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Genesis of a soil seed bank on a primary succession in the Central Alps (Ötztal, Austria)

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Abstract

Soil seed bank and standing vegetation were investigated on the Rotmoos Glacier foreland (Ötztal, Tyrol, Austria) along the chronosequence (i.e. on the pioneer, early, and late successional stage) as well as on a subalpine pasture beyond the glacier foreland (old successional stage). We aimed to answer the following questions: (1) How large are soil seed banks along the successional gradient? (2) Do the seed banks reflect the actual standing vegetation or do they remember earlier successional stages or do they represent already the next successional stage?

Soil samples were collected in late spring and a germination experiment was performed. The differences in seed bank size between succession stages and soil layers were proved by a two-way ANOVA. Similarities between seed bank and standing vegetation were tested by the Morisita–Horn index.

Our results indicated that seed bank size significantly increased along the chronosequence, from 273 seedlings/m^2 in the pioneer stage, 820 seedlings/m^2 in the early successional stage, to 3527 and 3674 seedlings/m^2 in the late and old successional stage, respectively. The seed bank size was correlated with the vegetation cover along the successional gradient. The early succession stages were more similar to the standing vegetation as the later stages. A persistent soil seed bank has been found all along the successional gradient; however, size and composition changed from the pioneer to the old successional stage.

Keywords: Diversity; Germination; Glacier foreland; Persistence; Similarity index

Introduction

Glacial retreat releases new land making it available for plant colonization (Walker and Del Moral, 2003). These areas offer the opportunity to investigate the development and succession of communities from the very beginning (Matthews, 1992). In this context, glacier forelands may be regarded as unique model systems for soil seed bank size and pattern. For the colonization of bare habitats, availability of seeds and vegetative propagules or a soil seed bank are essential (Fenner and Thompson, 2005; Whittaker, 1993). In the Alpine glaciers front, barren moraines without buried soils are characteristic; soils develop only several decades after deglaciation (Erschbamer et al., 1999). Thus, a soil seed bank was assumed to be absent on recently deglaciated moraines (Chapin, 1993; Stöcklin and Bäumler, 1996). With immigration of seeds the genesis of a seed bank begins. The seed sources can be either in the surrounding

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vegetation along the glacier valley itself, the valley slopes, or parallel glacial valleys (Matthews, 1992; Raffl et al., 2006a). If the newly deglaciated terrain is not far away from well-established vegetation and hence the seed sources, the ability to reach them should not be a limiting factor (Tackenberg and Stöcklin, 2008).

Chapin (1993) emphasized that seeds of early colonizers do not become incorporated into buried seed banks. However, based on the observations of others (Stöcklin and Bäumler, 1996; Weppler et al., 2006), who recorded accumulations of persistent seeds of pioneer species, we assumed that a persistent soil seed bank will develop immediately after the first colonization, due also to unpredictable reproduction possibilities (Cavieres, 1999), and the seed bank size should increase along the successional gradient. A seed burial experiment carried out in the same area already showed the persistence potential for seeds of some glacier foreland species (Schwienbacher et al., submitted).

The similarity between the seed bank and the standing vegetation is expected to be rather high at the beginning of the succession (Grandin and Rydin, 1998) and subsequently it decreases, once the plant community has reached a stable state (Fenner and Thompson, 2005). There, the dominating above-ground species are mostly graminoids which are thought to be absent in the persistent seed bank due to their prevailing clonal growth (Fenner and Thompson, 2005; Stöcklin, 1992) or due to heavy grazing regimes (Sternberg et al., 2003).

Most of the available studies describing the importance of seed banks in successional processes are concerning secondary successions (Klug-Pümpel and Scharfetter-Lehrl, 2008; Looney and Gibson, 1995). Many were carried out on abandoned fields (Jemenéz and Arnesto, 1992; Kiirikki, 1993) or on secondary successions following major disturbances (del Moral and Wood, 1993). However, little is known about the characteristics of a seed bank along a primary succession (Kneringer, 1998; Erschbamer et al., 2001; Grandin and Rydin, 1998; Rydin and Borgegard, 1991; Stöcklin and Bäumler, 1996).

Main aims of the present study were to analyze the size and species composition of the soil seed bank along the primary succession of a central Alpine glacier foreland (from the pioneer stage, ice-free for 33 years, to the late successional stage, ice-free for 146 years) and to compare it to an old successional stage beyond the moraines (ice-free for >5000 years).

Based on the fact, that potential seed sources are available on the adjacent valley slopes and beyond the glacier foreland, we assumed that a soil seed bank may be already present in the pioneer stage. We expected a gradual accumulation of seeds in the soil along the successional gradient with a changing composition according to the standing vegetation.

We aimed to answer the following questions:

1. How large are soil seed banks along the successional gradient?
2. Do the seed banks reflect the standing vegetation or do they remember earlier successional stages or do they represent already the next successional stage?
3. Do seeds occur in deeper soil layers, i.e. do persistent seed banks occur?

Material and methods

Study site

The study area lies in the Central Alps of Austria on the glacier foreland of the Rotmoos Valley (Obergurgl, Ötztal, Tyrol, 46°49′N 11°02′E) at 2270–2390 m asl. The U-shaped valley is almost levelled and only slightly ascending nearby the glacier tongue (Table 1). The largely well-preserved chronosequence of the glacier foreland exhibits a series of moraines (e.g. 1971, 1923, 1870), delimitated by a terminal moraine ridge dated 1858 (Gernot Patzelt, University of Innsbruck, unpubl. data, 1995). The mean monthly air temperature in summer ranges from 5.9 to 8.4 °C; the mean annual precipitation amounts to approximately 1460 mm (Kaufmann, 2001). Permanent snow cover lasts from October to late May or beginning of June with differences of 3 weeks between the young and the late successional stage. Although the onset of the vegetation period varies from year to year, spatial snowmelt patterns are rather constant over years within sites (Kölbel, 1984).

The study sites comprise the chronosequence from a pioneer stage via an early to a late successional stage (Raffl and Erschbamer, 2004; Raffl et al., 2006b). Outside the glacier foreland a subalpine pasture is present, being free of permanent ice for more than 5000 years (Bortenschlager, 1984). Exhibiting a slow progressive development from a Syrozem on the youngest moraines to Pararendzinas on the oldest sites (Erschbamer et al., 1999) the soil development along the glacier foreland is rather slow. The soils beyond the moraines were characterized as alpine brown earths and 'Eisen-Humus-Podsols' (Neuwinger, 1987).

The sampling sites are labelled according to their deglaciation time (Table 1). The pioneer stage, ice-free since 33 years, is characterized by the presence of pioneer species such as *Saxifraga aizoides, S. oppositifolia* and *Linaria alpina* (Raffl and Erschbamer, 2004; Raffl et al., 2006b). With increasing distance to the glacier, i.e. on moraines ice-free for 81 years, the pioneers are replaced by early successional species such as *Trifolium pallescens* and *Poa alpina*. In the late