



Succession of vascular plants in front of retreating glaciers in central Spitsbergen

Karel PRACH^{1,2} and Grzegorz RACHLEWICZ³

¹ Faculty of Science, University of South Bohemia,
Branišovská 31, CZ-37005 České Budějovice, Czech Republic <prach@prf.jcu.cz>

² Institute of Botany, Academy of Sciences of the Czech Republic,
Dukelská 135, CZ-37982 Třeboň, Czech Republic

³ Uniwersytet im. Adama Mickiewicza, Instytut Geoekologii i Geoinformacji, ul. Dziegielowa 27,
PL-61-680 Poznań, Poland <grzera@amu.edu.pl>

Abstract: Vegetation succession in front of five retreating glaciers was studied using phytosociological relevés (60) located at different distances between the Little Ice Age (LIA) moraines and the present glacier fronts around Petunia Bay. Approximate dating of succession stages was based on a study of the changing position of glacier fronts in the past approximately 100 years. The described succession corresponds to the uni-directional, non-replacement model of succession. All constituent species, except one, present in the nearby old tundra have colonized the glacier forelands since the end of the LIA. The first species appeared about 5 years after deglaciation. The latest succession stages closely resemble the old tundra.

Key words: Arctic, Svalbard, climate warming, glacier forelands, vegetation succession.

Introduction

Vegetation succession in front of retreating glaciers has been rather frequently studied in the case of both alpine and arctic glaciers (Matthews 2008). Any new case study can contribute to deepening our knowledge about the responses of both glaciers themselves and vegetation to ongoing climate change (Parmesan 2006; Thuiller *et al.* 2008). Many detailed mechanisms and processes of plant succession and relations to environmental factors are not yet known (Walker and del Moral 2003).

Succession in glacier forelands is a typical primary succession where we cannot expect any relevant biotic legacy just after melting of the ice (Walker and del Moral 2003). Thus, the newly exposed terrain is available for colonization from

outside. The rate of colonization varies greatly and can be generally expected to be slower with increasing extremity of a site in terms of the character of the exposed substratum and the external environment, especially climate (Matthews 2008). Distance to and the character of the surrounding vegetation also play important roles; see, for example Bullock *et al.* (2002) and Jones and del Moral (2009) for glaciers; del Moral and Erin (2004) and Řehounková and Prach (2006) in general.

Classical studies on vegetation succession in front of retreating glaciers were especially intense in Alaska (*e.g.* Cooper 1939; Boggs *et al.* 2010), the Alps (*e.g.* Burga *et al.* 2010; Erschbamer *et al.* 2008) and the Scandinavian Mountains (*e.g.* Matthews and Whittaker 1987). In Svalbard, several studies were performed in the northwestern part near Ny-Ålesund (*e.g.* Hodkinson *et al.* 2003; Moreau *et al.* 2009; Nakatsubo *et al.* 2011), the central-western near Longyearbyen (Ziaja and Dubiel 1996), the southwestern part (Olech *et al.* 2011) and in southeastern Svalbard (Ziaja *et al.* 2009). Around Petunia Bay, where our study was performed, detailed data exist on the rate of glaciers retreat (Rachlewicz *et al.* 2007). That study served as the basis for dating the respective succession stages described here. The retreat of these glaciers started with the end of the LIA about the beginning of the 20th century (Rachlewicz *et al.* 2007).

In the recent study, we addressed the following questions: How fast is the newly exposed terrain colonized by plants? Which species of the local flora participate and which not? Is any species turnover obvious? How do the late succession stages differ in species composition from that of permanent (old) tundra which existed in front of foreland moraines in the time of the LIA?

Material and methods

Site description and data collection. — Vegetation was sampled in front of five main glaciers terminating on land around Petunia Bay (central Spitsbergen, Svalbard): Ferdinand, Sven, Hørbye, Ragnar and Ebba (Fig. 1). The particular glaciers and their marginal zones were described by Rachlewicz *et al.* (2007). Vegetation samples (phytosociological relevés) were located at different distances between the LIA moraines and the present glacier fronts, avoiding sites obviously additionally eroded, flooded or buried with sediments from streams or landslides, being homogenous in their substratum and geomorphology and nearly flat (up to a slope of 20°). The coordinates of the central point of phytosociological relevés (5×5 m) were recorded by GPS with an accuracy up to 3 m. The cover of each presented vascular plant species was estimated visually (Kent and Coker 1992). Five phytosociological relevés were taken in the nearby old tundra. Altogether, 60 phytosociological relevés were studied. Nomenclature of vascular plants follows Rønning (1996).

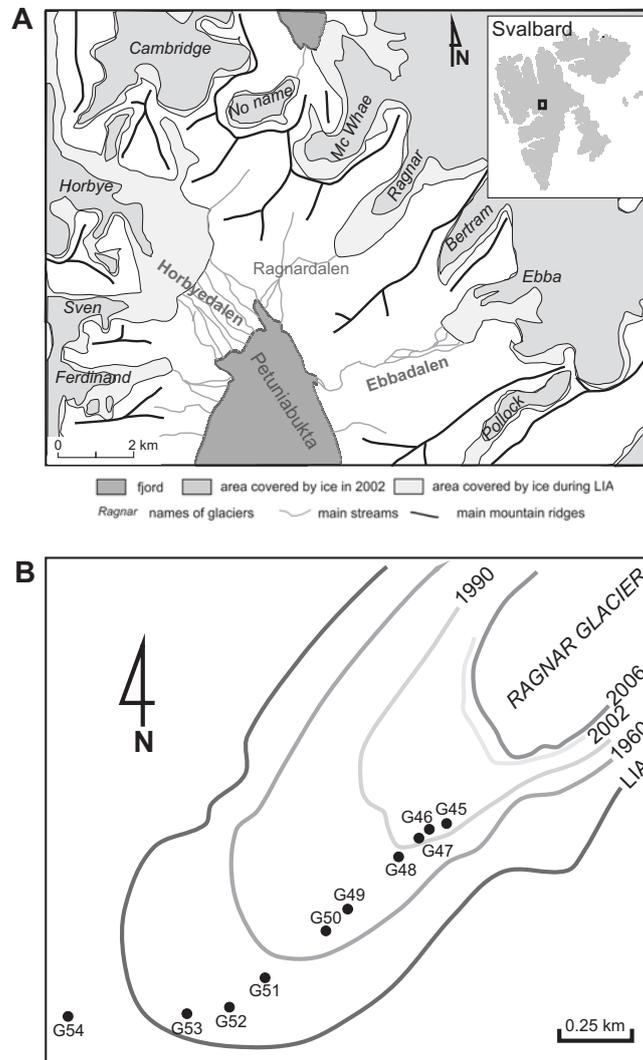


Fig. 1. Location of the studied glacial forelands around Petunia Bay (A), central Svalbard (the inset map) and detailed situation in one of the forelands of the Ragnar Glacier (B), with positions of the glacier front at different times (from Rachlewicz *et al.* 2007) and location of vegetation records (relevés).

Data elaboration. — Seven zones in each of the studied glacial forelands were delimited according to Rachlewicz *et al.* (2007). The approximate age of the respective succession stages was related to the year of vegetation data collection as listed below.

Inside each zone, the particular succession stages which were sampled were approximately dated regarding their positions inside the zone, assuming a constant rate of glacial front retreat. Thus, the succession age must be considered as only approximate estimates.

(I) The zone deglaciaded since 2007, *i.e.* between the present and 2007 positions of the glaciers. This zone was always without vegetation, thus it was not considered further in the analyses.

(II) The zone deglaciaded between 2002 and 2007 (5 years).

(III) The zone deglaciaded between 1990 and 2002 (15 years).

(IV) The zone deglaciaded between 1960 and 1990 (35 years).

(V) The zone deglaciaded between the beginning of the 20th century and 1960 (75 years). On aerial pictures from 1936, the terminal positions of the glaciers were still near the LIA border.

(VI) The zone just on the LIA moraine dated to the beginning of the 20th century (100 years).

(VII) Nearest old tundra arbitrarily dated as 200 years old.

Detrended Correspondence Analysis (DCA) was used for data elaboration as a unimodal, unconstrained ordination technique (Ter Braak and Šmilauer 2002). The constrained Canonical Correspondence Analysis (CCA) was used to test the effect of succession age on species composition. The length of the gradient (3.38 SD-units) justified using unimodal methods (Lepš and Šmilauer 2003).

Results

In total, 32 species of vascular plants were recorded, but only nine species attained >5% cover and just half of the species (16) had cover values <1% (Table 1).

Results of the DCA ordination are presented in Fig. 2. The samples were clearly arranged along the first axis (eigenvalue 0.765) which reflects their succession age. Age explained 19.5% of the vegetation variability in the CCA ordination. The highest vegetation heterogeneity between sites is seen among the youngest stages and then convergence is evident. The second axis (eigenvalue 0.330) is not interpretable by any environmental gradient. Succession is clearly unidirectional.

Constituent species were arranged from those being typical for initial and young succession stages on the left side of the diagram in Fig. 2 to those characterizing late succession stages and old tundra on the right side. The only species that occurred only in the old tundra and not in the succession stages was *Cassiope tetragona*.

The species sequence roughly corresponds to the time of the maximum occurrence of a species in the succession sequence. *Saxifraga oppositifolia* was often the first colonizer, but because of its common presence also in late succession stages and old tundra, its position is fairly in the middle of the temporal gradient. The first species appeared about 5 years after deglaciation, thus the first succession stage (0–2 years after deglaciation) was without vascular plants. The latest succession stages, *i.e.* those just on the LIA moraine, were nearly identical in species composition with the nearby old tundra. Even the total cover of vascular plants was the same, reaching in both cases approximately 60%.

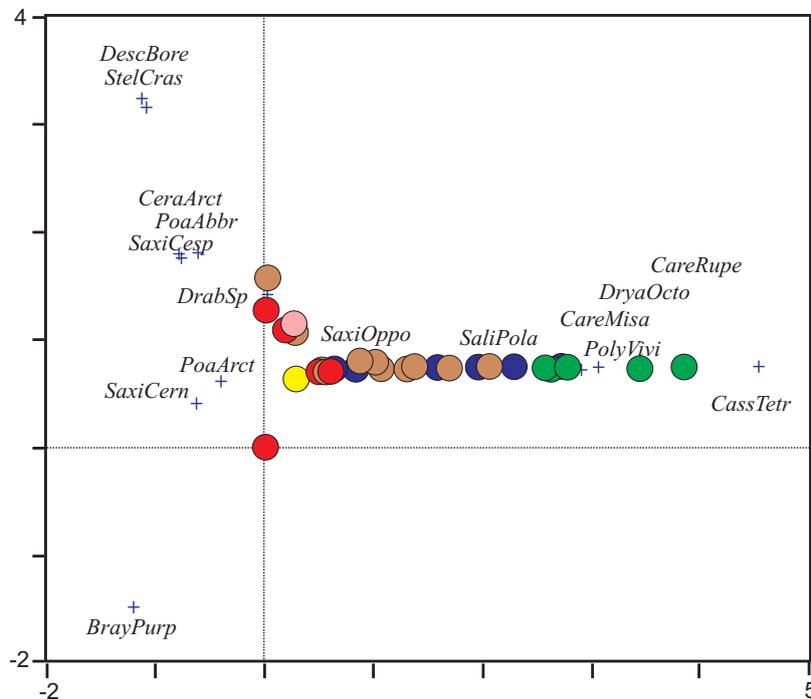


Fig. 2. Ordination (DCA) of vegetation samples and species which best fit the model. The different colours represent differently aged succession stages (average year since deglaciation is indicated): yellow – II (5 years); pink – III (15 years); red – IV (35 years); brown – V (75 years); blue – VI (100 years); green – VII (old tundra). Abbreviations of species names are composed of the first four letters of the generic and specific names (see Table 1). Due to overlaps, not all 60 relevés are visible.

The species number per relevé gradually increased during the first approximately 50 years of succession and then more or less stabilized as shown in Fig. 3, though a great variability existed. A slight decline in species number in the late succession stages is probably a stochastic artefact. The relationship between the number of species and succession age was significant.

Discussion

The recorded succession pattern is one of the best examples of the unidirectional, non-replacement model of succession described already from the Canadian High Arctic by Svoboda and Henry (1987) and recently from Iceland by Cutler (2010). We did not observe any species turnover which is an usual feature of succession (Walker and del Moral 2003). The environmental extremity and limited local species pool, manifested in establishment failure and dispersal limitation, respectively, probably together determine the rather simple course of succession in the high Arctic glacial forelands (Jones and del Moral 2009).

Table 1
 List of the recorded vascular plant species with their participation in the succession; + indicates cover below 1%, r indicates a negligible cover.

| Species | Occurrence in succession stages | Maximum cover [%] |
|--------------------------------|---------------------------------|-------------------|
| <i>Braya purpurascens</i> | II–VII | 1 |
| <i>Carex misandra</i> | V–VII | 5 |
| <i>Carex nardina</i> | V | r |
| <i>Carex rupestris</i> | VI–VII | 40 |
| <i>Cassiope tetragona</i> | VII | 40 |
| <i>Cerastium arcticum</i> | II–V | 5 |
| <i>Cerastium regeli</i> | IV–VI | + |
| <i>Deschampsia borealis</i> | IV, V, VII | 5 |
| <i>Draba</i> sp. | II–VII | 1 |
| <i>Dryas octopetala</i> | IV–VII | 30 |
| <i>Equisetum variegatum</i> | VI, VII | + |
| <i>Eutrema edwardsii</i> | VII | r |
| <i>Festuca vivipara</i> | VI | + |
| <i>Juncus biglumis</i> | V | + |
| <i>Minuartia biflora</i> | V | r |
| <i>Minuartia rubella</i> | III–VI | + |
| <i>Papaver dahlianum</i> | II, IV–VI | + |
| <i>Pedicularis dasyantha</i> | V–VII | + |
| <i>Poa abbreviata</i> | II–VI | 1 |
| <i>Poa alpina</i> | VI | + |
| <i>Poa arctica</i> | IV, VI | 1 |
| <i>Polygonum viviparum</i> | V–VII | 20 |
| <i>Salix polaris</i> | IV–VII | 30 |
| <i>Saxifraga aizoides</i> | IV–VI | + |
| <i>Saxifraga cernua</i> | II–V | 1 |
| <i>Saxifraga cespitosa</i> | II, IV, V | 1 |
| <i>Saxifraga oppositifolia</i> | II–VII | 40 |
| <i>Silene acaulis</i> | IV, VI, VII | + |
| <i>Silene apetala</i> | V | r |
| <i>Silene furcata</i> | IV, V | + |
| <i>Stellaria crassipes</i> | II–VII | 1 |
| <i>Trisetum spicatum</i> | IV | r |

In studies conducted in NW Svalbard, a certain species exchange was observed (Hodkinson *et al.* 2003) or at least some early succession species decreased in their cover while some late succession species increased in sites repeatedly sampled after 30 years (Moreau *et al.* 2009). We also observed the latter trend. Al-

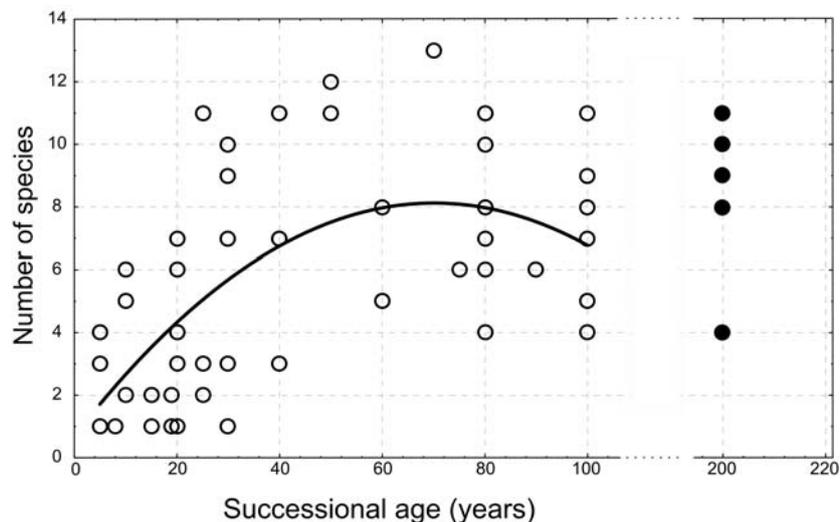


Fig. 3. Relationship between the number of species in the vegetation records and successional age (polynomial function, $p > 0.0002$). Full points on the right represent old tundra samples. Due to overlaps, not all 60 relevés are visible.

though some species occurring in succession stages were not present in the reference five vegetation records from the nearby old tundra (see Table 1), they were recorded elsewhere in the old tundra (Prach *et al.* 2012 this issue). Thus, all the species which occurred in the glacial forelands also occurred in the nearby old tundra and the only species from the old tundra, which we did not observe in the glacier forelands, was *Cassiope tetragona*. This can be explained by the fact that this species is a calcifuge, while the substratum in the studied area is mostly alkaline (Elvevold *et al.* 2007). This species probably needs a sufficient organic layer to accumulate over the alkaline substratum (Acock 1940), which has not yet occurred in our case. In the study conducted in NW Svalbard (Hodkinson *et al.* 2003), *C. tetragona* colonized deglaciated sites after more than 150 years.

The most common first colonizer in our case was *Saxifraga oppositifolia* similarly as in the studies from NW Svalbard (Hodkinson *et al.* 2003; Moreau *et al.* 2005). In those studies, vascular plants represented only a minor component of ground cover for the first 100 years of succession, while cryptogams dominated. This can be attributed to the more oceanic climate than in our case, having 386 vs ca 200 mm of precipitation, respectively (Rachlewicz and Szczuciński 2008; Nakatsubo *et al.* 2010; Láska *et al.* 2012 this issue), and possibly also to the presence of some acidic substrate. Moreau *et al.* (2009) observed a very similar list of vascular plant species as we did. The authors expected a long-lasting succession towards a mature stage taking probably several thousands of years (Moreau *et al.* 2009, p. 373, fig. 7). In our case, succession seems to have nearly reached a mature stage after only approximately 100 years.

In the other parts of Svalbard, succession was only partly similar to our sequence with a higher occurrence of cryptogams in the more oceanic parts (Olech *et al.* 2011) and the absence of *Dryas octopetala* on acidic substrates (Ziaja and Dubiel 1996).

We did not observe any other interpretable gradient except time in our data set. This is probably because our study was not sufficiently detailed regarding micro-site heterogeneity. The 5 × 5 m sampling area probably encompassed different micro-sites which could not be distinguished at this scale. Usually, substrate moisture and structure play a role (Mori *et al.* 2008; Moreau *et al.* 2009). Moreover, we avoided very wet and other extreme (very inclined) sites (see above). But the environment in the studied glacial forelands, as well as in the whole area around Petunia Bay and the respective vegetation, were generally highly uniform (Prach *et al.* 2012 this issue). Thus, the succession trajectory was also uniform in contrast to some other studies conducted in glacial forelands in less extreme geographical areas (*e.g.* Doležal *et al.* 2008; Garibotti *et al.* 2011).

Succession in glacial forelands is in any case the fastest vegetation change we can nowadays observe in Svalbard, and the only obvious one which can be related to climate warming. Average annual temperature increased about 1.8°C between 1912 and 2002 at the airport in Longyearbyen some 60 km south-west of the area studied (Karlén 2005), with some temperature maxima just in the past several years (Láška *et al.* 2012 this issue). Thus, also the melting of glaciers is accelerating (Rachlewicz *et al.* 2007). In the case of further warming, further and faster glacial retreat can be expected, resulting in the increased occurrence of new deglaciated areas to be colonized by plants, but probably by the same species and in the same sequence, and possibly by the same rate as described here. We do not expect expansion of any non-native species, which are still very restricted in their occurrence and abundance in central Svalbard (Liška and Soldán 2004; own observations), nor species from regional hot-spots (Elvebakk 2005). The vegetation in central Svalbard still seems to be highly resistant to warming (Prach *et al.* 2010). These predictions can be confirmed or rejected by future repeated studies in the same sites.

Finally, we can answer the questions stated in the Introduction. All, except one constituent species present in the nearby old tundra colonized the glacial forelands since the end of LIA, *i.e.*, approximately during the past 100 years. The first species appeared about 5 years after deglaciation. No species turnover was observed. The latest succession stages closely resembled the old tundra.

Acknowledgements. — We thank Alena Bartošová and Alex Bernardová for support in the field and Alena Jírová for her help with data elaboration. Keith Edwards kindly corrected our English. We thank Wiesław Ziaja and two anonymous reviewers for their helpful comments. The research was supported by the following grants INGO-LA341, LM2010009 Projekt CzechPolar, MSM6007665801 and AVOZ60050516, and the Polish Ministry of Science project no. N N305 098835 led by Józef Szpikowski.

References

- ACOCK A.M. 1940. Vegetation of a calcareous inner fjord region in Spitsbergen. *Journal of Ecology* 28: 81–106.
- BOGGS K., KLEIN S.C. and GRUNDBLATT J. 2010. Alpine and subalpine vegetation chronosequences following deglaciation in coastal Alaska. *Arctic, Antarctic and Alpine Research* 42: 385–395.
- BULLOCK J.M., MOY I.L., PYWELL R.F., COULSON S.J. and NOLAN A.M. 2002. Plant dispersal and colonization processes at local and landscape scales. In: J.M. Bullock, R.E. Kenward, R.S. Hails (eds) *Dispersal Ecology*. Blackwell, Oxford: 279–302.
- BURGA C.A., KRUSI B., EGLI M., WERNLI M., ELSENER S., ZIEFLE M., FISCHER T. and MAVRIS C. 2010. Plant succession and soil development on the foreland of the Morteratsch glacier (Pontresina, Switzerland): Straight forward or chaotic? *Flora* 205: 561–576.
- COOPER W.S. 1939. A fourth expedition to Glacier Bay, Alaska. *Ecology* 20: 131–155.
- CUTLER N. 2010. Vegetation-environment interactions in a sub-arctic primary succession. *Polar Biology* 34: 693–706.
- DEL MORAL R. and ERIN E.E. 2004. Gradients in heterogeneity and structure on lahars, Mount St. Helens, Washington, USA. *Plant Ecology* 175: 273–286.
- DOLEŽAL J., HOMMA K., VYATKINA M.P., YAKUBOV V., VETROVA V.P. and HARA T. 2008. Primary succession following deglaciation at Koryto Glacier Valley, Kamchatka. *Arctic, Antarctic and Alpine Research* 40: 309–322.
- ELVEBAKK A. 2005. “Arctic hotspot complexes” – proposed priority sites for studying and monitoring effects of climatic change on arctic biodiversity. *Phytocoenologia* 35:1067–1079.
- ELVEVOLD S., DALLMANN W. and BLOMEIER D. 2007. *Geology of Svalbard*. Norwegian Polar Institute, Tromsø: 36 pp.
- ERSCHBAMER B., NIEDERFRINIGER SCHLAG R. and WINKLER E. 2008. Colonization process on a central Alpine glacier foreland. *Journal of Vegetation Science* 19: 855–862.
- GARIBOTTI I.A., PISSOLITO C.I. and VILLALBA R. 2011. Spatiotemporal pattern of primary succession in relation to meso-topographic gradients on recently deglaciated terrains in the Patagonian Andes. *Arctic, Antarctic and Alpine Research* 43: 555–567.
- HODKINSON I.D., COULSON S.J. and WEBB N.R. 2003. Community assembly along proglacial chronosequences in the high Arctic: vegetation and soil development in north-west Svalbard. *Journal of Ecology* 91: 651–663.
- JONES C.C. and DEL MORAL R. 2009. Dispersal and establishment both limit colonization during primary succession on a glacier foreland. *Plant Ecology* 204: 217–230.
- KARLÉN W. 2005. Recent global warming: An artefact of a too-short temperature record? *Ambio* 34: 263–264.
- KENT M. and COKER P. 1992. *Vegetation Description and Analysis*. Belhaven Press, London: 225 pp.
- LÁSKA K., WITOSZOVÁ D. and PROŠEK P. 2012. Weather patterns of the coastal zone of Petuniabukta, central Spitsbergen in the period 2008–2010. *Polish Polar Research* 33 (4): 297–318.
- LEPŠ J. and ŠMILAUER P. 2003. *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press, Cambridge: 284 pp.
- LIŠKA J. and SOLDÁN Z. 2004. Alien vascular plants recorded from the Barentsburg and Pyramiden settlements, Svalbard. *Preslia* 76: 279–290.
- MATTHEWS J.A. 2008. *The Ecology of Recently-Deglaciated Terrain*. Cambridge University Press, Cambridge: 386 pp.
- MATTHEWS J.A. and WHITTAKER R.J. 1987. Vegetation succession on the Storbreen glacier foreland, Jotunheimen, Norway: a review. *Arctic, Antarctic and Alpine Research* 19: 385–395.
- MOREAU M., LAFFLY D., JOLY D. and BROSSARD T. 2005. Analysis of plant colonization on an arctic moraine since the end of the Little Ice Age using remotely sensed data and a Bayesian approach. *Remote Sensing of Environment* 99: 244–253.

- MOREAU M., LAFFLY D. and BOSSARD T. 2009. Recent spatial development of Svalbard strandflat vegetation over a period of 31 years. *Polar Research* 28: 364–375.
- MORI A.S., OSONO T., UCHIDA M. and KANDA H. 2008. Changes in the structure and heterogeneity of vegetation and microsite environments with the chronosequence of primary succession on a glacier foreland in Ellesmere Island, high arctic Canada. *Ecological Research* 23: 363–370.
- NAKATSUBO T., FUJIYOSHI M., YOSHITAKE S., KOIZUMI H. and UCHIDA M. 2010. Colonization of the polar willow *Salix polaris* on the early stage of succession after glacier retreat in the High Arctic, Ny-Ålesund, Svalbard. *Polar Research* 29: 385–390.
- OLECH M., WĘGRZYN M., LISOWSKA M., SŁABY A. and ANGIEL P. 2011. Contemporary changes in vegetation of polar regions. *Papers on Global Change* 18: 35–51.
- PARMESAN C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* 37: 637–669.
- PRACH K., KLIMEŠOVÁ J., KOŠNAR J. and HAIS M. 2010. High Arctic vegetation after 70 years: a repeated analysis from Svalbard. *Polar Biology* 33: 635–639.
- PRACH K., KLIMEŠOVÁ J., KOŠNAR J., REDCHENKO O. and HAIS M. 2012. Variability of contemporary vegetation around Petuniabukta, central Spitsbergen. *Polish Polar Research* 33 (4): 383–394.
- RACHLEWICZ G. and SZCZUCIŃSKI W. 2008. Changes in permafrost active layer thermal structure in relation to meteorological conditions, Petuniabukta, Svalbard. *Polish Polar Research* 28 (3): 261–278.
- RACHLEWICZ G., SZCZUCIŃSKI W. and EWERTOWSKI M. 2007. Post-“Little Ice Age” retreat rates of glaciers around Billefjorden in central Spitsbergen, Svalbard. *Polish Polar Research* 28 (3): 159–186.
- ŘEHOUNKOVÁ K. and PRACH K. 2006. Spontaneous vegetation succession in disused gravel-sand pits: role of local site and landscape factors. *Journal of Vegetation Science* 17: 583–590.
- RØNNING O.I. 1996. *The Flora of Svalbard*. Norsk Polarinstitut, Oslo: 184 pp.
- SVOBODA J. and HENRY G.H.R. 1987. Succession in marginal Arctic environments. *Arctic Antarctic and Alpine Research* 19: 373–384.
- TER BRAAK C.J.F. and ŠMILAUER P. 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.52)*. Microcomputer Power, Ithaca, New York: 500 pp.
- THULLER W., ALBERT C., ARAÚJO M.B., BERRY P.M., CABEZA M., GUISAN A., HICKER T., MIDGLEY G.F., PATERSON J., SCHURR F.M., SYKES M.T. and ZIMMERMANN N.E. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology Evolution and Systematics* 9: 137–152.
- WALKER L. R. and DEL MORAL R. 2003. *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press, Cambridge: 456 pp.
- ZIAJA W. and DUBIEL E. 1996. Vascular plant succession during contemporary deglaciation in the mountain of Nordenskiöld Land, Spitsbergen. In: W.E. Krawczyk (ed.) *23rd Polar Symposium*, Sosnowiec: 99–104.
- ZIAJA W., MACIEJOWSKI W. and OSTAFIN K. 2009. Coastal landscape dynamics in NE Sørkapp Land (SE Spitsbergen), 1900–2005. *Ambio* 38: 201–208.

Received 14 October 2011

Accepted 23 October, 2012