Plant succession and soil development on the foreland of the Morteratsch glacier (Pontresina, Switzerland): Straight forward or chaotic?

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Abstract

As study area we selected the glacier foreland of Morteratsch (approx. 1900 - 2100 m a.s.l.) near Pontresina northwest of the Bernina pass, Upper Engadine, Grisons (Switzerland). The aim of this study is a multimethodological approach using floristic inventories, vegetation and soil mapping of the pro-glacial area, also the detection of crucial parameters of plant resettlement in recently deglaciated areas related to time, local microtopography and soil development.

The following methodological approaches were included in this study: (i) floristic relevés along a chronosequence covering 134 years (1857-1990); (ii) dendrochronological data on tree establishment, collected on a grid with a mesh width of 40m in the area, which became ice-free between 1857 and 1980; (iii) vegetation mapping; (iv) soil analyses including physical and chemical properties of 11 typical profiles; (v) soil mapping and (vi) data evaluation using GIS.

Retreating glaciers successively expose mineral substrates that are colonised within a few years by vascular plants, mosses, lichens and soil biota. With increasing plant cover, also the abundance of soil

organic matter increases. At first sight, the large-scale patterns of vegetation and soil seem to be driven by the time since deglaciation, whereas the small scale patterns may appear chaotic since they depend on local site conditions, which may change dramatically over short distances.

The large-scale pattern seems to develop as follows. About seven years after deglaciation the first pioneer plants establish themselves and form after an additional 20 years the *Epilobietum fleischeri* community, which today dominate the recently deglaciated areas but may be found in patches more or less on the whole pro-glacial area. By contrast, the first elements of the short living *Oxyrietum digynae* community appear after approximately 10 years after deglaciation and persist for only about 30 years. Dendrochronology showed that the first European larch and Swiss stone pine trees established themselves 15 and 31 years, respectively, after deglaciation. Surprisingly, on the study area, Swiss stone pine is about twice as frequent as the typical pioneer species European larch (88 vs. 45 stems per ha), despite the fact that larch starts earlier and grows faster than Swiss stone pine (annual height increment: 21 vs. 8 cm). Up-to-now, however, nowhere in the 150 year old glacier foreland a near-to-mature larch-Swiss stone pine forest can be found.

Besides large-scale factors such as time since deglaciation, topography and disturbance (floods, rockfalls, avalanches), also small-scale factors such as grain size and water content of the substrate, micro-relief and micro-climate seem to be crucial for the development of both vegetation and soil. Time since deglaciation and a straight forward single-pathway succession model are clearly not sufficient for understanding the small-scale patterns of succession. A non-linear succession model with different starting points and different “pathways” of potential primary successions for the different ecological niches is more promising for describing accurately the spatio-temporal vegetation dynamics of the pro-glacial area of Morteratsch.

Keywords: glacier foreland, primary plant succession, soil development, grain size, Upper Engadine, Swiss Alps

Nomenclatures: Frahm and Frey (1983), Lauber and Wagner (2007), Wirth (1995), Braun-Blanquet (1948), Delarze and Gonseth (2008), Runge (1994)

1 Introduction

Since approx. 1850 AD, most Alpine glaciers show phases of marked recessions, temporarily interrupted by smaller glacier advances (cf. e.g. Kinzl, 1932; Röthlisberger, 1986; Patzelt, 1985; Burga, 1987; Zumbühl and Holzhauser, 1988; Furrer, 1991; Maisch, 1992; Holzhauser and Zumbühl, 1996). Locally, large deglaciated surfaces arose where vegetation development, i.e. primary plant succession, may be investigated. Where accurate data of glacier movements are available, soil development and vegetation dynamics along time-gradients (chronosequences) and/or using permanent plots can be studied (e.g. Aletsch, Grindelwald, Rhone, Morteratsch, Roseg, Sesvenna glaciers). First investigations on this topic in Swiss and Austrian Alps have been published e.g. by Coaz (1887), von Klebelsberg (1913), Lüdi (1921, 1934) and Oechslin (1935). Mainly Lüdi (1945, 1950, 1955, 1958) studied vegetation development of Swiss glacier forelands (Aletsch, Gries, Hüfi, Grindelwald, Rhone, Morteratsch, Roseg). Friedel (1938, 1956) made similar investigations in the Austrian Alps (Hintereisferner, Pasterze). Later studies of Alpine glacier forelands have been done by e.g. Jochimsen (1963), Richard (1973, 1987), Bäumler (1988), Schubiger (1988), Gafner and Hess (1994), Burga (1999), Fischer (1999), Münch (2001), Schwarz (2001), Caccianiga et al. (2001), Rehberger (2002), Treter et al. (2002), Wellstein et al. (2003), Bianchi (2005), Raffl et al. (2006), Krüsi et al. (2007) and others.

Similar investigations of vegetation dynamics were also carried out in other European areas like e.g. Norway (see e.g. Burrows, 1990; Matthews, 1992) and North America, notably in Alaska (e.g. Cooper, 1923 and others, see references in Burrows, 1990 and Stuart et al., 1994), in other parts of the USA (e.g. Jones and Moral, 2005) and in Canada (e.g. Jones and Henry, 2003). In Glacier Bay (Alaska),

Cooper (1923) established in 1916 the first permanent plots to monitor vegetation development following deglaciation.

Investigations (field experiments) on seed rain, soil seed bank, germination and establishment of seedlings of pioneer plants growing on Swiss Alpine glacier forelands have been carried out e.g. by Fossati (1980), Urbanska and Schütz (1986), Bäumler (1988), Stöcklin and Favre (1994), Stöcklin and Bäumler (1996), Erschbamer et al. (2001) and Marcante et al. (2009). There are also monitoring field experiments on glacier foreland vegetation related to global change (e.g. Erschbamer, 1997, 2007). Phytosociological approaches of primary plant colonisation of Swiss alpine glacier forelands have been used e.g. by Richard (1973, 1987), Bäumler (1988) and Schubiger (1988).

Generally, two main approaches have been used for the study of primary plant succession on glacier forelands, viz. (i) permanent plots and (ii) chronosequences ('space-for-time-substitution'). Local site conditions are crucial for establishing first plant settlers. In most cases, grain size and moisture of the substrate are crucial parameters of plant establishment. A multimethodological approach using vegetation data, soil data and a spatial analysis is however missing in most cases.

According to Landolt (2003) the glacier foreland Morteratsch lies within the Swiss supra-subalpine coniferous belt (European larch-Swiss stone pine forest), its colonisation by larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) is a part of the primary plant succession processes. At this elevation in the Central Swiss Alps, larch is considered to be the typical pioneer on raw soils, whereas Swiss stone pine is generally believed to require more developed soils. Consequently, we expect larch to dominate the only recently deglaciated areas and stone pine the more advanced successional stages with more developed soils. Contrary to expectations, however, Bianchi (2005) and Elsener (2006) showed that the glacier foreland of Morteratsch is today dominated by Swiss stone pine due to a zoochorous spread by the bird *Nucifraga caryocatactes* (Mattes, 1982, 1988; Holtmeier, 1993; Kratochwil and Schwabe, 1994).

Using dendrochronology, also Bleuler (1986) investigated germination dates of larch trees on the glacier foreland Morteratsch in relation to the historical glacier extensions. He distinguished three sub-populations, which started their growth 10, 10-20 and 20-30 years, respectively, after deglaciation. On

undisturbed and otherwise favourable micro-sites, larch can rapidly colonise recently deglaciated areas. Both Bianchi (2005) and Fischer (1999) compared the most advanced successional stages on the glacier foreland of Morteratsch with near-to-undisturbed forests in its immediate surroundings and concluded that 150 years are definitely not sufficient for the formation of mature larch-stone pine forest (*Larici-Pinetum cembrae*) with a well developed shrub and herb layer.

Plant succession is tightly bound to the underlying substrate and other site factors. Anderson et al. (2000), Matthews and Whittaker (1987), for instance, showed that factor complexes like snow melt, exposure, moisture, terrain and time control vegetation succession. However, only few studies deal with substrate characteristics (parent material) in pro-glacial areas and little is known about the rates of physical and chemical changes of soils in such areas and their consequences for plant growth. Arn (2002), Egli et al. (2003) or Hosein et al. (2004) measured high rates of mineral formation, transformation and chemical denudation, especially on young surfaces, indicating rapid soil development in proglacial areas. In order to explain primary plant succession on glacier forelands many authors suggested, therefore, a micro-site approach, taking small-scale differences in microclimate, disturbance levels, water supply, grain size of the substrate and soil development into account (e.g. Gafner & Hess 1994, Burga (1999 a,b), Böhmer 1999, Elsener 2006, Ziefle 2006, Wüthrich 2008).

The present study aims at elucidating the crucial factors governing plant establishment on recently deglaciated areas such as time since deglaciation, micro-relief or soil development, using a multi-method approach including (i) floristic relevés along a chronosequence covering 134 years (1857-1990); (ii) dendrochronological data on tree establishment collected using a grid with a mesh width of 40m in the area which became ice-free between 1857 and 1980; (iii) vegetation (iv) soil analyses; (v) soil mapping and (vi) spatial analyses using a GIS. Related to our main question “Straight forward or chaotic?” we try to establish a generalised model explaining the patterns of primary plant succession observed on the glacier foreland Morteratsch.

2 Study area

The investigation area consists of the glacier foreland Morteratsch (approx. 1900 - 2100 m a.s.l.) near Pontresina northwest of the Bernina pass, Upper Engadine, Grisons (Switzerland) (**fig. 1, photo 1**). The backwall of the glacier is formed by high mountain peaks of the South Raetian Alps like Piz Bernina (4048.6 m asl, the highest peak of the Grisons and the Eastern Alps) and Piz Palü (3901 m asl). The glacier foreland is easily accessible by a trail beginning at the railway station Morteratsch. The area between Pontresina and Morteratsch belongs to the Lower Austroalpine Bernina Nappe s.l. and comprises mainly various plutonic rock types, like granodiorites and alkali-granites, further syenites, diorites and gabbros (Staub 1946, Rageth 1984, Büchi 1987 and 1994, Spillmann 1993). Palaeo-glaciological and palaeo-ecological studies near the Bernina pass and in the Upper Engadine region were been done by Beeler (1977), Gamper and Suter (1982), Heitz et al. (1982), Kleiber (1974), Punchakunnel (1983), Fitze (1984), Burga (1987), Burga and Perret (1998) and Zoller et al. (1998). The Swiss Glaciological Commission of the Swiss Academy of Natural Sciences scnat (Gletscherberichte 1881-2008) recorded historical and recent glacier length fluctuations (**fig. 2**). Rübél published 1912 the first detailed monograph to the plant geography of the Bernina pass area. Herzog (1912) described already the moss flora of the glacier forelands of Morteratsch and Roseg. The first detailed vegetation map (scale 1:10'000) of the glacier foreland Morteratsch was established by Bäumler (1988). A slightly generalised map on a smaller scale (1:13'700) of the actual vegetation cover (modified and completed after Fischer, 1999) gives an overview to the vegetation pattern of the glacier foreland (**fig. 1**).

Soils in the pro-glacial area are weakly developed and have a maximum age of 150 years. Forested areas outside the glacier stage of 1857 are characterised by Podzols having an age of 10000 years or more.

3 Methods

For the present study, we used a multi-method approach combining (i) floristic relevés along a chronosequence covering 134 years (1857-1990); (ii) dendrochronological data on tree establishment collected using a grid with a mesh width of 40m in the area, which became ice-free between 1857 and 1980; (iii) vegetation; (iv) soil analyses including physical and chemical properties of 11 typical soil profiles; (v) soil mapping and (vi) spatial analyses using a GIS.

3.1 Vegetation

Burga established in 1999 10 permanent plots within the glacier foreland to monitor the vegetation dynamics of deglaciated areas (**fig. 1**, Burga, 1999a, b). With the help of the vegetation cover of permanent plots and the time since ice retreat (chronosequence 1857-1990), a generalised model of primary plant succession could be established (**figs. 3 - 4**). A clear correlation between vegetation and grain size of the substrate on consolidated sites could be shown (Burga, 1999a, b). Less obvious is the correlation between plant establishment and the age of the sites (time since deglaciation) due to the great small-scale heterogeneity of factors such as erosion and other disturbances, micro-relief, soil moisture, microclimate etc.

In 2004, a grid with a mesh width of 40 m was established with the help of the Swiss Federal Research Institute WSL, Birmensdorf, consisting of a total of 464 grid points and covering most of the glacier foreland between the stages 1857 and 1980 (**fig. 2**). At each grid point, 21 site and vegetation parameters were recorded. By superimposing a deglaciation map (data based on the Gletscherberichte 1881-2008 and Burga, 1999a,b), the year of deglaciation was assigned to each grid point. On circular plots with a radius of 1 m, 2 m and 5 m respectively, vegetation and site parameters of the herb, shrub and tree layers were recorded (unpublished data of Elsener, 2006). Using the closest-individual method (Greig-Smith 1983), individuals of larch and Swiss stone pine that were at least 10 cm tall were sampled at each grid point the closest, measuring the distance to the grid point, tree height, basal stem diameter, tree age and vitality (Elsener, 2006).

At 110 of the grid points, Ziefle (2006, unpublished data) studied the establishment of herbaceous plants and shrubs (mainly willows [*Salix spec.*]). For this, Ziefle (2006) subdivided the glacier foreland

into nine deglaciation and two flooding strata viz. ice free since (1) 1986-1995, (2) 1976-1985, (3) 1966-1975, (4) 1956-1965, (5) 1946-1955, (6) 1936-1945, (7) 1926-1935, (8) 1916-1925 and (9) 1857-1915), flooded in (10) 1955 and (11) 1987, respectively (**fig. 2**). In each stratum, ten of the established grid points were selected randomly. At each of the selected grid points, age and size of the closest individuals of *Salix myrsinifolia* and *S. helvetica* were measured.

As a control study, Bianchi (2005, unpublished data) investigated the establishment of Swiss stone pine and larch in the area outside of the actual pro-glacial area of the Morteratsch glacier, i.e. close to the end moraine of the 1857 stage, located at the edge of the grid mentioned above.

3.2 Soils

3.2.1 Soil mapping

Soil mapping (scale 1 : 10000) within the pro-glacial area was carried out based on aerial photographs and field investigations. Soil cartography and classification were performed according to the FAL system (Brunner et al., 1997). Soil mapping already includes a certain generalisation as small-scale variations (approx. < 100m²) could not be considered (Egli et al. 2006).

Based on the soil (Egli and Kneisel, unpubl.) and vegetation (Bäumler, 1988; Burga, 1999a; Fischer, 1999) maps, spatio-temporal soil and vegetation properties could be compared, both qualitatively and quantitatively. Area calculations (proportions of different soil and vegetation types between two deglaciation isochrones) were performed using ArcGIS 9.3 (ESRI) with modules programmed in Visual Basic for Applications (VBA). Input data sets were the digital soil and vegetation maps, data on historical glacier extensions (Burga, 1999 a,b) and the digital elevation model (20 m grid) within the pro-glacial area.

3.2.2 Soil analyses

11 pits were excavated for chemical and physical analyses of the soil material. 10 of them were located next to the permanent vegetation monitoring plots of Burga (1999 a,b). About two to four kilograms of soil material were collected per soil horizon, and the following parameters were measured: organic C and N, pH, granulometry, skeleton content, bulk density. At four sites (two Skeletic Leptosols and two Humi-Skeletic Leptosols), water tension (water potential) was monitored during 5 periods within one summer. The water potential was measured at a depth of 0-10 cm using two to three tensiometers at each site (Jet Fill Tensiometer, Eijkelkamp).

Total C and N contents of both the soil and the parent material were measured with a C/H/N analyzer (Elementar Vario EL). Soil pH (in 0.01 M CaCl₂) was determined on air-dried fine earth samples using a soil to solution ratio of 1:2.5.

Particle size distribution was determined on some selected soil samples. After a pre-treatment of the samples with H₂O₂ (3%), particle size distribution was determined by sieving the coarser particles (2000 - 32µm) and measuring the finer particles (< 32µm) with help of an X-ray-sedimentometer (SediGraph 5100/micromeritics/Germany).

4 Results

Primary plant succession of the pro-glacial area of Morteratsch with its predominantly siliceous parent material starts with the pioneer plant communities *Oxyrietum digynae* (**photo 2**) and *Epilobietum fleischeri* (**photo 3**; Lüdi, 1958; Braun-Blanquet, 1973; Bäumler, 1988; Burga, 1999a,b) and ends with the larch-Swiss stone pine forest (so-called climax vegetation; **photo 4**) after substantially more than 150 years. The investigations of Burga (1999a, b), based on ten permanent plots covering the chronosequence from about 1857 to 1990, give a general picture of plant succession on the glacier foreland and stress the crucial role of the grain size of the substrate. (**figs. 3 and 4**, Burga, 1999a). The following results are based on the vegetation and soil data, collected on a systematic grid, as well as on the detailed vegetation and soil maps (ArcGIS, **fig. 5**).

4.1 Primary plant succession

4.1.1 Large-scale pattern

The first plants, i.e. *Epilobium fleischeri*, *Oxyria digyna*, *Linaria alpina*, *Saxifraga aizoides*, *Rumex scutatus*, appear about 7 years after deglaciation and reach greater cover-abundance values after about 27 years (**fig. 3**). Together they form the long-living *Epilobietum fleischeri* plant community, which dominates the recently deglaciated areas but of which fragments can be found almost everywhere on the foreland of the Morteratsch glacier (**figs. 1, 5, 7**). The first species of the short living *Oxyrietum digynae* appears approx. 10 years after deglaciation and disappears approx. 30 years later (**figs. 3, 5, 7**). In the two above-mentioned pioneer communities, frequently also the following plant species can be found: *Achillea moschata*, *Adenostyles leucophylla*, *Cardamine resedifolia*, *Cerastium uniflorum*, *C. pedunculatum*, *Geum reptans*, *Myricaria germanica*, *Poa nemoralis*, *Poa alpina*, *Saxifraga bryoides*, *S. paniculata*, *Trifolium pallescens* and the moss species *Pohlia* spec. and *Rhacomitrium canescens*. Moss cushions of *Rhacomitrium canescens* form the subassociation *Epilobietum fleischeri rhacomitrietosum* (Braun-Blanquet, 1973). The first small larch trees, the first shrubs of willows and green alder and the first dwarf-shrubs as e.g. the rust-leaved alpenrose are found on areas, which have been ice-free for about 12 to 15 years (**figs. 3, 4**). Surprisingly, lichens such as *Stereocaulon* cf. *dactylophyllum* need about 15-20 years to establish the first populations, and 150 years are definitely not sufficient for the establishment of a larch-Swiss stone pine stand (*Larici-Pinetum cembrae*) (**figs. 4, 5**).

Fig. 7 shows the development after deglaciation of the frequency of occurrence of the more important vegetation types, as shown on the vegetation map **fig. 1**. Data on the development of the cover of the more important species are given in **figs. 3 and 4**). **Fig. 7** clearly shows the dominant role of the *Epilobietum fleischeri* pioneer community during the first 100 years of succession. The second most important community is the green alder community, which starts early and grows continually in importance until it overtakes the *Epilobietum fleischeri* after about the 100 first years of succession. Until about 55 years after deglaciation, pioneer grass communities (*Poa nemoralis*, *P.*

alpina, *P. laxa*) develop like green alder but later they decrease, probably due to the increasing shrub cover. Grass heath communities on moister soils are far less frequent and occur only about 60 years after deglaciation.

The first members of the larch-Swiss stone pine climax community establish themselves already 5-10 years after the glacier retreat, but their importance remains low during the first 120 years of succession, and the tree growth is very slow. Approx. 40 years after deglaciation, the first open clusters of small larch and Swiss stone pine trees form. As already mentioned above, the establishment of more or less mature larch-Swiss stone pine forest requires more than 150 years.

4.1.2 Small-scale pattern in the herb layer

On areas, which have been ice-free for 10-19 years, Ziefle (2006, unpublished data) found an average of 11.5 plant species (vascular plants, bryophytes, lichens) per 3.14 m², i.e. on a circular plot with a radius of 1 m. Surprisingly, the small-scale floristic diversity differs only little among the ten strata distinguished along the chronosequence. In contrast to the small-scale floristic diversity, the large-scale diversity, as expressed by the cumulative species number on 10 of the above-mentioned plots of 3.14 m² each, doubled along the chronosequence as expected from 34 species on the youngest to 63 on the oldest stratum (ice-free for 90-150 years). Ziefle (2006, unpublished data) found the following species most often: *Rhacomitrium canescens* (frequency: 69%/ cover: 7.6%), *Poa nemoralis* (68%/ 3.9%), *Epilobium fleischeri* (73%/ 1.7%), *Stereocaulon* spec. (38%/ 2.7%), *Agrostis schraderiana* (28%/ 3.4%), *Achillea moschata* (55%/ 1.5%), *Hieracium staticifolium* (60/ 1.2%), *Rumex scutatus* (42%/ 1.1%), *Poa alpina* (58%/ 1.1%) and *Trifolium pallescens* (40%/ 1.0%).

Multivariate analyses revealed that the 110 vegetation surveys of the herb layer may be grouped into ten vegetation units, each characterised by one dominant or few co-dominant species: (1) *Oxyria digyna*, (2) *Rhacomitrium canescens*, (3) *Saxifraga* spec., (4) *Poa alpina*/ *P. nemoralis*, (5) *Festuca rubra* s.l., (6) *Agrostis schraderiana*, (7) *Adenostyles leucophylla*, (8) *Stereocaulon* spec., (9) *Achillea moschata*/ *Sempervivum* spec. and (10) *Rhododendron ferrugineum*.

Time since glacier retreat and thus a linear succession model are not sufficient to explain the pattern formed by the above-mentioned vegetation units. In addition to time since deglaciation also micro-site conditions (e.g. grain size of the substrate and water supply) seem to play a crucial role.

Consequently, a micro-site controlled succession model with several different starting points and converging pathways meeting at a common climax seems to describe best the situation observed in the pro-glacial area of Morteratsch (**fig. 8**).

4.1.3 Colonisation by larch and Swiss stone pine

In the foreland of the Morteratsch glacier, surprisingly, Swiss stone pines are twice as frequent as European larch trees (88 vs. 45 stems per ha), this despite the fact that larch trees were found to establish themselves much earlier (**fig. 4**) after glacier retreat than Swiss stone pines (15 vs. 30 years) and to grow much faster (mean annual height increment: 21 vs. 8 cm) (Elsener 2006, unpublished data). Today, the pioneer species larch prevails over Swiss stone pine only in the height class above 4m (7 vs. 1 stems per ha). Given the actual predominance of Swiss stone pine in all the other height classes, the relative importance of the shade-tolerant Swiss stone pine will likely further increase in the future. In the long-term, saplings of the light-demanding larch will only be able to establish successfully on areas subject to disturbances resulting e.g. from avalanches, flooding or local die-back of Swiss stone pines due to diseases or old age. The successional most advanced larch-stone pine clusters on the pro-glacial area differ distinctly from close-to-climax stands just outside the glacier stage of 1857. The larch-stone pine clusters consist by 8 stems per ha within the pro-glacial area and by 416 stems per ha outside of the pro-glacial area, i.e. a ratio of 8/416 stems per ha (**fig. 5**, Bianchi, 2005, unpublished data). A second surprise is the fact, that “time since ice retreat” explains only a comparatively small part of the observed variances in tree height and stem number. The zoochorous Swiss stone pine, considered as typical shade-tolerant climax species mainly germinating on raw humus, is already today much more frequent in the glacier foreland than the anemochorous and light-demanding larch, germinating on undeveloped raw soils.

4.2 Soil development

The longer a surface is exposed to weathering, the more developed are usually the soils. Although the extent of soil development greatly varies on the pro-glacial area, the above-mentioned general trend could be found and measured. The main soil types are Endoskeletal Fluvisols, Skeletic or Lithic Leptosols, Humi-skeletic Leptosols, including some sites with Ranker (FAO-Unesco, 1998; FAO, 1998) that have a weak B horizon and Dystric and Gleyic Cambisols (endoskeletal) and sites without soil (**fig. 5**). The youngest soils near today's edge of the glacier show almost no signs of chemical weathering and alteration products. They are usually characterised by a very thin and often discontinuous humus layer. The soils are in general skeleton-rich (defined as the fraction $>2\text{mm}$). The fine earth of the soils has a high sand content (usually between 50 and 90%) and partially contains some silt (eolian attribution, grinding due to fluvial transport?). The Fluvisols partially show slightly increased silt content. In all other soils, granulometry is rather uniform. A significant trend of soil physical characteristics with time could be measured: The younger the soils, the greater the skeleton and sand contents (**tab. 2, fig. 6a**). The decrease in grain size with exposure time is a concomitant effect of weathering. Due to the high proportion of skeleton in the soil, the water content remains low ($< 30 \text{ vol.-%}$) in all soils. In general, water permeability of all soils is very high. Two different types of soil water regimes could be discerned: (1) soils drying out relatively quickly (**tab. 3**) and (2) soils remaining moist during the whole summer period due to north-exposure, concave topographical situation or water supply from subsurface flow (see our micro-site primary succession model, **fig. 7**). The 'dry' soils lose relatively quickly the gravitational water ($< 100 \text{ hPa}$), which locally may limit plant growth substantially.

Due to the increasing vegetation cover and plant productivity with time since deglaciation, increasingly more organic carbon is transferred into the soils; consequently, the older the soils, the greater the abundance of soil organic matter (**fig. 6b**). After about 150 years of soil formation, the soil organic matter stock reaches around $1.5 - 5 \text{ kg m}^{-2}$, which is quite considerable. In alpine environments, soils originating from siliceous parent material may contain more than $40 \text{ kg organic C m}^{-2}$ (see also Hitz,

2002) while the C-content of soils on calcareous parent material is often distinctly lower (15 – 20 kg C m⁻²; Egli et al., 2008).

Mean annual rates of organic C accumulation during 150 years of soil development are in the range of 10 - 33 g C/m²/y. These values are high compared to rates reported from other Holocene chronosequences (Egli et al., 2001: 6.7 - 9 g C/m²/y for soils older than 400 years; Lichter, 1998: 9 g C/m²/y). In Podzols of the Swiss Alps, the long-term accumulation rates (i.e. approx. 10000 years) are in the range of 2 - 4 g C/m²/y (Egli et al., 2001).

4.3 Relationships between vegetation and soil data

Comparison of the vegetation and the soil maps (**fig. 5**) shows similar general succession patterns. There is a good agreement between the vegetation types green alder/ willow scrub/ pioneer grass communities and the occurrence of Humi-Skeletal Leptosols. This vegetation/ soil pattern related to recessional moraines reflects partly some historical glacier stages (**figs. 1, 5**). The *Oxyrietum digynae* settles on Skeletal/ Lithic Leptosols or on “no soil” substrate after approx. 10 years after ice retreat and disappears approx. 30 years later (**fig. 5, tab. 5**). The distribution pattern of the *Epilobietum fleischeri* with single willow shrubs matches fairly well the distribution of the Skeletal/Lithic Leptosols, which are very poor in nutrient and dry out both quickly and frequently (**tabs. 3, 5**). The pioneer community *Oxyrietum digynae* grows preferentially on sites without soil. Undeveloped soils and scarce vegetation is also found on sites repeatedly flooded by the Morteratsch torrent (**fig. 2**). Likewise nearly free of vegetation and soil are the glacially moulded rock mounds (*roche moutonnée*). But nevertheless, the following plant species can be found on rock crevasses: e.g. *Sempervivum arachnoideum*, *Agrostis rupestris*, *Silene rupestris*, *Veronica fruticans*, and also *Pinus cembra*. On areas covered by medium-sized boulders, however, pockets with fine soil material exist where species grow, as for instance *Adenostyles leucophylla*, *Rumex scutatus*, *Dryopteris filix-mas*, *Athyrium filix-femina*, and *Gymnocarpium dryopteris*. Gleyic Cambisols are found in mire micro-biotopes and small ponds (**figs. 5, 8**). On the NE boundary of the older pro-glacial area (glacier stages 1878-1920) and close to the stage of 1980 Endoskeletal Fluvisols developed due to the floods of 1955 and 1987 (**fig. 2**). These

soils with slightly greater contents of carbon and water content are primarily occupied by green alder and willow shrubs. Open larch-Swiss stone pine stands with fairly dense herb layer occur on Dystric Cambisols (**tab. 4**). In general, concomitant with plant cover also soil organic matter increases. A fast increase in soil organic carbon in young soils within a few decades was also described by Conen et al. (2007), Egli et al. (2002) and in an early study of Jenny (1980).

In conclusion, time since glacier retreat, extent of soil development, grain size distribution of the substrate and local water supply seem to be the principal drivers of vegetation development and, therefore, the basis for a simple, mechanistic, non-linear plant succession model. A more detailed comparison between the occurrence of vegetation units and plant species, on the one hand, and soil data, on the other hand, is given in **tabs. 4, 5 and 6**. The *Oxyrietum digynae* occurs only on sites having a strongly gravely substrate. Also the *Epilobietum fleischeri* predominantly grows on sites rich in gravels and stones. Also pioneer grass communities can be recorded at sites with a high gravel or stone occurrence, although they grow also at sites with smaller grain sizes. Grass heath prefers sites with a lower stone and gravel content. The green alder scrub can be mostly found at periodically moist stony sites (**tab. 6**). According to the expectancies, rock vegetation is found at sites that are strongly stony or rocky. In local pockets, rock vegetation grows on a substrate that has a much lower grain size (i.e. silt and clay).

On the whole, local site conditions are highly variable, and the linear primary succession models proposed by Lüdi (1958), Braun-Blanquet (1973) and Bäumler (1988) are not sufficient for explaining accurately the complex spatio-temporal vegetation dynamics of the pro-glacial area of Morteratsch.

For this,

a better succession model with several different starting points and the larch-Swiss stone-pine community as common climax is needed (**fig. 8**).

5 Discussion and conclusion

Retreating glaciers successively expose mineral substrates that are colonised within a few years by vascular plants, mosses, lichens and soil biota. Soil development proceeds quickly in the pro-glacial area. 150 years of soil development lead to Ranker (Humi-Skeletal Leptosols) followed by Dystric Cambisol. On the pro-glacial area Morteratsch, we observed significant soil-forming processes such as alteration of parent material, formation of weathering products and accumulation of organic matter (weak B-horizons in Ranker). The rate of soil formation in the Morteratsch area is in the same order of magnitude as reported by other authors (e.g. Haugland, 2004). Fitze (1982) and Patzelt (1973) described Rankers that have been formed in the time span of 200 - 350 years after deglaciation. In Central Alpine areas, Dystric Cambisols usually form within 250 - 300 years after glacier retreat (Egli et al., 2001), whereas Podzols require a minimum duration of about 1200 years (Egli et al., 2003). In general, a fairly good agreement between the spatial patterns of soil types and vegetation units was found.

At first sight, the small-scale vegetation pattern of the pro-glacial area seems to be chaotic. At larger scales, patterns and processes seem clearer (chrono- and topo-sequences, regarding Morteratsch; see Bäumler, 1988; Burga, 1999a; Krüsi et al., 2007). Bäumler (1988) and Burga (1999a) established a rather linear succession model starting with one initial stage, followed by different development pathways and ending with coniferous forest as climax of the subalpine forest belt.

In the present paper we propose a more complex succession model with different, micro-site-dependent starting points and one climax stage, i.e. the larch-Swiss stone pine community (**fig. 8**). This model is quite elegant and accurate but it has also its weaknesses. For instance, some plant species reflect the grain size of soils, soil moisture or other characteristics of substrate (*Rhacomitrium canescens* and *Pohlia* spec. patches: clay, silt; *Adenostyles leucophylla* stands; coarse boulders; *Agrostis rupestris* and *Sempervivum* spec. patches; mainly rock surfaces). On the other hand, the model includes different types of micro-sites where primary successions in pro-glacial sections can start (**fig. 8**). *Oxyria digyna* is only dominant at initial stages and builds up the typical short-living pioneer plant community Oxyrietum digynae. Epilobietum fleischeri is a wide-spreading and long-lived

plant community of primary plant succession on glacier forelands dispersed across most of the chrono-sequence (e.g. Lüdi, 1958; Braun-Blanquet, 1973; Bäumler, 1988; Burga, 1999a).

Regarding the growth of larch and Swiss stone pine, the latter tree species is roughly twice as numerous as larch (Elsener, 2006, unpublished data), even though larch is a typical pioneer tree starting earlier after deglaciation and growing faster than Swiss stone pine on ice-free areas of the glacier foreland (Krüsi et al. 2007). This rather unusual situation in the pro-glacial area of Morteratsch may be explained by the local dominant wind direction and by the role of nutcracker (*Nucifraga caryocatactes*) regarding the seed dispersal of *Pinus cembra* (Mattes 1982, 1988; Holtmeier 1993, 2000).

The use of a plant-sociological approach on primary succession patterns of glacier forelands will not be in all cases successful, this due to heterogeneous environmental conditions and due to repeated local disturbances (floods, rockfalls, avalanches), which hinder a continuously progress until full development of plant communities. Therefore, mostly permanently stable plant communities, such as *Epilobietum fleischeri*, will in most cases not develop to the subalpine climax stage of *Larici-Pinetum cembrae*. Locally defined plant communities or 'types' seem to be better suited for describing the complex spatio-temporal vegetation patterns on the foreland of the Morteratsch glacier.

Raffl et al. (2006) showed in their study on the Rotmoosferner (Ötztal, Austria) the influence of different environmental conditions on primary plant succession. They postulate two different successional pathways depending on a multitude of factors (e.g. sunny vs. shaded side). Furthermore, Erschbamer et al. (2001) and Marcante et al. (2009) stressed the high degree of heterogeneity regarding the establishment of seedlings, depending on seed rain, variability of soil seed bank, germination, mortality rates of the remaining seedlings and other factors.

Patterned structures may be associated with abrupt thresholds that either enhance or stop/hinder soil formation and vegetation development. This might be due to several causes such as microclimatic conditions, micro-relief, deposition of physically inhomogeneous parent material (sites with a more fine-grained deposit close to rock debris), disturbance and probably also to brief periglacial processes (cf. Haughland, 2004).

Although the small-scale soil and the vegetation patterns in the pro-glacial area are very patchy and heterogeneous, the statistical and geographical comparison of the soil and vegetation maps revealed several significant trends and interrelationships among soil development, vegetation cover and composition and time since deglaciation. This is a valuable basis for further modelling of vegetation and soils development. Grain size of the substrate, water supply, microclimate and the time since glacier retreat seem to be the main drivers of plant successions on the young, pro-glacial areas.

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Captions to figures and tables

Figures

Fig. 1: Investigation area and vegetation map of the glacier foreland Morteratsch (1900 – 2100 m a.s.l). The lines mark the approximate position of the end of the glacier between 1857 and 1997 (after Burga, 1999b). Note the special edition of the Swiss stamp 2009 dedicated to the Morteratsch glacier. Source: @Die Post.

Fig. 2: Investigation area of the glacier foreland Morteratsch with more accurate former positions of the glacier for the time span 1940-2000 and with the established grid with a mesh width of 40 m (bright dots).

Fig. 3: Generalised chronosequence of pioneer plants 1857-1990 (vascular plants and lichens, after Burga, 1999a,b)

Fig. 4: Generalised chronosequence of subalpine forest and dwarf shrub heath species 1857-1990 (after Burga, 1999a,b)

Fig. 5: Comparison between the spatial distribution of soil types and vegetation units.

Fig. 6 a, b: Temporal evolution of a) the soil skeleton content (material with a diameter $> 2\text{mm}$; referred to a standardised soil depth of 15cm) and b) abundance of soil organic matter ($\text{kg/m}^2 \text{C}$) in the pro-glacial area

Fig. 7: Temporal development of the relative proportion of the most important vegetation types (see also Fig. 1) of the vegetation-covered area of the glacier foreland Morteratsch as a function of time (data from figs. 2 and 5)

Fig. 8: Primary plant successions of the glacier foreland Morteratsch: model based on different starting points of different potential primary successions and grain size classes (non-linear micro-site primary succession model)

Tables

Tab. 1: Ecological properties of pioneer plants occurring in the glacier foreland Morteratsch

Tab. 2: Selected chemical and physical properties of 11 typical soil profiles in the pro-glacial area

Tab. 3: Soil moisture of four monitored sites (two different soil types) in the pro-glacial area

Tab. 4: Comparison of vegetation with soil data of the glacier foreland Morteratsch

Tab. 5: Absolute and relative distribution of vegetation units within the pro-glacial area with respect to the soil types

Tab. 6: Relative distribution of the vegetation types in respect to the grain sizes (soil)

- Larch-Swiss stone pine forest (*Larici-Pinetum cembrae*), partially Swiss stone pine forest
- Open larch-Swiss stone pine forest
- Dwarf shrub heath (*Rhododendro-Vaccinietum*, *Empetro-Vaccinietum*, *Junipero-Arctostaphyletum*)
- Mosaic structure of dwarf shrub heath with *Juniperus communis* ssp. *nana* and *Nardus stricta* grass heath
- Green alder scrub (single stands of shrubs and *Alnetum viridis*)
- European dwarf-pine scrub
- Grass heath on moister soils (Dystic Cambisols, grass species e.g. *Festuca violacea*, *Calamagrostis villosa*, *Phleum rhaeticum*, *Poa alpina*)
- Pioneer grass communities. Outside of the pro-glacial area grass heath (*Geo montani-Nardetum* and *Poion alpinae*, above approx. 2400 m *Caricetum curvulae*)

- Epilobietum fleischeri* with single willow shrubs (on older sites with alpenrose)
- Oxyrietum digynae* with *Myricaria germanica*, *Saxifraga aizoides*, *Linaria alpina* and moss cushions (*Rhacomitrium* spec., *Pohlia* spec.)
- Boulder plant communities, partially *Epilobietum fleischeri*, *Adenostyles leucophylla* and several fern species
- Rock vegetation (e.g. *Agrostis rupestris*, *Silene rupestris*, *Sempervivum arachnoideum*)
- Peat bog, ancient lake mire
- No vegetation, bedrock, rock debris, glacier ice, brooks
- Glacier stages 1857 - 1997
- Number 1-10 permanent vegetation monitoring plots (16m² - 400m²)

Glacier foreland Morteratsch

Glacier stages 1857 – 2004

Grid of investigated area (bright dots) 40 m

Floods of 1955 and 1987

Legend to the tables 1–3 (plant species occurrence along the chronosequence of the glacier forefield)

Cover-abundance

- present rarely (Br.–Bl. >r and <+)
- present infrequently, low cover-abundance (Br. –Bl. +)
- present frequently, low cover-abundance (Br.–Bl. 1, <5%)
- present frequently, moderate cover-abundance (Br.–Bl. 2, 5–25%)
- present frequently, high cover-abundance (Br.–Bl. 3–4, >25%)
- o o o o locally higher cover-abundance (>75%)

Glacier stage (years A.D.)	~1990	1985	1980	1970	1960	1950	1940	1920	1900	1878	1857
Age of icefree areas 1857–1997 (years)	~7	12	17	27	37	47	57	77	97	119	140
Approx. distance (metres) from the present (1997) end of glacier (axis of the valley)	100	150	200	500	800	970	1170	1440	1660	1920	2050
Subalpine forest and dwarf shrub heath species (selection)											
Larix decidua											
Rhododendron ferrugineum											
Juniperus communis ssp. alpina											
Betula spec.											
Vaccinium myrtillus											
Athyrium distentifolium											
Dryopteris filix-mas											
Pinus cembra											
Empetrum nigrum s.l.											
Phyteuma betonicifolium											
Vaccinium uliginosum s.l.											
Avenella flexuosa											
Solidago virgaurea s.l.											
Homogyne alpina											
Calamagrostis villosa											
Arctostaphylos uva-ursi											
Peucedanum ostruthium											
Hieracium murorum											
Vaccinium vitis-idaea

Vegetation

Larch-Swiss stone pine forest (Larici-Pinetum cembrae), partially Swiss stone pine forest	Epilobietum fleischeri with single willow shrubs (on older sites with alpenrose)
Dwarf shrub heath (Rhododendro-Vaccinium, Empetro-Vaccinium, Junipero-Arcostaphyllum)	Oxycietum dignae with Myricaria germanica, Saxifraga aizoides, Linaria alpina and moss cushions (Rhacomitrium spec., Pohlia spec.)
Green alder scrub (single stands of shrubs and Alnetum viridis)	Boulder plant communities, partially Epilobietum fleischeri, Adenostyles leucophylla and several fern species
Grass heath on moister soils (Dystic Cambisols, grass species e.g. Festuca violacea, Calamagrostis villosa, Phleum rhaeticum, Poa alpina)	Rock vegetation (e.g. Agrostis rupestris, Silene rupestris, Sempervivum arachnoideum)
Pioneer grass communities, Outside of the pro-glacial area grass heath (Geo montani-Nardetum and Poion alpinae, above approx. 2400 m Caricetum curvulae)	No vegetation, bedrock, rock debris, glacier ice, brooks

Soil

Skeletic/Lithic Leptosol	No soil
Humi-Skeletic Leptosol	Glacier stages 1857 - 1997
Dystic Cambisol	
Endoskeletic Fluvisol	
Gleyic Cambisol	

A)

B)

area proportion of vegetation types

Primary plant successions of the glacier foreland Morteratsch: different starting points

Table 1. Ecological properties of pioneer plants occurring in the glacier foreland Morteratsch

Plant species	Ecological indicator values (Landolt 1977)					Life form	preferred sites (dominant grain size of substrate)				
	F	R	N	L	D		1 clay / silt- fine sand	2 coarse sand-gravel	3 coarse gra- vel-boulders	rock sites	small ponds/ mires
Rhacomitrium canescens	—	—	—	—	—	c	x				
Pohlia spec.	—	—	—	—	—	c	x				
Saxifraga aizoides	4w	5	2	4	x	c	x				x
Epilobium fleischeri	3w	4	3	5	2	c	x	x			
Linaria alpina	4	4	2	5	2	c	x	x			
Oxyria digyna	3	3	2	5	2	h	x	x			
Hieracium staticifolium	2w	3	2	4	2	h	x	x			
Cardamine resedifolia	3	2	2	4	2	h	x	x			
Saxifraga bryoides	3	2	1	5	2	c	x	x			
Cerastium uniflorum	3	2	2	5	2	c	x	x			
Cerastium pedunculatum	3	2	2	5	2	c	x	x			
Leucanthemopsis alpina	3	2	2	5	4	h	x	x			
Poa alpina	3	3	4	4	4	h	x	x			
Poa nemoralis	2	3	3	3	3	h	x	x			
Festuca rubra s.l.	3	3	3	4	4	h	x	x			
Phleum rhaeticum	3	3	4	4	4	h	x	x			
Avenella flexuosa	2	2	2	2	4	h	x	x			
Deschampsia caespitosa	4w	3	4	3	5	h	x	x			
Myricaria germanica	3w	4	2	4	3	en	x	x			
Larix decidua	3	3	2	4	4	p	x	x			
Salix nigricans	4w	3	3	4	4	p	x	x			
Salix daphnoides	4w	4	2	4	3	p	x	x			
Salix appendiculata	4w	3	3	3	5	p	x	x			
Salix purpurea	3w	3	3	4	3	p	x	x			
Salix hastata	4	3	3	3	3	n	x	x			
Rumex scutatus	2	3	2	4	2	h		x			
Geum reptans	3	2	2	5	2	h		x			
Achillea moschata	3	2	2	5	2	h		x			
Lotus alpinus	3	3	3	5	3	h		x			
Trifolium badium	3	4	3	4	4	h		x			
Trifolium pallescens	3	2	2	4	2	h		x			
Trifolium pratense ssp. nivale	3	3	3	4	4	h		x			
Saxifraga paniculata	2	4	2	5	1	c		x		x	
Alnus viridis	4w	2	4	4	5	n		x			
Pinus cembra	3	2	2	3	4	ep		x			
Betula pubescens	x	x	2	4	5	p		x			
Populus tremula	3	2	3	4	4	p		x	x		
Salix herbacea	4	2	2	5	4	h		x	x		
Salix retusa	3	3	3	5	3	wc		x	x	x	
Salix serpyllifolia	2	4	2	5	3	wc		x	x	x	
Rhododendron ferrugineum	3	2	2	3	4	en		x	x		
Calluna vulgaris	3	1	1	3	4	wc		x	x		
Vaccinium myrtillus	3	1	2	2	4	wc		x	x		
Vaccinium gaultherioides	3	1	2	3	4	wc		x	x		
Vaccinium vitis-idaea	3	2	2	3	4	wc		x	x		
Empetrum nigrum s.l.	1	2	2	4	4	wc		x	x		
Juniperus communis ssp. nana	2	2	2	4	3	en		x	x		
Adenostyles leucophylla	4	2	2	5	2	h			x		
Dryopteris filix-mas	3	3	3	2	4	h			x		
Dryopteris dilatata	4	2	3	2	4	h			x		
Athyrium filix-femina	3	2	3	2	4	h			x		
Athyrium distentifolium	3	2	3	2	3	h			x		
Gymnocarpium dryopteris	3	2	3	2	3	g			x		
Cystopteris fragilis	3	4	2	3	1	h			x	x	
Polystichum lonchitis	3	4	3	3	2	h			x		
Sempervivum arachnoideum	1	2	1	5	1	c		x		x	
Sempervivum montanum	2	2	1	4	3	c		x		x	
Sempervivum tectorum ssp. alpin	1	3	2	5	3	c		x		x	
Arabis alpina s.l.	3	5	2	4	2	c		x		x	
Silene rupestris	2	2	2	4	3	h				x	
Veronica fruticans	2	3	2	4	3	wc		x		x	
Agrostis rupestris	2	2	2	5	4	h				x	
Pinguicula leptoceras	4w	3	2	4	5	cp					x
Pinguicula alpina	4w	4	2	4	5	cp					x
Eriophorum vaginatum	4w	1	1	4	5	h					x
Eriophorum angustifolium	5w	2	2	5	5	g					x
Trichophorum caespitosum	4w	2	2	4	5	h					x
Carex spec.	—	—	—	—	—	h					x
Hydrurus spec.(green algae)	—	—	—	—	—	a					x
Stereocaulon cf. dactylophyllum	—	—	—	—	—	l	x	x			

Ecological indicator values: F=humidity value, R=reaction value, N=nutrient value, L=light value, D=dispersion value

Life form: p=deciduous phanerophyte, ep= evergreen phanerophyte, n=deciduous nanophanerophyte, en=evergreen nanophanerophyte

c=herbaceous chamaephyte, wc=woody chamaephyte, h=hemicryptophyte, g=geophyte, cp=carnivorous plant, a=algae, l=lichen

Grain sizes: 1= 0.002 - 0.2 mm, 2= >0.2-20.0 mm, 3= >20.0->63.0 mm

Typical pioneer plants are in **bold**

Table 2. Selected chemical and physical properties of 11 typical soil profiles in the pro-glacial area

[illegible]

7/Skeletal Leptosol	60	CA	0-12	1.5	55	85	13	2	5.1	6
	30	AC	0-6	1.5	53	92	6	2	5.2	1.9
		C	6-25	1.4	70	83	14	3	5.4	0.7
8/Skeletal Leptosol	30	(A)C	0-15	1.6	66	82	17	1	5.7	2
9/Skeletal Leptosol	20	(A)C	0-18	1.8	77	n.m.	n.m.	n.m.	5.7	2
10/Lithic Leptosol	10	C	0-9	1.7	75	75	22	3	5.8	0.9

¹⁾ soil skeleton = diameter of the material > 2mm.

²⁾ size fractions: sand (2000 – 63µm), silt (<63 – 2µm), clay (<2µm)

n.m. = not measured

Table 3. Soil moisture of four monitored sites (two different soil types) in the pro-glacial area Morteratsch

Soil type (FAO, 1998)	Soil age (y)	Mean moisture (hPa; $\pm$ SD)	Moisture (max hPa)
Humi-Skeletal Leptosol	108	243 ($\pm$ 113)	440
	98	176 ($\pm$ 35)	210
Skeletal/Lithic Leptosol	48	249 ($\pm$ 132)	425
	58	158 ($\pm$ 21)	180

Table 4. Comparison of vegetation with soil data of the glacier foreland Morteratsch

Vegetation data (see vegetation map)	Soil data (see soil map)
<p>Mainly moss pioneers <i>Racomitrium canescens</i>, <i>Pohlia</i> spec., <i>Saxifraga aizoides</i></p> <p>Oxyrietum digynae AC <i>Oxyria digyna</i>, <i>Linaria alpina</i>, <i>Saxifraga bryoides</i>, <i>Cerastium uniflorum</i>, <i>Cardamine resedifolia</i>, <i>Poa alpina</i>, <i>P. nemoralis</i></p> <p>Epilobietum fleischeri AC <i>Epilobium fleischeri</i>, AC <i>Hieracium staticifolium</i>, AS <i>Geum reptans</i>, <i>Rumex scutatus</i>, <i>Trifolium pallescens</i>, <i>T. pratense</i> ssp. <i>nivale</i>, <i>Achillea moschata</i>, <i>Saxifraga bryoides</i>, <i>Cerastium uniflorum</i>, <i>Cardamine resedifolia</i>, <i>Poa alpina</i>, <i>P. nemoralis</i>, <i>Lotus alpinus</i>, <i>Larix decidua</i>, <i>Myricaria germanica</i>, <i>Alnus viridis</i>, <i>Salix</i> spec., <i>Rhododendron ferrugineum</i>, <i>Stereocaulon</i></p> <p>Boulder vegetation <i>Adenostyles leucophylla</i>, <i>Rumex scutatus</i>, <i>Dryopteris</i> spec., <i>Athyrium</i> spec., <i>Gymnocarpium dryopteris</i>, <i>Polystichum lonchitis</i></p>	<p>Skeletal / Lithic Leptosol or 'no soil' grain size: clay/ silt - fine sand, 0.002 - 0.2 mm</p> <p>grain size: clay / silt - fine sand 0.002 - 0.2 mm, coarse sand-gravel >0.2 - 20.00 mm weakly developed soil with some humus in small pockets</p> <p>coarse gravel-boulders >20.00 - >63.0 mm</p>
<p>Alnetum viridis, Alnus viridis stands, Adenostylin, Salix shrubs, grass AC <i>Alnus viridis</i> and tall perennial herbs, <i>Salix</i> spec., <i>Poa</i> spec., <i>Deschampsia caespitosa</i>, <i>Avenella flexuosa</i>, <i>Nardus stricta</i>, <i>Festuca</i> spec., <i>Phleum rhaeticum</i>, <i>Anthoxanthum alpinum</i>, <i>Calamagrostis villosa</i></p>	<p>Humi-Skeletal Leptosol weakly developed soil with continuous humus layer</p>
<p>Larici-Pinetum cembrae (climax vegetation) AC <i>Pinus cembra</i>, AC <i>Larix decidua</i>, AII C <i>Rhododendron ferrugineum</i>, <i>Luzula sylvatica</i>, OC <i>Calamagrostis villosa</i>, AS <i>Vaccinium</i> spec., <i>Clematis alpina</i>, <i>Homogyne alpina</i>, <i>Oxalis acetosella</i>, <i>Avenella flexuosa</i></p>	<p>Dystic Cambisol relatively stable surface and better developed soil</p>
<p>Alnetum viridis, Salix shrubs, Epilobietum fleischeri, flood vegetation AC <i>Alnus viridis</i>, <i>Salix</i> spec., <i>Adenostyles leucophylla</i>, AC <i>Epilobium fleischeri</i>, AC <i>Hieracium staticifolium</i></p>	<p>Endoskeletal Fluvisol alluvial soil, continuous erosion and flood deposition</p>

Key of symbols: AC=Association character species, AllC=Alliance character species, OC=Order character species, AS=Accessory species

Table 5. Absolute and relative distribution of vegetation units within the pro-glacial area with respect to the soil types

Vegetation	Vegetation distribution on soil types: Absolute area						Vegetation distribution on soil types: Relative area						
	Skeletal/ Lithic Leptosol	Humi- Skeletal Leptosol	Endo- skeletal Fluvisol	Dystic Cambisol	Gleyic Cambisol	No soil	Skeletal/ Lithic Leptosol	Humi- Skeletal Leptosol	Endo- skeletal Fluvisol	Dystic Cambisol	Gleyic Cambisol	No soil	Sum
	(m ²)	(m ²)	(m ²)	(m ²)	(m ²)	(m ²)	%	%	%	%	%	%	%
Larch-Swiss stone pine forest (Larici-Pinetum cembrae), partially Swiss stone pine forest	4247	3897	395	596	0	10005	22	20	2	3	0	52	100
Dwarf shrub heath (Rhododendro-Vaccinietum, Empetro-Vaccinietum, Junipero-Arctostaphyletum)	269	0	0	0	0	0	100	0	0	0	0	0	100
Green alder scrub (Alnetum viridis)	70120	109073	1788	2175	0	25531	34	52	1	1	0	12	100
Grass heath on moist soils (grass species e.g. <i>Festuca violacea</i> , <i>Calamagrostis villosa</i> , <i>Phleum rhaeticum</i> , <i>Poa alpina</i>)	6408	14950	773	1791	0	4660	22	52	3	6	0	16	100
Pioneer grass communities	58858	48402	217	1322	256	26048	44	36	0	1	0	19	100
Epilobietum fleischeri with single willow shrubs and alpenrose	212542	88809	8873	993	191	350398	32	13	1	0	0	53	100
Oxyrietum digynae with <i>Myricaria germanica</i> , <i>Saxifraga aizoides</i> , <i>Linaria</i>	9310					7839	54	0	0	0	0	46	100

alpina and moss
cushions
(*Rhacomitrium* spec.,
Pohlia spec.)

Boulder plant communities, partially <i>Epilobietum fleischeri</i> , <i>Adenostyles</i> <i>leucophylla</i> and several fern species	18148	24619	0	100	0	38797	22	30	0	0	0	48	100
Rock vegetation (e.g. <i>Agrostis rupestris</i> , <i>Silene rupestris</i> , <i>Sempervivum</i> <i>arachnoideum</i>)	4435	2003	0	0	0	70409	6	3	0	0	0	92	100

Table 6. Relative distribution of the vegetation types in respect to the grain sizes (soil)

Vegetation types / Grain sizes	Skeleton free (< 5 v.-%)	Skeleton present* (5-10 v.-%)	Weakly gravely * (10-20 v.-%)	Stony* (10-20 v.-%)	Strongly gravely (20-30 v.-%)	Strongly stony (20-30 v.-%)	rich in gravels (30-50 v.-%)	rich in stones (30-50 v.-%)	Debris, boulders (> 50 v.-%)	Sum
Oxyrietum digynae with <i>Myricaria germanica</i> , <i>Saxifraga aizoides</i> , <i>Linaria alpina</i> and moss cushions (<i>Rhacomitrium spec.</i> , <i>Pohlia spec.</i>)	0.0%	0.0%	0.0%	0.0%	100.0%	0.0%	0.0%	0.0%	0.0%	100%
Epilobietum fleischeri with single willow shrubs and alpenrose	2.4%	0.6%	0.7%	3.9%	24.6%	8.6%	13.1%	42.2%	4.0%	100%
Pioneer grass communities. Outside of the pro-glacial area grass heath (Geo montani-Nardetum and Poion alpinae, above ca. 2400 m Caricetum curvulae)	6.5%	1.2%	4.8%	7.8%	38.6%	9.9%	10.7%	17.0%	3.6%	100%
Grass heath on moist soils (Dystic Cambisols, grass species e.g. <i>Festuca violacea</i> , <i>Calamagrostis villosa</i> , <i>Phleum rhaeticum</i> , <i>Poa alpina</i>)	3.2%	2.8%	4.8%	42.0%	18.9%	5.7%	0.2%	22.5%	0.0%	100%
Green alder scrub (Alnetum viridis)	1.5%	0.4%	3.0%	16.6%	31.2%	4.7%	3.1%	38.9%	0.6%	100%
Boulder plant communities, partially Epilobietum fleischeri, <i>Adenostyles leucophylla</i> and several fern species	0.0%	0.0%	0.6%	11.9%	29.8%	26.2%	0.7%	30.7%	0.0%	100%
Rock vegetation (e.g. <i>Agrostis rupestris</i> , <i>Silene rupestris</i> , <i>Sempervivum arachnoideum</i>)	21.2%	0.0%	7.7%	3.1%	13.0%	46.8%	8.0%	0.2%	0.0%	100%
Larch-Swiss stone pine forest (Larici-Pinetum cembrae),	4.3%	6.5%	13.4%	12.1%	17.2%	23.8%	0.0%	22.7%	0.0%	100%

partially Swiss stone pine forest

*soil skeleton: material > 2 mm in diameter; gravely: predominantly material < 5 cm in diameter; stony: predominantly material > 5 cm in diameter