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THE UNIVERSITY OF ALBERTA

MAJOR ENVIRONMENTAL INFLUENCES ON THE PATTERN OF *LEDUM GROENLANDICUM* IN MIRE SYSTEMS

by

© Eric F. Karlin

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY
IN
PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA
FALL, 1978

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 "Major Environmental Influences on the Pattern of Ledum Groenlandicum in Mire Systems" submitted by Eric F. [illegible] in partial fulfilment of the requirements for the degree of Doctor of Philosophy in plant ecology.

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ABSTRACT

This study was undertaken in order to determine the cause of the pattern of Ledum groenlandicum in mires (peatlands). The plant is a prominent mire shrub in North America, occurring primarily in the raised-peat portions of mires. Field research centered primarily in two mire systems located in central Alberta.

A series of field and laboratory experiments involving the seed dispersal, germination, seedling, juvenile and mature plant stages was conducted in order to establish which stage(s) limited the plant's distribution. The influence of several major environmental variables on the above stages of the plant's life cycle was studied; these included water level, pH, substrate chemistry and physical characteristics, temperature and light.

None of the abiotic environmental parameters tested was found to be of primary importance in limiting the plant's spread into low-peat substrates which have relatively well aerated surface layers. Instead, a combination of biotic environmental parameters (i.e. growth of other plants) and the growth characteristics of L. groenlandicum was found to be the primary cause of the pattern. Abiotic parameters (especially high substrate water content) played an indirect role, largely by influencing the growth rates of the plants.

The mature plant and seedling stages of L. groenlandicum were found to be the critical points in the formation

of the pattern. Vegetative spread of mature plants of *L. groenlandicum* into the low-peat communities was largely limited by the plant's growth pattern rather than by its physiological tolerances.

Although germination and initial seedling establishment occurred in all low and raised-peat substrates tested, no naturally established juvenile plants (≤ 3 years old) were found in the low-peat communities. The small size of the seedlings and their slow rates of growth puts the plant at a competitive disadvantage in relation to the faster growing plants which naturally occur in low-peat areas (primarily mosses). In addition, the extended period of time spent in a "seedling" environment by the young plants heightens the probability of mortality due to climatic extremes. The combination of these two variables is largely responsible for the lack of long term survival of *L. groenlandicum* seedlings in low-peat environments.

Successful seedling establishment (long term) was limited to habitats where moss growth is reduced, such as in disturbed areas or on senescent moss hummocks.

These results indicate that a re-examination of the general conclusion that abiotic parameters are the direct determinants of the distributional patterns of mire plants and plant communities needs to be made. Because the abiotic environmental gradients are often very steep in mire systems and change in parallel with the distributional patterns of many mire plants, it would at first appear that they were of primary importance in causing the pattern. However, for *Ledum groenlandicum* (and perhaps for other mire plants limited to raised-peat communities), it is the biotic environment that directly determines the final distributional pattern of [illegible]

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Finally, my wholehearted thanks go to my wife, Lois, (who typed this thesis) and to my daughter, Gaylyn, for their support and patience.

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I. INTRODUCTION

One of the more notable characteristics of mire systems is the distinctness of their vegetation from that of the adjacent upland communities. This is especially true of *Sphagnum* dominated mires. Major changes of vegetation within a small area are indicative of the presence of a steep environmental gradient (Hill 1973; McNaughton and Wolf 1973). Not only are there large differences between the environmental regimes of mire and non-mire systems, but there also exist major environmental gradients within most mires. Consequently, the patterning of mire plants and plant communities is frequently quite evident. It is generally assumed that the more obvious parameters of these internal gradients (degree of aeration, depth to water level, peat and water chemistry) are the direct determinants of the patterns observed (Sjörs 1950; Heinselman 1970; Jeglum 1971; Moore and Bellamy 1974).

Ledum groenlandicum is a prominent shrub in *Sphagnum* dominated mires in North America. It has one of the most distinctive distributional patterns within a given mire system, being limited to the less wet and more acidic areas of mires (the raised-peats). It is therefore primarily found in the later stages of mire succession, where there usually is a considerable development of raised peat (Bray 1921; Lewis et al. 1928; Moss 1949; Dansereau and Segadas Vianna 1952).

Bray (1921) observed that the spread of L. groenlandicum into recently formed raised-peat areas was not rapid, despite the fact that the plant grew vigorously in older raised-peats, especially where conifer establishment was taking place. Dansereau and Segadas-Vianna (1952) observed the same pattern and concluded that the dominance of L. groenlandicum led to the suppression of moss growth in such sites, thus enabling the successful establishment of trees.

The plant is able to exist under a relatively closed coniferous canopy, although in reduced numbers (Bray 1921; La Roi 1967; Jeglum 1972). It is most prominent in coniferous-ericaceous communities where tree cover is low and in disturbed raised-peat areas of mires. After a disturbance (fire, logging) L. groenlandicum often becomes the dominant vascular species present, particularly in central Canada (Lewis et al. 1928; Moss 1949; Jeglum et al. 1974).

Other dominant mire shrubs which have similar distributional patterns include Vaccinium vitis-idaea[1], V. angustifolium Ait., Kalmia angustifolia L., and Calluna vulgaris (L) Hull. Shrubs which are often associated with L. groenlandicum, but which also extend into low-peat areas are Andromeda polifolia, Betula pumila var. glandulifera, Chamaedaphne calyculata, Kalmia polifolia, Myrica gale,

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[1] Unless otherwise indicated, nomenclature for vascular plants follows Moss (1959), that for Sphagnum follows Vitt and Andrus (1977), and for mosses, Crum et al. (1973).

Vaccinium oxycoccus L. and V. macrocarpon Ait. (Lewis et al. 1928; Moss 1949; Dansereau and Segadas-Vianna 1952; Gimingham 1960; Sjörs 1963; Karlin 1975; Vitt et al. 1975; Vitt and Slack 1975).

As I observed patterns of species in the field, I began to wonder why L. groenlandicum has such a limited distribution, while others (A. polifolia and C. calyculata) are more extensive. At first glance it appeared to be simply due to different tolerances to high water levels and/or the chemistry of the primary water, which generally has a higher pH and greater mineral concentration than that found in secondary water. But this was an assumption based on only the readily apparent evidence, and not taking the total life cycle of the plant into account.

The pattern of L. groenlandicum is determined by the tolerance limits of one (or a combination) of five stages in its life cycle: seed production, seed dispersal, germination, seedling establishment, and the mature plant. It may be that the pattern displayed by the mature plant is not only indicative of its tolerances, but also of those of an earlier stage of development. The pattern is thus not to be explained by a single factor approach, but by a combination of several variables impinging on the plant, each with varying degrees of influence at different stages in the plant's life cycle (Billings 1952).

The primary objective of this study was to determine which environmental variables limit the spread of Ledum _groenlandicum_ into low-peat communities. A secondary objective was to quantify the diagnostic features of water and substrate chemistry in two mire systems representing the relative extremes in mire chemistry present in central Alberta.

II. THE PLANT

Ledum groenlandicum is a low (3-10 dm), erect, evergreen shrub endemic to North America and Greenland (Fig. 1). It is broadly distributed across the northern portions of the continent (Fig. 2). The plant is most commonly found in areas with acidic and moist organic substrates. It is a prominant component of the alpine tundras of the New England mountains, of boreal Feather moss-coniferous forests, and on Sphagnum hummocks in mires.

The genus Ledum is placed by Stevens (1971) in the Rhododendroideae subfamily of the Ericaceae, and is most closely related to Rhododendron and Menziesia. There are two other species of Ledum, both occurring in North America (Savfle, 1969). Ledum palustre is a circumpolar arctic species, with L. paulstre ssp. palustre in Eurasia and L. palustre ssp. decumbens (hereafter referred to as L. palustre) in North America and northeastern Asia. Ledum glandulosum is primarily found in the Pacific Northwest region of the United States.

Anthesis occurs in late May and early June, as does initiation of leaf expansion. Aspects of pollination have been studied by Lovell and Lovell (1936) and Reader (1975). Leaves are fully extended by late June to early July. On mature plants the majority of leaves remain for two growing seasons, being shed in the fall of the second year (Reader 1978). A small fraction (< 1%) are retained for a third

Figure 1. Ledum groenlandicum

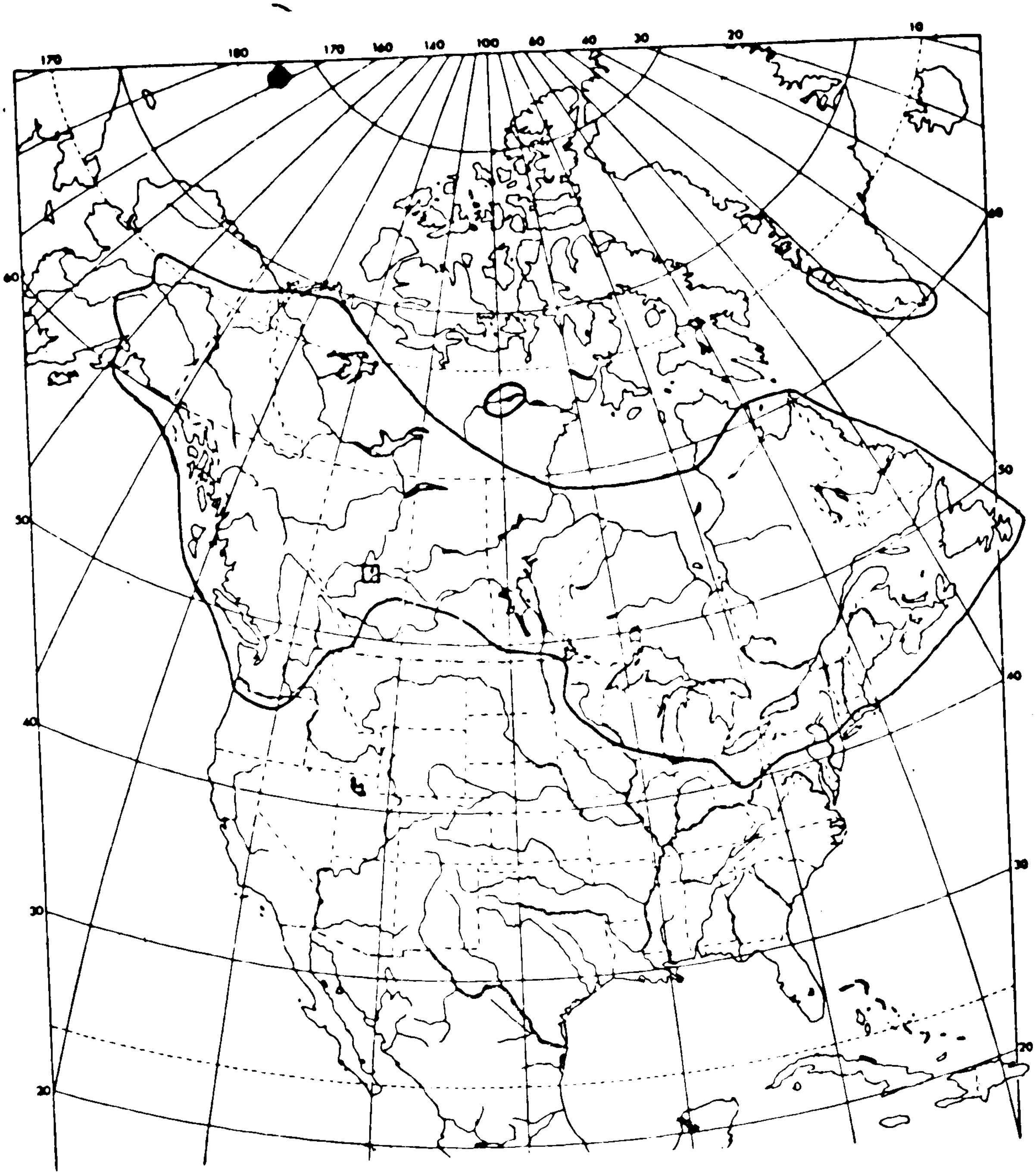

Figure 2. Distribution of *Ledum groenlandicum* according to Hultén (1968) and J.G. Packer (personal communication). The general location of the study sites is indicated by the square.

growing season (personal observation). Seed release begins in late August. The seed is very small (2.5 mm by 0.4 mm) and is wind dispersed (Ridley 1930).

Net photosynthetic rates are low. Maximum rates are generally about 4 mg CO_2 $g^{-1}h^{-1}$ ($\approx$ 4 mg CO_2 $dm^{-2}h^{-1}$) (Smith and Hadley 1974; Wilkinson 1977; Reader 1978). Small (1972a) reported rates twice as high, while Hadley and Bliss (1964) found that maximum rates were only 2 mg CO_2 $g^{-1}h^{-1}$ in an alpine environment. Maximum net photosynthetic rates of ericaceous plants have been found to be between 4 and 12 mg CO_2 $dm^{-2}h^{-1}$ (Mooney 1972).

Reader (1978) found that the second season leaves had a positive rate of net photosynthesis, although it was much lower than that of first season leaves. His research indicated that the overwintering leaves play a major role in supporting the growth and development of new shoots. Under harsh environmental regimes, however, the photosynthetic capability of the overwintering leaves may be considerably reduced (Hadley and Bliss 1964).

The photosynthetic apparatus of the plant has been shown to acclimate with temperature (Table 1) (Smith and Hadley 1974; Wilkinson 1977). Light (photosynthetically active radiation: .4 - .7 μm) saturation occurs around 800 μ Einstein $m^{-2}s^{-1}$ and light compensation at roughly 20 μ Einstein $m^{-2}s^{-1}$ (Wilkinson 1977). The above values roughly correspond to 47 klx and 1 klx respectively.

The xeromorphic characteristics of the leaves of

Table 1. Optimum temperature for maximum net photosynthetic rates in four different temperature regimes (° C).

Temp. Regime		Optimum Temp.	Net Photosynthesis	Reference
Day/Night				
30	25	25	4 mg CO_2 $g^{-1}h^{-1}$	Smith & Hadley 1974
25	15	25	4 mg CO_2 $g^{-1}h^{-1}$	Wilkinson 1977
15	10	20	4 mg CO_2 $g^{-1}h^{-1}$	Smith & Hadley 1974
15	5 to-2	15	1.8 mg CO_2 $g^{-1}h^{-1}$	Wilkinson 1977*

* Plants in the coolest temperature regime were in the process of going dormant and were not in the same phenological stage as the other temperature regimes.

L. groenlandicum (and those of other mire ericads) have evoked much interest, especially since hydromorphic adaptations are also present (Sifton 1940; Metcalfe and Chalk 1957). No evidence of summer drought stress was found, however, for L. groenlandicum plants growing in several different habitats, with minimum summer xylem pressure potentials being between -10 and -20 bars (Small 1972b; Marchand 1975; Wilkinson 1977; Mayo and Hartgerink, unpublished data). However, values indicating severe water stress (< -60 bars) were observed from early November to mid-March (Wilkinson 1977). Stomatal resistance on a hot summer day was only 1.2 s cm^{-1} (Small 1972b), while it was > 30 s cm^{-1} in March (Wilkinson 1977). It would appear that the xeromorphic characteristics are of adaptative significance for severe winter drought conditions (Gates 1914;

Small 1972b; Wilkinson 1977) and/or are a response to low nutrient levels (Loveless 1962; Beadle 1966; Small 1972a, 1972b).

The mature plant is quite cold hardy, with minimum survival temperatures ranging from -9°[2] in summer to < -40° in winter (Wilkinson 1977).

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[2] All temperatures are in Centigrade.

III. THE ENVIRONMENT

A mire is any wetland system in which autochthonus peat forms the primary substrate for the plant species present. Minerotrophic mires (fens) are those with substrate surfaces subject to the direct influence of mineral soil water (Sjörs 1963). The chemistry of the water and peats of fen systems depends largely on the chemical characteristics of the mineral soil water which flows into them. There is thus a gradient of fen types, ranging from poor fens (water pH 4-5, Ca = 2-5 ppm) to rich fens (water pH 7-8, Ca $\geq$ 30 ppm) (Gorham 1967; Moore and Bellamy 1974).

Mires in which peat has accumulated to such an extent that precipitation is the only major source of water are ombrotrophic mires (bogs). Such mires are acidic, nutrient poor systems (water pH 3-4.5, Ca $\leq$ 2 ppm), as mineral inputs are solely from atmospheric sources (Gorham 1967; Heinselman 1970; Moore and Bellamy 1974).

Raised-peat refers to peat which has accumulated more than 10 cm above the general water table, with low-peats being $\leq$ 10 cm. Two classes of water exist in mires with raised-peat systems. One, primary water, is the general water table above which the raised-peats have formed. Secondary water is the water elevated above the water table and located in the raised-peats. The direct source of the secondary water (and also minerals) varies along a continuum from being totally generated by precipitation (ombrotrophic) to being largely supplied by the primary water (minerotrophic).

Primary water chemistry is one of the best abiotic indices for mire classification, in that it is easy to obtain and less variable than peat chemistry. However, a peatland classified only on the basis of this parameter could have a vastly different secondary water chemistry, which might be more important ecologically. Because of this, data on the chemistry of both the primary water and secondary water (and/or peat chemistry) are necessary in order to get a true picture of the mineral nutrient status of a mire.

The concentration of Ca and the pH level have been found to be the most diagnostic components of mire water and peat chemistry (Sjörs 1963; Heinselman 1970; Moore and Bellamy 1974; Stanek and Jeglum 1977).

The study region is located in central Alberta, where <u>Ledum groenlandicum</u> is the dominant shrub in raised-peat areas and the patterning of the plant is especially evident. Its robustness indicates that there is no major limitation by the macro-climatic environment on the growth and distribution of the plant in this area. As a broad spectrum of mire types occur there, radically different mire environments could be utilized without extensive traveling.

The mire systems of the portion of the boreal forest located on the Interior Plains of central Canada have not been extensively studied. This area would include central Saskatchewan and central and northwestern Alberta (Rowe 1972). As this area is southwest of the Canadian Shield and largely underlain by calcareous bedrock, the mires present are predominantly fens and rich fens. This is in contrast to mire systems occurring on the Canadian Shield (largely poor fens and bogs) where the bedrock is poor in minerals.

Moss (1955) gave a general description of the mire vegetation of Alberta and reviewed the pertinent literature up to that date. Early botanical studies provided qualitative descriptions of the mires of central Alberta as well as observations on successional dynamics and the impact of various disturbances (Lewis and Dowding 1926; Lewis et al. 1928). Both studies reported that retrogressive succession in response to upwelling of calcareous spring water appeared to be taking place in some mires. After 33 years of observation, however, it was found that such succession was no longer actively occurring (Moss and Turner 1961). Mire systems of northwestern Alberta were found to be quite similar to those in the central portions of the Province (Moss 1953).

Intensive studies dealing with vegetation-environmental relationships in mire systems have been done in central Alberta (Moss 1949; Vitt et al. 1975; Busby 1976) and central Saskatchewan (Jeglum 1971, 1972, 1973). Research conducted in the region in related botanical disciplines includes taxonomic studies on *Sphagnum* (Moss 1949; Vitt and Andrus 1977) and *Tomenthypnum* (Vitt and Hamilton 1975), and eco-physiological studies on the following prominent mire species:

Tomenthypnum nitens and Feather Mosses (Busby 1976), Ledum groenlandicum (Wilkinson 1977), and Picea mariana (van Zindern Bakker 1974).

Studies on chemical and physical aspects of peat from central Alberta mires demonstrate that most peats have high Ca concentrations (Newton 1934; Walker 1936). Gardner (1967) and Christensen and Cook (1970) provide detailed information on the microbiology and selected physical-chemical parameters of representative peat types in Alberta. Although just outside of the study region, a thorough study on the chemical and physical parameters of the primary water and peat of several mires in southern Yukon demonstrated that ombrotrophic mires occur there (Walmsley and Lavkulich 1975).

Recent studies have classified Canadian wetlands on a largely physiognomic basis and provide general descriptions of the types of mire systems present and their distribution (Jeglum et al. 1974; Zoltai et al. 1975; Zoltai and Tarnocai 1975).

Study Sites

Field reconnaissance of mire systems occurring in central Alberta was conducted during Fall, 1975 and Spring, 1976. Two mires were selected as study sites based on the following major criteria: (1) that they be in a natural state; (2) that each contained both the wetter and dryer extremes of mire communities; (3) that one be representative of mineral rich mires (rich fens) and the other representative of mineral poor mires (poor fens to bogs); and (4) that they be readily accessible. A brief description of the sites is provided below (see also Appendix I).

Heatherdown Fen (HF): This is a rich mixed mire system, with rich fen low-peats and fen to ombrotrophic raised-peat "islands" (Fig. 3a). It is located 48 km west of Edmonton (53 37' N, 114 16' W; 765 m elevation). The system occurs on a slight slope (northwest aspect) and is fed by calcareous springs. It is a patterned mire, having several series of flarks (pools) oriented at right angles to the slope, in a terrace fashion. The level between consecutive flarks varies from 5 cm to almost 100 cm. The flarks and the more extensive sedge fens comprise the low-peat communities, which separate the coniferous-ericaceous dominated raised-peat islands. In the low-peat areas, from 0-10 cm (much thicker in some areas) of peat is present and this directly overlays marl. The raised-peat areas generally have 50 to 100 cm of peat above the marl layer. The mire has been subjected to fire and light logging within the last 50 years, but has not been greatly disrupted.

The natural upland vegetation is dominated by *Populus tremuloides* with an admixture of *Populus balsamifera*, *Betula papyrifera* and *Prunus pennsylvanica*. Major understory species are *Corylus rostrata*, *Amelanchier alnifolia*, *Aralia nudicaulis*, *Mertensia paniculata* and *Cornus canadensis*. The site is in the forest-transition area between the

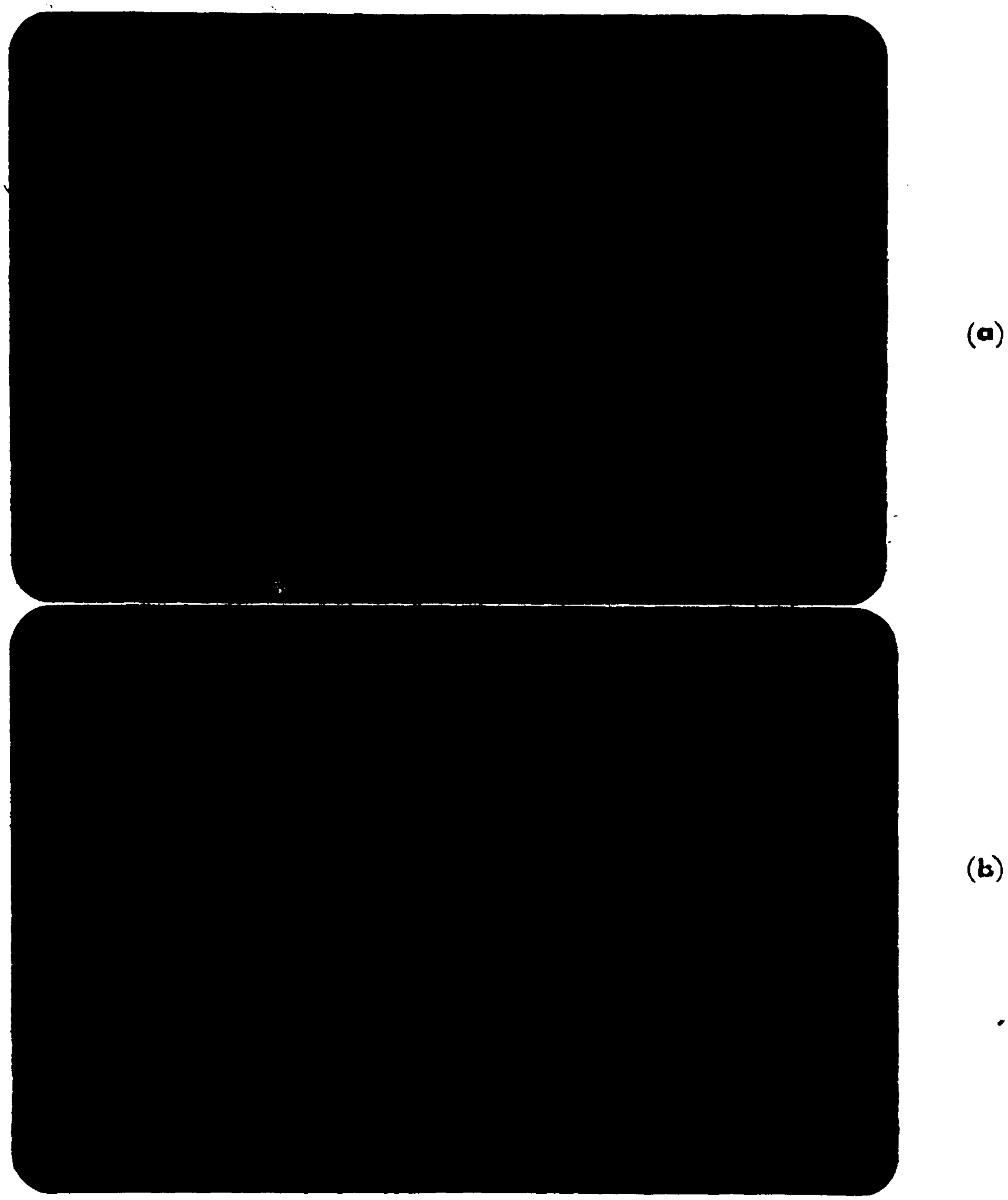

Figure 3. Study areas, (a) Heatherdown fen (b) Kestow fen: *Eriophorum*/*Sphagnum* community type.

boreal forest to the north and grassland to the south (Rowe 1972).

Nestow Fen (NF): This mire system occurs in a stabilized dune complex located 8 km north of Edmonton (54 14' N, 113 36' W; 633 m elevation). The mires and dunes form an intricate mosaic. It is a poor mixed mire system, with ombrotrophic *Sphagnum* hummocks rising out of graminoid dominated poor fens and fens (Fig. 3b). Zonation of mire community types is quite distinct, with coniferous-ericaceous dominated raised-peat areas at the outer margin of the mires. These grade (inward) into *Eriophorum-Sphagnum* dominated raised-peat communities. Low shrub fens (raised-peat) and sedge fens (low-peat) predominate in the central areas.

The dune vegetation is dominated by *Pinus banksiana*, *Cladina mitis*, *C. unciales*, *Vaccinium vitis-idaea* and *Arctostaphylos uva-ursi*. Less dominant, but quite prominent, species include *Anemone patens*, *Maianthemum canadense* and *Campanula rotundifolia*. In the moist transitional areas between the outer mire margins and the dry upper portions of the dunes, *Populus tremuloides*, *Vaccinium myrtilloides*, *Amelanchier alnifolia* and *Ledum groenlandicum* are dominant.

Vegetation

Methods

In order to quantitatively assess the distributional pattern of L. groenlandicum, several transects (eight at Heatherdown, two at Nestow) were established. These were placed such that each ran through at least one low-peat community (wet end of gradient) and up into at least one raised-peat community (dry end of gradient). Quadrats (1 m^2) were located on alternate sides of a meter tape every other meter along the transects. Transect length varied in order to adequately sample the pattern at each location, with the number of quadrats for each transect ranging from 13 to 30. At each quadrat, ground cover estimates were made for vascular and bryophyte species present using nine cover classes: +, < 1%; 1, 1-5%; 2, 6-10%; 3, 11-20%; 4, 21-30%; 5, 31-40%; 6, 41-50%; 7, 51-75%; 8, 76-100%. Depth to water level from the lowest point in the quadrat and the surface relief within each quadrat were also determined.

Community types were subjectively delineated on the basis of vegetation structure and floristic composition. To obtain a quantitative description of species composition and structure, one or two 200 m^2 plots (10 x 20 m) were located in major community types. Along the central axis of the plot, ten quadrats (1 m^2) were sampled. Species present in the plot but not sampled in the quadrats were noted and included in the data as being present (< 1% cover).

Community composition

Heatherdown: The sedge fens at Heatherdown are dominated by *Scirpus caespitosus*, *Carex aquatilis*, *Triglochin maritima*, *Andromeda polifolia* and *Betula pumila* var. *glandulifera* (Table 2). Dominant bryophytes include *Campylium stellatum*, *Drepanocladus revolvens* and *Scorpidium scirpoides*. *Tomenthypnum nitens* is prominent in drier areas transitional to the raised-peat. The raised-peat islands have *Picea mariana* and *Larix laricina* in the overstory, with *Ledum groenlandicum*, *Vaccinium vitis-idaea*, *Empetrum hermaphroditum* Hagerup and *Carex gynocrates* being major understory species. Dominant mosses here include *Sphagnum fuscum*, *Pleurozium schreberi*, *Hylocomium splendens* and *Aulacomnium palustre*.

The flarks are of various sizes and depths, although the majority have < 15 cm of standing water. They are largely devoid of vascular vegetation, with *Scirpus validus*, *Carex aquatilis*, *Utricularia intermedia* and *Scorpidium scirpioides* (includes *S. turgescens*) being the major plants encountered there. The flark bottoms are covered by a thick mat of algae (Lewis and Dowding 1926).

Similar rich fen areas were studied by Lewis and Dowding (1926) and Lewis et al. (1928) in the same re[illegible] Sjörs (1961b) found that rich fens with marl format[illegible] also occurred in the Hudson Bay Lowlands in eastern Canad[illegible] There are many species in common between the rich fens [illegible]t Heatherdown and those in Europe (Sjörs 1963; Bellamy and

Table 2. Mean ground cover class (+ to 8, see Methods) of prominent species in the major community types at Nestow and Heatherdown fens.

	Heatherdown		Nestow				
	Low-peat	Raised-peat	Raised-peat			Low-peat	
Community #	1	2	3	4	5	6	7
Species							
Bryophytes							
Scorpidium scorpioides *	2						
Campylium stellatum	6						
Drepanocladus sp.	3				1	1	4
Tomenthypnum nitens	1	1	+		1		
Sphagnum warnstorfii	+	+	+				
Pleurozium schreberi		3	+				
Sphagnum fuscum		3	1	1			
Hylocomium splendens		1	+				
Polytrichum strictum		1	2	1	+	+	
Aulacomnium palustre		2	1	+	5	1	3
Sphagnum angustifolium			4	3	2	4	
Sphagnum magellanicum			2	7	2	1	
Sphagnum subsecundum				+	2	4	
Trees and shrubs							
Andromeda polifolia	3	1	1	3	3		
Empetrum hermaphroditum		3					
Vaccinium vitis-idaea	+	3	3	+			
Salix sp.	1	1		1	3	2	1
Betula glandulifera	2	2	1	1	4	+	
Ledum groenlandicum	+	5	7	1	+		
Vaccinium oxycoccus	+	1	1	3	3	+	
Larix laricina	1	2	1	+	+		
Picea mariana	1	4	4	2	+	+	
Herbs							
Scirpus caespitosus	5						
Pingicula vulgaris	+						
Scirpus validus	1						
Viola nephrophila	1						
Dodecatheon radicatum	1						
Tofeldia glutinosa	1						
Muhlenbergia glomerata	2						
Rubus acaulis	1	2					
Juncus balticus	1	1					
Triglochin maritima * *	2	+					
Galium boreale	2	+					
Geocaulon lividum		1					
Drosera rotundifolia		1					
Carex gynocrates		1					
Carex aquatilis	2	2	+	1	1	1	
Smilacina trifolia	+	1	1	3	+		
Calamagrostis canadensis	+	1		+	+		2
Eriophorum spissum			2	2			
Rubus chamaemorus			2	+			
Carex lasiocarpa				1	4	6	4
Potentilla palustris					1		+
Eriophorum angustifolium				+		+	
Carex rostrata			+				3
No. 1 m^2 plots	20	20	20	20	10	10	10

* includes S. turgescens
** includes T. palustris

Reilly 1967; Moore and Bellamy 1974) It is interesting to note the presence of *Scirpus caespitosus* in rich fens in central Alberta, as it is characteristic of poor fens and bogs in eastern North America and Europe (Sjörs 1963; Moore and Bellamy 1974).

Nestow: The graminoid fens at Nestow are characterized by *Carex lasiocarpa*, *Carex rostrata*, *Calamagrostis canadensis* and *Equisetum fluviatile*. In the fen areas, *Drepanocladus* spp. and *Aulacomnium palustre* are the dominant mosses, while *Sphagnum subsecundum* and *S. angustifolium* are dominant in the poor fens. The low shrub fen is a raised peat area with *Betula pumila* var. *glandulifera*, *Andromeda polifolia*, *Salix* spp. *Vaccinium oxycoccus*, *Carex lasiocarpa*, *Aulacomnium palustre*, and *Sphagnum* spp. being prevalent. The *Eriophorum-Sphagnum* type is a *Sphagnum* hummock system, with *Eriophorum vaginatum* ssp. *spissum*, *Smilacina trifolia*, *Andromeda polifolia*, *Vaccinium oxycoccus*, *S. magellanicum* and *S. angustifolium* being dominant. This grades into a coniferous-ericaceous mire, characterised by *Picea mariana*, *Ledum groenlandicum*, *Vaccinium vitis-idaea*, *Rubus chamaemorus*, *Sphagnum angustifolium*, *S. magellanicum* and *Polytrichum strictum*.

Lewis et al. (1928) and Moss (1949) studied similar mire systems in the Nestow area. The mires of this area are similar in composition and structure to those in other areas of North America (Sjors 1963; Jeglum 1972; Karlin 1975; Vitt and Slack 1975).

Community structure

Information on community structure and diversity is listed in Table 3. Diversity is measured as species richness (r) and the Shannon index (H') (Peet 1974). Although H' is similar in low-peat and raised-peat communities at Heatherdown, species richness is much higher in the low-peat areas. This indicates that the raised-peat communities have a more equitable distribution of species importance.

The rich mixed mire system at Heatherdown has a greater richness and H' than the poor mixed mire system at Nestow. This is largely due to the low number of vascular species present at the latter site. In both systems, woody cover increased from wetter to drier sites, with monocot cover decreasing along the same gradient.

Climate

Methods

The macroclimate of central Alberta is characterised by long, cold winters with moderate snow fall, and cool summers with a frost-free period of 80-100 days. Mean monthly temperatures range from -14° to -17° in January and 16° to 17° in July. Mean annual precipitation ranges from 460-510 mm, of which 30% is received as snow. Mean potential evapotranspiration ranges from 508-559 mm, exceeding

Table 3. Characteristics of the plant community types at Heatherdown (HF) and Nestow (NP).

	Community	(n)	Species richness		H' (all species)	$\bar{X}$ Cover class					
			Bryophyte	Vascular		Lichen*	Bryophyte	Monocot	Dichot	Shrub	Tree
1	HF *Scirpus*/*Campylium* (LP)**	20	5	41	2.49-2.77	0	7	7	3	6	2
2	HF *Picea*/*Ledum* (RP)	20	8	29	2.64-2.79	2	6	3	2	8	5
3	NP *Picea*/*Ledum* (RP)	20	11	14	1.80-2.33	1	7	3	2	8	4
4	NP *Eriophorum*/*Sphagnum* (RP)	20	7	16	1.69-2.24	0	8	5	+	5	2
5	NP *Betula*/*Aulacomnium* (RP)	10	8	15	2.33	0	7	5	1	7	+
6	NP *Carex*/*Sphagnum* (LP)	10	6	14	1.81	0	7	7	1	2	+
7	NP *Carex*/*Drepanocladus* (LP)	10	3	18	1.93	0	6	7	1	1	1

* refers to lichens on ground substrates only

** LP = low-peat; RP = raised-peat

precipitation (Longley 1972).

Air temperature and humidity were recorded at Heatherdown with a Belfort Hygrothermograph during June to October, 1976 and May to October, 1977. The hygrothermograph was placed in a white-painted, louvered shelter, and the shelter was placed on the moss canopy surface in a low-peat community. The temperature was checked weekly in the field against a mercury-in-glass thermometer, while humidity was checked every two to three weeks with a sling psychrometer. Precipitation data were obtained from the Stony Plain meteorological station (53° 33' N, 114° 06' W; 767 m elevation), located 5 km southeast of Heatherdown.

Results

Meteorological data recorded at the Stony Plain weather station by Environment Canada are summarized in Fig. 4 (12 year mean). Data from the Rochester weather station 18.6 km northeast of Nestow (54° 27' N, 113° 32' W; 655 m elevation) indicate that the macroclimate characteristics at Nestow were approximately the same as those at Heatherdown, being only slightly cooler (Table 4 and Table 5).

The weather of the year preceeding the study (1975) and during the study period (1976-1977) closely corresponded to the twelve year mean at Stony Plain. Major climate differences occurring from 1975 to 1977 were a much higher than average precipitation in 1975 (Table 5) and an early snow melt in 1977, which led to a high mortality of the exposed overwintering leaves of *L. groenlandicum*.

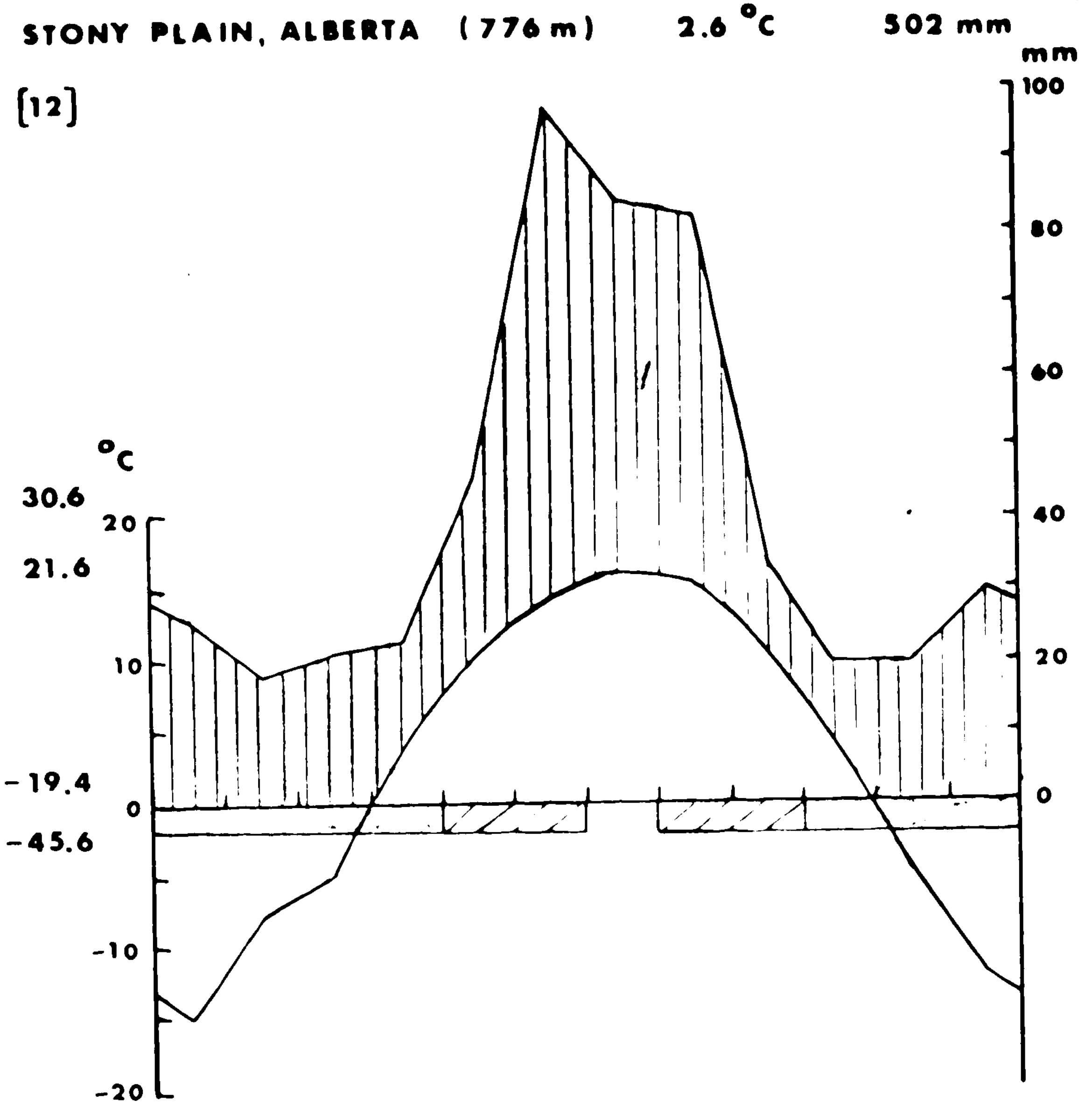

Figure 4. Climate diagram for Stony Plain, Alberta, after Walter (1973). Mean annual temperature 2.6° C; total annual precipitation 502 mm; years of observation 12; upper line is monthly precipitation; lower line is mean monthly temperature; solid bar is months with mean minimum temperature < 0° C; diagonally hatched bar is months with absolute minimum temperature < 0°C. Temperatures on left (in ascending order): absolute minimum, mean minimum coldest month, mean maximum warmest month, absolute maximum.

Table 4. Mean monthly (May-September) temperatures for 1975-1977 at Heatherdown, Stony Plain and Rochester (°C).

Station	May	Jun	Jul	Aug	Sept
1966-1977 (mean)					
Stony Plain	10.5	14.5	16.0	15.5	10.5
1975					
Stony Plain	9.4	13.9	18.3	13.3	11.7
Rochester	8.9	12.8	17.2	12.2	10.6
1976					
Heatherdown		12.0	14.5	15.4	10.0
Stony Plain	11.7	12.8	16.7	16.7	12.8
Rochester	10.0	11.7	15.0	16.1	11.1
1977					
Heatherdown		15.0	15.4	13.4	10.1
Stony Plain	11.0	15.2	14.8	13.0	9.6

Table 5. Annual and May-September precipitation for 1975-1977 at Stony Plain and Rochester (mm).

Station	May	Jun	Jul	Aug	Sept	Annual
1966-1977 (mean)						
Stony Plain	46	97	84	82	34	502
1975						
Stony Plain	55	152	58	166	8	602
Rochester	51	119	99	113	23	569
1976						
Stony Plain	33	117	87	88	27	500
Rochester	29	74	74	125	43	514
1977						
Stony Plain	167	40	45	100	45	500

Mean monthly air temperature at Heatherdown was closely correlated to that at Stony Plain (Table 4). The site had a greater range of temperature, however, with maximum summer temperature being about 2-3° higher and minimum summer temperature being about 4-5° lower. Many mire systems occur in areas of cold air drainage and thus tend to be cooler than the surrounding landscapes (Norgaard 1951; Geiger 1966; Joyal 1972). At Heatherdown, > 70% (1976 and 1977) of the minimum daily temperatures (for June, July and August) were < 10°, with > 30% (1976 and 1977) being < [illegible] Frosts occurred in June for both years and in all three months during 1977 (Table [illegible]). In contrast, only 45% and 4% of the minimum daily temperatures at Stony Plain were < 10° and < 5° respectively during the same time period in 1976.

Water Regime

Methods

Staff gauges and PVC water wells were utilized in the determination of water level fluctuations. Water levels were recorded on a weekly basis at Heatherdown from June through October, 1976. Water levels were recorded from May through October, 1977 at Heatherdown and Nestow, on a weekly basis at the former and on a less frequent schedule for the latter.

Samples of primary water were collected several times throughout the 1976 and 1977 field seasons at Heatherdown

Table 6. Number of days with minimum temperatures < 10°, < 5°, and ≤ 0°C at Heatherdown (HF) and Stony Plain (SP) during June to September, 1976. Data for 1977 at Heatherdown are in parentheses.

Month	< 10°C		< 5°C		≤ 0°C	
	HF	SP	HF	SP	HF	SP
June	26(24)	28	14(14)	4	3(1)	0
July	28(20)	6	12(6)	0	0(1)	0
August	19(27)	7	6(14)	0	0(3)	0
September	30(30)	25	25(16)	3	13(7)	0

and Nestow. They were analyzed for pH either in the field or in the laboratory (within 4 h of sampling) with a Metrohm E 280A portable pH meter. Samples were frozen and later analyzed for Ca and Mg by an atomic absorption spectrophotometer (Appendix II). In September, 1977, water samples were obtained from Heatherdown and Nestow analyzed (Appendix II) for a broad range of chemical parameters using techniques prescribed in Standard Methods (Anonymous 1971).

Results

Water level dynamics at Heatherdown were complex, with portions of the peatland having somewhat independent water level fluctuations (Fig. 5). This was probably due to the presence of a slight slope and differences of hydraulic conductivities in the substrates (Rycroft et al. 1975; Boelter and Verry 1976). Water level fluctuations in the raised peat islands were more extreme than those of the meadows. This could be caused by the increased transpirational loss of water from trees and the increased absorption of water by the larger amount of peat present above water level. Maximum drawdown in meadow sites ranged from 7 to 25.5 cm during the two year study period, while in the raised-peat islands it ranged from 16.5 to 31.5 cm.

The water regime at Nestow was more straightforward. The mires here were developed in depressional areas between the dunes, and water level changes were quite similar throughout the areas studied. Maximum drawdown for the

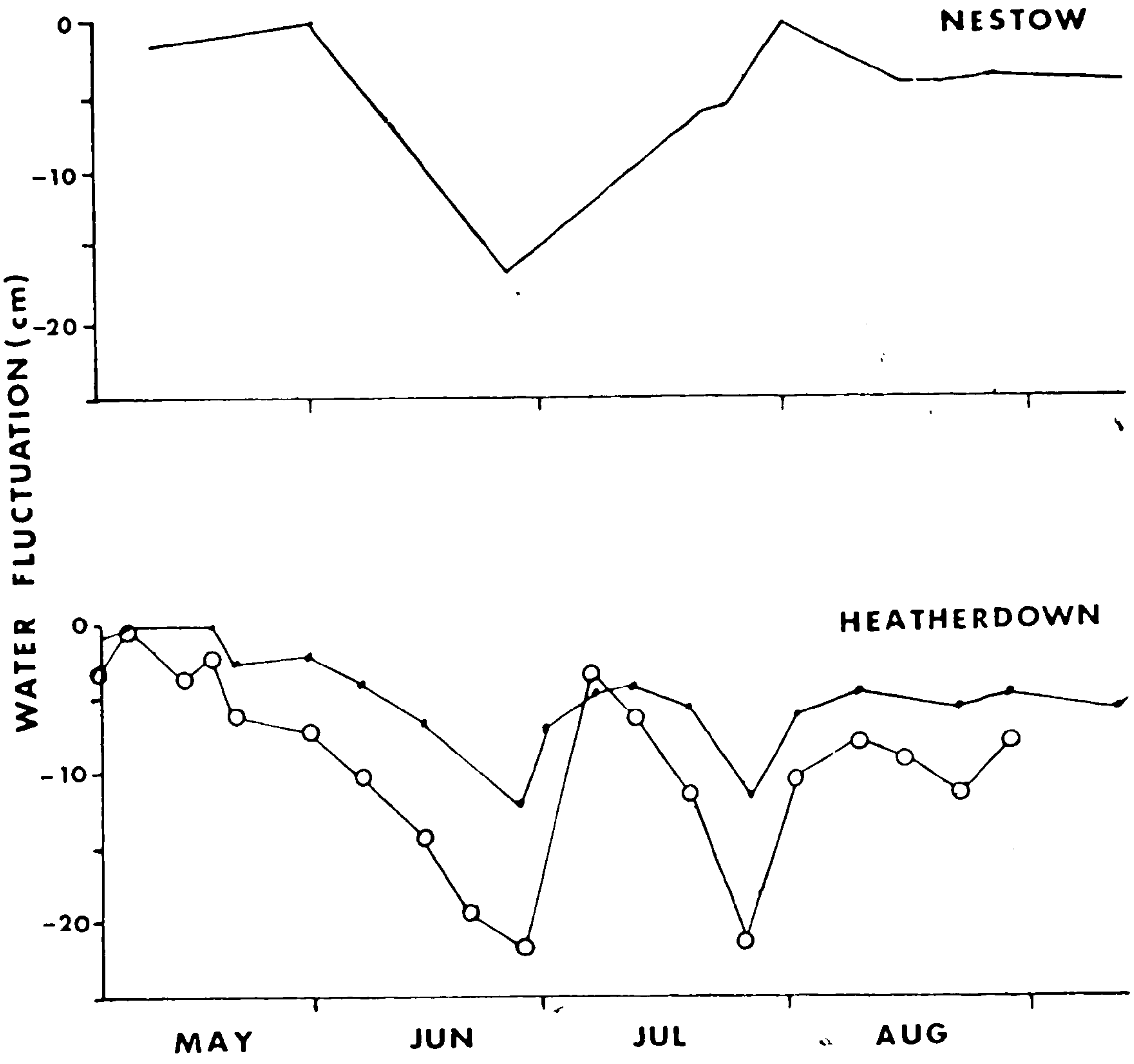

Figure 5. Seasonal water levels (1977) in relation to maximum water level at Heatherdown and Nestow fens (O = raised-peat location; • = adjacent low-peat location).

1977 season was 17 cm. Similar drawdown levels were found in the low-peat and raised-peat communities.

All of the communities sampled had microsites which were not inundated by primary waters, even at maximum water levels (Table 7 and Fig. 6). The low-peat communities at both study sites had moss hummocks >10 cm above maximum primary water levels. In terms of water level, such locations should theoretically be suitable for the establishment and survival of _L. groenlandicum_. But the plant is rarely found in the low-peat communities and is often largely absent from "young" raised-peat communities (Fig. 6).

The chemical characteristics of the primary water at Heatherdown would place it in a rich fen category (Table 8). As the raised-peat chemistry indicates that fen to ombrotrophic situations are also present (Table 12, page 21), the whole system is best considered as a rich mixed mire.

Water pH was fairly stable at each sampling location during the field season. Concentrations of Ca and Mg varied considerably, although seasonal changes in water chemistry were not evident. At one location the calcium concentrations were usually around 40 ppm, but were observed to be as high as 94 ppm. All of the primary water calcium concentrations determined at Heatherdown were >38 ppm.

In terms of calcium and magnesium, the primary waters of the Nestow mire system are minerally impoverished (Table 8). This system is a poor mixed mire, having fen to poor fen primary waters and ombrotrophic raised-peats.

Table 7. Mean relief and water level characteristics for the plant community types at Heatherdown and Nestow.

		Relief* (cm)		Maximum water** level (cm)		Minimum water** level (cm)	
Community	(n)	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD
HF *Scirpus*/*Campylium* (LP)	20	15.5 ±	6.9	6.3 ±	9.6	-12.5 ±	19.0
HF *Picea*/*Ledum* (RP)	19	25.7 ±	10.2	-9.7 ±	15.2	-34.3 ±	53.7
NF *Picea*/*Ledum* (RP)	20	26.3 ±	6.9	-19.2 ±	4.2	-36.7 ±	8.0
NF *Eriophorum*/*Sphagnum* (RP)	20	23.5 ±	9.8	-15.1 ±	6.6	-32.6 ±	14.2
NF *Betula*/*Aulacomnium* (RP)	10	25.0 ±	4.1	- 3.7 ±	6.4	-21.2 ±	36.7
NF *Carex*/*Sphagnum* (LP)	10	22.1 ±	5.4	2.1 ±	4.3	-15.4 ±	31.5
NF *Carex*/*Drepanocladus* (LP)	10	12.5 ±	6.0	6.6 ±	1.3	-10.9 ±	2.1

* lowest to highest points within each subquadrat
** in relation to the lowest point in each subquadrat

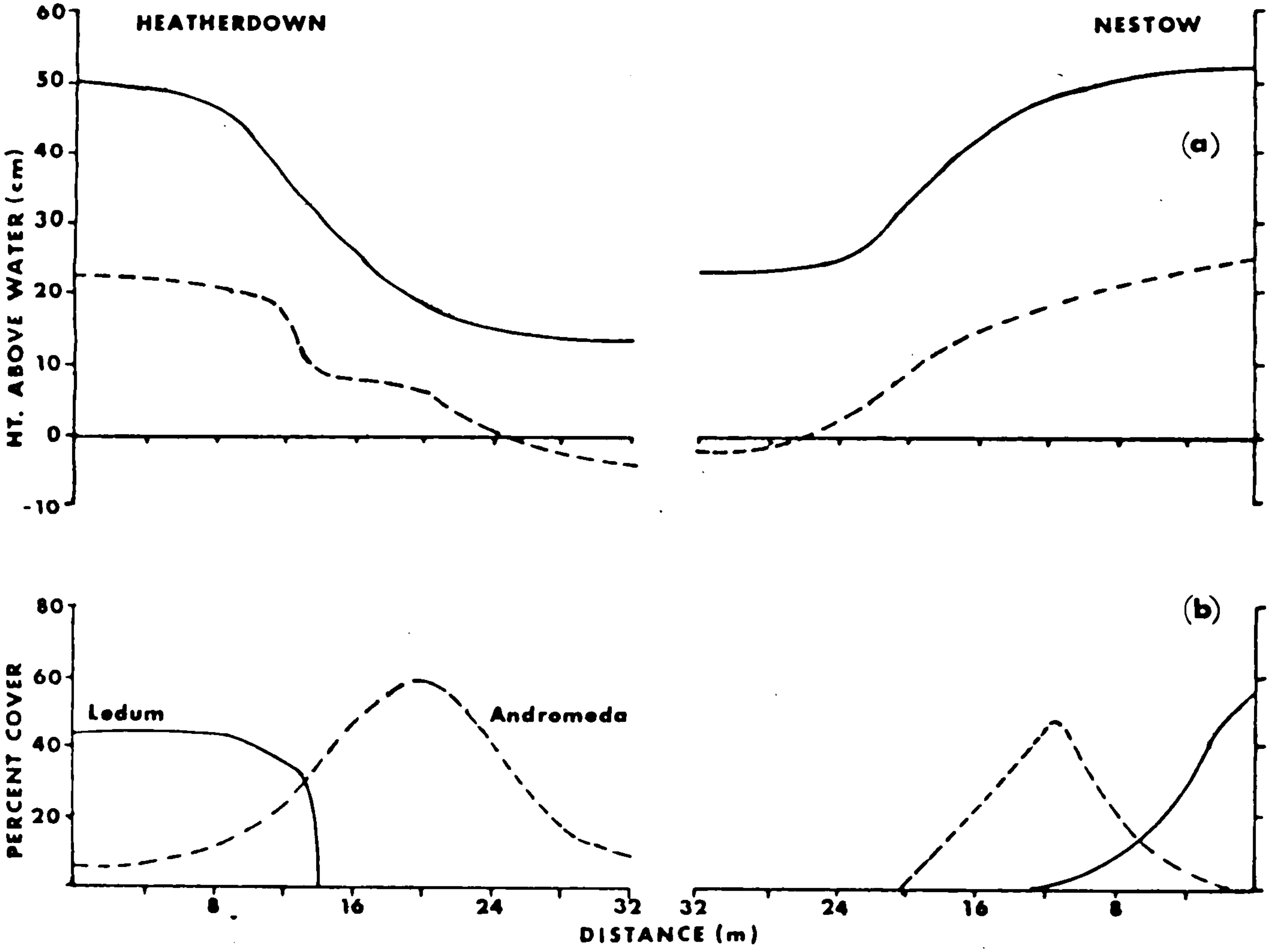

Figure 6. Distribution of Ledum groenlandicum in relation to substrate relief and maximum primary water level at Heatherdown and Nestow fen: (a) maximum (solid line) and minimum (dashed line) relief above maximum primary water level along typical transects at Heatherdown and Nestow, and (b) cover of L. groenlandicum and A. polifolia along the same transects.

Fluctuations of water pH during the growing season were slight at a given location. Calcium and magnesium concentrations varied both across time and space, but not enough data were collected to establish if any seasonal trends existed. While Heatherdown's primary water was richer in calcium, magnesium and sulfates, that at Nestow had higher levels of nitrates, phosphates, iron and chloride.

The primary water chemistry of both Heatherdown and Nestow fens is representative of the poor fen and rich fen systems in the study region (Table 9). The entire range of primary water chemistry is found in the region, ranging from bog to rich fen systems. Based solely on primary water chemistry, fens and rich fens predominate.

Substrate Chemical and Physical Parameters

Methods

Substrate bulk density and moisture content (upper 5 cm) were determined gravimetrically at several points during the 1976 and 1977 field seasons at Heatherdown. A metal cylinder (5 cm deep, area = 18 cm^2) was pushed (or persuaded) into the peat and a core was extracted. This was placed in a soil tin which was then put in a plastic bag. The peat was weighed within 3 h of sampling and then dried at 105 for 24 h and reweighed.

Volumetric samples (area = 100 cm^2) of the top 20 to 30 cm of major substrate types were collected in the fall of 1976 at Heatherdown and in June of 1977 at Nestow. The

Table 8. Primary water chemistry of the Heatherdown and Nestow mires, with data on other rich fens in central Alberta. Values for pH, Ca, Mg, and conductance represent the range across time and space during the study. All mineral values are in mg/l. Number of samples is given in parenthesis.

Factor	Other Rich fens[1]	Heatherdown	Nestow
pH	7.4- 8.0 (7)	7.2- 8.2 (60)	3.6- 6.1 (24)
Conductance (umho cm^{-1}, 20°C)	—	595 -928 (22)	30 -65 (13)
Ca:Mg (molar)	8.1- 3.7 (12)	.6- 2.1 (60)	2.5- 3.8 (24)
Ca	31.2-103.6 (12)	38.3-120.2 (60)	2.3-11.7 (24)
Mg	10.0- 41.2 (12)	26.0- 53.0 (60)	.5- 2.7 (24)
Na	1.2- 9.6 (5)	10 (1)	2 (1)
K	—	4 (1)	0 (1)
Fe	0.0- 0.4 (5)[2]	0.2 (1)	0.6 (1)
CO_3	139.5-253.3 (5)	140.6 (1)	20.0-24.0 (2)
SO_4	53.0- 74.2 (5)	205 (1)	0 (1)
NH_3-N	—	0.0 (3)	0.0- 0.01 (3)
NO_3-N	—	0.0- 0.1 (3)	0.1- 0.2 (3)
Total PO_4	—	0.1- 0.2 (3)	0.3- 1.4 (3)
Cl	—	4.1 (1)	8.7 (1)

1. In part adapted from Lewis and Dowding (1926) and Lewis et al. (1928).
2. Fe-oxide and aluminum

Table 9. Primary water chemistry of mires in west-central Canada. Number of mires sampled is given in parentheses. All mineral concentrations are in mg l^{-1}.

Location	n	pH	Ca	Mg
Yukon				
Watson Lake[1]	18 (6)	4.2-7.2	0.8- 43.0	0.3-20.0
N.W.T.				
Nahanni Park	5 (5)	5.1-6.4[4]	1.2- 10.4	0.1- 3.4
Alberta (north)				
Caribou Mountains	5 (5)	4.1-7.5	2.6- 29.7	0.4- 8.9
Lake Athabasca	4 (2)	5.5-7.3	4.4- 28.0	1.1-13.0
Alberta (central)				
Swan Hills[2]	63 (10)	4.1-6.0	1.2- 8.7	0.3- 2.0
Slave Lake	6 (1)	6.5-6.8	7.2- 49.0	0.5- 6.3
Westlock	9 (6)	3.6-7.1	5.9- 50.0	3.6- 7.1
Nestow Dunes	24 (9)	3.5-6.1	2.3- 11.7	0.5- 2.7
Elk Island - Cooking Lake	9 (4)	3.8-7.3	6.3- 72.6	1.2-33.0
Wabamun -[3] Heatherdown	92 (13)	4.4-8.2	4.0-120.2	1.8-53.0

1 adapted from Walmsley and Lavkulich (1975)
2 largely adapted from Vitt et al. (1975): 61 (8)
3 partly adapted from Lewis and Dowding (1926) and Lewis et al. (1928): 7 (3)
4 pH values for Nahanni were made on samples stored for up to 2 months at room temperature.

samples were divided into 0-5, 5-10, 10-20 and 20-30 cm fractions. The pH was determined on the fresh peat by the glass electrode method, with slight additions of distilled water when necessary. Samples were frozen until there was time to dry and rub them through a 4 mm sieve. Exchangeable metallic cations (Ca and Mg) were determined on an atomic absorption spectrophotometer following extraction from 5 g samples with 1 N ammonium acetate (Chapman 1965).

Results

Bulk density of the major substrate types at Heatherdown was quite variable (Table 10). Sphagnum substrates had the lowest values, although their density was comparable to that of the Feather mosses and the lighter of the Tomenthypnum substrates. The higher bulk densities of Campylium and Tomenthypnum were in part due to the presence of marl within the top 5 cm of substrate. All of the bulk densities were considerably lower than those characteristic of mineral soils (≥ 1 g cm^{-3}).

In terms of water content on a dry weight basis, the Feather mosses were the driest and Sphagnum the wettest. But this index of moisture is misleading when dealing with substrates with large differences in bulk density. A more meaningful index based on volume demonstrates that although the Feather mosses retain the dry spot, the low-peats (Tomenthypnum and Campylium) contain the most water. Moisture content of Sphagnum and Tomenthypnum overlapped

Table 10. Mean bulk density and water content (seasonal) of major substrate types at Heatherdown fen (upper 5 cm).

Substrate	n	Bulk density			Water content Percent of volume*			Water content Percent dry weight		
		g cm^{-3}	SD	range	%	SD	range	%	SD	range
Feather moss	27	.039	± .014	(.022-.091)	11.1	± 5.4	(1.3-20.2)	294	± 144	(34- 535)
Sphagnum fuscum	31	.026	± .011	(.011-.046)	22.9	± 5.1	(12.0-34.1)	866	± 194	(455-1289)
Tomenthypnum nitens	33	.051	± .041	(.020-.243)	28.4	±11.4	(10.2-66.9)	498	± 222	(191-1322)
Campylium stellatum	32	.143	± .078	(.054-.359)	61.2	±24.4	(23.5-100.0)	404	+ 163	(164- 803)

* adjusted to the mean bulk density of each substrate type

considerably. The range of water content in the substrates indicates that water potentials were all >-.33 bar. The Feather moss substrates were an exception, having several samples with a water content corresponding to < -15 bars (Walmsley and Lavkulich 1975; Boelter and Verry 1976; Busby 1976).

The chemical characteristics of the major substrate types are summarized in Tables 11 and 12. Although no major difference is found between the low-peat and raised-peat substrates at [illegible]tow, a sharp gradient exists at Heatherdown. The [illegible]mum concentration (volumetric) of calcium in the top [illegible] of the low-peat substrate (C. stellatum) is 34 times greater than the minimum and 10 times greater than the maximum value for calcium in Sphagnum substrates (Table 11). This gradient often occurs within an area as small as 30 cm horizontally and 40 cm vertically. It is generated by the upward growth of S. fuscum (and T. nitens to a minor extent). The peat that accumulates tends to isolate the upper substrate layers from primary water influence. The degree of isolation (ombrotrophy) depends on:

1. the amount of precipitation;
2. the evapo-transpiration: precipitation ratio;
3. how high the peat accumulates above the primary water level and the type of peat being produced;
4. the extent of primary water level fluctuation;
5. the chemistry of the primary water.

Table 11. Chemical characteristics of major substrate types at Heatherdown and Nestow fens.

Substrate	Depth (cm)	pH n	pH range	Bulk density g cm^{-3}	Exchangeable Cations n	Exchangeable Cations Ca meq dm^{-3}	Exchangeable Cations Mg meq dm^{-3}	cm above water
Heatherdown Feather Moss	0- 5	3	4.4-5.6	.022-.043	3	5.9- 9.0	9.0- 2.4	40-45
(S. fuscum)	5-10	1	4.0	.047	1	8.9	2.1	
(")	10-20	1	4.1	.017	1	2.4	1.0	
(")	20-30	1	4.2	.018	1	3.1	1.1	
Sphagnum fuscum	0- 5	6	3.8-4.5	.016-.043	4	3.5- 11.8	1.3-10.5	22-45
" "	5-10	6	3.7-6.3	.014-.034	4	3.1- 15.2	1.6-11.1	
" "	10-20	4	3.9-7.6	.022-.028	4	2.5- 18.4	2.3-11.2	
" "	20-30	4	6.1-7.8	.020-.058	4	7.2- 44.2	4.7-11.6	
Tomenthypnum nitens	0- 5	3	5.4-7.7	.008-.026	3	4.7- 21.8	0.5- 6.0	20-27
" "	5-10	3	6.9-7.8	.019-.069	3	9.6- 95.7	2.4-18.5	
Marl	10-20	3	7.4-7.7	.037-.177	3	35.4- 229.5	8.7-28.3	
Marl	20-30	3	7.2-7.3	.090-.189	3	76.6- 217.5	8.6-18.4	
Campylium stellatum	0- 5	3	7.3-7.8	.100-.346	3	119.7- 324.8	16.3-39.7	13-20
Marl	5-10	3	7.1-7.6	.119-.438	3	121.8- 385.7	23.3-30.9	
Marl	10-20	3	7.1-7.2	.119-.602	3	80.9- 252.8	10.1-25.6	
Nestow Sphagnum*	0- 5	4	3.3-3.9	.009-.015	4	1.3- 2.2	0.7- 1.0	20-43
"	5-10	4	3.4-4.4	.010-.022	4	1.0- 2.5	0.6- 0.9	
"	10-20	4	3.4-4.5	.010-.[illegible]	4	0.9- 5.7	0.3- 2.5	
Sphagnum/** Aulacomnium	0- 5	2	3.6	.0[illegible]-.011	2	1.3- 1.4	0.5- 0.6	13
"	5-10	2	3.9-4.0	.011-.021	2	1.8- 3.1	0.7- 1.1	
"	10-20	2	4.2-5.4	.019-.052	2	2.8- 7.8	0.8- 2.3	
Carex/Drepanocladus	0-10	2	5.8-5.9	.018-.030	2	3.4- 5.3	1.7- 3.3	0- 2

* Sphagnum angustifolium, S. magellanicum, S. subsecundum (s.s.

** Sphagnum subsecundum (s.s.) Aulacomnium palustre

Table 12. Exchangeable calcium and magnesium concentrations in Heatherdown and Nestow substrates on a dry weight basis (meq 100 g^{-1}).

Substrate	Depth (cm)	(n)	Calcium	Magnesium
Heatherdown				
Feather mosses	0- 5	3	21.05- 36.25	3.49- 5.53
	5-10	3	19.07- 51.23	4.51-11.27
	10-20	1	14.53	6.07
	20-30	1	17.00	6.03
Sphagnum fuscum	0- 5	6	9.35- 33.01	5.79-29.51
	5-10	6	9.23- 45.23	5.37-32.79
	10-20	5	8.79- 74.20	8.63-49.59
	20-30	4	35.93- 99.49	20.08-27.05
Tomenthypnum nitens	0- 5	3	48.35- 83.86	6.48-22.95
	5-10	3	51.19-137.84	12.70-26.64
	10-20	3	96.65-129.60	15.98-23.77
	20-30	3	62.56- 99.49	2.46-20.49
Campylium stellatum	0- 5	3	79.60-119.38	9.84-20.90
	5-10	3	88.13-106.88	5.33-22.54
	10-20	3	41.82- 71.93	2.87-18.44
Nestow				
Sphagnum	0- 5	4	10.34- 15.15	5.25- 8.93
	5-10	4	4.42- 14.84	3.81- 7.02
	10-20	4	4.81- 10.69	3.00- 8.68
Sphagnum/ Aulacomnium	0- 5	2	13.31- 14.83	5.57- 5.70
	5-10	2	14.53- 18.35	5.21- 6.68
	10-20	2	14.87- 14.98	3.98- 4.31
Carex/ Drepanocladus	0-10	2	17.93- 19.09	9.22-11.27

Because of the interactions of the above variables, the chemistry of ombrotrophic peats formed in different environments will vary, but less so than the chemical parameters of minerotrophic peats. In general, the exchangeable Ca content of ombrotrophic peats is ≤ 13 meq/100 g, with a pH range of 3.0-4.5 (Sjörs 1961a, Bellamy and Reiley 1976; Mornsjo 1968; Karlin 1975; Pakarinen and Tolonen 1977). Profiles of three ombrotrophic peats formed under different environmental regimes are given in Table 13.

A major diagnostic feature of ombrotrophic peats is a discontinuity in mineral composition in the peat profile (Table 13). Mineral content is high in the lower portions of the profile, which are in contact with the primary water. Above this zone the mineral content decreases until reaching a minimum value at a variable distance from the peat surface. Mineral content increases again in the surface layers of the peat, especially in the upper 5-10 cm (Sjörs 1961a, Bellamy and Reily 1967).

This increase in the surface layers has been attributed to nutrient retention and cycling abilities of the plants (Bellamy and Reily, 1967). Other researchers hypothesize that it is due to increased atmospheric input of nutrients due to man's activities (Mattson and Koutler-Anderson, 1954; Sjörs 1961a). The growth rates of the mosses (Bellamy and Reiley 1967; Clymo 1973) and the sharp break in chemistry near the peat surface suggest that the former theory is correct. There are probably greater atmospheric inputs

Table 13. Chemistry of ombrotrophic peats developed in three different environmental regimes, Ca and Mg are expressed as meq 100 g^{-1})

	Profile 1*	Profile 2	Profile 3
Location:	England	Heatherdown, Alberta	Nestow, Alberta
Precipitation:	1375 mm	500 mm	500 mm
Primary H_2O:	pH = 7.3; Ca = 29 ppm	pH = 7.5; Ca = 40 ppm	pH = 5.0; Ca = 5 ppm

Height of sample above primary H_2O (cm): 50, 40, 30, 20, 10, 0

Profile 1*

pH	Ca	Mg
4.0	56.1	10.1
3.7	13.6	9.
3.7	8.5	7.6
3.7	6.7	5.9
3.6	5.1	5.3
3.5	5.6	5.8
3.4	7.1	6.1
3.6	7.5	7.9
3.7	8.3	8.2
3.4	6.8	7.4
3.6	8.5	7.4
3.7	9.4	6.8
4.0	28.6	16.6
6.5	138.5	40.2

Profile 2

pH	Ca	Mg
4.2	9.3	5.8
4.3	9.2	5.4
4.5	8.6	7.0
4.5	9.0	10.3
4.7	20.8	17.4
6.1	51.0	30.2
7.0	73.5	28.9
7.4	88.5	26.9

Profile 3

pH	Ca	Mg
3.9	10.3	7.0
4.4	11.8	7.0
4.6	11.1	5.0
4.4	6.6	3.4
4.3	6.0	3.6
4.1	4.1	3.3
4.1	4.7	3.3
4.2	11.4	5.2
4.0	12.7	6.4

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* Adapted from Bellamy and Reily (1967)

of nutrients into mire systems because of man's recent activities, but these increases are not primarily responsible for the high concentrations of Ca and Mg in ombrotrophic peat surfaces.

The chemistry of minerotrophic peats is far more variable than ombrotrophic peats. Rough ranges would be: poor fen peat (Ca = 8 - 41 meq/100 g, pH 4.0-5.3), fen peat (Ca = 34-64 meq/100 g, pH 4.7-6.5) and rich fen peats (Ca $\geq$ 65 meq/100 g, pH 6.5-8.0) (Malmer and Sjörs 1955; Sjörs 1961a, Mörnsjö 1968). There is a broad overlap between most of the types, and consequently data on peat profile chemistry and nutrient status of the primary and/or secondary water is needed in order to classify the peat.

Only some of the Sphagnum raised-peats (primarily the upper 20 cm) at Heatherdown are ombrotrophic. Most of the raised-peats there are minerotrophic (poor fen to fen peats). The large variation in chemistry is due to differences in height above the primary water, extent of water level fluctuation, and size (in area) of the raised-peat system. The Feather mosses tend to be richer (poor fen to fen), which is surprising as they are largely dependent on atmospheric nutrient input (Tamm 1953; Busby 1976). The T. nitens and C. stellatum peats were all fen to rich fen peats.

At Nestow, small variability in peat chemistry is found. The peats range from ombrotrophic to poor fen in chemistry, with the raised-peat being ombrotrophic and the other peats being typical of poor fen peat. It is interesting to note that the upper 5 cm of Sphagnum at Nestow is similar in nutrient content to ombrotrophic Sphagnum peats at Heatherdown (Table 13).

Looking at peat chemistry from a volumetric point of view (Table 1) , a slightly different picture emerges. The chemistry of the Sphagnum, Feather moss and T. nitens (top 10 cm) substrates overlap to a greater extent. The gulf between the raised-peats (Sphagnum, Feather mosses and some Tomenthypnum) and the rich fen peats (T. nitens, C. stellatum and Drepanocladus) is greatly widened. The Sphagnum basal peats, which have comparable maximum calcium concentrations to rich fen peats on a dry weight basis have almost one tenth as much calcium on a volumetric basis.

Another interesting aspect is the high concentration of Mg in Heatherdown minerotrophic S. **fuscum** peats. This indicates either a preferential adsorption and retention of magnesium by Sphagnum, or the influence of leaching by rain, which tends to lower the Ca:Mg ratio in peat (Mörnsjö 1968). The maximum Mg concentration (volumetric) in the top 5 cm of Sphagnum peat is 25% of the maximum in C. stellatum (top 5 cm), while the maximum Ca concentration is only 3% of that in the C. stellatum peat.

The chemical composition (total) of marl from two rich fens similar to Heatherdown fen is presented in Table 14. The major components are $CaCO_3$ and organic matter.

Table 14. Chemical composition (total) of marl substrates from two rich fens in central Alberta. Taken from Lewis et al. (1928). Values are percent dry weight.

	Mire 1	Mire 2
Organic Matter	30.6	18.9
$CaCO_3$	64.2	80.3
$MgCO_3$	.1	.4
Silica	4.5	.4
Iron oxide and aluminum	.4	.0

Substrate Temperature

Methods

Substrate temperature at Heatherdown was measured at 1 h intervals with a Grant Recorder and thermister probes during selected periods of the 1976 and 1977 field seasons. The probes were situated at a depth of -3 cm, with two in raised peat substrates (Sphagnum fuscum hummocks, north and south aspects) and two in low-peat substrates (Tomenthypnum and Campylium). In late August, 1976, the probes were placed at -2 and -10 cm positions in a Sphagnum hummock (north exposure) and Campylium substrates.

Results

Characteristic trends in daily maximum and minimum temperatures for the three substrates are shown in Fig. 7 and Table 15. The Campylium substrate experienced the least fluctuation in temperature, primarily because of its higher water content. The Sphagnum and Tomenthypnum sub-

Table 15. Mean (± SD) daily maximum and minimum air (10 cm) and substrate temperatures (-3 cm) during the 1976 field season. Temperatures are in ° C.

	June 9-21	July 16-30	Aug. 25-Sept. 13
Air	22.6±2.4 (3.7±3.3)	23.0±4.5 (5.9±2.8)	18.0±5.1 (3.1±2.9)
Campylium	17.0±1.7 (9.2±1.8)	17.6±2.9 (12.2±2.2)	12.1±2.8 (7.4±2.5)
Tomenthypnum	23.3±2.9 (8.4±2.6)	22.8±4.7 (11.7±2.4)	— —
Sphagnum (N)*	19.7±2.8 (4.9±2.6)	19.5±4.1 (8.2±2.6)	16.9±4.9 (2.6±2.6)
Sphagnum (S)*	22.3±3.6 (5.8±3.2)	— —	— —

* N = north aspect; S = south aspect

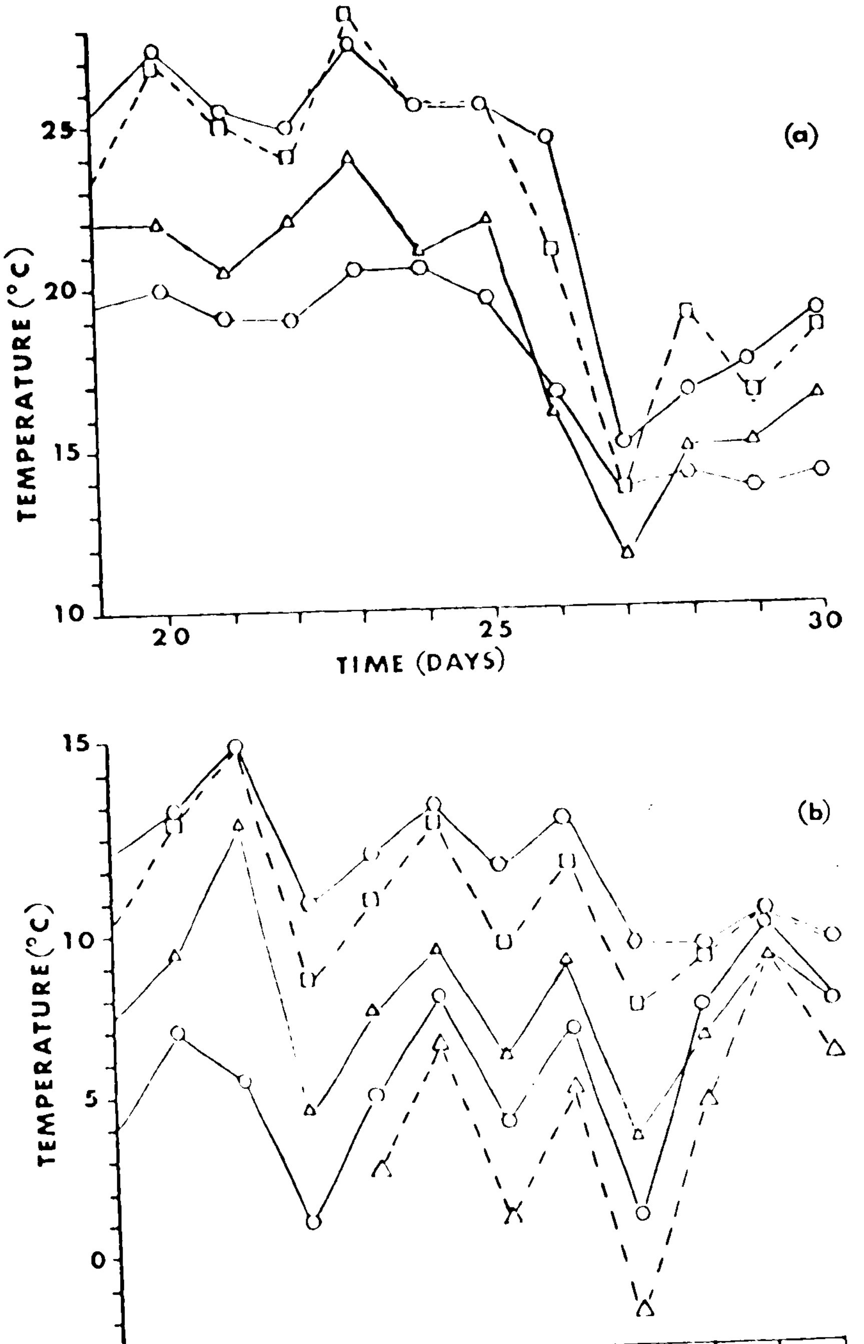

Figure 7. Maximum (a) and minimum (b) substrate temperatures at -3 cm depth during July 19-30, 1976. (□ = *Tomenthypnum*; ▵ = *Sphagnum*; ○ = *Campylium*; ○ = *air temperature*; △ = *Sphagnum* (0 cm)

strates had similar ranges of temperature variation, with southern exposures experiencing the most extreme fluctuations. Maximum substrate temperatures of Sphagnum at -3 cm were generally higher than those of Campylium and those of Tomenthypnum. Minimum temperatures in the Sphagnum hummocks were lower than the low-peat substrates. The higher minimum temperatures of the low-peat substrates were due to their proximity to the primary water and its heat buffering influence.

Data on temperature profiles in representative raised-peat (Sphagnum) and low-peat (Campylium) substrates is provided in Fig. 8. The raised-peat profile was subject to greater temperature extremes than the low-peat profile. In spite of having higher maximum temperatures, the Sphagnum substrates froze earlier in the fall than did the low-peat substrates.

Substrate temperature tracked air temperature fairly closely. However, variation in temperature at -2 cm, -3 cm and -10 cm was less than the variation in air temperature for all substrates monitered. Surface temperatures of unshaded moss substrates usually have much higher temperature variations than the air, with elevated maximum and depressed minimum temperatures (Norgaard 1951; Busby 1976). Daily minimum surface temperatures on a Sphagnum hummock in late July, 1976 were substantially lower than the corresponding minimum air temperatures (Fig. 7).

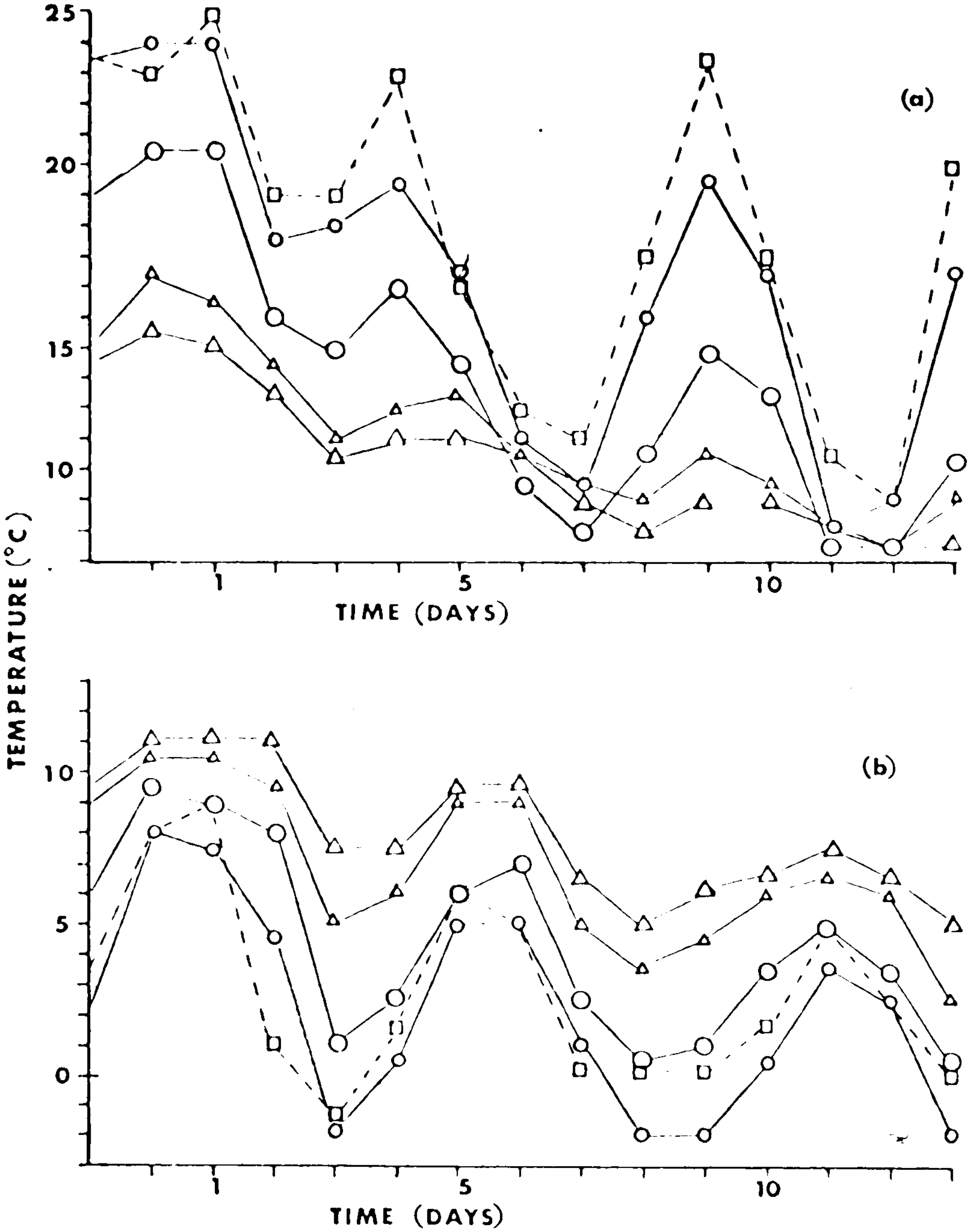

Figure 8. Maximum (a) and minimum (b) substrate temperatures at -2 cm and -10 cm depths during Aug. 30-Sept 13, 1976. (○ = -2 cm *Sphagnum*; ◯ = -10 cm *Sphagnum*; △ = -2 cm *Campylium*; ∠ = -10 cm *Campylium*; □ = air temperature)

IV. THE MATURE PLANT

Transplants Into Low-Peat

Methods

In order to establish whether mature plants of *L. groenlandicum* could tolerate the environmental regime of the low-peat communities at Heatherdown, transplantings were made several times throughout the study. On June 6, 1976, 5 clumps of mature plants were transplanted from raised-peat communities to each of two low-peat locations (site 1 and site 2). An additional 5 transplants were made within the raised-peat system so that the impact of transplantation could be determined. Plants with intact root systems were transplanted. The clumps were placed such that their rooting systems experienced a hydrological regime similar to that of the adjacent naturally occurring low-peat plants. A third low-peat transplant location (site 3) was established at a wetter site than either site 1 or 2 in fall, 1976 (4 clumps).

Observations on survival and vigor were made during the 1976 field season. In August, 1977, length of the ten longest leaves and stems produced that season was determined for each transplant clump and an equal number of undisturbed (control) clumps. These data were compared with an analysis of variance and Duncan's New Multiple Range Test to determine whether significant differences occurred between the three treatments (Steel and Torrie 1960; Sokal and Rohlf

1969). The level of significance used for this study is $\alpha = .05$.

A possibility existed that the peat transplanted along with the original transplants might be buffering their rooting systems from the chemistry of the wet meadow peat and primary water. Because of this, 22 rooted L. groenlandicum twigs were taken from greenhouse sand cultures and planted in two locations in the wet meadow in June, 1977 (11 at each site). All sand was washed from the roots so that they were in direct contact with the meadow peat. Survival and vigor of these plants was observed through June, 1978.

In order to help separate the influence of water chemistry and water level on the plants, transplants from raised-peat to low-peat at the Nestow mire were made in May, 1977. A total of 10 clumps of mature plants were transplanted to the meadow, while another 5 were transplanted within the raised-peat system as controls. Data on survival and vigor were obtained through June, 1978.

Results

All of the June, 1976 transplants at Heatherdown survived three growing seasons. The foliage appeared healthy and many of the plants flowered and produced viable seed. In general, the phenology of the low-peat transplants was the same as that of the undisturbed plants. Results of the August, 1977 measurements of current stem and leaf lengths indicate that the transplantation had a more serious impact on the plants than did the low-peat environment (Tables 16 and 17).

Table 16. Relationships of stem length in transplanted and control (non-disturbed) plants.

$F = 19.52$ ($p < .001$)

	Stem length (Mean)		
Treatment	RPT*	LPT	Control
Length (mm)	21.1	22.5	29.4
Non-significant ranges ($\alpha = .05$)			

* RPT = raised-peat transplants; LPT = low-peat transplants

Table 17. Relationships of leaf length in transplanted and control (non-disturbed) plants.

$F = 53.14$ ($p < .001$)

	Leaf length (Mean)		
Treatment	LPT*	RPT	Control
Length (mm)	20.3	22.0	27.5
Non-significant ranges ($\alpha = .05$)			

* LPT = low-peat transplants; RPT = raised-peat transplants

Data on site 3 transplants were not included in the statistical analyses. These had been transplanted in the fall and were thus not given a chance to establish a new rooting system, and were more vulnerable to the winter environment. As noted earlier, there was a lack of snow cover during the latter part of the 1976-1977 winter. Most of the leaves as well as many of the upper buds of the site 3 transplants did not survive to spring, 1977. Consequently, it was not possible to distinguish between the effects of late transplantation, the severe winter stress, and the low-peat environment on subsequent survival and growth. However, the overriding impact appeared to be the lack of snow cover in late winter. In spite of that stress, all of the site 3 transplants survived the 1977 and 1978 growing seasons.

By the end of the first growing season, 12 of the 22 rooted twigs planted appeared to be alive, 3 ± alive, 5 dead and 2 missing. In July, 1978, 8 plants (40% of 20) were alive, and 11 were dead. As the 8 surviving plants appeared very healthy, the death of the other plants was probably due more to the impact of transplantation than to the water and nutrient regimes of the Heatherdown low peat.

All of the Nestow transplants survived the 1977 and 1978 field seasons, and appeared quite healthy throughout the entire period (Fig. 9).

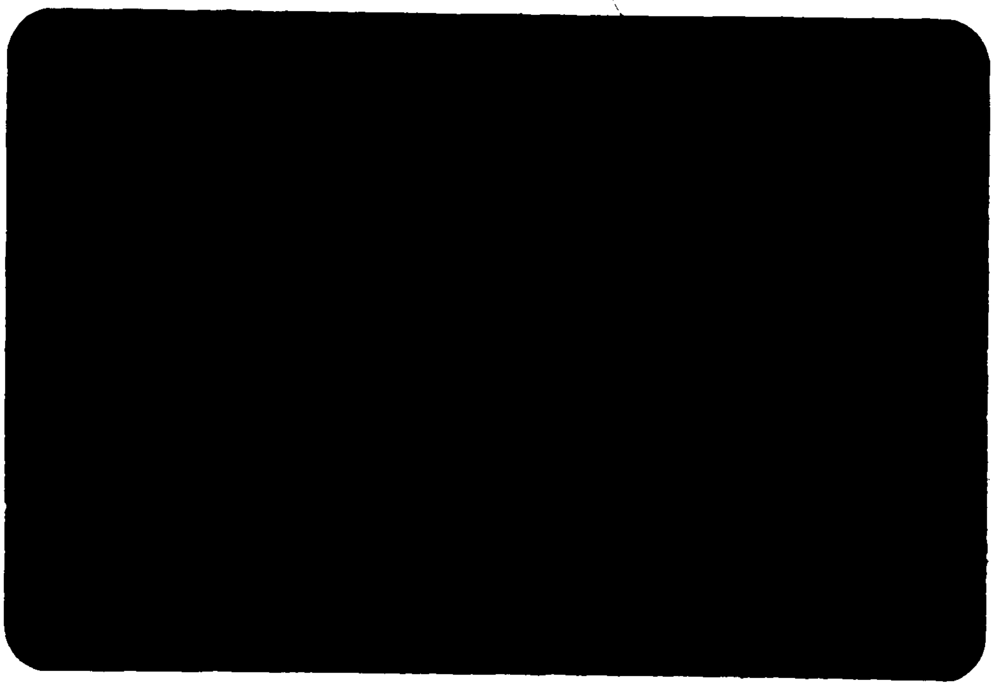

Figure 9. Clump of transplanted *Ledum groenlandicum* in Nestow low-peat environment. Picture taken in fall, 1977, after the transplants had been there for one growing season.

Adventitious Root Formation

Methods

In order to determine whether the vegetative spread of L. groenlandicum was restricted from the low-peat areas because of inhibition of adventitious root formation, the following experiment was carried out. On June 1, 1977, when the leaf buds were starting to expand, L. groenlandicum twigs which had active growing points and healthy leaves present from the 1976 growing season were collected. The twigs were cut such that at least 5 cm of stem would extend into the peat. The twigs were placed in four major substrate types: 110 twigs in each of Sphagnum, Tomenthypnum and Campylium-Drepanocladus and 86 twigs in Feather mosses. These were observed for survivorship and rooting in early July and mid-September, 1977 and in June, 1978.

Results

The unrooted twigs had a high mortality rate in all of the substrate types in which they were placed (Table 18). By the end of the 1977 field season, those placed in low-peats had the highest survival rates. Those in Tomenthypnum, Sphagnum and Feather Moss had survival rates decreasing in that order. All of the twigs in the Feather mosses died within a month of placement. This was probably due to the much lower moisture content of Feather moss substrates (see p. 38).

The survival rate had greatly changed by June, 1978.

Table 18. Survival of cut twigs in the adventitious root formation experiment after one growing season.

	Substrate			
	Fm	Sf	Tn	Cs*
Observed live	0	7	16	34
Expected live	12	15	15	15
Chi-square=39.94 ($p < .005$)				
Percent survival				
Sept., 1977	0	6	15	31
June, 1978	0	5	0	1

* Fm = Feather moss; Sf = S. fuscum; Tn= T. nitens; Cs = C. stellatum.

Most of the twigs in the C. stellatum - D. revolvens and T. nitens substrates did not survive the winter environment. All 5 plants which survived in the S. fuscum hummocks appeared healthy, as did the one in the low-peat moss mat. There were also 6 plants ± alive in the Campylium - Drepanocladus mats and 1 ± alive in the Tomenthypnum mats.

The initial higher survival rates in the low-peat substrates may have been due to the abundance of water there. Although adventitious roots had formed on all living twigs checked in the S. fuscum and T. nitens substrates (in September, 1977), many of those observed in the wet meadow substrates had not formed any detectable roots. That the low-peat plants were not healthy is indicated by the fact that the stems and leaves produced that growing season fell off easily when touched in late September, 1977. The ready availability of water in the wet meadow substrates may have enabled a high number of twigs to leaf out successfully and then gradually die during the rest of the growing season. Twigs which were in the other substrates did not have their stems immersed directly in water saturated substrates and most likely died quickly due to high water stress. There is also the more extreme range of daily temperatures experienced in the raised-peat substrates than in the low-peat substrates, which would mean that the low-peat twigs were subjected to less temperature stress as well.

Lab Experiments With Water Level and Chemistry

Methods

Two experiments were carried out to study the influence of water levels and chemistry on the mature plant under more controlled conditions. In October, 1976, several clumps of mature L. groenlandicum were obtained from the field and put in a growth chamber (Environmental Growth Chamber Co., Model M-15) at -4°. The substrate-root systems of the plants were left intact. They were removed from that temperature regime in December, 1976 and placed in a controlled environment (Trop-Arctic) greenhouse with a cool temperature regime (17° day/8° night) until bud break (May, 1977). On May 13, 1977, 5 plants were placed in each of the following water level regimes: wet (0 cm, constant); wet-moist (0 cm for 3 days,

-5 cm for 4 days); moist (-5 cm, constant); and dry (-10 cm, constant). The plants were grown through the equivalent of 2 (25° day/15° night field seasons with a fall-winter-spring season from August 4 to November 17. The experiment was terminated on February 9, 1978 (a total of 277 days). At this time, the number of leaves produced in the second season was compared with the number produced in the first by analysis of variance.

The second experiment dealt with water chemistry. Based on data obtained from the field and the literature, four nutrient culture solutions were made:

Solution 1) pH 3, Ca = 100 ppm
Solution 2) pH 3, Ca = 4 ppm
Solution 3) pH 7.5, Ca = 100 ppm
Solution 4) pH 7.5, Ca = 4 ppm

The other minerals were present at half the concentrations of that in Hoagland's solution. Rooted twigs of L. groenlandicum of approximately the same size were placed in the solutions (5 to each treatment). Nutrient solutions were replaced bi-weekly from June 21 to August 26, and then at monthly intervals until October 30, 1977.

This experiment was carried out in a growth chamber regulated to have a similar temperature regime as that at Heatherdown in July (25° day/8° night). Unfortunately iron was omitted from the solutions during the course of the experiment and therefore the experiment was not successfully completed.

Results

In the greenhouse water level experiment, all of the plants survived the first growing season, with all plants in the dry, moist and wet/moist regimes surviving to the end of the experiment. Three (of five) plants in the wet regime did not survive the dormant period. Leaf production in all treatments was considerably lower in the second growing season when compared with the first (Table 19). This was in part due to the higher number of flower buds present in the second growing season, which usually inhibit leaf production at those stem apices for that season.

The wet regime plants were the most severely affected. Only a few stunted leaves were produced during the second growing season by the two surviving plants. One flower bud started to expand, but never developed fully. Root development was not extensive and limited to the moss mat (0 to -2 cm). Both the wet and wet/moist regimes developed a moss mat on the substrate surface because of the high water levels. The moss mat in the wet regime was about 2 cm thick, while in the wet/moist it was about 1 cm thick.

The plants in the other three regimes produced normal flowers and leaves. The percent change in leaf production was not significantly different among them (Table 19). There was greater root development in these three regimes than in the wet regime. Roots in the wet/moist regime

Table 19. Relationship of second season leaf production to the first season's in the mature L. *groenlandicum* water level experiment.

F = 4.86 (p = .014)

	Percent changes (Mean)			
Water regime	Dry	Moist	Moist/wet	Wet
Percent Change	-47.1	-67.3	-74.7	-99.8
Non-significant ranges (α = .05)				

were concentrated in the upper 2 cm, being especially plentiful in the moss mat at the substrate surface. The moist and dry regime plants had extensive root development throughout the substrate down to the respective water levels (-5 cm and -10 cm).

As the plants appeared to be healthy at the end of their first season, the mortality of the wet regime L. *groenlandicum* may not be solely due to the high water level. Ice formation during the winter cycle caused much soil heaving in the wet and wet/moist regimes. It may be that extensive root damage from frost heave coupled with a continually saturated soil led to the death of the plants.

Even though the original purpose of the pH versus Ca concentration experiment was not accomplished, interesting data on Fe deficiency in L. *groenlandicum* were gathered. Minor deficiency symptoms in leaves produced during the experiment developed within two months. The two high pH regimes displayed the most severe symptoms, with interveinal chlorosis being prominent. Plants in the two low pH regimes appeared fairly healthy after the first two months, although slight interveinal chlorosis was noted in a few of the younger leaves.

After five months, only plants in the two low pH regimes had produced a second crop of leaves which were not severely iron deficient (four plants in solution 1 and three plants in solution 2). In fact, only one plant in the two high pH regimes produced a second set of leaves, and these were all white. Three (of five) of the plants in the solution 4 regime had died by the fifth month.

Discussion

Except for continuously saturated substrates, mature _L. groenlandicum_ is capable of tolerating high water levels. Several studies have shown that other mire shrubs are capable of surviving high water levels. Gimingham (1960) found that _Calluna vulgaris_ could tolerate a constant -2 cm water regime, with its roots being limited to the unsaturated upper 2 cm of peat. Although optimum growth of _Vaccinium macrocarpon_ under cultivation occurs at water levels between -20 cm to -30 cm (Beckwith 1940; Hall 1971; Eck 1976), good growth was also obtained with a -5.5 cm water regime (Hall 1971).

Completely saturated substrates (0 cm water regime) have been found to limit the growth of many mire shrubs. Stems of *Chamaedaphne calyculata* are capable of surviving at just above water level in floating peat mats, but rapidly die when submerged by water (Swan and Gill 1970). Rutter (1955) found that a fluctuating water table enabled plants to grow more successfully in wet substrates. A constant 0 cm water adversely affected *Empetrum nigrum* (Bell and Tallis 1974), *Erica cinera* (Bannister 1974b; Jones 1971), and *Calluna vulgaris* (Bannister 1964b), species which are characteristic of moist to dry portions of mires. *Erica tetralix* (Bannister 1964b) and *Andromeda polifolia* (Karlin, unpublished data), which are both often found in wet sites, survived the waterlogged regime quite well.

Ericaceous plants tend to have shallow root systems. The majority of roots occur in the upper 15 cm of substrate for *L. groenlandicum*. Rosswall et al. (1975) found that > 80% of the roots of mire shrubs (predominantly ericaceous) in northern Sweden occurred in the top 10 cm, with > 99% in the top 20 cm. Most of the active portion (> 90%) of the root systems (in terms of nutrient uptake) of *Calluna vulgaris* and *Erica tetralix* are located in the upper 15 cm of substrate (Boggie et al. 1958).

Plants possessing shallow root systems would be able to evade to some extent the anaerobic portions of wet substrates. The rooting systems of woody mire plants are usually situated above the general water table level (Emerson 1921; Rigg and Harrar 1931). Even though *Erica* *tetralix* is sensitive to poor aeration, its shallow root system allows it to survive in the wet portions of English bogs (Sheikh 1970). As there are extensive areas in the low-peat communities where the surface 3-10 cm of substrate are usually not inundated by water, it would appear that survival of the mature *L. groenlandicum* in such low-peat areas is not directly limited by the water regime present there.

As *L. groenlandicum* is characteristically found in acidic, nutrient poor, organic substrates (Fernald 1907; Wherry 1920; Jeglum 1971), it could be argued that the chemistry of the primary water limits the vegetational spread of the plant. If this hypothesis were true, one would expect to find the most distinct distributional patterns in rich fens (calcareous primary water) and hardly any pattern in poor fens and bogs, where the plant would extend into wetter areas. The same pattern has been observed, however, in both rich fen and poor fen systems (Fig. 6; Vitt and Slack 1975).

Survival of transplants subjected to the primary water regimes at Heatherdown and Nestow, and the formation of adventitious roots in Heatherdown low-peat environments provides further evidence that the vegetative spread of the mature plant is not greatly limited by primary water chemistry.

That *L. groenlandicum* was able to tolerate the calcareous substrates of the Heatherdown low-peats is surprising.

Rhododendron and most ericaceous plants have been found to be unable to tolerate calcareous substrates (Lunt et al. 1956; Bowers 1960; Holmes 1960; Oertli 1963; Lee 1965). It is believed that this is largely due to their inability to take up sufficient iron from substrates having a pH > 6 (Spencer and Shive 1933; Brown 1955; Holmes 1960; Oertli 1963). Ferrous iron is rapidly oxidized to the ferric form around pH 6, and the solubility of ferric iron decreases 1000 fold for each pH unit increase (Oertli 1963). Aeration also plays a role, however, and the reduced conditions found in water saturated substrates tend to offset the influence of high pH values on Fe (Buckman and Brady 1969). A mottled layer (rust-orange colored) occurs about 5 cm down from the surface of the low-peat substrates at Heatherdown, indicating that the reduced form of Fe is present below that depth.

Recent evidence indicates that high concentrations of HCO_3 (a dominant anion in many calcareous substrates) hinders the translocation of iron in *Rhododendron* (Rutland 1971). However, the environmental relationships underlying the exclusion of acid loving plants from calcareous substrates are complex and not entirely understood (Brown 1956; Epstein 1972; Larcher 1975).

The data from the nutrition study indicate that the Fe deficiency symptoms in *L. groenlandicum* are similar to those observed in other plants (Epstein 1972). They would be expected to show up relatively quickly (by the second growing season) if Fe was not readily available in the substrate environment. Deficiency symptoms had not developed in the Heatherdown low-peat transplants after 3 growing seasons. The availability of Fe is thus not a major limiting variable in such environments for the mature plant. It may play a role in seedling survival, as the seedling root environment would be limited to the surface layers of the low-peat substrate, where Fe would primarily be in the oxidized form.

It would appear that the slight amount of Fe contamination in the chemicals used to make the nutrient solutions was of sufficient quantity to allow L. groenlandicum to survive in the low pH regimes. The ability of the plant to do as well as it did with such low concentrations of Fe indicates that L. groenlandicum has an efficient uptake mechanism for that element and that the plant does not require it in great quantities. In the high pH regimes, any iron in the solution would have been precipitated out and unavailable to the plants.

Although no published mineral nutrition studies are available on L. groenlandicum, there have been several on Rhododendron (Stuart 1947; Twigg and Link 1951; Bell 1952; Leiser 1959). Twigg and Link (1951) found that R. kiusianum Makino (Syn. R. obtusum f. japonicum) developed characteristic nutrient deficiency symptoms, which appeared in the following order: N, K, B, Mg, Ca, Fe and P. The requirements of R. kiusianum for P, K, Ca and Mg are relatively low (Twigg and Link 1951), which has also been observed in other ericaceous species (Bailey et al. 1949). The most frequently encountered nutritional disorders of Rhododendron (cultivated) are caused by lack of nitrogen and unavailability of iron (Stuart 1947).

The N, P and K concentrations in healthy L. groenlandicum foliage (Gerloff et al. 1964; Small 1972a, 1972c; Reader 1978) were ≤ those of R. kiusianum exhibiting the respective mild to severe deficiency symptoms (Twigg and Link 1951) while Ca and Mg concentrations were ≥ those of healthy R. kiusianum. This indicates that L. groenlandicum is likely to have lower N, P and K requirements than does R. kiusianum, and that concentrations of these minerals in L. groenlandicum may normally be only slightly greater than the "critical concentration". Through the retention of its leaves for two growing seasons, L. groenlandicum maximizes its use efficiency of N, P, K and other minerals which may not be readily available in raised-peat substrates (Small 1972a; Reader 1978).

Nitrogen is available primarily as NH_4 in acidic conditions, while in less acidic sites a higher percentage of NO_3 may be present (Alexander 1965; Saebo 1970; Griedanus et al. 1972; Moore and Bellamy 1974). Both nitrogen forms have been shown to be utilized by Rhododendron, with NH_4 being the superior form, especially in less acidic substrates (Colgrave and Roberts 1956; Leiser 1959; in Oertli 1963; Oertli 1960; in Oertli 1963). Other ericaceous plants have also been found to be capable of utilizing both nitrogen forms (Kender and Childers 1959; Oertli 1963).

The subject is not clearly settled, however, as a recent study has indicated that V. macrocarpon is not able to utilize NO_3 (Griedanus et al. 1972), in direct contrast to earlier studies (Addoms and Mounce 1931; Kender and Childs 1959).

The major form of nitrogen available to the low-peat transplants was NO_3 (Table 8, page 35). As the plants grew for up to three growing seasons without developing any nitrogen deficiency symptoms, it would appear that either L. groenlandicum is able to utilize both the NH_4 and NO_3 forms of nitrogen, or that the plant is able to obtain sufficient NH_4 for survival in such environments.

V. SEED GERMINATION

Natural Establishment

Methods

A close visual examination of substrate surfaces in the major community types was undertaken to locate *Ledum groenlandicum* seedlings. This was done to determine the frequency of natural seedling establishment by *L. groenlandicum*, and the types of micro-habitats in which establishment occurred. Data on maximum rates of seedling establishment were obtained by sampling sites which were found to have large numbers of seedlings. Density of *L. groenlandicum* seedlings within 0.25 m^2 quadrats was determined and categorized into first, second-third, and $\geq$ fourth year age classes.

A disturbed mire near the Nestow Fen was discovered to have an extremely abundant crop of *L. groenlandicum* seedlings and was also sampled for seedling density. This mire had been affected by fire and road building activities within the last 25 years. It is a raised-peat system with a relatively flat and uniform surface. A solid mantle of *Polytrichum strictum* covers the mire forming a 5-8 cm thick layer on top of the original *Sphagnum* peat surface. Vascular plant cover is low (24%).

The small annual growth of *P. strictum*, coupled with its open canopy (when compared to that of *Sphagnum*) seemed to favor successful establishment of *L. groenlandicum*.

The tomentum of the Polytrichum stems and fungal mycelium form a compact layer about 2-3 cm beneath the moss canopy, and was the primary substrate for L. groenlandicum germination. In some cases, seed lodged and germinated on a sub-canopy leaf of Polytrichum. It would remain balanced there until the roots grew into the fungal-peat layer ± 1 cm below.

Many raised-peat "islands" isolated in the wet meadows from the major raised-peat areas occurred at Heatherdown and Nestow. If L. groenlandicum occurred on such an island, it must have been directly established by seed. In June, 1977, 120 of these islands were sampled at Heatherdown for the presence of L. groenlandicum, major substrate type, and maximum island height above water.

Results

Only a small number (< 12) of L. groenlandicum seedlings were found at Heatherdown during the 1976 season. This was in part due to my lack of knowledge about the minute size of the seedlings (Fig.13, p.103) and the kinds of micro-habitats where they occurred. In a greenhouse environment, the average ($\bar{X} \pm$ SD) height of 1 month old seedlings was 2 ± 0.5 mm, and by 4 months they had reached a mean height of 4 ± 0.6 mm (25^{c} day/16^{o} night).

After becoming acquainted with the characteristics of L. groenlandicum seedlings via preliminary laboratory experiments (in spring, 1977) and observing those present at the disturbed mire, I found a substantial number at Heatherdown. Due to the patchy nature of suitable germination sites, seedlings were only locally present. Generally they were absent in the mire system as a whole.

Germination usually occurred on a moss or peat substrate. In some cases, the moss layer was < 1 cm thick and directly overlaid marl. Most successful establishment took place in sites where moss growth rates were not high, such as on the tops of senescent raised-peat hummocks, at the base of fallen trees, and in moist (not wet) sites lacking a continuous moss cover (raised marl) which occurred infrequently between the low-peat and the raised-peat.

In the raised [illegible] there were mean densities ($\bar{X}$ ± SD) of 8 ± 7, 8 ± 2 and 19 ± 5 seedlings per 0.25 m^2 in first, second-third and ≥ fourth year age classes respectively. These values are of sites selected because of high density of seedlings and are not representative of seedling densities in the raised-marl site as a whole. .

Seedlings at the disturbed mire were quite evenly distributed and the following values are representative of that system: 14 ± 7, 33 ± 19, and 69 ± 24 seedlings per 0.25 m^2 in the first, second-third and ≥ fourth year age classes respectively.

As the sampling took place in late August, the first year seedling population data do not represent total germination for that year. Many current seedlings may have died previous to sampling and may, therefore, not have been observed at the time of sampling.

The results of the island study are presented in Tables 20 to 22 and in Fig. 10. *Sphagnum*, *Tomenthypnum* and peat proved to be the most favorable substrates for successful establishment (in that order). Practically no establishment occurred on *Campylium* and *Drepanocladus* mats.

Island height above water level is a second variable which might influence successful establishment (Tables 21 and 22). There is a significant difference in height between the two above substrate groupings. A comparison between island height and the corresponding rooting height of the *L. groenlandicum* plants nearest to the water level on that island showed a non-significant correlation (n = 35, r = .189). The mean rooting height of the lowest rooted *L. groenlandicum* was 17.6 ± 7.3 cm, which is lower than the mean maximum heights for islands dominated by *Campylium* and *Drepanocladus*. No significant difference was found among the mean heights of those *Campylium*, *Tomenthypnum* and *Sphagnum* dominated islands which supported *L. groenlandicum*, with the mean heights of the *Campylium* and *Tomenthypnum* islands being larger than the respective total means for each.

Discussion

The infrequent and patchy occurrence of seedlings indicates the importance of longevity and vegetative reproduction in population maintenance. Both are the primary

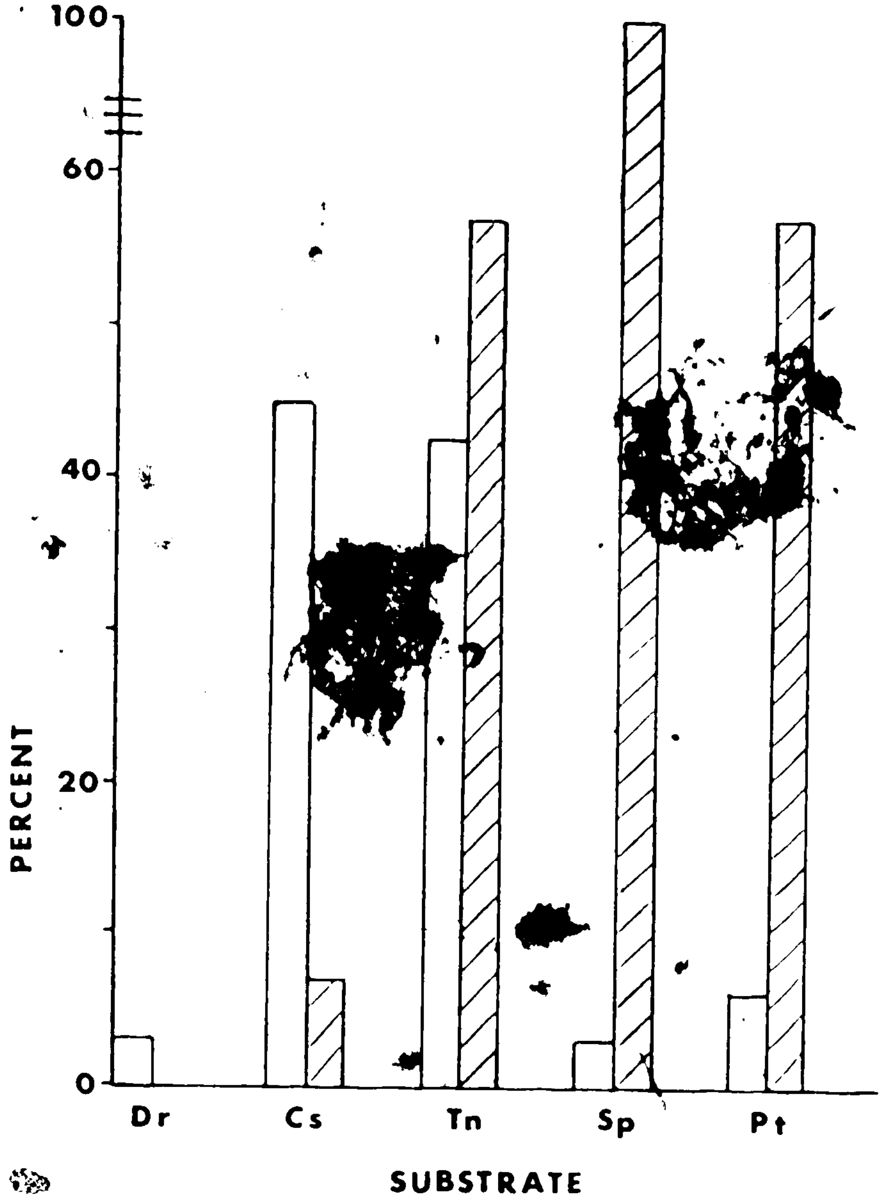

Figure 10. Substrate types (percent of total) sampled in island study and percent of each type with *Ledum groenlandicum* present. Columns with diagonal slashes represent the latter data.

Table 20. Data on raised-peat islands at Heatherdown. Number of islands sampled categorized by substrate and maximum height of islands above the water level (mean ± SD, cm).

Substrate	(n)	No. with Ledum	Mean Max. height (total)	Mean Max. height (with Ledum)
Drepanocladus	4	0	20 ± 3	---
Campylium	54	4	24 ± 7	30 ± 9
Tomenthypnum	51	29	35 ± 11	38 ± 13
Sphagnum	4	4	42 ± 13	42 ± 13
Peat	7	5	58 ± 12	61 ± 11

means of population maintenance for most ericaceous plants characteristic of mires. Seedling establishment is not common and usually is limited to disturbed sites. This is not due to low seed viability, as relatively high germination percentages under laboratory conditions have been found (Ritchie 1955; Bliss 1958; Hansen 1964; Bannister 1966; Swan and Gill 1970; Bell and Tallis 1973).

In contrast to the above trend, *Calluna vulgaris* reproduces primarily by seed (Gimingham 1960; Barclay-Esterup and Gimingham 1969). Bannister (1974a) found that successful germination and establishment of *C. vulgaris*, *Erica cinera* and *E. tetralix* was most favored in raised-peat substrates in comparison to humus and mineral soil. However, the raised-peat environment was not as favorable for promoting the growth of older seedlings of *C. vulgaris*

Table 21. Mean heights of all islands sampled.

F = 24.86 ($p < .001$)

Substrate	Dr*	Cs	Tn	Sp	Pt
Height (cm)	20	24	35	42	58
Non-significant ranges ($\alpha = .05$)	———	———	———	———	

* Dr = *D. revolvens*, Cs = *C. stellatum*, Tu = *T. nitens*, Sp = *Sphagnum*, Pt = peat.

and *E. tetralix* as that of adjacent better drained wet heath substrates (Loach 1968).

Seed produced in, or subjected to, harsh environments may have reduced viability. Seed collected from arctic populations of *A. polifolia*, *Empetrum hermaphroditum*, *Vaccinium uliginosum* L., and *V. vitis-idaea* failed to germinate, although both *L. palustre* and *Cassiope tetragona* seed had > 50% germination (Bliss 1958). Latimer and Smith (1938) found that allowing seeds of *Vaccinium angustifolium* to dry caused them to enter a prolonged secondary rest period that lasted for two years.

Dispersal of seed from the raised-peat areas into adjacent low-peat sites should readily occur, as the seed is small and easily dispersed by wind (Ridley 1930). The presence of *L. groenlandicum* on isolated raised-peat islands and the regular distribution of seedlings throughout the disturbed mire confirms that such dispersal does occur.

Table 22. Mean maximum heights of islands with *L. groenlandicum*.

F = 6.76 (p = .001)

Substrate	Cs*	Tn	Sp	Pt
Height (cm)	30	38	42	61
Non-significant ranges ($\alpha = .05$)	———	———	———	

* Cs = *C. stellatum*, Tn = *T. nitens*, Sp = *Sphagnum*, Pt = peat.

As a large number of seeds are produced per flower (> 50 seeds) and extensive flowering occurs each year, there should be substantial annual additions to the seed banks of both the low-peat and raised-peat substrates. The apparent annual seedling recruitment experienced by seedling populations in favorable sites for germination and establishment indicates that a significant amount of viable seed is also dispersed annually.

Although successful propagation of *L. groenlandicum* from seed has been reported under horticultural conditions (Bailey 1910; Gorer 1976), it has not been previously observed in the field. The extensive growth of *L. groenlandicum* and *L. palustre* in disturbed sites has been largely attributed to vegetative reproduction (Lewis et al. 1928; Lutz 1956; Moss 1948; Viereck 1973; Flinn and Wein 1977). Soil seed bank studies have not yielded any germination of *L. groenlandicum* seed (or of any other ericaceous species present), even though the plant was a prominent component of the vegetation (Johnson 1975; Moore and Wein 1977). A wide array of substrate types was tested, ranging from Sphagnum peats to sandy soils. No germination at all was observed in the Sphagnum peats. This is surprising, as it is believed that cold, acid and poorly aerated substrates are favorable for seed preservation, although they inhibit germination under normal field conditions (Turner 1933; Champness and Morris 1948). In a greenhouse environment, live Sphagnum is an excellant medium for the germination and establishment of many plants, especially the Ericaceae (including Menziesia and Rhododendron) (Close 1937; Childs 1946; Bowers 1960).

It may be that the seed bank studies mentioned above were biased by short germination periods (56 days and 35 days respectively). Soil seed bank studies carried out for longer periods have not only yielded germination in peat substrates, but also germination of several ericaceous species (Milton 1939; Champness and Morris 1948).

Seed Viability

Methods

Seed of Ledum groenlandicum was collected in late August - early September in 1976 and 1977 from Heatherdown and Nestow. All seed was stored dry. The 1976 seed was stored at -4° until October 1977, after which it was kept at 4°. The bulk of the 1977 seed was stored at 4°, with a small subsample being kept at 23°.

A sample of <u>Ledum palustre</u> seed collected in the Mackenzie Delta of the N.W.T. in August, 1977 was provided by John Campbell of the Botany Department, University of Alberta. This was stored at 4°.

The set up for germination was ~~as~~ follows: fifty seeds were placed on a wet folded Kimwipe in a 5 cm diameter Petri dish. This was then placed inside a 9 cm diameter Petri dish so that moisture loss would be minimized. Distilled water was added as required to keep the seeds moist. This same method was employed in all of the laboratory germination experiments.

In order to determine the relat[illegible] of viability to seed age, four treatments were established: <u>L. groenlandicum</u> seed 1 month old (6 replicates); seed eight months old (7 replicates); and seed 13 months (3 replicates) old; and <u>L. palustre</u> seed 1 month old (3 replicates). The 9 month old treatment was run at a different time than were the other 3. Germination took place in a growth chamber (Environmental Growth Chamber Co., Model M-15) with a 25° day/8° night temperature regime and 14 h of light.

In conjunction with the germination of 8 month old seed (stored at 4°) in the above experiment, 2 replicates of 8 month old seed stored at 23° were also established. This was done in order to determine whether storage temperature had any affect on seed viability.

Results

High levels of germination occurred in both species without cold stratification (Table 23 and Fig. 11). Most germination had occurred by 25 to 30 days. Germination of L. palustre seed required less time and was more synchronized than that of L. groenlandicum.

Seed viability decreased rapidly with age. Mean germination for 13 month old seed was only 1/3 that of 1 month old seed, and it required a longer period to germinate. Germination of seed stored at 4° for 8 months was not significantly different from that of seed stored at 23° for the same time period ($F = .16$, $p = .703$).

Discussion

These data indicate that the seed of both species is quite viable. While I am not aware of any previous studies on germination counts for L. groenlandicum, Bliss (1958) found that 7 month old seed of L. palustre had 51% germination at 22°. Nichols (1934) and Bliss (1958) also found that most germination occurred within 25 to 30 days under laboratory conditions for L. groenlandicum and L. palustre (respectively). That pretreatment is not necessary for germination to occur has been previously noted for L. groenlandicum (Nichols 1934). Other related genera (in the same subfamily) which are known to readily germinate without pretreatment include Epigaea (Blum and Krochmal 1974), Kalmia (Olson and Barnes 1974), and Rhododendron (Bowers

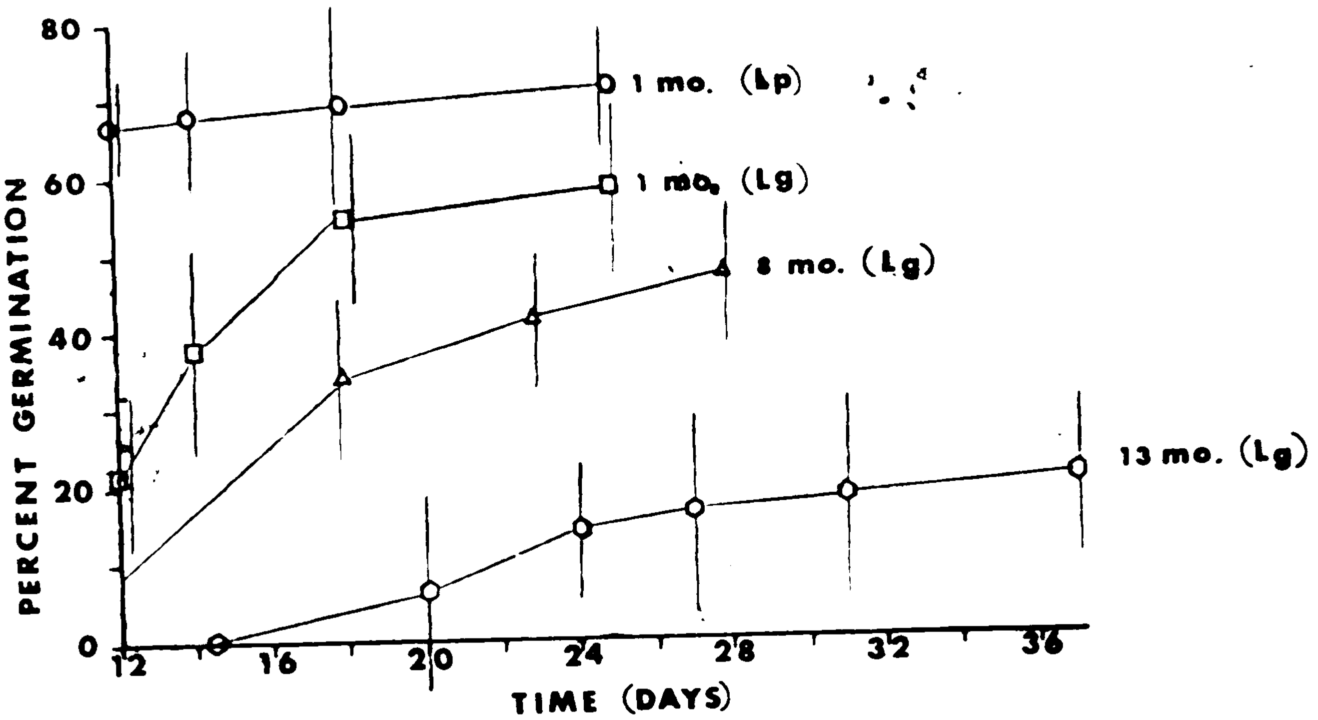

Figure 11. Mean percent germination in relation to seed age. (Lp = *Ledum palustre*; Lg = *Ledum groenlandicum*.)

Table 23. Mean germination in relation to seed age.

F = 19.70 (p < .001)

	Germination percents (Mean)			
Seed age (months)	13	8	1	1*
Germination	20	46	58	71
Non-significant ranges (α =.05)			—	—

* *Ledum palustre*

1960; Olson 1974).

Although mean germination of 8 month old seed was significantly lower than that of 1 month old seed at $\alpha = .05$, it was not significantly different at $\alpha = .01$. This fact, coupled with the large drop in germination between 8 and 13 month old seed, suggests that the germination for a given cohort of seeds largely occurs within one year of their production. Long term survival of the seed in the soil is not likely. This may be due largely to a lack of sufficient food reserves because of small seed size (2.5 mm by 0.4 mm). Germination of *Rhododendron* seed follows a very similar pattern in respect to age of seed and viability (Bowers 1960).

Field Germination Experiments

Methods

Field germination rates were studied during the 1977 and 1978 field seasons. Seed was obtained from Heatherdown in the fall of 1976 and 1977, and at Nestow in the fall, 1977. It was stored in paper bags placed inside plastic containers at -4°. In June, 1977, three circular plots 12 cm in diameter were placed in each of four substrate types at Heatherdown (*T. nitens*, *S. fuscum*, *C. stellatum-D. revolvens* and marl. One hundred seeds were sown in each plot. Observations on germination were made throughout the rest of the study period.

On October 10, 1977, a second sowing at Heatherdown was carried out at different sites with 100 seeds in circular plots 5 cm in diameter. Three plots were placed in each of *Campylium-Drepanocladus* and *Tomenthypnum* substrates, while two plots were placed in each of living *Sphagnum* and *Sphagnum* peat. All of the plots were covered with 5 cm diameter plastic Petri dish tops, which had several small holes cut in their surfaces. This was done to prevent the seeds from being blown or washed away during the fall/early spring periods. The Petri dishes were removed on April 25, 1978 so that any greenhouse affects would be limited to early spring. A third Heatherdown sowing similar in set up to the second one (without the Petri dishes) was established in late April, 1978. Five plots were placed on peat (*Drepanocladus* and *Campylium*) in the meadow, and four plots on *Sphagnum fuscum* hummock tops (one of which was on *Sphagnum* peat).

Germination plots were also established at Nestow in late April, 1978. These were the same in design as the third Heatherdown sowing. Three plots were established in both *Picea*-*Ledum* and *Eriophorum*-*Sphagnum* raised-peat community types on *Sphagnum* (*S. magellanicum*, *S. angustifolium*). Seven plots were established on *Aulacomnium palustre* hummocks in the wet meadow communities, with another 3 on *Sphagnum* peat which had been exposed at the disturbed mire in fall, 1977. Additional *Sphagnum* peat exposures (9 plots, each 1 dm^2) were watched for natural establishment rates of *L. groenlandicum*.

Results

The field germination data collected underestimates total germination. As only seedlings were observed, seeds which germinated but did not become established were overlooked. In some substrates it was difficult to locate seedlings (*T. nitens*, *Sphagnum* spp.) and a substantial number of seedlings may have been missed. Observations on germination were infrequent, and some seedlings may have appeared and died between countings. As seedlings were left in the germination plots, some that died may have been replaced by new seedlings which would, therefore, not have been counted.

Thus, the germination data might best be considered as percent successful initial establishment, rather than actual percent germination.

Initial establishment occurred in all substrates tested except the *S. angustifolium* and *S. magellanicum* raised-peats at Nestow (Table 24). Maximum establishment occurred in C. stellatum - D. revolvens peat in low-peat communities at Heatherdown. The range of values for establishment varied widely within each substrate type. Maximum values of establishment were of similar magnitude in all substrates except Sphagnum spp., which had very low values (Table 24).

Natural seedling establishment on exposed peat at the Nestow disturbed mire averaged 22 seedlings per 1 m^2.

Discussion

Germination and initial establishment is capable of occurring in low-peat substrates, perhaps at higher rates than in Sphagnum spp. and Feather moss dominated raised-peat substrates. The initial rate of seedling growth and development appeared to be the same in all substrates tested.

As the seedlings are quite small and delicate, it might be expected that they would be easily damaged by heavy rain storms if in an exposed location, or to dry periods as their rooting systems are small and shallow. Surprisingly, a large majority of the seedlings survived one of the most severe rainstorms in 25 years, including several seedlings in a relatively unsheltered area of marl substrate. As the substrates in the low-peat areas were moist even at the driest times throughout the three years of this study, it would be expected that some seedling

Table 24. Mean field germination in different substrate types.

F = 3.54 (p = .009)

	Germination percents (Mean)						
Substrate	Sf	Ml	Sfp	Tn	Cs	Ap	Csp**
Germination*	.1	1.3	2.8	4.2	4.9	6.4	10.0
Non-significant ranges (α =.05)			—	—	—	—	—
		—	—	—	—	—	
	—	—	—				
Max. % germination	1	13	12	10	13	22	16
n	6	5	6	5	5	5	5

* Mean % germination has been subjected to Arc-Sin transformation. This alters the final value, and is often different from a straight arithmetic mean.

** Sfp = Sf peat; Csp = Cs peat (see Table 26 for others).

survival would occur.

It appears that the germination and initial establishment phases of L. groenlandicum do not primarily limit its spread into low-peat locations. Since older age classes ($\geq$ 2-3 years) are not found in such areas, some environmental parameter limits the successful long term establishment of the seedling at some time between initial establishment and the end of the third year, at which time the seedling is usually large enough to be easily noticed.

Influence of Substrate

Methods

In fall 1977, three samples each of 8 different substrate types from Heatherdown (Campylium stellatum/

Drepanocladus revolvens, *Tomenthypnum nitens*, *Sphagnum fuscum*, Feather mosses and marl) and Nestow (*Aulacomnium palustre*, *Polytrichum strictum*, *Sphagnum magellanicum*) were collected. These were placed in 7.5 cm diameter plastic pots. One hundred seeds were sown in each pot; the substrates were watered immediately before sowing. The experiment was run in a 24° day/17° night temperature regime in controlled environment greenhouse. The planted seeds were cooled to -4° for 4 days and allowed to thaw in a 16° day/8° night regime for 1 day before being placed in the final temperature regime. Plastic Petri dish covers were placed on the pots during the first 21 days of the experiment to enhance germination. The substrates were watered with distilled water at the base of the pots. Germination was observed over an 80 day period.

In order to separate the influence of substrate physical parameters (i.e., water content, canopy structure) and growth rates on germination from possible allelochemic inhibitions, the following study was performed. Samples of *C. stellatum*, *S. fuscum* and *T. nitens* were collected at Heatherdown in April, 1978. An amount of distilled water equivalent to twice the fresh weight of *S. fuscum* and *T. nitens*, and equal to that of *C. stellatum* (less added because of high initial moisture content) was added to the substrates. The samples were shaken for 5 days on a reciprocating shaker (at 23°). The leachate was separated from the moss utilizing Buchner funnels and suction.

Six leachate treatments were established, consisting of 5 replicates with 100 seeds each. The treatments were: C. stellatum (pH 7.3); C. stellatum-adjusted pH (pH 6.0); T. nitens (pH 4.9); T. nitens-adjusted pH (pH 5.5); S. fuscum (pH 4.7); distilled water. Ten ml of the respective leachate (or distilled water) were used to provide the moisture for germination. Distilled water was used sparingly during the latter part of the experiment to keep the seeds moist. The experiment lasted for 35 days, with a constant 23° temperature regime and natural light.

Results

Germination occurred in all substrates, with lower percentages than those obtained in experiments which utilized the Petri dish-Kimwipe method (Table 25). Significant differences in germination only occurred between the P. strictum and T. nitens substrates. Germination in the first experiment was observed over an 80 day period as the seed used was 13 months old (and had been observed to take longer to germinate) and because the environment was not as conducive to rapid germination as that of the Petri dish method. The most favorable substrates were T. nitens and S. fuscum. The low value for P. strictum is surprising, as it was found to be one of the more favorable substrates for successful natural germination and establishment in the field.

Inhibition of germination only occurred with the

Table 25. Mean germination response to substrate type.

F = 1.35 (p = .29)

	Germina[illegible]ean)							
Substrate	Ps*	Ap	Fm	Cs	Ml	Sm	Sf	Tn
Germination	5	7	8	8	10	10	14	16
Non-significant ranges (α=.05)								

* See Table 26 for explanation of abbreviations.

unadjusted _C. stellatum_ leachate (Table 26). Although they were not significantly different, germination means in the remaining leachate treatments were all greater than that of the control.

Table 26. Mean germination response to leachates from three different substrates.

F = 5.64 (p = .002)

	Germination percents (Mean)					
Leachate	Cs*	Cl	TnA	CsA	Sf	Tn
Germination	18	38	42	47	48	51
Non-significant ranges (α =.05)						

* Ap = _A. palustre_
Cl = Control
Cs - _C. stellatum_
CsA = Cs-adjusted pH
Fm = Feather moss
Ml = Marl

Ps = _P. strictum_
Sf = _S. fuscum_
Sm = _S. magellanicum_
Tn = _T. nitens_
TnA = Tn - adjusted pH

Discussion

The physical and chemical parameters of major substrate types present at Heatherdown and Nestow do not totally limit the germination of L. groenlandicum. Although a high pH reduces germination (page 91), such substrates had germination percentages similar to more acidic ones.

Allelochemic interactions do not appear to play a major role in germination inhibition of L. [illegible]landicum. Leachates of S. fuscum and T. nitens possibily provide a more favorable germinating medium than does the distilled water control, perhaps by supplying more minerals to the seed. The data do not rule out the possibility that subsequent establishment is influenced by some allelochemic interaction.

The contrasting results of the adjusted and unadjusted C. stellatum leachates indicate that a high pH is probably the major parameter reducing germination in the latter treatment. This conclusion is further supported by the similarity of the germination percents of the unadjusted C. stellatum leachate (pH 7.3) and the pH 7.5 regime of the germination-pH experiment (page 91).

Influence of pH

As a sharp gradient (pH 4.0-7.6) in substrate and water pH existed at Heatherdown between communities with and without L. groenlandicum, an experiment was performed to determine the influence of pH on germination.

Methods

Four pH regimes (3.5, 5.5, 7.5, 8.5) were established using buffer solutions (see Appendix III). Kimwipes were soaked in the respective buffer solutions for 24 h before the "planting". Five replicates were prepared for each treatment. The buffer solutions were used to moisten the seeds when necessary. The seeds were germinated under a 25° day/8° night temperature regime, with 14 h of light. Germination and survival were noted for 28 days. Preliminary germination studies had indicated that most germination had occurred by 25-30 days.

Results

There was a significant influence of pH on germination and seedling survival (Tables 27 and 28, Fig. 12). The most favorable regimes were acidic, with pH 5.5 having the highest germination and survivorship. None of the seed which germinated in the 8.5 regime survived to day 28.

Discussion

Germination of Calluna vulgaris showed a similar response to pH, with a marked reduction in germination at values greater than pH 6.6 (Poel 1949; Brien 1950: in Gimingham 1960).

Although substrate pH may have considerable influence on germination and seedling survival in rich fens, it is not totally responsibile for the absence of L. groenlandicum

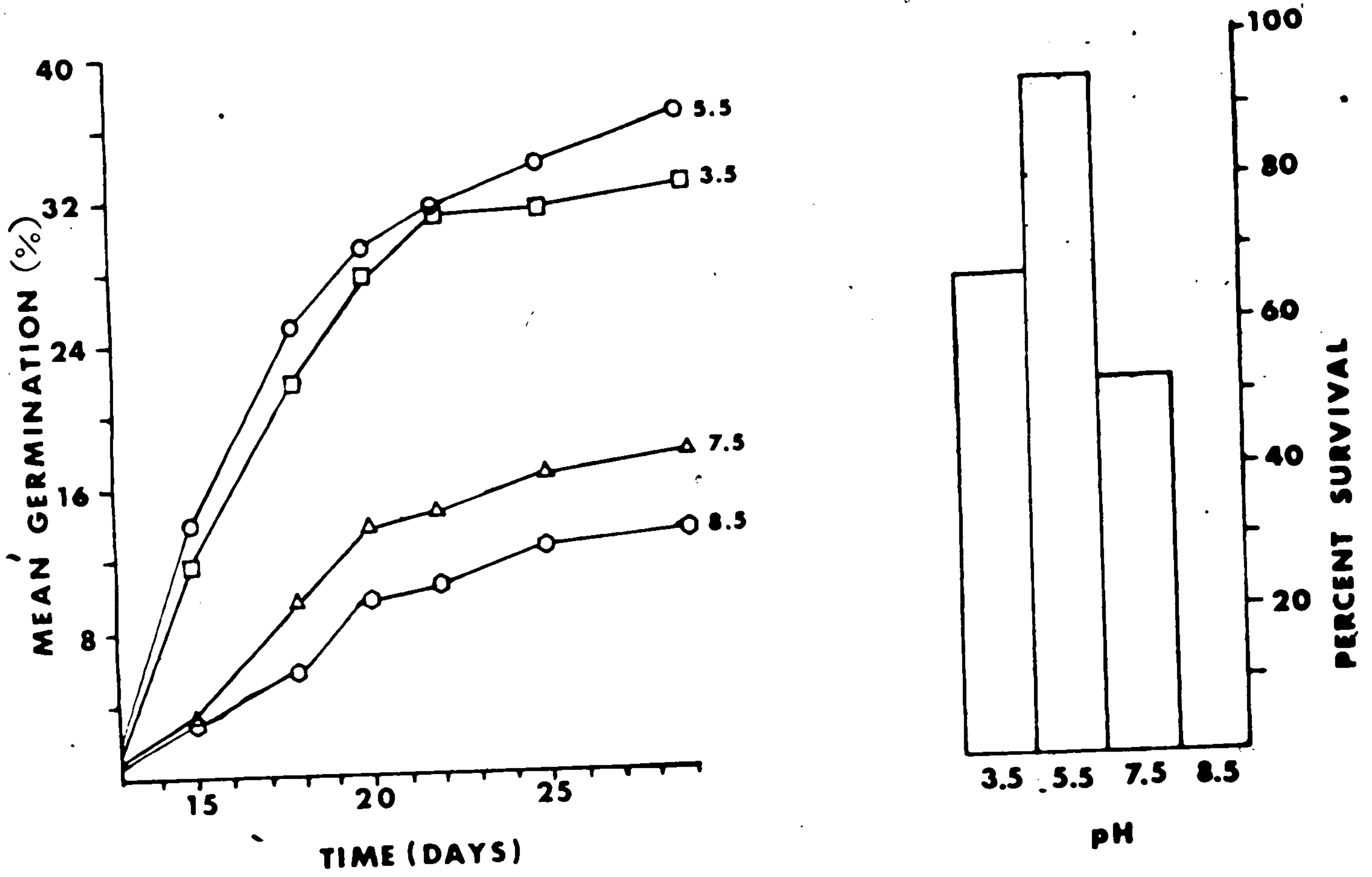

Figure 12. Mean percent germination and survival in relation to pH.

Table 27. Mean germination response to pH.

F = 14.71 ($p < .001$)

	Germination percents (Mean)			
pH	8.5	7.5	3.5	5.5
Germination	13	18	32	36
Non-significant ranges (α =.05)				

in low-peat communities. The small difference in substrate pH between raised-peat and low-peat communities in both fen and poor fen systems, plus the presence of seedlings in substrates with pH values of 7.5 at Heatherdown, indicate that other environmental parameters are important.

Table 28. Mean seedling survival in relation to pH.

F = 10.63 ($p = .002$)

	Survival percents (Mean)			
pH	8.5*	7.5	3.5	5.5
Survival	0	48	69	97
Non-significant ranges (α =.05)				

* not included in the anlysis of variance

Influence of Temperature

Methods

The same germination method used in the pH experiment was used, with distilled water employed to moisten the seeds and Kimwipes. Five constant temperature regimes (5, 10, 15, 17, 19°) and 5 diurnal temperature regimes (6/-1, 16/8, 25/8, 24/17, 40°/20°) were established. The constant temperature regimes were conducted in growth chambers (12 h light regimes) for 27 days while the diurnal regimes were placed in controlled environment greenhouses for 25 days. At the end of the experiment, seed from the 6° day/-1° night regime was placed in a 25° day/8° night regime for 22 days.

Results

Fairly high temperatures were required for germination in the temperature regimes (Table 29). Germination at and below 15° was low, with none occurring at 5°. There was a sharp increase in percentage germination between 15° to 17° constant temperature. The 5° and 10° treatments were allowed to continue for an additional 17 days. Mean germination in the 10° regime increased from 5% to 7%, and no germination occurred in the 5° regime.

The diurnal temperature regime showed a slightly different pattern (Table 30). No germination occurred in the 2 cooler regimes even though one had temperatures at which germination in the constant temperature experiment

Table 29. Mean germination response to constant temperature regimes.

$F = 142.95$ ($p < .001$)

	Germination percents (Mean)				
Temperature (°C)	5*	10	15	17	19
Germination	0	5	8	48	45
Non-significant ranges (α =.05)				———	———

* not included in the analysis of variance

had occurred. Maximum germination took place in the 25° day/8° night regime. Mean germination at 40° day/20° night was significantly less than it was in the 25°/8° regime at $\alpha = .05$, although not at $\alpha = .01$. Germination may have been reduced in the 24° day/17° night and 40° day/ 20° night regimes because of substantial contamination by fungi.

Table 30. Mean germination response to diurnal temperature regimes.

$F = 10.28$ ($p = .002$)

	Germination percents (Mean)				
Temperature (°C)	6/-1*	16/8*	24/17	40/20	25/8
Germination	0	0	25	40	58
Non-significant ranges (α =.05)			———	———	

* not included in the analysis of variance

Substantial germination (37%) was obtained from the cold stratified (6°/-1°) seed after 22 days in a 25° day/8° night regime. Mean germination, however, was significantly less than that of non-stratified seed (Table 31).

Discussion

Temperature has a major influence on germination of *L. groenlandicum*. Both daily maximum and minimum temperatures are important. Minimum daily temperatures of $\approx 8^\circ$ require high daily maxima in order for germination to occur. Temperatures $< 8^\circ$ would further limit germination. Exposure to daily minimum temperatures $\leq 4^\circ$ prevent germination of *Rhododendron* (Powers 1960).

Even though the seeds are mature when shed and do not require cold stratification, it is unlikely that much germination occurs in the fall. Substrate surface temperatures are too low to allow germination (Table 15, page 47) and the relatively long period required for germination would tend to buffer against exposure to short warm periods. Germination would not occur in the spring until daily maximum and minimum substrate temperatures were greater than 16° and 5° respectively.

The results of the cold stratification experiment indicate that the seed is capable of surviving the winter environment. An earlier study found that not only could *L. groenlandicum* seed survive winter temperature regimes, but that germination was enhanced by it (Nichols 1934). This is in contrast to the present data and, as no

Table 31. Mean germination response to cold stratification.

F = 6.93 (p = .008)

	Germination percents (Mean)		
Treatment	CS-22*	NS-18	NS-25
Germination	37	$\underline{55}$	$\underline{58}$
Non-significant ranges (α =.05)			

* CS-22 = cold stratified, germination at 22 days;
NS-18 = not stratified, germination at 18 days;
NS-25 = not stratified, germination at 25 days.

replicates were run in the previous study, it is likely that the small sample size biased the results.

The absence of L. groenlandicum from low-peat sites can not be explained on the basis of germination inhibition due to substrate temperature. The low-peat substrates generally had more favorable temperature regimes for germination than did the raised-peat substrates. Daily temperature fluctuation was not as extreme and minimum temperatures were higher than were those of unshaded raised-peats. Densely shaded raised-peat substrates would probably have a comparable temperature regime to that of the low-peat (Busby 1976).

Influence of Water Level

Methods

Two constant water level regimes (0 cm and -5 cm from the substrate surface) were established in the

25° day/16° night greenhouse. Three replicates of 100 seeds (10 months old) each were placed in each regime. The seeds were planted on a peat-sand mixture in 7.5 cm diameter plastic pots. Germination was observed over an 84 day period as little had occurred within 30 days in either regime. As an index of growth, the number of leaves produced per plant in each regime was determined at the end of the experiment.

Results

Mean germination and growth were not significantly different in the 0 cm and -5 cm regimes (Table 32). The low germination may have been partly due to the nature of the substrate (Childs 1946). Germination was first observed in the -5 cm regime on the 18th day, while it was not noted until the 28th day in the 0 cm regime. Seedlings were still alive and healthy 225 days after the date of planting.

Table 32. Mean, standard deviation, and t-test of data on the relationship of germination to water level. ($\alpha = .05$)

	Water Regime				
	0 cm	-5cm	df	T	Prob.
Percent germination	4.7±1.2	6.7±2.1	4	1.455	n.s.
No. leaves produced	2.7±2.5	2.0±1.0	4	.426	n.s.

Discussion

Water saturated substrates did not prevent germination and seedling establishment of *L. groenlandicum*. Percent germination was low in both regimes, and it was not possible to conclude that water saturated substrates significantly limit germination and seedling establishment. The seedling root systems in the 0 cm regime were all on the surface, however, and the seedlings would be quite vulnerable during dry periods. The surface rooting system would also not provide much support to the seedling if water levels temporarily became higher than the substrate surface.

Influence of Light

Methods

Two experiments were set up to study the effect of light on germination. For the no light regime, the outer Petri dishes were wrapped in aluminum foil and placed under a box in a growth chamber with a 25° day/8° night temperature regime. Three replicates (50 seeds each) were placed in the dark regime (35 days) while 3 controls (exposed to light) were placed on top of the box (25 days). Two replicates of *L. palustre* were also placed in the dark regime and one in the light.

In order to determine whether germination would be inhibited by the far-red light dominated environment of shaded habitats, an experiment was set up utilizing red rich (red: far-red = 3.31) and far-red rich (red:far-red = .23) light regimes (temperature = 20° day/15° night; PhAR = $100 \mu E\ m^{-2}\ s^{-1}$) established in 2 growth chambers by Dr. J. Hoddinott of the Botany Department, University of Alberta. Three replicates were placed in each regime, and germination observed for 33 days. Two replicates of L. palustre were also put in each regime.

Results

Germination did not occur in the dark regime for either species. Mean germination in the light was 37% for L. groenlandicum and 64% for L. palustre. Germination occurred in both red and far-red light regimes (Table 33). Although germination of L. groenlandicum was significantly reduced in the far-red regime, that of L. palustre was not significantly different from germination in the red light regime.

Table 33. Germination response to red and far-red light regimes.

F = 10.78 (p = .008)

	Germination percents (Mean)			
Treatment	Lg-FR*	Lg-R	Lp-FR	Lp-R
Germination	24	45	50	46
Non-significant ranges (α =.05)		—	—	—

* Lg-FR: L. groenlandicum-far red
Lg-R : L. groenlandicum-red
Lp-FR: L. palustre-far red
Lp-R : L. palustre-red

Discussion

Previous studies have demonstrated that both subspecies of L. palustre require light for germination (Hegi 1909; Bliss 1958). This is also known to be true of Kalmia (Olson and Barnes 1974) and Rhododendron (Olson 1974). The data from the second experiment suggest that exposure to red light enhances germination of L. groenlandicum, but does not affect the germination of L. palustre. Further studies are necessary to elucidate just what the specific light requirements are.

It does appear that L. groenlandicum would have lower germination in shaded environments. The seed would have to be fairly near the substrate surface in order to receive enough light of the necessary wavelengths to be able to germinate. This is of adaptive significance, as its seedlings are delicate and slow growing. They would not be capable of penetrating through much overlying substrate to reach the surface if they were buried.

VI. SEEDLING STUDIES

Three experiments testing the ability of Ledum groenlandicum seedlings to tolerate high water levels and the influence of substrate in relation to this tolerance were established. They were conducted in a Trop-Arctic greenhouse with a 24° day/16° night temperature regime.

Influence of High Water Level

Methods

Seedlings 1 month old were planted in a sand-peat mixture in 5 small plastic pots. Three days later, 3 of the pots (10 seedlings in each) were placed in a 0 cm constant water regime (in relation to the substrate surface) and 2 (9 and 10 seedlings) in a -5 cm regime. Seedling survival and leaf production were observed for 82 days.

Results

Seedling survival was high in both regimes (0 cm = 89%; -5 cm = 74%), with no significant difference in percent survival (F = .61, p = .49). Leaf production was significantly lower in the 0 cm regime, although seedlings in both regimes grew appreciably (Table 34). The seedlings appeared to be healthy after 225 days in the 0 cm water regime. Although additional seedlings had died (percent survival = 67%), a substantial number of new leaves had been produced (total no. leaves = 72) by the surviving plants.

Table 34. Chi-square test on the total number of leaves produced in relation to water level.

	0 cm	-5 cm
Number leaves observed	23	27
Number leaves expected	32	18

Chi-square = 5.06 (prob < .03)

Influence of Substrate

Methods

Three pots of seedlings from the terminated germination-substrate experiment (page 85) were placed in a constant 0 cm water regime. The substrates used were marl, *T. nitens* and *S. fuscum*. The number and location of seedlings present was noted for each pot at the start of the experiment. A fourth pot with a *C. stellatum* substrate was also established, with 10 seedlings being transplanted into the moss. They were at the same stage of development as those in the 3 other treatments. The plants were subjected to the water regime for 65 days. Seedling survival was observed during the experiment and 80 days after being removed from the water regime. The *C. stellatum* pot remained in the water regime for 84 days and was not observed at the later date.

Results

Seedling survival was high in all 4 treatments (Table 35). Mortality in the moss substrates appeared to be

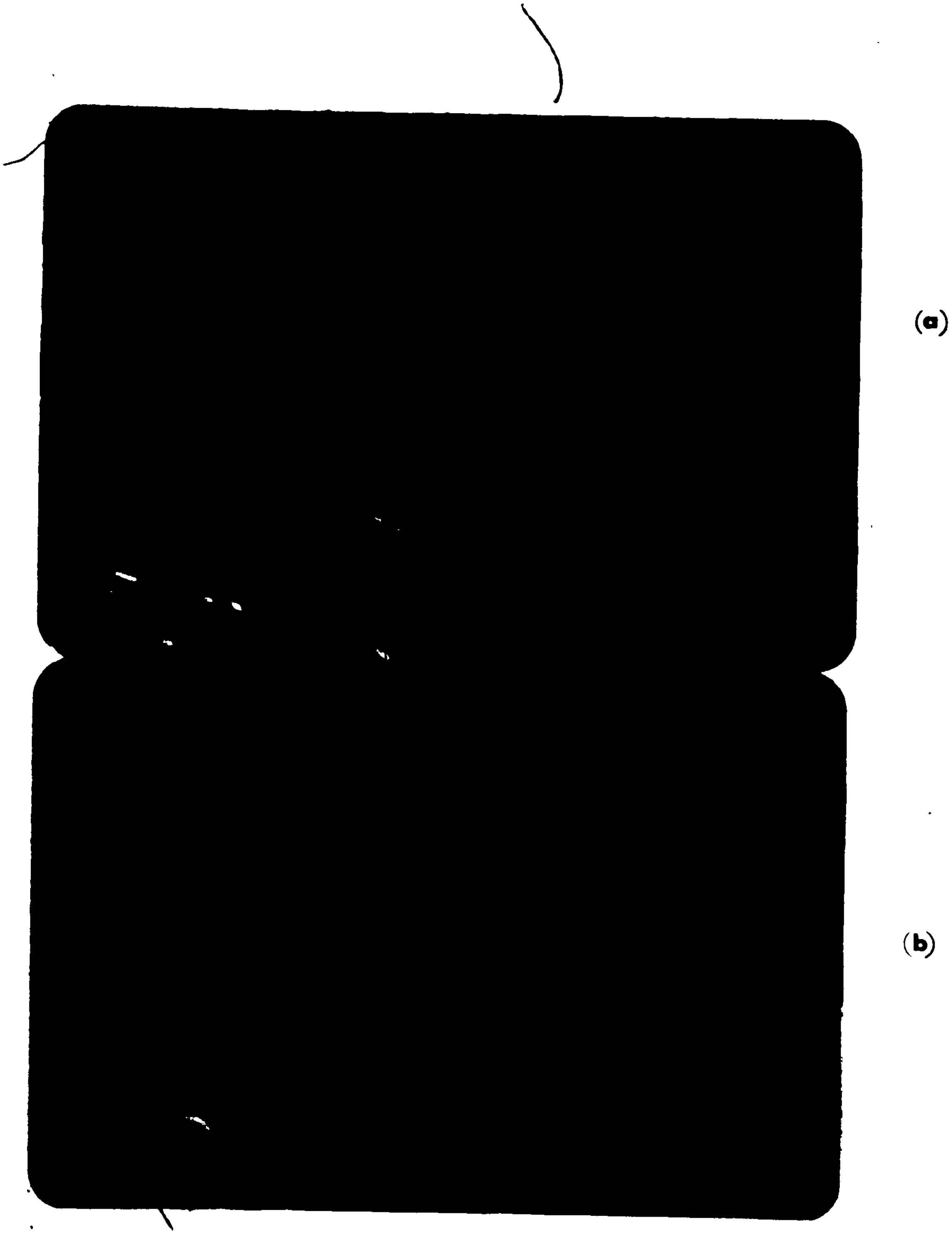

Figure 13. Ledum groenlandicum seedlings. (a) four month old seedlings reared in a greenhouse; (b) five month old seedlings, grown under the following regimes (from left to right): sand/peat, H_2O -5 cm; C. stellatum, H_2O -5 cm; C. stellatum, H_2O 0 cm; C. stellatum, H_2O -2 cm; sand/peat, H_2O 0 cm.

primarily due to being overgrown by the vigorous growth of the mosses. Leaf production was much higher in the T. nitens and S. fuscum substrates than in the other 2 treatments. As a considerable number of leaves had been overgrown by the moss in the T. nitens and S. fuscum substrates, and were not included in the live leaf count, the difference in leaf production between the 2 groups is underestimated.

Seedling growth in the C. stellatum substrates was very reduced. Their root systems were much smaller and leaf production less than those of seedlings transplanted into a sand-peat substrate with a 0 cm water regime (Fig. 13). Seedlings grown in C. stellatum with a -5 cm water regime (for 84 days) had produced somewhat larger root systems and some leaves, but were still smaller than were those in the sand-peat substrate with a 0 cm water regime.

Water Level and Field Established Seedlings

Methods

Seedlings and young L. groenlandicum plants (< 7 years old) were obtained from Heatherdown in fall, 1977. They were kept at 5° for 5 days, at 1° for 3 days (with 2 periods at -2° for 2 h) and then at -4° for 30 days. They were then placed in a 16° day/8° night Trop-Arctic greenhouse for 20 days. Nine pots of seedlings were selected, with 3 being placed in each of a 0 cm, -2 cm and -5 cm constant water regime (temperature = 25° day/17° night).

Table 35. Chi-square tests on seedling survival and number of leaves in relation to high water levels and 4 different substrate types.

	Cs	Ml	Tn	Sf
Initial number seedlings	10	12	11	13
	Number surviving			
Observed	7	12	10	9
Expected	8.2	9.9	9.1	10.8
Chi-square = 1.01 (prob > .75)				
	Number live leaves pot^{-1}			
Observed	0	15	32	25
Expected	13.2	22.8	18.9	17.1
Chi-square = 28.60 (prob < .005)				

* Cs = _C_. _stellatum_; Ml = marl, Tn = _T_. _nitens_, Sf = _S_. _fuscum_

The position and number of live leaves for each _L_. _groenlandicum_ plant in every pot was determined at the start and termination (140 days later) of the experiment. While in the 5° temperature regime, the plants were subjected to 2 extended periods (4 h and 7 h) of temperatures between 40° and 44°, due to a growth chamber malfunction.

Results

Plants not put into any of the water regimes produced new growth, but appeared to be somewhat affected by the exposure to 40° temperatures. That stress may have had a negative influence on the ability of the plants to tolerate the additional stress of high water levels.

Plant survival was highest in the -5 cm regime, although there was no significant difference among the treatments (Table 36). Mortality in the two wetter regimes appeared to be largely due to the marked increase in moss growth (*C. stellatum* and *D. revolvens*). Most of the smaller plants and many of the leaves of larger plants were overgrown by moss. The plants (and substrates) were collected from a drier (moist) site where moss growth was normally slight.

Many of the surviving plants did not produce new leaves during the course of the experiment. Either exposure to the elevated temperature lowered their tolerance to stress from high water levels and/or the over all environmental regime was not conducive to good growth. The mature plants in the water level study (page 58) which were in the same greenhouse also had a decline in growth for all treatments. Leaf production was not high in any of the treatments (Table 37).

Table 36. Mean field established seedling survival in relation to water level.

F = 3.20 (p = .11)

	Percent survival (Mean)		
Water regime	0 cm	-2 cm	-5 cm
Percent survival	48	64	89
Non-significant ranges (α = .05)	————	————	————

Table 37. Ratio of live leaves present at the end of the field established seedling-water level experiment to those at the beginning.

F = 3.84 (p = .025)

	Leaf number ratios (Mean)		
Water regime	0 cm	-2 cm	-5 cm
Ratio (end:beginning)	.78	1.01	1.12
Non-significant ranges (α = .05)	————	————	
		————	————
Percent change	-22	+1	+12

Discussion

High substrate water level does not directly prevent the establishment and growth of *L. groenlandicum* seedlings. Growth is somewhat reduced in water saturated regimes however, and root development is very shallow.

The interaction of substrate chemistry and high water content has a major influence on seedling growth. Seedlings in the calcareous and high pH substrates (*C. stellatum* and marl) had much less growth than those in the acidic and less nutrient rich substrates (*S. fuscum* and *T. nitens*).

The lack of leaf production in the *C. stellatum* substrates may be due to the impact of transplantation and moss growth, or could be indicative of an allelopathic interaction. As some *L. groenlandicum* occurred in *C. stellatum* mats in the field, it would appear that the former is probably the case. The seedlings transplanted into the sand-peat substrate probably grew better because of the more favorable substrate chemistry (acidic and non-calcareous) and the absence of mosses.

VII. GENERAL DISCUSSION

The environmental regime experienced by a plant is not a constant, but varies over time and space. In order for a plant to become established and survive in a given location, it must be able to tolerate the entire range of environmental variation which occurs at that site. In terms of a single plant, allogenic variables (e.g. climate, substrate, other organisms) largely control environmental variation over time, while autogenic variables (e.g. growth) primarily influence the exposure to spatial variation. Thus the microenvironment of a seedling is often quite different from that of the mature plant. The physiological characteristics of these two phases of the life cycle (as well as other phases) may consequently be quite different (Bazzaz 1974).

To assume that a plant's distributional pattern is solely generated by the physiological capabilities of the mature plant is to ignore the fact that its life cycle is a continuum, with different phases often experiencing radically dissimilar environmental regimes. Harper et al. (1965) found that small scales of pattern developed for three Plantago spp. due to differential germination occurring in response to variations in substrate microtopography. Each species had maximum establishment occurring under different sets of microtopographical conditions.

Seed dispersal and germination phases were found to be of primary importance in establishing the distributional patterns of early successional plant populations in abandoned fields (Raynal and Bazzaz 1973). Working with a larger scale of pattern, Black (1977) showed that the northern limit of tree line at the tundra-boreal forest interface in North America is generated primarily by characteristics of the seed production, dispersal, germination and seedling phases of Picea mariana.

The distributional patterns of species which reproduce primarily by vegetative reproduction are less influenced by the non-mature phases of the life-cycle than are plants which propagate principally via sexual reproduction. But even the predominantly vegetative reproducers are initially dependent on the ability of seed to reach the site and for successful seedling establishment to occur.

Mature Plant Stage

Mature Ledum groenlandicum is capable of tolerating the low-peat environments of both poor and rich fen systems. High water levels do not limit the survival of the plant as long as there are portions of the substrate which are relatively well aerated. This is also the case for Calluna vulgaris, which is found in habitats similar to those in which L. groenlandicum is found (Gimingham 1960). The plant is also able to endure the primary water chemistry of both poor and rich fens. The availability of Fe in the anaerobic portions of rich fen low-peat substrates may enable L. groenlandicum to survive there. Well aerated substrates of similar chemistry (high pH and high concentrations of Ca and HCO_3) are often deleterious to ericads (Oertli 1963; Lee 1965).

Vegetative spread of L. groenlandicum into the low-peat communities is limited primarily by the plant's growth pattern rather than by its physiological tolerances. The plant grows primarily in an upward direction and does not possess rhizomes. Consequently, each plant forms a compact clump of stems with little horizontal extension occurring. When L. groenlandicum forms a relatively closed canopy over the moss substrates, moss growth is reduced and the shrub's stems are not engulfed by a moss hummock. In actively growing Sphagnum substrates, shrubs are often hard pressed to manage more than a couple of year's growth emergent from the moss surface (Bray 1921; Dansereau and Segadas-Vianna 1952; Walter 1973). It is in such situations that vegetative reproduction may often occur for L. groenlandicum, as the emergent stems become separated from the parent plant via the death of the buried stems.

Germination and Establishment Stage

Seed production, dispersal, germination and initial seedling establishment stages were not found to be of primary importance in limiting the spread of the plant into low-peat environments. The seed was quite viable (> 50%

germination when fresh) and capable of surviving the winter environment. The presence of L. groenlandicum on small hummock islands in low-peat communities of both poor and rich fens indicates that dispersal of viable seed into low-peat areas does take place. The occurrence of naturally established seedlings and young plants of many age classes demonstrates that successful reproduction by seed readily occurs when the requirements are met. Germination and initial seedling establishment also occurred in all low-peat substrates tested.

Juvenile Stage

The juvenile stage (and established seedling stage) were found to play a major role in limiting the spread of L. groenlandicum. Naturally established juvenile plants (≥ 1 year and ≤ 4 years) of L. groenlandicum were not observed in low-peat substrates at either Heatherdown or Kestow. As 3 year old plants would be readily observed were they present, it appears that something prevents the survival of young L. groenlandicum plants before the end of their third growing season.

The small size of the juvenile plants, coupled with their extremely slow growth rates, means that they are subjected to a "seedling" environment for several years. This environment is located in the upper 3 cm of substrate and ≤ 1 cm above the substrate surface. Such micro-sites have a rigorous environmental regime, far more severe than that experienced by the mature plant (Norgaard 1951; Bazzaz 1974; Busby 1976). Prolonging the period spent in this microhabitat heightens the probability of mortality due to the occurrence of extreme climatic conditions. However, in respect to the temperature and water regimes, the moist low-peat substrates provide a far more favorable environment than do the raised-peat substrates.

Substrate chemistry and water content were not found to be of primary importance in limiting the survival of juvenile plants in low-peat environments. The juvenile plants had a similar response to high water levels as did the mature plants, being capable of surviving when a portion of the substrate was aerated. The presence of naturally established seedlings and juvenile plants on moss mats < 1 cm thick and directly overlaying marl suggests that the young plants manage to obtain enough Fe to survive and to grow in rich fens despite their shallow root systems. No Fe deficiency symptoms were observed in these plants.

Variables Limiting Seedling-Juvenile Plant Survival

High rates of moss growth are a major variable influencing the survival of the young plant. Annual growth rates of many mire bryophytes (Table 38) are usually much greater than that of L. groenlandicum seedlings. Even under a favorable temperature and water regime in a greenhouse, mean height of 4 month old seedlings was only .4 cm. The influence of moss growth on the survival of vascular plants

Table 38. Annual growth in length of mosses which are dominant in mire systems of central Canada.

Species	Mean length increment (cm)	Region	Source
T. nitens	.4 - 1.6	Alberta	(Busby 1976)
P. strictum	1.3 - 2.4	Manitoba	(Longton 1972)
S. fuscum	.1*	Manitoba	(Reader & Stewart 1971)
S. fuscum	.4 - 2.1	Finland	(Pakarinen 1978)
S. fuscum	1.0 - 1.3	England	(Bellamy & Rieley 1967)
S. fuscum	.1 - 1.0	Sweden	(Sonesson 1972)
S. angustifolium	3.0 - 8.0	England	(Clymo 1970)
S. angustifolium	11.6	Germany	(Overbeck & Happach 1957)
S. magellanicum	1.0	Norway	(Pederson 1975)
S. fuscum	$\geq$.1 - $\geq$1.0	** Heatherdown	
S. angustifolium/ *S. magellanicum*	$\geq$.2 - $\geq$2.0	*** Nestow	
A. palustre	$\geq$.5 - $\geq$1.2	*** Nestow	

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* Estimated from net annual production values, the range of which is low for this species. Either the site sampled was not conducive to growth of *S. fuscum* or there was a sampling error. Growth rates of *S. fuscum* similar to those found in other parts of the northern hemisphere were found at Heatherdown.

** Based on observations of moss growth around twigs in the adventitious root experiment (upper range of growth) and of liverwort covered hummock tops (lower range of growth). Growth measured (with wires inserted in the moss) during the month of April, 1978, ranged from 0 to 0.4 cm.

*** Growth produced during the months of May and June, 1978, measured by wires inserted into the moss.

(both seedling-juvenile and mature stages) has been noted by other researchers (Bray 1921; Walter 1973; Black 1976).

The major variable controlling moss growth and production is water availability (Clymo 1970, Busby 1976, Vitt and Pakarinen 1977). Due to the accumulation of peat in a low-peat area, the moss mat surface is gradually raised higher above the primary water level. As increasingly drier conditions develop, the growth rates of the low-peat moss species (Drepanocladus, Campylium, Scorpidium) decrease and other moss species, more tolerant of drier environments, become established (Tomenthypnum, Aulacominium, Sphagnum). As these invading bryophyte species have higher growth rates in wetter environments (Clymo 1973; Vitt and Pakarinen 1977), there would not be much of a chance for seedlings of L. groenlandicum to get successfully established during the transitional stage from low-peat to raised-peat systems. Successful establishment of L. groenlandicum in undisturbed portions of mires would be limited until the growth rate of the raised-peat bryophytes is reduced (via the upward accumulation of peat). Thus the plant is largely absent from young raised-peat hummocks, but is prevalent in the older raised-peat areas where moss growth rates are reduced to the point that L. groenlandicum seedlings and juvenile plants can successfully compete. Substrate surfaces are more diversified in raised-peat areas than they are in low-peat, and may thus contain a greater array of potential micro-sites for seedling establishment (Bray 1921).

There are two observations which further substantiate the influence of moss growth rates on L. groenlandicum. One is that several mires in the study region have young raised-peat areas (dominated by A. palustre) in which numerous isolated young raised-peat hummocks of S. angustifolium and S. magellanicum occur. Ledum groenlandicum is quite prominent on these Sphagnum hummocks. Jeglum (1972) also observed similar hummocks in Saskatchewan and found that fallen trees and stumps acted as sites of origin for such hummocks. The substrate surface resulting from a tree fall would primarily be exposed peat rather than a layer of living moss, and would have a large number of different micro-habitats which would be conducive to the successful establishment of L. groenlandicum. The re-establishment of mosses in such a site evidently is not rapid enough to prevent the development of L. groenlandicum to the stage (≥ 5 years) where its growth rate would equal or exceed that of the Sphagnum species which eventually form the hummock. The presence of L. groenlandicum in such actively growing Sphagnum hummocks is in contrast to the absence of the plant in equally productive Sphagnum hummocks which have develo. directly from non-disturbed moss mats in low-peat areas.

The second observation deals with the seedlings and juvenile plants of L. groenlandicum that occurred in certain transitional low-peat areas (raised-marl, probably a disturbed site) where moss growth was greatly reduced (pages 71 and 106). The seedlings and juvenile plants were relatively abundant in such sites and apparently were capable of outgrowing the mosses. When seedlings and juvenile plants, along with the moss-marl substrate, were transplanted to a greenhouse and were placed in a higher water level regime than that which they normally experienced in the field, the moss mat began to grow rapidly and soon engulfed most of the smaller seedlings of L. groenlandicum that were present.

It would appear that the raised marl site is too "dry" for the rapid growth and establishment of the low-peat moss species. Thus the substrate there is primarily exposed marl, with a few thin and scattered mats of low-peat mosses (where the L. groenlandicum seedlings and juvenile plants are located). The absence of raised-peat bryophytes indicates that they are probably not capable of directly invading bare marl surfaces. Therefore, they are excluded from that site until a thicker and more extensive peat layer is developed by the low-peat mosses. In this case, Ledum groenlandicum is capable of invading the site because competition from the bryophyte species is largely eliminated.

Both of these examples are in contrast to the theory that perturbations tend to cause a regression in successional processes (the degree of the regression depending on the degree of perturbation) (McNaughton and Wolf 1973). Perturbations in earlier successional stages may allow for an invasion of L. groenlandicum (as well as Sphagnum and other raised-peat species) into younger successional communities, consequently leading to an acceleration of the successional process.

In water saturated substrates, fall and spring freeze-thaw cycles may also limit survival. Ledum groenlandicum seedlings are small and delicate and would be easily damaged by such activity. Mortality of P. mariana seedlings in wet substrates due to freeze-thaw phenomena has been observed (Black 1977). But extensive areas of low-peat substrates occur which are not water saturated in the Heatherdown and Nestow fens. As P. mariana and Larix laricina seedlings were frequently observed in such sites at Heatherdown Fen, it is probable that seedling mortality of L. groenlandicum due to ice formation does not occur at those sites either.

In addition to mortality due to frost heaving, seedling root systems in water saturated substrates are very superficial. Such seedlings would be quite vulnerable to the hot dry periods which occur every summer. Periods of high water levels would also be quite damaging because of the lack of support from the shallow roots.

Like Erica tetralix (Sheikh 1970), Ledum groenlandicum is capable of tolerating low levels of mineral nutrients (which may be related to its slow seedling growth rate) and is able to survive in substrates with low nutrient levels. It thereby avoids competition from faster growing and more nutrient demanding species. Maximum volumetric concentrations of exchangeable Ca in the upper 20 cm of the raised peat substrates are only 1/3 that of the lowest value found in loam soils (Luvisol) (Table 39). Raised-peat substrates also contain less Ca than do most sandy soils (Luvisol), although the range of concentrations overlap. The volumetric concentration of N is similar in both soils, but the C:N ratio indicates that much of the N in the raised-peats may be unavailable.

Ledum groenlandicum is thus a plant with a limited ability to compete in environments other than those of mature raised-peat systems in mires. The plant is capable of tolerating the abiotic environmental regime of low-peat communities (except the continually water saturated areas) in both rich and poor fen systems, but is excluded from such environments primarily because of its extremely slow seedling growth rate and small seedling size. The limited ability of the mature plant to spread horizontally via vegetative means also limits the plant's distribution. It is largely absent from non-mire environments for the same reasons, and also because such environments are often too dry for the survival of the seedling and juvenile plants. The raised-peat substrates of mires are a refuge rather than a preferred environment for L. groenlandicum.

The characteristics of L. groenlandicum's sexual reproduction biology are similar to those of a fugitive species. The production of large numbers of wind dispersed seed capable of initial establishment under a wide range of substrate characteristics would be expected of a plant

Table 39. Comparison of volumetric content of nitrogen and exchangeable Ca in the top 20 cm of raised-peat substrates and mineral soils in central Alberta.

Substrate	Ca (meq dm^{-3})	N (g dm^{-3})	C:N
Raised-peat	1-18	.5-2.7*	16-94*
Luvisol (sand)**	6-43	______	______
Luvisol (loam)**	52-420	.4-3.8	8-17

* from Gardner 1967
** from Lindsay et al. (1968) and Twardy and Lindsay (1971)

dependent on "fleeting" habitats for successful establishment by seed. The slow growth rate and high moisture requirement of the seedlings severely limit establishment to certain fleeting habitats, however. Moist sites which require a long period to become revegetated would be favorable, which is often the case in northern environments, particularly in mires (Lutz 1956; Scotter 1964; Black 1977).

Because of the small seedling size and their patchy occurrence (in non-disturbed mires), seedlings of L. groenlandicum are probably often overlooked and assumed to be absent. This is the case for many ericaceous species. Even when looking specifically for the seedlings, it is often difficult to find them, particularly in mires (Bray 1921). In an intensive study on revegetation of burned heaths, Hansen (1964) frequently observed seedlings of several species that had previously been reported to only rarely occur.

The relatively high numbers of L. groenlandicum seedlings occurring in disturbed areas of mires indicates that successful seedling establishment readily occurs when a "favorable" environment is encountered. Colonization of small scale disturbances (such as at the base of fallen trees) within a mire community thus serves as a means of replacing those mature plants which may die and of increasing the genetic diversity of the L. groenlandicum population present in that community, as well as becoming established in successionally younger areas of the mire. Due to the large amount of seed produced annually, there is a high probability that seed will reach the majority of disturbed areas within a given mire system. Such seed saturation of local available sites would maximize the number of new plants established and assure that some seedling recruitment would occur annually. Large scale disturbances (e.g. fire, logging) would also be important in terms of providing a favorable environment for the successful establishment of seedlings.

Successional processes in mire systems occur slowly. Perturbations (e.g. fire) often prolong the various developmental stages, sometimes almost indefinitely (Moss 1955; Karlin 1975). Once established in such a system, L. groenlandicum would be likely to experience a fairly lengthy period of survival. The ability of the mature plant to survive fires (and other disturbances) by means of the buried stems further decreases the need for frequent successful reproduction by seed.

The plant's longevity and low light requirements for photosynthesis enable it to endure in forested areas, especially in the boreal _Picea_-Feather moss forests, which often culminate mire succession in central Canada. The reduced ground cover of _L. groenlandicum_ in stands with a relatively closed canopy indicate that the plant is not thriving in such an environment (Bray 1921; La Roi 1967). But many plants do survive, and with the advent of a disturbance _L. groenlandicum_ is able to recolonize the disturbed area fairly rapidly via sprouting and seedling establishment.

The plant's cold hardiness characteristics also enable it to successfuly compete in mire systems, which are usually much cooler than are the adjacent upland areas (Norgaard 1951, Joyal 1972). The fact that the minimum survival temperature in the summer is ≈ -9° (Wilkinson 1977) suggests that the northern limit of the plant may not be due to the characteristics of the mature plant. Some preliminary data show that seedlings of _L. groenlandicum_ are killed by rapid exposure to -4°, while those of _L. palustre_ survived. While these data are preliminary, they indicate one possible reason why _L. groenlandicum_ has a more southern distribution than does _L. palustre_.

The spread of _L. groenlandicum_ into non-mire systems would be limited by the slow growth rate of the seedlings and the high moisture requirement for germination and initial establishment. Communities dominated by deciduous trees would not be likely sites for successful establishment. The annual shedding of leaves would cover and kill any L. groenlandicum seedlings established during that growing season. The presence of L. groenlandicum in stands dominated by deciduous trees indicates either that the forest has invaded a peatland community, or that a major disturbance (e.g. a severe fire) occurred which did not allow a rapid recovery of the vegetation.

The restricted distribution of some plant species to certain harsh habitats is postulated to be due to the inability of such species to successfully compete in more favorable environments (Walter 1973). This is the case with L. groenlandicum, with seedling and juvenile establishment being the limiting phases in its competitive ability in more favorable (for other species) environments.

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APPENDIX I

Legal Descriptions of Study Site Locations

Legal description (quarter, section - township - range-meridian):

Heatherdown: NW24-53-2-W5 (The study site was largely situated in the southeast quadrant of the NW quarter.)

Nestow: SW31-60-24-W4 (The study site was located about 300 m north of a dump ground and 13 m east of the road. The dump ground is roughly 1.5 km south of Nestow.

Appendix II

Soil and Water Analysis Lab Facilities

Soils

John Konwicki (technician)
Soils Department
University of Alberta
(samples were diluted with 1% lanthanum oxide)

Water

G. Hutchinson (technician)
Zoology Department
University of Alberta

Appendix III

Composition of Buffer Solutions Used in Germination-pH Study

Buffer	Composition
pH 3.5	250 ml .05 M KH_2PO_4
	1 ml N HCl
pH 5.5	250 ml .05 M KH_2PO_4
	8 ml .05 M K_2HPO_4
pH 7.5	250 ml .05 M K_2HPO_4
	60 ml .05 M KH_2PO_4
pH 8.5	250 ml .05 M K_2HPO_4