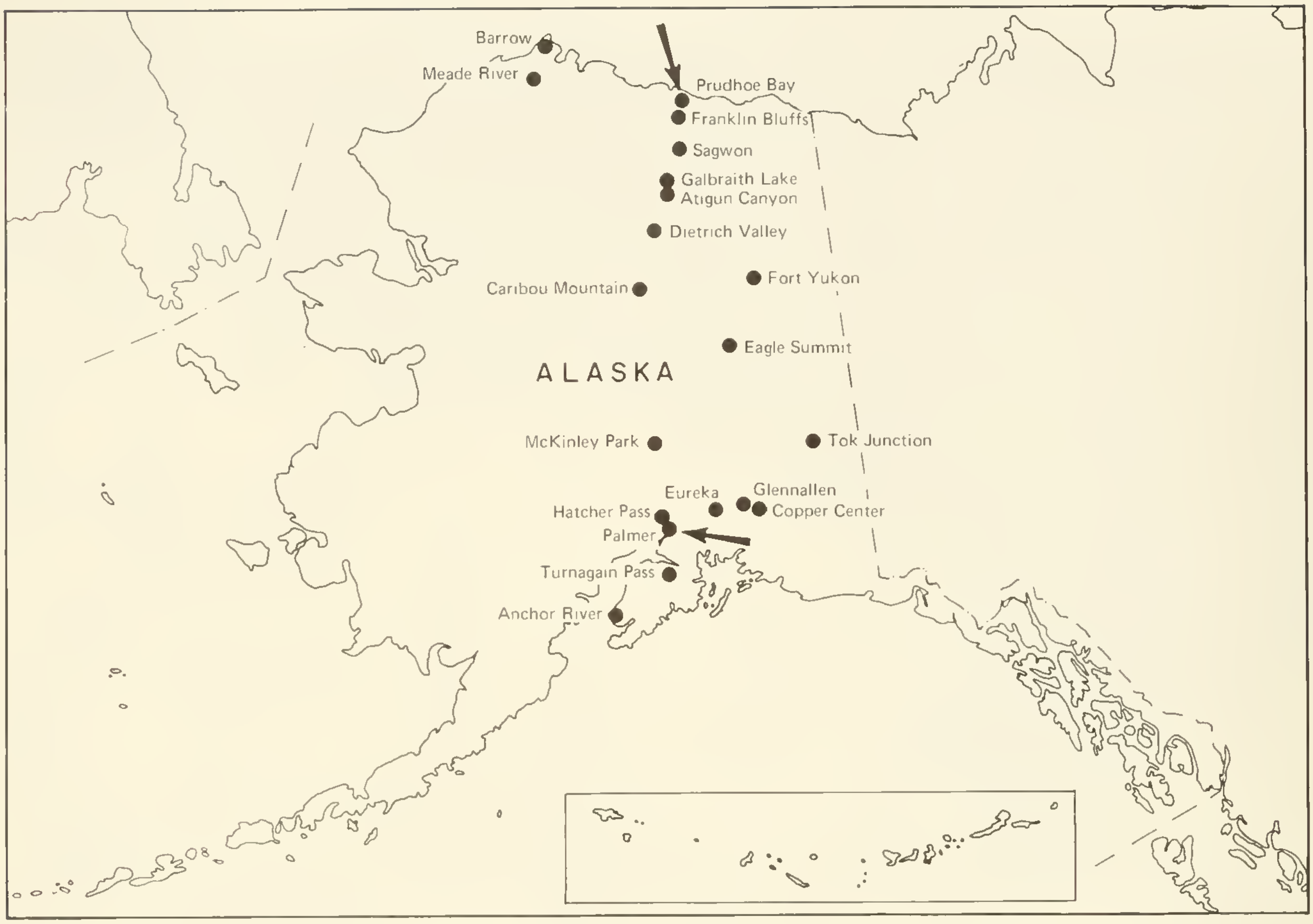


Fig. 2. *Map of Alaska with locations of transplant gardens (denoted by arrows) and collection sites for plant materials entered in transplant study.*

remarkably prolific. Some of the arctic entries produced more flowering culms at Palmer than at Prudhoe.

Shoot weights generally were greater at Palmer, but leaves often were longer at Prudhoe, particularly in the third year. As a rule, leaves were slightly to considerably wider at Prudhoe. Plants generally spread more in basal growing area at Palmer.

No definite patterns were reflected in the performances of the different polyploid races.

More detailed discussions of performances by species follows. Morphological and other data are presented in Table 1.

Alopecurus alpinus

The Colorado entries winter-killed at Prudhoe while surviving at Palmer. The Alaskan entry from the Kenai Peninsula was severely winter injured at Prudhoe.

The north to south gradient in collection sites for this species was reflected in plant height (or leaf lengths) in the experimental gardens (Fig. 4). Plants from the more southern locations in Alaska grew taller at both Palmer and Prudhoe. However, shoot heights of the Colorado entries were less than that of the south-central Alaska entry at the Palmer site. Those relationships did not hold true for the other parameters. Some of the arctic entries were as productive in shoot weight as the boreal and Colorado entries at Palmer and Prudhoe.

The arctic entries produced a short, dense growth at the boreal site and a decidedly taller growth at the arctic site. The plants had spread throughout the pot at both sites, but generally grew less dense at Prudhoe. This was consistent with results obtained in 1973. Two plants of the Kenai Peninsula entry recovered sufficiently from winter injury to produce seed heads in 1974, which grew the tallest at the Prudhoe site followed by an entry from a northern boreal station (Fort Yukon). The plants in the Prudhoe garden bore wider leaves than those in the Palmer garden, as they did in 1973.

Three of the arctic entries produced from about two to almost five times as many flowering culms as the other entries in both the Palmer and Prudhoe gardens (Fig. 5). This represented a tremendous increase in flowering culm production from the previous year. One arctic biotype from the Brooks Range (Atigun Canyon) resembled the Fort Yukon entry more than the coastal arctic forms in flowering culm production.

The arctic and boreal entries generally differed little in shoot weights (Fig. 6). All of the entries except the Barrow entry produced more top growth at the boreal site than at the arctic site. A Prudhoe Bay biotype and Fort Yukon biotype were the highest producers at both sites. The arctic biotypes compensated for their shorter growth with the production of more flowering culms and generally a more dense growth to yield as much as the boreal types.

Deschampsia caespitosa

The three Colorado entries and one from the Kenai Peninsula (Turnagain Pass) in southcentral Alaska, all tetraploids, winter-killed at both stations in 1973. An octoploid boreal entry from the southern interior region of Alaska (Copper Center) was severely winter injured in the Palmer garden in 1974.

The arctic and alpine entries grew shorter at Palmer than they did at Prudhoe, which generally was consistent with results obtained in 1973 (Fig. 7). The single boreal entry (IAS 145, Copper Center) that survived in both gardens grew considerably taller than the other entries at Palmer. The boreal entry grew longer leaves but shorter and much fewer flowering culms at Prudhoe than it did at Palmer.

The arctic and alpine entries increased appreciably in flowering culm production over the previous year at Prudhoe (Fig. 8). The tetraploid boreal entry (Copper Center, 145) declined in

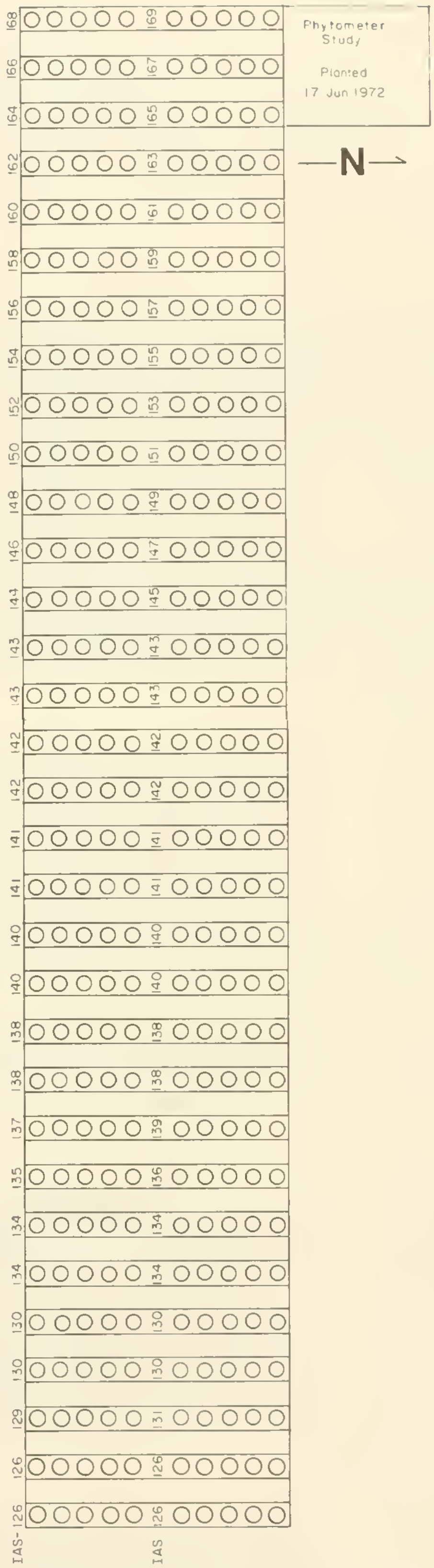


Fig. 3. *Plan of transplant garden at Prudhoe Bay.*

Table 1

Morphological, cytological, flowering, and biomass data on grasses grown in transplant gardens at Palmer (Pa) and Prudhoe (Pr), 1974 results. Entries are ordered along general north to south gradient within each species according to origin.

Species & Origin (2n No.)	Acc. No.	Ht (cm) Leaf/Culm		Leaf width (mm)		No. of Flw. culms per plant		Basal width* (cm)		Total dry weight of top growth	
		Pa	Pr	Pa	Pr	Pa	Pr	Pa	Pr	Pa	Pr
Alopecurus alpinus											
Alaska:											
Barrow (c. 102)	126	5/9	13/30	3.0	4.0	87	114	32/4.0	32/4.0	13.6	18.5
Prudhoe Bay (c. 100)	134	10/13	14/29	3.0	5.0	146	126	32/4.5	32/2.5	36.8	21.5
Prudhoe Bay (c. 100)	135	10/13	13/26	4.0	4.0	127	94	32/4.0	32/2.0	28.4	15.0
Atigun Canyon (c. 114)	136	11/17	20/33	3.5	4.5	54	30	32/3.5	32/3.0	24.7	15.5
Ft. Yukon (98)	129	17/34	25/40	3.5	6.0	27	40	29/4.5	32/2.5	38.8	19.5
Kenai Peninsula (98)	137	31/61	36/52	3.0	7.0	31	7	30/3.0	24/1.5	30.8	10.5
Colorado:											
Summit Lake (c. 104)	130	23/46	X	3.5	X	18	X	32/3.0	X	28.9	X
Summit Lake (c. 105)	131	22/43	X	4.0	X	15	X	30/3.0	X	29.3	X
Deschampsia caespitosa											
Alaska:											
Meade River (26)	138	14/20	25/31	3.0	3.0	43	49	15/5.0	10/5.0	35.4	35.0
Prudhoe Bay (52)	142	12/22	19/30	2.0	2.0	65	194	16/5.0	12/5.0	89.5	40.0
Franklin Bluffs (52)	147	14/28	21/39	3.5	3.0	95	120	14/5.0	12/5.0	49.7	42.5
Caribou Mt. (26)	143	9/30	16/30	2.0	2.0	131	112	14/5.0	11/5.0	23.1	31.5
Caribou Mt. (52)	144	11/28	15/28	2.0	2.5	74	92	10/5.0	9/5.0	18.9	25.0
Copper Center (26)	145	19/67	27/32	2.5	3.0	45	8	12/3.5	9/5.0	25.4	9.0
Copper Center (52)	146	XX	16/31	XX	2.0	XX	120	XX	13/5.0	XX	34.5
Turnagain Pass (26)	148					DEAD					
Colorado:											
Niwot Ridge (26)	140					DEAD					
Summit Lake (26)	141					DEAD					
Rollins Pass (26)	139					DEAD					
Arctagrostis latifolia											
Alaska:											
Prudhoe Bay (56)	155	19/36	24/35	6.0	9.0	13	15	22/1.0	22/2.5	3.2	8.5
Prudhoe Bay (28)	156	XX	24/31	XX	8.5	XX	53	XX	32/2.0	XX	22.5
Eagle Summit (56)	154	32/52	27/42	9.0	8.5	25	16	32/1.0	26/3.0	42.9	14.0
Tok Junction (28)	149	XX	45/40	XX	9.0	XX	8	XX	32/2.0	XX	14.0
Tok Junction (56)	150	40/70	34/27	12.0	12.0	22	7	31/3.0	32/3.0	55.1	8.0
Tok Junction (42)	151	40/74	X	10.0	X	22	X	32/2.0	X	32.2	X
Eureka (28)	153	32/57	26/31	7.5	9.0	39	2	31/3.0	25/2.0	35.9	3.5
Hatcher Pass (28)	152	32/60	32/38	6.0	11.0	24	7	32/3.0	24/2.5	37.3	8.5
Calamagrostis inexpansa											
Alaska:											
Sagwon (63)	158	18/36	41/44	3.0	6.0	28	18	32/2.0	22/4.0	21.2	32.0
Sagwon (56)	159	20/39	31/0	3.5	6.0	33	**	32/2.5	32/3.0	37.4	8.0
Sagwon (28)	128	16/35	29/28	2.0	4.0	116	13	30/2.5	32/3.0	28.0	19.5

Table 1 (continued)

Species & Origin (2n No.)	Acc. No.	Ht (cm) Leaf/Culm		Leaf width (mm)		No. of Flw. culms per plant		Basal width* (cm)		Total dry weight of top growth	
		Pa	Pr	Pa	Pr	Pa	Pr	Pa	Pr	Pa	Pr
Calamagrostis inexpansa											
Alaska:											
Galbraith (28)	164	18/39	38/36	2.5	4.5	46	20	32/3.0	32/2.0	35.3	18.5
Dietrich Valley (42)	160	30/54	44/42	4.0	6.0	68	9	19/4.0	26/2.0	28.2	17.0
Glennallen (28)	161	24/53	23/0	3.0	3.5	98	0	31/3.0	28/2.0	49.9	5.5
Glennallen (42)	165	27/54	34/0	3.5	7.0	72	0	32/1.5	26/2.0	44.0	7.0
Palmer (105)	163	38/57	XX	4.0	XX	61	XX	30/3.5	XX	63.9	XX
Festuca rubra											
Alaska:											
Franklin Bluffs (42)	166	15/22	15/23	2.5	2.5	2	7	23/3.5	8/5.0	19.7	3.5
Sagwon (42)	168	8/39	12/24	2.5	2.7	34	5	14/4.5	7/4.5	17.1	1.0
McKinley Park (42)	167	15/34	16/27	2.0	2.0	21	28	27/3.5	9/5.0	23.4	5.0

* Figure preceding slash (/) is basal width (cm); figure following slash is density estimate of basal growth judged according to 5 classes (1-5, sparse to dense).

X Dead

XX Seriously injured or unhealthy

** Grazing prevented accurate determination; believed not to have produced any culms.

flowering culm production at both sites while the octoploid (Copper Center, 146), winter injured at Palmer, increased at the Prudhoe site. The octoploid boreal entry produced many more flowering culms at Prudhoe than the tetraploid originating from the same location (Copper Center). The arctic octoploids also were considerably more productive in flowering culms than the arctic tetraploid. However, the alpine tetraploid from Caribou Mountain outproduced, by a smaller margin than the above instances, the octoploid from the same location.

The two arctic entries from Prudhoe Bay and Franklin Bluffs yielded the most top growth at both sites (Fig. 9). This was consistent with 1973 results. The tetraploid boreal entry declined significantly in top growth from the previous year at both sites.

Arctagrostis latifolia

A boreal entry died in the arctic garden during the first year. An arctic entry and a boreal entry did very poorly in the Palmer garden and were omitted from the analysis there. A boreal entry which recovered from an unhealthy start that excluded it from analysis in 1973 was included in the 1974 analysis.

The alpine and boreal biotypes grew taller (Fig. 10), bore more flowering culms (Fig. 11), and produced much more shoot weight (Fig. 12) than the surviving arctic biotype in the Palmer garden. The boreal entries produced longer leaves but fewer flowering culms than the arctic entries at Prudhoe. An arctic tetraploid entry produced the most flowering culms and top growth in the arctic garden. A boreal octoploid yielded the most top growth at Palmer. The boreal entries from central to southcentral Alaska grew more densely than the more northern entries at Palmer. Shoot weights and numbers of flowering culms were much greater at Palmer than at Prudhoe for most of the boreal entries. The arctic entries increased in number of flowering culms in both gardens and increased in shoot weight in the arctic garden in the third season, whereas the boreal entries were variable in this regard. Leaf lengths decreased in the third season.

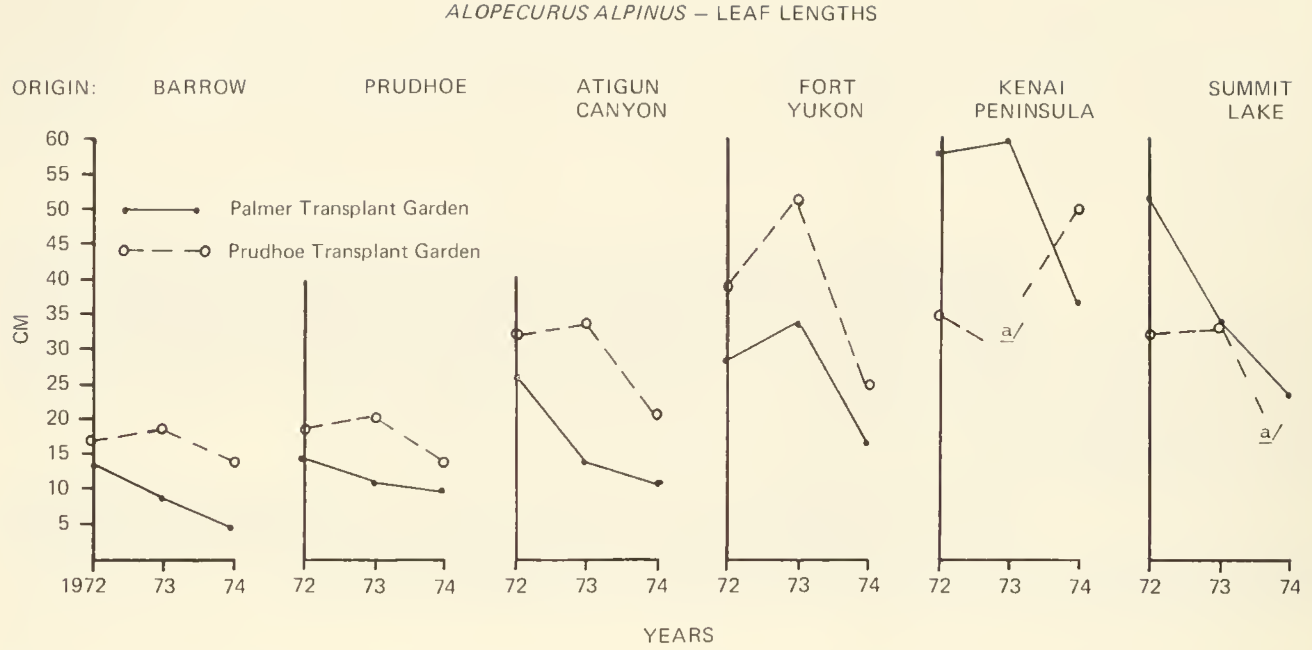


Fig. 4. *Leaf lengths of* Alopecurus alpinus *in the Palmer and Prudhoe transplant gardens over 3-year period.* ᵃ*/Entry severely injured or winter-killed.*

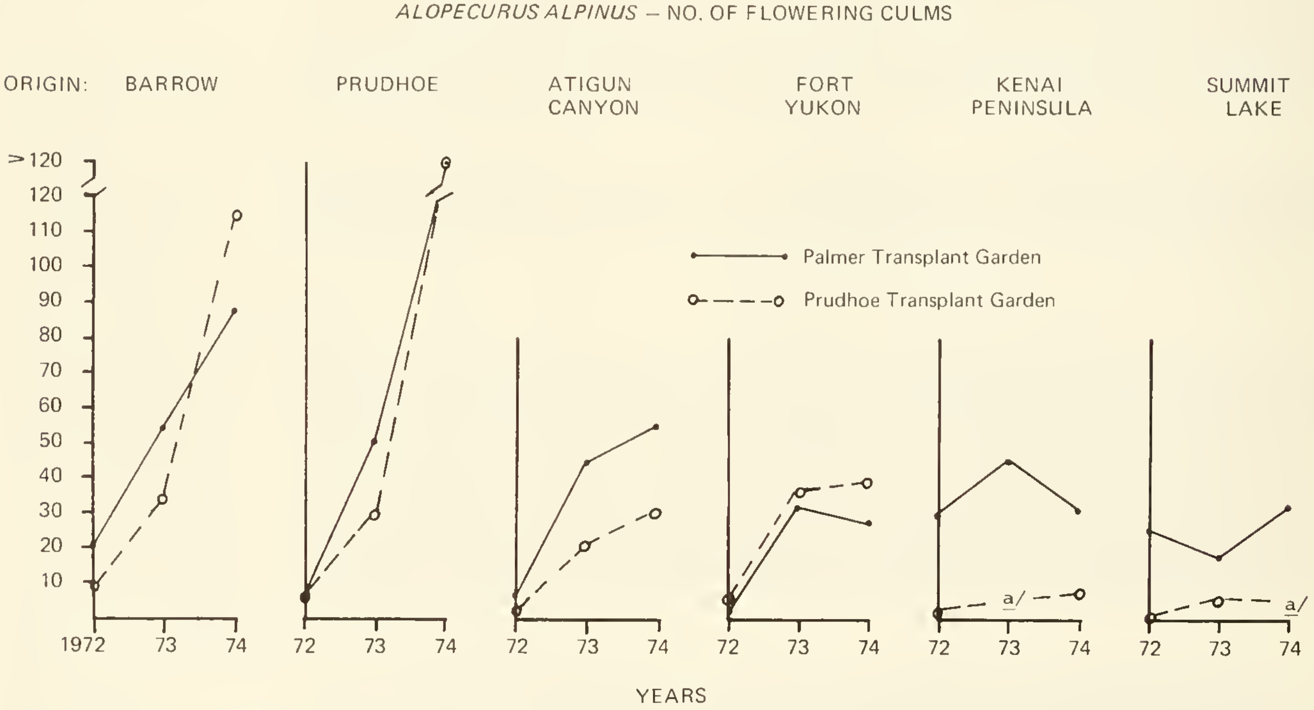


Fig. 5. *Flowering culm production of* Alopecurus alpinus *over the 3-year period.* ᵃ*/Entry severely injured or winter-killed.*

An alpine entry from northern interior Alaska (Eagle Summit) appeared the most ecologically plastic in being second in shoot weight and flowering culm production in both gardens in 1974.

Calamagrostis inexpansa

A boreal entry was severely winter injured in the arctic garden in 1974 and was excluded from the analyses at that site. All other entries were analyzed at both sites.

The boreal entries of northern reedgrass grew taller than the arctic entries at Palmer; results were mixed at Prudhoe (Fig. 13). In most cases leaf growth was longer and wider at Prudhoe than at Palmer, whereas flowering culms were longer at Palmer. Two of the boreal entries from southern interior Alaska failed to produce flowering culms at Prudhoe. An arctic entry might have been denied flowering through grazing activity. Flowering culm production was much more abundant at Palmer than at Prudhoe (Fig. 14). Except for one arctic entry, shoot weights were also greater at the boreal site (Fig. 15). In most cases, the rhizomatous grass spread throughout much of the growing area within the pots at both sites. A nine-ploid entry produced the most top growth at Prudhoe, while a 15-ploid boreal (tidal flat) entry was the highest yielder at Palmer.

Arctic and boreal tetraploids were the most prolific flowering culm producers at Palmer in the third season. A northern boreal hexaploid was outstanding in the second year but declined in the third year.

All entries decreased in leaf length in the third season at Palmer, as did most of the boreal entries at Prudhoe. Most of the arctic entries increased in leaf length, shoot weight, and flowering culm production at Prudhoe and in number of flowering culms at Palmer in the third season. They showed little improvement in shoot weight at Palmer. The boreal entries decreased in shoot weight and number of flowering culms at Prudhoe. Most of them increased in culm production at Palmer, but results were mixed in shoot weights.

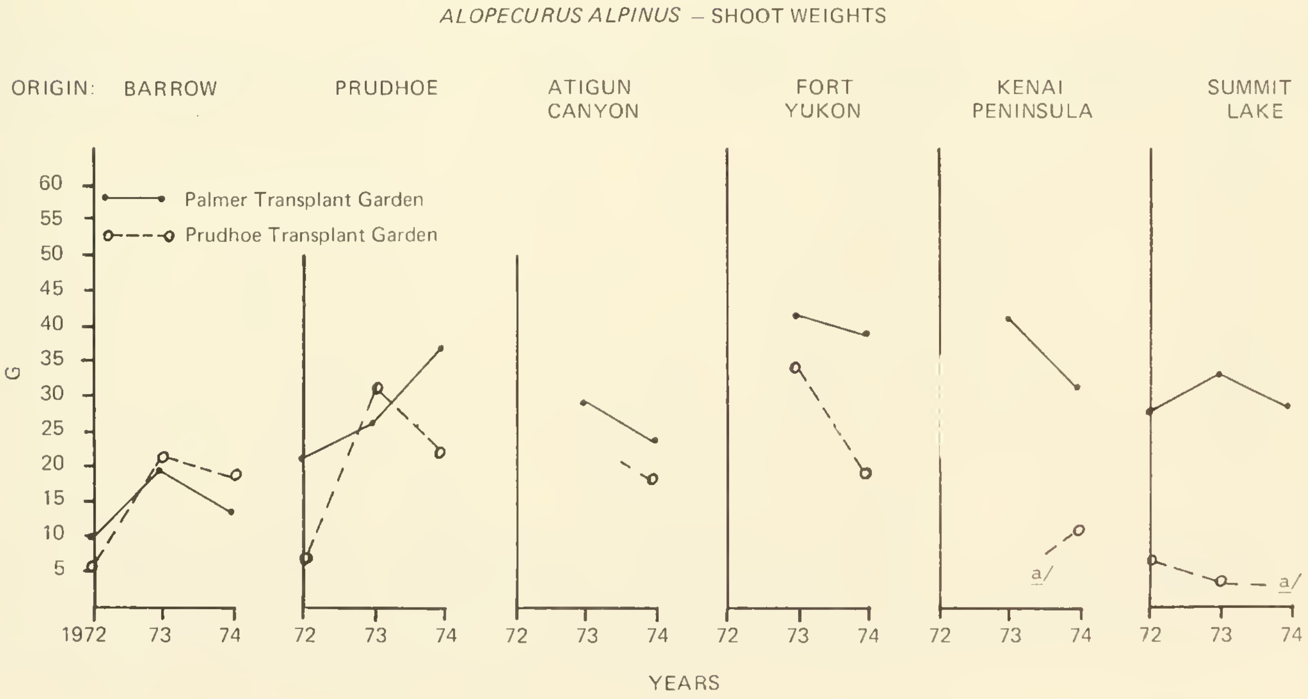


Fig. 6. *Shoot weights of* Alopecurus alpinus *over 2- or 3-year period. a/ Entry severely injured or winter-killed.*

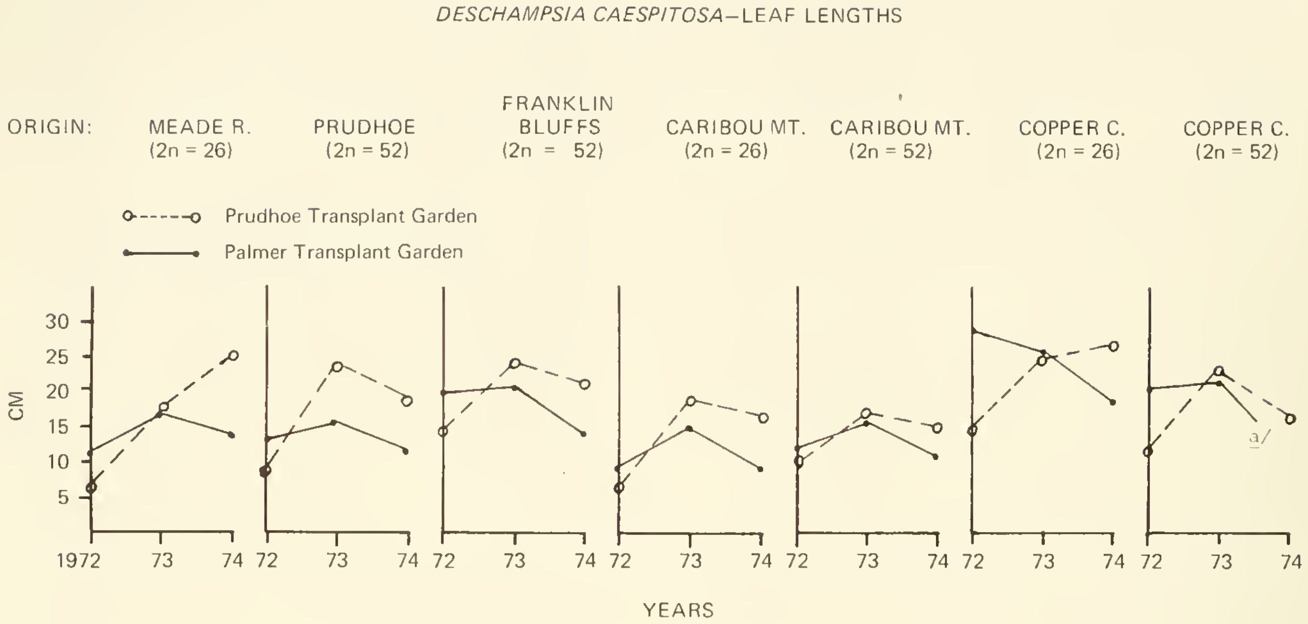


Fig. 7. *Leaf lengths of* Deschampsia caespitosa *over the 3-year period.* [a] */ Entry severely injured or winter-killed.*

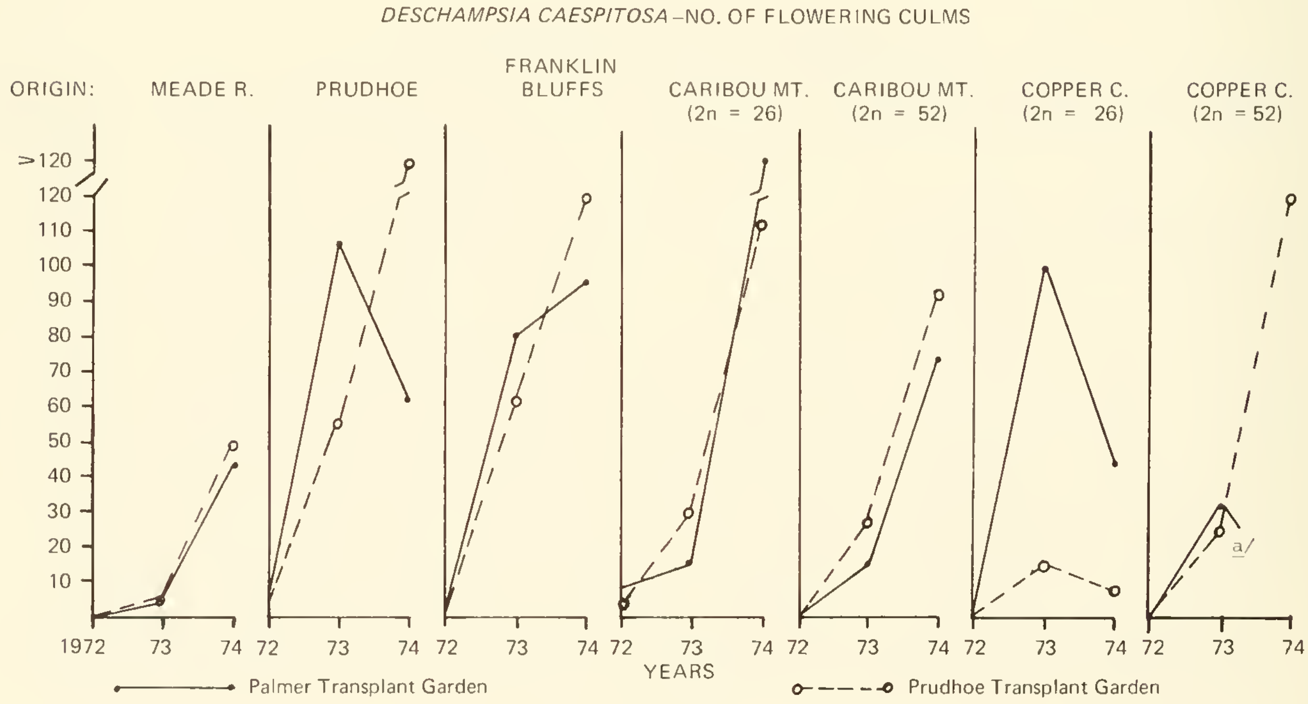


Fig. 8. *Flowering culm production of* Deschampsia caespitosa *over the 3-year period.* [a]*/Entry severely injured or winter-killed.*

Festuca rubra

Most of the red fescue entries declined appreciably in leaf length (Fig. 16), production of flowering culms (Fig. 17), and shoot weight (Fig. 18) at both sites. A McKinley Park entry yielded the most in shoot weight at both sites and produced the most flowering culms at Prudhoe. An arctic entry (Sagwon) bore the most flowering culms at Palmer.

Poa alpina

An entry of *Poa alpina* from Niwot Ridge, Colorado, became well established in both gardens in the initial year, but was winter-killed during the ensuing winter.

Seed set and phenology

A small amount of matured seed was found in some entries from the Prudhoe garden in 1973, but none was found in any of the entries in 1974. Only the arctic entries of *Alopecurus alpinus*, nos. 126, 134, 135, and 136, set seed in 1973. All surviving entries with healthy growth matured in the Palmer garden.

Approximate flowering dates (anthesis) were obtained for the entries in the Palmer garden in 1973 and 1974. *Arctagrostis latifolia* was omitted because of poor initial development of many of the plants.

Alpine foxtail was the earliest to flower followed by tufted hairgrass, with red fescue and northern reedgrass being the last to flower (Fig. 19).

The arctic entries generally commenced flowering about 2 to 3 weeks earlier than the boreal forested region entries and the Colorado alpine entries. The boreal alpine entries as a rule initiated flowering about 5 to 10 days after the earliest arctic entries and sometimes overlapped with their flowering times. The latest flowering entries were the high polyploid biotype of northern reedgrass (no. 163, 2n = 105), from the Cook Inlet tideland flats, and the coastal forest entry of red fescue.

Discussion

Most of the alpine entries from Colorado perished in the two transplant gardens in Alaska.

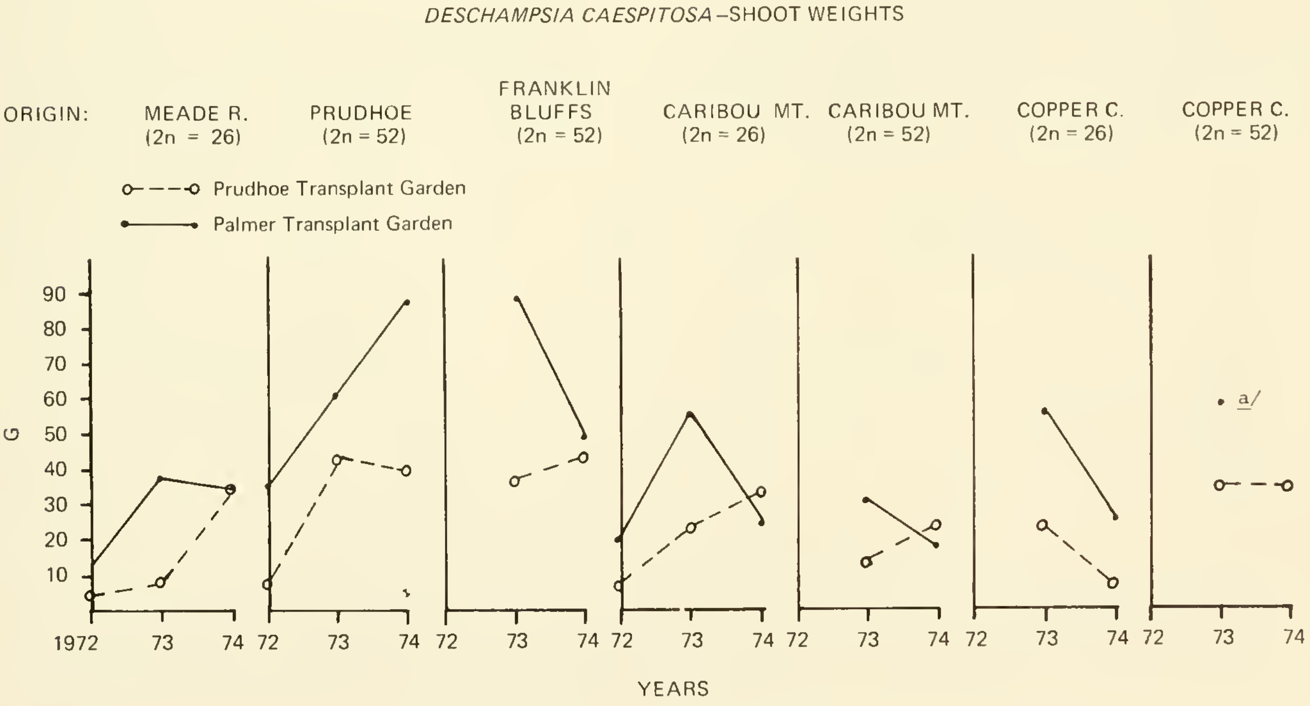


Fig. 9. *Shoot weights of* Deschampsia caespitosa *over 2- or 3-year period.* [a] *Entry severely injured or winter-killed.*

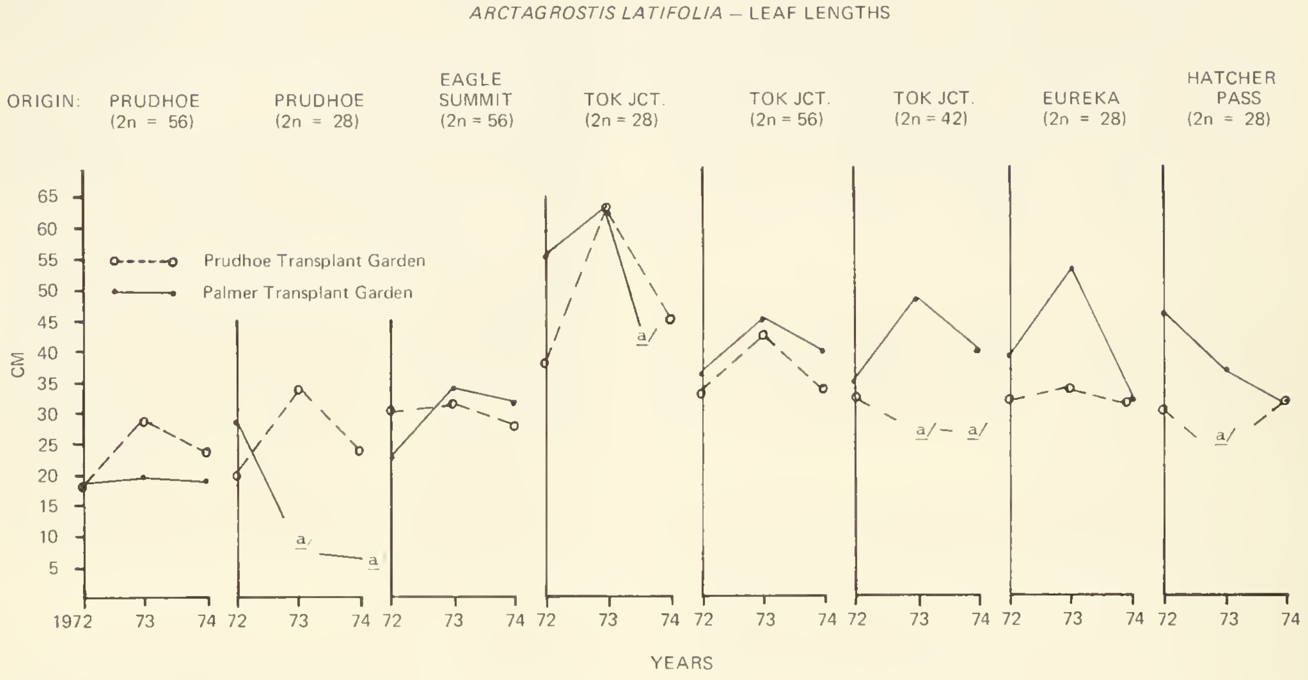


Fig. 10. *Leaf lengths of* Arctagrostis latifolia *over 3-year period.* a/ *Entry severely injured or winter-killed.*

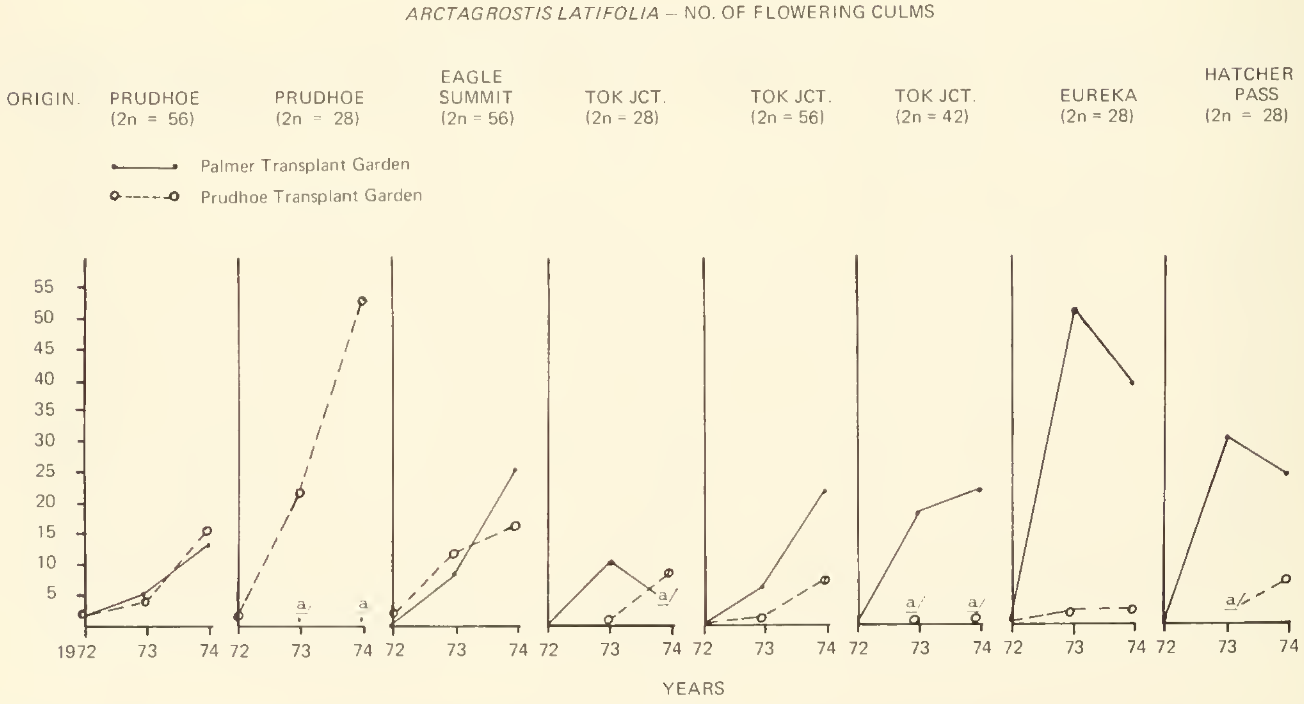


Fig. 11. *Flowering culm production of* Arctagrostis latifolia *over 3-year period.* a/*Entry severely injured or winter-killed.*

The two entries of *Alopecurus alpinus* survived in the boreal garden at Palmer, but winter-killed at Prudhoe. The entries of *Deschampsia caespitosa* and *Poa alpina* winter-killed in both gardens. Not all of the Alaska entries thrived in both gardens. A hairgrass biotype from a southcentral Alaska subalpine meadow winter-killed in both gardens. A southcentral coastal entry of *Alopecurus* experienced considerable injury at Prudhoe. Arctic entries of *Arctagrostis latifolia* had a difficult time at Palmer.

As would be expected, production was generally greater at Palmer than at the Prudhoe site. Differences in production between the two sites were often greater for the boreal entries than the arctic entries. Greater dry weights at Palmer were due to more abundant tillering and, in most cases, flower culm production. The hairgrass entries, however, tended to converge in dry weight production at the two sites in the third year.

Though dry matter production was generally greater at Palmer, leaves tended to grow longer and wider at Prudhoe. In some cases leaves were appreciably wider at the arctic site. This probably can be attributed to longer photoperiods with lower evaporative stresses in the Arctic.

The degree to which arctic limitations on growth also restrict the effective range of genetic variability and plasticity of plants requires clarification. Mosquin (1966) and Savile (1972) proposed that members of the arctic flora are genetically uniform. Such constancy was thought to be an inevitable consequence of means adapted by plants to speed up seed production. Bocher (1963) observed, however, that ". . . all species are more or less variable . . ."

In this study a great deal of variability was expressed in the number of flowering culms and amount of top growth produced. For example, shoot weights of arctic biotypes of *Deschampsia caespitosa* ranged from 40 g to almost 90 g at Palmer in 1973, and from 35 g to 90 g in 1974. Production at Prudhoe varied from 10 g to 40 g in 1973, but only from 35 g to 43 g in 1974. Variability in flowering culm production was even greater for these entries — from 3 to 106 at Palmer and 3 to 62 at Prudhoe in 1973, and from 43 to 95 at Palmer and 49 to 194 at Prudhoe in 1974. The boreal entries of hairgrass also varied a great deal in their performance at both sites, as did entries of other species.

The study has provided some information on the phenotypic plasticity of northern ecotypes. Plasticity in metabolic reactions with temperature has been demonstrated in arctic and alpine ecotypes of *Oxyria digyna* (Billings et al. 1971).

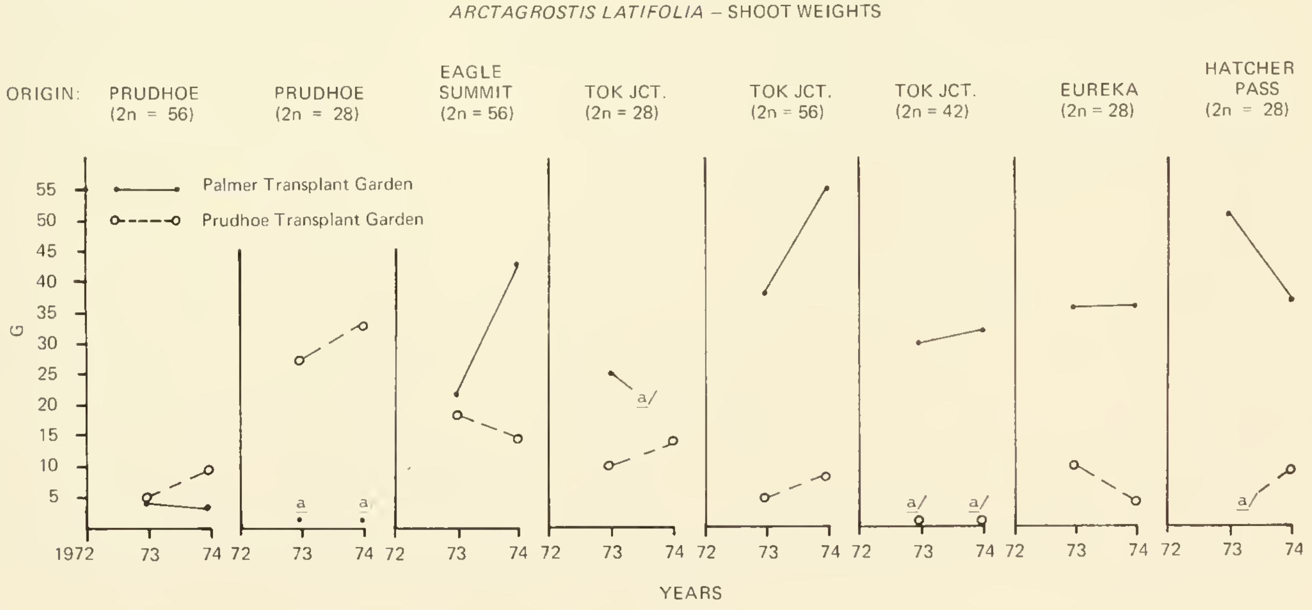


Fig. 12. *Shoot weights of* Arctagrostis latifolia *over 2-year period.* [a]/ *Entry severely injured or winter-killed.*

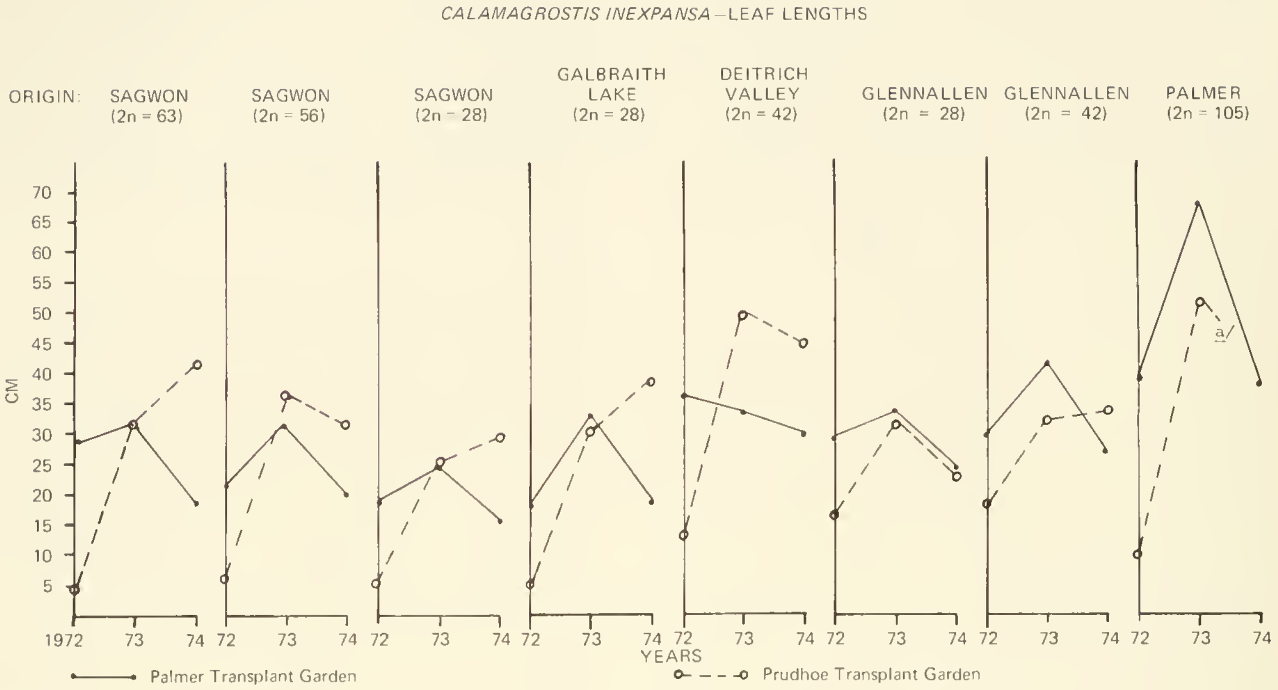


Fig. 13. *Leaf lengths of* Calamagrostis inexpansa *over 3-year period.* [a]/ *Entry severely injured or winter-killed.*

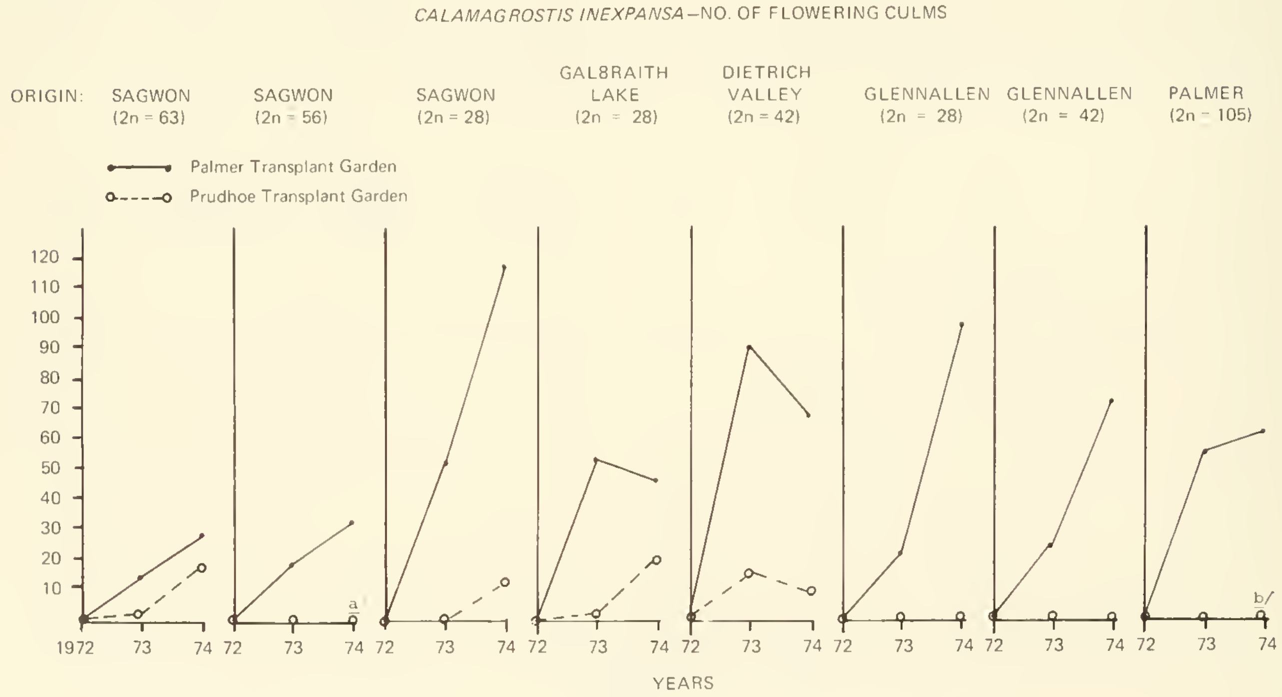


Fig. 14. *Flowering culm production of* Calamagrostis inexpansa *over 3-year period.* [a]/ *Entry grazed but believed not to have produced culms.* [b]/ *Entry severely injured or winter-killed.*

Some of the arctic entries in this study manifested considerable latitude in adaptations to the boreal site, with many of them achieving appreciably greater shoot weight and flowering culm production at Palmer than at Prudhoe. This agrees with the responses obtained by Clausen et al. (1940) and Mark (1965) when growing alpine biotypes at lower altitude stations. But these workers also found increased growth in height at the lower, less severe sites, whereas in our study all of the arctic entries grew taller in the Prudhoe garden. Some of them produced a dense but very short growth at Palmer.

The alpine entries varied in their adaptive responses to the two sites, but generally appeared suited to both. Two alpine biotypes of *Deschampsia* from northern interior Alaska grew taller at Prudhoe than at Palmer in the third year, but alpine biotypes of the other species from more central and southcentral Alaska grew taller and were more productive in the Palmer garden. Some alpine biotypes of arcticgrass, hairgrass, and red fescue from interior Alaska performed well in both the Palmer and Prudhoe gardens. However, alpine entries of hairgrass from southcentral Alaska and Colorado were unadapted to either site, failing to survive the first winter.

The two arctic entries of *Arctagrostis* appeared to be the most adversely affected in transplanting to the boreal region. They experienced difficulty in establishing at Palmer in their first year, and one of the entries eventually succumbed. This may indicate a genotype that is more narrowly adapted to the arctic environment, with less plasticity than the others.

These results have some practical significance in the possible application of native plant materials in various regions of Alaska. Those materials with sufficient plasticity to perform well in non-agricultural areas where they may be needed for rehabilitation, and in an agricultural area where they could be grown for seed, offer good potential for practical applications. In red fescue, for instance, a non-arctic entry of alpine origin was the best performer of that species both at Prudhoe and Palmer, thus pointing to the possibility of alpine entries being the source of material for tundra uses over a wide latitude. The relative merits of local vs. non-local seed sources were assessed in an altitudinal transect study with *Pinus ponderosa* (Conkle 1973). In that study, seed of yellow pine from a select zone outperformed local seed sources at altitudes lower and higher than that zone.

The diverse environments, particularly as they involved different altitudes, along the latitudinal transect sampled in Alaska confounded the delineation of ecoclinal gradients for most entries. However, such a gradient was rather

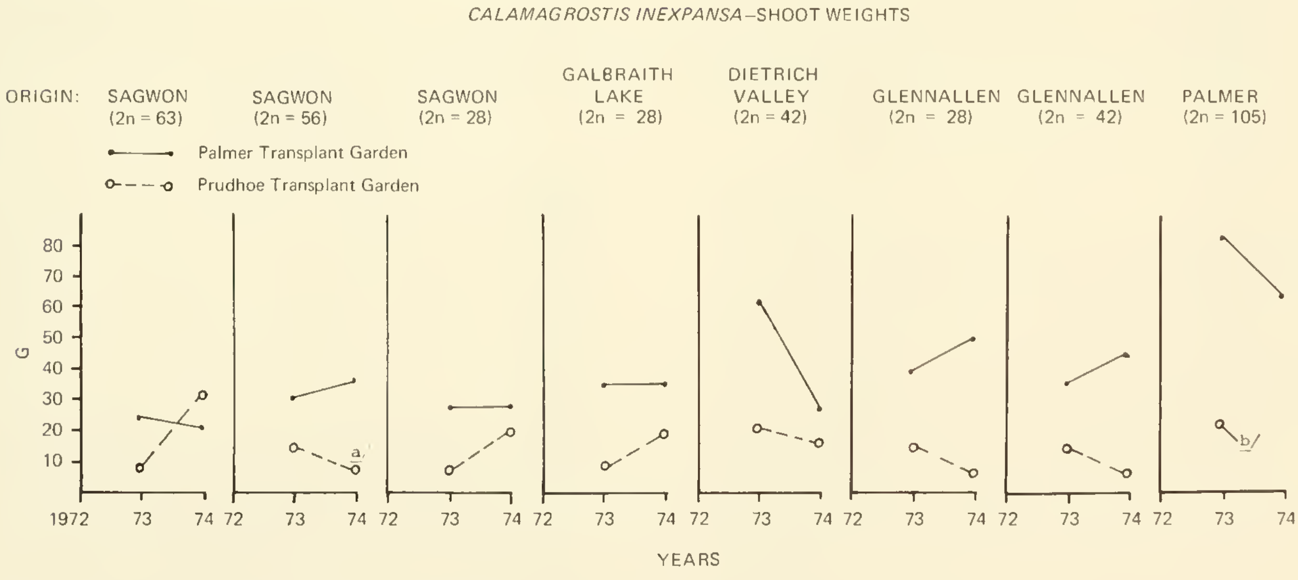


Fig. 15. *Shoot weights of* Calamagrostis inexpansa *over 2-year period.* [a]*/ Entry grazed.* [b]*/Entry severely injured or winter-killed.*

clearly evident in the height development of *Alopecurus alpinus*. The shortest forms in both gardens originated in the coastal tundra region followed by the Brooks Range entry, northern interior biotype, and Kenai Peninsula entry, in order of increasing heights. The Kenai Peninsula entry of this species resembled the Colorado entries more than the other Alaskan entries. The Colorado and southcentral Alaska entries grew tall, spread rather loosely from a dense central tuft at Palmer, and adapted poorly to the arctic site. The other Alaskan entries produced a more dense and shorter growing mat of material at Palmer and grew well at Prudhoe. The southcentral coastal material of Alaska may be more closely related to the alpine forms of the Rocky Mountains than to the northern Alaskan material.

No apparent conclusions can be drawn from the study regarding the possible significance of different ploidy levels within a species. In *Deschampsia* the diploid (2n = 26) appeared somewhat superior in both gardens to the tetraploid (2n = 52) collected from an alpine site on Caribou Mountain. However, the tetraploid race from Copper Center outperformed the diploid race from there in the arctic garden, whereas at Palmer the reverse was true. The

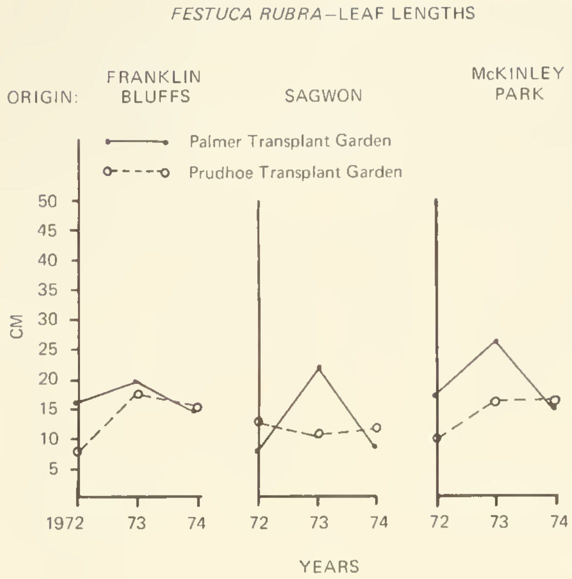


Fig. 16. *Leaf lengths of* Festuca rubra *over 3-year period.*

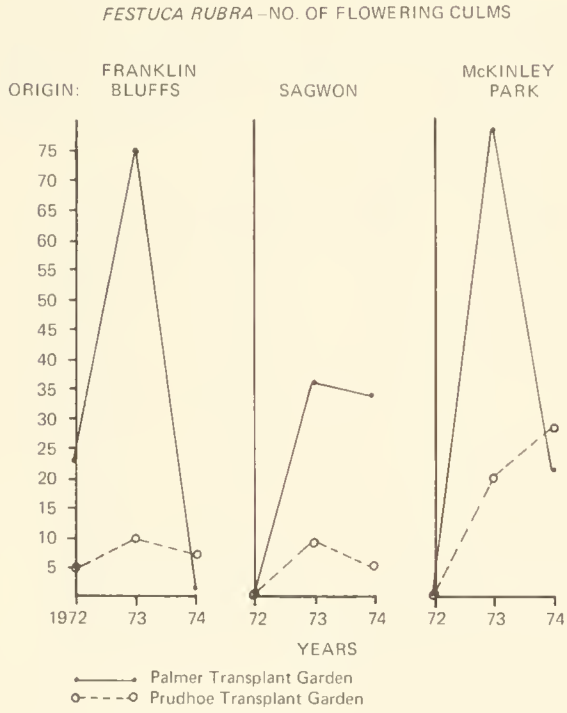


Fig. 17. *Flowering culm production of* Festuca rubra *over 3-year period.*

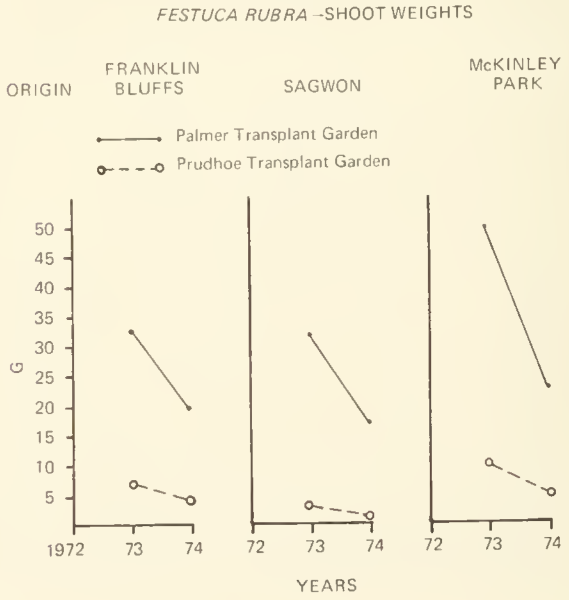


Fig. 18. *Shoot weights of* Festuca rubra *over 3-year period.*

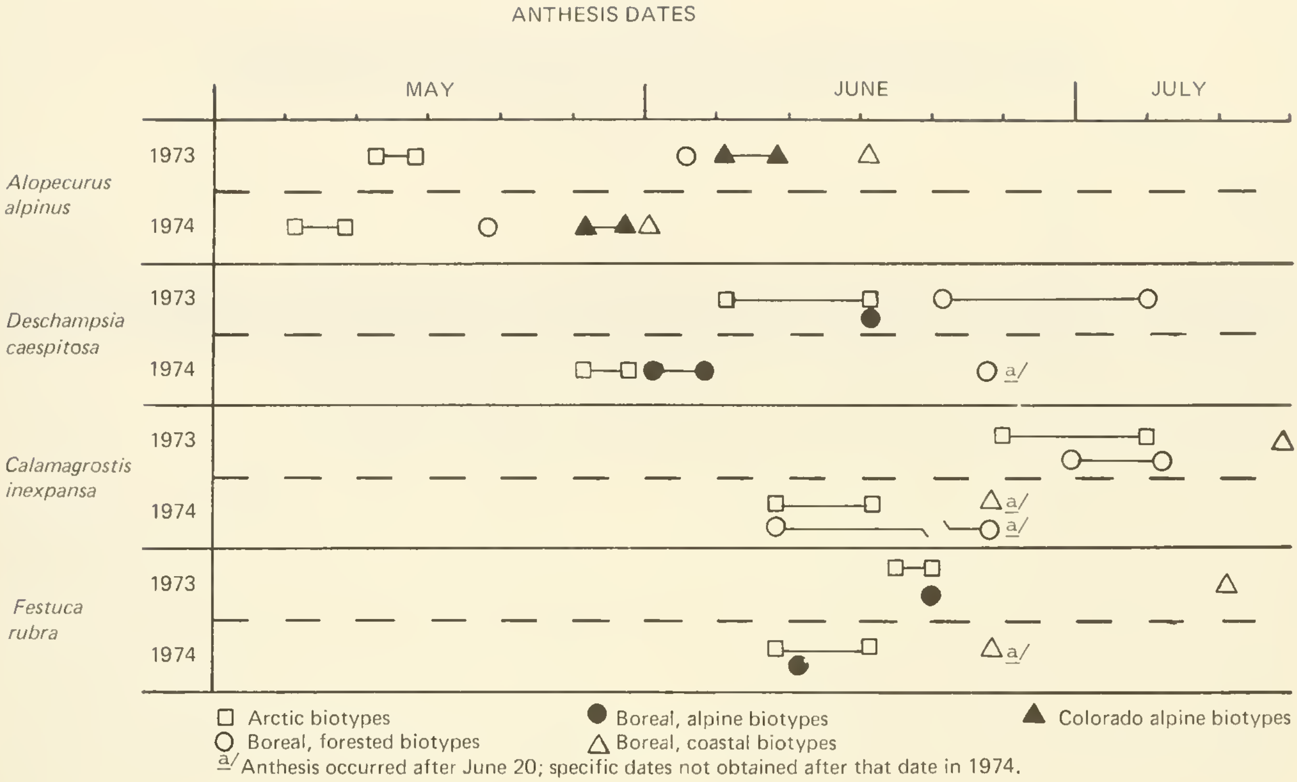


Fig. 19. *Anthesis dates of transplant entries in Palmer garden in 1972 and 1973 organized according to type of origin.*

highest polyploid in *Calamagrostis inexpansa* grew the most at Palmer but failed at Prudhoe. Extensive sampling and testing at the population level would be necessary to better define differences related to ploidy levels.

A comprehensive transplant study involving populations of *Agrostis tenuis* led Bradshaw (1959) to emphasize the roll of small populations interacting with their particular environment to produce local differentiation. He found natural selection effective in distinguishing populations occupying habitats very short distances apart. Though conditions in the North, particularly in the Arctic, are thought to limit differentiation in favor of systems that maintain successful genotypes, the results obtained in this study suggest greater variability than is suspected. Conclusions drawn from the performance of only one or a few genotypes out of a given population must be guarded, but it is possible that interactions of local populations with their environments are producing significant differentiation. Such differentiation would result in a flora better able to meet future exigencies than were it genetically uniform.

Phytometer Study

Procedures

Three species were grown from seed in plastic pots, 20 cm across and 21 cm deep, filled with a mica peat mix and sunk to ground level at Palmer and Prudhoe in 1973. Seed of "Engmo" timothy, annual ryegrass, and "Sprite" peas were sown on the surface of the mix on June 26 at both sites. The pots were fertilized about every week with 250 ml of Hoagland solution containing an additional 200 ppm of P. After germination the seedlings were reduced to five in each pot. The material was harvested 65 days from planting at Prudhoe and 66 days at Palmer. Various morphological and biomass measurements were made.

Table 2

Dry matter accumulations in grams per plant (1973 phytometer) of whole plant, and shoot and root components for Sprite pea, Engmo timothy, and annual ryegrass at Palmer and Prudhoe.

	Palmer (Boreal)				Prudhoe (Arctic)			
Entry	Whole Plant	Shoot	Root	Shoot/Root Ratio	Whole Plant	Shoot	Root	Shoot/Root Ratio
Sprite pea	9.5	8.4	1.1	7.6	1.14	.78	.36	2.2
Engmo timothy	7.4	3.5	3.9	.9	.046	.026	.020	1.3
Annual ryegrass	18.9	10.7	8.2	1.3	.352	.187	.165	1.1

Results and discussion

Results were consistent with those of 1972 in that annual ryegrass produced the most root and shoot dry matter at the boreal location while Sprite pea was the highest producer at the arctic site (Table 2). Yields at the arctic site were greatly reduced from those at the boreal site. There was a greater reduction in root growth than in shoot growth of timothy, thus resulting in a higher shoot/root ratio at Prudhoe; whereas in the pea, shoot growth decreased considerably more than root growth, thus producing a lower shoot/root ratio. That ratio remained about the same in annual ryegrass at both sites, as it did in 1972. The grasses produced more root growth than the pea at Palmer, but the reverse was true at Prudhoe. The pea produced less root growth with respect to shoot growth than the grasses at both sites. Total reduction in biomass at the arctic site was much greater for the perennial than the annuals. Sprite pea produced about 9x the biomass at the boreal site than it did at the arctic site; annual ryegrass accumulated about 50x and Engmo timothy about 150x their arctic production.

Biomass production of the two annuals at Palmer in 1973 exceeded that of the previous year (Table 3) in spite of a shorter growing period with fewer growing degrees (Table 4). Periodic fertilization with nutrient solution in 1973, as compared with one-time fertilization in 1972, probably accounted for the difference. Apparently the shorter growing period of 1973 was more significant in its effect in the Arctic. There yields were all lower in 1973 despite more abundant fertilization and the accumulation of more growing degrees. Increasing the frequency of fertilizer applications apparently did not influence growth as much where climatic conditions severely limited growth from seed. (Figures for the 1972 Eagle Summit phytometer study were included in Table 6 to demonstrate the intermediate position in biomass production of this alpine site).

Table 3

Productivity at arctic (Prudhoe) and alpine (Eagle Summit) sites in Alaska as a percentage of production at Palmer, a boreal site, in 1972 and 1973.

	Sprite Pea		Annual Ryegrass		Engmo Timothy	
Location	Biomass (g)	% of Palmer Production	Biomass (g)	% of Palmer Production	Biomass (g)	% of Palmer Production
1972						
Palmer	5.7	100	10.2	100	8.04	100
Prudhoe	2.2	38.6	.6	5.9	.06	.7
Eagle Summit	4.3	75.4	3.0	29.3	.34	4.2
1973						
Palmer	9.5	100	18.9	100	7.40	100
Prudhoe	1.1	11.6	.4	2.1	.05	.7

Table 4

Mean monthly air temperatures (°C) for summer months and growing degrees accumulated above daily mean of 0 C for phytometer growing periods at Palmer and Prudhoe in 1972 and 1973.*

Location & Year	Monthly Means June	Monthly Means July	Monthly Means Aug.	Phytometer Growing Period No. Days	Phytometer Growing Period Growing Degrees
Prudhoe					
1972	2.1**	6.7	6.4	76	447
1973	2.6	7.8	7.3	65	473
Palmer					
1972	10.9	15.5	13.4	76	1063
1973	11.6	13.8	11.6	66	852

* Monthly means and growing degrees were based on daily means derived from daily maxima and minima obtained at about 2 m above the ground. The Prudhoe data were furnished by the Atlantic Richfield Co. from readings taken at their base camp in the Prudhoe Bay region.

** In all cases except June, 1972 at Prudhoe the monthly mean temperature also equaled the mean number of growing degrees for the month. The average number of growing degrees for June, 1972 at Prudhoe was 2.3. The lower monthly mean temperature was due to 7 days averaging 0°C or below.

Only Sprite pea matured to the stage of seed production at Palmer. Annual ryegrass produced inflorescences in the emerging to emergent condition but did not develop beyond the early flowering stage. Timothy did not flower. None of the species flowered at Prudhoe.

Acknowledgments

These studies were jointly funded from the Tundra Biome Center, University of Alaska, utilizing both State of Alaska and Prudhoe Bay Environmental Subcommittee funds. Considerable savings in costs to all projects were accomplished by combining our Prudhoe schedules with non-Biome sponsored research at Prudhoe. The alpine plant materials from Colorado were kindly furnished by Erik K. Bonde and Maxine F. Foreman, who are conducting a similar study along an altitudinal transect in Colorado.

References

Billings, W. D., P. J. Godfrey, B. F. Chabot, and D. P. Bourque (1971). Metabolic acclimation to temperature in arctic and alpine ecotypes of *Oxyria digyna*. *Arct. and Alp. Res.*, 3:277-289.

Böcher, T. W. (1963). Phytogeography of middle west Greenland. *Meddelelser Om Gronland*, 148:1-289.

Bradshaw, A. D. (1959). Population differentiation in *Agrostis tenuis* Sibth. I. Morphological differentiation. *New Phyt.*, 58:208-227.

Clausen, J., D. D. Keck, and W. M. Hiesey (1970). Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. of Washington, Pub. No. 520, 452 pp.

Conkle, M. T. (1973). Growth data for 29 years from the California elevational transect study of ponderosa pine. *Forest Sci.*, 19:31-39.

Mark, A. F. (1965). Ecotypic differentiation in Otago populations of narrow-leaved snow tussock *Chionochloa rigida*. *New Zealand J. Bot.*, 3:277-299.

Mosquin, T. (1966). Reproductive specialization as a factor in the evolution of the Canadian flora. Pages 43-65 *in* The Evolution of Canada's Flora (R. L. Taylor and R. A. Ludwig, eds.). University of Toronto Press.

Savile, D. B. O. (1972). Arctic adaptations in plants. Canada Dept. Agric., Monog. 31:1-81.

Animal Investigations

Collecting data on adult insect populations. In the foreground is an emergence trap, used to document daily emergence of adult craneflies (Tipulidae). *In the background, observers examine a "sticky board" trap.*

David Atwood, USACRREL

Ecology of Tundra Invertebrates at Prudhoe Bay, Alaska

STEPHEN F. MacLEAN, JR.
Department of Biological Sciences
and Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska 99701

Introduction

Research on tundra invertebrates at Barrow has emphasized three main points: (1) the abundance and biomass of invertebrates in various tundra habitats; (2) adaptations of invertebrates to tundra conditions, and (3) their functional role in the tundra ecosystem. The tundra at Prudhoe Bay, while structurally similar to that of Barrow in a number of ways, offers milder summer conditions and a wider variety of habitats than is found at Barrow. Thus, research was planned to extend the observations made at Barrow and to determine the similarity in taxonomic structure, abundance, and function of the invertebrate community at the two sites. Observations were made in two seasons, 1971 and 1972.

Study Areas

Five study plots were selected for intensive study in 1971 in the Prudhoe Bay area. The plots were chosen to provide at least visually homogeneous stands of major topographic-vegetation features of the region. Two study plots (Nos. 4 and 5) were on the drained lake basin that was intensively sampled for primary production data. The remaining three plots were on the elevated bench west of the lake basin.

Plot 1: *Dryas integrifolia* dry heath
Plot 2: *Carex aquatilis* wet swale
Plot 3: *Dryas integrifolia* and graminiform mesic heath
Plot 4: Drained lake basin
Plot 5: Drained lake basin

Vegetational features of this area are reported in greater detail by Webber and Walker (this volume).

The above study plots were again sampled in 1972. In addition, two new plots were established north of drilling pad F. They were selected to avoid any possible influence of human activity and were located on avian study plot C (Norton et al., this volume).

Plot 6: *Carex aquatilis* wet meadow
Plot 7: *Dryas integrifolia* and graminiform mesic heath.

Methods

1. Species Diversity. An extensive collection of insects was made in 1971 in an effort to sample all habitats in the Prudhoe Bay area. Identification of specimens by authorities on the various taxonomic groups is still in progress, and only partial results can be presented at this time.

2. **Abundance of soil fauna.** Four sod cores, each 182.4 cm^2, were removed from points chosen at random in each study plot at 10-day intervals in 1971 and 1972. Cores were shipped to Fairbanks, where macroarthropods were removed by drying and heating the core under a 60-watt light bulb. Extracted specimens were preserved in alcohol until they could be counted.

On 29 August 1972, a set of cores, each 22.9 cm^2, was taken from plots 11, 14, 15, 16, and 17. These were brought to Fairbanks where replicate cores were subjected to O'Conner wet funnel extraction for Enchytraeidae and to Macfadyen high-gradient extraction for Acarina and Collembola. Each core was divided into 2.5 cm depth increments to determine distribution of invertebrates with depth below the tundra surface.

3. **Phenology.** Following a technique used at Barrow (MacLean and Pitelka 1971), two "sticky boards" (each 1x0.1 m), were placed level with the ground surface on each study plot. The boards were replaced at 3-day intervals. Arthropods captured on the sticky surface were identified and counted under a dissecting microscope. Since most arctic insects have a very short adult life-span, the distribution of "sticky board" catches through the season corresponds closely with the actual emergence of adult insects. The total number of captures in any plot provides an index of abundance that can be used in comparing year-to-year and between-habitat differences.

Results

1. **Species composition and diversity.** Although identification of the collection of Prudhoe Bay insects is far from complete, it is obvious that species diversity is much higher at Prudhoe Bay than at Barrow. For example, collecting in one season produced 13 species of craneflies (two never before collected) at Prudhoe Bay; collecting in many seasons at Barrow has produced only four species (Table 1). The greatest disparity between Barrow and Prudhoe occurs in the Dolichopodidae (long-legged flies); 20 species were collected at Prudhoe Bay in 1971, while the Barrow list has but one species. Prudhoe Bay has at least 12 butterfly species; Barrow has five. This difference is apparently due to higher within-habitat diversity and to the greater variety of habitats available in the Prudhoe Bay region.

David Atwood, USACRREL

Adult insects captured on "sticky board" trap. Trap consists of 1x0.1 m board covered with a sticky resin and placed flush with tundra surface.

Certain faunal groups that are scarce or lacking at Barrow are abundant and conspicuous at Prudhoe Bay. In walking across dry tundra, one is quickly struck by the abundance of large wolf spiders (Lycosidae), at least four forms of which are easily recognizable. At Barrow there is but one uncommon wolf spider *(Tarentula mutabilis),* and the true bugs (Homoptera) are represented by a single, uncommon leafhopper (Cicadellidae) species *(Hardya youngi).* At Prudhoe Bay leafhoppers are very abundant on drier habitats, occurring in lower numbers elsewhere (Fig. 7). In addition, at least one species of leaf bug (Miridae) was found.

2. **Abundance of soil fauna.** Larvae of various cranefly species (Diptera: Tipulidae) are an abundant component of many tundra ecosystems. At Barrow larvae of *Pedicia hannai*

Table 1

Comparison of species diversity of some insect families at Barrow and Prudhoe Bay. Barrow list after Hurd (1957) with additions. Prudhoe Bay specimens determined as indicated.

Barrow	Prudhoe Bay
Diptera: Tipulidae	(Det. by G. C. Byers and C. P. Alexander)
Tipula carinifrons Holm.	*Tipula begrothiana* Alex.
Tipula aleutica Alex.	*Tipula arctica* Curtis
(Det. by C. P. Alexander)	*Tipula pribilofensis* Alex.
	Tipula diflava Alex.
	Tipula besselsi OstenSacken
	Tipula macleani (sp. nov.) Alex.
	Prionocera parii OstenSacken
Prionocera gracilistyla Alex.	*Prionocera gracilistyla* Alex.
	Nephrotoma lundhecki (Nielsen)
Pedicia hannai antennata Alex.	*Pedicia hannai antennata* Alex.
	Erioptera kluane Alex.
	Erioptera forcipata Lundstrom
	Limnophila sp. nov.
Diptera: Culicidae	(Det. by R. Gorham)
Aedes nigripes	*Aedes cataphylla*
	Aedes impiger
	Aedes nigripes
Diptera: Dolichopodidae	(Det. by F. Harmston)
	Dolichopus amnicola
	Dolichopus consanguineus
	Dolichopus ohcordatus
	Dolichopus eudactylus
	Dolichopus ramifer
	Dolichopus plumipes
	Dolichopus occidentalis
	Dolichopus aldrichii
	Dolichopus humilis
	Campsicnemus nigripes
	Hydrophorus gratiosus
	Hydrophorus sodalis
	Hydrophorus signiterus
Hydrophorus fumipennis	*Hydrophorus fumipennis*
	Gymnopternus californicus
	Aphrosylus nigripennis
	Aphrosylus fumipennis
	Aphrosylus praedator
	Raphium tripartitum
	Raphium sp.
Lepidoptera: Pieridae	(Det. by K. W. Philip)
Colias palaeno	
	Colias hecla
	Colias thula
	Colias nastes
Lepidoptera: Papilionidae	
Papilio machaon	
(Det. by K. W. Philip)	
Lepidoptera: Lycaenidae	(Det. by K. W. Philip)
	Lycaeides argyrognomon
	Agriades aquilo
Lepidoptera: Nymphalidae	
(Det. by K. W. Philip)	(Det. by K. W. Philip)
Boloria frigga	*Boloria frigga*
Boloria polaris	*Boloria polaris*
Boloria chariclea	*Boloria chariclea*
	Boloria napaea
Lepidoptera. Satyridae	(Det. by K. W. Philip)
	Oenis melissa
	Erebia rossii
	Erebia fasciata

reaches densities of 250 m^{-2} in wetter habitats, while *Tipula carinifrons* larvae may number 100 m^{-2} in more mesic habitats. Their biomass at such densities may exceed 0.5 g dry weight in each case. The density of cranefly larvae was far lower in all habitats at Prudhoe Bay than in comparable habitats at Barrow (Table 2). The greatest density was achieved in the drained lake basin (plots 4 and 5); there, as in wet meadow habitats at Barrow, *Pedicia hannai* was the dominant species. The low density of cranefly larvae may explain the low breeding populations or absence of such shorebird species as the dunlin *(Calidris alpina)* and pectoral sandpiper *(C. melanotos)* (Norton et al., this volume) which prey heavily upon cranefly larvae at Barrow.

Table 2

Abundance of cranefly larvae (Diptera: Tipulidae) in Prudhoe Bay tundra in 1971 and 1972.

Plot	1971	1972	Major forms
1	9.8 m^{-2}	0	*Tipula*
2	2.0	10.0 m^{-2}	*Prionocera*
3	3.9	5.0	*Tipula, Pedicia*
4	17.6	40.2	*Pedicia*
5	27.4	39.1	*Pedicia*
6		22.3	*Pedicia*
7		3.4	*Tipula*

MacLean (1973) suggested that the high density of cranefly larvae at Barrow may be partly a result of the causal sequence:

low temperature → low productivity → prolonged life cycle → overlapping larval generations.

For example, larval development of *Pedicia hannai* at Barrow requires 4 or 5 years. If the warmer summer conditions at Prudhoe Bay allow individuals to shorten the life cycle, the result would be lower biomass at any one time in relation to population productivity. Thus, care must be taken in interpreting density and biomass values from different sites; however, even allowing for possible differences in life cycle length, it is clear that productivity of craneflies is less at Prudhoe Bay than at Barrow.

On 29 August 1972, a visit was made to Prudhoe Bay to collect samples to determine the abundance of microfauna (mite, Collembola, and enchytraeid worm). These groups consist of very small invertebrates which, because of their great abundance, collectively comprise the most important element of the soil fauna in many ecosystems. A limited sample processing capability prevented us from sampling all plots. We selected plots which appeared to span the range of moisture and vegetation features available at Prudhoe Bay. The results, shown in Table 3, are contrasted with results of similar sampling on nine study plots at Barrow.

Prudhoe Bay plot 1, a dry *Dryas integrifolia* heath, represents a habitat not found at Barrow; we might expect it to have greater faunal affinities with the *Dryas* fell-field alpine habitat at Eagle Summit in central Alaska. This plot contained an exceptionally high number of prostigmatid mites, but low numbers (in contrast to Barrow) of mesostigmatic and cryptostigmatid mites, and low numbers of the two major superfamilies of Collembola—the Entomobryidae and Poduridae—and of enchytraeid worms. At Barrow mites tend to increase in abundance in passing from wetter to drier plots, while Collembola and Enchytraeidae decline in abundance along such a moisture gradient. Thus, in general, the Prudhoe Bay plot 1 pattern was predictable on the basis of patterns seen at Barrow.

Prudhoe Bay plot 6 is the wettest plot sampled for all three major microfaunal groups. It has a very low abundance of both mites and Collembola, which seems to reflect the "polygon basin syndrome." There are other resemblances: *Carex aquatilis* is the only vascular plant species; there is very little, if any, moss or lichen cover; the top 10 or more cm consist of saturated sod with very high organic matter accumulation. The habitat represented by plot 6 differs from the typical Barrow polygon basins in its greater spatial extent and more robust but widely spaced shoots of *Carex aquatilis*. At Barrow the low invertebrate productivity in polygon basins is symptomatic of (and perhaps causally related to) a general reduction in the rate of ecosystem function relative to other tundra habitats. Primary productivity, microbial activity, and nearly all parameters that have been measured reach minimum values in such habitats. The existence of analogous, and perhaps homologous, habitats occupying greater area at Prudhoe Bay suggests that we may be addressing a general limiting feature of tundra ecosystem function.

Prudhoe Bay plot 7, a *Dryas*-graminiform mesic mixed heath, is closer to the Barrow dry meadows in gross appearance and in microfaunal composition. Prostigmatid mites are abundant; entomobryid Collembola and Enchytraeidae are rather low in abundance. It contained a surprising number of podurid Collembola—more than were found in eight of the nine Barrow plots.

In nearly all ecosystems that have been studied, the cryptostigmatid mites, especially

Table 3

Abundance of major invertebrate groups (number m^{-2}) at Barrow (seasonal mean) and Prudhoe Bay. Samples taken 29 August 1972.

	Barrow			Prudhoe Bay			
Group	Maximum	Minimum	Mean	Plot 1	Plot 6	Plot 7	Plots 4/5
Acarina							
Prostigmata	42,500	4,350	18,000	63,200	1,090	38,700	
Mesostigmata	7,080	603	3,260	1,090	109	3,710	
Cryptostigmata	38,900	1,600	20,000	11,900	5,790	4,040	
Total Acarina			41,300	76,200	7,000	46,500	
Collembola							
Entomobryidae	172,000	22,400	83,000	11,900	2,180	31,100	
Poduridae	33,200	1,150	8,110	3,820	436	21,400	
Sminthuridae	2,850	0	1,170	3,490	0	7,750	
Total Collembola			92,300	19,200	2,620	60,300	
Enchytraeidae	95,300	11,600	46,900	15,900	30,900	20,900	32,900

the Oribatei, are by far the predominant group of Acarina. At Barrow, however, Douce (1973) reports that the prostigmatid mites comprised 55% of the individuals and 16 of the 37 species found. Prudhoe Bay is even more extreme in the predominance of prostigmata; 79% of the mites on plots 1, 6, and 7 belonged to this group. This may be a general feature of tundra ecosystems: examination of data produced from other sites of the international Tundra Biome should allow resolution of this point.

The total number of Collembola on all Prudhoe Bay plots was lower than the Barrow mean. Thus, this system is not Collembola-dominated, as is the Barrow system. Differences in faunal composition occur within the Collembola. At Barrow the Entomobryidae comprise 90% of the total individuals; at Prudhoe Bay they comprise 55% of the total.

Sminthurid Collembola are rather uncommon at Barrow and somewhat more abundant at Prudhoe Bay, although they still do not form a numerically important part of the microfauna. Interestingly, they reach greatest abundance on wet plots at Barrow, but on the two dry plots at Prudhoe Bay. They are missing altogether from the polygon basin plot at Barrow, as they are from Prudhoe Bay plot 2. All of this suggests that there may be areas of wet tundra at Prudhoe Bay not suffering from the "polygon basin syndrome," in which sminthurid Collembola may reach even greater abundance.

Biomass was not measured directly at Prudhoe Bay. The numeric estimates of Table 3 were converted to biomass estimates using the mean dry weights per individual of 4 μg for Collembola, 5 μg for Acarina, and 20 μg for Enchytraeidae. The results are presented in Table 4. As at Barrow, the Enchytraeidae strongly dominate in all habitats sampled. Each of the Prudhoe Bay plots is well below the Barrow mean of 1,514 mg dry wt m^{-2}; however, Prudhoe Bay plot 6 corresponds precisely with the Barrow polygon basin which it otherwise resembles, and Prudhoe Bay plot 7, the *Dryas*-graminiform mesic heath, corresponds precisely with the Barrow raised polygon. Thus, when comparing similar habitats, the biomass of soil microivertebrates at Barrow and Prudhoe Bay is similar. However, the habitats sampled in this study represent a significant proportion of the Prudhoe Bay tundra, whereas comparable habitats at Barrow are limited in spatial extent. In other words, habitats low in invertebrate biomass are the rule at Prudhoe Bay, but the exception at Barrow. As a whole, Prudhoe Bay tundra supports a lower biomass of soil invertebrates than does Barrow tundra, in spite of the more temperate summer season climate and greater faunal and floral diversity found at Prudhoe Bay.

Table 4

Estimated biomass of major invertebrate groups (mg dry wt m^{-2}) at Prudhoe Bay, 29 August 1972.

Group	Plot 1	Plot 6	Plot 7	Plots 4/5
Acarina				
Prostigmata	316	5	194	
Mesostigmata	5	0.5	19	
Cryptostigmata	60	29	20	
Total Acarina	381	35	233	
Collembola				
Entomobryidae	48	9	124	
Poduridae	15	2	86	
Sminthuridae	14	0	31	
Total Collembola	77	11	241	
Enchytraeidae	636	1236	836	1316
TOTAL	1094	1282	1310	

The depth distribution of microfauna (Table 5) closely paralleled results found at Barrow. The majority of the fauna occurs close to the surface, which is most evident in the mites. All

Table 5

Depth distribution of soil microfauna (percent of total occurring in upper 2.5 cm of litter and soil).

Group	Plot 1	Plot 6	Plot 7	Plots 4/5
Acarina				
Prostigmata	93	30	93	
Mesostigmata	100	0	74	
Cryptostigmata	100	100	100	
Collembola				
Entomobryidae	83	100	87	
Poduridae	80	50	57	
Sminthuridae	100		82	
Enchytraeidae	87	87	61	82

specimens of cryptostigmatid mites occurred in the top 2.5 cm of the litter and soil. Unlike the north temperate regions, in the arctic soil animals cannot descend to escape the winter freeze. By remaining near the surface, they experience an earlier onset of activity in spring and warmer temperatures during the summer season.

3. **Phenology.** One of the striking features of tundra ecology is the synchronous emergence of adult insects (MacLean and Pitelka 1971; MacLean, in press). The peak of emergence at Barrow, particularly of the conspicuous Diptera, usually falls in the second week of July approximately one month after melt-off. We were interested in comparing emergence patterns at Prudhoe Bay where snow melt-off is generally earlier and summer temperatures warmer.

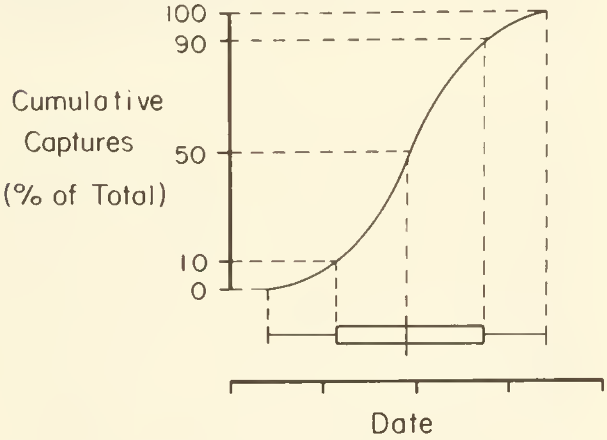


Fig. 1. *Derivation of the figure used to describe seasonal pattern of insect activity. Central line represents date of median capture; bar encloses central 80% of captures; total length of horizontal line indicates total period of capture. An open-ended line (see Fig. 3) indicates that the first (or last) capture occurred in the first (last) period sampled; a closed line, as shown here, indicates that at least one sample period with no captures preceded (or followed) the first (last) capture.*

The 2 years of observation at Prudhoe Bay yielded very different results. In 1971 melt-off was nearly complete when observations began in early June. The average of the daily mean air temperatures recorded at the BP-Mukluk based camp during the first week of June was 6.1° C. In 1972 melt-off was delayed by at least 10 days and occurred at approximately the same time as melt-off at Barrow. The average daily mean temperature for the first week of June 1972 was 0.5° C. Thus, invertebrate activity began much earlier in 1971. Air temperatures in the two seasons were then roughly comparable until late July, when 1971 was warmer than 1972. August 1972 was much warmer than August 1971, reversing the earlier trend; thus, temperature differences averaged out for the season.

All taxa examined showed a significant delay in emergence in 1972 relative to 1971 (Figs. 2-7). This delay approximately equals the difference in melt-off in the 2 years. This again demonstrates the unimportance of photo-related cues as a timing mechanism for arctic tundra invertebrates. Rather, it appears that emergence follows the completion of a certain amount of metabolic activity which begins at or soon after melt-off.

No consistent between-habitat differences are evident in the timing of emergence. In most cases, the dates of median capture of any taxon on all plots fell within a 5-day period. The synchrony of emergence is particularly evident in the Tipulidae, where 80% of the captures occurred within 10-day periods in both years (Fig. 2). Craneflies are important prey for breeding sandpipers, and the timing of sandpiper breeding activities has probably evolved so that the hatching of sandpiper young coincides with the appearance of their major prey. The synchronous nature of the emergence allows little room for error. The period of cranefly

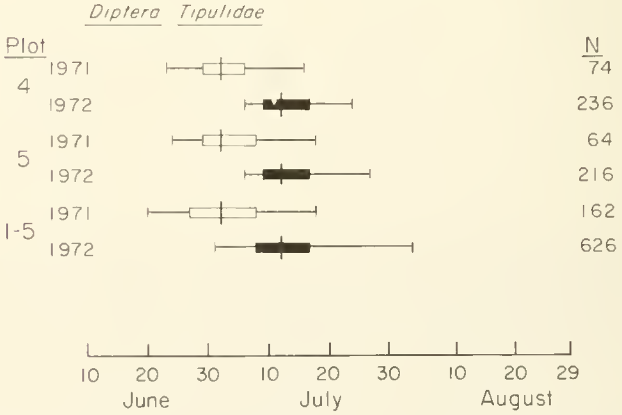


Fig. 2. *Seasonal distribution of "sticky-board" captures of adult craneflies (Diptera: Tipulidae) in 1971 and 1972.*

emergence, and thus the optimum period for sandpiper breeding, differed by 10 days between 1971 and 1972. Norton et al. (this volume) showed that avian breeding was delayed somewhat in 1972, thus preventing severe dissynchrony between predator and prey; however, it is possible that large, year-to-year differences in sandpiper breeding success relate to differences in the timing of cranefly and other insect emergence. The short summer season that characterizes arctic tundra makes timing or phenological relationships especially important; this may be one area in which the tundra is particularly sensitive to small disruptions.

The total number of captures in any plot provides an index of abundance that can be used for between-plot and between-year comparisons. The delayed melt-off and prolonged flooding of the lake basin (plots 4 and 5) in 1972 produced no major decline in insect abundance. In fact, Tipulidae and Dolichopodidae (Fig. 3) increased in abundance from 1971 to 1972. Only the parasitic Hymenoptera (Fig. 6) declined from 1971 to 1972, and this occurred on all plots.

Captures of leafhoppers (Cicadellidae) were concentrated on the drier plots (Fig. 7). On

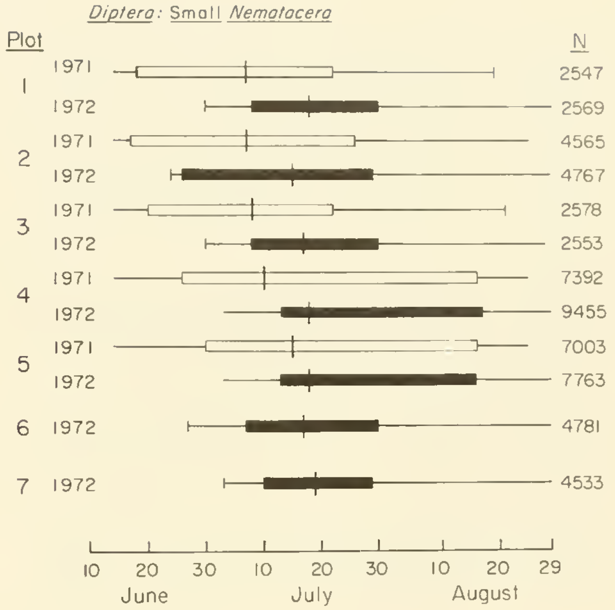


Fig. 4. *Seasonal distribution of "sticky-board" captures of other species of Diptera, suborder Nematocera in 1971 and 1972.*

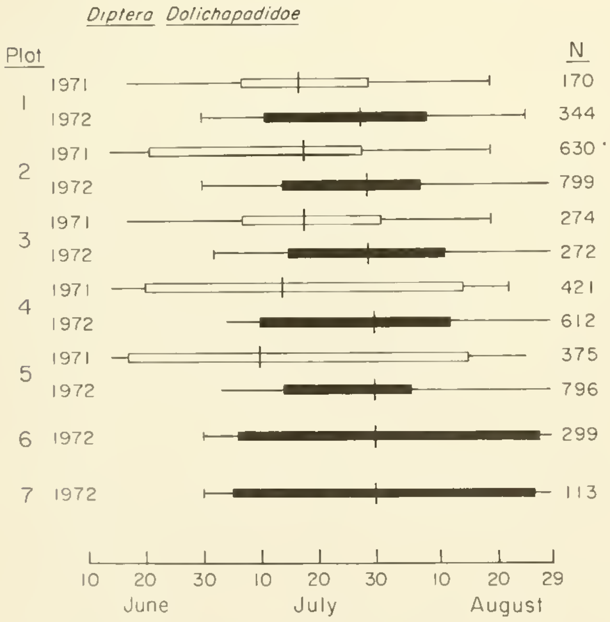


Fig. 3. *Seasonal distribution of "sticky-board" captures of long-legged flies (Diptera: Dolichopodidae) in 1971 and 1972.*

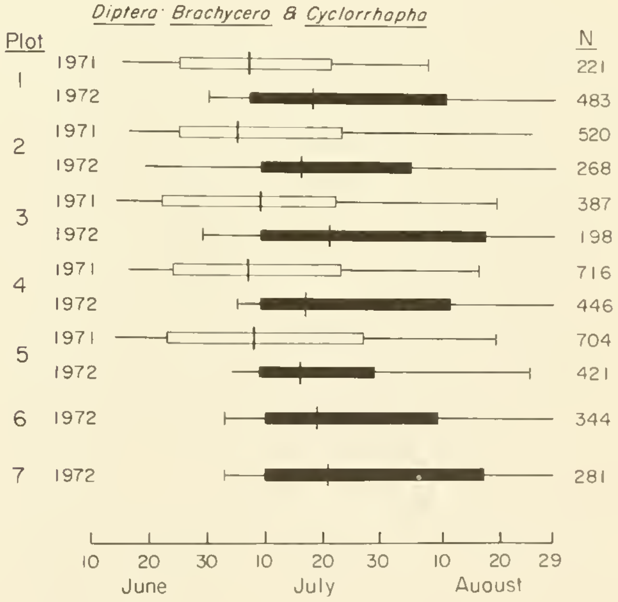


Fig. 5. *Seasonal distribution of "sticky-board" captures of "higher" flies (suborders Diptera, Brachycera and Cyclorrhapha) in 1971 and 1972.*

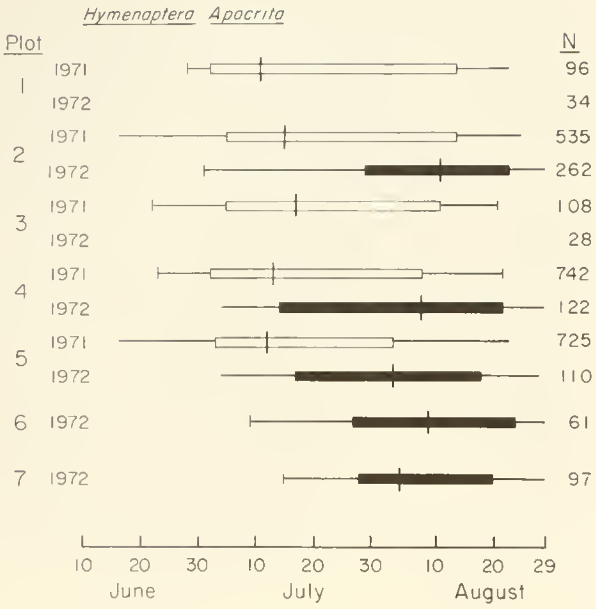


Fig. 6. *Seasonal distribution of "sticky-board" captures of "narrow-waisted" parasitic Hymenoptera (suborder Apocrita) in 1971 and 1972.*

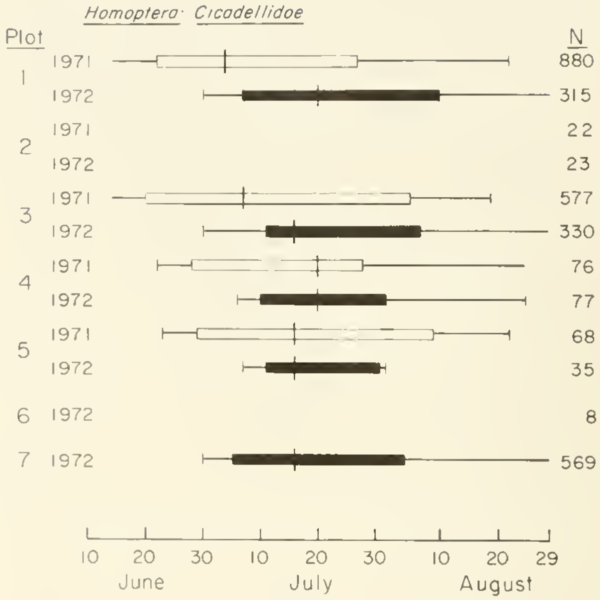


Fig. 7. *Seasonal distribution of "sticky-board" captures of leafhoppers (Homoptera: Cicadellidae) in 1971 and 1972.*

these plots they declined in abundance from 1971 to 1972. Leafhoppers have gradual (indirect, or hemimetabolic) development. Captures included adults and immatures (nymphs) at various stages of development; thus, the capture period is long. Year-to-year changes in number of captures may reflect differences in activity related to ambient temperature as much as actual differences in abundance.

Taking the insect fauna as a whole, the lake basin plots (4 and 5) seem to be the most productive. Only the leafhoppers show a preference for the drier plots (1, 3, and 7). Plots 4 and 5 tended to show a greater abundance of adult insects than the other wet plots, 2 and 6. This is strongly the case in the Tipulidae, and less so in other groups. It is interesting to note that Enchytraeidae, the only microfaunal group sampled in plots 4 and 5, were slightly more abundant there than elsewhere, but still well below the Barrow mean (Table 3). We conclude that, as at Barrow, wet plots support more invertebrate biomass than dry plots; however, biomass of the most favorable plots at Prudhoe Bay is well below biomass of the most favorable plots at Barrow.

General Conclusions

In general, results obtained at Prudhoe Bay support our more intensive observations at Barrow and reinforce their validity for northern Alaskan coastal tundra as a whole. It is interesting to note that the Prudhoe Bay tundra tends to be of lower productivity than Barrow tundra despite the longer and warmer growing season and greater floral and faunal diversity of Prudhoe Bay. Thus, we must conclude that the low productivity of tundra systems is not a direct and simple result of the severity of the climate. The distribution of individual species (as reflected in diversity), however, may be more directly influenced by climate. The link between ecosystem complexity (diversity) and function is clearly a complex one, and we must avoid simplistic statements relating diversity and productivity, stability, or other integrative ecosystem parameters.

Acknowledgments

The field work was performed with enthusiasm and diligence by Mark E. Deyrup in 1971 and Craig Hallingsworth in 1972. The micro-invertebrate sampling and identifications were the responsibility of G. Keith Douce (Acarina), Maggie E. Skeel (Collembola), and Edward A. Morgan (Enchytraeidae).

This project was primarily supported by the National Science Foundation grant GV-29342 to the University of Alaska, under the auspices of The U.S. Tundra Biome Program. Field logistics were provided through the Prudhoe Bay Environmental Subcommittee's support through the Tundra Biome Center.

References

Douce, G. K. (1973). The population dynamics and community analysis of the Acarina of the arctic coastal tundra. M.S. thesis. University of Georgia, Athens, 69 pp.

Hurd, Jr., P. D. (1957). Analysis of soil invertebrate samples from Barrow, Alaska. Final Project Report to A.I.N.A., 24 pp. mimeo.

MacLean, Jr., S. F. (1973). Life cycle and growth energetics of the arctic crane fly *(Pedicia hannai antenatta). Oikos,* 24(4):436-443.

_____(1975). Ecological adaptations of tundra invertebrates. Pages 269-300 *in* (J. Vernberg, ed.) Proc. E.S.A./A.I.B.S. Symp., Amherst, Mass. June, 1973. Intext Press, New York.

MacLean, Jr., S. F. and F. A. Pitelka. (1971). Seasonal patterns of abundance of tundra arthropods near Barrow. *Arctic*, 24:19-40.

Norton, D. W., I. W. Ailes, and J. A. Curatolo (This volume). Ecological relationships of the inland tundra avifauna near Prudhoe Bay, Alaska.

Webber, P. J. and D. A. Walker (This volume). Vegetation and landscape analysis at Prudhoe Bay, Alaska: A vegetation map of the Tundra Biome study area.

C.D. Evans, Arctic Environmental Information and Data Center, University of Alaska

Adult Black-bellied plover (Pluvialis squatarola), *a characteristic breeding bird of vegetation type 1 (Webber and Walker, this volume).*

Ecological Relationships of the Inland Tundra Avifauna near Prudhoe Bay, Alaska

DAVID W. NORTON*
Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska 99701

IRVIN W. AILES
Department of Wildlife and Fisheries
University of Alaska
Fairbanks, Alaska 99701

JAMES A. CURATOLO
Alaska Cooperative Wildlife Research Unit
University of Alaska
Fairbanks, Alaska 99701

Introduction

Two motivations prompted a quantitative study of terrestrial birds at Prudhoe Bay. The first was a basic comparison of abundance, species composition, diversity, phenology, and productivity at that site with similar observations at Point Barrow, Devon Island, and other northern sites where birds have been studied in relation to their resources. The second purpose was to examine generally the applied problems of tundra birds' coexistence with recent and projected oil and gas developments in arctic North America.

The nearest well-known avifauna is that of Point Barrow, some 320 km WNW of Prudhoe Bay. A series of behavioral, ecological, and energetic studies of various species has been under way since the early 1950s. Information generated by these studies has been enveloped by the U.S. Tundra Biome, resulting in an evaluation of the Barrow avifauna in the broad ecosystems context. We now know that the unique species composition and trophic dynamics there are the result of a largely saprovore-based food chain. That is, many of the terrestrial avian consumers depend on soil-dwelling, saprovorous arthropods, principally the dipteran families Tipulidae and Chironomidae (Holmes 1966; MacLean and Pitelka 1971; Norton 1973). Breeding shorebirds dominate the tundra in summer, as they seem especially capable of acquiring soil-dwelling larvae and surface-dwelling adult insects in quantities sufficient to support the high energy requirement of breeding in cold environments.

The factors making insectivory a feasible strategy for breeding birds at Barrow appear to be the unusual proportion of primary production entering the litter category susceptible to consumption by saprovores, the consequent high standing crops of larval saprovores, and the interdigitation of moist and dry tundra on a fine scale ("fine-grained mosaic" of MacLean 1969) that permits birds to select from radically different feeding habitats within short distances.

Prudhoe Bay tundra differs from that of Barrow, lacking the extreme variability of microrelief and moisture over short distances. Nevertheless, we expected an important saprovore-based trophic system favoring a shorebird-dominated avifauna at Prudhoe Bay.

---

*Current address: Outer Continental Shelf Project, University of Alaska, Fairbanks, Alaska 99701.

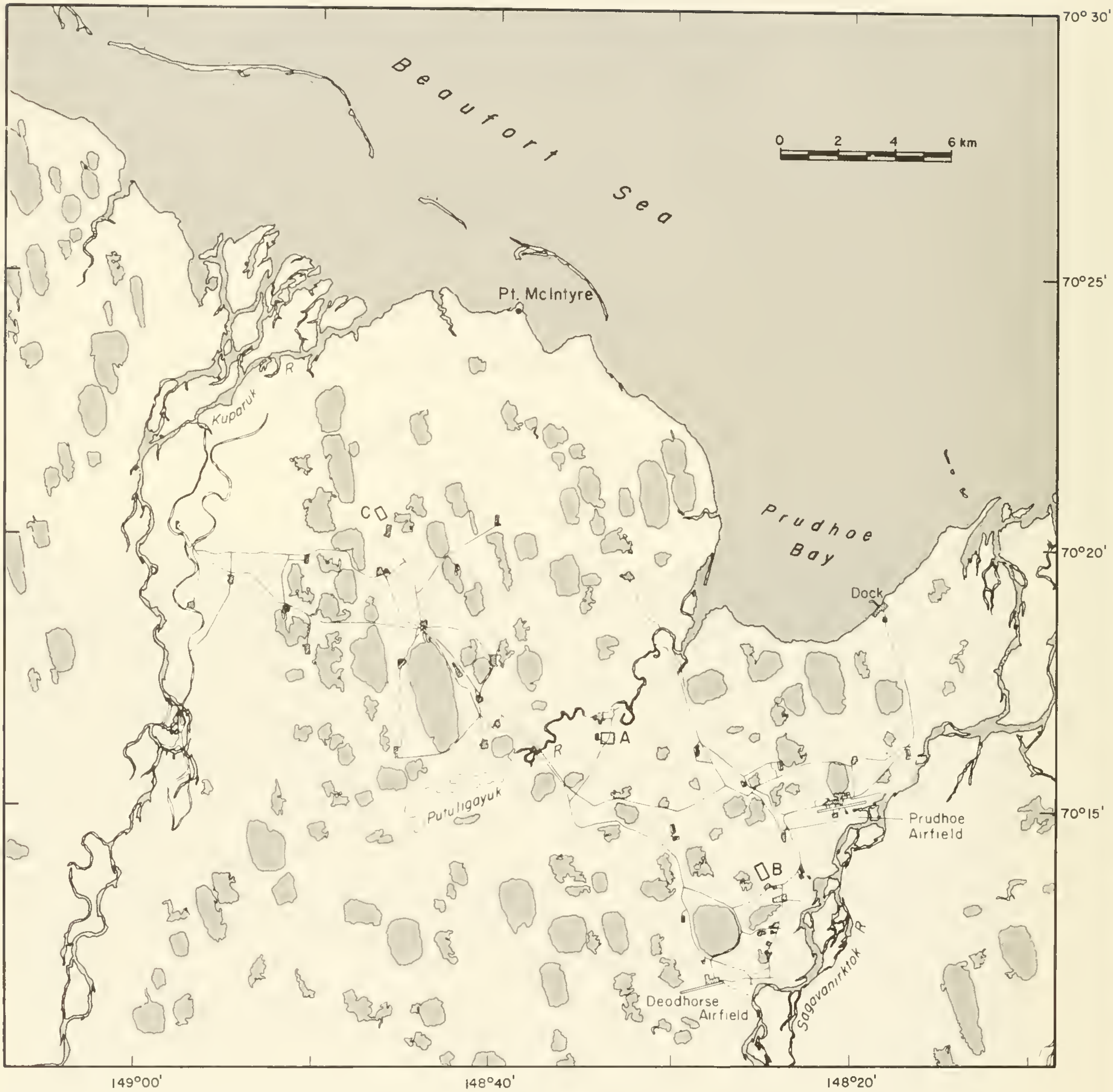


Fig. 1. *Avian census plots in the Prudhoe Bay Region, 1971, 1972.*

Actual or potential impacts of exploitation and transportation of arctic oil and gas on biological systems have gained a great deal of attention, but sufficient time and funding for serious, long-term scientific evaluation of these impacts have not been available. Consequences of such activity which may directly and negatively affect resident birds include noise disturbance; loss, destruction, or alteration of habitat, and spills of toxic materials. But these are obvious effects which could be offset with obvious countermeasures. One can argue that the extirpation of a few breeding species from a limited area may be unimportant. Historically, the less obvious effects of human activities have had far greater consequences for ecological systems. We therefore tried to identify any such systems effects as we encountered them in the course of this 2-year study. We viewed the small species with which we were dealing more as ecological indicators than as valuable resources in themselves. This approach is basically different from a resource management approach such as that of a waterfowl biologist, whose mandate is to protect and enhance productivity.

Methods

Visual census coverage of measured tracts, as developed for avifaunal studies at Point Barrow (Norton 1973), was used to evaluate the dynamics of bird populations using Prudhoe Bay tundra. Two census plots, A and B, each measuring 500x700 m (0.35 km^2), were erected and marked in 1971. A third plot, C, measuring 200x500 m (0.1 km^2), was erected in 1972 and deliberately located away from the lee, or west, side of nearby roads (Fig. 1).

Each plot was censused systematically by one to three observers who walked the grid and recorded locations of each bird encountered. The intervals between formal censusing (4-12 days depending on weather, level of activity, and estimated rates of change in populations present) were used in searching for nests, colorbanding adult and young birds trapped at their nests, and recording the progress of nests under observation. The proportion of birds, either unbanded or unaccounted for as nesting, theoretically should drop to near zero if the technique is successful.

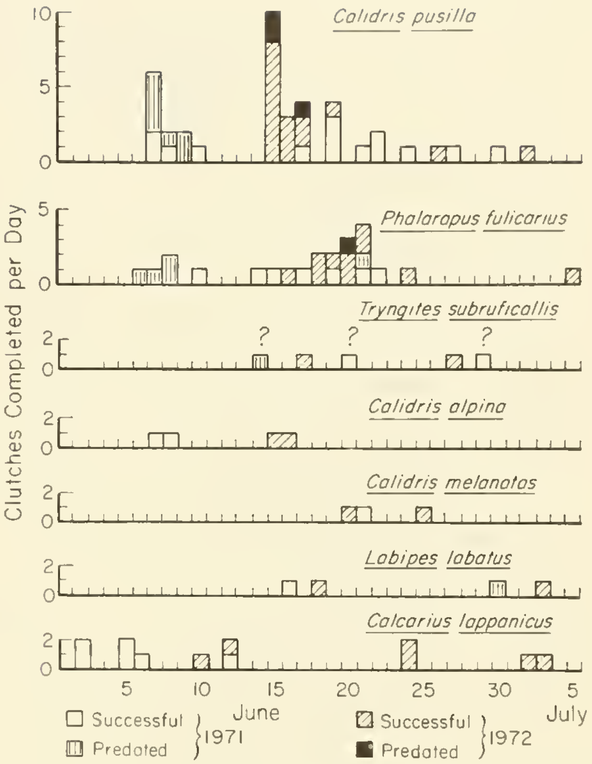


Fig. 2. *Breeding phenology measured by clutch completion dates for seven species at Prudhoe Bay, 1971, 1972.*

General observations outside the census plots also were made regularly over the wide area accessible by the road system. This study thus complements that of Gavin (1971), which deals primarily with waterfowl. Gavin lists 54 species observed in 1969 and 1970 over a much wider geographical area. However, his treatment of small terrestrial species was incomplete.

Results

Table 1 lists the 53 species of birds encountered during the two-season survey and distinguishes known breeding, suspected breeding, regularly and casually occurring species. Although we could certainly have expanded this list through attentive observation, particularly during the spring influx of species, we were preoccupied with the regularly occurring species that accounted for the major share of tundra resource use in this region.

Of 34 known or suspected breeding species in Table 1, only seven regularly used primarily terrestrial resources to support breeding within

Table 1

Species observed in the Prudhoe Bay region, 1971-72.

Gavia adamsii	Yellow-billed loon	C, SB
G. arctica pacifica	Arctic loon	KB
G. stellata	Red-throated loon	KB
Cygnus columbianus	Whistling swan	KB
Branta canadensis minima	Canada goose	KB
Branta nigricans	Black brant	KB
Anser albifrons frontalis	White-fronted goose	KB
Chen caerulescens caerulescens	Snow goose	KB
Anas platyrhynchos platyrhynchos	Mallard	C
Anas acuta	Pintail	KB
Anas americana	American wigeon	C
Anas clypeata	Shoveler	C
Aythya marila nearctica	Greater scaup	C
Clangula hyemalis	Oldsquaw	KB
Polysticta stelleri	Steller's eider	SB
Somateria mollissima v-nigra	Common eider	KB
Somateria spectabilis	King eider	KB
Somateria fischeri	Spectacled eider	KB
Melanitta perspicillata	Surf scoter	C
Mergus serrator serrator	Red-breasted merganser	C
Buteo lagopus sanctijohannis	Rough-legged hawk	C
Lagopus lagopus alascensis	Willow ptarmigan	KB
L. mutus nelsoni	Rock ptarmigan	KB
Grus canadensis canadensis	Sandhill crane	M
Charadrius semipalmatus	Semipalmated plover	SB
Pluvialis dominica dominica	American golden plover	M, SB
P. squatarola	Black-bellied plover	KB
Arenaria interpres (subsp)	Ruddy turnstone	M, SB
Capella gallinago delicata	Common snipe	C
Micropalama himantopus	Stilt sandpiper	M
Limnodromus scolopaceus	Long-billed dowitcher	M
Calidris alpina sakhalina	Dunlin	KB
C. pusilla	Semipalmated sandpiper	KB
C. bairdii	Baird's sandpiper	M, SB
C. mauri	Western sandpiper	C
C. melanotos	Pectoral sandpiper	KB
C. alba	Sanderling	M
Tryngites subruficollis	Buff-breasted sandpiper	KB
Phalaropus fulicarius	Red phalarope	KB
Lobipes lobatus	Northern phalarope	KB
Stercorarius pomarinus	Pomarine jaeger	SB
S. parasiticus	Parasitic jaeger	SB
S. longicaudus	Long-tailed jaeger	M
Larus hyperboreus barrovianus	Glaucous gull	KB
Xema sabini sabini	Sabine's gull	SB
Sterna paradisea	Arctic tern	SB
Nyctea scandiaca	Snowy owl	SB
Asio flammeus flammeus	Short-eared owl	SB
Corvus corax principalis	Common raven	M
Motacilla flava tschutschensis	Yellow wagtail	M
Acanthis (sp.)	Redpoll	SB
Calcarius lapponicus alascensis	Lapland longspur	KB
Plectrophenax nivalis nivalis	Snow bunting	KB

KB — Known breeding in Prudhoe region
SB — Suspected breeding
M — Regular movement or migration through region
C — Casual movement or migration through region

the census plots during this study. Shorebirds dominated this group (six of seven species) even more strikingly than is the case at Barrow (seven of 11 species—Norton 1973). The two seasons, 1971 and 1972, differed in weather: the first was comparatively mild with an early and regular snowmelt, whereas the second was cold with a delayed and prolonged snowmelt. This difference between seasons was reflected in delayed onset of nesting by most or all of the species, as indicated in Fig. 2.

Overall nesting success (eggs hatched/eggs laid) was universally higher in 1972 (Table 2). This improvement may be related to a reduction in local arctic fox *(Alopex lagopus)* populations during the winter of 1971-72 through a deliberate trapping program conducted around Prudhoe Bay (W. Hanson, pers. comm.) to remove nuisance animals attracted to refuse disposal areas. Foxes were observed more frequently on the plots in 1971 and were strongly suspected to be the major (if not sole) agents of nest predation that year.

Nesting densities of Prudhoe Bay birds were lower than those of their ecological counterparts at Barrow (Table 3), with the exception of the semipalmated sandpiper *(Calidris pusilla)* and red phalarope *(Phalaropus fulicarius)*. It is very difficult, however, to circumscribe the appropriate species as being ecologically equivalent in the two localities. Although the nine species listed in Table 3 are the major insectivores (and granivores) in each region, there are additional insectivorous species in the Barrow system, such as the ruddy turnstone *(Arenaria interpres)*; golden plover *(Pluvialis dominica)*, and non-nesting long-tailed jaegers *(Stercorarius longicaudus)*. These three species are omitted from Table 3 because of their absence as significant elements at Prudhoe in 1971 or 1972. Their inclusion in this analysis would demonstrate more clearly the greater use of tundra arthropod resources by birds in the Barrow area. Data in Norton's (1973) bioenergetic studies of Barrow shorebirds may be used to estimate that insectivorous species there ingest some 4×10^5 kcal km^{-2} yr^{-1} from the tundra arthropod resources. The same estimation procedure for Prudhoe Bay would probably put energy ingested by comparable members of the community at somewhat less than 75% of the Barrow system, or about 3×10^5 kcal km^{-2} yr^{-1} in 1971 and 1972.

Various inter- and intra-plot comparisons of census information may be used to discern the spatial and temporal patterns of resource use by Prudhoe Bay birds. For example, Plots A and B became snow-free early and approximately simultaneously each year, and bird counts dropped to less than 10% of peak abundance by late July on each plot. By contrast, Plot C was slower by 7-10 days to become snow-free in 1972. Its bird populations remained at 20-25% of peak numbers until the end of July. This situation is parallel to that found in different plots at Barrow (Norton 1973, p. 21). Late season resource use seems to be concentrated on areas unavailable earlier in the season. Another way to demonstrate this assertion is to break down census information from Plot B by individual rows within the plot (Figs. 3a, 3b, 4).

Table 2

Nesting densities (nests km^{-2}) and hatching success (eggs hatched/eggs laid) by species and year at Prudhoe Bay.

	Year 1971		Year 1972	
Species	Density (nests km^{-2})	Success	Density (nests km^{-2})	Success
C. pusilla	37.1	0.52	42.4	0.84
P. fulicarius	37.1	0.31	22.2	0.83
T. subruficollis	2.8	0.0	5.7	1.0
C. alpina	4.3	0.0	5.0	1.0
C. melanotos	5.7	0.33	5.7	1.0
L. lobatus	4.3	0.33	5.7	1.0
C. lapponicus	8.6	0.47	6.7	0.73
Overall	99.9	0.38	93.4	0.86

Table 3

Nesting densities and success compared between similar avifaunal components at Prudhoe Bay and Barrow.

Species	PRUDHOE BAY Density (nests km^{-2})	Success	BARROW Density (nests km^{-2})	Success
C. alpina	4.6	0.5	13.9	0.72
C. pusilla	39.8	0.68	9.8	0.73
C. bairdii	–	–	24.8	0.39
C. melanotos	5.7	0.67	13.6	0.69[1]
T. subruficollis	4.3	0.50	–	–
P. fulicarius	29.7	0.57	[26.4	0.50] [2]
L. lobatus	5.0	0.67	–	–
C. lapponicus	7.7	0.60	[30.0	0.63] [3]
P. nivalis	–	–	[15.0	0.80] [4]
Overall	96.7	0.62	[133.5	0.65]

[1] *Calidris* species data based on Norton (1973).

[2] Phalarope data from 1971 at Barrow only–preliminary.

[3] Longspur information from T. W. Custer (pers. comm.).

[4] Snow bunting data from 1971 IBP census plot only–incomplete.

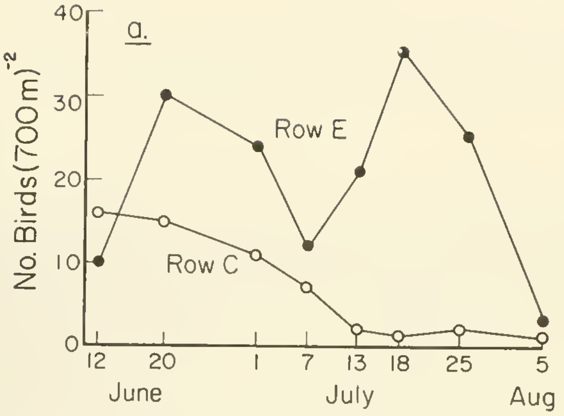
Row E represents the interface between terrestrial and aquatic systems that was partially underwater until about 20 June 1971, and until 1 July 1972. By those dates, most nesting birds were in late stages of commitment to territories on the western and central rows of Plot B. As soon as the sizeable lake east of Plot B was partially drained, heavy use of the formerly submerged land began. Shorebirds with broods of young could be found abundantly in Row E and eastward thereafter. In summary, tundra birds appear to move seasonally through a series of habitats that are successively later to emerge from either snow or water.

Recaptures of semipalmated sandpipers banded in 1971 have confirmed findings by U. N. Safriel (1971, pers. comm.) on the mating system of this species. Fig. 4 shows the recapture histories of the 14 *pusilla* that returned in 1972. All 14 returning birds nested successfully in 1971, although three of them only did so by renesting following predation of their first 1971 nest. In three cases, both banded members of pairs returned, and the 1972 nests of these six birds were all less than 100 m from the 1971 nest. Only one known case of remating occurred between the two seasons. No young of 1971 returned as breeding adults in 1972. The semipalmated sandpipers at Prudhoe Bay therefore are similar to those breeding at Barrow—monogamous, site-tenacious, and mate-faithful. They are especially faithful to mates and territory following reproductive success in the previous season. Young birds do not breed until at least their second year.

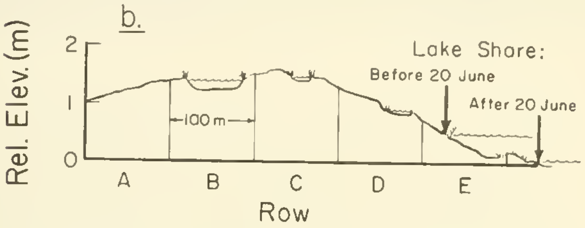
No Lapland longspurs *(Calcarius lapponicus)* or snow buntings *(Plectrophenax nivalis)* banded in 1971 returned to Prudhoe Bay plots in 1972, but this may be explained by the small sample size. Banding of male red phalaropes and female pectoral sandpipers *(Calidris melanotos)* in 1971 and an absence of returning birds in 1972 indicates that these species at Prudhoe, as at Barrow, display no site-tenacity.

Discussion

Tundra resource use by terrestrial birds at Prudhoe Bay is essentially similar in pattern to that of Barrow birds despite difference in species composition, density, and reproductive success. Information from this study places Prudhoe Bay on a continuum of sorts, relating to terrestrial



a. Numbers of birds counted (all species) by date and row of census plot.



b. Schematic cross section of Plot B, showing approximate elevation above lowest point on the east margin of the plot.

Fig. 3. *Spatial and temporal patterns of avian abundance, Plot B, Prudhoe Bay, 1971.*

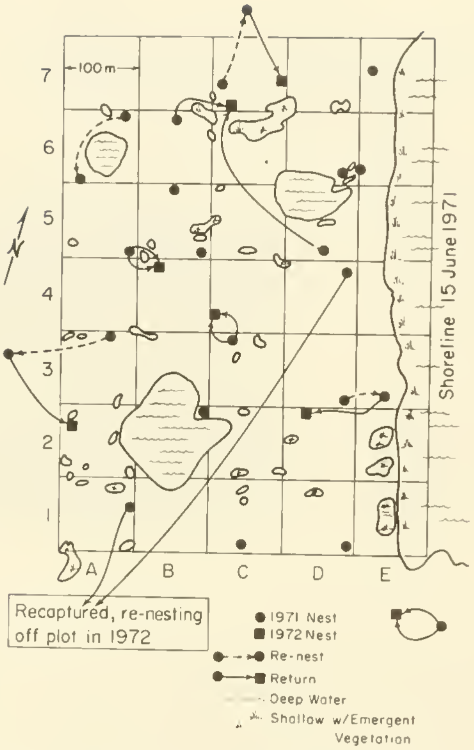


Fig. 4. *Schematic recapture histories of Semipalmated sandpipers from 1971 nests on Plot B, showing site-tenacity and mate-faithfulness.*

productivity and species diversity of sites at different latitudes and dominated by various physical factors. At one end of this continuum are the preliminary results of Pattie (1972) from Devon Island in the Canadian arctic. The other end of the continuum would presumably lie in tropical rain forests. Table 4 summarizes population estimates and such energy flux estimates as exist from nine northern community types for approximately ecologically equivalent components of the avifauna (insectivores and granivores), as discussed in this study. Farther south, species diversity, the relative importance of passerines, total avian biomass, and energy flux through avian populations may be expected to increase. Holmes and Sturges (1973), for example, estimated that a minimum of 5×10^6 kcal km^{-2} yr^{-1} was ingested by temperate forest birds at Hubbard Brook, N. H. The pieces of this global picture will probably continue to come into sharper focus with the present emphasis on measuring productivity at many sites.

All breeding birds at Devon Island, Barrow, and Prudhoe Bay are subjected periodically to widespread reproductive failure because of predation and probably physical factors. In the case of nest predation at Prudhoe Bay in 1971, it is likely that human activities were at the base of a chain of events leading from garbage disposal through attraction of foxes and abnormally heavy predation pressure by them to avian reproductive failure. Garbage disposal is a critical problem for industrial development in Alaska, as elsewhere. Improper disposal, leading to unnatural attraction of potentially nuisance or noxious species, is a quick, sure, and subtle modifier of ecosystem function, especially where the volume of garbage is great.

Another form of human impact on systems function has arisen from ground transportation developments in the Prudhoe Bay region. Raised roadbeds alter the accumulation of wind-driven snow and may significantly impound water during spring runoff. Downwind fallout of dust and

Table 4

Partial compilation of species diversity, population densities, and energy flux through northern avian communities.

Site	No. Lat. (°)	Habitat	Total spp.	Proportion passerines	Pr. or nests km^{-2}	Ingested E km^{-2}	Source
Devon Island (Canada)	76	tundra	3	0.33	2 (?)	6x10^4 kcal	Pattie (1972)
Barrow (USA)	71	tundra	9	0.22	134	4x10^5 kcal	Norton (1973)
Prudhoe Bay (USA)	70	tundra	7	0.14	97	3x10^5 kcal	This study
Cape Thompson (USA)	68	tundra	5	0.20	160	–	Williamson et al. (1966: Table 10)
Fairbanks A (USA)	65	taiga	22	0.91	133	5x10^6 kcal	West & DeWolfe (1974)
Fairbanks B (USA)	65	bog-taiga	10	1.0	53	1.8x10^6 kcal	West & DeWolfe (1974)
Great Slave Lake (Canada)	62	taiga	12-15	0.74	180-428	–	Carbyn (1971)
Vaksvik I (Norway)	62	subalpine	[18] *	?	380	–	Ytreberg (1972)
Vaksvik II (Norway)	62	subalpine	[12] *	?	91	–	Ytreberg (1972)

[ ] * passerines only.

gravel from winter traffic changes the reflectance of the snow cover, leading to altered rates of melting and sublimation of snow in the spring. We have not been able to quantify such effects, nor to identify alarming results on local avian ecology *per se*. The clear movements of individual birds from early- to late-emerging habitats (Fig. 4), however, suggest that spatio-temporal patterns of abundance and resource use will be altered by such structures on the arctic coastal plain. Furthermore, these may be only the first, few, short-term results of many subtle and longer-term changes in local biotic systems.

Acknowledgments

This study was largely supported by the National Science Foundation grant to the University of Alaska under the Tundra Biome Program. Field logistics were provided through the Prudhoe Bay Environmental Subcommittee's support through the Tundra Biome Center.

References

Carbyn, L. N. (1971). Densities and biomass relationships of birds nesting in boreal forest habitats. *Arctic*, 24:54-61.

Gavin, A. (1971). Ecological survey of Alaska's north slope, summer 1969 and 1970. Unpubl. brochure, Atlantic Richfield Co. 13 pp.

Holmes, R. T. (1966). Feeding ecology of the red-backed sandpiper *(Calidris alpina)* in arctic Alaska. *Ecology*, 47:32-45.

Holmes, R. T. and F. W. Sturges. (1973). Annual energy expenditure by the avifauna of a northern hardwoods ecosystem. *Oikos*, 24:23-28.

MacLean, S. F., Jr. (1969). Ecological determinants of species diversity of Arctic sandpipers near Barrow, Alaska. Ph.D. dissertation, University of California, Berkeley, 194 pp.

MacLean, S. F., Jr. and F. A. Pitelka. (1971). Seasonal patterns of abundance of tundra arthropods near Barrow, Alaska. *Arctic*, 24:19-40.

Norton, D. W. (1973). Ecological energetics of calidridine sandpipers breeding in northern Alaska. Ph.D. dissertation. University of Alaska, Fairbanks, 163 pp.

Pattie, D. L. (1972). Preliminary bioenergetic and population level studies in high arctic birds. Pages 281-292 *in* Devon Island I.B.P. project, high Arctic ecosystem (L. C. Bliss, ed.).

Safriel, U. N. (1971). Population study of the semipalmated sandpiper, *Calidris pusilla*. Page 35 *in* 1971 AAAS Mtgs. Proc. 22nd Alaska Sci. Conf.

Webber, P. J. and D. A. Walker (This volume). Vegetation and landscape analysis at Prudhoe Bay, Alaska: A vegetation map of the Tundra Biome study area.

West, G. C. and B. B. DeWolfe (1974). Populations and energetics of taiga birds near Fairbanks, Alaska. *Auk,* 91:757-775.

Williamson, F. S. L., M. C. Thomson, and J. Q. Hinds (1966). Avifaunal investigations. Pages 437-480 *in* Environment of the Cape Thompson region, Alaska, Wilimovsky and Wolf, eds.) U. S. A.E.C., Oak Ridge, Tenn.

Ytreberg, N. J. (1972). The stationary passerine bird populations in the breeding season, 1968-1970, on two mountain forest habitats on the west coast of southern Norway. *Norw. J. Zool.*, 20:61-89.

Brown lemming [Lemmus Sibericus (=trimucronatus)] *at edge of snow patch.*

Dr. John Koranda, Lawrence Radiation Laboratory

Population Studies of Lemmings in the Coastal Tundra of Prudhoe Bay, Alaska

DALE D. FEIST
Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska 99701

Introduction

Previous studies of microtine rodents on the arctic coastal tundra at Barrow have demonstrated marked fluctuations of lemming populations and considerable impact of high numbers of lemmings on local habitat (Pitelka 1957, 1973). However, the importance of microtine rodents in the total flow of energy and nutrients in the tundra ecosystem remains to be evaluated (Batzli, in press). Furthermore, it is not clear whether we can generalize from the limited studies at Barrow as to the species and numbers of microtine rodents and their importance in the tundra ecosystem at other sites along the arctic coast of Alaska.

The present studies of lemming populations were initiated on the arctic coastal tundra near Prudhoe Bay in the summer of 1971 to provide comparative data in conjunction with other investigations of the tundra ecosystem conducted by the U. S. IBP Tundra Biome Program. The initial objectives were to assess: (1) the productivity of microtine rodent populations; and (2) the effect of microtine rodent populations on the net primary production. The Prudhoe Bay area was of interest both for basic studies of coastal tundra and for the potential impact of local human activities (exploration and extraction of oil) on the tundra ecosystem.

Materials and Methods

Study area

The general area of arctic coastal plain near Prudhoe Bay selected for studies by the U. S. IBP Tundra Biome Program lies at about 75° 15′N latitude and is bounded on the west by the Kuparuk River and on the east by the Sagavanirktok River (Fig. 1). Much of the land surface consists of ponds and shallow lakes. The terrestrial habitat has limited relief and is dominated by drained lake basins with varying degrees of polygonization. The summer climate is notably warmer than that of Barrow; rapid snowmelt generally occurs in early June, and mean summer air temperatures are +2.6, +6.4, and +4.8°C in June, July, and August, respectively (Brown et al., this volume). The vegetation is typical of the arctic coastal plain and has been described in detail by several investigators (Neiland and Hok, this volume; Webber and Walker, this volume).

During the summer the area serves as a breeding ground or temporary stopping place for as many as 53 different avian species, mostly shore birds and waterfowl (Norton et al., this volume). Several species of jaegers (*Stercorarius* sp.), the snowy owl *(Nyctea scandiaca)*, and the short-eared owl *(Asio flammeus)* may act as predators on microtine rodents.

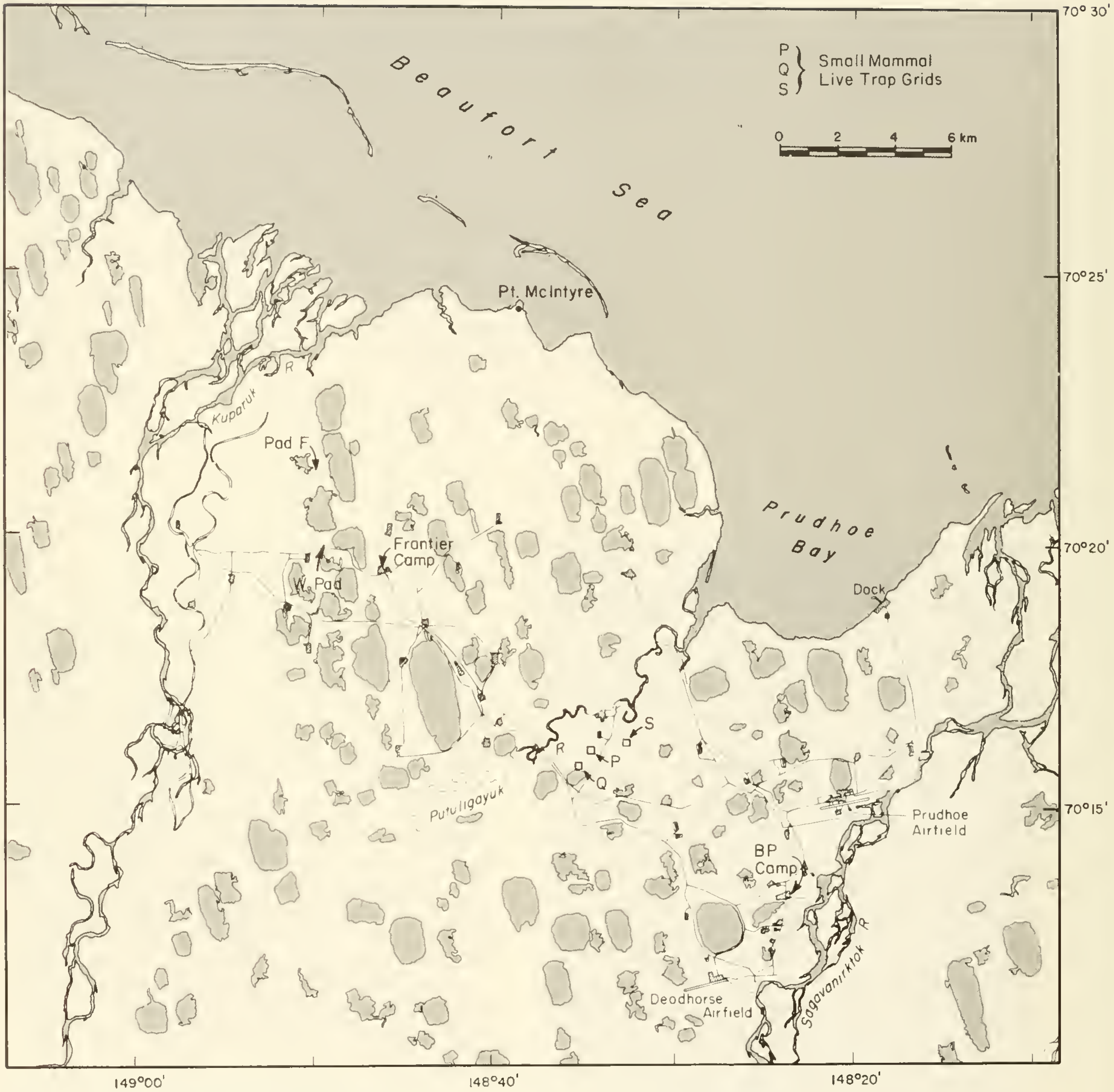


Fig. 1. *Small mammal trapping sites within the Prudhoe Bay area designated for U. S. IBP Tundra Biome studies.*

In addition to microtine rodents, arctic ground squirrels *(Citellus undulatus)* reside in the area. Arctic fox *(Alopex lagopus)* roam as predators of these small mammals (Underwood, this volume). Populations of caribou *(Rangifer tarandus granti)* graze the area during the summer (White et al., this volume). About a dozen other species of mammals, including the grizzly bear *(Ursus horribilis)* and wolf *(Canis lupus)*, have been occasionally reported in the general vicinity of Prudhoe Bay (Bee and Hall 1956).

Live trapping: Capture-mark-recapture

To assess numbers and demographic features of the microtine rodent populations, live trapping grids for small mammals were established in early June 1971 at locations shown in Fig. 1. The primary study areas were near the intensive IBP sites on the west side of the road leading NE to the Putuligayuk River. Live trap grid P was set at about 70°16'N, 148°34'W in a habitat with low relief polygons and tussocks. Live trap grid Q was set about 1 km SW of grid P in a flatter habitat of low relief tussocks. In June 1972 a third live trap grid S was established across the road (1 km NE of grid P) on a low pingo and the surrounding, very low relief tussocks.

The live trapping, mark, and recapture approach was similar at all locations. Live trapping grids consisted of 100 trap stations (10 rows x10 rows) at 5 to 6 m intervals (total area = 0.25 ha). One large, Sherman live trap and a nest can with cotton bedding and oats was placed at each station. During each trapping period of 2 to 5 days, traps were checked in the morning and afternoon. In some instances traps were checked more frequently (as often as every 4 hours) to reduce or eliminate trap mortality. Traps were locked open during the interval of 2 or 4 weeks between trapping periods. At first capture in each period, animals were tagged on the right ear with a fingerling tag, weighed with a Pesola spring scale, and examined for reproductive status before release at the site of capture. Females with a perforate vagina or vaginal plug, open pubic symphysis, and/or enlarged teats (nipple more than 1 mm in diameter) were considered in breeding conditions, as were males with scrotal testes (Krebs 1964; Batzli and Pitelka 1971). Trapping usually was continued in a period until all tagged animals were recaptured.

Temporary live and snap trapping

In addition to maintaining these permanent live trap grids, attempts were made to capture microtine rodents at other locations by temporary snap trapping and live trapping. In June 1971, snap trapping grids were set out at two sites: (1) on the area later established as live trap grid S; and (2) across the main road from the intensive sites to the SW of the live trap grids. These snap trap grids consisted of 100 stations (10 rows x 10 rows) at 10 m intervals with two Victor-type snap mousetraps per station. The closed traps were prebaited with peanut butter 3 days prior to trapping. They were checked at least twice per day for 5 days during the trapping period. These same two sites were trapped again in August 1971, but with temporary live traplines consisting of two parallel rows of 25 stations at 5 m intervals and one large Sherman live trap per station. Rows were about 25 m apart, and traps were checked twice per day for 5 days. In July 1971 two new areas about 10 km NW of the Putuligayuk River, just NE of Frontier Camp and just N of Western Pad, were explored and trapped with the same type of temporary live traplines. In August 1972 attempts were made to capture lemmings near pad F with temporary live traps.

Estimates of density

Estimates of density were calculated from the number of animals captured during a trapping period and the effective trapping area. The effective trapping area was calculated for each "sex-age" group of lemmings by adding a boundary strip around the actual 0.25 ha grid area. The size of the boundary strip was based on previous studies of collared lemming *(Dicrostonyx groenlandicus)* movements and range by Brooks and Banks (1971). It was assumed, but remains to be confirmed, that the range lengths found for different sexes and ages of collared lemming at Churchill, Man., Canada (Brooks and Banks 1971) apply to the lemmings at Prudhoe Bay as well. Thus, for each "sex-age" group a boundary strip of approximately half the average range length was added to the original grid size to give the effective trapping areas shown under Table 3.

Table 1

Numbers* of collared lemmings on three grid areas near Prudhoe Bay during the summers of 1971 and 1972.

		June 1971	July 1971	Aug. 1971	mid-June (19-23) 1972	early July (5-9) 1972	late July (24-31) 1972	mid-Aug. (21-25) 1972
						Numbers		
Grid P								
Male:	< 25g**				2	1	0	
	25-50g				1	4	1	
	> 50g				2	0	0	
Female:	< 25g				1	0	0	
	26-50g				2	2	0	
	> 50g				0	0	1p	
TOTAL		0	0	0+	8	7	2	0
(New)					(8)	(5)	(1)	
Grid Q								
Male:	< 25g	0			0	0	2	
	25-50g	1			2	3	1	
	> 50g	0			0	0	0	
Female:	< 25g	0			0	0	0	
	25-50g	1			3	1	1	
	> 50g	0			0	1p	0	
TOTAL		2	0	0	5	5	4	0
(New)		(2)			(5)	(3)	(3)	
Grid S								
Male:	< 25g				0		1	0
	25-50g				0		0	1
	> 50g				0		0	0
Female:	< 25g				0		0	0
	25-50g				0		0	0
	> 50g				1p		1p	0
TOTAL		0	0	0	1	0	2	1
(New)					(1)		(2)	(1)

*Numbers given represent estimated minimum numbers present 0.25 ha^{-1} grid area at each time, based on numbers captured.

**Each sex has been grouped into three weight classes which are assumed to approximate the age classes of juvenile (< 25g), subadult (25-50g), and adult (> 50g).

p = pregnant.

+In late August two arctic ground squirrels *(Citellus undulatus)* were captured in grid P.

Analyses of predator scats and pellets

To help determine what species of microtine rodents inhabit the Prudhoe Bay area, owl pellets, jaeger pellets, and fox scats were collected during the summer of 1971. About 80% of the 224 fox scats came from outside a den about 200 m NW of live trap grid Q. The remainder of scats and the 11 pellets were from other locations away from the live trap grids. The scats and pellets were teased apart, and the skeletal remains of prey were identified by species when possible (Bee and Hall 1956; Burt and Grossenheider 1964).

Results

Numbers, biomass, density

As shown in Table 1, only two lemmings were captured during the entire summer of 1971. During the first trapping period in June, two collared lemmings were captured, marked, and recaptured on grid Q. Although fresh fecal droppings were found around and in some of the traps in June and July, no other lemmings or other microtines were captured during the remainder of the summer on either grid. In late August, two arctic ground squirrels were captured on grid P. No animals were captured on any of the temporary live trapping or snap trapping sites during the summer of 1971.

In June 1972 an increased activity of microtine rodents over the previous summer was apparent from the fresh signs of burrows and fecal pellets. Observations over a wide area of Prudhoe Bay road system suggested a low to moderate level of activity and a very patchy distribution. Live trapping revealed a definite increase in numbers of collared lemmings in June 1972 [5-8$(0.25 \text{ ha})^{-1}$ grid area] over the level in June 1971 [0-2$(0.25 \text{ ha})^{-1}$ grid area] (Table 1). The presence of three juveniles of 12-14 g on grid P indicated that breeding had begun before the snowmelt. Although subadults and adults of both sexes remained in breeding condition with adult females pregnant through late July, the numbers captured declined from 5-7$(0.25 \text{ ha})^{-1}$ grid area in early July (Table 1) to 0-1$(0.25 \text{ ha})^{-1}$ grid area by late August. Biomass of live lemmings captured on each grid is shown in Table 2 and simply follows the trend in numbers captured through the summer of 1972.

Density estimates of collared lemmings based on the number captured and the assumed range of movements (Brooks and Banks 1971) are shown in Table 3. Densities were generally higher on grids P and Q and reached maximums of 10.2 and 6.6 lemmings ha^{-1} respectively, in July.

Lemming species in predator scats and pellets

Although there were many pieces of unidentifiable microtine remains in the predator scats and pellets (about 50%), of the total 16% were identified as collared lemming, 13% as brown lemming [*Lemmus sibericus (=trimucronatus)*] and 25% unidentified bird remains. *Microtus oeconomus* (tundra vole) could not be positively identified in these samples, although it had been previously found by MacLean (pers. comm.) in raptor pellets.

Discussion

Species composition and numbers

The results suggest that at Prudhoe Bay, in contrast to Barrow, the collared lemming may be more abundant than the brown lemming and that the lemming populations at Prudhoe Bay may never reach the magnitude seen at Barrow. Examination of the tundra for fresh signs of microtine rodent activity by S. MacLean in July 1970 (pers. comm.) and P. Whitney (pers. comm.) in September 1970, revealed little evidence of small mammal activity. In early September 1970, Whitney (pers. comm.) established two live trapping grids near the sites of grids P and Q in the present study, but captured no microtines during 2 days of trapping. Thus, it appears that the lemming populations were quite low in 1970, remained low in 1971, and reached trappable numbers as high as 8 collared lemmings $(0.25 \text{ ha})^{-1}$ grid area, or a maximum density of about 7-10 lemmings ha^{-1} during the summer of 1972.

One or two isolated instances of hand capturing of brown lemmings were reported in bird censusing areas in 1971 (I. Ailes, pers. comm.) and 1972 (J. Curatolo, pers. comm.). In addition, brown lemmings were identified as a prey item in the diet of the arctic fox in 1971-72. However, the amount of lemming prey sign was considered sparse at Prudhoe Bay fox den sites compared to sign at den sites in other areas of the Alaskan North Slope (Underwood 1974). In spite of evidence for the presence of brown

Table 2

Biomass[*] (grams) of collared lemmings on three grid areas near Prudhoe Bay during the summers of 1971 and 1972.

	June 1971	July 1971	Aug. 1971	mid-June 1972	early July 1972	late July 1972	mid-Aug. 1972
Grid P							
Biomass:							
Male				194(5)[+]	155(5)	32(1)	
Female				84(3)	95(2)	70(1)	
TOTAL	0	0	0	278	250	102	0
Grid Q							
Biomass:							
Male	31(1)			62(2)	108(3)	60(3)	
Female	36(1)			103(3)	100(3)	48(1)	
TOTAL	67	0	0	165	208	108	0
Grid S							
Biomass:							
Male				0		15	32(1)
Female				80(1)		62(1)	0
TOTAL	0	0	0	80	0	77	32

[*] Live weight biomass of lemmings captured on the 0.25 ha grid area.

[+] Numbers in parentheses are the number of lemmings for each biomass value.

lemmings, this species was never seen or captured in the present study.

Maximal densities reported for lemmings in tundra habitats at Barrow have been 1-30 ha^{-1} for *Dicrostonyx groenlandicus* (Batzli, in press) and 75-200 ha^{-1} for *Lemmus sibericus* (Schultz 1969; Maher 1970). In contrast to the predominance of *Dicrostonyx* found at Prudhoe Bay in 1971-72, the numbers of *Lemmus* generally have exceeded those of *Dicrostonyx* at Barrow and the brown lemming is considered the only grazer of significance in the grass-sedge tundra of the Barrow region (Pitelka 1973). Pitelka (1973) has suggested that the higher densities of *Dicrostonyx* may be reached only occasionally (every 20 years) at some locations.

Maximal densities of *Dicrostonyx* estimated at tundra sites in Canada range from 2-3 ha^{-1} at Devon Island, N.W.T. (Speller 1972), to 25 ha^{-1} at Baker Lake, N.W.T., (Krebs 1964) and southern Hudson Bay (Brooks 1970), to 35-40 ha^{-1}, also in southern Hudson Bay (Shelford 1943).

Factors which may limit lemming distribution and abundance

Bee and Hall (1956) have suggested that on the Arctic Slope of Alaska fluctuation in the population of collared lemmings seems to occur less often and to be of lesser degree than in the brown lemming. The microtine rodent population levels found in 1971-72 at Prudhoe Bay may indicate that populations of these small herbivores have always been low (relative to Barrow). The possibility that the low numbers in 1971-72 may reflect a trough (or fluctuation) in a lemming cycle cannot yet be eliminated. No systematic trapping for microtines was done in 1973. However, live trapping efforts by D. Holleman over a 4-5 day period in mid-July 1973 at Prudhoe Bay suggest that numbers were similar to or, in some areas, higher than those reported there for 1972 (D. Holleman, pers. comm.). In July 1973, although he captured no lemmings in the temporary live traplines near the BP camp, Holleman captured five *Dicrostonyx* on grid area Q, using the outer perimeter of 40 traps (of original 100 traps). On grid area S, using 90 of the original 100 traps, he caught eight *Dicrostonyx*. Three of the eight were small juveniles, which indicated recent, active reproduction. Comparison of these 1973 numbers on grid area S with those found in mid-July 1972 (Table 1) suggests that, at least on grid area S, numbers of collared lemming were higher in 1973. But this number does not exceed the highest found on grid areas P and Q in 1972 (Table 1). Holleman found no brown lemmings at any of the trapping sites.

If lemming populations around Prudhoe Bay always remain relatively low, perhaps the most important factor may be the presence and the movement during the summer of caribou in the habitat of the lemming. Although they do not give any quantitative data from their observations of collared lemming communities on the North Slope of Alaska, Bee and Hall (1956) claim that in certain areas the caribou controls the lemming population. At Barrow, where high populations of lemmings occur regularly, caribou are not an important element in the tundra ecosystem. At Prudhoe Bay, caribou annually migrate into the area in June, graze the area until September, and migrate out again to wintering grounds (White et al., this volume). In 1972, between 30 June and 30 July, at least several thousand caribou moved across the area near Prudhoe Bay which included the live trapping grid sites in the present study (White et al., this volume). On 10 July 1972, 1,600 caribou were seen slowly traversing the area which included our lemming trapping grids, during a period of several hours, grazing intermittently as they moved. MacLean (pers. comm.) reported that the passage of large numbers of caribou, as was seen at Prudhoe Bay in mid-July 1970, resulted in heavy grazing pressure on the vegetation as well as severe physical disturbance from trampling. It is reasonable to assume that the impact of these large herbivores on the local lemming populations through competition for food and space and through physical disturbance or destruction of habitat may be great. However, this remains conjecture until clarification by further studies.

In addition to the probable effect of caribou on depressing lemming population numbers, certain predators may play a significant role in affecting lemming numbers (Pitelka 1957, Maher 1970). No quantitative data are available for avian predators (Norton et al., this volume) or for mustelid predators at Prudhoe Bay. The arctic fox *(Alopex lagopus)* may prey upon a significant portion of the available lemmings (Underwood, this volume). During the winter of

Table 3

Density estimates for collared lemmings on three grid areas near Prudhoe Bay. Numbers in parentheses are the actual number captured on grid area.

	+Numbers ha^{-1}						
	June 1971	July 1971	August 1971	mid-June 1972	early July 1972	late July 1972	mid-August 1972
Grid P* (low relief polygons and tussocks)	0	0	0	7.4(8)	10.2(7)	3.3(2)	0
Grid Q* (low relief tussocks)	2.2(2)	0	0	4.3(5)	6.6(5)	5.3(4)	0
Grid S* (shallow pingo and surrounding area of very low relief tussocks)	0	0	0	1.6(1)	0	3.3(2)	1.6(1)

*Grid area = 0.25 ha; effective trapping area estimated as follows to compensate for lemming movements (re: Brooks and Banks 1971). See methods section for further explanation.

adult and subadult females probably without homesite	2.89 ha (60 m strip)
adult and subadult pregnant females probably with homesite, and juvenile females	0.61 ha (14 m strip)
subadult and juvenile males	0.61 ha (14 m strip)
adult males	10.0 ha (134 m strip)

+Values are estimated minimum number of animals present per effective trapping area.

1971-72 a deliberate trapping program was conducted around Prudhoe Bay to reduce the populations of arctic fox (W. Hanson, pers. comm.). Perhaps this reduction of canid predators facilitated the increase in collared lemmings found in the summer of 1972.

The impact of several years of human activity in the area on the populations of microtine rodents remains to be determined. It is conceivable that the elevated road systems, which facilitate field studies, have modified drainage patterns and altered the habitat conditions. Assessment of the significance of this disruption to the reproductive success and survival of local populations requires further studies both near Prudhoe Bay and in areas of the coastal tundra yet undisturbed by man.

Conclusion

The impact of the lemmings at Prudhoe Bay on the net primary production and upon the integrity of the tundra habitat would appear to be very small compared to that of lemmings at Barrow if the population numbers of these small herbivores normally remain as low as found in 1971 and 1972.

Acknowledgments

This research was supported by the National Science Foundation under Grant GV 29342 to the University of Alaska. It was performed under joint sponsorship of the International Biological Program and the Office of Polar Programs and was directed by the U. S. Tundra Biome. Logistic support at Prudhoe Bay was made available through a grant to the Tundra Biome Center, University of Alaska from the Prudhoe Bay Environmental Subcommittee. I am grateful to the late Scott Parrish for his assistance in logistics as site coordinator at Prudhoe Bay. I would like to thank Wayne Couture and Thomas Lahey for able field assistance, and Dr. Stephen F. MacLean, Jr. for helpful comments.

References

Batzli, G. O. (In press). The role of small mammals in arctic ecosystems. Submitted to: Small Mammals, Their Population Structure and Impact on World Ecosystems. IBP Series, Cambridge University Press.

Batzli, G. O. and F. A. Pitelka. (1971). Condition and diet of cycling populations of California vole *(Microtus californicus). J. Mammal.*, 52(1);141-163.

Bee, J. W. and E. R. Hall. (1956). Mammals of Northern Alaska. University of Kansas, Mus. Nat. Hist. Misc. Pub. 8, 309 pp.

Brooks, R. J. (1970). Ecology and acoustic behavior of the collared lemming *(Dicrostonyx groenlandicus)* (Trail). Ph.D. thesis. University of Illinois, 299 pp.

Brooks, R. J. and E. M. Banks (1971). Radiotracking study of lemming home range. *Commun. Behav. Biol.*, 6A, 1:1-5.

Brown, J., R. K. Haugen, and S. Parrish (This volume). Selected climatic and soil thermal characteristics of the Prudhoe Bay region.

Burt, W. H. and R. P. Grossenheider (1964). A Field Guide to the Mammals. Houghton Mifflin Co., Boston, 284 pp.

Krebs, C. J. (1964). The lemming cycle at Baker Lake, Northwest Territory, during 1959-62. Arctic Inst. No. Amer. Tech. Pap. No. 15, 104 pp.

Maher, W. J. (1970). The pomarine jaeger as a brown lemming predator in Northern Alaska. *Wilson Bull.*, 82:130-157.

Neiland, B. J. and J. R. Hok (This volume). Vegetation survey of the Prudhoe Bay region.

Norton, D. W., I. W. Ailes, and J. A. Curatolo (This volume). Ecological relationships of the inland tundra avifauna near Prudhoe Bay, Alaska.

Pitelka, F. A. (1957). Some aspects of population structure in the short term cycle of the brown lemming in Northern Alaska. Pages 237-251 *in* Cold Spr. Harb. Symp. Quant. Biol., Vol. 22.

______. (1973). Cyclic pattern in lemming populations near Barrow, Alaska. Pages 199-215 *in* Alaskan Arctic Tundra (M. E. Britton, ed.). Arct. Inst. North Amer. Tech. Pap. No. 25.

Schultz, A. M. (1969). A study of an ecosystem: the arctic tundra. Pages 77-93 *in* The ecosystem concept in natural resource management (G.Van Dyne, ed.). Academic Press, NY.

Shelford, V. E. (1943). The abundance of the collared lemming *(Dicrostonyx groenlandicus)* in the Churchill area, 1929 to 1940. *Ecology*, 24:472-484.

Speller, S. W. (1972). Biology of *Dicrostonyx groenlandicus* on Truelove Lowland, Devon Island, N.W.T. Pages 257-271 *in* Devon Island I.B.P. project, high Arctic ecosystem (L. Bliss, ed.). University of Alberta.

Underwood, L. S. (This volume). Notes on the Arctic Fox *(Alopex lagopus)* in the Prudhoe Bay area of Alaska.

Webber, P. J. and D. A. Walker (This volume). Vegetation and landscape analysis at Prudhoe Bay, Alaska: A vegetation map of the Tundra Biome study area.

White, R. G., B. R. Thompson, T. Skogland, S. J. Person, D. E. Russell, D. F. Holleman, and J. R. Luick (This volume). Ecology of caribou at Prudhoe Bay, Alaska.

Adult arctic fox in summer pelage defending a den site at Prudhoe Bay.

Notes on the Arctic Fox *(Alopex lagopus)* in the Prudhoe Bay Area of Alaska

LARRY S. UNDERWOOD
Naval Arctic Research Laboratory
Barrow, Alaska 99723

Introduction

This report is the result of some observations on the den site ecology of the arctic fox, *Alopex lagopus*. The purposes of the study were to assess the possible effects of this carnivore on small mammal populations in the Prudhoe Bay area and to gather baseline data on the arctic fox population in a portion of the Alaskan North Slope that will probably experience a considerable increase in human activity in the near future. Data were collected on the location and topography of den sites, signs of food items associated with the dens, and behavior of pups at the den site.

Study Area

The study area consisted of Point McIntyre, at the northwest corner of Prudhoe Bay, and the Deadhorse area, located about 30 km inland. Both of these locations are considered to be part of the Prudhoe Bay area. The terrain is a typical Alaskan coastal plain, with numerous lakes and ponds; wet meadows, and slightly elevated beach, bank, and hummock areas.

The soils and vegetation are also typical of the Alaskan coastal plain and are discussed elsewhere in this volume (Everett; Webber and Walker).

Approximately 150 species of birds nest in this area during summer months. Many species of waterfowl and shorebirds, and two species of passerines (Lapland longspur and snow bunting) are present in relatively large populations (Norton, this volume).

Mammal populations apparently are less reliably present. While bands of caribou *(Rangifer tarandus granti)*, varying from a few individuals to several hundred, are common in the area, they may be absent at a given time (White et al., this volume). Small mammals consist of an apparently expanding population of arctic ground squirrels *(Citellus undulatus)* and a relatively low level population of lemmings (Feist, this volume). Grizzly bears *(Ursus horribilis)*, grey wolves *(Canis lupus)*, and 13 other species are occasionally reported. (Bee and Hall 1956).

Methods

In the summers of 1971 and 1972, data were collected during a series of 3-day field trips. More extensive observations were made within a 3-week period in August 1972.

As soon as dens were located, each site was described and mapped (Table 1). Carcasses and other signs of food were noted but left in place at each den site. Fresh fecal pellets were collected for later analysis of prey species content. Behavioral data were collected during three 6-hour observation periods from tent or truck blinds located several hundred meters from the den sites.

Results

A total of eight arctic fox dens have been located in the Prudhoe Bay area. Six of these dens are within 2.5 km (four are within 100-200 m) of the road system that was constructed in the area in 1968-70. The two dens located near Point McIntyre are in an area of low level human activity.

Four of the dens are associated with pingos (geomorphic structures resembling small hills) ranging in height from approximately 2 m to 9 m in the Prudhoe Bay area. These structures, which are formed from the refreezing of lake bottoms following drainage, have a core of segregated ice. Dens near the tops of these structures have a commanding view of the surrounding tundra.

The remaining dens are also located in relatively high, dry ground. Two of them are in ridge banks which are probably the banks of ancient, drained lakes. The vegetation at all den sites was considerably more robust than that of the surrounding territory and "greened up" noticeably earlier, indicating a richer soil and more favorable growing conditions for plants. Following the age classification system of Chesemore (1967), it was determined that all of the dens located ranged from young to mature. Den site DH4, located in a large pingo nearly 9 m high, has two den systems. Although both were utilized by the pups, the one near the top with 10 entrances seemed to be used preferentially.

In the 1971 summer season, five dens were examined, two of which supported young. At den site DH3, at least two young were heard, but apparently the litter was moved during the night following discovery, before an accurate count of the pups could be made. In 1972 eight den sites were examined, and four contained pups. It is likely that two of these dens contained pups from the same litter. After several days of observation at site DH3, the litter of three apparently disappeared. The following day a new den containing three pups was discovered (den site DH6) in a riverbank not far from a well-traveled road. Although the den faced away from the road and could not be seen easily the pups were quite obvious when active. It is doubtful that the den could have existed all summer without being noticed.

For the four litters observed during the 2-year period in which accurate counts could be made, the average litter size was 5.5. This is somewhat smaller than the average number of seven reported by MacPherson (1969) for arctic foxes in the Lake Baker region of Canada.

Table 1

Densities in the Prudhoe Bay area

Code number[1]	Location[2]	Facing direction	Approximate dimensions	No. of entrances	No. of pups	
					71	72
DH 1	11.7	NW	7.5x 4.5m	15	none	none
DH 2	1.9	N	15.3x 9.9	50	5	10
DH 3	8.7	S	18.0x14.1	18	2(?)	3[3]
DH 4	20.4	E	9.0x 9.0	10		4
		E	4.5x 3.0	7		
DH 5	21.4	n/a[4]	n/a	25		none
DH 6	10.3	n/a	n/a	10		3[3]
MI 1	23.5	E	14.0x 4.0	56	none	none
MI 2	21.4	SE	8.0x 5.0	8	none	none

1. DH refers to Deadhorse area; MI refers to Point McIntyre area.
2. Distance in kilometers from Deadhorse air terminal.
3. Probably same litter. See text.
4. n/a indicates data not available.

The average number is increased considerably by the litter of 10 observed in 1972. Curiously, the animals in this litter were only approximately one-fourth grown in late July, while all other litters observed were nearly three-fourths grown. It is not known whether the animals were small because they had been born abnormally late in the season, or because the adults were not supplying them with enough food. However, their behavior appeared normal, and the three individuals that were trapped and examined seemed to have normal alertness, "fatness," and quality and thickness of pelage.

Behavioral Observations. Adult foxes were encountered relatively infrequently—only four times during approximately 50 visits or observation sessions at active dens. The earliest of these encounters occurred on 12 June 1972. Upon initial examination, no foxes were in evidence, although fresh diggings and patches of molted fur were associated with several of the den entrances. After several minutes, an adult fox exited one of the entrances and quickly left the den area. Approximately 10 minutes later, the fox returned and attacked the observer as he tried to retrieve an object deep in one of the dens. The attack consisted of grabbing and jerking the observer's hair. Thereafter, the fox approached from the rear to within a meter of the observer several times, and was noticeably aggressive (i.e., threat displays, vocalizations and snapping). As the observer left the den site, the fox reentered the den. No pups were seen or heard, but six weeks later a litter of three pups which were more than half-grown were observed.

The second adult fox was encountered on 20 July 1972. Carrying two brown lemming carcasses, it approached two observers sitting quietly on a den site. At a distance of approximately 9 m, the adult became aware of the observers, dropped the lemmings, barked, picked up the prey, ran behind a small hummock, and buried the prey under a light coat of moss and lichen. The fox then approached the den aggressively, but with less intensity than in the encounter described above (i.e., the second adult approached the observers less frequently and never closer than 4 m). The fox seemed more defensive of the prey than the den site.

The third encounter occurred on 21 July 1972. An adult fox observed the approach of two observers, barked once, and left the den site when they were within 45 m of it. The adult moved off for approximately ½ km, hid behind some relatively high tundra grass, and observed the den. The fox soon became distracted by a golden plover, which he unsuccessfully tried to capture.

The fourth encounter occurred on 3 August 1972 at den site DH6, when an adult was observed for 4½ hours. Behavior consisted almost entirely of resting approximately 15 m from the den site. During this period, a person who is not associated with the project approached the den to take photographs. The adult fox sat up and watched the person, but was not aggressive, and returned to a resting position as soon as the individual left. One of the pups that was playing actively in the area approached the adult fox only once. The adult snapped and growled, and the pup moved off.

It appears from these limited data that the adults become less attached to the den as the litter matures. Reaction of adults to the presence of humans in the den areas seems to progress from strongly defensive and aggressive in early June to nearly indifferent in early August. Casual human activity in the den area does not appear to seriously inhibit litter raising. On the other hand, frequent human activity may cause the adults to move the litters to new locations.

Pup behavior was observed for a total of 33 hr, 44 min, during approximately half of which time the pups were inside the den. When out of the den, the pups rested half of the time (sleeping, lying, sitting, standing, and often staring out across the tundra), and were active for the other half (walking, running, playing moderately or intensely). During active periods, the pups explored the den site and surrounding area. Solo play consisted of pouncing on grass clumps and other objects in the den site area and occasionally tossing objects into the air. Group play, which rarely involved more than two interacting individuals, often consisted of chases and wrestling. Wrestling matches were usually preceded by a "tail display" (upright tail, arched back, sideways walk), followed by a quick pounce by the displaying individual onto the more passive one. Wrestling consisted of rolling and biting in the region of the back of the neck and, less frequently, the tail and legs.

The data are too meager to identify well-defined patterns in pup activity. However, it appeared that early morning, early afternoon, and evening were relatively quiet, while late morning and late afternoon were active periods. Activity seemed to be inhibited by inclement weather and mosquitoes.

Prey species utilization. In marked contrast to similar data collected from den sites in other areas of the North Slope in past years, where as many as 30 lemming carcasses have been found associated with a single den, the amount of prey sign found associated with the Prudhoe Bay dens in 1971-72 was disappointingly sparse. This was probably a result of the relatively low population level of lemmings in these years. Prey signs consisted primarily of bits of lemming fur, partially eaten lemming carcasses, isolated feathers, and eggshells.

The most significant observations occurred on 22 July 1971 at den site DH2, when one whole and from one to three broken swan eggs were found which had been brought to the den the previous night. All signs of the eggs had disappeared 24 hours after their discovery. A large wing, probably of swan and partially desiccated (i.e., not freshly killed), was brought to the den, and the pups fed on it. Food items that could positively be identified were lemming, fledgling snow buntings, fledgling shore birds and swans. Several old caribou bones and antlers were associated with the dens, and were occasionally gnawed on by the pups, but were doubtless of small nutritional value.

The age of fecal pellets of arctic fox can be determined by noting color. Fresh scat is usually shiny, black, and moist. Within 24 hours of production, barring rain or heavy fog, the pellets tend to dry out, but retain their color. After about 6 weeks, the pellets begin to show signs of greying, and become dark grey after about 3 months. Pellets that have over-wintered are generally white or light grey. Thus, it is possible to distinguish scat of the year from scat of previous years.

Table 2 shows an analysis of prey content from scat of the year collected in 1971 at active dens in the Deadhorse area, and scat of the year found at random in the Point McIntyre area, where no pups or adults were observed.

Table 2

Contents of fresh fecal pellets

Prey sign	Deadhorse area (n=50)	Point McIntyre (n=24)
Small mammal	86%	75%
Caribou	2	0
Ground squirrel	12	4
Birds	56	63
Insects	8	8
Plants	46	42
Nondigestible material	14	0

Small mammal sign (either of the two lemming species), consisting of fur, long bones, skull parts, teeth, and whole paws, in that order of occurrence, were found in four out of five pellets. The differences between Deadhorse and Point McIntyre were probably not significant. Ground squirrel sign was relatively low. Both Deadhorse and Point McIntyre are approximately equidistant from the nearest known ground squirrel colony.

The occurrence of one sample of caribou hair may indicate some summer scavenging but, with caribou actively molting in the area during the summer, it seems likely that caribou hair could be ingested accidentally. Stephenson (1970) reports that arctic foxes did not take scavenge on St. Lawrence Island during the summer, when both live prey and carcasses were available.

The second most common occurrence in the pellets was bird sign found in more than half of the pellets. Signs consisted of mature feathers, in parts or whole, pinfeathers, eggshells, egg membranes, and hollow bones. No attempt has been made to identify the species of birds.

The six samples of insects consisted of two partially digested bumblebees (Bombas), one set of cranefly (Tipulidae) wings, and three unidentifiable insect carapaces.

Plant remains usually consisted of isolated plant fibers, but included a large number of *Salix rotundifolia* leaves which, although common in the area, are not as common as their occurrence in the pellets suggests.

Nondigestible items included bits of plastic, rubber, cork, and wire insulation. It is tempting to conclude that the differences in nondigestibles found in the two areas, Deadhorse and Point McIntyre (Table 2), are related to the differences in degree of human activity. However, it should be noted that in the Point McIntyre area, an abandoned DEW-Line site and the remains of oil exploration activities conducted at a time when environmental issues were not as popular as at present, have resulted in at least an equal availability of nondigestible items in the two areas.

Discussion

During the breeding season, adult foxes appear to spend large blocks of time away from the den site; they are infrequently seen in the denning area. These observations can be explained if one assumes that breeding foxes occupy large, overlapping feeding ranges. The use of swan eggs as food for fox pups fits this assumption. During the summer of 1971, ornithologists were documenting the nest locations of birds in the Deadhorse area. It is doubtful that breeding swans, whose large size and white color make them quite conspicuous on the treeless tundra, could have escaped detection at the time the eggs appeared at the fox den. The nearest known swan nest, 13 km from the den site, was not predated during July 1972. Thus, in this case at least, adult foxes probably traveled more than 13 km to secure food for the den. The impact of foxes on populations of small mammals and nesting birds is probably spread over an area of at least 500 square km. It should be reemphasized that the lemming population was relatively low during these years, which may have influenced the size of the feeding range. Considerably more data are needed on range size and prey species utilization before definitive statements can be made on the impact of the arctic fox on small mammal and bird populations.

Acknowledgments

These observations were conducted in conjunction with a Barrow based research project sponsored through the Arctic Institute of North America (AINA) and the NSF Tundra Biome grant to the University of Alaska. Support at Prudhoe was provided by the Tundra Biome Center through Prudhoe Bay Environmental Subcommittee funding.

References

Bee, J. W. and E. R. Hall (1956). Mammals of Northern Alaska. University of Kansas, Mus. Nat. Hist. Misc. Publ. 8, 309 pp.

Chesemore, D. L. (1967). Ecology of the arctic fox in northern and western Alaska. M.S. thesis. University of Alaska, 148 pp.

Everett, K.R. (This volume). Soil and landform associations at Prudhoe Bay, Alaska: A soils map of the Tundra Biome area.

Feist, D. D. (This volume). Population studies of lemmings in the coastal tundra of Prudhoe Bay, Alaska.

MacPherson, A. H. (1969). The dynamics of Canadian arctic fox populations. Canadian Wild. Rep. Scr. 8, Can. Wild. Ser., Ottawa, 52 pp.

Stephenson, R. O. (1970). A study of the summer food habits of the arctic fox on St. Lawrence Island, Alaska. M.S. thesis. University of Alaska, 76 pp.

Webber, P. J. and D. A. Walker (This volume). Vegetation and landscape analysis at Prudhoe Bay, Alaska: A vegetation map of the Tundra Biome study area.

White, R. G., B. R. Thomson, T. Skogland, S. J. Person, D. E. Russell, D. F. Holleman, and J. R. Luick (This volume). Ecology of caribou at Prudhoe Bay, Alaska.

Institute of Arctic Biology, University of Alaska

Weighing a tranquilized caribou at Prudhoe Bay.

Ecology of Caribou at Prudhoe Bay, Alaska

ROBERT G. WHITE, BRIAN R. THOMSON*, TERGE SKOGLAND**,
STEVEN J. PERSON, DONALD E. RUSSELL***,
DAN F. HOLLEMAN, AND JACK R. LUICK

Institute of Arctic Biology
University of Alaska
Fairbanks, Alaska 99701

Introduction

The U. S. IBP Tundra Biome study area at Prudhoe Bay, Alaska, is located on the northern coastal plain bordered by the Kuparuk River in the west and the Sagavanirktok River in the east. This same area is the site of oil exploration, and the road system which has been constructed for this purpose allows easy access to most of the area between these rivers and to approximately 7 km inland (Fig. 1).

Prudhoe Bay lies on the periphery of the summer range of two large populations of barren-ground caribou *(Rangifer tarandus granti).* The western part of the Arctic Herd may move into the area from the west in June-July (Hemming 1971), and occasionally the outer (western) periphery of the Porcupine Herd moves in from the east. However, most movement into the Prudhoe Bay area is thought to be from a large central section of the Arctic Herd (Hemming 1971). These animals move through Anaktuvuk Pass and down the Colville River, or through the Dietrich and Atigun areas and down the Canning, Sagavanirktok and Kuparuk Rivers (Hemming 1971; Gavin 1975) to graze on the coastal plains from late June through September. There is also evidence of a small population which remains in the Prudhoe Bay area year-round (Child 1973; Gavin 1975).

The summer vegetation of the Arctic tundra is thought to be of high nutritive value. Rapidly growing vegetation is of high soluble carbohydrate, soluble nitrogen (N), and phosphorus (P) levels because of the long daylight hours. Thus, the relatively short growing season is complemented by high relative growth rates. Since it is considered that summer nutrition is important in affecting the body condition of animals entering the winter, the quality and quantity of forage removed from the summer range is potentially important in affecting the productive performance of these caribou. This may be relatively more important to the calf crop, as growth rates of caribou calves are normally high, and any restriction in nutrition during this stage of rapid growth may lower the likelihood of surviving the winter.

---

*Current address: Department of Forestry and Natural Resources, University of Edinburgh, Scotland, U. K.

**Current address: Statens Viltundersøkelser, Elgeseter gt. 10, Trondheim, Norway.

***Current address: Faculty of Forestry, University of British Columbia, Vancouver 8, British Columbia, Canada.

There is increasing evidence that harassment by flying insects plays a major role in determining the movement and activity patterns of *Rangifer* in summer. Harassment leads to an increased energy expenditure because of avoidance movements and a corresponding decrease in the time spent grazing. However, whether this perturbation can materially affect the amount of herbage removed during a summer period has not yet been determined.

Finally, caribou may affect primary production through removal of preferred plant species and by trampling. Both natural (e.g., insect harassment) and human (e.g., construction of barriers) perturbations may cause temporarily high stocking rates, resulting in local overgrazing and physical damage from trampling. In extreme conditions, overgrazing and trampling may decrease the insulative effects of tundra vegetation, which would have long-term visual and topographically harmful consequences.

A recent report considers the effects of simulated pipelines on movement patterns (Child 1973), while the present report documents the normal grazing patterns of caribou in the Prudhoe Bay area.

The objectives of this study were: (1) to determine normal activity patterns of the resident and transient caribou populations; (2) to document the effects of insect harassment on activity and movement patterns; (3) to determine plant preferences by caribou in relation to vegetation phenology and nutrient content, and (4) to determine the amount of plant material harvested and returned to the ecosystem.

Methods

Source of abiotic data

Daily observations of dry and wet bulb temperature (°C), wind speed (km hr^{-1}), wind direction (degrees true N) and atmospheric pressure (mmHg) were obtained from climatologic data recorded at the Deadhorse and Prudhoe Bay airports. These observations were recorded on a 2 hourly basis from 0500 to 1800 hr.

Supplementary field observations of ambient temperature and wind speed were made with a hand held thermometer and anemometer at approximately 1.5 m from the tundra surface.

Determination of caribou population composition

In 1972 the study area was surveyed mainly from the road system (every 1-2 days), and four aerial surveys were made. In 1973 composition counts were made from the road system each 2-3 days.

In road surveys, all animals within binocular (10x50) or spotting-scope (25x60) range were classified according to age (calf, yearling, and adult) and sex. In addition, notes were made on group aggregations, locations, and movement patterns.

During periods of high insect harassment, caribou numbers, ages, and sex classes were also noted from a series of vantage points in the sand dunes associated with the Sagavanirktok River.

Documentation of behavioral and activity patterns

Observations on behavior and recordings of activity patterns were made as described for wild reindeer in Norway by Gaare et al. (1970) and Thomson (1971, 1973). Briefly stated, a suitable herd or group of caribou was located and, by following unobtrusively, observed for as long as possible. At 15 min intervals throughout this period, caribou were classified according to the number of individuals engaged in each of seven categories of activity (eating, lying, standing, walking, trotting, running, and other). Between these activity counts, observations were made on weather data, caribou behavior, movement patterns, and external disturbances. Similar and concurrent observations were made on grazing preferences, time spent on different plant communities, and monitoring of grazing intensity (Gaare et al. 1970; Gaare and Skogland 1971).

Grazing intensity

Previous workers have defined grazing periods in two ways; either the activity associated with eating *per se* (Thomson 1971), or the activity associated with searching and eating (Gaare and Skogland 1971). In the present report, the former activity is described as eating, and the latter as grazing. Grazing intensity was estimated as the fraction of a grazing period that was spent in eating [i.e., grazing intensity = eating time/(eating time + searching time)].

Description of vegetation

Following preliminary survey of the vegetation, an intensive study was made by describing and estimating plant species composition in plots (33x100 cm), as described by Gaare (1968). The 108 plots from the typical plains were analyzed with description of 5-15 plots per vegetation type. Plant groups were arranged into phyto-sociological vegetation types according to the European phyto-sociological system. Dominance, constancy, and Sorensen's index of similarity were used to distinguish types (Dahl 1956; Grieg-Smith 1964; Hanson and Churchill 1961). Nomenclature follows Hultén (1968). Moss cover was not described in detail.*

Tranquilizing caribou and field rumenotomy

Caribou were tranquilized with 3 ml M99 (Etorphine), which could be counteracted with 3 ml of antidote M50-50 (Diprenorphine) [American Cyanamid Corp., Princeton, N. J.] at the end of the sampling protocol. Once the caribou was fully tranquilized, 3 ml of Acepromazine [Ayerst Lab, N. Y., N. Y.] was given intramuscularly, and field rumenotomy was performed using the first stage of a rumen fistulation technique as described by Dieterich (1975). This involved shaving the operating area, disinfecting the site with Zepharin chloride [Winthrop Lab., N. Y., N. Y.], and locating the rumen through a 5-7 cm incision. The rumen wall was sutured to the skin, and an incision was made through the rumen wall for collecting mixed rumen samples, using a plexiglass tube of 3.2 cm in diameter (O.D.) and 55 cm in length. After sampling, the exposed edges of the rumen were folded into the rumen, and the rumen fistula was closed by suturing the rumen wall. Muscle tissue and skin was then sutured to close the incision. Care was taken to minimize spillage of contents, and the wound was dressed topically with Furacin Powder [Eaton Veterinary Lab., Norwich, N. Y.] to minimize infection. Long acting penicillin, 5 m Longacil S [Fort Dodge Lab, Inc., Fort Dodge, Iowa], was given intramuscularly to provide long-term protection. Caribou from all five field rumenotomy operations survived at least until the end of the study period (3 weeks).

Description of reindeer

Female reindeer of 2-5 yr of age were flown to Prudhoe Bay from the University of Alaska, Fairbanks. In 1972 two esophageal fistulated (EF) animals (Nos. 31 and 37), and two rumen fistulated (RF) animals (Nos. 10 and 12), were held in a small corral for the first week (July 6-10), until they were accustomed to being tethered and had adapted to the available herbage. No supplementary feed was given after July 10. Body weight measurements were made in July. Following experience gained in 1972, only two animals (Nos. 9 and 31) were taken to Prudhoe Bay in the summer of 1973. Both were supplemented with 2.5-3.0 kg d^{-1} Purina Cattle Starter No. 1 for the entire season, and body weights were recorded every 3 days (see below).

During periods of severe insect attack, reindeer were sprayed with insect repellant ("OFF," S. C. Johnson and Son Inc., Racine, Wisc., or Insect repellant Type IIB, Federal Specification 0-1-503) and were tethered in the most windy areas or were allowed freedom of movement in the holding corral.

Body weight determinations

Estimates of body weights of caribou and reindeer were made using a system involving four bathroom scales. An army stretcher or a wooden platform (2.5x1 m) was placed on the scales, which were then turned to zero. Tranquilized caribou were lifted onto the stretcher, and live reindeer were trained to stand on the platform while the four scales were read concurrently. Reproducibility of the technique was ± 1.0 kg.

Esophageal fistula collections

Samples from esophageal fistulated animals were collected over 10 or 20 min time periods. The esophageal plug was removed during a collection, and upon swallowing, egesta was extruded through the fistula and collected in a plastic bag fitted with a liner of nylon mesh (10-12 threads cm^{-1}). The nylon mesh served to retain the forage and allowed saliva to strain into the plastic bag. This apparatus was fitted into a canvas bag (30x18 cm) which supported the plastic bag and liner and which could be attached to the neck of the reindeer.

---

*This scheme of classification is compared with a more detailed study by Webber and Walker (this volume).

At the end of a collection period, the apparatus was taken from the animal, and saliva was forced from the forage sample by squeezing. Wet weights of forage and saliva samples were determined, and the forage was subdivided for determinations of plant species composition, dry matter content, and chemical composition.

Identification of plant material in rumen and esophageal egesta samples

Rumen and esophageal egesta samples were preserved in 80% ethanol. Since chlorophyll is removed from plant parts by alcohol, identifications were made within 2 days of sampling to determine live and dead plant parts. Samples in the preservative were added to an enamel tray (25x40 cm), and 200 point identifications were made with a binocular (x10) as described by Galt et al. (1969); Gaare et al. (1970); Gaare and Skogland (1971).

For comparison with samples of rumen contents and esophageal egesta, the plant species composition of communities on which the animals were grazing was also determined (see Description of vegetation, above).

Estimation of plant biomass and primary production

Biomass estimates were made by clipping all vegetation above the moss layer in 30x30 cm plots. Clipped vegetation was sorted into green (live) and dead material, weighed, and dried at 50° C.

Above-ground vascular production was estimated through the season from changes in biomass; total yearly above-ground production was estimated, assuming that peak green biomass represents total annual production (Tieszen 1972).

Chemical analyses

Dry matter content of vegetation, rumen samples, and esophageal egesta samples were determined by drying to constant weight in a forced air oven at 40-55° C.

Estimates of cell contents, hemicellulose, and ligno-cellulose in vegetation were made using the acid detergent/neutral detergent technique of Goering and Van Soest (1970). Lignin content was determined on the acid detergent residue using concentrated H_2SO_4 (Goering and Van Soest 1970).

Estimation of *in vitro* digestibility

The two stage, micro-digestion, *in vitro* technique of Tilley and Terry (1963) was used to determine the approximate digestibility of forage samples. Rumen liquor for the first stage of the digestibility was obtained from tranquilized caribou and the rumen fistulated reindeer. Strained liquor samples were incubated anaerobically with buffer and 0.5 g samples of forage. The second stage digestion with a pepsin-HCl solution was carried out as recommended by Tilley and Terry.

Results

Caribou numbers and populations composition at Prudhoe Bay

The location of the study area at Prudhoe Bay relative to the river systems is shown in Fig. 1. The 300 ft (91.5 m) contour indicates the most northern limit of the foothills of the Brooks Range. The heavily shaded area represents that area which could be surveyed from the road system at Prudhoe Bay. A map prepared from aerial photographs of this road network and gravel pads is shown in Fig. 1a, with individual study sites marked on the map.

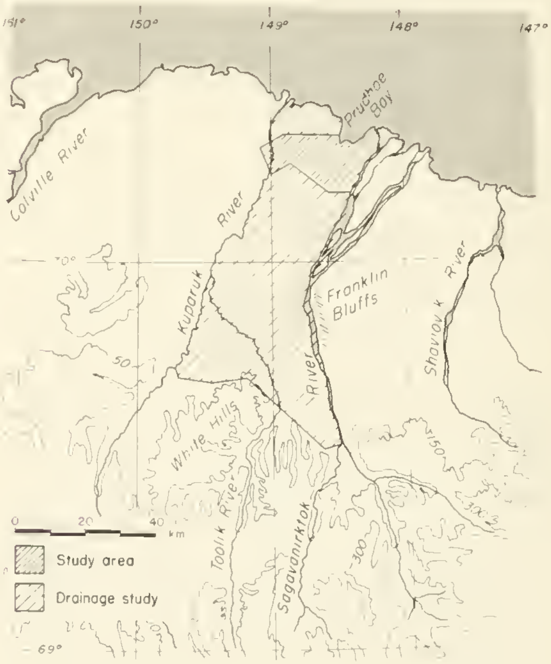
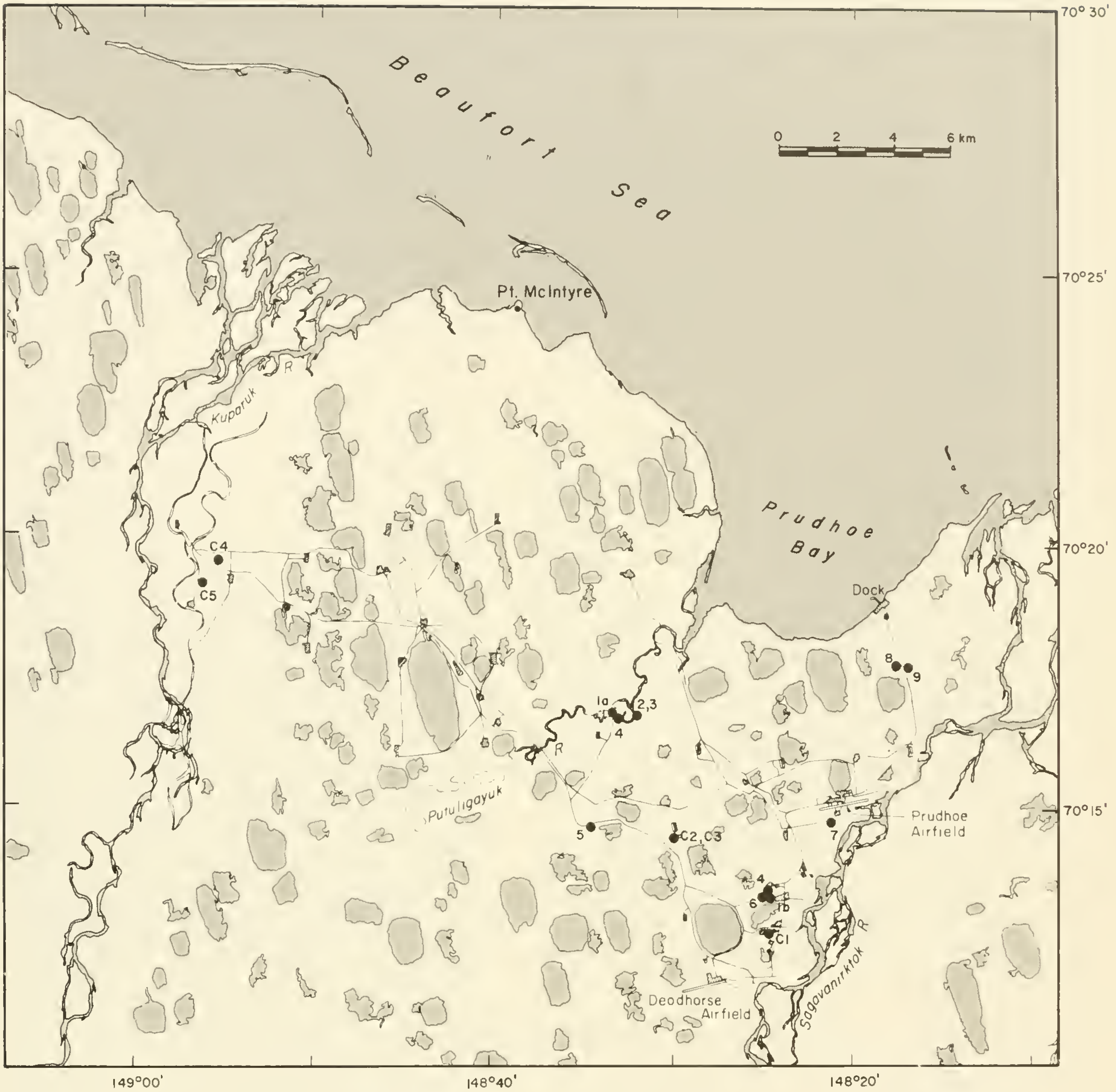


Fig. 1. *Location of study area relative to the drainage system of the Kuparuk and Sagavanirktok Rivers at Prudhoe Bay.*



Site no.	Description	Designation on vegetation map
1a	Location of reindeer corral 1972	$P_F3;\rightarrow;4$
1b	Location of reindeer corral 1972	$L3 \rightarrow L4$
2, 3	*Dryas* heath and *Salix rotundifolia* snowbed communities (Table 8, Table 12, Appendix Table 2)	$F_1 \rightarrow F_3, F_W9$
4	*Eriophorum* marsh communities (Table 8, Table 12, Appendix Table 1)	$P_H3; 4d \rightarrow F_f2, 8$
5	*Dupontia fisheri* brook meadow (Table 8, Table 12, Appendix Table 3)	$S_{12} \rightarrow F_3, 4$
6,7	Lake vegetation – *Carex* marsh (Table 8, Table 12)	$L6 \rightarrow L13$ or $F_r5, 3$
8	Sand dunes (Table 8, Appendix Table 4)	$D15 \rightarrow D17$
C1–C5	Location of caribou capturing activities (Table 11, Appendix Tables 5-10)	

Fig. 1a. *Location of sites associated with reindeer and caribou studies at Prudhoe Bay in 1972 and 1973.*

The number of caribou present in the Prudhoe area varied daily depending on the extent of immigration into and emigration out of the area. Thus, in 1972 between eight and 1,500 animals were observed on any single day in the study area, and in 1973 between one and 130 animals. In both years maximum numbers occurred on days of insect harassment, and caribou were observed to move into the area. Lowest numbers were observed in insect-free periods, and frequently caribou were tending to disperse out of the area.

In 1972 groups harassed by insects would move towards the coast; under severe harassment, large herds would assemble, particularly on the sand dunes and the sand or gravel banks of the river deltas. Herds moving under insect harassment would sometimes swim the Sagavanirktok or Kuparuk rivers.

In summer 1973 maximum numbers observed again corresponded with days of insect harassment (Fig. 2), but the large "invasions" did not occur. High water levels in the Sagavanirktok and Kuparuk rivers conceivably could have inhibited movement into the study area in the upper reaches of the rivers. Large herds under insect harassment were observed 35 km inland on the moderate heights of the Franklin Bluffs (Gavin, pers. comm.).

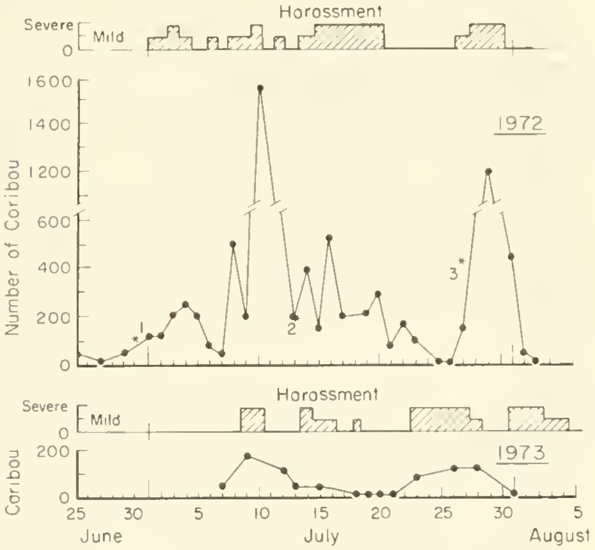


Fig. 2. *Relationship of caribou numbers and intensity of insect harassment at Prudhoe Bay. Caribou numbers were obtained from a census of caribou within binocular range of the road; 1, 2, 3; aerial surveys between coast and Franklin Bluffs.*

Population composition sample counts in both years were taken to be representative of the animals present in the Prudhoe Bay area, but not necessarily representative of any whole population, such as the Porcupine Herd, the Arctic Herd, or a "resident" Prudhoe Bay population.

For 1972 a calf:female ratio of 67:100 was estimated. This estimate was based on an observed ratio of 51.2 ±4.0 calves per 100 females plus yearlings (counts of 941 calves/1,831 females + yearlings in 26 herds of size greater than 24 females + yearlings per herd) and an estimated yearling: female ratio of 24:100 (counts of 22 yearlings/90 females). A male:female ratio of 101:100 was based on an observed ratio of 77 males per 100 females plus yearlings (counts of 1,103 male/1,429 females + yearlings). The nearly equal sex ratio was the result of a large herd of more than 1,000, of which 60% of animals (excluding calves) were males, which were classified as they moved into the area under severe insect harassment in 1972.

From the fewer animals present in 1973, three separate counts of at least 120 animals found the calf:female ratio to be 31:100, the yearling:female ratio 25:100, and the male: female ratio 37:100.

A comparison of the herd proportions recorded at Prudhoe Bay with previous estimates of herd proportions is shown in Table 1. The proportion of calves in caribou herds at Prudhoe Bay (16-23% of the herd) is similar to the calf percentage (15-26%) noted for major counts on the Arctic and Porcupine Herds.

When the herd proportion of calves is adjusted to a calf:female ratio, the data suggest that the survival of calves to the end of July 1973 at Prudhoe Bay was low compared with either the results for 1972 at Prudhoe Bay, or for the Arctic and Porcupine Herds in June. Moreover, the calf:female ratio of the Porcupine Herd in October 1972 (31:100), following a known high rate of mortality of calves in July and August, was the same as that for the Prudhoe Bay animals in 1973. Survival of yearlings was apparently similar for both years of the Prudhoe Bay counts and was slightly higher than that for the Porcupine Herd.

Table 1

Comparison of estimates of herd proportions (% of total number of animals) of Prudhoe Bay with estimates for the large arctic herds.

Herd	Year	Female	Male	Calves	Yearlings	Approximate no. classified	Reference
Prudhoe Bay	1972	34(100)	35(101)	23(67)	8(24)	2,632	This study
	1973	52(100)	19(37)	16(31)	13(25)	248	This study
Arctic	1970	40(100)	26(65)	19(47)	15(37)	242,000	Pegau and Hemming (1972)
Porcupine	1972	–	–	24	–	50,000	LeResche (1973)
Porcupine	1972						
	July	52(100)	12(23)	26(50)	9(17)	11,721	Calef and
	October	49(100)	28(57)	15(31)	9(18)	2,997	Lortie (1973)

Values in parentheses are ratios expressed per 100 adult females.

Group activity patterns of caribou

In the 1972 season the number of individuals in a group or herd variously involved in the activities of eating, lying, standing, walking, trotting, or running was recorded at 456 separate 15 min intervals. Activity of adults (female, yearling, and male) over the whole observed period averaged 48% eating, 28% lying, 4% standing, 14% walking, 5% trotting, and 1% running. The disproportionately few observations on male activity, except under insect harassment, make an accurate comparison with female activity times difficult. However, the contrast between adult and calf activity times was quantified after recording the activity within 15 groups (containing females, yearlings, and calves) over 4 insect-free days in late June 1972. The result is summarized in Table 2a; analysis of variance on the full data (Thomson 1974) indicates that females plus yearlings spend significantly more time eating than do calves, while the calves spend significantly more time lying, standing, trotting, and running. Only walking time is not significantly different between the calves and older animals.

Calves at this age (approximately 2-4 wk by end of June) graze considerably more and lie less than do calves at 1-10 days of age (wild

Table 2a

Summary of activity patterns of female yearlings and calves during insect free periods (values are % of study period).

Sex/age class	Eating	Lying	Standing	Walking	Trotting	Running
Female-yearling	52.8 (4.8)	32.7 (4.5)	1.2 (0.9)	11.2 (3.0)	1.8 (1.3)	0.1 (0.2)
Calf	23.5 (5.9)	54.6 (6.9)	4.7 (3.2)	10.9 (4.4)	4.5 (2.8)	1.5 (1.3)
Comparison of classes	X	X	X	NS	X	X

Value in parentheses is the standard deviation. A total of 15 groups were observed: three groups were observed for more than 6 hr duration; the remainder were observed for less than 6 hr and were combined into five groups according to date. Calves were 3-7 wk of age.

NS, not significant; x, $P < 0.05$.

Table 2b

Comparison of activity patterns of calf and adult cohorts at Hardangervidda and Prudhoe Bay.

	Calves, reindeer (1-10 d)	Calves, caribou (3-4 wk)	Adult caribou (insect-free, July)	Adult reindeer (insect-free, August)
Grazing	7%	24%	53%	49%
Lying	66%	55%	33%	30%
Standing	9%	5%	1%	3%
Walking	12%	11%	11%	14%
Trotting	2%	5%	2%	3%
Running	2%	2%	<1%	3%
Suckling	4%	<1%	—	—
Reference:	Hardangervidda Thomson (1973)	Prudhoe Bay (Table 2a)	Prudhoe Bay (Figure 4)	Hardangervidda Thomson (1971)

reindeer in Norway; Thomson 1973). The gradual development of the *Rangifer* calf activity towards an adult pattern is illustrated in Table 2b.

Nursing behavior

A total of 55 successful suckling events were observed over the 6 wk study period in 1972, 35% of which were timed at between 10 to 85 sec duration (mean 33.3 sec). At the start of the study, calves were approximately 2-4 wk of age, assuming calving to be approximately June 8 (Lent 1966; Calef and Lortie 1973), and they were suckled significantly ($P < 0.05$) longer than calves at 6-7 wk of age (Table 3). These data confirm observations on wild reindeer in Norway and domesticated reindeer in Sweden. The general ontogeny of nursing behavior for members of the genus *Rangifer* is shown in Fig. 3. Unlike reindeer, in which a lactating female may nurse several calves at one event, only single nursing events were observed in caribou.

In a separate study on milk production of reindeer (White, Holleman, and Luick, unpub. obs.), it was shown that milk intake of reindeer calves was 1.5-2 $1d^{-1}$ for the first 2 weeks of age, after which it declined exponentially, *viz.*

$$M = 2.18e^{-0.0116A} \quad \text{———————————(1)}$$

where M = milk intake ($1d^{-1}$) and A = age of calf (d).

Table 3

Duration of single nursing events (±SD) of caribou calves at Prudhoe Bay.

Age of calf (wk)	Duration (sec)	Significance of difference
3-4	36.0±7.3	$P < 0.05$
6-7	26.7±4.4	

Insect harassment

(a) **Relationship of insect harassment with wind and temperature.** Insect harassment was observed to have a dominant influence on caribou social behavior, as evidenced by changes in gregariousness, activity times, speed of movement, and habitat selection. The presence and degree of insect harassment on caribou could be recognized (and classified as moderate or severe)

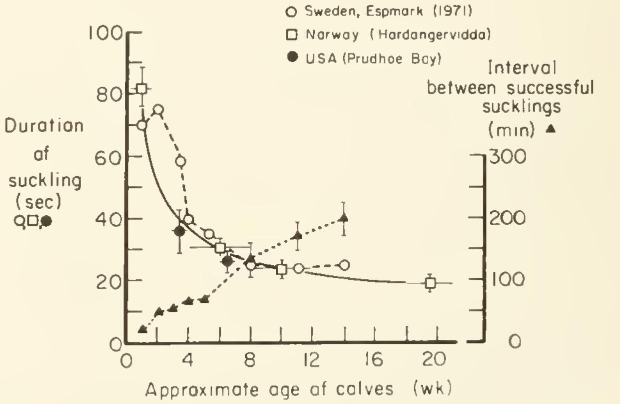


Fig. 3. *Comparison of the ontogeny of suckling behavior in domesticated (○) and wild (□) reindeer and caribou (●).*

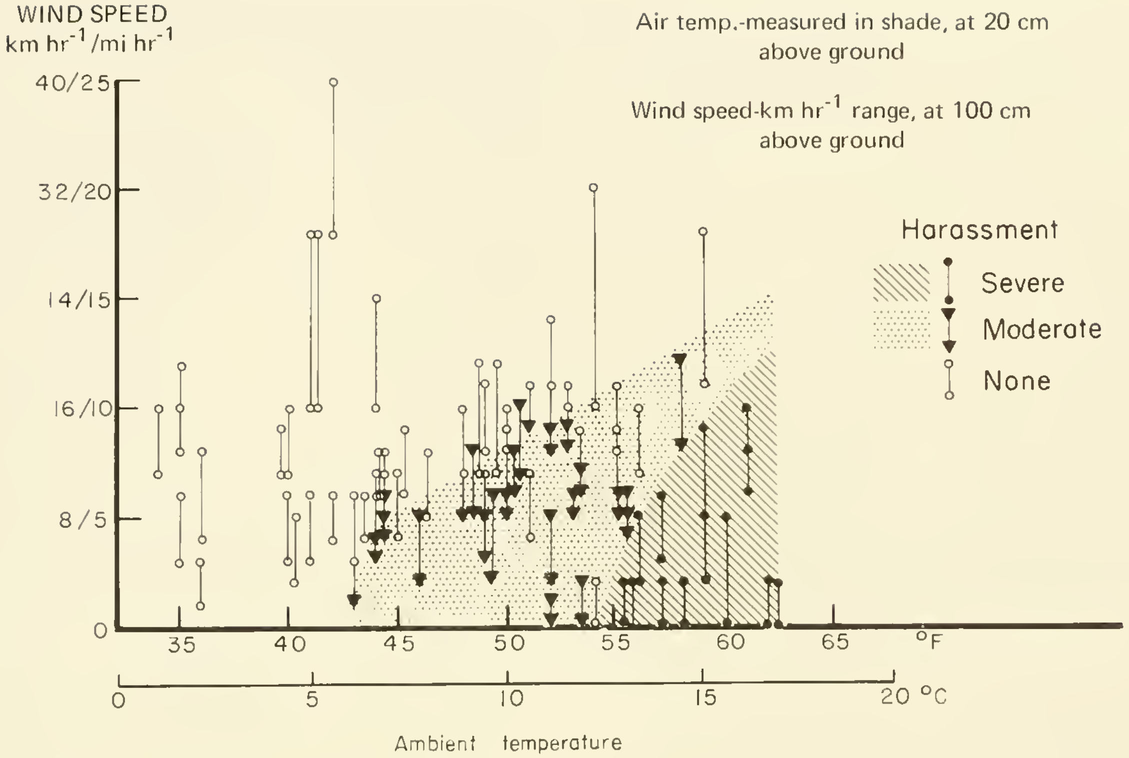


Fig. 4 *Relationship of intensity of insect harassment on caribou with ambient temperature and wind speed.*

from a variety of individual behavior responses, including tail wagging, ear flicking, head and body shaking, twitching, shuddering, leaping, and bounding, as described by Thomson (1971, 1973).

Mosquitos (*Aides* spp) became active, and the first signs of caribou harassment apparent, as shade air temperature increased above 6°C under still air conditions. With increasing temperature, mosquito harassment of caribou became progressively greater, as did the mosquitos' tolerance for wind. At shade air temperatures of over 13°C, usually on warm, sunny days, warble flies *(Oedemageon tarandi)* were observed to be active around caribou herds, causing avoidance responses typical of severe harassment. This relationship between intensity of insect harassment with ambient temperature and wind strength was quantified for the Prudhoe Bay area through frequent field recordings (Fig. 4). The regularity of the relationship made it possible to predict the degree of harassment from prevailing weather conditions on any day.

Unfortunately, the continuous data on air temperature and wind speeds at the small Prudhoe Bay meteorological station did not correspond to the same parameters measured on the field, because wind speed near the ground was not measured, and because local site variations accounted for a considerable variation in temperature. However, as an approximate guide, if a maximum daily temperature of 8.5°C or over was recorded, a day of moderate insect harassment could be predicted. If the maximum was 13.5°C or over, a day with severe insect harassment was predicted. The number of days in which caribou would experience insect harassment as predicted from meteorological data is listed in Table 4. Also shown in Table 4 are estimates of the cumulative duration of harassment for 1972 and 1973.

In all years, July is the peak month for insect harassment, with 20-25 days mild enough for harassment, during approximately half of which severe harassment on caribou can be expected. For mosquitos, the season extended

Table 4

Estimates of periods of possible insect harassment of caribou calculated from Prudhoe Bay weather data.

Period	Number of days when harassment was			Cumulative duration of insect harassment (hr)	
	nil	mild	severe	mild	severe
1970					
June	21	4	5	–	–
July	6	14	11	–	
August	21	6	4		
Summer Season 1970	48	24	20		
1971					
June	15	12	3	–	
July	8	13	10	–	
August	18	8	6	–	
Summer Season 1971	41	33	19		
1972					
June	23	7	0	–	
July	11	10	10	130(17)	12(2)
August	4	8	0	48(17)	0(0)
Summer Season 1972	38	25	20		
1973					
July	11	17	9	91(12)	101(14)
August	5	7	2	53(18)	13(4)
Summer Season 1973	16	24	11		

The index of insect harassment was estimated from temperature and wind speed records from the Prudhoe Bay weather station according to Fig. 4. Wind speed at 1.5 m from the ground (G, km hr^{-1}) was used in the estimation and was calculated from the weather station wind speed records (W, km hr^{-1}) *viz:* $G = 1.0 + 0.5\ W$.

Value in parentheses is duration of harassment as a percentage of the total period (i.e., 744 hr in July, 288 hr in August).

over nearly the whole study period from 25 June to 10 August, whereas warble flies were noted in suitable weather between 23 July and 15 August.

(b) **Effects of insect harassment on group size, composition, activity and movement.** On cool, non-insect days in June, July, and August, caribou were typically segregated into female-yearling-calf groups and male groups (Table 5). These groups noted under insect-free conditions had a mean size of 22 individuals, with only four groups (3%) of over 100 (Table 6). However, under insect harassment, groups readily coalesced, resulting in both a significantly higher proportion of mixed groups (Table 5) and an increase in group size. The 92 insect-harassed

Table 5

Effect of insect harassment on segregation of caribou into female-yearling-calf and male groups.

	Group Structure	
	Segregated	Integrated
No insects	59	17
Mild and severe harassment	39	26

Chi-square test shows these differences between level of harassment were significant ($X^2 = 5.18$ at 1 d.f. $P < 0.05$).

Values shown are the number of groups in each category.

groups noted had a mean size of 77, with 21 groups (23%) of more than 100 individuals (Table 6).

Caribou which were not harassed typically would be dispersed widely in a loosely coordinated group, alternating periods of concentrated grazing with lying, and often meandering only a few km in 24 hours. Caribou under mild insect harassment, a situation indicated by frequent tail flicking and head shaking, would move closer together in an oriented group, walking or trotting as they grazed. In a resting period, the animals would lie and stand close together; lying animals would often jump to a standing position and shake or scratch themselves. Under severe harassment, large massed herds would be seen making long, rapid movements, during which individuals would occasionally pause to quickly eat, then run or trot to rejoin the general movement.

Table 6

Effects of insect harassment on group size. Values shown are the number of groups noted in various size classes during the study period.

Group size	1-10	11-50	51-100	101-500	500+
No insects	70	42	11	4	0
Mild and severe harassment	40	18	13	18	3

The effect of increasing intensity of harassment on the activity budget was quantified and is illustrated in Fig. 5. Grazing and lying times declined markedly, and time spent standing *en masse* and in locomotion increased. These results parallel earlier findings for wild reindeer in Norway (Fig. 5).

Attempts were made to document the speed of movement under different levels of harassment by relating distance covered to time taken. Under insect-free conditions, caribou groups averaged 0.53 km hr^{-1} over several hours of alternating active and rest periods (Table 7). At this speed, undisturbed groups would move an estimated 14 km per day.

During insect harassment, the speed of movement of caribou depended on the time interval chosen. An insect-harassed individual or group was observed to run 25-35 km hr^{-1} over several minutes. Walking, trotting, or running by a harassed group averaged 8-16 km hr^{-1} over a longer interval (for example, during caribou movements along the Sagavanirktok River towards the coastal area). However, average speed of caribou movement was 3.14 km hr^{-1} for periods of severe harassment, and 1.36 km hr^{-1} during mild harassment. The differences were significant (Table 7). At these speeds, a caribou group harassed for 8 out of 24 hours would move a distance of 14 to 42 km, an average of 28 km.

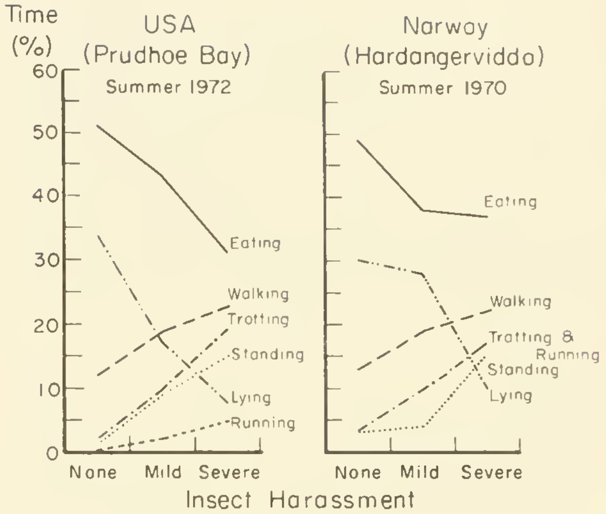


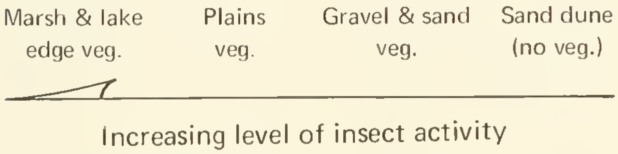
Fig. 5. *Effect of insect harassment on daily activity patterns of caribou at Prudhoe Bay (this study) and reindeer at Hardangervidda, Norway (Thomson 1971).*

Table 7

Effects of insect harassment on daily average rate of movement.

<table>
<tr><td></td><td colspan="3">Degree of fly harassment</td></tr>
<tr><td></td><td>none</td><td>mild</td><td>severe</td></tr>
<tr><td>Number of groups</td><td>13</td><td>12</td><td>8</td></tr>
<tr><td>Mean speed (km hr⁻¹)</td><td>0.53</td><td>1.36</td><td>3.14</td></tr>
<tr><td>t-test significance</td><td colspan="2">P < 0.05</td><td></td></tr>
<tr><td></td><td></td><td colspan="2">P < 0.1</td></tr>
<tr><td></td><td colspan="3">P<0.01</td></tr>
</table>

(c) **Habitat use.** Observed movements of caribou under insect harassment were not random in the Prudhoe Bay area. With the first indication of insect activity, grazing caribou would orient into the wind, but would otherwise remain grazing on the flat plains which constitute their major habitat. However, in their grazing patterns, they would avoid marshy areas and the lush vegetation of lake edges where mosquitos were more troublesome.



At an increased level of harassment, groups moved more quickly, heading toward areas of tundra with the least insect activity. Thus, inland groups moved north into the wind toward the coast, where the prevailing north wind reached its maximum velocity. During this movement, caribou frequently moved along river beds and on the numerous game trails. In the coastal areas, the caribou would find optimum relief by lying or standing in the wind-oriented "gullies" of the sand dune area or on the extensive sand or gravel bars of the river deltas where lack of plant growth was not conducive to mosquitos, or even by standing in the open water of the rivers and the Arctic Ocean. If harassment was not too severe at the coast, the caribou would remain there, grazing on the plants of the dry sand dune areas.

Under mild harassment, caribou would often remain on the flat plains which constitute the major habitat.

As insect harassment declined, normally in association with a reduction in air temperature or an increase in wind velocity, herds would leave the coastal area and slowly move inland, with concentrated grazing and dispersal into smaller-sized units, and males and females in increasingly segregated groups (Fig. 5). Following several days of freedom from insect harassment, groups would continue to disperse inland out of the study area, but with the return of warm, windless weather, the groups would predictably coalesce and move rapidly to the coast (Fig. 6).

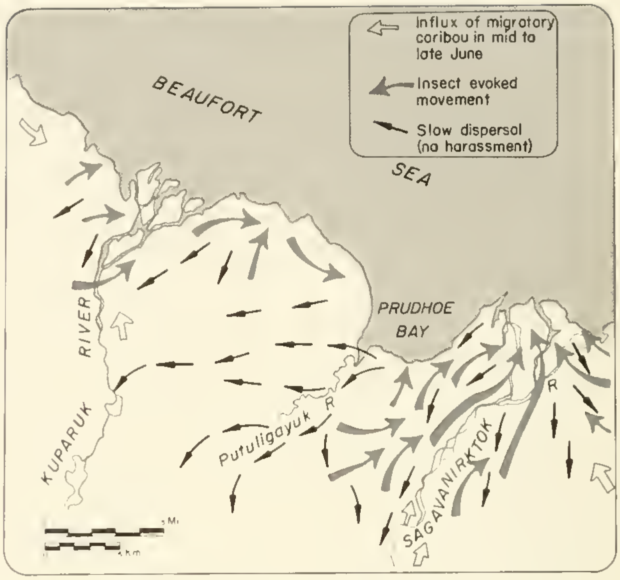


Fig. 6. *An assessment of the effects of insect harassment on observed movements of caribou in the Prudhoe Bay area.*

As an alternative to the use of coastal areas under fly harassment, males particularly, either singly or in groups, would often move onto the raised and bare gravel roads and pads of the oil development. Individual males could even be found standing or lying in the cool shade cast by the machinery and equipment around the camps. In 1973 higher winds associated with the Franklin Bluffs apparently attracted caribou seeking insect-relief areas.

As discussed above, Prudhoe Bay lies in the overlap between the summer ranges of two major caribou populations which make traditional seasonal movements and migrations (Hemming 1971). However, local summer movements and use of the tundra by caribou in the Prudhoe Bay area appeared to be dependent on the degree of insect harassment and, in insect-free periods, on the caribou's feeding preferences within the successional phenology of vegetation types (see below).

Classification of vegetation into phyto-sociological units

Fig. 7 shows diagrammatically the approximate pattern of vegetation types in the study area; six major terrestrial vegetation types (I_S)

Fig. 7. *Diagrammatic representation of Prudhoe Bay vegetation types in relation to moisture gradient and elevation. Numbers in brackets are vegetation types in accordance with the Webber/Walker scheme (this volume):*

Webber/Walker Vegetation Continuum

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Normal moisture gradient				→ increasing wetness			
Sand dunes	Type 15		Type 16		Type 17		
Streams			Type 13		Type 12		
Pingos	Type 10						
Snowbanks		Type 9					
Frost boils		Type 8					

The numbering of the sand dune communities is tentative and will probably change following more extensive mapping in the dunes. The following is a brief description of the current types:

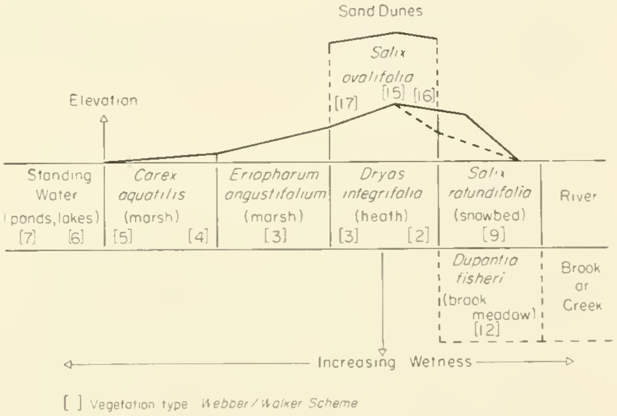
Type 15 — Pioneering communities consisting mainly of *Elymus arenarius, Artemisia* spp and *Salix ovalifolia*.

Type 16 — Drier communities on stabilized dune sand which has developed polygonal patterning. This type is similar to Type 2 and 3 but with much more *Salix ovalifolia* and *Artemisia* spp.

Type 17 — The wetter communities in the dunes which are similar to Type 4 but with abundance of *Salix ovalifolia*.

Vegetation Key: Webber/Walker Scheme for Prudhoe Bay (Key to the most common vegetation types of Prudhoe Bay)

1.	Lichens abundant	2.
	Lichens rare	3.
2.	Many fruticose *and* crust lichens	TYPE 1
	Mostly only fruticose lichens	TYPE 2
3.	*Dryas* and/or *Salix* spp. abundant	TYPE 3
	Dryas and/or *Salix* spp. rare	4.
4.	Mosses rare	TYPE 6
	Mosses abundant	5.
5.	*Drepanocladus* species dominant	TYPE 4
	Scorpidium scorpioides dominant	TYPE 5



---

were distinguished using Sørensen's index of similarity:

$$I_S = \frac{2.c.100}{a+b}$$

where *a* is the number of plant species in a stand of vegetation with a constancy ≥ 50; *b* is the equivalent value for the compared stand; *c* is the number of shared species. The mean index of similarity between stands within types was 64.7 (SD = 9.1) and between vegetation types 24.7 (SD = 17.6). The vegetation types correspond to the criteria of associations, but a formal classification was not attempted due to lack of data on the cryptogams. Vegetation types were named after the dominant species in each type.

Vegetation distribution in the study area was surveyed in four ground transects covering the land area between lakes. Lakes and sand dunes were recognized from aerial photographs and maps, and their distribution assessed in five map transects. The results of the ground transects are shown in Table 8, and the combined ground and aerial transects, in which free-water cover was deleted, is shown in column 8 of Table 8. Also shown in Table 8 are the same vegetation types with their appropriate designation, according to Webber's vegetation map for Prudhoe Bay (this volume).

Caribou grazing patterns and dispersion

(a) **Caribou preference for vegetation types.** Groups of caribou were observed for 10 min

Table 8

Percentage distribution of vegetation types along four transects of 15,168 m in total length. Also shown is the distribution across sand dunes excluding free-water cover (% of land cover).

Vegetation types	Designation from vegetation map*	Webber/Walker scheme	Transect				Mean(SD)	% of land cover
			1	2	3	4		
Dryas integrifolia heath type	$F_1 \rightarrow F_3$	Types 1,2,3	6	5	1	8	5(2.4)	5
Salix rotundifolia snowbeds	F_W9	Type 9	3	0.5	–	–	0.2	–
Dupontia fisheri brook/meadow type	$S_{12} \rightarrow F_{3,\underline{4}}$	Type 12	4	2	–	11	4(4)	4
Eriophorum angustifolium polygon marsh type	P_H3; $4d \rightarrow F_f2,8$	Type 3	72	56	46	30	51(15)	52
Carex aquatilis marsh type	$L_6 \rightarrow L_{13}$ or $F_r,\underline{5},3$	Types 4,5,6	8	23	41	50	31(16)	31
Sand dunes *(Salix ovalifolia)*	D15→D17**	Types 15,16,17	–		–	–	–	–
Water			9	13	11	1	8.5(4)	–
Roads			1	1	1	–	0.7	–

*See prefix and suffix descriptions, Webber and Walker (this volume).

**Tentative numbers.

Transects were established in mid- to late July 1972.

SD, standard deviation.

intervals to determine the vegetation types through which they grazed.

In late June a preference was shown for the *Dryas* heath and the adjacent snowbeds. These communities were slightly elevated, were well drained, and provided an early source of calciphilic vegetation composed of *Carex scirpoidea* on the heaths, with herbs, flowers of *Dryas integrifolia* and *Saxifraga oppositifolia*, lichen and *Salix rotundifolia* in the more protected depressions. Later in the season (after mid-July), the *Dupontia fisheri* wet meadow was preferred, perhaps because it had then contained a rich variety of herbs, salices, and grass-like species.

The combined observations of caribou dispersion in relation to plant vegetation types for the 1972 field season are shown in Table 9. Thus, 42% of all animals were noted on the *Eriophorum* marsh, the most available community (52%); almost 20% were grazing the *Dryas* heath/*Salix rotundifolia* snowbed community, and 12 to 14% were grazing the other communities. An assessment of caribou dispersion in relation to vegetation type was also available from the behavior study, and the distribution was confirmed. For example, 59% of caribou grazed the *Eriophorum* and *Dupontia* types; 15% grazed the *Dryas* heath and snowbed types; 8% grazed the *Carex* marsh, and 18% grazed the sand dunes. The latter observations were confined to periods of insect harassment.

When distribution is expressed as a function of the availability of the vegetation type in the area, it is clear that the *Dryas* heath/snowbed and the *Dupontia* wet meadows were used at almost 3 times their availability and the sand dunes at almost 2 times their availability, while the main community, the *Eriophorum* marsh, was used almost in proportion to availability. An apparent discrimination against the *Carex* marsh was noted. However, the *Carex* marsh was not available for grazing early in the summer because of the high water levels in it, which suggests the type may not be as available as shown in Table 7. From the above discussion, it is clear that the ratio of caribou dispersion in relation to vegetation type (Table 9, column 13) should not be interpreted as showing grazing preferences without accounting for the seasonal trends in the vegetation types with respect to phenology, and the probable presence of a prime mosquito habitat. Thus, the evident lack of preference for

Table 9

Dispersion of caribou on vegetation types in relation to group size. Values given are percentages of observations for the particular group or period.

	Caribou group size											
	1-10		11-20		21-99		100		All groups		Availability of vegetation type (%)**	Grazing dispersion relative to vegetation availability***
Vegetation types	N	%	N	%	N	%	N	%	N	%*(A_i)	(B_i)	(%) (X_i)
Dryas integrifolia heath/*Salix rotundifolia* snowbed	7	8.2	6	18.2	11	35.5	4	13.8	28	18.3	5	35.3
Dupontia fisheri brook meadow	9	10.6	7	21.2	3	9.7	5	17.3	24	14.2	4	35.4
Eriophorum angustifolium marsh	44	51.7	11	33.8	9	29.0	17	58.6	81	41.8	52	8.1
Carex aquatilis marsh	17	20.0	4	12.1	2	6.5	–	–	23	12.5	31	4.1
Salix ovalifolia sand dunes	8	9.4	5	15.2	6	19.4	3	10.3	22	13.2	8	17.1
	85	100.00	33	100.0	31	100.0	29	100.0	178	100.0	100	100.0

*Mean percentage normalized to give a total of 100% for all vegetation types.

**From Table 7.

***Values (X_i, column 13) were calculated from the normalized mean for all groups (A_i, column 11), the percentage distribution of vegetation type (B_i, column 12), where i = vegetation type (i = 1, 5), i.e. $X_i = A_i/B_i \times 100./\Sigma A_i/B_i$.

the *Eriophorum* and *Carex* marsh types could be due to their higher water table, which would be associated with mosquitos, and to the high proportion of standing dead plant material and mosses. When utilizing the *Eriophorum angustifolium* marshes, caribou characteristically grazed the raised micro-ridges on the polygons, where there was a richer plant growth than in the stagnant polygon trough.

The distribution of caribou on the vegetation types in relation to the caribou group size is also shown in Table 9. Most observations for the small group sizes (1-10 and 11-20 animals per group) were made on days when insect harassment was minimal or absent. Groups in excess of 100 individuals were noted under conditions of severe insect harassment (Table 6) and when grazing adjacent to the sand dunes after a period of severe harassment. During periods of mild to severe insect harassment, no animals were observed grazing the *Carex* marsh, while at other times the distribution of animals was similar to that noted for periods of zero to mild insect harassment.

(b) Botanical composition of EF samples. The reindeer were taken to the general locality of each vegetation type and allowed to graze freely while attached to a 20 m rope.

Site 1: July 4-6. This site was located in the *E. angustifolium* polygon marsh type. Seven EF samples were collected. The results of the botanical analysis are shown in Appendix Table 1. *E. angustifolium*, with a mean of 45.6% green tissue, constituted the largest portion of the contents at this time. Also, a large portion of dead tissue was collected. Of the total collection of *E. angustifolium*, 62% was green and 38% dead.

Site 2: July 15-16. This site was located on the raised dry heath beds along the river banks. *Dryas integrifolia* was the principal constituent of the heath, and *Salix rotundifolia* dominated the adjacent snowbeds. Although these vegetation types were distinguishable, their proximity to each other and overlapping occurrence made grazing so overlapping that they were considered as one unit. Five EF samples were collected from this site. The results are shown in Appendix Table 2. *Carex scirpoidea* from the dry heaths and *S. rotundifolia* from the snowbeds constituted 26.4 and 13%, respectively, of the sample compositions. Also noticeable were lichens, mainly *Thamnolia vermicularis,* which comprised about 5.7% of the diet. The relation between green and dead grass-like species was 65% green Cyperaceae and 35% dead Cyperaceae.

Site 3: July 23-27. This site was located in an area described as a wet meadow with a high water table early in the season, but drier with emerging green by the end of July. It was typically situated along brooks on sandy ground with a rich growth of willows and herbs. The dominant species was *Dupontia fisheri.* This vegetation type is situated close to the water, intermediate between the *Eriophorum angustifolium* type and the *Carex aquatilis* types. Six EF samples were collected from this site. Appendix Table 3 shows the botanical composition: grass-like plants (mainly family Cyperaceae) constituted 42.6% of the sample, with *C. aquatilis* and *E. angustifolium* at 11.7 and 17.1%, respectively. Salicaceae constituted 24.7% of the samples and herbs 18.3%. A wider variety of plant groups was chosen from this than other sites, and the amount of dead material was very small.

Site 4: July 28. This site was located in the sand dunes area near the coastline. Two EF samples were collected (Appendix Table 4), *Salix ovalifolia* at 79% was the main plant species. Most scattered herbs were picked. Reindeer fed by moving from one plant cluster to another. A low content of dead material was noted in the samples.

Direct comparison between compositions of EF egesta and available herbage was difficult because reindeer fed by slowly walking and nibbling at the ground cover in a non-random fashion. During a collection period, the animals might move over several vegetation types. Also, the distribution of plant species within vegetation types was commonly clustered, and a valid quantitative evaluation of plant species selection is rather dubious. However, 33x100 cm plots were subjectively laid out and analyzed along the approximate route of movement of the reindeer after the termination of EF collections.

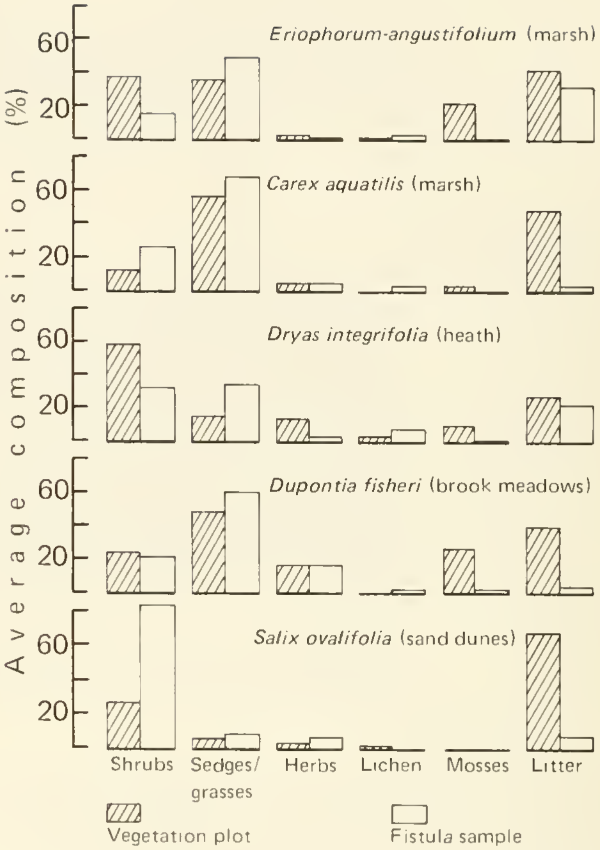


Fig. 8. *Frequency of occurrence of plant groups in esophageal fistula samples compared with vegetation grazed by reindeer.*

Fig. 8 shows the approximate preferences for the systematic plant groups from each study site. Each bar of the histogram represents the percentage composition of the particular plant groups from each sample. The horizontal crosslines represent the median value. Gaare (pers. comm.) suggested the use of the median value as a better representation of the average than the mean when outlying observations occur, as in this case.

From three study sites there was a median preference for the grass-like groups, respectively from the *D. integrifolia-S. rotundifolia* type, the *E. angustifolium* type, and the *D. fisheri* type. From the *S. ovalifolia* sand dunes there was preference for *S. ovalifolia.*

Table 10(a) shows the overall composition of 20 EF samples irrespective of vegetation type. Collectively, they constitute the main components of the diet in early, mid- and late July.

Table 10

Summary of botanical composition of 20 esophageal fistula collections from reindeer at Prudhoe Bay.

(a) Percentage occurrence of plant groups and parts present in more than 1% of fistula samples.

Cyperaceae			54.6
	green	(37.9)	
	dead	(16.7)	
Salicaceae			28.7
	green	(27.1)	
	dead	(1.6)	
Gramineae	green		1.9
Herbs			7.5
Lichens			2.2
Vascular bundles unidentified			1.5
Other dead unidentified			3.6
			100.0

(b) Percentage occurrence of plant species present in more than 1% of fistula samples.

Eriophorum angustifolium	36.6	
Salix ovalifolia	9.0	
Carex scirpoidea	6.6	
Salix arctica	5.7	
Salix rotundifolia	3.5	
Carex aquatilis	3.5	
Dupontia fisheri	1.8	
Dryas integrifolia	1.8	
Thamnolia vermicularis	1.8	
Carex rupestris	1.3	71.6
Trace and unidentified species	28.4	
	100.0	

Cyperaceae constituted more than 50% of the diet, while Salicaceae composed almost 30%. Herbs formed only 7.5% of the diet, while the contribution of lichen and Gramineae was insignificant. Table 10(b) shows the frequency of occurrence of the main plant species. Analysis of esophageal egesta indicates that *E. angustifolium* was the most frequently eaten plant during the summer season.

(c) Botanical composition of caribou rumen samples. During the last week of July, four caribou rumen samples were collected for botanical analysis (Table 11). Almost 35% of the sample was Salicaceae; 28% Cyperaceae (identifiable were 8% *Eriophorum* spp., 3% *Carex aquatilis*), and the balance was composed of herbs, lichen, and dead material. Approximately 14% of the sample was dead material. The nutritional history of the caribou was uncertain, but they were observed to graze mainly the *Dupontia* brook-meadow and, possibly, the surrounding *Eriophorum* marsh types preceding capture. From this standpoint, the analyses may be compared with esophageal egesta analyses obtained from reindeer grazing a *Dupontia* brook community at the same time. Comparison of values for the rumen samples in Appendix Table 5 with the values from the EF samples in Fig. 7 (*Dupontia* meadow) shows a greater amount of grass-like groups compared to willows in the EF samples, while the herb group is about equal. The caribou rumen samples show a higher content of lichen than the EF samples. Detection of quantitative differences in composition between the rumen and EF samples cannot be made due to the small sample sizes. Also, these differences in composition could be related to differential rates of ruminal turnover and/or digestion of the plant species. An absolute difference in selective patterns of reindeer and caribou cannot be determined, although preference for *Salix* spp. was apparently made by caribou.

Plant biomass estimates in relation to vegetation type and grazing behavior

Table 12 lists estimates of live, dead, and total biomass on five study sites at Prudhoe Bay. Peak biomass was recorded for each vegetation type in early to mid-July 1973. A marked decline in live biomass was noted in August. Insufficient sampling early in the season prevented the construction of precise growth curves for these sites. However, based on previous studies of the seasonal progression of primary production at Barrow, Alaska, a linear growth is expected from 20 June. Predicted seasonal patterns in primary production for the main vegetation types at Prudhoe Bay are shown in Fig. 9. Unfortunately, we were unable to estimate between site variations in the seasonal primary production of any one vegetation type. Subjective estimation suggests that variation within most vegetation types was high. For example,

Table 11

Botanical composition of rumen samples obtained by field rumenotomy on four caribou at Prudhoe Bay (July 1972).

Vegetation class	Plant species	Number of samples containing the species	Mean occurrence	
			species	class
	Salix arctica	2	2.3	
	S. lanata	1	3.0	
	S. reticulata	3	0.5	
	S. rotundifolia	1	0.3	
	S. pulchra	4	11.5	
	Miscellaneous*	2-3	16.7	
Shrubs		4		34.3
	Cyperaceae	4	16.6	
	Carex aquatilis	3	3.2	
	Eriophorum spp.	4	8.9	
	Dupontia fisheri	3	5.9	
	Equisetum spp.	3	1.1	
	Gramineae	3	2.8	
Grass-like				38.5
	Compositeae (flower heads)	1	0.3	
	Polygonium viviparum	2	0.6	
	Valeriana capitata	1	tr	
	Saxifraga spp.	1	tr	
	Stellaria spp.	1	tr	
	Miscellaneous*	2-3	8.9	
Herbs				9.8
	Cetraria spp.	2	1.4	
	Dactylina arctica	1	0.3	
	Sphaerophorus globosus	1	0.3	
	Thamnolia vermicularis	2	1.0	
Lichen				3.0
Dead plant parts			14.4	14.4
Totals			100.0	100.0

*Partially digested plant parts; could not be identified into species.

variation may be high within the *Dryas* heath/snowbed community, depending on the relative contribution of the snowbed species to the communities. Also, variations in the amount of willows in the *Dupontia* wet meadow/brook bank community could result in variations in live biomass of between 30 and 90 g m^{-2}.

Food intake of reindeer and caribou

In principle, an estimate of daily food intake by adult caribou could be made by: (a) determining the rate of eating (RI, g DM consumed per min eating time) of a tractable animal; and (b) relating RI to observations on the amount of time caribou spend eating. Thus, food intake (g d^{-1}) = RI (g min^{-1}) x average daily eating time (min d^{-1}).

(a) **Estimation of eating rates.** A quantitative estimate of food ingestion was made by assuming that all ingested food could be collected from an esophageal fistula during a grazing period of fixed, or known, duration. A summary of rates of esophageal egesta collection rates for experiments in 1972 is shown in Table 13. A considerable variation in rate of intake was noted within vegetation types (coefficient of variation = 34-75%), and the variance (1.52 g min^{-1}) was high relative to the mean rate of

Table 12

Seasonal changes in biomass of some vegetation types at Prudhoe Bay (1973).

Vegetation type	Date	Number of observations	Dry biomass (g/m^2)		
			Live	Dead	Total
Eriophorum angustifolium marsh	7/10/73	3	34.1± 6.5	87.1±22.1	121.2±23
	7/29/73	3	41.4± 1.6	33.9± 6.7	75.3± 7.4
	8/12/73	3	18.1± 4.4	66.2± 7.0	84.3± 8.9
	9/19/73	3	7.1± 2.8	111.1±18.9	118.5±21.5
Dryas integrifolia heath/ *Salix rotundifolia* snowbed	7/ 8/73	3	35.3± 4.8	45.5± 4.4	80.8± 4.9
	7/21/73	3	34.5± 5.9	76.3±22.7	110.8±28.1
	9/19/73	3	21.9±11.2	88.8±19.8	110.8±19.5
Dupontia fisheri brook meadow	7/19/73	3	71.3± 8.7	76.7±12.7	147.9±19.0
	8/12/73	3	30.4± 3.1	91.9±11.1	122.5±14.1
	9/19/73	3	7.1± 1.4	83.7± 7.9	91.8± 9.1
Carex aquatilis marsh	7/20/73	3	25.9± 3.2	55.2±12.6	81.4±15.5
	8/ 7/73	3	24.4± 1.4	39.4± 5.6	63.9± 6.7
	9/19/73	3	3.8± 2.9	63.1±36.4	66.9±17.1
Sand dunes	7/14/73	2	31.4± 7.6	20.5±12.1	51.9± 4.5

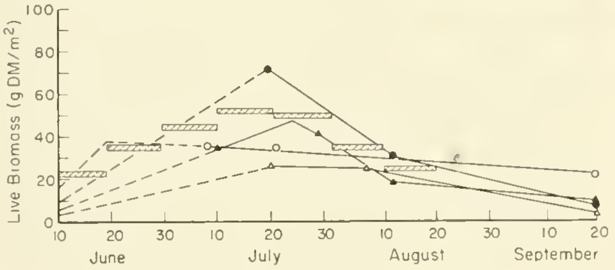


Fig. 9. *Predicted changes in live biomass availability based on data for late July (Table 12) and primary production rates for Barrow, Alaska (Tieszen 1971).* ▨ *, values used to calculate eating rate (Fig. 10) and eating time (Fig. 11) for the estimation of daily food intake (Table 15).* ▲ *, Eriophorum marsh; O, Dryas heath/Salix snowbed;* ● *, Dupontia brook bank;* Δ *, Carex marsh.*

food intake for all studies (2.92 g min^{-1}). From such a high degree of variance, it can be inferred that factors regulating food intake were not constant from one estimation to the next.

Changes were made in the experimental procedure in the following (1973) field season to increase the precision with which food intake could be estimated and to investigate some factors regulating food intake. Reindeer were fasted for 3-4 hr before using them in an intake experiment, and the collection period was reduced (e.g., from 20 min in 1972 to 10 min in 1973). Further, three to five collections were made on the one vegetation type, and a 20 min grazing period was allowed between collections. These experiments indicated that the rate of food intake declined at approximately 30% per hr during a grazing period. The peak rate of food intake increased in a curvilinear fashion with available live biomass, as shown in Figure 10a. Eating rate was apparently maximized at 6 g (DM) min^{-1} [6/83 = 0.072 g min^{-1} kg (BW)$^{-1}$] at and above a live biomass of 70 g (DM) m^{-2}.

It can be calculated that a reindeer confined to a small area has the potential to denude a range of live biomass 70 g m^{-2} at a rate of 11.7 min m^{-2}. This calculation assumes a simplistic approach to feeding, for the amount of time spent searching is not considered; however, the powerful harvesting potential of caribou is obvious.

At the Prudhoe Bay study site, peak live biomass was in the range of 30 to 70 g m^{-2} depending on the harvest date and the vegetation type (Fig. 9). Thus, some of the variance associated with the 1972 estimates of feeding rate (Table 13) could be attributed to variations in available biomass at the study sites.

(b) **Calculation of food intake from eating rates and time spent eating.** During all periods free of insect harassment, adult caribou spent 51% of the day eating (Table 2), and the female-yearling-calf group spent 53% of the day eating.

Table 13

Mean rates of forage collection from esophageal fistulated reindeer. A collection period was started when the reindeer terminated its lying period; esophageal samples were collected over a timed interval of 14-20 min.

Vegetation type	Sample identification	Number of observations	Mean (±SE) rate of dry matter collection (g/min)	CV (%)
Eriophorum polygon marsh	1-7	7	2.54 ± 0.35	36
Dryas heath and snowbeds	9-12	4	3.24 ± 0.94	58
Dupontia brook/meadow	14-17	4	2.36 ± 0.40	34
Carex marsh	13, 18	2	2.37 ± 1.26	75
Sand dunes *(Salix ovalifolia)*	19, 20	2	5.30 ± 1.76	47
Total	1-7, 9-20	19	2.92 ± 0.35	52

CV = coefficient of variation (SDx100/mean).

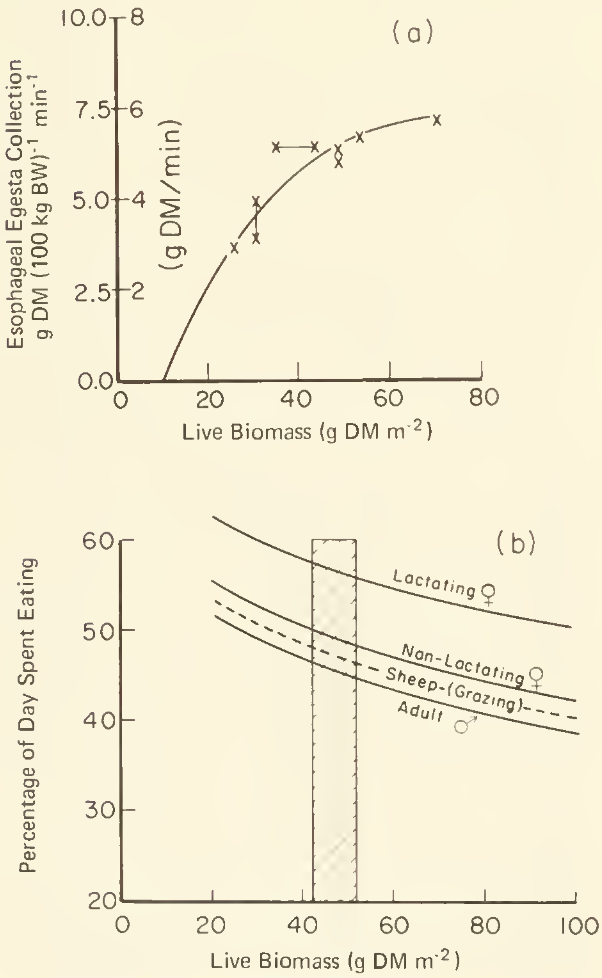


Fig. 10. *Relationship between rate of eating, as estimated by collection of esophageal egesta, and available live biomass (a). Forage samples were collected over a 10 min period following 3-4 hr fasting. Theoretical relationships between percentage of day spent eating and availability of live biomass (b). The general relationship was adapted from data for grazing sheep (---, Young and Corbett, 1972).* ▨, *average available live biomass at Prudhoe Bay in July (see Fig. 9).*

Unfortunately, we have no comparable detailed estimates for adult males. However, we have estimates of the grazing intensities of these cohorts (Table 14) which show that lactating caribou graze more intensively than non-lactating female caribou and caribou bulls. If it is assumed that all cohorts spend the same proportion of the day grazing (where grazing time = eating time + searching time), then estimates can be made of the relative amount of time spent eating (Table 14). This may be an oversimplification of grazing behavior under natural conditions, for it is known that the amount of time ruminants spend grazing decreases exponentially with increasing available biomass (Young and Corbett 1972). Since we were unable to determine this parameter, the general form of a relationship between grazing time and biomass

Table 14

Comparison of grazing intensity (±SE) and the predicted time spent eating by unharassed caribou groups and reindeer.

Group	Number of observation	Grazing intensity (%)	Predicted daily eating intensity* (%)	(min)
Caribou males	22	60.4±4.3	46(40-50)	662
Caribou, lactating females	22	79.5±2.3	57(53-60)	821
Caribou, nonlactating females and yearlings	4	67.5±6.0	49(45-53)	706
Caribou, calves (3-4 wk of age)	–	–	24	346
Esophageal fistulated reindeer, nonlactating females	19	68.2±3.9	–	–

Grazing intensity = (eating time/eating time + searching time) x 100.

Values in parentheses are the likely range for testing this model.

*Based on an observed value of 52.8% for the eating intensity of females (Table 2) and the assumption that all cohorts spend approximately 66-67% of the day grazing (see text).

availability was taken from previous studies on sheep (Allden and Whittaker 1970; Young and Corbett 1972) and adapted to the Prudhoe Bay site (Fig. 10b). It was assumed that (a) a mean live biomass of 45 g m^{-2} was available to the caribou in June, and (b) the relationship between percent of day spent eating and live biomass was similar for the three cohorts. Thus, three parallel lines were available for the calculation of the percent of day spent eating as the live biomass altered seasonally (Fig. 10b).

The simplistic expression for calculation of food intake is given as

food intake = eating rate x eating time.

From the above discussion, it is clear that both factors on the right side of the expression are proportional to available biomass, and the relationship between daily food intake as a function of live plant biomass is shown in Fig. 11.

In the present study, the mean seasonal change in biomass was estimated from the trends in Fig. 9 in five 10-day intervals commencing 20 June. At the extremes during late June to early July, the main vegetation type consumed was the *Dryas* heath/snowbed type of biomass 25 g m^{-2} (Fig. 9), while in late July to early August the *Dupontia* brook bank community of biomass 35 to 50 g m^{-2} was preferred. In the main, caribou were assumed to graze the *Eriophorum* marsh, with a live biomass in the range 25-45 g m^{-2}.

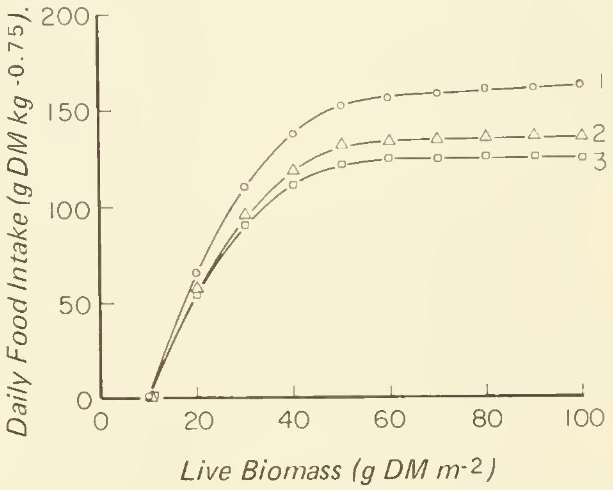


Fig. 11. *Theoretical relationships between daily food intake and availability of live biomass for lactating females (1), adult males (2), and non-lactating females (3). The relationships were calculated as the product of relationships shown in Figs. 10a and 10b.*

Summaries of expected biomass of live material, predicted mean daily food intake, and energy intake are shown in Table 15. For purposes of calculation, body weights of the adult cohorts—males, non-lactating females, and lactating females—were assumed to be respectively 115, 83, and 83 kg.

Table 15

Dry matter intake and energy available for fattening of caribou predicted from estimates of available live biomass and relationships between daily intake versus biomass (Fig. 11).

Cohort	Lactating females (83 kg BW)					Nonlactating female (83 kg BW)					Males (115 kg BW)				
Period	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Available live biomass (g m^{-2})	35	43	52	50	35	35	43	52	50	30	35	43	52	50	35
Dry matter intake (85% of peak, Fig. 11)															
(kg d^{-1})	2.90	3.35	3.10	3.55	2.90	2.54	2.88	2.08	3.02	2.54	3.09	3.48	3.65	3.62	3.09
[g d^{-1} $(kg^{0.75})^{-1}$]	105	122	131	129	105	92	105	112	110	92	88	99	104	103	88
Gross energy intake, GEI															
[kcal d^{-1} (kg 0.75)$^{-1}$]	514	598	642	633	514	451	516	550	541	451	429	483	508	504	429
Metabolizable energy intake, MEI															
(Mcal d^{-1})	6.35	7.37	7.95	7.86	6.35	5.55	6.41	6.82	6.71	5.55	6.78	7.66	8.04	7.97	6.78
[kcal d^{-1} (kg 0.75)$^{-1}$]	231	268	289	286	231	202	233	248	244	202	193	218	229	227	193
Energy requirements, ER [kcal d^{-1} (kg 0.75)$^{-1}$]															
maintenance	190	190	190	190	190	190	190	190	190	190	190	190	190	190	190
milk production	86	78	73	59	54										
total	276	268	263	249	244										
MEI/ER	0.84	1.00	1.10	1.15	0.95	1.06	1.23	1.30	1.28	1.06	1.02	1.15	1.21	1.20	1.02
Energy available for fattening															
(kcal d^{-1})			715	1017		330	1182	1595	1485	330	105	983	1370	1299	105
[kcal d^{-1} (kg 0.75)$^{-1}$]			26	37		12	43	58	54	12	3	28	39	37	3
Body weight gain															
(g d^{-1})			77	110		36	128	173	161	36	4	106	148	141	11
(kg 50d^{-1})	– 1.87 –					– 5.34 –					– 4.17 –				

Periods 1-5 were respectively 21-30 June 1, 1-10, 11-20, 21-31 July, 1-10 August.

Metabolizable energy intake = dry matter intake x gross energy of food (4.9 kcal g^{-1}) x energy digestibility (0.55) x metabolizability of digested energy (0.82).

Energy requirement for maintenance = 2 x fasting metabolic rate [97 kcal d^{-1} (kg 0.75)$^{-1}$]; energy requirements of lactation = energy output in milk/efficiency of milk synthesis (0.74).

Body weight gain = energy available for fattening x efficiency of fattening (0.39)/energy content of new tissue [3.6 kcal g (FW)$^{-1}$].

The calculations indicated that the duration of eating in lactating females (Fig. 10b) leads to intakes of 2.9 - 3.6 kg d^{-1} (105-131 [gd^{-1} $(kg^{0.75})^{-1}$], which were as high or higher than intakes estimated for bulls (3.1 - 3.6 kg d^{-1}). When expressed per unit metabolic body size [gd^{-1} $(kg^{0.75})^{-1}$] food intakes for non-lactating females were similar to the bulls but considerably lower than estimates for the lactating females.

(c) **Prediction of forage removed by the Prudhoe Bay caribou population.** To estimate the amount of forage removed by the caribou population at Prudhoe Bay, the estimates of individual food intakes in Table 15 must be multiplied by the number of animals in the cohort. Also, an estimate must be made of the amount of forage eaten by the yearlings and calves in the population. In the absence of empirical data on the grazing intake of calves and yearlings, the following assumptions were made:

(1) Food intake of calves was assumed to increase with age from 38 [g d^{-1} $(kg^{0.75})^{-1}$] at 3 wk to 88 [g d^{-1} $(kg^{0.75})^{-1}$] at 6 wk. These intakes were 30-70% of adult values. Body weight gain was set at approximately 400 g d^{-1} (calculated from data for reindeer calves).

(2) Intake of yearlings was assumed to be 114 [g d^{-1} $(kg^{0.75})^{-1}$], and body weight gain was set at 250 g d^{-1}.

Calculations were made on the likely food intake for each cohort for each period based on the mean population size for that period (Fig. 2) and the mean herd proportions for 1972 and

1973 as shown in Table 1. Estimates of the cohort and herd dry matter intakes for 1972 and 1973 are shown in Fig. 12. Thus, in 1972 when the average population on the study area was 155 animals, an estimated 25,000 kg of dry matter was consumed during the study period (21 June to 10 August). In 1973, the population was considerably lower, averaging 55 animals, and the amount of herbage consumed in the study period was approximately 5,400 kg.

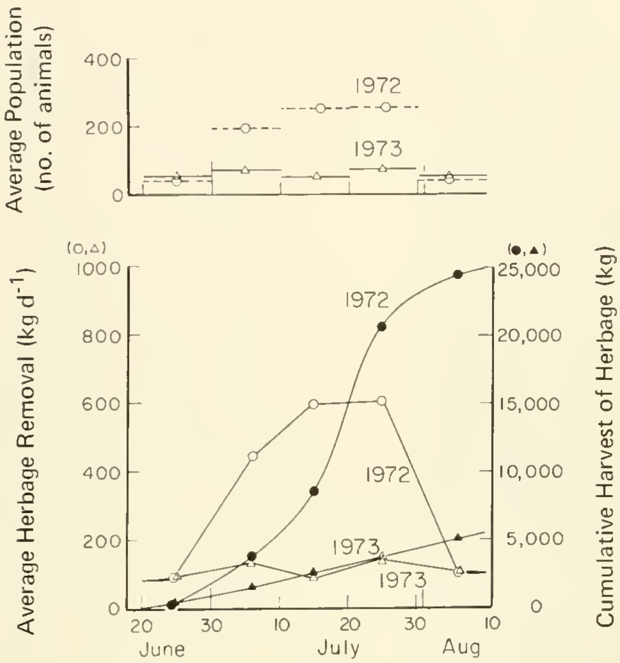


Fig. 12. *Predicted cumulative herbage consumption by caribou in the Prudhoe Bay study area in the summer of 1972 and 1973.*

(d) **Estimation of size of study area.** The interpretation given to harvest values has more meaning to the ecosystem as a whole if intake or harvest is expressed per unit area and in relation to primary production. As stated in the methods section, caribou populations at Prudhoe Bay were usually assessed by visual observation from the road system. The area under surveillance, 1.5 km on either side of the road, amounted to 530 km^2 and lay between the approximate boundaries of 149°05′ W in the east, 148°08′ W in the west, 70°08′ N in the south, and 70°22′ N in the north (Fig. 1). However, this area included riverbeds, ponds, and lakes as well as vegetated land. To estimate the relative amounts of each land type in the study area, 13 transects (6 north-south and 7 east-west) were drawn on a topographic map, and the relative occurrence of each area noted. The results, shown in Table 16, indicate that approximately 54% of the study area (i.e., 288 square km), was vegetated in late July and hence was available for grazing by caribou.

An effort was also made to calculate the total area of continuous habitat available to the caribou at Prudhoe Bay. An examination of topographic maps of the Prudhoe Bay/Beechey Point area suggested that the coastal tundra was bounded by the Kuparuk and Sagavanirktok rivers, on the W and E respectively, and by the White Hills (approximately 75 km away) and

Table 16

Approximate size of study areas and land classification.

	Total	Available for grazing	Lakes	River bed and dunes
Proportional distribution (±SE)		0.54 ±0.03	0.23 ±0.03	0.22 ±0.04
Study site (km^2) (Prudhoe Bay)	532	288	124	119
Kuparuk/Sagavanirktok River drainages (km^2)	2842	1540	665	637

Proportional distribution of land type was determined as fractional occurrence of each on 13 line transects drawn on a topographical map.

Study site includes all land visible 1.5 km either side of the Prudhoe Bay road system.

River drainage is bounded by the White Hills and Franklin Bluffs to the SE and S.

Franklin Bluffs (approximately 53 km away) to the SE and S respectively (Fig. 1). This drainage area was approximately 2,842 square km (Table 16). Thus, the study area was approximately 18% of the total drainage. It was anticipated that counts for the study area might be extrapolated to the drainage, and further, that on days of high insect harassment, the number of caribou observed moving to the coastal dunes should represent the total number in the drainage. Hence, observations of 20, 50, and 100 animals in the study area should yield estimates of respectively 110, 280, and 560 animals in the entire drainage. These latter values are similar to the numbers of animals moving to the coastal dunes on some days in 1972 and 1973 (Fig. 2). However, the estimate is very low compared with two peak values of 1,500 and 1,200 animals observed in 1972 (Fig. 2).

(e) **Estimation of caribou biomass and herbage intake in relation to seasonal primary production.** From the size of the study area and that portion containing grazeable herbage (Table 16), an estimate was made of caribou densities (Table 17). In 1972 a mean population of 155 animals was at a density of 3.4 km^2 animal^{-1}; the effective density was 1.9 km^2 vegetated area animal^{-1}. The following year (1973), total and effective stocking density were respectively 9.7 and 5.2 km^2 animal^{-1}. At a seasonal primary production of 50-70 g m^{-2} (mean 55 g m^{-2}), it can be calculated that during the respective summers of 1972 and 1973, approximately 0.16 and 0.03% of the aboveground vascular production was ingested. If the animals noted in 1972 and 1973 remained on the study site year-round, then approximately 1.1 and 0.2% of the respective seasonal vascular productions would be removed in the entire year.

In vitro digestibility of plant species consumed by caribou

Table 18 shows a comparison of indices of dry matter digestibility of selected plant species collected 12-25 July, 1972 at Prudhoe Bay. For the micro-digestion *in vitro* technique, rumen liquor was obtained by rumenotomy from tranquilized caribou, from rumen fistulated reindeer grazing vegetation at Prudhoe Bay, and from reindeer given prepared forages.

Table 17

Prediction of herbage intake by caribou in relation to seasonal primary production. Herbage intake was calculated over a period of 52 days (21 June through 10 August).

Parameter	1972	1973
Study area (km^2)		
a) total	532	532
b) vegetated	288	288
Population size (average July/August)	155	55
Caribou density (No. km^{-2})		
a) total	0.29 (3.4)	0.10 (9.7)
b) vegetated	0.54 (1.9)	0.19 (5.2)
Seasonal primary production*		
Prudhoe Bay (kg km^{-2})	55,000	55,000
(range 50-70 g m^{-2})		
Herbage intake (50 d study period)		
a) total (kg)	25,000	5,400
b) per unit area (kg km^{-2})	87	19
c) percentage of above-ground production	0.16	0.03

Value in parenthesis is caribou density expressed as km^2 caribou^{-1}.

*Calculated as peak above-ground, vascular live material.

Table 18

Estimates of dry matter digestibility (%±SE) of hand-picked plant samples and esophageal egesta from reindeer. Rumen innoculum for the *in vitro* technique was obtained from tranquilized caribou, reindeer grazing at the study site[1] or reindeer given a mixed diet[2].

		In vitro digestibility technique			
		Source of innoculum			
Plant sample		Caribou	Reindeer[1]	Mean	Reindeer[2]
Shrubs					
Salix arctica	leaves/buds	71	52±2	62	
S. pulchra	leaves/buds		54	54	24±0.3
S. reticulata	leaves/buds		38		
S. ovalifolia	leaves/buds	35	46±6	41	
S. lanata	live leaves		34±2		
Dryas integrifolia	leaves/stem base	33	33	33	
	heads		21		
D. octopetala	leaves and stems (alpine)				12±2
Sedge and cotton grass					
Carex aquatilis	live leaves	56	68±4	62	39±2
Eriophorum angustifolium	live leaves	48	59±3	55	32±3
	inflorescence + stem		56±3		
E. vaginatum	mature leaves				28±5
Grasses					
Dupontia fisheri	live leaves		79±2		
	inflorescences	67	70	68	
Arctophila fulva	live leaves	56	72	64	
Herbs					
Oxytropis sp.	live leaves		70		
Braya spp.	whole plant		68		
Parrya nudicalus	whole plant		67		
Artemisia richardsoiana sp.	leaves	62	66±3	64	
Pedicularis sp.	inflorescence + leaves		64±6		
Saxifraga oppositifolia	inflorescence + leaves		33±1		
Lichens					
Cetraria cucullata		74±3	48±1	68	77±9
_C, islandica_*					48±9
_Thamnolia vermicularis_*					59
_Alectoria nigricans_*					45
_Lobaria linita_*					45
_Peltigera aphthosa_*					44
_Stereocaulon alpinum_*					18
Cladonia alpestris		27±14	16±7	21	16±3
_C. uncialis_*					44
_C. arbuscula_*					10
_C. rangiferina_*					40
Mosses					
_Hylocomium splendens_*	entire gametophyte				19±6
_Sphagnum magellanicum_*	entire gametophyte				6
Other	entire gametophyte				13
Esophageal egesta					
Eriophorum meadow	reindeer No. 10		62±0.2		
Eriophorum meadow	reindeer No. 12		49±1.4		
Dryas heath	reindeer No. 12		49±3.3		
Dupontia brook bank	reindeer No. 31		50±0.6		
combined	reindeer				45±1.0
	caribou C2	37±2.2			
	caribou C3	43±1.6			

[1] Rumen fistulated reindeer were tethered on vegetation types at Prudhoe Bay.

[2] Rumen fistulated reindeer given a diet containing 67% (dry weight) lichens, 8% Carex aquatilis and 25% brome hay. The food was ground in a hammer-mill and thoroughly mixed.

*Samples obtained from Coal Creek and Nome, Alaska

As a group, the grasses *Dupontia fisheri* and *Arctophila fulva* were more highly digestible than the herbs, sedges, or shrubs (Table 18). With one exception, all herb samples proved highly digestible (64-70%), as were the sedges and cotton grass (48-68%). Digestibilities of salices were generally lower at 34-54%; however, a singularly high value of 71% was noted for *Salix arctica* when incubated with rumen liquor from caribou. *Dryas integrifolia* was of even lower digestibility (12-33%) than the willows.

Unfortunately, no mosses and only two lichens, *Cetraria cucullata* and *Cladonia alpestris,* were available for estimation of digestibility using inocula from caribou or reindeer at Prudhoe Bay. Both lichen samples were obtained from Coal Creek, Alaska. *C. cucullata* was highly digested (48-74%), whereas the digestibility of *C. alpestris* was low (16-27%). A more complete study using inoculum from reindeer given a prepared forage high in lichen showed that the digestibility of lichens was highly variable (10-77%) depending on the species. In contrast, the digestibility of three mosses was very low (6-19%) (Table 18).

Estimates of *in vitro* digestibility of forage samples obtained from esophageal fistulated reindeer were moderate to high at 45 to 62%. However, estimates using liquor obtained from caribou were lower at 37 to 43% (Table 18). The mean estimate of digestibility of the initial four esophageal egesta samples, 52 ± 3%, was higher than the estimate for a combined sample (45%), using liquor obtained from reindeer given a diet high in lichen.

In view of the wide range in digestibility of the vascular plant species and groups, it is difficult to predict a biologically meaningful average digestibility based on botanical composition, without incorporating the relative amounts of each plant species available or eaten. From the mean botanical composition for 20 esophageal fistula samples, shown in Table 10(b), and estimates of digestibility of the species (Table 18), a mean digestibility was calculated which was weighted for the relative abundance of each species (Table 19). For the esophageal samples, a mean digestibility of 56% was obtained; this estimate was 4% higher than the mean *in vitro* digestibility (52%) of four esophageal samples shown in Table 18, and is considerably higher than those estimated using inoculum from caribou rumen (37-43%). A similar calculation based on the botanical analysis of rumen contents from caribou (Table 11) indicated a dry matter digestibility of 52% for forage consumed by them.

Table 19

Comparison of *in vitro* digestibility of esophageal egesta samples with dry matter digestibility calculated from the summation of individual estimates of digestibilities (Table 15) and the % occurrence of species in the vegetation types.

		Predicted dry digestibility based on botanical composition of:			
	Type	(a) range: live material	total	(b) esophageal egesta	*In vitro* digestibility of esophageal egesta
Salix ovalifolia sand dunes	15-17	47	—	44	—
Dryas integrifolia heath	2,9	44	41	50	49
Salix integrifolia snowbed		53	50		
Dupontia fisheri brook meadow	12	59	49	58	50
Eriophorum angustifolium marsh	3-4	50	38	43	49-62
Carex aquatilis marsh	5	62	51	56	51

Table 20

Chemical composition of plant material collected at Prudhoe Bay, 12-25 June 1972. Components were analyzed according to the detergent technique of Goering and Van Soest (1970). Values are expressed as g $(100\ g)^{-1}$ dry matter.

Sample	NDF	ADF ligno-cellulose or crude fiber	CC cell contents	– – – – – –CWC– – – – – –			*In vitro* dry matter digestibility (%)
				Hemicellulose	Cellulose	Lignin	
Shrubs							
Salix arctica	18.5	16.4	81.5	2.1	11.9	4.5	52
S. pulchra	27.2	17.4	72.9	9.8	11.4	6.0	54
S. ovalifolia	31.2	27.3	68.8	3.9	18.6	8.7	46
S. lanata	20.6	17.9	79.4	2.7	13.2	4.7	34
Dryas integrifolia							
leaves/stem base	35.4	33.3	64.6	2.3	14.0	19.1	33
inflorescences	46.2	48.1	53.8	-2.0	21.1	27.1	21
Sedges							
Carex aquatilis	58.2	21.7	41.8	36.5	18.6	3.2	68
Eriophorum angustifolium							
live leaves/10% dead	68.5	24.6	31.5	43.8	19.1	5.1	59
inflorescence + stem	57.5	21.3	42.5	36.0	16.3	4.7	56
Grasses							
Dupontia fisheri							
live leaves/10% inflorescences	45.1	19.6	54.9	25.4	15.8	3.9	79
inflorescences + stem	62.1	31.0	37.9	31.1	25.5	5.5	70
Arctophila fulva	67.7	29.0	32.3	38.8	27.3	1.7	72
Herbs							
Artemisia richardsonii sp.	42.3	29.2	57.7	13.1	24.2	5.0	66
Pedicularis sp.	25.9	20.8	74.1	5.1	14.3	6.5	64
Saxifraga oppositifolia	26.9	35.9	73.1	-8.5	20.5	15.4	33
Lichens							
Cetraria cucullata	31.6	3.7	68.4	27.8	-0.6	4.3	77
Cladonia alpestris (Coal Creek)	83.0	4.6	17.0	78.3	1.7	2.9	16
C. alpestris (Nome)	83.3	2.3	16.7	81.0	-1.3	3.6	16
Esophageal fistula egesta							
Mixed samples EF C1	67.4	35.2	32.6	32.2	25.3	9.8	43
C2	69.9	36.2	30.1	33.6	26.7	9.4	43
C3	62.8	35.0	37.2	27.8	23.0	12.0	41
C4	52.5	32.9	47.5	19.7	25.5	7.2	41
Artificial food							
Mixed reindeer hay*	78.0	24.6	22.0	53.4	18.3	6.3	30
Purina cattle starter No. 1	48.6	27.4	51.4	19.1	24.4	2.9	68

NDF, neutral detergent fiber; ADF, acid detergent fiber; CC, cell contents; CWC, cell wall constituents; lignin was determined as the mineral acid resistant component of ADF.

In vitro digestibilities were taken from Table 16.

*78% lichen, balance of *Carex aquatilis* and brome hay.

Cell Constituents = 100 – NDF

Hemicellulose = NDF – ADF

Cellulose = ADF – lignin

In an analagous manner to that used to estimate digestibility of esophageal and rumen samples, average digestibilities were estimated for each of the vegetation types at Prudhoe Bay (Appendix Tables 5-10). These estimates, shown in Table 19, are the predicted digestibilities if caribou were to graze these communities, consuming the various vascular plant species in proportion to their availability. The estimates refer only to the time period 6-25 July. If caribou were to eat mainly the live plant material, the average digestibilities would be in the range of 44-62%, with the higher values noted for the wetter communities (the *Dupontia fisheri* brook bank/meadow and the *Carex aquatilis* marsh). The wetter communities also contain a substantially higher proportion of dead plant material. If such material is assumed to be 25% digestible, then the average digestibility for the community as a whole is reduced substantially (e.g., the *Eriophorum angustifolium* marsh, from 50 to 38%, and the *Carex aquatilis* marsh, from 62 to 51%) (Table 19).

Also shown in Table 19 are the average *in vitro* digestibilities of esophageal egesta collected from reindeer grazed on these communities, plus estimates of the digestibilities of the esophageal samples based on their botanical composition. In the drier habitats, it was apparent that digestibilities of selected material approximated that which was available as live material. However, in two of the wetter habitats, *Dupontia fisheri* brook meadow and *Carex aquatilis* marsh, the selected material was of a digestibility similar to that of the habitat as a whole (i.e., live + dead material). The suggestion that reindeer were consuming a significant proportion of dead plant material is not substantiated by the botanical analysis of the esophageal fistula samples, which indicated a low intake of dead plant material and litter (Fig. 7). We conclude that the *in vitro* digestibility estimates for these communities (*D. fisheri* brook meadow, *C. aquatilis* marsh), may be underestimated.

No evidence was found for selection of highly digestible material from within the community. However, the pattern of selection of vegetation types described in Table 9 suggests some selection for digestibility, based on preference for the *D. fisheri* brook meadow vegetation type. The lack of preference for the *C. aquatilis* marsh (Table 9), despite its predicted high quality (Table 19), suggests that its preferability may have been lowered by other factors, such as water ponding in early July, being a prime mosquito habitat, and containing a high proportion of dead plant material.

Chemical composition of plant material

To date, a limited number of analyses have been made on plant samples collected at Prudhoe Bay (Table 20), plus samples of lichen and moss collected at Nome and Cantwell, Alaska. These same samples were used in the *in vitro* digestion studies (Table 18). Analyses have been confined to the determination of acid detergent fiber (ADF) and neutral detergent fiber (NDF), further subdivided into hemicellulose, cellulose, and lignin. Future determinations will be made of energy, total N, P, Ca, and K.

The amount of cell contents in shrubs and herbs was high relative to hemicellulose. In grasses and sedges these components were similar, and in some lichens the hemicellulose component was high relative to cell contents. The cellulose and lignin components of all vascular plants were variable. Lichens were virtually free of cellulose, although they contained a small amount [3.4 g $(100\ g)^{-1}$] of acid resistant material which was allotted to the lignin component pending identification (Table 20). Table 20 indicates that ADF is quite variable in the vascular plants, but tended to be higher in the less digestible species. Lichens are generally thought to be high in crude fiber; the present analyses indicate that the ADF is low, and that the bulk of the cell wall constituents of lichen is a material which is extracted by neutral detergent in a manner similar to hemicellulose.

The prepared diets given the reindeer were either based on lichen or were of a medium to high crude fiber commercial pellet. The former food contained 78% lichen, and the high content of hemicellulose reflects this component in the ration.

Relationships between chemical composition and *in vitro* digestibility of vascular plants.

As stated above, it was apparent that *in vitro* digestibility was high for plants of low crude fiber (ligno-cellulose) content. A significant relationship between *in vitro* digestibility (D, %) and the acid detergent fiber, or crude fiber, content [F, $g\ (100g)^{-1}$] was noted for higher plants (eq. 3).

$$D = 95 - 1.6\ F \text{ ----------- } [3]$$

A relationship of higher predictive value was noted between *in vitro* digestibility (D, %) and lignin content [L, $g\ (100g)^{-1}$]. The data are shown in Fig. 13; a double exponential line (eq. 4) was fitted to the data, *viz.*

$$D = 32\ e^{-0.315\ L} + 68e^{-0.0433\ L} \quad [4]$$

Thus, for plants containing less than 4% lignin, digestibility declined with lignin content at a substantially faster rate than plants containing more than 6-8% lignin. Only one higher plant sample did not fit this relationship; the predicted *in vitro* digestibility of the sample of *Salix lanata* (61%) was almost twice the observed value (34%). No explanation can be given for this apparently aberrant result. However, this observation may be significant since *S. lanata* was seldom more than a trace constituent of esophageal egesta and rumen contents.

There are many previous studies in domestic sheep and cattle which show that the apparent dry matter digestibility of herbage depends on its degree of lignification. In wildlife studies, browse material consumed by herbivores is frequently high in chemicals (e.g., tannins) which limit digestibility (Longhurst et al. 1968). Thus, the general relationship between digestibility and lignification is not as common for browsers as for the temperate grassland grazers. Present evidence suggests that digestive processes of caribou in the tundra ecosystem at Prudhoe Bay may function under principles similar to those noted for ruminants in temperate grassland grazing systems.

Energy balance and energy flow through the Prudhoe Bay caribou population

(a) **Energy content of forage and intake by caribou.** From estimates of the energy content of forages, dry matter intake (Table 15), and dry matter digestibility (Table 18, 19), the amount of energy harvested by caribou at Prudhoe Bay can be calculated. Individual estimates of the energy content of sedges, grasses, and shrubs at the study site have not been made. However, previous studies (West and Meng 1966) show that for the months June through August, gross energy of most northern species which have been studied is between 4.83 and 5.02 kcal g^{-1} dry matter. In the present calculations, a mean energy content of 4.9 kcal g^{-1} was assumed. It was also assumed that the metabolizable energy content of forage was 82% of digestible energy (Blaxter 1962).

Table 21 shows a summary of assumed and calculated composition of late season (late July) forage at Prudhoe Bay. Values for the efficiency of utilization of net energy for milk synthesis and fattening were calculated from the predicted metabolizable energy content of the forage as proposed by Blaxter (1962).

Table 21

Summary of estimated values for the nutrient status of herbage harvested by caribou at Prudhoe Bay.

Dry matter digestibility	= 53%
Energy digestibility	= 55%
Gross energy content	= 4.90 kcal g^{-1}
Digestible energy content	= 2.69 kcal g^{-1}
Metabolizable energy content	= 2.21 kcal g^{-1}
Efficiency of utilization of net energy for	
(a) milk synthesis	= 74%
(b) body growth and fattening	= 39%

Table 15 lists a summary of expected intakes of gross and metabolizable energy by lactating females, non-lactating females, and adult males. It is clear that the intake of metabolizable energy per unit metabolic body size by the lactating females is considerably higher than in the other cohorts. Maximal intakes of gross and metabolizable energy were calculated for early to mid-July.

(b) **Maintenance energy requirement and energy expenditure of caribou.** No estimates were available of the daily maintenance energy requirement of grazing caribou. However, from our modeling efforts below (see **Modeling activities associated with the study of caribou at Prudhoe Bay**), we can predict a daily heat production of approximately 150 [kcal d^{-1} $(kg^{0.75})^{-1}$] which is 1.55 times the fasting metabolic rate of caribou—97 [kcal d^{-1} $(kg^{0.75})^{-1}$] (McEwan 1970). This estimate is low compared with the best empirical field estimates of the daily maintenance energy requirements (or heat production) of sheep at pasture, which are approximately 2.0 times the fasting metabolic rate (Young and Corbett 1972). Therefore, we have assumed a value of 190 [kcal d^{-1} $(kg^{0.75})^{-1}$] (or 1.97 x fasting metabolism) for caribou. The maintenance energy requirement, or daily metabolic rate, of caribou would be higher under conditions of insect harassment; hence the following estimates should approach favorable grazing conditions. For lactating animals, the amount of energy secreted in milk and associated with milk synthesis (i.e., the efficiency of milk synthesis), was also estimated as a component of the maintenance energy requirement of lactating females. Estimates of the amount of milk synthesized were taken from estimates for reindeer given by equation 1 (White, Holleman, and Luick, unpub. obs.), and an efficiency of 74% for synthesis was assumed (Blaxter 1962). The predicted maintenance energy requirements as shown in Table 15.

(c) **Net energy and predicted body-weight gain.** The amount of energy available for synthesis of body tissue (i.e., net energy) was estimated as follows:

Net energy = Metabolizable energy intake— Maintenance energy requirement————————[5]

Calculations from the present data suggest that lactating females were in positive energy balance for only periods 3 and 4 (11-31 June, approximately). For the non-lactating female and adult male segments of the population, a positive energy balance was noted for periods 1-5 (i.e., for the entire 50 days).

If it is assumed that net energy is used in the proportion of 80% for fattening and 20% for growth, then tissue would be synthesized at between 77 and 173 g d^{-1}, which amounts to cumulative body weight gains of 1.9, 5.3, and 4.2 kg for the lactating female, non-lactating female, and the male segments, respectively.

It was found in this study that the digestibility of the diet was an important determinant of the amount of food retained for fattening. For example, in the non-lactating female cohort, if the digestibility of the diet is increased by 10 units from 55 to 65% (i.e., by 18%), the amount of energy retained daily for fattening increased from 467 to 1,402 kcal (i.e., by 200%). This effect has previously been reported for domestic animals (Blaxter 1962); the powerful multiplier effect highlights the requirement for an accurately determined forage digestibility.

Modeling activities associated with caribou studies at Prudhoe Bay

It is clear from estimates of food intake, energy balance, and energy flow that many variables influence the final results. In the above calculations, it was necessary to assume values for variables (e.g., time spent grazing, eating rate, digestibility, caribou biomass) based on limited empirical estimates. It was not possible within the constraints of time to investigate the sensitivity of the calculated end product (e.g., food intake and body growth) to small changes in the magnitude of these variables. To investigate these limitations, a modeling effort was initiated in January 1973. The objectives of the modeling activities were to:

(a) determine the average daily metabolic rate, or heat production, of caribou cohorts based on (i) estimates of energy costs of activities such as standing, walking, grazing, etc.; (ii) time budgets of these activities, and (iii) changes in behavioral activities in response to abiotic and biotic variables. This submodel was termed ACTIVE.

(b) determine daily amounts of forage consumption and plant community/species selection, apparent digestibility, and metabolizable energy intake based on (i) estimates of eating rate as a function of plant live biomass; (ii) eating time as a basis of rumen fill, (iii) daily food intake as a function of eating rate and eating time, (iv) plant selection based on a matrix of chemical composition and biomass of plant types, and (v) digestibility and metabolizability of forage based on its chemical composition (% lignin). This model was termed GRAZE, and

(c) interface models ACTIVE and GRAZE to predict net energy available for growth and fattening of both adult and juvenile cohorts. Growth and fattening were calculated based on (i) estimates of daily net energy available for growth and fattening (i.e., metabolizable energy intake — average daily metabolic rate = net energy), and (ii) efficiency of growth and fattening based on the metabolizability of forage and milk. This interface model was termed GROWTH.

Models ACTIVE and GRAZE have been used in preliminary investigations (F. L. Bunnell, R. G. White, and D. E. Russell, unpub. obs.). From gaming runs with model ACTIVE, we predict that periods of severe insect harassment of more than 2 hr duration could increase the daily heat production by 1.6 to 3 times the average daily metabolic rate estimated for an insect-free day. It will be used in future studies to investigate harassment problems and, hopefully, to predict energy costs of harassment by human, vehicle, and aircraft interference in theoretically "habituated" and "non-habituated" caribou populations.

Model GRAZE is being used to investigate the range of possibilities that exist for caribou to select vegetation types, plant groups, and plant species at Prudhoe Bay. For example, what would be the expected change in grazing pattern and food intake if caribou were selectively grazing plants high in protein, phosphorus, or energy rather than selecting those of highest digestibility? Model GRAZE will also be useful in predicting the rate of diminution of plant biomass in the event of inadvertent or planned holding of caribou on the Prudhoe Bay development.

Model GROWTH is still in the coding stage. As soon as it has been interfaced with models ACTIVE and GRAZE, an attempt will be made to set limits on the upper stocking capacity which will ensure, firstly, a sustained population and, secondly, a sustained yield for this area.

Discussion

This project did not aim at determining the year-round population dynamics and movement of caribou at Prudhoe Bay. Hence, the herd or herds (Arctic or Porcupine) to which these caribou belong in the study years remains unknown. Our own studies on behavioral patterns, combined with local observations on the presence of animals on a year-round basis, indicate that there are two caribou populations at Prudhoe Bay. One may be considered resident, the other migratory. The resident herd is probably small in number, perhaps 5-30 being visible from the road system during most seasons. They also appear to become habituated to traffic on the road system, unlike the migratory animals. Based on an extrapolation of 55 animals in the study area, it is suggested that the maximum "resident" population may be 300 animals occupying the draining basin of the Kuparuk and Sagavanirktok rivers and bordered on the south by the Franklin Bluffs and the White Hills (Fig. 1). This is a total tundra area of approximately 2,840 km^2 (Table 18). The approximate stocking rate would be 0.1 caribou km^{-2} (0.3 caribou mile^{-2}) or 10 km^2 (3.9 mile^2) per caribou. This density is low compared with estimates of 1-3 caribou mile^{-2} for the Arctic, Porcupine, and Kaminuriak herds (Calef 1974), and must be considered a minimal estimate for it does not include the peak influx of migratory animals. The upper limit may be set by the availability of winter range because separate studies at Prudhoe Bay show that although there are a large number of lichen species, their actual distribution is limited to the dry habitats, and except for a peak biomass on one habitat of 88 g m^{-2} the biomass is generally low (0-55 g m^{-2}) (Williams et al., this volume). Therefore, resident caribou would have to supplement their winter diet with sedges, grasses, herbs, and willows in the more exposed communities. Again, the biomass would be small; plant material of high digestibility may be available at only 7-20 g m^{-2}. Dead material of much lower nutrient status would be present at 60-110 g m^{-2} (Table 12). A possible alternative source of winter range may be available on the Franklin Bluffs and in the White Hills.

In previous years large groups of caribou have been observed overwintering in the central arctic region (Collins 1937, cited by Skoog 1968; Olsen 1959, cited by Child 1973), and the same region is a calving area (Skoog 1968; Child 1973). Hence, in some years the "resident" population of caribou may be up to 10 times the assumed number (*ca.* 300) in this study.

In summer 1972 an average of 155 caribou were noted in the study area, and by extrapolation to the entire river drainage system, it was suggested that *ca.* 900 used the coastal plain at Prudhoe Bay. This number is only one-third of the peak numbers (*ca.* 3,000) reported by Child (1973). However, these latter reports were for animals moving through the area under insect harassment and presumably originating from outside the Kuparuk/Sagavanirktok drainage area. While it is not appropriate to base foraging and energy flow calculations on this peak number of animals, it may be appropriate to extrapolate to peak numbers in the 1972 and 1973 season to allow an assessment of the impact of the periodic high population numbers referred to by Skoog (1968).

Without estimates of calf, yearling, and adult rates of mortality, it is difficult to make a precise estimate of the productivity of a caribou herd. From a calf composition of 16% in August (Table 1), it can be argued that herd recruitment would be sufficient to meet losses; hence, a population increase would be expected. For Newfoundland caribou, Bergerud (1971) showed that a calf composition of 15% of the population in October could lead to a significant annual rate of increase.

The traditional migratory patterns of caribou of the Arctic and Porcupine herds have been described by Lent (1966) and Hemming (1971). More specific movement and migratory patterns of caribou in the central North Slope have been described by Child (1973) and Gavin (1975). Briefly, the animals move into the arctic tundra down the Colville and Canning rivers and spread out to enter the Prudhoe Bay area down the Kuparuk and Putuligayuk rivers in the south and southwest and across the Sagavanirktok delta in the east. Child (1973) generalizes this movement pattern as being from east to west in the 1971 and 1972 field seasons. However, superimposed on these general movement trends are the insect-evoked movement patterns, which result in caribou moving to the coast and occasionally to an inland relief area, followed by a slow dispersal inland once insect attack declines. During the rapid insect-evoked movements (Fig. 2), use is made of the numerous game trail systems (see Child 1973, Figs. 2a, 2b). On the other hand, during slow dispersal and grazing, caribou seldom use the trails. Trails intersect many of the roads at Prudhoe Bay, which necessitates several crossing points. Caribou readily crossed the roads and, in some cases, used them as insect-relief areas. The interaction of caribou with other man-made obstacles has been studied independently (Child 1973).

Observations on grazing behavior of caribou undisturbed by insects were confounded by group size and composition. In the smaller groups a general preference for vegetation in the drier habitats was noted. Groups comprising approximately 50 or more caribou showed no preference for vegetation type. This may have been due to the requirement for a certain minimum distance between individuals of the group. In this respect, it was observed that within groups of males, individuals were apparently more tolerant of each other than was the case in groups of lactating females and their calves. No unequivocal evidence could be gained for community selection because of the relatively small size of stands of vegetation of the various types and, except for the *Dupontia* brook/meadow type, because of lack of continuity between stands. However, the data in Table 9 indicate some preference for the *Dryas* heath/*Salix rotundifolia* snowbed and *Dupontia* brook meadow communities. Also, there was an apparent lack of preference shown for the *Carex aquatilis* marsh, which could be attributed to its being a prime mosquito habitat. In spite of apparent preferences for certain communities, their low availability resulted in the occurrence of grazing (42%) in the *Eriophorum* polygon marsh communities.

Within the plant communities, some preference was shown by esophageal fistulated reindeer for grasses and sedges (Fig. 7). Exceptions to this generalization were noted for the *Dupontia* brook meadow and *Salix ovalifolia* sand dunes, where preferences were also noted for willows. Thus, in summarizing the analyses of 20 esophageal fistula samples, it was found that *Eriophorum* spp and the salices made up respectively 37 and 29% of the diet (Table 10). Analyses of four caribou rumen samples yielded similar results, with grasses and sedges constituting 38% of the diet and salices 34% (Table 11). *Eriophorum* spp. constituted a lower proportion of the diet of caribou than of reindeer (Tables 10 and 11).

Preference for the *Dryas* heath and *Salix rotundifolia* snowbed communities was probably a reflection of their higher availability and more advanced phenology compared with other communities early in the season (late June-10 July). At this time the live biomass was relatively high (35 g m^{-2}), and dead material low (Table 12). However, the predicted, average apparent dry matter digestibility was relatively low (44-53%, Table 19). In early July the *Dupontia* brook meadow contains considerably more live plant material (71 g m^{-2}) than other communities

(26-41 g m^{-2}) (Table 12), and the predicted apparent dry matter digestibility of the live biomass was high at 59% (Table 19). This community also contains considerable amounts of *D. fisheri*, a grass which, until flowering, is potentially highly digestible (*ca.* 79%, Table 18), plus a wide range of willows and herbs which provide considerable variation in the diet.

In comparison with the *Dupontia* brook meadow, the most used community, the *Eriophorum* polygon marsh, was of only moderate nutritive value. The live biomass was moderate (34-41 g m^{-2}), which might limit eating rate and cause some compensatory increase in grazing time (Figs. 10a, 10b, 11), and the average digestibility of live material of the community was only 50% (Table 19). Selection within the community could lead to a higher digestibility of forage, but this must be balanced against increased searching time.

The apparent lack of preference for the *Carex aquatilis* marsh may be attributable to several factors: It is a prime mosquito habitat, is unavailable due to high water levels in early summer, is of low live biomass (24-26 g m^{-2}), and is relatively high in dead material (Table 12). In compensation, the predicted apparent dry matter digestibility of the live plant material was over 60% (Table 19). Thus, when mosquitos are not a problem, this community is potentially useful for grazing by caribou in late July and August.

Care should be taken in translating information based on the original vegetation analysis to the more detailed vegetation analysis of Webber and Walker. In Fig. 7 a comparison is shown between our present scheme and the more detailed scheme outline by Webber and Walker. In general, good agreement was noted between the schemes. However, because the cryptogams were not used in defining the vegetation and because *Carex aquatilis, Eriophorum angustifolium,* and *Dupontia fisheri* are found in most vegetation types (Appendix Table 10), some inconsistencies may arise in defining the *Carex aquatilis* and *Eriophorum angustifolium* marshes. The key used by Webber and Walker is shown in Fig. 7, and it is clear that, initially, the absence or presence of moss and, finally, the type of moss dictates the allocation of vegetation to types 4, 5, and 6. These vegetation types were placed in the *Carex* marsh type in Skogland's scheme.

A summary of the above characteristics of each community is shown in Fig. 14. Future gaming runs with model GRAZE may help to show the relative importance of each factor in affecting food intake by caribou. The present results are limited to the observation that above maintenance, an 18% increase in apparent dry matter digestibility can lead to a 200% increase in energy retention. The relative importance of small changes in other factors (e.g., community availability, live biomass, or the ratio of live/dead biomass) are not known. It can also be shown that caribou have the potential to denude the range of live biomass at a rate of 11 min m^{-2}. Thus, any inadvertent restriction of animals onto a small area could result in rapid removal of live plant material. Effects of trampling may also be important in destroying the habitat.

From the observed available live biomass (Table 12) and relationships between eating rate and biomass (Figs. 9 and 10), it is clear that available biomass limits forage intake on most plant communities. However, when not harassed by insects, caribou can apparently graze for extended periods of time. They spend up to 53% of the day eating, which is equivalent to a grazing period (eating plus walking) of 60-65% of the day (Tables 2a, 2b). Predictions based on grazing behavior (Tables 2 and 14) indicate that by virtue of their higher rates of grazing intensity, lactating females have a higher rate of ingestion of food than non-lactating females and males. Although this observation agrees with field studies on domestic sheep (Arnold and Dudzinski 1967), future work is required to verify this critical point in reindeer. Esophageal collections using lactating females should be compared with those for adult males and the current estimates of eating rate of non-lactating females. This type of experiment should be extended to weaned calves and yearlings, as we currently have no estimates on the relative eating activities of these cohorts. Similarly, more information is required on the interaction of grazing and eating times with available biomass and canopy structure (Fig. 10). More information on these factors will allow refinement on the current estimates of food intake.

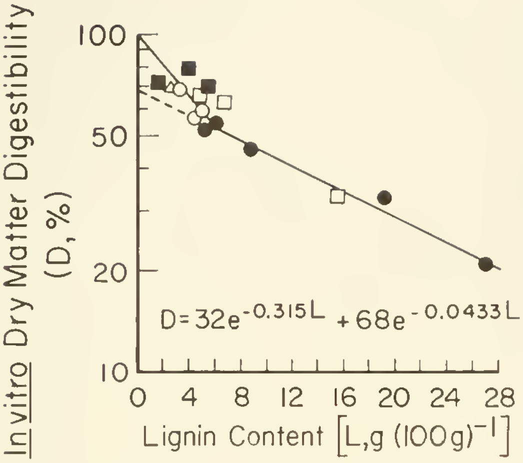


Fig. 13. *Correlation of* in vitro *digestibility with lignin content of vascular plants.* ●*, shrubs; O, sedges;* ■ *, grasses;* ☐ *, herbs;* Δ *, commercial pellets.*

Biomass estimates for July, August, and September (Table 12) are in general agreement with previous intensive studies at Barrow, Alaska (Tieszen 1972). Peak live biomass is noted in the last week of July, and biomass declines markedly in most communities after this date. Chemical analyses are not complete; hence, no trend with age in the degree of lignification can be shown. However, preliminary evidence, again at Barrow, indicates an increase in lignin and a decrease in soluble (cell constituents) components of the plant during August (B. H. McCown, L. L. Tieszen, and P. W. Flanagan, pers. comm.). At the start of the growing season, the effective productivity of herbivores is limited by the available biomass and the rate of biomass increase. At the end of the season (early to mid-August), productivity is also limited by the nutrient content of the available herbage.

The amount of energy which is harvested by caribou and which becomes available for production depends on the maintenance energy requirement of the animal. In turn, maintenance energy requirement is highly dependent on the activity pattern of the grazing animal. Insect harassment can increase substantially the daily heat production, the amount of the latter depending on the duration and intensity of harassment, the speed of movement, and the distance moved by the caribou. Following the present study, we are using simulation modeling (model ACTIVE) to give estimates of energy costs of insect harassment. Until this study is complete, we cannot calculate the loss in production (i.e., in potential milk production, growth, and fattening), which could be attributed to insect harassment in the 1972 and 1973 field seasons. Growth and fattening can only occur once the maintenance energy requirements have been reached. We have calculated that for mature caribou, net energy of growth and fattening may be available for only a limited time period, i.e., the month of July (Table 15). During July weather conditions favor mild to severe insect harassment 20% of the time. Hence, the potential productivity of a resident herd already subjected to a limited period of positive energy balance may be further limited by insect harassment. Also, during this period (July), the amount of energy diverted to growth and fattening is highly dependent on the dry matter digestibility, or the metabolizable energy content, of the forage. The mean metabolizable energy content of forage consumed by caribou was estimated at 2.2 kcal g^{-1} dry matter. This value compares with medium to good quality forage from other grassland systems. When availability is not limited, this would support good animal productivity.

It is clear from the present study that the Prudhoe Bay area is only moderately productive for caribou. Stability of the ecosystem is apparently achieved by low stocking densities, the latter resulting in consumption of less than 2% of the annual primary production (Table 17, Fig. 13). Thus, there is an adequate biomass "buffer" available to meet the infrequent and unpredictable entry of large caribou herds. The number of animals which apparently overwinter in the Prudhoe Bay area is small and is perhaps limited by nutritional as well as climatic factors. Adverse weather conditions plus lack of protection from strong winds may place a severe limitation on the time available for winter grazing on the arctic coastal plain. This, combined with minimal lichen distribution and biomass (0-88 g m^{-2}), a low biomass of frozen forage of high digestibility, and possibly a snow cover of high hardness index, would suggest an area of poor winter habitat for caribou. When a poor winter habitat is combined with a limited period

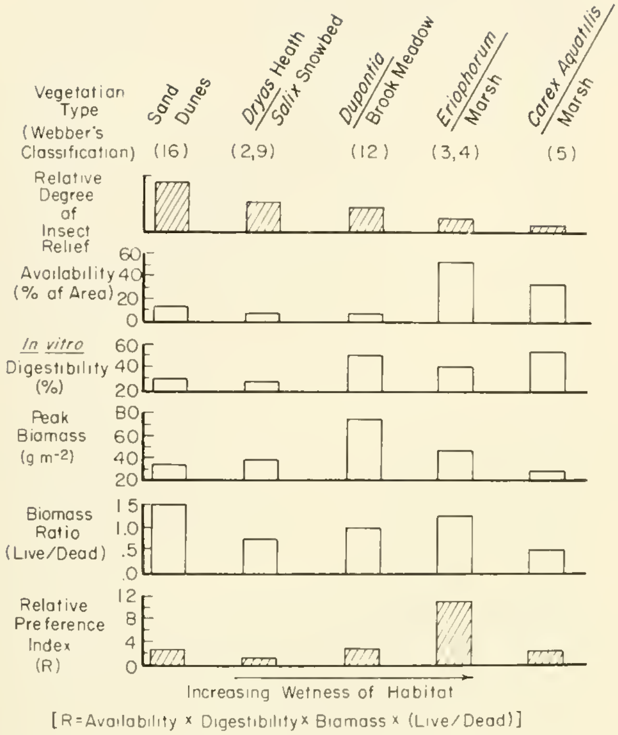


Fig. 14. *Summary of relative characteristics of vegetation types which appear pertinent to caribou habitat at Prudhoe Bay. Relative degree of insect relief is a subjective assessment; availability, see Table 8;* in vitro *digestibility, see Table 19; peak biomass, see Table 12 (live biomass); biomass ratio, calculated as ratio of live/dead, including litter at peak live biomass, see Table 12); relative preference index of herbage was calculated as the product of availability of community type,* in vitro *digestibility, peak biomass and ratio of live/dead.*

when energy is available for growth and fattening, low survival might be expected. Late July and August productivity would be higher if caribou followed the phenologic and primary production progression in vegetation types from south of the Prudhoe Bay study area into the foothills of the Brooks Range. This strategy might explain the adaptive significance of observed migration patterns of caribou, but why a small herd remains resident in the Prudhoe Bay area is less easily explained.

Acknowledgements

This project was supported by Grant No. GB-29342 to the University of Alaska under the auspices of the U. S. Tundra Biome Program from the Office of Polar Programs and the International Biological Program of the National Science Foundation. Logistic support at Prudhoe Bay was made available through the Tundra Biome Center, University of Alaska, from funds provided by the Prudhoe Bay Environmental Subcommittee; the Naval Arctic Research Laboratory, Barrow, Alaska, assisted in the transport of reindeer. Additional support was provided through contract with the U. S. Atomic Energy Commission (AEC Contract [(45-1)-2229-TA3]). The authors are grateful to the late Scott Parrish for his assistance in logistics as site coordinator at Prudhoe Bay. The skilled technical assistance of A. M. Gau, P. Frelier, and Sandra White is gratefully acknowledged.

R. G. White and J. R. Luick acknowledge international cooperation with the Grazing Programme of the Norwegian IBP Committee through exchange of data and personnel. The models ACTIVE and GRAZE were developed in cooperation with Dr. Fred Bunnell, Faculty of Forestry, University of British Columbia.

References

Allden, W. G. and I. A. McD. Whittaker (1970). The determination of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. *Aust. J. Agric. Res.*, 21:755-766.

Arnold, G. W. and M. L. Dudzinski (1967). Studies on the diet of the grazing animals. III. The effect of pasture species and pasture structure on the herbage intake of sheep. *Aust. J. Agric. Res.*, 18:657-666.

Bergerud, A. T. (1971). The population dynamics of Newfoundland caribou. Wildlife Monog. No. 25, 55 pp.

Blaxter, K. L. (1962). The energy metabolism of ruminants. C. C. Thomas, Springfield, Ill., 332 pp.

Brody, S. (1964). Bioenergetics and growth. Hafner Pub. Co. Inc., N. Y., 1023 pp.

Calef, G. W. (1974). The predicted effect of the Canadian Arctic Gas Pipeline Project on the Porcupine caribou herd. Pages 101-120 *in* Research Reports, Vol. 4. Environmental impact assessment of the portion of the MacKenzie gas pipeline from Alaska to Alberta. Environmental Protection Board, Winnipeg, Man., Canada.

Calef, G. W. and G. M. Lortie (1973). Observations of Porcupine caribou herd 1972. Sec. 1, Append. 1, Wildlife, to interim report No. 3: Toward an environmental impact assessment of a portion of the MacKenzie gas pipeline from Alaska to Alberta. Environment Protection Board, Winnipeg, Man., Canada, 127 pp.

Child, K. N. (1973). The reactions of barren ground caribou *(Rangifer tarandus granti)* to simulated pipeline and pipeline crossing structures at Prudhoe Bay, Alaska. A completion report of the Alaska Cooperative Wildlife Research Unit, 49 pp.

_______. (1975). A specific problem: the reaction of reindeer and caribou to pipelines. Pages 14-19 *in* Proc. 1st Int. Reindeer and Caribou Symp., Fairbanks, 9-11 August 1972, University of Alaska Biol. Papers, Special Report No. 1.

Dahl, E. (1956). Rondane: Mountain vegetation in South Norway and its relation to the environment. Det Norske Vid. Akademi 1. Mat. Naturv. Klasse No. 3, 374 pp.

Dieterich, R. A. (1975). Esophageal and ruminal fistulization of reindeer. Pages 523-527 *in* Proc. 1st Int. Reindeer and Caribou Symp., Fairbanks, 9-11 August 1972, University of Alaska Biol. Papers, Special Report No. 1.

Espmark, Y. (1971). Mother-young relationship and ontogeny of behaviour in reindeer (*Rangifer tarandus* L.) *Z. Tierpsychol.*, 29:42-81.

Gaare, E. (1968). A preliminary report on winter nutrition of wild reindeer in Southern Scandes Norway. Pages 109-115 *in* 21st Symp. Zool. Soc. London (M. A. Crawford, ed).

Gaare, E. and T. Skogland (1971). Villreinens naeringsvaner. Report from the grazing project of the Norwegian IBP committee. Statens viltundersokelser, Trondheim (English summary), 25 pp.

Gaare, E., T. Skogland, and B. R. Thomson (1970). Wild reindeer food habits and behavior, Hardangervidda, Jan.-July 1970. Report from the grazing project of the Norwegian IBP committee. Statens viltundersokelser, Trondheim (English summary), 97 pp.

Galt, H. D., P. R. Ogden, I. N. Ehrenreich, B. Theuer, and C. S. Martin (1969). Estimating botanical composition of forage samples from fistulated steers by a microscope method. *J. Range Mgmt.*, 21:397-401.

Gavin, A. (1975). Weather and its effect on caribou behavior patterns and migration. Pages 414-419 *in* Proc. 1st Int. Reindeer and Caribou Symp., Fairbanks, 9-11 August 1972, University of Alaska Biol. Papers, Special Report No. 1.

Goering, H. K. and P. J. Van Soest (1970). Forage fiber analyses. Agr. Handbook No. 379, U. S. Govt. Printing Office, Washington, D. C., 20 pp.

Grieg-Smith, P. (1964). Quantitative plant ecology, 2nd ed. Butterworths, London, 256 pp.

Hanson, H. C. and E. D. Churchill (1961). The plant community. Reinhold Pub. Co., New York, 218 pp.

Hemming, J. E. (1971). The distribution and movement patterns of caribou in Alaska. Alaska Dept. Fish and Game, Game Tech. Bull. No. 1., 60 pp.

Hultén, E. (1968). Flora of Alaska and neighboring territories. Stanford University Press, Stanford, Calif., 1008 pp.

Leng, R. A. and G. J. Leonard. 1965. Measurement of the rates of production of acetic, propionic, and butyric acids in the rumen of sheep. *Br. J. Nutr.*, 19:469-484.

Lent, P. C. (1966). The caribou of northwestern Alaska. Pages 481-517 *in* Environment of the Cape Thompson Region, Alaska (N. J. Wilimovsky and J. N. Wolfe, eds.). U. S. AEC Div. Tech. Inf. Ext., Oak Ridge, Tenn.

Le Resche, R. E. (1975). The international herds: present knowledge of Steese-Fortymile and Porcupine caribou herds. Pages

127-139 *in* Proc. 1st Int. Reindeer and Caribou Symp., Fairbanks, 9-11 August 1972, University of Alaska Biol. Papers, Special Report No. 1.

Longhurst, W. M., H. K. Oh, M. B. Jones, and R. E. Kepner (1968). A basis for the palatability of deer forage plants. *Trans. N. Am. Wildl. Nat. Resour. Conf.*, 33:181-192.

McEwan, E. H. (1970). Energy metabolism of barren ground caribou *(Rangifer tarandus)*. *Can. J. Zool.*, 48:391-392.

Pegau, R. E. and J. E. Hemming (1972). Caribou report, Vol. 12. Projects W-17-2 and 3. Alaska Dept. Fish and Game, Juneau.

Skoog, R. D. (1968). Ecology of the reindeer *(Rangifer tarandus granti)* in Alaska. Ph.D. thesis. University of California, Berkeley, 699 pp.

Thomson, B. R. (1971). Wild reindeer activity, Hardangervidda, July-Dec. 1970. Report from the grazing project of the Norwegian IBP committee. Statens viltundersokelser, Direktoratet for Jakt, Viltstell og Ferskvannsfiske, Trondheim, 83 pp.

______. (1973). Wild reindeer activity, Hardangervidda, 1971. Report from the grazing project of the Norwegian IBP committee. Statens viltundersokelser, Direktoratet for Jakt, Viltstell og Ferskvannsfiske, Trondheim, 76 pp.

Tieszen, L. L. (1972). The seasonal course of aboveground production and chlorophyll distribution in a wet arctic tundra at Barrow, Alaska. *Arct. Alp. Res.*, 4:307-324.

Tilley, J. M. A. and R. A. Terry (1963). A two-stage technique for the *in vitro* digestion of forage crops. *J. Br. Grassland Soc.*, 18:104-111.

Webber, P. J. and D. A. Walker (This volume). Vegetation and landscape analysis at Prudhoe Bay, Alaska: A vegetation map of the Tundra Biome study area.

West, G. C. and M. S. Meng (1966). Nutrition of willow ptarmigan in northern Alaska. *Auk*, 83:603-615.

White, R. G. and R. A. Leng (1968). Carbon dioxide entry rate as an index of energy expenditure in lambs. *Proc. Aust. Soc. Anim. Prod.*, 7:335-341.

Williams, M. E., E. D. Rudolph, and E. A. Schofield (This volume). Selected data on lichens, mosses, and vascular plants on the Prudhoe Bay tundra.

Young, B. A. and J. L. Corbett (1972). Maintenance energy requirement of grazing sheep in relation to herbage availability. 1. Calorimetric estimates. *Aust. J. Agric. Res.*, 23:57-76.

Appendix Table 1

Botanical composition of esophagus fistula samples from *Eriophorum angustifolium* polygon marshes. Percent.

Corresponding veg. plots	1-4	5-7		10-14		15-21			
EF samples	1	2	3	4	5	6	7	$\overline{x}$	S.D.
Shrubs	5.0	10.5	10.0	54.5	28.5	5.0	11.5	17.86	16.66
Dryas integrifolia	1.5	0.5	1.0	8.5	3.5			2.1	
Salix arctica				4.0	2.5	0.5	4.5	1.6	
Salix ovalifolia		1.0	1.0	10.5	2.0		0.5	2.1	
Salix reticulata				3.0	2.5	2.0	0.5	1.1	
Salix spp. leaves	2.5	9.0	7.5	23.0	17.0	2.0	5.0	9.4	
Salix spp. flowers			0.5	1.0			0.5	0.3	
Salix spp. stems	1.0			4.5	1.0	0.5	0.5	1.1	
Grass-like	59.3	49.0	61.5	23.0	40.5	45.5	59.5	48.33	12.71
Eriophorum angustifolium	59.3	41.5	55.5	21.0	40.0	44.0	58.0	45.6	
Eriophorum angustifolium culm		6.5	6.0	1.5	0.5	1.5	1.5	2.5	
Eriophorum angustifolium flower		0.5						tr	
Equisetum variegatum		0.5		0.5				0.2	
Herbs			1.5			0.5		0.33	0.55
Braya spp.						0.5		tr	
herb spp.			1.5					0.2	
Lichens		1.5		0.5	0.5	8.0	1.0	1.64	2.64
Cetraria islandica		1.0		0.5	0.5			0.2	
Dactylina arctica		0.5						tr	
Nephroma arctica							0.5	tr	
Thamnolia vermicularis						8.0	0.5	1.2	
Dead and Litter	35.7	39.0	27.0	22.0	30.5	41.0	28.0	31.89	6.4
Eriophorum angustifolium	33.7	34.5	22.0	18.5	26.0	39.0	26.0	28.5	
Dryas integrifolia						1.5	0.5	0.2	
Salix spp.				1.0				0.1	
Hair, *Rangifer*				0.5				tr	
Plant epidermis	1.0		1.0					0.2	
Vasc. bundles	1.0	4.5	3.5	2.0	4.5	0.5	1.5	2.5	
Insect, *Aedes* spp.			0.5					tr	

Appendix Table 2

Botanical composition of esophagus fistula samples from
Dryas-heath communities and *Salix rotundifolia* snowbeds. Percent.

Corresponding veg. plots		42.47 and 53-57		38-41			
EF samples	8	9	10	11	12	$\overline{x}$	S.D.
Shrubs	30.8	6.5	40.5	48.5	27.5	30.7	14.20
Dryas integrifolia flower				20.0	1.0	4.2	
Dryas integrifolia leaf	2.0		0.5	9.5	0.5	2.5	
Salix arctica	0.5		1.0	6.0	1.0	1.7	
Salix pulchra			34.5	2.0		7.3	
Salix reticulata					0.5	tr	
Salix rotundifolia	26.5	6.5	4.0	9.0	23.5	13.9	
Salix spp.			0.5			tr	
Salix spp. flower							
Salix spp. stem	1.5			2.0		0.7	
Vaccinium vitis-idaea					1.0	0.2	
Grass-like	44.0	47.0	28.0	27.0	27.0	34.6	8.96
Alopecurus alpinus		1.0				0.2	
Carex membranacea	1.5	0.5				0.4	
Carex rupestris	10.5	7.0	0.5	5.0	2.5	5.1	
Carex scirpoidea	26.0	37.0	24.0	21.0	24.0	26.4	
Carex spp.	2.0			1.0	0.5	0.7	
Carex spp. flower/fruit	4.0		0.5			0.9	
Eriophorum angustifolium			3.0			0.6	
Equisetum variegatum		1.5				0.3	
Herbs				7.5	0.5	1.6	2.96
Braya spp.					0.5	tr	
Draba alpina				2.5		0.5	
Lagotis glauca				0.5		tr	
Oxytropis spp.				2.0		0.4	
Parrya nudicaulis				0.5		tr	
Herb				2.0		0.4	
Lichen	6.0	4.5	9.0	1.0	10.5	6.2	3.35
Dactylina arctica	1.5	1.0				0.5	
Thamnolia vermicularis	4.5	3.5	9.0	1.0	10.5	5.7	
Dead and litter	19.5	41.5	22.5	16.0	34.5	26.8	3.63
Eriophorum angustifolium		1.5	1.0			0.5	
Dryas integrifolia	1.5		1.5	3.5		1.3	
Carex spp.	9.5	25.0	13.5	6.5	33.0	17.5	
Salix spp.	3.5	5.5	3.5	4.0	0.5	3.4	
Litter unspecified	0.5	0.5				0.2	
Epidermis	1.5	5.0		0.5		1.4	
Vasc. bundles	3.0	4.0	3.0	1.5	1.0	2.5	

Appendix Table 3

Botanical composition of esophagus fistula samples from the *Dupontia fisheri* type. (13 and 18 are from the *Carex aquatilis* type.) Percent.

Corresponding veg. plots	22-25		58-67			22-25		
EF samples	13	14	15	16	17	18	$\bar{x}$	S.D.
Shrubs	26.0	23.5	15.0	22.5	19.5	41.5	24.7	8.3
Dryas integrifolia		0.5					tr	
Salix arctica	14.5	13.0	10.5	14.0	14.0	27.5	15.6	
Salix lanata	1.5	2.0		0.5		3.5	1.4	
Salix reticulata	3.5	0.5	1.0				0.8	
Salix rotundifolia					0.5		tr	
Salix spp.	3.0	6.0	3.5	5.5	1.5	7.0	4.4	
Salix spp. stem	3.5	1.5		2.5	3.5	3.5	2.4	
Grass-like	67.0	19.0	69.0	54.5	64.0	11.0	47.42	23.48
Carex aquatilis	5.0		27.5	6.0	31.0	0.5	11.7	
Carex culm				0.5	0.5		0.2	
Dupontia fisheri		5.0	3.5	6.0	7.5		3.7	
Eriophorum angustifolium	6.0	8.0	27.5	33.5	20.0	7.5	17.1	
Eriophorum scheuchzeri flower		0.5					tr	
Eriophorum spp. flowers								
Cyperacea leaf	55.5	3.5	9.5	8.5	4.5	1.5	13.8	
Cyperacea culm			1.0		0.5	0.5	0.3	
Cyperacea fruit/flower	0.5	2.0					0.4	
Equisetum variegatum						1.0	0.2	
Herbs	3.5	54.0	11.0	15.5	9.0	38.5	21.9	18.1
Cardamine sp.					0.5		tr	
Pedicularis sudetica	3.0	1.0			1.5		0.9	
Polygonum viviparum		0.5	0.5		0.5		0.3	
Saxifraga hirculus leaf		3.5	0.5	0.5	0.5		0.8	
Saxifraga hirculus flower		2.0		0.5		1.0	0.6	
Stellaria spp.		0.5					tr	
Valeriana capitata		1.0		0.5	0.5		0.3	
Herb leaf				1.5			0.3	
Herb sepals	0.5	44.5	10.0	12.0	5.0	37.5	18.3	
Herb pistil		1.0		0.5	0.5		0.3	
Lichen	0.5						0.08	0.18
Thamnolia vermicularis	0.5						tr	
Dead and litter	2.5	0.5	5.0	4.5	8.0	7.5	4.67	2.62
Carex spp.			1.0	3.0	2.0		0.7	
Cyperaceae			3.0	1.5	2.5	1.0	1.3	
Dupontia fisheri								
Dryas integrifolia					0.5		tr	
Eriophorum angustifolium			1.0		2.5	3.5	1.2	
Vasc. bundles	0.5						tr	
Salix spp.	2.0	0.5			0.5	3.0	1.0	

Appendix Table 4

Botanical composition of esophagus fistula samples from *Salix ovalifolia* sand dunes. Percent.

Corresponding vegetation plots	97-106		
EF samples	19	20	$\overline{x}$
Shrubs	84.0	81.5	82.7
Salix ovalifolia leaf	80.0	78.5	79.3
Salix ovalifolia stem	4.0	2.0	3.0
Salix ovalifolia veins		1.0	0.5
Grass	9.0	6.5	7.75
Dupontia fisheri	9.0	5.0	7.0
Elymus arenarius		1.5	0.8
Herbs	3.0	5.5	4.25
Artemesia spp.		1.5	0.7
Chrysanthemum integrifolium	1.5		0.7
Parrya nudicaulis		1.0	0.5
Polemonium boreale		0.5	0.3
Primula spp.		0.5	0.3
Poligonum viviparum		1.0	0.5
Herb leaf	0.5		0.3
Herb flower	0.5	1.0	0.8
Herb pistil	0.5		0.3
Dead	2.5	6.5	4.5
Dupontia fisheri	1.0	0.5	
Salix ovalifolia	1.5	6.0	

Appendix Table 5

Botanical composition in 33 x 100 cm plots from *Dryas integrifolia* dry heaths. Percent.

Stand no.	1								2		
Corresponding EF samples											
Plot no.	31	32	33	34	35	36	37	$\bar{x}_1$	38	39	40
Shrubs	90	71	71	100	45	45	85.1	72.4	90	40	30
Arctostaphylos alpina		1			5	5	30	5.8			
Arctostaphylos rubra									70		
Dryas integrifolia	80	60	90	20	40	40	55	55.0	20	40	30
Cassiope tetragona				80				11.4			
Salix arctica											
Salix ovalifolia		10						1.4			
Salix reticulata	10		1				0.1	1.5			
Salix lanata											
Salix rotundifolia											
Grass-like		41	20	1	11	5.1	10	12.5			30
Arctagrostis latifolia		40						5.7			
Carex aquatilis											
Carex scirpoidea			20	1	5	5		4.4			
Dupontia fisheri											
Eriophorum angustifolium											
Festuca rubra		1			5			0.9			30
Carex rupestris					1	0.1	10	1.6			
Equisetum variegatum											
Herbs	2	5	11	6	6.1	32.1	1.7	9.1	10	5	18
Astragalus sp.			5		1	1	0.1	1.0			
Draba alpina											
Oxytropis arctica	1		5	1	5	1	1	2.0	10	5	10
Oxytropis sp.											
Pedicularis arctica	1	5	1	5			0.1	1.7			
Pedicularis capitata											3
Polygonum viviparum						0.1		tr			5
Polemonium boreale											
Saxifraga oppositifolia						30	0.5	4.4			
Silene acaulis					0.1			tr			
Papaver sp.											
Parrya nudicaulis											
Lichen	5	1	5	1	6			1.6			10
Dactylina arctica					1						
Cetraria ericetorum											
Thamnolia vermicularis	5	1	5	1	5			2.4			
Mosses	5	15	1	5	5	0.1	5	5.2			10
Bryum sp.		5	1	5		0.1	5	2.3			
Dicranum sp.	5	10			5			2.8			
Other											
Dead and litter					30	20		7.1	5		30
Bare ground					30	20		7.1	5		30
Standing dead							6	0.8	5		30

Appendix Table 5 (continued)

2		3									4				
		8, 11 and 12													
41	$\bar{x}_2$	42	43	44	45	46	47	48	49	$\bar{x}_3$	50	51	52	$\bar{x}_4$	$\bar{x}$
40	50.0	45.2	70	58	60	55	45	40	50	52.9	65.1	60.1	40	55.0	58.9
															1.8
1.0	17.5														3.2
40	11.8	40	40	50	30	50	30	30	40	38.8	55	55	40	50	44.3
															3.6
		0.1		3						0.4	0.1			tr	tr
								10	10	2.5					1.4
		2	20	5		5				4.0			0.1	tr	2.0
		3													tr
		0.1	10		30		15			6.9	10	5		5	3.2
	2.7	40.1	10	42	10.1	12	20	5	5	18.0	30	40.1	5	25.0	15.3
			2							0.3					1.9
												0.1		tr	tr
		10	5	20	–	10	20			8.1	30	20		16.7	6.
								5	5	1.3					0.5
		30								3.8					1.4
	2.7														tr
			3	20	10					4.1		20		6.7	2.9
		0.1		2	0.1	2				0.5			5	1.7	0.4
35	16.2	10	10	2.1	2.1	25.1	5.1	40	40	16.8	15	0.1	40	18.4	14.1
															tr
				2			3			0.6					0.2
						10				1.3					1.1
								30	5	4.4					1.6
						0.1	2			0.3					0.7
	0.8														tr
	1.3			0.1				10	5	1.9					1.6
30	2.7								30	7.2	10		5	5	3.4
		10	10	2		5	0.1								2.5
						10				1.3			30	10	2.3
				0.1						tr					tr
											5	0.1	5	3.3	0.5
	2.5	25.1		13			1.1			4.9					3.1
		2		2			0.1			0.5					0.2
		0.1		3			0.1			0.4					0.1
		23		8			1			4.0					2.2
	2.5	20		10	60	30	20			17.5	20	20	30	23.3	11.6
															0.7
															0.9
				10						1.3					0.5
20	13.7	70	40	60		10	30	30	10	31.3	30	30	40	23.3	20.7
20	13.7	10	10			10	30	30	10	12.5	10		20	6.7	10.7
20	13.7	60	30	60					6	11.3					9.3

Appendix Table 6

Botanical composition in 33 x 100 cm plots from *Eriophorum angustifolium* polygon marshes. Percent.

Stand no.																
Corresponding EF samples		1					2,3					4,5				
Plot no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Shrubs	—	20	0.2	15	15	50	1	15	25	35	77	45	57	65	30	60
Dryas integrifolia	—	15	0.1	10	5	30		3	20	15	30	20	30	20	20	40
Salix arctica	—	5	0.1	5	5	5		10		20	7		20	25	10	10
Salix lanata						10						20		15		
Salix ovalifolia																
Salix reticulata					5	5			5		40	5	7	5		10
Salix rotundifolia																
Salix pulchra																
Grass-like	50.1	40.1	75	35.1	35	5	60	35.1	25.1	25	13	40	23	20	32	20
Carex membranacea								5	5	5	3		3			
Eriophorum angustifolium	50	40	70	30	20		60	30	20	20	10	40	20	20	30	20
Eriophorum scheuzeri				0.1		5										
Equisetum variegatum	0.1	0.1	5	5	15			0.1	0.1						2	
Dupontia fisheri																
Herbs		0.1		5.2	0.1	5	4	0.1		5	0.1				5	2
Braya spp.				0.1												
Draba alpina		0.1														
Parrya nudicaulis				0.1												
Polygonum viviparum				2	0.1						0.1					
Pedicularis sudetica							4	0.1								
Saxifraga oppositifolia				3		5				5					5	2
Saxifraga cernua																
Stellaria crassifolia																
Lichen			0.1	15		0.1										15
Thamnolia vermicularis						0.1										15
Mosses	1	20	0.1	15	15	10		15	30	30	40	40	50	20	5	13
Bryum spp.	1	5								20	20				5	13
Dicranum sp.		10			15	10			30	10	20	20	20	20		
Other		5														
Standing dead	40	20	20	30	50	40	50	60	50	35	10	50	40	30	60	50
Humus	10		5		30	30	40	10	5						20	

Appendix Table 6 (continued)

		1								2						
	6,7					13,18										
17	18	19	20	21	$\bar{x}_1$	22	23	24	25	26	27	28	29	30	$\bar{x}_2$	$\bar{x}$
20	30.1	30	55	35	32.4	25	0.2	10.1	30	35	45	16	35	42	26.5	30.6
20	10	20	30	50.9	16.3	5	0.1	5	20	5	5		10		5.6	13.0
	20	5	5	10.0	7.7	5									0.6	5.6
		5			2.4			10		10					1.1	2.0
					0.1											tr
	0.1		20	20	5.8	15		0.1	10		10	10	10	2	6.3	6.0
						0.1	5					1	10		1.8	tr
										20	30	5	5	40	5.6	1.7
5	50	50.1	30	45	33.9	45	50	30	25	45.1	40	60.1	36	45	41.8	36.3
		0.1			0.9	5	10	10		5	5	30	5	5	8.3	2.5
	50	30	30	40	30.0	40	30	20	20	40	30	30	30	40	31.1	30.0
5		20			1.2		10								1.1	1.3
				5	1.5					0.1	5				0.5	1.2
									5			0.1			0.6	tr
15				1.0	2.0					5	5	10.1	0.1	–	2.2	2.1
				0.5	tr											tr
10					0.5											tr
					tr											tr
				0.5	0.1					5	5	5	0.1		1.7	tr
					0.2											tr
5					1.2											tr
												0.1			tr	tr
												5			0.5	tr
			5		1.6											1.2
			5		0.9											
	10	40	50	60	22.1	30	60	60	20	30	40	20	1	29.0	24.2	
			20		4.0											
			30		7.4											
					0.2											
40	40	60	60	60	42.6	40	20	20	60	30	30	70	50	70	43.3	42.8
50	10				10.0								15		1.7	

Appendix Table 7

Botanical composition in 33 x 100 cm plots from *Dupontia fisheri* meadows. Percent.

Stand no.	1											
Corresponding EF samples	14,15,16 and 17											
Plot no.	58	59	60	61	62	63	64	65	66	67	68	$\bar{x}_1$
Shrubs	50	31	35	35	20	25	30	10	10	–	30	25.1
Salix arctica	20	10	30		20	20	20	10		0.7		11.8
Salix lanata		1		20								1.9
Salix ovalifolia				15		5			10		30	5.5
Salix reticulata												
Salix rotundifolia			5				5					0.9
Salix pulchra	30	20					5	5		0.4		5.5
Grass-like	45	35	40	35	55	50	50	65	40	25.1	45	44.1
Carex aquatilis	–	5	10	10	10							3.2
Carex membranacea	15	10	10	10	5	10	20	5	15	5	20	11.5
Dupontia fisheri	10	10	10	10	30	30	20	30	5	10		15.0
Eriophorum angustifolium				5			10	30	20	10		6.8
Eriophorum scheuchzeri	20	10	10		10	10				0.5	20	7.3
Equisetum variegatum									5	0.1	5	0.9
Alopecurus alpinus												
Poa alpina												
Arctagrostis latifolia												
Juncus biglumis												
Herbs	8	27	30.4	15	15	25	21.1	0.2	15	15.1	3	15.8
Braya spp.			0.1			5		0.1				0.5
Cardamine pratensis		10	10			5						2.3
Melandrium apetalum		1	0.1									tr
Ranunculus nivalis										0.5		tr
Pedicularis sudetica	1		0.1			5	1			5	3	1.4
Polygonum viviparum	1	1	0.1				0.1	0.1	5			0.7
Saxifraga cernua		5		5	5	5	10		10			3.6
Saxifraga hirculus		5	10	10	10	5	10			10		5.5
Stellaria spp.	1											tr
Valeriana capitata	5	5	10									1.8
Oxytropis sp.										0.1		tr
Parrya nudicaulis												
Mosses	20	10		5	20	20	50	50	40		30	22.3
Mnium spp.	20	10		5	20	20	50	50	40		30	22.3
Standing dead	30	30	30	40	40	50	20	50	40	60	60	40.9
Humus/sand				10	5		15	5		40	30	9.5

Appendix Table 7 (continued)

2					3						
69	70	71	72	$\overline{x}_2$	73	74	75	76	77	$\overline{x}_3$	$\overline{x}$
40		10	40	22.5	0.1	0.1	5	5		2.5	18.8
		5		1.3							6.8
											1.1
											1.5
20		5	5	7.5							1.5
5			5	2.5							0.5
15			20	11.3	0.1	0.1	5	5	–	2.6	2.3
45.1	66	40.1	75	56.6	60	65	55	30.2	55	66.3	48.8
	10		10	5							2.8
10		5		3.7							7.0
5	30	0.1	30	16.3	10	25	5	5	5	12.5	14.0
30	20	30	30	22.5							9.3
											4.0
					50	30	30	20	5	33.8	7.3
		5	5	2.5				5		1.3	0.8
0.1				tr			5	0.1	5	2.5	0.5
	1			0.3			5		30	8.8	1.8
	5			1.3		10	10	0.1	10	5.0	1.8
5.2	6	10.1	10	7.8			0.2	5.1	0.1	1.3	10.6
							0.1			tr	
											1.3
		0.1		tr							tr
1				0.3						tr	tr
0.1				tr			0.1			tr	0.7
1			5	1.5				5	0.1	1.3	0.9
0.1				tr							2.0
	5	10	5	5.0							4.0
3				0.8							0.2
								0.1		tr	1.0
											tr
	1			0.3							tr
15	50	30	40	33.8						19.0	19.0
30	40	20	30	30	10	10	10	10	20	15.0	31.5
			30	7.5	35	30	30	40	30	41.3	

Appendix Table 8

Botanical composition in 33 x 100 cm plots from *Carex aquatilis* marshes. Percent.

Stand no.					1			
Corresponding EF samples					13, 18			
Plot no.	78	79	80	81	82	83	84	$\bar{x}_1$
Shrubs	0.5	30		30		30		8.6
Salix lanata								
Salix ovalifolia		30		30		30		
Salix rotundifolia	0.5							tr
Grass-like	70	60.1	55	45	60	60.1	55	57.9
Alopecurus alpinus								
Arctophila fulva			10				10	2.9
Carex aquatilis	40	50	40		30	50	40	35.7
Carex membranacea				20				2.9
Dupontia fisheri		5	5			5	5	2.9
Eriophorum angustifolium	30				20			7.1
Eriophorum scheuchzeri		5		20	10	5		5.7
Equisetum variegatum		0.1		5		0.1		0.7
Herbs	5	1.1		3	5		1.1	2.2
Cardamine pratensis		1					1	0.3
Pedicularis sudetica	5			3	5			1.9
Polygonum viviparum								
Viola sp.		0.1					0.1	tr
Lichen	5.5							0.8
Cetraria cucullata	1							0.1
Cetraria islandica	0.1							tr
Dactylina arctica	3							0.4
Thamnolia vermicularis	1							0.1
Mosses	25	20	30	30	40	20	30	27.9
Dicranum fuscescens	15							2.1
Mnium spp.		20	30	30		20	30	18.6
Standing dead	80	40	50	60	10	40	50	47.1
Sand/humus		40	30	30		40	30	
Water	20							

Appendix Table 8 (continued)

		2							3			
85	86	87	88	89	$\bar{x}_2$	90	91	92	93	94	$\bar{x}_3$	$\bar{x}$
11	5		10.1	20	11.5	5					1.3	8.8
1					0.3							tr
10	5		10	20	11.3							7.9
			0.1		tr	5					1.3	tr
71	80	80	70.1	20.1	80.3	65.1	80	70	80	50	86.3	63.0
1			0.1	0.1	0.3	0.1					tr	tr
												1.2
20	30	50	10	10	30	30	30	40	20	10	32.5	29.4
												1.2
30	30	20	30	5	28.8	5	10	20	20	30	21.3	12.9
						30	40	10	40	10	32.5	10.6
20	20	10	30	5	21.3							7.4
												tr
			0.1	0.1	tr							0.9
												tr
												0.8
			0.1	0.1	tr							tr
30	30	20	20	60	40	40	10	50	30	50	45.0	31.5
												7.6
40	20	20	30	10	30	20	30	20	20	30	30.0	33.5
		30			7.5	10					2.5	12.3
	5				1.3							tr

Appendix Table 9

Botanical composition in 33 x 100 cm vegetation plots from the *Salix ovalifolia* sand dunes. Percent.

Stand no.							1								
Corresponding EF samples						19,20									
Plot no.	95	96	97	98	99	100	101	102	103	104	105	106	107	108	x̄
Shrubs	30	10	30	15		30	5	15	20	15	55	30	50	50	25.4
Salix ovalifolia	30	10	30	15		30	5	15	20	15	55	30	50	50	25.4
Grass-like	15	2	0.1			5			1		0.1	0.2	15	40	5.6
Arctagrostis latifolia		1													tr
Dupontia fisheri	5	1	0.1								0.1	0.1	10	10	1.9
Elymus mollis	10					5			1			0.1	5	30	3.7
Herbs	5.3	0.1		5	0.3	0.1	5	5	5		5	0.1	5.1	5.2	2.9
Artemisia spp.	5			5			3	2	3		5		0.1		1.7
Aster spp.	0.1														tr
Braya spp.					0.1							0.1			tr
Cardamine pratensis					0.1										tr
Cerastium beeringianum														0.1	tr
Draba alpina						0.1									tr
Lupinus arcticus	0.1														tr
Oxytropis arctica															
Pedicularis capitata															
Polemonium boreale							2	2							0.3
Polygonum viviparum	0.1	0.1			0.1								0.1	0.1	tr
Primula borealis								1	2				5	5	0.9
Sand/gravel	50	90	70	75	100	65	90	80	74	85	40	60	30	10	65.6

Appendix Table 10

(Walker, S., Pers. Comm.). Distribution of *Dryas integrifolia, Eriophorum angustifolium* and *Carex aquatilis* through vegetation types making up the continuum at Prudhoe Bay. Mean cover score and frequency for 10 quadrants randomly selected from each vegetation type.

	Webber/Walker Vegetation Type					
Plant species	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Dryas integrifolia	48.7(100)	59.8(100)	20(90)			
Eriophorum angustifolium	2.4(40)	11.0(80)	11.6(90)	23.2(90)	7.5(70)	
Carex aquatilis		4.0(40)	11.2(60)	17.5(100)	19.0(100)	16.5(80)

Comments from Walker:

1. Type 2 may be equivalent to Skogland's *Dryas integrifolia* community, but Skogland may have been ignoring crustose lichens, which we use as an indicator for Type 1. Probably, plots were in both of Types 1 and 2. Also plot No. 34 was probably what we would call Type 9—snowbed community.
2. Although we show greatest coverage by *Eriophorum angustifolium* in Type 4, to say that Type 4 is equivalent to Skogland's *"Eriophorum angustifolium"* may be in error since the presence of *Dryas* is to be found in analyses of nearly all of his plots; we rarely recorded much *Dryas* in Type 4. Skogland's *Eriophorum angustifolium* marsh may correspond more closely to Type 3, but it should not be designated as "polygon marsh."
3. Skogland's *Carex aquatilis* marshes are probably a mixture of our Types 4 and 5. Type 4 is relatively dry by the end of summer (i.e., there's little or no standing water); whereas, Type 5 has standing water throughout the summer. These are both truly marshy types.

The *Dupontia fisheri* meadows seem to correspond most closely to Type 12 vegetation which was found mostly along streambanks and the edges of some lakes. It is not very common and probably does not fit into the generalized moisture continuum which occurs over the majority of the region.

Appendix A

Provisional Checklist to the Vascular, Bryophyte, and Lichen Flora of Prudhoe Bay, Alaska

BARBARA M. MURRAY and DAVID F. MURRAY
University of Alaska Herbarium
Fairbanks, Alaska 99701

Introduction

Prudhoe Bay is situated on the Arctic Coastal Plain, a distinct physiographic unit that extends from Point Lay east across northern Alaska to the Mackenzie Delta in Canada. The flora is characteristic of a wet lowland that is interrupted chiefly by thaw lakes, drained lake basins, and river systems. The differences between the Prudhoe flora and that of Barrow and environs can be attributed to the physical features associated with the large rivers that head in the Brooks Range, numerous pingos, and distinctly calcareous soils. The areas collected were adjacent to the road system that links drilling pads and related facilities between the Sagavanirktok and Kuparuk rivers. We and others were able to visit and examine gravel bars, riverbanks, sand dunes, pingos, thaw lakes, drained lake basins, saline marshes, and ice-wedge polygons. Thus, a full spectrum of habitats was included in the inventory.

Floristic studies of the Prudhoe Bay area are still in the exploratory stage, and the following list is provisional. The first plant collections resulted from Tundra Biome studies; since 1971 Tundra Biome participants and cooperators have been expanding our knowledge of the flora of the area through collections (Table 1) and reports. The only published list for the area is that of Rastorfer, Webster, and Smith (1973) who reported their own 1972 bryophyte collections. In a few cases they listed species without citing specimens, and according to J. R. Rastorfer *in litt.*, 1974, no vouchers were kept for these taxa. In the following list we have placed these undocumented reports in brackets, if we were unable to find a specimen to substantiate the occurrence of the species at Prudhoe Bay.

Table 1

Collectors of vascular plants (V), bryophytes (B), and lichens (L)

M. W. Battrum (1971) B, L
J. W. Batty (1973, 1974) V, B, L
J. Hok (1971) V
B. M. Murray (1971, 1972, 1974) B, L
D. F. Murray (1971, 1972, 1974) V
J. R. Rastorfer, H. J. Webster, and D. K. Smith (1972) B
D. H. S. Richardson (1974) L
E. Schofield (1972) V, L
W. C. Steere (1972); W. C. Steere and Z. Iwatsuki (1974) B
D. A. Walker (1973, 1974) V, B, L
H. J. Webster (1971) B
M. E. Williams (1972) V, L

This list represents the first report of vascular plants and lichens for the Prudhoe Bay area and includes further records of bryophytes. These records are excerpted from our Tundra Biome final project report. We have cited a single specimen of each taxon in order to document its presence in the Prudhoe Bay area and have not cited all collections seen. Unless otherwise stated, specimens are in the University of Alaska Herbarium (ALA), and identifications were made by the collectors. David F. Murray has verified the identification of all vascular plants cited. Other herbaria housing specimens cited are the University of Calgary Herbarium (UAC) and The New York Botanical Garden (NY). Generally, nomenclature follows Hultén (1968, 1973) for vascular plants; Worley (1970) for hepatics; Crum, Steere, and Anderson (1973) for mosses, excluding Mniaceae; Koponen (1968, 1972) for Mniaceae; and Hale and Culberson (1970) for lichens. Synonyms are included when they facilitate referral to specimens or when they are commonly used.

Acknowledgments

We wish to thank Tundra Biome personnel who sent us specimens and helped in the compilation of this report, especially M. W. Battrum, J. R. Rastorfer, D. A. Walker, and M. E. Williams. We are deeply indebted to John W. Thomson, University of Wisconsin, Madison, who determined or verified most of the lichen specimens cited. William C. Steere, of The New York Botanical Garden, generously provided help with identifications in the field and in the laboratory. We are also grateful to him for permitting us to cite his unpublished collections from Prudhoe Bay.

This project was supported through grants and contributions by the National Science Foundation under Grant GV 29342 to the University of Alaska, the State of Alaska, and the Prudhoe Bay Environmental Subcommittee. It was performed under the joint NSF sponsorship of the International Biological Program and the Office of Polar Programs and was directed under the auspices of the U. S. Tundra Biome.

Floristic Notes

Noteworthy discoveries are:

1. *Puccinellia andersonii* has been known in Alaska only from its type locality at Point Lay. The Prudhoe collection bridges a gap between Point Lay and Banks Island, Northwest Territories (A. E. Porsild, *in litt.*).

2. *Thlaspi arcticum* was found on a gravel terrace of the Kuparuk River. Numerous plants were seen which, in itself, is unusual. A collection by Spetzman from the Sadlerochit River (Wiggins and Thomas 1962) is the only other Alaskan collection. This taxon is currently under study to determine its relationship to the Asian *T. cochleariforme,* but sufficient material is not available from all stages of development to adequately describe it. We are now examining the series of *T. arcticum* we obtained, but viable seed would be most helpful. Since the locality of our collection is a gravel terrace adjacent to gravel deposits already mined for fill, this site should be identified so it can be protected. It is the only readily accessible source of this species. *Thlaspi arcticum* has now been placed on the Smithsonian list of threatened species, and this Prudhoe site should be protected from further disturbance.

3. The lichens *Lopadium fecundum, Polyblastia bryophila*, and *P. sendtneri* have not been previously reported for Alaska, according to J. W. Thomson *in litt.*

References

Crum, H., W. C. Steere, and L. E. Anderson (1973). A new list of mosses of North America north of Mexico. *Bryologist,* 76:85-130.

Hale, M. E., Jr. and W. L. Culberson (1970). A fourth checklist of the lichens of the continental United States and Canada. *Bryologist,* 73:499-543.

Halliday, G. and A. O. Chater (1969). *Carex marina* Dewey, an earlier name for *C. amblyorhyncha* Krecz. *Feddes Repertorium,* 80:103-106.

Hultén, E. (1968). "Flora of Alaska and Neighboring Territories." Stanford University Press, Stanford, 1008 pp.

Hultén, E. (1973). Supplement to Flora of Alaska and Neighboring Territories. *Bot. Not.*, 126:459-512.

Koponen, T. (1968). Generic revision of Mniaceae Mitt. (Bryophyta). *Ann. Bot. Fenn.*, 5:117-151.

———. (1972). Notes on *Mnium arizonicum* and *M. thomsonii*. *Lindbergia*, 1:161-165.

Mulligan, G. A. (1974). Confusion in the names of three *Draba* species of the Arctic: *D. adamsii*, *D. oblongata*, and *D. corymbosa*. *Can. J. Bot.*, 52:791-793.

Rastorfer, J. R., H. J. Webster, and D. K. Smith (1973). Floristic and ecologic studies of bryophytes of selected habitats at Prudhoe Bay, Alaska. The Ohio State University, Institute of Polar Studies, Report No. 49, 20 pp.

Steere, W. C. (1974). The status and geographical distribution of *Voitia hyperborea* in North America (Musci: Splachnaceae). *Bull. Torrey Bot. Club*, 101:55-63.

Steere, W. C. and B. M. Murray (1974). The geographical distribution of *Bryum wrightii* in arctic and boreal North America. *Bryologist*, 77:172-178.

Wiggins, I. L. and J. H. Thomas (1962). A flora of the Alaskan Arctic Slope. University of Toronto Press, Toronto, 425 pp.

Worley, I. A. (1970). A checklist of the Hepaticae of Alaska. *Bryologist,* 73:32-38.

VASCULAR PLANTS

AGROPYRON BOREALE (Turcz.) Drobov ssp. HYPERARCTICUM (Pols.) Meld. *D. Murray 4575*
ALOPECURUS ALPINUS Sm. ssp. ALPINUS *D. Murray 3410*
ANDROSACE CHAMAEJASME Host ssp. LEHMANNIANA (Spreng.) Hult. *D. Murray 3387*
ANDROSACE SEPTENTRIONALIS L. *D. Murray 4505*
ANEMONE PARVIFLORA Michx. *D. Murray 4531*
ANEMONE RICHARDSONII Hook. *D. Murray 4537*
ANTENNARIA FRIESIANA (Trautv.) Ekman ssp. ALASKANA (Malte) Hult. *D. Murray 4571*
ARABIS LYRATA L. ssp. KAMCHATICA (Fisch.) Hult. *D. Murray 3359*
ARCTAGROSTIS LATIFOLIA (R. Br.) Griseb. var. LATIFOLIA *D. Murray 4554*
ARCTOPHILA FULVA (Trin.) Anderss. *D. Murray 4555*
ARCTOSTAPHYLOS RUBRA (Rehd. & Wils.) Fern. *D. Murray 4561*
ARMERIA MARITIMA (Mill.) Willd. ssp. ARCTICA (Cham.) Hult. *D. Murray 3356*
ARTEMISIA ARCTICA Less. ssp. ARCTICA *D. Murray 4568*
ARTEMISIA BOREALIS Pall. (including *A. richardsoniana* Bess.) *D. Murray 3356*
ARTEMISIA GLOMERATA Ledeb. *D. Murray 4532*
ARTEMISIA TILESII Ledeb. ssp. TILESII *D. Murray 4569*
ASTER SIBIRICUS L. *D. Murray 4574*
ASTRAGALUS ALPINUS L. *D. Murray 4540*
ASTRAGALUS UMBELLATUS Bunge *D. Murray 4517*
BOYKINIA RICHARDSONII (Hook.) Gray *Walker 503*
BRAYA PILOSA Hook. *D. Murray 3383*
BRAYA PURPURASCENS (R. Br.) Bunge *D. Murray 3385*
BROMUS PUMPELLIANUS Scribn. var. ARCTICUS (Shear) Pors. *Walker 570*
CALTHA PALUSTRIS L. ssp. ARCTICA (R. Br.) Hult. *D. Murray 4512*
CAMPANULA UNIFLORA L. *D. Murray 3398*
CARDAMINE DIGITATA Richards. (= *C. hyperborea* Schulz) *D. Murray 3399*
CARDAMINE PRATENSIS L. ssp. ANGUSTIFOLIA (Hook.) Schulz *Walker 549*
CAREX AQUATILIS Wahlenb. (s.l., to include *C. stans* Drej.) *D. Murray 3586*
CAREX ATROFUSCA Schk. *D. Murray 3370*
CAREX BIGELOWII Torr. *D. Murray 3416*
CAREX MARINA Dewey (= *C. amblyorhyncha* Krecz., Halliday and Chater 1969) *Walker 4,* det. A. Batten
CAREX MARITIMA Gunn. *D. Murray 4514*
CAREX MEMBRANACEA Hook. *Walker s.n.,* 5 August 1974, det. D. Murray

Vascular Plants (continued)

CAREX MISANDRA R. Br. *D. Murray 3384*
CAREX RARIFLORA (Wahlenb.) J.E. Sm. *D. Murray 3364*
CAREX RUPESTRIS All. *D. Murray 4583*
CAREX SAXATILIS L. ssp. LAXA (Trautv.) Kalela *Walker s.n.,* 5 August 1974
CAREX SCIRPOIDEA Michx. *D. Murray 4519*
CAREX SUBSPATHACEA Wormsk. *Walker & Batty PB039*
CAREX URSINA Dew. *D. Murray 3406*
CAREX VAGINATA Tausch *Walker 526*
CASSIOPE TETRAGONA (L.) D. Don ssp. TETRAGONA *D. Murray 4539*
CERASTIUM BEERINGIANUM Cham. & Schlecht. var. BEERINGIANUM *D. Murray 4538*
CHRYSANTHEMUM INTEGRIFOLIUM Richards. *D. Murray 3394*
CHRYSOSPLENIUM TETRANDRUM (Lund) Th. Fr. *D. Murray 4525*
COCHLEARIA OFFICINALIS L. ssp. ARCTICA (Schlecht.) Hult. *D. Murray 4511*
DESCHAMPSIA CAESPITOSA (L.) Beauv. ssp. ORIENTALIS Hult. *D. Murray 3412*
DRABA ALPINA L. *D. Murray 3381,* det. G. A. Mulligan
DRABA CINEREA Adams *D. Murray 3402,* det. G. A. Mulligan
DRABA CORYMBOSA R. Br. *ex* DC. (= *D. bellii* Holm, *D. macrocarpa* Adams, Mulligan 1974) *D. Murray 3371,* det. G. A. Mulligan
DRABA LACTEA Adams *D. Murray 3382,* det. G. A. Mulligan
DRYAS INTEGRIFOLIA M. Vahl ssp. INTEGRIFOLIA *D. Murray 4533*
DUPONTIA FISHERI R. Br. ssp. PSILOSANTHA (Rupr.) Hult. *D. Murray 4563*
ELYMUS ARENARIUS L. ssp. MOLLIS (Trin.) Hult. var. VILLOSISSIMUS (Scribn.) Hult. *D. Murray 3411*
EPILOBIUM LATIFOLIUM L. *Walker 557*
EQUISETUM ARVENSE L. *D. Murray 4515*
EQUISETUM SCIRPOIDES Michx. *D. Murray 3380*
EQUISETUM VARIEGATUM Schleich. *D. Murray 4565*
ERIGERON ERIOCEPHALUS J. Vahl *D. Murray 4545*
ERIGERON HUMILIS Grah. *D. Murray 3378*
ERIOPHORUM ANGUSTIFOLIUM Honck. ssp. SUBARCTICUM (Vassil.) Hult. *Walker s.n.,* 5 August 1974
ERIOPHORUM SCHEUCHZERI Hoppe var. SCHEUCHZERI *D. Murray 3405*
ERIOPHORUM TRISTE (Th. Fr.) Hadac & Löve (= *E. angustifolium* ssp. *triste*) *D. Murray 3375*
ERIOPHORUM VAGINATUM L. *D. Murray 4550*
EUTREMA EDWARDSII R. Br. *D. Murray 3368*
FESTUCA BAFFINENSIS Polunin *D. Murray 3417*
FESTUCA BRACHYPHYLLA Schult. *D. Murray 4564*
FESTUCA RUBRA L. *D. Murray 3415*
GENTIANA PROSTRATA Haenke *D. Murray 4556*
GENTIANELLA PROPINQUA (Richards.) J. M. Gillett ssp. PROPINQUA (= *Gentiana propinqua*) *D. Murray 3407*
HIEROCHLOE PAUCIFLORA R. Br. *Walker 1*
HIPPURIS VULGARIS L. *D. Murray 4552*
JUNCUS ARCTICUS Willd. ssp. ALASKANUS Hult. *D. Murray 4553*
JUNCUS BIGLUMIS L. *D. Murray 4560*
JUNCUS CASTANEUS Sm. ssp. CASTANEUS *D. Murray 3404*
JUNCUS TRIGLUMIS L. ssp. ALBESCENS (Lange) Hult. *Walker & Batty s.n.,* August 1974
KOBRESIA MYOSUROIDES (Vill.) Fiori & Paol. *D. Murray 4557*
KOBRESIA SIBIRICA Turcz. *D. Murray 3352*
LAGOTIS GLAUCA Gaertn. ssp. MINOR (Willd.) Hult. *D. Murray 4526*
LESQUERELLA ARCTICA (Wormsk.) Wats. *D. Murray 3395*
LLOYDIA SEROTINA (L.) Rchb. *D. Murray 3390*
LUZULA ARCTICA Blytt *D. Murray 4580*

MINUARTIA ARCTICA (Stev.) Aschers. & Graebn. *D. Murray 3379*
MINUARTIA ROSSII (R. Br.) Graebn. *Schofield & Williams P-G16*
MINUARTIA RUBELLA (Wahlenb.) Graebn. *D. Murray 3403*
ORTHILIA SECUNDA (L.) House ssp. OBTUSATA (Turcz.) Böcher (= *Pyrola secunda* ssp. *obtusata*) *Walker & Batty PB005*
OXYRIA DIGYNA (L.) Hill *D. Murray 4520*
OXYTROPIS ARCTICA R. Br. *D. Murray 3396*
OXYTROPIS BOREALIS DC. *D. Murray 4559*
OXYTROPIS DEFLEXA (Pall.) DC. var. FOLIOLOSA (Hook.) Barneby *D. Murray 4584*
OXYTROPIS MAYDELLIANA Trautv. *D. Murray 4513*
OXYTROPIS NIGRESCENS (Pall.) Fisch. ssp. BRYOPHILA (Greene) Hult. *D. Murray 4541*
PAPAVER LAPPONICUM (Tolm.) Nordh. ssp. OCCIDENTALE (Lundstr.) Knaben *D. Murray 4521*
PAPAVER MACOUNII Greene *D. Murray 3377*
PARNASSIA KOTZEBUEI Cham. & Schlecht. *D. Murray 4570*
PARRYA NUDICAULIS (L.) Regel. ssp. NUDICAULIS *D. Murray 3408*
PEDICULARIS CAPITATA Adams *D. Murray 3386*
PEDICULARIS LANATA Cham. & Schlecht. (= *P. kanei* Durand) *D. Murray 3556*
PEDICULARIS LANGSDORFFII Fisch. ssp. ARCTICA (R. Br.) Pennell *D. Murray 3362*
PEDICULARIS SUDETICA Willd. *D. Murray 3391*
PEDICULARIS SUDETICA Willd. ssp. ALBOLABIATA Hult. *D. Murray 3372*
PETASITES FRIGIDUS (L.) Franch. *D. Murray 4582*
POA ABBREVIATA R. Br. *Walker 550,* det. D. F. Murray
POA ALPIGENA (Fr.) Lindm. *D. Murray 4576*
POA GLAUCA M. Vahl *D. Murray 3419*
POLEMONIUM BOREALE Adams *D. Murray 3353*
POLYGONUM BISTORTA L. ssp. PLUMOSUM (Small) Hult. *Walker 528*
POLYGONUM VIVIPARUM L. *D. Murray 3389*
POTENTILLA HOOKERIANA Lehm. ssp. HOOKERIANA *D. Murray 3401*
POTENTILLA PULCHELLA R. Br. *D. Murray 3358*
POTENTILLA UNIFLORA Ledeb. *D. Murray 4529*
PRIMULA BOREALIS Duby *D. Murray 4510*
PUCCINELLIA ANDERSONII Swallen *D. Murray 3414,* ver. A. E. Porsild
PUCCINELLIA PHRYGANODES (Trin.) Scribn. & Merr. *D. Murray 4567*
PYROLA GRANDIFLORA Radius *Walker 545*
RANUNCULUS NIVALIS L. *D. Murray 3555*
RANUNCULUS PEDATIFIDUS Sm. ssp. AFFINIS (R. Br.) Hult. *D. Murray 4536*
RANUNCULUS TRICHOPHYLLUS (E. Fr.) E. Fr. *Walker 532*
SAGINA INTERMEDIA Fenzl *D. Murray 4562*
SALIX ALAXENSIS (Anderss.) Cov. var. ALAXENSIS *D. Murray 4566*
SALIX ARCTICA Pall. *D. Murray 4523*
SALIX LANATA L. ssp. RICHARDSONII (Hook.) Skvortz. *D. Murray 3351*
SALIX OVALIFOLIA Trautv. var. OVALIFOLIA *D. Murray 3366*
SALIX PLANIFOLIA Pursh ssp. PULCHRA (Cham.) Argus var. PULCHRA *D. Murray 4522*
SALIX RETICULATA L. ssp. RETICULATA *D. Murray 4534*
SALIX ROTUNDIFOLIA Trautv. ssp. ROTUNDIFOLIA *D. Murray 4548*
SAUSSUREA ANGUSTIFOLIA (Willd.) DC. *Walker 555*
SAXIFRAGA CAESPITOSA L. *D. Murray 4546*
SAXIFRAGA CERNUA L. *D. Murray 4547*
SAXIFRAGA HIERACIFOLIA Waldst. & Kit. *D. Murray 4543*
SAXIFRAGA HIRCULUS L. *D. Murray 3369*
SAXIFRAGA OPPOSITIFOLIA L. ssp. OPPOSITIFOLIA *D. Murray 4524*

Vascular Plants (continued)

SAXIFRAGA TRICUSPIDATA Rottb. *D. Murray 4544*
SEDUM ROSEA (L.) Scop. ssp. INTEGRIFOLIUM (Raf.) Hult. *D. Murray 3354*
SENECIO ATROPURPUREUS (Ledeb.) Fedtsch. ssp. FRIGIDUS (Richards.) Hult. *D. Murray 3365*
SENECIO CONGESTUS (R. Br.) DC. *Walker s.n.,* July 1974
SENECIO RESEDIFOLIUS Less. *D. Murray 3376*
SILENE ACAULIS L. *D. Murray 4535*
SILENE INVOLUCRATA (Cham. & Schlecht.) Bocq. (= *Melandrium affine* J. Vahl) *D. Murray 3373*
SILENE WAHLBERGELLA Chawd. ssp. ARCTICA (Fr.) Hult. (= *Melandrium apetalum* (L.) Fenzl ssp. *arcticum* (Fr.) Hult.) *D. Murray 3363*
STELLARIA HUMIFUSA Rottb. *Walker & Batty PB037*
STELLARIA LAETA Richards. *D. Murray 4549*
TARAXACUM CERATOPHORUM (Ledeb.) DC. *D. Murray 3355*
TARAXACUM PHYMATOCARPUM J. Vahl *D. Murray 3397*
THALICTRUM ALPINUM L. *D. Murray 3392*
THLASPI ARCTICUM Pors. *D. Murray 4530*
TOFIELDIA PUSILLA (Michx.) Pers. *Walker & Batty PB028*
TRISETUM SPICATUM (L.) Richt. *D. Murray 3413*
UTRICULARIA VULGARIS L. ssp. MACRORHIZA (Le Conte) Clausen *Walker s.n.,* 5 August 1974, det. D. Murray
VALERIANA CAPITATA Pall. *D. Murray 4551*
WILHELMSIA PHYSODES (Fisch.) McNeill *D. Murray 4528*

BRYOPHYTES

Hepatics

ANEURA PINGUIS (L.) Dum. (= *Riccardia pinguis*) Rastorfer, Webster, and Smith 1973
ARNELLIA FENNICA (Gott.) Lindb. *Walker 52,* det. W. C. Steere
BLEPHAROSTOMA TRICHOPHYLLUM (L.) Dum. Rastorfer, Webster, and Smith 1973; var. BREVIRETE Bryhn & Kaalaas Rastorfer, Webster, and Smith 1973
[CEPHALOZIELLA ARCTICA Bryhn & Douin Rastorfer, Webster, and Smith 1973, no specimen cited]
CLEVEA HYALINA (Sommerf.) Lindb. *B. Murray 6215,* det. W. C. Steere
MARCHANTIA ALPESTRIS Nees *B. Murray 4417,* det. K. Damsholt
MARCHANTIA POLYMORPHA L. Rastorfer, Webster, and Smith 1973, no specimen cited, *B. Murray 4428*
MESOPTYCHIA SAHLBERGII (Lindb. & H. Arnell) Evans *Walker 37,* det. W. C. Steere
ODONTOSCHISMA MACOUNII (Aust.) Und. Rastorfer, Webster, and Smith 1973
PLAGIOCHILA ARCTICA Bryhn & Kaal. *Walker 71,* det. W. C. Steere
PREISSIA QUADRATA (Scop.) Nees *B. Murray 6243*
PTILIDIUM CILIARE (Web.) Hampe Rastorfer, Webster, and Smith 1973
RADULA PROLIFERA H. Arnell Rastorfer, Webster, and Smith 1973
[SCAPANIA IRRIGUA (Nees) Dum. Rastorfer, Webster, and Smith 1973, no specimen cited]
TRITOMARIA QUINQUEDENTATA (Huds.) Buch Rastorfer, Webster, and Smith 1973

Mosses

ALOINA BREVIROSTRIS (Hook. & Grev.) Kindb. *B. Murray 6231* (mainly *Polyblastia)*
APLODON WORMSKJOLDII (Hornem.) R. Br. (= *Haplodon wormskjoldii*) Rastorfer, Webster, and Smith 1973
AULACOMNIUM ACUMINATUM (Lindb. & H. Arnell) Kindb. Rastorfer, Webster, and Smith 1973
AULACOMNIUM PALUSTRE (Hedw.) Schwaegr. Rastorfer, Webster, and Smith 1973
AULACOMNIUM TURGIDUM (Wahlenb.) Schwaegr. Rastorfer, Webster, and Smith 1973
[BARBULA ICMADOPHILA Schimp. *ex* C. Muell. Rastorfer, Webster, and Smith 1973, no specimen cited]
[BRACHYTHECIUM TURGIDUM (C. J. Hartm.) Kindb. Rastorfer, Webster, and Smith 1973, no specimen cited]

BRYOBRITTONIA PELLUCIDA Williams *B. Murray 6247*

BRYOERYTHROPHYLLUM RECURVIROSTRUM (Hedw.) Chen (= *Didymodon recurvirostris*) Rastorfer, Webster, and Smith 1973

BRYUM ARCTICUM (R. Br.) B.S.G. Rastorfer, Webster, and Smith 1973

BRYUM ARGENTEUM Hedw. *B. Murray 6249*

BRYUM cf. CAESPITICIUM Hedw. *Walker 24,* det. W. C. Steere

[BRYUM CALOPHYLLUM R. Br. Rastorfer, Webster, and Smith 1973, no specimen cited]

BRYUM CRYOPHILUM Mart. *B. Murray 6248*

BRYUM PALLESCENS Schleich. *ex* Schwaegr. Rastorfer, Webster, and Smith 1973

BRYUM STENOTRICHUM C. Muell. (= *B. inclinatum*) Rastorfer, Webster, and Smith 1973

BRYUM WRIGHTII Sull. & Lesq. Steere and Murray 1974

CALLIERGON GIGANTEUM (Schimp.) Kindb. Rastorfer, Webster, and Smith 1973, no specimen cited, *Steere 72-718* (NY)

CALLIERGON ORBICULARICORDATUM (Ren. & Card.) Broth. *Steere 72-665* (NY)

CALLIERGON RICHARDSONII (Mitt.) Kindb. *ex* Warnst. Rastorfer, Webster, and Smith 1973; var. ROBUSTUM (Lindb. & Arn.) Broth em. Kar. *B. Murray 6220*

[CALLIERGON SARMENTOSUM (Wahlenb.) Kindb. Rastorfer, Webster, and Smith 1973, no specimen cited]

CALLIERGON TRIFARIUM (Web. & Mohr) Kindb. Steere *in litt.*, 1974 (NY)

CAMPYLIUM STELLATUM (Hedw.) C. Jens. Rastorfer, Webster, and Smith 1973

CATOSCOPIUM NIGRITUM (Hedw.) Brid. Rastorfer, Webster, and Smith 1973

CERATODON PURPUREUS (Hedw.) Brid. Rastorfer, Webster, and Smith 1973

CINCLIDIUM ARCTICUM (B.S.G.) Schimp. Rastorfer, Webster, and Smith 1973

CINCLIDIUM LATIFOLIUM Lindb. Rastorfer, Webster, and Smith 1973

CIRRIPHYLLUM CIRROSUM (Schwaegr. *ex* Schultes) Grout Rastorfer, Webster, and Smith 1973

CRATONEURON ARCTICUM Steere *Walker 49,* det. W. C. Steere

CRATONEURON FILICINUM (Hedw.) Spruce *Steere 72-739* (NY)

CTENIDIUM MOLLUSCUM (Hedw.) Mitt. *Walker 29,* det. W. C. Steere

[CYRTOMNIUM HYMENOPHYLLOIDES (Hueb.) Kop. (= *Mnium hymenophylloides*) Rastorfer, Webster, and Smith 1973, no specimen cited]

CYRTOMNIUM HYMENOPHYLLUM (B.S.G.) Holmen (= *Mnium hymenophyllum*) Rastorfer, Webster, and Smith 1973

DESMATODON HEIMII (Hedw.) Mitt. (= *Pottia heimii*) *B. Murray 4472*

DESMATODON LEUCOSTOMA (R. Br.) Berggr. (= *D. suberectus*) Rastorfer, Webster, and Smith 1973

[DICRANELLA CRISPA (Hedw.) Schimp. (= *Anisothecium crispum*) Rastorfer, Webster, and Smith 1973, no specimen cited]

DICRANUM ANGUSTUM Lindb. Rastorfer, Webster, and Smith 1973

DICRANUM ELONGATUM Schleich. *ex* Schwaegr. Rastorfer, Webster, and Smith 1973

DIDYMODON ASPERIFOLIUS (Mitt.) Crum, Steere & Anderson *B. Murray 4446*

DISTICHIUM CAPILLACEUM (Hedw.) B.S.G. Rastorfer, Webster, and Smith 1973

DISTICHIUM HAGENII Ryan *ex* Philib. Rastorfer, Webster, and Smith 1973

DISTICHIUM INCLINATUM (Hedw.) B.S.G. Rastorfer, Webster, and Smith 1973

DITRICHUM FLEXICAULE (Schwaegr.) Hampe Rastorfer, Webster, and Smith 1973

DREPANOCLADUS BADIUS (C. J. Hartm.) Roth Steere *in litt.*, 1974 (NY)

DREPANOCLADUS EXANNULATUS (B.S.G.) Warnst. *Steere & Iwatsuki 74-317* (NY)

DREPANOCLADUS LYCOPODIOIDES (Brid.) Warnst. *Steere 72-731* (NY); var. BREVIFOLIUS (Lindb.) Moenk (= *D. brevifolius*) Rastorfer, Webster, and Smith 1973

DREPANOCLADUS REVOLVENS (Sw.) Warnst. Rastorfer, Webster, and Smith 1973

DREPANOCLADUS UNCINATUS (Hedw.) Warnst. *Rastorfer, Webster, and Smith 28,* det. B. Murray

ENCALYPTA ALPINA Sm. Rastorfer, Webster, and Smith 1973, no specimen cited, *Steere 72-707* (NY)

ENCALYPTA PROCERA Bruch Rastorfer, Webster, and Smith 1973, no specimen cited, *B. Murray 6244*

ENCALYPTA RHAPTOCARPA Schwaegr. (= *E. vulgaris* var. *rhaptocarpa*) Rastorfer, Webster, and Smith 1973

ENCALYPTA VULGARIS Hedw. *B. Murray 6214*

Bryophytes (continued)

FISSIDENS ADIANTOIDES Hedw. *Steere & Iwatsuki 74-318* (NY)
FISSIDENS OSMUNDOIDES Hedw. Rastorfer, Webster, and Smith 1973
FUNARIA ARCTICA (Berggr.) Kindb. (= *F. hygrometrica* var. *arctica, F. microstoma* var. *obtusifolia*) *B. Murray 6251*
FUNARIA POLARIS Bryhn Rastorfer, Webster, and Smith 1973
GRIMMIA APOCARPA Hedw. *Battrum 304*
HYLOCOMIUM SPLENDENS (Hedw.) B.S.G. var. OBTUSIFOLIUM (Geh.) Par. (= *H. alaskanum*) Rastorfer, Webster, and Smith 1973
HYPNUM BAMBERGERI Schimp. Rastorfer, Webster, and Smith 1973
[HYPNUM CUPRESSIFORME Hedw. Rastorfer, Webster, and Smith 1973, no specimen cited]
HYPNUM PROCERRIMUM Mol. *B. Murray 4440*
HYPNUM REVOLUTUM (Mitt.) Lindb. *Walker 55,* det. W. C. Steere
HYPNUM VAUCHERI Lesq. Rastorfer, Webster, and Smith 1973
LEPTOBRYUM PYRIFORME (Hedw.) Wils. *B. Murray 4412*
MEESIA TRIQUETRA (Richt.) Angstr. Rastorfer, Webster, and Smith 1973
MEESIA ULIGINOSA Hedw. Rastorfer, Webster, and Smith 1973
MNIUM cf. BLYTTII B.S.G. *B. Murray 4426,* det. P. Gravesen
MNIUM THOMSONII Schimp. (= *M. orthorrhynchum*) *Steere 72-683* (NY)
MYURELLA JULACEA (Schwaegr.) B.S.G. Rastorfer, Webster, and Smith 1973
MYURELLA TENERRIMA (Brid.) Lindb. Rastorfer, Webster, and Smith 1973
ONCOPHORUS WAHLENBERGII Brid. Rastorfer, Webster, and Smith 1973
ORTHOTHECIUM CHRYSEUM (Schwaegr. *ex* Schultes) B.S.G. Rastorfer, Webster, and Smith 1973
ORTHOTHECIUM INTRICATUM (C. J. Hartm.) B.S.G. *B. Murray 6234,* det. W. C. Steere
ORTHOTHECIUM RUFESCENS (Brid.) B.S.G. *Steere 72-715* (NY)
PHILONOTIS FONTANA (Hedw.) Brid. var. PUMILA (Turn.) Brid. (= *P. tomentella*) *Steere 72-679* (NY)
PHILONOTIS sp. Rastorfer, Webster, and Smith 1973 (as possibly *P. fontana*)
[PLAGIOMNIUM RUGICUM (Laur.) Kop. (= *Mnium rugicum*) Rastorfer, Webster, and Smith 1973, no specimen cited]
PLATYDICTYA JUNGERMANNIOIDES (Brid.) Crum *Walker 51,* det. W. C. Steere
POGONATUM ALPINUM (Hedw.) Roehl. var. SEPTENTRIONALE (Brid.) Brid. Rastorfer, Webster, and Smith 1973
POHLIA CRUDA (Hedw.) Lindb. Rastorfer, Webster, and Smith 1973
[POHLIA NUTANS (Hedw.) Lindb. Rastorfer, Webster, and Smith 1973, no specimen cited]
RHACOMITRIUM LANUGINOSUM (Hedw.) Brid. Rastorfer, Webster, and Smith 1973
RHIZOMNIUM ANDREWSIANUM (Steere) Kop. (= *Mnium andrewsianum*) Steere *in litt.*, 1974 (NY)
RHYTIDIUM RUGOSUM (Hedw.) Kindb. Rastorfer, Webster, and Smith 1973
SCORPIDIUM SCORPIOIDES (Hedw.) Limp. Rastorfer, Webster, and Smith 1973
SCORPIDIUM TURGESCENS (T. Jens.) Loeske (= *Calliergon turgescens*) Rastorfer, Webster, and Smith 1973
SPLACHNUM SPHAERICUM Hedw. (= *S. ovatum*) Rastorfer, Webster, and Smith 1973
SPLACHNUM VASCULOSUM Hedw. Rastorfer, Webster, and Smith 1973, no specimen cited, *B. Murray 4415*
STEGONIA LATIFOLIA (Schwaegr. *ex* Schultes) Vent. *ex* Broth. var. PILIFERA (Brid.) Broth. *B. Murray 6246*
TAYLORIA ACUMINATA Hornsch. *B. Murray 6249*
TETRAPLODON MNIOIDES (Hedw.) B.S.G. Rastorfer, Webster, and Smith 1973; var. CAVIFOLIUS Schimp. (= *T. urceolatus*) Rastorfer, Webster, and Smith 1973
TETRAPLODON PARADOXUS (R. Br.) Hag. (= *T. mnioides* var. *paradoxus, T. pallidus*) *B. Murray 6252*
THUIDIUM ABIETINUM (Hedw.) B.S.G. (= *Abietinella abietina*) Rastorfer, Webster, and Smith 1973
TIMMIA AUSTRIACA Hedw. *B. Murray 4431,* det. V. B. Lauridsen
TIMMIA MEGAPOLITANA Hedw. var. BAVARICA (Hessl.) Brid. *B. Murray 6235*
TIMMIA NORVEGICA Zett. Rastorfer, Webster, and Smith 1973
TOMENTHYPNUM NITENS (Hedw.) Loeske (= *Homalothecium nitens*) Rastorfer, Webster, and Smith 1973
TORTELLA ARCTICA (Arn.) Crundw. & Nyh. *Rastorfer, Webster, and Smith 68,* det. B. Murray
TORTELLA FRAGILIS (Drumm.) Limpr. *B. Murray 6242*
TORTULA MUCRONIFOLIA Schwaegr. *B. Murray 6250*

TORTULA RURALIS (Hedw.) Gaertn., Meyer & Scherb. Rastorfer, Webster, and Smith 1973
TRICHOSTOMUM CUSPIDATISSIMUM Card. & Ther. *Walker s.n.*, 20 July 1974, det. B. Murray
VOITIA HYPERBOREA Grev. & Arnott Steere 1974

Rejected moss taxa

HYPNUM CALLICHROUM Funck *ex* Brid. Rastorfer, Webster, and Smith cited their collection number 28 as this species; the ALA specimen number 28 is *Drepanocladus uncinatus*.

ONCOPHORUS VIRENS (Hedw.) Brid. Rastorfer, Webster, and Smith cited this species, but the ALA specimen of the collection (No. 60) they cited is *O. wahlenbergii*.

VOITIA NIVALIS Hornsch. Rastorfer, Webster, and Smith cited their collections numbered 14, 73, and 85 as this species; Steere (1974) has recently discussed *V. hyperborea* and *V. nivalis* and cited Rastorfer, Webster, and Smith material as *V. hyperborea*.

LICHENS

ALECTORIA NIGRICANS (Ach.) Nyl. *Schofield Ak-86*, det. M. E. Williams
ALECTORIA OCHROLEUCA (Hoffm.) Mass. *B. Murray 6219*
ASAHINEA CHRYSANTHA (Tuck.) W. Culb. & C. Culb. *Williams Ak-652*, det. B. Murray
BUELLIA ALBOATRA (Hoffm.) Branth. & Rostr. *Battrum 325A* (UAC), det. C. D. Bird
BUELLIA PAPILLATA (Somm.) Tuck. *B. Murray 4355*, det. J. W. Thomson
CALOPLACA CINNAMOMEA (Th. Fr.) Oliv. *B. Murray 6245* in part, det. J. W. Thomson
CALOPLACA DISCOLOR (Will.) Fink *B. Murray 6227* in part, det. J. W. Thomson
CALOPLACA STILLICIDIORUM (Vahl) Lynge *B. Murray 6245* in part, det. J. W. Thomson
CANDELARIELLA AURELLA (Hoffm.) Zahlbr. *B. Murray 6228*, det. J. W. Thomson
CANDELARIELLA XANTHOSTIGMA (Pers.) Lett. *B. Murray 6241*, det. J. W. Thomson
CETRARIA CUCULLATA (Bell.) Ach. *B. Murray 4331*
CETRARIA DELISEI (Bory *ex* Schaer.) Th. Fr. *B. Murray 4345*
CETRARIA ISLANDICA (L.) Ach. *B. Murray 4335*
CETRARIA NIVALIS (L.) Ach. *B. Murray 4330*
CETRARIA RICHARDSONII Hook. *B. Murray 4332*
CETRARIA TILESII Ach. *B. Murray 4349*
CLADONIA AMAUROCRAEA (Flörke) Schaer. *Williams Ak-655*, det. J. W. Thomson
CLADONIA LEPIDOTA Nyl. *Richardson s.n.* (ALA 61969), det. J. W. Thomson
CLADONIA POCILLUM (Ach.) O. Rich. *B. Murray 4350*
CLADONIA SQUAMOSA (Scop.) Hoffm. *Schofield Ak-91*, det. M. E. Williams
CLADONIA SUBFURCATA (Nyl.) Arn. *Schofield Ak-90*, det. J. W. Thomson
COLLEMA BACHMANIANUM (Fink) Degel. (= *C. tenax* var. *bachmanianum*) *B. Murray 4328*, det. J. W. Thomson; var. MILLEGRANUM Degel. *B. Murray 4387*, det. J. W. Thomson
COLLEMA TUNAEFORME (Ach.) Ach. *B. Murray 4342*, det. J. W. Thomson
CORNICULARIA ACULEATA (Schreb.) Ach. *B. Murray 4326*
CORNICULARIA DIVERGENS Ach. *B. Murray 6237*
DACTYLINA ARCTICA (Hook.) Nyl. *B. Murray 4333*
DACTYLINA RAMULOSA (Hook.) Tuck. *B. Murray 4329*
EVERNIA PERFRAGILIS Llano *B. Murray 4344*, det. J. W. Thomson
FULGENSIA BRACTEATA (Hoffm.) Räs. *B. Murray 4363*
GYALECTA FOVEOLARIS (Ach.) Schaer. *B. Murray 4364*, det. J. W. Thomson
HYPOGYMNIA PHYSODES (L.) W. Wats. *B. Murray 4400*, det. J. W. Thomson – esorediate
HYPOGYMNIA SUBOBSCURA (Vain.) Poelt *B. Murray 4327*
LECANORA BERINGII Nyl. *Richardson s.n.* (ALA 61974), det. J. W. Thomson
LECANORA EPIBRYON (Ach.) Ach. *B. Murray 4337*
LECANORA VERRUCOSA Ach. *B. Murray 4339*
LECIDEA ASSIMILATA Nyl. *Richardson s.n.* (ALA 61975), det. J. W. Thomson

Lichens (continued)

LECIDEA VERNALIS (L.) Ach. *B. Murray 4361,* det. J. W. Thomson

LEPRARIA MEMBRANACEA (Dicks.) Vain. *B. Murray 6240,* det. J. W. Thomson

LEPTOGIUM TENUISSIMUM (Dicks.) Fr. *B. Murray 4347,* det. J. W. Thomson

LOPADIUM FECUNDUM Th. Fr. *B. Murray 4396,* det. J. W. Thomson

OCHROLECHIA FRIGIDA (Sw.) Lynge *B. Murray 4396* in part; f. THELEPHOROIDES (Ach.) Lynge *B. Murray 4395,* det. J. W. Thomson

OCHROLECHIA UPSALIENSIS (L.) Mass. *B. Murray 4360,* det. J. W. Thomson

PARMELIA OMPHALODES (L.) Ach. *B. Murray 4392*

PARMELIELLA PRAETERMISSA (Nyl.) P. James *Richardson s.n.* (ALA 61971), det. J. W. Thomson

PELTIGERA APHTHOSA (L.) Willd. *B. Murray 4397*

PELTIGERA CANINA (L.) Willd. *B. Murray 4382*

PELTIGERA MALACEA (Ach.) Funck *B. Murray 4325,* det. J. W. Thomson

PELTIGERA POLYDACTYLA (Neck.) Hoffm. *Richardson s.n.* (ALA 61970), det. B. Murray

PELTIGERA RUFESCENS (Weis.) Humb. (= *P. canina* var. *rufescens*) *B. Murray 4374,* det. J. W. Thomson

PELTIGERA SPURIA (Ach.) DC. f. SOREDIATA Schaer. (= *P. canina* var. *rufescens* f. *sorediata*) *B. Murray 4340,* det. J. W. Thomson

PERTUSARIA OCTOMELA (Norm.) Erichs. *B. Murray 4394*

PERTUSARIA PANYRGA (Ach.) Mass. *B. Murray 4358,* det. J. W. Thomson

PERTUSARIA SUBOBDUCENS Nyl. *B. Murray 4338,* det. J. W. Thomson

PHYSCIA DUBIA (Hoffm.) Lett. *B. Murray 6218*

PHYSCONIA MUSCIGENA (Ach.) Poelt *B. Murray 4348*

POLYBLASTIA BRYOPHILA Lönnr. *B. Murray 6227,* det. J. W. Thomson

POLYBLASTIA SENDTNERI Kremph. *B. Murray 4386,* det. J. W. Thomson

RAMALINA ALMQUISTII Vain. *B. Murray 4346*

RHIZOCARPON DISPORUM (Naeg. *ex* Hepp) Müll. Arg. *B. Murray 4351*

RINODINA ROSCIDA (Somm.) Arn. *B. Murray 4341*

RINODINA TURFACEA (Wahlenb.) Körb. *B. Murray 6238,* det. J. W. Thomson

SOLORINA SACCATA (L.) Ach. *B. Murray 4362*

SOLORINA SPONGIOSA (Sm.) Anzi *B. Murray 4356*

SPHAEROPHORUS GLOBOSUS (Huds.) Vain. *Walker s.n.,* 22 August 1974, det. W. A. Weber

STEREOCAULON ALPINUM Laur. *B. Murray 4375,* det. I. M. Lamb

? STEREOCAULON RIVULORUM Magn. *B. Murray 4365,* det. I. M. Lamb – too scanty to determine with certainty

THAMNOLIA SUBULIFORMIS (Ehrh.) W. Culb. *B. Murray 4336*

TONINIA LOBULATA (Somm.) Lynge *B. Murray 6216,* det. J. W. Thomson

VERRUCARIA DEVERGENS Nyl. *B. Murray 4354,* det. J. W. Thomson

XANTHORIA ELEGANS *B. Murray 4353*

Appendix B

Selected Data on Lichens, Mosses, and Vascular Plants on the Prudhoe Bay Tundra

MICHAEL E. WILLIAMS*, EMANUEL D. RUDOLPH,
and EDMUND A. SCHOFIELD**

Institute of Polar Studies and Department of Botany
The Ohio State University
Columbus, Ohio 43210

Vegetation study plots were established at Prudhoe Bay 5-14 July 1972 in eight sites selected for their apparent homogeneity in representing various floristic communities (Fig. 1 and Table 1). Six plots were 10 m on each side, while the remaining two were 5 m on each side. Samples of aboveground plant material, with the exception of loose vascular plant litter, were separated into moss, vascular plant, and lichen components, the latter by species. Ten 48 cm^2 samples were collected in each of the larger plots, and five samples in each of the smaller plots. The values for several abiotic parameters were also determined. Using random cores 7.2 cm in diameter and 10 cm deep, soil moisture, depth of thaw, and humus thickness were measured. Soil pH was obtained using the solution from a 5:1 dilution of air-dried soil in deionized water, which was filtered 18 to 19 hrs later through a No. 120 soil sieve (115 mesh, 125 μm opening). The pH was also determined for runoff water (i.e., the surface water nearest the study site to which the draining water would naturally flow). Conductivity was measured for both runoff water and aqueous extracts of soil. The results of these determinations are presented in Table 1.

No clear correlation exists between standing crop of mosses or vascular plants and soil moisture. Lichens showed a direct relationship with substrate water content, with the exception of plots IV and V. The presence of a large number of tussocks in plot IV, which were considerably drier than the surrounding wet depressions, formed a suitable base for lichen colonization. The bryophyte standing crop was also relatively low here, as compared to other sites with high moisture. The apparent reason for the absence of lichens in plot V, in spite of the relatively low soil moisture that normally favors lichen growth, was the extremely dense moss stand. The close proximity to the Prudhoe Bay coastline (ca. 75 m), however, does not permit the exclusion of direct marine effects, which are no doubt responsible for the barrenness of nearby plot IV. The presence of lichens in high moisture sites with low moss biomass (plot IV), and the absence of lichens in a site with favorably low substrate moisture but a dense moss stand (plot V), lead to the conclusion that, at least in certain sites, competition for space with bryophytes may be a limiting factor for lichen growth. Such competition was also observed in the case of adjacent high-center polygons in

---

[*] Current address: School of Public Health, Harvard University, Cambridge, Massachusetts 03128

[**] Current address: Ohio Department of Natural Resources, Columbus, Ohio 43224

Fig. 1. *Location of the eight study plots at Prudhoe Bay.*

Table 1

Prudhoe Bay Standing Crop data and plot description

		Ave. Standing Crop (g m^{-2})			% Total Standing Crop									
Plot***	No. of Lichen Species	Lichen	Mosses	Vascular Plants	Lichens	Mosses	Vascular Plants	% Soil Moisture	Depth of Thaw* (cm)	Humus Layer (cm)	Soil Conductivity** (μmho cm^{-1})	Soil pH	Runoff pH	Runoff Conductivity (μmho cm^{-1})
I	0	0.0	926.2	212.9	0.0	81.3	18.7	104	D=19.9 T=33.3	8.0	779	7.4	7.5	374
II	4	3.9	314.0	254.1	0.7	54.9	44.4	80	D=22.3 T=31.5	5.2	362	7.6	7.5	409
III	10	55.3	95.3	204.9	15.6	26.8	57.6	19	D=40.8 T=51.6	1.7	405	7.6	7.7	174
IV	11	44.1	281.7	247.1	7.7	49.2	43.1	108	D=11.6 T=21.4	4.6	390	6.6	7.8	143
V	0	0.0	1572.8	171.7	0.0	90.2	9.8	37	21.9	8.5	444	7.3	7.8	373
VI	1	(crustose)	0.0	14.9				24	43.5	1.1	2140	7.6	7.8	373
VII	14	83.1	27.5	470.0	14.3	4.7	81.0	26	D=33.1 T=46.8	2.1	270	7.1	7.1	222
VIII	8	54.6	461.3	251.8	7.1	60.1	32.8	52	D=15.6 T=35.5	4.3	421	7.6	7.1	222

* As of 7/13/72. D = depressions, T = tussocks

** 5:1 dilution (deionized water), 18-19 hrs. later filtered through No. 120 soil sieve

*** Plot I — wet meadow in old lake bottom; (T10N, R14E, Section 4)

Plot II — edge of ridge around old lake bed; moist meadow; (T10N, R14E, Section 4)

Plot III — top of "Fox Ridge" W of pingo; very dry, sandy soil; elev. 15 m (T11N, R14E, Section 33)

Plot IV — 100 m N of drill pad F; wet meadow; low-center polygons and many tussocks present (T11N, R13E, Section 2)

Plot V — near Prudhoe Bay docks, 75 m from coast; moist meadow, dense moss cover (T11N, R15E, Section 16)

Plot VI — (5 x 5 m) near Prudhoe Bay docks, 39 m E of plot V; very dry, barren high-center polygons; high salinity; crustose lichen cover (not weighed) more than 50% (T11N, R15E, Section 16)

Plot VII — S flank of Michele pingo, heavy vascular cover; very dry, sandy soil; elev. = 14 m (T11N, R13E, Section 5)

Plot VIII — (5 x 5 m) on stream terrace 0.7 km SW of Michele pingo; well drained, grassy area (T11N, R13E, Section 5)

U. S. Tundra Biome site 4 at Barrow, which had nearly identical moisture contents but highly divergent lichen standing crops that were inversely related to moss biomass.

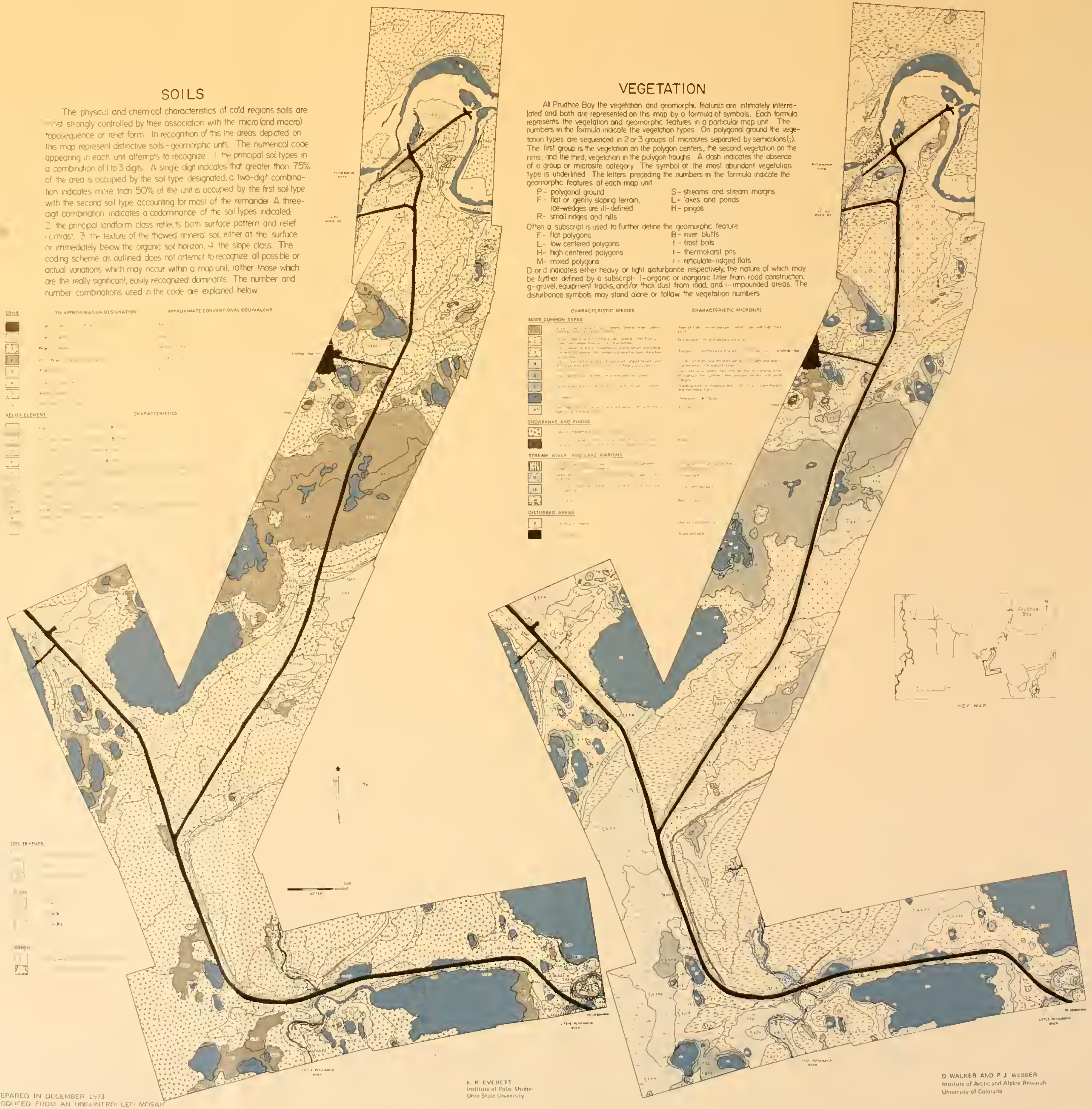
Several other abiotic parameters showed a correlation with lichen biomass, although these are interpreted as being secondary reflections of soil moisture. For example, somewhat higher lichen standing crops were observed on sites with a greater depth of thaw and on sites with a thinner humus layer. However, this was probably a ramification of the fact that dry sites generally had greater depth to permafrost and also less vascular plant and bryophyte cover, the latter of which would be responsible for thinner humus layers.

The pH and conductivity of soil and runoff water did not appear to have an effect on the differential distribution of plants, as there was little variation among the samples. The only exception to this was the high salinity of plot VI. On that site a sterile white crustose lichen covered more than 50% of the surface area, while mosses were completely absent, and vascular plants were present only as isolated shoots. The sparsity of plant life in plot VI is not surprising in view of the well-known fact that most terrestrial plants are intolerant of high salt concentrations.

Acknowledgments

These studies were supported by a National Science Foundation grant to Ohio State University, and logistics at Prudhoe were provided through the Prudhoe Bay Environmental Subcommittee support at the Tundra Biome Center, University of Alaska.

SOILS and VEGETATION, Tundra Biome Study Area, Prudhoe Bay, Alaska



SOILS

The physical and chemical characteristics of cold regions soils are most strongly controlled by their association with the micro (and macro) toposequence or relief form In recognition of this the areas depicted on this map represent distinctive soils–geomorphic units The numerical code appearing in each unit attempts to recognize 1 the principal soil types in a combination of 1 to 3 digits A single digit indicates that greater than 75% of the area is occupied by the soil type designated; a two-digit combination indicates more tndn 50% of the unit is occupied by the first soil type with the second soil type accounting for most of the remainder A three-digit combination indicates a codominance of the soil types indicated; 2 the principal landform class reflects both surface pattern and relief contrast, 3 the texture of the thawed mineral soil, either at the surface or immediately below the organic soil horizon, 4 the slope class. The coding scheme as outlined does not attempt to recognize all possible or actual variations which may occur within a map unit; rather those which are the really significant, easily recognized dominants The number and number combinations used in the code are explained below

VEGETATION

At Prudhoe Bay the vegetation and geomorphic features are intimately interrelated and both are represented on this map by a formula of symbols. Each formula represents the vegetation and geomorphic features in a particular map unit The numbers in the formula indicate the vegetation types On polygonal ground the vegetation types are sequenced in 2 or 3 groups of microsites separated by semicolons(;). The first group is the vegetation on the polygon centers, the second, vegetation on the rims; and the third, vegetation in the polygon troughs A dash indicates the absence of a group or microsite category The symbol of the most abundant vegetation type is underlined The letters preceding the numbers in the formula indicate the geomorphic features of each map unit

P – polygonal ground	S – streams and stream margins
F – flat or gently sloping terrain, ice-wedges are ill-defined	L – lakes and ponds
R – small ridges and hills	H – pingos

Often a subscript is used to further define the geomorphic feature

F – flat polygons	B – river bluffs
L – low centered polygons	f – frost boils
H – high centered polygons	t – thermokarst pits
M – mixed polygons	r – reticulate-ridged flats

D or d indicates either heavy or light disturbance respectively, the nature of which may be further defined by a subscript· l – organic or inorganic litter from road construction, g – gravel, equipment tracks, and/or thick dust from road, and i – impounded areas. The disturbance symbols may stand alone or follow the vegetation numbers

PREPARED IN DECEMBER 1973
PRODUCED FROM AN UNCONTROLLED MOSAIC

K. R. EVERETT
Institute of Polar Studies
Ohio State University

D WALKER AND P J WEBBER
Institute of Arctic and Alpine Research
University of Colorado