Vegetation and Production Ecology of an Alaskan Arctic Tundra

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3. Spatial and Temporal Variation of the Vegetation and Its Production, Barrow, Alaska

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Introduction and Site Overview

This chapter examines the factors which control the distribution of vegetation, growth-forms, species, broad productivity measures, seasonal patterns, and plant succession of the International Biological Programme (IBP) Tundra Biome site at Barrow, Alaska. It provides a framework against which the detailed physiological and modeling experiments of other production studies in this volume can be viewed. The pragmatic decisions of the program focused the experiments on a limited set of plant communities, growth-forms, and species. Since all vegetation and all species could not be modeled or studied to the depth desired, the project was designed to provide an ability to generalize spatially.

Systematic observations on the vegetation of the Arctic Coastal Plain have been made for the last 30 years (Wiggins, 1951; Spetzman, 1951, 1959; Churchill, 1955; Bliss and Cantlon, 1957; Britton, 1966; Koranda, 1954; Johnson et al., 1966). Only four pre-IBP era studies of primary production have been made (Thompson, 1955; Shanks in Bliss, 1962a; Pieper, 1963; Dennis, 1968), and all of these deal with Barrow. Since the start of the IBP program, several papers dealing briefly with vegetation composition and production in the Barrow area have appeared (Tieszen, 1972a and 1972b; Johnson and Tieszen, 1973; Smith, 1974; Neiland and Hok, 1975; Webber and Walker, 1975; Bunnell et al., 1975).

A general description of the environment, soils, geology, and history of the Barrow area was presented in Chapter 1. The IBP study sites (see Figures 2 and 3 in Chapter 1 of Tieszen, 1978) are approximately 110 ha in area and are characterized by shallow ponds, ice-wedge polygons, vertical relief less than a few meters, organic and acidic soils, and an active layer from 30 to 40 cm. The climatic data are summarized in Figure 1.

When compared with other regions of the Arctic Coastal Plain, the flora and number of plant communities of the Barrow area are impoverished (see Chapter 2, Murray, 1978; Chapter 5, Steere, 1978). This impoverishment is related to the combined effects of a severe climate and low habitat diversity. The immediate Barrow region is within the High Arctic Tundra Zone (*sensu* Webber, 1974) where there is an absence of erect shrubs on mesic sites; this is equivalent to the arctic subzone of the Tundra Zone (*sensu* Alexandrova, 1970; see Chapter 2,

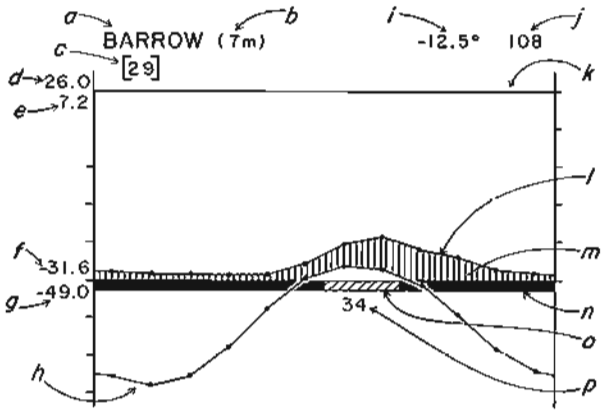


Figure 1. Climatic diagram for Barrow, Alaska (after Walter and Lieth, 1967) on the basis of data from the National Weather Service. Abscissa: months (Jan–Dec); ordinate: one division = 10°C or 20-mm precipitation. a, station name; b, elevation in meters; c, duration of observation in years; d, highest recorded temperature in °C; e, mean daily maximum temperature of the warmest month; f, mean daily minimum temperature of the coldest month; g, lowest recorded temperature; h, curve of mean monthly temperature; i, mean annual temperature; j, mean annual precipitation in mm; k, line of 100-mm precipitation; l, curve of mean monthly precipitation; m, the relative humid season; n, months with mean daily minimum temperature below 0°C; o, months with absolute minimum below 0°C; p, mean duration of frost-free period in days (after Walter, 1973).

Murray, 1978, for discussion). Wet, sedge meadows cover well over half of the land surface (Spetzman, 1959) and about three-quarters of the IBP study area. These meadows are dominated by one species, *Carex aquatilis*, and often have only a few secondary species such as *Eriophorum angustifolium*, *Eriophorum scheuchzeri*, and *Dupontia fisheri*. They also have a large moss component consisting of species of *Calliergon* and *Drepanocladus*. Lichens are only a minor component of these meadows.

The most striking feature of the vegetation of the IBP study site is that it changes character every few meters in response to changes of microrelief and drainage. The vegetation changes are not always reflected in the dominant species, many of which, for example *Carex aquatilis*, are ubiquitous, but in the subordinate species, especially the mosses and grasses.

Although much of the Barrow region is severely disturbed by construction and off-road vehicle traffic, the IBP site is relatively undisturbed. The principal disturbance has been the headward erosion by thermokarsting of Footprint Creek which flows eastward between sites 1 and 2 (see Figure 3 in Chapter 1). This erosion was initially triggered in the late 1940s by vehicle disturbance (Lewellen, 1972). The drainage for this creek has also been affected by the purposeful draining of Footprint Lake in 1950 which is 2 km to the south of the IBP site (Lewellen, 1972). The drained Footprint Lake provides a fortuitous analogue of a naturally drained *thaw lake* (Britton, 1966) basin. The entire IBP site is a series of overlapping former thaw-lake basins. Britton (1966) has

described the dynamic aspects of the thaw-lake cycle and the development of the ice-wedge polygon landscape. In this cycle polygonization occurs in the meadows of former lake basins, the low-centered polygons coalesce to form ponds which further coalesce to form lakes. Drainage of these lakes allows the cycle to repeat. The time frame of this cycle is on the order of hundreds of years. Thus the vegetation and surfaces in the study are very dynamic. The tundra is not only influenced by geomorphic changes but also by herbivore activities. A spectacular disruption is commonly seen with a frequency of 3 to 5 years when lemming *(Lemmus sibericus)* densities become very high, and their grazing causes widespread destruction of the vegetation (Thompson, 1955; Pitelka, 1957; Pieper, 1963). This heavy grazing may have many subsequent effects on the vegetation resulting from increased nutrient release and increased thaw depth (Schultz, 1964, 1969).

Methods

Vegetation may be viewed either as a continuum or as a series of distinct plant communities (Major, 1961; Whittaker, 1967; Webber, 1971; Shimwell, 1972). The continuum is studied through *gradient analysis* (Whittaker, 1967) and the vegetation units through *classification*. Each set of techniques gives different and useful information about vegetation and they are used to complement one another in this study. Classification, in which plant communities are recognized and named, permits easier communication, mapping, and plot replication and experimentation. Gradient analysis permits a more powerful identification of environmental controls and provides an environmental framework for the description of species distribution and production.

Sampling began during 1972 and continued for four growing seasons. Forty-three permanent plots (1 × 10 m) were established to represent the spectrum of undisturbed vegetation and to allow measurements of seasonal variations of biotic and abiotic factors. This plot size approximates the minimal area of most tundra vegetation and the shape is compatible with most tundra patterns: for example, along polygon rims, troughs, and bog-strings (Webber, 1971). Species composition, cover and frequency were established for each plot and an importance value called species index was derived for each species by summing their relative cover and relative frequency values within the plot (Webber, 1971). Both vascular plants and cryptogams were sampled. Simple abiotic descriptions such as aspect, slope, drainage characteristics, and stability were recorded for each plot at the time of sampling. Soil samples were collected from just below the vegetation mat to a depth of 10 cm. A one-time record was made in mid-August 1973 of the degree to which the smell of hydrogen sulfide was noticeable in soil at spade depth; a four-point subjective scale based on odor was used for this purpose. Chemical and physical analysis of soils was performed in the laboratory using standard techniques. Percentages of sands, silts, and clays, percentage of organic content, water holding capacity, and hydrogen ion concentration (pH) were determined for each soil sample. Soluble soil phosphate was determined for

a few selected soils. Gravimetric moisture was determined from two samples at a depth of 10 cm on each plot at intervals of 10 days during two growing seasons. Soil thaw surveys were conducted with a thin, graduated steel rod every 10 days. Snow depth, snow cover, and date of snowmelt surveys were conducted just prior to and at the start of each growing season. Soil thaw and snow depths were determined from 10 measurements in each plot.

Classification was achieved by clustering plots or stands on the basis of their species composition using the average linkage method of Sokal and Sneath (1963). The resulting clusters of stands have similar composition and were found to have a similar environment. These units represent broad vegetation types somewhat above the level of association (*sensu* Braun-Blanquet, 1932). Each cluster is called a *stand nodum* and is named on the basis of its species composition and habitat or physiognomic characteristics (Lambert and Dale, 1964; Webber, 1971). Nomenclature follows Murray and Murray (1978) in Appendix I except that *Salix pulchra* (= *Salix planifolia* ssp. *pulchra*) is retained in this volume to conform to recent use in the literature from the Alaskan arctic.

A map was made by outlining units of uniform landform assemblages. The vegetation map was made by coding these units on the basis of their most abundant nodum. This method solved the problem presented by the fine mosaic of geomorphic and vegetational patterns. A final scale of 1:5000 was found to be convenient.

Gradient analysis was achieved using the indirect stand ordination method of Bray and Curtis (1957). Ordinations based on stand species composition and subsequent correlation of the resulting ordination axes with measured stand environmental variables suggest and rank the major environmental controls of the vegetation. It is important to evaluate the use of the term environmental controls since a cause and effect relationship is not established because a correlation exists. However, in the present exercise those environmental factors which show high correlation with the ordination axes are hypothesized to be controlling. A further point of explanation with regard to ordination is required. The axes of the ordinations are best described as complex environmental gradients (*sensu* Whittaker, 1967). A complex gradient is a complex of interrelated and interdependent factors, some of which may be identified because they correlate with the axis while others may remain unknown because they have not been measured. Thus the factor with the highest correlation is unlikely to be the ultimate cause. An ordination is an expression of the variation within the sampled universe, here the Barrow tundra, and thus indicates the controls on the vegetation within the study site.

Since the early work of Raunkiaer (1934), the importance of plant growth forms as strategic adaptations to the tundra environment has always been emphasized (Bliss, 1956, 1962b; Tikhomirov, 1963; Chabot and Billings, 1972). The growth-forms shown in Figure 2 are based primarily on the nature of the shoot habit. Some categories, however, tend to be more systematic or phylogenetic in character, for example, *bryophytes* and *lichens*. Woody shrubs at Barrow are all of low stature and many are prostrate. Shrubs are subdivided on the basis of being evergreen or deciduous. The genus *Salix* is the principal

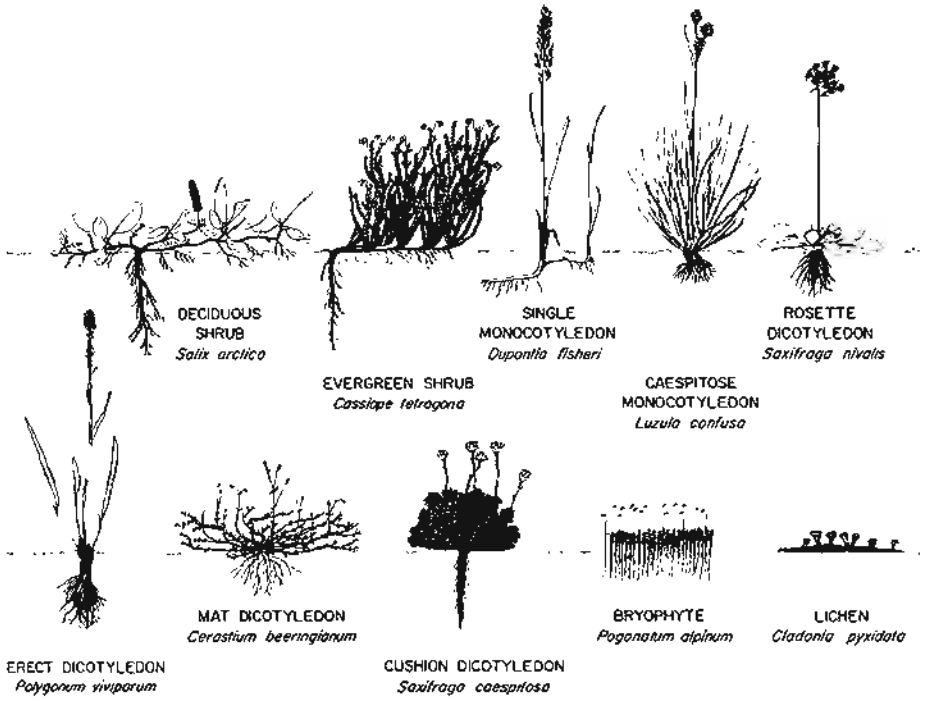


Figure 2. The 10 plant-growth forms of tundra plants which are recognized in this study (after Wielgolaski and Webber, 1973).

representative of the *deciduous shrubs* while *Cassiope* and *Vaccinium vitis-idaea* represent *evergreen shrubs*. Herbaceous plants with elongated, narrow leaves are represented by the monocotyledonous sedges, grasses, and rushes. These graminoids may be subdivided into those with crowded, bunched shoots, here called *caespitose monocotyledons*, and those with well-spaced individual shoots, here called *single monocotyledons*. *Luzula confusa* and *Eriophorum vaginatum* are examples of caespitose monocotyledons and *Dupontia fisheri* and *Carex aquatilis* represent the single monocotyledons. Four growth-forms are recognized for the broad-leaved herbs or forbs. Acaulescent (essentially stemless) plants with a rosette of radicle leaves are called *rosette dicotyledons*. *Saxifraga nivalis* and *Pedicularis lanata* are representative of this growth-form. Forbs with erect leaves or leaves supported into the canopy on long petioles or on an erect stem are called *erect dicotyledons*. Representatives of these are *Polygonum viviparum* and *Petasites frigidus*. The remaining forb growth-forms are *mat* and *cushion dicotyledons*. The former have tightly matted, often long, prostrate stems with leaves along the length of the stems. The latter have short crowded stems, often coming from a single tap root, which give a hemispheric shape. Examples of the mat form are *Cerastium jenisejense* and *Stellaria humifusa*. The cushion form is illustrated by *Saxifraga caespitosa* and *Silene acaulis*.

The spatial variation of standing crop and net primary production was established by harvesting two 0.1-m^2 (20 × 50-cm) quadrats from each plot during the period of peak aboveground vascular biomass. Standing crop refers to living plus dead plant material while biomass refers only to live material. Peak aboveground biomass usually occurs in the first week of August (Tieszen, 1972a). The herbage was clipped at soil level or just beneath any live moss carpet and the contents of each quadrat were kept separate and frozen for later processing. Two soil and root cores (7.6 cm in diameter) were taken to the maximum possible depth (usually 25 cm) in each quadrat. The soil cores were also frozen until they could be washed and sieved in order to retrieve the roots and other belowground organs. The thawed herbage was partitioned into vascular plants, lichens, and bryophytes. The vascular plants were further partitioned into 10 functional fractions. Current year's growth and previous standing material were separated into woody and herbaceous dead and live material. Stem bases and litter and prostrate dead comprised the remaining two fractions. Belowground material was separated into stem bases, rhizomes, live roots, and dead roots; the separation of roots into live and dead was made only on the basis of color and texture.

Estimates of net primary production were made only for the aboveground vascular plant portion of the vegetation. These estimates were based on the weight of the growth of the current season from the clipped material. These are, at best, crude because such small areas were clipped and no allowance was made for grazing, for shedding, for annual stem increments to perennial structures, or for current season die back of graminoid individuals. Turnover rates for various standing crop fractions were calculated by dividing the fraction in question by the estimate of its annual production.

Leaf area index (LAI) was estimated for each plot at the time of clip-harvesting. This includes petioles, stems, and floral structures in addition to blades proper. Sampling was done using a point-quadrat frame with 10 vertical pins spaced at regular intervals along a 1-m linear frame. Ten frames were sampled for each plot. Contacts were recorded for vascular plants, cryptogamic water, stones, bare ground, and lemming feces.

The temporal variation of standing crop and net primary production was only assessed for one vegetation type, a moist *Carex aquatilis*-dominated meadow. The course of standing crop and primary production for the 1971 growing season was compared with the peak season harvests of several years (1970–1974). Collection and analysis of the 1970 and 1971 data were supervised by Dr. John Dennis and results have been reported by Dennis and Tieszen (1972) and Dennis, et al. (1978).

A few measurements were made of the seasonal progression of plant stature of *Carex aquatilis* and the stem elongation of willow *(Salix pulchra)* at site 2. These were made in order to compare the year-to-year variation in plant growth. The plant stature measurements were made on 10 tagged individuals of *Carex aquatilis* at 5-day intervals throughout the growing seasons of 1972 and 1973. The willow measurements were derived from 10 plants harvested in the summer of 1974 and included measurements of stem increments for 1969 to 1973. Phenologi-

cal studies of a few selected flowering plants were made in 1972 and 1973. These plants were *Carex aquatilis, Dupontia fisheri, Petasites frigidus, Ranunculus nivalis, Pedicularis lanata,* and *Salix pulchra*. These species were chosen to represent a spectrum from early to late bloomers. Each species was recorded in its characteristic nodum; the same individuals were observed in each year. Weekly observations were made from snowmelt to late summer.

Results

Vegetation Units

Identity and Distribution. Eight noda were established (Figure 3) from the 43 plots representing the universe of the sedge meadow complex of the IBP site. Each nodum was given a Roman numeral and a name based on its characteristic species, position on the moisture gradient, and habitat or physiognomy (Table 1). The numbers I to VII are in a general sequence of increasing substrate moisture regime. Nodum VIII represents pioneer vegetation which occurs on recent alluvium. Figures 4–7 illustrate some of the noda. The units of a landform map of the study area were coded for their most abundant nodal vegetation cover (Figure 8). A planimetry estimate of the area occupied by each nodum is given in Table 1. A larger scale, more detailed version of this map is available elsewhere (Walker, 1977). A further picture of the spatial distribution of the noda is given by an idealized profile of the major landforms of the study area (Figure 9). The mean of Species Index, the total number of species in each of the major taxonomic entities, the mean relative cover of each growth-form, and some means of selected substrate variables for each nodum are given in Tables 2, 3, 4, and 5, respectively.

Vegetation dominated by *Carex aquatilis* forms most of the surface cover of the Barrow area. Noda III, IV, and VI, which are dominated by *Carex aquatilis*, occupy 77% of the mapped area. Although the noda seem fairly distinct in the dendrogram (Figure 3), it is difficult to single out clearly diagnostic or characteristic species for each nodum. Few species are unique to a nodum and most occur in several noda. The following descriptions point out the principal characteristics of each nodum.

Nodum I, which is called *Dry, Luzula confusa Heath*, is characteristic of high-centered polygons just to the south of site 1 (Figures 4 and 8). The use of the epithet heath refers to the barren steppe appearance of this vegetation (*sensu* Rübel, 1914) rather than the presence of ericaceous species. Ericaceous species such as *Cassiope tetragona* and *Vaccinium vitis-idaea* are rare at Barrow and are restricted to the flanks of the highest ridges such as raised beaches. This community occupies only 3% of the study area. Its barrenness is due to its dryness and elevation above the water table, low snow cover, and exposure to winds. The characteristic growth-forms are caespitose monocotyledons and

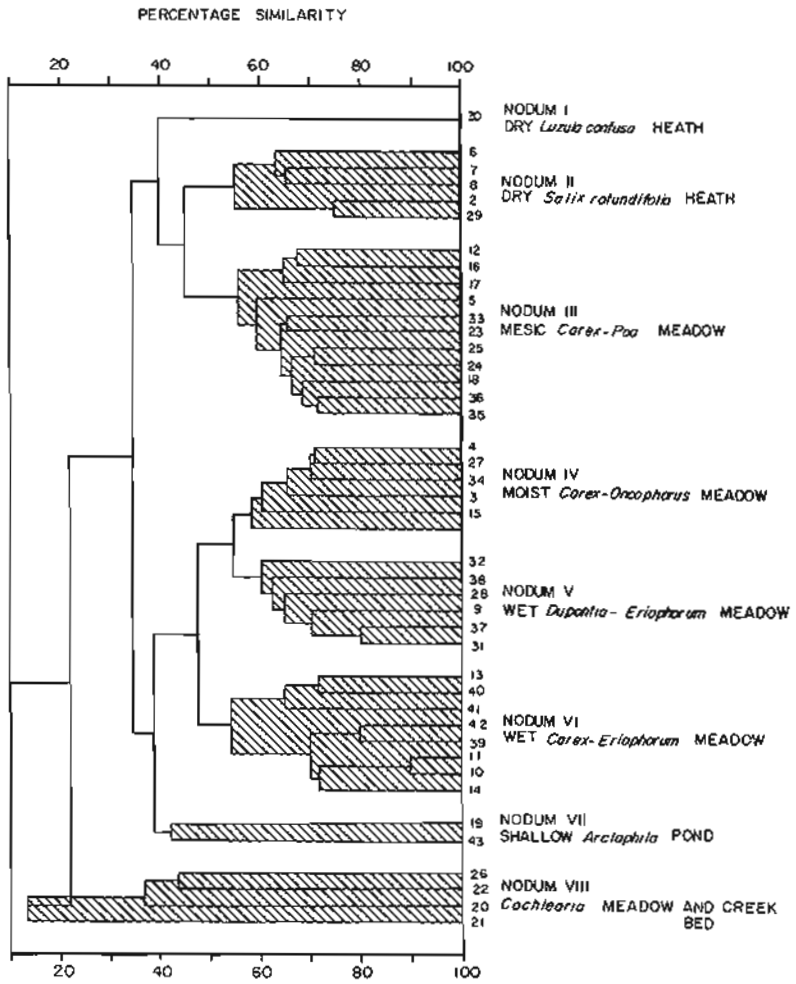


Figure 3. Dendrogram showing the similarity relationships between the 43 sampled vegetation stands. Eight clusters or noda are identified and have been named on the basis of habitat and characteristic species.

lichens (Table 5). In addition to *Luzula confusa* the following are characteristic species: *Potentilla hyparctica, Alectoria nigricans,* and *Pogonatum alpinum.*

Nodum II, *Mesic,* Salix rotundifolia *Heath,* is characteristic of the sloping creek banks between sites 1 and 2 (Figure 8). More abundant than Nodum I, but still small in extent (7%), this vegetation also occurs in the center of some low-centered polygons which drain readily. *Salix rotundifolia,* which is a prostrate deciduous shrub, characterizes this vegetation as do *Arctagrostis latifolia* and *Saxifraga punctata.* This nodum has the highest number of herbaceous dicotyledons (22) and the highest overall number of species (70) of any of the noda of the study area. The well-drained, sandy nature of the soils of this community leads to the deepest active layer of the principal noda.

Table 1. Numbers, Names, Characteristic Species, and Major Microrelief Types of the Eight Vegetation Noda Recognized for the Barrow IBP Site

Nodum		Characteristic species	Major microrelief type(s)
I.	Dry *Luzula confusa* heath	*Luzula confusa*, *Potentilla hyparctica*, *Alectoria nigricans*, *Pogonatum alpinum*, and *Psilopilum cavifolium*	High-centered-polygons
II.	Mesic *Salix rotundifolia* heath	*Salix rotundifolia*, *Arctagrostis latifolia*, *Saxifraga punctata*, *Sphaerophorus globosus*, and *Brachythecium salebrosum*	Low-centered-polygons and sloping creek banks
III.	Mesic *Carex aquatilis–Poa arctica* meadow	*Carex aquatilis*, *Poa arctica*, *Luzula arctica*, *Cetraria richardsonii*, and *Pogonatum alpinum*	Hummocky polygon rims and centers and dry, flat polygonized sites
IV.	Moist *Carex aquatilis–Oncophorus wahlenbergii* meadow	*Carex aquatilis*, *Oncophorus wahlenbergii*, *Dupontia fisheri*, *Peltigera aphthosa*, and *Aulacomnium turgidum*	Moist, flat sites and drained polygon troughs
V.	Wet *Dupontia fisheri–Eriophorum angustifolium* meadow	*Dupontia fisheri*, *Eriophorum angustifolium*, *Cerastium jenisejense*, *Peltigera canina*, and *Campylium stellatum*	Wet, flat sites and polygon troughs
VI.	Wet *Carex aquatilis–Eriophorum russeolum* meadow	*Carex aquatilis*, *Eriophorum russeolum*, *Saxifraga foliolosa*, *Calliergon sarmentosum*, and *Drepanocladus brevifolius*	Low polygon center and pond margins
VII.	*Arctophia fulva* pond margin	*Arctophila fulva*, *Ranunculus pallasii*, *Ranunculus gmelini*, *Eriophorum russeolum*, and *Calliergon giganteum*	Pond and stream margins
VIII.	*Cochlearia officinalis* pioneer meadow	*Cochlearia officinalis*, *Phippsia algida*, *Ranunculus pygmaeus*, *Stellaria humifusa*, and *Saxifraga rivularis*	Snowbeds, creek banks and creek sides

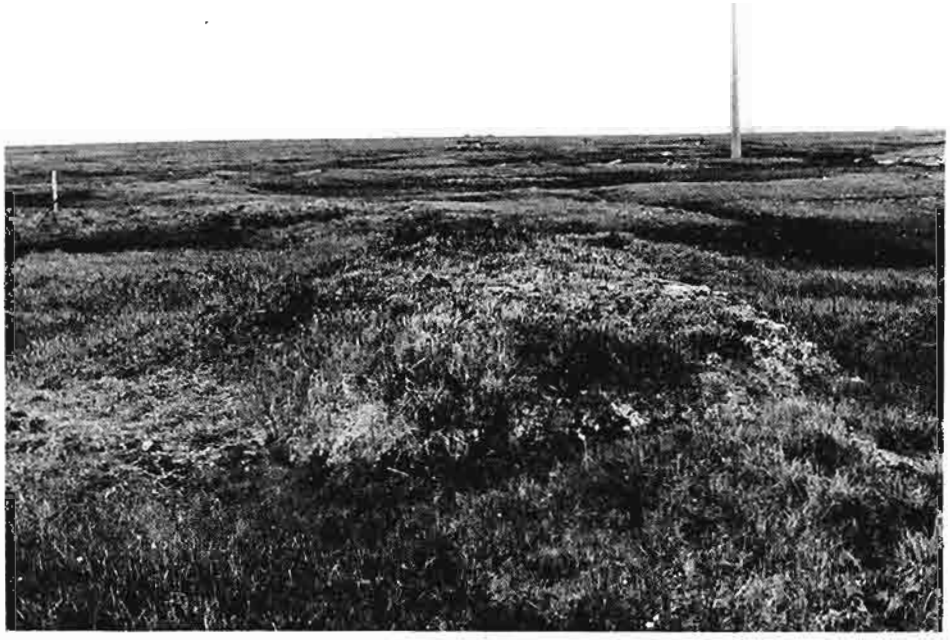


Figure 4. Nodum 1—*Dry Luzula confusa heath* situated on the higher center of a tundra polygon at site 1. White crust lichens *(Ochrolechia frigida)* are visible on the sides of the raised center. The trough in the left foreground contains vegetation of Nodum V.

Figure 5. Nodum V—*Wet Dupontia fisheri–Eriophorum angustifolium meadow*. This nodum is often found in wet polygon troughs, but it can form extensive meadows in suitably wet lowlands. Nodum IV occupies the polygon centers of this figure.

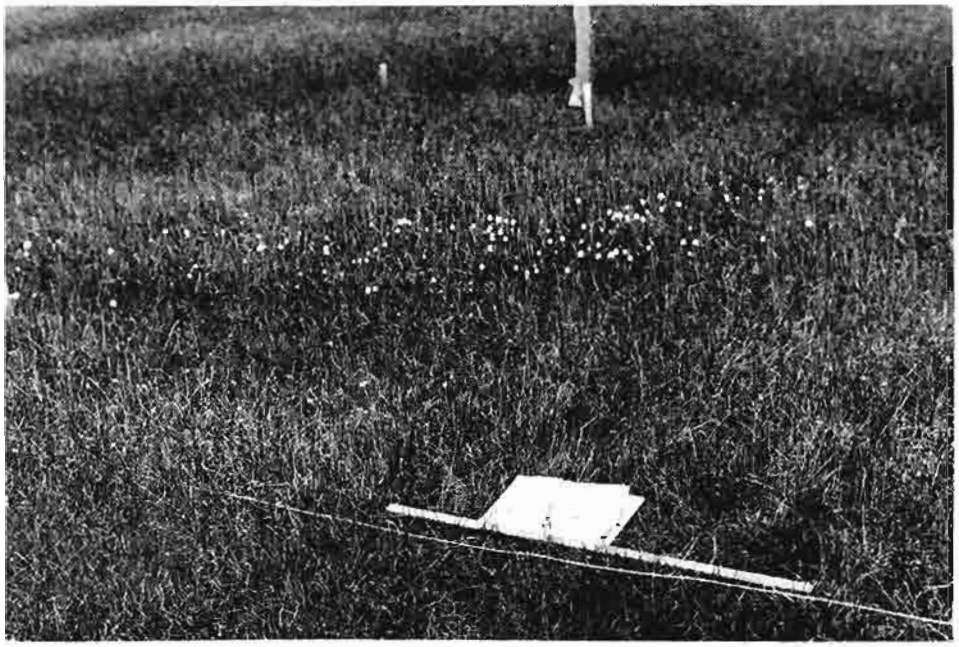


Figure 6. An extensive stand representing Nodum V. The white inflorescences of *Eriophorum russeolum* appear at the center of the figure.

Figure 7. Nodum VI—*Wet Carex aquatilis–Eriophorum russeolum meadow* in low center polygon. This is the barren extreme of this nodum and has a characteristic dark appearance.

Nodum III, *Mesic, Carex aquatilis–Poa arctica Meadow,* is the most extensive (41%) vegetation type of the study area. Bryophytes, primarily mosses, and lichens have greater relative covers (Table 5) than the more conspicuous graminoids. *Dicranum elongatum* and *Dactylina arctica* are a common moss and lichen, respectively. More characteristic of the nodum are the moss *Pogonatum alpinum* and the lichen *Cetraria richardsonii.* Noda IV, V, and VI all have the same superficial meadow physiognomy. The critical difference which separated Nodum III from them is the abundance of *Poa arctica,* which is very prominant when it is in anthesis, and the highest lichen diversity of any of the noda. Nodum III is best developed in the parts of the polygonized sedge meadow complex where it is fairly dry and where large, flat, and sometimes slightly raised polygon centers with barely discernible troughs and rims occur. It also occurs commonly on hummocky polygon rims in wetter areas with more pronounced polygon development as at site 4 (Figures 8 and 9).

Nodum IV, *Moist Carex aquatilis–Oncophorus wahlenbergii Meadow,* the second most extensive nodum (21%), develops on similar but moister sites than Nodum III and where thaw depth is slightly less. Most surfaces of sites 1 and 2 are classified in this nodum. It occurs on flat polygon centers and in drained, shallow polygon troughs. It appears very much like Nodum III but may be distinguished from it on the basis of less lichen cover and the presence of mosses such as *Calliergon sarmentosum* and *Oncophorus wahlenbergii.* The presence of *Dupontia fisheri, Peltigera aphthosa,* and *Aulacomnium turgidum* also distinguishes Nodum IV from III. Nodum IV has the most species of monocotyledons and it is the most intensively studied vegetation of the Tundra Biome program.

Nodum V, *Wet Dupontia fisheri–Eriophorum angustifolium Meadow,* occupies only 7% of the mapped area. It is characteristic of flat, slowly draining sites and wet polygon troughs. *Eriophorum russeolum* is also common in this nodum (Figure 6), but the low cover of *Carex aquatilis* and the greater abundance of *Dupontia* and *Eriophorum angustifolium* distinguish it from the other meadow noda. Woody dicotyledons are essentially absent but several herbaceous dicotyledons occur and *Cerastium jenisejense, Stellaria edwardsii,* and *Stellaria laeta* may form distinctive mats; *Saxifraga cernua* is a frequent erect forb.

The vegetation which is placed in Nodum VI is variable and is called *Wet Carex aquatilis–Eriophorum russeolum Meadow.* It includes the sparse vegetation of low-centered polygons (Figure 7) which contrasts with that of some pond margins, but there is an underlying floristic commonness between these examples and frequent intergrading stands. It has no woody species and only a few lichens. *Saxifraga foliolosa* is characteristic of the low-centered polygons while *Calliergon sarmentosum* is characteristic of the pond margin meadows. *Drepanocladus brevifolius* is common to all facies of this nodum. A thick organic mat, highly organic soils, and low species diversity also set this nodum apart from the other meadow noda. Spring snow cover on this nodum is moderately deep and late to recede.

Nodum VII is called *Arctophila fulva Pond Margin.* It is also found in slow-flowing streams; it is the most distinct of the principal noda, but it only occupies 2% of the area. Woody plants and lichens are totally absent from this nodum and

Figure 8. A vegetation map of the area surrounding the U.S. Tundra Biome terrestrial sites at Barrow, Alaska. In this map, land-units have been coded according to their most abundant vegetation nodum.

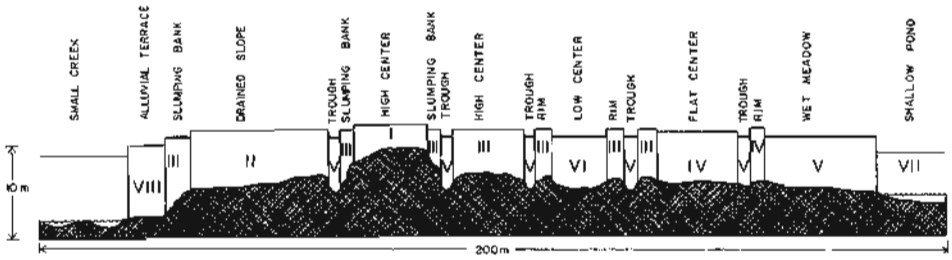


Figure 9. Idealized profile of the Intensive Study Site showing the principal microrelief features and the distribution of the vegetation noda.

the single monocotyledons, erect herbaceous dicotyledons, and bryophytes have an equal importance, although graminoid growth-form represented by the emergent *Archtophila* is most characteristic. *Ranunculus pallasii* and *Caltha palustris* are occasionally present. The pleurocarpous mosses *Calliergon giganteum* and *Drepanocladus brevifolius* are the principal bryophytes. Late in the growing season the substrate of this nodum may occasionally become noticeably anaerobic and have a characteristic odor of hydrogen sulfide.

Nodum VIII, *Cochlearia officinalis Pioneer Meadow,* is a rudimentary community which develops on recent alluvium in the creek bed which crosses the study area (Figure 8). Frequently these sites are in the shelter of the creek bank where snow may accumulate and be late to melt. Its sandy, moist alluvium thaws very deeply and the active layer may exceed 1 m in late summer. This nodum is floristically rich, but, as Figure 3 illustrates, the sampled plots comprising the nodum are extremely variable. *Cochlearia officinalis, Phippsia algida,* and *Stellaria humifusa* are the principal species.

Standing Crop and Production. Each nodum has a reasonably distinct standing crop composition at the period of peak aboveground biomass (Table 6). As a generalization the following aboveground pattern is seen for the dry weight (g m^{-2}) of the various fractions for Barrow tundra vegetation at the period of peak season: herbaceous dicotyledon biomass (4) < woody dicotyledon biomass (9) < lichen biomass (17) < monocotyledon biomass (35) < vascular standing dead (40) < bryophyte biomass (50) < total vascular biomass (50) < vascular litter and prostrate dead (80). If belowground standing crops are now considered, the sequence essentially continues: vascular stem base biomass (65) < rhizome biomass (95) < root biomass (560) < total belowground biomass (735) < belowground dead (2565).

Monocotyledon aboveground biomass increases from Nodum II *(mesic heath)* along the moisture gradient to Nodum VII *(pond margin).* Nodum I *(dry heath)* has a higher monocotyledon biomass than Nodum II *(mesic heath)* as a result of caespitose graminoids such as *Luzula confusa* which are abundant on dry sites. In all noda except Noda I and II *(heaths),* which are dry, the standing dead aboveground monocotyledon fraction is less than the live fraction at it is readily incorporated into litter and prostrate dead fractions. The same trend

Table 2. A Complete List of the Species Occurring in the 43 Sampled Stands and Their Nodal Occurrence[a]

Taxon	Growth-form	Vegetation I(1)	II(5)	III(11)	IV(6)	V(6)	VI(8)	VII(2)	VIII(4)
Shrubs									
Cassiope tetragona	ES	—	5.6	—	—	—	—	—	—
Dryas integrifolia	DS	—	1.0	—	—	—	—	—	—
Salix phlebophylla	DS	—	0.1	—	—	—	—	—	—
Salix pulchra	DS	—	0.9	3.0	2.6	—	—	—	—
Salix rotundifolia	DS	10.5	33.2	6.3	2.7	0.6	—	—	—
Vaccinium vitis-idaea	ES	—	—	—	—	—	—	—	0.4
Herbaceous dicotyledons									
Caltha palustris	ED	—	—	—	—	—	—	3.3	—
Cardamine pratensis	ED	—	—	—	1.7	4.7	1.3	0.4	1.9
Cerastium jenisejense	MD	—	—	—	0.3	4.8	—	1.9	8.7
Chrysosplenium tetrandrum	ED	—	—	0.1	0.4	0.2	—	—	0.5
Cochlearia officinalis	RD	—	—	—	0.1	—	—	—	7.0
Draba bellii	RD	—	0.5	—	—	—	—	—	—
Draba oblongata	RD	0.8	2.2	—	0.1	—	—	—	—
Eutrema edwardsii	ED	—	2.2	—	—	—	—	—	—
Papaver hultenii	RD	3.3	1.5	—	—	—	—	—	—
Papaver macounii	RD	—	1.1	—	—	—	—	—	—
Pedicularis lanata	ED	4.6	3.4	0.4	—	—	—	—	—
Pedicularis sudetica	ED	—	—	—	—	—	—	—	—
Petasites frigidus	ED	—	0.1	1.2	4.6	5.2	0.7	—	8.6
Polygonum viviparum	ED	—	1.5	—	0.8	—	—	—	1.3
Potentilla hyparctica	ED	16.1	2.0	—	—	—	—	—	0.2
Ranunculus gmelini	SG	—	—	—	—	—	—	0.4	—
Ranunculus nivalis	ED	0.8	0.9	1.6	1.6	2.5	—	—	0.3
Ranunculus pallasii	ED	—	—	—	—	0.9	—	61.0	—
Ranunculus pygmaeus	ED	—	—	—	—	—	—	—	4.2
Rumex arcticus	ED	—	1.5	—	—	—	—	—	—
Sagina intermedia	RD	—	0.2	—	—	—	—	—	—
Saxifraga caespitosa	CD	—	0.6	—	—	—	—	—	—

Table 2. A Complete List of the Species Occurring in the 43 Sampled Stands and Their Nodal Occurrence[a] (*Continued*)

Taxon	Growth-form	Vegetation I(1)	II(5)	III(11)	IV(6)	V(6)	VI(8)	VII(2)	VIII(4)
Saxifraga cernua	ED	0.8	1.2	5.2	6.7	10.5	5.5	—	9.9
Saxifraga foliolosa	RD	—	0.5	2.6	4.6	2.8	6.3	—	1.5
Saxifraga hieracifolia	MD	—	0.3	0.3	1.2	0.3	—	—	—
Saxifraga hirculus	ED	—	—	—	—	—	—	—	0.3
Saxifraga oppositifolia	MD	—	0.1	—	—	—	—	—	—
Saxifraga punctata	ED	—	4.8	0.1	1.2	0.1	—	—	—
Saxifraga rivularis	ED	—	—	—	—	—	—	—	3.1
Senecio atropurpureus	ED	—	4.4	0.9	—	—	—	—	—
Stellaria edwardsii	MD	5.4	4.1	1.4	3.4	4.3	0.4	—	1.9
Stellaria humifusa	MD	—	—	—	—	—	—	—	12.8
Stellaria laeta	MD	—	0.3	1.0	1.6	3.1	0.7	—	3.1
Monocotyledons									
Alopecurus alpinus	SG	—	1.5	0.5	—	0.5	0.6	—	2.5
Arctagrostis latifolia	SG	—	7.4	2.4	0.1	0.1	—	—	7.1
Arctophila fulva	SG	—	—	—	—	—	0.3	32.0	9.0
Calamagrostis holmii	SG	1.6	—	3.2	1.8	4.2	0.6	—	0.5
Carex aquatilis	SG	—	1.6	16.6	23.7	4.2	46.2	10.6	—
Dupontia fisheri	SF	—	0.1	5.2	8.3	18.3	7.7	10.0	17.4
Eriophorum angustifolium	SG	—	1.2	4.9	4.5	14.1	6.0	10.0	—
Eriophorum russeolum	SG	—	.2	4.8	8.0	8.7	17.3	7.3	0.5
Eriophorum scheuchzeri	SG	—	—	—	1.5	0.9	—	—	—
Festuca brachyphylla	CG	4.0	—	—	—	0.1	—	—	—
Hierochloë pauciflora	SG	—	0.1	—	0.9	—	—	—	—
Juncus biglumis	CG	—	0.4	—	3.4	0.5	0.8	—	—
Luzula arctica	CG	6.2	3.2	3.7	0.8	—	0.4	—	—
Luzula confusa	CG	20.9	5.0	0.6	1.3	—	—	—	0.3
Phippsia algida	CG	—	—	—	—	—	—	—	5.6
Poa arctica	SG	6.4	3.6	11.4	4.0	5.4	1.8	—	4.8

Bryophytes									
Aulacomnium palustre	BR	—	0.2	4.4	2.7	2.1	2.0	—	1.8
Aulacomnium turgidum	BR	—	3.0	3.3	1.4	—	0.2	—	—
Brachythecium cf. *turgidum*	BR	2.0	11.6	0.7	0.7	9.1	—	—	1.5
Bryum spp.	BR	—	3.6	11.8	14.5	24.5	10.8	7.3	27.4
Calliergon giganteum	BR	—	—	—	4.3	—	4.8	28.5	—
Calliergon sarmentosum	BR	—	—	0.6	12.4	15.7	34.4	—	7.5
Campylium stellatum	BR	—	0.2	—	0.2	4.3	—	13.6	7.4
Conostomum tetragonum	BR	—	0.3	0.3	—	—	—	—	—
Dicranum elongatum	BR	9.2	16.8	24.5	0.5	0.6	0.2	—	4.8
Distichium capillaceum	BR	—	3.5	0.3	—	—	—	—	—
Drepanocladus brevifolius	BR	—	—	0.8	7.4	7.2	28.2	13.6	6.5
Drepanocladus uncinatus	BR	—	6.1	2.5	2.1	—	0.2	—	0.5
Hepaticae	BR	—	0.2	4.4	2.7	2.1	2.0	—	1.8
Hylocomium alaskanum	BR	—	3.0	4.5	2.3	—	—	—	—
Myurella julacea	BR	—	0.6	0.7	1.6	—	—	—	—
Oncophorus wahlenbergii	BR	—	1.6	7.5	18.9	7.3	4.9	—	1.0
Pogonatum alpinum	BR	42.2	3.9	13.6	19.2	16.5	8.4	—	2.1
Polytrichum juniperinum	BR	18.9	4.5	4.7	4.6	3.9	0.2	—	—
Psilopilum cavifolium	BR	2.0	—	—	—	—	0.3	—	—
Rhacomitrium spp.	BR	—	3.9	—	0.5	—	—	—	—
Sphagnum spp.	BR	—	—	3.0	0.4	—	—	—	—
Tetraplodon mnioides	BR	—	0.5	0.3	0.6	—	—	—	—
Lichens									
Alectoria nigricans	LI	10.9	3.0	1.2	—	—	—	—	1.7
Cetraria andrejevii	LI	—	—	—	—	—	—	—	0.3
Cetraria cucullata	LI	7.6	4.5	4.0	0.5	1.0	0.4	—	1.5
Cetraria delisei	LI	0.8	0.1	0.3	0.2	0.1	—	—	0.2
Cetraria islandica	LI	3.7	4.9	6.1	3.3	1.1	1.8	—	2.6
Cetraria nivalis	LI	0.8	—	0.1	0.1	—	—	—	0.2
Cetraria richardsonii	LI	—	0.1	1.5	0.3	0.1	—	—	—
Cetraria simmonsii	LI	—	—	—	—	—	—	—	0.2

Table 2. A Complete List of the Species Occurring in the 43 Sampled Stands and Their Nodal Occurrence[a] (*Continued*)

Taxon	Growth-form	Vegetation I(1)	II(5)	III(11)	IV(6)	V(6)	VI(8)	VII(2)	VIII(4)
Cladonia amaurocraea	LI	—	—	1.9	—	—	—	—	1.6
Cladonia bellidiflora	LI	—	—	0.3	0.1	—	—	—	—
Cladonia carneola	LI	—	0.1	0.2	—	0.1	—	—	0.2
Cladonia cenotea	LI	—	—	—	—	—	—	—	—
Cladonia chlorophaea	LI	0.8	1.4	1.6	—	—	—	—	1.5
Cladonia cryptochlorophaea	LI	5.5	0.3	—	—	—	—	—	0.2
Cladonia mitis	LI	—	—	0.2	—	—	—	—	—
Cladonia pleurota	LI	0.8	—	0.2	—	—	—	—	—
Cladonia pyxidata	LI	—	—	0.1	0.3	—	—	—	—
Cladonia uncialis	LI	—	1.7	2.2	0.1	0.1	—	—	0.2
Cornicularia divergens	LI	—	4.4	2.1	—	—	—	—	0.3
Dactylina arctica	LI	4.7	5.6	8.1	2.1	1.3	2.8	—	3.5
Lobaria linita	LI	—	0.2	0.2	0.1	—	—	—	—
Peltigera aphthosa	LI	0.8	3.0	1.7	2.9	3.1	1.8	—	—
Peltigera canina	LI	—	0.2	1.4	1.1	3.6	0.2	—	—
Peltigera membranacea	LI	—	01.	—	—	0.1	—	—	—
Pseudoevernia consocians	LI	—	0.3	—	—	—	—	—	7.2
Solorina crocea	LI	—	0.1	—	—	—	—	—	—
Sphaerophorus globosus	LI	—	2.4	1.4	0.1	—	—	—	1.7
Stereocaulon cf. *tomentosum*	LI	—	1.5	0.1	—	—	—	—	1.0
Thamnolia vermicularis	LI	8.3	4.3	5.0	0.8	—	1.4	—	1.8

[a] The mean nodal values of Species Index are given. The number of stands per nodum is given in parentheses after the nodal number. The species are listed within the major groups and alphabetically arranged within these groups. Symbols are as follows: DS, deciduous shrub; ES, evergreen shrub; SM, single monocotyledon; CC, caespitose monocotyledon; RD, rosette dicotyledon; ED, erect dicotyledon; CD, cushion dicotyledon; MD, mat dicotyledon; BR, bryophyte; LI, lichen.

Table 3. The Total Number of Sampled Species in Each Growth-Form for the Vegetation Noda at Barrow

Growth-form	Vegetation noda								Total
	I	II	III	IV	V	VI	VII	VIII	
Woody dicotyledon	1	4	2	2	1	0	0	1	6
Herbaceous dicotyledon	7	22	11	14	12	6	5	16	33
Monocotyledon	5	11	10	12	11	10	5	9	16
Bryophyte	5	17	19	19	10	12	4	10	28
Lichen	11	16	25	15	10	6	0	19	29
Total	29	70	67	62	44	34	14	55	112

exists for the herbaceous dicotyledon standing dead material, and these patterns are interpreted as the result of slower decay rates on dry sites and the ease with which standing dead material gets incorporated into the prostrate dead and litter fraction on wetter sites. Herbaceous dicotyledon production is uniformly low in all noda except Nodum VIII *(pioneer meadow)*, but even here it does not exceed the production by monocotyledons. In only one nodum, Nodum II *(mesic heath)*, does the dicotyledon production exceed that of monocotyledons; here both herbaceous and woody dicotyledon productions are larger. Bryophyte biomass is highest in Nodum III *(mesic meadow)*, where many acrocarpous mosses such as *Dicranum* and *Pogonatum* are abundant; however, bryophyte biomass is fairly high in all noda. In all but the pioneer vegetation (Nodum VIII), the dry weight of dead belowground material is several times that of live belowground material. Presumably, the dead fraction is still accumulating in the pioneer sediments.

The belowground stem base component is variable from nodum to nodum. It is low to absent in those noda with little or no organic mat (Nodum II, *mesic heath;* Nodum VIII, *pioneer meadow*) and also in the pond vegetation (Nodum VII). In the sequence from Nodum I to Nodum V there is a general trend of increasing rhizome and total belowground biomass. From Nodum V *(wet Dupontia meadow)* through Nodum VI *(wet Carex meadow)* to Nodum VII *(pond margin)* the rhizome and total belowground biomass decreases. Belowground biomass is least in the *pioneer meadow* (VIII). The ratio of above- to belowground biomass does not change in such a clear fashion as that for belowground biomass alone. The ratio varies from a mean of 1:3.2 in the pioneer Nodum VIII to a mean value of 1:29.6 in Nodum I. The overall average ratio is 1:16.3 while that based on an average value for aboveground and belowground biomasses is 1:13.5.

Net aboveground production of vascular plants for the 1972 growing season ranged from 18.1 g m^{-2} yr^{-1} to 118.5 g m^{-2} yr^{-1} with a mean of 48.1 g m^{-2} yr^{-1}. Vascular production is positively correlated with site moisture regime and it essentially increases through the nodal sequence I through VII. *Dry heaths* (I) have a mean value of 18.1 g m^{-2} yr^{-1} and *pond margins* (VII) have a mean value of 115.0 g m^{-2} yr^{-1}. Pioneer vegetation is variable from a low of 20.7 g m^{-2} yr^{-1} to a high of 61.8 g m^{-2} yr^{-1}. Nodum VI, *moist Carex–Eriophorum meadow*, with a

Table 4. The Distribution of the Major Plant Growth-Form Types (Wielgolaski and Webber, 1973) in the Barrow Vegetation Noda[a]

Growth form	Examples	Vegetation noda							
		I	II	III	IV	V	VI	VII	VIII
Deciduous shrub	*Salix rotundifolia*	5.0	*16.5*	3.2	1.4	0.4	—	—	—
Evergreen shrub	*Cassiope tetragona*	—	3.3	1.5	1.3	—	—	—	0.2
Caespitose monocotyledon	*Luzula confusa*	*15.1*	4.4	2.1	2.8	0.4	0.6	—	2.8
Single monocotyledon	*Carex aquatilis*	4.0	8.1	*16.7*	*26.5*	*28.4*	*40.2*	*35.5*	20.8
Cushion dicotyledon	*Saxifraga caespitosa*	—	0.8	—	—	—	—	—	—
Mat-forming dicotyledon	*Cerastium beeringianum*	2.3	2.3	1.4	3.4	6.4	0.5	1.0	*12.9*
Rosette dicotyledon	*Saxifraga nivalis*	2.0	3.0	1.3	2.5	1.5	3.2	—	*4.3*
Erect dicotyledon	*Saxifraga cernua*	11.3	11.1	4.9	8.8	*12.1*	3.8	*32.3*	*15.2*
Bryophyte	*Pogonatum alpinum*	*37.0*	31.7	*45.3*	*46.2*	*45.4*	*47.4*	*31.2*	30.2
Lichen	*Cetraria islandica*	23.3	18.8	*23.6*	7.1	5.4	4.3	—	13.6

[a] Values are mean relative cover. For each nodum the value(s) of the characteristic growth-form or combination of growth-forms is (are) in italics.

Table 5. Some Selected Substrate Factors for the Eight Stand or Vegetation Noda from the Barrow Intensive Site[a]

Substrate factors	Vegetation noda							
	I(1)	II(5)	III(11)	IV(6)	V(6)	VI(8)	VII(2)	VIII(4)
Soil moisture (%) July 29, 1973	77	64	183	287	299	379	500	42
Snow depth (cm) June 6, 1973	0	4	21	29	43	36	28	86
Thaw depth (cm) August 17, 1973	37	54	36	32	32	32	37	76
Soil odor (scaled) August 17, 1973	0	0.4	0.3	2.2	1.7	1.7	2.0	0
Sand (%)	13	34	28	14	9	29	5	75
Soil reaction (pH)	3.9	5.3	4.2	4.1	4.4	4.2	4.5	5.1
Organic matter (%)	24	12	38	61	55	73	53	5
Organic horizon (cm)	4.4	3.7	6.5	11.8	9.5	18.2	2.0	1.2
Soluble phosphate (mg gdw^{-1} soil)[b]	15.5	21.5	18.5	10.1	59.8	4.5	41.2	6.0

[a] Values are means from the plots within each nodum. The number of stands per nodum is given in parentheses after the nodal number.

[b] Based on only two samples per nodum (except Nodum I with only one sample).

mean value of 43.9 g m^{-2} yr^{-1}, also does not fit the sequence. The variability of this nodum has already been noted. The low-centered polygons of this nodum may only produce 9.6 g m^{-2} yr^{-1} of vascular material while the better developed meadows as much as 106.8 g m^{-2} yr^{-1}.

The map permits an estimate of the overall productivity of the 110 ha of the study area, if an average value of net productivity for each nodum is used in conjunction with the estimates of areal extent (Table 7). This provides an average value of aboveground vascular productivity of 42.4 g m^{-2} yr^{-1} for the whole map area for the 1972 growing season.

Turnover rates of aboveground vascular biomass (biomass ÷ annual production) are close to 1 yr for the principally herbaceous noda (meadows) where there is little perennial aboveground living material (Table 6). For the drier noda where there are woody species and some rosette plants, the turnover rate of aboveground biomass reaches 1.6 yr. For the woody plants themselves this would be higher; several individuals of *Salix pulchra* had a minimum age of 20 yr based on counts of terminal bud scars of their branches. Turnover rates for standing crop of biomass plus standing dead are slower than for biomass alone (Table 6). The rates of the former reflect the rate of incorporation of aboveground biomass and standing dead into litter and prostrate dead. The dry noda (I, II, and III) have a mean turnover rate of biomass and standing dead of 3.2 yr while that for the remaining wetter noda is 1.8 yr. Thus rates of incorporation of biomass and standing dead into surface litter is higher in wet sites than in dry sites. The turnover rate of litter and prostrate dead has an average value of 2.1 yr while the average turnover rate of all aboveground vascular material (biomass + standing

Table 6. Some Selected Standing Crop Fractions, Production, and Derived Values (Ratios and Turnover Rates) for the Vegetation Noda[a]

Variables	Vegetation noda								
	I(1)	II(5)	III(11)	IV(6)	V(6)	VI(8)	VII(2)	VIII(4)	Mean
Aboveground biomass									
Herbaceous dicotyledon	4.5	5.2	0.9	3.3	3.4	1.8	40.3	14.7	9.3
Woody dicotyledon	5.4	31.0	31.1	2.6	0.8	0	0	0	8.9
Monocotyledon	9.4	4.1	31.1	41.4	49.1	44.8	78.8	32.9	36.1
Total vascular plant	19.3	40.3	63.1	47.3	53.3	4.8	118.6	47.6	54.3
Lichen	14.8	37.3	55.1	4.6	11.3	0.2	0	13.7	17.1
Bryophyte	15.6	7.5	244.0	40.0	19.1	36.7	18.0	20.0	50.1
Total biomass	49.7	85.1	362.2	91.9	83.7	81.7	136.6	81.3	121.5
Aboveground vascular annual production	18.1	25.3	39.3	45.1	51.1	43.9	115.0	47.0	48.1
Belowground biomass[b]									
Stem bases	112.6	0	64.4	259.6	76.8	111.2	2.2	3.0	66.2
Live rhizomes	59.2	108.1	110.0	91.3	219.8	77.1	43.4	44.2	94.1
Live roots	399.0	363.3	626.2	644.6	1008.3	866.2	466.4	105.9	560.0
Total biomass	570.8	471.4	800.6	995.5	1304.8	1054.5	512.0	153.1	733.5
Ratio[b]									
Above: belowground vascular biomass	29.6	11.7	12.7	21.1	24.5	23.5	4.3	3.2	16.3
Aboveground dead (vascular only)									
Standing dead	57.4	32.7	31.1	35.5	51.4	43.3	35.6	32.3	39.9
Litter + prostrate dead (L&PD)	41.4	126.8	121.4	67.0	75.2	46.9	63.9	84.6	78.4
Belowground dead[b]									
Intact plant organs	2804.9	1399.6	6367.4	3370.1	2105.6	2950.7	1227.5	291.3	2564.6
Turnover rates (years)									
Aboveground vascular biomass	1.1	1.6	1.6	1.1	1.0	1.0	1.0	1.0	1.4
Aboveground biomass + standing dead	4.2	2.9	2.4	1.8	2.1	2.0	1.3	1.7	2.3
Aboveground litter + prostrate dead[c]	2.3	5.0	3.1	1.5	1.5	1.1	0.6	1.8	2.1
Aboveground standing crop (+L&PD)	6.5	7.9	5.5	3.3	3.5	3.1	1.9	3.5	4.4
Belowground biomass	31.5	18.6	20.4	22.1	25.5	24.0	4.5	3.3	19.3

[a] Material was harvested at the period of peak aboveground vascular biomass in 1972. Values are means from the stands within each nodum. The number of stands per nodum is given in parentheses after the nodal number. Except for derived values, all units are g m^{-2}.

[b] Based on three stands per nodum except for Noda I and VII with only one and two stands, respectively, per nodum.

[c] Inverse of vascular decay index (Fig. 18).

Table 7. Net Aboveground Annual Vascular Primary Production of the Vegetation Noda and Their Percentage Contributions to the Total Aboveground Vascular Productivity of the Entire Mapped Area Surrounding the Biome Sites for the 1972 Growing Season[a]

Nodum	Number of plots[b]	Maximum observed	Mean (g m^{-2} yr^{-1})	Percentage of map	Percentage contribution
I	1	18.1	18.1	3.0	1.3
II	5	28.6	25.3	7.2	4.3
III	11	72.6	39.3	41.0	38.0
IV	6	74.5	45.1	20.9	22.2
V	6	74.9	51.1	6.9	8.3
VI	8	106.8	43.9	14.6	15.1
VII	2	118.5	115.0	2.3	6.3
VIII	4	61.8	47.0	4.1	4.5
Mean	—	—	48.1	—	42.4[b]

[a] The productivity estimates are based on a peak season harvest.
[b] The mean net aboveground productivity of the map (Fig. 8).

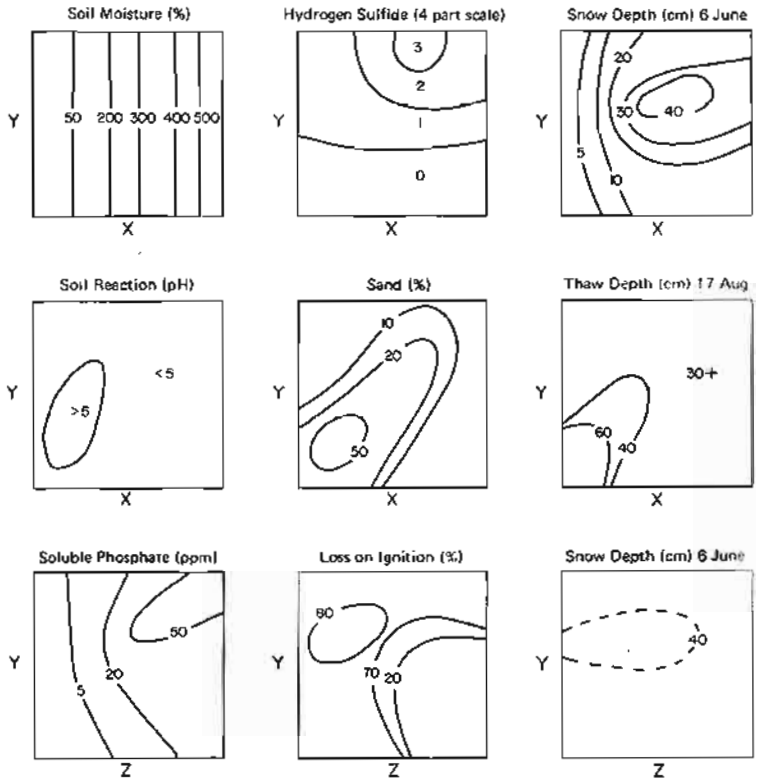


Figure 10. Distribution of eight significant abiotic factors within the space provided by the ordination. The substrate trends indicated are used to interpret the environmental distribution of various components of the vegetation. All measurements were made in 1973.

dead + litter and prostrate dead) is 4.4 yr. These last two derivatives may be regarded as indicators of surface decay rates.

Gradient Analysis

The Ordination and Its Gradients. The indirect ordination was constructed from 39 of the 43 sampled stands; four stands belonging to the pioneer vegetation of Nodum VIII were excluded as being too dissimilar from the central sedge meadow complex. The axes of the ordination were correlated with 16 measured substrate variables. Only those variables which had significant correlations are discussed. Figure 10 shows the distribution of these variables within the three-dimensional ordination space. This ordination framework provided by the phyto-sociological axes is the basis for describing the distribution of the vegetation noda, species, growth-forms, and various production and standing crop fractions in terms of the controlling environmental variables. The first axis of the ordination has the highest correlation with soil moisture, the second axis with the presence of hydrogen sulfide in the soil, and the third axis with soluble soil phosphate. These factors are thus used to name the major controlling complex gradients of the study area. In addition to the latter three factors, snow depth, pH of the surface horizon, percentage of sand, late season depth of thaw, and percentage of soil organic matter also show distinct patterns within the ordination space (Figure 10). The factors which correlate with the ordination axes are seldom, if ever, linear or orthogonal, and their interrelationships are complex (Figure 10). The nature of the complex gradients can also be seen when the substrate factors are clustered according to their intercorrelation with one another and with the ordination axes (Table 8 and Figure 11). Four clusters can be identified and each axis is a member of a separate cluster. A complete matrix of values for soluble soil phosphate is not available and in Figure 11 this factor is placed in an approximate position according to its highest correlation, which was with the third axis.

The diagonal trend of increasing concentration of hydrogen sulfide and soil moisture across the space provided by the first two axes reflects an intercorrelation and interdependence which is to be expected for these factors. Similar intercorrelating patterns are seen in Figure 10 between the amount of sand, soil reaction (pH), and depth of thaw. It should be noted that this latter group of variables cluster together (Figure 11).

Snow cover does not emerge from these analyses as a strong major controlling factor at Barrow because the variations in microrelief are insufficient to produce a pronounced snow effect. Where ravines, creek banks, ridges, and snowfences occur, snow cover appears as a controlling factor. Across the sedge meadow complex, shallow ponds, centers of low-centered polygons, and polygon troughs have the greatest snow accumulation and are the last sites to be free of snow, while raised polygon rims and centers of high-centered polygons have only a thin snow cover and are first to be snow free.

Plots from the different microrelief features or habitats have similar locations within the ordination space (Figure 12). Each vegetation nodum has a unique distribution within the ordination (Figure 13). The interpretation of the environment for each nodum from the ordination is compatible with the average value for environmental factors for each nodum (Table 5).

In addition to vegetation characteristics, other ecosystem phenomena such as consumer activities can be described within the ordination framework; for example, lemming activity (clipping, grubbing, and burrowing) and the amount of lemming feces show very distinct patterns within the ordination (Figure 14). Lemmings appear to use the drier sites and concentrate their activities in parts of Noda III and IV. There is a strong correspondence between the distribution of lemming feces and other lemming activities. It is interesting to note the concentration of lemming feces in the upper reaches of the phosphate gradient, but any connection between these is not established.

Distribution of Species and Growth-Forms. The distribution of 33 common species within the ordination is given in Figure 15. Each plot of a species within the ordination framework can be interpreted as a statement concerning the environmental tolerances or controls of that species. For example, *Salix rotundifolia* (top left, Figure 15) is most abundant on dry, well-aerated soils with high levels of soluble phosphate. Many species are wide ranging while others have restricted distributions. For example, *Saxifraga cernua, Carex aquatilis, Eriophorum angustifolium, Eriophorum russeolum, Poa arctica, Pogonatum alpinum,* and *Dactylina arctica* are wide ranging while *Cerastium jenisejense, Pedicularis lanata, Potentilla hyparctica, Eriophorum scheuchzeri, Calliergon*

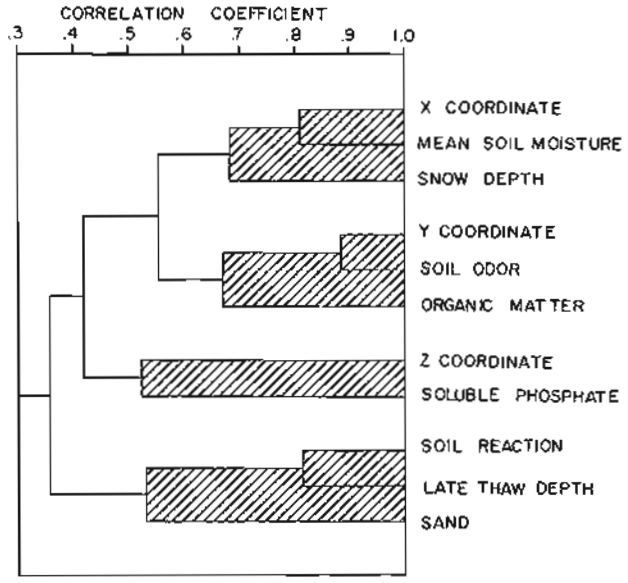


Figure 11. Dendrogram showing the clustering of the eight significant abiotic substrate factors and the three ordination coordinates. The position of soluble phosphate is based only on measurements from 15 plots. For $N = 39$ and $P = 0.001$, $r = 0.52$, and for $P = 0.05$, $r = 0.32$.

Table 8. List of Significant Correlations between Stand Ordination Coordinates and 16 Abiotic Variables[a]

Variable	Variables with significant correlations
Cluster 1	
First ordination coordinate (XAXIS)	LMOIS, MMOIS, YAXIS, SODOR, EMOIS, SNODE
Mean seasonal gravimetric water content (%) (MMOIS)	LMOIS, EMOIS, XAXIS, WABSO, BDENS, ORHORI, YAXIS, SODOR, ORMAT
Late season—August 17—water content (%) (LMOIS)	MMOIS, XAXIS, BDENS, WABSO, OHORI, SODOR, YAXIS, EMOIS
Early season—June 25—water content (%) (EMOIS)	MMOIS, WABSO, OHORI, XAXIS, SODOR, BDENS, LMOIS, YAXIS
Thickness of organic horizon (cm) (OHORI)	MMOIS, WABSO, EMOIS, LMOIS
Cluster 2	
Second ordination coordinate (YAXIS)	SODOR, XAXIS, MMOIS, WABSO, EMOIS, LMOIS
Soil odor on a four-part scale (SODOR)	YAXIS, XAXIS, MMOIS, WABSO, EMOIS, BDENS, LMOIS
Water absorption by dry sample (%) (WABSO)	ORMAT, MMOIS, EMOIS, OHORI, BDENS, LMOIS, SODOR, YAXIS
Loss on ignition (%) (ORMAT)	WABSO, BDENS, MMOIS
Cluster 3	
Third ordination coordinate (ZAXIS)	SPHOS
Soluble soil phosphate (ppm) (SPHOS)	ZAXIS
Early season—June 20—thaw depth (cm) (ETHAW)	SNODE
Early season—June 6—snow depth (cm) (SNODE)	SNOME, ETHAW, XAXIS
Duration of snow melt after June 6 (days) (SNOME)	SNODE
Cluster 4	
Sand in 2-mm soil fraction (%) (PSAND)	LTHAW
Bulk density of oven dry soil (BDENS)	MMOIS, LMOIS, WABSO, ORMAT, EMOIS, LTHAW, MTHAW, SODOR SOREA
Soil reaction of 2-m soil (pH) (SOREA)	MTHAW, LTHAW, BDENS
Late season—August 17—thaw depth (cm) (LTHAW)	BDENS, PSAND
Mean seasonal thaw depth (cm) (MTHAW)	BDENS

[a] Measurements from thirty-nine stands were used. Correlation was established with the Pearson's product–moment correlation coefficient (r) and significance was arbitrarily defined as any r-value with $P < 0.01$. All soil factors listed here were measured on the 0–5 cm soil core segments. Negative correlations are underlined. Correlation variables in each row are listed in sequence of decreasing correlation. All dates are for 1973.

giganteum, and *Alectoria nigricans* are narrow ranging. Some species may have similar distribution along one or two axes, but each is unique when all three axes are considered. For example, *Carex aquatilis* and *Eriophorum angustifolium* and *Dupontia fisheri* and *Eriophorum russeolum* have similar soil moisture and redox tolerances but differ with respect to phosphorus requirements or competition for phosphorus.

The floristic richness, as expressed by a number of species per 10-m^2 plot, of the vegetation varies from almost pure monospecific stands to rich stands with more than 40 species. There is a trend of decreasing floristic richness along the moisture gradient; dry-mesic sites have the most species, with very dry sites having slightly fewer and wet sites having the fewest species (Figure 16). Floristic richness is also lower in the phosphate-poor and anaerobic segments of the continuum such as low-centered polygons. Each major taxonomic entity has distinct diversity patterns within the continuum. Monocotyledons and bryo-

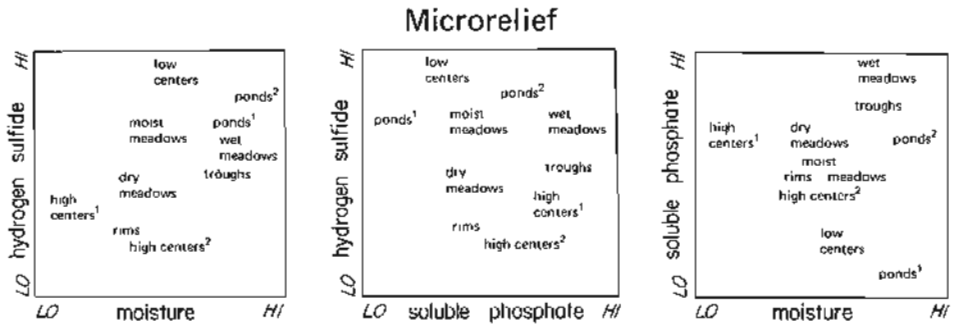


Figure 12. Generalized distribution of microrelief features and habitat types within the three principal elevations of the ordination. (Ponds[1], have no significant water flow: Ponds[2], have water flow; High Center[1], have mineral soil at surface; High Center[2], have thick peat.)

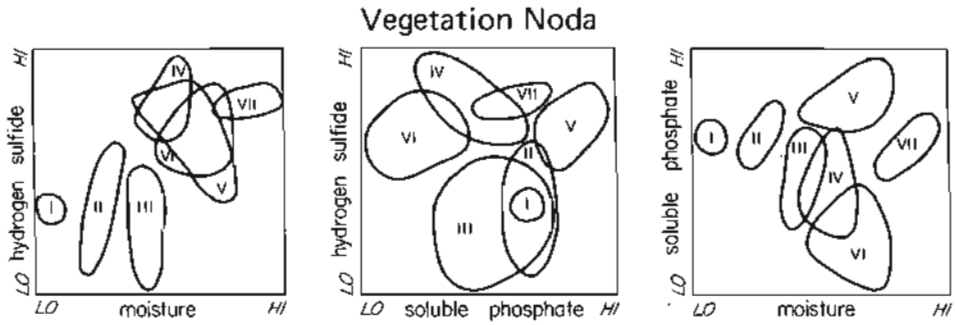


Figure 13. The distribution of the seven mature noda within the three principal elevations of the ordination. The nodal numbers are those given in Table 1.

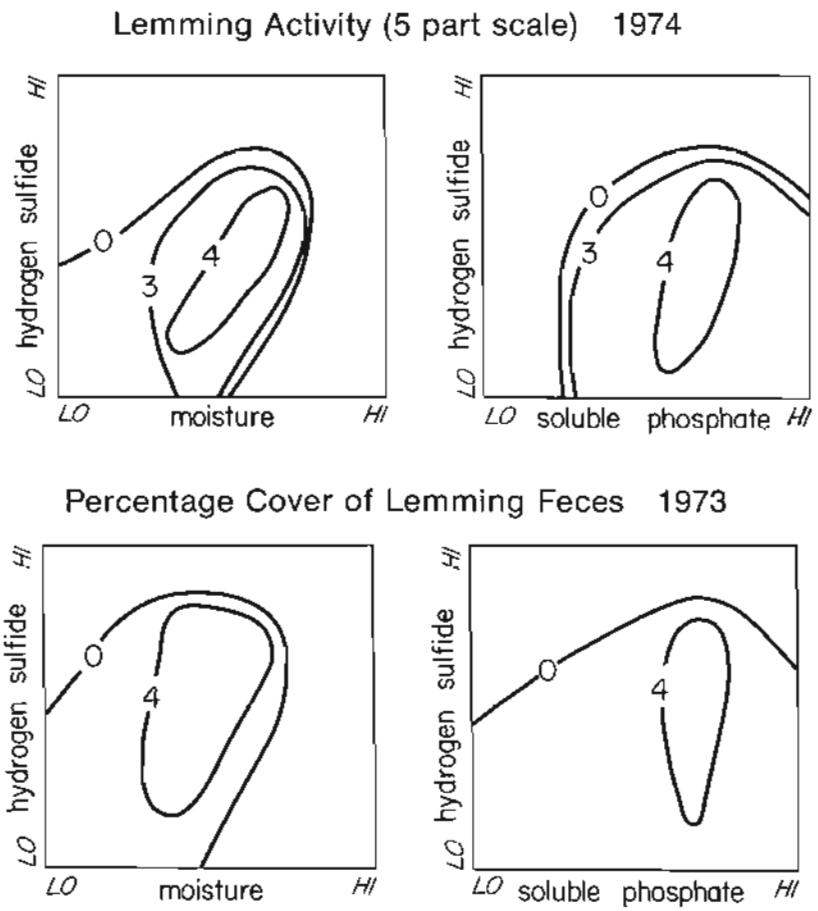
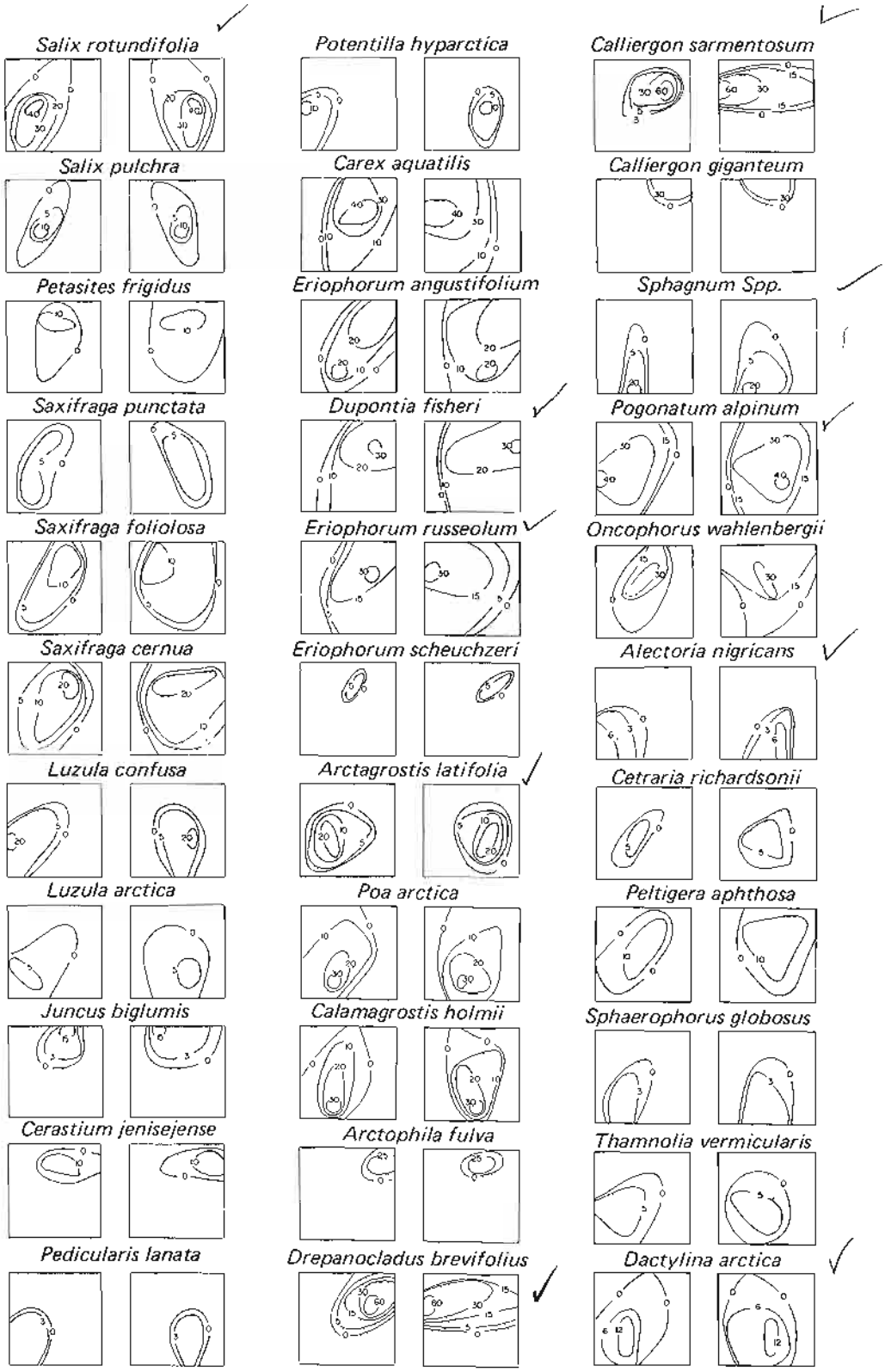


Figure 14. The distribution of lemming activities within the ordination. Lemming activity was based on evidence of the combined signs of grazing and burrowing. Activity was expressed on a four-part scale from 0 (no signs) to 4 (heavy signs). Percentage cover of feces was derived from the number of contacts of 100 vertical point quadrats per ordination plot.

phytes have most species in mesic sites, herbaceous dicotyledons have most species in dry to mesic sites, and woody dicotyledons have most species on dry, well-aerated sites.

Each growth form also has a distinct distribution within the ordination (Figure 17). Evergreen and deciduous shrubs, caespitose monocotyledons, rosette and cushion dicotyledons, and lichens are more abundant on the drier habitats. Single monocotyledons, erect and rosette dicotyledons, and bryophytes are more abun-

Figure 15. Distribution of 33 species within the three principal axes of the Barrow ordination. The axis positions correspond to those in the first two frames of Figure 10. Isoline values are Species Index.


Salix rotundifolia
Potentilla hyparctica
Calliergon sarmentosum
Salix pulchra
Carex aquatilis
Calliergon giganteum
Petasites frigidus
Eriophorum angustifolium
Sphagnum Spp.
Saxifraga punctata
Dupontia fisheri
Pogonatum alpinum
Saxifraga foliolosa
Eriophorum russeolum
Oncophorus wahlenbergii
Saxifraga cernua
Eriophorum scheuchzeri
Alectoria nigricans
Luzula confusa
Arctagrostis latifolia
Cetraria richardsonii
Luzula arctica
Poa arctica
Peltigera aphthosa
Juncus biglumis
Calamagrostis holmii
Sphaerophorus globosus
Cerastium jenisejense
Arctophila fulva
Thamnolia vermicularis
Pedicularis lanata
Drepanocladus brevifolius
Dactylina arctica

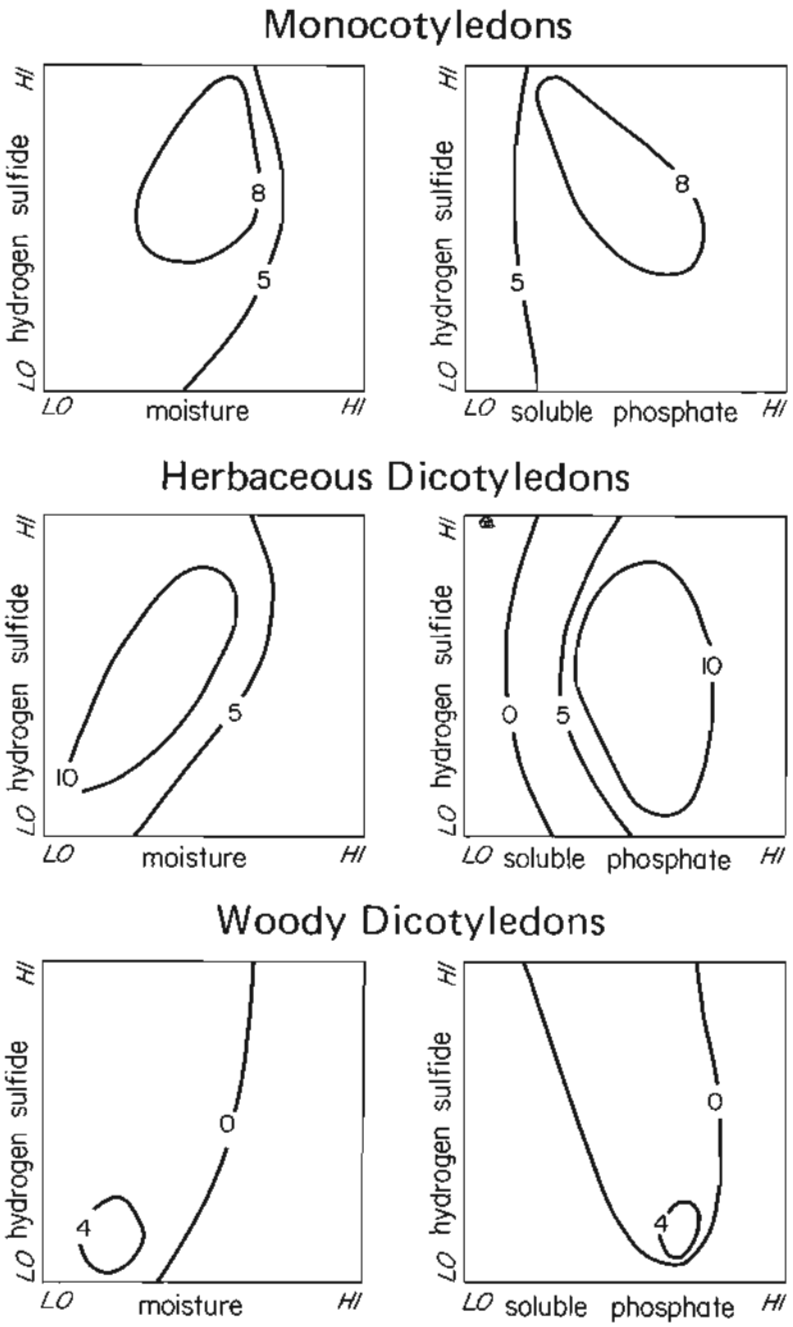


Figure 16. The distribution within the ordination of the number of species per 10-m^2 plot of each major taxonomic entity.

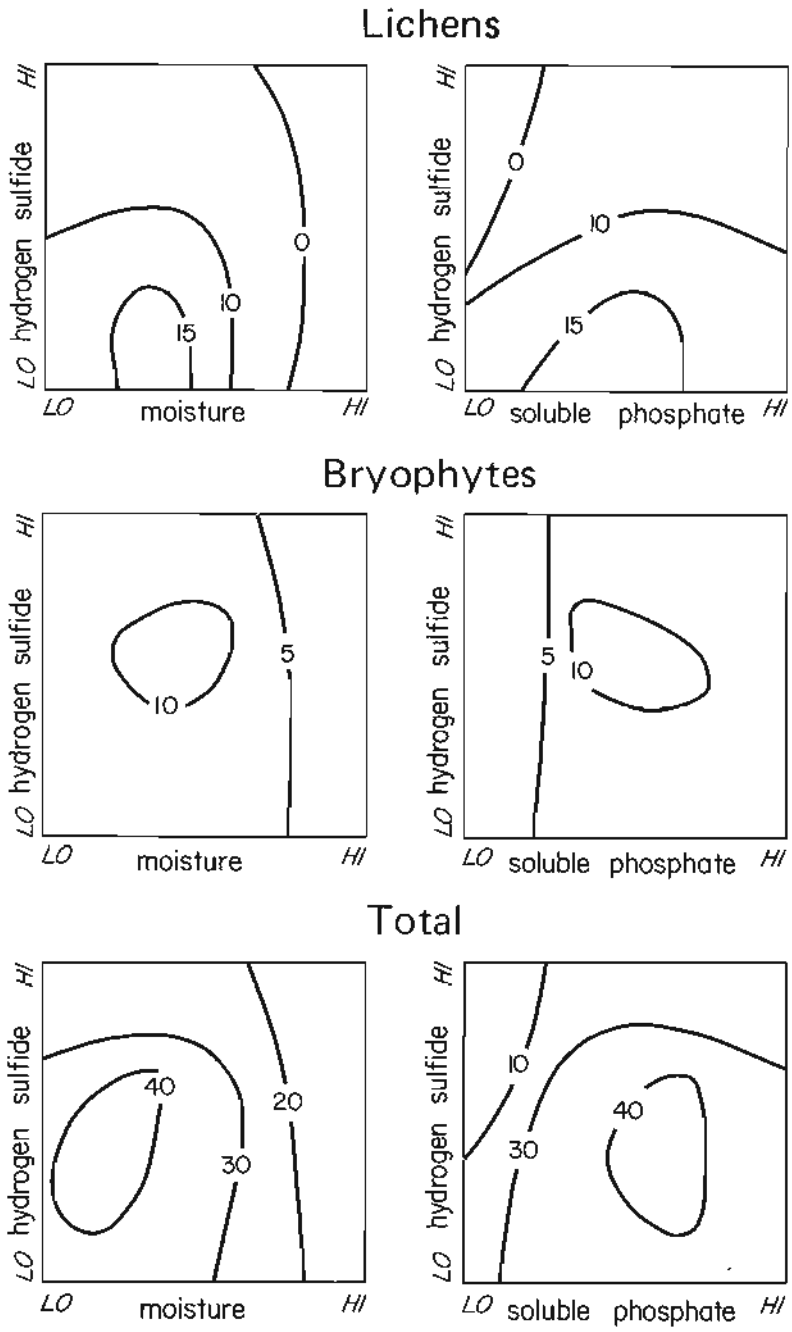


Figure 16 (continued).

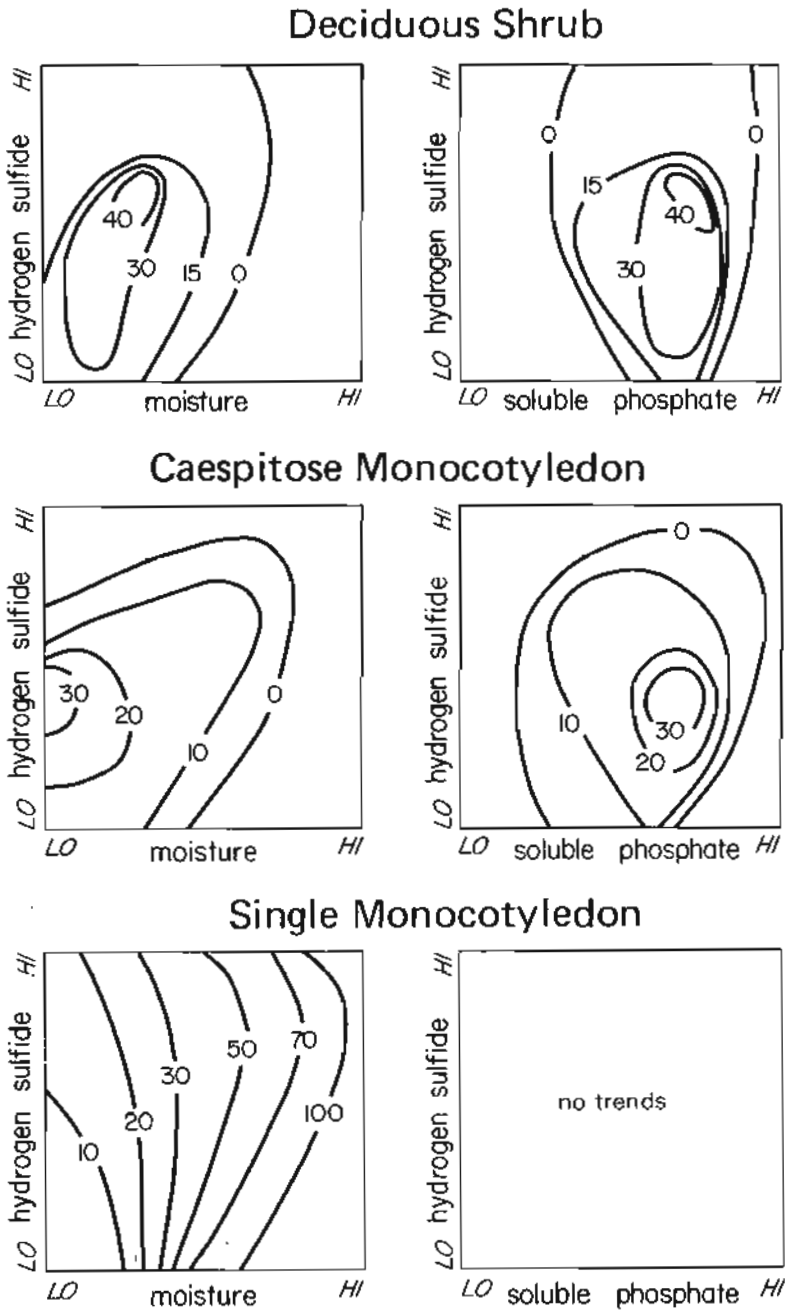


Figure 17. Distribution of 10 growth forms within the two principal elevations of the ordination. Isolines of Species Index have been drawn for each growth form.

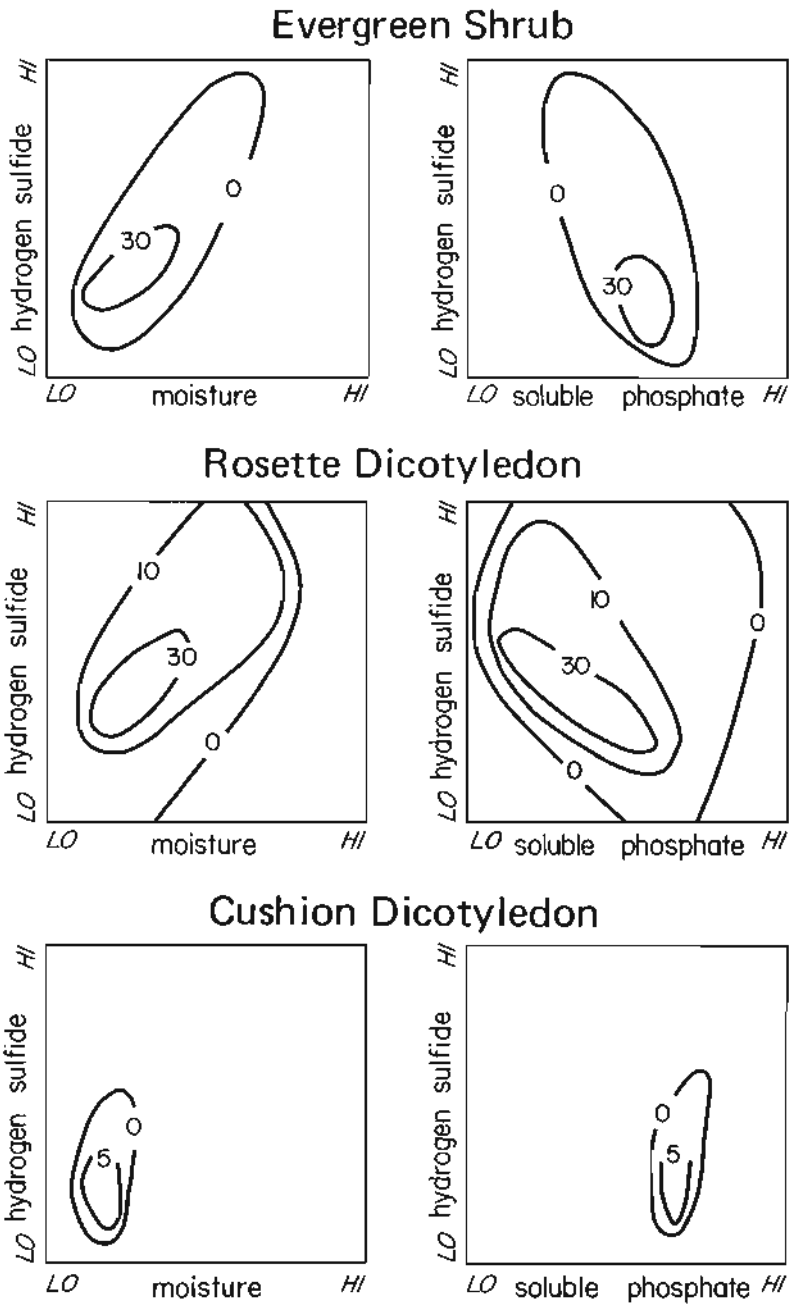


Figure 17 (continued).

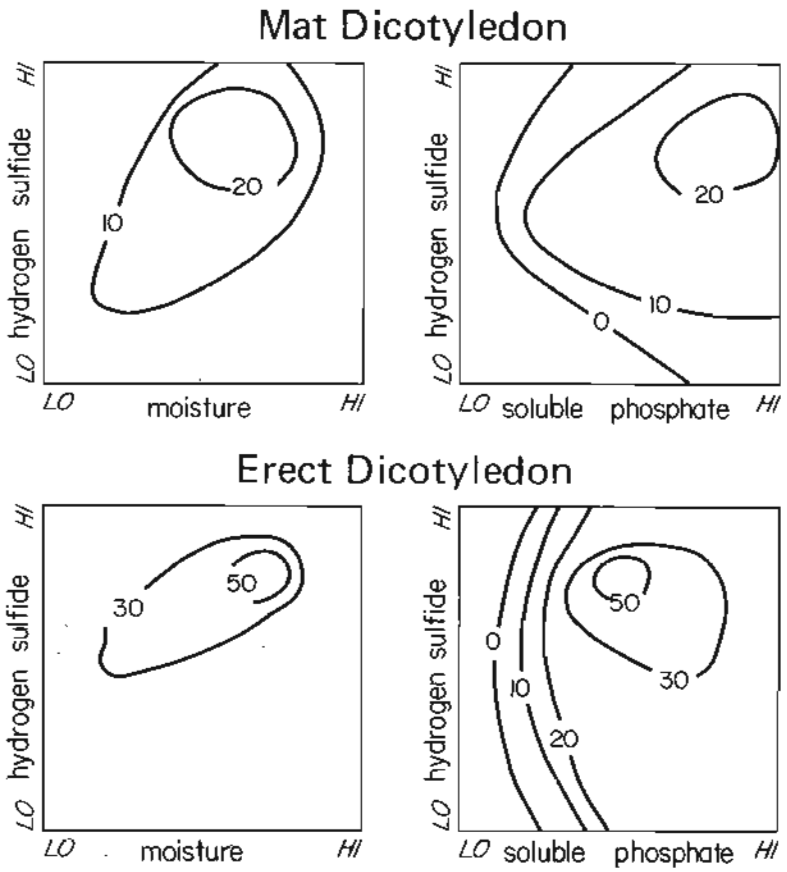


Figure 17 (continued).

dant on the wetter habitats. The cover of caespitose monocotyledons is highest on dry sites with moderate soil aeration and moderate phosphorus. The cover of the single monocotyledons increases with moisture and is independent of soil aeration and soil phosphorus. Evergreen shrubs occur with low moisture, moderately high aeration, and moderate phosphorus. Deciduous shrubs occur with slightly higher soil moisture, slightly lower soil aeration, and higher phosphorus than evergeen shrubs. Mat and erect dicotyledons reach their greatest abundance on moist, relatively anaerobic sites with moderate to high phosphate levels. Rosette dicotyledons are most abundant on dry to moist sites with medium levels of aeration and phosphate. Cushion dicotyledons have a distribution which is restricted to dry, well-aerated, phosphate-rich sites. Lichens occur with moderately low soil moisture, high soil aeration, and moderate phosphorus. Bryophytes, by contrast, occur with moderately high soil moisture, low soil aeration, and low phosphorus.

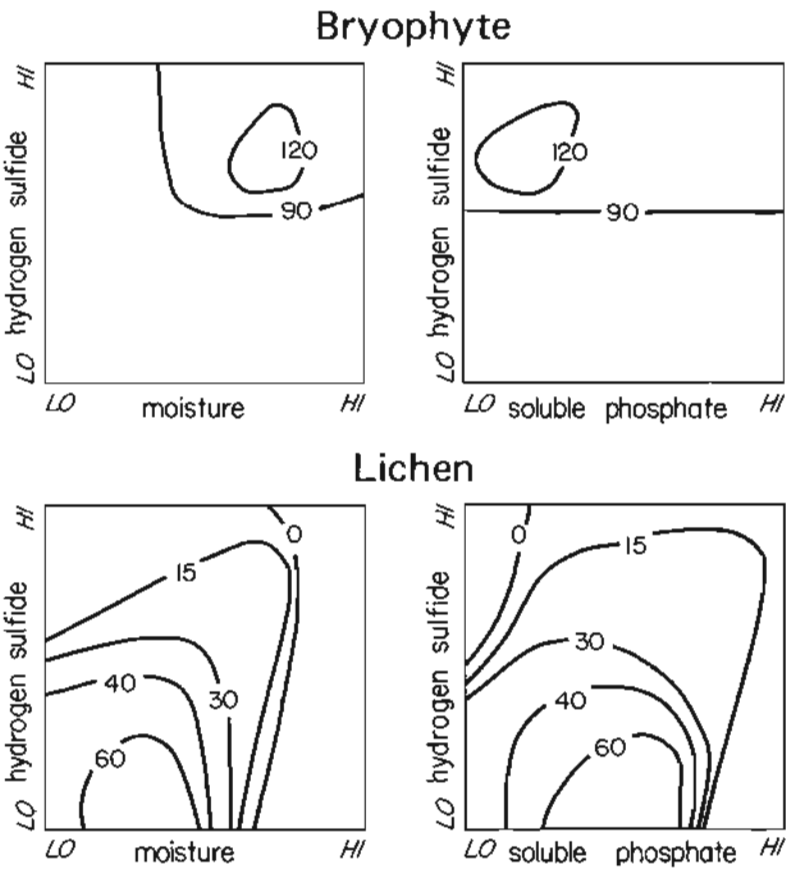


Figure 17 (continued).

The environment with the greatest diversity of a taxonomic entity is not the environment with the greatest abundance of that entity. For example, the number of bryophyte species is highest in mesic segments of each gradient and lowest in wet sites with low phosphate and high hydrogen sulfide levels (Figure 16).

Distribution of Standing Crop and Production. The quantity of the various harvested herbage fractions and of vascular plant leaf area index and net productivity also form clear interpretable patterns within the ordination (Figure 18). Net aboveground vascular production increases along the moisture gradient to a maximum of just over 100 g m^{-2} yr^{-1} in the wettest sites. These sites have highly reducing soils and intermediate to high phosphorus levels. The patterns of monocotyledon and herbaceous dicotyledon peak-season biomass are very similar to actual production patterns because only small amounts of herbaceous-live

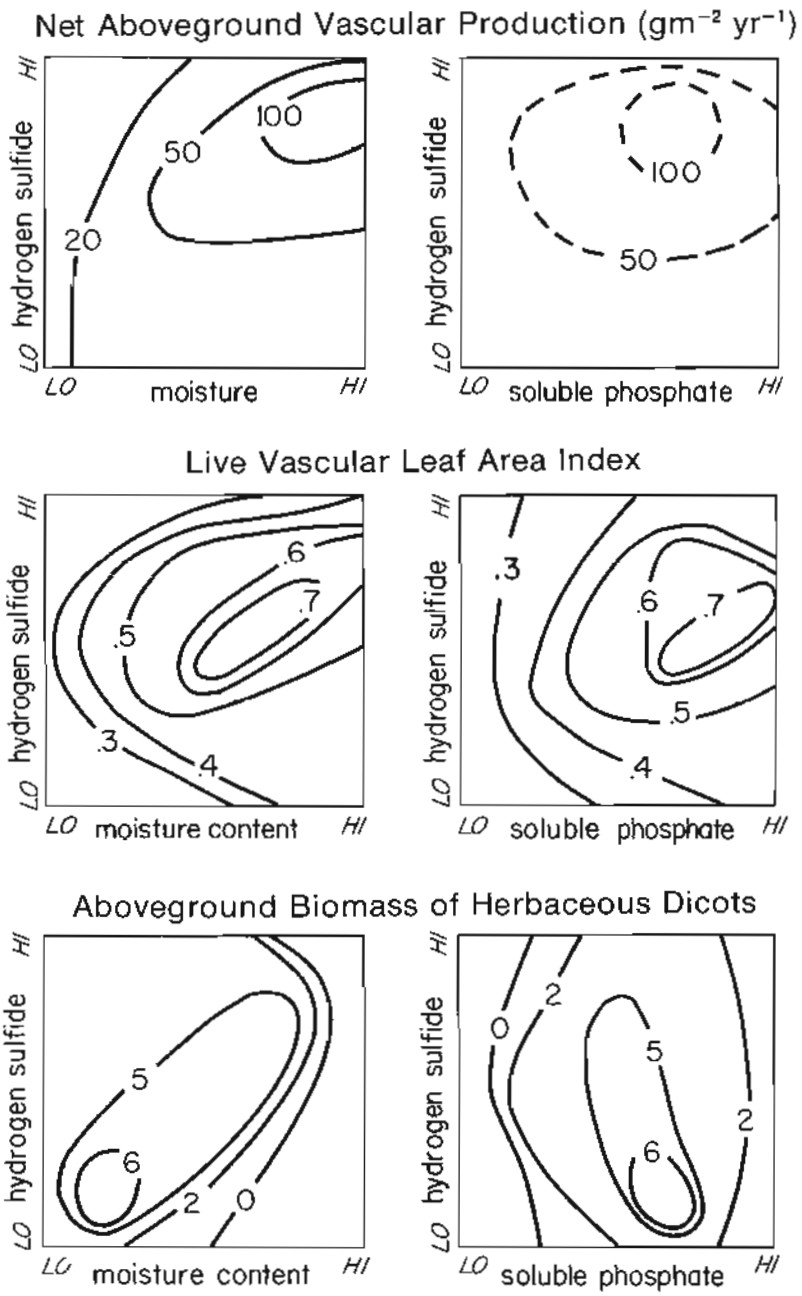


Figure 18. The distribution of several standing crop fractions and productivity related measures within the two principal elevations of the ordination. Measurements were made in 1972.

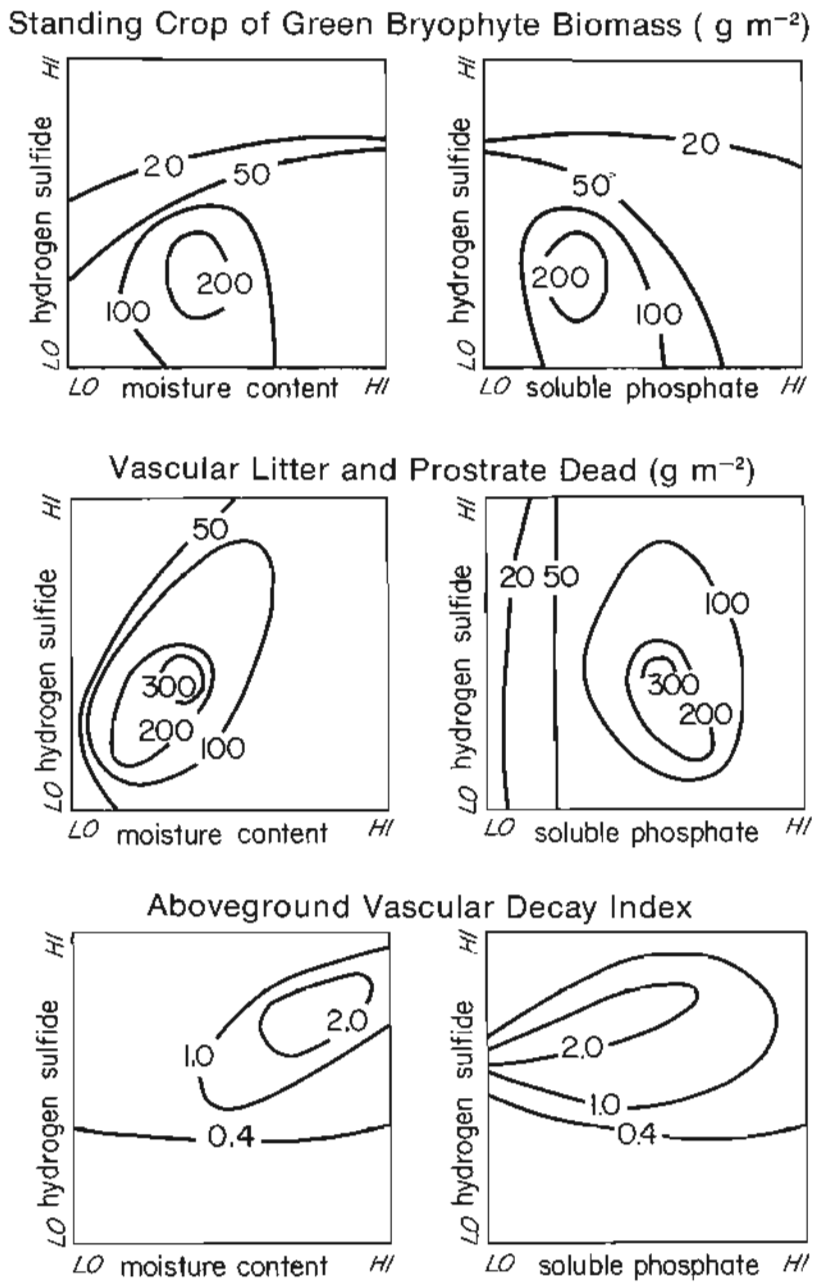


Figure 18 (continued).

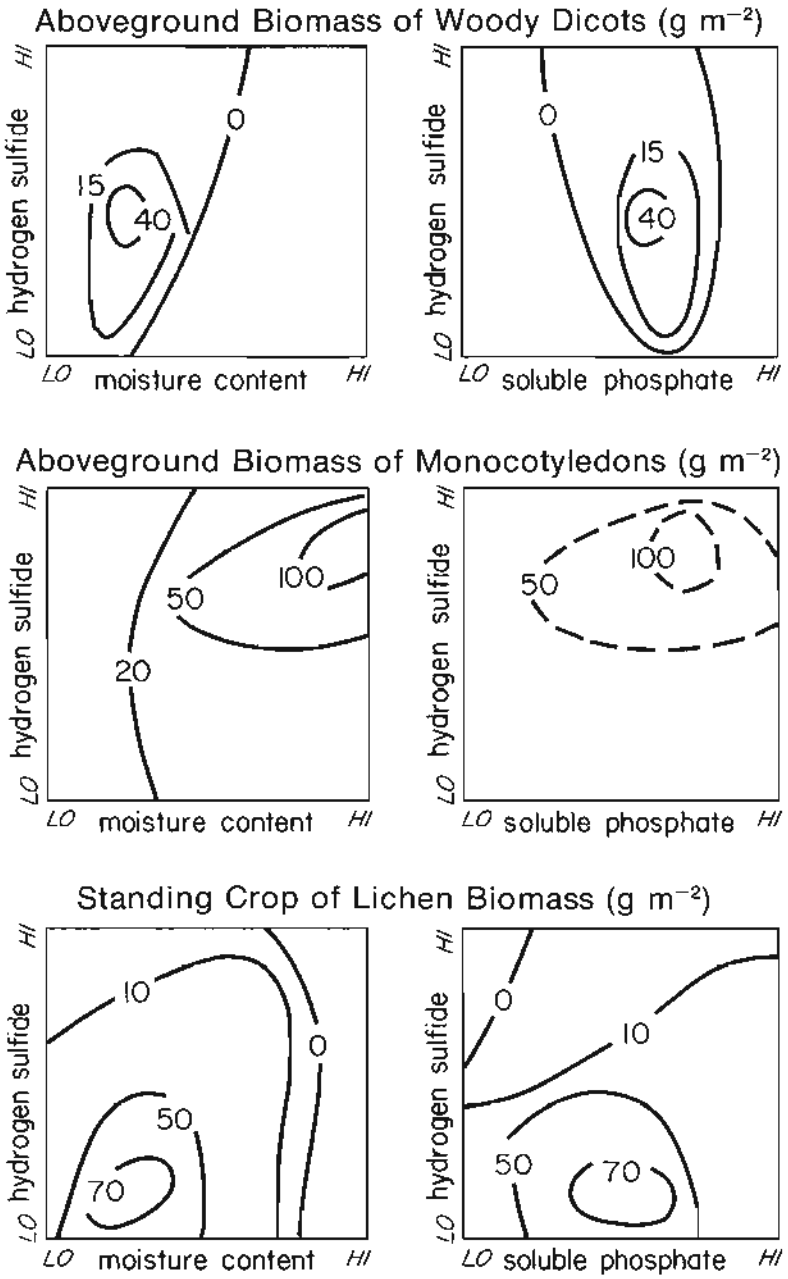


Figure 18 (continued).

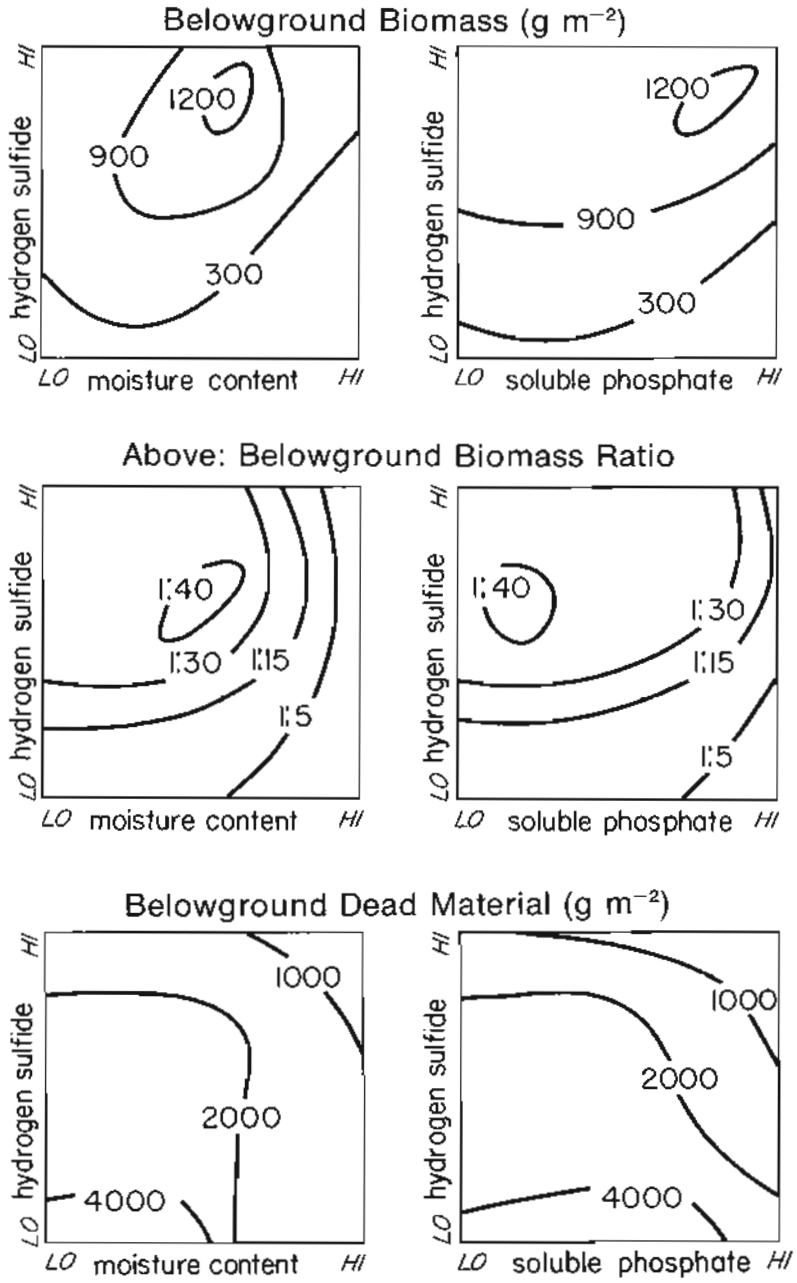


Figure 18 (continued).

material is carried over from previous years and only small amounts of the current year's growth will have been shed or have died or been grazed. Thus the similarity between the vascular production pattern and that of monocotyledon biomass with respect to both magnitude and distribution emphasizes the fact that monocotyledons contribute the majority of the vascular plant production of the IBP site. The production of herbaceous dicotyledons rarely exceeds 6 g m^{-2} yr^{-1} and is highest in dry, oxidizing sites with moderate levels of phosphate. Woody dicotyledon biomass has a similar distribution to that of herbaceous dicotyledons; in optimal sites it just exceeds 40 g m^{-2} and in dry sites the actual production of woody plants occasionally reaches 20 g m^{-2} yr^{-1}, which may equal the herbaceous production in these sites.

The distribution of lichen biomass within the ordination (Figure 18) mirrors that for the total species index of lichens (Figure 17); however, the distributions of bryophyte biomass and species index (Figures 17 and 18) do not correspond. Bryophyte species index, which is a fair measure of total bryophyte cover, is highest in wet, anaerobic, low phosphate sites, whereas biomass is highest on dry-mesic, well-aerated sites with low phosphate.

The distribution of belowground material within the ordination is different from that of aboveground material (Figure 18). Belowground living material is greatest in the most anaerobic sites. The ratio of above- to belowground biomass presents a different picture (Figure 18), with the lowest ratio (1:40) in moist, partly anaerobic sites with low soluble phosphate levels. The ratio of above- to belowground biomass increases along the moisture gradient and from anaerobic to aerobic sites.

Aboveground vascular litter and prostrate dead material and belowground dead material are both most abundant on dry sites and least abundant on wet sites. Litter accumulation is a function of the balance of production and decay. In order to examine this in terms of the principal controlling gradient, an index of aboveground vascular decay was plotted within the ordination (Figure 18). This index is the ratio of the peak season aboveground vascular litter and prostrate dead fraction to the annual aboveground vascular production. This index is the inverse of the litter and prostrate dead turnover rate (Table 6). The index, in the absence of surface transportation or grazing of litter, may be interpreted in terms of surface decay. This suggests that the highest decay rates are found on wet, anaerobic sites with low phosphate and that the lowest rates are found on dry, well-aerated sites with high phosphate. Similar trends for belowground decay are suggested by the distribution of belowground, intact dead matter (Figure 18). The highest accumulations of organic matter, up to 4000 g m^{-2}, occur on dry, well-aerated sites, and the lowest accumulations, about 1000 g m^{-2}, occur on wet, poorly aerated sites.

Seasonal Variation

The Growing Season. The data for the seasonal progression of vascular plant biomass were collected from ordination plots belonging to Nodum IV *(moist meadow)*. The growing season starts in the first or second week of June. In both

1970 and 1971, the onset of vascular plant growth corresponds with the point when the mean air temperature exceeds 0°C (Figure 19). Subsequent accumulation of aboveground vascular biomass is linear until it reaches a maximum or peak in the first week of August. The standing crop of aboveground vascular

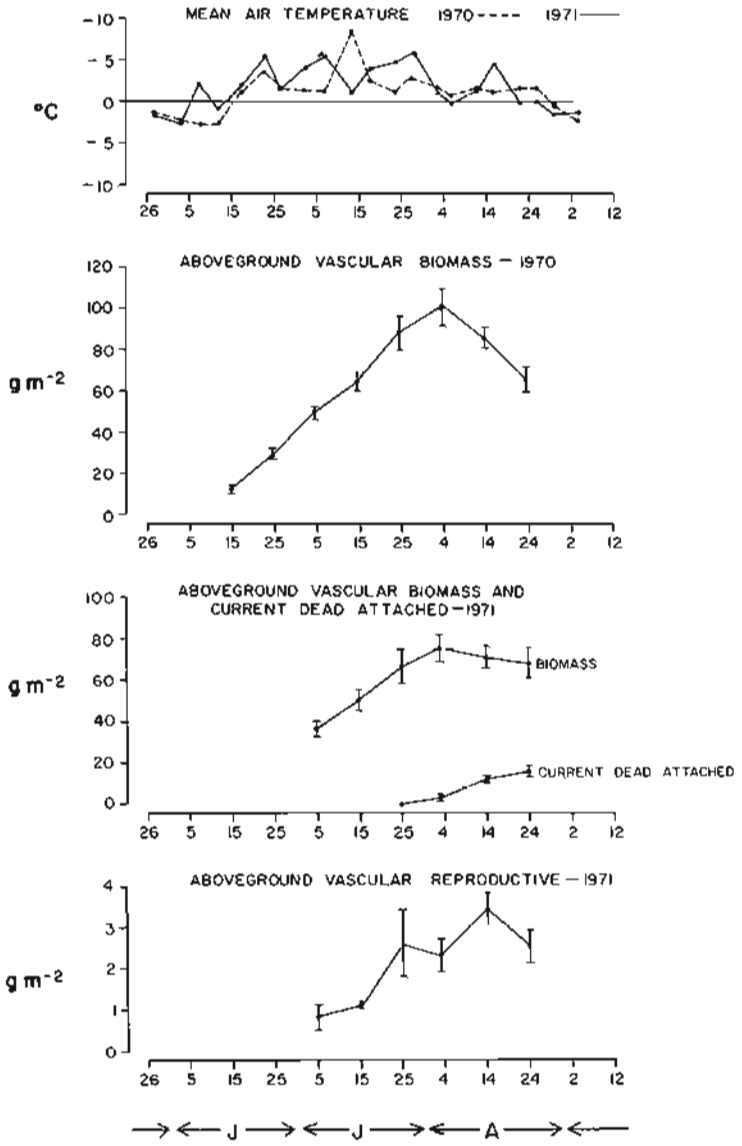


Figure 19. The seasonal progression of mean air temperature and some aboveground vascular plant standing crop fractions for the 1970 and 1971 growing seasons. Standing crop data are from Dennis and Tieszen (1972) and Dennis *et al.* (1978). The bars at each point represent standard errors of the mean.

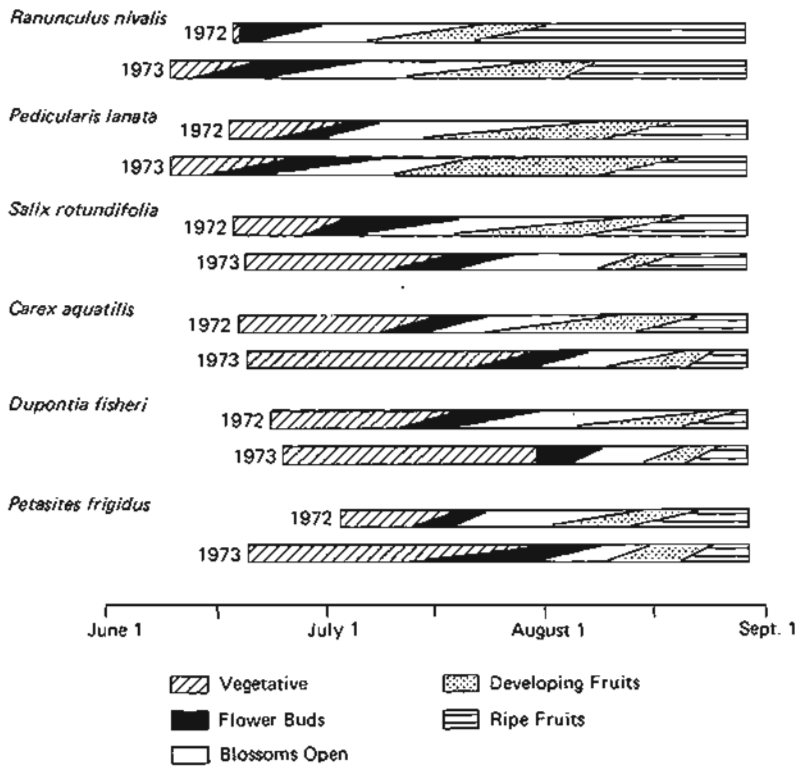


Figure 20. Phenophase diagrams of six common vascular plant species at Barrow, Alaska. The data for two growing seasons, 1972 and 1973, are compared. The species are arranged down the diagram in a sequence from early to late developing.

sexual structures (inflorescences) also reaches its peak in the first week of August.

The onset of vascular plant growth is also closely correlated with the disappearance of snow and the start of soil thaw (see Tieszen, 1974). Those sites which are the first to become free of snow show the first signs of new growth. These sites are the high-centered polygons and raised rims of polygons which belong to Noda I and II *(heaths)* (Figures 10 and 12). The first signs of growth on these sites is that of a little leaf growth followed closely by the flower bud expansion of *Pedicularis lanata* and *Salix rotundifolia*. However, the first prominent flower at the IBP site is that of *Ranunculus nivalis*. It is characteristic of Noda III and IV *(mesic and moist meadows)* which receive moderate snow cover. Nevertheless, the noda can be arranged in phenological sequence. The sequence corresponds to the numerical sequence of the noda, Nodum I *(dry heath)* being the first to begin growth and show mature fruits and Nodum VIII *(pioneer meadow)* being the last. This sequence corresponds to a gradient of increasing duration of snow cover and increasing soil moisture (Table 5). It is probably representative of a

complex temperature gradient. Nodum VIII, although well drained, is found in snowbank situations and is the last to be free of snow and hence the last to have blossoms.

A further description of plant responses within the growing season can be obtained from phenophase diagrams for six common species for the years 1972 and 1973 (Figure 20). The first signs of vegetative growth occur toward the end of the first week of June. Although some open blossoms appear toward the end of June, peak blooming for the Barrow tundra is not until mid- or late July. Fruits begin forming in mid-July, but few ripe fruits with well-formed seeds appear before mid-August. Most flowering is complete by the first week in August and the vegetation begins to senesce at this time. Although each species may begin growth and flowering at different times, there is less variation in the timing of the appearance of ripe fruits which is usually complete before the last week of August when freezing mean air temperatures return (Figure 19). *Ranunculus nivalis* produces well-formed seed within 35 days of snow melt. The period between onset of growth for a species and the appearance of the first mature fruits averages 53 days for the studied species. *Carex aquatilis* is one of the last species to produce mature fruits and it took 63 days in 1973 which was not a particularly cold year (Table 9). *Dupontia fisheri* seemed to be close to the last species to complete its fruit development, while *Pedicularis lanata* took the longest (73 days) to pass from onset of growth to final maturing of the last flower.

Variation between Seasons. Willow elongation for the years 1969 to 1973 showed a positive but insignificant correlation ($r = 0.6$) with the mean July temperature (Table 9). In the 1970 growing season which was cooler and later to start than the 1971 season (Figure 19, Table 9) the aboveground vascular production up to peak season was 34% less. This lack of positive correlation between production and growing season temperature is shown further by a comparison of 1972, when the mean July temperature was 2.34°C warmer than the normal (30-yr mean), with 1970, which was −0.50°C cooler than normal. In 1970, the production was 67% higher than in 1972; 1972 was the warmest of the 4 years.

Table 9. Comparison of Plant Growth from Site 2 and Some Climatic Parameters for the Years 1969–1973

Parameter	Season					Mean
	1969	1970	1971	1972	1973	
Willow elongation[a] (cm)	2.32	2.76	4.12	4.13	3.76	3.42
Deviation from 5-yr mean[a]	−1.10	−0.66	+0.70	+0.71	+0.34	—
Aboveground vascular net production (g m^{-2} yr^{-1})	—	101.5	80.1	74.7	57.4	78.43
Mean July temperature (°C)	1.50	3.22	4.67	6.06	4.28	3.94
Deviation of mean July temperature from normal[b] (°C)	−2.22	−0.50	+0.95	+2.34	+0.56	3.72

[a] *Salix pulchra* mean of 10 individual plants.
[b] Based on U.S. Weather Service records for 1941–1970.

In 1973, the onset of growth began earlier than in 1972 (Figure 20). However, the late blooming *Carex aquatilis* and *Dupontia fisheri* flowered later in 1973 and the final stature of *Carex* was less in 1973. Vegetation production was also less in 1973 than in 1972. The thaw season did begin earlier in 1973 than in 1972 but June and July were cooler in 1973 (Table 9).

Plant Succession

A Generalized Scheme. The scheme shown in Figure 21 is based on field observations and is thus inferential and untested. The vegetation noda are arranged in two connected sequences: one as it occurs on well-drained, fine-grained alluvium such as to be found in a floodplain of a small creek and the other on fine-grained, organic-rich, lacustrine sediments in former lake-basins. The successional changes are controlled primarily by changes in microrelief and thus drainage regimes. Only the most frequent and evident changes are shown; several possible interchanges or other sequences are omitted.

Plant colonization on stable floodplain alluvium is rapid. In a few years, an almost complete cover of species such as *Cochlearia officinalis, Stellaria laeta, Phippsia algida, Alopecurus alpinus, Poa arctica, Saxifraga cernua,* and *Bryum* develops. *Dupontia fisheri, Petasites frigidus,* and many other plants, including lichens, soon follow and stands belonging to Nodum VIII *(pioneer meadow)* result. In sites which are not dominated by snow accumulation, stabilization of sediments and consolidation of the vegetation form stands belonging to Nodum III *(mesic meadow).* These stabilized sites may become drier either by further alluvial deposition, by aeolian deposition, by raised polygon formation, or by increased drainage as local water courses deepen through thermokarsting. These drier sites will support the vegetation assemblages of Noda II and I *(heaths).*

The colonization of drained lake sediments is also rapid. The basin of Footprint Lake has become covered with highly productive vegetation within 25 yr. The present vegetation of the basin varies according to local drainage and substrate composition. It is generally representative of Noda IV, V, VI, and VII *(moist* to *wet meadows* and *pond margins*). Some vegetation seems to have changed very little since it was first colonized shortly after drainage, and it appears that once a surface has a complete cover of vegetation it seems slow to change to another type. Nevertheless, as the ice-wedge polygons form a variety of microrelief and moisture regime, the vegetation of the Footprint basin will become similar to the current IBP site. However, many decades or longer must elapse to provide the variety to be found at the IBP site. Nodum V, the *wet meadow,* is the most abundant vegetation in the Footprint basin. The annotations on the arrows in Figure 21 suggest the mechanisms necessary for change into other nodal types. The drier Nodum VI *(moist meadow)* can form when polygon troughs drain the polygon centers. Trough formation in Nodum IV can reverse the trend by producing wetter microsites. As polygonization continues, the diversity of surfaces increases. Drier polygon rims or slightly raised centers of

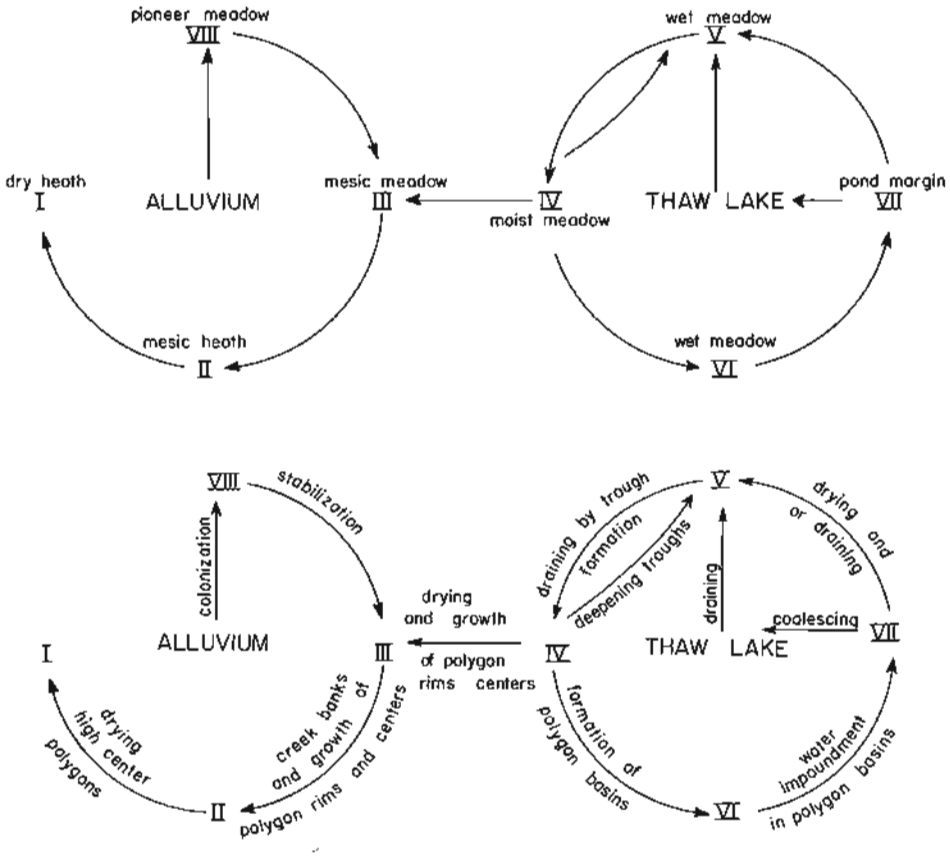


Figure 21. The principal successional trends of the vegetation noda and the principal allogenic geomorphic processes controlling these successional trends.

Nodum IV can transform to Nodum III *(mesic meadow)*. The creation of Nodum III from drained lake sediments forms a link with the alluvial succession. The formation of low polygon centers which may become wet and/or impounded can transform Nodum IV to Nodum VI *(wet Carex meadow)*. Further depression of centers and impounding of water readily produces ponds and the pond margin vegetation of Nodum VII. Some ponds may breach their impounding rims and drain while others may fill with sediments. In this manner Nodum V *(wet Dupontia meadow)* may be reformed. The cycle may also be closed by the coalescence of ponds as their margins or rims are eroded by thermokarsting, and thus large ponds and even thaw lakes may be reformed.

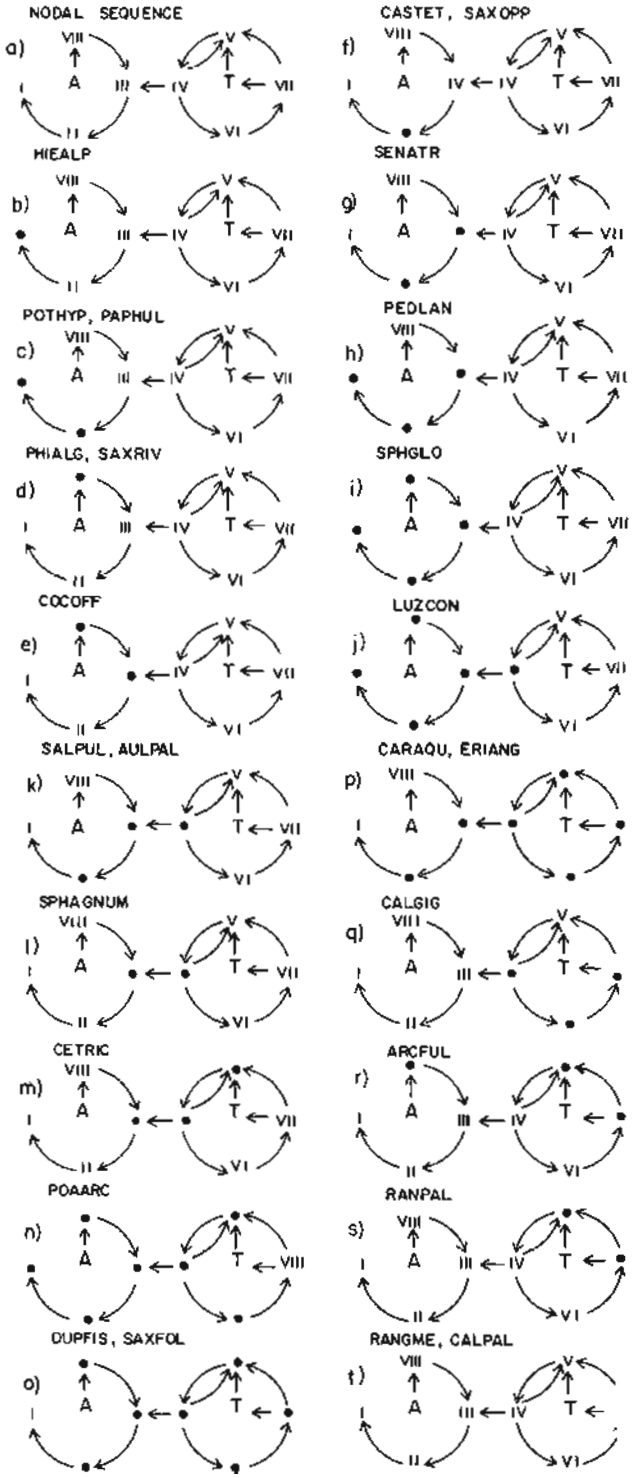
The draining of thaw lakes and the formation of extensive new alluvium in flood plains are relatively rare events in the study area. Both instances in this study are related to man's activities, but both processes can also be of natural occurrence. Several other examples of man's impact on plant succession are

available in the study area, for example, vegetation changes triggered by tracked vehicle damage and water impoundments resulting from road construction. These changes will fit into the successional scheme presented here. Catastrophic thermokarsting of any nodum would lead to either the alluvial or thaw lake starting points. The most frequent effect of moderate impact of impoundment in the IBP area is to cause a deepening of troughs through partial ice-wedge melting. In many instances this has caused drier intertrough areas (Nodum V to IV or Nodum IV to III) and wetter troughs (Nodum IV to V or Nodum V to VIII); these changes may occur within a very few years.

Patterns within the Succession. When the presence of various species is plotted on the basic successional frame formed by the nodal sequence, orderly patterns develop (Figure 22). Some species occur in only one nodum or successional stage [*Hierochloë alpinum* (Figure 22b), *Cassiope tetragona* (Figure 22f), *Caltha palustris* (Figure 22t), *Phippsia algida* (Figure 22d), *Saxifraga rivularis* (Figure 22d)]; other species occupy several noda [*Poa arctica* (Figure 22n), *Dupontia fisheri* (Figure 22o), *Saxifraga foliolosa* (Figure 22c), *Carex aquatilis* (Figure 22p), *Eriophorum angustifolium* (Figure 22p)]. The patterns of those species occurring in more than one nodum usually occur sequentially and are not interrupted or haphazard. The single exception to this generalization among the plotted species is *Arctophila fulva* (Figure 22r); it occurs in the wet noda (V and VII) and the pioneer nodum (VIII). Orderly patterns are also formed when the numbers of the various major taxa or growth forms per nodum and various production measures are plotted in the successional sequence (Figure 23). In the sequence from *pioneer meadow* (Nodum VIII) to *raised polygon center* (Nodum I), the number of most taxa increases from Nodum VIII through Nodum III to Nodum II but suddenly decreases from Nodum II to Nodum I. In the thaw-lake cycle from Nodum V through Noda IV, VI, and VII, the number of all taxa first increases from Nodum V to Nodum IV and then decreases from Nodum IV through Nodum VI to Nodum VII. Nodum VII has the lowest overall diversity.

The highest proportion of monocotyledons is found in Nodum VI and the least

Figure 22. The distribution of 26 species within the successional sequence diagram. A dot in the position of the nodal number indicates the presence of a species. Roman numerals represent the position of the vegetation noda and the letters A and T represent the starting points of alluvium and thaw lake successions. The six-letter codes for species are as follows: b, HIEALP—*Hierochloë alpina;* c, POTHYP—*Potentilla hyparctica,* PAPHUL—*Papaver hultenii;* d, PHIALG—*Phippsia algida,* SAXRIV—*Saxifraga rivularis;* e, COCOFF—*Cochlearia officinalis;* f, CASTET—*Cassiope tetragona,* SAXOPP—*Saxifraga oppositifolia;* g, SENATR—*Senecio atropurpureus;* h, PEDLAN—*Pedicularis lanata;* i, SPHGLO—*Sphaerophorus globosus;* j, LUZCON—*Luzula confusa;* k, SALPUL—*Salix pulchra,* AULPAL—*Aulacomnium plaustre;* l, SPHAGNUM—*Sphagnum* species; m, CETRIC—*Cetraria richardsonii;* n, POAARC—*Poa arctica;* o, DUPFIS—*Dupontia fisheri,* SAXFOL—*Saxifraga foliolosa;* p, CARAQU—*Carex aquatilis,* ERIANG—*Eriophorum angustifolium;* q, CALGIG—*Calliergon giganteum;* r, ARCFUL—*Arctophila fulva;* s, RANPAL—*Ranunculus pallasii;* t, RANGME—*Ranunculus gmelini,* CALPAL—*Caltha palustris.*


NODAL SEQUENCE
a)
HIEALP
b)
POTHYP, PAPHUL
c)
PHIALG, SAXRIV
d)
COCOFF
e)
SALPUL, AULPAL
k)
SPHAGNUM
l)
CETRIC
m)
POAARC
n)
DUPFIS, SAXFOL
o)
CASTET, SAXOPP
f)
SENATR
g)
PEDLAN
h)
SPHGLO
i)
LUZCON
j)
CARAQU, ERIANG
p)
CALGIG
q)
ARCFUL
r)
RANPAL
s)
RANGME, CALPAL
t)

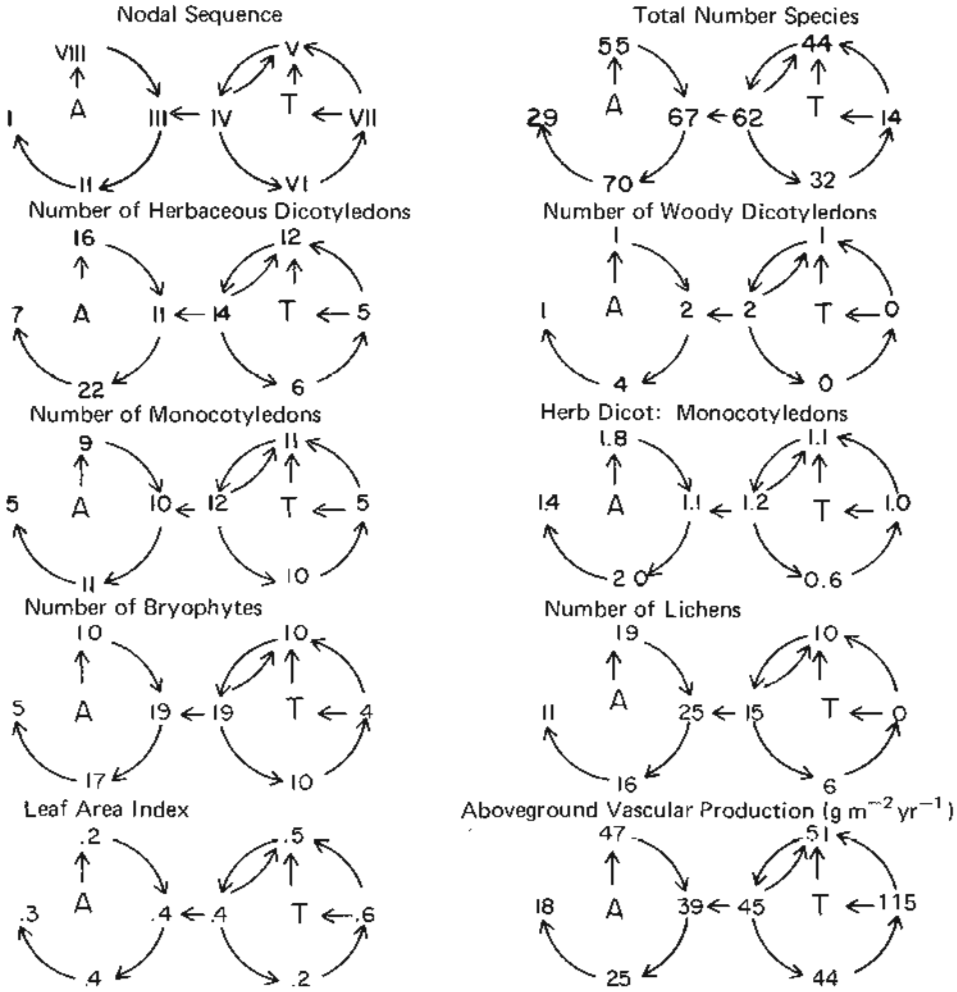


Figure 23. The distribution of the species diversity (number of species per 10 m^2) of the major life forms, leaf area index, and annual net aboveground vascular production within the successional sequence diagram. Roman numerals represent the position of the vegetation noda and the letters A and T represent the starting points of alluvium and thaw lake successions. Leaf Area Index only refers to vascular plants.

in Nodum II. The noda found on dry sites, that is those in the left half of Figure 23, have the highest proportion of dicotyledons. Nodum VIII has several typical pioneer species which are dicotyledons, for example, *Cochlearia officinalis*, *Saxifraga rivularis*, and *Stellaria humifusa*. Leaf area index has a low value of 0.2 in Nodum VIII, and this increases in a sequence to Nodum II and then decreases slightly to Nodum I. It has a high value of 0.6 in Nodum VII and this decreases around the thaw-lake cycle to Nodum IV where it has a value of 0.2.

Annual aboveground vascular production steadily decreases from a value of 47 g m^{-2} yr^{-1} in Nodum VIII to a value of 18 g m^{-2} yr^{-1} in Nodum I, and from Nodum VII through Nodum V to Nodum IV it decreases from a high of 115 g m^{-2} yr^{-1} to a low of 44 g m^{-2} yr^{-1}.

Discussion

Environmental Controls

The microrelief emerges as the principal control of the plant environment within the flat coastal tundra at Barrow. This is shown by the presence of distinct vegetation types, each of which occupies a distinct set of microrelief features. It is also shown by the grouping of points with similar microrelief within the continuum provided by the ordination of the vegetation (Figure 12). The microrelief controls the drainage and other substrate relations which in turn control distribution of the plants. This conclusion supports the earlier studies of the Barrow vegetation which emphasized the controlling influence of microrelief (Wiggins, 1951; Britton, 1966). Matveyeva et al. (1973), who have studied similar vegetation on the Western Taimyr Peninsula, have also stressed the importance of microrelief.

The interrelations of the substrate factors are very complex. The cluster diagram (Figure 10) shows them to be interdependent and the ordination (Figure 10) shows that they are not linearly related. Nevertheless, the cluster diagram shows four relatively independent complexes of substrate factors and the ordination serves to rank them in order of importance: a water complex > an aeration complex > a phosphate complex > a thaw complex (Figure 11). Three other complexes (wind, lemming activity, and soil stability) are also important. The interrelationships between these factors and their controls are summarized in Figure 24. The arrows indicate the direction of control. The complete matrix of arrows is not given and only the strongly substantiated or inferred controls are indicated. The thickness of the arrows indicates their relative importance. Thus the strong control of relief over the water complex and its subsequent control over vegetation and other substrate factors, such as aeration and soil thaw, is shown by heavy arrows. The term relief is used in Figure 24 in order to include the topographic features outside the immediate IBP site. This broadens the application of the diagram just beyond the microrelief of the polygon complex and the creek banks (Figure 9) to include raised beach ridges and lake bluffs.

In contrast to most studies of the controls of tundra vegetation, several factors, for example, wind, snow, active layer thickness, and disturbance (Sørenson, 1941; Gjaerevoll, 1956; Bliss and Cantlon, 1957; Bliss, 1963; Scott and Billings, 1964; Webber, 1971; Webber et al., 1976; Webber and May, 1977), do not emerge as major controls of the vegetation of the IBP site. This is not to say that they are unimportant; it only tells us that these factors may be relatively uniform across the site and do not contribute much to the variation of the vegetation.

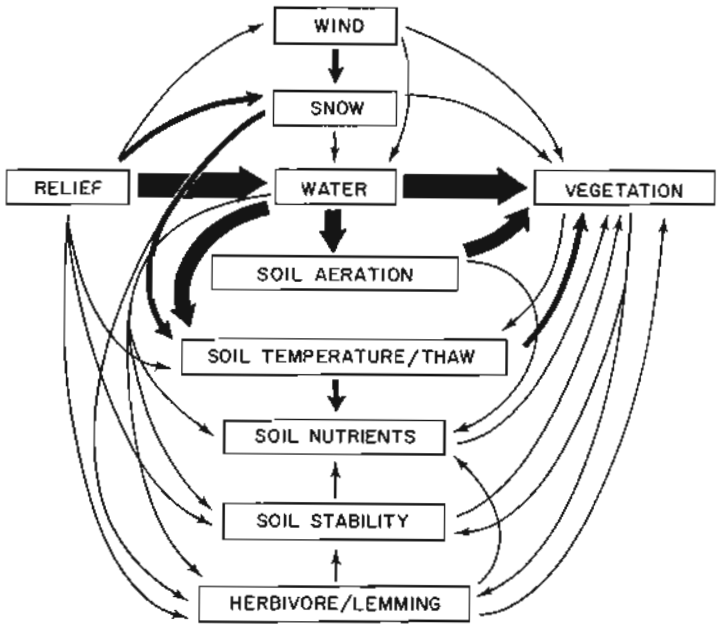


Figure 24. The principal components of the environmental complex as it controls the vegetation at Barrow, Alaska. The major controls are indicated by heavy arrows. The complex matrix of feedback arrows is not given; only substantiated or strongly inferred interactions are shown.

Wind is frequently strong enough to dry the vegetation and redistribute the snow, but these effects are seldom strong because of the moist soil, high relative humidities, and lack of great topographic relief. Nevertheless, the onset of plant growth in spring is strongly geared to the disappearance of snow.

The odor of hydrogen sulfide, used here as a measure of soil aeration, is crude and subjective. The fact that it emerged as a factor with a distinct pattern within the ordination, however, made it difficult to disregard. Gersper and Arkley's observations of soil oxygen levels across different features of microrelief agree broadly with the present observations on soil odor. The balance of oxidizing or reducing environments closely correlates with soil porosity and drainage and may be expected to have a major effect on the root environment and soil microbiology (Dennis, 1968).

Well-drained sites on mineral soils thaw deeply and are the warmest, and wet sites with organic soils have only shallow depths of thaw and are the coldest (Dennis, 1968). The thickness of the active layer and the presence of the permafrost barrier close to the surface must be a strong controller of vegetation type. However, like snowcover, it does not emerge from these studies as a major control.

Phosphate showed moderately distinct patterns with the various other factors and, because of its vital nature, it must have some effect on the vegetation, if it is present in less than adequate supply. Figure 24 shows a general nutrient box

which is under some control of thaw, water, and aeration. The deeper thaw provides a greater amount of substrate from which nutrients can be withdrawn, and sites with deeper thaw may have more microbial activity and greater nutrient release.

On the whole, the substrates of the study area are remarkably stable. Cryoturbation, which is active enough to disturb the vegetation, is limited to a few bare spots associated with frost boils, some polygon rims, and the centers of a few high-centered polygons. Surface instability is also a factor on new surfaces in creek bottoms or drained ponds. Where such unstable surfaces occur, the vegetation is very characteristic and hence instability can be a very important factor. It is closely tied to microrelief and topographic control.

It is important to note that in Figure 24 only a few arrows are shown from the vegetation to the substrate factors. Plant canopy development affects thaw depth by changing albedo and insulation regimes (Johnson, 1966; Ng and Miller, 1977). Also, soil stability is affected by the absence or presence of soil-binding vegetation roots. Similarly, lemming activity is dependent upon the availability of forage. Other feedback effects from the vegetation must exist for all factors, for example, wind and snow modification and rates of nutrient return from litter. However, these are relatively minor influences compared to the more direct effect of the substrates on the vegetation. This suggests that the principal forces affecting the vegetation are abiotic or related to animal activity.

Species, Growth Form, and Community Considerations

The wide ecological amplitude of these tundra species has been observed before at Barrow (Wiggins, 1951; Britton, 1966) and elsewhere (Oosting, 1948; Polunin, 1948; Böcher, 1954; Drury, 1962; McVean, 1969; Raup, 1969; Webber, 1971). Some wide-ranging species, for example, *Carex aquatilis*, *Pogonatum alpinum*, and *Poa arctica*, are dominant, while others, for example, *Saxifraga cernua*, *Dactylina arctica*, and *Cetraria islandica*, are subordinate (Figure 15, Table 10). It is the combination of ubiquity and dominance which, according to many botanists, has contributed to the difficulty in classifying tundra vegetation (Summerhayes and Elton, 1928; Griggs, 1934; Polunin, 1934, 1934–1935, 1948; Raup, 1941, 1951, 1953; Bruggeman and Calder, 1953; Dansereau, 1954; Savile, 1960, 1961). These botanists have also considered that physical environmental controls dominate tundra vegetation to such an extent that community patterns or clear vegetation associations do not develop and often vegetation is a bewildering array of species with little repetition over the landscape. Griggs (1934) and Savile (1960) argued that unstable surfaces with pioneer or rudimentary vegetation were largely the cause of the difficulty of dealing with tundra vegetation. This should not be the case at Barrow where most vegetation cover is complete and most surfaces are stable. The problem at Barrow originates with the flat terrain and the complexity of the patterns of the ice-wedge polygons (Brown and Johnson, 1965; Dennis, 1968). The presumed dominance of the physical environment over the vegetation composition is primarily the reason why many North American tundra botanists have relied on physical, habitat, and physiognomic descriptors

Table 10. The Percentage Cover and Percentage Frequency within the Mapped Area of the Most Abundant 40 of the 112 Sampled Taxa[a]

Rank	Taxon	Growth form	Percentage frequency	Percentage cover	Cumulative relative cover
1	*Carex aquatilis*	SG	72.09	18.78	12.91
2	*Pogonatum alpinum*	BR	76.74	14.44	22.84
3	*Bryum* spp.	BR	88.37	13.64	32.22
4	*Dicranum* spp.	BR	55.81	12.59	40.87
5	*Calliergon sarmentosum*	BR	53.49	8.72	46.86
6	*Oncophorus wahlenbergii*	BR	51.16	7.71	52.16
7	*Drepanocladus brevifolius*	BR	51.16	6.42	56.57
8	*Salix rotundifolia*	DS	44.19	6.27	60.88
9	*Poa arctica*	SG	74.42	5.29	64.52
10	*Polytrichum juniperinum*	BR	46.51	3.60	66.99
11	*Dupontia fisheri*	SF	74.42	3.58	69.45
12	*Eriophorum russeolum*	SG	72.09	3.31	71.73
13	*Eriophorum angustifolium*	SG	55.81	3.30	74.00
14	*Hylocomium alaskanum*	BR	20.93	2.80	75.92
15	*Hepaticae*	BR	58.14	2.57	77.69
16	*Saxifraga cernua*	ED	81.40	2.31	79.28
17	*Drepanocladus uncinatus*	BR	18.60	2.17	80.77
18	*Brachythecium* cf. *turgidum*	BR	41.86	2.10	82.21
19	*Salix pulchra*	DS	13.95	2.02	83.60
20	*Aulacomnium turgidum*	BR	37.21	1.85	84.87
21	*Dactylina arctica*	LI	69.77	1.84	86.13
22	*Calliergon giganteum*	BR	9.30	1.77	87.35
23	*Calamagrostis holmii*	SG	30.23	1.60	88.45
24	*Petasites frigidus*	ED	47.60	1.19	89.27
25	*Sphagnum* spp.	BR	13.95	1.11	90.03
26	*Arctagrostis latifolia*	SG	30.23	1.00	90.72
27	*Campylium stellatum*	BR	18.60	0.93	91.36
28	*Cetraria islandica*	LI	69.77	0.87	91.96
29	*Oncophorus* spp.	BR	4.65	0.86	92.55
30	*Myurella julacea*	BR	16.28	0.62	92.98
31	*Luzula confusa*	CG	37.21	0.61	93.40
32	*Ranunculus pallasii*	ED	9.30	0.55	93.78
33	*Stellaria edwardsii*	MD	58.14	0.50	94.12
34	*Peltigera aphthosa*	LI	58.14	0.49	94.46
35	*Arctophila fulva*	SM	11.63	0.47	94.78
36	*Juncus biglumis*	CG	23.26	0.41	95.06
37	*Cetraria cucullata*	LI	60.47	0.38	95.32
38	*Cassiope tetragona*	ES	6.98	0.37	95.57
39	*Distichium capillaceum*	BR	6.98	0.36	95.82
40	*Stellaria laeta*	MD	25.58	0.35	96.06
Totals for all 112 sampled taxa				145.48	100.00

[a] Percentage frequency is derived from the number of plots of occurrence of a taxon. The cover values are computed from the nodal averages and nodal areas in the vegetation map. Percentage cover values have been converted to relative cover and are accumulated in the last column. The taxa are arranged in order of their cumulative relative cover. Growth-form symbols are as in Table 2.

to name their plant communities rather than species alone (Polunin, 1934, 1934–1935, 1948; Churchill, 1955; Spetzman, 1959; Bliss, 1963; Britton, 1966; Johnson et al., 1966; Potter, 1972).

It is my opinion that tundra vegetation is no more difficult to classify or study than that of more temperate systems. This is in essential agreement with Bliss (1963) who felt that the mosaic of patterns may only appear exaggerated in low stature vegetation where there is an absence of trees. Some level of classification always seems possible after familiarization and detailed analysis. For example, Webber (1971), Barrett (1972), and Smith (1974) have made classifications of high arctic tundra vegetation. Webber (1971) used the same methods as used in this study on Baffin Island; Barrett (1972) used the more rigorous Zürich–Montpelier methods (Braun-Blanquet, 1932) on Devon Island; and Smith, who worked at Barrow on bryophyte communities, used an association analysis based on a χ^2 test (modified from Goodall, 1953).

The vegetation units or noda recognized here are rather broad and consist of several traditional associations or stand types. The *pioneer nodum* (VIII) is the most heterogeneous nodum (Figure 3). The distinct positions of the other noda in the ordination are seen as a reflection of environmental discontinuities and/or an oversampling of certain more frequent habitat types rather than as evidence for support of the association-unit hypothesis (Whittaker, 1962; Daubenmire, 1966). Because the noda are abstractions, it is not always possible to classify each new stand with confidence. However, the mapping experience has shown that the classification system works quite well within the sampled universe, but some difficulties were encountered toward the periphery. The vegetation assemblages of the polygonal ground areas of the Coastal Plain, which correspond to the universe of the IBP site and which have been described by the previous studies (Wiggins, 1951; Spetzman, 1959; Britton, 1966; Potter, 1972), fit into the present classification quite well.

The unique, nonrandom distribution of each species demonstrates that they are not haphazardly arranged, and this in itself is likely to allow for some measure of classification or division of the environmental or vegetational continuum. There is no evidence from these results to support the notion that the competitive exclusion principle is not operating at Barrow as implied for some more severe tundra situations (Savile, 1960). In fact, closely related species which would provide the best evidence for a violation of this test (Cole, 1960) have less similar distributions than unrelated species. For example, the distribution of *Luzula arctica* is more similar to that of *Potentilla hyparctica* than to *Luzula confusa*, and the distribution of *Eriophorum russeolum* is more similar to that of *Carex aquatilis* than to *Eriophorum scheuchzeri*. In a competitive exclusion context, it is unlikely that *Luzula confusa* and *Potentilla hyparctica* would be complete competitors because of their different growth forms. Even those species which do have somewhat similar distributions and aboveground form, for example, *Carex aquatilis, Dupontia fisheri,* and *Eriophorum angustifolium,* have different rooting patterns (Billings et al., 1978). The results on species distribution from this study are in close agreement with others from the same area (Wiggins, 1951; Koranda, 1954; Britton, 1966, Dennis, 1968; Smith,

1974; Rastorfer, 1978; Steere, 1978; Williams et al., 1978). The strength of the present study rests on its quantification of the response of individual species to the principal environmental controls of the IBP site proper.

Tundra is not unique with respect to the dominance of a few common species. Raunkiaer's Law of Frequency suggests that this pattern is generally universal (Kenoyer, 1927), as do other studies of dominance and diversity relations (for example, Patrick et al., 1954; Beschel and Webber, 1963; Whittaker, 1965). Nevertheless, the dominance by a few species seems particularly striking in tundra, especially because the floras are small in number of taxa. On the IBP site, 112 different taxa were sampled and of these 6 taxa make up 50% of the total plant cover, 14 make up 75%, 20 make up 85%, and 40 make up 96% (Table 10). The remaining 4% of the plant cover is provided by 72 species. On Bylot Island, N.W.T., Drury (1962) reported that 34 species comprised 85% of the plant cover, and on central Baffin Island, N.W.T., Webber (1971) found that 38 species comprised 85% of the plant cover. Both Bylot and central Baffin Island have overall floristic diversities similar to those of Barrow. However, the lower figure of 20 taxa comprising 85% of the cover at Barrow is a reflection of the low overall habitat diversity of the present study area compared to the Eastern Arctic sites.

The percentage cover values in Table 10 are means for each species obtained from nodal averages with a correction made for the areal extent of each nodum within the map. Perhaps the most striking feature of Table 10 in which the species are ranked according to their percentage cover is that although *Carex aquatilis* is dominant, the next six species are bryophytes. In fact, of the 10 most abundant species 7 are bryophytes. They comprise 58.1% of the total species cover of 100. Monocotyledons comprise 26.7%, shrubs 6.1%, forbs 5.3%, and lichens 3.8% of the remaining relative cover. In a similar analysis of some central Baffin Island vegetation, Webber (1971) found 5 of the 10 dominants to be bryophytes. Matveyeva et al. (1973) have noted that bryophytes are the dominant plants of their IBP site on the Taimyr Peninsula in the central Siberian Arctic.

The distribution of the major growth forms along the complex moisture gradient in terms of abundance and of number of species per plot in each growth form is very similar to that seen at two other quite different sites, Cape Thompson, Alaska (Johnson et al., 1966), and central Baffin Island, N.W.T. (Webber, 1971). The similarities are so strong that it is a fair assumption to consider these patterns to be universal to tundra. The patterns of growth form distribution corresponding to the redox and phosphate gradients have not been examined in any other studies. Because the growth forms are found in particular segments of the complex gradients, it appears that they provide a meaningful unit for the study of plant–environment responses in the tundra.

The observation that there is not necessarily a correspondence between growth form abundance as measured by the species index, the number of species, and the biomass of a growth form along the various gradients requires examination (Figures 15–17). The pattern for lichens is the same, that is, those segments of the gradients with the greatest number of lichen species also have the greatest species index and biomass. However, the patterns for bryophytes and monocotyledons are not the same when the distribution of these three

measures is considered. Several interpretations are possible. The first and most obvious interpretation is that the particular growth form category is invalid and does not comprise species with similar morphological and functional traits. Certainly the bryophyte category is as much phylogenetic as functional A splitting into acrocarpous mosses, pleurocarpous mosses, and leafy liverworts may provide more consistent results (see Rastorfer, 1978).

The plant growth forms recognized here are not unique to tundra (Lewis and Callaghan, 1976). No unique morphological or anatomical structures are known for tundra plants. Even the proportions of the various growth forms are unlikely to be unique although clearly certain combinations are characteristic of tundra as a whole and of specific habitats in particular (Bliss, 1962b; Tikhomirov, 1963). The absence of unique structural features should not be unexpected since it is generally agreed that the present tundra flora is young and is derived largely from preadapted more temperate forms (Savile, 1972; Billings, 1974; Löve and Löve, 1974). Perhaps the absence of specific growth forms such as annuals or trees deserves more attention.

Standing Crop, Production, and Seasonal Growth

There is a substantial number of measurements on standing crops and primary production of tundra (for example, Bliss, 1962b; Alexandrova, 1970; Webber, 1974; Wielgolaski, 1975), but there are only a few estimates of the production of large areas. Too often only the more productive communities have been measured rather than the impoverished communities which make up a large portion of the total arctic landscape (Webber, 1971). There are some measurements of unproductive sites; for example, Warren Wilson (1957) found only 3 g m^{-2} yr^{-1} in an arctic willow barren on Cornwallis Island, and Beschel (1970) estimated that the annual production of lichens on rocks may amount to only a few milligrams per square meter. The Canadian Tundra Biome program has been cognizant of this problem and each production paper in Bliss and Wielgolaski (1973) from Devon Island allowed for the areal extent of the various communities contributing to the total primary production.

The value for aboveground vascular production of 42.4 g m^{-2} yr^{-1} for the 1972 growing season obtained from the mapping estimates is a little less than the nodal mean of 48.1 and the nodal median of 50.2 (Table 7). This is an indication of the relatively few sites with low or high production, but it serves to indicate that significantly large areas of low or high production will significantly affect the productivity of the overall ecosystem. There is a general trend to agreement between measurements of live, vascular leaf area index, aboveground monocotyledon biomass, and aboveground monocotyledon production (Figure 18). Webber et al. (1976) and Dennis et al. (1978) have established a high level of correlation between vascular plant production and leaf area index of tundra. Aboveground biomass and production of vascular plants are also highly correlated in this tundra where so much of the aboveground biomass is an annual phenomenon. Woody plants, lichens, and mosses provide some departure from this generalization because they have a large fraction of aboveground perennial

tissue, but productivity for these forms with small or no root system is proportional to the biomass at the beginning of the season (Rastorfer, 1978; Williams et al., 1978). The discrepancy between moss abundance as shown by species index and biomass (Figure 17) may be explained by the greater specific weight of acrocarpous mosses compared to pleurocarpous mosses. Acrocarpous mosses are prevalent on drier sites, are erect, and provide less cover per unit weight than pleurocarpous mosses which dominate wet sites. Nevertheless, overall percentage cover and species index are fair surrogates of actual biomass or productivity. The ordination figures in which species index for various species or growth forms are plotted (Figures 15 and 17) may be interpreted in terms of relative biomass or productivity for their respective taxa.

The dominance of the site by Noda III, IV, and VI leads to the overall dominance of *Carex aquatilis* as previously indicated by Spetzman (1959). The importance of the various major growth forms has already been discussed using cover as a basis (Table 10). An estimate of the importance of these same growth forms with respect to biomass was also obtained from the mapping exercise which allowed the nodal mean biomass values to be corrected for the areal extent of each nodum (Table 11). Again, bryophytes are dominant with a mean value of 117.9 g m^{-2} or 60.8% of the total aboveground biomass. Monocotyledons form only 18.3% of the aboveground biomass with 35.5 g m^{-2}; shrubs form 5.0%, forbs 1.4%, and lichens, which are heavy in relation to their coverage, comprise 14.5%

Table 11. Percentage Cover, Relative Cover, Peak Season Aboveground Biomass, and Net Aboveground and Total Primary Production of the Principal Growth-Forms of the Terrestrial Vegetation of the IBP Site[a]

Variables	Principal growth-forms					
	Byrophytes	Monocotyledons	Woody shrubs	Herbaceous dicotyledons	Lichens	Totals
Percentage cover	84.5	38.8	9.0	7.7	5.5	145.5
Relative cover	58.1	26.7	6.1	5.3	3.8	100.0
Peak season aboveground biomass (g m^{-2})	117.9	35.5	9.7	2.7	28.1	193.9
Percentage of aboveground peak season biomass	60.8	18.3	5.0	1.4	14.5	100.0
Net production as a percentage of aboveground peak season biomass	21.3[b]	97.2	54.8	96.3	4.0[c]	—
Net aboveground production (g m^{-2} yr^{-1})	25.1	34.5	5.3	2.6	1.1	68.6
Percentage of net aboveground production	36.6	50.3	7.7	3.8	1.6	100.0
Net total production (g m^{-2} yr^{-1})	25.1	69.0	10.6	5.2	1.1	111.0
Percentage of net total production	22.6	62.1	9.6	4.7	1.0	100.0

[a] Cover and biomass values are derived from a consideration of nodal means and the areal extent of each nodum over the site map. Although it is probably an underestimate, belowground vascular production is assumed equal to that aboveground.

[b] Estimated from Rastorfer (1978).

[c] Estimated from Williams *et al.* (1978).

of the biomass. This ranking provides the same sequence as did the nodal means (Table 6), but the biomass values for bryophytes and lichens are higher for the entire map area (Table 11). This is because of the abundance of these growth forms in Nodum III *(mesic meadow)*, which occupies 41% of the map area and is thus the most extensive nodum. By estimating the percentage of peak season biomass, which represents net production of each growth form, an estimate of mean net production for the map area was obtained (Table 11). The productivity estimates for bryophytes were obtained from Rastorfer (1978) and for lichens from Williams et al. (1978). The values for the vascular plants were taken from the peak season clip harvest of 1972 by comparing the start of season biomass with annual net production. Rastorfer (1978) and Williams et al. (1978) derived their values from studies at site 2 in vegetation corresponding to Nodum IV. Using the mean biomass values of the present study, these percentage production values provide a net production value of 25.1 g m^{-2} yr^{-1} for bryophytes and 1.1 g m^{-2} for lichens. The aboveground net production of monocotyledons, shrubs, and forbs was 34.5, 5.3, and 2.6 g m^{-2} yr^{-1}, respectively, which represents an aboveground net production for vascular plants of 42.4 g m^{-2}. This value is the same as derived by slightly different means for the whole map area (Table 7). Therefore, vascular plants have greater production per unit of aboveground biomass. However, on a total end-of-season basis of, say, 750 g m^{-2} (that is, above- plus belowground) and assuming aboveground production equals that of belowground (Johnson and Kelley, 1970), the percentage would only be 11.3. The clip harvesting methods in this study estimated only 3% of the peak season herbaceous vascular material as originating from the previous year (Table 11). This agrees with Dennis and Tieszen (1972) and Tieszen (1972a) who show rather more than this and 8 to 10 g m^{-2} is recorded from site 2 (Figure 19). In the more northerly, but similar, ecosystem on Devon Island, Muc (1973) found from 4.0 to 7.1 g m^{-2} of green material at the onset of growth which represents 8.8 to 15.6% of the annual vascular production estimated to be 45.7 g m^{-2}.

The above discussion points to the importance of bryophytes in the Barrow ecosystem. Bryophytes not only comprise the largest portion of the plant cover, they also are the most productive in terms of a total perennial biomass and contribute to 36.6% of the aboveground net production and 22.6% to the total net production (Table 11). This supports Rastorfer's (1978) contention that bryophytes are an important major component in arctic tundra. Nevertheless, estimates of total production show that vascular plants contribute up to 61.8% of the aboveground or 76.4% of the above- and belowground productivity. The contribution of lichens is very low but may be important for herbivores (White et al., 1975) and nitrogen fixation (Alexander et al., 1974).

The above generalized values for the aboveground vascular production for the tundra of the IBP site are within the ranges reported by others for Barrow tundra (Thompson, 1955; Shanks in Bliss, 1962a; Pieper, 1963; Dennis, 1968; Dennis et al., 1978) and for similar ecosystems elsewhere in the Arctic (Bliss, 1956; Alexandrova, 1970; Wielgolaski, 1972, 1975; Muc, 1973; and Tikhomirov et al., 1975). There are few published values for cryptogams. However, the estimates presented here are very comparable to those for the wet sedge meadows of

Devon Island where Pakarinen and Vitt (1973) estimated a value of 30 g m^{-2} yr^{-1} for bryophytes and Richardson and Finegan (1973) estimated a value between 0.4 and 2.1 g m^{-2} yr^{-1} for lichens.

Our values for standing crop of belowground biomass and its proportion with that found aboveground at the time of peak aboveground vascular biomass are within the several published ranges. All studies of belowground biomass in tundra emphasize the tendency for small aboveground to belowground ratios (A:B) (Alexandrova, 1958, 1970; Bliss, 1962b, 1966, 1970; Mooney and Billings, 1960; Scott and Billings, 1964; Rodin and Basilevich, 1967; Dennis, 1968, 1977; Dennis and Johnson, 1970; Wielgolaski, 1972, 1975; Muc, 1973; Webber, 1974, 1977; Webber and May, 1977). It is appropriate to compare only data which deal with the same or similar vegetation [for example, Dennis (1977) for Barrow and Muc (1973) for Devon Island]. The magnitude of live rhizomes and roots reported by Dennis (1977) match very closely with those in this study. The values reported by Muc (1973) suggest that on Devon Island there is only about half the rhizome biomass but a similar amount of root biomass to that found at Barrow. Vascular aboveground production for wet meadows on Devon Island is about two-thirds that of Barrow. However, Muc (1973) reports a much higher belowground production of around four times that of aboveground. The A:B biomass ratios of Dennis and Johnson (1970), although sometime smaller, are generally similar to the present. The small values were explainable on the basis of unusually low aboveground current production. This points to the need to have either an average value from several years for aboveground production or a value representative of an average year. This need for an average value is not so critical for belowground biomass, which is a perennial system and which is more likely to be a damped system. On Devon Island, the A:B biomass ratios at peak season range from 1:6.1 to 1:13.6 and these seem, on the whole, a little larger than at Barrow. However, Muc (1973) did not include stem bases with the belowground portion. If stem bases are regarded as aboveground material the ratios at Barrow would change considerably from around 1:13.5 to around 1:5.5. This illustration emphasizes the need for further care in the use of A:B ratios and for the standardization of definitions, especially the boundary between above- and belowground in situations of aggrading substrates (Webber, 1977).

The present study did not measure belowground production at Barrow. Dennis (1977), using a regression approach, estimated that belowground production was 143 g m^{-2} yr^{-1} in 1971, which is 1.6 times greater than the aboveground vascular production. Previously, Dennis (1968) had used another indirect method of estimating belowground production, based on an estimate of decay rates. Using a decay rate of 140 g m^{-2} yr^{-1} (Douglas and Tedrow, 1959) and the assumption that the system was in steady state, he calculated on the basis of 70 g m^{-2} yr^{-1} aboveground production rate and an equal rate for belowground production. The current IBP effort has provided new estimates of total site decay. Flanagan et al. (in preparation) consider the average decay loss at Barrow to be 310 g m^{-2} yr^{-1}. If we use Dennis' (1968) method and the present estimate of average aboveground production for vascular plants and cryptogams to be 68.6 g m^{-2} yr^{-1} (Table 12), then belowground production would equal 241.4 g m^{-2} yr^{-1}

Table 12. Results of the Planimetry of the Three Available Vegetation Maps[a]

Nodum	Percentage cover		
	Map 1 (1:300) Lemming Grid (2.5 ha)	Map 2(1:300) Topographic Grid (4.3 ha)	Map 3 (1:5000) entire IBP site (110 ha)
I	0.8	0.5	3.0
II	13.0	11.2	7.2
III	30.3	22.1	41.0
IV	21.3	24.7	20.9
V	10.1	26.7	6.9
VI	23.8	14.4	14.6
VII	0.7	0.4	2.3
VIII	0	0	4.1
Mean production ($g\ m^{-2}\ yr^{-1}$)	41.1	43.0	42.4

[a] The percentage areal extent of each nodum and the mean aboveground vascular production per nodum (Table 7) were used to estimate mean overall aboveground vascular production of the area covered by each map. Map 3 is Figure 10.

or 5.7 times aboveground vascular production. Such an estimate is rather tenuous in the absence of knowledge of whether or not the system is in steady state (see Bunnell et al., 1975) and also because several reports indicate belowground production to range from equal to or half as much again as the aboveground vascular production (Wielgolaski, 1975). In this study, the more conservative estimate of Johnson and Kelley (1970) and Dennis and Johnson (1970) in which belowground production equals that aboveground has been used to estimate total production and to estimate various biomass and standing crop turnover rates.

There are only a few published turnover rates for tundra (Dennis, 1968, 1977; Dennis and Johnson, 1970; Johnson and Kelley, 1970; Bliss and Mark, 1974; Shaver and Billings, 1975; Webber and May, 1977). The previous estimates for Barrow tundra suggest that the aboveground vascular standing crop of live and dead material, including litter, takes between 4 and 5 yr to turn over (Dennis and Johnson, 1970; Johnson and Kelley, 1970). The values for this study range from 1.9 to 7.9 yr along the increasing moisture gradient with a mean of 4.5 yr. For drier alpine tundras, Bliss and Mark (1974) and Webber and May (1977) have estimated rates of turnover of aboveground standing crop to be respectively 8 and 15 yr and from 4.1 to 9.6 yr. These latter values also increased along a site moisture gradient. These above observations demonstrate the positive correlation of site moisture with aboveground turnover rate. Thus the turnover rate of the short-lived aboveground system, which is a measure of the rate of decay of surface material, is water limited. Surface decay rates are highest in the emergent Nodum VII and the pond margin vegetation (Nodum VII), and least in the much drier heaths (Noda I and II).

Dennis (1968) originally estimated turnover rates for belowground biomass to be at least 10 to 20 yr, but after further study (Dennis, 1977) he proposed 10 to 15

yr for rhizomes and 3 to 6 yr for roots. On this basis, the mean turnover time is likely to be less than 10 yr since roots represent the majority (ca. 70%) of the belowground biomass. In Table 6 belowground biomass turnover rates based on aboveground production range from 4.5 to 31.5 yr for the principal noda with a mean of 20.9 yr. If belowground production is substantially higher, then so would be the turnover rate. On the basis of a belowground production of 241.4 g m^{-2} yr^{-1} and a mean belowground biomass of 816.5 g m^{-2} for the principal noda, the turnover time or average residency for belowground structures would be 3.4 yr. Such a turnover rate seems too rapid in view of the expectation that in systems of low productivity one might expect low turnover rates of plant parts (Shaver and Billings, 1975). However, in view of the average ages of tundra plants to be obtained from the literature a mean turnover rate of 20 yr seems too slow. Sørenson (1941) found the shoots of most tundra geophytes, including *Carex aquatilis*, to live from 4 to 9 yr, and Shaver and Billings (1975) have shown that the roots of *Carex aquatilis* may live from 5 to 8 and even 10 yr, and that those of *Dupontia fisheri* may live from 4 to 6 yr, but that the roots of *Eriophorum angustifolium* are annual. Some woody roots may exceed 50 yr of age (Beschel and Webb, 1964), but these appear exceptional. At the present time the above evidence and arguments suggest that belowground production is greater than aboveground vascular production, and that a mean turnover rate of 5 to 10 yr would be reasonable. The same trends of decay can also be deduced from the distribution of belowground dead intact matter (Figure 18). Here, the driest sites, in spite of low production, have the highest concentrations and presumably accumulations of organic matter; the wet sites reverse this pattern.

The extreme values of standing crop fractions and aboveground production shown in Table 6 and Figure 18 do not always match. For example, litter and prostrate dead are higher and A:B biomass ratios are lower in the ordination than the nodal means. These discrepancies are the result of the nodal averaging which masks extremes while the ordination method is more likely to emphasize trends and extremes. Nevertheless, the nodal trends (Table 6) match those of the ordination quite closely, except perhaps for the A:B biomass ratios. In this instance, the within-nodal ranges were very large and have masked completely the pattern shown by the ordination.

Several factors contribute to the small ratios of A:B biomass in tundra. The growth form of tundra plants is the prime cause. These are predominantly hemicryptophytes or cryptophytes which have essentially annual aboveground systems and perennial, long-lived, belowground storing systems. Under experimental conditions and along gradients of increasing environmental severity, such as decreasing nutrients, low temperatures, increased wind, and high moisture levels, the A:B biomass ratio decreases in temperate and tundra plants (Scott and Billings, 1964; Whittington, 1967; Chapin, 1974; Wielgolaski, 1975). Thus the tundra environment may further reduce the size of the ratio. A study such as the present, where measurements have been made along several gradients, provides an opportunity to look for evidence of decreasing A:B ratios corresponding to gradients of environmental severity. The lowest ratios from the IBP site are from a few sites belonging to Nodum VI *(wet Carex meadow)*. These sites are not the

wettest although they have standing water in the spring. They also have low phosphate and low soil aeration. This supports the hypothesis that small A:B ratios may be a response to harsh environmental conditions and that a large belowground biomass is advantageous in nutrient-poor sites with poor aeration. The patterns of belowground biomass and the A:B biomass ratio in Figure 18 are distinctly different and clearly show the effect of the depressed aboveground peak season biomass in the few sites of Nodum VI which have low production. These sites, however, did not manifest themselves in the ordination framework depicting the distribution of production (Figure 18).

Webber and May (1977) have used identical analyses to examine the distribution of standing crop and productivity fractions on Niwot Ridge, Colorado. They found that A:B biomass ratios ranged from 1:3 to 1:25 and generally decreased along a complex moisture gradient. The smallest ratios (1:25) occurred in a moist tundra nodum and the largest ratios (1:3) in a shrub tundra nodum. The average ratio for this predominantly dry tundra is 1:10. This may be compared with the corresponding value of 1:13.5 for the Barrow tundra. The somewhat lower extremes at Barrow may well be a response to the more severe and especially wetter Barrow environment. Niwot on the average has three to four times greater aboveground net vascular production than Barrow and four to six times greater total vascular biomass. Alexandrova (1970) and Wielgolaski (1975) have noted that A:B biomass ratios tend to decrease along complex moisture gradients. This general trend is seen on Niwot Ridge but is not apparent at Barrow where the ratio first decreases and then increases (Figure 24). At the risk of pushing the results and the value of the A:B ratio too far, I submit that in general in the Arctic Coastal Plain the ratio will be found to decrease from dry, former beach ridges and lake and river bluffs to moist and wet meadows with poorer nutrient and oxygen levels and then increase again in the very wet meadows where nutrient supply is more favorable. Even on Niwot Ridge, the wettest sites show a tendency to have ratios a little larger than the less wet, moist tundra (Webber and May, 1977; Figure 1). However, the significance of the A:B biomass ratio is questionable (Dennis and Johnson, 1970; Dennis, 1977; Webber and May, 1977) and the measure has several serious weaknesses, for example: the difficulty of sampling belowground material; the uncertainties of distinguishing live from dead material; the problems of defining the actual ground level boundary; and finally, the problem associated with this relative measure which tells nothing of the absolute biomass values from which it was derived. Thus caution should be exercised against an overinterpretation of the A:B biomass ratio.

Although Muc (1972) has reported some growth to occur under snow cover on Devon Island, Tieszen (1974) has shown that plant growth does not begin at site 2 (Nodum IV) at Barrow until the snow has melted. The onset of soil thaw also matches very closely with the disappearance of snow (Brown et al., 1974). Thus, although the onset of plant growth as shown by Figure 19 coincides with the advent of nonfreezing air temperatures, the important trigger to growth is the warming of the ground. Nevertheless, over much of the IBP site, snow melt happens almost simultaneously and is closely correlated with air temperatures which are above freezing. The correspondence of growth with thawing soil

matches the very careful observations of Sørensen (1941) from Greenland. He found a noticeable lag of 3 to 4 weeks of positive mean air temperatures behind those of soil and found that plant growth was keyed to soil temperature rather than air temperature, although he acknowledged the causal effect of air temperature in the first instance. Sørensen (1941) also noted that soil thaw did not start until the snow had disappeared and he emphasized the great control of snow cover over plant life and development in the tundra. Holway and Ward (1965) have also noted the control of snow cover over plant phenology and the onset of growth.

Several studies at Barrow have noted the timing of the period of peak biomass to within the first week of August (Pieper, 1963; Dennis and Tieszen, 1972; Tieszen, 1972a). Tieszen (1972b) has shown this is also the time when there is an increase of translocation of products of photosynthesis to belowground organs and when photosynthesis is no longer positive throughout the day. Some sort of extrinsic or intrinsic timing mechanism comes into play but its nature is not known (Bunnell et al., 1975). The onset of plant growth varies from year to year (Figure 20), but the later phenophases such as the development and ripening of fruits are more synchronous. Experimental studies using snow-fences to increase snow cover and delay snow melt by up to 14 days in the Niwot Ridge alpine have also shown that the later phenophases are in close synchrony with the control plots which had no snow fences (Webber et al., 1976). Wielgolaski's (1974) data also show that the fruiting phenophases have a greater degree of synchroneity between sites than do the early phenophases. Again, some sort of timing mechanism which controls plant development and senescence is suggested.

The Barrow species seem remarkably adapted to the short growing season, as the first fruits are mature before the return of mean freezing air temperatures. The mean length of the thaw season with mean air temperatures above freezing is 87 days and the longest time needed for development was 73 days for *Pedicularis lanata* which occurs on those sites which are first to become free of snow. Pieper (1963) and Dennis (1968) made phenological observations on many of these same species in 1962, 1964, and 1965, respectively. They ranked the species in much the same phenologic sequence as the present one (Figure 22). The only remarkable difference was the very early development and flowering of *Petasites* in 1964 (Dennis, 1968). In spite of the ability of these plants to complete their sexual cycle within a short season an early frost often prevents seed set and will reduce germinability (Webber et al., 1976), and this may be quite frequent at Barrow where the frost-free period averages only 34 days (Figure 1). Late flowering species such as *Carex aquatilis* and *Dupontia fisheri* will thus be particularly vulnerable to early frost. In fact, Dennis (1968) stressed that these plants rely much more heavily on vegetative reproduction than some of the early developing species such as *Ranunculus nivalis*.

Temperature has a strong effect on plant growth and production. The onset and end of growth, the rate of phenological progression, the stature of plants, and the amount of willow stem elongation are all positively correlated with air temperatures. However, production as measured by the clip-harvesting showed

no clear correlation with the temperature of the current year or even, as Sørensen (1941) has noted, the previous year.

Plant Succession

Plant colonization of new surfaces or of disturbed surfaces and subsequent plant succession is an important topic in the Arctic, especially with the prospect of increasing disturbance and development of arctic resources. Unfortunately, the problem is complex and really no better understood at the present time than when Churchill and Hanson (1958) wrote their comprehensive review of tundra succession. Too often, as in this present report, successional patterns are interpreted by inference without either an adequate set of observations through time or dated surfaces (Drury and Nisbet, 1973; for tundra examples, see Oosting, 1956; Polunin, 1935; Billings and Mooney, 1959; Spetzman, 1959; Marr, 1969; Johnson and Tieszen, 1973). The scheme which has been adapted from Britton's (1966) observations to suit the present classification is oversimplified and may apply only to the immediate study area and no doubt will be revised.

The present observations on the rapid colonization of Footprint Lake concur with others at Barrow. For example, Carson (1968) observed drained lake strands to revegetate in 10 to 20 yr, and Britton (1966) has suggested that only a few decades are necessary to produce patterned ground and sorting of populations to create vegetation similar to surrounding, much older, former lake basins.

The entire successional scheme presented here emphasizes the dominance of the microrelief and geomorphic processes on the control of vegetation composition. The observation that the population of drained lake surfaces varies by species according to local microrelief drainage conditions and substrate composition and the fact that some of the resulting vegetation may be slow to change to another type suggests that Muller's (1952) concept of *Autosuccession* may apply in some situations. This concept, which was developed from tundra observations, allows for succession in which there are no intermediate stages so that the final stable self-perpetuating plant assemblage has a similar composition to that of the pioneer stand. However, it may be too soon to judge the stability of the Footprint Lake sediments since the lifespan of many of the individuals of a species may be close to 10 yr (Sørensen, 1941; Shaver and Billings, 1975). Autosuccession implies that competition between species and ensuing integration of the plant community is minimal and that environmental controls are dominant. In such a succession, *autogenic* (plant) controls are secondary to *allogenic* (environmental) controls (see Tansley, 1935). Dansereau (1954) has commented that in the Arctic, allogenic controls override autogenic controls in the determination of vegetation composition. Further evidence that environmental controls are predominant over plant controls is indicated by the rapid response of vegetation to even subtle changes in substrate conditions. For example, natural or man-induced nondestructive thermokarsting and road impoundments create changes in vegetation composition in a few seasons. However, as Tansley (1935) emphasized, both allogenic and autogenic controls

can act simultaneously and are not mutually exclusive. The closed nature of the vegetation at Barrow and the accumulation of organic material containing nutrients attest to at least a measure of control of the plants themselves over the environment. From time to time, *biogenic* (principally animal) controls (Tansley, 1935; Dansereau, 1957, 1974) are also striking; lemmings provide a documented example of such a control (Thompson, 1955; Dennis, 1968). Catastrophic changes are not regarded as part of succession. They are simply means of providing a new surface for succession (Tansley, 1935). Massive thermokarsting would be in this latter category.

The basic frame of the successional scheme presented here can be viewed as an ordination in which the various pathways are complex gradients. Time is one of the components of these gradients, but it is not a constant from step to step. The rates of change are extremely variable. On one hand, there are the rapid processes such as colonization of new, stable surfaces and responses to subtle changes of the substrate and also to fluctuating lemming pressures. These changes may all be clearly visible from between one to several years. On the other hand, however, there is an apparent steady state over most of the landscape and apart from normal, small, year-to-year fluctuations, the vegetation seems to have been unchanged for decades and even longer. Even many of the cryoturbating surfaces, such as frost boils, appear to have been almost indefinitely in their present state. It is generally thought that it has been several thousand years since the site was last occupied by a thaw lake (Brown, 1965) but the age of the site does not equate to surface stability, especially in the Arctic. Nevertheless, the ice-wedge polygons might be from 500 to 600 yr in age (Leffingwell, 1919; Lachenbruch, 1962), and the large accumulations of organic matter, which are frequently 100 to 500 times that of a liberal estimate of belowground annual production, suggest that several generations of tundra individuals have occurred. Therefore, as a working hypothesis, most of the Barrow vegetation is considered to be in a steady state. There is, however, little strong evidence for this steady state concept and the testing of this hypothesis must wait until the present permanent plots can be reexamined.

The present successional scheme, which is cyclic, precludes the identification of one climax type for the area because any one of the stable mesic stages might qualify as a climax. Both the *polyclimax* (Tansley, 1935) and the *climax pattern* (Whittaker, 1953) concepts would fit this scheme. The latter conforms best from a theoretical point of view because of the continuous nature of the vegetation along the various gradients. However, from a pragmatic viewpoint, the *polyclimax* concept is best. This allows for a practical application of the present nodal concept and accommodates the distinct pattern of habitats provided by the icewedge polygon complex. Thus any mature nodum is a topoedaphic climax (*sensu* Marr, 1961).

The orderly progression of species, number of species per plot, and various productivity and standing crop measures within the successional scheme give it a sense of credibility. However, the scheme is more a moisture gradient sequence than a time-controlled sequence and may remain so after testing. Therefore, at this time it is sensible to refrain from trying to interpret species diversity and

productivity trends in terms of successional sequences. The literature for temperate vegetation conflicts sufficiently (Whittaker, 1965; Pielou, 1966; Loucks, 1970) without attempting to test these data for generalizations such as those of Margalef (1968) and Odum (1969).

Representativeness

The earlier studies of the program were heavily process oriented and had to be based on the study of a few species (*Carex aquatilis, Dupontia fisheri, Eriophorum angustifolium, Pogonatum alpinum, Dicranum fuscescens,* and *Peltigera aphthosa*) at sites 1 and 2 (Miller and Tieszen, 1972; Tieszen, 1972a, 1972b; Collins and Oechel, 1973; Allessio and Tieszen, 1974; Oechel and Collins, 1974; Coyne and Kelley, 1975; Stoner and Miller, 1975; Billings et al., 1977). Later attention was turned to a greater diversity of habitats and some additional species (Alexander and Schell, 1973; MacLean, 1974; Miller and Laursen, 1974; Rastorfer, 1978; Williams et al., 1978). My assessment of the representativeness shows that indeed the experimental plots and species which underwent intensive examination were representative of the IBP site at Barrow.

The map records the distribution of landform assemblages and their most abundant nodal vegetation type. This can be misleading because the abundant vegetation type may occupy as little as 20% of the landform unit and five other noda might also be present in more or less equal amounts. In other words, is the map useful as a generalization of the distribution of the noda and as a means of estimating the primary production of the entire site? In an attempt to assess this problem, a comparative analysis was made of the nodal composition of some large scale maps which covered small areas and which mapped individual polygons and polygon parts. Two maps (1:300) were made of areas of site 4, which is the most complex and therefore problematical area to map at a smaller scale. One map, the Lemming Grid, was 2.5 ha (158 × 158 m) in area. The other map, the Topographic Grid, because it was the site of detailed vegetation, microrelief, and soil studies (Walker, 1977), was 4.3 ha (390 × 110 m) in area. The Lemming Grid is typical of the part of site 4 which is coded as Nodum III in the 1:5000 map, while the Topographic Grid ranges across several landform assemblages each dominated in turn by the major noda. The planimetric analyses of all three vegetation maps are provided in Table 12. The prevalance of Nodum III seen in the Lemming Grid and the more or less equal overall presence of Noda III, IV, and V in the Topographic Grid match with the information for the 1:5000 map. Apart from the absence of Nodum VIII in the two large scale maps, the relative representation of each nodal type is similar in all three maps. Also the mean aboveground production of each map calculated from the mean nodal production and the map area dominated by a nodum are very similar. The slightly higher mean productivity of the Topographic Grid is explainable on the basis of a higher occurrence of Nodum V in the Topographic Grids than in the other areas. Nodum V has a higher productivity than Noda III and IV (Tables 6 and 7). This mapping exercise indicates that the information provided for the overall IBP site by the 1:5000 map (Fig. 10) is both usable and representative with regard to the distribution of noda.

The 43 plots used for the ordination, production, and standing crop studies were selected to represent the overall range of undisturbed vegetation of the IBP site. These plots contained 112 taxa of which 55 were vascular plants, 28 were bryophytes, and 29 were lichens. In the entire Barrow region, the flora has been estimated at 295 taxa of which 125 are vascular plants, 95 are bryophytes, and 75 are lichens (Murray and Murray, 1978). Thus, of the total available flora, only 38% of the taxa were encountered and this comprised 44% of the available vascular plants, 29% of the available bryophytes, and 39% of the available lichens.

Such a low representation of the regional taxa by the sampled plots is primarily a result of the low diversity of the IBP sites compared to the whole Barrow region which contains habitats such as beaches, salt marshes, and extensive well-drained ridges which do not occur within the IBP area. Two other factors contribute to the low representation. These are the small number and size of the plots and my level of taxonomic competence. Undoubtedly, more and larger plots would have encountered additional species, but the dominance diversity curve plotted from the data in Table 10 and for the remaining 72 species makes a strong lognormal curve with a long asymptotic upper part, a good indication of a thorough sampling of an available universe (Patrick et al., 1954; Webber, 1971). I am experienced with the arctic vascular flora although less so with the cryptograms. Only those bryophytes and lichens which I felt we could recognize with certainty were documented. Several lichens and many mosses which occurred in the sampled quadrats were ignored. No attempt was made to collect exhaustively every unrecognized scrap or strand for later determination. Smith (1974) and Rastorfer (1978) have shown how many species of bryophytes can be added within the IBP site through meticulous testing of small sods of bryophytes. In conclusion, the 43 sampled plots do represent the IBP site with regard to the vascular species, but they were undersampled for cryptogams. The studies of Smith (1974) and Rastorfer (1978) make up for some of this deficiency.

The selection process of sites, species, and growth forms by the scientists has a natural tendency to ensure that the area is represented. This is because only those units which are sufficiently extensive or abundant to allow for adequate replication and control are selected. It is these abundant and extensive units which not only characterize the area but also provide the best clues to the understanding of the adaptation and functions of the regional ecosystem.

The majority of primary production process studies were made at sites 1 and 2. Sites 1 and 2 are located on landscape units dominated by Nodum IV *(moist Carex meadow)* which occupies an estimated 21% of the region (Table 7). Although Nodum IV is not as abundant as Nodum III, it offers larger, more uniform areas than Nodum III *(mesic meadow)*, which is often restricted to hummocky polygon rims and centers (Table 1). Nodum IV also offers a much more average aspect of the total vegetation in terms of species composition (Table 2, Figure 23), position on the major gradients (Table 5, Figure 13), and productivity (Table 6). Thus, sites 1 and 2, especially site 2, which is farther from vehicle and other disturbances, are well suited as locations for making detailed physiological experiments. Site 4 was selected to provide a greater diversity of

habitats and plant life than that provided by sites 1 and 2. The Topographic Grid covers much of site 4 and it contains all the noda except the *pioneer meadow* (Nodum VIII). Site 4 is a complex of ice-wedge polygons of all denominations ranging from incipient through flat center and low center to high-center types. Thus, site 4 provides a high degree of diversity and its study ensured representation of the area. The lack of Nodum VIII *(pioneer meadow)* is not considered critical.

The most intensively studied species were the monocotyledons *Carex aquatilis*, *Dupontia fisheri*, and *Eriophorum angustifolium* (for example, Tieszen, 1972a and 1972b; Allessio and Tieszen, 1974; Chapin and Bloom, 1976; Billings et al., 1978; Stoner et al., 1978). This decision seems fair since monocotyledons are the most important vascular plants of the region and *Carex aquatilis* is the most abundant species (Table 10). *Poa arctica*, which is the second most important monocotyledon, has not been studied so intensively as the other monocotyledons. If abundance is an important criterion for study, *Poa* should have been given preference over *Dupontia* as a tundra graminoid, especially as it is much more wide ranging. However, *Dupontia* is a uniquely arctic genus and this alone would be sufficient justification for its inclusion. The second most abundant vascular plant, according to Table 10, is *Salix rotundifolia*, which has been largely neglected. The principal woody plant to have been studied in physiological terms is the less abundant *Salix pulchra* (Stoner and Miller, 1975). The more massive stems and leaves of *Salix pulchra* compared to those of *Salix rotundifolia* may have been the reason for its selection. Herbaceous dicotyledons were somewhat neglected as experimental organisms. Some work was done with *Petasites frigidus* and *Potentilla hyparctica*. While *Petasites* is fairly frequent throughout the study area, *Potentilla* is restricted to the dry, slightly unstable surfaces of Nodum I *(dry Luzula heath)*. This latter point in itself may be reason enough for study. However, a better herbaceous dicotyledon for intensive study, at least on the basis of high frequency and abundance, would have been *Saxifraga cernua*. The principal bryophytes which were studied were *Pogonatum alpinum*, *Dicranum elongatum*, *Dicranum fuscescens*, and *Calliergon sarmentosum* (Collins and Oechel, 1973; Oechel and Collins, 1974). All four species are excellent choices as they together comprise 25% of the total relative cover of all taxa sampled by the 43 extensive plots (Table 10) and also they range across the complex moisture gradient with *Pogonatum* prevalent on dry sites, the *Dicranum* spp. on mesic sites, and *Calliergon* on wet sites. The principal lichens to be examined were *Dactylina arctica*, *Cetraria richardsonii* (Williams et al., 1978), and *Peltigera aphthosa* (Alexander and Schell, 1973). *Dactylina* is the most ubiquitous and abundant lichen on the IBP site. *Cetraria richardsonii* and *Peltigera aphthosa*, although occasional, are never abundant. *Cetraria* is an important arctic genus, but it would have been better represented by *Cetraria islandica*, which has a more typical lichen behavior. Both *Cetraria richardsonii* and *Peltigera aphthosa* occur in quite wet sites which is at odds with the distribution of the majority of tundra lichens (Table 2). *Cetraria richardsonii* does, however, have a large, strong thallus and *Peltigera* is able to fix nitrogen, and these characteristics may have played a part in their selection.

Summary and Conclusions

1. The site is characteristic of the seaward areas of the Coastal Plain physiographic province of the Alaskan Arctic Slope. It has a cool, moist climate and it is flat, poorly drained, and underlain by permafrost. The vegetation changes character every few meters in concert with the microrelief of ice-wedge polygon complexes.

2. Eight broad plant communities or noda were recognized for the study area on the basis of species composition: Nodum I, *dry Luzula heath;* Nodum II, *mesic Salix heath;* Nodum III, *mesic Carex–Poa meadow;* Nodum IV, *moist Carex–Oncophorus meadow;* Nodum V, *wet Dupontia meadow;* Nodum VI, *wet Carex–Eriophorum meadow;* Nodum VII, *Arctophila pond margin;* and Nodum VIII, *Cochlearia pioneer meadow*. The noda permit the classification of experimental plots and also the construction of a vegetation map of the IBP area. The map permitted an areal estimate to be made of the extent of each nodum and an estimate of the overall aboveground production.

3. The axes of a three-dimensional indirect stand ordination correlated with substrate complexes relating to moisture, aeration, and phosphate. The environmental framework provided by the axes of the ordination can be used to describe the distribution of species, growth forms, noda, various standing crop fractions and ratios, and production in terms of these gradients. Other environmental controls were identified; among these were wind, snow cover, temperature, depth of active layer, substrate stability, and the effects of lemming grazing. The interrelation of the environmental variables is complex but they are all initially controlled by the microrelief. Thus, within the climatic and historic setting of the region, it is the microrelief which determines the character and performance of the vegetation and its components.

4. The undisturbed vegetation cover of the site is complete and dominated by bryophytes and monocotyledons. Bryophytes form 58% of the cover, monocotyledons 27%, shrubs 6%, forbs 5%, and lichens 4%. The most abundant species is *Carex aquatilis,* which forms 13% of the cover. Six species form 50% of the total cover, 40 species form 96%, and the remaining 70 of the 112 species recorded form only 4% of the cover. The dominant species are wide ranging along the principal environmental gradients and occur in nearly all noda. Nevertheless, each species has a unique distribution and characteristic location within the ordination. Ten plant growth forms were recognized and each of these has a characteristic distribution.

5. The nodal means of aboveground net production of vascular plants ranged from 18.1 to 118.5 g m^{-2} yr^{-1}. On the basis of overall decay rates and longevity of belowground structures, the belowground production may be up to five to seven times higher than that aboveground. The mean nodal standing crop of belowground biomass ranges from 153 to 1305 g m^{-2} with a mean value of 734 g m^{-2}. Aboveground vascular production increases along the complex moisture gradient, but the ratio of aboveground to belowground biomass does not show such a simple pattern. The latter is lowest in wet anaerobic sites with low levels of soluble phosphate. It is higher in dry, well-aerated sites, and wet, phosphate high sites. Various turnover rates of above- and belowground standing crop

fractions show that decay rates increase with increasing site and soil moisture. The diversity or number of species per vegetation plot is highest on dry to mesic sites and low on very dry sites and on very wet sites. The first signs of plant growth occur soon after snowmelt. Plants can complete the majority of the production in 60 days and can produce seeds within 75 days. Although the mean length of the thaw season is 87 days, the frost-free season only averages 34 days. This emphasizes the importance of vegetative propagation and the perennial habit in tundra plants.

6. Colonization of new or disturbed surfaces takes place rapidly and a complete cover of vegetation can be produced in 20 yr. Physical rather than plant controls dominate the Barrow vegetation, and the principal noda appear to be able to persist in the landscape for long periods until changed by some physical process.

7. Several topics have emerged from this study as prime targets for future research on the producer component of the Barrow ecosystem. The principal topics in no special sequence are: plant succession including competition, assessment and study of tundra growth forms, production of bryophytes and lichens, production of the belowground system, and reproductive aspects of phenology.

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