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6

The Vegetation: Pattern and Succession

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INTRODUCTION

This chapter analyzes paths by which the environment acts upon tundra plants and interdependence between environmental factors and plant growth form characteristics (Figure 6-1). The analysis emphasizes the distinguishing characteristics and the environmental distributions of some of the principal growth forms recognized for tundra regions by Webber (1978) (Figure 6-2).

Although selection acts on whole individuals, growth form characteristics follow environmental gradients (Mooney et al. 1974) somewhat independently of each other. The objectives of this chapter are to identify the patterns of vegetation and plant growth forms in the coastal tundra at Barrow, the principal factors controlling these patterns, and the paths of influence between the major environmental controls and the plant growth forms which lead to the patterns of vegetation observed in the field. The major pathways of plant succession and the effect of natural and other perturbations are also examined.

To approach these objectives, the distribution of species, growth forms, and plant characteristics was determined along environmental gradients in the field, and the distribution of plant characteristics along environmental gradients was predicted from the physical and physiological information given in preceding chapters. The field distribution can be regarded as the realized niche, the predicted distribution as an indication of the fundamental niche (Hutchinson 1959).

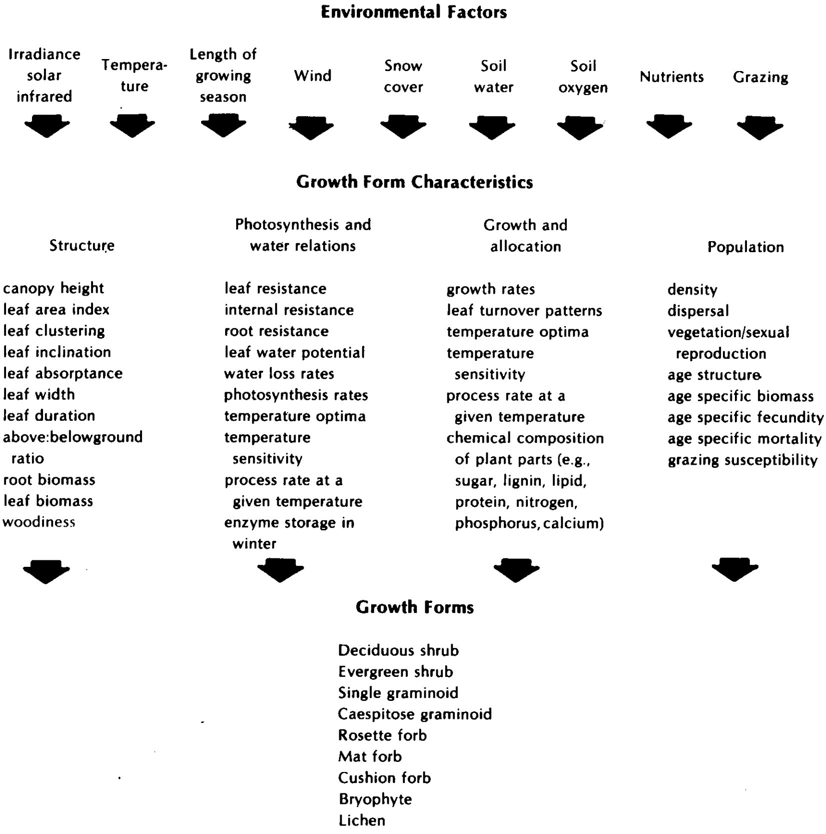


FIGURE 6-1. *The principal environmental factors, plant growth form characteristics, and plant growth forms in the coastal tundra at Barrow.*

TOPOGRAPHIC VARIATION AND VEGETATION PATTERNS IN THE COASTAL TUNDRA

Topographic and Environmental Variations

Topographic variation in the coastal tundra at Barrow causes variation in the environmental factors which control the growth and distribution of different plant species and growth forms (Table 6-1). The controlling factors can be indicated by the techniques of factor analysis or ordination (Whittaker 1967). The phytosociological gradients formed by indirect ordinations are interpreted as complex environmental gradients which represent the probable major controlling factors. Using these techniques, 9 of a total of 17 measured environmental factors were sig-

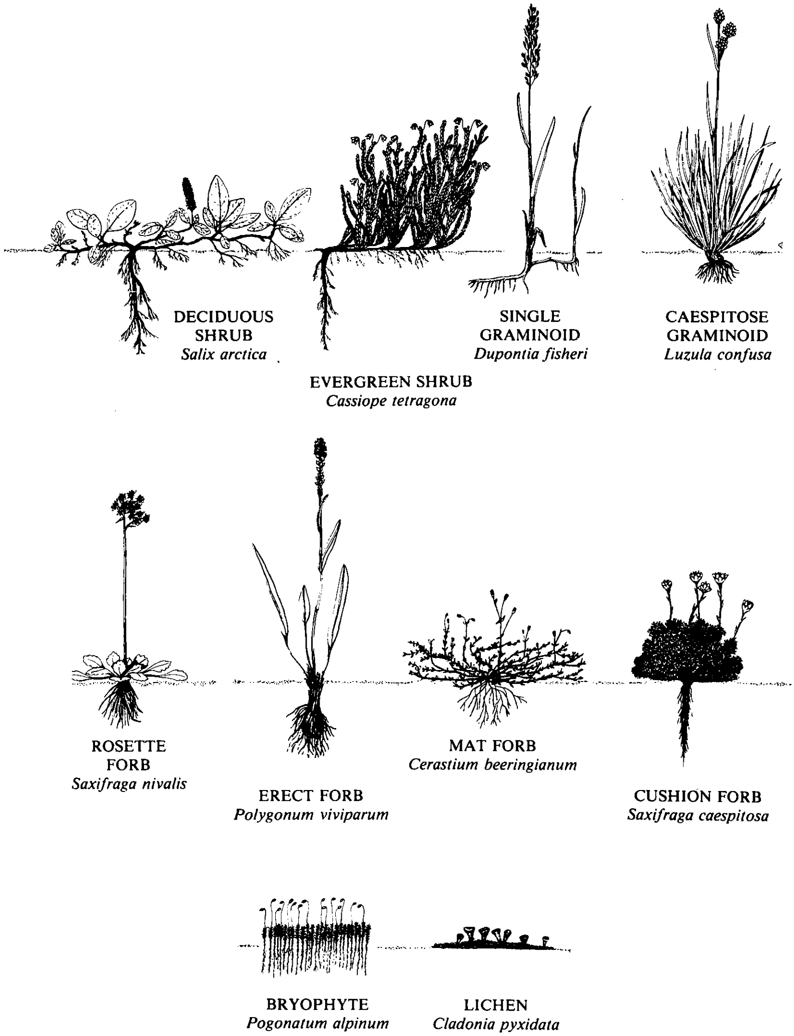


FIGURE 6-2. *Examples of the ten plant growth forms. (After Webber 1978.)*

nificantly correlated with the growth and distribution of different plant species and growth forms. The principal controlling factors were soil moisture, soil anaerobicity (indicated by soil odor of hydrogen sulfide), soluble phosphate in the soil and, to a lesser extent, snow cover.

Sampling sites were classified in terms of topography, hydrology and soil morphology. Samples were taken from six microtopographic units: ponds, meadows, polygon troughs, tops of high-centered polygons

TABLE 6-1. *Site Factors for Eight Vegetation Types Within the Biome Site at Barrow*

Site factor	Vegetation type							
	Luzula heath I (1)	*Salix* heath II (5)	*Carex–Poa* meadow III (11)	*Carex–Oncophorus* meadow IV (6)	*Dupontia* meadow V (6)	*Carex–Eriophorum* meadow VI (8)	*Arctophila* pond margin VII (2)	*Cochlearia* meadow VIII (4)
Snow depth (cm), 6 June 1973	0	4	21	29	43	36	28	86
Snow-free date	Before 1 June	13 June	23 June	23 June	30 June	20 June	13 June	12 July
Soil moisture (g cm^{-3}), 29 July 1973	0.31	0.45	0.97	0.92	0.96	0.80	0.90	0.38
Thaw depth (cm), 17 Aug 1973	37	54	36	32	32	32	37	76
Sand (g g^{-1} mineral soil)	0.13	0.34	0.28	0.14	0.09	0.29	0.05	0.75
Surface organic matter (kgdw m^{-2})	4.4	3.0	13.0	23.6	17.1	27.3	2.0	0.6
Surface organic matter thickness (cm)	4	4	7	12	10	18	2	1
Bulk density (g cm^{-3})	0.40	0.70	0.53	0.32	0.32	0.21	0.18	0.91
Soluble phosphate (g m^{-2} 10 cm^{-1} depth)*	0.62	1.51	0.98	0.32	1.91	0.09	0.74	0.55
Odor of hydrogen sulfide on 17 Aug 1973 (arbitrary scale: 0 = no odor)	0	0.4	0.3	2.2	1.7	17	2.0	0
Soil pH†	3.9	5.3	4.2	4.1	4.4	4.2	4.5	5.1

Note: Values are means from the plots within each type. The number of stands per type is given in parentheses.

*Water extract. Based on two samples per type except for I, in which only one sample was measured.

†Saturated water slurry.

Source: Webber (1978).

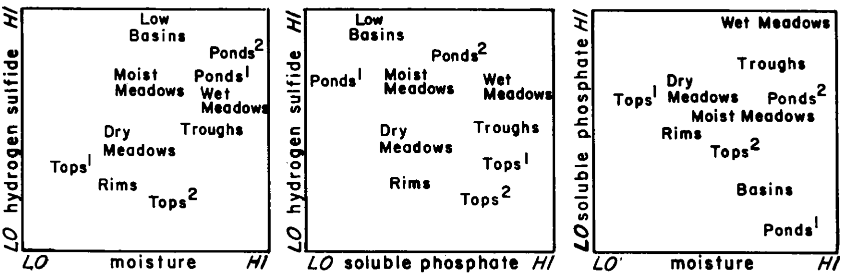


FIGURE 6-3. *The distribution of microtopographic units within the three principal axes of the ordination. The axes are soil moisture, soil odor of hydrogen sulfide, and soluble soil phosphate. Low basins are the centers of low-centered polygons, Tops^1 are the centers of high-centered polygons with little or no peat, Tops^2 are the centers of high-centered polygons with thick peat, Ponds^1 are those with no significant flow of water, and Ponds^2 are those with flowing water. (After Webber 1978.)*

and rims and basins of low-centered polygons. Two categories of ponds—those with and without flowing water—and three types of meadows—dry, moist and wet—were distinguished. Two categories of polygon tops—those with little or no peat at the surface and those with thick surface peat—were distinguished.

The different microtopographic units can be plotted within the axes of the indirect ordination (Figure 6-3). The sequence of units along the soil moisture gradient from low moisture to high is: tops of high-centered polygons with shallow soil, polygon rims, dry meadows, moist meadows, basins of low-centered polygons, tops of high-centered polygons with thick peat, polygon troughs, and wet meadows. The sequence along a gradient of soil hydrogen sulfide from low to high is: tops with thick peat, rims, tops with shallow soil, dry meadows, troughs, wet meadows, moist meadows and basins. The sequence along a gradient of soil soluble phosphate from low to high is: ponds with no flow, basins, dry meadows, moist meadows, rims, tops, troughs, and wet meadows. Basins of low-centered polygons and polygon troughs have the greatest snow accumulation and are the last microtopographic units to be free of snow, while polygon rims and tops of high-centered polygons have only a thin snow cover and are first to be snow-free. The duration of snow cover affects the length of the growing season, which varied from 30 to 42 days in 1973 (Table 6-1).

These observations coincide with the conclusions of Wiggins (1951) and Britton (1957) who emphasized the control by the microrelief of the substrate conditions, which in turn control the distribution of plants. In contrast to the results of most tundra ordinations (e.g. Webber 1971, Webber et al. 1976) and other tundra studies (Gjaerevoll 1956, Bliss 1963, Scott and Billings 1964), snow cover does not emerge as a major controlling factor from these analyses. The variations in microrelief among most of the sampled locations are insufficient to produce a pronounced variation in snow cover. However, where ravines, creek banks, beach ridges and snow fences occur, snow cover becomes an important factor influencing vegetation distribution.

Vegetation Turnover Patterns

As discussed in Chapter 1 (Table 1-4), eight major vegetation types or noda were distinguished in the vegetation of the coastal tundra at Barrow. Most species occur in more than one vegetation type, but the types are distinguished by the presence of certain indicator species and the consistent importance of other species. Each vegetation type has a reasonably distinct standing crop composition at the period of peak aboveground biomass (Table 3-2). The *Cochlearia* meadow is a rudimentary vegetation restricted to recent alluvium and disturbed sites; it is therefore not included in the discussion.

Each vegetation type has a unique distribution within the three axes of the ordination (Figure 6-4). The vegetation types are numbered from *Luzula* heaths to *Arctophila* pond margins, following the primary controlling gradient of increasing soil moisture which is associated with increasing snow cover. Along a gradient of increasing hydrogen sulfide, the sequence of vegetation types is from *Luzula* heath, *Salix* heath, and *Carex–Poa* meadow, all found on well-drained sites, to *Carex* and *Dupontia* meadows, *Arctophila* pond margin, and *Carex–Oncophorus* meadow, all found on poorly drained sites with still or stagnant water. Along

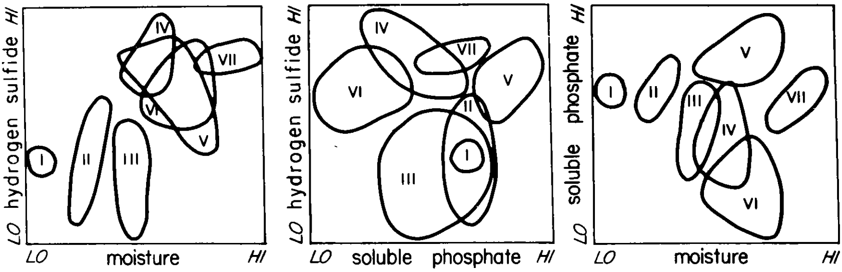


FIGURE 6-4. *The distribution of seven mature vegetation types within the ordination. I)* Luzula *heath, II)* Salix *heath, III)* Carex–Poa *meadow, IV)* Carex–Oncophorus *meadow, V)* Dupontia *meadow, VI)* Carex–Eriophorum *meadow, VII)* Arctophila *pond margin. (From Webber 1978.)*

TABLE 6-2 *Above- and Belowground Turnover Rates for the Eight Vegetation Types Based on Data of Tables 3-1 and 3-2*

	Vegetation type							
Variables	*Luzula* heath I	*Salix* heath II	*Carex–Poa* meadow III	*Carex–Oncophorus* meadow IV	*Dupontia* meadow V	*Carex–Eriophorum* meadow VI	*Arctophila* pond margin VII	*Cochlearia* meadow VIII
Vascular plants								
Aboveground biomass								
Graminoids	0.99	0.97	0.91	0.99	0.97	0.98	0.96	0.99
Forbs	0.96	0.96	0.89	0.91	0.94	0.89	0.97	0.97
Woody dicotyledons	0.83	0.53	0.33	0.46	0.50	a	a	a
Vascular biomass	0.94	0.63	0.62	0.95	0.96	0.98	0.97	0.99
Standing dead	0.32	0.77	1.26	1.27	0.99	1.01	3.23	1.46
Litter and prostrate dead	0.44	0.20	0.32	0.67	0.68	0.94	1.80	0.56
Aboveground dead	0.18	0.16	0.26	0.44	0.40	0.49	0.16	0.40
All aboveground matter	0.15	0.13	0.18	0.30	0.28	0.33	0.53	0.30
Belowground biomass	0.10	0.10	0.14	0.14	0.17	0.13	0.20	0.33
Mosses								
Green	0.23	0.23	0.23	0.23	0.23	0.23	0.23	0.23

Note: Turnover rates are in units of g g^{-1} yr^{-1}. Turnover rates were calculated assuming steady state conditions and no respiration losses.
a—Absent.

the gradient of increasing soluble phosphate, the sequence of vegetation types runs from *Carex-Eriophorum* meadow, *Carex-Oncophorus* meadow and *Carex-Poa* meadow to the heaths, *Arctophila* pond margin and *Dupontia* meadow. The three vegetation types associated with the lowest phosphate concentrations occur on sites that receive no drainage water or influx of minerals, while the types associated with higher concentrations are found on mineral soils on sites receiving an influx of drainage water.

Turnover rates (grams incorporated annually per gram standing crop) in a particular vegetation type depend on the species or growth forms present (Table 6-2). Turnover rates for aboveground biomass are about 1.0 yr^{-1} for those vegetation types that are mainly composed of graminoids and forbs. In the *Salix* heath and *Carex-Poa* meadow, woody dicotyledons are common and biomass turnover rates are about 0.6 yr^{-1}. The woody dicotyledons in these vegetation types have low turnover rates; several individuals of *Salix pulchra* were at least 20 years old, as determined by counts of terminal bud scars on the branches.

Turnover rates of standing dead range from 0.3 yr^{-1} in the *Luzula* heath to 3.2 yr^{-1} in the *Arctophila* pond margin. The turnover rates for standing dead in the *Carex-Oncophorus, Dupontia* and *Carex-Eriophorum* meadows are 1.0 yr^{-1} to 1.3 yr^{-1}. The turnover rate of standing dead is affected by the rates at which standing dead is blown or washed away from the site or pressed prostrate by snow and rain.

Turnover rates of litter and prostrate dead are from about 0.2 yr^{-1} in the *Salix* heaths to 1.8 yr^{-1} in the *Arctophila* pond margin. Turnover rates are 0.6 to 0.9 yr^{-1} in the *Carex-Oncophorus, Dupontia* and *Carex-Eriophorum* meadows. These turnover rates are affected by the rates of removal of material from the site, by rates of decomposition and by rates of incorporation of the vascular material into belowground material, which depends partly on the rate of vertical growth by moss.

The turnover rates for all aboveground dead material are about 0.2 yr^{-1} in the heaths, 0.4 yr^{-1} in the *Dupontia* and *Carex-Eriophorum* meadows, and 1.2 yr^{-1} in the *Arctophila* pond margin. These turnover rates imply residence times of dead material of less than a year in the *Arctophila* pond margin, to 2 to 2.5 years in the meadows, to 6.3 years in the heaths. Residence times of aboveground material in all vegetation types are between 1.9 and 7.7 years, and are about 3.4 years in the *Dupontia* and *Carex-Eriophorum* meadows.

Belowground turnover rates are estimated from root longevity data when available (Chapter 5). Root longevities are about 5 years in *Dupontia* and 8 years in *Carex aquatilis*, giving turnover rates of 0.2 to 0.12 yr^{-1} for the *Dupontia* and *Carex-Eriophorum* meadow types. Lower turnover rates are expected for the belowground parts of the woody dicotyledons.

GROWTH FORMS AND ENVIRONMENTAL CONTROL

Definition of Growth Forms

The factors controlling the distribution of plant populations could not be analyzed at the scale of resolution of individual species, however desirable such analyses might be, because of the lack of complete data on all species. Thus the plant species were grouped into growth forms based on aboveground characteristics (Figure 6-2). Since the early work of Raunkiaer (1934), the importance of plant growth forms as strategic adaptations to the tundra environment has been emphasized (Bliss 1962a, Tikhomirov 1963, Chabot and Billings 1972). The evidence is that growth forms are selected in different habitats, and therefore are a meaningful basis on which to analyze different plant–environment interactions. The growth form categories are based primarily on the nature of the shoot habit, although some categories, such as bryophytes and lichens, are systematic or phylogenetic in character. Nevertheless, bryophytes and lichens seem to be valid growth forms in the tundra.

Woody shrubs in the coastal tundra 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 representative of the deciduous shrub while *Cassiope tetragona* and *Vaccinium vitis-idaea* represent the evergreen shrub. Herbaceous plants with elongated, narrow leaves are represented by the graminoids, i.e. grasses, sedges and rushes. The graminoids are subdivided into those with crowded, bunched shoots, here called caespitose graminoids, and those with well spaced individual shoots, here called single graminoids. *Luzula confusa* and *Eriophorum vaginatum* are examples of caespitose graminoids and *Dupontia fisheri* and *Carex aquatilis* represent the single graminoids.

Four growth forms are recognized for the broad-leaved herbs or forbs. Acaulescent, or essentially stemless, plants with a rosette of radicle leaves, such as *Saxifraga nivalis* and *Pedicularis lanata*, are called rosette forbs. Broad-leaved herbs with erect leaves or leaves supported into the canopy on long petioles or on an erect stem are called erect forbs and are represented by *Polygonum viviparum* and *Petasites frigidus*. Mat forbs such as *Cerastium jenisejense* and *Stellaria humifusa* have tightly matted, often long, prostrate stems with leaves along the length of the stems. Cushion forbs have short, crowded stems, often coming from a single tap root, which give the plant a hemispherical shape illustrated by *Saxifraga caespitosa* and *Silene acaulis*.

Distribution of Growth Forms

An analysis of the distribution of plant growth forms along the environmental gradients shows that some growth forms have high fidelity for a vegetation type, e.g. the evergreen shrub in the heaths, while other growth forms are distributed through several vegetation types, e.g. the single-stemmed graminoids and the mosses.

The above- and belowground standing crops and foliage area indices of the vascular plants form clear patterns along the complex environmental gradients (Figure 6-5). A comparison of the patterns of foliage area index and productivity shows a general correlation between these two variables similar to that described by Miller et al. (1976).

The principal factor controlling the distribution of bryophytes appears to be slight differences in microrelief which influence soil moisture regimes. Bryophyte biomass is low on sites with high hydrogen sulfide and highest in the presence of moderately low values for soil moisture and soluble phosphate. The standing crop of forbs and woody dicotyledons is highest in dry, well-aerated sites with moderate levels of phosphorus.

Aboveground biomass of graminoids increases along the moisture gradient from the *Salix* heath to the *Arctophila* pond margin. The *Luzula* heath has a higher graminoid biomass than the *Salix* heath because of the caespitose graminoids, such as *Luzula confusa*, which are abundant on dry sites. In all types except the two heaths, which are relatively dry, the aboveground standing dead is less than the aboveground live for both graminoids and forbs. The decay index for litter and prostrate dead vascular plant material, which is the ratio of net aboveground productivity to litter and prostrate dead, is lower on dry sites than on wet sites, and standing dead material is incorporated into prostrate dead and litter fractions more easily on the wet sites.

The distribution of belowground biomass in relation to environmental factors differs from that of aboveground material. Belowground biomass is greatest in the most anaerobic soils, and in soils with moderate moisture and high concentrations of soluble phosphate (Figure 6-5). The ratio of aboveground to belowground biomass presents yet another picture, with the lowest ratios (1:40) in moist, partly anaerobic soils with low soluble phosphate concentrations. The ratio increases along the moisture gradient and from anaerobic to aerobic soils. These patterns of belowground biomass support the conclusion (Chapin 1974a, Wielgolaski 1975c, Chapter 5) that vascular plants develop greater amounts of absorptive root tissue on anaerobic, phosphate-poor soils. But they are also partly an artifact of the changing growth form spectrum along these gradients, i.e. a shift from woody-stemmed species to rhizomatous spe-

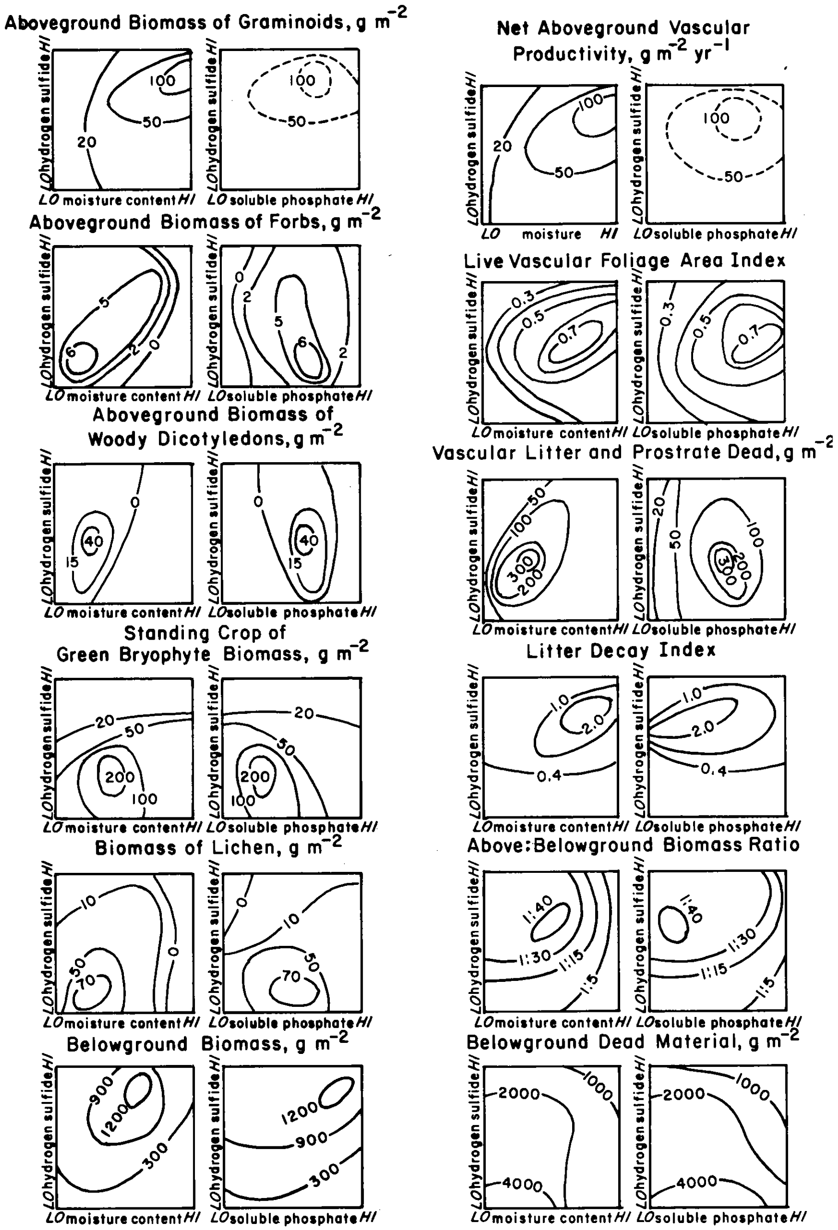


FIGURE 6-5. *Distribution within the principal axes of ordination of various above- and belowground standing crops, net aboveground productivity of vascular plants, foliage area index, above-to-belowground vascular biomass ratio, and vascular decay index. (After Webber 1978.)*

TABLE 6-3 *The Distribution of Major Growth Forms by Relative Cover for the Principal Vegetation Types of the Biome Sites at Barrow*

	Growth form/Example									
Site	Evergreen shrub *Vaccinium vitis-idaea*	Deciduous shrub *Salix lanata*	Caespitose graminoid *Luzula confusa*	Single graminoid *Carex aquatilis*	Cushion forb *Saxifraga caespitosa*	Mat forb *Cerastium beeringianum*	Rosette forb *Saxifraga nivalis*	Erect forb *Saxifraga cernua*	Bryophyte *Pogonatum alpinum*	Lichen *Cetraria islandica*
Luzula heath (I)	—	5.0	15.1	4.0	—	2.3	2.0	11.3	37.0	23.3
Salix heath (II)	3.3	16.5	4.4	8.1	0.8	2.3	3.0	11.1	31.7	18.8
Carex-Poa meadow (III)	1.5	3.2	2.1	16.7	—	1.4	1.3	4.9	45.3	23.6
Carex-Oncophorus meadow (IV)	1.3	1.4	2.8	26.5	—	3.4	2.5	8.8	46.2	7.1
Dupontia meadow (V)	—	0.4	0.4	28.4	—	6.4	1.5	12.1	45.4	5.4
Carex-Eriophorum meadow (VI)	—	—	0.6	40.2	—	0.5	3.2	3.8	47.4	4.3
Arctophila pond margin (VII)	—	—	—	35.5	—	1.0	—	32.3	31.2	—
Cochlearia meadow (VIII)	0.2	—	2.8	20.8	—	12.9	4.3	15.2	30.2	13.6

Source: Modified from Webber (1978).

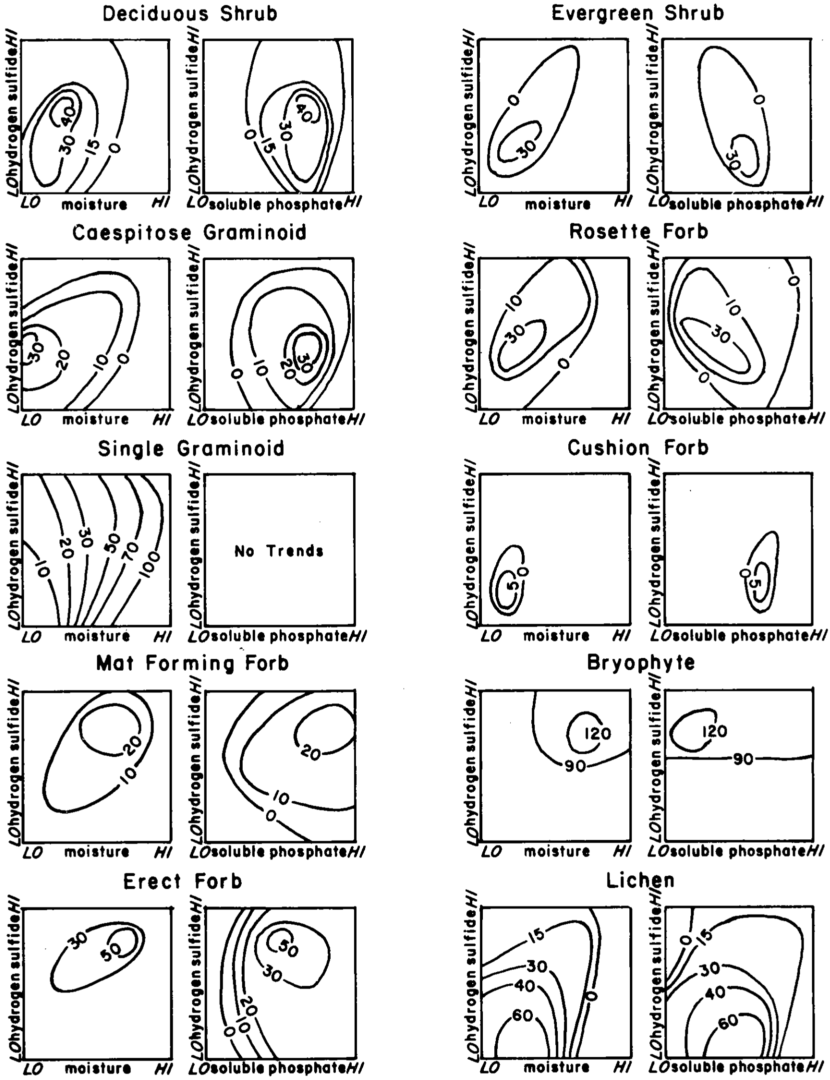


FIGURE 6-6. *The relative importance of growth forms within the principal axes of the ordination. The contour values are the sum of relative cover and relative frequency of the growth form. (After Webber 1978.)*

cies with increasing water-logging, and increasing moss growth which buries aboveground plant parts. The ratios and the magnitude of belowground biomass are similar to those reported by Dennis and Johnson (1970) and Dennis (1977).

The abundance of the graminoid-dominated vegetation types at the wet end of the moisture gradient is clearly apparent (Table 6-3). In wet meadows, single graminoids make up most of the vascular vegetation. Underlying the graminoid canopy is a discontinuous layer of moss. These two growth forms are the most important in primary production and nutrient cycling and have been studied the most intensively.

The importance of these growth forms, which is calculated from the relative cover plus relative frequency, varies in the different vegetation types and in the different microtopographic units, reflecting the different productivities of the growth forms along environmental gradients (Figure 6-6). Evergreen and deciduous shrubs, caespitose graminoids, cushion forbs, and lichens are more important on the drier microsites. The single graminoids, grasses, sedges and rushes, and the bryophytes are more important on the wetter sites. Caespitose graminoids occur with lower moisture, moderate soil anaerobicity, and moderate concentrations of soluble phosphorus (Figure 6-6). The importance of the single graminoids increases with moisture and is independent of soil aeration and phosphorus. Mat and erect forbs are most abundant in moist sites with moderate to high levels of phosphate and hydrogen sulfide, while rosette forbs prefer drier sites where phosphate and sulfide levels are moderate. Evergreen shrubs occur with low moisture, moderate concentrations of hydrogen sulfide and moderate phosphorus. Deciduous shrubs occur with slightly higher soil moisture, slightly higher hydrogen sulfide, and higher phosphorus. The importance of lichens is highest with moderately low moisture, low hydrogen sulfide, and moderate phosphorus. Bryophytes, by contrast, are most important with moderately high soil moisture, somewhat anaerobic soils, and low phosphorus.

Species Diversity Within Growth Forms

The number of species within a growth form, as well as overall cover and frequency, varies along the environmental gradients (Figure 6-7). The diversity of species within a given growth form does not always correspond with the importance of the form. The importance of single graminoids is highest in wet sites, and shows little relation to soil anaerobicity and phosphate. The species diversity is greatest with moderate moisture and phosphate and relatively high soil anaerobicity. Deciduous shrubs are more diverse with low soil hydrogen sulfide, but show high cover with higher soil hydrogen sulfide.

Production and diversity are related. Stands with lower diversity have high productivity; stands with moderate diversity have lower productivity. The highest diversity occurs on the drier sites, with growth forms of low productivity. The lowest diversity occurs at stream and pond edges, in monospecific graminoid stands with high production.

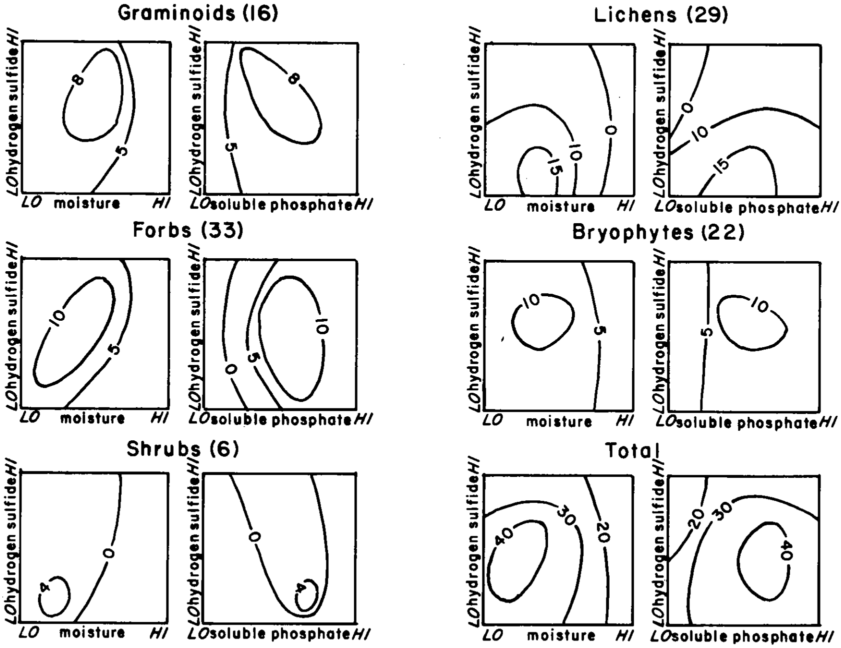


FIGURE 6-7. *The number of species per 10-m² plot of the most common growth forms and the total number of species within the principal axes of the ordination. The total number of species of each growth form is given in parentheses. (After Webber 1978.)*

FUNCTIONAL RELATIONSHIPS OF GROWTH FORMS AND ENVIRONMENTAL GRADIENTS

Functional Definition of Growth Forms

The growth forms defined on the basis of morphological habit differ in functional characteristics related to the environmental gradients. Functional characteristics include leaf longevity, timing of leaf growth, location of the perennating bud, location of stored organic and inorganic nutrients, leaf resistance to water loss, photosynthetic rates, carbon and nutrient costs of constructing new leaf material, and location of absorbing roots.

The graminoid forms are characterized by sequential leaf production and, for single graminoids, a rapid leaf turnover (Tieszen and Wieland 1975, Johnson and Tieszen 1976). The leaf longevity may be shorter than the growing season. This pattern results in a high annual growth respiration cost, and is generally associated with relatively high photosynthetic rates (Tieszen and Wieland 1975). Reserve materials are stored below ground (Allessio and Tieszen 1975a). The meristematic region that overwinters is either just below the moss or soil surface, or protected above ground by dead but persisting leaf sheaths. Forbs of the rosette, erect, mat or cushion types have high leaf growth rates and synchronous leaf production early in the season. The leaf duration is one growing season. The respiration rate during leaf growth is high, but net photosynthetic rates may be moderate (Tieszen 1973). Materials stored below ground in rhizomes and roots are mobilized early in the season to support the rapid growth (Mooney 1972). The perennating bud is located below ground or at the soil surface.

Deciduous shrubs have a high leaf growth rate and synchronous leaf production early in the growing season. Respiration rates are high during the leaf growth period, and photosynthesis rates are high; for example photosynthesis rates of *Salix* are higher than those of the graminoids (Chapter 4). The perennating buds are above ground and materials are stored in stems through the winter. The aboveground location of the perennating buds and stored materials makes the deciduous shrubs susceptible to grazing and to loss of plant parts due to abrasion by wind. The production of wood by the deciduous shrub involves a large biosynthetic cost, since the efficiency of lignin synthesis is comparatively low (Table 5-5). The deciduous shrub also has a relatively low root biomass (Chapter 3), which reduces the total maintenance cost.

Evergreen shrubs usually have synchronous leaf growth (Johnson and Tieszen 1976) with a low rate of leaf turnover, although some, e.g. *Dryas integrifolia*, have sequential but low rates of leaf production (Svoboda 1977). The respiration rates of evergreen woody shrubs are relatively low because of the low rates of growth. Photosynthesis rates based on leaf dry weight are also low, about half those of the graminoid form, but may be similar to the graminoid on a leaf area basis (Johnson and Tieszen 1976). Leaf resistance to water loss may be low in spite of their xerophytic appearance (Kedrowski 1976, Oberbauer 1978). Materials are stored in the stems and leaves through the winter, perhaps in the form of lipids. The perennating buds are located above ground. The evergreen form is found on exposed locations that are snow-free early in the season. It can photosynthesize early when the surface is warm, even though the soil and roots are frozen, since all the materials required for photosynthesis are stored in the leaf. It commonly survives desiccation and grows late in the season. The form also occurs in late-lying snowbeds.

The moss and lichen forms grow throughout the season whenever moisture and temperature conditions permit photosynthesis. Respiration and photosynthesis are low in relation to graminoids (Chapter 4). Materials are stored where they are formed; translocation is uncommon (Collins and Oechel 1974). The intake of minerals by moss depends largely upon inorganic nutrients being absorbed or deposited upon the moss surface or diffusing to the surface, since most mosses cannot absorb minerals through a root system from the soil profile.

Interrelations Between Environmental Factors and Plant Characteristics

The links between the major environmental factors and the patterns of plant characteristics can be diagrammed to clarify and assess the current state of understanding (Figure 6-8). Although the variation in environmental factors is continuous, a comparison of the interactions on exposed microtopographic units, such as tops of high-centered polygons, with those on more protected units, such as polygon troughs or sloping creek banks, provides some basis for assessing the direction of influence. Within the macroclimatic environment the patterns of vegetation are related to topographic gradients and associated environmental factors.

For example, the major environmental variables are all influenced by wind. Sites with relatively high wind have thin snow cover, low soil water and lower temperatures during the growing season (Table 6-1; Oberbauer and Miller 1979). High wind leads to increased removal of litter, which is indicated in the higher litter turnover rate of the unprotected *Luzula* heath relative to the *Salix* heath, and to reduced nutrients because of the wind-blown nutrient loss (Figure 6-4, Table 6-1). The low soil water also increases soil aeration, which can lead to increased acidity and phosphorus immobilization.

These environmental factors influence several plant processes. High wind and thin snow cover lead to increased loss of plant parts due to abrasion (Savile 1972), which favors low growth forms and species in which the buds are protected. The lower temperatures in the active season should lead to reduced growth (Warren Wilson 1966a, Larcher et al. 1973), although the relation between temperature and growth is poorly quantified for the Arctic (Miller et al. 1979). The reduced growth may also lead to low growth forms. The low growth forms lead to increased plant temperature, since ground surface temperatures are higher than air temperatures. The higher plant temperatures will cause higher vapor pressure differences from leaf to air, thus potentially increasing water loss and water stress unless compensated by high leaf resistance. High leaf resistances are associated with low photosynthesis rates, which lead to greater leaf longevity that provides time to recover the leaf construction costs (Johnson and Tieszen 1976, Miller and Stoner 1979). The need for greater leaf longevity is reinforced by the low nutrients (Beadle 1962, Monk 1966, Small 1972, Stoner et al. 1978b).

Thin snow cover results in earlier exposure of the surface in spring.

Leaf expansion cannot take place, since the ground may still be frozen and water unavailable, but photosynthesis is still possible (Larcher et al. 1973). In such a situation evergreen leaves containing photosynthetic enzymes stored through the winter are advantageous (Miller 1978). Thin snow cover also results in low soil water and the possibility of periodic summer drought, at least in the surface soil layers. The summer drought should select for leaves with structural thickenings and for plants with deep roots to exploit deeper, moister soil layers (Oberbauer 1978, Oberbauer and Miller 1979). Thus, on exposed sites the vegetation should comprise plants of low stature with long-lived leaves, low photosynthesis rates, high leaf resistance, buds protected by scales, hairs or persistent plant parts, rigid leaves and deep roots. These trends are exemplified in the vegetation turnover rate, growth form composition, and above- to belowground biomass ratios (Table 3-2, Table 6-2, Figure 6-5) of the heath vegetation types.

More protected sites have lower wind speeds, which lead to deeper snow cover, greater protection from winter abrasion, high soil water, higher temperatures in the active season, and increased litter deposition and nutrients. The decreased abrasion loss makes possible taller growth forms and the storage of nutrients above ground. The increased snow cover results in later exposure of the surface. Air and ground temperatures, when the surface is finally exposed, are higher than for the sites that are exposed earlier. Early in the season the ground is warmed by the influx of meltwater. Thus leaf expansion becomes possible as soon as photosynthesis is possible. Deciduous leaved plants, with nutrients stored in the aboveground stems, can occur. The vegetation of these sites includes many deciduous shrubs. With still greater snow cover the short snow-free season can favor evergreen forms which can regain the carbon cost of leaf construction through several seasons.

Increasing protection or impeded drainage leads to soils saturated with water, low soil aeration, and low soil temperatures because of the high heat capacity of the soil (Chapters 3 and 7). Low temperatures decrease mineralization and uptake ability, leading to reduced nutrient availability. The plant may compensate by increasing the number and biomass of absorbing roots. The lower soil oxygen can lead to greatly increased respiration demands to support the root biomass, unless aerenchyma are present. Thus, selection may be strong for plants with aerenchyma, which may have deep roots, or for plants with shallow roots, such as the evergreen shrub, or no roots, such as mosses. Saturated conditions are found in the *Dupontia* and *Carex–Eriophorum* meadows and in the *Arctophila* pond margins (Table 3-2, Table 6-2, Figure 6-5). Slightly better aeration allows plants without aerenchyma to occur and vegetation similar to *Salix* heath develops.

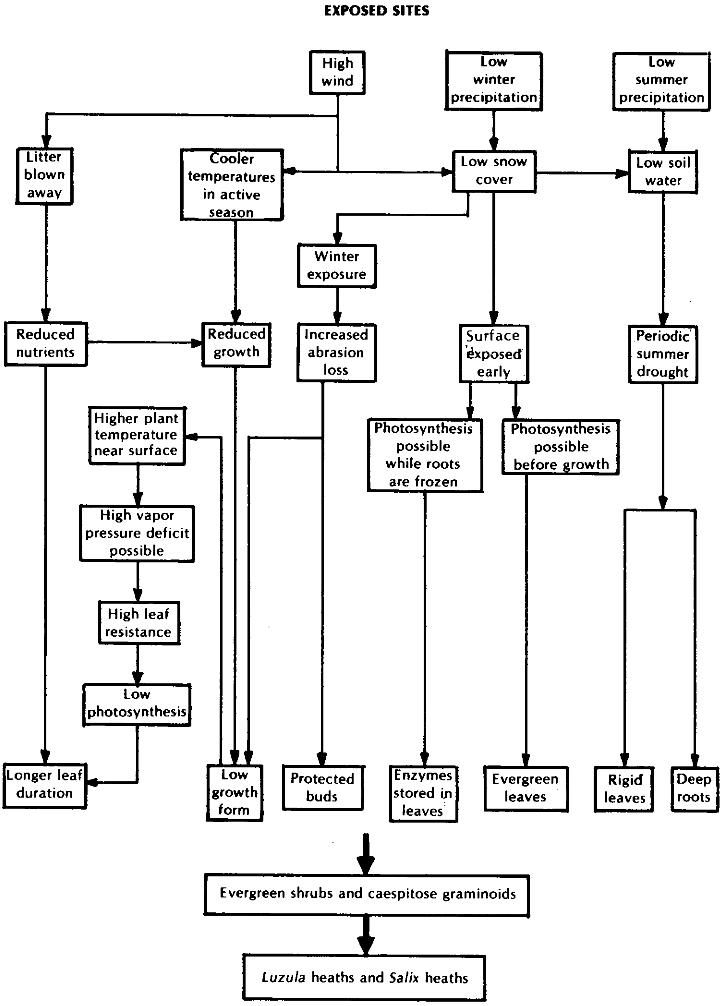
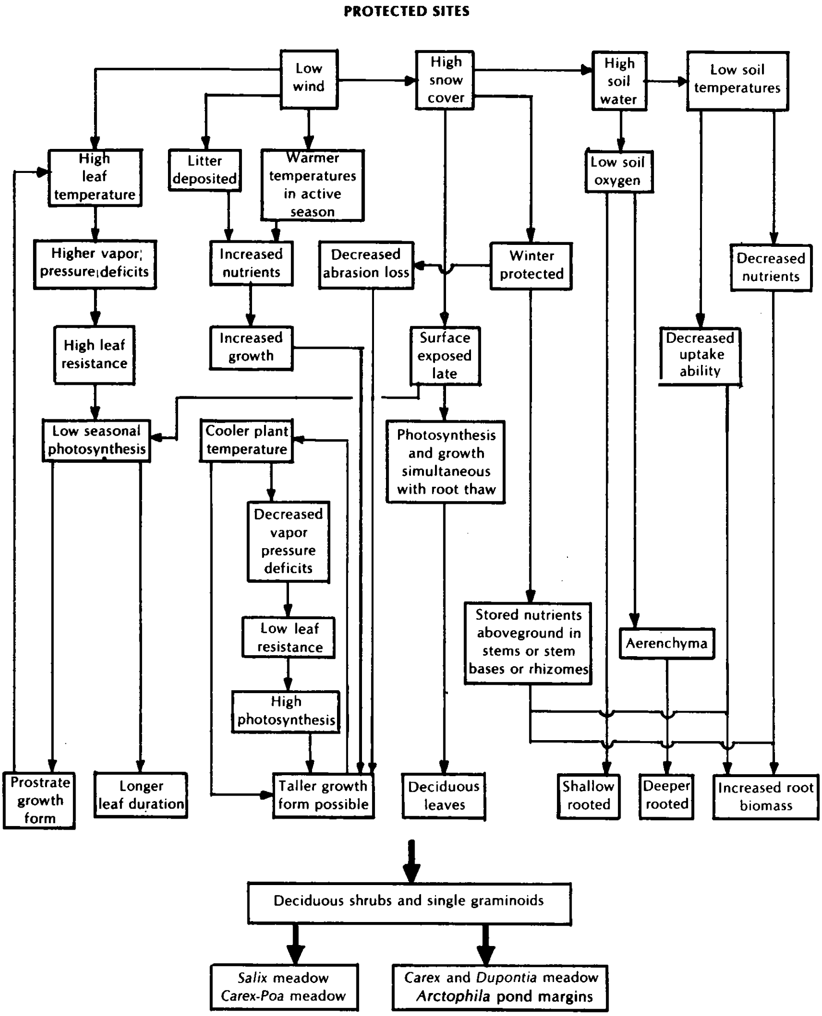


FIGURE 6-8. *Diagrammatic relationships between major environmental factors and plant characteristics. The diagram consists of two complexes: those for exposed sites which lead to plant characteristics to be found in evergreen shrubs and caespitose graminoids of* Luzula *and* Salix *heaths*



and those for protected sites which lead to the characteristics of the plants of Salix *and* Carex-Poa *meadows, for example deciduous shrubs and graminoids, and the plants of* Carex *and* Dupontia *meadows and* Arctophila *pond margins, for example single graminoids.*

PLANT SUCCESSION AND RESPONSE TO PERTURBATIONS

The explanation of vegetation patterns can lie in the physiological constraints of the species and growth forms as already discussed and in the change in plant populations as the vegetation recovers from disturbance or invades new territory.

Plant colonization of new or disturbed surfaces and subsequent plant succession is an important topic in arctic tundra, especially with the prospect of increasing disturbance associated with the development of natural 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 successional patterns are interpreted by inference without either an adequate set of observations through time or dated surfaces (Polunin 1935, Oosting 1956, Spetzman 1959, Johnson and Tieszen 1973). Although succession was not a main emphasis of the vegetation studies, a description of inferred succession patterns can be useful in interpreting such studies. The plant succession discussion is based largely on field inference and the literature. The rates of change in succession are variable and some changes may take a thousand years while others take only a few tens of years.

Thaw Lake Cycle

Short-term linear succession is apparent in the Biome research area, but the overriding patterns are cyclic and can be related either to the thaw lake cycle (Britton 1957) or to the colonization of alluvium (Figure 6-9). The resulting successional pattern is oversimplified and may only apply to the immediate Biome research area. Only the most commonly followed pathways are discussed; many others are possible. The successional changes are controlled primarily by changes in microrelief and thus drainage regimes.

Plant colonization on stable floodplain alluvium is rapid. In a few years a good cover develops, made up of species such as *Cochlearia officinalis, Stellaria laeta, Phippsia algida, Alopecurus alpinus, Poa arctica, Saxifraga cernua*, and *Bryum* spp. Other plants, including *Dupontia fisheri, Petasites frigidus* and lichens soon follow, and stands belonging to the *Cochlearia* meadow type develop. In areas that are not dominated by snow accumulation, stabilization of the sediments allows development of stands belonging to the *Carex–Poa* meadow type. Stabilized areas may become drier either by high-centered polygon formation, or by

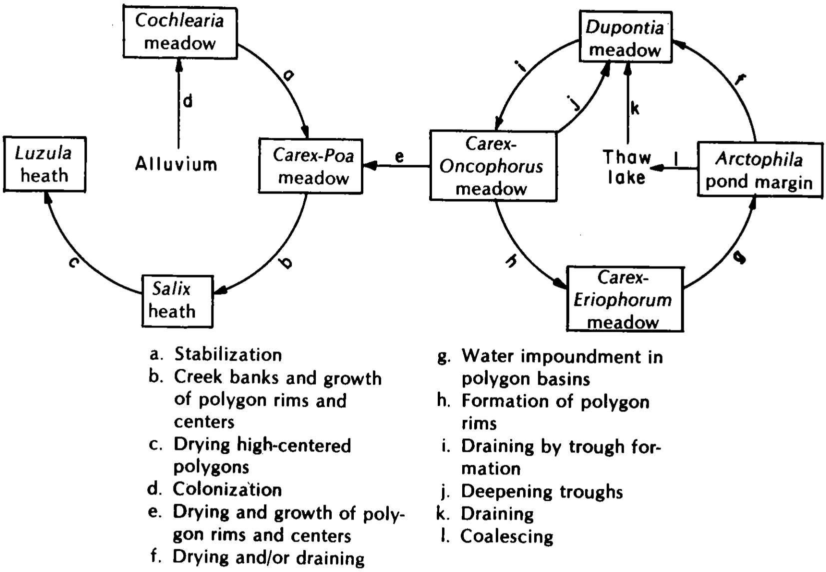


FIGURE 6-9. *Principal successional trends of vegetation types and principal allogenic geomorphic processes controlling them. (After Webber 1978.)*

increased drainage as local water courses deepen through thermokarst or frost heaving activity. Drier areas will support *Salix* and *Luzula* heaths. Although good field evidence exists for the transition to *Luzula* heath, such transitions are rare.

The colonization of drained lake sediments is also rapid. The basin of Footprint Lake has become covered with vegetation within 25 years (Dennis 1977). The present vegetation of the basin varies according to local drainage and substrate composition. It includes *Carex-Oncophorus, Dupontia* and *Carex* meadows, and *Arctophila* pond margins. The *Dupontia* meadow is the most abundant vegetation in the Footprint Lake basin at present. Once a surface has a complete cover of vegetation it seems slow to change to another vegetation type. As ice wedge polygons develop, with their attendant variety of microrelief and moisture regimes, the vegetation of the Footprint Lake basin should become similar to the highly polygonized Biome research area, but many decades must elapse before the same variety of vegetation types develops in the lake basin. The frequency with which thaw lakes drain and with which new alluvium is laid down is increased by man's activities.

The mechanisms responsible for changing vegetation types are predominantly geomorphic. The *Carex-Oncophorus* meadow can form when polygon troughs drain in a *Dupontia* meadow. The development of the *Carex* meadow from drained lake sediments forms a link with the alluvial succession. Trough formation in the *Carex–Oncophorus* meadow can reverse the trend by producing wetter areas and vegetation types in troughs and centers of low-centered polygons. As polygonization continues, the diversity of surfaces increases. Vegetation on the drier rims of low-centered polygons and tops of low-relief, high-centered polygons of the *Carex–Oncophorus* meadow can change to that of the *Carex–Poa* meadow. Further depression of centers and impounding of water produces ponds and *Arctophila* pond margin vegetation. Some ponds may breach their impounding rims and drain while others may fill with sediments. In this manner, the *Dupontia* meadow may be re-formed. The cycle may also be closed by the coalescence of ponds as their margins or rims are eroded by thermokarst activity, and large ponds and even thaw lakes may be re-formed.

When the presence of various species is plotted on this successional sequence of vegetation types, orderly patterns of species change emerge. Some species occur in only one type or successional stage, such as *Hierochloe alpina, Cassiope tetragona, Caltha palustris, Phippsia algida* and *Saxifraga rivularis.* Others occupy several types, such as *Poa arctica, Dupontia fisheri, Saxifraga foliolosa, Carex aquatilis* and *Eriophorum angustifolium.* Those species occurring in more than one type usually occur sequentially in the postulated successional sequences and this occurrence is not interrupted or haphazard. The single exception is *Arctophila fulva,* which dominates the pond margin vegetation, and also occurs in the *Dupontia* meadow and in the *Cochlearia* meadow.

Orderly patterns are also formed when the numbers of the species of different growth forms in each vegetation type and various productivity measures are plotted in the successional sequence (Figure 6-10). In the alluvial sequence from *Cochlearia* meadow to the *Luzula* heath on the tops of high-centered polygons, the total number of species increases from the *Cochlearia* meadow through the *Carex–Poa* meadow to the *Salix* heath but decreases abruptly from the *Salix* heath to the *Luzula* heath. In the thaw-lake cycle from the *Dupontia* meadow through the *Carex–Oncophorus* meadow, *Carex–Eriophorum* meadow and *Arctophila* pond margin, the total number of species first increases from the *Dupontia* meadow to the *Carex–Oncophorus* meadow and then decreases through the *Carex–Eriophorum* meadow to the *Arctophila* pond margin. The *Arctophila* pond margin has the lowest diversity in total number of species and in the number of species in each growth form. The highest proportion of graminoids is found in the *Carex–Eriophorum* meadow and the smallest in the *Salix* heath. The vegetation types found on dry sites have the highest proportion of dicotyledons. The *Cochlearia* meadow has several typical pioneer species which are dicotyledons, for example *Cochlearia officinalis, Saxifraga rivularis* and *Stellaria humifusa.*

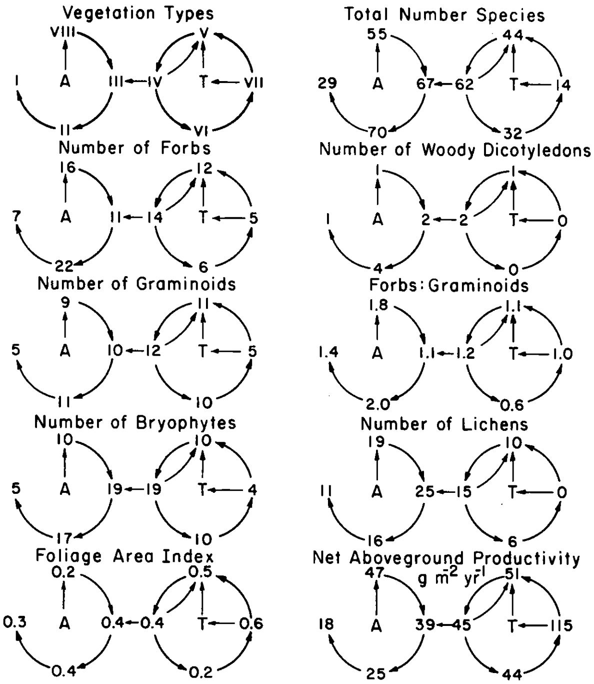


FIGURE 6-10. *The distribution of the species diversity (number of species per 10 m^2) of the major growth forms, foliage area index, and annual net aboveground vascular productivity within the successional sequence diagram. The Roman numerals represent the positions of the vegetation types and the letters A and T represent the starting points of alluvium (A) and thaw lake (T) successions. Foliage Area Index refers only to vascular plants. See Figure 6-9 for vegetation types. (After Webber 1978.)*

Foliage area index is low in the *Cochlearia* meadow, increases in the alluvial sequence to the *Salix* heath and then decreases slightly in the *Luzula* heath. It is highest in the *Arctophila* pond margin and decreases in the thaw lake cycle to the *Carex-Oncophorus* meadow. Annual aboveground vascular productivity decreases steadily with succession. From the *Cochlearia* meadow through the *Carex-Poa* meadow and *Salix* heath to the *Luzula* heath, productivity decreases from 47 g m^{-2} yr^{-1} to 18 g m^{-2} yr^{-1}. From the pond margin through the *Dupontia* meadow to the *Carex-Oncophorus* meadow productivity decreases from 115 g m^{-2} yr^{-1} to 45 g m^{-2} yr^{-1}.

Natural Perturbations

The control over ecosystem function exerted by various factors can best be studied when the system is perturbed. Enlargement and drainage of lakes may be viewed as natural perturbations occurring in the coastal tundra as part of the thaw lake cycle. Ecosystem function changes drastically in response to these alterations between aquatic and terrestrial environment, and thousands of years are required for completion of the thaw-lake cycle and return of the ecosystem to its original state.

Tundra is often viewed as easily disturbed or changed (Bliss et al. 1970) but it is quite stable and resilient to major environmental changes (Bliss et al. 1970, Webber and Ives 1978). It appears to be adapted to large, natural, often sudden environmental fluctuations. For example, the pulse of water runoff during snowmelt is dramatic but does not have immediate effects upon most other factors such as an efflux of nitrogen or phosphorus, even though 40% of the annual phosphorus return from litter to the soluble pool occurs during this 10-day period (Chapin et al. 1978). Apparently, the exchange capacity of the mosses and the nutrient demands of plants and microorganisms at this time are sufficient to extract most of the dissolved nitrogen and phosphorus from runoff. During the growing season, microbial populations in the soil may build up and crash, releasing a large proportion of the annual nutrient flux in brief periods. However, the rapid nutrient uptake by plants and the high exchange capacity of peat are sufficient to remove nutrients as they are made available.

The recurrent peaks in lemming abundance at 3- to 4-year intervals constitute another natural perturbation of the coastal tundra at Barrow (Chapter 10). Heavy winter grazing removes dead leaves from the canopy, and computer simulations predict that the associated increase in light intensity will stimulate photosynthesis and increase net production the following summer (Miller et al. 1976). Moreover, litter decomposes more rapidly once it is felled and in contact with the wet ground surface, releasing nutrients and further stimulating production.

Heavy grazing during summer, removing 50% or more of leaf biomass, depletes plant carbon and nutrient reserves as new leaves are produced and reduces the length of time that new leaves can photosynthesize (Mattheis et al. 1976, Chapin 1975); computer simulations predict a reduced annual production. The tundra vegetation recovers from intense grazing perturbations within 3 to 4 years, as discussed in Chapter 10 and by Schultz (1964, 1969). Briefly, grazing increases nutrient availability through leaching of urine and feces and more rapid decomposition of felled leaves and litter. The stimulation of primary production by increased nutrient availability returns the vegetation to its original state.

Controlled Perturbations

Experimental alteration of selected ecosystem variables reveals their relative importance in the resilience or fragility of tundra and provides clues to the recovery time and thresholds beyond which the system does not quickly recover. Heavy fertilization increases primary production and plant nutrient concentrations initially, but subsequent increases in standing dead and litter tie up nutrients and reduce light penetration and photosynthesis, so that within 3 to 8 years little treatment effect upon primary production can be observed (Schultz 1964, 1969). Clipping and removal of all aboveground vegetation or addition of excess litter (to stimulate accumulation of standing dead) alter primary production and plant nutrient concentrations only slightly (Chapin 1978). Even multiple defoliations of single tillers have relatively small effect upon regrowth (Mattheis et al. 1976). All the above manipulations cause changes that are within the normal range of conditions in lemming cycles, and the tundra is highly resilient to these perturbations.

The anticipated effect on the tundra of the Trans-Alaska Pipeline System, which carries hot oil, led to an experiment in which a wet meadow substrate was heated in situ. Alteration of soil temperature markedly affects ecosystem function, but the nature of the response depends upon the similarity of the perturbation to those that occur naturally. A 10 °C soil temperature rise for one summer month at Barrow increased thaw depth, decomposition rate, nitrogen availability, plant nutrient absorption rates, and primary production (Chapin and Bloom 1976). Ten years later little treatment effect could be observed. However, when soils were heated for one full year, the increased thaw depth caused melting of ice in permafrost, subsidence of the ground surface and ponding of water. Rapid decomposition depleted soil oxygen and soils became anaerobic, killing all vegetation within one year. The site did not recolonize during the 10 years following the experiment. Thus, although temporary summer changes in soil temperature stimulate nutrient cycling and primary production, a chronic year-round soil temperature change in ice-rich soils leads to ponding of water, death of the vegetation and a long-term change in ecosystem function. Experimental heating of a relatively ice-free soil in interior Alaska throughout the year caused no subsidence and increased primary production 3- to 5-fold (McCown 1973), an effect comparable to that caused by temporary heating of the ice-rich soil at Barrow. Thus the detrimental effects of soil heating appear to be caused primarily by a perturbation in excess of any natural fluctuation which triggers a chain of circumstances associated with melting of ice, soil subsidence, and change in soil chemical and physical environment.

Vehicle Tracks

Human impact in the Arctic is a subject of current concern because of both increasing human activity associated with arctic resource development and the unexpectedly severe ecological impact of human activity over the past 25 years. The severity of vehicle impacts upon tundra depends upon the nature of both the disturbance and the community and can be predicted from an understanding of natural and controlled perturbations of tundra (Figure 6-11).

Vegetation changes triggered by tracked vehicle damage and by water impoundments resulting from road construction fit into the thaw lake successional scheme presented here (Figure 6-9). Total destruction of any vegetation type because of catastrophic thermokarst activity leads to either the alluvium or the thaw lake starting points. Most commonly, water impoundment results in deepening of troughs through partial ice-wedge melting. In some instances this has caused both drier inter-trough areas and wetter trough areas. For example, at one site following disturbance by tracked vehicles the vegetation type has changed from the *Dupontia* meadow to both the *Carex–Oncophorus* meadow and the *Arctophila* pond margin, and from the *Carex–Oncophorus* meadow to both the *Carex* meadow and the *Dupontia* meadow. Vegetation changes may occur within a very few years.

Multiple passes by ACV's or a single pass by a Rolligon (balloon-tire vehicle) produce similar effects in winter or early spring. However, if the traffic occurs during the summer months, live vascular plants and mosses are crushed; passage of a wheeled vehicle may also produce some depression of the tundra surface (Abele et al. 1978, Everett et al. 1978). Soil temperature and, in following years, depth of thaw, nutrient availability and primary production increase. Recovery time is estimated at 2 to 4 years and is comparable to that associated with intense winter grazing by lemmings (Bliss and Wein 1972, Hernandez 1973, Wein and Bliss 1974, Challinor and Gersper 1975, Gersper and Challinor 1975, Brown and Grave 1979). The effect is greater in shrub tundra due to greater breakage of rigid stems, and recovery time is longer. Vehicle passage with greater frequency and later in the season increases damage to live leaves, prolongs recovery, and makes the impact more nearly comparable to that of summer lemming grazing by removing productive tissue and decreasing primary production.

Use of tracked vehicles, or repeated passage by low pressure wheeled vehicles, frequently compacts the low-bulk-density organic mat and depresses the soil surface below the water table, particularly in poorly drained meadow soils (Gersper and Challinor 1975). Standing water decreases albedo and increases soil temperature and thawing of permafrost,

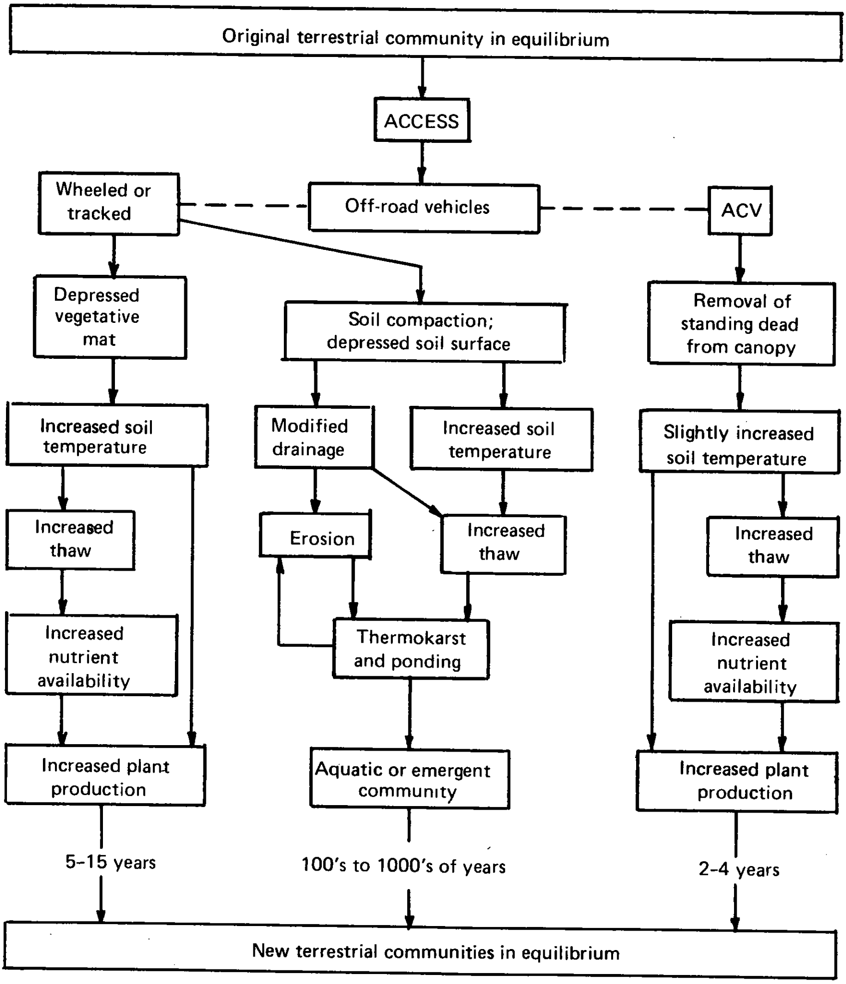


FIGURE 6-11. *Impact of air cushion vehicles (ACV) and wheeled and tracked vehicles upon the coastal tundra at Barrow. Recovery times are estimated from observations by Hok (1969), Hernandez (1973), Rickard and Brown (1974), Abele et al. (1978), and Lawson et al. (1978).*

causing increases in nutrient availability and primary production as well as further subsidence of the soil surface. Where the vehicle track crosses ice wedges or ice lenses, deep permanent ponds may form (Kryuchkov 1976, Peterson 1978). Sites with low ice content are less susceptible to this positive feedback and ponding (Webber and Ives 1978). On slopes, compaction by vehicles promotes drainage of water from surrounding areas, and thus speeds decomposition and permafrost thawing, increases nutrient availability, and changes community composition to that characteristic of wetter sites. Such communities are generally highly productive (Hernandez 1973, Wein and Bliss 1974). Drainage patterns also change naturally in tundra, with consequences similar to those described above, and are part of the thaw lake cycle (Britton 1957). Both natural and man-induced changes lead to irreversible permanent changes in the natural community, and recovery may require thousands of years until the landscape is modified by the thaw lake cycle. Vehicle impact upon various tundra communities can be predicted and mapped in order to manage vehicle use in areas of development (Everett et al. 1978, Webber and Ives 1978).

Vegetation and Organic Mat Removal

In general, tundra graminoids, if defoliated, regrow readily from belowground stems and rhizomes, especially in wet sites. Simulations suggest that wet meadow tundra can tolerate 50% foliage removal and still recover in 3 to 5 years. This situation is comparable to that which occurs naturally during lemming cycles (Bliss 1970, Babb and Bliss 1974). Vegetation in xeric sites generally recovers more slowly because of lower productivity, slower nutrient cycling, and greater exposure of dry-site species (e.g. evergreen shrubs) to disturbance (Hernandez 1973, Babb and Bliss 1974, Van Cleve 1977). The most serious consequences of removing aboveground vegetation are decreased albedo and increased heat penetration into the soil, which leads to thawing of permafrost, as described above, especially in wet sites.

The highly organic surface soil horizons of wet coastal tundra at Barrow serve an important function in nutrient retention. Removal of this organic mat from the tundra surface not only eliminates potentially resprouting vegetation but also removes a large proportion of the accumulated nutrient capital and most of the cation exchange capacity of the soil system. The 40 to 60% of the accumulated system nitrogen that is contained in the organic horizon of several tundra sites would require ? 5,000 to 10,000 years to replenish at current fixation rates (Chapin and Van Cleve 1978). In ice-rich permafrost, thermokarst continues over decades and relatively flat areas are recolonized by the native vegetation (Lawson et al. 1978). Perhaps the most serious consequence of organic mat removal has been serious erosion following thawing of permafrost on sloping terrain. An aquatic or emergent vegetation may eventually stabilize such erosion patterns (Hok 1969, Hernandez 1973, Haag and Bliss 1974), but the system probably will not return to its former state for thousands of years.

Although revegetation of naturally disturbed sites such as drained lake basins occurs by seedling establishment within 10 to 20 years in the Barrow area (Dennis 1968), seeding with grasses of temperate origin has often been attempted to speed the revegetation process in areas disturbed by man. These grasses have higher nutrient and soil temperature requirements than most native tundra graminoids (Chapter 5; McCown 1978) and become established only with heavy and repeated fertilization (Mitchell 1973, Younkin 1976, Van Cleve 1977). Such grasses are often effective in stopping erosion but generally slow down reinvasion by native species (Hernandez 1973, Younkin 1976, Johnson and Van Cleve 1976). The fertilization required to maintain cover of temperate-origin grasses may have secondary effects such as attraction of herbivores and eutrophication of adjacent aquatic systems.

Oil Spills

Oil is an environmental factor foreign to most tundra communities, so that recovery from oil spills cannot be readily predicted from our knowledge of the responsiveness of the natural vegetation. Alaskan crude oil and fuel oil are toxic to plant leaves, but if the oil does not penetrate the soil, the tundra system responds much as it would following 100% defoliation by lemmings (Figure 6-12). There is a temporary decrease in albedo and increased heating of the soil (Haag and Bliss 1974, Everett 1978), but regrowth of the vegetation allows the community to approach its original condition within a few years. Flooding of the community with water largely prevents oil penetration into the soil until toxic volatile fractions have evaporated and thereby minimizes the local impact of an oil spill.

Most of the live biomass of all trophic groups in the coastal tundra at Barrow is in the top 10 cm of the soil and is rapidly killed if oil penetrates into the soil before toxic volatile fractions evaporate (Jenkins et al. 1978). In wet soils, oil penetrates more slowly, much of the toxic fraction evaporates, and less vegetation dies than in dry sites (Walker et al. 1978). Species differ in their sensitivity to oil, and often the response is seen as decreased winter hardiness rather than as immediate mortality (Deneke et al. 1975, Linkins and Antibus 1978).

Other effects of oil upon system function are more subtle but equally important. Hydrocarbons may remain in the active layer for at least 30 years after an oil spill (Lawson et al. 1978). Addition of a large carbon-rich, nutrient-poor substrate to the soil increases the demands of microbes for nutrients from the available soil pools so that nutrients become less available to vascular plants. Moreover, oil kills at least certain mycorrhizal fungi, further decreasing the ability of plants to extract nutrients from the soil (Antibus and Linkins 1978). Thus, oil may effec-

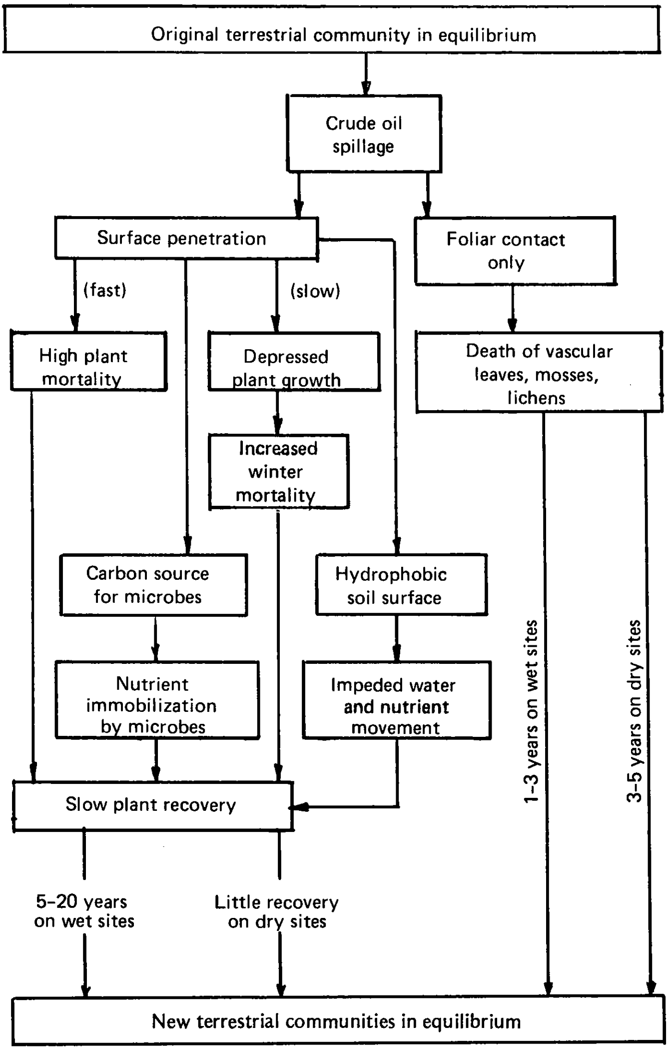


FIGURE 6-12. *Impact of crude oil upon the coastal tundra at Barrow. Recovery times are estimated from observations by Wein and Bliss (1973), Deneke et al. (1975), Hutchinson et al. (1976), and Walker et al. (1978).*

tively retard nutrient cycling and decrease nutrient availability in an ecosystem that is already nutrient-poor and highly dependent upon internal recycling of nutrients. Oil is hydrophobic and once within the soil greatly reduces water movement both into the soil and from the bulk soil to plant roots (Raisbeck and Mohtadi 1974, Everett 1978). Because nutrient movement within the soil is dependent upon water movement, the hydrophobic nature of oil-contaminated soil may decrease nutrient as well as water availability to plants.

SUMMARY

Within the prevailing coastal tundra macroclimate, the topographic position of a site causes the variation in environmental factors which in turn control the growth and distribution over the tundra surface of different plant species and growth forms. The complexes of controlling environmental factors were identified by indirect ordination. They are, in order of importance in explaining the overall variation of the vegetation, the complexes of soil moisture, soil anaerobicity, soil phosphate, and snow cover. The distribution of vegetation types, plant growth forms, and various vegetation and growth form attributes such as standing crop of above- and belowground material, productivity, foliage area, turnover rates, and diversity are described in terms of the controlling environmental complexes.

The principal growth forms recognized at Barrow are single graminoids, erect forbs, deciduous shrubs, and bryophytes. Others that may be locally abundant are caespitose graminoids; cushion, mat and rosette forbs; evergreen shrubs; and lichens.

Dry, exposed sites with little snow cover usually contain a preponderance of caespitose graminoids and lichens. They may also have evergreen and deciduous shrubs and cushion forbs. Mesic sites tend to have the most forbs but have an abundance of bryophytes and deciduous shrubs. Single graminoids are abundant over much of the tundra and are dominant in moist and wet sites along with bryophytes.

The distribution of plant growth forms within the tundra is related to structural and functional characteristics, such as leaf longevity, timing of leaf growth, location of perennating organs, location of stored nutrients, leaf resistance to water loss, photosynthetic rates, carbon and nutrient costs of making new leaf material, and the location of absorbing roots; to the availability or abundance of wind, water, light energy, heat, and inorganic nutrients; and to the influence of grazing animals.

A hypothetical scheme is presented for the major paths of plant succession in the Biome research area. The scheme is based on the thaw lake cycle, and the major vegetation types are seen as phases in the cycle. Plant colonization of stable surfaces may take only a few years, but the major vegetation types are generally long-lasting and change primarily in response to physical changes, such as microrelief and drainage, rather than in response to biological changes, as a result of competition.

Most human impacts upon tundra are within the range of natural perturbations, and their severity can be predicted from an understanding of the controls over ecosystem processes in natural tundra. Vehicle tracks that decrease canopy cover but do not destroy the vegetation or depress the soil surface create an impact comparable to intensive lemming grazing and the tundra may recover within a few years, or it may not. Disturbances that depress or destroy the vegetation mat initiate a series of changes in physical environment comparable to those occurring in the thaw lake cycle, and result in a corresponding recovery time, probably thousands of years.