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Seasonal vegetation changes in mountain pastures due to simulated effects of cattle grazing

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Abstract. Cattle influence grassland dynamics in three ways: herbage removal, dung deposition and trampling. The objective of this study was to assess the effects of these factors, separately or in combination, and to compare them with cattle grazing over a one year period in a field experiment conducted in the Jura Mountains of northwestern Switzerland.

A set of controlled treatments simulating the three factors was applied in a fenced area: (1) repeated mowing – three levels; (2) intensive trampling – two levels; (3) manuring with a liquid mixture of dung and urine – three levels. All treatments were applied homogeneously to the entire surface of each of the 40 plots inside the exclosure. Additionally, ten plots outside the fenced area represented reference plots with regular cattle pasturing. The multivariate response of species composition was assessed three times with the point-intercept method: in spring before the treatments, in autumn after one season of treatments and at the beginning of the following year after winter rest.

Multivariate analyses of vegetation data in the first year showed an overwhelming seasonal shift and significant differences induced by treatments. Abandoned and manured plots showed the largest deviation from the cattle grazed reference. Herbage removal, simulated by repeated mowing, appeared to be the most important factor for maintaining vegetation texture. Seasonal treatment effects were only partially carried over to the next spring, showing an unexpected resilience of the plant community, probably due to life-history traits and competition release following climatic disturbance in winter.

Keywords: Dunging; Field experiment; Herbage removal; Plant community; Plant trait; Trampling; Vegetation dynamics.

Nomenclature: Tutin et al. (1964-1980).

Abbreviation: PCA = Principal Component Analysis; RDA = Redundancy analysis.

Introduction

Spatial patterns of vegetation in pasture is strongly directed by human and cattle activities (Olff & Ritchie 1998; Olff et al. 1999). The effect of cattle on vegetation can be subdivided into three categories of stress factors (*sensu* Grime 1979): herbage removal, dunging and trampling. Many studies have addressed effects of grazing (e.g. Milchunas & Lauenroth 1993; Schlaepfer et al. 1998; Birch et al. 2000; Cingolani et al. 2003), trampling (e.g. Cole 1995; Guthery & Bingham 1996; Kobayashi et al. 1997), dung deposition (Malo & Suarez 1995; Dai 2000), or manuring or fertilizing (Gough et al. 2000), on grassland, heathland and woodland communities. Grazing is the main biotic factor affecting vegetation structure and dynamics in pastures (Olff et al. 1999; Bokdam & Gleichman 2000). It changes the arrangement of aboveground parts of plants in communities with consequences on several scales; on the community scale, growth forms of the component species are of major importance in predicting community responses to physical factors and to disturbance. Trampling leads to gap formation and promotes invasive species with high vegetative reproductive ability (Bullock et al. 1995). Cole (1995) has interpreted vegetation changes in various community types according to the concepts of resistance (ability to resist to change when trampled, observed after two weeks), tolerance (ability to tolerate a cycle of disturbance and recovery, observed after one year) and resilience (ability to recover following the cessation of trampling), which are the different components of stability. Dunging can also be considered as an important factor affecting vegetation changes in herbaceous or dwarf-shrub communities (Sougnez 1965) and their diversity (Grime 1973; Moore & Keddy 1989; Grace 1999; Gough et al. 2000). It changes the local nutrient balance, thus favouring nitrophilous species; it also contributes to seed transport. Initial species composition is a key factor in the community response to added nutrients and this response might be particularly strong where different life forms or functional groups co-exist (Hill & Carey 1997).

Among the cited studies, none considers the relative impacts of these biotic factors or their interactions in structuring the vegetation of pastures. Furthermore, there is evidence that spatial patterns of the three activities are not congruent. Cattle have, for example, favourite resting and dunging areas, which may be different from their preferred grazing areas (Bokdam & Gleichman 2000). Moreover, there is very poor information on the influence of these factors at a seasonal scale. Studies about grazing effects generally have a temporal resolution of one or more years (e.g. Bokdam & Gleichman 2000; Marriott et al. 2002) or are synchronic (e.g. Mitlacher et al. 2002; Vandvik & Birks 2002; Huebner & Vankat 2003). The spatial scale at which the three factors act is very fine (less than 1 m^2, bite and feeding station *sensu* Bailey et al. 1996). Consequently, to have an adequacy between time and space, we think that temporal resolution should be shorter than one year. Competition between species changes during the season. Thus, treatment effects should also differ at a seasonal scale. Furthermore, cattle management in mountains of temperate regions is generally limited to a short summer period (Dullinger et al. 2003). In the Jura Mountains, where the experiment was conducted, the herds are active between the end of May and the end of September. Thus, for almost eight months each year, vegetation is not disturbed by cattle activity. Nevertheless, the winter period with frost and snow events can be considered as another form of disturbance. On the other hand, in spring, when plant growth is at its maximum, interspecific competition is the main process in vegetation structuring, as in a mown meadow. It is usual to delay the transfer of the cattle to the mountain pastures until the end of the period of strongest plant growth. This traditional practice provides us with an additional argument to study the succession on a seasonal scale.

The objective of this study is (1) to assess, separately or in combination in an exclosure experiment, the effects of repeated mowing, manuring and trampling on herbaceous vegetation of a pasture used during the summer period and (2) to assess the effects of cattle activity over a one year period including winter disturbance and the following spring period free of cattle.

Our working hypotheses were that: (1) our treatments will induce, at a seasonal scale, a slight quantitative divergence by changing equilibrium between species of the community; (2) these changes will be partly hidden by a phenological shift among species; (3) changes induced by treatments will persist and become even more visible after the winter season, when comparing spring data sets before and after treatments; (4) at the seasonal scale, morphological traits of species are important to explain community dynamics.

Methods

Study site

The study was conducted in the Jura Mountains in NW Switzerland, near Les Ponts-de-Martel (46° 38' N, 6° 38' W), at 1200 m a.s.l. The climate is predominantly oceanic, with a mean annual rainfall of ca. 1600 mm and mean annual temperature of 7 °C. Mean daily temperature is below 0 °C on more than 60 days per year. There is snow during ca. 120 days from November to April. The climax vegetation is a *Fagus-Abies* forest. Soil is a Cambisol (FAO, Anon. 1988), with pH (H_2O) of 5.1.

The experiment was carried out in an exclosure of 300 m^2 in a flat pasture. The initial plant community was a homogeneous, mesotrophic, unfertilized, extensively grazed *Cynosurion* meadow. Dominant species of this community were *Festuca nigrescens*, *Anthoxanthum odoratum*, *Trifolium repens* and *Alchemilla monticola* (see App. 1 for details). This stand was an established community in equilibrium with decades of cattle summer activity, the stock density ranging from 0.6 to 0.9 adult bovine-unit.ha^{-1}.

Experimental design

In the exclosure, controlled treatments were applied, simulating herbage removal, trampling and dunging by cattle. The experimental area was fenced to prevent large herbivores from interfering with the treatments, but activities of small herbivores were not controlled. 0 plots (2 m × 2 m) separated by a 1-m pathway were arranged on a 5 × 8 grid. In the pasture around the exclosure, ten additional plots were established. The 50 plots were as similar as possible with respect to floristic composition, canopy structure and biomass. Soil homogeneity was checked by surface drilling. Three factors were introduced to be combined into treatments in the exclosure:

1. Repeated mowing with a lawn mower (Mo) at three levels:
Mo0 = no mowing; Mo1 = once a month; Mo2 = twice a month.
2. Trampling (Tr) with wooden shoes (1000 footsteps per m^2 with ca. 70 kg per footstep of 35 cm^2, representing a mean pressure of 2 kg.cm^{-2}):
Tr0 = no trampling; Tr1 = trampling once a month.
3. Manuring (Ma) with a liquid mixture of dung and urine given once a month at three levels:
Ma0 = no manuring; Ma1 = 0.5 L.m^{-2}; Ma2 = 2 L.m^{-2}.
Ma1 is equivalent to normal cattle activity, Ma2 to intensive cattle activity. The liquid mixture came from cattle that lived in the study area. It could possibly contain seeds from species already present in the study area.

Each treatment was a combination of the different levels of these three factors. From the 18 possible combinations, only eight were retained and randomly allocated in the 40 plots of the exclosure experiment with five replicates, giving:

- Five single treatments: Mo1(+Tr0+Ma0); Mo2(+Tr0+Ma0); Tr1(+Mo0+Ma0); Ma1(+Mo0+Tr0); Ma2(+Mo0+Tr0).
- Two coupled treatments: Tr1+Ma1(+Mo0); Mo1+Ma1(+Tr0).
- Abandoned plots with no intervention (Ab1 = Mo0+Tr0+Ma0).

All treatments were applied homogeneously to the entire surface of each plot, from the end of May to the end of September 2000. This period corresponded to the presence of cattle on the pasture land. Apart from this period, the vegetation was not artificially disturbed. The ten plots outside the fenced area represented reference plots with regular, uncontrolled, cattle activity (Ca).

Vegetation data

Records were made in a 1-m^2 central subplot, leaving a buffer strip of 50 cm around each plot. Of the 59 species present in all plots ca. 54% were found in each subplot, and 75% of the species with a mean cover > 5%. Absolute and relative cover of vascular plants were assessed using point-intercept frequency measurements (Goodall 1953; Daget & Poissonet 1969). The number of contacts of green parts with a vertical needle was counted, considering only the first hit for each species. The number of points, 80 - 190, was chosen after a preliminary test. A threshold of 120 point.m^{-2} was retained since it allowed efficient measurements, with a fair estimation of cover in ca. one hour per subplot. Since rare species are often missed by this method (Buttler 1992), a complete list of all species observed within each subplot was also recorded. In the data set, species found with no contact were allocated the minimum value 1 for their occurrence. To account for seasonal changes, the records were made at the end of spring of the first year of the experiment, when the vegetation started to grow, at the beginning of autumn of the same year, after one season of treatments, and again in May of the next season when cattle returned to the pasture. After having analysed the results of autumn records, we chose to consider only three replicates for each treatment (six for plots with cattle activity) for the final session.

Species traits

To test the relationship between vegetation dynamics and species morphological traits we compiled a set of simple morphological descriptions of the mature plants. These included leaf position (rosette, semi-rosette, leafy stem), plant height (four classes: 0-20 cm, 20-40 cm, 40 - 60 cm, > 60 cm) and capacity for lateral spread (four classes: none, < 10 cm, 10 - 25 cm, > 25 cm). Furthermore, we classified the species into the three classical taxonomical groups: grasses, forbs, legumes. Data were obtained from the literature (Grime et al. 1988; Lauber & Wagner 2001) and field observations.

Statistical analyses

Variation in the data set in relation to time and treatments was detected with Principal Component Analysis (PCA), programme CANOCO 3.12 (ter Braak 1987-1992). PCA was chosen because of the short vegetation gradient included (Legendre & Legendre 1998). First, PCA was conducted with the 100 records of spring and autumn of the first year to reveal seasonal shifts. Then separate PCAs were performed on the data set of each of the three periods to explore the treatment effect. Absolute species cover values were used after square-root transformation to improve the normality of the response variables. The plots with cattle activity were added as passive samples because they were not included in the experimental design. We used the coordinates of the records on the first ordination axis to test the overall treatment effect by means of ANOVA, whereas pair-wise comparisons were made with Tukey-Kramer HSD tests. The plots with cattle activity were excluded from this analysis. These tests were performed using JMP 4 software.

To measure the heterogeneity of the community before the treatments, asymmetric quantitative coefficients of Steinhaus were calculated from the absolute cover of species for all pairs of samples using the R Package 4.0 d6 (Legendre & Legendre 1998; Casgrain & Legendre 2001). This similarity index does not take into account the double absence of a species when calculating the resemblance between two records.

To analyse the variation in the data set in relation to treatments at the end of the growing season, Redundancy Analysis (RDA) was performed with CANOCO. The species data set was built with the 50 autumn records, using absolute cover of species (square-root transformed) and the correlation matrix was computed. The ten plots with cattle activity were added as passive samples. The environmental data set was built for each record with four explanatory quantitative variables coded as follows: 1. Mowing: Mo0 = 0, Mo1 = 1, Mo2 = 2; 2. Trampling: Tr0 = 0, Tr1 = 1; 3. Manuring: Ma0 = 0, Ma1 = 1, Ma2 = 4; 4. Abandoning: Ab0 (mowing, trampling and/or manuring) = 0, Ab1 = 1.

Interactions between trampling and manuring and between mowing and manuring were included in the model (CANOCO options). Furthermore, to assess the relationship between plant traits and treatments we added as passive species the absolute cover of each plant trait. This absolute cover was calculated by adding the absolute cover of each species belonging to each trait.

Finally, to compare the variation explained by the treatments at the end of the growing season and after one complete year, RDA was repeated for the 30 records from the spring period in the second year.

Results

Seasonal shift

The PCA with spring and autumn records of the first year (Fig. 1) clearly showed a seasonal shift. Axis 1 opposed records made in spring, on the right, and those made in autumn, on the left. Thus, seasonal changes appeared more important in this overall analysis than changes induced by treatments. Main species responsible for this change were: *Crocus vernus* ssp. *albiflorus*, which disappeared in the autumn, while *Agrostis capillaris* appeared (see App. 1). Species such as *Anthoxanthum odoratum*, *Campanula rotundifolia* and *Luzula campestris* were decreasing in cover during summer, while *Cynosurus cristatus* and *Plantago lanceolata* were increasing and others, such as *Festuca nigrescens,* remained constant.

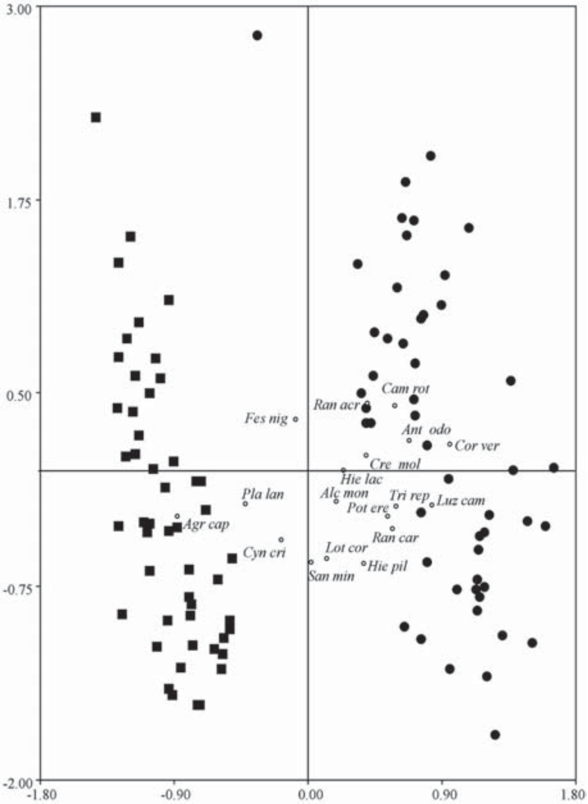

Fig. 1. Scatter diagram of the PCA of vegetation records made in spring (●) and in autumn (■). Explained variation: axis 1: 26.3%, axis 2: 10.9%. Species-arrows are represented by the end point of their vector. Only species with frequency > 90% are presented:
Agr cap = *Agrostis capillaris*; *Alc mon* = *Alchemilla monticola*; *Ant odo* = *Anthoxanthum odoratum*; *Cam rot* = *Campanula rotundifolia*; *Cre mol* = *Crepis mollis*; *Cro ver* = *Crocus vernus* ssp. *albiflorus*; *Cyn cri* = *Cynosurus cristatus*; *Fes nig* = *Festuca nigrescens*; *Hie lac* = *Hieracium lactucella*; *Hie pil* = *Hieracium pilosella*; *Lot cor* = *Lotus corniculatus*; *Luz cam* = *Luzula campestris*; *Pla lan* = *Plantago lanceolata*; *Pot ere* = *Potentilla erecta*; *Ran acr* = *Ranunculus acris* ssp. *friesianus*; *Ran car* = *Ranunculus carinthiacus*; *San min* = *Sanguisorba minor*; *Tri rep* = *Trifolium repens*.

There were ca. 32 species per plot in spring (max. 41, min. 25, SD = 3.6) and 27 in autumn (max. 33, min. 19, SD = 3.1). Ca. four species per plot appeared (e.g. *Agrostis capillaris*, *Prunella vulgaris*, *Pimpinella saxifraga*) and ca. nine disappeared (e.g. *Crocus vernus* ssp. *albiflorus*, *Coeloglossum viride*, *Primula veris*, *Orchis mascula*, *Gentiana acaulis*).

Changes induced by treatments

In spring of the first year, the Steinhaus similarity measures for all couples of records ranged from 0.47 to 0.90 (mean: 0.702; $n = 1225$) indicating that the starting vegetation was a homogeneous set of plots. Differences in species richness between records when comparing treatments were neither significant in autumn ($P = 0.07$), nor in spring of the second year ($P = 0.31$). A t-test for the number of species between the fertilized plots and all the others showed a significantly lower diversity ($P = 0.05$) in manured plots in autumn but this difference disappeared in the second spring.

The ANOVA on species scores along PCA axis 1 at each period showed that the treatments were significantly different ($P < 0.0001$) in autumn and in spring of the second year ($P = 0.03$), while the same grouping of plots yields no significant differences in spring of the first year ($P = 0.52$) (Fig. 2). Significant differences between treatments appeared with the Tukey-Kramer HSD in autumn and in spring of the second year. In autumn treatments were clustered into four groups (Fig. 2): (A) Ab1, Ma1, Ma2; (B) Tr1; (BC) Tr1+Ma1, Mo1+Ma1 and Mo1; (C) Mo2. Groups 2 and 4 were significantly different from each other but not from group 3. In spring of the second year this trend persisted but only Ab1 and Mo2 remained significantly different from each other.

The four explanatory variables of RDA using the autumn data set (Fig. 3) were significant in the forward selection (rank of explained variance: Mowing > Trampling > Manuring > Abandoning). Interactions (Manuring × Trampling and Mowing × Manuring) were not significant. The Monte Carlo permutation test was significant for the first ($P = 0.001$), the second ($P = 0.004$), and the third axis ($P = 0.015$). The explanatory variables explained 35% of the variation of the species matrix. Axis 1 was correlated with Abandoning and axis 2 positively correlated with Manuring and to some extent with Trampling. The variable Mowing was opposed to both Manuring and Abandoning. The interaction between Manuring and Trampling was close to Trampling and the interaction between Manuring and Mowing was positively correlated with Mowing.

The ordination scatter plot showed, on the left of the first axis, mown, trampled, mown + manured, trampled + manured plots, related to species such as *Hieracium lactucella*, *Hieracium pilosella*, *Trifolium repens* or *Luzula campestris*. Plots with cattle activity were also clustered in this area. On the right side of axis 1, manured and abandoned plots were found, in relation to species such as *Galium anisophyllon*, *Carex flacca*, *Carlina acaulis* or *Veronica chamaedrys*. Along the second axis, the most manured plots were related to *Dactylis glomerata*, *Festuca nigrescens* and *Arrhenatherum elatius*. Considering plant traits, mowing was related to rosette, small height and large lateral spread. On the opposite, manuring was characterized by semi-rosette species with small lateral spread and large size. Concerning taxonomical groups, forbs were related with abandoning, grass with manuring and legumes with trampling.

Compared to the RDA performed from records of autumn of the first year, the RDA from those of spring of the second year showed a lower percentage of explained variance but axes one and two remained significant (Table 1).

Discussion

Natural seasonal fluctuations of plant species are primarily dependent on life-history traits of species, but are also partly driven by environmental factors (Menzel & Fabian 1999). In our study, these life-history traits were modifying the community structure (Fig. 1) and this temporal shift was hiding changes induced by treatments at the seasonal scale. Results of the analyses using the autumn data set of the first year were relevant because of the relatively high homogeneity of the first spring data set and the fact that no significant differences appeared between groups before treatments (Fig. 2). This condition is very important in short-term experiments, in which the initial floristic composition determines the potential changes at community level. It is less important in the longer-term because species composition becomes more under control of the environmental regime rather than of the initial conditions (Hill & Carey 1997). In spring we recorded some typical vernal species, which were replaced in autumn by late growing species. Other species were always present but their contribution to cover changed through time. All species that appeared in plots after treatments belonged to the original plant community (*Cynosurion*) and were adapted to regular cattle activity. Thus, at the considered time scale, treatments did not affect the qualitative species composition, but they affected abundance of established species. Marriott et al. (2002) observed the same phenomenon in a five year grazing experiment.

Table 1. Summary of RDA of vegetation records made after treatments, in the autumn of the first year, and in spring of the following year, using three replicates. Plots with cattle activity were given as passive samples.

	Autumn	Spring
Explained variance (%)	46	41
Test of significance, P-value:		
Canonical axis 1	0.001	0.003
Canonical axis 2	0.030	0.004
Canonical axis 3	0.065	0.410

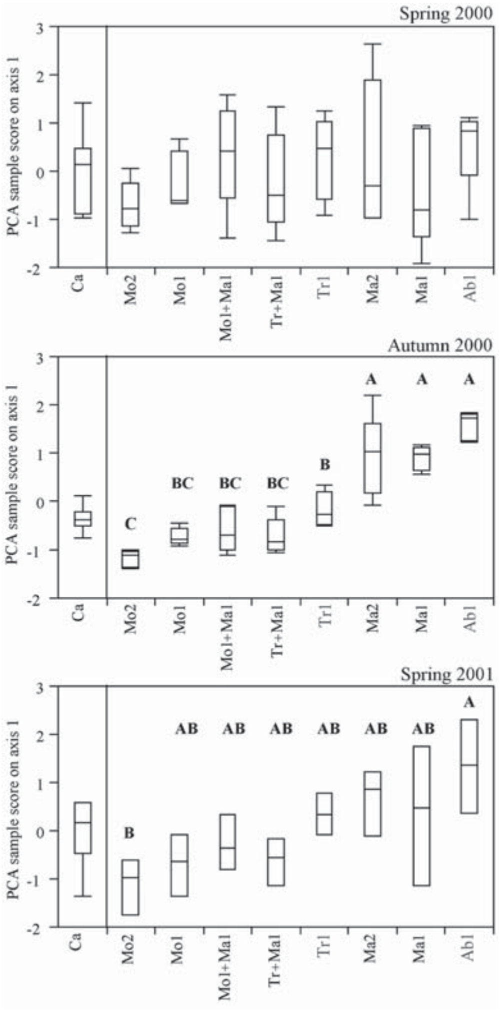

Fig. 2. Coordinates of records in the autumn of the first year and in spring of the following year, on the first ordination axis of each PCA, grouped by treatments. Plots with cattle activity were considered as passive samples. For autumn 2000 and spring 2001, significant differences ($P < 0.05$) with the Tukey-Kramer HSD are indicated with different characters (for spring 2000 there were no significant differences). Plots with cattle activity were excluded from this analysis because they were not included in the experimental design.

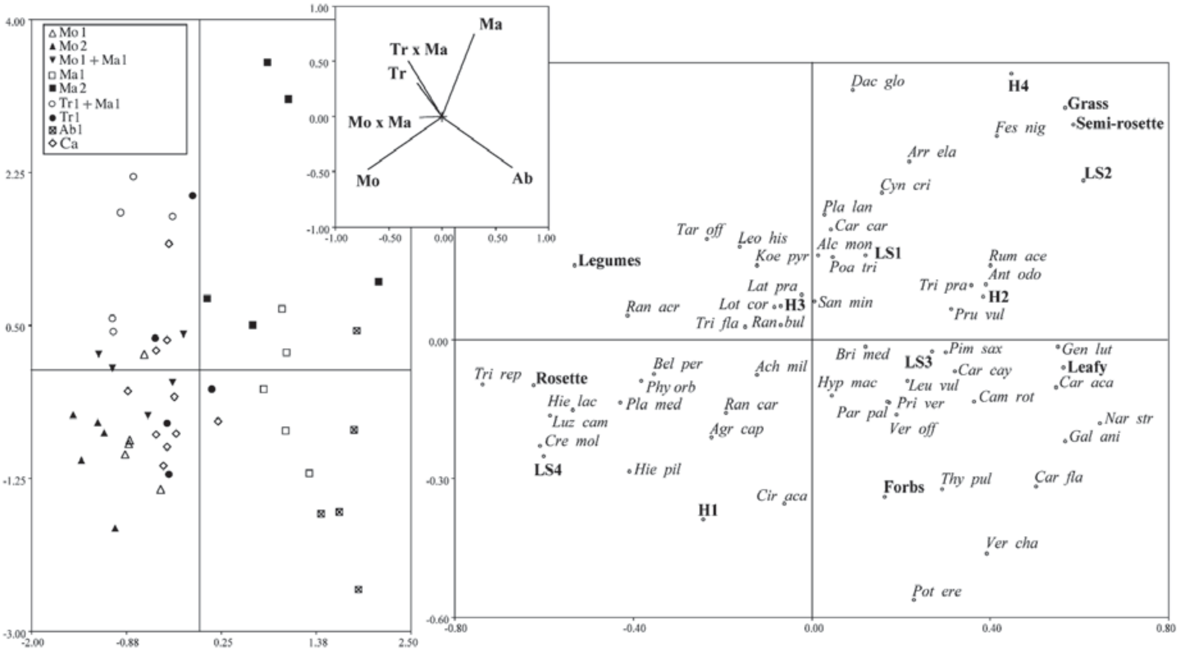

Fig. 3. Scatter diagram of the RDA of vegetation records made in autumn (for details see text). Symbols for records indicate the treatment. Plots with cattle activity are considered as passive samples. For clarity species-arrows are represented by the end point of their vector. Plant traits are indicated in bold, among them: LS(1 - 4): lateral spread (none - large); H(1 - 4): height (small - tall). Explained variation: axis 1: 16.1%, axis 2: 7.4%. Variation explained by all explanatory variables: 35.2%. The Monte Carlo permutation test was significant for the first axis ($P = 0.001$), for the second axis ($P = 0.004$) and for the overall regression ($P = 0.001$). Species with frequency higher than 10% are presented: *Ach mil = Achillea millefolium* ssp. *millefolium*; *Arr ela = Arrhenatherum elatius* ssp. *elatius*; *Bel per = Bellis perennis*; *Bri med = Briza media* ssp. *media*; *Car aca = Carlina acaulis* ssp. *simplex*; *Car car = Carum carvi*; *Car cay = Carex caryophyllea*; *Car fla = Carex flacca*; *Cir aca = Cirsium acaule*; *Dac glo = Dactylis glomerata*; *Gal ani = Galium anisophyllon*; *Gen lut = Gentiana lutea*; *Hyp mac = Hypericum maculatum* ssp. *maculatum*; *Koe pyr = Koeleria pyramidata*; *Lat pra = Lathyrus pratensis*; *Leo his = Leontodon hispidus*; *Leu vul = Leucanthemum vulgare*; *Nar str = Nardus stricta*; *Par pal = Parnassia palustris*; *Phy orb = Phyteuma orbiculare*; *Pim sax = Pimpinella saxifraga*; *Pla med = Plantago media*; *Poa tri = Poa trivialis* ssp. *trivialis*; *Pri ver = Primula veris* ssp. *veris*; *Pru vul = Prunella vulgaris*; *Ran bul = Ranunculus bulbosus*; *Rum ace = Rumex acetosa*; *Tar off = Taraxacum officinale*; *Thy pul = Thymus pulegioides*; *Tri pra = Trifolium pratense*; *Tri fla = Trisetum flavescens*; *Ver cha = Veronica chamaedrys*; *Ver off = Veronica officinalis*. See also Fig. 1

Over the period of cattle activity, vegetation response to herbage removal, which was simulated with repeated mowing treatment, was comparable to that of reference plots with cattle activity. This suggests that herbage removal is the most determinant factor for maintaining typical pasture vegetation at a fine scale. As in long-term studies on grazing effects (Lavorel et al. 1999a, b), repeated mowing favoured rosette species such as *Hieracium lactucella* and *H. pilosella* against grass species. Furthermore, this treatment was favouring species with a great capacity for lateral spread and a small height. In Mediterranean pastures, Hadar et al. (1999) have shown that herbage removal was a selective agent, favouring small grasses, geophytes and species with early flowering. On the contrary, when the vegetation was not removed, as in manured or abandoned plots, these types of plants were hampered since they cannot capture sufficient light to grow among the stems and leaves of taller plants (Werger et al. 2002). Unpalatable species are affected by repeated mowing too, but this may not occur in a real grazed situation, since cattle selectivity results in neglecting species such as *Gentiana lutea* or *Carlina acaulis*.

Vegetation reaction to trampling was weak. No new species typical of trampled vegetation (e.g. *Poa supina*) appeared. Cole (1995) has demonstrated that plant morphological characteristics (vegetation stature, erectness, life form) explained more of the variation in response to trampling than the site characteristics. The most resistant plants were caespitose or matted graminoids and the least were forbs. At our time scale this was not clearly verified. There was a negative relationship with forbs (Fig. 3) and a positive one with legumes.

On RDA axis 1, vegetation response to manuring showed the same trend as that in abandoned plots. For these two treatments, there was no direct physical disturbance of the vegetation. The difference lies in the nutrient status whose gradient is represented on RDA axis 2. The manured plots were differentiated by nitrophilous species. In contrast to mown plots, which were clustered in the RDA scatter diagram, vegetation of fertilized plots reacted less homogeneously. Initial floristic composition and soil conditions might be more important in steering the resulting vegetation for this kind of treatment. The only new species in spring of the second year were *Urtica dioica* and *Galium album* and they appeared in a highly manured plot. Contrary to Luzuriaga et al. (2002), we found a significant negative effect of this treatment on species richness at a seasonal scale. The increase in biomass induced by nutrient addition could explain this local loss of species (Guo 2003). This loss was not, however, observed after the winter season, following the disappearance of most above-ground biomass and the reappearance of vernal species. Species favoured by this treatment were large and with a poor capacity for lateral spread. Grasses dominated and forbs were negatively related to the manure treatment. Concerning the potential seed input by this treatment there was no evidence of an effect (results not shown). Furthermore, in the closed canopy of this type of grassland there is little opportunity for seedling development (Marriott et al. 2002).

Abandoned plots were the most reactive because this treatment is furthest from the initial conditions prevailing under cattle activity. These dramatic changes after cessation of grazing have been observed in many other studies (e.g. Krahulec et al. 2001; Moog et al. 2002). Favoured species in these plots were forbs such as *Veronica chamaedrys*, a species which is frequent in overgrowing forest fringes.

Vegetation of the two combined treatments was more influenced by mowing or trampling than by manuring (Figs. 2 and 3). Mowing and trampling seem to have a more important impact on short-term vegetation dynamics than manuring.

Our multifactorial approach showed that all three factors were important in structuring the vegetation. Effects occurred at a seasonal scale but they were combined with shifts in plant community structure due to life-history traits of the composing species. Thus, these effects remained slightly weakened in the following spring. By homogeneously applying the treatments to 4 m^2 plots, we created artificially large patches of mown, trampled and manured surfaces, thus decomposing the successional sequences which may occur in a cattle grazed pasture, intermingled in a very fine vegetation mosaic or on larger patches on pasture units. In successive years, the cattle activity over the summer period may change spatially, starting from a vegetation mosaic that is not entirely the result of the patchiness created by the former pasturing season. Frost events during winter, as well as lasting snow cover, are suppressing most of the green parts of the plants, thus erasing to some extent the established patchiness, which becomes not entirely the initial condition for the growth start in spring. This is in contrast to temperate grassland without lasting snow cover (Bakker et al. 1984). Further, before the herds settle on the pasture, the vegetation is growing quickly, without cattle disturbance, which triggers temporary competition processes that are different from those under cattle pressure.

This seasonal approach clearly shows that cattle affects the vegetation dynamics of pastures at this temporal scale. However, it is clear that we cannot explain this by cattle activity only. Processes acting during winter and early spring are also key factors controlling community dynamics in mountain pastures. In the context of global change, such factors are certain to gain importance in the future.

In mountain pastures all these biotic and abiotic processes are at work and cause directional successional sequences to change to shifting mosaics (Olff & Ritchie 1998; Olff et al. 1999). Knowledge of these processes at various spatio-temporal scales will provide clues for calibration of spatially explicit models of vegetation dynamics in pastures.

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