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Did Debris-Covered Glaciers Serve as Pleistocene Refugia for Plants? A New Hypothesis Derived from Observations of Recent Plant Growth on Glacier Surfaces

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Abstract

This study proposes a new hypothesis: Debris-covered glaciers served as Pleistocene biological refugia. This is based on detailed studies of vascular plant growth on six debris-mantled glaciers, literally around the world, as well as many casual observations also across the globe. We find that such glaciers are quite common and are distributed globally. Using Carbon Glacier, Mount Rainier, U.S.A., as a type locality and case study, we show aspects of the floristic and structural diversity as well as spatial patterns of plant growth on the glacier surface. Migration strategies, root characteristics, and origin and dispersal strategies for vascular plant species are documented. Also reported are special microclimatic conditions in these areas allowing for this remarkable plant ecology. We find that alpine taxa can grow considerably below their usual altitudinal niche due to the cooler subsurface soil temperatures found on glacial debris with ice underneath, and that may have significantly altered the spatial distribution of such flora during full glacial conditions. This in turn creates previously undocumented areas from which alpine, and perhaps arctic, plant species reestablished in post-glacial time. This hypothesis is complementary to both the nunatak hypothesis and tabula rasa theory and possibly helps solve the ongoing controversy between them.

Introduction

Glaciological research is primarily focused on bare "white" glaciers without any or only slight debris cover on the surface. Conditions on "black" debris-covered glaciers, in contrast, are significantly less well known, as assessments of mass balance or reactions to climate are difficult due to the debris mantle. Sometimes it is even hard to say where a debris-covered glacier ends and ice-free morainal material begins. Nevertheless, it has been emphasized that "debris-covered glaciers comprise a significant fraction of the global population of glaciers and are particularly common in the Himalayas, Andes, Alaska and on stratovolcanoes worldwide" (International Commission on Snow and Ice, 2000). Debris on such glaciers commonly derives from surrounding wall rockfalls, existing medial moraines, and eroded lateral moraines. Debris from all sources can reduce glacial ablation if the mantle is thick enough. Other sources of debris on glaciers include solifluction, alluvial, and eolian sediment-transport processes, as well as basal thrusting. Therefore, debris-covered glaciers are generally characterized by a far less negative—in some cases even positive—mass balance than white glaciers under present-day climate. Debris-covered glaciers are not to be confused with rock glaciers, where ice and coarse rock material are cemented in a mélange (Barsch, 1996; Haeberli, 1985). Even if rock glaciers might develop from debris-covered glaciers (cf. Höllermann, 1982; Johnson, 1980; Whalley and Martin, 1992), they are genetically different phenomena. While plant growth on rock glaciers is not uncommon (e.g., Burga et al., 2004, for the European Alps; Giardino et al., 1984, for the Rocky Mountains; and Kokarev et al., 1997, for the Tian Shan), publications about the occurrence of plant growth on debris-covered glaciers are rare. Those known by the authors include the Casa Pangue Glacier on Monte Tronador in south-central Chile (Region X; Veblen et al., 1989), several examples from Langtang Himalaya in central Nepal (Miehe, 1990), as well as from Alaska (Stephens, 1969; Rampton, 1970; Post and Streveler, 1976; Birks, 1980; Benn and Evans, 1998) (Figs. 1 and 2). Mature forests with trees more than 50 cm in diameter grow on the debris-covered termini of more than a dozen glaciers in south-central Alaska, including the Bering, Malaspina, Fairweather, Grand Plateau, and Martin-River Glaciers. Younger vegetation was noted on more than three dozen debris-covered glaciers including LaPerouse, Bremner, Fan, Sherman, Casement, Tana, Yakataga, White River, and Carroll Glaciers (Molnia, 2006).

On many debris-covered glaciers around the world, vegetation of varying densities has been observed by the authors along with a debris cover supporting the growth of plants, and in many cases also of trees (Fig. 3). These mobile habitats for plants, which presumably migrate downhill with glacier movement, are much more common than previously thought, and plant growth can occur on very shallow debris cover (Birks, 1980). In the case of dense forests, such as on Malaspina, Fairweather, or Ruth Glaciers, cumulative ground-cover values (i.e. understory and canopy layers combined) of >100% are not unusual.

Study Sites and Methods

Plant growth on debris-covered glaciers is not limited to a particular region. Reports and our observations come from glaciers in semi-arid (Karakoram, Himalayan Zanskar Range, western Kunlun), semi-humid (Peruvian Cordillera Blanca), and humid (Cascade Range, Alaska, New Zealand Alps) environments. Detailed investigations for this study include the Hailuogou and Gonga Gomba Glaciers at the Gonga Shan in southwest China, the Ventisquero Blanco at Monte Tronador in south-central Chile, the

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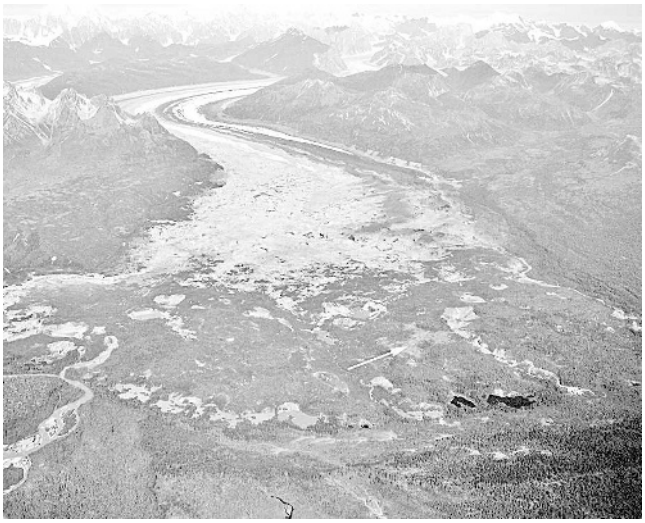


FIGURE 1. Densely forested terminus of Ruth Glacier south of Mount Denali (Alaska, U.S.A.). Note the light colored H-shaped area burned by a wildfire in summer of 1997 (white arrow). Photo: G. Adema, U.S. National Park Service, 6 August 2004.

Carbon Glacier at Mount Rainier (Washington, U.S.A.), as well as two examples from the European Alps: the Miage Glacier on the south side of Mont Blanc (Aosta Valley, Italy) and the Lang Glacier in Swiss Lötschental (Fig. 3; Richter et al., 2004).

Vegetation sampling was carried out on 100-m^2 quadrates along transversal transects across the debris-covered glaciers. The number of sampling sites as well as the distance between them varies depending on size, altitudinal range, and topography of the glacier surface. At all sites, ground cover (in percent) of all occurring plant species and Raunkiaer's life form-affiliation were recorded. In addition, site characteristics like aspect, slope angle, proportion of coarse rock, and—when possible—depth of debris cover were recorded.

At Carbon Glacier, Mount Rainier (Fig. 4), which is presented here in detail, 12 transects with a total of 68 plots between 1110 and 1530 m a.s.l. were sampled in vertical steps of 30 m, with a sampling gap between 1400 and 1500 m a.s.l. where an inaccessible serac zone deeply incised by crevasses prevented sampling (Fig. 4). Plant taxonomy follows Biek (2000). In addition to the botanical studies, surface- and soil-temperature measurements were carried out associated with analyses of basic physical and chemical soil parameters such as pH, nitrogen content, and organic matter.



FIGURE 2. Dense spruce forests (*Picea sitchensis*) on Fairweather Glacier (Alaska, U.S.A.). Individuals are up to 150 years old. Photo: B. F. Molnia, U.S. Geological Survey (http://pubs.usgs.gov/of/2004/1216/s/s.html).

Case Study: Carbon Glacier, Mount Rainier

Carbon Glacier (8 km^2) is the third-largest glacier on Mount Rainier in area, but has the greatest ice volume (0.8 km^3) and length (9.1 km; Fig. 4). The glacier reaches 900 m below the upper treeline to 1100 m. a.s.l., making its terminus the lowest in the contiguous United States (Driedger, 1986).

Compared to the other major glaciers on Mount Rainier, Carbon Glacier experienced the least recession after the neoglacial maximum between 1770 and 1860 (Burbank, 1981). This might be due to the exceptionally high precipitation on its northwest slopes (Franklin and Dyrness, 1988), the reduced radiation input due to its northern aspect, as well as the deeply carved Carbon River Valley creating increased shading and cold air drainage. However, these environmental factors alone do not explain why most of the glaciers around Mount Rainier retreated up to 3 km, while the Carbon glacier retreated only some hundred meters. For Mount Rainier, Burbank (1982) suggested that a climatically driven substantial thinning of the ice thickness occurred between 1850 and 1890, though without an obvious retreat of the glacier termini. Only after 1910, a rapid recession of the termini for most glaciers is verified with the exception of Carbon Glacier. In 1916 a major rockfall occurred where parts of Willis Wall at the head of Carbon Glacier (Fig. 4) collapsed and covered large parts of the glacier surface. Consequently, this debris insulates the ice and inhibits melting (Driedger, 1986). Emmons Glacier on the northeast side of

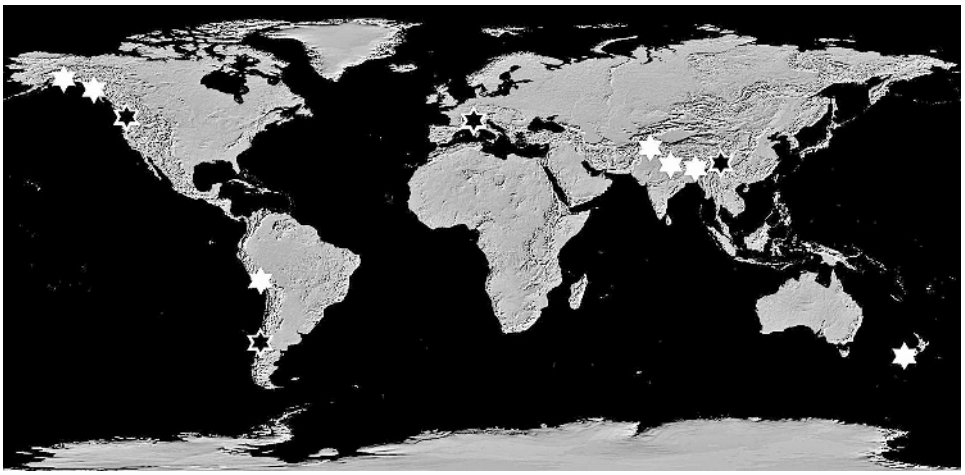


FIGURE 3. World map with location of detailed study areas (black stars) as well as anecdotally observed and reported sites of plant growth on debris-covered glaciers (white stars) (source: http://www.ngdc.noaa.gov/mgg/topo/img/toglshade2.gif).

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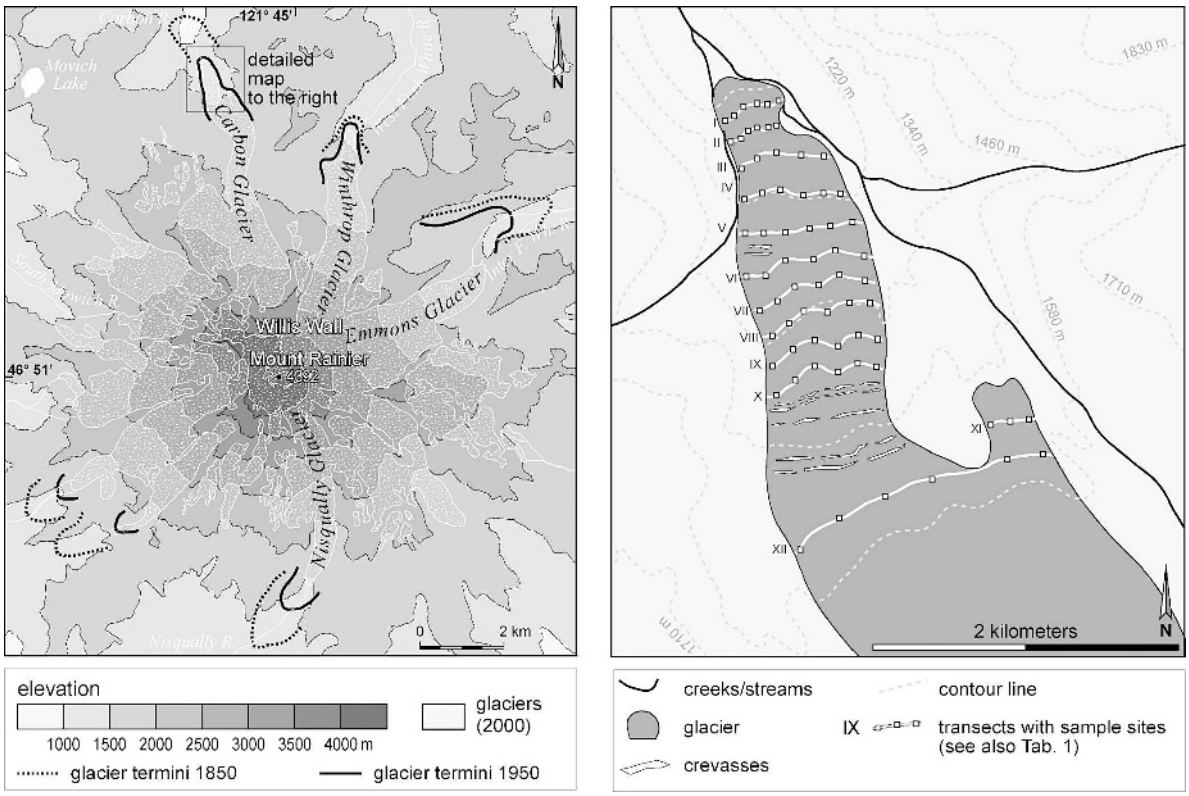


FIGURE 4. Map of Mount Rainier, Washington State, U.S.A. (left) and map of the lower part of the Carbon Glacier with location of the study transects (right). Note that Carbon Glacier extends several hundred meters lower in elevation than all others on Mount Rainier. It has the lowest elevation terminus of any glacier in the continental United States. The debris-covered portion of Carbon Glacier is extensively vegetated, whereas Nisqually and Winthrop glaciers have only a limited vegetative cover. All other glaciers lack significant vegetation cover. Year 2000 glacial terminus according to Earthwalk (2000).

Mount Rainier was even advancing for more than two decades after a comparable rockfall from nearby Tahoma Peak in 1963 (Driedger, 1986).

Our botanical studies on several glaciers around Mount Rainier showed that most lack plant growth either because the glacier tongue is too high in elevation for plants or because of an insufficient and/or too mobile debris cover. Vegetation was found on just three glaciers (Fig. 4): in addition to Carbon Glacier, the Nisqually Glacier on the south side supports a very sparse and species-poor vegetation, while on Winthrop Glacier a total of at least 15 different taxa was recorded.

With 41 species of higher plants plus several different mosses and lichens within the 68 study sites, Carbon Glacier harbors a rather diverse flora (Table 1). The favorable thermal growing conditions (i.e. mild air temperatures) due to the low-lying terminus at 1100 m a.s.l. and the surrounding montane coniferous forests seem to be responsible for this rich floristic inventory. In addition, the potential pool of species able to establish on the debris cover is increased by the number of vegetation belts a glacier passes through. Thus, on Carbon Glacier characteristic montane species like *Picea engelmannii*, *Tsuga heterophylla*, *Salix scouleriana*, *Antennaria rosea* ssp. *rosea*, *Calamagrostis purpurascens* var. *purpurascens*, or *Hieracium albiflorum*; and subalpine/alpine taxa (presumably favored by low soil temperatures) such as *Mimulus lewisii*, *Juncus filiformis*, *Luetkea pectinata*, and *Phyllodoce empetriformis* occur side by side.

Due to the location of Mount Rainier in close proximity to one of the global centers of conifer diversity (along the Pacific Coast of northern California and southern Oregon; Farjon, 1990), the high concentration of needle-leafed trees in the lower part of Carbon Glacier is not surprising. Pioneer species like *Tsuga heterophylla*, *T. mertensiana*, *Pseudotsuga menziesii* var. *menziesii*, *Abies amabilis*, *A. grandis* var. *grandis*, *Picea engelmannii*, and *Pinus contorta* var. *murrayana* are widespread and contribute much to ground cover and species diversity, but rarely exceed 1 m in height (Table 1). Besides those, the nitrogen-fixing *Alnus viridis* ssp. *sinuata* shows high ground-cover values (up to 10%) and at more than 3 m tall it is at the maximum height of all occurring taxa. The herbaceous *Anaphalis margaritacea* is significant as well.

Ground cover and species number decrease with increasing altitude (Figs. 5, 6a, and 6b), a well-known fact in high mountains in general and a trend appearing on other debris-covered glaciers as well (Richter et al., 2004). Below 1200 m a.s.l. a total ground cover of 10 to 20% is not uncommon. At higher elevations, ground-cover species number and structural diversity gradually decrease, particularly between 1260 and 1380 m a.s.l., approaching the steep serac zone, where plant growth probably is absent. Above the serac zone, the values slightly increase again before the uppermost plant limit is reached at 1530 m a.s.l. (see Fig. 5)

Most plants on Carbon Glacier appear to be part of an "autochthonous" vegetation type with *in situ* germination on the debris cover; i.e. seeds of plant individuals from the vicinity reached the glacial surface either by wind or by animals, established themselves successfully and might even be able to proliferate. However, this is not the only way for plants to vegetate glaciers. In many cases the plants found on glaciers derive from eroded, vegetation-covered lateral moraines and/or from landslides of the bordering mountain slopes (Veblen et al., 1989). In this case the plants are part of a clumped, "allochthonous" vegetation (Richter et al., 2004).

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TABLE 1

Species list of Carbon Glacier with family and life-form affiliation, ground cover in percent averaged by transect (x indicates values <0.1% ground cover). For life form abbreviations see Figure 5.

Taxa	Family	Life form	1110 ma.s.l.	1140 ma.s.l.	1170 ma.s.l.	1200 ma.s.l.	1230 ma.s.l.	1260 ma.s.l.	1290 ma.s.l.	1320 ma.s.l.	1350 ma.s.l.	1380 ma.s.l.	1500 ma.s.l.	1530 ma.s.l.
Asplenium trichomanes ssp. *Trichomanes*	Aspleniaceae	H	—	0.1	—	—	—	—	—	—	—	—	—	—
Agoseris aurantiaca var. *aurantiaca*	Asteraceae	H	—	—	—	—	—	—	—	—	—	—	—	x
Anaphalis margaritacea	Asteraceae	H	0.7	0.5	0.3	0.2	0.5	0.3	0.1	0.1	0.2	0.1	0.3	0.1
Antennaria rosea ssp. *rosea*	Asteraceae	H	0.1	x	—	x	—	—	—	—	—	—	—	—
Hieracium albiflorum	Asteraceae	H	x	0.1	x	x	—	x	—	x	—	—	—	—
Hieracium gracile var. *gracile*	Asteraceae	H	—	—	—	—	x	—	—	—	—	—	—	—
Alnus viridis ssp. *sinuata*	Betulaceae	MiP	3.0	1.8	0.7	—	x	—	x	—	—	—	—	x
Sedum divergens	Crassulaceae	H	—	—	—	—	—	x	—	—	—	—	—	—
Sedum oreganum ssp. *Oreganum*	Crassulaceae	Ch	—	—	—	—	—	—	—	x	—	—	—	—
Carex mertensii	Cyperaceae	H	x	—	—	—	—	x	—	—	—	—	—	—
Carex nigricans	Cyperaceae	H	—	—	—	x	—	—	—	—	—	—	—	—
Carex spec.	Cyperaceae	H	—	—	—	—	—	—	—	x	x	—	—	—
Polystichum muntium	Dryopteridaceae	H	—	—	x	—	x	—	—	—	x	—	—	—
Phyllodoce empetriformis	Ericaceae	Ch	—	—	—	—	—	—	—	—	—	—	1.5	0.1
Vaccinium parviflorum	Ericaceae	NP	—	x	—	—	—	—	—	—	—	—	—	—
Phacelia leptosepala	Hydropyllacea	H	—	—	—	0.2	—	—	x	—	—	—	0.1	x
Juncus drummondii ssp. *Subtriflorus*	Juncaceae	H	x	x	x	0.1	0.0	0.1	x	x	—	—	—	x
Juncus filiformis	Juncaceae	H	—	—	—	—	—	x	—	x	x	x	0.1	x
Juncus mertensianus	Juncaceae	H	x	0.1	x	x	0.1	0.1	0.1	0.1	x	x	—	x
Epilobium angustifolium ssp. *angustifolium*	Onagraceae	H	x	x	0.1	0.1	0.3	0.1	0.1	0.1	0.1	0.1	—	—
Epilobium hornemannii ssp. *Hornemannii*	Onagraceae	H	x	0.1	—	x	0.1	0.1	0.1	0.1	x	—	—	—
Abies amabilis	Pinaceae	MaP	0.2	0.2	0.2	x	—	—	—	—	—	—	—	x
Abies grandis var. *grandis*	Pinaceae	MaP	—	0.1	—	—	x	—	—	x	—	—	—	—
Picea engelmannii	Pinaceae	MaP	—	0.1	x	0.1	—	—	—	—	—	—	—	—
Pinus contorta var. *murrayana*	Pinaceae	MaP	x	—	—	—	—	—	—	—	—	—	—	—
Pseudotsuga menziesii var. *menziesii*	Pinaceae	MaP	1.3	1.0	0.9	0.1	—	—	x	—	—	—	0.1	—
Tsuga heterophylla	Pinaceae	MaP	0.5	1.9	0.8	0.4	0.1	x	x	x	—	—	—	—
Tsuga mertensiana	Pinaceae	MaP	—	0.3	—	—	—	—	—	—	x	x	—	—
Agrostis geminata	Poaceae	H	—	—	—	—	—	—	—	—	—	—	—	x
Calamagrostis purpurascens var. *purpurascens*	Poaceae	H	x	x	—	—	x	x	—	—	—	—	—	—
Poa secunda	Poaceae	H	—	0.2	—	—	x	x	—	—	x	—	—	—
Oxyria digyna	Polygonaceae	H	—	—	—	x	—	—	—	—	—	—	—	—
Actaea rubra ssp. *arguta*	Ranunculaceae	Ch	—	—	—	x	x	—	—	—	—	—	—	—
Holodiscus discolor	Rosaceae	MiP	—	0.2	—	—	—	—	—	—	—	—	—	—
Luetkea pectinata	Rosaceae	Ch	—	—	x	—	—	0.1	—	—	—	—	—	x
Populus balsamifera ssp. *Trichocarpa*	Salicaceae	MaP	—	—	—	0.1	—	—	—	—	—	—	—	—
Salix cascadensis	Salicaceae	Ch	—	—	—	—	x	—	—	—	—	—	—	—
Salix scouleriana	Salicaceae	NP	0.4	0.7	0.1	0.4	0.2	0.1	x	x	—	—	—	—
Saxifraga ferruginea var. *ferruginea*	Saxifragaceae	H	x	—	—	x	x	—	—	—	—	—	—	—
Mimulus lewisii	Scrophulariaceae	H	—	—	—	—	—	—	—	—	—	—	0.3	0.3
Penstemon davidsonii var. *menziesii*	Scrophulariaceae	Ch	—	—	—	0.1	—	—	—	—	—	—	—	—
	Transect number in Figure 2		**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**

The fairly high species number and ground cover suggest that putative negative factors for plant growth like low soil temperature, limited root horizon, or the high mobility of the surface must be compensated by positive ones such as mineral-rich, humus-free substrate with balanced soil and light conditions in the subnival zone. In general, a mixture of coarse grains (up to boulder size) and much finer material trapped in between prevails. Analyses of grain-size spectra on Carbon Glacier revealed no strong correlation between the proportion of coarse rocks and vegetation cover. Other factors, such as the depth of the rock layer (i.e. the depth of the root horizon above the ice table) or the mobility of the substrate, which strongly depends on the relief and the shape of

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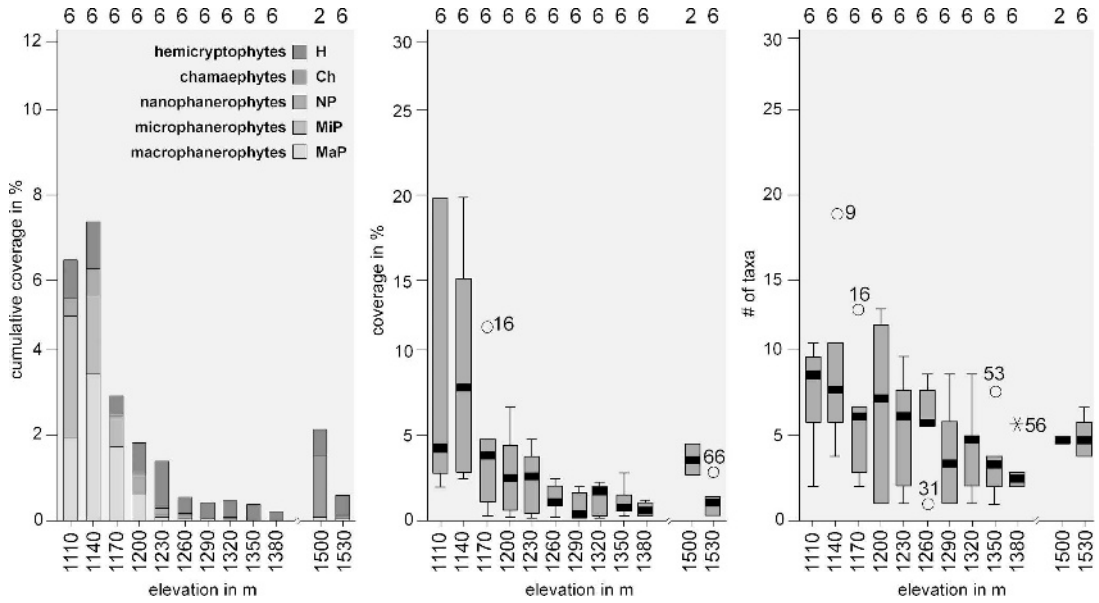


FIGURE 5. Life form spectra (left) averaged for all samples (100 m^2 plots) per transect indicating the contribution of the individual life forms to the mean total ground cover along the respective transect. The box plots show minimum and maximum values, the range of the middle half of the scores (25th to 75th percentile), the median, and outliers if present for ground cover (center) and species number (right) per transect. The number of samples included in calculation is given above each column.

the glacier surface, seem to be more important. Many phanerophytes appear well adapted having developed an extensive root system that manages to survive moderate tension without severe damage.

From a climatological point of view, the development of plant growth on glaciers is not tied to the macroclimate of the region as this phenomenon occurs in arid-continental (e.g., the Karakoram) and humid-maritime regions (e.g., Cascade Range, Southern Andes) as well as in high and low latitudes (Alaska and Cordillera Blanca, respectively). Moreover, densely vegetated glaciers often are in close proximity to glaciers without any plants, as is the case on Mount Rainier, and even on the same glacier vegetated and unvegetated sites occur side by side under comparable climatic circumstances. The length of snow cover, however, has an influence on the species composition and spatial patterns within glacier vegetation, as snow cover shelters the plants from low temperatures and temporarily increases the soil moisture but shortens the length of the growing season.

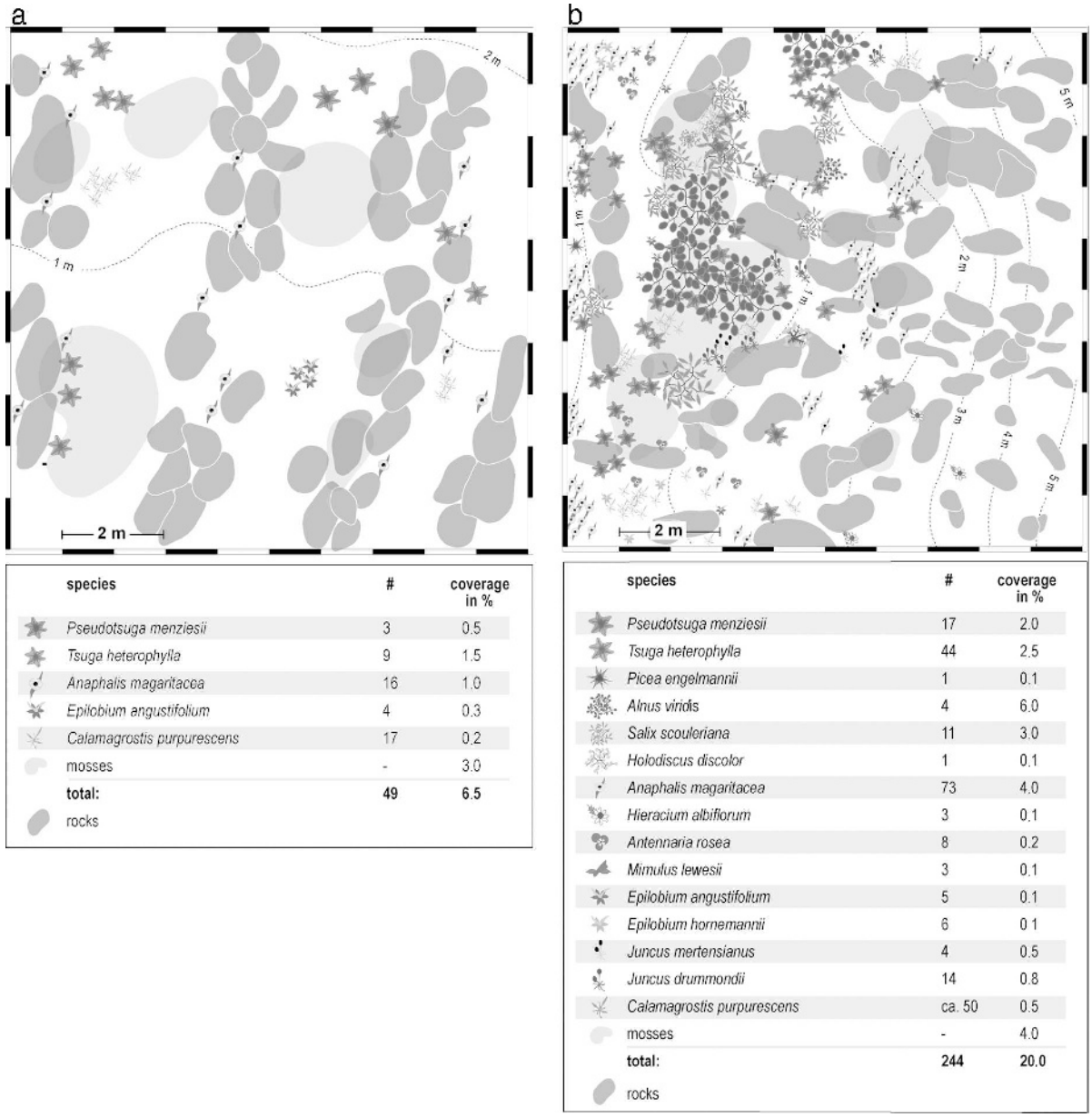
Microclimatic conditions seem to be more important for the establishment and survival of vascular plants. Temperature measurements on different surfaces on top of Carbon Glacier (Fig. 7) show situations similar to sites without underground ice. On sunny summer days, midday maximum temperatures of more than 50 °C on dark, dry surfaces occur regularly, and even at moist sites 30 °C is reached. These values are comparable to those found beside the glacier and therefore cannot be deemed as an obstacle for plant establishment. However, differences in hue and grain size of the substrate cause a highly diverse pattern of soil temperature and humidity conditions that affect plant growth, and in particular, plant diversity in space and time. On Carbon Glacier a mosaic of dry, south-facing and/or rocky sites with xerophytic, or at least desiccation tolerant, vegetation (e.g., *Anaphalis margaritacea*, *Antennaria rosea* ssp. *rosea*, *Hieracium* spp., *Sedum* spp., *Phacelia leptosepala*, and *Penstemon davidsonii* var. *davidsonii*) and fine-grained or north-exposed, more humid sites with hygrophilous plants (e.g., *Mimulus lewisii*, *Juncus mertensianus*, or *Epilobium hornemanii ssp. hornemanii*) frequently occur. Similar patterns are described for rock glaciers, which are also cool and mobile habitats for plants (e.g., Kokarev et al., 1997; or Burga et al., 2004).

An increasing influence of the underground ice becomes apparent at greater soil depths. While the temperature curves at −1 and −5 cm in Figure 8 do not indicate any major cooling by the underlying ice, such an effect is clearly visible at −35 cm, i.e. 5 cm above the ice table. Here, temperatures fluctuate between 3 and 7 °C on a generally rather low level for midsummer conditions. However, the temperature increase in late afternoon indicates a delayed heat flow from the glacier surface. As most of the montane forest trees in the vicinity succeed in establishment and grow to a certain height, plants with shallow root systems do not seem to be heavily disadvantaged by the low soil temperatures, a minimum of debris thickness is presumed. Once the roots come close to the ice table, the plants' physiological processes will be strongly affected or completely disabled (cf. Körner, 1999).

At sites with shallow debris cover, some plants clearly benefit from lowered soil temperatures. On Carbon Glacier several taxa such as the two rushes, *Juncus drummondii* var. *subtriflorus* and *J. mertensianus*, occur several hundred meters below their "usual" distribution within the subalpine and alpine communities (Biek, 2000). Further illustration of this phenomenon is *Ranunculus glacialis*, one of the highest growing vascular plants in the European Alps, thriving normally from 2300 up to more than 4200 m a.s.l. On Miage Glacier in the Italian Aosta Valley, however, this buttercup species was observed as low as 1850 m a.s.l. on the glacier surface, several hundred meters below its usual lower boundary. These and other examples (Richter et al., 2004) support our assertion that species characteristic of higher elevations can reach much lower elevations on glacial moraines, recently deglaciated surfaces, as well as on debris-covered glacier surfaces.

However, even if edaphic and microclimatic conditions may have a local influence on the development of the plant cover, the most important factor seems to be the ability of potential (i.e. available) taxa to resist the mobility of the substrate at the glacier surface. At least with perennial plants, a wide-spreading root

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species	#	coverage in %
Pseudotsuga menziesii	3	0.5
Tsuga heterophylla	9	1.5
Anaphalis margaritacea	16	1.0
Epilobium angustifolium	4	0.3
Calamagrostis purpurescens	17	0.2
mosses	-	3.0
total:	**49**	**6.5**
rocks		

species	#	coverage in %
Pseudotsuga menziesii	17	2.0
Tsuga heterophylla	44	2.5
Picea engelmannii	1	0.1
Alnus viridis	4	6.0
Salix scouleriana	11	3.0
Holodiscus discolor	1	0.1
Anaphalis margaritacea	73	4.0
Hieracium albiflorum	3	0.1
Antennaria rosea	8	0.2
Mimulus lewesii	3	0.1
Epilobium angustifolium	5	0.1
Epilobium hornemannii	6	0.1
Juncus mertensianus	4	0.5
Juncus drummondii	14	0.8
Calamagrostis purpurescens	ca. 50	0.5
mosses	-	4.0
total:	**244**	**20.0**
rocks		

FIGURE 6. The sketch maps show two representative 100 m^2 sampling plots on Carbon Glacier. Species composition, number of plants, and surface cover are indicated. The plot to the left is from transect V at 1230 m a.s.l.; note the low ground cover and species richness. At right is an exemplary plot from transect I at the lower elevation of 1110 m a.s.l. showing much greater plant cover and number of species.

system is clearly advantageous for surviving the permanent rearrangement of the habitat. Many species growing on debris-covered glaciers develop proportionally overlong roots, a phenomenon documented for other mobile habitats (e.g., Fickert and Grüninger, 2002, for sites affected by solifluction). In the case of Carbon glacier, willows (*Salix* spp.), alder (*Alnus viridis* ssp. *sinuata*), and most of the conifers show elongated root systems.

DID DEBRIS-COVERED GLACIERS SERVE AS BIOLOGICAL REFUGIA DURING GLACIAL TIMES?

General rules explaining which kind of plant might or might not grow on debris-covered glaciers do not exist. The taxa able to establish on glaciers most successfully are pioneer species of the surrounding plant communities with an extensive but shallow root system. Furthermore, many species of later successional stages or mature communities occur, although in a reduced frequency. Our observations include curious examples such as a cushion cactus (*Austrocylindropuntia floccosa*) or a terrestrial orchid (*Aa mathewsii*) on Glaciar Kinzl in Perú at 4400 m a.s.l. Thus, if there are not any particular ''glacier specialists,'' and if a rather diverse assemblage of different plant species and life-forms is able to grow on glacier surfaces today, the question arises whether debris-covered glaciers might have served as refugia for plants during the Pleistocene glaciations.

There is a long-lasting controversial discussion where plants might have survived Pleistocene glacial periods (cf. Ives, 1974). For the explanation of present-day distribution patterns of vascular plants, numerous scientists assume the existence of unglaciated refugia within extended ice sheets, the so-called ''nunatak hypothesis,'' where plants have endured glacial periods and from where expansion started after the ice retreated. Potential refugia are unglaciated mountain tops (''nunataks'' *sensu stricto*) or, in the case of the Fennoscandian or Laurentide ice sheets, small

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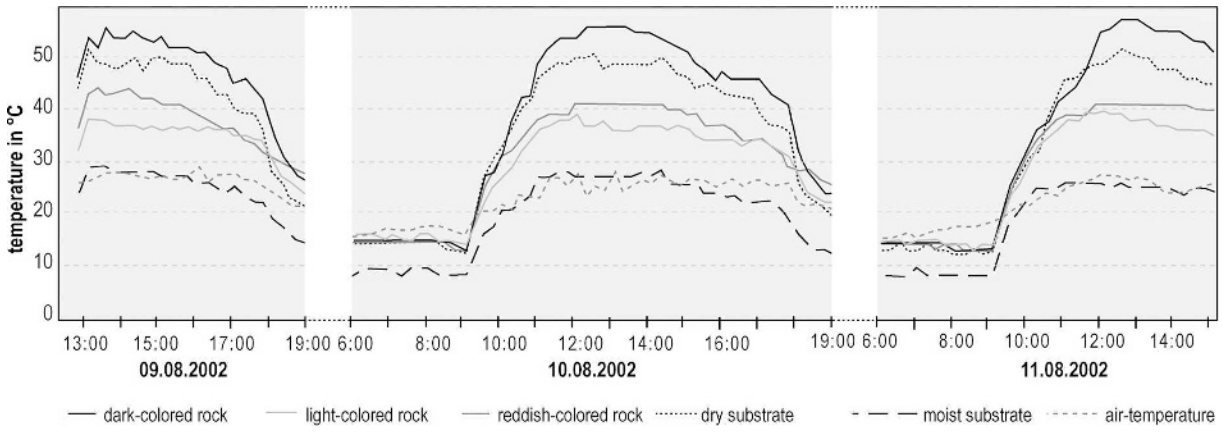


FIGURE 7. Surface temperatures of various rocks and substrates as well as air temperature recorded with cloudless skies on Carbon Glacier between 9 and 11 August 2002 (after Richter et al., 2004). Huge thermic differences depending on the hue of the substrate create a mosaic of different ecological conditions in close proximity. However, the patterns depicted on the glacier surface are similar, if not identical, to adjacent areas not underlain by ice, thus illustrating that the surface of debris-covered glaciers have a microclimatic regime conducive to plant growth.

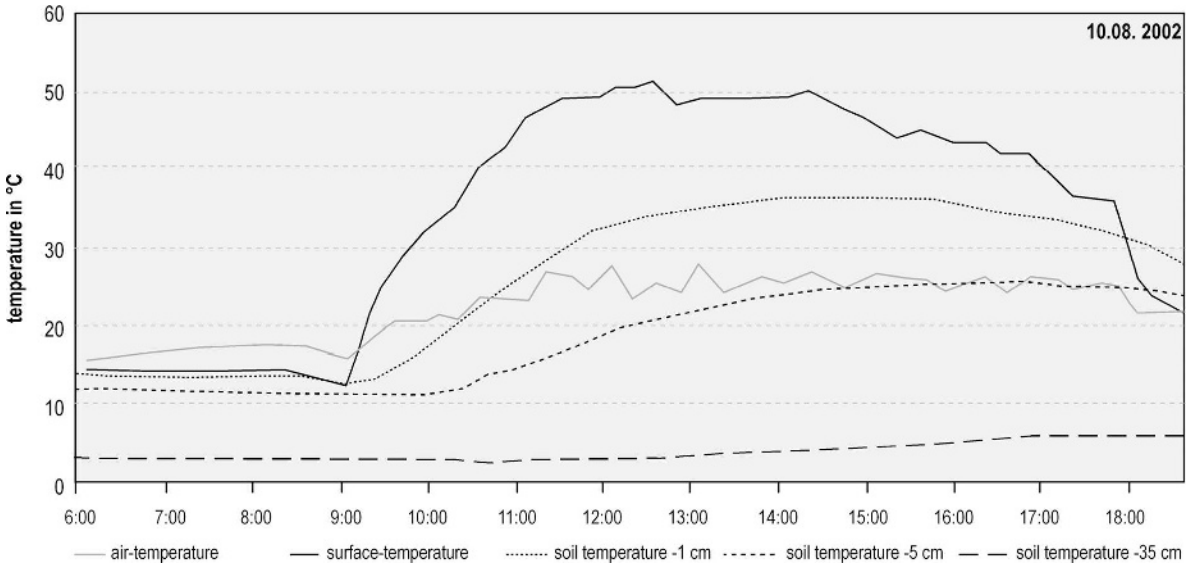


FIGURE 8. Air, surface, and soil temperature at various depths, recorded on 10 August 2002 with cloudless skies on Carbon Glacier (after Richter et al., 2004). Note the successively retarded warming (in the morning) and cooling (in the evening) at greater depths. At −1 and −5 cm the descent of temperature curves lag less than an hour behind air and surface temperatures; the respective lag at −35 cm is around five hours, but still detectable. Thus, even at greater depths, a warming effect from above is apparent.

ice-free areas in the coastal lowlands and islands offshore surrounded by ice (cf. Blytt, 1876; Rønning, 1963; Gjærevoll, 1963, 1990; Löve and Löve, 1974; and Dahl, 1987, for Scandinavia; Rundgren and Ingólfsson, 1999, for Iceland; and Schauffler and Jacobson, 2002; Brubacker et al., 2005, for North America). Opponents of the nunatak hypothesis, however, assume that plants were simply obliterated by the advancing ice during glacial times and revegetated their present-day habitats in post-glacial times only, i.e. the "tabula rasa theory" (cf. Nordal, 1987).

There are numerous papers pro and con for the two opposing hypotheses. Although plants are growing on nunataks in Greenland today (Frederiksen, 1971; Gjærevoll and Ryvarden, 1977), Ives (1974, p. 618) states as one of the major questions arising with the survival of plants on nunataks during the Pleistocene: "…would not the climate be so extremely severe as to preclude all possibility for plant survival?" Furthermore, a multivariate analysis carried out by Birks (1993) relating the distribution patterns of more than 100 mountain plants of Norway with several recent ecological factors (i.e. location, topography, geology, and climate) and with the abundance of unglaciated terrain (as historical variable) found that the "nunatak theory" is superfluous to explain the present-day distribution patterns of those species. Birks (1994) also showed that many of the so-called "nunatak-plants" grew close to the Pleistocene ice margin and from there readily invaded newly deglaciated terrain. Both facts, however, do not rule out the possibility of nunatak refugia.

In recent years the attempt was made to cast some light on the Pleistocene fate of plants by employing modern DNA analyses, which were carried out on a variety of arctic-alpine taxa. These molecular analyses treat low genetic similarity of species (or species groups) harboring distinct cpDNA genotypes as an indicator of low-level gene flow and thus for isolation (i.e. the survival on nunataks), whereas genetically more similar groups indicate high level of gene flow through survival in a continuous peripheral refugium. However, even with these modern methods, "…there is considerable controversy concerning the fate of Alpine plants [and this holds true for Nordic taxa as well] during Pleistocene glaciations. While some studies have found evidence

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for nunatak survival, others have explained the present genetic patterns by survival only in peripheral refugia'' (Schönswetter et al., 2004, p. 183). Examples of recent support for the tabula rasa theory include Gabrielsen et al. (1997), Holderegger et al. (2001), Brochmann et al. (2003), Schönswetter et al. (2002, 2004), and Ægisdóttir and þórhallsdóttir (2004), while the results of studies conducted by Füchter et al. (2001), Stehlik (2002), or Stehlik et al. (2001, 2002) are clearly ''pro nunatak.'' Finally, studies on the widespread high-alpine/subnival *Androsace alpina* by Schönswetter and Tribsch (2001) and on *Saponaria pumila* by Tribsch et al. (2002) in the European Alps showed that these species followed both strategies of survival depending on location, thus giving no clear evidence for either point of view.

Despite this long-lasting discussion, a conclusive answer has not yet arisen. The discovery of more than 8000-year-old macro- and megafossils of plants (in one case even 16,900 ± 170 ^{14}C yr BP) on nunataks and coastal refugia in the western part of the Scandinavian mountains nevertheless supports the assertion that in Northern Europe plants and even trees were not completely repelled to the southeast by the advancing ice during full glacial times, but must have found suitable refugia somewhere (Lindqvist, 1948; Kullman, 2000, 2006).

Discussion

Our observations of the sometimes rather dense and diverse vegetation growing nowadays on the debris-covered surfaces of mountain glaciers around the world make it reasonable to assume that comparable sites served as refugia in Pleistocene times. Such a ''debris-covered glacier hypothesis'' is between the two extremes, the nunatak hypothesis on the one side and tabula rasa on the other. Thus, our hypothesis complements the two existing assumptions without neglecting either one. If debris-covered glaciers are deemed as potential habitats for plants during the Pleistocene, this may help to explain some of the questions left unresolved by the two other opinions. One of those is associated with the issue of available space for plant growth. As Birks et al. (2005, pp. 279–280) noted for Scandinavia, ''it is universally agreed that the ice sheet extended beyond the Norwegian coast to the continental shelf edge at the LGM [last glacial maximum] (c. 22,000 ^{14}C yr. BP), … leaving nowhere for trees or other plants to grow.'' Comparable conditions have to be assumed for the western margin of the Laurentide ice sheet (Brubaker et al., 2005; Zweck and Huybrechts, 2003). Whereas the nunatak hypothesis (even in the broad sense) offers just small and disparate areas for the survival of plants, this spatial proportion would be considerably enlarged by debris-covered ice fields protruding from coastal mountains ranges.

Furthermore, as glaciers descend to a ''milder'' (by Pleistocene standards) climate of the lowlands, habitats on the glacier—a particular depth of debris presupposed—are thermally much more comfortable for plants than high-elevation nunataks. Reconstructions of climatic parameters for the LGM assume mean annual temperatures at sea level of −5 to −10 °C for the maritime western parts of the Eurasian and Laurentide ice sheets (Siegert and Marisat, 2001; Siegert and Dowdeswell, 2004; Hubberten et al., 2004; Bromwich et al., 2004, 2005). These are thermal conditions that exist or are even surpassed today at subpolar stations of Ny Ålesund (Spitsbergen), Thule (Greenland), and Barrow (Alaska) (Table 2); nevertheless, those areas' present-day climatic conditions allow a rather diverse assemblage of hardy plants to grow. Calculations of temperature conditions for several vegetated debris-covered glaciers are well above the subpolar localities (Table 2). However, it has to be kept in mind that all those selected glaciers harbor tree growth, i.e. they represent rather ''mild'' examples for plant growth on glaciers. In addition, the values are calculated for the glacier terminus, and plant growth in some cases reaches several hundred meters higher on the glacier surface, where temperatures approach subpolar means. This fact gives further support that from a climatological point of view plant growth on glacier surfaces was possible during the Pleistocene.

Of course, glaciers as Pleistocene refugia for plants are not equally necessary everywhere for the explanation of present-day vegetation. In the Americas, the continuous north-south-trending mountain chains have served as migrational pathways (e.g., Axelrod and Raven, 1985; Abbott et al., 2000, for North America; or Simpson, 1983; Simpson-Vuilleumier, 1971; Villagrán et al., 1998, for South America), giving (ant)arctic-alpine plants the chance to find suitable habitats by retreating to lower latitudes. In contrast, this was not possible in the same way in Europe, neither in the Alps—as they run west-east—nor in the Scandinavian mountains due to the continuous ice sheet and the surrounding sea. For these two regions, Figure 9 shows the juxtaposition of different potential refugia, i.e. high-elevation nunataks, glacial foreland, and debris-covered glaciers, varying in significance from place to place and mutually supplementing each other. Survival on debris-covered valley glaciers might have been particularly important along the west coast of Scandinavia, where only a few ice-free areas remained between the advancing ice and sea, serving as potential refugia, while in the eastern part of the Scandinavian mountains and also in the European Alps, plants were able to retreat to periglacial forelands. In those cases remigration of plants does not necessarily require a ''debris-covered glacier-theory'' for the recolonization of high-elevation habitats, although debris-covered glaciers might have accelerated the revegetation.

Three questions admittedly remain: (1) Where does the debris come from in areas with continuous ice sheets and only small rocky nunatak areas protruding from the ice, as was the case in many high mountains during the Pleistocene? At the beginning of a cold cycle, the amount of detritus provided by strong mechanical weathering is plenty, as there are still large unglaciated areas surrounding the slowly growing ice streams. A different picture appears during full glacial times, as few rockwall faces remain. The present south Alaskan coast may give a hint of how the coastal areas of higher latitudes, as well as the forelands of larger high mountain systems looked in the late Pleistocene. Similarly, large areas including most of the shelf were covered by piedmont glaciers during LGM. As on the Malaspina Glacier (Fig. 10), in many cases the source of debris has not been the interior part of the mountain system but rock falls originating from the outer, less glaciated mountain margins. Along the coastal escarpment of mountain ranges such as the Patagonian Andes, the Alaskan and Canadian coast ranges, and the Scandinavian mountains, the steep walls of deeply incised fjords created during earlier ice ages might have significantly contributed to the debris cover on glacier surfaces. In addition, basal thrusting frequently brings basal till and other basal sediment to the surface on many temperate glaciers. This basal thrusting is the primary source of sediment in the lower reaches of many present-day glaciers (e.g., Herbert and Mendenhall Glaciers). Finally, recent seismic activity (1964 and 2002) in Alaska caused over 100 rockfalls onto glaciers in the region (Post, 1967; Molnia, 2006), demonstrating that earthquakes readily create debris cover on glaciers, too.

(2) Did plants finally calve off the glacier into streams, oceans, or simply down the glacier front after migrating down-glacier and disappear? Many individuals surely did. Some of the

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TABLE 2

Climatic parameters, measured at subpolar climate stations, calculated for the termini of vegetated debris-covered glaciers and estimated values for the western margins of Fennoscandian and Laurentide ice sheets at last glacial maximum.

Time	Locality/region	Climate station	Elevation (m)	Ø T coldest month (°C)	Ø T warmest month (°C)	Ø annual T (°C)	Ø annual precip. (mm)	Sources*
Recent	Spitsbergen	Ny Ålesund	8	−14.6	4.9	−6.3	163	1
Recent	Greenland	Thule	77	−23.3	4.6	−11.2	124	2
Recent	Alaska	Barrow	9	−25.9	4.3	−12.2	114	3
Recent dcg	Lang Glacier (Alps)	Ried	2050	−6.6	9.1	0.9	>1000	4
Recent dcg	Miage Glacier (Alps)	Grd. St. Bernard	1850	−5.4	11.4	1.8	>1000	5
Recent dcg	Batura Glacier (Karakoram)	Misgar	2500	−3.7	22.4	10.0	<150	6
Recent dcg	Carbon Glacier (Cascades)	Carbon River Ent. St.	1100	−3.2	11.0	7.5	>1500	7
Recent dcg	Klultan Glacier (St. Elias Mts.)	Snag	1200	−29.2	12.8	−8.3	~400	8
Recent dcg	Ventisqu. Blanco (South Andes)	Puerto Montt	1000	?	?	4.6	>2000	9
Lgm	Scandinavia	—	sea level	?	?	−5 to −10	600–700	10
Lgm	North America	—	sea level	−10 to −15	3 to 5	−5 to −10	?	11

*Sources:

(1) http://www.scannet.nu/index.php?option=com_content&task=blogcategory&id=40&Itemid=137

(2) http://www.klimadiagramme.de/Europa/thule.html

(3) http://climate.gi.alaska.edu/Climate/Location/TimeSeries/Barrow.html

(4) Hörsch (2003).

(5) http://www.worldclimate.com/

(6) Reimers (1992).

(7) http://www.wrcc.dri.edu/

(8) Driscoll (1980).

(9) Villagrán (1980).

(10) Siegert and Marisat (2001), Siegert and Dowdeswell (2004), and Hubberten et al. (2004).

(11) Bromwich et al. (2004, 2005).

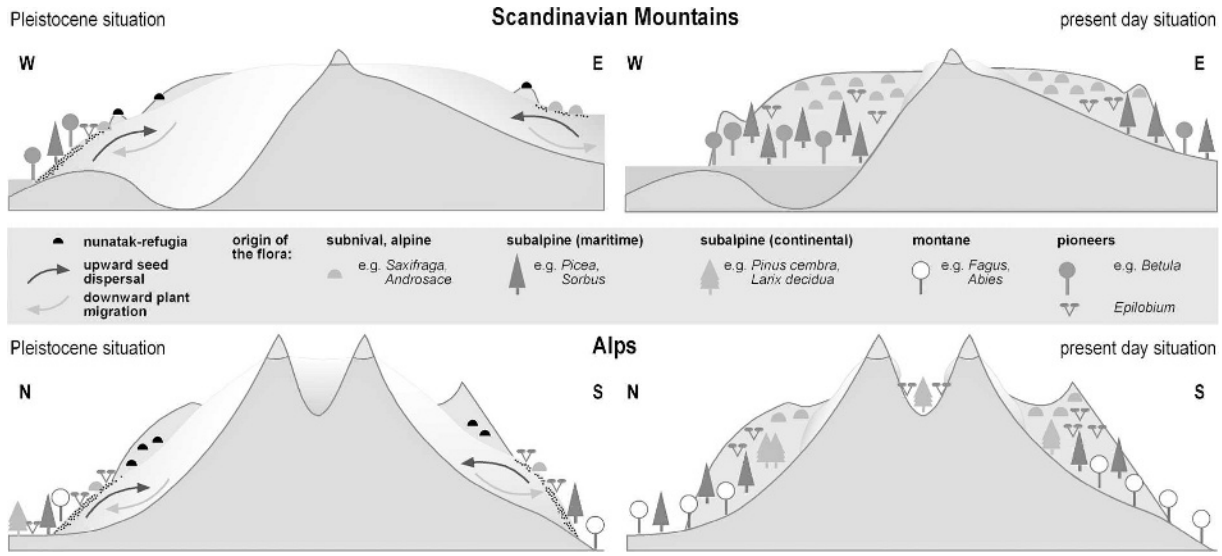


FIGURE 9. Modern (right) and hypothetical models of possible plant refugia during the Pleistocene glaciations (left) are shown for the Scandinavian mountains (above) and the European Alps (below). Survival of plants took place either in the ice-free forelands of major mountain systems (i.e. tabula rasa theory), or on unglaciated isolated mountain tops (nunatak hypothesis) and, as we believe, on the debris-covered surfaces of glaciers. The arrows indicate a cycle of downward migration and upward dispersal of plants. Strong anabatic valley winds support continuous seed dispersal to higher ground, thus providing the possibility for long-lasting colonization of the glacier surface by plants.

anemochorous (i.e. wind dispersed) species, however, without any doubt were able to spread seeds to higher parts of the glacier using strong anabatic valley winds as a transport pathway (Holtmeier, 2000). Quite frequently, vital plants with anemochorous dispersal mechanisms were found on top of the glacier far above their normal distribution range, creating a cycle of downward migration and upward dispersal of plants. Curiously, along with the fact that the large Pleistocene ice sheets continuously (and most pronounced at the peak of cold cycles) released icebergs to the ocean (Zweck and Huybrechts, 2003; Schäfer-Neth and Stattegger, 1999), our hypothesis also supports another theory about the floral history of the Holarctic, occasionally used in support of

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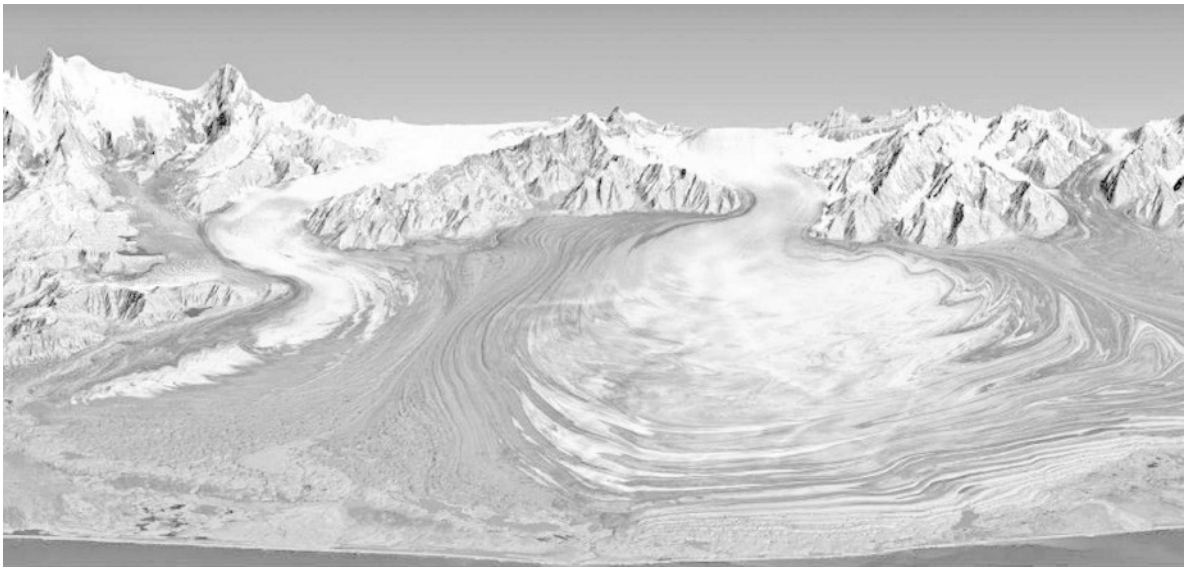


FIGURE 10. The largest piedmont glacier in the world, the Malaspina Glacier, composed of the Seward Lobe (to the right) and the smaller Agassiz Lobe (to the left), represents the largest debris-covered and partially vegetated glacier in Alaska. Similar conditions are likely to have existed on the surface of glaciers extending from high mountain terrain into the foreland during the Pleistocene glaciations, especially at the western margins of coastal mountain ranges such as the Scandinavian mountains, the Coast Ranges of northwestern North America, and western Patagonia. (source: http://www.jpl.nasa.gov/images/earth/alaska/malaspina-glacier-browse.jpg)

"tabula rasa:" long-distance dispersal. In addition to seed dispersal by wind, animals, or sea currents, propagation by icebergs and drift ice has been regarded as a possible dispersal mechanism for more than a century (Darwin, 1859; Blytt, 1876; Nordal, 1987; Buckland and Dugmore, 1991). Even vascular plants growing on ice islands were observed (Hultén, 1962; Fridriksson, 1975). Those plants have certainly been established on the glacier surface prior to their journey across the ocean, thus further illustrating the potential for growth of plants on and the dispersal of plants by drift ice. That said, a long-distance dispersal originating from plant refugia on debris-covered coastal glaciers during the Pleistocene is most likely; a simulation by Schäfer-Neth and Stattegger (1999) showed that icebergs caused circulation changes in the North Atlantic compared to present-day and that they can drift to almost any place in the North Atlantic from any given source area. By glacial-marine sedimentation, Molnia (1983) identified as many as 18 periods of increased iceberg transport of sediment to the eastern mid-Atlantic Ocean region during the past 300,000 years. During the Pleistocene, as much as 23 million cubic kilometers of glacierized Europe and North America drained into the North Atlantic Ocean. When these glaciers reached the sea, large icebergs carrying varying quantities of glacially eroded sediment—and probably plants—calved and drifted under the influence of surface currents. As the icebergs melted, frequently after transport for several thousand kilometers, sediment rafted from glacier termini was deposited into the oceanic water column where it settled to the bottom and was incorporated in the slowly accumulating, predominantly biogenic, pelagic sediment.

(3) Were all species living on debris-covered glaciers able to fruit for their self-dependent propagation? Our studies document that most of the herbaceous plants, as well as willows and alders, show vivid fructification. Conifers tend to possess a reduced growth rate (e.g., 25- to 35-year-old trees are characterized by a stunted shape and a maximum height of 2 m) and apparently are not able to produce cones during their first decades; however, trees of mature forest as shown in Figure 2 are definitely able to do so.

Conclusion

The hypothesis presented here is intended to stimulate paleobiogeographical and paleoecological research with unconventional ideas about the survival of plants during the Pleistocene. Our studies on plant growth on debris-covered glacier surfaces reveal a rather diverse vegetation both floristically and structurally. In some cases the plants growing on debris-mantled glacier

TABLE 3

Type of recent plant colonization on glacier surfaces around the world based on our direct observation.

	Autochthonous	Allochthonous	Both
European Alps	Miage Glacier, Lang Glacier, Roseg Glacier		
Western Kunlun/China	Oitagh Glacier		
Karakoram/Pakistan	Baltoro Glacier, Batura Glacier		
Himalaya/India & Nepal	Mayar Glacier		Annapurna III Glacier
Gonga Shan/China	Gonga Gomba	Hailuogou Glacier	
Cascade Range/North America	Carbon Glacier, Winthrop Glacier		
Alaska/North America	Ruth Glacier, Fairweather Glacier, Malaspina Glacier		
Southern Andes/Chile		Casa Pangue Glacier	Ventisquero Blanco
Cordillera Blanca/Perú			Glaciar Kinzl

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surfaces originate from vegetation-covered lateral moraines and/or from landslides of the bordering slopes, resulting in a clumped, allochthonous vegetation. Much more common, however, is an autochthonous colonization of the glacier surface by plants, i.e. seed dispersal (mainly by wind, to a lesser degree also by animals) of plants from the vicinity or of those already established on the glacier and *in situ* germination (Table 3). The latter fact is particularly important for our assumption; if plants are able to do such today, we assume similar mechanisms for the colder past. Such a ''debris-covered glacier hypothesis'' contributes to the contrasting nunatak and tabula rasa hypotheses.

We believe that in addition to nunataks and ice-free forelands (either close to the ice margin or farther away), the treatment of debris-covered glaciers as supplementary habitats for plants during glacial times helps to explain some of the questions left unresolved by the other two hypotheses. In both cases post-glacial recolonization of high mountains is hard to understand. While nunataks offer just small, disparate, and icy refugia for plants, the ice-free forelands might be located too distant for a fast recolonization of high-elevation terrain. Debris-covered glacier surfaces, in contrast, could have provided widespread non-peripheral refugia for mountain plants.

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