Compositional differentiation, vegetation-environment relationships and classification of willow-characterised vegetation in the western Eurasian Arctic

A.M. Pajunen, E.M. Kaarlejärvi, B.C. Forbes & R. Virtanen

Abstract

Question: How does willow-characterised tundra vegetation of western Eurasia vary, and what are the main vegetation types? What are the ecological gradients and climatic regimes underlying vegetation differentiation?

Location: The dataset was collected across a wide spectrum of tundra habitats at 12 sites in subarctic and arctic areas spanning from NW Fennoscandia to West Siberia.

Methods: The dataset, including 758 vegetation sample plots (relevés), was analysed using a TWINSPAN classification and NMDS ordination that also included analyses of vegetation-environment correlations.

Results: Based on the TWINSPAN classification, eight vegetation types characterised by willow (cover of upright willows >10%) were discerned: (1) *Salix glauca-Carex aquatilis* type, (2) *Aulacomnium-Tomentypnum* type, (3) *Salix-Betula-Hylocomium* type, (4) *Salix lanata-Brachythecium mildeanum* type, (5) *Salix-Pachypleurum* type, (6) *S. lanata-Myosotis nemorosa* type, (7) *Salix-Trollius-Geranium* type and (8) *Salix-Comarum palustre-Filipendula ulmaria* type. Willow-characterised vegetation types were compositionally differentiated from other tundra vegetation and were confined to relatively moist valley and sloping tundra sites, from mire to mineral soils. These vegetation types were encountered across a broad latitudinal zone in which July mean temperature ranged from 6 to 10°C.

Conclusions: Willow-characterised tundra vegetation forms a broad category of ecologically and geographically differentiated vegetation types that are linked to dwarf shrub tundra, shrub tundra or mire. Because of complex ecological gradients underlying compositional differentiation, predicting the responses of willow-characterised tundra vegetation to a warming climate may be complicated.

Introduction

In arctic and subarctic transitional regions, shrub thickets form the tallest type of vegetation and therefore play an important role in ecosystem functioning (Chernov 1985; Blanken & Rouse 1994; Sturm et al. 2001a). In the Eurasian Arctic, the dominant woody plants in these shrub-dominated vegetation types are willows, mainly *Salix glauca* and *S. lanata*. Vegetation consisting of upright willows has been postulated to form zonal vegetation north of the timberline, which corresponds approximately to the 10°C July isotherm, but in the most favourable conditions such as along riverbanks willow thickets occur still in areas with the ≈ 8°C July isotherm (Bliss & Matveyeva 1992; Walker 2000). Depending on habitat conditions, species present and stages of succession, willows form thickets in which canopy density varies from closed to fragmented, and height from very low-growing up to 3 m (Edlund & Egginton 1984; Wielgolaski 1997; Schickhoff et al. 2002; Pajunen 2009). Willow-characterised vegetation has been regarded as an element of shrub tundra (Bliss & Matveyeva 1992), and shrub communities have been viewed to form a mixture of birch- (*Betula nana* and *B. exilis*) and willow-characterised tundra. These are regarded as homogeneous in their structure and composition (Bliss & Matveyeva 1992), but it seems evident that their floristic differentiation has not been adequately resolved so far.

In the general Russian classification scheme, willow thicket is described as a type occurring on mineral soils and having a high and dense canopy

Pajunen, A.M. (corresponding author: anu.pajunen@oulu.fi), **Kaarlejärvi, E.M.** (elina.kaarlejarvi@emg.umu.se) & **Forbes, B.C.** (bforbes@ulapland.fi): Arctic Centre, University of Lapland, Box 122, FI-96101 Rovaniemi, Finland.
Virtanen, R. (risto.virtanen@oulu.fi): Department of Biology, University of Oulu, Box 3000, FI-90014 Oulu, Finland.

and rich herbaceous understorey (Meltzer 1984; Andreyashkina & Peshkova 1995; Chernov & Matveyeva 1997). Although a number of willow-characterised vegetation types have been recognized across circumpolar mountain and tundra areas (e.g. Holttum 1922; Kalliola 1939; Nordhagen 1943; Porsild 1951; Danilov 1958; Daniëls 1982; Sekretareva 1984, 2003; Anonymous 1994; Virtanen et al. 1999; Schickhoff et al. 2002; Koroleva 2006; Morozova et al. 2006), the relationships of compositional delineations and ecological characterisation between vegetation types in different areas have remained inadequately understood.

The occurrence, structure and species composition of willow vegetation are affected by climate, topography, depth of active soil layer, soil conditions and biotic factors (Oksanen & Virtanen 1995; Sturm et al. 2001a,b, Schickhoff et al. 2002; Totland et al. 2004; Pajunen et al. 2008). Each of these factors is likely to affect the characteristics of the willow canopy, which may also have effects on the compositional differentiation of the understorey vegetation. However, the role of the willow canopy in determining the floristic composition of understorey vegetation is unclear, as is the relationship between environmental variables and vegetation composition. Such knowledge, however, is essential for understanding the responses of willow-characterised vegetation to environmental variations such as the predicted changes in climate (ACIA 2005; IPCC 2007).

In this paper, we aim to analyse floristic variation in willow-characterised tundra vegetation (cover of upright willows > 10%) of western Eurasia, classify the main community types, identify the ecological gradients underlying vegetation differentiation, and explore the climatic regime of the vegetation types identified.

Material and Methods

Study sites

We combined datasets collected by the authors between 1994 and 2007 in a diverse spectrum of tundra habitats spread across a broad longitudinal region, ranging from NW Fennoscandia to the Yamal Peninsula in West Siberia (map in Appendix S1). In addition, we augmented the dataset with sample material from N Fennoscandia (site 2) published by Kalliola (1939). The geographical area of the entire dataset extends over several phytogeographic regions (Yurtsev 1994), bioclimatic tundra

zones and sections (Elvebakk 1985; Tuhkanen 1986; Virtanen et al. 1999; Walker et al. 2005). The sites in NW and N Fennoscandia (study sites 1 and 2) are mountainous, lying at elevations between 200 and 600 m a.s.l., whereas all the N Russian sites are located along hill slopes near river valleys at lower elevations (0-130 m a.s.l.). Mean annual temperature, mean July temperature, precipitation and depth of snow all decline from west to east (Appendix S2). Permafrost is present in the eastern study sites (4-12) and depth of the active layer decreases from west to east (Appendix S2). Among the sites studied, there are a variety of geographic conditions that create broad categories of soil types. These and other information on the study sites and datasets are presented in Appendix S2.

Sampling

The total dataset included 12 datasets and 758 vegetation plots (relevés) collected across a wide spectrum of tundra habitats. The plot size of the datasets varied from 0.5 m × 0.5 m to 10 m × 10 m. Despite the risk of potential bias in our results due to the plot size variation (Dengler et al. 2009), we preferred not to lose valuable available data. Also, according to Otýpková & Chytrý (2006), the variation in plot size affects ordination results, but in a case of heterogeneous datasets like ours, this distortion should be smaller than in more homogeneous datasets. In all the plots, the cover of all vascular and non-vascular plant species was visually estimated using the following classes: +, 1/2, 1, 2, 3, 4, . . . 10, 15, 20, 30, 40, . . ., 100%, and the height of the willow canopy was measured at three random points in each study plot. If the data were collected using different density classes, the formula of Oksanen (1976) was used to adjust these classes to the other datasets. The height of willows was measured at three random points in a plot. A thorough description on the sampling is given in Appendix S3.

The nomenclature for vascular plants, bryophytes and lichens follows Sekretareva (1999); Hill et al. (2006) and Andreev et al. (1996), respectively. The taxa representing geographically vicariant subspecies were combined.

Classification and ordination methods

We merged the datasets from the different study sites to yield a dataset with 758 plots and 506 species. The combined dataset was then classified into vegetation types using the polythetic divisive classi-

fication of the TWINSPAN program. To resolve problems indicated by Tausch et al. (1995), a WinTWINS version (2.3) based on strict convergence criteria (Hill & Šmilauer 2005) was used. The analyses were run using default options with five cut-off levels (0, 2, 5, 10 and 20) for pseudo-species. From the TWINSPAN clusters we discerned eight vegetation types with cover of upright willows > 10%. The clusters were interpreted as vegetation types following the Nordic convention of vegetation analyses (Haapasaari 1988; Økland 1990; Oksanen & Virtanen 1995).

Diagnostic species of the vegetation types were determined with the IndVal method, which calculates the indicator value (fidelity and species abundance) of species in clusters (Dufrêne & Legendre 1997; Chytrý et al. 2002). IndVal analyses were performed in the R statistical environment with function duleg (in Labdsv package) with default options including 1000 randomizations and 0.05 error probability level. The diagnostic species having indicator values > 0.13 were arranged in a synoptic table, where the hierarchy of TWINSPAN divisions is shown in the table header. The mean values of cover of plant life-form groups and environmental variables are also presented in Table 1.

To support the TWINSPAN analyses and to describe relationships between environmental factors and occurrence of willow vegetation, we performed two non-metric multidimensional scaling (NMDS) analyses using the vegan package of R statistical environment (Oksanen et al. 2008). In the first analysis, all 758 plots were included and in the second analysis only data including the plots belonging to the eight TWINSPAN clusters of willow-characterised vegetation (173 plots) were included. MetaMDS procedure was used with default options that include use of Bray-Curtis dissimilarity index and maximum 20 random starts in search of the stable solution. In addition, we allowed the function to perform Wisconsin double standardization and square-root transformation that are the default options for large values. To evaluate the ordination, correlation between fitted vectors and ordination values (R^2) was calculated using the stressplot function of vegan. The fitted environmental vectors and centroids were overlain using the envfit function of vegan. In order to further investigate the relationships between vegetation and environmental variables (July mean temperature, July precipitation, depth of active layer and height of upright willows), we overlaid these variables on the NMDS ordination using the ordisurf command in the vegan

package of R (Oksanen et al. 2008). Ordisurf fitted smooth surfaces on the ordination using generalized additive models (GAM) with thin plate splines (Wood 2000).

Results and Discussion

Ordination and classification

Willow-characterised vegetation types clustered in the left side of the NMDS ordination diagram of all the sample plots (stress = 24.3, $R^2 = 0.73$) (Appendix S4). The horizontal axis of the diagram reflects the variation in topography, in which willow-characterised vegetation prevails at valley and slope positions, whereas tundra heaths prevail at upper positions. Willow-characterised vegetation differentiated along the vertical NMDS axes showing considerable variation in geographic and climatic factors (lengths of the gradients are > 2 half-change units) (Appendix S4).

In the NMDS species ordination (stress = 24.3, $R^2 = 0.73$) for the whole dataset (Fig. 1), several forbs and horsetails scored within the left side of the ordination space, where cover and height of willow was greatest (Appendix S4). The presence of herbs such as *Viola biflora* indicates nutrient-rich organic soils (Wielgolaski 1997). This contrasts with oligotrophic tundra vegetation types dominated by dwarf shrub taxa on the right side of the diagram (*Empetrum*, *Vaccinium*). On the lower left of the plot is *Distichium capillaceum*, an indicator of calcareous soil (Steere 1978; Dierssen 2001). Grouped along the outer edges in the lower right portion of the plot are species indicators of acidic substrates (e.g. *Cetraria ericetorum*, *Cladonia cervicornis* ssp. *verticillata*, *Icmadophila ericetorum*, *Parmelia omphalodes* and *Stereocaulon paschale*; Thomson 1984). The occurrence of hygrophilic species such as *Meesia triquetra* and *Sphagnum teres* in the upper part of the diagram (Smith 1978) and *Arctostaphylos alpina* in the bottom part of the diagram (Wielgolaski 1997) indicates a decrease in soil moisture across the ordination space from top to bottom.

Supporting the ordination analyses, the first TWINSPAN division separates a cluster including willow-characterised vegetation types from a broad group of tundra heaths and mires described for the most part previously by Virtanen et al. (1999) and Pajunen et al. (2008). In the group of willow-characterised vegetation types, the next dichotomy separates willow-characterised tundra and mire ve-

Table 1. Synoptic table showing percentages of species occurrence in the TWINSPAN clusters. The values of environmental variables and covers and height of plant groups are mean values or typical values *. The diagnostic species are determined by IndVal ($P<0.05$) and are presented in order of descending indicator value. The species with IndVal <0.13, species with occurrence in less than four plots and genus level taxa are excluded from the table. The full list of species is presented in Appendix S7. The abbreviations B, L or V after a species name stands for bryophyte, lichen or vascular plant species. *Approximate values based on [28]Kalliola's (1939) descriptions

	1	2	3	4	5	6	7	8
	SgCaT	ATT	SBHT	SlBmT	SPT	SlMnT	STGT	SCFT
	Willow-characterised tundra and mire types				Forb-rich willow types			
Number of relevés	27	5	27	54	21	17	14	8
Mean July temperature (°C)	7	7	8	8	6	8	10	10
Mean July precipitation (mm)	43	47	46	46	44	40	71	55
Depth of thaw (cm)	40	100	88	76	87	111	200	189
Cover of willow (%)	14	15	22	55	25	47	37	94
Height of willow (cm)	18	3	31	71	13	98	55*	100*
Cover of dwarf birch (%)	10	0	20	4	0	0	0	3
Cover of deciduous dwarf shrubs (%)	0	11	4	2	12	8	1	0
Cover of evergreen dwarf shrubs (%)	0	0	5	0	0	0	0	0
Cover of forbs (%)	7	6	7	28	24	67	134	77
Cover of graminoids (%)	31	0	16	12	7	13	12	6
Cover of bryophytes (%)	91	75	62	65	26	21	40	23
Cover of lichens (%)	1	3	5	4	2	0.2	1	0
Diagnostic species of Salix glauca-Carex aquatilis type								
Sphagnum squarrosum (B)	59	0	0	0	0	0	0	0
Carex aquatilis (V)	78	0	11	52	0	6	0	25
Sphagnum fimbriatum (B)	41	0	4	4	0	0	0	0
Luzula wahlenbergii (V)	37	0	0	0	0	0	0	0
Polytrichum strictum (B)	37	0	7	13	0	0	0	0
Rubus chamaemorus (V)	52	40	30	24	0	18	0	13
Stramiergon stramineum (B)	30	0	7	6	0	0	0	0
Eriophorum angustifolium (V)	56	0	33	19	0	0	0	0
Senecio atropurpurea (V)	22	0	0	0	0	0	0	0
Diagnostic species of Aulacomnium-Tomentypnum type								
Tomentypnum nitens (B)	0	100	19	4	10	12	0	0
Plagiomnium ellipticum (B)	7	100	11	31	5	0	7	0
Equisetum scirpoides (V)	0	100	19	0	67	0	0	0
Salix arbuscula (V)	0	80	4	0	33	0	0	0
Lophozia incisa ssp. opacifolia (B)	0	40	0	0	0	0	0	0
Saxifraga hirculus (V)	0	40	0	0	0	6	0	0
Aulacomnium palustre (B)	89	100	59	24	24	0	0	13
Salix reticulata (V)	0	60	0	2	38	12	21	0
Peltigera leucophlebia (L)	0	60	15	2	19	0	7	0
Peltigera canina (L)	0	60	19	6	14	0	29	0
Petasites frigidus (V)	15	60	37	50	5	12	0	0
Pannaria pezizoides (L)	0	20	0	0	5	0	0	0
Diagnostic species of Salix-Betula-Hylocomium type								
Hylocomium splendens (B)	26	80	81	26	24	24	29	0
Betula nana (V)	59	20	78	59	0	6	14	25
Peltigera aphthosa (L)	4	0	33	20	0	12	0	0
Diagnostic species of Salix lanata-Brachythecium mildeanum type								
Brachythecium mildeanum (B)	19	0	11	70	0	18	0	0
Rubus arcticus (V)	0	0	19	44	0	6	0	0
Polemonium acutiflorum (V)	22	0	15	74	29	35	0	0
Sanionia uncinata (B)	33	80	67	96	71	12	71	63
Salix lanata (V)	30	80	59	89	76	71	50	88
Carex lachenalii (V)	0	0	0	24	0	0	14	0
Tritomaria quinquedentata (B)	11	40	33	54	24	24	0	0
Diagnostic species of Salix-Pachypleurum type								
Astragalus alpinus (V)	0	0	15	2	57	6	7	0
Polygonum viviparum (V)	22	80	52	61	90	24	93	13
Pachypleurum alpinum (V)	0	0	11	11	62	0	0	0
Senecio lugens (V)	0	0	11	0	43	0	0	0
Tanacetum bipinnatum (V)	0	0	22	24	48	12	0	0
Festuca rubra (V)	7	60	15	41	52	12	0	0
Syntrichia ruralis (B)	0	0	4	0	24	0	0	0

Table 1. *(Continued)*.

	1 SgCaT	2 ATT	3 SBHT	4 SlBmT	5 SPT	6 SlMnT	7 STGT	8 SCFT
	Willow-characterised tundra and mire types				Forb-rich willow types			
Myosotis asiatica (V)	0	0	4	7	48	6	0	0
Pedicularis sudetica (V)	7	0	15	15	19	0	0	0
Luzula multiflora (V)	0	20	7	17	29	12	7	0
Diagnostic species of Salix lanata-Myosotis nemorosa type								
Equisetum arvense (V)	7	20	52	96	38	100	7	0
Poa pratensis (V)	4	0	26	30	5	82	21	0
Myosotis nemorosa (V)	0	0	0	0	0	53	0	13
Veratrum album (V)	0	0	7	44	5	71	0	0
Adoxa moschatellina (V)	0	0	0	0	0	35	0	0
Aconitum septentrionale (V)	0	0	0	0	0	24	0	0
Chrysosplenium tetrandum (V)	0	0	0	4	0	24	0	0
Cardamine pratensis (V)	7	0	0	17	0	24	0	0
Brachythecium reflexum (B)	0	0	4	7	19	35	7	0
Achillea millefolium (V)	0	0	0	0	0	35	14	13
Diagnostic species of Salix-Trollius-Geranium type								
Geranium sylvaticum (V)	0	0	7	2	0	0	100	13
Trollius europaeus (V)	0	0	0	0	0	0	93	0
Anthoxanthum odoratum (V)	0	0	0	2	0	0	71	0
Cirsium helenioides (V)	0	0	0	0	0	0	93	38
Selaginella selaginoides (V)	0	0	7	0	0	0	64	0
Hylocomiastrum pyrenaicum (B)	0	0	0	0	0	0	57	0
Equisetum pratense (V)	0	0	0	0	0	0	57	0
Bartsia alpina (V)	0	0	4	0	0	0	57	0
Euphrasia frigida (V)	0	20	0	0	5	0	57	0
Poa alpina (V)	0	20	4	0	24	0	57	0
Solidago virgaurea (V)	0	0	0	4	0	0	57	0
Ranunculus acris (V)	7	0	26	52	67	88	93	13
Gnaphalium norvegicum (V)	0	0	0	4	0	0	50	0
Saussurea alpina (V)	0	20	7	2	10	6	57	0
Phleum alpinum (V)	0	0	0	0	0	0	43	0
Carex vaginata (V)	0	0	0	0	0	0	36	0
Viola biflora (V)	0	0	0	2	5	41	50	88
Carex atrata (V)	0	0	0	0	0	0	29	0
Veronica alpina (V)	0	0	0	0	0	0	29	0
Pyrola minor (V)	0	0	4	11	14	0	29	0
Campylium stellatum (B)	4	0	0	0	0	6	29	0
Philonotis fontana (B)	0	0	0	0	0	0	21	0
Oxyria digyna (V)	0	0	0	0	0	0	21	0
Agrostis mertensii (V)	0	0	0	0	0	0	29	13
Thalictrum alpinum (V)	0	0	4	0	0	6	21	0
Diagnostic species of Salix-Comarum palustre-Filipendula ulmaria type								
Salix lapponum (V)	4	0	0	4	0	0	43	88
Geum rivale (V)	0	0	0	0	0	0	57	75
Filipendula ulmaria (V)	0	0	0	0	0	0	29	63
Comarum palustre (V)	44	0	4	11	0	6	14	88
Rumex acetosa (V)	0	0	0	0	0	0	21	63
Trientalis europaea (V)	0	0	15	4	0	0	29	75
Equisetum sylvaticum (V)	0	0	4	0	0	0	7	38
Calamagrostis purpurea (V)	0	0	0	0	0	0	29	63
Rhizomnium pseudopunctatum (B)	15	20	7	9	10	0	14	38
Salix phylicifolia (V)	4	20	11	7	10	18	7	38
Myosotis decumbens (V)	0	0	0	0	0	0	14	25
Bryum pseudotriquetrum (B)	0	20	4	20	24	0	7	50
Viola epipsila (V)	0	0	4	0	0	18	14	25
Other common species								
Deschampsia flexuosa (V)	0	0	11	0	0	0	50	25
Salix glauca (V)	70	0	70	65	5	47	57	50
Cetraria islandica (L)	7	40	70	37	14	12	7	0
Psoroma hypnorum (L)	0	60	11	0	0	0	0	0

getation (types 1-4) from forb-rich willow vegetation (5-8). The subsequent TWINSPAN divisions are presented in Table 1 and described below. The complete list of species occurring in the vegetation types characterised by upright willows is presented in Appendix S7.
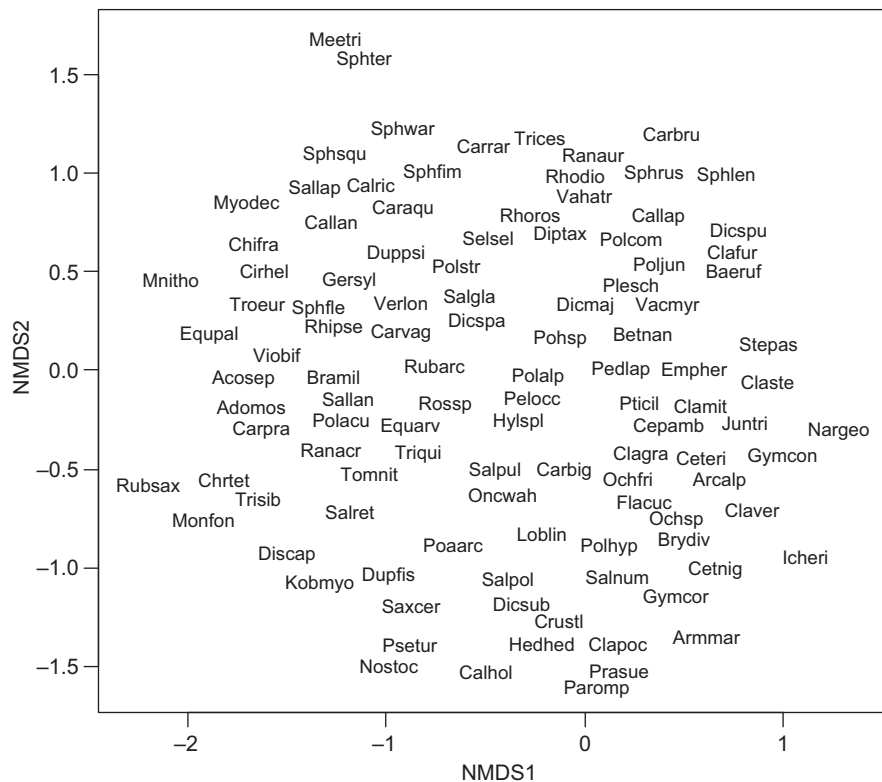
Fig. 1. NMDS ordination showing species from the combination of all datasets. Species codes are the first three letters of the genus and species (see Table 1 and Appendix S7 for full names). In the case of an overlap of species code, priority was given to labels of most abundant species by using the orditorp command in Vegan (Oksanen et al. 2008).

Willow-characterised tundra and mire types

TWINSPAN clusters 1-4 represent willow-characterised tundra and mire types having a lower abundance of willow than the remaining types. They have a high cover of bryophytes and generally relatively high number of species. The split between willow-characterised tundra and mire types (1-4) and forb-rich willow vegetation types (5-8) is comparable to the split between acidic soil types in higher riverbank terraces and more basic soils in lower riverbanks in Alaska (Schickhoff et al. 2002). The species ordination for NMDS ordination analyses of the willow types (stress = 27.2, $R^2 = 0.63$) also supported this division (for further information, see Appendix S5).

S. glauca-Carex aquatilis type (SgCaT)

The first TWINSPAN division among willow-characterised tundra and mire types separates this mire-like vegetation from drier willow-characterised tundra types (Table 1). The *S. glauca-C. aquatilis* type is a tundra mire type that mostly occurs in Yamal Peninsula, in relatively cold and dry conditions. It has a distinct but relatively low cover of upright willows dominated by *S. glauca*. The cover of willow

is slightly higher than the cover of *Betula nana*, whereas dwarf shrubs are practically absent. The mire-like characteristics of this vegetation type are indicated by the high abundance of *C. aquatilis*, *Eriophorum angustifolium* and an almost uniform layer of bryophytes, dominated by *Sphagnum* species (Table 1). The shallow depth of annual thaw indicates a thick turf layer typical of mires in cold climates. The species number of this type seemed to be highest among the tundra and mire types found in this study. A corresponding type has been described for the Yamal Peninsula as cottongrass-sedge-*Sphagnum* with willow mire type (Morozova et al. 2006). This type shares similar features with *Salix lapponum-S. glauca-C. aquatilis-C. rostrata* association (Kalliola 1939) and *Calliergonetum straminei* Dahl 1956 types described in Fennoscandia.

Aulacomnium-Tomentypnum type (ATT)

Among willow-characterised tundra types on drier sites, vegetation types dominated by *Salix lanata* are separated from *Salix polaris* tundra types described by Virtanen et al. (1999). Further, in a subsequent division of the *S. lanata* types, a cluster that closely resembles the *Aulacomnium palustre-*
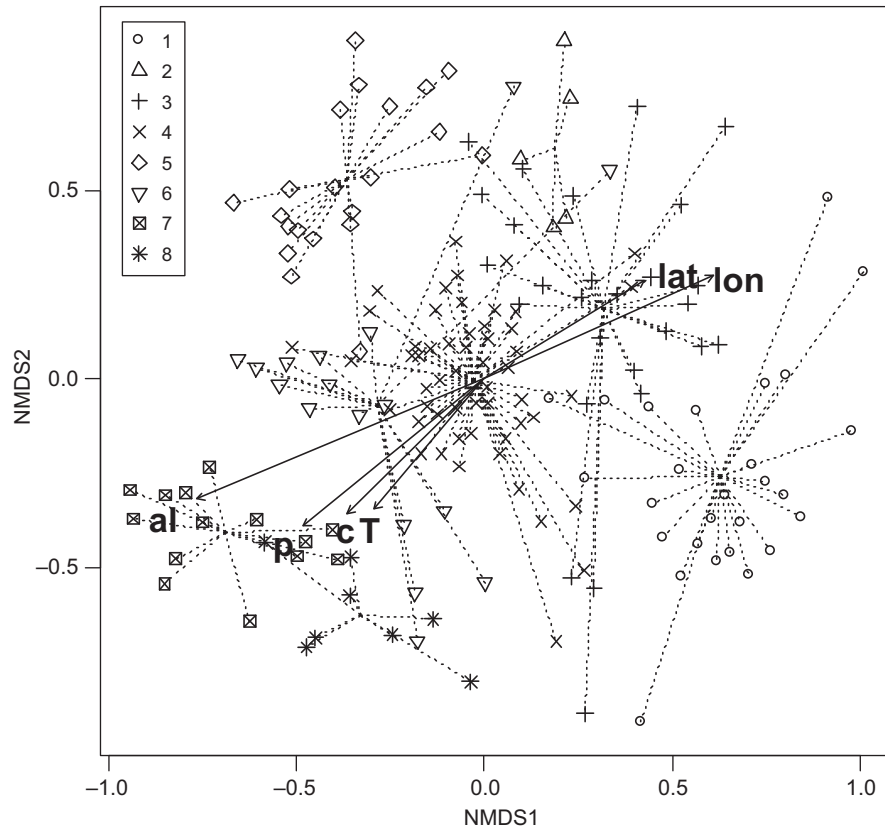
Fig. 2. NMDS ordination showing data for sites consisting of plots belonging to the willow vegetation types described in this research. Half-change scaling scales the configuration so that one unit means halving of community similarity from replicate similarity (Oksanen *et al.* 2008). The environmental factors are indicated with arrows, where **lat** is latitude, **lon** longitude, **al** mean depth of active layer, **p** mean July precipitation, **T** elevation-corrected mean July temperature (0.6° lapse rate per 100 m) and **c** cover of willow. The arrows point to the direction of most rapid change in the environmental variable. The vegetation types are based on TWINSPAN division hierarchy, where 1 = *S. glauca-C. aquatilis* type (SgCaT), 2 = *Aulacomnium-Tomentypnum* type (ATT), 3 = *Salix-Betula-Hylocomium* type (SBHT), 4 = *S. lanata-Brachythecium mildeanum* type (SlBmT), 5 = *Salix-Pachypleurum* type (SPT), 6 = *S. lanata-Myosotis nemorosa* type (SlMnT), 7 = *Salix-Trollius-Geranium* type (STGT) and 8 = *Salix-Comarum palustre-Filipendula ulmaria* type (SCFT).

Tomentypnum nitens type (Virtanen et al. 1999) is separated from other willow-characterised tundra types. ATT is found on Kolguyev Island, with relatively cold southern arctic conditions. The upright shrubs *Salix arbuscula* and *S. lanata* form a layer that is low in stature and has an open canopy. There is a relatively low abundance of forbs, whereas bryophytes are abundant. The occurrence of *Equisetum scirpoides* (Jonsell 2000) and *Salix reticulata* (Wielgolaski 1997) indicates nutrient-rich and moist conditions of these vegetation types. On the basis of the prominent bryophyte layer, Virtanen et al. (1999) considered ATT a transitional type between tundra vegetation and eutrophic mires. This type corresponds to the *Equiseto arvensis-Salicetum lanatae* association Cooper 1986 that is described for Alaska and found in habitats with shallow thaw but constant water supply.

Salix-Betula-Hylocomium type (SBHT)

In subsequent divisions among willow-characterised tundra types, TWINSPAN identifies a vegetation cluster in which *S. glauca* slightly dominates over *Betula nana*, with both having relatively low abundances (Table 1). In the ordination diagram, plots belonging to SBHT are clustered between the SgCaT and SlBmT types, thus supporting the result of the TWINSPAN analyses (Fig. 2). SBHT is found in several places across the entire geographical range of this study. The mean values of climatic variables suggest, however, that this type occurs in relatively cold and continental conditions. Graminoids dominate over dwarf shrubs and forbs and bryophytes are abundant (Table 1). This type partly corresponds to the *Betula nana* scrub type, *S. glauca* variant (BnS, Sg) of Virtanen et al. (1999). However, based on our cur-

rent more extensive sample material of the present study, we include this vegetation within the *Salix-Betula-Hylocomium* type. A corresponding vegetation type has earlier been described on Yamal as dwarf birch-willow-sedge-bryophyte type (Rebristaya et al. 1995) and dwarf shrub-lichen-moss tundra with willow and dwarf birch (Morozova et al. 2006).

S. lanata-Brachythecium mildeanum type (SlBmT)

TWINSPAN separates a cluster that belongs to the group of willow-characterised tundra types, but has many common features with forb-rich willow vegetation types. In contrast to the previous tundra types, it has relatively dense and high willow cover. In the NMDS ordination, the plots of this cluster score in the middle of the diagram, between the previous tundra types and the following forb-rich willow vegetation types (Fig. 2). Therefore, we consider this type as transitional between willow-characterised tundra vegetation and forb-rich willow vegetation types. SlBmT is mainly found on the Yamal Peninsula in similar climatic conditions as the previous type. Even though the abundance of forbs is relatively high, bryophytes dominate over them and lichens occur sporadically (Table 1). A corresponding type has earlier been described as willow (*S. glauca, S. lanata*)-dwarf birch-sedge (*Carex ensifolia* ssp. *arctisibirica*)-bryophyte tundra (Rebristaya et al. 1995) and forb-bryophyte willow thicket (Morozova et al. 2006) on Yamal Peninsula, and as *S. lanata-Nardosmia frigida* willow thicket in western Taimyr (Matveyeva & Zanoha 1986). In addition, *Pediculario lapponicae-S. lanatae* Sekretareva 2003 from Chukotka plateau and *Epilobio-Salicetum alaxensis polemonietosum acutiflori* Schickhoff et al. 2002 from Alaskan riparian habitats may be regarded as ecological counterparts of this type. Similar to the latter, our type occurred in areas with frequent disturbance, which relates to landslide activity in our case (Ukraintseva et al. 2003).

Forb-rich willow vegetation types

Types 5-8 have relatively dense and high willow cover and an abundant forb layer in the understorey. In contrast with the previous types, the active layer is deep and the cover of bryophytes low.

S. lanata-Pachypleurum alpinum type (SPT)

Among forb-rich willow vegetation types, TWINSPAN identifies a cluster that occurs in the southern arctic tundra zone (Kolguyev Island and W Yamal) and extends even up to cold middle arctic tundra (N Yamal). SPT prevails on well-drained slopes having a relatively deep thaw. In this vegetation type, *S. lanata* forms a relatively open and low canopy. Forbs and bryophytes are nearly equally abundant in the understorey vegetation (Table 1). Species composition of this TWINSPAN cluster closely resembles the *S. lanata-P. alpinum* type (Virtanen et al. 1999). As the species composition of this and other type of Kolguyev (ATT) suggest that the soils are relatively rich, it is possible that strong winds due to the proximity of the Barents Sea have caused vertical reduction of the willow canopy (see also Pajunen 2009).

S. lanata-Myosotis nemorosa type (SlMnT)

TWINSPAN separates a vegetation cluster having a more closed and tall willow canopy and more abundant forb flora in the understorey vegetation than SPT (Table 1). *S. lanata-M. nemorosa* type (SlMnT) is mainly found in Varandei and to some extent in SW Yamal in areas with a deep active layer (Fig. 2 and Appendix S6). Forbs are abundant and numerous in species number, while the cover of bryophytes is also relatively high compared to the other forb-rich willow vegetation types (Table 1). In the ordination diagram, sample plots representing this vegetation type score in the left side of the diagram (Fig. 2), where there are species indicating nutrient-rich conditions (e.g. *Distichium capillaceum*) (Appendix S5) (Steere 1978; Dierssen 2001). A corresponding vegetation type is described by Sekretareva (1984) and a very similar type is described by Matveyeva & Zanoha (1986) from Western Siberia. This type also shares similarities with *Myosoto-Aconitum* Dierssen 1996 described in Fennoscandia.

Salix-Trollius-Geranium type (STGT)

TWINSPAN separates a cluster containing exclusively the sample material of Kalliola (1939), with the forb-rich vegetation type of northern Fennoscandia. Kalliola (1939) originally separated two subtypes – a *Geranium-Trollius* tall herb meadow type and a *Salix-Geranium-Trollius* willow-rich, tall herb vegetation type – on the basis of the relative abundance of the grey willows *S. glauca, S. lanata* and *S. lapponum*. Our analyses suggest that these subtypes may not be clearly differentiated, and tall herb meadows and willow-rich tall herb vegetation could be treated as a single *Salix-Trollius-Geranium* type. In the ordination diagram, the plots belonging to this type are in the left corner and show a gradual shift towards the next type (SCFT), probably due to an increase in soil moisture (Fig. 2). The willow

cover of this type is lower and more open than in the previous type, which could be a result of reindeer grazing over a long period. On the other hand, tall herb meadow may also represent an earlier stage of succession, where willows occur in the later stages (Holttum 1922). Of the willow species, *S. glauca* dominates over *S. lanata* and *S. lapponum*. The cover of forbs is highest among the types described in this study, and the cover of bryophytes is also highest among the forb-rich willow vegetation types (Table 1). Earlier descriptions of corresponding vegetation types in Fennoscandia include *Geranietum sylvatici alpicolum* and *Salicetum geraniosum alpicolum* Nordhagen 1943, *Saussurea alpina-Carex vaginata-Sphagnum warnstorfii* type (Moen 1990) and *Myosoto-Aconitum* Dierssen 1996, and in Northern Russia, *Geranietum sylvatici* Koroleva 2006.

Salix-Comarum palustre-Filipendula ulmaria type (SCFT)

TWINSPAN forms a cluster containing almost exclusively sample material of Kalliola (1939) from N Fennoscandia. These plots belong to the *Salix-Comarum-Ulmaria* type of Kalliola (1939). This type vegetation prevails especially in riparian habitats along tundra streams and rivers, and can be ecologically interpreted as a riparian willow thicket type. In the ordination diagram, the plots belonging to this type score in the bottom part of the diagram, which is interpreted as having high soil moisture on the basis of the occurrence of *Warnstorfia sarmentosa* or *Sphagnum* species (Fig. 2, Appendix S5) (Dierssen 2001). In this type, the tall and very dense willow canopy is composed of *Salix lapponum* (dominant) together with *S. glauca*, *S. lanata* and *S. phylicifolia*. In the understorey vegetation, hydrophilic forbs and bryophytes are abundant (Table 1). Corresponding vegetation types in Fennoscandia include *Salicetum ulmariosum alpicolum* Nordhagen 1943; Dahl 1987, *Myosoto-Aconitum* Dierssen 1996 and *Rumici-Salicetum lapponi* Dahl 1956, which also occurs in northwest Russia (Koroleva 2006).

Vegetation-environment relationships

Our analyses revealed that despite the physiognomic uniformity of willow-characterised tundra vegetation across the western Eurasian Arctic, this vegetation includes tundra mires, heath-like types and productive forb-rich willow thickets that have floristically distinct ground and field layers. Given the important effects of upright willows (Sturm et al. 2001a) on ecosystem function, it is important to identify different types and examine their relations with one another. Most types have at least tentatively described counterparts in earlier studies, but our analyses of a large dataset from a geographically large area is the first attempt to reveal their ecological relationships and also to test the validity of some earlier delimitations. Indeed, some types turned out to be less supported, whereas others gained further support. One important outcome of the results is the first characterisation of the climatic regimes of different community types. We provide evidence here that willow-characterised vegetation occupies a wide climate regime, and that other ecological factors are likely to complicate prediction of the effects of changing climate on these vegetation types.

According to our analyses, willow-characterised vegetation occurs in areas where July mean temperature varies between 6 and 10°C and July mean precipitation is relatively high (Appendix S6a, b). According to Bliss & Matveyeva (1992); Walker (2000) and Walker et al. (2005), willow-characterised tall shrub communities occur in the Eurasian Arctic between the July isotherms 8 and 12°C. Our results support this, but also show that there are types floristically similar to tall shrub types that have low willow canopies (ATT and SPT) and can still be found in much colder areas (Fig. 2, Appendix S6). The described vegetation types are differentiated in relation to temperature gradients, but the climatic regimes of each type vary. Some of them seem to occupy relatively small niches in the ordination space (ATT, STGT, SCFT), whereas others are more heterogeneous (SBHT, SlMnT, SgCaT). It thus seems that other factors, such as topographic position and site moisture, affect the vegetation-climate relationships in tundra willow communities.

Depth of the active layer seems to be related to the thermal and precipitation regimes, but there is one notable anomaly. The tundra mires tend to have a shallow active layer (< 60 cm) and it seems clear that this factor is important in differentiating vegetation types. Most willow-characterised vegetation types were found to occur on sites where thaw depth was > 60 cm (Appendix S6c). There was also an association between the height of willow and depth of the active layer (Appendix S6c,d) that is in accordance with some earlier studies (Schickhoff et al. 2002; Walker et al. 2003; Pajunen 2009). As a consequence, the predicted permafrost thawing in the coming decades (ACIA 2005; IPCC 2007) is likely to alter the vertical structure of willow-characterised communities (Walker et al. 2003).

Our analyses strengthen earlier reports and studies (Holttum 1922; Kalliola 1939; Chernov 1985; Chernov & Matveyeva 1997; Wielgolaski 1997; Walker 2000) suggesting that topographic variability is among the main determinants underlying the occurrence of willow-characterised tundra vegetation. According to these reports, willow-characterised vegetation occurs in lower topographical positions for several reasons. First, the deep snow on slopes and in valleys protects willow shoots from wind, abrasion from ice crystals and winter browsing by herbivores. Deep snow also increases insulation and thus increases the depth of annual thaw. Further, it has recently been suggested that the structure of upright shrubs facilitates the trapping of snow and thus creates a positive snow-shrub feedback that leads to enhanced shrub growth and further snow capture (Sturm et al. 2001a, 2005). Second, the slopes and valley positions tend to have higher soil moisture and nutrient status, favouring willow growth (Shaver et al. 1996).

Our analyses show that the variation in canopy structure may mismatch with other compositional variation in willow-characterised vegetation types. For instance, the tall herb and willow tall herb types of Kalliola (1939) represent a relatively uniform vegetation unit. Also, the SPT type with an open and low willow canopy clustered together with other forb-rich types characterized by a more closed willow canopy. This does not preclude, however, that the willow canopy has any meaning for the structure and dynamics of these vegetation types. A closed willow canopy provides shelter and rapid turnover of nutrients, thus facilitating species that can tolerate limited light conditions (Epstein et al. 2004). Among the vegetation types we described, there was a tendency that the higher and denser the willow canopy, the more variable and abundant was the herbaceous cover in the understorey vegetation (Fig. 2, Appendices S5 and S6). Therefore, our results suggest that there are facilitative effects between willow and certain forb species (see also, Totland et al. 2004), and more effort should be directed towards understanding their role.

Recent analyses from Alaska and elsewhere have shown a considerable increase in the abundance of tundra shrubs, including willow (Sturm et al. 2001b; Tape et al. 2006). This has been mainly observed in regions of tall shrubs forming relatively dense canopies and has been attributed to recent climatic warming in tundra areas. Our analyses show that thermal conditions are one of the important drivers of community differentiation, and increasing summer temperatures will be reflected in willow vegetation structure and composition (see also Forbes et al. 2009). The association between temperature conditions and willow height shows some nonlinearity (curved surfaces in Appendix S6a and d). It is thus likely that other factors affecting willow abundance, such as effects of grazing by reindeer (*Rangifer tarandus*) (Oksanen & Virtanen 1995; Pajunen et al. 2008; Olofsson et al. 2009) may complicate the vegetation response to climatic warming in tundra regions.

References

ACIA 2005. *Arctic climate impact assessment*. Cambridge University Press, Cambridge, UK.

Andreev, M., Kotlov, Y. & Makarova, I. 1996. Checklist of lichens and lichenicolous fungi of the Russian Arctic. *Bryologist* 99: 137–169.

Andreyashkina, N.I. & Peshkova, N.V. 1995. Vegetation. In: Dobrinski, L.N. (ed.) *The nature of Yamal*. pp. 174–217. Yekaterinburg Nauka, Yekaterinburg, RU. (in Russian).

Anonymous 1994. *Vegetationstyper i Norden*. Nordiska Ministerrådet, Berlings, Arlöv, SE.

Blanken, P.D. & Rouse, W.R. 1994. The role of willow–birch forest in the surface energy balance at Arctic treeline. *Arctic and Alpine Research* 26: 403–411.

Bliss, L.C. & Matveyeva, N.V. 1992. Circumpolar Arctic vegetation. In: Chapin, F.S.III, Jefferies, R.L., Reynolds, J.F., Shaver, G.R. & Svoboda, J. (eds.) *Arctic ecosystems in a changing climate*. Academic Press, San Diego, CA, US.

Chernov, Y.I. 1985. *The living tundra*. Cambridge University Press, Cambridge, UK.

Chernov, Y.I. & Matveyeva, N.V. 1997. Arctic ecosystems in Russia. In: Wielgolaski, F.E. (ed.) *Ecosystems of the World III. Polar and alpine tundra*. pp. 361–507. Elsevier, Amsterdam, NL.

Chytrý, M., Tichý, L., Holt, J. & Botta-Dukát, Z. 2002. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science* 13: 79–90.

Cooper, D.J. 1986. Arctic–alpine tundra vegetation of the Arrigetch Creek Valley, Brooks Range, Alaska. *Phytocoenologia* 14: 467–555.

Dahl, E. 1956. Rondane Mountain vegetation in South Norway and its relation to the environment. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Matematisk.-Naturvidenskapelig. Klasse* 3: 1–374.

Dahl, E. 1987. Alpine–subalpine plant communities of South Scandinavia. *Phytocoenologia* 15: 455–484.

Daniëls, F.J.A. 1982. Vegetation of the Angmagssalik District, southeast Greenland. IV. Shrub, dwarf shrub and terricolous lichens. *Meddelelser on Grønland, Bioscience* 10: 1–78.

Danilov, D.N. 1958. Productivity of dwarf birch and upright willow vegetation in the east of the Bol's hezemel'skaya tundra. *Botanitcheskii Zhurnal* 43: 388–393 (in Russian).

Dengler, J., Löbel, S. & Dolnik, C. 2009. Species constancy depends on plot size – a problem for vegetation classification and how it can be solved. *Journal of Vegetation Science* 20: 754–766.

Dierssen, K. 1996. *Vegetation Nordeuropas*. Eugen Ulmer, Stuttgart, DE (in German).

Dierssen, K. 2001. *Distribution, ecological amplitude and phytosociological characterization of European bryophytes*. J. Cramer, Berlin, DE.

Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Edlund, S.A. & Egginton, P.A. 1984. Morphology and description of an outlier population of tree-sized willows on Western Victoria Island, District of Franklin. *Current Research Part A. Geological Survey of Canada Paper* 84-1A: 279–285.

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

Epstein, H., Beringer, J., Gould, W.A., Lloyd, A.H., Thompson, C.D., Chapin, F.S. III, Michaelson, G.J., Ping, C.L., Rupp, T.S. & Walker, D.A. 2004. The nature of spatial transitions in the Arctic. *Journal of Biogeography* 31: 1917–1933.

Forbes, B.C., Macias Fauria, M. & Zetterberg, P. 2009. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology*, doi:10.1111/j.1365-2486.2009.02047.x

Haapasaari, M. 1988. The oligotrophic heath vegetation of northern Fennoscandia and its zonation. *Acta Botanica Fennica* 135: 1–219.

Hill, M.O. & Šmilauer, P. 2005. *TWINSPAN for Windows version 2.3*. Centre for Ecology and Hydrology & University of South Bohemia, Huntingdon & České Budíjovice, CZ.

Hill, M.O, Bell, N., Bruggeman-Nannenga, M.A., Brugue, M., Cano, M.J., Enroth, J., Flatberg, K.I., Frahm, J.-P., Gallego, M.T., Garilleti, R., Guerra, J., Hedena, L., Holyoak, D.T., Hyvönen, J., Ignatov, M.S., Lara, F., Mazimpaka, V., Muñoz, J. & Söderström, L. 2006. An annotated checklist of the mosses of Europe and Macronesia. *Journal of Bryology* 28: 198–267.

Holttum, R.E. 1922. The vegetation of West Greenland. *Journal of Ecology* 10: 87–108.

IPCC 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Jonsell, B. (ed.) 2000. *Flora Nordica 1*. Bergius, Stockholm, SE.

Kalliola, R. 1939. Pflanzensoziologische Untersuchungen in der alpinen Stufe Finnisch Lapplands. *Annales Botanici Societatis Zoologicae – Botanicae Fennicae Vanamo* 13: 1–321 (in German).

Koroleva, N.E. 2006. Treeless plant communities of the East Murman shore (Kola Peninsula, Russia). *Rastitel'nost' Rossii* 8: 20–42 (in Russian).

Matveyeva, N.V. & Zanoha, L.L. 1986. Vegetation of southern tundra in Western Taimyr. In: Chernov, Y.I. & Matveyeva, N.V. (eds) *Southern tundra of Taimyr*. pp. 5–67. Leningrad, Nauka, RU (in Russian).

Morozova, L.M., Magomedova, M.A. & Ektova, S.N. 2006. The structure and phytocenotic diversity of vegetation cover. In: Magomedova, M.A., Morozova, L.M., Ektova, S.N., Rebristaja, O.V., Tsernajevo, I.V., Potemkin, A.L. & Knjazev, M.C. (eds), *Poluostrov Yamal: Rostitel'nii pokrov*. pp. 148–204. Citi-press, Tjumen, RU (in Russian).

Meltzer, L.I. 1984. Zonal division of tundra vegetation of the West Siberian plain. In: Belov, A.V. (ed.) *Vegetation of western Siberia and its mapping*. pp. 7–19. Akademia Nauk, Novosibirsk, RU (in Russian).

Moen, A. 1990. *The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands*. Universitetet i Trondheim, Vitenskapsmuseet, Trondheim, NO.

Nordhagen, R. 1943. Sikilsdalen og Norges fjellbeiter. En plantesosiologisk monografi. *Bergens Museums Skrifter* 22: 1–607 (in Norwegian).

Økland, R.H. 1990. Vegetation ecology: theory, methods and applications with reference to Fennoscandia. *Sommerfeltia* (Suppl 1): 1–233.

Oksanen, L. 1976. On the use of the Scandinavian type class system in coverage estimation. *Annales Botanici Fennici* 13: 149–153.

Oksanen, L. & Virtanen, R. 1995. Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. *Acta Botanica Fennica* 153: 1–80.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. 2008. *Vegan: Community Ecology*

Package. R package version 1.14-12. Available at http://vegan.r-forge.r-project.org/ Accessed 3 June 2008.

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T. & Suominen, O. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, doi:10.1111/j.1365-2486.2009.01935.x

Otýpková, Z. & Chytrý, M. 2006. Effects of plot size on the ordination of vegetation samples. *Journal of Vegetation Science* 17: 465–472.

Pajunen, A. 2009. Environmental and biotic determinants of height and growth of arctic willows along latitudinal gradient. *Arctic, Antarctic and Alpine Research* 41: 478–485.

Pajunen, A., Virtanen, R. & Roininen, H. 2008. The effects of reindeer grazing on the composition and species richness of vegetation in forest–tundra ecotone. *Polar Biology* 31: 1233–1244.

Porsild, A.E. 1951. Botany of southeastern Yukon adjacent to the Canol road. *National Museum of Canada Bulletin* 121: 1–400.

Rebristaya, O.V., Khitun, O.V., Chernyadjeva, I.V & Leibman, M.O. 1995. Dynamics of vegetation on the cryogenic landslips in the central part of the Yamal Peninsula. *Botanicheskii Zhurnal* 80: 31–48 (in Russian).

Schickhoff, U., Walker, MD. & Walker, D.A. 2002. Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: a classification and ordination analysis. *Phytocoenologia* 32: 145–204.

Sekretareva, N.A. 1984. The genus *Salix* (Salicaceae) in the vegetation cover of the middle reaches of the Syradasay River (western Taimyr). *Botanicheskii Zhurnal* 69: 1640–1651 (in Russian).

Sekretareva, N.A. 1999. *The vascular plants of the Russian arctic and adjacent territories.* Pensoft, Sofia, BG.

Sekretareva, N.A. 2003. Eutrophic shrub willow communities in the middle reaches of the Palyavaam River (the western part of the Chukotka Plateau, Northeastern Asia). *Rastitel'nost' Rossii* 5: 41–49 (in Russian).

Shaver, G.R., Laundre, J.A., Giblin, A.E. & Nadelhoffer, K.J. 1996. Changes in live plant biomass, primary production, and species composition along a riverside toposequence in arctic Alaska, USA. *Arctic and Alpine Research* 28: 361–377.

Smith, A.J.E. 1978. *The moss flora of Britain and Ireland.* Cambridge University Press, Cambridge, UK.

Steere, W.C. 1978. *The mosses of arctic Alaska.* J. Cramer, Vaduz, US.

Sturm, M., McFadden, J.P., Liston, G.E., Chapin, F.S. III, Racine, C.H. & Holmgren, J 2001a. Snow–shrub interactions in Arctic tundra: a hypothesis with climatic implications. *Journal of Climate* 14: 336–344.

Sturm, M., Racine, C.R. & Tape, K 2001b. Increasing shrub abundance in the Arctic. *Nature* 411: 546–547.

Sturm, M., Schimel, J., Michaelson, G., Welker, J.M., Oberbauer, S.F., Liston, G.E., Fahnestock, J. & Romanovsky, E. 2005. Winter biological processes could help convert arctic tundra to shrubland. *BioScience* 55: 17–26.

Tape, K., Sturm, M. & Racine, C. 2006. The evidence for shrub expansion in northern Alaska and Pan-Arctic. *Global Change Biology* 12: 686–702.

Tausch, R.J., Charlet, D.A., Weixelman, D.A. & Zamudio, D.C. 1995. Patterns of ordination and classification instability resulting from changes in input data order. *Journal of Vegetation Science* 6: 897–902.

Thomson, J.W. 1984. *American arctic lichens II. The macrolichens.* Columbia University Press, New York, NY, US.

Totland, Ø., Grytnes, J.A. & Heegaard, E. 2004. Willow canopies and plant community structure along an alpine environmental gradient. *Arctic, Antarctic and Alpine Research* 36: 428–435.

Tuhkanen, S. 1986. Delimitation of climatic–phytogeographical regions at the high-latitude area. *Nordia* 20: 105–112.

Ukraintseva, N.G., Streletskaya, K.A., Ermokhina, K.A. & Yermakov, S.Y. 2003. Chemical properties of plant–soil permafrost system on landslide slopes, Yamal, Russia. In: Phillips, M., Springman, S.M. & Arenson, L.U. (eds.) *Proceedings of the 8th International Conference on Permafrost, Zurich, Switzerland, 21–25 July 2003.* Vol. 1, pp. 1149–1154. Swets & Zeitlinger, Lisse, NL.

Virtanen, R., Oksanen, L. & Razzhivin, V. 1999. Topographic and regional patterns of tundra heath vegetation from northern Fennoscandia to the Taimyr Peninsula. *Acta Botanica Fennica* 167: 29–83.

Walker, D.A. 2000. Hierarchical subdivision of arctic tundra based on vegetation response to climate, parent material and topography. *Global Change Biology* 6(Suppl 1): 19–34.

Walker, D.A., Jia, G.J., Epstein, H.E., Raynolds, M.K., Chapin, F.S. III, Copass, C., Hinzman, L.D., Knudson, J.A., Maier, H.A., Michaelson, G.J., Nelson, F., Ping, C.L., Romanovsky, V.E. & Shiklomanov, N. 2003. Vegetation–soil–thaw depth relationships along a Low-Arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies. *Permafrost and Periglacial Processes* 14: 103–123.

Walker, D.A., Raynolds, M.K., Daniëls, F.J.A., Einarsson, E., Elvebakk, A., Gould, W.A., Katenin, A.E., Kholod, S.S., Markon, C.J., Melnikov, E.S., Moskalenko, N.G., Talbot, S.S. & Yurtsev, B.A. 2005. The Circumpolar Arctic Vegetation Map. *Journal of Vegetation Science* 16: 267–282.

Wielgolaski, F.E. 1997. Fennoscandian tundra. In: Wielgolaski, F.E. (ed.), *Ecosystems of the World III. Polar and alpine tundra.* pp. 27–83. Elsevier, Amsterdam, NL.

Wood, S.N. 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. *Journal of the Royal Statistical Society* Series B 62: 413–428.

Yurtsev, B.A. 1994. Floristic division of the Arctic. *Journal of Vegetation Science* 5: 765–776.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The study sites are located across northwestern Fennoscandia and Russia. 1 = NW Fennoscandia; 2 = N Fennoscandia; 3 = Kola Peninsula; 4 = Kanin peninsula; 5 = Kolguyev island; 6 = Pechora delta; 7 = Varandei; 8 = S Yamal; 9 = SW Yamal; 10 = Bovanenkovo; 11 = W Yamal; 12 = N Yamal.

Appendix S2. The geographical characteristics of the study sites.

Appendix S3. Detailed information on the sampling protocol used in datasets belonging to this study.

Appendix S4. NMDS ordination showing sites for the combination of all the datasets. Half-change scaling scales the configuration so that one unit means halving of community similarity from replicate similarity (Oksanen et al. 2008). The sites belonging to the TWINSPAN clusters described in this research are indicated in black, while non-willow communities are shown in grey. The environmental factors are indicated with arrows, where **lat** stands for latitude, **lon** longitude, **al** mean depth of active layer, **p** mean July precipitation, **T** elevation corrected mean July temperature (0.6 degree lapse rate per 100 m), **sn** mean depth of snow cover, **to V/-S/-T** topographical position valley/slope/top, **c** cover of willow and **h** height of willow.

The arrows point to the direction of most rapid change in the environmental variable.

Appendix S5. NMDS ordination showing species for the part of the data including only the plots belonging to the types described in this work. Species codes are the first three letters of the genus and species (see Table 1 and Appendix S7 for the full names). Only common species are shown. Species scored are weighted averages of site scores in NMDS that show the centre of gravity of species occurrences in ordination space. Therefore, the arrows of environmental variables in the Figure 2 may be used to interpret also the species ordination.

Appendix S6. The ordination diagrams of the plots belonging to the willow-characterised types described in this study are overlain by isotherms of environmental variables, July mean temperature (a), July precipitation (b), Depth of active layer (c) and Height of upright willows (d).

Appendix S7. The mean cover (mean), standard deviation (sd) and relative frequency (freq %) of plant species in the willow-characterised vegetation types.

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