

# IMPACTS OF GEOMORPHIC DISTURBANCES ON PLANT COLONIZATION IN EBBA VALLEY, CENTRAL SPITSBERGEN, SVALBARD

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**ABSTRACT:** Global warming observed nowadays causes an increase in geomorphic activity in polar regions. Within the areas influenced by cold climatic conditions, relief dynamics and vegetation development are the main landscape shaping processes. The study is limited to the Ebba Valley (78°43'N; 16°37'E) in central Spitsbergen (Svalbard), where geomorphologic observations and vegetation sampling were conducted in 2007. The valley was divided into three zones differentiated by dominating geomorphic activity and stability of deposits. The settlement and the evolution of plant cover have been documented there. The main factors that control well developed vegetation cover within raised marine terraces are frost heave and solifluction. In deeper parts of the valley, aeolian processes dominate and high differentiation of microsite conditions causes high variability in plant coverage. The area close to the Ebba glacier marginal zone is characterized by initial stages of plant colonisation where disturbance to vegetation is mainly caused by hydrological processes.

**KEY WORDS:** plant colonization; glacier foreland; climate change; Spitsbergen

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## Introduction

The on-going climate change is expected to be most pronounced in high latitudes (ACIA 2004) and greatly affect tundra ecosystems (Forbes et al. 2010), which are considered as vulnerable. The average Arctic surface temperatures have been rising faster than those of the rest of the Northern Hemisphere (IPCC 2013) and therefore there is expected further increase of growth, abundance and cover expansion of arctic woody plants (Forbes et al. 2010, Natali et al. 2012) as well as changes in the structure of the Arctic tundra

(Chapin et al. 2005). Since global warming is now one of the main factors affecting tundra ecosystems (Zwoliński, Dobiński 2008), it is important to investigate not only vegetation establishment on recently quite rapidly deglaciated areas but also plant responses to changing habitat conditions, especially to intensified geomorphic activity reported from periglacial environments (Zwoliński et al. 2008a, Mercier 2009).

Plant succession has long been the object of research in the Arctic, yet many of the studies dealing with the subject are focusing on the mechanism of plant succession (i.e. Chapin et al. 1994). A

number of studies review the succession patterns (Churchill and Hanson 1958, Hodkinson et al. 2003, Jones and Henry 2003), or relationships between plant cover and microrelief (Anderson and Bliss 1998, Canoe et al. 2004, Jónsdóttir 2005). Plant colonisation on newly exposed terrain is considered to be the main factor in stabilising glacier foreland deposits, but it was also proved that the influence is reciprocal: habitat disturbances on glacier forelands play a significant role in determining the rate of colonisation, distribution of pioneer species, as well as high species diversity in the initial phase of succession (Matthews 1992, Komárková 1993, Prach and Rachlewicz 2012). Physical stress to plants is one of the main mechanisms determining the course of succession while the intensity of surface disturbance determines its starting point (Connell and Slatyer 1977). Current vegetation structure and relief shape represent temporary equilibria which are slowly developing and adapting to environmental stresses until the next disturbance destroys them to different rates and initiates development of a new equilibrium state (Gutierrez and Fay 1980). Such cycles may be accelerated due to climate change, and therefore more attention should be paid to how arctic vegetation varies in relation to relief dynamics in various spatial scales and in changing environment (Prach et al. 2012).

The area of glacier forelands is increasing and undergoes intense modifications caused mainly by two types of dynamics: the above mentioned plant colonisation and active remodelling of glacial deposits (Szpikowski et al. 2014). On Spitsbergen, valley glaciers have been retreating since the end of the Little Ice Age which occurred 600–100 years ago (Kłysz et al. 1989 Rachlewicz et al. 2007) and its maximum occurred on Svalbard in the 1900s (Fleming et al. 1997, Moreau et al. 2008). It means that the glacier retreated there relatively recently and within the areas affected by that cold climatic period, the vegetation may have started to re-establish only some decades ago (Svoboda and Henry 1987). An example of such environment can be Ebba Valley.

The aims of this paper are to analyze the valley of Ebba glacier in central Spitsbergen in terms of (1) recognizing factors that control vegetation cover development in periglacial zone and (2) investigating the spatial differentiation of this cover. The next step is (3) the analysis of plant cover

density and its vertical structure on the valley bottom of increasing age and (4) determination of species composition and successional stages along Ebba Valley.

## Study area

The study was conducted in Ebba Valley which is located in the central part of Spitsbergen (Svalbard Archipelago, Fig. 1). The valley is situated on the eastern coast of Petunia Bay which is the northern end of Billefjord – a northeastern Isfjord branch (78°43'N, 16°37'E) (Rachlewicz et al. 2013).

The bedrock geology is dominated by dislocations along the Billefjorden Fault Zone of which most characteristic formations are metamorphic and carbonate outcrops (Rachlewicz et al. 2013). Sediments are mainly of marine, glacial, slope and fluvial origin (Dallmann et al. 2004). Permafrost is present in the soils of the study area and active layer can reach up to 1.2 m thickness during summer period (Rachlewicz and Szczuciński 2008, Mazurek et al. 2012).

Despite of being generally influenced by the warm West Spitsbergen Current, the climate of the study area is characterized by quasi-continental features such as higher temperatures in the ablation period (1–2°C more in comparison to western part) and very low precipitation throughout the year (not exceeding 60 mm during summer), which is characteristic for the central and eastern parts of the island (Rachlewicz 2003, Rachlewicz and Styszyńska 2007, Rachlewicz et al. 2013, Nordli et al. 2014).

According to the bioclimatic classification made by Elvebakk (1999), Ebba Valley is located in middle Arctic tundra zone. The vegetation within the study site is classified as the high Arctic *Dryas octopetala* tundra type (Rønning 1996), where the dominant species are polar willow (*Salix polaris*) and white dryas (*Dryas octopetala*).

## Methods

### Location of sampling sites

From the moraine edge, westward for 5 km to the coast of Petunia Bay, seventeen sites were

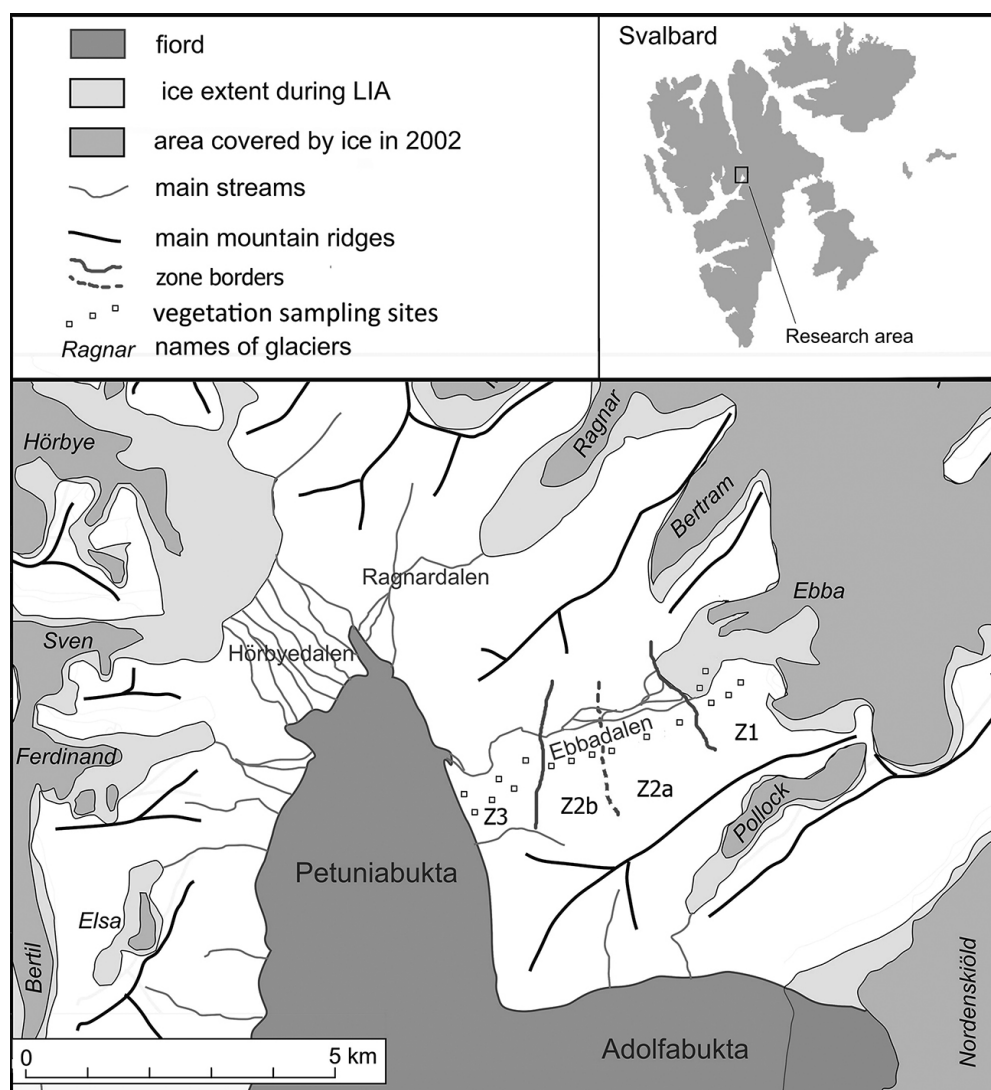


Fig. 1. Study site location and its division into zones of different geomorphic activity (modified after Rachlewicz et al. 2007).

chosen for vegetation sampling along the longitudinal profile of Ebba Valley (Fig. 1) at the distance of 200 or 400 m from each other, depending on variability of vegetation cover. Differences of microsite conditions such as type of sediments and their stability, geomorphic processes and age of surface were taken into account when choosing sites (Tab. 1). Then, quadrat sample plots were established within each site. Such linear type of sampling, from glacier marginal zone to the mouth of the valley, gives an adequate means to investigate the successional stages of vegetation which are the consequence of glacier retreat and soil development through time (Moreau et al. 2005) while random distribution of sample plots within sites makes it possible to assess the influence of different types of

geomorphic activity on the development of plant cover.

### Geo-botanical environment

Ebba valley, stretching from east to west, has a form of a "funnel" from which waters are quickly discharged (Kostrzewski et al. 1989, Szpikowski et al. 2014, Rachlewicz et al. 2016). Geomorphological forms of such type are characterized by the dominance of dry and very dry habitats. Snow thickness during winter is rather low. The vegetation is usually fragmentary due to abrasion and dominated by communities with a large proportion of *Saxifraga oppositifolia*, *Dryas octopetala*, *Cassiope tetragona*, *Carex rupestris* and *Deschampsia alpina* (Prach et al. 2012).

Table 1. Physical environment of delimited zones in Ebba Valley.

Zone	Site number	Terrain age	Geological substrate	Landform	Dominant processes	Stability of deposits
Z1	I–III	Holocene, with Precambrian rock outcrops	till, deposits of gravitational, aeolian and fluvial origin	outwash plain	runoff, flooding, wash-out, channel bank erosion, debris flow, aeolian accumulation	high instability
Z1	IV–V	Holocene	till, deposits of gravitational, aeolian and fluvial origin	area of contact of alluvial fan and outwash plain	runoff, flooding, wash-out, channel bank erosion, debris flow, fluvioglacial and aeolian accumulation, landslides	high instability
Z2a	VI–VIII	Holocene	till, deposits of gravitational, aeolian and fluvial origin	rear slope of marine terraces	aeolian accumulation, deflation, debris flow,	average stability, locally unstable
Z2b	IX–XI	Holocene/late pleistocene	marine deposits, deposits of gravitational, aeolian and fluvial origin	raised marine terraces remodelled by glacier transgression	deflation, debris flow, surface runoff	average stability, locally unstable
Z3	XII–XVII	Holocene	marine and aeolian deposits	raised marine terraces	solifluction, frost heave, surface runoff	rather stable

At each site the age of deglaciated terrain and destructive factors for vegetation were documented, along with other environmental variables such as soil type and its permeability, exposition, wind exposure conditions and stability of deposits. Terrain age and geomorphic processes were considered as the main factors affecting plant colonisation, while other environmental factors as secondary influence variables for plant cover development. The collected data and recognition of dominant geomorphic processes (Kostrzewski et al. 2006, Rachlewicz et al. 2012) were the basis for dividing the Ebba Valley into three zones (Fig. 1) differentiated in terms of vegetation cover characteristics. Zone 1 is the youngest part of the valley. The terrain is constantly reworked by glacier and snow melting water. Zone 2 was internally divided into two sub-zones on the basis of dominating sediment type. Zone 3, i.e. raised marine terraces is the oldest part of the valley (more than 5000 years old, according to deglaciation and sea level changes dating e.g. by Kłysz et al. 1989, Long et al. 2012, Rachlewicz and Szczuciński 2013).

### Vegetation sampling

Vegetation sampling was conducted in 2007 on total 425 quadrat sampling plots: 25 1×1 m plots located in each of seventeen study sites along the Ebba Valley. Six sites were located in Zone 2 and Zone 3, 5 were located in Zone 1. Quadrant sample

plots within different sites were established to quantify the distribution of vascular plant species among microsites (quadrates) within each site and to register species diversity. The quadrats were randomly placed, regardless of microtopography, within a study site. Plant cover, plant size, frequency, and density were estimated for each species. Cover estimates of lichens and bryophytes, cryptogamic crust, percentage of bare ground and sediment type were recorded. Additionally, five quadrat plots from each site were examined in more detail: the number of shoots of particular species was counted. The density of each species was expressed in amount of aboveground shoots/0.5 m<sup>2</sup>, in the case of vegetative reproduction, as separate individuals were considered plants having their own root system (cf. Robotnov 1964). Species encountered were divided by occurrence frequency in sample plots.

Nomenclature for plant names follows Rønning 1996 and Elven and Elvebakk 1996.

## Results

### Habitat disturbances determining plant colonisation

The set of geomorphological processes in the vicinity of east coast of Petuniabukta (Kostrzewski et al. 2006, Rachlewicz et al. 2012) having crucial



influence on vegetation cover within three delimited in the Ebba Valley zones are as follows:

1. Zone 1 (Z1) – upper stream: runoff zone. Located in the vicinity of glacier marginal zone. Dominant processes: ice and snow melting water eroding outwash plain and surrounding slopes.
2. Zone 2 (Z2) – middle stream: aeolian activity zone. Divided into two subzones: Z2a where accumulation processes dominate: deposition of fine textured material and gravity flow deposits, Z2b where erosion processes dominate: deflation of fine textured material, drying impact of wind.
3. Zone 3 (Z3) – lower stream: frost heave and solifluction zone. Located within raised marine terraces in the mouth of the valley.

Z1 proves to be most disturbed by geomorphic processes. Multiple seasonal channels cut into the deposits causing wash-out of sediments and plants or the sediment load is accumulated and covers vegetation. Similar effects occur due to spring floodings. In the area of contact with lower slopes of alluvial fans, multiple landslides destroying plant cover occur. Within Z2 and Z3 the geomorphic processes are less intensified and of less abrupt character.

### Plant cover: percent space occupancy

In Z1 plant coverage is between 1–10% and only locally exceeds this value. In some plots it is near 25%, but only at the spots sheltered by boulders of crystalline rock, preventing wash-out.

Z2 is characterized by high variability in plant coverage. The lowest, not exceeding 10% occurs within the exposed ridges of raised marine terraces. In terrain depressions sheltered from the wind and being local deposition sites for fine-textured material, the plant coverage may reach up to 75%. On the slightly sloping area of the rear slope of marine terraces and flat contact area to the outwash plain, the coverage is usually about 25%, locally reaching 50%.

Within Z3, the oldest part of the valley which was not under the direct influence of Ebba Glacier transgression during the LIA, plant cover is well developed and the percentage of covered ground is often close to 100%. High percentage of bare ground is characteristic only for exposed ridge crests where deflation has a significant impact.

### Species diversity

A total of 22 vascular plant species were recorded in the plots (Tab. 2). Bryophytes and lichens were also present, but only their cover percentage was estimated. Species richness increased with increasing relief age and distance from the glacier front. Within the youngest and most disturbed Zone 1, 7 species were documented, of which only 4 were encountered in the vicinity of glacier marginal zone. In Z2, where deposits were more stable and locally favourable moist conditions were recorded, 12 species were documented, of which 3 were not common for the two subzones: *Minuartia* sp. and *Potentilla pulchella* were encountered only within subzone Z2b. The oldest part of the valley, Z3, was characterized by the highest species diversity: 20 species were documented.

Only three species i.e. *Saxifraga oppositifolia*, *Bistorta vivipara* and *Salix polaris* occurred in all the sites along the transect. All the zones were differentiated in terms of species occurrence and sociability within sample plots (Table 3).

*Saxifraga oppositifolia*, *Bistorta vivipara* and *Salix polaris* were most abundant in zones 2 and 3, along with absent in Z1 *Dryas octopetala*. Similar, but lower occurrence frequency in zones 2 and 3 had also *Draba corymbosa*, *Minuartia biflora*, *Potentilla pulchella* and *Silene furcata*. The other common for all zones species were more frequently encountered within sample plots of Zone 3. Only three of documented species are specialised ones. *Dryas octopetala* and *Potentilla pulchella* preferred calciferous substrates, while *Saxifraga aizoides* demanding hygrophilous habitat was documented only along the banks of surface runoff channels. Most common and dominant species i.e. *Saxifraga oppositifolia*, *Dryas octopetala* and *Salix polaris* were forming two different growth forms depending on habitat conditions. If the percent of plant cover was low, *Dryas octopetala* and *Salix polaris* formed cushions. Whenever these species were growing in dense plant cover they formed wide patches or carpets but without superseding other species. *Saxifraga oppositifolia* preferred a prostrate form when colonizing areas where plant cover did not exceed 30% and in dense plant cover it formed carpets accompanied by *Dryas octopetala* and *Salix polaris*. In favourable moisture conditions and where plant cover was on the average level, it preferred a cushion form.

Table 2. Vascular plants documented in Ebba Valley within particular study sites.

Zone	Site number	Rate of percentage cover	Dominant processes	Species																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																				
				<i>Arenaria pseudofrigida</i>	<i>Braya glabella</i>	<i>Cassiope tetragona</i>	<i>Cerastium arcticum</i>	<i>Carex misandra</i>	<i>Carex rupestris</i>	<i>Deschampsia alpina</i>	<i>Draba</i> sp.	<i>Draba corymbosa</i>	<i>Dryas octopetala</i>	<i>Equisetum variegatum</i>	<i>Minuartia biflora</i>	<i>Minuartia rubella</i>	<i>Pedicularis hirsuta</i>	<i>Bistorta vivipara</i>	<i>Potentilla pulchella</i>	<i>Salix polaris</i>	<i>Saxifraga aizoides</i>	<i>Saxifraga oppositifolia</i>	<i>Silene acaulis</i>	<i>Silene furcata</i>	<i>Silene uralensis</i>																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																															
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### Percent participation and abundance

Species percent participation in total flora of the research area compared with shoot density made it possible to distinguish three groups of species:

- of participation not exceeding 10%, as *Arenaria pseudofrigida*, *Cassiope tetragona*, *Cerastium arcticum*, *Deschampsia alpina*, *Draba sp.*, *Equisetum variegatum*, *Minuartia rubella*, *Minuartia biflora*, *Pedicularis hirsuta*, *Silene furcata* and *Silene uralensis*, presence of these species (except for *Silene furcata*) was limited to the youngest marine terraces,
- of participation of 10 – 25%, as *Carex misandra*, *Carex rupestris* and *Silene acaulis*,
- of participation of more than 40% in at least ten sample plots, such as: *Dryas octopetala*, *Bistorta*

*vivipara*, *Salix polaris*, *Saxifraga oppositifolia* and *Saxifraga aizoides*, all of them (except *Saxifraga aizoides*) were widespread in the whole valley.

### Horizontal and vertical spatial organisation

In Zone 1, high percent of bare ground was characteristic for all sites. Plant cover formed small patches, or the individuals were growing singly. Most preferred growth form was cushion. Loosely organized assemblages were characteristic for channel banks and the vicinity of large boulders where they found shelter against the wind and wash-out. None of the species was distinctly dominant.

Zone 2a was similar to Zone 1 in terms of spatial organisation. Vegetation was assembled in small patches or individuals were growing

Table 3. Occurrence frequency (% of sample plots), sociability, local abundance, ecological indicator value, average shoot density and phytoecological features of species.

Species	Feature							
	Occurrence frequency (% of plots)			Sociability <sup>1</sup>	Local abundance <sup>2</sup>	Ecological indicator value <sup>3</sup>	Average shoot density /0.5 m <sup>2</sup>	Soil moisture preferences <sup>4</sup>
	Z1	Z2	Z3					
<i>Arenaria pseudofrigida</i>	–	–	20%	growing singly	sparse	euryoic	Z3: 49	xerophyte
<i>Bistorta vivipara</i>	100%	100%	100%	growing singly	subdominant	euryoic	Z2: 54 Z3: 49	mesophyte
<i>Braya glabella</i>	–	10%	10%	growing singly	sparse	euryoic	Z2: 2,2	mesophyte
<i>Cassiope tetragona</i>	–	–	15%	carpet forming	dominant	intermediate	Z3: 347,7	mesophyte
<i>Cerastium arcticum</i>	–	10%	–	growing singly	dominant	euryoic	Z2: 8	mesophyte
<i>Carex misandra</i>	–	–	20%	tussocks	subdominant	intermediate	Z3: 5	mesophyte
<i>Carex rupestris</i>	–	–	60%	tussocks	dominant	intermediate	Z3: 37,6	mesophyte
<i>Deschampsia alpina</i>	–	20%	5%	tussocks	dominant	intermediate	Z2: 3, Z3: 0,3	mesophyte
<i>Draba</i> sp.	–	10%	30%	tussocks	sparse	intermediate	Z2: 14 Z3: 16	xerophyte
<i>Draba corymbosa</i>	–	5%	5%	tussocks	sparse	intermediate	Z2:10 Z3: 8	xerophyte
<i>Dryas octopetala</i>	–	60%	80%	large patches or tussock	dominant	intermediate	Z2: 170 Z3: 430	xerophyte
<i>Equisetum variegatum</i>	–	–	5%	growing singly	sparse	intermediate	Z3: 3	higrophyte
<i>Minuartia biflora</i>	–	3%	4%	growing singly or forming patches	subdominant	intermediate	Z2: 0,5 Z3: 0,9	mesophyte
<i>Minuartia rubella</i>	–	1%	3%	growing singly	sparse	intermediate	Z2: 0,4 Z3: 0,4	xerophyte
<i>Pedicularis hirsuta</i>	–	–	35%	growing singly	sparse	euryoic	Z3: 2,1	mesophyte
<i>Potentilla pulchella</i>	–	5%	5%	tussocks	dominant	specialised	Z2: 0,1 Z2: 0,1	xerophyte
<i>Salix polaris</i>	30%	80%	100%	large patches or tussock	dominant	euryoic	Z1: 111 Z2: 347 Z3:578	mesophyte
<i>Saxifraga aizoides</i>	5%	–	–	growing singly	subdominant	specialised	Z1:26	higrophyte
<i>Saxifraga oppositifolia</i>	100%	100%	100%	carpet forming or singly	dominant	euryoic	Z1:30 Z2:345 Z3: 642	xerophyte
<i>Silene acaulis</i>	–	–	1%	growing singly	subdominant	intermediate	Z3: 0,5	mesophyte
<i>Silene furcata</i>	–	30%	25%	tussocks	sparse	intermediate	Z2: 0,7 Z3: 0,8	mesophyte
<i>Silene uralensis</i>	–	–	3%	singly	sparse	intermediate	Z3: 0,2	mesophyte

<sup>1</sup> Reference: Braun-Blanquet 1964, sociability scale.<sup>2</sup> Reference: Elven and Elvebakk 1996.<sup>3</sup> Reference: Elven and Elvebakk 1996.<sup>4</sup> Reference: Kojima and Wada 1999, Saville 1964.

singly. Higher percentage of plant cover was characteristic for more stable substrate where older individuals forming bigger cushions were common. In Zone 2b the patchiness was more

evident. In the open areas of mostly fine textured substrate vegetation was formed in poorly defined, loosely arranged assemblages and some individuals were growing singly. Sheltered terrain



depressions were occupied by vegetation patches while exposed ridges with coarse material were rather bare.

Almost all of the plots in Zone 3 had a uniform plant cover. Gaps of bare ground occurred only on exposed ridges, cracks of humus layer or surface eroded by intense wash-out. *Saxifraga oppositifolia*, *Dryas octopetala* and *Salix polaris* were dominant within all study sites but coexisting with other species. Only *Cassiope tetragona* formed large patches, thoroughly superseding other species. Bryophytes were dominant in water seepage areas at the foot of the slopes and melting snow bedded surfaces.

In Ebba Valley, only four of six existing vegetation strata were documented i.e. dwarf shrubs <0.5 m, herbs, mosses and lichens, bare ground (Fig. 2). Within the youngest part of the valley, i.e. Zone 1, no visible mosses and ground lichens were encountered. Area of bare ground usually exceeded 90%. Herbs were dominant within all sample plots and dwarf shrub cover did not exceed 3%.

In Zone 2, the same rate of the four strata as in Zone 1 occurred within the sites where plant cover did not exceed 10%. Within the sites where the percentage of bare ground was about 75%, the

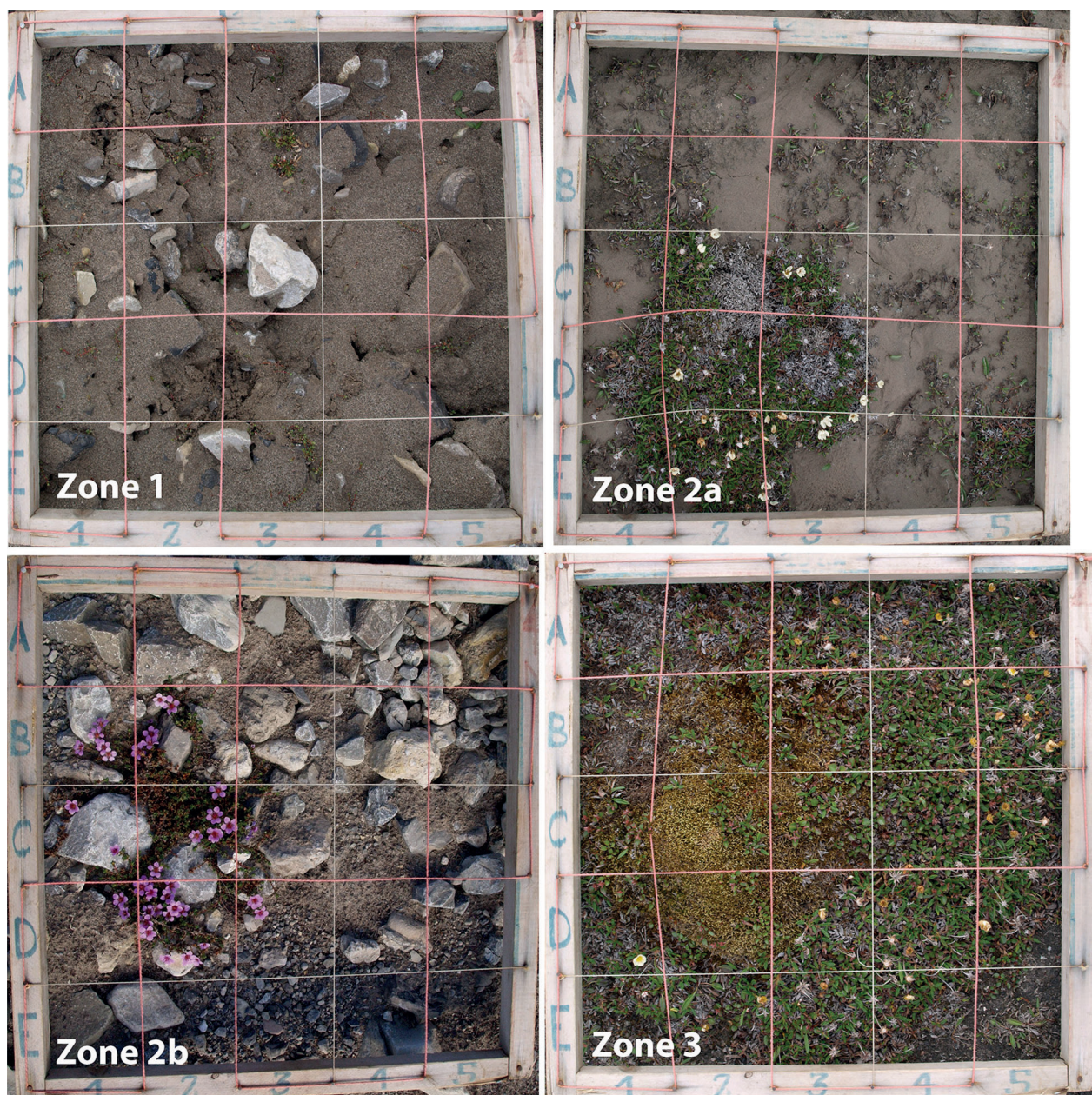


Fig. 2. Example of sample plots from delimited zones – differences in vegetation cover.



average rate of herbs and dwarf shrubs was 14 and 11% respectively. Mosses and lichens were documented sporadically.

Characteristic for Zone 3 was high percentage of mosses in both moist and quite dry sites. Moss cover in several sample plots reached up to 20%. Ground lichens were also documented. Dwarf shrub cover reached up to 55% in several sampling plots.

## Discussion

### Colonisation potential

Species of the Ebba Valley which proved to have the greatest potential for colonization are: *Bistorta vivipara*, *Salix polaris* and *Saxifraga oppositifolia*. These three species occur in all the sites along the transect. Dwarf shrubs such as *Salix polaris* had well developed root systems and many of them reaches the age of several decades (Buchwał et al. 2013). Marcante et al. (2009) points out that survival of adult perennials of this type serves as a buffer against temporal variations. This has particular relevance in disturbed habitats as a factor facilitating stabilisation of populations and their increase in size. It gives in Ebba Valley a possibility for establishing to species characteristic for later successional stages, as *Bistorta vivipara*. According to Hodgkinson et al. (2003), this species is typical for the final stages of succession, yet it was present within almost all sampling plots. Its prevalence in the whole profile of the valley results most probably from high tolerance to environmental stress and high reproduction ability. *B. vivipara* is often reported to have the highest seedling density in both intact and disturbed habitats (e.g. Cooper et al. 2004) and the results from the study area agree with suggestions made in literature.

*Saxifraga oppositifolia* was present within all the plots of the transect and dominant in most of them. It is a pioneer species within its entire geographical range (Pirożnikow 1996). *Saxifraga oppositifolia* is resilient to being covered by fine sediments and colonizes new terrains by producing single long shoots (prostrate form) instead of forming a cushion (Kume et al. 1999). This prostrate form was observed in the majority of sample plots in Zone 1. Creeping stems allowed

it to expand and to find places sheltered from winds. Most individuals also developed secondary root systems, allowing for a fuller use of resources and better anchorage in the substrate. Other characteristics of the species as a very high growth rate, often self-compatibility, substantial regeneration capacity and longevity of up to 25 years (Pirożnikow 1996) also contribute to its high abundance in the study area.

The main pioneer species in alluvial areas and in the vicinity of watercourses was *Saxifraga aizoides*, present only on moist or wet habitats and prevailing in all plots on which it was observed.

Species of lower abundance characteristic for later stages of succession were *Dryas octopetala*, *Deschampsia alpina* and *Silene fuscata*. *Deschampsia alpina* occurred in large numbers only on moist soils, with a high proportion of fine-grained sediments. *Dryas octopetala* being a specialized species was documented only in calcareous habitats. *Carex rupestris* and *Cassiope tetragona* were species of significant coverage on moist and relatively fertile sites. They were characteristic for mature stages of succession. *Cassiope tetragona* locally occupied the areas of several square meters. Other taxa occurred sporadically and were highly dispersed. The spatial arrangement of vegetation and its structure depends in Ebba Valley on local chronosequence, but it is mainly a result of ecological limits imposed by local environmental conditions and by the destructive disturbances of the environment. The dispersal of other taxa may be a result of poorer tolerance to environmental stress and limitations or lack of safe, stable places, as they are not crucial for germination but are crucial for establishment (Marcante et al. 2009).

### Successional stages

On the basis of the collected data on the number of species within sampling plots and their abundance and/or dominance determined on the grounds of space occupancy and shoot density, the attempt to distinguish successional stages in the Ebba Valley has been made. The age of landforms documented for the valley (Kłysz 1985, 1989, Long et al. 2012, Rachlewicz and Szczuciński 2013, van der Meij et al. 2016) and indicator species were also taken into account in the case, as well as disturbance regime, soil depth and moisture regime. In Ebba Valley, three

stages of succession may be specified. There is a clear correspondence between increasing surface age, distance from the glacier and the increase in vegetation cover (Table 2). The increasing total number of species and the mean number of species within the sample plots, along with increasing percent of covered ground and shoot density confirms in this case chronosequential occurrence of plants from upper to lower stream of the river. This successional sequence refers also to the concept of geosuccession developed for Antarctic oases by Zwoliński (2007).

As sites covered by vegetation in an initial stage of development in the Ebba Valley can be considered these which were characterized by:

- number of species  $\leq 4$ , without occurrence of *Cassiope tetragona*,
- short distance to the glacier snout and terrain disturbances conditioned by its vicinity
- strong wind action
- expiry of less than 600 years since the glacier recession,
- vegetation cover of up to 10%,
- presence of specialized species,
- presence of species characteristic for the initial stage of succession, such as: *Saxifraga oppositifolia*, *Saxifraga aizoides* and *Salix polaris* (Hodkinson et al. 2003, Raffl et al. 2006).

Such features were characteristic for all the plots in Zone 1 and 50% in Zone 2. The later deglaciated area and more reworked by active geomorphic processes, the higher percentage of bare ground was observed (Fig. 3). Plant succession begins in such environments almost immediately

after deglaciation (Matthews 1992). In Z1 and parts of Z2 disturbance events repeatedly destroy existing plant cover and secondary plant colonisation takes place. Establishing of vegetation cover is highly dependent on microsite conditions, especially on the presence of undisturbed sites, sheltered from wind activity and runoff ("safe sites", as defined in Jumpponen et al. 1999). The main factor limiting plant colonisation in this area, except for geomorphic disturbances, is rapidly changing moisture conditions, from wet and moist at the beginning of vegetation season to very dry towards its end. Strong wind action has also a negative influence on plant establishment within this area - it causes mechanical injuries and burial in carried sediments, while cold air from the glacier combined with intense radiation on soil surface cause extreme fluctuations in soil temperature and desiccation (Jumpponen et al. 1999).

As the intermediate level of tundra development in the Ebba Valley can be considered sites characterized by:

- number of species from 5 to 7, without occurrence of *Cassiope tetragona*,
- expiry of about 2000-600 years since glacier recession,
- degree of vegetation cover in range of 25-75%,
- presence of dominant species (representing over 45% of documented vegetation cover),
- presence of species characteristic for the intermediate stage of succession, such as *Cerastium arcticum* and *Minuartia rubella* (Hodkinson et al. 2003),
- visible blue-green algae and lichens on the substrate.

Such features were characteristic for 50% of the plots in Zone 2 and 15% in Zone 3. In Zone 2 it is intense wind activity having influence on the development of plant cover. Winds sweep down from the glacier, carrying away fine textured sediments from the moraines, glacialfluvial surfaces and instabilised areas of Zone 1. Zone 2a is the area where sand and silt is being accumulated. Most of the sites where succession stage can be considered as intermediate were found in this subzone. In Zone 2b debris pavement is being exposed. Coarse textured, permeable substrate prevents germination while cold and strong winds have destructive impact on already growing plants. Despite the longer distance from

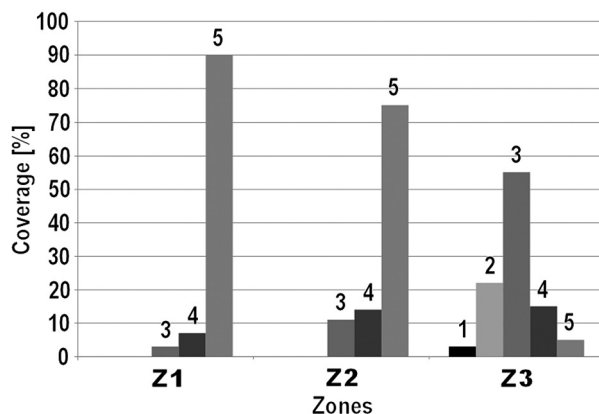


Fig. 3. Vertical vegetation structure.

1 - ground lichens, 2 - mosses, 3 - dwarf shrubs,  
4 - herbs, 5 - bare ground.

the glacier and increasing terrain age, succession in Z2b may be in many places characterised as initial.

The characteristics of the mature or close to mature stage in Ebba Valley are:

- amount of species that excess 10, one of which is *Cassiope tetragona*, considered as a determinant of mature communities in the investigated area (Elvebakk 1999, Ohtsuka et al. 2006),
- expiry of at least 4000 years since the glacier recession and relative sediment cover stability,
- degree of vegetation cover in the range of 75 – 100%,
- presence of the dominant species, but not exceeding 45%,
- presence of species characteristic for advanced stages of succession, such as: *Cassiope tetragona*, *Dryas octopetala* and *Pedicularis hirsuta* (Hodkinson et al. 2003).

This successional stage was observed in 85% of sample plots in Zone 3. The total development time of the vegetation cover in the region of Isfjorden on raised marine terraces is, according to Tishkov (1986), from 3000–3500 years. Given that the marine terraces within this zone are considered to be older (Kłysz 1985, 1989, Long et al. 2012, Rachlewicz and Szczuciński 2013, van der Meij et al. 2016) along with the fact that *Cassiope tetragona* was observed, and even dominating within several sample plots, vegetation here should be considered as fully developed. However, only a few sites within the Z3 area can be considered as mature due to local disturbances.

### Succession type

On the basis of the abovementioned facts, the type of succession in the Ebba Valley can be determined (according to the nomenclature proposed by Svoboda and Henry 1987) as directional, non-replacement. The progress of this type of succession is characterized by the coexistence of species and quantitative expansion in its successional stages. Species do not replace each other, but those typical for later successional stages start to accompany the pioneer ones. In the studied area, the total number of shoots per 0.5 m<sup>2</sup> and percentage of plant cover increased towards mature stages of succession in Zone 3 (Table 2). Species colonizing areas lately released from the

ice cover in the Ebba Valley were *Saxifraga oppositifolia*, *Salix polaris* and *Bistorta vivipara*. They were not replaced by other species but gradually began to be accompanied by *Dryas octopetala*, *Draba sp.* and *Silene furcata*. All these species also occurred in the plots within Zone 3, where the succession has nearly reached a mature stage, and were accompanied by *Cassiope tetragona*, *Carex misandra* and *Carex rupestris*.

### Disturbance regime

Although the general impression of the succession in Ebba Valley as being linear and consistent with time and distance from the glacier, many discontinuities have been observed. Investigation of sample plots within homogenous sites (at the first sight) proves that calling into question the chronosequence approaches which “are based on the implicit assumption that spatial and temporal variations are equivalent” (Pickett 1989, Rydgren et al. 2014:1367) is well justified. Matthews (1978) and Whittaker (1989) emphasize that other variables than time and distance from the glacier may play the main role in creating vegetation spatial pattern. Also Rydgren et al. (2014) proves that terrain age is not the main factor that explains present-day variation in species composition but local environmental variables may be more deterministic for vegetation structure. This also seems to be the case in Ebba Glacier foreland within all the zones. In Z1, the plots situated in the vicinity of outwash channels were characterized by slightly higher rates of plant cover and shoot density, which suggest that water availability is the most important factor influencing variation of vegetation cover. However, the plots located on waterlogged substrate, often disturbed by intense wash-out, were characterised by higher rate of bare ground.

Within the Z2, the influence of local environmental factors and disturbance regime is most explicit. Differentiation between fine-grained and moist substrate in Z2a and coarse, well-drained and desiccated by wind activity substrate in Z2b, is the most important cause of delimiting the two subzones, where successional stages are nonlinear with terrain age and distance from the glacier. Vegetation cover is much more developed on younger terrain of Z2a, again suggesting that moisture conditions and grain size of the



substrate have crucial role for plant establishment. In Z2b, the destructive influence of winds from the glacier causes that better developed vegetation is restricted to sheltered sites.

Within considerable parts of the Z3 it can be observed that soil movements caused by repeated freeze-thaw cycles in active layer of permafrost area result in destroying root systems. Root tension caused by such movements may be a significant stress factor for plants (Scurfield 1973, Zoltai 1975, Schweingruber and Poschlod 2005) and limit the establishment of vegetation. Frost creep, which is the main stress factor for existing vegetation cover, causes death of plants in case of severe root injuries or root tension. The occurrence of water seepage areas at the foot of the terrace slopes and accumulation of snow melting water in terrain depressions in the form of tundra lakes (Zwoliński et al. 2008b, Mazurek et al. 2012) also lead to transformation of existing plant cover. Thus, it should be concluded that most of the area undergoes periglacial reworking and vegetation cover is still being transformed at many sites.

## Concluding remarks

The major determinant of the degree of development of tundra vegetation is the time since the release of land from the glacier ice cover and stabilization of sediment cover. However, there is also a number local factors that can influence the linear development of plant cover, such as climate, substrate features as parent material, nutrient availability, pH, moisture content, particle size variability, landform differentiation, and geomorphic activity. The results from Ebba Valley confirm previous studies on the subject, but also indicate that more attention should be paid to geomorphic activity as a factor disturbing chronosequences. Initiation of plant colonization may be delayed and linear chronosequences of plant succession may be disturbed mainly by high geomorphic activity, especially cryoturbation, mass movements and fluvial processes. Within sites of well-developed vegetation cover, such disturbances cause severe damages in it and result in patchiness: within dense tundra cover some sites are characterized by initial succession stages and where plant re-development is also affected by

surrounding vegetation. Future studies on the relationship between geomorphic processes and succession should focus on combining phytosociological data with quantitative geomorphological studies on the intensity of the processes.

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