

Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: A classification and ordination analysis

by Udo SCHICKHOFF, Greifswald, Marilyn D. WALKER, and Donald A. WALKER, Fairbanks/Alaska

with 16 figures and 10 tables

Abstract. We present the first analysis of riparian vegetation types on the Arctic Slope of Alaska including classification and ordination. We classified riparian willow communities according to the Braun-Blanquet approach, and analysed environmental relationships of associations to complex environmental gradients using Detrended Correspondence Analysis. We also examined synecological differences in terms of community characteristics (e.g. growth form distributions, species richness, soil pH and climatic affinities, phytogeographic patterns) to better understand ecological alteration processes and changing species compositions along successional gradients. Data were collected along a transect from the Brooks Range to Prudhoe Bay, primarily in the watersheds of Sagavanirktok River and Kuparuk River. Riparian vegetation in arctic Alaska mainly consists of willow shrub communities which are functionally important components of arctic landscape ecosystems. A combination of edaphic conditions (soil pH, soil moisture) and factors related to topography, disturbance regime and landscape evolution (river terrace/stream bank development) controls spatial patterns and floristic compositions of riparian plant communities. Classification resulted in three associations and four subassociations, each occupying distinct riparian habitats, and, thus, indicating distinct environmental conditions.

The *Epilobio-Salicetum alaxensis* ass. nov. is a true pioneer community along mountain creeks (subass. *polemonietosum acutiflori*) and on gravel bars, floodplains and lower terraces of rivers (subass. *parnassietosum kotzebuei*). This tall willow association indicates sites with frequent disturbances and coarser-textured, relatively dry, initial alluvial soils with basic reaction that have deep active layers and relatively high soil temperatures. The association may persist on river banks as long as erosion and deposition of new increments of alluvium occurs, i.e. as long as predominantly allogenic processes are operative in succession cycles. It is characterized by relatively low species richness, considerable percentage of North American endemics, higher amount of more thermophilous species and comparatively higher cover percentage of forbs.

Higher terraces show the paradoxon of better developed soils and decreasing productivity of the shrub layer. With decreasing river influence and the transition to finer-textured, more nutrient-rich, less basic soils, the tall willow community is replaced by the *Anemono-Salicetum richardsonii* ass. nov. (subass. *lupinetosum arctici*). Decreasing active layer depth, caused by the insulation of a thick moss layer and consequently lower soil temperatures, as well as lower root activity and rooting space, and higher soil moisture reduce the competitiveness of *Salix alaxensis*-stands and are thus key factors for this successional replacement with low willows. The *Anemono-Salicetum richardsonii* characterizes later stages of succession on river alluvium with predominantly autogenic processes resulting inter alia in a uniquely arctic soil thermal regime.

Shrubs and mosses are dominant growth forms in this association, which is further characterized by comparatively highest species richness. It also occurs on upland tundra stream banks (subass. *salicetosum pulchrae*), where environmental conditions and floristic composition point to a certain affinity to the *Valeriano-Salicetum pulchrae* ass. nov.

The latter association is distributed on older, long-deglaciated land surfaces with paludified, loamy, acid soils with massive ground ice and thick moss layers, resulting in cold soils, decreased depth of thaw, and increased soil moisture. It typically occupies the immediate margins of smaller tundra streams and creeks with a specific streamflow regime (low disturbance level), originating in the gentle topography of the foothills. Water saturation of the soils lead to reduced decomposition of organic residues and thus to high contents of organic matter. Percentage of acidophilous species and of more cold-adapted species as well as moss cover and bryophyte species richness are comparatively very high. This terminal riparian vegetation type seems to be connected to long-established hydrologic patterns and associated riparian ecosystem evolution along headwaters in upland tundra, and has developed in other time scales compared to the above associations.

Due to synecological and physiognomic correspondences and floristic similarities in supraregional and circumpolar perspective, North Alaskan riparian willow associations can be assigned to existing higher syntaxonomic units of the Braun-Blanquet system, established in Europe and Greenland. Strong affinities do exist to alluvial willow associations of the *Salicetea purpureae*. We propose to extend the range of this class to the North American Arctic.

Keywords: Alaska, arctic, DCA, riparian, *Salix*, soil pH, soil moisture, succession, syntaxonomy.

1 Introduction

Global-scale research on arctic ecosystems has been intensified considerably in recent years. Research initiatives like the International Tundra Experiment, the US Arctic Systems Science project, or the IGBP-Global Change Terrestrial Ecosystems programme, greatly contribute to our still deficient understanding of arctic environments. The tremendous surge in research on arctic systems is largely motivated by predictions that global warming is expected to be most extreme in high latitudes and to result in relatively faster and greater environmental changes (e.g. FITZHARRIS 1996; OECHTEL et al. 1997). In fact, recent climate patterns in the Arctic are generally consistent with those projected by global circulation models under increased atmospheric CO₂ concentrations (MAXWELL 1997). It follows, that, due to the high susceptibility of the temperature-dominated arctic systems (BILLINGS 1997a), global change will have large effects on sea ice, snow, glaciers, permafrost, and tundra ecosystems, including riparian ecosystems and adjacent rivers and streams (OSWOOD et al. 1992). Tundra ecosystems, mainly characterized by the qualitative and quantitative composition of their vegetation types, are likely to change (e.g. EPSTEIN et al. 2000), before their structure and function, having been relatively stable for thousands of years, can be precisely assessed.

Therefore, there is an immediate need for more detailed vegetation studies in the vast, remote circumpolar Arctic. Studies on the composition

and classification of plant communities as well as on their synecology, symorphology, synchorology and syndynamics become increasingly important, but are missing for many areas; they concentrated on a few relatively small regions near human settlements and infrastructure (WALKER, M. D. et al. 1994a). This holds true in particular for the North Slope of Alaska with only one permanent road (see below) in an area of more than 200,000 km², a very low population density, and a long and severe winter. Whereas the majority of vegetation studies in northern Alaska dealt with zonal tundra vegetation types, riparian plant communities have been rather neglected so far. In order to accomplish a more detailed inventory of the North Slope's vegetation, this study focusses on hitherto phytosociologically undescribed riparian plant communities.

Since the vegetation of the North Slope is dominated by perennial forbs, grasses, sedges, dwarf shrubs, mosses and lichens, taller willow shrublands along river margins and streamsides form a prominent feature of the tundra landscape. Riparian vegetation must be considered an extremely important component of arctic landscape ecosystems. Riparian shrublands are the most productive arctic vegetation types (SHAVER & CHAPIN 1991), they provide stream bank stability, and may reach, together with floodplains, a considerable spatial extent (up to 20% of the total landscape cover; cf. MULLER et al. 1998). Moreover, riparian corridors play a vital role as reservoirs of species diversity in a relatively species-poor environment (WALKER, M. D. 1995; GOULD & WALKER 1997, 1999; see also NAIMAN et al. 1993; WARD 1998 for general considerations on riparian biodiversity). Additionally, riparian shrublands provide organic matter for the aquatic food chain, and they are of primary importance as winter forage resource, cover, nesting and denning habitat for abundant wildlife in the open tundra, including moose (*Alces alces*), caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*) and barren ground grizzly bear (*Ursus horribilis*) (cf. MOULD 1977; WHITE & TRUDELL 1980).

Riparian vegetation of the North Slope predominantly consists of *Salix*-shrublands. Almost all riparian habitats – cutbanks, river bars, floodplains and lower terraces along major rivers, upper terraces with further developed alluvial soils, margins of smaller upland streams and creeks, and sites along fast-flowing, gravelly creeks in the mountains – are occupied by different *Salix*-communities. Only on some microsites, e.g. locally along stream channels, along pools of beaded streams or in flooded areas, minor riparian vegetation types like *Carex aquatilis*- or *Carex rotundata*-communities occur. This paper concentrates on *Salix*-communities, for which, like for most of the vegetation in northern Alaska, a comprehensive phytosociological analysis is lacking up to now. There is hardly any detailed information on the synecological characteristics or on the floristic-sociological differentiation of *Salix*-communities. Preliminary observations of riparian *Salix*-shrublands of arctic Alaska were included in the studies of HANSON (1953), CHURCHILL (1955), BLISS & CANTLON (1957), SPETZMAN (1959), KORANDA (1960), CANTLON (1961), DREW & SHANKS (1965), BRITTON (1967), HETTINGER & JANZ (1974), BATTEN (1977), PETERSON & BILLINGS

(1978, 1980), KOMAROVÁ & WEBBER (1980), WALKER, D. A. et al. (1982, 1989), WALKER, D. A. (1985, 1987), WALKER, D. A. & ACEVEDO (1987) and WALKER, M. D. et al. (1989). *Salix*-shrublands in western Alaska were described by HANSON (1951), YOUNG (1974), RACINE (1976), RACINE & ANDERSON (1979) and BINKLEY et al. (1997). MOORE (1982) investigated *Salix alaxensis*-stands along the Sagavanirktok River, the major river in the study area, with regard to floristics, structure and population biology. At the same river a willow shrub ecosystem was incorporated in ecosystem-level studies of nutrient cycling, hydrology, plant biomass, and primary production (GIBLIN et al. 1991; SHAVER et al. 1996). Primary succession of *Salix alaxensis*-habitats at Umiat, Colville River, was discussed by BLISS & PETERSON (1992) and BLISS (2000).

Riparian vegetation and environmental conditions of the headwaters of an upland tundra stream (Imnavait Creek) were studied in detail by WALKER, D. A. & M. D. WALKER (1996). WALKER, M. D. et al. (1994b) presented the first application of the Braun-Blanquet approach to the vegetation of the Alaskan arctic foothills. They included in their survey two riparian plant communities (*Eriophorum angustifolium*-*Salix pulchra*-community and *Salix alaxensis*-*Salix lanata*-community resp.) without formally describing it according to the Braun-Blanquet approach. The only other application of this approach on the North Slope so far resulted in publications of KOMAROVÁ & WEBBER (1980), KOMAROVÁ (1981, 1993) and KOMAROVÁ & MCKENDRICK (1988) on the vegetation of the wet coastal plain at Atkasook. These papers, however, do not contain the descriptions of associations, which are not yet published. In the entire North American Arctic there are very few studies that have used the Braun-Blanquet approach including unpublished dissertations of LAMBERT (1968), GILL (1971), BARRETT (1972) and ODASZ (1983), the studies of THANNHEISER (e.g. 1984, 1987) and his collaborators (e.g. THANNHEISER & WILLERS 1988; THANNHEISER & HELLFRITZ 1989) in the Canadian Arctic, and COOPER'S (1986) classification of the arctic-alpine tundra vegetation of the Arrigetch Creek area in the southern Brooks Range. The latter includes brief descriptions of different riparian *Salix*-communities. Recently, GOULD (1998) and GOULD & WALKER (1999) analyzed the vegetation of the Hood River corridor (Northwest Territories, Canada), applying the Braun-Blanquet approach. They described twenty-four communities including several *Salix*-communities.

A reinforced application of the Braun-Blanquet approach in the North American Arctic would be highly desirable in order to lay the foundation for a circumpolar classification of arctic vegetation (cf. DIERSSEN 1996 for northern Europe) as well as for the intended circumpolar arctic vegetation map (cf. WALKER, D. A. 1995; WALKER, D. A. et al. 1995; WALKER, D. A. & LILLIE 1997). The importance and ecological relevance of the Braun-Blanquet syntaxa in this respect is highlighted by DANIËLS (1997). Since the international "Workshop on Classification of Arctic Vegetation" in Boulder/CO, U. S. A., 1992, the completion of a circumpolar phytosociological/ecological synthesis of arctic vegetation is a main research focus (WALKER,

M. D. et al. 1994a). Moreover, a circumpolar database of well-defined vegetation types with a consistent nomenclature would be an integral part of a hierarchic GIS for circumpolar ecosystem management (cf. WALKER, D. A. 1997). The use of accurately defined syntaxa makes the combination of vegetation studies and ecosystem studies a lot easier. It enables a better extrapolation of site measures of ecosystem fluxes and dynamics to larger areas, which is a unique opportunity in the Arctic due to the pronounced continuity of its vegetation. In view of the presently changing arctic environment the potentials of a common framework of arctic vegetation and ecosystem studies with regard to circumpolar ecosystem management should be completely exhausted.

In this paper a classification and ordination analysis of riparian shrub communities on the North Slope of Alaska is presented. It is based on 85 relevés along a transect from the Brooks Range to Prudhoe Bay and includes the first formal Braun-Blanquet descriptions of riparian associations. The study aims at analyzing the floristic-sociological differentiation of extremely diverse streamside communities (WALKER, M. D. et al. 1994b) and at revealing their relationships to complex environmental gradients at various scales. It is a baseline study of riparian vegetation ecology that may serve as a foundation for future assessments of status and dynamics of arctic environments.

2 Study area

The study was conducted along a S-N-transect from the southern slope of the Brooks Range (Endicott Mountains/Philip Smith Mountains) to the arctic coast in the vicinity of Prudhoe Bay/Deadhorse. The transect follows the northern segment of Dalton Highway, the only permanent road in the area (Fig. 1). This gravel access road ("haul road"), completed in 1974 after the discovery of oil at Prudhoe Bay, parallels the Trans-Alaska Pipeline System (TAPS). It crosses the major ecoregions of northern Alaska (Brooks Range, Arctic Foothills, Arctic Coastal Plain; GALLANT et al. 1995) and makes accessible a relatively undisturbed series of ecosystems along a latitudinal-elevational gradient. It provides the only opportunity for studying a ground-accessible transect of arctic and alpine tundras of northern Alaska (cf. BROWN & BERG 1980; BROWN & KREIG 1983).

The major portion of the transect lies within the drainage system of Sagavanirktok River, the second-largest river (267 km length), after the Colville, on the North Slope of Alaska (BOOTHROYD & TIMSON 1983). The drainage system has its headwaters in the northern Brooks Range, including Atigun River as the major tributary along the transect. Numerous smaller mountain and tundra streams and creeks flow into the system on its way to the Arctic Ocean. Additionally, the transect traverses headwaters of the Kuparuk River basin in the Arctic Foothills as well as headwaters of the Chandalar and Dietrich Rivers on the southern slope of the Brooks Range.

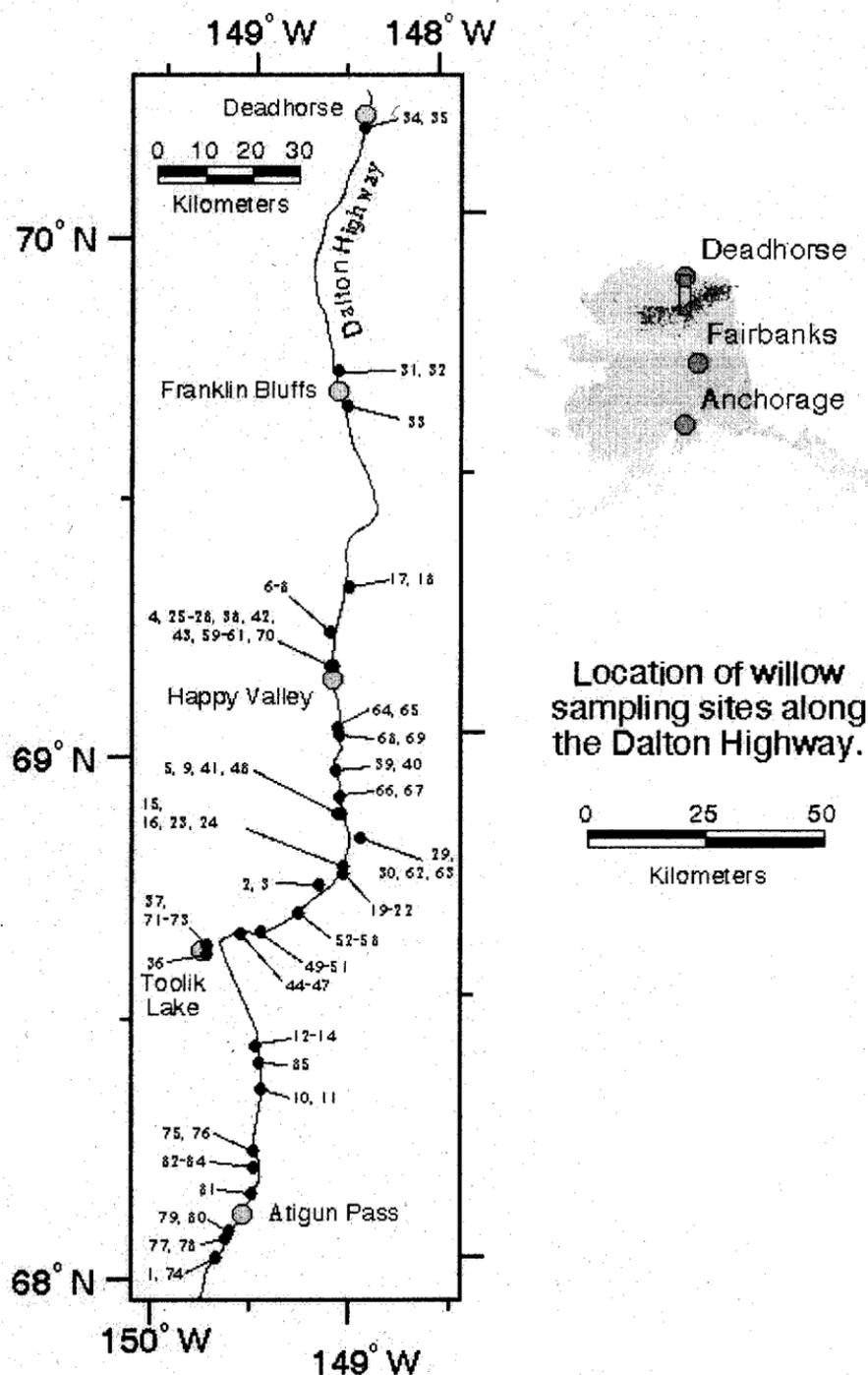


Fig. 1. Location of the willow transect in northern Alaska.

2.1 Physiography

The Brooks Range, a northwestern extension of the Rocky Mountain Cordillera, consists of rugged, east-trending, linear mountain ranges, ridges, and hills. In the Atigun Pass area (1550 m above sea level), where the transect crosses the Brooks Range, glacially sculptured peaks attain an elevation of more than 2200 m. The physiography has been considerably modified by repeated late Tertiary and Quaternary glacial advances, indicated by numerous cirques at low altitudes, well integrated glacial-valley systems and abraded and streamlined landforms (see HAMILTON 1986 for further details on the major glacial episodes). At present, only small glaciers persist at higher elevations. The mountains are deeply dissected and drained by north- and south-flowing rivers in flat-floored, U-shaped valleys.

North of the Brooks Range at Galbraith Lake the mountains abruptly give way to the rolling hills and plateaus of the Arctic Foothills, which are dissected by numerous water tracks, beaded and meandering streams, and partly braided rivers. This ecoregion can be topographically separated into southern and northern sections (cf. GALLANT et al. 1995). In the southern section, elevations vary from 350 to 1050 m and the topography is characterized by irregular buttes, knobs, mesas, east-trending ridges and intervening, gently undulating tundra uplands. Small-scale differences in topography and landscape age result from different glacial histories. Large areas are covered by drift sheets of Sagavanirktok River glaciation (mid-Pleistocene), younger landscapes were deglaciated ca. 60,000 years BP (Itkillik I phase) and ca. 10,000 years BP (Itkillik II phase), respectively (cf. HAMILTON 1986). The northern foothills are marked by broad, rounded, east-trending ridges and mesa-like uplands, reaching elevations of 180 to 350 m.

North of Sagwon, near the confluence of the Sagavanirktok and Ivishak Rivers, the foothills ecoregion grades to the Arctic Coastal Plain, which slopes gently to the Arctic Ocean. This ecoregion is mainly a smooth, poorly drained and marshy plain. However, the flat topography is locally broken by pingos (ice-cored mounds), low hills, and occasional bluffs bounding river terraces. The terrain is marked by permafrost-related features, such as ice-wedge polygons, elongated and oriented thaw lakes, peat ridges, and frost boils. The Sagavanirktok River becomes a braided and distributary river in the plain and builds a delta into the Arctic Ocean.

2.2 Climate, permafrost, soils, and hydrology

The climate in northern Alaska is strongly influenced by the ocean throughout the year. On the basis of currently available data three major climatic zones (Arctic Foothills, Arctic Inland, Arctic Coastal) can be differentiated along the transect on the North Slope of Alaska (Tab. 1). The Arctic Coastal zone, which extends inland about 20 km from the ocean, is characterized by cool summers and relatively warm winters, due to presence of the ocean, sea ice, and prevailing northeast winds. The Arctic Inland zone, which extends about 100 km along the transect to the south (from

Table 1. Climatic differentiation of the North Slope of Alaska (adapted from ZHANG et al. 1996).

	Arctic Foothills	Arctic Inland	Arctic Coast
Distance to the ocean (km)	150 to 300	200 to 150	<20
Elevation (m)	300 to 1000	50 to 400	<50
Air temperature (°C)			
Mean diurnal amplitude	10 to 15	8 to 14	4 to 8
Range (extreme low-high)	-50 to +30	-65 to +35	-50 to +26
Mean annual	-8.6	-12.4	-12.4
Annual amplitude	16.8	21.1	17.5
Degree-day (°C-day)			
Freeze	4000	5300	4930
Thaw	800	930	420
Precipitation (mm)			
Snow	156	126	113
Rain	168	103	85
Annual total	324	229	198
Seasonal snow cover			
Average starting date	27 Sep.	1 Oct.	27 Sep.
Range	11 Sep. to 15 Oct.	19 Sep to 12 Oct.	4 Sep. to 14 Oct.
Average duration (days)	243	236	259
Range (extreme)	226 to 261	198 to 260	212 to 288
Average maximum thickness (cm)	-	43	32
Range (extreme)	-	28 to 70	10 to 83
Thaw season			
Average starting date	28 May	25 May	6 Jun.
Range (extreme)	18 May to 15 Jun.	28 Apr. to 6 Jun.	26 May to 19 Jun.
Average length (days)	122	129	106
Range (extreme)	104 to 139	105 to 167	77 to 153

the coastal plain at Deadhorse to the northern foothills near Sagwon), has considerably higher diurnal and annual amplitudes of air temperature leading to extremely cold winters and relatively warm summers.

The climate of the Arctic Foothills zone (extending from Sagwon to the south into the Brooks Range) is marked by higher precipitation and much higher winter temperatures. Increases in temperature and precipitation must be attributed to the higher elevation of the foothills, which is about 900 m on average in the southern part. This is close to the average height of the top of the atmospheric temperature inversion layer on the Arctic Slope of Alaska. As a result of the weaker atmospheric temperature inversion, mean annual air temperature in this zone is about 4 °C warmer than in the two zones to the north, although summer temperatures are slightly cooler than in the Inland zone (cf. ZHANG et al. 1996). Total annual precipitation increases to 640 mm at Atigun Pass (1550 m) and decreases again to 300–450 mm on the southern slope of the Brooks Range (HAUGEN 1982).

As a consequence of below-freezing mean annual temperatures and the long period of winter cold, the Arctic Slope is underlain by continuous

permafrost. Active layer thicknesses vary roughly between 30 and 70 cm, and increase from the coast to the Arctic Foothills (ZHANG et al. 1997). The largest thaw depths occur along major rivers (NELSON et al. 1997). Soils of the North Slope are thus permafrost-affected, i.e. their genesis is dominated by cryopedogenic processes (freeze-thaw cycles, cryoturbation, ice segregation, frost cracking etc.) resulting from cold soil temperatures. Other soil-forming processes, such as podzolization or gleyzation, may be present, but they are of secondary importance. The majority of the soils are poorly drained, have an upper organic horizon of variable thickness, and have developed on fine-textured materials, silt loams and silty clay loams. A few moderately well-drained and well-drained gravelly soils occur on ridges and on terraces marginal to the larger rivers. The soils can be broadly differentiated into calcareous and acidic soils (cf. BOCKHEIM et al. 1998). Apart from higher soil pH and concomitantly greater amounts of extractable Ca and Mg, and a higher base saturation, soils of moist nonacidic tundra differ from soils of moist acidic tundra in some other key properties. They have thinner organic horizons, a significantly thicker active layer, and greater cryoturbation. These pergelic nonacidic and acidic tundra soils, formerly described as upland tundra soils and meadow tundra soils by TEDROW (1977), comprise ca. 70 % of the North Slope's landcover. Like minor soil types, such as lithosols, regosols, arctic brown soils, and bog soils, they are now classified according to the recently proposed and adopted Gelisol order of the US Soil Taxonomy (BOCKHEIM et al. 1994).

Due to the presence of permafrost as an impermeable layer, the hydrologic cycle is characterized by a very shallow subsurface system with a severely limited water storage capacity. All water leaves the drainage basins either through runoff or evapotranspiration. Every spring a major, dramatic ablation runoff event can be observed (KANE et al. 1989; EVERETT et al. 1996), that leads to extreme differences between seasonal maximum and minimum streamflow rates. E.g., peaks of 439 and 566 m³ sec⁻¹ during spring floods contrasted with winter flows of only 0.4 m³ sec⁻¹ in the Sagavanirktok River (downstream of Lupine River) in 1971 and 1972 (CRAIG & McCART 1975). CRAIG & McCART classified stream types with different streamflow regimes on the North Slope according to the origin of flow. Their characteristics are summarized in Tab. 2. In tundra streams and creeks, originating in the foothills and coastal plain, flow peaks sharply during the snowmelt period in late May, and falls off dramatically for the remainder of the summer. Freezeup occurs in September. In larger rivers like the Sagavanirktok River, originating in the Brooks Range (mountain streams), flow decreases more gradual after spring breakup before approaching zero in fall. Some flow may continue through unfrozen riverbed gravels during winter. Furthermore, the hydrograph of mountain streams reflects higher intensity of rainfall events in the Brooks Range throughout the summer season. As will be discussed below, different streamflow regimes and related disturbances are critical for understanding riparian vegetation ecology.

Table 2. Characteristics of mountain streams (originating in the Brooks Range) and tundra streams (originating in upland tundra), based on data from 55 locations in 17 Beaufort Sea drainages (adapted from CRAIG & MCCART 1975).

Features	Mountain streams	Tundra streams
Physical and chemical		
Surface flow	late May to mid-October	late May to mid-September
Groundwater flow	minimal	none
Summer discharge (m ³ /sec)	0.3–100+	0.1–7+
Temperature (°C)		
– Summer	10 (4–15)	10 (5–20)
– Winter	0–1 or frozen	frozen
– Annual variation	10	17
Color	clear/turbid	stained
pH	8.0 (7.0–8.5)	7.6 (6.4–8.5)
Conductivity (umhos/cm)	176 (78–285)	116 (17–230)
Ca (mg/l)	28 (16–37)	9 (3–16)
Benthic invertebrates		
Standing crop (no./m ²)	100	1000
Relative diversity	low	moderate
Fish		
Most abundant species	Arctic char (<i>Salvelinus alpinus</i>)	grayling (<i>Thymallus arcticus</i>)

2.3 Flora and vegetation

The circumpolar arctic flora consists of about 900 vascular species (ca. 0.4% of all vascular plants on Earth), distributed over a land area of ca. 13 million km² or almost 15% of the earth's land surface (BILLINGS 1997b). Considering this relatively small flora, the North Slope of Alaska is relatively rich floristically. WIGGINS & THOMAS (1962) and HULTÉN (1968) listed 450–500 vascular species occurring on the North Slope – about half of the entire arctic flora. The relatively high plant diversity is mainly due to the dynamic landscape history of Beringia (the area between Lena and Mackenzie rivers) during the late Tertiary and Quaternary (cf. HOPKINS et al. 1982). During glacial maxima and concomitant periods of lower sea levels, land connections between Asia and America provided an immigration route for a huge amount of Asiatic taxa, including steppe, forest and tundra species. Moreover, large areas of Beringia remained unglaciated throughout the Pleistocene and served as refugia for the regional arctic flora. The Beringian species pool was further extended by taxa that returned from areas south of the continental icesheets as well as by newly evolved taxa of Pleistocene and Holocene age (MURRAY 1992, 1995). Approximately half of the recent North Slope flora consists of Beringian species, the other half has circumpolar distributions.

According to recent phytogeographic zonations of the Arctic, the study area falls within the Southern Tundra Zone of MATVEYEVA (1998), the Southern Arctic Tundra Zone and Arctic Shrub Tundra Zone proposed by ELVEBAKK et al. (1999), and within the Erect Dwarf Shrub and Low Shrub Subzones proposed by WALKER, D. A. (2000) respectively. The vegetation of the North Slope can be broadly differentiated into lowland tundra on the coastal plain and upland tundra in the Arctic Foothills and mountains of the Brooks Range. Lowland tundra is predominantly a wet sedge-moss tundra, upland tundra mainly consists of tussock tundra (WALKER, M. D. 1995), a widespread vegetation type on imperfectly drained lands that is also common in adjacent upland regions of northwestern Canada and northeastern Russia (BLISS & MATVEYEVA 1992; CHERNOV & MATVEYEVA 1997). WALKER, M. D. et al. (1994b) published the hitherto most detailed account of the tussock tundra vegetation of the North Slope. They described the Sphagno-Eriophoretum vaginati as the zonal vegetation on mesic, acidic slopes throughout the foothills, dominated by the tussock-forming sedge *Eriophorum vaginatum*, low shrubs (*Betula nana*, *Rubus chamaemorus*) and mosses (*Sphagnum* spp., *Hylocomium splendens*). Its non-acidic counterpart is the Dryado integrifoliae-Caricetum bigelowii, which is widespread on circumneutral mesic uplands and hillslopes, primarily in younger landscapes. Mountain slopes of the Brooks Range are covered by *Betula-Salix*-shrub tundra, giving way to *Dryas octopetala*-dominated dwarf shrub communities at higher elevations (1100–1200 m a.s.l.).

2.4 Human impact

Much of arctic Alaska still consists of relatively pristine tundra and riparian ecosystems, only slightly modified by anthropogenic disturbances. As far as riparian systems are concerned, Alaska can still be termed a “warehouse of pristine running water systems” (OSWOOD 1997). All rivers are free-flowing, unregulated rivers; most river corridors are undisturbed over the whole of the river continuum, from headwaters to mouth. Although arctic ecosystems have been relatively stable for thousands of years, they are very susceptible to anthropogenic interferences (e.g. BILLINGS 1997). This susceptibility is mainly due to a short growing season, low temperatures, low primary productivity, the presence of permafrost, and the extreme sensitivity of the vegetative and organic surface layers to any disruption of their physical integrity and thermal regime (REYNOLDS & TENHUNEN 1996).

Common anthropogenic disturbances on the North Slope result from energy development, following the discovery of oil at Prudhoe Bay in 1968, and concentrate along the Trans Alaska Pipeline haul road and in the coastal plain oil fields respectively. Impacts of energy development include disturbance of rivers and riparian vegetation by gravel mining and crossings, removal and modification of vegetation by road and drilling pad construction and off-road vehicle trails, snow and ice roads on tundra for winter transportation, dust loads on vegetation from oil drilling operations, mining

activities, and truck traffic, and other impacts such as oil spills, road salting, surface mining, spoil siting, thermal erosion, and waste disposal (WALKER, D. A. et al. 1987; WALKER, D. A. 1996). During construction of the pipeline, roads, worksites and camps, large areas of *Salix*-shrublands in the Atigun and Sagavanirktok river valleys were destroyed, mostly through shallow mining of vegetated river bars for gravel. 23 % of tall (>1 m) *Salix alaxensis*-stands were disturbed; subsequent restoration of these habitats was only partially successful (DENSMORE et al. 1987).

Additionally, large-scale indirect impacts from sources at lower latitudes, including climate change, ozone loss, air pollution, and bioaccumulation of heavy metals, pesticides and PCBs, adversely affect the North Slope's environment. Effects of these impacts are being increasingly detected in the Arctic (e.g. BRAUNE et al. 1999; see YOUNG & CHAPIN 1995; HANSELL et al. 1998 for effects on biodiversity). This illustrates the pervasiveness of global environmental threats, and shows that remote Arctic Alaska can no longer be considered an untainted wilderness.

3 Methods

3.1 Field sampling

In order to cover the full variety of riparian shrubland habitats between the Brooks Range and the coastal plain, study sites were selected along rivers and streams of different orders; in total 85 relevés were completed according to the Braun-Blanquet approach (BRAUN-BLANQUET 1964), which has become a fairly standardized method (cf. MUELLER-DOMBOIS & ELLENBERG 1974; DIERSCHKE 1994). The southernmost relevé was spaced at Dietrich Creek (68°02'N, 149°39'W), just north of the arctic treeline on the southern slope of the Brooks Range, the northernmost study site was at the Sagavanirktok River (braided section of delta plain) in the vicinity of Deadhorse (70°11'N, 148°26'W).

Phytosociological and environmental data collection was conducted by the first author during the period of 9 July to 17 August 1997. After a reconnaissance of the study area locations of sample plots were carefully selected along the transect in order to fulfill the requirements of homogeneity and minimal area. Sample plots were of square or rectangular shape. Representative samples of the *Salix*-communities required minimal areas between 50 m² (low shrublands) and 100 m² (tall shrublands). After establishing a sample plot, height and actual cover of the separate vegetation layers (shrub, field, moss, and lichen layer) were measured or estimated. A detailed inventarisation of taxa followed, including all vascular, bryophyte, and lichen species. Species cover was estimated according to the traditional Braun-Blanquet cover-abundance scale (7 classes). A voucher specimen of each species was collected on the relevé sites for final identification in the herbaria of the University of Alaska at Fairbanks/AK (*Salix* spp.) and of the University of Colorado at Boulder/CO. Nomenclature of vascular plants follows ARGUS (1973) for *Salix* spp. and HULTÉN (1968) for most of the

vasculars. For recent revisions we consulted CODY (1996). Mosses, hepatics and lichens are named according to STEERE (1978), STEERE & INOUE (1978) and THOMSON (1979, 1984) respectively.

Since vegetation is understood as a plant community-habitat-system (phytogeocoenosis) sensu GLAVAC (1996), vegetation sampling was complemented by a detailed characterization of habitat conditions. Altitude was measured with a Thommen altimeter. Information on slope and aspect was negligible in most riparian habitats, but was noted when considered to be important. Estimates of a number of habitat factors, such as frequency of flooding, flow speed/discharge regime of running water, soil moisture, site moisture, snow cover, % cryoturbation, and animal disturbance, were carried out in decimal scales (1–10 or 1–4) in order to ease the intended transfer of data to the ordination matrix. Additionally, the vertical distance to the water table was measured, and information on the locality, on the entire size of the sample stand, on microtopography and geomorphic processes, and on the surrounding vegetation types was noted. A soil pit was dug on each relevé site. Soil profiles were described according to SCHLICHTING et al. (1995) with regard to depth of active layer, thickness and type of horizons, color (Munsell Soil Color Charts), texture, humus contents, moisture conditions, and root patterns. To be in accordance with previous studies in the region, soil samples ($3 \times 100 \text{ cm}^3$ cylinder samples) were collected from 10 cm depth in each soil pit. Fresh field samples were oven-dried at 105°C for 72 h in camp (Toolik Field Station) to determine percentage weight loss and soil moisture. Laboratory soil analyses (carried out in the Soil, Water and Plant Testing Laboratory, Colorado State University, Fort Collins/CO) comprised soil pH (saturated paste method), EC, lime estimate, % organic matter, $\text{NO}_3\text{-N}$, plant available P, K, Zn, Fe, Mn, Cu, and % gravel, sand, silt, and clay.

3.2 Classification and ordination

Vegetation was classified according to the Braun-Blanquet sorted table method, i.e. the relevés were arranged in phytosociological tables to differentiate and characterize associations and subassociations (MUELLER-DOMBOIS & ELLENBERG 1974; DIERSCHKE 1994). On the basis of field impressions, the 85 relevés were arranged in two separate raw tables. All records of tall shrublands (*Salix alaxensis*-stands) were placed in one table and all records of low shrublands in another. Table work was carried out by means of a common table calculation program (Microsoft Excel), where it is easy (i) to obtain bipartite or tripartite divisions in each table by dragging and dropping rows and columns and (ii) at the same time to fully realize the classification procedure step by step. An intimate knowledge of the data structure can be attained this way. It is recommended for smaller, manageable data sets. Differentiations of vegetation units are based on diagnostic species (character species, differential species, and constant companions). Determinations of differential species as well as assessments of degrees of fidelity of character species followed the criteria proposed in

DIERSCHKE (1994). Tabular presentation and nomenclature of the described syntaxa are in accordance with WEBER et al. (2000).

In order to analyze relationships between variation in vegetation and environmental variation, Detrended Correspondence Analysis (DCA) ordinations were carried out using PC-ORD (3.0 for Windows) program (MCCUNE & MEFFORD 1997). DCA was considered a more appropriate technique than a constrained (direct) ordination like Canonical Correspondence Analysis (CCA) because the focus was on generation, not on testing of hypotheses about vegetation-environment relationships, i.e. the problematic dependency of constrained ordination axes on recorded environmental variables should be avoided (problematic regarding an unbiased interpretation of all explanatory variables of complex-gradients; cf. ØKLAND 1996). Performing DCA, all species and environmental data were used. Rare species were downweighted; axes were rescaled based on program defaults. DCA produces first axes showing major directions of variation in the data and revealing the relationship of the classification to major environmental gradients. The latter is considered very important in the present study. Classification and ordination were perceived as interactive, complementary procedures. E.g., preliminary assignments of particular relevés to subassociations during table work could be later revised and corrected according to positions of samples in the ordination space. DCA ordinations were compared with parallel applications of other ordination techniques available in PC-ORD (e.g. Bray-Curtis, CCA), using the same data set. Comparable or nearly congruent configurations of ordination diagrams indicated the appropriateness of DCA for this general-purpose ecological study.

The community tables provided a valuable data base for further analyses at community level, including inquiries into species richness (alpha diversity), growth form distributions (shrubs, forbs, graminoids, mosses, lichens), geographic range (circumpolar, North American, North American-Asian distributions) and physiographic unit (arctic, arctic-alpine, arctic boreal distributions) analyses, and investigations into affinities to climatic zones and soil pH. Regarding climatic affinity, we assessed the northern limits of species areas and correlated them to climatic zones developed by YOUNG (1971), based on the sum of mean monthly temperatures above 0 °C. Regarding soil pH affinity, we followed the method of ELVEBAKK (1982) to group species into one of six categories of pH values (considering mean and range, within a 95 % confidence interval) based on all relevé sites where a species occurred.

4 Results

Classification of *Salix*-shrublands resulted in three associations and four subassociations. These community types are not only marked by their characteristic species combinations, but also by distinct habitat conditions (Tab. 3). The floristic differentiation of the community types is clearly reflected in the ordination diagram of all relevés, even on subassociation level

Table 3. Mean values of selected environmental variables for the differentiated associations and subassociations.

Selected environmental variables	Epilobio-Salicetum alaxensis	subass. parnassie-tosum kotzebui	subass. polemonie-tosum acutiflori	Anemono-Salicetum richardsonii	subass. lupine-tosum arctici	subass. salice-tosum pulchrae	Valeriano-Salicetum pulchrae
Soil pH (paste)	7.2	8.8	6.6	6.6	6.8	5.8	5.0
Soil moisture (vol. %)	24.1	25.4	23.2	47.1	45.1	53.1	61.7
Bulk density (g/cm ³)	1.4	1.3	1.5	0.9	1.0	0.7	0.5
Gravel (g/100 cm ³)	26.0	3.4	41.6	0.6	0.9	0.0	0.6
% Sand	70.4	66.0	73.5	49.0	50.1	45.8	41.2
% Silt	22.2	24.2	20.9	37.5	36.2	41.6	32.7
% Clay	7.3	9.8	5.6	12.9	13.0	12.7	15.0
% Org. matter	3.9	1.9	5.3	13.5	12.9	15.3	24.2
NO ₃ -N (ppm)	2.1	2.0	2.1	3.0	3.0	3.1	3.2
P (ppm)	4.6	5.1	4.2	8.5	9.6	5.3	8.1
Mn (ppm)	98.0	16.0	154.4	136.9	72.8	322.0	514.6
Fe (ppm)	53.2	48.4	56.6	232.0	214.6	282.2	594.8
Flowspeed index	2.1	1.0	2.9	1.6	1.2	2.8	2.3
Vertical distance water table (m)	0.8	1.1	0.6	1.7	2.0	0.9	0.5
Moss layer (cm)	1.8	0.6	2.5	8.4	7.4	11.2	12.3
n	27	11	16	35	26	9	23

(Fig. 2). Actually, this ordination diagram can be considered a graphic representation of the similarity structure of a combined phytosociological table of all relevés. Each of the community types occupies a distinct range within the ordination space. Thus, the ordination results corroborate the results of the classification. A considerably narrow range is occupied by the Valeriano-Salicetum pulchrae, indicating a floristically very homogeneous vegetation type with a comparatively narrow ecological amplitude. In contrast, the Anemono-Salicetum richardsonii and the Epilobio-Salicetum alaxensis show a much more heterogeneous species composition and occur over a broader range of environmental conditions. As a consequence, both associations can be further differentiated into two subassociations.

The diagram represents not only the floristic similarity structure, but also indicates relationships of relevés and communities to the most important environmental gradients. Axis 1 corresponds to a complex edaphic gradient primarily representing soil pH and soil moisture. Relevés of moist acidic stream banks are concentrated in the right corner of the diagram, whereas those of edaphically drier, nonacidic sites increase in abundance towards the left side. Vertical distance to the water table and frequency of

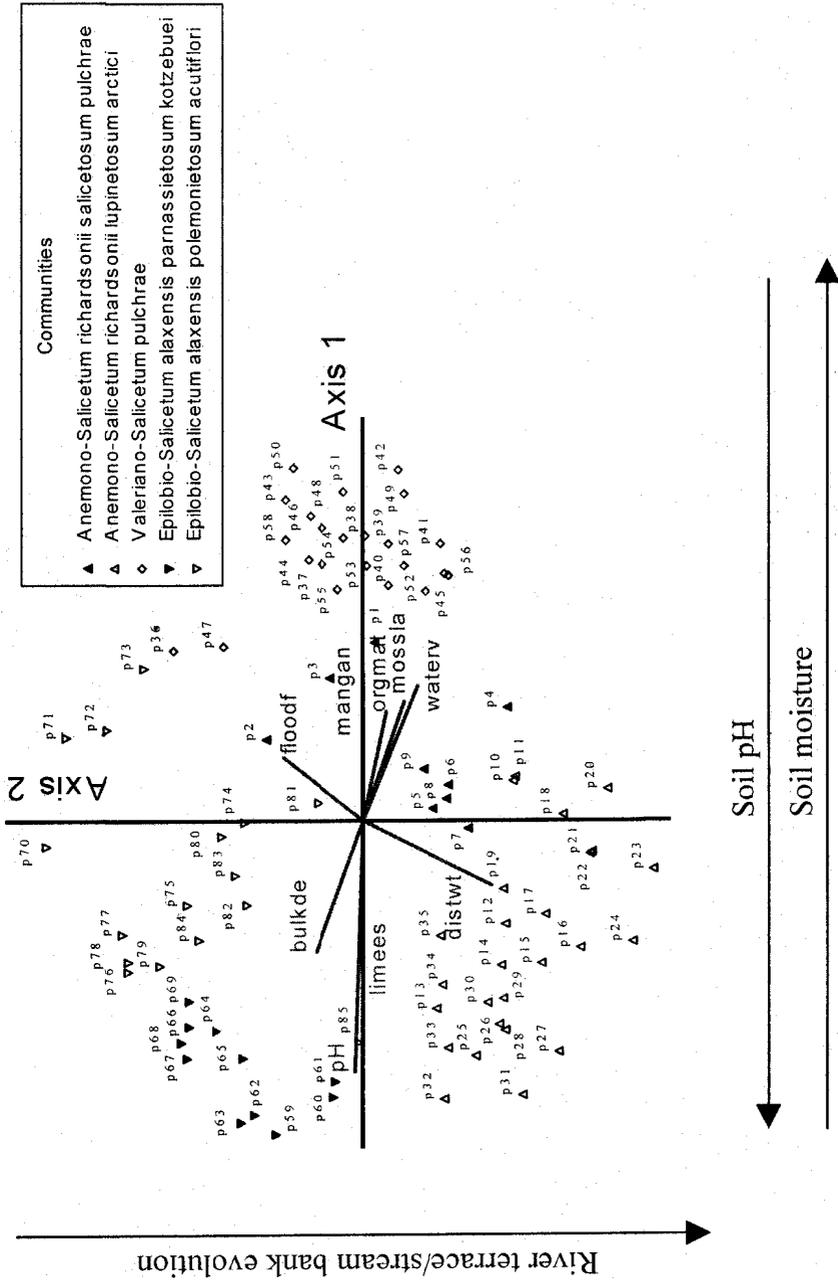


Fig. 2. DCA ordination of *Salix* associations and subassociations in the study area.

flooding show highest correlation with axis 2, which has to be interpreted as a complex gradient of river terrace/stream bank evolution or successional gradient with relevés of young, gravelly mountain streamsides or floodplain sites of rivers in the upper half of the diagram and relevés of higher river terraces with better developed alluvial soils in the lower half. However, this interpretation is only valid for the *Epilobio-Salicetum alaxensis* and *Anemono-Salicetum richardsonii* on river alluvium. Relevés of head-water stream banks on old land surfaces in upland tundra, mainly belonging to the *Valeriano-Salicetum pulchrae*, do not fit into this successional scheme since they have developed in different temporal scales. The influence of landscape history (deglaciation ages) on riparian vegetation differentiation will be discussed below. Relevé positions of the *Valeriano-Salicetum pulchrae* along the vertical axis mainly reflects the intermediate position in terms of height above river/stream water level and associated flooding frequency.

The ordination diagram of all relevés (Fig. 2) is placed together with the correlation coefficients of environmental variables with species axes (Tab. 4)

Table 4. Correlation coefficients (Pearson's r) of environmental variables with species axes derived by DCA ordination.

All <i>Salix</i> samples (N = 85)	Axis 1	Axis 2	Axis 3
Eigenvalue	.043	.026	.143
Gradient length	2.85	2.65	1.99
Soil pH	-.871	.152	-.188
Ca	-.718	.006	-.147
Mn	.668	.035	.026
Soil water	.634	.407	-.228
Bulk density	-.629	.376	.281
Moss layer	.596	-.349	.013
Soil organic matter	.568	.265	-.067
Flow speed	.462	.384	.289
Vertical distance water table	-.442	-.627	.003
Frequency of flooding	.436	.491	-.261
Fe	.435	-.107	.030
Sand	-.409	.320	.060
K	.390	.089	.281
Silt	.345	-.286	.179
Zn	.318	-.003	-.092
Altitude	.312	.377	.574
Electric conductivity	.306	-.189	.003
Clay	.276	-.168	.142
Snow cover	.243	.393	.478
NO ₃ -N	.233	-.168	-.031
Gravel	-.158	.372	.550
P	.120	-.201	-.011
Cu	.113	-.512	-.067

Table 5. (cont.)

Releve-No.	parnassietosum kotzebuei										polemoniotosum acutiflori																		
	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	
<i>Ditrichum flexicaule</i>						+	1	2	2	+																			
<i>Senecioia uncinata</i>				1	1	2																							
<i>Bistorta vivipara</i>																													
<i>Stellaria covarskii</i>																													
<i>Pyrola grandiflora</i>							1	1																					
<i>Pelligera rufescens</i>																													
<i>Elymus pseudocytretum</i>																													
<i>Pentaptyliodes floribunda</i>																													
<i>Wilhelmsia physodes</i>																													
<i>Pohlia nutans</i>																													
<i>Aconitum delphinifolium</i> ssp. <i>delphinifolium</i>																													
<i>Poa alpina</i>																													
<i>Poa alpigena</i>																													
<i>Hylocomium splendens</i>																													
<i>Solidago multiradiata</i> var. <i>multiradiata</i>																													
<i>Bromus pumpehianus</i>																													
<i>Callimagrostis canadensis</i>																													
<i>Climacium cendroides</i>																													
<i>Pedicularis capitata</i>																													
<i>Juncus castaneus</i>																													
<i>Gentianaella propinqua</i> ssp. <i>arctophylla</i>																													
<i>Carex rolundata</i>																													
<i>Anemone richardsonii</i>																													
<i>Physcia albolba</i>																													

Additional taxa: *Deschampsia flexuosa* (rel. 66+; 72+); *Encalypta hepaticarpa* (66:1); *Orthotrichum chryseum* (68:1, 67:1); *Hepaticae* indet. (65-); *Lomatogonium rotatum* (67+); *Plagiobryum denticulatum* (67+); *Carex glacialis* (64+; 76+); *Dicranodiscus polygamum* (64+); *Helodium blandinum* (62+, 64+); *Carex vaginata* (65+); *Lupinus arcticus* (61+, 65+); *Cerastion purpureus* (65+; 64+); *Carex aquatilis* (68+); *Carex acutiflora* (68+); *Hyprnum hamulosum* (68+); *Eriophorum schroeteri* (77:1, 78:1); *Juncus arcticus* ssp. *sealei* (76+); *Carex saxatilis* (78:1); *Aulacomnium turgidum* (78:4, 81+); *Luzula arctica* (75+; 76+); *Pollia albicans* (75+); *Tortula microfolia* (75+); *Poa pseudobreviflora* (76:1, 81+); *Astragalus eucomis* ssp. *sealei* (76+); *Ledum palustre* ssp. *greenlandicum* (74+); *Alnus crispus* (74:1, 74:2); *Vaccinium vitis-idaea* (74+); *Empetrum nigrum* ssp. *pernaphroditum* (74+); *Ledum palustre* ssp. *decumbens* (74+); *Festuca brachyphylla* (74+; 81+); *Arnica grisea* ssp. *frigida* (74+); *Pogonatum dentatum* (74+); *Cladonia fimbriata* (74+); *Cladonia gracilis* (74+; 80+); *Bistorta palmifolia* (74+); *Lecum elongatum* (79+; 83+); *Cladonia mitis* (83+; 85+); *Potentilla hookeriana* (82+); *Poa lanata* (83:2); *Saxifraga tricuspidata* (83+; 85+); *Epiobium argusifolium* (73:2, 83:1); *Dicranum (70:2)*; *Pedicularis verticillata* (59+; 70+); *Hypnum cupressiforme* (70:2); *Viole episcopa* ssp. *repens* (70+); *Potentilla hyperbatica* (84+); *Saxifraga trichoclasis* ssp. *funstonii* (81+; 84:1); *Spiraea beauriviana* (70+); *Gallium boreale* (70:2); *Pedicularis virens* (80+); *Dicranum bonjeani* (80+); *Rhynidium rugosum* (79+; 85:1); *Eriodon concoloris* ssp. *jordani* (80+; 85:2); *Bupleurum triadatum* ssp. *arcticum* (85:1); *Polytrichum juniperinum* (85+); *Pleurozium schreberi* (85:1); *Syntrochia norvegica* (85+); *Cerastia tlesii* (65+); *Plantanthera obtusata* (60:1); *Plagiobrya spec.* (61+); *Salix rotundifolia* (81+); *Acomasyle rossii* (81+); *Poa arctica* (81+); *Salix brachycarpa* ssp. *niphocida* (59:1); *Scorpidium revolvens* (59+); *Mnium rugicum* (72+); *Draba longipes* (73+); *Leptobryum pyriforme* (67:1); *Oncophorus wahlenbergii* (67:1); *Blepharostoma trichophyllum* (64+; 65+).

Localities: rel. 59-61: Sagavaniktok River at Happy Valley Landing Strip; 62-63: Sagavaniktok River south of Pump Station 3; 64, 65+ 68-69: Sagavaniktok River bars between Oil Spill Hill and Ice Cut; 66-67: Sagavaniktok River north of Pump Station 3; 70: Lower Happy Valley Creek; 71, 73: Toxik Lake Inlet; 74: Deutch Creek below Chandler Shelf; 75-76: Upper Algon River north of Algon Camp; 77-78: Braided floodplain of Chandalar River south of D.O.T. station; 79, 80: Unnamed Creek north of Chandler Camp; 81: Algon River bed just north of Algon Pass; 82, 83: Upper Algon River south of Pump Station 4; 84: Unnamed Creek north of Algon Camp; 85: Route Moutonnee Creek.

at the outset of the results to give a first overview of community type differentiation and vegetation-environment relationships as well as to ease understanding of the following discussions.

4.1 *Epilobio-Salicetum alaxensis* Schickhoff et al. 2001 ass. nova Nomenclatural type relevé: Tab. 5, rel. 63

This tall willow shrub association occupies two distinct riparian habitat types along the transect: It occurs on floodplains, gravel bars and lower terraces of the Sagavanirktok River as well as on upland and montane stream banks. Along the Sagavanirktok River to the north, this community is well developed up to the Happy Valley area in the northern foothills section (Fig. 3); however, the name-giving taxon, feltleaf willow (*Salix alaxensis*), occasionally occurs further to the north, where the individuals become less vigorous and the shrub stature is reduced. Towards the coast, the ecological conditions (climate, depth of active layer) become unfavorable for the development of the *Epilobio-Salicetum alaxensis*: It is replaced in comparable habitats by low willow stands (*Anemono-Salicetum richardsonii*; see below). The other main distribution area of this tall willow community comprises upland and montane stream banks. It occupies in particular gravelly banks of fast-flowing creeks in the Brooks Range, where it is well developed up to an elevation of ca. 1200 m a.s.l.



Fig. 3. The *Epilobio-Salicetum alaxensis* (subass. *parnassietosum kotzebuei*) is widely distributed on floodplains, gravel bars and lower terraces along the Sagavanirktok River; phot. U. SCHICKHOFF, 26.07.1997.

before it gives way to pioneer herb communities. Occasionally, it occurs along upland tundra streams in the southern foothills, where it is largely restricted to geomorphologically active sites on younger land surfaces. Within the "Alaska Vegetation Classification" (VIERECK et al. 1992), this association falls into the categories "closed tall willow shrub" and "open tall willow shrub" respectively.

The habitats of the *Epilobio-Salicetum alaxensis* are pioneer habitats. Along a gradient of river terrace/stream bank evolution (cf. Fig. 2), this association occupies the least developed sites, e.g. gravelly creek margins, bare gravel bars with initial sand and silt accumulation or lower terraces with well to moderately drained, coarse-textured soils. Tab. 3 shows the comparatively high gravel content, the predominant sand fraction (70%), the high bulk density, and thus the relative edaphical dryness in the soils under this association. The soils are generally non-acidic with a mean soil pH of 7.2. They are further characterized by low available nitrogen, a very low organic matter content, high base saturation and cation exchange capacity. Floodplain and lower terrace soils show a very deep active layer of about 1 m in late July. This provides large rooting space as well as favorable soil temperatures for the tall willows, what in turn is reflected in a higher biomass and a higher net annual production compared to the low willow stands on upper terraces (see below). It is evident from the above habitat description that the *Epilobio-Salicetum alaxensis* is a true pioneer community.

This pioneer association is marked by a characteristic species combination including character and differential species as well as a whole array of companions with high presence (see Tab. 5). There are four character species, all showing pronounced pioneer character. The amphibi-Beringian, thicket-forming feltleaf willow is able to colonize bare gravels, accelerates the deposition of sand and silt, and thus facilitates further succession (BLISS & PETERSON 1992). Large amounts of early summer seeds, having no dormancy requirements, can germinate on newly exposed substrate after the floodwaters from spring thaw subside (cf. GILL 1971; ARGUS 1973; see also EBERSOLE 1985 for the capability to rapidly colonize disturbed areas). Moreover, *Salix alaxensis* develops adventitious roots readily so that growth of sprouts from buried branches often produces dense stands (cf. VIERECK 1970; ZASADA & DENSMORE 1978).

Likewise, the circumpolar, arctic-alpine species *Epilobium latifolium* (syn. *Chamaenerion latifolium*) is among the first taxa to colonize gravel bars and stream banks (cf. MOORE 1982). E.g., it forms distinct communities along glacier streams in SE-Greenland (LÜNTERBUSCH et al. 1997). It shows higher presence degree and higher cover along gravelly creeks in the mountains, whereas the amphibi-Beringian *Aster sibiricus* has its main distribution along lowland river banks on sandy-loamy soils.

The above described two distinct habitats of the association and the concomitant diverging species combination results in a differentiation of two subassociations:

1) *Epilobio-Salicetum alaxensis parnassietosum kotzebuei*
 Schickhoff et al. 2001 subass. nova
 Nomenclatural type relevé: Tab. 5, rel. 62

This is the subassociation of floodplains and lower terraces of lowland rivers (Tab. 5; rel. no. 59–69). It is on these habitats where the association has its optimum ecological conditions, and where thus most extensive and productive *Salix alaxensis*-stands (3–4 m tall) can be found. Accordingly, shrubs are the most prominent growth form, reaching the highest percentages on the total sum of plant cover among all differentiated communities (Fig. 4). Species richness of vascular plants and mosses is higher, too (Fig. 5). Habitat conditions differ from montane stream banks e.g. in higher summer temperatures, a much deeper active layer, a slightly higher soil moisture, more fine-textured, deeper soils (sandy loam) with much lower gravel content, and a considerably higher soil pH (cf. Tab. 3). As evident from the DCA ordination (Fig. 6), soil pH is the decisive ecological factor for differences in floristic composition of both subassociations. There is a regular supply of base cations during every spring breakup when the lowland river banks are flooded with water flowing down from the Brooks Range and its foothills. Due to prevailing limestone bedrock in the headwaters this water is moderately hard and rich in calcium and magnesium ions (CRAIG & MCCART 1975; KLING et al. 1992). The sedimentation on lowland river banks of the suspended inorganic load of the annual spring flood provides regular mineral nutrient supply and thus contributes to the productivity of *Salix alaxensis*-stands of these habitats.

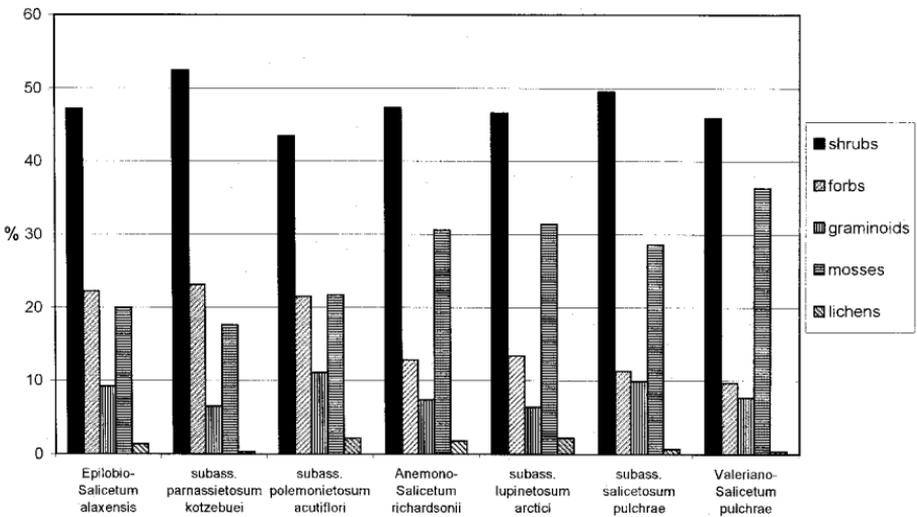


Fig. 4. Weighted growth form spectra of *Salix*-communities. Percentage of each growth form was calculated on the basis of transformed cover/abundance values of species in relevés (transformed into average cover percentage according to ELLENBERG 1956) in order to reflect actual dominance conditions.

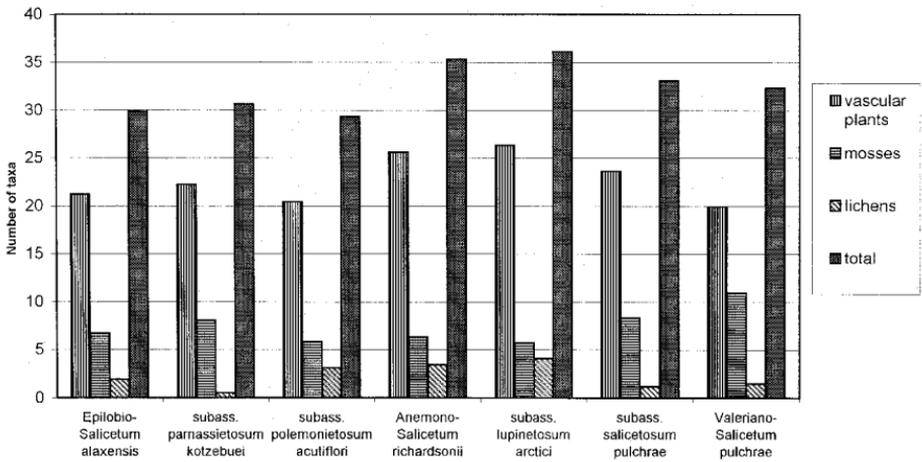


Fig. 5. Species richness of *Salix*-communities.

The composition of differential species is a fine expression of the above described habitat conditions. Most of the taxa have their main distribution on sandy or gravelly soils along stream and river banks, e.g. *Parnassia kotzebuei*, *Equisetum variegatum* ssp. *variegatum*, *Hedysarum alpinum* ssp. *americanum*, *Astragalus nutzotinus* or *Elymus alaskanus*. Moreover, the vast majority of differential taxa indicates calcareous substrata and basic conditions. Compared to the other *Salix* associations/subassociations, this subassociation shows the highest amount of basiphilous taxa (Fig. 7). Along the successional gradient to higher terraces and upland tundra streamsides the percentage of species defined as basiphilous to circumneutral considerably decreases, whereas weakly acidophilous and acidophilous taxa show a distinct increase.

Within this subassociation a variant could be differentiated (Tab. 5; rel. no. 59–65) that occurs on higher ground (1.0–2.3 m above water table) with slightly drier and coarser-textured soils, i.e. with a higher content of sand fraction and less silt. On these sites, *Salix alaxensis* is very vigorous and reaches up to 3.5 m in height. The herb layer shows higher cover and is more species-rich. This variant of *Castilleja caudata* is represented by differential taxa, which are mostly endemic to North America (*Shepherdia canadensis*, *Zygadenus elegans*, *Leymus velutinus*, *Hedysarum mackenzii*, *Carex concinna*) or whose distribution extends a bit further to NE-Asia (*Castilleja caudata*, *Anemone parviflora*). The species composition might point to a lower competitiveness of circumpolar taxa under these specific habitat conditions, and/or it might be the result of symphylogenic developments among taxa of a more or less common evolution in space and time. Actually, the *Salix alaxensis*-association comparatively shows the highest amount of North America endemics (Fig. 8). This percentage sharply decreases along the successional gradient, whereas the percentage of circumpolar taxa increases. The latter taxa are obviously favored by environ-

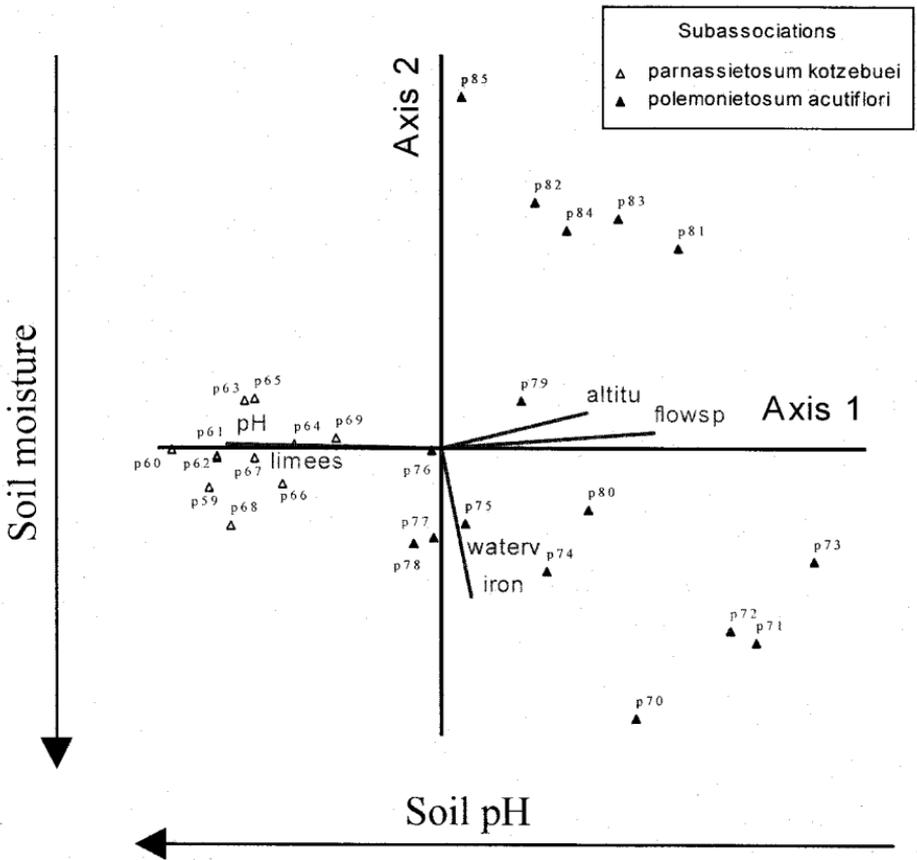


Fig. 6. DCA ordination of *Epilobio-Salicetum alaxensis*.

mental conditions in upland tundra, similar to vast circumpolar regions. The higher competitiveness and richness of endemics in pioneer communities has serious implications for nature conservation: The destruction of *Salix alaxensis*-habitats (as happened in the course of Dalton Highway building on the Arctic Slope) endangers a particularly valuable component of Alaskan biodiversity.

2) *Epilobio-Salicetum alaxensis polemonietosum acutiflori*
 Schickhoff et al. 2001 subass. nova
 Nomenclatural type relevé: Tab. 5, rel. 75

This subassociation (Tab. 5; rel. no. 70–85) occurs primarily on gravelly montane stream banks in the Brooks Range up to an elevation of c. 1200 m a.s.l. (Fig. 9). Compared to lowland river banks, stand productivity and vigor of *Salix alaxensis* is reduced. On the one hand, this must be attributed

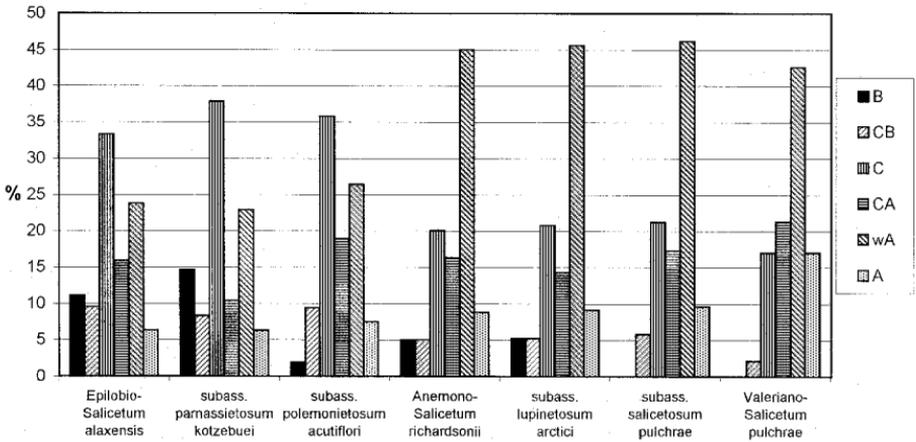


Fig. 7. pH affinities for vascular species of *Salix*-communities. Species were placed into one of six affinity groups (B = basiphilous, CB = circumneutral to basiphilous, C = circumneutral, CA = circumneutral to acidophilous, wA = weakly acidophilous, A = acidophilous) by determining mean pH value and a range of pH values (based on 95 % confidence intervals) of all occurrences for each species according to ELVEBAKK (1982).

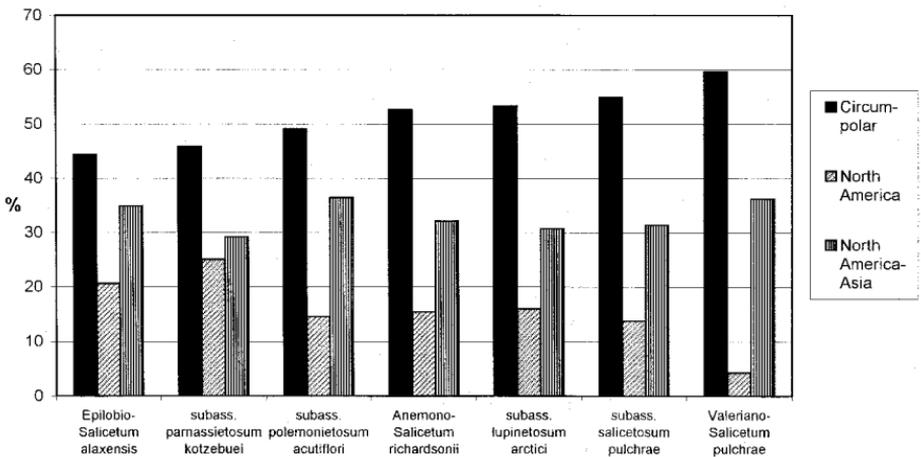


Fig. 8. Geographic range analysis for vascular species of *Salix*-communities.

to lower summer temperatures and a shorter vegetation period. On the other, mineral nutrition and hygric conditions in the shallow active layer are more unfavorable (cf. Tab. 3). Much higher gravel content and higher bulk density in the coarser-textured soils (loamy sand) along mountain creeks lead to edaphically drier conditions, although vertical distance to the water table is considerably reduced. Mean soil pH decreases to 6.6, i.e. lower base saturation, lower cation exchange capacity, and slight acidification of the topsoil is indicated. Basiphilous species percentage sharply

decreases (cf. Fig. 7). This superficial acidification is enhanced by the fact, that the annual spring flood in the headwaters is mainly restricted to the stream/creek beds or flows over still frozen ground, and that perpetual allogenic mineral supply is not given. Due to higher litter fall (higher cover of herb and moss/lichen layer) and slower decomposition rates in these higher-elevated habitats, the soil organic matter content is higher than along lowland rivers.

Interestingly, the majority of differential taxa of this subassociation does not indicate a special adaptation to the more gravelly, coarser-textured soils. E.g., only *Poa glauca*, *Astragalus alpinus* ssp. *alpinus*, *Artemisia arctica* ssp. *arctica*, and *Cerastium beeringianum* primarily occur on sandy, gravelly places. More important regarding the composition of differential taxa, that mainly show amphi-Beringian or circumpolar distributions, is their ability to thrive under conditions that are much less basic. Soil reaction is the ecologically decisive difference to the subass. *parnassietosum kotzebuei* (cf. Fig. 6). This is clearly demonstrated by the high presence of the name-giving taxon *Polemonium acutiflorum*, of *Valeriana capitata*, and by the occurrence of *Salix planifolia* ssp. *pulchra*. These taxa are not only differential species of the Anemono-Salicetum *richardsonii* salicetosum *pulchrae*, but also character species of the Valeriano-Salicetum *pulchrae*, both occurring on acidic soils (see below).



Fig. 9. *Salix alaxensis*-communities are not restricted to lowland river banks. As true pioneer communities they occupy gravelly montane stream banks in the Brooks Range, which might show only periodical streamflow (subass. *polemonietosum acutiflori*). Stand productivity and vigor of *Salix alaxensis* is reduced; phot. U. SCHICKHOFF, 18.07.1997.

Table 6. (cont.)

Relevé-No.	salicetosum pulchrae									10	11	12	13	14	
	1	2	3	4	5	6	7	8	9						
Variant of <i>Oxytropis maydelliana</i>															
<i>Oxytropis maydelliana</i>
<i>Salix arctica</i>	1	2
<i>Carex capillaris</i>	+	1	+
<i>Trisetum spicatum</i>	.	+
Companions															
<i>Arctous rubra</i>	.	.	.	2	1	2	2	2	2	.	.	1	2	1	.
<i>Dryas integrifolia</i>	+	+	2	+	1	1	1
<i>Salix glauca</i>	+	5	.	3	1	.	2	1	2	2	1	3	2	3	.
<i>Salix reticulata</i>	.	.	2	.	2	1	1	2	.	1	2	2	2	2	2
<i>Pedicularis capitata</i>	+	+	+	+	.	1	1	+	1	+	+
<i>Tomenthypnum nitens</i>	.	.	1	1	4	3	3	4	2	.	.	.	4	4	4
<i>Vaccinium uliginosum</i>	1	3	2	1	3	2	2	3	3
<i>Carex bigelowii</i>	+	.	1	3	2	+	1	2	.	+	+	1	+	+	1
<i>Arctagrostis latifolia</i>	1	2	1	2	+	.	.	.	+	+	1
<i>Hylocomium splendens</i>	1	+	.	3	.	2	1	1	.	2	3
<i>Betula nana</i> ssp. <i>exilis</i>	2	1	1	2	1	+	+	+	+	2	1	+	+	+	+
<i>Bistorta vivipara</i>	+	+	+	.	.	1	+	.	+	.	.	+	1	+	+
<i>Pentaphragma floribunda</i>	.	1	+	.	+	1	1	1	1	+	.
<i>Equisetum arvense</i>	.	+	2	2	+	2	2	1
<i>Saussurea angustifolia</i>	+	+	1	1	.	1	1
<i>Ditrichum flexicaule</i>	1	2	2	.	1	.	2	1	+	.
<i>Pyrola grandiflora</i>	+	+	.	+	+	1	+	1	+
<i>Empetrum hermaphroditum</i>	+	.	+	+	.	1	+	.	+
<i>Cardamine digitata</i>	+	+	+	+	.	+
<i>Petigera rufescens</i>	+	.	+	+	+	+
<i>Aulacomnium turgidum</i>	.	.	.	+	1	.	.	1	1	.	1	2	.	.	.
<i>Festuca rubra</i>	.	1	1	+	.
<i>Rhytidium rugosum</i>	+	1	3	.	.	.
<i>Cladonia pyxidata</i>	.	.	.	+	+	+	.	.	+
<i>Stereocaulon tomentosum</i>	+	+	+	.	.
<i>Ledum palustre</i> ssp. <i>decumbens</i>	1	.	.	1	+
<i>Senecio atropurpureus</i> ssp. <i>frigidus</i>	+	+	+	.	+	.	.	r	.
<i>Distichium capillaceum</i>	1	+
<i>Sanionia uncinata</i>	.	.	3	3	+	1
<i>Abietinella abietina</i>	2	2	2	2
<i>Senecio lugens</i>	.	+	+	+	.
<i>Campyladelphus stellatus</i>	.	.	.	2	.	+	.	+	+
<i>Astragalus alpinus</i> ssp. <i>alpinus</i>	.	.	.	+	.	+
<i>Dicranum elongatum</i>	+	+	1	.	.	.
<i>Pohlia nutans</i>	1	+	.	.	.
<i>Aster sibiricus</i>	.	+	+	.
<i>Andromeda polifolia</i>	+	.	+
<i>Vaccinium vitis-idaea</i> ssp. <i>minus</i>	+	.	+	1
<i>Luzula kjelmanniana</i>	+	+	.	.	+	1	.	.	.
<i>Cladonia gracilis</i>	+	.	.	.
<i>Polytrichum juniperinum</i>	+	.	.	+	.	+
<i>Aulacomnium acuminatum</i>	1	.	.	+	.	.	3	.	.	.
<i>Parnassia palustris</i> ssp. <i>neogaea</i>	.	.	.	+	.	+
<i>Bryum</i> spp.
<i>Oncophorus virens</i>	1
<i>Cetraria delisei</i>	1	.	.	.	1
<i>Poa glauca</i>
<i>Papaver macounii</i>
<i>Pedicularis albobabiata</i>	+	.	+
<i>Saxifraga hieracifolia</i>	+	+	.	.
<i>Drepanocladus aduncus</i>	+	.	.	+
<i>Hypnum hamulosum</i>	.	.	+	.	.	1	1
<i>Encalypta rhaptoarpa</i>	+	.	.	+
<i>Racomitrium lanuginosum</i>
<i>Eriophorum vaginatum</i>
<i>Petigera aphthosa</i>	+	+	.	.
<i>Equisetum scirpoides</i>
<i>Carex rotundata</i>	.	.	.	+
<i>Silene acaulis</i>	r
<i>Saxifraga hirculus</i>	+	+	.	.
<i>Arnica griscomii</i> ssp. <i>frigida</i>
<i>Carex vaginata</i>
<i>Astragalus eucosmus</i> ssp. <i>sealei</i>	1
<i>Brachythecium turgidum</i>	2	.	1

Table 6. (cont.)

Additional taxa: *Cladonia unicalis* (rel. 22: +); *Cladonia fimbriata* (22: +); *Calamagrostis lapponica* (16: +, 20: 1); *Anastrophyllum minutum* (20: +); *Lepraria neglecta* (20: +); *Cladonia subulata* (21: +); *Cladonia carneola* (21: +); *Polytrichum strictum* (11: 1, 19: +); *Cladonia scabriuscula* (19: +); *Boykinia richardsonii* (15: 1, 16: +); *Epilobium latifolium* (15: +, 16: +); *Parnassia kotzebuei* (15: +, 16: +); *Lagotis glauca* ssp. *minor* (15: +, 16: +); *Didymodon asperifolius* (15: +, 16: 2); *Pedicularis langsдорffii* (16: +, 23: +); *Cynodontium strumiferum* (23: +); *Carex krausei* (24: +); *Amphidium lapponicum* (24: 1); *Tortella fragilis* (24: +); *Tortella tortuosa* (5: 1, 24: +); *Myurella julacea* (24: +); *Lecanora epibryon* (24: +, 27: +); *Solorina saccata* (24: +); *Salix arbusculoides* (29: +, 30: 1); *Platanthera obtusata* (26: +, 30: +); *Peltigera leucophlebia* (30: +); *Shepherdia canadensis* (25: +); *Androsace chamaejasme* ssp. *lehmannaiana* (25: r); *Cetraria tilesii* (27, +); *Pleurozium schreberi* (28, +); *Bryum pseudotriquetrum* (5: +, 17: +); *Entodon concinnus* (3: +, 17: +); *Fissidens adianthoides* (17: +); *Eutrema edwardsii* (18: +); *Deschampsia brevifolia* (3: +, 18: +); *Taraxacum phymatocarpum* (18: +); *Ceratodon purpureus* (18: +, 34: +); *Castilleja caudata* (33: +); *Hedysarum mackenzii* (31: 1, 32: 2); *Pohlia cruda* (13: +, 31: 1); *Carex glacialis* (32: +); *Lomatogonium rotatum* (32: r); *Mnium blytii* (32: +); *Leptobryum pyriforme* (32: 1); *Salix ovalifolia* (34: 2, 35: 2); *Dendranthema integrifolium* (34: +, 35: +); *Oxyria digyna* (34, +); *Poa alpigena* (34: +); *Artemisia arctica* ssp. *arctica* (1: +, 34: +); *Artemisia glomerata* (34: +); *Alsinanthe rossii* (34: +, 35: +); *Salix chamissonis* (35: 2); *Poa alpina* (35: +); *Carex podocarpa* (7: +, 8: +); *Dodecatheon frigidum* (7: +, 8: +); *Blepharostoma trichophyllum* (7: 1); *Hypnum cupressiforme* (5: +, 7: 1); *Thuidium recognitum* (8: +); *Mnium hymenophylloides* (3: +, 5: 1); *Racomitrium canescens* var. *ericoides* (5: 1, 9: 1); *Catascopium nigratum* (5: +); *Sphagnum squarrosum* (9: +); *Stereocaulon alpinum* (9: +); *Aconitum delphinifolium* ssp. *paradoxum* (3: +); *Sphagnum teres* (2: +, 3: 2); *Klaeria starkei* (2: +, 3: +); *Salix hastata* (2: 1); *Viola epipsila* ssp. *repens* (2: 1); *Timmia megapolitana* var. *bavarica* (2: +); *Chondrophylla prostrata* (14: +); *Philonotis fontana* (14: +); *Bryum lisaie* var. *cuspidatum* (14: 1); *Peltigera didactyla* (14: +); *Alnus crispa* (1: +); *Ledum palustre* ssp. *groenlandicum* (1: +); *Deschampsia caespitosa* (1: 1); *Thalictrum alpinum* (10: +, 11: +); *Potentilla hyparctica* (10: +); *Hierochloa alpina* (10: +, 11: +); *Hepatic. indet.* (10: +); *Cetrelia alaskana* (10: +); *Eriophorum scheuchzeri* (11: +).

Localities: rel. 1: Dietrich Creek below viewpoint; 2, 3: Oksrukuyik Creek at Slope Mt., left bank; 4: Lower Happy Valley Creek, upper terrace, right bank; 5: Lower Oksrukuyik Creek, near Pump Station 3, left bank; 6–8: Lower Dan Creek near Dalton Highway, left and right bank; 9: Lower Oksrukuyik Creek, near Pump Station 3, left bank; 10–11: Atigun River above Pump Station 2, right bank; 12–14: Atigun River in front of Atigun Gorge, right bank; 15–16: Sagavanirktok River near Slope Mt. Maintenance Station, left bank; 17–18: Sagavanirktok River south of Sagwon, left bank; 19–24: Sagavanirktok River near Slope Mt. Maintenance Station, left bank; 25–28: Sagavanirktok River near Happy Valley Landing Strip, left bank; 29–30: Sagavanirktok River south of Pump Station 3, left bank; 31–32: Sagavanirktok River near Franklin Bluffs, left bank; 33: Sagavanirktok River south of Franklin Bluffs Camp, left bank; 34–35: Sagavanirktok River south of Deadhorse, left bank.

Within this subassociation, a variant could be differentiated which occurs on edaphically drier sites with higher gravel and sand content, and which is characterized by an extraordinarily high cover/abundance of lichens (Tab. 5; rel. no. 79–85). Correspondingly, lichen species richness is much higher compared to the subass. *parnassietosum* (cf. Fig. 5). Most of the lichens are indicators of acidity, e.g. *Stereocaulon tomentosum*, *Cetraria nivalis*, *Peltigera aphthosa*, *Thamnolia subuliformis*, and *Cetraria cucullata* (WIRTH 1992). However, since they are poikilohydric plants without roots or rhizoids, and their behaviour differs from that of vascular plants, these indications only apply to their immediate environment (often they are attached to moss tissues). This corroborates the above mentioned slight acidification of the topsoil. That the mineral soil is still weakly basic, is proved by the occurrence of base indicators like *Dryas octopetala* or *Hypnum bambergeri*. So the differentiation within this subassociation must be attributed to soil moisture rather than to soil pH as indicated by axis 2 in Fig. 6.

In the lower section of Tab. 5 companion species are listed. Some of the most abundant taxa like *Salix glauca*, *Arctous rubra*, *Equisetum arvense*, or *Bistorta vivipara* are at the same time most frequent companions of the *Anemono-Salicetum richardsonii*, indicating floristic and ecological affinities between both associations.

4.2 *Anemono-Salicetum richardsonii* Schickhoff et al. 2001 ass. nova Nomenclatural type relevé: Tab. 6, rel. 26

This more or less open low willow shrub association is widely distributed on banks of upland tundra streams as well as on upper terraces of Sagavanirktok River, adjoining to *Salix alaxensis*-stands on lower terraces. It occurs over a wide altitudinal range, from mountain stream banks at an elevation of 900–950 m down to upper river terraces on the coastal plain. In contrast to *Salix alaxensis*-communities it occupies better developed sites along the successional gradient of river terrace/stream bank evolution (cf. Fig. 2, axis 2). It follows in the course of succession, when pioneer tall willow shrub communities have prepared the ground in terms of soil development and/or when sites reach a certain vertical distance to the water table due to river erosion. The association corresponds to low willow stands of the categories “closed low willow shrub” and “open low willow shrub” respectively by VIERECK et al. (1992).

The soils under the *Anemono-Salicetum richardsonii* are considerably further developed compared to feltleaf willow stands (cf. Tab. 3): Gravel content is negligible, and the soils are much more fine-textured (loam to sandy loam) with a considerable increase in silt and clay fractions. Thus, the soils have much higher water capacity and higher soil moisture, further enhanced by a thick, water-storing moss layer. Mosses become much more prominent in the growth form spectrum (cf. Fig. 4). Organic matter and nitrogen content likewise show a remarkable increase. At the same time, the C/N-ratio widens, indicating lower decomposition rates. As indicated by a mean soil pH of 6.6, base saturation and cation exchange

capacity ensure a sufficient nutrient supply. Summing up, soil conditions improve from lower to upper terraces, where a comparatively higher number of taxa (many weakly acidophilous species; cf. Fig. 7) finds suitable habitat conditions. Total species richness (Δ 35.3), vascular species richness (Δ 25.6), and lichen richness (Δ 3.4) is higher than in *Salix alaxensis*-communities (Δ 29.8, Δ 21.2, Δ 1.9 resp.) (cf. Fig. 5). Paradoxically, the productivity of the shrub layer decreases in the same direction from tall to low willow shrub communities. This must be attributed to the decrease in depth of the active layer. Thicknesses of only 40–50 cm (reduced rooting space) and shorter thaw seasons on upper terraces hamper the development of tall woody structures and thus the competitiveness of *Salix alaxensis*.

In its optimum development, this association is characterized by a 1–1.5 m tall shrub layer with a cover of 70–80% (Fig. 10). Towards the coastal plain, where the climatic conditions become more unfavorable, the average shrub height decreases to 20–30 cm near Deadhorse (see WALKER, D. A. 1985 for a detailed study on stature changes along a Sagavanirktok River transect). Among the two character species, the amphi-Beringian *Salix lanata* ssp. *richardsonii* is present in all relevés, but by far less dominant compared to the name-giving *Salix* taxa in the other two associations (Tab. 7). The character species are more or less homogeneously distributed in both subassociations (cf. Tab. 6), i.e., they occur with comparable cover and abundance on lowland, upland, and mountain streambanks and river



Fig. 10. The low willow community *Anemono-Salicetum richardsonii* (subass. *lupinetosum arctici*) is widely distributed on upper terraces along the Sagavanirktok River; phot. U. SCHICKHOFF, 15.07.1997.

Table 7. Dominance values of five highest ranked species in each association as expressed by percentage on the sum of the total species cover. Calculation is based on cover/abundance values of species in relevés transformed into average cover percentage according to ELLENBERG (1956).

Most dominant species	Percentage on total cover of respective community
Epilobio-Salicetum alaxensis	
<i>Salix alaxensis</i>	35.0 %
<i>Abietinella abietina</i>	4.7 %
<i>Aster sibiricus</i>	3.5 %
<i>Hypnum bambergeri</i>	2.6 %
<i>Salix glauca</i>	2.5 %
Anemono-Salicetum richardsonii	
<i>Salix lanata</i> ssp. <i>richardsonii</i>	14.1 %
<i>Tomenthypnum nitens</i>	11.4 %
<i>Salix glauca</i>	11.0 %
<i>Hylocomium splendens</i>	7.6 %
<i>Dryas integrifolia</i>	5.1 %
Valeriano-Salicetum pulchrae	
<i>Salix planifolia</i> ssp. <i>pulchra</i>	30.1 %
<i>Hylocomium splendens</i>	7.7 %
<i>Aulacomnium palustre</i>	6.9 %
<i>Sphagnum teres</i>	4.9 %
<i>Sanionia uncinata</i>	4.3 %

terraces, indicating that altitude does not play a major role in community characteristics, at least at the association level. The above mentioned edaphic conditions much better characterize the synecology of this association.

Tabular processing resulted in two subassociations on upland tundra stream banks (*salicetosum pulchrae*) and on upland and lowland river terraces (*lupinetosum arctici*) respectively:

1) **Anemono-Salicetum richardsonii salicetosum pulchrae**
 Schickhoff et al. 2001 subass. nova
 Nomenclatural type relevé: Tab. 6, rel. 3

This subassociation (Tab. 6; rel. no. 1–9) is distributed on upland tundra stream banks. It is a transitional vegetation type, already mediating to the *Valeriano-Salicetum pulchrae* on most humid and acid stream banks (cf. Fig. 2). Edaphic parameters are close to those of the latter association (see Tab. 3). Soil pH and vertical distance to the water table are much lower, and soil moisture of the more loamy soils is much higher than in the second subassociation (*lupinetosum arctici*). These are crucial factors deter-

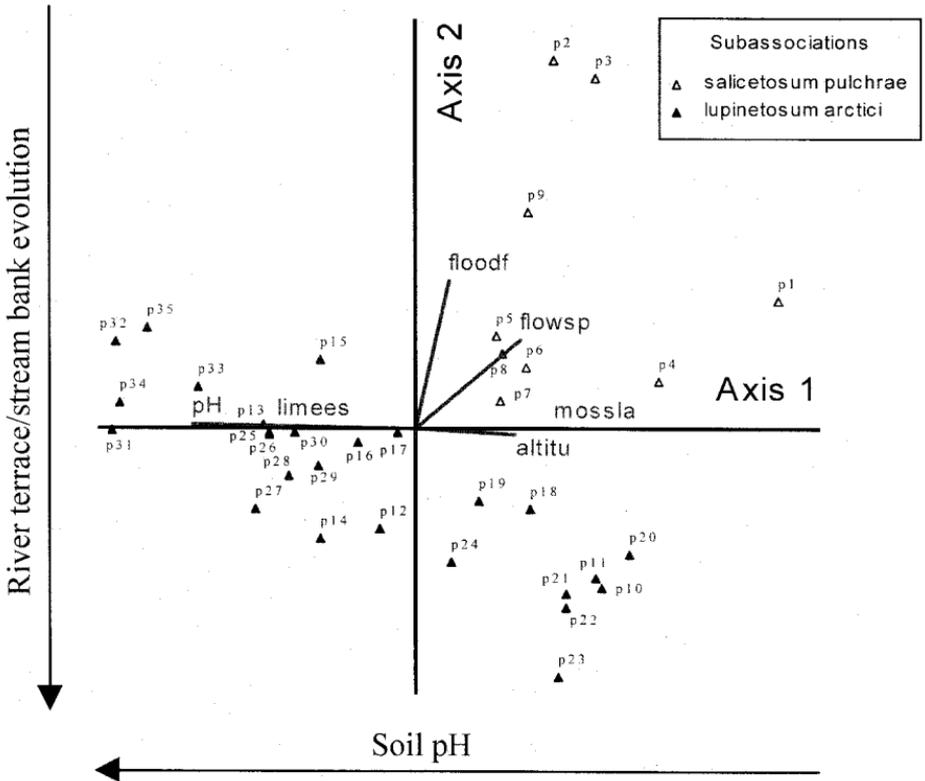


Fig. 11. DCA ordination of *Anemono-Salicetum richardsonii*.

mining the differentiation pattern in the ordination diagram (Fig. 11). Moreover, soil texture, content of organic matter, nitrogen, Mn- and Fe-ions, and thickness of moss layer (Tab. 3) differentiate the two subassociations, and give evidence of the transitional position to *Salix pulchra*-communities. This position is likewise reflected in community characteristics like growth form percentage (cf. Fig. 4), species richness (cf. Fig. 5) or pH-affinities of the species composition (cf. Fig. 7).

The name-giving taxon of this subassociation, the amphi-Beringian *Salix planifolia* ssp. *pulchra*, as well as other differential species like *Polemonium acutiflorum*, *Valeriana capitata*, *Anemone richardsonii*, *Aconitum delphinifolium* ssp. *delphinifolium*, *Saxifraga nelsoniana* ssp. *nelsoniana*, and *Climacium dendroides* are at the same time character species of the Valeriano-*Salicetum pulchrae* (see Tab. 7 below). Additionally, they point to similar habitat conditions regarding soil moisture and soil reaction. The majority of the differential species show amphi-Beringian distribution. They indicate moist, rich, peaty-humous soils, and moderately acid to acid conditions. The latter holds true not only for vascular plants rooting in

the mineral soil, but also for mosses covering the soil surface (*Oncophorus wahlenbergii*, *Aulacomnium palustre*).

2) *Anemono-Salicetum richardsonii lupinetosum arctici*

Schickhoff et al. 2001 subass. nova

Nomenclatural type relevé: Tab. 6, rel. 26

This subassociation (Tab. 6; rel. no. 10–35) is widely distributed on upper river terraces in both lowland and upland. It represents the typical form of the association, occupying better developed sites with advanced soil development along the successional gradient of river terrace/stream bank evolution (see above). Sites are characterized by comparatively higher soil pH, lower soil moisture, and considerably higher vertical distance to the water table. The more moderate habitat conditions obviously lead to more favorable living conditions for a greater variety of species, except for mosses. Total species richness as well as vascular and lichen species richness is higher compared to the other subassociation (cf. Fig. 5).

Along the transect from the Brooks Range to Prudhoe Bay, a sequence of variants (cf. Tab. 6) represents gradients of decreasing altitude, decreasing soil moisture, increasing vertical distance to the water table, and increasing nitrogen content. The variant of *Kobresia myosuroides* (Tab. 6; rel. no. 10–14), occurring along upland rivers, is characterized by differential taxa with arctic-alpine and mostly circumpolar distribution, indicating harsh climatic conditions. Moreover, taxa like *Kobresia myosuroides*, *Dryas octopetala*, and *Festuca brachyphylla* indicate weakly basic conditions of less developed montane river terrace soils (mean soil pH of sites of this variant is 6.7).

The variant of *Lupinus arcticus* (Tab. 6; rel. no. 15–30), occurring along lowland rivers in the northern foothills section, represents the optimum development of this subassociation. It occupies intermediate sites in terms of soil moisture and soil pH (cf. Fig. 11). It is common on occasionally flooded broad upper river terraces with well developed, nutrient-rich soils at an altitudinal range between 260 and 550 m a.s.l. Mean soil pH of the sites is 6.5, and the sandy-loamy soils are characterized by relatively high amounts of organic matter (Δ 16.8% o.m.). The majority of the differential taxa are indicators of weakly basic to basic soils. At the same time they indicate fresh soils or moist soils; pronounced dry-site or wet-site indicators are missing.

Some differential taxa (*Zygadenus elegans*, *Leymus velutinus*, *Carex concinna*) are at the same time differential taxa of the variant of *Castilleja caudata* within the *Epilobio-Salicetum alaxensis parnassietosum kotzebuei* (cf. Tab. 5; rel. no. 59–65). This floristic-sociological affinity, also expressed by neighbouring positions of relevés in the ordination diagram (cf. Fig. 2), reflects similar site conditions of adjoining vegetation types along the gradient from lower to upper river terraces.

The third variant (Tab. 6; rel. no. 31–35) is developed on terraces of lowland rivers in the coastal plain section below 200 m a.s.l. The sites of this variant, often ice-wedge polygons, are characterized by basic condi-

Table 8. Community table of *Valeriano-Salicetum pulchrae* ass. nova.

Relevé-No.	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
Relève Size (m²)	60	60	60	60	60	60	100	60	60	60	60	100	60	60	60	60	100	60	60	60	60	60	60
Altitude (m a.s.l.)	820	790	330	410	400	460	350	350	800	810	790	810	460	890	870	800	870	790	780	790	810	820	800
Cover Shrub Layer (%)	90	80	70	75	80	70	90	80	80	85	90	80	80	90	75	80	70	80	85	80	90	70	90
Cover Herb Layer (%)	70	40	30	25	15	35	30	30	20	30	20	30	20	20	30	20	30	20	15	20	20	30	25
Cover Moss/Lichen Layer (%)	25	75	80	90	90	90	90	80	35	20	30	20	70	90	35	90	85	95	90	90	30	40	15
Total number of taxa	26	47	43	40	31	38	28	41	25	26	19	23	29	28	30	30	37	35	38	42	31	29	28
Number of vascular taxa	21	27	21	19	24	16	22	16	17	13	19	13	16	20	19	24	22	24	24	22	21	16	16
Number of bryophyte taxa	5	14	15	13	12	11	11	16	9	8	6	4	15	9	9	10	12	12	13	18	9	8	10
Number of lichen taxa	-	6	7	6	-	3	1	1	-	1	-	-	1	3	1	1	1	1	-	-	-	-	-
Ch/D ass.	5	4	4	4	3	5	4	4	4	4	5	4	4	5	4	4	4	4	4	4	4	4	5
<i>Salix planifolia</i> ssp. <i>pulchra</i>	1	2	1	1	1	1	-	+	-	+	-	+	1	1	2	+	+	1	1	2	+	1	2
<i>Valeriana capitata</i>	1	1	+	-	+	-	+	+	+	+	+	+	1	1	+	+	+	+	+	+	+	+	1
<i>Polemonium acutiflorum</i>	1	1	+	-	+	-	+	+	+	+	+	+	1	1	+	+	+	+	+	+	+	+	1
<i>Acentium delphinidium</i> ssp. <i>delphinidium</i>	1	1	+	-	+	-	+	+	+	+	+	+	1	1	+	+	+	+	+	+	+	+	1
<i>Arenaria richardsonii</i>	1	1	+	+	+	-	+	+	+	+	+	2	+	+	+	+	-	+	+	+	+	+	+
<i>Saxifraga neilsoniana</i> ssp. <i>neilsoniana</i>	+	+	-	-	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Climacium dendroides</i>	+	+	-	-	+	-	+	+	+	+	+	+	+	+	+	+	+	1	1	+	+	+	+
<i>Luzula rufescens</i>	+	+	-	-	+	-	+	+	+	+	+	+	+	1	1	+	1	+	+	+	+	+	1
Variant of <i>Vaccinium uliginosum</i>	+	2	1	3	2	3	2	1	3	2	1	2	1	2	1	2	1	2	1	2	1	2	1
<i>Vaccinium uliginosum</i>	+	1	+	1	+	1	+	1	2	1	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Vaccinium vitis-idaea</i> ssp. <i>minus</i>	-	2	-	2	2	1	-	-	-	-	-	-	1	1	2	1	-	-	-	-	-	-	-
<i>Rubus chamaemorus</i>	-	+	1	2	2	1	+	+	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Ledum palustre</i> ssp. <i>decumbens</i>	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Equisetum arvense</i>	-	+	+	+	+	+	+	+	+	+	+	2	+	+	+	+	+	+	+	+	+	+	+
<i>Calluna vulgaris</i>	2	2	2	1	-	+	1	2	1	2	1	+	+	+	+	+	+	+	+	+	+	+	+
<i>Calluna vulgaris</i> canadensis	-	+	+	1	1	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Andromeda polifolia</i>	-	+	+	1	1	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Empetrum hermaphroditum</i>	-	+	+	1	1	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Pentaphragma forficata</i>	2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Carex poeppocarpa</i>	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Salix lanata</i> ssp. <i>richardsonii</i>	1	2	1	+	+	+	+	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Variant of <i>Salix chamissonis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Salix chamissonis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	2	1	2	3	2	-
<i>Salix reticulata</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	1	2	3	2	-
<i>Carex bigelowii</i>	-	-	-	-	-	-	-	-	-	-	-	-	2	+	-	1	+	2	2	1	1	1	-
<i>Pyrola grandiflora</i>	-	-	-	+	2	1	-	-	-	-	-	-	-	-	-	+	-	-	1	1	1	1	1
<i>Bistorta plumosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	1	1	1	1	1
<i>Sphagnum squarrosum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	1	+	+	+	+
<i>Bistorta vivipara</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+
<i>Thuidium recurgitum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+
Companions	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	+	+	+	+	+	+
<i>Betula nana</i> ssp. <i>exilis</i>	+	1	1	2	2	2	2	2	1	1	1	+	2	2	+	1	+	+	+	+	+	1	2
<i>Aulacomnium palustre</i>	-	1	2	2	1	4	1	-	1	1	1	3	3	1	-	2	4	3	2	2	2	2	1
<i>Hylacomnium splendens</i>	-	3	2	2	3	3	1	2	2	1	2	+	2	2	+	3	3	2	3	3	1	+	+
<i>Acrotagrostis latifolia</i>	-	-	-	1	2	1	+	+	1	1	1	-	1	2	1	2	1	2	1	1	1	+	2
<i>Petastites frigidus</i>	-	1	2	+	1	2	2	3	+	2	+	-	-	1	-	2	+	+	+	1	1	+	1
<i>Pedicularis capitata</i>	-	+	+	-	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Thymus praenoxanthus</i>	-	1	-	-	1	3	+	1	1	1	1	+	2	-	-	3	2	1	+	3	1	1	1

tions (mean soil pH 7.8), and they are relatively rich in available nitrogen and phosphorus. The favorable nutrient supply has to be attributed to the runoff peak in spring, when the banks of the lower Sagavanirktok River are flooded and provided with minerals and nutrients. Moreover, airborne nutrients from loess depositions upwind contribute to the remarkable nutrient supply. Basic soil conditions are indicated in particular by *Trisetum spicatum*, *Carex capillaris*, and *Salix arctica*. On the other hand, harsh climatic conditions restrict the productivity of the shrub layer resulting in very prostrate, creeping growth forms of several *Salix* species (*S. arctica*, *S. lanata* ssp. *richardsonii*, *S. ovalifolia*). The shrubs do not grow higher than 15 cm.

The floristic composition of the most frequent companions mirrors the intermediate position of this association. Some are at the same time most frequent companions in the *Salix alaxensis*-communities (e.g. *Arctous rubra*, *Salix glauca*, *Equisetum arvense*, *Bistorta vivipara*), others share the same status in the *Salix pulchra*-stands (e.g. *Betula nana* ssp. *exilis*, *Hylocomium splendens*, *Pedicularis capitata*). Some taxa like *Arctagrostis latifolia*, *Festuca rubra*, *Tomenthypnum nitens*, and *Sanionia uncinata* are abundant in all three *Salix* associations. At least the latter are supposed diagnostic taxa of higher syntaxonomic units.



Fig. 12. The Valeriano-*Salicetum pulchrae*, here along the upper Kugaruk River, is common on paludified, acid banks of upland tundra streams and creeks in the Arctic Foothills, especially on older land surfaces; phot. U. SCHICKHOFF, 25.07.1997.

4.3 Valeriano-Salicetum pulchrae Schickhoff et al. 2001 ass. nova Nomenclatural type relevé: Tab. 8, rel. no. 37

This conspicuous low willow community is restricted in its distribution to most humid and acid banks of upland tundra streams and creeks of the Arctic Foothills zone (roughly between 400 and 800 m a.s.l.). It occupies the immediate margins of smaller tundra streams and creeks originating in the gentle topography of the foothills and not in the Brooks Range (Fig. 12). Thus, it is typical for a specific tundra stream type with a specific streamflow regime (sharp peakflow in late May), which governs the environmental conditions in terms of disturbance, soil moisture, soil reaction, nutrient fluxes and the like. The higher elevation of community habitats is clearly reflected in a slightly higher amount of species with arctic-alpine distribution compared to the two other associations (Fig. 13) as well as in the lowest percentage of thermophilous species (Zone 4 species), whereas more cold-adapted species (Zone 2 species) show the highest percentage (Fig. 14).

Adjoining to this association, shrub tundra (mostly dominated by *Betula nana*) or tussock tundra on paludified soils prevails with increasing distance from creeks. Along somewhat larger streams, where a stream terrace is developed and where regular disturbances occur, this association is replaced by *Salix richardsonii*-stands. The latter are restricted to less humid and acid terrace sites with higher vertical distance to the water table, especially on younger land surfaces. *Salix pulchra*-communities occupy a distinct, delimited space within the ordination diagram of all relevés (Fig. 2), indicating the narrowest synecological amplitude of all *Salix*-communities and a more homogeneous floristic composition. As a result, they are much better defined by character species. *Salix pulchra*-stands are subsumed by VIERECK

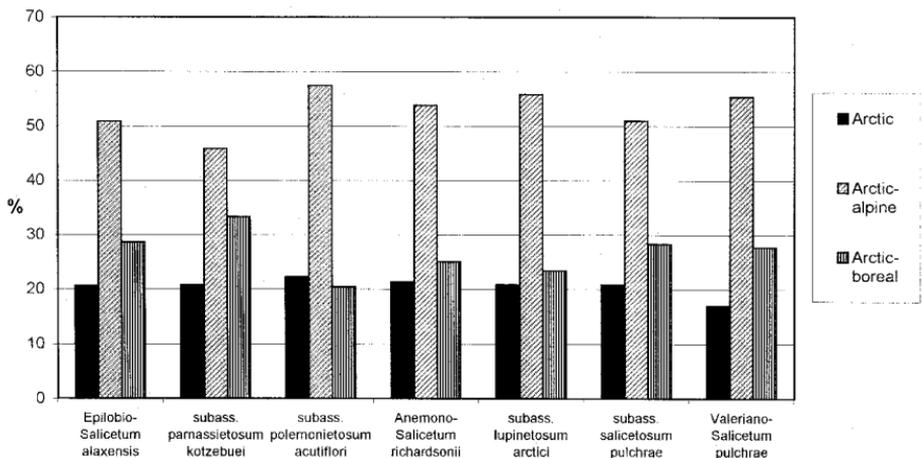


Fig. 13. Physiographic unit analysis for vascular species of *Salix*-communities.

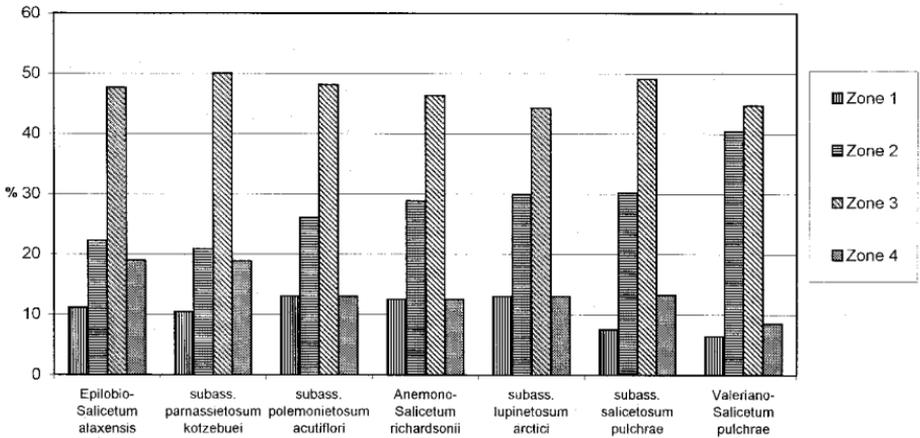


Fig. 14. Climatic affinity for vascular species of *Salix*-communities. Northern limits of plant distributions were assessed within the four climatic zones developed by YOUNG (1971). The differentiation of zones is based on the sum of mean monthly temperatures above 0 °C (zone 1 = 0 to < 6 °C; zone 2 = 6 < 12 °C; zone 3 = 12 < 20 °C; zone 4 = 20 < 35 °C).

et al. (1992) under “closed low willow shrub” and “open low willow shrub” respectively without separating it from *Salix lanata*- and *S. glauca*-stands.

Most riparian habitats show pioneer-like characteristics, the habitats of this association, however, cannot be termed pioneer habitats. As a rule, they are located on older land surfaces, which are geomorphologically not very active. As the smaller streams and creeks drain smaller watersheds, the water volume is relatively low and so is its erosional impact. They do overflow their banks, but flooding is less severe compared to mountain streams. This is reflected in lower levels of turbidity and suspended silt loads of these waters (tundra streams), which show distinct differences in chemical characteristics (esp. Ca- and Mg-ions, pH, conductivity) compared to mountain streams originating in the Brooks Range (Tab. 9). Moreover, the sharp peakflow in the melting period occurs at a point in time, when most of the ground is still frozen and thus protected from erosion. Nevertheless, snowmelt runoff provides a certain ionic enrichment, which may lead to a certain accumulation in organic surface soils during later melting phases. The rather stable habitats of this association show comparatively most progressive soil development like leached loamy soils with very low soil pH (Δ 5.0), low bulk density, and relatively high content of silt and clay fractions (cf. Tab. 3). On the other hand, the sites are characterized by a very shallow active layer (30–35 cm), which is mainly due to perfect insulation by extremely thick moss and mor layers with high water storage capacity (Fig. 15). Mosses nearly equal shrubs in cover percentage (cf. Fig. 4), and bryophyte species richness is comparatively very high (cf. Fig. 5). Water saturation of the soils and lower oxygen content lead to reduced decompo-

sition of organic residues and thus to the development of thick mor layers and to high percentage of organic matter (Δ 24.2%). Considerably high amounts of Mn- and Fe-ions (cf. Tab. 3; Mn-concentrations in plant tissues may reach toxic levels; see MARION et al. 1989), point to reduction and oxidation processes in these strongly humous, peaty soils, resulting in redoximorphic features in the subsoil (iron and manganese concretions, characteristic color patterns). Both Mn- and Fe-ions are reduced and possibly complexed with organic acids in the organic-rich soils (EVERETT et al. 1996). Under these conditions, *Salix pulchra*-shrubs are remarkably vigorous. They reach high cover/abundance values and average heights of 80–100 cm. As a consequence of the hygric and acid, paludified soil conditions and the decreased rooting space, taller willows (*S. alaxensis*, *S. glauca*, *S. lanata* ssp. *richardsonii*) are no longer competitive. *Salix planifolia* ssp. *pulchra* exclusively dominates the stands.

Those character species which show highest presence degree are at the same time differential species of the Anemono-Salicetum richardsonii salicetosum (cf. Tab. 6), indicating floristic-sociological and synecological affinity to that subassociation (cf. Fig. 2; Tab. 3). Most of the character taxa are amphi-Beringian in their distribution and indicators for acidophilous soils and moist sites (Tab. 10). Two variants could be preliminarily differentiated: the typical variant is that of *Vaccinium uliginosum*, which shows the characteristic species composition (Tab. 8; rel. no. 36–50). The sites of this variant cover the whole distributional range of the association. Compared to those of the *Salix chamissonis*-variant (Tab. 8; rel. no. 51–58), they are characterized by slightly lower soil moisture and organic matter contents, and slightly higher amounts of nutrients (N, P) and soil pH. The only major difference in site conditions between the two variants is the amount of Mn-ions, which is considerably higher in the soils under the *Salix chamissonis*-variant (848.8 vs. 336.4 ppm). This may be attributed to higher water saturation, lower soil pH and a slightly higher degree of reduction in the soil. However, the regional validity of the *Salix chamissonis*-variant has to be elaborated by further studies. It may merely be a

Table 9. Chemical analysis of water samples from mountain and tundra streams in Sagavanirktok and Kuparuk River drainages. Ions are reported in $\mu\text{mol L}^{-1}$ (data from KLING et al. 1992).

	Conductivity ($\mu\text{S/cm}^{-1}$)	pH	HCO_3^-	Ca^{2+}	Mg^{2+}	Na^+	K^+
Mountain streams							
Atigun River	166.0	8.0	1105	524	227	144	12
Sagavanirktok River	148.0	8.2	1163	324	189	10	2
Tundra streams							
Upper Kuparuk River	29.2	7.1	200	95	35	33	8
Upper Oksrukuyik Creek	37.9	7.3	298	125	46	28	10



Fig. 15. Sites of *Salix pulchra*-stands are characterized by a very shallow active layer (30 cm in this example). Thick moss and mor layers provide perfect insulation of the subsoil; phot. U. SCHICKHOFF, 10.08.1997.

local variant, since the majority of its relevés were recorded along the upper Oksrukuyik Creek. Therefore we refrain from describing it as a subassociation.

The differential species of the *Vaccinium*-variant are strong indicators of moist, peaty-turfy, acid soils. This holds true especially for *Vaccinium uliginosum*, *Vaccinium vitis-idaea* ssp. *minus*, *Rubus chamaemorus*, *Ledum palustre* ssp. *decumbens*, *Andromeda polifolia*, and *Empetrum hermaphroditum*. In their majority, the differential taxa show circumpolar distribution. On the other hand, the differential species group of the *Salix chamissonis*-variant contains more amphi-Beringian elements (*Salix chamissonis*, *Carex bigelowii*, *Bistorta plumosa*). This might point to slight differences in the phylogenetic evolution of these phytocoenoses.

The most frequent companion species (e.g. *Betula nana* ssp. *exilis*, *Petasites frigidus*, abundant mosses) also indicate hygric and acid soil conditions. Bryophyte species richness is exceptionally high (cf. Fig. 5). Moreover, frequent mosses like *Aulacomnium palustre*, *Hylocomium splendens*, *Sanionia uncinata*, and *Sphagnum teres* reach high cover/abundance values and all belong to the most dominant species in this association (cf. Tab. 7).

Table 10. Attributes of character species of *Salix*-communities. Abbreviations for pH affinity and northern limit are those used in Figs. 7 and 14 resp.

Character species	Growth form	pH affinity	Physiographic unit	Geographic range	Northern limit
Epilobio-Salicetum alaxensis					
<i>Salix alaxensis</i>	shrub	C	Arctic	North America–Asia	3
<i>Epilobium latifolium</i>	forb	C	Arctic-alpine	Circumpolar	2
<i>Aster sibiricus</i>	forb	CB	Arctic-alpine	North America–Asia	3
<i>Trisetum spicatum</i>	graminoid	C	Arctic-alpine	Circumpolar	2
Anemone-Salicetum richardsonii					
<i>Salix lanata</i> ssp. <i>richardsonii</i>	shrub	C	Arctic	North America–Asia	3
<i>Anemone parviflora</i>	forb	C	Arctic-alpine	North America	3
Valeriano-Salicetum pulchrae					
<i>Salix planifolia</i> ssp. <i>pulchra</i>	shrub	wA	Arctic-alpine	North America–Asia	2
<i>Valeriana capitata</i>	forb	CA	Arctic-alpine	North America–Asia	2
<i>Polemonium acutiflorum</i>	forb	CA	Arctic-alpine	North America–Asia	2
<i>Aconitum delphinifolium</i> ssp. <i>delphinifolium</i>	forb	CA	Arctic-boreal	North America–Asia	3
<i>Anemone richardsonii</i>	forb	wA	Arctic	North America–Asia	3
<i>Saxifraga nelsoniana</i> ssp. <i>nelsoniana</i>	forb	A	Arctic-alpine	North America–Asia	2
<i>Climacium dendroides</i>	moss	CA	Arctic-boreal	Circumpolar	2
<i>Luzula rufescens</i>	graminoid	A	Arctic	North America–Asia	3

5 Discussion

Our study reveals distinct relationships of riparian *Salix* associations and subassociations with major landscape-level environmental variables along a transect from the Brooks Range to Prudhoe Bay. A combination of edaphic conditions (soil pH, soil moisture) and factors pertaining to topography, disturbance regime and landscape evolution (river terrace/stream bank development) controls spatial patterns and floristic compositions of these riparian vegetation units. Principal environmental gradients at work in riparian ecosystems are, thus, included (cf. MALANSON 1993; HUGHES 1997). Landscape age, topography, substrate and disturbance effects like annual flooding, erosion and sedimentation are crucial underlying parameters for the present-day differentiation of the riparian vegetation mosaic. Environmental gradients affecting the vegetation in this study correspond to those well-known to control plant distribution across the Arctic (esp. soil moisture, soil pH, landscape age; cf. WEBBER et al. 1980; WALKER, D. A. 1985; WALKER, M. D. et al. 1994b; GOULD 1998). Specific riparian replacement successions can be derived from floristic-sociological traits, synecological characteristics, and spatial patterns of *Salix*-communities. The Epilobio-Salicetum alaxensis is a true pioneer community along mountain creeks and on gravel bars, floodplains and lower terraces of rivers, where it is favored by frequent disturbances, coarser-textured soils with a deep active

layer and relatively high soil temperatures. Corresponding to the permanent habitat disturbances, this self-perpetuating pioneer association may persist on river banks as long as erosion and deposition of new increments of alluvium occurs, i.e. as long as predominantly allogenic processes are operative in succession cycles. It is replaced by the *Anemono-Salicetum richardsonii* (subass. *lupinetosum arctici*) on higher terraces with better developed soils (however, with a shallower active layer due to insulation by a thick moss cover and lower soil temperatures) (Fig. 16). This association characterizes later stages of succession on river alluvium with predominantly autogenic processes resulting inter alia in an uniquely arctic soil thermal regime.

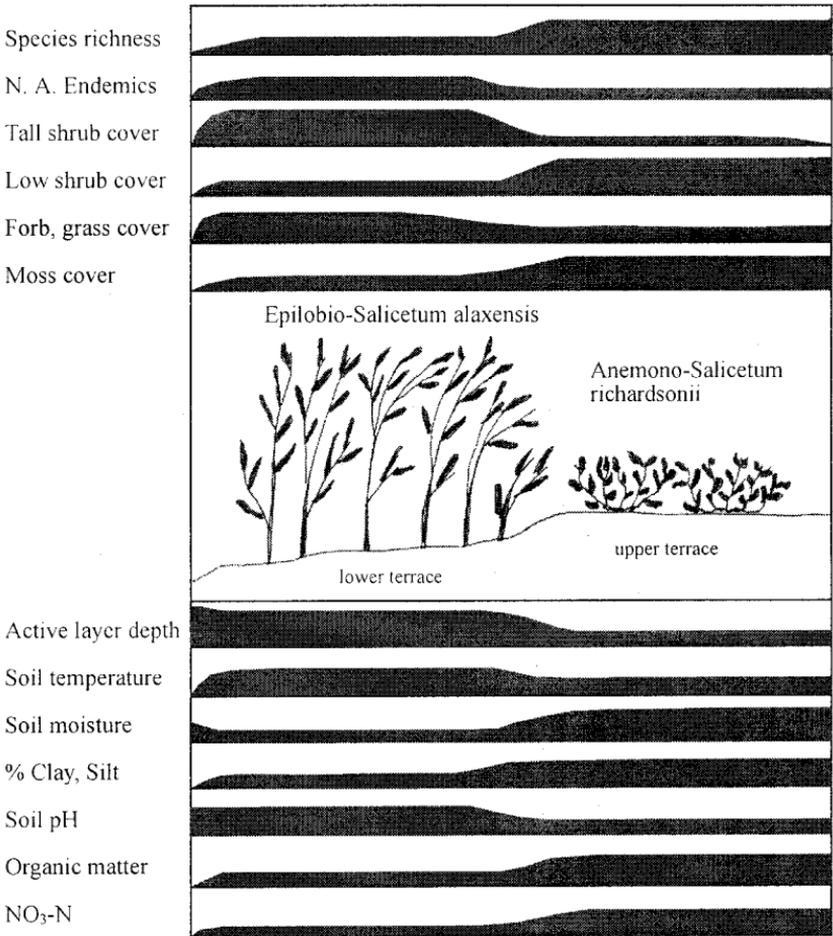


Fig. 16. Idealized pattern of willow succession along the Sagavanirktok riverside illustrating environmental alterations, concomitant directional community replacement and changing community characteristics.

In the riparian successional seres within the gently rolling terrain of upland tundra, the *Anemone-Salicetum richardsonii* (subass. *salicetosum pulchrae*) is replaced on streamsides with more progressive soil development by the *Valeriano-Salicetum pulchrae*. The latter association is found on older land surfaces with paludified, loamy, acid soils with massive ground ice and thick moss layers, resulting in cold soils, decreased depth of thaw, and increased soil moisture. However, since the overall Arctic Foothills vegetation pattern is not a simple successional sequence due to the diverse glacial history (cf. WALKER, M. D. 1995), riparian vegetation likewise has to be seen in the light of a landscape mosaic of contrasting deglaciation ages. Terminal riparian vegetation types like the *Salix pulchra*-communities seem to be connected to long-established hydrologic patterns and associated riparian ecosystem evolution along headwaters in upland tundra (up to mid-Pleistocene; cf. HAMILTON 1986), and have, thus, developed in other time scales compared to riparian communities in younger landscapes. The present-day pattern of riparian plant communities reflects a mosaic of developmental states governed by landscape age heterogeneity. Both spatial and temporal environmental heterogeneity influence this pattern.

The result of a combined control of macroscale and microscale environmental gradients on distribution, floristic differentiation and successional developments of *Salix*-communities is corroborated by comparisons with other ecological research on northern alluvial habitats. BLISS & CANTLON (1957) and BLISS & PETERSON (1992) found the same pattern of plant succession with tall *Salix alaxensis*-stands on gravel bars and floodplains and low greenleaf willow communities on higher terraces along the Colville River near Umiat. As associated with these floristic and productivity changes they stressed an increase of organic matter, a decrease in the active layer, colder and wetter soils, and decreasing direct river influence. Depending on texture of the alluvium, rate of meander migration, stream size, latitude and altitude, the successional gradient can be steep or gradual (BLISS & CANTLON 1957, p. 466). Comparable patterns have been reported from Nome and Snake Rivers (HANSON 1951), from Mackenzie River (GILL 1971), from NE-Alaskan rivers (HETTINGER & JANZ 1974), and from Meade River near Atkasook (PETERSON & BILLINGS 1978, 1980). Several further studies (e.g. SPETZMAN 1959; VIREECK et al. 1992) attributed the degeneration of tall willow stands with increasing distance to the stream channel to accumulation of organic debris, rise of permafrost table and decreasing soil temperatures. Feltleaf willow communities obviously need an ameliorated soil temperature environment. Even within *Salix alaxensis*-stands soil temperatures decrease with distance to the river. Soil temperatures in a young gravel bar stand (recorded at 50 cm depth in June) were 5–6 °C higher than in an adjacent inland decadent stand at the Sagavanirktok River (MOORE 1982). The data in GILL (1971) clearly show that soil temperatures decrease inland as soon as a certain accumulation of organic material or a moss layer provides an insulating blanket and moisture retention. As a result, the active layer decreases in thickness along the succes-

sional continuum. Regarding decreasing river influence, GILL (1971) supposed that low willows (*Salix lanata* ssp. *richardsonii*, *S. arbusculoides* in his study), succeeding *Salix alaxensis* inland, cannot withstand alluviation. They do not grow on sites which receive annual increments of alluvium, and show decreased ability to place adventitious roots.

BLISS & PETERSON (1992) point out the decrease in nutrients with time as a major factor favoring higher competitiveness of heath shrubs and low deciduous shrubs. However, in floodplain environments, early successional soils are generally lower in N and P (e.g. VAN CLEVE et al. 1996). Our data show an increase in nitrogen and phosphorus in later successional soils on higher terraces: P-concentrations nearly double (cf. Tab. 3). Nutrient availability is likely to increase because of lower mean pH levels (8.0 vs. 6.8 in our study). Results of GIBLIN et al. (1991) also show comparatively favorable nutrient supply (N, P) for *Salix lanata* ssp. *richardsonii*-stands. According to our data, the paradoxon of a decrease in productivity (standing biomass) on higher terraces with further developed soils, expressed by the replacement of tall willow by low willow shrub communities, is more a question of decreasing active layer, insulation by a thick moss layer, lower soil temperatures, lower root activity and rooting space, and higher soil moisture rather than one of enhanced competition for limited nutrients. SHAVER et al. (1996) showed along a riverside toposequence that only the combination of favorable soil fertility, soil thaw and low soil moisture warrants high productivity. Even when the outer crust of the moss layer dries in mid-summer, warming of the underlying soil is prevented due to a low thermal conductivity. High contents of silt and clay further retard thermal exchange between soil horizons compared to the coarser, drier deposits under *Salix alaxensis*. *Salix richardsonii*-stands are, thus, more tolerant of lower soil temperatures and more poorly drained soils.

Along this successional gradient, soil pH decreases whereas species richness simultaneously increases. This is remarkable, since in most tundra habitats higher soil pH is associated with higher vascular plant species richness (GOUGH et al. 2000). This holds also true along longitudinal river profiles at the landscape scale (GOULD & WALKER 1997). Under extreme environmental conditions like in floodplain and lower river terrace habitats, the number of species found, however, is limited. On upper terraces with progressive soil development the species pool increases. Other factors connected with further developed soils (higher soil moisture, nitrogen, percentage clay and silt) as well as biotic factors (vegetation structure, competition) obviously overcompensate the effect of decreasing soil pH on species richness. By contrast, riparian willow communities in upland tundra follow the general pattern of higher richness with higher pH, as far as richness of vasculars and lichens is concerned. *Salix pulchra*-stands on old land surfaces with paludified soils have lower vascular plant species and lichen richness compared to *Salix richardsonii*-communities. However, they have the comparatively highest bryophyte species richness. Bryophyte richness seems to be more positively correlated with soil moisture rather than soil pH (cf. GOULD & WALKER 1999).

Regarding the time frame of succession on river alluvium, 20–30 years are reported for early successional stages (MOORE 1982). According to BLISS & CANTLON (1957) and HETTINGER & JANZ (1974), who counted annual rings, feltleaf willow stands become decadent after 45–50 years (see also WALKER, L. R. et al. 1986 for interior Alaska), and low willow shrub communities are subsequently beginning to replace them. However, ages of willow stems are not very suitable as indicators for successional time frames, since some of the riparian willows are able to survive repeated burials by river alluvium and send up new sprouts (GILL 1971; MOORE 1982). Compared to the Subarctic, where later successional stages are dominated by poplars, spruces or other trees, willows continue to play the dominant role in arctic riparian succession throughout successional seres. Alluvial successions in the Subarctic are similarly governed by a decrease in depth of thaw, lower soil temperatures, and deteriorating drainage (e.g. BENNINGHOFF 1952; DRURY 1956; VIERECK 1970; VAN CLEVE et al. 1996)

The dependence of upland streamside communities on substrate, streamflow and disturbance regime was already intimated by WALKER, M. D. et al. (1994b), who assigned *Salix alaxensis*-*S. richardsonii*-community types to creek margins within rocky till surfaces. The distinction to *Salix pulchra*-communities on less disturbed streamsidcs of older land surfaces with loamier soils and along hillslope water tracks is in agreement with our observations in a wider region. Our consideration of *Salix pulchra*-communities as terminal riparian vegetation types contrasts with the general conception that willows characterize labile, earliest successional stages and become less and less important as vegetational succession continues. Our view is corroborated e.g. by BLISS & CANTLON (1957), who found the most poorly drained, less disturbed sites, most inland along a transect from the Colville River, covered with *Salix pulchra* intergrading into wet tundra meadows (see also CHURCHILL 1955). JOHNSON et al. (1966) described *Salix pulchra* as the dominant willow in later successional stages on infrequently flooded terraces of Ogotoruk Creek (Cape Thompson region). ARGUS (1973) studied a transect from the sandy-gravel floodplain of a creek to the upper terrace in the Cape Beaufort area, where *Salix pulchra* dominated the relatively stable vegetation on the uppermost terrace with minimal disturbance and siltation, and poor drainage. HETTINGER & JANZ (1974) considered the wet sedge-low willow shrub (*Salix pulchra*) community the end point of riparian successional trends at lower elevations in the southern Brooks Range.

With regard to the classification of riparian plant communities in arctic Alaska, the Braun-Blanquet approach used in this study proved to be an appropriate analytical tool to define vegetation types based on accurate floristic information, supported by correlations of relevé groups with environmental variables via DCA ordination. As a result, we define associations on a floristic **and** ecological basis. As already stressed by KOMÁRKOVÁ (1993), the Braun-Blanquet approach is an effective method to delimit and classify arctic vegetation types despite of its relatively high number and allegedly poor definition. Our results give evidence that a clear delimitation

and description of types for North American arctic vegetation is possible. Previous phytosociological/vegetation ecological studies already came up with delimitations of arctic riparian vegetation types, that partially show remarkable correspondences to the above defined associations in terms of floristic structure and synecological characteristics. GOULD (1998) described an *Epilobium latifolium-Salicetum alaxensis*-community from the Hood River, Northwest Territories, Canada, as a common pioneer community of gravel bars and active floodplains, disturbed by flooding and ice-scouring. GOULD's data show numerous floristic and synecological correspondences (see also BLISS & CANTLON 1957, DREW & SHANKS 1965, GILL 1971, HETTINGER & JANZ 1974, MOORE 1982 for further *Salix alaxensis*-communities in the region). Similar vegetation types are also found in mountainous environments, exemplified by COOPER's (1986) description of the *Elymo innovatis-Salicetum alaxensis*, best developed on broad, gentle alluvial fans of limestone sands in the central Brooks Range. A specific set of species assemblages (e.g. *Salix alaxensis*, *Aster sibiricus*, *Shepherdia canadensis*, *Hedysarum alpinum* ssp. *americanum*, *Castilleja caudata*, *Zygadenus elegans* a.o.) can even be found on floodplains of interior Alaska (cf. FARJON & BOGAERS 1985).

Previous descriptions of low willow shrub communities also show more or less corresponding findings regarding the above defined associations. GOULD (1998) described *Salix niphoclada-Hedysarum mackenzii* and *Equisetum arvense-Salix lanata* ssp. *richardsonii*-communities from protected river banks above the floodplain of the Hood River, resembling the *Anemone-Salicetum richardsonii* of our study. They occur on neutral to basic to basic/cation-rich substrates, i.e. in comparable habitats, regardless that mean soil pH is higher compared to this study (7.2 and 7.6 vs. 6.8). This suggests that the succession model with *Salix alaxensis*-communities on floodplains and lower terraces to *Salix lanata* ssp. *richardsonii*-communities on higher terraces is valid in a wider region of the North American Arctic. *Salix niphoclada*, taxonomically closely related to and presumably hybridizing with *Salix glauca* (ARGUS 1973), forms communities, which are synecologically (cf. GOULD 1998) closely related to *Salix lanata* ssp. *richardsonii*-communities and which might be vicariant in this successional seres. Floristically similar *Salix richardsonii*-communities have been reported in northern alluvial habitats e.g. by BLISS & CANTLON (1957), GILL (1971), CORNS (1974).

Salix pulchra-dominated riparian communities are not restricted to smaller tundra streams and creeks. WALKER, M. D. et al. (1994b) and WALKER, D. A. & M. D. WALKER (1996) described a related *Salix pulchra*-shrub community (*Eriophorum angustifolium-Salix pulchra*-community) along channels of better developed hillslope water tracks in upland tundra with similar floristic composition. Further studies have to show syntaxonomical relationships in detail. Similar community types were also described by LAMBERT (1968) and HETTINGER & JANZ (1974).

The above described correspondences and floristic similarities of willow communities in a wider region underline supraregional and point to cir-

cumpolar relationships of arctic community organization, that applies in particular to azonal habitats. KOMÁRKOVÁ (1981) already mentioned riverbank and riverbar vegetation in this respect. Moreover, Alaskan riparian *Salix*-associations show in many respects affinities to other Arctic riparian *Salix*-communities beyond North America so that it seems possible to assign them to existing higher syntaxonomic units of the Braun-Blanquet system. In terms of physiognomy and synecology, our associations largely correspond to alluvial shrub communities described from northern Eurasia (e.g. MØLHOLM HANSEN 1930; NORDHAGEN 1943; SECRETAREVA 1979; KLOKK 1981; KOZHEVNIKOV 1989; DIERSSEN 1996). Moreover, as azonal vegetation types, these riparian shrub communities show close similarities with regard to floristics, even in a circumpolar perspective. Therefore, we propose an integration of our associations into the existing Braun-Blanquet classification scheme based primarily on phytosociological work in Scandinavia and Greenland.

In view of the existing classification scheme of willow shrub and forest vegetation on river alluvium in northern Europe (class Salicetea purpureae; cf. Tab. 19 in DIERSSEN 1996), it is obvious that the North Alaskan riparian willow associations can be added to the order Salicetalia purpureae. Within this order, they show strongest similarities to boreal-(montane-alpine)-arctic riparian willow communities, which are integrated into the alliance Salicion phylicifoliae. The associations of this alliance are characterized floristically by taxa with more or less closed circumpolar distribution like *Salix glauca*, *S. hastata*, *S. lanata*, *S. lapponum*, and *S. phylicifolia*. Mainly distributed in alluvial pioneer habitats of middle and northern boreal regions, their range extends into the southern Arctic and upslope to the lower alpine belt. They typically occupy headwater streamsides and creek margins as well as geomorphologically active river deltas with strong water currents and water table fluctuations (DIERSSEN 1996).

On older land surfaces with gentle topography these willow communities (composed of the same species) occur in moist colluvial basins, fens and peaty valley bottoms along creek margins, often interspersed with tall herb stands. Therefore, geobotanists working in those landscapes mostly assigned these willow communities to the classes Betulo-Adenostyletea or Scheuchzerio-Caricetea nigrae, as we also tentatively did, when we tried to assign riparian communities of Toolik Lake and Innvait Creek region/Alaska or Hood River/Canada (cf. WALKER, M. D. et al. 1994b; GOULD & WALKER 1999; see also DANIÉLS 1982 for *Salix callicarpaea*-communities in SE-Greenland). However, when considering the appearance of riparian willow communities over a wide range of circumpolar riverine habitats, the affinities to alluvial associations of the Salicion phylicifoliae with regard to physiognomy, ecology, and floristics are more pronounced. We follow DIERSSEN (1996) to include those associations (e.g. the Filipendulo-Salicetum phylicifoliae described by NORDHAGEN 1943, which is e.g. additionally dominated by *Salix lanata* and *S. glauca* ssp. *callicarpaea* on Iceland; DIERSSEN 1996) into the Salicion phylicifoliae and Salicetea purpureae respectively. *Salix callicarpaea*-communities in Green-

land may also be assigned to the *Salicetea purpureae*, as indicated by DANIELS et al. (2000). Comparing structural, floristic and ecological characteristics, stronger affinities do exist to other alluvial willow associations of the *Salicetea purpureae* (including those of montane/subalpine belts of the temperate zone) rather than to open woodland, shrub, tall herb or fen communities of the classes *Betulo-Adenostyletea* or *Scheuchzerio-Caricetea nigrae*. We therefore propose to extend the range of the *Salicetea purpureae* to the North American Arctic.

The Braun-Blanquet approach bears the potential for a common framework to accommodate vegetation units of the entire Arctic that often show strong floristic similarities in similar habitats throughout the circumpolar region (WALKER, M. D. et al. 1994b), especially at higher taxonomic levels. The floristic ties between Scandinavia, the Russian Arctic, Greenland and Beringia are strong enough to make an application of hitherto described vegetation units or modifications of them to Alaska possible. Further extending the existing vegetation classification of Eurasia and Greenland to the North American Arctic, a comprehensive and manageable circumpolar system could be established that avoids an inflation of regional community types not fitting into supraregional classifications (e.g., 17 *Salix alaxensis*-community types and a total of 888 community types were listed only for Alaska by VIERECK et al. 1992). By extending the results of regional vegetation studies to the entire arctic biome on a common classification platform we would also come closer to a circumpolar ecological synthesis of arctic vegetation since floristic similarities or variations of (vicariant) syntaxa represent to a great extent synecological affinities or deviations.

6 Conclusions

Combining phytosociological and gradient analyses, i.e. using classification and ordination of arctic riparian plant communities as complementary procedures, a wealth of information on floristic-sociological structure and environmental relationships of floristically defined vegetation types can be inferred. To reveal differentiations in arctic vegetation cover, whose vegetation types are often hardly distinguishable at first sight, the above described combined procedure is recommended. It combines advantages of major approaches in vegetation science seeking to explore maximum vegetation ecological relationships, whereas at the same time contributing to a common framework of arctic vegetation and ecosystem studies. A major implication of our results is the possibility to use *Salix*-communities as indicators for riparian habitat characteristics and landscape evolution.

The above vegetation ecological analyses and formal descriptions of associations and subassociations form a further step in taxonomical and synecological research on the North Slope of Alaska. Conducted on the only easily accessible gradient from the Brooks Range to the Arctic Ocean, it would be of high scientific interest to extend the scope of this study to other regions north of the Brooks Range and to subject the above findings to supraregional comparisons. We agree with MATVEYEVA (1994) and de-

mand to first publish more data on lower units of syntaxa (i.e. associations, subassociations, vicariants, variants) before definitely assigning them to existing higher units or to introduce new higher-level units within the taxonomical hierarchy in a circumpolar perspective. Considering the need for arctic ecosystem studies in view of rapid environmental changes (e.g. climate warming, pollution from various sources, etc.), the completion of a circumpolar phytosociological/ecological synthesis of arctic vegetation should be a top priority on the arctic research agenda.

Acknowledgements: This research was supported by the Max Kade Foundation grant KADE-OCG 3088 to U. SCHICKHOFF, by the U. S. National Science Foundation grant OPP-9400083 to M. D. WALKER, and by the U. S. National Science Foundation grant 9908829 to D. A. WALKER. We are grateful to R. ANDRUS, Binghamton, NY, for identifying *Sphagnum*-mosses, and to W. A. WEBER, Boulder, CO, for identifying all other bryophytes. We thank F. J. A. DANIELS and J. OKSANEN for their valuable comments on a previous version of this paper.

References

- Argus, G. W. (1973): The Genus *Salix* in Alaska and the Yukon. – National Museum of Natural Sciences Publ. in Botany, No. 2, Ottawa.
- Barrett, P. E. (1972): Phytogeocoenoses of a coastal lowland ecosystem, Devon Island, N. W. T. – Ph.D. thesis, University of British Columbia, Vancouver.
- Batten, A. R. (1977): The vascular floristics, major vegetation units, and phytogeography of the Lake Peters area, northeastern Alaska. – M.Sc. thesis, University of Alaska, Fairbanks.
- Benninghoff, W. S. (1952): Interaction of vegetation and soil frost phenomena. – *Arctic* 5: 34–44.
- Billings, W. D. (1997a): Introduction: challenges for the future: arctic and alpine ecosystems in a changing world. – In: Oechel, W. C., Callaghan, T., Gilmanov, T., Holten, J. I., Maxwell, B., Molau, U. & B. Sveinbjörnsson (eds.): *Global Change and Arctic Terrestrial Ecosystems*, pp. 1–18. – Springer, New York.
- (1997b): Arctic phytogeography: plant diversity, floristic richness, migrations, and acclimation to changing climates. – In: Crawford, R. M. M. (ed.): *Disturbance and Recovery in Arctic Lands*, pp. 25–45. – Kluwer, Dordrecht.
- Binkley, D., Suarez, F., Stottlemyer, R. & B. Caldwell (1997): Ecosystem development on terraces along the Kugururok River, northwest Alaska. – *Ecoscience* 4: 311–318.
- Bliss, L. C. (2000): Arctic tundra and polar desert biome. – In: Barbour, M. G. & W. D. Billings (eds.): *North American Terrestrial Vegetation*, 2nd ed., pp. 1–40. – Cambridge University Press, Cambridge–New York.
- Bliss, L. C. & J. E. Cantlon (1957): Succession on river alluvium in northern Alaska. – *Am. Midl. Nat.* 52: 452–469.
- Bliss, L. C. & N. V. Matveyeva (1992): Circumpolar arctic vegetation. – In: Chapin, F. S. III, Jefferies, R. L., Reynolds, J. F., Shaver, G. R., Svoboda, J. & E. W. Chu (eds.): *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*, pp. 59–89. – Academic Press, San Diego, CA.
- Bliss, L. C. & K. M. Peterson (1992): Plant succession, competition, and the physiological constraints of species in the Arctic. – In: Chapin, F. S. III, Jefferies, R. L., Reynolds, J. F., Shaver, G. R., Svoboda, J. & E. W. Chu (eds.): *Arctic Ecosystems in a Changing*

- Climate: An Ecophysiological Perspective, pp. 111–136. – Academic Press, San Diego, CA.
- Bockheim, J. G., Ping, C. L., Moore, J. P. & J. M. Kimble (1994): Gelisols: a new proposed order for permafrost-affected soils. – In: Kimble, J. M. & R. Ahrens (eds.): Proceedings of the Meeting on the Classification, Correlation, and Management of Permafrost-Affected Soils – July 1994, pp. 25–44. USDA, Soil Conservation Service, National Soil Survey Center, Lincoln, NE.
- Bockheim, J. G., Walker, D. A., Everett, L. R., Nelson, F. E. & N. I. Shiklomanov (1998): Soils and cryoturbation in moist nonacidic and acidic tundra in the Kuparuk river basin, Arctic Alaska, U. S. A. – *Arct. Alp. Res.* **30**: 166–174.
- Braun-Blanquet, J. (1964): Pflanzensociologie. – 3. Aufl., Springer, Wien.
- Braune, B. & 20 coll. (1999): Spatial and temporal trends of contaminants in Canadian Arctic freshwater and terrestrial ecosystems: a review. – *The Science of the Total Environment* **230**: 145–207.
- Britton, M. E. (1967): Vegetation of the arctic tundra. – In: Hansen, H. P. (ed.): Arctic Biology, pp. 67–130. – Oregon State Univ. Press, Corvallis, OR.
- Cantlon, J. E. (1961): Plant cover in relation to macro-, meso-, and micro-relief. – Final Report, Grants No. ONR-208 a. **216**, Office of Naval Research, Washington.
- Chernov, Y. I. & N. V. Matveyeva (1997): Arctic ecosystems in Russia. – In: Wielgolaski, F. E. (ed.): Ecosystems of the World, Vol. 3: Polar and Alpine Tundra, pp. 361–507. – Elsevier, Amsterdam.
- Churchill, E. D. (1955): Phytosociological and environmental characteristics of some plant communities in the Umiat region of Alaska. – *Ecology* **36**: 606–627.
- Cody, W. J. (1996): Flora of the Yukon Territory. – NRC Research Press, Ottawa.
- Cooper, D. J. (1986): Arctic-alpine tundra vegetation of the Arrigetch Creek valley, Brooks Range, Alaska. – *Phytocoenologia* **14**: 467–555.
- Corns, I. G. W. (1974): Arctic plant communities east of the Mackenzie Delta. – *Can. J. Bot.* **52**: 1731–1745.
- Craig, P. C. & P. J. McCart (1975): Classification of stream types in Beaufort Sea drainages between Prudhoe Bay, Alaska, and the Mackenzie Delta, N. W. T., Canada. – *Arct. Alp. Res.* **7**: 183–198.
- Daniëls, F. J. A. (1982): Vegetation of the Angmagssalik District, Southeast Greenland, IV. Shrub, dwarf shrub and terricolous lichens. – *Meddelelser om Grønland, Bioscience* **10**. Copenhagen.
- (1997): Braun-Blanquet syntaxa and their importance for the legend of a circumpolar arctic vegetation map. – In: Walker, D. A. & A. C. Lillie (eds.): Proceedings of the Second Circumpolar Arctic Vegetation Mapping Workshop, Arendal, Norway, 19–24 May 1996 and the CAVM-North America Workshop, Anchorage, Alaska, US, 14–16 January 1997, pp. 15–17. – Occasional Pap. No. 52, Inst. of Arctic and Alpine Research, University of Colorado, Boulder.
- Daniëls, F. J. A., Bültmann, H., Lünterbusch, C. & M. Wilhelm (2000): Vegetation zones and biodiversity of the North-American Arctic. – *Ber. d. Reinh.-Tüxen-Ges.* **12**: 131–151.
- Densmore, R. V., Neiland, B. J., Zasada, J. C. & M. A. Masters (1987): Planting willow for moose habitat restoration on the North Slope of Alaska, U. S. A. – *Arct. Alp. Res.* **19**: 537–543.
- Dierschke, H. (1994): Pflanzensociologie. – Ulmer, Stuttgart.
- Dierssen, K. (1996): Vegetation Nordeuropas. – Ulmer, Stuttgart.
- Drew, J. V. & R. E. Shanks (1965): Landscape relationships of soils and vegetation in the forest-tundra ecotone, upper Firth River valley, Alaska-Canada. – *Ecol. Monogr.* **35**: 285–306.

- Drury, W. H. (1956): Bog flats and physiographic processes in the upper Kuskokwim River region, Alaska. – *Contr. Gray Herb. No. 178*, Harvard University.
- Ebersole, J. J. (1985): Vegetation disturbance and recovery at the Oumalik oil well, arctic coastal plain, Alaska. – Ph.D.-Thesis, University of Colorado at Boulder.
- Ellenberg, H. (1956): *Grundlagen der Vegetationsgliederung. Aufgaben und Methoden der Vegetationskunde.* – Ulmer, Stuttgart.
- Elvebakk, A. (1982): Geological preferences among Svalbard plants. – *Inter-Nord 16*: 11–31.
- Elvebakk, A., Elven, R. & V. Y. Razzhivin (1999): Delimitation, zonal and sectorial subdivision for the Panarctic Flora Project. – *Det Norske Videnskaps-Akademi. I. Mat.-Naturv. Klasse Skrifter Ny Serie 38*: 375–386.
- Epstein, H. E., Walker, M. D., Chapin III, F. S. & A. M. Starfield (2000): A transient, nutrient-based model of arctic plant community response to climatic warming. – *Ecol. Appl. 10*: 824–841.
- Everett, K. R., Kane, D. L. & L. D. Hinzman (1996): Surface water chemistry and hydrology of a small arctic drainage basin. – In: Reynolds, J. F. & J. D. Tenhunen (eds.): *Landscape Function and Disturbance in Arctic Tundra*, pp. 185–201. – Springer, Berlin–Heidelberg.
- Farjon, A. & P. Bogaers (1985): Vegetation zonation and primary succession along the Porcupine River in interior Alaska. – *Phytocoenologia 13*: 465–504.
- Fitzharris, B. B. & coll. (1996): The cryosphere: changes and their impacts. – In: Watson, R. T., Zinyowera, M. C. & R. H. Moss (eds.): *Climate Change 1995. Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses*, pp. 241–265. – Cambridge University Press, Cambridge.
- Gallant, A. F., Binnian, E. F., Omernik, J. M. & M. B. Shasby (1995): *Ecoregions of Alaska.* – U. S. Geol. Surv. Prof. Pap. 1567. Govt. Printing Office, Washington.
- Giblin, A. E., Nadelhoffer, K. J., Shaver, G. R., Laundre, J. A. & A. J. McKerrrow (1991): Biogeochemical diversity along a riverside toposequence in arctic Alaska. – *Ecol. Monogr. 61*: 415–435.
- Gill, D. (1971): Vegetation and environment in the Mackenzie River Delta, Northwest Territories. – Ph.D.-Thesis, University of British Columbia, Vancouver.
- Glavac, V. (1996): *Vegetationsökologie.* – Fischer, Stuttgart.
- Gough, L., Shaver, G. R., Carroll, J., Royer, D. L. & J. A. Laundre (2000): Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. – *J. Ecol. 88*: 54–66.
- Gould, W. A. (1998): A multiple-scale analysis of plant species richness, vegetation, landscape, and spectral diversity along an arctic river. – Ph.D.-Thesis, University of Colorado at Boulder.
- Gould, W. A. & M. D. Walker (1997): Landscape-scale patterns in plant species richness along an arctic river. – *Can. J. Bot. 75*: 1748–1765.
- (1999): Plant communities and landscape diversity along a Canadian Arctic river. – *J. Veg. Sci. 10*: 537–548.
- Hansell, R. I. C., Malcolm, J. R., Welch, H., Jefferies, R. L. & P. A. Scott (1998): Atmospheric change and biodiversity in the Arctic. – *Environmental Monitoring and Assessment 49*: 303–325.
- Hanson, H. C. (1951): Characteristics of some grassland, marsh, and other plant communities in western Alaska. – *Ecol. Monogr. 21*: 317–378.
- (1953): Vegetation types in northwestern Alaska and comparisons with communities in other arctic regions. – *Ecology 34*: 111–140.
- Haugen, R. K. (1982): Climate of remote areas in north-central Alaska. 1975–1979 summary. – *CRREL Rep. 82–35*. U. S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH.

- Hettinger, L. R. & A. J. Janz (1974): Vegetation and soils of northeastern Alaska. – Arctic Gas Biol. Rep. Ser. Vol. 21, Canadian Arctic Gas Studies Ltd., Calgary, Alberta.
- Hopkins, D. M., Matthews, J. V., Schweger, C. E. & S. B. Young (eds.)(1982): Paleocology of Beringia. – Academic Press, New York.
- Hughes, F. M. R. (1997): Floodplain biogeomorphology. – *Progr. Phys. Geogr.* 21: 501–529.
- Hultén, E. (1968): Flora of Alaska and Neighboring Territories. A Manual of the Vascular Plants. – Stanford University Press, Stanford, CA.
- Johnson, A. W., Viereck, L. A., Johnson, R. E. & H. Melchior (1966): Vegetation and flora of the Cape Thompson-Ogotoruk Creek area, Alaska. – In: Wilimovsky, J. J. & J. N. Wolfe (eds.): Environments in the Cape Thompson Region, Alaska, pp. 277–354. – U. S. Atomic Energy Comm., Washington, DC.
- Kane, D. L., Hinzman, L. D., Benson, C. S. & K. R. Everett (1989): Hydrology of Imnavait Creek, an arctic watershed. – *Holarct. Ecol.* 12: 262–269.
- Kling, G. W., O'Brien, W. J., Miller, M. C. & A. E. Hershey (1992): The biogeochemistry and zoogeography of lakes and rivers in arctic Alaska. – *Hydrobiologia* 240: 1–14.
- Klokk, T. (1981): Classification and ordination of river bank vegetation from middle and upper parts of the River Gaula, Central Norway. – *K. Norske Vidensk. Selsk. Skr.* 2: 1–43.
- Komárková, V. (1981): Holarctic alpine and arctic vegetation: circumpolar relationships and floristic-sociological, high-level units. – In: Dierschke, H. (Red.): Syntaxonomie. Ber. Int. Symp. d. Int. Ver. f. Veg.-kde, S. 451–476. – Cramer, Vaduz.
- (1993): Vegetation type hierarchies and landform disturbance in arctic Alaska and alpine Colorado with emphasis on snowpatches. – *Vegetatio* 106: 155–181.
- Komárková, V. & J. D. McKendrick (1988): Patterns in vascular plant growth forms in arctic communities and environment at Atkasook, Alaska. – In: Werger, M. J. A., van der Aart, P. J. M., During, H. J. & J. T. A. Verhoeven (eds.): Plant Form and Vegetation Structure, pp. 45–70. – SPB Acad. Publ., The Hague.
- Komárková, V. & P. J. Webber (1980): Two low arctic vegetation maps near Atkasook, Alaska. – *Arct. Alp. Res.* 12: 447–472.
- Koranda, J. J. (1960): The plant ecology of the Franklin Bluffs area, Alaska. – Ph.D. thesis, University of Tennessee, Knoxville.
- Kozhevnikov, Y. P. (1989): Geography of Vegetation of Chukotka. – Nauka, Leningrad. (in russ.)
- Lambert, J. D. H. (1968): The ecology and successional trends in the Low Arctic subalpine zone of the Richardson and British Mountains of the Canadian western Arctic. – Ph.D. thesis, University of British Columbia, Vancouver.
- Lünterbusch, C., Bültmann, H. & F. J. A. Daniëls (1997): Eine pflanzensoziologische Übersicht der *Oxyria digyna*- und *Chamaenerion latifolium*-Vegetation im küstennahen Bereich Südostgrönlands. – *Polarforschung* 65: 71–82.
- Malanson, G. P. (1993): Riparian Landscapes. – Cambridge University Press, Cambridge.
- Marion, G. M., Hastings, S. J., Oberbauer, S. F. & W. C. Oechel (1989): Soil-plant element relationships in a tundra ecosystem. – *Holarctic Ecology* 12: 296–303.
- Matveyeva, N. V. (1994): Floristic classification and ecology of tundra vegetation of the Taymyr Peninsula, northern Siberia. – *J. Veg. Sci.* 5: 813–828.
- (1998): Zonation in Plant Cover of the Arctic. – Proceedings of the Komarov Botanical Institute, Issue 21: 1–219. Russian Academy of Sciences.
- Maxwell, B. (1997): Recent climate patterns in the Arctic. – In: Oechel, W. C., Callaghan, T., Gilmanov, T., Holten, J. I., Maxwell, B., Molau, U. & B. Sveinbjörnsson (eds.): Global Change and Arctic Terrestrial Ecosystems, pp. 21–46. – Springer, New York.

- McCune, B. & M. J. Mefford (1997): PC-ORD. Multivariate Analysis of Ecological Data, Version 3.0. – MjM Software Design, Glenden Beach, Oregon.
- Møllholm Hansen, H. (1930): Studies on the vegetation of Iceland. – In: Kolderup Rosvinge, L. & E. Warming (eds.): *The Botany of Iceland* 3 (1), pp. 1–186. – Copenhagen.
- Moore, N. J. (1982): Pioneer *Salix alaxensis* communities along the Sagavanirktok River and adjacent drainages. – M.Sc. thesis, University of Alaska, Fairbanks.
- Mould, E. D. (1977): Movement patterns of moose in the Colville River area, Alaska. – M.Sc.-Thesis, University of Alaska, Fairbanks.
- Mueller-Dombois, D. & H. Ellenberg (1974): *Aims and Methods of Vegetation Ecology*. – Wiley & Sons, New York.
- Muller, S. V., Walker, D. A., Nelson, F., Auerbach, N. A., Bockheim, J., Guyer, S. & D. Sherba (1998): Accuracy assessment of a land-cover map of the Kuparuk river basin, Alaska: considerations for remote regions. – *Photogrammetric Engineering and Remote Sensing* 64: 619–628.
- Murray, D. F. (1992): Vascular plant diversity in Alaskan arctic tundra. – *Northwest Environ. J.* 8: 29–52.
- (1995): Causes of arctic plant diversity: origin and evolution. – In: Chapin III, F. S. & C. Körner (eds.): *Arctic and Alpine Biodiversity: Patterns, Causes and Consequences*, pp. 21–32. – Springer, New York.
- Naiman, R. J., Décamps, H. & M. Pollock (1993): The role of riparian corridors in maintaining regional biodiversity. – *Ecol. Appl.* 3: 209–212.
- Nelson, F. E., Shiklomanov, N. I., Mueller, G. R., Hinkel, K. M., Walker, D. A. & J. G. Bockheim (1997): Estimating active-layer thickness over a large region: Kuparuk River basin, Alaska, U. S. A. – *Arct. Alp. Res.* 29: 367–378.
- Nordhagen, R. (1943): *Sikilsdalen og Norges fjellbeiter*. En plantensosiologisk monografi. – Bergens Mus. Skr. 22, Bergen.
- Odasz, A. M. (1983): Vegetation patterns at the treelimit ecotone in the upper Alatna River drainage of the Central Brooks Range, Alaska. – Ph.D. thesis, University of Colorado, Boulder.
- Oechel, W. C., Cook, A. C., Hastings, S. J. & G. L. Vourlitis (1997): Effects of CO₂ and climate change on arctic ecosystems. – In: Woodin, S. J. & M. Marquiss (eds.): *Ecology of Arctic Environments*, pp. 255–273. – Blackwell Science, Oxford.
- Økland, R. H. (1996): Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? – *J. Veg. Sci.* 7: 289–292.
- Oswood, M. W. (1997): Streams and rivers of Alaska: a high latitude perspective on running waters. – In: Milner, A. M. & M. W. Oswood (eds.): *Freshwaters of Alaska*. Ecological Syntheses, pp. 331–356. – Springer, New York.
- Oswood, M. W., Milner, A. M. & J. G. Irons III (1992): Climate change and Alaskan rivers and streams. – In: Firth, P. & S. G. Fisher (eds.): *Global Climate Change and Freshwater Ecosystems*, pp. 192–210. – Springer, New York.
- Peterson, K. M. & W. D. Billings (1978): Geomorphic processes and vegetational change along the Meade River sand bluffs in northern Alaska. – *Arctic* 31: 7–23.
- (1980): Tundra vegetational patterns and succession in relation to microtopography near Atkasook, Alaska. – *Arct. Alp. Res.* 12: 473–482.
- Racine, C. H. (1976): Flora and vegetation. – In: Melchior, H. R. (ed.): *Biological Survey of the Proposed Kobuk Valley National Monument*, pp. 39–139. – University of Alaska, Fairbanks.
- Racine, C. H. & J. H. Anderson (1979): Flora and vegetation of the Chukchi-Imuruk area. – In: Melchior, H. R. (ed.): *Biological Survey of the Bering Land Bridge National Monument*, pp. 38–113. – University of Alaska, Fairbanks.

- Reynolds, J. F. & J. D. Tenhunen (1996): Ecosystem response, resistance, resilience, and recovery in arctic landscapes: Introduction. – In: Reynolds, J. F. & J. D. Tenhunen (eds.): *Landscape Function and Disturbance in Arctic Tundra*, pp. 3–18. – Springer, Berlin–Heidelberg.
- Schlichting, E., Blume, H. P. & K. Stahr (1995): *Bodenkundliches Praktikum*. – 2. Aufl., Blackwell, Berlin–Wien.
- Secretareva, A. (1979): Willow shrub communities in the east of Chukotka Peninsula. – *Bot. Zh.* **64**: 957–970.
- Shaver, G. R. & F. S. Chapin III (1991): Production:biomass relationships and element cycling in contrasting arctic vegetation types. – *Ecol. Monogr.* **61**: 1–31.
- Shaver, G. R., Laundre, J. A., A. E. Giblin & K. J. Nadelhoffer (1996): Changes in live plant biomass, primary production, and species composition along a riverside toposequence in arctic Alaska, U. S. A. – *Arct. Alp. Res.* **28**: 363–379.
- Spetzman, L. A. (1959): *Vegetation of the Arctic Slope of Alaska*. – U. S. Geol. Surv. Prof. Pap. **302-B**. Govt. Printing Office, Washington.
- Steere, W. C. (1978): *The Mosses of Arctic Alaska*. – *Bryophytorum Biblioth.* **14**. Cramer, Vaduz.
- Steere, W. C. & H. Inoue (1978): *The Hepaticae of Arctic Alaska*. – *J. Hattori Bot. Lab.* **44**: 251–345.
- Tedrow, J. C. F. (1977): *Soils of the Polar Landscapes*. – Rutgers University Press, New Brunswick, NJ.
- Thannheiser, D. (1984): *The coastal vegetation of eastern Canada*. – Memorial University of Newfoundland, *Occasional Papers in Biology* **8**: 1–212.
- (1987): *Die Vegetationszonen in der westlichen kanadischen Arktis*. – *Hamburger Geogr. Stud.* **43**: 159–177.
- Thannheiser, D. & K. P. Hellfritz (1989): *Die Vegetation der Salzwiesen auf den Queen Charlotte Islands (Westkanada)*. – *Essener Geogr. Arb.* **17**: 153–175.
- Thannheiser, D. & T. Willers (1988): *Die Pflanzengesellschaften der Salzwiesen in der westlichen kanadischen Arktis*. – *Hamburger Geogr. Stud.* **44**: 207–222.
- Thomson, J. W. (1979): *Lichens of the Alaskan Arctic Slope*. – University of Toronto Press, Toronto.
- (1984): *American Arctic Lichens. I. The Macrolichens*. – Columbia University Press, New York.
- Van Cleve, K., Viereck, L. A. & C. T. Dyrness (1996): *State factor control of soils and forest succession along the Tanana River in interior Alaska, U. S. A.* – *Arct. Alp. Res.* **28**: 388–400.
- Viereck, L. A. (1970): *Forest succession and soil development adjacent to the Chena River in interior Alaska*. – *Arct. Alp. Res.* **2**: 1–26.
- Viereck, L. A., Dyrness, C. T., Batten, A. R. & K. J. Wenzlick (1992): *The Alaska vegetation classification*. – USDA Forest Service, Pacific Northwest Research Station, Gen. Techn. Rep. **286**. Portland, OR.
- Walker, D. A. (1985): *Vegetation and environmental gradients of the Prudhoe Bay region*. – CRREL Rep. **85-14**. U. S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH.
- (1987): *Height and growth-ring response of Salix lanata ssp. richardsonii along the coastal temperature gradient of northern Alaska*. – *Can. J. Bot.* **65**: 988–993.
- (1995): *Toward a new circumpolar arctic vegetation map: St. Petersburg Workshop*. – *Arct. Alp. Res.* **31**: 169–178.
- (1996): *Disturbance and recovery of Arctic Alaskan vegetation*. – In: Reynolds, J. F. & J. D. Tenhunen (eds.): *Landscape Function and Disturbance in Arctic Tundra*, pp. 35–71. – Springer, Berlin–Heidelberg.

- (1997): Arctic Alaskan vegetation disturbance and recovery. – In: Crawford, R. M. M. (ed.): *Disturbance and Recovery in Arctic Lands*, pp. 457–479. – Kluwer, Dordrecht.
- (2000): Hierarchical subdivision of arctic tundra based on vegetation response to climate, parent material, and topography. – *Global Change Biology* **6**: 19–34.
- Walker, D. A. & W. Acevedo (1987): Vegetation and a landsat-derived land cover map of the Beechey Point Quadrangle, Arctic Coastal Plain, Alaska. – CRREL Rep. **87-5**, U. S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH.
- Walker, D. A. & A. C. Lillie (eds.) (1997): Proceedings of the Second Circumpolar Arctic Vegetation Mapping Workshop, Arendal, Norway, 19–24 May 1996 and the CAVM-North America Workshop, Anchorage, Alaska, US, 14–16 January 1997. – Occasional Pap. No. **52**, Inst. of Arctic and Alpine Research, University of Colorado, Boulder.
- Walker, D. A. & M. D. Walker (1996): Terrain and vegetation of the Innavait Creek watershed. – In: Reynolds, J. F. & J. D. Tenhunen (eds.): *Landscape Function and Disturbance in Arctic Tundra*, pp. 73–108. – Springer, Berlin–Heidelberg.
- Walker, D. A., Everett, K. R., Acevedo, W., Gaydos, L., Brown, J. & P. J. Webber (1982): Landsat-assisted environmental mapping in the Arctic National Wildlife Refuge, Alaska. – CRREL Rep. **82-37**, U. S. Army Cold Regions Research and Engineering Laboratory, Hanover, NH.
- Walker, D. A., Webber, P. J., Binnian, E. F., Everett, K. R., Lederer, N. D., Nordstrand, E. A. & M. D. Walker (1987): Cumulative impacts of oil-fields on northern Alaskan landscapes. – *Science* **238**: 757–761.
- Walker, D. A., Binnian, E. F., Evans, B. M., Lederer, N. D., Nordstrand, E. & P. J. Webber (1989): Terrain, vegetation and landscape evolution of the R4D research site, Brooks Range Foothills, Alaska. – *Holarct. Ecol.* **12**: 238–261.
- Walker, D. A., Bay, C., Daniels, F. J. A., Einarsson, E., Elvebakk, A., Johansen, B. E., Kapitsa, A., Kholod, S. S., Murray, D. F., Talbot, S. S., Yurtsev, B. & S. C. Zoltai (1995): Toward a new arctic vegetation map: review of existing maps. – *J. Veg. Sci.* **6**: 427–436.
- Walker, L. R., Zasada, J. C. & F. S. Chapin III (1986): The role of life history processes in primary succession on an Alaskan floodplain. – *Ecology* **67**: 1243–1253.
- Walker, M. D. (1995): Patterns and causes of arctic plant community diversity. – In: Chapin III, F. S. & C. Körner (eds.): *Arctic and Alpine Biodiversity: Patterns, Causes and Consequences*, pp. 3–20. – Springer, New York.
- Walker, M. D., Daniëls, F. J. A. & E. van der Maarel (1994a): Circumpolar arctic vegetation: introduction and perspectives. – *J. Veg. Sci.* **5**: 758–764.
- Walker, M. D., Walker, D. A. & N. A. Auerbach (1994b): Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. – *J. Veg. Sci.* **5**: 843–866.
- Walker, M. D., Walker, D. A. & K. R. Everett (1989): Wetland Soils and Vegetation, Arctic Foothills, Alaska. – U. S. Fish Wildl. Serv. Biol. Rep. **89(7)**, Washington, DC.
- Ward, J. V. (1998): Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. – *Biol. Conserv.* **83**: 269–278.
- Webber, P. J., Miller, P. C., Chapin III, F. S. & B. H. McCown (1980): The vegetation: pattern and succession. – In: Brown, J., Miller, P. C., Tieszen, L. L. & F. L. Bunnell (eds.): *An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska*, pp. 186–218. – Dowden, Hutchinson & Ross, Stroudsburg, PA.
- Weber, H. E., Moravec, J. & J. P. Theurillat (2000): *International Code of Phytosociological Nomenclature*. 3rd edition. – *J. Veg. Sci.* **11**: 739–768.
- White, R. G. & J. Trudell (1980): Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. – *Arct. Alp. Res.* **12**: 511–529.
- Wiggins, I. L. & J. H. Thomas (1962): *A Flora of the Alaskan Arctic Slope*. – University of Toronto Press, Toronto.

- Young, O. R. & F. S. Chapin III (1995): Anthropogenic impacts on biodiversity in the Arctic. – In: Chapin III, F. S. & C. Körner (eds.): *Arctic and Alpine Biodiversity: Patterns, Causes and Consequences*, pp. 183–196. – Springer, New York.
- Young, S. B. (1974): Vegetation of the Noatak River valley. – In: Young, S. B. (ed.): *The Environment of the Noatak River Basin, Alaska: Results of the Center for Northern Studies Biological Survey of the Noatak River Valley, 1973*, pp. 58–84. – Center for Northern Studies, Wolcott, VT.
- Zasada, J. C. & R. A. Densmore (1978): Rooting potential of alaskan willow cuttings. – *Can. J. For. Res.* **8**: 477–479.
- Zhang, T., Osterkamp, T. E. & K. Stamnes (1996): Some characteristics of the climate in northern Alaska, U. S. A. – *Arct. Alp. Res.* **28**: 509–518.
- – – (1997): Effects of climate on the active layer and permafrost on the North Slope of Alaska, U. S. A. – *Permafrost and Periglacial Processes* **8**: 45–67.

Addresses of the authors:

Dr. Udo SCHICKHOFF, Prof., Institute of Botany and Landscape Ecology, University of Greifswald, Grimmer Str. 88, D-17487 Greifswald, Germany;

e-mail: schickho@mail.uni-greifswald.de (corresponding author).

Dr. Marilyn D. WALKER, Leader, Boreal Ecology Coop Research Unit, School of Agriculture and Land Resources Management, University of Alaska Fairbanks, P. O. Box 756780, Fairbanks, AK 99775-6780; e-mail: mwalker@lter.uaf.edu

Dr. Donald A. WALKER, Prof., Institute of Arctic Biology, University of Alaska Fairbanks, P. O. Box 757000, Fairbanks, AK 99775-7000; e-mail: ffdaw@uaf.edu