

Effects of red deer on secondary succession in the Swiss National Park.



Key words: Secondary succession, SNP, Red deer (*Cervus elaphus*), vegetation monitoring, seed production, seed bank.

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Abstract

In the Swiss National Park (SNP) the secondary succession proceeds very slowly on abandoned cattle pastures after the foundation of the Park in 1914. A lack of seeds of late successional species in the seed bank of early successional vegetation stages could be an important reason for this observation. In this study we therefore investigated the seed bank dynamics on the former cattle pastures in the SNP and the eventual role of red deer on this seed banks by removing inflorescences and modifying local seed production or by import of seeds via dung. Red deer are today the most important ungulate in the SNP and re-immigrated into the area shortly after the Park foundation.

We conducted an exclosure experiment and compared the composition of the vegetation, local seed production and seed bank composition in the protected area inside of permanent exclosures with unprotected reference plots outside of the exclosures. We found that late successional species are lacking in the seed banks of the pastures in the SNP. The input of late successional species through the dung of red deer seems to be negligible as no significant difference was found between the protected and unprotected plots. Though red deer did have an effect on the amount of inflorescences by preferring plant species of early successional stages, this behaviour did not alter the composition of the seedbank between protected and unprotected plots.

Introduction:

In the area of the Swiss National Park (SNP) cattle and sheep were grazing for several centuries (Parolini 1995). As a result, distinct spatial patterns developed on subalpine pasture areas. Nutrients were e.g. enriched around cattle resting places and stables (Schütz et al. 2006) and enabled tall-herb and meadow communities to develop (Achermann 2000). With the foundation of the SNP in 1914, the grazing regime changed dramatically: cattle and sheep pastures were abandoned, but red deer (*Cervus elaphus* L.) re-immigrated into the area (Haller 2002). While the herded cattle was forced to graze in large areas, the wild red deer (in particular hinds) preferred to graze in the nutrient-rich small areas of the former cattle resting places. These distinct grazing patterns still exist today (Leuzinger 1999), i.e. red deer grazing is still determined by former agricultural use of the pastures (Schütz et al. 2003). In their preferred grazing sites, red deer were driving succession from agricultural tall-herb and meadow communities towards short-grass pastures with red fescue (*Festuca rubra*: Nomenclature after Lauber and Wagner 1996) as the dominant species (Achermann 2000, Schütz et al. 2003). The much larger nutrient poor parts of the former cattle pastures remained almost ungrazed by red deer and vegetation did not change since the Park foundation (Stüssi 1970). The development of the vegetation in the SNP is very well known, since vegetation monitoring started in 1917 on permanent plots (Braun-Blanquet 1931, Grämiger and Krüsi 2000). The main reason for this vegetation survey was to demonstrate the rapid encroachment of trees on the former cattle pastures (Braun-Blanquet 1931). The sites chosen in this study are located on pastures which are as early in succession as possible. However, all the cattle pastures are still almost completely free of trees (Risch et al. 2001). Apart from the development of agricultural tall-herb and meadow communities towards short-grass pastures (early successional stages), succession in general proceeded very slowly in the whole SNP from these heavily grazed short-grass through rarely grazed tall-grass pastures and mountain pine forests to stone pine/larch forests (late successional stages), Schütz et al. 2000a, Wildi and Schütz 2000, Risch et al. 2004). This observation gave rise to fears that the whole succession and forest regeneration in particular, might be negatively affected by deer activities (e.g. Blankenhorn et al. 1979). However, several studies found no negative correlations between both tree regeneration in forests and tree encroachment on pastures with increasing numbers of red deer, suggesting that in the SNP other factors are responsible for the slow succession and tree encroachment in open areas (Bigler 1997, Sieber 2000, Krüsi and Moser 2000).

One of these other factors could simply be seed limitation. Especially the lack of late successional (LS) species in the seed rain or soil seed bank at early succession (ES) sites. In general, two possible pathways for seed bank dynamics during succession can be distinguished: i) the seed bank is mainly composed of early successional species during the whole succession and ii) the seed bank composition varies according to the changing vegetation (Bossuyt and Hermy 2004). In the first case, early successional species produce many persistent seeds, which remain present in the soil even after the species disappear from the vegetation. Seeds of ES species may also arrive during LS stages (by wind or animals). If LS species produce less and less persistent seeds, total viable seed density will decline with time as a result of seed senescence and decreasing seed input. Consequently, species of the first successional stages will remain dominant in the seed bank. In the second case, early successional species disappear from the seed bank as they disappear from the vegetation and the seeds of species appearing later in the succession gradually become incorporated in the soil. As a result, both seed density and species composition in the seed bank follow the changes in species composition in the vegetation. Which pathway the seed bank assembly follows during succession depends on the ratio of seed persistence characteristics (Reiné et al.

2004) and seed arrival (by local production and dispersal) between early and later successional species (Bossuyt et al. 2002).

Large herbivores may have a significant effect on soil seed banks. They can reduce local seed production by the direct removal of flowers and seeds (Sternberg et al. 2003). However, they can also be an important seed predator and seed source since they can transfer seeds endo and exozoochorously (Malo and Suarez 1995; Mouissie et al. 2005) over large distances, due to their large home ranges (VonOheimb et al. 2005). Since red deer consume about one third of their daily diet in the forests of the SNP (Suter et al. 2004), they could potentially be important vectors that transfer seeds of LS (forest) species into early succession stages (pastures) and vice-versa (Bokdam 2003, thesis).

In order to study the role of i) seed bank composition in secondary succession of the SNP and ii) the effects of red deer altering seed bank composition in early successional sites, we selected six exclosure sites, each established 20 years ago in ES sites. By comparing the composition of i) the vegetation, ii) the local seed production, and iii) the local seed bank in the protected area inside the exclosures with the unprotected areas of reference plots outside the exclosures, we want to address the following hypotheses:

- 1) Succession proceeds very slowly in the Swiss National Park due to missing seeds of late succession species in the seed bank of early vegetation stages.
- 2) Ungulates and in the study area red deer in particular stimulate succession by altering the composition of the seed bank by input of late successional species via dung and reduction of inflorescences of early successional species by grazing. If so, both the local seed production and the local seed bank are significantly different inside ungulate exclosures compared to unprotected reference plots outside the exclosures.

Methods:

Study area:

The SNP (Swiss National Park) is located in the south eastern part of Switzerland. The Park has a size of 170 km². 50 km² are comprised with forests, of which almost all is coniferous, 33 km² alpine and 3 km² subalpine grasslands. The other half of the park is covered with ice, snow and rocks (Schutz et al 2003). It's elevation extends from 1500m.a.s.l. to 3170m.a.s.l. . Over the last two decades, about thirty permanently installed exclosures were built in the SNP (Langenegger 2004). Mesh size measures 20cm x 20 cm.

In our study we collected data from 6 exclosure sites (Table 1): Il Fuorn, Stabelchod 1, Stabelchod 2, Trupchun (NP32), Grimmels, Channels. Channels and NP32 are located in the valley of Trupchun, the others in the valley of Il Fuorn. The six sites are chosen in a way that they differ from each other in grazing intensity, dung density and characteristics of vegetation in order to represent as many different grassland ecosystems of the Park as possible.

Table 1: View of permanent exclosures (Langenegger 2004, modified)

Name	Characterization	Elevation	Exclosure size (m x m)	Co-ordinates X/Y	year of establishment of exclosure
Il Fuorn	Short-grass pasture	1800	6x6	811890 / 171750	1984
Stabelchod 1	Short- to tall-grass pasture	1908	6x6	814290 / 171385	1984
Stabelchod 2	Short- to tall-grass pasture	1908	4x4	814655 / 172125	1984
Trupchun (NP32)	Short- to tall-grass pasture	2130	12x20	798825 / 165825	1992
Grimmels	Short-grass pasture	2000	4x4	810225 / 171875	1984
Channels	Short- to tall-grass pasture	2140	12x25	801830 / 164775	1992

Composition of the vegetation:

The composition of the vegetation was assessed in June and July 2006. Inside and outside of each exclosure, 5 relevés, 1m x 1m, were sampled systematically (Fig. 1). The 5 relevés outside of the exclosure are located 20 meters away from the fence, except from Grimmels and Stabelchod 2, where the distance measures 5 meters. In each plot all plant species were recorded and the percentage cover of each species was estimated.

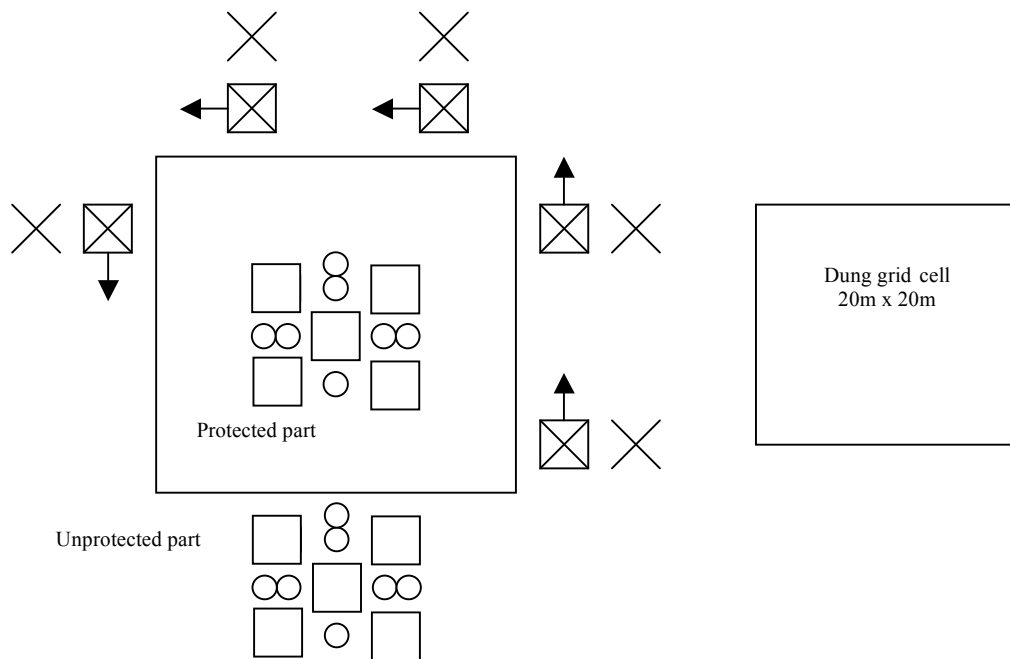


Figure 1: Experimental design..

□ = Relevé plots, ○ = Sampling of soil cores ⊠ = fenced plot for grazing × = reference plot

Composition of the seed bank:

Inside and outside of each enclosure, 7 soil samples were taken systematically between the vegetation plots by the end of May 2006.(Fig. 1). The soil core diameter measured 4.8cm and the depth 10 cm (soils in the park are mainly shallow). Total sampled area = 127 cm² per site/treatment. All of the soil samples were sieved with a mesh width of 4mm, removing coarse and fine soil material, roots and vegetative parts.

The samples were spread in thin layers (+/- 2mm) on trays and exposed in the greenhouse. A fleece cloth separated the soil samples from the sterilized substrate. Soil moisture was controlled daily and watering was done manually if necessary. The light regime followed the natural long-day cycle from beginning of June until half of September. Three control trays with sterilized substrate were also placed in the greenhouse but no contamination was found. Seedlings were identified, counted and removed as soon as possible after germination. The ones which could not be identified were transplanted in other pots to make sure that there was no competition for germination of the seedlings.

Local seed production:

To estimate local seed production, we recorded inflorescences for each plant species separately end of July and end of August. This was done again at all 6 sites for protected and unprotected area, in each vegetation relevé plot (Fig. 1).

Grazing intensity:

To estimate the grazing intensity at the different sites, the moveable cage method described by McNaughton et al. (1996) was used. Each month the vegetation was clipped down at each site, to 1.5 cm at 5 protected plots and on 5 unprotected reference plots, each with a surface of

1m². Then the plots were moved to be able to count for compensatory regrowth. This was done with a sequence of 4 weeks, i.e. end of June, end of July and end of August. The clipped material was collected and dried to constant weight at a permanent temperature of 105°C. Adding up the harvest from all of the five protected plots over the growing season and comparing it to the unprotected reference plots provided information about the intensity (expressed as gram dry weight year⁻²) of red deer grazing.

Dung density:

The number of faecal-pellet groups was counted on a plot of 20m x 20m outside of each enclosure (Fig. 1). End of May old faeces were cleared off. Since red deer doesn't graze on these sites during winter time, new faeces were counted from the end of May till half of September. Yearly dung input was estimated using a linear regression (Acherman 2000) of the number of faecal-pellet groups (x) on dung dry weight (y).

$$y = 274.9x + 142.06$$

Data handling

All three datasets on i) the composition of the vegetation, ii) the composition of the locally produced seeds, and iii) the composition of the seed bank consisted of 12 relevés each, one relevé inside and one relevé outside of each of the six enclosures. We calculated centroids of average cover of the five plots inside and the five plots outside of each enclosure to generate vegetation relevés. Frequency centroids were calculated for seed production relevés while seed bank relevés consisted of the number of seedling per recorded species from 1 l of soil from inside and outside of each enclosure.

To determine the succession age of each relevé, we applied the method described in Schütz et al. (2000a). Each present plant species is multiplied with a species probability table. This means the probability of a plant species to appear in a certain successional stage. All the plant species for each site/treatment are grouped and the overall probability to appear in a successional stage is calculated. By calculating the Euclidean distance between our own calculated successional ages and the successional ages out Schütz et al 2000, the succession age is determined. The succession age bases on succession models developed for the SNP (Schütz et al. 2000a, Wildi and Schütz 2000), which have been derived from data of the permanent plots established after the foundation of the Park (Braun-Blanquet et al. 1931). The models demonstrate how vegetation patterns on resting and feeding places caused by former cattle use of the pastures will develop back into forest vegetation. In this study, we distinguish two main succession stages, early and late. In the early stage, we comprise remnants of the former agricultural use of the pastures, such as tall-herb communities on former cattle resting places and meadow communities (Achermann 2000). Driven by heavy grazing impact of red deer, these nutrient-rich agricultural communities developed into still nutrient-rich short-grass pastures (Schütz et al. 2000, 2006), which we include in the early succession stage. Nutrient-poor communities developed by nutrient removal by cattle and red deer including rarely grazed tall-grass pastures and all forest communities, belong to the late succession stage (Schütz et al. 2000a, Wildi and Schütz 2000, Risch et al. 2004).

Statistical analysis

All statistical analysis were done with the free software package "R".(R Development Core Team. 2004)

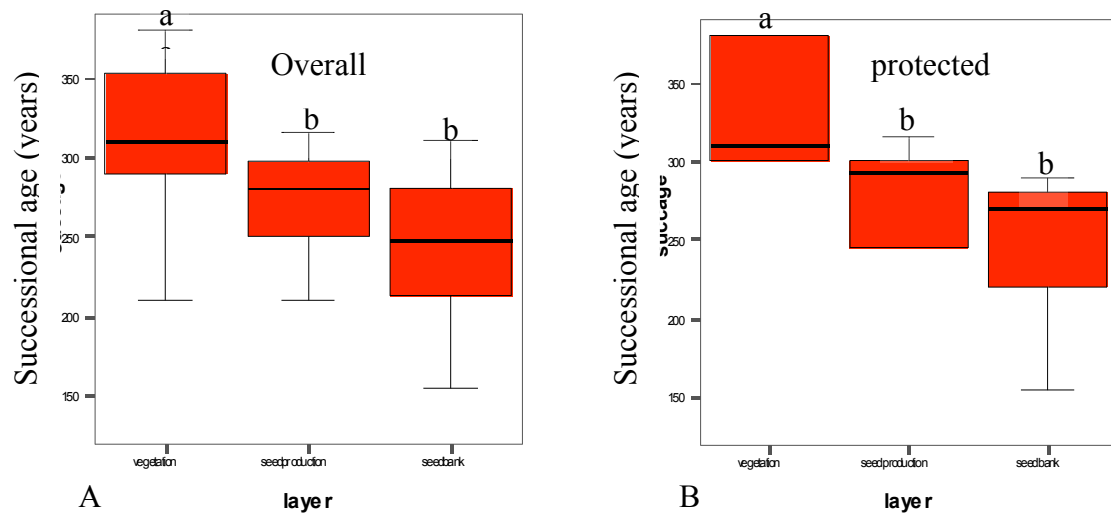
Differences in grazing treatments (= inside vs. outside enclosures) and between the three layers (vegetation, seed production, seed bank) in function of the response variable “successional age” were tested with a repeated measures ANOVA. In the formula we used an error term for the different layers per enclosure.

One way ANOVA, followed by a post hoc tukey test was used to test for significant differences between layers. Two way ANOVA, followed by a post hoc tukey test was used to test for interactions between grazing treatment x layers. Regression analysis was applied to study the relationship between grazing intensity and layers, and dung density and layers outside of the enclosures.

Results

Layer effect

We found highly significant ($p < 0.001$) differences in successional age between the three layers composition of the vegetation, the locally produced seeds and the seedbank. The succession age of the vegetation is the highest with 303 years, followed by the succession age of the produced seeds (265 years) and the seed bank (241 years, Fig. 2a).



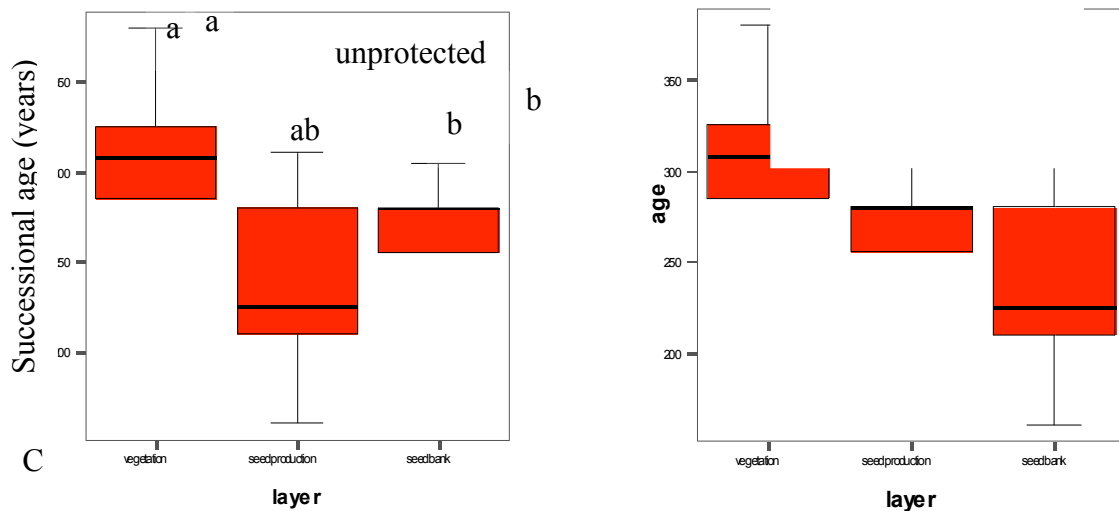


Figure 2: Boxplot diagram of succession ages of the three layers for the overall data (A), for the protected plots inside the permanent exclosures (B), and for the unprotected plots outside the permanent exclosures a,b=data with different letters are significantly different at $p<0.05$.

These patterns in succession age are based on differences between the vegetation and the seed production layer ($p<0.05$) as well as on differences between the vegetation and the seedbank layer ($p<0.05$). However, there are no significant differences in succession age between seed production and seed bank layer. This result reflects exactly the patterns in succession age, which we found inside the exclosures in protected samples (Fig. 2b). In unprotected samples outside the exclosure, however, the patterns were slightly different (Fig. 2c): we only found significant differences between vegetation and seedbank layers ($p<0.05$) but no differences between vegetation and seed production layer.

On the species level, many of these observed patterns become even more obvious, since each of the three layers has its specific characteristics. Out of the 127 plant species found over all the layers, 123 species were recorded in the vegetation relevés, 98 species produced seeds and only 56 species were recorded from the seedbank. Whereas 89 out of the 127 plant species were found in low frequencies in any of the three layers, i.e. are of less importance for explaining the patterns mentioned above, 38 species showed high frequencies at least in one of the layers. 14 plant species are common in all the layers, i.e. they were found in many vegetation relevés, produced inflorescences in a similar number of plots and were also found in many seedbank samples. In this group, species that are characteristic for early succession stages dominate over species from later stages. With *Phleum pratense* and *Cerastium caespitosum*, we found two species that represent meadow communities, the remnants of the former agricultural use of the pastures. A second group comprising 13 species were often found in the vegetation and in the seed production layer, but was almost missing in the seedbank layer. This species group is characterised by species of the tall-grass pastures such as *Elyna myosuroides* or *Sesleria coerulea*, which belong to the late succession stage. In the third group of important species, which was only reported from the vegetation, but neither from the seed production nor from the seedbank layer, plants that are characteristic for forest communities such as the tree species *Pinus mugo* or the dwarf shrub *Polygala chamaebuxus* were found. This group comprises 11 plant species.

Grazing effect

Comparison of the successional age of each layer separately between the protected versus the unprotected plots, did not reveal any significant differences ($p > 0.05$). This highly remarkable result is also reflected on the species level: in the vegetation relevées 107 plant species were for example found in the protected plots and almost the same number (103 species) in the unprotected plots. For the species, which produced inflorescences this was respectively 84 in the protected and 89 in the unprotected area. For the seed bank 48 species were found in protected and 49 in the unprotected part.

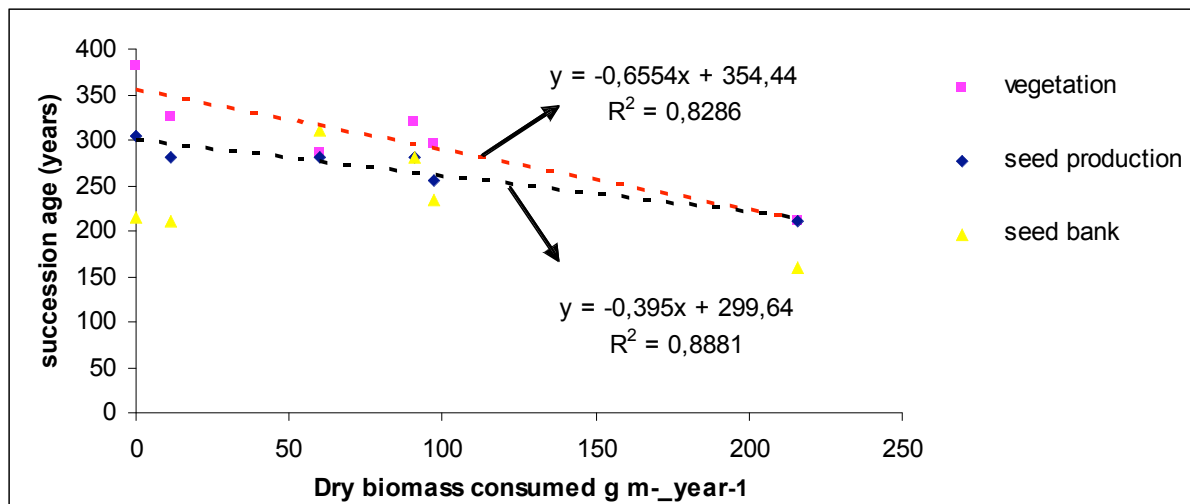


Fig 3: Linear regression of successional age of the three layers vegetation, seed production and seedbank in dependence of dry biomass ($\text{g m}^{-2} \text{ year}^{-1}$) consumed by red deer.

We also tested the relation between successional age of the different layers and grazing intensity with a linear regression model (Fig. 3). The relation between successional age of the vegetation and grazing intensity is significant ($p=0.01$)

With increasing successional age of the vegetation, consumption is decreasing, i.e. red deer prefer to graze in earlier successional stages. The highest grazing intensity $215 \text{ g consumed dry biomass m}^{-2} \text{ year}^{-2}$, was measured at il Fuorn with an age of 210 years. On Channels, in contrast, there was no consumption at all and the successional age of the vegetation was with 380 years much older. Consequently, the composition of the vegetation of the two study sites il Fuorn and Channels is quite different: out of 78 species, only 20 plant species were found on both sites, 39 plant species were recorded from il Fuorn but not from Channels. 19 plant species appeared on channels, but not on il Fuorn..

The relation between the successional age of seed production and grazing intensity is significant as well ($p=0.004$). At the highest grazing intensity, the successional age of the produced seeds is 210 years (il Fuorn), at the lowest grazing intensity 305 years (Channels), i.e. we found again a negative relationship. On il Fuorn only 28 plant species which produced inflorescences were found compared to 42 at Channels. Only seven plant species, which produced inflorescences appeared on both sites. The total number of inflorescences is markedly lower at high grazing intensity compared to sites with lower grazing intensity, i.e. many inflorescences are consumed by red deer. In addition, red deer seem to prefer inflorescences of species that represent earlier successional stages since the difference between the successional age of the vegetation and the seed production decreases with increasing grazing pressure.

For the successional age of the seed bank, no significant relationship with grazing intensity was found (Fig. 3, $R^2=0.07$, $n=6$, $p=0.46$).

Since seed input by dung could be an important source for the seedbank, we compared the successional age of the seed bank with the dung density in a linear regression model. The model, however, showed no significant correlation ($R^2=0.05$, $n=6$, $p=0.32$).

Dung density is significantly correlated with grazing intensity ($R^2=0.83$, $n=6$, $p=0.03$), i.e. we found highest dung density at the site of il Fuorn (36.1 g dung dry weight $m^{-2} year^{-2}$), the lowest at the site of Channels (0.01 g dung dry weight $m^{-2} year^{-2}$). The number of pellet groups on il Fuorn and Channels were respectively 52 and 1.

Discussion

Potential errors. Reliability of the results

The conclusions about the grazing effect of the red deer is only based on the last 20 years. The average age of establishment of the exclosures is 20 years old. It is e.g. possible that persistent zoochorous plant species are present in the soil from before the establishment of the exclosures. Also the effect of e.g. rodents is not excluded as the mesh size measures 20 x 20 cm. On 2 out of 6 sites, the plots outside are only 5 meters far from the fence. This means that rodents could forage during the night on the plots and influence e.g. the seed production.

Hypothesis 1: Pathway, Layer effect

In general two possible pathways for seed bank dynamics during succession can be distinguished: i) the seed bank is mainly composed of early-successional species in all successional stages or ii) the seed bank composition varies according to the changing vegetation (Bossuyt and Hermy 2004).

In our study the vegetation represents an older successional stage than the seed bank and seems to follow the first pathway. Seeds of species of late successional stages were in confirmation with our hypotheses completely missing in the seedbank. This could therefore be a possible reason for the slowly proceeding succession observed in the SNP after abandonment of the pastures (Schütz et al. 2000, Wildi and Schütz 2000, Risch et al. 2004). Similar results are also reported from numerous other grassland studies, which compared the similarity between the aboveground vegetation and the soil seed bank (Falinska 1998; Amiaud et al. 2004, Diaz et al. 2003, Bekker et al. 2000). Funes et al. (2003) found that the similarity between the composition of the seed bank flora and that of the established vegetation in tall tussock grasslands was low throughout an altitudinal gradient in the mountains of central Argentina. Another high altitude study conducted by Marage et al (2006) pointed in an opposite direction. They found that similarity of seed bank and vegetation was low in early succession but increased with proceeding succession. Also studies conducted in mixed prairie vegetations found the same dissimilarity between vegetation and seed bank (Romo et al 2004). It seems to be a general pathway that similarity between seed bank and vegetation is general low in grasslands. Other factors than successional stage may play a role in the similarity. Similarity and dissimilarity is also found to be susceptible to the season and seasonal conditions. (Kemeny et al 2005). Some studies found that the similarity in the seed bank was higher in autumn than in spring, as the seed rain is concentrated in autumn. Hereby we can ask if they measured the seed bank or if there is influence due to the seed rain on the ground.

Explanation of the pathway

A reason (causal mechanism) for the observed pathway could possibly be found in different reproduction strategies of plant species of early succession stages compared with species from later succession stages. The species from early succession stages (see appendix) produce in general many but small seeds (Grime 1979), which persist in the soil even after the disappearance of the respective species from the vegetation (Bossuyt and Hermy 2004). Very well known hereby is the strategy of the ruderals. Succession starts by definition after a disturbance event (e.g. Grime 1979), (in our case the sudden release from livestock grazing , followed by an increasing Red deer grazing). Disturbances create gaps and these gaps are usually quite fast closed by ruderals. The ruderals consist mostly out of herbs with a rapid growth rate but the longevity of the established phase is very short because most of the annual production is devoted to seeds. The flowers are produced in the early life-history and are marked by a high frequency of flowering. The main regenerative strategies of the ruderals are i) seasonal regeneration in vegetation gaps, ii) numerous small wind-dispersed and zoochorously dispersed seeds or spores and a ii) persistent seed bank (Grime 1979, Graham and Hutchings 1988a, Graham and Hutchings 1988b). The ruderals which establish during secondary succession are recruited from the seed bank since they form in many ecosystems the main part of the seedbank or seeds from ruderals are the first to arrive in primary succession Grime 1979).

In high alpine ecosystems (altitudinal range 1800-2150m) ruderals do not play an important role since the vegetation period is too short for this strategy. However, though ruderals (or annuals) are almost completely missing in our ecosystem, species of early succession stages are still dominant in the seed bank in the study area (see appendix). Our ES species represent the tall herb and meadow communities, i.e. so called competitors. This is in contrast to most other studies, in which ruderals are the main species of early stages and not competitors. In later stages our competitors are replaced by stress-tolerators. Later successional (e.g. Swiss stone pine, European larch) species produce generally less but larger seeds and they are less persistent.

There are many different events (e.g. spatial dynamics, seed migration), in the course of time, which influence composition and amount of seeds in the soil (Falinska 1998). The soil seed bank will be assembled as a result of the balance between seed input, local seed production or seed rain, seed dispersal- and seed output, i.e. seed germination, decay and predation (Bossuyt and Hermy 2004).

Hypothesis 2: Grazing (Exclosure) effect

No difference between protected and unprotected soil seed banks was found in our study. We expected to find a difference between the protected soil seed bank inside of our permanent exclosures compared to the unprotected soil seed bank outside of the exclosures. We expected that red deer would have had an impact on the soil seed bank because many studies revealed interactions between seed bank dynamics and large herbivore activities. Ungulates grazing activities showed relations with pre-dispersal seed predation and long-distance seed dispersal (Wang and Smith 2002) and may affect rodents density and related post-dispersal seed predation (Smit et al 2001). Grazing can reduce seed production of plants by affecting the allocation of plant resources for reproduction due to reduction of photosynthetic surface and by the direct removal of flowers and seeds (Sternberg et al 2003). Under heavy grazing, the removal of reproductive structures may even lead to situations in which seed banks become a limiting factor for the recovery or persistence of the palatable vegetation (Benjamin and Sanderson 2000; Sternberg 2003). Studies have consistently shown that grazing changes

the relative abundance of species in the seed bank, indicating that grazing causes a persistent change in the vegetation. (O'connor and Pickett 1992; Meissner and Facelli 1999; Kinloch and Friedel 2005). Red deer in the SNP stays in the forest during the day due to disturbance by visitors and 30% of the total food intake consists of forest species (Suter et al. 2004). Since a substantial quantity and range of seeds are dispersed by large herbivores in grassland ecosystems (Malo and Suarez 1995; Pakeman et al. 2002, Myers et al. 2004; Cossyns and Hoffmann 2005; Mousissie et al. 2005; von Oheimb et al. 2005), we expected that many forest species, i.e. late successional species, would be dispersed by dung into our unprotected plots. We expected therefore to find more late successional species outside of the enclosure as studies demonstrated that large herbivores dung could be an important seed source for plant colonisation in grasslands (Welch 1985; Malo and Suarez 1995b; Pakeman et al. 1999).

Explanation for the absence of the expected effect

There are several possibilities why the forest species, which we expect to be in the dung, are not able to move towards the soil seedbank: i. they are not ingested. ii they cannot survive the digestive tract (Von Oheimb 2005),... it could be that the seeds of late successional species are not persistent (Grime 1979), ii) seeds are not able to move towards the soil because there are not enough gaps available (Kohler F. et al 2006), iii) post-dispersal predation of late successional species is high (Chambers et al 1994) (iiii) too much late successional seeds get crushed and damaged in the mouth of red deer.

In addition to the expected seed input of late successional species by dung, we also expected that grazing activities of red deer outside of our enclosures would reduce seed production and local seed rain of early successional species, since red deer prefer to feed on early successional species (Achermann 2000). We expected that this impact would enhance the differences in the soil seed bank between protected and unprotected plots, i.e. the successional age of the seedbank would further increase on unprotected plots outside the enclosures. Indeed, heavy grazing pressure reduced inflorescences of early successional species in our study. However, this reduction in inflorescences had no significant impact on the soil seedbank. One possible reason is that the inflorescences are reduced by grazing but density of seeds increases in the inflorescences. Plant species which are partially grazed produce more seeds as a defence strategy and have a lower abortion rate of flowers and fruits compared to ungrazed plants. (Fang XW et al). i.e the influence of grazing on the seed production is lower than we expected. Another explanation is that the ingested ES seeds are excreted in dung, and transferred to the local soil seedbank.

Recommendations for further research

As mentioned above, there could be many reasons why seeds of late succession are not able to move towards the soil seed bank. i) seeds are not ingested or transported by red deer, ii) seeds do not survive the passage through the digestive tract, iii) seeds get predated after their dispersal (iiii) or seedlings of late successional species are consumed immediately after germination.

Further useful research could focus on those reasons e.g. the content of the red deer dung in order to assess the contribution of these animals on the dispersal of late-successional species. Also a seed sowing experiment can learn us if seed limitation is the problem or if it is a problem of seed germination or a lack of gaps in the vegetation.

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