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TITLE OF THESIS..Autecology of *Kobresia bellardii*:
"Why winter snow accumulation
patterns affect local distribution

UNIVERSITY....University of Alberta.............

DEGREE FOR WHICH THESIS WAS PRESENTED.....Ph.D........

YEAR THIS DEGREE GRANTED.......1974..............

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THE UNIVERSITY OF ALBERTA

AUTECOLOGY OF *KOBRESIA BELLARDII*: WHY WINTER SNOW ACCUMULATION PATTERNS AFFECT LOCAL DISTRIBUTION

by

KATHERINE L. BELL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING, 1974

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Autecology of Kobresia bellardii: why winter snow accumulation patterns affect local distribution, submitted by Katherine L. Bell in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Lawrence C. Bliss
Supervisor

External examiner

Date: 22 October 1973

ABSTRACT

In the Colorado Front Range Kobresia bellardii (All.) K. Koch is restricted to alpine meadows which are neither extremely wind-exposed nor buried under snow throughout the winter.

The kobresia meadow environment is distinguished by ephemeral microdrifts in winter. Winds within the tussock are strong year-round, averaging 0.4 m/sec in summer, 1.2 m/sec in winter. Summer soil surface temperatures vary rapidly, especially at mid-day when they may briefly exceed 35°C. Winter surface temperatures usually closely resemble air temperatures above. Summer vapor pressure deficit profiles are generally uniform with low mean deficits of about 2.0 mb. Soil water potentials (Ψ_{soil}) at 10 cm depth average -8 bars in summer. Winter Ψ_{soil} is frequently below -30 bars, but rises above -20 bars in 33% of readings. During spring melting, Ψ_{soil} rises to near 0 bars for about 3 wks. Soil at 2 cm depth is usually drier than -20 bars except in spring.

Among kobresia's adaptations to this environment is the ability to use an extended season for development, approximately 1 April to 20 October. Short green leaves in winter allow aboveground storage of carbohydrates so that translocation is not necessary for elongation. Water stress is tolerated by efficient maintenance of leaf water potential (Ψ_{leaf}) even when passive uptake from soil is impossible and by water uptake from soils at 0° and possibly much colder.

In contrast to the kobresia meadow, a fellfield had much higher winds and drier soils in all seasons. Temperature profiles were

similar in the two microsites. Snow microdrifts were more shallow and less durable. Moderate (70 cm) and deep (140 cm) snow accumulation areas had lower summer winds and daily heating at the surface was 3 to 6° higher than in the kobresia meadow. Summer Ψ_{soil} at the deep snow accumulation site was higher than the kobresia meadow, while gopher disturbed soil in the moderate snow accumulation area was usually drier. In both snow accumulation sites, soil remained deeply frozen and Ψ_{soil} below -20 bars through the winter until June. Summer vapor pressure deficits in all sites resembled those of the kobresia meadow.

Kobresia does not survive in the fellfield primarily because of mechanical damage from wind-blown sand and prolonged low Ψ_{soil} leading to wilting. Under deep and moderate snow, fall die-back is incomplete before snow accumulation starts, and freezing destroys carbohydrate reserves and meristems of unhardened shoots. Spring elongation does not begin until snowmelt is complete. Shallow snow cover, with early saturation in April, permits elongation and apparent loss of hardiness before the final hard freezes of spring. Under temporarily deep snow, leaves elongate, but die back with loss of carbohydrate reserves if snow is removed before spring thawing. Interspecific competition is unimportant in kobresia's absence from snow accumulation areas. All habitat alterations result in decreased production and carbohydrate reserves.

Grazing by elk, although heavy, had no apparent adverse effect at these study sites.

Seed and flower production are reducted up to 99% by habitat alteration. It is questionable whether kobresia presently reproduces

sexually in the Front Range. Seed of undisturbed plants did not germinate in field and laboratory tests. Young tussocks are absent in most places.

Kobresia is well adapted to a particular microenvironment, but intolerant of changes. Its apparent inability to reproduce by seed implies that its destruction may be irreversible.

ACKNOWLEDGMENTS

I am grateful to Dr. L. C. Bliss for his guidance and patience in supervising this research.

Others for whose help I am indebted include: Dr. J. M. Mayo for advice on many aspects of this problem; Dr. P. R. Gorham and Mr. J. Svoboda who provided the carbohydrate analysis techniques; Drs. R. C. Stutz and D. L. Pattie for helpful conversations and criticisms; and members of the examining committee for their comments.

Kveta Svoboda carried out the laboratory portion of the carbohydrate analyses.

Year-round field studies became possible through the help of many people. Rocky Mountain National Park provided permission for research and the use of Park facilities. I appreciate the generous support and encouragement given by many Park personnel, including Mr. Tom Thomas and Mr. Dwight Hamilton, Chief Naturalists; Mr. Jim Randall, Chief Ranger, and Mr. Dave Stevens, Park Biologist. Martha Bell's work as a summer field assistant and Emily Dixon's winter assistence and persistence were invaluable. Others who helped with field work were Jean Weaver, Bernice Weldon, and Bill Gregg. Skip and Joyce Greene, Robert Haines, and Drs. Julia Martin and Sam Luce gave useful advice on working under winter alpine conditions. I would like to express my gratitude to these individuals.

The Institue of Arctic and Alpine Research of the University of Colorado furnished logistic support during preliminary studies.

Financial support for this study was provided by the National Science Foundation (Grant GB 7899 to Dr. Bliss).

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I. INTRODUCTION

Meadows dominated by Kobresia bellardii comprise an important portion of alpine vegetation in the Colorado Front Range. Kobresia dominates the plant cover in many sites which are neither extremely wind-exposed such as fellfields nor buried under snow throughout the winter. The well-delineated microtopographic preferences of this species raise questions concerning its adaptations to so specialized an environment, or, conversely, reasons for its intolerance of other microhabitats. This study was undertaken to identify those aspects of the environment which prevent occurrence of kobresia under snow accumulations and in fellfields and to describe some of the adaptations that allow this species to be successful in its normal habitat.

Kobresia bellardii inhabits relatively snow-free sites throughout its wide geographical distribution. The species is found in eastern Siberia, Japanese and Chinese mountains, mountains of southeastern Europe and the Alps the Urals, much of the North American arctic and western mountain ranges (Hulten, 1968). It is associated with exposed tundra slopes with deep turf in many areas including the Alps (Guyot, 1920; Braun-Blanquet, 1954), Norway (Nordenhagen 1936), Yugoslavia (Grebenschchikov, 1960), the Urals (Igoshina, 1966), the eastern coast of Siberia (Tikhomirov and Gavrilyuk, 1966), the Canadian Rockies (Hrapko, 1970; Trottier, 1972), the southern Rocky Mountains (Cooper, 1908; Cox, 1933; Kiener, 1967; Osburn, 1958; Willard, 1963; Eddleman, 1967; Marr, 1967a), Iceland (Falk, 1940), and Greenland (Gelting, 1934; Bocher, 1954). A few exceptions to this distribution are described: in the Verkhoyansk Mountains of Siberia, the species is associated with river banks and terraces (Kil'Dyushevskii, 1966); in Iceland, with moderate snow accumulations (Steindorsson, pers. comm.); and it occurs under deep snow in the White Mountains of California (Major and Bamberg, 1965) and the Wind River Range of Wyoming (Major, pers. comm.). A few authors describe *Kobresia bellardii* as preferring calcareous soil (Selander, 1950; Böcher, 1951; Gaerevoll, 1954). Others, however, note no such preference (Osburn, 1958; Willard, 1963; Eddleman, 1967; Trottier, 1972).

The role of kobresia in the alpine vegetation of the Colorado Front Range has been especially well-defined. In 1933, Cox described the species as dominant in "climax" meadows. Subsequent workers have recognised these meadows to be exceptionally stable and many of them quite ancient (Osburn, 1958; Willard, 1963). Osburn (1958) described a successional sequence after gopher disturbance. Cushion plants are replaced by forbs in a *Geum turbinatum* dominated turf which eventually gives way to dense kobresia tussocks. Kiener (1967), in a less specialized case, described meadows of increasing age as becoming more strongly dominated by kobresia at the expense of species diversity. He suggested that this was the outcome of competition for water in which its dense but shallow root system gave it an advantage over other species. Willard (1963) noted that young kobresia plants were rarely found and that some meadows may have taken as long as 1000 years to develop to their present state. Even if kobresia could not properly be considered a climax species, these meadows are extremely stable and long-lived.

The presence of kobresia often has a profound effect on meadow structure and microclimate. Kobresia forms up to 55% of the cover (Willard, 1963). Tussocks are dense and closely spaced. The character of the environment between and around the tussocks is controlled by their activities and shape. Kiener (1967) hypothesizes that kobresia is primarily responsible for the soil moisture regime in its meadows since it is efficient in removing soil water. The tussocks' influence on the microenvironment is most clearly visible in winter when microdrifts are usually present in the lee of each clump (Osburn, 1958).

From these earlier studies it appears that Kobresia bellardii is well-adapted to a particular environment and may be incapable of growing outside of it. This investigation attempted to determine some of the adaptive features of the species and the limits to its tolerances that prevent its occurrence outside its normal habitat. Environment may limit development of a species in any part of its life cycle. The implied importance of snow cover and a preliminary finding that kobresia has green leaves in winter underlined the desirability of winter studies. Thus a year-round field study examining various stages of kobresia's life cycle was undertaken. Microenvironment was examined in four tundra microhabitats including a kobresia meadow. Transplant experiments and use of snowfences permitted comparisons of kobresia behavior from snowfree to snow accumulation habitats.

II. STUDY SITES

Three areas on Trail Ridge (Fig. 1), Rocky Mountain National Park, Colorado, were selected for study areas.

In the study area near Tombstone Ridge four sites were chosen representing a variety of microhabitats: a fellfield, a kobresia meadow with shallow ephemeral winter snow cover, a moderate snow and a deep snow accumulation site. Despite considerable differences in wind exposure and snow cover, the sites were separated by a maximum distance of 0.5 km and had similar elevation and slope angle (Table 1). These representative microhabitats were used for transplant studies. The fellfield transplant site was located in a broad flat area on the ridge top where a slight dip in the ridgeline tended to funnel winds. The kobresia meadow at the transplant control site was about 50 by 15 m, tapering in width at its ends with well-defined edges. A meteorological station, transplants, and control plants were located near its center. The transplant site with moderate winter snow accumulation was placed near the inner edge of a solifluction terrace where the riser of the terrace above provided a lee for snow accumulation. This area was marked with old soil disturbances caused by pocket gophers, but no activity was observed during the period of study. The fourth transplant site was in a deep snow accumulation area formed in the lee of ridgetop tors.

The Sundance study area was used as a second control meadow and as the location for snowfence studies. Here the kobresia meadow occupied the lower exposed edge of a broad snow accumulation basin on the southeast slopes of Sundance Mountain at about 3500 m. Slope

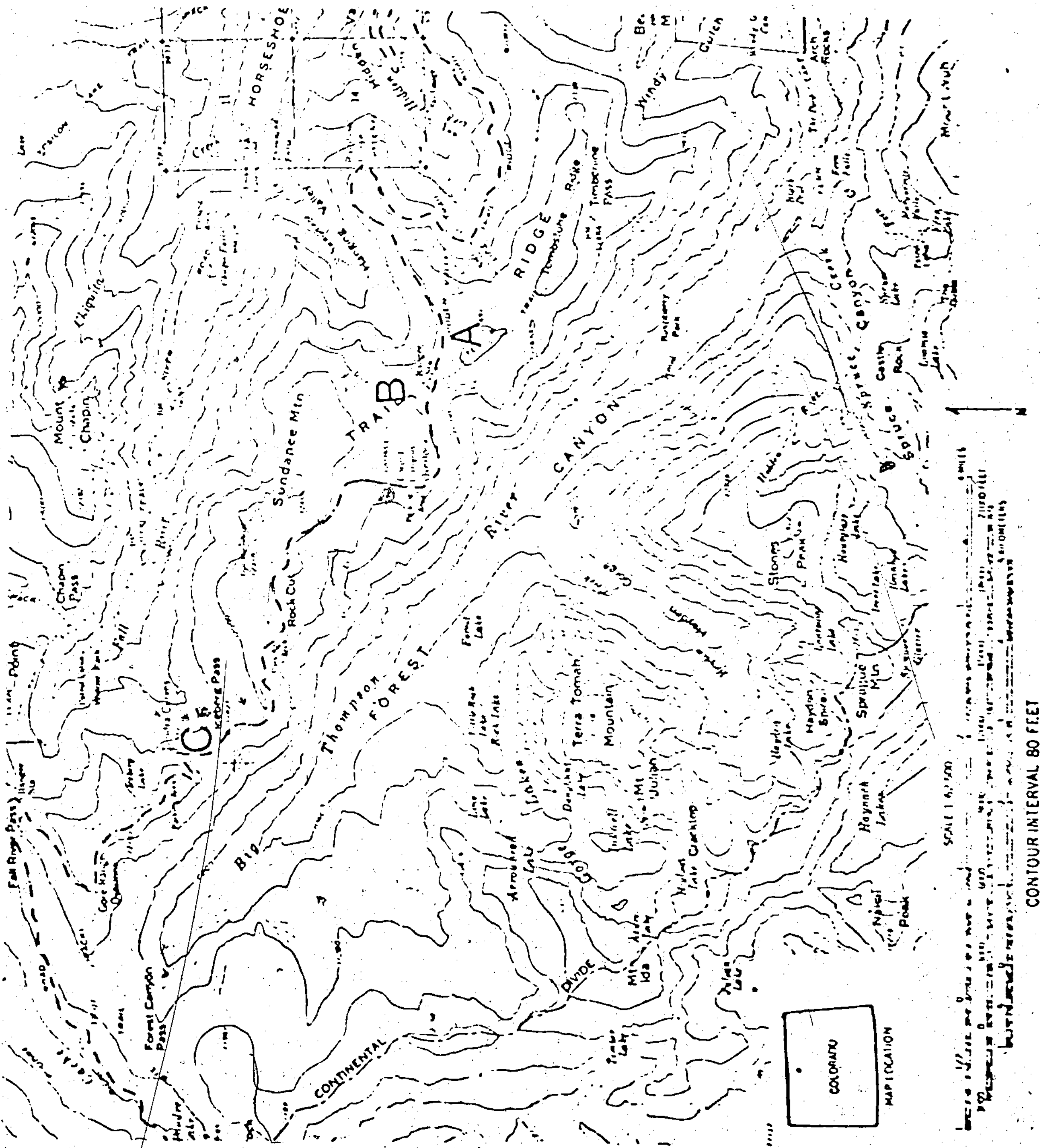

Fig. 1. Location of study sites on Trail Ridge, Rocky Mountain National Park. A. Transplant study areas. B. Sundance Mountain site. C. Tundra Curves site.

Table 1. Some physiographic characteristics of transplant sites in Tombstone Ridge study area.

Site characteristic	Site			
	Fellfield	Kobresia control	Moderate snow	Deep snow
Elevation (m)	3555	3545	3545	3560
Slope angle	2-6°	0-3°	3-5°	0-5°
Directions of protection from wind	NE and S	W	W	W and NW
Angle to top of hill to the west	0° within 3 km	8°	23°	42°
Distance from control site (m)	300	0	80	200

angle was 5-8°.

The Tundra Curves site was located at the lowest switchback on this section of Trail Ridge Road. Here a large drift forms in the lee of a road embankment. The drift cuts across an extensive stand of kobresia. Elevation of the site is 3600 m, and it slopes to the NNE at 5-12°.

While detailed soil descriptions were not made, soils in all three kobresia meadows appeared to resemble closely those in kobresia stands described by Osburn (1958) and Eddleman (1967). Parent material in all cases was metamorphic rock, primarily gneisses and schists on Trail Ridge. An _L_ horizon varied from 0 to 3 cm thick. _Ah_ horizons were as much as 20 cm thick. Depth of the organic horizons was variable; occasionally it was completely absent between widely spaced tussocks. The _A_ horizons were somewhat acid (pH 5.5-6.5). _B_ horizons had a high fraction of coarse fragments.

Plant Communities of the Study Sites

The plant communities of each were examined using the line intercept method. Stratified random sampling was made with transects placed entirely within the community of the site. Five lines of 5 m length were run at each site. At the Tundra Curves site lines were placed parallel to and one meter outside the snowdrift area. Plant cover was determined by species; and litter, rock, and mineral soil cover noted.

All three control meadows had similar kobresia cover and a relatively high cover of _Carex drummondiana_[1], _Geum turbinatum_, and

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[1] Nomenclature follows that of Harrington (1964) except for _Kobresia bellardii_ which follows that of Hitchcock _et al_. (1955-1969).

Table 2. Percent cover by species in three *Kobresia* meadows and three other microhabitats used as study sites.

Species	Percent Cover					
	Kobresia meadows			Other habitats		
	Sundance Mountain	Tundra Curves	Transplant control	Deep snow	Moderate snow	Fellfield
Selaginella scopulorum	2.6	0.0	0.8	0.0	0.7	P
Festuca ovina var. *brachyphyllum*	0.4	0.8	0.4	2.0	2.8	0.0
Poa rupicola	0.0	0.1	1.2	0.2	0.0	0.0
Calamagrostis purpurascens	0.0	0.2	0.3	2.2	0.0	0.0
Kobresia bellardii	53.6	54.8	50.9	0.0	0.0	0.0
Carex obtusata	0.0	0.0	0.0	0.0	0.4	0.0
C. elynoides	0.0	0.0	0.0	0.0	2.2	0.0
C. drummondiana	9.9	7.5	11.2	0.0	0.0	0.0
C. phaeocephala	0.0	0.0	0.0	3.9	0.0	0.0
C. scopulorum	0.0	0.0	0.0	15.3	0.0	0.0
Luzula spicata	0.0	0.0	0.2	0.4	0.5	P
Zygadenus elegans	0.0	0.0	0.1	0.0	0.0	0.0
Lloydia serotina	0.0	0.2	0.0	0.0	0.2	0.0
Salix planifolia	2.7	0.0	0.0	0.0	0.0	0.0
Polygonum viviparum	0.8	0.5	0.6	0.0	0.1	0.0
P. bistortoides	0.0	1.2	0.0	1.1	0.2	0.0
Silene acaulis	1.1	0.3	0.2	0.0	0.1	4.1
Paronychia pulvinata	0.0	0.0	0.0	0.0	0.0	11.2
Cerastium beeringianum	0.0	0.0	0.0	0.2	0.0	0.0
Arenaria obtusiloba	1.3	0.4	1.7	0.8	8.8	6.0
A. fendleri	0.2	0.0	0.1	0.0	0.3	0.0
Anemone globosa	0.0	0.0	0.0	0.0	4.0	0.0
Ranunculus adoneus	0.3	0.6	0.0	8.2	0.6	0.0

Table 2, cont.

Species	Sundance Mountain	Tundra Curves	Transplant control	Deep snow	Moderate snow	Fellfield
Draba aurea	0.2	0.1	0.2	0.0	0.0	0.0
Sedum stenopetalum	0.2	0.0	0.2	0.0	0.2	0.0
Saxifraga rhomboidea	0.2	0.0	0.0	0.0	0.5	0.0
Heuchera parviflora	0.0	0.0	0.0	0.2	0.0	0.0
Potentilla diversifolia	0.2	0.0	P	1.0	1.1	0.0
Geum turbinatum	5.2	15.9	1.6	36.0	7.6	1.0
Sibbaldia procumbens	0.0	0.0	0.0	21.0	0.8	0.0
Trifolium dasyphyllum	5.2	4.8	2.8	0.0	0.1	4.1
T. nanum	0.0	0.0	0.0	0.0	0.0	P
Oreoxis alpina	0.8	0.9	1.8	0.0	0.0	0.0
Primula angustifolia	0.0	0.0	0.0	0.0	0.0	P
Androsace septentrionalis	0.1	0.0	0.0	0.0	0.2	0.0
Gentiana romanzovii	0.4	0.0	0.0	0.0	0.0	0.0
Phlox caespitosa	1.4	0.0	0.5	0.0	0.2	0.0
Eritrichium elongatum	0.4	0.0	0.6	0.0	0.0	0.0
Mertensia viridis	0.0	0.6	0.0	0.0	0.0	0.0
Castelleja occidentalis	0.0	0.0	0.0	0.4	0.0	0.0
Solidago nanum	0.0	0.0	0.0	0.0	1.4	0.0
Happlopappus pygmaeus	0.0	0.0	0.0	0.0	0.0	P
Erigeron simplex	0.2	0.0	1.1	5.7	0.0	0.0
Artemisia scopulorum	[illegible]	3.9	0.0	9.9	3.2	0.0
A. norvegica	[illegible]	0.2	0.0	6.8	19.6	0.0
Hymenoxis acaulis	0.0	0.0	0.2	0.0	0.0	0.0
Total vascular plant cover	88.2	93.0	76.7	115.3	55.8	26.4
moss	0.0	[illegible]	0.0	14.8	6.6	P
lichen	1.7	0.5	2.7	2.0	1.4	13.2

Table 2, cont.

Species	Sundance Mountain	Tundra Curves	Transplant control	Deep snow	Moderate snow	Fellfield
rock	0.0	0.0	7.4	3.4	0.6	14.6
gravel and soil	3.6	2.5	6.0	3.5	0.6	41.6
litter (except *Kobresia*)	3.1	1.7	2.6	0.2	3.4	0.0
dead *Kobresia*	3.5	2.3	2.4	0.0	0.0	0.0

Γ indicates a cover less than 0.1%

Trifolium dasyphyllum (Table 2). Salix planifolia was present only at the Sundance meadow. Kobresia meadows described by Willard (1963), Eddleman (1967), Kiener (1967), and Marr (1967a) vary considerably in their associated species; those described here most closely resemble meadows described by Willard (1963). Gentiana prostrata, which Kiener (1967) suggests indicated the optimal stage of development of the kobresia association, is present in all three meadows; but only in very small numbers.

The fellfield community is dominated by cushion plants, including Paryonychia pulvinata, Silene acaulis, and Arenaria obtusiloba. Trifolium dasyphyllum, which Marr (1967a) considered restricted to areas of moderate snow accumulation, is relatively important, despite the obvious exposure of the site. Much of the area is rock and mineral soil (56%).

The moderate snow accumulation area is dominated by Artemesia norvegica, Geum turbinatum and Arenaria obtusiloba. Soil disturbance by gophers has probably contributed to the rather unusual group of plants. The community is quite dissimilar to Osburn's (1958) "gopher gravel mulch". The closet likeness to previously described stands is with gopher gardens (Willard, 1963), but the species present in the moderate snow accumulation site are more commonly found in areas of deeper snow accumulation than in gopher disturbed locations.

Cover at the deep snow accumulation site is very high; in places the community has several layers. Geum turbinatum and Sibbaldia procumbens were dominant. Geum is fairly ubiquitous in the slpine zone, but Sibbaldia is restricted to snow accumulation areas, where it is often dominant (Willard, 1963; Eddleman, 1967; Marr, 1967a).

III. CLIMATE AND MICROCLIMATES OF A KOBRESIA MEADOW

Introduction

A considerable body of data has been amassed describing the Front Range alpine climate. Barry (1973) compared the alpine zone with lower elevations. He found the alpine area on Niwot Ridge, 65 km south of Trail Ridge, to be windier and colder than lower elevations; precipitation was about 25% higher than in a subalpine forest; but solar radiation was comparable over the whole eastern slope. Marr (1967b), Marr et al. (1967a and b), and Barry (1973) have quantified the climate at 3740 m on Niwot Ridge between 1952 and 1970. The kind of climate they describe appears representative of the Front Range alpine zone since studies of shorter duration by Judson (1965) and Marr and Willard (1970) found similar climates about 65 km north and south of Niwot Ridge at Berthoud Pass and Trail Ridge. The climate of a kobresia meadow on Trail Ridge used in this study was examined so that this site could be compared with Niwot Ridge and Berthoud Pass.

In other alpine areas, profiles of environmental character at the height of plants have indicated that a different climate prevails near the ground from that a meter or two above it (e.g. Bliss, 1966; Courtin, 1968). Information obtained by Salisbury et al. (1968) shows that a similar phenomenon could be expected in the Front Range. Previously climates surrounding alpine plants have been described in summer only. Thus a second part of the study dealt with environmental profiles through the year.

Methods

The climate and microclimate of a kobresia meadow were examined using a combination of recording instruments and frequent spot readings. A station was maintained consisting of a standard meteorological shelter housing a Belfort 31-day recording hygrothermograph at 1.2 m, a standard 3-cup anemometer at 2 m, a Belfort pyrheliometer, an unshielded Taylor maximum-minimum thermometer at 50 cm, and in summer months an unshielded Tru-chek rain gauge at 50 cm. [illegible]ause of problems with snow accumulation some modification of the shelter was necessary. Muslin (180 threads/inch) was placed over the slats on the north and west sides and sealed around the edges. The vents between slats in the floor of the shelter were sealed with cold-resistant tape. These changes did not appear to cause damping or a noticeable lag in temperature or humidity recordings.

Summer precipitation was measured daily. Snow accumulation in winter proved to be variable over short periods and accurate estimates of snowfall were impossible. Depth of snow surrounding kobresia tussocks was measured at intervals ranging from 2 hr to several days. Measurements were made at 5 points on each of the windward and leeward sides of tussocks. Snow density was measured using a small can with 3 cm diameter and 33 ml volume. Samples were taken in triplicated for weighing indoors. Use of the small can permitted density measurements in very small drifts.

Solar radiation was recorded with a Belfort pyrheliometer placed on the ground. No attempt was made to keep it above the snow level, but the sensor was never buried more than one day. The dome had to be cleared of frost daily in winter.

Profiles of wind, temperature, and summer vapor pressure deficit were run with 5 replicates, repeating the sequence from lowest to uppermost point. Wind profiles were read in 60 sec for each sequence; temperature, 90 sec; and wet and dry bulb temperatures at 2 to 3 min intervals.

Windspeeds were measured at 2 cm (inside a kobresia tussock), 5 cm (at the top of the tussock), 20 cm and 2 m (the level of the 3-cup anemometer) with a Hastings-Raydist thermopile anemometer with a directional probe. Only rarely were winds so light or variable that determination of direction became difficult. When direction was uncertain or winds exceeded 30 m/sec, length of time between profile readings was increased to 2 min. Anemometer data were corrected from instrument readings calibrated to sea level to that for air pressure of 495 mm Hg (3500 m altitude) using the following equation supplied by Hastings-Raydist (pers. comm.):

$$\text{Corrected velocity} = \text{Measured velocity}\ \frac{P_o}{P_x} \qquad \text{(Eq. 1)}$$

where P_x = actual atmospheric pressure at altitude, and P_o = 1 atm.

Temperature profiles were measured with a 20 mil copper-constantan thermocouple and a Honeywell portable potentiometer with an electronic reference junction. In summer, readings were taken at -1 cm, soil surface, in the plant tussock at 2 cm, 5, 20, and 120 cm above the surface. Winter profiles omitted the reading below the soil surface and added readings of 1 cm below and at the snow surface when appropriate. The thermocouple was hand held about 10 cm from the junction and shielded from sun and wind by hand. Paired tests with a 3 mil and a 20 mil thermocouple gave equivalent readings. Since the thicker wire proved more durable in winter conditions, it was used.

Wet and dry bulb temperatures were measured at 2, 20 and 120 cm with and electric psychrometer (Atkins). Vapor pressure deficit was calculated directly from wet and dry bulb temperatures (T_w and T_a). Since

$$VPD = e^o - e \qquad \text{(Eq. 2)}$$

and (after Slatyer, 1967)

$$e = e^o - \frac{P\ c_p}{0.622\ l}\ (T_a - T_w) \qquad \text{(Eq. 3)}$$

where e = actual vapor pressure, e^o = saturation vapor pressure of the wet bulb temperature; P = pressure; c_p = specific heat of air; and l = latent heat of evaporation, then

$$VPD = \frac{P\ c_p}{0.622\ l}\ (T_a - T_w). \qquad \text{(Eq. 4)}$$

At 3500 m, P = about 495 mm Hg. Slatyer (1967) gives c_p = 0.242 cal g $^{-1}$ deg $^{-1}$, and l = 590 cal gm^{-1}. Thus with altitude correction

$$mb\ VPD = 0.433\ (T_a - T_w). \qquad \text{(Eq. 5)}$$

Soil moisture at each site was measured with porous cup thermocouple psychrometers (Wescor) and a microvoltmeter (Keithley-Wescor). Soil psychrometers were given a one-point calibration test and placed at 2 and 10 cm depths. In summer, 1970, gravimetric soil moisture samples with 2 replicates wer taken from 7 to 10 cm depth; stones over about 2 cm at their greatest dimension were discarded; and drying was done for 48 hr at 95°.

Some additional practices that aided in winter instrument use are discussed in Appendix I and other difficulties in carrying out winter studies in Appendix I.

Results and Discussion

A. Precipitation and Snow Cover

Summer precipitation is received from storms which may be divided into two classes: convectional thunderstorms and frontal storms. Convectional thunderstorms tend to occur regularly in early afternoon. Precipitation from these is usually light and localized, often in the form of hail or graupel. Widespread storms associated with large scale frontal systems account for the bulk of precipitation received in summer. An extended dry period did occur over the entire month of June, 1971, but this was not observed at any other time. Maximum precipitation from convectional storms was 0.8 and averaged 0.06 cm; from frontal storms 2.3 and 0.6 cm respectively. This precipitation pattern is similar to that described by Marr (1967a). Periods of stormy weather described by Salisbury et al. (1968) in late May, early June and late July did not occur in 1971 or 1972; but large September storms occurred in both years.

Total precipitation in July and August was 10.0 cm in 1970, and 7.8 in 1971. This is less than the 12-year average of 14.6 cm at 3740 m on Niwot Ridge, but greater than the minimum of 6.1 during that period (Marr et al., 1968b). Barry (1973) points out the necessity for gauge shieling in windy alpine sites. Unshielded gauges on Trail Ridge may have reduced the amount measured there.

Seasonal change in precipitation from snow to rain or rain to snow is not abrupt. Although most precipitation in May, 1972, was in the form of snow, 1.3 cm of rain fell during a thunderstorm on 3 May. Major snowstorms occurred in June, 1969. September snow in 1970 was

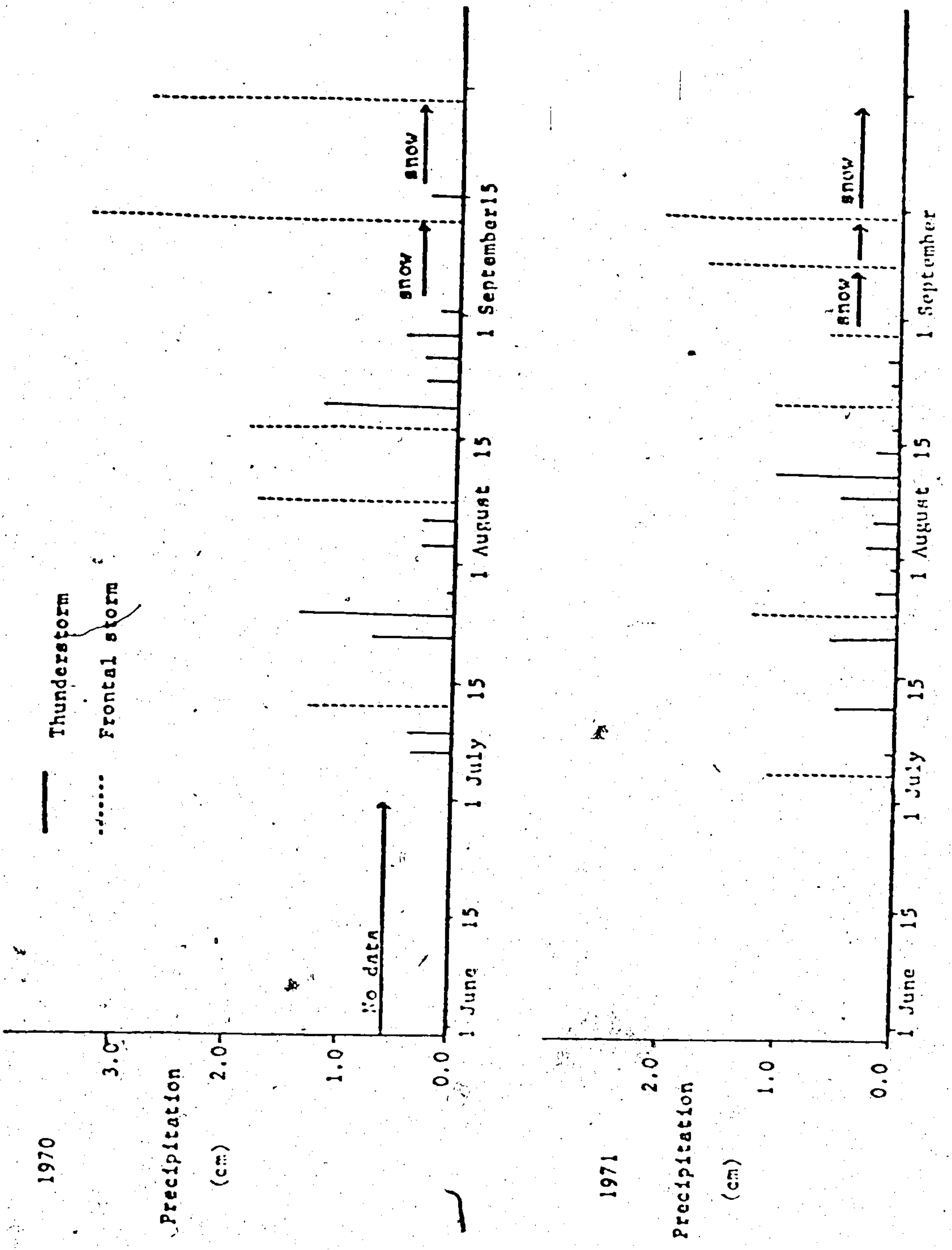


Fig. 2. Three day precipitation totals for periods ending on day indicated. The type of storm yielding most of the precipitation during each period is indicated.

melted by rain.

Measurement of winter precipitation is extremely difficult since snow is constantly being redistributed by wind. The amount of snow actually falling probably has little biological significance since it is so rapidly drifted. Accumulation of snow, however, is of considerable importance since it alters the environment beneath it.

Snowfalls in September were wet and melted in 1 to 6 days without much drifting except into very sheltered areas.

In mid-winter, low temperatures create dry snow conditions which combine with strong winds to produce a complex pattern of snow accumulation. A typical sequence involves deposition of deep snow (up to 50 cm) in a storm from the east followed by extensive drifting by strong wind from the west as the easterly storm subsides. In kobresia meadows, winter wind near the ground is usually not strong enough to remove all the snow for a period of several days. A system of microdrifts forms in the lee of kobresia tussocks. Snowfall associated with storms from the west assumes microdrift configuration during deposition. Microdrifts had a hard crust of 1 to 2 cm thickness underlain by unconsolidated crystals (density 0.15 to 0.22 g cm^{-3} in drifts examined in January through March.

In April and May higher temperatures and lighter winds produced less drifting. Snow formed microdrifts less frequently in spring than in winter (Fig. 3).

B. Solar Radiation

Mean daily radiation totals varied between a low of 252 lys day^{-1} in January to a high of 704 lys day^{-1} in June (Table 3). Summer

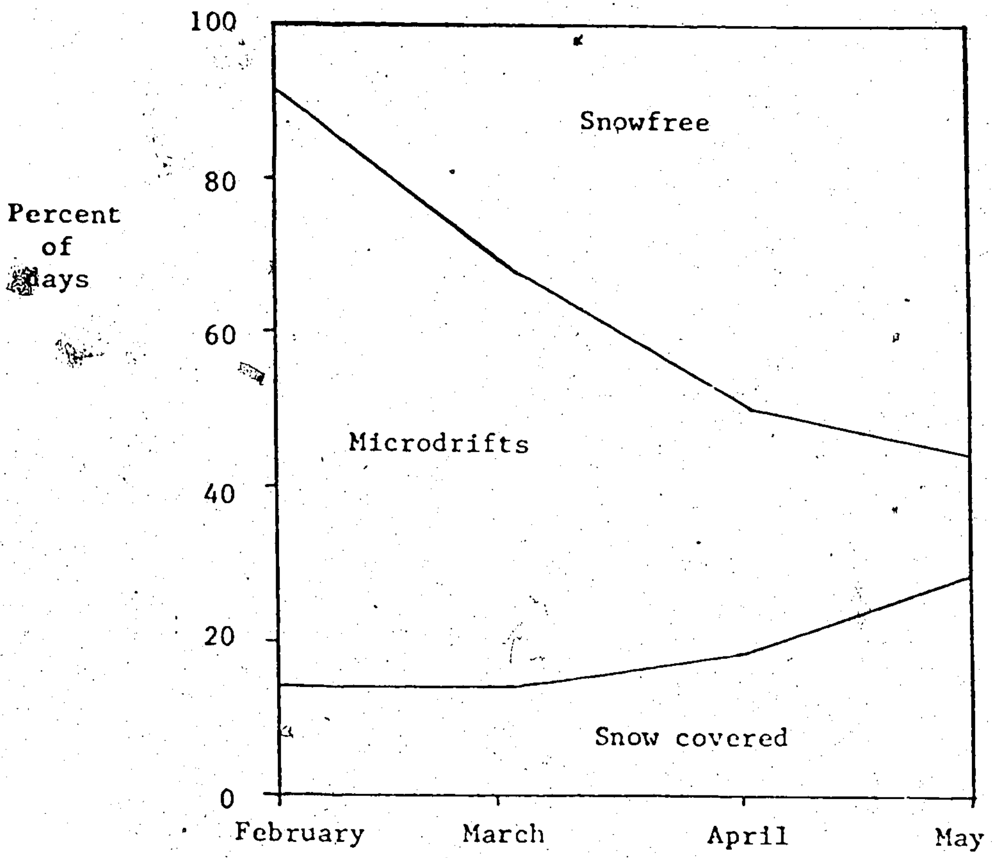


Fig. 3. Distribution of snow cover in a kobresia meadow, February-May.

Table 3. Mean monthly radiation, wind, and relative humidity in a Trail Ridge kobresia meadow. Wind was was measured at 200 cm height, relative humidity at 120 cm. Radiation cycles indicate frequency of change from sunny to cloudy to sunny conditions (after Salisbury _et al._, 1968).

Month	Solar radiation Lys/day	Solar radiation % of potential lys/day	Cycles/ day	Wind m/sec	Relative humidity (%) Daily mean	Relative humidity (%) Daily maximum	Relative humidity (%) Daily minimum
January	252	74	-	14.3	--	--	--
February	352	72	8.6	9.3	87	94	67
March	378	56	10.7	10.3	84	94	69
April	563	68	12.1	6.5	76	90	58
May	631	66	19.9	3.9	87	90	67
June	704	69	18.8	4.1	59	85	34
July	596	60	26.0	3.5	62	94	37
August	508	56	20.1	2.9	67	93	42
September	507	67	10.2	6.5	61	84	44

radiation means are comparable to those observed in summer at other alpine stations in Colorado, Wyoming, and the Sierra Nevada Range in California (Bliss, 1966; Barry, 1973), in contrast to summer means of 300 to 500 lys day^{-1} in the cloudy Presidential Range (Bliss, 1966). Measured radiation compared to the potential maximum (derived from Frank and Lee, 1966) was highest in mid-winter and spring (Table 3). The effects of cloudiness were least in January and February and greatest in August.

Diurnal patterns of radiation vary seasonally (Fig. 4). Summer days most frequently had clear mornings and broken clouds in the afternoon. Passage of frontal storms was also characterized by rapid and frequent fluctuations of radiation. These rapid changes from sun to cloudy conditions have been termed "radiation cycles" by Salisbury _et al_. (1968). Winter solar radiation tended to be less dramatically variable; daily curves were more nearly smooth. Fall and spring tended to be intermediate between winter and summer in the amount of rapid change (Table 3). Salisbury _et al_. (1968) concluded that total energy and the number of radiation cycles are the most meaningful components of radiation in an alpine environment similar to that of Trail Ridge. Incoming radiation is high in April through September, and number of daily cycles is greatest in May through August. Thus, four seasons are partially defined by radiation: a low, stable radiation winter; constant, high radiation in spring and fall; and high variation and total radiation in summer.

C. Wind

Winter windspeeds considerably exceeded those of summer (Table 3).

Fig. 4. Typical diurnal radiation patterns in various weather conditions in four seasons.

Winter

A.	9 February 1971	Clear
B.	18 February 1971	Easterly storm
C.	23 February 1971	Westerly storm

Spring

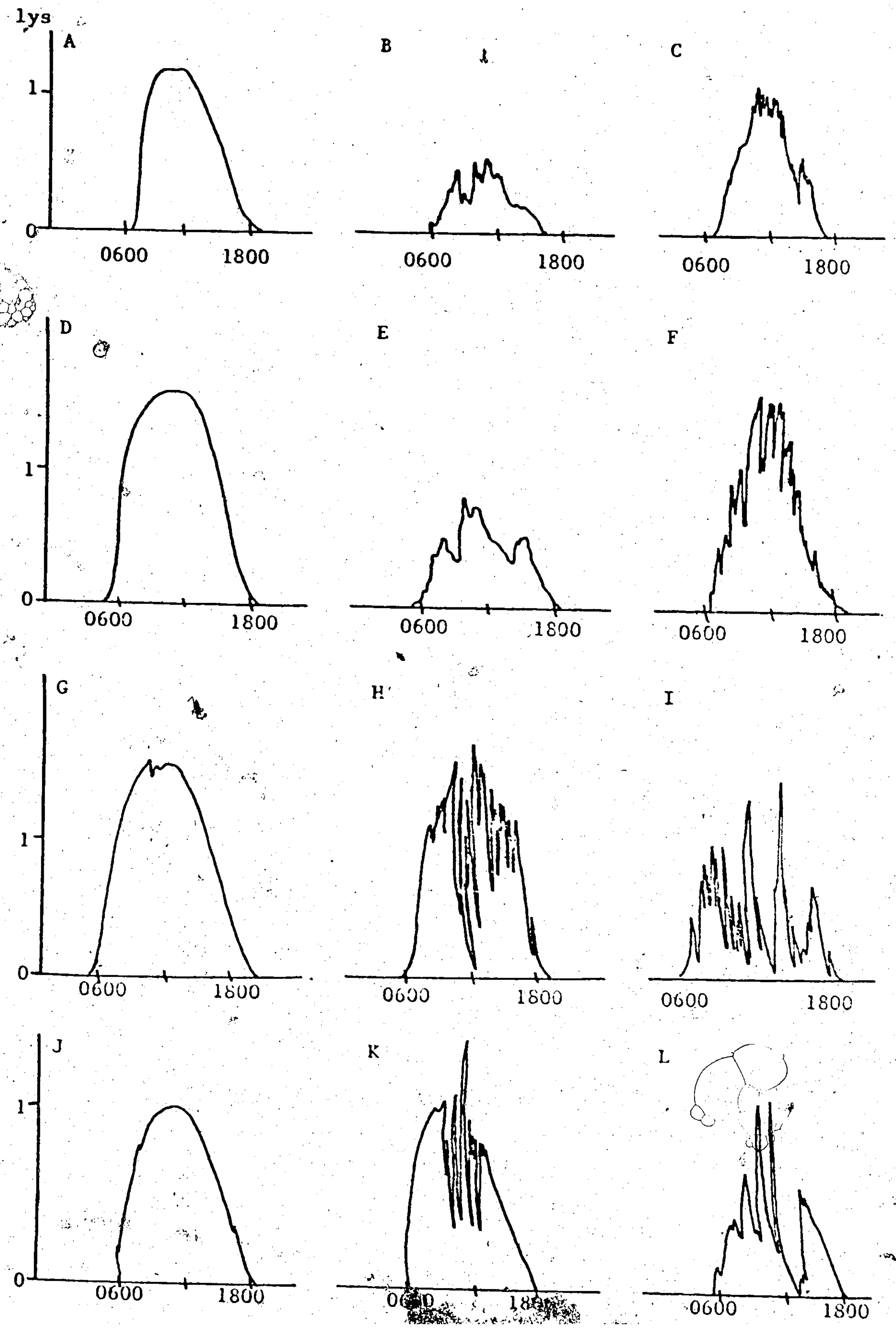
D.	23 April 1972	Clear
E.	26 April 1972	Easterly storm
F.	10 April 1972	Westerly storm

Summer

G.	11 July 1971	Clear
H.	27 July 1970	Afternoon thunderstorms
I.	23 July 1971	Frontal storm

Spring

J.	8 September 1970	Clear
K.	3 September 1970	Afternoon thunderstorm
L.	4 September 1970	Frontal storm


lys
A
1
0
0600
1800
B
0600
1800
C
0600
1800
D
1
0
0600
1800
E
0600
1800
F
0600
1800
G
1
0
0600
1800
H
0600
1800
I
0600
1800
J
1
0
0600
1800
K
0600
1800
L
0600
1800

Summer wind conditions prevail May through August with average speeds between 3 and 4 m sec^{-1}. Periods of high winds occur briefly in association with afternoon thunderstorms, reaching 8 m sec^{-1}, and daily averages as high as 5.6 m sec^{-1} were recorded. In summer, brief periods of calm occur occasionally with wind as low as 0.2 m sec^{-1} at 2 m for periods of several minutes and 0.7 m sec^{-1} over 1 hr. Wind direction was recorded only with spot readings. The strongest summer winds were from the west, but easterly and northeasterly winds accounted for 38% of readings in 1970, and 48% in 1971.

Measured monthly winds in winter averages 9 to 14 m sec^{-1} (Table 3) with daily averages between 1.8 and 17.5 m sec^{-1}. Windspeeds as low as 0.1 m sec^{-1} and exceeding 45 m sec^{-1} were measured for periods of 1 min at 2 m above the surface. Winds from the east were never measured exceeding 16 m sec^{-1}. The strongest winds were always from the west or southwest.

September and April winds were intermediate between those of summer and winter.

Average monthly windspeeds on Trail Ridge in the kobresia meadow follow the seasonal variation reported by Marr _et al_. (1967b) and Barry (1973), but are about 20% lower than those they observed. Part of the discrepancy may be related to a slightly lower anemometer position (2 m _vs_. 2.4 m) on Trail Ridge and part to the exposed ridge-top position of the Niwot Ridge station.

Front Range summer alpine winds are comparable to or lighter than those of other ranges. Bliss measured means of 4.4 m sec^{-1} on a ridge in the Medicine Bow Mountains of Wyoming (1956) and between 2.4 and 5.4 m sec^{-1} on a ridge on Mt. Washington in the Presidential

Range (1966). In the Sierra Nevada, ridge-top winds average about 3 m sec^{-1} (Klikoff, 1965). Means of summer spot readings in exposed alpine sites in the Canadian Rockies were 5.5 m sec^{-1} (Hrapko, 1970).

Wind Profiles

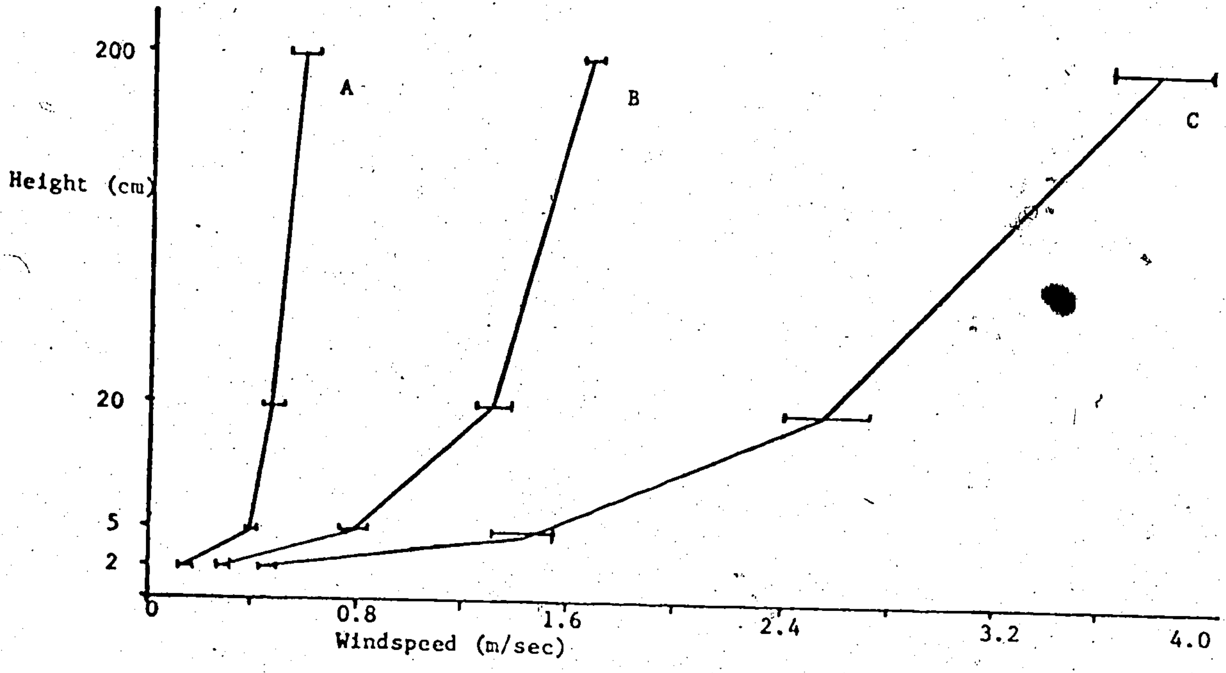
Profiles tended to exhibit the typical J-shaped curve, which approaches a straight line when plotted on the $\log_{10}$ of height (Figs. 5 and 6). The shape of profile curves and their slope varied. Summer curves had a more pronounced J-shape than those of winter, and profiles at high windspeeds had a gentler slope. The seasonal variation in profile curves is not solely related to change in windspeed at 2 m; a comparison of profiles for similar windspeeds in summer and winter (Fig. 7) indicates the flattening and depressed angle of curves regardless of windspeed. A transition from the typical winter to summer curves occurs in May when the profile at low speeds resembles summer; at high speed, winter; and at intermediate speeds assumes a complex curve that has the slope of winter profiles combined with the more pronounced J of summer near the surface (Fig. 6). This condition appeared only in May.

In April (with winter profile conditions prevailing) wind was measured directly over a tussock (the normal practice for other wind profiles) and at the edges of kobresia tussocks, the 2 cm readings being within the leaf canopy and the 5 cm at its top in all cases. A small venturi effect appeared to be produced by the slightly raised tussock, seen at the 2 cm points but greatly lessened at 5 cm (Fig. 8). In addition, the tussock acted as a windbreak, lowering velocity on the leeward side. These effects increased with higher windspeeds.

Fig. 5. Summer and fall wind profiles in a kobresia meadow.

Season	Curve	Windspeed at 2 m m/sec	Sample size
Summer	A	< 1.1	15
	B	1.8-2.9	26
	C	> 3.8	18
Fall	A	< 3.8	4
	B	3.8-7.7	6
	C	7.7-11.6	3

Summer


200
20
5
2
Height (cm)
A
B
C
0
0.8
1.6
2.4
3.2
4.0
Windspeed (m/sec)

Fall

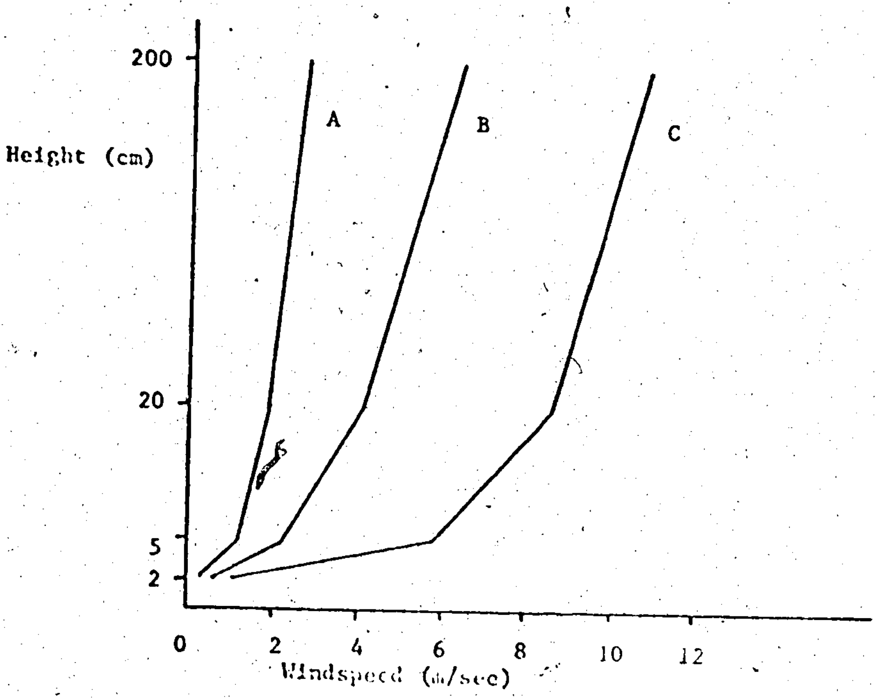
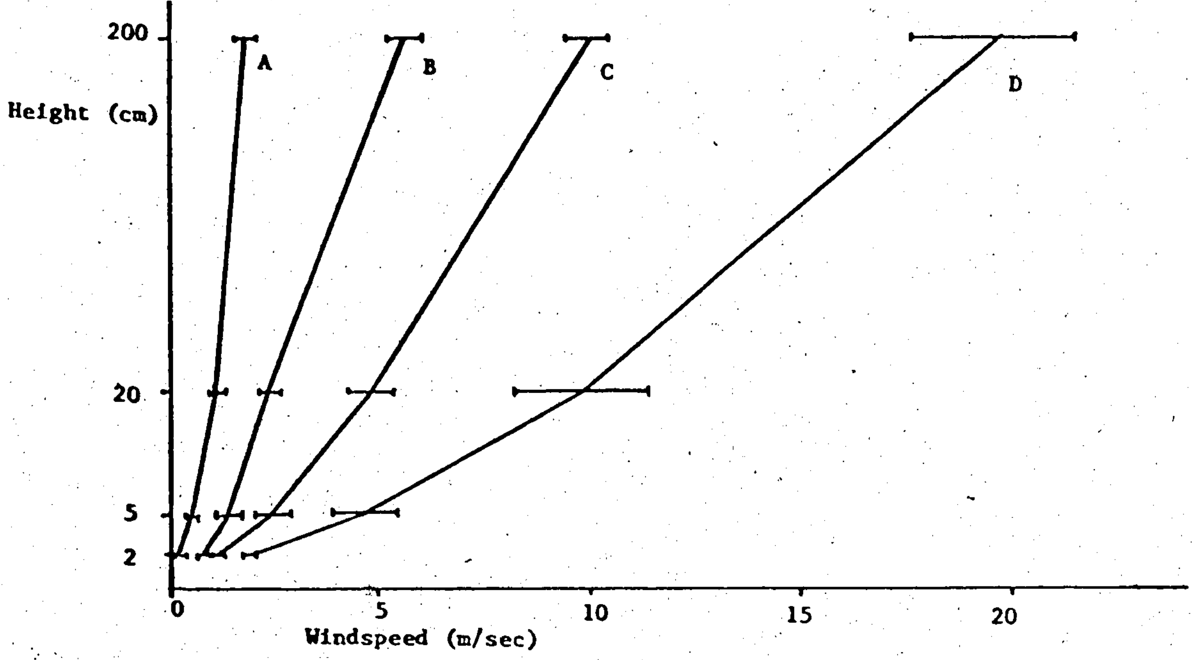

200
20
5
2
Height (cm)
A
B
C
0
2
4
6
8
10
12
Windspeed (m/sec)

Fig. 6. Winter and spring wind profiles in a kobresia meadow.

Curve	Windspeed at 2 m m/sec	Sample size Winter	 April	 May
A	3.8	7	4	8
B	3.8-7.7	5	6	8
C	7.7-15.4	18	6	3
D	15.4	8	6	1

Winter (January-March)



Spring

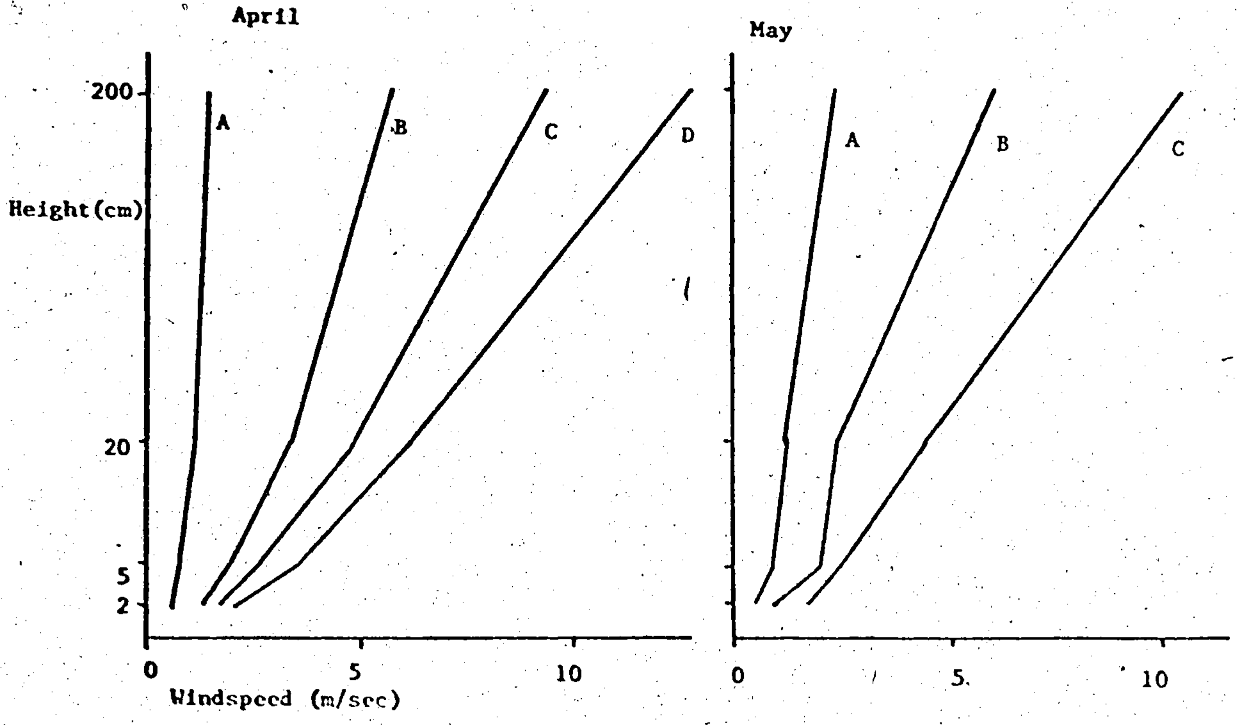
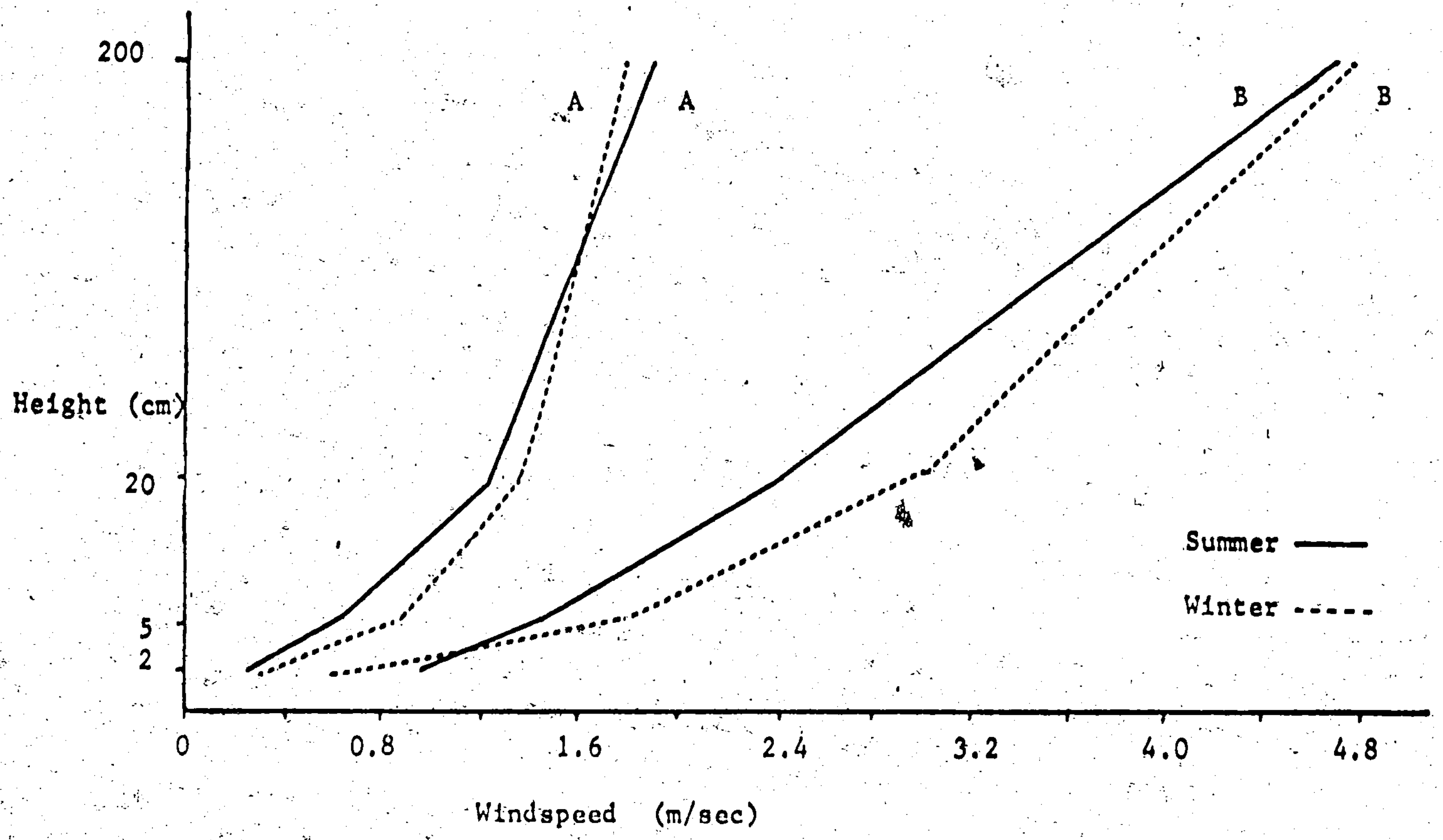


Fig. 7. Comparison of wind profile curves at similar 2 m windspeeds in summer (July-August) and winter (January-March).

Curve	Windspeed at 2 m m/sec	Sample size Summer	Sample size Winter
A	< 3.8	41	5
B	3.8-7.7	18	5


200
Height (cm)
20
5
2
0
0.8
1.6
2.4
3.2
4.0
4.8
Windspeed (m/sec)
A
A
B
B
Summer
Winter

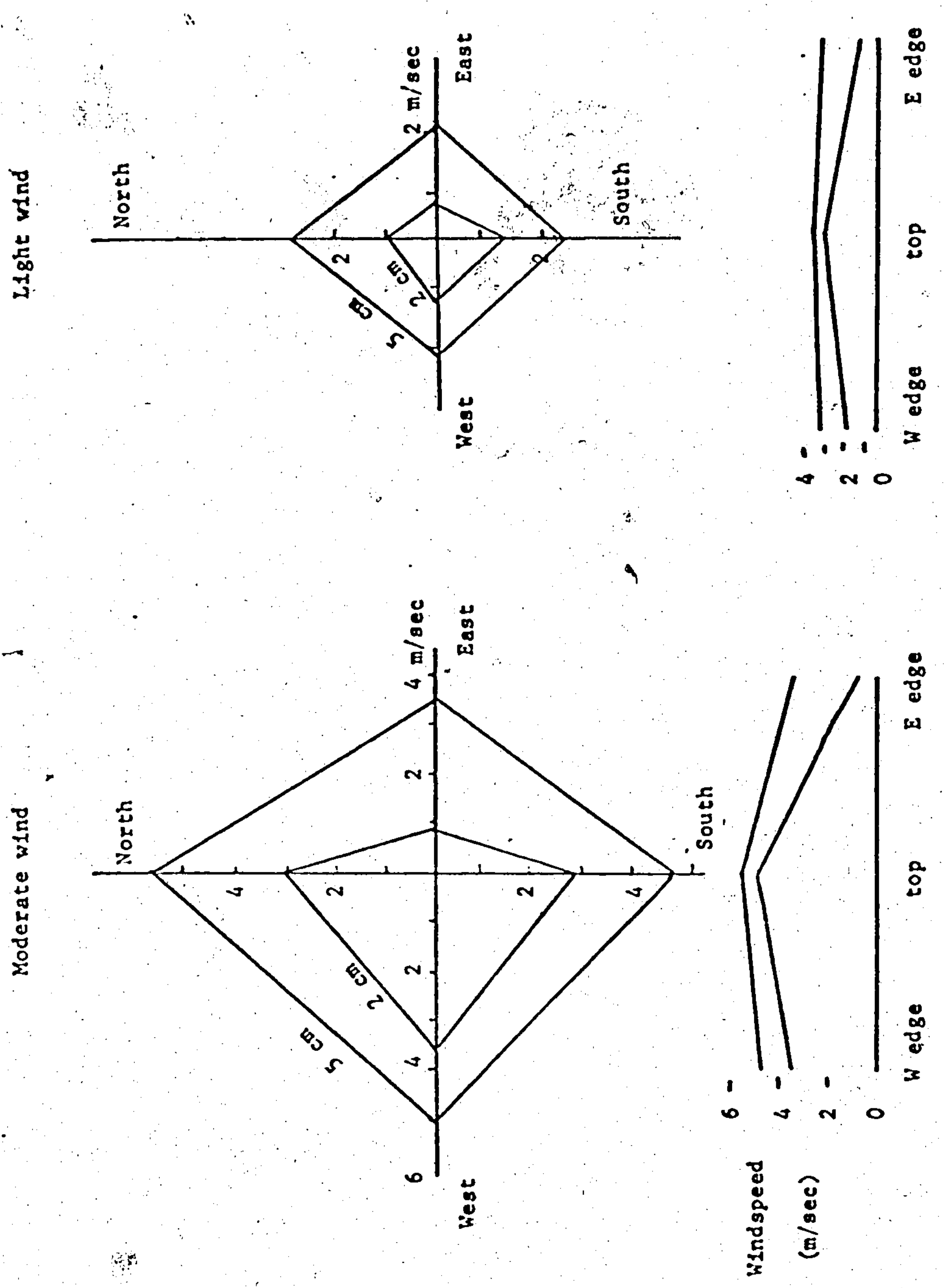


Fig. 8. Windspeeds around and over a kobresia tussock, 10 April 1972. Windspeeds are means of 10 measurements at edges of and over the tussock base at 2 cm and 5 cm height.

While J-shaped curves are usually considered the most common form of wind profile in both alpine areas (Bliss, 1966; Courtin, 1968) and elsewhere (Geiger, 1966) other curve shapes have been observed. Deacon (1953) suggested that profiles could be described by the equation

$$\frac{du}{dz} = cz^{-\beta} \qquad \text{(Eq. 6)}$$

where u is windspeed; z is height; and c a constant determined by von Karman's constant, a roughness parameter, and the velocity of shear. In such a description the value of β determines the shape of velocity profile curves; and a number of studies have been made of methods for determining β to relate it to other environmental variables (Longley, 1954; Deacon, 1953). β was found to have a variety of values and to be unpredictable (Longley, 1954). As Fig. 7 suggests, temperature and wind velocity may have a role in determining β. Tussock roughness, while it alters windspeeds at 2 cm appears to have little effect at 5 cm, at least in winter. Although the data presented seem to offer these possible explanations for the value of β, it should not be predicted on these bases because of the extreme accuracy of data required for this determination (Longley, 1954 and pers. comm.). Thus profile curve shape must be treated as an independent variable, and only such empirical generalizations as those above can be made.

D. Temperature

Mean monthly temperatures (Table 4) closely resemble those on Niwot Ridge. Trail Ridge temperature means were usually within 3° of the means measured on Niwot Ridge by Marr et al. (1967b) and Barry

Table 4. Monthly temperatures at 120 cm in a kobresia meadow: mean daily maxima and minima, monthly maxima and minima, and mean number of cyclic fluctuations greater than 1°C during midnight to midnight periods.

Month	Temperature (°C)				Cycles/ day
	Daily maximum	Daily minimum	Monthly maximum	Monthly minimum	
February	-8	-16	0	-29	3.4
March	-7	-15	2	-26	2.4
April	-2	-10	7	-18	2.7
May	2	-7	7	-15	3.7
June	7	-3	15	-11	4.9
July	12	2	18	-3	6.8
August	14	6	18	3	6.3
September	7	-1	16	-11	3.7
October	-3	-10	4	-16	3.9

(1973). Bliss (1966) noted the similarity of summer alpine temperatures in the Rocky Mountains, Sierra Nevada and Presidential Ranges. Summer means of 7 to 9° have also been observed in the Olympic Mountains (Bliss, 1969) and in the Canadian Rockies (Hrapko, 1970). In New Zealand, summer alpine temperatures are a little lower (4.4-6.2°) and night freezing occurs more frequently than in North American alpine zones (Bliss, 1966, 1969).

Average temperatures alone do not indicate the severity of the temperature regime. In a Colorado alpine environment, rapid changes in solar radiation produce cyclic temperature variation with periods of a few minutes (Salisbury <u>et al.</u>, 1968). This temperature instability was quite noticeable on Trail Ridge. The minimum period for cycles that could be observed in data recorded at 120 cm was about 1 hr. The frequency of such cycles was highest in summer, about twice that of winter (Table 4). May, September, and October showed intermediate cycle numbers.

Temperature Profiles

Temperature profiles are the most variable of any environmental profile examined because of the amny factors determining temperatures. They are partially an independent variable because large-scale air masses set up basic temperature ranges. The details of profiles, however, are determined by windspeed, solar radiation, evaporation after a rainstorm, presence and depth of snow cover, meltwater or ice sheets, and the short-term history of the profile. Variations over profiles, especially near the soil surface, are so rapid and great that description of temperature profiles using means of readings from a number of days obscures the complexity of the temperature regime around kobresia plants.

Summer temperatures present the fastest rate of change and, as a rule, the most highly differentiated profiles (Fig. 9). Night profiles are usually uniform. Immediately after sunrise the air warms a little more rapidly than the soil, setting up a cooler air mass around the plant tussock than in the air above. By midmorning, however, the profile is reversed as the soil warms rapidly on clear days. Mid-day profiles are affected by cloud conditions. Surface heating is greater on clear days than during cloudy or partly cloudy periods. This surface warming produced the highest temperature observed, 40.3° at the soil surface. Profiles under partly cloudy conditions with rapid insolation fluctuation often exhibited extremes typical of profiles for cloudy and clear weather within periods under 6 min. Well-developed temperature layers persist into the afternoon under various cloud conditions, and fade as the sun nears the horizon.

Windspeed affects the thickness and degree of warming of the heated air layer near the surface (Fig. 10). When windspeed at 2 m is less than about 3 m sec^{-1}, wind velocity has little effect on the formation of heated layers. The top of these layers is well established at 5 cm, directly above the top of the dense portion of the kobresia tussock. A windspeed of 7 m sec^{-1} at 2 m keeps the top of the tussock cool. This thinner heated layer is more clearly defined: temperatures above the tussock are more uniform than at lower windspeeds. As this 7 m sec^{-1} approaches the summer maximum it is probably rare that wind destroys the heated layer in the tussock during that season.

Fig. 9. Representative temperature profiles during summer in a kobresia meadow.

Curve	Time	Sky	Wind at 2 m m/sec	Date
A	0310	Clear	2.1	21 July 1970
B	0535	Clear	1.0	20 July 1970
C	0932	Clear	1.1	20 July 1970
D	1230	Partly cloudy	5.9	26 July 1971
E	1210	Clear	0.9	16 July 1971
F	1245	Cloudy	1.0	21 August 1971
G	1450	Clear	2.2	11 August 1970
H	1340	Cloudy	0.8	9 August 1971
I	1700	Clear	3.7	9 August 1971
J	1700	Cloudy	2.2	30 July 1971

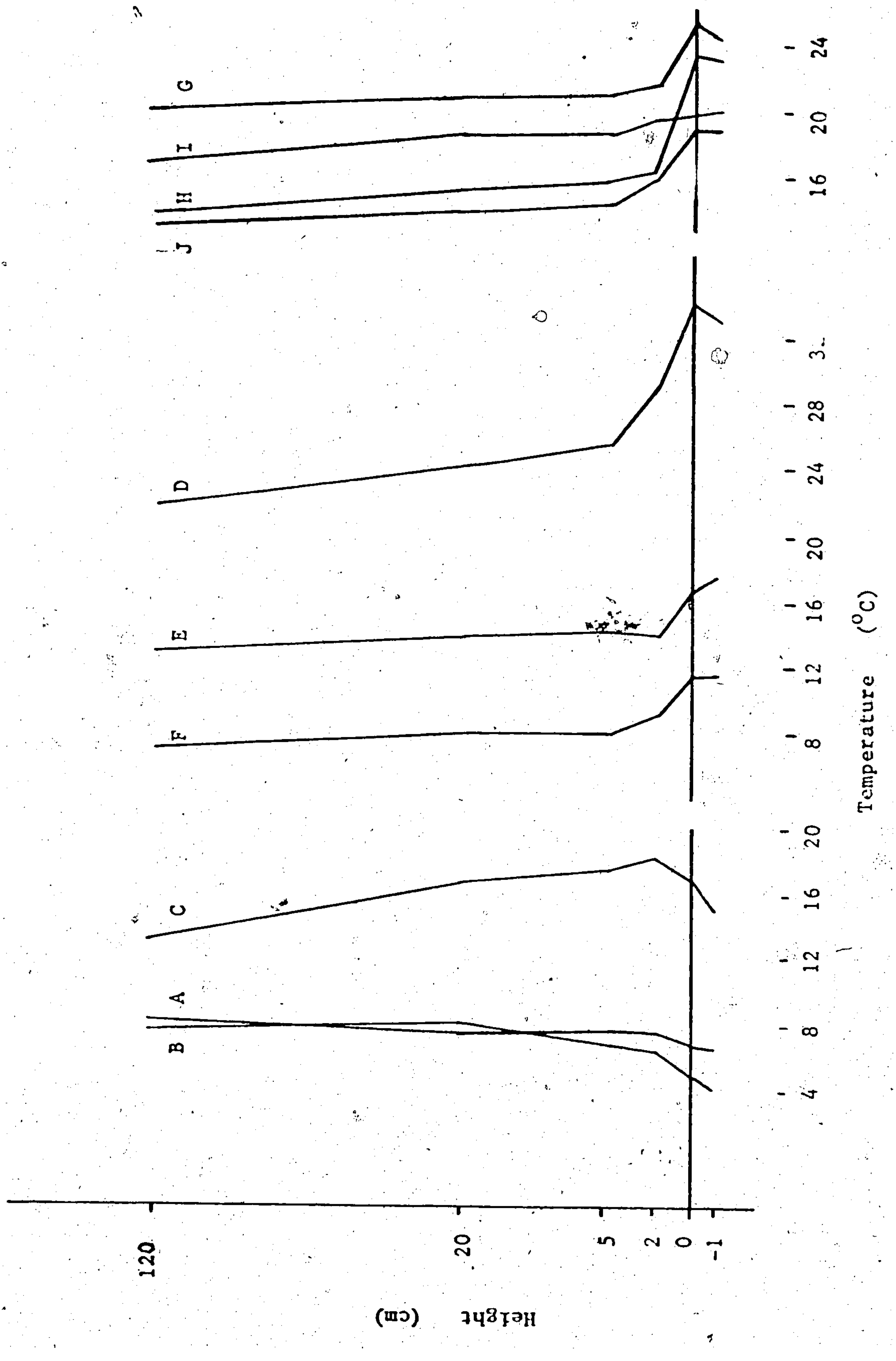
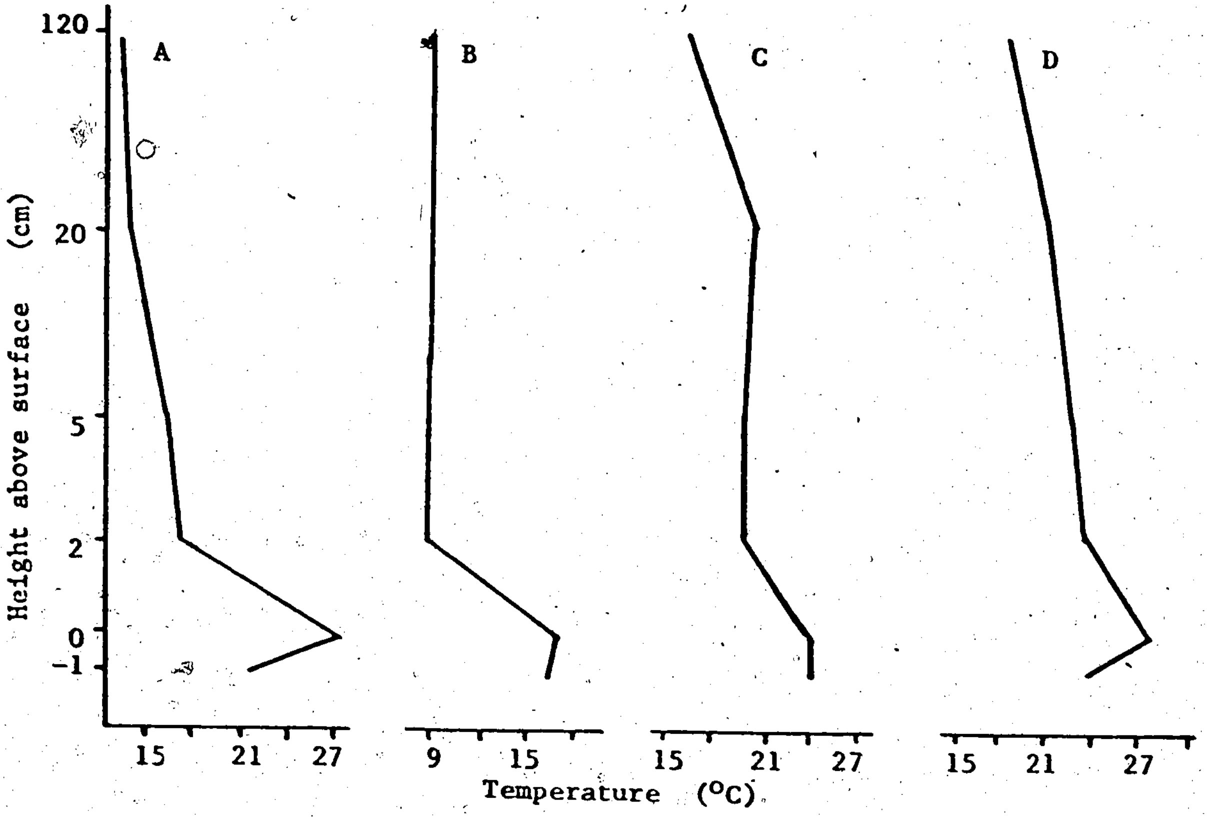

Height (cm)
120
20
5
2
0
-1
B
A
C
F
E
D
J
H
I
G
4
8
12
16
20
8
12
16
20
24
28
3..
16
20
24
Temperature (°C)

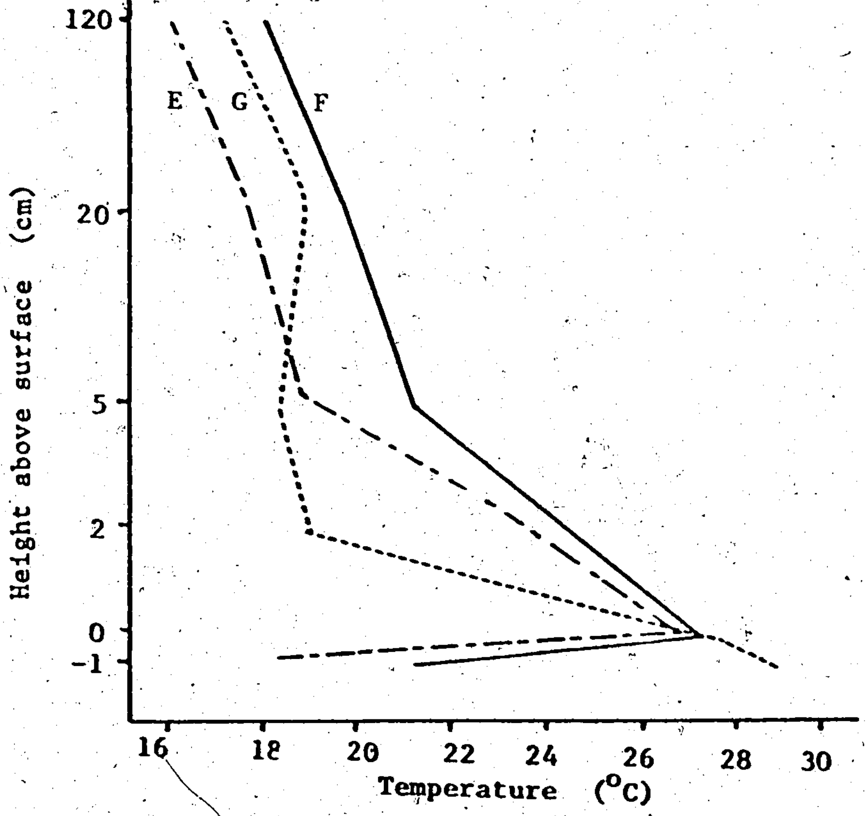
Fig. 10. Effects of an afternoon thunderstorm and of windspeed on summer temperature profiles in a kobresia meadow.

Profile	Sky condition	Windspeed at 2 m m/sec	Time	Date
A	Clear	1.4	10:00	27 July 1970
B	Cloudy, rain	1.6	12:10	27 July 1970
C	Overcast	2.7	13:55	27 July 1970
D	Partly cloudy	2.2	15:30	27 July 1970
E	Clear	1.6	10:00	10 Aug 1970
F	Clear	3.1	10:10	19 Aug 1970
G	Clear	7.3	09:45	13 Aug 1970

Effect of a thunderstorm



Effect of windspeed



The frequent afternoon thunderstorms also influence temperature profiles. These are complex events involving changes in wind, clouds, and moisture at the soil surface. A sequence of temperature profiles during the course of such a stormy afternoon (Fig. 10) shows that the advent of the storm reduces the thickness of the heated layer; and as stormy conditions persist they diminish the degree of heating in this layer, making surface temperatures closer to those of the air above. The passing of the storm allows partial restoration of the warm air layer, but it is rarely as well developed after the storms as before they begin.

Summer temperature profiles are sometimes subject to extremely rapid and intense variation, especially under the partial cloudiness that is common in early afternoon. For periods of 1 hr, temperature profiles were recorded once every 2 min and variation among these profiles described by calculation of standard deviations. Variation was most rapid near the soil surface and declined rapidly within the kobresia tussock (Fig. 11). Mean temperature change over 5 hr in early afternoons was 1.5° $\min^{-1}$ at the soil surface. Maximum change was 14° in 2 min when the sun was covered by cloud. Temperature fluctuations less than 2 min in duration [illegible] evident but not measured.

Winter temperature profiles are generally much more uniform than those of summer (Fig. 12). While the soil surface and the air immediately above it vary in temperature from the air at 120 cm, the difference rarely exceeds 1 or 2°. In winter the soil becomes important as a heat source or sink determining temperatures near plants. On clear days, temperatures rise in the morning near the

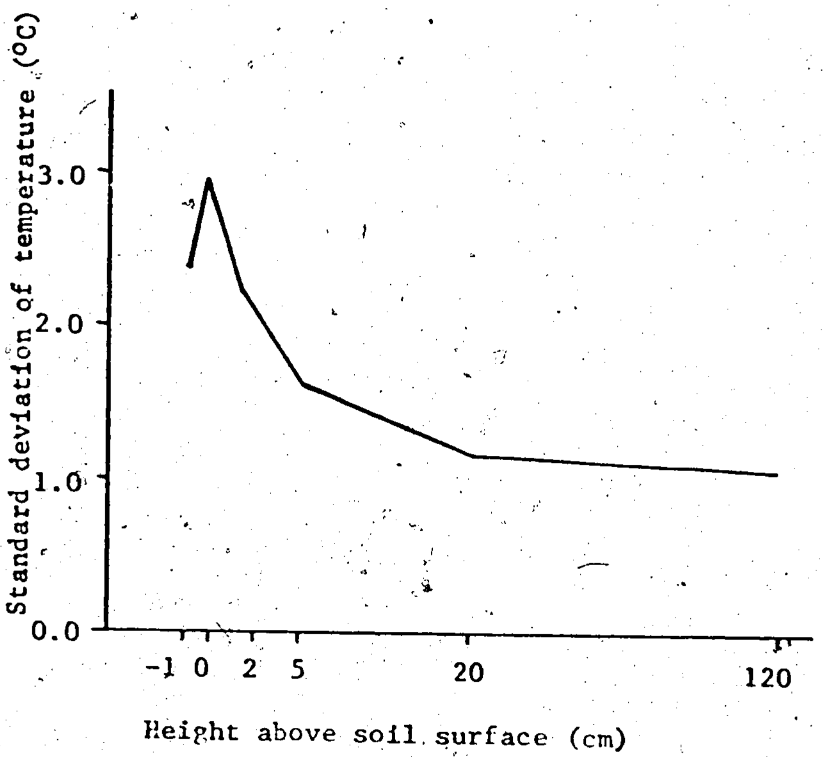
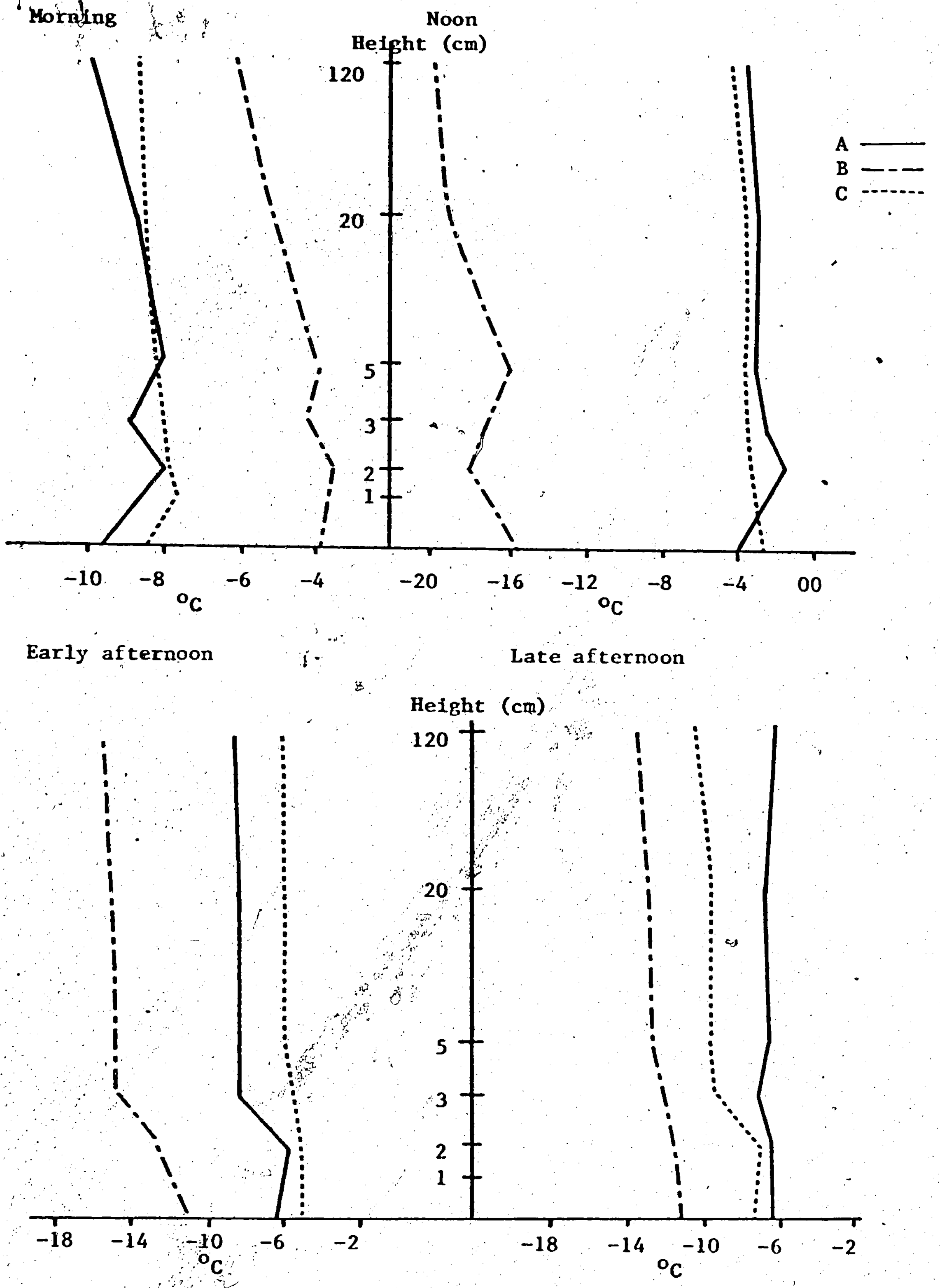


Fig. 11. Standard deviation of temperatures from a mean of 30 readings at 2 min intervals over a 6-point profile. Curve represents the mean of 5 hrs measured on 5 days during the period of maximum solar radiation variation (11:30-15:00).

Fig. 12. Representative temperature profiles, winter, 1971.

Profile	Weather	Snow depth cm	Wind at 2 m m/ sec	Time	Date
Morning					
A	**Clear**	1-5	4.7	10:00	9 Feb
B	**Easterly storm**	0-1	3.2	10:20	2 Feb
C	**Westerly storm**	1-2	10.3	10:30	13 Mar
Noon					
A	**Clear**	1-5	13.1	12:00	12 Feb
B	**Easterly storm**	1-2	1.2	12:15	1 Mar
C	**Westerly storm**	0-2	28.6	12:15	11 Mar
Afternoon					
A	**Clear**	1-5	8.9	14:20	24 Feb
B	**Easterly storm**	2-5	1.8	14:40	1 Mar
C	**Westerly storm**	2-4	5.6	14:30	25 Mar
Evening					
A	**Clear**	1-5	4.7	16:45	9 Feb
B	**Easterly storm**	2-6	1.9	17:15	19 Feb
C	**Westerly storm**	1-6	21.7	16:35	25 Feb


Morning
Noon
Height (cm)
120
20
5
3
2
1
-10
-8
-6
-4
-20
-16
-12
-8
-4
00
°C
°C
A
B
C
Early afternoon
Late afternoon
Height (cm)
120
20
5
3
2
1
-18
-14
-10
-6
-2
-18
-14
-10
-6
-2
°C
°C

surface, but the soil acts as a heat sink. Temperatures at the snow surface remain colder than those immediately above or below it. By early afternoon maximum air temperatures are reached and the soil surface is slightly warmed; but by late afternoon the profile becomes uniform with rapid re-radiation from both air and soil. Storms from the east, with low winds and heavy clouds, show a morning profile development similar to that of clear days. By noon, the soil begins to act as a heat source, and cooling at the snow surface is quite strong. In storms with strong winds, usually those from the west, relatively little profile differentiation is observed, especially above the snow surface. High winds and cloudy conditions slow the heating of the soil surface and the wind accelerates soil cooling in the afternoon. The net effect of these windy storms is thus to reduce the total heating in the space near the soil surface and to shorten the period of relative warmth during the day.

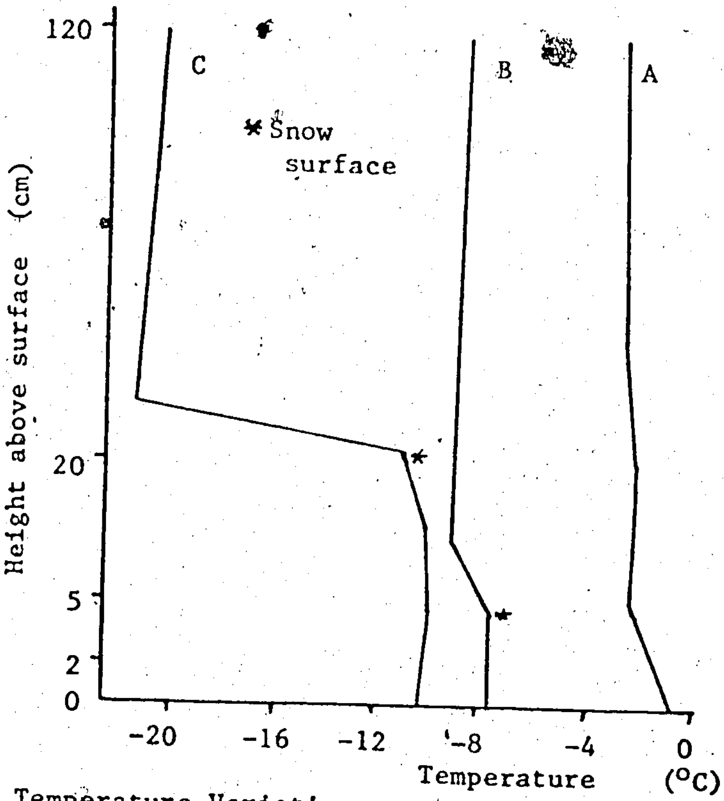
Three factors have considerable influence on winter temperature profiles: windspeed, snow depth and quality, and temperature of wide area air masses of different temperatures. High winds reduce the thickness of layers that are warmed during the day (Fig. 13). In low winds, a layer of warmer air develops above the snow, while at increased speeds more typical of winter, cooling from the air above affects points below the snow surface.

Snow cover has two effects on temperature: it is an insulator and its surface is often cooled, probably by sublimation. Three temperature profiles measured after daily maxima had past illustrate the effectiveness of snow as an insulator (Fig. 13). With no snow, heat loss from soil and plants is rapid; and, while the soil may

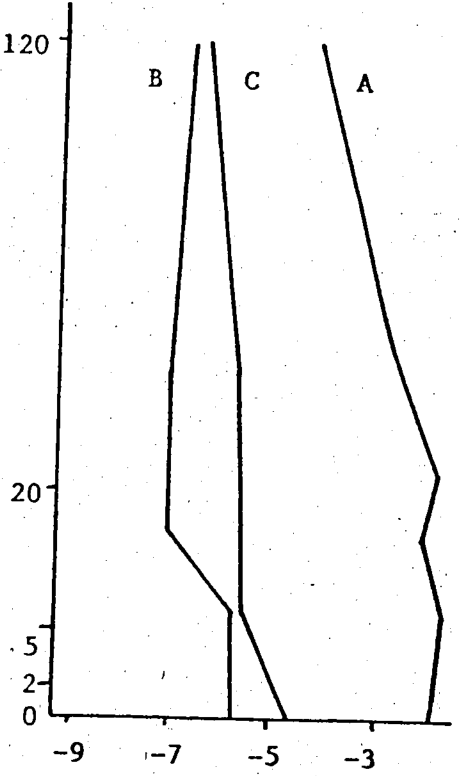
Fig. 13. Effects of snow cover, wind and temperature on temperature profiles, winter, 1971.

	Curve	Snow depth cm	Wind at 2 m m/sec	Time	Date
Snow cover variation					
Continuous cover	A	22	1.5	11:20	22 Feb
Microdrifts	B	1-5	6.6	12:50	25 Feb
Snowfree	C	0	7.9	10:25	30 Jan
Windspeed variation					
Calm	A	0-3	0.3	11:00	3 Feb
Moderate	B	1-4	10.3	10:30	13 Mar
Strong	C	0-3	27.6	12:15	11 Mar
Temperature variation					
High	A	0	2.2	11:00	1 Feb
Average	B	0-2	4.7	11:30	19 Feb
Low	C	0-2	2.0	12:00	1 Mar

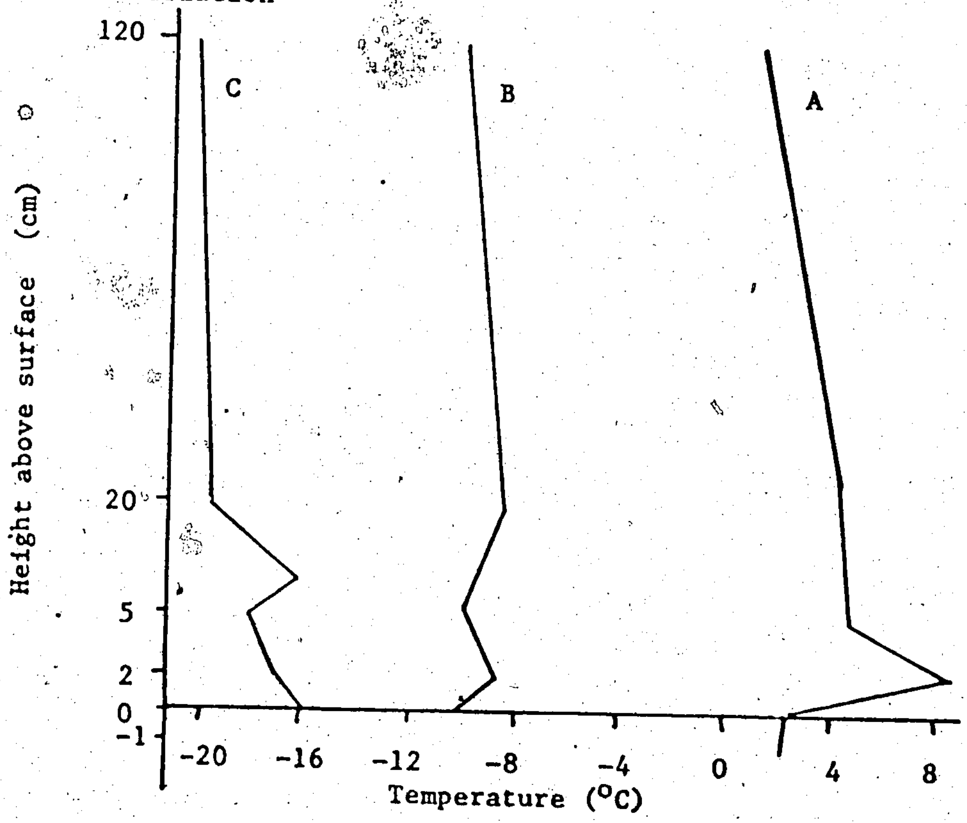
Snow cover variation



Windspeed variation



Temperature Variation



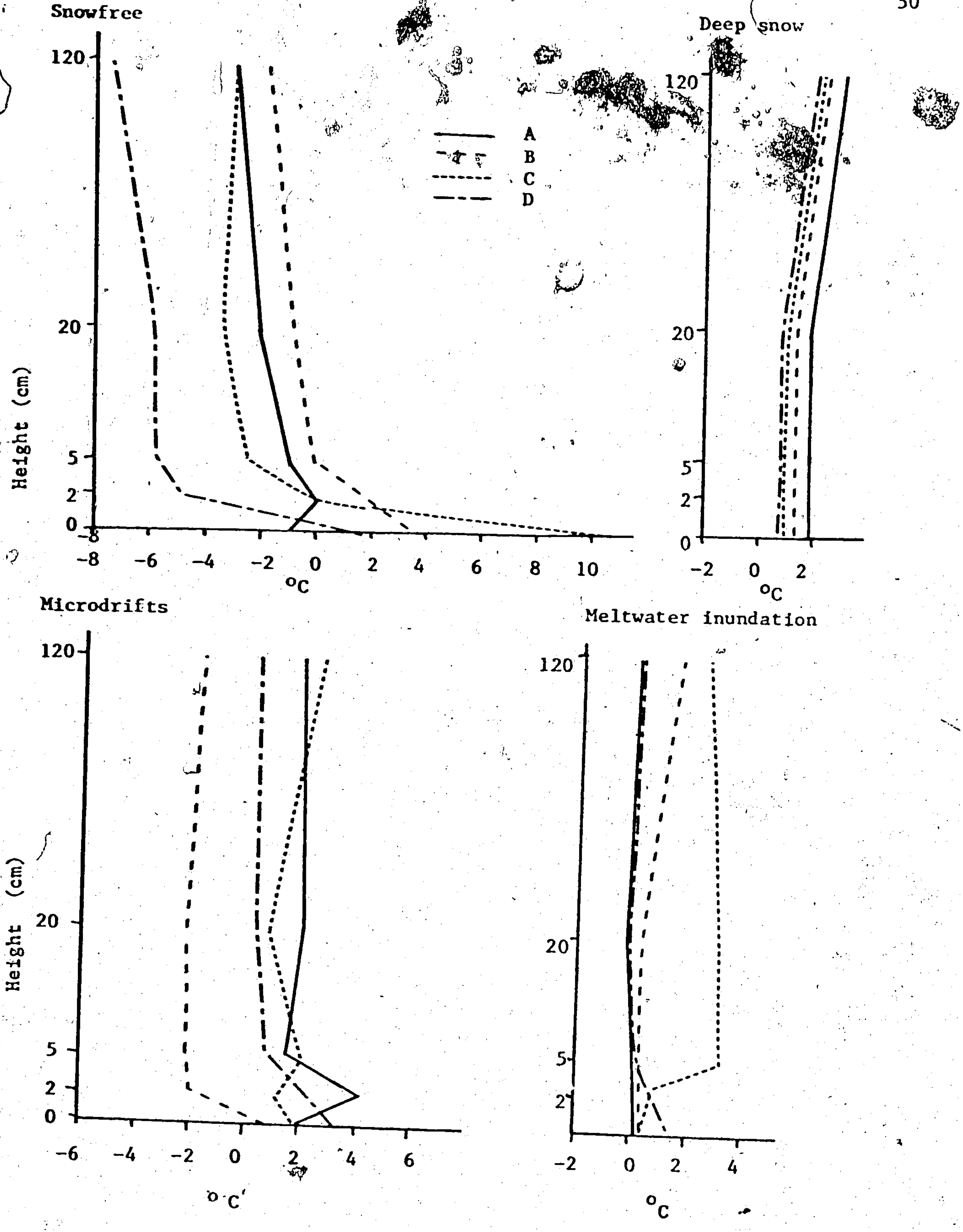
act as a heat source, it cannot heat air as high as 2 cm above it. The presence of as little as 3 cm of snow permits the lower portion of kobresia tussocks to benefit from soil heating. Deeper snow permits even greater departure of plant-level temperatures from air temperatures at 120 cm. The presence of crusts of snow or ice near the surface of the ground may permit a significant warming beneath this layer. Readings of temperature 0.5 cm above and below ice sheets and snow crusts showed air temperature beneath the ice averaged 1.0° higher than above it and 0.7° higher below snow crusts. Although the differences above and below are small they are very highly significant statistically ($p>99.9\%$). As temperature of the air approached the melting point, however, differences above and below snow crusts became negligible while those above and below ice sheets continued to average 1.0°

If other factors are constant, the temperature of air masses that cover large regions may alter the role of the soil in profile definition (Fig. 13). At unusually high temperatures associated with chinook conditions, the soil acts as a heat sink and maximum temperatures are found in the air within the kobresia tussock. In exceptionally low temperatures, the soil acts as a heat source and temperatures are highest at its surface throughout the day.

Spring temperature profiles frequently had greater variability than those of winter (Fig. 14). With diminished winds, a heated layer developed daily near the soil surface when snow and meltwater were absent. Soil surface temperatures were as much as 15° above those at 120 cm even under cloudy skies, and temperatures were frequently far above the freezing point at plant level in April and May. The

Fig. 14. Representative spring temperature profiles in a kobresia meadow.

Profile	Time	Date	Snow depth (cm)	Sky conditions
Snowfree				
A	09:20	10 April 1972	0	Overcast
B	11:30	3 April 1971	0	Overcast
C	14:00	5 April 1971	0	Overcast
D	17:00	5 April 1971	0	Overcast
Microdrifts				
A	08:15	29 April 1972	0-2	Overcast
B	11:50	21 April 1972	2-5	Clear
C	13:30	17 April 1972	0-3	Partly cloudy
D	15:50	28 April 1972	0-3	Clear
Deep snow				
A	08:50	10 May 1972	20	Fog
B	10:20	9 May 1972	20	Cloudy
C	13:00	8 May 1972	25	Clear
D	16:00	8 May 1972	25	Clear
Meltwater inundation				
A	08:00	23 May 1972	0	Overcast
B	11:50	23 May 1972	0	Overcast
C	13:55	24 May 1972	0	Cloudy
D	18:15	22 May 1972	0	Cloudy


Snowfree
Deep snow
A
B
C
D
Height (cm)
120
20
5
2
0
-8
-6
-4
-2
0
2
4
6
8
10
°C
120
20
5
2
0
-2
0
2
°C
Microdrifts
Meltwater inundation
Height (cm)
120
20
5
2
0
-6
-4
-2
0
2
4
6
°C
120
20
5
2
-2
0
2
4
°C

presence of even slight snow cover, however, held temperatures near 0°. Meltwater from nearby snow flowing across the meadow prevented formation of a heated surface layer. Since snow and meltwater are common in late spring, surface heating occurs principally in early April and late May when meadows are dry.

Heating at and near the soil surface in summer is typical of alpine environments. Bliss (1966) found surface temperatures on Mt. Washington 4 to 8° warmer than 10 cm air temperatures. Salisbury and Spomer (1964) report 5 to 15° differences on Mt. Evans in the Front Range, and Peterson (1971) found similar conditions in the Olympic Mountains. Klikoff (1965) reports surface temperatures much higher than air temperature when Sierra Nevada meadows are dry. Winter temperature profiles have not been reported from other snowfree alpine sites. The slight insulation of snow cover is unusual. Gieger (1966) reports that even 3 cm of snow can maintain differences of several degrees during diurnal fluctuations. The high winds of Trail Ridge appear to be responsible for the lessened effect of snow cover on temperature profiles.

E. Atmospheric Moisture

Relative humidity recorded at 120 cm was high in February through May and much lower in summer and early autumn (Table 3). Marr et al. (1967b) observed a similar, if less abrupt, seasonal transition on Niwot Ridge. June, 1970, had exceptionally little precipitation, and this dryness is reflected in a low relative humidity.

Vapor Pressure Deficit Profiles

Vapor pressure deficit (VPD) profiles showed little variation between 2, 20 and 120 cm levels. Average differences between VPD at 2 and 20 cm and at 120 cm were 0.4 and 0.7 mb, respectively. Deficits were usually low, although under partly cloudy conditions in early afternoon maxima exceeded 4 mb at 2 cm and 2.6 mb at 120 cm (Table 5). Representative VPD profiles (Fig. 15) illustrate this uniformity. VPD is lowest near the soil surface through the night, early morning and late afternoon. The gradient is reversed with the highest VPD near the soil only with soil surface heating. VPD rises to a peak by mid-afternoon on clear days; but under normal afternoon thunderstorm conditions, rain decreases VPD and produces a uniform profile. After rain, evaporation and lowered soil and air temperatures tend to keep the 2 cm CPD lower than the air above. Wholly cloudy days often fail to exhibit gradient reversals.

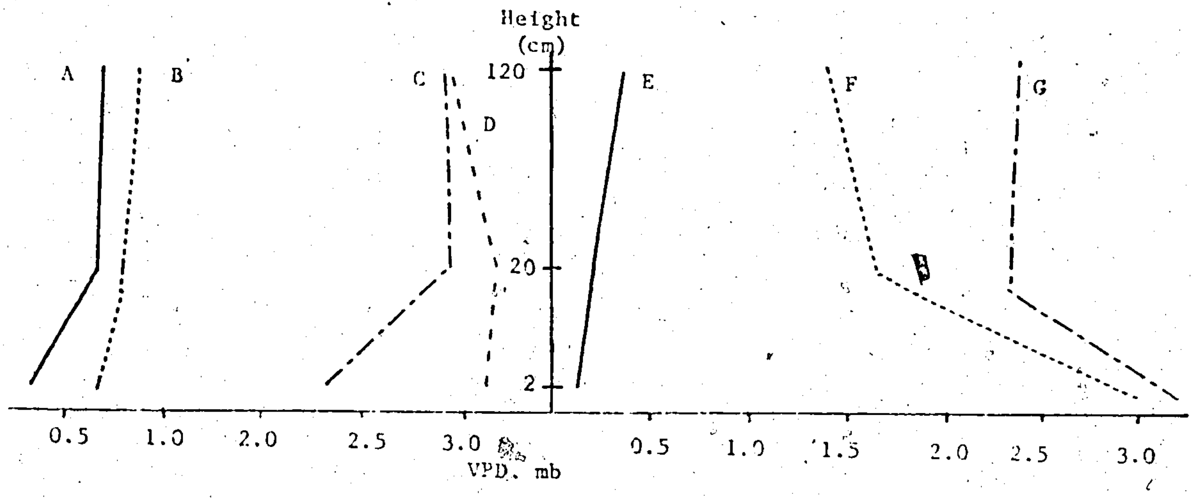
Vapor pressure deficits on Trail Ridge were much less than those described in other dry alpine sites. Values of 8 to 11 mb have been reported for the False Mummy Pass area of Rocky Mountain National Park (Holway and Ward, 1964); about 9 mb for a ridgetop in the Medicine Bow in Wyoming (Bliss, 1966); and 10 to 20 mb in a dry meadow in the Sierra Nevada (Klikoff, 1965). Even the relatively moist Presidential Range has average alpine VPD as high as 3 mb. The apparent high atmospheric moisture levels on Trail Ridge result from the computation method used to obtain VPD from wet and dry bulb temperatures. Direct calculation allows for altitude correction. Methods used for deriving values are not usually described by other investigators. Klikoff (1965) and Bliss (1966, by pers. comm.) first converted wet and dry bulb temperatures to relative humidity, then to VPD. One method for the latter conversion is described by Williams

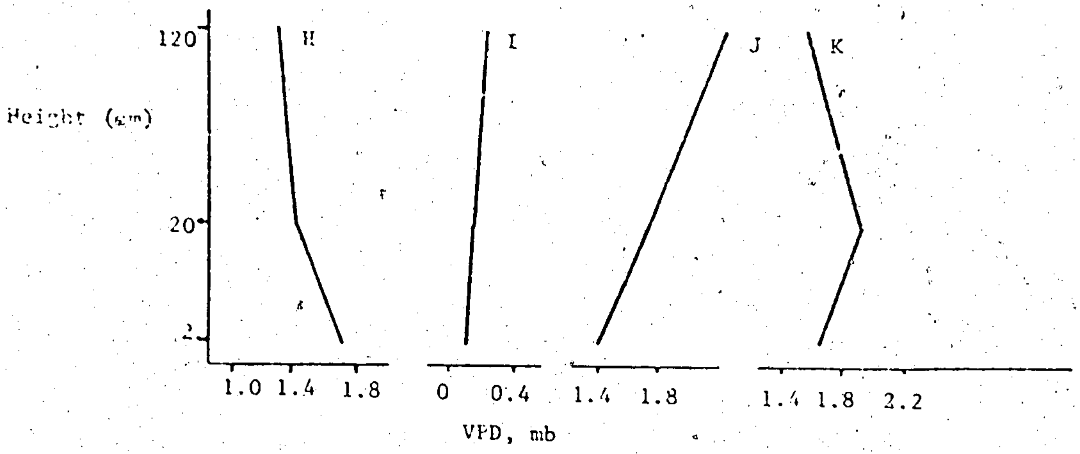
Table 5. Means with standard error and ranges of vapor pressure deficits (mb) in 92 profile measurements in a kobresia meadow, July and August, 1970 and 1971.

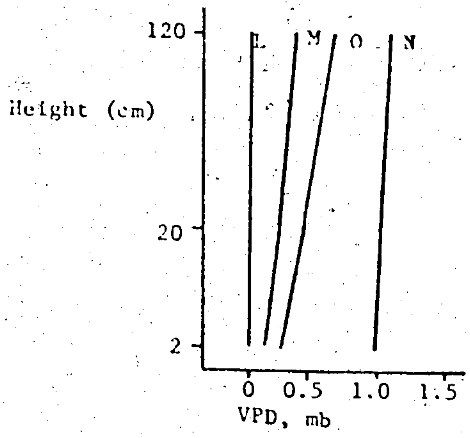
	Height above soil surface		
	2 cm	20 cm	120 cm
Mean	1.88±0.12	1.97±0.09	1.88±0.09
Maximum	6.52	4.65	3.97
Minimum	0.00	0.00	0.00

Fig. 15. Representative summer vapor-pressure deficit profiles.

	Time	Weather	Date
A.	03:00	Clear	21 July 1970
B.	05:35	Clear	2 July 1970
C.	09:30	Clear	10 August 1970
D.	12:20	Clear	11 August 1970
E.	12:40	Partly cloudy	6 August 1971
F.	15:25	Clear	11 August 1970
G.	19:30	Clear, after sunset	26 July 1970
H.	10:30	Clear	27 July 1970
I.	12:40	Cloudy, rain and hail	27 July 1970
J.	14:30	Overcast	27 July 1970
K.	16:00	Partly cloudy	27 July 1970
L.	08:10	Fog, partly cloudy	23 July 1970
M.	10:35	Cloudy, rain	22 July 1970
N.	14:10	Cloudy,	19 July 1970
O.	18:00	Cloudy	24 August 1971


Height
(cm)
120
20
2
A
B
C
D
E
F
G
0.5
1.0
2.0
2.5
3.0
VPD, mb
0.5
1.0
1.5
2.0
2.5
3.0


120
20
2
Height (cm)
H
I
J
K
1.0
1.4
1.8
0
0.4
1.4
1.8
1.4
1.8
2.2
VPD, mb


120
20
2
Height (cm)
L
M
O
N
0
0.5
1.0
1.5
VPD, mb

and Brochu (1969). Their method yields much higher values than the direct calculation. For Trail Ridge data

$$c = 0.209 \frac{f}{T} \qquad \text{(Eq. 7)}$$

where c is VPD calculated directly; f is the VPD derived from relative humidity corrected for altitude using the Williams and Brochu nomogram; and T is dry bulb temperature (°C). Since Williams and Brochu make no allowance for pressures other than 1 atm, calculation with altitude correction is preferable for describing VPD in high mountain areas. Calculations not corrected for altitude in this fashion, however, yield Trail Ridge VPDs most frequently between 8 and 20 mb, making this site comparable to other southern Rocky Mountain areas.

F. Soil Moisture

Average gravimetric soil moisture on Trail Ridge during July and August, 1970, was 44%. This is about 14% higher than on Niwot Ridge, although minima in the two locations are comparable (Marr et al., 1967b). Measurements of soil water potentials (Ψ_{soil}) in 1971 (Fig. 16) showed great variation at 2 cm where values below -40 bars were common, but highs of 0 to -5 bars occurred after rain. At 10 cm depth, Ψ_{soil} varied between -27 and -1.7 bars. Ψ_{soil} was above -20 bars only occasionally at 2 cm but fairly consistently at 10 cm depth during at least a portion of most days.

On a summer day Ψ_{soil} drops sharply during the day, rises abruptly for a short period after a rainstorm, then drops again (Fig. 17). During the night, Ψ_{soil} rises to levels very near those of early morning of the previous day. Reasons for this rise at night are not

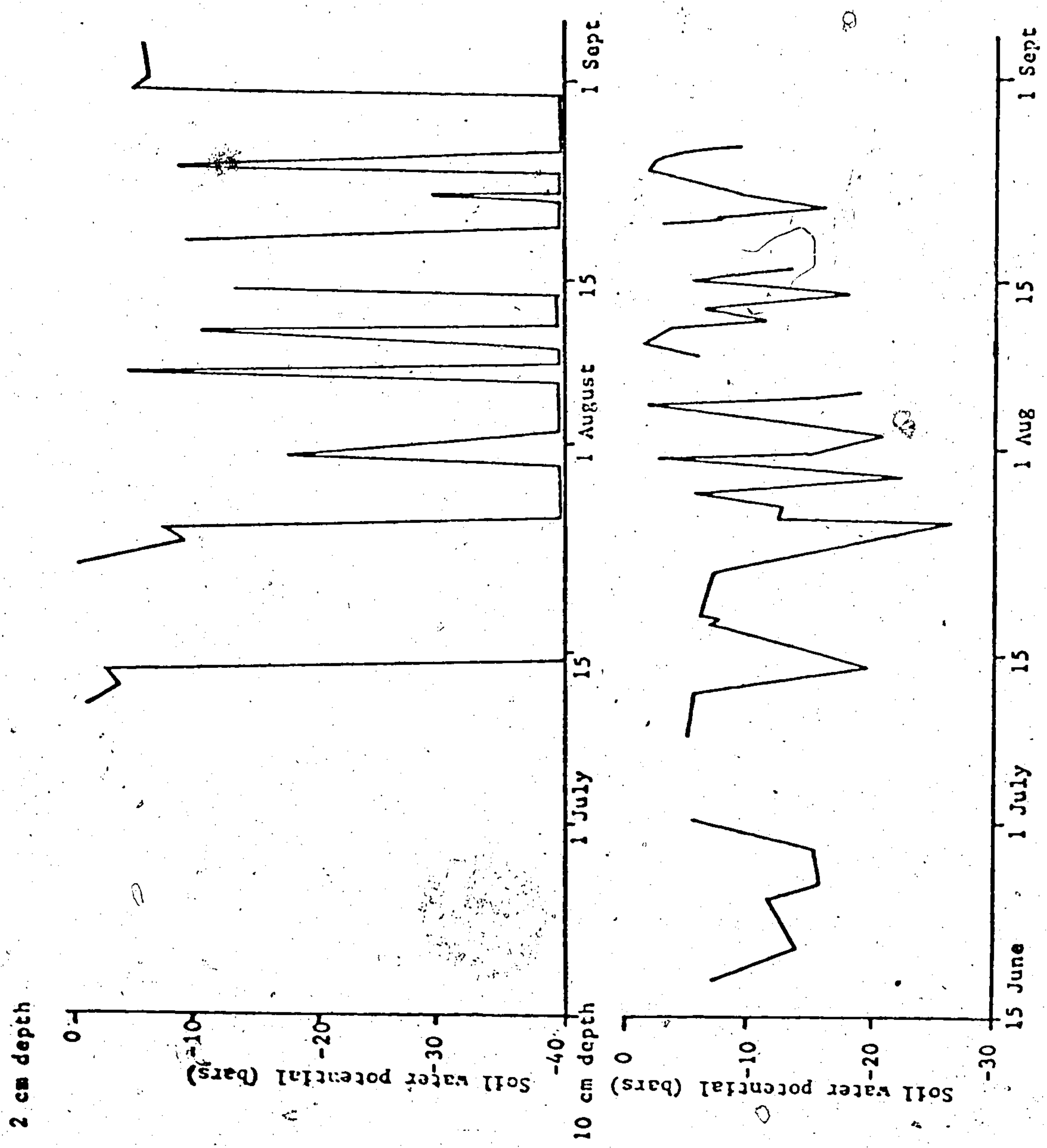


Fig.16. Soil water potentials at 2 and 10 cm depths in a kobresia meadow, summer, 1971. All readings were made before 10:30, and those below -40 bars are indicated as equal to -40 bars.

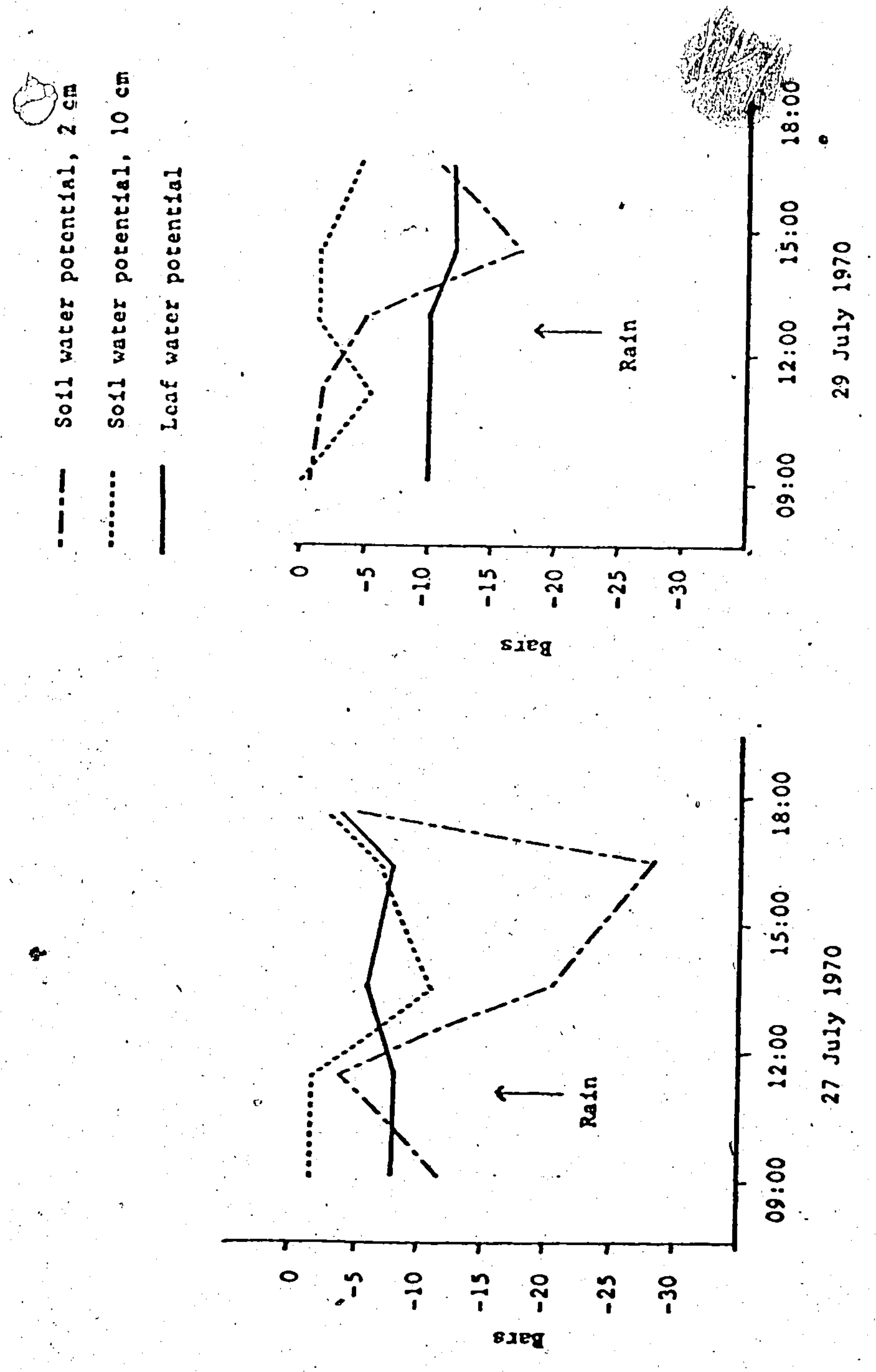


Fig. 17. Changes in soil water potentials in a kobresia meadow at 2 and 10 cm depth and leaf water potentials of undisturbed kobresia over two summer days.

known, but it could result from movement of water along temperature gradients (Taylor, 1962).

Low soil moisture on Trail Ridge is typical of Rocky Mountain alpine areas. Bliss (1966) and Johnson and Billings (1962) report soil moistures lower than -15 bars in exposed sites. Soil drying is even more extreme in the Olympic Range where Peterson (1971) found Ψ_{soil} minima between -20 and -40 bars on a ridge-top. Klikoff (1965) reports no soil moistures below -15 bars in an exposed site of the Sierra Nevada. Mt. Washington, with high precipitation, also rarely drops below -15 atm (Bliss, 1966). Patterns of intense diurnal change in Ψ_{soil} have not been reported elsewhere. Daily changes in other ranges reflect extended periods without precipitation as in the Sierra Nevada (Klikoff, 1965) or consistently wet weather as in the Presidential Range (Bliss, 1966).

Winter soil water potential readings (Fig. 18) were calculated in the same manner as those of summer. Use of this formula rests on assumptions which are rather dubious: (1) that the cooling cycle of the Wescor-Keithley meter is actually producing adequate condensation (more likely frost formation) on the psychrometric thermocouple; (2) that at the conclusion of the cooling period, the rate of sublimation is rapid enough to yield readings within a few minutes; (3) that the ceramic cup acts in frozen soil as it does in non-frozen (Formation of an ice coat was seen on one sensor at another location; though the ceramic appeared ice-free in the kobresia meadow, ice within pores might not be visible. This would prevent proper equilibration with soil vapor pressures, and readings could indicate only the vapor pressure over ice at the sensor temperature.);

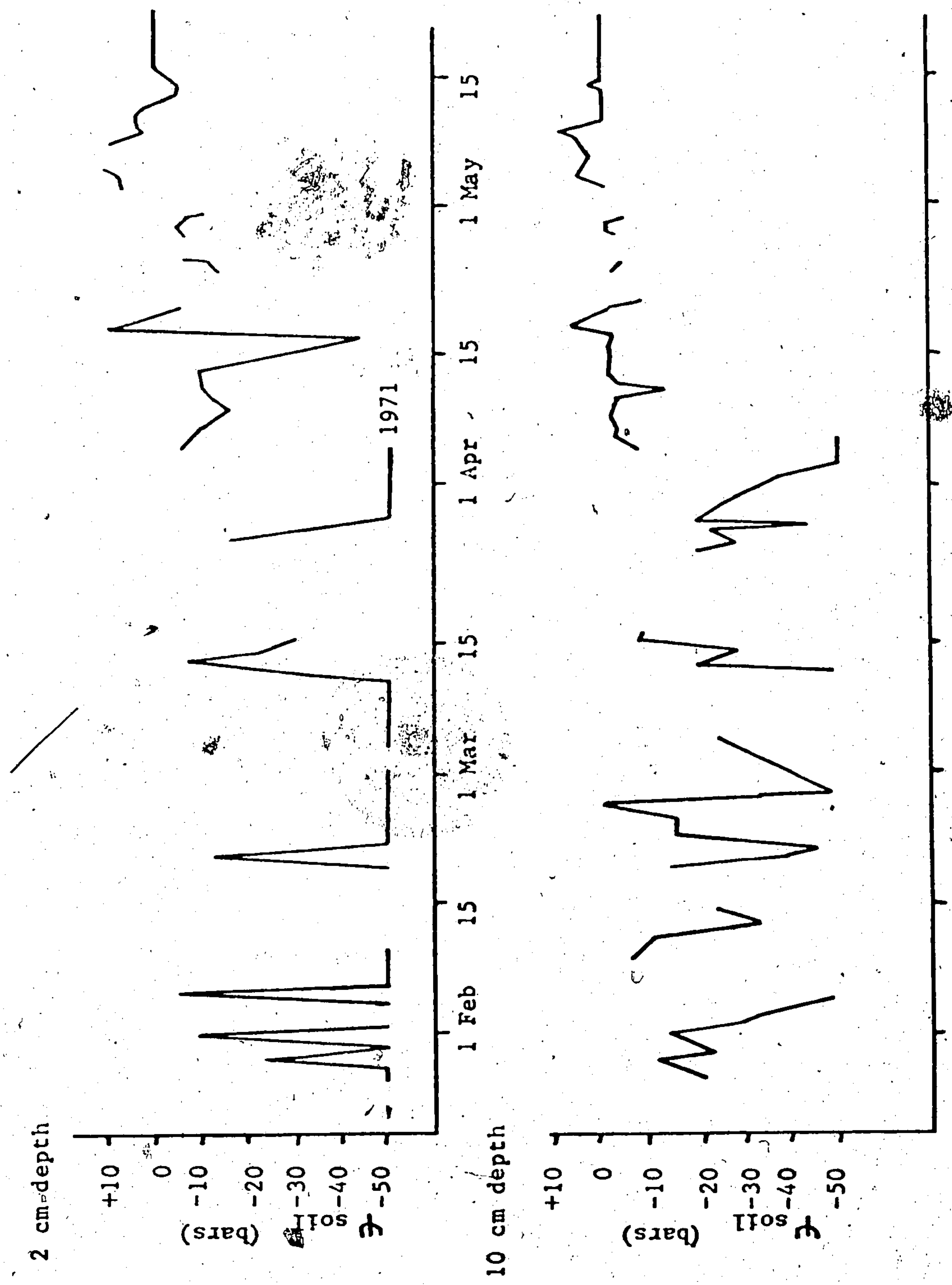


Fig. 18. Soil water potentials at 2 and 10 cm depths in winter, 1971, and spring, 1972. Readings below -50 bars are treated as equal to -50.

(4) that latent heat of fusion will not be reflected in meter readings.

Given these reservations, the winter and spring readings show some surprisingly credible values. Those with very low Ψ_{soil} in deeply frozen soil are reasonable, although they may only reflect instrument failure. The readings at temperatures approaching the freezing point could be accurately showing partial thawing of the soil solution with some freezing point depression. Readings of 0 bars during May were made in soil that was thawed and under water, a plausible measurement. Positive soil water potentials, however, are quite suspect. Mr. Eric Campbell of Wescor, Inc. has suggested (pers. comm.) that they result from resistance heating of lead wires during an extended cooling phase and should, therefore, be discarded. There remains a fairly large group of readings taken at temperatures considerably below 0° with Ψ_{soil} values between -5 and -25 bars. These readings, if accurate, are interesting in that they may represent water (or vapor) available to plants from the soil. Van Haveran (paper presented to the Symposium on Thermocouple Psychrometers: Theory and Applications to Water Relations Research, March, 1971, Logan, Utah) suggests that thermocouple psychrometers of the kind used on Trail Ridge produce accurate measurements at least to -5.5°. There were some indications that thermocouple psychrometers were working normally during alpine winter use. The cooling period required was 30 to 60 sec, 3 to 6 times longer than that used in summer. In addition, the sensor covered with ice gave readings much higher than others not so coated. Water potentials of frozen soils have not been reported for other alpine areas, so these measurements cannot be substantiated through comparisons with other work.

Soil thawing at the surface occurs occasionally through the winter. A comparison of Ψ_{soil} at 2 cm and 10 cm indicates that thawing is probably relatively unimportant as a potential winter water source for plants. At 2 cm, Ψ_{soil} tended to remain below −50 bars. The soil surface thawed on 5 days between 26 January and 1 April 1971. These were days with dry, windy chinook conditions. Even then, Ψ_{soil} was close to −50 bars. The consistently higher 10 cm Ψ_{soil} despite low temperatures appreas to offer more readily available moisture than the uppermost soil layers.

Melting became important in early May, 1972. During the month, high Ψ_{soil} was measured under melting snow. The meadow remained inundated with meltwater until about 17 June 1971 and 25 May 1972. These saturated meadows at about 0° had soil water potentials near 0 bars.

Conclusions

The environment of a kobresia meadow is characterized by rapid change. Some of this variation is evident in parameters measured on Niwot Ridge, Berthoud Pass, and in this study. Instrument shelter records, however, do not define the environment at plant levels. The description of the kobresia microenvironment obtained through repeated spot readings suggests that the following should be considered in an attempt to draw conclusions about the plant environment from the normal sorts of environmental recordings:

1. Temperature, VPD, and windspeed at plant level are not directly

related to temperature, humidity and wind at 1 or 2 m above the ground surface. Other factors such as radiation, snow cover, and interaction of these factors modify the tussock environment.

2. Rates of change over time are not the same over a distance of 2 vertical meters. In the case of temperature and VPD, changes occur most rapidly near the soil surface; wind is most stable near the ground.

3. While actual conditions around plants at any time may be difficult to predict, their ranges and variability can perhaps be defined. Individual parameters show the following characteristics:

A. Solar radiation. Frequency of variation is greatest in summer with intermediate cycle frequency in fall and spring. Magnitude of variation in summer is about 8 to 10 times greater than in winter.

B. Wind. Among profiles examined those of wind seem to be most predictable. Changes in profiles curves with the season have been moted; and while factors which control the curve shape cannot be positively identified, an empirical distinction between seasons has been made. The presence of snow in winter must be considered in relating surface winds to those above. Variation in windspeed is least near the soil surface and variability increases with increasing speed.

C. Temperature. At 120 cm, frequency of cyclic variation is greater in summer than in winter. Differences within a profile from 1 to 120 cm above the soil are greatest in summer. The most rapid temperature variation occurs at the soil surface in early afternoon in summer. Rapidity of solar radiation cycles, history of the temperature profile be considered in predicting summer temperature around plants. Winter temperature profiles show less differentiation and less rapid change because of lower frequency and amplitude in solar radiation cycles, frequent high winds mixing the air, and the presence at times of snow cover. Spring profiles are less variable than those of summer because of the presence of snow or meltwater.

D. Vapor pressure deficit. Summer profiles tend to be relatively uniform. Variation is greatest near the soil surface. Gradient reversals occur both with a dirunal pattern and in short-term cycles during periods of maximum radiation variation on partly cloudy summer afternoons. Frequency of snort-term cycles cannot be estimated from data obtained, but their amplitude is slight, rarely exceeding 1.5 mb.

E. Soil moisture. At all, seasons, Ψ_{soil} variation has greater amplitude at 2 cm than at 10 cm. Diurnal fluctuations occur at both levels, as well as longer range ones determined by precipitation in summer and precipitation and temperature in winter. Summer Ψ_{soil} at 2 cm frequently is below -40 bars, while that at 10 cm tends to remain between -5 and -15 bars. Winter soil melting gives brief and occasionally high Ψ_{soil} at 2 cm, but values otherwise are below -50 bars. At 10 cm, some moisture may be available throughout much of the winter since Ψ_{soil} values of -10 to -25 bars were measured regularly. During melting in spring, soil water potentials remain constant near 0 bars.

4. Because of the varying conditions, environmental extremes in the kobresia microenvironment may be expected to be quite different from those 1 or 2 m above. Some idea of these extremes, however, may be derived from profiles measured under extreme conditions. For

example, at high air temperatures of 16 to 18°, soil surface temperatures are much higher, often 35 to 40°. On the other hand, surface lows in winter do not tend to be so far removed from low air temperatures above.

The examination of the environment around a kobresia tussock suggests both features that are potentially harmful and others that offer advantages to plants. In summer, temperatures around plants are often higher than the air at 1 or 2 m, but are only briefly lower. Rapid temperature fluctuations in summer might be deleterious if plant leaves have low heat transfer capacities. Movement of water caused in part by temperature gradients could result in excessive loss from leaves. Warm temperatures near the soil may begin as early as the first of April, allowing some extension of the growing season if plants can tolerate later frosts. When meadows are inundated, plants are not subjected to temperatures much below 0°, even when air temperature drops. On the other hand, winter temperatures are low because surface warming is minimal; thus a high degree of frost hardiness or bud protection is advantageous. Soil moisture is not excessively low, and vapor pressure deficits are relatively high. Wind at the level of the plants is usually light in summer, much stronger in winter.

Plant adaptations to the kobresia microenvironment may include an ability to tolerate rapid temperature change in summer and low winter temperatures. Plants should be able to function normally in 0.3 to 0.4 m sec^{-1} wind in summer and be unharmed by gusts up to 5 m sec^{-1} in winter. They should not be permanently injured by summer soil water potentials between -15 and -25 bars, and ability to photosynthesize under such conditions would be advantageous. An ability to take up water in very cold soils could reduce the possibility of winter drought damage and permit early spring growth, thereby lengthening the growing season.

IV. BEHAVIOR OF UNDISTURBED KOBRESIA

Introduction

Within the microclimate of a kobresia meadow described above, a number of factors appear to be potentially limiting to plant growth. A plant living in such a habitat might be expected to have a variety of adaptations to permit survival under some of the extreme conditions encountered. Previously *Kobresia bellardii* has received virtually no physiological study which would permit an assessment of its adaptations to its restricted habitat. Thus this study included examination of aspects of normal kobresia behavior so that adaptive characteristics could be identified.

Methods

Seed germination

Inflorescences were collected within 5 days after the beginning of seed dispersal at collection sites adjacent to the kobresia meadow transplant site and above Upper Hidden Valley. These were air-dried under field conditions. Harvested seeds were placed in small nylon bags among kobresia tussocks in early September, 1971. Samples were placed under small rocks to discourage marmot disturbance. Seeds used for laboratory examinations of germination were stored at -7, +5 and +25°C. Viability tests were made using 0.1% solutions of 2,4,5-triphenyltetrazolium chloride. Gibberellic acid (GA_3) solutions of various strengths were used in an attempt to break dormancy. Germination and viability tests were made with 25 seeds in tests replicated once or twice.

Leaf lengths

Leaf lengths were measured at 1 to 3 wk intervals beginning January, 1971. Length was measured between the top of tightly packed dead leaf sheaths which form a well-defined base in the tussock and the clearly delineated top of the green portion of the leaf. Twenty leaves were measured on both the windward and leeward sides of each tussock.

Tetrazolium response

Reaction time with 0.1% solutions of 2,4,5-triphenyltetrazolium chloride was measured at 2 wk intervals in winter and spring and 3 times each summer. Tests had 1 or 2 replicates. In winter, leaf material had sufficiently little pigmentation to allow a response to be seen throughout the leaf, but roots had to be sectioned for reaction color to be visible. In summer, root reactions could be seen in young roots without sectioning.

Leaf water potentials

Determinations of leaf water potentials were done with 2 methods which yielded very similar results in simultaneous tests. In summer, 1970 and winter 1971, the Schardakov dye method (Barrs, 1968) was done with sucrose solutions. In summer, leaves were placed in sucrose solutions immediately after collection, and equilibration reached in 4 to 5 hr. Most winter tests were made by packing leaves in snow at the time of collection and holding them frozen for about an hour (occasionally as long as 3 hr). They were taken indoors, wiped free of snow and green leaf portions placed in solutions. As indoor temperatures were usually well below 0°, little warming occurred during these processes. Equilibration in winter was exceedingly slow, requiring 6 to 12 hr, the longer times being used when solution temperatures were below -4°. Solution freezing point depression was sometimes adequate to prevent ice formation. Frozen samples were discarded. Final solution density determinations were mostly done at -2 to +5°. Considerable care was necessary to assure that test and stock solutions were not at different temperatures because of handling.

In summer, 1971, and spring, 1972, leaf water potentials were measured with a psychrometric sample chamber (Wescor) and Keithley-Wescor psychrometric microvoltmeter. In summer equilibration time was 30 min; at cooler spring temperature, up to 1.5 hr. During equilibration the chamber was kept in field conditions in an insulated box.

In all cases, leaf water potential was determined using portions of several leaves in each test. Only green, or in winter yellow, leaf tissue was used with approximately equal amounts taken from leaves developed in the current year or previous summer and leaves older than one year.

Leaf surface temperature

At the time temperature profiles were measured, leaf surface temperatures were also determined with the same 20 mil thermocouple. A cluster of 12 to 15 leaves was wrapped tightly around the thermocouple and held by hand while temperature was read within 5 sec.

Carbohydrate determinations

Samples were taken of green shoot material and of roots attached to these. Leaves and roots were separated and cleaned. Samples collected in summer, 1970, were boiled for 15 min in 85% ethanol with a small amount of $NaCO_3$, then stored for analysis within 6 months. Those collected after September, 1970, received similar treatment except that the boiling was omitted. Determinations of alcohol soluble reducing sugars were made with the method of Somogyi (1945). Oligosaccharides were measured using the same method following mild acid hydrolysis, boiling with 2N HCl for 20 min. Starch concentration was determined by hydrolysis of alcohol insoluble material with α-amylase followed by reducing sugar determinations with the modified Somogyi and Nelson test. Dry weight was determined using alcohol insoluble materials.

Results

Seed germination

As in earlier studies (Sorensen, 1941; Amen, pers. comm.) kobresia seeds showed a deep dormancy which has not been broken. Germination tests were made within 2 wks of collection. Seeds did not germinate in 3 wks at field temperatures or at 22°. Later germination tests with seeds subjected to scarification, leeching, removal of the seed coat, storage for 1 yr at 5°, and a variety of temperatures during germination tests also failed. Treatment with gibberellic acid ($3X10^{-5}M$) solutions had no effect. Seeds left over winter in the Tombstone Ridge kobresia meadow in September, 1971, did not germinate in 1972. Repeated searches for germinating seeds were made in and around kobresia tussocks on Trail Ridge and a number of other alpine ridges nearby. About 200 seeds identified as kobresia by the persistent split perigynium were found, but none had germinated.

A large fraction of seed collected had apparently incompletely developed embryos. In 1970 and 1971 respectively, 72 and 52% of seeds had abnormally small embryos which deliquesced upon imbibition. These embryos were in seeds of normal size.

Viability tests were made with a 0.1% 2,4,5-triphenyltetrazolium chloride solution. Seeds yielded very faintly positive tests on the embryos only after extended periods of immersion in tetrazolium. Neither the degree of coloration nor the speed of reaction were affected by the same treatments used in germination tests. All treatments began to yield the slightly positive tests only after a minimum of 4.5 hr and maximum coloration required 21 hr at both 5 and 25°. (Avena embryos became pink in 10 min when placed in the same solution.)

The lack of germinability appears related to weak viability. The faintness of response to tetrazolium suggests a very low oxidative reduction rate, sufficiently low so that germination might well be unlikely. Failure to carry out respiration does not appear related to a gibberellin-regulated hormonal inhibition. A high frequency of clearly immature embryos suggests that embryos in all seeds tested may be immature at dispersal and fail to after-ripen.

Support for this hypothesis is seen in the failure of germination under natural conditions.

Phenology

Kobresia is a sedge having filiform leaves clustered in a dense tussock. The leaves are sheathed at the base. After the death of the leaf, its sheath remains intact and becomes a part of the mass of tightly packed sheaths which partially protects the base of the leaves. Over the long lifespan of tussocks, this base accumulates to thicknesses up to 5 cm, and the boundary with the soil under the tussock becomes increasingly difficult to distinguish. The gradual accretion of leaf sheaths often raises the tussock slightly above the surrounding soil, increasing exposure on the windward side and protection of the lee.

The pattern of development observed resembles that described by Sørensen (1941) for Kobresia bellardii in Greenland. In Colorado, a greater number of leaves are produced during the life of an individual tiller. For 3 yrs a typical tiller produces 2 new leaves each fall and 2 more in early summer. In the fourth summer, it produces one or two new tillers; only about 10% produce two. In the fifth and terminal year, a single inflorescence appears and the tiller dies at the end of the summer. Leaves initiated in the fall only partially expand before the following summer. They survive 2 winters and die during their third fall. Leaves initiated in summer live through one winter and the following summer.

While tillers have a limited life-span, tussocks are very long-lived. The observation that number of tillers in a tussock increased by about 3.3% annually permits approximate aging. Tussocks with about 300-500 tillers, or 200 to 250 years old, are fairly common. Many tussocks are probably still older, but the death of tillers at their centers makes their ages uncertain.

The frost-free period of the Front Range alpine area is short, but kobresia uses a much longer portion of the year for development (Table 6). Vegetative development proceeds from late May into October; floral development [illegible] early April to mid-August. Leaves that survive the winter often have green leaf tissue above the protecting leaf sheaths. Changes in lengths of the green portion of leaves occur throughout the winter. Both die-back and elongation were observed in all months of winter field studies. Thus it appears that kobresia is active in all seasons.

A more quantitative assessment of vegetative phenology was derived from measurements of leaf lengths. Leaves on the windward side were usually shorter than those on the leeward except in mid-summer when they were statistically indistinguishable (Fig. 19). Maximum length occurred in late July, just before development of fall coloration. Lengths fluctuated throughout winter. Changes at the transplant control meadow were highly significant (Table 7). The [illegible] of changes on the leeward side was usually greater than in wind-exposed leaves. Leaf lengths varied between sites, but a comparison of the Sundance and Tombstone Ridge meadow plants shows some similarities of changes in lengths (Fig. 19).

Table 6. Dates of major phenological events in *Kobresia bellardii*, 1968-72. Observations prior to 1970, were made at 3500 m on Niwot Ridge, Boulder Co., Colorado. Later ones are based on plants in Trail Ridge kobresia meadows.

Event	1968-69	1970	1971	1972
Floral bud expansion begun	-	-	31 Mar	15 Apr
Spring leaf elongation begun	20 May-5 June 1969	-	20 May-5 June	18 May-3 June
Anthesis begun	-	10 July	8 July	3 July
Fall coloration begun	3 Aug 1969	1 Aug	4 Aug	28 July
Seed dispersal begun	-	10 Aug	11-12 Aug	6-14 Aug
Initiation of new leaves and tufts begun	-	15 Aug	17 Aug	-
Fall die-back complete	22 Oct 1968	(incomplete 23 Sept)	(incomplete 18 Sept)	-

A dash indicates lack of data.

Fig. 19. Length of green leaves in undisturbed kobresia.

A. Spring and summer, 1971, transplant control meadow.

B. Winter, 1971, and spring, 1972, transplant control meadow.

C. Winter, 1971, and spring, 1972, Sundance kobresia meadow.

Lengths in the transplant control meadow are means of 120 leaves each; in the Sundance meadow, of 200 leaves.

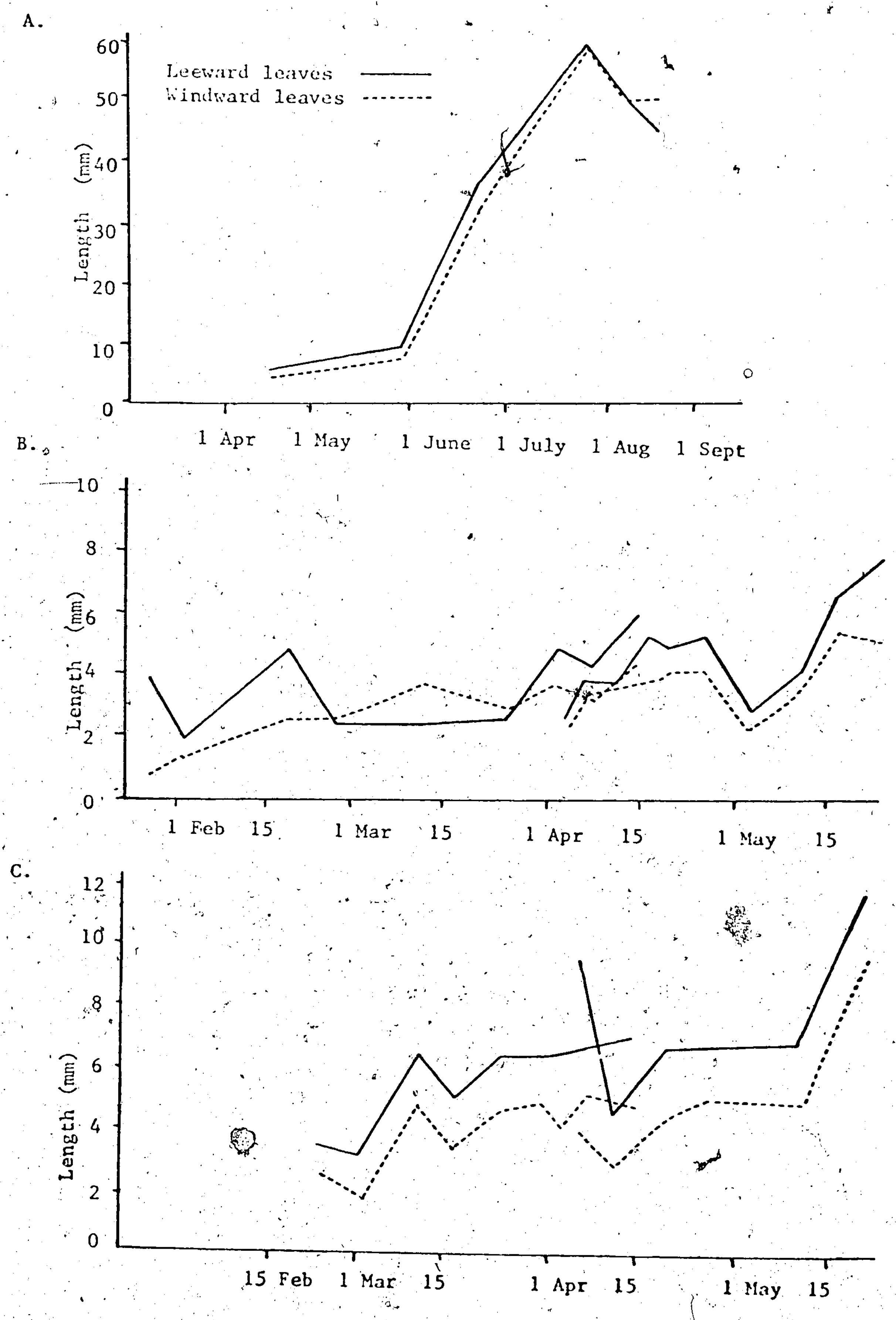

A.
Leeward leaves
Windward leaves
Length (mm)
60
50
40
30
20
10
0
1 Apr
1 May
1 June
1 July
1 Aug
1 Sept
B.
Length (mm)
10
8
6
4
2
0
1 Feb
15
1 Mar
15
1 Apr
15
1 May
15
C.
Length (mm)
12
10
8
6
4
2
0
15 Feb
1 Mar
15
1 Apr
15
1 May
15

Table 7. Significance of change in leaf length in sequential winter measurements of green leaf lengths of undisturbed kobresia.

Dates	Windward leaves		Leeward leaves	
	Change in mean leaf length (mm)	t	Change in mean leaf length (mm)	t
1971				
2 Feb. - 19 Feb.	+1.3	5.216**	+1.9	5.491**
19 Feb. - 26 Feb.	-0.1	0.565	-2.3	7.289**
26 Feb. - 12 Mar.	+1.2	5.775**	-0.1	0.388
12 Mar. - 26 Mar.	-0.8	3.079**	+0.3	1.286
26 Mar. - 3 Apr.	+1.0	3.013**	+2.3	9.943**
3 Apr. - 9 Apr.	-0.5	2.775**	-0.6	2.143*
9 Apr. - 16 Apr.	+1.2	6.910**	+1.7	6.274**
1972				
5 Apr. - 12 Apr.	+1.3	3.215**	+1.1	2.787**
12 Apr. - 18 Apr.	+0.3	1.432	+1.5	7.501**
18 Apr. - 27 Apr.	+0.3	1.502	-0.1	0.431
27 Apr. - 4 May	-2.1	8.997**	-2.1	10.543**
4 May - 12 May	+1.2	7.052**	+1.1	5.388**
12 May - 18 May	+0.9	8.518**	+2.5	10.384**
18 May - 25 May	-0.2	0.670	+1.2	2.935**

Significance at 95% indicated by *; at 99.9% by **. For all tests n = 248.

Inflorescence development

Kobresia normally produces great numbers of inflorescences on each tussock, but not all are successful in producing seeds. Some fail to set seed because of the development of the smut *Cintractia caricis*[1]. In others, apparently normal gynecia fail to produce embryos or endosperm for other unidentified reasons. Numbers, fertility, and infection differ among tussocks, between sites, and from year to year (Table 8). All these factors varied between sites in such a way that it is apparent that inflorescence density is unrelated to rates of infertility or infection. Nor is a heavy smut infection always accompanied by increased failure in seed development from other causes.

Tetrazolium response time.

Leaf reaction time varied with the season. In January and February, color first appeared at injuries in 16 hr and over the whole leaf base in 30 hr. Reaction times decreased until in April and May, injured and uninjured tissue yielded positive reactions in 1 and 4 hr respectively. Summer leaf reaction times were between 10 and 25 min.

Root reactions were much slower, averaging 2 hr in summer and 1 hr in September. Roots gave no response in winter until mid-April.

Leaf water potentials

Leaf water potentials in undisturbed kobresia varied throughout the year between 0 and -21 bars. Low potentials were observed in

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[1] Identified by James Traquair.

Table 8. Infertility associated with incomplete maturation, infection with smut and density of inflorescences in kobresia at three sites on Trail Ridge. Means and standard errors are shown for 15 to 20 tussocks at each site.

Inflorescence condition	1970	1971	1972
Percent infertile			
Tombstone Ridge	Less than 1 (est.)	3.9 ± 1.0	2.7
Sundance Mountain		11.4 ± 2.7	
Tundra Curves		8.6 ± 0.5	
Percent smut infected			
Tombstone Ridge	21.2 ± 3.2	1.3 ± 0.0	
Sundance Mountain		13.6 ± 3.0	
Tundra Curves		0.5 ± 0.2	
Floral density (inflorescences/cm^2)			
Tombstone Ridge	0.867	1.047	1.012
Sundance Mountain		1.042 ± 0.064	
Tundra Curves		0.690	

both summer and mid-winter, minima in each being between -15 and -21 bars. When plants were inundated in spring, Ψ_{leaf} rose to 0 bars, the annual minimum.

Leaf water potentials were quite uniform within the Tombstone Ridge meadow. Maximum variation between 8 plants was 2 bars in summer and 3 bars in winter. Water potentials in leaves from the Tombstone Ridge meadow and the Sundance meadow were usually within 2 bars. In July and August, old leaves consistently had water potentials 2 bars lower than young leaves.

Seasonal trends show that during snow melt in May and June, Ψ_{leaf} was quite high, falling gradually toward the end of June (Fig. 20). Through the remainder of the summer, large and sometimes rapid fluctuations were observed between minima of about -20 bars and maxima of about -5. Diurnal variation was usually 2 to 4 bars (Fig. 17). Early fall Ψ_{leaf} values were comparable to those of summer. Winter leaf water potentials were lowest in January and February, when they reached -18 to -20 bars. Potentials gradually rose until with snow melt in May, Ψ_{leaf} was 0 bars for 12 consecutive days. Winter diurnal changes of Ψ_{leaf} were small, rising 2 bars on 4 days and remaining constant (within 1 bar) on three others. The rise at midday in spring averaged 3 bars on 5 days.

Carbohydrates

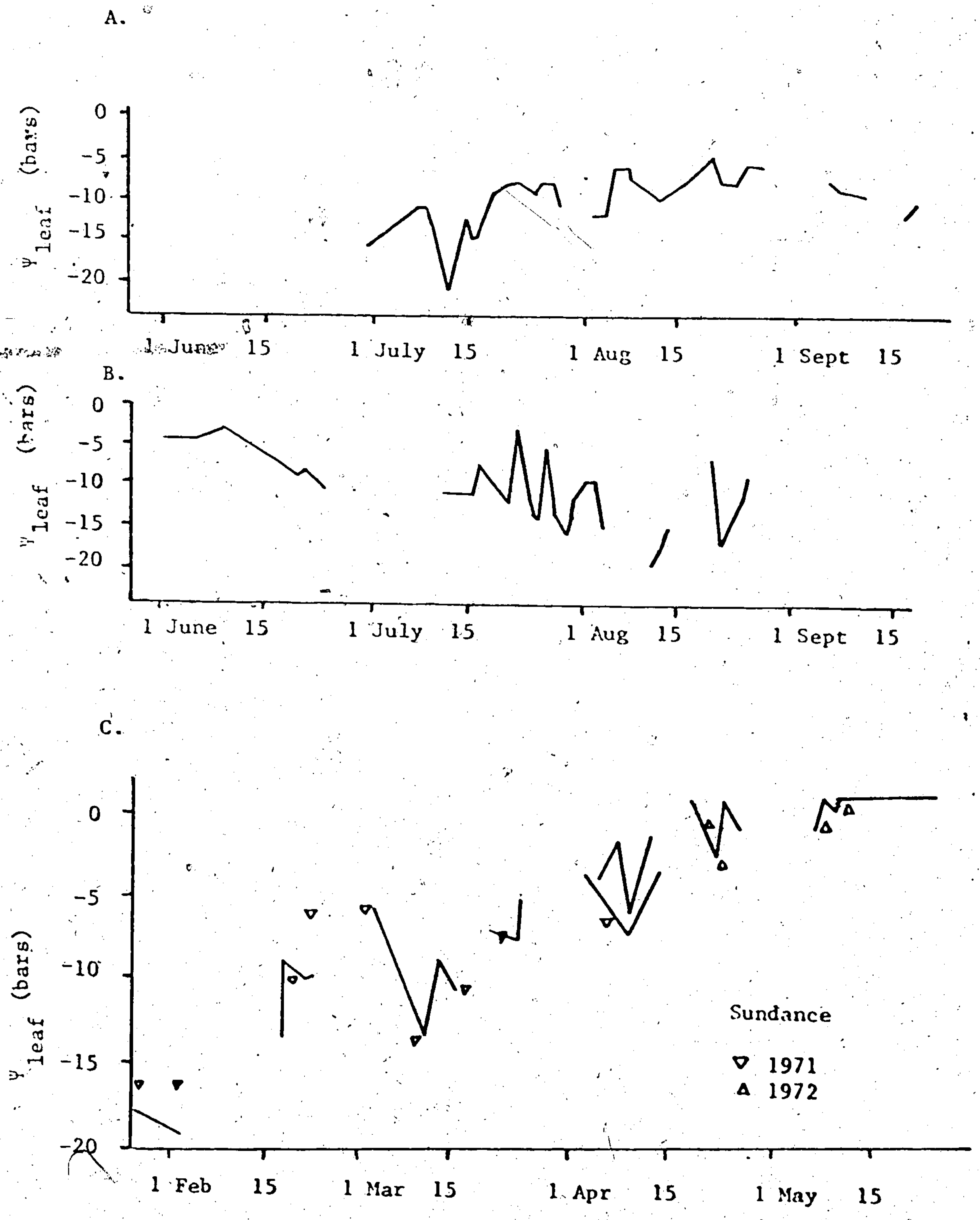
The principal carbohydrate storage products in kobresia are non-reducing, alcohol soluble sugars (presumably mostly oligosaccharides) (Fig. 21). In shoots, starch never accounts for

Fig. 20. Seasonal changes in Ψ_{leaf} of undisturbed kobresia plants. All measurements were made before 11:00 in summer and between 12:00 and 16:00 in winter.

A. Summer, 1970, transplant control kobresia meadow plants.

B. Summer, 1971, transplant control kobresia meadow plants.

C. Winter, 1971, and spring, 1972, transplant control and Sundance kobresia meadow plants.


A.
Ψleaf (bars)
0
-5
-10
-15
-20
1 June 15
1 July 15
1 Aug 15
1 Sept 15
B.
Ψleaf (bars)
0
-5
-10
-15
-20
1 June 15
1 July 15
1 Aug 15
1 Sept 15
C.
Ψleaf (bars)
0
-5
-10
-15
-20
1 Feb 15
1 Mar 15
1 Apr 15
1 May 15
Sundance
▽ 1971
△ 1972

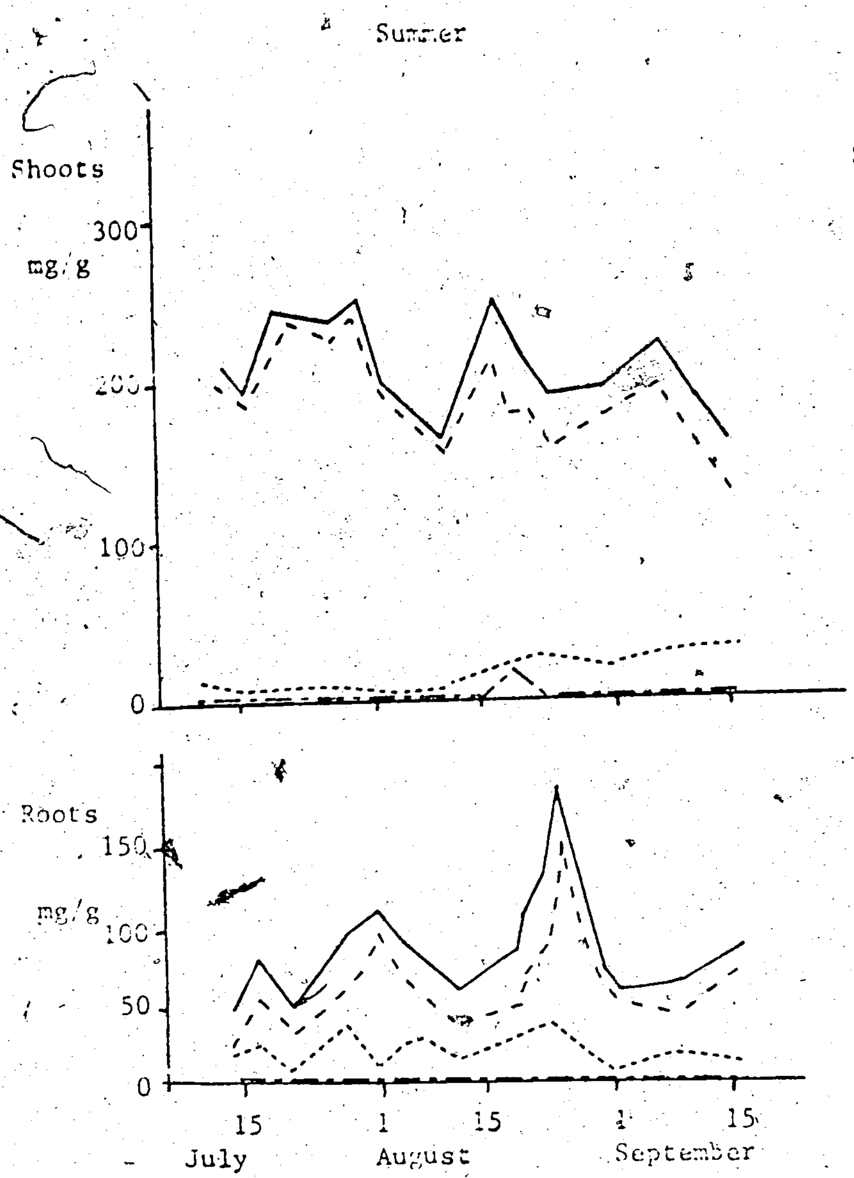
[illegible] Carbohydrate levels in kobresia roots and shoots,
[illegible]0, and winter, 1971.

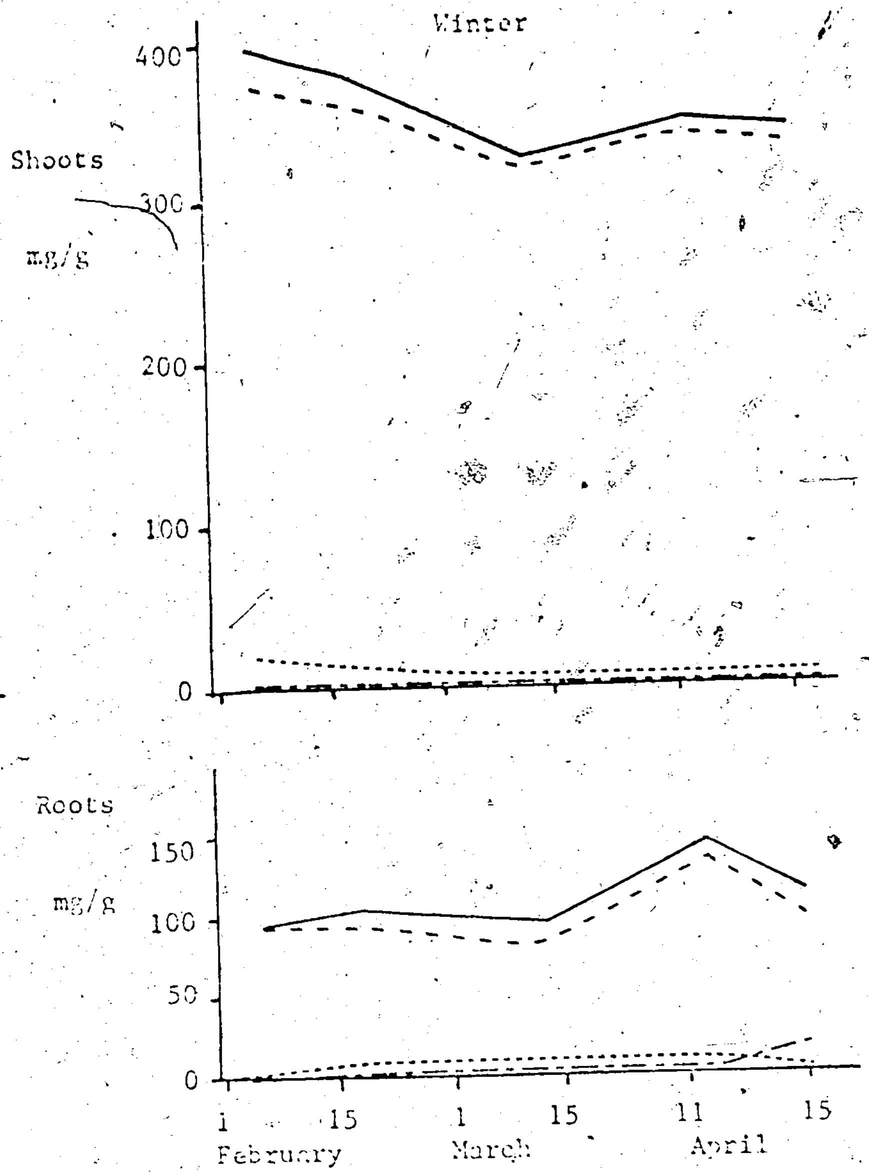
——— Total carbohydrates

- · - Oligosaccharides and non-reducing sugars

····· Starch

- - - - - - Reducing sugars


Summer
Shoots
mg/g
300
200
100
0
Roots
mg/g
150
100
50
0
15
July
1
August
15
1
September
15


Winter
Shoots
mg/g
400
300
200
100
0
Roots
mg/g
150
100
50
0
1
February
15
1
March
15
11
April
15

more than 20% of the total carbohydrate content in summer and 3% in winter. The roots have starch as an important carbohydrate component during summer, but not in winter. Sugars were almost always a very small component of dry weight; in most cases the concentration was so low that it was not detected by the test used. Total carbohydrate content was high in shoots, and much lower in roots. In summer it ranged between 15 and 25% of dry weight in shoots and 8 to 18% in roots. The rather woody character of the roots suggests a high fraction of their dry weight may be cellulose.

Carbohydrate contents appear to be intermediate between the low concentrations in other alpine monocots, Carex biglowii, C. elynoides, and Luzula spicata, and the high concentrations of various alpine dicots of Mt. Washington (Fonda and Bliss, 1966) and the Medicine Bow Range (Mooney and Billings, 1960). Kobresia differs from other alpine species reported in the relative importance of shoots as storage organs and in a high oligosaccharide content, although it is similar in the latter respect to an arctic sedge, Carex nardina (Svoboda, 1972).

Diurnal carbohydrate changes were measured on two summer days (Table 9). The first of these (17 July 1971) was a typical su[illegible] day with afternoon thunderstorms. Carbohydrates peaked in both shoots and roots at mid-day and declined in the afternoon. Near noon, relatively high concentrations of sugars suggest rapid photosynthesis and potential for translocation. On a wholly sunny day (21 July 1971) evening measurements were much higher than those in the morning in shoots. Root carbohydrate content, both

Table 9. Carbohydrate content variations in kobresia through two summer days in 1970. Afternoon cloudiness and thunderstorms occurred on 17 July; 21 July was generally clear. Total solar radiation on 17 and 21 July was 485 and 660 lys, respectively. Values represent the mean of three determinations.

Date and Time	Carbohydrates - mg/gm dry wt.							
	Shoots				Roots			
	Sugar	Oligosaccharides	Starch	Total	Sugar	Oligosaccharides	Starch	Total
17 July								
0600	1	167	10	178	0	39	18	57
1230	4	184	3	191	1	47	18	66
1800	1	180	2	186	0	42	14	57
21 July								
0500	5	170	7	186	0	41	23	64
1800	0	218	7	225	0	28	12	39

starch and oligosaccharides, declined possibly indicating use in root growth or transfer to ripening seeds.

Analysis of Results

Leaf Water Potentials

Readings of Ψ_{leaf} were frequently made simultaneously with Ψ_{soil} measurements. There was a high positive correlation (r=0.8367; n=31) between Ψ_{leaf} and Ψ_{soil} in summer. If one assumes that when Ψ_{soil} exceeds Ψ_{leaf} passive uptake of water may occur, it is clear that plants may usually obtain water (Fig. 22). In summer passive uptake was possible in 82% of measurements. One exception (Point A, Fig. 22) was a transient condition shortly after a thunderstorm. The soil was still warm and dry at 10 cm depth because the storm had been brief, but the leaves were surrounded by rapidly melting graupel. All other exceptions were in measurements made when Ψ_{soil} was less than -20 bars. These may indicate a system for maintaining Ψ_{leaf} in extremely dry soil, possibly via stomatal closure. A t-test indicates that there is a highly significant difference between Ψ_{soil}: Ψ_{leaf} ratios above and below Ψ_{soil} of -20 bars (p<99%).

Winter Ψ_{leaf}:Ψ_{soil} relationships are similar to summer (Fig. 22). When Ψ_{soil} was below -19.5 bars, Ψ_{leaf} was less than Ψ_{soil}. A condition of potential passive uptake was observed in 7 of 15 simultaneous measurements of leaf and soil water potentials in February and March. This high fraction reflects in part the relative ease of obtaining measurements during warmer weather, but still

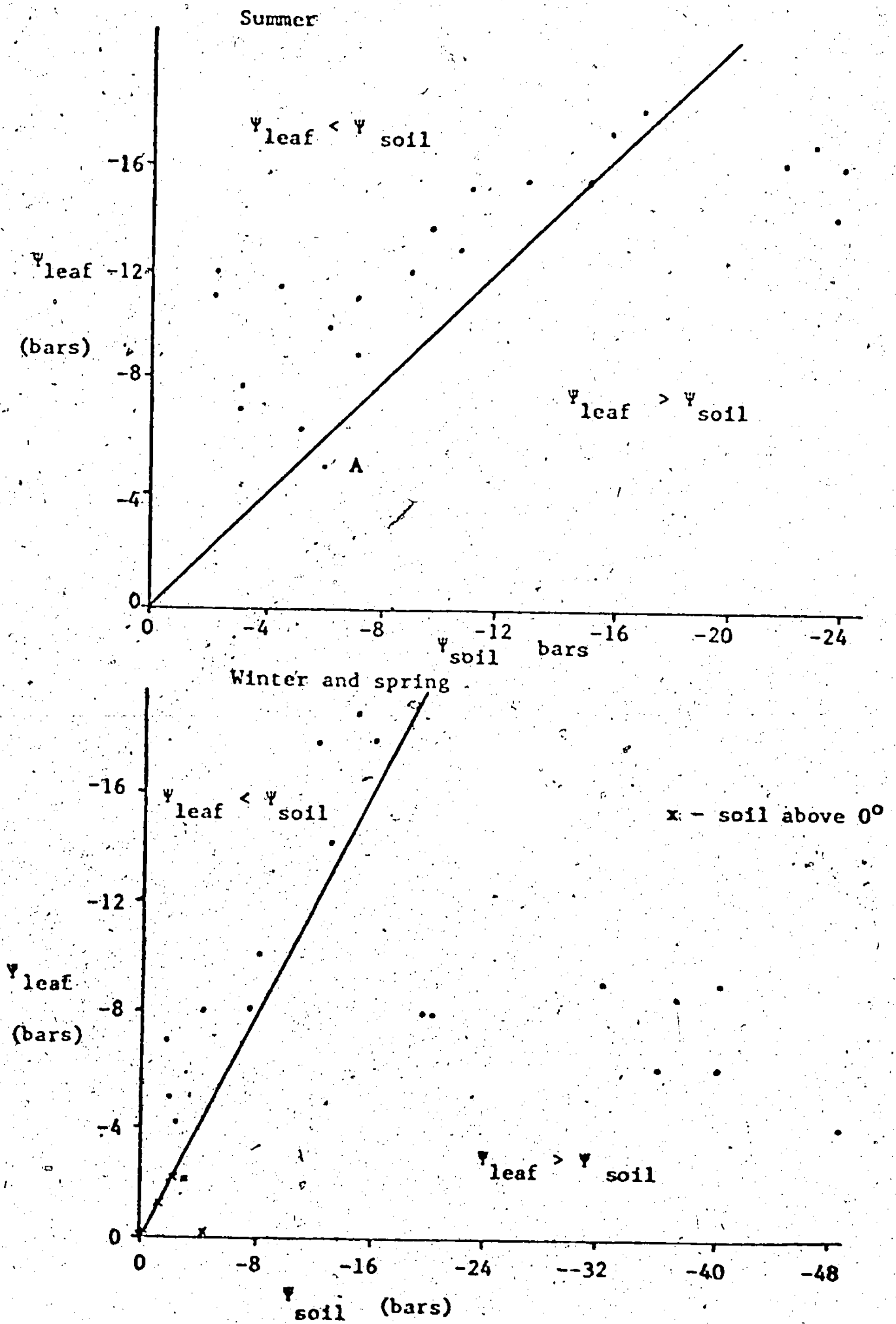


Fig. 22. Relationship of Ψ_{leaf} to Ψ_{soil} in simultaneous measurements.

indicates that passive uptake is possible during considerable portions of mid-winter.

In spring, meltwater near 0° flows over thawing soil. Leaf and soil water potentials both rise to near 0 bars. This contrasts sharply with observations of arctic species in cold soil. Haag (1972) found that Carex rariflora and Eriophorum russeolum maintained leaf water potentials about 10 bars lower than soil potentials in saturated soil slightly above 0°. Unlike these arctic species, alpine kobresia appears well adapted to water uptake from cold soils, possibly the result of lower root resistance to water movement.

Leaf surface temperatures

Leaf surface temperatures closely resembled those of the adjacent air in all seasons. These temperatures were measured with a 20 mil thermocouple, but the thermocouple did not appear to conduct heat. Twelve pairs of readings revealed no significant differences in measurements made with the 20 mil thermocouple and those with a 3 mil sensor (t=0.241 in summer and t=1.022 in winter).

The correlation of leaf surface temperature to air temperature at 2 cm was very highly significant in summer (r=0.970; n=157), winter (r=0.966; n=47), and spring (r=0.958; n=49). Of 100 samples in summer, 75 were within 1° of equality between leaf and air; maximum difference was 2.8°. When differences exceeded 1°, leaf temperature was almost as frequently below as above ambient.

During periods of rapid air temperature change in summer afternoons, leaf temperatures varied a little more than the adjacent air (std. deviation in 30 consecutive measurements at 2 min intervals at 2 cm = 2.18; at leaf surfaces, 2.32 in five variation profiles). This difference was significant ($p > 95\%$).

Salisbury and Spomer (1968), Courtin (1968), and Peterson (1971) have all reported temperatures of leaves in alpine plants exceeding ambient. Kobresia does not follow this trend, despite environmental conditions very similar to those described by Salisbury and Spomer. Leaf temperatures coupled to ambient have also been observed in Carex biglowii on Mt. Washington, but only when wind exceeded 5 m/sec (Courtin, 1968). Except for these two sedges, alpine plants observed previously have been either broadleaved or cushion plants. Gates (1968) states that small leaf size and exposure to wind are highly influential in allowing leaf temperatures to remain near ambient, despite radiation and transpiration conditions. Kobresia leaves are very narrow (less than 2 mm wide), are exposed to high windspeeds despite the shortness of the plant, and have a low angle of solar incidence at midday. All these may play a role in preventing the warming of leaves observed in other alpine species.

Carbohydrates

Factors controlling carbohydrate levels are complex, and might be expected to include solar radiation, temperature, wind, Ψ_{soil}, and the developmental state of the plant. All except the last can be described quantitatively. A statistical comparison of environment characteristics with carbohydrate level changes revealed no significant correlations in either summer or winter. It appears, therefore, that phenological conditions, which cannot be quantified should also be considered. Such an analysis is somewhat subjective, but it does permit suggestions of mechanisms influencing carbohydrate levels.

Carbohydrate concentrations generally rose in July, 1970, but fell in early August during a period of low solar radiation and seed dispersal. Following this, first shoot, then root, carbohydrate levels rose as new shoots and roots developed in early fall. When snow covered the plants through most of the period 3 to 14 September, there was a slight increase in root carbohydrate content, but a decrease in the shoots. A comparison of September and February carbohydrate levels suggests that fall die-back involves little change in roots, but a strong concentration of carbohydrates in the portions of shoots which will remain green over winter. Plants under snow gave no indication of carrying out such processes in September. Carbohydrate concentration must have occurred in late September and early October. This corresponds well with the observation that fall die-back did not appear to be complete until late October in 1968. Thus, presence of a prolonged heavy snow cover in September and October appears deleterious by preventing proper onset of winter carbohydrate status.

In winter, carbohydrate content declined in leaves through the period February through mid-March, during which winds were strong and temperatures low. Amelioration of the environment in late March permitted a renewal of reserves simultaneously with leaf elongation. The rise in root carbohydrate levels after mid-March occurred in frozen soil.

The high winter concentrations of carbohydrates, especially oligosaccharides, suggests that their levels may be associated with frost hardening. High concentrations of sugars, especially sucrose, have been observed to be associated with frost hardiness in a large number of species (Mazur, 1969; Levitt, 1972). Failure to build up adequate concentrations of sucrose, or some other low molecular weight saccharides, might be expected to prevent adequate hardening.

Use of shoots as storage organs may facilitate spring development by obviating the need for translocation from roots in frozen soil. Tieszen (1972) suggests that any such means of lengthening the growing season has great advantage for a tundra plant species.

Leaf lengths

Winter and early spring leaf lengths appear determined by a complex of environmental conditions. The single most important factor in determining change in leaf length is mean windspeed (r= -0.5218 for windward leaves; -0.6643 for leeward; n=18). While correlation with temperature alone is insignificant, a combined temperature-wind factor yields a better correlation than wind alone. As an example, correlation with Siple's windchill index, a factor based on rate of heat loss as a function of both temperature and wind (Siple and Passel, 1945), was -0.7164 for windward leaves, -0.6718 for leeward. Leaf length changes were usually measured over weekly periods or longer. Changes over 3.5 days measured in April, 1972, were not as well correlated with either wind or wind-temperature as were weekly changes. For example, wind and wind-temperature were related to changes in windward leaves by r= -0.461 and -0.512 respectively for 3.5 day intervals. Weekly changes during thise period, however, could be relat[illegible] these factors about as well as in other winter months. Thi[illegible]sts that, while these factors are important in determining leaf length, more than 3 days are required for leaves to come into equilibrium with changes in the average environment.

More difficult to assess is the role of Ψ_{soil} in influencing leaf length. Since Ψ_{leaf} and Ψ_{soil} were measured intermittently, no means can reasonably be calculated. Leaf length change is, however, fairly closely correlated with estimated 7-day mean noon Ψ_{leaf} ($r=0.7855$ for windward leaves, 0.5198 for leeward). This Ψ_{leaf} has been shown to be highly dependent on Ψ_{soil} when the latter exceeds -20 bars. When Ψ_{soil} dropped below -20 bars and remained there, leaf lengths decreased or remained unchanged (e.g. in early April, 1971, Fig. 26). Direct correlation is impossible because of lack of continuous readings, but it may be reasonable to hypothesize that elongation occurs only when Ψ_{soil} rises above -20 bars at some time during a 7 day period. Rate and extent of elongation and die-back would be determined by wind and to a lesser extent by temperature.

This model, developed by statistical considerations, seems plausible for biological reasons. Water uptake appears to occur even in frozen soil. Periods of uptake combined with efficient prevention of transpiration might result in restoration and maintenance of turgor even through subsequent periods of stress. Strong winds would increase rate of water loss and lower respiration rates. All metabolic and physical actions would be expected to be low in lower temperatures. Thus, some uptake would be necessary, but not sufficient, for elongation. By reducing heating near the surface, wind would affect rates of physical and biochemical activities. Mean thickness of the tussock boundary layer might determine maximum potential winter-green leaf length. The system would be dynamic and would require considerable controlled environment study for verification of the model.

Summary

Undisturbed kobresia was examined both as a control for studies of the species' behavior in non-normal habitats and for development of a model of potentially limiting factors. The results suggest that undisturbed kobresia shows the following limitations in its adaptations to its customary environment:

1. The species is physiologically active through the year, so that environmental conditions could be deleterious at any season.
2. Available soil moisture may be limiting at any season. Soil water potentials less than about -20 bars consistently appear deleterious. Plants maintain Ψ_{leaf} higher than Ψ_{soil} during periods of low Ψ_{soil}, possibly by closing stomates. Decreased stomatal opening could hinder photosynthesis and thereby reduce productivity. Extreme drought in winter may produce excessive die-back, damaging leaf tissue needed in spring elongation.
3. In spring, leaf elongation occurs after an extended period during which Ψ_{soil} approaches 0 bars. While it has not been proved that this is necessary for elongation, it would seem reasonable to hypothesize that high soil moisture must precede spring growth.
4. In winter, leaf elongation and die-back provide something of an

indicator of environmental suitability. Soil water potentials below -20 bars for extended periods of time, high winds and low temperatures combine to cause die-back.

5. A long snow-free period after early September appears to be required for proper onset of normal winter carbohydrate status in shoots, a condition which may well be associated with proper frost hardiness.

6. Sexual reproduction may be reduced by failure to produce large numbers of flowers, development of a smut infection, or failure of flowers to set seed. Only smut seems to affect seed production in normal habitats, but germination studies indicate that many seeds which are dispersed are very immature and will not germinate.

V. COMPARISON OF PLANT ENVIRONMENTS IN FOUR TUNDRA MICROSITES

Introduction

Kobresia tends to be restricted to a specialized microenvironment characterized by the presence of microdrifts through much of the winter. Marr (1967b) has demonstrated differences in wind, temperature, soil moisture and snow depth between a kobresia meadow and other alpine sites on Niwot Ridge. He made no attempt to distinguish the nature of the environment immediately around plants. As was seen in the study of the kobresia environment, this cannot be completely predicted from the climate at 1 or 2 m height. Microclimate studies were planned to provide a description of the plant environment in four microsites used for transplant studies. These were designed to distinguish the environment of a kobresia meadow from other tundra microsites and to provide a basis for examining plant responses to these various environments.

Methods

Microclimate was examined in each of 4 sites: a fellfield, a kobresia meadow, moderate (ca. 70 cm) and deep (ca. 140 cm) snow accumulation sites. Comparisons were based on spot readings of temperature, wind, vapor pressure deficits, soil moisture, precipitation and snow depth. These were measured as in the study of the kobresia meadow microclimate. Winter temperature profiles under snow were read using fixed thermocouples with 2 m of lead wire in the snow to minimize heat conduction.

Results

Precipitation and snow cover

Slight differences appeared in summer precipitation at the 4 sites (Table 10). Variations appeared related to the extreme localization of thunderstorms and to windspeed and direction. Frontal storms yielded relatively uniform precipitation. Storms with strong westerly wind gave the heaviest rain to the kobresia meadow; easterly storms, to the fellfield. Over an entire summer, total differences between sites were about 25%; but totals for two summers were similar at all sites.

Sites had been chosen to represent varying amounts of winter snow cover. In the fellfield and kobresia meadow accumulations did not last more than 2 weeks and were only microdrifts through most of the winter period of study. The fellfield was snowfree 38% of February and March compared with 22% in the kobresia meadow. Periods of complete cover were equivalent in the two sites. Microdrifts in the fellfield site were very shallow, usually 1 to 3 cm less deep than in the meadow. Snow in the moderate and deep accumulation areas formed persistent drifts ranging from 30 to 80cm and 90 to 175 cm deep respectively (Table 10). Hoar developed at the bottom of both drifts and remained until 14 April 1971 and 8 May 19[illegible]. A hard wind crust (specific density = 0.34 - 0.42) usually covered the surfaces and 2 or 3 buried surfaces persisted. In spring, the snowbanks became saturated with meltwater except the lowest 4 to 10 cm which became layers of ice for about 4 wks. Accumulations lasted from late September to early July in the deeper snowbank and

Table 10. Rain and snow accumulations at four tundra microsites.

A. Summer (July and August) precipitation in four microsites.

Year	Total precipitation (cm) Fellfield	 Kobresia meadow	 Moderate snow	 Deep snow
1970	7.85	9.98	--	8.94
1971	9.89	7.75	7.06	7.57

B. Snow depth in four microsites, representative winter dates.

Date	Snow depth (cm) Fellfield	 Kobresia meadow	 Moderate snow	 Deep snow
1 Feb 1971	0	0	60	120
1 Mar 1971	0-2	1-5	60	120
1 Apr 1971	0	0	80	175
1 May 1972	8-12	4-14	45	110
1 June 1972	0	0	30	90

C. Duration of snow cover in four microsites.

Winter	Duration of snow cover Fellfield	 Kobresia meadow	 Moderate snow	 Deep snow
1969-70	?	?	?-28 June	?-10 July
1970-71	ephemeral	ephemeral	?-22 June	21 Sept-4 July
1971-72	ephemeral	ephemeral	?-10 June	14 Sept-23 June

probably from early October to late June in the moderate bank.

Wind

Increasing exposure from the deep snow accumulation area to the fellfield was evident at all points of wind profiles from 2 to 200 cm height (Fig. 23). At all sites summer profiles had a J-shaped curve which became less pronounced with increasing windspeed. Maximum winds at 2 cm, within the plant canopy, ranged from 0.08 m/sec in the deep snow area to 0.50 in the fellfield.

Windspeed increased in the fall at all sites, but the profile curves lost some of their summer regularity. While windspeed in the kobresia meadow and fellfield approximately tripled, it did not quite double near the surface. Thus, the fall increase may have had less effect on the plant environment than later in the winter.

In mid-winter, profile curves were quite flat, especially in the fellfield. Fellfield winds were frequently above 35 m/sec, the upper limit of accuracy for the Hastings-Raydist meter. Gusts estimated at about 50 m/sec (by extrapolation with meter readings) were not uncommon. Under such conditions, winds near the surface were also quite strong, despite the flattened profile curves. A number of gusts exceeding 7 m/sec were measured at 2 cm. In February and March, 22% of readings at 2 cm showed wind faster than 5 m/sec. These winds picked up quantities of sand and saltation often occurred.

Calmer conditions returned in April and May in both the fellfield and the kobresia meadow. The presence of wet snow in

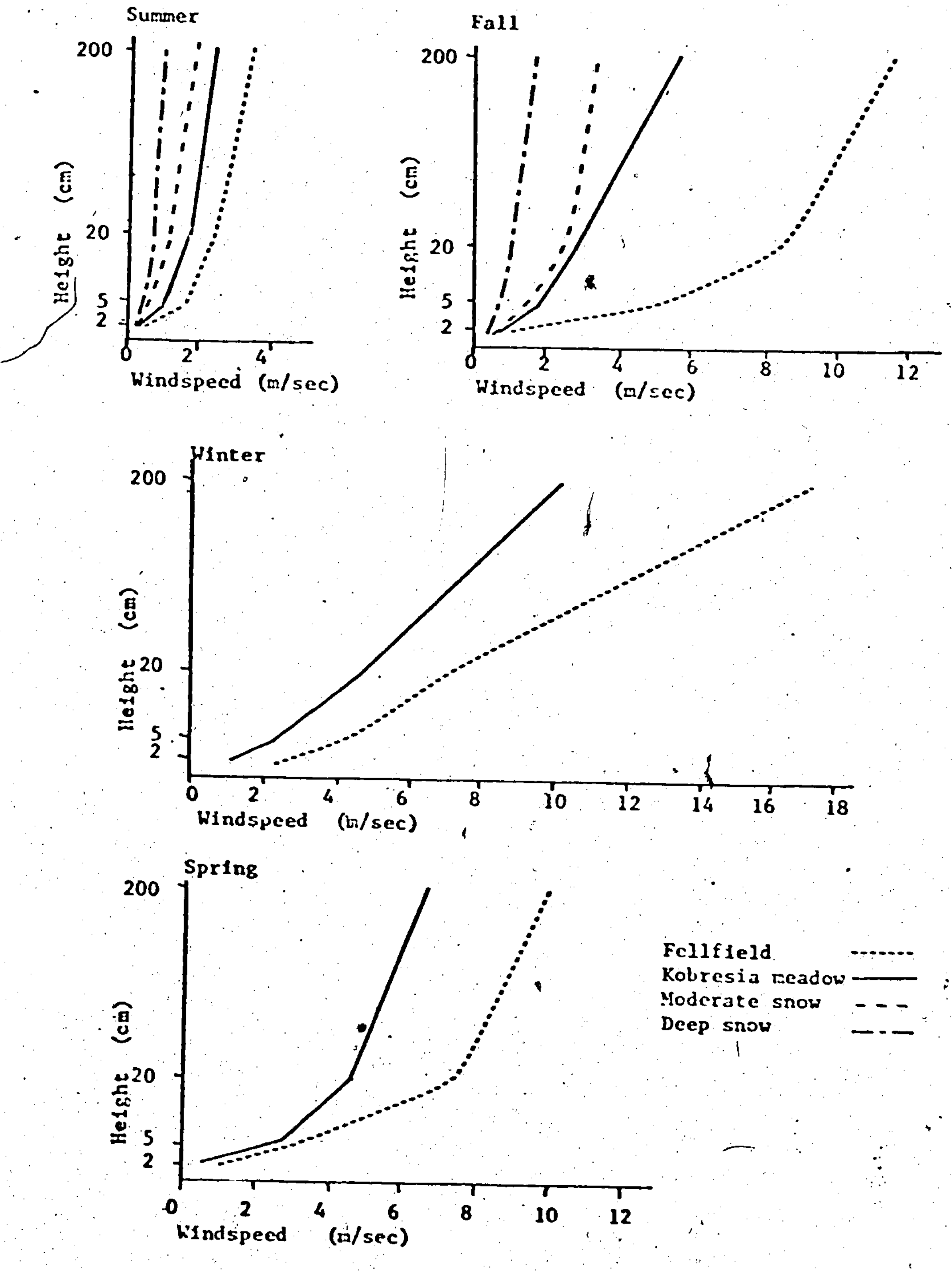


Fig. 23. Windspeed profiles, four tundra microsites in four seasons. Sample sizes: summer (July-August), 84-96; fall (September), 14; winter (January-April), 42-65; spring (May), 22.

May was partially responsible for the rapid drop of average windspeed near the surface in both the meadow and fellfield.

Temperature profiles

Temperature profiles in all four microsites resembled those of the kobresia meadow in being complex and unstable in summer. During summer the sites with less wind exposure experience the greatest heating near the soil surface and the most stable temperatures (Table 11). Variation under partly cloudy afternoon conditions was greatest in the fellfield, least in the deep snow accumulation site. Plants in the deep and moderate snow accumulation areas had early afternoon temperatures averaging 3 to 6° higher than the other sites. Heating in the morning and cooling in late afternoon were more rapid in the sheltered sites. Night profiles at all areas were uniform throughout. Thus, average daily temperatures became slightly higher with decreasing wind exposure. The one exception was that at the warmest part of the day, soil temperature was lowest in the kobresia meadow despite lower windspeed than in the fellfield. This suggests that kobresia meadow vegetation sufficiently shades the soil to keep it cooler than the bare ground surface of the fellfield.

The presence of winter snow prevented diurnal warming in the snow accumulation sites (Table 12). At least 2 days with a change of 10° from the preceding days were required to alter the temperature at the base of the moderate snowbank, and 3 or 4 days for the deeper one. In the kobresia meadow and the fellfield, temperature profiles

Table 11. Means of summer temperature profiles at four tundra microsites.

Time	Number of samples	Temperature, °C Height above soil surface, cm -1	0	2	5	20	120
Fellfield							
0800-1000	9	14.4	16.0	15.8	14.9	14.9	13.7
1000-1200	15	17.8	19.7	17.3	16.8	16.6	15.3
1200-1500	24	22.4	23.1	19.8	18.6	18.1	16.8
1500-1800	30	18.6	18.4	16.9	16.2	15.9	15.0
Kobresia meadow							
0800-1000	22	17.2	20.1	17.2	15.7	15.3	13.9
1000-1200	19	20.0	21.7	17.2	16.6	16.3	15.2
1200-1500	34	20.7	21.1	17.3	16.4	15.6	15.4
1500-1800	19	19.3	19.3	17.2	16.3	16.2	15.1
Moderate snow accumulation area							
0800-1000	9	21.2	21.6	21.9	19.1	18.1	16.6
1000-1200	18	22.9	23.7	21.1	18.8	18.0	16.6
1200-1500	18	27.9	27.6	21.2	18.6	17.7	16.3
1500-1800	27	17.9	17.9	15.0	14.6	14.6	13.9
Deep snow accumulation area							
0800-1000	7	20.0	21.5	18.1	17.2	17.6	17.7
1000-1200	20	19.8	21.7	18.6	17.3	17.0	16.1
1200-1500	19	24.0	26.6	22.4	20.2	19.1	17.4
1500-1800	29	17.7	18.1	15.9	15.1	15.0	14.6

Table 12. Means of winter temperature profiles at four tundra microsites.

Time	Number of samples	Temperature °C Height above soil surface (cm) 0	2	5	20	120
Fellfield						
0800-1200	10	-6.7	-7.5	-8.0	-8.5	-9.0
1200-1500	9	-5.9	-5.7	-6.1	-6.8	-7.0
1500-1800	10	-5.6	-5.8	-6.2	-6.3	-6.8
Kobresia meadow						
0800-1200	19	-4.4	-4.3	-5.4	-5.6	-6.2
1200-1500	10	-5.8	-7.0	-7.7	-8.1	-8.4
1500-1800	15	-5.7	-6.1	-6.7	-7.0	-7.7
Moderate snow accumulation area						
0800-1200	9	-4.5	-4.5	-4.5	-4.7	-6.1
1200-1500	8	-4.6	-4.6	-4.6	-4.9	-7.3
1500-1800	9	-4.8	-4.8	-4.7	-4.7	-5.2
Deep snow accumulation area						
0800-1200	16	-4.6	-4.5	-4.6	-4.7	-5.9
1200-1500	14	-4.5	-4.5	-4.6	-4.5	-6.2
1500-1800	17	-5.5	-5.5	-5.5	-5.2	-5.2

remained nearly uniform except in periods of deep snow. Fellfield profiles showed slightly less daily surface warming than the kobresia meadow.

Spring temperature profile characteristics were primarily a function of snow conditions. When the deep snow accumulation became saturated with meltwater temperature in the snow above 5 cm was 0° until snowmelt was complete. Below 5 cm, temperature during melting was initially near -4° and gradually rose to 0° over 24 days. Temperatures in the moderate snow accumulation area were similar except that a freeze in mid-May lowered temperature to -3° in the whole accumulation. Fellfield May snow accumulation was like that of the kobresia meadow, and there were no significant temperature differences between these two sites.

Vapor pressure deficit profiles

At 120 cm height, summer vapor pressure deficits were equal at all sites (Table 13). Nearer the soil surface, however, differences were apparent. At the plant level VPD was consistently lowest in the deep snow accumulation area. Both VPD and temperature profiles suggest a more pronounced diurnal stratification in the relatively still air of this site. The moderate snow accumulation and kobresia meadow sites both had quite uniform mean VPD profiles, but the moderate snow accumulation site never experiences the high VPD occasionally observed in the meadow. The fellfield often showed a well developed profile with the air at 2 cm having a higher mean VPD here than elsewhere. This high VPD may be related to the

Table 13. Vapor pressure deficit profiles at four tundra microsites, July and August: means with standard errors and ranges.

ite	Number of samples	Vapor pressure deficit (mb) Height above surface (cm)		
		2	20	120
Fellfield	49			
mean		2.24±0.17	2.12±0.15	1.89±0.12
range		0.32-4.95	0.55-4.13	0.59-3.93
Kobresia meadow	92			
mean		1.88±0.12	1.97±0.09	1.88±0.09
range		0.00-6.52	0.00-4.65	0.00-3.97
Moderate snow accumulation area	48			
mean		1.91±0.13	1.88±0.12	1.88±0.12
range		0.27-3.83	0.32-3.81	0.47-3.59
Deep snow accumulation area	48			
mean		1.77±0.16	2.03±0.16	1.96±0.15
range		0.00-3.91	0.00-4.00	0.00-3.96

relative dryness of the soil surface at this site.

Mean VPD values did not exceed 2.3 mb nor extremes 7.5 mb at any site. These small deficits are related to the method of calculating VPD previously discussed.

Soil Water Potentials

Summer soil moisture was lowest in the fellfield and the moderate snow accumulation site (Table 14). In these sites, the surface was primarily gravel; A horizons were lacking. This appeared to allow rapid percolation after rain and to reduce nightly upward water movement. Diurnal drops in water potential became quite severe in the fellfield where Ψ_{soil} at 10 cm dropped below -50 bars on several occasions. After such extreme drying, Ψ_{soil} rose only after a heavy rain. The deep snow accumulation area had relatively high Ψ_{soil} throughout the summer.

In winter, Ψ_{soil} was constantly very low under snow accumulations (Table 14). Unlike in snowfree areas, Ψ_{soil} never rose above -20 bars before the end of April in either the deep or moderate snow accumulation sites. Fellfield soil temperatures were comparable to those of the kobresia meadow ($r = 0.877$; $n = 24$), but Ψ_{soil} was much lower. Soil water potential exceeded -20 bars only half as frequently as in the kobresia meadow, probably because high winds dried the soil quickly.

Spring snow melted simultaneously in the fellfield and kobresia meadow, raising Ψ_{soil} to 0 bars. Under snow accumulations Ψ_{soil} rose only to about -8 bars by late May, 1972. Meltwater inundated

Table 14. Comparison of soil water potential at 10 cm depth in four alpine microsites.

Time	Mean soil water potential (bars)			
	Fellfield	Kobresia meadow	Moderate snow	Deep snow
Summer				
0800-1100	-15.1	-8.0	-9.6	-4.6
1100-1400	-22.2	-7.2	-12.2	-7.0
1400-1800	-17.1	-8.9	-7.9	-6.3
Winter				
0800-1100	-66	-23	-36	-28
1100-1400	-77	-28	-41	-35
1400-1700	-49	-31	-49	-26

	Percent of readings above -20 bars Ψ_{soil}			
	Fellfield	Kobresia meadow	Moderate snow	Deep snow
Summer (July-August)	73	90	76	100
Winter (Jan-April)	17	33	0	0
Spring (May)	95	100	11	10

the fellfield from mid-May for 12 days; the kobresia meadow at the same time for 17 to 20 days; the moderate snow accumulation area from early June for about 10 days; and the deep snow accumulation area from early July for 4 to 6 days.

Discussion

The plant environments afforded by the four microsites examined offer a variety of conditions potentially deleterious to kobresia (Table 15).

Both drought and wind may make the fellfield poor kobresia habitat. A Ψ_{soil} above -20 bars appears necessary for stomatal opening, and Ψ_{soil} in the fellfield was often lower than this even in summer, down to -40 bars. With increased wind and vapor pressure deficits at 2 cm, water loss might be severe. Winter wind was very strong; and plants might, therefore, be expected to have difficulty in maintaining normal winter leaf conditions. Temperatures in the fellfield would probably not cause difficulties because in all seasons they closely resemble those of the kobresia meadow. The increased rate of temperature variation in summer could be tolerated because increased wind would speed equilibration of leaf temperatures with ambient.

In the moderate snow accumulation area, kobresia might be expected to have problems associated with low soil moisture in summer. Summer maximum temperatures at the plant level are higher than in the kobresia meadow, but the effects of this cannot be predicted from normal kobresia behavior. The date of the first persistent snow accumulation is unknown, but it was likely before

Table 15. Comparison of environmental characteristics potentially deleterious to kobresia in four alpine microsites.

	Fellfield	Kobresia meadow	Moderate snow	Deep snow
Annual snowfree period	Ephemeral drifts	Ephemeral drifts	20 June-1 Oct (?)	5 July-15 Sept
% snowfree days, Feb-Mar	38	22	0	0
Wind at 2 cm height (m/sec)				
Summer: mean	0.7	0.5	0.4	0.2
Winter: mean	2.4	1.2	0.0	0.0
maximum	7.7	5.1	0.0	0.0
Temperature at 2 cm (°C)				
Summer: mean, 12:00-15:00	23.1	21.1	27.6	26.6
maximum	33.5	29.9	31.0	35.6
Winter: mean, 12:00-15:00	-5.7	-7.0	-4.6	-4.5
maximum (Feb-Mar)	+6.8	+8.2	-3.1	-3.5
Temperature at soil surface Variability (std. deviation) 12:00-15:00	3.2	2.9	1.8	1.6

Table 15, cont.

	Fellfield	Kobresia meadow	Moderat[illegible]now	Deep snow
Soil water potentials at 10 cm				
% of readings -20 bars				
Summer (July-Aug)	73	90	76	100
Winter (Jan-Mar)	17	33	0	0
Spring (May)	95	100	11	10
Beginning of spring soil saturation	14 May	9 May	13 June	3 July
Duration of soil saturation (days)	12	17-20	10	4-6

late October so fall die-back could be interrupted. Soil moisture appears effectively unavailable under winter snow accumulations, and temperatures remain far below the maxima of snowfree areas. Spring soil thaw was retarded by about 3 wks under moderate snow depth and temperatures near 0° persisted until late June when snow was completely melted. Both would probably delay spring elongation. Thus, the moderate snow accumulation area offers a combination of a shortened growing season and unfavorable conditions during both summer and winter.

The deep snow accumulation produces a similar array of problems for kobresia except that summer soil water potentials were consistently above the critical point of -20 bars. Snowmelt was incomplete until early July. Soil remained cold and saturated until the end of melting, so that spring leaf elongation would probably be delayed by about 5 wks until early to mid-July. Snow accumulation beginning in mid-September might halt fall die-back 6 wks early.

VI. KOBRESIA BEHAVIOR IN ALTERED HABITATS

Introduction

The study of undisturbed kobresia indicated a number of conditions which appear potentially deleterious. Kobresia is normally absent from alpine habitats affording some of the conditions such as early snow cover or high winds. Tolerance for several unfavorable environments was examined by placing plants in a variety of habitats not naturally occupied by the species. Studies of these plants paralleled observations of undisturbed kobresia so that behavioral alterations under these abnormal microenvironments could be identified.

Methods

Three methods of environment alteration were used: the transplanting of kobresia tussocks to non-normal habitats, the erection of snow fences in a kobresia meadow, and the long-term alteration produced by the construction of an embankment along Trail Ridge Road, producing a deep drift across a kobresia meadow.

Fifteen tussocks from the transplant control meadow were transplanted into each of four sites: a fellfield, the control kobresia meadow, a moderate and a deep snow accumulation area. Nine were placed between 4 and 10 July 1970, and six more between 12 and 18 September 1970. Transplants were made with an intact soil block about 3 cm wider than the tussock and about 25 cm deep. This appeared to encompass the entire root mass of the tussock. Plants were watered daily throughout the summer of 1970; September transplants were watered only 2 or 3 times.

Snowfences were erected in the Sundance Mountain site kobresia meadow. Two fences, 3.6 m long and 1.2 m high, were used. One was maintained in place the whole of the winters of 1970-71 and 1971-72. The second was erected on 3 February 1971 and left in place for six weeks. After its removal the snowbank behind it was dispersed in about two weeks.

Vegetation was described using the transect method along five 5 m lines.

Productivity was compared between transplants, snow-buried plants and controls from each site. Samples were collected from 10 plants for each treatment between 9 and 13 September 1971. A ring 2.5 cm in diameter was placed over each tussock and all shoot material originating in this area harvested. The current year's production was separated from the standing dead, samples oven-dried at 85°C and weighed.

Other techniques employed were those used in the study of undisturbed kobresia.

Results

Effect of Long-term Snow Accumulation on Vegetation

A part of the kobresia meadow at the Tundra Curves site has been buried by snow each winter since 1932 or 1933 when a switchback embankment was constructed. Within a very well-defined area plant community changes are obvious (Fig. 24). These were examined quantitatively using paired transects parallel to and one meter to each side of the boundary of the changed community. The data show that kobresia was almost completely eliminated, and many of the dead bases remain firmly in place and uninvaded by other species (Table 16). *Carex drummondiana*, a common member of kobresia meadows, also suffered a significant loss of cover, while *Geum turbinatum* and *Artemisia scopulorum* partially replaced the cover lost by the sedges.

Summer data are insufficient to explain the presence of the sharp edge of the dead kobresia area. Three visits in winter, however, revealed that the drift consistently has very steep edges, rising from 20 cm to about 200 cm depth in a distance of 2 m. Snow was deeper along the edges, up to 75 cm, for about 2 weeks in May, 1972, but this quickly melted and the portion of the meadow having normal appearance was snow-free within 2 days of the remainder of the undamaged meadow.

When the Tundra Curves meadow was examined in 1962, Willard (1963) concluded that it was not changing into a snow accumulation type of community. Nine years later the increase of *Geum turbinatum* and *Artemisia scopulorum* make this more like the disturbed moderate snow accumulation transplant site of this study and other disturbed sites described by Osburn (1964). It appears that if snow accumulation increases, kobresia tussocks die back from microclimatic changes rather than competition from other species. Dead kobresia and mineral soil may remain for longer than ten years before being colonized by more snow tolerant species.

Fig. 24. Vegetation changes under a snowdrift present for 40 winters at Tundra Curves, 29 May 1972. Surviving kobresia still has light-colored dead leaf tops as in winter. A well-defined edge of the damaged area parallels the retreating snowbank edge.

Table 16. Significant changes in cover produced in a kobresia meadow by winter snow cover forming in the lee of an embankment of Trail Ridge Road, constructed 39 years previously. Drift and control areas were compared using t-tests. Changes shown are significant at 95%; changes in starred species are significant at 99.9%

Species	Percent Cover	
	Control	Snowbank
Kobresia bellardii	54.8	0.4*
dead *K. bellardii*	2.3	18.5
Carex drummondiana	7.5	0.6
Silene acaulis	0.3	3.0
Geum turbinatum	15.9	26.7
Artemisia scopulorum	3.9	15.3*
Mineral soil	2.5	9.7

Phenology

A comparison of phenological events in transplanted and control tussocks indicates that abnormal habitats exert a profound influence over the timing of vegetative and floral development (Table 17). Transplantation *per se* appears to produce little change; dates of developmental processes in control transplants were usually within 3 days of control plants. Plants in the fellfield site showed a slightly shortened season of spring-summer-fall development. Floral bud and spring leaf expansion were delayed about one week and fall die-back was about ten days advanced. Where snow did not melt until late June, leaf expansion was 3 weeks delayed; where snow persisted until 9 July, spring development was 6 to 7 weeks late. The initial phases of fall die-back were also delayed in snow accumulation sites, to the extent that snow cover began before die-back was complete. Floral development and seed dispersal were only slightly modified in the fellfield, but they were altered even more than vegetative development in snow accumulation sites. Floral bud expansion did not begin until after snow release and so was up to 3.5 months late. Development was rapid, however, and anthesis was only 2 to 3 weeks late. Seed dispersal was delayed, and in the case of the deep snow accumulation site was only partially complete when the first lasting snow came.

Leaf length measurements in summer also point up the phenological effects of the experimental transplanting. Undisturbed plants and control transplants had no significant differences in leaf lengths. Fellfield plant leaves, however, lengthened slowly and remained

Table 17. Dates of phenological events in 1971, for undisturbed Kobresia and tussocks under four transplant treatments.

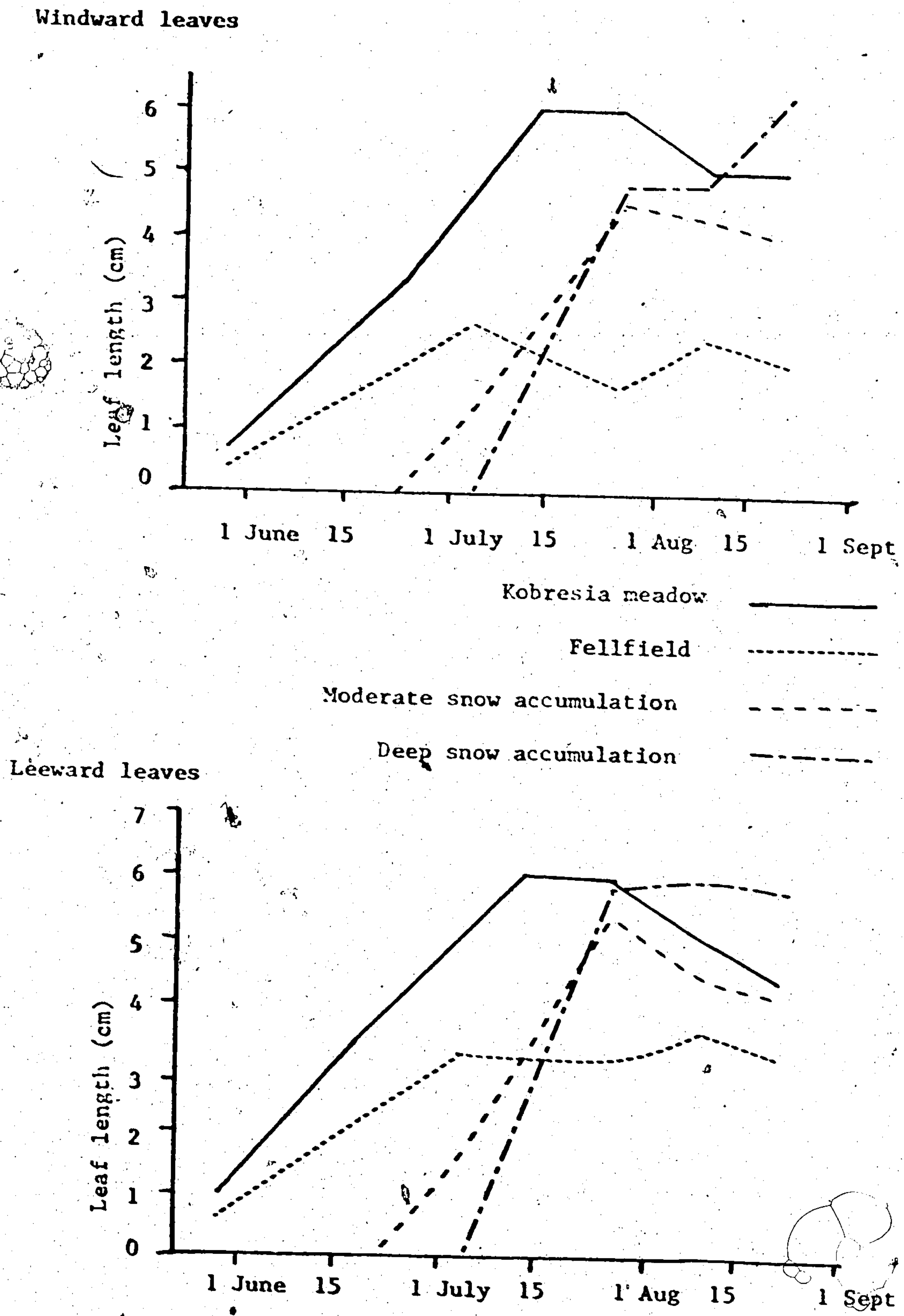
Event	Kobresia meadow		Transplants		
	Undisturbed	Transplants	Fellfield	Moderate snow	Deep snow
Floral bud expansion begun	31 Mar	31 Mar	8 Apr	25 June	15 July
Spring leaf expansion begun	20 May-5 June	20 May-5 June	1 June	23 June	12 Jul
Anthesis begun	8 July	8 July	10 June	18 July	1 Aug
Fall coloration begun	4 Aug	1 Aug	20 July	12 Aug	17 Aug
Seed dispersal begun	11 Aug	9 Aug	7 Aug	20 Aug	30 Aug
Initiation of leaves and roots begun	17 Aug	15 Aug	9 Aug	18 Aug	20 Aug
Fall die-back complete	? Oct	? Oct	20 Sept	None	None
Snow release	None	None	None	20 June	8 July
First lasting snow accumulation	None	None	None	?	14 Sept

short. Unlike control plants, differences in leaf lengths on windward and leeward sides persist through the summer in fellfield tussocks. Elongation was delayed in snow accumulation transplants (Fig. 25). After snow release recovery and elongation are faster than normal so that leaves on the leeward sides were almost equal to controls by late July. The failure to initiate die-back at the normal time is especially obvious in transplants in the deep snow accumulation site.

Plants in the moderate and deep snow accumulation sites, in failing to complete die-back, were buried under snow with rather long green leaves. During winter these leaves showed signs of very severe frost damage. Leaves collected and thawed in winter had lost their turgor. When growth resumed after snowmelt, elongation began from below the top of leaf sheaths.

Plants in the fellfield maintained live leaves in winter, but length of green leaves and rate and degree of change in length were reduced (Fig. 26). Windward leaves often suffered from severe erosion by windblown particles. Often no living leaf extended above the leaf sheaths. Several tussocks were eroded to the level of the roots, and one was partially blown out of the soil. By late May of the second winter in the fellfield, 60% of the surface area of tussocks was eroded below the tops of the leaf sheaths (Fig. 27). Sand accumulated up to the top of the leaf sheaths on the leeward side.

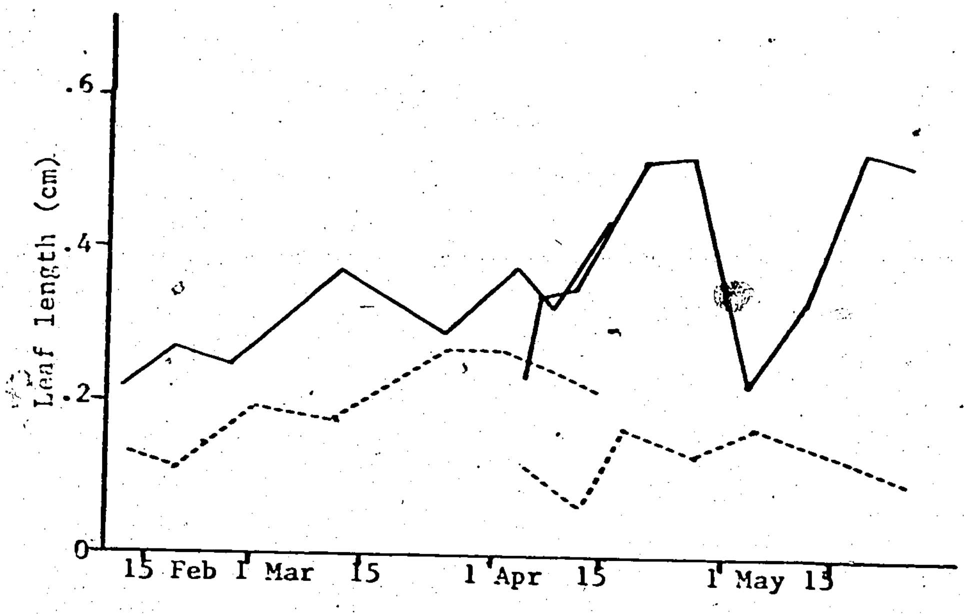
The presence of a shallow drift permitted more normal winter plant phenology. Leaf lengths under a 30 to 50 cm deep artificial drift closely resembled those of control plants but were more stable


Windward leaves

Leeward leaves

Fig. 25. Effect of altered habitats on summer leaf lengths of kobresia in four transplant sites, 1971. Undisturbed and control transplants did not vary significantly and are plotted together.

Windward Leaves



Leeward Leaves

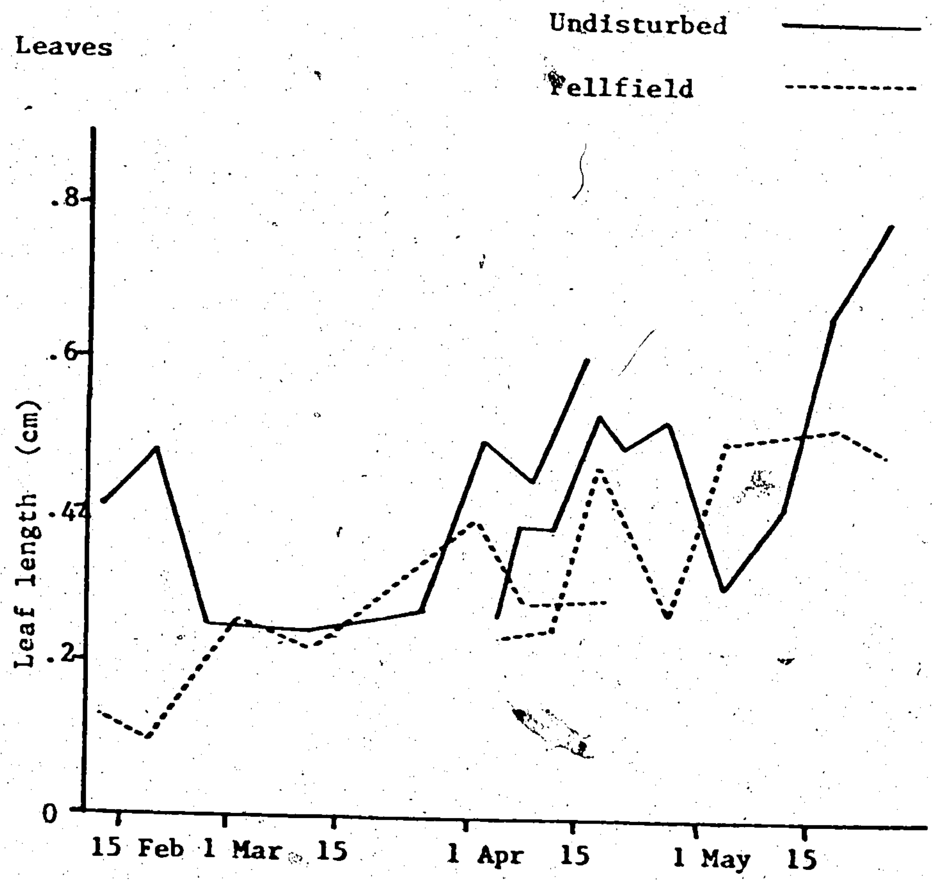
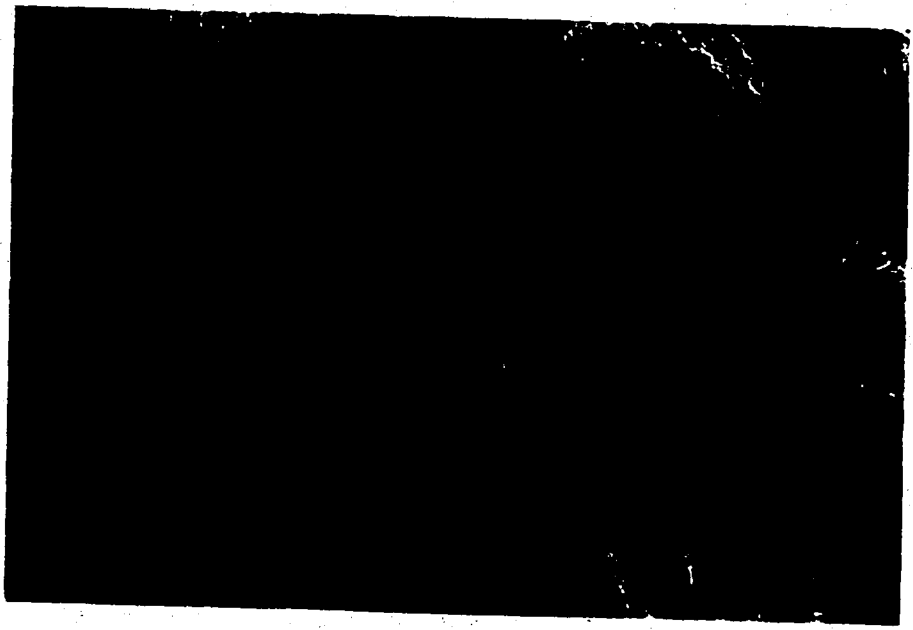


Fig. 26. Leaf lengths of undisturbed kobresia and transplants into a fellfield, winter, 1971, and spring, 1972.

A.



B.

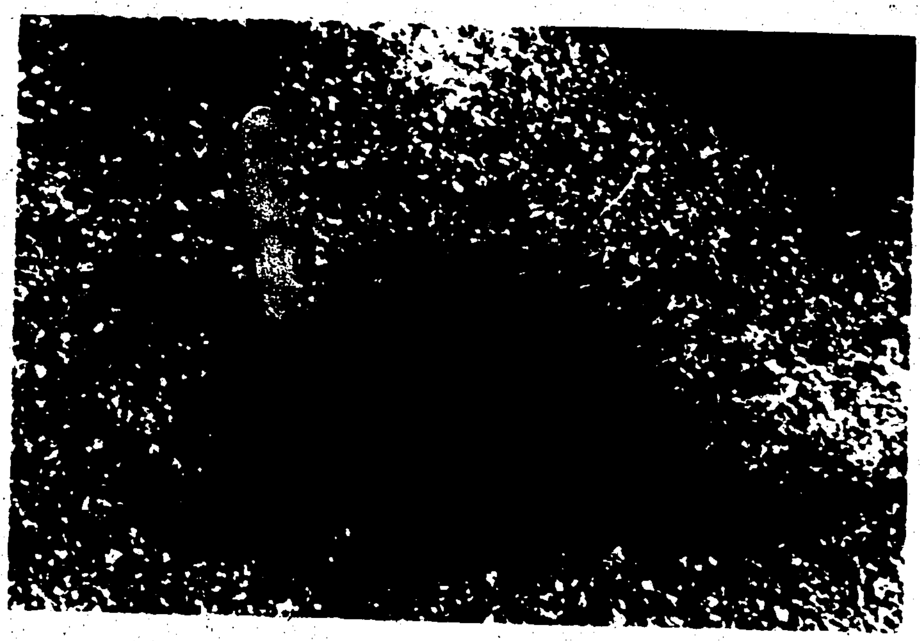


Fig. 27. Erosion of a fellfield transplant tussock. A. undisturbed kobresia meadow tussock, 25 May 1972; B. fellfield transplant tussock, 27 May 1972.

until snowmelt began (Fig. 28). When meltwater became available at the base of the drift, however, leaf lengths increased rapidly and leaves appeared somewhat etiolated. By late May leaves which had elongated under snow appeared frost-damaged by spring freezing.

Protection under a shallow temporary drift permitted leaves to elongate significantly more than controls in February. Leeward leaves responded to protection more quickly than windward. Leaves died back to the length of control leaves when the drift was dispersed.

Inflorescence Development and Success

The production and success of flowers are severely decreased in altered environments (Table 18). Transplantation had no effect on either characteristic, but in all other treatments inflorescence density and fertility fell. Changes were greatest under deep snow, but were only slightly less in other non-normal habitats.

In the first summer of transplantation, flowering was normal in all experimental plants. Fertility, although not measured, was uniformly high. After one winter, floral density was reduced by at least 50%. Of these flowers, about half successfully produced seeds. Following a second winter, transplants outside the kobresia meadow produced almost no flowers, but the percent fertility rose. This suggests that floral initiation, which occurs in autumn, is only partially reduced in response to summer and autumn conditions. The following summer, there was dense flowering but incomplete seed development. Floral bud initiation at the end of that summer was almost completely suppressed. Efficiency of seed production improved

Fig. 28. Winter, 1971, and spring, 1972, leaf lengths under shallow snow. Drifts of 35-60 cm were created behind snowfences, one of which remained in place through the whole winter in 1970-71 and 1971-72; the other from 3 Feb to 17 Mar 1971. Points represent the mean of 200 leaves.

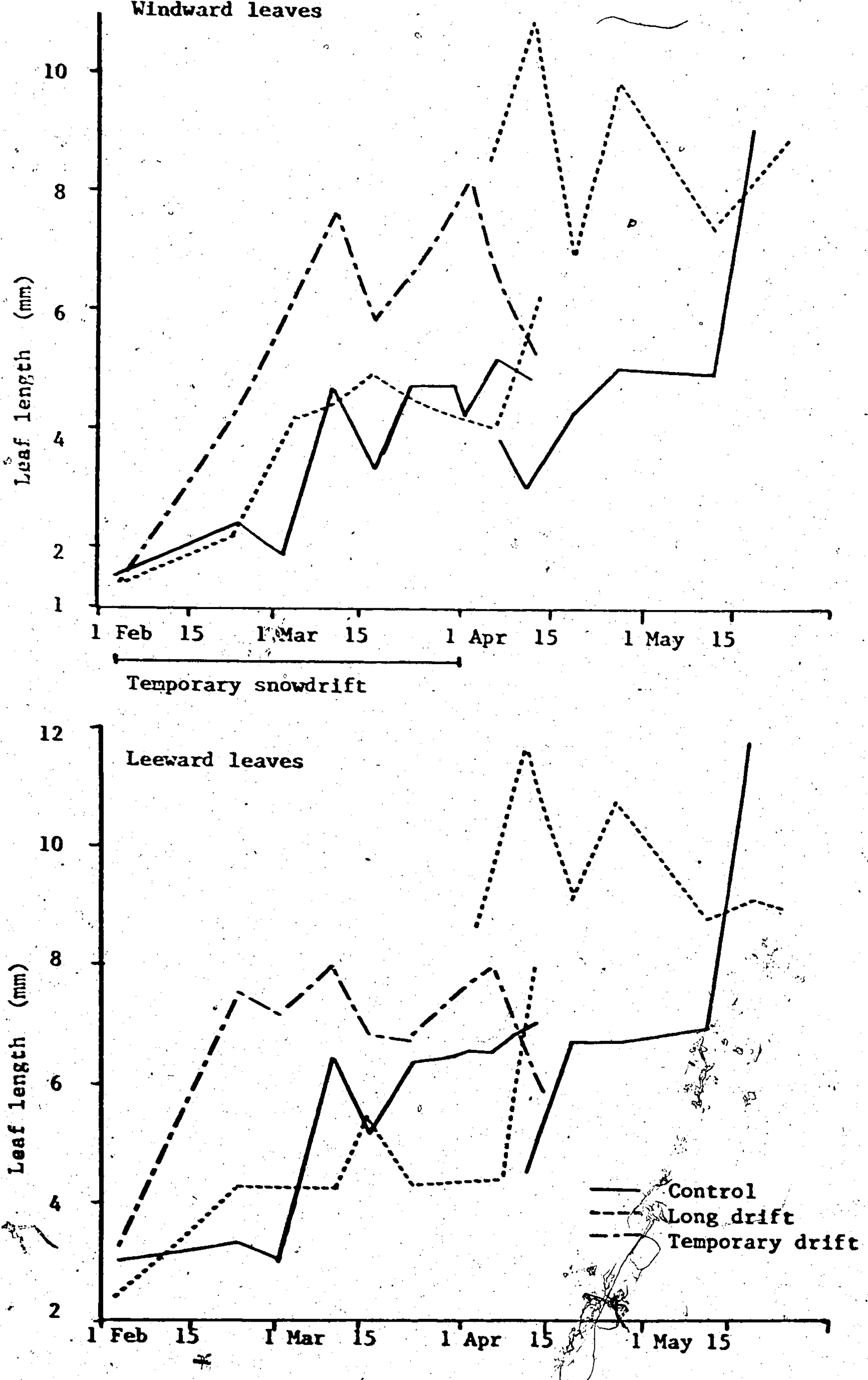

Windward leaves
Leaf length (mm)
10
8
6
4
2
1
1 Feb
15
1 Mar
15
1 Apr
15
1 May
15
Temporary snowdrift
Leeward leaves
Leaf length (mm)
12
10
8
6
4
2
1 Feb
15
1 Mar
15
1 Apr
15
1 May
15
Control
Long drift
Temporary drift

Table 18. Inflorescence density, infertility and smut infection in undisturbed *Kobresia* and plants under various environmental alteration and transplant treatments. Data are means of 15 to 20 tussocks per treatment.

Treatment	Inflorescences/cm^2			Percent infertile			Percent infected	
	1970	1971	1972	1970	1971	1972	1970	1971
Transplants								
Undisturbed controls	0.86	1.10	1.01	1	3.9	2.7	35.0	1.3
Control transplants	0.70	1.06	0.93		1.4	1.6	26.8	1.4
Fellfield	0.83	0.44	0.05		46.9	23.6	28.3	7.4
Moderate snow	0.54	0.56	0.02		49.7	31.7	11.4	0.0
Deep snow	0.93	0.33	0.01		57.4	38.1	36.0	0.0
Sundance Mountain								
Undisturbed controls		1.04			11.4			6.6
Permanent snowfence		0.65			31.8			4.8
Temporary snowfence		1.17			32.9			3.3
Tundra Curves								
Undisturbed controls		0.69			8.6			0.5
Snowbank		0.02*			52.4			0.5

* Based upon living plants only.

with decreased flowering. The short-duration snowdrift, allowing proper fall and spring floral development, permitted normal flower numbers, but fertility was reduced.

Smut infection rates appeared uniform between natural and altered environments in a particular year.

Tetrazolium Response

Variation in tetrazolium response rates between plants in various habitats were observed in winter only. Response time of fellfield plants was 10 to 20% longer than controls, January through April. In May, 1972, when plants were snowfree, reaction time was 50% longer than controls. Snow accumulation plants showed abnormally rapid responses, with a fairly strong reaction being visible throughout thawed leaves in 8 to 12 hrs in February and March, compared to 30 hrs for a similar reaction in controls. This was comparable to reaction rates in injured control tissues.

The slow reaction time in fellfield plants suggests maintenance of a slightly lower rate of physiological activity in these plants in winter. The rapid response of snow accumulation transplants may be an indicator of freezing injury.

Leaf Water Potentials

Leaf water potentials in all treatments were within the range observed in control plants. Transplant leaf water potentials during July and August the year after transplanting averaged 2 to 3 bars higher than controls or control transplants. Transplants in snow accumulation areas consistently had higher Ψ_{leaf} than controls.

while those in the fellfield were either above or below controls (Table 19). A comparison of Ψ_{leaf} and Ψ_{soil} under summer conditions showed that plants in the fellfield behaved much as did control plants; leaf water potentials consistently exceeded soil water potentials at Ψ_{soil} below -20 bars and only then (Fig. 29). The frequency of Ψ_{soil} below -20 bars was greater than in the control meadow. Thus, while Ψleaf in fellfield transplants was often higher than in the undisturbed plants, this probably reflects a condition of closed stomata rather than a more efficient water uptake. When Ψ_{soil} was below -30 bars, fellfield plants maintained leaf water potentials of about -10 bars, suggesting that this is the water potential of wilted leaves. Wliting might not be obvious since the leaves are quite stiff. In snow accumulation areas the summer pattern of Ψleaf:Ψsoil relationships is somewhat altered. Soil water potential rarely fell below -20 bars during summer, 1971; but Ψ_{leaf} was often higher than Ψ_{soil} (Fig. 29). This unusual condition appeared only after a winter of burial under snow and it suggests failure of normal stomatal control mechanisms. In both fellfield and snow accumulation area transplants stomatal closure might be expected to reduce productivity.

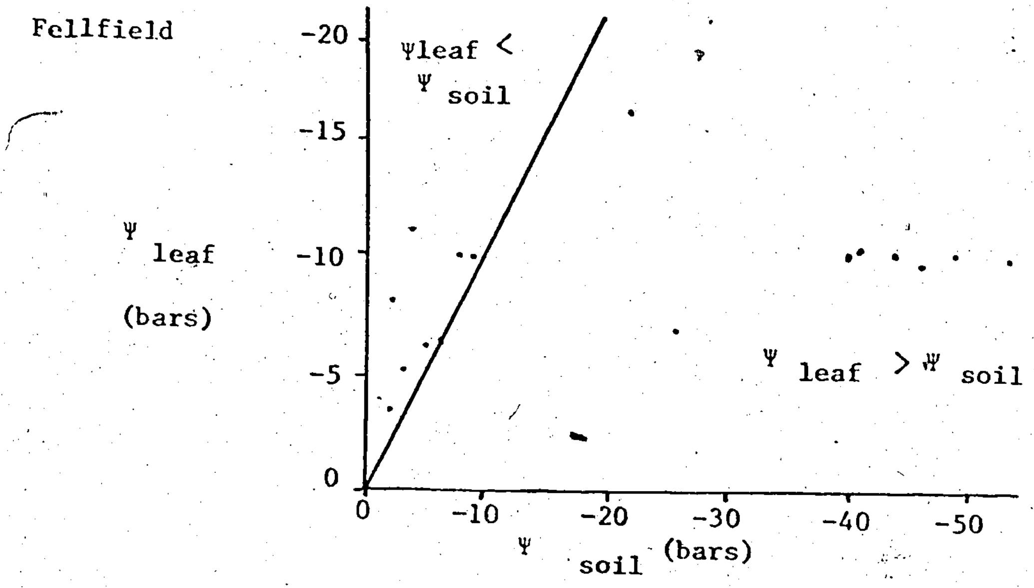
Other than in summer, fellfield leaf water potentials closely resembled those of controls. In September, they remained constant under snow, dropping gradually through the month. Winter Ψ_{leaf} of fellfield plants was usually within 1 or 2 bars of kobresia meadow plants. Simultaneous measurements of leaf and soil water potentials

Table 19. Some representative Ψ_{leaf} values from nearly simultaneous measurements at four transplant sites. These were selected from 204 determinations, each with one replicate. Those on 19 July 1970 were taken within 1 wk after transplantation.

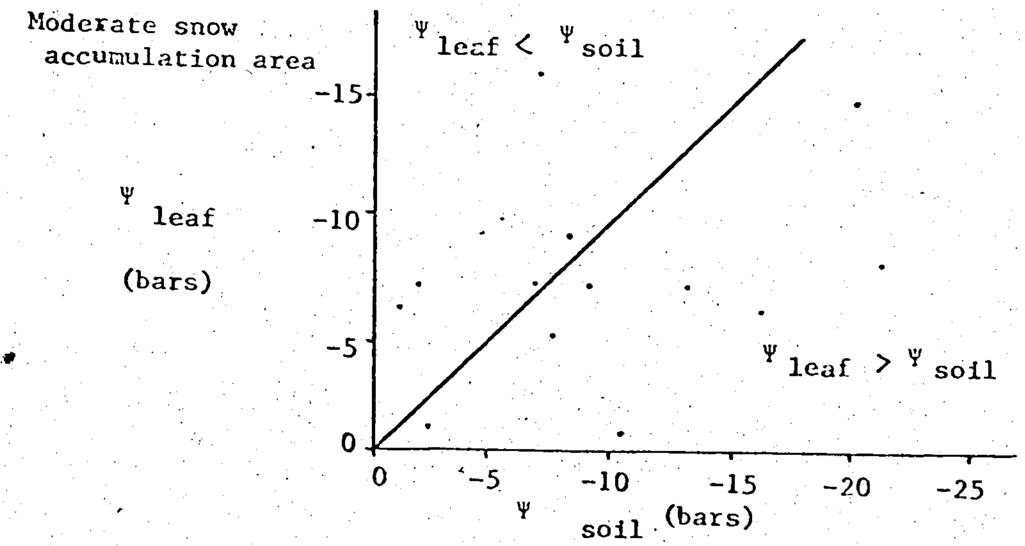
Date	Undisturbed	Leaf water potential (bars)			
		Transplants			
		Fellfield	Kobresia meadow	Moderate snow	Deep snow
19 July 1970	-10	-8	-12	-12	-10
19 Sept 1970	-11	-12	-12	-9	-8
27 Jan 1971	-18	-22	-20	-	-
20 Feb 1971	-9	-11	-10	-7	-8
13 Mar 1971	-8	-14	-10	-	-
17 Apr 1971	-4	-5	-5	-	-9
5 June 1971	-4	-13	-5	-1	-1
21 July 1971	-10	-16	-12	-7	-2
30 July 1971	-17	-10	-15	-11	-15
14 Aug 1971	-15	-7	-16	-3	-6
7 Apr 1972	-6	-5	-6	-4	-8
16 May 1972	0	0	0	0	-4

Fig. 29. Relationship of kobresia Ψ_{leaf} to Ψ_{soil} in three transplant sites, summer, 1971. The diagonal line separates the region of potential passive uptake above from that of impossible passive uptake below.

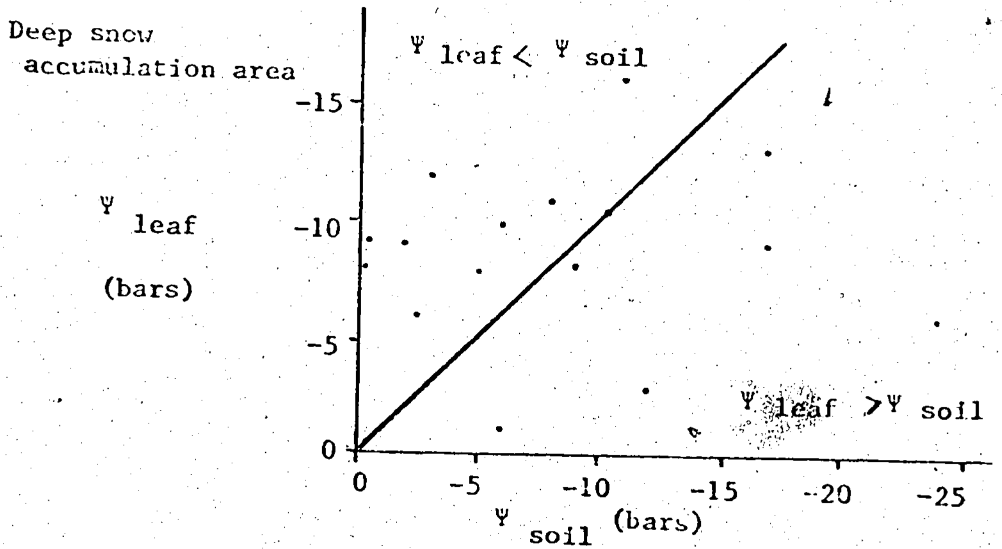
Fellfield



Moderate snow accumulation area



Deep snow accumulation area



in winter and spring showed passive uptake possible when Ψ_{soil} was above -20 bars and impossible when it was below. In spring, Ψ_{soil} and Ψ_{leaf} rose to 0 bars for a period of 17 days during the slow melting of a deep spring snow cover.

Kobresia plants placed under snow accumulations tended to have more constant and higher winter leaf water potentials than controls. Leaf water potentials remained close to -8 bars under fall snow accumulations and through the winter. The significance of these winter measurements is questionable since the leaves were melted from ice at the base of snowbanks. Although tests were made at temperatures below 0°, this thawing may have altered Ψ_{leaf}. Further, thawed leaves appeared severely damaged and tetrazolium tests suggested extensive injuries. While values are high, they do not reflect real conditions, and are probably not comparable to Ψ_{leaf} of undamaged plants.

Under shallow snow, leaf water potentials tended to be similar to those of normally exposed plants (Fig. 30). The high Ψ_{leaf} associated with spring conditions was reached much earlier under snowbanks and was accompanied by premature elongation.

Leaf Surface Temperatures

Plant leaf temperature was generally coupled with ambient air in summer (Table 20). The only significant departures were in fellfield transplants during the second summer, when leaf surface temperature was significantly lower than air temperature ($p<99.9\%$). This may represent cooling during periods when stomates were open and high winds enhanced transpiration rates. Winter leaf surface

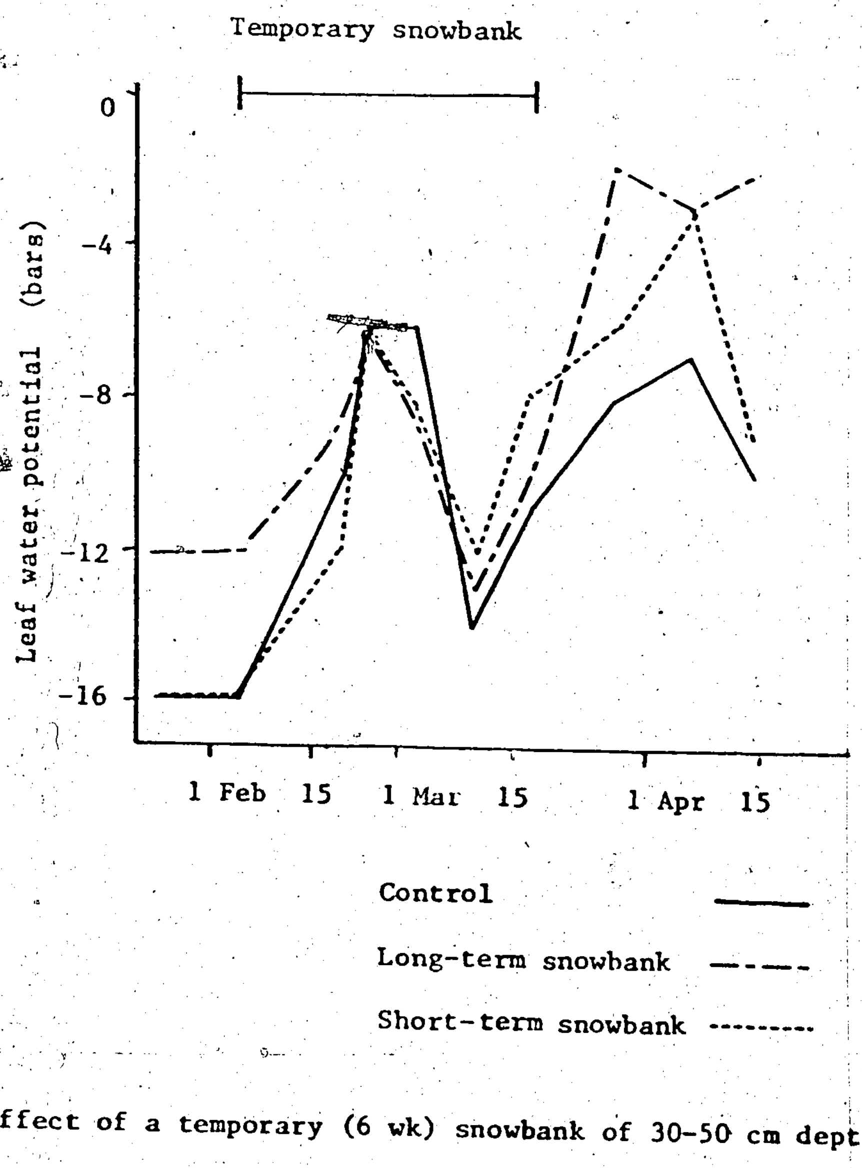


Fig. 30. Effect of a temporary (6 wk) snowbank of 30-50 cm depth on Ψ_{leaf} in kobresia at the Sundance site, winter, 1971.

Table 20. Kobresia summer leaf surface temperature differences from 2 cm air temperatures in four transplant treatments. Plants were transplanted and watered in 1970; not watered in 1971. Differences of less than $1^{o}C$ are treated as equalities. Symbols used: =, leaf surface temp. = air temp.; >, leaf surface temp. > air temp.; <, leaf surface temp. < air temp.

Site	Year	Percent of occurrences			Number of samples
		=	>	<	
Control	1970	83	11	6	83
	1971	76	12	12	33
Fellfield	1970	78	17	5	58
	1971	54	0	46	24
Moderate snow	1970	73	25	2	59
	1971	71	12	17	24
Deep snow	1970	74	24	2	53
	1971	73	14	14	22

temperatures were the same as the surrounding snow at 2 cm under deep and moderate snow accumulations ($p<95\%$) and as ambient 2 cm temperatures in the fellfield ($p<99\%$).

Carbohydrates

Some characteristics of carbohydrate budgets remained similar in controls, transplants and snowfence treatments: carbohydrate levels were quite high with the greatest concentrations in the shoots rather than in roots; and oligosaccharides formed the principal storage product, especially in the shoots.

Changes in carbohydrate levels over the summer varied from controls according to the transplant treatment (Fig. 31). Control transplants were insignificantly different from undisturbed tussocks. Plants in the fellfield usually had slightly higher concentrations of carbohydrates, possibly associated with the failure of leaves to elongate normally. The early die-back is indicated in the high carbohydrate levels attained by early September. Carbohydrate concentrations of plants in snow accumulation areas dropped to 30 to 50 mg g^{-1} during early leaf elongation, compared with a low of 100 mg g^{-1} in controls at the same stage of development. In all sites September carbohydrate levels were low. It was suggested earlier that in undisturbed plants a long snow-free period in September or October would be necessary for the concentration of oligosaccharides associated with fall die-back. This concentration failed to develop in plants under both moderate and deep snow accumulations. Since high oligosaccharide levels may be associated with frost hardiness

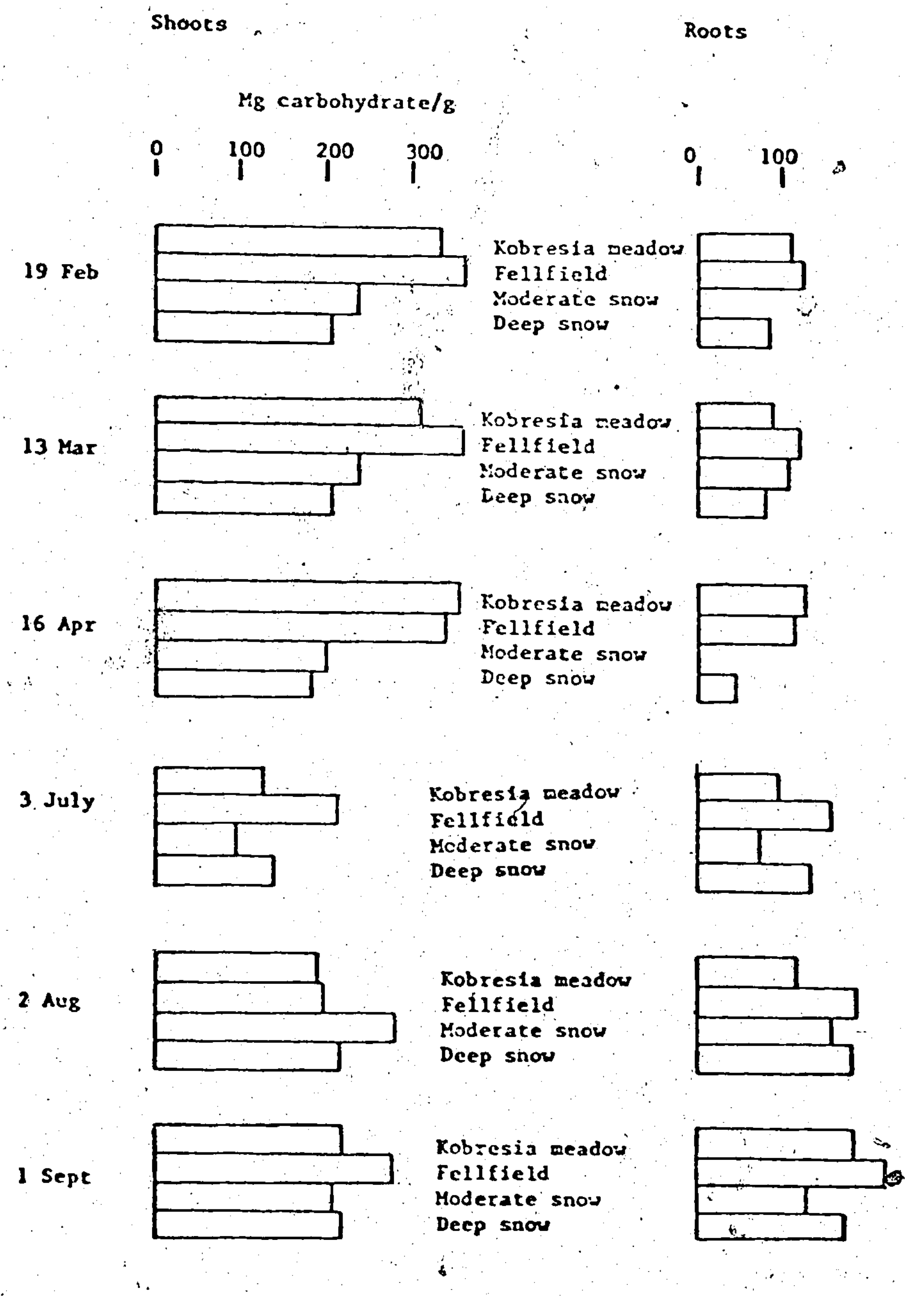


Fig. 31. Total carbohydrates in shoots and roots of undisturbed and transplanted kobresia in

Mazur, 1969; Levitt, 1972), failure to attain normal oligosaccharide levels may cause the extensive frost kill observed in these transplants in winter and spring. This may also delay elongation after snowmelt. In early September, however, carbohydrate concentrations in snow accumulation area transplants nearly equalled those of control plants, indicating at least partial recovery.

Plant Production

Shoot production dropped in all treatments, including control transplants the year after transplantation and erection of snowfences (Table 21). Variation between tussocks, especially in undisturbed plants, was great. Samples of 10 tussocks were inadequate for statistically significant distinctions between transplants and controls, except in the case of fellfield transplants. Those had production reduced by 70%, standing dead by 40%. Transplants in snow accumulation areas and plants under snowfence drifts showed lower production than controls ($p<80\%$), except under deep snow where reduction was only 0.7 g m^{-2}. Long-term effects of deep snow, however, were obvious at Tundra Curves where annual shoot production of plants under snow for 40 winters was about 15% of adjacent controls. Standing dead was slightly lower in snow accumulation transplants, but this was quite insignificant ($p>40\%$). In the fellfield and at Tundra Curves, however, standing dead was reduced by about 30%.

Carbohydrate contents on a weight basis were determined for standing shoot material less than 1 year old and a carbohydrate m^{-2} factor derived. Shoot carbohydrate m^{-2} was low in all treatments

Table 21. Annual shoot production, standing dead, and carbohydrate/m^2 in kobresia under various treatments. Measurements were made in September, 1971. Carbohydrate/m^2 was based upon 2 determinations of carbohydrate levels in shoots produced during the previous year times mean shoot production. Standard errors are indicated for production and standing dead for 6 to 10 tussocks per treatment.

Treatment	Shoot production g/m^2	Standing dead g/m^2	Carbohydrate g/m^2 basal area
Transplants			
Undisturbed	8.4±1.1	45.0±7.1	1.82
Control transplants	7.0±1.3	46.0±8.2	1.76
Fellfield	3.1±0.4	28.2±5.4	0.82
Moderate snow	6.8±0.5	41.9±1.8	1.36
Deep snow	7.7±0.5	37.9±5.1	1.55
Snowfence			
Undisturbed	9.2±1.2	35.0±4.7	1.76
Short-term drift	6.7±1.2	33.3±3.6	–
Long-term drift	7.0±0.6	41.1±6.1	0.84
Tundra Curves			
40 winters under snow	1.3±0.5	27.4±5.3	–

except control transplants, being greatest in the fellfield.

These measurements of production, standing dead, and carbohydrate m^{-2} suggest that kobresia performs most poorly under fellfield conditions. The effect of abrasion is quite evident in the reduction of standing dead. Over a number of year the presence of snow cover will also be deleterious. Plants in snow accumulation areas recovered from the initial winter damage and achieved near-normal levels of production, but this is at the expense of carbohydrate reserves which are critical for the next summer's growth and probably for frost hardiness.

Effect of Elk Grazing

During the winter from 15 to 32 elk used the alpine area of Trail Ridge. Bite counts indicated that about 75% of their diet is kobresia. Most kobresia meadows showed signs of heavy grazing by early April, 1971, and 1972. Of several hundred tussocks examined, however, none were grazed below about 2.5 cm above the basal leaf sheaths. Thus, green leaf tissue was not taken. Comparisons of green leaf lengths in grazed and ungrazed tussocks at the transplant control meadow in April and May, 1972, showed no significant effects of grazing on either leaf length or rates of change in length. Seven comparison of Ψ_{leaf} and 2 of the late winter carbohydrate contents showed no differences associated with grazing. Inflorescence production and seed set were the same in both groups of plants in 1972. Therefore, it appears that winter grazing by elk has no deleterious effects.

Discussion and Summary

Outside of kobresia's usual habitat, modifications in its behavior vary according to the character of the environment. The most conspicuous changes are related to abridgement of the growing season. Factors triggering the initiation and end of the growing season for kobresia cannot be defined on the basis of this study, but some hypotheses can be made. Soil moisture appears to determine the beginning of rapid spring activity, but under field conditions this is inextricably related to soil temperature. Variations in the initiation of die-back suggest that its timing may also be regulated by soil moisture. Low soil moisture levels have been shown to speed the onset of dormancy in <u>Geum turbinatum</u> (Billings and Bliss, 1959; Holway and Ward, 1965). Kobresia cannot be considered completely analogous since no dormant bud develops; but from the data available lack of soil moisture may trigger fall die-back. Its onset is advanced in the fellfield and started in control plants after a period of drought in late July in both 1970 and 1971. Die-back was most delayed in the moist deep snow area. If drought does trigger die-back, this would explain the absence of kobresia in relatively snowfree but poorly drained sites.

Shortening of the growing season is not the only cause of difficulties associated with timing of development. Under shallow snow, spring leaf elongation began before the final hard freezes. This appeared to be a response to high soil moisture produced by April melting. The partial loss of hardening permitted frost damage during freezing periods in late April and May.

Leaf tissue and carbohydrate reserves were reduced outside normal habitats. In the fellfield, leaves and the protective leaf sheaths were lost through wind erosion. Failure to complete fall transfer of carbohydrates and frost killing in leaves under snow accumulations reduced carbohydrate reserves available for future leaf production.

Water balance regulation was altered in both fellfield and snow accumulation sites so that stomates often appeared closed, again suggesting a reduction in the amount of photosynthesis possible. Only in fellfield transplants were leaf surface temperatures lower than the adjacent air, probably because of transpirational cooling. Water loss from these plants thus may be quite rapid while stomates are open. More importantly, fellfield plants were often forced to close stomates because of low soil water potentials. Below Ψ_{soil} of about -30 bars, leaves appeared to be wilted because Ψ_{leaf} became independent of Ψ_{soil} and remained near -10 bars.

While soil water potentials below -20 bars were rare in the snow accumulation sites, Ψ_{leaf} frequently exceeded Ψ_{soil}, indicating stomatal closure. This suggests that regulation of stomates may be somewhat abnormal in these plants. Let us assume, on the basis of the evidence of control and fellfield plants, that wilted leaves have a Ψ_{leaf} of about -10 bars and that when turgor pressure approaches 0 bars stomatal closure ensues. Stomatal closure appears to be associated with much higher Ψ_{leaf} in plants in snow accumulation areas. It may be that wilting Ψ_{leaf} is much higher for these plants than in controls. Such a condition is not unlikely because the period of rapid elongation is associated with extremely low carbohydrate concentrations. These low solute concentrations would raise the minimal osmotic potential. Then when turgor pressure approaches 0, Ψ_{leaf} will be relatively high and stomates will be closed at a high water potential. Low carbohydrate concentrations occur during a period of minimal water stress in control plants. In snow accumulation areas, however, rapid elongation is incomplete before early August. Prior to this, Ψ_{leaf} often exceeds Ψ_{soil}, especially in the drier moderate snow accumulation area. Increased stomatal closing might be expected to reduce photosynthesis, reducing carbohydrate reserves and the effect would tend to increase with each year under snow.

All these changes, and perhaps others, could be expected to reduce photosynthesis more or less directly. Reduced production did occur in the first year after environmental alteration, although apparently there were some compensations for changes. The extremely rapid leaf expansion in moderate and deep snow accumulation areas permitted use of a large portion of the snow-free period by a large total leaf surface area. The relatively low expenditure of energy on seed production permitted a more nearly normal leaf production. High soil moisture in the deep snow accumulation site may have aided elongation and increased the frequency of stomatal opening. But despite these, net photosynthesis appears to have declined in altered environments since production declined and carbohydrate reserves were low at the end of the summer.

One result of this may be the reduced flower and seed production seen in these environments. Both proved very sensitive to any change in habitat. The only other characteristic which is so consistently altered is carbohydrate m^{-2}. Mark (1969) and Hadley and Bliss (1964) offer evidence that floral production in some alpine grasses and sedges may be related to photosynthesis, and so by implication to carbohydrate reserves. Numbers of flowers, especially in the second summer after treatment, and success of seed set both appear dependent upon a high level of carbohydrate reserves in kobresia.

VII. CONCLUSIONS

Limitations to Vegetative Development

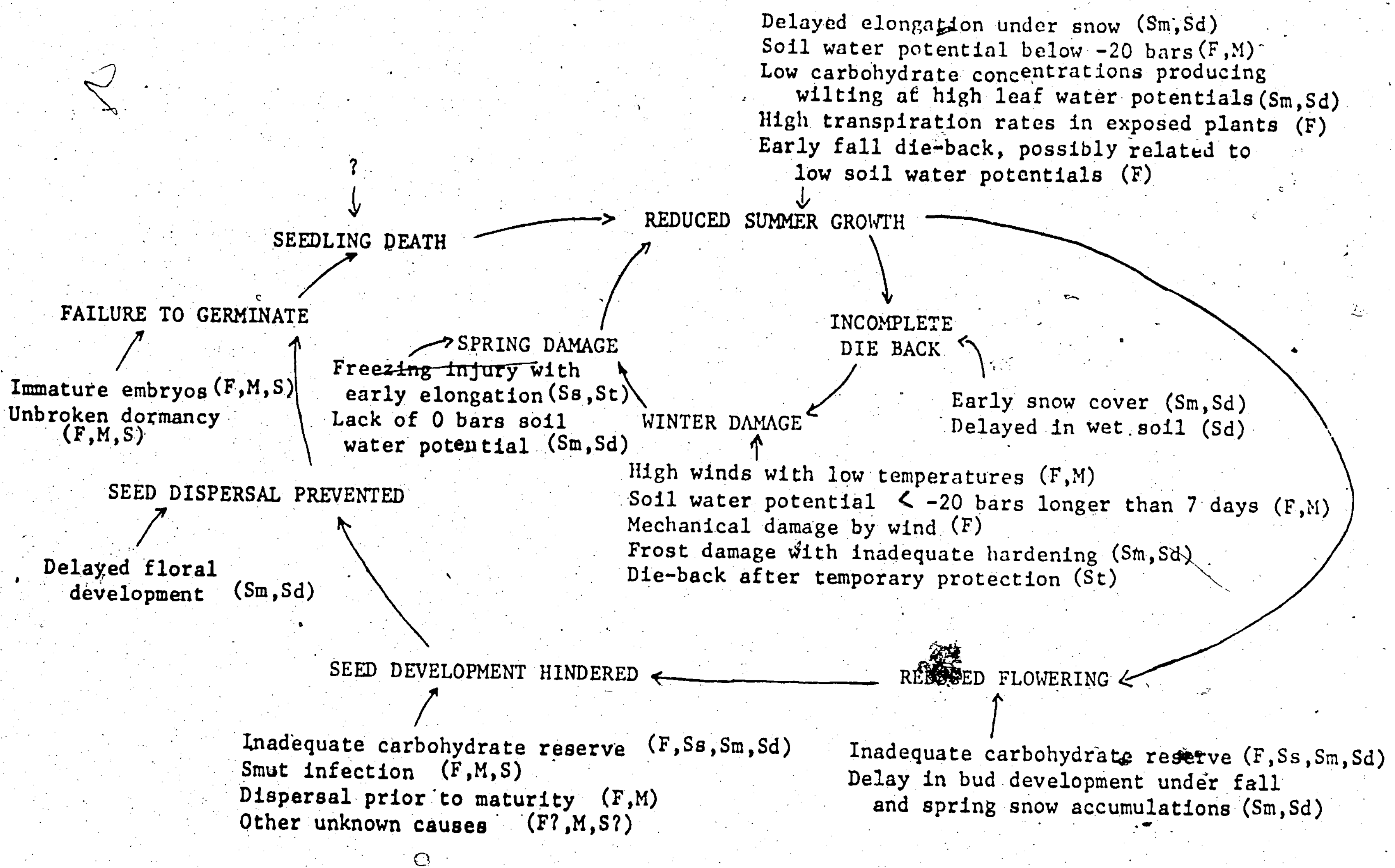
Reasons for the failure of kobresia to occur outside its customary habitat are complex. Many conditions may be deleterious (Fig. 32). In particular habitats a number of factors are damaging, and often these interact synergistically. Factors detering kobresia's vegetative development in habitats outside its normal distribution are as follows:

Fellfield. Survival is most stringently reduced here, primarily because of the abrasive effects of winter winds and low summer soil moisture. Other problems are related to apparently high summer transpiration rates; early fall die-back, possibly initiated in response to low soil water potential; and the limitations on winter leaf length by strong winds.

Shallow snow. Development is normal except in early spring when elongation begins too early in the wet environment during early snowmelt. This is apparently accompanied by some reduction in frost hardiness since subsequent freezing in the snowbank damages the elongating leaves.

Moderate and deep snow. Snow accumulating in September or early October prevents completion of die-back and hardening. Later, as temperatures drop, unhardened leaves are frozen and killed. Spring elongation does not begin until after snow release, shortening the time available for photosynthesis. Low leaf carbohydrate levels associated with early summer growth raise the wilting leaf water

Fig. 32. A model of factors implicated in faliures of kobresia to carry out maximal vegetative growth and sexual reproduction. Factors are associated with particular microenvironments as follows: F, fellfield; M, kobresia meadow; S, all snow accumulation conditions; Ss, shallow snow accumulation; Sm, moderate snow accumulation; Sd, deep snow accumulation; St, temporary snow accumulation dispersing before spring.


Delayed elongation under snow (Sm,Sd)
Soil water potential below -20 bars (F,M)
Low carbohydrate concentrations producing wilting at high leaf water potentials (Sm,Sd)
High transpiration rates in exposed plants (F)
Early fall die-back, possibly related to low soil water potentials (F)
?
SEEDLING DEATH
REDUCED SUMMER GROWTH
FAILURE TO GERMINATE
INCOMPLETE DIE BACK
SPRING DAMAGE
Immature embryos (F,M,S)
Unbroken dormancy (F,M,S)
Freezing injury with early elongation (Ss,St)
Lack of 0 bars soil water potential (Sm,Sd)
WINTER DAMAGE
Early snow cover (Sm,Sd)
Delayed in wet soil (Sd)
High winds with low temperatures (F,M)
Soil water potential < -20 bars longer than 7 days (F,M)
Mechanical damage by wind (F)
Frost damage with inadequate hardening (Sm,Sd)
Die-back after temporary protection (St)
SEED DISPERSAL PREVENTED
Delayed floral development (Sm,Sd)
SEED DEVELOPMENT HINDERED
REDUCED FLOWERING
Inadequate carbohydrate reserve (F,Ss,Sm,Sd)
Smut infection (F,M,S)
Dispersal prior to maturity (F,M)
Other unknown causes (F?,M,S?)
Inadequate carbohydrate reserve (F,Ss,Sm,Sd)
Delay in bud development under fall and spring snow accumulations (Sm,Sd)

potential, further reducing photosynthetic capability. These factors and perhaps others which affect kobresia directly are responsible for its absence from snow accumulation areas rather than any effects of interspecific competition.

Poorly drained soil or meltwater drainage areas. Low soil moisture levels may be the trigger for fall die-back. If die-back is delayed, the result may be inadequate frost hardening. This may contribute to preventing growth in snow accumulation areas which remain saturated until late July or later.

Temporarily deep snow. Protection may permit considerable leaf elongation in winter. If snow cover is removed, die-back ensues with an apparent loss of carbohydrate reserve.

Close grazing. While elk grazing has little effect, any extremely close grazing such as that of domestic sheep in late summer could remove a large fraction of carbohydrate reserves since much of this is stored in shoots. In addition to disturbing energy balance, this might affect frost hardening.

Limitations to Sexual Reproduction

Although restrictions to the growth of mature kobresia plants are numerous, it seems reasonable to expect that germination and seedling survival requirements would also affect local distribution of the species. But these requirements are not known since neither germination nor seedlings have been observed.

The evidence available suggests that at present in the Front Range, kobresia does not reproduce sexually. No seedlings or young plants can be found in the areas examined on Trail Ridge and adjacent areas in Rocky Mountain National Park, and Osburn (1958) has observed the same on Niwot Ridge. Seeds placed in various microsites on the tundra failed to germinate. Clearly, however, kobresia must have reproduced by seeds in the past. Osburn (1958) reports the presence of a kobresia stand in a timberline area that burned between 1890-1900 on the north side of Niwot Ridge. Since kobresia is never found under trees in the Front Range, Osburn concludes that this stand developed after the fire. In certain stands described and photographed by Kiener (1967, based on research done in 1935-39) young kobresia plants were common. An examination of several areas on Long's Peak in August, 1972, revealed kobresia plants in several areas pictured by Kiener. These plants were relatively young but did have well developed basal leaf sheath mats, suggesting that these too are many years old.

Their precise age is difficult to determine. Based upon the observation that there is about a 10% increase in number of tillers in a tussock over three years, the age of these Longs Peak tussocks was estimated to be between 72 and 84 years. It is interesting to note that this approximate aging technique dates the establishment of these plants near the time of the stand which Osburn was able to age. It may be possible that prior to this date germinable seed was produced, but that some climatic change at that time has since prevented development of germinable seeds. The large number of tussocks about 200 years old may be associated with the Gannet Peak Stade of Neoglaciation between 1650 and 1859 (Benedict, 1968). The most recent establishment of kobresia in the late nineteenth century conincides with a world-wide cool period between about 1883 and 1895 (Callendar, 1961; Lamb, 1966). The relatively warm climates since 1900 could be preventing seed maturation in this century.

It is clear that when kobresia is placed in an unfavorable environment, the first normal functions to be impaired are those associated with seed production. Presently, plants usually disperse seeds with extremely immature embryos, and those in unsuitable environments show still more incomplete seed development. Even the largest embryos show only a very low level of physiological activity. Seed dispersal appears to be regulated by factors other than seed maturity. In three summers, initial seed dispersal occurred 10 days after the first day with a temperature maximum of 17°. High temperature, therefore, might play a role in triggering seed dispersal. If this proves to be the case, then only in a summer when temperature maxima were below some critical point at least well into August would kobresia produce germinable seed. A very slightly cooler climate might then restore seed reproduction in the species.

Kobresia cannot now seed in an area after disturbance or in the course of succession, its role as a climatic climax species is historical rather than current. Plants live for very long periods so large kobresia meadows can be expected to persist for hundreds of years should present conditions continue. During this period, if climatic fluctuations produced a more favorable environment, seed reproduction could be resumed. Willard (1963) has suggested that both kobresia and Carex elynoides form climax associations, and that [illegible]y be a relict climax. While lack of sexual reproduction seems to support Willard's hypothesis with kobresia assuming the position of a relict, two factors argue against this designation. The relict status of kobresia would have persisted for a relatively brief time in terms of the hundreds of years required for alpine successional sequences as suggested by Willard (1963). In addition, winter observations suggested that Carex elynoides may require a somewhat less exposed habitat than kobresia since tussocks were damaged and leaves died back whenever snow was completely absent from around them (Bell, 1974) whereas kobresia was quite tolerant of this condition.

Regardless of whether these hypotheses concerning reasons for lack of seedlings are true, it seems apparent that present distribution of kobresia is at least partially independent of germination and seedling establishment requirements.

Adaptations to the Preferred Habitat

Although kobresia is unable to maintain itself outside a narrowly defined range of environmental conditions, it has a number of adaptations which make it quite efficient in its use of suitable habitat. Its competitive advantage over other species is suggested by the high degree to which it dominates meadows, often forming 50% of cover. Its suggested role as a climax species indicates its stability even in the presence of other species. Tussock life-spans of several hundred years are indicative of kobresia's ability to survive environmental extremes.

The phenology of kobresia offers opportunity for utilization of an unusually long season for development. Maintenance of wintergreen leaves allows spring development with minimal energy expenditure. Above-ground storage of carbohydrate reserves used in spring leaf expansion make translocation from roots in frozen soil unnecessary. Die-back in late September and October allows some increase in carbohydrate reserves after seed dispersal. Slight increases in carbohydrates during leaf expansion in winter even offer the possibility that there may be a low rate of photosynthesis then, but this would probably be most difficult to demonstrate in field measurements.

These phenological adaptations are not found only in kobresia. Growth outside the frost-free period extends the growing season in many alpine species, especially those in relatively snow-free habitats (Bell, 1974). Kobresia, however, has one of the longest annual periods of development. Two other species, Arenaria obtusiloba and Sedum stenopetalum, are also active to a slight extent in winter; but kobresia's winter leaf expansion is unique. Tieszen (1972) argues that ability to lengthen the growing season gives a tundra plant species considerable competitive advantage. Thus, the long growing season for kobresia may partially explain its dominance in areas where it can survive.

The short tussock may also form an adaptation to the normal kobresia habitat. Survival is reduced in the windy fellfield as tussocks are eroded to a cushion shape with loss of wintergreen tissue. Wintergreen species occurring in the fellfield are either cushion plants (e.g. Arenaria obtusiloba) or are found behind rocks or in small depressions (e.g. Festuca ovina). In the kobresia meadow, however, the low tussock form holds microdrifts reducing abrasion and probably water loss in winter. The cushion plants of the fellfield do not hold such drifts in the meadow. While the tussock for is deleterious under extreme wind exposure it may be advantageous in less exposed sites.

Kobresia also appears well-adapted to use the xeric environments in which it is found. Its efficiency in preserving high water potentials under conditions of low soil moisture allow it to tolerate periods of drought in all seasons. It is able to recover from some wilting throughout the year. Roots are effective in uptake even from very cold or frozen soils. Efficiency in uptake combined with an extensive root mass beneath tussocks produces the success of kobresia in competing for water postulated by Cox (1933) and Kiener (1967).

Management Implications

Some management applications can clearly be drawn from this behavioral description. The species is well-adapted to its particular habitat. Kobresia is a species with considerable potential value as cover, as a food source for natural animal populations, and for aesthetic reasons in an area of great beauty. It is, however, extremely susceptible to damage or death from environmental alteration. An increase in snow cover, even for a brief period, may seriously reduce normal growth. Close grazing could remove critical carbohydrate reserves. In fall or spring, when this grazing damage would be most severe, kobresia might be heavily grazed because of its snowfree habitat. Even recreational use can destroy kobresia, although it appears to be damaged by trampling more slowly than many alpine species (Willard and Marr, 1971). Once it has been injured, its recovery would be very slow. Willard and Marr (1971) suggest that periods up to 1000 years could be required.

The most serious problem, however, is not that of recovery, but of a source of plants in areas denuded of kobresia. If, as suggested here, kobresia is not presently capable of reproduction by seeds, natural recovery would be impossible. Even extremely low levels of germinable seed production would present essentially insurmountable difficulties in natural replacement. Transplants would be feasible, but vegetative development is very slow and effects on vegetation at the source of transplants would also be long lasting. For these reasons, it seems prudent to consider present kobresia meadows effectively irreplaceable and to preserve them intact.

REFERENCES

Barrs, H. D. 1968. Determination of water deficits in plant tissues. 236-246. In: Water deficits and plant growth, Vol. I. T. T. Kozlowski (ed.). Academic Press, New York. 390 p.

Barry, R. G. 1973. A climatological transect on the east slope of the Front Range, Colorado. Arctic Alpine Res. 5: 89-110.

Bell, K. L. 1974. Autumn, winter and spring phenology of some Colorado alpine plants. Amer. Midl. Nat. In press.

Benedict, J. B. 1968. Recent glacial history of an alpine area in the Colorado Front Range, U.S.A. II. Dating the glacial deposits. J. Glaciol. 7: 77-87.

Billings, W. D. and L. C. Bliss. 1959. An alpine snowbank environment and effect on vegetation, plant development, and productivity. Ecology 40: 388-397.

Bliss, L. C. 1966. Plant productivity in alpine microhabitats on Mt. Washington, New Hampshire. Ecol. Monogr. 36: 125-155.

Bliss, L. C. 1969. Alpine community patterns in relations to environmental parameters. 167-184. In: Essays in plant geography and ecology. K. N. H. Greenridge (ed.). Nova Scotia Museum. Halifax, N. S. 184 p.

Böcher, T. W. 1951. Distribution of plants in the circumpolar area in relation to the ecological and historical factors. J. Ecol. 39: 376-395.

Braun-Blanquet, J. 1954. La vegetation alpine et nivale des Alpes Francaises. Stat. Intern. de Geobot. Mediterr et Alp. 125. 77 p.

Callendar, G. S. 1961. Temperature fluctuations and trends over the earth. Quart. J. Roy. Met. Soc. 87: 1-12.

Cooper, W. S. 1908. Alpine vegetation in the vicinity of Long's Peak, Colorado. Bot. Gaz. 45: 319-337.

Courtin, G. M. 1968. Evapotranspiration and energy budget of two alpine microenvironments, Mt. Washington, New Hampshire. Ph.D. Thesis. Univ. of Illinois. 172 p.

Cox, C. F. 1933. Alpine succession on James Peak, Colorado. Ecol. Monogr. 3: 299-372.

Deacon, E. L. 1953. Vertical profiles of mean wind in the surface layers of the atmosphere. Geophysical Memoirs 91.

Eddleman, L. E. 1967. A study of phyto-edaphic relationships in alpine tundra of northern Colorado. Ph.D. Thesis, Colorado State Univ. 148 p.

Falk, P. 1940. Further observations on the ecology of central Iceland. J. Ecol. 28: 1-41.

Fonda, R. W. and L. C. Bliss. 1966. Annual carbohydrate cycle of alpine plants on Mt. Washington, New Hampshire. Bull. Torrey Bot. Club 93: 268-277.

Frank, E. C. and R. Lee. 1966. Potential solar beam irradiation on slopes. Tables for 30° to 50° latitude. U. S. For. Serv. Res. Paper RM-18.

Gates, D. M. 1968. Transpiration and leaf temperature. Ann. Rev. Plant Physiol. 19: 211-238.

Gieger, R. 1966. The climate near the ground. Harvard Univ. Press. Cambridge, Mass. 611 p.

Gelting, P. 1934. Studies on the vascular plants of east Greenland between Franz Joseph Fjord and Dove Bay. Medd. om Gronl. 101: 1-341.

Gjaervoll, O. 1954. Kobresieto-Dryadion in Alaska. Nyttmagasin Botanikk 3.

Grebenschchikov, O. S. 1960. Vegetation of the high mountain areas of Yugoslavian Macedonia (The Vardar Basin). In: Studies on the flora and vegetation of high mountain areas. V. N. Sukachev (ed.) Problems of Botany 5: 106-140. Trans. by Israel Program for Sci. Transl., Jerusalem.

Griggs, R. F. 1956. Competition and succession on a Rocky Mountain fellfield. Ecology 37: 8-20.

Guyot, H. 1920. Le Valsorey; esquisse de botanique, geographique, et ecologique. Comm. Phytogeog. Soc. Helvetique des Sci. Nat. 8. Zurich. 166 p.

Haag, R. W. 1972. Mineral nutrition and primary production in native tundra communities of the Mackenzie Delta region, N. W. T. M.Sc. Thesis. Univ. of Alberta. 89 p.

Hadley, E. B. and L. C. Bliss. 1964. Energy relations in alpine plants on Mt. Washington, New Hampshire. Ecol. Monogr. 34: 331-357.

Harrington, H. D. 1964. Manual of the plants of Colorado. Swallow Press, Chicago. 666 p.

Hitchcock, C. L., A. Cronquist, M. Ownby, and J. W. Thompson. 1955-69. Vascular plants of the Pacific Northwest. Univ. of Washington Press, Seattle. 5 vol.

Holway, J. G. and R. T. Ward. 1963. Snow and meltwater effects in an area of Colorado alpine. Amer. Midl. Nat. 69: 189-197.

Hrapko, J. O. 1970. An ecological study of the alpine plant communities of Signal Mountain, Jasper National Park. M. Sc. Thesis, Univ. of Alberta. 283 p.

Hulten, E. 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press, Stanford, California. 1008 p.

Igoshina, K. N. 1966. Flora of the mountain and plain tundras and open forests of the Urals. 189-339. In: Vascular plants of the Siberian North and the northern Far East. A. I. Tolmachev (ed.). Moscow. Trans. by Israel Program for Sci. Transl., Jerusalem.

Judson, A. 1965. Weather and climate of a high mountain pass in the Colorado Rockies. U. S. For. Ser. Res. Paper RM-16. 28 p.

Kiener, W. 1967. Sociological studies of the alpine vegetation on Longs Peak. Univ. of Nebraska Studies, new ser. 34. 75 p.

Kil'Dyushevskii, I. D. 1966. The flora of the Verkhoyansk Mountains. 145-164. In: Vascular plants of the Siberian North and northern Far East. A. I. Tolmachev (ed.) Moscow. Transl. by Israel Program for Sci. Transl., Jerusalem.

Klikoff, L. G. 1965. Microenvironmental influence on vegetational pattern near timberline in the Central Sierra Nevada. Ecol. Monogr. 35: 187-211.

Lamb, H. H. 1966. The changing climate. Methuen. London. 236 p.

Levitt, J. 1972. Responses of plants to environmental stress. Academic Press. New York. 697 p.

Major, J. and S. A. Bamberg. 1965. Some Cordilleran plants disjunct in the Sierra Nevada of California and their bearing on Pliestocene ecological conditions. 171-188. In: Arctic and alpine environments. H. E. Wright and W. S. Osburn (eds.). Indiana Univ. Press, Bloomington.

Mark, A. F. 1969. Ecology of snow tussocks in the mountain grasslands of New Zealand. Vegetatio 18: 289-306.

Marr, J. W. 1967a. Ecosystems of the east slope of the Front Range in Colorado. Univ. of Colorado Studies, Ser. in Biol. 8. 134 p.

Marr, J. W. 1967b. Data on mountain environments I. Front Range, Colorado, sixteen sites, 1952-1953. Univ. of Colorado Studies, Ser. in Biol. 27. 110 p.

Marr, J. W., A. W. Johnson, W. S. Osburn, and O. A. Knorr. 1968a. Data on mountain environments. II. Front Range, Colorado, four climax regions, 1953-1958. Univ. of Colorado Studies, Ser. in Biol. 28. 171 p.

Marr, J. W., J. M. Clark, W. S. Osburn, and M. W. Paddock. 1968b. Data on mountain environments. III. Front Range, Colorado, four climax regions, 1959-1964. Univ. of Colorado Studies, Ser. in Biol. 29. 181 p.

Marr, J. W. and B. E. Willard. 1970. Persisting vegetation in an alpine recreation area in the southern Rocky Mountains, Colorado. Biol. Conservation 2: 97-10.

Mazur, P. 1969. Freezing injury in plants. Ann. Rev. Plant Physiol. 20: 419-448.

Mooney, H. A. and W. D. Billings. 1960. The annual carbohydrate cycle of lapine plants as related to growth. Am. J. Bot. 47: 594-598.

Nordenhagen, R. 1936. Versuch einer neuen Einteilung der Subalpinen-alpinen vegetation Norwegens. Bergens museums Arbok, Natur Rekke 7. 88 p.

Osburn, W. S. 1958. Ecology of winter snow-free areas of the alpine tundra of Niwot Ridge, Boulder County, Colorado. Ph.D. Thesis, Univ. of Colorado. 77 p.

Peterson, S. M. 1971. Microenvironment and water relations of two alpine species, Olympic National Park. M. Sc. Thesis, Univ. of Alberta. 57 p.

Salisbury, F. B. and G. G. Spomer. 1968. Leaf temperatures of alpine plants in the field. Planta 60: 497-505.

Salisbury, F. B., G. G. Spomer, M. Sobral, and R. T. Ward. 1968. Analysis of an alpine environment. Bot. Gaz. 129: 15-32.

Selander, S. 1950. Floristic phytogeography of South-western Lule Lappmark, I. Swedish Lappland. Acta Phytogeographica Suecica 27: 1-200.

Siple, P. A. and C. F. Passel. 1945. Dry atmospheric cooling in subfreezing temperatures. Proc. Am. Philos. Soc. 89: 177-199.

Slatyer, R. O. 1967. Plant-water relationships. Academic Press, London. 366 p.

Somogyi, M. 1945. A new reagent for the determination of sugars. J. Biol. Chem. 160: 61-68.

Sorensen, T. 1941. Temperature relations and phenology of the Northeast Greenland flowering plants. Medd. om Gronl. 125. 305 p.

Svoboda, J. 1972. Vascular plant productivity studies of raised beach ridges (semi-polar desert) in the Truelove Lowland. 146-184. In: Devon Island I. B. P. Project, Project Report 1970 and 1971. L. C. Bliss (ed). Edmonton, Alberta.

Taylor, S. A. 1962. The influence of temperature upon the transfer of water in soil systems. Overdruk uit de Mededelingen van de Landbouwhogeschool ende Opzoekingsstations van de Staat te Gent. 27: 535-550.

Tieszen, L. L. 1972. The seasonal course of aboveground production and chlorophyll distribution in a wet arctic tundra at Barrow, Alaska. Arctic Alpine Res. 4: 307-324.

Tikhomirov, B. A. and V. A. Gavrilyuk. 1966. The flora of the Bering Coast of the Chukchi Penninsula. 74-105. In: Vascular plants of the Siberian North and northern Far East. A. I. Tolmachev (ed.) Moscow. Transl. by Israel Program for Sci. Transl., Jerusalem.

Trottier, G. C. 1972. Ecology of the alpine vegetation of Highwood Pass, Alberta. M. Sc. Thesis. Univ. of Calgary. 229 p.

Willard, B. E. 1963. Phytosociology of the alpine tundra of Trail Ridge, Rocky Mountain National Park, Colorado. Ph.D. Thesis, Univ. of Colorado. 243 p.

Willard, B. E. and J. W. Marr. 1970. Effects of human activities on alpine tundra ecosystems in Rocky Mountain National Park, Colorado. Biol. Sonservation 2: 257-265.

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

Williams, G. C. V., and J. Brochu. 1969. Vapor pressure deficit vs. relative humidity for expressing atmospheric moisture content. Natur. can. 96: 621-636.

APPENDIX I. INSTRUMENT USE IN WINTER ALPINE CONDITIONS

Many instruments were difficult to use under alpine winter conditions. Both blowing snow and cold presented problems. Wind-driven snow penetrates even tiny openings, so that instrument cases had to be thoroughly sealed with tape. Spot-reading instruments that required repeated exposure for use (e.g., the Honeywell potentiometer) were also placed in a deep clear plastic sack through which dials could be read and control knobs turned. This sack proved useful as a sort of small tent in which readings could be made when blowing snow reduced visibility even at very close range. Despite such precautions, it was necessary to remove snow from the inside of almost all instruments once or twice daily. Blowing snow made winter use of the sample chamber psychrometer outdoors impossible.

Temperature tolerance limits for some instruments used were frequently higher than ambient temperatures. It was necessary to warm all spot-reading instruments at least twice a day until mid-April, and on some days after that. A Grant recorder drained large 6V dry cells in a few days with low temperatures less than -15°C. Contacts in the range switches failed below about -8°, and some plugs from thermistor sensors had erratic contact below -10°. These failures, combined with snow filling the instrument box during period checks, made use of this machine impractical. Use of other equipment was facilitated in the following ways:

1. Honeywell portable potentiometer. The liquid in the reference cell is very cold-sensitive (Fig. 33). We attempted to keep this cell warm by taping a lit handwarmer inside the instrument body near

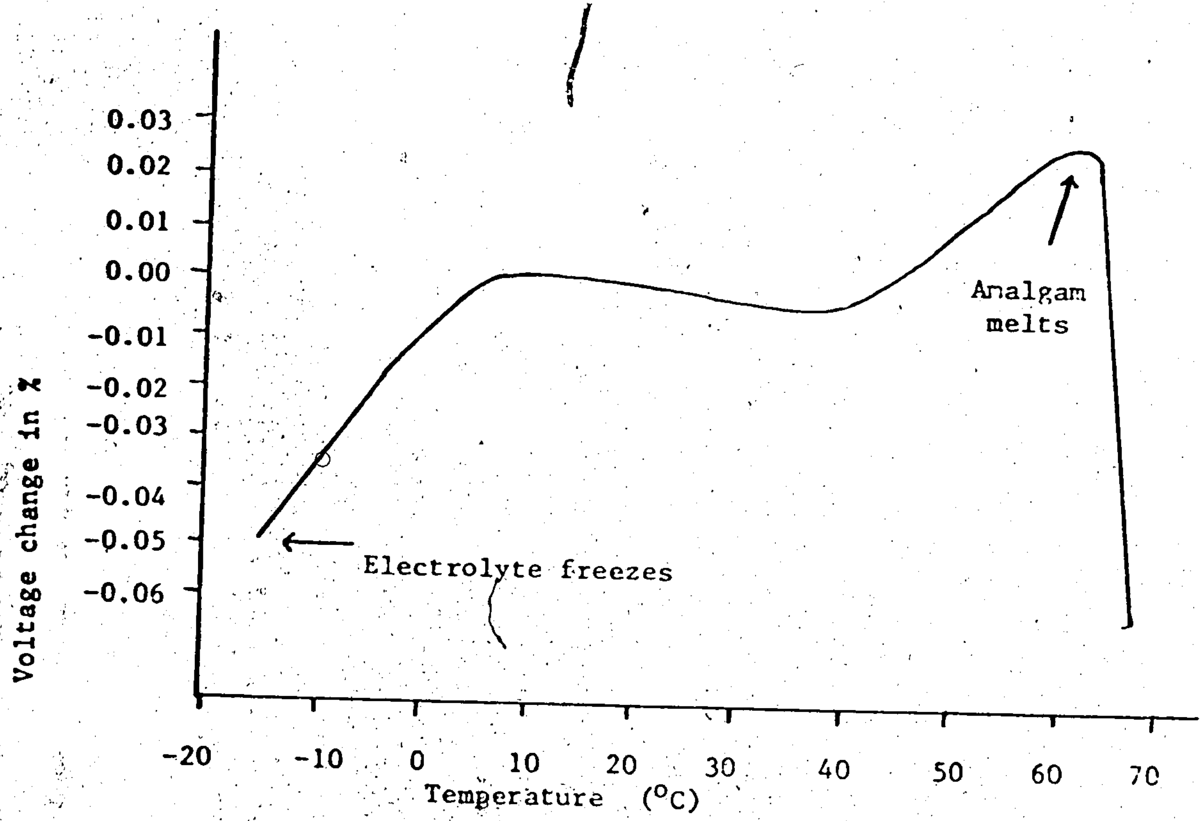


Fig. 33. Temperature response of the standard reference cell used in the Honeywell portable potentiometer. (Information supplied by the Eppley Laboratory, <u>via</u> pers. comm. from Honeywell, Inc.).

the reference cell and insulating the machine with about 5 cm of crumpled newspaper inside a box. At about -15° with a wind between 10 and 20 m/sec, the instrument could be used for about 45 min over a period of 3.5 to 4 hr. Alkaline cells were more reliable than other power sources.

2. Wescor-Keithley psychrometric microvoltmeter. Van Haveran (pers. comm.) determined this meter to be accurate to about -5.5°. Heavy newspaper packing, a handwarmer beneath the machine and short periods of use made the instrument credible for somewhat longer than the Honeywell meter during any one day.

3. Thermocouples. Thermocouples frequently broke while being handled at temperatures below about -12°. Heavy gauge (20 mil) wires proved considerably more durable than 3 mil. Even so, it was helpful to have a large supply of thermocouples constantly with the potentiometer since thermocouple repair is difficult under winter conditions. Duplicate porous cup psychrometers for each point to be measured proved valuable not only because they provided a check of values obtained, but also because they compensated for losses when psychrometric thermocouples broke.

4. Belfort hygrothermograph. The clock tended to freeze below about -15° and required warming to a much higher temperature before it again operated.

APPENDIX II. SOME PROBLEMS OF WINTER ALPINE FIELD STUDIES

Living and working conditions on Trail Ridge during late January through March, 1971, were rigorous. During this period, Emily Dixon, my assistant, and I lived in one of the stone huts of the Rock Cabin Ranger Station. The cabin was equipped with a Norge fuel oil furnace and a butane kitchen range, but lacked electricity. Adequate snow for water was available nearby. The hut was located at 3500 m in a pass exposed to wind off the Continental Divide, an ideal location to keep it from being buried by snow. Heating the cabin was a difficult task, and indoor temperatures were often well below freezing.

Outdoor temperatures and winds were also chilling (Fig. 34). I attempted to work outside a minimum of two 3-4 hr periods daily for 11 or 12 days followed by 2 or 3 days at Estes Park. In retrospect, this was far too much. Four day weeks and fewer hours outside would have been less detrimental to our health.

Mountaineering and arctic literature abound with recommendations concerning cold weather clothing. While most choice of apparel under our working conditions could be based on personal preferences, we found a number of items particularly helpful. An outer windproof layer, a parka hood with a deep tunnel and ruff, and boots with good traction on slippery snow surfaces were essential. My typical dress for -15°C with wind about 15 m sec^{-1} gusting to 45 m sec^{-1} included two knit shirts, a wool shirt, 2 or 3 pairs of long underwear, jeans or wool slacks, wind pants, 3 pr of socks, snowmobile boots with 2 pr of extra insoles, balaclava, a scarf for additional face protection, doubled wool inner mitts, leather and nylon windproof

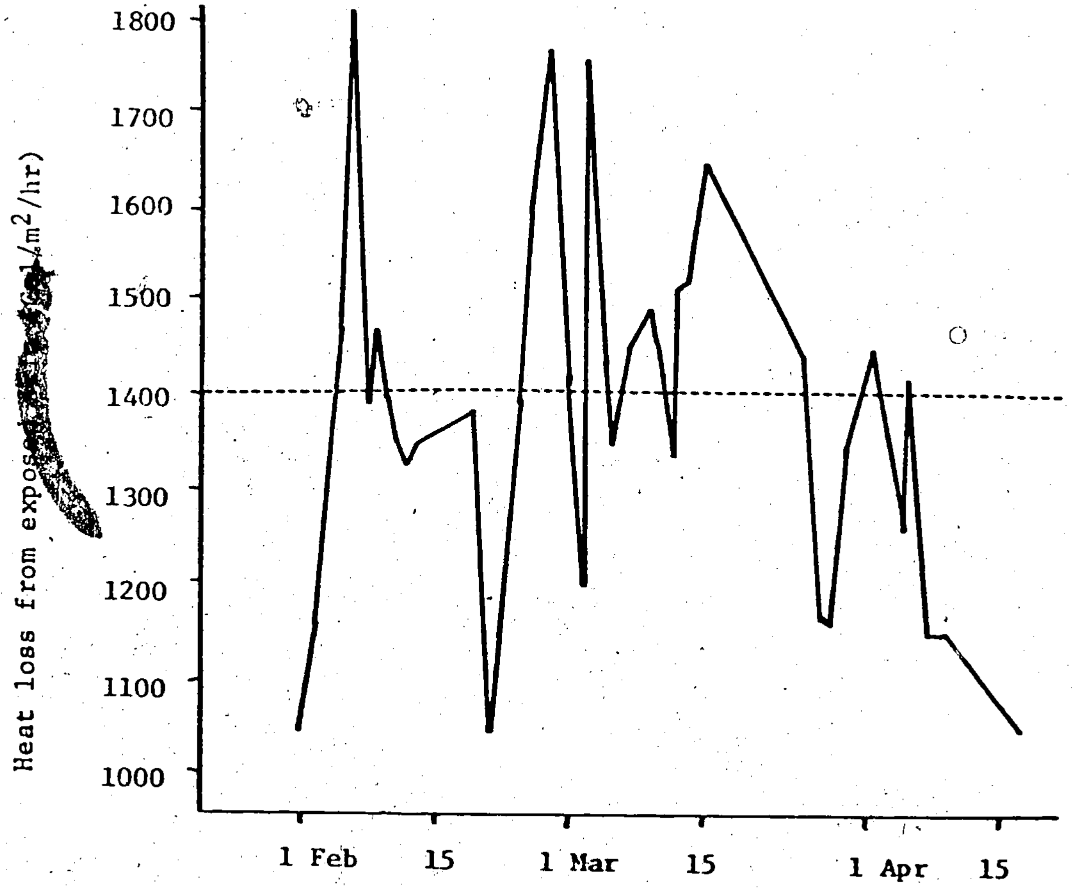


Fig. 34. Mean windchills on Trail Ridge, winter, 1971. Windchill factor was derived after Siple and Passel (1945) using mean wind and temperature for daily periods or groups of days. The broken line at 1400 Cal/m^2/hr represents the approximate lower limit for frostbite danger to exposed flesh. Siple and Passel describe 1100 Cal/m^2/hr as "bitterly cold" in cloudy conditions.

mittens, and an expedition-type down parka with tunnel and fur ruff. We rarely needed snowshoes because the tundra was either snowfree or covered with hard-packed snow.

Apart from maintaining general body warmth, the most critical problems lay in the use of hands. Down mittens are warm, but their bulk makes only clumsy manipulation possible. Wool inner mittens with windproof covers were not quite as warm, but with practice we did such delicate tasks as taking field notes, attaching lead wires to a potentiometer, and opening plastic sacks without removing the mittens. It was usually futile to plan work requiring use of silk gloves or insulated ski gloves before late March. Removing outer mittens was not wise either, since hands numbed within a minute or two and snow blew into the empty mitten openings. It was helpful to carry a pair of thin gloves in a snowfree pocket, but we rarely used them except in relatively good weather.

Frost-covered glasses also caused major problems, and these remained unsolved. Emily was dependent on glasses, and she was unable to deep them cleared. I had difficulty using sunglasses. Their protection from both light and painful blowing snow was offset in mid-winter by their tendency to ice up. A solid steam-deterent product helped somewhat, but was not completely satisfactory.

A few other items of equipment were most helpful. Soft lead pencils wrote best at low temperatures. When paper tended to ice up, soft-surfaced note cards could be scratched and read later. A heavy dandelion digger was (to a limited extent) effective in removing roots from frozen soil. Electrical tape (especially Scotch Brand 300) held better than other sorts, but even that had to be replaced frequently. An ensolite foam pad provided protection while we were kneeling or lying, but it tended to blow away. The high winds demanded that we lower our packsacks on the frame so that they were at shoulder level.

An appropriate diet proved as necessary as adequate clothing. Although we more than doubled our caloric intake over our normal diet, we both lost considerable weight. A very high proportion of fats and carbohydrates helped us stay warmer. Hedbloom (no date) recommends a cold weather diet of 40% fat, 40% carbohydrate, and 20% protein. I estimated ours to have about 35% fat and a little extra carbohydrate and protein. We should have used vitamin supplements. After a large meal, we tended to chill more quickly than usual. Dr. Julia Martin suggested numerous small meals during the day instead of a large lunch so that circulation in peripheral body areas would not be reduced during digestion. This proved beneficial. It became necessary to carry nibbling food (peanuts, raisins, small candies high in glucose) in our parka pockets against sudden fatigue during outdoor work. Finally, our fluid intake was high, approaching 4 liters daily. Sweet warm drinks had obvious physiological as well as psychological benefits.

The psychological environment was almost as stressful as the physical. The greatest problems were with boredom and motivation. Trail Ridge in winter offered steady strong winds, cold, and blowing snow. Glimpses of snow-plumed peaks only occasionally broke the monotony of ground blizzard and roaring wind. Cold inside and out demanded heavy clothing which blunted the sense of touch. Our work was repetitive; and since only simple tasks could be carried out in the cold, it offered little mental stimulation. Only the sense of taste remained a source of pleasant novel experience, and the difficulty of cooking in temperatures below freezing made us frequently avoid the effort necessary to concoct tasty dishes. My personal reaction was to avoid the physical environment and withdraw in my mind to others, at first through reading, then increasingly through daydreams as turning pages with gloved hands demanded too much motivation. "Civilization" became difficult to deal with, and short weekends twice a month did not force me to come completely out of this mental retreat. Emily wisely dealt with the problems she faced by taking a 10 day break in March. Thus at the end of the three month period I became heavily dependent on her to make almost all decisions.

Despite the often unpleasant surroundings, my drive to achieve certain goals was almost always strong enough to keep me working. I was motivated both by curiosity and by a desire to prove that I could work under any conditions. This probably was necessary to accomplish research objectives. On the other hand, such a high level of motivation clouded my judgement; and I tended to put field work ahead of both comfort and safety. If I knew that 20 min more work would give me some data I wanted, I let my toes get frost-bitten. Emily, with somewhat less at stake in the research, was not motivated to work this way. Her reluctance often helped to balance my fanaticism.

The winter months on Trail Ridge were not unrewarding. The location is spectacular, and winter storms have their own beauty. Emily and I shared many jokes and many prayers, and our friendship was warm. Both of us developed in self-confidence and in faith in God. And some of my curiosity about what alpine plants do in winter was satisfied.