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Hierarchical subdivision of Arctic tundra based on vegetation response to climate, parent material and topography

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Abstract

Current land-cover classifications used for global modelling portray Arctic tundra as one or two classes. This is insufficient for analysis of climate–vegetation interactions. This paper presents a simple three-level vegetation-map legend system useful for modelling at global, regional, and landscape scales. At the highest level (global scale: 10^7–10^8 km^2) the Tundra Zone is divided into four subzones based on vegetation response to temperature along the latitudinal temperature gradient from north to south: (1) Cushion-forb, (2) Prostrate Dwarf-shrub, (3) Erect Dwarf-shrub, and (4) Low Shrub subzones. The boundaries follow a modification of Yurtsev's phytogeographic subzones. Parent material and topography are also major considerations at global, regional, and landscape scales. Soil pH is a key variable for many ecosystem responses, and a division into acidic (pH 5.5 or less) and nonacidic soils is used. A conceptual mesotopographic gradient is used to characterize the influence of soil-moisture and snow regimes. The example legend framework focuses on the Northern Alaska floristic subprovince, and could be expanded to other floristic provinces using local expert knowledge and available literature. Dominant plant functional types within each habitat type within the four subzones are also presented. Modellers could include or ignore different levels of resolution depending on the purpose of the model. The approach resolves conflicts in terminology that have previously been encountered between the Russian, North American, and Fennoscandian approaches to Arctic zonation.

Keywords: Arctic, classification, climate change, climate, geology, plant functional types, soils, tundra, vegetation mapping, vegetation, zonation

Introduction

There is growing evidence that the effects of global climate change will be particularly strong in the Arctic and that numerous difficult-to-predict indirect responses to climate change are likely to occur (Chapin *et al*. 1992; Oechel *et al*. 1997). The effects could vary considerably across the Arctic because of different regional climate responses and major differences in vegetation types and other ecosystem properties that occur across about 30° of latitude and a 10 °C mean-July temperature gradient. For example, there is about a five-fold increase in vascular plant species along the gradient (Young 1971; Rannie 1986). Within the soils, the amount of organic carbon varies from negligible amounts in the far north to an average of nearly 50 kg m^{-2} near treeline (Bockheim *et al*. 1996). There is approximately a 25× increase in average plant canopy height, a 10× increase in primary production, a 30× increase in biomass, and similar increases in the number of invertebrate and vertebrate taxa (Bazilevich *et al*. 1997; Chernov & Matveyeva 1997). The major differences in vegetation are not depicted on any existing global map. Current global land-cover classifications usually portray tundra regions as one or two broad land-cover categories (e.g. Olson 1985; Prentice *et al*. 1992; Steffen *et al*. 1996). Additionally, tundra vegetation and soils are also the product of climate, parent-material and soil-moisture factors operating at a variety of spatial scales (Cantlon 1961; Walker 1985; Edlund & Alt 1989; Elvebakk 1994). The influence of soil pH is particularly important and often overlooked. The combined effects of climate, parent material and topography need to be

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considered in models of vegetation response to climate change. This paper first summarizes the response of Arctic vegetation to these influences, and then presents a framework for a circumpolar legend, using the Northern Alaska floristic subprovince as an example.

Climatic influences

> First and foremost is the separation of subzones and the drastic changes of many parameters (productivity, diversity, abundance) from the forest tundra up to the polar deserts. These changes are so great, that averaged values for the communities and ecosystems over the tundra zone as a whole are of little value. (Chernov & Matveyeva 1997)

In tundra regions, cooler shorter growing seasons poleward create a transition from relatively diverse and lush vegetation near tree line to barren 'polar deserts' with low diversity in the coldest areas. Different approaches for describing this gradient have been used in Russia, North America, and Fennoscandia (Table 1). A unification of these approaches is essential for global vegetation mapping and modelling efforts. Although there is much conflicting terminology between the various approaches, there is rough agreement on the basic vegetation transitions from north to south.

For this paper, the Tundra Zone is defined broadly as the vegetation region north of the Arctic tree line, and includes the 'polar deserts' and 'Arctic tundras' of other approaches. Other authors have divided the region into as few as two subdivisions (Bliss 1997) and as many as seven (Alexandrova 1980). Here, the Tundra Zone is divided into four subzones with boundaries that generally follow Yurtsev's phytogeographic subzones (Yurtsev 1994) (Fig. 1). These boundaries have evolved through a long tradition of Russian Arctic geobotanists (Gorodkov 1935; Lavrenko & Sochava 1954; Sochava & Gorodkov 1956; Alexandrova 1980; Yurtsev 1994; Chernov & Matveyeva 1997). There is, however, conflicting terminology and different boundary delineations even among Russian geobotanists that are not easily resolved (e.g. Yurtsev's High Arctic Tundra vs. Alexandrova's Polar Desert, Table 1). Treeless oceanic boreal areas are also shown in Fig. 1. These areas have cool summers and relatively warm winters. Although the low-growing vegetation is physiognomically similar to tundra, these oceanic areas show little floristic resemblance to tundra because of the dominance of boreal species (Tuhkanen 1984).

The names of the units in Fig. 1 are based on the transitions in the stature of woody plants on mesic sites along the temperature gradient. The height of woody plants has been shown to have a strong correlation with summer temperature (Walker 1987; Edlund & Alt 1989). Just north of tree line, low shrubs, 40–200 cm tall, dominate most mesic vegetation types, and northward there is a gradual reduction to first erect dwarf shrubs, and then prostrate forms, until in subzone 1 woody plants are totally absent in all habitats. There are also other changes in the nature of the plant canopy that are discussed in the descriptions below.

The main criterion for defining the four subzones of Fig. 1 is the vegetation type occurring on mesic sites found on plains with fine-grained soils, where the vegetation has developed fully under the prevailing macroclimate without alteration due to excessive or depleted drainage, snow, nutrients, disturbance or other factors. Such sites are referred to as the 'plakor' in Russia (Vysotskyi 1909). Some authors have subdivided the subzones based on difference of the vegetation in intrazonal areas, such as wetlands, snowbeds, and streamside areas. (For an example, see northern and southern variants of subzone 2 below.) These variants are not shown in Fig. 1 because, in most cases, the circumpolar natures of the variants are not well known at present.

The concepts of zonal vegetation in the Arctic have been developed mainly in Russia, where the patterns have been well-known since the 1930s (Sochava 1934). Perhaps the best area for observing the transitions between all four subzones is the broad Taimyr Peninsula, where the zonal patterns have been recently described in English (Chernov & Matveyeva 1997). Zonal patterns have also been described from more maritime climates, such as Svalbard (Elvebakk 1985), Fennoscandia (Ahti *et al*. 1968), and southern Greenland (Feilberg 1984; Tuhkanen 1984). Very steep coastal temperature gradients and associated vegetation gradients occur in some areas where continental landmasses are adjacent to the cold waters of the polar seas (Sorensen 1941; Walker 1987). On large islands, such as Greenland, Svalbard, Ellesmere, and Axel Heiberg, the zonal patterns form narrow bands parallel to the coast (Feilberg 1984; Tuhkanen 1984; Brattbakk 1986). In northern Canada, zonal patterns are less clear than in the Russia because of the many islands and complex topography (Bliss 1997). Nonetheless, even in such conditions, vegetation patterns are clearly associated with temperature gradients (Edlund & Alt 1989).

Mean July temperatures at the southern boundaries of subzones vary between continental and oceanic areas. In continental areas, the mean July temperatures show roughly a 3 °C separation between the subzones (Edlund 1996; Matveyeva 1998) (Tables 1 and 2). In continental areas of Alaska, Canada and Russia, the treeline occurs at about the 12 °C mean July isotherm. In more maritime

Table 1 Terminology cross-walk for Arctic Tundra subdivisions

Subzone	Russia			North America			Fennoscandia	
	Alexandrova (1980)	Yortsev (1994)	Matveyeva (1998)	Polunin (1951)	Edlund (1996) Edlund & Alt (1989)	Bliss (1997)	Tuhkaner (1986)	Elvebakk (1999)
1. Cushion forb	Northern polar desert	High Arctic tundra	Polar desert (1.5–2°C)[1]	High Arctic[2]	Herbaceous and cryptogam (1–3°C, 50–150 TDD)	High Arctic	Inner polar zone C = 0.0[4]	Arctic polar desert zone
	Southern polar desert						Outer polar zone C = 0.5	
2. Prostrate dwarf shrub	Northern Arctic tundra	Arctic tundra: northern variant	Arctic tundra (5–6°C)	Middle Arctic	Herb-prostrate shrub transition (3–4°C, 150–250 TDD) Prostrate shrub (4-6°C, 250–350 TDD)		Northern Arctic zone C = 1.0	Northern Arctic tundra zone Middle Arctic tun-dra zone
	Middle Arctic tundra	Arctic tundra: southern variant	Typical tundra (8–10°C)		Dwarf and prostrate shrub (5–7°C, >350 TDD)		Middle Arctic zone C = 1.75	Southern Arctic tundra zone
	Southern Arctic tundra							
3. Erect dwarf shrub	Northern sub-Arctic tundra Middle sub-Arctic tundra	Northern hypo-Arctic tundra		Low Arctic	Low erect shrub (7–10°C)	Low Arctic	Southern Arctic zone C=2.5	Arctic shrub-tundra zone
4. Low shrub	Southern sub-Arctic tundra	Southern hypo-Arctic tundra	Southern tundra (10–12°C)					

[1]Mateveyeva (1998): Range of mean July temperature at southern boundary of subzone.
[2]Polunin (1951): Zones based roughly on openness of ground cover. High Arctic, very sparsely vegetated; Middle Arctic, open vegetation carpet; Low Arctic, closed vegetation carpet.
[3]Edlund & Alt (1989): Zones defined on the bases of mean July temperature and sum of mean temperature of days exceeding 0°C (thawing degree days, TDD).
[4]Tuhkanen (1986): Southern boundary of zones defined by Holdridge biotemperature as the sum of mean monthly temperatures >0° C divided by 12.

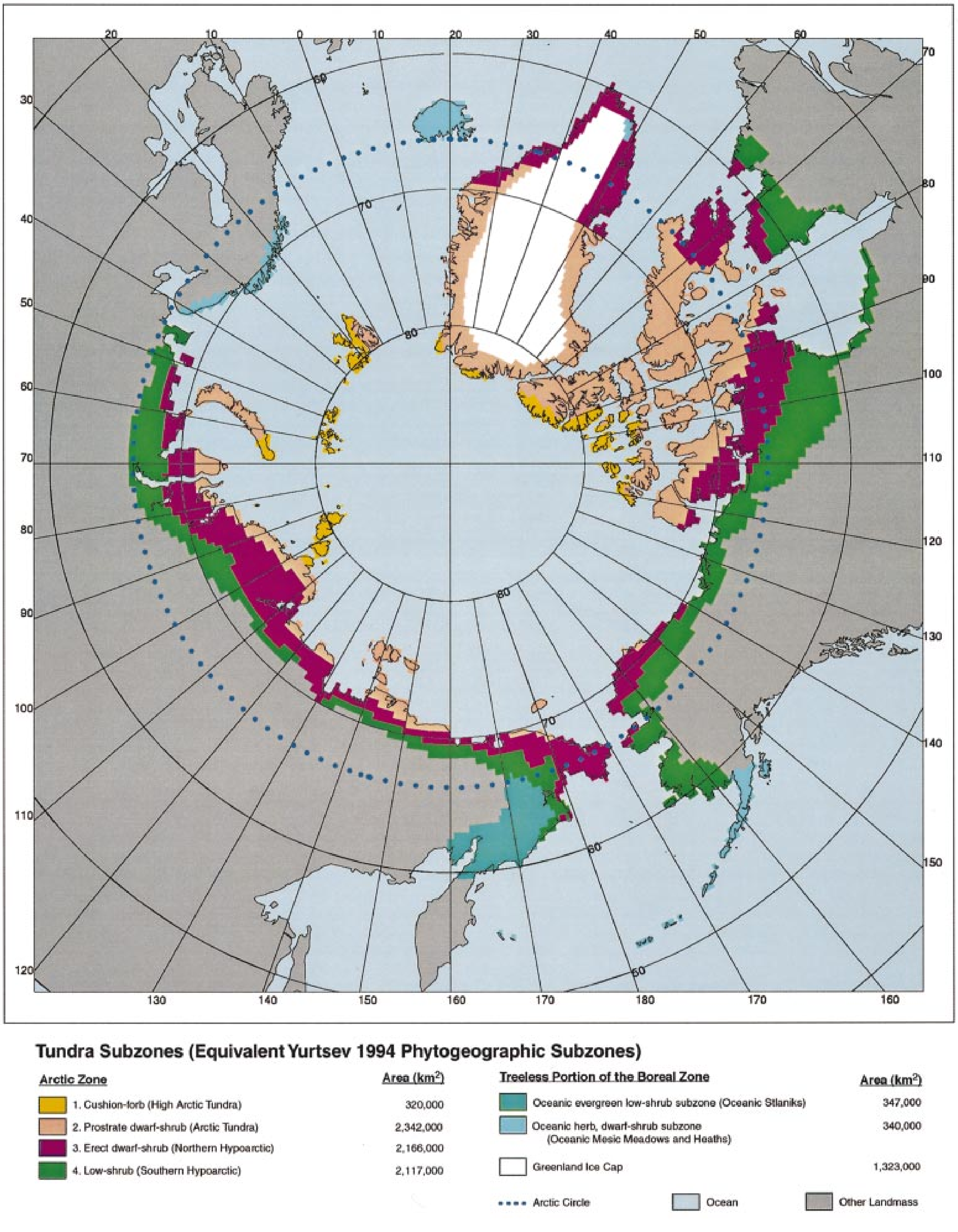

Fig. 1 Subzones of the Arctic Tundra Zone. The subzone boundaries are modified slightly from Yurtsev's (1994) phytogeographic boundaries. This map portrays Arctic tundra and treeless boreal subzones using a 0.5° × 0.5° grid-cell size, the same as that used in numerous global modelling efforts.

areas, mean July temperatures are closer to 10 °C. Some authors consider the total amount of summer warmth to be a better index for defining the subzonal boundaries. For example, Young (1971) used the sum of the mean monthly temperatures greater than 0 °C to define Arctic floristic zones. Other authors have used the seasonal total of daily mean temperatures above freezing (thawing degree days, TDD) (Edlund & Alt 1989), or the Holdridge biotemperature, which is the sum of the monthly temperatures exceeding freezing divided by 12 (Tuhkanen 1986). The boundaries shown in Fig. 1 will require further adjustment as better climate and vegetation information become available. For example, observations made at Expedition Fiord and other sites on north-western Axel Heiberg Island during the 1999 Canadian Circumpolar Arctic Vegetation Mapping transect indicate that subzone 1 just touches the coldest, foggiest, outer edge of the fjords. The inner fjords are all in subzone 2. In Russia, where there is a long heritage of using this zonal approach, such adjustments will be relatively minor, but in North America, more severe adjustments of the boundaries may be required.

Descriptions of the subzones

Subzone 1: cushion-forb subzone. In the coldest portions of the Arctic, the major parts of the land surface are largely barren, often with <5% cover of vascular plants. Permanent ice covers large areas of the land. Woody plants are absent. Lichens, bryophytes, cyanobacteria, and scattered forbs (e.g. *Papaver, Draba, Saxifraga, Stellaria*) are the dominant plants of the sparse vegetation cover. Many of the forbs, lichens and mosses have a compact cushion growth form. In midsummer, the Arctic poppy, *Papaver radicatum* s.l., is the most conspicuous plant over large portions of this subzone. Soil lichens, mosses, and liverworts can cover a high percentage of the surface, particularly in more maritime areas such as Novaya Zemlya (Alexandrova 1980). Rushes (*Luzula* and *Juncus*) and grasses (*Alopecurus, Puccinellia, Phippsia,* and *Dupontia*) are the main graminoid groups. Sedges are rare and wetlands lack organic peat layers. Well-vegetated surfaces occasionally occur on mesic sites, but there is little contrast in the composition of vegetation on mesic sites, streamside sites, and snowbeds The vascular-plant flora is extremely depauperate, consisting of only about 50–60 species (Young 1971). On fine-grained soils, the extremely cold temperatures and the thin sparse plant canopy induce intense frost activity, which forms networks of small (<50 cm diameter) nonsorted polygons, and plants are confined mainly to the depressions between the polygons (Chernov & Matveyeva 1997).

Subzone 1 occupies a small portion of the Arctic Tundra zone (4.6%), where July mean temperatures are less than about 3 °C. It includes mostly fog-shrouded islands within the permanent Arctic ice pack, such as Ellef Ringnes Island, Amund Ringnes Island, and nearby islands in the north-west corner of the Canadian Archipelago. It also includes the coastal fringe of northernmost Greenland and Ellesmere Island, the north-eastern portion of Svalbard, Franz Josef Land, Severnaya Zemlya, the northern tips of the Taimyr Peninsula, and northern tip of Novaya Zemlya. In Greenland, the most recent study explicitly addressing the status of subzone 1 is that of Bay (1997), who argues for a very limited delineation along Greenland's northern coast.

This subzone is called 'polar desert' in Russia (Alexandrova 1980), Fennoscandia (Elvebakk 1985), and Greenland (Bay 1997), but this is not a good term for this subzone globally. In North America, 'polar desert' has been used to describe vegetation types (Bliss 1977) and zones (Tedrow 1977) with similar barren aspect, but many of these areas would not be considered 'polar desert' elsewhere. Desert-like barren landscapes are exceedingly common in subzone 1, but also occur extensively in subzones 2 and 3 in association with wind-blown plains or coarse-grained highly alkaline limestone, strongly acidic shales, and other surficial materials that are not conducive to plant growth (Edlund & Alt 1989). The vegetation types of these areas are not the same as in subzone 1 because they contain woody plants (e.g. *Dryas* and *Salix*), richer floras, and are part of more diverse regional mosaics of vegetation types. Floristic data and available meteorological data from these areas do not support placing them in subzone 1. Additionally, the term 'desert' implies an area with a deficit of moisture for plant growth. Despite low precipitation, most soils in subzone 1 are continuously moist during the summer due to fog, low evapotranspiration, and the presence of permafrost, which retain moisture at the soil surface. Cold arid grass-dominated deserts occur in some continental areas of subzones 2 and 3, such as the inner fiords of northern Ellesmere in the vicinity of Eureka and probably also Peary Land in north Greenland. Vegetation in these areas consist of sparse grasses and forbs (*Pucinellia angustata*, *P. poaceae*, *Poa hartzii*, *Braya thorild-wulffii*, *Gastrolychnis triflora*, *Potentilla pulchella*).

Subzone 2, prostrate dwarf-shrub subzone. In subzone 2, mesic, low-elevation surfaces with fine-grained soils generally have open, patchy plant cover, generally with 5–50% cover of vascular plants. Throughout the subzone, erect shrubby vegetation is lacking on mesic sites. Over broad areas, abundant nonsorted circles, stripes, and ice-wedge polygons interrupt the plant cover. In mesic areas,

Table 2 Climate, vegetation structure, annual production, standing crop and species richness for representative zonal sites in Tundra subzones

Subzone	Mean July temp. at southern sub-zone boundary (°C) [compromise value][1]	Sum of mean monthly temps above freezing at southern boundary[2] (°C)	Vertical structure of plant cover[3]	Horizontal structure of plant cover[3]	Total phyto-mass[4] (above ground + below ground and live + dead) ($t\,ha^{-1}$)	Net annual production[4] (above ground + below ground) ($t\,ha^{-1}\,y^{-1}$)	Number of vascular plant species in local floras[5]
1. Cushion forb	2–3 [3]	6	Mostly barren. In favourable microsites, 1 lichen or moss layer <2 cm tall, very scattered vascular plants hardly exceeding the moss layer; no woody plants	<5% cover of vascular plants, up to 40% cover by cryptogams mostly associated with cracks in polygonal patterns and protected microsites. No closed root systems	3	0.3	<50
2. Prostrate dwarf shrub	5–7 [6]	12	2 layers, moss layer 3–5 cm thick and herbaceous layer 5–10 cm tall, prostrate and hemi-prostrate dwarf shrubs	5–50% cover of vascular plants, open patchy vegetation	20	2.3	75–125
3. Erect dwarf shrub	8–10 [9]	20	2 layers, moss layer 5–10 cm thick and herbaceous/dwarf-shrub layer 10–40 cm tall	50–80% cover of vascular plants, interrupted closed vegetation	57	3.3	150–250
4. Low shrub	10–12 [12]	35	2–3 layers, moss layer 5–10 cm thick, herbaceous/dwarf-shrub layer 20–50 cm tall, sometimes with low-shrub layer to 80 cm	80–100% cover of vascular plants, closed canopy	107	3.8	200 to >450

[1] Mean July temperatures based on Edlund (1996) and Matveyeva (1998) with a compromise value for global modeling in continental areas.
[2] Sum of mean monthly temperatures from Young (1971).
[3] Vertical and horizontal structure from Chernov & Matveyeva (1997).
[4] Based on Bazilovich & Tishkov (1997) for Russian Arctic.
[5] Number of vascular species in local floras based on Young (1971).

vascular vegetation is often confined to protected habitats provided by cracks and depressions in the polygonal network, and areas irrigated by runoff from snow patches. The dominant growth forms on mesic sites are prostrate and hemi-prostrate (<10 cm) dwarf shrubs (e.g. *Dryas*, *Salix arctica*, *S. polaris*, *Cassiope tetragona*), forbs (e.g. *Draba*, *Saxifraga*, *Minuartia*, *Cerastium*, and *Papaver*), graminoids (e.g. *Carex stans*, *Carex rupestris*, *Alopecurus alpinus*, *Deschampsia borealis*, *Luzula confusa*), mosses and lichens. *Dryas* and prostrate dwarf willows (*Salix polaris*, *S. arctica*) are the primary shrubby species in the northern part of subzone 2. Arctic and Arctic-alpine floristic elements are dominant. Ericads (excluding *Cassiope*) and dwarf birch (*Betula*) are nearly absent. Sedges are often important on mesic sites, and are dominant in wet areas. Rushes (*Luzula*) are also an important component of many mesic vegetation types. *Cassiope* becomes more important in the southern part of the subzone, particularly in early melting, well-drained snow beds, and in areas with acidic parent material. Some authors subdivide subzone 2 into two variants (Yortsev 1994) or two zones (Elvebakk 1999; Fredskild 1998). Subzone 2 is not subdivided here because in much of North America, especially where nonacidic soils are prevalent, the vegetation on mesic sites is not sufficiently different to justify such subdivision, although there are significant differences in the vegetation of snow-bed, wetland, and streamside areas.

The mean July temperature at the southern boundary of subzone 2 is approximately 6 °C. This subzone covers about 35% of the Tundra Zone, including most of the islands in the Canadian Archipelago, most of northern Greenland, south-western Svalbard, Novaya Zemlya, most of the northern fringe of mainland Russia, and the New Siberian Islands.

Subzone 3, erect dwarf-shrub subzone. The boundary between subzones 2 and 3 is considered of highest rank because it separates the northern dry tundras on mineral soils from the southern relatively moist tundras with moss carpets and peaty soils (Alexandrova 1980). The major difference in pedology causes dramatic changes to the vegetation. The plants in subzone 3 have strong hypo-Arctic affinities (*sensu* Yurtsev *et al*. 1978). Important hypo-Arctic species such as birch, alder, willow, and heath plants extend their ranges from the lower layer of sub-Arctic woodlands. Dwarf birch (*Betula nana*, *B. exilis*, *B. glandulosa*) is common in subzone 3 except on calcareous soils, where it is often absent.

The plant canopy is usually interrupted by patches of bare soil caused by nonsorted circles, stripes, and a variety of other periglacial features ('spotty tundra' in the Russian literature). Vascular plants generally cover about 50–80% of the surface. Zonal vegetation on gently sloping upland surfaces consists of sedges (e.g. *Carex bigelowii, Carex membranacea, Eriophorum triste, E. vaginatum, Kobresia myosuroides*), prostrate and erect dwarf (<40 cm tall) shrubs (e.g. *Salix planifolia, S. lanata* ssp. *richardsonii*, *S. reticulata, S. arctica, Betula exilis, Dryas integrifolia*), and mosses. Woody hypo-Arctic species (erect *Salix* species, *Betula, Vaccinium, Ledum, Empetrum,* etc.) occur but are not dominant. Low shrubs (>40 cm tall) occur along streams, but tall (>200 cm) shrub thickets are rare. The role of shrublands is much less prominent than in subzone 4. Prostrate-dwarf-shrub communities, which were common in subzone 2, are confined mainly to wind-swept sites, snowbeds, and calcareous rocks. The moss layer, consisting primarily of *Tomentypnum, Hylocomium, Aulacomnium*, and *Sphagnum*, contributes to the development of organic soil horizons on fine-grained soils. Soils on most mesic surfaces have peaty surface horizons and are often acidic (pH below 5.5), except where the soils are influenced by loess or other factors that maintain a higher soil pH.

There is also more regional variation in the zonal vegetation than in subzones 1 and 2. Tussock tundra consisting of cottongrass tussocks (*Eriophorum vaginatum*) and dwarf shrubs is common on fine-grained acidic soils over much of north-eastern Siberia and northern Alaska (Walker *et al*. 1994), particularly in areas that were unglaciated during the last part of the Pleistocene. In transitional areas to subzone 2 and on nonacidic loess, *Dryas* spp. and *Cassiope tetragona* are important (Walker & Everett 1991). Some continental areas of Russia have dry steppe tundras that are relicts of a cold, dry Pleistocene vegetation (Yurtsev 1982).

Climatically, subzone 2 receives predominately Arctic air masses, while subzone 3 receives relatively temperate air during the summer. The mean July temperatures in subzone 3 are about 6–9 °C. Subzone 3 covers about 33% of the Arctic Tundra Zone, including much of northern Alaska, the southern parts of Banks Island and Victoria Island, much of Keewatin, southern Baffin Island, most of southern Greenland, and a broad band across Siberia and Chukotka.

Subzone 4, low-shrub subzone. In subzone 4, the zonal vegetation is dominated by hypo-Arctic low shrubs that are often greater than 40 cm tall (e.g. *Betula nana*, *B. exilis*, *B. glandulosa*, *Salix glauca*, *S. phylicifolia*, *S. planifolia*, *S. richardsonii*, *Alnus* spp.). In some moister areas such as west Siberia and north-west Alaska, thickets of birch or willow species over 80 cm tall occur on zonal sites. In more continental areas and areas with less snow cover, the shrubs are shorter and form a more open canopy (Alexandrova 1980). In northern Alaska and eastern Siberia, tussock tundra is common and has more shrubs than in subzone 3. True shrub tundra with dense canopies of birch, willows, and sometimes alder (*Alnus*) occur in many areas. Low shrubs are abundant along most water courses. Toward the southern part of subzone 4, in flat areas that are continuous with the boreal forest, patches of open forest penetrate into this area along riparian corridors. These woodlands consist of a variety of species of spruce (*Picea*), pine (*Pinus*), cottonwood (*Populus*), and larch (*Larix*) and tree birches (*Betula*) Peat plateaus (palsas) up to 1.5 m tall are common in lowland areas. Subzone 4 is the warmest part of the Arctic Tundra Zone with mean July temperatures of 9–12 °C, and covers about 32% of the zone.

East–west floristic variation within the zones

Russian geobotanists have described longitudinal subdivisions within the subzones that are based primarily on floristic differences (Yurtsev 1994). These divisions are useful for characterizing the considerable E–W floristic variation within the subzones, particularly in subzones 3 and 4. In the more northern two subzones, the Arctic has a remarkably consistent core of circumpolar Arctic plant species that occur around the circumpolar region. Further south, local E–W variation is related to a variety of factors, including different palaeohistories and the greater climatic heterogeneity. Large N–S trending mountain ranges, primarily in Asia, have also restricted the exchange of species between parts of the Arctic (Alexandrova 1980). Yurtsev (1994) delineated six floristic provinces and 20 subprovinces and has discussed their characteristics. The Northern Alaska subprovince is used later in this paper in an example of a framework for a circumpolar Arctic vegetation map. This area covers the region north of the Brooks Range, from the Mackenzie River westward to about Point Lay.

Altitudinal belts

Mountains and plateaus in the Arctic show pronounced altitudinal belts that reflect the latitudinal zonation. For example, in the Alaskan Brooks Range, which lies within subzone 4, an altitudinal belt that is dominated by *Dryas octopetala*, occurs between about 1000 m and 1500 m and is similar to the vegetation of subzone 2. Above 1500 m the vegetation takes on a distinctly polar-desert physiognomy, dominated by lichens, mosses and cushion forbs, similar to subzone 1 (Cantlon 1961). For continental areas, the approximately 3 °C mean July temperature separation between the subzones and the environmental adiabatic lapse rate (6 °C per 1000 m; Barry 1981) can be used to model the vegetation with respect to elevation within each subzone (Fig. 2). With more data, a diagram using thawing-degree-days or Holdridge biotemperatures could be constructed that would apply to both continental and oceanic areas.

Geological influences

> Within each of the…subzones and altitudinal belts, geological processes have produced a rather wide range of soil parent materials which exert a segregating action on the biota producing vegetation patterns of various sizes. (Cantlon 1961)

Vegetation patterns related to parent-material differences are extensive and therefore important to global- and regional-scale modelling efforts. There is a rich literature describing the peculiarities of floras and vegetation on carbonate and ultramafic rocks, saline soils, and fine- vs. coarse-textured soils in the Arctic and sub-Arctic (see for example, Edlund 1982a; Elvebakk 1982; Cooper 1986; Edlund & Alt 1989; Walker & Everett 1991). Unfortunately, the effects of parent material on Arctic

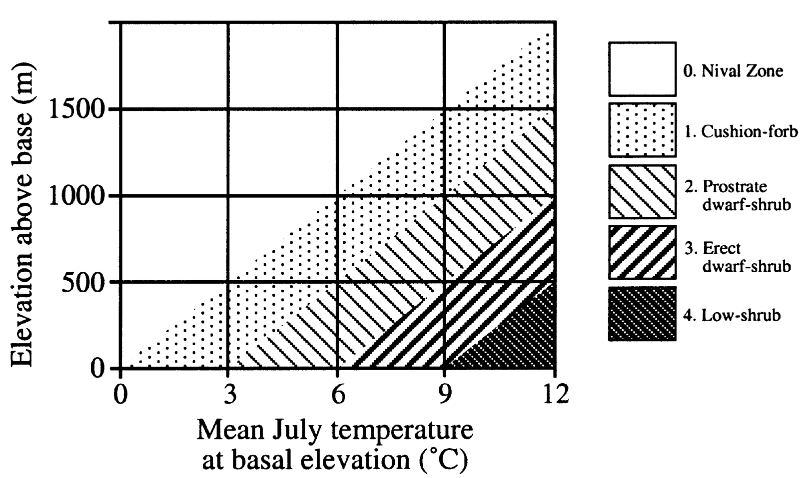

Fig. 2 Altitudinal belts for continental sites in the Arctic. The figure applies to continental areas with an approximately 3 °C mean July temperature separation between the subzones and an environmental adiabatic lapse rate of 6 °C per 1000 m.

vegetation have rarely been mapped. A notable exception is Edlund's (1990) map of the Queen Elizabeth Islands in the Canadian Archipelago. Limestone and dolomite deposits in this region are highly alkaline and coarse textured and support sparsely vegetated barrens (Edlund 1982a,b; Edlund & Alt 1989). Edlund's map portrays the differences of vegetation on acidic and alkaline substrates. *Luzula*-dominated communities occur in the acidic areas and *Dryas, Salix,* and *Saxifraga oppositifolia* communities occur on the alkaline areas (Fig. 3).

In northern Alaska, extensive acidic aeolian and marine sands have vegetation types that are distinct from those on nonacidic fine-grained loess deposits (Walker & Everett 1991; Muller *et al.* 1999). Walker *et al.* (1998) compared ecosystem properties and processes on adjacent acidic and nonacidic tundras in northern Alaska (Table 3). The nonacidic tundra had 28% greater heat flux, half the primary production, 70% less net CO_2 uptake, about half the organic horizon thickness, half the shrub biomass, 30% lower leaf-area indices, 50% deeper active layers, and 15% of the methane flux. These differences are in many cases greater than the changes that could be expected from a change in subzone designation. In northern Alaska, alkaline areas of subzone 3 have many ecosystem properties similar to those of zonal sites in subzone 2. Substrate can thus essentially modify the zonal boundaries, in a fashion similar to that described from taiga regions of Russia (Isachenko 1973).

Glacial history and landscape evolution also strongly affect substrate chemistry and ecosystem properties. In northern Alaska, older landscapes have lower soil pH, poorer nutrient regimes, shallower permafrost tables, wetter soils, lower biodiversity, and greater NDVI than younger landscapes (Walker *et al.* 1995).

Currently, it is difficult to treat these differences globally. As noted above and by numerous other authors, some of the most important vegetation effects are related to substrate pH. A simple break separating nonacidic and acidic parent materials can be carried out in most regions of the Arctic using available soil and surface-geology maps in a GIS context (Walker 1999). Other parent-material subdivisions could be made for global mapping if they were found to be regionally extensive and important to ecosystem processes.

Topographic influences: hill-slope gradients

> Within each of the above subzones, altitudinal belts and areas of different parent material, relief features of various sizes occur. Differences in sharpness of relief and direction of slope exposure associated with these features operate to influence soil drainage, soil depth, surface insolation, snow depth and duration, wind velocity and other environmental phenomena. In turn, these environmental phenomena exert a segregating action on

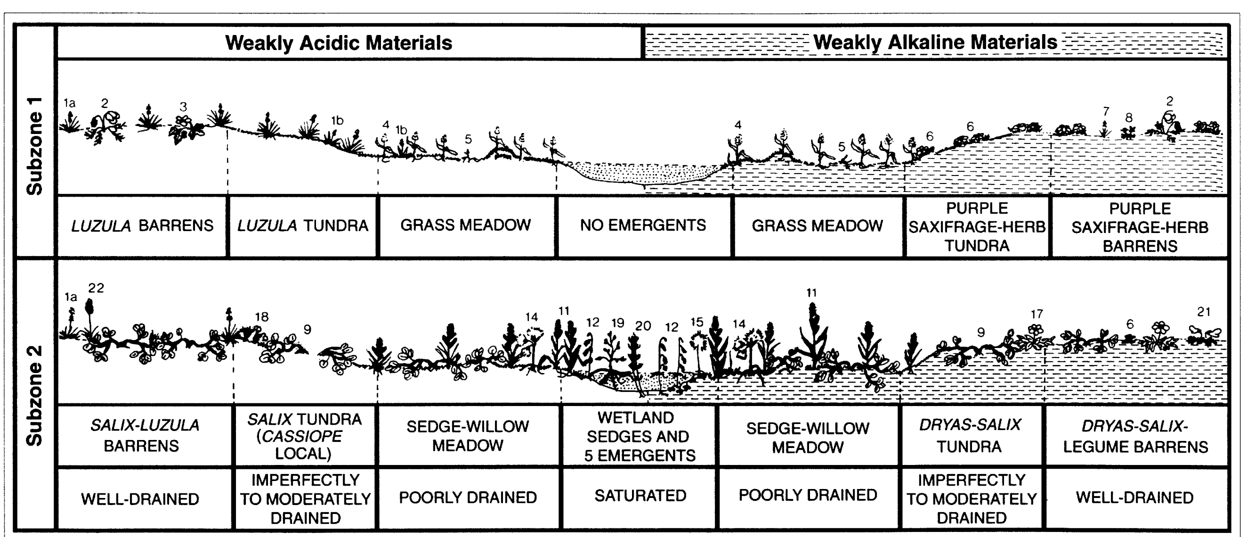

Fig. 3 Catenas of vegetation on weakly acidic and weakly alkaline materials in subzones 1 and 2. Modified from Edlund & Alt (1989). Numbered species: 1, *Luzula confusa*; 1b, *L. arctica*; 2, *Papaver radicatum*; 3, *Potentilla hyparctica*; 4, *Alopecurus alpinus*; 5, *Phippsia algida*; 6, *Saxifraga oppositifolia*; 7, *Poa abbreviata*; 8, *Draba* sp.; 11, *Carex aquatilis var. stans*; 12, *Pleuropogon sabinei*; 14, *Eriophorum triste*; 15, *E. scheuchzeri*; 17, *Dryas integrifolia*; 18, *Cassiope tetragona*; 19, *Arctophila fulva*; 20, *Hippuris vulgaris*; 21, *Oxytropis arctobia*; 22, *Hierochloe alpina*.

Ecosystem property	MNT	MAT
pH of top mineral horizon	7.0	5.3
Average vascular plant species richness (no.)	26	14
Average height of plant canopy (cm)	3.9	6.5
Leaf area index ($m^2 m^{-2}$)	0.57	0.81
NDVI	0.28	0.41
Cover of nonsorted circles (%)	36.5	1.4
Soil heat flux (19–29 Jun 1995, $MJ m^{-2} d^{-1}$)	1.39	1.09
Maximum thaw depth (1995, cm)	57	37
Moss cover (%)	65	79
Net CO_2 uptake (1996, mgCO_2-C m^{-2} $season^{-1}$)	3.3	55.2
Evapotranspiration (19–29 Jun 1995, mm d^{-1})	1.06	1.16
Methane emission[3] ($mg cm^{-2} y^{-1}$)	69	449
Soil organic carbon to 1 m depth ($kg C m^{-3}$)	40	88

Table 3 Ecosystem properties of moist nonacidic tundra (MNT) and moist acidic tundra (MAT). Unless otherwise noted, most values are from two sites on either side of a soil pH boundary in the Arctic Foothills Alaska, measured in 1995. Climate on either side of the boundary was nearly identical. (Based on Walker *et al*. 1998.)

> the available biota resulting in vegetation patterns that are strongly relief-correlated. (Cantlon 1961)

At landscape scales (1–100 km^2), soil moisture has an overwhelming influence on soil development, patterns of tundra plant communities, and tundra ecosystem processes (Zoltai & Pettapiece 1973; Webber 1978; Reynolds *et al*. 1996). This is largely an effect of topography and can be portrayed along hill-slopes as a mesotopographic gradient (Billings 1973) (Fig. 4). Principal landforms – plains, hills, mountains, and tablelands – form first-level geological divisions (Bailey 1996). The vegetation within these divisions is primarily a function of drainage and soil-moisture regime. For example, in northern Alaska, the plains are mainly wet; the hills moist, and the mountains dry. These same changes can be seen at microscales, where small differences of a few centimetres of elevation above or below the water table can influence the plant community composition and function dramatically. In flat areas, such as flat coastal plains or broad river deltas, the influence of microtopography associated with patterned ground features, such as ice-wedge polygons is predominant.

Geochemical migration of elements down slopes is an important influence along mesotopographic gradients. The cold wet soils of the Arctic severely constrain decomposition and nutrient mineralization and availability of nutrients to plants (Chapin *et al*. 1980; Nadelhoffer *et al*. 1997). Areas that have high nutrient flux, such as along streams, water tracks, bird cliffs, or animal dens, often exhibit strikingly different plant growth and structure to zonal tundra habitats (Walker 1987; Chapin *et al*. 1988; Odasz 1994). Snow distribution is controlled largely by wind and mesotopographic features and has a wide variety of ecosystem influences, including effects on soil moisture, soil chemistry, growing-season length, soil temperatures, and subnivian animal activity (Walker *et al*. 1999). There are important differences between the well-drained, early melting portion of snow beds and poorly drained, late-melting portions (Razzhivin 1994). Streams and snow beds occupy large components of most Arctic landscapes, and any realistic portrayal of landscape variation associated with hill slopes should include dry, mesic, wet, snowbed and streamside habitats (Fig. 4).

Relevance to Arctic vegetation mapping

Currently, there is no map of any detail that portrays the vegetation of the whole Arctic. Such a map is needed for a wide variety of purposes, including modelling efforts to predict the consequences of climate change. A circumpolar Arctic vegetation map is currently in progress (Walker 1995). An integrated mapping procedure will incorporate climate, parent-material, and topography information in a unified legend approach (Walker 1999). A hierarchical legend framework based on climate, parent material, and topography is presented here using northern Alaska as an example (Table 4). The table shows the dominant plant communities occurring in the five habitats of the mesotopographic gradient on acidic and nonacidic substrates, within subzones 2, 3 and 4 of the Northern Alaska Subprovince (Yurtsev 1994). Similar tables could be constructed for each subzone–subprovince combination within the Tundra zone. An important element of Table 4 is that each plant community has a two-species name that includes the publication where the community is described. Plant communities that are only described locally are given 'plant community type' (communication) designations. Those that have 'association' (suffix *–etum*) names have been compared globally to types described from other areas and have been incorporated into the Braun–Blanquet

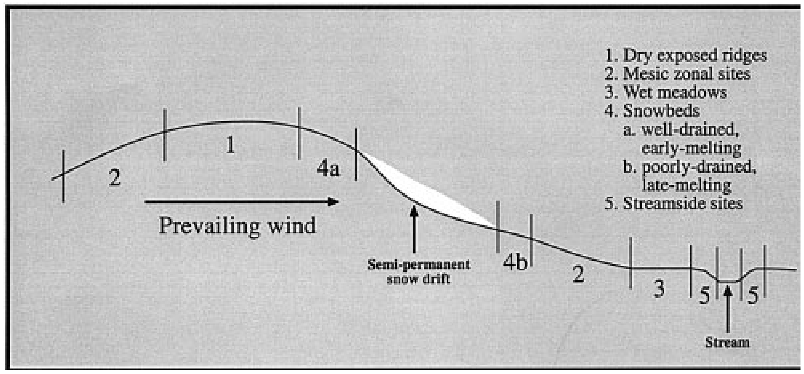

Fig. 4 An idealized mesotopographic gradient for the Arctic that includes five habitats: dry, mesic (zonal), wetland, snowbed, and streamside vegetation.

syntaxonomic nomenclature system (Westhoff & van der Maarel 1978). The European phytosociological approach has a long history in the European Arctic, whereas North Americans have traditionally favoured a gradient approach using informal or individual classification systems (Walker *et al*. 1994a). The European approach has many advantages as an international classification system at the plant-community level because of its well-established procedures, long history, and wide application throughout the Arctic (e.g. Thannheiser 1988; Daniëls 1994; Elvebakk 1994; Walker *et al*. 1994a; Dierssen 1996; Matveyeva 1998).

Relevance to global modelling efforts

Many current approaches to modelling vegetation response to climate change use plant functional types (PFTs) to group the multitude of plant species into more manageable groups of plants that are considered important with respect to ecosystem function (Solomon & Shugart 1993; Box 1996; Noble & Gitay 1996; Woodward & Cramer 1996; Smith *et al*. 1997). Simple mathematical step functions can then be parameterized such that a bioclimatic 'envelope' describes the range of climatic conditions under which a group can survive (Cramer 1997). Under modelled climate-change scenarios, these PFT groups can then form different assemblages that can be interpreted as resembling vegetation types. This approach is a compromise between the now-outdated assumption that climate change will cause wholesale shifts in vegetation types corresponding to current bioclimatic relationships and the assumption that it is necessary to model the response of all key plant species so that they respond individualistically to climate. The PFT categories can be based on a variety of plant characteristics, including growth forms, life forms, taxonomic groups, or other characteristics depending on the application. Several authors have discussed PFTs and growth forms specific to the Arctic (Webber 1978; Komárková & McKendrick 1988; Cramer & Leemans 1993; Hobbie *et al*. 1993; Chapin *et al*. 1996; Cramer 1997; Shaver *et al*. 1997). Figure 5 provides a key to the PFTs that several Arctic vegetation ecologists have arrived at through various workshops in response to the needs of global vegetation modelers. This group of PFTs is modified from a list of Arctic tundra vascular plant growth forms (Komárková & McKendrick 1988). These 14 PFTs plus barrens are extensive and potentially useful for global modelling efforts to predict vegetation change to the zonal types. Table 5 contains a first approximation of the dominant PFTs in major habitat classes within each subzone. Some modelling approaches may desire a shorter list of PFTs, which could be developed by reference to Fig. 5. The table is currently developed only for nonacidic substrates in subzones 1, 2 and 3, and acidic substrates in subzone 4.

Conclusions

More detailed land-cover maps of the tundra regions are needed to portray the large differences in ecosystems that occur across approximately 30° of latitude and 10° differences in mean July temperature. At the coarsest global scale, with pixel sizes of $0.5° \times 0.5°$, four subzones are perhaps sufficient for most modelling considerations. These subzones portray the major transitions on mesic (zonal) sites, from the coldest barren portions of the Arctic to relatively warm lush shrub tundra near treeline. They are named according to changes in the stature of the woody plants on zonal sites. The subzones could be subdivided further to portray more subtle changes related to variation within intrazonal sites, such as wetlands, snow beds, and streamside areas.

Within the subzones, parent-material chemistry is much more significant than is generally realized. A simple division is used here that shows the contrasts between acidic and nonacidic soils. The framework presented in Table 4 could be expanded to include other geological substrates if they were found to be regionally extensive and important to ecosystem processes.

Table 4 Dominant plant communities occurring in major habitats along the mesotopographic gradient on acidic and nonacidic substrates in subzones 2, 3 and 4 of the Northern Alaska Floristic Subprovince. Subzone 1 is missing in northern Alaska. The break between acidic and nonacidic soils is approximately pH 5.5

Habitat along mesotopographic gradient	Acidic substrates	Nonacidic substrates
	Subzone 2	
	Acidic substrates (Barrow)	Nonacidic substrates (Prudhoe Bay, coast)
Dry exposed sites	*Sphaerophorus globosus-Luzula confusa* comm. (Elias *et al.* 1996; Webber 1978)	*Carex rupestris–Dryas integrifolia* comm. (Walker 1985) (Type B12)
Mesic zonal sites	*Sphaerophorus globosus-Luzula confusa* comm. (Elias *et al.* 1996; Webber 1978)	*Carex aquatilis–Dryas integrifolia* comm. (Walker 1985) (Type U12)
Wet sites	*Eriophorum angustifolium-Carex aquatilis* comm. (Elias *et al.* 1996; Webber 1978)	*Carex aquatilis–Dupontia fisheri* comm. (Walker 1985) (Type M10)
Snow beds	*Salix rotundifolia-Cetraria delesii* (Elias *et al.* 1996) (moderate snow beds) Phippsia algida-Cochlearia officinalis comm. (Walker 1977) (deep snow beds)	*Dryas integrifolia–Cassiope tetragona* comm. (Walker 1985) (Type U6, well-drained snow beds) *Equisetum scirpoides–Salix rotundifolia* comm. (Walker 1985) (Type U7, Late-melting snow beds)
Streamsides	*Dupontia fisheri-Alopecurus alpinus* comm. (Walker 1977)	*Juncus arcticus–Salix ovalifolia* comm. (Walker 1985) (Type M6)
	Subzone 3	
	Acidic substrates (Atqasuk)	Nonacidic substrates (Prudhoe Bay, inland)
Dry exposed sites	*Diapensia lapponica–Dryas integrifolia* comm. (Komárková & Webber 1980)	*Oxytropis nigrescens–Dryas integrifolia* comm. (Walker 1985) (Type B1, dry gravelly sites) *Saxifraga oppositifolia–Dryas integrifolia* comm. (Walker 1985) (Type B2, dry organic soil)
Mesic zonal sites	*Betula nana* ssp. *exilis–Eriophorum vaginatum* comm. (Komárková & Webber 1980)	*Eriophorum triste–Dryas integrifolia* comm. (Walker 1985) (Type U3)
Wet sites	*Carex aquatilis* ssp. *stans* comm. (Komárková & Webber 1980)	*Carex aquatilis–Drepanocladus brevifolius* comm. (Walker 1985) (Type M2)
Snow beds	*Boykinia richardsonii–Cassiope tetragona* comm. (Komárková & Webber 1980)	*Dryas integrifolia–Cassiope tetragona* comm. (Walker 1985) (Type U6, well-drained snowbeds) *Equisetum scirpoides–Salix rotundifolia* comm. (Walker 1985) (Type U7, Late-melting snow beds)
Streamsides	*Salix planifolia* ssp. *pulchra.* (Komárková & Webber 1980)	*Epilobio latifolii–Salicetum alaxensis* ass. prov. [Schikoff, in prep.] (active floodplains) *Carex aquatilis-Salix lanata* comm. (Walker 1985) (Type U8)
	Subzone 4	
	Acidic substrates (Imnavait Creek)	Nonacidic substrates (Toolik Lake)
Dry exposed sites	*Selaginello sibiricae–Dryadetum octopetalae* (Walker *et al.* 1994b) (dry gravelly sites) *Salici phlebophyllae–Arctoetum alpinae* (Walker *et al.* 1994b) (dry organic soils)	*Oxytropis bryophila–Dryas integrifolia* comm. (Walker, in prep.) (dry gravelly sites) *Astragalus maydelliana–Dryas integrifolia* comm. (Walker, in prep.) organic dry sites)
Mesic zonal sites	*Sphagno–Eriophoretum vaginati* (Walker *et al.* 1994b) (Tussock tundra) *Sphagno–Eriophoretum vaginati betuletosum nanae* (Walker *et al.* 1994b) (Shrub tundra)	*Dryado integrifoliae–Caricetum bigelowii* (Walker *et al.* 1994b)

Table 4 Continued

Habitat along mesotopographic gradient	Subzone 2	
	Acidic substrates (Barrow)	Nonacidic substrates (Prudhoe Bay, coast)
Wet sites	*Sphagnum orientale–Eriophorum scheuchzeri* comm. (Walker & Walker 1996) *Sphagnum lenense–Salix fuscescens* comm. (Walker & Walker 1996)	*Eriophorum angustifolium–Carex aquatilis* comm. (Walker & Walker 1996)
Snow beds	*Carici microchaetae – Cassiope tetragona* comm. (Walker *et al.* 1994b) *Salix rotundifolia–Saxifrage nivalis* comm. (Walker *et al.* 1989)	*Dryas integrifolia–Cassiope tetragona* comm. (Walker *et al.* 1994b) *Salix rotundifolia–Saxifraga nivalis* comm. (Walker *et al.* 1989)
Streamsides	*Valeriano capitatae–Salicetum planifoliae* ass. prov. (Schikoff, in prep.) (=*Eriophorum angustifolium-Salix purlchrae* comm. (Walker *et al.* 1994b)	*Epilobio latifolii–Salicetum alaxensis* ass. prov. (active floodplains) *Salicetum glauco–richardsonii* ass. prov. (stable floodplains) *Climaceum dendroides–Alnus viridis* comm. (Walker *et al.* 1997) (alder floodplains)

[1]Surface deposits at the representative sites: Barrow, Acidic marine sands and gravels; Prudhoe Bay (coast), calcareous glacial outwash; Atqasuk, acidic eolian sands; Prudhoe Bay (inland), calcareous loess; Imnavait Creek, acidic mid-Pleistocene glacial till; Toolik Lake, calcareous late-Pleistocene glacial till.

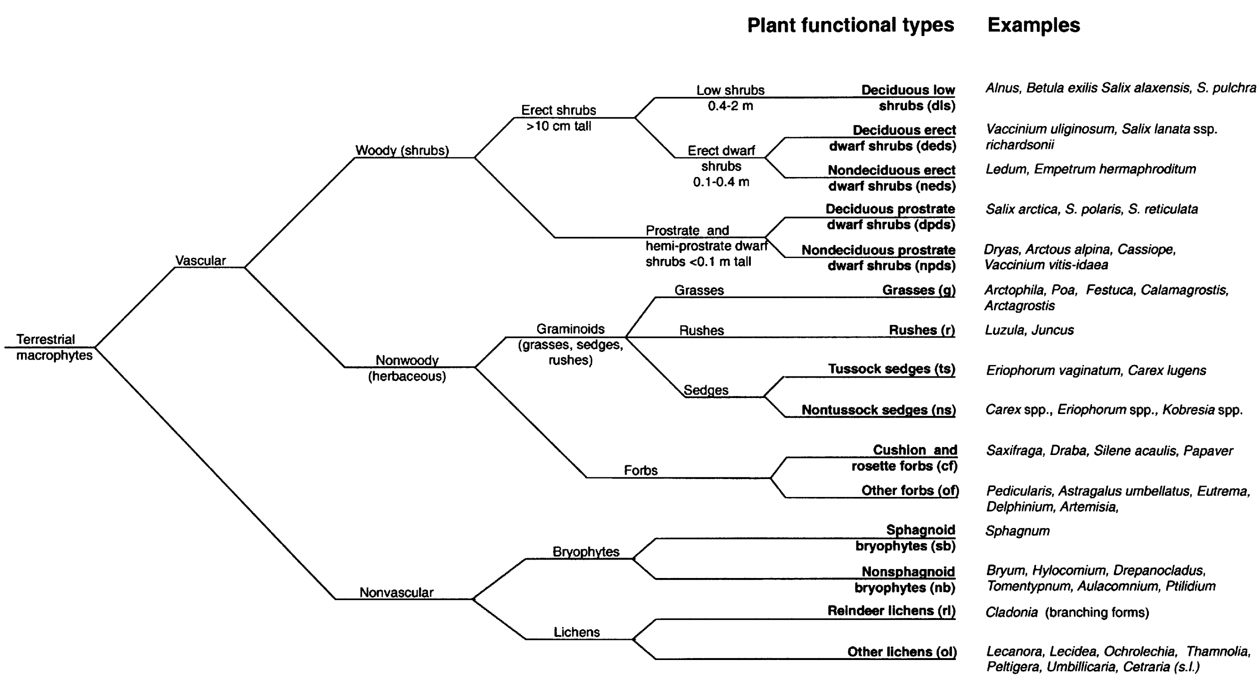

Fig. 5 Key to plant functional types for tundra ecosystems.

At landscape scales, soil-moisture and snow gradients are predominant. A five-habitat mesotopographic gradient is useful to portray the principal components of most Arctic landscapes. This includes dry, mesic (zonal), wet, snowbed, and streamside environments.

The forthcoming circumpolar Arctic vegetation map will take into consideration climate, parent material and topographic factors. The example hierarchical legend presented in Table 4 will be extended to other floristic subprovinces based on the literature and expert knowl-

Table 5 Plant functional types (PFTs) for modelling vegetation in the four tundra subzones and five major habitats. Underlined PFTs are dominant and a suggested minimum for global and regional modelling efforts

Subzone	Habitat				
	Dry, wind swept	Mesic (zonal)	Snowbed (early melting, well-drained)	Wet (non-emergent)	Streamside (stable sites)
1. Cushion-forb	b, cf, of, g	b, g, r, cf, of, ol, c (>95% barren or lichen covered)	b, g, of, c	nb, g	b, g, cf
2. Prostrate dwarf shrub	b, npds, ns, dpds, cf, of, ol	npds, dpds, b, ns, cf, of, ol (50–95% barren or lichen covered)	npds, dpds, nb, ol	ns, nb, dpds, of	npds, dpds, ns, cf, of, nb
3. Erect dwarf shrub	npds, dpds, b, ns, cf, of, ol	ns, nb, npds, dpds, deds, neds, cf, of, ol, b (20–50% barren)	npds, dpds, nb, ol	ns, nb, dpds, of	deds, npds, dpds, of, ns, nb , of
4. Low shrub	dpds, npds, g, ol	dls, ts*, ns, deds, neds, sb, nb, rl, ol (<20% barren)	npds, dpds, nb, ol	ns, sb, nb, dpds, of	dls, neds, deds, npds, dpds, nb, of

*In Beringia.
PFT codes: b, barren; cf, cushion or rosette forb; deds, deciduous erect dwarf shrub; dls, deciduous low shrub; dpds, deciduous prostrate dwarf shrub; g, grass; nb, nonsphagnoid bryophyte; neds, nondeciduous erect dwarf shrub; npds, nondeciduous prostrate dwarf shrub; ns, nontussock sedge; of, other forb; ol, other lichen; r, rush; rl, reindeer lichen; sb, sphagnoid bryophyte; ts, tussock sedge. Parent material conditions are assumed to be nonacidic in subzones 1–3 and acidic in subzone 4.

edge from these regions. The compiled list of dominant plant communities within each climatic subzone, parent material type, and major habitat type will provide concrete information for a wide variety of users including climate-change modellers

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References

Ahti T, Hamet-Ahti L, Jalas J (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, **5,** 169–211.

Alexandrova VD (1980) *The Arctic and Antarctic: Their Division Into Geobotanical Areas*. Cambridge University Press, Cambridge.

Bailey RG (1996) *Ecosystem Geography*. Springer, New York.

Barry RG (1981) *Mountain Weather and Climate*. Methuen, London.

Bay C (1997) Floristical and ecological characterization of the polar desert zone of Greenland. *Journal of Vegetation Science*, **8,** 685–696.

Bazilevich NI, Tishkov AA, Vilchek GE (1997) Live and dead reserves and primary production in polar desert, tundra, and forest tundra of the former Soviet Union. In: *Polar and Alpine Tundra* (ed. Wielgolaski FE), pp. 509–539. Elsevier, Amsterdam.

Billings WD (1973) Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbances. *Bioscience*, **23,** 697–704.

Bliss LC (1977). *Truelove Lowland, Devon Island, Canada: a High Arctic Ecosystem*. University of Alberta Press, Alberta, 714pp.

Bliss LC (1997) Arctic ecosystems of North America. In: *Polar and Alpine Tundra* (ed. Wielgolaski FE), pp. 551–684. Elsevier, Amsterdam.

Bockheim JG, Walker DA, Everett LR (1996) Soil carbon distribution in nonacidic and acidic soils of arctic Alaska. *Advances of Soil Science. Proceedings of the International Symposium on Carbon Sequestration in Soil*, pp. 143–155.

Box EO (1996) Plant functional types and climate at the global scale. *Journal of Vegetation Science*, **7,** 309–320.

Brattbakk I (1986) *Vegetation Regions — Svalbard and Jan Mayen*, Map 1:1,000,000 scale. Norsk Polarinstitutt/MAB

Cantlon JE (1961) Plant cover in relation to macro-, meso- and micro-relief. Final Report, Grants #ONR-208 and 216, Office of Naval Research.

Chapin FS III, Bret-Harte MS, Hobbie S, Zhong H (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, **7,** 347–358.

Chapin FS III, Fetcher N, Kielland K, Everett KR, Linkins AE (1988) Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. *Ecology*, **69,** 693–702.

Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J

(1992). *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective*. Academic Press, New York.

Chapin FS III, Miller PC, Billings WD, Coyne PI (1980) Carbon and nutrient budgets and their control in coastal tundra. In: *An Arctic Ecosystem: the Coastal Tundra at Barrow, Alaska* (eds Brown J *et al*.), pp. 458–482. Dowden, Hutchinson and Ross, Stroudsburg.

Chernov YI, Matveyeva NV (1997) Arctic ecosystems in Russia. In: *Polar and Alpine Tundra* (ed. Wielgolaski FE), pp. 361–507. Elsevier, Amsterdam.

Cooper DJ (1986) Arctic-alpine tundra vegetation of the Arrigetch Creek Valley, Brooks Range, Alaska. *Phytocoenologia*, **14,** 467–555.

Cramer W (1997) Modeling the possible impact of climate change on broad-scale vegetation structure: examples from Northern Europe. In: *Global Change and Arctic Terrestrial Ecosystems* (eds Oechel WC *et al*.), pp. 312–329. Springer, New York.

Cramer W, Leemans R (1993) Assessing impacts of climatic change on vegetation using climate classification systems. In: *Vegetation Dynamics and Global Change* (eds Soloman AM, Shugart HH), pp. 190–217. Chapman & Hall, New York.

Daniëls FJA (1994) Vegetation classifications in Greenland. *Journal of Vegetation Science*, **5,** 781.

Dierssen K (1996) *Vegetation Nordeuropas*. Ulmer, Stuttgart.

Edlund SA (1982a) *Plant Communities on the Surficial Materials of North-Central District of Keewatin, Northwest Territories.* Geological Survey of Canada, Paper no. 80-33.

Edlund SA (1982b) *Vegetation of Eastern Melville Island.* Geological Survey of Canada, Paper no. 852.

Edlund SA (1996) Legend for vegetation of Canadian arctic islands and adjacent mainland. In: *Circumpolar Arctic Vegetation Mapping Workshop, St. Petersburg, Russia,* 21–24 *March* 1994. USGS Open File Report 96-251.

Edlund SA, Alt BT (1989) Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. *Arctic*, **42,** 3–23.

Edlund SA (1990) *Vegetation, central Queen Elizabeth Islands, Northwest Territories*. Map 1755A, 1:000,000 scale. Geological Survey of Canada, Alberta.

Elias SA, Short SK, Walker DA, Auerbach NA (1996) *Final report: Historical biodiversity at remote Air Force sites in Alaska.* Report to Department of Defense, Legacy Resource Management Program, Project 0742, 60 + appendices. Institute of Arctic and Alpine Research, Boulder, CO.

Elvebakk A (1982) Geological preferences among Svalbard plants. *Inter-Nord*, **16,** 11–31.

Elvebakk A (1985) Higher phytosociological syntaxa on Svalbard and their use in subdivision of the Arctic. *Nordic Journal of Botany*, **5,** 273–284.

Elvebakk A (1994) A survey of plant associations and alliances from Svalbard. *Journal of Vegetation Science*, **5,** 791.

Elvebakk A (1999) Bioclimatic delimitation and subdivision of the Arctic. *Det Norsk Videnskaps-Akademi. I Matematisk Naturvitenskapelige Klasse, Skrifter, Ny serie*, **38,** 81–112.

Feilberg J (1984) A phytogeographical study of South Greenland. Vascular plants. *Meddelelser Om Grønland, Bioscience*, **15,** 3–70.

Fredskild B (1998) The vegetation types of Northeast Greenland. *Meddelelser Om Grønland, Bioscience*, **49,** 1–84.

Gorodkov BN (1935) *Rastitelnost tundrovoi zony SSSR [The vegetation of the tundra zone of the USSR],* 142pp. Cited in Alexandrova (1980).

Hobbie SE, Jensen DB, Chapin FS III (1993) Resource supply and disturbance as controls over present and future plant diversity. In: *Biodiversity and Ecosystem Function* (eds Schultze E, Mooney HA), pp. 385–408. Springer, Heidelberg.

Isachenko AG (1973) *Principles of Landscape Science and Physical-Geographic Regionalization*. Melbourne University Press, Melbourne.

Komárková V, McKendrick JD (1988) Patterns in vascular plant growth forms in arctic communities and environment at Atkasook, Alaska. In: *Plant Form and Vegetation Structure* (eds Werger MJA *et al*.), pp. 45–70. SPB Academic Publishing, The Hague.

Komárková V, Webber PJ (1980) Two Low Arctic vegetation maps near Atkasook, Alaska. *Arctic and Alpine Research*, **12,** 447–472.

Lavrenko EM, Sochava VB (1954) *Geobotanicheskaya karta SSSR, m 1:4,000,000* [Geobotanical map of the USSR, 1:4,000,000 scale].

Matveyeva NV (1998) *Zonation in Plant Cover of the Arctic*. Russian Academy of Science, St Petersburg (In Russian).

Muller SV, Racoviteanu AE, Walker DA (1999) Landsat–MSS-derived land-cover map of northern Alaska: extrapolation methods and a comparison with photo–interpreted and AVHRR-derived maps. *International Journal of Remote Sensing*, **20,** 2921–2946.

Nadelhoffer KJ, Shaver GR, Giblin A, Rastetter EB (1997) Potential impacts of climate change on nutrient cycling, decomposition, and productivity in arctic ecosystems. In: *Global Change and Arctic Terrestrial Ecosystems* (eds Oechel WC *et al*.), pp. 349–364. Springer, New York.

Noble IR, Gitay H (1996) A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science*, **7,** 329–336.

Odasz AM (1994) Nitrate reductase activity in vegetation below an arctic bird cliff, Svalbard, Norway. *Journal of Vegetation Science*, **5,** 913.

Oechel WC, Callaghan T, Gilmanov T *et al*. (1997) *Global Change and Arctic Terrestrial Ecosystems*. Springer, New York.

Olson J (1985) *Major World Ecosystem Complexes Ranked by Carbon in Live Vegetation: A Database.* Carbon Dioxide Information Center.

Polunin N (1951) The real Arctic: suggestions for its delimitation, subdivision and characterization. *Journal of Ecology*, **39,** 308–315.

Polunin N (1960). *Introduction to Plant Geography*. Oxford University Press, London.

Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19,** 117–134.

Rannie WF (1986) Summer air temperature and number of vascular species in arctic Canada. *Arctic*, **39,** 133–137.

Razzhivin VY (1994) Snowbed vegetation of far northeastern Asia. *Journal of Vegetation Science*, **5,** 829–842.

Reynolds JF, Tenhunen TD, Leadley PW *et al*. (1996) Patch and landscape models of arctic tundra: potentials and limitations. In: *Landscape Function and Disturbance in Arctic Tundra* (eds Reynolds JF, Tenhunen JD), pp. 293–346. Springer, Berlin.

Schikoff U (in press) Vegetation and ecology of riparian habitats on the Arctic Slope of Alaska: a classification and ordination analysis. *Phytocoenologia*, in press.

Shaver FR, Giblin AE, Nadelhoffer KJ, Rastetter EB (1997) Plant functional types and ecosystem change in arctic tundras. In: *Plant Functional Types* (eds Smith TM *et al.*), pp. 153–173. Cambridge University Press, Cambridge.

Smith TM, Woodward IA, Shugart HH (1997) *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. Cambridge University Press, Cambridge.

Sochava VB (1934) Botaniko-geograficheskie podzony v zapadnykh tundrakh Yakutii [Botanical-geographical subzones in the western tundras of Yakutia]. *Botanchisky Zhurnal*. Cited in Alexandrova (1980).

Sochava VB, Gorodkov BN (1956) Arkticheskie pustyni i tundry [Arctic deserts and tundras]. In: *Poyasnitel'ny Pokrov SSSR. Poyasnitel'ny Tekst K 'Geobotnicheskoy Karte SSSR' M. 1:4,000,000* [Explanatory Text to Geobotanical Map of the USSR, Scale 1:4,000,000]. *Part 1: Moscow–Leningrad.* Cited in Alexandrova (1980).

Solomon AM, Shugart HH (1993) *Vegetation Dynamics and Global Change*. Chapman & Hall, New York.

Sorensen T (1941) Temperature relations and phenology of the northeast Greenland flowering plants. *Meddelelser Om Grønland, Bioscience*, **125,** 1–315.

Steffen WL, Cramer W, Plöchl M, Bugmann H (1996) Global vegetation models: incorporating transient changes to structure and composition. *Journal of Vegetation Science*, **7,** 321–328.

Tedrow JCF (1977) *Soils of the Polar Landscapes*. Rutgers University Press, New Brunswick.

Thannheiser D (1988) Eine landschaftsökologische Studie bei Cambridge Bay, Victoria Island, N.W.T., Canada. *Mitteilungen der Geographischen Gesellschaft in Hamburg*, **78,** 1–51.

Tuhkanen S (1984) A circumboreal system of climatic-phytogeographical regions. *Acta Botanica Fennica*, **127,** 1–51.

Tuhkanen S (1986) Delimitation of climate-phytogeographical regions at the high-latitude areas. *Nordia*, **20,** 105–112.

Vysotskyi GN (1909) O fitotopologiqeskikh kartakh, sposobakj ikh sostavleniya i ikh prakticheskoe znachenie [Phytotopological maps, their drawing and their meaning for practice]. *Pochvovedenie*, **1,** 97–124.

Walker DA (1977) *The analysis of the effectiveness of a television scanning densitometer for indicating geobotanical features in an ice-wedge polygon complex at Barrow, Alaska*. MA thesis, University of Colorado, Boulder.

Walker DA (1985) *Vegetation and environmental gradients of the Prudhoe Bay region, Alaska.* Report 85-14. U.S. Army Cold Regions Research and Engineering Laboratory.

Walker DA (1987) Height and growth-ring response of *Salix lanata* ssp. *richardsonii* along the coastal temperature gradient of northern Alaska. *Canadian Journal of Botany*, **65,** 988–993.

Walker DA (1995) Toward a new circumpolar arctic vegetation map. *Arctic and Alpine Research*, **31,** 169–178.

Walker DA (1999) An integrated vegetation mapping approach for northern Alaska (1:4,000,000 scale). *International Journal of Remote Sensing* (in press).

Walker DA, Everett KR (1991) Loess ecosystems of northern Alaska: regional gradient and toposequence at Prudhoe Bay. *Ecological Monographs*, **61,** 437–464.

Walker DA, Walker MD (1996) Terrain and vegetation of the Imnavait Creek Watershed. In: *Landscape Function: Implications for Ecosystem Disturbance, a Case Study in Arctic Tundra* (eds Reynolds JF, Tenhunen JD), pp. 73–108. Springer, New York.

Walker DA, Binnian E, Evans BM, Lederer ND, Nordstrand E, Webber PJ (1989) Terrain, vegetation, and landscape evolution of the R4D research site, Brooks Range foothills, Alaska. *Holarctic Ecology*, **12,** 238–261.

Walker MD, Daniëls FJA, van der Maarel E (1994a) Circumpolar arctic vegetation – introduction and perspective. *Journal of Vegetation Science*, **5,** 757–764.

Walker MD, Walker DA, Auerbach NA (1994b) Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science*, **5,** 843–866.

Walker DA, Auerbach NA, Shippert MM (1995) NDVI, biomass, and landscape evolution of glaciated terrain in northern Alaska. *Polar Record*, **31,** 169–178.

Walker DA, Auerbach NA, Bockheim JG *et al*. (1998) Energy and trace-gas fluxes across a soil pH boundary in the Arctic. *Nature*, **394,** 469–472.

Walker DA, Billings WD, Molenaar JGD (1999) Snow–vegetation interactions in tundra environments. In: *Snow Ecology* (eds Jones HG *et al.*). Cambridge University Press, Cambridge.

Webber PJ (1978) Spatial and temporal variation of the vegetation and its productivity, Barrow, Alaska. In: *Vegetation and Production Ecology of an Alaskan Arctic Tundra* (ed. Tieszen LL), pp. 37–112. Springer, New York.

Westhoff V, van der Maarel E (1978) The Braun-Blanquet approach. In: *Classification of Plant Communities* (ed. Whittaker RH), pp. 287–399. Dr W. Junk, Den Haag.

Woodward FI, Cramer W (1996) Plant functional types and climatic changes: Introduction. *Journal of Vegetation Science*, **7,** 306–308.

Young SB (1971) The vascular flora of St. Lawrence Island with special reference to floristic zonation in the arctic regions. *Contributions from the Gray Herbarium*, **201,** 11–115.

Yurtsev BA (1982) Relicts of the xerophyte vegetation of Beringia in northeastern Asia. In: *Paleoecology of Beringia* (eds Hopkins DM *et al.*), pp. 157–177. Academic Press, New York.

Yurtsev BA (1994) Floristic division of the Arctic. *Journal of Vegetation Science*, **5,** 765–776.

Yurtsev BA, Tolmachev AI, Rebristaya OV (1978) The floristic delimitation and subdivision of the Arctic. In: *The Arctic Floristic Region* (ed. Yurtsev BA), pp. 9–104. Nauka, Leningrad.

Zoltai SC, Pettapiece WW (1973) Terrain, vegetation and permafrost relationships in the northern part of the Mackenzie River valley and northern Yukon. In: *Environmental Social Program Task Force on Northern Oil Development Report*.