CANADIAN THESES ON MICROFICHE

I.S.B.N.

THESES CANADIENNES SUR MICROFICHE

National Library of Canada
Collections Development Branch

Canadian Theses on
Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Direction du développement des collections

Service des thèses canadiennes
sur microfiche

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

NL-339 (r. 82/08)

Canadä

113

0-315-16022-5

National Library
of Canada

Bibliothèque nationale
du Canada

Canadian Theses Division

Division des thèses canadiennes

Ottawa, Canada
K1A 0N4

63931

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

- Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur

JOHN SINCLAIR CAMPBELL

Date of Birth — Date de naissance June 18, 1949	Country of Birth — Lieu de naissance USA

Permanent Address — Résidence fixe

1703 7 Ave South
Lethbridge, Alberta
T1J 1C9

Title of Thesis — Titre de la thèse

Growth, BIOMASS PARTITIONING, AND CARBON ALLOCATION OF THREE DWARF SHRUBS IN THE CANADIAN LOW ARCTIC

University — Université

University of Alberta

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

PhD

Year this degree conferred — Année d'obtention de ce grade 1983	Name of Supervisor — Nom du directeur de thèse L. C. Bliss

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date April 25, 1983	Signature John S. Campbell

NL-91 (4/77)

THE UNIVERSITY OF ALBERTA

GROWTH, BIOMASS PARTITIONING, AND CARBON ALLOCATION OF THREE DWARF SHRUBS IN THE CANADIAN LOW ARCTIC

by

John S. Campbell

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
SPRING, 1983

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: JOHN S. CAMPBELL

TITLE OF THESIS: GROWTH, BIOMASS PARTITIONING, AND CARBON ALLOCATION OF THREE DWARF SHRUBS IN THE CANADIAN LOW ARCTIC

DEGREE FOR WHICH THESIS WAS PRESENTED: DOCTOR OF PHILOSOPHY

YEAR THIS DEGREE GRANTED: 1983

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(Signed) John S. Campbell

PERMANENT ADDRESS:

1703 7 Ave. South
Lethbridge, Alberta
T1J 1L9

DATED Apl 25, 1983

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 "Growth, Biomass Partitioning, and Carbon Allocation of Three Dwarf Shrubs in the Canadian Low Arctic" submitted by John S. Campbell in partial fulfilment of the requirements for the degree of Doctor of Philosophy in plant ecology.

Lawrence C. Bliss

Supervisor

Dale H. Vitt

Wayne Pettapiece

James M. Mayo

Kenneth Higginbotham

F. Stuart Chapin, III

External Examiner

DATE Dec. 15, 1982

ABSTRACT

Growth, biomass partitioning and carbon allocation of *Betula nana*, *Ledum palustre* and *Vaccinium vitis-idaea* were studied in a low arctic, dwarf shrub tundra on uplands east of the Mackenzie River Delta, N.W.T. Net annual aboveground production was; vascular community, 54 g m^{-2} yr^{-1}; *B. nana*, 31 g m^{-2} yr^{-1}; *L. palustre*, 6 g m^{-2} yr^{-1}; *V. vitis-idaea*, 4 g m^{-2} yr^{-1}. Stems were a larger portion of biomass in *B. nana* (>75%) than in the evergreen species (*L. palustre* = 60%, *V. vitis-idaea* = 20%), while leaves were a much smaller fraction in the deciduous shrub (<25%) than in *L. palustre* (<40%) or *V. vitis-idaea* (<75%). Reproductive tissue was <5% of aboveground biomass in all three species. The ratio of net production to biomass was lower in the evergreen species (.14) than in *B. nana* (.29). Leaf expansion in *B. nana* began shortly after snowmelt and was completed rapidly. Expansion of current leaves in the evergreens started later and was completed more slowly. Stem elongation in all species occurred largely after leaf expansion had been completed.

Carbon allocation to aboveground tissue was examined using ^{14}C as a tracer. Different patterns were exhibited by the two growth forms. Most carbon fixed by *B. nana* shortly after leaf expansion remained in leaf tissue until

abscission, though some export did occur. With full expansion, less carbon was retained by leaves and greater amounts were exported to current and non-current stems. Maximum ^{14}C recovered from reproductive organs of B. nana was <3%.

Except for a short early period of high carbon retention, non-current leaves were a source of carbon throughout the growing season for development of stems, current leaves, and reproductive tissue in the evergreen shrubs. Current leaves remained a carbon sink until August. Commitment of carbon to reproductive tissue was high in L. palustre and V. vitis-idaea, with up to 40% of recovered ^{14}C in that tissue.

In all three species, leaves were the major aboveground carbon sink over the growing season, and at least small amounts of carbon assimilated early in the season remained mobile and were translocated to other aboveground tissue before dormancy.

ACKNOWLEDGEMENTS

This study was completed with the help of many fine people who generously gave of their time, ideas, money, and muscles. All are deserving of more than the thanks I can offer here.

Drs. W. Pettapiece and K. Higginbotham provided necessary guidance and criticism at all stages in the work as members of my thesis committee. Dr. F.S. Chapin III supplied new perspectives and refreshing insights with his manuscript review and through his enthusiastic and friendly role as external examiner. Dr. D.H. Vitt was a committee member who gave biological and editorial advice, but also kindly acted as my in-house administrator for the last few years. For pleasant humor, endless stories, philosophical forays, and an unselfish giving of time and ideas, few could surpass Dr. J.M. Mayo.

As the person who gave me the opportunity to pursue the ideas in this work, who allowed me to wander towards my goal without letting me get too far astray, and who showed unbelievable patience, Dr. L.C. Bliss deserves much praise for his role as my major supervisor. His model as a thoughtful, careful biologist and a fine, caring person has had a deep influence on my life.

Over the years I have benefited from contact with a great many fellow workers and friends. Valerie Loewen was an efficient field assistant, a useful memory prompter, and a very good friend. Peter Kosko, Al Black, John Harter, Peter Lee, Bill Lee, and Bob Ellis all listened, suggested, or helped work through problems at many stages. Eric Karlin helped oversee the jerky beginnings of the project and Victor Lieffers was able to smooth the ending. David Somers kept me on my toes with alternate ways of seeing everything and gave me an important lift at the bottom. The input of these people went well beyond pure scientific application.

Thanks must also go to my parents, Dr. and Mrs. John S. Campbell, for unending support before and during this effort.

Gulf Oil Canada Ltd. generously provided financial support that made this project possible through a grant to L.C. Bliss. The company was also there with logistic assistance that took the work from idea to reality. Jim Gutherie was particularly helpful in field support.

Final thanks must go to Cathy Campbell for help of every form at all stages. She was field assistant, graphics creator, editor, and much else, always providing the moral support that allowed this to be completed.

TABLE OF CONTENTS

CHAPTER PAGE

I. INTRODUCTION 1

II. SITE DESCRIPTION 5

- Vegetation 5
  - Methods 7
  - Results and Discussion 8
- Soils 10
  - Methods 10
  - Results and Discussion 10
- Climate 14
  - Methods 15
  - Results and Discussion 18
    - Temperature 18
    - Radiation 26
    - Precipitation 29
    - Water Relations 33
    - Wind 35
    - Active Layer 36

III. THE PLANTS-DISTRIBUTION AND PHENOLOGY 40

- *Betula nana* 40
- *Ledum palustre* 47
- *Vaccinium vitis-idaea* 52

IV. LEAF AND STEM GROWTH 56

- Methods 56
- Results 62
- Discussion 84

TABLE OF CONTENTS continued

V. BIOMASS PARTITIONING 99
- Introduction 99
- Methods 101
- Calorimetry 101
- Biomass Partitioning 101
- Results 103
  - Caloric Content 103
  - Biomass Partitioning 106
    - *[illegible]a nana* 106
    - *[illegible] palustre* 109
    - *Vaccinium vitis-idaea* 113
- Discussion 118
  - Calorimetry 118
  - Biomass Partitioning 120
    - *Betula nana* 120
    - *Ledum palustre* 124
    - *Vaccinum vitis-idaea* 129

VI. NET PRODUCTION 133
- Introduction 133
- Methods 134
- Results 138
- Discussion 148

VII. CARBON ALLOCATION 156
- Introduction 156
- Methods 157
- Results 160

TABLE OF CONTENTS continued

Betula nana 160

Ledum palustre 169

Vaccinium vitis-idaea 179

Discussion 190

Betula nana 190

Ledum palustre 194

Vaccinium vitis-idaea 201

VIII. SYNTHESIS 205

IX. LITERATURE CITED 231

LIST OF TABLES

Table | Page

1. Percent frequency, aerial cover, and presence of species in sampled quadrats. 9

2. Representative soil profile description of a soil hummock, Parsons Lake, N.W.T. 13

3. Degree day sums June 1 to August 30, 1970-1979. 20

4a. Monthly mean, mean maximum, and mean minimum air and soil temperatures at the Parsons Lake study site in 1977. 24

4b. Monthly mean, mean maximum, and mean minimum air and soil temperatures at the Parsons Lake study site in 1978. 25

5. Mean daily irradiance at Parsons Lake, N.W.T. 31

6. Caloric values for various tissue types in _Betula nana_, _Ledum palustre_, and _Vaccinium vitis-idaea_. 104

7. Non-current biomass of _Betula nana_, _Ledum palustre_, and _Vaccinium vitis-idaea_ in the four fertilizer treatment plots. 137

8. Soil test results for N, P, Al, Mn, and pH from experimental and control plots one year after fertilization. 139

9. Peak season biomass and net annual production of _Betula nana_, _Ledum palustre_, _Vaccinium vitis-idaea_, all remaining vascular species, and the total vascular community. 141

LIST OF FIGURES

Figure Page

1. Map of study region. 6

2. Representative soil profile of the study area, including sections of a soil hummock and an inter-hummock trough. 12

3. Climadiagrams for Inuvik and Tuktoyaktuk, N.W.T. 16

4. Degree days accumulated in 1977 and 1978 at the Parsons Lake study site. 19

5. Five-day air temperature means 150 cm above the ground. 21

6. Representative mean, mean maximum, and mean minimum air and soil temperature profiles. 23

7. Monthly means of total daily short-wave radiation at Inuvik, N.W.T. 27

8. Daily total short-wave radiation at Parsons Lake in June, July and August, 1977 and 1978. 28

9. Five-day means of total daily short-wave radiation in 1977 and 1978. 30

10. Precipitation and weekly mean soil moisture of hummocks and inter-hummock troughs at -5 and -10 cm in 1977 and 1978. 32

11. Mean weekly dawn xylem tensions of Betula nana, Ledum palustre, and Vaccinium vitis-idaea in June, July and August, 1978. 34

12. Mean weekly active layer thickness in 1977 and 1978. 37

13. Mean weekly active layer thickness in hummocks and inter-hummock troughs in 1978. 38

14. North American distributions of Betula nana subsp. exilis and Betula glandulosa. 41

15. Reproductive and vegetative phenophases of Betula nana, Ledum palustre, and Vaccinium vitis-idaea in 1977 and 1978. 45

16. North American distribution of Ledum palustre subsp. decumbens. 48

17. North American distribution of Vaccinium vitis-idaea subsp. minus. 53

LIST OF FIGURES continued

Figure Page

18. Leaf blade elongation in Betula nana. 63

19. Mean surface area of leaf blade (one side only) in Betula nana. 65

20. Mean leaf dry weight (blade and petiole) in Betula nana. 67

21. Mean leaf dry weight (blade and petiole) by position in the bud of Betula nana in 1977 and 1978. 69

22. Mean surface area of leaf blade (one side only) by position in the bud of Betula nana in 1977 and 1978. 70

23. Leaf blade elongation in Ledum palustre. 71

24. Mean surface area of leaf blade (one side only, current leaves) in Ledum palustre. 73

25. Mean leaf dry weight (blade and petiole) of current leaves of Ledum palustre. 74

26. Leaf blade elongation in Vaccinium vitis-idaea. 76

27. Mean surface area of leaf blade (one side only, current leaves) in Vaccinium vitis-idaea. 78

28. Mean leaf dry weight (blade and petiole) of current leaves of Vaccinium vitis-idaea. 79

29. Leaf longevity in Ledum palustre. 81

30. Elongation of stems (long shoots) of Betula nana, Ledum palustre, and Vaccinium vitis-idaea in 1977 and 1978. 83

31. Annual stem elongation (long shoots) in Ledum palustre from 1967 to 1978. 85

32. Partitioning of total aboveground biomass of Betula nana in 1977, based on dry weight of tissue. 107

33. Partitioning of total aboveground biomass of Betula nana in 1978, based on dry weight of tissue. 108

34. Partitioning of total aboveground biomass of Ledum palustre in 1977, based on dry weight of tissue. 111

35. Partitioning of total aboveground biomass of Ledum palustre in 1978, based on dry weight of tissue. 112

LIST OF FIGURES continued

Figure		Page
36.	Partitioning of total aboveground biomass of *Vaccinium vitis-idaea* in 1977, based on dry weight of tissue.	114
37.	Partitioning of total aboveground biomass of *Vaccinium vitis-idaea* in 1978, based on dry weight of tissue.	115
38.	Effect of N and P on elongation of current year stems in *Betula nana*, *Ledum palustre*, and *Vaccinium vitis-idaea*.	143
39.	Effect of N and P on dry weight of current tissue in *Betula nana*.	145
40.	Effect of N and P on dry weight of current tissue in *Ledum palustre*.	146
41.	Effect of N and P on dry weight of current tissue in *Vaccinium vitis-idaea*.	147
42.	Percent of ^{14}C recovered in leaves from total aboveground biomass of *Betula nana*.	162
43.	^{14}C activity of leaf tissue in *Betula nana*.	163
44.	Percent of ^{14}C recovered in current and non-current stems of *Betula nana*.	165
45.	^{14}C activity of current stem and reproductive tissue in *Betula nana*.	166
46.	Percent of ^{14}C recovered in preformed buds and reproductive tissue of *Betula nana*.	168
47.	Percent of ^{14}C recovered in current and non-current leaves of *Ledum palustre*.	170
48.	^{14}C activity of current, one year old, and three year old leaf tissue in *Ledum palustre*.	171
49.	Percent of ^{14}C recovered in current and non-current stems of *Ledum palustre*.	173
50.	^{14}C activity of current stem tissue in *Ledum palustre*.	175
51.	Percent of ^{14}C recovered in preformed buds and reproductive tissue of *Ledum palustre*.	177
52.	^{14}C activity of reproductive tissue in *Ledum palustre*	178

LIST OF FIGURES continued

Figure — Page

53. Percent of ^{14}C recovered in current and non-current leaves of _Vaccinium vitis-idaea_. 180

54. ^{14}C activity of current leaf tissue in _Vaccinium vitis-idaea_. 182

55. ^{14}C activity of one year old, two year old and three year old and older leaf tissue in _Vaccinium vitis-idaea_. 184

56. Percent of ^{14}C recovered in current and non-current stems of _Vaccinium vitis-idaea_. 185

57. ^{14}C activity of current, one year old, two year old and three year old and older stem tissue in _Vaccinium vitis-idaea_. 186

58. ^{14}C activity and percent of ^{14}C recovered in reproductive tissue of _Vaccinium vitis-idaea_.

INTRODUCTION

The continued survival of a plant species in a specific environment depends on the ability of the species to maintain vegetative growth and to reproduce under the constraints of that system. These constraints include the potential limitation of such important resources as radiation, water, nutrients, and space. The ability of a species to use the available resources is ultimately expressed through the maintenance of existing tissues and the production of new tissues, both vegetative and reproductive. Within a plant community, members have evolved many different patterns of growth and reproduction in response to the physical limitations of environmental resources.

The concept of plant growth form has been well established in description of geographical plant distributions and their relationship to general environmental conditions (Cain 1950, Daubenmire 1978). The early definitions of growth form have been expanded to include characteristics of reproduction and leaf and stem growth. This broadened concept has been used to interpret the adaptations of plant species to their existing environment (Harper and Ogden 1970, Grime 1977, Harper 1977).

Much of the interest in strategies of different growth forms has focused on the adaptiveness of evergreen and deciduous leaves to plants. Chabot and Hicks (1982) have summarized the hypotheses that attempt to explain the different patterns of leaf longevity among growth forms. These hypotheses variously relate the value of a particular leaf longevity pattern to competition for nutrients internally among plant compartments, avoidance of environmental stresses during part of the growing season, nutrient cycling, nutrient use efficiency, compensation for different photosynthetic rates, cost of leaf development and the resulting effect on net carbon balance, and the storage of nutrients and carbohydrates. In some cases (e.g. Mooney et al. 1975, Chabot and Bunce 1979), the examination of these hypotheses have been more pertinent to moderate temperate and tropical environments than arctic situations.

Comparative studies of strategies in different low arctic growth forms have concentrated on nutrient cycling and nutrient use efficiency (Stoner et al. 1978, Chapin et al. 1980a, Shaver and Chapin 1980), and photosynthetic life spans and carbon balance (Johnson and Tieszen 1976). Through an understanding of resource allocation patterns in structural, photosynthetic, and reproductive tissues, and the resulting partitioning of this biomass within plants, a more clear understanding can be developed of how these plants respond to the limitations in their growing conditions (Mooney 1972).

The severe limitations to growth and reproduction of plants imposed by the physical environment of the North American Arctic are reflected by the low species diversity in the region, and by the low net annual productivity of the plant communities (Bliss et al. 1973). Characteristic of this environment are a short growing season (Lewis and Callaghan 1976), limited radiation (Bliss 1971), low soil and air temperatures (Bliss 1956, 1966) and low levels of available nutrients (Chapin et al. 1980b).

In North America, the Low Arctic includes southwestern Baffin Island, and mainland Canada and Alaska north of the tree line (Aleksandrova 1980, Bliss 1981), and consists of a mosaic of different plant communities. Evergreen and deciduous shrubs, low shrubs, and dwarf shrubs are important members of many of these communities. In the Mackenzie River Delta region of western Canada, low shrub and dwarf shrub communities dominate relatively well drained, rolling upland sites. The deciduous shrub, Betula nana L. subsp. exilis (Sukatsch.) Hult., and the evergreen shrubs Ledum palustre L. subsp. decumbens (Ait.) Hult., and Vaccinium vitis-idaea L. subsp. minus (Lodd.) Hult. have high frequency and cover in the Low Shrub-Heath community on upland sites that provide adequate winter snow cover (Corns 1974). In these upland sites, L. palustre and V. vitis-idaea form sub-canopies under an upper canopy created by B. nana. Thus, both evergreen and deciduous dwarf shrubs successfully coexist in the environment of the Mackenzie Delta region.

This study was initiated to quantify the relationships of leaf and stem growth, biomass partitioning, net production, and carbon allocation in three dominant deciduous and evergreen dwarf shrubs, B. nana, L. palustre, and V. vitis-idaea in the Low Shrub-Heath community of the Mackenzie River Delta uplands.

SITE DESCRIPTION

The study site was situated on uplands along the northwestern shore of Parsons Lake, District of Mackenzie, Northwest Territories, Canada, at 68° 59'N and 133° 34'W (Fig. 1). This is east of the present Mackenzie River Delta, approximately 71 km north of Inuvik and 55 km southwest of Tuktoyaktuk. The gently rolling topography of the region is physiographically in the Morainic Hills subdivision of the Pleistocene Coastland (McKay 1963). Elevations generally are under 75 m and relief ranges up to 50 m. The entire region was glaciated during the last Wisconsin advance (Hughes 1972), with deglaciation occurring before 12,000+/-170 radiocarbon years B.P. (Ritchie and Hare 1971). The area is treeless tundra and is approximately 70 km north of the open boreal forest treeline. Trees, krummholz forms of Black Spruce, Picea mariana, extend to the study area only in relatively well protected sites. The actual study site was a 0.75 ha hilltop plot at 55 m elevation, sloping gently to the northwest.

Vegetation

The plant communities of these uplands east of the Mackenzie Delta have been classified previously by Corhs

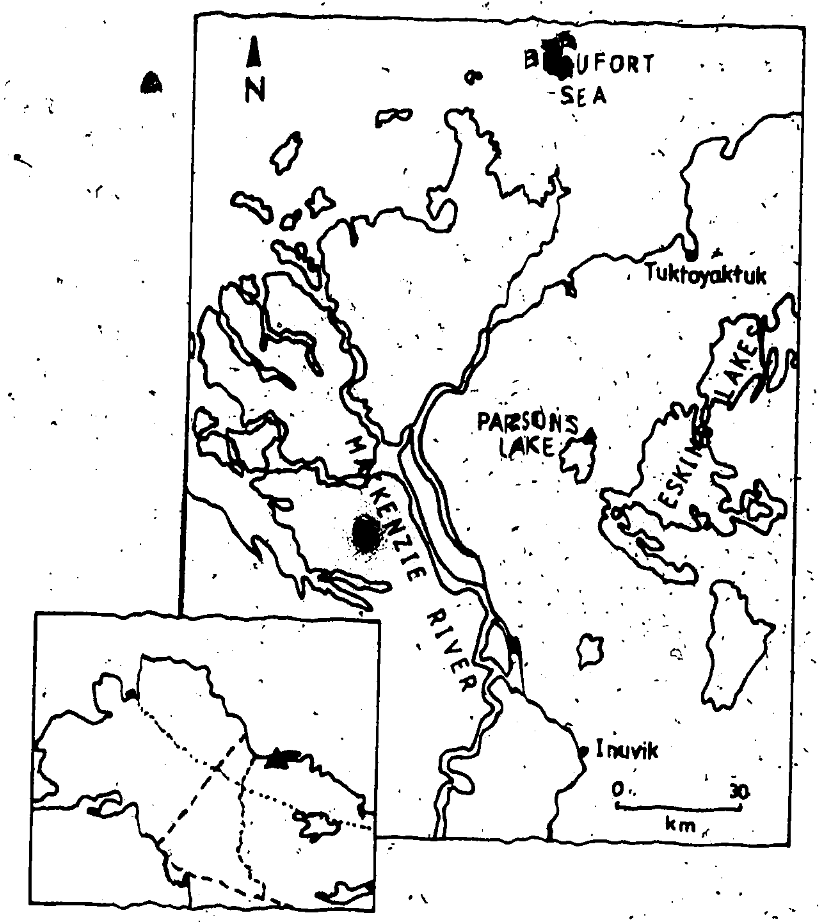


Figure 1. Map of study region. Triangle marks the Parsons Lake study site.

(1974) into five major types on the basis of physiognomy and floristics. All five types were present in the region of the study site. The Tall Shrub-Herb community type contains shrubs >1.5 m in height and is limited to lakeshores and streambanks. *Salix lanata* and *S. alaxensis* provide most of the shrub cover in these communities. The Medium Shrub-Heath type is dominated by shrubs <1.5 m. This type is best developed on slopes which have a deep winter snow pack and late snowmelt. *Alnus crispa*, *Betula nana* subsp. *exilis*, and *Ledum palustre* subsp. *decumbens* are well represented here. The Low Shrub-Heath type with shrubs 35 to 100 cm is similar to the Medium Shrub-Heath type, but occurs more frequently on drier hilltop sites which have less winter snow cover. *Betula nana*, *Salix glauca*, *S. acutafolia*, and *S. pulchra* dominate this community type. Several subgroups of the Herb-Low Shrub-Heath community type occur in the study region, primarily on impeded to well drained sites, or on polygonal patterned ground. The Herb type is represented in the Parsons Lake area by wetland communities dominated by *Carex* spp. and *Eriophorum* spp. Vegetation sampling was carried out in August 1977, to relate the vegetation of the study area to Corn's units.

Methods

Three parallel transects were randomly placed perpendicular to a 100 m baseline and each transect was divided into four parts. Thirty-four 50 x 50 cm (0.25 m^2) quadrats were stratified randomly along the three, quartered transects (ie. three quadrats located in most quarters). Cover of each vascular plant species as well as cover of lichen and bryophyte components were visually estimated to the nearest 1% within each quadrat. Frequency values for all vascular plant species were also calculated. Nomenclature follows Hulten (1968) for vascular plant species.

Results and Discussion

The plant community of the site is classified as a Low Shrub-Heath type, Birch-Heath subgroup according to the scheme of Corns (1974). This community type is typical of most well-drained uplands and slopes in the region north and east of Parsons Lake. Species diversity was low, with less than 20 vascular plant species forming the community. Betula nana, Ledum palustre, and Vaccinium vitis-idaea all occurred with high frequency and cover in this community (Table 1).

These shrub communities contain several recognizable canopy strata. Betula nana dominates the upper canopy, growing to heights of 0.5 m. No Salix pulchra or S. glauca

Table 1. Percent frequency, aerial cover, and presence of species in sampled quadrats (T=0-0.5%, n=34).

Species	Mean Cover	Range	Frequency
Betula nana	39.9	0-85	94
Ledum palustre	14.5	0-45	85
Vaccinium vitis-idaea	23.0	T-30	100
Empetrum nigrum	6.5	0-30	79
Arctostaphylos rubra	4.8	0-51	38
Petasites frigidus	1.4	0-10	50
Pyrola secunda	1.0	0-6	32
Pyrola grandiflora	T	0-5	38
Saussarea angustifolia	2.0	0-8	82
Oxytropis maydelliana	T	0-<1	3
Rosa acicularis	T	0-5	9
Stellaria longipes	T	0-T	53
Pedicularis kanei	T	0-5	3
Carex bigelowii	2.8	0-10	77
Arctagrostis latifolia	<1.0	0-7	50
Poa arctica	T	0-<1	15
Calamagrostis canadensis	1.3	0-9	88
Lichens	26.6	2-74	100
Mosses	3.9	0-12	94
Dead Material	26.9	4-80	100

occurred in the study area, and they were infrequent in the immediate area. A subcanopy is formed by L. palustre, although its distribution is less uniform than that of B. nana. A third stratum near ground level is dominated by V. vitis-idaea with other herbaceous and graminoid species having lesser importance. Cover at ground level consists primarily of such fruticose lichens as Cetraria cucullata, and Cladina arbuscula, along with decomposing organic material. Bryophytes were infrequent and of limited cover, except on the moist organic material of some interhummock troughs.

Soils

Methods

A pit which included two soil hummocks and the trough area between was dug to permafrost in late August, 1977. A soil profile description was made from the exposed profile with the classification following the Canadian system (Canada Dept. Agriculture 1978).

Results and Discussion

The ground surface of the site was covered with a matrix of earth hummocks. Similar hummocks cover approximately 95% of the landscape in the lowlands around the Mackenzie Delta (Tarnocai and Zoltai 1978) and are cryogenic in origin. The hummocks were formed by displacement of mineral and organic materials due to cryostatic pressures formed during fall freezeup. Soil characteristics of texture, temperature, and moisture, in combination, determine the degree of hummock formation (Tarnocai and Zoltai 1978). Radiocarbon studies indicate these surface features probably formed 3,000 to 5,000 yr B.P. (Zoltai et al. 1979) during a colder climatic period (Ritchie and Hare 1971). Although such hummocks are associated with dynamic soil processes, Zoltai (1975) and MacKay and MacKay (1976) suggest that they have been relatively stable for at least two decades. No evidence of surficial disturbance from any cryoturbation was observed at the study site. Vegetation formed a nearly complete cover, with little bare soil present.

The distance between hummock centers on the study site ranged from 0.75 to 1.5 m and the hummock tops were approximately 0.5 m higher than the troughs between adjacent hummocks (Fig. 2). The core of the hummocks was composed primarily of fine grained minerals, clays and silts, overlain by a thin layer of organic material (Table 2). Trough areas between hummocks are usually filled with organic matter extending down to the base of the active

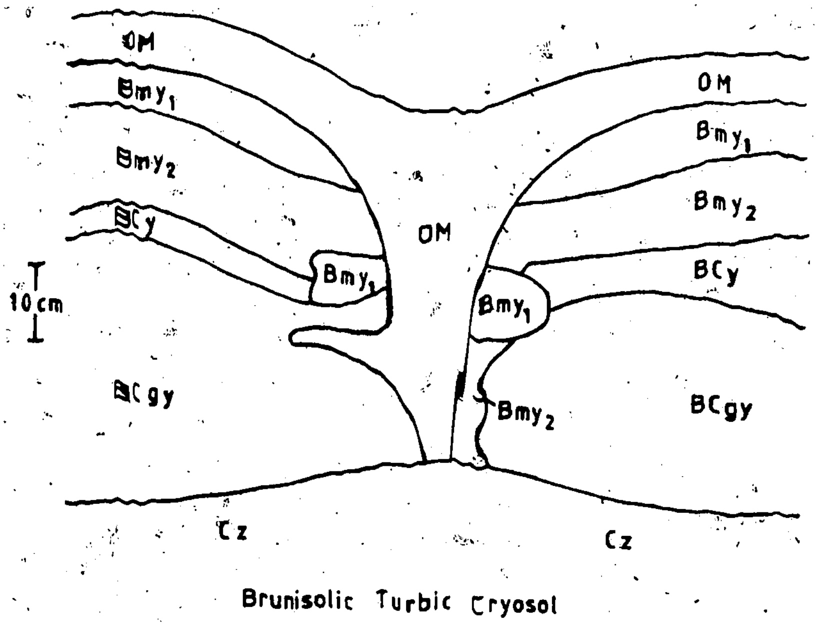


Figure 2. Representative soil profile of the study site, including sections of a soil hummock and an inter-hummock trough. Symbols representing soil horizons are after the Canadian Soil Classification System (1978). y indicates cryoturbated layers and z indicates frozen horizons.

Table 2. Representative soil profile description of a soil hummock, Parsons Lake, N.W.T. Color notation after Munsell (1971).

Horizon	Depth (cm)	Description
OM	0-10	Very dark brown (10YR 2/2 m), very dark grayish brown (10YR 3/2 d) semi-decomposed organic matter; abundant very fine, random fine, plentiful medium, and few coarse roots; amophous boundary; 3-10 cm thick; pH 4.8
Bmy$_1$	4-12	Very dark grayish brown (10YR 3/2 m), brown-dark brown (10YR 4/3 d) clay loam; fine granular; friable when moist, slightly plastic when wet; plentiful very fine and random fine roots; amorphous boundary; 2-4 cm thick; pH 4.6
Bmy$_2$	6-12	Dark brown (10YR 3/3 m), pale brown (10YR 6/3 d) clay loam; coarse granular; friable; plentiful fine and very fine roots; amorphous boundary; 5-8 cm thick; pH 4.9
BC$_y$	13-20	Dark brown (10YR 3/3 m), pale brown (10YR 6/3 d) clay; amorphous; sticky, very plastic; 1-8 cm thick; pH 5.9
BC$_{gy}$	16-35	Very dark grayish brown (10YR 3/2 m), brown (10YR 5/3 d) clay; amorphous; sticky, very plastic; 25-35 cm thick; pH 5.6

layer. Involutions of both organic matter and mineral horizons along the sides of the hummocks are evidence of cryoturbation sometime in the past. The permafrost surface is a mirror image of the ground surface, with greatest thaw occurring beneath the mineral cores. Soils of the site are classified as Brunisolic Turbic Cryosols. The BCgy horizon reflects the effect of impeded drainage caused by the permafrost.

Climate

Parsons Lake is at the interface of three major climatic zones: Marine Tundra occurring to the north, Taiga to the south and Continental Tundra to the east (Burns 1973). The climate of the region is affected by several different air masses which dominate at different times of the year. Continental Arctic air dominates the region in winter, but retreats in summer as solar radiation increases and pools of meltwater form on the surface of the arctic ice. Weather of the growing season is modified, primarily by cold maritime arctic air masses (Burns 1973). Bryson (1966) and Larsen (1971) have suggested a correspondence between the location of these air masses and position of the boreal forest.

Long cold winters with short cool summers, both associated with low precipitation, are typical of the region (Fig. 3). Inuvik's mean July temperature of 13.3 $^{\circ}$C and January mean of -29.4 $^{\circ}$C would be similar to those of the Parsons Lake area because of similarities in elevation. Precipitation, averaging 260 mm at Inuvik, would also be roughly similar at Parsons Lake.

Methods

Meso- and microclimate were monitored on the study site during June, July, and August of 1977 and 1978. Air temperature and relative humidity were measured continuously with a Belfort hygrothermograph (Model 5-594) housed in a louvered, white shelter at ground level. The instrument was calibrated weekly with a mercury in glass thermometer and a sling psychrometer.

Soil and air temperatures were measured hourly with a Grant multipoint recorder (Model D). Air temperature probes with self-ventilating shields were located at +1.5, 0.25, 0.05, and 0.01 m. In 1977, soil probes were located within a soil hummock at -0.05, -0.10, -0.15, and -0.20 m. In 1978, soil probe installations were changed to -0.05 and -0.10 m in a soil hummock, and -0.05 and -0.10 m in a trough area between hummocks.

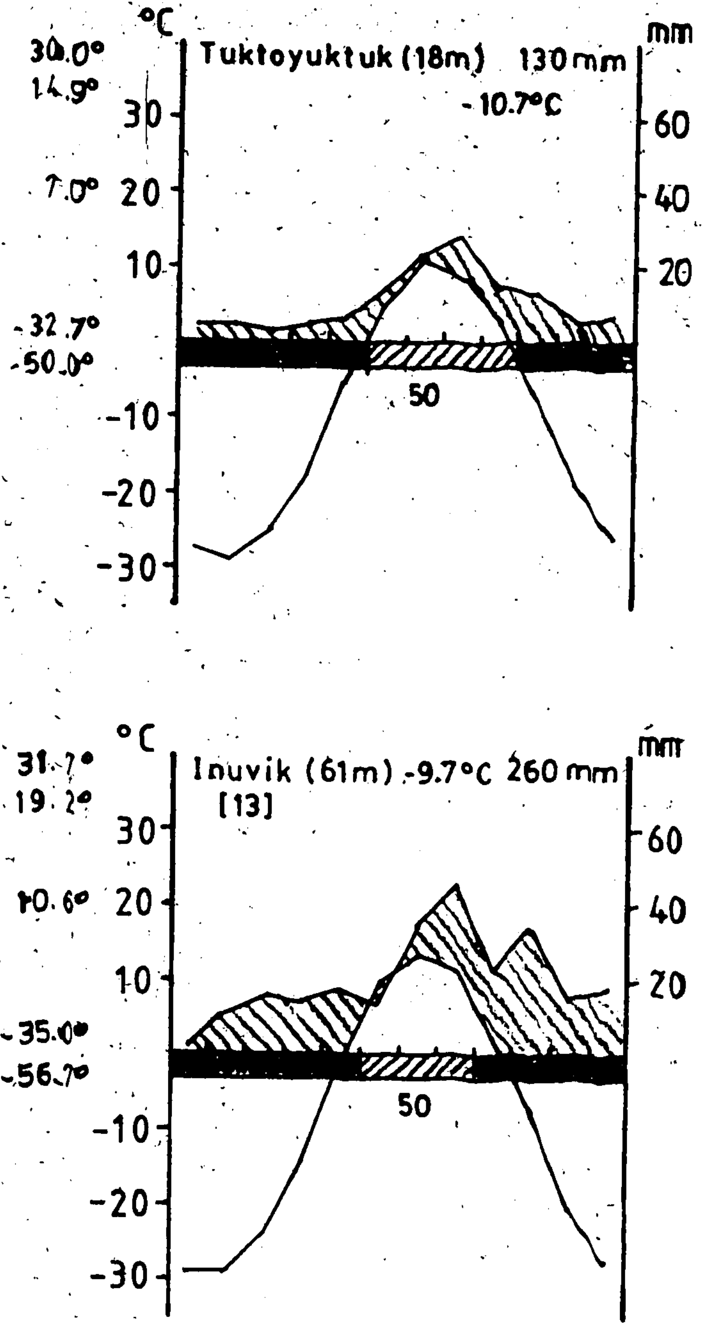


Figure 3. Climadiagrams for Inuvik and Tuktoyaktuk, N.W.T., after Walter (1973). Mean annual temperature -10.7°C; total annual precipitation 260 mm; years of observation 13; upper line is monthly precipitation; lower line is mean monthly temperature; frost-free growing season 50 days; solid bar is months with mean minimum temperature below 0°C; bar with diagonal lines marks months with absolute minimum below 0°C; other diagonal lines mark relatively humid season. Left column of temperatures in descending order; absolute maximum, mean maximum warmest month, mean diurnal temperature range, mean minimum coldest month, absolute minimum.

Precipitation was measured with a Taylor Clear Vu rain gauge (Model 2701) with the opening 0.25 m above the shrub layer.

Wind speeds were measured at 1 m above ground level using a Belfort three-cup totalizing anemometer (Model 5-349A) that was read daily.

Incoming shortwave radiation was recorded with a Belfort actinograph (Model 5-3850) located on top of the instrument shelter.

Soil moisture was determined weekly at -0.05, -0.10, and -0.20 m, with three samples per depth, using gravimetric techniques. In 1977, samples were collected from hummocks, while samples were collected from both hummocks and troughs in 1978.

In 1978, dawn stem xylem tensions for Betula nana spp. exilis, Ledum palustre subsp. decumbens, Vaccinium vitis-idaea were measured weekly using a Scholander type pressure bomb to evaluate the amount of water stress experienced by the plants. Shoots of random plants were clipped and placed in a closed, humidified chamber until they could be tested.

The active layer depth was measured weekly with a 1.3 cm diameter steel probe at 100 points randomly placed along three 30 m transects. The same 100 points were measured at each sampling interval in both 1977 and 1978.

Results and Discussion

Temperature

Accumulated degree days (0°C base) during the primary growing months of June, July, and August suggest different conditions were present in the two years of the study (Fig. 4). The 960 degree days accumulated at the study site in 1977 were probably representative of an average growing season. Growing season degree days at Inuvik and Tuktoyaktuk in 1977 are midpoint in the range of degree days accumulated in the years 1970 to 1979 (Table 3). However, the 771 degree days at Parsons Lake in 1978 represented a relatively cool year as indicated by the second lowest accumulation in the 10 yr time span at both Inuvik and Tuktoyaktuk. The major differences in rate of accumulation between the two years occurred during the months of June and August. July temperatures were similar both years (Fig. 4).

Five-day and monthly mean air temperatures at 150 cm reflect the same pattern shown in degree day data (Fig. 5,

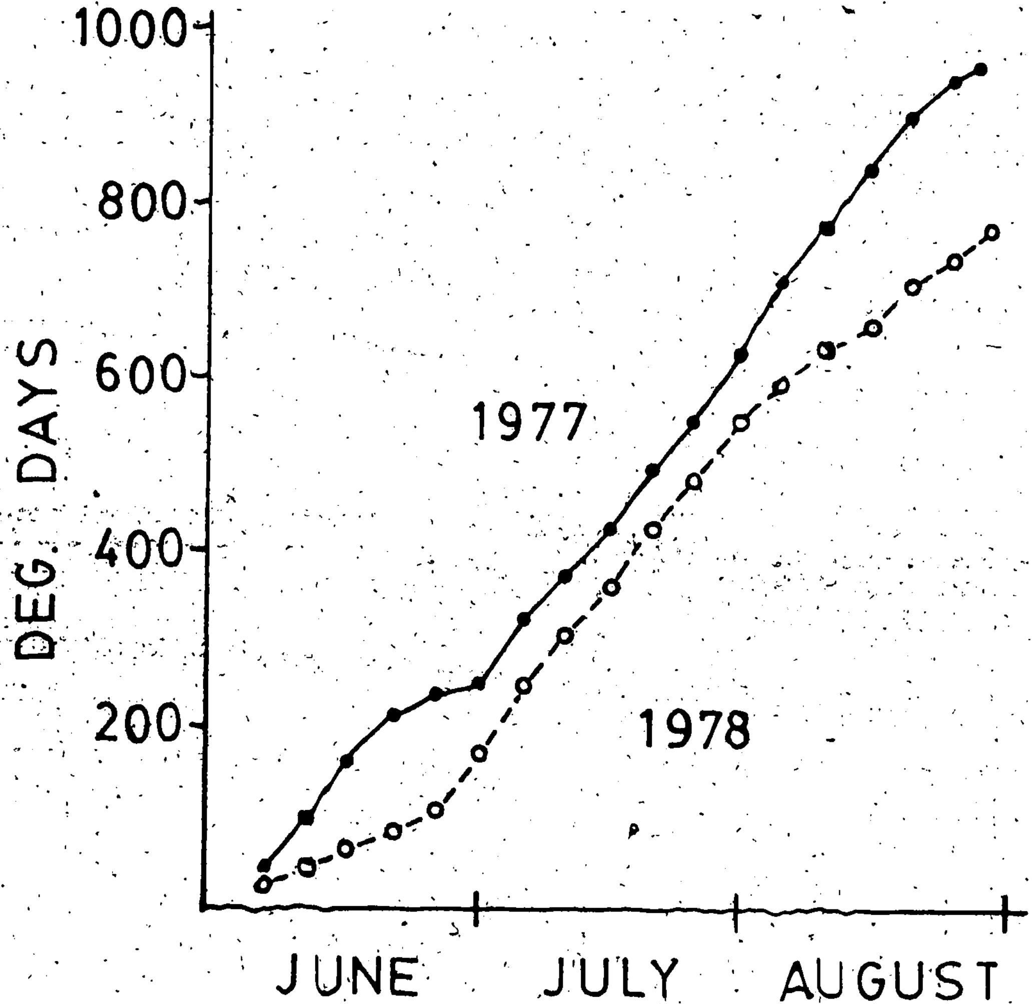


Figure 4. Degree days (0°C base) accumulated in 1977 and 1978 at the Parsons Lake study site.

Table 3. Degree day sums (0° C base) June 1 to August 30, 1970-1979.

Year	Inuvik*	Tuktoyaktuk*	Parsons Lake
1970	1107	743	
1971	1068	821	
1972	1139	795	
1973	1107	849	
1974	930	585	
1975	1038	751	
1976	1099	849	
1977	1071	829	960
1978	944	640	771
1979	1275	953	
Mean	1078	782	866

* Data from Environment Canada

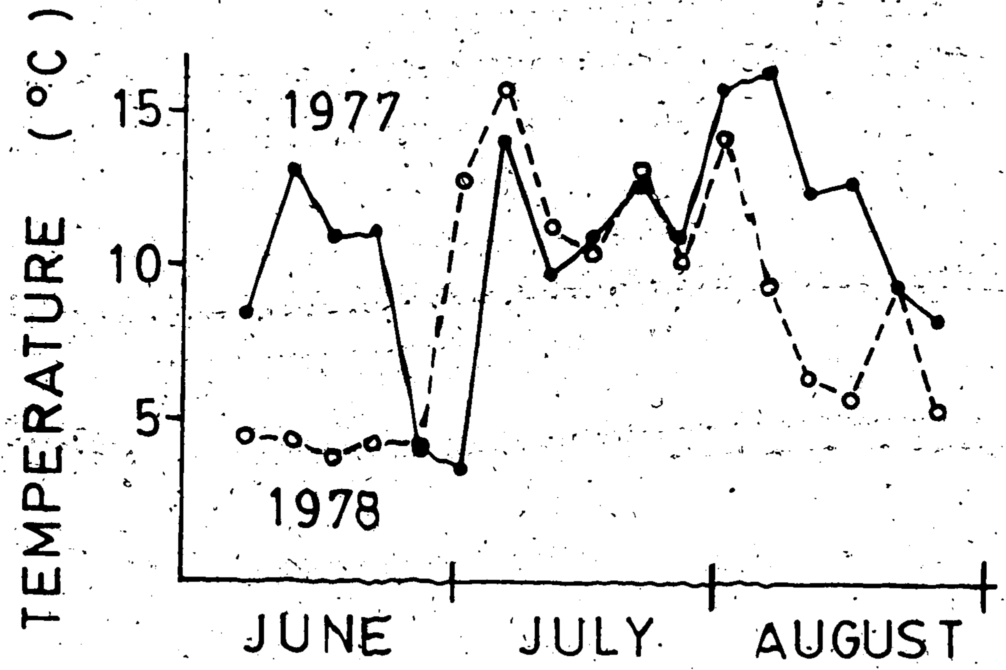


Figure 5. Five-day air temperature means 150 cm above the ground at the study site. Means calculated from hourly measurements.

Table 3). The low temperatures in June and August of 1978 represented cooler-than-average conditions. This is also shown by the lower-than-average values recorded in Inuvik at the same time.

Temperatures outside of the active period of growth can also affect the growth performance of a plant through such indirect means as control of snow melt (Billings and Bliss 1959). A cool May (4° C below normal at Inuvik) in 1978 delayed snow release by about two weeks and therefore shortened the effective growing season experienced by the plants. Snow release on the study site had been completed at some time before May 30, 1977, when it was first viewed, but was not completed until June 4 in 1978.

The July 1977 mean monthly, mean maximum, and mean minimum temperature profiles above and below ground (Fig. 6, Table 4) are representative of general profile patterns found in the three months of the growing season in both years. The mean monthly temperature in the boundary layer (1 cm) was slightly more than 1° C warmer than at 150 cm; 125 cm above the surface of the shrub layer. A larger boundary layer effect was observed in mean maximum temperature values. The mean maximum temperature at 1 cm was more than 7° C higher than at 150 cm and more than 3° C higher than at 5 cm. However, these data were collected on a relatively open

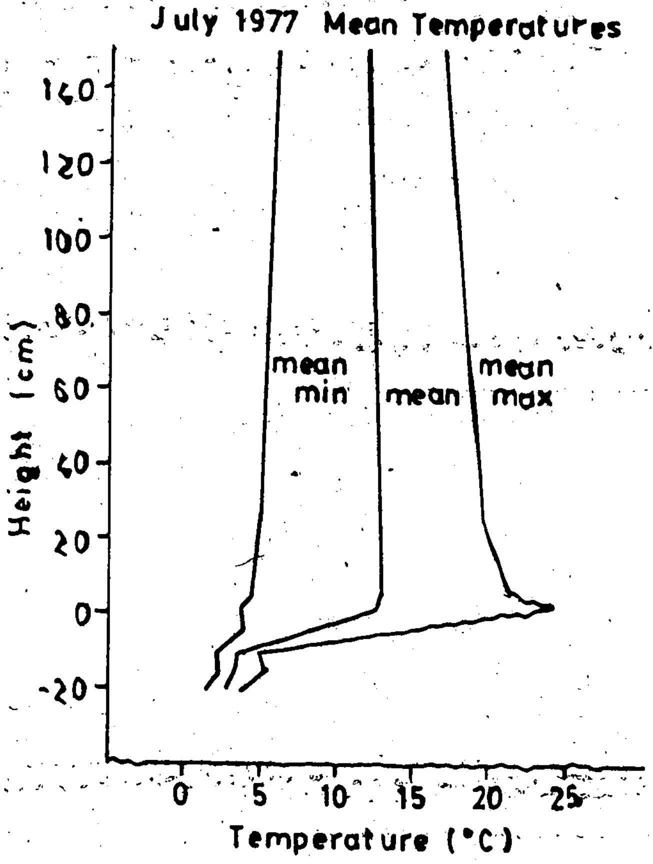


Figure 6. Representative mean, mean maximum, and mean minimum air and soil temperature profiles at the study site. Profiles of July, 1977.

Table 4a. Monthly mean, mean maximum, and mean minimum air and soil temperatures at the Parsons Lake study site in 1977. Height in cm. 0 = groundlevel.

		June		July		August	
	Ht.	°C	SE	°C	SE	°C	SE
Mean	150	7.8	1.4	11.5	0.8	11.1	0.9
	25	8.5	1.5	12.5	0.8	11.3	0.9
	5	8.8	1.5	12.8	0.8	11.0	0.9
	1	8.8	1.5	12.6	0.7	10.7	0.8
	-5	3.6	0.5	6.9	0.4	6.6	0.4
	-10	2.1	0.3	3.7	0.2	4.1	0.3
	-15	0.3	0.1	3.8	0.6	3.8	0.2
	-20	0.3	0.1	2.6	0.5	3.0	0.2
Maximum	150	11.9	1.9	16.9	1.1	16.5	1.1
	25	13.6	2.1	19.7	1.1	17.9	1.2
	5	14.4	2.2	20.8	1.0	17.8	1.2
	1	15.5	2.3	23.9	1.1	19.0	1.2
	-5	6.1	0.8	10.6	0.6	10.1	0.6
	-10	3.4	0.5	5.1	0.3	5.5	0.5
	-15	1.7	0.2	5.5	0.9	4.8	0.5
	-20	0.9	0.1	3.7	0.7	3.6	0.2
Minimum	150	3.2	0.7	5.9	0.5	5.7	0.6
	25	3.1	0.7	5.2	0.5	4.9	0.6
	5	2.9	0.7	4.5	0.4	4.0	0.7
	1	2.8	0.6	3.9	0.4	3.5	0.6
	-5	1.7	0.2	3.9	0.3	3.6	0.3
	-10	0.9	0.2	2.4	0.2	2.9	0.2
	-15	0.2	0.2	2.3	0.3	3.1	0.3
	-20	0.1	0.1	1.6	0.2	2.6	0.2

Table 4b. Monthly mean, mean maximum, and mean minimum air and soil temperatures at the Parsons Lake study site in 1978. Height in cm. 0 cm = groundlevel T = trough H = hummock.

		June		July		August	
	Ht.	°C	SE	°C	SE	°C	SE
Mean	150	4.8	0.7	12.6	0.7	8.1	0.8
	25	5.8	0.7	12.8	0.7	8.5	0.8
	5	6.4	0.8	13.7	0.6	8.3	0.8
	1	6.5	0.6	12.7	0.5	7.8	0.7
	-5T	1.7	0.2	5.2	0.2	4.2	0.3
	-10T	0.7	0.1	4.0	0.2	3.6	0.3
	-5H	2.0	0.2	6.2	0.2	4.7	0.3
	-10H	1.4	0.1	4.0	0.1	3.5	0.2
Maximum	150	9.8	1.0	19.0	1.0	12.6	1.1
	25	12.9	1.0	20.6	0.9	14.4	1.2
	5	14.5	1.2	22.2	0.9	15.6	1.2
	1	16.1	1.2	22.4	0.9	15.1	1.2
	-5T	3.2	0.3	7.2	0.2	5.6	0.4
	-10T	1.4	0.2	5.6	0.2	4.8	0.4
	-5H	3.6	0.4	9.0	0.5	6.8	0.5
	-10H	2.3	0.2	5.4	0.2	4.7	0.3
Minimum	150	0.4	0.4	6.3	0.5	3.7	0.5
	25	0.3	0.4	5.6	0.4	2.9	0.5
	5	0.0	0.4	4.7	0.5	1.8	0.5
	1	0.1	0.3	4.8	0.4	2.4	0.5
	-5T	0.6	0.2	3.3	0.2	2.9	0.3
	-10T	0.1	0.1	2.6	0.2	2.5	0.2
	-5H	0.5	0.1	3.9	0.1	3.0	0.3
	-10H	0.5	0.2	2.8	0.2	2.6	0.2

hummock top and the boundary layer effect would undoubtedly have been more pronounced underneath the canopy of Betula nana, resulting in warmer conditions at the soil surface.

Diurnal fluctations of soil temperature decreased in amplitude with increasing depth and increasing proximity to the upper surface of the permafrost table (Fig. 6). This is reflected in the decreasing range between mean maximum and mean minimum temperature with increasing depth. The decrease in soil temperature was most rapid in the first 10 cm below the soil surface.

Radiation

At this latitude (69° N, Inuvik), total annual shortwave radiation is 3374 MJ m^{-2} (Environment Canada); however, only 51% of this is received in the three months that constitute the active growing season of tundra plants (Fig. 7). Of the remaining radiation, 40.5% is received prior to snowflush and 8.5% is received after active growth has stopped (Environment Canada). Mean monthly shortwave radiation at this latitude peaked in June, generally corresponding with the melting of the snow cover, and initiation of plant growth. After this peak, in the two years of the study, the radiation received at the study site decreased in roughly a linear fashion (Fig. 8).

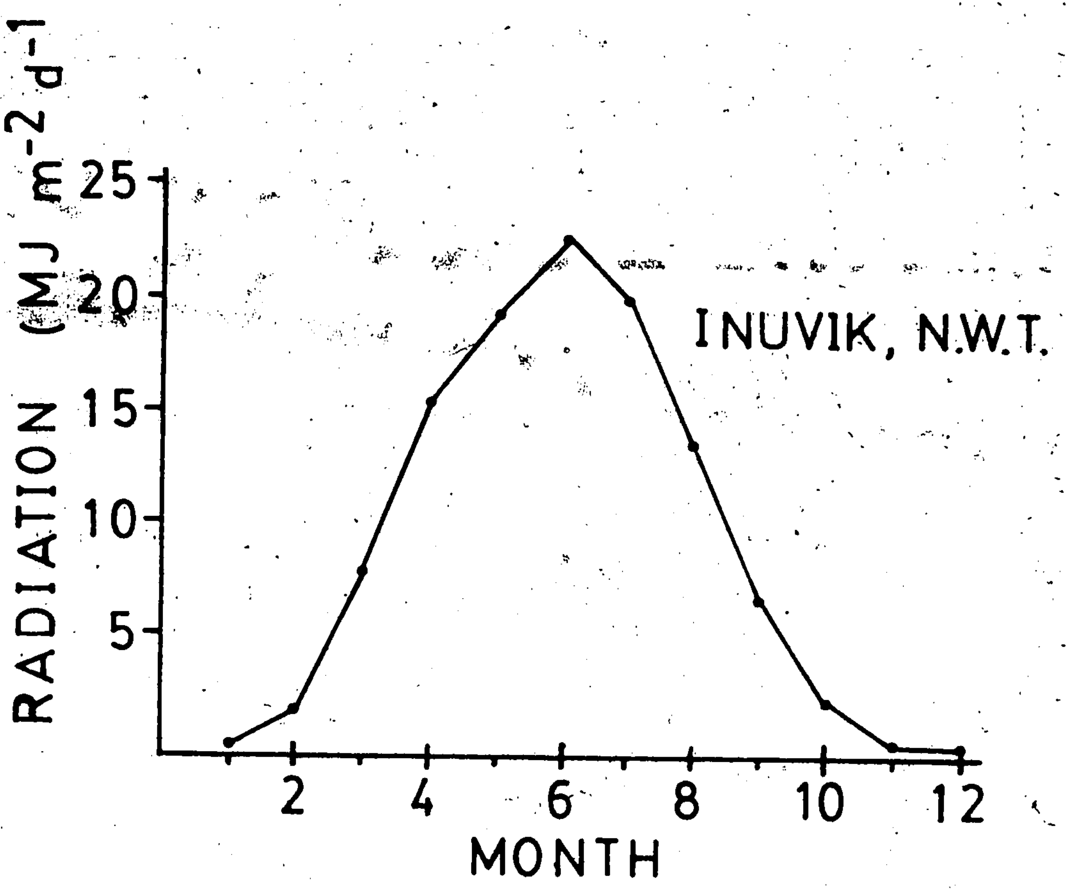


Figure 7. Monthly means of total daily short-wave radiation at Inuvik, N.W.T. Data from Environment Canada.

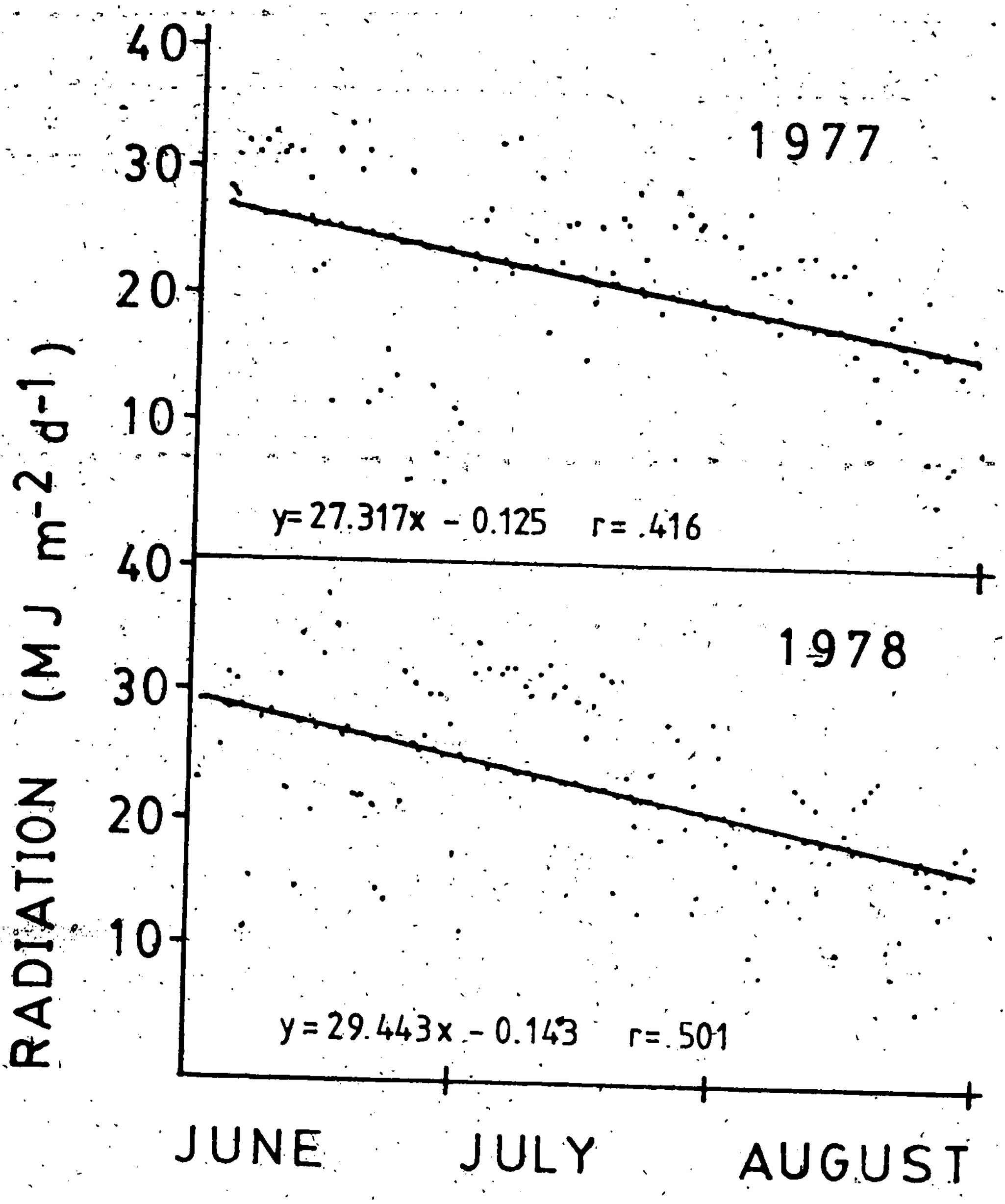


Figure 8. Daily total short-wave radiation at Parsons Lake study site in June, July, and August, 1977 and 1978.

Mean daily irradiance at Inuvik during June, July, and August is 18.8 MJ m^{-2}. Irradiance at Parsons Lake was from 2.9 MJ m^{-2} d^{-1} (August, 1977) to 6.6 MJ m^{-2} d^{-1} (June, 1978) higher. The difference in the two sites may have been a product of fog and cloud patterns associated with the Mackenzie River channel which passes near Inuvik.

Irradiance patterns at Parsons Lake for 1977 and 1978 are shown in Fig. 9 and Table 5. Cloudy and rainy weather in 1977 reduced incoming radiation, particularly in June.

Precipitation

Accumulation of measureable precipitation was greater in June, July, and August of 1977 (130 mm) than in the same months of 1978 (70 mm). In 1977, over 92% of the summer precipitation was evenly distributed between June and August, with July remaining comparatively dry. Precipitation in 1978 was more evenly distributed over the three months, with no single month significantly wetter or drier than the others (Fig. 10). Rainfall patterns at Parsons Lake differed in some respects from those recorded at Inuvik. While the amount of rainfall received daily at the two sites had a positive correlation (r=.55), the occurrence of rainfall events was negatively correlated (r=-.25). Inuvik and Parsons Lake often differed in timing

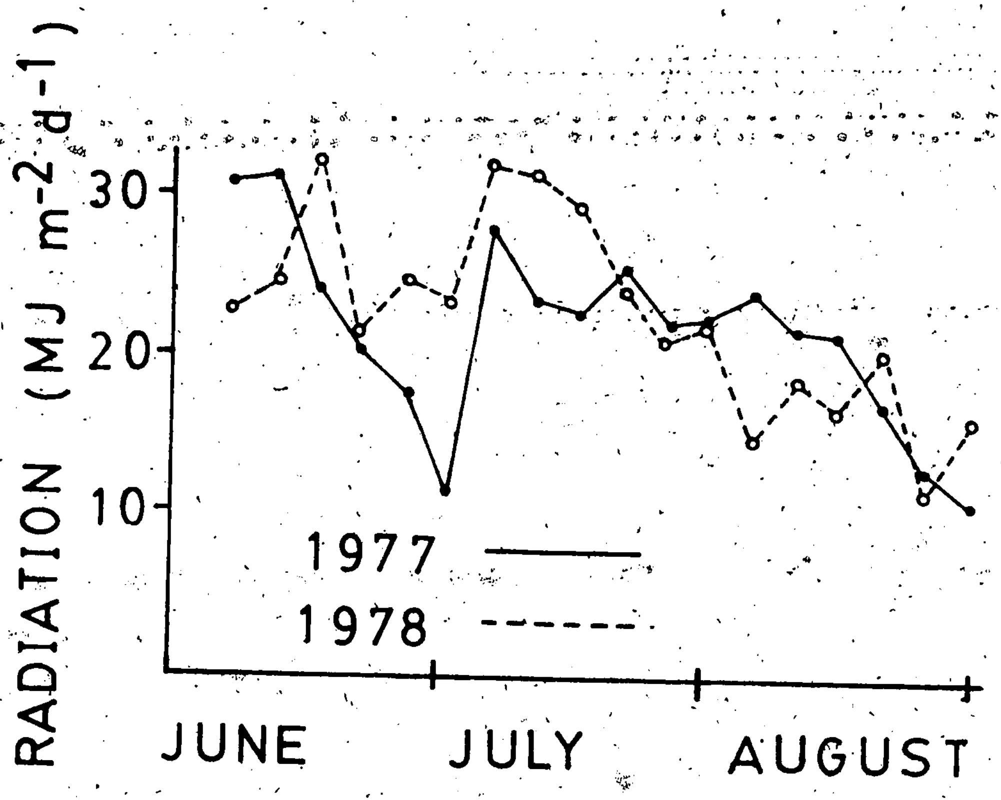


Figure 9. Five-day means of total daily short-wave radiation at study site in 1977 and 1978.

Table 5. Mean daily irradiance (MJ m^{-2}) at Parsons Lake, N.W.T. Parenthetical values are deviations from the 10 year mean at Inuvik (*n=28, ** n=29).

Month	1977	1978
June	22.97 *	25.65 (-3.53)
July	23.65 (+0.62)	26.09 (+0.89)
August	17.70 ** (+1.27)	16.70 (-0.70)

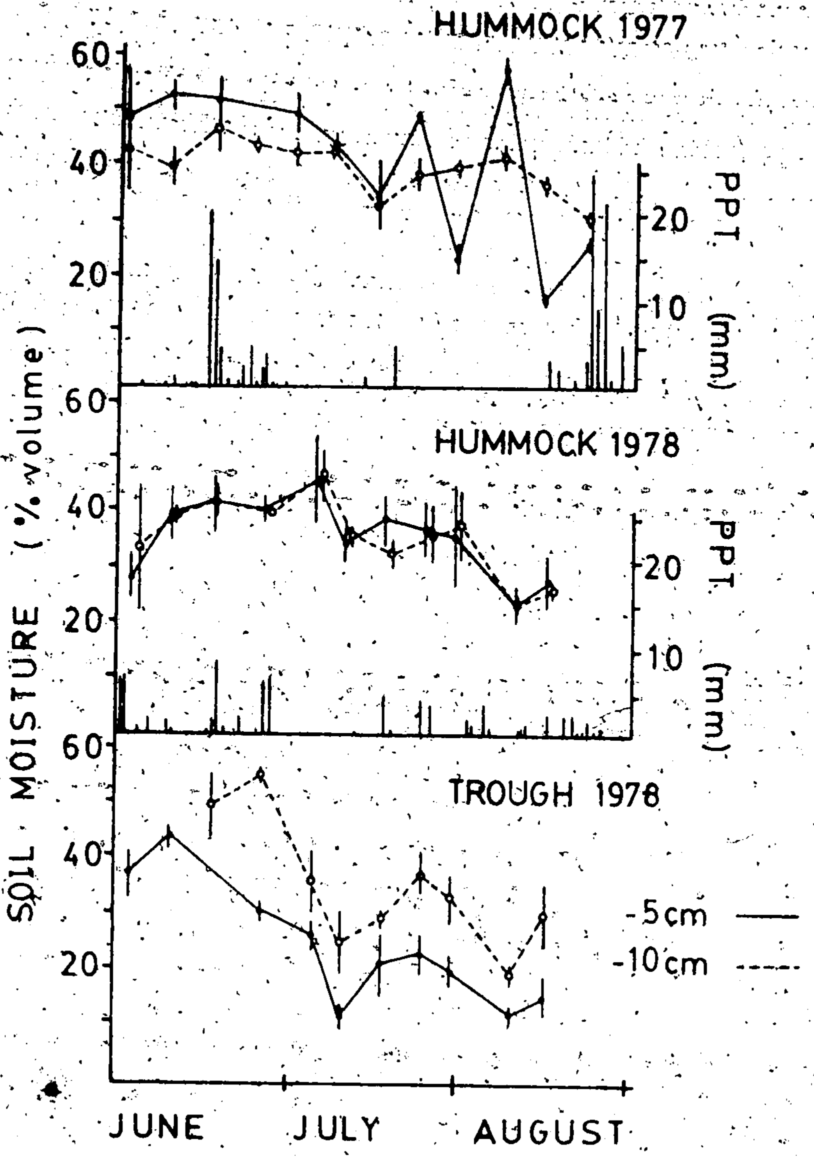


Figure 10. Precipitation and weekly mean soil moisture (±SE) of hummocks and inter-hummock troughs at -5 and -10 cm in 1977 and 1978.

of low accumulation precipitation events, with Inuvik recording many trace level events on days when Parsons Lake had none. These small amounts of precipitation at Inuvik may result from its closer proximity to the Richardson Mountains or its position near the Mackenzie River channel. Heavier rainfalls appeared to be more regional in nature, and both recording stations reflected these major events.

Though precipitation at Parsons Lake may not exactly reflect patters at Inuvik, June accumulations in Inuvik were three to five times greater than normal in both years of the study, a large enough deviation to suggest wetter conditions probably existed throughout the region. However, this additional rainfall may have had little effect on the plants. In June, permafrost near the soil surface impedes drainage of meltwater from winter precipitation, and soils normally have high water contents (Fig. 10).

Water Relations

Xylem tensions for all three species generally remained above 800 kp and below 2500 kp throughout June and July 1978 (Fig. 11). Xylem tensions of the species decreased in August, remaining below 1000 kp. _Vaccinium_ _vitis-idaea_ had higher tensions in June and July than _L_. _palustre_ or _B_. _nana_, but in August xylem tensions of all three species were

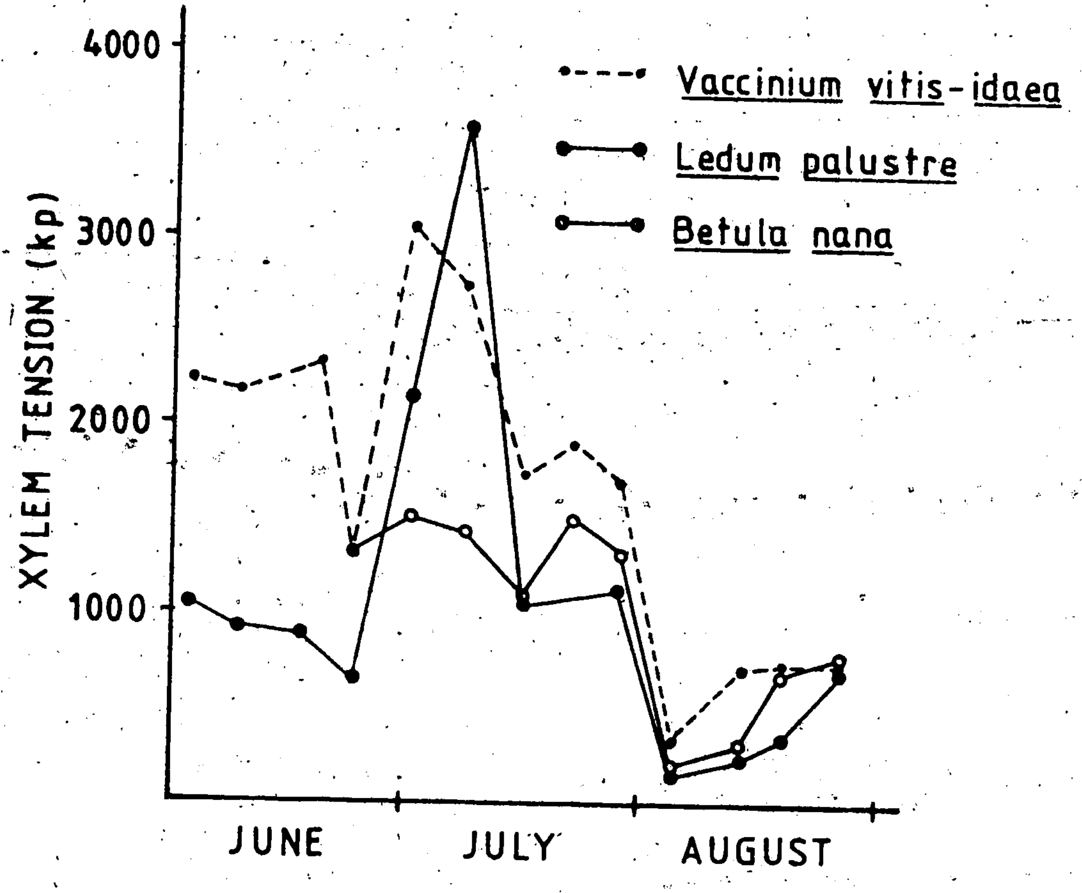


Figure 11. Mean weekly dawn xylem tensions of Betula nana, Ledum palustre, and Vaccinium vitis-idaea in June, July, and August, 1978.

relatively similar. Low values in *L. palustre* and *V. vitis-idaea* in early July were associated with depressed soil moisture levels at the same time in inter-hummock troughs, the primary rooting region for the plants. *Betula nana* did not exhibit this early July rise in xylem tension. *Ledum palustre* and *V. vitis-idaea* tend to have shallower roots than *B. nana* and may have experienced lower soil water potentials than the more deeply rooted deciduous shrub.

Similarly low water potentials have been reported for other arctic species (Oberbauer and Miller 1979,1981) and particularly for dwarf evergreen shrubs and cushion plants (Courtin and Mayo 1975). Low correlations between growth and plant water potentials led Oberbauer and Miller (1982) to conclude that water stress, while present at times in Alaskan arctic plants, was not a major limiting factor to growth. Courtin and Mayo (1975) and Miller et al. (1978) came to similar conclusions.

Wind

The hilltop study site was nearly always windy, with both calm air and heavy winds relatively rare. Wind speeds averaged 3.1 $m\ s^{-1}$ in 1977 and 2.8 $m\ s^{-1}$ in 1978. Since these data were collected 0.75 m above the vegetation canopy, wind speeds could be expected to be significantly less within the shrub strata.

Active Layer

Differences in June air temperatures in the two years of the study were also reflected in the differential melt rates of the active layer. Fig. 12 shows the thawed portion of the active layer was 30% larger at the end of the relatively warm June of 1977 than at the same point after the cool spring of 1978. Depth of thaw was nearly identical by the middle of July in both years, however, and remained so through the remainder of the growing season.

The active layer is considerably deeper under hummock tops than in the troughs between hummocks (Fig. 13). The active layer in hummocks also develops more rapidly in the spring than in troughs. The differences in thaw patterns are probably related to thermal conductivity and heat flux differences between hummock tops and troughs (Crampton 1977, Black and Bliss 1980). Thermal conductivity is higher in the mineral core of the hummocks than in the organic matter in the troughs. Tarnocai and Zoltai (1978) found trough areas of earth hummocks were the coldest portion of the hummocks and temperatures decreased more rapidly with depth in the troughs than on hummock tops.

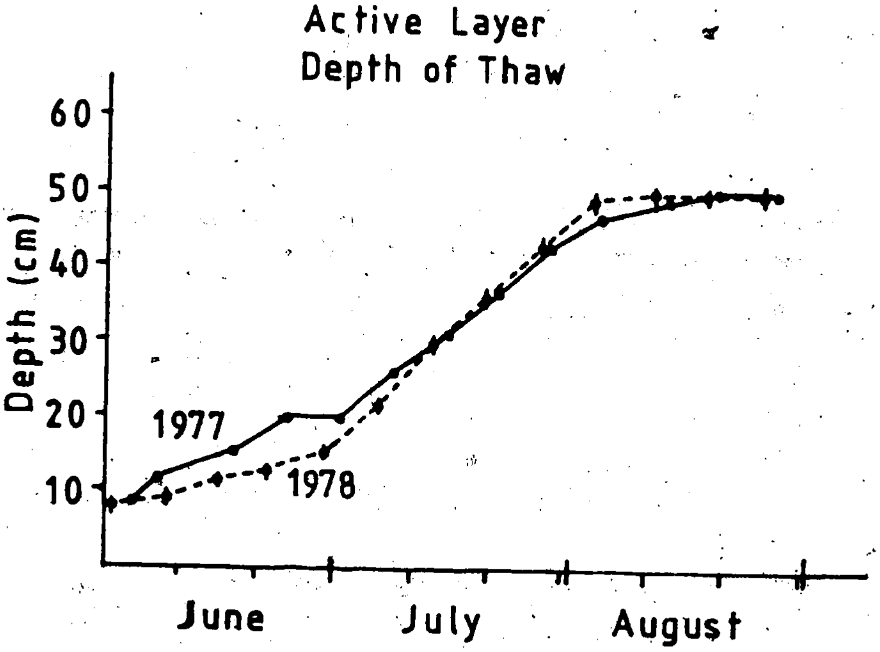


Figure 12. Mean weekly active layer thickness (±SE) in 1977 and 1978.

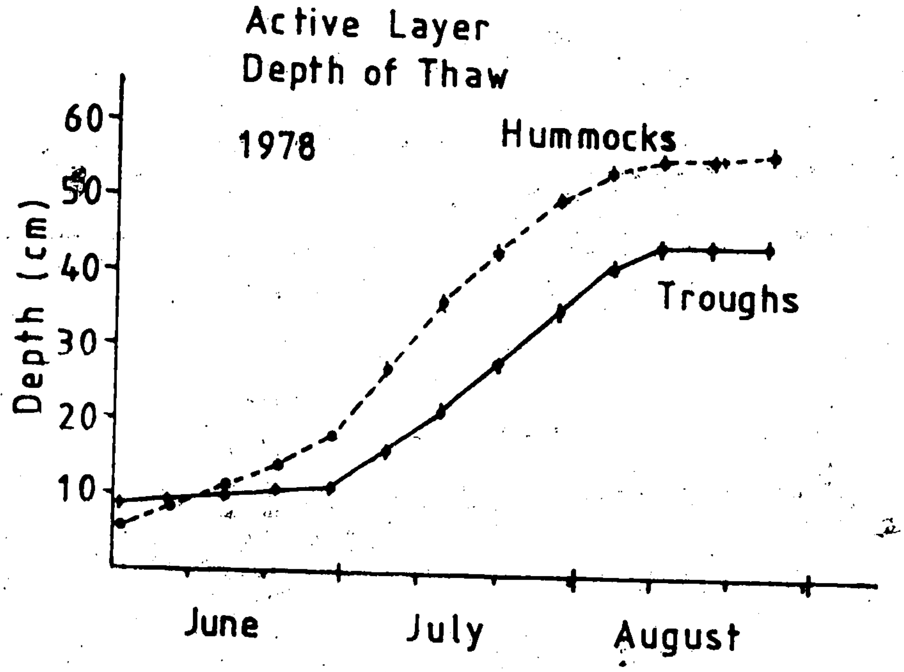


Figure 13. Mean weekly active layer thickness (±SE) in hummocks and inter-hummock troughs in 1978.

The immediate influence of active layer depth on plants of the study site is related to its effect on soil temperatures and length of time the soil is thawed. The temperature of the rooting environment will, in part, be determined by the proximity of the frozen layer below. The majority of plant roots are in that section of the active layer that melts out earliest.

Although the rooting zone becomes ice-free very quickly, there can be significant differences in the melt rate from year to year. Twelve additional days were required to melt the top 15 cm, the prime rooting zone, in the cool spring of 1978 compared to the more normal spring in 1977. This difference in melt rates would have been greater if only trough areas, where most roots grow, had been compared. This lag of 12 days is a significant part of the short growing season experienced by these plants.

THE PLANTS - DISTRIBUTION AND PHENOLOGY

Descriptions of the three species are from Hulten (1968), Porsild and Cody (1980) and my own observations.

Betula nana L. subsp. exilis (Sukatsch.) Hult.

Betula nana subsp. exilis, hereafter referred to as B. nana, is a deciduous dwarf shrub and a member of the Betulaceae. The shrub birches of northern North America are a taxonomically confusing group, with frequent and common introgressive hybridization between adjacent taxa (Hulten 1968). The common hybridization between B. glandulosa Michx., and B. nana in the MacKenzie Delta region makes stands of pure species difficult to find or recognize. Although other names have been applied to the shrub birch complex of the area (Wiggins and Thomas 1962, Vierick and Little 1972, Porsild and Cody 1980), B. nana will be used in this study to agree with other recent ecological work in the Mackenzie Delta area (Janz 1973, Haag 1974, Black and Bliss 1980).

The distribution of B. nana is circumboreal and amphi-beringian, with the range extending to the southwestern coast of Greenland and to northeastern Siberia (Fig. 14). Its habitat in arctic North America ranges from

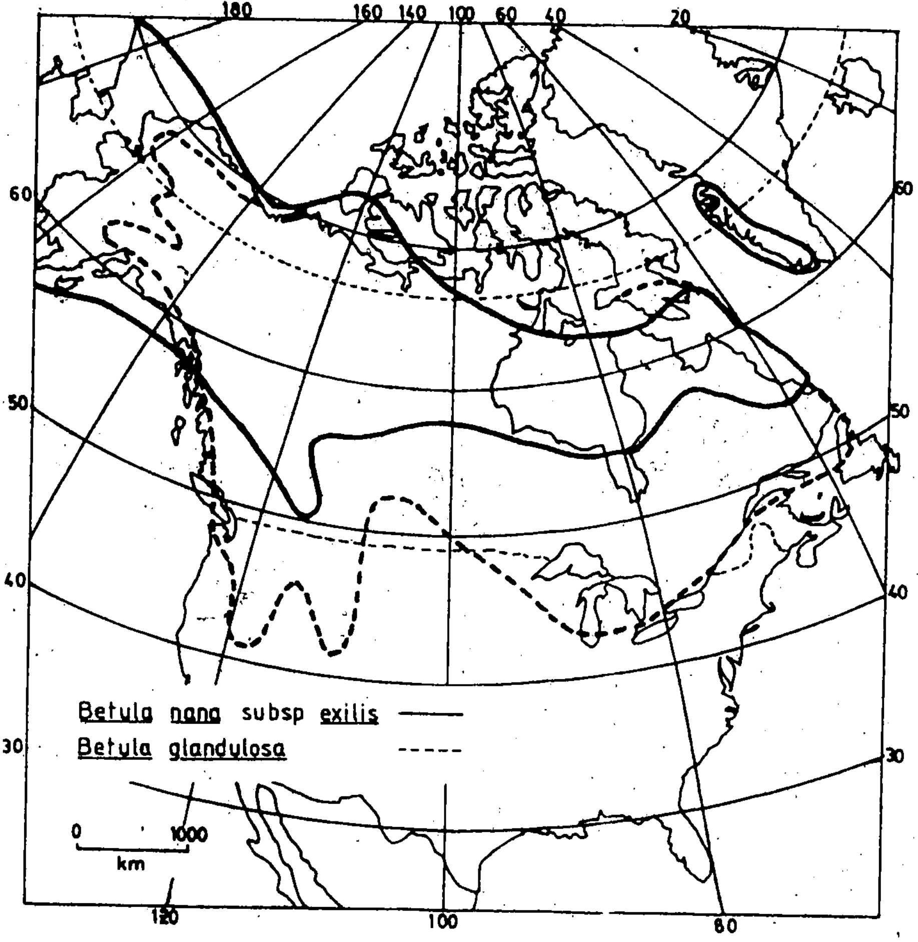


Figure 14. North American distributions of Betula nana subsp. exilis and Betula glandulosa according to Hulten (1968).

poorly or moderately drained upland tundra, to wet and boggy marshes. In the study region, B. nana is found in greatest abundance and cover on moderately drained, convex, hummocky slopes with winter snow cover adequate to cover the plants. The study site had better development of the species than in most sites in the region.

The plants are decumbent to upright, and generally less than 1.5 m tall. Basal stem diameters rarely exceed 4 cm. Young stems are covered with resin spots that obscure terminal bud scars after one to two years. One to five thin orbicular leaves are clustered at each node. Plants are monoeceous, with catkins arising from lateral buds along the stem. Seeds are small, narrowly-winged nutlets that are shed in late fall or during the winter.

Field observations suggest sexual reproduction of B. nana is rare in the study region; no seedlings were observed during two summers of field research. However, McGraw and Shaver (1982) reported B. nana seedling densities of 2.9 m^{-2} in Eriophorum vaginatum tussock tundra in Alaska. That tussock tundra was similar in many characteristics to the tundra in the present study. Most of these seedlings were not surviving, however (F. S. Chapin III, per. comm.).

Asexual reproduction occurs when decumbent branches are covered by lichens, mosses, or decomposing organic debris. Adventitious roots appear at nodes, and new branches arise from the newly rooted section. Underground portions of B. nana are primarily buried stem sections and adventitious roots that have arisen from these stems. A buried stem can be several meters long, with many branches arising from it and appearing aboveground as a 'plant' or genet. The portion of the stem from which branches arise often becomes thickened into a burl-like structure. The oldest section of these underground stems eventually dies and decomposes, leaving viable growing tips.

Thus, what appears to be many plants in an area may actually be multiple branches originating from the same stem. Plants arising in this manner are genetically identical, and may be considered members of a clone. Because of the decomposition of older underground stem sections, all members of a clone may not be interconnected. The clonal nature of the species is apparent in the fall when leaves of some clones begin to change color before those in the rest of the population. Clonal sizes, as indicated by fall coloration, ranged from 0.75 m to 5 m in diameter.

Rooting of B. nana occurs primarily in the organic material of inter-hummock troughs. From these troughs, aboveground branches grow out and over many of the hummock tops, giving an appearance of nearly uniform distribution, even though only an occasional stem is actually rooting in the drier and thinner organic material that overlies the mineral core of the hummock. For field sampling and descriptive purposes, a B. nana individual was defined as any stem section that appeared above a continuous ground cover of lichens, mosses, or organic debris.

Both vegetative and reproductive buds are formed the summer before the growing season in which they will develop into leaves, stems or flowers. The preformed buds are visible by early to late July in the year before their final development. Leaf buds form as small orbicular organs in the axils of leaves. Floral buds look similar, but are slightly larger, more cylindrical, and are not associated with leaf clusters.

Both types of buds begin enlarging very quickly after snow release (Fig. 15), and, at this time, are sticky and resinous. Leaf buds on sections of stem that either supported female flowers, or grew rapidly the previous summer, enlarge more slowly than buds on stem sections that had little elongation or had supported no flowers. As the leaf bud continues to enlarge, bud scales separate, exposing the resinous leaf blades of the nodal cluster. Although

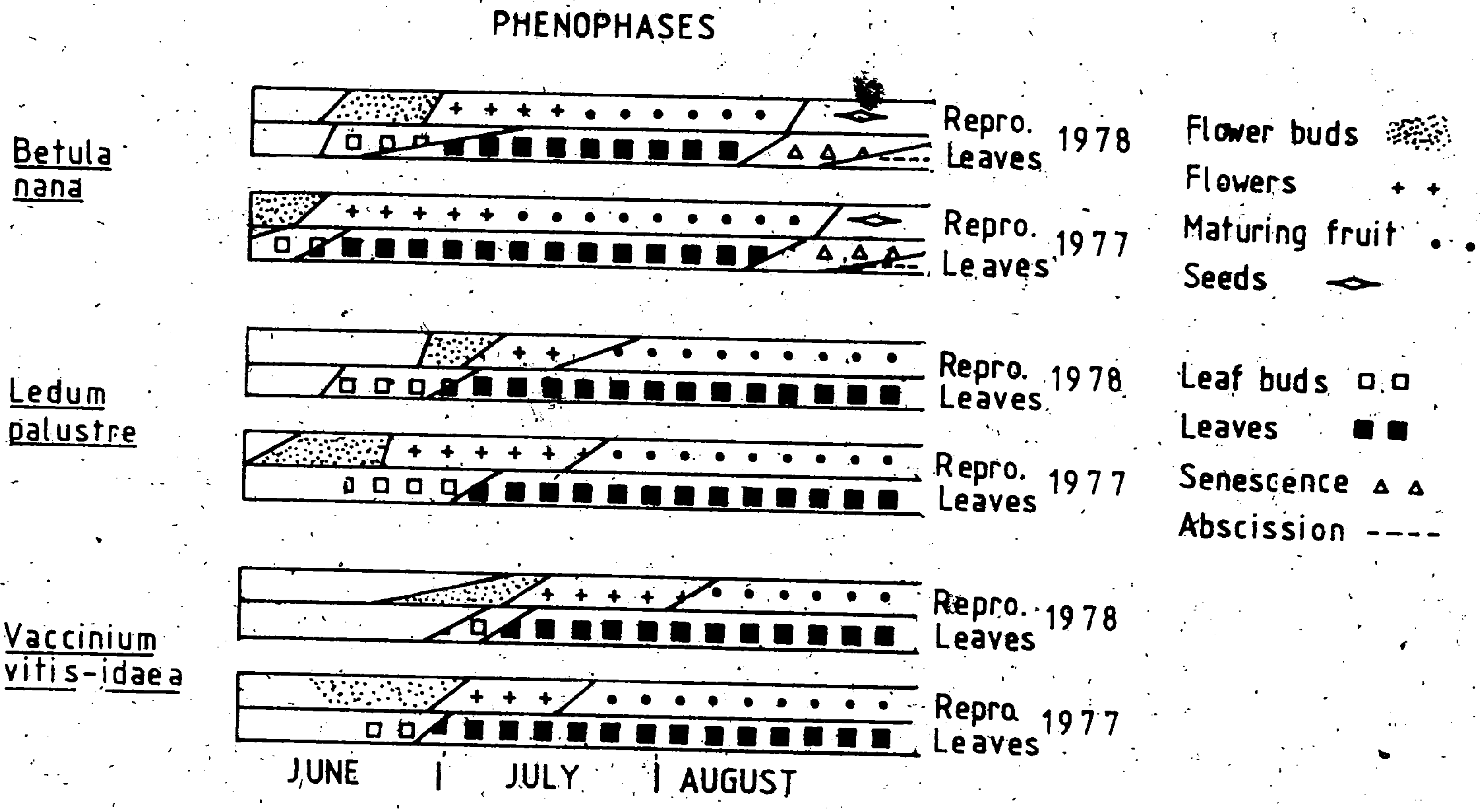


Figure 15. Reproductive and vegetative phenophases of Betula nana, Ledum palustre, and Vaccinium vitis-idaea at Parsons Lake in 1977 and 1978. Observations were halted in the fall before all phases were completed.

three to five leaves generally form at each cluster, only one leaf usually forms at nodes on long shoots that grew or supported flowers the previous summer. As blade elongation continues, the leaves slowly lose their resinous nature. The time from initiation of bud enlargement to 80% of maximum blade expansion can vary from days to several weeks, depending on environmental conditions (see Chapter 4). When leaves are well expanded, male flowers begin to develop from within the leaf clusters. Female flowers begin to develop after visible development of male flowers has been initiated. Pollen release occurs near the end of June, after most leaf expansion has occurred. Catkins continue to mature through the remainder of the growing season. Flowers begin to dry after mid-August, and seed release occurs from late August through winter. Seeds and catkin parts found in the snowpack indicate that some seeds are dispersed over winter.

Elongation of current stems is usually initiated somewhat synchronously with initiation of leaf blade expansion, and continues at differing rates through the entire growing season (see Chapter 4). The young stems remain soft and fleshy until mid-July when they slowly take on a woody character. Two types of shoots are formed; long shoots which generally form leaders and grow more than 1 cm in a season, and short shoots which are often laterals and usually grow less than 1 cm.

Leaf coloration on some *B. nana* clones in mid-August marks the onset of leaf senescence. Leaf fall from some nodes occurs shortly thereafter, although most leaves are retained until early September.

Ledum palustre L. subsp. *decumbens* (Ait.) Hult.

Ledum palustre subsp. *decumbens*, hereafter referred to as *L. palustre*, is an evergreen, dwarf shrub member of the Ericaceae. Distribution of *L. palustre* is circumboreal and amphi-beringian, with the range also extending to southeastern Greenland (Fig. 16). In arctic North America it occurs on moderately to well-drained upland tundra. In the Mackenzie Delta region, *L. palustre* is best developed on hummocky, convex, upland slopes which maintain a snow cover sufficient to bury the shrubs in winter. *Ledum palustre* is a low, many-branched shrub up to one meter in height. Basal stem diameter rarely exceeds 1 cm. Young stems are covered with a fine, rust-colored pubescence, while older stems are grey and smooth barked. The evergreen, sclerophyllous leaves are linear, with strongly revolute margins. The leaves are borne singly in whorls on the stem. Upper surfaces are dark green, while lower surfaces are cinnamon

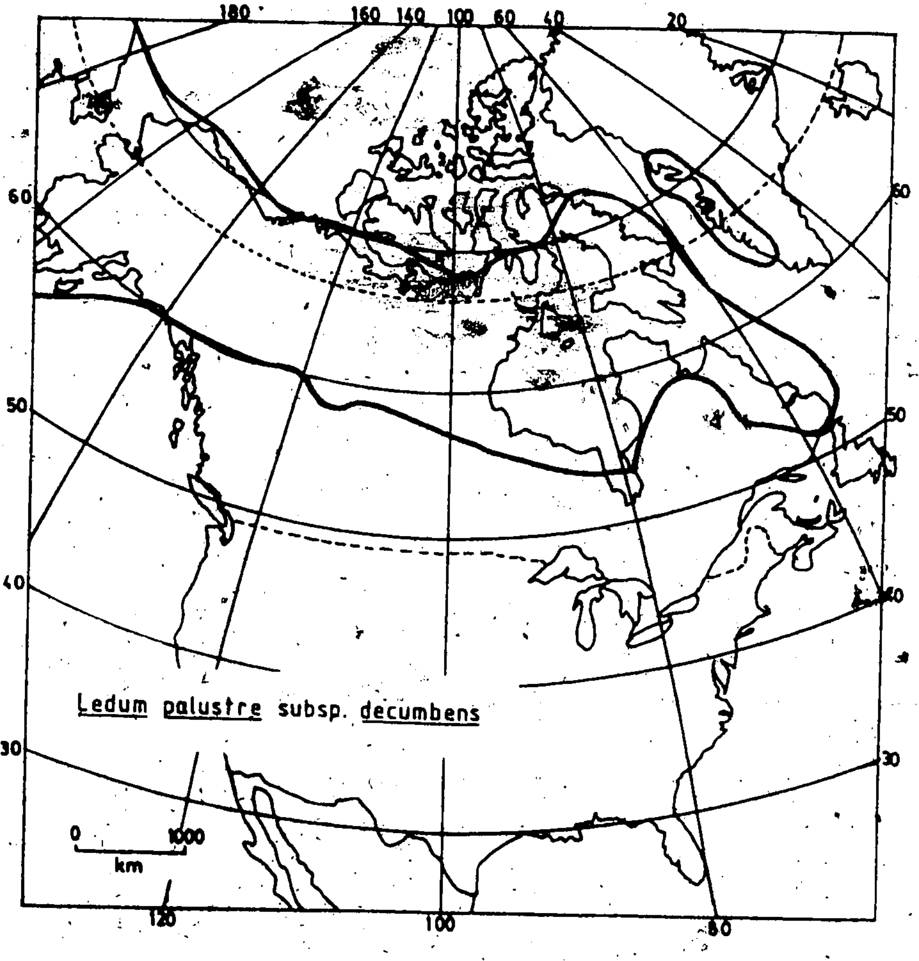


Figure 16. North American distribution of Ledum palustre subsp. decumbens according to Hulten (1968).

brown and densely wooly. Leaves are commonly retained up to five growing seasons.

Inflorescences are borne terminally and consist of an umbel-like cluster of white to pink flowers. Sexual reproduction of L. palustre in the Mackenzie Delta region appears to be uncommon. Only one plant positively identifiable as having developed from a seedling was observed during two summers of field research. McGraw and Shaver (1982) reported over 180 seedlings m^{-2} in a more open Eriophorum vaginatum tussock community. In that community, seedlings over 20 years old often retained juvenile morphological characteristics.

The pattern of vegetative reproduction is very similar to that of B. nana. Adventitious roots are formed when lower branches are covered by lichens, mosses, or organic debris. New, isolated individuals arise when underground stems eventually die and decompose, leaving the living terminal ends of the shoots independent. As with B. nana, many shoots which appear to be individual plants are actually branches of the same plant that are connected beneath the ground surface. However, for this study, an individual plant was defined as any shoot emerging from the ground cover.

Rooting patterns of L. palustre are also similar to those of B. nana, though generally less deep. Most rooting occurs in the top 20 cm of moist organic material in the inter-hummock troughs. Shoots, both aboveground, and to a lesser extent, belowground, do grow onto the hummocks, but not frequently. Thus, an aerial view of the landscape would reveal corridors of L. palustre in the inter-hummock troughs surrounding L. palustre-free islands formed by the hummocks.

Floral and vegetative buds of L. palustre are preformed, becoming visible in late July of the year prior to their eventual opening. Both bud types are terminal on shoots, with floral buds being much larger and more globose.

Evergreen leaves of L. palustre overwinter in a pendulous, nearly vertical aspect. Anthocyanin in the leaf blades give overwintering leaves a deep purple cast. When plants are uncovered at snow release, usually at the end of May, leaves slowly regain a dark green color and the horizontal aspect of normal summer conditions. Leaves generally lose their winter coloration and pendulous orientation by July 1. Movement of leaves from the vertical winter position to the horizontal summer condition does not occur in the same sequence in all L. palustre individuals. Leaves on some plants are reoriented basipetally (top to bottom) or on other plants acropetally (bottom to top), with only those plants with very few leaves changing synchronously.

All current leaves of L. palustre begin elongation in the single preformed terminal bud. Visible enlargement of the bud does not immediately follow melt out, but begins after a lag of one to several weeks (Fig. 15). A large portion of total leaf elongation occurs while the leaves are still in a tight, vertical bud-like formation that is maintained after bud scales have abscised. The new leaves, and thus the new photosynthetic surfaces, are not exposed significantly until this vertical orientation changes to the normal horizontal orientation of summer leaves. This change in aspect is associated with stem elongation, and does not usually begin until after July 1.

Floral bud enlargement does not always occur concurrently with leaf enlargement. After flowering, maturation of the floral capsule continues through the remainder of the growing season, and seeds are released in late fall before snowfall.

Elongation of L. palustre stems begins at the end of June, and continues until maximum elongation is reached near the first of August. Development of a floral cluster on a stem stops all further elongation of that particular stem.

Lateral shoots may develop below the floral cluster, either the same year in which flowering takes place, or in the year after flowering. Lateral shoots that do develop in the same growing season are generally less robust than developing shoots not associated with a floral cluster.

Vaccinium vitis-idaea L. subsp. minus (Lodd.) Hult.

Vaccinium vitis-idaea subsp. minus, hereafter referred to as V. vitis-idaea, is a low, creeping, dwarf evergreen shrub in the Ericaceae. Worldwide distribution is circumboreal, with New World distribution amphi-beringian, with a range extending to Greenland's west coast (Fig. 17). The arctic North American habitats of V. vitis-idaea range from wet, moss-dominated bogs, to poorly to well-drained upland tundra. In the Mackenzie Delta region, V. vitis-idaea is best developed on moderately to well-drained slopes with little overstory cover. The study site represented typical habitat for the species, but not that in which the species achieved its greatest abundance or cover.

The shrubs are decumbent to creeping, and attain more than 10 cm in height only in the moist, low light conditions which occur in inter-hummock troughs under a dense canopy of

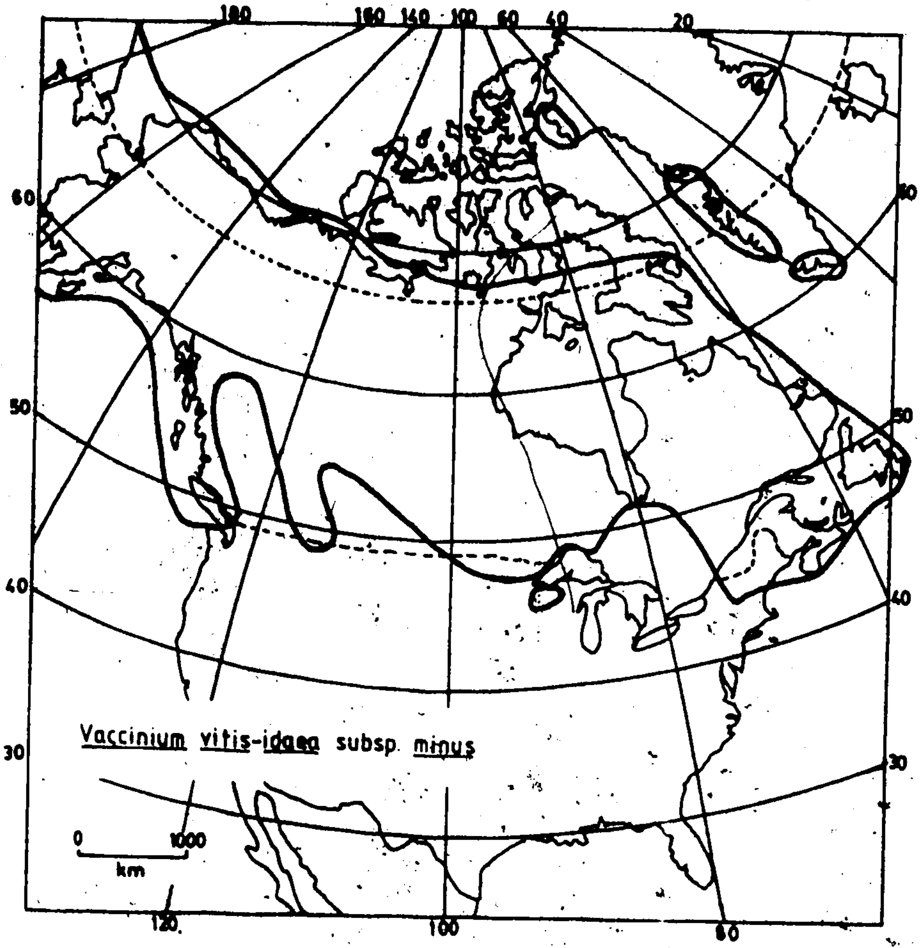


Figure 17. North American distribution of Vaccinium vitis-idaea subsp. minus according to Hulten (1968).

B. nana or L. palustre. Basal stem diameters rarely exceed 3 mm. The evergreen, coriaceous leaves are obovate, with reflexed margins, and are arranged alternately along the stem. Leaves can be retained for up to eight growing seasons, but three to five seasons is more common.

As with the other two species in this study, V. vitis-idaea infrequently reproduces via sexual means. Only one seedling or plant identifiable as having originated from a seedling was observed in two growing seasons. Fewer than two seedlings m^{-2} were found in a Eriophorum vaginatum tussock community in Alaska (McGraw and Shaver 1982). The inflorescence is a terminal cluster of pale to dark pink flowers. Fruit is a bright red berry.

Unlike B. nana and L. palustre, which root almost exclusively in the inter-hummock organic debris, V. vitis-idaea roots in nearly all microtopographic sites within this general habitat type. Vaccinium vitis-idaea has true rhizomes, and 90% of its rhizomes and adventitious roots grow in the top 5 cm of organic material on hummock tops, or the top 15 cm of the organic material in the troughs.

As with L. palustre, V. vitis-idaea leaf buds do not enlarge immediately after snow release, but exhibit a lag of several weeks (Fig. 15). Much leaf expansion occurs within a tight bud cluster, and individual leaf surfaces generally do not become exposed until stem elongation separates the individual leaves. The leaf blades are initially light green and non-sclerophyllous. The color of the leaves reddens with exposure to light after they begin to separate, and sclerophylly begins to develop several weeks after leaf exposure.

Flowering, and the exposure of the new leaf blades, begins after July. Green berries are visible in early August, and ripening extends into September. Many of the ripe berries do not abscise in the fall of their year of formation, but remain attached to the plants until the following spring.

The pattern of stem elongation in V. vitis-idaea is very similar to that of L. palustre, starting in late June, continuing through July, and ending near the beginning of August. Development of the terminal floral cluster also halts all further elongation of that stem. Unlike L. palustre however, no lateral shoots regularly appear below the floral cluster. In later years, a lateral shoot may develop somewhere along the stem, but its position or time of apppearence cannot be predicted.

LEAF AND STEM GROWTH

Methods

Seasonal leaf growth of the three shrub species was evaluated by determining leaf blade elongation, leaf weight gain, and increase in leaf surface at intervals from bud break in the spring to either leaf dormancy or leaf abscission in the fall. Sampling design for this leaf growth analysis was double sampling (two phase sampling) (Cochran 1977). Length of leaf blades was measured directly while weight and surface area were derived by regression estimation from the leaf length measurements.

In 1977, 20 individual plants of each species were selected in a 10 x 10 m plot and marked with an identification tag. On each B. nana plant, leaf buds at three nodes were additionally selected and marked. All nodes selected were on stem sections which had significant elongation the previous year and which were in the upper part of the leaf canopy. Each node produced three to five leaves, and thus 9 to 20 leaves were measured on each plant.

As leaves expanded, lengths of leaf blades were measured to the nearest 0.005 cm using hand held calipers. Maps of individual leaf positions at each node were drawn to allow each leaf to be re-identified and remeasured at later sampling periods. Betula nana leaves undergo significant elongation while still within a relatively unexpanded bud in the early portions of the growing period. Measurement with calipers at this time would have resulted in leaf tissue damage that may have affected later growth.

In order to avoid this damage, yet still obtain an estimate of leaf elongation within the expanding bud, a regression technique was used. Twenty buds from non-tagged plants were harvested, the lengths of the buds measured, and then the buds were carefully dissected. A mean length of the enclosed leaves was calculated, and these values used in a linear regression of length of leaf on length of bud. This linear relationship was then used to convert bud lengths measured at the marked nodes on the tagged plants to a mean leaf length value for the enclosed leaves. When buds had expanded sufficiently to allow measurement of the leaves without damage, measurements were made every five days during the period of rapid elongation and every 10 days in the remainder of the growing season.

Three to four times during the growing season, leaves were collected randomly from plants growing near the plot of tagged plants. The length of these harvested leaves was measured and each leaf was weighed. Leaf surface area (one side) was determined with a planimeter. Natural logarithmic transformations of length, weight, and area were made, and linear regressions were calculated to describe length on weight, and length on area relationships. These linear relationships were then used to estimate mean leaf weight and leaf area from the measured leaf length values at each sampling period.

Estimates of parameters calculated with linear regressions based on logarithms tend to underestimate the true parameters, in this case mean leaf weight and mean leaf area, when retransformed to arithmetic values (Baskerville 1972, Beauchamp and Olson 1973). To correct this bias in the estimated values, mean leaf weights and mean leaf areas were calculated from a formula derived by Baskerville (1972):

$$\hat{y} = e^{(\bar{y} + \hat{\sigma}^2/2)}$$

where: $\hat{y}$ = estimated mean in arithmetic units
$\bar{y}$ = mean of dependent variable in linear regression
$\hat{\sigma}^2$ = sample variance of the logarithmic equation

When using a double sampling technique to estimate means, two sources of error must be accounted for; error associated with the linear regression, and error associated with the primary sampling, here, on leaf length measurements on the original 20 plants. To account for both error sources, Cochran's modified formula (1963), for use when regression samples are selected independently from primary samples, was used in the calculation of the sample variance of the logarithmic equation:

$$\hat{\sigma}^2 = Sy^2(1-r^2)\left[\frac{1}{n} + \left(\frac{1}{n} + \frac{1}{n'}\right)\frac{1}{(n-3)}\right] + (r^2 \cdot Sy^2)$$

where: $\hat{\sigma}^2$ = sample variance of the logarithmic equation
Sy^2 = Σy^2 / degree of freedom
r^2 = regression coeficient of determination
n = sample size in measured sample
n' = sample size in regression sample

This calculation produced a variance estimate expressed in natural logarithms which is an underestimate of the true value when converted to arithmetic units. Baskerville's (1972) correction for this bias was used:

$$\hat{\sigma}_A^2 = e^{(2\hat{\sigma}^2 + 2\bar{y})} - e^{(\hat{\sigma}^2 + 2\bar{y})}$$

where: $\hat{\sigma}_A^2$ = estimated variance in arithmetic units
$\hat{\sigma}^2$ = sample variance from Cochran's formula
$\bar{y}$ = mean of independent variable in regression equation

A series of these computations was thus used in the conversion of leaf lengths, measured _in situ_ each sampling period, to estimates of leaf weight and leaf area and their associated variances. Initially 200 leaves were used for the regression procedure, but analysis of covariance revealed that 50 leaves produced a relationship that was not significantly different from that derived using the larger number. Fifty to eighty leaves were used for all later computations.

In 1978 methods were changed only slightly. To reduce measurement time, 10 plants instead of 20 were used, reducing the number of nodal leaf groups from 60 to approximately 30. Of the B. nana nodes tagged in 1978, 63% had also been tagged the previous year. The measurement of leaf length was halted in 1978 when 90% of blade elongation had occurred (July 17), based on the previous year's data. A final measurement of blade lengths was made in late August during leaf senescence.

Procedures for L. palustre were similar to those described above. For L. palustre, leaf clusters from the terminal bud on three shoots of each individual were chosen instead of three nodes as in B. nana. Only the outermost four to six leaves from each bud were measured in 1977, and the outermost seven to eleven leaves in 1978. In addition, seven to nine overwintered leaves produced in a previous season were measured on each stem at the beginning and end of the growing season. In 1978 the number of plants sampled was reduced to 10, and no overwintered leaves were measured.

The analysis of covariance suggested little biological difference between the ratio of leaf weight to leaf length in the evergreen leaves of L. palustre in the two years of the study and thus the regression equation of 1977 was used again in 1978.

Techniques used in the measurement of V. vitis-idaea were similar to those used for L. palustre. Only one bud per V. vitis-idaea plant was selected, and all leaves within that bud were measured. Several overwintered evergreen leaves were also included in 1977. No regression estimate of leaf length inside unexpanded buds was completed because of the small size of such buds and leaves. Twenty plants were used for measurements in 1977, and 10 plants in 1978.

Stem elongation was the only characteristic of stem growth directly measured in the field. Stem elongation was determined by measuring the distance between terminal bud scars and the base of the terminal bud. Measurements were made on the same dates leaf growth measurements were taken. In 1977, three marked stems on each of the 20 B. nana plants were measured. In 1978, one stem per plant of L. palustre and V. vitis-idaea were measured in situ.

However in 1978, an additional indicator of stem elongation was used. All current year stems from plants harvested at intervals throughout the growing season for biomass estimation (see Chapter 5) were separated, measured, and a mean length calculated. In 1978, 30 L. palustre plants were harvested and annual stem length increments measured using old bud scale scars. A maximum of 12 years of increments were measured on each stem, with fewer increments measured on some stems. Because the growth of stems stops after development of a terminal floral bud in L. palustre, only stems which had not flowered in those years could be used as a record of past growth. Correlation analysis with estimators of environmental conditions was completed.

Results

In all three species, differences in pattern and magnitude of growth, as measured by leaf and stem elongation, leaf weight gain, and leaf area development, existed between the two years of the study. Patterns and magnitude of growth also differed between the three species and between deciduous and evergreen growth forms.

Leaf elongation in B. nana was initiated nearly two weeks earlier in 1977 than in 1978 (Fig. 18). Visible expansion of the leaf bud on most plants occurred in the first week of June 1977, while in 1978 expansion in most plants was not visible until the third week of the month. Expansion was relatively synchronous in 1977, with leaves expanding at about the same time in all plants, and at the same time amongst all canopy positions on an individual plant. Leaf expansion was less uniform in 1978. Bud enlargement was first noted in the second week of June in

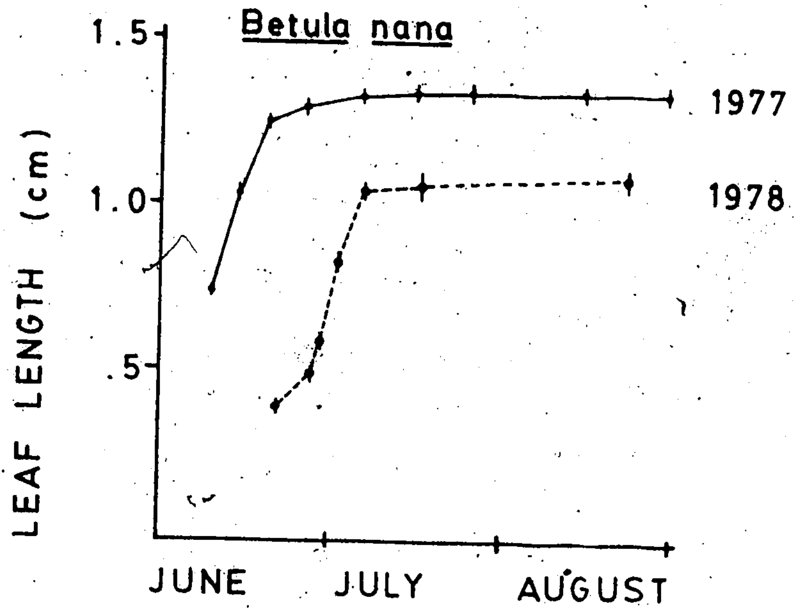


Figure 18. Leaf blade elongation in Betula nana. Values ± 1SE.

those buds on branches in the topographic depression of the inter-hummock troughs, while the buds on upper, exposed canopy branches did not generally begin expanding until the third week of the month. By June 19, 1977, 95% of maximum expansion had been reached while in the next year, full expansion did not occur until July 7. Leaves developing in upper canopy positions achieved full expansion later than the lower, more protected, leaves in 1978.

Once initiated, the rate of leaf expansion in 1977 was more rapid, with 95% of maximum leaf length being achieved in under two weeks, while the same degree of expansion required nearly three weeks in 1978. Maximum leaf length in 1977 was 25% larger than the maximum leaf length developed the next year. Both the maximum and the minimum size of sampled leaves was reduced in the second year of the study.

The pattern of B. nana leaf area development closely followed that of leaf length (Fig. 19). Leaf surface area developed rapidly after initiation of growth in the spring, reached a maximum by the first week of July, and remained constant until leaf abscission in late August and September. In 1978, areal development was initiated two weeks later than the previous summer and the expansion of the leaf blade was more gradual during the first week. Though a period of slower expansion was initially noted in 1978, the majority

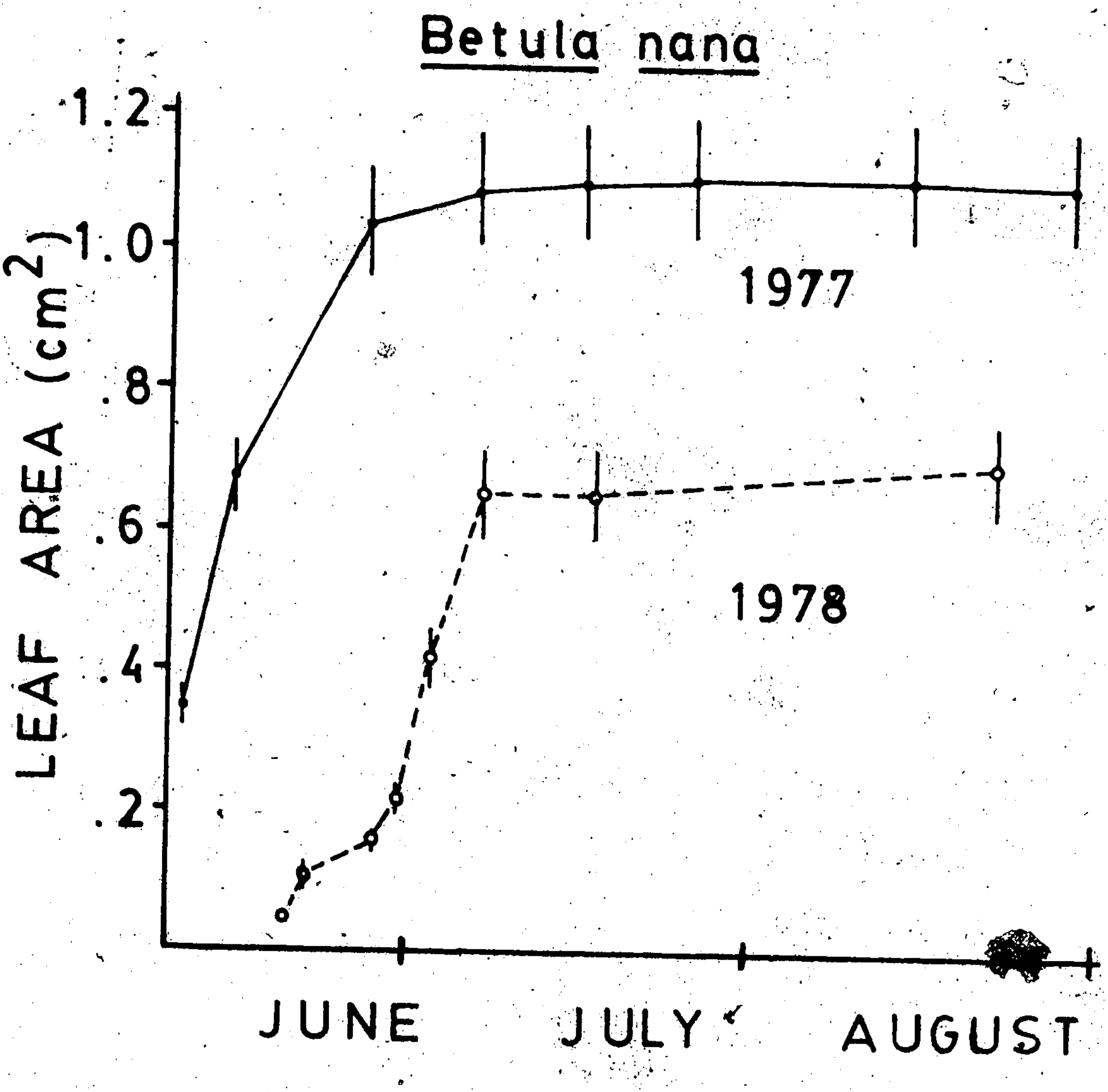


Figure 19. Mean surface area (±SE) of leaf blade (one side only) in *Betula nana*.

of total expansion occurred at the same rate as the previous year. Leaves reached 95% of their maximum surface area by June 27, 1977, but the same level of expansion was not recorded until July 16, 1978. Leaves that developed in 1978 were significantly smaller than those in 1977, with maximum mean leaf area being 63% less.

This general pattern of leaf length and leaf area development was also present in weight gain of B. nana leaves through the growing season (Fig. 20). Weight gain in 1977 began shortly after snowmelt. Leaf weight rose rapidly until the first week of July and then remained constant until mid August. A weight loss of 13% was noted just prior to leaf drop in the fall. In 1978, weight was initially gained more slowly, but most of the total weight of leaf tissue was eventually gained at the same rate as 1977. As with the other leaf growth characteristics, weight gain in 1978 lagged behind that of 1977 by approximately three weeks. Mean leaf weight at peak season in 1978 was 40 to 50% less than that attained the previous summer. No weight drop was noted before leaf fall in 1978.

The position of a leaf within a nodal cluster affected the final size of the leaf. Leaves on the outside of the nodal cluster, the first to be exposed when emerging from the bud scales, were smaller in surface area and lighter

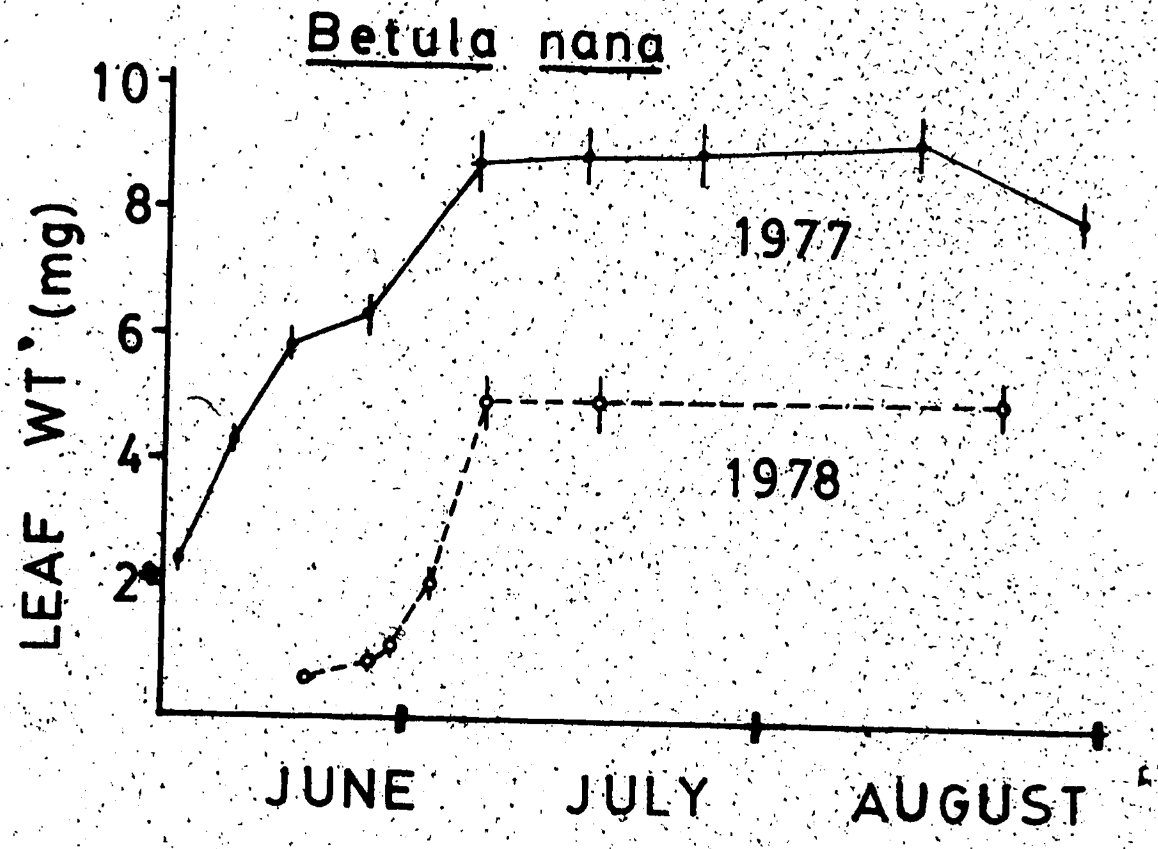


Figure 20. Mean leaf dry weight (blade and petiole)(±SE) in *Betula nana*.

than those developing in the center of the cluster (Figs. 21 and 22). The inner leaves continued growth for slightly longer than the outer leaves, and their growth occurred at a higher rate. This development pattern was similar in both years of the study except for that of leaves in position four, the inner most leaves in the cluster. Leaves in this position were the largest in 1977, and the smallest in 1978. The accuracy of the estimate of mean area and weight for position four was reduced in both years by the relatively small sample sizes (n=4), and thus this difference between years was probably not meaningful.

The growth of current L. palustre leaves began later in the growing season than the growth of B. nana leaves, and much of the early leaf elongation (50-70%) occurred while the leaves were still tightly bunched together as they expanded from the bud (Fig. 23). Time of leaf growth initiation did not differ significantly in 1977 and 1978. Bud scales covered the elongating leaves until the first week of July in both years of the study. After expansion from beneath the bud scales, leaves continued elongating until maximum length was reached in the last week of July; a period of one month from exposure to full expansion. In general, leaves on the outside of a bud began development before those in the center of the bud. Thus, the last leaves to expand were those nearest the terminal bud. The

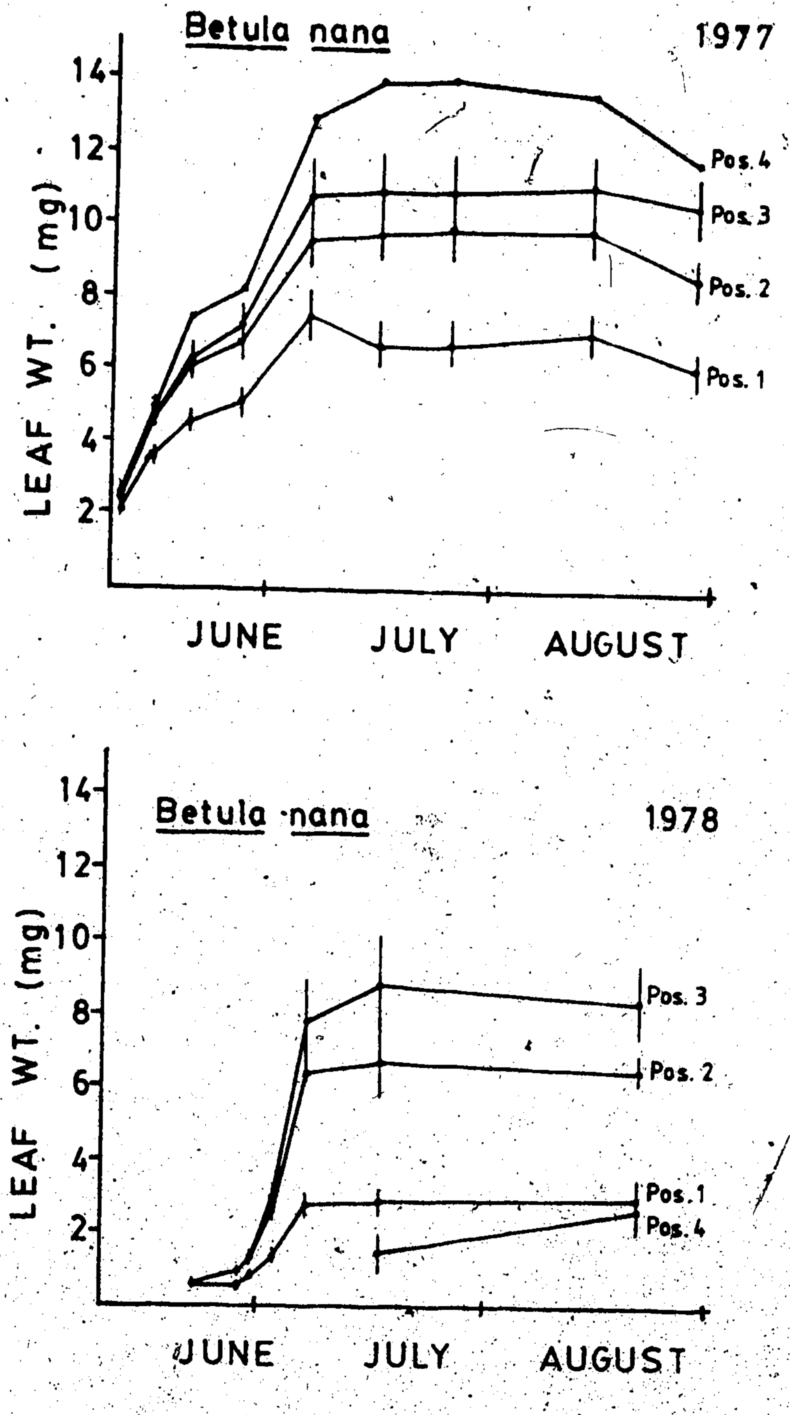
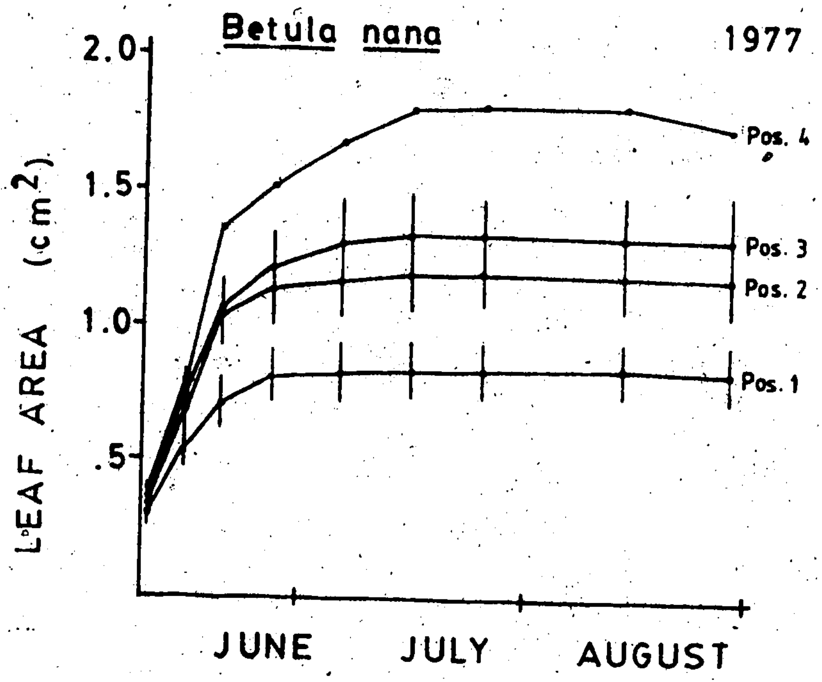


Figure 21. Mean leaf dry weight (blade and petiole)(±SE) by position in the bud of Betula nana in 1977 and 1978. Position one was on the outside of the bud, and position four was on the inside.



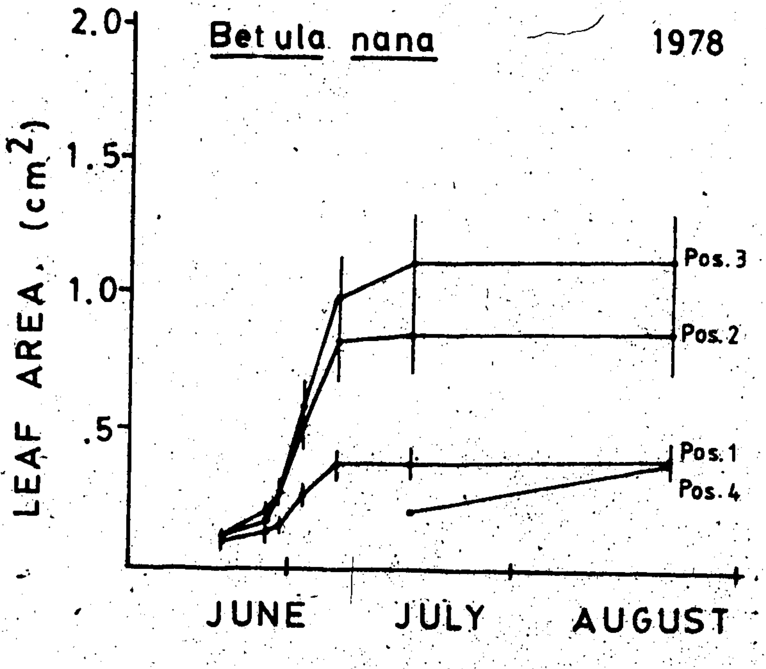


Figure 22. Mean surface area (±SE) of leaf blade (one side only) by position in the bud of *Betula nana* in 1977 and 1978. Position one was on the outside of the bud and position four was on the inside.

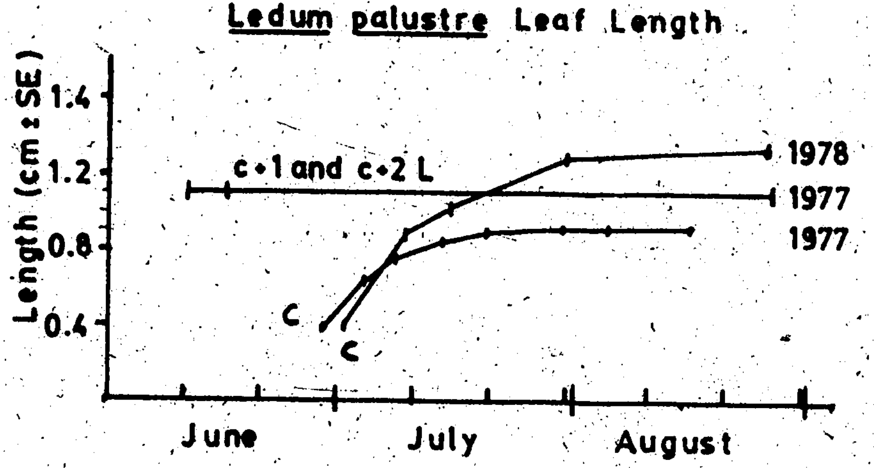


Figure 23. Leaf blade elongation in *Ledum palustre*. Values ±SE. c indicates leaves produced in the current growing season; c+1L indicates one year old leaves; c+2L indicates two year old leaves.

rate of elongation in L. palustre was slower than the rate in B. nana. Maximum length of measured leaves was greater in 1978 than in 1977, reaching 0.9 cm in the first year and 1.3 cm in the second year. One and two year leaves showed no evidence of continued growth beyond that of the first growing season.

Development of current leaf area in L. palustre followed a pattern similar to that of leaf elongation (Fig. 24). Surface area increased slowly from the initiation of bud expansion in late June until maximum expansion was achieved. This rate slowed in late July of both 1977, and 1978, but expansion did continue until just before leaf dormancy in the fall. Most leaves were near full expansion for the whole month of August. Maximum leaf area (one side) in 1978 was nearly twice that of 1977.

Weight gain in current year L. palustre leaves did not follow the pattern set by leaf elongation and leaf surface area development (Fig. 25). Weight did not approach a maximum in late July, but continued to increase until the end of the growing season. The rate of this weight gain was relatively uniform throughout the growing season. There was no difference in the time of onset of weight gain in 1977 and 1978. However, current leaves in 1978 weighed more than those developed in 1977. Mean maximum weight in 1978 was

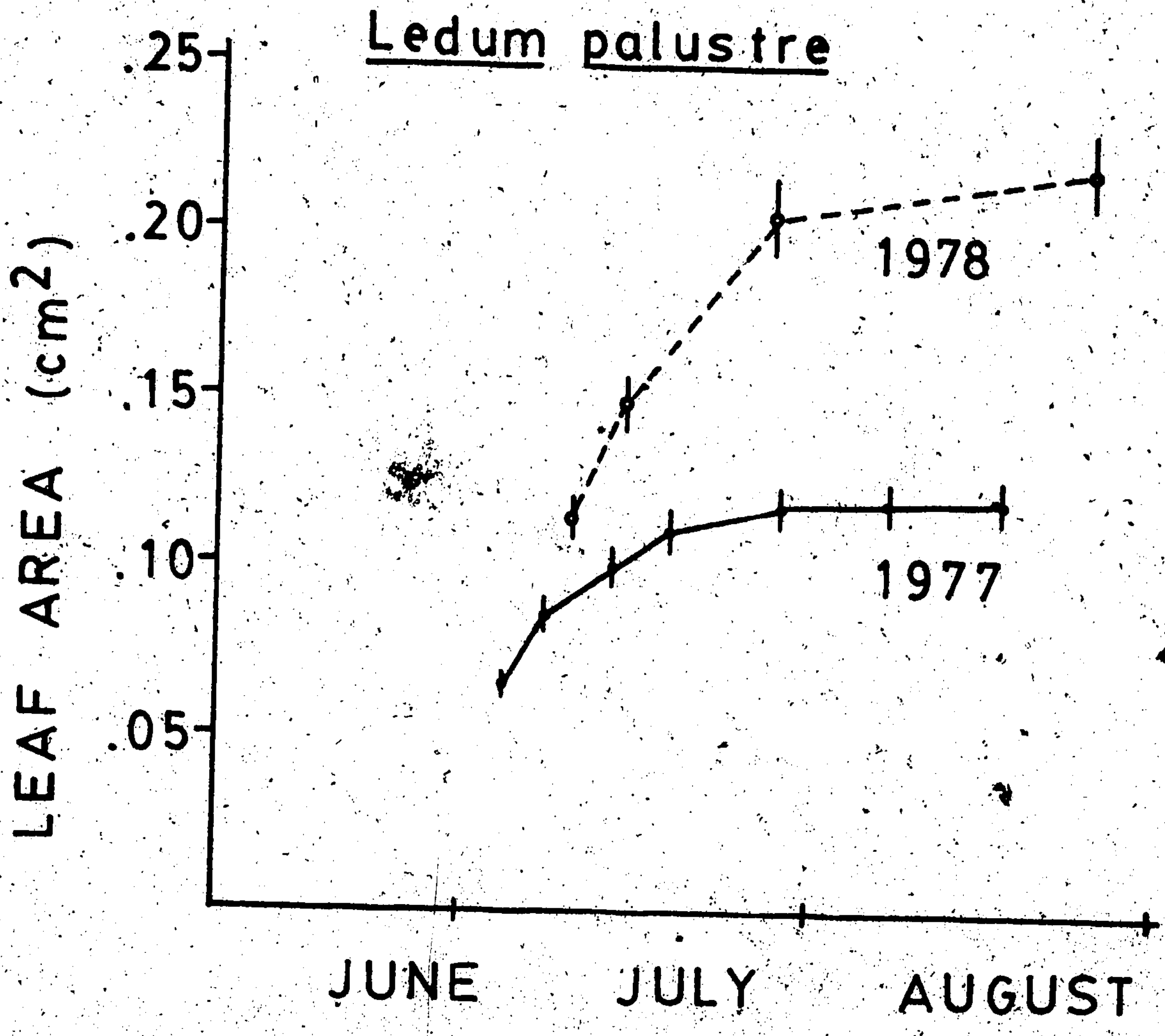


Figure 24. Mean surface area (±SE) of leaf blade (one side only, current leaves) in *Ledum palustre*.

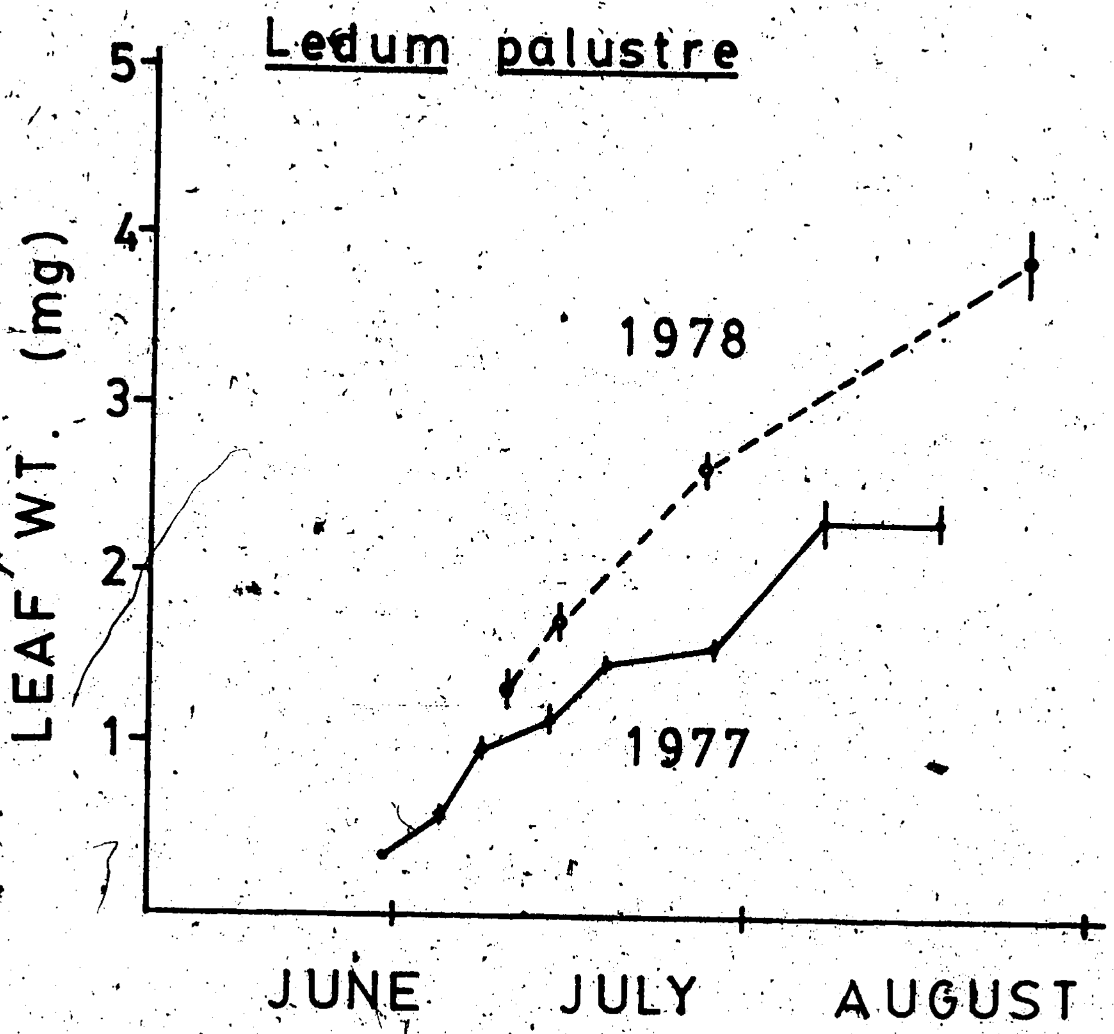


Figure 25. Mean leaf dry weight (blade and petiole)(±SE) of current leaves of *Ledum palustre*.

greater than 3.75 mg while mean maximum weight in 1977 was less than 2.40 mg. Density of leaves, based on dry weight, was similar in the two years; 0.0194 mg cm^{-2} in 1977, 0.0176 mg cm^{-2} in 1978.

The pattern of leaf growth during the growing season in *V. vitis-idaea* was very similar to the other evergreen species in the study, *L. palustre*. Elongation of the leaf blade began in late June and continued until maximum size was reached in mid to late July (Fig. 26). Quantitative measurements of *V. vitis-idaea* leaves in early stages of development were difficult because of the extremely small leaf sizes, and thus no data are available for this period. However, bud expansion and leaf growth did begin several weeks after that in *B. nana* and about the same time as *L. palustre*. Time from bud elongation to maximum leaf size was the same as for *L. palustre*, about one month. A lag of 7 to 14 d in the initiation of blade elong[illegible]n was noted in 1978 relative to 1977, and this lag in gr[illegible] continued until maximum size was reached. No furthur blade elongation was evident after the last week in July in either year. Mean maximum leaf length was slightly greater in 1977, but this difference was not statistically significant.

Leaf growth did occur in a sequential manner in *V. vitis-idaea*. The outermost primary leaves were the first to

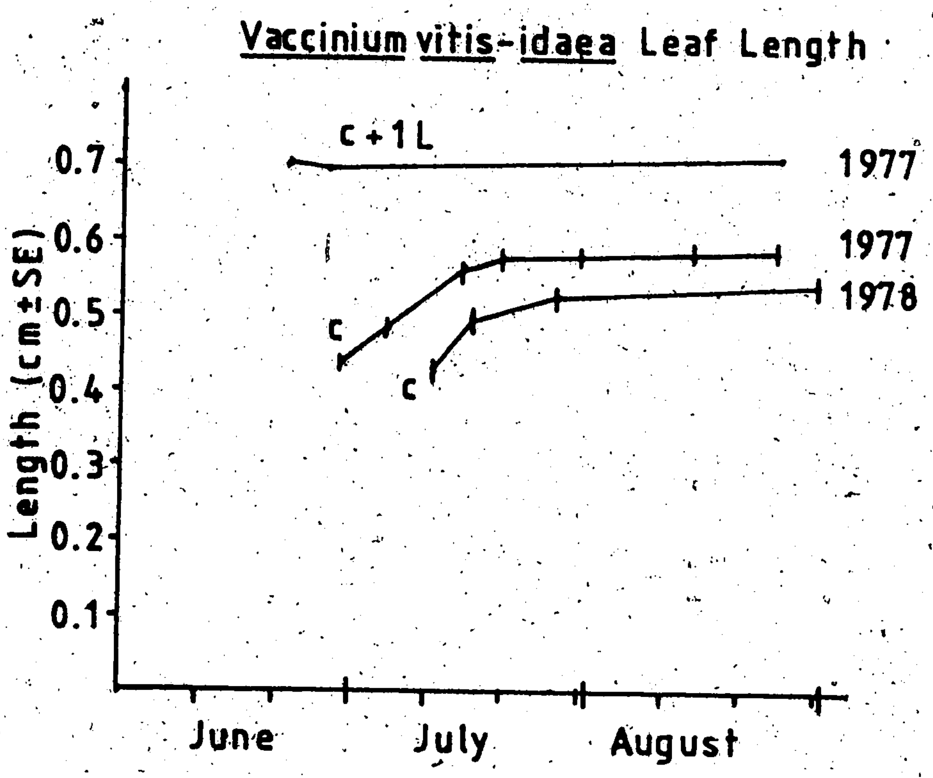


Figure 26. Leaf blade elongation in Vaccinium vitis-idaea. Values ±SE. c = leaves developed in the current growing season; c+1L = one year old leaves.

expand, and expansion of inner leaves occurred later as the stem elongated. Thus leaf expansion in V. vitis-idaea was not synchronous, but developed in relationship to position within the bud, and therefore position along the stem. Current leaves at the tip of a vegetative shoot had the shortest exposure and thus photosynthetic period, and leaves near the bud scale scars of the previous year had the longest. The outermost leaves in the bud grouping were generally bract like, and usually abscised by mid growing season. A small photosynthetic surface was present on these bracts, however their contribution to the total carbon budget of the plant could not have been large. No evidence of elongation of one or two year overwintered leaves was noted.

Surface area increase of V. vitis-idaea current leaves essentially paralleled that of linear leaf growth (Fig. 27). Photosynthetic surface of the leaves was first exposed in late June and reached a maximum by the end of July. A lag in development of surface area was noted in 1978 relative to that in 1977. Current leaves grown in 1977 had a larger surface area than those grown in 1978, but the difference was not significant.

Weight gain in V. vitis-idaea did not parallel the gain in leaf blade surface area or blade length (Fig. 28).

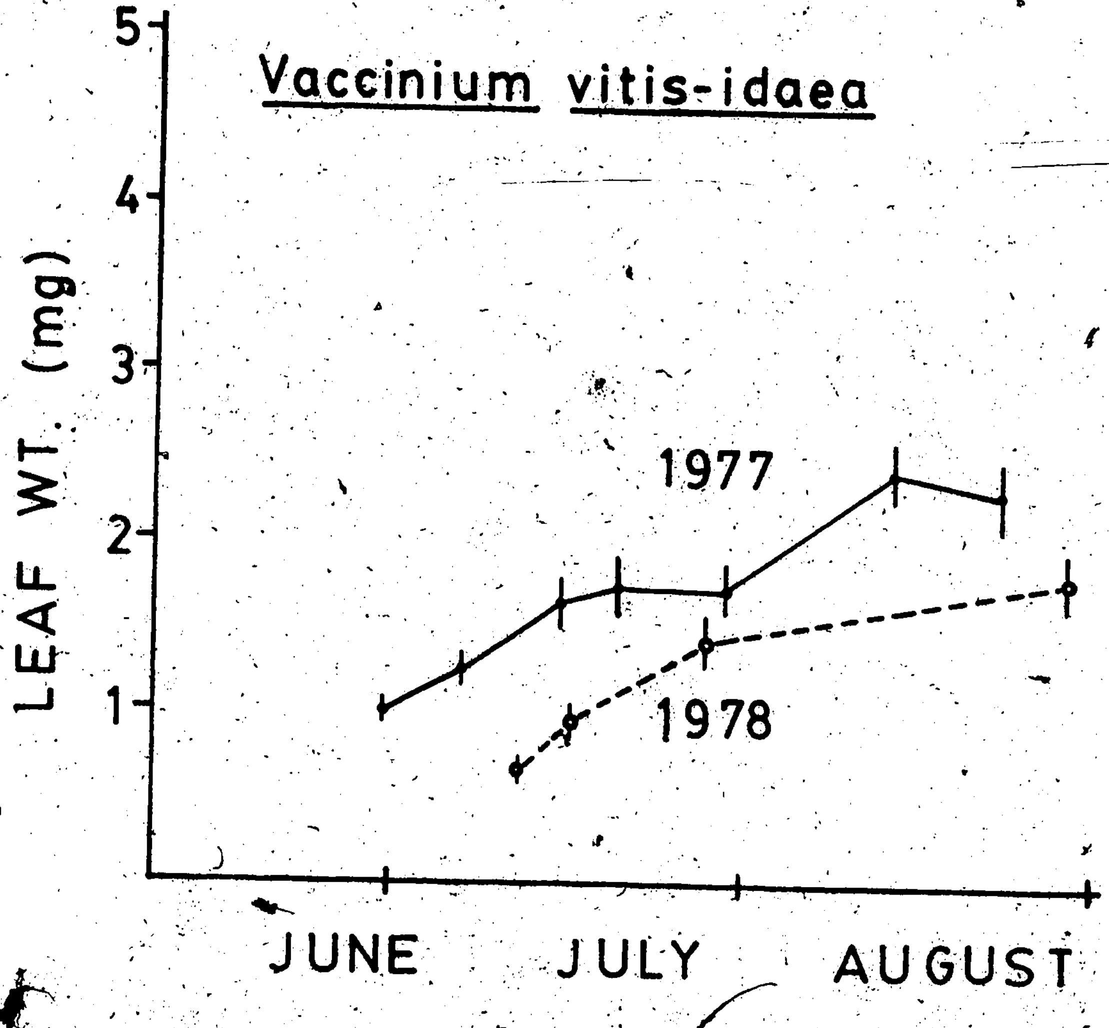


Figure 27. Mean surface area (±SE) of leaf blade (one side only, current leaves) in *Vaccinium vitis-idaea*.

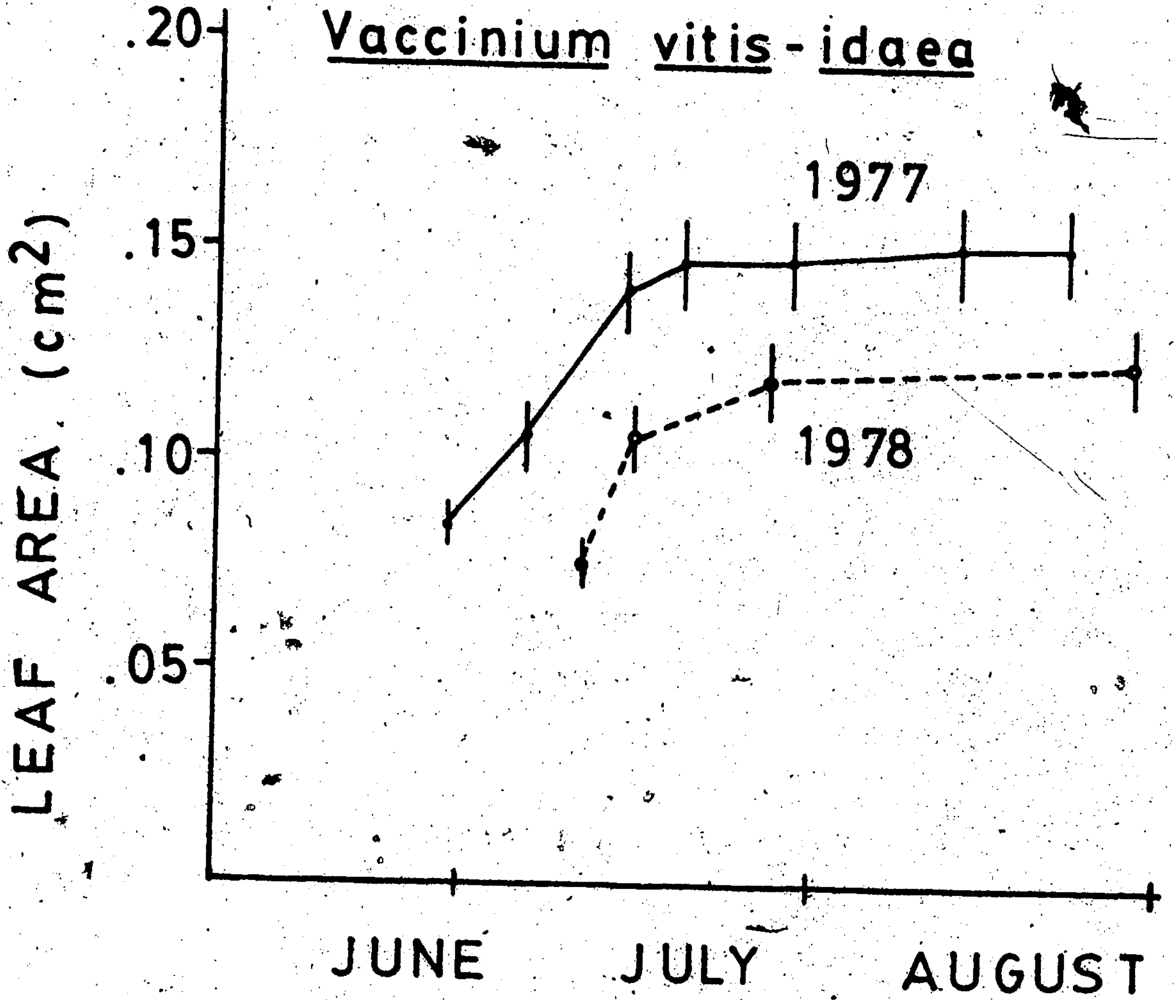


Figure 28. Mean leaf dry weight (blade and petiole)(±SE) of current leaves of *Vaccinium vitis-idaea*.

Weight of leaf tissue increased at a relatively constant rate throughout most of the growing season with no plateau in early August as occurred in B. nana. Peak leaf weight was reached at the end of the 1978 growing season, however in 1977, a slight decrease in mean leaf weight was observed at the end of August. This weight drop was not significant statistically. Lack of mid August sampling data in 1978 may have prevented the observation of such a drop, if it did exist, in that year. Growth rates were similar in both years, though weight gain in 1978 was delayed by one to two weeks. Though leaves were heavier in 1977 than in the next summer, the difference was not significant. Peak tissue density was 0.0163 mg cm^{-2} in 1977 and 0.0146 mg cm^{-2} in 1978.

Leaf longevity in B. nana was generally less than 90 d, with leaves being retained on the plant from the first or second week in June, to the first to third week in September. Leaf longevity in L. palustre was evaluated by counting leaves and leaf scars in different leaf age classes at mid season (July 10, 1977) (Fig. 29). A large percentage (42%) of leaves were still present in their fourth photosynthetic season (current + 3 yr age class). Many fewer remained in their fifth photosynthetic season, and most of those abscised by the end of that year. Thus, over half of the leaves of L. palustre survived for three

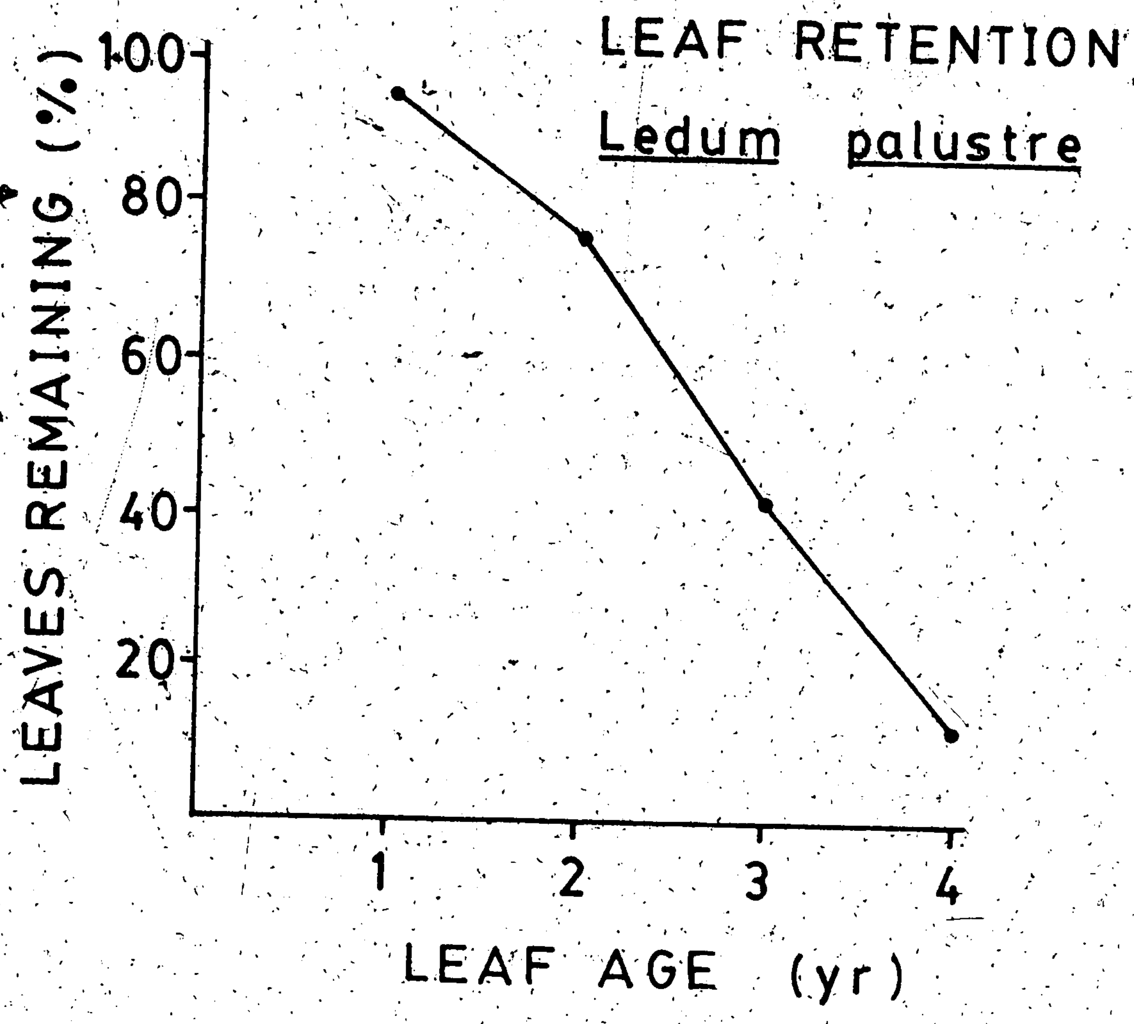


Figure 29. Leaf longevity in Ledum palustre. Leaf scars and remaining leaves in each age class were counted in mid-July, 1978.

photosynthetic seasons.

Evaluating V. vitis-idaea leaf longevity was more difficult because of its determinate growth (see Chapter 2). Stems stopped growing after producing a flower, and therefore estimating age of leaves on most stems was impossible. In some cases, however, it could be seen that leaves survived at least four to eight years.

General patterns of stem elongation were similar in all three species, with timing of initiation differing between growth forms (Fig. 30). Ledum palustre and V. vitis-idaea had nearly identical patterns of stem growth. Elongation of stems began in early July, with stems reaching maximum lengths by the end of the month. Betula nana stem growth began much earlier in the growing season, with elongation noted at the end of the first week in June, 1977. The elongation phase in B.nana was longer than in the evergreen shrubs, extending to the beginning of August when maximum lengths were reached. Stem growth of B.nana had a similar pattern in both years of the study. The much smaller stem lengths in 1978 are an artifact of the sampling procedures used. In 1977, stem lengths on shoots that had been actively elongating the previous year were chosen for measurement, and the same shoots were measured at each sampling. In 1978, shoots measured were subsamples of all

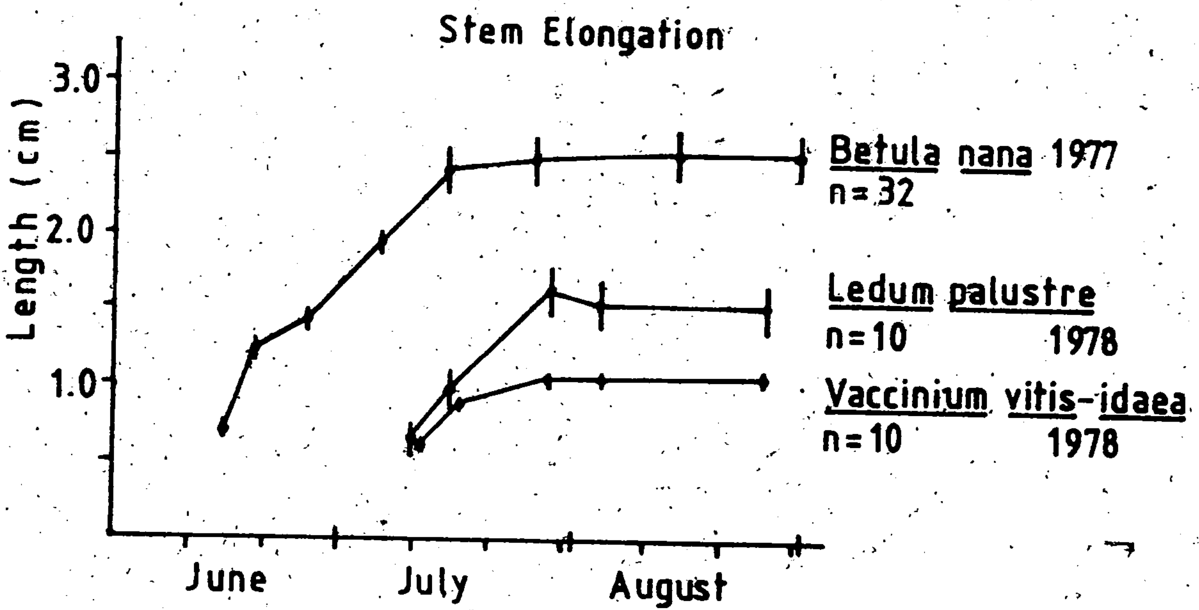


Figure 30. Elongation of stems (long shoot~~s~~) of *Betula nana*, *Ledum palustre*, and *Vaccinium vitis-idaea*. Data ±1SE. The same stem sections were measured at each sampling.

shoots on harvested plants used in an analysis of biomass partitioning. These subsamples included many smaller shoots with much less elongation than those measured in 1971.

Stem elongation in L. palustre from 1966 to 1978 is presented in Fig. 31. Much year to year variation in stem growth was present. Mean annual stem growth over the 12 years sampled was 0.87 cm with a mean maximum growth of 1.08 cm in 1975 and a mean minimum growth of 0.69 cm in 1971.

Discussion

A dominant feature of all B. nana leaf growth characters in this study, was the very short time period from initiation of bud expansion to near maximum development. Leaf length, weight, and area all increased very rapidly over most of their expansion phase. The first leaves to develop, those on the outer edges of a bud leaf cluster began growth the earliest and achieved maximum levels in the shortest period of time. Leaf longevity in deciduous arctic shrubs such as B. nana is usually 90 days or less. A net positive carbon gain must be exhibited by the leaf at the end of this period if the leaf is to make a beneficial contribution to the plant. Compressing leaf development into a very short period after the initiation of

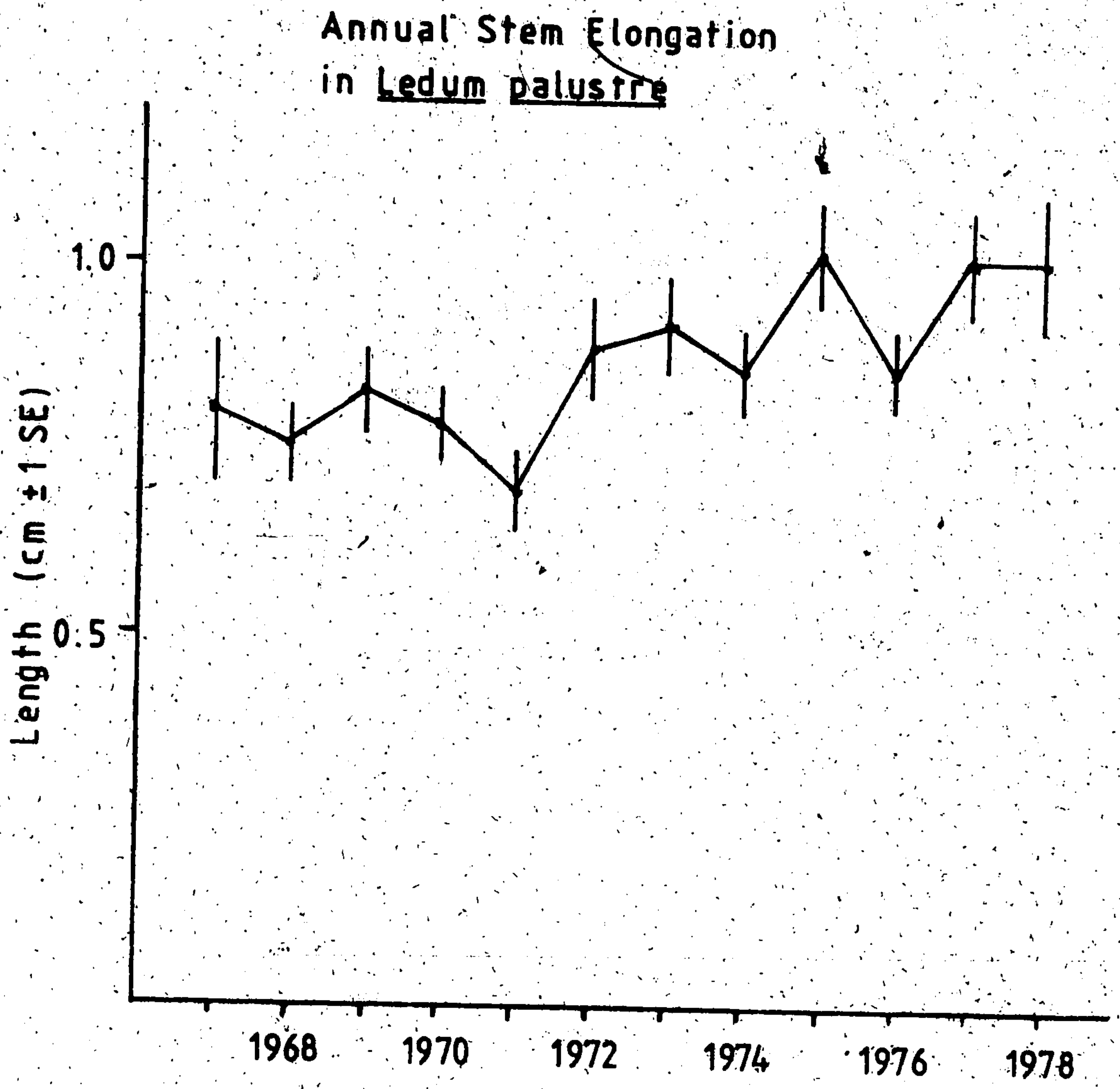


Figure 31. Annual stem (long shoot) elongation (±SE) in *Ledum palustre* from 1967 to 1978. Only stems which had not flowered in those years were included.

growth maximizes the time of full photosynthetic competency and the opportunity for repaying the carbon debt incurred from tissue development and maintenance. Mooney and Gulmon (1982) define the net benefit a plant receives from a leaf to be the rate of leaf carbon gain times the carbon gain period minus carbon cost of leaf growth and minus the losses from herbivory. Thus an increase in the period of carbon gain provided by a shorting of development time would increase the potential for an individual leaf to make a net positive contribution to a plant within the limits of the 90 day functional period.

Leaf expansion in B. nana generally occurred at or after the annual peak in incoming solar radiation. Mean monthly shortwave radiation at Inuvik in August is only 62% of that received in June, and July's radiation is only 93% of the June amount (Fig. 7). The rapid rate of leaf expansion in B. nana soon after snowmelt insured that maximum photosynthetic surface was exposed near this period of peak insolation.

B. nana has a photosynthetic capacity typical of many temperate deciduous shrubs (37+/-4 mg CO_2 dry wt^{-1} hr^{-1} (Johnson and Tieszen 1976, Limbach et al. 1982). This potential for relatively rapid carbon gain is another positive character in Mooney and Gulmon's leaf cost-benefit analysis. A high photosynthetic capacity increases the potential of a plant for photosynthesis at high rates and thus the ability to achieve a net positive carbon gain over a short leaf life. Both high air and upper soil temperatures can be present in early to mid-June (Fig. 5) at the study area, and combined with high radiation levels and adequate soil moisture from melting snow and ground ice, conditions can be present that would support high rates of photosynthesis. Thus rapid leaf growth in B. nana allows it to take advantage of these appropriate conditions and maximize the possible carbon gain.

The carbon cost of leaf development in B. nana, as represented by dry matter deposition in leaf tissue primarily occurred early in the growing season (Fig. 20). Additional costs at this time came from high metabolic rates that exist during periods of rapid growth (Mooney 1972). These are not accounted for when using dry matter deposition as an indicator of development costs. This concentration of dry matter production in early season also coincided with the maximum radiation load. If the maximum photosynthetic potential of B. nana exists in June and July because of the higher levels of radiation, temperature, and moisture, then it would be beneficial for structural development in such a deciduous leaf to take place very rapidly before or during this period to maximize this potential. In this way, the fully developed leaf could very rapidly begin making a carbohydrate contribution to the maintenance of its own tissue as well as potentially exporting excess carbon to other compartments of the plant to replace that used in leaf construction.

The rate and timing of leaf development in _B. nana_ appeared to be partially dependent on temperature, as indicated by differences in development in the two years of the study. With a delayed snowmelt in 1978, and the cooler temperatures that followed the eventual snowmelt, there was also a concomitant delay in leaf development. Rapid leaf expansion did not occur in either year until approximately 100 degree days had passed after snow release (Fig. 4), however, this point was passed nearly three weeks later in 1978 than in 1977. In the cool June of 1978, expansion was delayed, and then began slowly and only in selected leaves, until warmer temperatures arrived. Once temperatures increased, expansion and growth rates were similar to those noted in June of 1977.

Additional evidence for temperature dependency of leaf growth came from the differential timing of initiation of expansion in 1978. The time when leaf growth began varied with topographic and canopy positions. Though only qualitatively observed, those leaves near the ground in lower canopy positions and in hummock troughs did begin growth substantially before the more exposed upper canopy leaves. These earlier expanding leaves also reached maximum expansion before other leaves. These leaves were developing within the earth's boundary layer, which has reduced air turbulence and less mixing of warm surface air with that from cooler upper areas, and resulted in significantly warmer temperatures near the surface (Campbell 1977)(Fig. 6). The temperature differential that was created by the boundary layer only appeared to affect leaf development in the early part of the growing season and at temperatures in the lower range experienced in 1978 (five day means generally between 4 and 5 ^{o}C). No significant difference in onset of leaf expansion was noted amongst canopy positions in June of 1977, nor later in the growing season.

Low soil temperatures may also have had a role in delaying leaf development in 1978. Much evidence appears in the literature suggesting that low soil temperatures can inhibit water uptake (Kuiper 1964, Courtin and Mayo 1975), and reduce nutrient availability (Chapin 1978, Ulrich and Gersper 1978), both of which could easily reduce growth rates of aboveground plant parts. Thus, the reduced and delayed growth rates of *B. nana* leaves in early and mid-June 1978 may have been an expression of both lower soil and air temperatures.

Mooney and Gulmon (1982) noted that deciduous plants produce leaves with a lower specific weight (ratio of dry weight to unit area) than evergreen leaves. Leaf specific weights of between 0.0005 and 0.0008 for B. nana at peak season in 1977 and 1978 were generally half or less than those recorded for the two evergreen species in the study. Thus in the deciduous shrub, less carbon is committed per unit of photosynthetic surface area than in the evergreen shrubs. That deciduous leaves have a lower initial carbon cost than do evergreen leaves (Miller and Stoner 1979) can be partially explained by this lesser carbon commitment per unit of photosynthetic surface. If carbon committed to leaf structure was greater in these leaves, their ability to provide a net positive carbon gain to the whole plant by the end of their 90 day photosynthetic lifespan would be reduced.

Johnson and Tieszen (1976) found that B. nana leaves in the wet tundra of northern Alaska lost weight throughout August after reaching a peak at the beginning of the month. Leaves they measured dropped from a peak weight of approximately 2.0 mg to under 0.2 mg before leaf fall. This weight loss occurred in all leaf positions at a node. Other deciduous species in their study, Eriophorum sp. and Salix sp., also exhibited this major drop in leaf weight at the end of the growing season. This pattern is very different from that of the *B. nana* in this present study, and I can offer no biological explanation for this difference. Johnson and Tieszen failed to present any error estimates with their data however, and thus no evaluation of the significance of their findings can be made. It seems unlikely that a leaf would lose enough structural material in the fall to allow its weight to approach zero as suggested by their data.

Th[illegible]fference in peak leaf weights between those at the Al[illegible]an site and at the Mackenzie Delta site may be explained by the occurrence of hybridization in *Betula*. Hybridization between *B. nana* and *B. glandulosa* is common (Hulten 1968), and results in a plant with larger leaves than *B. nana*. Such hybrids were common in the study region, and were among the sampled plants.

Both evergreen dwarf shrubs in the study started leaf growth several weeks after deciduous *B. nana* started leaf growth. When the snow melted in the spring, the active layer had thawed and overwintering plants came out of dormancy, such evergreen shrubs as *L. palustre* and *V. vitis-idaea* already had in place a set of fully developed leaves with photosynthetic potential. There was no need for immediate carbon commitment to development of new competent photosynthetic structures. During the period of metabolic activity after snowmelt, carbohydrate reserves of the plant are used instead to reactivate photosynthetic structures in the one year and older overwintered leaves (Mayo et al. 1975). Internal changes that are needed to regain photosynthetic competency include production of chlorophyll (Tieszen 1972) and resynthesis of such enzymes as carboxylase (Tieszen ,1974, 1978).

This development of photosynthetic competency in overwintering leaves occurred rather quickly in L. palustre and V. vitis-idaea. Older leaves of both species exhibited active photosynthesis by mid-June, 1978 when they were checked for the first time (Figs. 47 and 53) (see Chapter 7). Mayo et al. (1977) demonstrated that high arctic populations of Dryas integrifolia, another evergreen species, could fix CO_2 positively within four or five days of snowmelt. Although older leaves of L. palustre and V. vitis-idaea began to photosynthesize shortly after snowmelt, active and rapid growth of current leaves began only after the start of carbon export from older leaves.

Elongation of current leaves in L. palustre and V. vitis-idaea began at the same time and proceded fairly rapidly once initiated, though at a slightly slower rate than B. nana. Current leaves of both species had reached near maximum length and near maximum surface areas by the third week in July, slightly past the midpoint of the growing season, and well past the period of maximum insolation. Because the evergreen leaves of L. palustre and V. vitis-idaea are retained on average for several growing seasons, an individual leaf does not need to have a net positive carbon contribution in its first growing season. Therefore, the relatively late season development of leaf surface in the evergreen shrubs does not limit their potential contributions nearly as much as would a delayed development in a deciduous shrub. A one week delay in an evergreen leaf is a much smaller percentage of its active life than is a similar delay in growth of a deciduous leaf.

The cool June of 1978 did not appear to affect the timing of leaf growth in L. palustre and V. vitis-idaea as much as in B. nana. L. palustre leaf expansion was initiated at approximately the same time in both years. However, leaves measured in 1978 were significantly larger than those measured in the summer of 1977; opposite the pattern observed in B. nana. The leaf primordia of 1978 leaves were formed during that warmer season, which may have been partially responsible for their larger size. Warm years with favorable photosynthetic conditions such as those in 1977 have been shown to favor other growth characteristics such as floral activity in the following year (Mark 1970).

Light may also be more important than temperature for leaf growth in L. palustre, whereas temperature may be relatively more important in B. nana, which develops leaves in a region with less boundary layer. If L. palustre leaf growth is dependent on photosynthesis of the current year, then the slower leaf growth of B. nana in 1978 may have increased light penetration through the canoopy and thus resulted in a greater net carbon gain for L. palustre.

The differences in the size of leaves in the two years may also have been an artifact of the sampling technique. Leaf sizes within a bud cluster were not uniform, and because more leaves were sampled in 1978 per cluster, a similar population of size classes may not have been sampled for measurement. Additionally, many L. palustre individuals measured in 1978 were different than those measured in 1977, and thus most leaf clusters were on different shoots than the previous summer.

Leaf growth of V. vitis-idaea did show a slight delay of about one week in 1978 relative to the previous summer, however, no significant differences in leaf sizes were noted. Because of the difficulty in measuring V. vitis-idaea leaves during the early stages of leaf expansion, a quantification of the differences in growth in this period between the years of the study was not possible.

In neither L. palustre or V. vitis-idaea was a difference in leaf growth noted in 1978 that could be correlated with either topographic position or position within the canopy, as was seen in B. nana. Both L. palustre and V. vitis-idaea primarily grew within the surface boundary layer, the region in which the early expansion of B. nana buds and leaves occurred. L. palustre and V. vitis-idaea were thus exposed to the warmer temperature regime associated with this region during the early, cool weeks of June 1978, and may not, therefore, have been affected by the lower air temperatures as was B. nana.

A major difference in patterns of leaf growth between B. nana and the two evergreen species did occur regarding weight gain of leaf tissue. Rather than an early and rapid attainment of maximum tissue weight as in B. nana, L. palustre and V. vitis-idaea both gained leaf weight up to the onset of leaf dormancy in the fall. By the end of their first growing season, current leaves of L. palustre and V. vitis-idaea had reached specific leaf weights of 0.0019 and 0.0016 respectively, both nearly twice that of the deciduous B. nana. The heaviness of these leaves, and their gradual weight gain over their first growing season is primarily associated with sclerification of leaf tissue, and to a lesser extent the development of tannins and aromatics (Jung et al. 1979, Batzli and Jung 1980). Miller and Stoner

(1979) suggest that these leaf characteristics are associated with higher carbon costs of initial leaf development in evergreen leaves.

Sclerophylly and other xeromorphic characters such as thickened cuticles and cell walls, high fiber content, and tomentose leaves have been associated with conditions of low nitrogen and phosphate availability, typical in many arctic habitats (Loveless 1961, Beadle 1966, Small 1972, Haag 1974). These characters, along with evergreeness, appear important in efficient use and cycling of nutrients of low availability.

Aromatics and other chemical compounds common in evergreen leaves have also been suggested as evolutionary deterents to grazing by insects (Rohringer and Samborski 1967, Swain 1977), and mammals (Batzli and Jung 1980). Neither L. palustre nor V. vitis-idaea showed any evidence of leaf damage from herbivores in either current or older age class leaves in either year of the study. B. nana, however, showed a total surface reduction of 4.3% in late August of 1978 due to herbivore damage. Of the leaves remaining on the plant at the end of August, 25% showed some insect damage, with a mean leaf surface reduction of 17.3% per damaged leaf. Young leaves of B. nana were coated with a sticky resin which may have protected the leaves from herbivory in early season. This protection may ensure that entire leaves are present long enough to at least recover their investment cost, without the energy expense of protection throughout the life of the leaf.

Stem elongation in the three species differed in the absolute time of onset. However, all three species began stem elongation at the same time relative to the growth of their leaves. _B_. _nana_ stems experienced the majority of growth after most leaf expansion had occurred. Stems were elongating through the latter half of June and reached a maximum length several weeks before leaf fall. Thus, stem growth was delayed until after the demands of leaf structural development had been met, and the new leaves had begun contributing carbohydrates to the system.

At the beginning of the growing season, evergreen species already have a complement of leaves that are able to provide carbohydrates for growth. Yet, _L_. _palustre_ and _V_. _vitis-idaea_ both also initiated stem elongation after the majority of current leaf expansion had occurred.

In a region with such a limited growing season and low energy regime as the Low Arctic, the development of photosynthetic structures that are capable of increasing the carbohydrate supply may have a higher priority than such supportive tissue as stems. Thus, some stem growth in all three species was delayed until adequate carbon had been supplied to the leaf tissue. In L. palustre and V. vitis-idaea however, some stem growth is needed to arrange current leaves in a manner useful for photosynthesis.

Ledum palustre was the only species for which a record of past stem length increments could be produced. Mean annual increments of the 12 years between 1967 and 1978 varied from under 0.7 cm to over 1.0 cm. However, there was no significant correlation between the size of stem increment and environmental conditions of either the year in which the growth took place, or the year previous. Conditions considered included; degree days in a growing season, degree days of each month, mean temperatures of each month, and precipitation. Much variability in growth increments existed among stems in a given year, and this large variance may have obscured any correlations with environmental conditions if they did exist.

These non-flowering stems may be a non-random sample from the population. Individuals which showed significant growth in a particular year may have flowered the following season, and thus, would have been eliminated from this sample.

BIOMASS PARTITIONING

Introduction

Growth, development, and maintenance of plant tissue requires an energy expenditure by the plant. The allocation of this energy to different tissue types within a plant, and the role of this allocation pattern in the ecological strategy of the plant has received much attention in recent years. Harper and Ogden (1970) separated individual plants into different components based on tissue function. Energy allocation to these tissues was expressed as a function of their proportion of the total tissue weight. This technique has since been applied to differences in allocational strategy between annual and perennial, and between evergreen and deciduous growth forms (Ogden 1974, Johnson and Tieszen 1976, Abrahamson 1979), and to the effect of habitat on energy allocation strategies (Gadgil and Solbrig 1972, Abrahamson and Gadgil 1972, Gaines et al. 1974, Hickman 1975, 1977, Pitelka 1977, Bostock and Benton 1979, Kawano and Masuda 1980).

Most studies have involved non-woody herbs, and most have been from temperate or desert habitats. Arctic studies have been relatively infrequent. Flower-Ellis (1975) investigated energy allocation of the dwarf evergreen shrub

Andromeda polifolia, in a subarctic mire at Stordalen, Sweden; Weilgolaski and Kjelvik (1975) studied energy allocation to green and non-green tissue in many shrub and non-shrub species from Finnish and Norwegian IBP sites; and Johnson and Tieszen (1976) determined biomass allocation patterns for B. nana, L. palustre, and V. vitis-idaea from an upland tussock tundra at Atkasook, Alaska.

Harper and Ogden's (1970) technique assumes that energy allocation to plant tissue is accurately estimated by tissue weight, i.e. caloric content of different tissues are similar. In many cases, this assumption appears to be valid. Hickman and Pitelka's (1975) study of the relationship between energy allocation patterns based on tissue caloric values and those based on dry weights of plant parts concluded that for plants with primarily carbohydrate, rather than lipid, seed reserves, tissue dry weight analysis produced results nearly as accurate as the much more laborious caloric analyses.

In the following discussion, biomass refers to all living aboveground plant tissue of a species or of a community. Phytomass or standing crop refer to all aboveground tissue, living or dead.

Calorimetry Methods

To validate the use of the biomass separation technique to estimate energy content in B. nana, L. palustre, and V. vitis-idaea, the energy content of the different tissue types in the three species was measured with oxygen bomb calorimetry. Measurement of caloric (energy) values of tissue samples followed the general recommendations of Leith (1975). Each tissue type analyzed was a composite of randomly selected material from 1977 biomass harvests. Tissue from two harvests, one in early June and one in early to mid-August, was analyzed for each species. Samples were prepared by grinding in a Wiley mill and drying at 80 °C for 24 hr, and then pelletized. The pellets were ignited in a Parr adiabatic oxygen bomb calorimeter (Parr Instrument Co.). Ash residue was negligible and no correction for it was made. Two to three samples per tissue type were analyzed unless material was limited, in which case, only one sample was burned. Error estimates were generally 0.1 to 0.6%.

Biomass Partioning - Methods

Changes in seasonal aboveground biomass partitioning were investigated using a harvest technique. Aboveground parts of B. nana, L. palustre, and V. vitis-idaea were harvested from random quadrats by clipping stems rooted in the quadrat at ground level. Because the rhizomatous nature and frequent vegetative reproduction by layering in the three species obscured the concept of individual plants, an individual plant in this study was defined as any shoot that emerged aboveground from the litter, or ground layer.

Because stem densities of the three species were different, a different quadrat size was used for each species to ensure multiple quadrat placements (up to 17) would be required to harvest 40 stems. Quadrat sizes were 0.1 m^2 for B. nana, 0.05 m^2 for L. palustre, and 0.025 m^2 for V. vitis-idaea. Harvests were made at five day intervals from early June until mid-July each year, the period in which plants were growing most rapidly, and then approximately every 10 days until the end of August.

Phytomass compartment categories separated for B. nana were: current leaves, current stems, one year old stems, greater than one year old stems, floral or reproductive tissue, and dead tissue. Compartment categories for L. palustre were: current leaves, one year, two year, three year, and greater than three year old leaves, current stems, one year, two year, three year, and greater than three year old stems, floral or reproductive tissue, and dead tissue. Compartments separated from V. vitis-idaea were essentially the same as those for L. palustre. Samples were dried at 60 °C for 24 hr and weighed to 0.001 g on an electronic balance.

All compartments were not necessarily present at each sampling period, e.g. no current leaves existed at the first June harvest. Also, the reproductive compartment was often subdivided into male and female flowers, or preformed buds.

Results

Caloric Content

Caloric values for component tissues of B. nana, L. palustre, and V. vitis-idaea are presented in Table 6. Some care must be taken in the interpretation of these energy estimates. Since each sample analyzed consisted of well mixed ground tissue from more than one plant, values for standard errors of the mean represent the variance in the calorimetric technique more than the variance within tissues. Also, because some tissue types, e.g. flowers, were a very small proportion of the total plant and, therefore, were in limited supply, the analyses of these compartments were occasionally limited to one composite sample.

Table 6. Caloric values for various tissue types in Betula nana, Ledum palustre, and Vaccinium vitis-idaea. Values expressed as J g-1 ±1SE. Compartments are cl, current leaf;c+1L, one year older than current; c+2L, current plus two year leaf; OL, greater than c+2L; cs, current stem; c+1s, one year older than current; c+2s, current plus two year stem; Os, greater than c+2s; mr, male reproductive; fr, female reproductive; PFB, preformed buds.

Species and compartment	Date	
	June 11, 1977	August 1, 1977
Betula nana		
leaves	1291.4 (1.6)	1174.5 (1.4)
cs	---	1430.0 (1.6)
c+1s	1476.9 (5.9)	1418.6 (3.2)
Os	1296.4 (3.1)	1283.7 (0.4)
mr	1201.5 *	
fr	1246.9 *	
Ledum palustre		
cl	1257.1 (0.3)	1305.2 (6.7)
c+1L	1289.7 (3.0)	1288.8 (0.6)
c+2L	---	1271.5 (4.7)
OL	1287.7 (2.0)	1243.9 *
cs	---	1166.2 *
c+1s	1195.6 (6.5)	1240.0 (4.9)
c+2s	---	1275.3 (0.2)
Os	1271.1 (6.6)	1288.7 (4.6)
PFB	---	1295.3 *
Vaccinium vitis-idaea		
cl	---	1149.5 (2.2)
c+1L	1179.6 (0.2)	1173.6 (0.5)
OL	1178.7 (2.3)	1187.0 (4.9)
c+1s	1194.1 *	---
Os	1175.2 (4.5)	1163.8 (1.3)

---

* one sample only

Relatively little variation in energy content of the different tissue compartments existed in any of the species. In B. nana, the tissue with the lowest energy content, the June sample of old stems, was only 18.6% less than the tissue with the greatest energy value, the June sample of current stems. Maximum variation was much less in L. palustre and V. vitis-idaea tissues. The August sample of L. palustre current stems was only 10.6% less than the energy content of the August sample of current stems, and the August sample of V. vitis-idaea current leaves was only 3.2% less than the content of the greater than one year old leaves.

The energy value of different tissue types also changed very little between June and August. The maximum change in caloric content occurred in the leaf compartment of B. nana. The June 11 energy value was 1291 J g^{-1} and by August 1, the value had dropped to 1175 J g^{-1}, a decrease of only 9%. Most other tissue types in the three species changed less than 50 J g^{-1} between the sample dates. Of the 11 tissues sampled twice in the growing season, seven decreased by August, and four increased. No consistent directional change occurred in any tissue type. For example, energy content of old stems in L. palustre increased, while that of B. nana and V. vitis-idaea decreased between June and August.

Biomass Partitioning

Betula nana

The largest and dominant biomass compartment at all times of the year in *B. nana* was that used for structural support; the stem component (Figs. 32 and 33). In both years of the study, stems of all ages were always at least 70% of the total aboveground biomass. During winter and at snowmelt, when the only other aboveground compartments present were leaf and floral buds, stems represented nearly 100% of the biomass. As leaves developed in June, the stem portion of aboveground tissue gradually decreased. This decrease continued through the growing season, but the rate of decrease slowed in late July and August as leaf tissue development slowed, and as the current stem compartment increased. The current stem compartment began to increase in mid-June 1977, but not until early July in the cooler weather of 1978. The current stems continued to increase until growth halted in late August. Current stems reach near maximum development at the end of their first growing season, and no change in the current plus one year compartment was noted in either year of the study.

The leaf compartment in *B. nana*, represented only by buds at the beginning of June, increased rapidly in the

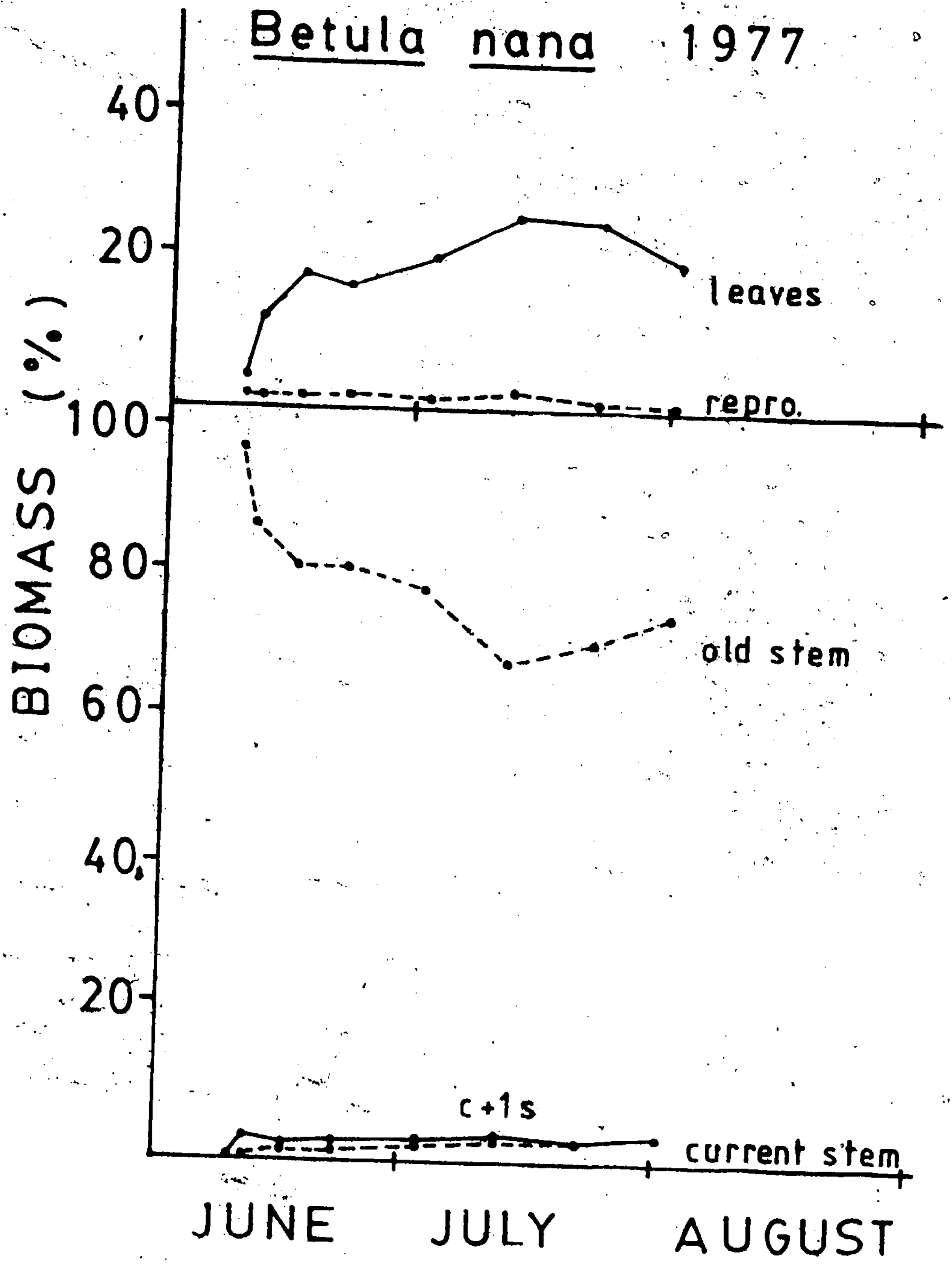


Figure 32. Partitioning of total aboveground biomass of Betula nana in 1977, based on dry weight of tissues. Repro. = reproductive tissues; c+1s = one year old stem; old stem = stems > one year old.

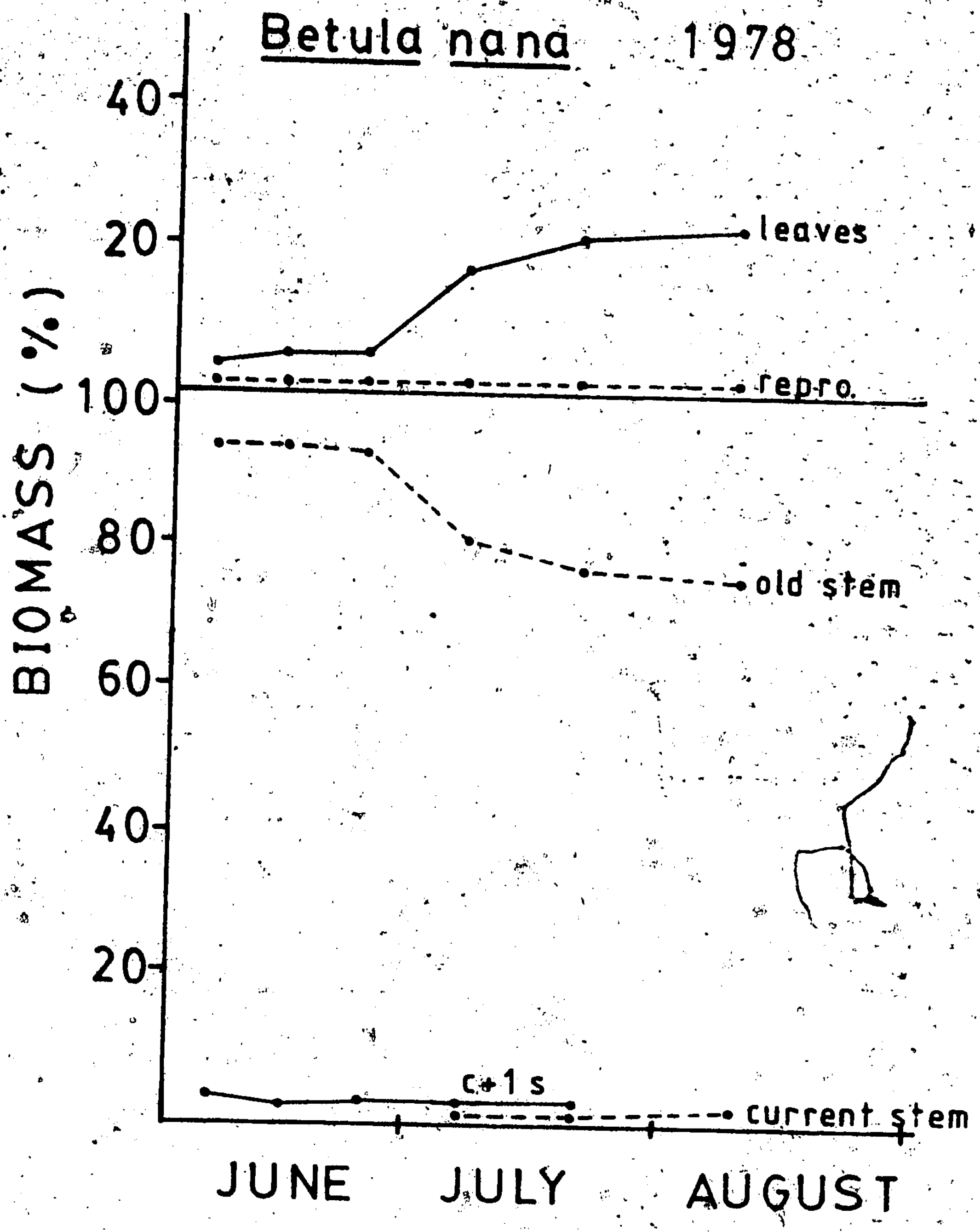


Figure 33. Partitioning of total aboveground biomass of Betula nana in 1978, based on dry weight of tissues. Repro. = reproductive tissues; c+ls = one year old stem; old stem = stems > one year old.

first two weeks, and then increased at a slower pace until a maximum was reached in mid-July, 1977. A small decrease in the leaf compartment was noted at the last two sampling points, but this decrease was not significant.

The pattern of leaf increase was modified slightly in the much cooler June of 1978. Partitioning of biomass to leaves was very slow in June, and increased more rapidly in the last week of the month after the arrival of warmer weather. This more rapid rate continued until the third week of July, beyond which little additional increase was noted.

The reproductive compartment as a portion of biomass was always small in all parts of the growing season, and in both 1977 and 1978. However, in the warmer 1977 season, 51% of the sampled plants (n=322) had flowered, while in 1978, only 21% (n=204) had any reproductive component. Even among those plants which did produce flowers, the maximum mean floral component at any sampling period was only 3%. The reproductive component was less than 1% for most sample periods.

Ledum palustre

Biomass in L. palustre, as in B. nana, was largely in some stem compartment (Figs. 34 and 35). Stems of all ages generally contributed between 50 and 70% of aboveground biomass. This proportion remained relatively steady throughout the growing season, with no major trends appearing. The current stem component appeared in mid-July in both years, and increased to an August maximum of 16.1% in 1977 and 10% in 1978. No significant change in current plus one or two year stems was observed.

While differences in biomass partitioning did exist on a seasonal basis between the different age classes of leaves, the total proportion partitioned to leaves remained relatively constant. The current leaf compartment, represented only by preformed buds at the onset of the growing season, increased to approximately 10% of the biomass by season's end in 1977 and 1978. In 1977 the current plus one year leaf compartment remained essentially constant; however the compartment of oldest leaves dropped slowly through the growing season, reaching a low point at the end of August. A similar pattern existed in 1978, except that the oldest category of leaves showed no drop at the end of the growing season as occurred the previous summer. The current plus one year leaf compartment in 1978 was smaller by about 5% at most sampling dates compared with the sample dates in 1977.

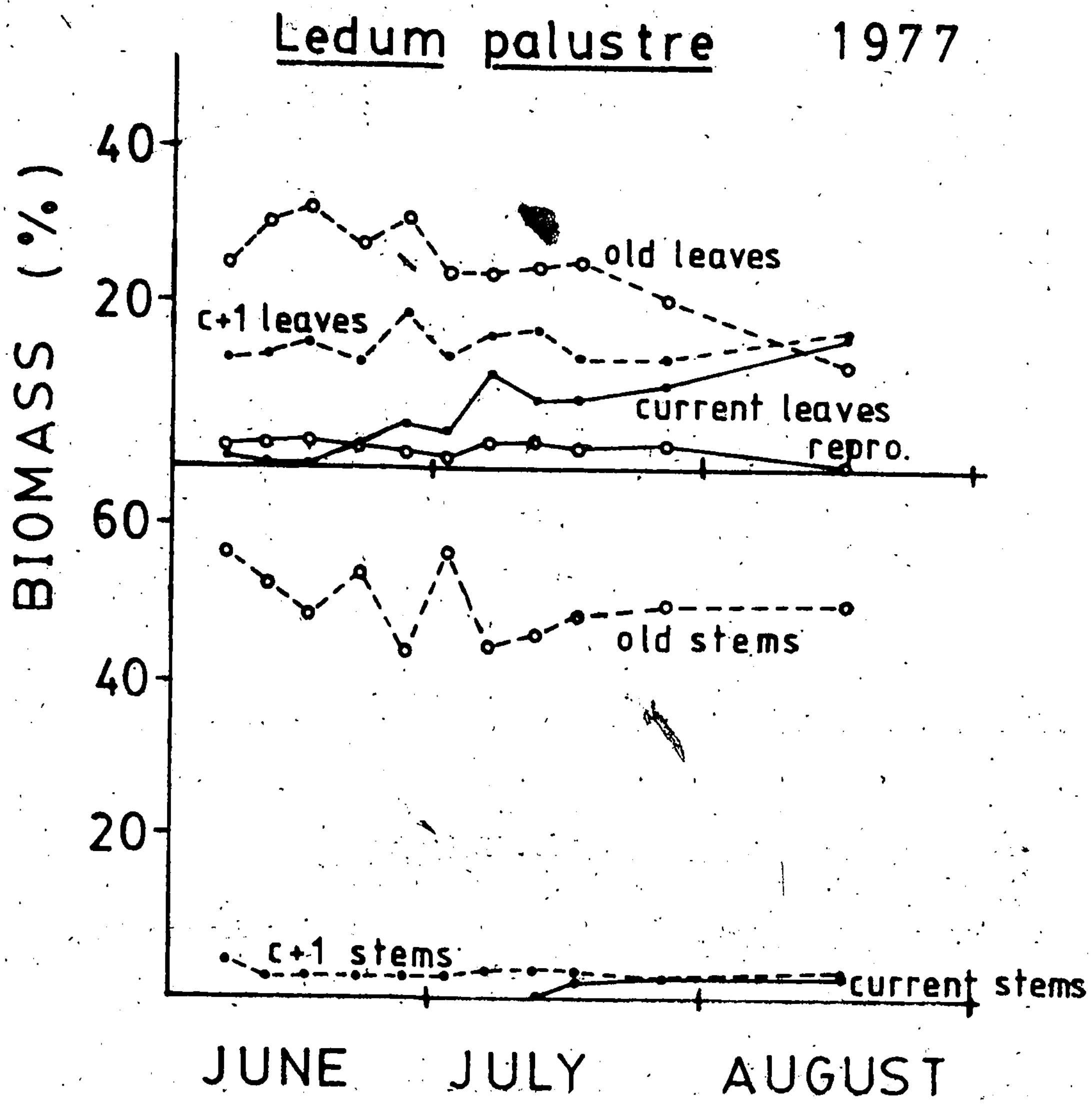


Figure 34. Partitioning of total aboveground biomass of Ledum palustre in 1977, based on dry weight of tissues. Repro.= reproductive tissues; c+1L = one year old leaves; old leaves = leaves > one year old; c+1s = one year old stems; old stems = stems > one year old.

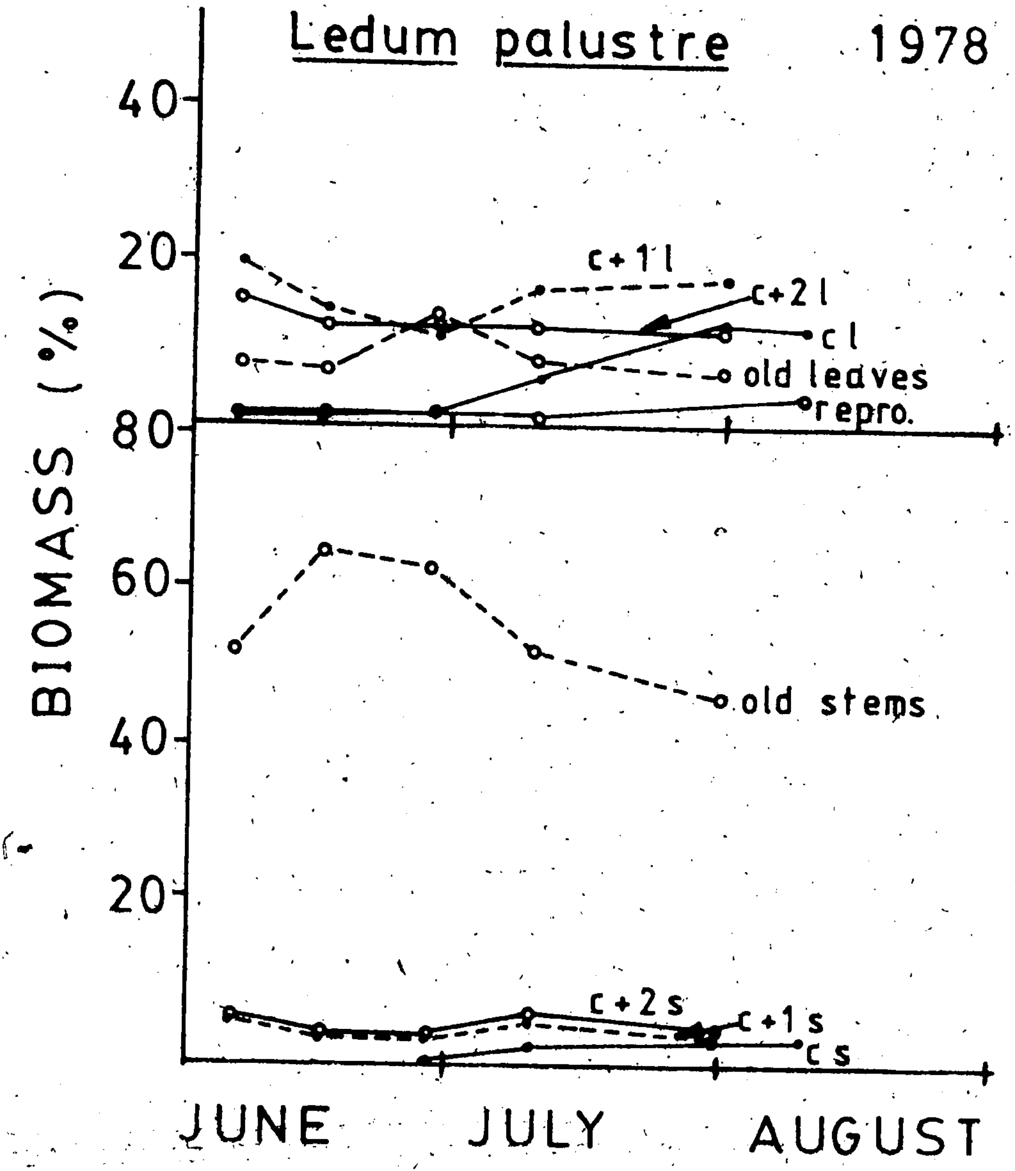


Figure 35. Partitioning of total aboveground biomass of Ledum palustre in 1978, based on dry weight of tissues. Repro. = reproductive tissues; c+1L = one year old leaves; c+2L = two year old leaves; old leaves = leaves > two years old; c+1s = one year old stems; c+2s = two year old stems; old stems = stems > two years old.

As in B. nana, the reproductive compartment was relatively small in L. palustre, remaining under 5% at all times. In 1977, 15% (n=358) of L. palustre plants produced some floral structures, while in 1978, only 12% (n=209) flowered. Though commitment of biomass to reproduction in the whole population of L. palustre was relatively low, those plants that did flower often had more than 12% of their aboveground biomass represented as reproductive tissues. In these flowering plants, commitment of biomass produced in the current year to reproduction was often very high. On July 7, 1977, flowering individuals had mean current biomass commitments of 67% (n=6) to floral tissue, with some plants having 100% of current growth as flowers, indicating that flowering often precedes leafing in this species.

Vaccinium vitis-idaea

Biomass partitioning of V. vitis-idaea in 1977, and 1978 is presented in Figs. 36 and 37. Relative to B. nana and L. palustre, V. vitis-idaea had a relatively small portion of aboveground biomass in stems. Total stem commitment was a maximum of 26% on July 17, 1977, but generally was less than 20% for both the 1977 and 1978 growing season. The noncurrent stem compartments were all relatively unchanged through the growing seasons. Current

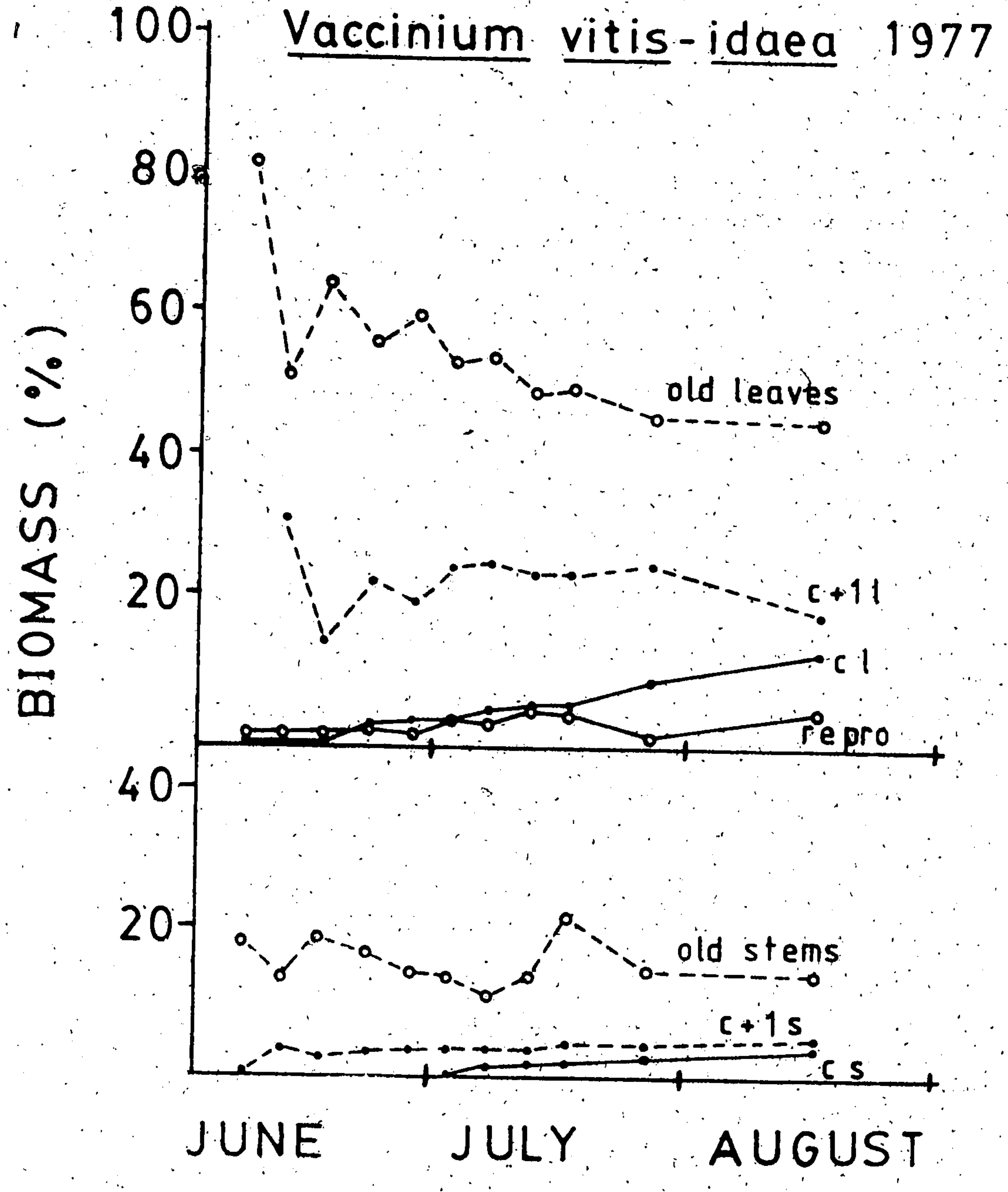


Figure 36. Partitioning of total aboveground biomass of *Vaccinium vitis-idaea* in 1977, based on dry weight of tissues. Repro.= reproductive tissue; cl = current leaves; c+lL = one year old leaves; old leaves = leaves > one year old; cs = current stems; c+ls = one year old stems; old stems = stems > one year old.

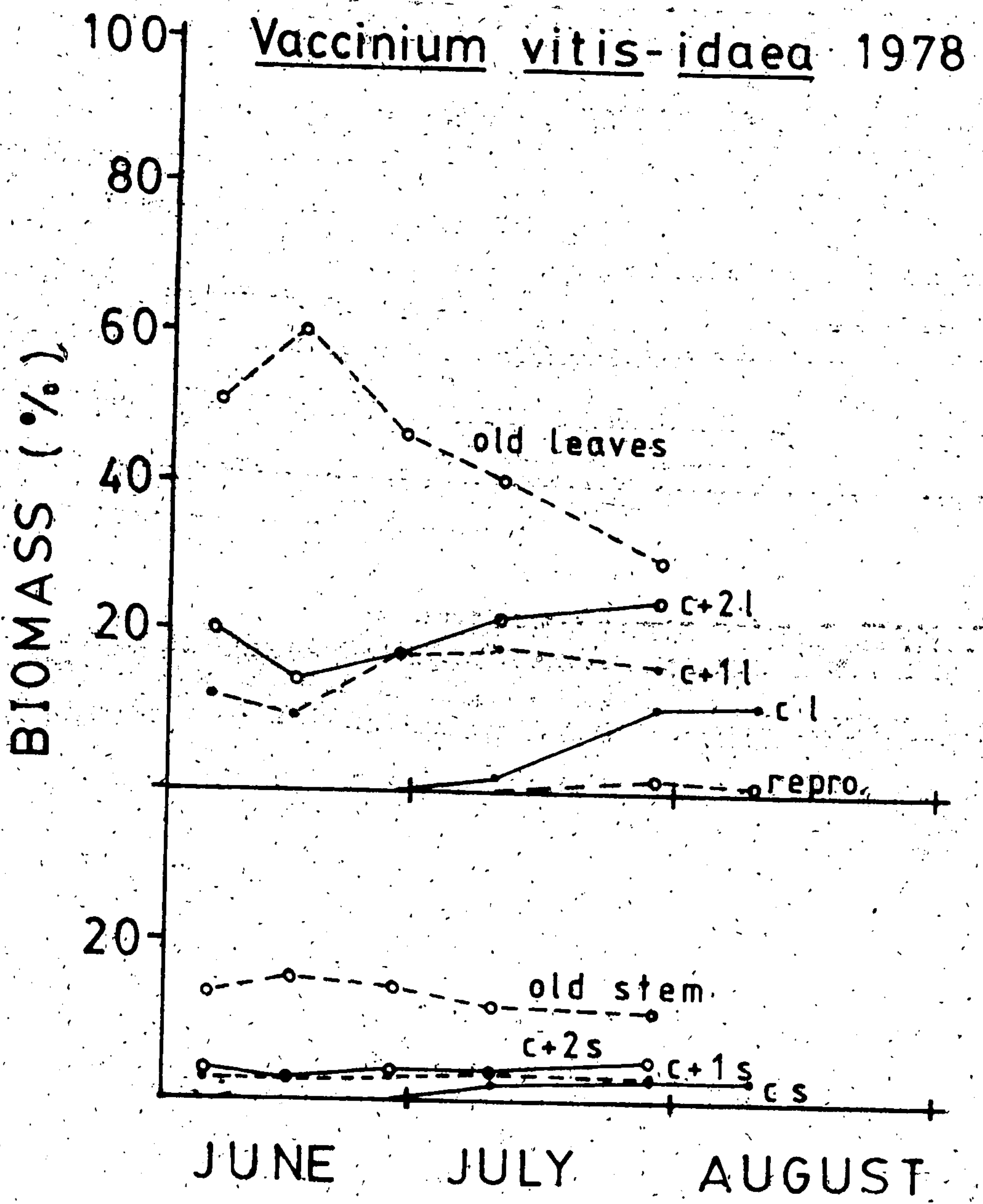


Figure 37. Partitioning of total aboveground biomass of *Vaccinium vitis-idaea* in 1978, based on dry weight of tissues. Repro.= reproductive tissue; cl = current leaves; c+1L = one year old leaves; c+2L = two year old leaves; old leaves = leaves > two years old; cs = current stems; c+1s = one year old stems; c+2s two year old stems; old stems = stems > two years old.

stem components appeared near July 1 in both years, and increased slowly to an August maximum of 3% in 1977, and 2% in 1978. The size of the current stem compartment reached nearly that of the current plus one year stem compartment by the end of the growing season.

The current year leaf compartment was represented by very small preformed buds at the beginning of the growing season, but increased as the season progressed, reaching a maximum of slightly more than 10% at the last sampling date in both years. This compartment began to increase in size several weeks earlier (mid-June) in 1977 than it did in 1978 (late June). The current plus one year leaf compartment remained relatively unchanged in both 1977 and 1978, staying at a level slightly greater than achieved by the current year compartment at season's end. The oldest leaf compartment (greater than or equal to current plus two years in 1977, and greater than or equal to current plus three years in 1978) gradually declined as the growing season progressed, with a low point occurring just before dormancy in the fall. The leaf compartment (all age classes) represents the largest component of living aboveground biomass in V. vitis-idaea. Leaves were more than 70% of the biomass in all parts of the growing season.

As with the other two shrub species, the reproductive compartment of V. vitis-idaea was small compared to leaf and stem compartments, always representing less than 5% of the biomass. In 1977, the reproductive compartment was more than 4% by the end of the growing season, but was never larger than 1% in 1978. In 1977, 13.6% of the sampled plants (n=316) supported some reproductive tissue, while in 1978 only 9% (n=209) did. Of those plants that did flower, the reproductive compartment was much larger than in the population as a whole. In flowering individuals, the mean portion of aboveground biomass that was reproductive tissue was over 17% during peak flowering (July 17, 1977), and was 46% on August 17, 1977 when fruits were nearly fully developed. These values were reduced in 1978 when 7% of the tissue of flowering plants was reproductive on July 10, and 8% on July 29. No data were available for V. vitis-idaea when fruits were fully developed in 1978.

Data for V. vitis-idaea include shoots which supported current growth and shoots which did not have current growth. Thus, these data differ from those for B. nana and L. palustre which generally had a greater percentage of stems actively growing.

Discussion

Calorimetry

Caloric content of *B. nana*, *L. palustre*, and *V. vitis-idaea* showed little variation on either a seasonal basis, among tissue types within a species, or between species. Though the caloric content of these three arctic dwarf shrubs were generally higher than reported for temperate and tropical species (Golley 1961), the values were very similar to those reported for other plants from higher elevation sites at lower latitude, as well as other arctic sites (Bliss 1962, Sonesson 1975, Dennis et al. 1978).

Vaccinium vitis-idaea from dry meadows at five Norwegian tundra sites averaged 1172 J g^{-1} for green tissue and 1123 J g^{-1} for non-green, compared to 1170 J g^{-1} and 1164 J g^{-1} for the same tissue types in the current study. For mixed stems and leaves of *V. vitis-idaea* from alpine tundra of Mt. Washington, Bliss (1962) calculated caloric contents as 1191 J g^{-1} in late June and 1209 J g^{-1} ~~in~~ mid-August compared to 1182 J g^{-1} and 1169 J g^{-1} for these sample types from the Mackenzie Delta uplands.

Similarities also existed for *Betula minor* from the Mt.

Washington site and B. nana at the Mackenzie Delta site. Bliss (1962) reported caloric contents of leaf and stem tissue as 1230 J g^{-1} and 1249 J g^{-1} in June and August respectively, while similar samples in the current study had 1317 J g^{-1} and 1327 J g^{-1}.

Though no data are available on caloric content of L. palustre from other arctic sites, L. palustre tissue energy values from this study were very similar to those of L. palustre subsp. groenlandicum at the alpine Mt. Washington site (Bliss 1962).

The higher energy contents of arctic and alpine plants have been attributed to higher percentages of lipid in the tissue (Hadley and Bliss 1964), and to the greater amounts of soluble carbohydrates relative to structural material that occur under low temperature stress (Mooney and Billings 1960, Berg et al. 1973, Wielgolaski and Kjelvik 1975).

The low variance of caloric content in different tissues of B. nana, L. palustre, V. vitis-idaea and the similarly low variance of energy content within a tissue type throughout the growing season have important implications in the evaluation of energy allocation in these species. Because the energy content of the different tissues is similar, data for biomass partitioning within a plant should provide nearly as accurate an evaluation of differences in energy allocational patterns as the more laborious conversion to tissue energy contents. In a study of annual and perennial herbs, Hickman and Pitelka (1975) concluded that no significant differences in energy allocation patterns were found when using caloric or dry weight measures of species with low lipid levels in seed reserves. The remaining analyses and discusssion of energy allocation patterns in this study shall, therefore, be based on patterns of biomass partitioning.

Biomass Partitioning

Betula nana

The general pattern of partitioning of the aboveground biomass of B. nana in the Mackenzie Delta uplands is very similar to that found in the tussock tundra of Alaska's north slope (Johnson and Tieszen 1976), and of other deciduous shrubs in various other arctic sites (Wielgolaski and Kjelvik 1975, Stoner et al. 1982). The dominant feature of this partitioning pattern in B. nana and most other deciduous shrubs is the large biomass commitment to woody sructural tissue, and the much smaller one to leaves. On the current study site, B. nana always had more than 70% of living aboveground tissue represented as woody stems. . .

Betula nana in the Mackenzie Delta region is very near the northern limit of its range (Fig. 14). Farther north, the shorter growing season (45-50d), low temperatures, and low levels of available radiation (Courtin and Labine 1977) are probably inadequate to support the strategy of annual replacement of photosynthetic tissue (the leaf compartment). Obviously, the deciduous growth form can successfully exist in the Mackenzie Delta area, as indicated by the widespread occurrence of B. nana and several species of Salix. Except for Alnus crispa, another deciduous shrub occurring on moister sites with greater winter snow cover, B. nana is the tallest upland shrub in the area, with heights of up to 0.75 m. This height, which requires large amounts of supportive stems, allows B. nana to present its photosynthetic surfaces above the canopy of all other species, and, therefore, maximize radiation interception. Combined with a relatively high photosynthetic potential (Johnson and Tieszen 1976), this ability to maximize radiation interception helps B. nana fix sufficient carbon each growing season to allow the high annual carbon turnover associated with the deciduous growth form.

The fraction of the aboveground biomass that was stems dropped as the growing season progressed and the photosynthetic fraction increased when the current crop of leaves developed. This same pattern occurred in both years of the study (Figs. 32 and 33), however the cool period in early June, 1978, delayed the development of leaves. This delay was reflected in the lower percentage of leaf tissue in June 1978, and by the higher percentage of stems during that same period. This rapid increase in the leaf compartment reflects the need for a deciduous leaf to maximize its photosynthetic life so a net positive carbon contribution can be made. The rate of increase in compartment size is slower than shown for leaf growth in Chapter 4 (Fig. 18). Leaves from all canopy positions, including the leaves from inner bud positons with delayed development, were measured in the compartment technique. Thus, leaf development appears to occur over a longer period than when only outer leaf positions are sampled, as with the individual leaf technique. Partitioning of biomass was similar by mid-August of both years however.

A slight decrease in the leaf fraction after mid-July 1977 was not significant statistically. However, there was a real loss of tissue in both years of the study after that point. The precision of the sampling technique used did not allow identification of this loss. As reported in the previous chapter, a mean reduction of 4% of leaf surface from herbivore damage occurred on those leaves present just before autumn abscission. Additionally, entire leaves were lost by abscission due to various unknown causes, and by severance of the petiole by insects.

The reproductive compartment of B. nana was very small in 1977 and 1978; however, these data do not fully represent carbon committed to this compartment. In June, male catkins developed and eventually released pollen, after which the catkins generally dried and dropped from the plant. After fertilization, the female catkins increased in size and weight as the seeds matured. Since the male catkins and their pollen are no longer present in August, these late season values do not represent the total allocation of carbon to reproduction. However, even if an adjustment for this carbon loss was made, reproductive effort in B. nana relative to structural or photosynthetic development was still very small.

The significant reduction in number of plants flowering in 1978 relative to that in 1977 was not as well correlated with environmental conditions in the year of floral bud development as it was with environmental conditions in the season of actual flowering. Floral buds of flowers blooming in 1977 and 1978 were preformed in 1976 and 1977 respectively. In both 1976 and 1977, Inuvik received near average numbers of degree days (Table 3). Thus flowers blooming in both years of this study developed from buds formed under similar conditions. However, in 1977, 51% of sampled individuals flowered, while only 21% flowered in 1978. A below average number of degree days were received in Inuvik in 1978. This reduction in flowering may have been caused by abortion of floral initiatives in the cooler June of 1978.

Ledum palustre

The general pattern of partitioning of aboveground biomass in L. palustre in the Mackenzie Delta uplands was similar to that found in L. palustre growing in tussock tundra of Alaska (Johnson and Tieszen 1976, Archer and Tieszen 1980). Aboveground biomass was divided about evenly between woody stems and leaf tissue, with reproductive tissue relatively low at all points in the growing season. Ledum palustre is a canopy subdominant in the community, overtopping all species except B. nana and an occasional Salix individual. The maintenance of this canopy position requires significant structural support, resulting in a relatively large stem component. In most microsites, L. palustre leaves are shaded by the taller B. nana, resulting in less than maximum radiation interception. This reduction appears to be less of a limitation for evergreen dwarf shrub growth forms than for deciduous species. Johnson and Tieszen (1976) have suggested that the lower photosynthetic rates of these evergreen shrubs are compensated for by the retention of leaves for more than one season, increasing the photosynthetic life and thus allowing the leaves to make a net positive carbon contribution to the plant, though not necessarily in one growing season.

Nutrient limitations may be greater limitation to plant growth in the arctic than low levels of radient energy (Chapin et al. 1980b). Retention of leaves for several years may be an advantage in a nutrient limited environment. Evergreen species such as L. palustre and V. vitis-idaea are more efficient and conservative in their use of the limited nutrients than are deciduous plants because evergreen species retain and use these nutrients within their tissues for multiple years (Reader 1978, Chapin 1980b, Shaver 1981).

The interception of subcanopy radiation by the photosynthetic surfaces of L. palustre was maximized by their position high in this subcanopy, even though they were shaded by B. nana in many cases. Frequently in this community, where B. nana is not present, L. palustre did form the upper canopy and thus received the maximum available radiation. No differentiation between shaded and unshaded L. palustre was made during sampling, and thus no differences in growth were noted.

The large stem compartment was also important in the vegetative reproduction of L. palustre. Layering frequently occurred when weight of leaves and stem tissue brought the stem into contact with the ground, or when lichens, mosses, or organic debris covered stems, and adventitious roots formed from the node. Long stem sections and relatively long distances between layering nodes, thus allowed "dispersion" of offspring from the "parent" ramet. While establishment of L. palustre seedlings appeared rare, a fair proportion of individual plants did flower each year, and of those that did flower, a large fraction of their current year's growth was commited to reproduction (up to approximately 70% in some cases). Ledum palustre is a common understory component of the taiga to the south, where sexual reproduction and seedling establishment may be more successful. It may, therefore, have been successfully reproducing in these uplands of the Mackenzie Delta when an overstory of black spruce, Picea mariana, was present, as recently as 5,500 years B.P. (Ritchie and Hare 1971, Ritchie, 1976, 1977). As cooler environmental conditions prevailed, the trees receded south (Black and Bliss 1980). Many of the understory species remained, although perhaps with a diminished sexual reproductive success as expressed by the plants in the current study.

A second explanation of the presence of large carbon commitments to an infrequently successful reproductive effort may be maintenance of genetic diversity within the population. Successful establishment of L. palustre may occur only rarely, and only when several years of proper temperature, moisture, length of growing season, and appropriate seedbed coincide. Appropriate seedbeds may be formed by fire, natural slumpages, or such disturbances by man as seismic lines, winter roads, or gas well drilling pads. Yet these infrequent occurrences of successful establishment may be adequate to maintain sufficient genetic diversity to provide ecotypes that could survive in the marginal environment near the northern limit of the species' range in this part of the Arctic.

The reduction in the portion of individuals flowering in the second year of the study is better correlated with environmental conditions present in the year of flowering than in the year of floral bud development. The percentage of plants flowering dropped to 12% in 1978 from 15% in 1977, corresponding to a drop in degree days received. Floral buds for these flowering periods were all preformed under similar conditions. This reduction in flowering may have been caused by the abortion of the floral initiatives in the early, cooler portion of the 1978 growing season.

Changes in the leaf compartment of L. palustre through the season, and differences between years are very similar to the patterns expressed by leaf growth analysis (Chapter 4). The late development of the current leaves in 1978 was associated with later snowmelt and lower temperatures in early June of that year. The compartment grew larger throughout the season, with the early growth in size associated with sclerophyllization near the end of the growing season. This development of sclerophylly ended growth of the leaf and thus, the leaf compartment, as indicated by the similarity between the sizes of the current compartment at the end of the two growing seasons, and by the similarity of that compartment with the size of the current plus one year leaf compartments. The relatively uniform size of the current plus one year leaf compartment throughout the growing season also suggests that no further growth occurred in a leaf after the end of its initial season.

The oldest leaf compartment (greater than or equal to current plus two years) showed a gradual drop in total percentage through the growing season in 1977, reflecting both the increasing amount of current leaves present as well as the abscission of older leaves in their third and fourth years. These older leaves usually shifted from deep green coloration to yellow and orange in July, immediately before abscission. The increased rate of leaf loss in the latter half of the growing season is also reflected in the rapid drop in size of the oldest leaf compartment at that time. This loss of leaves does not represent a loss of net photosynthetic surface, since the current year leaves are nearing full expansion at this time.

No similar decrease in the oldest leaf compartment was indicated in 1978 as would be expected, even though coloration and abscission of older leaves was observed in the field. The plants sampled in June may either have had an abnormally small complement of older leaves or those sampled in August had an abnormally high complement, and thus obscured the loss observed in the field. Leaf abscission in L. palustre may perhaps also be retarded in cool years.

Vaccinium vitis-idaea

Unlike B. nana and L. palustre, stems are a relatively small compartment in V. vitis-idaea (Figs. 36 and 37), and do not provide a major supportive structure that raises the leaves into the upper canopy. It generally has a low, sometimes prostrate growth form, rarely more than 10 cm high. Only in low-light situations under a dense overstory canopy did V. vitis-idaea ever have upright growth, and even then was seldom over 15 to 20 cm high. Thus in areas dominated by one of the taller shrubs, V. vitis-idaea would only be exposed to lower levels of incoming radiation and thus have less radiant energy available for growth. Johnson and Tieszen (1976) suggest that long leaf retention (up to eight years in V. vitis-idaea) allows evergreen species to successfully maintain lower photosynthetic rates by postponing attainment of net positive carbon contributions by the leaves. This same argument would explain the success of this species as an important understory shrub.

Of the three species studied, V. vitis-idaea has the greatest leaf longevity, though an accurate estimate of the average photosynthetic life is not available because of the difficulties associated with the determinate growth of stems. This long leaf life is also associated with the lowest photosynthetic potential (Johnson and Tieszen, 1976) as well as a physiognomic position in the lower strata where radiation levels are reduced. The long retention time for V. vitis-idaea leaves may thus be a compensation for this reduced potential for energy fixation. A net positive carbon cost to the plant may only be achieved after several years of carbon contributions at a lower rate. Additionally, the relatively high percentage of leaves in the biomass reduces maintenance costs by minimizing such non-carbon fixing structures as stems.

While there was a delay in production of the current leaf component in the cool June of 1978, this delay was probably less significant to V. vitis-idaea than for B. nana, both because the leaves have a longer photosynthetic life and because of the more gradual development of this compartment in V. vitis-idaea under average conditions.

The gradual decrease in the oldest leaf compartment throughout the growing season of both years reflects the abscission of some older leaves. The more rapid decrease in 1978 is probably the result of the manner in which the data are presented. Current plus two year leaves are included in the 1977 data, and this class had a very low abscission rate, while current plus three year leaves were the youngest included in this data class in 1978, and had a higher abscission rate.

Though the portion of tissue allocated to reproductive purposes is small relative to that used in support and carbon fixation, particularly in 1978, those plants that did flower, had surprisingly large amounts of carbon committed to reproduction. The value to V. vitis-idaea of such a large energy commitment to a relatively unsuccessful reproductive effort, at least in the two years of the study, may be the same as that described for L. palustre in this chapter. That is, the reproductive effort may be a trait useful to V. vitis-idaea over a large part of its range where it is a boreal forest understory species, and sexual reproduction may be more successful.

Or it may be worthwhile in the long run because of the genetic diversity that it generates in those few, uncommon years when proper conditions are met and sexual reproduction is more successful. The value and efficiency of a reproductive trait may appear different when the base of comparison changes. Chester and Shaver (1982) found that many arctic species were actually more reproductively efficient than temperate species when viable seed reproductive effort was analyzed rather than simple total reproductive effort.

As with the other two species studied, flowering in V. vitis-idaea was sensitive to low June temperatures. The number of plants flowering, and the percentage of aboveground biomass in floral structures was higher when floral buds were formed in a summer of average degree days (1976, Table 3), and more flowering took place in a summer of average degree days (1977) than when flowering was in a year of below average degree days (1978) and the floral buds had been formed in an average summer (1977). Thus, environmental conditions in the year of flowering appear more important in determining the reproductive effort than those in the year of floral bud initiation.

NET PRODUCTION

Introduction

Relative to many temperate plant communities, those in arctic environments generally have low productivity. Net annual aboveground production of vascular plants is often under 20 g m^{-2} yr^{-1} in polar semi-desert sites in the High Arctic, while most shrub communities in low arctic tundra are under 200 g m^{-2} yr^{-1} (Wielgolaski et al. 1981). Limits to arctic plant productivity include low temperatures (Bliss 1956, 1966, Miller et al. 1976), a short growing season (Lewis and Callaghan 1976), and soil nutrient deficiencies (Shultz 1964, Bliss 1971, Babb and Whitfield 1977, Chapin 1980b, Chapin et al. 1980a, 1980b).

The low nutrient levels in arctic soils are a function of several factors. Nutrient input to most tundras is low because of low precipitation, slow rates of mineral decomposition, and low levels of nitrogen fixation (Dowding et al. 1981). Most nutrients in the tundra ecosystem are tied up in organic matter (Chapin et al. 1980b, Dowding et al. 1981), and release of these nutrients is limited by low rates of decomposition due to low soil temperatures (Chapin et al. 1980b). Low pH in most tundra soils also favors adsorbtion of H^+ to the cation exchange complex rather than metallic cations (Gersper et al. 1981). Additionally, low soil temperatures may lower rates of nutrient uptake by the plant roots (Chapin 1978), though this limitation may be less important than the others (Dowding et al. 1981). Most inorganic nitrogen in tundra soils is in the form of ammonium, though in drier sites nitrate levels may equal ammonium levels (Gersper et al. 1981). Nitrification appears to proceed more slowly than mineralization in these soils; the latter having been shown to occur in the cold, anerobic conditions common to most tundra soils (Gersper et al. 1981). Soil phosphorus is primarily in an organic form and levels of inorganic phosphorous are generally very low (Chapin et al. 1978).

Nutrient supplementation of arctic soils by fertilization has been used to evaluate the role of these low nutrient levels in limiting productivity. Addition of nitrogen and phosphorous by fertilization has been demonstrated to increase productivity of a low arctic dwarf shrub community and its component species (Haag 1974), and an Alaskan graminoid-dominated tundra which included dwarf shrubs (Chapin et al. 1975, Shaver and Chapin 1980).

Methods

To assess the amount of aboveground biomass present, rates of net annual production, and the effect of nutrient addition on productivity and stem elongation, four 10 x 10 m experimental plots were delineated. Each plot was subdivided into four 5 x 5 m subplots. One 10 x 10 m plot was reserved as a control (no treatment) and the remaining three plots were each fertilized on July 25, 1977 with one of the following treatments: nitrogen as ammonium nitrate (34% N); phosphorous as Superphosphate (20% P); or a combination of both nitrogen and phosphorous. In each case, N and P were applied at a rate of 200 kg of the element per hectare.

A composite sample of the organic soil from 5-20 cm in the inter-hummock troughs from each experimental plot was collected at the end of August, 1978 and analyzed by the Alberta Soil and Feed Testing Lab (Alberta Government, Edmonton). Nitrate nitrogen and phosphorous were analyzed using a Bray extraction of ammonium floride with weak sulfuric acid at 5:1. Sodium and potassium were analyzed with a 1N ammonium acetate extraction at pH 7.0. Aluminum and manganese were extracted with a 0.02 M $CaCl_2$ solution.

Plants were harvested from the plots between August 10 and August 22, 1978. Within each 5 x 5 m subplot, all vascular plants rooted in five 20 x 100 cm random quadrats were clipped at ground level and the plants from the five quadrats were combined. Thus each sampling unit represented vegetation from a total area of 1.0 m^2 in each subplot. Mosses and lichens at ground level within the quadrats were also combined for each subplot. Vascular plant species in the sample were separated into four groups: B. nana, L. palustre, V. vitis-idaea, and all remaining species.

The three individual species were each subdivided into the following tissue categories: current leaves, current stems, current reproductive tissue (flowers or preformed floral buds), non-current living tissue, and standing dead tissue. Current stems were further subsampled by random selection, and the length of each stem in the subsample was measured. All tissue samples were dried at 60 °C for 24 hr and then were weighed.

The 10 x 10 m treatment plots varied in the amount of non-current live tissue present in them. This non-current live tissue was largely stems, but also included non-current leaves in L. palustre and V. vitis-idaea (Table 7). Since large plants with many shoots will produce more new stems and leaves than small plants with few shoots, a correction for this lack of uniformity would make recognition of fertilizer effects more clear.

To evaluate the effect of the fertilizer treatments on

Table 7. Non-current biomass of *Betula nana*, *Ledum palustre*, and *Vaccinium vitis-idaea* in the four fertilizer treatment plots. Data expressed as g m^{-2} ± (1SE). n=4

Species	Treatment			
	Control	N	P	N+P
Betula nana	105.0 (34.9)	172.0 (8.5)	114.3 (18.3)	78.1 (10.6)
Ledum palustre	35.8 (6.8)	65.6 (25.8)	58.1 (9.9)	37.1 (4.5)
Vaccinium vitis-idaea	27.8(7.0)	16.7 (8.8)	21.1 (2.8)	29.4 (5.4)

net annual production and to adjust for this variance in non-current tissue among plots, an analysis of covariance (ANCOVA)(Snedecor and Cochran 1967) was completed. The amount of non-current living tissue, a rough estimate of plant size, was used as the covariate in the adjustment of treatment means. Tukey's multiple range test (Snedecor and Cochran 1967) determined the significance of existing differences between treatment means.

The effect of fertilization on stem elongation was evaluated with an analysis of variance, (ANOVA) (Snedecor and Cochran 1967). Tukey's multiple range test determined the significance of differences in stem lengths between treatments.

An underestimate of net annual production results from this method of clipping and separating current growth because it ignores radial growth of stems (Whittaker 1963, Bliss 1966). This error should be similar in all treatments, and a comparison of growth differences among treatments, but not species, would still be appropriate.

Results

Results of the soil nutrient analyses of samples from control and fertilized plots are presented in Table 8. The

Table 8. Soil test results for NO^{3-}, P, K, Al, Mn, and pH from experimental and control plots one year (August 31, 1978) after fertilization (July 25, 1977). Samples collected at 10 cm from inter-hummock troughs. * OM + Ah from hummock. Data expressed as ppm.

Treatment	Test Parameter					
	N	P	K	Al*	Mn*	pH
Control	0.5	19.0	186.5	9.2	16.8	4.5
Nitrogen	0.5	15.5	138.5			4.6
Phosphorous	0.5	26.0	260.0			4.3
Nitrogen + Phosphorous	0.5	18.5	158.0			4.5

samples represent organic material from inter-hummock troughs, where most rooting occurred. Estimates of biomass and net annual production of B. nana, L. palustre, V. vitis-idaea, the combined group of all remaining species in the community, and the total community are presented in Table 9. The biomass of the total community was 277 g m^{-2} at peak season (August 10, 1978). The three dwarf shrubs represented 88% of the community biomass. The estimated net annual production for the whole community was 54 +/- 7 g m^{-2}. Of this net annual production, 76% was contributed by B. nana, L. palustre, and V. vitis-idaea. Standing crop of lichens was 108 +/- 23 g m^{-2}, of moss 40 +/- 13 g m^{-2} and of litter 272 +/- 33 g m^{-2}.

Betula nana accounted for 49% of the biomass (136 g m^{-2}) and the net annual production of 31 +/- 9 g m^{-2} was 57% of the total. Large amounts of dead stem tissue (81 +/- 31 g m^{-2}) were present in the canopy of B. nana. The severely weathered character of this dead material indicated that it was not dropped from the plant until many years after its death.

The biomass of L. palustre was 42 g m^{-2} (15% of the entire community), and the 1978 net annual production of 6 +/- 1 g m^{-2} was 11% of that of the community. Though less dead material was retained in the canopy of L. palustre than

Table 9. Peak season biomass and net annual production of *Betula nana*, *Ledum palustre*, *Vaccinium vitis-idaea*, all remaining vascular species, and the total vascular community.

Species	Parameter	g m^{-2}(± 1SE)
Betula nana		
	current leaves	27.8 (7.9)
	current stems	1.9 (0.3)
	current flowers	0.4 (0.2)
	preformed buds	0.4 (0.2)
	biomass (non-current)	105.0 (34.8)
	standing dead	81.1 (31.3)
	total biomass	135.5
	net production	6.0 (1.2)
Ledum palustre		
	current leaves	4.4 (1.0)
	current stems	0.7 (0.1)
	current flowers	0.9 (0.2)
	preformed buds	0.1 (0.02)
	biomass (non-current)	35.8 (6.8)
	standing dead	12.3 (5.8)
	total biomass	41.8
	net production	6.0 (1.2)
Vaccinium vitis-idaea		
	current leaves	3.6 (0.9)
	current stems	0.5 (0.1)
	current flowers	0.2 (0.04)
	biomass (non-current)	27.8 (7.0)
	standing dead	0.8 (0.2)
	total biomass	32.0
	net production	4.2 (1.0)
Remaining vascular species		
	current tissue	12.8 (1.1)
	biomass (non-current)	19.4 (5.4)
	standing dead	14.8 (2.4)
	total biomass	32.3
Total vascular community		
	biomass	241.7
	net production	53.6 (7.0)

in *B. nana* on an absolute weight measure, it did represent a fair percentage of the aboveground standing crop of the total community. The biomass of *V. vitis-idaea* was 32 $g\ m^{-2}$ or 12% of the entire community. Net annual production of *V. vitis-idaea* (4 +/- 1.0 $g\ m^{-2}$) was 8% of the community production. Standing dead tissue was very small relative to that in the two other shrubs.

The ratio of net annual production to biomass varied amongst the species studied. The two evergreen species, *L. palustre* and *V. vitis-idaea*, had similar ratios; .144 and .132 respectively. Deciduous *B. nana* had a ratio of .291, while the remaining vascular plant species in the community, which included many graminoids, had a ratio of .397.

Fertilizer addition had different effects on stem growth, as measured by stem elongation, in the three species, and amongst the deciduous and evergreen growth forms (Fig. 38). Stem growth of *B. nana* was not significantly affected by any treatment. *Ledum palustre* showed significantly increased stem growth under all fertilizer treatments relative to the control. The smallest increase (22%) occurred with P addition, and the largest (40%) was displayed with N+P fertilization. No significant increases in stem elongation were exhibited by *V. vitis-idaea* after any of the treatments.

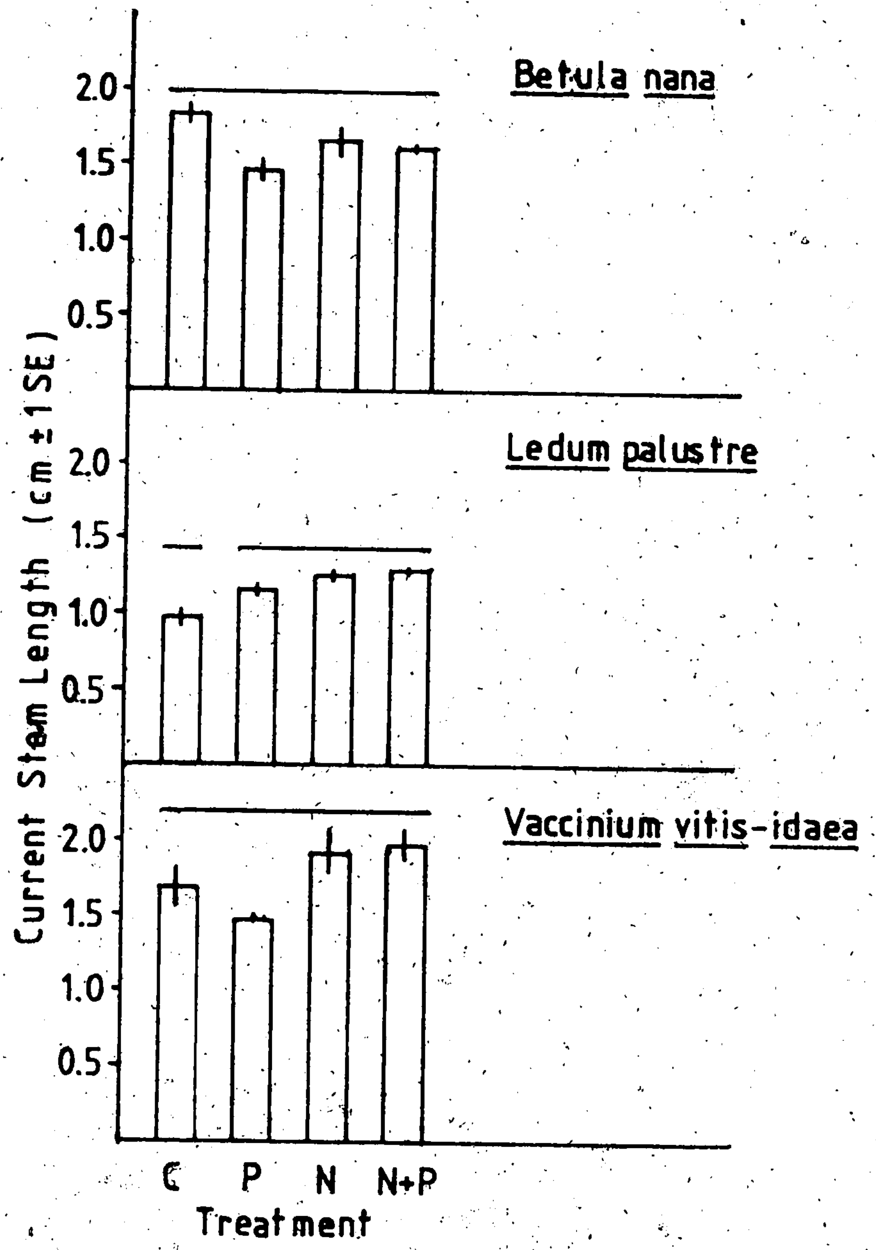


Figure 38. Effect of N and P on elongation of current year stems in Betula nana, Ledum palustre, and Vaccinium vitis-idaea. C = control. Columns under a single horizontal line are not significantly different at $P = 0.05$.

Results of the analysis of covariance (ANCOVA) and the multiple range tests on the effect of fertilization on net annual production of the different tissue compartments of B. nana, L. palustre, and V. vitis-idaea are presented in Figs. 39, 40, and 41. Adjustment of treatment means using ANCOVA produced no trends in net annual production that were not shown by the unadjusted means. Only relative amounts of change in production were modified by the ANCOVA analysis.

Fertilization had no significant effect on the net production of either current stems, current leaves, or total current tissue of B. nana, even after correction for differences in non-current biomass per treatment. Nor did any trends in net production appear amongst the tissue types, except for an increase in current stems after N fertilization.

The adjusted means of net annual production for different tissue types in the evergreen species showed greater differences after fertilization than did those of the deciduous B. nana. Net annual production of L. palustre was not significantly affected by any of the nutrient additions when compared with the control.

Fertilization did increase current stem production in L. palustre. Relative to the control, addition of N+P

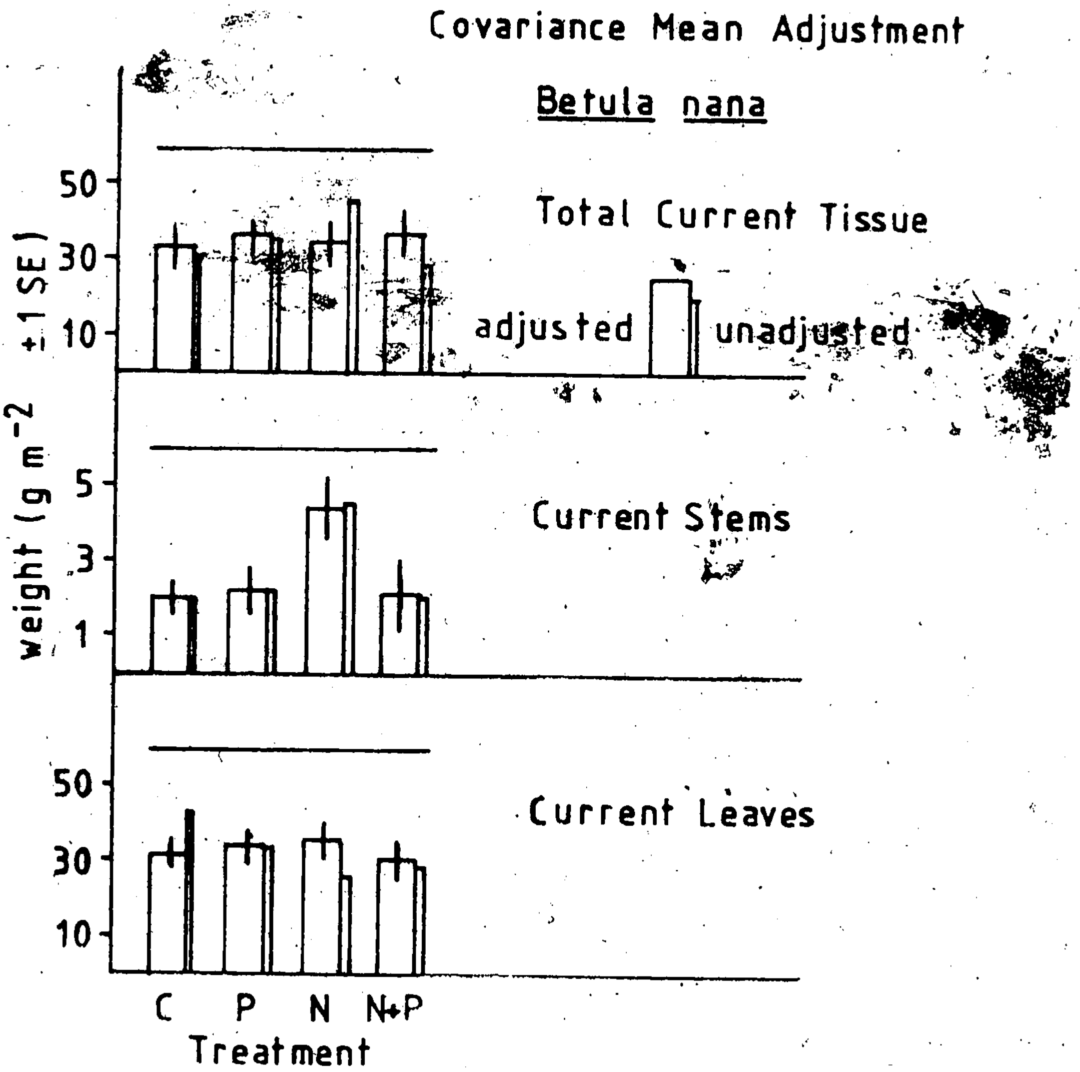


Figure 39. Effect of N and P on dry weight of current tissue in *Betula nana*. C = control. Adjusted refers to data adjusted by ANCOVA to account for differences in non-current tissue among plots. Columns under a single horizontal line are not significantly different at P = 0.05.

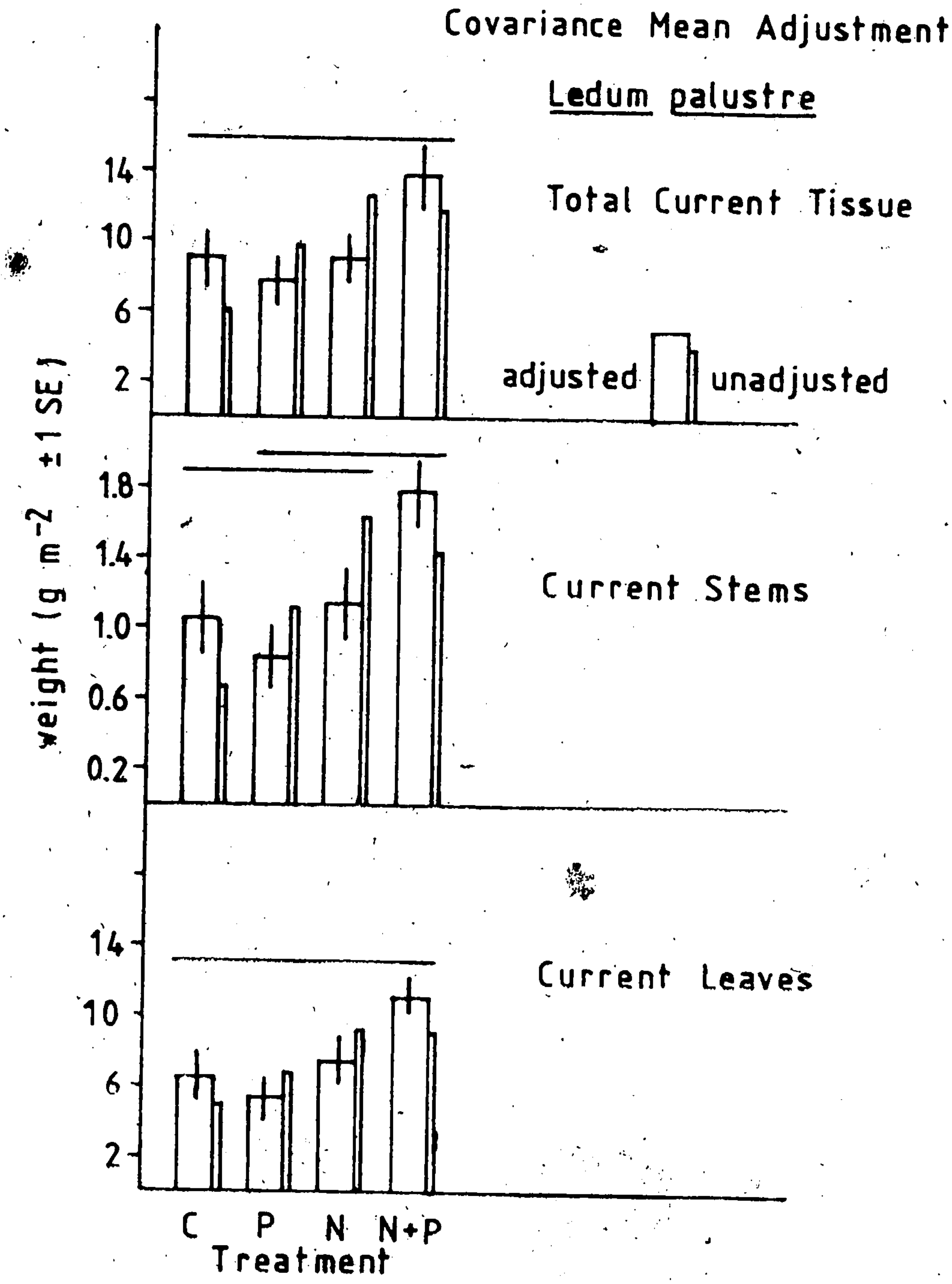


Figure 40. Effect of N and P on dry weight of current tissue in *Ledum palustre*. C = control. Adjusted refers to data adjusted by ANCOVA to account for differences in non-current tissue among plots. Columns under a single horizontal line are not significantly different at $P = 0.05$.

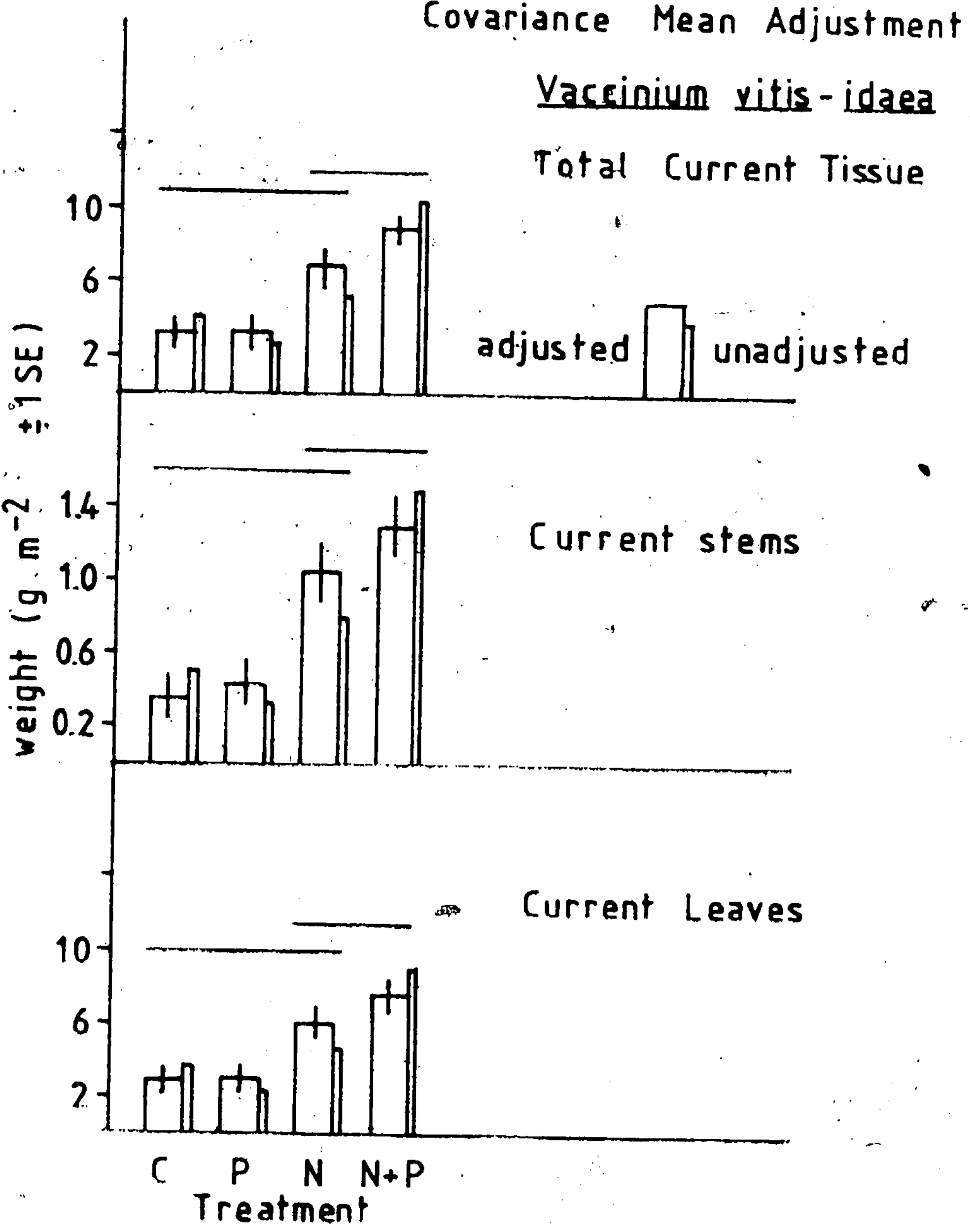


Figure 41. Effect of N and P on dry weight of current tissue in _Vaccinium vitis-idaea_. C = control. Adjusted refers to data adjusted by ANCOVA to account for differences in non-current tissue among plots. Columns under a single horizontal line are not significantly different at $P = 0.05$.

resulted in a significant production increase of 71%. Fertilization with N and P had no significant effect on stem growth.

Fertilization affected total production and production of current stems and current leaves in V. vitis-idaea more strongly than in either B. nana or L. palustre. Net annual production was unchanged with N or P addition. The combined addition of N+P significantly increased production of current tissue by 182%. This same pattern of significance and increases occurred in the individual tissue compartments of current stems and current leaves. Stems and leaves had no significant production increases with fertilization with N only. Addition of N+P together increased annual production of stems and leaves 255% and 182% respectively; both increases being statistically significant. Application of P alone caused little or no change in production of either tissue.

Discussion

The aboveground biomasss of vascular plant communities at arctic sites around the world vary widely. They range from lows of near zero g m^{-2} within polar deserts in the Canadian Arctic Archipelago, to highs above 2200 g m^{-2} in low shrub communities at Disko Island, Greenland

(Wielgolaski et al. 1981). The biomass of 278 g m^{-2} in this study was nearly identical to that reported by Haag (1974) in a similar community 70 km north (285 g m^{-2}), and very similar to a dwarf shrub/heath in the Low Arctic at Harp, USSR (275 g m^{-2}) (Gorchakovsky and Andreyashkina 1972). It was greater than a dwarf shrub heath in a highly productive high arctic site on Devon Island (145 g m^{-2}) (Bliss et al. 1977) and that of a wetter, coastal dwarf shrub community near Barrow, Alaska (63 g m^{-2}) (Webber in Wielgolaski et al. 1981).

The estimate of net annual aboveground production of vascular plants at Parsons Lake (54 g m^{-2}) was slightly less than reported in Haag's (1974) work (62 g m^{-2}), but greater than Gorchakovsky and Andreyashkina (1972) reported from Harp, USSR (42 g m^{-2}). Production was only 25 g m^{-2} at the coastal Alaskan site (Webber in Wielgolaski et al. 1981), and 18 g m^{-2} in the dwarf shrub heath at the Devon Island high arctic site (Bliss et al. 1977); both much less than the low arctic site in the present study.

The dominance of both aboveground biomass, and net annual production by B. nana in this community reflect characteristics associated with its deciduous growth form. The large stem component that gave upper canopy dominance to B. nana leaves contributed nearly half of the community biomass. The retention of this supportive structure after its death produced a low ratio of living to dead aboveground tissue (107 g m^{-2} living stems vs. 81 g m^{-2} dead stems). The retention of this old woody tissue may have some adaptive advantages. Shrubs in the Mackenzie River Uplands are generally limited to areas where a protective winter snow cover exists, and in these sites, shrub height is limited to the depth of the snow cover (Corns 1974). Branches extending above the snow are exposed to winter desiccation, abrasion of blowing snow crystals, and perhaps increased herbivory by birds and mammals. The stems themselves should slow wind speeds and cause deposition of snow crystals on the shrubs, forming a protective cover. The dead stems of B. nana nearly double the material that remains aboveground, thus greatly enhancing the "snowfence" effect, and improving the protective winter snow cover.

The relatively high ratio of net annual production to biomass in B. nana is a function of the production of large numbers of leaves each year, none of which are retained over winter. The subshrubs L. palustre and V. vitis-idaea contributed significantly smaller percentages of the total community biomass and net annual production, reflecting their smaller stature relative to B. nana. Both species receive the benefit of the snow stopping ability of B. nana and are well covered by winter snow, but only at a cost of reduced radiation during the growing season in the lower canopy positions below the leaves of B. nana.

However, limited data on photosynthetic light response curves for such understory shrubs as L. palustre and V. vitis-idaea indicate that they may be photosynthetically adapted for this shaded sub-canopy environment. Limbach et al. (1982) showed that V. vitis-idaea reaches light saturation at lower levels of intensity than B. nana, whose leaves receive greater amounts of radiation in their upper-canopy position. Additionally, they found that the optimum temperature for photosynthesis was lower in V. vitis-idaea. Thus, V. vitis-idaea appears to have photosynthetic characteristics that would be adaptive in the understory environment.

In the lower energy regime of the sub-canopy, L. palustre and V. vitis-idaea exhibited a lower annual turnover of carbon as indicated by the lower ratios of net annual production to live standing crop than in B. nana. Carbon that was fixed during a growing season was retained within the plant longer in the evergreen species than in the deciduous species. And importantly, retained tissues were primarily photosynthetic in nature, as opposed to the supportive tissue retained by B. nana. This supports the hypothesis of an evergreen strategy of efficient use of photosynthetic tissue over a long period of time (Johnson and Tieszen 1976).

Most arctic tundra soils have very low levels of many plant nutrients, and those soils upon which the dwarf shrub communities of the Mackenzie Delta uplands grow are no exception (Haag 1974, Table 8 this study). Total available nitrogen in all four experimental plots was less than 1 ppm, and available phosphorous was less than 26 ppm. Such low levels of available nutrients are partially responsible for the relatively low growth rates and low productivity of these tundra areas (Shultz 1964, Janz 1973, Haag 1974, Shaver and Chapin 1980).

An increase in growth in response to artificial supplementation of these nutrients has been used as indication that they are indeed limiting (Shultz 1964, Haag 1974). Chapin (1980a) however, cautions that this test may not be entirely valid because slowly growing plants adapted to low nutrient regimes may not show the same large increases in growth observed in crop plants with high growth rates. These slowly growing plants are adapted to low nutrient situations and may respond by increasing tissue nutrient concentrations through luxury consumption more than by increasing productivity (Grundon 1972, Chapin 1980a, Shaver and Chapin 1980).

In this study, the response of plants to fertilization was variable, but the increases in growth and production with nitrogen addition suggest that nitrogen is among the resources limiting production. The greatest and most significant increases occurred when N and P had been applied together, while the addition of P alone was not associated with production increases in any of the three species. This interaction of P and N, and the lack of response to P alone suggests that production limitation in the tundra is not a function of any single factor. Low levels of P do not appear to have been a limiting factor by themselves, rather the low levels of N appear to have limited the incorporation or use of P.

Stoner et al. (1978) suggested that the deciduous growth form should exhibit greater response to nutrient supplementation than does the evergreen growth form because of the annual loss of nutrients during leaf senescence. The results from this current study do not support this hypothesis. The response of deciduous _B_. _nana_ to nutrient addition was far less than in either of the two evergreen species, _L_. _palustre_ or _V_. _vitis-idaea_. In fact, the lack of response of either stem elongation or production of current tissue in _B_. _nana_ to any of the fertilizer treatments is in contrast to the results of Haag (1974) and Shaver and Chapin (1980), both of whom reported increase in production, particularly with a combination of N and P. Ledum palustre and V. vitis-idaea both showed trends of increased growth and production after fertilization with N and N+P, particularly the latter. Only V. vitis-idaea exhibited significantly greater amounts however.

Direct comparison of these three species and their response to fertilization may not be very instructive since each has a different rooting pattern and may thus be exposed naturally to a different temperature, moisture, and nutrient regime. Vaccinium vitis-idaea, which showed the greatest response to nutrient addition, roots in the uppermost 10 cm of the soil, where fertilization may have had the greatest effect. The two larger species root primarily at greater depth, with B. nana roots occurring down to 30-50 cm. The additional nutrients may have reached these depths in much lower amounts.

The relative lack of response to fertilization in this study, in contrast to the response observed by Shultz (1964), Haag (1974), and Shaver and Chapin (1980), may have occurred because of low soil nutrient levels, even after fertilization. Fertilization rates in this current study were similar to those used by Haag and Shaver and Chapin. Analysis of soil nutrient levels (Table 8) one and one-half years after fertilization indicated little effect from N addition, and only a slight elevation in P levels when P was added alone. No increase in P was noted with the combined N+P treatment. This lack of response of soil nutrient levels to fertilization was also noted in a similar study by Shaver and Chapin (1980, F. S. Chapin III, pers. comm.) These low levels may have been caused by removal of the nutrients during melt water runoff, complexing of the nutrients with organic components of the soil, or by uptake of all additional nutrients by the plants themselves. The lack of response of the vascular plants may also have been caused by N and P being taken up by such other organisms as microbes and, thus, not be available to the vascular species.

CARBON ALLOCATION

Introduction

The partitioning of photoassimilated carbon among functional tissue compartments is an important adaptive characteristic in the survival strategy of plants (Grime 1979). Although allocation of carbon to different compartments has long been estimated indirectly from measurement of biomass (Johnson and Tieszen 1976, Flower-Ellis 1980), the availability of radioisotopes has made the direct measurement of partitioning in plants possible. Radiocarbon has been used for several decades as a tracer in studies of carbon allocation patterns in agricultural and economically important plant species (Wardlaw 1968) and the use of ^{14}C as a tracer has aided determination of carbon movement in seedling and mature evergreen, needle-leaf conifers (Dickmann and Kozlowski 1968, Gordon and Larson 1970).

Only recently has the technique been applied to arctic or alpine plant species. Svoboda and Bliss (1974) used autoradiography to determine viability of Dryas integrifolia roots. Collins and Oechel (1974) used ^{14}C to determine growth and translocation patterns in an arctic moss Polytrichum (Pogonatum) alpinum. Using the technique, Johansson (1974) noted differences in allocation patterns between a small evergreen shrub, Andromeda polifolia, and a dwarf deciduous woody species, Rubus chamaemorus, in northern Sweden. Berg et al. (1975) reported distribution of photosynthates in woody and herbaceous species from a Norwegian alpine site. In an arctic graminoid from northern Alaska, Dupontia fisheri, Allessio and Tieszen (1975a, 1975b) demonstrated similar patterns of carbon distribution among different age classes of leaves as well as varying degrees of interdependence among tiller types.

These studies, including the current one, discuss in a qualitative manner the distribution and movement of assimilated radiocarbon over a short period of time, usually less than one year. Rosberg et al. (1981) recently estimated the carbon flow for several years through a Calluna heath ecosystem in Norway using similar pulse labelling by $^{14}CO_2$.

Methods

To assess allocation of carbon fixed at different times during the growing season to aboveground biomass compartments, plants were allowed to assimilate ^{14}C. Individual plants were labelled by sealing them into a 2.6 L plastic cuvette and injecting 0.025 mCi of $^{14}CO_2$ into the cuvette. The $^{14}CO_2$ was generated by acidification of 0.5 ml Na^{14}CO3 solution (activity 0.05 mCi ml^{-1}) with excess 1N HCl. A small electric fan in the cuvette minimized boundary layer effects. Plants were exposed for 20 min, after which the cuvette was flushed with fresh air and then removed. All B. nana and L. palustre individuals that were labelled had both flowering and vegetative shoots. Labelled V. vitis-idaea had either flowering and vegetative shoots or a flowering and a vegetative plant were each labelled.

Betula nana was labelled with $^{14}CO_2$ three times in the growing season; July 4, when leaves were beginning to expand, August 1, when leaves were fully expanded, and August 30, 1978, after growth had halted. Ledum palustre and V. vitis-idaea were labelled four times in the growing season; June 13-17, before current leaves had expanded but after regreening of older leaves, July 5-6, when current leaves were beginning to expand, August 2-4, after current leaves had expanded, and August 30, 1978, after growth had halted.

Pairs of labelled plants of each species were harvested 3, 24, and 48 hr, 1, 2, 3, 4, 6, 8, and 11 wk after exposure, as appropriate. For example, no plants were harvested after September 3, and thus plants exposed on

August 30 were only harvested 24 and 48 hr after labelling. After harvest, plants were separated into biomass compartments based on age and function (see Chapter 4), dried at 40° C for 24 hr, and weighed to the nearest 0.001 g. Tissue samples from each compartment were combusted in a Packard TriCarb Sample Oxidizer (Model 306, Packard Instrument Co.) with the $^{14}CO_2$ absorbed into Carbosorb (Packard Instrument Co.), and automatically mixed in a scintillation vial with a Permaflor II scintillation cocktail (Packard Instrument Co.). Activity of the recovered sample was determined with standard scintillation counting techniques (Wang et al. 1975, Horrocks 1976).

Frequent combustion of a standard of known activity indicated the sample oxidizer recovered more than 98% of the ^{14}C in a given tissue. However, estimates of sample variance were high for many biomass compartments at most sampling dates because of the small number of samples (two in most cases). Data are expressed as concentrations of radiocarbon (disintegrations min^{-1} g^{-1}) of plant tissue, and relative quantities of radioactivity recovered from each plant biomass compartment (percent of total ^{14}C recovered).

Because of the great difficulty in both determining the extent of a whole plant in these vegetatively reproducing species, and of harvesting the entire underground tissue of an individual plant, no estimate of total carbon allocation to underground tissues was made. The concentration of radiocarbon in samples of underground stem or rhizome from each plant varied greatly, and showed no pattern regarding either time when labelled, or time after labelling.

In general, relative concentrations of ^{14}C are an indication of the sink strength of each biomass compartment, while relative proportions (%) describe movement of radiocarbon between biomass compartments (Milchunas et al. 1982). Levels of tissue concentrations of radioactivity are calculated independantly of other tissue compartments, and changes in activity represent real increases or decreases in carbon. Decreases in tissue concentrations are caused by respirational losses of carbon, the majority of which occurs in the first 48 hr (Tieszen et al. 1974, and Berg et al. 1975), dilution of the radiocarbon within a tissue by nonradioactive carbon associated with continued growth, and actual translocation of ^{14}C out of the tissue.

Results

Betula nana

^{14}Carbon assimilated in early July, shortly after leaf expansion, accumulated primarily in leaf tissue, and largely remained there until leaf fall (Fig. 42). This stability indicates little translocation of carbon out of the leaves relative to other aboveground tissues. The proportion of recovered ^{14}C in these leaves dropped slowly from over 96% just after labelling, to 82% at the end of the growing season, eight weeks later. The concentration of radioactivity in these leaves dropped rapidly for one week after this exposure, but then remained relatively constant for the remainder of the growing season (Fig. 43). This rapid drop was likely due to carbon losses associated with respiration or to translocation to belowground tissues. The fraction of ^{14}C recovered from leaves after the August 1 exposure, when leaves were well developed, decreased from 95% to 56% after one week, but remained at this level until the end of the growing season. This drop suggests movement of carbon from leaves to other aboveground tissues. Like those exposed in July, the concentration of radiocarbon in these leaves also dropped rapidly after labelling, but did not stabilize until two weeks later.

Since plants labelled at the end of August, just before leaf fall, were sampled only twice, changes in recovery patterns are not obvious. A large portion of carbon was recovered from leaf tissue (over 78%) after this exposure, but the concentration of ^{14}C in the tissue was initially much lower than after the two ~~previous~~ exposures, as might

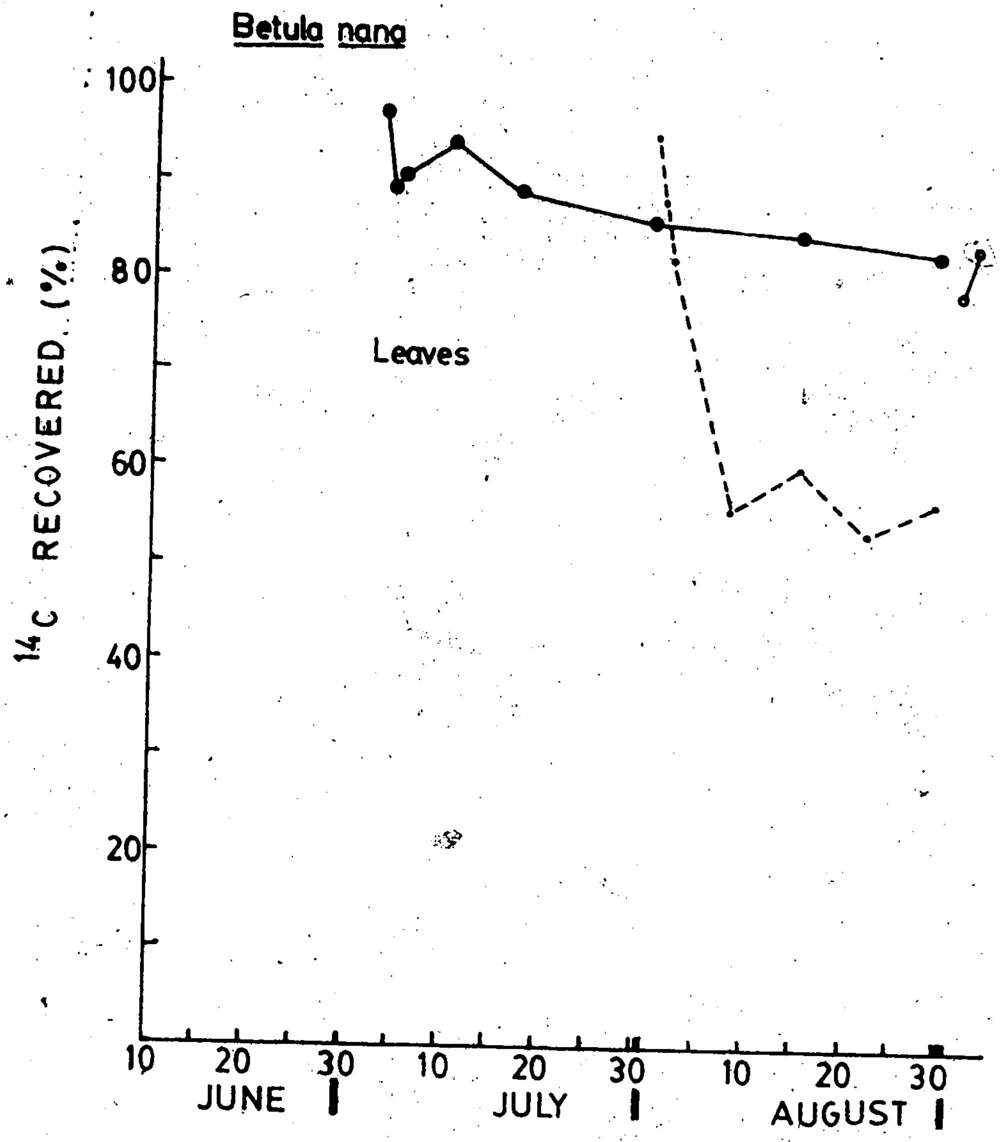


Figure 42. Percent of ^{14}C recovered in leaves from total aboveground biomass of Betula nana. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

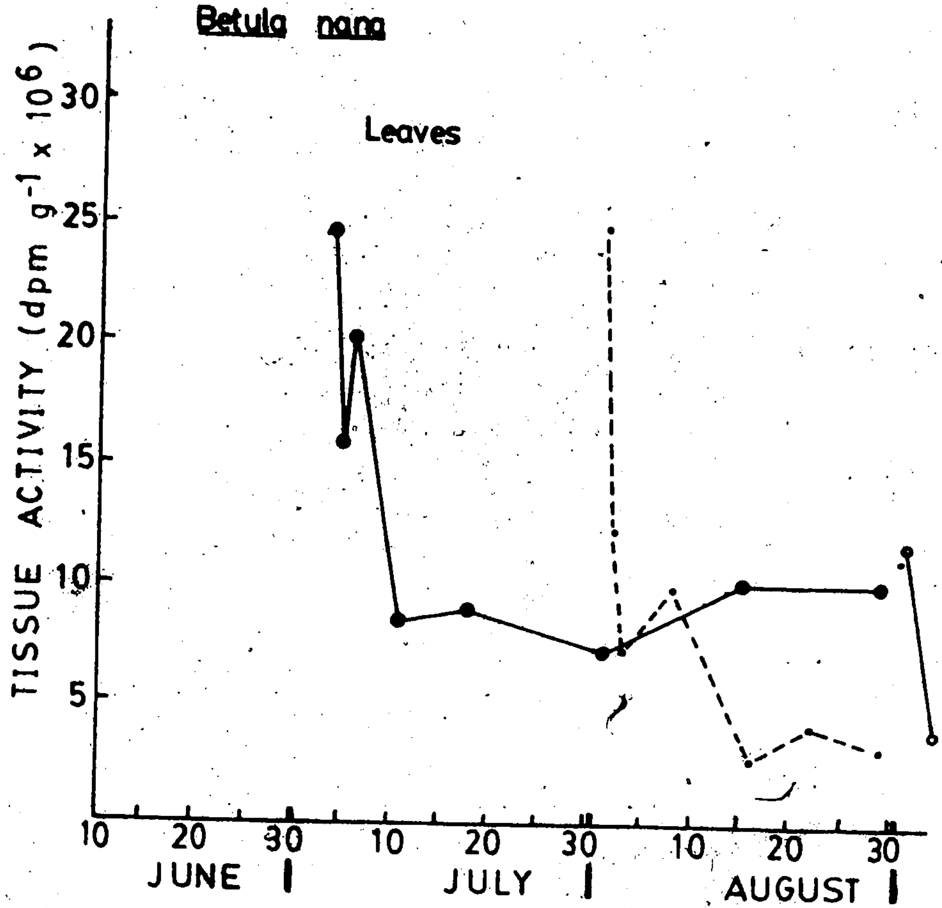


Figure 43. ^{14}C activity of leaf tissue in Betula nana. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

be hypothesized for leaves with reduced photosynthetic competence.

The proportion of assimilated radiocarbon recovered from current and non-current stems of B. nana increased with time after both July 4 and August 1 labellings; however the fraction recovered from non-current stems was much larger than that from current stems (Fig. 44). The increased recovery rate after labelling was much greater after the August 1 exposure. This labelling coincided with the stem weight gain that occurred after most elongation had halted. rapid stem growth.

Changes in radiocarbon concentrations in current stems were similar following both the July 4 and August 1 assimilations (Fig. 45). After an initial rise, concentrations leveled off in the range of 5.0×10^3 DPM g^{-1}, which was similar to concentrations in leaf tissue at the same time. This leveling of radiocarbon concentrations at a time when stems were still gaining weight suggests that translocation of ^{14}C into stem tissue occurred, and countered the dilution with new carbon characteristic of continued tissue growth.

By August 1, preformed leaf buds appeared which would develop into expanded leaves the following summer. Carbon

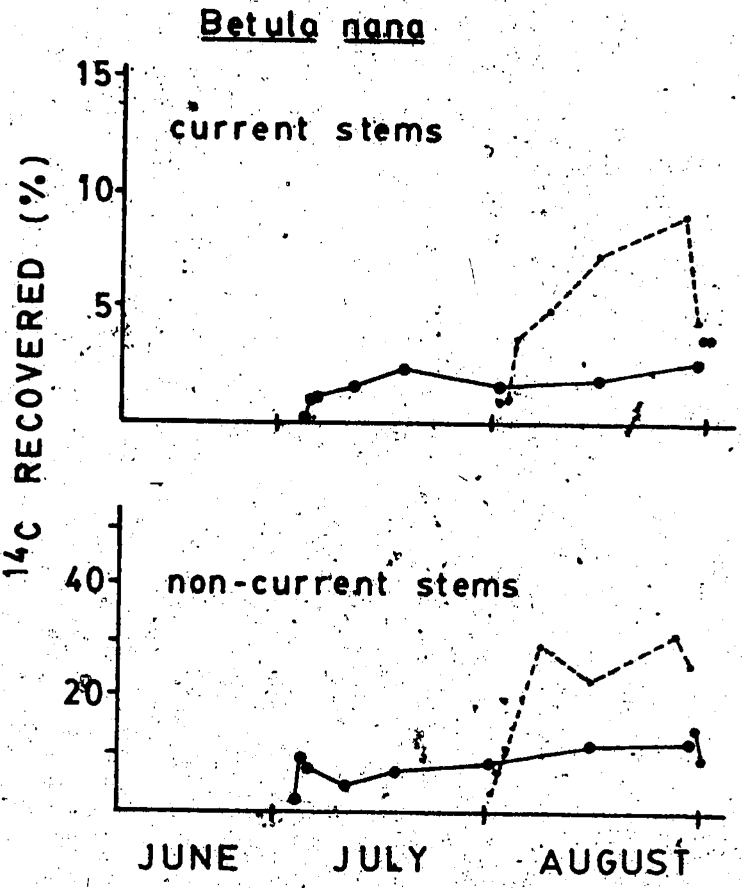


Figure 44. Percent of ^{14}C recovered in current and non-current stems from total aboveground biomass of Betula nana. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

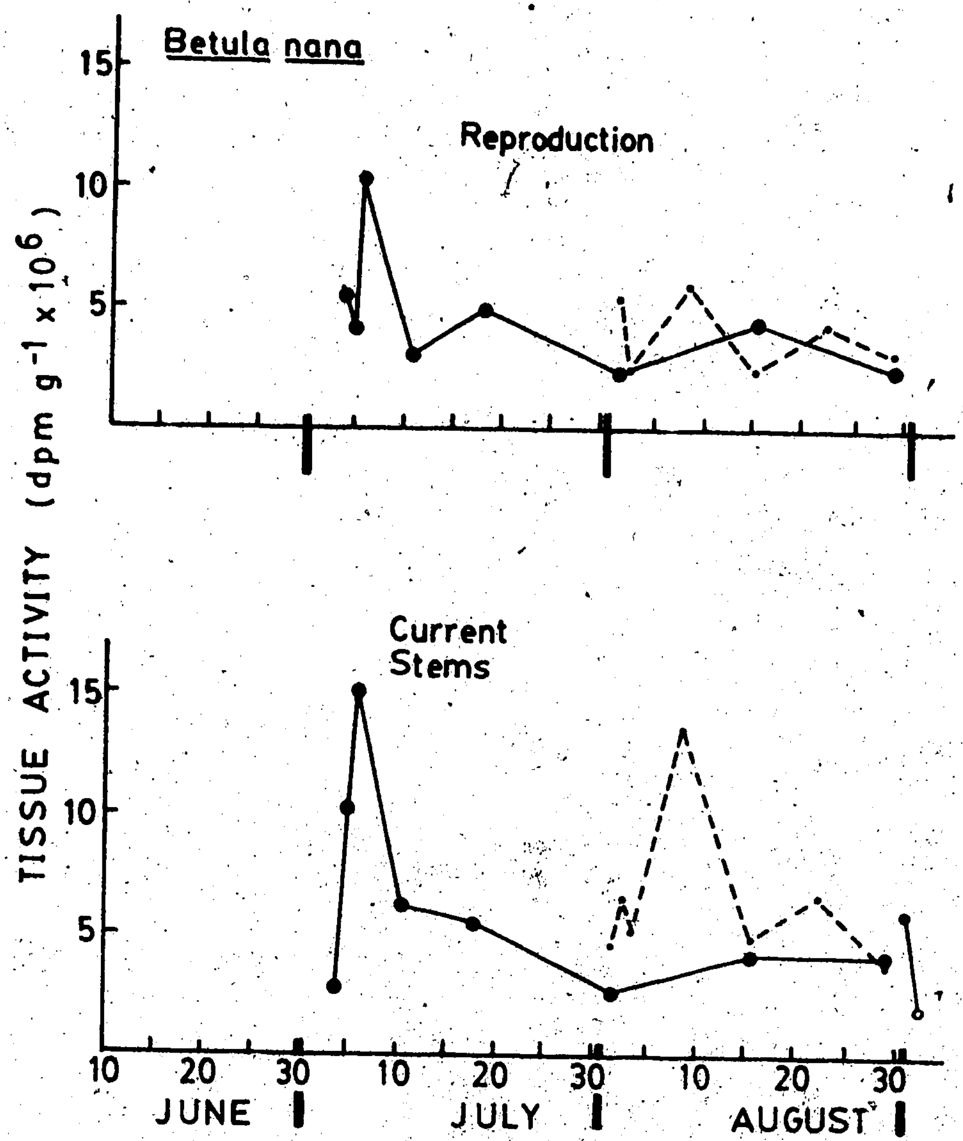


Figure 45. ^{14}C activity of current stem and reproductive tissue in Betula nana. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

assimilated in early July appeared in this bud tissue when harvested four weeks later. Both tissue concentrations and the portion of total activity recovered were low in all tissue samples from this exposure (Fig. 46). In contrast, carbon assimilated on August 1 was recovered in increasingly larger portions from these preformed buds at later harvests, eventually representing 13% of the total recovered four weeks after labelling (August 29). The radiocarbon concentration in this tissue was high compared to most non-current tissue samples, but similar to that found in other such rapidly developing tissues as leaves and current stems. Carbon was thus translocated to these buds from other tissues throughout August.

Reproductive tissue represented a very small portion of the aboveground biomass in <u>B</u>. <u>nana</u> (see Chapter 4), and likewise, only a small proportion of ^{14}C recovered from the plants was found in either male or female reproductive tissue (Fig. 46). Concentration of radiocarbon in these reproductive organs remained relatively constant through the growing season after both the July and early August labellings (Fig. 45). This tissue activity of about 4×10^6 DPM g^{-1} was similar to that in current year stems, the other major non-photosynthetic current tissue.

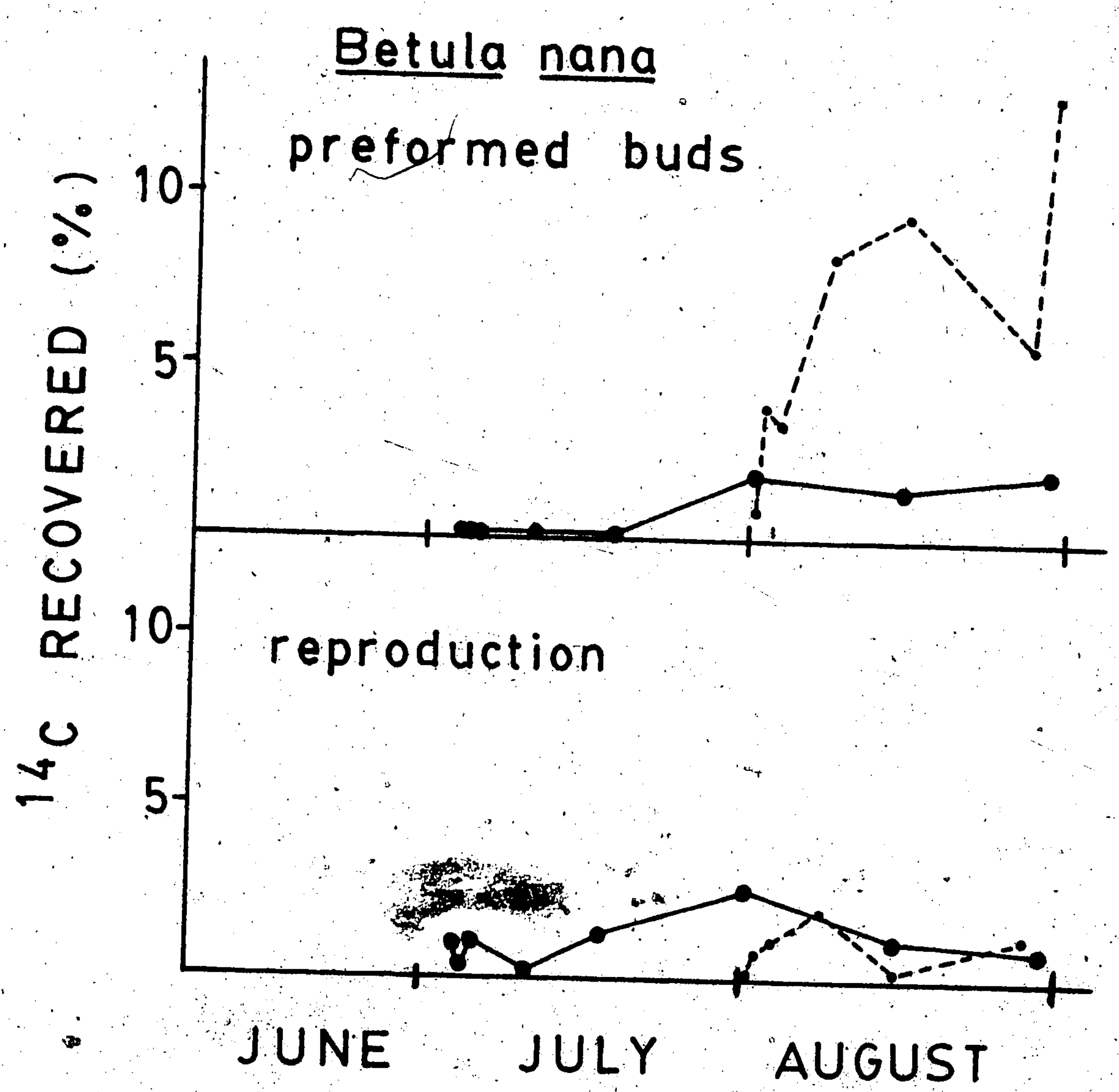


Figure 46. Percent of ^{14}C recovered in preformed buds and reproductive tissue from total aboveground biomass of Betula nana. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

Ledum palustre

Leaf tissue was the primary site of radiocarbon accumulation in L. palustre after labelling with $^{14}CO_2$ (Fig. 47). The increasing percentage of radiocarbon recovered from current leaf tissue in the periods after all three exposures indicates translocation into these sites throughout the growing season. Virtually no radiocarbon was recovered from current leaves immediately after the early June exposure, when leaves were still within a bud, but eventually reached a maximum of 11% in late August. When current leaves had at least partially expanded, as at the July 5 and August 2 labellings, the amount of ^{14}C recovered from the tissue increased rapidly, reaching plateaus after 48 hr. The increase in concentrations of radiocarbon in current leaves (Fig. 48) in the 48 hr after exposure indicates their strength as a sink for carbon. The gradual drop in concentration after this initial period, and in the first 48 hr after the August 2 exposure probably was a function of dilution of the ^{14}C in the tissue with continued growth, and from respirational losses.

Non-current L. palustre leaves of all age classes translocated ^{14}C to other biomass compartments in the plant following all exposure dates (Fig. 47). This outward translocation continued throughout the growing season, and

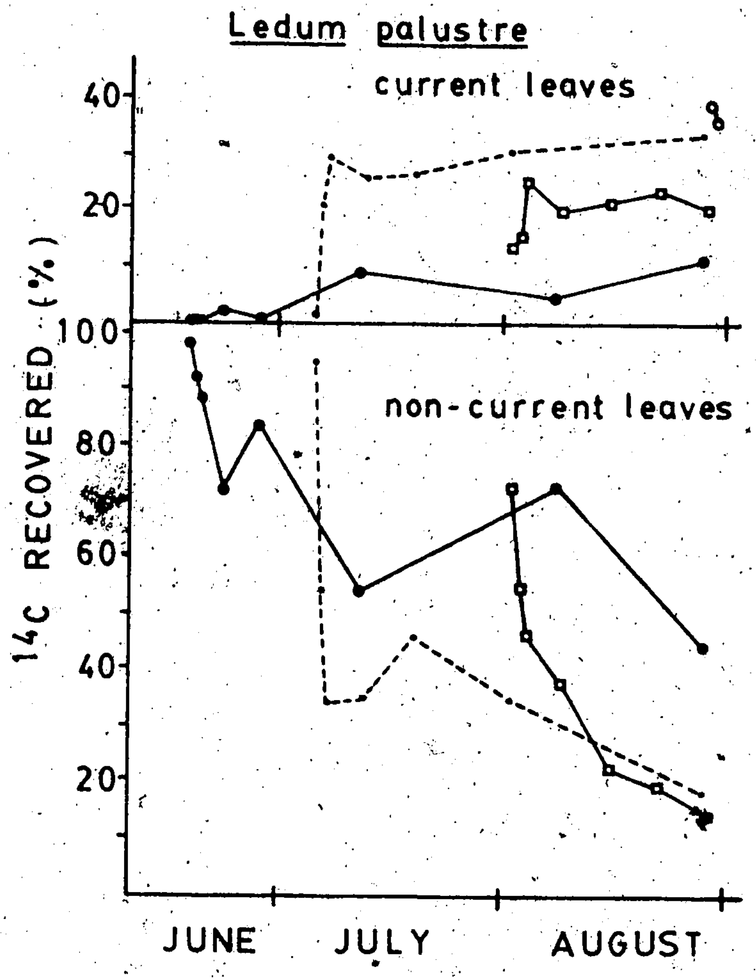


Figure 47. Percent of ^{14}C recovered in current and non-current leaves from total aboveground biomass of Ledum palustre. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

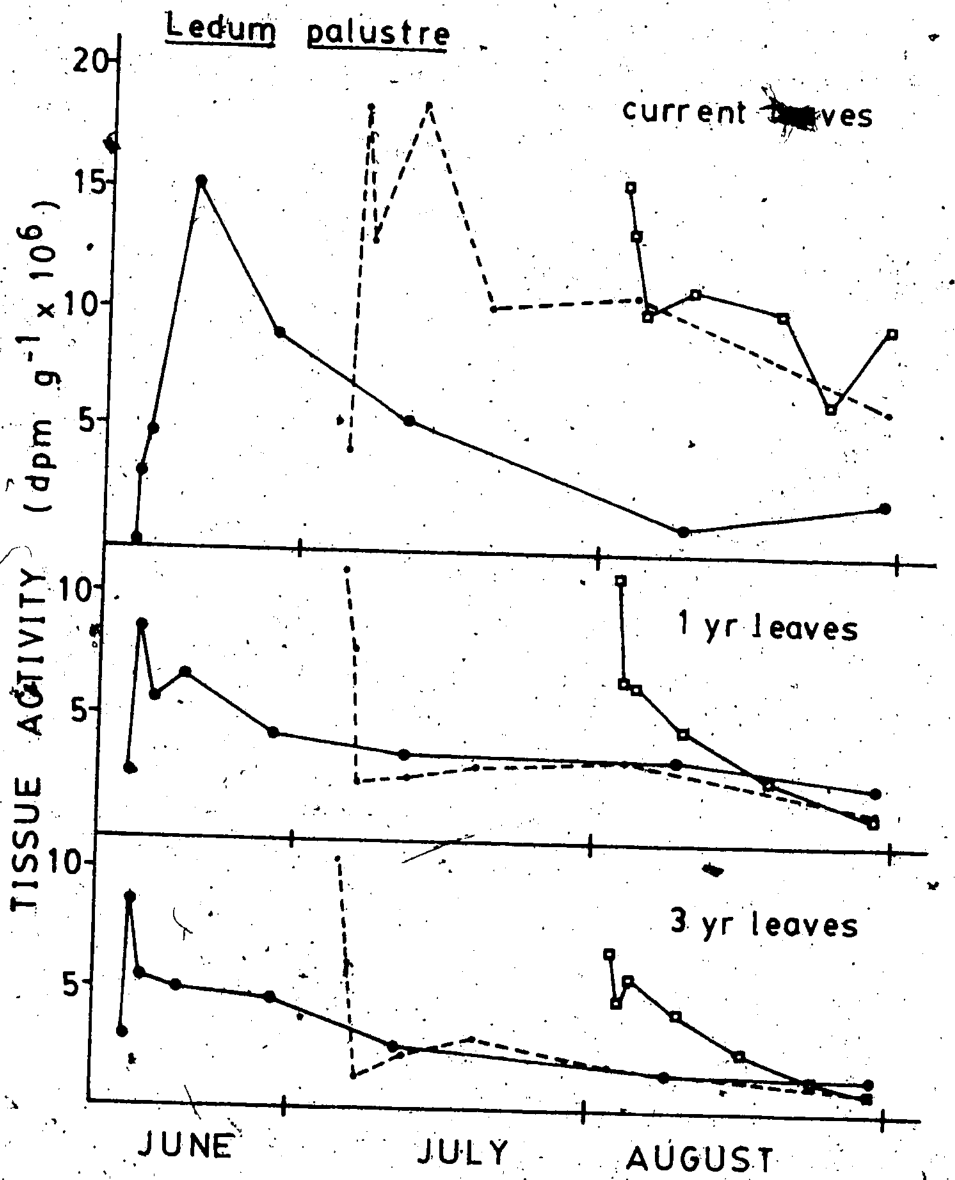


Figure 48. ^{14}C activity of current, one year old, and three year old leaf tissue in Ledum palustre. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

with increasing rapidity after each successive exposure. At the end of August, 44% of radiocarbon recovered from plants exposed on June 13 was found in non-current leaves, while only 14% was recovered from non-current leaves from plants exposed on August 2. This same rapid translocation from non-current leaves was observed in plants labelled on August 30, when leaf senescence had begun.

Tissue concentration of radiocarbon was similar in all age classes of non-current leaves (Fig. 48), and this concentration decreased in a similar pattern in all age classes after the different exposures. Concentrations in the 3 yr leaf classes were about one-half of those in 1 yr leaves at the end of the growing season.

Allocation of ^{14}C to stem tissue, both current and non-current, occurred after all four labelling dates, as indicated by the increases in proportion of radiocarbon recovered from those tissues [illegible]r exposure (Fig. 49). Significant accumulations of [illegible] in current stem tissue did not occur until at least one week after the plant had assimilated the radiocarbon. Current stems labelled June 13 showed accumulations of ^{14}C only after 8 and 11 wk, with only 1% of the radiocarbon recovered on the latter date from current stem tissue.

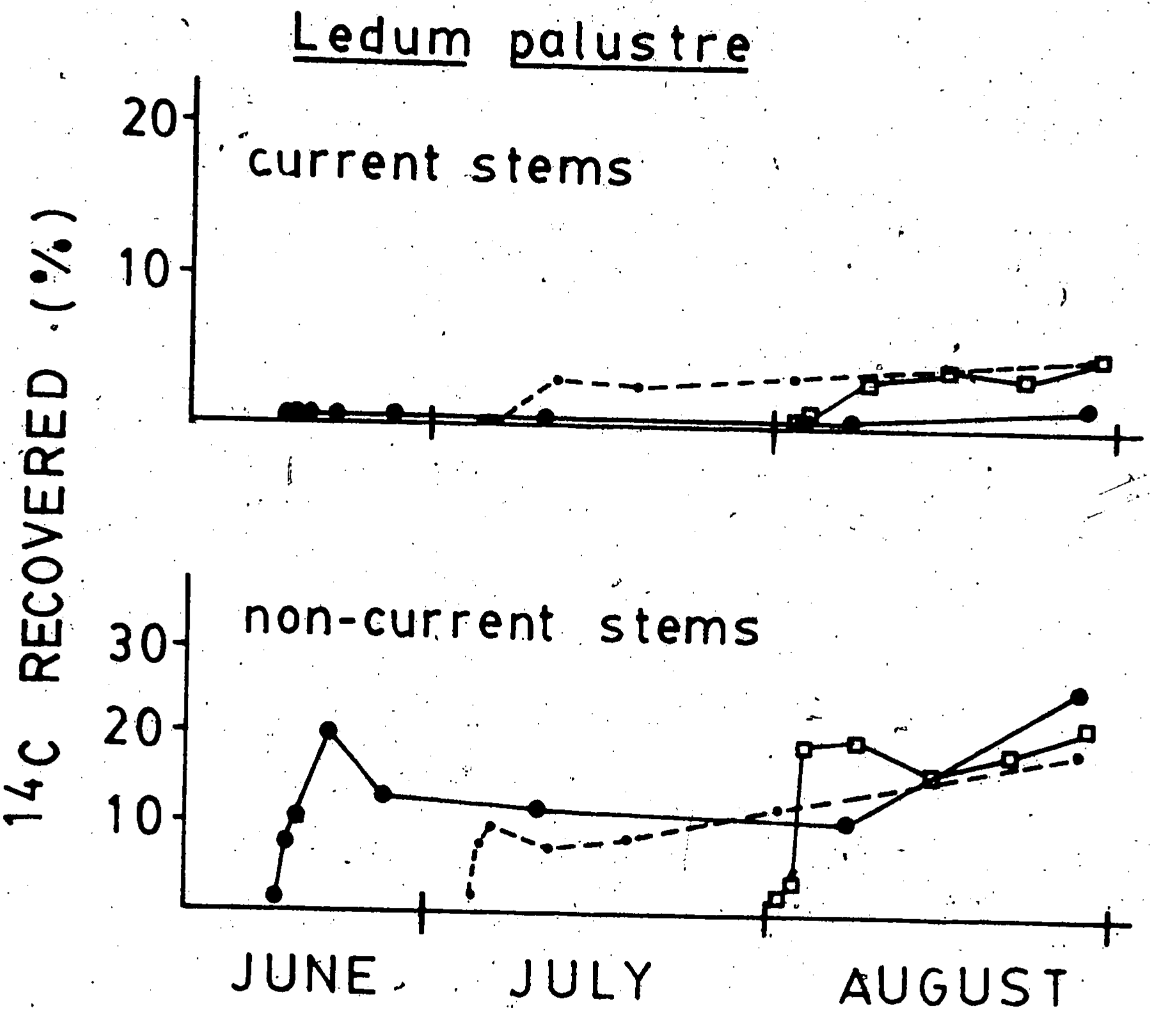


Figure 49. Percent of ^{14}C recovered in current and non-current stems from total aboveground biomass of Ledum palustre. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

Non-current stem compartments had larger amounts of radiocarbon translocated to them than did current stems. Radiocarbon was evident in these tissues within 48 hr of exposure. Over 50% of the maximum allocation to non-current stems had been received by the end of 48 hr after the June 13, July 5, and August 2 labellings. The maximum percentage of total radiocarbon recovered from non-current stems came from the last plants harvested from all four exposure groups, those collected on August 30.

Tissue concentrations of ^{14}C in current stems exposed before expansion of current leaves (June 13 exposure) rose above zero only near the end of the growing season (Fig. 50). This lack of current stem allocation early in the growing season was partially the result of difficulties in physically separating current stem and leaves at this stage of development, as well as the small amount of stem growth that occurred then. The tissue activity of current stems rose very rapidly in the 48 hr period after the July 6 and August 2 exposures, indicating that the tissue was a strong sink for assimilated carbon at that time. The concentration of radiocarbon in current stem tissue continued to rise for two weeks after the August 2 exposure, reflecting a continued movement of radioactive carbon into the tissue. The decreases in concentration toward the end of August probably reflected a dilution of the ^{14}C in the rapidly

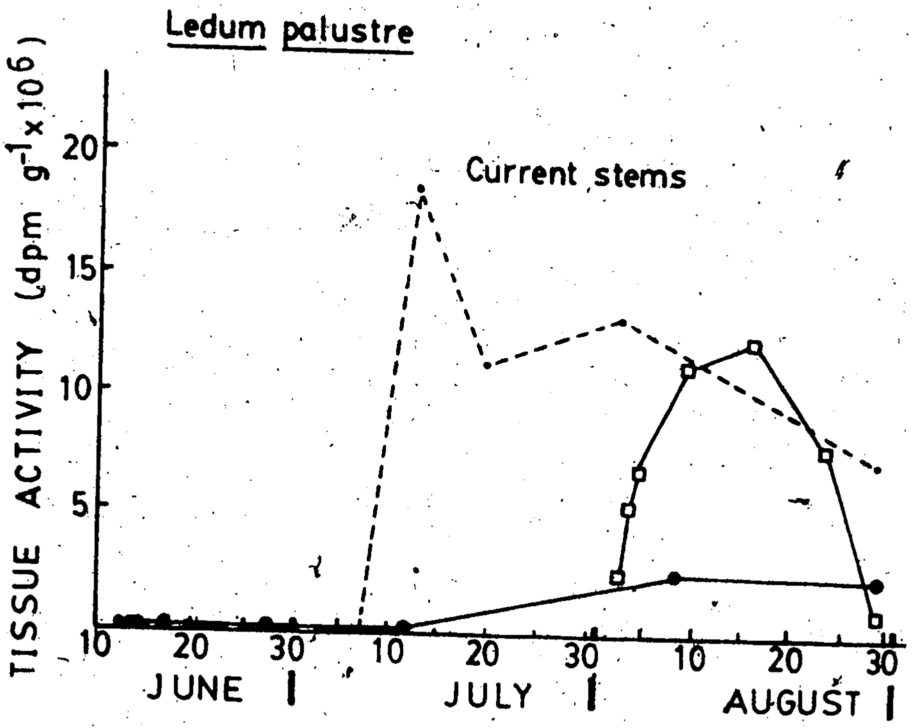


Figure 50. ^{14}C activity of current stem tissue in Ledum palustre. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

growing tissue with non-radioactive carbon fixed after the initial labelling.

Movement of ^{14}C to reproductive tissue is indicated by the increases in the portion of radiocarbon recovered from that tissue relative to that recovered from the entire plant, especially in the first week after labelling (Fig. 51). Only a small fraction of the total ^{14}C recovered in the first 48 hr after the early summer exposure came from reproductive tissue; however only 3 hr after exposure, 3 and 12% were recovered from these tissues following the July 5 and August 2 assimilation periods. The accumulation of radiocarbon in reproductive tissue was eventually relatively large, with final values on August 30 ranging from a low of 16% (June 13 exposure) to a high of 39% (August 2 exposure), excluding those labelled on August 30.

The patterns of ^{14}C concentration in the reproductive tissue following exposure were similar to the patterns of recovery of ^{14}C from the same tissues (Fig. 52). Maximum levels of tissue concentration were reached one week after exposure, and generally remained near this level until the end of August, suggesting that ^{14}C was continuing to be moved into the tissue.

Radiocarbon assimilated during the various exposure

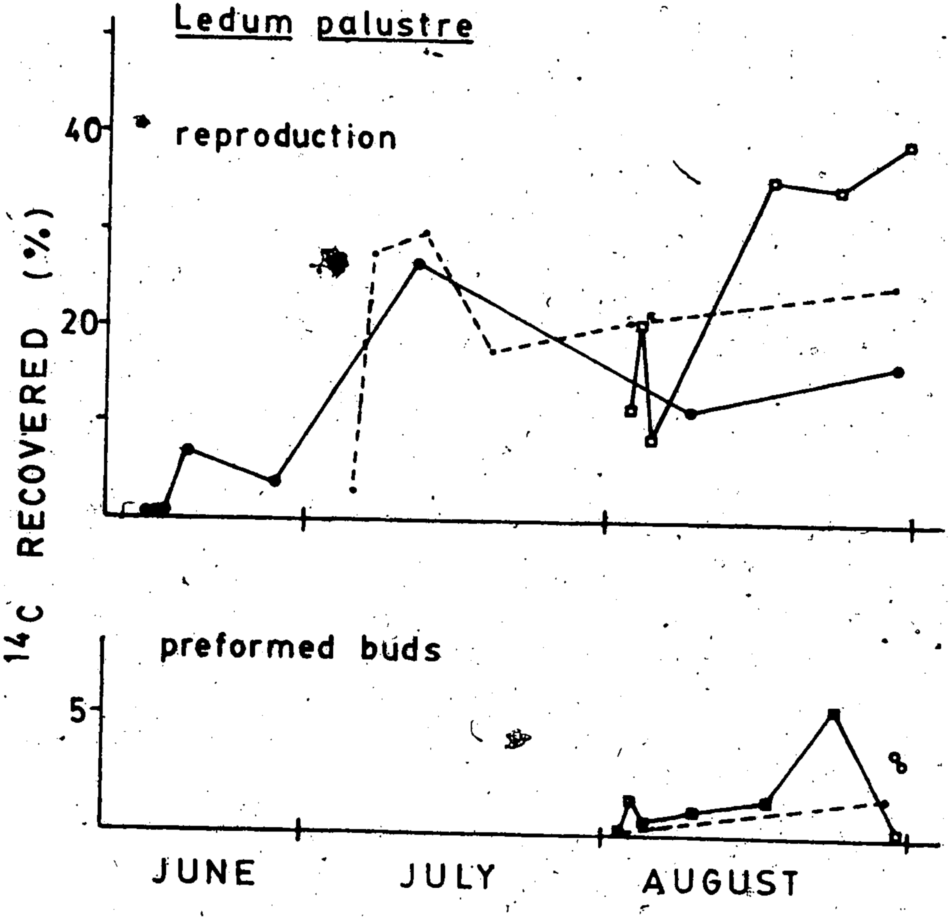


Figure 51. Percent of ^{14}C recovered in preformed buds and reproductive tissue from total aboveground biomass of Ledum palustre. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

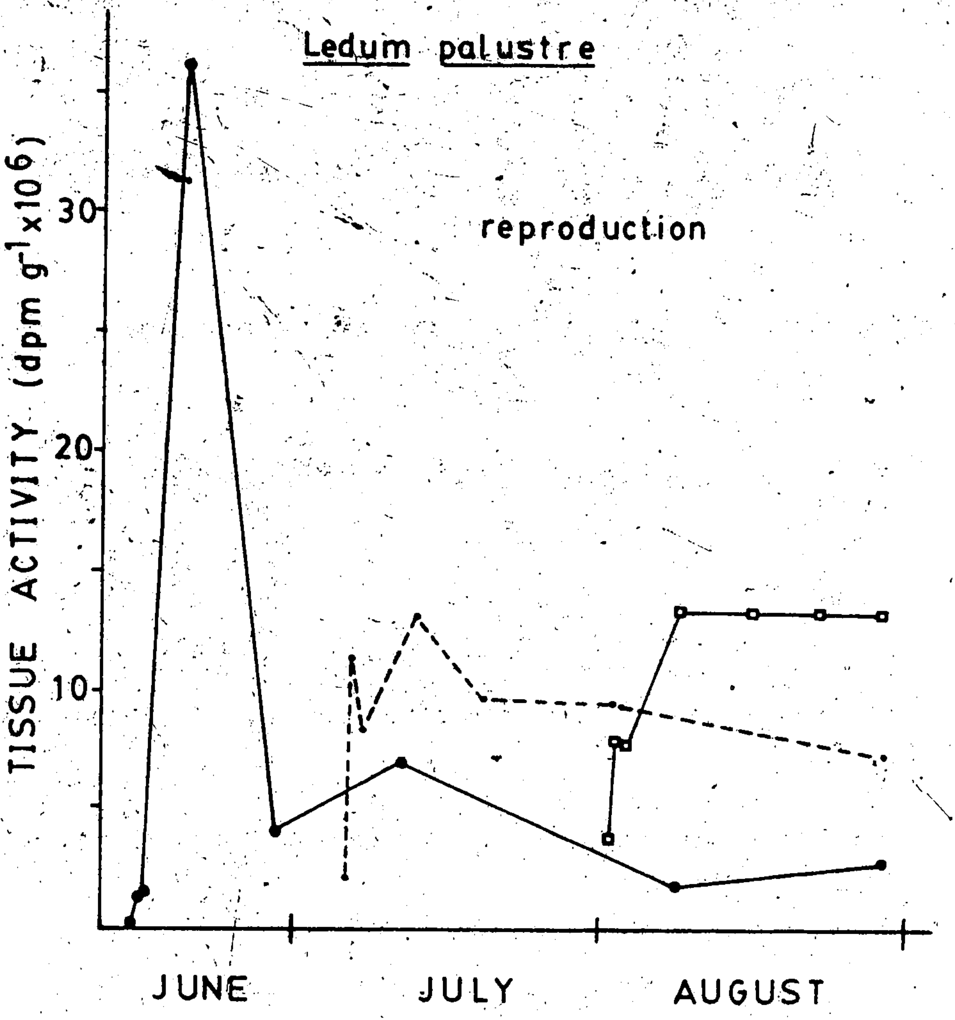


Figure 52. ^{14}C activity of reproductive tissue in Ledum palustre. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

periods was also allocated to preformed buds, current tissue associated with growth the following year (Fig. 51). Only a small amount of ^{14}C was ever recovered from these preformed vegetative and reproductive buds; values were always under 6% of the total. The greatest amounts recovered from the preformed buds were from samples harvested in the last two weeks of August. Two of the larger fractions of total ^{14}C recovered were from samples harvested only 24 and 48 hr after the August 30 exposure (3% in both samples).

Vaccinium vitis-idaea

The allocation of ^{14}C among aboveground tissues in *V. vitis-idaea* was very similar to that in the other evergreen shrub, *L. palustre*. At all harvest dates and after all labellings nearly all radiocarbon was recovered from leaf tissue, with the majority recovered from non-current leaves (Fig. 53).

Very little radiocarbon was initially recovered from current leaves labelled on June 17 (Fig. 53). After eight weeks this recovery rose to 7%, and finally to 11% on August 30. At least 2% of the ^{14}C recovered from the three later exposures was found in current leaves after only three hr. This difference between the first labelling and the later three reflects the lack of photosynthetic competence of

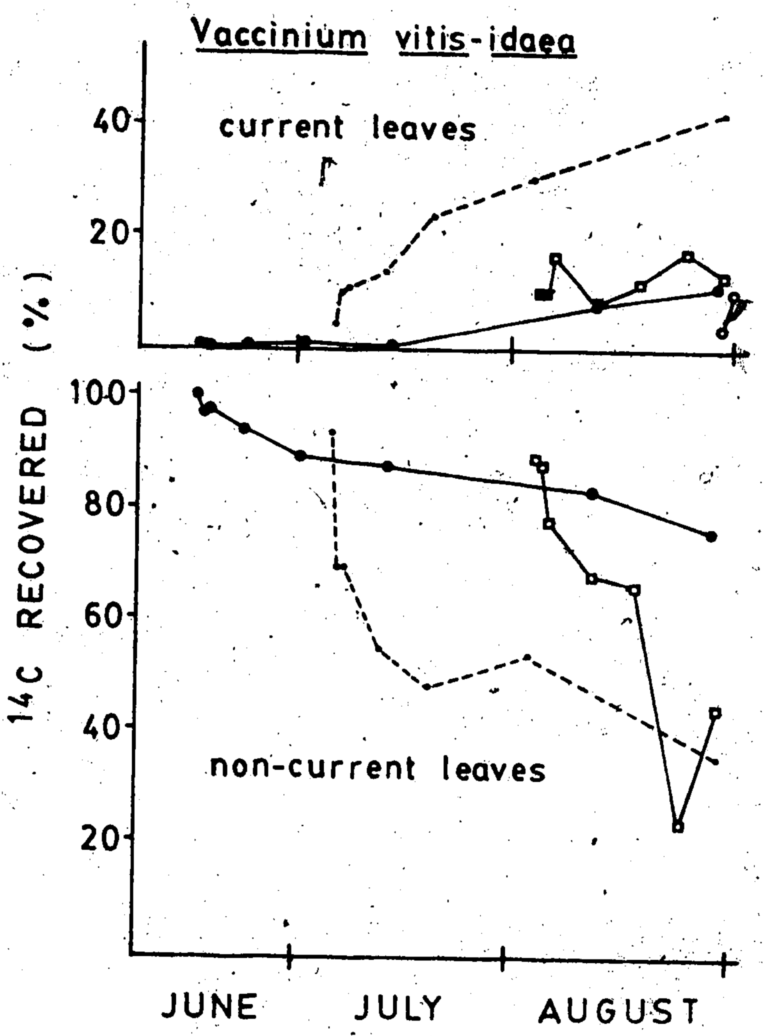


Figure 53. Percent of ^{14}C recovered in current and non-current leaves from total aboveground biomass of Vaccinium vitis-idaea. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

current leaves in June. The portion found in leaves exposed July 6 increased with each succeeding harvest, eventually reaching a maximum of 41%. The majority of this increase came during expansion of current leaves. Leaves labelled on August 4 reached their maximum recovery rate within one week of exposure.

Old leaf compartments contributed the greatest amount of recovered radiocarbon three hr after each exposure, with a decrease thereafter, suggesting translocation from the tissue throughout the growing season. The rate of this decrease was different after each labelling. The fraction of ^{14}C found in non-current leaves labelled on June 17 decreased throughout the growing season, but only to 76% by August 30. The contribution of leaves labelled on July 6 had decreased to about 50% after one week, and eventually reached a low of 35% by August 30. After the August 4 exposure, the amount of radiocarbon recovered from non-current leaves decreased at a rate similar to that after the July 6 labelling.

Tissue concentrations of ^{14}C in _V_. _vitis-idaea_ current leaves also followed a different pattern after each of the separate labellings (Fig. 54). During the period of primary leaf growth (June 17 and July 6 exposures), the current leaves were strong sinks for carbon and showed an initial

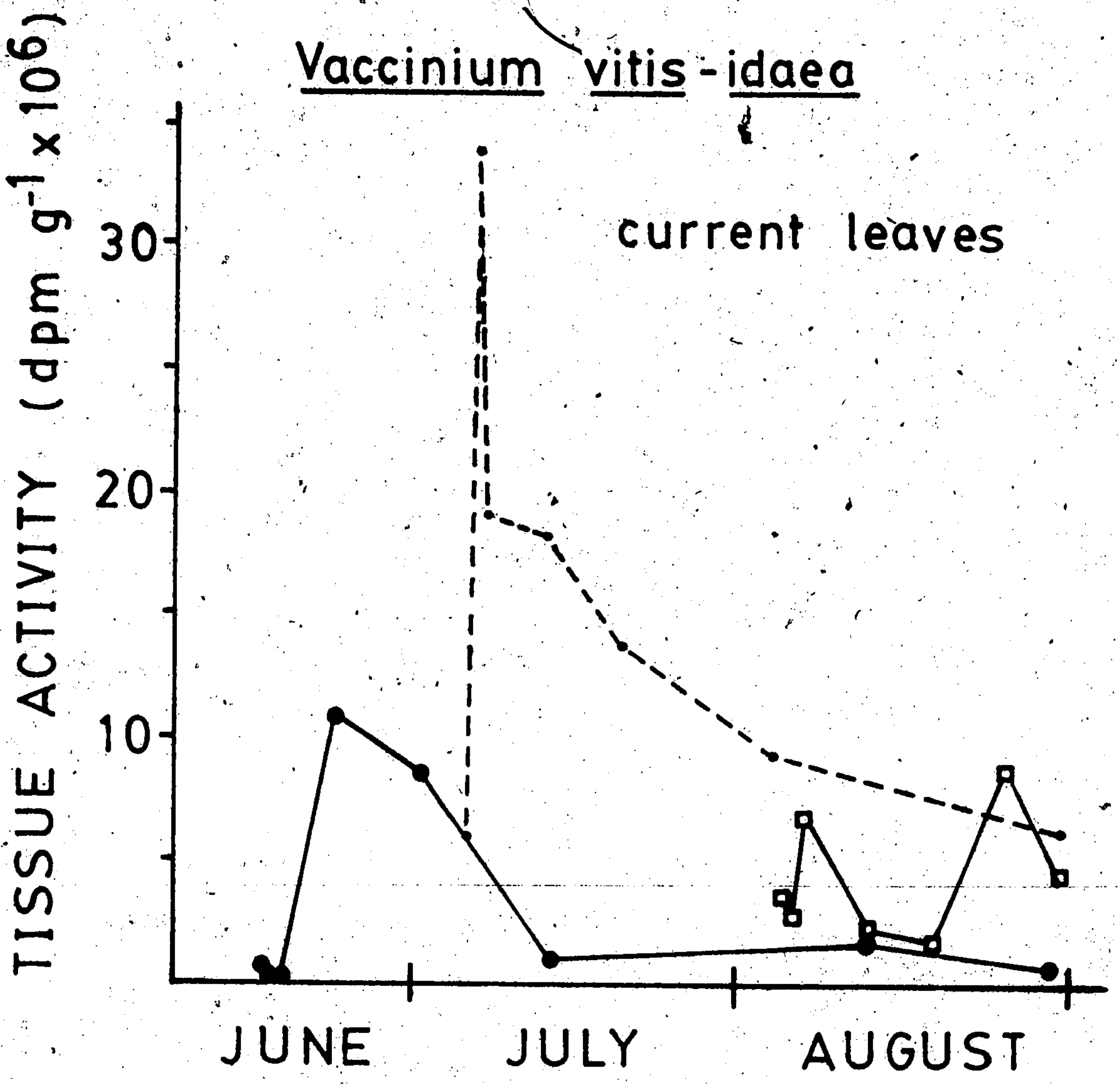


Figure 54. ^{14}C activity of current leaf tissue in Vaccinium vitis-idaea. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

increase in radiocarbon tissue concentrations. This increase was followed by a gradual drop in concentration, primarily associated with the dilution of ^{14}C with more recent, non-radioactive assimilates in the growing tissue. Carbon assimilated later in the growing season (August 4), after leaves had fully expanded, remained at about the same concentration from 48 hr after exposure until the end of the season.

All older leaves exhibited similar patterns of radiocarbon tissue concentrations following the four labellings (Fig. 55). Concentrations dropped in the first two weeks from the initial high levels reached after 48 hr, to a lower plateau at which they remained until the end of the growing season. All older leaf classes had similar tissue concentrations of ^{14}C.

~~Accumulation of radiocarbon in stem tissue of V.~~ *vitis-idaea* was similar to accumulation in stems of *L. palustre*. Translocation of ^{14}C from leaves to stems occurred very rapidly after exposure of a plant to $^{14}CO_2$, and in most cases, this translocation continued for the remainder of the growing season (Figs. 56 and 57). No major translocation to current stems occurred after the June 17 labelling for several weeks, but did occur immediately after assimilation later in the growing season. The greatest

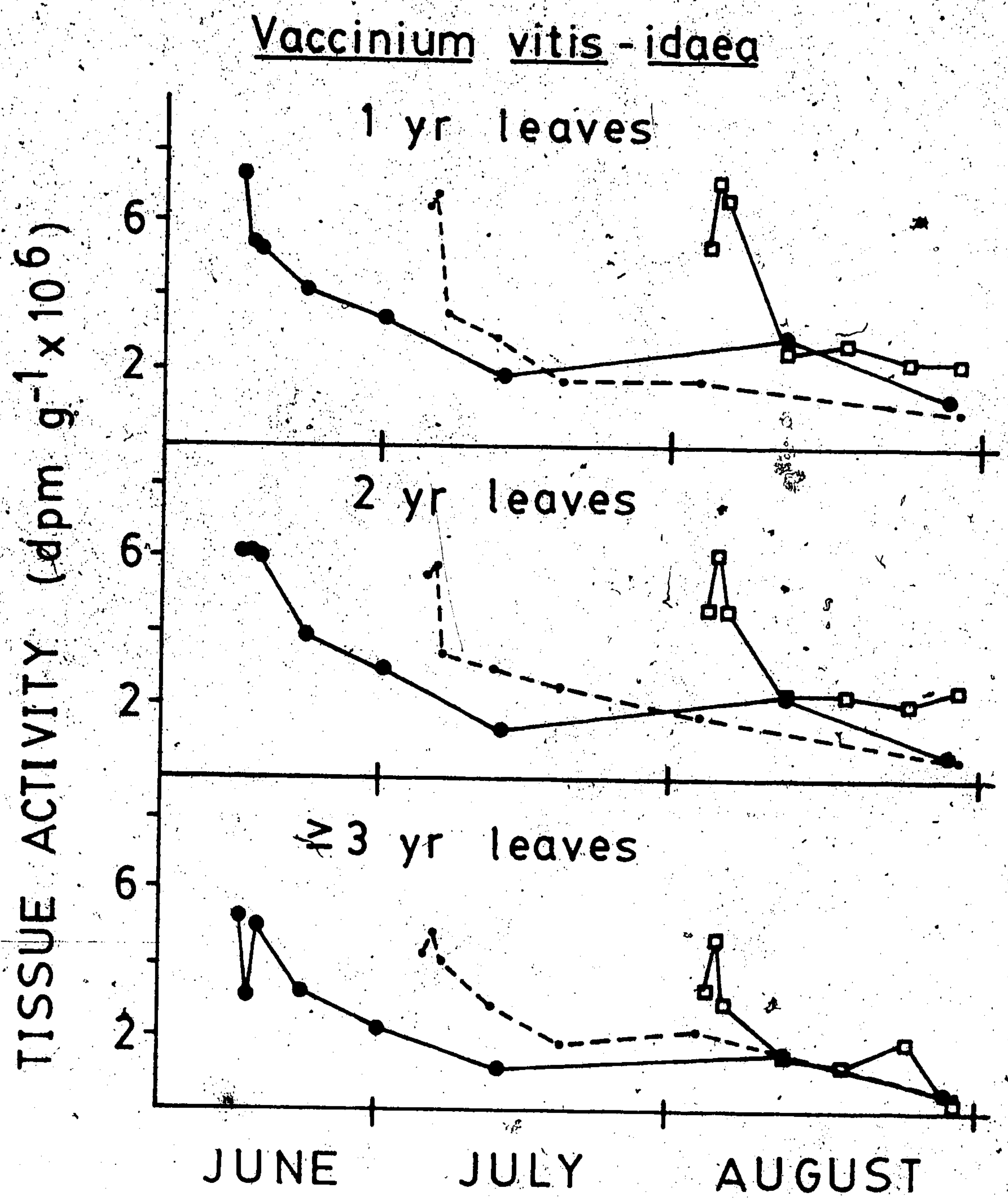


Figure 55. ^{14}C activity of one year old, two year old , and three year and older leaf tissue in *Vaccinium vitis-idaea*. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

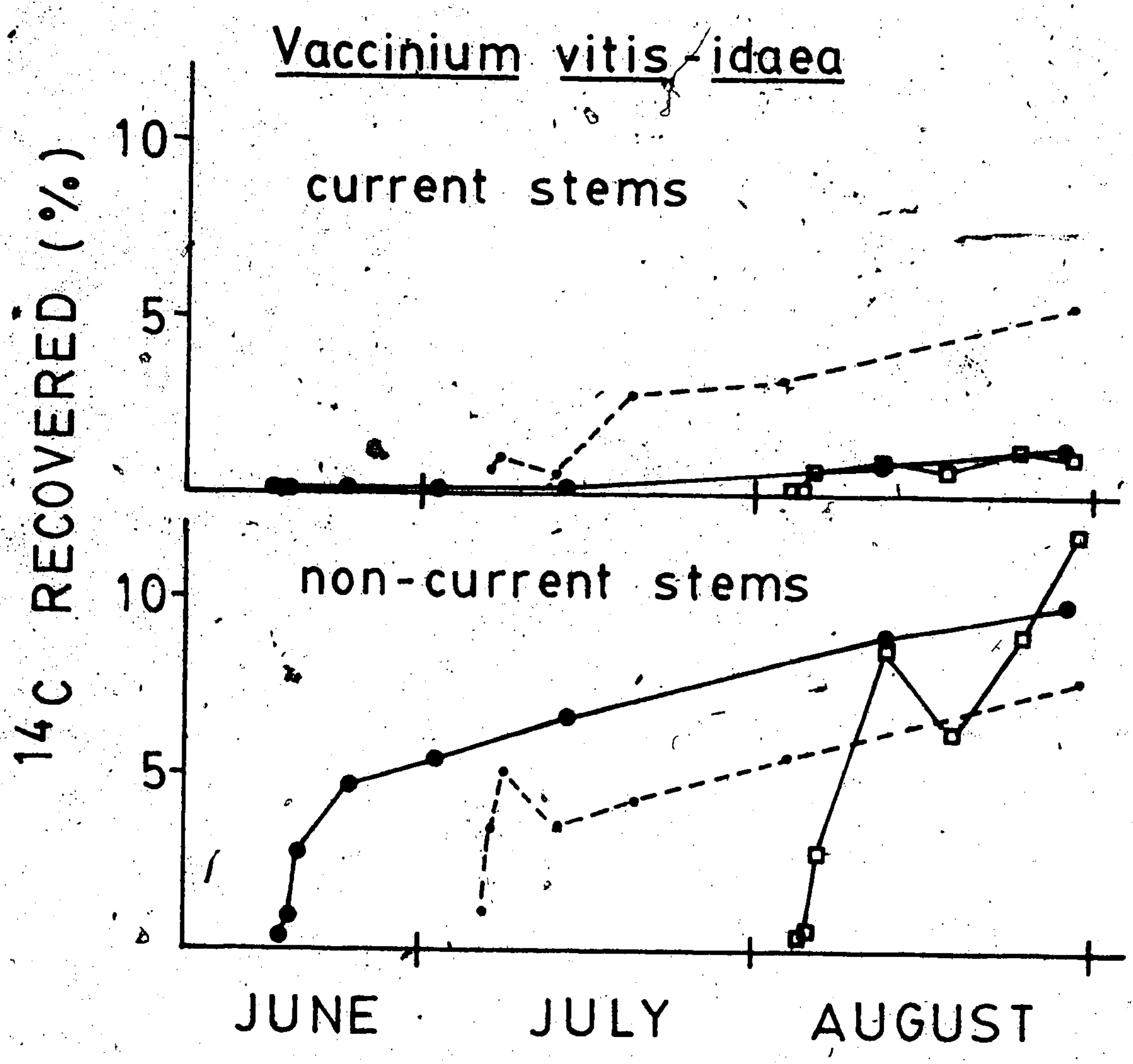


Figure 56. Percent of ^{14}C recovered in current and non-current stems from total aboveground biomass of Vaccinium vitis-idaea. Each line represents a series of plant harvests from a different exposure date. Most points represent N. = 2.

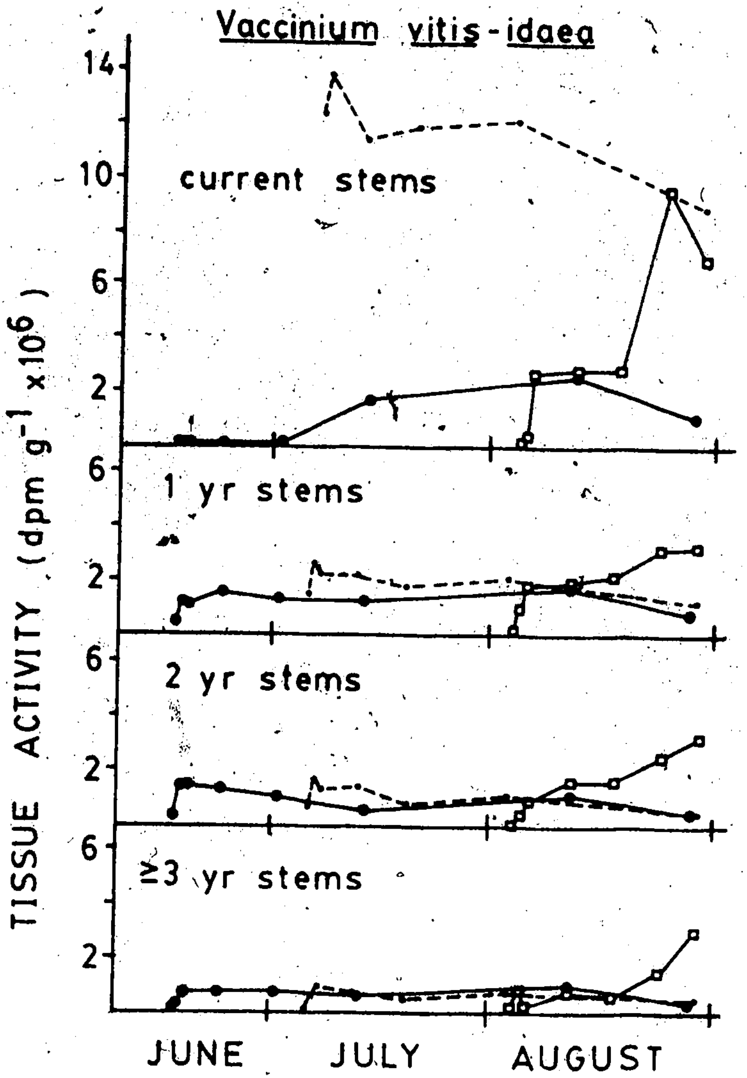


Figure 57. ^{14}C activity of current, one year old, two year old, and three and older stem tissue in Vaccinium vitis-idaea. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

accumulation occurred after the early July labelling, when stems were actively growing, and the fraction of total recovered carbon eventually reached 5% by the end of the season. Non-current stems accumulated appreciably more ^{14}C than did current stems, and this accumulation began immediately after all four labellings. The percentage of radiocarbon recovered from the non-current stems generally increased over the whole growing season, with the rate of increase rising with each successive exposure.

The concentration of radiocarbon in stem tissue reflected this movement of carbon into the tissue after assimilation. Little tissue activity was noted in the first two weeks after the June exposure, a time when little stem growth was occurring. Increases in radiocarbon concentration in current stems after two weeks indicate translocation to the tissue, as growth was initiated.

When young stems were beginning to elongate (July 4 exposure), labelling led to a high concentration of ^{14}C within 24 hr. The concentration dropped slightly towards the end of the growing season, with the decrease probably associated with dilution of ^{14}C by more recently assimilated carbon as growth continued. When radiocarbon was assimilated after the majority of current stem growth had occurred (August 4), concentration in the tissue still rose until late August, suggesting continued movement of ^{14}C into the tissue from other compartments of the plant.

Radiocarbon concentrations in all non-current stem compartments remained relatively low and constant throughout the growing season after an initial increase in the first 24 to 48 hr following labelling (Fig. 57). The non-current stem compartment increased slightly after the August 4 labelling, paralleling a similar rise in current stems.

Carbon accumulated in reproductive tissue at all times in [illegible] growing season (Fig. 58). The concentration of radiocarbon in floral tissue rose immediately after the June 16 exposure, but this carbon did not become a significant portion of the total recovered in a plant until two weeks later. A large percentage of carbon fixed on July 4 was soon recovered from floral tissue, a pattern also exhibited by tissue concentration, indicating allocation to this compartment. A drop in both concentration and amount recovered in the latter portion of the growing season after this exposure suggests no further July 4 carbon was translocated to the tissue. In addition, carbon already present was diluted by non-radioactive carbon. Carbon assimilated during fruit development (August 14 exposure) continued to move to the strong sink of the fruit for the remainder of the growing season, increasing tissue

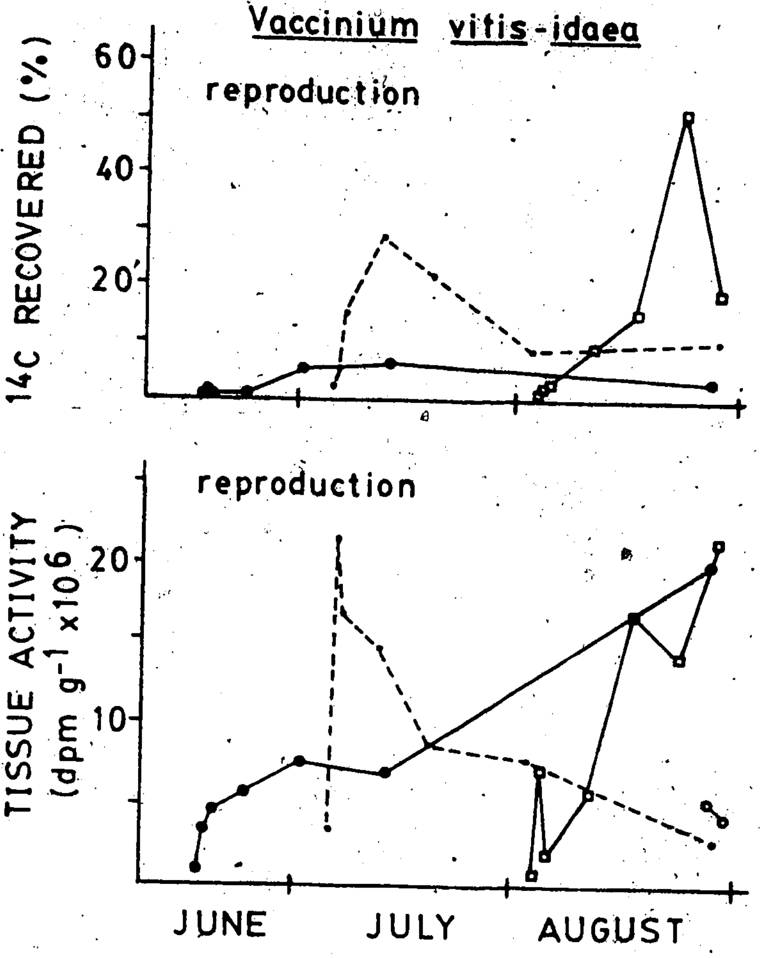


Figure 58. ^{14}C activity and percent of ^{14}C recovered in reproductive tissue from total aboveground biomass of Vaccinium vitis-idaea. Each line represents a series of plant harvests from a different exposure date. Most points represent N = 2.

concentrations of radiocarbon. This also resulted in greater percent recovery of radiocarbon from the fruit.

Discussion

Betula nana

Allocation of ^{14}C to aboveground biomass compartments of *B. nana* reflected the deciduous growth form of the plant. With no photosynthetic apparatus in place at the breaking of dormancy, deciduous species must rapidly produce leaves if net assimilation is to occur with the production of carbohydrates. Carbohydrates stored in underground stems and roots are used to initiate this development of new photosynthetic tissue when dormancy is broken (Chapin 1980a). High concentrations of ^{14}C within 3 hr of assimilation in these newly expanded leaves (Fig. 42) indicates they attained photosynthetic competency very rapidly. The similar concentrations in 3 hr harvests from early July, when leaves had just expanded, and from those in early August, after full expansion, suggest that the photosynthetic apparatus was fully active in early July. This radioactive carbon represented nearly 50% of the total ^{14}C generated (5.5 X 10^{7} DPM) in the cuvette. Johansson and Linden (1975) reported high photosynthetic rates in *B. nana* in recently expanded leaves. A rapid drop in ^{14}C recovered from leaves within the first week after exposure was also noted in various northern species by Allessio and Tieszen (1974), Berg et al. (1975), and Rosberg et al. (1981). Rosberg et al. (1981), working in a Norwegian Calluna heath, concluded that this drop in recovered ^{14}C represented respirational losses, rather than translocation, because no radiocarbon to account for the losses was found in either aboveground or belowground compartments.

Carbon assimilated as the leaves were completing their expansion was probably incorporated into leaf structural components, rather than entering the pool of total non-structural carbohydrates. The large percentage of radiocarbon from this early July exposure recovered from leaves through the remainder of the growing season, as well as the stability of tissue concentrations after the first week, indicate that much of this July carbon was retained in leaves until leaf fall and was never transported to overwintering compartments.

Once leaf structures were well developed, less carbon was retained within the leaves themselves, and more was translocated to other developing tissues. Though more than 50% of carbon recovered from the early August assimilation was still found in leaves just before they fell, this may not reflect carbon retention in all leaves. Leaf development in B. nana largely occurred synchronously in spring; however, additional leaves were still forming at some nodes in early August, and some of the high recovery represented structural material in the late forming leaves. No drop in radiocarbon concentration in leaf tissue was noted after mid-August as might be expected if carbohydrates or other organic compounds were exported to storage areas elsewhere in the plant before the loss of the leaves.

The low tissue concentration, but relatively high percentage of carbon recovered from leaves 48 hr after the August 30 exposure, probably reflects low levels of photosynthetic competency late in the growing season. Fall coloration of leaves had begun by this time, and reduced chlorophyll levels undoubtedly contributed to lower photosynthetic capacities. Reduced photosynthetic rates on the approach of leaf senescence in B. nana were reported by Johansson and Linder (1975).

Some carbon was being translocated to developing stems in early July, indicating that export of carbon was occurring while leaf structures were still a major sink for assimilates. As leaf development slowed in early August, and stem growth continued, carbon was translocated to stem tissues at greater rates than earlier in the season, and in larger amounts. The movement of carbon to both current and non-current stems continued to the end of the growing season. Approximately equal amounts of carbon were moving to current stems as they developed in length and diameter, and to non-current stems. The carbon translocated to non-current stems was probably used in part for radial increases. No sudden increase in carbon allocation to aboveground stem tissue occurred in the period before leaf senescence that would suggest movement of carbohydrates to storage areas in these stems that would prevent loss of that carbon in falling leaves.

Temporal differences in aboveground carbon allocation of *B. nana* reflected a priority in carbon demands. Large amounts of the first photosynthates produced after leaf expansion were committed to further development of essential structures needed for survival. Only after photosynthetic tissues were completed did the majority of carbon get distributed to such structures of less immediate importance, as stems.

Neither the deciduous male or female catkins ever represented a significant portion of aboveground biomass in *B. nana*. And likewise, allocation of radiocarbon to these tissues was relativley low throughout the year. Movement of assimilates to reproductive compartments was rapid, with ^{14}C appearing within 3 hr of fixation, but also appeared to be limited in duration, with little further transfer beyond the first week after assimilation.

Both leaves and catkins expanded rapidly in early stages of the growing season from buds that had been formed during July and August of the previous summer. Relatively small amounts of carbon fixed in early July were incorporated into these buds, but significant amounts (over 12% of the aboveground recovery) were used in the development of these buds later in the season, when leaf and much stem growth had been completed.

The presence of preformed leaf and flower buds when the soil was beginning to thaw, and when soil moisture, soil nutrients, and carbohydrates were available, would be an advantage in producing functional tissues very rapidly after snowmelt. Allocation of carbon to the buds in the fall, when photosynthates were available and conditions for translocation were favorable, avoided potential problems with mobilization and translocation of carbohydrates in the early part of the growing season because of low temperatures and frozen soil.

Ledum palustre

The allocation of carbon to aboveground compartments of

L. palustre was generally dominated by leaf tissue, with over 50% of assimilates in aboveground tissue found in leaves at most points during the growing season. Unlike B. nana which supported a single age class of leaf, L. palustre maintained current year leaves, and leaves two or three years old, to which carbon was committed differently.

Shortly after plants broke dormancy, as indicated by bud expansion and reorientation of leaves to a horizontal position, older leaf classes were photosynthetically active, with large amounts of assimilates remaining within the leaves until the end of the season. This retained carbon was probably used in synthesis of compounds and membranes that were modified upon entering dormancy and were necessary to regain full metabolic and photosynthetic competence in the spring (Tieszen 1972, 1974, Penning de Vries 1975). Few differences were noted in the response of 1 yr and 3 yr leaves at any time during the growing season. As growth of current tissue commenced in other compartments, increasingly less carbon was recovered from old leaves, both immediately after fixation, and weeks later. Once the immediate carbon demands within old leaves were met, carbon was exported in response to the strong sinks of other growing tissues.

The major sink to which this carbon was initially exported was to the developing current leaves. Because L.

palustre had a functioning photosynthetic apparatus in the overwintered leaves, there was no need to produce a new set of leaves very rapidly after snowmelt as in deciduous species. Once photosynthetic competence had been restored to the older leaves, synthesis of both structural and physiologically active components in current leaves created a strong demand for carbon. In mid-June, these developing leaves were still in a tight bud cluster and were not photosynthetically active, as shown by the lack of radiocarbon recovered from them 3 hr after exposure. But increasing radioactivity and amounts of carbon recovered from this tissue with time illustrates the translocation of photosynthates from older leaves to current leaves. Since only photosynthates from the current season were tagged with ^{14}C, no estimate of carbon contributions from storage areas of the plant to the production of current leaves could be made.

By early July, the buds had opened and leaves were beginning to expand. The relatively high level of activity in the leaves 3 hr after assimilation indicates that they were at least partially photosynthetically active. However, increasing activity and increasing percentages of carbon recovered from the leaves during the 48 hr after exposure indicates that carbon was still being imported from older leaves. Current leaves were thus making some contribution to their carbon budget at this time, but this contribution was complemented with that from other tissues to meet high demands of the rapid growth. As the growing season progressed, current leaves remained a sink for photoassimilates as carbon was used in the synthesis of structural material during continued elongation of the leaves, and in the development of sclerophylly once expansion had been completed. The high level of tissue activity 3 hr after assimilation indicates however, that current leaves could meet most of their carbon demands internally by early August.

Johnson and Tieszen (1976) reported decreasing photosynthetic capacities in non-current leaves of increasing age. The lack of major differences in radioactive concentrations in 1 yr and 3 yr leaves 3 hr after assimilation suggests there may have been no differences in photosynthetic rates between those age classes in this study. However, since some time had passed between assimilation and harvest, tissue concentrations may reflect respirational and translocational losses as well as photosynthetic rates.

Stems, both current and non-current, were a sink for photosynthates throughout the growing season. Carbon moved rapidly to old stem tissue after assimilation at all four sample exposures. The amount of radiocarbon recovered leveled off after one week, suggesting that movement of carbon to stems was largely completed within a short time after photosynthesis. Most of this translocated carbon was likely used for radial growth of the old stems and synthesized into cell structural material that was no longer transportable, as the relatively constant values after one week suggest. Slight increases in the amount of carbon recovered from old stems at the final harvests in late August perhaps indicates that some soluble carbohydrates have been moved to this stem tissue for storage over winter.

Though current stems were never a large portion of aboveground standing crop of L. palustre, or a source of a large percentage of recovered radiocarbon, they were a strong sink for photosynthates, particularly during their period of rapid growth in July and August. Carbon was translocated to areas of current stem growth at all times during the growing season, but only small amounts were committed to this tissue when the carbon demand for leaf growth was high, e.g. after the June 16 exposure. The drop in tissue activity after the July 7 exposure indicates that ^{14}C was probably being diluted by an influx of other carbon with continued growth. However, the relatively slow drop in activity for the last portion of the growing season, when active stem elongation was still occurring, suggests that more ^{14}C was moving into the tissue from another source, probably leaves, countering the dilution effect.

In contrast, the two week rise in tissue activity after the August 2 exposure, marking an influx of ^{14}C, was followed by a rapid decrease near the end of the growing season, indicating a lack of carbon flow into the tissue to balance the dilution effect. The stability of the amount of radiocarbon recovered from current stems at this time suggests that this drop was caused by the dilution factor of new carbon in rapid growth, rather than an export from this tissue to elsewhere in the plant, which would have caused a similar drop in activity.

Increasingly large amounts of carbon were committed to reproductive efforts through the growing season, and after each succeeding exposure period. In June, when leaves were strong sinks for carbon, allocation to reproductive tissue was initially slow, with significant amounts found in the tissue only after one week had passed. Later in the growing season, when leaves retained less photosynthate, movement of carbon into reproductive tissue occurred most rapidly in the first 48 hr after assimilation. The greatest translocation to this tissue occurred in August, when fruits were maturing and most leaf growth had occurred, and current leaves were exporting carbon. Allocation of significant amounts of carbon to reproductive effort came only after the requirements of old leaves had been met, and current leaves had become photosynthetically competent.

Though reproduction via seed was a rare occurrence in 1977 and 1978, nearly 40% of carbon fixed by L. palustre in early August was committed to reproduction. While the many wind dispersed seeds may not become established in most years on vegetated terrain, the annual production of many seeds would be advantageous in those infrequent years when conditions are proper for germination and seedling establishment. These conditions may occur when such environmental parameters as temperature or moisture are adequate, or when large areas of disturbed ground conducive to seedling establishment develop through slumping of banks and slopes or frost action.

In a manner similar to B. nana, L. palustre also committed photosynthates in August to the development of preformed vegetative and floral buds. Thus, there was a temporal separation between allocation of carbon to production of current photosynthetic tissue in early season, and to the less immediate needs of the next year later in the season. The deferral of carbon commitments to these buds until after sink strengths of most other tissues had diminished minimized intercompartment competition and, in effect, priorized the distribution of the potentially limited resources.

Vaccinium vitis-idaea

Patterns of carbon distribution to aboveground compartments of *V. vitis-idaea* were very similar to the other evergreen species, *L. palustre*. More photoassimilates were committed to photosynthetic tissue at all times of the year in *V. vitis-idaea* than in *L. palustre*, but this reflected the high ratio of leaves to stems in the former. Most carbon assimilated shortly after the breaking of dormancy was used by and retained in overwintered leaves, presumably for the rejuvenation of intracellular metabolic and photosynthetic apparatus. Once these commitments had been met, carbon was translocated from old leaves to such developing tissues as current leaves and stems as the demand arose. The gradual increases in the amounts of ^{14}C recovered from these developing tissues as well as older stems indicates that carbon was being translocated to them over a period of time and not just in a short pulse after assimilation.

Differences in allocation patterns were greater between current and non-current tissue, both stems and leaves, than within the different age classes of non-current tissue. Thus, once a structure was mature, as marked by woodiness in stems, or sclerophyllization in leaves, carbon budgets were similar among different age groups.

However, age of leaves may have affected photosynthetic rates as noted by the slight decreases in radiocarbon tissue concentrations 3 hr after exposure with increasing age of the leaf. This decreased concentration may also have been caused by increased rates of translocation from the tissue within the first 3 hr, reflecting a less strong sink in aging leaves. Tieszen et al. (1974) reported 50% of initial photosynthates were removed from Dupontia fisheri in as little as 4.8 hr, suggesting that differences at 3 hr in V. vitis-idaea may indeed be caused by differential rates of translocation rather than differential photosynthetic rates.

Recovery of radiocarbon and tissue activity in non-current stem tissue increased with time after assimilation, particularly after exposure in early August. This late season increase was greater than that observed in L. palustre, and represented a strong flow of carbon to the tissue at the time before onset of dormancy. Some of this carbon accumulation can be accounted for by radial growth of stems, with the sharp concentration rise accentuated by the high ratio of current tissue to old tissue in these old stems of V. vitis-idaea. Yet a similar rise in all three age classes of non-current stems suggests that much of this carbon was placed in storage areas in the stem as well as being used for radial growth. Higher concentrations of soluble carbohydrates in stem tissue of V. vitis-idaea than in some other evergreen shrubs supports the concept of the stem being a storage site for carbohydrates (Bannister 1980). Nitrogen budgets of L. palustre suggest 50% of N storage occurrs in stems rather than leaves (F. S. Chapin III, pers. comm.). If this pattern also occurred in V. vitis-idaea, it would also suggest substantial organic storage in stems.

Vaccinium vitis-idaea was the only species to have a fleshy fruit and movement of carbon to this compartment throughout the growing season reflected its development. As much as 50% of the recovered carbon from the August 4 exposure was in the developing fruit three weeks later; a large commitment relative to B. nana, but similar to L. palustre.

The increase in tissue activity in late August in fruits exposed to ^{14}C on June 16 indicates that this carbon had been resident elsewhere in the plant for most of the growing season, and only as the fruit began to mature was it redistributed. Similar increases in plants exposed in early

August correspond well to decreases in non-current leaves at that time.

Vaccinium _vitis-idaea_, like _B_. _nana_, and _L_. _palustre_, produced preformed floral and vegetative buds in late summer. These buds were too small to easily separate and analyze, and, thus, the lack of data is a reflection of technical problems and not of an absence of production of preformed buds.

SYNTHESIS

The arctic tundra environment is generally considered to have severe limitations for plant growth and development. Many parameters of the physical environment have been described as limiting factors in the growth and development of tundra vascular plants. Low air and soil temperatures (Bliss 1956, 1966), limited radiation (Bliss 1971), short growing season (Lewis and Callaghan 1976), and low levels of ~~nutrients (~~Chapin et al. 1980b) all contribute to the limited productivity of the tundra.

Many areas of the Low Arctic, nevertheless, are well vegetated with both herbs and woody shrubs, and through time, many vascular plants have evolved a wide range of adaptations and strategies for successful exploitation of this environment. Physiological constraints associated with different plant growth forms have been proposed as adaptive modifications in this environment (Bliss 1962, Johnson and Tieszen 1976, Shaver and Chapin 1980). Since the vascular plant community studied at Parsons Lake was dominated by dwarf shrubs of both deciduous and evergreen growth forms, adaptations of each form appear to have survival value in this environment.

The Parsons Lake study site had a short growing season

(90–100 d) typical of tundra environments. Mean temperatures were higher than other low arctic sites (Dingman et al. 1980, Barry et al. 1981), perhaps as a function of the site's higher elevation, and the resulting decrease in impact of coastal fogs. Air temperatures during the growing season had a wide range, with five day means as high as 16°C, and as low as 3.5°C. June, July, and August mean daily temperatures at 150 cm were 7.8, 11.5, and 11.1°C respectively in 1977, and 4.8, 12.6, and 8.1°C in 1978. Shortwave radiation and precipitation showed similar variability. Mean daily shortwave irradiance at Parsons Lake in June, July, and August respectively was 23.0, 23.7 and 17.7 MJ m^{-2} in 1977, and 25.7, 26.1, 16.7 MJ m^{-2} in 1978. Accumulated measureable precipitation over the same three months was 130 mm in 1977 and 70 mm in 1978. Degree day data from the two years of the study, and from the ten year period preceding the study also indicate an environment with large annual differences. From June to August, 960 degree days (0°C base) accumulated in 1977 and 771 in 1978, while the 10 yr mean from 1970 to 1979 for the same period at Inuvik was 1078 degree days.

The study site had a large amount of spatial as well as temporal variability. The soil of the study area was a Brunisolic Turbic Cryosol which formed a hummock-trough surface topography typical of the general region (Tarnocai and Zoltai 1978). Hummocks consisted of a mineral matrix overlain by a thin organic layer. Troughs were entirely organic matter down to permafrost. Nutrient contents of mineral and organic soil fractions were low. Late August available nutrient levels in trough organic material, where most rooting occurred, were 0.5 ppm (N), 19 ppm (P), and 187 ppm (K). These levels were in the general range of other low arctic sites (Haag 1974, McKendrick et al. 1978), though levels of N were higher in the wetter Alaskan site of McKendrick et al. (1978).

The hummock and trough surface topography created a wide range of soil temperatures, active layer depths, soil moisture, and thicknesses of the soil organic layer. Mean June 1978 soil temperatures were 1.4°C on hummocks and 0.7°C in troughs. At the end of the growing season in that year, the active layer was 56 cm on hummocks and 44 cm in troughs. The organic layer on hummock tops was generally less than 8 cm and more than 50 cm in troughs.

Use of this spatially diverse habitat by the three species was also different. Although aboveground parts of all three species were relatively uniformly distributed over the surface, rooting patterns reflected the surface variability. *Betula nana* and *Ledum palustre* rooted primarily in the moister and cooler deep organic material in the inter-hummock troughs. Vaccinium vitis-idaea rooted both in this trough area and in the thin layer of organic material overlying the mineral core of the hummocks themselves. This latter site was quicker to thaw in the spring, and warmer during the growing season, but less uniformly moist between precipitation events.

Rooting depths of the three species at Parsons Lake were similar to those of dwarf shrubs at other arctic and alpine tundra sites. Betula nana, L. palustre, and V. vitis-idaea roots were primarily in the upper 10 cm of organic material, above mineral soil (Bliss 1956, Shaver and Cutler 1979). Other dwarf shrubs like Salix pulchra and Empetrum nigrum had similar rooting patterns, while such graminoid roots as those of Carex bigelowii often penetrated over 40 cm (Bliss 1956). The roots of dwarf shrubs and graminoids in Mt. Washington alpine tundra had the same pattern as at the arctic sites (Bliss 1966). At Parsons Lake, maximum rooting depths were the greatest in B. nana and the shallowest in V. vitis-idaea.

The temporal variability present in the tundra environment was also reflected in growth rates and production of tundra species. Phenological stages of all three species were initially retarded by several weeks in 1978, when a cooler spring than average prevailed, compared to phenological development in 1977 when an average spring occurred.

Net annual aboveground production at Parsons Lake for the three species were: B. nana, 31 g m^{-2} yr^{-1}, L. palustre, 6 g m^{-2} yr^{-1}, and V. vitis-idaea, 4 g m^{-2} yr^{-1}. These production levels were in the general range of those reported in other low arctic production studies (Wein and Bliss 1972, Haag 1974, Shaver and Chapin 1980). Production of B. nana in the upland shrub community at Parsons Lake was higher than in Eriophorum tussock communities, but production of L. palustre and V. vitis-idaea at Parsons Lake was lower than at many tussock sites.

Patterns of leaf and stem growth, biomass partitioning, and carbon allocation varied among the three species and among the two growth forms in this study. The largest difference in these characteristics was between the deciduous shrub, B. nana, and the evergreen shrubs, L. palustre, and V. vitis-idaea. Each growth form exhibits a distinctive strategy for carbon and energy usage under the limiting parameters of low energy input, short growing season, and low nutrient supplies of the tundra environment in which they grow.

The partitioning of aboveground biomass into tissue compartments was different in the two growth forms. Stems represented a larger portion of biomass in _B_. _nana_ (>75%) than in the evergreen species (_L_. _palustre_ = 60%, _V_. _vitis-idaea_ = 20%), while leaves were a much smaller fraction in the deciduous shrub (<25%) than in the evergreen shrubs _L_. _palustre_ = 40%, _V_. _vitis-idaea_ = 75%). Reproductive tissue was less than 5% of the aboveground biomass in all three species throughout the growing season.

The partitioning of biomass into the various compartments was relatively constant over the growing season in the evergreen shrubs as new leaves gradually replaced abscised older leaves. In contrast to this even distribution, the leaf and stem compartments of _B_. _nana_ varied widely with time, as relative proportions changed with development of leaf tissue each spring. Additionally, the ratio of net production to biomass was lower in the evergreen species (_L_. _palustre_ = .14, _V_. _vitis-idaea_ = .13) than in _B_. _nana_ (.29), indicating a slower biomass turnover in the former. These patterns of biomass partitioning in the three species at Parsons Lake are similar to the patterns of the species elsewhere in the Low Arctic and to other dwarf shrub species in the same region: Northwest Territories (Haag 1974), Alaska (Johnson and Tieszen 1976, Stoner et al. 1982), Finland and Norway (Wielgolaski and Kjelvik 1975).

At the break of dormancy, B. nana has no functional photosynthetic apparatus. Within a relatively short growing season, B. nana must develop a set of leaves which can produce enough carbohydrate before they abscise in the fall to at least equal the cost of production and maintenance of those leaves and all other tissues in the plant. After snowmelt, leaf development from preformed buds was rapid, with fully expanded leaves present within one to two weeks. Leaf development was primarily synchronous, with only a limited number of leaves continuing to develop beyond the first several weeks of the growing season. This rapid expansion creates functioning photosynthetic surfaces during that part of the year when solar radiation is at a maximum, and maximizes the photosynthetic life of the leaves. Though the development of leaves was delayed by 10 to 14 d in 1978 due to a late, cool spring, the general pattern of development was similar in both years and was the same as that observed by Johnson and Tieszen (1976) in Alaskan B. nana.

Ledum palustre and V. vitis-idaea began the growing season with an intact photosynthetic apparatus, and showed no such rapid leaf flush after snowmelt as in B. nana. Development of current leaves in the evergreen shrubs was less rapid and asynchronous, beginning several weeks after leaf expansion in B. nana. Although they also expanded from preformed buds, leaf development continued to some degree over much of the growing season. Leaves older than one year exhibited well developed sclerophylly, and showed no significant growth after their first summer. The evergreen shrubs, which begin leaf expansion in early July, showed fewer differences in timing of phenophases in the two years of the study than did B. nana.

The source of carbon used in the development of these current leaves differed in the two growth forms. Betula nana, without a current assimilatory source of carbon, relied upon a storage pool of carbohydrates elsewhere in the plant for the initial development of the leaves. Once the leaves were photosynthetically active, a very rapid occurrence (Johansson and Linder 1974), much of the carbon used in further structural development of the leaves came from current photoassimilates. The carbon assimilated early in the growing season largely remained in the leaves until leaf abscission. Once the leaf tissue, and thus the photosynthetic apparatus, was well developed in B. nana, carbon was exported to other regions of the plant undergoing growth, ie. stems, reproductive tissue, rhizomes and roots.

The one year old and older leaves of evergreen shrubs did have photosynthetic competency after the break of dormancy, but the assimilates from these leaves did not initially move to newly developing tissues. Most of the early season assimilates remained in the old leaves where they were probably used in the synthesis of such structures as cellular membranes damaged or destroyed over winter (Tieszen 1972, 1974). Some of these early season carbohydrates were exported to current leaves and used in their development, however. Export of early season assimilates to support growth of new tissue continued for some time after assimilation, indicating that the old leaves functioned as storage organs for carbon in the first part of the growing season. Thus, carbon could be gained in that part of the season when radiation input was at its peak, and then used later, when the potential for photosynthesis might be reduced. Once expansion of current leaves began, carbon used for their continued development came both from their own photoassimilates as well as those imported from older leaves. Non-current leaves play an important role in the carbon and nutrient budgets of evergreen tundra plants. These leaves have been proposed as storage sites for carbohydrates (Hadley and Bliss 1964), and nutrients (Small 1972), and as a mechanism for assimilation in years of little or no production of new tissue (Chapin et al. 1980a calculated from Johnson and Tieszen 1976).

The two growth forms thus had contrasting patterns of carbon allocation. Allocation in deciduous shrubs had two general phases, the first consisting of carbon allocation for leaf development and the second for stem and reproductive tissue. Evergreen shrubs tended to carry on development of all three tissue types concomitantly. Carbon was committed to leaves, stems, and reproductive tissues simultaneously, rather than separately. These general patterns are typical of shrub development reported elsewhere in the Low Arctic (Wein and Bliss 1974, Haag 1974, Johnson and Tieszen 1976, Chapin et al. 1980a, Stoner et al. 1982).

The higher levels of ^{14}C recovered from B. nana leaves shortly after assimilation than those found in either of the evergreen shrubs reflects the higher photosynthetic rates of deciduous shrubs (Johnson and Tieszen 1976, Limbach et al. 1982). However, while B. nana had higher rates of photosynthesis, the large amounts of ^{14}C recovered from non-current leaves of L. palustre and V. vitis-idaea in mid-June, before B. nana leaves had fully expanded, illustrates that these shrubs with evergreen leaves had a longer season of carbon assimilation. Betula nana produced no photosynthates at this time because no leaves had yet developed.

In this upland tundra, deciduous shrubs as B. nana and Salix spp. generally form the canopy layer, while such evergreen shrubs as L. palustre and V. vitis-idaea form the understory or sub-canopy. The evergreen shrubs are thus able to begin photosynthetic activity earlier in the growing season, before the canopy leaves of B. nana begin to shade them. The evergreen leaves of L. palustre and V. vitis-idaea also presumably allow assimilation of photosynthates later in the growing season, after abscission of the deciduous leaves in late August and early September.

Betula nana, with a shorter period available for photosynthesis and a higher carbon cost associated with the annual leaf carbon turnover, benefits from its upper canopy position. Once leaves have developed in June, B. nana leaves have the potential to photosynthesize at higher rates without shading from other species.

Temperature appears to affect photosynthesis and growth of evergreen and deciduous shrubs differently. The evergreen shrubs, V. vitis-idaea and L. palustre subsp. groenlandicum have lower optimum temperatures for photosynthesis than does B. nana (Smith and Hadley 1974, Limbach et al. 1982). This ability to photosynthesize at lower temperatures allows the evergreen leaves to begin assimilating carbon in the cool period shortly after snowmelt. This process is additionaly aided by the shallow root systems of the evergreen shrubs, which are concentrated in that portion of the active layer which first develops.

Later in the growing season, when the canopy of B. nana shades many of the evergreen shrubs and potentially limits their leaf temperatures, photosynthesis can still proceed at near maximum rates because of the ability of evergreen species to photosynthesize efficiently at lower temperatures.

Though B. nana has a higher optimum temperature for photosynthesis than the evergreen shrubs, it may also maintain a higher average leaf temperature through interception of greater amounts of radiation than L. palustre and V. vitis-idaea. The unshaded upper canopy position of B. nana aids this interception.

The sensitivity of growth in B. nana to temperature in the early part of the growing season was reflected in the differential rate of leaf development on different parts of the same plant. Leaves near the ground and in the warmer boundary layer developed earlier and more rapidly than did those in the cooler, upper portions of the plant.

General distribution patterns of carbon and energy between aboveground and belowground compartments in tundra plants is extremely difficult to determine, and few reports of such have appeared. The large number of intertwined underground stems and rhizomes make separation of them tenuous at best. Both deciduous and evergreen shrubs appear to have large portions of biomass belowground (Bliss 1971, Shaver and Billings 1975, Chapin et al. 1980a), in contrast to many high arctic subshrubs and herbs (Svoboda 1977, Bell and Bliss 1978).

These large underground biomass compartments may provide increased surface area for nutrient absorption in the nutrient deficient environment (Chapin et al. 1980b). The contrast between biomass patterns in low arctic and high arctic sites, both low nutrient situations, and evidence of both accelerated and reduced root growth at low soil temperatures (Shaver and Billings 1975, Bell and Bliss 1978) make the situation unclear.

Information on carbon movement to and from the underground portions of the three species is not generally available, but Chapin et al. (1978, 1980a) reported different patterns of nutrient movement to and from these compartments in evergreen _L. palustre_ and deciduous _B. nana_. Carbohydrate movement might be expected to be similar to that of nutrients. The deciduous shrubs have strong nutrient and carbon sinks in aboveground tissue shortly after snowmelt, when rapid leaf growth is occurring. However, at this time, the soil is largely frozen and conditions for translocation from underground tissue are unfavorable. This, and changes in concentrations of mobile nutrients in stem tissue over time, led Chapin et al. (1980a) to conclude that most storage was in aboveground stems. Leaf development of *B. nana* does not begin until the top few cm of soil are unfrozen, an area where many buried stems occur. The high carbohydrate demands of rapid leaf development in deciduous shrubs may also be met by movement from these belowground or shallowly buried stems.

Carbohydrate demands in evergreen shrubs in early season are more easily met by the old leaves which, at that time, rapidly gain photosynthetic competence, and thus potentially lessen the significance of unfavorable conditions for translocation from underground tissues. In *L. palustre*, nutrients appear to be stored *in situ* in overwintering leaves (Chapin et al. 1980a, Reader 1980) and carbohydrates may also be stored there (Hadley and Bliss 1964, Reader 1978). Large amounts of ^{14}C retained in both current and non-current leaves of *L. palustre* at all times in the growing season indicate that they may be important organs for storage of photoassimilates. In *V. vitis-idaea*, retention of large amounts of ^{14}C in leaves and stems in this current study, and high levels of total nonstructural carbohydrates in aboveground compartments (Bannister 1980) suggest that aboveground tissues in general may be important storage sites for carbohydrates over winter. With nutrients and carbohydrates stored aboveground, their translocation might easily take place when large amounts of underground tissue were still frozen.

Though deciduous species must produce new leaves each year, the cost of these leaves may differ from the cost of evergreen leaves. Because of the lower cost partially associated with the presence of few secondary chemical compounds (Jung et al. 1979) which are used as antiherbivore defenses in evergreen species (Rhoades and Cates 1976, Batzli and Jung 1980, Chapin et al. 1980a, Mooney and Gulmon 1982), the initial cost of leaf development in deciduous species appears lower than for evergreen species (Miller and Stoner 1979).

The relative lack of antiherbivore defense compounds in deciduous leaves relative to evergreen leaves is reflected in differences in herbivore damage observed in the two growth forms during the study. While losses were low in all three species, four percent of leaf surface area in _B. nana_ was lost to herbivores during the growing season. Nearly all damage was caused by insects. Most shrubs are snow-covered in winter and winter grazing appears minimal.

Photosynthetic surfaces of deciduous shrubs lost to herbivores can be replaced during the growing season.

Although the pattern of leaf development was basically synchronous, some leaves continued to form relatively late in the growing season. Dormant lateral buds may also respond to defoliation by the production of new leaves (Archer and Tieszen 1980). Because herbivore losses are low, leaf longevity is short, and some replacement of losses can occur, the cost of antiherbivore defenses to B. nana and other deciduous shrubs may be greater than the actual carbon losses to the plants.

Carbon losses from both L. palustre and V. vitis-idaea to to herbivores were very low during the study (estimated to be under 1%). Both evergreen shrubs have large amounts of defensive chemicals present in leaf tissue (Jung et al. 1976). Because evergreen leaves are usually present for more than one growing season, additive annual losses of photosynthetic surface to herbivores might be significant without such defenses. Thus, the carbon, nutrient, and energy cost of developing such defensive mechanisms may be more effective for evergreen plants than for deciduous species with an annual leaf carbon turnover.

In discussing physiological strategies of evergreen and deciduous growth forms, much attention has been paid to rates of carbon fixation (Johansson and Linder 1975, Johnson and Tieszen 1976) and the adaptive significance of the rates. Carbohydrate production may not be a limiting factor to plant growth in the Mackenzie Delta region of the Low Arctic, and such impediments to assimilation as low rates of fixation or herbivore caused reduction in photosynthetic surface area may be less important than other environmental factors. Most tundra species have high levels of total nonstructural carbohydrates throughout most of the growing season (Mooney and Billings 1960, Fonda and Bliss 1966, Haag 1974). Among the exceptions to this general pattern are cushion plants in the High Arctic (Svoboda 1977).

Chapin et al. (1980b) believed that this carbon surplus present in the plants may be a result of limitations to carbohydrate use caused by low nutrient supplies, rather than being a function of low temperature inhibiting carbohydrate use as proposed by Warren Wilson (1966) and Haag (1974). If such a nutrient limitation to metabolism or use of nonstructural carbohydrates exists, then differences in photosynthetic capacity, carbon uptake rates, or reduction of photosynthetic surface area may be less important to growth and primary production of deciduous and evergreen plants than the nutrient regime in which the plants are growing.

Evergreens become increasingly important in low nutrient habitats, both in temperate and arctic environments

(Loveless 1961, 1962, Monk 1966, Small 1975, Shaver and Chapin 1980, Shaver 1981). Most explanations of this phenomenon center around more efficient use of limited nutrients by evergreens (Small 1975, Reader 1978). This interpretation suggests nitrogen retained by the leaves and used for several years increases nutrient use efficiency. A net positive benefit relative to the cost of nutrient acquisition, leaf development and leaf maintenance is attained by evergreens through long term use of the nutrients at low photosynthetic rates rather than in one growing season at higher photosynthetic rates as for deciduous species (Johnson and Tieszen 1976).

However, Chapin et al. (1980a), using a different method of calculating the nitrogen investment of a plant, demonstrated similar carbon gains for a unit of nutrient invested in both _B. nana_ and _L. palustre_. They suggest that the dominance of evergreens in low nutrient environments may originate from lower annual nutrient requirements or reduced nutrient losses from leaching and abscission rather than through a relationship between photosynthetic rate and nutrient investment. Though low nutrient levels exist in the soils of the study area, and in similar habitats in the region (Haag 1974), both growth forms do well as indicated by the relatively large standing crops of both types. In this situation, neither growth form appears to have a distinct advantage over the other.

Energy expended by all three species in total reproductive effort was very high relative to reproductive success. Only two seedlings, one each of V. vitis-idaea and L. palustre were noted in the two years. Deciduous B. nana committed the least energy to reproduction, while L. palustre committed the greatest amount. In contrast to this pattern, Chester and Shaver (1982) reported a reproductive effort six times greater in V. vitis-idaea than in L. palustre in a central Alaskan cotton grass tundra community. However, in this study at Parsons Lake, the return on this energy investment was equally low in both growth forms. These low rates of seedling establishment were in sharp contrast to those at Eagle Creek, Alaska where seedling densities were between 1.5 m^{-2} in B. nana and V. vitis-idaea and 180 m^{-2} in L. palustre (McGraw and Shaver 1982).

Reproduction and seedling establishment have high heat requirements in tundra plants (Bliss 1971). Reproductive success of these plants may thus reflect current environmental conditions. Betula nana, L. palustre, and V. vitis-idaea are all major understory components of the taiga flora to the south, and were well establshed in the Parsons Lake region when a tree overstory existed between 8,500 and 4000 years ago (Ritchie and Hare 1971, Ritchie 1976, 1977).

At that time when the plants occurred as understory shrubs and more moderate environmental conditions existed, the success rate of sexual reproduction in the species may well have been higher. With the subsequent cooling of the climate, treeline retreated to the south, but the ericaceous and deciduous shrub understory remained (Ritchie and Hare 1971, Nichols 1976). A less significant advance and retreat occurred subsequently as the climate again ameliorated and then cooled (Black and Bliss 1980). In those past times of climatic amelioration, and under an overstory canopy of trees, sexual reproduction of the three species may have been more frequently successful. The carbon cost of the reproductive effort would have resulted in a payback of established seedlings.

With the present cooler climate, sexual reproduction is not frequently successful, even though the effort, in terms of carbon allocation, is still made. Successful seedling establshment may still occur at Parsons Lake in occasional years when appropriate environmental conditions exist. Black and Bliss (1980) have demonstrated that seed production and germination of <u>Picea mariana</u> along a treeline gradient to the south of the present study, are in part limited by low temperatures. Trees at treeline are no longer reproducing sexually as a result of a slight decrease in recent summer temperatures, while trees a short way south along a temperature gradient were reproducing successfully. A similar situation may exist with the dwarf shrubs at Parsons Lake. With appropriate conditions, represented perhaps by a year or series of years with a slightly warmer growing season, the shrubs might increase their reproductive success significantly.

The high rates of successful seedling initiation among the three shrub species and successful establishment in L. palustre reported by McGraw and Shaver (1982) reflect some of their reproductive potential under warmer conditions. The retention of annual commitments of carbon to a currently nonproductive compartment would thus be advantageous in a region where either a long term climatic cycling or short term fluctuations would again present environmental conditions appropriate to seed germination and seedling establishment.

Few studies are available regarding seed banks or the viability of buried seeds for arctic or subarctic species. Johnson (1975) reported that while seeds of many species, including Betula spp. and V. vitis-idaea, from a subarctic forest were commonly present in the soil, most seeds were not viable. Seeds collected from plants at maturity, however, have had greater degrees of viability and germination. Seeds of V. vitis-idaea collected in the boreal forest had >75% germination (Hall and Shay 1981). Germination rates of these seeds decreased rapidly within one year. Seeds of L. palustre from the Parsons Lake area had >90% germination six months after harvest (E. Karlin, pers. comm.). Bliss (1958) reported germination rates of B. nana seeds at >50%. Thus, these shrub species produce viable seeds which germinate freely under the appropriate conditions.

The low number of seedlings found in most field studies, therefore, is not the result of few viable seeds being produced. The rapid decline in viability of seeds with time reported by Hall and Shay (1981) and the low number of viable seeds in buried seed banks (Johnson 1975) suggest that an appropriate seedbed and proper environmental conditions for germination must very shortly follow a growing season in which a supply of viable seeds is produced if seedling establishment is to occur.

The reestablishment of the three species after natural or man-caused disturbances depends on either sexual reproduction via seedling establishment or asexual reproduction via rhizomes or root sprouting. A disturbed surface with recolonization potential can result from natural phenomena as the slumping of soil associated with melting of permafrost or the removal of vegetation by fire.

Disturbed surfaces may also result from such man-induced changes as development of seismic lines and winter roads. The method for reestablishment used by the three species probably depends on external conditions relating to the environment and on the nature and frequency of the original disturbance.

Tundra fires commonly occur (Lutz 1956, MacKay 1970), though their frequency and extent are difficult to establish. With the cool summer temperatures of the arctic and a low fuel load relative to temperate forests, fires intense enough to kill all plant roots and rhizomes may be infrequent (Wein and Bliss 1972). Such fires probably do occur when conditions are very dry and the organic material in inter-hummock troughs can easily burn, thus, destroying roots and rhizomes that are established there. Shrub species in burned areas show rapid and extensive sprouting from the roots and rhizomes which are not killed during a fire (Wein and Bliss 1972, Black and Bliss 1982). Ledum palustre particularly reestablishes well by sprouting after fire (Wein and Bliss 1973).

Reestablishment of dwarf shrubs after man-induced physical disruption is frequently similar to that after fire. The creation of seismic lines and winter roads tends to shear off the stems of the shrubs near ground level, leaving belowground parts relatively undisturbed (Hernandez 1973). Betula nana, L. palustre, and V. vitis-idaea all exhibit the ablity to successfully reestablish on such disturbed ground via sprouting from the undisturbed underground parts (Bliss and Wein 1972, Hernandez 1973, Sims and Steward 1981). The rate and degree of recolonization depends on many factors, including the type of disturbance, and its frequency and duration.

Shrub recolonization of disturbed areas by seeds appears to be less common than by vegetative means. Germination of dicot seeds on bare, disturbed tundra is poor (Chester and Shaver 1982). Thus, reestablishment of the shrubs on these disturbed areas, particularly when no belowground organs exist as in a recently slumped area or after an intense fire, may not occur immediately. Instead, the site may first be colonized by graminoids. In contrast to dicots, graimoid seeds do germinate and seedlings do become established on bare tundra soil (Chester and Shaver 1982).

Both evergreen and deciduous growth forms are successful exploiters of the Mackenzie Delta uplands. The dominance of B. nana in the study area indicates that the carbon and nutrient demands of an annual leaf turnover are able to be met by the plant in this environment. Mooney and

Gulmon (1982) have suggested that the net benefit of a leaf to a plant can be considered as a function of the rate of carbon gain, times the period of that gain, minus the cost of growth and maintenance of the leaf, minus losses to herbivores. Relative to the evergreen shrubs, the period of carbon gain for B. nana is short; limited to a single growing season. However, this short growing season is offset by a much higher potential for carbon gain, represented by a higher photosynthetic capacity, than that of evergreen species (Johansson and Linder 1975, Johnson and Tieszen 1976, Limbach et al. 1982). Thus, though the carbon gain period may be short, sufficient amounts of carbon can be fixed during the life of the leaf because of higher photosynthetic rates.

Evergreen species become increasingly important with increasing latitude (Bliss 1981). In the High Arctic, nearly all herb and shrub species are either evergreen or wintergreen. In the Low Arctic, where deciduous shrubs are common, the cost of rapid biomass turnover resulting from annual leaf abscission can be met by the plants. The deciduous shrubs maintain a comparatively high rate of photosynthesis when air temperatures and radiation intensities are sufficient. Soils in these lower latitude regions thaw early and rapidly, allowing translocation of water, nutrients, and carbohydrates to the developing leaves.

With increasing latitude, and the associated lower air temperatures, shorter growing season, and shallower and more slowly developing active layer, evergreen species are favored. No translocation of nutrients or carbohydrates is needed immediately for production of new photosynthetic tissue in these species, since photosynthetic tissue is already present at snowmelt in the form of over-wintered evergreen leaves. In this shorter and cooler growing season, the high carbon turnover of deciduous shrubs appears less adaptive.

LITERATURE CITED

Abrahamson, W. G. 1979. Patterns of resource allocation in wildflower populations of fields and woods. Amer. J. Bot. 66:71-79.

Abrahamson, W. G. and M. Gadgil. 1973. Growth form and reproductive effort in goldenrods (Solidago, Compositae). Am. Nat. 107:651-661.

Allessio, M. L. and L. L. Tieszen. 1975a. Leaf age effect on translocation rate and distribution of ^{14}C photoassimilate in Dupontia at Barrow, Alaska. Arctic Alp. Res. 7:3-12.

Allessio, M. L. and L. L. Tieszen. 1975b. Patterns of carbon allocation in an arctic tundra grass, Dupontia fisheri (Graminae), at Barrow, Alaska. Amer. J. Bot. 62:797-807.

Archer, Steve and Larry L. Tieszen. 1980. Growth and physiological responses of tundra plants to defoliation. Arctic Alp. Res. 12:531-552.

Babb, T. A. and D. W. A. Whitfield. 1977. Mineral nutrient cycling and limitation of plant growth in the Truelove Lowland ecosystem. In L. C. Bliss (ed.) Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem. Univ. of Alberta Press, Edmonton. 714p.

Bannister, Peter. 1980. The non-structural carbohydrate contents of ericaceous shrubs from Scotland and Austria. Acta OEcol. OEcol. Plant. 1:275-292.

Barry, R. G., G. M. Courtin and C. Labine. 1981. Tundra climates. In L. C. Bliss, O. W. Neal and J. J. Moore (eds.) Tundra Ecosystems: a Comparative Analysis. Cambridge Univ. Press, Cambridge. 813p.

Baskerville, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. 2:49-53.

Batzli, George O. and Hans-Joachim G. Jung. 1980. Nutritional ecology of microtine rodents: resource utilization near Atkasook, Alaska. Arctic Alp. Res. 12:483-499.

Beadle, N. C. W. 1966. Soil phosphate and its rôle in molding segments of the Australian flora and vegetation with special reference to xeromorphology and sclerophylly. Ecology 47:991-1007.

Beauchamp, John J. and Jerry S. Olson. 1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54:1403-1407.

Bell, Katherine L. and L. C. Bliss. 1978. Root growth in a polar semidesert environment. Can. J. Bot. 56:2470-2490.

Berg, A., S. Kjelvik and F. E. Wielgolaski. 1975. Distribution of 14C photosynthates in Norwegian alpine plants. <u>In</u> F. E. Wielgolaski (ed.) Fennoscandian Tundra Ecosystems. Pt. I. Plants and Microorganisms. Springer-Verlag, New York. 366 p.

Berg, A., O. Skre, F. E. Wielgolaski and S. Kjelvik. 1973. Leaf areas and angles, chlorophyll and reserve carbon in alpine and subalpine plant communities, Hardangervidda, Norway. <u>In</u> L. C. Bliss and F. E. Wielgolaski (eds.) Primary Production and Production Processes, Tundra Biome. I. B. P. Tundra Biome Steering Committee, Edmonton-Oslo.

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

Black, R. Alan and L. C. Bliss. 1980. Reproductive ecology of <u>Picea mariana</u> (Mill.) BSP., at treeline near Inuvik, Northwest Territories, Canada. Ecol. Monogr. 50:331-354.

Bliss, L. C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. Ecol. Monogr. 26:303-337.

Bliss, L. C. 1958. Seed germination in arctic and alpine species. Arctic 11:180-188.

Bliss, L. C. 1962. Caloric and lipid content in alpine tundra plants. Ecology 43:753-757.

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

Bliss, L. C. 1971. Arctic and alpine plant life cycles. Ann. Rev. Ecol. Syst. 2:405-438.

Bliss, L. C. 1981. North American and Scandanavian tundras and polar deserts. in L. C. Bliss, O. W. Heal, and J. J. Moore (eds.) Tundra ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge. 813 p.

Bliss, L. C. and Ross W. Wein. 1972. Plant community response to disturbances in the western Canadian arctic. Can. J. Bot. 50:1097-1109.

Bliss, L. C., G. M. Courtin, D. L. Pattie, R. R. Riewe, D. W. A. Whitfield and P. Widden. 1973. Arctic tundra ecosystems. Ann. Rev. Ecol. Syst. 4:359-399.

Bostock, S. J. and R. A. Benton. 1979. The reproductive strategies of five perennial Compositae. J. Ecol. 67:91-107.

Bryson, R. A. 1966. Air masses, streamlines and the boreal forest. Geogr. Bull. 8:228-269.

Burns, B. M. 1973. The climate of the Mackenzie Valley-Beaufort Sea. Vol. I & II. Environment Canada, Climatological Studies No. 24., Ottawa.

Campbell, Gaylon. 1977. An Introduction to Environmental Physics. Springer-Verlag, New York. 159 p.

Canadian Soil Survey Committee. 1978. The Canadian system of soil classification. Agriculture Canada Pub. No. 1646. 164 p.

Chapin, F. S. III. 1978. Phosphate uptake and nutrient utilization by Barrow tundra vegetation. In Larry L. Tieszen (ed.) Vegetation and Production Ecology of an Alaskan Arctic Tundra. Springer-Verlag, New York. 686 p.

Chapin, F. S. III. 1980a. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-260.

Chapin, F. Stuart III. 1980b. Nutrient allocation and responses to defoliation in tundra plants. Arctic Alp. Res. 12:553-563.

Chapin, F. S. III, R. J. Barsdate and O. Barel. 1978. Phosphorous cycling in Alaskan coastal tundra: a hypothesis for the regulation of nutrient cycling. Oikos 31:189-199.

Chapin, F. Stuart III, Douglas A. Johnson and Jay McKendrick. 1980a. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. J. Ecol. 68:189-209.

Chapin, F. S. III, L. L. Tieszen, M. C. Lewis, P. C. Miller and B. H. McCown. 1980b. Control of tundra plant allocation patterns and growth. In Jerry Brown, Philip C. Miller, Larry L. Tieszen and Fred L. Bunnell (eds.) An Arctic Ecosystem. The Coastal Tundra at Barrow, Alaska. Dowden, Hutchinson, and Ross, Stroudsburg, Penn. 571 p.

Chapin, F. Stuart III, Keith Van Cleve and L. L. Tieszen. 1975. Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska. Arctic Alp. Res. 7:209-226.

Chester, A. L. and G. R. Shaver. 1982. Reproductive effort in cotton grass tussock tundra. Holarctic Ecol. 5:200-206.

Chester, Ann L. and Gaius R. Shaver. 1982b. Seedling dynamics of some cotton grass tussock tuncra species during the natural revegetation of small disturbed areas. Holarctic Ecology 5:207-211.

Cochran, William G. 1963. Sampling Techniques. 2nd ed. Wiley, New York. 413 p.

Cochran, William G. 1977. Sampling Techniques. 3rd ed. Wiley, New York. 428 p.

Corns, Ian G. W. 1974. Arctic plant communities east of the Mackenzie Delta. Can. J. Bot. 52:1731-1745.

Collins, N. J. and W. C. Oechel. 1974. The pattern of growth and translocation of photosynthate in a tundra moss, *Polytrichum alpinum*. Can. J. Bot. 52:355-363.

Courtin, G. M. and C. L. Labine. 1977. Microclimatological studies on Truelove Lowland. *In* L. C. Bliss (ed.) Truelove Lowland, Devon Island, Canada: a High Arctic Ecosystem. Univ. of Alberta Press, Edmonton. 714 p.

Courtin, G. M. and J. M. Mayo. 1975. Arctic and alpine plant water relations. *In* F. John Vernberg (ed.) Physiological adaptation to the environment. Intext Educational Pub., New York. 576 p.

Crampton, C. B. 1977. A study of the dynamics of hummocky microrelief in the Canadian north. Can. J. Earth Sci. 14:639-649.

Dennis, J. G., L.L. Tieszen and M. A. Vetter. 1978. Seasonal dynamics of aboveground production of vascular plants at Barrow, Alaska. *In* L. L. Tieszen (ed.) Vegetation and Production Ecology of an Alaskan Arctic Tundra. Springer-Verlag, New York. 686 p.

Dickmann, D. I. and T. T. Kozlowski. 1968. Mobilization by *Pinus resinosa* cones and shoots of ^{14}C photosynthate from needles of different ages. Amer.

J. Bot. 55:900-906.

Dickmann, D. T. and T. T. Kozlowski. 1970. Mobilization and incorporation of photoassimilated ^{14}C by growing vegetation and reproductive tissues of adult Pinus resinosa Ait. trees. Plant Physio. 45:284-288.

Dingman, S. L., R. G. Barry, G. Weller, C. Benson, E. F. LeDrew and C. W. Goodwin. 1980. Climate, snow cover, microclimate, and hydrology. In Jerry Brown, Philip C. Miller, Larry L. Tieszen and Fred L. Bunnell (eds.) An Arctic Ecosystem, The Coastal Tundra at Barrow, Alaska. Dowden, Hutchinson and Ross, Stroudsburg, Penn. 571 p.

Dowding, P. F. S. Chapin III, F. E. Wielgolaski and P. Kilfeather. 1981. Nutrients in tundra ecosystems. In L. C. Bliss, O. W. Heal and J. J. Moore (eds.) Tundra Ecosystems: a comparative analysis. Cambridge Univ. Press, Cambridge. 813 p.

Environment Canada. 1977-1978. Monthly Record. Meteorological Observations in Canada.

Flower-Ellis, J. G. K. 1975. Growth in populations of Andromeda polifolia on a subarctic mire. In F. E. Wielgolaski (ed.) Fennoscandian Tundra Ecosystems. Part I, Plants and Microorganisms. Springer-Verlag, New York. 366 p.

Flower-Ellis, J. G. K. 1980. Diurnal dry weight variation and dry matter allocation of some tundra plants. 2. Rubus chamaemorus L. In M. Sonesson (ed.) Ecology of a Subarctic mire. Ecol. Bull. (Stockholm) 30:163-179.

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

Gadgil, M. and O. T. Solbrig. 1972. The concepts of r and K selection: Evidence from wildflowers and some theoretical considerations. Am. Nat. 106:14-31.

Gaines, M. S., K. J. Vogt, J. L. Hamrick and J. Caldwell. 1974. Reproductive strategies and growth patterns in sunflowers (Helianthus). Am. Nat. 108:889-894.

Gersper, P. L., V. Alexander, S. A. Barkley, R. J. Barsdate, and P. S. Flint. 1980. The soils and their nutrients. *In* Jerry Brown, Philip C. Miller, Larry L. Tieszen and Fred L. Bunnell (eds.) An Arctic Ecosystem. The Coastal Tundra at Barrow, Alaska. Dowden, Hutchinson, and Ross, Stroudsburg, Penn. 571 p.

Golley, F. B. 1961. Energy values for ecological materials. Ecology 42:581-584.

Gorchakovsky, P. L. and N. I. Andreyashkina. 1972. Productivity of some shrub, dwarf shrub and herbaceous communities of forest-tundra. *In* F. E. Wielgolaski and T. Rosswall (eds.) Proceedings IVth International Meeting on the Biological Productivity of Tundra. Tundra Biome Steering Committee, Stockholm.

Gordon, J. C. and P. R. Larson. 1968. Seasonal course of photosynthesis, respiration, and distribution of ^{14}C in young *Pinus resinosa* trees as related to wood formation. Plant Physiol. 43:1617-1624.

Gordon, J. C. and P. R. Larson. 1970. Redistribution of ^{14}C labelled reserve food in young red pines during shoot elongation. Forest Science 16:14-20.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, New York. 222 p.

Grundon, N. J. 1972. Mineral nutrition of some Queensland heath plants. J. Ecol. 60:171-181.

Haag, Richard W. 1974. Nutrient limitations to plant production in two tundra communities. Can. J. Bot. 52:103-116.

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

Hall, Ivan V. and Jennifer M. Shay. 1981. The biological flora of Canada, 3. Vaccinium vitis-idaea L. var. minus Lodd. Supplementary account. Can. Field Nat. 95:434-464.

Harper, J. L. and J. Ogden. 1970. The reproductive capacity of higher plants. I. The concept of strategy with special reference to Senecio vulgaris L. J. Ecol. 58:681-698.

Hernandez, Helios. 1973. Natural plant recolonization of surficial disturbances, Tuktoyaktuk Peninsula Region, Northwest Territories. Can. J. Bot. 11:2177-2196.

Hickman, James C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual Polygonum cascadense (Polygonaceae). J. Ecol. 63:689-701.

Hickman, James C. 1977. Energy allocation and niche differentiation in four co-existing annual species of Polygonum in western North America. J. Ecol. 65:317-326.

Hickman, J. C. and L. F. Pitelka. 1975. Dry weight indicates energy allocation in ecological strategy analysis of plants. Oecologia 21:117-121.

Horrocks, Donald L. 1976. The mechanisms of the liquid scintillation process. In A. A. Noujaim, C. Ediss, L. I. Weibe (eds.) Liquid Scintillation. Science and Technology. Academic Press, New York. 352 p.

Hughes, O. L. 1972. Surficial geology of northern Yukon Territory and northwestern District of Mackenzie, Northwest Territories. Geol. Surv. Can., Paper 69-36. 11 p.

Hulten, E. 1968. Flora of Alaska and Neighboring Territories. Stanford Univ. Press, Stanford, Ca.

1008 p.

Janz, A. 1973. Topographic influence on soil and plant nutrients in the Low Arctic. In L. C. Bliss (ed.) Botanical Studies of Natural and Man Modified Habitats in the Mackenzie Valley, Eastern Mackenzie Delta Region and the Arctic Islands. Dept. Indian Aff. North. Dev. Ottawa.

Johansson, L. G. 1974. The distribution and fate of ^{14}C photoassimilated by plants on a subarctic mire at Stordalen. Progress Report 1973. Swedish I. B. P. Tundra Biome Project Tech. Rep. 16:165-172.

Johansson, L. F. and S. Linder. 1975. The seasonal pattern of photosynthesis of some vascular plants on a subarctic mire. In F. E. Wielgolaski. Fennoscandian Tundra Ecosystems. Part I. Plants and Microorganisms. Springer-Verlag, New York. 366 p.

Johnson, Douglas A. and Larry L. Tieszen. 1976. Aboveground biomass allocation, leaf growth, and photosynthesis pattern in tundra plant forms in arctic Alaska. Oecologia 24:159-173.

Johnson, E. A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. Can. J. Bot. 53:2933-2941.

Jung, H. G., G. O. Batzli and D. S. Seigler. 1979. Patterns in the phytochemistry of arctic plants. Biochemical Syst. Ecol. 7:203-209.

Kwano, Shoichi and Junzo Masuda. 1980. The productive and reproductive biology of flowering plants. VII. Resource allocation and reproductive capacity in wild populations of Heloniopsis orientalis (Thumb.) C. Tanaka (Liliaceae). Oecologia 45:307-317.

Kuiper, P. J. 1964. Water uptake of higher plants (bean) as affected by root temperature. Weiner Tierarztliche Monatsshrift 51:1-11.

Larsen, J. A. 1971. Vegetational relationships with air mass frequencies: Boreal forest and tundra. Arctic 24:177-194.

Leith, Helmut. 1975. Measurement of caloric values. In Helmut Leith and Robert Whittaker (eds.) Primary Productivity of the Biosphere., Springer-Verlag, New York. 339 p.

Lewis, M. C. and T. V. Callaghan. 1976. Tundra. In J. L. Monteith (ed.) Vegetation and the Atmosphere. Academic Press, London.

Limbach, W. E., W. C. Oechel and P. C. Miller. 1982. Photosynthetic and respiratory responses to temperature and light of three Alaskan tundra growth forms. Holarctic Ecol. 5:150-157.

Loveless, A. R. 1961. A nutritional interpretation of sclerophylly based on differences in chemical composition of sclerophyllous and mesophytic leaves. Ann. Bot. N. S. 25:168-176.

Loveless, A. R. 1962. Further evidence to support a nutritional interpretation of sclerophylly. Ann. Bot. 26:551-561.

Lutz, H. J. 1956. Ecological effects of forest fires in the interior of Alaska. U. S. Dept. of Agriculture Tech. Bull. 1133.

MacKay, J. R. 1963. The Mackenzie Delta areas, N. W. T. Can. Dept. Mines, and Tech. Surveys, Memo 8. 202 p.

MacKay, J. R. 1970. Disturbances to the tundra and forest tundra environment of the western arctic. Can. Geotech. J. 7:420-432.

MacKay, J. R. and D. K. MacKay. 1976. Cryostatic pressures in nonsorted circles (mud hummocks), Inuvik, Northwest Territories. Can. J. Earth Sci. 13:889-897.

Mark, A. F. 1970. Floral initiation and development in New Zealand alpine plants. New Zealand J. Bot. 8:67-75.

Mayo, J. M., A. P. Hartgerink, Don G. Despain, Robert G. Thompson, Eduard M. van Zinderen Bakker Jr., and Sherman D. Nelson. 1977. Gas exchange studies of <u>Carex</u> and <u>Dryas</u>, Truelove, Lowland. <u>In</u> L. C. Bliss (ed.) Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem. Univ. of Alberta Press, Edmonton. 714 p.

McGraw, J. B. and G. R. Shaver. 1982. Seedling density and seedling survival in Alaskan cotton grass tussock tundra. Holarctic Ecol. 5:212-217.

Milchunas, D. G., W. K. Lavenroth and J. L. Dodd. 1982. The effect of SO_2 on ^{14}C translocation in <u>Agropyron smithii</u> Rydb. Envir. Exp. Bot. 22:81-91.

Miller, P. C. and W. A. Stoner. 1979. Canopy structural and environmental interactions. <u>In</u> O. T. Solbig, S. Jain, G. B. Johnson and P. Raven (eds.) Topics in Plant Population Biology. Columbia Univ. Press, New York.

Miller, P. C., W. A. Stoner, and J. R. Ehleringer. 1978. Some aspects of water relations of arctic and alpine regions. <u>In</u> Jerry Brown, Philip C. Miller, Larry L. Tieszen and Fred L. Bunnell (eds.) An Arctic Ecosystem. The Coastal Tundra at Barrow, Alaska. Dowden, Hutchinson and Ross, Stroudsburg, Penn. 571 p.

Miller, P. C., W. A. Stoner, and L. L. Tieszen. 1976. A model of stand photosynthesis for the wet meadow tundra at Barrow, Alaska. Ecology 57:411-430.

Miller, P. C. and L. L. Tieszen. 1972. A preliminary model of processes affecting primary production in arctic tundra. Arctic Alp. Res. 4:1-18.

Monk, Carl D. 1966. An ecological significance of evergreenness. Ecology 47:504-505.

Mooney, H. A. 1972. The carbon balance of plants. Ann. Rev. Ecol. Syst. 3:315-346.

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

Mooney, H. A. and S. L. Gulmon. 1982. Constraints on leaf structure and function in reference to herbivory. Bioscience 32:198-206.

Munsell Soil Color Charts. 1971. Munsell Color Division. Kollmorgen Corp. Baltimore, Maryland.

Nichols, H. 1976. Historical aspects of the northern Canadian treeline. Arctic 29:38-47.

Oberbauer, Steve and Philip C. Miller. 1982. Growth of Alaskan tundra plants in relation to water potential. Holarctic Ecology 5:194-199.

Oberauer, S. and P. C. Miller. 1981. Some aspects of plant water relations in Alaskan arctic tundra species. Arctic Alp. Res. 13:205-218.

Oberbauer, S. and P. C. Miller. 1979. Plant water relations in montane and tussock tundra vegetation types in Alaska. Arctic Alp. Res. 11:69-81.

Ogden, J. 1974. The reproductive strategy of higher plants. II. The reproductive strategy of Tussilago farfara L. J. Ecol. 62:291-324.

Penning De Vries, F. W. T. 1975. The cost of maintenance processes in plant cells. Ann. Bot. 77-92.

Pitelka, Louis F. 1977. Energy allocation in annual and perennial lupines (Lupinus: Leguminosae). Ecology 58:1055-1065.

Porsild, A. Erling and William J. Cody. 1980. Vascular plants of continental Northwest Territories, Canada. Nat. Museums Can., Ottawa. 667 p.

Reader, R. J. 1978. Contribution of overwintering leaves to growth of 3 broad leaved, evergreen shrubs belonging to the Ericaceae family. Can. J. Bot. 56:1248-1261.

Reader, R. J. 1980. Effects of nitrogen fertilizer, shade, and the removal of new growth on longevity of overwintering bog ericad leaves. Can. J. Bot. 58:1737-1743.

Rhoades, D. F. and R. G. Cates. 1976. Toward a general theory of plant antiherbivory chemistry. Recent Adv. Phytochem. 10:168-213.

Ritchie, J. C. 1976. The late-Quaternary vegetation history of the western interior of Canada. Can. J. Bot. 54:1793-1818.

Ritchie, J. C. 1977. The modern and late Quaternary vegetation of the Campbell-Dolomite uplands, near Inuvik, Northwest Territories, Canada. Ecol. Monogr. 47:401-423.

Ritchie, J. C. and F. K. Hare. 1971. Late-Quaternary vegetation and clmate near the arctic treeline of northwestern North America. Quat. Res. 1:331-342.

Rohringer, R. and D. J. Samborski. 1967. Aromatic compounds in the host-parasite interaction. Ann. Rev. Phytopath. 5:77-86.

Rosberg, Ingvald, Dag Ovstedal, Reidun Seljelid, Olivind Schreiner and Jostein Goksoyr. 1981. Estimation of carbon flow in a Calluna heath system. Oikos 37:295-305.

Shaver, Gaius R. 1981. Mineral nutrition and leaf longevity in an evergreen shrub, Ledum palustre ssp. decumbens. Oecologia 49:362-365.

Shaver, G. R. and W. D. Billings. 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. Ecology 56:401-409.

Shaver, G. R. and F. S. Chapin III. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61:662-675.

Shaver, G. R. and J. C. Cutler. 1979. The vertical distribution of live vascular phytomass in cottongrass tussock tundra. Arctic Alp. Res. 11:335-342.

Shultz, A. M. 1964. The nutrient recovery hypothesis for arctic microtine cycles. II. Ecosystem variables in relation to arctic microtine cycles. In D. J. Crisp (ed.) Grazing in Terrestrial and Marine Environments. Blackwell Scientific Pub., Oxford.

Sims, R. A. and J. M. Steward. 1981. Aerial biomass distribution in an undisturbed and disturbed subarctic bog. Can. J. Bot. 59:782:786.

Small, E. 1972. Photosynthetic rates in relation to nitrogen recycing as an adaptation to nutrient deficiency in peat bog plants. Can. J. Bot. 50:2227-2233.

Smith, Edward M. and Elmer B. Hadley. 1974. Photosynthetic and respiratory acclimation to temperature in *Ledum groenlandicum* populations. Arctic Alp. Res. 6:13-28

Snedecor, George W. and William G. Cochran. 19 . Statistical Methods. Iowa St. Univ. Press, Ames, Iowa. 593 p.

Sonesson, 1975. In F. E. Wielgolaski (ed.) Fennoscandian Tundra Ecosystems. Part I. Plants and Microorganisms. Ecological Studies Vol. 16. Springer-Verlag, New York. 366 p.

Stoner, W. A., P. Miller and P. C. Miller. 1982. Seasonal dynamics and standing crops of biomass and nutrients in a subarctic tundra vegetation. Holarctic Ecol. 5:172-179.

Stoner, W. A., P. C. Miller, S. P. Richards and S. A. Barkley. 1978. Internal nutrient cycling as related to plant life-form: a simulation approach. In D. Adriano and I. L. Brisbin (eds.) Environmental Chemistry and Cycling Processes. Dept. of Energy Symposium. Series CONF-760429. Washington, D. C.

Svoboda, J. 1977. Ecology and primary production of raised beach communities, Truelove Lowland. In L. C. Bliss (ed.) Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem. Univ. of Alberta Press, Edmonton. 714 p.

Svoboda, Josef and L. C. Bliss. 1974. The use of autoradiography in determining active and inactive roots in plant production studies. Arctic Alp. Res. 6:257-260.

Swain, T. 1977. Secondary compounds as protective agents. Ann. Rev. Plant Physiol. 28:479-501.

Tarnocai, C. and S. C. Zoltai. 1978. Earth hummocks of the Canadian arctic and subarctic. Arctic Alp. Res. 10:581-594.

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

Tieszen, L. L. 1974. Photosynthetic competence of the subnivian vegetation of an arctic tundra. Arctic Alp. Res. 6:253-256.

Tieszen, L. L. 1978. Photosynthesis in the principal Barrow, Alaska species: A summary of field and laboratory responses. In Larry L. Tieszen (ed.) Vegetation and Production Ecology of an Alaskan Arctic Tundra. Springer-Verlag, New York. 686 p.

Tieszen, L. L., D. A. Johnson and M. L. Allessio. 1974. Translocation of photosynthetically assimilated $^{14}CO_2$ in three arctic grasses *in situ* at Barrow, Alaska. Can. J. Bot. 52:2189-2193.

Ulrich, A. and P. L. Gersper. 1978. Plant nutrient limitations of tundra plant growth. *In* Larry L. Tieszen (ed.) Vegetation and Production ecology of an Alaskan Arctic Tundra . Springer-Verlag, New York. 686p.

Viereck, L. A. and E. L. Little. 1972. Alaska Trees and Shrubs. Agric. Handbook No. 410. Forest Service U. S. D. A. Washington, D. C. 265 p.

Walter, H. 1973. Vegetation of the Earth in Relation to Climate and the Eco-physiological Conditions. Springer-Verlag, New York.

Wang, C. H., David L. Willis and Walter D. Loveland. 1975. Radiotracer Methodology in the Biological, Environmental, and Physical Sciences. Prentice Hall, Englewood Cliffs, N. J. 480 p.

Wardlaw, I. F. 1968. The control and pattern of movement of carbohydrates in plants. Bot. Rev. 34:79-105.

Warren Wilson, J. 1966. An analysis of plant growth and its control in arctic environments. Ann. Bot. 30:383-402.

Wein, Ross W. and L. C. Bliss. 1974. Primary production in arctic cottongrass tussock tundra communities. Arctic Alp. Res. 6:261-274.

Whittaker, R. H. 1963. Net production of heath balds and forest heaths in the Great Smoky Mountains. Ecology 44:176-182.

Wielgolaski, F. E, and S. Kjelvik. 1975. Energy content and use of solar radiation of Fennoscandian tundra plants. In F. E. Wielgolaski. (ed.) Fennoscandian Tundra Ecosystems. Pt. I. Plants and Microorganisms. Springer-Verlag, New York. 366 p.

Wielgolaski, F. E., L. C. Bliss, J. Svoboda and G. Doyle. 1981. Primary production of tundra. In L. C. Bliss, O. W. Heal and J. J. Moore (eds.) Tundra Ecosystems: A Comparative Analysis. Cambridge Univ. Press, Cambridge. 813p.

Wiggins, I. L. and J. H. Thomas. 1962. A Flora of the Alaskan Arctic Slope. Arctic Inst. of North Amer., Spec. Pub. No. 4. Univ. Toronto Press, Toronto. 425 p.

Zoltai, S. C. and W. W. Pettapiece. 1973. Terrain, vegetation and permafrost relationships in the northern part of the Mackenzie Valley and northern Yukon. Environmental-social Program, Task Force on Northern Pipeline Development, Gov't of Canada Report 73-4. 105 p.

Zoltai, S. C., C. Tarnocai and W. W. Pettapiece. 1979. Age of cryoturbated organic materials in earth hummocks. In Proceedings of the Third International Conference on Permafrost. Edmonton, Can. July 1978.

Zoltai, S. C. 1975. Tree ring record of soil movements on permafrost. Arctic Alp. Res. 7:331-340.