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Seed bank studies in the Swiss Alps

II. Restoration plots on a high-alpine ski run

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Abstract

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Soil seed banks in trial plots, installed on a machine-graded downhill ski run at ca. 2500 m were studied about 10 years after restoration in spring and autumn samples. This is the first report on post-restoration development of the soil seed reserve in a high-alpine site Unless otherwise specified, the data presented below refer to means ± standard error values.

The density of the germinable fraction of the seed reserve recorded in the autumn samples averaged 916 ± 210 seeds per m^2 in the plots RPF; the corresponding value in the plots RPG was lower (611 ± 333 seeds per m^2). After the spring snowmelt in the following year a diminished density (698 ± 270 seeds per m^2) was observed in the plots RPF, but in the plots RPG a considerable increase (3580 ± 1701 seeds per m^2) was recorded. The differences between the two plot groups and between sampling seasons were not statistically significant because of the large variance.

In the autumn samples, seven species were identified among the retrieved seedlings, and two further species were registered in the small un-germinated fraction. The spring samples included only four identified species within the germinable fraction; no further species were determined among many dormant seeds. The α-diversity studies revealed some salient features: (1) the soil seed reserve included mostly immigrant species, and only few species used in the restoration were represented; (2) compared to the standing vegetation, much fewer species occurred in the soil samples: (3) the relative frequency of species in the seed reserve did not correspond to the species frequency in the plant cover of the plots.

Considered both in the terms of diaspore accumulation and increase of α-diversity, the soil seed reserve developed within only ca 10 years after restoration represents an important symptom of active plant population processes occurring in the restoration plots.

Key words: Seed bank, soil seed reserve, restoration, machine-graded ski run, transplants, immigrants, α-diversity.

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Introduction

Restoration trials carried out in degraded high-alpine ski runs by our group demonstrated a considerable increase of plant cover and species diversity in the restored plots. This development was clearly enhanced by installation of transplants as population founders and also the manipulations which provided safe-site conditions favourable to plant establishment. The recovery process in the restoration plots was influenced both by population development of the introduced species, and by unassisted colonisation (Urbanska et al. 1987; Schütz 1988; Flüeler 1992; Hasler 1992; Tschurr 1992; Urbanska and Hasler 1992; Urbanska 1995a, b; Fattorini 1996). We assumed accordingly that accumulation of seed reserves in soil may begin soon after the restoration work has been completed; however, no study has ever been carried out on the subject.

The aim of this paper is to provide for the first time information about accumulation of seeds in soil of the trial plots where regular reproduction by seed and a considerable colonisation was recorded soon after the restoration. The issues specifically addressed are (1) density as well as α-diversity and species composition of the soil seed reserve in different restoration plots, (2) the seed reserve in soil cores respectively taken towards the end of one growth period and at the beginning of the following one, (3) differences between the occurrence and frequency of species in the seed reserve and those in the standing vegetation in each plot, and (4) relative contribution of species used in restoration and colonisers to the soil seed reserve.

The soil seed banks are exceedingly important to plant population and community dynamics, especially with regard to extreme environmental conditions. This importance was already stressed in the first paper of this series dealing with seed banks of intact alpine grassland and a degraded ski run (see Urbanska and Fattorini 1998 and also the reference therein). An information on a possible build-up of the soil seed reserve in restored plots was therefore of a particular interest.

Materials and methods

The soil cores were collected at about 2500 m in surroundings of Davos, Grisons, NE Swiss Alps (for general description of the area see Urbanska and Fattorini 1998). The restoration plots were located on SW-facing slope of Jakobshorn Mountain (Fig. 1) within a downhill ski run bordered on the one side by a natural grassland of the Caricion curvulae type (Table 1) and on the other side by a narrow boulder field which separated the ski run from the intact grassland. The two plots RPF were situated in a flat part of the ski run rather close to the grassland; on the other hand, the two plots RPG were installed in the middle of the ski run. Plants which spontaneously colonised the un-restored ski run were largely scattered over the soil surface (Table 1). According to the information provided by the cable car company, the ski run was machine-graded in the early 70s and no commercial revegetation was attempted since. The ski run is extensively used every winter by skiers heading downhill from the neighbouring top station of a skilift. It also serves as exercise slope for beginner ski classes. The daily maintenance is done with track vehicles.

Prior to the restoration trials, the few plants naturally growing on the ski run and also larger rocks occurring on the soil surface were removed. Clonal transplants obtained from single-ramet-cloning were used as population founders in various species combinations. The plots RPF were planted in 1985 with grasses only (Urbanska et al. 1987), whereas the plots RPG installed in 1987 included various graminoids and forbs (Gasser 1989). The transplants were pre-grown in garden soil, but no fertilizer amendment was included in the restoration trial. After the pocket-planting, the plots were covered with biodegradable wood-fibre mats (CURLEX®) to provide safe sites for survival and establishment and also to improve seed entrapment. The installed restoration plots remained open to the same use and maintenance work as did the surrounding un-restored ski run.

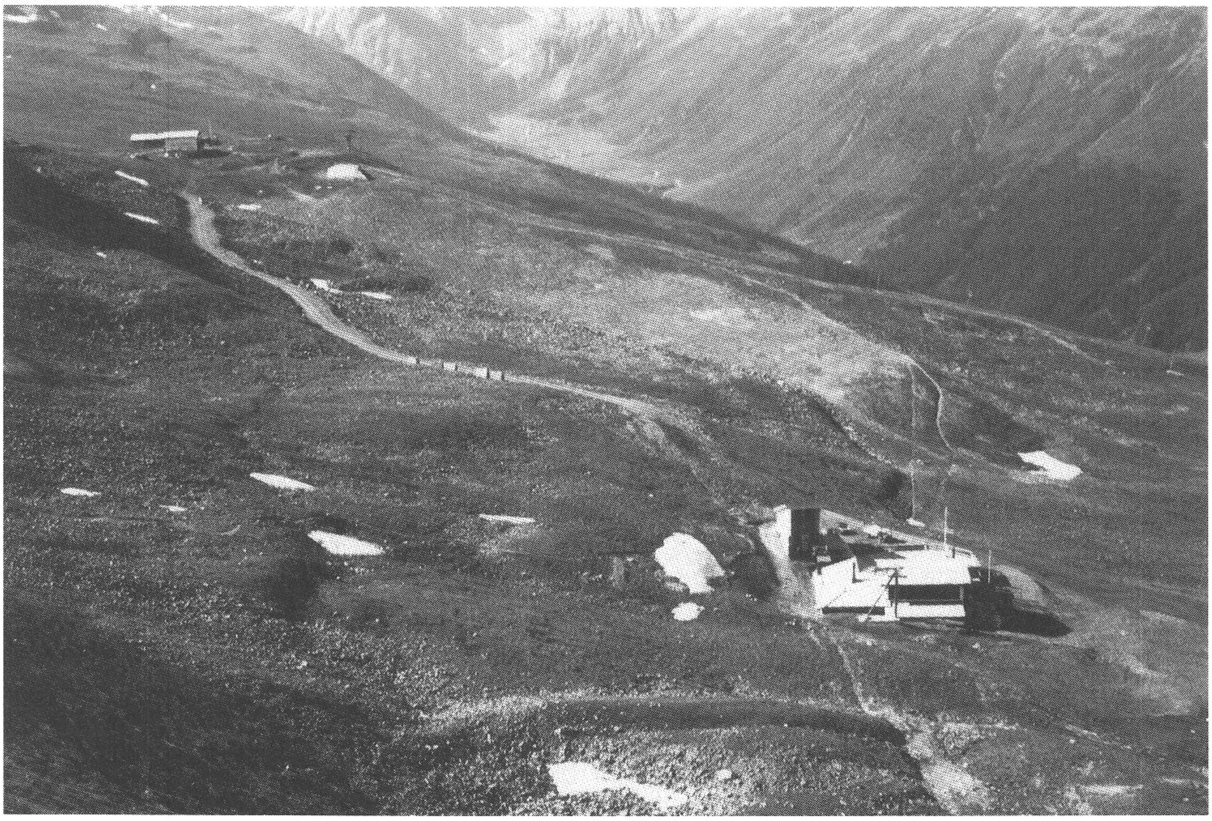

Fig. 1. Jakobshorn Mountain, ca. 2500 m. a.s.l.: Machine-graded ski run with the studied restoration plots and the surrounding landscape.

Soil samples within the restoration plots measuring ca 5 m × 1 m each were taken in places indicated by coin throwing. To spare the restored sites as much as possible, the sampling was limited to an absolute minimum of five cores per plot. The plots were sampled first in early autumn (September 3, 1996) just before an extensive snowfall heralded the end of the growing period; the sampling was repeated in the following spring, a few days after the snowmelt (mid June 1997). Each circular core measured 5.4 cm in diameter and about 5 cm in depth, the plant litter on the surface included. The soil volume of a single core was 114.5 cm^3.

Each sample was air-dried, then passed through two sieves of 0.4 cm and 0.2 cm mesh, respectively. The sieved soil of either fraction was spread to an approximate depth of 0.7 cm in Petri dishes. The samples were incubated during 110 days in a growth chamber under light-dark regime of 16:8 hrs, controlled air humidity and day/night temperature of 17.3 °C and 8.7 °C, respectively. The Petri dishes were regularly aerated and watered with tap water from above. Mosses appearing in some samples were removed. To bring deeper buried seeds close to the light, the soil samples were thoroughly re-mixed three times in ca 7–8-week-intervals, for the first time by the 37^{th} day of the trial. Seedlings were counted and determined to species or genus; not immediately identifiable seedlings were potted and grown until determination. The few seedlings or young plants which could not have been positively determined were registered as mono- or dicotyledons.

The present study mainly focused upon the germinable fraction of the seed reserve but partly included the un-germinated component of the seed reserve as well. After the germination trial was concluded, randomly selected soil samples were examined under a dissecting microscope to detect possible dormant or unviable diaspores. The autumn series included three samples per site, whereas the number of samples in the spring series was increased to five per site.

For comparison of species composition of the seed reserve and that of the standing vegetation, the lists of the plants occurring in the plots were drawn up to prior to the sampling of soil cores in 1996.

Table 1. SW-exposed slope of the Jakobshorn Mountain (ca. 2500 m): Vegetation in the un-restored ski run and intact grassland nearby. Phytosociological relevés according to the method of Braun-Blanquet (1964). Status as of July 1996.

Species	Phytosociological relevés						
	Ski run			Natural grassland nearby			
	1	2	3	4	5	6	7
Agrostis rupestris	+	1	+	1	·	2	1
Agrostis schraderiana	·	·	+	·	·	·	·
Antennaria dioica	·	·	·	·	·	·	+
Anthoxanthum alpinum	·	·	·	·	+	·	·
Arabis alpina	+	·	·	·	·	·	·
Arenaria biflora	+	·	+	·	·	·	·
Arnica montana	·	·	·	+	·	·	+
Botrychium lunaria	·	·	·	·	·	+	·
Cardamine resedifolia	1	+	1	·	·	+	+
Carex curvula	+	+	+	3	3	2	3
Carex sempervirens	·	·	·	·	·	·	+
Cerastium trigynum	+	·	·	·	·	·	·
Chrysanthemum alpinum	1	1	1	1	1	1	1
Daphne striata	·	·	·	·	·	·	·
Deschampsia flexuosa	·	·	·	·	+	·	1
Doronicum clusii	+	+	+	·	·	·	·
Euphrasia minima	·	·	·	1	+	2	+
Gentiana kochiana	·	·	·	·	·	·	+
Gentiana punctata	·	·	·	1	2	r	·
Gentiana purpurea	·	·	·	·	·	·	+
Gnaphalium supinum	+	+	·	2	·	+	·
Helictotrichon versicolor	·	·	+	+	2	2	2
Hieracium alpinum	·	·	+	·	+	1	+
Hieracium glanduliferum	·	·	·	·	·	·	+
Homogyne alpina	·	+	·	+	1	·	+
Juncus trifidus	·	·	·	·	·	·	1
Leontodon helveticus	+	+	+	2	2	2	2
Ligusticum mutellina	·	·	·	+	+	·	+
Linaria alpina	·	·	+	·	·	·	·
Loiseleuria procumbens	·	·	·	·	2	+	2
Luzula lutea	·	·	+	·	+	+	1
Luzula spadicea	·	+	+	·	·	·	·
Luzula spicata	·	·	·	·	·	1	·
Nardus stricta	·	·	·	+	1	·	+
Phyteuma hemisphaericum	·	·	·	+	+	2	1
Poa alpina	2	+	·	+	·	1	·
Poa laxa	+	1	+	·	·	·	·
Polygonum viviparum	·	·	·	·	·	+	·
Potentilla aurea	·	·	·	·	+	+	·
Primula integrifolia	·	·	·	·	·	·	·
Pulsatilla vernalis	·	·	·	·	·	+	·
Rhododendron ferrugineum	·	·	·	+	·	·	·
Salix herbacea	·	·	·	2	·	·	·
Sedum alpestre	+	·	1	·	·	+	·
Senecio carniolicus	1	+	+	+	·	1	1
Sesleria disticha	·	·	+	·	·	1	1
Sibbaldia procumbens	+	+	+	1	·	+	·
Soldanella pusilla	·	·	·	2	1	+	+
Trifolium alpinum	·	·	·	·	·	+	·
Vaccinium gaultherioides	·	·	·	·	2	·	1
Vaccinium myrtillus	·	·	·	·	·	·	·
Vaccinium vitis-idaea ssp. *minus*	·	·	·	·	·	+	1
Veronica alpina	+	·	·	·	·	·	·
Veronica bellidioides	·	·	·	·	·	1	+
Species number	16	13	18	19	18	27	28

Table 2. Current species composition of the plant cover in the restoration plots RPF (upper part) and RPG (lower part). Status as of late summer 1996.

Species used in restoration *	Immigrant species
plots RPF	
Deschampsia flexuosa	*Agrostis rupestris*
Helictotrichon versicolor	*Anthoxanthum alpinum*
Phleum alpinum	*Arenaria biflora*
Poa alpina ssp. *vivipara*	*Cardamine resedifolia*
Trisetum distichophyllum	*Chrysanthemum alpinum*
Trisetum spicatum	*Doronicum clusii*
	Euphrasia minima
	Gnaphalium supinum
	Hieracium alpinum
	Leontodon helveticus
	Poa alpina
	Salix herbacea
	Senecio carniolicus
	Sibbaldia procumbens
	Silene rupestris
	Taraxacum alpinum
plots RPG	
Agrostis schraderiana	*Agrostis rupestris*
Biscutella levigata	*Anthoxanthum alpinum*
Carex curvula	*Arenaria biflora*
Carex sempervirens	*Cardamine resedifolia*
Chrysanthemum alpinum	*Chrysanthemum alpinum*
Doronicum clusii	*Festuca rubra*
Elyna myosuroides	*Gentiana punctata*
Hieracium pilosella	*Gnaphalium supinum*
Luzula lutea	*Leontodon helveticus*
Poa laxa	*Ranunculus grenierianus*
Trifolium nivale	*Senecio carniolicus*
Trifolium repens	*Veronica bellidioides*

* According to data of Urbanska et al. (1987) for the plots RPF and those of Gasser (1989) for the plots RPG.

The species listed represented on the one hand the material used in restoration, and on the other hand the immigrants (Table 2).

For the density assessment, data on seedlings were converted to seedlings per square metre; since the cores were not divided into depth layers, the data for unit area of soil surface represented also the density of seedlings per unit volume. The non-parametric U-test of Mann-Whitney was used to evaluate differences between plots and sampling seasons; statistical significance was set a $p = 0.05$.

Terminology

As in the first paper of this series (Urbanska and Fattorini 1998), the terms "seed banks" and "seed reserve" are respectively understood as (a) seed populations of single species, and (b) seeds of all species i.e. species community occurring in one soil core or in all cores from a given site. The term "seed" is used in a generalised way to design various diaspore types (genuine seeds, achenes, kernels, etc.). The taxonomic nomenclature follows that of Hess et al. (1967–1972).

Results

Most seeds germinated within the first two months. The subsequent increase in number of seedlings recorded at the end of the trial corresponded roughly to 17% in the autumn series but it was considerably larger in the spring series (ca 28%). The seed reserve in the soil was apparently not fully used up throughout the trial duration; this applied in particular to the spring samples.

Density of seed reserve

Density assessments provided in the following part of this paper include only the germinable fraction of the seed reserve and are accordingly referred to as minimum values. Unless otherwise specified, the data presented below refer to means accompanied by the SE values. The non-parametric test used in the study did not reveal any significant differences between various means. This was clearly due to the large variance influenced both by a strong clumping of seeds in the soil cores, and also by the limited number of samples. Regardless of these limitations, the data presented here have an important indicative value.

In the autumn samples, the minimum density of seed reserve averaged 916±210 seedlings per m^2 in the plots RPF, and 611±333 seedlings per m^2 in the plots RPG (Fig. 2). The few samples examined after the trial included altogether only five un-germinated diaspores.

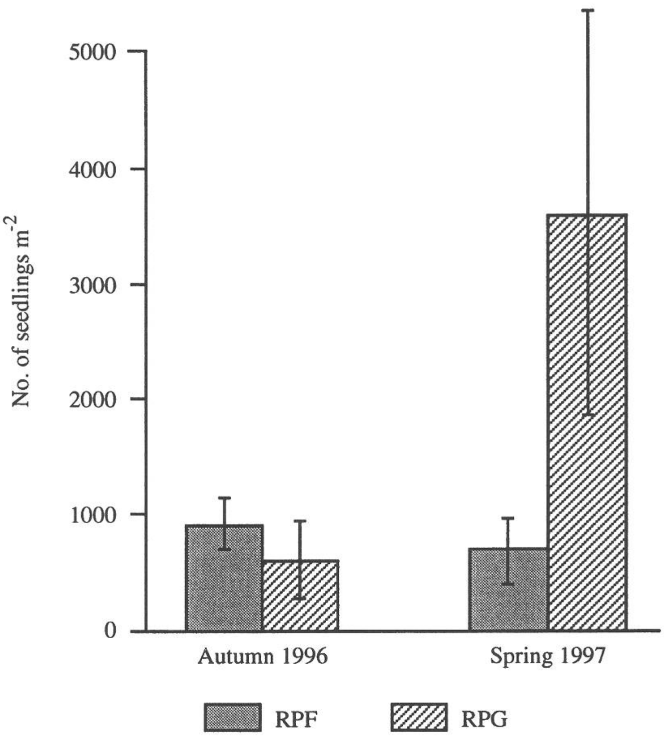

Fig. 2. Restoration plots: Seedling density in the germinable fraction of the seed reserve (means±SE). RPF = plots installed in 1985, RPG = plots installed in 1987.

In the spring samples, the mean seedling density in RPF plots was 698±270 per m^2, but it was more than five times higher in the younger plots RPG (3580±1701 seedlings per m^2, Fig. 2). The dormant diaspores found in the spring series after the trial were very numerous and irregularly distributed among samples.

Calculated globally for either of the two sampling seasons, mean minimum densities totalled 763±194 seedlings per m^2 in the autumn samples, whereas the corresponding value for the spring samples was 2139±901 seedlings per m^2.

α-diversity (species richness)

The estimations of α-diversity include the data from the germinable fraction of the seed reserve and also un-germinated diaspores. Since some seedlings remained unidentified, it is likely that further species remained undetected.

Seven species identified in the germinable fraction of the seed reserve in all samples taken in autumn 1996 occurred in different combinations on the two plot groups studied (four species in the plots RPF and five species in the plots RPG). In addition, *Lotus alpinus* and *Festuca rubra* were found in the tiny un-germinated fraction of the RPG plots. *Cardamine resedifolia* constituted the majority of all seedlings in the samples taken in the plots RPF; on the other hand, no distinct dominance pattern occurred in cores from the plots RPG.

The samples taken spring 1997 included four identified species. Only *Cardamine resedifolia* and one seed of *Trisetum spicatum* were recorded in the plots RPF; a single dicotyledonous seedling remained undetermined. The cores from the plots RPG included three identified species; of those, *Poa laxa* represented about 78% of the germinable fraction and all but one of the numerous un-germinated diaspores.

α-diversity in seed reserve vs. standing vegetation

The comparison of the α-diversity in the soil seed reserve and that of the standing vegetation revealed some consistent features. They may be summed up as follows:

- the soil seed reserve included mostly seed banks of immigrant species;
- the soil seed reserve included much fewer species than the vegetation in restoration plots;
- the relative frequency of species in the seed reserve did not correspond to the species frequency in the standing vegetation of the plots.

The immigrant species occurring in the seed reserve represented various categories (Fig. 3). Most of them already formed well-established populations in the plots; on the other hand, more recent immigrants represented only by a few plants each were less frequent. A special category was represented by species which actually did not occur in the standing vegetation of the plots but colonised the un-restored ski run nearby.

The plant cover of the plots RPF totalled 23 species (Table 2), but only four of these species were identified in the seed reserve (Fig. 4). *Trisetum spicatum* used in restoration of the plots (Table 2) and also well represented in their standing vegetation was identified only in a low frequency within the seed reserve. The three immigrant species *Cardamine resedifolia*, *Gnaphalium supinum* and *Poa alpina* were long-established in the plant cover of the plots. However, *C. resedifolia* constituted a large majority of the seed reserve whereas *Gnaphalium supinum* and *Poa alpina* were rather poorly represented (Fig. 4).

The vegetation in the plots RPG inclued 22 species (Table 2). However, only three of those were recorded also in the germinable fraction of the seed reserve (Fig. 5). *Poa laxa* which was extensively used as restoration material (Table 2) and constituted a large part of the plant cover in the plots, also largely prevailed in the soil samples. On the other hand, *Car-*

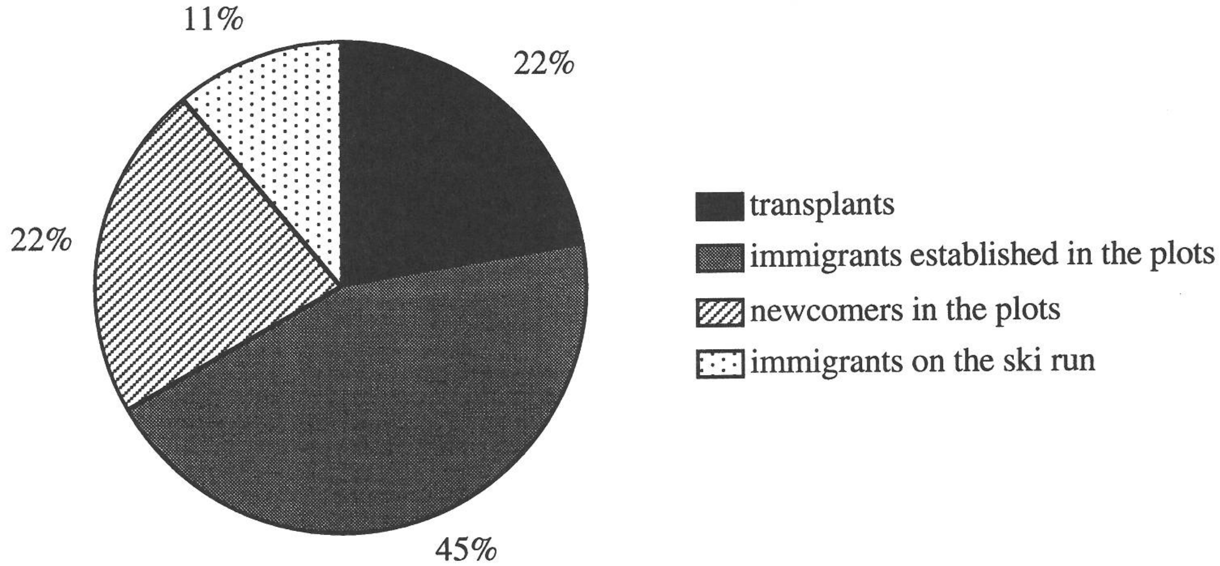

Fig. 3. Contribution (%) of transplant and immigrant species to the seed reserve. Data include species identified both among seedlings and the un-germinated seeds.

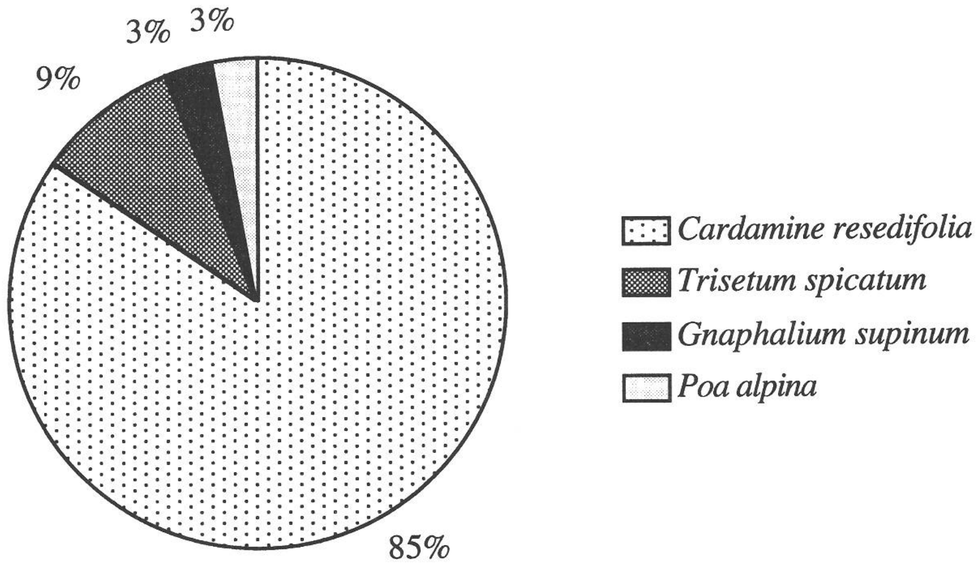

Fig. 4. Plots RPF: Species identified in the germinable fraction of the soil seed reserve.

damine resedifolia and *Gnaphalium supinum* successfully colonised the plots soon after restoration but were much less frequent in the soil cores. Of the two further species identified as seedlings, *Cerastium trigynum* did not grow within the plots but was found on the neighbouring un-restored ski run, whereas *Galium anisophyllum* was not found either in the plots or in the immediately adjacent area despite repeated search. The immigrant *Festuca rubra* found among the non-germinated diaspores was also well-established in the vegetation of the plots. On the other hand, *Lotus alpinus* did not grow there but flourished in a nearby restoration plot forming part of another research project.

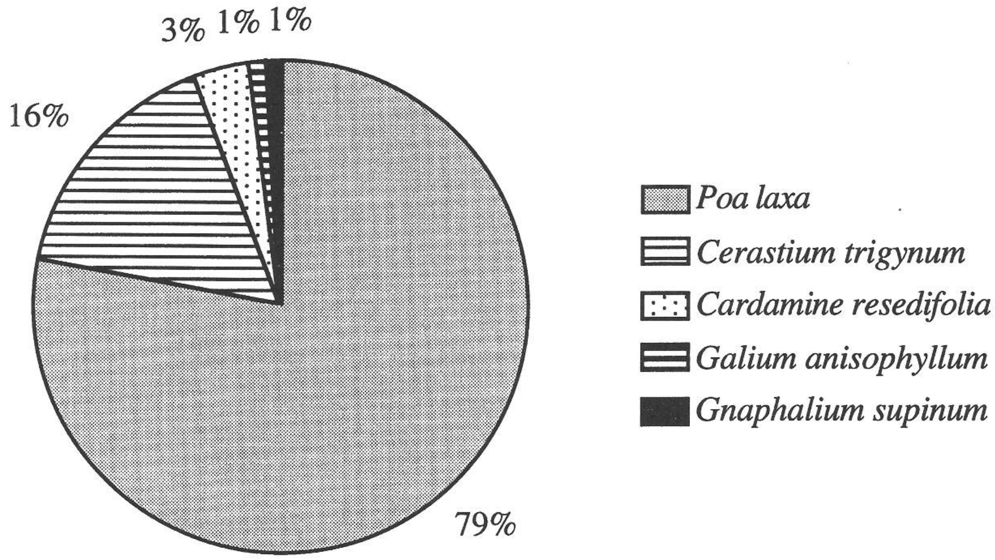

Fig. 5. Plots RPG: Species identified in the germinable fraction of the soil seed reserve.

Discussion

Seed density

The restoration plots were characterized by a very promising soil seed reserve. A direct comparison with other restoration sites is not possible so far; however, the minimum seedling density in the studied plots was to some extent comparable to data on natural alpine grassland (Hatt 1991; Niederfriniger-Schlag and Erschbamer 1995; Urbanska and Frattorini 1998, and further references therein). Compared to our recent findings on an un-restored ski run (Urbanska and Frattorini 1998), the build-up of the soil seed reserve in the restoration plots was much better. However, this assessment is given under caution because considerable small-scale variation is a rule rather than an exception in the alpine vegetation belt and may as well apply to the seed banks. Our data originate from a single restoration area, and therefore do not permit any broad speculations. Only further, urgently needed studies will help to clarify this issue.

Differences in seed reserve densities between samples taken in the autumn and those collected after the spring snowmelt were rather negligible in the plots RPF, but the spring samples taken in plots RPG were characterized by a considerable increase of seed reserve resulting mostly from the copious seed input of *Poa laxa*. This species is one of so-called "winter standers" (germ. *Wintersteher*) known to produce ripe diaspores only by the very end of the growing period. They often remain on the mother plant throughout the winter (Müller-Schneider 1986). It is thus fairly possible that the large increase of the seed reserve recorded in the spring samples included the seed input from late autumn which did not show up in the September samples. A comparable situation was recently recorded in a seed rain of high-alpine grassland (Pflugshaupt 1997). On the other hand, the diminished seed reserve in the plots RPF might be largely influenced by limitations of the seed input in autumn resulting from the strong grazing in late summer (Fattorini 1998).

α-diversity

The differences between the two studied plot series were recognisable both in the actual species number and in the plant groups they belonged to. The four identified species in the seed reserve of the plots RPF represented two grasses and two forbs belonging to Asteraceae and Brassicaceae, respectively. On the other hand, the seven species identified on the whole in the samples from plots RPG included two grasses, one legume, and four forbs representing four different families, viz. Asteraceae, Brassicaceae, Caryophyllaceae, and Rubiaceae. The two plot groups had only *Cardamine resedifolia* and *Gnaphalium supinum* in common, otherwise their species composition was different. These differences might have been influenced by dispersal timing of numerous species and the situation of the plots relative to the diaspore sources; the latter factor may be decisive in colonisation (Howe and Smallwood 1982; Ernst et al. 1992; Hensen and Müller 1997; Pflugshaupt 1997; Urbanska 1997c).

The immigrant species dominating the soil seed reserve were for the most part already established in the plots or in their close vicinity. The results of the present study confirm some previous data on short-distance dispersal in high-alpine sites (Spence 1990; Urbanska 1995a, 1997a; Pflugshaupt 1997; Kofler 1997; Urbanska et al. in press). They support the assumption that colonisation of alpine disturbances mostly proceeds via "stepping-stone" pattern rather than by large jumps (Urbanska 1997d).

Only two of many species used as restoration material in ths studied plots were actually identified in the seed reserve in these plots. This result was rather surprising because numerous transplant species in the plots began to reproduce by seed one year after restoration, and seedling recruitment within the restored plots was consistently recorded over years (Hasler 1992; Tschurr 1992; Urbanska 1994a, b; 1995a, b; 1996; 1997a, b, c, d; Fattorini 1996, 1998). The occurrence pattern of the two transplant species was rather consistent in the autumn and spring samples but it is possible that the time of sampling influenced to some extent the absence of other species used in restoration. It would be helpful to consider this aspect in future studies on restoration plots.

Safe site conditions and seed reserve development

The data on the soil seed reserve indicate ongoing population processes which are mostly more advanced than the actual population founding. This development was undoubtedly influenced by safe site availability in the plots improved first by the initial site manipulations (introduction of grown plants and use of biodegradable covers) and then by the subsequent development of plant cover.

Diaspore trapping represents an exceedingly important element in colonisation, especially in windy environments (Chambers 1995, 1997; Chambers et al. 1991; Kolb 1993; Urbanska 1997b, c; Urbanska et al. in press). The biodegradable wood-fiber mats used in our trials apparently functioned as seed traps because colonisation of restored plots was consistently observed soon after restoration in various trials carried put by our group e.g., in the studies of Schütz (1988), Hasler (1992) or Tschurr (1992). The results of the present study further confirm the usefulness of these covers. It seems that the development of seed banks in the plots was on the one hand enhanced by an input of diaspores from outside, and on the other hand by a direct deposition of diaspores produced in situ by the immigrant individuals which already became established within plots (Urbanska et al. in press). It would be most interesting to study the genetic structure in the immigrant populations.

Compared to the un-restored ski run nearby, the percentage cover of vegetation in the study plots was significantly higher (Fattorini 1998). The same results were recently obtained in another restoration site (Urbanska unpubl.). The occurrence of neighbour plants is often beneficial to seedling recruitment, and the nurse effect represents an important aspect of safe site in extreme environments (Urbanska 1992, 1997c). This aspect of seed bank dynamics should be further investigated.

Soil seed reserve as a sign of restoration success

Occurrence of a seed reserve revealed in restoration plots is particularly noteworthy as the restored plots are obviously very young compared with the intact grassland vegetation which may be several hundred years old (Grabherr et al. 1978; Reisigl and Keller 1987).

The results presented in this paper may be regarded as first symptoms of site recovery within only a decade or so after restoration. The time frame coincides rather well with the "deadline" for appearance of the first signs of restoration success (Jackson et al. 1995). The present study demonstrates that ecological restoration leads to accelerated development of self-sustaining vegetation and increase of species diversity. We strongly suggest that soil seed bank studies be included as an important component of planning and implementation of restoration (Pywell and Putwain 1996) and also in post-restoration monitoring.

Professor Elias Landolt greatly helped with phytosociological relevés and determination of seedlings. Anita Hegi took exceptional care of the samples throughout the trial. Free transport offered by Jakobshorn Bahnen AG, Davos, is gratefully acknowledged. Constructive remarks of an anonymous reviewer greatly improved the manuscript.

Zusammenfassung

Samenbanken im Boden der 1985 bzw. 1987 auf einer Skipistenplanierung (rund 2500 m ü.M.) installierten Renaturierungsflächen wurden etwa zehn Jahre danach in Herbst- und Frühjahrproben untersucht. Dies ist der erste Bericht über die Entwicklung des Samenvorrates im Boden nach der Renaturierung eines hochalpinen Standortes.

Die mittlere Dichte des keimungsfähigen Anteils der Samenreserve in Herbstproben aus elfjährigen Versuchsflächen betrug 916±210 Samen pro m^2; der entsprechende Wert in den zwei Jahre jüngeren Flächen erwies sich als etwas niedriger (611±333 Samen pro m^2). Nach der Schneeschmelze im folgenden Frühjahr wurde in Proben aus älteren Flächen eine Dichte von 698±270 Samen pro m^2 beobachtet, während jene in jüngeren Flächen auffällig hoch war (3580±1701 Samen pro m^2). Die Verteilung der Samen in den Proben war sehr verklumpelt.

In den Herbstproben bestand der keimfähige Anteil der Samenreserve aus sieben bestimmbaren Arten; zwei weitere Arten wurden nach Abschluß des Keimungsversuches als ungekeimte Samen gefunden. In den Frühjahrproben traten lediglich vier identifizierte Arten als Keimlinge auf, und es wurden keine weiteren Arten unter den ungekeimten Samen gefunden. Die Samenreserve im Boden war durch die folgenden Merkmale gekennzeichnet: (1) Es traten vorwiegend die eingewanderten Arten auf; (2) die Arten in der Samenreserve entsprachen nur teilweise der Pflanzendecke der jeweiligen Versuchsflächen, und (3) die Häufigkeit der Arten in der Samenreserve war nicht gleich der Arten-Häufigkeit in der Pflanzendecke.

Die im Boden der Versuchsflächen gefundene, innerhalb von etwa zehn Jahre nach der Renaturierung gebildete Samenreserve kann sowohl in Bezug auf die Ansammlung der Samen wie auch auf die Erhöhung der Artenvielfalt als ein wichtiges Zeichen der aktiven Populationsprozesse in den Versuchsflächen betrachtet werden.

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