

EFFECT OF CATTLE ACTIVITIES ON GAP COLONIZATION IN MOUNTAIN PASTURES

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Abstract: Cattle influences gap dynamics in pastures in two ways: (1) by creating gaps and (2) by affecting the colonization process. This effect of cattle activity on gap revegetation can be subdivided in three main factors: herbage removal, trampling and dung and urine deposition. The objective of this study was to assess how these three effects moderate the plant succession following gap creation.

In an enclosure, four controlled treatments simulating cattle activity (repeated mowing, trampling, manuring and untreated control) were applied on plots of 2 × 2 m. In the centre of each plot, one artificial gap of 60 × 60 cm was created. During three years, vegetation changes were monitored in spring and in autumn, with a square grid of 100 cells of 0.01 m² centred on the gap.

Our experiment confirmed that fine-scale gap creation may have a high impact on relative abundances of species in the community. The gap environment acts on species as a filter and this filtering was described in terms of regenerative attributes. Colonizers were species with small seeds, unspecialized seed dispersal, persistent seed bank and high vegetation spread. However, the role of dung deposition, herbage removal or trampling by cattle did not seem to be of primary importance in the revegetation process, but could moderate vegetation response. Therefore, the different cattle effects act as secondary filters that selectively favoured or disadvantaged different species from the gap-regenerating community. These complex interactions are probably keys to understand plant coexistence in perennial grasslands.

Keywords: Biodiversity, Environmental filters, Plant functional traits, Principal response curves, Spatial monitoring, Swiss Jura Mountains

Nomenclature: TUTIN et al. (1964–1980)

INTRODUCTION

Gap creation is part of disturbances participating in the dynamics of a wide range of plant communities such as forests (e.g. HUBBELL et al. 1999, WRIGHT et al. 2003) or grasslands (e.g. WILLIAMS 1992, LAVOREL et al. 1994, VANDVIK 2004). This disturbance, by removing biomass, reduces competition intensity and allows species that are poor competitors to persist in the community through a competition-colonization trade-off (e.g. HOBBS & HOBBS 1987, TILMAN 1994). Moreover, SUDING & GOLDBERG (2001) pointed out that beyond removing

biomass, gap creation may change the abiotic and biotic environment in a multitude of ways (soil compaction, microtopography, microclimate, herbivores, disease, mycorrhiza, and many others). SUDING (2001) concluded that gap creation might affect species competitive rankings, possibly due to changes in the environment where the interactions occur and not only due to reduction of competition.

In contrast with forest vegetation where most gap colonists are of seed origin (BROKAW & BUSING 2000), colonists of gaps in perennial grasslands can be of seed or clonal origin (BULLOCK et al. 1995). The proportion of seed-derived and clonal colonists varies with gap size. Increased gap size increases the density and size of seed-derived plants (BULLOCK et al. 1995, ROGERS & HARTNETT 2001, VANDVIK 2004). The high proportion of species with clonal reproduction in grasslands (KLIMEŠ et al. 1997, TAMM et al. 2002) allows adult plants to colonize gaps. It is thus clear that the ability of species to colonize gaps depends on regenerative traits. Traits that provide advantages in a closed canopy are not necessarily an advantage for gap colonization. In perennials grasslands rapid vegetative spread (KOTANEN 1997, MARIOTT et al. 1997) and smaller seed mass (KALAMEES & ZOBEL 2002, SUDING et al. 2003) generally characterize gap colonizers. Consequently, plant species often occur with different relative frequencies in recently colonized gaps than they do in the surrounding vegetation (MARTINSEN et al. 1990, BULLOCK et al. 1995). This gap colonization is potentially an important source of vegetation change in grassland. These communities can be seen as a patchwork of microsites in different stages of revegetation (VANDVIK 2004). At landscape and long time scales these small-scale disturbances appear to be effective in maintaining high plant diversity as a result of the interplay of differences in regeneration niches and a lottery for establishment together with the incidence of different conditions in time and space (LAVOREL et al. 1994).

In pastures, large herbivores participate in gap dynamics in two ways. First they directly create the gaps by hoof action (BAKKER & OLFF 2003). SILVERTOWN & SMITH (1988) showed that heavier grazing increased the frequency of canopy gaps. Second, cattle activities such as dung deposition, herbage removal (grazing s.str.) and trampling differently affect vegetation dynamics at a very fine scale (KOHLER et al. 2004a). With the gap environment, these three factors induced by cattle activity can be considered as supplementary environmental filters (*sensu* ZOBEL 1997) that exclude different subsets of the total grassland flora from the gaps. Dung and urine deposition influence gap colonization in two ways: (1) fertilization involving a stimulation of plant growth, (2) addition of seeds promoting new species (MALO et al. 1995, BAKKER & OLFF 2003). Herbage removal induces a loss of biomass and a change in light competition between species (GRIME 2001). Finally, trampling affects the vegetation through detaching or killing plant material by hoof action and by influencing water regime in the firming soil (ABDELMAGID et al. 1987). Most studies on gap colonization were done in fields without herbivores (e.g. ROGERS & HARTNETT 2001, KALAMEES & ZOBEL 2002, VANDVIK 2004) or by considering grazing as a general factor combining the three cattle activities (e.g. WILLIAMS 1992, BULLOCK et al. 1995). Therefore there is poor information on to what extent these different cattle activities act as filters in the gap revegetation processes.

The aim of the present study was to investigate at seasonal and square decimetre scale the revegetation of artificial gaps under different treatments simulating cattle activity (fertilizing, herbage removal and trampling). We explored the role as filters of cattle activities in the colonization process at species and functional traits levels. Furthermore we were interested in the role of gaps in maintaining biodiversity and in promoting new species.

Our working hypotheses were: (1) different effects (the three simulated cattle activities) impose different filters resulting in different community compositions of gaps; (2) these different community compositions can be described by traits of the regenerative phase; (3) these different filters have various effects on the species number appearing in the gaps.

MATERIALS AND METHODS

Study site

This study was conducted in the Jura Mountains of north-western Switzerland in a pasture grazed by cattle from May to September. In this ecosystem, gaps are naturally created by late-lying snow beds, fossorial mammals and large herbivores (principally cows and wild boars) and sizes vary from a few square centimetres to about one square meter. The study site is located in La Métairie d'Évilard (Orvin BE, 47°09' N, 7°10' W) at an elevation of about 1200 m a.s.l. The climate is predominantly temperate oceanic, with a mean annual rainfall of about 1600 mm (with more than 400 mm snow precipitation) and a mean annual temperature of 7 °C. The ground is covered with snow from November to April. The climax vegetation is a *Fagus-Abies* forest. The experiment was carried out in an enclosure on a flat pasture. The initial plant community was a homogeneous, mesotrophic, unfertilized, and extensively grazed *Cynosurion* meadow composed of mainly perennial species. Dominant species of this community were *Festuca nigrescens*, *Agrostis capillaris*, *Trifolium pratense* and *Alchemilla monticola* (see Fig. 3 for a more complete list) and biomass production was about 200 g DM m⁻². This stand was an established community in equilibrium after decades of cattle summer activity. Soil is a cambisol (DECKERS et al. 1998) with a water pH of about 5. Management of the pasture is a rotational grazing system (the animals pass from one paddock to another after variable periods of grazing) with heifers; the stock density ranging from 0.6 to 0.9 adult bovine units per hectare.

Experimental design

Controlled treatments, simulating herbage removal, trampling and dunging by cattle were applied in enclosures. The experimental area was fenced to prevent cattle and other large herbivores from interfering with the treatments, but activities of small herbivores were not controlled since they were negligible. Eight plots (2 × 2 m) separated by a 1-m pathway were arranged along a line. The eight plots were as similar as possible with respect to floristic composition (mean Jaccard's binary similarity index before the experiment = 0.75, SD = 0.07), canopy structure and biomass. Soil homogeneity was checked by surface drillings. Four treatments with two replicates were allocated randomly in two blocks of four plots: (1) repeated mowing with a lawn mower twice a month with a cutting height at 30 mm and removal of the cut biomass, (2) trampling with wooden shoes (1000 footsteps per m² with

ca. 70 kg per footstep of 0.0035 m², representing a mean pressure of 20 000 kg m⁻²) once a month and (3) fertilizing with a liquid mixture of dung and urine given once a month (2 l m⁻²), (4) untreated control, with no intervention at all, simulating abandonment. The frequency and the height of the cutting allowed the maintenance of a vegetation height below 0.1 m. This corresponds to the vegetation height of the most grazed parts in the paddock surrounding the experiment. Moreover, as we showed in another study, cattle do not seem to select plants species at this fine scale (KÖHLER et al. 2004b) except for big species such as *Gentiana lutea*. The selection seems to occur at the scale of plant community types. For trampling, pressure was equivalent to that of a heifer (about 400 kg on at least two hoofs of about 0.01 m² each). Moreover, the quantity of liquid mixture was equivalent to intensive cattle activity (RYSER et al. 2001). The liquid mixture came from cattle that lived in the study area and it may have contained seeds from species already present in the study area.

The number of replicates was low because the sampling process with a resolution of 0.01 m² was very time consuming (see below). All treatments were applied homogeneously at plot scale to the entire surface of each plot, from the end of May to the end of September in 2001 and 2002. This period corresponded to the presence of cattle on the pastureland. Apart from this period, the vegetation was not artificially disturbed. Furthermore, at the beginning of the experiment in spring 2001, a gap of 0.6 × 0.6 m was created in the centre of each plot. Gaps were created by removing the first 3 centimetres of the soil (humus and the very top of A horizon). We chose this large size to obtain an area in the middle of the gap, that cannot rapidly be colonized from the border. Wild boar or high cattle trampling created similar gaps in the surrounding area (F. KÖHLER, pers. observation).

Vegetation sampling

We chose a spatial resolution of 0.01 m² and an extent of 1 m² using a square grid with 100 cells. The grid was positioned at the beginning of the experiment in order to have the 6 × 6 central cells exactly above the gap of 0.6 × 0.6 m. It was not possible to lay the grid down on the soil because of the density of the vegetation. So the grid was kept 15 cm above the ground on four perforated plastic tubes. In order to place the grid in the same position every time, we fixed two other perforated plastic tubes in the soil at opposite corners. A wooden rod was then placed through the two superposed tubes to adjust the grid. In each cell we recorded the exhaustive list of species present in the aboveground and we estimated the cover of each species with the Braun-Blanquet dominance scale. The observations were made vertically above the cells so as to avoid recording twice the margins of contiguous cells. Each record of 1 m² required five hours of labour or more, depending on the species richness and on the state of development of the vegetation. The eight plots were recorded by the same observer in spring (before gap creation) and autumn 2001, in spring and autumn 2002, and finally in spring 2003. Therefore, we collected a total of 4000 cell samples.

Plant functional traits

Plant functional traits were used to detect general trends in trait promotion and inhibition during the gap colonization. We selected four traits of the plant regenerative phase with two to four attributes each that were supposed to respond to gap colonization (Table 1). We focused

Table 1. Plant functional traits (63 species in total). ^a – Vegetative spread: None: CLOPLA1 (1, 2, 4, 12, 16–19, 100), < 0.1 m: CLOPLA1 (6, 7, 9, 13, 15), > 0.1 m: CLOPLA1 (3, 5, 8, 10, 11, 14). CLOPLA1 is the database of KLIMEŠ et al. (1997) and the numbers refer to types of clonal growth. ^b – Seed bank longevity: Transient: “Transient” in more than 80% of all records, Persistent: “Short or long term persistence” in more than 20% of all records. Following the database of THOMPSON et al. (1997).

Trait	Attribute	Number of taxa with attribute	Data source	Missing values
Vegetative spread ^a	none	16	KLIMEŠ et al. 1997	0
	< 0.1 m	21		
	> 0.1 m	26		
Seed mass	< 0.2 mg	14	GRIME et al. 1988	6 (10%)
	0.2– 0.5 mg	11	KLOTZ et al. 2002	
	0.5– 1 mg	13		
	> 1 mg	19		
Type of seed dispersal	Wind-dispersed	12	JULVE 1998	0
	Zoochore	26		
	Unspecialized	25		
Seed bank longevity ^b	Transient	21	THOMPSON et al. 1997	7 (11%)
	Persistent	35		

on traits widely used and easily accessible in databases or literature. Attribute classes were large enough to include a sufficient number of species. Each plant species was graded for each trait according to the attributes. The traits were “vegetative spread”, “seed mass”, “seed agency of dispersal” and “seed bank longevity”. See Table 1 for details and data sources.

Statistical analysis

For each plot, three area types were defined for data analysis: (1) centre of the gap: square of 4 × 4 cells in the centre of the grid, (2) edge of the gap: the band of 20 cells around the square of the first area type and (3) around the gap: the band of 64 cells around the second area type. These three area types were analyzed as three subplots per plot.

To measure the effect of treatments on species number at different scales, we calculated the number of species appearing in the centre of the gap between two successive observations, in three ways: (1) the total number of species observed in the centre of the gap; (2) the number of species in the centre of the gap, which were not found at this place before gap creation; (3) the number of species in the centre of the gap, which were not found in all plots before gap creation. Differences in species number represent a colonization rate, which can be viewed as a Poisson process. To test the effect of treatments on these species counts, generalized linear models (GLMs) with Poisson distribution and log link were used. Models included the following ordered terms: time (period number), season (winter or summer), block and treatment. Calculations were performed with R 2.1.1 (R DEVELOPMENT CORE TEAM 2005).

To measure the multivariate response of the plant community, principal response curves (PRC – principal response curves) (VAN DEN BRINK & TER BRAAK 1999, TER BRAAK & ŠMILAUER 2002) were used (see FRAMPTON et al. 2000 or VANDVIK 2004 for ecological examples). This recent method derived of partial redundancy analysis (pRDA) made it possible to analyze the effect over time of one or more treatments relative to a reference. It is

coded as a partial redundancy analysis that allows for time-specific treatment effects while controlling for the overall temporal trend. Time (coded as dummy variable) is considered as covariable and only the interactions time \times factor (coded also as dummy variable) are considered as explanatory variables. This analysis was done at species and functional traits levels with three models: (1) Time \times Gap effects, (2) Time \times Simulated cattle activity and (3) Time \times Gap effects \times Simulated cattle activity. For the first model, records around the gap were chosen as references. For the second, records of untreated plots were chosen as references and for the third, references were records around the gap in untreated plots. The species matrix was built as follows: for each sampling date, cell records from each plot were aggregated over each subplot by calculating the average cover of each species from Braun-Blanquet codes (transformed to percentage cover as follows: 1 \rightarrow 3%; 2 \rightarrow 14%; 3 \rightarrow 32%; 4 \rightarrow 57% and 5 \rightarrow 90%). These average covers were used as raw data. Furthermore, because redundancy analysis (RDA) is not appropriate to analyze matrices with a high number of zeros (LEGENDRE & LEGENDRE 1998), the species data matrix was Hellinger transformed (LEGENDRE & GALLAGHER 2001). For the functional trait matrix, relative cover of each trait was calculated by adding the absolute cover of each species belonging to attributes and by dividing these values by the total absolute cover. Like at species level, the same aggregation of data was done. In this case data were not transformed because there were only a few zeros in the matrix. To evaluate the statistical significance of each PRC, permutation tests were done. Depending on the model, permutations were restricted in different ways. For the first model (Time \times Gap effects), the whole time series of each subplot was permuted freely within each plot. For the second (Time \times Simulated cattle activity), the whole time series of the 3 subplots of each plot was permuted freely within each block. For the third (Time \times Gap effects \times Simulated cattle activity) the design did not permit to do restricted permutations in a rigorous way. Nevertheless to have an estimate of the *P*-value, the whole time series of each subplot was permuted freely within each block. This may result in inflated Type I error (ANDERSON 2001). The resulting *P*-value has therefore to be interpreted cautiously. Overall differences among blocks were removed in all analyses. PRC were performed using the software package CANOCO 4.5 (TER BRAAK & ŠMILAUER 2002).

RESULTS

Species richness

Before gap creation, 53 species were observed in the eight plots. The mean richness was 37.4 species per plot (SD = 3.3; range 34–43, $n = 8$) and 10.0 species per cell (SD = 1.8; range 5–17, $n = 800$). The impact of gap creation on richness was low at the plot scale with a mean loss of 1.9 (SD = 1.5) species per plot. The effect of gap creation on plant cover and species number was always visible at the end of the experiment (Fig. 1). Concerning the evolution of the total absolute cover at cell scale in the three area types (Fig. 1A), cover increased regularly on the edge and in the centre up to the end of the observation with a higher increase on the edge. There were no important differences between treatments. The evolution of the species number did not show any trend around the gap (Fig. 1B). For the edge of the gap, there was an important increase of species richness in the first summer, but the increase was less important

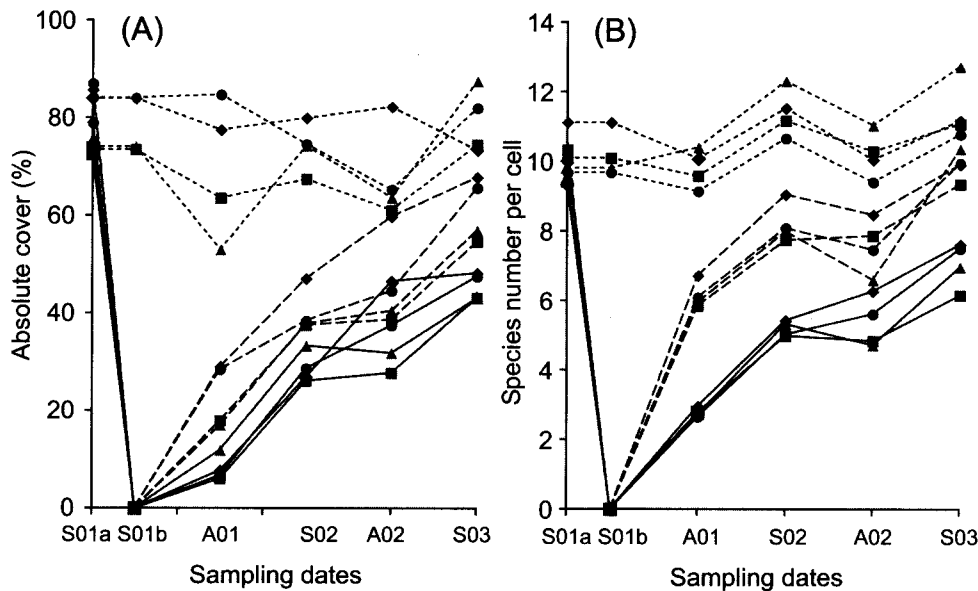


Fig. 1. Mean absolute cover of all species per cell (A) and mean species number per cell (B) during time ($n = 2$). S – spring; A – autumn; 01, 02, 03 – years; for 01: a – before gap creation, b – after gap creation. Solid lines – centre of the gap; dashed lines – edge of the gap; dotted lines – around the gap. ● – trampling; ▲ – repeated mowing; ■ – untreated control; ◆ – manuring.

between the following sampling dates. Finally, in the centre of the gap the increase was lower and more regular than on the edge. Treatments showed the same trends.

Before gap creation there was an average of 24.1 (SD = 3.4) species in the area that will become the centre of the gap (0.16 m²). In this area an average of 24.0 different species (SD = 5.5) were observed during the study. GLM on species colonization rate showed no evidence for a treatment effect (χ^2 test, residual d.f. = 25, $P = 0.726$) but a highly significant effect of time ($P < 0.001$) and season ($P < 0.001$) was found. Most of the species were already observed in spring 2002 after the first winter and the cumulative number of species increased only slightly in autumn 2002 and in spring 2003 (Fig. 2).

An average of 6.0 (SD = 2.1) new species, which were not found in the gap area before its creation, were observed between autumn 2001 and spring 2003 (Fig. 2). There was no significant treatment effect ($P = 0.630$), but a strong season effect ($P = 0.001$). A total of 26 new species were observed, mostly after winter periods. The most frequent new species were *Veronica serpyllifolia* (in 6 of 8 gaps) and *Cerastium fontanum* subsp. *triviale* (in 5 of 8 gaps).

If we refer to the entire community recorded in the eight plots in spring 2001, the average number of new species appearances was 1.4 (SD = 1.5). With such a low colonization rate, GLM only showed a slight treatment effect ($P = 0.086$). Trampling and repeated mowing showed the highest number of new species at the end of the experiment (Fig. 2). These appearances were observed only from the second spring (Fig. 2) and concerned only four different species (*Poa alpina*, *Poa supina*, *Rhinanthus minor* and *Stellaria graminea*). Among these species, *Poa supina*, which appeared in four of the eight gaps (repeated mowing and trampling plots), presented the most important cover.

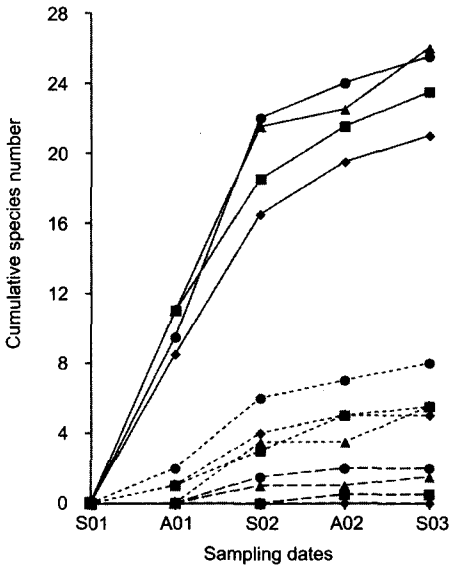


Fig. 2. Mean cumulative species number ($n = 2$) in the centre of the gap (0.16 m^2) during time. S – spring; A – autumn; 01, 02, 03 – years. Solid lines – all species appearing after gap creation included; dotted lines – only species, which were not present on the gap emplacement before its creation included; dashed lines – only species, which were not in all entire plots before gaps creation included. ● – trampling; ▲ – repeated mowing; ■ – untreated control; ◆ – manuring.

importance in the gap. There were some exceptions (e.g. *Hieracium pilosella* and *Agrostis capillaris*), which were dominant species (principally in autumn for *Agrostis capillaris*) in both the non-perturbed area and in the gap. On the first PRC axis there was no difference between treatments but differences appeared on the second axis (Fig. 3). This axis explained 12% of the total variation. Trampling showed the highest deviation from the reference (around the gap area in plots without intervention). Between trampling and untreated control, we found repeated mowing. Manuring was mixed with the reference. *Agrostis capillaris* played an important role in gap colonization (axis 1), especially in trampled plots (axis 2). By contrast, *Alchemilla monticola* was mainly found in the area around the gap (axis 1) and in trampled plots (axis 2).

Functional traits

At functional traits level, differences between the gaps and references over time accounted for 68% of the variance and were highly significant (Table 2). At this level, variance explained by treatments was not significant. The full model explained 79.4% of the variation and was highly significant (Table 2). The first axis of the PRC is presented in Fig. 4. Axis 2 is not presented because almost all the variation is explained by axis 1 (Table 2). In this case

Species composition

For PRC, differences between the gaps and references (around the gap) over time accounted for 38.4% of the variance and were highly significant (Table 2). For the treatments, explained variance was lower but also significant (25.8%). The PRC model for both treatment and gap effects over time explained 67.1% of the variance. This effect was highly significant but the Type I errors of these P -values may be inflated (see Methods section). The first axis (Fig. 3) shows that species composition was changed by gap creation particularly for the central area, and that gaps tend slightly to become more similar to the control with time, particularly for the edge area of the gap. This process was slow with differences persisting after two years. Species involved in gap colonization presented positive weights on the first axis (Fig. 3). Spearman rank coefficient between species weight on the PRC axis 1 and species cover (calculated from the eight plots at the first session) was equal to -0.47 ($P < 0.001$), which is to say there was a tendency for species with low cover to increase in relative

Table 2. Summary of PRC of vegetation data to quantify the effect of different factors included in the model (see text for details). For the species dataset, axes 1 and 2 of the full model of PRC (Time \times Gap effect \times Simulated cattle activity) are presented in Fig. 3 and for the functional traits dataset, axis 1 of the full model is presented in Fig. 4. Variations explained were expressed in percentage relative to the total inertia minus variance explained by the covariables. *P* (999): Significance tested by Monte-Carlo permutation test with 999 permutations (see details in the Methods section). ^a – The Type I error of these *P*-values may be inflated (see Methods section).

Model	Total	Variance explained (%)		
		<i>P</i> (999)	PRC axis1	<i>P</i> (999)
Species dataset				
Time \times Gap effect	38.4	0.001	32.4	0.001
Time \times Simulated cattle activity	25.8	0.042	11.0	0.042
Time \times Gap effect \times Simulated cattle activity	67.2	0.001 ^a	24.4	0.001 ^a
Functional traits dataset				
Time \times Gap effect	68.0	0.001	66.3	0.001
Time \times Simulated cattle activity	11.3	0.15	6.5	0.08
Time \times Gap effect \times Simulated cattle activity	79.3	0.001 ^a	66.3	0.001 ^a

differences between the three area types were also clear. Like at species level the centre and the edge of the gap became more and more similar to the undisturbed area around the gap during the study. This process was slow and differences persisted up to the end of the experiment. Colonizer traits were very light seeds (< 0.2 mg), unspecialized seed dispersal, persistent seed bank and high vegetative spread.

DISCUSSION

Species richness

At the plot scale, gap creation had almost no impact on the species number, although the gap destroyed 36% of the vegetation cover. The low impact of gap creation at 1-m² scale was due to a very high number of species per 0.01 m² and a rather homogeneous distribution of plant species. Similarly, KLIMEŠ (1995) observed in a subthermophilous meadow an average number of ca. 3 species in squares of 0.0025 m² with a maximum of 8 species. On an extensively grazed limestone grassland, VAN DER MAAREL & SYKES (1993) observed a maximum of 40 species on 1 m² and of 27 on 0.01 m². This scale-dependent response to gap creation means that gap-creation events do not affect the general texture of the plant community. PICKETT et al. (1989) pointed out that to alter the structure of the higher-level system (in this case the entire grassland) some change in the disturbance regime (frequency of gap creation in space and time) would be required because this change would affect the overall plant composition.

The number of new species appearing in the central area of the gap during the study was similar between treatments. This number (between 3 and 9 in 0.16 m²) was comparable to those observed at this scale in undisturbed vegetation. For the same community type, KOHLER et al. (2004b) showed at the decimetre scale an average of about 6 new species appearing during only four months. VAN DER MAAREL & SYKES (1993) observed in a square of 0.25 m² an average of 4.4 new species appearing within two years. The rate of appearance of new

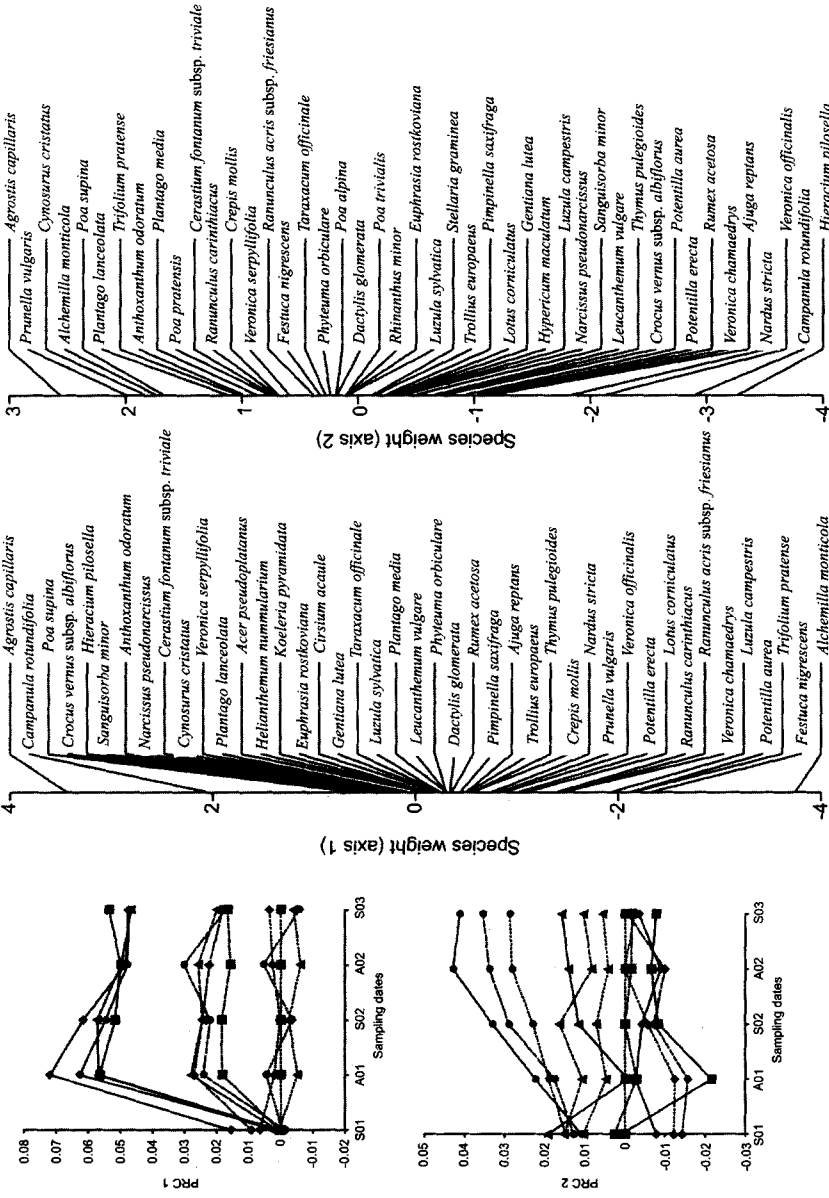


Fig. 3. PRC diagram of vegetation data and species weights on PRC axes 1 and 2 for the species records aggregated by area types after Hellinger transformation. Area around the gap of untreated plots was used as reference. Solid lines: centre of the gap; dotted lines: edge of the gap; dashed lines: around the gap. S: spring; A: autumn; 01-02-03: years; ● - trampling; ▲ - repeated mowing; ■ - untreated control; ◆ - manuring. Only species with weight outside the range -0.08 to +0.08 are presented. For percents of explained variation and permutation tests see Table 2.

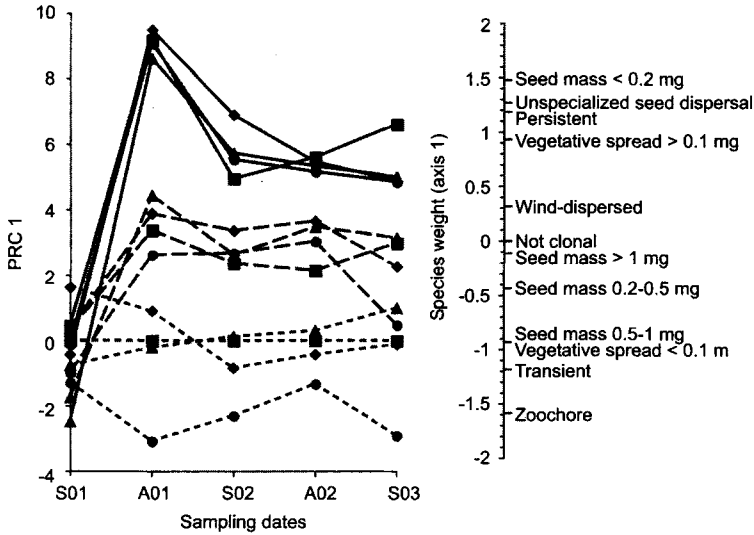


Fig. 4. PRC diagram and species weights on PRC axes 1 for the functional traits matrix. Around the gap for abandoned plot was used as reference. Solid lines – centre of the gap; dashed lines – edge of the gap; dotted lines – around the gap. S – spring; A – autumn; 01–02–03 – years; ● – trampling; ▲ – repeated mowing; ■ – untreated control; ◆ – manuring. For percents of explained variation and permutation tests see Table 2.

species is thus not particularly different in the gap and in the closed surrounding vegetation where the turnover is high (HERBEN et al. 1993, KLIMEŠ 1999, OTSUS & ZOBEL 2002). Differences between gaps and intact vegetation are rather in the species type than in their turnover (see below).

Surprisingly, at the community scale new species seemed to appear principally in mown and trampled gaps. Manuring treatment did not seem to promote biodiversity despite potential addition of seeds with the liquid mixture and nutrient enrichment. By contrast, in a chalk grassland, BONIS et al. (1997) demonstrated that some typical gap species cannot grow in gaps without nutrient enrichment by animals. Even if trampling and mowing seemed to promote new species at community scale, the number of new species was very low (only four different species). ŠPAČKOVÁ & LEPŠ (2004) observed no change in the community composition after four years of moss and litter removal and explained this by the fact that meadows are already species rich (the regional species pool contained no or few species that could enrich the established vegetation). In our case, the studied community had been for decades submitted to a similar kind of gap creation and so gap colonizers were already present. The most important new species was *Poa supina*, which is a typical ruderal species of trampled area with sparse vegetation. This species seems to colonize new favourable habitats very quickly, particularly in trampled and mowed plots where plants are frequently partly destroyed. Gaps have therefore only little impact on site or landscape biodiversity, but they permit the long-term maintenance of species favoured by this disturbance. In the absence of gap creation these species will disappear more or less rapidly depending on their ability to maintain their population in the closed canopy.

Species composition

The gap environment affected the relative contribution of species in the community and this effect persisted up to the end of the observation period, principally in the centre of the gap. Species composition in the gap was a subset of the species around the gap. Apart from the four new species cited above, all species in the gap were also present in the closed community surrounding the gaps. Species filtered by the gap environment were generally well-known colonizers also cited in other studies. VANDVIK (2004) showed also that *Veronica serpyllifolia* and *Cerastium fontanum* subsp. *triviale* were gap colonizers in subalpine grasslands, but not *Agrostis capillaris*, which however played an important role in our case. This stoloniferous species was defined by ARNTHORSDDOTTIR (1994) and PAKEMAN et al. (1998) as a good colonizer and LAVOREL et al. (1998) described it as a representative species of pig disturbance. *Cerastium fontanum* subsp. *triviale* was also recognized as a colonizer by MILBERG (1993) who found this species only in gaps. GIGON & LEUTERT (1996) showed that *Sanguisorba minor* and *Plantago lanceolata* had significantly larger cover on vole colonies in limestone grassland than in control vegetation. Furthermore BULLOCK et al. (1995), in a species-poor sward dominated by grasses, showed that *Cynosurus cristatus* had a greater colonization ability and that the proportion of seed-derived colonizing tillers was for this species about 95% of the total colonizing tillers. Otherwise, two species with bulbs (*Crocus vernus* subsp. *albiflorus* and *Narcissus pseudonarcissus*) appeared as important species in the gaps. Bulbs were probably not destroyed by gap creation because they were located deeper than 3 cm. So it was impossible, in this case, to say if they were really gap colonizers or if they corresponded to regrowth. The dominant species *Festuca nigrescens*, *Alchemilla monticola* and *Trifolium pratense* were excluded from the gap. BULLOCK et al. (1995) showed also that *Festuca rubra* (*Festuca nigrescens* belongs to the *Festuca rubra* aggregate) had a low colonization ability. GIGON & LEUTERT (1996) showed that *Trifolium pratense* had more cover in control vegetation than on vole colonies.

Our treatments, which simulated cattle activities, clearly did not play a primary role in filtering species during gap revegetation despite that they have significant effects in a closed community (KOHLENER et al. 2004a). Differences between treatments appeared, but with secondary importance at species level (Fig. 3). In PRC the variance explained by gap area types and treatments was higher than the variance explained by gap area types only. It is interesting to note that gap colonizers were dispatched on the second axis. *Agrostis capillaris* and *Poa supina* were favoured by trampling and mowing, whereas *Campanula rotundifolia* and *Hieracium pilosella* responded positively to manuring and untreated control. This last result was surprising because these two low-statured species usually develop on nutrient-poor soils and thus should not be favoured by manuring. It seems therefore that such species, which are clearly disadvantaged by manuring in a closed canopy (KOHLENER et al. 2004a) could become key-species in gap revegetation under the same treatment. Nevertheless, the interpretation of such results has to be done carefully because of the low number of replicates.

Functional traits of the regenerative phase

Small seed, unspecialized seed dispersal, persistent seed bank and strong vegetative spread were identified as characteristic functional traits of gap colonizers. Among the species

present, *Agrostis capillaris*, *Veronica serpyllifolia* and *Campanula rotundifolia* combined these four attributes. However, it was not possible with our method to know if these attributes played a direct role in colonization. BURKE & GRIME (1996) showed that smaller-seeded species were more dependent on disturbance for establishment, large seed size permitting seedling establishment in closed vegetation. KALAMEES & ZOBEL (2002) and SUDING et al. (2003) also showed that gap colonizers had smaller seed mass. In contrast, GOLDBERG (1987) and LAVOREL et al. (1999) found no association between small seed and colonization. Surprisingly, zoochorous species were more common in intact vegetation. We expected that, like species with wind-dispersed seeds, this type of dispersal would permit colonization at greater distances than non-specialized seeds. MALO et al. (1995) showed, for example, that rabbit endozoochory could contribute significantly to the build-up of the seedbank in small "seed-free" disturbances. Zoochore species present in the study site were principally epizoochore and myrmecochore (dispersal by ants) species. For epizoochore species the exclusion of large herbivores of the study area could explain the lack of dispersal. Furthermore, ants are probably not attracted by these vegetation-free areas. Our results showed that a persistent seed bank was clearly associated with colonizers. In a calcareous grassland, KALAMEES & ZOBEL (2002) found that the soil seed bank density was about 3000 seeds per m² and they concluded from a field experiment that the soil seed bank plays an important role in gap regeneration. Furthermore, PAKEMAN & SMALL (2005) showed in acid grassland that removing the seed bank significantly slowed regeneration. By contrast, in wet grassland, MILBERG (1993) concluded that the seed bank was the main source of seedlings emerging after gap creation but these seedlings contributed very little to the colonization, which was clearly dominated by vegetative regrowth. In our case and as reported from perennial grasslands elsewhere (RAPP & RABINOWITZ 1985, MILBERG 1993, KOTANEN 1997, MARIOTT et al. 1997), rapid vegetative spread was also a characteristic trait of species present in gaps. The importance of this trait was not surprising considering the high proportion of species using this strategy in perennial grasslands (KLIMEŠ et al. 1997, MACEK & LEPSŠ 2003).

At functional traits level, treatments showed only a very weak effect. This means that by aggregating species following their regenerative attributes, effects observed at species level disappeared. This is probably due to the high selection of gap environment on regenerative attributes, this main filter explaining a large part of the variation of the functional attributes matrix (Table 2). It seems then that supplementary constraints such as trampling and mowing did not induce a higher selection on regenerative plant traits. Therefore, species having reacted to treatments were not selected according to our choice of traits. It is almost certain that the tested traits do not include all those of major relevance for the studied process although largely recognized to be important in vegetation dynamics. Moreover, it is at present difficult to obtain complete trait data for rich mountain meadows. Furthermore, because we studied a colonization process, our chosen traits were voluntarily centred on the regenerative phase and not on traits of the established phase. This could also explain the lack of treatment effects. Indeed, KOHLER et al. (2004a) observed effects of the same treatments on plant height and stature in the closed canopy of a similar pasture.

CONCLUSION

Our experiment confirmed that fine-scale gap creation can have a strong impact on the relative abundance of species in the community. The continuous creation of gaps of several decimetres by cattle or other large herbivores and colonization of these gaps by a specialized set of species from the surrounding area may be seen as a series of microsuccessions contributing to biodiversity and long-term stability (VANDVIK 2004). Cattle may influence vegetation change by affecting the rate of gap creation (BULLOCK et al. 1995). This rate is also dependent on other factors like small herbivores (BAKKER & OLFF 2003) or snow quantity during the winter. However, the filtering role of dung deposition, herbage removal or trampling by cattle does not seem to be of primary importance but may moderate vegetation response. First, species are filtered by gap environment according to their regenerative attributes. Second, the colonizer species are filtered by the different cattle activities. These complex dynamics are probably keys to understand plant species coexistence in pastures.

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