

4 Terrain and Vegetation of the Imnavait Creek Watershed

D. A. WALKER and M. D. WALKER

4.1 Introduction

The Imnavait Creek watershed is within a large region of tussock-tundra vegetation that covers much of northern Alaska, northwestern Canada, and northeastern Russia (Bliss and Matveyeva 1992). Tussock tundra has been described in numerous areas of northern Alaska (e.g., Hanson 1951, 1953; Churchill 1955; Bliss 1956, 1962; Spetzman 1959; Douglas and Tedrow 1960; Koranda 1960; Johnson et al. 1966; Lambert 1968; Hettinger and Janz 1974; Holowaychuk and Smeck 1974; Racine 1981; Walker et al. 1982). Some of these studies have touched on the variation that occurs within tussock tundra with regard to topography, hydrology, and soils, but there remains a general impression that tussock tundra is a fairly uniform vegetation type that varies little over vast areas of the Low Arctic. This impression is often reinforced from the air as one flies over the seemingly endless expanse of tussock tundra.

On the ground, however, tussock tundra often defies description because of subtle changes in dominant growth forms and species. Although techniques such as geostatistics (Chap. 1, this Vol.) and gradient analysis (Walker et al. 1994) are useful to study these changes, it is often desirable to define discrete vegetation types and portray that variation in a map format. This is particularly valuable for exploring the spatial patterns of vegetation in relation to terrain as well as hydrological and geological variables using geographic information systems (GIS; e.g., Ostendorf 1994), and a thorough understanding of vegetation variation along natural gradients is an important starting point for developing predictive models of terrain sensitivity to disturbance (Chap. 18, this Vol.). This chapter uses a geoecological approach to describe and map the terrain and vegetation along a hillslope gradient at Imnavait Creek. It includes descriptions of all the major terrain and vegetation types within the Imnavait Creek watershed, and focuses on the changes in vegetation along a west-facing hillslope gradient.

4.2 Terrain

Our studies focused on an area within the Imnavait Creek UTM grid, a 1-km² section of watershed with 100 m between grid points, which serves as a

reference for much of the data presented in this book. Hereafter, we refer to the portion of the grid that we sampled as the Intensive Research Site (IRS; Fig. 4.1). To place these data into a regional context, we also present comparative data for the Imnavait Creek watershed (2.2 km^2) and the R4D region (22 km^2 ; see Fig. 1.1 in Chap. 1 this Vol.).

The hills near Imnavait Creek rise less than 100 m from the valley bottoms to the crests, and are elongated in SSE to NNW trending ridges. The west-facing aspects of these ridges are much gentler and longer than the east-facing aspects; in fact, over 60% of the terrain in the R4D region has NW/SW-facing aspects.

4.2.1 Glacial Deposits

Hills in this region are covered with smoothly eroded mid-Pleistocene-age glacial deposits, fine colluvium, and tussock-tundra vegetation. Shallow peat deposits are found in the basins between the ridges. Small bedrock outcrops,

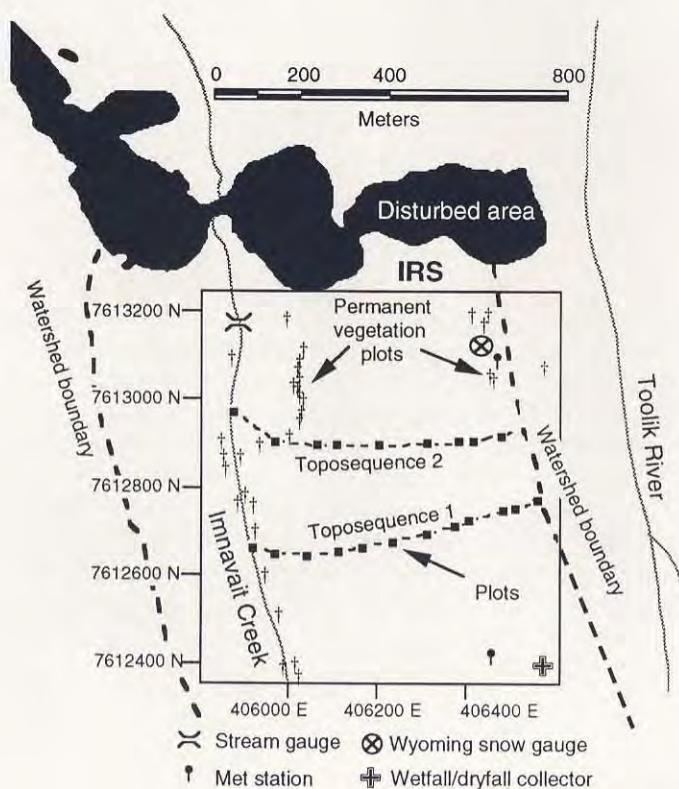


Fig. 4.1. Map of the intensive research site, showing location of the permanent vegetation plots, toposequences, and meteorological sites. UTM grid as in Fig. 1.1, Chap. 1 (this Vol.).

glacial till of late-Pleistocene age, and glaciofluvial outwash surround the Imnavait Creek watershed (Fig. 4.2). The glacial till in the Imnavait Creek watershed was deposited during the Sagavanirktok Glaciation (deglaciated about 125 000 years ago; Hamilton 1986). Glacial till is exposed primarily on ridgecrests and scattered sites on the hillslopes. About 9% of the R4D region, 4% of the watershed, and 5% of the IRS contains exposed till deposits (Fig. 4.2). These till surfaces are generally rocky and gently undulating with small blockfields (areas with greater than 50% cover of moderate-to-large-sized angular rocks; Washburn 1980) and nonsorted circles (patterned ground features composed of regularly spaced circular patches of bare ground with diameters 0.5–3 m that are formed by frost heaving of the soil; Washburn 1980). The till on most slopes is covered by fine-grained colluvium that has been retransported from upslope.

4.2.2 Retransported Hillslope Deposits

About 70% of the R4D region, 76% of the watershed, and 83% of the IRS consist of retransported hillslope deposits (Fig. 4.2). The till on the hillslopes of the watershed is covered by a clay loam that has been moved from upslope and topped with about 20–40 cm of peat. This unit is frozen and commonly contains massive ice (Kreig and Reger 1982). Scattered glacial erratics protrude up to 1 m above the tundra surface.

A variety of surficial geomorphological features are superimposed on the hillslope deposits as shown in a detailed map of the IRS (Fig. 4.3). Nonsorted stripes occur on the upper slopes and shoulders of most of the hillslopes in this region. From the air these features have a pattern oriented toward the downslope (Fig. 4.4d). The more barren stripes are relatively dry with nonsorted circles. The vegetation on these stripes, which are probably caused by combinations of cryoturbation, erosion, and gelifluction (Washburn 1980), is dominated by dwarf-shrubs and fruticose lichens (see Chap. 5, this Vol.). The interstripe areas are poorly drained, peaty, and covered with tussock-tundra vegetation. Ten percent of the R4D region, 15% of the watershed, and 4% of the IRS are covered by nonsorted stripes.

Hillslope water track, shallow drainage channels spaced tens of meters apart, are common features on the mid-to-lower portions of most hills giving them a ribbed appearance (Fig. 4.4). We distinguish hillslope water tracks (also termed horsetail drainages; Cantlon 1961) from the lowland water tracks described in mires of Minnesota, Labrador, and northern Europe where the term *water track* applies to minerotrophic drainage channels in flat peatlands (Heinselman 1970; Glaser et al. 1981; Glaser 1983). Lowland water tracks also occur in the colluvial basins of our study area. We distinguish well-defined hillslope water tracks, which have distinct channels, from weakly defined tracks, which are more subtle and do not have incised channels (Fig. 4.4b,c). Weakly defined tracks are discernible because of a greater abundance of dwarf

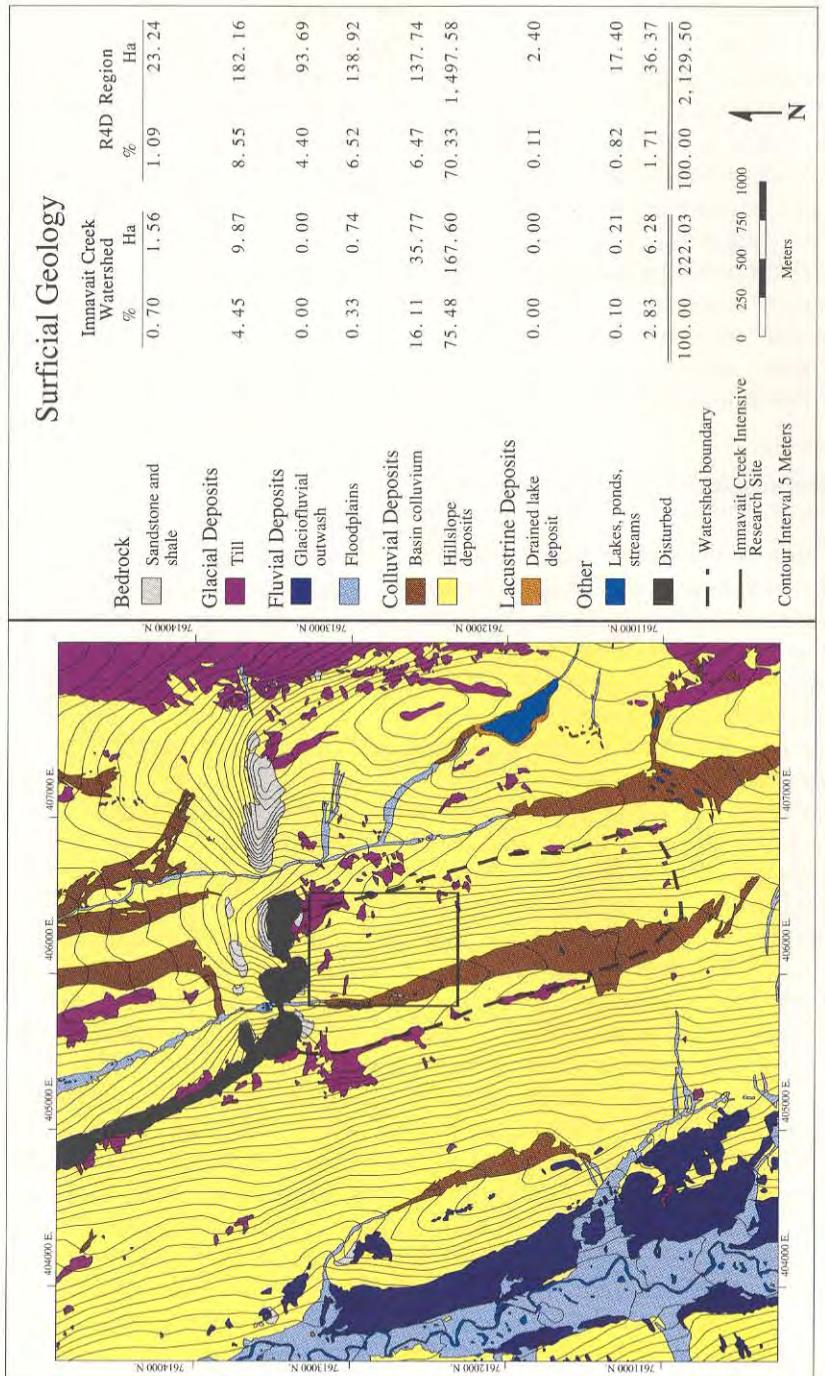


Fig. 4.2. Surficial geology of the R4D region. *Dashed line* indicates Immavait Creek watershed boundary. *Solid line* indicates intensive research site of Fig. 4.1.

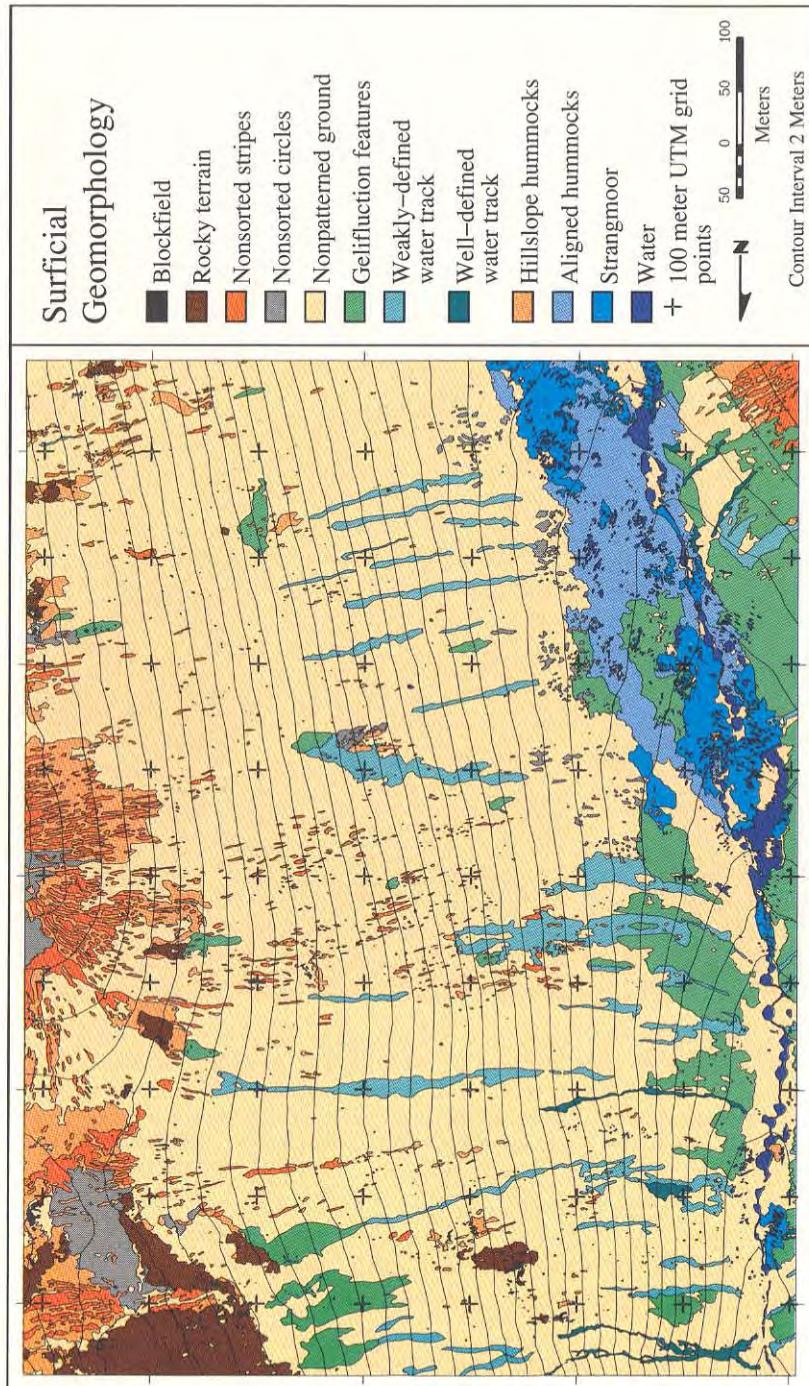


Fig. 4.3. Surficial geomorphology of the R4D intensive research site shown in Fig. 4.1

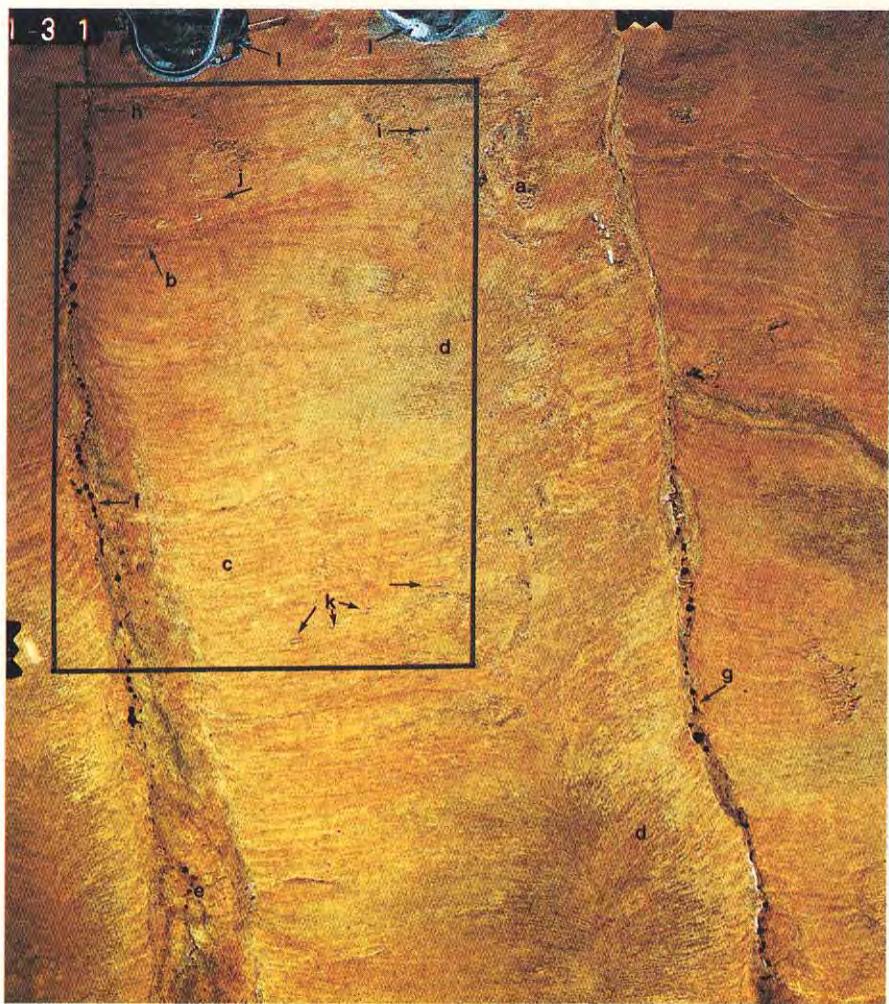


Fig. 4.4. Aerial color-infrared photograph of the Imnavait Creek research site. The black rectangle delineates the boundary of the geobotanical map (Fig. 4.6). *a* Exposed Sagavanirktock-age glacial drift; *b* well-defined hill-slope water tracks; *c* weakly defined water tracks; *d* nonsorted stripes; *e* colluvial basin; *f* beaded channel of Imnavait Creek; *g* Toolik river; *h* weir; *i* Wyoming snow gage; *j* pipeline for tundra watering experiment; *k* runoff plots; *l* gravel pad

willows and dwarf birch along the track path compared with the adjacent tundra. Well-defined water tracks cover only about 1% of the watershed and 6% of the R4D region.

Nonsorted circles are common on interfluve areas between water tracks, and are more common on upper hillslopes. Even many areas we describe as "nonpatterned" have small nonsorted circles between tussocks, i.e., they are

concealed by vegetation and are therefore not detectable on aerial photographs (Walker et al. 1989a).

Gelifluction features are earth lobes, terraces, and benches formed by the slow downslope flow saturating soil in permafrost regions (Washburn 1980). Gelifluction features are common on wetter hillslopes at the IRS and are predominantly small features, less than 20 cm high, consisting of terraces or aligned hummocks oriented perpendicular to the slope.

4.2.3 Colluvial Basin Deposits

Most of the hillslope water tracks drain into a gently sloping basin that forms the headwater of Imnavait Creek (Fig. 4.4). Similar basins occur in the bottom of valleys between smoothly rounded slopes throughout the arctic foothills. They consist of fine-grained, organic-rich deposits that appear to have moved into smaller basins from the surrounding slopes by solifluction, creep, and/or slope wash (Kreig and Reger 1982). The basins have a complex microtopography consisting of string bogs (peatlands characterized by low ridges of peat and vegetation interspersed with depressions that often contain shallow ponds; Washburn 1980), palsas (small ice-cored mounds), high-centered ice-wedge polygons, and wet areas with lowland water-track patterns. Basin colluvium covers 6% of the R4D region, 16% of the watershed, and 11% of the intensive research site.

4.2.4 Floodplain Deposits

Imnavait creek is a beaded stream (Chap. 13, this Vol.), composed of a series of small pools connected by short water courses (Fig. 4.4). The pools result from the thawing of ice masses that occur at ice-wedge polygon intersections, and the connecting drainage is commonly along the thawing ice wedges (Washburn 1980). The creek has a narrow floodplain, and only about 0.3% of the watershed has floodplain deposits. Within the surrounding R4D region extensive alluvial and glaciofluvial deposits occur along the Kuparuk River.

4.3 Vegetation

4.3.1 Flora

Imnavait Creek is in the hypoarctic zone, which lies between the boreal forest to the south and the arctic tundra zone to the north (Yurtsev 1994). The hypoarctic zone is south of the 7°C mean July isotherm (the mean July temperature at Imnavait Creek is 10.9°C). This zone is characterized by a closed vegetation cover compared with the generally open and interrupted vegetation

cover of the arctic tundra zone. Low and dwarf shrubs are a major component of the plant canopy over much of the landscape, whereas they are much less common in the arctic tundra zone (e.g., *Betula nana*, *Empetrum hermaphroditum*, *Ledum palustre* ssp. *decumbens*, *Vaccinium uliginosum*, *V. vitisidaea*, *Andromeda polifolia*). Other important boreal species include *Eriophorum vaginatum*, *Calamagrostis canadensis*, *Comarum paluster*, *Linnaea borealis*, and *Sparganium hyperboreum*. Willow thickets (e.g., *Salix planifolia* ssp. *pulchra*) occur in protected riparian areas. Tussock tundra, dominated by the cottongrass, *Eriophorum vaginatum*, or *Carex bigelowii* and the boreal shrub species mentioned above, cover the uplands and interfluves between streams.

Along an east–west floristic gradient, Imnavait Creek lies within the North Alaska subprovince of the Alaska province of the Beringian sector, which includes arctic Chukotka, east of the Indigirika River, and arctic North America, west of the Mackenzie River delta (Yurtsev 1994). During the Pleistocene glacial interval, the eastern and western parts of Beringia were linked by an unglaciated land bridge that was a corridor for many Asiatic species moving into North America (Hopkins 1982). It is one of the floristically richest areas in the Arctic. Many of the Beringian species that occur in the Imnavait Creek flora are found on dry, exposed, south-facing sandstone outcrops outside the watershed (e.g., *Astragalus umbellatus*, *Douglasia ochotensis*, *Eritrichium aretioides*, *Festuca altaica*, *Oxytropis bryophila*, *Smelowskia calycina*, *Anemone drummondii*, *Bupleurum triradiatum*, *Phlox sibirica*, *Spiraea stevenii*). Although these outcrops cover only about 1% of the region, they account for 32 species (20% of the known flora) including the endemic-to-Alaska and threatened plant *Erigeron muirii* (Murray and Lipkin 1987). The documented flora of the R4D region consists of 174 vascular plants (Appendix A). The combined flora of the Toolik Lake and Imnavait Creek regions is about 300 species (Walker, unpubl. data), of which only about 120 occur within the Imnavait Creek watershed.

4.3.2 Vegetation Types

The diversity of the vegetation physiognomy in the R4D region is shown in Fig. 4.5. This vegetation classification is based on 72 study plots at Imnavait Creek and 81 plots at the Toolik Lake site (Walker et al. 1994). Community types and subtypes were defined using the Braun-Blanquet tabular analysis approach (Westhoff and van der Maarel 1978).

A total of 22 vegetation map units occur within the IRS (Fig. 4.6). Community types are characterized by groups of species that are normally found in one type of community and are uncommon or absent in other community types. The names of the community types include two species associated with them; the second is usually the dominant species. Many types are divided into subtypes and facies. The subtypes have no characteristic taxa that separate

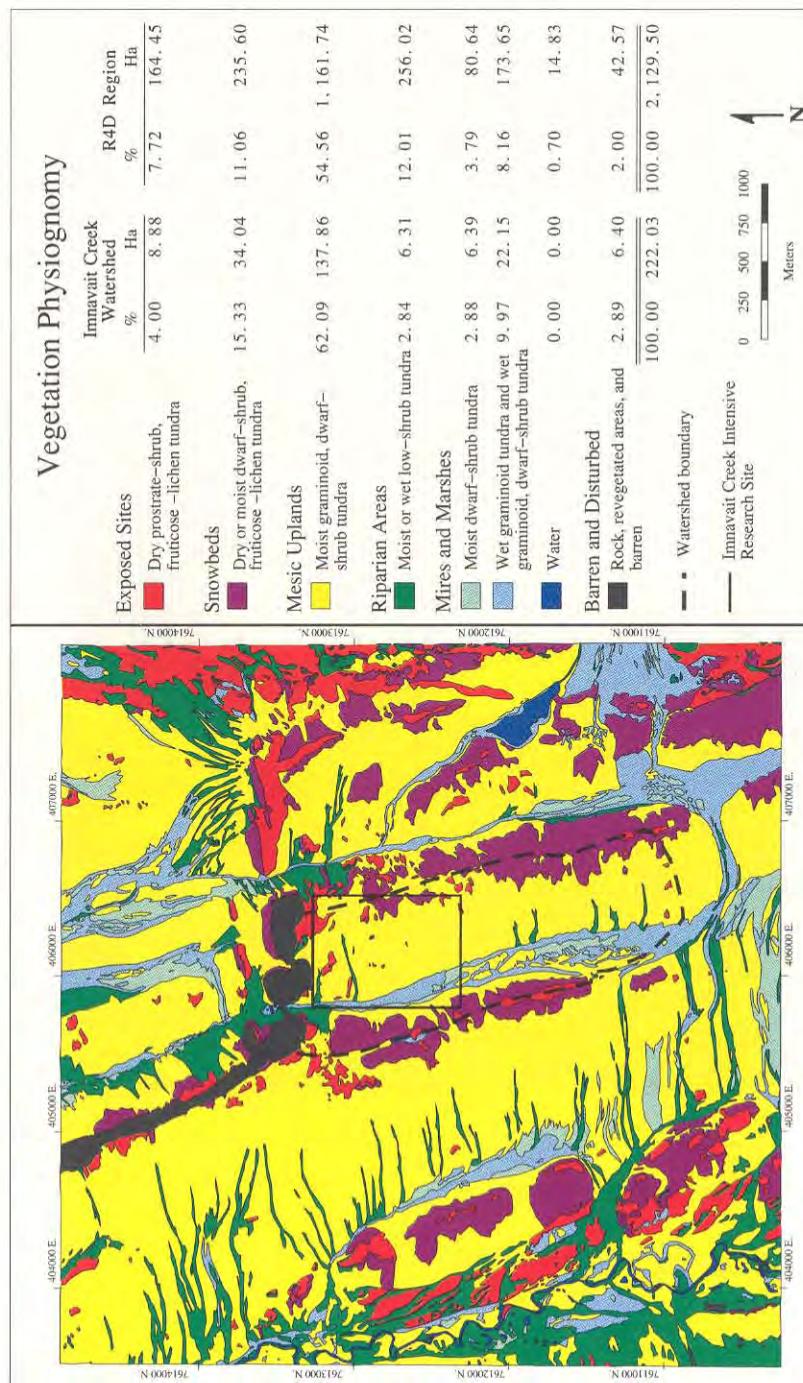


Fig. 4.5. Vegetation of the R4D region. Dashed and solid lines indicate watershed boundary and intensive research site, respectively

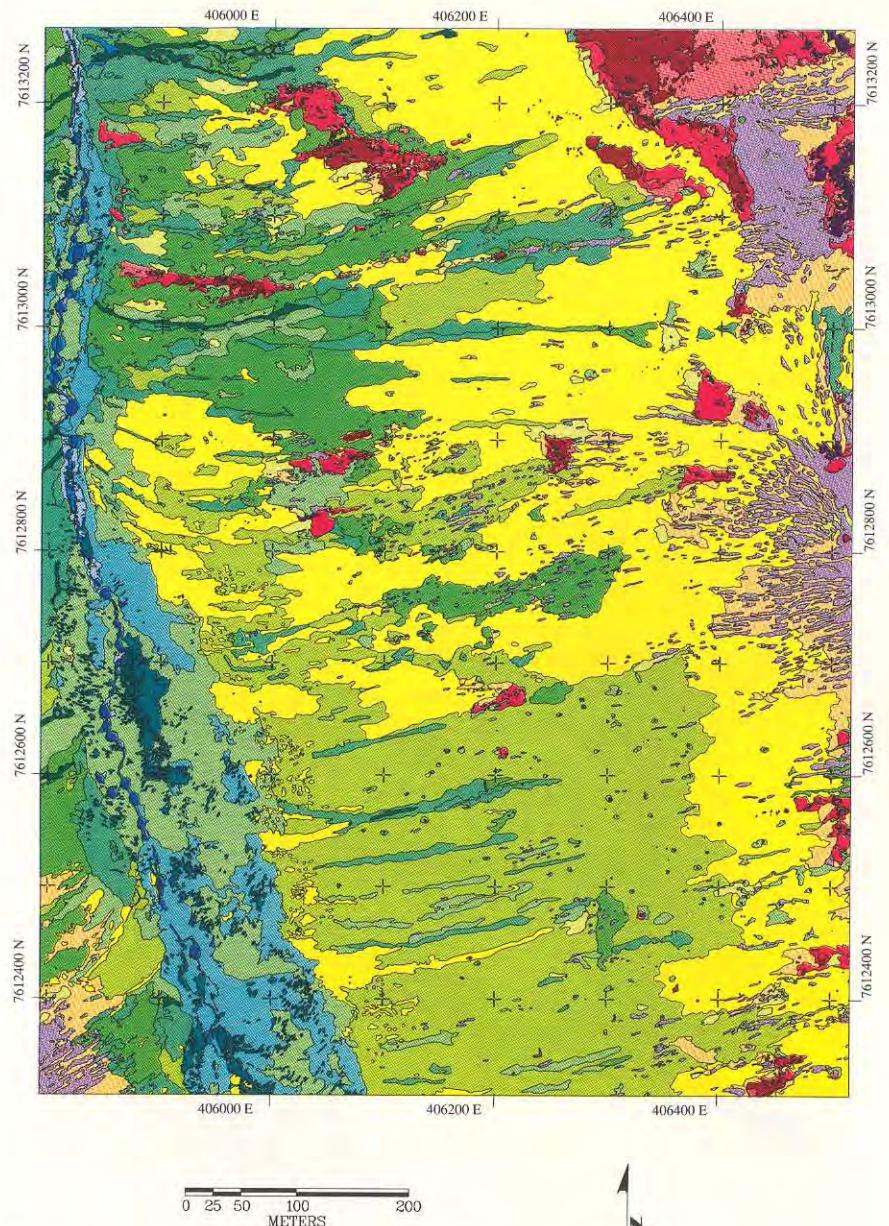


Fig. 4.6. Vegetation of the Imnavait Creek intensive research site

Vegetation, Imnavait Creek Intensive Study Area

Community Type (GIS codes)	Ha	% of Map
<i>Cetraria nigricans-Rhizocarpon geographicum</i> (07)	0. 15	0. 22
<i>Hierochloe alpina-Arctous alpina</i> , subtype <i>Arctous alpina</i> (01)	0. 89	1. 29
<i>Hierochloe alpina-Arctous alpina</i> , subtype <i>Salix phlebophylla</i> (02)	0. 06	0. 09
<i>Hierochloe alpina-Arctous alpina</i> , subtype <i>Vaccinium vitis-idaea</i> (03, 04)	0. 82	1. 18
<i>Hierochloe alpina-Betula nana</i> (06)	1. 52	2. 21
<i>Diapensia lapponica-Cassiope tetragona</i> , subtype <i>Calamagrostis inexpressa</i> (05)	3. 34	4. 85
<i>Diapensia lapponica-Cassiope tetragona</i> , subtype <i>Nephroma arcticum</i> (09)	0. 17	0. 25
<i>Sphagnum rubellum-Eriophorum vaginatum</i> , subtype <i>Eriophorum vaginatum</i> (10)	20. 50	29. 74
<i>Sphagnum rubellum-Eriophorum vaginatum</i> , subtype <i>Carex bigelowii</i> (11)	1. 04	1. 51
<i>Sphagnum rubellum-Eriophorum vaginatum</i> , subtype <i>Cassiope tetragona</i> (14)	3. 09	4. 48
<i>Sphagnum rubellum-Eriophorum vaginatum</i> , subtype <i>Betula nana</i> (tussock tundra facies) (12)	15. 17	22. 01
<i>Sphagnum rubellum-Eriophorum vaginatum</i> , subtype <i>Salix planifolia</i> ssp. <i>pulchra</i> (tussock tundra facies) (13)	6. 16	8. 94
<i>Sphagnum rubellum-Eriophorum vaginatum</i> , subtype <i>Betula nana</i> (shrubland facies) (15)	6. 21	9. 01
<i>Sphagnum rubellum-Eriophorum vaginatum</i> , subtype <i>Salix planifolia</i> ssp. <i>pulchra</i> (shrubland facies) (16, 17)	4. 96	7. 20
<i>Eriophorum angustifolium-Salix planifolia</i> ssp. <i>pulchra</i> (26)	0. 33	0. 48
<i>Salix chamissonis-Carex aquatilis</i> (25, 19)	0. 23	0. 34
<i>Eriophorum angustifolium-Carex aquatilis</i> (21, 22)	0. 08	0. 12
<i>Sphagnum lenense-Salix fuscescens</i> (23, 24)	3. 04	4. 41
<i>Sphagnum orientale-Eriophorum scheuchzeri</i> (20, 28)	0. 85	1. 22
<i>Hippuris vulgaris-Sparganium hyperboreum</i> (29)	0. 05	0. 08
Barren and miscellaneous vegetation types (08, 18, 30, 33, 34)	0. 23	0. 34
Water (31)	0. 03	0. 03
Totals	68. 92	100. 00

Table 4.1. Environmental and soil information for community types at the Innavaït Creek intensive research site (values are mean \pm standard error.)

	Cetnig-Rhigeo ^a (n = 2)	Hiealp-Arcalp (n = 12)	Hiealp-Betnan (n = 4)	Dialap-Castet (n = 13)	Sphrub-Erivg (n = 33)	Eriang-Saplpa (n = 6)	Sphlien-Salfus (n = 6)	Sphori-Erisch (n = 3)	Eriang-Caraqu (n = 5)	Hipvul-Spahyp (n = 3)
<i>Environment</i>										
Slope (°)	1 \pm 1	5 \pm 2	2 \pm 1	17 \pm 4	4 \pm 0	10 \pm 4	2 \pm 1	1 \pm 0	1 \pm 0	0 \pm 0
Aspect (°)	90	210 \pm 39	90 \pm 90	161 \pm 38	199 \pm 22	173 \pm 54	316 \pm 14	325 \pm 25	355 \pm 5	n.d.
Exposure (scalar) ^b	2.0 \pm 0.0	3.0 \pm 0.2	2.4 \pm 0.4	2.1 \pm 0.2	2.0 \pm 0.1	1.7 \pm 0.1	1.8 \pm 0.0	1.8 \pm 0.0	1.7 \pm 0.1	1.0 \pm 0.0
Site moisture (scalar) ^c	1.5 \pm 0.0	3.8 \pm 0.1	4.3 \pm 0.3	4.6 \pm 0.2	6.8 \pm 0.1	8.3 \pm 0.5	7.7 \pm 0.3	8.3 \pm 0.3	8.7 \pm 0.4	10.0 \pm 0.0
Snow duration (scalar) ^d	3.8 \pm 0.3	3.2 \pm 0.4	3.9 \pm 0.5	5.0 \pm 0.4	4.3 \pm 0.1	4.2 \pm 0.6	4.8 \pm 0.4	4.0 \pm 0.0	4.4 \pm 0.2	4.0 \pm 0.0
Stability (scalar) ^e	1.0 \pm 0.0	1.3 \pm 0.1	1.1 \pm 0.1	2.2 \pm 0.2	2.1 \pm 0.2	3.7 \pm 0.2	2.1 \pm 0.4	1.5 \pm 0.3	3.0 \pm 0.8	3.7 \pm 0.9
Thaw depth (cm)	n.d.	82 \pm 18	45 \pm 15	71 \pm 7	36 \pm 3	50 \pm 4	30 \pm 5	40 \pm 2	51 \pm 8	43 \pm 13
Bare soil (%)	0.0 \pm 0.0	0.6 \pm 0.3	0.0 \pm 0.0	0.1 \pm 0.1	0.4 \pm 0.3	7.0 \pm 4.8	0.3 \pm 0.3	9.3 \pm 3.5	11.0 \pm 6.0	20.0 \pm 5.8
Rock cover (%)	95.0 \pm 0.0	6.1 \pm 2.1	0.0 \pm 0.0	1.4 \pm 0.7	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
<i>Soil characteristics at 10 cm depth</i>										
Organic matter (%)	n.d.	9.10 \pm 2.76	39.15 \pm 13.46	29.62 \pm 5.03	53.81 \pm 5.46	29.15 \pm 8.86	76.27 \pm 4.12	79.40 \pm 8.36	55.91 \pm 11.99	70.83
Sand (%)	n.d.	54.1 \pm 3.0	58.0	39.0 \pm 6.3	15.9 \pm 4.5	11.8 \pm 5.5	21 \pm 0.5	4.1 \pm 2.3	30.9 \pm 21.4	n.d.
Silt (%)	n.d.	30.4 \pm 2.2	30.0	38.5 \pm 3.4	40.6 \pm 4.9	37.1 \pm 4.3	51.9 \pm 6.6	52.6 \pm 6.8	43.4 \pm 14.9	n.d.
Clay (%)	n.d.	15.5 \pm 3.1	12.0	22.5 \pm 4.5	42.4 \pm 5.1	51.0 \pm 8.1	46.1 \pm 6.3	43.3 \pm 9.1	25.7 \pm 6.5	n.d.
Soil moisture (%) ^f	n.d.	19.3 \pm 4.1	111.2 \pm 48.5	84.0 \pm 25.1	318.8 \pm 48.2	302.7 \pm 109.0	507.4 \pm 35.2	631.5 \pm 14.5	508.2 \pm 100.5	407.0
pH ^g	n.d.	4.0 \pm 0.1	3.8 \pm 0.2	4.4 \pm 0.2	4.6 \pm 0.1	4.0 \pm 0.2	4.4 \pm 0.2	4.3 \pm 0.2	5.1 \pm 0.4	4.1

n.d., no data.

^aCommunity types: abbreviations use the first three letters of the species name plus the first three letters of the species name, e.g. Cetnig-Rhigeo is community type *Cetraria nigricans* – *Rhizocarpon geographicum*.

^b1 (protected) to 4 (very exposed).

^c1 (extremely xeric) to 10 (hydric).

^d1 (snow-free all year) to 10 (deep snow all year).

^e1 (stable) to 5 (disturbed more than once annually).

^fGravimetric soil moisture.

^gSaturated paste method.

them from other subtypes; they are defined mainly on the basis of differences in species dominance. Facies are finer divisions of subtypes that relate to the general physiognomy of the plant canopy.

The dominant vegetation types that generally follow a moisture gradient from dry-to-wet sites along an idealized hillslope gradient within the IRS (Fig. 4.7) are described in Sections 4.3.2.1–4.3.2.6. A summary of key environmental and soil variables is given in Table 4.1.

4.3.2.1 Lichen-Covered Rocks

Crustose and foliose lichens are abundant on most rocks and dominate vegetation communities on blockfields, sorted stone polygons, and isolated glacial erratics. Most of the rocks within the IRS are acidic conglomerate sandstone derived from the Kanayut formation. We sampled only two of these rocky sites, and defined a single community type, *Cetraria nigricans-Rhizocarpon geographicum*. This unit comprises only about 0.2% of the IRS. A detailed analysis of lichen communities and non-rock substrates, including species composition and aboveground biomass, is given in Chap. 5 (this Vol.).

4.3.2.2 Dry Heath

Dry heaths occur on windblown ridge tops and on early-melting snowbed areas. Prostrate shrubs and fruticose lichens are the primary growth forms. Winter snow cover strongly affects the relative dominance of species within the heath vegetation types. Very exposed windblown sites with *Selaginella sibirica-Dryas octopetala* communities are common on sandstone outcrops within the R4D region (Chap. 5, this Vol.), but do not occur within the IRS. Somewhat less exposed sites with shallow snow cover occupy about 4.8% of the IRS; the main plant communities are *Hierochloë alpina-Arctous alpina*, and *Hierochloë alpina-Betula nana*. Areas with deeper snow (50–150 cm) have the *Diapensia lapponica-Cassiope tetragona* community type.

Fig. 4.7a–f. Common vegetation types in the intensive research site. a Dry acidic glacial till with community type *Hierochloë alpina-Arctous alpina*; subtype *Arctous alpina*; b moderately deep snowbeds with community type *Nephroma arcticum-Cassiope tetragona*; c moist uplands with shrub-rich tussock tundra, community type *Sphagnum rubellum-Eriophorum vaginatum* subtype *Betula nana*; d well-developed water track with community type *Eriophorum angustifolium-Salix planifolia* ssp. *pulchra*; e Elevated microsites in colluvial basins have community type *Sphagnum lenense-Salix fuscescens*, and wet microsites between hummocks have community type *Sphagnum orientale-Eriophorum scheuchzeri*; f Beaded pond with *Eriophorum angustifolium-Carex aquatilis* around margin of pond (vegetation in the pond is *Sparganium hyperboreum-Hippuris vulgaris*)

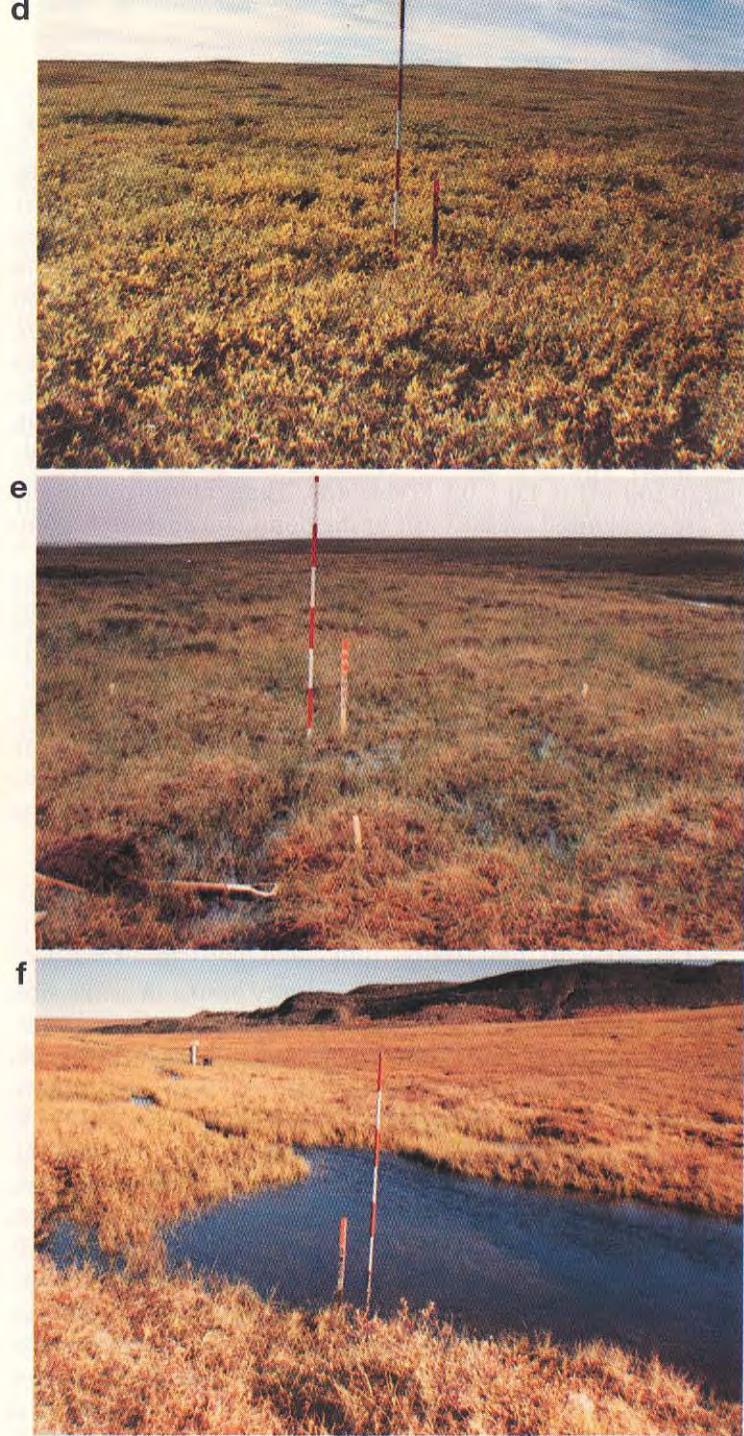
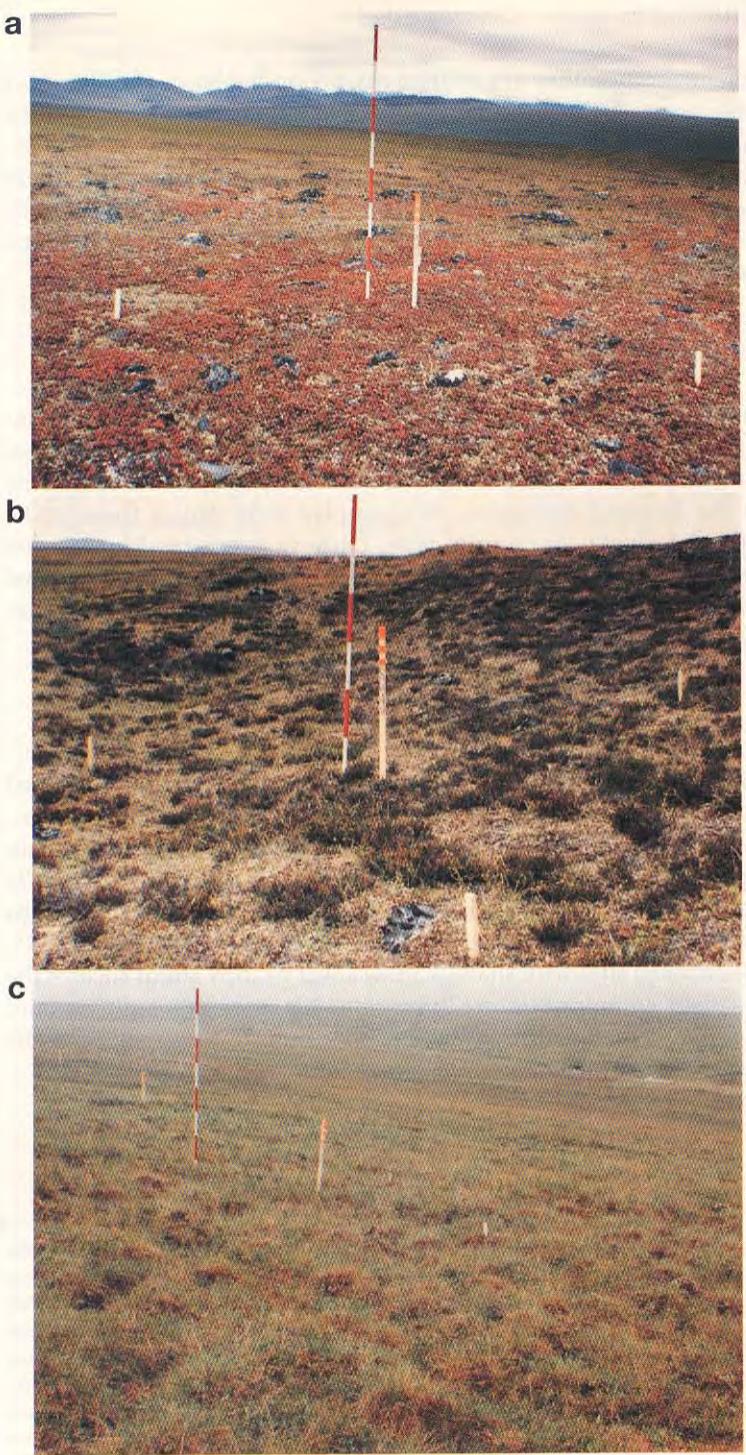


Fig. 4.7 (continued).

4.3.2.2.1 Exposed Sites

The *Hierochloë alpina-Arctous alpina* community (Fig. 4.7a) occurs on dry, rocky, windblown, acidic glacial deposits that cover about 2.6% of the IRS (Fig. 4.6); common species include *Arctous alpina*, *Hierochloë alpina*, *Salix phlebophylla*, *Vaccinium vitis-idaea*, *V. uliginosum* ssp. *microphyllum*, *Ledum palustre* spp. *decumbens*, the mosses *Dicranum cf. elongatum*, *Polytrichum strictum*, *P. piliferum*, and the lichens *Alectoria ochroleuca*, *Asahinea chrysantha*, *Bryocaulon divergens*, *Cetraria cucullata*, *Cetraria nivalis*, *Cetraria islandica*, *Cladonia amaurocraea*, *C. coccifera*, *C. gracilis*, *Dactylina arctica*, *Masonhalea richardsonii*, *Sphaerophorus globosus*, and *Thamnolia subuliformis*. The soils are rocky, deeply thawed, acidic, mineral soils with shallow organic-rich surface horizons. The depth of thaw at the end of summer is 82 ± 18 cm; mean soil pH is 4.0 ± 0.1 (Table 4.1). Three physiognomically similar subtypes are recognized on the basis of the dominant species: *Arctous alpina* (Fig. 4.7a), *Salix phlebophylla*, and *Vaccinium vitis-idaea*.

The *Hierochloë alpina-Betula nana* community is dominated by dwarf birch. This community type is found in dry, somewhat protected sites such as depressions in the till or in the lee of larger rocks on till deposits. It covers about 2.2% of the IRS. It has a suite of moist species that thrive in the protection of the birch overstory including *Pedicularis labradorica*, *Aulacomnium turgidum*, *Dicranum angustum*, and *Hylocomium splendens*. The soils are moister and have thicker organic surface horizons (Table 4.1) than those of the *Hierochloë alpina-Arctous alpina* community, due to the presence of moss carpets.

4.3.2.2.2 Snowbeds

The *Diapensia lapponica-Cassiope tetragona* community occurs in acidic sites with shallow to moderately deep snowbeds (0.3–4.0 m of snow). It is characterized by a high cover of dwarf and prostrate shrubs (e.g., *Cassiope tetragona*, *Diapensia lapponica* ssp. *obovata*, *Ledum palustre* spp. *decumbens*, *Loiseleuria procumbens*, *Salix phlebophylla*, *Vaccinium vitis-idaea*, *V. uliginosum*) and fruticose lichens (e.g., *Cladina rangiferina*, *C. arbuscula*, *Cetraria cucullata*, *C. nivalis*, *C. islandica*, *Cladonia gracilis*, *C. amaurocraea*, *Dactylina arctica*, *Peltigera aphthosa*, *Stereocaulon tomentosum*, and *Sphaerophorus globosus*). Common forbs include *Pedicularis capitata*, *P. langsdorffii* ssp. *arctica*, and *Polygonum bistorta*. *Cassiope tetragona* is typically found in moderately deep snowbeds in much of the Arctic (Nordhagen 1943; Churchill 1955; Rönning 1965; Alexandrova 1980; Cooper 1986; Evans et al. 1989; Walker 1990). Although it occurs outside of snowbeds as well, it reaches its greatest cover and abundance on moderately deep snowbeds. It is relatively insensitive to substrate pH (Böcher 1954). Two subtypes were recognized: *Calamagrostis inexpansa* and *Nephroma arcticum*.

The *Calamagrostis inexpansa* subtype occurs primarily on the dry mineral element of nonsorted stripes, which often also holds shallow snow drifts. Highly variable, this type is intermediate between the dry heath and the true snowbed communities. It covers about 4.9% of the IRS (Fig. 4.6). This subtype has a high cover of dry species and species occurring on mineral soils (e.g., *Cladonia coccifera*, *Dicranum cf. elongatum*, *Petasites frigidus*, *Salix phlebophylla*, and *Sphaerophorus globosus*), and a relatively low cover of mesic species (e.g., *Cassiope tetragona*, *Hylocomium splendens*, and *Aulacomnium turgidum*). The soils are deeply thawed (>100 cm).

Subtype *Nephroma arcticum* occurs in moderately deep snowbeds, often on north-facing slopes where the snow cover may persist through late June to early July. A few poorly developed versions of this type occur on east-facing depressions within the study area, where snow depths are about 75 cm in early May (Fig. 4.7b). This unit covers only 0.3% of the IRS. The moss carpet is better developed than in the *Calamagrostis inexpansa* subtype, and therefore harbors a relatively high cover of mesic taxa such as *Hylocomium splendens*, and a relatively low cover of dry taxa such as *Salix phlebophylla*. Other common taxa include *Carex microchaeta*, *C. tetragona*, *Dicranum scoparium*, *Dactylina ramulosa*, *Huperzia selago*, *Nephroma arcticum*, *Novosieversia glacialis*, *Parrya nudicaulis*, *Pogonatum urnigerum*, *Ptilium crista-castrensis*, *Pyrola grandiflora*, *Rhytidium rugosum*, *Saxifraga nelsoniana*, *Senecio atropurpureus*, and *Abietinella abietina*.

4.3.2.3 Tussock Tundra

Tussock tundra is the zonal vegetation on mesic slopes throughout the foothills. Considerable variations in species and growth-form dominance within this broad physiognomic unit correspond to variations in substrate pH, site stability, snow, and soil moisture (Walker et al. 1994). *Sphagnum rubellum-Eriophorum vaginatum* is the most common community type on acidic uplands (Fig. 4.7c), and covers about 58% of the IRS (Fig. 4.6). Important vascular species associated with this community include *Eriophorum vaginatum*, *Betula nana*, *Salix planifolia* ssp. *pulchra*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Rubus chamaemorus*, *Carex bigelowii*, *Cassiope tetragona*, *Ledum palustre* spp. *decumbens*, *Petasites frigidus*, *Bistorta vivipara*, and *Pedicularis lapponica*. Common mosses include *Sphagnum angustifolium*, *S. balticum*, *S. lenense*, *S. rubellum*, *S. teres*, *Dicranum* spp., *Polytrichum strictum*, *Hylocomium splendens*, *Aulacomnium turgidum*, and *A. palustre*. Common lichens are *Cetraria cucullata*, *C. islandica*, *Cladina rangiferina*, *C. arbuscula*, *Cladonia amaurocraea*, *C. gracilis*, *Dactylina arctica*, and *Peltigera aphthosa*.

The soils are wet with shallow organic horizons generally 10–25 cm thick. The mineral portion of the soils are generally high in clay ($42 \pm 5\%$) and are gleyed (neutral gray color due to waterlogging and lack of oxygen) with abun-

dant orange mottles due to intermittent saturation. The average depth of the active layer is 36 ± 3 cm (Table 4.1).

Nonacidic uplands (community type *Tomentypnum nitens-Carex bigelowii*) are rare within the Imnavait Creek region, but they are found in few sites outside of the watershed where the groundwater pH is relatively high, such as at the base of some steep slopes. Although the physiognomies of acidic and nonacidic moist tundra are similar, few species occur in both types (e.g., *Eriophorum vaginatum*, *Carex bigelowii*, *Aulacomnium turgidum*, and several lichen species). Minerotrophic species dominate the nonacidic sites (e.g., *Dryas integrifolia*, *Salix reticulata*, *Salix arctica*, *Eriophorum triste*, *Lagotis glauca*, *Tofieldia pusilla*, *Rhododendron lapponicum*, *Pedicularis oederi*, *Equisetum variegatum*, *Saussurea angustifolia*, *Tomentypnum nitens*, *Orthothecium chryseum*, and *Ditrichum flexicaule*).

Five acidic tussock tundra subtypes can be consistently recognized on the basis of species and growth-form dominance: subtypes *Eriophorum vaginatum*, *Betula nana*, *Carex bigelowii*, *Salix planifolia* ssp. *pulchra*, and *Cassiope tetragona*. These subtypes show distinct distribution patterns with regard to micro- and mesotopographic slope positions, moisture, snow, and site stability. The *Cassiope tetragona* subtype occurs mainly on gentle ($<4\%$) slope shoulders in interstripe elements of nonsorted stripe complexes and in association with shallow snow drifts. Subtype *Eriophorum vaginatum* characterizes gentle upper slopes and footslopes, reaching its peak abundance on slopes of less than 9%, whereas subtypes *Betula nana* and *Salix planifolia* ssp. *pulchra* are more common near water tracks and on steeper slopes ($>12\%$). Similar trends have been noted for the distribution of *Eriophorum vaginatum*, *Carex bigelowii*, and dwarf shrubs on a southwest-facing toposequence on the Seward Peninsula (Racine 1981).

4.3.2.4 Riparian Areas

Most of the IRS consists of a mosaic of poorly-defined water track communities and tussock tundra – only a few well-defined water tracks are present. Vegetation in the water tracks varies with the degree of channel development. Weakly developed water tracks have communities that are scarcely distinguishable from tussock tundra, whereas well-developed tracks contain distinctive willow and dwarf-birch communities. The common sequence of communities associated with well-defined water tracks is (1) *Sphagnum rubellum-Eriophorum vaginatum* subtype *Eriophorum vaginatum* on the interfluvia, grading into (2) subtype *Betula nana* (tussock-tundra faces), grading into (3) subtype *Betula nana* (shrubland facies), grading into (4) subtype *Salix planifolia* ssp. *pulchra* (shrubland facies), grading into (5) community-type *Eriophorum angustifolium-Salix planifolia* ssp. *pulchra* in the channel of the water track (Fig. 4.7d). In addition, tracks where the water flows all summer long harbor a sixth community in the track channel dominated by almost pure stands of *Eriophorum angustifolium*.

Sphagnum rubellum-Eriophorum vaginatum, subtype *Betula nana* (shrubland facies), forms distinctive margins along many well-developed water tracks. It occupies about 9% of the IRS. It is easily recognized by the dominance of *Betula nana* and *Rubus chamaemorus*, and thick *Sphagnum* moss carpet. It is particularly noticeable in the fall when the *Betula nana* turns red and contrasts with the yellow willows in the center of the tracks. Although this community type is characterized by the high constancy and abundance of *B. nana* and *R. chamaemorus*, and the sporadic occurrence and low cover of *Eriophorum vaginatum* and *Carex bigelowii*, there are no characteristic taxa that distinguish it from other tussock tundra subtypes. Soil pH is low, averaging 4.4. The soils have deep organic horizons that cause reduced summer thaw relative to the adjacent tussock tundra areas (e.g., thaw in the birch subtype averaged 35 ± 1 cm and that in the *Eriophorum vaginatum* tussock tundra averaged 48 ± 4 cm). This may tend to hydrologically isolate the water track from the surrounding tussock tundra.

Subtype *Salix planifolia* ssp. *pulchra* (shrubland facies) covers 7.2% of the IRS. It occurs in upland water tracks and on lower slopes, areas with a somewhat higher seasonal water flux than areas with subtypes *Eriophorum vaginatum* and *Betula nana*. These stands are characterized by high constancy and a cover of *Aulacomnium palustre*, *Petasites frigidus*, *Rubus chamaemorus*, *S. planifolia* ssp. *pulchra*, and *Sphagnum rubellum*, as well as the differential taxa *Saxifraga nelsoniana*, *Bistorta vivipara*, *Poa arctica*, *Sanionia uncinatus*, *Scapania paludicola*, and *Sphagnum warnstorffii*. Soil characteristics differ between the *Betula* and *Salix* subtypes, reflecting their different positions in the landscape. Greater water flux in the *S. planifolia* ssp. *pulchra* subtype results from a deeper summer thaw (56 ± 2 cm) and soils that are relatively minerotrophic and aerobic. Soil pH is relatively high (5.1 ± 0.9 compared with 4.2 ± 0.2 for the *Betula nana* subtype).

The distinctive community type *Eriophorum angustifolium-Salix planifolia* ssp. *pulchra* (Fig. 4.7d) occurs in the channels of well-defined water tracks, and covers about 0.5% of the IRS. These stands have medium-height (50–100 cm) *S. planifolia* ssp. *pulchra* with *Eriophorum angustifolium* understories. Species diversity is relatively low, and the stands are floristically distinct from tussock tundra areas, with several differential taxa, including *Calliergon stramineum*, *C. giganteum*, *Eriophorum angustifolium* var. *subarcticum*, *Valeriana capitata*, and *Polemonium acutiflorum*. These sites accumulate snow because of depressions associated with the water tracks (mean snow depth in early May is 66 ± 3 cm).

Riparian areas along upper Imnavait Creek are representative of headwaters of many high-elevation tundra streams. They lack well-developed willow shrublands that occur along the lower reaches of these streams. The riparian vegetation grades into the mire vegetation types found in the colluvial basin at the head of Imnavait Creek (see Sect. 4.3.2.5). The streamside community *Salix chamissonis-Carex aquatilis* covers about 0.3% of the IRS and is physiognomically similar to the mire communities, but it has species that are

rare elsewhere including *Aconitum delphinifolium* ssp. *paradoxum*, *Anemone richardsonii*, *Aster sibiricus*, *Calamagrostis canadensis*, *Climacium dendroides*, *Dodecatheon frigidum*, *Gentianella propinqua* ssp. *arctophila*, *Festuca altaica*, *Lycopodium annotinum*, *Paludella squarrosa*, *Philonotis fontana* var. *pumila*, *Plagiognathus ellipticum*, *Polemonium acutiflorum*, *Rubus arcticus*, *Senecio lugens*, *Salix chamissonis*, *Solidago multiradiata* var. *multiradiata*, *Valeriana capitata*, *Wilhelmsia physodes*, and *Zygadenus elegans*. These species become more common downstream from the IRS. Better-developed riparian willow shrublands (*Salix lanata* spp. *richardsonii*, *S. planifolia* ssp. *pulchra*, and *S. alaxensis*) occur along the meandering Kuparuk River.

4.3.2.5 Mires

The Imnavait Creek colluvial basin exhibits complex patterns of plant communities that are related to microtopography and the relative position of microsites with regard to the water table. The basin is relatively acidic compared with, for example, colluvial basins near Toolik Lake. Most wetlands in the Imnavait Creek watershed have soil pH ranging from 4.1 to 4.8; at Toolik Lake, soil pH ranges from 4.6 to 6.6. The acidity of the soil and water is presumably derived from the cation exchange system of *Sphagnum* (Clymo 1963; Clymo and Hayward 1982) and the concentration of organic acids from decomposition (Gorham et al. 1985).

The colluvial basin at the head of Imnavait Creek is a mosaic of poor fens and bogs. The pH of the water in Imnavait Creek averages 5.9 ± 2.0 , and Ca ion concentration averages $55.3 \pm 11.2 \text{ } \mu\text{eq l}^{-1}$ (Chap. 9, this Vol.). If these values can also be used for the surface waters in the nearby colluvial basin, then Ca ion concentrations are sufficiently low to satisfy the criteria for a bog, but the pH values are those of an intermediate fen (Heinselman 1970). Some low microsites even have a few rich-fen plant species such as *Sphagnum warnstorffii*, *Scorpidium scorpioides*, and *Aneura pinguis*. Permafrost hydrologically isolates some palsas and raised microsites above the groundwater table due to permafrost, and pH of these sites is very low (<4).

We mapped three broad mire community types, one that occurs in slightly minerotrophic sites, and two in acidic mires. *Eriophorum angustifolium-Carex aquatilis* occurs in somewhat minerotrophic water tracks and the channel of Imnavait Creek between beaded ponds. This type consists of almost pure stands of *C. aquatilis* and *E. angustifolium* ssp. *subarcticum*. These stands are floristically depauperate. There are no unique faithful taxa nor any differential taxa. Similar communities inhabit the shallow water of the mires in the colluvial basin. These communities occupy only about 0.1% of the IRS.

Acidic mires predominate in most of the colluvial basin. Community-type *Sphagnum lenense-Salix fuscescens* (Fig. 4.7e) occurs on raised microsites, such as strangs and hummocks, and covers about 4.4% of the IRS. It includes the characteristic acidic-wetland taxa: *Carex rariflora*, *C. rotundata*,

Eriophorum scheuchzeri, *Polytrichastrum alpinum*, *Sphagnum fimbriatum*, *S. imbricatum*, and *S. rubellum*, plus the differential species found in slightly less-wet microsites, *Andromeda polifolia*, *Salix fuscescens*, *Sphagnum aongstroemii*, and *S. lenense*.

Community-type *Sphagnum orientale-Eriophorum scheuchzeri* (Fig. 4.7e) occurs in low microsites of wet meadows, pond margins, and lowland water tracks. It has a single faithful taxon, *Sphagnum orientale*; it covers 1.2% of the IRS. *Pedicularis albolabiata* and *Carex rotundata* reach their peak abundance in this type.

4.3.2.6 Beaded Ponds

Several beaded ponds in Imnavait Creek have aquatic communities. The *Hippuris vulgaris-Sparganium hyperboreum* community occurs in water up to 2 m deep, and occupies less than 0.1% of the IRS. The shallower pond margins have a group of characteristic aquatic taxa including *Caltha palustris*, *Comarum palustre*, *Hippuris vulgaris*, *Sparganium hyperboreum*, *Sphagnum squarrosum*, and *S. lindbergii* (Fig. 4.7f). The soils are generally thick mats of undecomposed peat moss.

4.4 West-Facing Toposequence

The trends in surface forms, vegetation structure, species composition, and soil characteristics along west-facing hillslope gradients are summarized in the idealized toposequence (Fig. 4.8; see Fig. 4.1 for location of the transects). Generally, the crests of the hills have rocky glacial till with frost scars, acidic mineral soils with organic horizons surface horizons (Pergelic Cryumbrepts in the US soil taxonomy; Soil Survey Staff 1975), and dry, dwarf-shrub, fruticose-lichen tundra (dry heath vegetation). The hillslope shoulders have nonsorted stripes with frost-scar complexes, Pergelic Cryumbrept soils, and dry, dwarf-shrub, fruticose-lichen tundra on the stripes. Between the stripes are wet nonacidic soils with thin organic horizons (Pergelic Cryaquepts) and moist, sedge, dwarf-shrub tundra. The upper backslopes have nonpatterned surfaces, acidic Pergelic Cryaquept soils, and tussock tundra. The interfluves between water tracks show an abundance of gelification features and thicker surficial organic layers downslope, so that soils near the footslope are classified as acidic Histic Pergelic Cryaquepts (organic horizons >25 cm thick). The vegetation becomes increasingly dominated by dwarf shrubs (e.g., *Betula nana* and *Rubus chamaemorus*) and *Sphagnum* moss. The gradual hillslope interfluvе transition often culminates on the footslope with a moist or wet dwarf-shrub moss tundra. The transition from the hillslope to the colluvial basin or stream floodplain is generally abrupt.

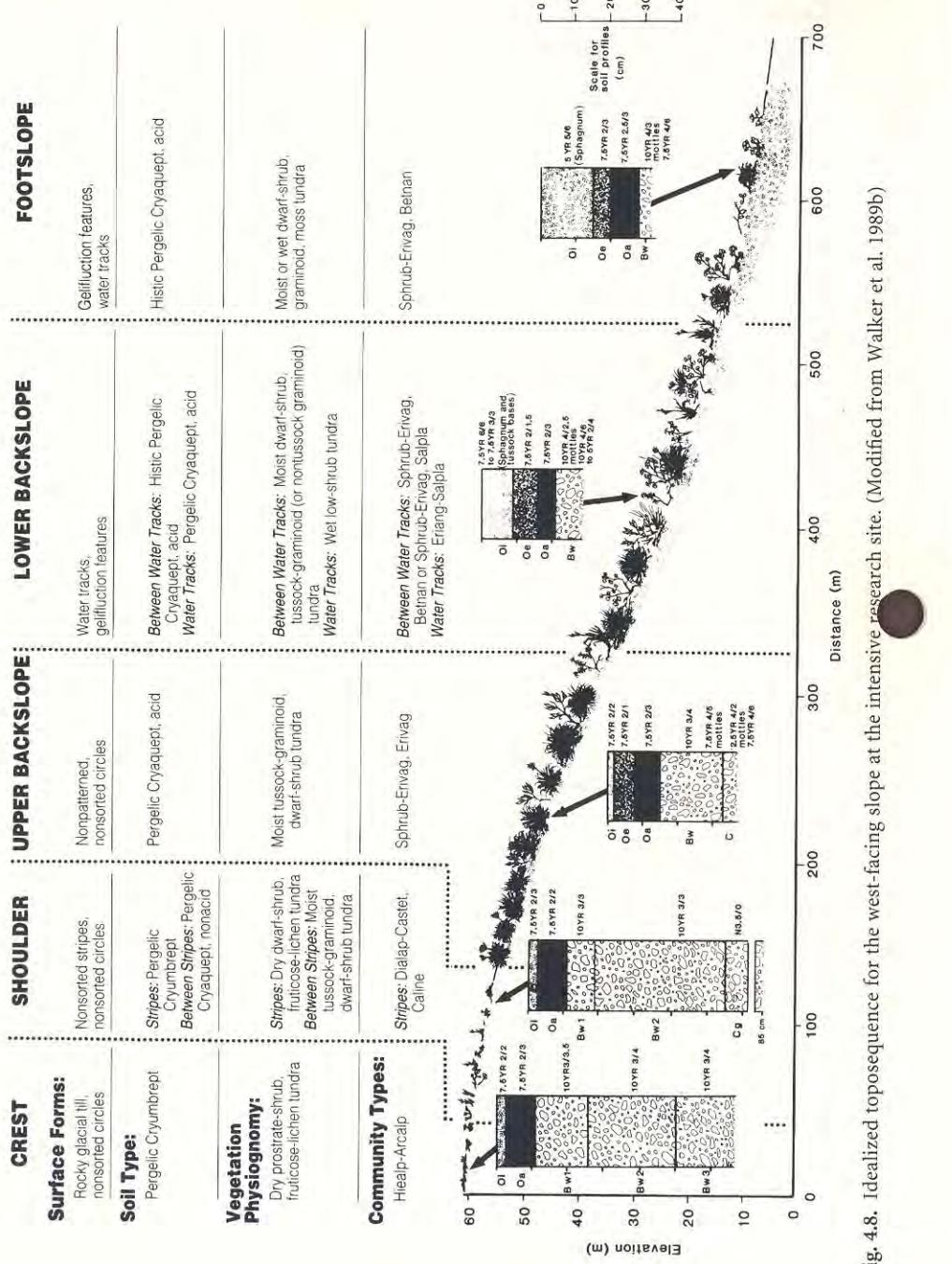


Fig. 4.8. Idealized toposequence for the west-facing slope at the intensive research site. (Modified from Walker et al. 1989b)

There are a number of downslope trends in vegetation along the toposequence. These are illustrated in Fig. 4.9a–e: (a) an overall decrease in species richness, due mainly to (b) a bimodal distribution for dwarf shrubs; (c) a maximum of graminoid species (mostly sedges) on the upper backslope; (d) the abundance of lichens on the hillcrest and shoulder; and (e) a general increase in mosses, primarily *Sphagnum*. On the ridges prostrate ericaceous species (e.g., *Arctous alpina*, *Vaccinium vitis-idaea*, *Diapensia lapponica*) are abundant, whereas deciduous dwarf shrubs (e.g., *Betula nana* and *Salix planifolia* ssp. *pulchra*) dominate the footslope.

The abundant mosses on the lower slopes strongly affects the hydrological regimes, soil nutrient regimes, and permafrost conditions. The soils are more organic downslope; active layers are thinner, and pH and nutrients decline (Fig. 4.9f–j). *Sphagnum* moss is thought to be a keystone species controlling the patterns of several soil and vegetation parameters along the slope gradient. The moss is able to establish on hillslopes with sufficient soil moisture and low soil pH. Older landscapes have more leached nutrient-poor and organic-rich soils, ideal conditions for the establishment of *Sphagnum*. Once it becomes established, it tends to further promote the conditions for *Sphagnum* growth, because it can hold 10–25 times its dry weight in water (Vitt et al. 1975) and acidify the soil (e.g., Clymo 1963). This process by which peatlands develop on previously well-drained sites is termed paludification, and has been described from boreal forested ecosystems worldwide (e.g., Auer 1928; Lawrence 1958; Heinzelman 1970; Ugolini and Mann 1979; Noble et al. 1984; Klinger 1990). Viereck (1966) has described a similar process leading to *Sphagnum*-rich tussock-tundra vegetation on the outwash gravels of the Muldrow Glacier.

An important consequence of the thicker organic mats and shallower active layers downslope is that thawed mineral material decreases to an almost negligible thickness on the footslope (Fig. 4.8). Runoff passes through the organic horizons, which contributes to the decline in pH and soil nutrients downslope. On the Imnavait Creek hillslope, the pH on the hillcrest at the top of the mineral horizon is 4.7 rising to 5.3 on the mineral-rich slope shoulder, and then decreases steadily to pH 3.8 on the footslope. There is also a trend of lower pH in the lower soil horizons and higher pH for the interstitial waters (Fig. 4.9h). The soil water pH values on the footslope are comparable to values reported from Imnavait Creek waters (Oswood et al. 1989). Soil nutrients (e.g., Ca and NO₃; Figs. 4.9i,j) measured at the top of the Bw horizon generally peak in the shoulder area and then decrease downslope with very low values on the footslope. For example, nitrate-nitrogen declined from 2.6 µg g⁻¹ on the shoulder to negligible values on the lower backslope and footslope (Fig. 4.9j). The formation of *Sphagnum*-rich peat on the hill slopes is, thus, a prerequisite to the development of poor-fen vegetation in the lowlands, because the water entering the colluvial basins is acidified by passing through the *Sphagnum* peat on the hill slopes.

The toposequence at Imnavait Creek has many of the same characteristics that Hamilton (1986) described for Sagavanirktok-age (mid-Pleistocene)

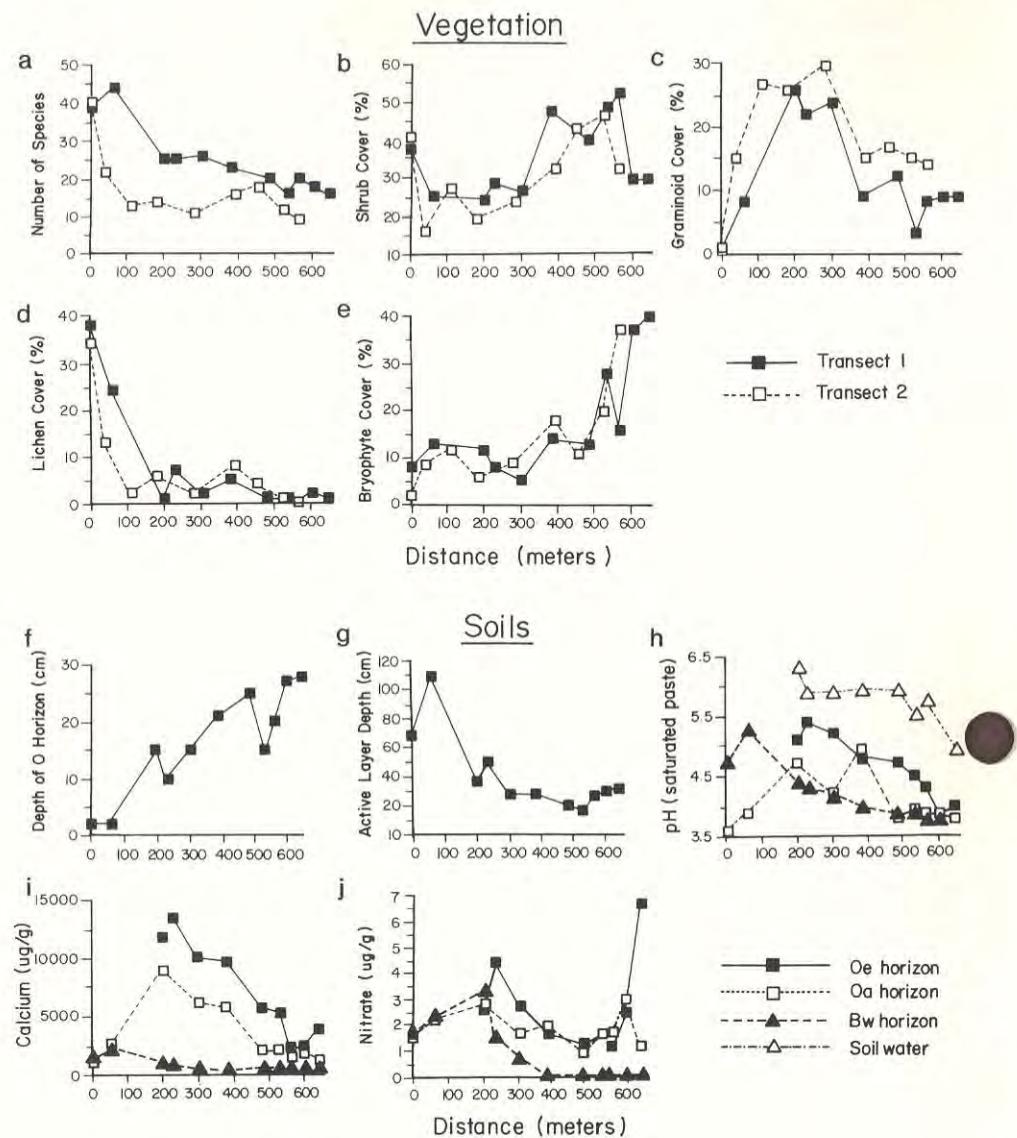


Fig. 4.9a–j. Trends in key vegetation and soil characteristics downslope along the west-facing toposequence. See text for explanation. (Modified from Walker et al. 1989b)

moraines on the North Slope. Terrain of this age is dominated by acidic tussock tundra, thaw depressions, bogs, and water-track complexes (Jorgenson 1984; Hamilton 1986). The hill crests are generally sites of dry heath vegetation and are usually free of tussock tundra. Older landscapes to the north of Imnavait Creek that were glaciated during Anaktuvuk Glaciation

(early Pleistocene, deglaciated about 250 000 years ago) have broader, more rounded moraine crests with tussock tundra overtopping the hill crests, few glacial erratics protruding above the tundra surface, better integrated stream networks, and few lakes.

The nearby Sagavanirktoq River valley and the Toolik Lake region have Itkillik glacial till deposits (late-Pleistocene, deglaciated 11 500 to 60 000 years ago). The geomorphological contrast between the Itkillik and Sagavanirktoq drifts is strong. The Sagavanirktoq surfaces are generally more highly eroded with smooth slopes, broad hill crests, few glacial erratics, mature drainage systems, and a more extensive tussock tundra. In contrast, the younger Itkillik surfaces have a more irregular topography, stony surfaces, steeper slopes, deranged drainage systems, and more heterogeneous vegetation cover (Hamilton 1986). These areas are dominated by dry heath vegetation, nonacidic tundra on moist sites, nonsorted stripe complexes, and less tussock tundra (Jorgenson 1984).

Based on our experience while mapping the region's vegetation, the vegetation trends described for this toposequence are representative of other long west-facing slopes in the region. Slopes of other aspects are less common and show distinctively different zonal vegetation with regard to slope position. For example, east facing slopes tend to be shorter and steeper, and accumulate snow because of the westerly and southwesterly winter storm winds and less solar heating (Chap. 6, this Vol.). Consequently, east-facing slopes tend to be wetter with more snowbed plant communities and more abundant shrubs. North-facing slopes also accumulate snow because of the prevailing southerly winds. More than 4 m of snow can accumulate on the steeper north-facing slopes, and snowbed plant communities are common. Gentle north-facing slopes downslope of large snowdrifts are generally covered by well-developed water tracks formed by meltwater from the drifts. In contrast, the few south-facing slopes occurring on bedrock outcrops are steep, dry, blown free of winter snow, and offer mineral substrates for communities dominated by *Dryas octopetala* (Chap. 5, this Vol.).

4.5 Terrain Sensitivity to Disturbance

Thermokarst is the melting of massive ground ice to form a topography of depressions, hummocks, and small ponds (Washburn 1980), often an undesirable consequence from construction in arctic regions (see Chap. 3, this Vol.). The distribution of ground ice along hillslope gradients is related to landscape age and slope position. Older glacial deposits on the North Slope generally have greater amounts of massive ground ice because older till is generally finer grained and has had more time to form segregated ice (Brown and Kreig 1983). According to Jorgenson's (1984) hypothesis of landscape evolution for the glaciated foothills, the accumulation of organic matter on well-drained sites

reduces heat flux and the depth of summer thaw, and leads to the accumulation of aggradational ice at the permafrost/active-layer boundary.

On the Imnavait Creek toposequence the organic layer increases from about 2 cm on the hill crest to about 30 cm on the footslope. The thawed zone (active layer) is over 100 cm thick on the hill shoulder and declines to about 25 cm on the footslope (Figs. 4.8 and 4.9f-j). Soil pits along the toposequence were dug to penetrate the top of the permafrost/active-layer boundary. Although no quantitative assessment of ice was made, there was an obvious trend toward greater amounts of clear ice encountered at the permafrost boundary on the lower slope positions. Thickening of the organic mat and reduced heat flux are known to contribute to an aggrading permafrost table, which, combined with large amounts of water flowing from upslope, favor the accretion of ice layers near the top of the permafrost table (Washburn 1980). The combination of thin active layers and large amounts of ice near the soil surface make the lower slopes particularly sensitive to disturbance. This sensitivity is enhanced by the thick moss mats that are easily compressed or removed by physical disturbance. This alters the local microtopography and hydrology, and influences the heat budget and leads to thermokarst.

4.6 Conclusions

The Imnavait Creek IRS is a high-altitude, acidic tussock-tundra site that is representative of large regions of foothills that were glaciated during the mid-Pleistocene. The site contains good examples of typical features of the Arctic Foothills physiographic province including broad smooth hill slopes, glacial till surfaces, water tracks, nonsorted stripes, colluvial basins, and beaded streams.

The known flora for the region is 174 vascular plants, 81 mosses, 20 liverworts, and 95 lichens. Imnavait Creek is in the hypoarctic zone, and the North Alaska subprovince of the Alaska province of the Beringian sector (Yurtsev 1994). The relative depauperate flora of the watershed is due primarily to the acidic substrates and low habitat diversity.

A detailed vegetation map of the research site contains 22 map units, 7 of which are tussock-tundra subtypes and facies. Imnavait Creek is dominated by acidic tussock tundra that has few species in common with nonacidic tussock tundra areas. Tussock tundra is much more variable than has been generally assumed; there is considerable variation in species and growth-form dominance related to local site factors including soil pH, snow regime, site stability, and hydrological regime.

An idealized toposequence on the west-facing slope of the study area is useful for examining geoecological interactions between terrain, soil, vegetation, and ground-ice conditions. Paludification is an important process controlling vegetation distribution on hillslopes in the Low Arctic, and strongly

influences the occurrence of massive ground ice. The older foothill landscapes glaciated during the early- and mid-Pleistocene generally have greater amounts of ground ice and are more susceptible to disturbance (Kreig and Reger 1982). Within these old landscapes, upper slopes, particularly hill shoulder areas with nonsorted stripes, are less susceptible to disturbance because of coarse-grained, deeply thawed soils and less ice in the soils, whereas the footslopes and areas with deep *Sphagnum* moss mats are more susceptible because of thin active layers and the presence of considerable pure ice near the soil surface.

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Appendix A. List of Plants for Imnavait Creek, Alaska¹

Vascular Plants (174)

- Acomastylis rossii* (R. Br.) Greene
 (= *Geum rossii*)
- Aconitum delphinifolium* DC. ssp.
 delphinifolium
- Aconitum delphinifolium* DC. ssp.
 paradoxum (Reichb.) Hult.²
- Alopecurus pratensis* L.
- Andromeda polifolia* L.
- Anemone drummondii* S. Wats.
- Anemone parviflora* Michx.
- Anemone richardsonii* Hook²
- Antennaria alpina* (L.) Gaertner
 var. *media* (Greene) Jepson (= *A. friesiana*)
- Arctagrostis latifolia* (R. Br.) Griseb.
 var. *latifolia*
- Arctophila fulva* (Trin.) Anderss.
- Arctous alpina* (L.) Niedenzu
 (= *Arctostaphylos alpina*)
- Arnica angustifolia* M. Vahl ssp.
 angustifolia (= *A. alpina* ssp.
 angustifolia)
- Arnica griscomii* Fern. ssp. *frigida*
 (C. A. Mey.) S. J. Wolf (= *A. Frigida*)
- Arnica lessingii* Greene
- Artemisia arctica* Less. ssp. *arctica*
- Artemisia tilesii* Ledeb. ssp. *tilesii*
- Aster sibiricus* L.

¹ Nomenclature is according to species list provided by the University of Alaska Herbarium, Fairbanks, Alaska.

² Species recorded in sample plots, but not documented with collection at the University of Alaska Herbarium.

Astragalus alpinus L. ssp. *alpinus*
Astragalus umbellatus Bunge
Betula glandulosa Michx.
Betula nana L. ssp. *exilis*
 (Sukatsch.) Hult.
Bistorta plumosa (Small) Greene
 (=*Polygonum bistorta* ssp.
plumosum)
Bistorta vivipara (L.) S. F. Gray
 (=*Polygonum viviparum*)
Bupleurum triradiatum Adams ssp.
arcticum (Regel) Hult.
Calamagrostis canadensis (Michx.)
 Beauv.
Calamagrostis inexpansa Gray
Calamagrostis purpurascens R. Br.
Caltha palustris L. ssp. *arctica*
 (R. Br.) Hult.²
Campanula lasiocarpa Cham.
Cardamine bellidifolia L.
Cardamine digitata Richards.
 (=C. *hyperborea*)
Cardamine pratensis L.
Carex aquatilis Wahlenb.
Carex atrofusca Schkuhr.
Carex bigelowii Torr.
Carex chordorrhiza Ehrh.
Carex lachenalii Schkuhr.
Carex michrochaeta Holm
Carex misandra R. Br.
Carex obtusata Lilj.
Carex podocarpa R. Br.
Carex rariflora (Wahlenb.) J. E. Smith
Carex rotundata Wahlenb.
Carex rupestris All.
Carex saxatilis L. ssp. *laxa* (Trautv.)
 Kalela
Carex scirpoidea Michx.
Carex vaginata Tausch
Cassiope tetragona (L.) D. Don ssp.
tetragona
Chrysosplenium tetrandrum (Lund)
 T. Fries
Comarum palustre L. (=*Potentilla*
palustris)

Crepis nana Richards.
Diapensia lapponica L. ssp. *obovata*
 (F. W. Schmidt) Hult.
Dodecatheon frigidum Cham. &
 Schlecht.
Douglasia ochotensis (Willd.) Hult.
Dryas integrifolia M. Vahl
Dryas octopetala L. var. *octopetala*
Empetrum hermaphroditum (Lange)
 Hagerup (=E. *nigrum* ssp.
hermaphroditum)
Epilobium angustifolium L.
Epilobium davuricum Fisch.
Epilobium latifolium L.
Equisetum arvense L.
Equisetum palustre L.
Equisetum scirpoides Michx.
Equisetum variegatum Schleich.
Erigeron muirii Gray (=E.
grandiflorus ssp. *muirii*)
Eriophorum angustifolium Honck.
 ssp. *subarcticum* (Vassiljev) Hult.
Eriophorum callitrix Cham.
Eriophorum russeolum E. Fries
Eriophorum scheuchzeri Hoppe var.
scheuchzeri
Eriophorum triste (Th. Fries) Hadac
 & Love (=E. *angustifolium* ssp.
triste)
Eriophorum vaginatum L.
Eritrichium aretoides (Cham.) DC.
Eutrema edwardsii R. Br.
Festuca altaica Trin.
Festuca brachyphylla Schult.
Festuca rubra L.
Gastrolychnis macrosperma (Pors.)
 Tolm. & Kozh. (=*Melandrium*
macrospermum)
Gentiana glauca Pall.
Gentianella propinqua (Richards.)
 Gillett ssp. *arctophila* (Griseb.)
 Hult. (=*Gentiana propinqua* ssp.
arctophila)²
Hierochloë alpina (Sw.) Roem. &
 Schult.

Hippuris vulgaris L.
Huperzia selago (L.) C. Martius ssp.
appressa (Desv.) D. Löve
 (=*Lycopodium selago* ssp.
appressum)
Juncus biglumis L.
Kobresia myosuroides (Vill.) Fjori &
 Paol.
Koeleria asiatica Domin
Lagotis glauca Gaertner
Ledum palustre L. ssp. *decumbens*
 (Ait.) Hult.
Linnaea borealis L.
Loiseleuria procumbens (L.) Desv.
Luzula arctica Blytt
Luzula confusa Lindeb.
Luzula kjellmaniana Miyabe &
 Kudo (=L. *tundricola*)
Luzula multiflora (Retz.) Lej.
Luzula wahlenbergii Rupr.
Lycopodium annotinum L. ssp.
pugens (La Pyl.) Hult.²
Minuartia arctica (Stev.) Aschers. &
 Graebn.
Minuartia macrocarpa (Pursh)
 Ostorf.
Minuartia obtusiloba (Rydb.) House
Minuartia rubella (Wahlenb.)
 Graebn.
Novosieversia glacialis (Adams)
 Bolle (=*Geum glaciale*)
Orthilia secunda (L.) House ssp.
obtusata (Turcz.) Böcher
 (=*Pyrola secunda* ssp. *obtusata*)
Oxytropis bryophila (Greene)
 Yurtsev (=O. *nigrescens* ssp.
bryophila)
Papaver macounii Greene
Parrya nudicaulis (L.) Regel
Pedicularis albolabiata (Hult.) Kozh.
 (=P. *sudetica* ssp. *albolabiata*)
Pedicularis capitata Adams
Pedicularis labradorica Wirsing
Pedicularis lanata Cham. & Schlecht
 (=P. *kanei* ssp. *kanei*)

Pedicularis langsdorffii Fisch.
Pedicularis lapponica L.
Pedicularis oederi M. Vahl²
Pentaphylloides floribunda (Pursh)
 Löve (=*Potentilla fruticosa*)²
Petasites frigidus (L.) Franch.
Phlox sibirica L.
Poa alpigena (E. Fries) Lindm.
Poa alpina L.
Poa arctica R. Br.
Poa glauca M. Vahl
Poa lanata Scribn. & Merr.
Poa paucispicula Scribn. & Merr.
Poa pseudoabbreviata Roshev.
 (=P. *branchyanthera*)
Polemonium acutiflorum Willd.
Potentilla uniflora Ledeb.
Pyrola grandiflora Radius
Ranunculus eschscholtzii Schlecht.
Rhododendron lapponicum (L.)
 Wahlenb.
Rubus arcticus L. ssp. *acaulis*
 (Michx.) Focke²
Rubus chamaemorus L.
Salix alaxensis (Anderss.) Cov.
Salix arbusculoides Anderss.
Salix arctica Pall.
Salix brachycarpa Nutt. ssp.
niphoclada (Rydb.) Argus
 (=S. *niphoclada*)
Salix chamissonis Anderss.
Salix fuscescens Anderss.
Salix lanata L. ssp. *richardsonii*
 (Hook) A. Skvortsov²
Salix phlebophylla Andress.
Salix planifolia Pursh ssp. *pulchra*
 (Cham.) Argus (=S. *pulchra*)
Salix reticulata L. ssp. *reticulata*
Salix rotundifolia Trautv. ssp.
rotundifolia
Saussurea angustifolia (Willd.)
 DC.
Saxifraga bronchialis L. ssp.
funstonii (Small) Hult.
Saxifraga cernua L.

- Saxifraga flagellaris* Willd. ssp.
setigera (Pursh) Tolm.
- Saxifraga foliolosa* R. Br. var.
foliolosa
- Saxifraga hieracifolia* Waldst. & Kit.
- Saxifraga hirculus* L.
- Saxifraga nelsoniana* D. Don ssp.
nelsoniana (=*S. punctata* ssp.
nelsoniana)
- Saxifraga nivalis* L.
- Saxifraga reflexa* Hook.
- Saxifraga rivularis* L.
- Saxifraga tricuspidata* Rottb.
- Selaginella sibirica* (Milde) Hieron.
- Senecio atropurpureus* (Ledeb.)
Fedtsch. ssp. *frigidus* (Richards.)
Hult.
- Senecio kjellmanii* Pors. (=*S.*
atropurpureus ssp. *tomentosus*)
- Senecio lugens* Richards.²
- Silene acaulis* L.
- Smelowskia calycina* (Stephen) C. A.
Mey.
- Solidago multiradiata* Ait. var.
*multiradiata*²
- Sparganium hyperboreum* Laest.
- Spiraea stevenii* (Schneid.) Rydb.
(=*S. beauverdiana*)
- Stellaria crassifolia* Ehrh.
- Stellaria edwardsii* R. Br.
- Stellaria laeta* Richards.
- Stellaria longipes* Goldie
- Tofieldia pusilla* (Michx.) Pers.
- Trisetum spicatum* (L.) Richter
- Vaccinium uliginosum* L. ssp.
alpinum (Bigel.) Hult.
- Vaccinium uliginosum* L. ssp.
microphyllum Lange
- Vaccinium vitis-idaea* L. ssp. *minus*
(Lodd.) Hult.
- Valeriana capitata* Pall.
- Viola epipsila* Ledeb.
- Wilhelmsia physodes* (Fisch.)
McNeill
- Zygadenus elegans* Pursh²

Mosses [81]

- Abietinella abietina* (Hedw.)
Fleisch. (=*Thuidium abietinum*)
- Aulacomnium palustre* (Hedw.)
- Aulacomnium turgidum* (Wahlenb.)
Schwaegr.
- Brachythecium groenlandicum*
(C. Jens.) Schljak.
- Brachythecium turgidum* (Hartm.)
Kindb.
- Bryum algovicum* Sendtn.
- Bryum pseudotriquetrum* (Hedw.)
Gaertner et al.
- Calliergon giganteum* (Schimp.)
Kindb.
- Calliergon stramineum* (Brid.)
Kindb.
- Campylium stellatum* (Hedw.) C.
Jens.
- Catoscopium nigritum* (Hedw.)
Brid.
- Ceratodon purpureus* (Hedw.) Brid.
- Cirriphyllum cirrosum* (Schwaegr.)
Grout
- Dicranella varia* (Hedw.) Schimp.
(= *Anisothecium varium*)
- Climaciun dendroides* (Hedw.)
Web. & Mohr²
- Dicranum acutifolium* (Lindb. &
Arnell) C. Jens.
- Dicranum angustum* Lindb. (= *D.*
laevidens)
- Dicranum elongatum* Schleich.
- Dicranum groenlandicum* Brid.
- Dicranum muehlenbeckii* Bruch &
Schimp.
- Dicranum scoparium* Hedw.
- Dicranum spadiceum* Zett. (= *D.*
neglectum)
- Drepanocladus brevifolius* (Lindb.)
Warnst. (= *D. lycopodioides* var.
brevifolius)

- Encalypta brevicolla* Bruch &
Schimp.
- Encalypta rhaftocarpa* Schwaegr.
(= *E. vulgaris* var. *rhaftocarpa*)
- Hylocomium splendens* (Hedw.)
Schimp. (= *H. splendens* ssp.
obtusifolium)
- Hypnum bambergeri* Schimp.
- Hypnum procerrimum* Mol.
(= *Pseudostereodon procerrimum*)
- Limprichtia revolvens* (Sw.) Loeske
(= *Drepanocladus revolvens*)
- Loeskyphnum badium* (Hartm.) Paul
(= *Drepanocladus badius*)
- Meesia uliginosa* Hedw.
- Orthothecium chrysaeum* (Schwaegr.)
Schimp.²
- Paludella squarrosa* (Hedw.) Brid.
- Philonotis fontana* (Hedw.) Brid.
var. *pumila* (Turn.) Brid. (= *P.*
tomentella)²
- Plagiomnium ellipticum* (Brid.) T.
Kop. (= *Plagiomnium rugicum*)²
- Plagiomnium medium* (Bruch &
Schimp.) T. Kop. (= *Mnium*
medium)
- Pleurozium schreberi* (Brid.) Mitt.
- Pogonatum urnigerum* (Hedw.)
Beauv.
- Pohlia andrewsii* Shaw
- Pohlia crudoides* (Sull. & Lesq.)
Broth.
- Pohlia elongata* Hedw. var. *greenii*
(Brid.) Shaw
- Pohlia nyuans* (Hedw.) Lindb. (= *P.*
schimperi)
- Polytrichastrum alpinum* (Hedw.)
G. L. Sm. var. *alpinum*
(= *Pogonatum alpinum*)
- Polytrichum commune* Hedw.
- Polytrichum hyperboreum* R. Br.
- Polytrichum juniperinum* Hedw.
- Polytrichum longisetum* Brid.
(= *Polytrichastrum longisetum*)
- Polytrichum piliferum* Hedw.
- Polytrichum sexangulare* Brid.
- Polytrichum strictum* Brid
(= *P. juniperinum* var. *gracilis*)
- Polytrichum swartzii* Hartm.
(= *P. algidum*)
- Pseudobryum cinclidiodes* (Hüb.)
T. Kop.
- Ptilium crista-castrensis* (Hedw.) De
Not.
- Racomitrium lanuginosum* (Hedw.)
Brid.
- Rhizomnium andrewsianum*
(Steere) T. Kop.
- Rhytidium rugosum* (Hedw.) Kindb.
- Sanionia uncinata* (Hedw.) Loeske
(= *Drepanocladus uncinatus*)
- Sarmenthypnum sarmentosum*
(Wahlenb.) Tuom & T. Kop.
(= *Calliergon sarmentosum*)
- Scorpidium scorpioides* (Hedw.)
Limpr.²
- Sphagnum angustifolium* C. Jens.
(= *S. recurvum* var. *tenue*)
- Sphagnum aongstroemii* Hartm.
- Sphagnum balticum* (Russ.) C.
Jens.
- Sphagnum capillifolium* (Ehrh.)
Hedw. (= *S. nemoreum*)
- Sphagnum compactum* DC.
- Sphagnum fimbriatum* Wils. var.
fimbriatum
- Sphagnum girgensohnii* Russ.
- Sphagnum imbricatum* Hornsch.
(= *S. steerei*)
- Sphagnum lenense* H. Lindb.
- Sphagnum lindbergii* Schimp.
- Sphagnum magellanicum* Brid.
- Sphagnum obtusum* Warnst.
- Sphagnum orientale* Sav.-Ljub. (= *S.*
perfoliatum)
- Sphagnum rubellum* Wils. (= *S.*
Capillifolium var. *tenellum*)
- Sphagnum squarrosum* Crome
- Sphagnum subsecundum* Nees var.
subsecundum

Sphagnum teres (Schimp.) Ångstr.
Sphagnum warnstorffii Russ.
Splachnum sphaericum Hedw. (=*S. ovatum*)
Tetraplodon pallidus Hag.
Tomentypnum nitens (Hedw.) Lowske
Tortula ruralis (Hedw.) Gaertner et al.

Liverworts [20]

Anastrophyllum minutum (Schreb.) Schust.
Aneura pinguis (L.) Dum.
Barbilophozia binsteadii (Kaal.) Loeske (=*Lophozia binsteadii*)
Barbilophozia quadriloba (Lindb.) Loeske (=*Lophozia quadriloba*)
Blepharostoma trichophyllum (L.) Dum. ssp. *brevirete* (Bryhn & Kaal.) Schust. (=*B. trichophyllum* var. *brevirete*)
Chandonanthus setiformis (Ehrh.) Lindb. (=*Tetralophozia setiformis*)
Diplophyllum albicans (L.) dum.
Diplophyllum plicatum Lindb. (=*Microdiplophyllum plicatum*)
Gymnomitrion concinnum (Lightf.) Corda
Lophozia guttulata (Lindb. & Arnell) A. Evans (=*L. porphyroleuca*)
Lophozia opacifolia Culm.
Lophozia ventricosa (Dicks.) Dum.
Mylia anomala (Hook.) S. F. Gray
Plagiochila arctica Bryhn & Kaal.
Pseudolepicolea fryei (Perss.) Grolle & Ando
Ptilidium ciliare (L.) Hampe
Radula prolifera S. Arnell
Scapania paludicola Loeske & K. Müll.
Scapania simmonsii Bryhn & Kaal.
Tritomaria quinquedentata (Huds.) Buch

Lichens [95]

Alectoria nigricans (Ach.) Nyl.
Alectoria ochroleuca (Hoffm.) Massal.
Arctoparmelia centrifuga (L.) Hale (=*Xanthoparmelia centrifuga*)
Arctoparmelia separata (L.) Hale (=*Xanthoparmelia separata*)
Asahinea chrysantha (Tuck.) Culb. & C. Culb.
Asahinea scholanderi (Llano) Culb. & C. Culb.
Bryocaulon divergens (Ach.) Kärnuf (=*Cornicularia divergens*)
Caloplaca jungermanniae (Vahl) Th. Fr.
Catapyrenium lachneum (Ach.) R. Sant. (=*Dermatocarpon lachneum*)
Cetraria andrejevii Oxner
Cetraria commixta (Nyl.) Th. Fr.
Cetraria cucullata (Bellardi) Ach.
Cetraria delisei (Bory) Nyl. (=*C. hiascens*)
Cetraria fastigiata (Del.) Kärnuf.
Cetraria hepatizon (Ach.) Vainio
Cetraria inermis (Nyl.) Krog
Cetraria islandica (L.) Ach.
Cetraria kamczatica Savicz.
Cetraria laevigata Rass.
Cetraria nigricans Nyl.
Cetraria nivalis (L.) Ach.
Cetraria tilesii Ach.
Cladina arbuscula (Wallr.) Hale & Culb. (=*Cladonia arbuscula*)
Cladina mitis (Sandst.) Hustich (=*Cladonia mitis*)
Cladina rangiferina (L.) Nyl. (=*Cladonia rangiferina*)
Cladina stellaris (Opiz) Brodo (=*Cladonia alpestris*)
Cladonia alaskana A. Evans
Cladonia amaurocraea (Flörke) Schaerer

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Cladonia carneola (Fr.) Fr.
Cladonia cenotea (Ach.) Schaefer
Cladonia chlorophaea (Flörke) Sprengel
Cladonia coccifera (L.) Willd.
Cladonia cornuta (L.) Hoffm.
Cladonia deformis (L.) Hoffm.
Cladonia ecmocyna Leight.
Cladonia fimbriata (L.) Fr.
Cladonia gracilis (L.) Willd.
Cladonia macrophylla (Schaerer) Stenh.
Cladonia pleurota (Flörke) Schaefer
Cladonia pocillum (Ach.) O. Rich
Cladonia pyxidata (L.) Hoffm.
Cladonia subulata (L.) Weber
Cladonia sulphurina (Michx.) Fr.
Cladonia uncialis (L.) Weber
Coleocaulon aculeatum (Schreb.) Link (=*Cornicularia aculeata*)
Dactylina arctica (Richards.) Nyl.
Dactylina beringica Bird & Thomson
Dactylina madreporeiformis (Ach.) Tuck.
Dactylina ramulosa (Hook.) Tuck.
Haematomma lapponicum Räsänen
Hypogymnia subobscura (Vainio) Poelt (=*Parmelia subobscura*)
Lecanora epibryon (Ach.) Ach.
Lecidoma demissum (Rutstr.) G. Schneider & Hertel (=*Lecidea demissa*)
Lobaria linita (Ach.) Rabenh. (=*Sticta linita*)
Masonhalea richardsonii (Hook.) Kärnuf (=*Cetraria richardsonii*)
Melanelia septentrionalis (Lynge) Essl. (=*Parmelia septentrionalis*)
Melanelia stygia (L.) Essl. (=*Parmelia stygia*)
Mycoblastus sanguinarius (L.) Norman
Nephroma arcticum (L.) Torss
Nephroma expallidum (Nyl.) Nyl.

Ochrolechia frigida (Swartz) Lyngé (=*O. gonatodes*)
Ochrolechia upsaliensis (L.) Massal.
Parmelia omphaloalodes (L.) Ach.
Parmelia sulcata Taylor
Peltigera aphthosa (L.) Willd.
Peltigera canina (L.) Willd.
Peltigera horizontalis (Huds.) Baumg.
Peltigera leucophlebia (Nyl.) Gyelnik
Peltigera malacea (Ach.) Funck.
Peltigera polydactyla (Necker) Hoffm.
Peltigera scabrosa Th. Fr.
Pertusaria bryontha (Ach.) Nyl.
Pertusaria dactylina (Ach.) Nyl.
Pertusaria panyrga (Ach.) Massal.
Physconia muscigena (Ach.) Poelt
Porpidia flavocaerulescens (Hornem.) Hertel & Schwab. (=*Lecidea flavocaerulescens*)
Polyblastia gelatinosa (Ach.) Th. Fr.
Pseudephebe pubescens (L.) M. Choisy
Psoroma hypnorum (Vahl) S.F. Gray
Rhizocarpon geographicum (L.) DC.
Rinodina turfacea (Wahlenb.) Körber
Solorina bispora Nyl.
Solorina crocea (L.) Ach.
Solorina saccata (L.) Ach.
Sphaerophorus fragilis (L.) Pers.
Sphaerophorus globosus (Huds.) Vainio
Stereocaulon alpinum Laur.
Stereocaulon paschale (L.) Hoffm.
Stereocaulon tomentosum Fr.
Thamnolia subuliformis (Ehrh.) Culb.
Tuckermannopsis pinastri (Scop.) Hale (=*Cetraria pinastri*)
Tuckermannopsis sepincola (Ehrh.) Hale (=*Cetraria sepincola*)
Umbilicaria caroliniana Tuck.

Umbilicaria hyperborea (Ach.)
Hoffm.

Umbilicaria proboscidea (L.)
Schrader

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