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WILLOW-CHARACTERISED
SHRUB VEGETATION IN
TUNDRA AND ITS RELATION
TO ABIOTIC, BIOTIC AND
ANTHROPOGENIC FACTORS

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ANU PAJUNEN

**WILLOW-CHARACTERISED SHRUB
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RELATION TO ABIOTIC, BIOTIC
AND ANTHROPOGENIC FACTORS**

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Abstract

Deciduous shrubs form the tallest type of vegetation in arctic-alpine areas and are important for ecosystem function. In the southern part of the Eurasian tundra zone, willows (*Salix* spp.) are the most common species in the shrub layer. In the alpine areas of Northern Fennoscandia, willow shrubs are characteristic to areas between tree line and treeless tundra heaths. Vertical structure and composition of willow-characterized tundra vegetation is affected by a variety of ecological factors including climate and herbivory. In turn, the abundance of the willow canopy affects understory species in several ways that still remain inadequately understood.

In this PhD work I describe compositional differentiation of willow-characterized vegetation by using a large data set spanning from north-western Fennoscandia to the Yamal Peninsula in north-western Siberia. I studied environmental factors affecting willow-characterized vegetation and willow growth by using correlative analyses. The factors under investigation were latitude, distance from the sea, depth of thaw, position in the slope, industrial disturbance and reindeer grazing. In addition, I examined the relationships between the shrub biomass estimate and composition and species richness of understory vegetation. The effects of reindeer grazing on vegetation in an alpine forest-tundra ecotone were studied experimentally using reindeer-proof exclosures.

I found that willow-characterized vegetation is floristically variable and comprises at least eight vegetation types. The most abundant willow thickets typically have a forb-rich understory. The growth of willow increased along with increasing summer temperatures. However the height of willow was more determined by distance from the sea, thaw depth and slope position. Reindeer grazing decreased the abundance of willow and changed the composition of understory vegetation. In addition, industrial activities were detected to have destructed shrub vegetation and turned it into graminoid-dominated vegetation. Shrub canopies facilitated forbs but decreased the cover of all the other groups including dwarf shrubs, bryophytes and lichens. The species richness of vegetation decreased along with increasing shrub abundance.

My study shows that arctic-alpine willow vegetation is more diverse than previously thought. There is a predictable relationship between summer temperatures and willow growth. However, the results also show that there are many factors, both physical and anthropogenic, that are likely to complicate this pattern. Most important of these counteracting effects are industrial activities and reindeer grazing. In the areas where shrubs grow in abundance, the species richness of understory vegetation is likely to decrease and forbs are likely to replace other tundra species.

Keywords: arctic-alpine areas, climate change, competition, disturbance, facilitation, industrial impacts, latitude, plant community, reindeer grazing, species richness, thaw depth, topography

To my parents

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My inspiration for studying northern willows started already during my master's thesis in 2000 in Kilpisjärvi. While measuring willows, my supervisor Risto Virtanen and his collaborator Heikki Roininen told me that they had seen vast areas of fragmented shrubs after the migration of reindeer on their Siberian trip. Even though I forgot this image for many years, there was some fascination and curiosity that stayed. Risto also supervised my doctoral thesis all the way. He was there whenever I came with my questions and showed me the way to do science in a brilliant way by combining guidance and tasks to be resolved by myself. I truly admire his way of working and am ever grateful for having the possibility to do my theses under his example and guidance. Risto was a co-author on three of my articles, and during this co-operation I learned very much and had a most inspiring time. I am also grateful for having the possibility use part of Risto's data as a part of two of my studies. I thank Heikki for the possibility to use the enclosure experiment in Kilpisjärvi and also for the fruitful co-operation in writing an article together.

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Helsinki, January 2010

Anu Pajunen

List of original articles

This thesis is based on the following articles, which will be referred to in the text by their Roman numerals:

- I Pajunen A, Kaarlejärvi E, Forbes BC & Virtanen R (2010) Compositional differentiation, vegetation-environment relationships and classification of willow- characterised vegetation in the western Eurasian Arctic. *J Veg Sci* 21: 107–119.
- II Pajunen A (2009) Environmental and biotic determinants of growth and height of arctic willow shrubs along a latitudinal gradient. *Arct Ant Alp Res* 41:478–485.
- III 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 Biol* 31: 1233–1244.
- IV Kumpula T, Pajunen A, Kaarlejärvi E, Forbes BC & Stammer F. Land use and land cover change in Arctic Russia: ecological and social implications of industrial development. Manuscript.
- V Pajunen A, Oksanen J & Virtanen R. Impact of shrub canopies on understory vegetation in western Eurasian tundra. Manuscript.

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1 Introduction

1.1 Shrub vegetation in Arctic-alpine systems

In the transition from latitudinal and altitudinal tree line to tundra heaths there is a zone where deciduous shrubs form the tallest canopy layer and create a variety of habitats that are important for ecosystem functioning (Chernov 1985, Bliss & Matveyeva 1992, Blanken & Rouse, 1994). In the Eurasian Arctic, the dominant species in this shrub zone are grey-leaved willows, mainly *Salix glauca* and *S. lanata*. In alpine areas and in southern parts of arctic tundra, willows typically form mixed stands with dwarf birch (*Betula nana*).

Vegetation characterized by willow shrubs forms zonal vegetation north of the timberline, which corresponds approximately to the 10° C July isotherm (Bliss & Matveyeva 1992, Walker 2000). However, in the most favorable conditions, such as along river banks, this vegetation still occurs in areas with an 8° C July mean temperature (Bliss & Matveyeva 1992, Walker 2000). In the higher slopes and drier soils, willows grow mixed with and lower-growing dwarf birch that is an assumably inferior competitor to willow in the moist habitats with a deep snow cover (Jonasson 1982). Depending on the 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 meters (Edlund & Egginton 1984, Wielgolaski 1997, Schickhoff *et al.* 2002). In the understory of dense willow canopies, forbs and graminoids are the most frequent species, whereas dwarf shrubs and cryptograms generally abound in association with more open canopies (Schickhoff *et al.* 2002). Despite structural similarities between willow-characterized vegetation types described in different parts of the circumpolar Arctic (*e.g.* Holtum 1922, Kalliola 1939, Nordhagen 1943, Porsild 1951, Danilov 1958, Daniëls 1982, Anonymous 1994, Virtanen *et al.* 1999, Schickhoff *et al.* 2002, Sekretareva 1984, 2003, Koroleva 2006, Morozova *et al.* 2006), variation is expected in species composition caused by differences in local conditions and geographical areas. This variation, however, has received relatively little attention and this vegetation is often regarded as a physiognomic entity (Bliss & Matveyeva 1992).

1.2 Abiotic factors affecting willow growth

The radial growth of trees and shrubs has been found to correlate with mean summer temperatures and length of the growing season (Walker 1987, Kirilyanov *et al.* 2003, Chapin *et al.* 2005, Knorre *et al.* 2006, Forbes *et al.* 2009). This explains the general vertical reduction of woody plants along increasing latitude and altitude. It may also be behind the observations of increasing shrub abundance in the past decades in some parts of Arctic (Sturm *et al.* 2001a, Tape *et al.* 2006) and alpine (Kullman 2002) areas that have experienced summer warming during the past decades. However, there remains uncertainty as to the exact cause of the increase in the shrub cover. Other factors such as delayed snow-melt in some areas, due to the increase in winter precipitation, may interfere with the linear climate-shrub growth relationship (Kirilyanov *et al.* 2003, Schmidt *et al.* 2006). In addition, a decrease in the intensity of herbivory may have been at least partly behind these observations (see chapter 1.3). Warm air and soil temperature directly enhance the metabolic rate and photosynthetic activity of plants, and have indirect effects through changes in soil resources such as water and nutrient availability and the depth of annual thaw (Nadelhoffer *et al.* 1991, Jarvis & Linder 2000). These direct and indirect effects of temperature on vegetation are highly species and site specific (Hobbie & Chapin 1998, Bret-Harte *et al.* 2002), and in many cases still remain inadequately understood.

Permafrost in tundra areas affects plants through changes in available rooting space and changes in hydrological, chemical and thermal conditions of soils. Willows and other deciduous shrubs may effectively utilize areas with discontinuous or deep permafrost, where they have plenty of rooting space, available nutrients and good drainage (Schickhoff *et al.* 2002, Lloyd *et al.* 2003, Walker *et al.* 2003, Schuur *et al.* 2007). If the observed warming of permafrost (Osterkamp & Romanovsky 1999, Pavlov & Moskalenko 2002) will lead to degradation of permafrost and deepening of the active layer as predicted (ACIA 2005, Anisimov & Reneva 2006), then shrub abundance is likely to increase. However, in predicting vegetation changes in relation to permafrost, local conditions including vegetation type, small-scale topography, snow conditions and soil characteristics should be taken into account as they are likely to complicate the relationship (Smith & Riseborough 1996, Walker *et al.* 2003).

Despite the latitude of an area, wind and snow patterns create microclimate variability along slopes which is likely to affect the growth of shrubs (Seppälä 2004). In addition, soil conditions and nutrient availability vary along toposequences

thereby affecting the growth of plants. In turn, shrubs may also change the conditions of slopes, for instance by increasing the trapping of snow (Liston *et al.* 2002, Sturm *et al.* 2005) and enhancing the turn-over of nutrients (Epstein *et al.* 2004, Wookey *et al.* 2009). On a broader geographical scale, the distance from the sea is likely to affect the growth of shrubs due to strong winds often associated with areas near arctic seas (Seppälä 2004).

1.3 The effects of reindeer grazing and industrial activities

In the Eurasian Arctic, reindeer (*Rangifer tarandus*) is the most important herbivore affecting the growth of willow (Chernov 1985, Oksanen & Virtanen 1995). Willows are important for reindeer especially at the beginning of the growing season when herbs and graminoids are scarce and reindeer suffer from protein and mineral deficiency after the winter (Vakhtina 1964, Warenberg 1999). Reindeer tend to suppress the growth of their forage shrubs and fragment their distribution within a given landscape (den Herder *et al.* 2004, 2008, Manseau *et al.* 1996). This has led to suggestions that the effects of grazing may even counteract the possible effects of climatic warming on shrubs (Moen & Danell 2003, den Herder *et al.* 2004, Post & Pedersen 2008, Olofsson *et al.* 2009).

Summer grazing by reindeer is likely to also alter the composition of understory vegetation in the shrub-characterized vegetation (Suominen & Olofsson 2000, Kitti *et al.* 2009). Grazing has been found to reduce the cover of dwarf shrubs (Manseau *et al.* 1996, Olofsson 2006a) and forbs (Olofsson 2001, Olofsson *et al.* 2001). On the other hand, grazing has either increased (Oksanen & Virtanen 1995, Manseau *et al.* 1996, Olofsson *et al.* 2001) or decreased (Olofsson *et al.* 2002, Olofsson 2006a, Hansen *et al.* 2007) the cover of bryophytes. According to earlier studies, grazing effects on the vegetation of unproductive mountain heaths are stronger than the effects on the vegetation of more productive tundra meadows (Moen & Oksanen 1998, Olofsson 2001, Olofsson *et al.* 2002). However, in some other systems without natural enemies, grazers have moderated differences between habitats differing in productivity (Virtanen *et al.* 2002, Bråthen *et al.* 2007, Eskelinen 2008) thereby supporting the theory of Oksanen *et al.* (1981), according to which herbivore effects are stronger in relatively productive habitats if grazers are not regulated by their predators.

Reindeer grazing has generally increased species richness of vegetation by reducing the dominance of few palatable plant species and thus increasing the number of coexisting species (Helle & Aspi 1983, Oksanen & Virtanen 1995, Suominen &

Olofsson 2000). Some contrasting negative effects of grazing on species richness have also been found in the case of very intensive grazing (Austrheim & Erikson 2001) and in low-productive habitats, whereas positive effects have mostly been found in relatively productive habitats (Gough & Grace 1998, Proulx & Mazumder 1998). Canopy-forming willows are likely to be important mediators of grazing effects on understory species richness due to their shading and amelioration effects (Epstein *et al.* 2004, Wookey *et al.* 2009). However, experimental evidence on the effects of grazing on species richness in shrub communities remains scarce.

The main areas of semi-domesticated reindeer are Fennoscandia and northern Russia, where reindeer numbers have collapsed in many areas after the break-up of the Soviet Union (Baskin 2005). In some areas of northern Russia industrial activities related to the production of oil and gas have caused fundamental changes to vegetation, including shrub thickets that tend to be vulnerable and regenerate more slowly after disturbance in comparison with other tundra vegetation types (Rebristaya *et al.* 1993). The industrial activities that cause disturbance affecting the composition and cover of vegetation include off-road traffic, roads, railroads, quarries and chemical disturbance (Sumina 1998, Forbes *et al.* 2001, Khitun & Rebristaya 2002, Lavrinenko *et al.* 2003). Earlier studies show that plant groups particularly vulnerable to disturbance include shrubs, certain groups of bryophytes (*e.g.* *Sphagnum* spp.) and fruticose lichens, whereas many graminoids (*Carex* spp., *Eriophorum* spp., certain *Poaceae* spp.), especially rhizomatous forms regenerate more easily (Oksanen & Virtanen 1997, Forbes *et al.* 2001). In some areas, such as the Yamal Peninsula, industrial development also concentrates the effects of grazing and trampling since the spreading of industrial activities push the reindeer herds into smaller areas. In the Yamal Peninsula, reindeer numbers have also steadily grown in the past decades for a variety of reasons (Baskin 2005). Consequently, the overlapping of these two livelihoods may lead to degradation of the pastures (Vilkhek & Bykova 1992).

1.4 The effects of shrub canopies on understory vegetation

Alteration in abundance of canopy-forming deciduous shrubs is likely to have pronounced effects on vegetation patterns through competition and facilitation, and yet, the relative roles of these processes remain an unresolved issue in tundra ecosystems (Callaway *et al.* 2002, Brooker *et al.* 2008). Shrub canopies considerably decrease the amount of solar radiation reaching the understory vegetation (Totland & Esæte 2002), which is likely to create competition for light

(Fargione & Tilman 2003). On the other hand, shrubs facilitate understory plants by amelioration of stress, accumulation of nutrients and water and by protection from wind and herbivores (Brooker & Callaghan 1998, Callaway 1992). The response of an understory species to shading created by canopies is likely to depend on the life strategy of a species. Therefore, it has been suggested that functional groups and plant traits describing different ecological strategies could be useful in predicting species-specific association between plants (Eskelinen 2009, Maestre *et al.* 2009).

The large leaf area typical to many forbs has been associated with competitiveness in terms of high photosynthetic capacity and short leaf turnover time, which is likely to be beneficial in patchy light conditions (Grime 1979). In addition, canopy height is generally accepted as a useful measure of competitive advantage (Hodgson *et al.* 1999), albeit greater height also implies a greater sensitivity to disturbance (Westoby *et al.* 2002). In their study of forest succession, Dahlgren *et al.* (2006) showed a positive correlation between specific leaf area of an understory species and forest canopy density. This gives reason to assume that simple traits such as leaf size or canopy height may be useful in explaining species co-occurrence patterns in relation to canopy.

An experimental study simulating the effects of a warming climate showed that most functional groups of plants, except deciduous shrubs and graminoids, decreased in abundance under warmer conditions and that the overall species richness declined together with increasing dominance of shrubs (Walker *et al.* 2006). This supports the view according to which competition is the prevailing process driving canopy-understory relations in tundra (Oksanen 1990) and that the relative role of competition increases in association with decreasing environmental stress (Bruno *et al.* 2003, Brooker *et al.* 2008). On the other hand, Totland *et al.* (2004) found that in a relatively favorable arctic plant community species richness was higher outside than inside of the willow canopies, but in a more severe community the species richness did not vary in and outside the canopies. Presumably this was due to the counteracting effects of facilitative and competitive processes, the previous being relatively more important in the severe community (Brooker & Callaghan 1998). Despite the increasing need for broad-scale syntheses on canopy effects on understory vegetation, the utilization of geographically extensive datasets in association studies in a correlative manner is scarce (see however, Cornelissen *et al.* 2001). In addition, especially the traits of cryptograms, an important constituent component of the arctic vegetation, have been more neglected than vascular plants in most previous studies (Cornelissen *et al.* 2007).

1.5 Aims of this study

The aim of this PhD work was to describe willow-characterized vegetation types across western Eurasian tundra and to examine the ecological and anthropogenic factors affecting their growth, composition and species richness. In addition, the aim was to examine how deciduous shrub canopies affect the composition and species richness of understory vegetation. In particular, I addressed the following questions:

- 1) How does physiognomically relatively uniform tundra willow vegetation differentiate floristically? What are the patterns of differentiation in relation to climatic and local factors?
- 2) What is the relative importance of climate, soil thaw, slope position, distance from the sea and reindeer grazing for the growth and height of willow shrubs in Arctic conditions?
- 3) How does reindeer grazing affect the composition and species richness of shrub-characterized vegetation in a forest-tundra ecotone?
- 4) How does tundra vegetation including shrub thickets regenerate after mechanical industrial disturbance? How do industrial impacts affect the quality of reindeer pastures?
- 5) How do shrub canopies affect the composition and species richness of understory vegetation and can the variation in the effects be predicted by using simple plant traits?

2 Material and Methods

2.1 Study areas

The geographical area of this study spans over 1000 km from northwestern Fennoscandia to the Yamal Peninsula, northwestern Siberia (Fig. 1). It thus extends over several bioclimatic tundra zones and phytogeographic sections (Elvebakk 1985, Tuhkanen 1986, Yurtsev 1994, Walker *et al.* 2005). The study sites in Fennoscandia (study sites 1 and 2) are mountainous, lying at elevations between 200–600 m a.s.l., whereas all the Russian sites are located along hill slopes near river valleys at lower elevations (0–130 m a.s.l.). All the study sites are treeless due to the altitude in Fennoscandia or latitude in northern Russia. The mean annual temperature, the mean July temperature, precipitation and the depth of snow decline eastwards (Virtanen *et al.* 2006). Permafrost is present in the eastern study sites (4–12) (Goryachin *et al.* 1994) and the depth of the active layer decreases eastwards among these sites. All the areas are extensively grazed by reindeer. A variety of geographical conditions creates broad categories of soil types among the study sites.

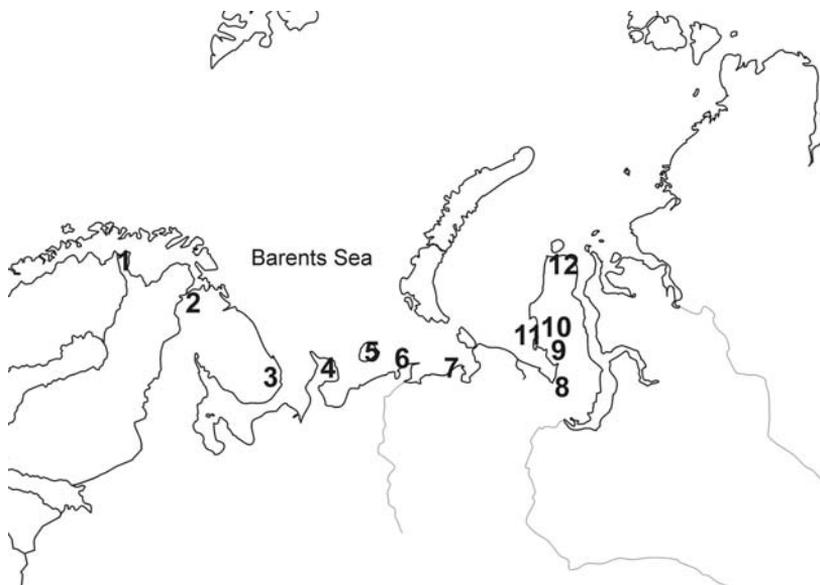


Fig. 1. The study sites span from north-western Fennoscandia to the Yamal Peninsula in West Siberia.

2.2 Research methods

I collected parts of the vegetation data during 2005–2007 in northwestern Siberia (papers II and IV corresponding to sites 7–10). For studying the vegetation effects of reindeer grazing, I used an ongoing enclosure experiment in a forest-tundra ecotone in the vicinity of the village of Kilpijärvi in northwestern Fennoscandia (paper III, site 1). In the geographically large-scale papers I and V, I used all the datasets mentioned above and in addition available data sets from western Eurasian tundra (Virtanen *et al.* 1999, 2006). This data has been collected across gradients of tundra habitats from the Kola Peninsula to the northern Yamal Peninsula and corresponds to the study sites 3–6 and 11–12 (Fig. 1). In addition, a part of the data published by Kalliola (1939) from northern Fennoscandia, corresponding to site 2 (Fig. 1), was augmented in papers I and V.

2.2.1 Growth of willow (II)

To study the growth patterns of willow I sampled willow thickets at 13 locations along a latitudinal transect spanning from the central Yamal Peninsula to the northern Polar Urals in the summers of 2006–2007. The total length of the transect was over 300 km and it consisted of two parts: 1) an approximately 125-km-long section in the more northern area (study site 9 in Fig. 1) and 2) an approximately 30-km-long section in the more southern area (site 8 in Fig. 1). The transects followed the only two available access routes into the region, an all-terrain vehicle trail in the more northern area and a road in the more southern area.

The study sites were situated along the nearest slope of a watershed from a road / all terrain vehicle trail where willow shrubs were growing. At each study site, willows in three distinct topographical positions were sampled: (1) the uppermost position (hereafter called top) (2) the mid-slope position (hereafter called middle) and (3) the down slope position (hereafter called bottom). In each position of the study site, 1–3 study plots 10 x 10 m in size were chosen by using a randomization procedure. In each study plot, the height of 10 random willow ramets per species (*Salix glauca* or *S. lanata*) representing the prevalent uppermost canopy was measured from the ground. The top shoots with at least four years of growth increments of the measured individuals were collected for later retrospective growth measurements. The number of reindeer droppings was counted along a side of one randomly chosen plot (10 x 2 m) at each at segment (top, middle, bottom) of each study site. In addition, the depth of thaw (five measurements) was measured within each study plot.

In the retrospective measurements, the length of shoots was measured starting from the leading shoot and proceeding annually back to the shoot that had been growing in 2003. The shoot diameter was measured using cross measurements in 2003. Prior to the statistical analyses, the mean value of each response variable – the height of willow shrubs and the length and diameter of willow shoots – was calculated for each plot. The explanatory variables were latitude (distance from the Equator (km), distance from the sea (km), position on the slope (“top”, “middle”, “bottom”), depth of thaw (cm), the mean number of reindeer droppings on the study slope and the identity of *Salix* species (*S. lanata* or *S. glauca*).

Linear mixed effects (LME) models (Pinheiro & Bates 2000) were used to investigate the relationships between response and explanatory variables. In the models, a study site (1–13) was set as a random factor, whereas all the explanatory variables mentioned above were set as fixed factors. The quadratic terms of all the continuous explanatory variables were included as explanatory variables in the initial models. To obtain minimum adequate models (Crawley 2002), non-significant terms were removed, and final models contained only significant explanatory variables or their interaction terms. In order to obtain satisfactory residual plots of the models, the data of length and diameter of willow shoots were log-transformed prior to the modeling. To graphically illustrate the results, linear or curvilinear regression models with only one variable were used to draw the prediction lines for each variable. Statistical parts of this study, as for most of the rest of the papers, were carried out using the R statistical environment (R Development Core Team 2008).

2.2.2 The effects of reindeer grazing (III)

The enclosure-experiment for investigating the effects of reindeer grazing on the vegetation in the forest-tundra ecotone was conducted at Mt. Muotkantakka (69° 07'N, 20° 45' E) in northwestern Finnish Lapland (site 1 in Fig. 1). In this area, reindeer are present throughout the year. The experimental sites ranged from valleys with mountain birch (540 m a.s.l.) including frost heath and riparian habitats to treeless tundra heath above the timberline (560–585 m a.s.l.). The experimental system was established in 1998. In total, 102 plots of the size 2 x 2 m (1 x 1 m in the tundra heath) with each plot containing at least one willow genet growing approximately in the middle of the plot were randomly chosen in the study area. There were 22 plots in the tundra heath, 56 in the frost heath and 24 in the riparian area. From every two neighboring plots, one randomly chosen plot was fenced in by a reindeer-proof enclosure (mesh size of 38–150 mm) in 1999.

The vegetation sampling was conducted in 2006. In order to analyse the effect of microhabitat on vegetation responses in the frost heath and in the riparian area, hummocks and hollows were sampled separately from each experimental plot. Four subplots (two in tundra heath) of the size 50 x 50 cm were sampled at each plot. In each subplot, the cover of plant groups and the cover of all the plant species were estimated visually using the following classes: +, 1/2, 1, 2, 3, 4 ...15, 20, 30, 40, ..., 100%. The plant groups, determined on the basis of growth form, were: upright willow (*Salix* spp.), dwarf birch (*Betula nana*), prostrate dwarf shrubs (woody plants height under 20 cm), forbs, sedges (*Carex* spp. and *Eriophorum* spp.), grasses (*Poaceae* spp.), bryophytes and lichens. The height of the plant groups was measured from five random individuals / subplot. In addition, the area of bare soil was estimated. The mean values of the two subplots (hummocks and hollows) from each study plot were used in the statistical analyses.

I used generalized linear modeling with quasi-Poisson error structure for statistical testing of the treatment effects on vegetation composition (R Development Core Team 2008). The cover of plants groups (see above) and species richness of vegetation (vascular plants, bryophytes and lichens) were response variables, whereas treatment (exclosure/control), habitat (factor with 3 levels) and hummock-hollow structure (factor with two levels referred to as “microhabitat”) were explanatory variables. In the initial models, exclosure, habitat, microhabitat and their interactions were included as explanatory variables. To obtain minimum adequate models (Crawley 2002), non-significant terms were removed and the final models contained only significant explanatory variables.

2.2.3 Case studies on industrial activities (IV)

I conducted the studies on the industrial activities in the Bovanenkovo gas field (study site 10) and in the Toravei oil field (study site 7) in close co-operation with a geographer applying satellite image analyses and a social anthropologist conducting participant observation and interviews among nomadic Nenets reindeer herders. This approach was used as a tool for finding a more thorough understanding on industrial effects on reindeer pastures in these two areas. To characterize the vegetation change around mechanically affected industrial areas I used off-road vehicle tracks that separate disturbed patches with sharp boundaries enabling comparisons with adjoining undisturbed vegetation. In both areas, there is an extensive network of off-road tracks resulting from the use of all terrain vehicles

during the growing season. Individual tracks vary in width from 4 to 8 m, whereas patches resulting from multiple tracks can be much larger in area. Until the early 1990's the tracks were used so intensively that the original vegetation cover was destroyed and mineral soils were visible in archival satellite images. By the time of sampling they were naturally revegetated.

The vegetation sampling was conducted at Bovanenkovo in July 2005 and at Toravei in July 2006. Three 15–20 year old multi-pass vehicle tracks were randomly chosen with the aid of satellite images within each of the three major vegetation types in each study area. These vegetation types were willow thicket, dwarf shrub tundra and mire. Within each track six treatment plots (50 x 50 cm) were set up in the middle of the track and six control plots were situated along a parallel transect in undisturbed vegetation. The distance between all the plots was 12 m. Within the plots the cover of each species, also including bryophytes and lichens, was estimated visually using the following scale: +, ½, 1, 2, 3, ..., 10, 15, 20, 25, ...100.

The cover estimates of plant species were pooled on the basis of their functional group (Chapin *et al.* 1996 with few exceptions). The covers of dwarf shrubs and lichens were not analyzed, because they were infrequent overall and almost absent in mires. They were, however, included in the group of reindeer forage plants together with upright deciduous shrubs, forbs and graminoids. The impact of disturbance, area, vegetation type and their mutual interactions on the cover of functional groups of species and species richness of vegetation (total number of species, number of vascular plants, number of cryptogram species) was tested with mixed linear models (LME) (Pinheiro & Bates 2000). In order to obtain satisfactory residual plots of the models, square root transformation was applied to the data of deciduous shrub and forb cover prior to modeling. I used track as a random factor in the analyses, whereas disturbance, area, vegetation type and their interactions were set as fixed factors in the initial models. According to principles of the minimum adequate model (Crawley 2002), non-significant terms were removed, and final models contained only significant explanatory variables. To investigate the relations of species composition between disturbed and undisturbed plots and among different vegetation types in Bovanenkovo, we performed detrended correspondence analysis (DCA) for the species data by using the Vegan package of R (Oksanen *et al.* 2008). We also performed DCA analyses for disturbed and undisturbed plots of shrub thickets in both study areas.

2.2.4 Classification and facilitation studies (I and V)

To classify willow-characterized tundra vegetation into types and to study the associations between deciduous shrub abundance and composition and species richness of the understory vegetation, I used a large dataset encompassing all of the datasets described above, with the exception of the disturbed plots from study IV. In addition, I also used other vegetation data available (Kalliola 1939; Virtanen *et al.* 1999, 2006). In total, there were 758 plots and 506 species included in this combination of datasets.

For the classification study (I), the combined data were classified into vegetation types by the polythetic divisive TWINSpan program with default options (WinTWINS version 2.3; Hill & Šmilauer 2005). From the TWINSpan clusters I discerned eight vegetation types with a distinct willow cover (cover of willow > 10 %) to describe in detail. Diagnostic species of these willow-characterized vegetation types were determined with the Indval method that calculates the indicator value of species in clusters (Dufřene & Legendre 1997, Chytrý *et al.* 2002). Indval analyses were performed with default options including 1000 randomizations and usage of a 0.05 error probability level. To support the TWINSpan analyses and to describe the relationships between environmental factors and occurrence of willow vegetation, I performed two non-metric multidimensional scaling (NMDS) analyses with default options using the vegan package of the R statistical environment (Oksanen *et al.* 2008). In the first analyses, all the plots were included and in the second analyses only the data including the plots belonging to the eight TWINSpan clusters of willow-characterized vegetation (173 plots) were included. 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), I overlaid fitted environmental vectors and centroids on the NMDS ordination (Oksanen *et al.* 2008).

To study the relationship between shrub abundance (biomass estimate) and composition and species richness of understory vegetation (V), I used subdata (359 plots) including the samples having a deciduous shrub cover above zero. The associations were tested using linear mixed effects (LME) models (Pinheiro & Bates 2000). As an appropriate estimation of shrub biomass, I counted the vegetation volume (mean cover x height) and used its cube root ($x^{1/3}$) in the analyses. Study site (1–12) was set as a random factor and shrub biomass estimate as a fixed factor. To control the effect of variable plot size, I used the logarithm of plot size as an additional fixed factor.

The relationship between individual species and shrub biomass estimate was examined by using the entire data set (758 plots) and analysing it with the *wascor* function from the *vegan* library (Oksanen *et al.* 2008) that computed the weighted average value of shrub abundance for all plots in which a species occurred, weighted by the species abundance. This method showed whether a species had a positive or negative association with the deciduous shrub biomass estimate with an error possibility of 0.001 % using 999 unrestricted permutations.

To investigate the canopy effects on species representing certain morphological plant traits, I divided the vascular plant species into the following classes on the basis of literature: high (≥ 50 cm) vs. low (< 50 cm) and big-leaved (≥ 10 cm²) vs. small-leaved (< 10 cm²) plants (Polunin 1959, Flora of North America Editorial Committee 1993, Hämet-Ahti *et al.* 1998, Aiken *et al.* 1999, Mossberg & Stenberg 2003). For some species, not all the leaf size information could be found in the literature, and in these cases, I measured them from the Herbarium collection in the Botanical Museum of Oulu. The width and length of the most common type of leaf (if many) was measured from five random specimens collected from arctic-alpine habitats. In bryophytes, the contrast was made between high (≥ 5 cm) and low (< 5 cm) and broad-leaved (≥ 10 cm²) vs. narrow-leaved (< 10 cm²) species on the basis of literature (Dierssen 2001, Ignatov & Ignatova 2003). Since all the lichen species were expected to show a constant association with shrub abundance, they were treated as a single group. In order to examine the relationships between plant traits and shrub abundance, contingency tables and Fisher's exact test were used. These analyses tested whether plant traits were randomly distributed with regard to positive, negative or neutral association ($df=2$) with the shrub abundance. A species was included in the Fisher's exact test, if its frequency was 5 or more.

2.2.5 Nomenclature

In the Fennoscandian study (III) the nomenclature for vascular flora, bryophytes and lichens follows Hämet-Ahti *et al.* (1998), Ulvinen *et al.* (2002) and Vitikainen *et al.* (1997), respectively. For the datasets including study areas across the Eurasian tundra the nomenclature for vascular plants, bryophytes and lichens follows Sekretareva (1999), Hill *et al.* (2006) and Andreev *et al.* (1996), respectively.

3 Results

3.1 Differentiation of willow-characterized vegetation (I)

Willow-characterized vegetation types (cover of upright willows >10%) were clearly differentiated from other tundra vegetation. However, they occurred across a variety of conditions and showed great compositional variation among them. The presence and abundance of TWINSPAN indicator species of the first split separating willow-characterized vegetation from other tundra vegetation were *Equisetum arvense*, *Salix glauca*, *S. lanata* and *Sanionia uncinata*. This split was also supported by the ordination analysis of the whole data set. Among the willow-characterized vegetation the TWINSPAN separated eight types, half of which were tundra and mire types having a relatively low abundance of willow and a high cover of bryophytes in the understory. These types were: 1) *Salix glauca-Carex aquatilis* type (SgCaT), 2) *Aulacomnium-Tomentypnum* type (ATT), 3) *Salix-Betula-Hylocomium* type (SBHT) and 4) *Salix lanata-Brachythecium mildeanum* type (SIBmT). In comparison, the rest of the types had relatively dense and high willow cover and an abundant forb layer in the understory. In contrast to the previous types, the active layer was deep and the cover of bryophytes low. These types were: 5) *Salix-Pachypleurum* type (SPT), 6) *Salix lanata-Myosotis nemorosa* type (SIMnT), 7) *Salix-Trollius-Geranium* type (STGT) and 8) *Salix-Comarum palustre-Filipendula ulmaria* type (SCFT).

The ordination analysis revealed that willow-characterized vegetation occurred in valleys and slopes in comparison with other tundra vegetation occurring in higher topographical positions. Willow-characterized vegetation types were found in areas where July mean temperature varied between 6 to 10 °C. There were types that resembled one another floristically (*e.g.* SPT and SIMnT), but occurred in areas differing in terms of their July mean temperature (6 and 8 °C, respectively). Some of the types clearly clustered the ordination space (ATT, STGT, SCFT), whereas others were more heterogeneous (SBHT, SIMnT, SgCaT) indicating a greater variation in their geographical distribution. Most willow-characterized vegetation types were found to occur on sites where thaw depth was > 60 cm. However, the tundra mires tended to have a shallow active layer (< 60 cm). There was also an association between the height of willow and the depth of the active layer.

3.2 Growth and height of willow (II)

The primary (shoot length) and secondary (shoot diameter) growth of willow decreased northwards, but the height of willow was not determined by latitude. Height and secondary growth increased with increasing distance from the sea, while the effect of distance from the sea on the primary growth of willow depended on the depth of thaw. At shallow thaw depths, primary growth increased as a response to the increasing distance from the sea, whereas in substrates with deeper thaw only minor effects were observed. At the top of the slope and in areas with shallow thaw, all the growth parameters of willow were low compared to the other slope positions and to areas with deep thaw. The decline in primary growth northwards and towards shallower thaw depths was stronger for *S. glauca* than for *S. lanata* (Table 1).

The reindeer grazing effects on the growth and height of willow in all cases depended on an additional environmental factor. An increase in grazing intensity was associated with a decrease in the height of willow in the areas of deep thaw, whereas at shallow thaw depths, the increase in the grazing intensity was associated with an increase in the height of willow. Reindeer grazing had a negative effect on the primary growth of willow and this effect was stronger at the middle and the bottom of the slope than at the top of the slope. The increasing intensity of grazing was associated with a decrease in the secondary growth of willow and this effect was more pronounced in areas distant from the sea than in areas closer to the sea (Table 1).

Table 1. The effects of environmental determinants and their interactions on the growth and height of willow. In the direction of effects, + indicates positive effect, - negative effect and 0 no effect. Two signs in sequence indicate stronger effects on a certain level in comparison with another level in case of significant interactions between variables. The statistics are drawn from LME-models simplified according to the minimal adequate principles.

Environmental factor	Growth variable	Direction of effect	Statistics
Latitude	secondary growth	-	$F_{1,9}=451.0, p<0.0001$
Latitude x species	primary growth	S. glauca- - S. lanata -	$F_{1,226}=10.0, p=0.002$
Distance from the sea	height	+	$F_{1,46}=4.9, p=0.03$
Distance x thaw depth	primary growth	deep thaw 0 low thaw +	$F_{1,226}=5.7, p=0.02)$
Depth of thaw	secondary growth	+	$F_{1,46}=24.3, p<0.0001$
Depth of thaw x species	primary growth	S. glauca+ + S. lanata+	$F_{1,226}=3.8, p=0.05$
Slope position	height	middle>bottom>top	$F_{2,46}=12.8, p<0.0001$
	secondary growth	bottom>middle>top	$F_{2,46}=27.6, p<0.0001$
Reindeer grazing x thaw depth	height	deep thaw - low thaw +	$F_{1,46}=4.6, p=0.04$
Reindeer grazing x distance from the sea	secondary growth	far from sea - - close to sea-	$F_{1,46}=22.5, p<0.0001$
Reindeer grazing x slope	primary growth	middle- - bottom- - top -	$F_{2,226}=6.0, p=0.003$

3.3 The effects of reindeer grazing on vegetation (III)

The total cover of vegetation, cover of upright willows, dwarf birch, dwarf shrubs, forbs and grasses increased in exclosures (Fig. 2). In addition, the height of willow, dwarf shrubs, forbs, grass foliage, bryophytes and lichens increased in exclosures. The increase in the total cover of vegetation and in the covers of willow and dwarf birch was greatest in the least productive tundra heath (Fig. 2). In contrast, the increase in the height of willows and grass foliage was strongest in the most productive riparian area. The effects of exclosures on the cover and height of willow were clearest on hummocks, where they grew more abundantly. The cover of bryophytes and the area of bare soil decreased in exclosures, whereas the covers of sedges, lichens and litter were not affected by the exclosure experiment.

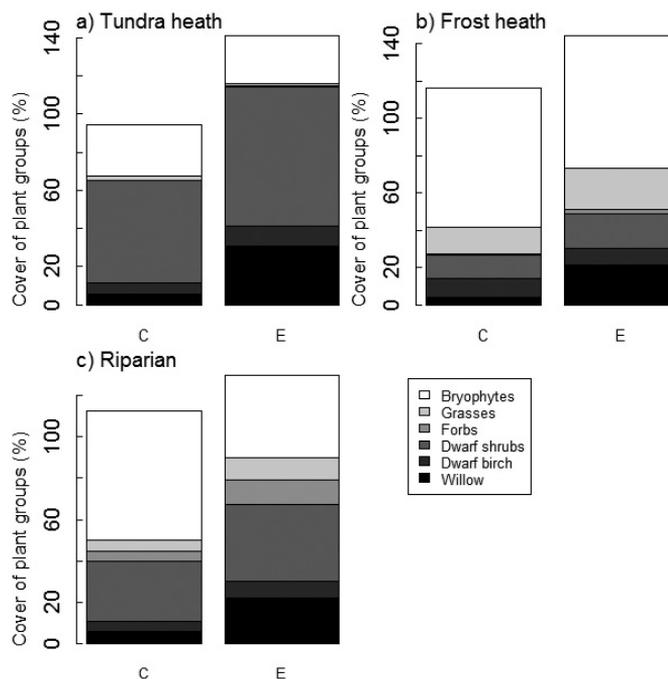


Fig. 2. The cover of plant groups in exclosures (E) and in control plots (C) in different habitats of forest-tundra ecotone. All these illustrated plant groups responded significantly to the exclosure treatment.

The exclosures had no significant effect on the total number of species. The number of vascular plant species decreased in exclosures in the hollows of the riparian area, whereas in the hummocks and in the other two habitats, the exclosures did not have an effect. The number of bryophyte species decreased in exclosures in all habitats, whereas the number of lichen species was not affected by the exclosure experiment.

3.4 The effects of industrial activities (IV)

Most species groups regenerated poorly during the 15 years after severe mechanical disturbance. This most clearly held true for deciduous shrubs that showed the greatest difference between disturbed and undisturbed sites in willow thickets. In contrast with the other plant groups, the cover of graminoids was greater on disturbed ground than in the adjoining undisturbed vegetation. Due to the strong revegetation of graminoids, the cover of reindeer forage plants in Bovanenkovo was

approximately the same in disturbed and undisturbed vegetation, albeit in Toravei the opposite held true. The recovery of bryophytes after disturbance depended on the study area, being stronger in Toravei than in Bovanenkovo. The total species richness and the species richness of vascular plants and cryptograms were all lower in disturbed vegetation than in undisturbed vegetation.

In the DCA ordinations, the plots from the disturbed areas clustered near to each other, revealing that anthropogenic disturbance homogenizes vegetation across geographical areas and vegetation types. In the ordination including only the willow thickets of Bovanenkovo and Toravei, the disturbed plots clustered in the middle of the diagram, whereas the plots of undisturbed vegetation showed greater variation in relation to the second DCA axis. In the area corresponding to the disturbed plots in the species ordination, there was a cluster of hydrophilic graminoids such as *Carex aquatilis* and *Eriophorum vaginatum*. In addition, there were hydrophilic bryophytes such as *Calliergon cordifolium* and *Plagiomnium ellipticum* in the sector of the disturbed plots. In the DCA ordination for all the vegetation types at Bovanenkovo, the disturbed plots clustered near each other, whereas original vegetation clustered according to the respective types in relation to the first and second axis. The species ordination of Bovanenkovo revealed that hydrophilic graminoids such as *Arctophila fulva*, *Carex aquatilis* and many other graminoids clustered in the sector corresponding to the area of disturbed plots.

According to the satellite image analysis, the amount of willow vegetation had declined 15–20% in the vicinity of industrial areas due to the mechanical disturbance. The graminoid-dominated secondary vegetation was seen by reindeer herders as potentially good reindeer pasture. Especially in early summer, the emerging graminoid shoots have high forage value for reindeer. However, industrial waste and other industrial disturbance limited the utilization of the revegetating tracks.

3.5 Canopy effects on understory vegetation (V)

The cover of forbs positively associated with the biomass estimate of deciduous shrubs. Conversely, the cover of dwarf shrubs, graminoids, bryophytes and lichens had a negative relationship with shrub biomass. The total species richness of vegetation and the species richness of bryophytes and lichens decreased along with increasing abundance of deciduous shrubs. The species richness of vascular plants did not associate with shrub biomass.

Large-leaved vascular plants and bryophytes occurred more frequently beneath a dense deciduous shrub canopy. Large-leaved vascular plant species included many forbs, *e.g.* *Petasites frigidus*. In addition, tall-statured vascular plants such as *Veratrum album* had a positive association with willow canopy. Among bryophytes, large-leaved species that benefitted from shrub canopies included, *e.g.* *Plagiomnium ellipticum* and *Rhizomnium pseudopunctatum*. However, according to the weighted averaging analysis, one bryophyte species also showing a distinct association with dense willow canopy was *Brachythecium mildeanum*, a pleurocarpous species with relatively small leaves. All the lichen species showed an either negative or indifferent association with the shrub canopy.

4 Discussion

4.1 Variation in willow-characterized vegetation types

My study showed that despite the physiognomic similarity of willow-characterized 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. The first TWINSpan division among willow vegetation – that was also supported by the ordination analyses – was the separation between tundra and mire types and forb-rich types. In the forb-rich types, the abundance of willow was generally higher than in the tundra and mire types. The drivers behind this differentiation may be related to vegetation succession that in some areas leads to accumulation of bryophytes, which – via decreasing the depth of annual thaw – reduce shrub growth overall. In other areas where conditions favor shrub growth the canopy effects may regulate the composition of understory vegetation and favor the occurrence of forbs. The division between tundra and mire types and forb-rich types is comparable with the split between acidic soil types in higher riverbank terraces and more basic soils in lower riverbanks in Alaska (Schickhoff *et al.* 2002).

Most willow-characterized tundra vegetation types have at least tentatively described counterparts in the earlier studies. Especially the forb-rich types have ecological counterparts described throughout the Arctic with a similar vegetation structure albeit different species composition (Nordhagen 1943, Dahl 1956, 1987, Sekretareva 1984, 2003, Matveyeva & Zanoza 1986, Moen 1990, Schickhoff *et al.* 2002, Koroleva 2006). This structural similarity of distant plant communities supports the idea of a strong role for canopies in the regulation of understory vegetation and also the positive feedback between shrub abundance and nutrient cycling in soils (Wahren *et al.* 2005). However, my analyses also show that the variation in canopy structure may mismatch with other compositional variation in willow-characterized vegetation types. For instance, the tall herb and willow-tall herb types of Kalliola (1939) represented a relatively uniform vegetation unit in our analyses (*Salix-Trollius-Geranium* type), although there were plots with discontinuous willow canopies. Also, the *Salix-Pachypleurum* type with an open and low willow canopy clustered together with forb-rich types characterized by a more closed willow canopy. Therefore, the split between tundra and mire types and forb-rich types is also related to soil characteristics as found by Schickhoff *et al.* (2002).

My results support earlier reports in which willow-characterized tall shrub communities occur in the Eurasian Arctic between the July isotherms 8 °C and 12 °C (Bliss & Matveyeva 1992, Walker 2000, Walker *et al.* 2005). However, my results also show that there are types floristically similar to tall shrub types that have low willow canopies (*Aulacomnium-Tomentypnum* type and *Salix lanata-Pachypleurum alpinum* type) and may still be found in much colder areas. The described vegetation types differentiated in relation to temperature gradients, but the climatic regimes of most types were relatively variable. The willow vegetation was restricted to valleys and slopes and to the areas of deep thaw. It thus seems that, in addition to climate, other factors such as topographic position and depth of thaw affect the vegetation-climate relationships in tundra willow communities.

4.2 Effects of abiotic environmental factors on willow growth

The observed associations between July mean temperature and the occurrence of willow-characterized vegetation types (I) and between latitude and the primary and the secondary growth of willow (II) suggest a correlation between willow growth on the July isotherm. These results are in line with dendrochronological and experimental studies showing that an increase in mean summer temperatures causes an increase in shrub abundance and radial growth (Walker 1987, Knorre *et al.* 2006, Walker *et al.* 2006, Forbes *et al.* 2009). These findings may aid in the understanding of the observations from Alaska and elsewhere, where the abundance of shrubs has increased in recent decades, when the summer temperatures have increased (Sturm *et al.* 2001a, Tape *et al.* 2006, Forbes *et al.* 2009, Olofsson *et al.* 2009). In addition, observations of indigenous people, such as Nenets from the Yamal Peninsula, confirm these observations of increasing shrub abundance (Forbes & Stammer 2009). It is noteworthy that several positive feedbacks may be involved in the observed increase in shrub abundance: first the enhancement of nutrient cycling caused by shrubs (Wahren *et al.* 2005) and also a decrease in albedo of solar radiation due to the increased amount of foliage (Chapin *et al.* 2005). The positive correlation between the height and growth of willow and increasing distance from the sea supports this same trend and also earlier observations according to which most abundant arctic willow communities are found in continental areas (Young 1971, Walker 1987, Bliss & Matveyeva 1992). As the suppressing effect of the cold sea on the primary growth of willow was stronger in the areas with shallow thaw, the results suggest that several factors may simultaneously reduce willow growth.

The primary (shoot length) and secondary growth (shoot width) of willow were significantly greater in sites with deeper thaw (II). This result conforms to earlier reports according to which most of the arctic willow communities are found in southern tundra areas, where there is either discontinuous permafrost or the active layer is deep (Bliss & Matveyeva 1992). Also, in Alaskan riparian habitats, the height of willows decreased along topographical gradients, along which the depth of thaw decreased (Schickhoff *et al.* 2002). These findings suggest a dependency of willow on rooting space and on the nutrients and water that are more available in the soils characterized by deep thaw. According to the results found here, the depth of thaw explains the growth of willow more clearly than the direct effect of latitude. As a consequence, the predicted permafrost thawing in the coming decades (ACIA 2005, IPCC 2007) may alter the vertical structure of willow-characterized communities. However, the depth of thaw is determined by temperature regimes at variable levels including also snow conditions and vegetation (Smith & Riseborough 1996, Walker *et al.* 2003). Therefore, the prediction of thaw-depth-vegetation patterns is complicated, and sometimes an increase in vegetation cover may reverse the effects of climate on thaw depth (Walker *et al.* 2003)

The willow-characterized vegetation types were found to occur along slopes and in valleys in contrast with other tundra vegetation (I). In addition, the growth and height of willow were lowest on the tops of the slopes compared to lower slope positions (II). My analyses thus strengthen earlier reports and studies suggesting that topographic variability is among the main determinants underlying the occurrence of willow-characterized tundra vegetation (Holttum 1922, Kalliola 1939, Chernov 1985, Wielgolaski 1997, Chernov & Matveyeva 1997, Walker 2000). This may be a result of wind-driven snow accumulation at the bottom parts of slopes and the ability of snow to protect willow shoots from the wind, abrasion from ice crystals and winter browsing by herbivores. This would support the traditional way of seeing snow depth as the main determinant of height of woody plants in arctic and subarctic environments (Kihlman 1890, Chernov 1985). On the other hand, at the top part of slopes there tends to be low nutrient availability (Shaver *et al.* 1996) and a reduction in soil moisture that may reduce the growth of willow. In this case, snow trapping by shrubs (Sturm *et al.* 2001b, 2005, Liston *et al.* 2002) would cause the accumulation of snow at the bottom parts of slopes instead of the other way around (Seppälä 2004). Snow cover insulates soils in the winter, thereby retarding the freezing process and causing higher winter ground temperatures than in adjacent sites of shallow snow (Seppälä 2004). This, further enhanced by increased drainage

related to steepness of slope, promotes the development of deep thaws, further promoting the growth of willows (Liston *et al.* 2002, Sturm *et al.* 2005).

4.3 The role of reindeer grazing on willow vegetation

The results from the enclosure experiment (III) and from the willow growth and height measurements (II) show that reindeer grazing decreases the abundance of willow in arctic-alpine areas. This result is in line with earlier studies from arctic-alpine areas (Quellet *et al.* 1994, Manseau *et al.* 1996, den Herder *et al.* 2004, 2008, Kitti *et al.* 2009). The effect of reindeer exclusion (III) on the cover of willow was greater in tundra heath than in the other two habitats suggesting that under harsh climatic conditions and unproductive soils grazing suppresses the growth of woody plants more strongly than in more productive habitats (den Herder & Niemelä 2003, Oksanen & Moen 1994, den Herder *et al.* 2008). However, the enclosure effects on willow height (III) and associations between grazing and willow growth and height (II) show that the effects of grazing are most pronounced in areas where other environmental factors are most favorable, as found in earlier studies (Gough *et al.* 2007, Eskelinen 2008, Post & Pedersen 2008). These findings may contribute to the understanding of the observed nonlinear relationship between height of willow-characterized vegetation types and temperature conditions (I) suggesting that the effects of grazing by reindeer may complicate the vegetation response to climatic warming in tundra regions (Oksanen *et al.* 1981, Post & Pedersen 2008, Olofsson *et al.* 2009).

The exclusion of reindeer generally increased the total cover of vegetation, and height and cover of dwarf shrubs, forbs and grasses, but decreased the cover of bryophytes. In addition, the exclusion of reindeer decreased the area of bare soil. Similarly to willow, the cover of dwarf birch most strongly increased in the absence of reindeer in the least productive tundra heath, albeit the overall effect was weaker. In the hummocks of frost heaths, the cover of dwarf birch was greater in the control plots than in enclosures and it seems possible that lower-growing dwarf birch is an inferior competitor to willow in the absence of reindeer, and intensified competition by willow may have reduced the growth of dwarf birch in the hummocks of enclosures. The suppressing effect of reindeer grazing on the growth of dwarf birch (Oksanen & Moen 1994, Manseau *et al.* 1996, Cretê & Doucet 1998) and dwarf shrubs (Manseau *et al.* 1996, Väre *et al.* 1996, Olofsson 2006a) is in line with earlier studies from arctic-alpine environments.

The cover and height of forbs increased in the absence of reindeer, supporting earlier studies showing that grazing reduces the abundance of forbs (Olofsson 2001, Eskelinen & Oksanen 2006, Eskelinen 2008, see however Manseau *et al.* 1996, Olofsson *et al.* 2001). The effects of exclosures were quantitatively greatest in the most productive riparian area, where the cover and height of forbs was greatest. Similarly, the increase in the height of grasses was greatest in the exclosures of the most productive riparian area. These results are in accordance with findings from other systems that show the greatest grazing effects on vegetation in the most productive habitats thus moderating differences between habitats contrasting in productivity (Milchunas & Lauenroth 1993, Virtanen *et al.* 2002, Bråthen *et al.* 2007, Aunapuu *et al.* 2008). Graminoid expansion and productivity enhancement after intensive grazing suggested by Zimov *et al.* (1995), and found in some tundra areas (Olofsson *et al.* 2001, van der Wal & Brooker 2004), was not detectable in my study system. I assume that in our study area grazing causes a decline in the cover and height of grasses, because the combination effects of nutrient deficiency and intensive grazing outweigh the good compensation ability of grasses after disturbance (Archer & Tiezen 1980, Mulder 1999, van der Wal & Brooker 2004). However, Bråthen *et al.* (2007) found a reindeer-driven decline in the grass abundance also in nutrient-rich tundra habitats.

The exclusion of reindeer decreased the cover of bryophytes, as found in earlier studies (Helle & Aspi 1983, Oksanen & Virtanen 1995, Manseau *et al.* 1996, but see Olofsson *et al.* 2002). The effect was strongest in the most productive riparian area, where the increased competition by forbs – the covers of which strongly increased in the absence of grazing – is likely to have reduced the cover of bryophytes (van der Wal *et al.* 2005). My results support the idea of van der Wal (2006) according to which grazing promotes a vegetation shift from lichen-dominated tundra into bryophyte-dominated tundra. However, if grazing pressure is strong enough, even bryophytes are likely to decrease (Oksanen & Moen 1994, van der Wal & Brooker 2004, Hansen *et al.* 2007). It is noteworthy that although the cover of bryophytes decreased in the absence of grazing, the height of bryophytes increased in exclosures. The discrepancy between cover and thickness of bryophyte cover may complicate the evaluation of the role of the bryophyte layer regarding the temperature and decomposition rates of soils (Olofsson *et al.* 2004, van der Wal & Brooker 2004).

The exclusion of reindeer did not affect the cover of lichens as a group. However, the cover of lichens in my study system was at most less than 15%

of the ground cover, which is much less than has been found earlier in a similar type of vegetation (Haapasaari 1988). This suggests that reindeer have strongly reduced the cover of lichens and that eight years without grazing has not been a long enough time for lichen recovery. Earlier studies confirm that reindeer grazing and trampling strongly reduce the abundance of lichens (Helle & Aspi 1983, Väre *et al.* 1996, Suominen & Olofsson 2000, Hansen *et al.* 2007) and that the recovery of lichens after disturbance is slow (Henry & Gunn 1991, Hansen *et al.* 2007). Even though the cover of lichens did not respond to grazing exclusion, lichen mats were considerably thicker in the plots inaccessible to reindeer. This implies that the lichen biomass, and thus the forage value of winter pastures, may recover on a relatively short time-scale as suggested by Kumpula *et al.* (2000).

The exclusion of reindeer had no effect on the total number of species as found in an earlier study (Olofsson & Oksanen 2003). However, the number of vascular plant species decreased in enclosures in the hollows of the most productive riparian area, where there was a tendency for accumulation of soil moisture and nutrient input from melt water. In contrast, in the hummocks and in the other two habitats, grazing had only a modest effect on vascular plant richness. This result conforms to a general pattern according to which grazing increases species richness especially in the most productive habitats by decreasing dominance, while it may have a negative effect on species richness in low-productive habitats (Grime 1973, Proulx & Mazumder 1998, Austrheim & Eriksson 2001, see however Olofsson 2006b). The species richness of bryophytes decreased in the absence of grazing across all habitats. This finding is consistent with earlier studies suggesting that grazing promotes an increase in the species richness of bryophytes (Olofsson *et al.* 2001, Jasmin *et al.* 2008), even though under very heavy grazing the number of bryophytes is likely to decrease (Hansen *et al.* 2007). The species richness of lichens was not affected by the exclusion of reindeer, which contradicts an earlier study that showed a negative correlation between reindeer pressure and species richness of lichens (Eskelinen & Oksanen 2006). Presumably, the highest number of lichen species is found in areas of intermediate grazing intensity as suggested by Grime (1973) and Helle & Aspi (1983). In my experiment, we found that neither intensive year-round grazing nor exclusion of grazers is likely to support high species richness of lichens.

4.4 Industrial impact on reindeer pastures

In many Arctic areas, industrial disturbance decreases the amount of land suitable for pastures thereby increasing the effects of reindeer on the remaining pastures (Forbes 1999, Nellemann *et al.* 2001). According to my case studies from Arctic Russia (IV), the shrub vegetation decreased 15–20% in landscapes as a consequence of the mechanical effects of industry. This supports earlier studies reporting that shrubs are among the plants most vulnerable to industrial impact (Rebristaya *et al.* 1993). After the initial construction phase, many disturbed areas are left to regenerate naturally, but according to my comparisons between disturbed and the original sites, regrowth of vegetation is very slow for most plant groups. In the 15–20 years since the cessation of widespread off-road vehicle traffic, the cover of most plant groups was significantly lower in tracks compared to the original vegetation. However, graminoids including grasses (*Poaceae* spp.) and sedges (*Carex* spp. and *Eriophorum* spp.) regenerated readily and there had been a wide transformation from shrub-willow vegetation, tundra heaths and mires to graminoid-dominated vegetation supporting earlier studies from different parts of the Arctic (Forbes 1992, Khitun 1997, Sumina 1998, Forbes *et al.* 2001, Khitun & Rebristaya 2002, Lavrinenko *et al.* 2003).

The capacity of graminoids for rapid regrowth after disturbance is mainly due to the ability of rhizomatous graminoids to reproduce effectively primarily by vegetative means (Oksanen & Virtanen 1997, Forbes *et al.* 2001). The recovery of graminoids was generally higher in mires than in other vegetation types, supporting earlier studies that have shown that the more moisture there is in the soil, the faster the vegetation regenerates (Rebristaya *et al.* 1993, Andreyashkina & Peshkova 1995, Forbes *et al.* 2001). Despite the occurrence of some hydrophilic bryophyte species on tracks, the total cover of bryophytes had regenerated poorly after the disturbance. A common response to the removal or thinning of the bryophyte layer is an increase the depth of the active layer (Kevan *et al.* 1995, Pavlov & Moskalenko, 2002), which may have profound impacts on the thermal regime of the soils including the potential to induce thermokarst (Forbes 1998, Pavlov & Moskalenko 2002). In the revegetated secondary communities, the cover of reindeer forage species was relatively high, in mires of Bovanenkovo even much higher than in the adjoining undisturbed vegetation. This suggests that if only considering forage species, these swards could be relatively high-value pastures. However, as the results from participant observation and interviewing reindeer herders show, the suitability of reindeer summer pastures depends not only on the nutrient values

of forage plants, but also on factors such as accessibility of herders to good fishing places and amount of disturbance including industrial waste, feral dogs, noise and traffic, which can diminish so called “grazing peace” (see also, Kitti *et al.* 2006). In practice, herders have to avoid the disturbed areas, even though they otherwise could use the disturbed vegetation for grazing.

The revegetating tracks had a similar species composition regardless of the original vegetation type and the species richness was lower in the tracks than in the undisturbed vegetation. Therefore, the ordination analyses showed that anthropogenic disturbance lowers species diversity and homogenizes vegetation composition within and among geographically distant areas. Earlier studies have reported similar results, according to which a decrease in species richness has been related to different forms of industrialization, off-road traffic, roads, railroads, quarries, and chemical disturbance (Sumina 1998, Forbes *et al.* 2001, Khitun & Rebristaya 2002, Lavrinenko *et al.* 2003). Coupled with the raising of the herder perspective, my study supports the holistic landscape approach, where lowering of biological diversity is linked with the lowering of indigenous use and so called ecodiversity within the same areas (Naveh 1995).

4.5 Effects of shrub canopies on understory vegetation

My results show that the relationships between shrubs and understory species are competitive (negative), facilitative (positive) or indifferent (neutral) depending on plant groups based on life form and identity of species (V). The cover of forbs increased in association with an increasing shrub biomass estimate, whereas the cover of all the other plant groups declined. In accordance with this, among the willow-characterized vegetation types we described (I), there was a tendency that the higher and denser the willow canopy, the more variable and abundant was the herbaceous cover in the understory vegetation. According to my results simple plant traits are useful in explaining why co-occurring species do not show consistent responses to changing canopy abundance. Shade from deciduous shrub cover retains moisture at the soil surface, which facilitated broad-leaved vascular plants and bryophytes at the expense of plant groups and species with more xerophytic characteristics.

The positive association between leaf size of vascular plants and shrub biomass estimate is probably caused by the increasing proportion of shade tolerant species, which are able to cope with the densest willow canopies. This result is in line with earlier studies, where broad- and thin-leaved species having high specific leaf

areas (SLA) benefitted from low-light conditions (Grime 1979, Wilson *et al.* 1999, Dahlgren *et al.* 2006, Dormann & Woodin 2002, see however Reich *et al.* 2003). A large leaf area typical to many forbs has also been associated with rapid growth and a need for a relatively high soil nutrient status. Therefore broad-leaved species are likely to be favored by the rapid turnover of nutrients underneath the shrub canopies (Wilson *et al.* 1999, Epstein *et al.* 2004, Diaz *et al.* 2004). In addition to leaf size, the stature of vascular plants was positively associated with deciduous shrub cover. Tall stature is advantageous in competing for light, but may also include increasing risk to vulnerability to herbivores (Grime 1979, Westoby 1998, Westoby *et al.* 2002). Therefore, shrubs may facilitate tall broad-leaved species by providing associational shelter against herbivores. Forbs are often tall and generally preferred by herbivores such as reindeer. Beneath the protective shrub canopies, palatable forbs such as *Rumex acetosa* and *Geum rivale*, which showed positive associations with shrub abundance, may avoid the negative effects of being grazed (Olofsson 2001, Anthelme *et al.* 2007).

Even though the total cover of bryophytes decreased in association with increasing shrub biomass similarly in the exclosure experiment (III), the effect of canopies depended on the plant traits and identity of species. In general, the large-leaved species such as *Plagiomnium ellipticum* and *Rhizomnium pseudopunctatum* showed positive associations with shrub canopies, whereas liverworts and mosses having smaller leaves showed a negative association. My results thus suggest that large-leaved bryophytes may tolerate shade and therefore utilize the improved water retention, due to the canopy cover, better than other bryophytes. This is in accordance with Bates (1998), who suggests that bryophytes inhabiting shady environments typically have open life-forms since there is a lower risk of drying than in full light conditions. Consequently, in shade, typical bryophytes are richly branched robust pleurocarpic mosses or leafy liverworts (Bates 1998, Grime *et al.* 1990). However, the positive association with the shrub canopy of some species such as *Brachythecium* may also be due to their relatively fast growth rate, which is advantageous in coping with leaf litter (Grime *et al.* 1990). The positive effects of canopy on bryophyte cover may also depend on the moisture regime of soils (Russell 1990), which was not controlled for in this study.

Dwarf shrubs, graminoids and lichens showed a negative correlation with the shrub biomass estimate. The negative response of dwarf shrubs contradicts some earlier studies reporting facilitation among shrubs and dwarf shrubs (Jonasson 1992, Shevtsova *et al.* 1995), but support others which have demonstrated that dwarf shrubs were outcompeted by upright shrubs (Totland *et al.* 2004, Wahren

et al. 2005). The negative response of lichens conforms to the earlier-reported negative correlation between lichens and vascular plants (Cornelissen *et al.* 2001, Wahren *et al.* 2005, Walker *et al.* 2006). It has been suggested by Wookey *et al.* (2009) that when nutrients are taken in lesser amounts by cryptogams under low light levels, nutrient supply to vascular plants increases, thus further promoting their dominance. Photosynthetic tissues comprise a small part of lichen structure, and therefore they easily suffer from the increased shade created by shrub canopies. In addition, lichens may also suffer from an increased amount of litter under shrub canopies (Chapin *et al.* 1995).

There was a negative relationship between shrub canopies and the overall species richness of understory vegetation suggesting that an increasing dominance of willow leads to a reduced number of coexisting species within the community. This is assumably due to suppression by dominants that out compete subordinates in the competition for light and is in line with earlier studies reporting decreased species richness along an increasing shrub canopy gradient (Anthelme *et al.* 2007). Especially among lichens, species richness strongly declined in association with increasing shrub biomass as also found earlier (Cornelissen *et al.* 2001). The finding supports the Stress-Gradient-Hypothesis according to which the role of competition in relation to facilitation grows in importance as a driver of the community scale patterns along a gradient of decreasing environmental stress (Bruno *et al.* 2003, Brooker *et al.* 2008). Therefore, our results support earlier studies from elevation gradients (Choler *et al.* 2001), gradients of increasing nutrient availability (Bret-Harte *et al.* 2004), warmed vs. non-warmed conditions (Klanderud & Totland 2005, Wahren *et al.* 2005, Walker *et al.* 2006) and comparisons between more productive vs. less-productive conditions (Totland *et al.* 2004), where the overall role of facilitation has been greater in more severe environmental conditions (see however, Shetvsova *et al.* 1997). The results also conform to the findings of Jumpponen *et al.* (1998) and Totland *et al.* (2004), who found that arctic willows do not serve as nuclei that facilitate diverse understory vegetation as has been often observed in arid environments (Pugnaire *et al.* 1996, López *et al.* 2009). However, the experiment from the forest-tundra ecotone (III) does not show significant effects of exclosures – where shrub abundance increased – on the species richness of vegetation. In this study, however, the understory vegetation was not sampled along a changing canopy gradient, as the study was designed for another purpose.

My results imply that not only abiotic factors, but also dominance, is important for species richness and composition of a given plant community. As evident from the papers II and III, the dominance in plant communities is also affected by

herbivory. It should be noted that my study does not allow distinguishing positive canopy effects from other habitat stress amelioration effects. Therefore, it is possible that other abiotic factors, most importantly water and nutrient availability, simultaneously affected the abundance of shrubs and the composition and species richness of vegetation and caused the above outlined responses. Especially the suppression in the growth of lichens may be due to surface drying instead of the light competition (Wookey *et al.* 2009).

4.6 Conclusions and future perspectives

My study shows that willow vegetation is variable in terms of its species composition and occurs in a broad belt across relatively favorable arctic and alpine conditions. Even though most willow-characterized types that I reported have counterparts in earlier studies, this analysis deriving from such a geographically extensive data set is the first attempt to reveal ecological relationships between vegetation types in different areas. The forb-rich types having a high abundance of willow turned out to be common in the most favorable conditions and their structure resembled other willow thickets described in different parts of the circumpolar Arctic. To deepen understanding of floristical differentiation of willow-characterized tundra vegetation, it would be useful to include even more already existing datasets from different parts of the arctic and alpine regions in the analyses.

The main results concerning the interaction between environmental factors and shrub abundance are summarized in Fig. 3. The growth of willow shrubs was strongly associated with latitude, although the growth and height of willow also depended on other environmental factors such as distance from the sea, depth of annual thaw, slope position and reindeer grazing. In light of my findings, it is evidently likely that the predicted climatic warming in the Arctic (ACIA 2005, IPCC 2007) will enhance the growth of shrubs, but the complexity of interactions between environmental factors may challenge the more simple cause and effect predictions. The correlative results of associations between climatic factors, reindeer grazing and willow growth that I found suggest a need for more experimental studies, where climatic factors, reindeer density and competition between canopy-forming willow and dwarf birch are controlled.

My study supports earlier notions, according to which reindeer grazing reduces willow abundance under arctic-alpine conditions. The study sites in Fennoscandia and on the Yamal Peninsula are hotspots in reindeer density, where the suppressing effects of grazing were strong. My results suggest that the effects of reindeer

grazing may regionally counteract the effects of climate. In the areas with high reindeer densities, such as the Yamal Peninsula, industrial activities are likely to further enhance the effects of grazing by decreasing the area of available pastures. Industrial activities also destroy vegetation, after which regeneration for most plant groups is slow. After industrial disturbance, vegetation is easily transformed into floristically homogeneous graminoid-dominated swards which, in practice, have low value as reindeer pastures. To gain a more thorough understanding of the regeneration of arctic-alpine vegetation after disturbance, species-level analyses would be useful to match with life strategies of species (Oksanen & Virtanen 1997).

Tundra vegetation contains a broad spectrum of growth forms and therefore a shift in dominance may fundamentally change structural and functional properties of the ecosystem. The results found in this study imply that if shrubs gain more dominance – either due to climatic changes or changes in reindeer densities – the functional composition of understory vegetation is likely to shift towards a higher dominance of broad-leaved and tall forbs and broad-leaved bryophytes at the expense of dwarf shrubs, lichens and bryophytes of smaller size. In addition, the species richness of understory vegetation is likely to decline along with increasing dominance of shrubs (Fig. 3). It is possible that in the areas of increased shrub abundance certain forbs and bryophytes would replace many shade-intolerant and more “genuine” tundra species. To obtain further confirmation of canopy effects on understory vegetation, one should carry out experiments where canopy density is manipulated at constant moisture and nutrient levels.

Although the zone of willow-characterized vegetation is relatively small in area, being confined to the Low Arctic (Walker 2000) and the alpine forest-tundra ecotone, it has a high value for the wildlife and people of the Arctic-alpine regions. For instance, willow is an important source of firewood (Prokof'yeva 1964, Tuisku 1999). For animals, the willow zone is critical for nesting and foraging, resembling the forest habitat in more southern areas (Formozov 1973, Chernov 1985). The arctic and alpine areas are expected to be especially responsive to climatic changes in the coming decades (ACIA 2005, Serreze *et al.* 2000, IPCC 2007). The changes in dominance of vegetation will inevitably lead to complicated changes in the whole ecosystem (Wookey *et al.* 2009) and therefore it is important to draw attention to the shrub zone and the factors affecting it. The multidisciplinary study approach that proved to be useful in my research would benefit studies related to pasture use and utilization of willow by people and reindeer.

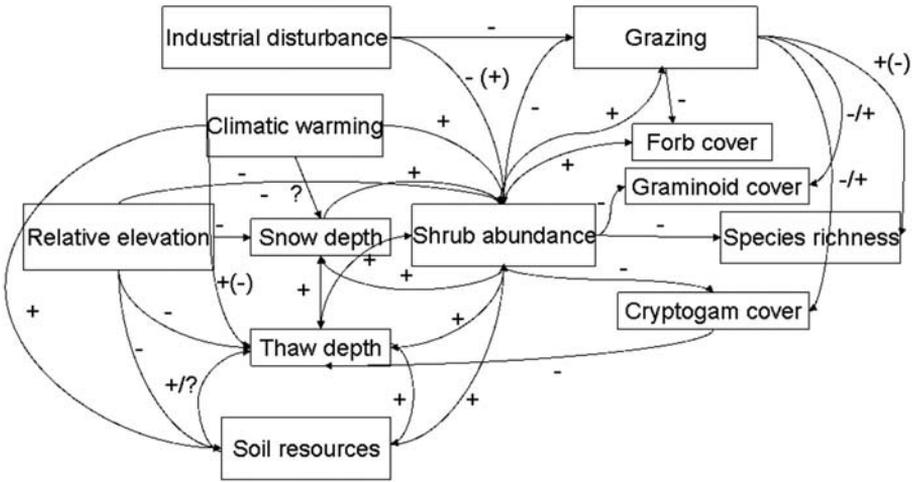


Fig. 3. The diagram shows interactions between tundra shrub abundance and environmental factors affecting it. In addition, some associations between shrub abundance and cover of other plant groups are indicated. Soil resources refer to water and nutrient availability. +/- signs symbolize the direction of an interaction. In the case that both + and - characterize a certain association, the sign written first, is the main direction of the interaction according to this study. The direction of interactions between environmental variables is based on current literature. If the latter sign is written within brackets, it has a relatively minor role. In the case of reindeer grazing effects on cryptogams, the negative effects mainly concern lichens and positive effects mainly bryophytes.

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List of original articles

- I Pajunen A, Kaarlejärvi E, Forbes BC & Virtanen R (2010) Compositional differentiation, vegetation-environment relationships and classification of willow- characterised vegetation in the western Eurasian Arctic. *J Veg Sci* 21: 107–119.
- II Pajunen A (2009) Environmental and biotic determinants of growth and height of arctic willow shrubs along a latitudinal gradient. *Arct Ant Alp Res* 41:478–485.
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