WATER LIMITATIONS AND PLANT COMMUNITY DEVELOPMENT IN A POLAR DESERT[1]

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Abstract. Polar deserts of the High Arctic contain vast areas of minimal plant cover and low primary productivity. Significant development of polar desert plant communities is largely restricted to areas with considerable cover of a cryptogamic soil crust, which develops in sites exposed to continued surface runoff from melting snow for some of the short growing season. Thus, soil drought and plant water stress have often been assumed to be major constraints to plant community development in polar deserts. To examine this issue, water availability and plant water relations of common herbaceous perennial plants were studied over three growing seasons in a typically barren ("noncrusted") site and a site with a well-developed cryptogamic crust and vascular plant community ("crusted"). Soil water content was consistently higher in the crusted site than the noncrusted site through all growing seasons. These differences had limited biological relevance because subsurface soils at both sites remained effectively saturated (soil water potential > -0.1 MPa) through each growing season, despite low amounts of precipitation that varied nearly twofold from year to year. However, the surface soils (0.5–2.0 cm in depth), especially in noncrusted sites, dry considerably in some years. There were no significant differences in plant water potential and midday values of whole-plant transpiration and water vapor conductance for adult plants growing in crusted vs. noncrusted sites. Water stress for established plants was minor in both sites. Greater plant community development in crusted areas of this polar desert does not result from a reduction in plant water stress by a greater supply of meltwater through the growing season. Instead, surface meltwaters probably benefit vascular plants indirectly by facilitating the growth, development, and nitrogen fixation activities of cryptogamic organisms in the soil crust. The presence and activity of these cryptogams favor vascular plant success through increased nutrient availability, soil organic matter, surface temperatures, reduced soil cryoturbation, and more favorable sites for germination and seedling establishment.

Key words: arctic; cryptogams; Devon Island, Canada; plant community development; polar deserts; soil crusts; soil moisture; water availability; water relations.

INTRODUCTION

Large expanses of the High Arctic are occupied by polar deserts (Aleksandrova 1983, Bliss and Matveyeva 1992). These landscapes are characterized by a sparse cover (<5%) of prostrate vascular plants scattered within a matrix of frost-sorted features. The floristic diversity and cover of mosses, cyanobacteria, fungi, and lichens are considerably greater than those of the vascular species, but cryptogam distribution is largely restricted to sites of higher moisture availability (Bliss et al. 1994). In such sites, these cryptogams form a thin (<1 cm) crust layer on the soil surface. Vascular plant diversity and production reach a maximum in these areas of high cryptogamic cover.

Short growing seasons and low temperatures provide an overall limitation to biological productivity in the High Arctic. Low summer precipitation is also characteristic, especially in the North American portion. However, there are areas of the High Arctic that support much higher plant diversity and primary productivity

than do the polar deserts. These include widespread semideserts and isolated coastal and valley areas ("polar oases") that are comparable to wet tundras of the Low Arctic (Bliss 1988, Svoboda and Freedman 1994). The major constraints to plant community development on polar deserts are poorly understood, but it has commonly been assumed that soil drought is quite important (Bliss et al. 1984). It is obvious on the landscape that the maximum development of vascular and nonvascular plant cover is closely associated with greater moisture input during the growing season. Sites with well-developed communities are generally located downslope from persistent snow banks or in seasonal stream beds (Bliss et al. 1984, 1994).

Moisture availability has an important role in controlling the range of community productivity in low arctic tundras (Chapin and Shaver 1985). Plant water stress often correlates with community composition and production on a local mesotopographic scale (e.g., Oberbauer and Miller 1979). In addition to such direct moisture limitations on the vegetation, indirect moisture effects, such as the control of nutrient supply rates by water flux (Chapin et al. 1988), can be important. Variation in community composition, cover, and pro-

duction within a high arctic polar oasis, Truelove Low-
land, is highly correlated with patterns of water flow
and retention controlled by local topography (Muc and
Bliss 1977). These patterns of moisture availability also
correspond to patterns of plant water stress (direct ef-
fects) and nutrient availability (indirect effects). Mois-
ture limitations have frequently been cited as a major
controlling factor in Russian polar deserts but few data
are available (Aleksandrova 1983). Moisture avail-
ability has been qualitatively identified as the most in-
fluential environmental factor in the distribution of spe-
cies and life-form assemblages on an upland of Elles-
mere Island, Canada (Batten and Svoboda 1994). The
degree of water limitations and the relative importance
of direct and indirect effects have not been quantita-
tively assessed for polar desert areas.

The objective of this study was to examine the nature
of moisture limitations for vascular plants in a polar
desert landscape. Is the correlation of moisture avail-
ability and vegetation patterns evident on the polar des-
ert landscape a result of direct impacts on plant water
status, or are indirect effects also important? We mon-
itored soil moisture content and availability, plant wa-
ter status, and plant water use through three growing
seasons at a high arctic polar desert location. The in-
vestigations were part of an integrated study of polar
desert ecosystem development, including research on
nutrient cycling, soil genesis, nitrogen fixation, insect
communities, and vascular plant ecology.

SITE DESCRIPTION

Our study was located on a plateau (330 m above
sea level) above the northeast coast of Devon Island,
N.W.T., Canada (75°39′ N, 84°24′ W). This plateau site
is immediately adjacent to Truelove Lowland, a mosaic
of lush coastal graminoid meadows and dry raised
beach ridges, which has been the focus of much inten-
sive research (Bliss 1977).

The Devon Island plateau consists mainly of Arctic
Platform sediments (mostly fine-grained dolomite)
above the basement crystalline rocks (Krupicka 1977).
The landscape of this plateau is dominated by networks
of sorted stone nets and stripes which have formed on
the dolomitic substrate. Cryogenic processes are re-
sponsible for the segregation of finer grained (silt) par-
ticles from the coarser fraction, resulting in these pat-
terns. Such cryogenic features are common in the polar
desert of the Queen Elizabeth Islands and Svalbard.
Horizon development is absent in the soils, which are
classified as Pergelic Cryochrepts by the USDA soil
taxonomy system (Soil Survey Staff 1992). These soils
have almost no organic matter, low levels of macro-
nutrients, and are mildly to moderately alkaline (pH
from 7.4 to 8.6; R. Sletten and F. Ugolini, *unpublished
data*).

The short growing season is characterized by dry,
cool weather but is also highly variable (Fig. 1). The
1991 season was one of the warmest in the past 25 yr,

while 1992 was the coldest, with only 16 d snowfree
on the plateau. Meteorological data gathered during our
brief 1993 sampling period were insufficient for pre-
sentation. Mean daily air temperatures at 50 cm ranged
from −1° to 14°C through the summer for these two
years. Daily fluctuations in air temperature are small
(usually <5°C), due to continuous solar irradiance, but
surface temperatures can fluctuate by up to 20°C
through the day. Mean daily soil temperatures in the
rooting zone (5 cm depth) follow variations in air tem-
perature closely, ranging from 1° to 13°C during the
growing season. Daily integrated irradiance ranged
from 54 to 57 mol/d photosynthetic photon flux density
(PPFD) on clear days, to 8 to 10 mol/d PPFD under
heavy cloud cover. Hourly mean PPFD ranged from
150 to 1200 μmol·m^{-2}·s^{-1} during a clear day in the
middle of the growing season. The highest readings of
instantaneous PPFD occurred on days that were partly
cloudy (1600 to 1800 μmol·m^{-2}·s^{-1}) rather than cloud-
less (1300 to 1400 μmol·m^{-2}·s^{-1}), possibly as a result
of enhanced Rayleigh scattering (Monteith and Uns-
worth 1990). Precipitation was low, infrequent, and
highly variable between years. Total precipitation for
July was 33 mm in 1991 and 55 mm in 1992. The
atmospheric water vapor pressure deficit was generally
low (<12 mmol/mol). Winds are usually minor through
the early and middle portions of the growing season,
while brief periods of intense foehn winds can occur
in the late season of some summers.

Vascular plant cover on the Devon Island plateau is
generally quite low (<3%) except in limited areas near-
er the coastal edge, where it may approach 10–15%
(Bliss et al. 1994). These biologically richer sites are
characterized by a well-developed soil surface crust of
nonvascular species (cyanobacteria, fungi, lichens, and
mosses) which can provide a total cover of the fine
material in some areas. Areas of well-developed crust
usually occur downslope of persistent snowbanks and
in drainages. Only 16 species of vascular plants have
been described from this site, but many more species
of nonvascular plants are present (N. Matveyeva, *per-
sonal communication*). Vascular plant nomenclature
follows that of Porsild and Cody (1980).

METHODS

In order to examine the importance of water avail-
ability, we selected two major sampling locations to
represent extremes along a continuum of biological de-
velopment on the local polar desert. We compared wa-
ter availability and water relations of dominant vascular
species in a typically barren ("noncrusted") site with
those growing in an area of well-developed crypto-
gamic crust ("crusted" site) composed of a variety of
nonvascular plant species. The designation of sites as
crusted or noncrusted in this study refers only to the
presence or absence of a thin biological surface crust
rather than a physical crust of the soil surface. Plant
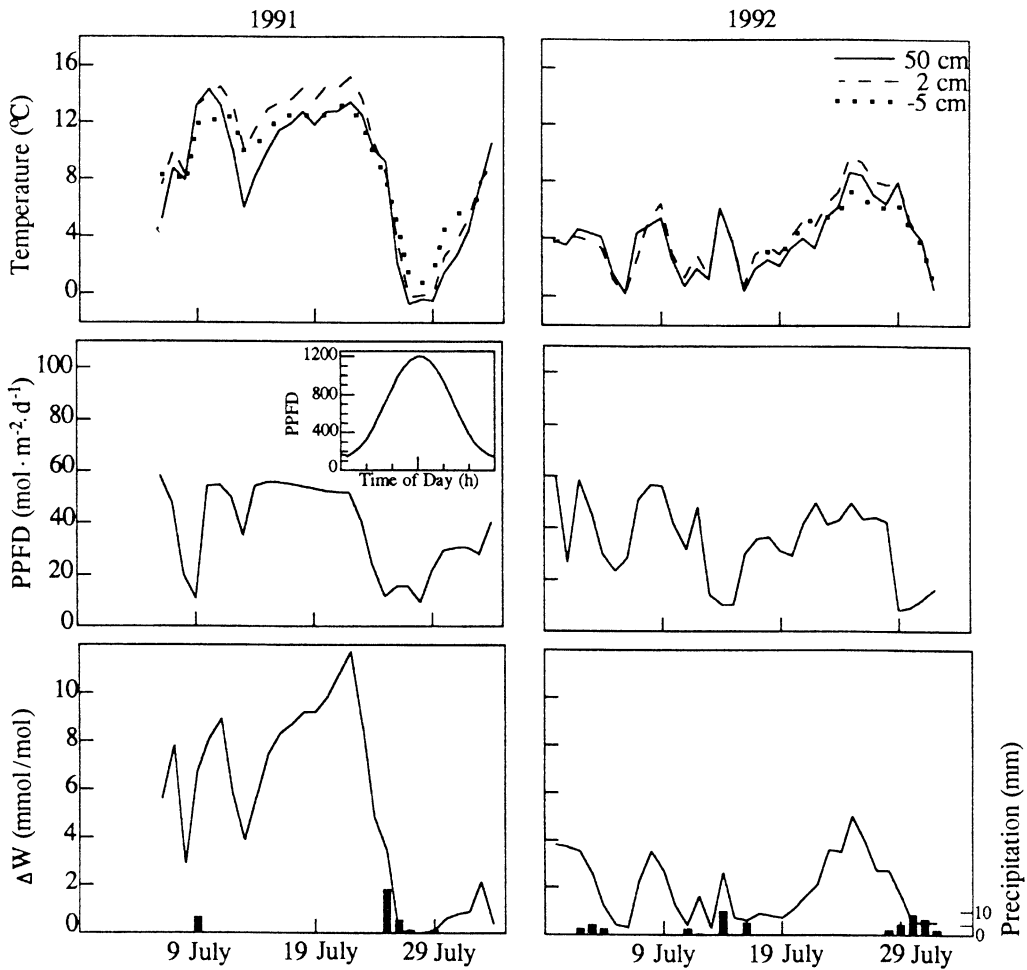cover was evaluated for each site with thirty 20 × 50

FIG. 1. Seasonal courses of mean daily air temperature at 50 cm and 2 cm above the ground surface, soil temperature at −5 cm depth, total daily photosynthetic photon flux density (PPFD), mean daily atmospheric water vapor deficit (ΔW), and precipitation (solid bars) in 1991 and 1992 at the Devon plateau research location. Inset figure depicts one 24-h period (at 4-h intervals) of mean hourly PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$) during a clear day in the middle of the growing season (15 July 1991).

cm quadrats in a stratified random design (Bliss 1963). Although >77% of the ground surface was occupied by biological material in the crusted site, vascular plants accounted for only 9.1%, with the remainder being the cryptogamic soil crust (Table 1). The surface of the noncrusted site was nearly all occupied by rock or bare soil, with only 3.3% vascular plant cover.

TABLE 1. Percent ground surface cover (mean ± 1 SE) of crusted and noncrusted sites from 30 randomly located 20 × 50 cm quadrats in each site on the Devon Island plateau, Canada. Cover values for all plants and rocks are vertical projections.

	Crusted site	Noncrusted site
Vascular plants	9.1 ± 0.8	3.3 ± 0.9
Nonvascular plants	68.3 ± 2.9	2.7 ± 0.6
Litter	2.3 ± 0.5	1.7 ± 0.5
Rock	20.7 ± 2.3	67.7 ± 1.7
Bare soil	0.0 ± 0.0	24.8 ± 1.4

Soil moisture

Gravimetric soil moisture content was monitored by extracting 2 cm diameter soil cores (n = 4 in 1991; n = 12 in 1992 and 1993) through the major rooting depth (0–10 cm). Cores were transported to the lowland laboratory for weighing and drying over a heating stove to a constant weight (>48 h). In 1993, subsamples of dried soil were returned to Seattle for further drying at 105°C in a forced air oven for 48 h. No significant differences were found between dry weights measured in the field laboratory and those obtained following drying under standard conditions in Seattle.

The relationship of gravimetric water content to soil water availability was determined with a pressure plate apparatus (Soil Moisture Equipment). Intact soil cores (5 cm diameter) were excised from the upper 10 cm of the soil, preserving the physical structure as much as possible, and returned to Seattle in closed metal containers. Segments 1 cm thick were carefully removed

from each core at the 5–6 cm depth, and each sample was run through a sequential series of pressures (0.03, 0.1, 0.3, 0.5, 1.0, 1.5 MPa) while water content was monitored (Richards 1949). Four replicate soil cores from each site were used in both 1991 and 1992.

Plant water relations

A comparison of maximum soil moisture availability in crusted and noncrusted sites was accomplished by measuring shoot xylem pressure potential of plants that had been covered from 0400 to 0800 h. Individual cushions of *Draba corymbosa* and *Saxifraga caespitosa* were covered with a plastic container coated with aluminum foil on the outside to reduce heating. Cushion temperatures in the covered containers averaged only 2°–3°C higher than exposed cushions during that time period. Measurements were done twice during the 1992 season (12 and 19 July) on four plants of each species at each site. These are analogous to predawn xylem pressure potential measurements where the plant, with a given hydraulic resistance, is assumed to have come into moisture equilibrium with the soil during nighttime stomatal closure. Such nighttime darkness does not occur at our site during the growing season, and nighttime stomatal opening was considered possible. Preliminary measurements with a gas exchange system (modified LI-6200, LI-COR) demonstrated that stomatal closure occurred on the two species used within 10 min of darkening.

Shoot xylem pressure potential of vascular plants was measured with a Scholander-type pressure chamber (PMS). Entire shoots of selected species were excised by severing the main stem at the ground surface, and the shoots were rapidly enclosed in the pressure chamber. The small size and cushion plant morphology of most of the vascular species made it impossible to use individual leaves or branches for such measurements. Midday pressure potential measurements were taken on five major species (*D. corymbosa, Minuartia rubella, Papaver radicatum, Saxifraga caespitosa,* and *S. oppositifolia*) in both crusted and noncrusted sites through the growing season of 1991 and 1992.

Patterns of whole-shoot xylem pressure potential were corroborated by parallel measurements of leaf tissue water potential of three species (*D. corymbosa, S. caespitosa,* and *S. oppositifolia*) on 12 and 19 July 1992. Seven to ten green mature leaves were clipped from plants at midday, the same day of the xylem pressure potential measurements and immediately placed into a small stainless steel chamber of a Decagon model SC-10A thermocouple psychrometer sample changer. Samples were transported to the lowland laboratory, where the water potential of each sample was measured along with KCl standards under controlled-temperature conditions (20°–25°C). Three replicates from different plants of each species were measured at each date.

Water vapor flux

Instantaneous plant water vapor fluxes were measured with a modified LI-COR LI-6200 closed gas exchange system. A specially-designed cuvette (0.93 L) was constructed for use with these cushion-form species. The chamber was built as a rectangular design with a clear teflon-coated polycarbonate frame incorporating large windows on the top, front, and two sides. These windows were covered with Propafilm-C, a thin plastic sheeting which is highly transparent to infrared radiation. This reduced problems of solar heating inside the chamber during measurements. All measurements were done within 3°C of ambient temperature. A fan mounted on one side at average cushion height provided air mixing. Leaf temperature was monitored with a fine wire thermocouple, and chamber air temperature and water vapor concentration with a thermistor and solid state capacitance sensor (Vaisala), respectively. Measurements were made with chamber [CO_2] within 12 μL/L of ambient air concentration (358–363 μL/L).

Entire shoots of these species were enclosed in the chamber by placing a split polycarbonate baseplate around the central stem after gentle excavation of the surrounding soil surface (<1 cm). Terostat putty (Teroson) was added around the stem to ensure an airtight seal. The seal was tested prior to each measurement by monitoring chamber [CO_2] while a high-concentration CO_2 source was introduced at potential leakage points. Ambient air was pumped through the chamber in an open configuration for 5 min before the system was placed in a recirculating (closed) mode for measurements. Three measurement periods of 1–2 min each were interspersed with 5-min periods of open circulation to check for repeatability. The change in chamber water vapor concentration was minimized by adjusting the portion of air flow returning to the chamber that was passed through a desiccant column. Because of the small leaves and complex architecture of these cushion plants (*Saxifraga caespitosa* and *S. oppositifolia*), we did not partition water vapor conductance into stomatal and boundary layer components. Whole-shoot total conductance (stomatal plus boundary layer) was calculated from the measured rates of water vapor flux and environmental conditions within the chamber. This probably overestimates conductance under natural conditions because the chamber fan disrupts the canopy boundary layer. Estimates of whole-canopy transpiration under ambient conditions were made by multiplying values of shoot conductance by the leaf-to-air vapor pressure gradient for plants outside the chamber. Relative humidity and leaf and air temperatures necessary for the calculation of leaf-to-air vapor pressure gradients were continuously monitored at canopy height with fine wire thermocouples and resistance humidity sensors (Phys-Chem Scientific). Estimated transpiration and water vapor conductance of *S. caespitosa* are expressed relative to the total leaf area (one-sided) of
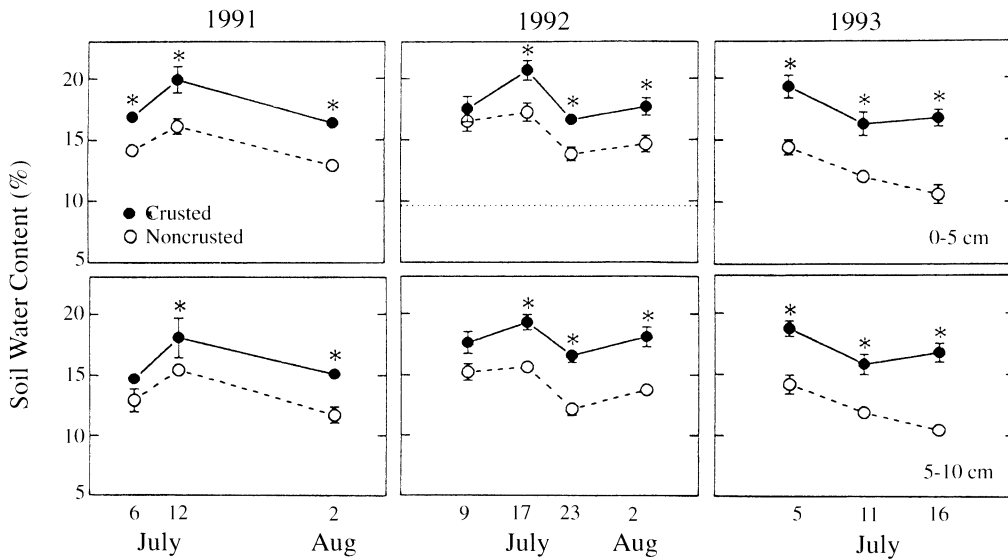
FIG. 2. Seasonal pattern of gravimetric soil water content at crusted and noncrusted sites on the Devon plateau for three summers at two depth increments, 0–5 cm (upper row) and 5–10 cm (lower row). Means ($n = 4$ in 1991 and $n = 12$ in 1992 and 1993) are presented with ± 1 SE bars. Asterisks indicate significant differences ($P < 0.05$) between sites at each date by Student's t test. Note different time scale on abscissa for 1993. The dotted line indicates the estimated soil water content for either site equivalent to a soil water potential of -0.1 MPa as calculated from least squares exponential curve fits to soil moisture release data (Fig. 3).

each plant measured. Following water vapor flux measurements, each plant was harvested and green leaves were isolated and pressed. Leaf area was later determined on a leaf area imaging system (Delta-T). Values for *S. oppositifolia* are expressed on the basis of a horizontal projection of the green leaf area exposed at the tip of each branch.

Leaf tissue and soil total nitrogen and phosphorus concentrations were determined on a Technicon autoanalyzer following a modified Kjeldhal digestion (Parkinson and Allen 1975).

RESULTS

Soil moisture

Soil water content in the most densely-occupied portion of the rooting zone (0–10 cm) remained significantly higher (by up to 7.7%) in crusted sites than noncrusted sites through most of the 1991, 1992, and 1993 growing seasons (Fig. 2). Within-sites soil moisture content was similar through the three years despite large differences in growing-season precipitation (33 mm and 55 mm, respectively, in 1991 and 1992, and only 1 mm in the brief sampling period of 4–20 July 1993). Seasonal patterns of soil moisture differed among years due to variation in the timing of snow melt and subsequent weather patterns. Soil drying occurred at similar rates in crusted and noncrusted sites during 1991. Little drying occurred in 1992, due to low temperatures and greater precipitation. In 1993, there is an indication of more rapid soil drying in the noncrusted site by mid-July, but the driest soils still ex-

ceeded 10% moisture content despite low precipitation. The surface soils (0–1 cm), particularly in the noncrusted site, dried more rapidly than the subsurface soils in July 1993.

Moisture-retention characteristics differed between soils taken from crusted and noncrusted sites in both 1991 and 1992 (Fig. 3). However, these differences occurred only at moisture contents of $\leq 7\%$, which were never observed in the field. Above 10% moisture content, soil water potential remained > -0.1 MPa in both soils. Field soil water potentials were estimated from the measurements of soil water content by fitting a least squares exponential curve to the 1991 moisture retention data (Fig. 3; $R^2 = 0.93$ for either crusted or noncrusted sites).

Plant water relations

Midday shoot water potentials of four major polar desert species declined through the summer of 1992 (Table 2), in parallel with a seasonal decline in soil moisture content during July (Fig. 2). However, these declines were not large, ranging from 0.04 to 0.29 MPa. There were no significant differences in shoot water potential among plant species, and few differences between plants in crusted and noncrusted sites. Crusted-site plants had lower midday water potentials on 19 July, but these differences were small: from 0.09 to 0.25 MPa. The low water potentials observed early in 1991 were indicative of earlier snow melt and drier, sunnier conditions. In all cases, plant water stress appeared minor, with minimum average shoot pressure
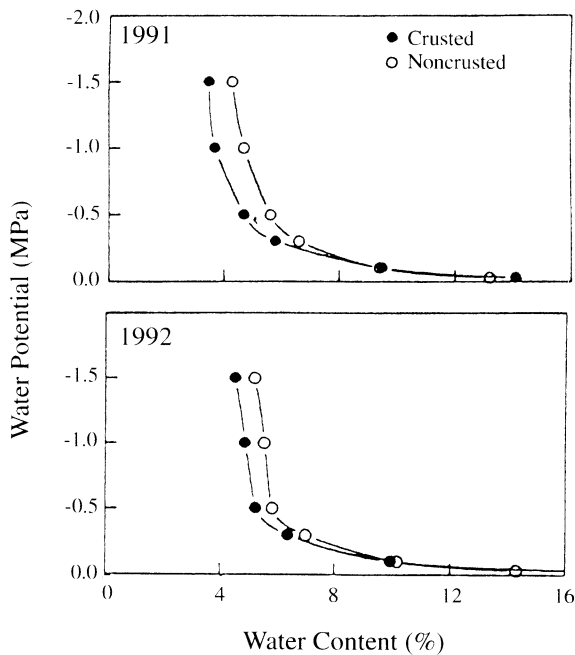
FIG. 3. Soil moisture release curves for soils collected in 1991 and 1992 from crusted and noncrusted sites. Each data point is a mean of six replicates.

TABLE 3. Comparison of plant water potential (MPa) in crusted vs. noncrusted sites on the Devon Island plateau, as measured by a thermocouple psychrometer (leaf tissue) and a pressure chamber (whole shoot) for two species in 1992. Means ($n = 4$) are presented $\pm$ 1 SE. Superscript letters indicate significant ($P < 0.05$) differences between sites within each technique by species combination. Differences were evaluated with Tukey's multiple comparison test following ANOVA.

Water potential	Site	12 July 1992 Draba corymbosa	19 July 1992 Saxifraga caespitosa
Leaf	Crusted	$-.61 \pm .61$	$-.82 \pm .49$
	Noncrusted	$-.57 \pm .38$	$-.77 \pm .48$
Shoot	Crusted	$-.43 \pm .07$	$-.65 \pm .04$[b]
	Noncrusted	$-.45 \pm .03$	$-.46 \pm .05$[a]

potentials for all species of only -0.92 and -0.71 MPa for 1991 and 1992, respectively (Table 2).

In 1992, there were no differences in leaf tissue water potential of plants in crusted and noncrusted sites. Measurements of leaf tissue water potential were much more variable and consistently lower (0.12 to 0.31 MPa) than measures of whole-shoot water potential (Table 3). Little seasonal variation in leaf tissue water potential was apparent (data not shown), although the 1992 growing season was unusually short and moist.

Diurnal patterns of plant water status in 1992 showed declines in water potential from early morning through late afternoon for plants in both crusted and noncrusted sites (Fig. 4). The timing and severity of these water potential declines were usually similar for plants in both sites (e.g., Fig. 4A), but on 19 July the decline was

greater at the crusted site for most species (e.g., Fig. 4B). Both soil moisture content and estimated rooting-zone soil water potential remained constant through the day. Plants that were covered for the period from 0400 to 0800 h had shoot water potentials ≈ 0.20 to 0.25 MPa lower than the saturated soil, indicating a small but consistent hydraulic resistance. Preliminary gas exchange results showed that stomatal closure in these species took place within minutes of darkening. Thus, covered plants should have achieved maximum stomatal closure for a substantial period of time prior to water status measurement. Despite this period of stomatal closure, the water potential of these covered plants was not significantly different from that of plants measured at 0400 h prior to covering. This suggests that substantial stomatal closure takes place at night in these species, despite the natural nighttime irradiance (see inset in Fig. 1).

Midday maximal whole-shoot water vapor conductance of plants in crusted and noncrusted sites did not differ late in the 1991 growing season (Table 4). There were no significant differences between the two Saxifraga species, although a rosette species, Papaver radicatum, had considerably higher maximum whole-shoot conductance values (370 and 320 mmol·m^{-2}·s^{-1} for crusted and noncrusted sites, respectively) than the cushion-form saxifrages. Estimated midday maximum

TABLE 2. Midday whole shoot pressure potentials (MPa) of major polar desert species in 1991 and 1992 on the Devon Island plateau. Data are mean $\pm$ 1 SE ($n = 3–5$). Superscript letters indicate significant differences ($P < 0.05$) between sites for a species on one date. Differences were evaluated with Tukey's multiple comparisons test following ANOVA.

| Date	Site	Draba corymbosa	Papaver radicatum	Saxifraga caespitosa	Saxifraga oppositifolia	Minuartia rubella
10 July 1991	Crusted	$-.77 \pm .02$	$-.58 \pm .06$	$\cdots$	$-.78 \pm .04$	$-.82 \pm .04$
	Noncrusted	$-.75 \pm .05$	$-.83 \pm .26$	$\cdots$	$-.73 \pm .05$	$-.92 \pm .04$
12 July 1992	Crusted	$-.43 \pm .07$	$-.55 \pm .06$	$-.47 \pm .02$	$-.40 \pm .03$	$\cdots$
	Noncrusted	$-.45 \pm .03$	$-.42 \pm .04$	$-.43 \pm .04$	$-.40 \pm .03$	$\cdots$
19 July 1992	Crusted	$-.40 \pm .04$[a]	$-.65 \pm .04$[b]	$-.60 \pm .03$[b]	$-.67 \pm .08$[b]	$\cdots$
	Noncrusted	$-.49 \pm .04$[a]	$-.46 \pm .05$[a]	$-.43 \pm .05$[a]	$-.42 \pm .03$[a]	$\cdots$
24 July 1992	Crusted	$-.65 \pm .03$	$-.67 \pm .04$	$-.51 \pm .02$	$-.62 \pm .03$	$\cdots$
	Noncrusted	$-.58 \pm .01$	$-.71 \pm .04$	$-.54 \mp .03$	$-.69 \pm .04$	$\cdots$
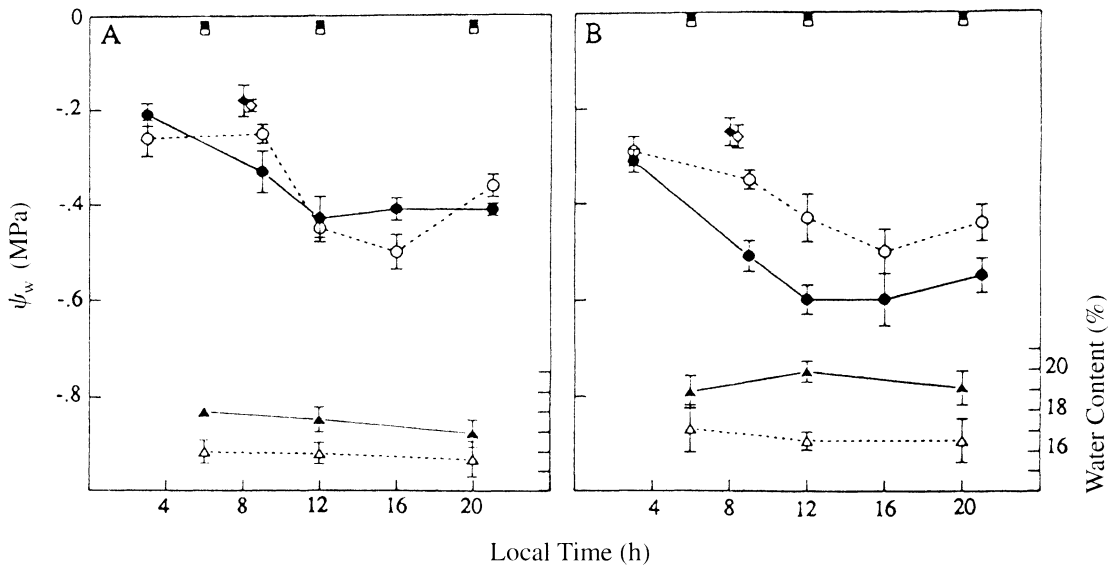
FIG. 4. Diurnal patterns of shoot water potential (circles) of (A) *Draba corymbosa* on 12 July 1992, and (B) *Saxifraga caespitosa* on 19 July 1992 (*n* = 5 in both cases). Diurnal patterns of soil water content (triangles) are given for (A) 9 July 1992, and (B) 17 July 1992 (*n* = 4). Squares indicate rooting-zone mean soil water potential estimated from water content data and least squares exponential curve fits to soil moisture release data (see Fig. 3). Diamonds show measured shoot water potential of covered plants (see *Methods: Plant water relations; n* = 4). Closed symbols indicate measurements taken in the crusted site, while open symbols indicate the noncrusted site. Means are presented with ± 1 SE bars.

transpiration for entire shoots followed similar patterns, with no differences between plants in crusted or noncrusted sites. Similar patterns were seen late in the short 1992 growing season, but inclement weather patterns prevented sufficient data from being gathered.

DISCUSSION

The remote locations and severe environment of polar deserts have proved to be formidable barriers for biological research. Most of the ecological investigations in the High Arctic have focused on semidesert landscapes (e.g., Sohlberg and Bliss 1984, Grulke and Bliss 1988) and isolated, highly-productive coastal polar oases, such as Truelove Lowland (Bliss 1977, Dawson and Bliss 1989) and Alexandra Fiord on Ellesmere Island, N.W.T., Canada (Svoboda and Freedman 1994). Plant cover and community development are much greater in these areas than in the polar desert landscapes. Vascular plant cover in our upland Devon Island study sites never exceeded 22% (even in the species-rich snowflush area) and was usually much less than 10%. The cover of vascular species in our noncrusted site (0–5%) was comparable to many of the polar barren sites described by Zoltai and Woo (1976) and Bliss et al. (1984) in a survey of the Canadian arctic islands. Net annual production in such barren areas averages just 1 g/m^2 (Bliss and Svoboda 1984, Bliss and Matveyeva 1992). In comparison, semidesert and oasis areas (sedge–moss mires) typically have 35 and 140 g/m^2 of net annual primary production, respectively (Bliss and Matveyeva 1992).

Moisture limitations

In addition to having low maximum development of vascular plant communities, polar deserts show patchy distribution of the most productive areas. Previous vegetation surveys have suggested that the development of such areas of greater productivity is limited by moisture availability (Aleksandrova 1983, Bliss et al. 1984, 1994). Sparse growing-season precipitation and rapid development (<2 wk) of a dry surface soil layer following snow melt in many areas have suggested poor moisture availability for plants. Further, the restriction of more highly productive areas to "snowflush" sites has caused some to propose water as the major limitation to plant communities on the polar desert. These snowflush sites receive a continuing water supply from melting snow for a considerable time during the summer, and have well-developed cryptogamic soil crusts

TABLE 4. Whole-shoot water vapor conductance (H$_2$O in mmol·m^{-2}·s^{-1}) and estimated transpiration (H$_2$O in mmol·m^{-2}·s^{-1}) at midday from 1–3 August 1991, Devon Island. Means (*n* = 3–4) are presented ± 1 SE. No significant (*P* < 0.05) differences were detected between sites within species by Student's *t* test.

Species	Site	Conductance	Transpiration
Saxifraga caespitosa	Crusted	200 ± 2	2.8 ± .5
	Noncrusted	170 ± 4	2.4 ± .5
Saxifraga oppositifolia	Crusted	220 ± 2	3.0 ± .9
	Noncrusted	180 ± 2	2.4 ± .3

along with richer vascular plant communities. Our re-sults indicate that, indeed, soil moisture content is high-er in such snowflush sites throughout the summer. En-hanced soil water content in snowflush areas is a well-known phenomenon in alpine areas (Billings and Bliss 1959, Oberbauer and Billings 1981, Isard 1986). This is often associated with both increased productivity and a change in community composition to more hydro-phytic species (Oberbauer and Billings 1981, Isard 1986). Batten and Svoboda (1994) have recently con-cluded that soil moisture is the most influential envi-ronmental variable affecting the distribution of plant communities on an upland site (475–975 m a.s.l.) on Ellesmere Island, Canada (79° N latitude). Discrete changes in plant communities with reduced water avail-ability are evident on dry, raised gravel beach ridges within the adjacent lowland polar oasis on Devon Is-land (Muc and Bliss 1977). However, such discrete changes in plant communities from barren areas to snowflush sites are not so evident within this polar desert area. Rather, snowflush communities include the species found in more barren locations along with ad-ditional species restricted to the snowflush locations (see Bliss et al. 1994).

Although the differences in soil water content of crusted and noncrusted sites seem to support the notion of water limitations, these differences were of little direct biological consequence to the adult vascular plants. The water potential of soils in both sites re-mained >-0.1 MPa, effectively saturated, throughout all three growing seasons. Soil water content must fall below 6–8% before appreciable soil moisture stress de-velops (see Fig. 3). The minimum water contents ob-served in the rooting zone were consistently 10–13% in all three years, despite large differences in precip-itation, temperature, and insolation. Data from a nearby site on the same plateau through the 1974 growing season also showed an early-season decline in soil moisture (0–5 cm depth) from 22% to 13%, a steady value of 12% for 4 wk, and a recovery to 19% with the onset of late-season precipitation in August (Schul-ten 1981). Thus, despite the visually-obvious drying of the soil surface (0–1 cm deep) following snow melt, subsurface soils remain effectively saturated, and mois-ture availability to adult vascular plants is high. Con-sequently, the measures of plant water potential indi-cated only small seasonal changes and minor moisture stress of adult plants. Plants growing in snowflush (crusted) sites did not experience less water stress than those in barren areas. This was reflected by similar whole-plant and leaf tissue water potentials for plants in these areas. The shoot water potentials of these polar desert species are well within the range of values re-ported for high arctic plants from wet habitats such as sedge–moss meadows (Bliss 1995). In fact, our shoot water potentials of *S. oppositifolia* are comparable to leaf water potentials reported for that species from nearby wet meadows of Truelove Lowland, Devon Is-

land (−0.2 to −0.9 MPa; Teeri 1972). Raised gravel beach ridges within Truelove Lowland provide the most xeric local habitats, with mean leaf water potentials of *S. oppositifolia* populations reported from −0.5 to −1.7 MPa, and some individuals as low as −4.4 MPa (Teeri 1972).

Polar desert soils that remain saturated through the summer are well-known in the Russian literature (see Aleksandrova 1983). Soil moisture is thought to be maintained by absorption of water from the thaw front at the base of the active layer. We have observed a very rapid wicking capacity of the dolomitic soils from our sites in laboratory experiments. Lateral flow of water in soils underlain by permafrost is well-described (Woo 1986), but little is known about vertical transport of water from the thaw front up to the shallow rooting zone of high arctic herbaceous perennials.

Diurnal patterns of plant water deficits and instan-taneous water fluxes were also remarkably similar for plants in these sites. Maximum whole-shoot water va-por conductances of these cushion species are similar to maximal stomatal conductances reported for other high arctic species in typically more moist and more productive habitats, such as sedge–moss meadows and semideserts (Oberbauer and Dawson 1992). This re-flects the high degree of moisture availability for these plants and the minimal boundary layer present within the cuvette during measurements. Alpine cushion plants, including *Saxifraga oppositifolia*, have been re-ported to have lower canopy water vapor conductances than our results in wind-exposed habitats (40–60 mmol·m^{-2}·s^{-1}), and higher values (300–400 mmol·m^{-2}·s^{-1}) in wind-protected locations (Körner and De Moraes 1979). Cushion plants on the Devon Island plateau generally occupy exposed habitats, but typical wind speeds at plant canopy height are only 0.5 m/s in July. Low soil temperatures and concomitant reduced water uptake, common to both arctic and alpine sites, may be principally responsible for the overall low rates of transpiration and conductance (Dawson and Bliss 1989).

Plant community development

It is clear that moisture availability and the water relations of adult vascular plants are not improved in areas of maximum community development (crusted sites) at this polar desert site. However, it is also evident that these isolated patches of greater plant cover are closely associated with snowmelt. They are often lo-cated below persistent snow banks or in seasonal drain-ages, where surface water flow remains for a portion of the growing season (Bliss et al. 1994). Most of the greater plant cover and productivity in these areas (rel-ative to the more common barren polar desert sites) results from the greater biomass and diversity of moss-es, lichens, algae, and cyanobacteria (N. Matveyeva, *personal communication*). These cryptogams reside at the soil surface and rely on the presence of surface

moisture for their water needs. With little means of regulating water loss, the mosses, algae, and cyanobacteria are often restricted in distribution to areas of higher surface-moisture availability. Prolonged surface-water flow in snowflush areas provides favorable conditions for proliferation of such species. Included in this surface crust of poikilohydric organisms are substantial quantities of nitrogen-fixing cyanobacteria, principally *Nostoc commune* (L. Dickson, *unpublished manuscript*). The nitrogen supplied through cyanobacterial fixation is the only significant source of this principal nutrient to the polar desert communities. The typical, noncrusted soils of the polar desert have extremely low concentrations of total soil nitrogen (0.04%). However, in crusted areas soil N concentrations are more than double (0.09%). Much of this is due to accumulation of organic nitrogen, but large differences in inorganic constituents such as nitrate also exist (13.0 μg/g in crusted sites vs. 4.3 μg/g in noncrusted sites). The availability of other mineral nutrients (e.g., P, K) is also poor in both of these soils, particularly at noncrusted sites. These communities, along with most arctic ecosystems, are recognized as highly nutrient limited (Haag 1974, Shaver and Chapin 1986, Nadelhoffer et al. 1992). Prolonged periods of moist surface soils can therefore have a substantial indirect influence on vascular plant success through facilitation of nitrogen-fixing organisms. Preliminary data suggest that this nutrient enhancement effect is manifested in some species (e.g., *Papaver radicatum*) through higher leaf tissue nitrogen concentrations and light-saturated net photosynthetic rates in the crusted sites (W. Gold, *unpublished data*).

Indirect effects of soil moisture on vegetation have also been documented in low arctic wet sedge meadows at Barrow, Alaska. Soils there remain saturated through the growing season, vascular plant water stress is minor (Stoner and Miller 1975), and yet soil moisture is highly correlated with variations in primary productivity (Webber 1978). Similar to our conclusion, Chapin et al. (1988) suggested that the influence of soil water content on the vascular plants is mediated through alterations in nutrient availability. In their case, high soil water contents were associated with increased lateral subsurface water flow, enhancing nutrient fluxes to the surface of plant roots. It is unlikely that lateral subsurface or surface water flow is causing direct nutrient enrichment to our snowflush areas. Chemical analyses of subsurface water collected with lysimeters indicate very low nutrient concentrations of water originating in barren areas underlying persistent snowbanks (R. Sletten and F. Ugolini, *unpublished data*).

Besides enhancing the physiological function of nitrogen-fixing organisms, long periods of moist soil surfaces may have important direct implications for seed germination and seedling survival. Successful reproduction and colonization is highly periodic in such a severe, variable environment (Bell and Bliss 1980,

Chapin and Shaver 1985). The availability of surface and near-surface water may be crucial for both environmental amelioration and seedling water balance.

Water limitations, both direct and indirect, are only one portion of the environmental milieu with which plants must contend. Low temperatures and a short growing season, common throughout the High Arctic, are clearly two of the most selective agents which have helped to shape the nature and composition of plant communities on the polar deserts. Dark-colored soil crusts can substantially elevate soil and surface temperatures (W. Gold, *unpublished data*), possibly enhancing seedling establishment and growth. Soil movement resulting from frost action can be a substantial source of stress and mortality (Bliss et al. 1984, 1994). Uprooted seedlings and adult plants are not uncommon on this landscape. The presence of cryptogamic crusts reduces cryoturbation through surface stabilization (W. Gold, *unpublished data*). Past soil cryogenic processes have created a complex microtopography on polar desert landscapes (Washburn 1956, 1980). Topographic microrelief has often been recognized as a primary influence on arctic vegetation patterns (Webber 1978, Sohlberg and Bliss 1984).

Polar deserts have a circumpolar distribution, occupying more than 0.8×10^6 km^2 of land (Bliss and Matveyeva 1992). Despite their consistently sparse plant cover, they occur across a variety of substrates and physical environments on both a local and regional scale (Aleksandrova 1983, Bliss et al. 1984, 1994). Although the subsurface soils of our sites provided little moisture limitation for adult vascular plants, this may not be true throughout all polar desert landscapes. More arid and exposed sites also exist within the High Arctic region (Teeri 1972, Aleksandrova 1983, Bliss et al. 1984, Maycock and Fahselt 1992). However, saturated soils overlying permafrost have been described from a number of locations in both the Russian Arctic and Antarctic (Aleksandrova 1983). Conditions on the Devon Island plateau are broadly representative of large areas in the eastern and central North American High Arctic, where silty soils derived from dolomite predominate. In such areas, low summer precipitation does not necessarily impose drought stress for adult vascular plants, but may for seedlings, especially when the thin surface layer of the soil dries. The maintenance of surface moisture is apparently very important for germination and seedling development. In 1994, an unusual proliferation of seedlings and rapid root development of those seedlings (up to 3 cm in 3 wk) accompanied an unusually moist growing season. The soil surface showed little drying in 1994, and periodic warm periods provided an unusual combination of warm, wet conditions. The occurrence of such uncommon growing seasons is probably very influential in the recruitment of new individuals and plant community development.

The effects of moisture limitations on the established

vascular plant community occur indirectly, probably through their association with the cryptogamic flora, whose function and establishment are tightly coupled to surface water availability. The successful establishment of such nonvascular species may facilitate localized recruitment of vascular species and community development through environmental amelioration (raised surface temperatures, reduced cryoturbation) and enhanced nutrient availability. Nutrient addition experiments in the High Arctic (Henry et al. 1986) have demonstrated the importance of low nitrogen availability in limiting plant community development and production. Nitrogen-fixing organisms within the biological surface crusts are the only significant source of nitrogen in these landscapes. Thus, in these polar desert sites, with little moisture limitation to established vascular plants, patterns of community development closely parallel the enhanced nutrient availability and favorable microsites for seedling establishment associated with the presence of cryptogamic crusts.

LITERATURE CITED

Aleksandrova, V. D. 1983. Vegetation of the Soviet polar deserts. Cambridge University Press, New York, New York, USA.

Batten, D. S., and J. Svoboda. 1994. Pages 97–110 in J. Svoboda and B. Freedman, editors. Ecology of a polar oasis, Alexandra Fiord, Ellesmere Island. Captus University Publications, Toronto, Canada.

Bell, K. L., and L. C. Bliss. 1980. Plant reproduction in a high arctic environment. Arctic and Alpine Research 12:1–10.

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

Bliss, L. C. 1963. Alpine plant communities of the Presidential Range, New Hampshire. Ecology 44:678–697.

———, editor. 1977. Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton, Alberta, Canada.

———. 1988. Arctic tundra and polar desert biome. Pages 1–32 in M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, New York, New York, USA.

———. 1995. Arctic ecosystems of North America. In F. E. Wielgolaski, editor. Polar and alpine tundra ecosystems. Elsevier, New York, New York, USA, in press.

Bliss, L. C., G. H. R. Henry, J. Svoboda, and D. I. Bliss. 1994. Patterns of plant distribution within two polar desert landscapes. Arctic and Alpine Research 26:46–55.

Bliss, L. C., and N. V. Matveyeva. 1992. Circumpolar arctic vegetation. Pages 59–89 in F. S. Chapin, III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, New York, New York, USA.

Bliss, L. C., and J. Svoboda. 1984. Plant communities and plant production in the western Queen Elizabeth Islands. Holarctic Ecology 7:325–344.

Bliss, L. C., J. Svoboda, and D. I. Bliss. 1984. Polar deserts, their plant cover and plant production in the Canadian High Arctic. Holarctic Ecology 7:305–324.

Chapin, F. S., III, N. Fetcher, K. Kielland, K. R. Everett, and A. R. Linkins. 1988. Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. Ecology 69:693–702.

Chapin, F. S., III, and G. R. Shaver. 1985. Arctic. Pages 16–40 in B. F. Chabot and H. A. Mooney, editors. Physiological ecology of North American plant communities. Chapman and Hall, New York, New York, USA.

Dawson, T. E., and L. C. Bliss. 1989. Intraspecific variation in the water relations of Salix arctica, an arctic–alpine dwarf willow. Oecologia (Berlin) 79:322–331.

Grulke, N. E., and L. C. Bliss. 1988. Comparative life history characteristics of two high arctic grasses, Northwest Territories. Ecology 69:484–496.

Haag, R. W. 1974. Nutrient limitations to plant production in two tundra communities. Canadian Journal of Botany 52:103–116.

Henry, G. H. R., B. Freedman, and J. Svoboda. 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. Canadian Journal of Botany 64:2502–2507.

Isard, S. A. 1986. Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, U.S.A. Arctic and Alpine Research 18:83–96.

Körner, Ch., and J. A. P. V. DeMoraes. 1979. Water potential and diffusion resistance in alpine cushion plants on clear summer days. Oecologia Plantarum 14:109–120.

Krupicka, J. 1977. Bedrock geology of the Truelove River area. Pages 63–72 in L. C. Bliss, editor. Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton, Alberta, Canada.

Maycock, P. F., and D. Fahselt. 1992. Vegetation of stressed calcareous screes and slopes in Sverdrup Pass, Ellesmere Island, Canada. Canadian Journal of Botany 70:2359–2377.

Monteith, J. L., and M. H. Unsworth. 1990. Principles of environmental physics. Second edition. Chapman and Hall, New York, New York, USA.

Muc, M., and L. C. Bliss. 1977. Plant communities of Truelove Lowland. Pages 143–154 in L. C. Bliss, editor. Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. University of Alberta Press, Edmonton, Alberta, Canada.

Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver, and A. E. Linkins. 1992. Microbial processes and plant nutrient availability in arctic soils. Pages 281–300 in F. S. Chapin, III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, New York, New York, USA.

Oberbauer, S. F., and W. D. Billings. 1981. Drought tolerance and water use by plants along an alpine topographic gradient. Oecologia (Berlin) 50:325–331.

Oberbauer, S. F., and T. E. Dawson. 1992. Water relations of arctic vascular plants. Pages 259–279 in F. S. Chapin, III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, New York, New York, USA.

Oberbauer, S. F., and P. C. Miller. 1979. Plant water relations in montane and tussock tundra vegetation types in Alaska. Arctic and Alpine Research 11:69–81.

Parkinson, J. A., and S. E. Allen. 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Communications in Soil Science and Plant Analysis **6**:1–11.

Porsild, A. E., and W. J. Cody. 1980. Vascular plants of the continental Northwest Territories, Canada. National Museum of Canada Publication, Ottawa, Canada.

Richards, L. A. 1949. Methods of measuring soil moisture tension. Soil Science **68**:95–112.

Schulten, R. B. 1981. Ecology and nitrogen nutrition of two polar desert populations of *Cerastium alpinum,* Devon Island, N.W.T., Canada. Dissertation. University of Massachusetts, Amherst, Massachusetts, USA.

Shaver, G. R., and F. S. Chapin, III. 1986. Effect of fertilizer on production and biomass of tussock tundra, Alaska, U.S.A. Arctic and Alpine Research **18**:261–268.

Sohlberg, E. H., and L. C. Bliss. 1984. Microscale pattern of vascular plant distribution in two high arctic plant communities. Canadian Journal of Botany **62**:2033–2042.

Soil Survey Staff. 1992. Keys to soil taxonomy. Fifth edition. Soil Management Support Services Technical Monograph Number 19. Pocahontas Press, Blacksburg, Virginia, USA.

Stoner, W. A., and P. C. Miller. 1975. Water relations of plant species in the wet coastal tundra at Barrow, Alaska. Arctic and Alpine Research **7**:109–124.

Svoboda, J., and B. Freedman, editors. 1994. Ecology of a polar oasis, Alexandra Fiord, Ellesmere Island. Captus University Publications, Toronto, Canada.

Teeri, J. A. 1972. Microenvironmental adaptations of local populations of *Saxifraga oppositifolia* in the High Arctic. Dissertation. Duke University, Durham, North Carolina, USA.

Washburn, A. L. 1956. Classification of patterned ground and review of suggested origins. Geological Society of America Bulletin **67**:823–865.

———. 1980. Geocryology: a survey of periglacial processes and environments. Holstead, Wiley, New York, New York, USA.

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

Woo, M. 1986. Permafrost hydrology in North America. Atmosphere-Ocean **24**:201–234.

Zoltai, S. C., and V. Woo. 1976. Soils and vegetation of Somerset and Prince of Wales Islands, District of Franklin. Pages 143–147 *in* Geological Survey of Canada Paper 76-1B, Geological Survey of Canada, Ottawa, Canada.