Vegetation Succession Pattern and Diversity Changes in a Glacier Valley, Central Alps, Austria

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Abstract

The aim of this study was to assess the influence of comparable unequal environmental conditions on primary vegetation succession in an alpine glacier valley by the means of transects. Two longitudinal transects were established along the glacier foreland of the Rotmoosferner, Tyrol, Austria, and two transverse transects were established across the valley on the 1923 and 1858 moraines. The progressions of alpha- and beta-diversity were compared, and vegetation data within the glacier foreland were analyzed. Moraine age emerged as the primary factor within a canonical correspondence analysis (CCA), while the second axis separated the two valley sides. A clearly differentiated development of plant communities became obvious especially within the early development stages. Early development of vegetation cover and alpha diversity was further developed on the shaded valley side, and progression of beta diversity differed significantly among the valley sides. The results indicate two different successional pathways, on both the qualitative and the quantitative level. These can be attributed to differences in the extent of solar irradiation (sunny vs. shaded side), lithology, geomorphic processes, and a multitude of other factors, reinforcing the dissimilarity between the valley sides. Our approach highlights the necessity of a deliberate sampling design within different glacier forelands sensitive to environmental conditions created by the topography that may impact comparisons among the forelands.

Introduction

The alpine landscape is characterized by its diversity of landforms, parent rock types, soils, and vegetation (Molau, 2003). The prevailing extreme conditions in these landscapes limit the number of species (Whittaker, 1972, 1999; Chapin and Körner, 1995; Gaston, 2000). Thus, species numbers decrease with elevation (Ozenda, 1988; Grabherr et al., 1995, 2000; Holten, 2003; Theurillat et al., 2003). Due to increases of annual mean temperature, 75% of all glaciers are estimated to have been in a retreat for the last 150 years, exposing abundant bare substrate for colonization (Walker and del Moral, 2003). This retreat is most extensive in high mountain areas with steep slopes and can thus be identified as one of the conspicuous signs of climate change in alpine landscapes in the last century (Haeberli, 1995). Glacier forelands exhibit the unique opportunity for examining the development of diversity from the very beginning (Matthews, 1992).

Primary vegetation succession on glacier forelands has been a subject of ecological studies since the early 20th century, and comprehensive worldwide information exists (see review in Matthews, 1992). Glacier forelands in the European Alps have been well studied (e.g., Caccianiga, 1999; Caccianiga et al., 2001; Sigler et al., 2002; Tscherko et al., 2003; Raffl and Erschbamer, 2004).

The investigation of Foster and Tilman (2000) supported the validity of the chronosequence approach (space-for-time substitution) as a viable tool to obtain integrated information within succession studies, confirming previous assumptions for glacier foreland research (Matthews, 1992). Because considerable effort is required to record vegetation as a whole, data collection along transects is a popular approach (Vetaas, 1994, 1997; Rydin and Boregard, 1995; Frenot et al., 1998; Ohtonen et al., 1999). However, it is crucial to establish the transects for subsequent analyses in locations that are representative of the chronosequence. Valley glaciers in the Alps and their forelands are tightly constrained by adjacent valley slopes. The immediate proximity of steep slopes fundamentally influences colonization processes and hence the ensuing succession pattern. Increased input of plant fragments, seeds, and soil by snow avalanches and landslides is likely. But first of all, it leads to pronounced local differences on the valley bottom with respect to the extent of solar radiation and thus snow cover duration and water supply. Körner (1999) found a major impact on vegetation development within a glacier foreland near Furka pass, Switzerland. He observed that the valley side receiving more direct solar irradiation exhibited accelerated vegetation development and thus a higher species turnover compared to the more shaded side. Walker and del Moral (2003) pointed out that comparisons among time series of primary succession within the same research area would be highly interesting, yet such comparisons are very rare. So far there have been few attempts to compare directly the changes on two parallel transects along the same chronosequence.

The present study aimed to observe diversity and succession pathways along two valley sides on the glacier foreland of the Rotmoosferner in the Central Alps, Ötztal, Austria, using two transects. One transect was established on the sun-exposed valley side (southwest-facing) and the other one on the side with much less direct solar irradiation (northeast-facing). The two valley sides also differ in soil pH (Rudolph, 1991; Erschbamer et al., 1999; Mallaun, 2001; Raffl and Erschbamer, 2004; Schwienbacher, 2004). Differing soil pH is a common phenomenon in the European Alps, owing to the sometimes adjacent co-occurrence of acidic and more basic bedrocks. Since the two transects were restricted to undisturbed areas, they provide an insight into primary succession on a well-preserved chronosequence by omitting local disturbances such as floods or erosion. Apart from changes in community composition (qualitative level), the development of quantitative parameters (cover, alpha- and beta-diversity) was measured along the chronosequence. The valley sides (i.e. the lateral
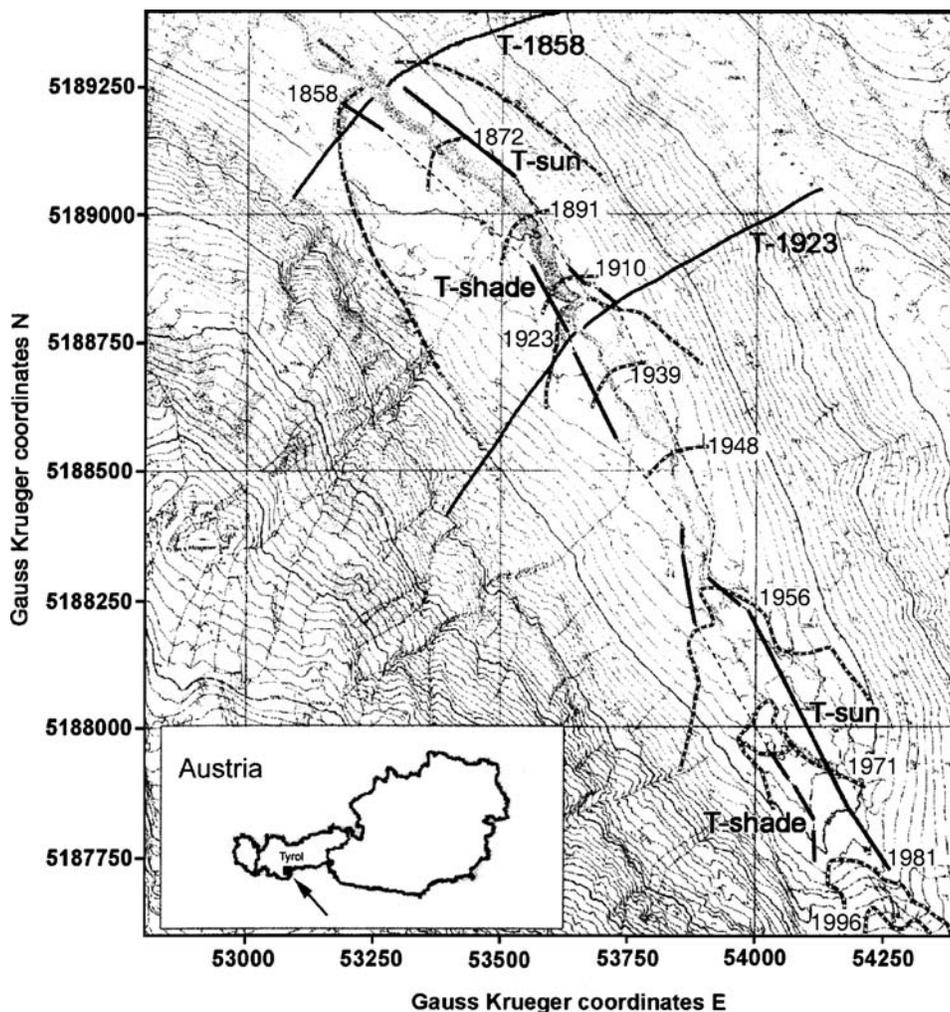
FIGURE 1. Locations of the four transects on a map of the Rotmoos valley (see Mallaun 2001, with modifications). The dotted thick lines represent the neoglacial moraine stages (dated by Patzelt 1995, University of Innbruck, unpubl. data), the thick lines represent the transects: T-sun and T-shade follow the chronosequence along the valley bottom, while T-1923 and T-1859 cross it on the respective moraines.

moraines and the adjacent slopes) were included in the quantitative analyses using additional data of two transverse transects crossing the glacier foreland (Raffl and Erschbamer, 2004).

In this present paper we aim (1) to investigate the development of alpha and beta diversity of the primary succession along the foreland of an alpine valley glacier; and (2) to compare the development of the communities especially concerning the differences on the two valley sides.

## Material and Methods

STUDY AREA

The Rotmoosferner is a valley glacier situated in the Austrian Central Alps (46°52′N, 11°02′E). The study area includes the glacier foreland at 2300 to 2450 m a.s.l as well as the adjacent valley slopes (2600 m a.s.l.). The generally northeast exposure of the valley provides ideal conditions for comparison between a valley side with high solar irradiation and one with low solar irradiation. Available climatic data taken from a weather station in the Rotmoos valley indicate a mean summer temperature of 7.6°C; mean annual precipitation is estimated to be approximately 1460 mm yr^{-1} (Kaufmann, 2001).

The bedrock of the glacier foreland is dominated by feldspathic rocks and micaschists, with outcrops of metacarbonates near the glacier terminus (Frank et al., 1987). Over the last 140 yr the glacier retreated more than 2 km, with an average rate of 14 m yr^{-1}. The largely well preserved chronosequence exhibits a series of glacial moraines (e.g.

glacier stages of 1923, 1971), delimited by a terminal moraine ridge dated 1858 (Patzelt, 1995, University of Innsbruck, unpubl. data). The glacier retreat has been measured yearly since 1892 by the Austrian Alpine Club (Juen, 1998). The valley slopes that have been free of permanent ice for at least 10,000 yr (Bortenschlager, 1984) are quite different in character: While the northeast-facing side exhibits immediately steep valley walls and bears many bare rockfalls, the incline of the southwest-facing valley slope is comparatively smooth and it is vegetated by various types of alpine grasslands (Raffl and Erschbamer, 2004). In addition to the central creek, numerous smaller brooks, which strongly vary in size during the year, originate on both sides of the Rotmoos valley (Wallinger, 1999). The glacier foreland vegetation was already recorded before, i.e. 40 and 10 years ago (Jochimsen, 1962; Rudolph, 1991).

SAMPLING DESIGN

Vegetation was recorded in four successive summers (1996–99). Four transects were established (Fig. 1). The longitudinal transects, T-sun and T-shade, follow the chronosequence on the orographically right (= sun exposed) and left (= more shaded) side of the valley, respectively (Mallaun, 2001). Sampling started at moraines deglaciated since 1990 and ended at the terminal moraine of 1858. The transects T-1923 and T-1858 ran transverse to the glacier valley, crossing the 1923 and 1858 moraines, respectively. They ended at the valley slopes beyond the lateral moraines of the glacier foreland (Raffl and Erschbamer, 2004).
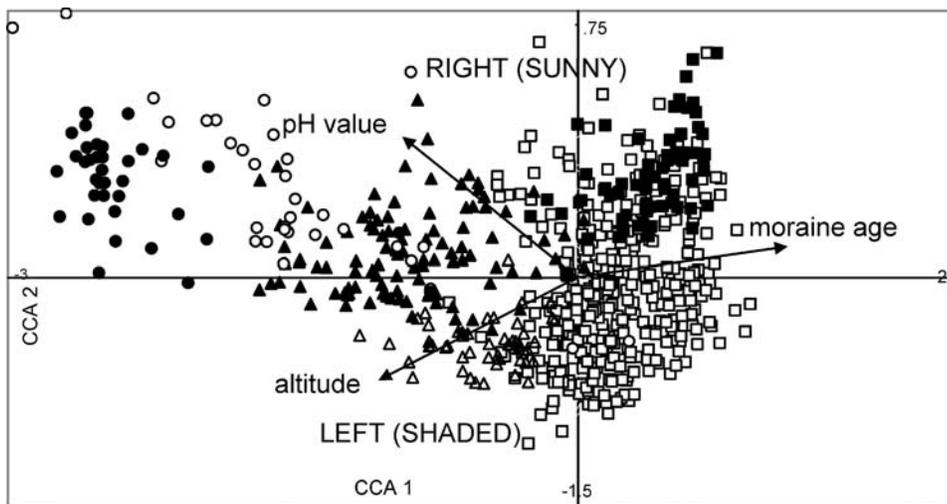
FIGURE 2. CCA plot of sample scores and environmental variables. The environmental parameters are shown by vectors, and, the valley sides are shown as centroids. ● Species poor pioneer stage; ○ Species rich pioneer stage; ▲ Early successional stage; △ Transient stage; □ Initial grassland; ■ Initial grassland with *Kobresia*.

Along the chronosequence (T-sun and T-shade), the series of plots were continuous in undisturbed regions. However, transects were interrupted in several places (Fig. 1), where the chronosequence was obliterated by relocating creeks, scree slopes or stochastic events like snow and rock avalanches and floods (Mallaun, 2001). The plot sequences transverse to the valley (T-1858 and T-1923) were continuous within the glacier foreland and the northeast-facing valley slope in order to sample the patchy vegetation pattern present there. On the southwest-facing valley slopes within sections of homogeneous vegetation, however, data were sampled in representative discontinuous plots every 10 m, and means were calculated. Thus more plots were sampled in sites with high physiognomic heterogeneity (Raffl, 1999; Raffl and Erschbamer, 2004).

The plot size was uniformly 1 meter square, in which the abundance of each plant was estimated according to the method of Braun-Blanquet (1964) on a nine-degree scale (Reichelt and Willmanns, 1973). A small set of environmental factors was also recorded comprising site age, pH-value, altitude, and total vegetation cover per 1 m².

CLASSIFICATION AND ORDINATION

The classification and ordination procedure was restricted to the data collected in the glacier foreland, by omitting the samples on the valley slopes beyond the lateral moraines. The classification of 643 samples with 204 species was performed using TWINSPAN (Hill, 1979), at three levels of division. The plots were further ordinated by canonical correspondence analysis (CCA; Ter Braak and Smilauer, 1998), where age since deglaciation, soil pH, and affiliation to one of the valley sides were implicated as environmental parameters. A Monte Carlo Permutation Test was used to test the significance of each environmental variable. Additionally, the vectors for vegetation cover and species richness were added as passive variables.

DIVERSITY

All calculations concerning plant diversity were computed for the whole data set including the valley slopes (857 samples in total). Alpha diversity was derived from the species number per plot. In recording the progression of species richness along a gradient the calculations of Beta diversity along each transect were performed according to Shmida and Wilson (1985).

NOMENCLATURE

Nomenclature for vascular plants follows Adler et al. (1994); macrolichens, Wirth (1995); and mosses, Frahm and Frey (1983).
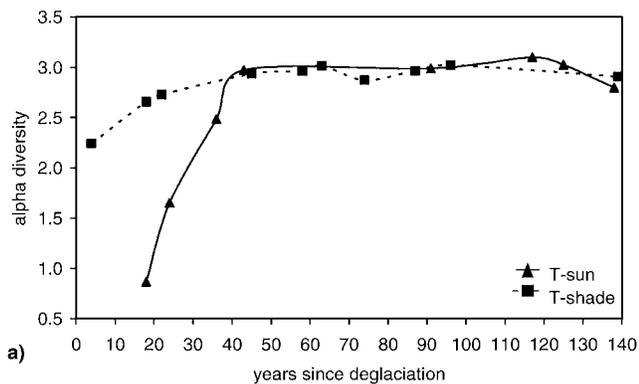
Results

A clear separation of pioneer, early and late successional stages was obtained by CCA of the data from longitudinal transects (Fig. 2). The first axis (Eigenvalue = 0.373) is strongly correlated to moraine age and soil pH-value. It exhibits a comparable long gradient, where the pioneer communities (species-poor stage, species-rich stage) and the early successional stage are clearly distinct, whereas the older stages are more densely crowded. As indicated by the centroids, the two valley sides split along the second axis (Eigenvalue = 0.262). A similar ordination was obtained from the two transverse transects (Raffl and Erschbamer, 2004), the pioneer and the late successional stages being also separated along the first canonical axis (Eigenvalue = 0.385), while the second axis (Eigenvalue = 0.299) divided the two valley sides.

The species-poor pioneer stage (average species number per square meter = 3) was mainly formed by *Saxifraga oppositifolia* and *S. aizoides* on the sites deglaciated for about 25 yr. Vegetation cover was very low at these sites (Fig. 3) and the average soil pH was 7.5. The pH-value of the species-rich pioneer stage was similar (7.4). This stage occurred on comparable older habitats, already deglaciated for up to 40 yr. Beside the two *Saxifraga* species, *Linaria alpina*, *Artemisia genipi*, and *Poa alpina* exhibited high constancy values as well, yielding in comparable increased vegetation cover and a higher alpha diversity (Figs. 3, 4a).
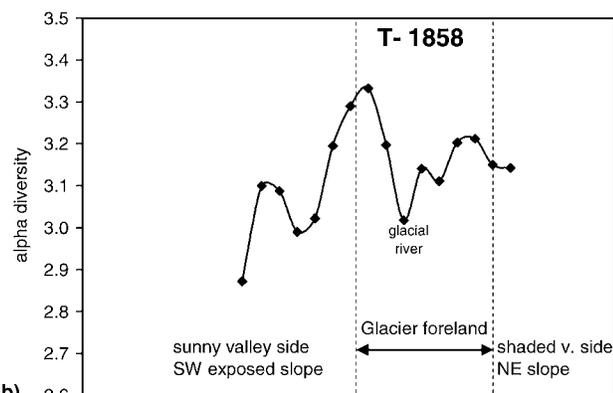
On the shaded valley side, no pioneer stage was recorded. Although less sun exposed, that side exhibited distinctly higher values in vegetation cover and a higher alpha diversity on the youngest sites
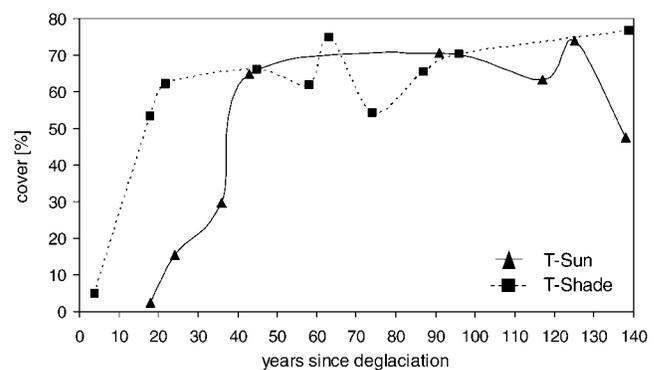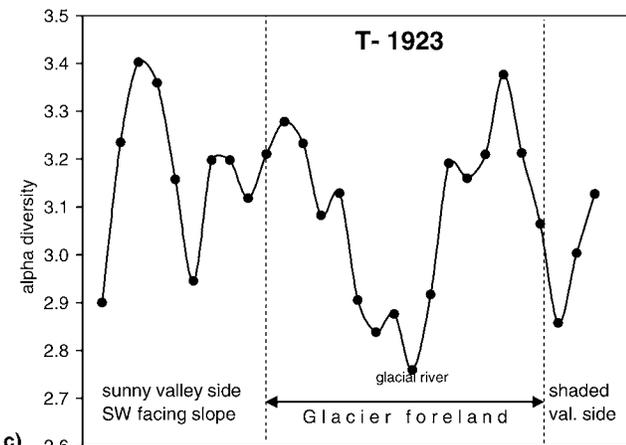

FIGURE 3. Development of total vegetation cover on T-sun and T-shade, starting from the recently deglaciated terrain to the terminal moraine. The age since deglaciation refers to the 1990.
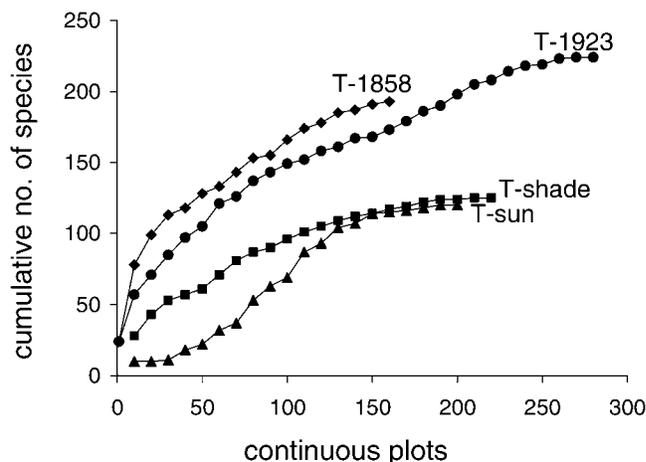
a)

b)

c)

FIGURE 4. Alpha diversity along the four transects. a. T-sun and T-shade follow the chronosequence along the valley bottom. For b. T-1858 and c. T-1923 the diagram starts with the samples located on the southwest-facing mountain ridge and ends with the northeast-facing ridge.

FIGURE 5. Cumulative number of species recorded on the four transects. For T-1923 and T-1858 the graph starts with the samples located by the glacial river and ends with the ones located on the adjacent mountain ridges. For T-sun and T-shade the graph starts with the youngest moraine stages and ends on the terminal moraine.

the small ridges, species indicating moister conditions (*Gnaphalium supinum*, *Salix herbacea*, *Sagina saginoides*, *Leucanthemopsis alpina*, and *Oxyria digyna*) were established in the depressions. In spite of this persisting differentiation on community level, vegetation cover and alpha diversity equalize around 45 yr after deglaciation on both valley sides (Figs. 3, 4a).

The subsequent older parts of the glacier foreland were covered by initial grasslands on both sides of the valley, with highest species numbers and vegetation cover (Fig. 3). Beside *Trifolium pallescens* and *Poa alpina*, which already exhibited high constancy values in earlier stages, *Campanula scheuchzeri* and *Leontodon hispidus* ssp. *alpinus* were highly frequent, whereas *Stereocaulon alpinum* and *Racomitrium canescens* decreased. The initial grasslands of the two valley sides differed significantly in pH value ($P < 0.001$). The average pH of 6.5 demonstrates the sustaining influence of calcareous bedrocks on the sunny valley side compared to the shaded side (pH 5.75). *Agrostis rupestris*, *Trifolium badium*, *Leucanthemopsis alpina*, and *Salix herbacea* yielded high constancy levels on the shaded side whereas, *Achillea moschata*, *Erigeron uniflorus*, *Minuartia gerardii*, and *Saxifraga paniculata* were more present on the sunny side.

On the sunny side, the oldest moraine stages of about 140 yr were covered by the initial grassland with *Kobresia myosuroides* (Fig. 3) which exhibited the highest vegetation cover (mean 70%). Characteristic species with high constancy levels were *Kobresia myosuroides*, *Agrostis apina*, *Myosotis alpestris*, and *Anthyllis vulneraria* ssp. *alpestris*.

On T-1858, alpha diversity was lower on the valley slopes compared to the glacier foreland (Fig. 4b). However, on T-1923 alpha diversity was rather variable exhibiting low values close to the glacial river and high values on the valley slopes beyond the lateral moraines (Fig. 4c).

To get a general impression of species increase from younger stages to older stages, the development along the chronosequence was compared, as well as from the sites near the glacial river, to the valley slopes on both sides (Fig. 5). Both longitudinal transects (T-shade, T-sun) exhibited fewer species than the transverse transects (T-1858, T-1923).

The progression of beta diversity within the glacier valley confirms the pattern found in alpha diversity: A different initial development between the two valley sides and an alignment of the values

(Figs. 3, 4a). The community can be described as an early successional stage. Still, early colonizers such as *Saxifraga oppositifolia* and *S. aizoides* exhibited high constancies in the early successional stage, as did *Linaria alpina*, *Cerastium uniflorum*, and *Arabis caerulea*. The cryptogams *Racomitrium canescens* and *Stereocaulon alpinum* also became prominent. In addition, species which are more common in the later successional stages invaded: *Trifolium pallescens*, *Silene acaulis* agg., and *Minuartia gerardii*. On the sunny valley side the early successional stage did not occur until 40 yr after deglaciation.

The transient stage only occurred on the shaded valley side. The species composition mirrors the spatial micropattern, which is attributed to previous movements of the glacier. While *Saxifraga bryoides*, *Agrostis rupestris*, and *Luzula alpinopilosa* were found on

around 45 yr after deglaciation can be observed (Fig. 6). While on T-shade a stepwise increase of beta diversity was present reaching its maximum 100 yr after deglaciation, a constant incline until 140 yr was present on T-sun. Beta diversity exhibited a quite similar progression in both directions on T-1858, whereas the maximum of beta diversity on the sunny valley side of T-1923 was almost twice as high as on T-1858 (Fig. 6b, c).

Discussion

Primary succession occurs in response to many relatively fixed parameters, such as surface age, exposure to solar radiation, and moisture availability (Matthews, 1992), as well as more random or stochastic factors, such as disturbance by landslides or avalanches. Together these factors in glacier forelands yield regular vegetation succession patterns in which the influence of age may be modulated by the distribution of other factors (e.g., sunlight, moisture) and be interrupted by perturbations (Mizuno, 1998). In fact, the ecological processes present within a glacier foreland are highly complex, to the extent that it is difficult to define the causes of the emerging pattern (Tilman, 1988). Del Moral and Wood (1993) ascertained that successional stages primarily depend on local habitat differences, such as age and soil stability. Freezing and thawing processes which are widespread on glacier forelands influence moisture supply, grain size characteristics, and thus the distribution of vegetation (Matthews, 1992).

First colonizers are initially exposed to high light but low nutrient availability. Except for nitrogen all of the minerals required by plants occur in the parent material, so that most of the early dominants, which occur immediately after the pioneers, are capable of nitrogen fixation (Tilman, 1988; Miles and Walton, 1993). In the glacier foreland of the Rotmoosferner, nitrogen-fixing species (e.g., *Trifolium pallescens*) become dominant on the areas deglaciated for 40 yr. Reiners et al. (1971) also mentioned lichens such as *Stereocaulon alpinum* in this context, which is also widespread on the younger stages on the foreland of the Rotmoosferner. Together with nitrogen from atmospheric sources, various soil-forming processes provide an increased level of total soil nitrogen (Insam and Haselwandter, 1989; Bekku et al., 1999; Tscherko et al., 2003) facilitating biodiversity increases as succession proceeds. The nitrogen mineralization rates are dependent on various determinants, such as soil pH, moisture, and temperature among others (Tilman, 1988; Walker, 1993). With respect to these factors, the two sides of the Rotmoos valley are quite unequal, which leads to the two distinct successional pathways that became evident in the present study (see also: Rudolph, 1991; Mallaun, 2001; Schwienbacher, 2004).

Fastie (1995) observed two separate successional pathways within the foreland of Glacier Bay, in relation to the presence of *Alnus crispa*. Within the Rotmoos valley the differentiation was especially obvious in the initial and transient stages of colonization. Compared to the gradual increase of plant biomass and diversity on the sunny valley side, the development was more "explosion-like" on the shaded valley side. Within the early successional stage, various species played a prominent role as colonizers apart from classical pioneers. Despite the higher extent of solar irradiation, on the sunny valley side the development of a community similar to the shaded valley side took over 40 yr longer. This fact might be attributed to the steepness of the barely vegetated adjacent northeast-facing slopes, from which material is constantly input from the upper regions. Melting avalanches leave plant material and clods of earth containing seeds and tillers, which contribute to the colonisation processes on the pioneer sites (personal observations). Besides, conditions for plant establishment seem to be more favorable on the shaded valley side. The larger stones there represent safe sites for seedling recruitment and establishment, which is
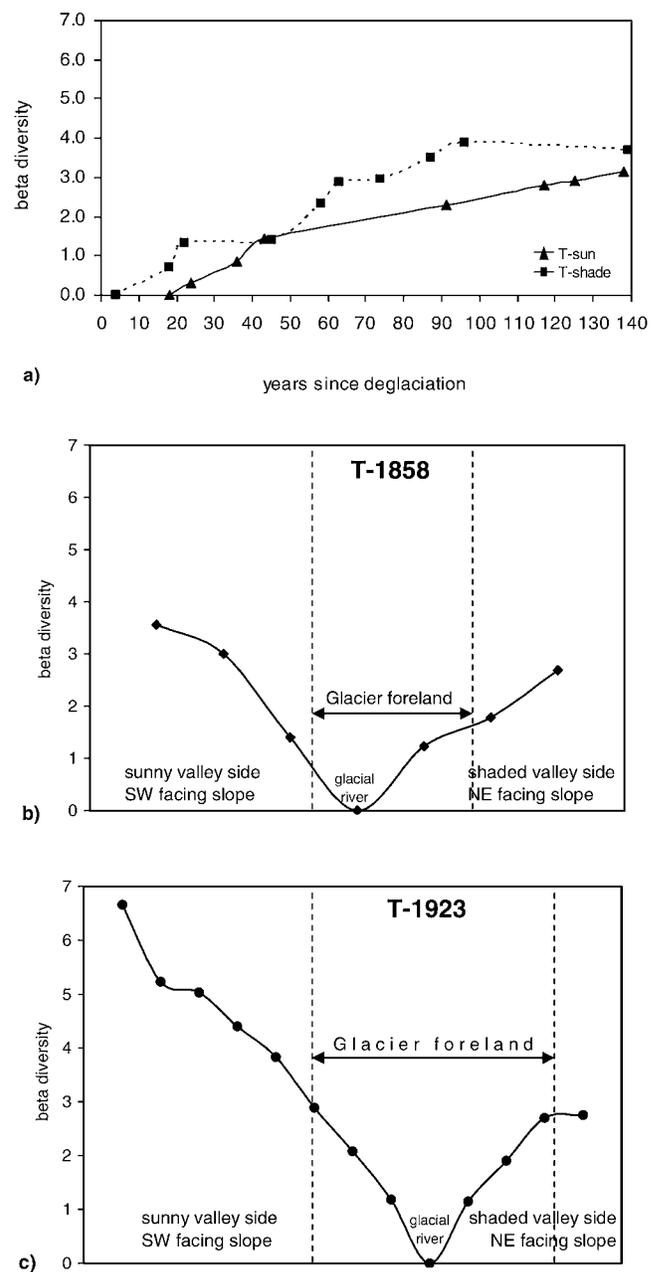
FIGURE 6. Beta diversity along the four transects. a. T-sun and T-shade follow the chronosequence along the valley bottom. For b. T-1858 and c. T-1923 the diagram starts with the samples located on the southwest-facing mountain ridge and ends with the northeast-facing ridge.

essential considering the harsh conditions present in front of the glacier terminus (Frenot et al., 1998; Jumpponen, 1999; Niederfriniger Schlag and Erschbamer, 2000). In addition, the shadowing effects of the slopes allow a better water supply, a crucial aspect considering the high seedling mortality ascribed to drought (Chapin and Bliss, 1989; Niederfriniger Schlag and Erschbamer, 2000). The presumption is also confirmed by the high percentage of species characteristic for snow-bed communities within the transient stage, a community which is completely lacking on the sunny valley side. The succession of microbial colonizers, facilitating the emergence of pioneers, is much more rapid on sheltered and moist soils (Miles and Walton, 1993). Because of the weak capability of water retention of raw soils and the scattered vegetation cover, the risk of desiccation is comparably high.

Already Jochimsen (1975) and Krause (1996) have identified water supply as the key factor in limiting vegetation occurrence and modifying successional pathways in glacier forelands (Matthews and Whittaker, 1987; Kaufmann, 2001). Although detailed information about the local water situation would be desirable, sampling of information about the abiotic factors faces great technical obstacles, as in most studies concerned with alpine vegetation, given the highly variable character of this habitat (Gerdol, 1990).

Within the first 50 yr vegetation catches up in respect of cover and diversity on the sunny valley side, which receives direct solar irradiation to a distinctly higher extent than the shaded one, also leading to a prolongation of the vegetation period. The opportunities for soil development are enhanced in early melting sites (Stanton et al., 1994) and within 50 yr the soil has reached a temporary steady state and a stable ecosystem (Tscherko et al., 2003). Since these soils provide a higher water-retention capacity, more demanding species become prominent forming the later successional stages, in turn leading towards a climax community of initial grassland with *Kobresia myosuroides*, *Caricetum sempervirentis*, and *Caricetum curvulae* (Raffl and Erschbamer, 2004; Caccianiga and Andreis, 2004).

The accumulation of species towards a temporary balance was interpreted as the most prominent feature of development on newly formed surfaces (Walker and del Moral, 2003). Within 40 to 50 yr of succession, alpha diversity reached a plateau on both valley sides for many years. That pattern was also observed in the development of microbial diversity (Tscherko et al., 2003) and with invertebrates (Kaufmann, 2001) and it seems to be generally valid for glacier forelands not only in Europe (Bekku et al., 1999; Sigler et al., 2002) but also in North America (Helm et al., 1999; Jumpponen et al., 2002). The early peak indicates a relatively large number of species colonizing the virgin soils and the subsequent stabilization can be ascribed to competition increases (Insam and Haselwandter, 1989; Matthews, 1992). But in the Rotmoos valley a sigmoid progression in alpha diversity was confirmed only on the sunny valley side. On this valley side a persistent increase of beta diversity was also observed albeit clearly smoother after 50 yr of deglaciation. The continuing increase of beta diversity (Shmida and Wilson, 1985) at constant alpha diversity indicates that despite species numbers remaining stable, community development still proceeds. On the shaded valley side, however, the continuing frequent disturbances below the rocky slopes and the prolonged snow cover (Rudolph, 1991) result in a more stepwise turnover of communities within succession, so that up to now potential sites for demanding communities like the initial grassland with *Kobresia myosuroides* are rare. Zollitsch (1969) also described such differences in diversity development at the glacier foreland of the Pasterze in the National Park Hohe Tauern (Austria).

On the valley slopes the progression of alpha diversity on T-1858 can be ascribed to the shift from an early vegetation stage within the glacier foreland towards to the more mature vegetation types beyond the side moraine. The declines in alpha diversity are attributed to an increase of competition in later successional stages (Whittaker, 1972; Sommerville et al., 1982; Tilman, 1988; Frenet et al., 1998). However, the reverse pattern on T-1923 with higher alpha diversity on the side moraine relies on the multitude of local habitat conditions and the larger extent of local disturbances present there, especially on the northeast-facing valley side (intermediate disturbance hypothesis). Among disturbances, avalanche occurrence also plays a significant role in influencing communities' distribution and affecting alpha diversity (Erschbamer, 1989; Patten and Knight, 1994). Besides, the higher extent of beta diversity on the sunny valley side of T-1923 compared to T-1858 can be mainly ascribed to the occurrence of additional communities on the valley slopes (*Caricetum frigidae*, *Caricetum sempervirentis*, and *Caricetum curvulae*), which are absent in the glacier foreland (Raffl and Erschbamer, 2004).

Conclusions

We agree with Foster and Tilman (2002) that the chronosequence approach provides an integrative picture in succession studies. Comparable to soil chronosequences, the succession rate of vegetation is not only determined by terrain age but also climate, organisms, relief, and parent material (Matthews, 1992). So a particular correlation between vegetation and site age could arise from multiple successional pathways. To evaluate what determines diversity development and resulting community constitution, one must consider local topography and geomorphology as well as individual interactions such as facilitation and inhibition (Connel and Slatyer, 1977). The consideration of local environmental differences might contribute to a better understanding of the interplay between the multiple driving forces.

Although the investigation of the changes of alpine diversity has increased in the last few decades, particularly with regard to climatic change (Körner and Spehn, 2002), understanding which factors determine and influence the progression of diversity within a given complex alpine community remains a challenge. Alpine glacier forelands provide a basis for the investigation of the genesis of diversity in alpine environments from the very beginning. They can be seen as a model for the development of alpha and beta diversity by the means of succession from virgin soils to relatively complex plant communities. Our results indicate that various pathways in primary succession presently coexist, even when the observed sites are not far apart. This applies on the qualitative (community composition) but also on the quantitative level (vegetation cover, alpha and beta diversity). Our approach represents a step towards repetitive, standardized data collection to provide reliable comparisons among different glacier forelands. It may contribute to a more appropriate sampling design for future studies from which real comparisons can be made.

Acknowledgments

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