

Zeitschrift: Bulletin of the Geobotanical Institute ETH
Herausgeber: Geobotanisches Institut, ETH Zürich, Stiftung Rübel
Band: 67 (2001)

Artikel: Spatially specific simulation of the long-term development of a subalpine pasture in the Swiss National Park
Autor: Risch, Anita C. / Krüsi, Bertil O. / Grämiger, Helena
DOI: <https://doi.org/10.5169/seals-377836>

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 23.12.2025

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

Spatially specific simulation of the long-term development of a subalpine pasture in the Swiss National Park

ANITA C. RISCH, BERTIL O. KRÜSI, HELENA GRÄMIGER & MARTIN SCHÜTZ

Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland;
anita.risch@wsl.ch

Summary

1 Due to economic pressure on agriculture and forestry, more and more areas in the mountainous regions of Europe will no longer be managed. In the Swiss National Park (SNP), this process started in 1914 when all agricultural, silvicultural and hunting activities were abandoned. Understanding the concomitant changes in vegetation at the landscape, ecosystem and species levels is crucial for pinpointing undesired developments and designing effective remedial actions.

2 In this study, a general succession model for grassland vegetation within the SNP was modified to simulate the development of the small-scale patterns of vegetation and plant species diversity on a small subalpine pasture in the SNP for the period from 1900 to 2500. The simulation was based on both present and historic data on the abundance of vascular plants, micro-relief and grazing intensity by red deer (*Cervus elaphus* L.). Present-day vegetation data consisted of 149 relevés on systematically arranged 1-m² plots. Historic data and vegetation maps dating back to 1917 allowed a detailed calibration of the model.

3 Our results show that on the whole, the pace of succession is extremely slow. In order to accurately model the past development, the succession rate proposed by the general succession model had to be increased or decreased, depending on the microrelief and on the grazing intensity observed in 1998. Our calculations predict that by the year 2500, plant species associated with the herb layer of mountain pine forests will be predominant on 98% of the area sampled, even though the trees will not yet form a closed canopy.

4 Between 1917 and 1998, the total number of vascular plant species present on the pasture increased by 50%, despite the massive re-immigration of red deer into the area and the associated high grazing pressure. According to the model, maximum diversity will be reached in the year 2200 with twice as many species as in 1917. Between 2200 and 2500 the number of species will slightly decrease to a level still significantly higher than today. A more substantial decrease in the number of vascular plant species, e.g. to the level observed in 1917, will probably only occur once the trees form a closed canopy.

Keywords: biodiversity, *Cervus elaphus* L., long-term succession, space-time model, subalpine grasslands, Swiss National Park

Bulletin of the Geobotanical Institute ETH (2001), 67, 27–40

Introduction

In many mountainous regions of Europe traditional agricultural and silvicultural systems are no longer economically viable (Price 1995; Bätzing 1996; Rieder 1996; Broggi 1998). Thus, large areas will be used less intensively or will be abandoned completely, while others will be exploited more intensively. Studies concerning potential impacts of increased agricultural and silvicultural activities on ecosystems are quite numerous (e.g. Pohl 1996), but few studies have dealt with how a reduction in intensity of management affects the diversity of ecosystems and landscapes in mountain areas.

A number of studies on succession in subalpine grasslands have been performed in the past (Braun-Blanquet 1931; Stüssi 1970; Cernusca 1989; Hegg 1992; Krüsi *et al.* 1995; Krüsi *et al.* 1996; Chapin & Körner 1998; Achermann 2000; Schütz *et al.* 2000a,b,c). Spatially detailed succession studies, however, are extremely rare. In order to be able to assess how land abandonment will affect the future development of mountain regions, it is crucial to understand the successional processes of the main ecosystems in these areas.

In the Swiss National Park (SNP) all grazing by sheep and cattle stopped when the Park was founded in 1914. During the subsequent 80 years former pastures were allowed to develop without any human interference. As of 1914, the successional development on the pastures was affected only by the steadily increasing number of wild ungulates, mainly red deer (Krüsi *et al.* 1995, 1996; Achermann *et al.* 2000; Schütz *et al.* 2000c). Fortunately, monitoring of the vegetation development started right after the foundation of the Park. Over time, more than 160 permanent plots were established on which vegetation relevés were made approximately every ten years (Stüssi 1970; Grämiger & Krüsi 2000). In ad-

dition, ungulate populations were counted every summer (Schloeth 1972).

The knowledge of vegetation patterns and processes within the Park was used to establish a general succession model for the Park's grasslands (Schütz *et al.* 2000a,b; Wildi and Schütz 2000), further referred to as the SNP-vegetation-model, simulating the development from tall herb communities (resting places on the abandoned cattle pastures) to forests dominated by mountain pine. Until now, however, the model has never been applied to or tested on any specific pasture or area in the park. The goal of this study was to simulate the potential long-term vegetation change in space and time on one particular subalpine pasture, Plan Praspöl, using detailed local vegetation data and the SNP-vegetation-model. Further, we examined if the simulation could be improved by including into the model spatially detailed data on microrelief and grazing intensity. Using the calibrated and validated model, long-term change on Plan Praspöl was studied for the 600-year period between 1900 and 2500 in terms of (1) vegetation, i.e. small-scale spatial pattern of vegetation types or succession phases, (2) species abundance, i.e. relative average abundance of the 96 vascular plant species present on the pasture, and (3) floristic diversity, i.e. number of plant species present on the pasture studied.

Study area and methods

STUDY AREA

The Swiss National Park is located in the southeastern part of Switzerland and covers an area of approximately 170 km²; of these, 50 km² are covered with forests, 33 km² with alpine grasslands and 3 km² with subalpine grasslands. Ice, snow and rocks occupy the

other half of the Park area. The elevation ranges from 1350 to 3170 m.a.s.l. Between 1917 and 1998, the meteorological station located in the Park (Buffalora, 1977 m.a.s.l.) recorded a mean annual precipitation of 925 ± 162 mm and a mean annual temperature of 0.2 ± 0.7 °C. The study area, the subalpine pasture Plan Praspöl, is located at 1680 m.a.s.l. and covers an area of approximately 0.4 ha (co-ordinates 808.508/171.451). Up to 1910, Plan Praspöl was grazed by sheep (Parolini 1995). In 1917, Braun-Blanquet established a 3000-m² permanent plot, where floristic vegetation relevés were made once every ten years until present (Braun-Blanquet 1931; Braun-Blanquet *et al.* 1954; Grämiger & Krüsi 2000). Plan Praspöl is surrounded by subalpine spruce and mountain pine forests (*Piceetum subalpinum*, *Mugeto-Ericetum*) (Kurth *et al.* 1960; Campell & Trepp 1968).

In addition to the vegetation, ungulates in the Park were also permanently monitored. Chamois (*Rupicapra rupicapra* L.) and roe

deer (*Capreolus capreolus* L.) were already there when the Park was founded. Shortly after 1914, red deer (*Cervus elaphus* L.) began to re-colonise the Park, and since 1965 it has become the most important large herbivore in the area (Schütz *et al.* 2000c). Ibex (*Capra ibex* L.) were successfully re-introduced into the Park around 1930. Today, red deer have by far the greatest impact on vegetation on Plan Praspöl (Märki *et al.* 2000).

SAMPLING DESIGN

In the summer of 1998, a grid of 5 m x 5 m was established on Plan Praspöl covering the entire permanent plot established in 1917 by Braun-Blanquet (1931). At each of the 149 grid points, a vegetation relevé was made on a 1 m x 1 m plot, considered to represent the vegetation of the surrounding 5 m x 5 m plot. Species abundance was recorded in percent cover; nomenclature followed Hess *et al.* (1991). In addition, grazing intensity was estimated at each grid point based on vegetation

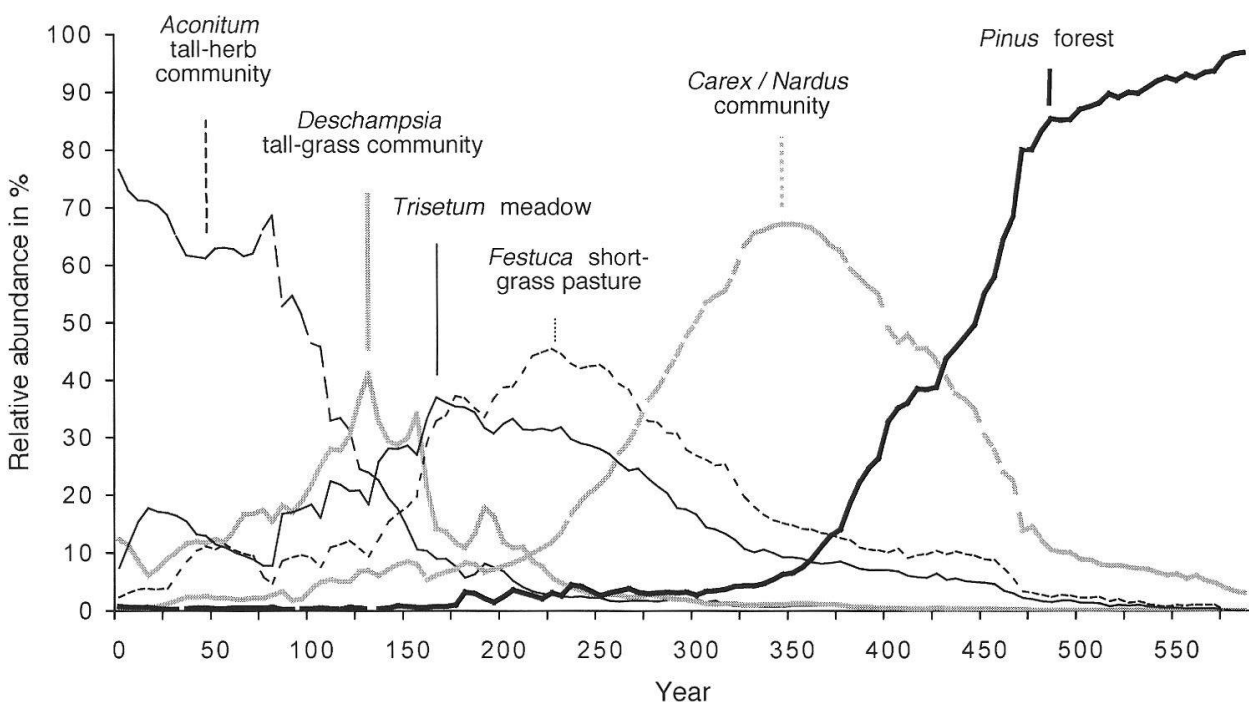


Fig. 1. The general succession model (SNP-vegetation-model) established by Schütz *et al.* (2000a,b) for all the grasslands of the Swiss National Park, based on a total of 456 original relevés from 59 long-term permanent plots.

height: high grazing intensity = vegetation height 2 to 5 cm, medium grazing intensity = vegetation height 5 to 10 cm, low grazing intensity = vegetation height 10 to 30 cm. Finally, relief position was recorded for each point as a means to estimate nutrient supply: convex or slope = relatively nutrient-poor, concave = relatively nutrient-rich, flat = intermediate nutrient supply.

THE SNP-VEGETATION-MODEL

The basis for establishing a space-time model for Plan Praspöl was the existing SNP-vegetation-model (Schütz *et al.* 2000a,b; Wildi & Schütz 2000). The model is based on 456 original relevés collected between 1917 and 1998 on 59 long-term permanent plots distributed over the whole area of the Park (Schütz *et al.* 2000a,b; Grämiger & Krüsi 2000). The SNP-vegetation model distinguishes six major succession phases or vegetation units, namely, in order of appearance, *Aconitum* tall-herb community, *Deschampsia* tall-grass community, *Trisetum* meadow, *Festuca* short-grass pasture, *Carex/Nardus* grassland and *Pinus* forest (Fig. 1). The succession of these six vegetation units describes the development from abandoned cattle pastures to forest over a time period of 585 years. The successional development of the vegetation during the 585 years covered by the model is described by 118 relevés, each representing a 5-year period.

VEGETATION PATTERN ON PLAN PRASPÖL

For each of the 149 vegetation relevés made on Plan Praspöl in 1998, the present successional stage, i.e. the succession year (1–585) in the SNP-vegetation-model was determined as follows: first, the relative presences of the six succession phases distinguished by the SNP-vegetation-model were calculated for each relevé, i.e. each *n*-species relevé was

transformed into a six-phases relevé. This was done (1) by multiplying the cover percentage of each species as recorded in 1998 (0–100%) by the relative importance (0–1) of that species in each of the six succession phases, (2) by summing up the resulting values for each of the six succession phases, and (3) by normalising the sums to 100 percent total cover. Second, each of the resulting 149 six-phases relevés was assigned to the 5-year period in the general SNP-vegetation-model to which it resembled most, using the statistical package Mulva-5 with the “van der Maarel” similarity coefficient as resemblance measure (Wildi & Orlóci 1996).

Once the 149 relevés made in 1998 had all been assigned to a 5-year period in the SNP-vegetation-model, for each plot, a first simulation of the past and future vegetation development was made, using the general SNP-vegetation-model. The results of this simulation were then compared with historic vegetation relevés (3000 m²) from 1917, 1927, 1938, 1947, 1958, 1975, 1979 and 1995 as well as vegetation maps from 1927 (Braun-Blanquet 1931) and 1947 (Stüssi 1970). In order to minimise the observed differences between simulated and historic data, the 149 plots were assigned to nine strata. The stratification was made based on the data on grazing intensity (3 categories) and relief position (3 categories) collected in 1998. Subsequently, for each stratum past succession was simulated using seven different succession speeds, namely 0.25, 0.5, 0.75, 1.00, 1.25, 1.5, and 1.75 times the rate of the general SNP-vegetation model (Risch 1999). The outcomes of these simulations were once again compared with the historic data (1) by calculating the “van der Maarel” similarity coefficient (Wildi & Orlóci 1996) between historic relevés (3000 m²) and the combination of the simulated relevés (25 m²)

of all 149 plots, and (2) by checking for each plot whether or not the historic vegetation maps from 1927 and 1947 corresponded to the simulated predominant succession phase, derived from the simulated relevés according to the procedure described above (Risch 1999). For each stratum the succession rate leading to the best fit between simulated and historic data was identified. These stratum-specific succession rates were then used to adjust the general SNP-vegetation-model to the specific conditions of the study area Plan Praspöl. With the adjusted model the development of the vegetation between 1917 and 2500 was then simulated for each of the 149 plots. Finally, vegetation maps of Plan Praspöl were constructed for different points in time by assigning to each point in space and time the predominant succession phase, derived from the simulated relevés according to the procedure described above.

SPECIES ABUNDANCE

Based on our adjusted successional model and on the 118 relevés describing the SNP-vegetation-model, expected species composition was calculated for each of the 149 grid points for each year in which relevés had been taken on Plan Praspöl, i.e. 1917, 1927, 1938, 1947, 1958, 1975, 1979 and 1998, as well as for every 50th year from 2050 until 2500. This simulation included only those 96 species of the SNP-vegetation model which are known to grow on Plan Praspöl or in the herb layer of the immediately adjacent forests. For each of these 96 species and for each of the above-mentioned years, cover values from the 149 simulated relevés were averaged. Subsequently, the cover values of each species were normalised by dividing them by the maximum value obtained during the simulated succession between 1917 and 2500. The

normalised values were compiled in a table showing for each species how its abundance changed during succession.

FLORISTIC DIVERSITY

Based on the relevés generated to describe the abundance of individual plant species during the simulated succession, it was possible to establish the total number of vascular plant species present on the pasture at different points in time. This was done for 1917, 1927, 1938, 1947, 1958, 1975, 1979 and 1998, as well as for every 50th year from 2050 until 2500. Again, only those 96 species were taken into account which (1) are present on Plan Praspöl or in the herb layer of the immediately adjacent forests and (2) which are considered in the SNP-vegetation-model. We calculated several regression models (linear, logarithmic and second-order polynomial) to (1) find the best fit between simulated and observed species numbers for the period from 1917 to 1998, and (2) to best describe the simulated development of the species number during the 600-year period covered by the model.

Results

VEGETATION PATTERN

In order to simulate the pattern indicated on the vegetation map of 1927 (Braun-Blanquet 1931), the rate of succession predicted by the general SNP-vegetation-model had to be decelerated or accelerated on some of the 149 plots, depending on grazing intensity and relief position (Table 1). The rate of change was found to be only half the one predicted by the SNP-vegetation-model on 98 plots in nutrient-losing (convex or slope) and flat relief positions subjected to high or medium grazing intensity. In contrast, on the 23 plots in nutrient-accumulating (concave) relief positions subjected to medium to low grazing intensity

Table 1. Factors by which the succession rates given in the general SNP-vegetation-model of Schütz et al. (2000a,b) had to be multiplied in order to obtain a spatially detailed simulation of the vegetation development observed on Plan Praspöl between 1917 and 1998. The relief-position "convex or slope" was considered to be conducive to nutrient loss, the position "concave" to nutrient gain.

		Grazing pressure		
		High	Medium	Low
Relief position:	Convex or Slope	0.5	0.5	1.0
	Flat	0.5	0.5	1.0
	Concave	1.0	1.5	1.5

the rate of change was 1.5 times higher. On the remaining 28 plots, succession proceeded as predicted by the SNP-vegetation-model (Table 1).

Adjusting the succession rate resulted in a marked increase in resemblance between simulated and historic data if the 149 plots were considered individually. Based on the original succession rate of the SNP-vegetation-model, only 66 of the 149 simulated relevés corresponded to the vegetation unit mapped in 1927 (Braun-Blanquet 1931), whereas 115 of the 149 simulated relevés showed the corresponding unit if the plot-wise adjusted succession rates were used. However, if the 149 plots were considered together (averaging cover values of species), the species composition predicted by the model with plot-wise adjusted succession rates was hardly more similar to the species composition actually recorded in 1927 (similarity coefficient = 0.586) than the species composition predicted without this adjustment (0.585). In conclusion, this means that, at a larger scale, there was no need to adjust the general SNP-vegetation-model. At the plot scale, however, succession could be modelled accurately only when the general SNP-vegetation-model was modified.

After adjusting the SNP-vegetation-model to small-scale patterns within the study area, the past and future development of vegetation

pattern on Plan Praspöl was simulated (Fig. 2). In the year 1917, the vegetation present on Plan Praspöl was a mix of the succession phases *Aconitum* tall-herb community, *Deschampsia* tall-grass community, *Trisetum* meadow and *Festuca* short-grass pasture. As of 1975, the *Aconitum* tall-herb community did no longer dominate any of the 149 plots, and the *Carex/Nardus* community had become the most prominent succession phase on some plots. In 1998, the two dominant succession phases were *Festuca* short-grass pasture and *Carex/Nardus* community. By 2200, according to the model, the study area will be dominated by *Carex/Nardus* community but the plant community typical for the herb layer of *Pinus* forests will already play an important role. In 2500, the herb layer community of *Pinus* forests will dominate on 98% of the plots, though remnants of all other succession phases will still be present. According to the model, in the year 2500, the relative presence of the six succession phases will be as follows: herb layer community of *Pinus* forest 87.0%, *Carex/Nardus* community 9.6%, *Festuca* short-grass pasture 2.0%, *Trisetum* meadow 1.2%, *Deschampsia* tall-grass pasture 0.1% and *Aconitum* tall-herb community 0.1% (Fig. 2).

SPECIES ABUNDANCE

Analysis of the development of the relative abundance of different plant species on the

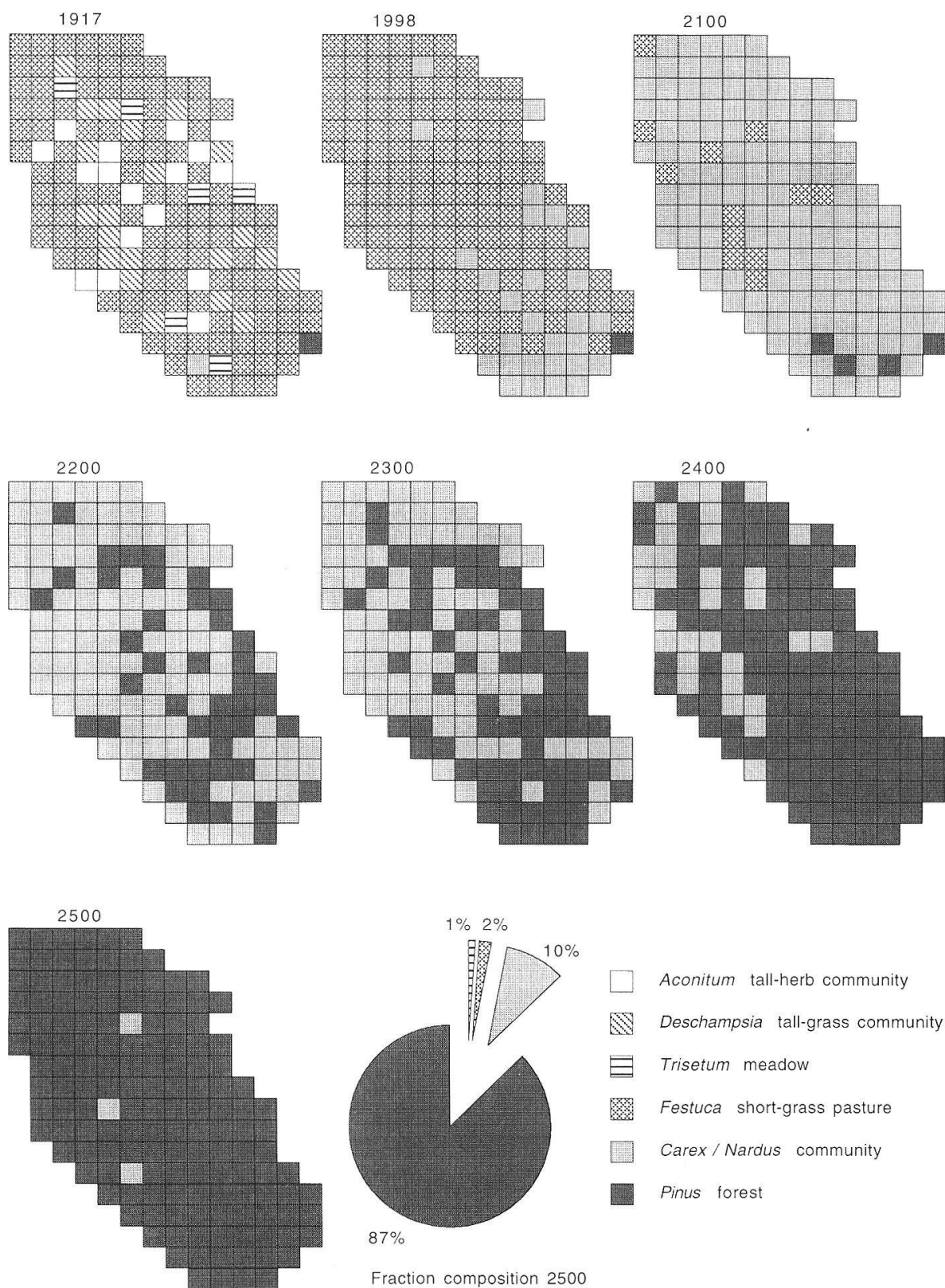
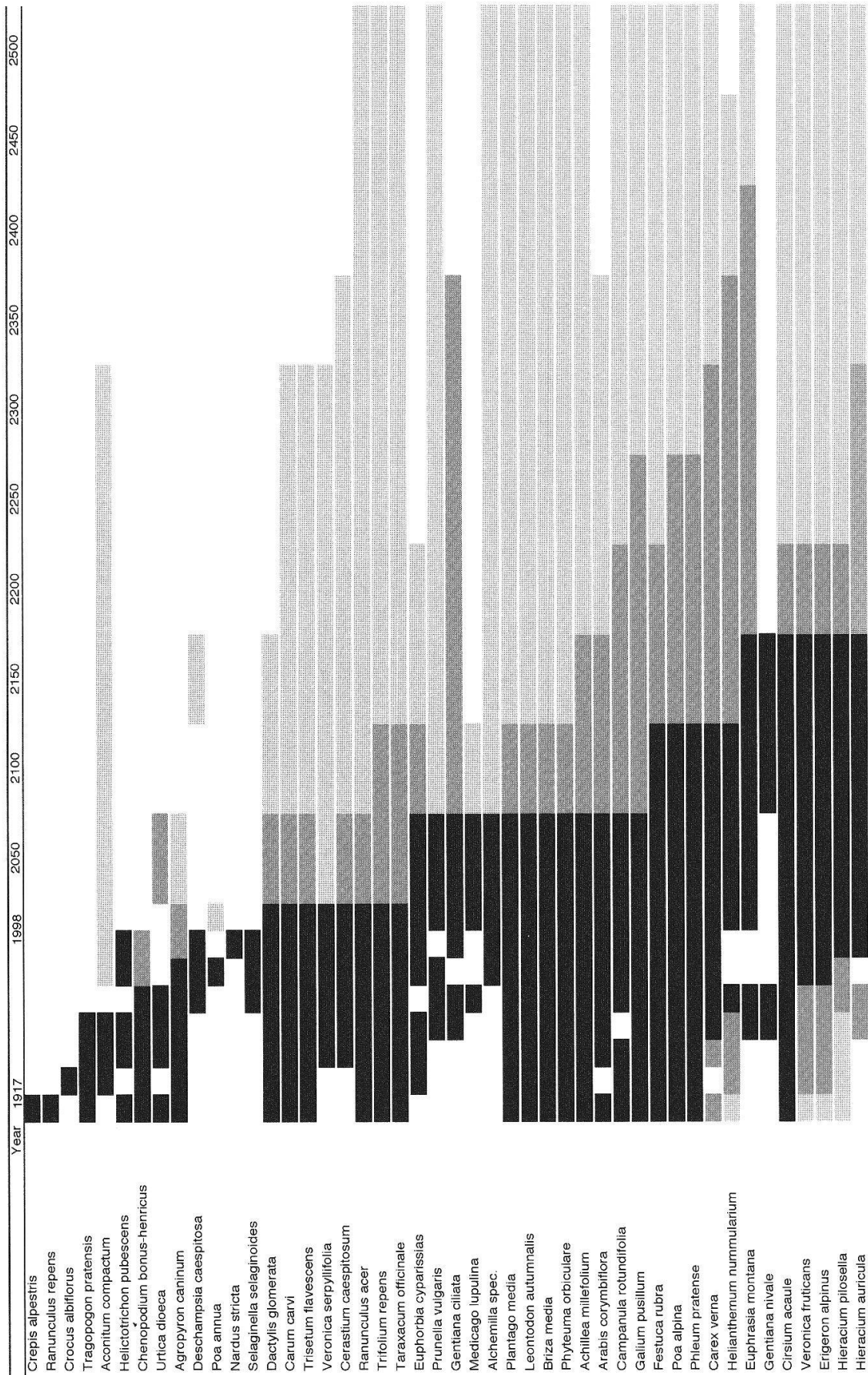
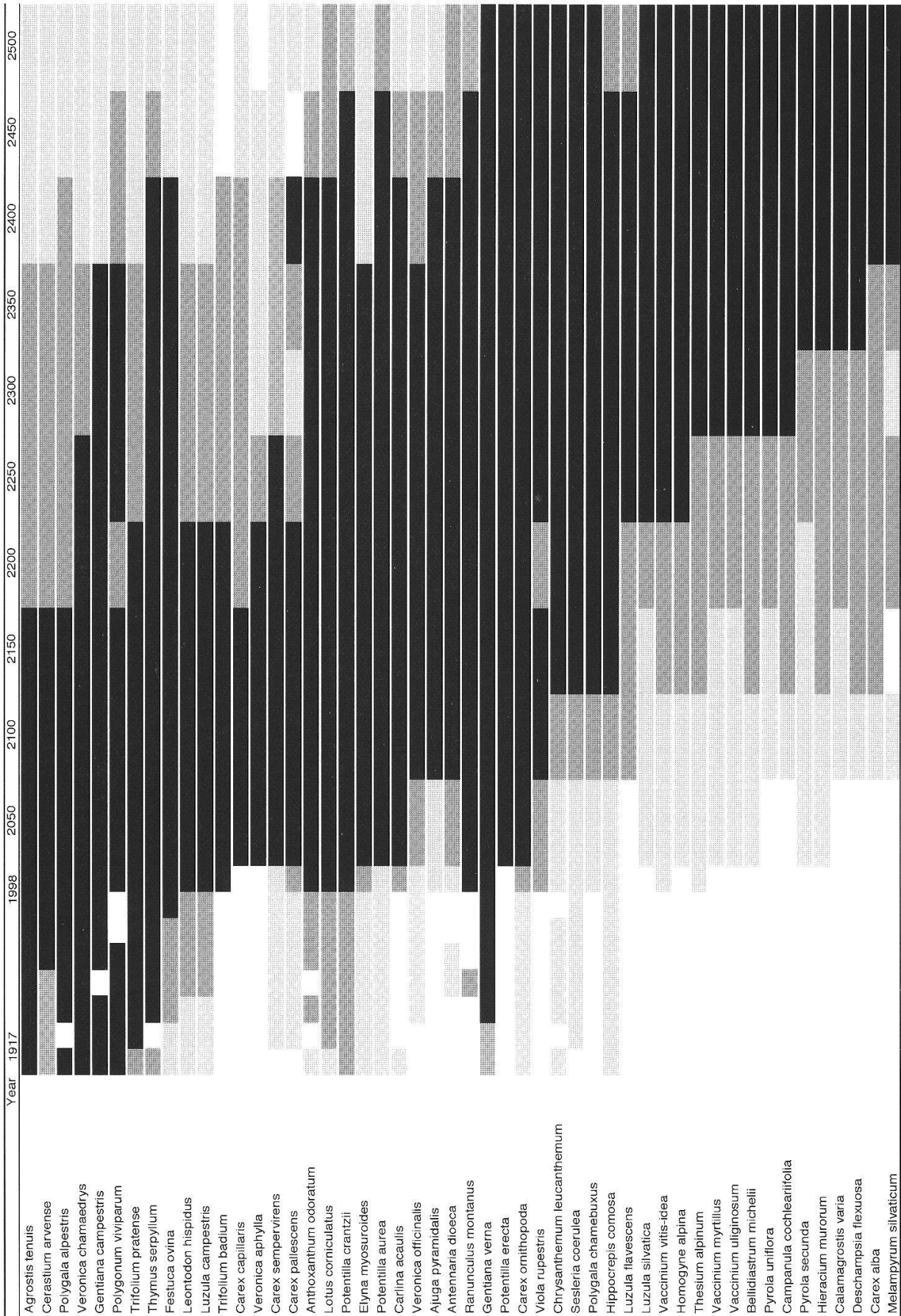


Fig. 2. Spatially detailed simulation of the succession on Plan Praspöl from 1917 to 2500. On the maps, the predominant succession phase is shown only for each of the 149 25-m² plots, even though usually other succession phases are present as well. The pie-chart shows the true presence of the different succession phases on the study area in the year 2500.

Table 2. Simulated development of the relative abundance of individual plant species on the pasture Plan Praspöl between 1917 and 2500. Black: 100–50% of maximum cover reached by the species between 1917 and 2500, dark grey: 50–25%, light grey: 25–1%.





pasture during the 600 years of simulated succession (Table 2) reveals that some species reach their maximum abundance during the first 150 years of simulated succession (species typical for the nutrient-rich areas occupied by the *Aconitum* tall-herb community or the *Deschampsia* tall-grass community), some species attain their highest cover between 2050 and 2250 (species typical for the succession phases *Festuca* short-grass pastures or *Carex/Nardus* community), and some are most abundant towards the end of the simulated period (species associated with the succession phase *Pinus* forest).

FLORISTIC DIVERSITY

The simulated long-term development of floristic diversity on Plan Praspöl shows a substantial increase in the number of vascular plant species between 1917 and 1998, which will continue up to the year 2200 (Fig. 3). Later, the number of vascular plant species will slowly decrease (Fig. 3). The high number of species predicted for the year 2500 is due to the fact that remnants of all succession phases will still be present, even though by then 98% of the plots will be dominated by the herb layer community of *Pinus* forests. As the forest becomes denser, floristic species richness will probably decrease considerably. A highly significant correlation between the simulated and the observed developments of

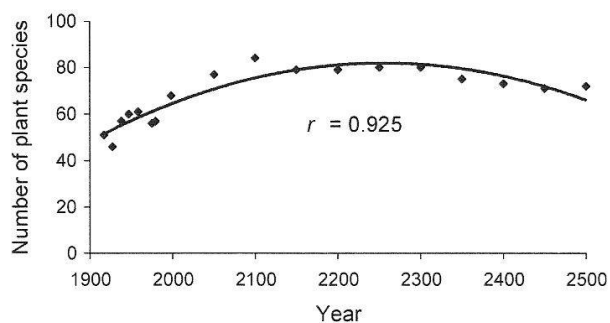


Fig. 3. Simulated development of species diversity on Plan Praspöl between 1917 and 2500. The second-order polynomial regression line is indicated.

species richness between 1917 and 1998 ($r = 0.934$; $P < 0.001$; $n = 8$) indicates that the simulation is meaningful and realistic.

Discussion

Our simulation shows that, during the past 80 years, different areas of the subalpine pasture Plan Praspöl have developed at different rates. In particular, we found that areas in a relief position conducive to nutrient loss and subject to high to medium grazing in 1998 developed at half the rate predicted by the general SNP-vegetation-model. Most likely, this was due to the fact that the grazing pressure observed on Plan Praspöl differed from the pressure on the permanent plots used by Schütz *et al.* (2000a,b) to develop their model: in the general SNP-vegetation-model, plots on nutrient-poor sites were generally only subject to light grazing. The observation that heavy grazing on sites with intermediate to poor nutrient supply slows down succession during the second half of the *Festuca* phase and prevents the transition into the *Nardus/Carex* phase has also been made on Plan Mingèr, another small pasture in the Swiss National Park (Wirth 2000). In the Swiss National Park, in general, the current combination of grazing pressure and nutrient supply seems not to be adequate for maintaining the nutrient regime of the short-grass pasture in equilibrium, which, in turn, would be the prerequisite for a prolonged persistence of this succession phase. Given the abundance of nutrient-rich grasslands in the Park, up to now, wild ungulates can in general afford to abandon a pasture before nutrients are depleted to equilibrium conditions. So far, the only exception seems to be Plan Mingèr, an isolated small pasture in the forests, which because of its low elevation plays a crucial role during the seasonal migration of red deer

between summer and winter habitats (Wirth 2000).

McNaughton *et al.* (1997), studying interactions between ungulates and vegetation in the Serengeti, Tanzania, report that large ungulate herds grazing are indeed able to prolong substantially or even maintain indefinitely certain succession phases. Augustine & McNaughton (1998) explained their observation that the large ungulate herds of the Serengeti do not deplete their pastures as follows: grazing by ungulates increases nutrient cycling in the soil, which in turn increases the amount of nutrients available for plant growth. Similar results were found by Frank & McNaughton (1993) investigating the influence of elk on meadows in the Yellowstone National Park, USA, as well as by Pastor *et al.* (1988) and Collins *et al.* (1998) studying moose and bison impact in different areas of the USA. In addition to stimulating nutrient cycling in the soil by grazing, herbivores can also improve the nutrient supply in an area via faeces, especially, if a sizeable part of their food intake occurs elsewhere (Georgiadis & McNaughton 1990). Again, more available nutrients in the soil will lead to increased biomass production and therefore more forage will be available for grazers. Further, due to co-evolution between plants and ungulates (Owen & Wiegert 1982), many grasses are able to compensate grazing damage with increased nutrient uptake (Wallace & Macko 1993) and increased biomass production (Georgiadis & McNaughton 1990).

Between 1917 and 1998 the number of vascular plant species present on the study area increased by roughly 50%. This increase in floristic diversity is most likely due to the activities of red deer, which re-immigrated into the Park from 1920 to today in steadily increasing numbers. The concomitant increase in grazing pressure broke the dominance of

large-leaved species such as *Chenopodium bonus-henricus* L., *Urtica dioeca* L. or *Aconitum compactum* Rchb. which had become abundant in the study area after commercial grazing with sheep was stopped in 1910. The fact that grazing can break the dominance of large-leaved species and subsequently lead to increased species diversity has been reported by many authors from grasslands both in Europe and the USA (Dirzo 1985; Scherfose 1993; van Wieren 1995; ten Harkel & van der Meulen 1995; Willems & van Nieuwstadt 1996; Schiess & Schiess-Bühler 1997; Collins *et al.* 1998; Schütz *et al.* 2000c).

According to our simulation, floristic diversity will peak around 2200 when half of the 149 plots will be dominated by species of the herb layer community of *Pinus* forests, i.e. when succession from grassland to forest will have reached its mid-point. This corresponds very well to the findings of Bazzaz (1975) and Sousa (1979, 1980) who reported diversity to be highest in mid-succession. During later succession stages when the forest canopy closes, many light-demanding species will disappear from the herb layer (Bazzaz 1975; Barnes *et al.* 1998; Schütz *et al.* 2000b). In addition, once slow-growing and long-lived species such as trees replace the fast-growing, and mostly shorter-lived herbaceous plants, changes in abundance and floristic composition will proceed at slower rates. Consequently, the number of unoccupied niches and, thus, opportunities for the establishment of new species become smaller (Grime 1979; Foster & Tilman 2000). A further reason for the decrease in species richness during later succession stages is the fact that many herbaceous species associated with forests are more vulnerable to grazing than typical grassland species (Tilghman 1989).

Overall, our model shows that under the grazing regime of wild ungulates as observed

today and as implemented in our model, the floristic diversity of abandoned subalpine grasslands is likely to be maintained for a very long period of time. Therefore, our findings support the hypothesis that the ungulate densities observed in the Swiss National Park during the past 30 years (1968–1998), with on average 22.2 red deer, 14.2 chamois, 3.1 ibex, and 0.6 roe deer per vegetation-covered square kilometre, are still in an order of magnitude where the beneficial impacts exceed the harmful ones. Other studies made in the Park both on grasslands and in the forests support this hypothesis (Krüsi *et al.* 1996; Krüsi & Moser 2000; Schütz *et al.* 2000c).

In conclusion, we found that at the scale of the whole study area (3000 m²) the general SNP-vegetation-model of Schütz *et al.* (2000a,b) correctly simulates the floristic changes. However, for a spatially more detailed simulation (25 m²) it is of crucial importance to take into account factors such as grazing intensity and microrelief to accurately predict the successional development of the vegetation, as well as changes in species number and species composition of a pasture in the study area.

Acknowledgements

We thank Martin F. Jurgensen, Margaret R. Gale, Heidi Anderson, Blake Ketchum (Michigan Technological University), Deborah S. Page-Dumroese (USDA Forest Service, Rocky Mountain Research Station) and Otto Wildi (WSL Birmensdorf) for many valuable comments on successive drafts of the manuscript. The funding provided by the Swiss National Science Foundation (grant 3100-045944.95) is gratefully acknowledged. Last but not least we want to thank the Park Service for the administrative and logistic support of our research in the Swiss National Park.

References

- Achermann G., Schütz M., Krüsi B.O. & Wildi O. (2000) Tall-herb communities in the Swiss National Park: long-term development of the vegetation. *Nationalparkforschung in der Schweiz*, **89**, 67–88.
- Augustine, D.J. & McNaughton, S.J. (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management*, **62**, 1165–1183.
- Barnes, B.V., Zak, D.R., Denton, S.R. & Spurr, S.H. *Forest Ecology*, 4th ed. John Wiley & Sons, New York.
- Bätzing, W. (1996) Landwirtschaft im Alpenraum: unverzichtbar, aber zukunftslos? *Landwirtschaft im Alpenraum – unverzichtbar, aber zukunftslos: Eine alpenweite Bilanz der aktuellen Probleme und der möglichen Lösungen* (ed. W. Bätzing), pp. 9–11. Blackwell, Berlin.
- Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, **56**, 485–488.
- Braun-Blanquet, J. (1931) Vegetationsentwicklung im Schweizerischen Nationalpark. *Jahrbuch der Naturforschenden Gesellschaft Graubündens*, **69**, 3–82.
- Braun-Blanquet, J., Pallmann, H. & Bach, R. (1954) Pflanzensoziologische und bodenkundliche Untersuchungen im Schweizerischen Nationalpark und seinen Nachbargebieten. II Vegetation und Böden der Wald- und Zwergstrauchgesellschaften (Vaccinio-Piceetalia). *Ergebnisse der wissenschaftlichen Untersuchungen im schweizerischen Nationalpark*, **28**, 1–200.
- Broggi, M.F. (1998) SOS für bedrohte Kulturlandschaften. *I. Alpenreport: Daten, Fakten, Probleme, Lösungsansätze* (eds. CIPRA), pp. 152–162. Haupt, Bern.
- Campbell, E. & Trepp, W. (1968) Vegetationskarte des Schweizerischen Nationalparks. Beschreibung der Pflanzengesellschaften. *Ergebnisse der wissenschaftlichen Untersuchungen im schweizerischen Nationalpark*, **58**, 1–42.
- Cernusca, A. (ed.) (1989) Struktur und Funktion von Graslandökosystemen im Nationalpark Hohe Tauern. *Veröffentlichungen des Österreichischen MaB-Programms*, **13**, 1–625. Universitätsverlag Wagner, Innsbruck.
- Chapin, F. S. III & Ch. Körner (1996) Arctic and alpine biodiversity: its patterns, causes, and eco-

- system consequences. *Functional roles of biodiversity: a global perspective* (eds. H.A. Mooney, J.H. Cushman, E. Medina, O.E. Sala & E.-D. Schulze), pp. 7–32. John Wiley and Sons, New York.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. (1998) Modulation of diversity by grazing and mowing in native tall-grass prairie. *Science*, **280**, 745–747.
- Dirzo, R. (1985) The role of the grazing animal. *Studies in plant demography: a festschrift for John L. Harper* (ed. J. White), pp. 343–355. Academic Press, New York.
- Foster, B. L. & Tilman, D. (2000) Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. *Plant Ecology*, **146**, 1–10.
- Frank, D. A. & McNaughton, S.J. (1993) Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia*, **96**, 157–161.
- Grämiger, H. & Krüsi, B.O. (2000) Balthasar Stüssi, 17 July 1908–24 October 1992, *Nationalparkforschung in der Schweiz*, **89**, 27–38.
- Georgiadis, N.G. & McNaughton, S.J. (1990) Elemental and fiber contents of savanna grasses: Variation with grazing, soil type, season, and species. *Journal of Applied Ecology*, **27**, 623–634.
- Grimes, J. (1979) *Plant species and vegetation processes*. John Wiley and Sons, Chichester.
- Hegg, O. (1992) Long-term influence of fertilization in a Nardetum. The experimental field of Dr. Werner Lüdi on Schynige Platte. *Vegetatio*, **103**, 133.
- Hess, H.E., Landolt E. & Hirzel, R. (1991) *Bestimmungsschlüssel zur Flora der Schweiz und angrenzender Gebiete*. 3rd Ed. Birkhäuser, Basel.
- Krüsi, B.O. & Moser, B. (2000) Impacts of snow and ungulates on the successional development of a mountain pine forest in the Swiss National Park (Munt La Schera). *Nationalparkforschung in der Schweiz*, **89**, 131–164.
- Krüsi B.O., Schütz M., Grämiger H. & Achermann G. (1996): Was bedeuten Huftiere für den Lebensraum Nationalpark. Eine Studie zu Nahrungsangebot und Waldverjüngung. *Cratschla*, **4**, 51–64.
- Krüsi B.O., Schütz M., Wildi O. & Grämiger H. (1995): Huftiere, Vegetationsdynamik und botanische Vielfalt im Nationalpark. *Cratschla*, **3**, 14–25.
- Kurth, A., Weidmann, A. & Thommen, F. (1960) Beitrag zur Kenntnis der Waldverhältnisse im Schweizerischen Nationalpark. *Mitteilungen der schweizerischen Anstalt für das forstliche Versuchswesen*, **36**, 221–378.
- McNaughton, S.J., Banyikawa, F.F. & McNaughton, M.M. (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science*, **278**, 1798–1800.
- Owen, F.D. & Wiegert, R.G. (1982) Grasses and grazers: is there a mutualism? *Oikos*, **38**, 258–259.
- Parolini, J.D. (1995) *Zur Geschichte der Waldnutzung im Gebiet des heutigen Schweizerischen Nationalparks*. Ph.D. thesis, ETH Zürich.
- Pastor, J., Naiman, R. J., Bradley, D. & McInnes P. (1988) Moose, microbes, and the boreal forest: through selective browsing, moose change plant communities and ecosystem properties. *BioScience*, **38**, 770–776.
- Price, M.F. (1995) Mountain research in Europe: an overview of MAB Research from the Pyrenees to Siberia. *Man and the Biosphere Series*, **14** (ed. J.N.R. Jeffers). UNESCO, Paris.
- Pohl, B. (1996) Die Landwirtschaft im Südtiroler Alpenraum. *Landwirtschaft im Alpenraum – unverzichtbar, aber zukunftslos: Eine alpenweite Bilanz der aktuellen Probleme und der möglichen Lösungen* (ed. W. Bätzing), pp. 57–71. Blackwell, Berlin.
- Rieder, P. (1996) Berglandwirtschaft in der Schweiz. *Landwirtschaft im Alpenraum – unverzichtbar, aber zukunftslos: Eine alpenweite Bilanz der aktuellen Probleme und der möglichen Lösungen* (ed. W. Bätzing), pp. 117–139. Blackwell, Berlin.
- Risch, A. (1999) *Raum-Zeit-Modell der Vegetationsentwicklung auf zwei subalpinen Kleinweiden im Schweizerischen Nationalpark*. M.S. thesis, ETH Zürich and WSL Birmensdorf.
- Scherfose, V. (1993) Zum Einfluss der Beweidung auf das Gefäßpflanzen-Artengefüge von Salz- und Brackmarschen. *Zeitschrift für Ökologie und Naturschutz*, **2**, 201–211.
- Schiess, H. & Schiess-Bühler, C. (1997) Dominanzminderung als ökologisches Prinzip: eine Neubewertung der Tagfalterfauna eines Auenwaldes in der Nordschweiz. *Mitteilungen der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft*, **72**, 1–127.
- Schloeth, R.F. (1972) Die Entwicklung des Schalenwildbestandes im Nationalpark von 1918–1971.

- Schweizerische Zeitschrift für Forstwesen*, **123**, 565–571.
- Schütz M., Wildi O., Achermann G., Krüsi B.O. & Nievergelt B. (2000a) Predicting the development of subalpine grassland in the Swiss National Park: how to build a succession model based on data from long-term permanent plots. *Nationalparkforschung in der Schweiz*, **89**, 207–235.
- Schütz M., Wildi O., Achermann G., Krüsi B.O. & Nievergelt B. (2000b) From tall-herb communities to pine forests: distribution patterns of 121 plant species during a 585-year regeneration process. *Nationalparkforschung in der Schweiz*, **89**, 237–255.
- Schütz M., Wohlgemuth, T., Achermann G., Krüsi B.O. & Grämiger, H. (2000c) Influence of increasing grazing pressure on species richness in subalpine grassland in the Swiss National Park. *Nationalparkforschung in der Schweiz*, **89**, 39–65.
- Sousa, W.P. (1980) The responses of a community to disturbance: the importance of successional age and species' life histories. *Oecologia*, **45**, 72–81.
- Sousa, W.P. (1979) Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. *Ecology*, **60**, 1225–1239.
- Stüssi, B. (1970) Naturbedingte Entwicklung subalpiner Weiderasen auf Alp La Schera im Schweizer Nationalpark während der Reservatsperiode 1939–1965. *Ergebnisse wissenschaftlicher Untersuchungen im Schweizerischen Nationalpark*, **13**, 1–385.
- ten Harkel, M.J. & van der Meulen, F. (1995) Impact of grazing and atmospheric nitrogen deposition on the vegetation of dry coastal dune grasslands. *Journal of Vegetation Science*, **6**, 445–452.
- Tilghman, N.G. (1989) Impacts of white-tailed deer on forest regeneration in north-western Pennsylvania. *Journal of Wildlife Management*, **53**, 524–532.
- van Wieren, S.E. (1995) The potential role of large herbivores in nature conservation and extensive land use in Europe. *Biological Journal of the Linnean Society*, **56**, 11–23.
- Wallace, L.L. & Macko, S.A. (1993) Nutrient acquisition by clipped plants as a measure of competitive success: the effects of compensation. *Functional Ecology*, **7**, 326–331.
- Wildi, O. & Schütz, M. (2000) Reconstruction of long-term recovery process from pasture to forest. *Community Ecology*, **1**, 25–32.
- Wildi, O. & Orlóci, L. (1996) *Numerical exploration of community patterns. A guide to use MULVA-5*. SPD Academic Publishing, The Hague.
- Willems, J.H. & van Nieuwstadt, M.G.L. (1996) Long-term after effects of fertilization on above-ground phytomass and species diversity in calcareous grassland. *Journal of Vegetation Science*, **7**, 177–184.
- Wirth, A. (2000) *Raumnutzung des Rothirsches auf der Kleinweide Plan Minger*. M.S. thesis, ETH Zurich and WSL Birmensdorf.

Received 6 April 2001

Revised version accepted 21 June 2001